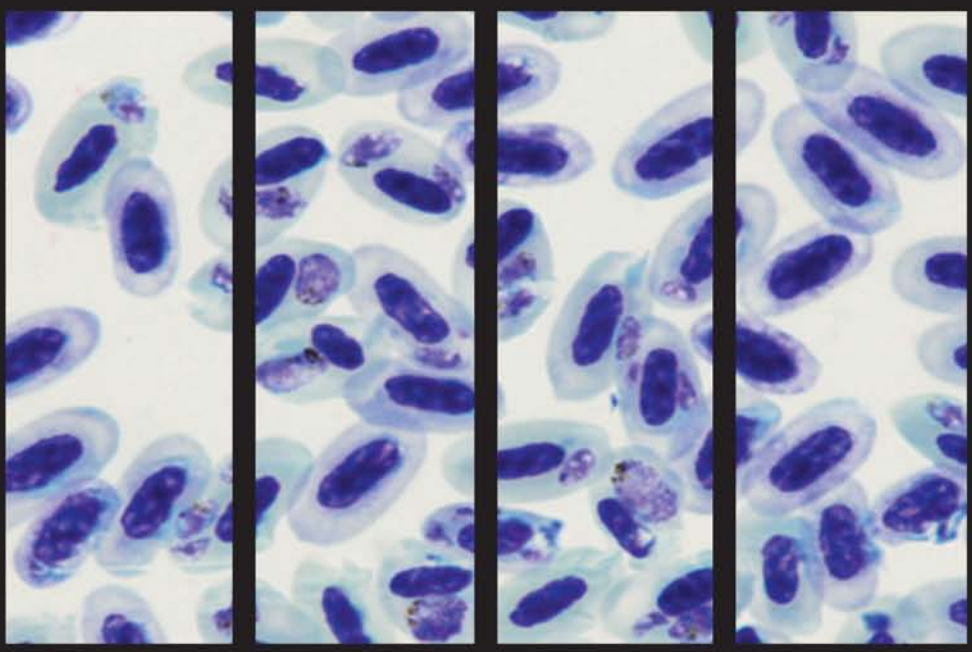

AVIAN MALARIA PARASITES AND OTHER HAEMOSPORIDIA

Gediminas Valkiūnas

CRC PRESS

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Preface to the English Edition

This book summarizes the work carried out during more than a hundred year period of research on bird haemosporidians, discovered by a Russian physiologist V.Ya. Danilewsky in 1884 near Kharkov (Ukraine). Intensive investigations by the Russian scientist were generalised in his well known monograph *'La parasitologie comparée du sang'* published in Russian (1888) and French (1889). In this book a wide distribution of intracellular blood parasites of birds was shown for the first time and analysis was made with information available at that time. From this point of view, the book offered to the reader may be reckoned as the latest publication of the monograph by V.Ya. Danilewsky.

For a long time bird haemosporidians have been used as important models to study human malaria and, therefore, became objects of intensive investigation. Indeed, the great Sir Ronald Ross gained much of his reputation by studying the malaria parasites of sparrows. This period of investigation culminated in 1966 when P.C.C. Garnham published his outstanding monograph '*Malaria parasites and other Haemosporidia*,' which included the information about all species of *Plasmodium* and some other well investigated bird haemosporidians discovered by that time. Nevertheless, no complete illustrated review about the world fauna of these parasites has been prepared. Bird haemosporidians as models for the research of human malaria were largely replaced by the discovery of malaria parasites of rodents and then by the development of culture techniques in the second half of the 20th century. Unfortunately, these developments have markedly hampered biological investigations of this fascinating group of protists in birds. The great body of knowledge remained, however, so that when ecologists and evolutionary biologists sought models to illustrate their theories, avian haematozoa provided some of the best existing databases. Avian haematozoa fulfil many of the specifications of an ideal model for the study of the effects of parasites on natural populations. They are widespread, abundant, diverse, and are easily sampled without disrupting of the host population. In addition, they show a diversity of pathogenic potential, which is still insufficiently investigated, especially in wildlife. No doubt these parasitic organisms deserve more thorough notice as fascinating objects of scientific research and they are also important from a practical point of view. The author hopes that the material collected in this book will be useful for planning and performing future investigations.

The author would like to note that bird haemosporidians in Russia and adjacent countries have been under investigation since the time of V.Ya. Danilewsky. The results of these investigations, however, were published in Russian, often in rare publications, thus many of them appeared beyond the reach and knowledge of the western reader. The English version of this book brings to English-speaking readers information, much of which has been taken from inaccessible Russian sources and has never previously been accumulated in one volume. This book may be regarded as a summary of the existing information on the biology of bird haemosporidian parasites indicating some directions in which investigations can proceed in the future.

As a fascinating group of protists inhabiting a fascinating group of vertebrate hosts, the bird haemosporidians have not been only a field of professional interests to the author but also one of his hobbies for over a 25-year period. The author warmly welcomes all suggestions to improve the work, which will be acknowledged in any other edition. In spite of over a century of investigations into this group of parasites conducted by numerous scholars all over the world, the reader will quickly realise that there are many gaps to be filled in the life histories, epidemiology, pathogenicity, and taxonomy of these bird parasites even by means of traditional parasitological methods. The main objective of this book was to specify such gaps, which may stimulate future research. It is noteworthy that, at present, with rare exceptions (see, for example, Bensch *et al*., 2000; Ricklefs and Fallon, 2002; Waldenström *et al.*, 2002; Fallon *et al.*, 2003), there is limited information on the molecular biology and genetics of bird haemosporidians. This situation is clearly reflected in the contents of the book. However, methods are available to describe valid taxonomic characters in the DNA of parasites in blood films. Certainly, molecular biology methods are an inexhaustible reserve for future investigations into species of the Haemosporida.

The author acknowledges the generosity of Robert D. Adlard (Queensland Museum, South Brisbane, Australia), Ali (M.) Anwar (University of Oxford, Oxford, UK), Richard W. Ashford (Liverpool School of Tropical Medicine, Liverpool, UK), Lester R.G. Cannon (Queensland Museum, South Brisbane, Australia), Alex Kacelnik (University of Oxford, Oxford, UK), and Peter Nansen (Danish Centre for Experimental Parasitology, Frederiksberg, Denmark) for their support of the English edition of the book. The author is also pleased to thank William D. Hamilton (University of Oxford, Oxford, UK) for giving him a chance to work in his Laboratory in Oxford in 1998 when the idea to prepare the English version of this book was launched and for giving him a hand to obtain a subsidy toward the translation. The author is grateful to the Royal Society of London, the Systematics Association, the Gordon Getty Foundation, and the Lithuanian State Science and Studies Foundation, whose grants toward the preparation and costs of the translation made publication of the English version of this book possible.

Introduction

Haemosporidians (Sporozoa: Haemosporida) is a peculiar and clearly phylogenetically detached group of obligate heteroxenous protists, that inhabit the amphibians, reptiles, birds, and mammals and use blood-sucking dipteran insects (Insecta: Diptera) as vectors. We do not exaggerate if we say that haemosporidians are one of the most well known and well studied groups of parasitic protists because they include the agents of malaria, which remains one of the common human diseases in warm climate countries, whose imported cases are known worldwide. At the same time, the level of our knowledge of different groups of haemosporidians is extremely uneven. Practical concern is the reason that the overwhelming number of works are devoted to the agents of human malaria and a small number of species belonging to the family Plasmodiidae, used as model objects in the research of this disease. The other groups of haemosporidians, and primarily the representatives of the Haemoproteidae, Leucocytozoidae, and Garniidae families have been studied relatively less. In recent years the asymmetry of knowledge about haemosporidians has become even more polarized. This manifests itself in the overwhelming domination of information about species of medical importance and those used as experimental models in the study of malaria. This prevents the development of the integral concept about the group of parasitic organisms considered, which, in its turn, slows down progress in scientific research, especially in protistology.

In this book we summarize the results of the research on bird haemosporidians, the largest group of the order Haemosporida by number of species. This review, written from the standpoint of a zoologist and protistologist, is based on the 25-year personal study by the author as well as the investigations of other authors carried out over more than a hundred years. At present, according to our data there are 206 species[†] of bird haemosporidians, which is about half of the known species of this order.

Bird haemosporidians played an important role as models in the study of human malaria, being a stimulus for the development of medical parasitology. Important investigations such as the study of the life cycles, development of chemotherapy, cultivation *in vitro*, vaccination during malaria, and a number of other research projects, were initially carried out with models of bird haemosporidians. Even now, low cost models of bird *Plasmodium* spp., available for any laboratory, have not lost their significance, primarily in immunological, genetic, and biochemical investigations. Besides, bird haemosporidians are characterized by some unique, frequently fascinating properties and therefore they are important not only as models, which is usually emphasized, but as interesting objects of protistological studies. The use of haemosporidians in ecological investigations reveals a unique opportunity for repeated investigation of the same free living specimens during their lifetime, including the ringed ones, which are of great informational importance. It is not a

[†] See also Appendix 2.

coincidence that in the last two decades haemosporidians attracted the particular attention of scholars working on the problems of evolutionary and populational biology of birds (Hamilton and Zuk, 1982; Ashford *et al*., 1990; Johnson and Boyce, 1991; Kirkpatrick *et al*., 1991; Vysotsky and Valkiūnas, 1992; Møller, 1997, and others).

The practical importance of bird haemosporidians is obviously underestimated. First of all it should be emphasized that the group considered includes many agents of the diseases of domestic birds. These parasites cause a decrease in their productivity and even become a reason for high mortality. Among these agents, *Leucocytozoon caulleryi*, *L. simondi*, *L. smithi*, *L. struthionis*, *Haemoproteus mansoni*, *Plasmodium durae*, *P. juxtanucleare* should be mentioned first of all, and to this list many other species of practical importance can be added. Birds kept in zoos and aviaries worldwide fall ill and die of haemosporidioses of known and unknown etiology (Griner, 1974; Cranfield *et al*., 1990; Bennett *et al*., 1993e; Earlé *et al*., 1993). The role of haemosporidioses in the pathology of birds in captivity cannot be currently correctly estimated due to poor organization of the veterinary inspection of haemosporidians in many zoos, aviaries, and private collections. Haemosporidians should be taken into account when domestic and wild birds are imported into regions historically free from these parasites, but where conditions for the transmission of the parasites and creation of new nidi of infection are favorable. A graphic example of this situation is the introduction of *Leucocytozoon smithi,* a dangerous agent of leucocytozoonosis in turkeys, into many northern and central states of the USA, Ukraine, and South Africa (Glushchenko, 1961; Vatne, 1972; Huchzermeyer, 1993a). It is noteworthy that the quarantine services of many countries do not take bird haemosporidians into account in their programs. Projects to reintroduce rare and disappearing species of birds to the regions of their previous habitat, which have become popular in recent decades, are frequently under the threat of failure because of the active transmission of pathogenic species of haemosporidians. Experience shows that the introduction of a small group of genetically similar birds bred in captivity into the endemic regions leads to bursts of outbreaks of lethal haemosporidioses (Herman *et al*., 1975). The successful implementation of projects to restore decaying populations of birds requires the control of the parasitological situation.

Lack of keys to the identification of species and summarizing ecological works on bird haemosporidians hampers the solution of related theoretical and practical important problems. The data on the species of these parasites accumulated during more than 100 years of scientific research are spread over many sources in the literature, some of which are hardly available even for specialists. Up to now, there are no illustrated reviews on the world fauna of the majority of birds' haemosporidians genera. Species of *Plasmodium* is an exception, the available reviews of which (Hewitt, 1940; Garnham, 1966) have not yet lost their significance, but they need to be supplemented. The widest reviews on the biology of the species of *Haemoproteus* and *Leucocytozoon* (Fallis *et al*., 1974; Fallis and Desser, 1977; Desser and Bennett, 1993) contain incomplete information about the fauna and do not reflect the morphological diversity of the stages which are important in species identification. Catalogues of the specific names of bird haemosporidians that appeared in the last two decades (Bennett *et al*., 1982b; Bishop and Bennett, 1992) contribute to but do not solve the problem of species identification because they lack information on the morphology of parasites.

It is noteworthy that due to the worldwide distribution, practical importance, and scientific appeal of the research conducted with birds and blood-sucking dipteran insects, haemosporidians may be excellent objects for scientific research by students at the corresponding faculties of universities and colleges. The work with haemosporidians

requires broad erudition and mastering a wide complex of traditional parasitological methods available in any laboratory. It is enough to mention that a great number of important discoveries associated with the life cycle of haemosporidians made at the end of the 19th and the beginning of the 20th century were made by students, postgraduates, and young scientists using models of bird haemosporidians. It is our opinion that the difficulty in species identification is one of the reasons why this fascinating group of parasitic protists, which is easily available for investigation in wildlife all over the world, is almost completely missing in the scope of interest of zoologists, protistologists, and specialists in relative disciplines at universities and other institutions of higher education. A summary of the vast information in the literature on the ecology and peculiarities of the distribution of haemosporidians is required along with the solution to taxonomic problems, which will furnish the keys to understanding the parasitological situation in each specific region.

Over the last two decades there was an active accumulation of information on various aspects of bird haemosporidians biology, which is to a great extent associated with the activity of the International Reference Centre for Avian Haematozoa (St. John's, Canada). The references, check-lists of specific names, descriptions of new species, and redescription of the known species of bird haemosporidians published by the scientists of the Centre (Herman *et al*., 1976; Bennett *et al*., 1981; Bennett *et al*., 1982b; Bishop and Bennett, 1992) made a great contribution to facilitating the analysis of literature data and significantly influenced the formation of the author's scientific views on the problem (that are sometimes different from the position of Canadian colleagues, which is discussed in the book in detail).

The main objective put forward, when writing this book, is to generalize, summarize, and systematize information on the fauna, ecology, and pathogenicity of bird haemosporidians on the basis of the results of the author's personal investigations and analysis of the collection materials and data from the literature, as well as to give grounds for the hypotheses about their origin and phylogeny. The primary objective was to formulate general regularities in the analysis of each specific problem, and to identify the most poorly studied aspects of the biology, which are important for further research. It is apparent that securing this objective required a wide outlook on the group and analysis of a number of problems, which, strictly saying, go beyond the scope of this book, but they are necessary for the writing of certain chapters and for the formation of the integral outlook of the reader on the protists considered. First of all, this refers to such problems as ultrastructure, immunity, treatment, and some others, which are discussed by the author only to an extent needed to attain the main objective.

The basis for this research is the materials collected by the author on the Curonian Spit in the Baltic Sea [the Biological Station of the Zoological Institute, Russian Academy of Sciences (ZIN RAS), 1977–1992, 1994, 1996, 1998–2002], in Southern Kazakhstan (the Chokpak Ornithological Station of the Institute of Zoology, Academy of Sciences of Kazakhstan, 1986–1987), in the multidisciplinary expedition of ZIN RAS to Middle Asia (1988), and collections in Lithuania and Latvia. The author investigated more than 14,000 specimens of birds belonging to 136 species and 14 orders. The collected material was the basis for the collection of haemosporidians including over 10,000 preparations, which are deposited at the Institute of Ecology, Vilnius University, Vilnius (Lithuania). In addition, we investigated the material deposited in the two greatest world depositories of haemosporidians: the collection of P.C.C. Garnham (London, UK) and the International Reference Centre for Avian Haematozoa (St. John's, Canada). Individual preparations were kindly given to the author for research by specialists from Great Britain: A. (M.) Anwar (Oxford),

R.W. Ashford (Liverpool), M.A. Peirce (Wokingham) as well as G.F. Bennett (St. John's, Canada), and some museums. The author investigated all genera, subgenera, and 92% of the described species. Reinvestigation of the type material was carried out as far as possible.

The work was started under the supervision of R.E. Nikitina, who familiarized the author with bird haemosporidians when he was a student (1977–1979) at Kaliningrad State University (Kaliningrad, Russia). The research was continued at the Institute of Zoology and Parasitology, Academy of Sciences of Lithuania (the present name is Institute of Ecology, Vilnius University) thanks to P. Zajančkauskas and S. Biziulevičius who took an active interest in the investigations. The discussions with M.V. Krylov (St. Petersburg, Russia), the supervisor of the author's thesis for a degree of candidate of biological sciences greatly influenced the author. The discussion of problems of general parasitology at regular seminars held by V. Kontrimavičius for postgraduate students of the Institute of Zoology and Parasitology, Academy of Sciences of Lithuania in 1984–1985 had a fruitful influence on formation of the author's ecological concept. The consultations and exchange of opinions on various problems with I.M. Kerzhner (St. Petersburg, Russia), E.E. Shuikina (Moscow, Russia), and R.W. Ashford (Liverpool, UK) were very important. A. (M.) Anwar and W.D. Hamilton were cordial hosts of the author during his work at Oxford University, while R.W. Ashford hosted and helped in the work at Liverpool School of Tropical Medicine. It was the cordial invitation of G.F. Bennett that the author could visit the International Reference Centre for Avian Haematozoa (St. John's, Canada), which helped to enlarge the collection of literature and to correct descriptions of some species. Discussion of the systematics of haemosporidians with G.F. Bennett (Canada) and M.A. Peirce (Great Britain) were very useful although the opinion of the author on certain problems does not coincide with their opinion. A.O. Frolov (St. Petersburg, Russia) read the section 'A Brief Outline of the Ultrastructure' and made important critical remarks. This book would hardly have been written without the help and collaboration of scientists from the Biological Station of ZIN RAS (V.R. Dolnik, A.V. Bardin and C.V. Bolshakov were the directors during my work at the Station) on capturing and investigation of birds. The scientists at the station A.V. Bardin, C.V. Bolshakov, N.V. Vinogradova, T.V. Dolnik, V.P. Diachenko, V.D. Efremov, T.A. Ilyina, D.S. Lyuleyeva, M.Yu. Markovets, V.A. Payevsky, L.V. Sokolov, A.P. Shapoval, M.E. Shumakov, and M.L. Yablonkevich were teachers and consultants to the author on the problems of ornithology and carried out identification of the species, sex, age, level of migratory fat, and other parameters in the investigation of almost all birds on the Curonian Spit. The investigation of birds at the Chokpak Ornithological Station of the Institute of Zoology, Academy of Sciences of Kazakhstan (Alma-Ata, Kazakhstan) were carried out thanks to the support of E.I. Gavrilov. The researchers and assistants at the station, D.K. Alimzhanov, S.A. Brochovich, A.B. Goloschapov, and P.V. Pfander, rendered their assistance in the capture and identification of birds in Southern Kazakhstan. Some blood smears were kindly collected and given to the author by C.V. Bolshakov, V.G. Vysotsky, M.Yu. Markovets, S.V. Mironov, L.V. Sokolov, N.S. Chernetsov, A.P. Shapoval (St. Petersburg), S.A. Brochovich (Alma-Ata), N.G. Lisina (Tomsk), G.V. Grishanov (Kaliningrad), and A. Sruoga (Vilnius). Many foreign colleagues sent essential material and literature to the author providing the information required. J. Virbickas and V. Kontrimavičius continuously rendered their help in the course of the entire work at the Institute of Ecology and contributed to the organization of a number of expeditions as well as visiting foreign scientific centers. T.A. Iezhova, co-author of a series of articles, rendered her help in the search of vital scientific

publications in the libraries and proof-reading. M. Eaves (Oxford, UK) edited the English abstract in the Russian version of this book.

All illustrations are originals prepared by the author and T.A. Iezhova. Some of them are modifications of published data (as a rule old papers published 15 to 80 years ago) by means of using microphotographs, color illustrations, corrections, and introduction of new details, and unified to one scheme for this book. As a rule, the author studied additional material (preparations) and (or) carried out additional experimental research before preparing such modifications which are accompanied with corresponding references.

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The author gives his cordial thanks to everybody who helped him in this work.

General Section

Brief Historical Summary

In 1884, V.Ya. Danilewsky, a professor of Kharkov University, published a small article 'About Blood Parasites (Haematozoa)' in the *Russian Medicine* journal which marked a qualitatively new stage in the development of protozoology. V.Ya. Danilewsky validated the main concepts of his doctrine about the comparative parasitology of the blood in a series of papers published between 1884 and 1896 in Russian, French, and German journals, making a contribution to the solution of some fundamental problems of general biology and medicine, and primarily the problem of malaria.[†]

V.Ya. Danilewsky (1852–1939), being a physician by his education, went down in history of the medical and biological sciences thanks to his studies in the field of physiology and protistology. He spent about 12 years of his life investigating the intracellular blood parasites of vertebrates. This research has played a great role in the study of haemosporidians. While working with amphibians, reptiles, and birds in the vicinities of Kharkov and other southern regions of the Russian Empire, V.Ya. Danilewsky discovered and studied in great detail the morphology of various stages of the development of the blood intracellular protists, and described and excellently illustrated the recorded parasites. It is noteworthy that the drawings of V.Ya. Danilewsky surprise modern scientists with their accuracy and thoroughness of the picturing of details of the parasites' structure, although classical methods of staining the blood parasites introduced by D.L. Romanowsky were yet to be discovered. The studies of V.Ya. Danilewsky were based on different groups of haemosporidians, which he did not differentiate taxonomically. The nomenclature that V.Ya. Danilewsky established and used is complicated; it includes the descriptive terms, which characterize not the taxa but the stages of the life cycle of various groups of the parasites. The main importance of these investigations is the fact that he confirmed the wide distribution of intracellular blood protists in vertebrates. Even more, V.Ya. Danilewsky clearly expressed his opinion about the relationship of the discovered parasites favouring joining them into one group Haemocytozoa, including the agents of human malaria. Not being a taxonomist V.Ya. Danilewsky did not take part in the construction of the classification of haemosporidians, which was later elaborated by other scholars. Nevertheless, he formulated the main characters of haemosporidians definition. The importance of this scientist in the description of Haemosporida is undoubtedly acknowledged in each of the modern systems of Protista.

V.Ya. Danilewsky described in detail the exflagellation process of microgametocytes of haemosporidians in fresh blood, and in 1888 he already expressed his surmise about the relation of the flagella of his '*Polimitus*' with spermatozoids (microgametes). At the same time he formulated his suggestion about the possibility of the development of the blood

[†] For details, see Valkiūnas (1985c).

protists beyond the blood stream; development in the exoerythrocytic way. V.Ya. Danilewsky carried out the first investigation of pathology during avian malaria. He showed by dissecting infected birds that this disease is accompanied by an acute anaemia, enlargement of the liver and spleen, as well as the accumulation of pigment and the presence of parasites and infected erythrocytes in the phagocytes of these organs. Further investigations of pathology during bird malaria confirm and expand on the data obtained. The ecological observations of V.Ya. Danilewsky associated with the seasonal dynamics of bird infection with blood parasites are of undoubted interest. His conclusion that intracellular blood parasites prevail in birds in the warm seasons and that parasitemia correlates with temperature of the environment, put forward the idea that vectors take part in the spreading of the parasites. The facts obtained and the hypotheses and surmises suggested gain a general biological importance together with the clear statements by V.Ya. Danilewsky about the similarity between human malaria parasites and the parasites of other vertebrates, and birds in particular. His investigations laid a foundation for the comparative parasitological and experimental studies of haemosporidioses. It is not a coincidence that the most important discoveries related to the life cycle of these parasites and human malaria parasites, which are most important practically, were made with model protists discovered by V.Ya. Danilewsky. The articles and the monographs written by this scientist (Danilewsky, 1888, 1889) are full of new ideas and hypotheses, and were cited by all prominent malariologists of that time. It is noteworthy that the investigation, impressive by its scope and thoroughness, illustrating a wide distribution of intracellular blood protists in amphibians, reptiles, and birds, was also performed by A.P. Shalashnikov (1888), a veterinarian working in the laboratory of V.Ya. Danilewsky. Unfortunately, this work was published only in Russian and remained unnoticed by European scholars, while its author did not complete it and died of lung tuberculosis in the prime of his life.

E. Marchiafava and A. Celli (1885) established the first genus of haemosporidians, *Plasmodium*, and attributed human malaria parasites to it. Their priority was, however, recognized only at the beginning of the 20th century. The taxonomic position of haemosporidians was defined by I.I. Metchnikov (1887), who determined that they are close to coccidians.

The further study of bird haemosporidians is associated with a relatively short but fruitful interest of W. Kruse (1890), B. Grassi and R. Feletti (1890a, 1890b, 1891, 1892) in these parasites, who continued the morphological and taxonomic investigations. W. Kruse established the genus *Haemoproteus* for the crescent-like intracellular parasites described by V.Ya. Danilewsky and also described the first three species of this genus: *H. danilewskii*, *H. columbae*, and *H. passeris*. B. Grassi and R. Feletti placed human and bird malaria parasites into one genus, *Haemamoeba* (at present, a partial synonym of *Plasmodium*), which was important principally for the development of the taxonomy. These researchers described the first two species of bird malaria parasites (*Haemamoeba relicta* and *H. subpraecox*). Thorough morphological investigations of W. Kruse, B. Grassi, and R. Feletti stimulated the activity of morphologists and taxonomists.

In 1890, D.L. Romanowsky discovered, and for the first time applied a new technique for staining erythrocytic stages of malaria parasites. He prepared the stain, which clearly differentiates the nucleus and the cytoplasm of haemosporidians colouring them pink and blue, respectively. The active staining component of this stain (the so-called ‘polychrome methylene blue’) in different modifications of its production is widely used in a number of modern stains (azure-eozin after Romanowsky, Leishman’s and Giemsa’s stains, etc.). Moreover, some of these stains are indispensable in the production of collection

preparations of haemosporidians and some other protists. The discovery by D.L. Romanowsky stimulated the beginning of precise morphological investigations of haemosporidians.

F. Schaudinn (1900) contributed much to the elaboration of the terminology for many of stages of the development of haemosporidians, which has been used with minor changes until the present time. The contribution of A. Laveran (Laveran, 1902; Laveran and Lucet, 1905), the discoverer of the human malaria parasites, into the problem of bird haemosporidians investigation is not large but original. This scholar found and described *Leucocytozoon smithi,* the first discovered agent of severe haemosporidiosis in domestic birds. He also discovered such widely distributed parasites as *L. majoris* and *Haemoproteus majoris*. It is noteworthy that the attention paid by this prominent parasitologist to bird haemosporidians is important because it stimulated the interest of physicians and veterinarians to the parasites considered.

Italian scholars A. Celli and F. Sanfelice (1891) described the next two species of haemosporidians *Haemoproteus alaudae* and *H. noctuae*. The significant contribution of these scientists into the development of malariology is that they were the first who managed to infect birds with malaria by subinoculation of infected blood. This was the basis for further experimental investigations of malaria.

A well illustrated work of A. Labbé (1894), which was once one of the most cited monographs on malariology, is mainly of historical importance, being the most complete summary of the data and literature on bird haemosporidians at that time. It is noteworthy that A. Labbé was the first professional zoologist who defended his doctoral dissertation on bird haemosporidians. He was the first to focus his attention on the fact that early classifications of haemosporidians contradict each other, but he failed to solve these contradictions. He established the genera *Halteridium* and *Proteosoma,* which are synonyms to *Haemoproteus* and *Plasmodium*, respectively. Even more, the fact that he joined all bird malaria parasites known by that time into one species, *Proteosoma grassii,* even slowed down to a certain extent the study of the fauna of haemosporidians. Nevertheless, the enthralling and well published monograph of A. Labbé focused the attention of the specialists and no doubt stimulated an interest in this group of protists.

Several brilliant discoveries were made by the students of the John Hopkins University (Baltimore, USA). E.L. Opie (1898) found wide distribution of haemosporidians in North American birds which principally widened the concept of their geographical distribution. This scholar was one of the first who studied in detail the influence of malaria parasites on infected cells. W.G. MacCallum (1897, 1898), using as a model *Haemoproteus* sp. taken from crows, discovered the sexual process in haemosporidians and described and explained the sexual dimorphism of their gametocytes. The credit for the discovery of the sexual process in human malaria parasites is also given to this scientist. W.G. MacCallum also made a detailed investigation of the pathological changes in infected birds, which confirmed the observations and conclusions of V.Ya. Danilewsky.

The discovery and description of the development of the malaria parasite (*Plasmodium relictum*) in 'grey' mosquito (genus *Culex*) and the confirmation of the transmissive way of spreading malaria made by R. Ross (1898) became the peak achievement of malariology in the 19th century. Ronald Ross was awarded the Nobel Prize in Medicine in 1902 for this discovery, gained world-wide recognition, and received the title Sir Ronald following his honour of Knight Commander of the Bath in 1911 (Laird, 1998). Since the discovery by R. Ross, bird malaria parasites began to attract the attention of scholars as an experimental model for the investigation of human malaria, and they were used for this purpose in many laboratories of that time. R. Koch (1899) was one of the first to confirm the results obtained

by R. Ross infecting domestic canaries with malaria by means of mosquito bites. After that, canaries became, for many decades, the most attractive experimental hosts for malaria research in the laboratories and retained this status up to the discovery of the domestic chicken's parasite *Plasmodium gallinaceum* in the second half of the 1930s.

The first results of the detailed morphological investigation of leucocytozoids were published by N. Sakharoff (1893) who worked with crows, magpies, and rooks near Tbilisi (Georgia). H. Ziemann (1898) following his research gave a detailed description of the first species of leucocytozoids developing in the little owl *Athene noctua* calling it *Leukocytozoen danilewskyi*. It is noteworthy that H. Ziemann was the first scholar who studied the structure of the leucocytozoids gametocytes, stained according to Romanowsky, in detail and published the excellent colour drawings of gametocytes and their host cells. N.M. Berestneff (1904) was the first person to make the nominal genus *Leucocytozoon* available. He used it in binomen *Leucocytozoon danilewskyi*, and described several leucocytozoids from the blood of owl, rook, and crow using this name. L.W. Sambon (1908) was the first to distinctly formulate the definition of the genus *Leucocytozoon* and made the first brilliant illustrated review of the entire group clarifying the generic grouping of each species discovered by that time that contributed to the final stabilisation of the *Leucocytozoon* nomenclature. The nomenclature confusion with the genera *Haemoproteus* and *Plasmodium* was solved later mainly after the publication of the outstanding monograph by C.M. Wenyon (1926). Since that time, bird Haemosporida almost invariably included two families: Plasmodiidae Mesnil, 1903, with the genus *Plasmodium* and Haemoproteidae Doflein, 1916, with the genus *Haemoproteus*. The third family, Leucocytozoidae was established relatively recently by A.M. Fallis and G.F. Bennett (1961b). In 1965, two new genera *Parahaemoproteus* and *Akiba* were established for the species of haemosporidians whose vectors are biting midges (Bennett *et al.*, 1965). At present, they are often considered as subgenera of the genera *Haemoproteus* and *Leucocytozoon,* respectively. A. Corradetti with co-authors (Corradetti *et al*., 1963a) suggested the classification of bird malaria parasites on the basis of the morphological peculiarities of their gametocytes and erythrocytic meronts distinguishing four subgenera: *Haemamoeba*, *Giovannolaia*, *Novyella*, and *Huffia*, which are still current. R. Lainson with co-authors (Lainson *et al*., 1971, 1974) discovered reptile haemosporidians with merogony in blood cells, but developing without formation of residual malarial pigment (hemozoin) even when they inhabit erythrocytes. A new family Garniidae was established for these parasites, which included the genera *Garnia* and *Fallisia*. A. Gabaldon *et al.* (1985) found the first representative of garniids, *Fallisia neotropicalis* developing in birds. These discoveries had a major importance for the understanding of the evolution of haemosporidians.

The first information about exoerythrocytic development of haemosporidians was obtained in Brazil by H.B. Aragão (1908), who described large meronts with cytomeres in the endothelial cells of lungs in pigeons infected with *Haemoproteus columbae*. This scholar showed that merozoites produced by meronts invade erythrocytes and develop into gametocytes. Later S.P. James and P. Tate (1937) described exoerythrocytic meronts of bird *Plasmodium* sp. This way, the theory of exoerythrocytic development of malaria parasites was confirmed and later predominated. Much later, these stages were found in human malaria parasites. It is noteworthy that megalomeronts of leucocytozoids were found for the first time and studied in detail by C.G. Huff (1942) and then by K.G. Wingstrand (1947) performed with *Leucocytozoon simondi* and *L. sakharoffi*, respectively. These discoveries contributed to the understanding of the high virulence of some species of leucocytozoids. Not long ago, F. Miltgen with co-authors (Miltgen *et al*., 1981) made an important

discovery. They found that the exoerythrocytic meronts of *Haemoproteus desseri* (*=H. handai*) develop in fibres of the skeletal muscles, heart, tongue, and other muscle organs, which significantly widened the concept about the types of the tissues incorporated by haemosporidians.

Since R. Ross discovered the vectors of *Plasmodium* spp., about 60 years were needed to determine the range of invertebrate hosts of other bird haemosporidians. The Sergent brothers (Sergent and Sergent, 1906) showed that the hippoboscid fly *Lynchia maura* (*=Pseudolynchia canariensis*) is able to transmit *Haemoproteus columbae* from one domestic pigeon to another. Soon after this, the sporogony of this parasite was studied and described in detail (Adie, 1915). A limited geographical distribution and relatively narrow range of vertebrate hosts of hippoboscid flies belonging to the family Hippoboscidae did not explain the worldwide distribution and high rates of prevalence of bird infection with haemoproteids. Success in a search for additional vectors of these parasites was finally achieved, in 1957, when A.M. Fallis and D.M. Wood (1957) showed that *Haemoproteus nettionis* uses biting midges belonging to the family Ceratopogonidae as vectors. American scholars E.C. O'Roke (1930a) and L.V. Skidmore (1931) almost simultaneously and independently discovered the vectors of *Leucocytozoon* sp. Blood-sucking simuliid flies (family Simuliidae) were found to be the vectors. Present day knowledge about the range of invertebrate hosts of bird haemosporidians was formulated after K. Akiba (1960) showed that one species of leucocytozoids (*Leucocytozoon caulleryi*) uses biting midges as vectors.

As already mentioned, systematic study of the bird haemosporidians fauna started in 1890. It was performed extremely nonuniformly and not always successfully. At present, more than half of the species described are not really considered to exist. It is our opinion that in addition to the scientists mentioned above, the following scholars made the greatest contribution in the study of bird haemosporidian fauna. They are: C. Mathis and M. Léger (a number of publications in 1909–1912), I.F. Mello (a number of publications in 1916–1937), C.G. Huff (a number of publications in 1927–1967), R.D. Manwell (a number of publications in 1926–1975), G.R. Coatney and R.L. Roudabush (a number of publications in 1932–1949), J. Tendeiro (1947), and others. The first most detailed species lists of bird haemosporidians and their hosts and the reference lists of the literature most important in the taxonomic respect were compiled by G.R. Coatney and R.L. Roudabush (Coatney, 1936, 1937; Coatney and Roudabush, 1936, 1949) and later supplemented with the active participation of N.D. Levine, G.F. Bennett, and other scholars (Levine and Campbell, 1971; Hsu *et al*., 1973; Bennett *et al*., 1982b). The monographs of R. Hewitt (1940), A.-H.H. Mohammed (1958), and P.C.C. Garnham (1966), predominantly containing information about the species of *Plasmodium* remain one of the most thoroughly prepared illustrated reviews on bird haemosporidians.

The investigation of the fauna and distribution of bird haemosporidians became notably more active after the organisation of the International Reference Centre for Avian Malaria Parasites in 1968 in St. John's, Canada, initiated by M. Laird under the aegis of the World Health Organization (WHO) [in 1975 it was reorganised and renamed into the International Reference Centre for Avian Haematozoa (IRCAH)]. A broad collection of the literature on bird blood parasites and a unique vast collection of preparations, which are available for access by researchers, were gathered in the Centre with the active participation of M. Laird and G. F. Bennett. A significant part of the type material, primarily of species of *Haemoproteus* and *Leucocytozoon* are deposited in the collection. It is noteworthy that a significant part of the preparations in the Centre were collected between 1963

to 1971 during the implementation of the project called the *Migratory Animal Pathological Survey* covering the vast region of Eastern and Southern Asia and coordinated by H.E. McClure (see McClure *et al*., 1978). The investigations within this program were supported by the military research institutions of the USA, and are an interesting example of the significant contribution of the army into the development of traditional zoology and protistology. The material collected during the implementation of the project is the basis of our present-day knowledge about the bird blood parasites in Eastern and Southern Asia. Many new species of haemosporidians were described on this basis, while a significant part of the material has not yet been processed. The scientists of the Centre prepared and published complete catalogues of the literature on bird blood parasites (Herman *et al*., 1976; Bennett *et al*., 1981; Bishop and Bennett, 1992). In addition, they prepared refined versions of the lists of the specific names of haemosporidians, and complete lists of vertebrate hosts of all parasites ever mentioned in the literature (Bennett *et al*., 1982b; Bishop and Bennett, 1992), which facilitated the further taxonomic and ecological investigations. In 1972 to 1995, the scientists of the Centre headed by G.F. Bennett with the active participation of the British protistologist M.A. Peirce published a number of articles with the description of new species and redescriptions of many known species of *Haemoproteus* and *Leucocytozoon*. As a result of the research conducted by G.F. Bennett and his colleagues, a foundation for the development of the current faunistics of these groups was laid down. In 1995, the collection (over 64,000 stained blood films) and the library of the IRCAH were donated to the Queensland Museum in Brisbane (Australia), where they retain integrity, and are available for investigation. In addition, it is worth mentioning that the perfectly organised collection of haemosporidians gathered by P.C.C. Garnham (Garnham and Duggan, 1986) became a unique depository of the types of species belonging to the genus *Plasmodium* and some other genera. It is deposited in the British Museum (Natural History), London.

In this chapter, we briefly touched upon the main discoveries and works, which, in our opinion, have major priority in the study of bird haemosporidians. This research was the 'framework' for a number of subsequent works that revealed various aspects of the biology of haemosporidians. Let us mention some of them that played an important role in the development of malariology. T. Wasielewski was first to use bird *Plasmodium* spp. to test antimalarial preparations (Wasielewski, 1904). These parasites were widely used for this purpose in a number of developed countries during World War II. For example, G.R. Coatney with co-authors (Coatney *et al*., 1953) used the model of *P. gallinaceum* to test the antimalarial properties of about 4000 compounds. This research laid the foundations of malaria chemotherapy. The cultivation methods of the tissue and erythrocytic stages of malaria parasites *in vitro* were elaborated using models of *P. lophurae* and *P. gallinaceum* (Hawking, 1944; Trager, 1947, 1950). It was relatively recently that the model of *P. gallinaceum* was used to develop a method that allows the study of sporogony *in vitro* (Warburg and Miller, 1992). The prominent success in the development of an antimalarial vaccine was also gained using the model of *P. gallinaceum* (see for example McGhee *et al*., 1977).

The list of discoveries made with the use of bird haemosporidians models is impressive, and its presentation in more detail goes beyond the objectives of this work. It is noteworthy that after the discovery of the rodent malaria parasites in 1950 and successful infection of the *Aotus trivirgatus* monkey with human malaria in 1966, the interest of malariologists to bird haemosporidians significantly decreased. The number of scholars working with bird parasites sharply decreased, while many aspects of the biology of haemosporidians still remain unstudied. We should not forget, however, that bird haemosporidians are not only model organisms for the research on malaria (although they did not

lose their importance in this respect), but they are also a unique group of parasitic protists with many surprising properties, awaiting their discoverers, that deserve the interest of scholars without any relation to malaria.

Life Cycle and Morphology

Poljansky (1986) has formulated the definition of the 'life cycle' that is one of the closest to the preconceived idea of the author. The life cycle or the cycle of development is the mode of the parasite existence realised by means of a set of strictly ordered stages of development, which, in aggregation, correspond to the ontogenesis of the species.

The life cycles of haemosporidians are obligate heteroxenous and rather complicated. During their development they change hosts, ways of reproduction, and form various stages of development from the morphofunctional point of view. The general scheme of bird haemosporidians development is clear as a whole. The parasites develop in two groups of hosts, the vertebrates (birds) and vectors (blood-sucking dipterans, Insecta: Diptera). The sexual process takes place in the vectors, and thus the birds are intermediate hosts and the vectors are final (definitive) ones. While feeding, the vectors inoculate sporozoites in birds giving rise to agamic stages, which undergo asexual division in the cells of the fixed tissues of the host. These stages are known as exoerythrocytic meronts or schizonts. As a result of multiple or agamous division (merogony or schizogony) in meronts, uninuclear merozoites are formed which are asexual stages of distribution within the organism of the host. Usually, there are several generations of the exoerythrocytic development, during which the parasite gradually adjusts to the host. As a result of the merogony, there is an avalanche growth of the initial infectious source. Exoerythrocytic merozoites induce a new cycle of the merogony and (or) the development of sexual stages in the blood cells (gametocytes or gamonts). Gametocytes possess the sexual potency (they produce gametes). The cells, which produce macrogametes, are known as macrogametocytes, as distinct from microgametocytes, which produce microgametes. Macrogametocytes are usually easily distinguished from microgametocytes due to their sexual dimorphic characters. Among the latter, a more intense staining of the cytoplasm and a compact nucleus with clear contour in macrogametocytes should be noted first of all. In addition, the nuclei of macrogametocytes possess a nucleolus, which is not present in microgametocytes. However, the nucleolus is not easily seen in all groups of haemosporidians under a light microscope. Moreover, Haemoproteidae and Plasmodiidae species possess pigment granules (hemozoin), which have a tendency to gather at the ends of elongated microgametocytes, which is not generally characteristic of macrogametocytes (there are exceptions). The named characters of sexual dimorphism of gametocytes are the distinguishing features of haemosporidians most easily seen. Gametocytes are infective for the vectors.

To a first approximation, the infection in birds includes the following main periods: 1 – prepatent, when the parasites develop beyond the blood; 2 – acute, characterized by the appearance of parasites in the blood and by a sharp increase of parasitemia; 3 – crisis, when the parasitemia reaches its peak; 4 – chronic, and 5 – latent, when the parasitemia sharply decreases and later eliminates under the impact of the immune response of the host.

As a rule, the parasites persist in birds. A bird once infected usually maintains the parasites for many years or even for life thus being the source of infection for vectors. A relapse of parasitemia occurs in most of the haemosporidian species during the reproduction period of the vertebrate hosts, which facilitates the infection of vectors and the transfer of infection to offspring (see p. 185 for a more detailed description).

Shortly after feeding on infected birds, the gametocytes initiate gametogenesis in the midgut of the vectors, resulting in a sexual process of the oogamy type. As this takes place, the gametocytes are freed from the host cells. One of the main stimuli for the beginning of the gametogenesis is the change in oxygen and carbon dioxide concentration, when the blood is transferred from the vertebrate host to the vector. A macrogametocyte produces one rounded macrogamete, while a microgametocyte undergoes exflagellation, as a result of which eight motile thread-like microgametes are formed. Fertilization occurs extracellularly. The zygote is transformed into an elongated motile ookinete. The latter penetrates through a peritrophic membrane and through the epithelial layer of the midgut. The ookinete rounds up under the basal lamina and develops into an oocyst, which is surrounded by a capsule-like wall built from the material of the host. During the process of oocyst development (sporogony), numerous uninuclear elongated bodies (sporozoites) are formed in the oocyst. After maturation of the oocysts, the sporozoites move into the haemocoele and then penetrate the salivary glands of the vector. Sporozoites are infective to birds. Transmission occurs when sporozoites are injected by the vector into vertebrate hosts with salivary gland secretion during its blood meal. It should be noted that ookinetes frequently contain one or several vacuole-like spaces, which are also present in young oocysts and occasionally in zygotes in some species. These spaces are gatherings of lipoproteins which are washed out after fixation with alcohol and look like empty spaces in stained smears.

During each stage of development, excluding the zygote stage, the haemosporidians are haploid. Only the zygote has a diploid ($2n$) set of chromosomes. Reduction division (meiosis) occurs in the initial stages of the ookinete development.

Along with the similar features of the life cycles of the representatives of the families Haemoproteidae, Plasmodiidae, Garniidae, and Leucocytozoidae included in the order Haemosporida, which parasitize birds, they have significant differences that require separate consideration. Below, only concise general characteristics of the development for the representatives of the families are given. Frequently the life cycles and morphology of some stages of development of the different species of haemosporidians belonging to the same family have distinct characteristic features. At present, due to the available fragmentary data about the cycles of development for most of the species described, it is not always possible to determine whether these features are characteristic of the families considered as a whole. In this context, the peculiar features of the development cycles and structure of the individual stages are considered in more detail later in the book in the Systematic Section.

LIFE CYCLE AND MORPHOLOGY OF HAEMOPROTEIDAE SPECIES

The life cycle of the bird haemoproteids has been studied in not more than 7% of the species known at present. The general scheme of the life cycle is shown in Fig. 1.

Biting midges (Diptera: Ceratopogonidae) (Fig. 2) and hippoboscid flies (Hippoboscidae) (Fig. 3) are the vectors of bird haemoproteids. Exoerythrocytic merogony occurs in

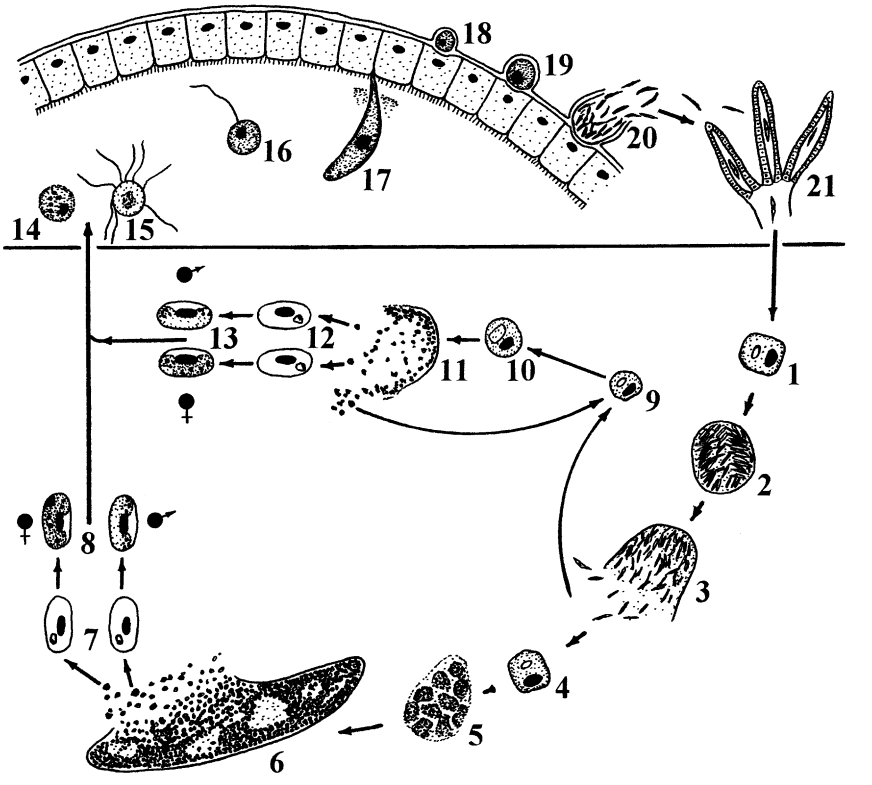


Figure 1 Diagrammatic representation of the life cycle of bird haemoproteids (*Haemoproteus mansoni* as an example).
Upper part, in vector; lower part, in bird: *1* – sporozoite in endothelial cell; *2*, *3* – exoerythrocytic meronts of the first generation with elongated merozoites; *4* – merozoite in endothelial cell; *5*, *6* – growing and mature megalomeronts in skeletal muscles, respectively; *7* – merozoites in erythrocytes; *8* – mature gametocytes; *9* – merozoite in reticuloendothelial cell in spleen; *10*, *11* – growing and mature meronts in spleen, respectively; *12* – merozoites in erythrocytes; *13* – mature gametocytes; *14* – macrogamete; *15* – exflagellation of microgametes; *16* – fertilization of macrogamete; *17* – ookinete penetrating the peritrophic membrane; *18* – young oocyst; *19*, *20* – sporogony; *21* – sporozoites in the salivary glands of vector.

birds in the endothelial cells and probably in fixed macrophages, while in certain species it also occurs in myofibroblasts. Gametocytes develop in mature erythrocytes. The merogony does not occur in the blood cells.

Sporozoites injected into the bird's blood circulation by vectors initiate the development of exoerythrocytic meronts (Wenyon, 1926; Mohammed, 1967; Baker, 1966; Bradbury and Gallucci, 1972; Ahmed and Mohammed, 1977; Atkinson *et al*., 1986). Most frequently meronts are found in the lungs, and less often in the liver, spleen (Pl. I, *1*), kidneys, heart, skeletal musculature, and other organs. The meronts are variable in shape in the endothelium of lungs. Oddly branching (Fig. 4, *1–3*) and worm-like serpentine (Fig. 4, *2*) parasites are common. During the development of meronts they can split into separate parts (cytomeres) containing several nuclei (Fig. 4, *8, 9*). The sizes of the meronts vary significantly, but their length generally does not exceed 100 μm. In certain species

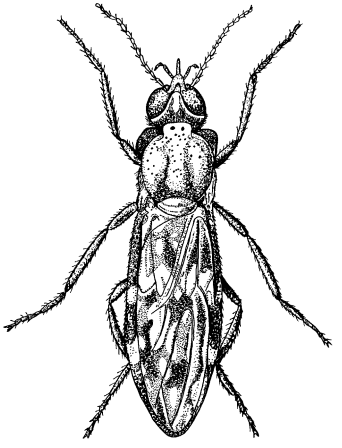


Fig. 2

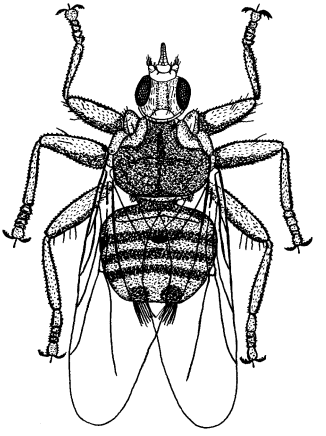


Fig. 3

Figure 2 Vector of haemoproteids, the biting midge *Culicoides nubeculosus* (modified from Gutsevich, 1973).

Figure 3 Vector of haemoproteids, the blood-sucking hippoboscid fly *Pseudolynchia canariensis* (=*Lynchia maura*) (modified from Krylov, 1994).

[*Haemoproteus handai, H. mansoni* (=*H. meleagridis*)] megalomeronts develop in the endothelial cells of the capillaries and in myofibroblasts of the skeletal musculature, and in the heart muscle (Miltgen *et al*., 1981; Atkinson *et al*., 1986). Megalomeronts are significantly larger than meronts in the lungs. The length of the largest parasites exceeds 400 μm. They are stretched along the muscle fibres and surrounded by a thick hyaline wall (Fig. 5, *2–4*).

The number of generations of exoerythrocytic meronts preceding the appearance of gametocytes is never less than two. For example, at least two generations of exoerythrocytic meronts of *H. mansoni* develop in the skeletal musculature and heart muscle (Atkinson *et al*., 1986, 1988b). The first generation of meronts develops in the endothelium of capillaries and in myofibroblasts (Fig. 5, *1*). These meronts reach 20 μm in diameter and produce elongated (about 5 to 6 μm in length) merozoites. The development of first generation meronts is completed approximately five days after infection. Elongated merozoites induce secondary merogony in the endothelial cells of the capillaries and myofibroblasts and also give rise to meronts in the reticular cells of the spleen. It is likely that the latter are responsible for the maintenance of chronic parasitemia and for the relapse. The meronts of the second generation (megalomeronts) (Fig. 5, *4*) mature approximately 17 days after infection. They possess numerous roundish merozoites with a diameter of about 1 μm. The merozoites developed in megalomeronts penetrate into erythrocytes giving rise to the gametocytes.

The prepatent period for the majority of the haemoproteids species studied varies within 11 days and three weeks.

Only gametocytes develop in the blood cells (Fig. 6; Pl. II, *1–3*). Infection of vertebrate hosts by subinoculation of infected blood is impossible due to the absence of merogony in the blood, except in the case when exoerythrocytic merozoites are present in the blood circulation. More than one (sometimes up to 15) merozoites may penetrate into an individual erythrocyte. Multiple infection of one erythrocyte by several parasites is a

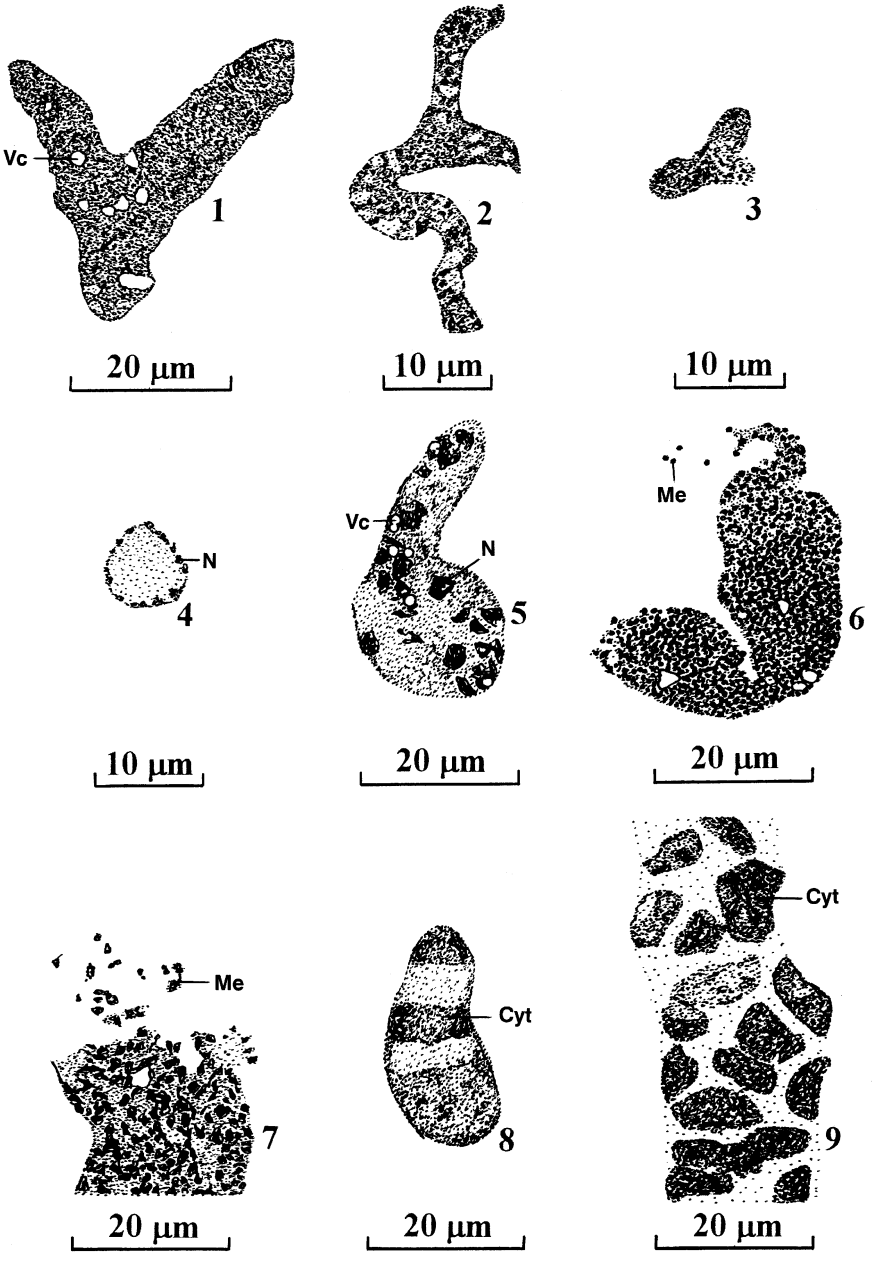


Figure 4 Exoerythrocytic meronts of *Haemoproteus columbae* from the lungs of experimentally infected *Columba livia:*
1–3 – meronts of irregular form; *4* – meront with nuclei located on the periphery of the parasite; *5* – growing meront; *6* – mature meront; *7* – a fragment of mature meront; *8* – young meront with cytomeres; *9* – a fragment of large meront with numerous cytomeres; Cyt – cytomere; Me – merozoite; N – nucleus; Vc – vacuole (modified from Ahmed and Mohammed, 1977).

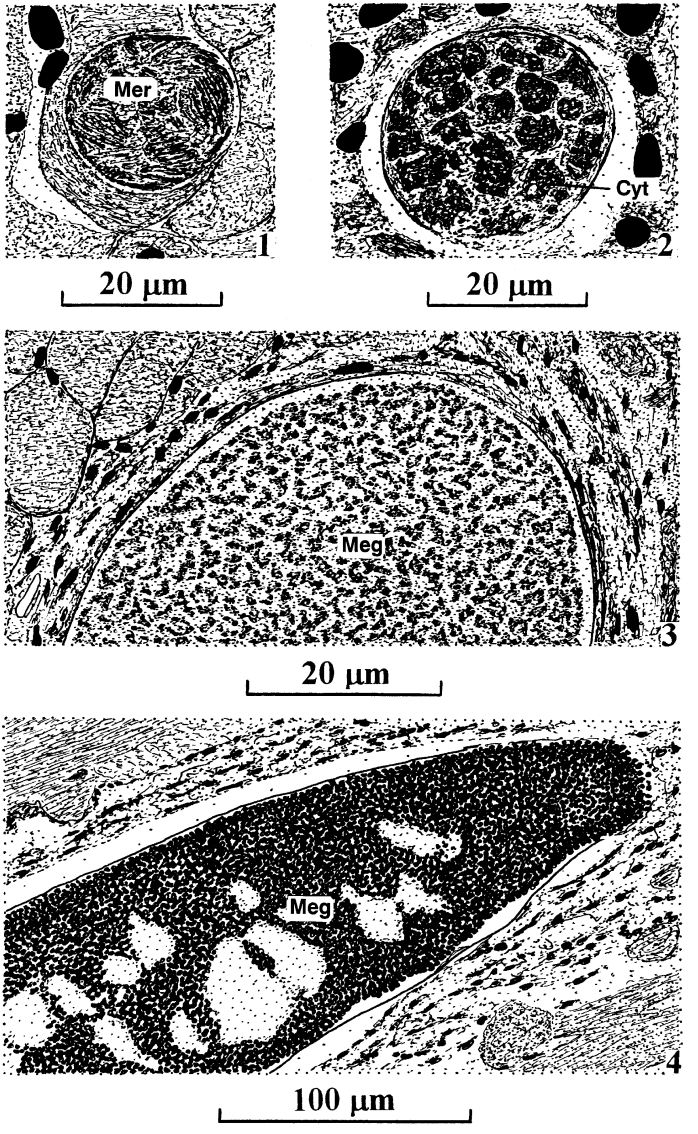


Figure 5 Exoerythrocytic meronts of *Haemoproteus mansoni* from the pectoral muscle of turkey: *1* – mature meront of the first generation with elongated merozoites (the parasite develops within a muscle fibre); *2* – growing megalomeront with cytomeres; *3* – a fragment of nearly mature megalomeront with merozoites developing inside branching cytomeres; *4* – a fragment of mature megalomeront packed with numerous merozoites (vacuolated areas are seen); Cyt – cytomere; Meg – megalomeront, Mer – meront (modified from Atkinson *et al*., 1986).

function of the intensity of parasitemia. When the intensity of the infection increases, the probability of penetration of several merozoites into one cell grows. Usually not more than two parasites gain maturity. Malarial pigment (hemozoin) is formed in gametocytes in the form of granules of golden-brown, brown, or black colour. The number, form, and position of pigment granules in the gametocytes are important characters used to determine the

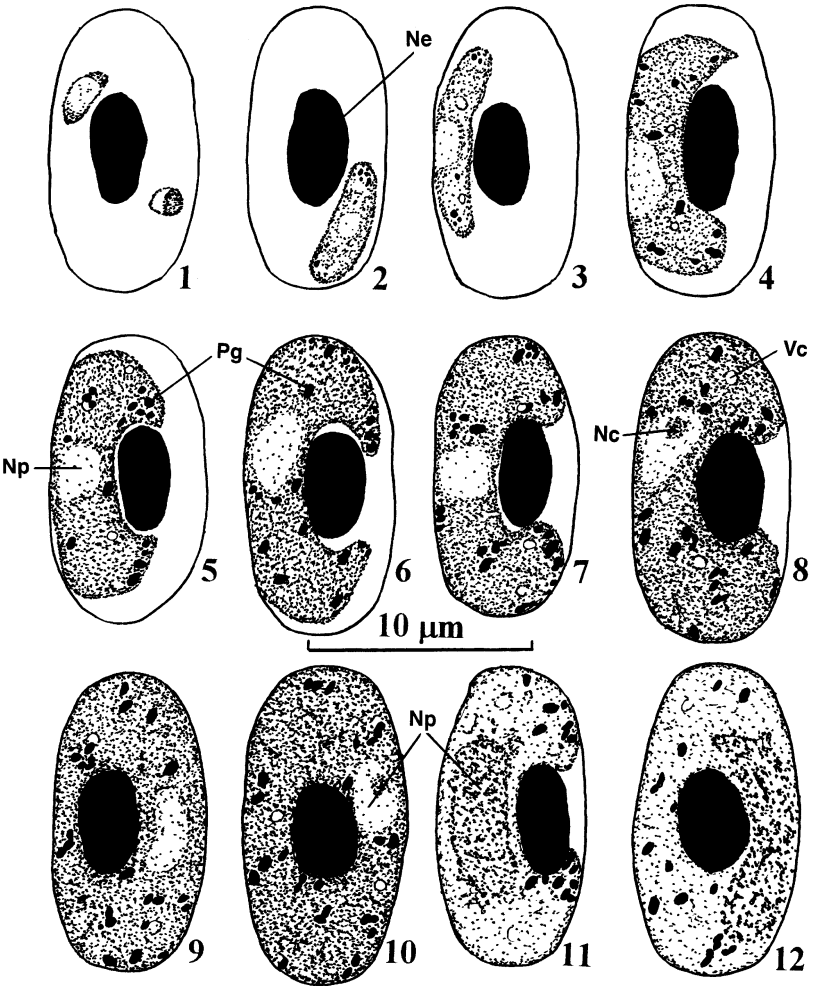


Figure 6 Gametocytes of *Haemoproteus mansoni* from the blood of *Tetrastes bonasia: 1–3* – young; *4–10* – macrogametocytes; *11*, *12* – microgametocytes; Nc – nucleolus; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Vc – vacuole.

species. Together with true malarial pigment, more or less compact gatherings of matter called valutin are often seen in the gametocytes of certain species. The granules of valutin, if stained by different modifications of the Romanowsky method, usually develop various hues of violet and sometimes have azurophilic tints (Pl. II, *3*). The nature of the valutin granules is still not completely understood. They are usually clearly distinguished from pigment granules by their lesser light refraction.

Gametocytes capable of gametogenesis appear within two to six days of the merozoites penetrating the erythrocytes. Afterward, the ability of gametocytes to produce gametes decreases. A small number of viable gametocytes in the blood of infected birds (frequently less than 1 per 1000 erythrocytes) is maintained due to the weak merogony in the internal organs during the period when transmission of infection takes place in the wild. During the entire 80 days of observations (from the beginning of May till the end of July), we recorded

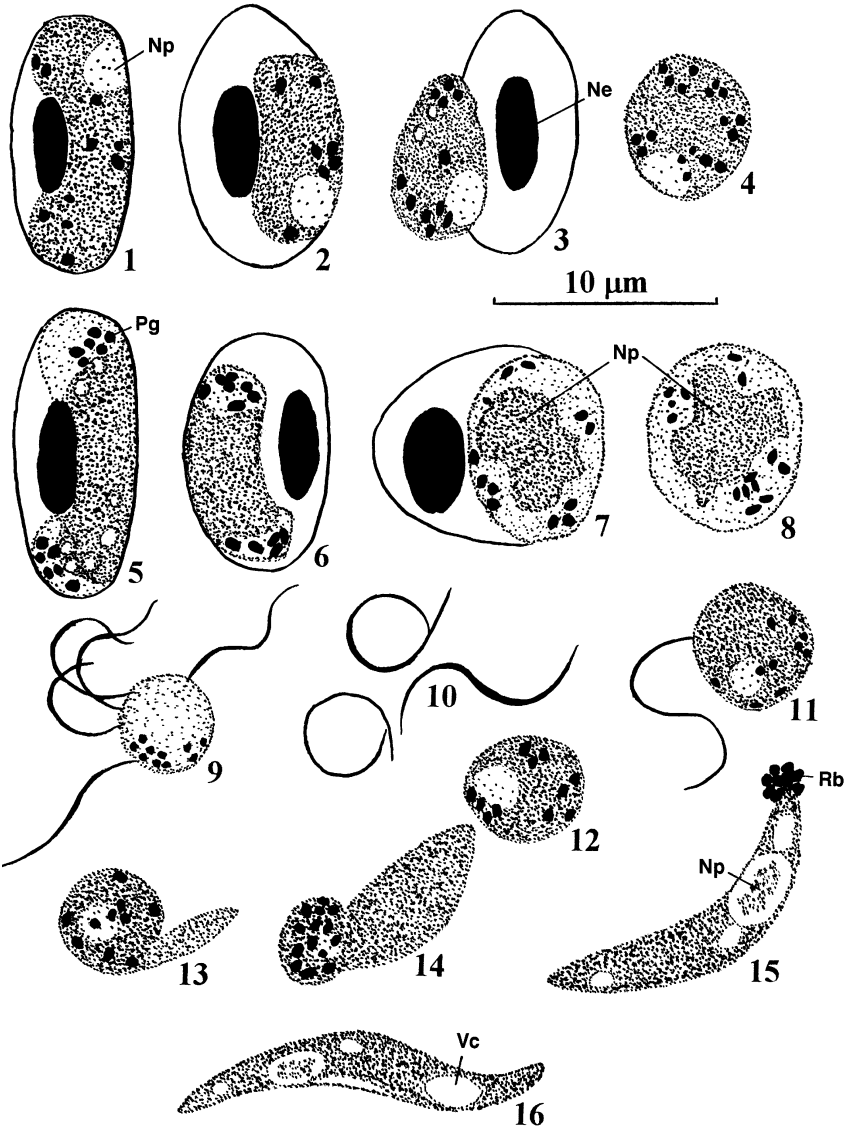


Figure 7 *Haemoproteus majoris* gametogenesis, zygote, and ookinete development *in vitro:* *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the peripheral blood of birds before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of development of ookinete; *14* – medium grown ookinete; *15* – ookinete with a residual body; *16* – ookinete without the residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1994).

viable gametocytes of *Haemoproteus fringillae* in the blood of naturally infected *Fringilla coelebs* kept in captivity, which indicates that there are several cycles of merogony maintaining a small number of gametocytes in the peripheral blood.

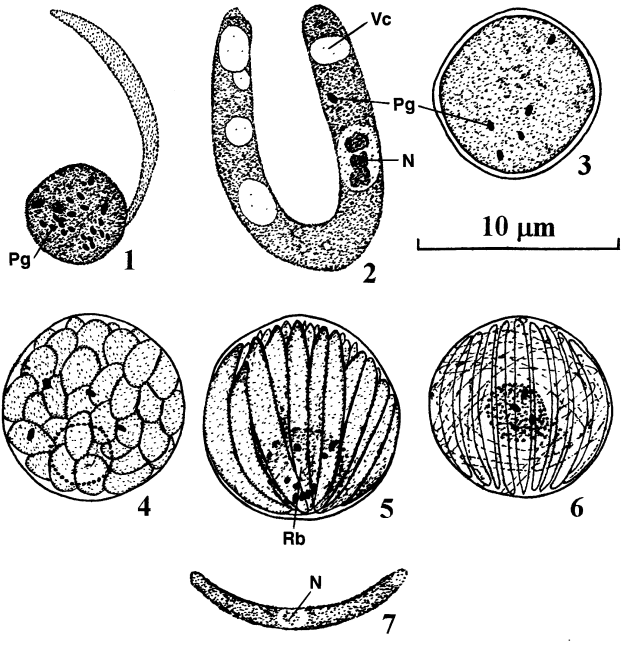


Figure 8 *Haemoproteus mansoni* in the vector *Culicoides sphagnumensis:*
1 – initial stage of the development of ookinete in midgut contents 12 h after the ingestion of gametocytes; *2* – full grown ookinete in midgut contents 36 h after the ingestion of gametocytes; *3* – young oocyst in midgut wall four days after the ingestion of gametocytes; *4* – diagrammatic representation of oocyst six days after the ingestion of gametocytes (discrete masses of the cytoplasm, a residual body and pigment granules are seen); *5* – mature oocyst six days after the ingestion of gametocytes (characteristically arranged and completely developed sporozoites and a residual body with pigment granules are seen); *6* – mature oocyst seven days after the ingestion of gametocytes (irregularly arranged sporozoites, which can move about within the oocyst, and a residual body with pigment granules are seen); *7* – sporozoite from the salivary glands; N – nucleus; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Fallis and Bennett, 1960).

At the present level of knowledge, the morphology of gametocytes and the character of their impact on infected erythrocytes (Fig. 6; Pl. II, *1–3*) is the basis for species identification.

The parasite persists in birds. Relapses take place during a period at the beginning of bird reproduction.

The stages responsible for relapses and maintaining of chronic parasitemia are still insufficiently studied. Atkinson *et al*. (1988b) believe that meronts of *H. mansoni,* causing relapses and maintaining a chronic parasitemia in turkeys, develop in reticular cells of the spleen (for more details, see p. 306).

Several minutes after feeding on infected birds, or even earlier, mature gametocytes in the midgut of vectors become round and escape from erythrocytes (Fig. 7, *3, 7*). Gametogenesis, fertilization, and development of zygotes and ookinetes occur according to the uniform scheme for all haemosporidians (Fig. 7; Pl. III, *1–4*). It is noteworthy that a residual body is formed on the distal end of the ookinete during its development. This body possesses a portion of the cytoplasm and a part or all of the pigment granules (Fig. 7, *15*). The residual body separates from the parasite (Pl. III, *2*).

The length of microgametes, structure of zygotes, morphological peculiarities of the zygote transformation into the ookinete, the sizes of ookinetes, and the rate of the ookinete development under standard conditions *in vitro* differ for various species (Valkiūnas and Iezhova, 1995). For example, for the majority of the bird haemoproteids studied, the length of microgametes varies within 10 to 18 μm. The shortest microgametes (less than 10 μm on average) are characteristic of *Haemoproteus pallidus* and *H. minutus*, while the longest (greater than 20 μm on average) were found in *H. palumbis.* The size of macrogametes in all species studied is almost the same (the diameter is about 6 to 7 μm). At the same time, the size of gametocytes differs significantly in many species. These data provide reasons to assume that during the stage preceding fertilization, the size of macrogametes is equalised. One large 'vacuole' is found in zygote of *H. balmorali* and *H. fringillae*, which is not observed in zygotes of other species studied so far. The presence of the 'vacuole' in zygotes is a significant diagnostic character of *H. balmorali* and *H. fringillae.* On the basis of the parasites' morphology at the initial stage of transformation of zygote into ookinete, the species studies can be divided into three main groups. The first one, being the largest, includes *H. balmorali, H. belopolskyi, H. dolniki, H. lanii, H. majoris,* and *H. tartakovskyi.* Development of ookinete in these parasites starts with the appearance of a finger-like outgrowth (Figs. 7, *13*; 8, *1*). The second group includes *H. fringillae.* In this species, a short blunt outgrowth appears in the middle part of the zygote, which elongates and shapes the forming ookinete in a form of a pear (or skittle). The third group includes *H. pallidus* and *H. minutus.* Development of ookinete in these species occurs without formation of any clearly expressed outgrowths. The transforming ookinete of these parasites is gradually elongated. The species studied can also be divided into three groups based on the rate of their ookinetes development *in vitro*. At temperatures of 18 to 20°C ookinetes of *H. pallidus* and *H. minutus* are formed faster than any others (within 1 to 1.5 h), while the formation of *H. dolniki* and *H. tartakovskyi* ookinetes is the slowest (during 24 to 48 h). *Haemoproteus balmorali, H. belopolskyi, H. fringillae, H. lanii,* and *H. majoris* occupy an intermediate position between these two groups. In this group, ookinetes with a residual body are formed approximately in three to six hours. The sizes of ookinetes vary significantly for different species. For example, the length of fixed ookinetes of *H. minutus* and *H. pallidus* developed *in vitro* is 8 to 9 μm on average, while for *H. tartakovskyi*, it is 18 μm.

Ookinetes (Figs. 8, *2*; 9, *1–3*) migrate through the epithelial layer of the midgut of the vector and round up under the basal lamina giving rise to oocysts (Fig. 8, *3*). Sporogony of the species developing in biting midges and hippoboscid flies is not the same. The majority of the species of bird haemoproteids, whose life cycle has been studied, develop in biting midges. In this case, small oocysts (less than 20 μm in diameter) with one germinative center (Fig. 8, *5*) are formed. Less than 100 sporozoites usually develop there. The average length of sporozoites usually exceeds 10 μm. Their ends are more or less approximately equally pointed (Fig. 8, *7*). Sporogony in biting midges usually completes in less than ten days, which is the adjustment to a relatively short (seven to ten days) gonadotrophic cycle of the midges (Atkinson, 1991b). As a result, by the time of the next blood meal, the sporozoites get into the salivary glands of the vector. *Haemoproteus mansoni* and *H. nettionis* are the best studied species, which develop in biting midges.† Sporogony of the species developing in hippoboscid flies is characterized by a longer development of oocysts (usually exceeding ten days), where multiple germinative centers and several hundreds of

† See also Valkiūnas *et al*. (2002b).

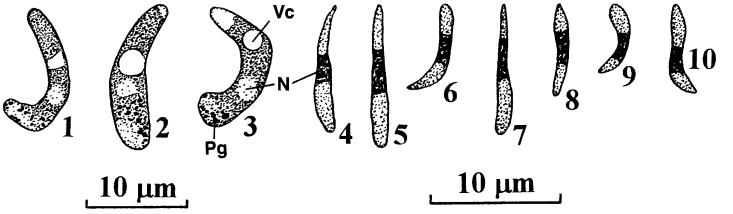


Figure 9 *Haemoproteus palumbis:*
1–3 – ookinetes which developed *in vitro* 3.5 h after exposure of blood with mature gametocytes to the air at a temperature of 35°C; *4–10* – sporozoites from the salivary glands of the hippoboscid fly *Ornithomyia avicularia*; N – nucleus; Pg – pigment granule; Vc – 'vacuole' (*1–3* are modified from Baker, 1966b; and *4–10* are modified from Baker, 1963).

sporozoites are formed. This type of development, which is not exactly synchronized with the blood meal, is an adjustment to the mode of life of relatively long living hippoboscid flies, which spend a long time on birds. The diameter of mature oocysts usually exceeds 20 μm. For example, oocysts of *H. columbae* reach 40 μm or even more in diameter. The average length of sporozoites is less than 10 μm. One end of sporozoites is more pointed than the other (Fig. 9, *4–10*). *Haemoproteus columbae* and *H. palumbis* are the best studied species, which develop in hippoboscid flies.

Mature oocysts usually burst, and sporozoites penetrate into the haemocoele of the vectors. Gradual release of sporozoites from oocysts is also observed in several species of haemoproteids. Some sporozoites penetrate into the salivary glands of the blood-sucking insects, which become capable of infecting the birds during their next blood meal.

LIFE CYCLE AND MORPHOLOGY OF PLASMODIIDAE SPECIES

The present day knowledge of the life cycle of avian malaria parasites was accumulated mainly in the 1930 to 1950s, when these protists were widely used as experimental laboratory models to study human malaria. The data about the development of the malaria parasites of birds, which became the property of science during the same period and earlier, were generalized by Garnham (1966). Later, the interest of malariologists in this group of parasites significantly decreased mainly due to the discovery of malaria parasites of rodents, which are more close to the malaria parasites of human in their biological properties and more convenient for experimental research. Thus, by now, the life cycles of many species of bird malaria parasites have been either investigated fragmentarily or not studied at all. This refers primarily to the species of the subgenus *Novyella*. The development of species of the subgenus *Haemamoeba* is the most well studied. In the text below, the general characteristics of the life cycle of Plasmodiidae species is given by example of *Haemamoeba* species.

Blood-sucking mosquitoes (Diptera: Culicidae) are vectors of malaria parasites of birds. Only the females of these dipterans feed on blood and, consequently, participate in spreading the infection. The major part of the vector species belongs to the genera *Culex* (Fig. 10), *Aedes,* and *Culiseta.* Mosquitoes of the genus *Anopheles* are also vectors of

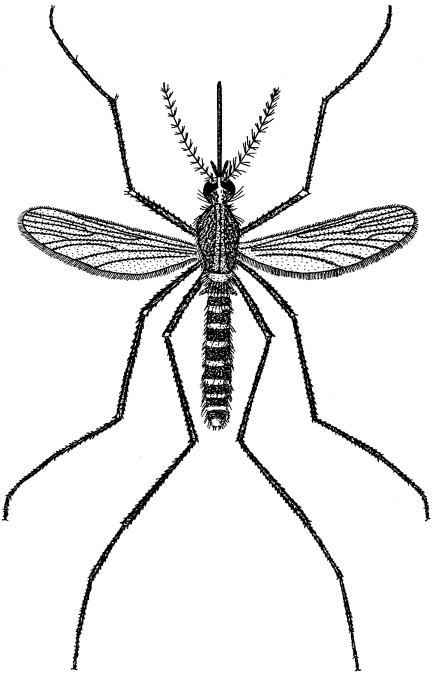


Figure 10 Vector of bird malaria, the mosquito *Culex pipiens* (modified from Gutsevich *et al*., 1970).

certain species. Exoerythrocytic merogony occurs in birds in the cells of mesodermal origin, that is in the endothelial cells lining the capillaries, in the cells of hemopoietic and lymphoid macrophage systems. Erythrocytic meronts develop in the cells of the erythrocytic series, while gametocytes develop mainly in mature erythrocytes. Below, the characteristics of the malaria parasites' life cycle are presented mainly in the example of *Plasmodium relictum,* which is distributed worldwide in a broad range of vertebrate hosts and has been studied quite well (Garnham, 1966; Corradetti *et al.,* 1970). The general scheme of its life cycle is shown in Fig. 11.

As a first approximation, the development in birds may be divided into exoerythrocytic merogony, erythrocytic merogony, and formation of gametocytes. In its turn, the exoerythrocytic merogony is arbitrarily divided into primary (preerythrocytic) and secondary (posterythrocytic) ones. Primary exoerythrocytic merogony consists of two generations of meronts, which are called cryptozoites and metacryptozoites, respectively. Secondary exoerythrocytic merogony includes several generations of meronts, which are called phanerozoites.†

Sporozoites injected by the vector into birds give rise to the first generation of primary exoerythrocytic meronts (cryptozoites). They develop predominantly in the reticular cells

† Strictly speaking, the term 'zoite' used for the representatives of the Sporozoa phylum designates asexual spreading stages (merozoites, sporozoites). In this connection, the terms 'cryptozoites,' 'metacryptozoites,' and 'phanerozoites' used to designate different generations of exoerythrocytic meronts of bird malaria parasites, are not very appropriate. Nevertheless, these terms were accepted in the literature and are used to characterize the complex life cycles of malaria parasites of birds (Garnham, 1966; Carter and Graves, 1988). We also kept to this traditional terminology.

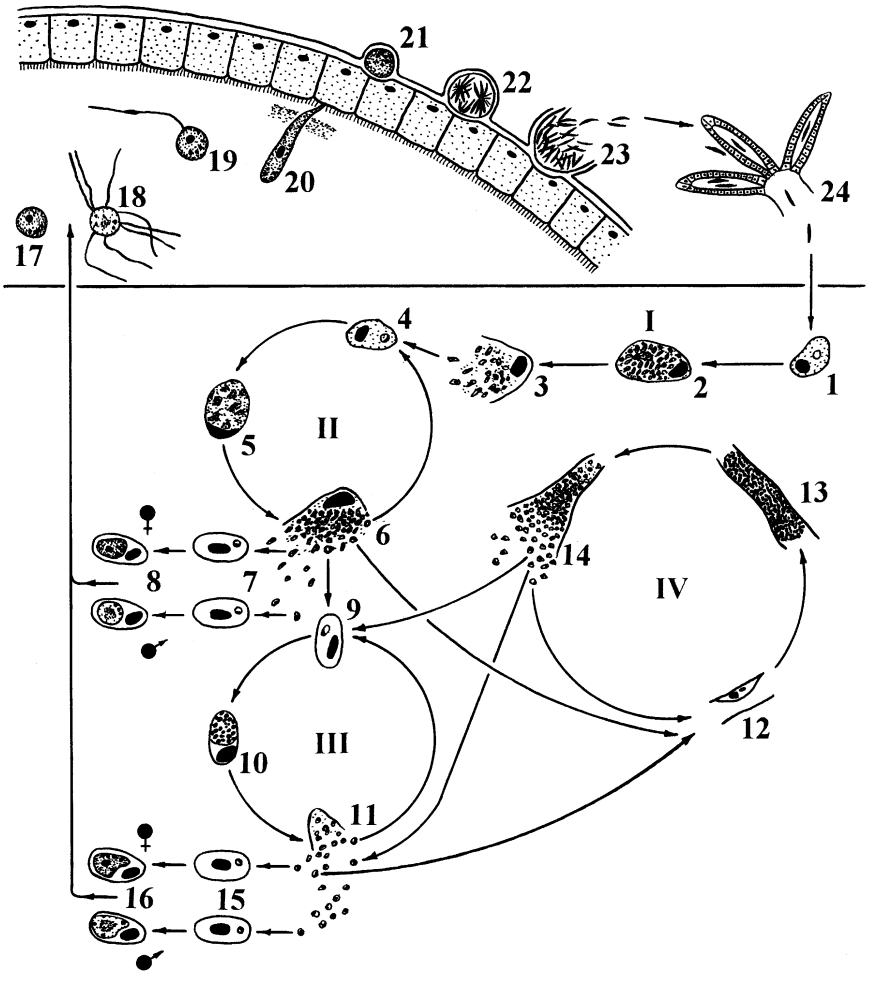


Figure 11 Diagrammatic representation of the life cycle of bird malaria parasites (*Plasmodium relictum* as an example):
Upper part, in vector; lower part, in bird: I, II – primary exoerythrocytic merogony; III – erythrocytic merogony; IV – secondary exoerythrocytic merogony; *1* – sporozoite in reticuloendothelial cell; *2*, *3* – cryptozoites; *4* – merozoite in macrophage; *5*, *6* – metacryptozoites; *7* – merozoites in erythrocytes; *8* – gametocytes; *9* – merozoite in erythrocyte; *10*, *11* – erythrocytic meronts; *12* – merozoite in endothelial cell of capillaries; *13*, *14* – phanerozoites; *15* – merozoites in erythrocytes; *16* – gametocytes; *17* – macrogamete; *18* – exflagellation of microgametes; *19* – fertilization of macrogamete; *20* – ookinete penetrating the peritrophic membrane; *21* – young oocyst; *22*, *23* – sporogony; *24* – sporozoites in the salivary glands of vector.

of many organs and tissues including skin. Frequently cryptozoites are found in the spleen. Usually, the diameter of cryptozoites does not exceed 30 μm. Fewer than 100 merozoites are formed there. They cannot infect the blood cells yet. The merozoites developing in cryptozoites induce the second generation of primary exoerythrocytic meronts (metacryptozoites), which develop in macrophages in many organs. Metacryptozoites are very much like cryptozoites, but usually contain a greater number of merozoites (Pl. I, *2*). The

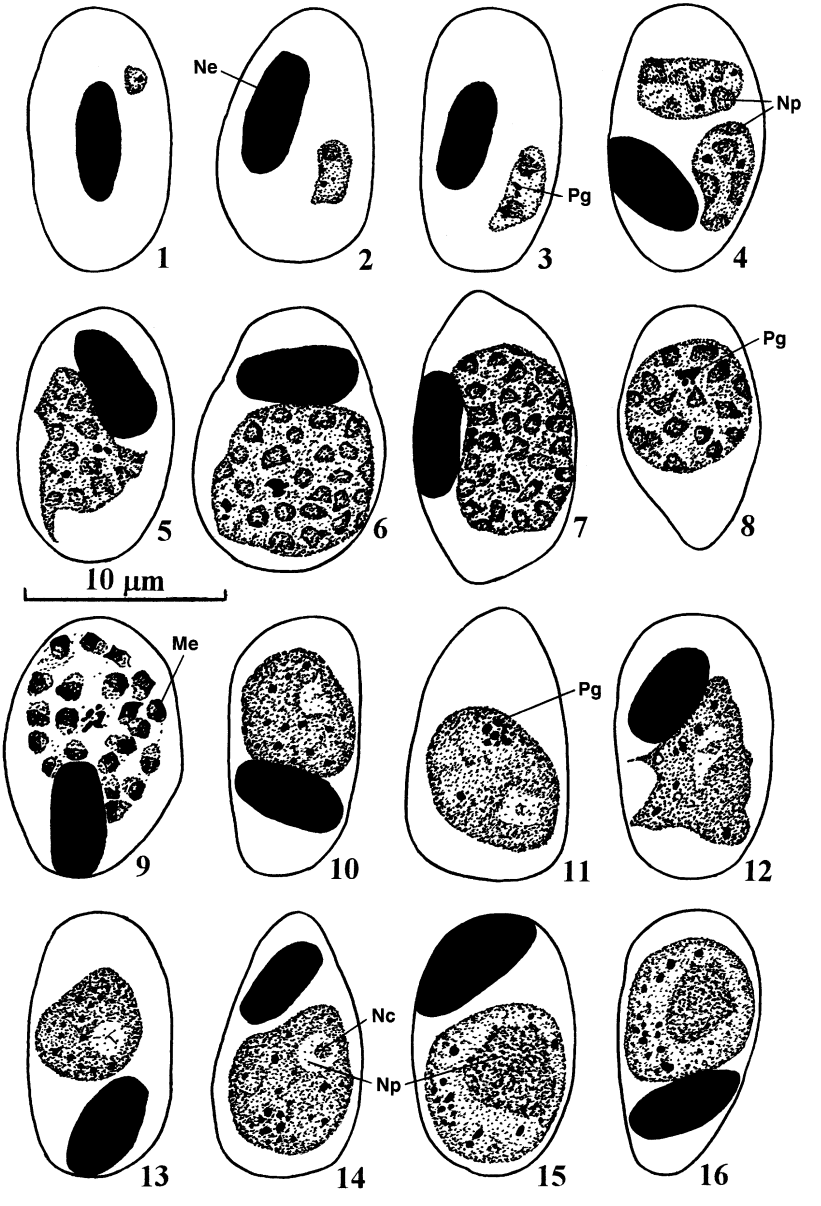


Figure 12 *Plasmodium relictum* from the blood of *Passer hispaniolensis:*
1, *2* – trophozoites; *3–9* – erythrocytic meronts; *10–14* – macrogametocytes; *15*, *16* – microgametocytes; Me – merozoite; Nc – nucleolus; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule.

merozoites formed in metacryptozoites are able to infect the cells of the erythrocytic series. One part of merozoites developed in metacryptozoites induces the next generations of metacryptozoites and phanerozoites, while another part invades the erythrocytes, giving rise to agamic stages and gametocytes, which simultaneously appear in the blood. At this

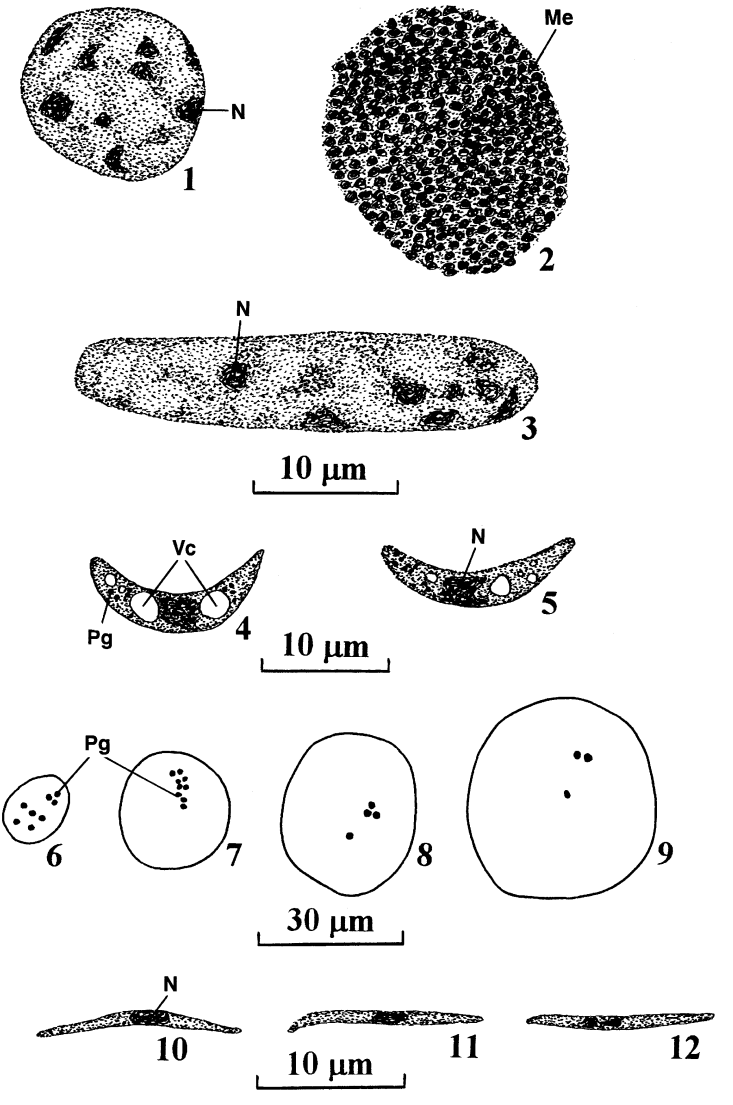


Figure 13 *Plasmodium relictum:*
1–3 – exoerythrocytic meronts in canaries who were infected experimentally by the inoculation of sporozoites (first passage from *Passer hispaniolensis* through *Culex pipiens*): growing (*1*) and mature (*2*) meronts of the first generation in the spleen, and growing phanerozoite (*3*) in brain; *4*, *5* – ookinetes which developed *in vitro*; *6–9* – oocysts at three, four, six and seven days after the ingestion of gametocytes by vector, respectively; *10–12* – sporozoites from salivary glands of *Culex pipiens*; Me – merozoite; N – nucleus; Pg – pigment granule; Vc – 'vacuole' (*6–9* are modified from Garnham, 1966).

stage of development, the number of parasites in the blood cells is not large yet. The time from the inoculation of sporozoites into birds until the maturation of the first generation of metacryptozoites is called a prepatent period of the development, which usually does not exceed 120 h for *Plasmodium relictum.*

Merozoites developed in metacryptozoites induce agamic development in erythrocytes. The parasites, penetrated into the young and (or) mature erythrocytes, become roundish in form and give rise to the growing nonfissionable parasites, which are called trophozoites (Fig. 12, *1–2*). Sometimes, young trophozoites possess a large vacuole and an eccentric nucleus, which makes them look like a 'ring.' The 'rings,' however, are not formed by all species of bird malaria parasites. The form of growing trophozoites varies. The amount of the cytoplasm and the size of the nucleus increase with the growth of the parasite, and, later, granules of malarial pigment (hemozoin) appear. From the moment of first nucleus division (Fig. 12, *3*), the parasite develops into a stage called erythrocytic meront. As a result of asexual multiple division, uninuclear merozoites are formed in erythrocytic meronts (Fig. 12, *9*). Their number is one of the major characters in the identification of species. Erythrocytic meronts of malaria parasites contain pigment granules of golden, brown, or black color (Fig. 12, *3–9*), which frequently group together in mature meronts. The pigment is insoluble residuum formed in the process of hemoglobin digestion (Yamada and Sherman, 1979). The pigment granules are easily distinguished under the light microscope due to their property of strong light refraction.

The duration of the erythrocytic merogony and the degree of its synchronization differ for various species. The cycle of the erythrocytic merogony in the majority of parasites terminates after 24 to 36 h. There are species with a clearly expressed periodicity (*Plasmodium cathemerium, P. gallinaceum, P. matutinum*) and a weakly expressed one (*P. relictum, P. rouxi, P. vaughani*). All agamic stages are usually found in the same blood film. For the species with clearly expressed periodicity, the relative ratio of different stages,

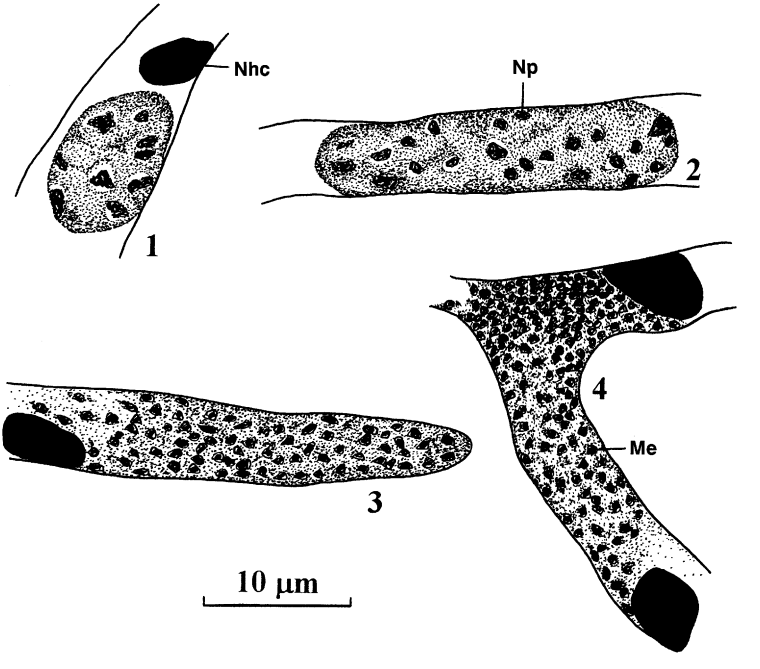


Figure 14 Young (*1*, *2*) and mature (*3*, *4*) phanerozoites of *Plasmodium relictum* in the brain of experimentally infected canaries:
Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite.

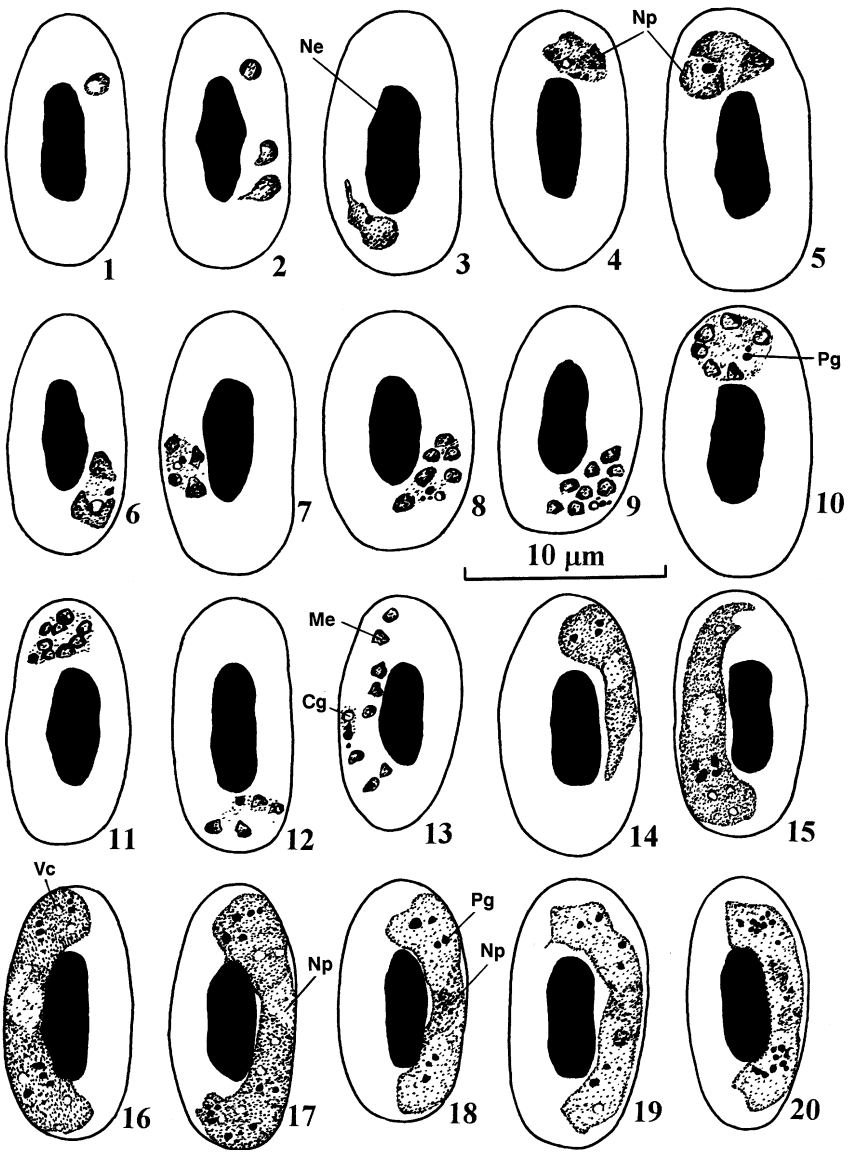


Figure 15 *Plasmodium vaughani* from the blood of *Turdus migratorius* and *T. merula:* *1–3* – trophozoites; *4–13* – erythrocytic meronts; *14–17* – macrogametocytes; *18–20* – microgametocytes; Cg – colourless refractive globule; Me – merozoite; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Vc – vacuole.

however, varies significantly depending on the time of the day. During the rupture of erythrocytic meronts, no indications of fever are found in birds. Infection of vertebrate hosts can be easily achieved by subinoculation of infected blood due to the presence of merogony in the blood.

A part of the merozoites formed in the erythrocytic meronts induces the next cycles of erythrocytic merogony and gives rise to gametocytes (Fig. 12, *10–16*), while the other

part penetrates the endothelial cells of the capillaries of many organs including the brain, initiating secondary exoerythrocytic merogony (phanerozoites). Part of merozoites developing in the metacryptozoites also induces the secondary exoerythrocytic merogony. Maturation of the first generation of phanerozoites usually coincides with the period of the sharp increase of parasitemia (Pl. II, *4*). Phanerozoites together with erythrocytic meronts produce merozoites maintaining the parasitemia during the chronic stage of the infection. In addition, phanerozoites are responsible for the relapses (see p. 185 for more details).

Exoerythrocytic meronts (cryptozoites, metacryptozoites, and phanerozoites) are usually roundish or oval bodies containing a variable number of merozoites (Fig. 13, *1–2*; Pl. I, *2*). Phanerozoites developing in the endothelial cells of brain usually have an elongated form (Fig. 14; Pl. I, *3*). The number of merozoites formed in the exoerythrocytic meronts is a character used for the identification of certain species. Less than 1000 merozoites usually develop in the exoerythrocytic meronts of malaria parasites, but sometimes there are many fewer.

Erythrocytic meronts and gametocytes of different species are variously shaped and characterized by distinct differences according to their influence on host cells, which is widely used in the systematics. For example, the species of the *Haemamoeba* subgenus usually have roundish exoerythrocytic meronts and gametocytes which markedly deform infected erythrocyte, displace its nucleus, and can even enucleate the host cell (Fig. 12, *6–16*). All species of the subgenus *Novyella* have small erythrocytic meronts of variable form and elongated gametocytes, which have no or little influence on the infected cells and their nuclei (Fig. 15, *4–20*).

The general scheme of the parasitemia dynamics of malaria parasites of birds is shown in Fig. 16. The period, when an increased number of parasites is present in the blood of birds infected once (the acute stage of the primary or initial parasitemia), varies from one week to several weeks and occasionally even months, depending on the species and strain of the parasite, the species of the vertebrate host, and other factors. Later, a decrease of the parasitemia takes place in surviving specimens and the parasitemia turns into the chronic stage, whose duration also varies significantly. During this period, only few parasites are found in the blood. Weakening of immunity during the chronic stage of the parasitemia frequently leads to a short-term increase in the number of parasites in the blood (recrudescence). The chronic stage of the parasitemia is frequently followed by the latent stage of infection, when the parasites disappear completely from the peripheral blood. In this case, malaria parasites usually persist in the internal organs. Relapses lead to the secondary parasitemia. It is noteworthy that the relapses are synchronized with the breeding period of birds, which is important for infection of the offspring and maintenance of the parasite in the wild.

Several minutes after feeding on infected birds, mature gametocytes in the midgut of mosquitoes round up and escape from the erythrocytes. Gametes are formed, fertilization occurs, and then the motile ookinete develops. This process occurs according to the same scheme as for all haemosporidians. After 24 to 48 h the ookinetes of *Plasmodium relictum* (Fig. 13, *4*, *5*) are recorded in the midgut of the vectors at a temperature of about 24°C. They take the shape of worm-like bodies containing a nucleus, several ‘vacuoles,’ and granules of pigment. The latter are inherited from macrogametes and macrogametocytes. The average length of the fixed ookinetes is about 16, and the width is about 3 μm.

Ookinetes move toward the epithelial cells of the midgut, reach the basal lamina, become round and transform into the oocysts surrounded by a capsule-like wall. During the process of development, the oocysts significantly increase in size. On average, the diameter

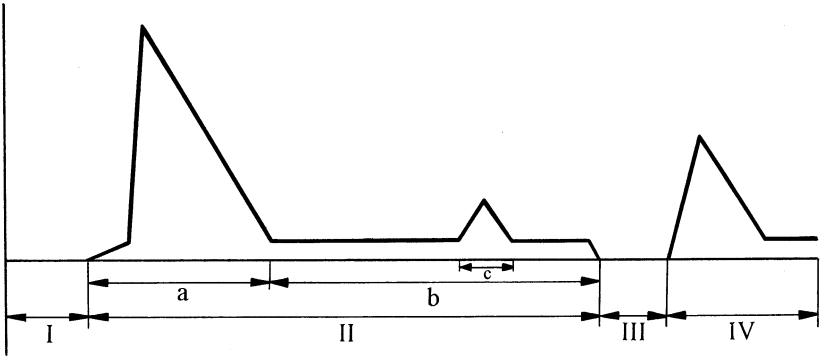


Figure 16 Diagrammatic representation of the dynamics of parasitemia of malaria parasites in birds:
I – prepatent period (parasite develops in internal organs); II – primary parasitemia; III – latent stage of infection (parasites are absent in the blood but persist in internal organs); IV – secondary parasitemia due to relapse; *a–c* – stages of parasitemia: *a* – acute including the crisis, *b* – chronic, *c* – recrudescence. The abscissa is a calendar and the ordinate is a relative parasitemia.

of mature oocysts of *P. relictum* is about 40 μm, or even more. They significantly stretch the basal lamina and can be clearly seen at the surface of the midgut (Pl. III, *5*). Several germinative centres are formed, and many hundreds of sporozoites develop during the sporogony. The oocysts usually possess granules of pigment, whose capabilities for grouping may differ in various species (Fig. 13, *6–9*). The rate of sporogony depends on the species and strain peculiarities of the parasites and vectors, on temperature, and other factors. It is worth noting that among the abiotic factors, temperature is very important. There are different optimal temperatures for various species developing in the vector. Temperatures close to 25°C are optimal for *P. relictum.* The viability of sporozoites developed at higher temperatures decreases. Degeneration of the oocysts occurs, if the mosquitoes are kept at temperatures close to 4°C.

At a temperature of about 24°C, the sporogony of *P. relictum* in *Culex pipiens* mosquito is completed in seven days after ingestion of mature gametocytes. When mature oocysts rupture, the sporozoites get into the haemocoele, penetrate into the salivary glands, where they locate extracellularly, intracellularly, and in the ducts of the glands. Sporozoites have a form of elongated bodies with a nucleus located approximately at the center (Fig. 13, *10–12*). The average length of *P. relictum* sporozoites is about 13 μm, while the width is about 1.4 μm. The sporozoites persist in the salivary glands of the mosquitoes for several weeks. Infection of new hosts occurs by means of injection during a blood meal of infected vectors.

The life cycles of different species of bird malaria parasites have a series of distinctive peculiarities. This primarily relates to the representatives of the subgenus *Huffia*, whose exoerythrocytic merogony occurs in cells of the haemopoietic system. The peculiarities of the development of various species are discussed in the Systematic Section.

LIFE CYCLE AND MORPHOLOGY OF GARNIIDAE SPECIES

The life cycle of garniids has been studied only fragmentarily. The vectors of these parasites have not yet been discovered. Indirect data indicate that it is likely that *Fallisia neotropicalis* completes its development in the mosquito *Aedeomyia squamipennis* (Diptera: Culicidae), but this requires verification (Gabaldon *et al.,* 1985).

The majority of the garniid species develop in reptiles. Only one species, *Fallisia neotropicalis*, was discovered in birds. The development of this parasite in vertebrate hosts is similar to the development of bird *Plasmodium* spp. (Gabaldon *et al.,* 1985). Primary exoerythrocytic meronts, whose development is induced by sporozoites, have not yet been described. Secondary exoerythrocytic merogony (phanerozoites) is easily induced by merozoites developing in the cells of the peripheral blood. The phanerozoites are similar to the ones in bird malaria parasites. It is likely that they are developing in the reticular cells and in the histiocytes of the connective tissues in many organs including the brain. In the peripheral blood, the trophozoites, meronts, and gametocytes mainly develop in thrombocytes; they are less frequently seen in lymphocytes and monocytes. There is no pigment (hemozoin) at any stage of development. Gametogenesis, the development of zygote and ookinete occurs according to the same scheme as for other haemosporidians.

The development and morphology of *F. neotropicalis* are discussed in detail in the Systematic Section (see p. 731).

LIFE CYCLE AND MORPHOLOGY OF LEUCOCYTOZOIDAE SPECIES

The life cycles of the leucocytozoids have been more or less completely studied in approximately 1/3 of the species described so far. Blood-sucking simuliid flies (Diptera: Simuliidae) are the vectors of these parasites (Fig. 17). One of the species (*Leucocytozoon caulleryi*) uses biting midges (family Ceratopogonidae) as vectors. The exoerythrocytic merogony in birds occurs in the parenchymal cells of the liver (hepatocytes), in macrophages and various other reticuloendothelial cells, including endothelial cells of the capillaries. The gametocytes and all other stages of development do not possess malarial pigment (hemozoin). The gametocytes develop in erythroblasts, erythrocytes, and mononuclear leukocytes. Merogony does not occur in blood cells.

In the example below, we describe the life cycle of *Leucocytozoon simondi*, one of the best studied species which has a great practical importance (Huff, 1942; Chernin, 1952; Desser, 1967; Desser *et al*., 1968; Khan *et al*., 1969; Aikawa *et al*., 1970; Yang *et al*., 1971; Eide and Fallis, 1972; and others). The general scheme of development of this parasite is shown in Fig. 18.

Sporozoites injected into birds by simuliid flies during their blood meal can develop only in the parenchymal cells of the liver. Viable sporozoites are found in the birds for several days. The role of this persistence has not yet been studied to a conclusion. Gradual penetration of sporozoites into the hepatocytes is one of the reasons of asynchronous property of the merogony in liver. Sporozoites give rise to the hepatic meronts of the first generation (Fig. 19, *1–3*). The growth of meronts is accompanied by an increase of the amount of cytoplasm and multiple division of the nucleus. The cytoplasm of the parasite

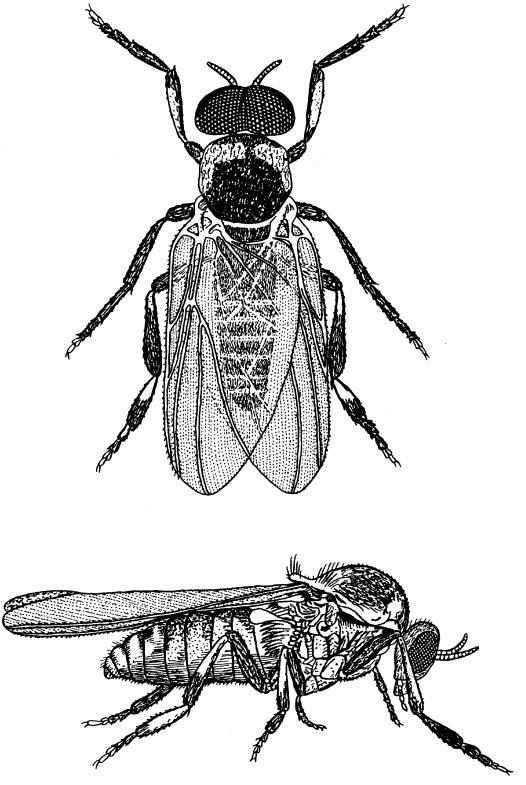


Figure 17 Vector of leucocytozoids, blood-sucking simuliid fly. A general view (modified from Rubtsov and Yankovsky, 1984).

achieves a great number of invaginations and breaks down into separate parts containing a great number of nuclei (Fig. 19, *2*). These parts are called cytomeres. Further invagination of the cytoplasm and nuclei division in the cytomeres lead to the appearance of uninuclear merozoites, whose diameter is about 1 to 2 μm. The cytoplasmic fragments, which are surrounded by a plasma membrane and contain several nuclei, develop simultaneously. These 'fragments' are called syncytia. Mature hepatic meronts reach 45 μm in diameter, but are usually smaller. The nuclei of the infected cells are markedly enlarged. The development of the hepatic meronts is completed in four to five days.

After the merozoites get into the blood, they penetrate into immature and mature erythrocytes giving rise to the gametocytes. The prepatent period is equal to approximately five days. Young gametocytes cause marked hypertrophy and deformation of the host cells and their nuclei. They are located in the infected cells in the indentation of the nucleus. The growth of the gametocytes is completed within two days. The fully grown undeformed gametocytes are roundish or oval. The host cells are roundish in form and do not produce any fusiform processors. Their nuclei acquire a cup-like or band-like form, and they are closely appressed to the gametocytes (Fig. 20, *4, 6, 7*).

It seems likely that some of the merozoites from the hepatic meronts induce secondary exoerythrocytic merogony in the hepatocytes. However, there is no conclusive proof of that due to the asynchronous character of the merogony.

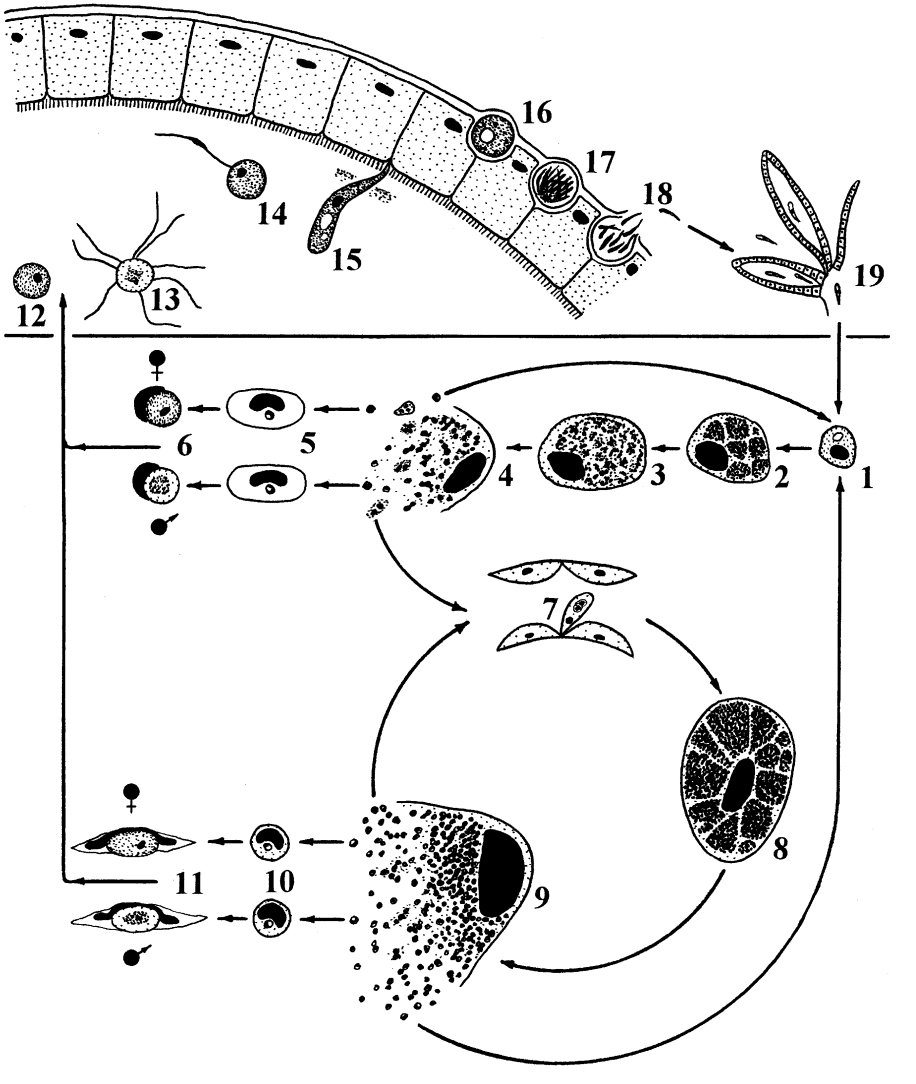


Figure 18 Diagrammatic representation of the life cycle of leucocytozoids (*Leucocytozoon simondi* as an example):
Upper part, in vector; lower part, in bird: *1* – sporozoite or merozoite in the parenchymal liver cell (hepatocyte); *2–4* – hepatic meronts; *5* – merozoites in erythrocytes; *6* – gametocytes in roundish host cells; *7* – syncytium (=a fragment of hepatic meront with two or more nuclei) or merozoite in reticuloendothelial cell; *8*, *9* – megalomeronts; *10* – merozoites in mononuclear leukocytes; *11* – gametocytes in fusiform host cells; *12* – macrogamete; *13* – exflagellation of microgametes; *14* – fertilization of macrogamete; *15* – ookinete penetrating the peritrophic membrane; *16* – young oocyst; *17*, *18* – sporogony; *19* – sporozoites in the salivary glands of vector.

The syncytia get into the blood and spread into many organs. They are phagocytized by macrophages and other cells of the reticuloendothelial system giving rise to the second generation of meronts, which were called ‘megalomeronts’ or ‘megaloschizonts’ due to their large size (Fig. 19, *4–7*). This term defines the ‘host cell–parasite’ complex. Strictly

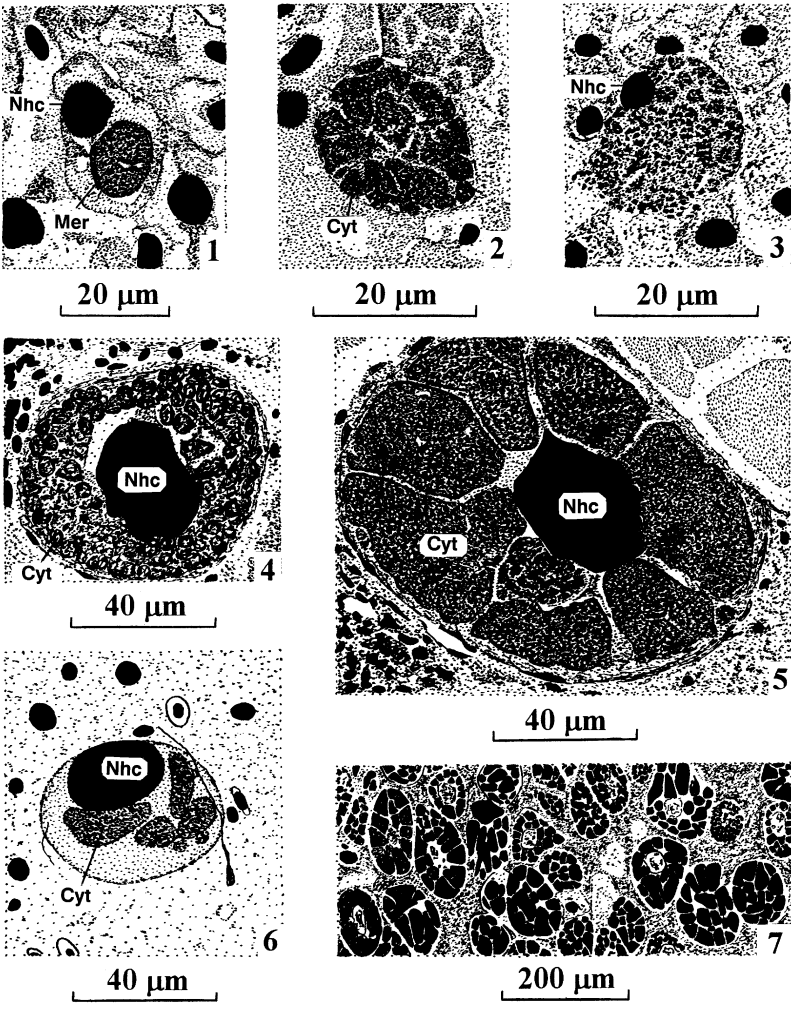


Figure 19 Exoerythrocytic meronts of *Leucocytozoon simondi* from the internal organs of experimentally infected domestic ducks:
1–3 – hepatic meronts: young parasite (*1*), growing parasite with numerous cytomeres (*2*), mature parasite dividing into merozoites and syncytia (*3*); *4–6* – megalomeronts in spleen (*4*), liver (*5*) and brain (*6*) (numerous cytomeres and markedly enlarged nucleus of the host cell are seen), *7* – diagrammatic representation of a histological section of heavily infected spleen overfilled with megalomeronts; Cyt – cytomere; Mer – meront; Nhc – nucleus of host cell (*1*, *2*, *4* to *7* are modified from Desser, 1967).

speaking, the term ‘megalomeront’ should be used only for the parasite dividing asexually. This term in its present day meaning was initially used by Huff (1942). This term is rather informative. It has been accepted into the literature and scholars have used it by present to define the ‘host cell – large exoerythrocytic meront’ complex, which is characterized by complicated relations. The main features of the megalomeront are its large size (from 50 to 400 μm or greater) and the markedly hypertrophied nucleus of the host cell (which is sometimes called a central body of the megalomeront) (Pl. I, *4*).

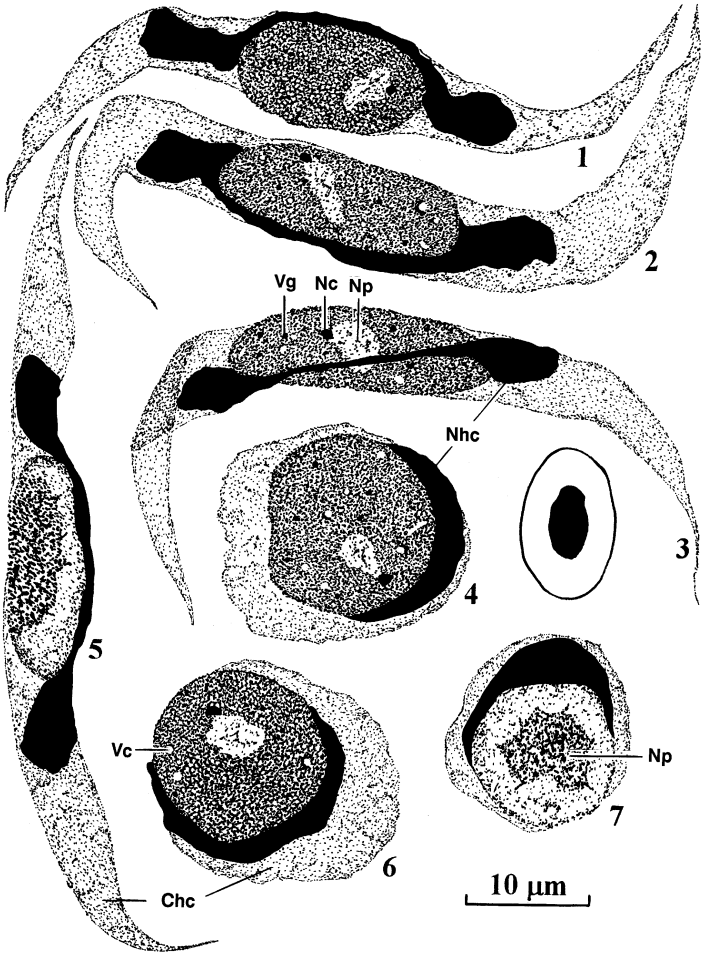


Figure 20 Gametocytes of *Leucocytozoon simondi* from the blood of *Anas penelope:* *1–4*, *6* – macrogametocytes; *5*, *7* – microgametocytes; Chc – cytoplasm of host cell; Nc – nucleolus; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – vacuole; Vg – valutin granule. An uninfected erythrocyte is shown in the centre for comparison (modified from Valkiūnas *et al*., 1990).

Megalomeronts can be seen anywhere in the bird organism, but the majority are in the spleen (Fig. 19, *7*; Pl. I, *4*) and in the lymph nodes. Numerous cytomeres are formed during the development of the parasites. Megalomeronts become mature within four to five days. They possess hundreds of thousands of uninuclear merozoites with a diameter of approximately 1 μm. Merozoites penetrate into the lymphocytes and other leukocytes of the mononuclear type giving rise to gametocytes. Infected cells become fusiform, while their nucleus markedly deforms and displaces to the periphery (Fig. 20, *1–3, 5*). A part of the merozoites formed in megalomeronts is absorbed by the reticuloendothelial cells. These merozoites slow down their development, periodically forming megalomeronts, due to which the chronic parasitemia is maintained and the spring relapses of the infection are developed. It is not inconceivable that a part of merozoites from megalomeronts can induce secondary merogony in the liver.

As noted above, the form of the *Leucocytozoon* gametocytes is roundish, oval, or elongated oval. There are two types of gametocytes, in the roundish (Fig. 20, *4;* Pl. II, *5*) and fusiform (Fig. 20, *1*; Pl. II, *6*) host cells. In the latter case, infected cells obtain more or less expressed spindle-like cytoplasmic processes, that is characteristic only of the leucocytozoids. There are species with gametocytes only in the roundish host cells (for example, *L. dubreuili, L. fringillinarum, L. majoris*) and ones with gametocytes only in fusiform host cells (*L. neavei, L. sousadiasi*), as well as those with gametocytes found in both types of host cells (*L. danilewskyi, L. lovati, L. simondi*). It is noteworthy that the host cells become fusiform during the growth of young gametocytes, but not when they gain maximum size. One of the characteristic features of the impact of gametocytes on the host cells is strong deformation and hypertrophy of its nucleus. This indicates that the host cells are intensively participating in the growth of gametocytes. The nucleus usually relocates to the periphery and locates close to the gametocyte. Dust-like azurophilic inclusions are found in the gametocytes of many species. They are usually called valutin or 'pseudopigment'. The nature of valutin has not been studied yet in detail. Valutin weakly refracts light, unlike malarial pigment (hemozoin) which is not present in leucocytozoids because the parasites digest hemoglobin completely when they develop in red blood cells.

The ratio of the macro- and microgametocytes in the same individual birds significantly differs in the course of parasitemia. The reasons of this are unknown. A small number of gametocytes in the blood of birds infected once is frequently found within the entire year. During the breeding period of birds, relapses are observed. In this period of parasitemia, the gametocytes in the fusiform cells predominate. Relapses are associated with the renewal of exoerythrocytic merogony of parasites persisting in the internal organs, and they are stimulated at least in part by sexual hormones (see p. 185). The synchronization of relapses with the breeding period of birds is important for the infection of vectors and next for the infection of the bird offspring and finally for the survival of parasites in nature.

Infection of vertebrate hosts by infected blood subinoculation is impossible due to the fact that there is no merogony in the blood cells excluding the instance, when exoerythrocytic merozoites are present in the blood.

Many species of blood-sucking simuliid flies, including those species that do not generally feed on birds, are vectors of *L. simondi.* It is likely that the restrictions for the development of parasites in one or other species of simuliids are ecological rather than physiological (Desser and Yang, 1973).

Gametocytes developing both in roundish and fusiform host cells are infective for the vectors. Development of the gametes, fertilization, development of ookinetes, and sporogony take place in the midgut of the simuliids, which ingested mature gametocytes. Each generation of the gametocytes keeps the ability for exflagellation for at least five days.

Parasitemia of *L. simondi* and *L. smithi* is characterized by clearly expressed diurnal cycles (Roller and Desser, 1973a; Noblet and Noblet, 1976). The peak of gametocytemia takes place in the daytime, which coincides in time with the period of activity of blood-sucking simuliids who are the vectors of infection. This is the adjustment to complete the development in the optimal way.

The process of exflagellation *in vitro* has been studied by Desser with co-authors (Desser, 1970c; Desser *et al*., 1976). After the blood containing mature gametocytes is exposed to the air, microgametocytes escape from the erythrocytes within a few seconds and become round. At this time the chromatin in the nucleus obtains the form of net-like threads (Fig. 21, *2*), but later it concentrates into a compact mass (Fig. 21, *3*). Shortly after

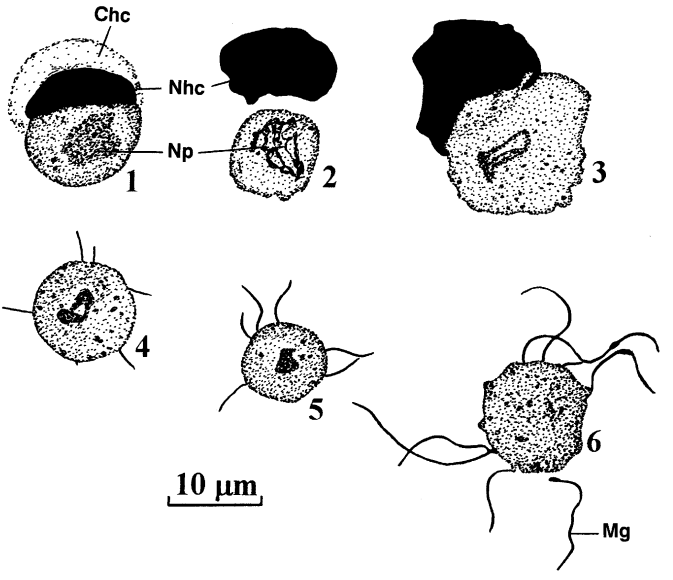


Figure 21 Microgametogenesis of *Leucocytozoon simondi:*
1 – mature microgametocyte in the peripheral blood of birds before the onset of gametogenesis; *2*, *3* – free microgametocyte (the nucleus of host cell still locates close to the gametocyte); *4–6* – exflagellation of microgametes; Chc – cytoplasm of host cell; Mg – microgamete; Nhc – nucleus of host cell; Np – nucleus of parasite (modified from Desser *et al*., 1976). Description of nuclear changes of microgametocytes are given in the text.

this, exflagellation of microgametes starts (Fig. 21, *4–6*). The chromatin divides. One portion of chromatin penetrates into each of the eight forming microgametes. This process is rapid and can be completed within one minute. Developing microgametes keep contact with the microgametocyte for some time making active snake-like motions. Shortly after this they free themselves, and they move actively by means of sinusoidal bending of their body. The average length of the microgametes in fixed preparations is about 23 μm, while the width is about 1 μm (see also p. 793).

The conditions necessary for the successful exflagellation of the microgametocytes, were studied by Roller and Desser (1973b). They showed a clearly expressed inverse relation between the temperature of the environment and the time necessary to start the exflagellation. Exflagellation is rarely observed at temperatures lower than 15°C. If the temperature increases from 15 to 20°C, the time needed for the preparation of microgametocytes for exflagellation is reduced. If the temperature is in the range of 26 to 40°C, exflagellation starts in 1 to 1.5 min. This process is most successful at temperatures close to the temperature of the bird's body. This indicates that no decrease of the blood temperature is needed to stimulate gametogenesis, as was believed before.

The ability of gametocytes for exflagellation at high temperatures is biologically important, because when the simuliids are feeding, their temperature may reach the temperature of the bird's body. To feed with blood, the simuliids approach the skin of the bird, where they can stay up to 30 min. The blood meal action lasts 4 to 10 min (Fallis, 1964). At this time the temperature of the simuliids' body increases, which supports successful exflagellation. As a result, inhibition of exflagellation *in vivo* does not occur at

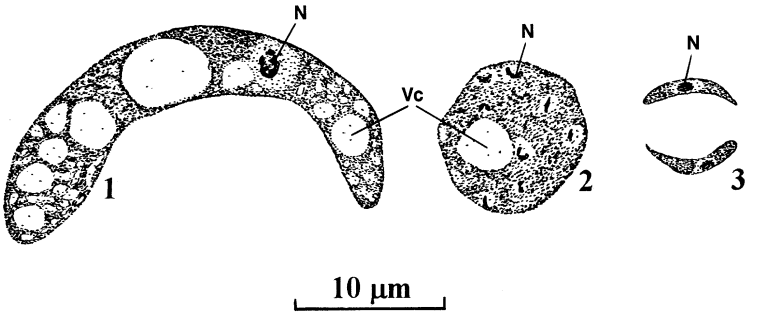


Figure 22 *Leucocytozoon simondi:*
1 – ookinete; *2* – young oocyst; *3* – sporozoites; N – nucleus; Vc – 'vacuole' (modified from Fallis *et al*., 1951).

low temperatures of the natural environment, and this contributes to the successful transmission of leucocytozoids in the Northern Holarctic. The change of the partial pressure of the air components is the other factor stimulating the process of gametogenesis. Regardless of environmental temperature, the process of exflagellation does not start without access to the air. It was shown experimentally that oxygen supply and a decrease in carbon dioxide concentration are needed to initiate exflagellation. Exflagellation takes place in the atmosphere where the content of CO_2 is less than 3%. Decrease of its concentration, when the blood is exposed to the air or gets into a vector, is one of the main prerequisites for the beginning of exflagellation.

Zygote is formed when microgamete fertilizes the macrogamete. Within 6 to 12 h at a temperature close to 20°C, the zygote transforms into a motile ookinete (Fig. 22, *1*). The average length of fixed ookinetes is about 30 μm, while their width is about 4 μm. Ookinetes possess a nucleus and several clear vacuole-like spaces, which are grouping of lipoproteins washed out during the alcohol fixation. The development of ookinetes and oocysts is not synchronized. Ookinetes move toward the layer of epithelial cells of midgut, reach the basal lamina, and transform into spherical oocysts surrounded by a capsule-like wall. The fate of the ookinetes, which did not leave the midgut before the formation of the peritrophic membrane, is not clear. Some of them perish, but it is likely that some of them survive and continue development after the breaking of the peritrophic membrane. The long (up to 7 to 18 days) period of sporogony in simuliids infected only once confirms this.

Sporogony is completed after three to five days at a temperature of 20°C. It is noteworthy that sporogony of *L. simondi* occurs successfully at relatively low temperatures. Additionally, a temperature of 15°C is the optimal temperature for the development of certain strains (Eide and Fallis, 1972), which is an adjustment for development in the high latitudes of the Holarctic. A large vacuole-like structure is present in young oocysts which is a gathering of lipoproteins that are washed out during the alcohol fixation (Fig. 22, *2*). The sizes of oocysts only slightly increase in the process of their development. The diameter of mature oocysts varies between 9 and 14 μm. Few sporozoites (usually fewer than 100) are formed in each oocyst.

A general scheme of the development of an oocyst is shown in Fig. 23. The oocysts locate extracellularly inside the layer of epithelial cells touching their plasma membrane. Usually, the oocyst stretches the basal lamina slightly in the direction of the haemocoele, but its major part is located in the area of the epithelial cells. Some oocysts are located

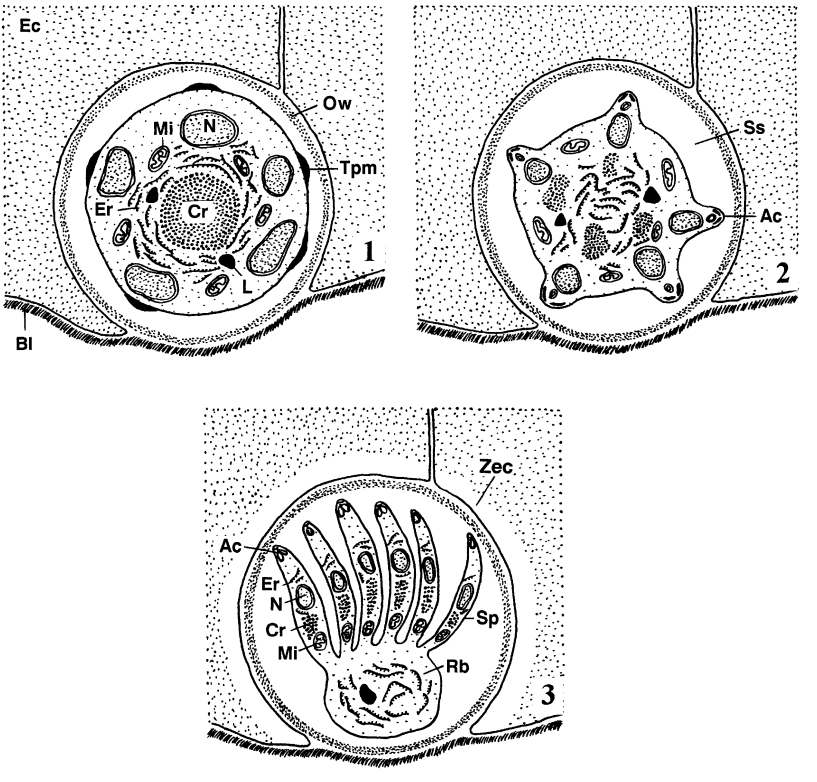


Figure 23 Diagrammatic representation of the development of oocyst of *Leucocytozoon simondi: 1–3* – successive stages of development of oocyst; Ac – organelles of the apical complex of developing sporozoites; Bl – basal lamina of midgut of vector; Cr – crystalloid; Ec – epithelial cell of midgut; Er – endoplasmic reticulum; L – lipid; Mi – mitochondrion; N – nucleus; Ow – oocyst capsule-like wall; Rb – residual body; Sp – sporozoite; Ss – subcapsular space; Tpm – thickening beneath the plasma membrane of oocyst; Zec – zone of epithelial cell lacking organelles (modified from Desser and Wright, 1968).

completely between the epithelial cells and, thus, it is not easy to find them. A zone free from organelles is located in the epithelial cells adjacent to the oocyst (Fig. 23, *3*). During the early stages of the oocysts development, such a zone has not been recorded (Fig. 23, *1, 2*), while its width can be as large as 1 μm in the oocysts with sporozoites. No other distinctions are found between the epithelial cells adjacent and not adjacent to the oocyst. It is not improbable that this zone is involved in the transport of metabolites.

Sporozoites free themselves from the oocysts, get into the haemocoele, and penetrate into the salivary glands. Sporozoites are elongated bodies with one rounded and one end more or less pointed (Fig. 22, *3*). The average length of the sporozoites is 8 μm, while their width is 1 μm. Infection of birds occurs by means of the infection of sporozoites with salivary gland secretion, when infected simuliids are feeding on birds. It is noteworthy that within 11 days after infection, sporozoites of *L. dubreuili* are found in the peripheral blood of experimentally infected thrushes (Khan *et al*., 1969). Limited data indicate that sporozoites of *L. dubreuili* are able to a transit pass through the cells of infected birds. They move by bending their bodies and by sliding in a gregarine-like way (Wong and Desser, 1977).

Development in the vectors of all species of leucocytozoids so far studied occurs according to the scheme described above, while their development in the vertebrate host significantly differs. The general regularity is that the first generation of exoerythrocytic meronts in all species, excluding *L. caulleryi,* develops in the parenchymal cells of the liver, although in several species (for example, *L. dubreuili*) the first generation of the meronts also develops in the endothelial cells of the kidneys. *Leucocytozoon smithi* is the only species known at present, where the merogony occurs only in the hepatocytes (Steele and Noblet, 1992).

The role of megalomeronts in the life cycle of leucocytozoids has not yet been completely understood. They are found in *L. caulleryi, L. danilewskyi, L. sakharoffi, L. simondi*, and in some other species. Megalomeronts of *L. caulleryi* are characterized by the fact that they complete their development in an extracellular way (see p. 845). It is important to note that the formation of megalomeronts and gametocytes in fusiform host cells is not required to complete the life cycle of *L. simondi* (Desser and Ryckman, 1976). These stages are not formed in some vertebrate hosts (see p. 790 for more details). It is worth noting in this connection that megalomeronts of *L. sakharoffi* were also found not in all of its vertebrate hosts. The megalomeronts are not found in *L. dubreuili, L. fringillinarum, L. smithi,* and in many other species. Moreover, there is no strict correlation of the development of megalomeronts and gametocytes in the fusiform host cells. Gametocytes in the fusiform host cells do not develop in *L. sakharoffi*, which has megalomeronts (Wingstrand, 1947, 1948), but they are formed in *L. smithi,* which do not produce megalomeronts (Steele and Noblet, 1992). Additional investigation is required for the understanding of the role of megalomeronts in the development of the leucocytozoids.

The life cycle of *L. caulleryi* is characterized by a series of peculiarities that differentiate this species from the others. First, biting midges of the family Ceratopogonidae are the vectors of the parasite. Second, exoerythrocytic meronts of the first and following generations develop in the endothelial cells of the capillaries of many organs. Third, merozoites of the first generation are elongated, and their average length reaches 7 μm. Fourth, megalomeronts complete their development extracellularly and they do not have the so-called 'central body.' Fifth, the prepatent period is long (approximately two weeks).

It follows from this brief review that there are still many 'blank spots' in the problem of the life cycles of leucocytozoids, and thus further studies are needed. The peculiarities of the development of individual species are considered in more detail in the corresponding essays about species in the Systematic Section.

A Brief Outline of the Ultrastructure

The organization and development of bird haemosporidians at the ultrastructure level are difficult. Detailed consideration of these problems is beyond the scope of this book. One can find the main information on the ultrastructure of bird haemosporidians in a number of reviews and monographs (Aikawa, 1971; Aikawa and Sterling, 1974; Fallis *et al*., 1974; Seed and Manwell, 1977; Aikawa and Seed, 1980; Meis and Verhave, 1988; Wernsdorfer and McGregor, 1988; Paterson and Desser, 1989; Desser and Bennett, 1993). Below, a general characteristic of the ultrastructure of bird haemosporidian parasites is given that is important to solve a series of theoretical problems including those which facilitate the understanding of the phylogenetic relations and evolution of the groups of protists considered.

Haemosporidians are characterized by a similar ultrastructure, although the details of the organization of certain stages of development may significantly differ. In the course of description, the main peculiarities of the structure of the objects considered will be indicated. It is noteworthy that the ultrastructure of *Fallisia neotropicalis,* the only representative of the family Garniidae parasitizing birds, has not been studied yet. Information available on the ultrastructure of species belonging to the genera *Fallisia* and *Garnia*, developing in reptiles, indicates that garniids and other haemosporidians have similar structure (Boulard *et al*., 1987; Paperna and Boulard, 1990; Dizin *et al.*, 2000). The peculiarities of the ultrastructure of the reptilian garniids are not analyzed in this book.

SPOROZOITES AND MEROZOITES. THE PECULIARITIES OF THEIR PENETRATION INTO THE HOST CELLS

Sporozoites and merozoites are spreading stages, whose ultrastructure demonstrates more similarities rather than differences (Garnham, 1966; Aikawa, 1971; Desser, 1972c; Desser and Allison, 1979; Morii *et al*., 1981, 1987; Atkinson, 1991a). Let us discuss their structure separately.

S p o r o z o i t e s develop in the vector and initiate parasite development in the birds. They are elongated fusiform cells whose length in different species usually varies within 7 to 16 μm, while the width is on average about 1 μm. The structure of sporozoites in all groups of haemosporidians is quite conservative (Fig. 24). The organelles of sporozoites can be arbitrarily divided into two groups of general and special purposes. The organelles of general purposes are responsible for the fundamental processes of vital activity in the cell. Among these are primarily the nucleus, mitochondria, Golgi apparatus, endoplasmic reticulum, ribosomes, and some others. The organelles of special purposes (complex pellicle with a micropyle, polar rings, subpellicular microtubules, rhoptries, micronemes, etc.) facilitate extracellular existence and the spreading of the parasites as well as their

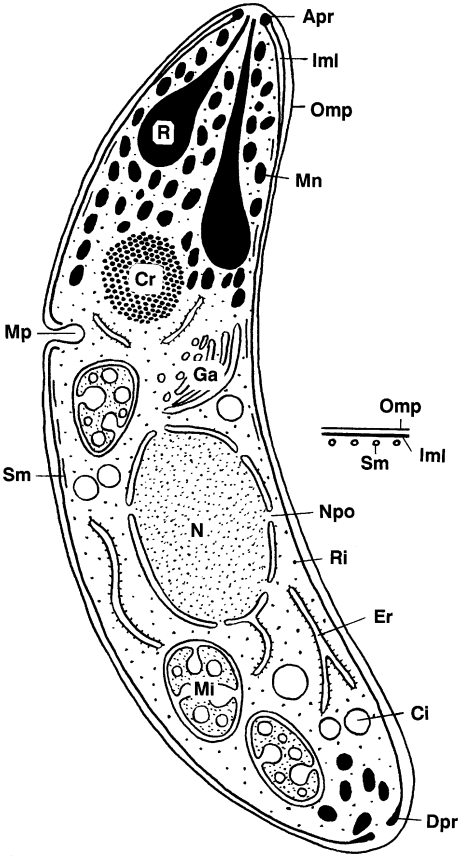


Figure 24 Diagrammatic representation of the structure of sporozoites of bird haemosporidians: Apr – anterior polar ring; Ci – cell inclusion; Cr – crystalloid; Dpr – distal polar ring; Er – endoplasmic reticulum; Ga – Golgi apparatus; Iml – inner interrupted membrane layer; Mi – mitochondrion; Mn – microneme; Mp – micropyle (ultracytostome); N – nucleus; Npo – nuclear pore; Omp – outer membrane of pellicle; R – rhoptry; Ri – ribosome; Sm – subpellicular microtubule. A fragment of the cross-section of pellicle with adjacent subpellicular microtubules is shown on the right.

penetration into the host cell. The organelles of special purposes are characteristic of the spreading stages of all sporozoans, which is one of the main systematic characters of the phylum Sporozoa (=Apicomplexa) (Levine, 1970; Krylov and Dobrovolsky, 1980; Levine *et al*., 1980; Beyer, 1989; Krylov, 1992). Let us analyze the structure of some of these organelles in more detail.

The nucleus is located in the center of the sporozoite, and it is rather large in proportion to the size of the cell. The nuclear envelope is composed of two membranes with nuclear pores. The mitochondria are small. They possess tubular cristae. In addition to the structures listed above, the cytoplasm of the cell contains lysosomes, lipid droplets, bubble-shaped structures bounded with a membrane, and some other cellular inclusions. It is noteworthy that sporozoites of *Haemoproteus* and *Leucocytozoon* spp. possess peculiar inclusions that are called a crystalloid material (Desser, 1970b; Desser and Allison, 1979;

Atkinson, 1991a). The crystalloid of sporozoites is composed of more or less space-ordered particles with a size of about 20 to 40 nm (see also p. 65). These particles contain lipoproteins, but do not contain DNA or RNA, nor are they surrounded by a membrane (Trefiak and Desser, 1973). Crystalloid was not found in the *Plasmodium* spp. sporozoites. It is likely that crystalloid performs energy functions and takes part in the metabolism of lipids.

The pellicle consists of three membranes. The outer membrane (plasmalemma) is continuous, while the two inner ones are interrupted in the region of the poles and a micropyle. These two membranes form the inner double interrupted membrane layer.

The micropyle (ultracytostome) is formed by invagination of plasmalemma in the area of the sporozoite's cytoplasm. As mentioned above, an inner double membrane layer interrupts in the area of the invagination. The micropyle plays the role of the 'cell's mouth,' which probably is out of operation at the spreading stage.

The polar rings are located at the anterior (apical) and posterior (distal) ends of the sporozoite. The anterior polar ring is a complex structure, where subpellicular microtubules originate. Two more apical rings are located over the anterior polar ring. The posterior polar ring is the area where the inner membrane layer terminates.

Subpellicular microtubules are an important part of the cytoskeleton. They pass under the inner membrane layer at an equal distance from each other stretching out from the anterior polar ring in the direction to the distal end, but not reaching it. The number of subpellicular microtubules varies in different species. For example, there are 22 of them in *Haemoproteus mansoni* (=*H. meleagridis*) (Atkinson, 1991a), 30 in *Leucocytozoon tawaki* (Desser and Allison, 1979), and 12 in *Plasmodium gallinaceum* (Garnham *et al*., 1963).

Rhoptries and micronemes are electron-dense structures. The largest of them are called rhoptries. They have a more or less elongated form and are located in the anterior one third of the sporozoite. The more numerous and smaller in size structures are called micronemes. The major part of them is located in the anterior one third of the cell, but they can also be located in the center and at the distal end of the sporozoite. The distinct boundary between rhoptries and micronemes cannot always be indicated. The ducts of rhoptries and micronemes are stretched in the direction of the plasmalemma of the apical end where they open.

One of the characteristic peculiarities of the ultrastructure of haemosporidian sporozoites and merozoites is the absence of conoid. Nevertheless, this peculiar organelle is found in the ookinetes of haemosporidians and it is described below when the ookinetes' ultrastructure is considered.

Sporozoites invade the receptive cells of a vertebrate host giving rise to actively growing nonfissionable stages (trophozoites), which later transform into exoerythrocytic meronts. Merozoites develop intracellularly by asexual division of meronts. Merozoites are released from the host cells, when the latter are ruptured.

M e r o z o i t e s usually have an oval or roundish form. Their diameter does not generally exceed 2 μm. The exclusion are exoerythrocytic merozoites of the first generation in *Haemoproteus mansoni* and *Leucocytozoon caulleryi,* which are elongated in form. Their length reaches 5 μm and even more (Atkinson *et al*., 1986; Morii and Fukuda, 1992).

Ultrastructure of haemosporidian merozoites is similar to the structure of sporozoites. The organization of merozoites in different groups of haemosporidians is, however, much more pleomorphic. The ultrastructure of *Plasmodium* and *Haemoproteus* spp. merozoites is the most similar to the one of sporozoites (Fig. 25, *1*). Merozoites of these parasites are covered with a pellicle composed of three membranes; they have a micropyle, subpellicular microtubules, three apical polar rings, rhoptries, and micronemes. There is no conoid. The

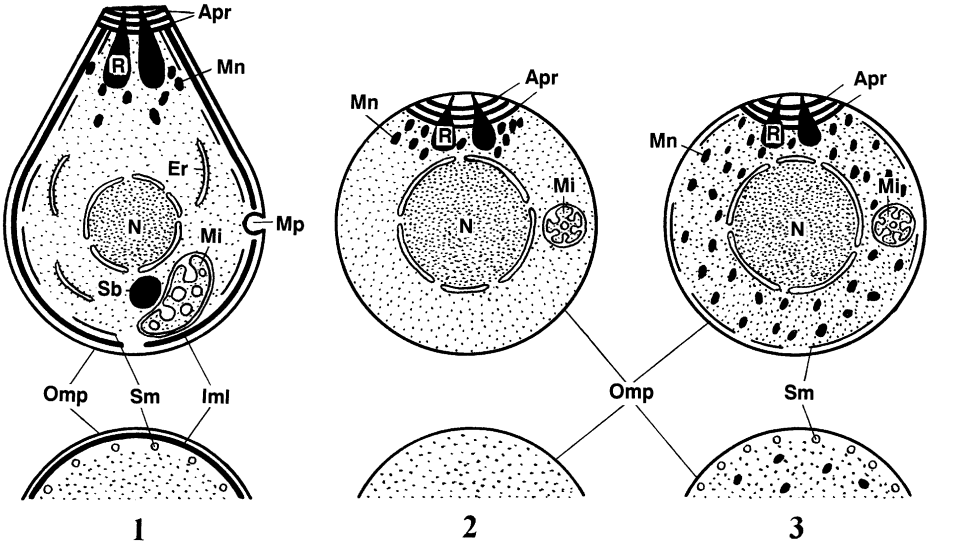


Figure 25 Diagrammatic representation of the structure of merozoites of bird haemosporidians: *1 – Haemoproteus* and *Plasmodium* spp.; *2 – Leucocytozoon simondi*; *3 – L. dubreuili*; Apr – anterior polar rings; Er – endoplasmic reticulum; Iml – inner interrupted membrane layer; Mi – mitochondrion; Mn – microneme; Mp – micropyle; N – nucleus; Omp – outer membrane of pellicle; R – rhoptry; Sb – 'spherical body' associated with a mitochondrion; Sm – subpellicular microtubule (modified from Wong and Desser, 1978).

nucleus is large. It is located in the center of the merozoite. A nucleolus was found and described in the exoerythrocytic merozoites but not in the erythrocytic ones. There is one crescent-shaped mitochondrion, with tubular cristae. It is located closer to the distal end of the merozoite. A so-called 'spherical body,' whose function has not been completely understood, is located near the mitochondrion. There is a suggestion that the 'spherical body' is associated with the energy functions of the cell (Aikawa and Seed, 1980). The ribosomes are numerous. The endoplasmic reticulum is weakly developed. The Golgi apparatus is difficult to distinguish.

The ultrastructure of merozoites of certain species of *Leucocytozoon* is characterized by distinguishing peculiarities (Fig. 25, *2, 3*). The structure of *L. caulleryi* merozoites is almost identical to that of *Plasmodium* and *Haemoproteus* spp. (Morii *et al*., 1981, 1987; Morii and Fukuda, 1992). There is no inner membrane layer in *L. dubreuili* and *L. simondi* merozoites. The micropyle is not found (Wong and Desser, 1978, 1981). Even more, there are no subpellicular microtubules in *L. simondi* merozoites. It is interesting to note that there are subpellicular microtubules in the renal merozoites, but none in the hepatic merozoites of *L. dubreuili.* In this respect *L. dubreuili* occupies an intermediate position between *L. simondi* on the one hand, and *L. caulleryi* and the species of *Plasmodium* and *Haemoproteus* on the other hand. It is likely that the partial simplification of the structure of merozoites in certain species of *Leucocytozoon* is associated with the lack of their mobility. It should be remembered in this connection that motile sporozoites of all haemosporidian groups have similar structure of their pellicle and possess subpellicular microtubules. The presence of a spherical mitochondrion and the lack of a 'spherical body' are also distinguishing peculiarities of the structure of *Leucocytozoon* spp. merozoites.

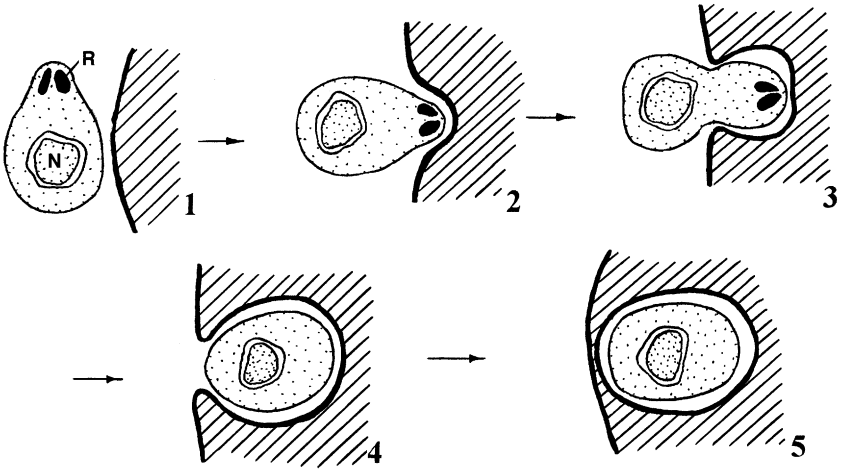


Figure 26 Diagrammatic representation of the penetration of merozoites of haemosporidians into erythrocytes (modified from Breuer, 1985).
N – nucleus, R – rhoptry. Explanation is given in the text.

The merozoites formed in the *L. simondi* megalomeronts differ in the electron density of their cytoplasm. It is believed that merozoites with a lesser electron density of cytoplasm give rise to the microgametocytes, while those with a greater density give rise to the macrogametocytes (Desser, 1970a). Merozoites of *L. simondi* developing in the hepatic meronts do not differ in this character.

The existence of differences in the ultrastructure of *Plasmodium, Haemoproteus,* and *Leucocytozoon* spp. merozoites as well as in the ultrastructure of the same species of *Leucocytozoon* at different stages of their development indicate that one should be careful in generalizing the ultrastructure within the same genus and even within the same species of haemosporidians.

Among the bird haemosporidians, the process of penetration of zoites into a host cell have been studied in detail for *Plasmodium gallinaceum* in the 'merozoite–erythrocyte' model (Ladda *et al*., 1969). It passes in a uniform way for each of the malaria parasites, and it is likely that it is the same for all haemosporidians (Breuer, 1985; Kostenko, 1992). Penetration of merozoites into erythrocytes is a complex process that occurs with energy consumption. It is controlled by a set of cellular reactions. The penetration takes place by means of induced phagocytosis without perforation of the plasma membrane of the host cell. Briefly, this process can be described as follows (Fig. 26). Free merozoites initially get into contact with an erythrocyte by any part of their cell (Fig. 26, *1*), and next, they reorient themselves so that their apical end is slightly pressed into the plasma membrane of the erythrocyte (Fig. 26, *2*). The deepening into the plasmalemma increases as the merozoite penetrates into the erythrocyte (Fig. 26, *3*). During this process, the integrity of the host cell's membrane is maintained. At the final stage of the penetration, the erythrocyte's membrane closes up, while the parasite appears enclosed in the parasitophorous vacuole that is restricted by the inverted host cell's membrane (Fig. 26, *4*). The parasitophorous vacuole performs the functions of a buffer creating the necessary conditions for the intracellular development of trophozoites, meronts, and gametocytes.

TROPHOZOITES AND MERONTS

After penetration into the host cell, the haemosporidians sporozoites and merozoites transform into actively growing t r o p h o z o i t e s (Aikawa, 1971; Seed and Manwell, 1977; Aikawa and Seed, 1980). Some of the merozoites are capable of penetrating the blood cells and giving rise to gametocytes. The process of the transformation of sporozoites and merozoites into trophozoites includes a rapid degeneration of the inner double membrane layer, subpellicular microtubules, polar rings, rhoptries, and micronemes. The crystalloid material characteristic of *Haemoproteus* and *Leucocytozoon* spp. sporozoites is not found in trophozoites. The trophozoite is surrounded only by plasmalemma and enclosed in the parasitophorous vacuole. Thus, trophozoites and then meronts are separated from the cytoplasm of the host cell by a membrane of the parasitophorous vacuole, which is produced from the plasma membrane of the infected cell and the plasmalemma of the former sporozoites or merozoites. The growth of the trophozoite is accompanied by the increase of the nucleus size and the amount of the cytoplasm. The nucleolus is clearly expressed. The endoplasmic reticulum is relatively weakly developed.

Trophozoites feed themselves by means of absorption and digestion of the cytoplasmic content of the host cell. Hemoglobin is one of the main components of erythrocytic trophozoites and meronts nutrition. Erythrocytic trophozoites of *Plasmodium* and *Haemoproteus* spp. as well as erythrocytic meronts of *Plasmodium* spp. absorb hemoglobin via micropyles. An opportunity of selective absorption of hemoglobin by means of plasma membrane intrusion with further separation of small bubbles (pinocytosis) also cannot be excluded. Digestion of nutrients occurs inside food vacuoles with participation of lysosomal hydrolytic enzymes. Hemozoin or the so-called malarial pigment is a by-product of the hemoglobin digestion. Hemozoin contains the ferrous part of hemoglobin that is not digested by species of *Plasmodium* and *Haemoproteus.* The pigment is packed in the vacuoles surrounded by one membrane. The number, form, dimension, location, and some other features of the pigment granules are the characters used in the systematics. It is likely that the lack of food vacuoles in the exoerythrocytic trophozoites and meronts accounts for the peculiarities of their nutrition. Most likely, nutrients get into the *Leucocytozoon* spp. trophozoites by means of diffusion and (or) directed transport (Wong and Desser, 1981). This is favored by the lesser density of the host cell cytoplasm as compared to the one of the erythrocytes containing hemoglobin (Aikawa, 1971).

Following the period of the active growth, trophozoite undergoes the division of its nucleus passing to the next stage of development transforming into m e r o n t. The process of merogony illustrated by the example of the *Plasmodium* spp. erythrocytic meronts, studied in the greatest detail is considered below (Aikawa, 1971; Aikawa and Seed, 1980).

The division of the nucleus occurs by means of closed intranuclear pleuromitosis. During this process, the nuclear envelope remains intact, and bundles of microtubules of the division spindle are attached to the nuclear envelop from inside by means of the electron-dense material (centriolar plaques). One of the first morphological characteristics of the division is transformation of the nuclear chromatin from the inactive form (heterochromatin) to the active one (euchromatin). From the viewpoint of morphology, this looks like transformation of the coarse-granular chromatin of the nonmitotic nucleus to the finely-fibrous chromatin structure of the mitotic nucleus. Active synthesis of the DNA takes place during the growth of meronts and in the course of merogony. The mitotic apparatus has spindle microtubules which radiate from the centriolar plaques inside the nucleus

in a clear fan-like fashion. The spindle microtubules are arranged in the manner usually seen in the spindle fibres of the metaphase of mitosis. The centriolar plaques are tightly connected with the envelope of the nucleus. Two sets of spindle microtubules meet approximately midway between the centriolar plaques. Small electron-dense bars are occasionally observed close to the spindle microtubules, and they were initially thought to be chromosomes. These structures are called kinetochores. They participate in the binding of the chromosomes to the spindle microtubules (Aikawa, 1971). It should be noted that haemosporidian chromosomes have been insufficiently studied. It is usually difficult to see chromosomes in a nucleus that undergoes division, because during the major part of the fission period they are in a diffusive state. The nucleus elongates, becomes dumbbell-shaped, and splits into two parts. The mitochondria also undergo division by means of budding simultaneously with the fission of the nucleus. The division of cytoplasm follows shortly after nuclear division. The buds appear on the surface of the developing meront surrounded by a plasmalemma. Apical organelles of the future merozoites start to form beneath these buds, and the inner double membrane layer is laid down. The buds grow in size. A nucleus, a mitochondrion, a 'spherical body,' a portion of endoplasmic reticulum, and ribosomes penetrate into each bud. The developing merozoites grow in size and separate from the residual body. Exoerythrocytic merogony in all groups of haemosporidians happens in a way similar to the erythrocytic one (Aikawa, 1971; Bradbury and Gallucci, 1971, 1972; Desser, 1973; Fallis *et al*., 1974; Fallis and Desser, 1977; Wong and Desser, 1978; Morii *et al*., 1987; Meis and Verhave, 1988; Morii and Fukuda, 1992) except for the difference mentioned above, i.e., that food vacuoles and pigment granules are absent in the exoerythrocytic meronts. The process of exoerythrocytic merogony goes in accordance with the strictly coordinated sequence of the following events: active mitotic division of the nucleus, division of the mitochondria, increase of the endoplasmic reticulum and the number of ribosomes, differentiation of the membranes of the pellicle, subpellicular microtubules, micropyles and rhoptries, division of the cytoplasm. Segmentation of the cytoplasm usually passes through the stage of the formation of multinuclear interconnected or separated cytomeres surrounded by a plasma membrane. The process of cytomeres formation in all the groups studied, excluding *Leucocytozoon* spp., takes place within one parasitophorous vacuole whose membrane surrounds the entire meront. The appearance of cytomeres leads to the increase of the meront's surface. This in its turn leads to the activation of metabolism processes and also to the increase of the surface of the plasmalemma, which facilitates the differentiation of merozoites. The further mitotic division of the nuclei and fragmentation of the cytoplasm in cytomeres lead to the appearance of the uninuclear merozoites. The merozoites are formed synchronously. During merogony, the membrane of the parasitophorous vacuole remains intact.

The process of cytomere formation discovered in certain exoerythrocytic meronts of *Leucocytozoon* sp. is unique (Desser, 1973). The meront, which undergoes division, splits into a multitude of cytomeres, separated from each other not only by the content of the parasitophorous vacuole but also by the cytoplasm of the host cell. Each of these cytomeres is surrounded by its own plasmalemma and the membrane of the parasitophorous vacuole. The further merogony within these cytomeres occurs in a similar fashion to the other haemosporidians as described above.

It is noteworthy that merozoites in all bird haemosporidians studied up to the current time, except for *Leucocytozoon dubreuili*, bud-off at the periphery of the persisting cytomeres, which achieve extremely irregular shapes. In the renal meronts of *L. dubreuili,* the merozoites are formed simultaneously in a multitude of the spherical centers located within

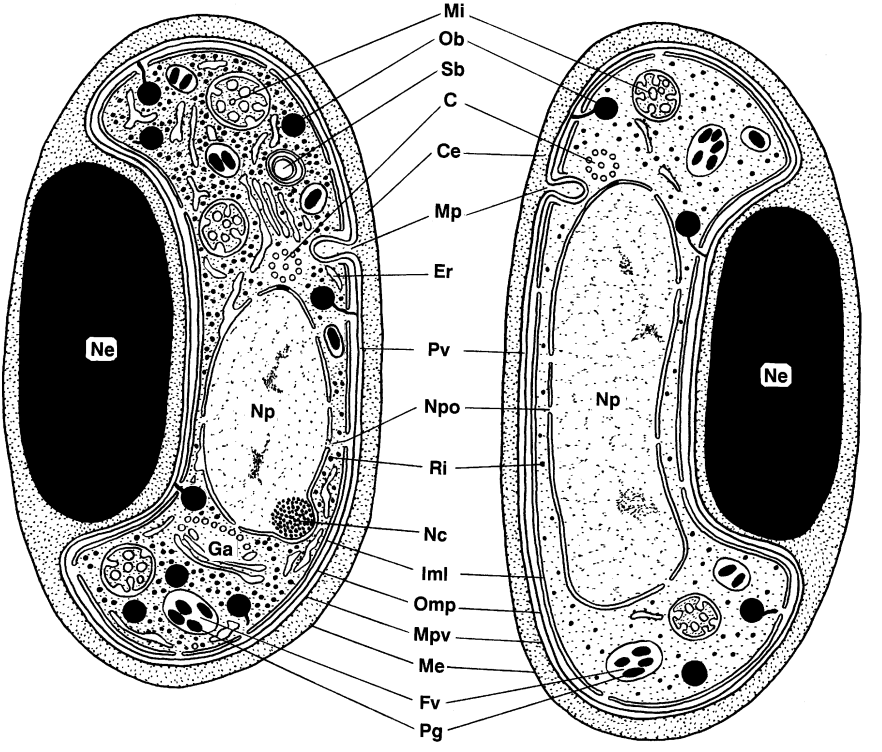


Figure 27 Diagrammatic representation of the structure of gametocytes of bird haemosporidians: On the right – microgametocyte, on the left – macrogametocyte; C – centriole; Ce – cytoplasm of erythrocyte; Er – endoplasmic reticulum; Fv – food vacuole; Ga – Golgi apparatus; Iml – inner interrupted membrane layer; Me – membrane of erythrocyte; Mi – mitochondrion; Mp – micropyle; Mpv – membrane of parasitophorous vacuole; Nc – nucleolus; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Npo – nuclear pore; Ob – osmiophilic body; Omp – outer membrane of pellicle; Pg – pigment granule; Pv – parasitophorous vacuole; Ri – ribosome; Sb – 'spherical body' (modified from Carter and Graves, 1988).

the cytomeres whose boundaries are yet not already distinguishable (Wong and Desser, 1978). The other distinguishing peculiarity of the *L. dubreuili* merogony is the presence of electron-dense ring-shaped thickenings in the locations of the joints of the budding merozoites and the maternal cytoplasm. It is likely that these thickenings facilitate pinching off of the merozoites from the central residual body.

The hypertrophy of the nucleus and cytoplasm of the infected cells is a characteristic feature of *Leucocytozoon* spp. merogony. This process is extremely well expressed during the development of megalomeronts. During this process, in particular, the increase of the amount of chromatin in the nucleus as well as the increase of the endoplasmic reticulum and the number of mitochondria in the cytoplasm, takes place. All this indicates the active participation of the host cell in the metabolism processes of the parasite (Desser, 1973; Wong and Desser, 1978).

It is likely that the *Plasmodium* and *Haemoproteus* spp. meronts feed themselves mainly via micropyles, which is particularly clearly expressed in the *Plasmodium* spp. erythrocytic meronts. The micropyles are not found in the *Leucocytozoon* spp. exoerythrocytic

meronts. It is likely that in the latter case, nutrition is performed by diffusion and (or) by directed transport (Bradbury and Gallucci, 1972; Aikawa and Seed, 1980; Wong and Desser, 1980, 1981).

GAMETOCYTES, GAMETOGENESIS, AND GAMETES

The ultrastructure of gametocytes and gametes as well as the process of ultrastructural transformation of these cells during gametogenesis of bird haemosporidians are relatively well studied (Garnham *et al*., 1967; Bradbury and Trager, 1968a, 1968b; Aikawa *et al*., 1969, 1970; Bradbury and Roberts, 1970; Desser, 1970c; Desser *et al*., 1970; Desser, 1972a; Milhous and Solis, 1973; Sterling and Aikawa, 1973; Gallucci, 1974a; Kocan and Kocan, 1978; Morii *et al*., 1981, 1984a; Steele and Noblet, 1993). Intracellular g a m e t o c y t e is enclosed in the parasitophorous vacuole bounded by one continuous membrane formed from the plasmalemma of the host cell (Fig. 27). The membrane of the parasitophorous vacuole is closely opposed to the pellicle of the gametocyte. The pellicle consists of a continuous plasmalemma and inner interrupted membrane layer formed by two membranes. The inner membrane layer is interrupted in many points. The presence of the inner double membrane layer is a characteristic feature of the structure of the gametocyte pellicle that clearly distinguishes the ultrastructure of gametocytes from the one in trophozoites and meronts. The inner double membrane layer develops in young gametocytes. Thus, gametocytes are surrounded by the membrane of the parasitophorous vacuole and possess a pellicle. The cavity of the parasitophorous vacuole is not clearly pronounced.

Subpellicular microtubules are not usually found in the fully grown gametocytes of bird haemosporidians, but they are recorded in the young gametocytes of certain species.

There are micropyles in the gametocytes, and they function in the majority of investigated species. Food vacuoles are formed in *Plasmodium* and *Haemoproteus* spp. through the micropyles. The digestion of hemoglobin and other nutrients as well as the storage of pigment granules takes place inside food vacuoles.

The nucleus of microgametocyte is significantly larger than that of macrogametocyte. The envelope of the nucleus consists of two membranes with numerous pores. Some of the pores are plugged with electron-dense material. The outer nuclear membrane is connected with the endoplasmic reticulum in the female gametocyte.

A structure termed an ‘atypical centriole’ embedded in an electron-dense matrix is located on the cytoplasmic side of the nuclear envelope. A complex of ten microtubules is clearly distinguished on the cross sections of this structure. One of the microtubules is located in the center, while the others are arranged in a circle around the central one.

A large number of electron-dense organelles are present in the cytoplasm of gametocytes. They are bounded by a unit membrane, and they are described in the literature as ‘dense’ or ‘osmiophilic’ bodies. These occur in largest numbers near the periphery of the cell, and each of them is connected with the plasmalemma of the pellicle via a thread-like duct. The ducts pass through the inner membrane layer in those points, where the latter interrupts. The electron density and the structure of the osmiophilic bodies are similar to those in micronemes and rhoptries of the spreading stages of haemosporidians (sporozoites, merozoites, and ookinetes). It is likely that the osmiophilic bodies are responsible for the changes in the membranes of the host cells, when gametocytes escape from them in the process of gametogenesis.

Mitochondria are numerous and possess tubular cristae. In the *Leucocytozoon* species, the mitochondria are located in microgametocytes in the indentations of the nuclear envelope (Desser *et al*., 1970; Kocan and Kocan, 1978). Ribosomes are also numerous. The endoplasmic reticulum is well developed. There are food vacuoles. It is worth noting that among the cytoplasmic inclusions there are gatherings of amorphous dense material found in certain species. It is likely that this material is a precursor of the crystalloid inclusions found in ookinetes, oocysts, and sporozoites (Desser, 1970c; Desser *et al*., 1970; Steele and Noblet, 1993).

Besides the size of the nucleus, the main distinguishing peculiarities of the structure of macrogametocyte compared to microgametocyte are the following. First, the nucleus of macrogametocyte possesses a nucleolus. Second, macrogametocyte possesses significantly more ribosomes, and the endoplasmic reticulum is developed significantly better. A more intensive basophilic staining of the macrogametocytes' cytoplasm by Giemsa's stain is mainly due to these peculiarities of the gametocytes' structure. Third, the macrogametocyte possesses the Golgi apparatus and 'spherical body.' Forth, osmiophilic bodies in macrogametocyte are significantly more numerous.

The process of development of unique fusiform host cells of the *Leucocytozoon* spp. gametocytes is not studied in detail yet. It is not inconceivable that compactly packed 'bunches' of parallel located microtubules take part in the formation of spindle-like cytoplasmic processes of the host cells of *L. smithi.* These microtubules are formed inside the nucleus of the gametocyte and eventually project into the parasite cytoplasm area. They are situated parallel to the long axis of the elongating parasite. It is likely that they also take part in the division of the *L. smithi* host cell nucleus (Steele and Noblet, 1993). Similar compactly packed microtubules, although absent in the nucleus, are found in the *L. simondi* gametocytes' cytoplasm (Desser *et al*., 1970).

Nutrition of gametocytes is performed by means of absorption of nutrients through the micropyles. Diffusion and pinocytosis are likely to have lesser importance. Residual pigment (hemozoin) is accumulated in the food vacuoles of *Plasmodium* and *Haemoproteus* spp. gametocytes, which develop only in the cells of the erythrocytic series and feed primarily with hemoglobin. The *Leucocytozoon* species have a significantly wider range of the host cells, which indicates that their digestive specialization is not so narrow. The *Leucocytozoon* species developing in erythrocytes completely digest the hemoglobin. There is no hemozoin in their gametocytes.

The process of gametogenesis in haemosporidians is difficult. It is similar in all groups of the Haemosporida except for rare exceptions. Gametocytes round up within several seconds or minutes after the stimulation by corresponding external factors and escape from the infected cells. As this takes place, the membranes of the host cell rupture. Anomalous development of microgametocytes is frequently observed, when the plasmalemma of the host cell remains intact, and gametogenesis occurs within the infected cell. It is likely that rupture of the membranes of the host cells occurs under the influence of the secretion of osmiophilic bodies (Carter and Graves, 1988).

The macrogametocytes, which have escaped from the host cells actually become macrogametes. They are surrounded by a pellicle whose structure is identical to the structure in macrogametocytes. At present, the exception is *Haemoproteus columbae,* whose macrogametocytes undergo significant transformation in the process of gametogenesis (Gallucci, 1974a). In the latter case, microtubules of the division spindle appear in the nucleus of the macrogametocyte. The nucleus elongates and a constriction divides it into two portions. The nuclear envelope remains intact. Main intranuclear structures remain

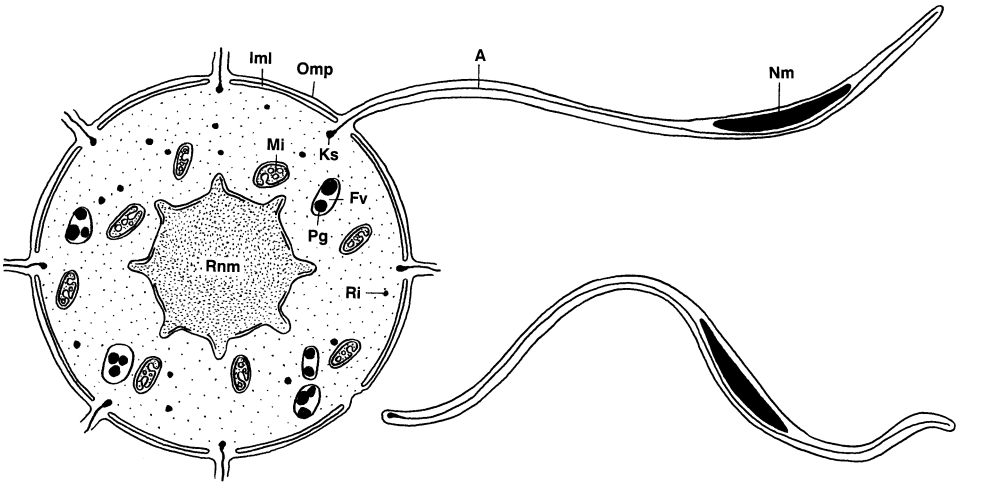


Figure 28 Diagrammatic representation of the final stage of the exflagellation of microgametes of haemosporidians:
A – axoneme; Fv – food vacuole; Iml – inner interrupted membrane layer; Ks – kinetosome; Mi – mitochondrion; Nm – nucleus of microgamete; Omp – outer membrane of pellicle; Rnm – remnants of nucleus of microgametocyte; Pg – pigment granule; Ri – ribosome (modified from Garnham *et al*., 1967).

in the greatest part of the dumbbell-like nucleus. The role of this process has not yet been understood.

The process of microgametes development is much more complicated than that of macrogametes. For the majority of species studied, it conforms to the following scheme. Microtubules of the division spindle apparatus appear rapidly in the nucleus of the rounded up microgametocyte. The nucleus of the gametocyte divides forming eight nuclei. Kinetosomes (basal bodies) are formed in the cytoplasm. The kinetosomes initiate axonemes with a usual structure (two central microtubules and nine double microtubules at the periphery). Thus, all the components needed for the development of eight microgametes are formed. Formation of microgametes occurs by means of their protrusion from the body of microgametocyte in those places, where the inner membrane layer is interrupted (Fig. 28). In this manner, primary flagella buds appear and then extend. This stage of development is called exflagellation. Each axoneme sticks out together with a kinetosome and 'covers' with the plasmalemma of the microgametocyte. A portion of the nucleus moves to the outgrowth formed. The nuclear membrane of the microgametocyte remains intact during the process of microgametogenesis for all species studies excluding *Leucocytozoon simondi* and *L. caulleryi* (Aikawa *et al.,* 1970; Morii *et al.,* 1984a).

Microgametogenesis of *Haemoproteus columbae* occurs in a different way (Bradbury and Trager, 1968b). After escaping from the host cell, microgametocyte assumes a dumbbell-like form. One part of the dumbbell is surrounded only by plasmalemma and contains a part of the nucleus. The other part of the dumbbell is surrounded by a three-layer pellicle of the microgametocyte, and contains the major part of the nucleus. Gametogenesis in the latter part occurs approximately in the same way as described above, but the envelope of the microgametocyte nucleus disappears during the process. Formation of dumbbell-like structures in the process of microgametocyte transformation was recorded in *H. dolniki,*

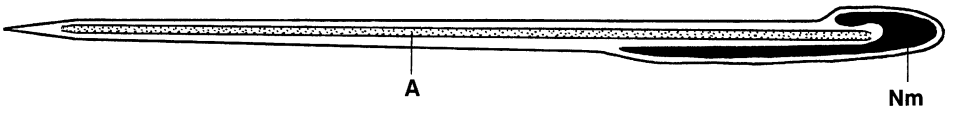


Figure 29 Diagrammatic representation of the structure of microgamete of *Leucocytozoon simondi:*
A – axoneme; Nm – nucleus of microgamete (modified from Aikawa *et al*., 1970).

H. fringillae, H. velans (Desser, 1972a; Valkiūnas and Iezhova, 1993a, 1994). It is likely that this type of microgametogenesis in bird haemosporidians is not rare. Moreover, it is interesting to note that microgametocytes of *Leucocytozoon simondi* developing in roundish host cells do not obtain a dumbbell-like form in the process of gametogenesis, while those in the fusiform host cells do obtain this form (Aikawa *et al*., 1970; Desser, 1970c).

Microgamete is surrounded by a plasmalemma and possesses one axoneme and one nucleus, which is bounded by two layer envelope without pores (Fig. 29). The cytoplasm of microgametes possesses no other organelles except a fine granular matrix. The microgametogenesis process is complicated, but it passes rapidly. That is why a greater or lesser number of anomalous microgametes, which possess several axonemes and even several nuclei, is always formed. Microgametes move actively with a snake-like body motion. The energy source for this motion is not clear yet.

FERTILIZATION, ZYGOTE, AND INITIAL STAGES OF OOKINETE DEVELOPMENT

Fertilization, formation of zygote, and the initial stages of ookinete development have been studied quite well for *Plasmodium gallinaceum, Haemoproteus columbae,* and *Leucocytozoon caulleryi* (Garnham *et al*., 1962; Gallucci, 1974b; Mehlhorn *et al*., 1980; Aikawa *et al*., 1984; Morii *et al*., 1984a). Fertilization starts when the microgamete attaches itself by one end to the plasmalemma of the macrogamete. Shortly after this, the membranes of both gametes merge together. The axoneme and the nucleus of the microgamete penetrate into the cytoplasm of the macrogamete. After the fusion of the gametes, the surface of the plasmalemma of the macrogamete increases markedly due to the joining of the plasmalemma of the microgamete. The surface of the inner double membrane layer remains unchanged with the result that a significant part of the macrogamete appears surrounded only by the plasmalemma. The nucleus of the *P. gallinaceum* microgamete moves in the direction of the macrogamete's nucleus along a special channel of the endoplasmic reticulum. Fusion of the nuclei occurs in a special region of the macrogamete nuclear envelope consisting of a complex of convoluted folds. The axoneme of microgamete persists for a certain time in the cytoplasm of the zygote and later disintegrates. The axoneme of *L. caulleryi* penetrates into the nucleus of the macrogamete together with the microgamete's nucleus.

The transformation of zygote into an ookinete starts with the polarization of nucleus of the former. Nucleolus is located at one of the ends of the elongated nucleus, while the other end elongates toward the zygote's plasmalemma, where there is no inner double membrane layer. Microtubules appear near the envelope of the nucleus, while the electron-dense material is deposited below the plasmalemma. As the zygote transforms into the

ookinete, the microtubules of the spindle apparatus appear in the nucleus, and reduction division (meiosis) takes place (Gallucci, 1974b; Aikawa *et al.,* 1984; Sinden and Hartley, 1985; Sinden *et al*., 1985; Paterson and Desser, 1989). Polar rings and conoid are formed from the electron-dense material in the region where the nucleus is close to the plasmalemma. The other structures characteristic of the apical end of the ookinete also start to form. By that time the nucleus of the parasite returns to its central position for the second time. The endoplasmic reticulum significantly increases, and the crystalloid particles appear. Electron-dense structures, which look like the osmiophilic bodies of the gametocytes, appear in the region of the apical organelles of the developing ookinete. These structures are precursors of future micronemes. The further development of the ookinete is characterized by the elongation of its apical end, until it obtains the elongated form typical of the mature ookinete. At the final stage of the ookinete development, a residual body separates from its distal end.

OOKINETE

Ookinete of haemosporidians is an extremely specialized stage responsible for the penetration of the parasite from the content of the vector's midgut through the epithelial layer to the place of sporogony under the basal lamina. Sometimes the stages of zygote and ookinete are identified one with the other in the literature, and ookinete is called a motile zygote. In our opinion, the stages of zygote and ookinete should not be equated. Zygote is a stage formed immediately after fertilization of the macrogamete by the microgamete. It is characterized by a diploid ($2n$) set of chromosomes and does not have apical organelles which are characteristic of the spreading stages of all sporozoans. Apical organelles are formed in the process of transformation of zygote into ookinete, and meiosis takes place, as was already mentioned. Thus, ookinete differs from zygote not only structurally but also genetically. It is difficult to draw a clear distinction between a zygote and young ookinete. From the practical point of view, it is more convenient to call the stages from the moment of formation of the complex of apical organelles as young ookinetes. As this takes place one can clearly see under a light microscope that the transforming zygotes of the majority of species develop a more or less pronounced outgrowth. This differs them from the early zygotes. There is a period of relative 'rest' between the stages of the zygote and young ookinete, when under the light microscope zygotes look like morphologically unchanged roundish bodies. The preparation for the future complex morphological changes occurs during this period contributing to the rapid changes, which later take place in the growing ookinetes. The duration of the 'resting' period clearly differs for various species of haemosporidians, which can be used in the systematics (Valkiūnas and Iezhova, 1993a).

Ookinetes are elongated bodies, whose length in different species usually varies on average from 7 to 30 μm, while the width is within the range 2.5 to 7 μm. The ultrastructure of completely developed ookinetes is similar to the structure of sporozoites and merozoites, although the structure of these stages also has differences. The ultrastructure of *Plasmodium, Haemoproteus*, and *Leucocytozoon spp.* ookinetes is in general conservative (Garnham, 1966; Desser, 1970b, 1972b; Gallucci, 1974a; Desser and Allison, 1979; Mehlhorn *et al*., 1980; Aikawa *et al*., 1984; Atkinson, 1989; Paterson and Desser, 1989; Atkinson, 1991b).

The pellicle of ookinete consists of plasmalemma and inner double membrane layer, which is interrupted at the apical and distal ends (Fig. 30). Micropyles are not found.

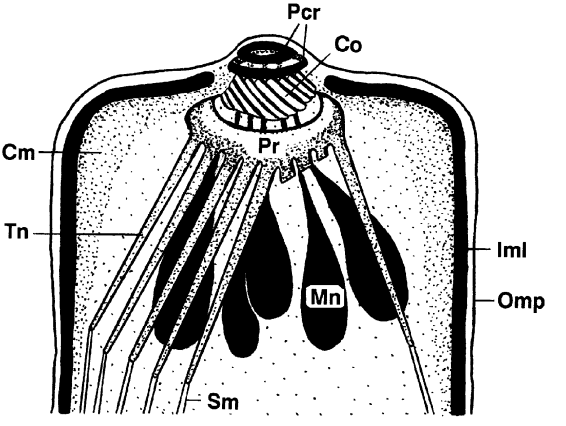


Figure 30 Diagrammatic representation of the structure of apical end of ookinete of *Leucocytozoon simondi:*
Cm – dense material coating cytoplasmic surface of Iml; Co – conoid; Iml – inner interrupted membrane layer; Mn – microneme; Omp – outer membrane of pellicle; Pcr – preconoidal rings; Pr – polar ring; Sm – subpellicular microtubule; Tn – tine (modified from Paterson and Desser, 1989).

Subpellicular microtubules connected to the apical polar ring pass under the inner membrane layer. The micronemes are numerous, concentrated in the anterior one third of the ookinete. Rhoptries are not found. The nucleus is large. The nucleolus is well pronounced. The mitochondria are elongated with tubular cristae. The endoplasmic reticulum is well developed. The other organelles of the 'general' purpose and cytoplasmic inclusions are similar to the ones in sporozoites.

The inner membrane layer of the pellicle in the region of the apical end is covered by a wide band of electron-dense material consisting of two layers each containing differently packed microfilaments (Atkinson, 1989). It is likely that this double layer, which resembles a collar or a dome, plays an important supporting function in the process of penetration of ookinete through the peritrophic membrane and epithelial layer of the vector's midgut.

Peculiar supports or tines shaped like pitchfork prongs radiate from the apical polar ring posteriorly at even distances from each other (Fig. 30). These tines are of round shape in cross section. They are made of electron-lucent material and outwardly do not differ from the material of the polar ring. From the inner side, the tines are covered with an electron-dense material. The number of tines is different in different species of haemosporidians. There are 34 of them in *Leucocytozoon simondi*, 25 in *Haemoproteus mansoni*, and 31 in *Plasmodium gallinaceum* (Aikawa *et al.*, 1984; Atkinson, 1989; Paterson and Desser, 1989). Interestingly, the structure of the tines differs in the ookinetes of various haemosporidian groups. For example, in *H. columbae* (the vectors are hippoboscid flies) the tines stretch along the entire length of the ookinete and finally branch into two (Gallucci, 1974b). The tines do not reach the middle of the ookinete and do not branch in *H. mansoni, H. velans* (the vectors are biting midges) and in *L. simondi* (the vectors are blood-sucking simuliid flies) (Desser, 1972b; Atkinson, 1989; Paterson and Desser, 1989). Atkinson (1991b) suggested that these characters can be used in the systematics.

The polar ring and its associated tines are defined as the polar ring complex (Paterson and Desser, 1989). This complex is present in ookinetes of haemosporidians. There are no tines in sporozoites and merozoites of these parasites.

Subpellicular microtubules originate from the inner surface of the apical polar ring. They extend posteriorly, lying against a band of electron-dense material that is opposed to the inner surface of the tines. It is important to note that subpellicular microtubules are not adjacent to the pellicle in the region of the tines. It is likely that, as a result, the apical end of the ookinete partly loses its elasticity and frequently deforms. The number of subpellicular microtubules varies in the ookinetes of different groups of bird haemosporidians (they are usually more than 40 but less than 100).

Conoid is an important peculiarity of the structure of ookinetes, which is absent in sporozoites and merozoites of haemosporidians. The conoid of haemosporidians is an empty structure in the form of a small frustum cone formed of fibres twisted in a spiral. Two preconoidal rings are located over the conoid. Ducts of micronemes pass inside the conoid and preconoidal rings. It is likely that the conoid plays an important role when ookinete penetrates to the place of sporogony through the peritrophic membrane and tissues of the midgut of the vector. This organelle is found only in sporozoans, who retained the gut phase of development in their life cycle (Beyer, 1989). The electron density of the material constituting the conoid of haemosporidians is relatively low, thus it is quite difficult to find the conoid. Owing to this, the presence of this organelle in the ookinetes of haemosporidians was clearly demonstrated not long time ago (Gallucci, 1974b; Atkinson, 1989; Paterson and Desser, 1989).

A region lined with electron-dense granular matrix should be mentioned among the peculiarities of the structure of ookinete. This region is located between the polar ring complex and the electron-dense material covering the inner double membrane layer of the pellicle (Fig. 30). It is noteworthy that the food vacuoles containing amorphous masses of pigment (hemozoin) and several portions of crystalloid material are found in ookinetes. This pigment is 'inherited' from macrogametes and macrogametocytes. In the investigations carried out with a light microscope, the parts of ookinetes containing crystalloid are usually described as 'vacuoles.'

The recent data (Torii *et al*., 1992) indicate that ookinete of *Plasmodium gallinaceum* on its way to the place of sporogony under the basal lamina first penetrates into the epithelial cells of the midgut. Parasitophorous vacuole is absent around the intracellular ookinete. The cytoplasm of the host cell adjacent to the apical end is substituted by fine-granular material, which is free from organelles characteristic of the intact cytoplasm. After penetration into the epithelial cell, ookinete moves into the intercellular space to migrate there in the direction of the basal lamina. Thus, ookinetes penetrated into the epithelial cells clearly differ from intracellular sporozoites and merozoites by the absence of the parasitophorous vacuole around them. This indicates that the mechanisms of the penetration of these stages into the cells are different. It is possible that ookinetes can perforate the membrane barrier of the vectror's epithelial midgut cells due to the presence of the conoid.

OOCYST AND SPOROGONY

The structure of oocysts and the process of their development during sporogony is studied in the species of *Plasmodium, Haemoproteus,* and *Leucocytozoon* (Terzakis *et al*., 1967; Wong and Desser, 1976; Desser and Allison, 1979; Mehlhorn *et al*., 1980; Atkinson, 1991a, 1991b). After reaching the place of sporogony near the basal lamina of the vector's midgut, haemosporidian ookinetes round up and transform into the oocysts. At this time the

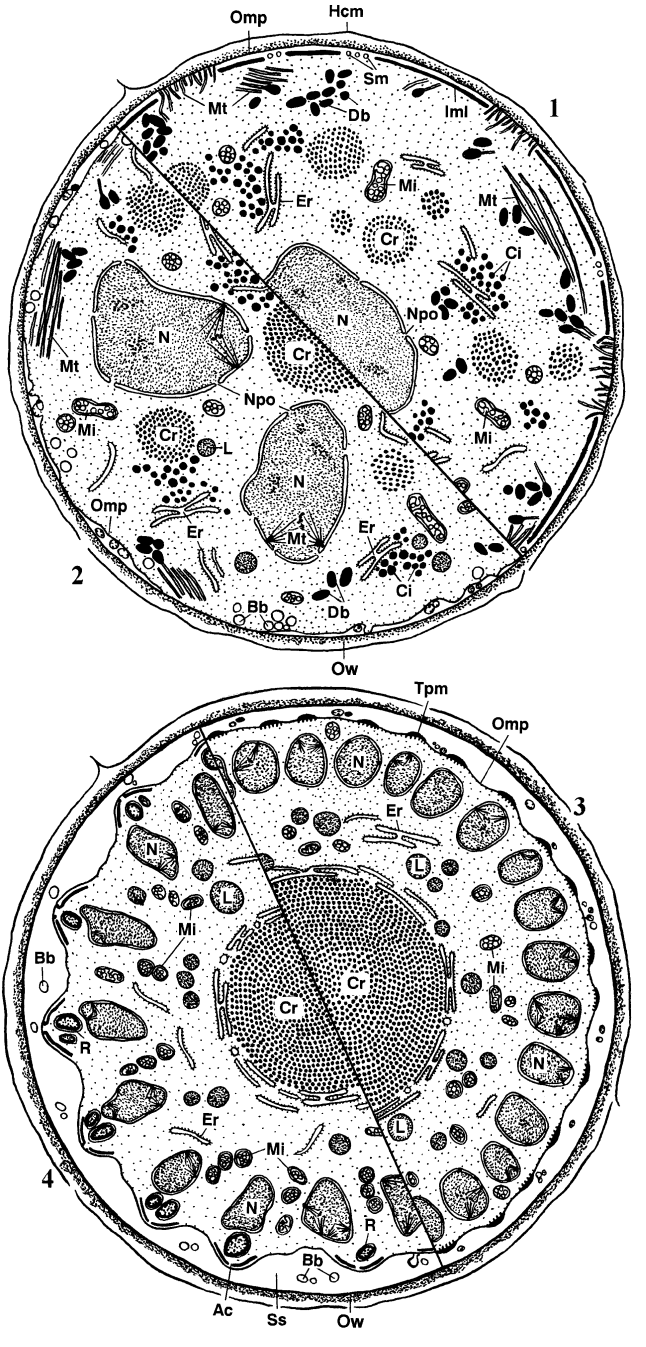
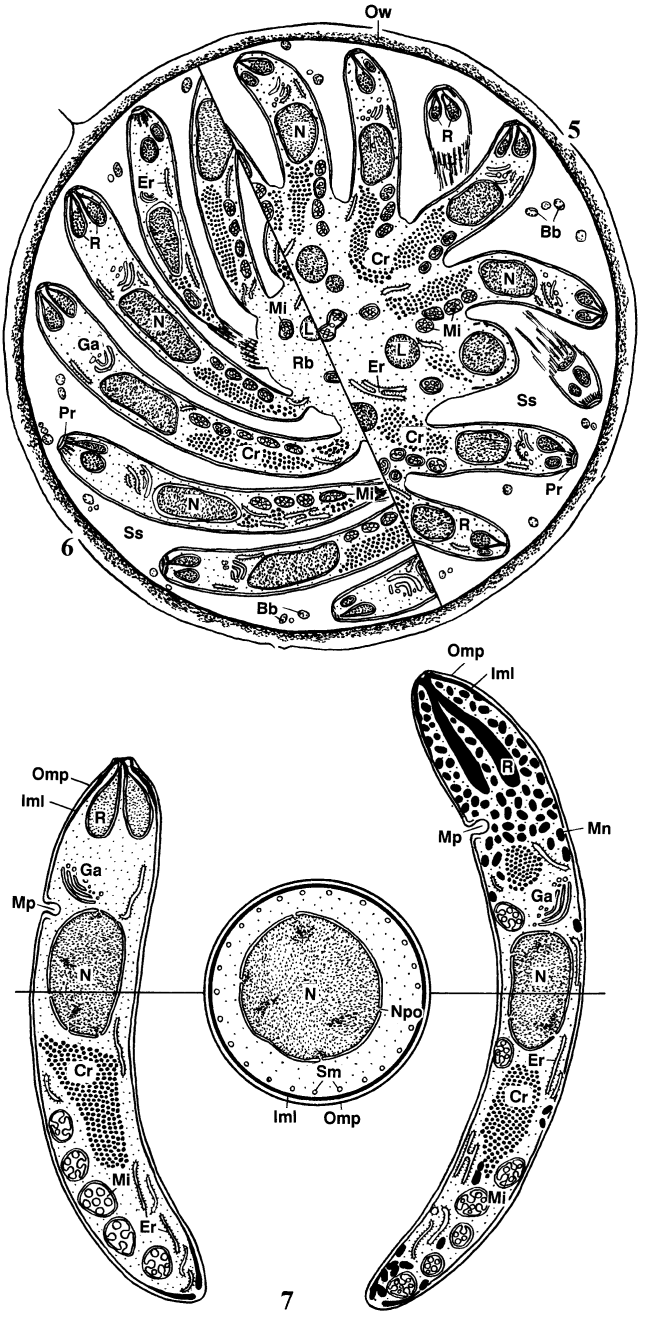


Figure 31 Diagrammatic representation of the development of sporozoites within oocyst of *Leucocytozoon dubreuili:*
1–6 – successive stages of the development of sporozoites; *7* – diagrammatic representation of the structure of sporozoites in oocyst (on the left) and in the salivary glands of vector (on the right); Ac – organelles of apical complex of developing sporozoites; Bb – membrane-bound body; Ci – cell inclusion; Cr – crystalloid; Db – electron-dense body; Er – endoplasmic reticulum; Ga – Golgi



apparatus; Hcm – membrane of host cell; Iml – inner interrupted membrane layer; L – lipid; Mi – mitochondrion; Mn – microneme; Mp – micropyle; Mt – microtubule; N – nucleus; Npo – nuclear pore; Omp – outer membrane of pellicle; Ow – oocyst capsular-like wall; Pr – polar ring; R – rhoptry; Rb – residual body; Sm – subpellicular microtubule; Ss – subcapsular space; Tpm – thickening beneath the plasma membrane of oocyst (modified from Wong and Desser, 1976).

organelles of the apical complex, inner double membrane layer of pellicle, and subpellicular microtubules are rapidly disintegrated. The developing oocyst is thus surrounded only by plasmalemma of the former ookinete. In addition, the oocyst is also surrounded by a thick (up to 1 μm) layer of amorphous material, whose composition includes polysaccharides. This layer is a capsule formed from the material of the invertebrate host. The capsule contains electron-dense granules and membrane-bound bubbles. The process of formation of sporozoites (sporogony) takes place within the capsule.

In different groups of haemosporidians sporogony takes place according to two schemes. In the species with large oocysts (a diameter greater than 20 μm), the contents of the oocyst initially divides into several sporoblasts (germinative centres) from which sporozoites bud off. Many hundreds of sporozoites are formed in each oocyst. This process is characteristic of all *Plasmodium* spp. as well as of the species of *Haemoproteus*, whose vectors are hippoboscid flies. In haemosporidians with small oocysts (usually less than 20 μm in diameter), all the contents are transformed into one germinative centre from which sporozoites bud off. In this case, less than 100 sporozoites usually develop in each oocyst. This type of sporogony is characteristic of all the species of *Leucocytozoon* as well as of the species of *Haemoproteus,* whose vectors are biting midges.

The structure of oocysts and the process of sporogony is described below by the example of *Leucocytozoon dubreuili,* a common parasite of passerine birds (Wong and Desser, 1976). An active process of disintegration of the inner double membrane layer of pellicle, subpellicular microtubules, and organelles of the apical complex of ookinete takes place in young oocysts. These structures are well distinguished in young oocysts for a certain time, but later they either disappear or only their fragments are present (Fig. 31, *1*). The nucleus and mitochondria undergo active division. The nuclear division occurs in the same way as in meronts. Numerous lipid droplets appear in the cytoplasm. Crystalloid material begins to concentrate in the center of the oocyst (Fig. 31, *2*). Compression of the oocyst's contents takes place simultaneously. The plasmalemma develops uneven outline and exfoliates from the capsule forming subcapsular space where sporozoites bud off. The development of the subcapsular space is accompanied by the appearance of a large number of small roundish membrane-bound bodies, and roundish gatherings of granular electron-dense material. Later, numerous smaller nuclei form a line along the circumference immediately under the plasma membrane of the oocyst (Fig. 31, *3*). The crystalloid material is concentrated in the center of the oocyst as a uniform compact mass surrounded by the endoplasmic reticulum. Thickenings then appear near the nuclei under the plasma membrane, where the processes of budding off of sporozoites initiate, and the organelles of the apical complex of the future sporozoites start to form (Fig. 31, *4*). The thickenings initiate the formation of an inner double membrane layer of the sporozoites. A nucleus, several small mitochondria, a portion of the crystalloid material, and some other organelles penetrate into each of the forming 'buds' (Fig. 31, *5*). The size of sporozoites grows larger, while the size of the residual body decreases. As a result, sporozoites finally separate from the residual body (Fig. 31, *6*).

Morphology of sporozoites significantly differs in the mature oocysts and in the salivary glands of the vectors (Fig. 31, *7*). Formation of the organelles of the apical complex completes in the salivary glands, and clearly pronounced rhoptries and micronemes appear.

As was mentioned earlier, certain distinguishing peculiarities are characteristic of the sporogony process in *Plasmodium* spp. and of those species of *Haemoproteus*, which have large oocysts (Terzakis *et al*., 1967; Mehlhorn *et al*., 1980; Atkinson, 1991b). Sporogony starts with the division of the nucleus, and next the subcapsular space is formed. The

plasmalemma is drawn inside the oocyst forming the clefts, which split the cytoplasm with nuclei and organelles inside it into multiple sporoblasts. The further development of sporozoites in the sporoblasts occurs in the same way as described above.

The crystalloid material is found in ookinetes and oocysts in all the species of bird haemosporidians studied until now. Two types of crystalloid particles have been described: Type I and Type II. Crystalloid particles of Type I are found most frequently. They are small (about 20 to 40 nm in diameter) structures containing lipoproteins. They are not surrounded by a membrane. Crystalloid of the Type II was found only in *Plasmodium* spp. In this case, the crystalloid particles usually exceed 40 nm in diameter, and they are surrounded by a membrane. It is not inconceivable that crystalloid of Type II represents viruses. Nucleic acids are found in this type of crystalloid (Trefiak and Desser, 1973; Terzakis *et al*., 1976; Desser and Allison, 1979).

It is noteworthy that the gathering of the crystalloid material in the center of the growing oocysts is found only in the species of *Leucocytozoon.* The crystalloid is washed out during fixation with alcohols and looks like an empty space which is usually described as a ‘vacuole’ in stained preparations under a light microscope. The particles of the crystalloid material in the young oocysts of *Haemoproteus mansoni* are dispersed, while in the sporozoites, which bud off, they are located in rows along the inner membrane layer of pellicle between subpellicular microtubules (Atkinson, 1991a). The crystalloid material is found in *Plasmodium gallinaceum* only at the early stages of the development of the oocysts. It is absent in the fully grown oocysts and in sporozoites (Mehlhorn *et al*., 1980).

Specificity and General Principles of Species Identification

Parasites occupy a peculiar place in nature because they inhabit living organisms who become an environment for their existence at one or all stages of their development. The hosts actively respond to the presence of the alien agents. Haemosporidians belong to a group of extremely specialized parasites, which never leave the organism of their hosts, but regularly change the habitat passing from vertebrate hosts to invertebrate ones and back. In this case, the factors of external habitat (the habitat of the second order) influence the parasites only in an indirect way through their hosts. The obligatory change of hosts, the complicated morphological and functional transformations in the organisms of birds and vectors, the diversity of response mechanisms of hosts to the presence of the parasites, the necessity to develop adequate mechanisms of protection, and the complicated biology of the hosts, all these factors combined lead to the restrictions of the range of haemosporidians' hosts, which is limited by a certain group of organisms occupying a certain position in the taxonomic system. The characteristic feature of parasites to inhabit a limited group of hosts is referred to in parasitology as specificity. Specificity is one of the fundamental categories of parasitology whose essence and contents are no doubt familiar to the reader. It should be emphasized that specificity is realized by means of at least two groups of factors. First, the biological properties of the parasites should provide an opportunity to exist in such a highly organized and dynamically changing environment as living organisms, that possess a complex system of protection. Second, the ecological conditions of the existence of parasites and their hosts limit the propagation of infective stages from one group of hosts to another in a specific way. The first group of factors determines the maximum possible range of hosts (the so called potential specificity), while the second one is responsible for the realization of this opportunity in the specific ecological conditions (occurrence of the parasites).

The solution of the problem of specificity is important to understand the evolution, phylogeny of the parasites, peculiarities of their relations with the hosts, problems of the species, etc. It is not surprising that the problem of specificity is one of the central problems in parasitology. It is discussed widely from the different standpoints (Kirshenblat, 1941; Bychovsky, 1957; Dogiel, 1962; Kontrimavičius, 1969; Kennedy, 1975; Price, 1980; Krylov, 1981; Balashov, 1982; Alekseev and Kondrashova, 1985). From the standpoint of the problems discussed in this book, it is important that the knowledge of specificity gives additional information to solve some problems of systematics and, in particular, the problem of the species. The problem of specificity is considered in this book in a relatively narrow aspect concerning the use of data on the relationship of certain parasites with a certain group of hosts to use these data in the taxonomy, and, in particular, in the identification of haemosporidian species. However, it should be remembered that the natural host range of

a parasite is not a valid taxonomic character (Valkiūnas and Ashford, 2002). Natural host distribution, like geographical distribution, is not solely a reflection of the genotype of the parasite, but depends on many circumstantial events. If these characters were used in taxonomy, the study of host specificity and of zoogeography would risk becoming circular and invalid. However, the experimental data on the specificity of parasites may be helpful to designate their possible maximum host range. That may be helpful for species identification. For example, avian malaria parasites have never been experimentally transmitted directly to mammals, and thus they are solely bird parasites. This eliminates the necessity to compare avian species of *Plasmodium* with the parasites of mammals during identification and description of their species. It is important to note that the intraspecific polymorphism of the specificity of the group of parasites under consideration cannot be analyzed in detail yet because there is not enough information about the problem. The problem of intraspecific variability of bird haemosporidians is a pressing one and needs further research. We mention this problem here as a reminder.

The lack of experimental data and the lack of detailed morphological studies have led to the long-term existence of two opposing alternative points of view in the literature regarding the specificity of bird haemosporidians. One group of scholars considered these protists as strictly specific. As a result, until the middle of the 20th century, a number of the haemosporidian species were described according to the principle 'new host – new species' of the parasite, which led to the accumulation of a large number of specific names in the literature that name parasites with minor differences or even no differences. This position led the taxonomy of the group under consideration to a dead end, taking away any biological sense from the category of species. At present, we can consider valid only 132 specific names in the family Haemoproteidae, 35 in the Leucocytozoidae, and 38 in the Plasmodiidae of the 280, 143, and 89, respectively found in the literature.† The other scholars used one or another specific names for absolutely different morphological forms considering (frequently without sufficient grounds) that the haemosporidians are not specific. They attributed to one species many clearly distinguished parasites. As a result the data from the literature concerning the distribution of many species (for example, *Haemoproteus danilewskii, Leucocytozoon danilewskyi, Plasmodium relictum,* etc.) appeared extremely intricate. Thus, the data about the distribution of the parasite species by the host species accumulated up to now can not be always used to investigate the problem of specificity. This is also complicated by numerous mistakes made by certain scholars in the identification of the species of haemosporidians. Further, the problem is that the following approach has been applied to identify the haemosporidians even at present, when the bird parasites are attributed to the species previously found in certain hosts or to those that are systematically close to them. By now, it has been proved that several species of haemosporidian parasites belonging to one genus can parasitize the same host. The cases are known of mixed infection of the same vertebrate host by several species of *Haemoproteus* (Valkiūnas and Iezhova, 1991, 1992a; Peirce and Bennett, 1993), *Leucocytozoon* (Bennett and Cameron, 1975; Valkiūnas, 1985b), *Plasmodium* (Garnham, 1966; Beier and Stoskopf, 1980). It follows from this that the approach to identification of species mentioned above may be regarded as discredited. The availability of many erroneous and doubtful identifications in the literature, which usually cannot be checked, became the main reason that the occurrence of haemosporidians in birds of different systematic groups is not analyzed in this book in detail, when we discuss specificity.

† See also Appendix 2.

The present day taxonomy of bird haemosporidians at the species level is almost exclusively based on parasite morphology in the peripheral blood, and on experimental data about the parasite specificity. At present, the identification of species is based primarily on the detailed study of the morphology of blood stages of the parasites with necessary account for many characters. All other stages of development, including exoerythrocytic meronts, are described for a few species and cannot be currently widely used to distinguish not only between the species but also between some subgenera and even genera of haemosporidians (Garnham, 1966; Valkiūnas, 1985a, 1985b; Bennett and Peirce, 1988; Atkinson, 1991b) although these characters are often informative and may be used in species identification in the future. In addition, specificity is taken into account during identification of the species. The theoretical maximum possible range of vertebrate hosts, which occupy a certain position in the biological system, is distinguished on the basis of the experimental data available. All morphologically identical forms within a given range of the hosts are considered as one species, while those, which are morphologically different, are related to different species. Morphologically identical forms in different ranges of hosts are considered as different species. Not numerous cases are distinguished as exclusions with experimentally confirmed deviations according to the suggested scheme. For example, experimental confirmation of the existence of narrowly specific and morphologically similar species (*Haemoproteus palumbis, H. columbae*), and morphologically similar species, which have clearly different ranges of distribution (*Leucocytozoon lovati, L. macleani*). The scheme suggested has no claims to finally solve the problem, but it restricts the description of the morphologically identical forms as new species and consequently makes the synonymy easier allowing us to bring the systematics of certain groups out of the dead end at the first stage of the bird haemosporidian species composition revision. In addition, distinguishing the morphologically identical forms within a definite range of vertebrate hosts paves the way for the future theoretical, experimental, and molecular biology research to construct a more advanced classification. The implementation of this scheme in various haemosporidian families is performed specifically.

Before starting the analysis of the specificity peculiarities in the representatives of various families, it should be emphasized that normally all species of bird haemosporidians do not develop in amphibians, reptiles, and mammals, thus they are strictly bird parasites (see, however, p. 649). Additionally, the molecular methods were not used in the systematics of bird haemosporidians on the species level and, thus, they are still an inexhaustble reserve for future research, and the solution of numerous complicated questions.

SPECIFICITY AND GENERAL PRINCIPLES OF THE IDENTIFICATION OF HAEMOPROTEIDAE SPECIES

The overwhelming majority of the haemoproteid species has been described on the basis of the morphology of blood stages, the gametocytes. The other stages of their life cycle are described only for a small number of species and cannot be currently widely used for the identification of species.† Thus, we are currently restricted mainly by the morphology of gametocytes in the blood and peculiarities of their influence on host cells. Despite the disadvantages of this method, it has certain merits. First, this is a rapid and inexpensive

† See also Valkiūnas *et al.* (2002b).

method. Second, it gives good results in the diagnostics because gametocytes are present in the bird blood for a relatively long period of time, while the number of diagnostic characters used is rather large. Third, the use of blood allows wide application of collecting the parasite material from live hosts, which opens wide opportunities to carry out parasitological studies along with ornithological investigations and consequently to solve the problem of collection of material without any harm to the avifaune. The latter is important in mass observation of birds.

During the last two decades, the specificity of haemoproteids has been widely discussed in the literature. Bennett *et al*. (1972) after the analysis of experimental data (the authors cite the papers of Fallis and Wood, 1957; Fallis and Bennett, 1960; Khan and Fallis, 1971a) postulated the specificity of haemoproteids at the level of bird families, which was supported by many scholars. Nevertheless, this conclusion can hardly be considered sufficiently supported if it is based only on the mentioned papers. Khan and Fallis (1971a) used the same bird species, *Sphyrapicus varius*, both as the donor and recipient of infection in their experiments with *Haemoproteus velans*. Thus, the specificity of haemoproteids cannot be judged on the basis of this work only; compare the work of Fallis and Wood (1957), where they used domestic white Pekin duck as the donor and recipient of *H. nettionis.* The information about haemoproteids specificity can be found only in the paper by Fallis and Bennett (1960). They managed to infect experimentally *Bonasa umbellus* (Galliformes: Tetraonidae) with *H. canachites* (=*H. mansoni*), which was originally found and described from *Canachites canadensis* (Tetraonidae), by injection of sporozoites. They could not however infect three ducks (Anseriformes), one Jawa sparrow (Passeriformes), and one pigeon (Columbiformes). It is difficult to make a conclusion about the specificity of haemoproteids at the level of bird families only on the basis of the results of this work. Nevertheless, it can be definitely said that there is no infection transmission between the hosts belonging to different bird orders. Wenyon (1926) also failed to infect *Serinus canaria* (Passeriformes) with *H. columbae* by means of inoculation of sporozoites, although *Columba livia* (Columbiformes) was successfully infected.

Atkinson (1986) performed a series of elegant experiments showing that *H. mansoni* (=*H. meleagridis*) isolated from *Meleagris gallopavo* (Galliformes: Meleagrididae) successfully develops in *Alectoris chukar* and *Phasianus colchicus* (Galliformes: Phasianidae) thus transmitting between different families of the order Galliformes. The author of the same work showed that *H. mansoni* has a selective specificity and does not infect *Gallus gallus, Colinus virginianus* (Galliformes: Phasianidae) and *Numida meleagris* (Galliformes: Numididae). The example discussed is important in the sense that it demonstrates the possibility for one species of haemosporidians to infect the representatives of various families of the same order.[†]

The results of our research carried out on the Curonian Spit in the Baltic Sea show that *Haemoproteus fringillae* isolated from *Emberiza citrinella* (Passeriformes: Emberizidae) successfully infects *Fringilla coelebs* (Passeriformes: Fringillidae). The biting midge *Culicoides impunctatus* was used in this case as the vector. Thus, *H. fringillae* can also develop in birds belonging to different families within one order.

[†] Atkinson (1986) accepts the bird classification according to which the groups Meleagrididae, Numididae, and Phasianidae are included in the family Phasianidae as subfamilies (Check-list of North American Birds, 1983). It follows from these facts that the author restricts the level of haemoproteids specificity by the bird families. The problem of the influence of the Aves classification reconstruction on the problem of bird haemosporidians specificity will be discussed in the text below.

In this connection, it is interesting to mention the data about the absence of *Haemoproteus* and *Leucocytozoon* spp. in 107 specimens (the 95% confidence limit of the infection prevalence is 0.0 to 3.6) of the Palearctic *Cuculus canorus,* which we have investigated in the Eastern Baltic region. This bird being a representative of the order Cuculiformes is characterized by brood parasitism. *Cuculus canorus* lay eggs mainly in the nests of birds of the order Passeriformes, which bring up the young cuckoos. Despite a high prevalence of haemoproteids and leucocytozoids in the main feeders of the cuckoo: *Erithacus rubecula, Phoenicurus ochruros, Saxicola rubetra* and other small passerine birds (Malchevsky and Pukinsky, 1983; Lietuvos fauna. Paukščiai, 1990), the cuckoos do not gain the infection, most probably due to the narrower specificity of the haemoproteids and leucocytozoids, while a relatively low density of their populations and individual spatial allocation (Žalakevičius *et al*., 1995a) hinder the infection spreading between adult and young *C. canorus* after the young ones fly from the nest. The case considered favors that there is no transmission of *Haemoproteus* and *Leucocytozoon* spp. between birds of different orders, which is being found in the course of regular 'experiments' carried out in nature. On the other hand, the results of our field observations on infection of *Troglodytes troglodytes* on the Curonian Spit, the place of active transmission of *Haemoproteus* spp., call into question the practice of naming the bird haemoproteid species according to the family identity of their hosts as a general device used in the current systematics. A single case (1.5%) of *Haemoproteus* sp. infection was recorded in 67 investigated birds during a 12-year period of the investigations. This bird is very sedentary and the only member of the family Troglodytidae in Europe. There is no potential source of infection within the family on the study site. It is likely that the parasite came from birds belonging to another family of the Passeriformes. Some passerine birds are infected there with haemoproteids up to 100% during the breeding period (Valkiūnas, 1987c).

At present, we can assume on the basis of the data available that it would be more correct to consider the order of birds as the maximum theoretical possible level of the haemoproteids specificity. In doing so, when there is no experimental or molecular biology information about the range of vertebrate hosts of the parasites under study, the forms of haemoproteids gametocytes that cannot be distinguished within one order of birds should be attributed to one species, while those from the different orders should be attributed to different species.

It is noteworthy, however, that the point of view on the bird's families as the maximum range of the haemoproteids' hosts discussed above is currently common in the literature. This position is based only on the facts discussed above, and it is our opinion that it is not well enough justified. However, the assumption about haemoproteids specificity at the level of the bird families has been so often repeated in the literature during the last two decades without additional experimental facts to justify it (Bennett *et al.*, 1986a, 1986b, 1987; Bennett and Peirce, 1988; Bennett, 1989b; Bennett and Peirce, 1989; Bishop and Bennett, 1989; Bennett *et al.*, 1990; Bennett and Bishop, 1990b; Bennett and Peirce, 1990c; Bishop and Bennett, 1990; Peirce *et al.*, 1990; Bennett *et al.*, 1991b; Bennett and Peirce, 1991; Burry-Caines and Bennett, 1992; Bennett *et al.*, 1994a) that it gradually became to be taken for granted. It is noteworthy that in this case there is a usual alternative perception of the same limited experimental facts.

During the last two decades, the problem of specificity of Haemoproteidae species has started to be even more complicated by the fact that bird classification reconstruction was activated in ornithology, which was relatively weakly reflected on the taxa of the order level, but strongly impacted the taxa of families and subfamilies (Check-list of North

American Birds, 1983; Edwards, 1986; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). As a result, the groups of birds, with which the experiments on specificity testing were carried out, remained in one group of systems in the rank of families, while the others obtained the status of subfamilies. This could not avoid influencing the concept of parasitologists, which adhere to the opinion of haemoproteids specificity at a level lower than the orders of birds. For example, transition of Meleagrididae, Numididae, and Tetraonidae to the rank of subfamilies of the family Phasianidae and correspondingly the fact of no transmission of *H. mansoni* (=*H. meleagridis*) from the representatives of the Meleagridinae to certain species of the Phasianinae and Numidinae (Atkinson, 1986) were used to justify the assumption of the haemoproteids specificity at the level of subfamilies of birds (Bennett and Peirce, 1989). However, as already mentioned, it was not emphasized that *H. mansoni* from *Meleagris gallopavo* (Meleagridinae using the scheme considered) was successfully transmitted to certain representatives of the Phasianinae, namely *Alectoris chukar* and *Phasianus colchicus* (Atkinson, 1986). Thus, even in this case we cannot theoretically exclude a possibility of infection transmission between the birds of different subfamilies. Restriction of the specificity level of haemoproteids to subfamilies of birds brought about the description of a series of morphologically identical 'new species' which differ from the previously described only by the fact that they parasitize birds belonging to different subfamilies, for example, *Haemoproteus coereba, H. paruli, H. phodili, H. thraupi,* etc. It should be noted that not all changes in classification based mainly on the data of molecular methods are universally recognized (The Birds of the Western Palearctic, 1988, 1992; Potapov, 1992; Kurochkin, 1993). Leaving aside the problem of the birds' taxonomy, it should be emphasized that the parasitologists who accepted the position on the haemoproteids specificity at a level below the order were trapped into the dependence on the bird taxonomy reconstruction. Unfortunately, this inevitably leads to the contradictions, incorrect actions, and unjustified exclusions from the point of view on the specificity that they accepted. Let us analyze some examples.

In 1984, Peirce (1984b) described *Haemoproteus balmorali,* found in passerine birds of the families Turdidae and Muscicapidae. Soon after the concept of the specificity at the level of subfamilies was accepted by some scholars, *H. balmorali* was excluded from the list of Turdinae parasites (Bennett and Peirce, 1989), and the range of its hosts was limited by the birds of the subfamily Muscicapinae (Bennett *et al.*, 1991b). Nevertheless, the morphology of this parasite in both groups of birds is so similar and in some points unique that afterward Peirce and Bennett (1993) indicated that they missed *H. balmorali* in the representatives of the Turdinae. In the latter paper they admitted that *H. balmorali* parasitize birds of the subfamilies Turdinae and Muscicapinae belonging to the family Muscicapidae, thus present in birds of different subfamilies of the same family. In other words, these taxonomists had to admit that *H. balmorali* is characterized by the specificity at the family level, not at the subfamily level of birds. It is noteworthy that there were no additional experimental data about the specificity of *H. balmorali.* The range of the hosts of this species was widened despite the statements about haemoproteids specificity at the level of bird's subfamilies (Bennett and Peirce, 1989; Bennett *et al*., 1991b). It was done only on the basis of the data on the morphology of gametocytes and their host cells in the peripheral blood. At the same time, certain haemoproteids have still been described as new species only on the basis that they are found in birds of different subfamilies of the same bird family (Burry-Caines and Bennett, 1992). It is obvious that such a free interpretation of the haemoproteids specificity level without additional experimental or molecular biology data negatively influences the development of the systematics.

It is our opinion that the postulate about haemoproteids specificity at the level of subfamilies of birds (Bennett and Peirce, 1989; Bennett *et al*., 1991b; Burry-Caines and Bennett, 1992) does not stand up under scrutiny as the fundamental approach to the problem of species identification. This approach inevitably leads to the appearance of new specific names in the literature, which name morphologically indistinguishable parasites. For example, at present, two species of haemoproteids *H. greineri* and *H. nettionis* are accepted as developing in the representatives of the family Anatidae. Several subfamilies of anseriform birds are included in the family Anatidae (we shall name only Anatinae, Anserinae, Cygninae), where the above mentioned parasites were found. If one consistently adheres to the position of haemoproteids specificity at the level of bird's subfamilies, the number of species parasitizing Anatidae would be automatically increased several times. Nevertheless, even the supporters of the conception of narrow specificity do not dare to do this and name only *H. greineri* and *H. nettionis* as parasites of birds belonging to the Anatidae (Bishop and Bennett, 1992).

The contradictory position of the scholars operating with specificity at a level below the order with the objectives of systematics is also in the fact that the range of hosts for the parasites of different groups of birds is arbitrarily limited either by subfamilies or by families (summarized by Bennett *et al.,* 1994).

At present, it is clearly obvious that different species of haemoproteids are characterized by a different level of specificity. An example of experimentally proved wide but selective specificity of *H. mansoni* was considered above. The group of widely specific species also includes *H. fringillae* parasitizing passerine birds. *Haemoproteus palumbis* parasitizing *Columba palumbus* is a good example of a strictly specific parasite, which does not develop even in a closely related bird species belonging to the same genus, *C. livia.* Interestingly, *H. columbae* isolated from *C. livia* does not complete development in *C. palumbus* (summarized by Baker, 1975). Further investigations are needed to evaluate the range of hosts of the individual species of haemoproteids. At the same time, one should not forget about the existence of intraspecific variability of specificity in the parasites. In this relation, negative results of the experiments on cross infection (especially when a limited number of experimental hosts are used) should be carefully extended to the category of the species as a whole. This fact is usually not taken into the account by the specialists investigating the bird haemosporidians. In addition, one should carefully apply the data of experimental works with negative results in theoretical constructions, because by now it was not completely understood how keeping wild birds in captivity reflects on their physiological condition as well as how the viability of sporozoites is influenced by vectors kept in artificial conditions. At the same time, evaluating the maximum theoretically possible range of hosts for different groups of haemosporidians is important at the present stage of taxonomy development. It has already been mentioned that it is our opinion that it would be more correct to consider the orders of birds as the maximum level of specificity for haemoproteids, because at present there are no scientific indications of the infection of birds belonging to different orders by the same species of parasites, while there are examples, although not numerous (because the experimental works on haemoproteids are not numerous), when individual species are transmitted between the birds of different families belonging to one order. It is important that qualitative information about the distribution of haemoproteid species among the birds, which is gradually being accumulated, indicates that the range of hosts for many species is likely to be limited by the families of birds. For example, such 'good' species from the point of view of their morphology as *H. payevskyi*, *H. lanii*, and *H. orioli* were found exclusively in representatives of

the order Passeriformes belonging to the families Sylviidae, Laniidae, and Oriolidae, respectively. There are more such examples. Nevertheless, the experimental data on the possibility of certain haemosporidians to develop in the representatives of different families belonging to one order are of supreme significance in the evaluation of the theoretically possible range of hosts for a species with unknown specificity. In this relation, the objective of the stability of taxonomy while describing the new species requires adherence to the principle of haemoproteids specificity at the level of order of birds, unless something else can be proved regarding each individual species. Molecular biology methods are a promising technique for this purpose.†

From the point of view of the parasite's taxonomy, the postulation about haemoproteids specificity at the level of bird's order has several advantages over the others discussed above. First, it is almost insensitive to the changes in the classification of birds, which mainly deal with the taxa ranks lower than the orders. Second, in this case the identification and description of the species presume the necessity of detailed analysis and comparison of all species described for birds of the same order, which requires a peer morphological analysis and permanent improvement of the set of characters used in the systematics. Third, this approach restricts the possibility of the description of morphologically indistinguishable species performed merely on the basis that they were found in previously unknown hosts. Under the condition of thorough investigation and a wide set of morphological characters, the likelihood of the description of 'assembled' species decreases. All this is important for the future development of the taxonomy.

The range of invertebrate hosts (vectors) of bird haemoproteids is limited by blood-sucking dipteran insects of the Ceratopogonidae and Hippoboscidae families, and the role of the hippoboscid flies as vectors is convincingly proved only for the haemoproteids parasitizing birds belonging to the order Columbiformes (*Haemoproteus columbae, H. sacharovi, H. palumbis*). It is likely that only biting midges are the vectors of haemoproteids parasitizing other groups of birds. In the last decade, it has been speculated that certain species of haemoproteids can probably use both the biting midges and hippoboscid flies as vectors (Atkinson, 1991b; Desser and Bennett, 1993). This suggestion has not been tested yet.

The haemoproteids species that were studied with the greatest detail use many species of biting midges as vectors. For example, *H. mansoni* successfully completed its development in *Culicoides arboricola, C. edeni, C. haematopotus, C. hinmani, C. knowltoni,* and *C. sphagnumensis* (Fallis and Bennett, 1960; Atkinson *et al.,* 1983; Atkinson, 1988). The development of the parasite, however, is interrupted at the oocyst stage in the biting midges *C. baueri, C. nanus, C. paraensis, C. scanloni,* while it is not recorded in *C. crepuscularis*. The reasons of the selective development of haemoproteids in various species of the biting midges have not been explained yet in detail. Valkiūnas *et al.* (2002b) recorded that sporogony of five species of *Haemoproteus* is completed in the experimentally infected biting midge *C. impunctatus*.

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† At the time of preparing this book for publication, the mitochondrial DNA analysis of avian species of *Haemoproteus* was carried out (Bensch *et al.*, 2000). It was shown that tits (*Parus:* Paridae) harbor lineages of *Haemoproteus* sp. that are nested within parasite clades recovered from a variety of Old World warblers (*Acrocephalus, Phylloscopus:* Sylviidae) suggesting that some species of haemoproteids have been transmitted, at least in an evolutionary sense, between avian hosts belonging to different families. Fallon *et al.* (2003) recorded three identical lineages of *Haemoproteus* spp. in passeriform birds belonging to the Fringillidae and Vireonidae in the Lesser Antilles.

SPECIFICITY AND GENERAL PRINCIPLES OF THE IDENTIFICATION OF PLASMODIIDAE AND GARNIIDAE SPECIES

By the first third of the 20th century, two opposite points of view on the bird malaria parasites (genus *Plasmodium*) were common in the literature: all parasites found in new hosts were either attributed to one species (*Plasmodium praecox* or *Proteosoma grassii*) or described as new species. As a result, the taxonomy of these parasites appeared rather intricate. Species identification of malaria parasites compared to the identification of haemoproteids and leucocytozoids on the one hand is facilitated by the opportunity to study the morphology not only of gametocytes but also of erythrocytic meronts, while on the other hand, it becomes more complicated by the difficulty in finding infections in heavy form in wild birds, where gametocytes and meronts of the parasites are numerous enough in the blood. The acute stage of parasitemia in malaria is short and rarely recorded in wild birds. Erythrocytic meronts are not always found during the long chronic stage of the infection, while the gametocytes of many bird *Plasmodium* spp. (subgenera *Giovannolaia, Huffia*) are morphologically similar to the gametocytes of some species of *Haemoproteus.* Experiments with bird malaria parasites are facilitated by the possibility of infecting the recipient hosts by subinoculation of blood from infected birds, which is almost impossible in the case of *Haemoproteus* and *Leucocytozoon* spp. infections. The application of the subinoculation methods is, however, difficult during the mass investigation of wild birds. The microscopy of stained blood films gives only an idea about the relative distribution of bird malaria parasites.

Many species of *Plasmodium* develop in birds belonging to various families and even orders (Garnham, 1966, 1980; Waldenström *et al.*, 2002) thus being catholic in their host range. Strictly speaking, specificity does not play a decisive role in species identification, while the main attention is focused on the detailed study of the morphology of blood and some other stages (if information on the latter is available) and then on the host–parasite relationships including experimental tests on birds' susceptibility to infection. In field conditions, the researchers are limited by the first group of characters. The information about the susceptibility of canaries, chickens, ducklings, and other domestic birds to the *Plasmodium* species under study may be used for species identification in the experiments.

The specificity of *Fallisia neotropicalis*, the only representative of the family Garniidae parasitizing birds, has not been experimentally studied. The parasite has been recorded only in the Neotropical zoogeographical region (Gabaldon *et al*., 1985). *Columba livia,* the type vertebrate host of this parasite was introduced into the Neotropics and no doubt gained the infection in a secondary way. Taking into account that this haemosporidian parasite was not found in wild species of the Columbiformes but common in the representatives of the order Ciconiiformes of the local fauna, the transmission of this species among the birds of different orders is possible. Most likely, *F. neotropicalis* has a wide range of vertebrate hosts and in this relation it is similar to the *Plasmodium* species.

The range of invertebrate hosts (vectors) of bird malaria parasites is limited only to blood-sucking dipterans of the family Culicidae. The majority of well-studied *Plasmodium* species successfully develop in many species of mosquitoes. For example, *P. gallinaceum* completed its development in approximately 40 species of mosquitoes, while *P. relictum* completed it in more than 20 species belonging to the genera *Aedes, Anopheles*, *Armigeres*, *Culex*, *Culiseta*, and *Mansonia.* Certain species of *Plasmodium* are however more selective

with respect to the vectors. For example, sporogony of *P. juxtanucleare* failed to be induced in any species of the above-listed genera of mosquitoes, except *Culex* spp. The general rule for the majority of the malaria parasites is that the most effective vectors usually belong to one or two genera of the Culicidae.

SPECIFICITY AND GENERAL PRINCIPLES OF THE IDENTIFICATION OF LEUCOCYTOZOIDAE SPECIES

Much of what has been discussed about the specificity of the Haemoproteidae species and their identification principles may be related to the Leucocytozoidae. One faces the same difficulties in species identification of leucocytozoids as was the case with haemoproteids. It should be noted that the identification of the leucocytozoid species is also complicated by other circumstances. First, the intensity of infection with leucocytozoids in free-living birds is usually low, and prolonged microscopy is needed to find gametocytes, especially not distorted ones, in the blood smears. Second, the leucocytozoid gametocytes are easily deformed when blood films are prepared, which has to be taken into account if one finds gametocytes of unusual form. Third, a significantly lesser number of morphological characters can be used for leucocytozoids species identification than for *Haemoproteus* or *Plasmodium* spp., thus the likelihood of the description of assembled species increases. Moreover, the morphology of the host cell is more valuable in the systematics of leucocytozoids on the species level than the morphology of gametocytes itself. Fourth, morphometric parameters should be used with particular care, because they overlap in the majority of the species and cannot be used as a reliable feature of the species not associated with other characters of the gametocytes (Bennett and Campbell, 1975). Finally, the possibility to use the morphology and peculiarities of the development of exoerythrocytic meronts in the systematics of the Leucocytozoidae should be called into question after it was shown that there are strains of *Leucocytozoon simondi,* whose megalomeronts are always developed in ducks, but sometimes do not develop when geese are infected (Desser and Ryckman, 1976; Desser *et al*., 1978). In other words, the peculiarities of exoerythrocytic merogony for certain strains of *L. simondi* may be determined to a great degree by the properties of the host organism (for details, see p. 790). It is noteworthy in this relation that megalomeronts of *L. sakharoffi* have not been found in all vertebrate hosts (Wingstrand, 1947, 1948; Khan and Fallis, 1971b). The information about the existence of strains differing in the exoerythrocytic development in a certain way currently restricts the use of the peculiarities of the exoerythrocytic merogony and morphology of the meronts in the systematics. This situation is unique for haemosporidians and requires additional investigation.

At present, there are no scientific facts available which confirm the possibility that the same species of *Leucocytozoon* infect birds belonging to different orders (see, however, pp. 806 and 828 about possible exceptions which need to be tested). Let us consider some of the examples.

It is possible to infect only domestic ducks and geese (order Anseriformes) with *L. simondi* by exposure of the birds in the regions where the leucocytozoonosis is endemic as well by experimental inoculation of suspensions containing exoerythrocytic merozoites or sporozoites. It is not possible to infect domestic chickens, turkeys, guinea fowls, pheasants, hazel grouses (representatives of the order Galliformes), as well as domestic pigeons (Columbiformes), plovers (Charadriiformes), owls (Strigiformes), and passerines

(Passeriformes) (Stephan, 1922; Fallis *et al*., 1953, 1954; Anderson *et al*., 1962; Fallis and Bennett, 1966; Eide and Fallis, 1972; Fallis *et al*., 1974). Similar results were obtained in the experiments with *L. smithi.* This parasite infects turkeys, but does not develop in ducks and geese (Skidmore, 1932; Byrd, 1959; Solis, 1973). The penguin (Sphenisciformes) parasite *L. tawaki* does not infect domestic chickens and ducklings if they are exposed in an endemic region (Allison and Desser, 1978). A negative result was obtained after the exposure of guinea fowls for the whole summer in the territory with active transmission of *L. simondi* in anseriform and *L. sp.* in passeriform birds (Fallis *et al*., 1974). A series of experiments was performed by Fallis and Bennett (1958, 1966) on cross infection by means of sporozoites inoculation. The results are the following. *Leucocytozoon lovati* (=*L. bonasae*) develops in *Bonasa umbellus* (Galliformes), but does not develop in ducklings (Anseriformes) and *Zonotrichia leucophrys* (Passeriformes); *L. fringillinarum* isolated from *Z. albicollis* and *Quiscalus quiscula* (Passeriformes) does not develop in ducklings; *L. leboeufi* (=*L. ardeae*) isolated from *Ardea herodias* (Ciconiiformes) does not infect ducklings; *L. dubreuili* (=*L. mirandae*) isolated from *Turdus migratorius* (Passeriformes) does not infect ducklings; *L. danilewskyi* develops in *Aegolius acadicus* (Strigiformes) but neither infects *Lonchura oryzivora* (Passeriformes) nor ducklings. Thus, the species of *Leucocytozoon* studied cannot complete their development in birds belonging to different orders. An example showing no transmission of *Leucocytozoon* spp. between birds belonging to the orders Cuculiformes and Passeriformes in nature was also discussed above (see p. 71).

There was usually no success in experimental infection of birds belonging to different families of one order with the same species of *Leucocytozoon.* For example, *L. smithi* develops in turkeys (Galliformes: Meleagrididae) but does not develop in domestic chickens, quails, or chukars whose are representatives of galliform birds of the family Phasianidae (Skidmore, 1932; Solis, 1973). Fallis with his co-authors (Fallis *et al.*, 1974) kept guinea fowls (Galliformes: Numididae) during the whole summer in a region with active transmission of *L*. sp. among hazel grouses (Tetraonidae), but the guinea fowls were not infected. Fallis and Bennett (1966) in the experiments on cross infection by means of sporozoites inoculation obtained the following results: *L. sp.* (most likely *L. berestneffi*) isolated from *Cyanocitta cristata* (Passeriformes: Corvidae) infects *Perisoreus canadensis* (Corvidae) but does not complete its development in *Lonchura oryzivora* (Estrildidae), *Hesperiphona vespertina* (Fringillidae), *Melospiza georgiana* (Emberizidae); *L. dubreuili* isolated from *Turdus migratorius* (Passeriformes: Turdidae) does not infect *Lonchura oryzivora* (Estrildidae). Nevertheless, there are species of *Leucocytozoon* infecting birds of different families belonging to one order, which is of theoretical importance related to the problems considered here. For example, Fallis and Bennett (1962) managed to infect the representatives of three families belonging to the order Passeriformes: *Zonotrichia albicollis* (Emberizidae), *Quiscalus quiscula* (Icteridae), and *Lonchura oryzivora* (Estrildidae) with *L. fringillinarum* by means of sporozoites inoculation. Later these scholars confirmed again that *L. fringillinarum* can be transmitted among the passeriform birds belonging to different families (Fallis and Bennett, 1966). This parasite isolated from *Q. quiscula* by experimental inoculation of sporozoites developed in the simuliid fly *Cnephia ornithophilia* was successfully transmitted to *L. oryzivora.* The examples considered are of particular theoretical interest, because they demonstrate the ability of one species of *Leucocytozoon* not only to develop in the representatives of at least three different families belonging to the order Passeriformes, but also to infect the representatives of phylogenetically well differentiated groups, for example, the Estrildidae

and Icteridae, which evolved in the Old and New World, respectively. This conclusion is especially important for the parasites of small passerines, in which a lot of morphologically indistinguishable species of leucocytozoids have been described.

The leucocytozoids whose range of hosts is narrower than the families of birds (Khan and Fallis, 1971b)† are also known. There was no success to transmit *Leucocytozoon sakharoffi* isolated from *Corvus corax* and *C. brachyrhynchos* (Passeriformes: Corvidae) to *Cyanocitta cristata* (Corvidae) by inoculation of sporozoites, while *L. berestneffi* from *C. cristata* does not infect *C. brachyrhynchos.*

Leucocytozoon caulleryi is a strictly specific species. This parasite develops only in domestic chickens. It does not infect ducks, geese, turkeys, and domestic pigeons (Mathis and Léger, 1910d). Experimental inoculation of exoerythrocytic merozoites and sporozoites failed to infect nine species of birds belonging to the order Galliformes: *Bambusicola thoracica, Chrysolophus pictus, Colinus virginianus, Coturnix japonica, Numida meleagris, Phasianus colchicus, P. versicolor, Syrmaticus reevesi, S. soemmerringii* by *L. caulleryi.* Interestingly, the removal of spleen from *C. japonica* does not facilitate suppression of the natural immunity to *L. caulleryi* (Morii and Kitaoka, 1971).

The examples considered show that there are species among the Leucocytozoidae both with a narrow specificity (*L. caulleryi*) and with a broad one (*L. fringillinarum*) as well as species that occupy an intermediate position between these two by their level of specificity (for example, *L. simondi*). Experimental investigations and other numerous observations allow us to consider the bird orders as a theoretically maximum range of the vertebrate hosts of *Leucocytozoon* species. The property to parasitize mainly birds of one order can be regarded at present as a universal one for all *Leucocytozoon* species known, both with narrow and wide specificity. At the present level of knowledge, we consider that it is possible to use this property for *Leucocytozoon* species identification while strictly observing it for species whose specificity was not experimentally proved. In the light of present knowledge, all morphologically identical parasites in the hosts belonging to one bird order should be related to one species, while those which are morphologically different should be related to different species. An exception from this general scheme is made only in those cases when a narrower specificity of certain species was experimentally proved (for example, *L. caulleryi, L. sakharoffi*). It is not inconceivable that certain *Leucocytozoon* species identified this way will appear 'aggregated' in the future. To minimize confusion in the systematics of leucocytozoids before additional experimental and molecular biology studies have been carried out, and primarily to restrict the possibility of describing parasites with minor or even no morphological differences as new species, it is reasonable to consider the bird orders as the maximum theoretically possible range of vertebrate hosts of the leucocytozoids species.

Bennett and Campbell (1975) were the first who practically implemented the idea that it is necessary to restrict the maximum theoretically possible range of the *Leucocytozoon* species hosts by the bird orders with the objective to develop the systematics further. These scholars admitted that *L. fringillinarum* can parasitize birds of different families of the order Passeriformes. They carried out a detailed morphometric analysis of *L. simondi, L. dubreuili,* and *L. fringillinarum* gametocytes and their host cells and showed that using morphometric characters only is not enough for the identification of even these 'good' species. These scholars were first to publish the results of a vast and well-grounded work on the synonymy

† The authors do not identify the parasites up to the level of species. The species were identified by us.

of the parasite specific names, which indicate morphologically indistinguishable forms described in birds of one order. In particular, the synonyms for *L. fringillinarum* included seven specific names of *Leucocytozoon*, which, in our opinion, is quite well grounded.

Later, however, Bennett with co-authors (Bennett *et al*., 1991c) reconsidered their views regarding the specificity of species of the Leucocytozoidae. As was the case with species of the Haemoproteidae, this was done primarily not on the basis of new facts found about the parasites, but as a consequence of the changing of bird classification by certain ornithologists (Check-list of North American Birds, 1983; Edwards, 1986). In particular, such families of the order Galliformes as Meleagrididae, Numididae, Tetraonidae, Phasianidae were transferred into the rank of subfamilies of the family Phasianidae, which was not accepted by all ornithologists (The Birds of the Western Palearctic, 1980, 1992; Stepanyan, 1990; Potapov, 1992). The general propositions about the influence of the bird classification changes on the problem of specificity of haemosporidians that we considered in the analysis of specificity of the Haemoproteidae species are fully applicable to the Leucocytozoidae species. The parasitologists, who introduced the new and sometimes debatable concepts of ornithology about Aves classification into their researches, had to reconsider the maximum possible level of the specificity and limit it to the families or even subfamilies of birds. The logic of this action is the following. For example, as it was already mentioned, the results of the experimental observations indicate that *L. smithi* develops in turkeys (Meleagrididae) but does not infect representatives of the family Phasianidae. If the rank of Meleagrididae and Phasianidae is lowered to the rank of a subfamily of the family Phasianidae, the level of specificity of *L. smithi* and consequently the level of the entire group of the Leucocytozoidae would be limited to the subfamilies of birds. After making this step, some of the scholars had to decline the results of their previous investigations, which in our opinion was not well enough grounded. For example, Bennett with co-authors (Bennett *et al*., 1992c) say that admittance of the possibility of *L. fringillinarum* development in passerine birds of various families accepted earlier (Bennett and Cameron, 1975) is to a great extent based on morphological data rather than on the results of experimental research. It is, however, difficult to admit this statement, because the authors in the paper published in 1975 cite the previously mentioned paper by Fallis and Bennett (1962), who showed experimentally the possibility of the development of *L. fringillinarum* in passerine birds belonging to the families Emberizidae, Icteridae, and Estrildidae. It is important to note that the results of some field investigations also call into question the practice of naming *Leucocytozoon* species according to the family identity of their hosts. For example, *Cinclus cinclus* is an extremely rare host of *Leucocytozoon* sp. in Scotland. Since this bird is sedentary and the only member of the family Cinclidae in Europe, there is no potential source of infection within the family, and it is reasonable to assume that the infection came from another family (Logie *et al.*, 1998).

Admission of the postulation about the specificity of leucocytozoids at the level of bird families and even subfamilies (Bennett *et al*., 1991c) and its subsequent use in the practice of taxonomy led to a series of publications (Bennett *et al.,* 1992c; Bennett and Peirce, 1992b; Bennett and Squires-Parsons, 1992; Bennett *et al*., 1993d and others) where numerous parasites were described under new names mainly on the basis that they were found in birds of other families and subfamilies unlike previously described species, e.g., *L. deswardti, L. dutoiti, L. icteris, L. irenae, L. nectariniae, L. parulis, L. pittae, L. prionopis, L. sturni, L. thraupis, L. timallae, L. whitworthi* and others parasitizing passerine birds.[†]

[†] See also Appendix 2 (p. 867).

It is noteworthy that scholars, while describing these leucocytozoids, besides the thesis about the specificity lay special emphasis on the morphometric characters which cannot be a basis to describe new taxa, as shown in a previous paper by Bennett and Campbell (1975).

It is our opinion that, at present, the position about the specificity of the Leucocytozoidae species at the level of families and subfamilies of birds considered above cannot be accepted as the basis for taxonomic investigations, because it ignores a series of facts. Let us remind once more that *L. fringillinarum* can infect passerine birds belonging to the families Emberizidae, Icteridae, and Estrildidae (Fallis and Bennett, 1962, 1966). It is important that in the majority of the present classifications of Aves, the groups Emberizidae and Estrildidae are either distinguished as individual families or have the rank of subfamilies belonging to different families. In other words, the presence of mutual *Leucocytozoon* species infecting the representatives of these groups of birds favours the point of view about the specificity of leucocytozoids at a level higher than families, taking no account of the opinion of ornithologists about the classification of Aves. It is worth noting the fact that transmission of *L. simondi* between the representatives of the family Anatidae belonging to the subfamilies Anatinae and Anserinae is a universally recognized and experimentally proved fact (Fallis *et al*., 1974), which becomes a force to reckon with in particular by the followers of the theory of narrow specificity of *Leucocytozoon* spp. (Bennett and Squires-Parsons, 1992; Bishop and Bennett, 1992) who make an exception for this species including it in the list of the parasites of several subfamilies of the Anatidae.

Thus, to stabilize the taxonomy on the specific level, as was the case with the Haemoproteidae species, and to restrict the overwhelming amount of literature by morphologically identical forms described under new specific names, it seems reasonable to limit the maximum theoretically possible range of the hosts for the Leucocytozoidae species by the orders of birds. The further investigation of the leucocytozoids' specificity and the use of molecular biology methods are extremely valid in clarifying the status of the majority of specific names, which are available in the literature. It is important to remember that there is almost no information about the intraspecific variability and specificity of *Leucocytozoon* spp.

The range of invertebrate hosts (vectors) of leucocytozoids is limited by blood-sucking dipteran insects belonging to the Simuliidae and Ceratopogonidae. Only one species (*Leucocytozoon caulleryi*) uses biting midges as vectors. All other species of *Leucocytozoon* studied up to the present are transmitted by simuliid flies.

Relatively well-studied species, for example, *L. dubreuili*, *L. fringillinarum*, *L. simondi*, *L. smithi*, and others, successfully develop in numerous species of simuliids. The great majority of the leucocytozoid species are transmitted by simuliid flies belonging to the genus *Simulium*, while the simuliids of the genera *Cnephia*, *Prosimulium* and some others are vectors for a minor number of species, which have been studied so far. On the other hand, the majority of species of simuliid flies studied may be the vectors for several species of *Leucocytozoon.* For example, *L. danilewskyi*, *L. dubreuili*, *L. fringillinarum*, *L. lovati*, *L. sakharoffi*, and some other leucocytozoids successfully completed their development in *Simulium aureum* and *S. latipes.* It is most likely that the restrictions on the infection of many species of simuliids by *Leucocytozoon* spp. are frequently ecological rather than physiological (Bennett, 1960; Barrow *et al.,* 1968; Desser and Bennett, 1993). For example, the factor sufficiently hampering the infection of simuliids is their feeding specialization and vertical distribution during the period of their maximum activity. In this connection, mammalophylous species of simuliids appear ecologically isolated from the birds, while the species, which prefer to feed in the tree canopy, have fewer opportunities to gain parasites

from birds, who spend most of their time on the ground. All this is of great epidemiological importance.

Pathogenicity

The category of pathogenicity is used here in its broadest meaning as the impact of parasites, which is not advantageous to the host and in its extreme manifestation can lead to illness or even death of the host. It is obvious that this definition as well as any other is conventional and does not reflect all the aspects of the complex interrelations between the parasites and their hosts. The notions of 'advantage' and 'benefit' themselves are relative and bear a different sense at the level of organisms, populations, and cenoses (Beklemishev, 1970; Kennedy, 1975; Anderson and May, 1978, 1982; Kontrimavičius, 1982, 1983; Balashov, 1991). The choice of this standpoint on the problem of pathogenicity was caused by the framework of the problems touched in this book and also by the fact that it provides the maximum liberty to interpret the ecological relationships between the parasites and both domestic and wild birds.

The pathogenic impact of haemosporidians on their hosts is extremely complicated and diverse, which is mostly determined both by their complex life cycles and the complicated epidemiology of the diseases. It is noteworthy that the relationship between the parasites and vectors has been studied to a lesser extent than their relationship with birds. Consideration of the entire frame of problems related to this vast field of knowledge requires special research. In this work we shall limit ourselves by a single objective, which has always intrigued zoologists and naturalists. Namely, the separate facts accumulated up to the present will be used to make an attempt to illustrate that none of the groups of haemosporidians are neutral for their hosts including free-living ones. The solution of this problem is valid in relation to the plans for future research. In the last decade, the notion that haemosporidians are relatively harmless (with rare exceptions) to wild birds has been expressed with a growing insistence (Peirce, 1989; Bennett and Bishop, 1990a; Bennett *et al.*, 1993e; Desser and Bennett, 1993). It is our opinion that this idea does not represent all facts available at present, but even more to some extent it slows down the research to investigate the role of haemosporidians and parasites in the natural biocenoses as a whole. Despite the global distribution of parasitic organisms, their great diversity, and high density of their populations, ecologists frequently ignore parasites or do not give much consideration to them while explaining the processes occurring in the wild. This is especially true in ornithology.

In this book, the facts are grouped in four main sections and described in the following sequence. First, we present the general information about the comparative pathology of haemosporidioses, which is the basis for the understanding of the main mechanisms of the pathogenic influence on birds. Then, the general characteristics of the diseases of domestic birds are given. The greatest consideration is given in regard to distinguishing the influences of haemosporidians on wild birds. This problem has attracted less study. In the final chapter, the data on the pathogenic impact of haemosporidians on vectors are presented.

COMPARATIVE PATHOLOGY

The fundamentals of comparative pathology for bird haemosporidioses were laid by a Russian scientist, V.Ya. Danilewsky, who in 1888 published his monograph 'Research on the Comparative Parasitology of the Blood. I. Zooparasites in Bird Blood' (in Russian). This book was republished in 1889 in French and was cited by the leading malariologists of that time. This was the first fundamental work on comparative pathology, where the author showed for the first time that haemosporidioses in wild birds are accompanied by anaemia, enlargement and whitening of the spleen and liver, and accumulation of pigment in these organs. The data on comparative pathology of bird haemosporidians accumulated by science by the 1960s were analyzed by a prominent British malariologist, P.C.C. Garnham (1966). During recent decades a series of new discoveries were made in the field of bird haemosporidians life cycles, and new, previously unknown or underestimated forms of pathology were found that await scientific generalization.

Pathological changes in birds caused by certain species of haemosporidians are diverse. In this book they are considered in the corresponding essays on species in the Systematic Section, where the literature on the problem is cited most fully. This chapter considers the most general regularities of pathology during haemosporidioses and shows how different the impact of the representatives of different haemosporidian groups on their avian hosts can be.

Exoerythrocytic meronts

A characteristic feature of the development of first-generation exoerythrocytic meronts, which are induced by sporozoites, is that as a rule they do not cause serious pathology in infected birds regardless of the group of haemosporidians. The number of these meronts is usually not large; their size is small, development is rapid, and the inflammatory reaction is usually not pronounced. An exception are, e.g., the first-generation exoerythrocytic meronts in *Haemoproteus mansoni* (=*H. meleagridis*), which cause the necrosis of adjacent muscle fibres (Atkinson *et al*., 1986, 1988b). If the infection with the *Leucocytozoon* species is heavy, numerous meronts of the first generation may cause stretching or even blockage of the liver sinusoids, but no inflammatory reaction is observed around these meronts (Newberne, 1957; Wehr, 1962; Desser, 1967). Pathological changes are pronounced the most during the development of next-generations meronts. Moreover, the character of pathological changes significantly differs in various groups of haemosporidians.

The most severe pathology caused by *Plasmodium* spp. is associated with the blockage of the brain capillaries and capillaries of other vital organs by phanerozoites and sometimes by metacryptozoites. As a result of this, the blood supply of the affected organs is disturbed, the tissues surrounding the meront suffer from anoxia, and the cells die off. Infiltrates develop. The tissues surrounding the meronts become oedemic and die off. Necrosis of the tissues adjacent to meronts is usually significant. The birds often perish with the indications of cerebral paralysis. Similar pathological changes are characteristic of malaria caused by *Plasmodium gallinaceum*, *P. cathemerium*, *P. durae*, *P. lophurae*, *P. elongatum*, *P. octamerium*, and other species of malaria parasites.

The pathology associated with the development of *Fallisia neotropicalis* has not been studied in detail yet. Numerous phanerozoites develop in many organs including the brain during heavy infections, and young birds can perish (Gabaldon *et al*., 1985).

In the case of *Leucocytozoon* infection, the pathological changes are mostly associated with the development of megalomeronts in the spleen, liver, lungs, heart, brain, and many other organs (Wingstrand, 1948; Cowan, 1957; Newberne, 1957; Desser and Fallis, 1967b; Akiba, 1970; Miller *et al*., 1983). Megalomeronts are found in *L. caulleryi*, *L. danilewskyi*, *L. sakharoffi*, *L. simondi*, and some other species. Mature megalomeronts reach 200 μm in diameter and more. They are surrounded by a fibrous capsule-like wall and contain many thousands of merozoites. A clearly expressed inflammatory reaction is usually observed around megalomeronts. Infiltrates frequently contain erythrocytes, macrophages, plasmatic cells, heterophils. After the termination of the merogony, the capillaries adjacent to the parasite burst. Haemorrhages develop in place of the ruptured megalomeronts, which may be heavy. If the parasite develops in the brain, then indications of cerebral paralysis are found. The haemorrhages during the development of megalomeronts are usually clearly expressed. This is why the disease caused by *L. caulleryi* in domestic chickens in Southeast Asia is often called Bangkok haemorrhagic disease. During the final stages of merogony, necrotic centers are formed in place of ruptured megalomeronts, and calcificates are found. The species of *Leucocytozoon*, which do not produce megalomeronts (for example, *L. fringillinarum*, *L. dubreuili*, *L. berestneffi*), induce a notably less pronounced pathology in birds (Khan and Fallis, 1970a).

There is not as much information about pathology associated with the development of *Haemoproteus* spp. exoerythrocytic meronts. It is based mainly on the data obtained in the observation of naturally infected birds. The pathology in pigeons infected with *H. columbae* has been studied in more detail (Mohammed, 1967; Garnham, 1966; Bradbury and Gallucci, 1972; Ahmed and Mohammed, 1977). During heavy infections, the lungs of birds are filled up with meronts, which block up the capillaries. As a result, pneumonia-like symptoms develop, which may cause death of young birds. The inflammatory reaction around meronts is well pronounced.

The development of *Haemoproteus handai* (=*H. desseri*) in parrots, *H. mansoni* in turkeys, and probably *H. columbae* in doves, is accompanied by the formation of megalomeronts in the endothelial cells of capillaries, in the myofibroblasts of the skeletal muscles, and in the heart muscle (Miltgen *et al*., 1981; Atkinson *et al*., 1986, 1988b; Earlé *et al*., 1993). A capsule-like wall is formed around megalomeronts, a heavy inflammatory reaction is observed, and erythrocytes and lymphocytes are concentrated here. Rupture of megalomeronts leads to the formation of large necrotic nidi. Myopathy develops. Calcificates appear in the tissues adjacent to meronts. The number of *Haemoproteus* species, which produce megalomeronts is not known exactly. It is not inconceivable that the numerous cases of megalomeronts recorded in the muscle tissues in many species of naturally infected birds (Becker *et al*., 1956; Farmer, 1964; Levine *et al*., 1970; Walker and Garnham, 1972; Opitz *et al*., 1982; Gardiner *et al*., 1984) are also exoerythrocytic stages of *Haemoproteus* spp. Further study of the role of megalomeronts in the life cycle of various species of *Haemoproteus* is important in theoretical and practical aspects. Nevertheless, it is clear that the opinion that haemoproteids as a whole group are relatively benign for birds (Bennett, 1993b) can hardly be accepted. See also Appendix 2, p. 868.

Blood stages

The most serious pathological consequence of the development of haemosporidians in the blood is the destruction of blood cells and anaemia (Garnham, 1966; Kocan, 1968; Akiba, 1970; Maley and Desser, 1977). One of the general causes of anaemia during bird

haemosporidioses is the active removal of infected erythrocytes from the blood circulation by the cells of the reticuloendothelial system in the spleen, liver, bone marrow, and some other organs. Acute anaemia is developed in those cases, when the processes of erythropoiesis and introduction of erythroblasts in the blood do not compensate for the losses of erythrocytes. Anaemia is less pronounced during the infection with *Haemoproteus* sp. (Atkinson *et al*., 1988b), although in the unfavourable and critical periods of the host's life it is likely that acute anaemia may develop due to the decrease of the organism's ability to compensate for the losses of erythrocytes.

Destruction of erythrocytes during the development of *Plasmodium* spp. is also associated with the development of numerous erythrocytic meronts (Pl. II, *4*). The change in the chemical composition of the blood plasma is also observed during malaria, which enhances the effect of erythrocytes destruction (Seed and Manwell, 1977). Decrease in the plasma pH and increase in the concentration of proteins in the blood is observed during the increase of parasitemia. This leads to the decrease of the oxygen-binding capacity of hemoglobin and to the lessening of effective circulation in the capillaries.

During the *Leucocytozoon* infection, anaemia is intensified because of the destruction of uninfected erythrocytes due to the appearance of the so-called anti-erythrocyte factor in the blood plasma, whose nature has not been completely understood yet (Kocan, 1968). The increase of the osmotic fragility of uninfected erythrocytes and hemolysis are also observed during bird malaria (Seed and Manwell, 1977), but these processes are however significantly less pronounced in malaria than during leucocytozoonosis.

The other peculiarity of *Leucocytozoon* infection is that serious pathological changes in birds may induce gametocytes circulating in the blood, which form large host–parasite complexes together with the infected cells (in certain species, their length reaches 40 μm and even longer). For example, gametocytes of *L. smithi* block up the alveoli and overfill the lungs during heavy parasitemia, which leads to the distortions of respiratory functions and the development of pneumonia-like symptoms (Siccardi *et al*., 1974).

The enlargement of the spleen and liver associated with the hyperplasia of lymphoid-macrophage cells is a characteristic feature of haemosporidioses. During certain heavy infections, these organs enlarge up to 20 times in volume which can cause them to rupture. The greatest enlargement of the spleen and liver is observed during malaria and leucocytozoonosis (Garnham, 1966; Seed and Manwell, 1977; Gabaldon *et al*., 1985; Atkinson *et al*., 1988b). In cases of severe *Plasmodium* and *Haemoproteus* spp. infections, a great amount of insoluble pigment is accumulated in the macrophages of the spleen and liver, and these organs acquire a black hue.

GENERAL CHARACTERISTICS OF HAEMOSPORIDIOSES OF DOMESTIC BIRDS

Haemosporidians are responsible for some serious diseases of domestic birds including lethal ones. The agents of leucocytozoonosis of geese and ducks (*Leucocytozoon simondi*), domestic chickens (*L. caulleryi*), and turkeys (*L. smithi*) are of great practical importance. Poultry farming losses from the diseases caused by other haemosporidians are not as great.

Young highly susceptible birds suffer and die mostly of leucocytozoonoses (Tartakovsky, 1913; Wickware, 1915; Knuth and Magdeburg, 1922; Stephan, 1922; O'Roke,

1930a, 1931; Skidmore, 1932; O'Roke, 1934; Ivanić, 1937b; Johnson *et al*., 1938; Fallis *et al*., 1951; Newberne, 1955; Cowan, 1957; Akiba, 1960; Fallis and Bennett, 1966; Kocan and Clark, 1966; Desser, 1967; Akiba, 1970; Novilla *et al*., 1971; Jones *et al*., 1972; Morii *et al*., 1986; Morii, 1992). Lethargic features, loss of appetite, breathing difficulties, anaemia, debilitation, and diarrhoea can be distinguished among clinical manifestations common for the leucocytozoonoses of various etiology. Haemorrhages and defecation with greenish faeces are also frequently observed. Convulsions and paralysis are usually observed before death. The death rate in juveniles less than one month old can reach 50 to 100%, while it significantly decreases in birds of greater age. Adult birds tolerate the disease more easily and usually survive. The productivity of birds that passed the disease is decreased.

Leucocytozoon macleani (=*L. sabrazesi*) and *L. schoutedeni* (=*L. andrewsi*) should be mentioned among the leucocytozoids parasitizing domestic birds. These parasites of domestic chicken cause relatively mild diseases with weakly pronounced pathology, which rarely have a lethal end. Nevertheless, there is a decrease in the productivity of heavily infected chickens (Lee *et al*., 1969). If one takes into account a wide geographical distribution of the agents of these infections, then it should be admitted that the attention of scholars, which has been drawn to these parasites is likely to be insufficient.

The diseases of domestic birds caused by *Haemoproteus* and *Plasmodium* spp. are recorded much rarely than leucocytozoonoses. *Haemoproteus mansoni* causes severe haemoproteosis in domestic turkeys (Atkinson *et al*., 1988b). Heavily infected birds can perish, while those who survive slow down in growth and their egg-laying qualities decrease. Megalomeronts of this parasite develop in the skeletal muscles causing necrosis of the muscular tissues. A clearly expressed lameness is one of the characteristic clinical manifestations of the disease.

It is likely that the exoerythrocytic meronts recorded in the heart and other organs of domestic ducks, *Cairina moschata*, are also stages of the development of haemoproteids (Commichau and Jonas; 1977; Kučera *et al*., 1982). The ducklings probably become infected with the parasites which normally develop in wild birds. After penetration into the organism of unusual hosts, the parasite causes lethal disease, but develops only up to the stage of exoerythrocytic meronts without forming gametocytes. The mortality rate of ducklings from this disease reached 50% in certain cases recorded in Germany. The myopathy associated with the development of megalomeronts in the skeletal muscles and heart described in domestic chickens (Opitz *et al*., 1982) is similar to myopathy in turkey poults during the development of *Haemoproteus mansoni.* It is likely that in this case the agent of the disease in chicken is also an unknown species of *Haemoproteus*.

Heavy infection of *Haemoproteus columbae* can become lethal for domestic pigeon *Columba livia* (Coatney, 1933). The combination of conditions, when the birds perish, has not been studied yet. It is frequently impossible to see the symptoms of the disease even in heavily infected pigeons (the intensity of parasitemia may be about 50% of erythrocytes) (Ahmed and Mohammed, 1978a, 1978b). Decrease of glycogen, protein, and RNA in the liver, spleen, and brain is recorded in infected birds, which indicates significant changes of the metabolism (Reddy *et al*., 1980).

Among malaria parasites, *Plasmodium durae*, *P. juxtanucleare*, and *P. gallinaceum* are responsible for most frequently observed outbreaks of especially severe malaria in domestic birds. Not only young but also adult birds perish from malaria (Garnham, 1980; Huchzermeyer, 1993b). The breeds of domestic birds, primarily chickens and turkeys introduced into countries with a hot climate, where transmission takes place, suffer most of

all. The disease usually develops rapidly, and it cannot be always controlled. Among the clinical symptoms common for many severe forms of bird malaria, a sharply expressed weakness, worsening of motion coordination, cerebral symptoms, and paralysis should be noted first of all.

Plasmodium relictum, *P. cathemerium*, *P. circumflexum*, *P. matutinum*, *P. fallax* and some other species cause severe forms of malaria in canary *Serinus canaria*, which has been bred in captivity for many centuries and is a good experimental host for research on bird malaria.

All haemosporidioses of domestic birds excluding the disease caused by *Leucocytozoon caulleryi* are naturally focal infections. *Leucocytozoon caulleryi,* a dangerous agent of leucocytozoonosis in domestic chickens, has not been found up to the present in wild birds. If susceptible domestic birds get into the natural nidi of infection, the epizooties develop, which lead to severe economical losses. Let us consider several examples. In the 1950s the Canada Department of Agriculture made an attempt to establish domestic pilgrim geese near Fort Chimo (Ungava Bay, Quebec province, Canada) in order to provide year-round supply for Eskimos with meat (Laird and Bennett, 1970). This region is endemic for *L. simondi*. The epizooties of leucocytozoonosis led this program to failure. Similar devastating epizooties of leucocytozoonosis appeared in a number of states in the southeastern part of the USA after large turkey farms were established on the territories endemic for *L. smithi* (Stoddard *et al*., 1952; Kissam *et al*., 1973, 1975). The epizooties considered clearly demonstrate the necessity to account for the haemosporidioses under the conditions of the anthropogenic transformation of ecosystems. The development of new branches of poultry farming and the occupation of new territories for industrial breeding of poultry require an explanation for the appearance of haemosporidioses outbreaks and the chances of their initiation. For example, the farms of domestic ostriches, *Struthio camelus,* which became popular in Africa in the last decades, suffer losses from leucocytozoonosis caused by *L. struthionis*. Only young ostriches are recorded to be infected, sick with the disease and die. It is not inconceivable that the reservoir hosts of the infection are domestic hens, which are bred at the same farms as ostriches, but do not get sick or tolerate the infection in a mild way (Bennett *et al*., 1992d) (for more details, see p. 806).

The diseases of domestic birds caused by various species of haemosporidians are considered in more detail in the corresponding essays on species in the Systematic Section.

THE IMPACT OF HAEMOSPORIDIANS ON WILD BIRDS

The information on the pathogenicity of haemosporidians accumulated to the present is almost completely based on the results of laboratory experiments with domesticated birds (canaries, chickens, ducklings, pigeons, turkey poults). The direct extension of these data on free-living hosts is impossible. Wild birds and their parasites passed a long period of their co-evolution and mutual adaptation. The interaction of various factors (genetic and immunologic status, age, food resources, stresses, availability of shelters, etc.) may have an unexpected influence on the development of infection in wildlife. Under natural conditions, the animals are involved in complicated competitive interrelations, which determine the principal differences of the status of similar individuals leading an active life in the natural environment and those kept in captivity. In the latter case, the protection from predators and infections is guaranteed; they are provided with abundance of water, food,

etc. Thus, the parasites, which seem neutral for the animals kept in captivity, may be the reason of weakening or even illness, when the animals are 'at home.' Analysis of the data available allows us to state that the representatives of all haemosporidian groups are most likely pathogenic for their free-living hosts. Nevertheless, the mechanism of influence of infections on the physiology, ecology, and behaviour of birds in the natural conditions has not yet been studied well enough. Let us discuss the available data in more detail.

Haemosporidioses of wild birds in zoos and aviaries

One can quite frequently find information about the illnesses and even deaths of birds from suspected cause of haemosporidians in the annual reports from well organized zoos worldwide. Due to many reasons, most of these reports present no convincing evidence that the haemosporidians are precisely the main reason of the death of birds. However, some haemosporidioses are well studied and thoroughly documented in the zoos and there is no doubt that they cause economical losses (Griner, 1974; Cranfield *et al*., 1990).

Haemosporidioses in the zoos are characterized by the following main features. First, exotic birds imported from territories where there is normally no haemosporidian parasites transmission or they are presented with other groups of haemosporidians that cause illnesses in the zoos, suffer most of all. In other words, the birds not adapted evolutionarily and physiologically to the local species of haemosporidians become infected, when they appear in the nidi of their transmission. Second, malaria is the main haemosporidiosis in zoos. This is accounted for by the worldwide distribution of malaria parasites and the wide range of their vertebrate hosts. In the zoos, there are often vectors (blood-sucking mosquitoes belonging to the Culicidae) and donors of malaria parasites (usually small wild passerines). Favourable conditions for outbreaks are thus created, when susceptible birds not adapted to the parasites appearing in the local nidi of malaria. The range of vertebrate hosts of haemoproteids and leucocytozoids is significantly less than for malaria parasites, while some of their vectors (hippoboscid flies, simuliid flies) are less frequent in zoos than mosquitoes. As a result, haemoproteosis and leucocytozoonosis are recorded in zoos much less frequently than malaria. Let us consider some examples of bird haemosporidioses in zoos.

In 1964, four keas *Nestor notabilis* (order Psittaciformes) were put into the Malaysian National Zoo in Kuala Lumpur. The birds were caught in New Zealand, where, apart from minor exceptions, there are no haemosporidians in the local fauna. There were numerous blood-sucking mosquitoes in the zoo and the keas were not protected from them. Three weeks after the keas were put in the zoo, all four of them had died. Each of the birds was infected at least by two species of *Plasmodium* (Bennett *et al*., 1993e).

Severe illnesses and even devastating outbreaks of malaria among penguins (*Aptenodytes patagonica*, *Spheniscus demersus*, *S. humboldti*, *S. magellanicus,* etc.), whose agents are *Plasmodium relictum* and *P. elongatum*, were recorded in many zoos of North America, Europe, and Asia (Scott, 1927; Rodhain, 1939; Huff and Shiroishi, 1962; Griner and Sheridan, 1967; Fleischman *et al*., 1968; Herman *et al*., 1968; Sladen *et al*., 1979; Stoskopf and Beier, 1979; Beier and Stoskopf, 1980; Beier and Trpis, 1981; Bak *et al*., 1984; Fix *et al*., 1988; Cranfield *et al*., 1990; Graczyk *et al*., 1994b). Both species of malaria parasites have a wide range of vertebrate hosts and vast ranges of distribution. The evolution and habitat of the major number of penguin species are related to the regions of cold climate with dominating windy weather. In these conditions, there is usually no transmission of bird malaria. Thus, the penguins are not adapted to malaria, but they are easily infected and

severe disease develops. All this leads to the situation when insufficiently prepared programs to establish artificial colonies or to keep small groups of these birds in zoos with local nidi of malaria transmission are accompanied with severe diseases and high mortality rate. Let us illustrate this with some examples.

In 1986, a large group of penguins *Spheniscus magellanicus* was caught in one of the islands in the south of Chile. Some of these birds ware transported to Japan, where they did not fall ill. The major part of the penguins put in the zoos of North America died of malaria caused by *Plasmodium relictum*, which was recorded in detail in the Blank Park Zoo in Des Moines (Iowa, USA) (Fix *et al*., 1988).

The illness and death of penguins *Spheniscus demersus* caused by *Plasmodium relictum* and *P. elongatum* in the Baltimore Zoo (Maryland, USA) have been recorded regularly from the time when this colony was established in 1967. As a result, the zoo had to spend additional funds to maintain this colony of *S. demersus,* largest in the USA (Cranfield *et al*., 1990). The source of infection is wild passerine birds living free in the zoo (*Cardinalis cardinalis*, *Melospiza melodia*, *Toxostoma rufum*, *Turdus migratorius*, and others), while the vectors are the mosquitoes *Culex pipiens* and *C. restuans* (Beier and Stoskopf, 1980).

As already mentioned, due to a narrower specificity of haemoproteids to their vertebrate hosts in comparison to *Plasmodium* spp., the probability is low that the former parasites from the local fauna (most frequently passerines are the source of infection) would complete their development in birds kept in zoos (many of the latter belong to the orders of nonpasserine birds). However, it is not inconceivable that the inhabitants of the zoos can gain haemoproteids not typical for them, which develop only up to the stage of exoerythrocytic meronts without forming gametocytes. The cases of mortality among psittaciform and other birds, when meronts are found in their skeletal muscles and (or) in the heart, but no parasitemia is observed, illustrate this hypothesis (Borst and Zwart, 1972; Fowler and Forbes, 1972; Markus, 1972; Smith, 1972; Walker and Garnham, 1972; Garnham, 1973; Gardiner *et al*., 1984). Formerly, these meronts were usually described as 'aberrant *Leucocytozoon* infection.' After megalomeronts were discovered in *Haemoproteus handai* and *H. mansoni* (Miltgen *et al*., 1981; Atkinson *et al*., 1988b), it became clear, however, that they better suit the description of *Haemoproteus* spp. If the hypothesis of birds' death in the zoos associated with the development of *Haemoproteus* spp. megalomeronts is to be confirmed, the veterinary importance of haemoproteosis requires significant reconsideration. In relation to this it should be emphasized that new findings appeared about the death of dove *Gallicolumba luzonica* in the aviaries in South Africa (Earlé *et al*., 1993). It is likely that the death was caused by megalomeronts of *H. columbae* developing in large numbers in the skeletal muscles, in the muscle of the heart, and in the lungs and some other organs. See also Appendix 2 (p. 868) for additional information.

The examples considered, or at least some of them, illustrate the role of haemosporidians as a factor stabilizing ecosystems by means of hampering the penetration of alien organisms in certain ecosystems.

Examples of severe pathology and death of wild birds

There is information in the literature about dying and dead wild birds with a clearly pronounced pathology, which confirms the conclusions of laboratory investigations about the potential pathogenicity of haemosporidians. It is not by chance that the number of works devoted to this problem is a minor part of the total publications on haemosporidians in wild

birds. A catch of a severely ill bird in nature is a great luck, because weak individuals are rapidly eliminated by predators (Holmes, 1982). The discovery of sick wild birds is unusual. That is why the few works about the pathology caused by haemosporidians in wild birds, which became the property of science, are to a certain degree the reflection of human abilities shown in the 'competition' with a keen network of predators for their 'prey.' It is not by chance that most discoveries of sick birds occurred in human-inhabited localities, where there is the transmission of infection, the press of predators is decreased, while the level of culture of the population and investigators is enough not only to register the ill birds, but also to provide a time-consuming procedure of processing and understanding the material with a final result of publishing it in the scientific journals.

Seven cases of severe illness and deaths of young and adult wild birds were described in the USA, the main reason for which was malaria, most likely caused by *Plasmodium cathemerium* (Stone *et al*., 1971). Weak *Corvus brachyrhynchos*, *Passer domesticus*, *Quiscalus quiscula*, and *Turdus migratorius* that could not fly or dead ones were found on the ground and investigated in the laboratory. The intensity of parasitemia in various individuals varied from 28 to 74% of erythrocytes. Numerous phanerozoites were found in the brain of the majority of the birds, which was the main reason of severe neurological symptoms.

Garnham (1966) described a case of severe infection of *Plasmodium* sp. in a dying *Tyto alba*, which was found in San Spirito Island in the Pacific Ocean during World War II. Manwell (1951a) recorded a similar example of acute malaria caused by *P. cathemerium* in the Colorado Mountains.

The examples of illnesses associated with infection by *Haemoproteus* and *Leucocytozoon* spp. are also available in the literature.

Haemoproteus sp. causes seasonal lethal myopathy in *Strepera graculina* in Australia (Hartley, 1992). Numerous megalomeronts develop in skeletal, cardiac, and gizzard musculature. Gametocytes appear in the blood only in birds who survived acute myopathy.

A sick, weak, wild turkey was caught by hand in Florida (USA) and soon died in the laboratory (Atkinson and Forrester, 1987). Its skeletal musculature was, in a literal sense, larded with megalomeronts of *Haemoproteus mansoni* (*=H. meleagridis*), which became one of the reasons of its death.

A young weak *Delichon urbica* with the indications of heavy anaemia and ruffled plumage was found on the ground in Zambia (Peirce, 1984a). A high *Haemoproteus* sp. parasitemia was recorded in this bird. About 40% of erythrocytes including young ones were parasitized. By the way, Bennett with co-authors (Bennett *et al*., 1993e) described a case where an adult ringed male *Carpodacus purpureus* infected with *H. coatneyi* with an intensity of 60 to 80% of erythrocytes was repeatedly caught during three years. This case is a rare exception from the rule. We could not distinguish such a high intensity of parasitemia in the Palearctic in any of over 14,000 specimens of investigated wild birds, who led an active life in the nature. Usually, the intensity of parasitemia did not exceed 10% in any of the caught and observed birds in the spring–summer season and generally it is much less. It is interesting to note that one male *Parus major* heavily infected with *Haemoproteus majoris* was recorded in the north of Lithuania. This bird was caught by a domestic cat (Valkiūnas, 1998). In this case the intensity of parasitemia exceeded 30% of erythrocytes, which is significantly more than was ever recorded in this bird species caught by mist nets at the study site. Experimental observations indicate that heavy infections of *H. lophortyx* lead to emaciation, weakening, and may become the reason of death for *Lophortyx californica* (O'Roke, 1930b). A high intensity of *Haemoproteus* and *Leucocytozoon* spp.

parasitemia was recorded in weak *Columba livia*, *Streptopelia senegalensis*, and *Chrysococcyx caprius*. Some of them were found in a lethargic condition and could be caught by hand (Oosthuizen and Markus, 1968; Markus and Oosthuizen, 1972). Interestingly, the experience of rehabilitation of traumatized falconiform birds in captivity indicates that the birds infected with *Haemoproteus* sp. recover slower than not infected ones (Olsen and Gaunt, 1985).

Leucocytozoonosis caused by *Leucocytozoon simondi* is considered one of the reasons of death of immature *Cygnus olor* in Sweden (Mörner and Wahlström, 1983). It is important to note that it has been proved experimentally that anseriform wild birds suffer from the leucocytozoonosis. The sporozoite-induced infection of *L. simondi* leads to the death of immature wild anseriform birds (*Anas rubripes, A. platyrhynchos)* (Khan and Fallis, 1968).

The clinical signs of the disease and severe emaciation caused by *Leucocytozoon* and *Haemoproteus* spp. infections were found in one specimen of *Turtur chalcospilos* in Zambia (Peirce, 1984a). The weight of the sick bird was less than the average weight for this species by approximately 25%.

A young wild *Anas platyrhynchos* was found in field condition in the Ontario province (Canada) and examined histologically (Karstad, 1965). The bird was weak and emaciated with clearly expressed neurological symptoms and anaemia. Numerous megalomeronts were found in the brain, while gametocytes of *Leucocytozoon simondi* were found in the blood. From 300 to 400 megalomeronts with a diameter of 160 to 190 μm were found in the histological sections of the brain with an area of 1 cm^2. Blockage of blood vessels and haemorrhages in place of rupture of megalomeronts were frequently observed. There is no doubt that the leucocytozoonosis was the reason for the sickness and weakening of the bird, which became completely noncompetitive.

The examples of weakening, illness, and death of wild birds from severe haemosporidioses considered do not allow us to support the viewpoint of Bennett with co-authors (Bennett *et al*., 1993e), who think that the mortality caused by haemosporidians is observed almost totally in domesticated birds or those kept in unfamiliar conditions. From our point of view, these scholars hold to the very strict approach to the assessment of the available zoological data about the pathogenicity of haemosporidians for wild birds, considering them not sufficient enough to state that the death of birds was caused precisely due to haemosporidioses.

Epizooties of haemosporidioses in wild birds in nature

Information on outbreaks in wild birds caused supposedly by haemosporidians is not rare in the literature. However, the convincingly proved cases of epizooties caused by haemosporidians in wildlife are not numerous though rather impressive. Let us consider some examples.

Epizooties caused by *Leucocytozoon simondi* among immature *Branta canadensis* are described at the Seney National Wildlife Refuge in the Michigan Lake (USA) (Herman *et al*., 1975). *Branta canadensis* breeding at the study site disappeared in 1929. The population was restored in 1936 by introduction of 332 birds bred in captivity. After six years, more than 400 individuals lived in the refuge. Approximately half of them were migratory and returned for breeding. In 1956 there were about 3000 birds in the population. The mass death rate of goslings was recorded soon after the beginning of the work to restore the population. Epidemiological investigations showed that since 1960 epizooties caused by

L. simondi occurred among the immature birds approximately every four years. The highest mortality rate was recorded in spring, which coincides with the appearance of a large number of highly susceptible goslings and with the increase of density of blood-sucking simuliid flies, the vectors of infection. It is likely that the epizooties in the case considered were caused by the appearance of a large group of genetically monomorphic birds bred in captivity in the region endemic for leucocytozoonosis. This example indicates that the account of haemosporidioses is important in the implementation of programs of wild bird reintroduction into the regions of their previous habitat.

Garnham (1950) described an outbreak caused by *Leucocytozoon* sp. in a colony of weaver finches *Ploceus jacksoni* located near his laboratory in Kenya. Chronic parasitemia was found almost in each adult individual of the colony. Young birds (about three weeks of age) were regularly found dead under the trees. A high parasitemia of *Leucocytozoon* sp. was recorded in dying or dead fledglings, while exoerythrocytic meronts were found in their enlarged spleen. The parasitemia passed into the chronic stage in those young birds who survived the primary attack of the parasites.

Epizooties caused by *Plasmodium* and *Fallisia* spp. accompanied by high mortality rate among nestlings are described for ciconiiform birds in Venezuela (Gabaldon and Ulloa, 1980, 1985). The parasites were found in 23 species of birds. The transmission of infection occurs year round, but most actively takes place during the rain season (from September to December). During this season, the birds' breed and offspring appear. In total, the haemosporidians were found in 5.8% of adult birds and in 53.6% of nestlings by the method of microscopy of blood smears. As the nestlings grow older, the prevalence of infection increases from 36.3 to 74.6%. Young birds are often found dying under the trees. Mixed infection by several species of the parasites is common. The intensity of infection in young birds may reach 70% of erythrocytes and even more. The situation resembles holoendemic human malaria found in tropical Africa and in some other regions. When this takes place, the transmission of parasites occurs year round. The major part of adult individuals in the population are chronic infection carriers without clearly pronounced clinical symptoms, while a high mortality rate is recorded among highly susceptible nonimmune young individuals. In this case, the parasites play an active role in the control of the population. It is noteworthy that migrating birds of the Nearctic come to the wintering areas in South America in September–December, that is during the period of the activation of malaria transmission in Venezuela. The long term stay of nonimmune Nearctic migrants, the major part of which are highly susceptible young specimens, in the active nidi of infection at wintering sites cannot pass without traces. However, there is still no convincing information about the fate of Holarctic migrants, when they get into the holoendemic malaria nidi during wintering.

The introduction of *Plasmodium relictum* and its active vector *Culex quinquefasciatus* into the Hawaiian Islands is an example of dramatic impact of haemosporidians on the number of population, ranges of distribution, and even on the survival of many native species of birds (Warner, 1968; van Riper *et al*., 1986; van Riper, 1991). This case illustrates the dangerous result of human activity associated with the penetration of parasites into ecosystems new for them. Haemosporidians were, probably, occasionally transported into the Hawaiian Islands by migrating birds, but lack of vectors prevented the spreading of infection in the endemic fauna. *Plasmodium relictum* and its vector were accidentally introduced by whale hunting and other ships after the islands were discovered in the second half of the 18th century. As the mosquitoes were spreading in the islands inhabiting the moist and warm lowlands at a height up to 1000 m over the sea level, malaria also started

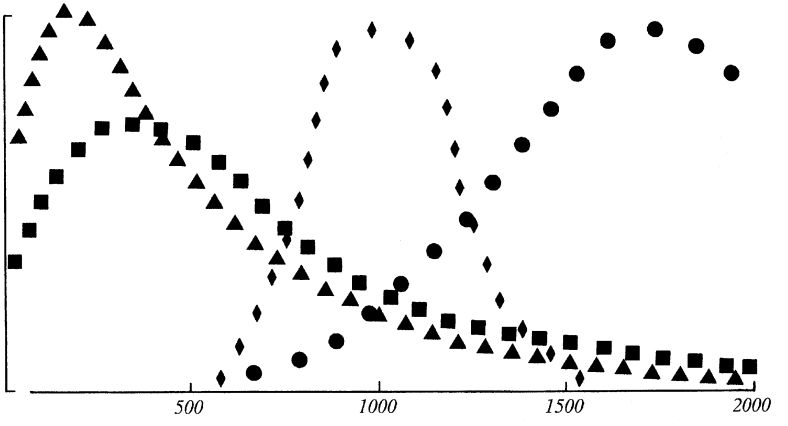

Figure 32 Relative abundance of introduced (■) and native (●) species of birds as well as malaria parasites (♦) and their vectors (▲) at different altitudes on Mauna Loa in the Hawaiian Islands: The abscissa is the altitude above sea level (m) and the ordinate is the relative value of the parameter under consideration (modified from van Riper *et al*., 1982).

to spread. Endemic species of birds, whose ranges of distribution coincided with the area of parasite transmission, died out or were forced out to the territories located above 1000 m, where *P. relictum* and its vector did not manage to penetrate (Fig. 32). Since the introduction of the infection to the Hawaiian Islands, which was new for the local fauna, more than half of the endemic bird species, and primarily the Drepanididae species, died out. It is important to note that it happened earlier than the places of their habitat disappeared or changed significantly under the impact of human activity. Among the dangerous transmissive diseases introduced to the islands, the avian pox virus, which, no doubt, plays an important role in the elimination of many species of endemic avifauna, should be also mentioned. The dramatic impact of malaria on the distribution of birds on the Hawaiian Islands was proved experimentally by moving endemic birds from highlands to lowlands. Their exposure in the zone of the active transmission of *P. relictum* during several days led to the development of lethal malaria (van Riper *et al*., 1986). Interestingly, that the introduced bird species, which are more resistant to malaria, successfully got acclimatized in the area of the distribution of *P. relictum* and its vectors in the lowlands of the islands, where there is no strong competition with the endemic avifaune (Fig. 32).

The results of the observations carried out in recent years (van Riper, 1991) indicate that endemic Hawaiian species of birds gradually acquire resistance to *Plasmodium relictum* and slowly start secondary penetration into the territories previously 'conquered' by malaria. Moreover, the birds elaborate new behaviour adjustments leading to the decrease of the probability of malaria infection. For example, *Himatione sanguinea* and *Vestiaria coccinea* perform regular daily migrations to spend the night in the highlands. This decreases the probability of their contact with the vector whose activity manifests itself after 8 PM. In addition, during the night sleep, the birds mask the most vulnerable parts of the body by plumage, which to a certain degree decreases the probability of infection.

The examples considered are interesting from the point of view of the role of parasites in the evolution of the birds' behaviour and also from the standpoint of the certain realization of the geographical distribution of birds. From this point of view, an original hypothesis is

worth mentioning, namely, that the current distribution of certain bird species in Africa may be understood on the basis of the zoogeography of their diseases (Markus, 1974).

In most examples considered, the parasite factor influences the mortality rate of the birds without a clearly expressed dependence on the extreme conditions of the environment. In this case, the participation of haemosporidians in the control of the host population is clearly manifested. In the wild, such antagonistic relations between the populations of haemosporidians and their hosts are rarely recorded, and thus the assessment of the role of the parasite load on free-living hosts is not an easy task because it manifests itself by means of other biotic and abiotic factors. In this case, a problem arises in estimating how much the parasite weakens and makes its host vulnerable compared to noninfected individuals.

Influence of haemosporidians on the competitiveness of wild birds in nature

Competitiveness is one of the fundamental properties of living organisms, which primarily manifests itself in the ability to survive in extreme conditions and leave viable offspring. It can be regarded as one of the main components of the definition of the 'living organisms.' In the last decade, new facts appeared due to the widening of long-term research of free-living populations, which indicate that the competitiveness of birds infected with haemosporidians decreases compared to those noninfected. Let us consider several examples.

Field observations indicate that reproductive activity decreases in males of *Centrocercus urophasianus* infected with *Plasmodium pedioecetae*. The birds infected with malaria parasites rarely attend leks which is correlated with the reproductive success. In addition, the copulation by infected males is less successful and more frequently occurs with young females and takes place in the less favourable (later) part of the reproductive period (Johnson and Boyce, 1991).

Infection by *Leucocytozoon danilewskyi* (=*L. ziemanni*) leads to the decrease in egg numbers in clutches of *Aegolius funereus* in those years, when the number of rodents they eat decreases (Korpimäki *et al*., 1993).

Males of *Parus major* spending more energy during the period of reproduction have greater indices of intensity of infection with *Leucocytozoon* spp. (Norris *et al*., 1994). This was tested experimentally by manipulation of the number of eggs in the nests. It is most likely that the increase in expending energy weakens the immune abilities of the organism, which leads to the enhancement of the recrudescence of chronic infections and thus to increase of the parasitemia. The ecological consequences of this phenomenon for birds have not been specifically studied in the wild.

It is important to note that the influence of haemosporidians on wild birds is not always detected even in the source of well organized populational investigations (Ashford *et al*., 1990, 1991; Davidar and Morton, 1993; Korpimäki *et al*., 1993). This problem is much more complicated than it looks at first, and this can partly explain quite contradictory results of investigations into relationships between haemosporidians and some other parasites on the one hand and free-living avian hosts on the other hand (summarized by Møller, 1997). The pathogenicity of the majority of species of bird haemosporidians is poorly investigated. Different parasite species and their strains are characterized by different virulence, which is well known for *Plasmodium* spp., but this phenomenon is still insufficiently investigated and rarely discussed in ecological and evolutionary biology studies. However, at present, it is obvious that one of the main problems in the estimation of host–parasite relationships in wildlife is that the application of a combination of only

such methods as the microscopy of stained blood films obtained from naturally infected birds and the analysis of recaptures of infected and noninfected ringed birds, combined with their correlations with parameters of bird life histories, are not enough for understanding the influence of parasites on their free-living hosts. This is mainly due to the fact that only bird specimens with low chronic (relatively benign) infections are available using traditional methods of bird sampling and specimens with an acute stage of infection are usually undersampled (see p. 140 for more details). Usually, additional experimental investigations and more 'precise' field observations are needed to solve this problem (Valkiūnas, 1993a, 1996, 1998). It is also important to note that from the point of view of parasitology, methodological errors are being made in certain research works even on the level of bird populations when preparing the parasitological facts for the analysis. Some scholars appreciated the advantages of using the data on bird's infection with blood parasites when solving the problems of ecology and evolutionary biology, but underestimated the complexity of haemosporidians biology and, thus, were frequently 'trapped.' This problem is considered separately (see p. 181).

With rare exceptions, there is almost no information in the literature about the influence of haemosporidians on the behaviour of wild birds. This is accounted for by the difficulties of observing birds and by the difficulties of controlling dynamic infections in the animals actively moving in the wild. It is methodologically easier to carry out investigations using lizards and their malaria parasites as laboratory test animals. The *Sceloporus occidentalis* lizards infected with *Plasmodium mexicanum* more frequently obtain a subordinate social status rather than noninfected ones (Schall *et al*., 1982; Schall, 1983; Schall and Dearing, 1987). In particular, this manifests itself in their losses during social conflicts and in the fact that they inhabit worse territories. In addition, infected lizards are characterized by the changes of the process of lipids accumulation, decrease in the size of ovaries and egg production, decrease in hemoglobin level, and increase of the mortality rate.

In the last two decades, new facts appeared and new hypotheses were put forward about the influence of acute and chronic infections by haemosporidians on the behaviour of wild birds associated with the decrease of their competitiveness. Let us discuss them in more detail because they are important from the theoretical point of view to find the methodological approaches to the solution of the problems considered.

Influence of haemoproteids on young passerine birds

The data of the long-term field investigations and the results of observations of experimental young small passerines infected and noninfected with *Haemoproteus* spp. indicate that the parasites have a pathogenic impact on birds (Valkiūnas, 1991, 1993a). In this case, the peculiarities of host–parasite relations manifest themselves only when the results of field observations and the experiments carried out with birds and parasites of the same population are compared. Let us analyze this case in more detail.

The work was carried out at the Biological station of the Zoological Institute, Russian Academy of Sciences on the Curonian Spit in the Baltic Sea. *Fringilla coelebs,* the most common and well-studied bird of the forest zone of Europe and *Haemoproteus fringillae,* its parasite, were used as models. The choice of these objects and the place for investigations was determined not only by wide distribution of haemoproteids in *F. coelebs* on the Curonian Spit (Valkiūnas, 1984b), but also by the fact that the ecology of the Curonian population of this bird had been well studied (Payevsky, 1971; Dolnik and Gavrilov, 1982; Dolnik and Payevsky, 1982; Dolnik and Yablonkevich, 1982; Ilyina, 1982a, 1982b;

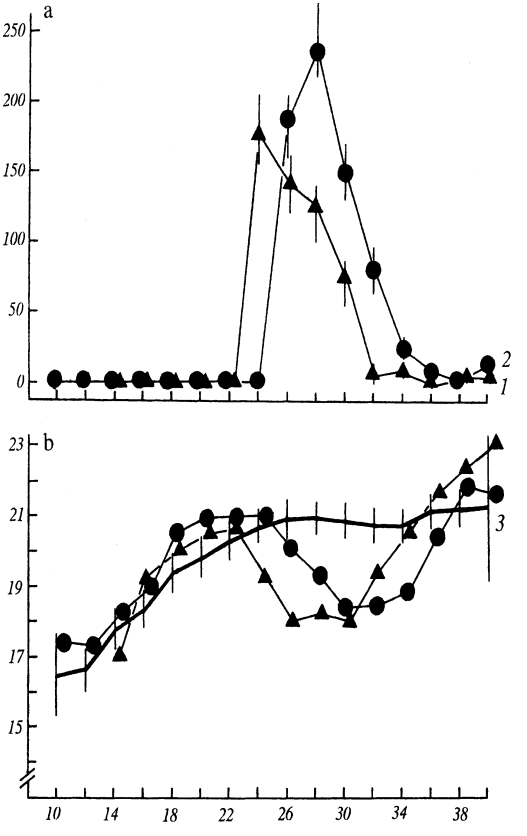

Figure 33 Parasitemia (*a*) and body mass (*b*) changes in two *Fringilla coelebs* nestlings infected (*1*, *2*) with *Haemoproteus fringillae* and in a group ($n = 29$) of noninfected (*3*) *F. coelebs* nestlings raised by hand:
The abscissa is the birds' age in days and the ordinate: *a* – intensity of parasitemia, number of parasites per 1000 erythrocytes, and *b* – body mass (g). Vertical lines are 95% confidence limits.

Payevsky, 1985; Sokolov, 1991). As a result, there was an excellent opportunity to use this vast information on the ecology of the vertebrate host to plan and carry out the experiments and analysis of the parasitological data obtained.

Thirty-three *Fringilla coelebs* nestlings aged from 6 to 12 days were taken from nests within a radius of 1 km from the field station and ringed. The nestlings were raised by hand according to the demands of each specimen. Thirty-one birds lived to the age of 40 days (the period of observations). Two nestlings died at the ages of 17 and 23 days. One of them choked while swallowing food. No haemosporidian parasites were found in the dead nestlings at autopsy. Gametocytes of *Haemoproteus fringillae* were found in the blood of two birds at the age of 23 and 25 days. No other blood parasites were recorded. No doubt the infection of *F. coelebs* occurred in the nests, because gametocytes appeared in the blood in the laboratory, where transmission of haemosporidians was excluded. When these birds were taken from the nests, their age was 10 and 12 days. It is impossible to determine the duration of the prepatent period of infection. According to the initial data it cannot be less than 13 and greater than 23 to 25 days.

Table 1 Reliability of differences between chaffinches infected and noninfected with *Haemoproteus fringillae* in demonstration of secret reaction after frightening on different days of parasitemia.

Days of parasitemia	Number of secret reactions per 10 frightenings during a day							
	First pair				Second pair			
	Noninfected	Infected	Criterion of reliability of differences, t_f	Differences	Noninfected	Infected	Criterion of reliability of differences, t_f	Differences
2	0	9	5.00	+++	1	8	2.90	++
3	1	8	2.90	++	1	9	3.47	++
4	1	7	2.42	+	0	7	3.14	++
5	1	3	0.56		2	6	1.40	
6	3	2	0.00		3	5	0.46	
7	2	4	0.48		1	2	0.00	
8	1	2	0.00		1	3	0.56	
10	0	0	0.00		0	1	0.00	
14	2	0	0.77		1	3	0.56	
16	1	2	0.00		0	0	0.00	

Note: The first and second pairs include infected birds. The dynamics of parasitemia in these birds are marked in Fig. 33 as '*1*' and '*2*,' respectively. Significant differences which correspond to 95, 99%, and higher probability are marked as +, ++, and +++, respectively.

Below, the characteristics of the parasitemia, behaviour, and certain peculiarities of the physiological state of infected and 29 noninfected (control) *F. coelebs* are given.

The parasitemia increased rapidly (Fig. 33). A large number of merozoites and young gametocytes were found in the blood already in the first day of the parasitemia. In the second day, the number of young gametocytes increased and mature gametocytes appeared, which were able to gametogenesis. The peak of the parasitemia was recorded on the second and fourth day after the registration of parasites in the blood. At this time, the intensity of infection reached 175 gametocytes per 1000 erythrocytes in one bird (the 95% confidence limit is 156 to 205), and 235 in the other (217 to 272). Later, the parasitemia decreased sharply. The increased number of gametocytes (more than 50 per 1000 erythrocytes) was observed in the blood of infected *F. coelebs* during eight days. After a lapse of this time, the intensity of the parasitemia decreased and by the end of the period of observations fluctuated within the limits of 1 to 35 gametocytes per 1000 erythrocytes.

No clinical sign of infection was recorded in the infected birds, which could be attributed to the symptoms of the disease in the usual sense of this term. Infected *F. coelebs* continued to eat actively and looked healthy, although there were clear changes in the mass of their body and behaviour.

From the age of ten days up to the appearance of gametocytes in the blood, the body mass of the infected and noninfected growing birds was increasing synchronously (Fig. 33). It is likely that the early exoerythrocytic development had no negative influence on the body mass of the growing *F. coelebs*. A decrease in the body mass of infected birds was observed during the peak of the parasitemia. The peak of parasitemia occurred

approximately two days ahead of the period of the maximum body weight decrease. After the decrease of parasitemia, the body mass of infected birds started to grow and rapidly reached the average values characteristic of noninfected coevals. The body mass decrease during the peak of parasitemia clearly indicated the changes in physiological state of the birds. It is important to note that the changes in the physiological state are not accompanied by clinical manifestations of the infection.

The changes in the behaviour of infected birds during the peak of parasitemia are manifested primarily in the changes of their reaction to frightening and in the tactics of search for food. Let us explain this. The peak of parasitemia was recorded in birds at the age of 24 to 30 days (Fig. 33). At this age the majority of noninfected birds were feeding by themselves and the birds flew quite well in a large cage. The *F. coelebs* raised by hand did not get used to people. When people approached the cage quickly, the birds showed anxiety and flew away. When infected birds were frightened during the peak of parasitemia, they showed a clearly expressed reaction to hide themselves. The results of testing this indication for two randomly chosen noninfected and two infected *F. coelebs* are presented in Table 1. The birds were frightened by the sudden approach of people to the cage with birds and (or) by means of its slight jogging. The significant differences in the demonstration of the reaction to hide themselves after being frightened between the infected and noninfected *F. coelebs* are observed within three days. Later the infected and noninfected specimens could not be distinguished by this indication.

The other characteristic feature of infected birds during the peak of parasitemia is the change in their feeding behaviour. Unlike noninfected specimens who were actively moving and feeding themselves in the cage, the infected ones preferred a sedentary posture, and, when being slightly irritated, demanded food from the people who fed them by hand or from birds of the same age who were sitting nearby. The infected birds were feeding willingly from the hand at the peak of parasitemia but avoided going down to the feeding-rack and, as a rule, were not feeding themselves. Unlike noninfected birds, the infected ones clearly displayed a decrease of locomotive activity and an increase in the calls with the aim of attracting the attention of bread-winners during two to three days of the parasitemia peak at the age of 24 to 30 days. Such behaviour is not characteristic of healthy experimental birds of the same age and of young birds in nature, where at this time the broods of *F. coelebs* start to break up, and the young birds gradually start an independent mode of life (Dolnik and Yablonkevich, 1982; Ilyina, 1982a). The changes in behaviour of infected birds is a sort of a temporary return to the behaviour of healthy nestlings at the age of 15 to 17 days; that is, their behaviour resembles the behaviour of the fledglings. Namely, during the peak of parasitemia, the infected birds are weakly mobile, they display a reaction to hide themselves when frightened, and prefer begging behaviour to independent feeding, i.e., they almost do not feed by themselves. These changes in the behaviour of the birds cannot be directly attributed to the signs of illness in the usual sense of this term.

The comparison of intensity of the parasitemia in the experimental birds and those caught in nature during the breeding period showed the following. Among the total 1018 young birds caught by mist nets and large stationary traps, 493 birds were infected with *H. fringillae*. All of them were investigated at daytime. The maximum intensity of infection never exceeded 30 to 40 gametocytes per 1000 erythrocytes. This index ranged from less than 1 to 20 parasites per 1000 erythrocytes in the majority of the captured young birds that corresponded to the period of the decrease of parasitemia in the experimental birds (Fig. 33). The lack of infected *F. coelebs* specimens with a heavy parasitemia (more than 50 gametocytes per 1000 erythrocytes) in the large number of captured infected birds

suggests that there is a threshold level of parasitemia in young birds leading an active life in the wild. Let us consider this situation in more detail. As shown experimentally, the primary parasitemia of *H. fringillae* develops with a clearly pronounced peak of parasitemia (Fig. 33). A similar dynamic of parasitemia is known for some other species of haemoproteids (Ahmed and Mohammed, 1978a; Atkinson, 1986). It should be emphasized that the intensity of parasitemia in two infected *F. coelebs* reached 175 (95% confidence limit is 156 to 205) and 235 (217 to 272) gametocytes per 1000 erythrocytes. Such high indices of infection intensity were not found in any of the 493 infected birds captured at the study site. A hypothesis was put forward on the basis of these data that intensively infected birds are undersampled by mist nets or stationary traps. The principle of bird catching by these methods is based on the active motion of birds. The absence of infected *F. coelebs* with the high level of parasitemia among the large group of captured specimens can be explained by making an assumption that they are inactive or weakly mobile unlike the healthy ones and, as a result of this, they are not captured by mist nets or stationary traps. The decrease of locomotive activity during the peak of parasitemia in *F. coelebs* infected with *H. fringillae* is clearly visible within several days in the experimental conditions. There are no grounds to exclude such influence of the parasite in the field conditions. If this is true, the rate of intensively infected birds among the captured ones should decrease, because they are not available for the mist nets or for the stationary traps.

This hypothesis was tested by comparison of intensity of parasitemia in young wild birds obtained by catching and shooting. In the vicinity of the Biological station, there were total 57 young *F. coelebs* shot. Thirty-six of these were infected with *H. fringillae*. The parasitemia in 33 birds fluctuated from less than 1 to 30 gametocytes per 1000 erythrocytes, while in 3 birds it was equal to 82 (95% confidence limit is 64 to 98), 88 (73 to 109), and 70 (55 to 87). The value of the index of intensity in these three birds, which were shot in the field, corresponds to that in the experimental birds during the peak of parasitemia (Fig. 33). The difference between the proportion of birds with an intensity of parasitemia of more than 50 gametocytes per 1000 erythrocytes in the samples of the captured ($N = 493$, $n = 0$) and shot ($N = 36$, $n = 3$) birds is significant ($P < 0.001$). These data indicate that parasitemia in birds living in the wild develops in the same way as in birds in cages, while *F. coelebs* at the peak of parasitemia are undersampled by the traditional methods of their catching, but can be obtained by shooting on the endemic territories. With regard to this, there are grounds to think that at the top of parasitemia, the young *F. coelebs* are lowering their locomotion activity and probably transferring effort on getting food to the bread-winners (parents) in the field conditions in a similar way as it takes place during the experiments in the cage.

The decrease of locomotive activity even for a short period of time in birds living in nature inevitably leads to losses in the competitiveness of the infected individuals compared to noninfected ones, which indicates the negative influence of the infection on birds. It is noteworthy that after the age of 30 days, the broods of *F. coelebs* break up in the wild, and young birds start an independent mode of life (Dolnik and Yablonkevich, 1982; Ilyina, 1982a; Sokolov, 1982). Birds older than 30 days cannot rely on parents. As a result, survival of even the short term peak of parasitemia can become a problem for them. As already mentioned, signs of illness are not found in the infected birds in the caged situation, and both experimental birds successfully survived the peak of parasitemia. The fate of infected birds after the break up of broods in nature is probably not so successful, and some of the birds perish. It is likely that predators play a large role in this process, which is confirmed by the data of the birds shot.

The results of the investigation favour the concept about the negative influence of *H. fringillae* infection on *F. coelebs* in nature. The locomotive activity of birds decreases for several days during the peak of parasitemia. As a result, intensively infected *F. coelebs* are not taken into account by traditional methods of catching them based on the active motion of birds, but can be obtained by shooting. The mobility restriction of *F. coelebs* during the peak of parasitemia on the one hand alleviates the survival of the acute stage of infection, while on the other hand makes the birds more vulnerable for predators, unfavourable climate, feeding, and other factors which leads to the decrease of competitiveness in natural conditions and the increase of the probability of elimination of the heavily infected specimens. In experimental conditions (in the cage), the infected birds successfully survive the peak of parasitemia.

The facts obtained can be theoretically explained in the following way. It is known that the energy for birds' existence is predetermined physiologically. Its value is the same for the birds in the cage and in the wild. In nature, this energy is spent on the maintenance of the vital functions for the existence of the individual. In the cage, where a lesser amount of energy is needed to maintain existence, the rest of the energy is spent by means of spontaneous locomotion activity (Dolnik and Gavrilov, 1982). The parasites transfer their metabolic functions on the host enhancing its main metabolism and, thus, spending part of its energy for existence. In the conditions of the cage, infected birds may compensate the losses of the energy needed for existence by eliminating the efforts to find food, to defend themselves from predators, decreasing locomotive activity, etc. Thus, in the cage, infection can develop in the form of asymptomatic presence of parasites without expressed signs of the disease. In nature, the bird cannot spend less energy to maintain its existence without loss of competitiveness. The host bird, accepting the metabolic functions of the parasite, inevitably spends part of its energy on the parasite, which inevitably leads to the loss of competitiveness during the acute stage of infection. Concerning this, the observations on canaries during the peak of *Plasmodium relictum* parasitemia are of particular interest (Hayworth *et al*., 1987). It was shown that during the period of maximum parasitemia, the ability for thermoregulation and oxygen consumption decreases in experimentally infected birds. The impact of haemosporidian infections on birds during the period of thermal stress and other extreme situations (sharp cooling, rains, etc.) is likely to be underestimated.

Influence of haemoproteids on the accumulation of migratory fat in small passerine birds

The results of investigation on the Curonian Spit in the Baltic Sea with a large number of small passerine birds during their seasonal migration indicate that high parasitemia of *Haemoproteus* spp. is associated with the decrease of accumulation of migratory fat in the birds (Valkiūnas, 1983, 1993a). The fatness of the birds during migration was determined visually using a semiquantitative method by estimating the level of fat filling the underskin fat depots (Vinogradova *et al*., 1976). It is known that underskin fat makes up for about a half of all the amount of migratory fat in the body of migrating birds. Moreover, the fat locates mainly on apteriums. These phenomena are often used by ornithologists for live visual estimation of the level of migratory fatness. The level was divided into several steps with the following limits: 'no-fat': the hypodermic fat is not found, 'low-fat': the fat occupies less than half of the depots, 'medium-fat': the fat occupies more than half of the depots, 'high-fat': the fat occupies all the depots.

The data on infection of all of the bird species studied (families Hirundinidae, Motacillidae, Laniidae, Turdidae, Sylviidae, Muscicapidae, Emberizidae, Fringillidae) are

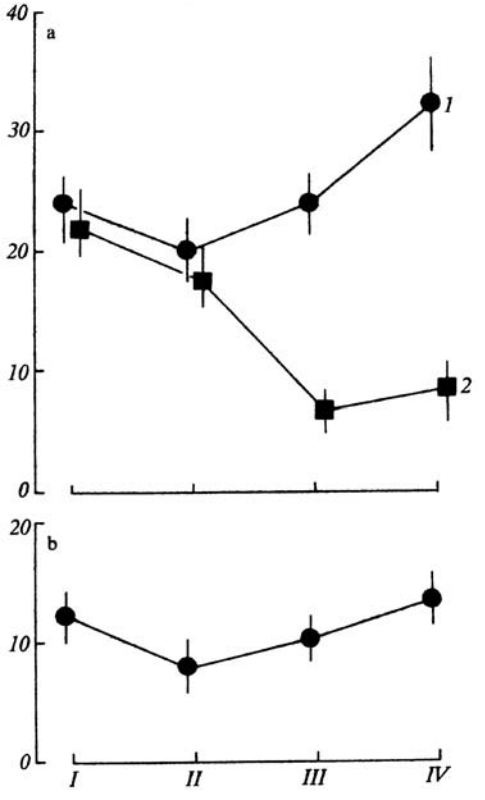

Fig. 34

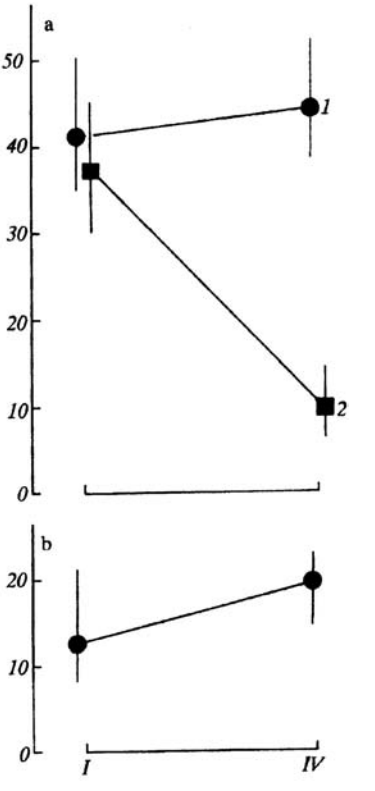

Fig. 35

Figure 34 Infection of birds of different level of fatness (*I–IV*) with haemoproteids at different intensity of parasitemia (*1*, *2*) in spring (*a*) and autumn (*b*):
Intensity of parasitemia: *1* – <20 gametocytes per 1000 erythrocytes, *2* – >20 gametocytes per 1000 erythrocytes. The abscissa is the level of fatness: *I* – 'no,' *II* – 'low,' *III* – 'medium,' *IV* – 'high,' and the ordinate is the number of infected birds, %. Vertical lines are 95% confidence limits.

Figure 35 Infection of sylviid birds of different levels of fatness with *Haemoproteus belopolskyi* at different intensity of parasitemia in spring and autumn (symbols are as in Fig. 34).

presented in Fig. 34. The proportions of infected birds with a different level of fatness do not differ statistically, when the parasitemia is low (less than 20 gametocytes per 1000 erythrocytes), while at high parasitemias (more than 20 gametocytes per 1000 erythrocytes), the proportions of infected birds with the degrees of fatness 'medium' and 'high' do significantly decrease. This indicates that there is a possibility to inhibit the accumulation of migratory fat in birds during the period of high parasitemia. It is noteworthy, that the intensity of parasitemia is always low during the autumnal migration (less than 10 to 15 gametocytes per 1000 erythrocytes, but is usually even less than 1 per 1000). In autumn, there are no statistically significant differences in the proportion of infected birds with a different level of fatness (Fig. 34).

Similar results are obtained in the investigation of birds only of the family Sylviidae infected with *Haemoproteus belopolskyi*. During the spring migration (in May), the share of intensively infected sylviids is significantly less in a group with the 'high' level of

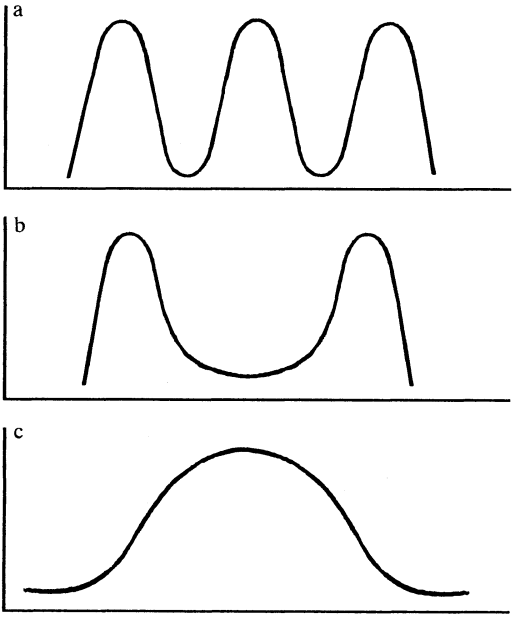

Figure 36 Diagrammatic representation of the possible relationships between migratory fat accumulation (*a*, *b*) and parasitemia of *Haemoproteus* spp. (*c*) during the spring migration of birds: *a* – normal dynamics of the level of migratory fat; *b* – dynamics of the level of migratory fat in heavily infected birds; *c* – dynamics of parasitemia of *Haemoproteus* spp. The abscissa is the calendar, and the ordinate is the relative value of parameters under consideration.

fatness than in a group with the 'no' level of fatness (Fig. 35). The proportions of infected specimens in these two groups of birds did not differ significantly at low parasitemia both in spring and autumn.

Thus, the data obtained indicate the negative impact of haemoproteids on migratory birds. It is likely, that when the intensity of parasitemia is high (more than 20 gametocytes per 1000 erythrocytes), there is an inhibition of migratory fat accumulation in birds in nature. It is likely that this results in the fact that the proportion of the birds with the 'high' level of fatness is significantly less than the share of the birds with the 'no' level of fatness at the high parasitemia (Figs. 34 and 35). In relation to this, it is noteworthy that infection with *Plasmodium mexicanum* negatively influences the metabolism of lipids in lizards *Sceloporus occidentalis* (Schall, 1983). The amount of fat in infected lizards decreases by 17 to 45% compared to noninfected ones.

The dependence of the two dynamic factors (parasitemia and accumulation of migratory fat) considered can be presented in the general form in a diagram shown in Fig. 36. Only fat birds are capable for a migration flight (Dolnik, 1975). They use the fat during migration. Scraggy birds make a stop on their way of migration and accumulate fat. Only after this they become capable for the next migratory flight. Each migrating bird makes several stops on the way, thus both 'scraggy' and 'fat' state are a norm for them (Fig. 36a). According to our data, heavy infections with *Haemoproteus* spp. (Fig. 36c) lead to the reduction of migratory fat accumulation (Fig. 36b). As a result, probably at high level of infection intensity, the share of fat birds becomes significantly less than at low levels of infection. The biological aspect of this fact has not been studied in detail yet. It is apparent,

however, that high parasitemia should have a negative impact on migrants, because migratory fat is the main energetic material used during seasonal migrations. It is not inconceivable that heavily infected birds slow up during migration. As the parasitemia goes down, the ability of birds to accumulate fat and to continue the flight restores, but they fly to the breeding areas later (when the time for breeding is not so favourable). It is likely that this can partly explain the fact that a part of European birds are still at their wintering grounds, while the other specimens of the same species are already incubating eggs in their breeding areas (Earlé, 1993). This can also explain the well known fact that low parasitemias are more frequently recorded in migrating birds.

The reasons why the accumulation of migratory fat is slowed down during seasonal migrations have not been found yet. It is likely that at high levels of parasitemia migratory hyperphagia is broken either directly or through a system of intermediate steps. Anorexia is a common response of the organism to parasite infections (Symons, 1985). It is noteworthy that in spring we observed the accumulation of fat to the level of 'medium' and 'high' in each of 16 experimental birds (*Fringilla coelebs*, *Sylvia atricapilla*) kept in captivity with an intensity of infection reaching 40 to 80 gametocytes per 1000 erythrocytes in them. This stands for the fact that it is likely that high parasitemia slows down the accumulation of migratory fat only in nature by means of mechanisms, which are still not understood.

The influence of haemoproteids on the accumulation of migratory fat in birds was recorded only during spring migration (Figs. 34 and 35). Thus, from the point of view of the pressure of heavy *Haemoproteus* spp. infection, the spring migration should be less favourable for birds than the autumnal one. If we assume that the elimination of infected birds occurs during seasonal migrations, then it should be much more pronounced in spring. It is noteworthy in this relation, that the spring death rate of birds is significantly higher than the autumnal one (Shapoval and Shapoval, 1983; Payevsky, 1985). Thus, there is a distinct parallel between the dynamics of parasitemia and the peculiarities of the haemoproteids influence on migratory fat accumulation on the one hand, and natural death rate on the other hand. These data give grounds to put forward a hypothesis about the causative relationship between these two phenomena.

There are data in the literature that contradict the results of these investigations. Ashford (1971) compared the level of migratory fat in spring and the infection of two species of the Palearctic migrants with blood parasites and concluded that haemoproteids do not have a negative impact on the accumulation of the fat, and thus they are benign from this point of view. The author investigated the blood and determined the level of fatness in 65 specimens of birds. Twenty-seven of them were noninfected, while parasites were found in 28 birds with a low intensity reaching less than six parasites per 1000 erythrocytes. According to our data, such low intensity of infection does not yet display a notable influence on the accumulation of the fat. Only ten birds were infected more intensively (from six to 31 parasites per 1000 erythrocytes). Seven of these birds were related to the level of 'no-fat' and 'low-fat,' while only three were included in the groups with 'medium-fat' and 'high-fat' (the Ashford's classification of fatness is 1, 2, 3, 4, respectively). Thus, the tendency of the influence of haemosporidians on the accumulation of migratory fat can be seen in the work of R.W. Ashford. Nevertheless, the number of birds investigated was not large, and the data obtained are statistically insignificant ($P > 0.05$). This original work gave us the idea to collect larger samples to test the hypothesis.

Smith and Cox (1972) performed a similar work and did not find any negative influence of haemosporidians on the body mass of the Palearctic migrants. However, the intensity of parasitemia in their material was low (less than 1 parasite per 1000 erythrocytes). This

confirms the conclusion that low infections have no influence on the accumulation of fat in birds during migration.

Bennett with co-authors (Bennett *et al*., 1988) failed to obtain data confirming the influence of *Haemoproteus* and *Leucocytozoon* spp. infections on the body mass of small passerines caught and investigated in summer on Newfoundland Island. These authors summarized the results of long-term investigations in birds. A total of 3739 specimens of birds were examined. There is a distinct positive correlation between the body mass and the level of migratory fat (Dolnik, 1975). This correlation is observed, however, only during seasonal migrations, that is in spring and autumn. Thus, in the cited paper by Bennett and co-authors there are no data about the correlation of haemosporidian infection and the accumulation of migratory fat. It is noteworthy that according to the data available, the influence of haemoproteids on the body mass of *Fringilla coelebs* is complicated and manifests itself only within a short period of time (several days) during the peak of parasitemia (Fig. 33). No doubt this influence is diminished when the data of long-term observations are summarized. Bennett and co-authors (1988) noted in their paper that: 'There were no effects due to high intensity parasitemia for eight host species examined. Either parasitism does not cause loss of body mass, or the techniques used were too insensitive to separate effects of parasitism from other natural causes'. The latter explanation seems more convincible.

Peculiarities of the infection of irruptive species of passerine birds

In ornithology, the term 'irruption' means a mass invasion of birds on the territories that are not their potential wintering area. The general characteristics of this phenomenon is given according to Dolnik (1975) and Payevsky (1985). In this chapter, the term 'irruption' is used only in its ornithological interpretation. Irruptions are preceded by periods of sharp increase of the number of birds due to favourable conditions in their breeding areas. In unfavourable years, the birds fly away from this area and it is likely that many of them perish before the beginning of the next breeding season.

Irruption is a poorly studied phenomenon of ornithology and at the same time it is an unusual phenomenon from the point of view of parasitology, focusing special importance on the role of parasitic organisms in the regulation of the density of the host population (Anderson and May, 1978; Kennedy, 1975; Kontrimavičius, 1982; Hudson, 1998), however, there is also another opinion on the subject (Ashford, 1998). On the one hand, the study of infection of irruptive bird species with parasites gives additional information about the possible causes of the phenomenon, and on the other hand provides original information for a deeper understanding of the parasitism at the level of populations. Let us consider the data available on the infection of regular migrants (*Fringilla coelebs*, *F. montifringilla*, *Spinus spinus*, *Sylvia atricapilla*, *Parus major*) and irruptive species of birds (*Aegithalos caudatus*, *Nucifraga caryocatactes*) with blood parasites obtained on the Curonian Spit (Valkiūnas, 1987b, 1993a), noting that we analyze the data on infection of the young (subadultus) birds investigated during strict calendar periods of their autumnal migration (September–October). The main results of a microscopic examination of blood films are shown in Figs. 37 and 38. *Haemoproteus* and *Leucocytozoon* spp. are common parasites of regular migrants, while *Trypanosoma* spp. are found in these birds occasionally. An opposite situation is found in the irruptive bird species: *Haemoproteus* and *Leucocytozoon* spp. are not found, while the number of individuals infected with *Trypanosoma* spp. is large.

It is important to point out that in autumn the prevalence of infection with the groups of blood protists considered shows only a relative outline of the parasites' distribution. This

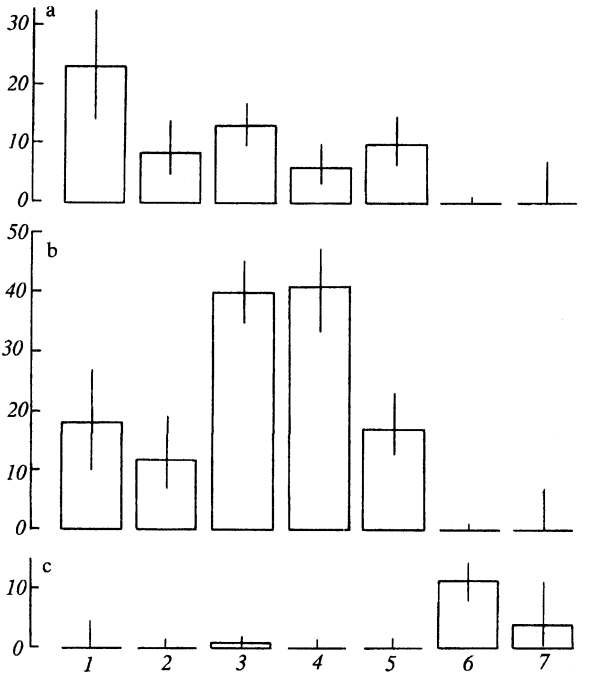

Figure 37 Infection of regular migrants (*1–5*) and irruptive species of birds (*6*, *7*) with blood protists:
1 – Sylvia atricapilla, *2 – Parus major*, *3 – Fringilla coelebs*, *4 – F. montifringilla*, *5 – Spinus spinus*, *6 – Aegithalos caudatus*, *7 – Nucifraga caryocatactes*; *a – Haemoproteus*, *b – Leucocytozoon*, and *c – Trypanosoma* spp. The ordinate is the prevalence of infection, %. Vertical lines are 95% confidence limits.

is associated, first, with the fact that haemoproteids and leucocytozoids develop like malaria infections with an increased parasitemia occurring during a warm period of the year. In autumn, infection becomes chronic or even latent, and gametocytes are rarely seen in the blood. As a result, the prevalence of infection appears underestimated. Second, the method of the microscopy of blood films for diagnostics of trypanosomes also gives underestimated results. The method of cultivation *in vitro* and molecular techniques provide an opportunity to find these parasites in a greater number of birds (Kirkpatrick and Lauer, 1985; Sehgal *et al.*, 2001). However, if we take into account that the work has been carried out with birds of the same age infected with the same or relative species of parasites found using the same method, the data could be considered comparable and as reflecting the relative outline of the parasites' distribution which is enough for this study.

The results of the research and the corresponding data from the literature allow us to put forward the following two hypotheses.

1. The sharp change of the parasitocenosis structure, which is usual for a certain group of birds, is one of the factors providing the growth of the number of birds during the years of birds' irruption.

As already mentioned, elimination of birds caused by various species of haemosporidians occurs in nature. Related to this, the analysis of the results of research allows us to consider that a sharp increase of the number of irruptive species of birds in the breeding

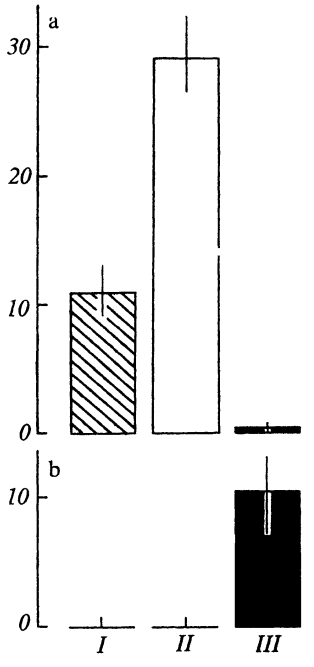

Figure 38 Infection of regular migrants (*a*) and irruptive species of birds (*b*) with blood protists (summarized data):
I – Haemoproteus, *II – Leucocytozoon*, and *III – Trypanosoma* spp. Other symbols are as in Fig. 37.

areas may be associated not only with the favourable food and climatic conditions, but also with a significant decrease of the pressure of certain groups of parasitic organisms (in our case these are haemoproteids and leucocytozoids). After the increase in the number of birds' population, favourable conditions are formed for the increase of population density of certain parasite groups, for example, trypanosomes. The normal structure of parasitocenosis destroys which probably weakens the regulatory parasite mechanisms facilitating the preservation of the number of irruptive species of birds at a high level, at least until the beginning of the autumnal irruptive movements.

2. Unusually high infection with trypanosomes is one of the factors influencing the unusual behaviour of irruptive species of birds and their mortality rate.

The data available allow us to make only hypothetical conclusions about the cause-and-effect relationships between unusually high prevalence of infection of birds with trypanosomes and the mechanisms of irruption. Trypanosomes are usually considered as parasites benign for birds (Baker, 1976). Nevertheless, some experimental investigations show that it is likely that trypanosomiasis does not pass into birds without effect. Enlargement of the spleen, lymphoid hyperplasia, and focal myocarditis are recorded in infected birds (Molyneux *et al*., 1983), which is reflected in the general physiological state of the host. With regard to this, the data obtained to a certain extent illustrate the opinion of the ornithologists according to which the irruptions of birds occur 'due to certain changes of their internal state, caused by high number of birds' (Dolnik, 1975). The problem of the influence of parasites on the ecology of the hosts has not been adequately studied. It is not inconceivable that increased infection with certain groups of parasites is one of the factors,

which directly or indirectly by means of a system of intermediate steps influence the behaviour of irruptive species and their mortality rate. According to the data obtained, the prevalence of infection of irruptive *Aegithalos caudatus* with trypanosomes is equal to 11.0% if diagnosed by the method of stained blood films microscopy (95% confidence limit is 8.3 to 14.6). It has already been discussed that the methods of cultivation give more precise results in the diagnostics. Their accuracy exceeds the accuracy of the former method at least by seven to ten times (Kučera, 1983; Kirkpatrick and Lauer, 1985). A simple calculation allows us to assume that, in fact, all investigated *A. caudatus* can be infected with trypanosomes in reality. Thus, irruptions from the point of view of parasitology can be regarded as the mechanism for the withdrawal of birds infected with trypanosomes from the breeding areas with the corresponding regulation of the density of the birds' and the parasites' population.

There is a theoretical interest to the study of these problems.

Peculiarities of the distribution of infected birds along flight waves during their autumnal migration

One of the surprising properties of the migration of birds is their wave-like or pulsing character. The number of birds flying over any point of observation is irregular in time. Days of intensive flights are intermittent with days of weak migration. Ornithologists have a consensus of opinion on the fact that the flight waves actually exist and they are not the artifacts of the observations methods. The wave-like character of migration in autumn is well pronounced on the Curonian Spit in the Baltic Sea and well studied there. The data of long term observations carried out on the Spit indicate that the number of waves and the time of their observation are relatively constant properties at the study site (Dolnik, 1975; Shumakov and Sokolov, 1982). There is no data in parasitology about the distribution of infected birds by flight waves across the entire period of a season. The data on infection of *Fringilla coelebs* with haemosporidians partly fill up this gap (Valkiūnas, 1989d, 1993a).

During the autumnal migration, leucocytozoids and haemoproteids were recorded in *F. coelebs* on the Curonian Spit. Malaria parasites were not found. Leucocytozoids are presented by *Leucocytozoon fringillinarum*, *L. dubreuili*, and *L. majoris* by the decrease in order of their occurrence, while haemoproteids are presented mainly by *Haemoproteus fringillae*. Gametocytes of haemoproteids and leucocytozoids, which could not be identified at a specific level, were also seen. The analysis of the distribution of birds infected with haemosporidians during the autumnal migration period allowed us to reveal the following patterns.

1. Birds infected with leucocytozoids and haemoproteids are uniformly distributed within each wave of migration (Fig. 39).

It is interesting to compare the results obtained with those of the ornithological investigations, according to which one of the characteristic features of the flight waves is the strict order from the point of view of bioenergetics. The birds taking part in the beginning and end of the wave of flight differ in the level of migratory fat, which as was already mentioned, is the main energetic material for the migrants. Fat birds with a high potential to migration predominate in the beginning of the wave, while scraggy birds predominate in the end of the wave (Dolnik, 1975; Shumakov and Sokolov, 1982). The uniform distribution of birds infected with leucocytozoids and haemoproteids within each wave of the flight (Fig. 39) indicates that there is no influence of these protists on the distribution of birds, or in other words, there is no influence on the process of migratory fat accumulation in birds during the

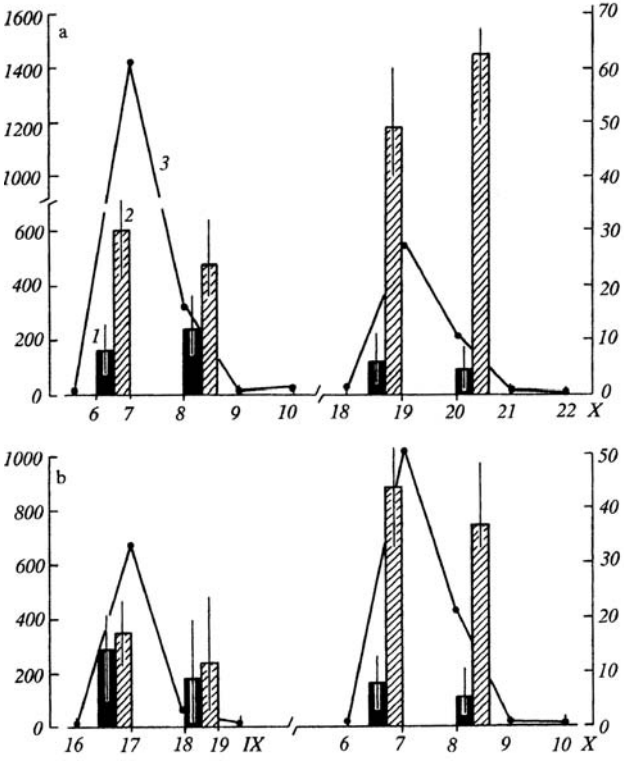

Figure 39 Infection of adult *Fringilla coelebs* with haemoproteids (*1*) and leucocytozoids (*2*) at the beginning and end of migratory waves (*3*) in 1978 (*a*) and 1979 (*b*):
The abscissa is the calendar (Arabic numerals indicate days, and Roman numerals indicate months) and the ordinate: on the left – the total number of caught birds; on the right – the prevalence of infection, %. Vertical lines are 95% confidence limits.

autumnal migrations. Otherwise, infected birds should gather at the end of the migratory wave, the main part of which is formed by birds with 'no' or 'low' level of fat (Dolnik, 1975).

It is likely that the reasons for this lie in the following. The prevalence and intensity of *F. coelebs* infection with haemoproteids are low in autumn. The prevalence of infection is 8.1%, while the intensity has never exceeded eight to ten parasites per 1000 erythrocytes. Thus, in the autumn, these protists cannot have any significant influence on the distribution of birds during migration or on the energetic structure of the waves of flight.

The prevalence of *F. coelebs* infection with leucocytozoids is high (Fig. 39). At the same time, the intensity of infection is always low in autumn (usually it is less than 1 parasite per 1000 erythrocytes). When infection by leucocytozoids is low, no significant differences in the prevalence of infection between the birds of different levels of fatness are found (Fig. 40). Thus, there are grounds to consider that low chronic infections of birds with leucocytozoids do not have any significant influence on the process of migratory fat accumulation in the birds. It is likely that this favours the uniform distribution of *F. coelebs* infected with leucocytozoids within each migratory wave.

2. The prevalence of *F. coelebs* infection with leucocytozoids in the late flight waves significantly increases compared with the early ones (Figs. 39 and 41).

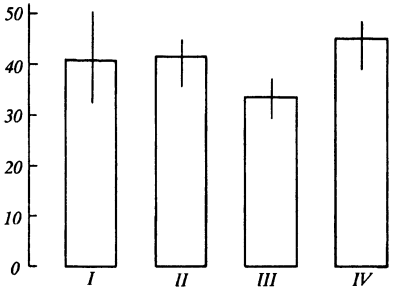

Figure 40 Infection of adult *Fringilla coelebs* of different level of fatness (*I–IV*) with leucocytozoids at intensity of parasitemia less than 1 gametocyte per 1000 erythrocytes during autumnal migration:
The ordinate is the number of infected birds, %. *I–IV* are levels of fatness: *I* – 'no,' *II* – 'low,' *III* – 'medium,' *IV* – 'high.' Vertical lines are 95% confidence limits.

The increase of the prevalence of *F. coelebs* infection with leucocytozoids during the autumnal migration on the Curonian Spit was recorded earlier (Valkiūnas, 1984b). The main reason for this phenomenon lies in the interaction of two factors. *Fringilla coelebs* of the northern populations (Karelian, Finnish, etc.) are infected with these parasites in greater prevalence than the southern ones (Baltic and Curonian) (Valkiūnas, 1984b). At the same time, there is a strict population sequence in the bird migration over one geographical point. The northern populations of *F. coelebs* migrate through the Curonian Spit later than the southern ones (Payevsky, 1985). Thus, the increase of *F. coelebs* prevalence of infection with leucocytozoids in the late waves of the flight is a result of participation in their formation of the greater number of birds with higher prevalence of *Leucocytozoon* infection from the northern populations.

3. The final flight wave, which takes place in the second half of October, consists mainly of the birds infected with leucocytozoids (Fig. 41).

The unusually high prevalence of bird infection with leucocytozoids during the last wave of migration in October is difficult to explain only from the standpoint that this wave consists mainly of the birds from the northern populations with high prevalence of infection. According to the observations of the ornithologists (Shumakov and Sokolov, 1982), the last flight wave of *F. coelebs* is mixed on the Curonian Spit. It consists of a large number of birds infected with ectoparasites. For example, the great part of birds with legs damaged by the tick *Knemidocoptes jamaicensis* have been accurately recorded in the latest migratory wave (Shumakov and Sokolov, 1982). The results of our investigations supplement these data (Valkiūnas, 1989d, 1993a). The prevalence of *F. coelebs* infection with leucocytozoids in the last wave of migration in 1978, 1979, 1984, and 1986–1989 was significantly greater than in the previous waves and it varied from 55.8 to 88.0% in different years. It seems likely that the birds, which experienced a disease, are left behind the main migration flow of their populations and gather at the end of the migratory stream forming the wave in the second half of October.

The mechanism of parasitic influence on migrating birds is probably associated with the distortion of the formation of the normal migratory state in birds, the state in which birds can migrate (Dolnik, 1975). Only low chronic (usually less than 1 parasite per 1000 erythrocytes) infections are recorded in each of the investigated *F. coelebs*. Thus, in this case we have to speak not as much about the influence of parasites on the birds during

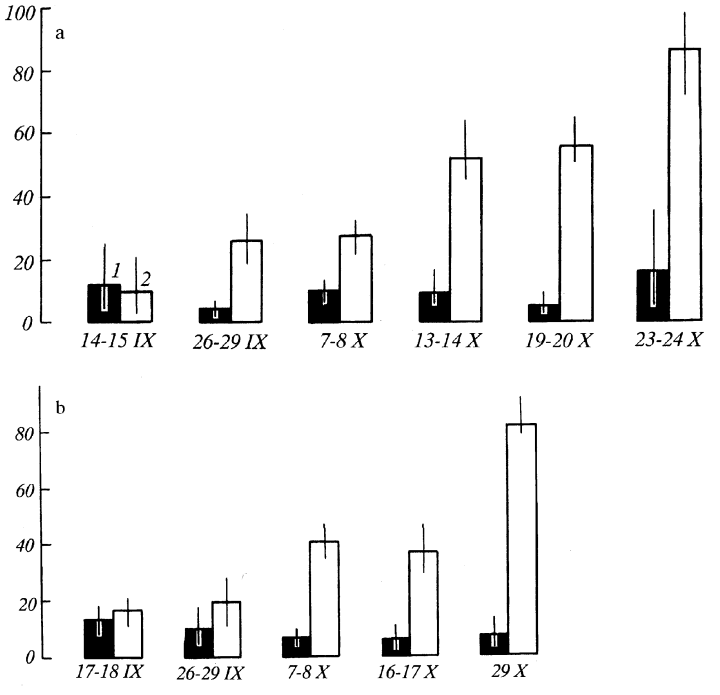

Figure 41 Infection of adult *Fringilla coelebs* with *Haemoproteus* (*1*) and *Leucocytozoon* spp. (*2*) in different flight waves during autumnal migration in 1978 (*a*) and 1979 (*b*):
The abscissa is the calendar (Arabic numerals indicate days and Roman numerals indicate months when the migratory waves were recorded) and the ordinate is the prevalence of infection, %. Vertical lines are 95% confidence limits.

migration, but mostly about the consequences of the diseases they experienced formerly. In the case of leucocytozoids, these may be distortions of the liver functions, which is where exoerythrocytic meronts localize (Khan and Fallis, 1970a) and, at the same time, plays an active role in the metabolism processes of the migratory fat (Dolnik, 1975). Probably, the delay in formation of the migratory state takes place in birds who had gone through a heavy leucocytozoonosis, comparing to the main part of a bird population. As a result, the infected birds gather at the end of the migratory flow when the climatic, feeding, and other conditions are worse. All this can promote the elimination of infected birds. The concentration of infected birds at the end of the migration flow may be considered as a sort of parasite 'filter' delaying the birds, which have been seriously ill, from flying away to wintering areas at the most favourable periods. It is not inconceivable that this is one of the regulatory parasitic mechanisms, which is realized in the period of seasonal migrations.

INFLUENCE OF HAEMOSPORIDIANS ON VECTORS

The relationships between bird haemosporidians and their vectors have not yet been sufficiently studied. It is likely that infection of the dipterans does not pass without leaving any

traces in them, which was shown in an example of various groups of blood-sucking arthropods and agents of infection (Alekseev, 1989, 1993). The data illustrating the peculiarities of the relationships between bird haemosporidians and their vectors are, however, poor.

Malaria parasites actively absorb carbohydrates from the haemocoele of mosquitoes, disturb the metabolism of amino acids, and induce mechanical distortions of the epithelial cells of the midgut (Alekseev, 1986). This influences the viability of females. Necrosis of the epithelial cells of *Culex pipiens* midgut under the influence of *Plasmodium cathemerium* is probably the main reason for increased mortality rate of infected mosquitoes compared to noninfected ones (Maier, 1973). There are data indicating that motility of females of *Aedes aegypti* infected with *Plasmodium gallinaceum* decreases when they transmit the infection to the vertebrate host compared with noninfected ones. It is not inconceivable that this increases the probability of their elimination (Alekseev *et al*., 1984). The mortality rate of the infected mosquitoes *A. aegypti* under relatively low infections (less than 40 oocysts per midgut) does not usually exceed the death rate of noninfected mosquitoes (Freier and Friedman, 1987). When there is no carbohydrate alimentation, the mosquitoes of both groups live four days. No significant differences are also found between infected and noninfected females in their dry body mass before and after extraction of lipids. Intensive reproduction of bacteria and pathological changes in midgut and salivary glands are observed in *Anopheles* spp. mosquitoes heavily infected with mammalian malaria parasites (Klein *et al*., 1982). It is likely that these processes also take place during heavy infection of mosquitoes with bird haemosporidians.

The life time of blood-sucking simuliid flies (Simuliidae) in the laboratory is inversely proportional to the intensity of parasitemia in birds on which they feed (Davies, 1953; Desser and Yang, 1973; Allison *et al*., 1978). For example, when *Simulium venustum* fed on birds with a high gametocytemia of *Leucocytozoon simondi* the majority of females died within 24 hours. However, an insignificant mortality rate was simultaneously observed in flies, which fed on the birds with low parasitemia. We obtained similar results when the biting midges *Culicoides impunctatus* were fed on *Fringilla coelebs* with high (about 20 to 30 gametocytes per 1000 erythrocytes) and low (less than 1 per 1000) gametocytemia of *Haemoproteus fringillae*. In one day after infection, the death rate of females in the first group was four times higher than in the second one ($P < 0.01$).†

FINAL NOTES ON PATHOGENICITY

The data on pathogenicity of haemosporidians accumulated up to the present prominently mirror the main concepts of the general parasitology about the important role of parasites in the elimination of the individual specimens, regulation of the density of populations of hosts, and stabilization of ecosystems (Beklemishev, 1970; Anderson and May, 1978, 1982; Kennedy, 1975; Price, 1980; Kontrimavičius, 1982, 1983; Balashov, 1991; Hudson, 1998). Devastating epizooties of haemosporidioses occur in wildlife. The majority of the species of haemosporidians being ‘moderately pathogenic’ do not cause, however, the death of their hosts directly. Mathematical modeling of the relations between parasites and

† See also Appendix 2 (p. 868) for additional information.

hosts indicates that such parasites perform the best regulation of the density of their hosts' population doing this in a more effective way than parasites that kill their hosts and undermine their own density (Anderson and May, 1982). Nevertheless, the specific mechanisms of the realization of this concept remain poorly understood in wildlife.

The available facts allow us to suggest that the influence of haemosporidians on free-living birds manifests itself mainly by means of decreasing the competitive ability of infected specimens. In nature this means the elimination of less 'optimal' genotypes (that is, not capable or less capable to withstand infection during its acute stage) under the pressure of extreme biotic and abiotic factors. This way of influence on the host is more justified from the energetic standpoint because it does not require additional expenditures of energy of the decease agents against the defense properties of individual host specimens and their populations. It is important to note that in the case of haemosporidians, selection is aimed to support the host specimens that are capable to successfully survive an acute stage of the infection but not completely eliminate the parasite from the organism. The exceptions are rare. For example, there is *Leucocytozoon caulleryi* that induces a complete immunity to reinfection in birds recovered from the disease. As a rule, the birds that survived an acute stage of the infection keep the parasite in the organism and maintain its number at a low (chronic) level. Many species of haemosporidians survive in once infected birds actually to the end of hosts' life. This state is mutually beneficial to the host and parasite. The infected birds acquire more or less expressed immunity (premunition), while the parasite obtains an opportunity for further transmission due to chronic parasitemia, which usually increases (but usually does not reach the maximum level of the acute stage of the initial infection) during the seasons of active transmission.

The situation considered leads to an important conclusion that has not yet been taken into account in ecological and evolutionary biological investigations. Namely, the pathogenic influence of haemosporidians on free-living birds clearly manifests itself mainly during the peak of initial development [merogony and (or) parasitemia] in the vertebrate host, or during acute relapses, which is a relatively short-time interval, but which is sufficient for the elimination of weak specimens in the wild. It is noteworthy from the point of view of ecology that the birds (primarily young ones) are not active during the acute stage of infection and thus, are not available for the researchers using traditional methods to catch them (mist nets, traps, and probably even the nest-boxes) (see p. 140 for details). Much information about the relations of birds and haemosporidians accumulated during the last two decades is thus based mainly on low (chronic) infections, and does not take into account birds during the acute stage of their infections; therefore, it only partially reflects the real outline of the relations between the hosts and parasites in nature. The conclusions of numerous works (summarized by Møller, 1997) about the presence (or absence) of the pathogenic influence of haemosporidians on wild birds can be accepted only with one significant correction; the overwhelming majority of the conclusions are based on only one stage of the infection (chronic), therefore, they cannot be automatically extended to the relations between the hosts and parasites in general, which is usually done and is an example of the errors in some ecological and evolutionary biology works from the point of view of epidemiology. On the one hand, the problem of the influence of haemosporidians on birds during the acute stage of infection remains insufficiently studied in wildlife, while on the other hand, it is fundamental for the understanding of the role of the parasites in nature. The understanding of the fact that both the presence and the absence of correlations between the prevalence of infection during the stage of chronic parasitemia (usually <3% of blood cells) and the ornithological parameters of fitness reflect only a minor part of the

host–parasite relationships is important to plan future investigations of the pathogenic influence of haemosporidians and other groups of parasites on their hosts in nature. At the same time a number of examples currently available to science, which were discussed in this chapter, illustrate the thesis about the influence of haemosporidians on selection in host populations that facilitates the implementation of genetic diversity (Hamilton, 1982). The participation of haemosporidians in the regulatory mechanisms of populations and cenoses acquires a significant importance due to the worldwide distribution of these parasites and high prevalence of infection in populations of many bird species. The complex life cycles of haemosporidians, diversity of the manifestation of their influence on the hosts, which is frequently performed indirectly through the complex ways of the interacting abiotic and biotic factors, requires principally new approaches to the understanding of the relationships of parasites with their hosts, which was also noted by Ashford (1998). A combination of traditional and the newest methods of research in parasitology and ornithology, together with a deep analysis of diseases epidemiology, is currently the only possible way to understand and evaluate the relationships between the hosts and their parasites in wildlife. It is noteworthy that the methods evaluating the immune status of wild birds, with rare exceptions (Nordling *et al.*, 1998), are not employed in the solution of the problem of pathogenicity. An opportunity to estimate numerous parasitological indices from living hosts, and the wide distribution of haemosporidians make them convenient model objects to solve the intricate problems of parasitology related to birds.

Anthropogenic changes occurring in the ecosystems lead to the distribution of haemosporidioses among domestic birds. As this takes place, unstable host–parasite systems are formed, which cause severe epizooties. Anthropogenically induced distortions of the balance in natural ecosystems also lead to the distribution of epizooties among wild birds. Programs to reintroduce wild birds bred in captivity to the wild, which gain greater and greater actuality at present, as well as projects to develop artificial colonies to preserve rare and disappearing species of birds are jeopardized by possible failure. The appearance of a small genetically similar group of specimens on the territories endemic for haemosporidioses creates favourable grounds for the development of severe diseases that can currently be controlled with difficulty. All this demonstrates the theoretical and practical importance of further research into bird haemosporidians and particularly their role in the certain populations of hosts and biocenoses.

Distribution

The study of regularities of the bird haemosporidians distribution is complicated due to several reasons, the main of which are the following. First, the fauna of haemosporidians in each of the zoogeographical regions has been studied irregularly. For example, there is almost no information about the peculiarities of the distribution of these parasites in the vast territories of Siberia and Far East. If we, however, take into account that a significant part of the Palearctic bird species are migratory, and blood samples were collected in the places of mass migration, the fauna of the Palearctic and Holarctic in total appeared to be studied rather well, although the peculiarities of the formation of faunae of certain subregions require further research. This problem is most pressing in relation with the study of the parasites in nonmigrating birds and their vectors. Second, the distribution of haemosporidians remains unknown in representatives of some orders and families of birds. Birds of economical importance and those that are easily available for mass catches have been studied relatively well. Third, migrating birds regularly transport parasites during their seasonal and other migrations. Such parasites often do not complete their life cycles in the breeding areas but enrich the local fauna becoming a sort of reserve for the future evolution (see p. 145 for details). This is especially characteristic of the far-distance Palearctic migrants wintering in the Ethiopian region. At present, it is not always possible to distinguish between these 'alien' elements of fauna in full scale, which hampers detailed analysis of the fauna in different regions of the planet. Fourth, certain species of bird haemosporidians were recorded only once at a certain geographical point. Similar to the majority of the well-studied species, one can expect that many of such 'rare' forms have wide ranges of distribution. Information in the literature about a large number of these 'unique' findings hampers the work of distinguishing the degree of the endemic character of faunae of certain regions and lessens the value of the results of quantitative estimates of the similarity and differences of the species composition, even in such global divisions of the world as zoogeographical regions. As a result of this, at the present level of knowledge, we have to abandon the intention to calculate the indices of faunae similarity in different regions, because it is inevitable that the input data for these mathematical calculations would, no doubt, disfigure the realistic situation in nature. Fifth, the distribution range of certain species has changed significantly under the impact of human industrial activity (introduction of birds and vectors, wide application of insecticides and pesticides in the agriculture, and so on). It is difficult to estimate the degree of these changes in the case of parasites of wild birds at present, and further investigations are required.

Nevertheless, it is our opinion that the main difficulties of haemosporidian research, mentioned above, do not mean that zoogeographical generalizations are made earlier than they should be done. At present, the fauna of bird Haemosporida includes 206 species.[†] The curves characterizing the decrement of the number of described species belonging to the

[†] See also Appendix 2.

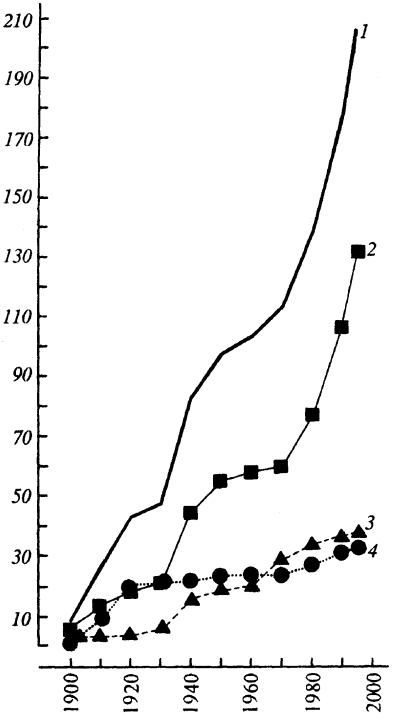

Figure 42 Number of described species of bird haemosporidian parasites: *1* – all species, *2* – *Haemoproteus*, *3* – *Plasmodium*, and *4* – *Leucocytozoon* spp. The abscissa is the calendar in years, and the ordinate is the total number of species.

families Plasmodiidae and Leucocytozoidae have practically reached a plateau (Fig. 42). This indicates that the number of existing species not yet known to science is not very large. At least, we should not expect a significant increase in the number of species of these parasites in the near future, if the traditional methods of systematics are applied and maximum level of specificity for haemoproteids and leucocytozoids is accepted at the level of bird orders (see pp. 69 and 76 for details). Due to many reasons, the modern methods of systematics (molecular biology, genetic, and others) are not widely applied in bird haemosporidians taxonomy on the species level, and we should not expect any cardinal change of this situation in the near future because of gradually decreasing funding for zoological research and systematics. During recent decades, the number of species belonging to the family Haemoproteidae has increased relatively quickly, and this is the main reason that the general number of bird haemosporidian species also increases (Fig. 42). We can expect that the number of haemosporidian species known to science would be increased primarily due to the study of fauna in the tropical and subtropical regions, especially in Australia. In this respect, the fauna of the Holarctic has been studied relatively well. Due to the fact that in the countries with warm climate, the access to mass research of the majority of bird species which have not been investigated yet is not an easy task, it is likely that this process will not be very fast. Experience leads us to conclude that within the next 10 to 20 years the number of newly described species of haemosporidians would not probably increase by more than 10 to 15%.

Table 2 Prevalence of haemosporidian parasites in birds in different zoogeographical regions (according to Greiner *et al.*, 1975; McClure *et al.*, 1978; White *et al.*, 1979; Peirce, 1981; Valkiūnas, 1987a; Bennett *et al.*, 1992a, and new data).

Zoogeographical region	Number of investigated birds	Infected					
		Haemoproteus sp.		*Plasmodium* sp.		*Leucocytozoon* sp.	
		Number	%	Number	%	Number	%
Holarctic	102590	18363	17.9	2981	2.9	16619	16.2
Ethiopian	11507	1887	16.4	368	3.2	529	4.6
Oriental	45091	5926	13.1	348	0.8	1327	2.9
Neotropical	54101	3841	7.1	865	1.6	66	0.1

Note: This table is based only on data of microscopy of blood smears. The precise data from the Australian region are not available.

According to Bennett with co-authors (Bennett *et al.*, 1982b) and our additions to their calculations, about 45% of bird species of the world fauna have been investigated so far for infection by haemosporidians. The number of specimens investigated in different zoogeographical regions is large (Table 2). It follows from this that we can estimate some general rules of bird haemosporidians distribution. In this work we shall analyze the two aspects of the problem: the geographical distribution and distribution by hosts.

GEOGRAPHICAL DISTRIBUTION

Irregularity of the fauna investigation in the subordinate regions within the zoogeographical regions forced us to analyze the distribution of bird haemosporidians mainly by the zoogeographical regions, without the analysis of smaller subordinate regions. Only the lists of faunae will be considered, because the analysis of the ecological faunistic complexes requires a deep knowledge of the ecology of parasites inhabiting various zoogeographical regions as well as detailed information about the species composition of their vectors, which is not provided by the current level of our knowledge. It is also noteworthy that the haemosporidians fauna of birds in the Nearctic and Palearctic regions of the Holarctic has more similar features than differences. Thus, we do not consider these parts of the Holarctic separately. The main distinguishing peculiarities of the Palearctic and Nearctic regions which currently manifest themselves will be emphasized in the course of the description of the material. We accept only one genus in each of the families Haemoproteidae, Plasmodiidae, Leucocytozoidae, and Garniidae, whose representatives parasitize birds. These genera are: *Haemoproteus*, *Plasmodium*, *Leucocytozoon,* and *Fallisia,* respectively. Thus all information discussed below is valid also for the families.

Bird haemosporidians are distributed worldwide (Table 3). They are found in each zoogeographical region excluding the Antarctic.† These parasites are widely distributed in each of the landscape zones. They penetrate up the mountains to a height of 3000 m above

† The Antarctic region is usually not mentioned in further description.

Table 3 Fauna of bird haemosporidian parasites in different zoogeographical regions.

Zoogeographical region	Number of species				
	Haemoproteus	*Plasmodium*	*Fallisia*	*Leucocytozoon*	Total
Holarctic	78 /24	19/6	0	26/9	123/39
Ethiopian	70/17	13/2	0	25/6	108/25
Oriental	70/11	20/8	0	16/1	106/20
Australian	11/1	3/0	0	8/0	22/1
Neotropical	28/9	18/8	1/1	5/0	52/18
Antarctic	0	0	0	0	0

Note: Total number of species is given in numerator, and the number of species, which have been recorded only in a certain zoogeographical region, is given in denominator. See also Appendix 2.

sea level. Certain species are actively transmitted even beyond the North Polar Circle. The representatives of the families Haemoproteidae, Plasmodiidae, and Leucocytozoidae are distributed in all zoogeographical regions, while the species of the Garniidae were found only in the Neotropics. *Fallisia neotropicalis* is the only species belonging to the family Garniidae which parasitize birds. It is endemic for the Neotropics.

The faunae of bird haemosporidians of the Holarctic (123 species), Ethiopian (108), and Oriental regions (106) are the richest ones (Table 3). The representatives of all genera except *Fallisia* are actively transmitted in these zoogeographical regions, and the greatest number of species characteristic only to these regions are found there (39, 25, and 20, respectively). It is important to emphasize that the number of haemosporidian species discovered to now only in one of the zoogeographical regions, gives only a partial characteristics of the fauna endemism at the present level of knowledge. As already mentioned, many of the species were found only once, and it is likely, similar to the well-studied species, that their actual range of distribution is significantly wider. As a whole, the faunae of the Holarctic, Ethiopian, and Oriental regions are similar in the richness of species diversity. The faunae of the Australian (22 species) and Neotropical regions (52) are much poorer.

The fauna of the Australian region is the poorest, which manifests itself at the level of each genus. This may be accounted, in some degree, for the fact that this region is less investigated. It can be expected that the number of species of bird haemosporidians known in the Australian region would increase in the future. Nevertheless, the quite poor character of haemosporidians fauna in this region probably reflects the real situation in nature. It is likely that the penetration of avian haemosporidians into this region was secondary. It is noteworthy that all groups of haemosporidians, excluding *Fallisia* sp., are actively transmitted in the Australian region, although their distribution is a question for future research.

Regardless that the number of species in the Neotropical region is relatively low, its fauna significantly differs from that of the Australian region. First, the number of *Plasmodium* species is six times greater here. The Neotropics are quite comparable with the Holarctic, Ethiopian, and Oriental regions in the number of malaria parasites species (Table 3). The poverty of Neotropics fauna is mainly accounted for by the lessening of the *Haemoproteus* species number, and especially the *Leucocytozoon* species. Only the leucocytozoids with a world-wide distribution penetrate into the Neotropics (*Leucocytozoon danilewskyi*, *L. dubreuili*, *L. fringillinarum*, *L. marchouxi*). Moreover, the majority of the species

were recorded in the Nearctic migrating birds in their wintering grounds. At present we can only report with more or less confidence about the low transmission of *L. danilewskyi* and *L. marchouxi* in the Neotropics.† It is likely that all the other leucocytozoid species are only temporarily present in the region together with the migrating Nearctic birds. The prevalence of *Leucocytozoon* spp. infection is low in the Neotropics (Table 2), which together with the poor species composition and complete lack of endemic species indicates that *Leucocytozoon* spp. appearance is secondary in this region. Leucocytozoids only start to inhabit the Neotropical region, and it is noteworthy that this process is not very successful, despite the fact that the parasites are regularly introduced there by Nearctic migrants. This is probably related to the lack of susceptible vectors (ornithophilous blood-sucking simuliid flies) in the Neotropics. The specific features of bird haemosporidian fauna in the Neotropics are the almost complete absence of *Leucocytozoon* spp. and presence of *Fallisia* spp.

The majority of bird haemosporidian species are associated with the Holarctic, Ethiopian, and Oriental regions. The proportions of species of *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* found in a vast region covering these three zoogeographical regions are 92, 79, and 100% of the fauna of these genera, respectively.

It is noteworthy that the *Leucocytozoon* fauna is connected to the global region including the Holarctic, Ethiopian, and Oriental regions, where, as mentioned, 100% of the currently known species have been recorded. The Holarctic is distinguished among them by its high indices of the overall prevalence of infection with leucocytozoids (Table 2). In the high and medium latitudes of the Holarctic, the prevalence of infection of many species and populations of birds with leucocytozoids reaches 25% and frequently even more (Greiner *et al*., 1975; Valkiūnas, 1989d; Valkiūnas *et al*., 1990; Valkiūnas and Iezhova, 1990a). The combination of such factors as rich fauna of leucocytozoids, high prevalence of bird infection, and regular seasonal mass migration of numerous species of the Holarctic birds for wintering to the southern latitudes differentiates the Holarctic from the other zoogeographical regions and allows us to consider it as the present-day center of *Leucocytozoon* spp. spreading (Valkiūnas, 1984a, 1987a, 1989c). On the contrary, the rich fauna of malaria parasites in the Ethiopian, Oriental, and Neotropical regions combined with the active transmission of the parasites and the regular appearance of Holarctic birds in the wintering areas, distinguish these regions as a vast center of *Plasmodium* spp. spreading. The Ethiopian region is primarily distinguished in this respect due to a higher overall prevalence of the infection (Table 2). The share of birds infected with malaria reaches 20 to 50% in some regions of the African tropics (Crewe, 1975). The holoendemic malaria nidi are described in the Neotropical region (Gabaldon and Ulloa, 1980). The relatively high overall prevalence of infection with bird malaria parasites (Table 2) and the rich species composition of *Plasmodium* (Table 3) in the Holarctic can be partly accounted for by the infection of the Holarctic birds in their wintering areas (for more details, see p. 145).

The geographical distribution of haemosporidians subgenera is in general similar to the distribution of the genera (Table 4). The majority of the subgenera are distributed worldwide. The exceptions are the species of the subgenera *Plasmodioides* and *Akiba*. *Plasmodioides* is an endemic of the Neotropics, while *Akiba* is distributed in the Oriental region and in the adjacent regions of the Palearctic. The present day data about the lack of *Bennettinia* and *Huffia* in the Australian region require verification. It is likely that these parasites could be found in the Australian region with a more thorough research.

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† See also Appendix 2, p. 867.

Table 4 Distribution of subgenera of bird haemosporidian parasites by zoogeographical regions.

Genus and subgenus	Number of species					
	Total	Zoogeographical region				
		Holarctic	Ethiopian	Oriental	Australian	Neotropical
Haemoproteus						
Parahaemoproteus	126	72	68	68	10	26
Haemoproteus	6	6	2	2	1	2
Plasmodium						
Haemamoeba	10	6	2	5	1	4
Giovannolaia	15	5	6	9	1	5
Novyella	9	5	3	4	1	6
Bennettinia	1	1	1	1	0	1
Huffia	3	2	1	1	0	1
Fallisia						
Plasmodioides	1	0	0	0	0	2
Leucocytozoon						
Leucocytozoon	34	25	25	15	8	5
Akiba	1	1	0	1	0	0
Total	206	123	108	106	22	52

Note: See also Appendix 2.

The analysis of the geographical distribution of the haemosporidian species showed that the major part of the representatives of all genera, excluding *Fallisia*, have vast ranges of distribution covering several zoogeographical regions. For example, the proportion of *Haemoproteus* species occurring in more than one zoogeographical region is equal to 54%, that of *Leucocytozoon* is 57%, and that of *Plasmodium* is 37% of the fauna of the certain genus. The total number of haemosporidian species occurring in more than one zoogeographical region is equal to 105, which is 51% of the world fauna. It is noteworthy, that the share of such species is likely to grow in the future, because some of the haemosporidians were recorder only once, and most probably have greater ranges of distribution than is currently known. The number of bird haemosporidian species found in three to four zoogeographical regions is equal to 52 or 25% of the world fauna. Such species as *Haemoproteus columbae*, *H. nettionis*, *H. noctuae, H. passeris*, *H. plataleae*, *Leucocytozoon danilewskyi*, *L. dubreuili*, *L. fringillinarum*, *Plasmodium circumflexum*, *P. relictum*, and *P. vaughani* are found in each of the continents. It should be kept in mind, however, that the distribution of most haemosporidian species is of a patchy character due to the irregular distribution of their hosts and influence of other factors.

The tendency to cosmopolitanism is one of the characteristic features of the geographical distribution of genera, subgenera, and species of bird haemosporidians. It is noteworthy that the ranges of distribution being vast, however, have quite clear boundaries. For example, the transmission of *Leucocytozoon simondi* occurs only in the Holarctic approximately north of 42° N, while *L. caulleryi* is transmitted in the Oriental region and in the adjacent regions of the Palearctic. The present day patchy distribution of *L. smithi* is an excellent example of rapid extension of the haemosporidians area of distribution under the

Table 5 Fauna of haemosporidian parasites in different bird orders.

No.	Order	Number of species				
		Haemoproteus	*Plasmodium*	*Fallisia*	*Leucocytozoon*	Total
1	Sphenisciformes	0	2	0	1	3
2	Struthioniformes	0	0	0	1	1
3	Tinamiformes	0	3	0	0	3
4	Pelecaniformes	0	1	0	1	2
5	Ciconiiformes	4	4	1	2	11
6	Anseriformes	2	9	0	1	12
7	Falconiformes	6	5	0	1	12
8	Galliformes	9	17	0	7	33
9	Turniciformes	0	1	0	0	1
10	Gruiformes	5	8	0	1	14
11	Charadriiformes	5	2	0	2	9
12	Columbiformes	6	11	1	1	19
13	Psittaciformes	2	5	0	0	7
14	Cuculiformes	1	2	0	1	4
15	Musophagiformes	1	1	0	1	3
16	Strigiformes	2	5	0	1	8
17	Caprimulgiformes	1	3	0	1	5
18	Apodiformes	4	3	0	0	7
19	Coliiformes	1	0	0	1	2
20	Trogoniformes	1	0	0	0	1
21	Coraciiformes	10	4	0	4	18
22	Piciformes	9	8	0	1	18
23	Passeriformes	63	16	0	7	86

Note: See also Appendix 2.

influence of the industrial activity of people. This parasite of turkeys was initially distributed only in the southeastern part of the Nearctic. At present, it has been introduced in many states of the USA, as well as in Europe, and South Africa. Unfortunately, the absolute definition and mapping of the areas of distribution for the majority of bird haemosporidian species are currently impossible due to the lack of necessary data.

Among the fundamental properties of the geographical distribution of haemosporidians, a clearly expressed tendency to the increase of the prevalence of *Leucocytozoon* infection from the tropical latitudes to the high latitudes of the Holarctic have to be noted (Greiner *et al*., 1975; White *et al*., 1978; Valkiūnas, 1984a, 1984b, 1989c; Valkiūnas and Iezhova, 1990a; Valkiūnas *et al*., 1990). It is likely that this is related primarily to the increase of the density of host populations as well as to the ability of the parasites to complete their development in the vectors at a relatively low temperature. This general rule has a certain realization in various bird species in different regions, and there are exceptions, but in general it is characteristic of *Leucocytozoon* spp. Certain species of leucocytozoids (for example, *L. lovati*, *L. simondi*) have managed to penetrate even beyond the North Polar Circle where they are actively transmitted. Species of the other haemosporidian genera have not yet adjusted to such severe conditions. For example, *Haemoproteus* spp. are absent in

the tundra region, and are rarely recorded in the forest tundra, which is accounted for by the poor fauna of vectors in these regions, and probably the lack of necessary total heat for the development in the invertebrate host. As already mentioned, the majority of malaria parasite species are heat-loving and do not penetrate as far north as *Leucocytozoon* and *Haemoproteus* spp.

DISTRIBUTION BY HOSTS

As we already mentioned, about 45% of bird species of the world fauna have been currently investigated with respect to infection with haemosporidians. *Haemoproteus* spp. are recorded in approximately in 50%, *Plasmodium* and *Leucocytozoon* spp. in 30%, and *Fallisia* sp. in 0.5% of the investigated bird species. The representatives of exotic birds and bird groups difficult to investigate are still not studied, for example: Heliornithidae, Rhinochetidae, Menuridae, Atrichornithidae, Philepittidae, Phytotomidae, Xenicidae, Oxyruncidae, Dulidae, Gallaeidae, and others. There are also no data about haemosporidians of many rare species of birds belonging to the widely distributed families, whose mass investigation is difficult. For example, the following Palearctic birds, are not yet investigated: *Gavia pacifica* (Gaviidae), *Podiceps nigricollis* (Podicipedidae), *Diomedea albatrus* (Diomedeidae), *Nipponia nippon* (Threskiornithidae), *Chen rossii* (Anatidae), *Elanus caeruleus* (Accipitridae), *Falcipennis falcipennis* (Tetraonidae), *Grus vipio* (Gruidae), *Porzana exquisita* (Rallidae), *Syrrhaptes paradoxus* (Pteroclididae), *Columba janthina* (Columbidae), *Hierococcyx fugax* (Cuculidae), *Otus sunia* (Strigidae), *Ceryle rudis* (Alcedinidae), *Dendrocopos hyperythrus* (Picidae), *Remiz macronyx* (Paridae), and many other relatively rare species. A significant increase (more than 10%) in the number of bird species investigated can only be achieved in the near future if special joint programs of ornithologists and parasitologists to study the fauna primarily of the tropical and subtropical countries are implemented.

The distribution of haemosporidian species by bird orders is shown in Tables 5 and 6.[†] Haemosporidians were not found in the Casuariiformes, Apterygiformes, Phoenicopteriformes, or Eurypygiformes. Sporadic findings of haemosporidians not yet identified to a specific level, which are likely to have a secondary origin, are known in species of the Rheiformes, Gaviiformes, Podicipediformes, Procellariiformes, and Cariamiformes.

The richest fauna of haemosporidians is found in birds belonging to the Passeriformes (86 species), Galliformes (33), Columbiformes (19), Coraciiformes (18), and Piciformes (18). A poorer species composition of haemosporidians (8 to 17 species) is recorded in birds belonging to the Ciconiiformes, Anseriformes, Falconiformes, Gruiformes, Charadriiformes, and Strigiformes. No more than seven species of haemosporidians develop in the representatives of each other order. The poorest fauna (not greater than three species) is characteristic of such relatively old groups as the Sphenisciformes, Struthioniformes,

[†] Bennett (1993b) carried out an analysis of *Haemoproteus* species distribution by the orders of birds. So far, we have a slightly different view on the status of some species; the distribution of *Haemoproteus* species by the orders of birds in this book is slightly different. Nevertheless, the total number of species belonging to the family Haemoproteidae, parasitizing birds according to G.F. Bennett (128 species) and our data (132) is close. See also Appendix 2.

Table 6 Distribution of species of haemosporidian parasites by orders of birds.

No.	Order	Species of haemosporidians
1	Sphenisciformes	1. *Plasmodium relictum* (Passeridae) 36. *P. elongatum* (Passeridae) 27. *Leucocytozoon tawaki* (Spheniscidae) Total: three species
2	Struthioniformes	16. *Leucocytozoon struthionis* (Struthionidae) Total: one species
3	Tinamiformes	1. *Plasmodium relictum* (Passeridae) 13. *P. polare* (Hirundinidae) 16. *P. pedioecetae* (Tetraonidae) Total: three species
4	Pelecaniformes	12. *Plasmodium circumflexum* (Turdidae) 21. *Leucocytozoon vandenbrandeni* (Anhingidae) Total: two species (see also Appendix 2)
5	Ciconiiformes	7. *Haemoproteus crumenium* (Ciconiidae) 30. *H. herodiadis* (Ardeidae) 34. *H. plataleae* (Threskiornithidae) 49. *H. pelouroi* (Threskiornithidae) 1. *Plasmodium relictum* (Passeridae) 26. *P. vaughani* (Turdidae) 30. *P. nucleophilum* (Mimidae) 36. *P. elongatum* (Passeridae) 1. *Fallisia neotropicalis* (Columbidae) 14. *Leucocytozoon leboeufi* (Ardeidae) 28. *L. nycticoraxi* (Ardeidae) Total: 11 species
6	Anseriformes	10. *Haemoproteus nettionis* (Anatidae) 84. *H. greineri* (Anatidae) 1. *Plasmodium relictum* (Passeridae) 12. *P. circumflexum* (Turdidae) 13. *P. polare* (Hirundinidae) 20. *P. anasum* (Anatidae) 22. *P. hegneri* (Anatidae) 24. *P. gabaldoni* (Columbidae) 26. *P. vaughani* (Turdidae) 30. *P. nucleophilum* (Mimidae) 36. *P. elongatum* (Passeridae) 12. *Leucocytozoon simondi* (Anatidae) Total: 12 species
7	Falconiformes	17. *Haemoproteus tinnunculi* (Falconidae) 27. *H. elani* (Accipitridae) 51. *H. buteonis* (Accipitridae) 69. *H. janovyi* (Accipitridae)

Table 6 (continued)

No.	Order	Species of haemosporidians
		81. *H. nisi* (Accipitridae) 99. *H. brachiatus* (Falconidae) 1. *Plasmodium relictum* (Passeridae) 11. *P. fallax* (Strigidae) 12. *P. circumflexum* (Turdidae) 13. *P. polare* (Hirundinidae) 36. *P. elongatum* (Passeridae) 9. *Leucocytozoon toddi* (Accipitridae) Total: 12 species (see also Appendix 2)
8	Galliformes	13. *Haemoproteus mansoni* (Tetraonidae) 18. *H. lophortyx* (Phasianidae) 38. *H. rileyi* (Phasianidae) 52. *H. pratasi* (Numididae) 66. *H. ortalidum* (Cracidae) 71. *H. stableri* (Tetraonidae) 75. *H. ammoperdix* (Phasianidae) 76. *H. megapodius* (Megapodiidae) 80. *H. cracidarum* (Cracidae) 1. *Plasmodium relictum* (Passeridae) 4. *P. gallinaceum* (Phasianidae) 8. *P. griffithsi* (Meleagrididae) 9. *P. tejerai* (Meleagrididae) 10. *P. coturnixi* (Phasianidae) 11. *P. fallax* (Strigidae) 12. *P. circumflexum* (Turdidae) 13. *P. polare* (Hirundinidae) 14. *P. lophurae* (Phasianidae) 15. *P. durae* (Meleagrididae) 16. *P. pedioecetae* (Tetraonidae) 17. *P. pinottii* (Ramphastidae) 18. *P. formosanum* (Phasianidae) 28. *P. rouxi* (Passeridae) 34. *P. kempi* (Meleagrididae) 35. *P. juxtanucleare* (Phasianidae) 38. *P. hermani* (Meleagrididae) 3. *Leucocytozoon smithi* (Meleagrididae) 4. *L. neavei* (Numididae) 5. *L. lovati* (Tetraonidae) 7. *L. macleani* (Phasianidae) 19. *L. schoutedeni* (Phasianidae) 24. *L. cheissini* (Phasianidae) 35. *L. caulleryi* (Phasianidae) Total: 33 species

Table 6 (continued)

No.	Order	Species of haemosporidians
9	Turniciformes	26. *Plasmodium vaughani* (Turdidae) Total: one species
10	Gruiformes	9. *Haemoproteus porzanae* (Rallidae) 22. *H. antigonis* (Gruidae) 28. *H. gallinulae* (Rallidae) 60. *H. balearicae* (Gruidae) 62. *H. telfordi* (Otididae) 1. *Plasmodium relictum* (Passeridae) 3. *P. cathemerium* (Passeridae) 6. *P. lutzi* (Rallidae) 18. *P. formosanum* (Phasianidae) 26. *P. vaughani* (Turdidae) 28. *P. rouxi* (Passeridae) 33. *P. bertii* (Rallidae) 36. *P. elongatum* (Passeridae) 25. *Leucocytozoon grusi* (Gruidae) Total: 14 species
11	Charadriiformes	19. *Haemoproteus scolopaci* (Scolopacidae) 59. *H. larae* (Laridae) 68. *H. contortus* (Scolopacidae) 70. *H. rotator* (Scolopacidae) 74. *H. abdusalomovi* (Glareolidae) 1. *Plasmodium relictum* (Passeridae) 12. *P. circumflexum* (Turdidae) 15. *Leucocytozoon legeri* (Scolopacidae) 23. *L. sousadiasi* (Charadriidae) Total: nine species (see also Appendix 2)
12	Columbiformes	127. *Haemoproteus columbae* (Columbidae) 128. *H. sacharovi* (Columbidae) 129. *H. turtur* (Columbidae) 130. *H. palumbis* (Columbidae) 131. *H. krylovi* (Pteroclididae) 132. *H. pteroclis* (Pteroclididae) 1. *Plasmodium relictum* (Passeridae) 3. *P. cathemerium* (Passeridae) 12. *P. circumflexum* (Turdidae) 13. *P. polare* (Hirundinidae) 14. *P. lophurae* (Phasianidae) 24. *P. gabaldoni* (Columbidae) 26. *P. vaughani* (Turdidae) 27. *P. columbae* (Columbidae) 30. *P. nucleophilum* (Mimidae) 31. *P. dissanaikei* (Psittacidae)

Table 6 (continued)

No.	Order	Species of haemosporidians
		36. *P. elongatum* (Passeridae) 1. *Fallisia neotropicalis* (Columbidae) 11. *Leucocytozoon marchouxi* (Columbidae) Total: 19 species
13	Psittaciformes	44. *Haemoproteus handai* (Psittacidae) 123. *H. psittaci* (Psittacidae) 1. *Plasmodium relictum* (Passeridae) 12. *P. circumflexum* (Turdidae) 26. *P. vaughani* (Turdidae) 30. *P. nucleophilum* (Mimidae) 31. *P. dissanaikei* (Psittacidae) Total: seven species
14	Cuculiformes	24. *Haemoproteus centropi* (Cuculidae) 1. *Plasmodium relictum* (Passeridae) 26. *P. vaughani* (Turdidae) 20. *Leucocytozoon centropi* (Cuculidae) Total: four species
15	Musophagiformes	56. *Haemoproteus montezi* (Musophagidae) 26. *Plasmodium vaughani* (Turdidae) 22. *Leucocytozoon dizini* (Musophagidae) Total: three species
16	Strigiformes	4. *Haemoproteus noctuae* (Strigidae) 14. *H. syrnii* (Strigidae) 2. *Plasmodium subpraecox* (Strigidae) 11. *P. fallax* (Strigidae) 19. *P. gundersi* (Strigidae) 29. *P. hexamerium* (Turdidae) 36. *P. elongatum* (Passeridae) 1. *Leucocytozoon danilewskyi* (Strigidae) Total: eight species (see also Appendix 2)
17	Caprimulgiformes	61. *Haemoproteus caprimulgi* (Caprimulgidae) 1. *Plasmodium relictum* (Passeridae) 3. *P. cathemerium* (Passeridae) 13. *P. polare* (Hirundinidae) 17. *Leucocytozoon caprimulgi* (Caprimulgidae) Total: five species
18	Apodiformes	42. *Haemoproteus archilochus* (Trochilidae) 72. *H. trochili* (Trochilidae) 73. *H. witti* (Trochilidae) 85. *H. apodus* (Apodidae) 1. *Plasmodium relictum* (Passeridae) 3. *P. cathemerium* (Passeridae)

Table 6 (continued)

No.	Order	Species of haemosporidians
		28. *P. rouxi* (Passeridae) Total: seven species
19	Coliiformes	124. *Haemoproteus undulatus* (Coliidae) 34. *Leucocytozoon colius* (Coliidae) Total: two species
20	Trogoniformes	106. *Haemoproteus trogonis* (Trogonidae) Total: one species
21	Coraciiformes	25. *Haemoproteus coraciae* (Coraciidae) 29. *H. halcyonis* (Alcedinidae) 36. *H. upupae* (Upupidae) 39. *H. fuscae* (Alcedinidae) 45. *H. meropis* (Meropidae) 57. *H. enucleator* (Alcedinidae) 64. *H. lairdi* (Meropidae) 65. *H. manwelli* (Meropidae) 88. *H. eurystomae* (Coraciidae) 103. *H. gavrilovi* (Meropidae) 1. *Plasmodium relictum* (Passeridae) 12. *P. circumflexum* (Turdidae) 21. *P. garnhami* (Upupidae) 26. *P. vaughani* (Turdidae) 18. *Leucocytozoon eurystomi* (Coraciidae) 30. *L. nyctyornis* (Meropidae) 32. *L. communis* (Upupidae) 33. *L. bennetti* (Coraciidae) Total: 18 species (see also Appendix 2)
22	Piciformes	35. *Haemoproteus thereicerycis* (Capitonidae) 41. *H. velans* (Picidae) 47. *H. xantholaemae* (Capitonidae) 50. *H. borgesi* (Picidae) 63. *H. bennetti* (Picidae) 77. *H. bilobata* (Capitonidae) 78. *H. cornuata* (Capitonidae) 86. *H. bucconis* (Bucconidae) 89. *H. indicator* (Indicatoridae) 1. *Plasmodium relictum* (Passeridae) 3. *P. cathemerium* (Passeridae) 12. *P. circumflexum* (Turdidae) 17. *P. pinottii* (Ramphastidae) 26. *P. vaughani* (Turdidae) 28. *P. rouxi* (Passeridae) 30. *P. nucleophilum* (Mimidae) 37. *P. huffi* (Ramphastidae)

Table 6 (continued)

No.	Order	Species of haemosporidians
		31. *Leucocytozoon squamatus* (Picidae) Total: 18 species
23	Passeriformes	1. *Haemoproteus danilewskii* (Corvidae) 2. *H. passeris* (Passeridae) 3. *H. alaudae* (Alaudidae) 5. *H. fringillae* (Fringillidae) 6. *H. majoris* (Paridae) 8. *H. hirundinis* (Hirundinidae) 11. *H. orizivorae* (Estrildidae) 12. *H. ptilotis* (Meliphagidae) 15. *H. queleae* (Ploceidae) 16. *H. wenyoni* (Passeridae) 20. *H. aegithinae* (Irenidae) 21. *H. anthi* (Motacillidae) 23. *H. beckeri* (Mimidae) 26. *H. dicruri* (Dicruridae) 31. *H. orioli* (Oriolidae) 32. *H. otocompsae* (Pycnonotidae) 33. *H. pastoris* (Sturnidae) 37. *H. lanii* (Laniidae) 40. *H. picae* (Corvidae) 43. *H. quiscalus* (Icteridae) 46. *H. sanguinis* (Pycnonotidae) 48. *H. zosteropis* (Zosteropidae) 53. *H. sequeirae* (Nectariniidae) 54. *H. globulosus* (Fringillidae) 55. *H. macropigmentatus* (Fringillidae) 58. *H. fallisi* (Turdidae) 67. *H. stellaris* (Hirundinidae) 79. *H. killangoi* (Zosteropidae) 82. *H. balmorali* (Muscicapidae) 83. *H. cublae* (Laniidae) 87. *H. circumnuclearis* (Tyrannidae) 90. *H. souzalopesi* (Tyrannidae) 91. *H. tartakovskyi* (Fringillidae) 92. *H. tyranni* (Tyrannidae) 93. *H. formicarius* (Formicariidae) 94. *H. furnarius* (Furnariidae) 95. *H. philippinensis* (Pycnonotidae) 96. *H. vireonis* (Vireonidae) 97. *H. attenuatus* (Turdidae) 98. *H. belopolskyi* (Sylviidae) 100. *H. parus* (Paridae)

Table 6 (continued)

No.	Order	Species of haemosporidians
		101. *H. sittae* (Sittidae) 102. *H. dicaeus* (Dicaeidae) 104. *H. motacillae* (Motacillidae) 105. *H. nucleophilus* (Dicaeidae) 107. *H. africanus* (Estrildidae) 108. *H. bubalornis* (Bubalornithidae) 109. *H. eurylaimus* (Eurylaimidae) 110. *H. monarchus* (Monarchidae) 111. *H. nipponensis* (Muscicapidae) 112. *H. pachycephalus* (Pachycephalidae) 113. *H. pallidus* (Muscicapidae) 114. *H. pittae* (Pittidae) 115. *H. timalus* (Timaliidae) 116. *H. uraeginthus* (Estrildidae) 117. *H. calandrellae* (Alaudidae) 118. *H. coatneyi* (Emberizidae) 119. *H. dolniki* (Fringillidae) 120. *H. magnus* (Fringillidae) 121. *H. minutus* (Turdidae) 122. *H. neseri* (Turdidae) 125. *H. kairullaevi* (Sturnidae) 126. *H. payevskyi* (Sylviidae) 1. *Plasmodium relictum* (Passeridae) 3. *P. cathemerium* (Passeridae) 5. *P. matutinum* (Turdidae) 7. *P. giovannolai* (Turdidae) 11. *P. fallax* (Strigidae) 12. *P. circumflexum* (Turdidae) 13. *P. polare* (Hirundinidae) 17. *P. pinottii* (Ramphastidae) 23. *P. octamerium* (Estrildidae) 25. *P. leanucleus* (Passeridae) 26. *P. vaughani* (Turdidae) 28. *P. rouxi* (Passeridae) 29. *P. hexamerium* (Turdidae) 30. *P. nucleophilum* (Mimidae) 32. *P. paranucleophilum* (Thraupidae) 36. *P. elongatum* (Passeridae) 2. *Leucocytozoon majoris* (Paridae) 6. *L. berestneffi* (Corvidae) 8. *L. sakharoffi* (Corvidae) 10. *L. fringillinarum* (Fringillidae) 13. *L. dubreuili* (Turdidae)

Table 6 (continued)

No.	Order	Species of haemosporidians
		26. *L. maccluri* (Turdidae) 29. *L. balmorali* (Laniidae) Total: 86 species (see also Appendix 2)

Note: The species from the same genus are given in chronological order. Chippers, which are given before the specific names, correspond to the numeration of the same species essay in the Systematic Section. The bird family, to which the type vertebrate host of the species belongs, is given in parentheses.

Tinamiformes, Pelecaniformes, Turniciformes, Musophagiformes, Coliiformes, and Trogoniformes. Thus, only two bird orders, i.e., the Passeriformes and Galliformes, are clearly distinguished by the richness of their haemosporidian fauna.

Haemoproteus parasites identified to a specific level are found in the representatives of 18 bird orders. The richest *Haemoproteus* fauna is recorded in birds belonging to the Passeriformes (63 species), Coraciiformes (10), Galliformes (9), Piciformes (9), Falconiformes (6), and Columbiformes (6).

The species composition of *Plasmodium* was studied in 20 orders of birds. The maximum number of species parasitize birds belonging to the Galliformes (17 species), Passeriformes (16), Columbiformes (11), Anseriformes (9), Gruiformes (8), and Piciformes (8).

Fallisia parasites identified to the specific level were found only in birds belonging to the Ciconiiformes and Columbiformes (one species in birds of each order). It is noteworthy that these rare bird parasites were also found in the Neotropics in the representatives of the orders Falconiformes and Pelecaniformes, but they were not identified to the specific level.

The species composition of *Leucocytozoon* has been investigated in birds of 18 orders. The maximum number of leucocytozoid species was found in birds belonging to the Passeriformes (seven species), Galliformes (seven), and Coraciiformes (seven). The fauna of leucocytozoids in birds of other orders is significantly poorer. It is represented by not more than two species.

The general characteristic of the fauna and peculiarities of the distribution of haemosporidians in birds belonging to the most well studied orders is given below. The information about the distribution of all species of haemosporidians is given in the corresponding essays on species in the Systematic Section.

Ciconiiformes

The fauna includes 11 species. It is presented by all genera of haemosporidians (Tables 5 and 6). *Haemoproteus* spp. are found in all zoogeographical regions. The widest geographical distribution is characteristic of *H. plataleae*, which is distributed worldwide. *Plasmodium* spp. are recorded everywhere. *Fallisia neotropicalis* is an endemic of the Neotropics. *Leucocytozoon nycticoraxi* has been recorded by the present time only in the Palearctic, while *L. leboeufi* is found in the Holarctic, Ethiopian and Oriental regions.

Anseriformes

There are 12 species of parasites belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). *Haemoproteus nettionis* is distributed worldwide, while

H. greineri has been recorded only in the Holarctic, though it is likely to have a wider range of distribution. Malaria parasites are distributed in each continent. *Plasmodium anasum*, *P. hegneri* were recorded only in the Oriental region, while *P. gabaldoni* was found only in the Neotropics. The other species of *Plasmodium* are characterized by greater ranges of distribution. *Leucocytozoon simondi* is an endemic of the Holarctic. This species penetrated beyond the North Polar Circle in the Palearctic, where it is actively transmitted. The southern boundary of *L. simondi* transmission in the Holarctic is to the north of 42° N.

Falconiformes

The fauna is presented by 12 species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). *Haemoproteus tinnunculi*, *H. elani,* and *H. nisi* are found in the Holarctic, Ethiopian, and Oriental regions. *Haemoproteus buteonis* and *H. brachiatus* were found only in the Holarctic, while *H. janovyi* was recorded only in the Ethiopian region. Malaria parasites are widely distributed. *Leucocytozoon toddi* is found in each zoogeographical region excluding the Australian one. The prevalence of infection with leucocytozoids in the representatives of the family Falconidae in any parts of the range of distribution of the parasites is usually significantly lower than in those of the Accipitridae. The leucocytozoids are usually found in the Accipitridae species ten times more frequently than in the Falconidae species. The tendency of the increase of the prevalence of infection of *L. toddi* in the direction from the tropical latitudes to the mid-latitudes of the Northern Hemisphere is clearly expressed. The majority of well studied populations of *Accipiter nisus* in the Palearctic are infected with *L. toddi* by 50 to 100%. The other species of the Accipitridae in the Holarctic, which have undergone mass investigation are also infected with *L. toddi* at a high prevalence (Greiner *et al*., 1975; Valkiūnas, 1989b).

Galliformes

Thirty-three species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6) are found. A relatively large number of species, with clearly bounded ranges of distribution, is a characteristic peculiarity of the distribution of *Haemoproteus* and *Leucocytozoon* spp. For example, *H. mansoni* and *L. lovati* are found only in the Holarctic, *H. pratasi* and *L. neavei* are recorded only in the Ethiopian region, *H. megapodius* is found only in the Oriental region, and *H. cracidarum* and *H. ortalidum* were found only in the Neotropical region. The range of distribution of *L. smithi* was initially limited by the southeastern part of North America. Currently, this parasite together with its host (turkey) has been introduced into Europe and South America. *Leucocytozoon caulleryi* is widely distributed only in Southeastern Asia. The widest ranges of distribution covering several zoogeographical regions are characteristic of the species developing in the representatives of the cosmopolitan family Phasianidae (*H. lophortyx*, *H. rileyi*, *L. macleani,* and *L. schoutedeni*). Malaria parasites are found in all zoogeographical regions, however, some of the species (*P. gallinaceum*, *P. griffithsi*, *P. tejerai*, *P. lophurae*, *P. durae*, *P. pinottii,* and *P. formosanum*) are distributed only in the countries with a warm climate.

Gruiformes

There are 14 species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). *Haemoproteus* spp. are distributed worldwide. *Haemoproteus*

antigonis and *H. gallinulae* have the widest ranges of distribution. They are found in the Holarctic, Ethiopian, and Oriental regions. *Plasmodium* spp. are distributed widely, while *P. formosanum* was found only in the Oriental region; *P. lutzi* and *P. bertii* were found only in the Neotropical region. *Leucocytozoon grusi* was recorded in the Holarctic and Ethiopian regions.

Charadriiformes

There are nine species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). *Haemoproteus* spp. are recorded in all zoogeographical regions excluding the Australian one. *Haemoproteus rotator* and *H. contortus* were found only in the Oriental region. *Haemoproteus scolopaci* and *H. larae* have larger ranges of distribution covering several zoogeographical regions. *Plasmodium* spp. were recorded rarely. *Leucocytozoon legeri* was found only in the Holarctic, while *L. sousadiasi* was recorded only in the Ethiopian region.

Columbiformes

The fauna includes 19 species belonging to the genera *Haemoproteus*, *Plasmodium*, *Leucocytozoon,* and *Fallisia* (Tables 5 and 6). The representatives of the subgenus *Haemoproteus* parasitize birds of this group only. *Haemoproteus columbae* is distributed worldwide; *H. sacharovi* and *L. marchouxi* are recorded in all zoogeographical regions excluding the Australian one. The other species of *Haemoproteus* have been found only in the Palearctic. It is noteworthy that *H. columbae* and *H. sacharovi* are more frequently recorded at the tropical and subtropical latitudes. Malaria parasites are widely distributed. *Plasmodium gabaldoni* and *P. columbae* were found only in the Neotropics. *Fallisia neotropicalis* is an endemic of the Neotropical region.

Psittaciformes

There are seven species belonging to the genera *Haemoproteus* and *Plasmodium* (Tables 5 and 6). *Haemoproteus handai* is distributed in all zoogeographical regions excluding the Holarctic; *H. psittaci* has been found only in the Ethiopian region. *Plasmodium* spp. are widely distributed. Leucocytozoids are recorded rarely and they are not identified to the specific level.

Strigiformes

The fauna includes eight species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). The characteristic peculiarity is a worldwide distribution of most haemosporidian species. *Haemoproteus noctuae* and *L. danilewskyi* are cosmopolitans, while *H. syrnii* is recorded in all zoogeographical regions excluding the Australian one. Malaria parasites are widely distributed. *Plasmodium gundersi* was found only in the Ethiopian region. The prevalence of bird infection with *Haemoproteus* and *Leucocytozoon* spp. is high in the Holarctic. Populations of birds with 50% and greater prevalence of the infection are usual for this region.

Caprimulgiformes

Five species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* are recorded (Tables 5 and 6). The characteristic peculiarity is a clearly expressed patchiness of the vast ranges of distribution of *H. caprimulgi* and *L. caprimulgi*, which were recorded in many zoogeographical regions.

Apodiformes

The fauna includes seven species belonging to the genera *Haemoproteus* and *Plasmodium* (Tables 5 and 6). All species of *Haemoproteus* are recorded only in the New World, mainly in the Neotropics. *Plasmodium* spp. were found relatively rarely. Leucocytozoids were recorded only sporadically, and they were not identified to the specific level.

Coraciiformes

The fauna is presented by 18 species belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). The peculiarities of geographical distribution are poorly studied. *Haemoproteus coraciae*, *H. halcyonis*, *H. fuscae*, *H. meropis*, *L. eurystomi*, *L. nyctyornis,* and *L. communis* have the greatest ranges of distribution covering the Holarctic, Ethiopian, and Oriental regions. In addition, the latter species was found in the Australian region. The other species of *Haemoproteus* and *Leucocytozoon* have lesser ranges of distribution; their boundaries have to be clarified. For example, *H. enucleator* and *H. lairdi* were found only in the Ethiopian region; *H. manwelli* was recorded only in the Oriental region. *Haemoproteus gavrilovi* and *L. bennetti* were found only once in the Palearctic. The ranges of distribution of these species are probably larger. *Haemoproteus eurystomae* was found only in the Ethiopian and Oriental regions. The distribution of *H. upupae* has not been studied yet. Malaria parasites are frequently recorded and they are widely distributed.

Piciformes

Eighteen species are found belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). *Haemoproteus* spp. were not found in the Palearctic, while only one species (*H. velans*) was found in the Nearctic. All the other described species of *Haemoproteus* are recorded in the Ethiopian, Oriental, and Neotropical regions. The peculiarities of the *Plasmodium* spp. distribution have not been studied yet. *Leucocytozoon squamatus* is transmitted in the Holarctic, Ethiopian, and Oriental regions. It was found rarely.

Passeriformes

This group of birds is the richest in the number of haemosporidian species. There are 86 species of parasites belonging to the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* (Tables 5 and 6). The representatives of all genera are found worldwide, although the peculiarities of the distribution of individual species and the infection of the representatives of certain families significantly vary. There are not enough data for the detailed analysis of these problems. The Corvidae, Fringillidae, Mimidae, Muscicapidae,

Table 7 Fauna of bird haemosporidian parasites in the order Diptera.

Family and genus	Number of described species			
	Haemoproteus	*Plasmodium*	*Leucocytozoon*	Total
Simuliidae				
Austrosimulium	0	0	1	1
Cnephia	0	0	4	4
Prosimulium	0	0	7	7
Simulium	0	0	12	12
Ceratopogonidae				
Culicoides	11	0	1	12
Culicidae				
Aedes	0	5	0	5
Anopheles	0	5	0	5
Armigeres	0	1	0	1
Culex	0	15	0	15
Culiseta	0	6	0	6
Mansonia	0	3	0	3
Psorophora	0	1	0	1
Wyeomyia	0	1	0	1
Hippoboscidae				
Microlynchia	1	0	0	1
Ornithomyia	1	0	0	1
Pseudolynchia	3	0	0	3

Paridae, Parulidae, Sylviidae, Turdidae, and Vireonidae are the families of birds with the highest overall prevalence of infection in the Holarctic, while the Certhiidae, Hirundinidae, Icteridae, Prunellidae, Regulidae, Sittidae, Troglodytidae, and Tyrannidae species are characterized with a low prevalence of infection. Nevertheless, there are species in each of the listed families which significantly differ in the prevalence of infection. *Haemoproteus passeris*, *P. relictum*, *P. circumflexum*, *P. vaughani,* and *L. fringillinarum* are cosmopolitans. The ranges of distribution for the majority of other species should be clarified. *Leucocytozoon maccluri* (the Oriental region) as well as *L. balmorali* and *H. stellaris* (the Ethiopian region) are the most probable candidates for the group of endemic species for certain zoogeographical regions.

DISTRIBUTION BY VECTORS

Different taxonomic groups of blood-sucking dipteran insects similar to the birds have uneven haemosporidian fauna both in the quantitative and qualitative aspects. The wide geographical distribution of the majority of haemosporidian species implies a wide species composition of the vectors. For example, *Plasmodium relictum,* one of the best studied species of bird malaria parasites, completes its development at least in 26 species of the Culicidae. The range of bird haemosporidian vectors has been studied satisfactorily only at

the level of genera and families of blood-sucking dipterans. The species of the vectors are not determined for the majority of haemosporidian species. The data presented in Table 7 give only a relative outline of the distribution of haemosporidian species by the vectors.

Haemoproteus spp. develop in the representatives of the families Ceratopogonidae and Hippoboscidae. The majority of haemoproteid species studied so far use the representatives of the genus *Culicoides* as vectors. Malaria parasites develop only in species of the Culicidae. The greatest number of the *Plasmodium* species studied are transmitted by the representatives of the genera *Culex* (these are frequently used in the laboratory experiments, thus they are well studied as vectors), *Culiseta*, *Aedes*, *Anopheles,* and *Mansonia*. The *Leucocytozoon* species develop in the representatives of the families Simuliidae and Ceratopogonidae. The vectors of most leucocytozoid species studied so far are blood-sucking simuliid flies belonging to the genera *Simulium*, *Prosimulium,* and *Cnephia*.

Certain Peculiarities of the Ecological Study of Bird Parasites

Much theoretical work in ecology and evolutionary biology has been based on the results of surveys of blood parasites, and first of all, on haemosporidians. The investigation of avian blood using methods harmless for the hosts gives a perfect opportunity to take large samples both from common and rare protected bird species. These parasitological methods are particularly attractive to ornithologists. However, the investigations have also presented potential theoretical traps due to the complicated life histories of these haematozoa, epidemiology of the diseases, and migratory behavior of their avian hosts. Our belief in the fact that birds and their parasites are extremely interesting and convenient objects of general parasitology made us analyze some of the main peculiarities of the biology of birds and their parasites, illustrating this research with examples of haemosporidians. The main objective of this chapter is to highlight some important aspects of the ecology of haemosporidian parasites that may await future research in ecology and evolutionary biology.

THE INFLUENCE OF MIGRATORY BEHAVIOUR OF BIRDS ON INFECTION PREVALENCE AT A STUDY SITE

Mobility is one of the characteristic features of bird biology. One has to keep this in mind while investigating the ecology of bird parasites. However, this obvious conclusion is relatively infrequently realized by the parasitologists in their practice. Actual difficulties of the recording or ignoring the peculiarities of the populational biology of birds discovered by ornithologists during recent decades frequently cause incorrect interpretation of the parasitological data and even disappointing conclusions (see p. 146). The solution of the problems of general parasitology in studies with birds assumes a thorough comprehension and account of the ornithological data on the migration of birds.

At present, it is known for certain that there is a definite sequence of flight of different bird populations of one species over one geographical point during seasonal migrations (Payevsky, 1985). Those who study the parasites of a certain species of birds should keep in mind that within different intervals of time at one study site a parasitologist deals with the representatives of different populations of hosts and, consequently, with different populations of their parasites. Overlap of the data on infection of birds belonging to different populations may cause significant fluctuations in the values of many parasitological indices without any relation to the peculiarities of the transmission of the parasites at the study site. The situation with *Leucocytozoon* spp. distribution on the Curonian Spit in the Baltic Sea is a clear example of this fact (Valkiūnas, 1984b). Consider as an example the peculiarities of *Fringilla coelebs* infection with *Leucocytozoon* spp. This is one of the best studied birds

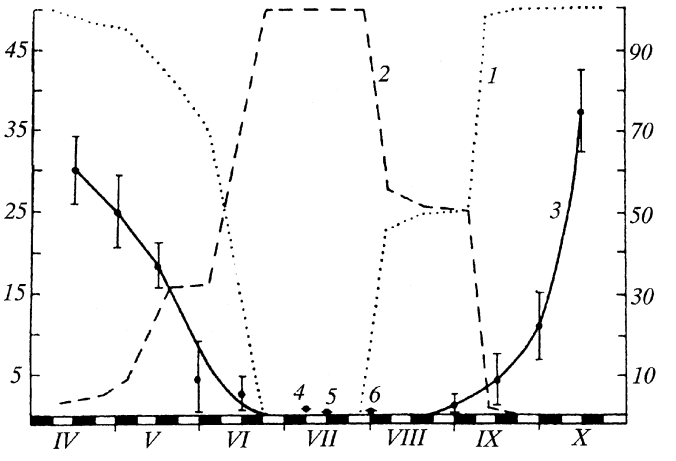

Figure 43 Infection of adult *Fringilla coelebs*, trapped on the Curonian Spit, with leucocytozoids in relation to the affiliation of the bird population:
1 – F. coelebs from the northern populations migrating over the Spit; *2 – F. coelebs* from the local Curonian population (modified from Sokolov, 1982); *3* – prevalence of *Leucocytozoon* spp.; *4–6* – several cases of *Leucocytozoon* infection recorded in birds of the Curonian population. The abscissa is the calendar in months, and the ordinate: on the right – the number of trapped birds, %; on the left – the prevalence of infection, %. Vertical lines are 95% confidence limits.

of the forest zone in Europe. In the summer time, when only the representatives of the local (breeding) population of birds are present on the Curonian Spit, *F. coelebs* infected with *Leucocytozoon* spp. are recorded extremely rarely (Fig. 43). This is explained in the following way. Due to several reasons, *Leucocytozoon* spp. are not transmitted on the Curonian Spit (see p. 151). Young birds born on the Curonian Spit are completely free from these parasites. Adult birds of the local population rarely get infected with *Leucocytozoon* spp. during seasonal migrations (Valkiūnas, 1993b). The Curonian population of *F. coelebs* is relatively stable in the sense that local birds return for breeding only on the spit, while those flying over do not incorporate into the population or their number is quite negligible (Sokolov, 1991). All this reveals that in summer *Leucocytozoon* spp. are rarely found in *F. coelebs* on the Curonian Spit. A great number of *F. coelebs* of all ages infected with *Leucocytozoon* spp. is recorded on the Curonian Spit in spring and autumn during seasonal migrations. Moreover, the greatest prevalence of infection is recorded in April and October that coincides with the period of mass migration of the northern populations (Karelian, Finnish, etc.). The ringing data indicate that in autumn the local population of *F. coelebs* leaves the Curonian Spit for wintering before the migration of the Baltic and the next northern population starts. Spring migration occurs in the opposite order: the northern populations migrate over the spit earlier than the southern ones (Shumakov and Sokolov, 1982). These data are in good agreement with the data on the seasonal dynamics of bird infection with *Leucocytozoon* spp. (Fig. 43). Different species of *Leucocytozoon* are common parasites on the Curonian Spit during the stay of migratory birds. Moreover, the more representatives of the northern populations stop in the region, the more infected birds are found. This conclusion leads to consequences interesting in the practical and theoretical aspects. First, to estimate the actual frequency of infection in a particular bird population, the data must be carefully analyzed with reference to the ornithological situation at the site

of investigation. Secondly, prevalence of infection in nonringed birds reflects the local parasitological situation only during a short period in summer, when migrating birds are absent from the region (for example, from June 10 to August 10 on the Curonian Spit in the Baltic Sea); however, the period might be prolonged for about a month by investigating the ringed specimens, females with signs of breeding (brood spots), and birds caught on the nests. Third, the change of the population composition of birds during seasonal migrations allows one to investigate in one geographical point the parasites originating from distant regions. Without taking into account the dynamics of the composition of the bird population, it is difficult to explain the peculiarities of the difference of infection of the same bird species with haemosporidians and many other groups of parasites found at the study site at different times.

Far inter-population dispersion is another feature of the biology of birds needed to be taken into account in the ecological studies of the parasitologists. Incorporation of immigrants from other populations, whose proportion is sometimes significant, into a population under study is a common feature for some bird species (Sokolov, 1991). As this takes place, parasites normal and abnormal in the local bird populations may be introduced. The share of the abnormal parasites, which normally do not complete their development cycle at the study site, is sometimes large. In the case of short-term field observations this makes the understanding of the peculiarities of the transmission of parasitic organisms and the analysis of epidemiological situation at the study site more difficult. For example, a great number of birds infected with *Leucocytozoon* spp. in the Curonian populations of *Parus major* (prevalence of the infection is 14.3%, 95% confidence limit is 7.6 to 23.7), *Phylloscopus sibilatrix* (14.2%, 4.8 to 30.3), *Sylvia atricapilla* (47.6%, 38.9 to 61.1) is a result of the incorporation of distant (inter-populational) immigrants (Valkiūnas, 1998). The young birds born on the Curonian Spit are not infected with these parasites (see p. 173 for details). It is important to take this fact into consideration because it sets up a situation where only chronic infections (relatively benign in comparison to acute ones) are present in populations of the above-mentioned species of birds on the Curonian Spit. No doubt, such territories are not suitable for investigating the parasite influence on free-living populations, because the initial acute infections are absent there.

And finally, we have already mentioned that the annual migrations of birds to southern latitudes provide an opportunity of regular import of parasites acquired by birds in the wintering areas and on the routes of their migration into the breeding areas of these birds. Different populations of the birds of one species are characterized by different time and routes of their migration that determines a different probability to record the so-called 'migration' and southern forms of parasites even in the sympatric populations of the hosts. The registration of 'alien' elements in the fauna of parasites in the breeding areas of birds may cause erroneous conclusions. The data on the prevalence of such infections should be carefully interpreted as they are not connected with transmission during the breeding season. As a result, acute infections may be absent at the study site, while only low chronic parasitemias may be recorded. For example, *Haemoproteus pallidus* is common in *Ficedula hypoleuca* on the Curonian Spit in the Baltic Sea, but a great majority of the birds of this population are infected in over-wintering sites in Africa (Valkiūnas, 1998). A special chapter of this book is dedicated to the discussion of the role of the seasonal migrations in the distribution of haemosporidians (see p. 145).

The investigation of the mechanism regulating the density of populations of parasites and their hosts is one of the main problems of general parasitology. It is important to find out the changes in the structure of the populations of hosts and parasites as well as the factors

determining these changes. Related to this, it is necessary to clearly distinguish between the changes of the parasite population due to purely external reasons related to the seasonal transformations of the populations of their hosts or those occurring in time and space after the breeding period, but not associated with the peculiarities of the transmission of parasites at the study site. It is difficult to understand the peculiarities of the transmission and dynamics of the populational structure of bird parasites without taking into account the data of the ornithological investigations and without analysis of the age and seasonal variations of the fauna of parasites and the prevalence of data. Further development of general parasitology can progress mainly on the basis of comprehensive long term populational investigations, carried out together with the representatives of various biological disciplines.

SAMPLING BIAS IN NETTING, TRAPPING, AND SHOOTING OF BIRDS

Most ecological investigations on haemosporidians and other parasites are based on birds caught in mist nets or stationary traps, for example, big Rybachy traps on the Curonian Spit in the Baltic Sea. Only relatively healthy specimens that have been leading an active life in nature are available for investigation using these methods of netting and trapping; but birds weak due to the parasitic infections are undersampled because they are inactive. All active birds are below a threshold level of parasitemia in the wild (Valkiūnas, 1993a). This value is about 40 to 50 parasites per 1000 erythrocytes (or 4 to 5%) in species of *Haemoproteus* in juvenile birds, and it is even less for *Plasmodium* and *Leucocytozoon* spp. This explains why the heavy parasitemia has been extremely rarely recorded in birds captured by netting and trapping even on the endemic territories, but it is common in experimental captive birds and may be detected in the wild using other methods. One example is analyzed here. The intensity of parasitemia of *Haemoproteus fringillae* on the Curonian Spit does not exceed 5% of the erythrocytes, and it is usually considerably less (about 1% or less) in juvenile *Fringilla coelebs* that were caught with mist nets and big Rybachy traps. The maximum level of parasitemia in adult birds may be higher, but usually it does not exceed 10%. Exceptions are extremely rare and were recorded only in adult birds (Bennett *et al.*, 1993e). However, the primary parasitemia significantly exceeds the above-mentioned level, and may reach 25% at the peak of parasitemia in naturally infected juvenile *F. coelebs* that have been monitored in the laboratory. Moreover, heavily infected young *F. coelebs* were shot (the recorded level of the maximum intensity of parasitemia was as high as 122 gametocytes per 1000 erythrocytes, or approximately 12%), and also found as road kills (the same value of the parameter 69/1000 or 7%) (Valkiūnas, 1998). It is interesting to note that a male *Parus major* heavily infected with *H. majoris* was recorded by the author in the north of Lithuania. This bird was caught by a domestic cat. In this case the intensity of the parasitemia exceeded 30% of erythrocytes. These facts can be explained in the following way. It was shown that infected young *F. coelebs* become less mobile at the peak of parasitemia (Valkiūnas, 1993a). Reduced mobility during the heavy stage of infection makes the birds more vulnerable to predators and during other unfavourable situations. It implies a reduced ability to compete and an increased mortality rate in nature. If birds survive the primary acute attack of the parasites, then they may be caught in mist nets. This situation leads to two important conclusions. First, only a relatively healthy part of the bird population is usually available both to the ornithologists and parasitologists who use

traditional methods of netting and trapping for catching the birds. The heavily infected specimens are undersampled because they are inactive. Therefore, special methods of investigation should be designed to measure the real impact of parasites. These methods must allow the observer to follow the fate of the birds during the acute stage of infection. Second, the data on recaptures of wild ringed infected and noninfected birds, based on netting and trapping, do not necessarily contribute to the understanding of the vitality of the individuals because infected birds are specimens that have already passed through an acute stage of the infection and have acquired premunition (Ahmed and Mohammed, 1978a; Garnham, 1980; Valkiūnas, 1998). Furthermore, the method does not give any information on the fate of birds from the group of noninfected specimens that gained the parasites between two periods of recapture. The data on recaptures of *F. coelebs*, either noninfected or infected (low chronic parasitemia) with *H. fringillae,* on the Curonian Spit were analyzed by Valkiūnas (1998). The proportion of recaptured chronically infected and not infected birds during the first year of their life based on ringing studies was almost identical. Surprisingly, the data shows that a significantly lesser number of noninfected than infected birds was recaptured in the successive year. One may speculate that some of the noninfected birds have subsequently gained the infection and did not survive the primary attack of the parasites. According to our data, over 20% of noninfected *F. coelebs* gain the infection in the second year of life on the Curonian Spit. Probably, some of the infected birds were eliminated as it was recorded in juvenile specimens during the first year of their life (Valkiūnas, 1993a). These examples show that, in order to measure the real impact of the parasites, the results on recaptures of infected and noninfected birds should be carefully interpreted taking into account all aspects of the disease epidemiology. Ideally, field studies should also be supplemented by the experimental work.

It is noteworthy that much of the research in general parasitology has been based on blood parasites of game birds obtained by shooting. The shooting season is usually strictly restricted to a nonbreeding period (early spring and late autumn in the Holarctic) when parasitemias are chronic or latent. This explains the rarity of recordings of heavy parasitemias in shot game birds. Consequently, the shooting data on infection intensity and prevalence in game bird populations should be carefully interpreted when used in ecology and evolutionary biology. It is noteworthy that, according to our data, the heavily infected (more than 5% of erythrocytes) *Ficedula hypoleuca* and *Parus major* were never sampled from nest-boxes. It is likely that they do not enter the boxes at the crisis of infection. These examples also show that new methods of investigations should be designed to monitor the heavily infected part of the bird population.

THE PROBLEM OF PARASITE SPECIES IDENTIFICATION

It is important to note that the identification of the species of bird Haemosporida is either rarely performed or not always correct in the studies on ecology and evolutionary biology. Some misidentifications are common. For example, *Haemoproteus pallidus* parasitizing *Ficedula hypoleuca* and *F. albicollis* has rarely been distinguished from *H. balmorali*. Correct identification is important because the ecology, life histories, and virulence of different species are different and insufficiently investigated or even unknown for many species of bird parasites. Papers on ecology and evolutionary biology based only on generic identification do not match the requirements of present day parasitology.

THE DIFFICULTY OF ESTIMATING THE TRUE PREVALENCE OF INFECTION BY BLOOD FILM SURVEYS

An advantage of the ecological research using haemosporidian parasites as a model is that, once infected, birds remain infected either for life or many years (Garnham, 1966; Desser and Bennett, 1993; Valkiūnas, 1996; 1998). This allows a long-term control of the infected ringed birds in natural populations. However, the period of patent infection is seasonally restricted and totally different in species of *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*. In the northern part of the Holarctic, most species of malaria parasites (genus *Plasmodium*) cannot be found in the blood in early spring and during the autumnal migration. The period of chronic parasitemia of *Haemoproteus* spp. is longer than that of *Plasmodium* spp.; however, gametocytes of most species of *Haemoproteus* are usually absent in the blood in the early spring migration, and they gradually disappear from the blood during the autumnal migration. Extensive examination of blood smears may reveal a few gametocytes of *Leucocytozoon* spp. in the early spring migration as well as during the late autumnal migration and even in winter. As a rule, birds infected with *Plasmodium* and *Haemoproteus* spp. cannot be found during early spring or late autumnal migration by blood film survey, but *Leucocytozoon* spp. are often recorded. That is why the data on prevalence of infection based on blood film microscopy should be critically analyzed in ecological investigations of haemosporidians. One should observe the rule that the absence of parasites in the blood does not necessarily mean that the birds investigated are not infected. In the northern part of the Holarctic, the best season for blood investigation using a microscope is May–July. During this period, most infections are patent. Moreover, for *Plasmodium* spp., the period of acute infection is short with few parasites present in the blood during the chronic parasitemia even during the season of active transmission. An extensive examination of blood films is necessary; however, this is not always enough to detect a *Plasmodium* infection. It should be mentioned that even when recorded, most of these chronic infections of *Plasmodium* spp. couldn't always be identified to the specific level, even by experts, due to low intensities and common mixed infections. Experimental subinoculation of blood from wild birds into susceptible captive hosts gives better results, but it is expensive. As a rule, examination of blood films reveals only a part of the real distribution of malaria. It is noteworthy that the same is true for *Trypanosoma* spp. as the intensity of *Trypanosoma* spp. parasitemia is usually low. The microscopy of blood smears is an insensitive method to determine the prevalence of *Trypanosoma* infection in birds. The method of cultivation of the parasites is at least five to seven times more sensitive (see Kirkpatric and Lauer, 1985; Valkiūnas, 1993a). Thus, the data on prevalence of *Plasmodium* and *Trypanosoma* spp. infections obtained by the blood-smear technique does not reflect the parasitological situation in free-living populations. Such data cannot be used to illustrate theories in evolutionary biology. Immunological methods and molecular techniques are applicable for the estimation of the prevalence of infection (Graczyk *et al.*, 1994b; Waldström *et al.*, 2002) and promising on the generic level, but are still inaccurate for identification of the parasite species.

The examples considered illustrate only some of the problems faced by the researchers in their field studies of bird parasites. It is clear that the solutions of the problems of general parasitology require a wider use of the data accumulated by particular sciences on migration, population structure, bioenergetics, alimentary and social behaviour, reproduction, and demography of the hosts. Without this, it is impossible to reach a high level in populational ecological investigations.

Where possible it is expedient to use birds with unique life histories in the solution of general parasitology problems because this facilitates the understanding of the processes occurring in nature (Valkiūnas and Iezhova, 2001b). These birds include, for example, *Loxia curvirostra*, whose breeding period in the Northern Palearctic frequently occurs in the winter and early spring months, when vectors are inactive, and haemosporidians are not transmitted (see p. 149), or *Cuculus canorus*, which is characterized by brood parasitism mainly in passerines (see p. 71). The peculiarities of the formation of fauna of parasites in animals with unique life histories is a key to the solution of some disputed ecological problems using relatively simple and inexpensive methods.

To stimulate progress in ecology and evolutionary biology using parasites as a model, joint projects on parasitology, ornithology, and evolutionary biology are to be recommended. The participation of parasitologists is important not only during the phase of investigation of blood smears and identification of species of parasites (as usually is the case), but also during the phases of planning and data analysis. This would reduce the epidemiological mistakes (see p. 181) in ecological and evolutionary studies using parasitological data.

The Role of Seasonal Migrations in the Distribution of Bird Haemosporidians

Migration is a common phenomenon in the animal world. There are species among crustaceans, insects, fish, amphibians, reptiles, mammals, and other animals that migrate more or less regularly. The seasonal migrations of birds, however, have no analogy in the animal world in their scale and regularity. In different seasons of the year, approximately half of all bird species changes their place of living (Curry-Lindahl, 1984). The major part of the migrating birds breed in the Holarctic. Migrations of birds in the tropics and such types of migrations as vertical, water and land, weather, recurrent, drinking, and others have been much less studied by ornithologists than seasonal migrations. The data of their influence on the distribution of the parasitic organisms are poor. The description below refers primarily to the seasonal migration of the Holarctic migrants to the southern latitudes and back. The accumulation of information about the spatial displacement of various groups of parasitic organisms developing in very motile migrating birds is interesting from the theoretical point of view in the understanding of the peculiarities of the distribution of parasites on the planet, their penetration into new hosts and distribution in new territories, which finally would allow scholars to approach the problem of forecasting the global parasitological situation.

It is well known in parasitology that seasonal migrations providing a long stay of the same individuals in regions with strongly different ecological conditions is one of the factors influencing the fauna of animals' parasites. V.A. Dogiel was first to start a wide study of the parasite fauna in migrating birds. The investigations carried out by Dogiel and Karolinskaya (1936), Dogiel and Navtsevich (1936), Dubinin (1938), Markov (1939), Dubinin and Dubinina (1940), were summarized by Dogiel (1949) and later supplemented by Belopolskaya (1956, 1959) and Bychovskaya-Pavlovskaya (1962). They allowed one to distinguish the important rules of the ecology of the migrating birds' parasites in association with the ecology of their hosts. The main results of the papers cited were generalized in one of the classical monographs on general parasitology (Dogiel, 1962, 1964). These studies became the foundation of investigating the relations of animal hosts with a wide range of parasites including the blood protists. Dogiel and Navtsevich (1936) were first to show that haemosporidians of *Delichon urbica* at the latitude of St. Petersburg are southern forms by the place of infection. Markov (1939) considered that migrations of *Sturnus vulgaris* played a main role in infecting with *Haemoproteus* sp. During the last 50 years, a great amount of data (some of them are contradictory) was accumulated in the literature about the influence of migrations on infecting the birds breeding in the Holarctic with blood protists. Some scholars consider that the migration of birds of England is an important factor of infecting with blood parasites (Bennett *et al*., 1974a; Peirce and Mead, 1976; Peirce, 1981b). Peirce (1981b) considers that this situation may be observed in birds of the other European countries. Many Baltic migrating birds were found to be infected with

haemosporidians beyond the breeding areas (Valkiūnas, 1984b, 1989c). Kučera (1981a, 1981b) considers that distribution of blood parasites in the birds of Central Europe is caused by mechanisms different from migrations. Similar conclusions were made in the analysis of birds infection with haemosporidians in Canada (Bennett *et al*., 1976, 1978; Bennett and Bishop, 1990a). Glushchenko (1963) recorded a greater infection prevalence in migrating birds compared to nonmigrating ones in Ukraine. Dilko (1966) holds the opposite opinion on the basis of investigating the birds in Belarus. Burtikashvili (1976) and Zeiniev (1975a) found that the percentage of infected birds is greater in Transcaucasian nonmigrating birds in comparison to migratory ones. In Middle Asia and Kazakhstan, one group of scholars finds that the prevalence of infection is greater in migrating birds (Abidzhanov, 1967; Subkhonov, 1973), while the others have the opposite results (Ulugzadaev and Abidzhanov, 1975). Madalov and Esikov (1974) consider that migrations of sparrows in Kirgizia does not play any significant role in their infection with blood parasites. Nevertheless, they show the data that prevalence of infection in migrating sparrows (*Passer indicus*, *P. hispaniolensis*) is two times greater than in nonmigrating ones (*P. domesticus*, *P. montanus*).

In many of the above cited works, the role of migrations in the infection of birds with blood parasites is estimated without any account for the data of the time and routes of migration and areas of wintering. Even more, unreliable methods are frequently used to solve the problem. For example, some scholars sum up the long term data obtained in different seasons during the investigation of birds of different age and species to find the difference in the overall prevalence of infection between migrating and nonmigrating birds. In this case they ignore that the previously mentioned factors taken by one have a sufficient influence on the problem considered. The values of infection prevalence obtained this way are often random and do not reflect the real parasitological situation. It is important also to mention that the comparison of infection in migrating and nonmigrating birds does not always allow one to estimate the peculiarities of the quantitative and qualitative contribution of migrations into the fauna and distribution of parasites at the study site. The problem lies in the fact that migrating and nonmigrating birds usually belong to different systematic groups with different life histories and ecology, and the species of their parasites are different due to the specificity of haemosporidians (Valkiūnas, 1984b). For example, we failed to find *Haemoproteus* spp. in more than 200 specimens of nonmigrating *Dendrocopos major*, *D. minor,* and *Certhia familiaris* studied in the Eastern Baltic region, although these parasites are common in small migrating passerines belonging to the families Sylviidae, Fringillidae, Muscicapidae and many others, and they infect a significant part of young birds at the breeding areas. Thus, the comparison of infection prevalence in migrating and nonmigrating birds is not always a reliable method to estimate the role of migrations in the distribution of haemosporidians. A wide application of these methods in some of the papers cited is one of the main reasons why there are so many alternative concepts in the literature concerning the same phenomenon.

Birds are extremely motile creatures. To get reliable facts about the transmission of one or other parasite on the study site, one has to know the structure of the bird populations studied (Valkiūnas, 1986a, 1996, 1998). When studying wild bird parasites, one should take into account the possibility that during seasonal migrations the representatives of different bird populations, and thus parasites, may be present at the study site as well as immigrants, which may incorporate into the bird population under study; this may lead to the introduction of parasites not characteristic for the study site. Sometimes the share of such immigrants is large (Vysotsky and Valkiūnas, 1992, 2001). Ignoring these and other peculiarities in the work with bird parasites sometimes becomes the reason of unfortunate

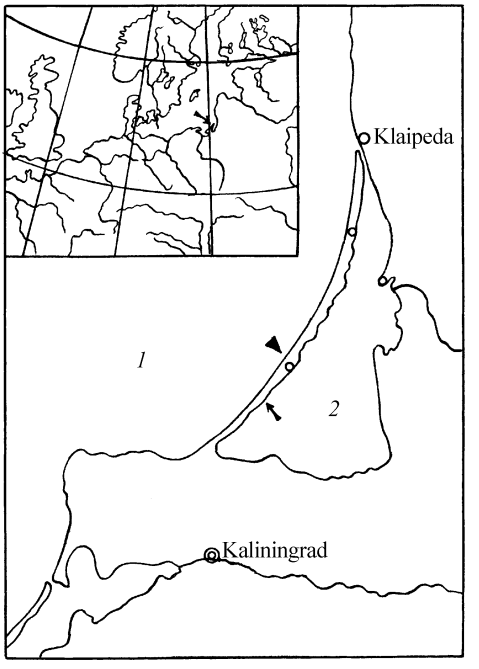

Figure 44 Location of the Biological Station (arrow-head) of the Zoological Institute, Russian Academy of Sciences, and the place of material collection (arrow):
1 – the Baltic Sea, *2* – the Curonian Lagoon.

incorrect conclusions. In natural conditions, it is difficult to understand the outline of the parasitic organisms transmission without using the ornithological methods of marking (ringing) the birds, as well as without studying the seasonal and age peculiarities of infection of the hosts from certain populations (see p. 137). The papers that study the role of seasonal migrations in the distribution of blood parasites carried out at the level of separate populations including ornithological methods of ringing are, however, not numerous (Bennett *et al*., 1976, 1978; Valkiūnas, 1984b, 1989c; Bennett and Bishop, 1990a; Valkiūnas and Vysotsky, 1991; Valkiūnas, 1993b).

In this chapter we analyze only the results of populational studies, of which a major part was obtained at the Biological Station of the Zoological Institute, Russian Academy of Sciences on the Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E) (Fig. 44). At present, this Palearctic region is one of the best studied from the point of view of the role of migrations in the distribution of haemosporidians. In this relation let us first consider the data obtained on the Curonian Spit (Valkiūnas, 1984b, 1989c; Valkiūnas and Vysotsky, 1991; Valkiūnas, 1993b).

Birds breeding on the Curonian Spit and those passing this region winter in Europe, Africa, and Near East. Only *Carpodacus erythrinus* fly to Southern Asia (Payevsky, 1971). According to the possibility of infection with bird blood parasites, the entire wintering territory can be conventionally divided into three zones significantly differing by the activity of vectors during the period that migrants stay in the regions: zone I is characterized by cold and moderate winters, zone II is characterized by mild winters, and zone III is the one with warm winters (Fig. 45).

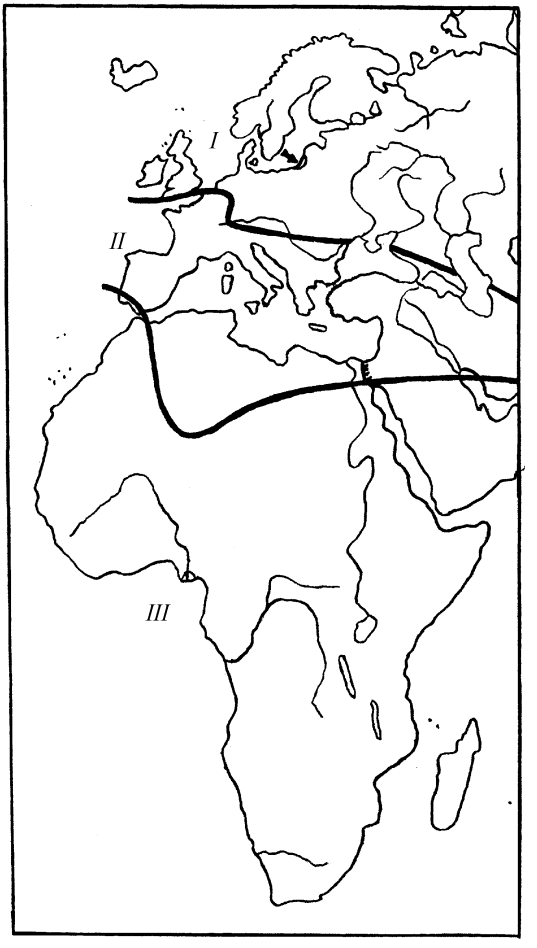

Figure 45 Sketch-map of wintering zones of birds of the Curonian populations and other ones migrating over the Curonian Spit:
I – zone of cold winters; *II* – zone of mild winters; *III* – zone of warm winters. Arrow indicates the site of material collection.

The southern boundary of zone I in Eastern and Central Europe approximately coincides with the mean January 0°C isotherm, while in Western Europe it is located slightly to the south of this isotherm. We include Great Britain in this zone, where there is no transmission of infection in the late autumn, winter, and early spring (Baker, 1975). The so-called nearest or near-distance migrants winter in this area. These are the birds belonging to the families Strigidae, Troglodytidae, Regulidae, Sturnidae, Corvidae, part of Paridae, and Fringillidae. The major part of them fly to the wintering areas late (October–December) and leave them early (February–March). During this period, the blood parasites are not transmitted in zone I because the vectors are inactive. The probability of infection of nearest migrants with blood parasites is thus low both in the wintering and migration areas. They are infected on the breeding territories. Few bird groups, that are known at present, are exclusions.

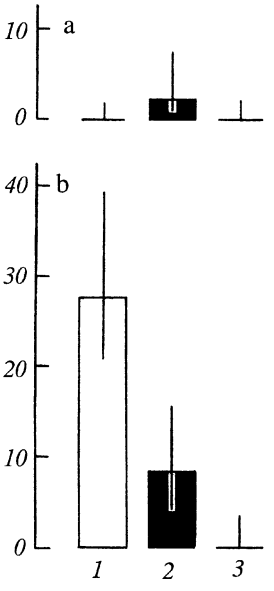

Fig. 46

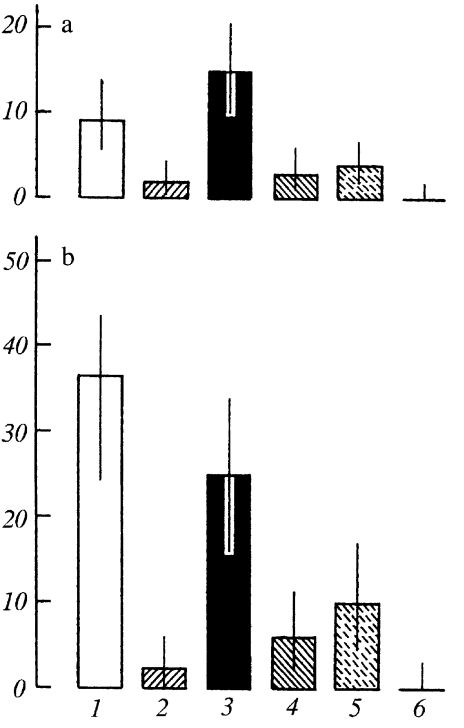

Fig. 47

Figure 46 Infection of young *Sturnus vulgaris* at the beginning of the seasonal migration toward wintering (*a*) and adult birds of this species after arrival from wintering (*b*) with haemosporidian parasites:
1 – Haemoproteus pastoris; *2 – Leucocytozoon* sp.; *3 – Plasmodium* sp. The ordinate is the prevalence of infection, %. Vertical lines are 95% confidence limits.

Figure 47 Infection of young (*a*) and adult (*b*) *Loxia curvirostra* with haemosporidian parasites during summer movements over the Curonian Spit:
1 – Haemoproteus tartakovskyi, *2 – H. fringillae*, *3 – Leucocytozoon fringillinarum*, *4 – L. dubreuili*, *5 – L. majoris*, *6 – Plasmodium* sp. Other symbols are as in Fig. 46.

The migrants which move to the wintering areas in summer are included in the first group. For example, movements of *Sturnus vulgaris* in the usual direction of autumnal migration start already in July (Payevsky, 1971). At this time young *S. vulgaris* are not infected with *Haemoproteus pastoris*. After the return from wintering this parasite is present in the blood of many *S. vulgaris* (Fig. 46). This gives reason to assume that the birds gain the haemoproteids during the summer migration towards their wintering areas. It is not likely that they gain the parasites in wintering areas (December–January) and on the route of their migration in spring (February–March) in zone I. Similar results were obtained by Markov (1939) while investigating the parasites of *S. vulgaris* in the vicinity of St. Petersburg.

Loxia curvirostra is a representative of the second group of birds infected with haemosporidians in zone I during migration (Valkiūnas and Iezhova, 2001b). The breeding period of these birds, migrating through the Curonian Spit where they do not breed, usually takes place in the end of winter and beginning of spring (Malchevsky and Pukinsky, 1983). At

Table 8 Prevalence of haemosporidian parasites in young birds which have been hatched on the Curonian Spit and do not yet migrate.

Family and species of birds	Number of examined birds	Infected					
		Haemoproteus sp.		*Leucocytozoon* sp.		*Plasmodium* sp.	
		Number	*p*, %	Number	*p*, %	Number	*p*, %
Fringillidae							
Fringilla coelebs	509	205	40.3 (35.7–44.4)	0	0.0 (0.0–0.7)	0	0.0 (0.0–0.7)
Sylviidae							
Hippolais icterina	348	143	41.1 (34.8–45.3)	0	0.0 (0.0–0.9)	0	0.0 (0.0–0.9)
Phylloscopus trochilus	296	51	17.2 (12.6–21.2)	0	0.0 (0.0–1.0)	0	0.0 (0.0–1.0)
Sylvia atricapilla	137	78	56.9 (48.7–65.4)	0	0.0 (0.0–2.1)	0	0.0 (0.0–2.1)
Muscicapidae							
Ficedula hypoleuca	164	13	7.9 (4.3–12.9)	0	0.0 (0.0–1.8)	0	0.0 (0.0–1.8)
Total	1454	490	33.7 (32.5–34.2)	0	0.0 (0.0–0.0)	0	0.0 (0.0–0.0)

Note: 95% confidence limits of prevalence of the infection are given in parentheses.

that time, the vectors of haemosporidians are not active in the Northern Palearctic. Thus, juvenile *L. curvirostra* may become infected with haemosporidians only during summer movements after breeding period. In summer, these birds actively move between the regions with a rich crop of fir and pine tree seeds. *Loxia curvirostra* gain all species of haemosporidians (Fig. 47) precisely during this period of the year.

Zone II is characterized by a short mild winter, late autumn, and early spring. The southern boundary of this zone in Western Africa, approximately coincides with the mean January 10°C isotherm, while in Eastern Africa it is located somewhat more to the south. The vectors usually are not active during the coldest period of the year. Let us conditionally call the birds wintering in this zone as middle-distance migrants. They include the major part of the Fringillidae, part of the Turdidae, Alaudidae, Accipitridae, and Charadriidae and some others. All these birds leave the breeding areas relatively late (September–November) and arrive at the breeding areas early (March–April). It is not likely that the birds are infected with blood parasites during the coldest months in the wintering areas in zone II, because the vectors are not active or weakly active. It is also not likely that they are infected with the parasites on their migration route in autumn, because the middle migrants cross zone I in September–November, when the vectors are already not active, and reach the wintering areas in November–December (Payevsky, 1971), when the activity of the vectors significantly decreases. In March–April, the migrants may be attacked by the vectors in zone II. In April, infection with blood parasites is observed in the nestlings of local birds (Mohammed, 1958). Middle-distance migrants may gain blood parasites in the wintering areas and on the migration route in spring mainly in zone II.

Table 9 Prevalence of *Plasmodium* and *Leucocytozoon* spp. in young birds of Curonian origin before autumnal migration.

Bird species	Number of examined birds	Infected, *p*, %
Ficedula hypoleuca	164	0 (0.0–1.8)
Fringilla coelebs	509	0 (0.0–0.7)
Hippolais icterina	348	0 (0.0–0.9)
Parus major	62	0 (0.0–6.0)
Phylloscopus trochilus	296	0 (0.0–1.0)
Total	1379	0 (0.0–0.0)

Note: 95% confidence limits of prevalence of the infection are given in parentheses.

Zone III is characterized by a warm winter. The blood parasites vectors are more or less active throughout the whole period of the stay of migrants. The so-called far-distance migrants, which are representatives of the families Caprimulgidae, Apodidae, Upupidae, Hirundinidae, Motacillidae, Muscicapidae, Sylviidae, Oriolidae, part of the Turdidae, and some others winter in zone III (Payevsky, 1971; Žalakevičius *et al*., 1995b). All of them leave the breeding areas early (August–September) and return to the breeding areas late (May), being attacked by the vectors not only during the entire wintering period in zone III, but also when they cross zone II in autumn and especially in spring. The majority of far-distance migrants spend about nine months beyond their breeding area. The likelihood that these birds acquire blood parasites outside the breeding areas is high.

The discussion below refers primarily to birds wintering in the Mediterranean zone and Ethiopian zoogeographical region.

Long-term observation of a large number of ringed birds (Valkiūnas, 1993b) show that the birds of the Curonian populations are infected with *Haemoproteus*, *Leucocytozoon,* and *Plasmodium* spp. Haemoproteids are actively transmitted on the spit, while leucocytozoids and many species of malaria parasites do not, however, complete their cycle of development in the region. This can be seen from the absence of *Leucocytozoon* and *Plasmodium* spp. in young birds hatched on the Curonian Spit, which did not make seasonal migrations (Tables 8 and 9). It is likely that a relatively low monthly mean temperature in summer, which does not exceed 18°C even in the warmest months (Dolnik and Payevsky, 1982), is one of the obstacles for the transmission of malaria parasites, especially those of south origin, on the spit in some years (see also p. 158). The absence of the vectors (simuliid flies) is an obstacle for the transmission of leucocytozoids here. There are no places for breeding of simuliids on the Curonian Spit (bodies of water with clean water rich with oxygen, quickly flowing brooks, etc.), while the isolation with water basins of the Baltic Sea and Curonian Lagoon prevents the penetration of the flies from the mainland (Fig. 44). The lack of transmission of leucocytozoids and the lack or weak transmission of malaria parasites on the Curonian Spit provides an opportunity to carry out a quite precise quantitative estimate with relatively simple methods of the role of seasonal migration of birds in the import of parasites of southern origin into the breeding areas. The birds of the Curonian populations not infected with leucocytozoids and malaria parasites at the breeding areas, which are distinguished by ringing, are indicators of parasites imported from the south after the birds return from wintering. As one can see from Table 10, after the birds of the Curonian origin arrive from over-wintering, they import parasites, which are not characteristic of the breeding area. All of them are acquired beyond the breeding area. On the Curonian Spit we distinguish

Table 10 Prevalence of haemosporidian parasites of the south origin in birds of the Curonian origin after arrival from wintering.

Bird species	Number of examined birds	Infected			
		Leucocytozoon sp.		*Plasmodium* sp.	
		Number	*p*, %	Number	*p*, %
Ficedula hypoleuca	70	0	0.0 (0.0–4.2)	4	5.7 (2.0–12.6)
Fringilla coelebs	200	9	4.5 (2.0–8.0)	2	1.0 (0.1–3.5)
Hippolais icterina	82	1	1.2 (0.0–6.7)	8	9.7 (4.3–17.6)
Phylloscopus trochilus	122	0	0.0 (0.0–3.6)	7	5.7 (2.7–13.0)
Sylvia atricapilla	38	0	0.0 (0.0–8.8)	4	10.5 (2.9–24.2)
Total	512	10	2.0 (0.9–3.6)	25	4.9 (3.2–7.0)

Note: 95% confidence limits of prevalence of the infection are given in parentheses.

the following parasites that birds gain in the south: *Leucocytozoon dubreuili*, *L. fringillinarum*, *L. majoris*, *Plasmodium circumflexum*, *P. fallax*, *P. relictum*, *P. rouxi*, *P. vaughani,* and *P. (Haemamoeba)* sp. Quantitative data about the prevalence of Curonian birds' infection with haemosporidians of southern origin (Table 10) contributes to the quantitative understanding of the role of seasonal migrations in the distribution of these parasites.

During seasonal migrations, the birds of the Curonian populations and more northern ones (Karelian, Finnish, Baltic, etc.) form the so-called West European migration flow. They have relatively stable, quite compatible routes of migration and areas for wintering (Menzbir, 1934; Payevsky, 1971; McClure, 1974; Žalakevičius *et al*., 1995b). Thus, the share of the Curonian origin birds infected with leucocytozoids and malaria parasites (Table 10) may be conventionally accepted as the reference level of the import of the protists into the western part of the North Palearctic and, in this way, we can make a first order quantitative approximation of the number of southern origin parasites in the fauna of northern origin. As one can see from Fig. 48, the birds infected with leucocytozoids in wintering areas and on their migration route (prevalence of the infection in birds of the Curonian origin) form only an insignificant part compared to the total number of birds infected with these parasites in the breeding areas (the prevalence of the infection in young birds of the northern populations during their early autumnal migration through the study site). It is noteworthy that the species composition of leucocytozoids, infecting *Fringilla coelebs*, *Phylloscopus trochilus,* and *Hippolais icterina* at their breeding areas, is similar to the species composition of leucocytozoids imported from the south to the Curonian Spit. It is presented by three species in decreasing order of their prevalence: *Leucocytozoon fringillinarum*, *L. dubreuili,* and *L. majoris*. Thus, annual seasonal migrations of birds into the regions of mild and warm winters do not contribute to the growth of the leucocytozoids

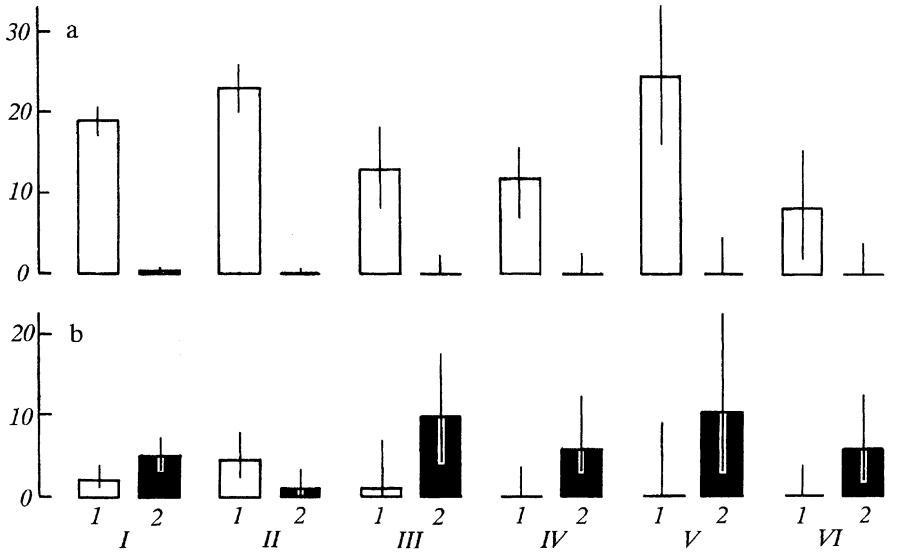

Figure 48 Infection of young birds of northern populations at early autumnal migration (*a*) and adult birds of the Curonian origin after arrival from wintering areas (*b*) with *Leucocytozoon* (*1*) and *Plasmodium* spp. (*2*):
I – summarized data on all investigated bird species; *II – Fringilla coelebs*; *III – Hippolais icterina*; *IV – Phylloscopus trochilus*; *V – Sylvia atricapilla*; *VI – Ficedula hypoleuca*. Other symbols are as in Fig. 46.

fauna richness, and only insignificantly increase the overall prevalence of infection with these protists. The data obtained confirm the concept about the existence of the modern Holarctic centre of leucocytozoids spreading (Valkiūnas, 1987a; Valkiūnas and Iezhova, 2001a). A principally opposing picture was found during the analysis of the infection of the Palearctic migrants with malaria parasites (Fig. 48). In the beginning of autumnal migration (August – beginning of September) *Plasmodium* spp. are rarely found in young birds of northern populations. In spring, however, regular import of these parasites into the breeding areas is done by migrants. Migration of birds to the southern latitudes is an important factor facilitating regular distribution of malaria parasites into Northern and Northwestern Europe. The birds wintering in zone II regularly import *Plasmodium vaughani*, *P. relictum,* and *P. (Haemamoeba)* sp. into the breeding areas. The species composition of the parasites regularly imported into the breeding areas by far-distance migrants is richer. Besides the named species, *P. circumflexum*, *P. fallax,* and *P. rouxi* are quite frequently found. No doubt that malaria parasites of the southern origin compose a significant part of their fauna in the western part of the Northern Palearctic. These data indicate that there is an Ethiopian centre of bird malaria spreading (Valkiūnas, 1987a).

According to the literature data, the greatest prevalence of infection with haemosporidians in birds is recorded in Zambia in December–January (Peirce, 1984h), which coincides with the period when far-distance migrants stay at wintering areas. In Nigeria, the prevalence of infection with *Plasmodium circumflexum* and *P. vaughani* in *Streptopelia senegalensis* reaches 20 and 50%, respectively, while in *Lonchura cucullata*, it is equal to 4 and 30%, respectively (Crewe, 1975). Malaria parasites are common in the birds of Ethiopia (Ashford *et al*., 1976), South Africa (Earlé *et al*., 1991a), and other African

Table 11 Prevalence of haemosporidian parasites in birds of the Curonian origin before and after seasonal migration.

Wintering zone	Bird species	Species of *Haemoproteus*	Group of birds						
			Young still not migrating			Differences	Adult after arrival from wintering		
			Number of examined birds	Infected			Number of examined birds	Infected	
				Number	*p*, %			Number	*p*, %
II	*Fringilla coelebs*	*H. fringillae*	509	191	37.5 (35.7–44.4)		200	92	46.0 (38.0–52.1)
		H. magnus		11	2.2 (1.1–3.7)			6	3.0 (1.1–5.9)
		H. dolniki		17	3.3 (2.0–5.2)			14	7.0 (3.8–11.0)
III	*Hippolais icterina*	*H. belopolskyi*	348	116	33.3 (29.3–39.4)	*	82	80	97.6 (91.5–99.7)
	Phylloscopus trochilus	*H. belopolskyi*	296	40	13.5 (9.7–17.5)	*	122	36	29.5 (21.3–37.8)
	Sylvia atricapilla	*H. belopolskyi*	137	69	50.4 (41.6–58.4)	*	38	38	100.0 (91.2–100.0)
	Ficedula hypoleuca	*H. pallidus*	164	1	0.6 (0.0–2.7)	*	70	24	34.3 (24.7–45.4)
		H. balmorali		6	3.7 (1.6–7.0)			2	2.9 (0.5–8.7)
		H. sp.		7	4.3 (2.0–7.8)			1	1.4 (0.0–6.6)

Note: Wintering zones are described in the legend to Fig. 45. The reliable differences are marked by an asterisk; 95% confidence limits of the prevalence of the infection are given in parentheses.

countries (Valkiūnas, 1987a). These facts form a theoretical basis for understanding the reasons of infection of the Palearctic migrants with malaria, when they get into the African nidi of infection. It is noteworthy that after the birds' arrival from wintering, parasites are found only in those birds that successfully withstood the disease during wintering. It is apparent that birds that perished from malaria, are not recorded. The death rate of the Holarctic migrants due to malaria and other haemosporidioses during wintering remains unknown. The share of infected specimens recorded after their return from wintering reflects only the minimum possible part of birds infected beyond the breeding area. This share, however, exceeds the share of birds infected with malaria in the breeding areas (Fig. 48).

It is likely that the activity of transmission of many species of *Plasmodium* decreases in Europe north of 55° N. While estimating the epidemiological situation on haemosporidioses at a study site, it is important to note that only young birds (that did not migrate yet)

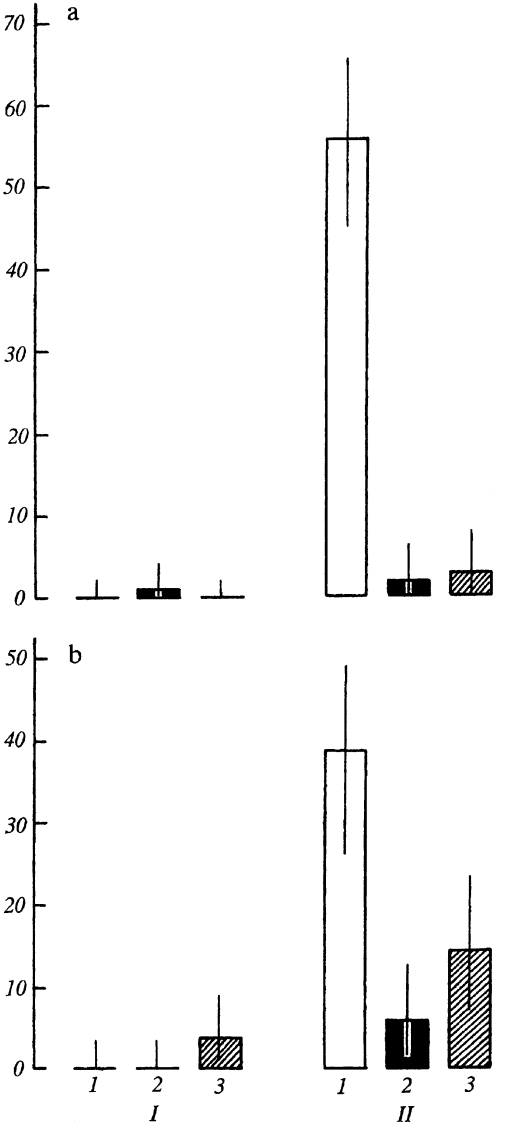

Figure 49 Infection of young *Delichon urbica* with haemosporidian parasites during early autumnal migration (*I*) and adult birds of this species during spring migration (*II*) on the Curonian Spit *(a)* and in the Western Tien Shan (*b*):
1 – Haemoproteus hirundinis; *2 – Leucocytozoon* sp.; *3 – Plasmodium* sp. Other symbols are as in Fig. 46.

can serve as indicators of the parasites transmission but not any birds captured in the region, which is sometimes not taken into consideration by the parasitologists.

The results of microscopic examination of stained blood smears (the main method used in the investigations on the Curonian Spit) reflect only the relative picture of *Plasmodium* spp. distribution, because the patent period is relatively short in many species. A more reliable method of subinoculation of blood was used to search malaria parasites in the

Curonian birds of local origin (Valkiūnas, 1993b). The blood taken from 50 young *Fringilla coelebs,* that did not migrate yet, was subinoculated into 17 birds of the same species kept in captivity and into 10 chickens of White Leghorn breed. We failed to induce *Plasmodium* infection in any of the 27 experimental birds. The intensive microscopic examination of stained blood smears and the results of experiments on blood subinoculation indicate that malaria, which is annually imported by migrating birds from the south, does not usually spread on the Curonian Spit or the transmission is weak and the malaria parasites are difficult to record with the methods used. No doubt the malaria parasites are transmitted in the Northern Palearctic where they have been recorded in numerous bird populations. However, the number of birds infected at breeding areas is significantly less than at wintering areas.

Haemoproteus spp. are actively transmitted on the Curonian Spit (Valkiūnas, 1984b). To evaluate the share of birds infected with these parasites beyond the breeding area and to determine the species composition of the parasites of southern origin, a seasonal-age analysis of infection in five species of birds during the period which follows breeding and after their return from wintering areas next year was carried out. As one can see from Table 11, the share of *Hippolais icterina*, *Phylloscopus trochilus,* and *Sylvia atricapilla* infected with *Haemoproteus belopolskyi*, and *Ficedula hypoleuca*, infected with *H. pallidus*, consistently increases after the birds return to the breeding areas from wintering. It is difficult to explain these facts without assuming that parasites are acquired at the wintering areas or on the route of birds' migration.

The increase of prevalence of infection in spring can be explained, if one assumes that infected birds are more viable and that the number of birds infected with haemosporidians exceeds the number of noninfected ones among those which return to breeding areas. This is, however, inconsistent with the data of immunology, especially for malaria (Garnham, 1966; Shuikina, 1979) and with available results of testing the viability of infected and non-infected birds in nature (see p. 95).

The species of haemoproteids, which are rare or those that have not been found in young birds that had not yet migrated, are regularly found in some birds of the Curonian origin after their arrival from wintering. For example, these are *Haemoproteus hirundinis* and *H. pallidus* (Table 11, Fig. 49). These facts indicate that quite a large number of birds can be infected beyond the breeding areas, because these parasites are found in many *Delichon urbica* and *Ficedula hypoleuca* after they return to the Curonian Spit from wintering. Interestingly, a similar outline of *D. urbica* infection with *H. hirundinis* was recorded in Southern Kazakhstan (Fig. 49). Dogiel and Navtsevich (1936) obtained the same results near St. Petersburg. It is likely that infection of *D. urbica* with haemoproteids occurs in African wintering areas.

The proportion of *Fringilla coelebs* infected with *Haemoproteus fringillae*, *H. magnus*, and *H. dolniki*, as well as *Ficedula hypoleuca* infected with *H. balmorali* and *H.* sp. does not change significantly after the birds arrival from wintering areas (Table 11). It is likely that active transmission of these species occurs mainly in the breeding areas. It is important to note that no significant increase in *Haemoproteus* infection prevalence is found in birds after they return from wintering in the Mediterranean region (*F. coelebs*). At the same time, the proportion of infected individuals significantly increases after migration among the birds wintering in the Ethiopian zoogeographical region (*F. hypoleuca*, *Hippolais icterina*, *Phylloscopus trochilus*) (Table 11). As already mentioned, the species of haemoproteids (*Haemoproteus hirundinis*, *H. pallidus*), which are absent or rare in young birds that had not yet migrated, are frequently found in birds of the second group. These data indicate that migrations to the Mediterranean area and to the Ethiopian

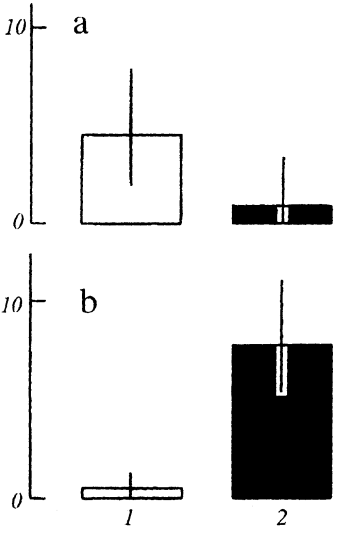

Figure 50 Unequal value of seasonal migrations in the Mediterranean zone (*a*) and in the Ethiopian zoogeographical region (*b*) for the infection of birds of the Curonian origin with *Leucocytozoon* (*1*) and *Plasmodium* spp. (*2*):
a – data on *Fringilla coelebs*; *b* – data on *Ficedula hypoleuca*, *Hippolais icterina*, and *Phylloscopus trochilus*. Other symbols are as in Fig. 46.

zoogeographical region are not equal from the point of view of their infection with *Haemoproteus* spp. The results of our research (Valkiūnas, 1993b) also indicate that the migrations to the west of the Southern Palearctic and to the Ethiopian zoogeographical region are not equal in the infection of birds with *Leucocytozoon* and *Plasmodium* spp. (Fig. 50). Birds wintering in the Mediterranean area have a reliably higher prevalence of infection with leucocytozoids and less prevalence of infection with malaria parasites, while the situation is the opposite for the birds wintering in the Ethiopian region.

The analysis of seasonal and age peculiarities of infection of the Curonian populations of birds with blood parasites as well as the birds migrating through this region (Valkiūnas, 1993b), shows that the Palearctic migrants are infected with haemosporidians in wintering areas and on the migration routes. The birds are more frequently infected with *Leucocytozoon* spp. during their migrations within the Palearctic, while they are infected with *Plasmodium* and *Haemoproteus* spp. mainly during wintering in the Ethiopian zoogeographical region. These data could be understood on the basis of general regularities of the geographical distribution of haemosporidians (Valkiūnas, 1984a, 1987a; Bennett *et al*., 1991d). During seasonal migrations, far-distance migrants only cross the Palearctic (the region of high prevalence of leucocytozoids). They spend the major time of wintering in the Ethiopian region (the region of high prevalence of infection with malaria parasites), while the wintering areas of middle-distance migrants do not spread beyond the Palearctic boundaries. The clear differences in the geographical location of wintering area for the middle-distance and far-distance migrants with respect to the regions of increased prevalence of infection with the parasites and different duration of the birds stay in these regions should influence the overall prevalence of infection with these protists.

The fauna of haemosporidians in far-distance Palearctic migrants is regularly enriched after their arrival from winterings primarily due to the species of haemoproteids and malaria

parasites. This, however, does not change the epidemiological situation in the birds' breeding areas which is confirmed by a relatively stable fauna of parasites in the young birds, where species of the southern origin usually do not penetrate. This indicates that there are reliable barriers in the breeding areas for further distribution of haemosporidians annually imported from the south in offspring.

A suggestion was put forward (Valkiūnas, 1984b) that abiotic factors, primarily temperature, limit the spreading of bird malaria on the Curonian Spit. The Curonian Spit is characterized by a cooler spring and cooler summer than the adjacent regions on the continent (Dolnik and Payevsky, 1982). Nevertheless, the results of 15-year studies carried out on the spit in summer indicate that the observed outline of bird infection with these protists is not accounted for by only the lack of corresponding abiotic factors because distribution of malaria among the young birds is usually not recorded on the Curonian Spit during the years with a relatively warm summer in 1977 to 1992. It is likely that absence or weak transmission of malaria parasites on the spit and in some other northern regions is caused by the interaction of at least two factors, which require further investigation. First, malaria parasites of southern origin often cannot complete their cycles of development in the breeding areas of birds due to the lack of mutually adapted 'parasite–vector' pairs, whose formation is hampered by strict geographic isolation of populations of the parasites imported from the south and the vectors present in the breeding areas. Nevertheless, formation of mutually adapted systems between hosts and parasites should occur due to the regularity of seasonal migrations and the import of malaria parasites into the breeding areas. This factor taken alone cannot restrict the spreading of southern origin malaria to the north. The second factor also contributes to the prevention of the parasites spreading. The protists of southern origin are adjusted to milder abiotic conditions in the vector, which are not regularly formed in the Northern Palearctic. The absence of mutually adjusted parasites and vectors prevents the distribution of bird malaria in the north in favourable years, while often unfavourable climatic conditions for parasite development at high latitudes prevent the formation of mutually adjusted 'host–parasite' systems. The causes of the absence of active transmission of malaria parasites and some other species of haemoproteids imported from Africa to the Curonian Spit should be sought in the interaction of at least these two factors.†

Due to the lack of restriction imposed by the second factor in the Southern Palearctic, the parasites of southern origin had a greater opportunity during the process of their distribution to develop the ability to complete their life cycles in the local populations of the vectors, which facilitated widening the areas of their distribution and probably species divergence. It is likely that this situation took place in the bird *Plasmodium* spp. during their spreading from the Ethiopian and other tropical centers.

It is likely that the fate of haemosporidians of northern origin imported by birds into the wintering regions is more favourable. Milder climatic conditions should facilitate a relatively fast formation of the mutually adjusted systems 'parasite–vector.' It is our opinion that this situation is formed with the leucocytozoids of the Passeriformes, Falconiformes species, and other birds being an evolutionary young group of haemosporidians widely distributed in the Holarctic and slowly spreading to the south, where the overall prevalence of

† Few cases of *Plasmodium* sp. infections in juvenile birds have been recorded by us on the Curonian Spit in the last decade after unusually warm summers. This testifies to the opportunity of increase of transmission of the parasites at the study site, and needs further research. It is possible that climate warming has an impact not only on the area of bird distribution in the Baltic region (Žalakevičius, 1999), but also on the epidemiology of bird haemosporidiosis.

bird infection with these protists is currently often less than in the Northern Holarctic (Greiner *et al*., 1975; McClure *et al*., 1978; White *et al*., 1978; Valkiūnas, 1987a). An illustration of this statement is the introduction of turkey parasite *Leucocytozoon smithi* by people from North America to South Africa, where this parasite managed to incorporate and strike roots (Huchzermeyer and Sutherland, 1978). At present, no cases have been recorded of the penetration of leucocytozoids, which are adapted to transmission in warm countries, to the north. Nevertheless, the northern forms of haemosporidians cannot freely widen their ranges of distribution to the south. For example, active transmission of *L. simondi* in the Palearctic occurs approximately north of 52° N (Valkiūnas *et al*., 1990). Annual seasonal migrations of wild anseriform birds and regular transport of *L. simondi* to the south could not yet overcome the ecological barriers for the distribution of the parasite beyond the Holarctic. A similar situation takes place with numerous species of leucocytozoids which are regularly imported by the Nearctic birds to the Neotropic wintering areas where many species of these parasites are not transmitted. It is likely that the availability of adaptive vectors is the main obstacle to the distribution of leucocytozoids in the south. Further study of the mechanisms preventing the spreading of parasites, which are regularly imported by migrating birds into regions where transmission does not occur, is of great theoretical importance.

The data analyzed above about the role of seasonal migrations into the Ethiopian region in the distribution of malaria parasites and haemoproteids are obtained during the investigation of birds migrating in the direction of Western Europe. The routes of migration and wintering areas of numerous species and populations of birds breeding in the Eastern, Central, and Southern Palearctic are also associated with the Ethiopian zoogeographical region (McClure, 1974; Mikheev, 1981). Thus, the concept about the Ethiopian centre of bird malaria spreading and about the important role of migration of birds into this region in infection with haemoproteids may be extended to the entire numerous group of the Palearctic migrants wintering in the Ethiopian region. Among the other factors, this is confirmed by a similar outline of the prevalence of infection of *Delichon urbica* with *Haemoproteus hirundinis* (a parasite of the southern origin) in various regions of the Palearctic (Fig. 49). It is noteworthy, however, that due to the variety of factors influencing the phenomenon, this general concept is realized in a specific way for different species and populations of birds inhabiting certain regions. The mere fact of birds' migration to the southern latitudes does not mean that the bird should be necessarily infected with blood parasites. Among the far-distance migrants, there are those weakly infected with haemosporidians (for example, *Apus apus*, *Hirundo rustica*, *Upupa epops* and others). The time and routes of migration are not the same for different species and populations of the same species of birds. They are also infected in different ways during breeding period (Valkiūnas, 1984b). Thus, it is more correct to find the solution of the problem about the role of bird migration in infection with blood protists at the level of populations. We are suggesting only that the probability of infection of far-distance migrants with blood parasites is significantly greater than that of the middle-distance and near-distance ones. The data considered above confirm this (see Table 11). It is apparent that malaria parasites obtained in the Ethiopian region make up only a part of the local origin protists in the Southern Palearctic, where bird malaria is actively transmitted (Mohammed, 1958; Garnham, 1966; Burtikashvili, 1978; Valkiūnas and Iezhova, 2001a). In the regions with the lack of transmission of one or another groups of the parasitic organisms, their fauna is composed of species of southern origin and (or) the species imported by birds immigrating from the other territories.

Many Palearctic bird species winter in the Oriental zoogeographical region, where, according to available information, the overall prevalence of infection with haemosporidians

is lower than in the Ethiopian region and the Palearctic (McClure *et al*., 1978; Mikheev, 1981; Valkiūnas, 1987a). This gives grounds to assume that import of all groups of haemosporidians by migrants from the Oriental region into the Palearctic may play a lesser role than their import from the Ethiopian region. The results of mass investigation of anseriform birds in the Northern Palearctic confirm this. Haemosporidians of the southern origin were coincidentally recorded in many species of the Anatidae breeding in the north of Russia and wintering in Southern and Southeastern Asia (Valkiūnas *et al*., 1990).

The populational investigations carried out in Canada (Bennett *et al*., 1976, 1978; Bennett and Bishop, 1990a) resulted in the conclusion that there is no significant exchange of haemosporidians between North and South America during seasonal migrations. At the same time, the data are available in the cited works, which testify to the opportunity of infection of some birds with malaria parasites outside the Nearctic breeding areas. For example, the authors found that prevalence of infection with *Plasmodium* spp. in migrating Nearctic fringillids is 3.8 times greater ($P < 0.01$) than in nonmigrating ones (Bennett *et al.*, 1976, 1978), while in migrating emberizids, this index is 5.8 times greater ($P < 0.001$) than in nonmigrating representatives of this family (Bennett and Bishop, 1990a). It is noteworthy that an active transmission of *Plasmodium* spp. occurs in wintering areas of Nearctic birds in Venezuela (Gabaldon and Ulloa, 1980), where holoendemic malaria nidi are formed with a high death rate among young birds of local species (see p. 93 for more details). The high prevalence of *Plasmodium* infection in birds is recorded in Panama (Galindo and Sousa, 1966) and other countries of South and Central America. It is likely that infection of Nearctic migrants with malaria parasites occurs in the Neotropics as it takes place with Palearctic migrants in the Ethiopian region.

Leucocytozoon spp. are rare in the Neotropical zoogeographical region (White *et al*., 1978; Valkiūnas, 1987a). It is likely that this occurs due to the absence of the appropriate vectors. This group of haemosporidians, young from the point of evolution, has not yet adjusted to the Neotropics. Thus, infection of Nearctic far-distance migrants with leucocytozoids may occur mainly in breeding areas and during their movements in the Nearctic, which is, in general, similar to the situation recorded in the Palearctic. Canadian colleagues (Bennett and Bishop, 1990a) think that infection of Nearctic birds with *Leucocytozoon* spp. occurs mainly in breeding areas, but they also admit (Bennett and Inder, 1972) that certain bird species (for example, *Somateria mollissima* on Newfoundland Island) get infected with these and other haemosporidians on the routes of migration beyond their breeding areas.

The information about the role of seasonal migrations of Nearctic birds in the distribution of *Haemoproteus* spp. on the level of bird populations is not large. The interesting results of the mass populational studies were carried out in Canada (Bennett *et al*., 1976, 1978; Bennett and Bishop, 1990a). However, the papers mentioned contain information mainly on the overall prevalence of infection calculated by summing up the results of investigation of many species of migrating and nonmigrating birds belonging to different systematic groups. As we showed above, the application of this method frequently diminishes the peculiarities of infection in individual species of birds. The increase in the prevalence of infection of *Progne subis* with *Haemoproteus hirundinis* (=*H. prognei*) in Maryland (USA) after the birds return from wintering in Brazil was not associated with seasonal migrations (Davidar and Morton, 1993) mainly because parasites were not found in 12 young birds at their wintering sites. Such a low sample is not sufficient for the detection of parasites (when $n = 12$, the 95% confidence limit of the prevalence for zero infected birds is 0.0 to 26.5). Besides, in this case, the possibility of infection in the

migration areas was not taken into account. Moreover, it was not proved that birds investigated in the USA and Brazil belong to the same population. We discuss this example partly with the aim of showing how difficult it is to investigate this problem in detail. It is noteworthy that the outline of *P. subis* infection with *H. hirundinis* in the USA is similar to the outline of infection of *Delichon urbica* in the Palearctic in general (Fig. 49). In both cases the parasites are not recorded in young birds at the breeding areas, but a great number of infected birds is found after their return from wintering. It is our opinion that the opportunity of infection at wintering and (or) migration areas cannot be excluded.

The import of parasites both of the southern and 'migratory' origin by Palearctic birds into their breeding areas is known for various groups of parasitic organisms (Belopolskaya, 1956, 1986; Bychovskaya-Pavlovskaya, 1962; Dogiel, 1962; Valkiūnas, 1993b). Fundamental ornithological investigations on bird migrations compose the methodological basis for understanding why the birds get infected with parasites during wintering and on their migration route many hundreds or thousand kilometers away from their breeding areas. To some extent, the data from ornithological research brings the results of the ecological parasitological investigations into consistence with the accumulated data on the genetic basis of functioning of the host–parasite systems. Seasonal migrations have a clearly pronounced periodicity, and the populations of regular migrants of one species are characterized by relatively constant time and migration routes, stopover sites on their migratory way, areas of wintering and even individual time of flying over a certain geographical point (Dolnik, 1975; Shumakov and Sokolov, 1982; Payevsky, 1985; Sokolov, 1991). As already mentioned, the majority of far-distance migrants spend about nine months away from their breeding areas. In the process of evolution, this should facilitate the susceptibility of long-distance migrants to infection with parasites beyond the breeding areas, when they regularly get into the same nidi of transmission of one or another groups of parasitic organisms in migration and wintering areas. In the course of evolution, this probably also contributes to mutual adjustment of the northern migrants and the parasites which are actively transmitted only in the southern ecosystems. So, the regularly migrating Holarctic birds should not be completely 'alien' hosts even for endemic parasites in the south zoogeographical regions.

It is important to emphasize the great potential role of the intermediate points on the route of migration in the bird infection with blood parasites, i.e. the sites where the birds stay for rest and feeding and thus become the objects of the attack of the vectors. There are well documented facts of migrating birds attacked by the vectors during their stay in migration areas (Forthey and Brust, 1988). Many passerine birds spend two thirds of their travel time from wintering to breeding areas on stopover sites. The halts of *Fringilla coelebs* on its migration route last 18 to 21 days (Blyumenthal, 1971; Shumakov and Sokolov, 1982). The opportunity for infection of birds in their migration areas cannot be excluded. This conclusion confirms the reality of distinguishing an ecological group of 'migratory' parasites on the basis of the place of birds' infection, whose existence was for the first time substantiated by Belopolskaya (1956, 1959) on the example of bird helminths. The results of research on the Curonian Spit (Valkiūnas, 1993b) indicate that *Haemoproteus pastoris* belongs to the group of haemosporidians infecting the birds on their migratory route. Even more, each of the haemosporidians of *Loxia curvirostra*, who breed during cold months of the year, also belongs to this ecological group of parasites (Fig. 47).

The data, which indicate that there is an opportunity to enrich the fauna of haemosporidians by bird-immigrants incorporating into the populations under study from other populations (frequently from far-distance ones) (Valkiūnas, 1988a; Vysotsky and

Valkiūnas, 1992, 2001), are related to a separate problem. They are considered in this book from a somewhat different point of view (see pp. 139, 173).

The analysis of facts mentioned in this chapter allows us to make the following main conclusions about the role of seasonal migrations in the distribution of bird haemosporidians. The wintering areas of Holarctic birds occupy vast territories of the Earth in various climatic zones. The time and routes of migration as well as wintering areas are different for different species and different populations of one species of birds. Thus, the conclusions about infection of birds associated with migrations cannot be considered reliable if they are not defined up to the level of wintering areas of certain species and even populations.

The representatives of all genera of haemosporidians with the exception of *Fallisia* sp. are more or less actively transmitted in the Holarctic. The role of seasonal migrations to the southern latitudes usually consists only in enriching the fauna and increasing the prevalence of infection, which is realized in different ways in various groups of birds and parasites.

The nearest migrants moving into the zone of cold winters are usually not infected with haemosporidians in wintering and migration areas. The birds that migrate in summer are exclusions. For example, *Sturnus vulgaris* infected with *Haemoproteus pastoris*, as well as *Loxia curvirostra* infected with *H. tartakovskyi*, *H. fringillae*, *Leucocytozoon fringillinarum*, *L. dubreuili,* and *L. majoris* are representatives of the nearest migrants infected with haemosporidians on the migration routes during their summer movements in the Palearctic.

The most important area where the Holarctic birds get infected is primarily the Ethiopian zoogeographical region. It is likely that seasonal migrations to the other zoogeographical regions are less important in this sense, although this problem needs additional research.

The role of Palearctic bird migrations to the Mediterranean zone and to the Ethiopian zoogeographical region is not the same with respect to their infection with haemosporidians. The birds more frequently get infected with leucocytozoids during their migrations within the Palearctic, while infection with malaria parasites and haemoproteids occurs mainly during their wintering in the Ethiopian region. It is likely that approximately the same situation occurs in the New World. It is most likely that Nearctic birds get infected with leucocytozoids mainly within the Nearctic, while malaria parasites infect them in the Nearctic and in the Neotropical region.

Far-distance migration of birds to the Ethiopian zoogeographical region is an important factor permanently influencing the fauna of haemosporidians in the Palearctic. The general rules of haemosporidians fauna genesis in the far-distance (trans-Saharan) Palearctic migrants are the following. Seasonal migrations of far-distance migrants do not contribute or they insignificantly contribute to enriching the fauna of leucocytozoids and increase of *Leucocytozoon* infection prevalence. The birds are usually infected with these protists mainly in the breeding areas. In those regions where there is no transmission of leucocytozoids, young birds are free of these parasites; this is recorded on the Curonian Spit. On the contrary, the long stay of far-distance migrants in the Ethiopian region facilitates their infection with haemoproteids and malaria parasites.[†] After far-distance migrants return from wintering, two groups of haemosporidians are imported into the breeding areas. The

[†] Infection of Palearctic birds with haemoproteids and malaria parasites in African wintering areas has been proved by molecular methods (Waldenström *et al.*, 2002).

first and the greatest group includes the species whose transmission has not been recorded in the Northern Palearctic (for example, *Haemoproteus hirundinis*, *H. payevskyi*, *Plasmodium rouxi*, *P. fallax*, and others). They do not infect young birds in the breeding areas. The other group is formed from the species whose transmission takes place in the breeding areas (for example, *H. belopolskyi*, *H. majoris*, *H. pallidus*, *P. relictum,* and others). In the latter case, the imported protists only increase the overall prevalence of bird infection. The fate of the imported parasites from the second group is not finally understood. It is not inconceivable that they can be transmitted in the north thus enriching the genofond (gene pool) of the species with a wide range of distribution.

Thus, after the far-distance Palearctic migrants return from wintering their fauna of haemosporidians is regularly enriched mainly due to the species of haemoproteids and malaria parasites. This, however, does not change the epidemiological situation in the breeding areas, which is indicated by a relatively stable fauna of parasites in the young birds, where parasite species of the southern origin do not penetrate. All this indicates that breeding areas are provided with strict barriers preventing further spreading of haemosporidians regularly imported from the south. It is likely that these barriers are formed primarily because there are no specific or adaptive vectors, insufficient total heat for the development of parasites in the invertebrate hosts, or as a result of these two factors combined. Even in the case of such motile animals as birds, the number of species of parasites associated with a certain biocenosis is relatively strictly determined and usually is not momentarily enriched due to regularly imported ‘alien’ elements. This situation is a good illustration for the biocenotic specificity of parasitic systems. In this sense, the haemosporidians of southern origin in the north and of northern origin in the south can be regarded as a kind of ‘preserved’ genofond, which is realized slowly and is of great importance for the evolution of parasites and new parasitic diseases. No doubt the regular mass spreading of parasites by migrating birds in the course of evolution plays an important role in their penetration into new hosts and new territories, which is one of the main peculiarities of the formation and development of bird parasite fauna.

Seasonal Peculiarities of Bird Infection

There are several factors needed for the successful completion of the haemosporidians' life cycle at a study site: parasite, susceptible vertebrate hosts and vectors, and favourable environmental conditions, primarily both the temperature and humidity necessary for the development of parasites in the vector and for the transmission of infection. In those cases, when seasonal changes are not manifested or are only slightly manifested in nature, and the factors listed above are available permanently, the haemosporidians can be transmitted throughout the year. This situation is observed in certain countries with a mild and humid climate, usually in the subtropics and tropics, where the vectors are active throughout the year, and the birds (donors and recipients of infection) are permanent residents. The subtropics of Florida (USA) is an example, where transmission of *Haemoproteus mansoni* (*=H. meleagridis*) among turkeys is observed throughout the whole year (Atkinson, 1988; Atkinson *et al*., 1988a). Venezuela is also an example, where transmission of malaria does not stop during the entire year (Gabaldon and Ulloa, 1980). Continuous transmission of *Leucocytozoon smithi* occurs in some regions of South Carolina (USA) (Noblet *et al*., 1975). Interestingly, the populations of hippoboscid flies in southern latitudes are relatively stable and are not subject to significant seasonal fluctuations. As a result, the prevalence of infection of columbiform birds with *Haemoproteus* species whose vectors are the hippoboscid flies, is also relatively stable in the countries with warm climate, and frequently reaches 90 to 100% during each season of the year (Markus and Oosthuizen, 1972; Ayala *et al*., 1977).

In regions with clearly expressed seasonal changes in nature, the transmission of haemosporidians is usually interrupted during the periods when the activity of vectors decreases. The transmission resumes as the vectors become active. At high latitudes, the period of active transmission of haemosporidians is usually connected with the warm seasons (Bennett and Cameron, 1974; Baker, 1975; Herman and Bennett, 1976; Burtikashvili, 1978; Valkiūnas, 1987a, 1987c; Atkinson *et al*., 1988a), while at low latitudes, it is often associated with the humid season that follows the period of rains (Bennett *et al*., 1966; Greiner and Mundy, 1979; Earlé *et al*., 1991a; Young *et al*., 1993). During this time, relapses are observed, the vectors appear, and the density of their population increases, while the birds begin reproduction, and a large number of young highly susceptible to infection vertebrate hosts appears, which favours rapid spreading of infection. Due to the fact that the activity of haemosporidians transmission depends on many aspects, whose formation and interaction differ in various regions, the peaks of infection prevalence do not occur simultaneously in different territories, while the infections sufficiently differ in many parameters (Valkiūnas, 1987a), which cause problems for the regional parasitology investigations. There are examples when significant differences in infection epidemiology are observed even on adjacent territories. For example, in South Carolina (USA) there are regions, where the transmission of *Leucocytozoon smithi* among turkeys is recorded throughout the entire year, but it is interrupted in other regions in winter (Noblet *et al*.,

1975), which is associated with the differences in the duration of activity of the vectors, simuliid flies.

It is likely that the increase of the likelihood of bird infection with *Plasmodium* spp. as well as infection of columbiform birds with *Haemoproteus* spp. in the second half of summer is a regular characteristic of the Central and Northern Holarctic. At this time, (i) the most favourable conditions are formed from the point of view of total heat needed for the development of malaria parasites in the invertebrate hosts, and (ii) the density of populations of hippoboscid flies, which transmit *Haemoproteus* spp. among species of the Columbiformes, significantly increases. Interestingly, the active transmission of haemoproteids among columbiforms by the hippoboscid flies, which spend much of their time on the birds, may occur at medium latitudes in the autumn or even in the winter months, as was recorded in Michigan (Klei and DeGiusti, 1975). This situation is unique for haemosporidians.

The highest indices of infection intensity of haemosporidians are observed in birds in those seasons when the active transmission of parasites starts in nature. At this time, parasitemia increases significantly due to relapses as well as to the appearance of acute primary parasitemia.

Age Peculiarities of Bird Infection

Several hundred papers have been published with the information about infection prevalence and fewer about the intensity of infection with haemosporidians in birds of different age groups. The authors usually distinguish between two age groups: young (juvenilis, subadultus) and adult (adultus) birds, differentiated by their plumage. Birds of less than one year old are usually related to the first group, while the second group includes birds aged one year and older. This division is conventional, which is primarily related to the category of adult birds including the specimens markedly differing by their lifetimes. It is noteworthy that the index of the average intensity of parasitemia sometimes used for the comparison of infection of birds of different ages with haemosporidians is not discussed in this book. It is our opinion that summation and averaging the data on the intensity of infection in the ecological research generally do not have enough validity, in particular, because daily cyclic fluctuations of the parasitemia are not taken into account. These properties are described for certain species (Noblet *et al*., 1980) but have not been studied well enough for the majority of bird haemosporidians. Besides, chronic parasitemia (less than 20 parasites per 1000 erythrocytes, but usually less than 1 parasite per 1000), which may be related to the category of low parasitemia, is usually found in the overwhelming majority of naturally infected birds captured by traditional methods (see p. 140 for details) in nature. Below, we shall discuss only the prevalence of infection.

Analysis of data from the literature shows a very patchy picture of infection of birds of different age by haemosporidians. In particular, one group of scholars (the majority) indicate that adult birds have a greater prevalence of infection by various groups of haemosporidians (Lyubinsky *et al*., 1940; Bauer, 1941; Levine and Hanson, 1953; Glushchenko, 1963; Subkhonov, 1973; Bennett *et al*., 1974a; Musaev and Zeiniev, 1974; Greiner, 1975; Burtikashvili, 1976; Peirce and Marquiss, 1983; Valkiūnas, 1987a; Davidar and Morton, 1993), the second group of scientists notes a greater infection prevalence in young birds (Levine and Hanson, 1953; Kobyshev and Chashina, 1972; Yakunin, 1972; Kučera, 1979; Thul *et al*., 1980), while the third ones advise that there are no reliable differences in the prevalence of bird infection in different age groups (Oliger, 1940b; Bennett *et al*., 1976; Bennett *et al*., 1980). These data, which are contradictory at the first glance may be understood from the point of view of haemosporidians' existence in nature.

The maintenance of haemosporidian species, with rare exceptions (see pp. 187, 206), is realized due to infection of vertebrate hosts and persistence in their organism. The lifetime of the vectors of haemosporidians is relatively short compared to that of birds. The parasites inhabit them only for a relatively short period of time during active transmission. A bird once infected that survives an acute stage of infection, maintains the infection for many months and even years, up to two to five years and even longer (Garnham, 1966; Fallis *et al*., 1974; our data). The mean lifetime of different species of birds significantly varies, but for the majority of species studied, it rarely exceeds ten years. For example, the mean lifetime of different species of small passerines, whose fauna of haemosporidians is

the richest, is usually 1.5 to 2.5 years (Payevsky, 1985). In this relation, it becomes clear that not only the elaboration of mechanisms for relatively long survival in the adult part of the vertebrate hosts, but also regular infection of a certain part of young birds is important for haemosporidians to survive in nature. The incorporation of haemosporidians to young birds is favoured by their high susceptibility to infection. According to the works cited above, the general rule is that a certain part of young birds is usually inevitably infected, and some part of adult birds is also infected and sometimes reinfected on the territories with the transmission of haemosporidians. The realization of this general rule, however, depends on numerous factors which interact in a complex way related to the peculiarities of the populational biology of vertebrate and invertebrate hosts and abiotic conditions, and thus is not subject to simple determinations or forecast in each specific case. This is the primary reason for a very patchy picture in the literature on the problem considered. It is clear that a certain number of infected specimens in bird populations is necessary to maintain a species of haemosporidians in nature, while at any specific moment of time the ratio between infected young and adult birds can often be random. Let us consider one example (Atkinson and van Riper, 1991). Mass hatching of wild turkeys in one well studied region of Florida (USA) usually occurs in the middle of May, when the peak of activity of *Simulium congareenarum,* the only vector of *Leucocytozoon smithi* in the region, decreases. Thus, the majority of young birds is usually infected only in the next spring, while during the first year of life they are not infected or a few of them are infected. During humid years, however, when the number of simuliid flies is large, or during the year, when young turkeys hatch earlier, a great proportion of young birds can be infected during the first months of their life. Another situation occurs in South Carolina (USA) (Noblet *et al*., 1975). Here in the majority of the regions studied, the vectors are active within the entire year, and the likelihood of infection of young turkeys is high during the first year of their lives. Thus, the seasonal, annual, and other variations in the time of birds breeding, activity of vectors, abiotic factors, and other reasons, may have a significant influence on the level of birds infection, primary of the young birds.

The adult birds being susceptible to infection (Garnham, 1966; Fallis *et al*., 1974; Ahmed and Mohammed, 1978a) and having a longer period of contact with the vectors than the young ones, usually have greater chances to be infected, and more important, they have more chances to maintain the infection during the periods of life unfavourable for the transmission of parasites. Most of them usually have low chronic (relatively benign) infections. This seems to be the main explanation for the fact that, as we mentioned above, different scholars often recorded that the prevalence of infection in adult birds is greater than in young ones. It is likely that the chronically infected adult birds, being the important source of parasites for the vectors, play a major role in the maintenance of haemosporidian species in nature because ornithologists identify this age group as a relatively stable part in any of bird populations (Payevsky, 1985).

Decoding the mechanism responsible for the realization of the certain level of bird infection at each study site is the subject of populational parasitology research, which goes beyond the limits of this book.

Biotic Factors Influencing the Probability of Bird Infection

As we already mentioned, the transmission of haemosporidians is determined by a number of factors interacting in a complex way, related to the biological properties of vertebrate and invertebrate hosts as well as to certain abiotic factors. As a result, the specific realization of the parasite fauna and parasitological indices frequently differs in many species of the birds living in similar conditions. Nevertheless, the infection of many species of birds distributed over vast regions is often similar in various points of their range of distribution. For example, in each of the regions of the Palearctic studied to date, the *Leucocytozoon toddi* infection prevalence in birds belonging to the family Accipitridae is consistently greater than in birds belonging to the Falconidae; the prevalence of *Delichon urbica* infection with haemoproteids is greater than in *Hirundo rustica*; the prevalence of infection of *Phylloscopus trochilus* with haemoproteids in each specific region is usually lower than in *Sylvia atricapilla* or *Hippolais icterina*; the prevalence of infection with leucocytozoids in species of the Strigidae is usually high and exceeds 25% in the Palearctic, while *Apus apus*, *Caprimulgus europaeus*, *Cuculus canorus*, *Dendrocopos major,* and *Upupa epops* are usually free from haemoproteids in this region (Valkiūnas and Iezhova, 2001b). All this indicates that there are certain general rules in distribution of haemosporidians. Experience and available facts lead us to conclude that a number of the peculiarities of the biology of birds to a certain degree favours their greater or lesser contacts with the vectors, which is reflected in the overall prevalence of infection. Below, some of these peculiarities will be analyzed. It is noteworthy that all the discussion refers only to the areas where transmission of the certain groups of haemosporidians takes place. Young birds, which do not migrate yet, are the convenient 'mirror' to measure the rate of transmission.

A prolonged time of nestlings' stay in the nest (more than 14 to 16 days) is a factor increasing the probability of their infection with haemosporidians. It is likely that this is due to the fact that older nestlings are more easily available and more attractive to the vectors. Let us analyze some examples. Infection of *Accipiter nisus* nestlings with *Leucocytozoon toddi* in England occurs mainly in the nest, where about a third of young birds and even more are infected (Peirce and Marquiss, 1983; Ashford *et al*., 1990, 1991). We observed a similar situation in the Eastern Baltic region where the prevalence of *L. danilewskyi* infection was found in *Asio otus* nestlings at the age of 18 to 25 days to be 70.8% (the 95% confidence limit is 48.8 to 87.4). A high prevalence of falconiform nestlings infection with haemoproteids (about 70%) and leucocytozoids (20%) was recorded in the Volgograd region of Russia (Kobyshev and Chashina, 1972).

The nestlings, which stay in the nest for a short time (less than 14 days), often do not have time to get infected with haemosporidians during this period even in the regions with active transmission of parasites. This is probably characteristic of many species of small Passeriformes. We confirmed this experimentally (Valkiūnas, 1991, 1993a, and

unpublished data). Sixty-seven nestlings of *Fringilla coelebs* were taken out of the nests on the Curonian Spit in the Baltic Sea at the age of 6 to 12 days and raised by hand in the laboratory. The blood of the hand-raised birds was tested for parasites every day up to the age of 40 days; that is enough to record the infection. *Haemoproteus* sp. gametocytes were found only in two experimental birds or in 3% of birds (the 95% confidence limit is 0.4 to 11.2), which means that these birds were infected in the nest. At the same time, the prevalence of infection in *F. coelebs* at the age of 25 to 50 days captured on the Curonian Spit during the years of the experiment reached 36.2% (28.0 to 39.5). These data show that active infection of a significant part of young birds occurs after they leave the nest. In other words, the period of their stay in the nest is not absolutely necessary to get infected with haemosporidians, which may actively infect young birds after they fly from the nests. In particular, this is also confirmed by the data of infection of young *Loxia curvirostra* migrating in summer through the Curonian Spit (Valkiūnas, 1993b). In the North Holarctic, *L. curvirostra* represents a specialized ecological group of birds that can breed in winter or in early spring (Malchevsky and Pukinsky, 1983) when the vectors of haemosporidians are inactive. Thus, the young generation of *L. curvirostra* born during the cold season can be infected only after the breeding period, in late spring or summer when the birds are actively moving between places with a good crop of pine and fir-tree seeds. On the Curonian Spit, *L. curvirostra* do not breed and they can only be captured during postreproductive dispersal and irruptions. The young *L. curvirostra* have been found infected on the Spit with *Haemoproteus tartakovskyi, H. fringillae, Leucocytozoon fringillinarum, L. dubreuili, L. majoris*, and *Plasmodium* sp. in June (Fig. 47). These young birds can only have been infected outside of the nest. These data show that *L. curvirostra* are often infected during active summer movements, and the period while the birds are in the nest does not play a decisive role in the infection. A diverse fauna of haemosporidians in *L. curvirostra* captured on the Curonian Spit is formed during the period that follows the breeding period.

Thus, two ecological groups of birds with a short and a long period of stay in the nests can be distinguished from the point of view of the probability of the young birds' infection with haemosporidians. The risk of infection of nestlings belonging to the first group is less than for the second. It is likely that the representatives of both groups can actively get infected with haemosporidians at the breeding area after they leave the nests, which finally determines the level of prevalence of infection in young birds at the end of the breeding period.

A large body size is the factor increasing the probability of infection with haemosporidians. This is clearly demonstrated in the example of *Leucocytozoon* spp. (Valkiūnas, 1984a, 1987c). For example, in the Eastern Baltic region, prevalence of infection of Turdidae birds of medium size (approximately like *Turdus merula* and larger) with leucocytozoids exceeds the infection of small ones (approximately like *Phoenicurus phoenicurus*) 2.7 times ($P < 0.001$). Prevalence of the infection in large nonpasserine birds is 2.9 times greater ($P < 0.001$) than in small passerines. It is likely that large birds are more attractive for vectors and (or) more convenient and available for feeding on them (Bauer, 1941). Under equal conditions, a greater number of vectors can feed on the birds of larger size, which increases the probability of sporozoites inoculation. It is apparent that the dependence of infection of birds on their size is not unique, because it is subject to the influence of many other factors. The prevalence of infection of phylogenetically close species of comparable sizes often significantly differs (Valkiūnas, 1987c, 1989b), while among small passerines, there are ones with extremely high prevalence of infection (for example, *Fringilla coelebs*, *Hippolais icterina*, *Luscinia luscinia,* and others)

as well as with low prevalence of infection (*Aegithalos caudatus*, *Certhia familiaris*, *Hirundo rustica* and others). We are speaking here only about the increased probability of infection of large size birds, which is not always practically realized.

The closed type of nests and their location at ground level are worth mentioning among the factors reducing the probability of birds' infection with haemosporidians (Ashford, 1974; Kučera, 1981a, 1981b; Valkiūnas, 1987c). It is likely that the first factor plays the role of mechanical protection of nestlings and adult birds on eggs, preventing in some extent the access of vectors. The second factor is probably associated with a certain zone of the feeding activity of vectors.

Decrease of the locomotion activity of birds during the nesting period is a factor increasing the probability of their infection with haemosporidians. This is possibly accounted for by the fact that inactive specimens are more accessible to the attacks of vectors (Valkiūnas, 1984a, 1987c). In particular, this accounts for a higher prevalence of *Haemoproteus* spp. infection in *Fringilla coelebs* females compared to males at the end of the breeding season. According to the data of ornithologists (Ilyina, 1982b), only females hatch the eggs and feed the offspring. *Fringilla coelebs* females spend a major part of the day on the eggs. As a result, the females are less active than males during the nesting period, and thus they have a greater chance to be infected. It is noteworthy that, with rare exclusions (Markov and Chernobai, 1968; Applegate, 1971; Burtikashvili, 1978; Valkiūnas, 1987c), the differences in prevalence of infection of birds of opposite sexes are usually insignificant (Glushchenko, 1963; Forrester *et al*., 1974; Burtikashvili, 1976, 1978; Thul *et al*., 1980, and many other authors). No doubt, this situation takes place in the wild and it is likely that it predominates in nature. Nevertheless, in certain cases, the absence of difference of infection in birds of opposite sexes is caused by a methodological error. While comparing the prevalence of infection of males and females, some authors summarize the data obtained during a long period of investigation, but not during specific periods of time when the differences in the ecology of sexes clearly manifest themselves. Moreover, the data on infection of birds of different ages are sometimes summarized. In these cases, the peculiarities of infection of males and females are often diminished or seem insignificant.

It is important to note that the differences in infection prevalence in opposite sexes at an investigation site may be due to the influence of such factors independent to the transmission of parasites as bird dispersal. The immigrants can introduce unusual parasites into a study site. The share of parasites introducing by the opposite sexes may differ significantly due to a different level of dispersal in the opposite sexes. The situation on infection with leucocytozoids of the opposite sexes of *Parus major* on the Curonian Spit is an example (see p. 178 for details). We mention this fact here to remind the reader that the processes, which take place in wildlife, are complicated, and the parasitological situation cannot be always understood only by simply capturing birds at the study site and determining the level of their infection with parasites. Deeper analyses of the processes, which take place in nature, are often necessary to solve the problem.

The probability of infection of marine and coastal birds with haemosporidians is low compared to the probability of infection of other ecological groups of birds. This is primarily due to the fact that the activity of blood-sucking dipteran insects markedly decreases or is limited by a lesser number of days in the land located on the coast, which in part is due to the lack of breeding places for the vectors, and windy or cold weather, especially on islands. Examples are the numerous species of birds belonging to the families Gaviidae, Podicipedidae, Pelecanidae, Pelecanoididae,

Charadriidae, Stercorariidae, Spheniscidae, a part of Laridae, and others, in which haemosporidians either were not found or are uncommon. However, there are some exceptions (see Appendix 2, e.g., pp. 860–862). It is important to note that the marine and coastal birds can be easily infected with malaria parasites when they are introduced on endemic territories. Numerous well documented cases of malaria in penguins are an example (see p. 89).

The probability of infection of birds with haemosporidians is decreased in the regions with increased anthropogenic load primarily due to the elimination or decrease of the density of vectors caused by the use of insecticides, pesticides, and total pollution of the environment. For example, after World War II, the prevalence of wild birds' infection with all groups of haemosporidians markedly decreased in Western Europe (at least two times and even more in some localities), while the species common before (for example, *Plasmodium cathemerium*) became rare in some countries (Corradetti, 1974; Kučera, 1981a). It is likely that the main reason for this is the wide use of DDT and other insecticides in the agriculture. Birds living in cities and towns are often less infected with haemosporidians and thus have an advantage in comparison to ones inhabiting the natural environment. It is likely that this is caused by increased pollution of environment in densely populated localities and the absence or low density of certain groups of vectors. For example, according to our data the overall prevalence of infection of young *Fringilla coelebs* after leaving the nests at the age up to 50 days is 2.4 less in the parks of Kaliningrad ($P < 0.05$) than on the Curonian Spit, which is the reserve located approximately 30 km from this city.

A colonial mode of life of birds contributes to the increase of the prevalence of their infection in regions where haemosporidians are actively transmitted and even contributes to the development of lethal outbreaks among the young birds (Garnham, 1966; Ashford, 1974; Gabaldon and Ulloa, 1980). One should, however, keep in mind that only the colonial mode of life itself is not enough for the spreading of infection. A combination of other factors considered above is needed, which provide the transmission of infection. There are many colonial species of birds, where haemosporidians were not found at all or were recorded occasionally. The examples are: *Apus apus*, *Egretta garzetta*, *Riparia riparia*, the majority of marine, coastal, and some other groups of birds which live near large water basins under conditions when, due to some reasons, the transmission of haemosporidians is interrupted. It is thus understandable why Ashford and co-authors (Ashford *et al*., 1994) came to the conclusion that colonial species of birds are not appropriate for the study of the ecology of haemosporidians due to the low prevalence of infection. This conclusion is hardly true for all colonial birds. For example, according to our data in South Kazakhstan, the overall prevalence of haemosporidian infection reaches up to 80% and even more in some large colonies of *Passer indicus* and *P. hispaniolensis* in the beginning of their breeding period (see also p. 93).

In conclusion, it is important to emphasize that none of the factors discussed influences the level of bird's infection fatally, and that there are many exceptions to these 'rules.' Even more, the degree of the influence of the factors considered on the infection of birds with different genera of haemosporidians is also unequal. We are speaking only about the fact whether the presence or absence of the corresponding factors can potentially place certain species of birds into a certain category of infection risk. It is our opinion that concise information on the problem considered is important in the sense that it facilitates the understanding of the epidemiological situation at each certain study site.

Haemosporidians as Biological Tags in Bird Population Studies[†]

During several decades of intensive research, vast data were accumulated in parasitology whose importance goes beyond the limits of this research. We emphasize only that parasitology gives original facts for the elaboration of certain concepts of the theory of evolution (Hamilton, 1982; Kontrimavičius, 1982). There are well known examples of data on the fauna, ecology, and distribution of parasitic organisms being successfully used as additional criteria in the study of the biology, phylogeny, zoogeography, and the structure of the populations of hosts of various systematic groups (Dubinin, 1958; Dogiel, 1962; MacKenzie, 1983). It must be admitted, however, that the results of parasitological investigations are only occasionally applied to solve the problems in other branches of biology. On the one hand, this can be accounted for by weak coordination of the fundamental investigations of parasitologists and specialists in other biological disciplines. On the other hand, this can be explained by the necessity in certain cases to kill a large number of animals under study to obtain reliable parasitological facts. The latter significantly restricts the organization and performance of wide range investigation of the parasitologists and specialists in other branches of biology, especially at the level of populations of the highest vertebrate animals and their parasites.

In this chapter we describe a method to estimate the structure of birds' populations using *Leucocytozoon* spp. as biological markers. This method avoids the necessity to kill the animals under investigation. The essence of the method is in the fact that the prevalence data on infection of birds with leucocytozoids can be used in ornithology to estimate the number of long-distance (inter-populational) immigrants in the populations of birds under study in those localities without breeding places of blood-sucking simuliid flies (Simuliidae), which are isolated by ecological barriers. A search for new, not traditional, markers for ornithology to study the range of bird's dispersal is on-going. Let us discuss the main reasons (Vysotsky and Valkiūnas, 1992, 2001).

Besides many other factors, the structure of the breeding population is determined by an inflow of immigrants from other populations estimated per one generation, which is a function of the mobility of individuals. Determination of the level of links between the populations becomes one of the main objectives of populational study in any groups of organisms. The study of the structure of avian breeding populations faces many difficulties due to the ability of birds to move free in space. The experience of ornithologists indicates that total ringing and recapture of adult specimens and their offspring in large territories is a problem beyond their capabilities. The majority of populational ecological works performed with small passerine birds covers areas of a few square kilometers. The results of these

[†] It is my pleasure to thank V.G. Vysotsky and L.V. Sokolov, the ornithologists from the Zoological Institute, Russian Academy of Sciences for their help in collecting the material and discussions of the data used in the preparation of this chapter.

investigations do not allow one to judge not only about the inter-populational exchange of the individuals but also about the exchange between the territories at a distance of several kilometers from one another as well. It is clear that the maximum size of the territory under study is a restriction for judgment about the dispersion of birds. No problems arise with the size of the latter only when one studies the displacements significantly less than the size of the territory under study. Statistical methods to study the dispersion of birds almost have not been worked out yet (North, 1988). Information about ringed birds coming from the regions beyond the territory studied (through the ringing centres, from other scholars, etc.) is always limited and forms only a small part of data, compared with information obtained at the study site. Certain works are carried out simultaneously in two or more regions located some distance apart, between which there is an exchange of offspring. This information about the dispersion is not complete. For example, if there are two regions, then only a part of the embracing territory (second region) surrounding the first region is under control. It is clear that in this case the number of specimens dispersed from the first region at a distance equal to the interval between these two regions is greatly underestimated. A full account of the breeding birds is possible only in small squares, because it is labor consuming. Increasing the size of the region under study is inevitably associated with a decrease of the quality of control. Therefore, the study of dispersion of birds by means of ringing and recapturing is not effective and gives a shifted estimate, especially over long distances.

It is emphasized almost in each corresponding publications on ornithology (see Vysotsky and Valkiūnas, 2001 for references) that the major part of the breeding birds is presented by specimens that have not been ringed. Ringing of the nestlings on the territory studied is rarely complete enough. Therefore, one can only make suggestions about the origin of unringed adult birds. With regard to this, any attempts to evaluate the real number of specimens appearing in the population as a result of long-distance dispersion are of significant interest. To do this, one needs markers, which allow one to differentiate the birds from vast long-distance territories. One can differentiate small passerine birds belonging to various populations by the different content of the microelements in the feathers (Dobrovolskaya, 1990). This method has not given prominent results yet. Bauer (1987) indicates in his review that many scholars ignore the fact that the spatial distribution of bird individuals, which were not registered, remains unknown and requires the need to investigate larger territories. Zimin (1988) also appeals for a search of more modern methods for mass marking of birds.

We used haemosporidians belonging to the genus *Leucocytozoon* as markers. The possibility to use leucocytozoids as biological tags to identify the populational origin of birds is based on the regularities of the distribution and peculiarities of the life cycle of these parasites. Leucocytozoids belong to a pecular group of haemosporidians with a small number of species, which is common in birds and widely distributed in the Holarctic. The parasites use blood-sucking simuliid flies as vectors.† The presence of at least each of the three components of the host–parasite system in one locality are needed for successful transmission: susceptible birds, agents of infection, and susceptible vectors. Despite an extremely complex life cycle of leucocytozoids (see p. 36), one can accurately judge its completion at the study site by the detection of gametocytes in the blood of young birds (the final stage of development in birds). During the breeding period, a relapse of infection is

† One species of leucocytozoids only (*Leucocytozoon caulleryi*), which belongs to the subgenus *Akiba* is transmitted by biting midges (Ceratopogonidae). This parasite by its distribution is restricted to Southeast Asia.

observed in birds, which were infected before. When this occurs, gametocytes appear in their blood. It is important to remember that birds once infected with *Leucocytozoon* species become a carrier of parasites for many years.

One of the components of the system 'host–parasite–vector' is missing in the regions where there are no appropriate places for breeding of simuliid flies (water bodies with clean water rich in oxygen, for example, rapid brooks, etc.), which are isolated by ecological barriers preventing the penetration of simuliids from other territories. Therefore, the transmission of *Leucocytozoon* spp. is interrupted. This situation occurs on the Curonian Spit in the Baltic Sea. This is a place of intensive bird migration, where the method considered was developed and tested (Valkiūnas, 1988a; Vysotsky and Valkiūnas, 1992, 2001).

The Curonian Spit is a narrow (0.7 to 3.7 km) long (97 km) sandy strip of land running into the Baltic Sea. It extends from northeast to southwest (Fig. 44). This region is described in detail by Dolnik and Payevsky (1982). There are no biotopes for the breeding of simuliid flies on the spit, while the isolation from the mainland by large water basins of the Baltic Sea and Curonian Lagoon prevents the penetration of these dipterans from the mainland (Valkiūnas, 1984b). As a result, the fauna of leucocytozoids on the Curonian Spit may be formed in only two ways. First, the import of these parasites by birds of the Curonian origin from wintering areas and migration routes cannot be excluded. Second, there is the possibility that birds infected with leucocytozoids immigrate into the Curonian populations and inhabit the territory following juvenile dispersal and seasonal migrations. The possibility to use this parasite as a biological marker is based on the estimates of the contribution of each of these ways to the infection of breeding birds with leucocytozoids. To do this, it is necessary to investigate several groups of breeding birds: with known (Curonian) and unknown origin. The birds hatched on the Curonian Spit may get infected with the parasite only at wintering areas and migration routes. The birds other than of the Curonian origin may get infected both in the places of their hatching and during migration and wintering. If these birds immigrate into the Curonian population, the prevalence of infection would be greater in them. The difference in the prevalence of the infection between these two groups of birds allows one to determine the share of inter-populational immigrants inhabiting in a population studied.

The method considered for the Curonian Spit was most completely tested in *Fringilla coelebs*, *Ficedula hypoleuca*, *Hippolais icterina,* and *Phylloscopus trochilus*. Let us consider these facts in more detail.

All birds investigated on the Curonian Spit were divided into the following four groups:

(I) Young (juvenilis) birds hatched on the Curonian Spit, which did not make seasonal migrations (Table 9). They are indicators of the epidemiological situation on leucocytozoonosis at the study site.

(II) Birds of northern populations (Baltic, Finnish, etc.) migrating in the autumn and spring through the Curonian Spit (Table 12). The dates of the observation were chosen to exclude birds of the Curonian origin from this group as much as possible.

(III) Birds breeding on the Curonian Spit with known (local) origin (Table 13). These are the birds, which made migrations, being previously ringed on the Spit before autumnal migrations, when they were nestlings (pullus) or young (juvenilis) birds. Each of them is an indicator of leucocytozoids imported to the region from wintering areas and migration routes.

(IV) Birds of unknown origin breeding on the Curonian Spit (Table 13). All nonringed adult (subadultus, adultus) birds during the breeding period (from June 11 to August 5), and

Table 12 Prevalence of *Leucocytozoon* spp. in young (autumn) and adult (spring) birds during seasonal migration on the Curonian Spit.

Bird species	Autumn			Spring		
	Number of examined birds	Infected		Number of examined birds	Infected	
		Number	*p*, %		Number	*p*, %
Ficedula hypoleuca	63	3	4.8 (1.3–11.9)	52	6	11.5 (5.1–21.7)
Fringilla coelebs	789	205	26.0 (22.0–28.1)	690	187	27.1 (25.3–31.9)
Hippolais icterina	116	9	7.8 (3.8–15.1)	241	30	12.5 (9.0–18.1)
Parus major	49	5	10.2 (4.1–20.4)	74	9	12.2 (6.5–20.3)
Phylloscopus trochilus	237	40	16.9 (12.2–22.0)	357	61	17.1 (13.3–21.4)

Note: 95% confidence limits of prevalence of the infection are given in parentheses.

Table 13 Prevalence of *Leucocytozoon* spp. in adult birds of known (Curonian) and unknown origin on the Curonian Spit during breeding periods.

Bird species	Bird origin					
	Curonian			Unknown		
	Number of examined birds	Infected		Number of examined birds	Infected	
		Number	*p*, %		Number	*p*, %
Ficedula hypoleuca	70	0	0 (0.0–4.2)	249	0	0 (0.0–1.2)
Fringilla coelebs	200	9	4.5 (2.0–8.0)	235	11	4.7 (2.6–9.1)
Hippolais icterina	82	1	1.2 (0.0–6.7)	102	1	1.0 (0.0–5.4)
Phylloscopus trochilus	122	0	0 (0.0–3.6)	82	0	0 (0.0–4.5)

Note: 95% confidence limits of prevalence of the infection are given in parentheses.

females with signs of breeding (brood spots) captured earlier were investigated. Each of *Ficedula hypoleuca* included in groups III and IV was caught in nest-boxes.

The first two groups are needed to evaluate the differences in infection with leucocytozoids of the birds belonging to the Curonian and more northern populations, which finally determine the possibility to apply the method described. As mentioned above, comparison of the leucocytozoid infection prevalence in birds belonging to groups III and IV allows us to estimate the presence or absence of immigrant birds, which immigrate to the

local Curonian bird population taking into account the share of parasites which are gained in the areas of wintering and on the routes of migration. The results of the analysis of infection of the groups indicated are as follows.

Young birds hatched on the Curonian Spit are not infected with leucocytozoids (Table 9). This is the main confirmation of the fact that there is no transmission of leucocytozoids on the spit due to the reasons mentioned above. The prevalence of infection in birds of northern populations migrating through the Curonian Spit is high (Table 12). The places closest to the region studied, where leucocytozoids are found in young individuals of some passerine birds, are located on the opposite coast of the Curonian Lagoon and in the vicinities of Klaipeda (Lithuania) (Fig. 44). No significant difference in the prevalence of infection was found between the birds hatched on the spit and in birds of unknown origin of the same species (Table 13) (the 95% confidence limit of infection prevalence for birds belonging to these groups markedly overlap). Thus, the results of researches performed allow us to state that the import of leucocytozoids by birds from areas of their wintering and migration is the main way of forming the fauna of these parasites in these species of birds studied on the Curonian Spit. The birds infected with leucocytozoids that pass through the spit either do not immigrate to the Curonian populations of *Fringilla coelebs*, *Ficedula hypoleuca*, *Hippolais icterina,* and *Phylloscopus trochilus*, or their share is insignificant. In other words, the data of the parasitological investigation indicate relative stability of the populations considered, in the sense that no birds from other distant populations are found here. This generally confirms the data of ornithological investigations (Sokolov, 1991).

Let us discuss one example in more detail (Vysotsky and Valkiūnas, 1992). According to the data obtained, the Curonian population of *Ficedula hypoleuca* is free of *Leucocytozoon* spp. (Table 13). This indicates that *F. hypoleuca* are not infected with the parasites during wintering or on the migration routes and that the share of these birds among those migrating through the spit and settling there becoming the members of the Curonian population is equal to zero or insignificant. Even if we assume that there is a possibility that 10% of *F. hypoleuca* migrating through the spit immigrate to the Curonian population, 11.5% of which are infected in spring (see Table 12), then after a simple calculation we demonstrate that parasites should be found in 1.15% of the group consisting of 249 birds of unknown origin (immigrants), which corresponds approximately to three individuals ($249 \times 0.1 \times 0.115 = 2.86$ individuals, or 1.15%). This calculation assumes that the infection of birds with parasites and the immigration of birds into the population are independent events. A possible share of infected birds (1.15%) calculated using this method coincides with the possible share of infected birds (1.2%), which could have been missed in a sample of 249 immigrants (the upper value of the 95% confidence limit for the possible share of infected birds) due to the limited number of the sample itself. None of *F. hypoleuca* infected are actually found. On the basis of this calculation, the proportion of the birds from the migration flow (specimens from distant populations) cannot exceed 10% in the population of *F. hypoleuca* on the Curonian Spit with a probability of 95%. Even the level of exchange of up to 10% of individuals per one generation cannot distort the peculiarity of the populations as genetic systems (Yablokov, 1987). Thus, the Curonian population of *F. hypoleuca* should be considered quite stable from the point of view of the presence of long-distance (inter-populational) immigrants. The Curonian Spit is a region of intensive migration for many bird species. In spring, *F. hypoleuca* belonging to northern populations stop here during their migration. Visual observations indicate that they occur exactly in the biotope of breeding near still uninhabited artificial nest-boxes. It seems that

these birds are provided here with everything needed to settle for breeding, but this however does not occur. The importance of these data for ornithology was earlier discussed in detail by Sokolov (1991) and Vysotsky and Valkiūnas (1992; 2001).

It is noteworthy that the use of *Leucocytozoon* spp. as biological tags facilitates the estimations of the presence of immigrants in the population of birds who make seasonal migrations over short distances into the regions of cold winters (for example, some species of *Parus*). Due to certain reasons, near-distance migrants are usually not infected with haemosporidians in the areas of their wintering or on the migration route (Valkiūnas, 1984b, see also p. 148). Therefore, all leucocytozoids recorded in them should be attributed to import by immigrants. This is also characteristic of birds, where the adult part of the populations consists of nonmigrating birds. In both cases, there is no need to have a reference group of birds of local origin to estimate the import of parasites from wintering areas, which allows one to apply this method without preliminary ringing of the birds at the regions with lack of *Leucocytozoon* spp. transmission.

This conclusion was taken into account in the estimation of the share of immigrants in the Curonian population of *Parus major* making seasonal migrations over short distances into the regions of cold winters (Vysotsky and Valkiūnas, 1992). Leucocytozoids were found in nine of 63 *P. major* investigated, which bred on the Curonian Spit (this makes 14.3%, while the 95% confidence limit of the infection prevalence is 7.6 to 23.7). The value of this index practically coincides with the same index recorded in *P. major* migrating through the spit in spring (12.2%) and autumn (10.2%), while their confidence limits markedly overlap (Table 12). Thus, birds of non-Curonian origin migrating through the spit predominantly take part in the formation of the Curonian population of *P. major*. Besides, less than 1% of the total number of *P. major* hatched at the study site were found here breeding in the following years. Similar values are also known for the other parts of the range of their distribution, for example in the Leningrad region of Russia (Noskov and Smirnov, 1981). At the same time, it is noteworthy that according to the data of ringing during certain years, specimens of *P. major* hatched at the study site make 10 to 20% of those, that breed on the Curonian Spit. In other words, the data of parasitological investigation indicate that there is strong mixing of *P. major* from different long-distance populations. This is in agreement with the results of ringing, which show that there is strong spreading of young *P. major* from the places of their hatching in the Northwestern Russia and Eastern Baltic (Noskov and Smirnov, 1981; Dobrynina, 1990). Interestingly, that leucocytozoids were found only in females (there were 45 females of 63 birds investigated) among *P. major* breeding on the Curonian Spit, while there is no difference in the infection of opposite sexes of this bird during seasonal migrations. These data indicate that mostly female immigrants penetrate into the Curonian population of *P. major*.

Interesting data are obtained during parasitological research of far-distance migrant *Phylloscopus sibilatrix*. In spring, 16 individuals of a total of 101 migrating through the Curonian Spit birds investigated were found to be infected with *Leucocytozoon* spp. (this makes 15.8%, while the 95% confidence limit of the infection prevalence is 9.9 to 25.6), which coincides with the infection of breeding *P. sibilatrix*: 5 birds of total 35 investigated (14.2%, 4.8 to 30.3). Since far-distance migrants are rarely infected with these parasites in wintering areas (Valkiūnas, 1993b; see also p. 162), and birds hatched on the spit cannot get infected at the locality of hatching, we can conclude that the Curonian population of *P. sibilatrix* is predominantly formed from the birds of non-Curonian origin. These results agree with the fact that *P. sibilatrix* rarely return to the places of their previous reproduction (Temrin, 1988). It is likely that the individuals of this bird intensively exchange between

distant populations. It is important to note from the point of view of parasitology that immigrating birds import parasites, and, as a result of this, the proportion of infected birds in the population studied may increase significantly without any relation to the parasite transmission at the study site.

Thus, according to the results of the parasitological investigation, the nature of the bird populations significantly differs for the species studied. *Fringilla coelebs*, *Ficedula hypoleuca*, *Hippolais icterina,* and *Phylloscopus trochilus* are characterized by quite isolated populations. Unlike the species mentioned, *Parus major* and *Phylloscopus sibilatrix* are characterized by a significant exchange of individuals between distant territories. It is noteworthy that in this respect, the two latter species are likely to be an exception rather than a rule among the small passerines investigated. These data have also a theoretical importance for the parasitology. For example, the information about the high prevalence of *Leucocytozoon* spp. infection in *P. major* and *P. sibilatrix* on the Curonian Spit quantitatively illustrates the important role of immigrant birds in the formation of the parasite fauna of certain regions. This peculiarity of the parasite fauna has not yet been taken into account in parasitological populational studies (see also p. 139).

On the Curonian Spit as well as in any other regions without reproduction of simuliids and isolated by ecological barriers (for example, Barsa-Kelmes Island in the Aral Sea, Gotland Island in the Baltic Sea, and many others), one can use leucocytozoids as convenient markers to estimate the structure of the populations of birds, especially in the Holarctic where the prevalence of bird infection with these parasites is high. The leucocytozoids of passerines not only meet all the requirements of the parasites as biological tags (MacKenzie, 1983), but they have the apparent advantage of the diagnostics among many other parasites, which is an opportunity to record parasites on a species level in living hosts. On the one hand, this increases the accuracy of the method applied, because repeated mass samplings do not distort the peculiarities of the distribution and allocation of the parasites in the wild host population, while on the other hand, it offers new opportunities to apply the method in the ornithological studies without damaging the bird populations and at the same time using ringed birds, which are of great informational value.

It is necessary to remember that the longevity of a relapsed parasitemia in leucocytozoids is usually much longer than in other groups of bird haemosporidians, and the patent parasitemia is usually available during the entire breeding period in previously infected birds. This fact also contributes to the use of the method described. The application of other groups of haemosporidians as markers is less possible because their vectors (species belonging to the Culicidae, Ceratopogonidae, Hippoboscidae) have less restriction to the places of reproduction and are distributed almost everywhere.

The example of the application of parasitological data to solve specific ornithological problems discussed in this chapter is theoretically important because it demonstrates unusual opportunities for multidisciplinary work by parasitologists and biologists of other specialties, which are still insufficiently realized. These multidisciplinary investigations generally do not require additional funding, while at the same time they significantly increase the databases and ideas of both groups of sciences. In this sense, the opportunities for general parasitology remain unrealized. Molecular biology methods are an inexhaustible reserve for future investigations into host–parasite relationships, including the use of parameters as biological tags in bird populational studies.

Haemosporidians as Objects for Analysis in the Evolutionary and Population Biology of Birds

Birds are the only group of vertebrates which is inhabited almost worldwide by haemosporidians, excluding the extreme northern and southern regions of the planet. Moreover, as we already mentioned, some species of parasites are even actively transmitted beyond the North Polar Circle, which is unique for haemosporidians (Valkiūnas *et al*., 1990). Wide geographical distribution, high prevalence of infection, a possibility for the analysis of many parasitological indices in living hosts, including ringed birds, which is of great informational importance, all these and some other factors mentioned already in this book separate bird haemosporidians into a group of promising objects to study the role of parasites in nature. At the same time, the complicated life cycles and the complex biology of haemosporidians, not all aspects of which have been currently investigated, require some experience of the researchers who use this group of protists in evolutionary biology studies. A formal collection of facts on bird infection with haemosporidians in the solution of the problems of evolutionary and populational biology leads to regrettably incorrect conclusions. Our belief in the fact that the analysis of the peculiarities of wild birds' infection with haemosporidians is promising toward the solution of a series of problems of parasitology and evolutionary biology made us consider some of the typically inaccurate conclusions or even mistakes made in the works of two recent decades.

A well-known paper by Hamilton and Zuk (1982) stimulated a wider use of the data on blood parasites in the works on the evolutionary biology of birds. The authors put forward one of the most brilliant hypotheses ever suggested to explain the causes of the evolution of bright plumage of birds. According to this hypothesis, the secondary sexual characters (bright plumage, peculiarities of song) evolved as signals of resistance to parasites, used by females to choose genetically most resistant partners for mating. The theses usually named as consequences of this hypothesis are that the bird species with the brightest plumage should be subject to a greater parasites load, while infection with parasites should correlate with the success of mating for individual males.[†] The actual analysis of this original hypothesis is beyond the range of this book. Discussion materials on this problem are published in several reviews (Endler and Lyles, 1989; Clayton, 1991; Toft, 1991; Møller, 1997), as well as in the articles cited in this chapter. We touched on this hypothesis because the data on bird infection with haemosporidians are widely used for its testing.

The Hamilton–Zuk hypothesis stimulated the development of parasitology and became a stimulus to conduct a series of excellent original population investigations (Schall and Dearing, 1987; Ressel and Schall, 1989; Ashford *et al.*, 1990; Johnson and Boyce,

[†] Both of these consequences are not easy to test in relation to haemosporidians. It is our opinion that both of them, as well as the hypothesis itself, cannot be tested directly by means of the analysis of the parameters of chronic parasitemia and their correlations, which is, however, frequently done (see pp. 113 and 140 for details).

1991; Kirkpatrick *et al*., 1991; Davidar and Morton, 1993; Korpimäki *et al.,* 1993; Rätti *et al.*, 1993; Allander and Bennett, 1994). At the same time there are works where the testing of this hypothesis and the solution of other problems of the evolutionary biology of birds using the data on their infection with blood parasites has been carried out on a perfect level from the point of view of evolutionary biology and mathematical statistics but do not stand up under scrutiny from the position of parasitology. This refers primarily to the materials, which are available in the review catalogs on the distribution of blood parasites in different zoogeographical regions (Greiner *et al*., 1975; McClure *et al*., 1978; White *et al*., 1978; Peirce, 1981b), which are used in evolutionary biology. These catalogs summarize the data from literature on the infection of many hundreds of bird species with numerous species of blood parasites at the level of their genera (mainly, *Haemoproteus*, *Leucocytozoon*, *Plasmodium,* and *Trypanosoma*). For each bird species, the data summarized on their infection (overall prevalence of infection) are given for hosts of different ages and sexes, which were investigated during various seasons, in different regions, etc. Each of the factors listed has its own specific influence on the prevalence data. Even more, the 'negative' results of investigations, when bird parasites are not allocated due to any of the reasons, are frequently not included in the catalogs. Scientific journals are reluctant to publish these 'negative' data (Ashford *et al*., 1994) as well as the data of certain narrow regional investigations. Therefore, the information presented in the catalogs is, to a great degree, random, and usually does not reflect the real parasitological situation, which takes place in nature and frequently differs markedly from the results of investigation with certain populations of birds. Nevertheless, in the last decades, the catalog data have been widely used in evolutionary biology for testing the Hamilton–Zuk hypothesis (Read and Harvey, 1989; Pruett-Jones *et al*., 1990; Zuk, 1991) and the solution of such specific problems as the explanation of the evolution of polygyny (Read, 1991) and birds' song (Read and Weary, 1990), the duration of embryonic development (Ricklefs, 1992) of birds, etc. The conclusions of these works based on perfect mathematical calculations may easily mislead those who do not have a deep knowledge of parasite biology. The manifestation of incorrectness in preparing the parasitological facts for analysis are conclusions that the prevalence of birds infection with blood parasites is comparatively insensitive to the influence of habitat and even to the season of the year (Ricklefs, 1992). The application of catalog data on the overall prevalence of infection as a basis for the solution of the problems of the evolutionary biology of birds is an example of how helpless the mathematical modeling and the use of the powerful means of mathematical statistics are in the cases when the data for analysis have been insuficiently prepared.

Some scholars were 'trapped' while testing the Hamilton–Zuk hypothesis at a higher populational level due to their underestimation of the complex biology of haemosporidians. For example, they used the intensity index in the investigation of the influence of haemosporidians on wild birds (Pruett-Jones *et al*., 1990) but did not take into account that this parameter is an extremely dynamic one and, in many aspects, it is a function of the stage of the infection development in each individual host. In relation to this, information about the intensity of parasitemia in birds investigated only once cannot be extended to the same individuals of birds in different periods of their lives. This is also the reason that data about the mean intensity of infection of certain bird species with haemosporidians are frequently random. This index is sometimes used in the investigations of the evolutionary biology (Pruett-Jones *et al*., 1990). While performing ecological investigations, one should operate the data on the intensity of infection carefully, because certain species of haemosporidians are characterized by diurnal cycles of parasitemia. This phenomenon is poorly studied in

bird parasites (Noblet *et al*., 1980). At the same time, it is noteworthy that the intensity of parasitemia is an informative parameter when studying host–parasite relations. It can be effectively used in the field conditions, however, only when the data are compared with the laboratory experimental observations.

Another common mistake in investigations performed at the populational level is summarizing the data of bird infection with different groups of parasites (for example, *Haemoproteus*, *Leucocytozoon,* and *Plasmodium* spp.) as well as summarizing the data on infection of various age groups of the hosts (Weatherhead and Bennett, 1992). In this case, apparent differences in the biology of haemosporidians related to different genera as well as the peculiarities of their influence on the birds of different age are ignored, which makes the entire analysis and its results doubtful. In some works (Weatherhead *et al.,* 1991), the parasitological data on parasites accurately collected at the level of the certain populations of birds lose their 'individuality' due to the summarizing of the data on infection of many bird species with various blood parasites, which practically equates the level of these investigations to the one, when catalog data are used.

The few examples considered are only some of the easily understood cases of the difficulties faced by scholars using haemosporidians in their research on the evolutionary and populational biology. There are other specific 'traps' in every case of the investigations of the host–parasite relationships. Some of them are discussed in the chapter 'Certain Peculiarities of the Ecological Study of Bird Parasites' (p. 137). Joint efforts and coordination by parasitologists and ornithologists are needed to overcome these difficulties.

In conclusion, it is worth emphasizing that the overwhelming majority of the works dedicated to testing the Hamilton–Zuk hypothesis using bird blood parasites as a model (summarized by Møller, 1997) are based on correlations with the application of the parameters of chronic infections (relatively benign), but the heavy infections (at their acute stage) for some reasons are usually underestimated (see p. 140 for details). It is our opinion that with regard to this, the main idea of the Hamilton–Zuk hypothesis remains untested and attractive, despite there being a number of works dedicated to this problem, including equally those that reject and confirm it. One of the possible ways of testing the Hamilton–Zuk hypothesis from the point of view of the application of bird haemosporidians for these purposes is the estimation of immune status and resistance to parasites in males with bright and dull plumage inside a population and among bird species, as well as testing the ability of birds from both these groups to survive the acute stage of the primary infection and the ability of their offspring to inherit this capability. At present, it is clear that the estimation of chronic parasitemia in wild birds is not enough to study these problems. Astonishingly, *K*-selected birds and their parasites in the tropics, where the loss of even few individuals may have a significant influence on the genofond (gene pool) of low-density populations, look to provide a good model for such investigations (Ashford, 1998).

Relapses

The content of the term 'relapse' differs in the representatives of various groups of haemosporidians, because there are major differences in their life cycles. Relapse during bird haemosporidiosis is the appearance of secondary parasitemia after a latent stage of infection or a significant increase of the parasitemia during the period of chronic parasitemia, which, in both cases, is associated with the activation of exoerythrocytic merogony.

The representatives of the Haemoproteidae and Leucocytozoidae families pass only the exoerythrocytic merogony, which is the only source of merozoites giving rise to the parasites in the blood cells. Consequently, any reliable increase of parasitemia of haemoproteids and leucocytozoids is associated with the activation of the exoerythrocytic merogony thus being a relapse. It is noteworthy that chronic parasitemia of Haemoproteidae and Leucocytozoidae species lasts many months following a one-off infection with sporozoites. For example, gametocytes were recorded in the blood of turkeys for 13 months following infection with a strain of *Leucocytozoon smithi* from South Carolina (USA) (Dick and Rice, 1975), which indicates a continuing exoerythrocytic merogony. Nevertheless, one can speak about a relapse only in the case of a marked intensification of the merogony that is usually observed for *L. smithi* in spring time (Alverson and Noblet, 1977).

Along with exoerythrocytic merogony, the species of the Plasmodiidae are also characterized by erythrocytic merogony. The increase of parasitemia in this content may be associated either with the activation of exoerythrocytic merogony (relapse) or with the resuming of the erythrocytic merogony. The latter case is a recrudescence of high parasitemia, but not a relapse. It is difficult to distinguish relapses from recrudescences in birds naturally infected with malaria parasites without using special experimental tests because the intensity of chronic parasitemia is often low. Therefore, it is not always possible to find parasites in the blood using the stained films microscopy method and thus to distinguish between the chronic and latent period of infections, which precede the recurrence of high parasitemia.

One of the main peculiarities of the *Plasmodium* spp. life cycle in birds is that the exoerythrocytic merogony (phanerozoites) can be initiated by merozoites from erythrocytic meronts. This property principally differentiates bird malaria parasites from the species developing in mammals. It was experimentally shown that relapses occur in birds subinoculated with the blood of infected individuals (Applegate, 1971). The relapses of *Plasmodium* spp. in mammals are recorded only after infection with sporozoites (Garnham, 1980; Krotoski, 1989).

The mechanism of relapses of bird haemosporidians has not yet been studied well enough. It should be noted, first of all, that the role of sporozoites in the formation of stages responsible for relapses have not yet been finally investigated. It is, however, clear that sporozoites is not the only source of forming the stages, which are responsible for relapses of bird haemosporidians. Merozoites from the exoerythrocytic and erythrocytic meronts take part in this process (Applegate, 1971; Yang *et al.*, 1971), which, as it was mentioned earlier, is not characteristic of *Plasmodium* spp. in mammals. It is likely that some exoerythrocytic trophozoites and meronts slow down their development becoming a

reservoir to maintain chronic parasitemia and relapses. It is difficult to find these inactive stages in naturally infected birds using traditional histological methods due to their small size and (or) low intensity of the infection. They have not been studied in the majority of the species of bird haemosporidians. Moreover, general regularities in the mechanism of relapses are still uncertain even at the level of genera of bird parasites. Both the morphology and the localization of the exoerythrocytic meronts responsible for the relapses are shown to differ significantly even in the representatives of one genus. For example, these are the most likely megalomeronts in lungs for *Leucocytozoon simondi* (Desser *et al*., 1968), meronts in kidneys for *L. danilewskyi* and *L. dubreuili* (Khan and Fallis, 1970b; Khan, 1975), while in *L. lovati* (=*L. bonasae*) these are meronts in liver (Clarke, 1938).

The data available indicate that there is no unique mechanism of relapses for all genera of haemosporidians. Relapses of bird haemosporidians may be conventionally divided into two groups: seasonal (usually spring ones) and nonseasonal. The former are characterized by a clearly manifested adaptive property being synchronized with the period, when the transmission of parasites resumes coinciding with the period of bird breeding and activation of the vectors in nature, while the latter may occur at any time of the year and have no clear connection with seasonal changes in nature.

Seasonal relapses are characteristic of the majority of bird haemosporidians studied, which are transmitted in the countries with temperate climate. Spring relapses are well documented for *Plasmodium relictum*, *Haemoproteus nettionis*, *H. mansoni*, *Leucocytozoon danilewskyi*, *L. dubreuili*, *L. lovati*, *L. simondi*, *L. smithi,* and other species (Huff, 1942; Chernin, 1952; Box, 1966; Desser *et al*., 1968; Khan and Fallis, 1970b; Applegate, 1971; Alverson and Noblet, 1977; Allan and Mahrt, 1989). Seasonal relapses have an important epidemiological role being the main and often the only source of infection during the period when transmission initiates in countries with well-manifested natural seasonal phenomena. It is noteworthy that during the period of spring relapses, the infectivity of gametocytes for vectors increases compared to the period of chronic parasitemia; this was experimentally shown on the example of *P. relictum* (Applegate and Beaudoin, 1969). Spring relapses are clearly synchronized and they depend neither on the time of the initial infection of birds nor on the internal rhythms of existence, but are determined by abiotic factors influencing indirectly through the organism of the vertebrate host (Applegate, 1971). One of the factors stimulating the spring relapse in birds is the increase of the quantity of sexual hormones in the blood during breeding season, which in its turn correlates with the increase of day duration in spring. By artificial prolongation of the daylight in laboratory conditions, it became possible to induce laying of eggs in anseriform birds one month earlier compared to the reference specimens. This was also accompanied by earlier relapse of *L. simondi* (Chernin, 1952). In those cases, when ducks lay eggs in autumn, the relapse is also recorded in the fall time (Khan and Fallis, 1970b). Injections of sexual hormones and corticosterone stimulate relapses (Haberkorn, 1968; Applegate, 1970). It is noteworthy that relapses of *L. tawaki* correlate with the beginning of molting of penguins (Fallis *et al*., 1976) and are probably stimulated by the corresponding hormones.

Nonseasonal relapses are poorly studied. They are common in those species of haemosporidians the transmission of which is strongly extended in time, which is especially characteristic of the countries with a warm climate. For example, no periodicity is found in the relapses of the Egyptian strain of *Haemoproteus columbae,* whose vectors are hippoboscid flies (Ahmed and Mohammed, 1978a). Similar results were obtained in the investigation of the American strains of *H. columbae* and *H. sacharovi* (Coatney, 1933; Farmer, 1962). The factors stimulating nonseasonal relapses are still poorly understood.

Stresses and associated decrease of immunity possibly have some influence in this case. There is information that relapses of *Leucocytozoon simondi* in anseriform birds during stress situations are related in particular, to the manifestation of aggression in the flock and may, in fact, be induced during any time of the year (Barrow, 1963).

The duration of the secondary parasitemia initiated by relapses in species of *Haemoproteus* and *Leucocytozoon* is usually several months. For example, the relapsed parasitemia lasts three and four months in *H. mansoni* and *L. lovati,* respectively (Allan and Mahrt, 1989) but this is not the maximum limit, which has been recorded so far. The duration of the parasitemia decreases, while the infection 'gets older' in the following years (Khan and Fallis, 1970b). The duration of the relapsed parasitemia in *Plasmodium* spp. is usually much shorter, although it varies in the representatives of different subgenera.

It is noteworthy that relapses are not characteristic of all species of bird haemosporidians. For example, domestic chickens that survive the infection of *Leucocytozoon caulleryi*, acquire complete resistance to reinfection, and relapses have not been observed yet for this parasite (Morii, 1992). Single inactive exoerythrocytic meronts of *L. caulleryi* are seldom found in the recovered birds. It is not inconceivable that relapses may occur in the case of decrease of immunity, but this should not have a great influence on the disease epidemiology due to the apparent fact that such inactive meronts are rarely formed (Fujisaki *et al*., 1982; Hashimoto, 1982; Kitani *et al*., 1983).

The role of the spleen and reticuloendothelial system of hosts in the control of relapses is not the same for different species of haemosporidians. For example, removal of the spleen induces the relapses of *Plasmodium gallinaceum*, *P. juxtanucleare,* and *P. cathemerium* (Huff, 1963) but not of *Leucocytozoon caulleryi* (Morii and Kitaoka, 1970). This is another example of the principal differences of immunity and the mechanisms of relapses in different groups of bird haemosporidians, which is apparently poorly studied.[†]

[†] Recently, we have studied the effects of a light-dark cycle on the relapse of *Haemoproteus* sp. in the naturally infected adult siskins *Spinus spinus*. During winter time, the relapse was induced by exposing the infected birds, in which the infection was latent, to the extended light cycle (16 : 8 h instead of 12 : 12 h). Gametocytes of *Haemoproteus* sp. were recorded in two experimental birds two to four days after this experiment was started. Two weeks after the exposure to the extended light cycle, the relapse of *Haemoproteus* sp. was recorded in six birds from the experimental groups (100% of infections were relapsed) but none of five infected birds from the control group, which were held at 12 : 12 h light-dark cycle, showed the relapsed parasitemia ($P < 0.01$). Intensity of the relapsed parasitemia was low (< 0.01% of erythrocytes). The parasitemia was seen for a month (the period of observation). Thus, extension of the light cycle has a rapid influence on the relapse of *Haemoproteus* sp. It is probable that the pineal hormone melatonin is one of the factors, which initiate the spring relapses of some species of avian haemosporidians. The concentration of this hormone in birds is very sensitive to the light–dark cycle. Melatonin is responsible for many circadian and circannual rhythms in birds (Gwinner and Hau, 2000). See also Valkiūnas *et al.* (2004) for additional information.

Peculiarities of Immunity

Innate and acquired immunity are distinguished in haemosporidioses as well as in other infections. Innate immunity usually includes the interaction of physiological and other biological factors influencing the susceptibility of the host to parasites. This form of resistance is a result of long evolution. Innate immunity determines the properties of the parasites, which, in particular, are manifested in their 'potential specificity.' The latter is realized indirectly (by means of the ecological factors) in the fact that the parasites have a certain range of hosts, which is one of the important objectives in the research of zoologists (for details see the chapter 'Specificity and General Principles of Species Identification'). Acquired immunity is formed as a result of the previous infection of the corresponding host individuals and may be maintained for a certain time restricting the development of the pathological process during repeated infections or completely preventing it.

Acquired immunity is poorly studied for haemoproteosis. Domestic pigeons with chronic parasitemia of *Haemoproteus columbae* acquire immunity (premunition) which is being lost while gametocytes disappear from the blood (Ahmed and Mohammed, 1978a). Bird malaria is practically always accompanied by the premunition state due to more or less prolonged presence of a small number of erythrocytic parasites (Garnham, 1966; Seed and Manwell, 1977). When *Leucocytozoon simondi* develops in ducklings, premunition is maintained by introduction of sporozoites into the blood, while the presence of exoerythrocytic meronts and gametocytes of the parasite in the bird's organism does not prevent their reinfection, which may even cause the death of the reinfected individuals (Fallis *et al*., 1974). The other situation is observed during the development of *L. caulleryi* in chickens. In this case, complete immunity to reinfection develops due to the total blocking of the development of the exoerythrocytic meronts of the second generation (Morii and Kitaoka, 1970; Morii *et al*., 1986, 1989). On the ten to fifteen days after the inoculation of sporozoites, serum-soluble antigens of the proteinaceus nature are found in the blood plasma of chickens, which originated from the second generation of the exoerythrocytic meronts (Morii, 1972, 1974). Precipitating antibodies against these antigens appear in the sera of the chickens on approximately the 17th day after the inoculation of sporozoites. Long-term presence of the antibodies to *L. caulleryi* in chickens infected once was proved experimentally (Isobe and Suzuki, 1987). Cell-mediated immunity plays an important role in the development of the resistance to reinfection with *L. caulleryi* in chickens (Isobe *et al.*, 2000). Relapses in chickens recovered from primary infection have not been recorded. Exoerythrocytic meronts of *L. caulleryi* of the second generation and serum-soluble antigens are characterized with high immunogenicity to chickens, which forms a basis for the development of a vaccine (Morii *et al*., 1989, 1990). A vaccine utilizing erythrocytic stages of *Plasmodium gallinaceum* has been developed (McGhee *et al*., 1977).

Wide distribution of mixed infections with the representatives of the genera *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* in wild naturally infected birds indicates that a cross immunity does not develop.

Prevention and Treatment

Prevention of haemosporidioses is based on the isolation of birds from the vectors whose period of activity is associated with the warm season of the year. During the period favourable for infection, small groups of birds and individual expensive specimens are kept indoors or put in cages or aviaries covered with fine-mesh bolting silk which prevents the blood-sucking dipteran insects from penetrating there.

The birds living in aviaries on endemic territories are regularly tested for infection with blood parasites. Infected specimens are isolated and treated, if possible. Dovecotes are regularly examined in the warm season (not less than once in three weeks) and cleaned of the puparium of hippoboscid flies. The aviaries infected with these insects and the birds may be processed with powder used against fleas. Newly introduced specimens are treated in the same way, as well as the birds returning from exhibitions, breeding, etc.

Prevention of haemosporidioses in industrial poultry farming is a difficult problem. One should keep in mind that young birds are more susceptible; they experience the illness harder and perish more often. The probability of infection decreases in the endemic regions if the young birds are bred indoors in the premises accessible by the vectors with difficulty, where repellents may be sprayed during the period of maximum activity of the vectors. If the birds are kept outdoors in the industrial farming, the control of vectors requires expensive global regular actions. For example, in South Carolina (USA), a reliable decrease in the number of blood-sucking simuliid flies, the vectors of *Leucocytozoon smithi*, was gained due to spraying of larvicide from a helicopter in a region of the location of several large farms breeding turkeys on the territory with an approximate diameter of 16 km. This led to a decrease of prevalence of birds' infection with this parasite (Kissam *et al*., 1975). The damaging impact on the nature caused by such global programs can be markedly reduced when larvicides of biological origin are used.

Administration of preventive compounds decreases the poultry damage caused by leucocytozoonosis (see Akiba, 1970; Siccardi *et al*., 1974). To prevent the disease caused by *Leucocytozoon smithi*, clopidol in a dose 0.025 or 0.0125% is added to the food during the period favourable for the transmission of the parasite. This effectively controls the parasitemia. A good result in prevention from *L. caulleryi* is obtained if pyrimethamine in dose 0.00005 to 0.0001% or sulphadimethoxine in dose 0.005% is added to food, or their combination is used in doses of 0.0001 and 0.001%, respectively. The chemotherapy is applied in the period of the year when the transmission takes place. Parasites develop resistance to preventive compounds, which requires permanent search of new ones. In addition, chemical preventive agents are accumulated in the food products; this requires the development of effective vaccines against haemosporidioses, which are not widely used at present in industrial production.

The methods of bird haemosporidioses treatments are not worked out well enough. Usually, chronic parasitemias are not manifested clinically, but they are dangerous as a source of infection for the vectors. In case of haemoproteosis, it was recommended to apply quinacrine hydrochloride or chloroquine phosphate (see Moucha, 1983). In the former

case, one tablet (100 mg) should be dissolved in 113 ml of drinking water and given to the birds every day during 7 to 14 days, repeating the treatment after two weeks. In the latter case, one tablet (250 mg) is dissolved in the same quantity of water and given to the birds daily for as long as 30 days. Atebrine and plasmochine were recorded to reduce the parasitemia of *Haemoproteus* spp., but have no influence on the exoerythrocytic meronts (Coatney, 1935). These preparations are toxic for birds and can hardly be recommended for wide use. Butalex (buparvaquone) was found to be effective against *H. columbae* in naturally infected domestic pigeons (El-Metenawy, 1999).

No reliable means of treatment of severe leucocytozoonosis has yet been found. In this relation, the administration of preventive compounds is important in endemic territories. Infections of *Leucocytozoon caulleryi* are treated with sulphamonomethoxine sodium by adding 1 g of the compound to one liter of drinking water. The same preparation at a dose of 1 g per 20 l of drinking water may be applied with prevention purposes (Soulsby, 1982).

Numerous preparations were tested to treat bird malaria (Seed and Manwell, 1977; Richards, 1984). Chloroquine phosphate (in dose 5 mg per 1 kg of the bird weight), paludrine (7.5 mg/kg), and pyrimetamin (0.3 mg/kg) are effective against *Plasmodium gallinaceum*. Below, we give a scheme of treating malaria caused by *P. relictum* and *P. elongatum,* which are the most widely distributed species of malaria parasites (see Stoskopf and Beier, 1979). A satisfactory result was obtained in treatment of penguins by oral intubation of chloroquine phosphate and primaquine phosphate suspension prepared in the normal (0.85%) saline. The dose of primaquine phosphate is 0.003 mg/kg daily during three days. The first dose of chloroquine phosphate introduced together with primaquine phosphate is 10 mg/kg. After 6, 18, and 24 h, the intubation of chloroquine phosphate is repeated at a dose of 5 mg/kg. Indirect effects were not recorded. Relapses of parasitemia occurred, the mechanism of which has not been investigated in detail. It is likely that many new compounds applied in treating human malaria, especially caused by *Plasmodium falciparum* which is phylogenetically close to the bird disease, may be also used to treat bird malaria but this needs testing with certain species of avian parasites.

Taxonomy and Classification

At present, the position of haemosporidians in the classification of living organisms is well determined, and with a few exceptions does not cause any serious disagreement, although the taxonomic rank of the group (Order, Suborder, and rarely Class and Subclass) are not uniquely defined in different systems (Wenyon, 1926; Kudo, 1947; Garnham, 1966; Levine, 1973; Krylov *et al.*, 1980; Levine *et al*., 1980; Euzeby, 1988; Levine, 1988; Sleigh, 1989; Cox, 1991; Euzeby, 1992; Krylov, 1992, 1996). In this book, we accepted the version suggested by Krylov (1996).

Kingdom Protista (Haeckel, 1866)
Phylum Sporozoa (Leuckart, 1879) (=Apicomlexa Levine, 1970)
Class Perkinsea (Levine, 1978)
Class Gregarinea (Dufour, 1828)
Class Coccidea (Leuckart, 1879)
Subclass Coccidia (Leuckart, 1879)
Order Agamococcidiida (Levine, 1979)
Order Protococcidiida (Cheissin, 1956)
Order Coccidiida (Leuckart, 1879)
Order Adeleida (Léger, 1911)
Order Haemosporida (Danilewsky, 1885)
Subclass Piroplasmia (Levine, 1961)
Order Piroplasmida (Wenyon, 1926)

The same plan of the ultrastructure realized to a greater or lesser degree in each of the representatives of the phylum Sporozoa at least during one stage of their development is the basis for establishment of the phylum. Among the characteristics of the sporozoans, the most important in the taxonomic respect, the pellicle with a complex structure consisting of a plasmalemma and inner double membrane layer, as well as micropyles, subpellicular microtubules, conoid (reduced in certain species), polar rings, micronemes and rhoptries (reduced in certain species) should be pointed out first of all.

We use the name Sporozoa for the phylum considered. R. Leuckart made this name available more than 100 years ago. He used it for the class of protists, whose rank was raised to the phylum by Krylov and Dobrovolsky (1980). Not long ago, Levine with co-authors (Levine, 1970; Levine *et al.*, 1980) introduced a new name Apicomplexa for this group by means of the description a new phylum of protists. No doubt, N.D. Levine's merit is that he was the first to focus attention on the similarity of the ultrastructure of sporozoans and to suggest the use of these data in the systematics. It is difficult to agree, however, with the position that new high-rank taxa are established on the basis of the appearance of principally new information on the biology of the objects belonging to the existing taxonomic groups. It should be noted that the union of the Perkinsea, a small group by the

number of species, with sporozoans into one phylum seems an insufficient argument to establish the new phylum of protists. The name Apicomplexa reflects better the structure of protists under consideration because all their species have organelles of the apical complex at least at one stage of their development but not all produce spores. However, in taxonomy, the category 'who is first' but not 'better' has priority. At present each protistologist knows what the name Sporozoa means, and in this case there is no need to establish new taxon and new name Apicomplexa. Let us remember that physicists successfully use the term 'atom' which means 'indivisible' but everyone knows that it is divisible. Unfortunately, the International Code of Zoological Nomenclature (1985, 1988) does not deal with taxa whose rank is higher than the family group. However, it would be logical to follow the same principles in nomenclature work both with the low and high rank taxa when possible. We discussed this question in more detail because, in our opinion, this is important in protistology, which currently experiences marked transformation of its classification at the level of higher taxa, and thus there is a threat against the stability of nomenclature. Some prominent protistologists expressed their opinion against using the name Apicomplexa for this group of protists, which includes many well-known agents of the diseases of human and domestic animals (Krylov and Dobrovolsky, 1980; Krylov *et al.*, 1980; Vivier, 1982; Sleigh, 1989; Cox, 1991; Krylov, 1994, 1996, and others). We agree.

The number of families of the order Haemosporida determined in the outstanding monograph by Garnham (1966) has currently been supplemented with the family Garniidae, including the genera *Garnia* and *Fallisia* (Lainson *et al*., 1971, 1974; see also Appendix 2, p. 868). It should be noted that P.C.C. Garnham accepted the validity of the garniids (Garnham and Duggan, 1986). The family Garniidae unites mainly the reptilian parasites whose merogony occurs in the blood cells and who developed the ability to digest hemoglobin completely and thus do not produce the malarial pigment (hemozoin) at all stages of their development, even when they inhabit erythrocytes. At present, taxonomists frequently distinguish four families of haemosporidians: Haemoproteidae, Plasmodiidae, Garniidae, and Leucocytozoidae, which reflects the divergence quite well, and this is accepted by us. Telford (1988a) considers the Garniidae to be a synonym to the Plasmodiidae, which we can hardly accept, because this requires a major change in the definition of the well defined family Plasmodiidae, which includes well investigated and quite specialized malaria parasites of human and other mammals. Levine (1988) joins all haemosporidians into one family Plasmodiidae, which in our opinion is not right, because this approach first of all ignores the difference in the life cycles of the parasites and leads to the loss of proportionality and descriptiveness of the classification. We also can hardly accept the joining of the Leucocytozoidae and Garniidae with piroplasmids into one order Achromatorida, as well as the separation of the order Chromatorida including the representatives of the Haemoproteidae and Plasmodiidae (Euzeby, 1988, 1992). The latter position ignores the similarity in the life cycles and structure of haemosporidians as well as their difference from piroplasmids. In particular, haemosporidians have oocysts and a conoid at the stage of ookinete, which is not characteristic of piroplasmids (Paterson and Desser, 1989; Krylov, 1992).

We accept one genus of parasites: *Haemoproteus*, *Plasmodium,* and *Leucocytozoon* in each of the families Haemoproteidae, Plasmodiidae, and Leucocytozoidae, respectively, which reflects the resemblance of the life cycles and structure of these protists. The genera *Parahaemoproteus* and *Akiba* are considered as subgenera of the *Haemoproteus* and *Leucocytozoon*, respectively, which was first suggested by Levine and Campbell (1971) and Hsu and co-authors (Hsu *et al*., 1973). This is currently the most popular position of

the taxonomists following Corradetti with co-authors (Corradetti *et al*., 1963a), according to which it is considered to be more preferable not to group close species within families of haemosporidians into numerous weakly differentiated genera, but to apply the subgenera category in the taxonomy. The status of subgenera for the groups mentioned above is accepted by many specialists (Bennett and Peirce, 1988; Atkinson, 1991b; Bishop and Bennett, 1992; Morii, 1992; Desser and Bennett, 1993). This position simplifies the generic identification of species whose life cycles are studied incompletely, especially in the vector. This is convenient for faunistic and applied research. Not all taxonomic problems are solved, however, in this situation, especially those related to insufficient study of the life cycles of the majority of species and with the impossibility of identifying the groups on the basis of the investigation of gametocytes, the most easily available stages for research. These problems are only transferred to the level of subgenera, which has significantly less influence on the nomenclature, and seems optimal at present.

Corradetti with co-authors (Corradetti *et al.*, 1963a) were first to suggest the division of bird parasites of the genus *Plasmodium* into subgenera. The division is still topical. We accept the following subgenera of bird malaria parasites: *Haemamoeba*, *Giovannolaia*, *Novyella,* and *Huffia.* A new subgenus *Bennettinia* was also established (Valkiūnas, 1997), which includes only one species, *Plasmodium juxtanucleare* characterized by small (smaller than the nucleus of the infected erythrocyte), roundish erythrocytic meronts and gametocytes as well as unique pedunculated oocysts.

Fallisia neotropicalis is the only representative of the family Garniidae which has been discovered in birds. A new subgenus *Plasmodioides* was established for this parasite (Gabaldon *et al*., 1985).

From the above reasoning, bird haemosporidians can be classified in the following way:

Order Haemosporida
- Family Haemoproteidae
  - Genus *Haemoproteus*
    - Subgenus *Parahaemoproteus*
    - Subgenus *Haemoproteus*
- Family Plasmodiidae
  - Genus *Plasmodium*
    - Subgenus *Haemamoeba*
    - Subgenus *Giovannolaia*
    - Subgenus *Novyella*
    - Subgenus *Bennettinia*
    - Subgenus *Huffia*
- Family Garniidae
  - Genus *Fallisia*
    - Subgenus *Plasmodioides*
- Family Leucocytozoidae
  - Genus *Leucocytozoon*
    - Subgenus *Leucocytozoon*
    - Subgenus *Akiba*

Origin and Phylogeny

At present, we have no exact answer to the questions: (i) in which ecological niche, (ii) when, and (iii) in which group of vertebrate hosts the parasitism of bird haemosporidians originated, because the corresponding paleontological and molecular biology data are not available. At present, these problems may be solved only at a hypothetical level. It is evident that bird haemosporidians could not appear earlier than their vertebrate and invertebrate hosts evolved, whose fossilized remains are available and can be exactly dated. Thanks to the data on species diversity, life cycles, ultrastructure, geographical distribution and distribution by hosts accumulated in the last decades and due to the associated character of the evolution of parasites and their hosts, the reconstruction of the evolution of this group of protists gets relatively reliable reference points.

It seems that most indisputable is the fact that bird haemosporidians take their origin from the haemosporidians of reptiles. The concept that bird and reptilian haemosporidians are close was put forward many times (Wenyon, 1926; Manwell, 1955, 1965; Baker, 1965; Garnham, 1966). Additional support was found thanks to new data obtained in the last 30 years. The following discoveries seem to be the priority ones.

First, the life cycles of some species of reptilian malaria parasites were studied (Ayala, 1971; Petit *et al*., 1983; Klein *et al*., 1987a, 1987b). It was found that these parasites develop according to the scheme general for all haemosporidians, and sporogony is completed in such relatively ancient groups of blood-sucking dipteran insects as species of the Phlebotomidae (*Plasmodium mexicanum*) and Ceratopogonidae (*P. agamae*), and also in more advanced Culicidae species (*P. floridense*). The use of representatives of several families of Diptera as vectors is recorded only in reptilian *Plasmodium* spp., which testifies to the ancient character of the host–parasite relations. It is noteworthy that the most primitive species of reptilian malaria parasites have not probably lost the ability to infect vertebrate hosts *per os*, when the vectors are eaten (Petit *et al*., 1983; Klein *et al*., 1987b). This also testifies to the ancient origin of the reptilian malaria parasites.

Second, intensive research of the fauna of reptilian haemosporidians in the 1970s to 1990s increased the number of species discovered in such well studied genera like *Haemoproteus* and *Plasmodium* more than two times (Telford, 1988a, 1988b; Paperna and Landau, 1991). Simultaneously, new haemosporidians were discovered in reptiles, which usually develop without forming the malarial pigment. New genera, *Saurocytozoon*, *Garnia,* and *Fallisia* were established for them (Lainson and Shaw, 1969; Lainson *et al.,* 1971, 1974; see also Appendix 2). Genus *Saurocytozoon* includes the reptilian haemosporidians which have neither merogony in the blood nor malarial pigment in the gametocytes. *Saurocytozoon* is close to the *Leucocytozoon* and currently it is often attributed to the family Leucocytozoidae, although additional research of the life cycle of its species is required to finally solve the issue. *Saurocytozoon* spp. were found in lizards of the Neotropical (two species) and Oriental (one) zoogeographical regions. The representatives of *Garnia* and *Fallisia* are united into the family Garniidae; they are characterized by merogony in the

Table 14 Fauna of haemosporidian parasites in vertebrate animals.

Class of vertebrates	Number of species of haemosporidians				
	Haemoproteidae	Plasmodiidae	Garniidae	Leucocytozoidae	Total
Teleostomi	1 (?)	1 (?)	0	0	2 (?)
Amphibia	3	2	0	0	5
Reptilia	25	69	15	2	111
Aves	132	38	1	35	206
Mammalia	36	56	0	0	92
Total	197	166	16	37	416

Note: See also Appendix 2.

blood cells and to a greater or lesser extent by the loss of ability to produce malarial pigment. Meronts and gametocytes of *Garnia* spp. develop in the cells of the erythrocytic and leukocytic series, while certain strains have not completely lost the ability to form hemozoin. The representatives of *Fallisia* develop only in the cells of the leukocytic series and contain no malarial pigment. *Garnia* (nine species) are currently known only in the Neotropical region, while *Fallisia* spp. have a wider range of distribution. They are found in the Neotropical (five species), Oriental (one), and Australian (one) regions. The discovery of haemosporidians capable of developing in the blood cells of reptiles without forming hemozoin, and also capable of inhabiting various cells of leukocytic series significantly extended the knowledge about the divergence of the entire group of haemosporidians, and it is our opinion that this, to a certain extent, clarified the origin of the genus *Leucocytozoon*, whose representatives parasitize only birds, they do not produce malarial pigment in gametocytes and can develop in leukocytes. At present, the fauna of reptilian haemosporidians consists of 111 species, and it includes all families of haemosporidians found in birds (Table 14). Most probably, bird haemosporidians originated from reptilian haemosporidians. The fauna of haemosporidians is poorer in other groups of vertebrate animals and is not so diverse as in reptiles and birds. In this relation, the search for ancestors of haemosporidians in fish, amphibians, and mammals is most likely unpromising. The data that haemosporidians parasitize fish (Misra *et al*., 1972) need confirmation requiring a detailed study of the life cycle of the parasites. It is not inconceivable that the fish may be accidental hosts infected by eating the vectors with sporozoites, which belong to reptilian or amphibian species of parasites. The fauna of haemosporidians in amphibians is poor, and infected animals are recorded exceptionally rarely. It is likely that amphibians gained the parasites from reptiles in a secondary way. Species of Haemoproteidae and Plasmodiidae are widely distributed in mammals where about 90 species have been described. Nevertheless, Garniidae and Leucocytozoidae species, which develop in reptiles and birds, do not parasitize mammals. In addition, not long ago a suggestion about the origin of certain species of mammalian malaria parasites from bird *Plasmodium* spp. was put forward on the basis of the data of molecular biology (Waters *et al*., 1991, 1993). All these facts indicate that mammalian haemosporidians is an evolutionary young group even compared to the fauna of these parasites in birds. A rich fauna and the presence of representatives of all known families of haemosporidians in reptiles indicate that these parasites have flourished in reptiles, and that the fauna of haemosporidians is of the secondary origin in other groups of vertebrate animals.

Third, the study of the ultrastructure of Haemoproteidae, Plasmodiidae, and Garniidae species in reptiles (Aikawa and Jordan, 1968; Aikawa, 1971; Scorza, 1971; Sterling, 1972; Sterling and DeGiusti, 1972, 1974; Moore and Sinden, 1974; Starling *et al*., 1974; Boulard *et al*., 1987; Paperna and Boulard, 1990; Dizin *et al*., 2000) revealed a striking similarity of the structure of these parasites with the haemosporidians developing in birds and mammals. This gives more grounds to discuss the relative relationship of haemosporidians, which inhabit various groups of vertebrate animals rather than speak about their convergent similarity.

Thus, the solution of the problem of the bird haemosporidians ancestors is rather clear. Reptiles were probably the primary hosts of these parasites. Relatively wide distribution of *Haemoproteus* and *Plasmodium* spp. in reptiles belonging to the order Squamata, whose present day families existed already in the Upper Mesozoic Era (Darlington, 1957), and the presence of fossilized remains of their vectors from that time (species of the Phlebotomidae, Ceratopogonidae) (Balashov, 1982) give grounds to think that the haemosporidians incorporated reptiles not later than the Cretaceous Period, that is long before the appearance of the majority of the present day orders of birds. It is much more difficult to reconstruct the sequence of how haemosporidians inhabited birds of different orders. Investigation of the distribution of species and genera of haemosporidians among vertebrate hosts belonging to different orders gives information for understanding this process (Tables 5 and 6). Two groups of facts seem to be most important.

The most ancient and relatively primitive groups of birds either do not have haemosporidians or the fauna of these parasites is poor in them and clearly has secondary origin. This refers to all groups of haemosporidians, for example, Sphenisciformes, Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes, Tinamiformes, Gaviiformes, Podicipediformes, Procellariiformes, and Pelecaniformes. Bennett (1993b) also indicates that the fauna of *Haemoproteus* spp. in primitive birds is poor. Interestingly, the Neotropical region is characterized by the maximum number of groups of primitive birds (Darlington, 1957) and the relatively poor fauna of haemosporidians (Table 3). The total number of species of haemosporidians found in the bird orders listed above is equal to nine, which is 4.4% of the world fauna. Moreover, it is clear that the majority of species of haemosporidians parasitizing primitive birds were gained in the secondary way. For example, malaria parasites *Plasmodium relictum* and *P. elongatum* successfully inhabited penguins kept in the zoos of the temperate zone of the Northern Hemisphere. *Leucocytozoon tawaki* also developing in penguins is found only in birds that penetrated into the Australian and Ethiopian zoogeographical regions. No doubt, these parasites were acquired by penguins as secondary infection from the local avifaunae. *Leucocytozoon struthionis* is recorded only in young ostriches. In this case, it is not clear how the parasite maintains itself in nature. There was a hypothesis put forward that *L. struthionis* may be a synonym of *L. schoutedeni* which is common in domestic chickens, kept together with the ostriches on the same farms (Bennett *et al*., 1992d). It is not inconceivable that, in this case, the parasite of chickens penetrated into young ostriches, while adult birds are resistant to the infection. The examples considered demonstrate a violation of one of the rules of evolutionary parasitology that primitive parasites occur in more primitive hosts from the phylogenetic point of view (Dogiel, 1962, 1964). In our case, there is the clear secondary penetration of haemosporidians, which are widely distributed in phylogenetically relatively young birds, into more primitive groups of birds.

The conclusion about the secondary character of the appearance of haemosporidians in primitive birds has an interesting consequence from the point of view of the evolution.

The majority of the birds of low phylogenetic level are related to the hydrophilous group (marine, coastal, and some others) (Chernov, 1988). These birds either do not have haemosporidians, or their fauna is extremely poor and has a clearly expressed secondary characteristic. These are, for example, Gaviidae, Podicipedidae, Diomedeidae, Procellariidae, Hygrobatidae, Pelecanoididae, Phaethontidae, Sulidae, Phalacrocoracidae, Anhingidae, Fregatidae, Stercorariidae, most of Laridae, Rynchopidae, and Alcidae. It is likely that the beginning of haemosporidians' penetration into birds is not associated with the most primitive birds among present ones including marine, coastal, and some other relatively primitive hydrophilous birds. It is important to note in relation to this that the majority of the species of reptilian *Plasmodium* are distributed in tropical rain forests, while *Haemoproteus* spp. are distributed on internal territories of the continents (Telford, 1988b). The majority of the groups of present primitive birds did not spread to the regions where reptilian haemosporidians are actively transmitted, and they often remain ecologically isolated from the infection until now. All this accounts for the fact that the fauna of haemosporidians in birds of low phylogenetic rank is poor. It is likely that mass penetration of haemosporidians into birds occurred some time after the appearance of birds and is not related to the incorporation in ancient groups of birds. It is most likely that the penetration of reptilian haemosporidians into birds occurred without the participation of marine, coastal, and some other relatively primitive hydrophilous birds, which have been living in the regions where reptilian parasites and their vectors are not distributed. The biotopes of the majority of primitive hydrophilous birds are located in the regions with no active transmission of haemosporidians due to the absence of agents of diseases and vectors, or more or less ecological isolation from the vectors (see also p. 171).

Interestingly, the maximum species diversity of all groups of haemosporidians is recorded in the birds youngest in the evolutionary respect. For example, 86 species of haemosporidians are found in passeriform birds, which make 42% of the world fauna. It is important that 73 species or almost 36% are recorded only in passerines. This example is important because it demonstrates the possibility of relatively quick evolution of haemosporidian species in young flourishing groups of birds. The order Passeriformes, latest from the evolutionary point of view includes more than half of the present species of birds and it is distinguished for a high taxonomic diversity being the dominant by the number of individuals. These birds were rapidly developing, radiated, and intensively spread mostly during the Miocene (Darlington, 1957). This process is continuing at present. Passerines inhabited each of the continents and landscape zones excluding the Antarctic. The parasites diverged together with the divergence of the bird species. The rich species composition of haemosporidians in passerines is most likely of secondary origin. In this respect, the passerines and their haemosporidians well illustrate the rule of evolutionary parasitology according to which the orders of hosts characterized by high taxonomic division and large number of species are also characterized by rich and diverse fauna of parasites (Dogiel, 1962, 1964). Due to the apparent young evolutionary age of the Passeriformes, we can assume that the divergence of the species of haemosporidians also occurred in this order of birds relatively not long ago. A similar but not so well expressed picture is observed in relatively phylogenetically young species of the Piciformes and Coraciiformes, in which 36 species of the parasites have been recorded; this is approximately 18% of the world fauna of bird haemosporidians.

Poor fauna of haemosporidians in most relatively primitive groups of birds and rich fauna in evolutionary advanced ones (Table 5) indicate that active penetration of these parasites from reptiles into birds and the period of their flourishing occurred not during the

initial period of the evolution of birds but later, when the main orders of terrestrial and arboreal birds have already appeared and the active divergence of their main groups took place, which is associated with a higher level of the evolution of Aves occurring approximately during the Eocene and Oligocene and even later (Darlington, 1957). It is important that all groups of vectors of haemosporidians known at present already existed at that time (Balashov, 1982). We can assume that birds gained haemosporidians from reptiles only during their period of active penetration in the tropical rain forests and other internal territories in the tropics and subtropics, in the regions of distribution of the major part of currently known reptilian haemosporidians. It is likely that blood-sucking dipteran insects, whose period of flourishing coincided with the appearance of homoiothermal animals, played the main role in the transmission of haemosporidians to birds as well as in the distribution of these parasites among various groups of birds. In other words, the birds obtained haemosporidians from reptiles possibly not as an 'inheritance' but most likely like a 'present' through blood-sucking dipteran insects, where the parasites penetrated earlier than in birds. A theoretically important problem in this consideration is to go slightly beyond the limits of the subject under discussion and analyze which hosts (vertebrate or invertebrate) are primary for the entire group of haemosporidians.

It is unlikely that invertebrates were historically the first hosts of Haemosporida species, as some scholars consider (Huff, 1945; Landau, 1974; Kallinikova, 1991). A more grounded hypothesis based on modern knowledge is the one that assumes the origin of haemosporidians from coccidia-like parasites of vertebrate animals, which currently demonstrate a clear tendency and practically unlimited potential to inhabit various organs and tissues of their hosts, illustrating the transition from typically intestinal coccidians to haemococcidians and through them to haemosporidians, which has been repeatedly discussed in the literature (Wenyon, 1926; Dogiel 1947; Manwell, 1955, 1965; Baker, 1965; Bruce-Chwatt, 1965; Garnham, 1966; Coatney *et al*., 1971; Krylov, 1981, 1992). The following facts favour the primary character of vertebrates as hosts of haemosporidians. First, the range of invertebrate hosts of haemosporidians is limited by blood-sucking dipteran insects (Diptera), where the representatives of the phylum Sporozoa, which could be the direct ancestors of modern Haemosporida species, are not found. They are numerous in vertebrate animals, flourish, and demonstrate transitions to blood parasitism as we already mentioned above. These are the representatives of the genera *Eimeria*, *Isospora*, *Schellackia*, *Lankesterella,* and others. Second, among the invertebrate hosts only those individuals that feed on blood are infected. In the majority of groups of the Diptera these are only the females, while the males are free from the parasites, which indicates the secondary character of penetration of haemosporidians into the dipteran insects. Third, haemosporidians are only temporary parasites of the invertebrate hosts. Persistence of the parasites and maintaining the species during the period unfavourable for transmission occur in vertebrates, that indicates more ancient relations of haemosporidians with vertebrates. Fourth, the range of vertebrate hosts of haemosporidians is incomparably wider than the invertebrate ones and includes the species of Amphibia, Reptilia, Aves, and Mammalia (Table 14), while all known vectors are presented only by the species of Diptera. This also indicates a longer evolutionary relation of haemosporidians with vertebrate animals. It is most likely that the fact that haemosporidians are less pathogenic for dipteran insects than for vertebrates (see also Appendix 2, p. 868) is not a consequence of a longer evolutionary relation between the vectors and parasites but probably can be accounted for by more intensive reproduction of the dipterans. Dipteran insects produce an incomparably greater number of generations and individuals than vertebrates per time unit, which, undoubtedly,

favours more rapid mutual adjustment of the parasites and vectors. We do not consider the argument serious enough, which favours more ancient relations of dipteran insects with haemosporidians, put forward on the basis that sexual process occurs in invertebrate hosts, because there are many examples in the evolution of parasites, when sexual processes occur at the stages developing in the evolutionary young hosts (for example, Trematoda).

On the basis of data available at present, it is difficult to say anything more definite about the sequence of penetration of parasites belonging to the genera *Haemoproteus* and *Plasmodium* into birds of different orders or about the time and place where these occurred. The ancestors of these parasites in reptiles have a worldwide although patchy distribution mainly in the tropical and subtropical regions, and it is likely that the birds were repeatedly infected with these parasites. Cosmopolitan distribution of *Haemoproteus* and *Plasmodium* spp. in birds, relative easiness of changing the vertebrate hosts, which is especially characteristic of *Plasmodium* species, practically unlimited possibilities of infected birds to move worldwide, uneven rate of divergence of parasite species in birds of various orders, are some of the facts significantly hampering the reconstruction of the ways of spreading of haemosporidians and the sequence of their penetration into their vertebrate hosts. The present day distribution of haemosporidians by the orders of birds (Tables 5 and 6) is the result of a complex process of their evolution, repeated and probable, very rapid spreading, adjustment, widening of the ranges of distribution, which is closely related to the climatic peculiarities, and the presence of vectors. It is likely that the penetration of *Haemoproteus* and *Plasmodium* spp. in birds occurred independently in any of significant ecological groups of birds. It is likely that in each of these groups there were the evolutionary rise, divergence into new species, and distribution and incorporation of new hosts, which penetrated into the new nidi of infection. As we already mentioned, the beginning of the evolution of bird *Haemoproteus* and *Plasmodium* spp. is most likely related to the regions of a relatively warm climate, where the representatives of these genera in reptiles flourish at present. Later, as the birds regularly and massively transported the parasites into the regions with a cooler climate and the vectors also penetrated there, the species and strains capable for the development at lower total heat evolved. Therefore, the present day ranges of bird *Haemoproteus* and *Plasmodium* spp. distribution are incomparably wider than those of the reptilian parasites.

Bennett and Desser (Bennett, 1989a; Desser and Bennett, 1993) think that haemosporidians of birds evolved to the present day state in the northern regions of the Holarctic, where the maximum prevalence of infection is currently observed, and that only later they moved to the equatorial regions with migratory birds during the northern winter, where their secondary divergence occurred. This approach, however, does not take into account the peculiarities of distribution of reptilian haemosporidians, which are heat-loving forms and, with rare exceptions, they are absent in reptiles in the moderate regions and high latitudes of the Holarctic as it was discussed above. It is likely that the current fauna of bird haemosporidians in the Holarctic northern regions is of secondary origin.

Bennett (1993b) analyzed the distribution of the species of haemoproteids and the frequency of occurrence of different types of gametocytes of these parasites in birds of various orders, and came to the conclusion that representatives of the genus *Haemoproteus* evolved in birds during the period of the formation of the Piciformes and Coraciiformes. We can hardly agree with this point of view because it does not take into consideration the information about the peculiarities of distribution of haemoproteids in reptiles. In spite of a smaller number of species of haemoproteids in reptiles than in birds (Table 14), as we discussed above, it is likely that Haemoproteidae species evolved in reptiles, and it looks

more logical to think that they inhabited birds in the secondary way. Interestingly, G.F. Bennett uses two criteria to measure the antiquity of birds of various orders as hosts of haemoproteids: the number of species of the parasites that inhabit them, and the degree of diversity that gametocytes form (halteridial, microhalteridial, circumnuclear, rhabdosomal, discoid) in the birds of the corresponding orders. The analysis carried out by this author showed that the richest fauna and most diverse forms of gametocytes are found in species of the Passeriformes, the youngest group of birds in the evolutionary respect. This fact indicates that the characters considered taken separately cannot be a measure of the antiquity of penetration of haemoproteids into birds of various orders. Above, we discussed that this is, to a great degree, determined by the secondary divergence of the hosts and parasites. The fact that the evolutionary young Piciformes and Coraciiformes species are characterized by a rich fauna of *Haemoproteus* spp., similar to the case with the Passeriformes, and diverse forms of their gametocytes can be accounted for by the significant taxonomic division of these orders, which was followed by the divergence of the species of the parasites rather than it can testify to ancient relations of haemoproteids with the birds of the named orders. It is noteworthy that the degree of diversity of the form of gametocytes can hardly be a good criterion for estimation of the antiquity of penetration of haemoproteids in birds, because main morphological forms of gametocytes distinguished in birds are also found in reptilian haemoproteids. It is important to emphasize that the character of pathogenicity used by G.F. Bennett in the estimation of the antiquity of the relation between haemosporidians and birds does not look reliable enough, because there are species among the genera *Haemoproteus, Plasmodium,* and *Leucocytozoon,* which markedly differ in the degree of their pathogenic influence on their host. Therefore, we do not use the data on pathogenicity in the analysis of the evolution of bird haemosporidians.

The data about the geographical distribution and the range of vertebrate hosts of Garniidae and Leucocytozoidae species provide more reliable means to consider the problem about the place and time when these parasites incorporated birds.

The representatives of the Garniidae in reptiles were found in the Oriental (1 species), Australian (1), and Neotropical (14) regions, while the entire fauna of *Garnia* known (9 species) is concentrated in the Neotropics. The most diverse and rich fauna of the Garniidae (88% of the total number of species) is characteristic of the Neotropical region, where probably the flourishing of this group of haemosporidians took place. It relation to this, it is not a surprise that *Fallisia neotropicalis,* the only representative of the Garniidae parasitizing birds, is also found only in the Neotropics. It is apparent that garniids are rare bird parasites. It is likely that these haemosporidians only start to incorporate birds, which is currently recorded only in the Neotropical region in the representatives of the Ciconiiformes and Columbiformes (Tables 5 and 6). It is noteworthy that *Fallisia* parasites not identified to the specific level were found also in the Neotropics in species of the Falconiformes and Pelecaniformes. Even more, it has been experimentally shown that *F. neotropicalis* can infect the representatives of different orders of birds; i.e., this parasite is close to the species of *Plasmodium* by its level of specificity (Gabaldon *et al*., 1985). All this shows that from an evolutionary viewpoint, there are potential abilities of a relatively fast enlargement of the range of avian hosts of *Fallisia* spp. In this relation, it should be emphasized that *Columba livia* (the only representative of the Columbiformes where *F. neotropicalis* is found) was introduced into the Neotropics by human beings and thus was infected with this parasite not long ago. Due to the migratory behaviour of birds we can expect that the range of distribution of *Fallisia* spp. in birds would be widened primarily in the New World. Also, there is a danger that these poorly studied parasites would be introduced into

the tropics of the Old World. At present, we cannot say anything more definite about the real possibilities of widening the range of distribution of bird *Fallisia* sp., because the range of invertebrate hosts of the parasite has not yet been determined. Due to the fact that the major part of the Garniidae fauna is concentrated in the Neotropics and because this area is the only place where *Fallisia* sp. is found in birds, the Neotropical zoogeographical region can be considered as the centre of origin and present day spreading of *Fallisia* species in birds.

The discovery of reptilian haemosporidians developing without formation of malarial pigment at all stages of their development (*Saurocytozoon, Garnia, Fallisia*) threw light on the problem of the ancestors of *Leucocytozoon* spp. The cycles of development of haemosporidians belonging to the genera listed have not been finally studied yet. Nevertheless, the peculiarities of the metabolism related to the ability to utilize hemoglobin without forming any residual pigment as well as by the ability to inhabit the cells of the leukocytic series definitely place *Leucocytozoon* spp. closer to *Saurocytozoon* spp. and other representatives of the Garniidae rather than to the Haemoproteidae or Plasmodiidae. The representatives of the Garniidae parasitize reptiles only in the tropics of the Old and New World. It is likely that the beginning of the evolution of *Leucocytozoon* species is also related to tropical latitudes.

Let us consider the facts which allow one to get closer, to a greater or lesser degree, to the solution of the problem of where bird *Leucocytozoon* species originated. As already mentioned (see p. 119), 100% of the species of *Leucocytozoon* are found in the Holarctic, Ethiopian, and Oriental zoogeographical regions. Endemic species of *Leucocytozoon* are not recorded in the Neotropics and Australian region, while the fauna of the parasites is presented there mainly by the species with a cosmopolitan or wide distribution (the range of their distribution covers several zoogeographical regions). It is likely that the penetration of bird leucocytozoids into the Neotropical and Australian regions was secondary. This primarily refers to the Neotropics, where the leucocytozoid species composition is the poorest (Table 3) and the overall prevalence of the infection in birds is low (Table 2). So far as the range of distribution and the great number of species of reptilian haemosporidians are nearly completely limited within the tropical latitudes, it is not likely that the beginning of the evolution of *Leucocytozoon* spp. is associated with the Holarctic. Most likely, it is connected with warm climate countries, either in the Oriental or Ethiopian regions. It should be remembered that the representatives of the Garniidae, the possible ancestors of leucocytozoids, were found in the Old World only in the Oriental and Australian regions. By means of this exclusion, we come to a conclusion that the most probable region for the beginning of the evolution of *Leucocytozoon* spp. is the Oriental region. It is important to note in this relation that this region and the adjacent territories of the Palearctic is the only place on the planet where species of the subgenera of *Leucocytozoon* and *Akiba* are found simultaneously, that is, the fauna of leucocytozoids in this area is most diverse.

As we already mentioned above, the phylogenetically most primitive birds either do not have *Leucocytozoon* parasites or their fauna is presented by no more than one species in each order (Tables 5 and 6), and their parasite fauna is of apparently secondary origin. This means that we have to look for the original hosts of *Leucocytozoon* species among the groups of phylogenetically younger birds. The study of the distribution of leucocytozoids by the vertebrate hosts shows that the richest fauna is found in birds belonging to the Passeriformes (seven species), Galliformes (seven), and Coraciiformes (four). In birds of other orders, species of *Leucocytozoon* are either absent or not more than two species of the parasites have been recorded. It is likely that the beginning of the evolution of leucocytozoids

in birds is related to one of the orders listed above. The Coraciiformes, and especially the Passeriformes, are phylogenetically relatively young groups, and it is not likely that *Leucocytozoon* spp. first appeared in these birds. It is likely that the rich fauna of leucocytozoids in the two latter orders is of a secondary character as in the case with the other groups of haemosporidians. It reflects the richness of the division of their hosts from the taxonomic point of view. The Galliformes is the most real contender for the ancient group, where *Leucocytozoon* spp. started their evolution. We are reminded that the Galliformes is the only order of birds where representatives of the subgenus *Akiba* parasitize. In addition, it is likely that the centre of origin of the Galliformes was the Oriental region (Darlington, 1957), which coincides with the hypothetical area of the origin of *Leucocytozoon* spp. The family Phasianidae clearly predominates among the galliform birds over the greatest part of the world. Radiation from the sole main centre in the Oriental region is well observed for this family. The galliform birds have a relatively weak ability for spreading, thus their present day distribution and the clearly well defined ranges of the distribution of their parasites reflect their early history to a certain degree. It is likely that *Leucocytozoon* species appeared in ancient species of the Phasianidae in the Oriental region. *Leucocytozoon macleani*, *L. schoutedeni,* and *L. caulleryi* should be noted among the leucocytozoids parasitizing the Phasianidae species in this region. As the Phasianidae species radiated from the Oriental region, the following leucocytozoids probably evolved: *L. neavei* (a parasite of the Numididae in Africa), *L. lovati* (a parasite of the Tetraonidae in the Holarctic), and *L. smithi* (a parasite of the Meleagrididae in the southeastern Nearctic). It is likely that the relatively long existence of *Leucocytozoon* species in the Oriental region favoured the origination of *L.* (*Akiba*) *caulleryi,* a unique representative of the Leucocytozoidae in many aspects, whose vectors are biting midges. In addition to the region mentioned, the range of distribution of *L. caulleryi* includes only the adjacent territories of the Palearctic, where most likely this parasite penetrated in the secondary way. The representatives of other bird orders probably gained leucocytozoids from the galliform birds via the vectors. The divergence of species of leucocytozoids has not yet occurred in the majority of the orders of vertebrate hosts (excluding the Passeriformes and Coraciiformes), and the fauna is presented by no more than two species, which indicates that the parasites incorporated these birds not long ago (Tables 5 and 6).

The appearance of a unique group of species (*L. simondi*, *L. lovati,* and some others), that penetrated into the high latitudes of the Holarctic up to the Polar Circle and even further to the north, is a characteristic peculiarity of the *Leucocytozoon* spp. evolution. This became possible due to the adjustment of the development of these species in the vectors at low temperatures and the significant acceleration of their development in the vertebrate and invertebrate hosts. For example, the prepatent period in the Norwegian strain of *L. simondi* is four to five days, while its sporogony completes in the vector in seven days at a temperature of 13 to 14°C (Eide and Fallis, 1972). The cycle of development of the parasite is completed at this temperature in less than two weeks, which is not found in any other haemosporidians at such low temperatures. If we take into account that the vectors of the parasite (blood-sucking simuliid flies) feed approximately every five to seven days (Fallis, 1964), then even during a short and cool northern summer, the parasite can infect a large number of birds. It is not a surprise that the prevalence of infection reaches 50% and even more among anseriform birds in the Palearctic near the Polar Circle (Valkiūnas *et al*., 1990). This indicates that this species flourishes there. The same properties of *Leucocytozoon* spp. are accounted for by the penetration of the parasites in the mountains, at least up to 3000 m over the sea level (Krylov and Krylova, 1979). It is important to

emphasize that not all species of *Leucocytozoon* achieved the ability to develop in such severe conditions. The temperature optimum for the sporogony of *L. schoutedeni* and *L. caulleryi* is equal to approximately 20 to 25°C (Morii *et al*., 1965; Fallis *et al*., 1973; Morii *et al*., 1986). These species did not penetrate into the regions of high latitudes of the Holarctic. It is likely that the thermophilic species (*L. macleani*, *L. neavei*, *L. schoutedeni,* etc.), which originated in the countries with a warm climate, seem to be more primitive. Species tolerant to low temperatures probably evolved as the climate became significantly colder approximately during the Pliocene (John, 1982). It is likely that they initially originated in the mountain regions, where they are found now, and later spread to the north, where they became widely distributed due to the high density of bird and vector populations, exposed to radiation, and are currently flourishing and slowly moving to the south for the second time. Unstable life cycles of the 'northern' species of *Leucocytozoon* indicate that these species are relatively young. The latter fact shows that the group is at the formation stage. For example, strains, which form megalomeronts not in each group of the vertebrate hosts, are found in *L. simondi* (Desser and Ryckman, 1976; Desser *et al*., 1978) (see p. 790 for details).

As we already mentioned, *Leucocytozoon caulleryi* is the only representative of the subgenus *Akiba* that is distributed only in the Oriental region and adjacent territories of the Palearctic. This parasite inhabited only one species of galliform birds *Gallus gallus.* It is adjusted to the development at relatively high temperatures in the vector. The temperature optimum is about 25°C (Morii *et al*., 1965, 1986). Thermophilic property is possibly one of the factors preventing the spread of this species to the high latitudes of the Palearctic, because both vertebrate hosts and vectors (biting midges of the genus *Culicoides*) of this parasite are distributed worldwide. It is likely that *L. caulleryi* originated not long ago in the Oriental region in *Gallus gallus* (the usual host of such species of *Leucocytozoon* as *L. macleani* and *L. schoutedeni*) due to the adjustment to a new group of vectors (the family Ceratopogonidae). It is important to note that birds that survive the infection of *L. caulleryi*, develop complete resistance to reinfection and relapses do not take place. In other words, the vectors is the main source of infection of this parasite in nature, which is a rare situation for haemosporidians. Presently, there is a danger that *L. caulleryi* can be introduced into the countries with a warm climate mainly by the introduction of infected vectors. Under natural conditions, the infected biting midges have a restricted opportunity to spread over long distances, which is realized in the well localized range of the geographical distribution of *L. caulleryi.* However, in the unpredictable economic activity of human beings, such an opportunity should be kept in mind.

The problem of the phylogenetic relationships between the main groups of bird haemosporidians can be considered mainly on the basis of data on their life cycles, distribution by hosts, and comparative morphology. Unfortunately, sufficient information on molecular biology is still poor. The following similar properties of the life cycle and morphology of the Haemoproteidae, Plasmodiidae, Leucocytozoidae, and Garniidae species (the latter group has been studied only fragmentarily) should be emphasized. Gametogenesis occurs extracellularly; each microgametocyte produces eight microgametes, while each macrogametocyte produces one macrogamete; ookinete is motile; oocyst changes its size and contains no spores; formation of gametocytes is followed by multiple asexual division (exoerythrocytic merogony); gametocytes develop in blood cells and are characterized by the clear sexual dimorphic characters; species of the blood-sucking Diptera are the vectors. The representatives of the families listed display the same plan of their ultrastructure (Aikawa, 1971; Aikawa and Sterling, 1974; Fallis *et al*., 1974;

Fallis and Desser, 1974; Seed and Manwell, 1977; Aikawa and Seed, 1980; Boulard *et al*., 1987; Meis and Verhave, 1988; Wernsdorfer and McGregor, 1988; Paterson and Desser, 1989; Paperna and Boulard, 1990; Desser and Bennett, 1993). Let us consider only its main features (for details see p. 47). The cell envelope of the spreading stages (sporozoites, merozoites, and ookinetes) consists of plasmalemma and an inner double membrane layer (there are exclusions); subpellicular microtubules originate from the polar ring located at the apical end, they end at the distal end in the region of the distal polar ring; electron-dense rhoptries and micronemes are located in the zone of the apical end, their ducts are stretched in the direction of the plasmalemma of the apical complex and they open there; sporozoites and merozoites contain no conoid but there is one in the ookinetes; intracellular stages are enclosed into the parasitophorous vacuole (except for ookinetes); the process of transformation of zoites into the dividing stages is accompanied by the loss of the inner double membrane layer and specialized organelles of the apical complex, which are newly created in the forming sporozoites and merozoites. The surprising similarity in the life cycles and structure of the Haemoproteidae, Plasmodiidae, Garniidae, and Leucocytozoidae species indicates their affinity and suggests that the courses of their evolution are much alike.

The Haemoproteidae and Plasmodiidae species are most close to each other. They are characterized with similar metabolism. They do not completely utilize the hemoglobin and deposit residual malarial pigment in the erythrocytic meronts and (or) gametocytes. Among the other characters of the ultrastructure of these groups we should emphasize the presence of micropyle in the merozoites and a 'spherical body' near the mitochondrion, which is probably associated with the energy properties of the cell (Aikawa and Seed, 1980). It is likely that the Haemoproteidae and Plasmodiidae species originated from the same ancestor. The Plasmodiidae species, which pass merogony in the blood cells, seems to be a more advanced group in the sense of incorporation in the blood. These parasites are a more advanced group of blood parasites, which perhaps originated from the primitive reptilian haemoproteids that have not yet specialized for exoerythrocytic merogony in the fixed tissues of the vertebrate host. The concept about the origination of malaria parasites from haemoproteids is not new; it has been discussed many times in the literature (for example, Wenyon, 1926; Dogiel, 1947; Manwell, 1955; Dogiel, 1962, 1964; Garnham, 1966; Coatney *et al*., 1971; Krylov, 1981, and others) and continues to draw the attention of the scholars.

The data available on the life cycle and morphology of the Garniidae species (Gabaldon *et al*., 1985; Telford, 1988b), undoubtedly indicate that they are close to the Plasmodiidae. Both groups of haemosporidians pass merogony in the blood cells, while certain species of *Garnia* have not yet completely lost the ability to produce malarial pigment. The number of species of Plasmodiidae is significantly larger (Table 14), while the range of their vertebrate hosts and geographical distribution is incomparably wider (Telford, 1988a, 1988b) than that of the Garniidae. A relatively poor species composition of the Garniidae and the relation of most species to the evolutionary young group of saurian reptiles with the richest fauna of the parasites in the Neotropical region, allows us to consider the Garniidae as a young group separated from the ancestors of the present day Plasmodiidae (about the origin of *Progarnia* sp., see Appendix 2, p. 868). It is likely that the main tendency of the evolution of garniids was that the primitive Plasmodiidae species gained the ability to completely utilize the hemoglobin when inhabiting erythrocytes and to develop in the cells of leukocytic series.

In addition to the most characteristic characters of the Leucocytozoidae species mentioned before, which distinguish them from Haemoproteidae and Plasmodiidae species,

the following should be named. The structure of the merozoite pellicle is markedly simplified in some species. For example, the pellicle is lost in merozoites of *Leucocytozoon dubreuili* and *L. simondi,* and the merozoites are covered only by the plasmalemma, while there is no inner double membrane layer. The micropyle is not found either. Even more, there are no subpellicular microtubules in the merozoites of *L. simondi* (Wong and Desser, 1978, 1981). In some species, the dividing exoerythrocytic meronts split into numerous cytomeres separated from each other not only by the contents of the parasitophorous vacuole but also with the cytoplasm of the host cell (Desser, 1973). Gametocytes of some species are capable to develop in leukocytes. Exoerythrocytic development and growth of gametocytes is accompanied by a strong hypertrophy of the nucleus and cytoplasm of the host cell, which indicates the active participation of the infected cell in the metabolism of the parasite. Mitochondria in the microgametocytes are frequently located in the indentations of the nuclear envelope of the host cell (Desser *et al*., 1970; Kocan and Kocan, 1978). In certain species, host cells containing gametocytes acquire a unique fusiform shape, which is accompanied by the appearance of bunches of parallel-located microtubules in the nucleus and (or) in the cytoplasm of the host cell (Desser *et al*., 1970; Steele and Noblet, 1993).

Leucocytozoon spp. are most close to reptilian *Saurocytozoon* spp. by the absence of pigment in the gametocytes, a strong influence on the nucleus of the host cell, and the absence of merogony in the blood cells. *Saurocytozoon* spp. are found only in the evolutionary young saurian reptiles, which indicates that this group is evolutionarily relatively young. It is likely that the Leucocytozoidae species originated from the ancestors of the Garniidae due to the secondary loss of merogony in the blood cells. The advanced system of defense immunity in birds may be a stimulus for this. Further study of the life cycles, ultrastructure, and molecular biology of *Saurocytozoon* spp. is important for working out the phylogenetic relations of these parasites.

It is likely that the parasites of the subgenus *Parahaemoproteus*, which use biting midges as vectors, are the most ancient among the subgenera of *Haemoproteus* parasitizing birds. Ceratopogonids are one of the most ancient groups of blood-sucking dipteran insects known from the end of the Cretaceous Period (Balashov, 1982). This subgenus is characterized by incomparably greater species composition and a wider range of their vertebrate hosts than the subgenus *Haemoproteus*. The latter subgenus currently includes only six species, and according to current knowledge, these parasites managed to incorporate only birds belonging to the order Columbiformes. It is noteworthy that an evolutionary young group of brachycerous blood-sucking dipteran insects of the family Hippoboscidae are the vectors of the representatives of the subgenus *Haemoproteus*. It is likely that *Haemoproteus* species originated from *Parahaemoproteus* species, with which they have more common features than different. Among the latter, the large size of the oocysts, which develop with the formation of multiple germinative centers, should be distinguished. Atkinson (1991b) put forward an interesting hypothesis that the representatives of the subgenus *Haemoproteus* can also develop in biting midges. This has not been proved yet.

Phylogenetic relations between subgenera of bird *Plasmodium* have not been found yet. In the last 30 years, the number of species of malaria parasites developing in reptiles known to science increased more than two times and, in addition to the already known subgenera (*Sauramoeba*, *Carinamoeba,* and *Ophidiella*), three new ones (*Asiamoeba*, *Lacertamoeba,* and *Paraplasmodium*) were described (Telford, 1988a). As a result of these discoveries, the majority of subgenera of bird *Plasmodium* with a greater or lesser degree of probability may originate from the subgenera of reptilian parasites. New data, primarily

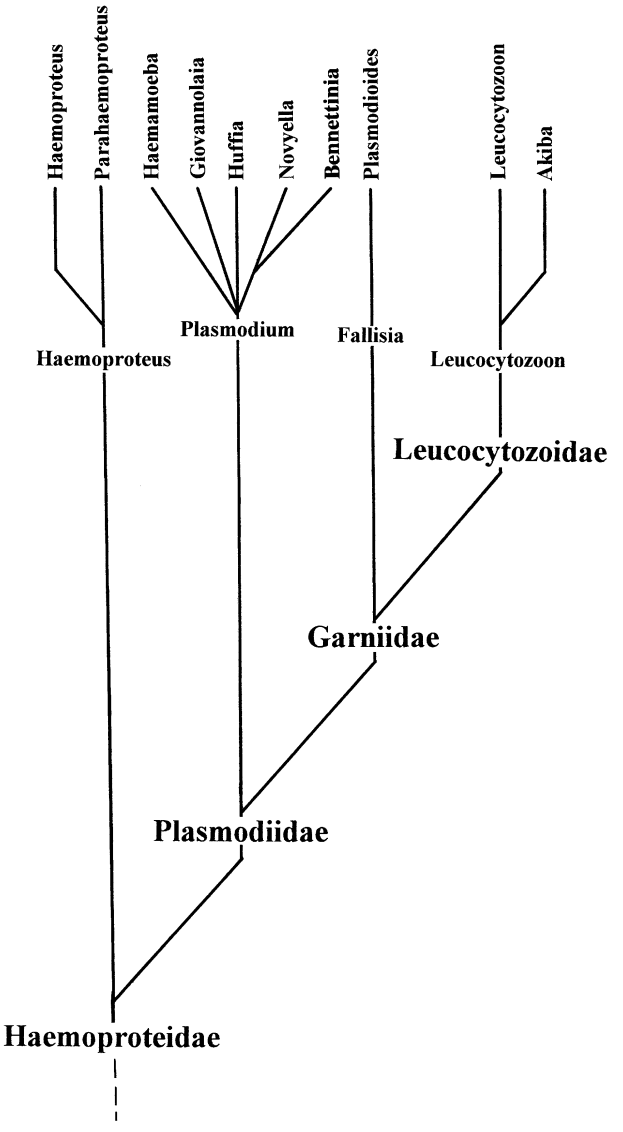

Figure 51 Diagrammatic representation of the possible phylogenetic relationships of haemosporidian parasites (only subgenera and genera of bird parasites are shown).

about the life cycles and molecular biology of reptilian malaria parasites, are required to distinguish the primitive and advanced subgenera of *Plasmodium.*

Subgenus *Bennettinia* with a single species *Plasmodium juxtanucleare* is distinguished for a unique feature, its oocysts are pedunculated (Bennett *et al*., 1966; Bennett and Warren, 1966), which should be regarded as a new character. The *Bennettinia* is perhaps one of the youngest among the subgenera of bird *Plasmodium*. The small size of the erythrocytic meronts and gametocytes makes *Bennettinia* species close to species of the subgenus *Novyella* to which *P. juxtanucleare* was formerly attributed.

The close relationship between leucocytozoids belonging to the subgenera *Akiba* and *Leucocytozoon* looks likely. These groups are related primarily due to their ability to completely utilize the hemoglobin without forming any residual pigment, the absence of merogony in the blood, and the strong influence on the host cell, which is manifested, in particular, in the hypertrophy of the nucleus and cytoplasm. There are, however, clear differences. Among these, the following should be distinguished first of all. Exoerythrocytic meronts of the first generation of *Leucocytozoon* species develop in the cells of the liver parenchyma, and they produce merozoites, which are roundish in form. The corresponding stages of *Akiba* species develop in the cells of the reticuloendothelial system and produce elongated merozoites. Megalomeronts of *Akiba* species can complete their development extracellularly, which is not characteristic of *Leucocytozoon* species. The vectors of *Akiba* are limited to biting midges (Ceratopogonidae), while for *Leucocytozoon* species, they are limited to blood-sucking simuliid flies (Simuliidae). To answer the question, which of the two groups is more ancient, one has to keep in mind that representatives of the subgenus *Leucocytozoon* have an incomparably wider range of vertebrate hosts than *Akiba* species and they are cosmopolitan in distribution, which testify to their greater age. As we already mentioned, *Akiba* species infects only one species of birds and has a relatively narrow range of distribution compared with other bird haemosporidians covering the Oriental region with adjacent territories of the Palearctic. It is likely that the *Akiba* is a younger group, whose evolution is associated with the adjustment to biting midges as vectors.

The general scheme of the possible phylogenetic relations between the subgenera of bird haemosporidians originating from the corresponding groups of ancestors developed in reptiles is shown in Fig. 51.

It should be noted in conclusion that only the data of the traditional research on biology of bird haemosporidians are analyzed in this chapter. The use of traditional methods to reconstruct possible ways of the evolution of organisms was shown to be productive in numerous branches of zoology, but this is obviously not enough to solve complicated questions. Methods of molecular biology have to be applied, but unfortunately they have only just started to be used in models of avian Haemosporida (see for example, Waters *et al*., 1991, 1993; Bensch et al., 2000; Ricklefs and Fallon, 2002) and the data available on the subject are still insufficient for deep analysis, particularly on the level of species and subgenera of haemosporidians. The author hopes, however, that the information presented in this chapter can be helpful in indicating directions, in which molecular biology methods can be applied in future.

Practical Importance

Haemosporidians are the agents of some dangerous diseases of domestic birds, which lead to the decrease of their productivity and are often accompanied with a high rate of mortality. Almost all haemosporidioses are diseases with natural focality. Usually the parasites persist in birds for many years, which provides the stability of the natural nidi of the infections. The agents of leucocytozoonosis in domestic geese and ducks (*Leucocytozoon simondi*), chickens (*L. caulleryi* and to a significantly lesser extent *L. macleani*), turkeys (*L. smithi*), and ostriches (*L. struthionis*) are of the greatest practical importance. *Haemoproteus mansoni* (=*H. meleagridis*) causes severe haemoproteosis in domestic turkeys. *Plasmodium gallinaceum*, *P. durae*, *P. lophurae*, and *P. juxtanucleare*, causing malaria in domestic gallinaceous birds in the countries with a warm climate are practically most important among the malaria parasites. Rapidly developing haemosporidioses, which cannot always be kept under control, occur in domestic birds, when they appear in the natural nidi of the infection. There are examples when projects failed or significant economical losses occurred during the attempts to establish poultry farming in the regions endemic for haemosporidioses (Stoddard *et al*., 1952; Laird and Bennett, 1970; Kissam *et al*., 1973, 1975). Haemosporidians check the development of poultry farming on the endemic territories because the highly productive breeds of nonimmune birds introduced into the area are most susceptible to infection, their diseases pass in acute form, and the birds often perish, which lay obstacles to their wide use (Lee *et al*., 1969; Garnham, 1980). Bird haemosporidioses and the peculiarities of the pathogenicity of certain species are discussed in the chapter 'Pathogenicity' and in the description of the species in the Systematic Section.

It is important to note that the ranges of distribution of the most practically important agents of diseases of domestic birds are quite clearly restricted to certain zoogeographical regions, and thus their practical significance for the poultry development in different countries differs markedly. In addition, due to significant transformation of ecosystems by industrial activity in many countries, there is a tendency for a decrease of the prevalence of infection in reservoir wild birds and thus the lowering of probability for outbreaks among domestic birds (see p. 172 for some details). On the other hand, it is also noteworthy that the role of haemosporidians in the pathology of domestic birds is likely to be underestimated. The documented cases of lethal haemosporidioses of nondetermined etiology (Commichau and Jonas, 1977; Kučera *et al*., 1982; Opitz *et al*., 1982) testify to this.

Birds kept in zoos and aviaries suffer from haemosporidioses and even perish almost everywhere in the world. For example, there are well documented facts of mass deaths of penguins and psittaciform birds of malaria caused by *Plasmodium relictum*, *P. elongatum* and other species of *Plasmodium* in the zoos of North America and Eurasia (Griner, 1974; Cranfield *et al*., 1990; Bennett *et al*., 1993e). The factor of haemosporidians should be taken into account, if domestic and wild birds are imported into regions historically free from these parasites but with the potential conditions for the formation of new nidi of infection. A well known example is the introduction of *Leucocytozoon smithi,* a dangerous

agent of leucocytozoonosis in turkeys, into many states of the USA, Ukraine, and South Africa. As we already mentioned, projects to reintroduce rare and disappearing species of birds into the regions of their previous habitat, popular in recent decades, are frequently under the threat of failure due to the transmission of haemosporidians in the regions. The introduction of a small group of genetically similar birds bred in captivity into endemic territories leads to the outbreaks of severe haemosporidioses. For example, this situation occurred in the Seney National Wildlife Refuge (USA) in course of the realization of a program to restore the population of *Branta canadensis* (Herman *et al*., 1975). The acute outbreak of malaria in partridges *Perdix perdix*, which were imported from Hungary to the endemic territory in France is another example (Garnham, 1966). Peirce *et al*. (1997) noted that *Leucocytozoon marchouxi* is of potential threat to the continued recovery of the population of *Columba mayeri* on Mauritius Island in the Indian Ocean. Successful realization of important projects to recover the decaying populations of birds requires the control of the parasitological situation. In the Holarctic, this is primarily related to the programs to reintroduce anseriform birds, which are highly susceptible to *Leucocytozoon simondi* widely distributed in the wild north of 42° N. This parasite causes severe and even lethal leucocytozoonosis in immature birds on endemic territories. Malaria parasites (*Plasmodium relictum*, *P. elongatum*, and some others) should be also taken into account.

It should be emphasized in conclusion that bird malaria parasites played an important role as models in human malaria research and were a stimulus for the development of medical parasitology. The practically important researches such as formation of chemical therapy (Wasielewski, 1904; Sergent and Sergent, 1921), cultivation *in vitro* (Trager, 1947, 1950), development of vaccine (McGhee *et al*., 1977), and many others were first successfully achieved precisely on the models of bird malaria parasites. At present, the low cost and easy availability of models of bird *Plasmodium* spp. have not lost their practical importance, primarily in immunological, genetic, biochemical, and ecological investigations.

Methods of Collection and Investigation

At present, haemosporidians is a group of protists under intensive study primarily due to the fact that it includes the agents of malaria, one of the widely distributed human diseases in the tropical regions. Accordingly, the set of scientific and practical methods applied to study haemosporidians is large. Besides traditional methods, there is a set of the newest immunological tests and techniques of molecular biology including the analysis of the DNA and RNA of parasites (Gilles and Warrell, 1993; Bensch *et al.*, 2000). None of the newest methods, however, is applied widely to identify the species of haemosporidians, and in particular, bird haemosporidians. With rare exceptions (see, e.g., Bensch *et al.*, 2000; Waldenström *et al.*, 2002; Fallon *et al.*, 2003), these methods have not been widely used so far to study the fauna, ecology, and other zoological aspects of these parasites biology. In recent years, the ELISA test has been applied to determine the prevalence of infection of birds with *Plasmodium* and *Haemoproteus* spp. (Graczyk *et al*., 1994a, 1994b), which is an intriguing and promising technique, but it does not solve the problem of species identification for the entire group of Haemosporida. At present, two main factors determine the success of species identification: the efforts of an experienced specialist and the application of the methods of light microscopy. Experience of the research carried out in recent years gives no grounds for hope that this situation would be drastically changed shortly, mainly because of decreasing funds for systematic research worldwide.

In this chapter, we briefly describe only those traditional methods of collection and investigation of bird haemosporidians which are used in the everyday work of zoologists and protistologists. Among the numerous modifications, the methods are described which, from our experience, are most effective for bird haemosporidians studies and available for any laboratory. The methods of haemosporidians research are also described in more detail in a series of handbooks (Hewitt, 1940; Garnham, 1966; Bruce-Chwatt, 1985; Gilles and Warrell, 1993).

Obtaining of blood from birds and preparation of blood smears

It is recommended to take blood only from live birds for zoological and protistological investigations. If one uses the blood of dead or shot individuals, it is difficult to avoid changes of mature gametocytes due to the onset of gametogenesis. Species identification of haemosporidians often becomes impossible in the latter case. If needed, it is possible to take blood directly from the heart from the birds just shot, although one should take into account that, in this case, morphologically changed parasites might be present in the smears.

If wild birds are investigated one time or the same individuals are investigated sporadically (one or two times a month) in the laboratory, it is convenient to take blood by clipping a tip of a claw of the middle toe of one of the feet with scissors. A drop of blood is pressed out on the glass slide from the claw several seconds after it is cut off, and then a film is prepared. Complete restoration of the claw occurs in one or two months. The method

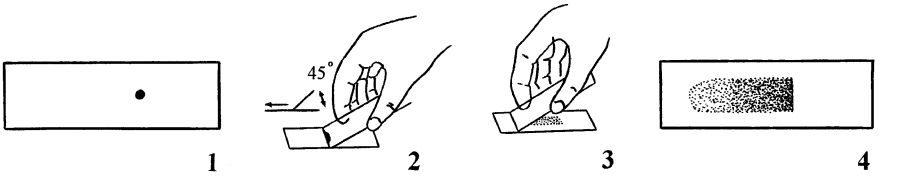

Figure 52 Successive stages (*1–4*) of the preparation of blood smears (modified from Gilles and Warrell, 1993). Explanation is given in the text.

is the easiest and gives good results after some training, allowing one to investigate more birds in a unit of time compared to the other known methods applied. This is especially useful during mass field investigations of small passerines. In the case of multiple investigations of the same individuals in the laboratory, and if big birds are investigated (the body mass greater than 300 g), it is more convenient to take blood from the vein (Campbell, 1995). It is easy to take blood from big birds by piercing the femoral vein below the knee. If one operates with small birds, the brachial vein of the wing in the area where it crosses the humerus is the most convenient source of blood. In the latter case, the bird is kept on its side or back with the left hand, its neck is fixed between the second and third fingers, while the left wing is stretched and fixed by the forefinger and thumb. The vein is pierced by a pin, needle, or any other sharp object, then a drop of blood is pressed out and the smear is prepared. It is not recommended to use the same syringe needles more than one time because their multiple use can cause contamination. The nonsyringe needles are kept in 70% ethanol.

The smears are prepared on standard clean glass slides that are free of grease and scratches. The slides should be numbered with a pen using special glass ink or pencil. Glass slides with one end frosted are the most convenient for this purpose. A drop of blood is placed on the glass slide left to the number. The size of the drop should not be greater than a pin hook. A glass slide with a polished edge (or the smooth edge of another clean glass slide) is attached to the drop at an angle of about 45°. Under the action of capillary force, the drop spreads along the edge as a thin stripe film between the two glasses. The glass with the polished edge is pushed then in the direction from the blood drop keeping it at the same angle. The movement should be rapid but not too brisk. The blood is spread as a thin film (Fig. 52). The manipulations described should be done as fast as possible, so that the blood does not clot. In certain cases, it is useful to touch the blood drop with the polished edge of the slide near the vein and then quickly make the smear with the same glass slide on the other glass slide. After each smear is prepared, it is necessary to wipe the polished edge of slide with a cotton wool tampon slightly wetted with water. This prevents contamination of other blood films during mass bird investigation. It is important that the film is thin and the blood cells make an even layer. The bird erythrocytes possess nuclei, which mask parasites in thick films that significantly hamper or even make it impossible to study their morphology in incorrectly prepared smears. The same reason accounts for the fact that the method of thick blood film widely used in the research of haemosporidians in mammals is not applicable in the work with birds and other lower vertebrates.

The blood films are air-dried; they should be protected from dust and insects. It is better to fix the smears in 100% methanol by immersing the preparation in the alcohol for about 1 min. If no methanol is available, it is possible to fix the smears in 96% ethanol for about 3 min. Fixed smears are air-dried and packed into paper bands so that they will not touch

each other. The blocks of preparations are then accurately wrapped into paper or put into a box with a tight cover for transportation to the laboratory, where they are stained. It is significant that the fixation of smears should be done soon after their preparation, because it influences the quality of staining. In the field, it is desirable to fix the smears at the end of each working day or even just after they have been dried in the humid environment. This ensures that accidental splashing of water does not ruin the blood films by hemolysis.

Staining of blood smears and their examination

In order to get a good quality of staining, prepared blood smears should be stained as soon as possible. A satisfactory staining of the smears is usually reached not later than one or two months after they are prepared. If the staining is delayed more than one week, it is better to keep the material in the refrigerator at a temperature of approximately 4°C.

Each good preparation is of scientific value, thus, it should be thoroughly prepared and saved. It is recommended to stain the smears in the collection purposes with Giemsa's stain. Rapid stains (for example, Field's stain) used in malaria research are less stable and fade faster with time. They are not suitable for taxonomic investigations. The easiest way is to use a commercially purchased stock solution of Giemsa's stain. To prepare the working staining solution for staining bird (as well as amphibian and reptilian) haemosporidians, it is necessary to add 10 ml of the standard stock solution to 100 ml of the phosphate buffered water with pH 7.2. To stain mammalian haemosporidians, 5 ml of the stock solution for the same quantity of the buffered water is enough. The staining solution must be freshly prepared before its use. The preparations are put on the edge in special plastic or glass containers and filled with the staining solution. The staining is performed for 1 h at a temperature of approximately 20°C. After the staining, the slides are taken out of the containers. The remains of the stain are gently washed off with tap water. The smears are thoroughly air-dried in an upright position and then examined in a light microscope. In well stained preparations, the cytoplasm of the erythrocytes should be pink with violet shimmer, the parasite nucleus stains red while the cytoplasm is blue. Minor differences, however, can be found when different brands of purchased commercial stock solutions of Giemsa's stain are used.

A buffered water with pH 7.2 for diluting the stock solution is prepared by diluting 1.0 g of disodium hydrogen phosphate Na_2HPO_4 and 0.7 g of potassium dihydrogen phosphate KH_2PO_4 in 1 liter of distilled water. The prepared solution should be tested. It keeps a stable pH value for a long time when kept in a tightly closed bottle made of neutral glass.

It is not recommended to mount the preparations made for collection purposes in Canada balsam, because in the course of time this leads to fading of the blood smears. Smears of particular value (the type preparations and others) may be covered by a coverslip glass so that the balsam would touch only the edges of the coverslip, but not the smear itself. This should be done by an experienced person.

It is convenient to examine the smears first with an ×40 oil immersion objective and ×10 ocular, which gives an opportunity to quickly find both the smallest (*Plasmodium* spp.) and largest (*Leucocytozoon* spp.) parasites. It is advised that approximately 2 cm^2 of the film are examined under the low ×40 oil immersion objective, and then 100 fields of microscope are investigated under high magnification (×100 oil immersion objective, ×10 ocular). It is important to use only the standard methods of slide examination to get comparable data. The investigation of the morphology and identification of the species of

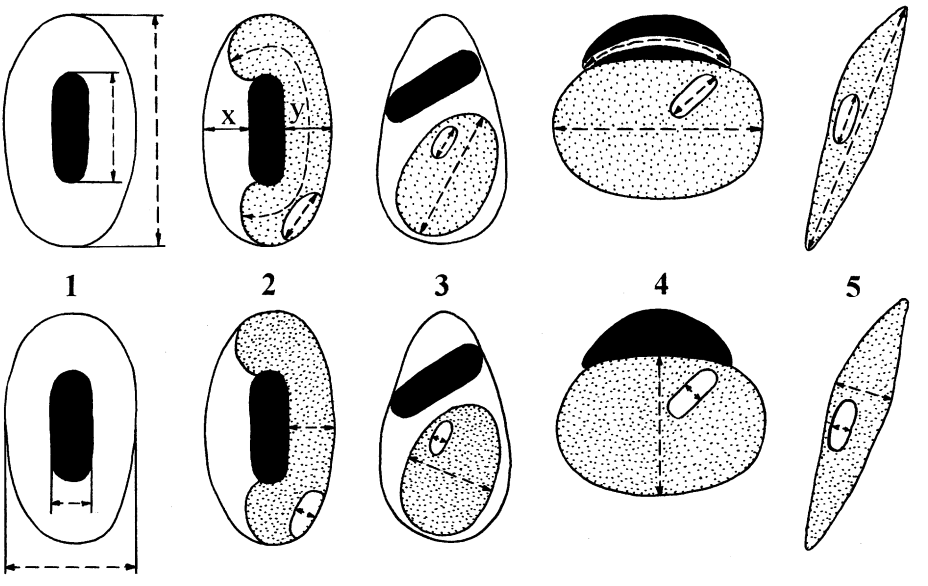

Figure 53 General diagram of measurement of the parameters of length (top) and width (bottom) which are used for the description of species of haemosporidian parasites:
1 – erythrocyte; *2*, *3* – gametocyte and meront of *Haemoproteus* and *Plasmodium* spp.: *2* – elongated form, and *3* – roundish and oval form; *4* – gametocyte of *Leucocytozoon* sp. and nucleus of its host cell; *5* – ookinete; *x*, *y* – parameters used for calculation of the Nucleus Displacement Ratio (NDR).

haemosporidians are carried out under high magnification. The immersion oil is easily removed from the preparations, either with a cotton wool tampon wetted in xylol or by immersing them into this liquid.

The intensity of parasitemia can be determined by actual calculating of the number of parasites per 1000 or 10,000 erythrocytes in randomly chosen fields of a thin blood film, as recommended by Godfrey *et al.* (1987).

It is advised to determine the relative intensity of infection during the first examination of blood smears under high magnification. This significantly simplifies the further work to select the most suitable preparations for a thorough analysis. The following symbols can be recommended in bird parasitological studies: +, 1–10 parasites per 100 thin film fields; ++, 11–100 parasites per 100 thin film fields; +++, 1–10 parasites in one thin film field; ++++, more than 10 parasites in one thin film field.

Measurement of parasites and their host cells can be done using various modifications of a screw ocular micrometer directly from the preparations as well as from the scale drawings or microphotographs. Computer analyzers of morphological parameters are, however, more convenient for this purpose. The recommended scheme for the measurement of different stages of the development of haemosporidians is shown in Fig. 53 (see also Fig. 298).

Preparations of gametes, zygotes, and ookinetes

Formation of gametes, zygotes, and ookinetes of many species of bird haemosporidians is easily induced *in vitro*, if the blood containing mature gametocytes is exposed to the air.

The blood of infected birds is taken either from the heart or from the vein, then it is quickly put on a watch glass and diluted with 3.7% solution of sodium citrate in a ratio of one part of the solution to four parts of blood. The smears are prepared as described above at set intervals of time after the blood exposure to the air (1, 3, 5, 10, 15, 30, 45 min and 1, 1.5, 3, 6, 12, 24, 48 h). They are air-dried, fixed in methanol, and stained with Giemsa's stain as described above. To prevent the drying of the solution with blood, the watch glass is placed in a Petri dish with a sheet of filter paper wetted in water on its bottom. The work is performed at 18 to 20°C. Exflagellation, fertilization, and development of ookinetes are induced this way most easily in the species of *Haemoproteus* and *Leucocytozoon*, while in some species of *Plasmodium* it is induced not so easily, and the use of special media is required (for example, those containing blood serum). In the case of *Plasmodium* spp., this process is easily induced by infecting mosquitoes, which are later dissected after a certain period of time. This method also gives good results with parasites belonging to all genera of bird Haemosporida.

Preparation of impression smears of birds' organs and tissues

The impression smears are made for the investigation of the tissue stages of haemosporidians. A small piece (not more than 1 cm^3) of an organ is removed with a scalpel or razor. The cut surface is then blotted gently with filter paper so that the excess of blood is removed. After this, the prepared surface is pressed onto a glass slide so that an impression smear or imprint is left. It is necessary to guarantee that the tissue cells make one layer in the imprint. Prepared imprint smears are air-dried, fixed, and stained in the same way as blood smears. The staining solution should be prepared by adding 4 to 5 ml of the stock Giemsa's solution to 100 ml of the phosphate buffered water with pH 7.2.

Preparation of histological sections of birds' organs and tissues

The preparations of tissue stages of haemosporidians of high quality are made when histological methods are used. It is recommended to make histological preparations from the material selected by the examination of impression smears, because the registration of the exoerythrocytic meronts in naturally infected birds is not an easy task, especially for the primary tissue stages. The methods of preparation of the histological preparations are described in numerous books on histology (see, for example, Ivanov *et al*., 1958; Lillie, 1965; Garnham, 1966; Kublickienė, 1978; Volkova and Ieletsky, 1982).

Infection of birds by subinoculation of infected blood and by sporozoites

The species of *Plasmodium* undergo merogony in the blood and can be easily subinoculated to uninfected susceptible birds by passing of infected blood. High parasitemia is usually reached this way, which allows one to study different aspects of the parasite biology more effectively. Obtaining blood from donor birds is not difficult although it requires some practice. The following methods can be recommended (Crewe, 1975). The tarso-metatarsal vein is cut near the ankle with a fine hypodermic needle and the blood is let to drip into a dish moistened with heparin. The blood can be also obtained by cutting the axilla vein and then collecting the blood into heparinized hematocrit tubes. The obtained blood is then

collected in a syringe rinsed out with heparin. The blood-anticoagulant mixture containing erythrocytic meronts is then intravenously injected in any of the large veins, or it is injected intramuscularly into the pectoral muscle, or intraperitoneally into the area under the sternum, or hypodermically in the neck area. The first three methods of subinoculation are most effective. About 0.2 to 0.3 ml of the mixture is injected into a bird of the canary size, while 0.5 to 1 ml of the mixture is injected into a bird of the thrush size. Heparin or 3.7% solution of sodium citrate are usually used as anticoagulant. Prepatent period significantly varies in subinoculated birds depending on the way of infection, virulence of parasite, species of recipient host and some other factors. High parasitemia develops most rapidly (usually within four to seven days) if the infection is made intravenously. It is noteworthy that a shock occasionally occurs with birds after the intravenous injection, which usually passes quickly.

Infecting birds with sporozoites is possible if the corresponding vectors are successfully infected. The experimentally infected vectors are first tested for presence of sporozoites in their salivary glands. Next, wings and legs are removed from the large insects and they are ground in a small amount of liquid consisting of equal parts of bird blood serum and normal (0.85%) saline. Insects can be homogenized only in the normal saline but the viability of the sporozoites usually decreases. The mixture obtained is filtered through two layers of gauze to remove debris. The filtrate with sporozoites is injected into the experimental birds, usually intramuscularly or intravenously.

Collection of blood-sucking dipteran insects and their experimental infection

The Bennett's trap is most frequently used for the collection of blood-sucking dipteran insects feeding with the blood of birds (Bennett, 1960). A modified version of this trap is described and illustrated by Baker (1970). Its main principle of operation is the following. The birds are put in a small wire-netting cage fixed to baseboard. After a certain time of the exposure at a certain height above the ground, the bird cage is covered with a cube-like insect cage covered with fine-mesh bolting silk. After blood meal, the blood-sucking dipteran insects concentrate in the upper part of the insect cage, where they are collected with an exhauster. The method gives good results when working with large birds (partridges, ducks, turkeys, rooks). When working with small passerine birds, the Bennett's trap is not so effective because these birds are less attractive for the blood-sucking dipterans than large birds. A longer exposure of the birds and the presence of the investigator near the trap is needed to collect the blood-sucking insects from small birds using the Bennett's trap, which is not always possible in the field experimental work. Moreover, this method has another disadvantage. After exposure in field conditions, it is not always possible to examine quickly the insect cage without damaging the small specimens. In the places of large density of dipterans, the samples from birds also include specimens attacking the investigator during the examination of the insect cage; therefore, this method does not always allow us to obtain 'pure' collections.

Glukhova and Valkiūnas (1993) suggested a simple construction of trap to collect biting midges from small birds (Fig. 54), which may be used also for the collection of other blood-sucking dipteran insects. It consists of two main parts: the trap itself (Fig. 54, *2*) and a wire frame (Fig. 54, *1*), with a piece of plywood in its lower part. The latter is the bottom. The trap is a cube sewed of fine-mesh bolting silk of about 40×40×40 cm in size. Ropes are sewed in the corners of the cube which are used to draw the trap inside the wire frame. The size of the latter is about 50×50×50 cm. When the trap is stretched inside the frame the

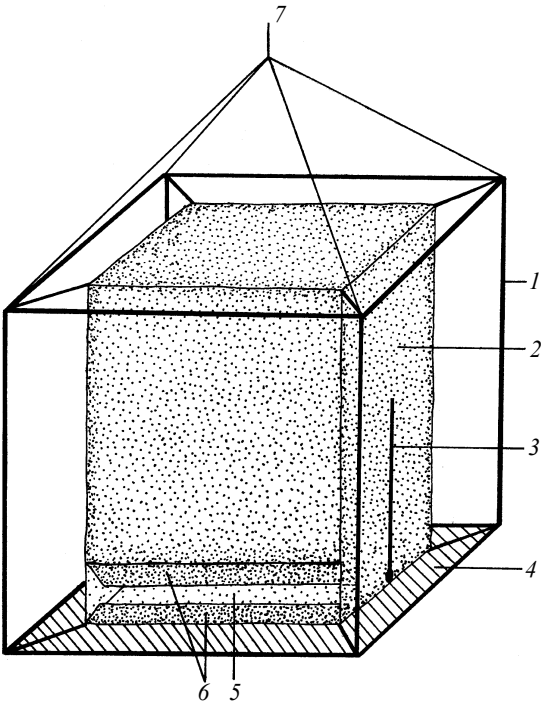

Figure 54 Sketch of the trap for the collection of blood-sucking dipteran insects from birds: *1* – wire frame; *2* – the trap made of fine-mesh bolting silk; *3* – zipper; *4* – bottom made of plywood; *5* – entrance to the trap; *6* – walls preventing the escape of insects from the trap; *7* – cord for the trap fastening. Description is given in the text.

tension of its sides can be easily regulated to avoid folds. This significantly simplifies the examination of the trap and collection of the blood-sucking dipteran insects. It is difficult to reach this, if the trap is pulled on the frame, which complicates the collection of small insects. Two slots about 10 to 15 cm wide are cut in the lower part of the trap on its opposite sides, through which the insects penetrate into the trap (Fig. 54, *5*). To decrease the probability of the insects flying out of the trap, two walls about 10 cm wide are sewed in the slot. They are sewed at an angle to each other and form a valve (Fig. 54, *6*), which does not prevent the insects to penetrate into the trap but decreases the probability of their flying out. To facilitate the access of the investigator into the trap, a zipper is sewed to one of its sides (Fig. 54, *3*), which allows one to get inside and perform the necessary manipulations, when it is unzipped. Small birds used as baits for the blood-suckers are put in small wire-netting cages with a size of about 15×10×15 cm. The latter are placed on the bottom of the trap near the valves. The entire trap can be raised to the necessary height on a branch of a tree and fixed there for a certain time with a twine (Fig. 54, *7*), one end of which is attached to the trap, while the other is thrown over a branch.

The main advantage of this trap compared to the Bennett's trap is that it can be left without care of an investigator for a long time, while its contents can be analyzed in the laboratory because it is easy to transport the trap. Moreover, the samples of blood-sucking dipterans include only the species attracted by the birds. To increase the effectiveness of work, the trap should be put in the biotopes with a relatively high density of blood-sucking

dipterans during a period of their maximum activity, because small passerine bird is not an effective bait for them and good samples cannot always be made. It was possible to catch from 6 to 74 of engorges biting midges in the places with their high activity on the Curonian Spit in the Baltic Sea, when the trap was exposed during 10 to 12 h at a height of 4 to 5 m over the ground (Glukhova and Valkiūnas, 1993). A part of the collected blood-sucking dipterans are dried for their subsequent identification.

When blood-sucking insects are collected with this trap, it is impossible to determine the exact time when they ingested gametocytes, which is important to determine the time of the development of the parasite in the vector. The time when the dipterans swallowed the gametocytes can be determined if the insects are collected directly from the birds, which the investigator holds in his hands in the places of their active attacking. The crown feathers of birds, who are used as donors of gametocytes for vectors, are plucked of from a surface of about 1 cm^2 to facilitate the observation of the dipterans taking blood meal, which is especially helpful during the work with biting midges. This procedure is easily endured by the birds if they are treated accurately, and the plumage is subsequently restoring. The bird prepared this way is held in a hand. For the convenience of the work, the head of the bird is thrust through a cone-like cover made of fabric, which bottom part is fastened with a safety-pin. This gives an opportunity to manipulate with good fliers without a fear to let them free in the field conditions. The biting midges and mosquitoes willingly attack the birds prepared this way and take blood meal at the places free of feathers. The engorged females are collected with an instrument for catching live blood-sucking dipterans and transported into small insect cages made of fine-mesh bolting silk with a glass pipe sewed in their upper part for the convenience of manipulations. The instrument for manipulations with live insects is a glass pipe with attached rubber tube and a piece of fine-mesh bolting silk between them. This procedure requires some practice. If the experimenter works alone, a part of the engorged females are damaged, while some of them are not caught. The gathering of insects can be improved to avoid this. The insect cage is made of fine-mesh bolting silk with a size of about 10×10×10 cm, which is stretched inside the wire frame with a size of 15×15×15 cm. A zipper is sewed in one wall of the cage. The bird head with plucked feathers as described above is placed into the unzipped insect cage after several specimens of dipterans start to take blood meal at its crown. The engorged insects fly off and concentrate in the upper part of the insect cage. This allows us to reduce the losses of the engorged females to the minimum and completely exclude any damage of these delicate insects, which is especially important with the work with biting midges. This way one can exactly determine the time when the insects swallowed the blood of infected birds. Transportation of the small insect cages is not difficult.

The insects fed on the birds with high parasitemia perish more often than those who fed on the birds with low parasitemia. For experimental infection of the vectors, it is recommended to select the donor birds with an intensity of parasitemia less than 40 gametocytes per 1000 erythrocytes (10 to 20 gametocytes per 1000 erythrocytes seems to be optimal for most groups of haemosporidians).

Cultivation of blood-sucking dipteran insects in the laboratory conditions is rather difficult, it requires practice and sometimes a significant funding. The information on this topic is available in the literature (Wenk, 1965; Morii and Kitaoka, 1968a; Gutsevich and Glukhova, 1970; Vanderberg and Gwadz, 1980; Edman and Simmons, 1985; Lacoursière and Boisvert, 1987; Fahrner and Barthelmess, 1988; Glukhova, 1989). The methods of laboratory keeping of hippoboscid flies and the peculiarities of the work with these flies used as vectors are described by Baker (1956).

Laboratory keeping of blood-sucking dipteran insects caught in nature

Usually, blood-sucking dipterans fed on infected birds need to be kept in the laboratory approximately five to ten days to study sporogony at a temperature optimal for certain parasite species. During this period, the majority of species of haemosporidians complete their development in the vectors. We have found that it is convenient to transport small cages with insects collected as described above to the laboratory and keep them at humidity and temperature optimal for completion of sporogony without any manipulations with them before their dissection, which is especially important during experimental work with biting midges (for details, see Valkiūnas *et al.*, 2002b). However, if it is necessary to divide the collected insects into several groups, the following procedure is recommended. The insects are transferred from the insect cage into cardboard boxes about 5×5×8 cm in size or less, depending on the species and the number of dipterans. The actions are performed with an instrument for manipulations with live insects. The upper part of each box is covered with fine-mesh bolting silk which is fixed with a rubber ring. A hole closed with a tampon is made in the middle of the box. It is used to put the insects in the box or remove them when necessary. A cotton wool tampon is put on the fine-mesh bolting silk well wetted with solution of sucrose, which is a source of food for the insects. The tampon is changed daily. The boxes with insects are placed in a dark place and kept at a temperature of about 20 to 25°C and relative humidity of 80 to 90%.

In field conditions, the insect boxes and cages are put into a tightly closed container of foam plastic. Boxes with insects and Petri dishes with sheets of filter paper wetted in water are put on the bottom of the container. The necessary regime of temperature, humidity, and illumination can be easily gained. Water, which is dangerous for small insects, is not condensed on the walls of the container. Instead of containers, plastic packs can also be used to keep the insect boxes and cages at appropriate humidity conditions.

The mortality of some groups of blood-sucking dipterans captured in nature and kept in the conditions of experiments can be high, especially among biting midges and simuliid flies, which should be taken into account in the planning of the experiment (see p. 112).

Dissection of blood-sucking dipteran insects and making preparations of ookinetes, oocysts, and sporozoites

The insects are lightly anesthetized by putting them for a few seconds into a tube closed with a cotton wool tampon wetted in chloroform, ethylacetate, or any other anesthetic. After this, identification of species is performed. It is advised to remove the wings and legs of the insects before dissecting them. Then, the insects are put on the glass slide and wetted with normal saline, which facilitates the further operations with them. The dissection is performed under the observation with a binocular stereoscopic microscope. The set of needles for dissection is chosen in advance and improved individually in the course of gaining the experience. Shute's needles can be recommended. Below, we describe the method of dissection of mosquitoes. Dissection of other groups of blood-sucking dipterans is performed in a similar way with slight modifications. It is noteworthy that this fine work requires some practice, and it takes some time for each investigator to find the most convenient way of the dissection. The final objective is the separation of the midgut and salivary glands of the dipterans. The general scheme of the arrangement of mosquito internal organs is shown in Fig. 55.

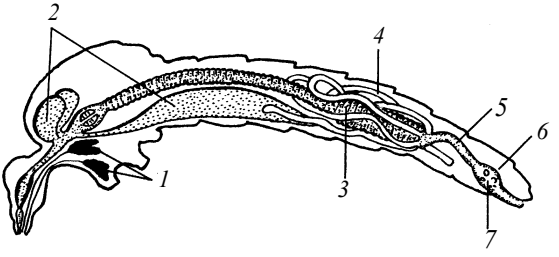

Figure 55 Diagrammatic representation of the arrangement of internal organs of blood-sucking mosquito:
1 – salivary glands; *2* – diverticula; *3* – midgut; *4* – Malpighian tubule; *5* – hindgut; *6* – rectum; *7* – rectal papilla. Ovaries are omitted (modified from Vanderberg and Gwadz, 1980).

Preparations of ookinetes are made most easily. The contents of the midgut is extracted for this purpose. Ookinetes locate in the semidigested contents of the midgut. Completely developed ookinetes of bird haemosporidians usually appear in 12 to 24 h at a temperature of about 20°C, although there are species that develop much faster and much slower, which one should bear in mind when working with different parasites. The extreme segment of the abdomen is cut off with a razor or dissecting cutting needle and the contents of the abdomen is pressed out on the glass slide using a dissecting needle by simultaneous pressing and rotating it from the anterior end of the abdomen to its posterior end. The insect is slightly held at the thorax during this process. The midgut is separated from the other organs, which are removed. The contents of the midgut is expressed on the slide and mixed with a minute drop of normal saline. A thin smear is prepared afterward. It is important to localize the blood clot, if the delicate midgut is torn when it is pressed out of the abdomen, which frequently happens. The quality of the preparations does not become worse. The smears are air-dried, fixed in methanol, and stained in the same way as blood smears.

Preparations of oocysts. Development of the oocysts of haemosporidians occur not synchronously, and it takes place with a different speed in different species of parasites. Small oocysts of *Leucocytozoon*, *Parahaemoproteus,* and *Akiba* species develop most rapidly. The process of their development starts in 48 h and they may become mature in three to four days after ingestion of gametocytes by the vector. The slowest development of oocysts is found in *Haemoproteus* and *Plasmodium* species whose sporogony may be as long as one week and even longer. All this should be taken into account while studying the sporogony.

A fresh preparation of midgut is initially prepared. For this purpose, one has to extract the midgut gently on a glass slide. Nicks are made with a dissecting cutting needle on one of the posterior segments of the abdomen (Fig. 56, *1*). The tip of the nicked abdomen is pulled out together with the abdominal contents (the ovaries, Malpighian tubules, midgut, and other adjacent organs) using a needle while the insect is held by its thorax with another needle. (Fig. 56, *2*). The midgut is gently separated, placed in a small drop of normal saline, covered by a small coverslip, and examined under a light microscope (×40 objective, ×10 ocular). A minute drop of 2% solution of mercurochrome (some investigators advise to use 0.5% solution) is put on the extracted midgut for staining to simplify the search of the oocysts, and only afterward it is covered with a coverslip. Oocysts are stained in a darker color than the tissues of the midgut. It is convenient to study the oocysts with a phase-

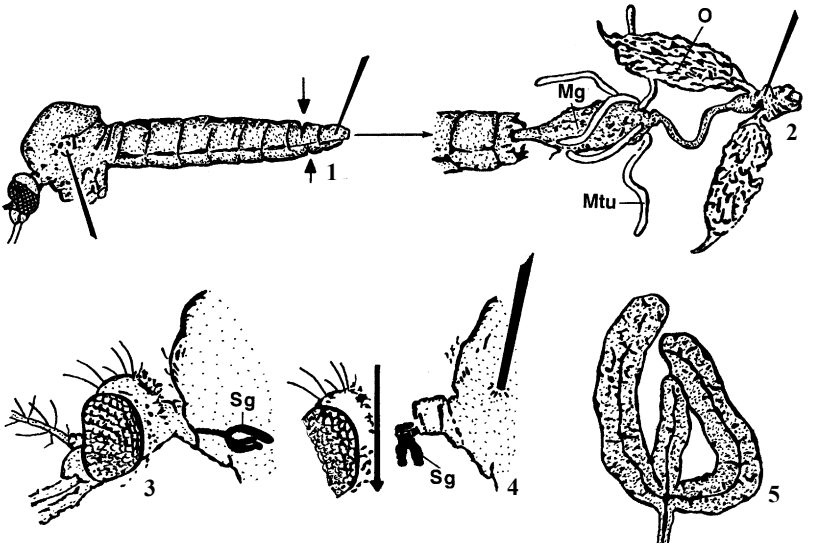

Figure 56 Successive stages of dissection of mosquito females for isolation of the midgut (*1*, *2*) and salivary glands (*3*–*5*):
5 – isolated salivary glands; Mg – midgut; Mtu – Malpighian tubule; O – ovary; Sg – salivary glands (modified from Service, 1993). Description of manipulations is given in the text.

contrast system of the microscope or in the transmitted light with closed iris diaphragm. The presence of pigment granules inherited by ookinetes from macrogametocytes helps to find young oocysts of some species of *Haemoproteus* and all species of *Plasmodium* investigated so far, although the pigment in oocysts is present not in all species of *Haemoproteus*. Certain practice is required to find small oocysts of species of the subgenera *Parahaemoproteus*, *Leucocytozoon*, and *Akiba*.

The best fresh preparations are used to make permanent preparations of oocysts. Below, we describe the method suggested by Garnham (1966) with minor modifications. First of all, the midgut with oocysts is fixed in 10% formalin in normal saline. A drop of the fixative is placed at one edge of the coverslip and then drawn through the specimen under the coverslip by applying a piece of filter paper to its opposite edge. The procedure is repeated if necessary gaining that the midgut under the coverslip would be soaked with the fixative. Next, the hole slide is immersed for the final fixation in a Petri dish with the fixative for 24 h. The coverslip floats off while the midgut remains fixed to the coverslip or sometimes to the glass slide itself. The fixative is then replaced with 70% ethanol, where the preparation is left for six to ten hours. It is then washed gently in distilled water and stained with Ehrlich's or Delafield's hematoxylin for 5 to 10 min. Before use, the hematoxylin is diluted in the ratio of one part of the stain in four parts of distilled water. The stained specimen is 'blued' gently in tap water with an added pinch of sodium bicarbonate for 5 min. Next, it is differentiated with acid ethanol until the specimen turns a rusty-reddish color, and then 'blued' again for 5 min. The acid ethanol is prepared by adding two to three drops of concentrated sulfuric acid into a Petri dish half-full with 70% ethanol. The specimen preparation processed this way is dehydrated in 70% and then 100% ethanol, cleared by putting a drop of clove oil over the preparation, placed in the Petri dish filled with xylol, and mounted in green Euparal or Canada balsam.

Preparations of sporozoites are made after extraction of salivary glands from the vectors. Dissection of salivary glands is a procedure that needs practice. It is important to bear in mind that the rate of sporogony and penetration of sporozoites into the salivary glands strongly differs in various species of haemosporidians. The sporozoites of the majority of species invade the salivary glands in four to ten days after ingestion of mature gametocytes by the vectors, and then their number gradually decreases. The optimum time for dissection is chosen for each of the species of parasite and the vector studied. The salivary glands are almost completely located in the thorax area of the vectors (Fig. 55, *1*). The head of the insect is cut off with a razor or dissecting cutting needle (Fig. 56, *3*, *4*). The salivary glands are gently pressed out with a slight pressure by a blunt needle on the thorax near the base of the fore-legs (Fig. 56, *4*, *5*), and placed in a small drop of the normal saline together with adjacent debris from the dissection place. The salivary gland of mosquitoes can be separated from the adjacent structures, but the salivary glands of biting midges are too minute in size to do this. To prepare a preparation of sporozoites, the salivary glands should be ruptured by the gentle pressure of a needle and they can be slightly mixed with a minute drop of normal saline to produce a thin small film. The preparation is then air-dried, fixed in methanol, and stained in the same way as the blood smears.

Methods of Species Identification and Recommendations for Their Description

MAIN DIAGNOSTIC CHARACTERS USED FOR SPECIES IDENTIFICATION

With rare exception, identification of the species of bird haemosporidians is performed only on the basis of the stages developing in the peripheral blood. As a rule the other stages of the life cycle of these parasites as well as the peculiarities of their development are studied only fragmentarily in a small number of species. Thus, many of these characters cannot be used for a detailed comparison between them and, therefore, at present, they cannot be used to compose keys to the species, although they should be taken into account when the final identification of a species is made and while describing new species. In well studied Plasmodiidae species, these characters include: the duration and degree of synchrony of erythrocytic merogony and the time of the day when the mass maturation of erythrocytic meronts takes place; the morphology and localization of exoerythrocytic meronts; the duration of the development in mosquitoes; the morphology of oocysts and sporozoites; the taxonomic position of vectors; the peculiarities of infection of experimental vertebrate hosts (canaries, domestic chickens, ducklings, turkey poults, pigeons, etc.). One has to keep in mind that some of the characters mentioned are variable and they differ in the representatives of different populations of parasites belonging to one species; but this is still poorly studied and, at present, limits the application of these characters in the systematics.

The minimums of morphological characters listed in the text below, which served as a basis to compile keys to the species of various families refer mainly to trophozoites, erythrocytic meronts, gametocytes, and to the peculiarities of their influence on infected cells. The data used to identify the species are obtained during examination of the objects under study with a light microscope. The importance of using the available experimental data on specificity of parasites in species identification was discussed earlier (see p. 67).

A character of the ‘area’ (area of the parasite; nucleus of the parasite; host–parasite complex; infected and noninfected erythrocyte, etc.) is frequently used in papers on systematics, when species of haemosporidians are described. It is our opinion that taxonomy of bird haemosporidians can do without the character of ‘area’ which is directly proportional to the product of such linear parameters as length and width. The two latter are calculated more easily and accurately by low cost traditional methods available in any laboratory. We do not use ‘area’ in the description of the species and in keys for their identification.

Qualitative characters are primarily used in this book in keys for identification of different taxa. Those, which are relatively most stable, are primarily recommended for use in the description of species. Qualitative characters in the protists considered are subject to lesser variability and they are determined significantly more easily than quantitative ones.

A scheme for measuring the parasites and their host cells is given in Fig. 53 (see also Fig. 298).

HAEMOPROTEIDAE

Young gametocytes.[†,‡] Shape: roundish; oval; irregular; elongate rod-like. Outline: even; angular; wavy; slightly ameboid; highly ameboid. Peculiarities of growth in infected erythrocytes: adhere to the nucleus and grow toward the envelope; adhere to the envelope and grow toward the nucleus; do not touch either the nucleus or the envelope.

Growing gametocytes.[*] Outline: even; angular; wavy; slightly ameboid; highly ameboid. Position of medium grown gametocytes in relation to the poles of infected erythrocytes: they fill the erythrocytes up to their poles; they do not fill the erythrocytes up to their poles. Position of medium grown gametocytes in infected erythrocytes: they do not touch either the nucleus or the envelope; they are appressed to the nucleus but do not touch the envelop along all of their margin; they are appressed to the envelope but do not touch the nucleus along all of their margin; they are appressed both to the nucleus and envelope; they adhere to the nucleus and envelop but the central part of the pellicle does not extend to the envelope of the erythrocytes, causing a 'dip' and giving a dumbbell-like appearance. Dumbbell-shaped gametocytes (with thickenings at the ends): present; absent. Percentage of the dumbbell-shaped gametocytes from the total number of growing gametocytes. Form of pigment granules: roundish; oval; irregular; rod-like. Dimensions of pig- ment granules: small or dust-like (<0.5 μm); medium (0.5 to 1.0 μm); large (1.0 to 1.5 μm); gigantic (>1.5 μm).

Fully grown gametocytes.[**] Staining of the cytoplasm: macrogametocytes clearly different from microgametocytes; macrogametocytes differ slightly from microgametocytes. Vacuoles: present; absent. Dimensions of vacuoles: small (<1 μm); large (>1 μm). Shape: roundish (discoid); elongate; bilobated, circumnuclear. Outline: even; angular; wavy; slightly ameboid; highly ameboid. Position in relation to the poles of infected erythrocytes: they fill the erythrocytes up to their poles; they do not fill the erythrocytes up to their poles. Peculiarities of position in infected erythrocytes: they do not encircle the nucleus completely; they encircle the nucleus completely but do not occupy all available cytoplasmic space; they encircle the nucleus completely and occupy all available cytoplasmic space.

[†] The essence of most characters listed is specifically rendered in keys to the species of the corresponding subgenera and also in the descriptions of species in the Systematic Section by means of references to the corresponding illustrations.

[‡] Parasites, whose length is usually less than the length of the nucleus of the infected erythrocyte, (or sometimes close to it) are referred to as 'young gametocytes.'

[*] Parasites, whose length usually exceeds the length of the nucleus of infected erythrocyte, are referred to as 'growing gametocytes.' A group of 'medium grown' gametocytes is distinguished among these. Their length is not more than 2/3 of the length of fully grown gametocytes. The length of 'medium grown' gametocytes is proportional to the length of fully grown gametocytes, therefore, it varies significantly in different species of haemoproteids.

[**] Parasites, whose length reaches the average length of the fully grown gametocytes known for the species considered or exceeds it are referred to as 'fully grown gametocytes.'

Position in relation to the nucleus and envelope of infected erythrocytes: they are closely appressed both to the nucleus and envelope; they are closely appressed to the nucleus but do not touch the envelope along all of their margin; they are closely appressed to the envelope but do not touch the nucleus along all of their margin. Dumbbell-shaped gametocytes (with a constricted central portion and thickenings at the ends): present; absent. Position of nucleus in macrogametocytes: median or submedian; subterminal; terminal. Position of nucleus of gametocytes in relation to the nucleus of infected erythrocytes: it is located close to the nucleus; it is not located close to the nucleus. Form of pigment granules: roundish; oval; irregular; rod-like. Range of variation and average number of pigment granules. Peculiarities of location of pigment granules in the cytoplasm: randomly scattered; tendency to aggregate into compact masses; aggregate in loose clumps; aggregate in well regulated groups which are rosette-like, fan-like, star-like, and others in form. Dimensions of pigment granules: small or dust-like (<0.5 μm); medium (0.5 to 1.0 μm); large (1.0 to 1.5 μm); gigantic (>1.5 μm). Average length and average width. Range of variation and the average value of the nuclear displacement ratio (NDR) of infected erythrocytes which is calculated according to the formula: $NDR = 2x/(x+y)$.† Influence on the nucleus of infected erythrocytes: absent (the nucleus is not displaced); displaced laterally; rotated to the normal axis; displaced towards one pole of the erythrocytes; pushed out (enucleated erythrocytes). Average length and average width of uninfected and parasitized erythrocytes. Average length and average width of the nucleus of uninfected and parasitized erythrocytes.

The investigation of all the characters mentioned above should be carried out separately for macro- and microgametocytes.

To characterize haemoproteids species, Bennett and Peirce (1988) use the shape of fully grown gametocytes. This is significant but not always enough to assist species identification because the fully grown gametocytes are not always present in smears prepared from naturally infected birds. The data on young and especially growing parasites, which are also informative, are needed for this. Let us analyze one example. In the article mentioned, the shape of gametocytes of *Haemoproteus mansoni* (=*H. meleagridis*) is characterized as halteridial. This shape of gametocytes is, however, characteristic only of the growing ones, which are usually most common in preparations, while fully grown gametocytes complete- ly encircle the infected erythrocyte (Atkinson, 1986) and according to the terminology used by these authors should be related to the group of circumnuclear forms. The application of the maximum possible set of characters, including all transition stages from young to fully grown gametocytes in the description and identification of the species, markedly facilitates the species identification and makes it more reliable.

PLASMODIIDAE

Trophozoites. Outline: even; irregular, ameboid. A long thread-like or finger-like outgrowth which length exceeds the length of the main body of trophozoite: present; absent. Position in infected erythrocyte: variable; a polar or subpolar. Position in relation to the nucleus of infected erythrocyte: adhere; do not adhere. Influence on infected erythrocyte: not evident or slightly evident; markedly evident.

† The NDR is given according to Bennett and Campbell (1972) (see Fig. 53, *2*).

Erythrocytic meronts. A long (>2 μm in length) thread-like or finger-like outgrowth in growing meronts: present; absent. Vacuoles: present; absent. Dimensions of vacuoles: small (<1 μm); large (>1 μm). Form of fully grown meronts: roundish; oval; elongate; irregular. Position of nuclei in fully grown meronts: fan-like; rosette-like; disorder; other. Peculiarities of position in infected erythrocyte: encircle the nucleus of erythrocyte completely; do not encircle the nucleus of erythrocyte completely. Position in relation to the nucleus of infected erythrocyte: adhere; do not adhere. Degree of occupation of the available cytoplasmic space in infected erythrocyte: they occupy less than half of the cytoplasmic space; they occupy more than half but not all the cytoplasmic space; they occupy all the cytoplasmic space. Residual body in mature meronts (segmentes): present; absent. Number of merozoites in mature meronts: range of variation and average number. Dimensions of fully grown meronts: range of variation and average length and width. Influence on infected erythrocytes: not evident or slightly evident; deformed. Influence on the nucleus of infected erythrocyte: not evident or slightly evident; displaced laterally; rotated to the normal axis; displaced towards one pole of erythrocyte; pushed out (enucleated erythrocytes).

Gametocytes. A long (>2 μm in length) thread-like or finger-like outgrowth in young gametocytes: present; absent. Vacuoles: present; absent. Dimensions of vacuoles: small (<1 μm); large (>1 μm). Form of fully grown gametocytes: roundish; oval; elongate. Peculiarities of position of fully grown elongate gametocyte in the infected erythrocyte: encircles the nucleus completely; does not encircle the nucleus completely. Position in relation to the nucleus of infected erythrocyte: adhere; do not adhere. Form of pigment granules: roundish; oval; irregular; rod-like. Peculiarities of location of pigment granules in fully grown gametocytes: randomly scattered; aggregated into one or several clumps; aggregated into one or several solid masses. Influence on infected erythrocyte: not evident or slightly evident; deformed. Influence on nucleus of infected erythrocyte: not evident; displaced laterally; rotated to the normal axis; displaced toward one pole of eryth- rocyte; pushed out (enucleated erythrocytes). Dimensions of fully grown gametocytes: range of variation and average length and width.

Phanerozoites. Localization and number of merozoites.

Main biological characters. Periodicity of erythrocytic merogony.

GARNIIDAE

The same characters as for Plasmodiidae species keeping in mind that for these bird parasites (i) host cells in the blood are mainly thrombocytes and mononuclear leukocytes and (ii) malarial pigment (hemozoin) is absent.

LEUCOCYTOZOIDAE

Fully grown gametocytes and their host cells. Form of host cell of gametocyte: roundish; fusiform. Form of nucleus of roundish host cell: cap-like (with a more or less evident thickening in the center); dumbbell-like (with thickenings at both ends); band-like (without clearly pronounced thickenings); irregular (distorted into filaments or other). Form of

nucleus of fusiform host cell: cap-like or almond-like (with a more or less evident thickening in the center); they resemble a nucleus of uninfected erythrocyte; band-like or crescent-like (without clearly pronounced thickenings); dumbbell-like with thickenings at both ends which are appressed to the gametocyte; dumbbell-like with thickenings at both ends, which do not adhere to the gametocyte. Degree of extension of nucleus of roundish host cell around the gametocyte: up to 1/2 of the circumference of gametocyte; more than 1/2 of the circumference of gametocyte. Degree of extension of nucleus of fusiform host cell around gametocyte: up to 1/3 of circumference of gametocyte; more than 1/3 but less than 2/3 of circumference of gametocyte; more than 2/3 of the circumference of gametocyte but not complete circumference; complete circumference. Peculiarities of influence of fully grown gametocyte on nucleus of host cell: deform; push aside but do not enucleate host cell; split into two more or less symmetrical portions; uniformly disperse along all circumference of gametocyte; enucleate host cell (see also Appendix 2, p. 866).

METHODS OF SPECIES IDENTIFICATION

Species identification is possible only by means of the analysis of a set of characters of the stages developing in the peripheral blood. The data about the specificity of the parasites given above (see p. 67) should be also taken into account. To identify the species, the thoroughly prepared and well stained blood smears containing the stages of development of haemosporidians, which form the basis for identification, are required. It is important that the blood film should be thin and the blood cells make an even layer and, ideally do not touch each other. This decreases the possibility of the deformation of parasites and their host cells. It is also advised that the blood for the smears is obtained from live birds. If the blood is exposed to the air, mature gametocytes of haemosporidians rapidly become round and leave the erythrocytes due to the onset of gametogenesis. Rounded parasites lose their main diagnostic characters and currently cannot be used for species identification. This should be taken into account when blood is taken from shot or dead birds. Besides, roundish gametocytes are frequently found in smears made in an atmosphere with a high humidity, when blood smears do not dry quickly enough. If one does not take these requirements into account, species identification is not reliable.

The intensity of parasitemia in naturally infected birds is usually low (frequently less than 1 parasite per 1000 erythrocytes), and not all stages necessary for species identification are always present in the smears. In these cases, species identification should be postponed until more complete material would be obtained.

If the preparations are good enough, the following sequence of tasks for species identification is recommended. The smear is examined under the high magnification (×100 oil immersion objective, ×10 ocular) of a light microscope and sketches of the most typical (frequently observed) cells of the parasite at each stage of its development are made. It is important to exclude not typical (deformed, destroyed, or extremely rarely seen) cells and artefacts, which are present in certain amounts in all preparations and frequently cause wrong identification. This is the most important stage of the identification, which is especially difficult to master. One should also keep in mind that the material under study can contain parasites belonging to other groups of sporozoan blood parasites (for example, species of the genera *Hepatozoon*, *Babesia*, *Atoxoplasma*, and some others), which should be differentiated from haemosporidians. This is in general not difficult to do, due to clear

sexual dimorphic characters observed in gametocytes of haemosporidians, which is not characteristic of other blood sporozoans. In addition, the same blood smear frequently contains several species of parasites belonging to one or several genera (subgenera) of haemosporidians, which makes identification significantly more difficult, especially in the former case.

After the general concept about the species under study is obtained, one is advised to prepare the plates of sketches of the most typical stages of development, which are recommended to be used for identification of species of certain genera (see, for example, Figs. 6, 12, and 20). The main diagnostic characters should be noted on the sketches. The tables of morphometric characters needed for identification are also prepared. Next, one chooses one of two main ways to determine the species.

The first one is used when the material under study contains the main diagnostic characters needed for identification of parasites. In this case, one can identify the species using the keys for their identification. The most difficult 'steps,' which do not exclude ambiguity, are accompanied in the keys with references to the corresponding schematic illustrations. This simplifies the comparison of diagnostic characters used in the keys to the species and those recorded in plates of sketches prepared by the scholar who performs the species identification.

If the available material does not contain some of the diagnostic characters necessary for identification, which is a common situation during the work with material collected in the wild, or the scholar doubts whether the typical characters needed for the species identification have been correctly distinguished, then we recommend the second way of species identification. It is based on the presence of a quite well defined range of the vertebrate hosts for the species of Haemoproteidae and Leucocytozoidae (see pp. 69 and 76). This method may be also recommended if one failed to identify a species using the keys. In this case, the species being identified is compared with the illustrations and descriptions of all species described for the birds of the order to which the vertebrate host of the species under study belongs. The data about the distribution of the species of haemosporidians by bird orders are presented in Table 6. In doing this, first of all, it is necessary to pay attention to the species of parasites, which are described in birds that are especially close, from the point of view of phylogeny, to the host of the species of parasite under identification. The range of vertebrate hosts of many *Plasmodium* species include representatives of several bird orders, thus, during the species identification of malaria parasites by the second method of identification, one has to compare the parasite studied with each representative of the subgenus to which it belongs rather than depend on the taxonomic position of the hosts. The second way of identification is labor-consuming, but it may become useful, especially for the scholars who master species identification.

The final identification is made after thorough comparison of the material under consideration with the one presented in the essays on species in the Systematic Section.

When one identifies the species of parasites in naturally infected birds, some additional difficulties arise. They are different in different families of haemosporidians. Below we describe them.

Plasmodiidae. Low intensity of parasitemia and difficulty in finding trophozoites and erythrocytic meronts. It is relatively easy to infect susceptible experiment birds (canaries, chickens, pigeons, ducklings, and wild birds) with the parasites in laboratory conditions by means of subinoculation of infected blood. As a result, heavy parasitemia can be achieved for detailed study. Some species can only be reliably identified using this method (see also p. 231).

Garniidae. The same difficulties as for identification of Plasmodiidae species. It is noteworthy that pigment granules in some species of *Plasmodium* are minute in size and hardly distinguishable, thus malaria parasites are sometimes erroneously identified as species belonging to the genus *Babesia* or even *Garnia*.

Haemoproteidae. The lack of all stages (necessary for identification) of the development of gametocytes and primarily lack of fully grown ones in blood smears is a common difficulty. If the scholar has certain experience, the use of the second way for identification allows one to distinguish many species only on the basis of morphology of the growing gametocytes. Gametocytes of some species contain a great amount of valutin, which masks the malarial pigment and can be erroneously distinguished as malarial pigment. It is important to note that at heavy parasitemia (usually over 10% of erythrocytes), minor morphological changes of parasites as well as their influence on host cells may be observed, due to occupation of immature erythrocytes and probably some other reasons which are still poorly understood. This should be taken into consideration during identifi- cation. The keys to haemoproteid species were compiled based on the preparations with parasitemia less than that mentioned above.

Leucocytozoidae. The main difficulties are low intensity of parasitemia combined with extreme fragility of the parasites and their host cells as well as an evident tendency to their deformation. It is not always possible to find the necessary number of cells suitable for identification. Preparations of high quality as well as long-time microscopy are required.

MAIN DIAGNOSTIC CHARACTERS USED FOR SPECIES DESCRIPTION

The main requirement imposed upon the descriptions is the possibility to use them for species identification. The description is effective if it allows the species, for which it is prepared, to be distinguished not only from the known ones, but also from those that will be described in the future. It is clear that the descriptions within the same genus should be done using the same scheme to simplify the comparison. It is advisable to use the main diagnostic characters listed above while describing new species or redescribing known species of haemosporidians. New morphological and other characters may be added in the future. In addition, if possible, it is desirable to describe in detail the main stages of development in the vertebrate and invertebrate hosts as well as to investigate the specificity and other biological aspects regardless that many of these characters cannot currently be used for identification because of their fragmentary study in the majority of species and lack of knowledge about the intraspecific variability. Nevertheless, this approach allows us to get closer to the understanding of naturally existing diversity and then to use this information in the taxonomy. This is also helpful in determining the most valuable diagnostic characters, which can be used in the future in preparing the keys for species identification.

It is important to note that, due to the wide range of vertebrate hosts, some avian species of the genus *Plasmodium*, within the host spectrum, may exhibit diverse morphological forms resulting in strain varieties and transmission by different vectors throughout their distribution range. Due to these morphological variants, it was conventionally accepted since P.C.C. Garnham's treatise (Garnham, 1966) that any new species should only be defined if supported at least by the full range of blood stages in experimentally

inoculated hosts but, ideally also by the data on exoerythrocytic merogony, periodicity, vectors, development in vector, and some other biological characters. Descriptions based solely on the blood stages recorded in naturally infected birds should be called into question. In this relation, the validity of some *Plasmodium* species, which are given in this book, should be proved by investigation of the parasites' morphology in subinoculated experimental hosts as well as by investigation of their biological characters. Among such parasites, *P. anasum, P. gundersi, P. hegneri, P. leanucleus*, and some others may be mentioned as an example. Blood stages of these plasmodiids have distinctive characters, but the degree to which development in other hosts affects the phenotype of the parasites is unknown. The so-called 'good' species of *Plasmodium* (for example, *P. nucleophilum, P. polare, P. rouxi*) usually maintain their main diagnostic characters when developed in various hosts, although some variations are always present. It looks reasonable at present to discourage description of new species of avian malaria parasites based solely on infections in naturally infected birds. In addition, morphometric data, which are useful for identification of high level specific reptilian *Plasmodium* spp. (Telford and Forrester, 1992), should be carefully used for identification of avian malaria parasites, which are of low level specificity. It has been proved experimentally (summarized in Garnham, 1966) that avian malaria parasites' development in different vertebrate hosts can markedly influence the shape and dimensions of blood stages (see, for example p. 600).

A search for new effective taxonomic characters applicable in different taxa is actually an urgent point. One of the main requirements for the new diagnostic characters is the availability of their study in many species of parasites under standard conditions. Only in this case can one compare the stages of development in many species of parasites, the majority of which develop in wild birds including exotic ones, which are accessible only with difficulty for laboratory investigation in captivity. In the case of haemosporidians, we attribute the peculiarities of gametogenesis and development of zygote and ookinete to the group of these characters. This process is easily induced *in vitro* and can be studied in detail under standard conditions (see also Valkiūnas *et al.*, 2002b).

It was found (Valkiūnas and Iezhova, 1993a, 1994, 1995; Iezhova and Valkiūnas, 1995) that the comparative study of gametogenesis, formation of zygote and ookinete in bird haemosporidians allows one to distinguish a series of useful characters, which can be used to make a more accurate and wide definition of the species. Among these characters, the length of microgametes, structure of zygotes, morphological peculiarities of the transformation of zygote into ookinete, the size of ookinetes and the rate of formation of the ookinete *in vitro* should be mentioned first of all. Combinations of these characters in various species of haemoproteids are rather different and informative, which gives a basis to identify many species even without the knowledge of the morphology of the gametocytes in the peripheral blood. This conclusion is illustrated in Table 15 presented in the form of a key for the identification of species, where the main diagnostic characters are given for nine species of bird haemoproteids, which so far have been studied in detail in this aspect. The data of Table 15 illustrate an opportunity to compile the key to the species of haemosporidians in which a set of data about the development of the parasites *in vitro* may be used together with other traditional characters. Further accumulation of information on gametogenesis, and the formation of zygote and ookinete under standard conditions *in vitro* is a promising method to develop more accurate and wider definitions of many species as well as to study their divergence. Molecular biology methods are also a promising technique for such purposes, but they have not been applied in bird haemosporidian taxonomy on the species level so far.

Table 15 Main diagnostic characters of gametes, zygotes and ookinetes of *Haemoproteus balmorali*, *H. belopolskyi*, *H. dolniki*, *H. fringillae*, *H. lanii*, *H. majoris*, *H. minutus*, *H. pallidus*, and *H. tartakovskyi* during their development *in vitro*.

1 (8). The average length of microgametes and fully grown ookinetes is greater than 10 μm.

2 (11). Zygotes do not possess large (2 μm in diameter and larger) 'vacuoles.'

3 (14). The average length of fully grown ookinetes is less than 17 μm. Ookinetes with residual bodies develop more rapidly than in 24 h at temperature of 18 to 20°C.

4 (15). Pigment granules in residual body of ookinete are not aggregated into a large solid mass. Ookinetes with residual bodies develop in 6 to 12 h at temperature of 18 to 20°C.

5(16). Ookinetes possess large (>1 μm in diameter) 'vacuoles.' The average width of fully grown ookinetes is greater than 2.5 μm.

6 (7). Ookinetes with residual bodies and fully grown ookinetes develop in less than 12 h at a temperature of 18 to 20°C.

. . . . . ***H. majoris***

7 (6). Ookinetes with residual bodies and fully grown ookinetes develop in more than 12 h at temperature of 18 to 20°C.

. . . . . ***H. dolniki***

8 (1). The average length of microgametes and fully grown ookinetes is less than 10 μm.

9 (10). Minimum size of macrogametes is less than 5 μm in diameter. Ookinetes possess 'vacuoles.' One end of fully grown ookinete is markedly pointed and the other end rounded.

. . . . . ***H. minutus***

10 (9). Minimum dimension of macrogametes is greater than 5 μm in diameter. Ookinetes do not possess 'vacuoles'. Both ends of fully grown ookinetes are more or less rounded.

. . . . . ***H. pallidus***

11 (2). Zygote possess a large (2 μm in diameter or even larger) 'vacuole.'

12 (13). A finger-like outgrowth develops at the initial stage of ookinete development.

. . . . . ***H. balmorali***

13 (12). A finger-like outgrowth does not develop at the initial stage of ookinete development.

. . . . . ***H. fringillae***

14 (3). The average length of fully grown ookinetes is greater than 17 μm. Ookinetes with residual bodies develop in more than 24 h at temperature of 18 to 20°C.

. . . . . ***H. tartakovskyi***

15 (4). Pigment granules in residual body of ookinete are aggregated into a large solid mass. Ookinetes with residual bodies develop in less than 6 h at temperature of 18 to 20°C.

. . . . . ***H. lanii***

16 (5). Ookinetes do not possess large (>1 μm in diameter) 'vacuoles.' The average width of fully grown ookinetes is less than 2.5 μm.

. . . . . ***H. belopolskyi***

Systematic Section

General Remarks

This section considers all species of bird haemosporidians known by the time the manuscript of this book was completed (see also Appendix 2). The sequence of the taxa belonging to the rank of subgenus and higher is determined by the opinion of the author on their phylogenetic relations. The species within the subgenera are given in chronological order.

As a rule, the descriptions of the species are composed from the following data.

1. Latin name according to the binomial nomenclature with indication of the subgeneric name in parenthesis and the name of the author and date of publication.

2. Main references given immediately after the Latin name include primarily the original description, synonymy and its argumentation, and new combinations. The names of the authors are given in the chronological order. All authors are given and the conjunction 'and' is put before the name of the last author in those cases when the reference is given after the Latin name of the new taxon established in the work. The other bibliographic references are given according to the standard form of this book. The page number, where the main text about the taxon starts, where the general definition of the species is written, or where the specific name is mentioned for the first time (mainly old works) is given after the year of publication and separated by a colon. Arabic numerals written after the page number indicate the number of illustrations that have an important diagnostic value. All synonyms including varieties as well as subspecies not considered in this book are given for each species. We accepted the following arrangement of the synonymy. The references start with the valid name of the taxon in the original combination. The names of the authors not related to the original establishment of the taxon are separated from the name with a colon. Previously allocated names (for example, nom. praeocc., non Kruse, 1890), a reference to a partial correspondence (partim), emendations (emend.), synonyms established earlier (with an equality sign ahead of them), newly established synonyms (syn. nov.) and some other notes are stipulated in parentheses after the bibliographical reference.

3. The type vertebrate host is given according to the original description of the taxon. The order to which the bird species belongs is given in parentheses (see also item 6).

4. Additional vertebrate hosts are distinguished on the basis of the collections, which the author managed to study, and also on the basis of publications containing the information (illustrations, descriptions, indications, etc.) that can, to a certain degree of probability, give grounds to a guess about the correctness of the identification. There are many works in the literature with the lists of 'faunae' for different regions including numerous traditional *nomina nuda* (for example, *Haemoproteus coraciatis* Tartakovsky, 1913; *H. erythropi* Tartakovsky, 1913; *H. meropis* Tartakovsky, 1913, etc.) without any other information about parasites, which can confirm the correctness of the identification. The use of unavailable specific names for naming the parasites takes place

when the work is carried out under the outdated principle, 'one species of parasite corresponds to one vertebrate host or group of hosts,' without sufficient attention to the morphology of the protists. In this case most critical attention should be focused on the lists of 'faunae' including unavailable specific names and not containing any information about the morphology of the parasites. Such works were not taken into account in the determination of the range of additional vertebrate hosts. Nor did we use directly for these purposes the information compiled in catalogs (Bennett *et al.*, 1982b; Bishop and Bennett, 1992), because they comprise a quite complete compilation of specific names of parasites ever mentioned in the literature including incorrect identifications as well as invalid and unavailable names. However, the catalogs mentioned were useful in showing directions how work may proceed. It is not likely that it was possible to avoid all incorrect identifications, while making the lists of additional vertebrate hosts using data from the literature, despite the fact that we spend much time attempting to solve this question. Therefore, one has to be especially critical when reading this section of the species essays. At the same time, taking into account the adequate level of present day knowledge and tendencies to accumulate information about bird haemosporidians, it seems reasonable to publish the results of the analysis performed. Because of the limited size of the manuscript, we had to exclude the lists of vertebrate hosts of the species of haemosporidians developing in a vast number of birds species.

5. Vectors. Natural vectors are listed as well as species, where the parasites develop to the stage of the sporozoites experimentally. The data about the peculiarities of development of haemosporidians in the vectors are analyzed separately (see item 12).

6. The type locality is indicated according to the original description. Neotypes of bird haemosporidians are sometimes designated in contradiction to the recommendations of the International Code of Zoological Nomenclature (1985, 1988). For example, some neotypes came from the places located far beyond the original type locality [frequently even from other zoogeographical regions and (or) from nontype vertebrate hosts]. The validity of certain neotypes listed in this book seems questionable. In each essay on species this problem is discussed separately. In relation to this, the place of origin of such neotypes can be accepted with difficulty as the neotype locality [Recommendation 75B(f), International Code of Zoological Nomenclature, 1985]. This contradiction reflects the actual nomenclatural problems related to the groups of protists studied, which the author could not always solve unambiguously.

7. Geographical distribution is characterised briefly by zoogeographical regions on the basis of the investigation of collections and critical analysis of the literature. A significant part of the species of bird haemosporidians has vast distribution ranges covering several zoogeographical regions. It is noteworthy that the distribution of parasites in the ranges indicated is restricted by the limits of the distribution of their vertebrate hosts and (or) vectors. Unfortunately, at present the data available with rare exceptions are not enough for exact mapping of the ranges of distribution of the species of bird haemosporidians.

8. Type material is given only for the valid name. For the overwhelming majority of species, these are dried fixed blood smears usually stained with Giemsa's stain and containing the stages of parasites' development in the cells of peripheral blood. If other stages of development are designated as type material, this is specifically noted. The following information is usually given for each preparation of the type series: (1) number, (2) name of the vertebrate host, (3) date and (4) place of collection of the material, (5) initials and family name of the collector, (6) place of deposition. In some cases, additional

information is also given (for example, the organs of the localization of exoerythrocytic meronts; species of vectors, where oocysts or other stages of parasite development are isolated from, etc.). The storage place of quality additional materials, which can be used for investigation if necessary, are also given for certain species.

List of abbreviations used for institutions and private collections, where the material is deposited according to the original description of the taxon

ANMS	Australian National Museum, Sydney, Australia
DBZU	Laboratory of Parasitology, Department of Biology, Zhongshan University, Guangzhou, China
GML	Gorgas Memorial Laboratory, Panama
IOCB	Institute Oswaldo Cruz, Rio de Janeiro, Brazil
IRCAH	Queensland Museum, South Brisbane, Australia (collection of the International Reference Center for Avian Haematozoa)
CDSA	Collection of Dr. L. Sacchi, Dipartimento di Biologia Animale, Università di Pavia, Pavia, Italy
CDVA	Collection of Dr. G. Valkiūnas, Institute of Ecology, Vilnius University, Vilnius, Lithuania
CPG	Collection of Prof. P.C.C. Garnham, Department of Zoology, British Museum (Natural History), London, Great Britain
CPGA	Collection of Prof. A. Gabaldon, Instituto Nacional de Higiene, Ministerio de Sanidad y Asistencia Social, Caracas, Venezuela
CPHU	Collection of Prof. F.W. Huchzermeyer, Pathology Section, Veterinary Research Institute, Onderstepoort, Republic of South Africa
CPM	Collection of Prof. R.D. Manwell, Department of Zoology, University of Syracuse, Syracuse, USA
CPW	Collection of Prof. C.M. Wenyon, Department of Zoology, British Museum (Natural History), London, Great Britain
MNHM	Muséum National d'Histoire Naturelle, Paris, France
NHRCB	Parasitology Section, Natural History Research Centre, Baghdad, Iraq
NMNZ	National Museum of New Zealand, Wellington, New Zealand
NZCC	National Zoological Collection, Zoological Survey of India, Calcutta, India
UAPRC	University of Alberta, Parasitology Reference Collection, Alberta, USA
USNPC	United States National Parasite Collection, Beltsville, USA
WMCL	Wellcome Museum Collection, London, Great Britain

9. Etymology.

10. Main diagnostic characters is a brief summary of the main features, which have the primary importance for the identification of species. Combined with the illustrations of parasites given in almost every essay on the species, this information is usually enough for species identification.

11. Development in vertebrate host. This unit includes the peculiarities of the exoerythrocytic development, all stages developed in the blood, relapses, and some other information.

12. Development in the vector is described from gametogenesis, development of zygote and ookinete to sporogony and development of sporozoites.

The information about the morphology of parasites given under items 10 to 12, is almost completely based on the data obtained, when the objects were examined with a light microscope. In this relation, one has to keep in mind that the terminology traditionally used for the description of the species does not always exactly correspond to the ultrastructure of the parasites and their host cells. It is also noteworthy that some of the morphological (and sometimes morphometric) data are not given in the text to maximally reduce the wordy description of the characters, but they can be easily found in the scaled illustrations.

13. P a t h o g e n i c i t y is considered in a very wide meaning of the term: from relations between the host and parasites on the population and organism levels to pathological changes at the level of tissues and even cells. This off-centre approach was chosen with the only objective to concentrate all the main information about the pathogenicity of the species, the majority of which are poorly studied in this aspect.

14. S p e c i f i c i t y. Usually only brief information is given about the experimentally determined range of the vertebrate hosts.

15. S u b s p e c i e s are characterized occasionally using the same scheme as for the species, but much more briefly.

16. C o m m e n t s include the logic of new synonyms, discussion of disputable problems on the taxonomy, nomenclature, comparison of the nearest species, and information about biology and ecology, which is of principal importance.

The species of bird haemosporidians have been studied nonuniformly. Information about the development in vectors as well as pathogenicity, specificity, and subspecies have not been studied for the majority of species. The data on the development in vertebrate hosts are usually limited to the morphology of the stages developing in the blood. Some original descriptions and redescriptions are incomplete, whereas reexamination of the type material was not always possible. Therefore, some of the items listed above are omitted from the essays on many species, or only brief information is given. The most detailed descriptions are given for the parasites that have practical importance.

The description of subgenera and genera is made in the same way as for the species; it includes (1) the valid name accompanied with the author and date of publication, (2) synonyms and the most important bibliographical references, (3) the type species and the method of its fixation, (4) etymology, (5) a brief definition. The description of the families includes: (1) the valid name accompanied with the author and date of publication, (2) the type genus, (3) a brief definition.

The keys to all taxa are compiled using the dichotomous system and are based on a set of characters where possible. We declined the use of polytomous (multi-entry) keys due to their extreme cumbersomeness and the necessity of using many sets of characters for the identification of the species of certain subgenera, first of all the species of the *Parahaemoproteus*. The name of a taxon in the key for its identification is given with the sequential number of the taxon description. The keys for identification of the lower rank taxa are given immediately after the characteristics of the higher rank taxa (the keys to the families are placed after the characteristic of the order, etc.).

Identification of the species of bird haemosporidians is difficult, and is especially complicated for haemoproteids of birds belonging to the Passeriformes and malaria parasites. The identification is based mainly on the characters of the stages of development in the peripheral blood, which is important from the practical point of view. Scaled illustrations of the blood stages (trophozoites, meronts, gametocytes), given in almost every species essay carry the greatest informational value in the identification of species. It is noteworthy that these illustrations include only the most typical cells for each particular

species, which are especially frequently found in preparations of good quality. The keys to the species for most subgenera are compiled for the first time. Unfortunately we could not completely avoid using relative characters (for example, 'usually contains – usually does not contain,' 'characteristic – not characteristic,' 'there is a tendency – there is no tendency,' etc.). Besides, wordy descriptions of certain characters may not always be uniquely understood due to insufficiently unified terminology and a lack of tradition to compile the keys for the haemosporidian species. This situation reflects the present day knowledge about the species and other taxa and is associated with the peculiarities of the structure of the stages of parasite development, on which basis the identification is currently performed (see 'Methods of Species Identification,' p. 229). Many wordy descriptions used in the keys are accompanied with illustrations with the aim to reduce the degree of the probability of misunderstanding while working with the keys to the species.

In conclusion, the reader should be reminded that the data on the morphology of haemosporidians given in the Systematic Section are obtained only using a light microscope. In all cases where the data about the staining of parasites are given, we mean the staining by different modifications of Romanowsky's method (usually Giemsa's stain and other relative stains were used). The cytoplasm of macro- and microgametocytes is usually stained blue and pale blue, and their nuclei are stained red and pink with Giemsa's stain, respectively. These sexual dimorphic characters in gametocytes' staining, which are typical of the great majority of haemosporidian parasites, are not repeated in the essays of species. The other methods of staining and the peculiarities of staining the gametocytes of some species of haemosporidians with Giemsa's stain are given a special note.

Systematic Index of Species[†]

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Class **COCCIDEA** (Leuckart, 1879)
Subclass **COCCIDIA** (Leuckart, 1879)
Order **HAEMOSPORIDA** (Danilewsky, 1885)

I. Family **HAEMOPROTEIDAE** Doflein, 1916

1. Genus **Haemoproteus** Kruse, 1890

1. Subgenus **Parahaemoproteus** Bennett, Garnham and Fallis, 1965

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25. *H. (P.) coraciae* Mello and Afonso, 1935 335
26. *H. (P.) dicruri* Mello, 1935 338
27. *H. (P.) elani* Mello, 1935 339
28. *H. (P.) gallinulae* Mello, 1935 342
29. *H. (P.) halcyonis* Mello, 1935 343
30. *H. (P.) herodiadis* Mello, 1935 345
31. *H. (P.) orioli* Mello, 1935 348
32. *H. (P.) otocompsae* Mello, 1935 350
33. *H. (P.) pastoris* Mello, 1935 352
34. *H. (P.) plataleae* Mello, 1935 355
35. *H. (P.) thereicerycis* Mello, 1935 358
36. *H. (P.) upupae* Mello, 1935 360
37. *H. (P.) lanii* Mello, 1936 361
38. *H. (P.) rileyi* Malkani, 1936 367
39. *H. (P.) fuscae* Mello and Fonseca, 1937 369
40. *H. (P.) picae* Coatney and Roudabush, 1937 372
41. *H. (P.) velans* Coatney and Roudabush, 1937 375
42. *H. (P.) archilochus* Coatney and West, 1938 379
43. *H. (P.) quiscalus* Coatney and West, 1938 381
44. *H. (P.) handai* Maqsood, 1943 383
45. *H. (P.) meropis* Zargar, 1945 386
46. *H. (P.) sanguinis* Chakravarty and Kar, 1945 387
47. *H. (P.) xantholaemae* Zargar, 1945 390
48. *H. (P.) zosteropis* Chakravarty and Kar, 1945 391
49. *H. (P.) pelouroi* Tendeiro, 1946 394
50. *H. (P.) borgesi* Tendeiro, 1947 395
51. *H. (P.) buteonis* Wingstrand, 1947 397
52. *H. (P.) pratasi* Tendeiro, 1947 400
53. *H. (P.) sequeirae* Tendeiro, 1947 401
54. *H. (P.) globulosus* Covaleda Ortega and Gállego Berenguer, 1950 403
55. *H. (P.) macropigmentatus* Covaleda Ortega and Gállego Berenguer, 1950 405
56. *H. (P.) montezi* Travassos Santos Dias, 1953 406
57. *H. (P.) enucleator* Bennett, Okia, Ashford and Campbell, 1972 408
58. *H. (P.) fallisi* Bennett and Campbell, 1972 410
59. *H. (P.) larae* Yakunin, 1972 412
60. *H. (P.) balearicae* Peirce, 1973 415
61. *H. (P.) caprimulgi* Williams, Bennett and Mahrt, 1975 417
62. *H. (P.) telfordi* Bennett, Forrester, Greiner and Campbell, 1975 418
63. *H. (P.) bennetti* Greiner, Mandal and Nandi, 1977 420
64. *H. (P.) lairdi* Bennett, 1978 422
65. *H. (P.) manwelli* Bennett, 1978 424
66. *H. (P.) ortalidum* Gabaldon and Ulloa, 1978 425
67. *H. (P.) stellaris* White and Bennett, 1978 429
68. *H. (P.) contortus* Bennett, 1979 430
69. *H. (P.) janovyi* Greiner and Mundy, 1979 431
70. *H. (P.) rotator* Bennett, 1979 434
71. *H. (P.) stableri* White and Bennett, 1979 435

72. *H. (P.) trochili* White, Bennett and Williams, 1979 437
73. *H. (P.) witti* White, Bennett and Williams, 1979 438
74. *H. (P.) abdusalomovi* Subkhonov, 1980 439
75. *H. (P.) ammoperdix* Subkhonov, 1980 441
76. *H. (P.) megapodius* Nandi and Mandal, 1980 443
77. *H. (P.) bilobata* Bennett and Nandi, 1981 444
78. *H. (P.) cornuata* Bennett and Nandi, 1981 446
79. *H. (P.) killangoi* Bennett and Peirce, 1981 448
80. *H. (P.) cracidarum* Bennett, Gabaldon and Ulloa, 1982 450
81. *H. (P.) nisi* Peirce and Marquiss, 1983 452
82. *H. (P.) balmorali* Peirce, 1984 454
83. *H. (P.) cublae* Peirce, 1984 459
84. *H. (P.) greineri* Bennett, Turner and Whiteway, 1984 460
85. *H. (P.) apodus* Bennett, Caines and Whiteway, 1986 462
86. *H. (P.) bucconis* Bennett, Caines and Whiteway, 1986 465
87. *H. (P.) circumnuclearis* Bennett, Caines and Whiteway, 1986 467
88. *H. (P.) eurystomae* Bishop and Bennett, 1986 468
89. *H. (P.) indicator* Bennett, Caines and Whiteway, 1986 470
90. *H. (P.) souzalopesi* Bennett, Caines and Whiteway, 1986 472
91. *H. (P.) tartakovskyi* Valkiūnas, 1986 474
92. *H. (P.) tyranni* Bennett, Caines and Whiteway, 1986 478
93. *H. (P.) formicarius* Bennett, Caines and Woodworth-Lynas, 1987 481
94. *H. (P.) furnarius* Bennett, Caines and Woodworth-Lynas, 1987 482
95. *H. (P.) philippinensis* Rahal, Bishop and Bennett, 1987 485
96. *H. (P.) vireonis* Bennett, Caines and Woodworth-Lynas, 1987 487
97. *H. (P.) attenuatus* Valkiūnas, 1989 489
98. *H. (P.) belopolskyi* Valkiūnas, 1989 492
99. *H. (P.) brachiatus* Valkiūnas and Iezhova, 1989 497
100. *H. (P.) parus* Bennett, 1989 499
101.*H. (P.) sittae* Bennett, 1989 501
102. *H. (P.) dicaeus* Bennett and Bishop, 1990 503
103. *H. (P.) gavrilovi* Valkiūnas and Iezhova, 1990 506
104. *H. (P.) motacillae* Bennett and Peirce, 1990 508
105. *H. (P.) nucleophilus* Bennett and Bishop, 1990 511
106. *H. (P.) trogonis* Bennett and Peirce, 1990 513
107. *H. (P.) africanus* Bennett and Peirce, 1991 515
108. *H. (P.) bubalornis* Bennett and Peirce, 1991 517
109. *H. (P.) eurylaimus* Bennett, Bishop and Peirce, 1991 519
110. *H. (P.) monarchus* Bennett, Bishop and Peirce, 1991 521
111. *H. (P.) nipponensis* Bennett, Bishop and Peirce, 1991 523
112. *H. (P.) pachycephalus* Bennett, Bishop and Peirce, 1991 525
113. *H. (P.) pallidus* Valkiūnas and Iezhova, 1991 527
114. *H. (P.) pittae* Bennett, Bishop and Peirce, 1991 532
115. *H. (P.) timalus* Bennett, Bishop and Peirce, 1991 534
116. *H. (P.) uraeginthus* Bennett and Peirce, 1991 537
117. *H. (P.) calandrellae* Valkiūnas and Iezhova, 1992 539
118. *H. (P.) coatneyi* Burry-Caines and Bennett, 1992 540
119. *H. (P.) dolniki* Valkiūnas and Iezhova, 1992 544

120. *H. (P.) magnus* Valkiūnas and Iezhova, 1992 549
121. *H. (P.) minutus* Valkiūnas and Iezhova, 1992 550
122. *H. (P.) neseri* Bennett and Earlé, 1992 555
123. *H. (P.) psittaci* Bennett and Peirce, 1992 556
124. *H. (P.) undulatus* Bennett and Earlé, 1992 559
125. *H. (P.) kairullaevi* Valkiūnas and Iezhova, 1993 560
126. *H. (P.) payevskyi* Valkiūnas, Iezhova and Chernetsov 1994 564

2. Subgenus **Haemoproteus** Kruse, 1890

127. *H. (H.) columbae* Kruse, 1890 567
128. *H. (H.) sacharovi* Novy and MacNeal, 1904 575
129. *H. (H.) turtur* Covaleda Ortega and Gállego Berenguer, 1950 577
130. *H. (H.) palumbis* Baker, 1966 581
131. *H. (H.) krylovi* Subkhonov, 1980 584
132. *H. (H.) pteroclis* Shamsuddin and Mohammad, 1980 586

II. Family **PLASMODIIDAE** Mesnil, 1903

1. Genus **Plasmodium** Marchiafava and Celli, 1885

1. Subgenus **Haemamoeba** Grassi and Feletti, 1890

1. *P. (H.) relictum* (Grassi and Feletti, 1891) 592
2. *P. (H.) subpraecox* (Grassi and Feletti, 1892) 597
3. *P. (H.) cathemerium* Hartman, 1927 600
4. *P. (H.) gallinaceum* Brumpt, 1935 605
5. *P. (H.) matutinum* Huff, 1937 612
6. *P. (H.) lutzi* Lucena, 1939 616
7. *P. (H.) giovannolai* Corradetti, Veroni and Neri, 1963 619
8. *P. (H.) griffithsi* Garnham, 1966 623
9. *P. (H.) tejerai* Gabaldon and Ulloa, 1977 625
10. *P. (H.) coturnixi* Bano and Abbasi, 1983 628

2. Subgenus **Giovannolaia** Corradetti, Garnham and Laird, 1963

11. *P. (G.) fallax* Schwetz, 1930 633
12. *P. (G.) circumflexum* (Kikuth, 1931) 637
13. *P. (G.) polare* Manwell, 1934 642
14. *P. (G.) lophurae* Coggeshall, 1938 646
15. *P. (G.) durae* Herman, 1941 650
16. *P. (G.) pedioecetae* Shillinger, 1942 653
17. *P. (G.) pinottii* Muniz and Soares, 1954 656
18. *P. (G.) formosanum* Manwell, 1962 660
19. *P. (G.) gundersi* (Bray, 1962) 662
20. *P. (G.) anasum* Manwell and Kuntz, 1965 665
21. *P. (G.) garnhami* Guindy, Hoogstraal and Mohammed, 1965 667
22. *P. (G.) hegneri* Manwell and Kuntz, 1966 671
23. *P. (G.) octamerium* Manwell, 1968 673
24. *P. (G.) gabaldoni* Garnham, 1977 677
25. *P. (G.) leanucleus* Huang, 1991 680

3. Subgenus **Novyella** Corradetti, Garnham and Laird, 1963

26. *P. (N.) vaughani* Novy and MacNeal, 1904 684
27. *P. (N.) columbae* Carini, 1912 690
28. *P. (N.) rouxi* Sergent, Sergent and Catanei, 1928 692
29. *P. (N.) hexamerium* Huff, 1935 696
30. *P. (N.) nucleophilum* Manwell, 1935 699
31. *P. (N.) dissanaikei* Jong, 1971 702
32. *P. (N.) paranucleophilum* Manwell and Sessler, 1971 705
33. *P. (N.) bertii* Gabaldon and Ulloa, 1981 708
34. *P. (N.) kempi* Christensen, Barnes and Rowley, 1983 711

4. Subgenus **Bennettinia** Valkiūnas, 1997

35. *P. (B.) juxtanucleare* Versiani and Gomes, 1941 714

5. Subgenus **Huffia** Corradetti, Garnham and Laird, 1963

36. *P. (Hu.) elongatum* Huff, 1930 720
37. *P. (Hu.) huffi* Muniz, Soares and Batista, 1951 724
38. *P. (Hu.) hermani* Telford and Forrester, 1975 728

III. Family **GARNIIDAE** Lainson, Landau and Shaw, 1971

1. Genus **Fallisia** Lainson, Landau and Shaw, 1974

1. Subgenus **Plasmodioides** Gabaldon, Ulloa and Zerpa, 1985

1. *F. (P.) neotropicalis* Gabaldon, Ulloa and Zerpa, 1985 731

IV. Family **LEUCOCYTOZOIDAE** Fallis and Bennett, 1961

1. Genus **Leucocytozoon** Berestneff, 1904

1. Subgenus **Leucocytozoon** Berestneff, 1904

1. *L. (L.) danilewskyi* (Ziemann, 1898) 741
2. *L. (L.) majoris* (Laveran, 1902) 746
3. *L. (L.) smithi* (Laveran and Lucet, 1905) 748
4. *L. (L.) neavei* (Balfour, 1906) 752
5. *L. (L.) lovati* Seligman and Sambon, 1907 754
6. *L. (L.) berestneffi* Sambon, 1908 758
7. *L. (L.) macleani* Sambon, 1908 764
8. *L. (L.) sakharoffi* Sambon, 1908 767
9. *L. (L.) toddi* Sambon, 1908 772
10. *L. (L.) fringillinarum* Woodcock, 1910 777
11. *L. (L.) marchouxi* Mathis and Léger, 1910 783
12. *L. (L.) simondi* Mathis and Léger, 1910 785
13. *L. (L.) dubreuili* Mathis and Léger, 1911 796
14. *L. (L.) leboeufi* Mathis and Léger, 1911 802
15. *L. (L.) legeri* França, 1912 804
16. *L. (L.) struthionis* Walker, 1912 805

17. *L. (L.) caprimulgi* Kerandel, 1913 807
18. *L. (L.) eurystomi* Kerandel, 1913 809
19. *L. (L.) schoutedeni* Rodhain, Pons, Vandenbranden and Bequaert, 1913 811
20. *L. (L.) centropi* Fantham, 1921 814
21. *L. (L.) vandenbrandeni* Rodhain, 1931 815
22. *L. (L.) dizini* Tendeiro, 1947 817
23. *L. (L.) sousadiasi* Tendeiro, 1947 818
24. *L. (L.) cheissini* Krylov and Trjapicina, 1965 819
25. *L. (L.) grusi* Bennett, Khan and Campbell, 1974 820
26. *L. (L.) maccluri* Greiner, 1976 822
27. *L. (L.) tawaki* Fallis, Bisset and Allison, 1976 824
28. *L. (L.) nycticoraxi* Shamsuddin and Mohammad, 1980 829
29. *L. (L.) balmorali* Peirce, 1984 830
30. *L. (L.) nyctyornis* Nandi, 1986 833
31. *L. (L.) squamatus* Nandi, 1986 834
32. *L. (L.) communis* Valkiūnas, 1989 836
33. *L. (L.) bennetti* Valkiūnas, 1993 838
34. *L. (L.) colius* Bennett, Earlé, Peirce and Nandi, 1993 841

2. Subgenus **Akiba** Bennett, Garnham and Fallis, 1965

35. *L. (A.) caulleryi* Mathis and Léger, 1909 843

Order HAEMOSPORIDA (Danilewsky, 1885)

Obligate heteroxenous. Merogony takes place in the blood cells and (or) fixed tissues of vertebrate hosts. Gametocytes develop in blood cells; are characterized by sexually dimorphic characters. Sexual process and sporogony take place in blood-sucking dipterans (Insecta: Diptera). Gametogenesis occurs outside the cells. Syzygy is absent. Each microgametocyte produces eight microgametes, and each macrogametocyte forms one macrogamete. Zygote transforms into motile ookinete. During development, oocyst changes in size. Spores are absent. Sporozoites concentrate in the salivary glands of the vector. Infection of vertebrate hosts takes place actively.

KEY TO THE FAMILIES

1 (4). Merogony occurs in blood cells.

2 (3). Malarial pigment (hemozoin) is present in meronts, which develop in blood cells, and in gametocytes, but it can be absent in some species during development in immature erythrocytes.

II. **Plasmodiidae**

3 (2). Malarial pigment is absent at all stages.

III. **Garniidae**

4 (1). Merogony does not occur in blood cells.

5 (6). Malarial pigment is present in gametocytes.

I. **Haemoproteidae**

6 (5). Malarial pigment is absent at all stages.

IV. **Leucocytozoidae**

I. Family **HAEMOPROTEIDAE** Doflein, 1916

Type genus. *Haemoproteus* Kruse, 1890.

Merogony takes place in cells of fixed tissues of vertebrate hosts. No merogony occurs in blood cells. Malarial pigment (hemozoin) is present in gametocytes. Sexual process and sporogony take place in hippoboscid and nycteribiid flies (Diptera: Hippoboscidae, Nycteribiidae), biting midges (Ceratopogonidae), and tabanid flies (Tabanidae).

Representatives of the genus *Haemoproteus* parasitize birds.

1. Genus **HAEMOPROTEUS** Kruse, 1890

Haemoproteus Kruse, 1890: 370. – *Haemamoeba* Grassi and Feletti, 1890b: 6 (partim). – *Laverania* Grassi and Feletti, 1890b: 6 (partim). – *Halteridium* Labbé, 1894: 129. – *Haemocystidium* Castellani and Willey, 1904: 84. – *Haemoproteus*: Castellani and Chalmers, 1910: 235 (=*Halteridium*, *Laverania*); Coatney, 1936: 88 (=*Haemocystidium*); Bhatia, 1938: 211 (=*Haemamoeba*). – *Parahaemoproteus* Bennett, Garnham and Fallis, 1965: 930. – *Haemoproteus*: Levine and Campbell, 1971: 476 (=*Parahaemoproteus*).

Type species. *Haemoproteus columbae* Kruse, 1890, according to subsequent designation (Bennett *et al.*, 1965).

Characteristics of the family. Gametocytes develop in erythrocytes. Sexual process and sporogony take place in biting midges (Ceratopogonidae) and hippoboscid flies (Hippoboscidae).

Representatives of two subgenera, *Parahaemoproteus* and *Haemoproteus*, parasitize birds.

KEY TO THE SUBGENERA

1 (2). Parasites of birds belonging to orders other than the Columbiformes. Sporogony takes place in biting midges (Ceratopogonidae). Exflagellation occurs at temperatures below 20°C. The diameter of fully grown oocysts is less than 20 μm. The average length of sporozoites is greater than 10 μm. Both ends of the sporozoites are approximately equally pointed.

1. ***Parahaemoproteus***

2 (1). Parasites of birds belonging to the Columbiformes. Sporogony takes place in hippoboscid flies (Hippoboscidae). Exflagellation does not occur at temperatures below 20°C. The diameter of fully grown oocysts is greater than 20 μm. The average length of sporozoites is less than 10 μm. One end of the sporozoites is more pointed than the other.

2. ***Haemoproteus***

1. Subgenus **PARAHAEMOPROTEUS** Bennett, Garnham and Fallis, 1965

Parahaemoproteus Bennett, Garnham and Fallis, 1965: 930 (pro gen.).

Type species. *Haemoproteus danilewskii* Kruse, 1890, according to the original designation.
Etymology. The subgeneric name reflects the closeness of the parasites to species of the subgenus *Haemoproteus*.

Vertebrate hosts are birds belonging to orders other than the Columbiformes. Sporogony takes place in biting midges (Ceratopogonidae). Exflagellation occurs at temperatures below 20°C. The diameter of fully grown oocysts is less than 20 μm. One germinative centre and less than 100 sporozoites develop in the oocysts. The average length of sporozoites is usually greater than 10 μm. Both ends of the sporozoites are approximately equally pointed.

KEY TO THE SPECIES

1. Vertebrate hosts:

1a (2). Anseriformes
1b (5). Apodiformes
1c (12). Caprimulgiformes
1d (13). Charadriiformes
1e (22). Ciconiiformes
1f (29). Coliiformes
1g (30). Coraciiformes, including the Upupidae
1h (49). Cuculiformes, Musophagiformes
1i (52). Falconiformes
1j (63). Galliformes
1k (80). Gruiformes
1l (89). Passeriformes
1m (214). Piciformes
1n (231). Psittaciformes
1p (234). Strigiformes
1r (237). Trogoniformes
1s (238). Pelecaniformes

2 (1a). Vertebrate hosts: A n s e r i f o r m e s.

3 (4). Fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally; they markedly enclose the nucleus with their ends and can completely encircle the nucleus. The average NDR is 0.5 or greater.
. . . . . 84. ***H. greineri***

4 (3). Fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally; they usually slightly enclose the nucleus with their ends but do not completely encircle the nucleus. The average NDR is less than 0.5.
. . . . . 10. ***H. nettionis***

5 (1b). Vertebrate hosts: A p o d i f o r m e s.

6 (10). Fully grown gametocytes do not completely encircle the nucleus of infected erythrocytes.

7 (11). The average number of pigment granules in gametocytes is less than 18.

8 (9). Growing gametocytes of dumbbell-like shape (Fig. 57, *6*) are present.
. . . . . 85. ***H. apodus***

9 (8). Growing gametocytes of dumbbell-like shape (Fig. 57, *6*) are absent.
. . . . . 72. ***H. trochili***

10 (6). Fully grown gametocytes completely encircle the nucleus of infected erythrocytes and occupy all available cytoplasmic space in the erythrocytes (Fig. 57, *7*).
. . . . . 42. ***H. archilochus***

11 (7). The average number of pigment granules in gametocytes is greater than 18.
. . . . . 73. ***H. witti***

12 (1c). Vertebrate hosts: Caprimulgiformes. One species has so far been described.
. . . . . 61. ***H. caprimulgi***

13 (1d). Vertebrate hosts: Charadriiformes. See also Appendix 2.

14 (15). Fully grown gametocytes, which rotate erythrocyte nuclei 45 to 90° to the normal axis (Fig. 57, *8*), are present.
. . . . . 70. ***H. rotator***

15 (14). Fully grown gametocytes, which rotate erythrocyte nuclei 45 to 90° to the normal axis (Fig. 57, *8*), are absent.

16 (20). Fully grown gametocytes, which completely encircle the nucleus of erythrocytes, are present. Large (1.0 to 1.5 μm) pigment granules are absent in gametocytes.

17 (21). Fully grown gametocytes are closely appressed to the nucleus of erythrocytes and occupy all available cytoplasmic space in the erythrocytes (Fig. 57, *7*).

18 (19). The maximum number of pigment granules in macrogametocytes is less than 30. Infected erythrocytes are significantly hypertrophied in length in comparison to uninfected ones.
. . . . . 19. ***H. scolopaci***

19 (18). The maximum number of pigment granules in macrogametocytes is greater than 30. Infected erythrocytes are not changed significantly in comparison to uninfected ones.
. . . . . 59. ***H. larae***

20 (16). Fully grown gametocytes, which completely encircle the nucleus of erythrocytes, are absent. Large (1.0 to 1.5 μm) pigment granules are present in gametocytes.
. . . . . 74. ***H. abdusalomovi***

21 (17). Fully grown gametocytes do not touch the nucleus of infected erythrocytes and do not occupy all available cytoplasmic space in the erythrocytes. A clear unfilled space (a 'cleft') is present between the fully grown gametocyte and the erythrocyte nucleus (Fig. 57, *9*).
. . . . . 68. ***H. contortus***

22 (1e). Vertebrate hosts: Ciconiiformes.

23 (27). Gametocytes, which completely encircle the nucleus of erythrocytes (Fig. 57, *7*, *9*), are absent. The average number of pigment granules in macrogametocytes is less than 25. Fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally. The average NDR is 0.5 or greater.

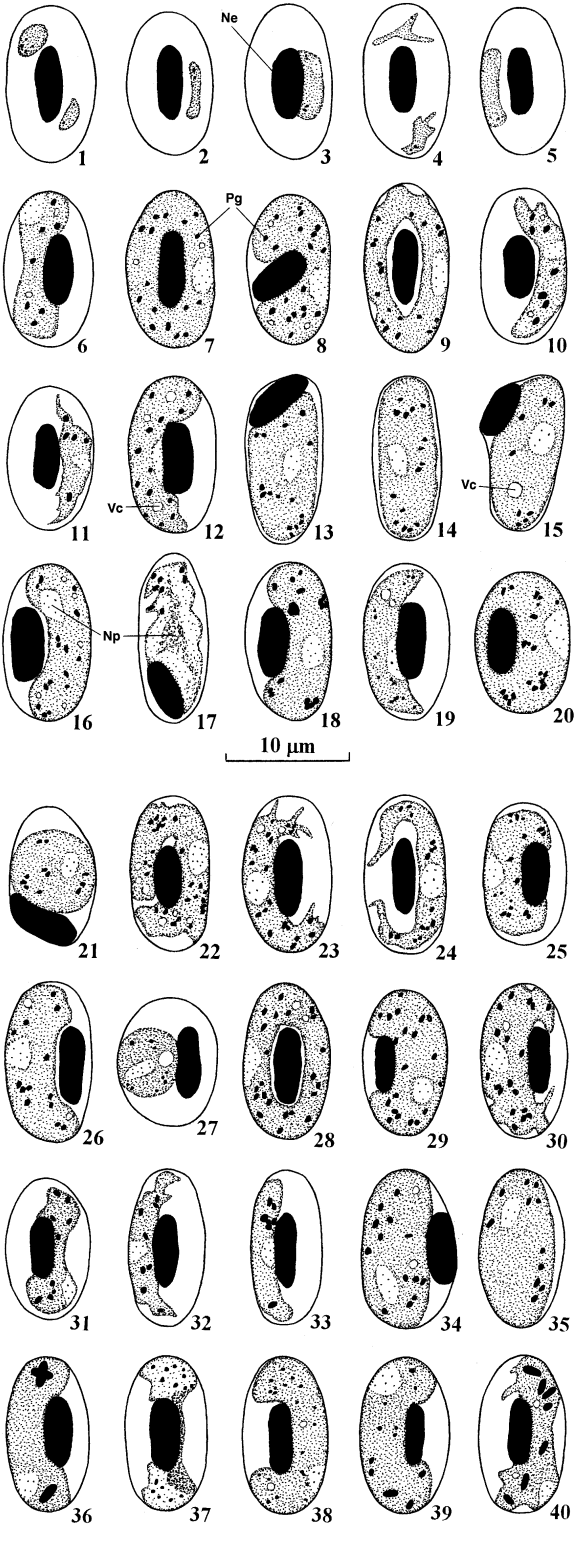
24 (28). Fully grown gametocytes do not fill the infected erythrocytes up to their poles (Fig. 57, *10*). The average number of pigment granules in macro- and microgametocytes is approximately the same.

25 (26). Gametocytes with a highly ameboid outline (Fig. 57, *11*) are present. Oval medium-size (0.5 to 1.0 μm) pigment granules are present in gametocytes.
. . . . . 49. ***H. pelouroi***

26 (25). Gametocytes with a highly ameboid outline (Fig. 57, *11*) are absent. Oval medium-size (0.5 to 1.0 μm) pigment granules are absent in gametocytes.
. . . . . 30. ***H. herodiadis***

27 (23). Gametocytes, which completely encircle the nucleus of erythrocytes (Fig. 57, *7*), are occasionally present. The average number of pigment granules in macrogametocytes is greater than 25. Fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally. The average NDR is less than 0.5.
. . . . . 34. ***H. plataleae***

28 (24). Fully grown gametocytes fill the infected erythrocytes up to their poles (Fig. 57, *12*). The average number of pigment granules in macrogametocytes is approximately 1.5 to 2 times greater than in microgametocytes.
. . . . . 7. ***H. crumenium***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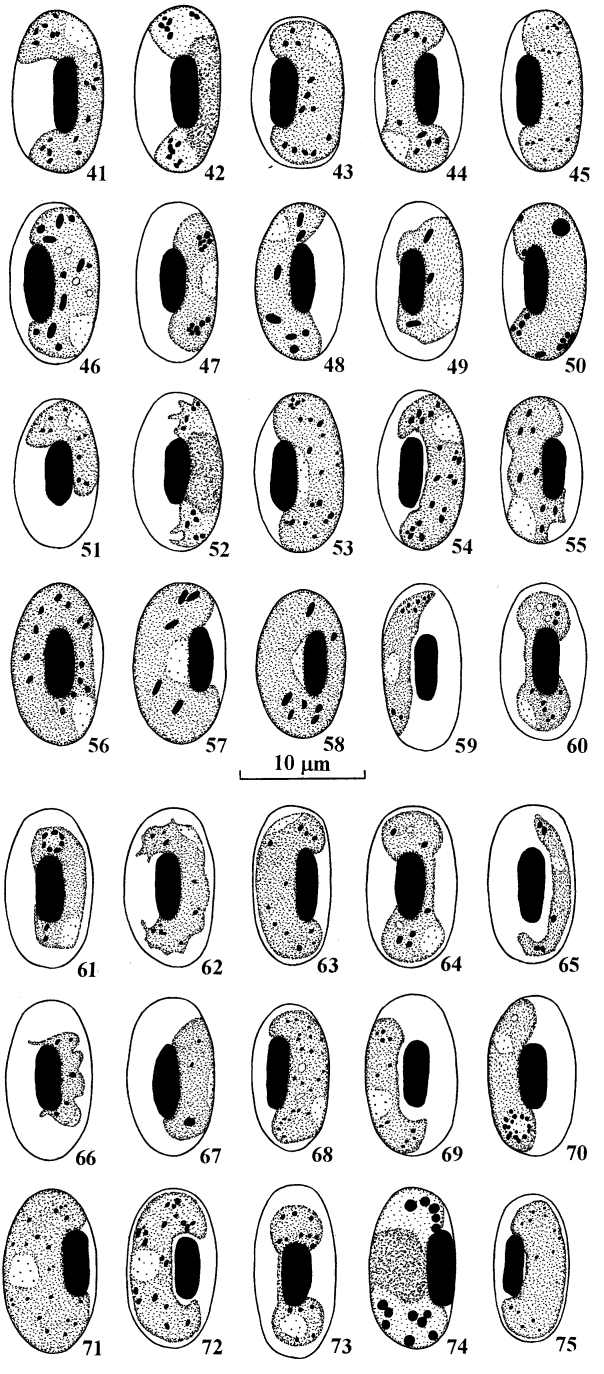

Figure 57 Main morphological peculiarities of the structure of *Haemoproteus* spp. gametocytes as well as the location of the parasites in the infected erythrocytes, which are used for identification of the species:
Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Vc – vacuole. Explanations are given in the text.

29 (1f). Vertebrate hosts: Coliiformes. One species has so far been described.
. . . . . 124. ***H. undulatus***

30 (1g). Vertebrate hosts: Coraciiformes, including the Upupidae. See also Appendix 2.

31 (36). Fully grown gametocytes, which displace the nucleus of infected erythrocytes towards one pole of the erythrocytes (Fig. 57, *13*, *15*, *17*) and finally enucleate the host cells (Fig. 57, *14*), are present.

32 (35). The average number of pigment granules in gametocytes is greater than 11. Macrogametocytes usually do not possess a clear large (>1 μm in diameter) vacuole. Microgametocytes with a highly ameboid outline (Fig. 57, *17*) are uncharacteristic.

33 (34). Erythrocytes with fully grown gametocytes are significantly atrophied in width in comparison to uninfected erythrocytes.
. . . . . 64. ***H. lairdi***

34 (33). Erythrocytes with fully grown gametocytes are not significantly atrophied in width in comparison to uninfected erythrocytes.
. . . . . 57. ***H. enucleator***

35 (32). The average number of pigment granules in gametocytes is less than 11. Macrogametocytes frequently possess one clear large (>1 μm in diameter) vacuole (Fig. 57, *15*). Microgametocytes with a highly ameboid outline (Fig. 57, *17*) are common.
. . . . . 103. ***H. gavrilovi***

36 (31). Fully grown gametocytes, which displace the nucleus of infected erythrocytes toward one pole of the erythrocytes (Fig. 57, *13*, *15*, *17*) and finally enucleate the erythrocytes (Fig. 57, *14*), are absent.

37 (48). The form and size of pigment granules in macro- and microgametocytes are approximately the same.

38 (41). Fully grown gametocytes markedly enclose the nucleus of infected erythrocytes with their ends (Fig. 57, *38*), and can completely encircle it.

39 (40). Fully grown macro- and microgametocytes completely encircle the nucleus of infected erythrocytes. The average number of pigment granules in gametocytes is greater than 20.
. . . . . 39. ***H. fuscae***

40 (39). Fully grown macro- and microgametocytes markedly enclose the nucleus of infected erythrocytes with their ends. Microgametocytes can completely encircle the nucleus of erythrocyte. The average number of pigment granules in gametocytes is less than 20.
. . . . . 25. ***H. coraciae***

41 (38). Fully grown gametocytes only slightly enclose the nucleus of infected erythrocytes with their ends (Fig. 57, *16*) and never encircle it completely.

42 (46). The average width of fully grown gametocytes is greater than 4 μm. The average NDR is 0.5 or less.

43 (47). The average number of pigment granules in gametocytes is greater than 15.

44 (45). Fully grown gametocytes, which do not touch the nucleus of infected erythrocytes and thus form a more or less pronounced unfilled space (a 'cleft') between the parasite and the nucleus of erythrocytes (Fig. 57, *16*), are present and common.
. . . . . 29. ***H. halcyonis***

45 (44). Fully grown gametocytes, which do not touch the nucleus of infected erythrocytes and thus form a more or less pronounced unfilled space (a 'cleft') between the parasite and the nucleus of erythrocytes (Fig. 57, *16*), are absent or are extremely rare.
. . . . . 88. ***H. eurystomae***

46 (42). The average width of fully grown gametocytes is less than 4 μm. The average NDR is greater than 0.5.
. . . . . 45. ***H. meropis***

47 (43). The average number of pigment granules in gametocytes is less than 15.
. . . . . 65. ***H. manwelli***

48 (37). The form and size of pigment granules in macro- and microgametocytes are clearly different. Fully grown gametocytes markedly enclose the nucleus of infected erythrocytes with their ends and are closely appressed to the nucleus.
. . . . . 36. ***H. upupae***

49 (1h). Vertebrate hosts: Cuculiformes, Musophagiformes.

50 (51). Pigment granules in fully grown gametocytes tend to aggregate into compact large masses or loosely aggregated clumps. The ends of the gametocytes are rounded (Fig. 57, *18*).
. . . . . 24. ***H. centropi***

51 (50). Pigment granules in fully grown gametocytes do not tend to aggregate into compact large masses or loosely aggregated clumps (Fig. 57, *18*). The ends of the gametocytes are narrowed (Fig. 57, *19*).
. . . . . 56. ***H. montezi***

52 (1i). Vertebrate hosts: Falconiformes.

53 (60). Fully grown gametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*, *9*, *20*, *28*), are present.

54 (57). Fully grown gametocytes, which occupy all available cytoplasmic space in infected erythrocytes (Fig. 57, *7*, *20*), are present.

55 (56). Staining of cytoplasm of macro- and microgametocytes is similar. Roundish (discoid) gametocytes (Fig. 57, *21*) are present.
. . . . . 69. ***H. janovyi***

56 (55). Staining of cytoplasm of macro- and microgametocytes is clearly different. Roundish (discoid) gametocytes (Fig. 57, *21*) are absent.
. . . . . 17. ***H. tinnunculi***

57 (54). Fully grown gametocytes, which occupy all available cytoplasmic space in infected erythrocytes (Fig. 57, *7*, *20*), are absent.

58 (59). The majority of gametocytes are characterized by clear finger-like ameboid outgrowths (Fig. 57, *23*). Over 50% of mature gametocytes are closely appressed to the nucleus of infected erythrocytes.
. . . . . 99. ***H. brachiatus***

59 (58). The majority of gametocytes are without clear finger-like ameboid outgrowths (Fig. 57, *23*). Over 50% of mature gametocytes do not touch the nucleus of infected erythrocytes (Fig. 57, *24*).
. . . . . 81. ***H. nisi***

60 (53). Fully grown gametocytes, which encircle the nucleus of infected erythrocytes completely (Fig. 57, *7*, *9*, *20*, *28*), are absent.

61 (62). Gametocytes are closely appressed to the nucleus of infected erythrocytes. Fully grown gametocytes do not fill the erythrocytes up to their poles (Fig. 57, *25*).
. . . . . 51. ***H. buteonis***

62 (61). Gametocytes are characterized by their variable contact with the nucleus of infected erythrocytes; together with mature gametocytes, which are closely appressed to the nucleus of erythrocytes, the mature gametocytes, which do not touch the nucleus or touch it only in some points, are common (Fig. 57, *26*). Fully grown gametocytes fill the infected erythrocytes up to their poles (Fig. 57, *26*).
. . . . . 27. ***H. elani***

63 (1j). Vertebrate hosts: Galliformes.

64 (79). Fully grown gametocytes of roundish (discoid) form (Fig. 57, *21*, *27*) are absent.

65 (70). Fully grown gametocytes encircle the nucleus of infected erythrocytes completely (Fig. 57, *7*, *28*).

66 (69). Fully grown gametocytes do not occupy all available cytoplasmic space in infected erythrocytes (Fig. 57, *28*), and a more or less evident unfilled space (a 'cleft') is present between the fully grown gametocyte and the nucleus of erythrocyte.

67 (68). The average number of pigment granules in macrogametocytes is greater than 15.
. . . . . 18. ***H. lophortyx***

68 (67). The average number of pigment granules in macrogametocytes is less than 15.
. . . . . 71. ***H. stableri***

69 (66). Fully grown gametocytes occupy all available cytoplasmic space in infected erythrocytes (Fig. 57, *7*), and an unfilled space (a 'cleft') (Fig. 57, *28*) is not present between the fully grown gametocyte and the nucleus of the erythrocyte.
. . . . . 13. ***H. mansoni***

70 (65). Fully grown gametocytes do not encircle the nucleus of infected erythrocytes completely.

71 (77). The average number of pigment granules in macrogametocytes is greater than 15.

72 (78). The outline of fully grown gametocytes is even (Fig. 57, *29*).

73 (76). Gametocytes with a highly constricted central portion, causing a 'dip' and giving a dumbbell-like appearance (Fig. 57, *6*), are absent.

74 (75). Fully grown macrogametocytes markedly displace the nucleus of infected erythrocytes laterally; the average NDR is less than 0.7.
. . . . . 52. ***H. pratasi***

75 (74). Fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally; the average NDR is greater than 0.7.
. . . . . 75. ***H. ammoperdix***

76 (73). Gametocytes with a highly constricted central portion, causing a 'dip' and giving a dumbbell-like appearance (Fig. 57, *6*), are present.
. . . . . 76. ***H. megapodius***

77 (71). The average number of pigment granules in macrogametocytes is less than 15.
. . . . . 38. ***H. rileyi***

78 (72). The outline of fully grown gametocytes is highly ameboid (Fig. 57, *30*).
. . . . . 80. ***H. cracidarum***

79 (64). Fully grown gametocytes of roundish (discoid) form (Fig. 57, *27*) are present.
. . . . . 66. ***H. ortalidum***

80 (1k). Vertebrate hosts: G r u i f o r m e s.

81 (86). Fully grown gametocytes, which completely encircle the nucleus of infected erythrocytes, are absent.

82 (87). The average number of pigment granules in macrogametocytes is less than 25.

83 (88). The average number of pigment granules in macrogametocytes is less than 12. The average NDR is greater than 0.5.

84 (85). Dumbbell-shaped gametocytes (Fig. 57, *31*) are present.
. . . . . 9. ***H. porzanae***

85 (84). Dumbbell-shaped gametocytes (Fig. 57, *31*) are absent. The gametocytes are elongated and slender (Fig. 57, *32*, *33*).
. . . . . 60. ***H. balearicae***

86 (81). Fully grown gametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*), are present.
. . . . . 62. ***H. telfordi***

87 (82). The average number of pigment granules in macrogametocytes is greater than 25.
. . . . . 28. ***H. gallinulae***

88 (83). The average number of pigment granules in macrogametocytes is greater than 12. The average NDR is 0.5 or less. . . . . 22. ***H. antigonis***

89 (11). Vertebrate hosts: P a s s e r i f o r m e s.

90 (160). Fully grown gametocytes of roundish (discoid) form (Fig. 57, *21*, *27*) are absent.

91 (163). Fully grown macro- and (or) microgametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*, *9*, *20*, *28*, *56*), are absent.

92 (180). Fully grown gametocytes, which markedly displace the nucleus of infected erythrocytes toward one pole of the erythrocytes (Fig. 57, *13*, *34*) and finally enucleate the erythrocytes (Fig. 57, *14*, *35*), are absent.

93 (183). Fully grown gametocytes, which are closely appressed to the nucleus of infected erythrocytes but do not touch the envelope of the erythrocytes along their entire margin (Fig. 57, *60–64*), are absent.

94 (188). Medium grown macrogametocytes, which are closely appressed to the nucleus of infected erythrocytes but do not touch the envelope of the erythrocytes along their entire margin (Fig. 57, *61*, *64, 66)*, are absent.

95 (211). Medium grown gametocytes, which are closely appressed to the envelope of infected erythrocytes but do not touch the nucleus of the erythrocytes along their entire margin (Fig. 57, *59, 69*), are absent.

96 (127). Medium grown macrogametocytes, whose pellicle in the centre does not extend to the envelope of infected erythrocytes causing a 'dip' and giving a dumbbell-like appearance (Fig. 57, *6*, *40*, *44*, *55*), are present; they represent more than 10% of the total number of growing macrogametocytes.

97 (125). Gigantic (>1.5 μm) pigment granules (Fig. 57, *36*) are absent in gametocytes. The average number of pigment granules in fully grown gametocytes is greater than five.

98 (126). Growing microgametocytes, which (i) fill the infected erythrocytes up to their poles and (ii) have a markedly pronounced dumbbell-like shape with the part of the parasite adjacent to the erythrocyte nucleus markedly narrowed (the width of the parasite at this part is less than 1 μm) (Fig. 57, *37*), are absent.

99 (100). Only small size (<0.5 μm) pigment granules are present in fully grown gametocytes (Fig. 57, *38*).

. . . . . 16. ***H. wenyoni***

100 (99). Pigment granules of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size are present in fully grown gametocytes (Fig. 57, *39*, *40*, *46*, *48*). Pigment granules of small (<0.5 μm) size are also present (Fig. 57, *39*) in some fully grown gametocytes, together with medium size pigment granules.

101 (106). Rod-like and large (1.0 to 1.5 μm) pigment granules are present in fully grown gametocytes (Fig. 57, *39*, *40*, *46*, *48*).

102 (103). Gametocytes with a highly ameboid outline (Fig. 57, *40*) predominate among growing macrogametocytes. Rod-like large (1.0 to 1.5 μm) pigment granules predominate in medium grown gametocytes (Fig. 57, *40*).

. . . . . 79. ***H. killangoi***

103 (102). Gametocytes with a highly ameboid outline (Fig. 57, *40*) are not present or only occasionally present and never predominate among growing macrogametocytes. Rod-like large (1.0 to 1.5 μm) pigment granules are not present or do not predominate in medium grown gametocytes.

104 (105). Rod-like large (1.0 to 1.5 μm) pigment granules predominate in fully grown gametocytes.

. . . . . 104. ***H. motacillae***

105 (104). Rod-like large (1.0 to 1.5 μm) pigment granules do not predominate in fully grown gametocytes, but roundish medium size (0.5 to 1.0 μm) pigment granules predominate.

. . . . . 40. ***H. picae***

106 (101). Rod-like and large (1.0 to 1.5 μm) pigment granules (Fig. 57, *39*, *40*, *46*, *48*) are absent in fully grown gametocytes.

107 (110). Macrogametocytes, which pull the nucleus of infected erythrocytes inside (Fig. 57, *41*), are present. The maximum NDR during the development of macrogametocytes is greater than unity.

108 (109). Microgametocytes, pulling the nucleus of infected erythrocytes inside (Fig. 57, *42*), are present. The maximum NDR during the development of microgametocytes is greater than unity.

. . . . . 119. ***H. dolniki***

109 (108). Microgametocytes, pulling the nucleus of infected erythrocytes inside (Fig. 57, *42*), are absent. The maximum NDR during the development of microgametocytes does not exceed unity.

. . . . . 101. ***H. sittae***

110 (107). Macrogametocytes, which pull the nucleus of infected erythrocytes inside (Fig. 57, *41*), are absent. The maximum NDR during the development of macrogametocytes does not exceed unity.

111 (112). Fully grown gametocytes, which do not fill the infected erythrocytes up to their poles (Fig. 57, *43*), are present.

. . . . . 5. ***H. fringillae***

112 (111). Fully grown gametocytes, which do not fill the infected erythrocytes up to their poles (Fig. 57, *43*), are absent.

113 (118). Fully grown gametocytes markedly displace the nucleus of erythrocytes laterally. The average NDR is 0.5 or less.

114 (115). Young gametocytes are usually clearly elongated rod-like in shape (Fig. 57, *2*). Numerous valutin granules are always present in growing and fully grown gametocytes. Numerous valutin granules always concentrate at the ends of microgametocytes, and, as a result, the ends of microgametocytes are much more intensively stained than their central portion.

. . . . . 82. ***H. balmorali***

115 (114). Young gametocytes are variable in shape (Fig. 57, *1*, *4*); the young gametocytes of clearly elongated rod-like shape (Fig. 57, *2*) are not characteristic. Valutin granules are not present or are uncommon in growing and fully grown gametocytes.

116 (117). The average number of pigment granules in fully grown gametocytes is 14 or less.

. . . . . 6. ***H. majoris***

117 (116). The average number of pigment granules in fully grown gametocytes is greater than 14.

. . . . . 15. ***H. queleae***

118 (113). Fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally. The average NDR is greater than 0.5.

119 (123). The outline of the earliest gametocytes is usually even (Fig. 57, *1*). The earliest gametocytes with a highly ameboid outline (Fig. 57, *4*) are not characteristic.

120 (124). Young gametocytes are closely appressed to the nucleus of infected erythrocytes and grow toward the envelope of the erythrocytes (Fig. 57, *3*). Dumbbell-shaped gametocytes (Fig. 57, *6*, *44*) occur with approximately equal probability among growing macro- and microgametocytes.

121 (122). Pigment granules in fully grown gametocytes are usually of medium size (0.5 to 1.0 μm). Small (<0.5 μm) pigment granules are not present or are uncommon in fully grown gametocytes.

. . . . . 118. ***H. coatneyi***

122 (121). Small (<0.5 μm) and medium (0.5 to 1.0 μm) size pigment granules occur with approximately equal probability in fully grown gametocytes.

. . . . . 96. ***H. vireonis***

123 (119). The outline of the earliest gametocytes is usually highly ameboid (Fig. 57, *4*).

. . . . . 115. ***H. timalus***

124 (120). Young gametocytes are not necessarily appressed to the nucleus of infected erythrocytes (Fig. 57, *3*); a considerable number of young gametocytes are closely appressed to the envelope of erythrocytes and grow toward the nucleus of the erythrocytes

(Fig. 57, *5*). Dumbbell-shaped gametocytes (Fig. 57, *6*, *44*) are much more common among growing macrogametocytes than microgametocytes.

. . . . . 2. ***H. passeris***

125 (97). Gigantic pigment granules (>1.5 μm) are present in fully grown gametocytes (Fig. 57, *36*). The average number of pigment granules in fully grown gametocytes is less than five.

. . . . . 67. ***H. stellaris***

126 (98). Growing microgametocytes, which (i) fill the infected erythrocytes up to their poles and (ii) have the pronounced dumbbell-like shape with the portion of the parasite adjacent to the erythrocyte nucleus markedly narrowed (the width of the parasite at this portion is less than 1 μm) (Fig. 57, *37*), are present.

. . . . . 97. ***H. attenuatus***

127 (96). Medium grown macrogametocytes, whose pellicle in the centre does not extend to the envelope of infected erythrocytes causing a 'dip' and giving a dumbbell-like appearance (Fig. 57, *6*, *40*, *44*, *55*), are not present or represent less than 10% of the total number of growing macrogametocytes.

128 (159). The nucleus in fully grown macrogametocytes is in a median (Fig. 57, *18*, *25*, *30*, *47, 53, 57, 71*) or subterminal (Fig. 57, *38–41*, *46, 55*) position, but is never strictly terminal (Fig. 57, *45*).

129 (135). Fully grown gametocytes usually do not fill the infected erythrocytes up to their poles (Fig. 57, *25*, *43*, *46*).

130 (158). Pigment granules in fully grown macrogametocytes are randomly scattered throughout the cytoplasm. The nucleus in microgametocytes is significantly larger than the nucleus in macrogametocytes.

131 (134). Rod-like (Fig. 57, *46*) large (1.0 to 1.5 μm) pigment granules are absent in fully grown gametocytes.

132 (133). The nucleus in fully grown macrogametocytes is in a median or submedian position.

. . . . . 107. ***H. africanus***

133 (132). The nucleus in fully grown macrogametocytes is in a subterminal position.

. . . . . 58. ***H. fallisi***

134 (131). Rod-like (Fig. 57, *46*) large (1.0 to 1.5 μm) pigment granules are present in fully grown gametocytes.

. . . . . 23. ***H. beckeri***

135 (129). Fully grown gametocytes always fill the infected erythrocytes up to their poles (Fig. 57, *29*, *39, 48*, *53, 57*).

136 (143). Pigment granules of large (1.0 to 1.5 μm) size are present in fully grown macrogametocytes.

137 (141). Pigment granules in fully grown gametocytes vary from medium (0.5 to 1.0 μm) to large (1.0 to 1.5 μm) size. Small (<0.5 μm) pigment granules are absent in fully grown gametocytes.

138 (142). Roundish and large (1.0 to 1.5 μm) pigment granules (Fig. 57, *74*) are absent in gametocytes. However, large and rod-like pigment granules (Fig. 57, *40, 49*) may occur.

139 (140). Medium grown gametocytes are usually with pointed ends; the ends markedly wrap the nucleus of infected erythrocytes but do not fill the erythrocytes up to their poles (Fig. 57, *49*). The poles of erythrocytes are filled up only at the final stages of gametocyte development.

. . . . . 108. ***H. bubalornis***

140 (139). Medium grown gametocytes are usually with rounded ends; the ends only slightly surround the nucleus of infected erythrocytes and fill the erythrocytes up to their poles (Fig. 57, *48*).

. . . . . 48. ***H. zosteropis***

141 (137). Pigment granules in fully grown gametocytes vary from small (<0.5 μm) to large (1.0 to 1.5 μm). Large pigment granules are present no in all fully grown gametocytes, while medium size (0.5 to 1.0 μm) pigment granules predominate (Fig. 57, *39*).
. . . . . 8. ***H. hirundinis***

142 (138). Roundish and large (1.0 to 1.5 μm) pigment granules (Fig. 57, *74*) are present in fully grown gametocytes.
. . . . . 55. ***H. macropigmentatus***

143 (136). Pigment granules of large (1.0 to 1.5 μm) size are absent in fully grown gametocytes.

144 (157). The nucleus in fully grown macrogametocytes is, as a rule, not located close to the nucleus of infected erythrocytes (Fig. 57, *38*).

145 (154). Pigment granules of medium (0.5 to 1.0 μm) size are present in fully grown gametocytes.

146 (153). A large (~1.5 μm) pigment granule (Fig. 57, *50*) does not develop in fully grown microgametocytes.

147 (152). The average number of pigment granules in fully grown gametocytes is less than 20.

148 (151). The average number of pigment granules in fully grown gametocytes is 14 or less. The asymmetrical position of growing gametocytes to the nucleus of erythrocytes at the pole of infected erythrocytes (Fig. 57, *51*) is not characteristic.

149 (150). Growing macrogametocytes with a highly ameboid outline (Fig. 57, *52*) are present and represent more than 10% of the total number of the growing macrogametocytes.
. . . . . 33. ***H. pastoris***

150 (149). Growing macrogametocytes with a highly ameboid outline (Fig. 57, *52*) are absent or represent less than 10% of the total number of the growing macrogametocytes.
. . . . . 21. ***H. anthi***

151 (148). The average number of pigment granules in fully grown gametocytes is greater than 14. The asymmetrical position of growing gametocytes to the nucleus of the erythrocytes at the pole of infected erythrocytes (Fig. 57, *51*) is characteristic.
. . . . . 92. ***H. tyranni***

152 (147). The average number of pigment granules in fully grown gametocytes is greater than 20.
. . . . . 11. ***H. orizivorae***

153 (146). A large (~1.5 μm) pigment granule (Fig. 57, *50*) sometimes develops in fully grown microgametocytes.
. . . . . 26. ***H. dicruri***

154 (145). Pigment granules of medium (0.5 to 1.0 μm) size in fully grown gametocytes are absent. Only small size (<0.5 μm) dust-like pigment granules are present in the fully grown gametocytes.

155 (156). The average number of pigment granules in fully grown gametocytes is 14 or greater. The average NDR is 0.6 or less.
. . . . . 102. ***H. dicaeus***

156 (155). The average number of pigment granules in fully grown gametocytes is less than 14. The average NDR is greater than 0.6.
. . . . . 3. ***H. alaudae***

157 (144). The nucleus in fully grown macrogametocytes is usually in a median or submedian position and, as a rule, is located close to the nucleus of the infected erythrocytes (Fig. 57, *53*).
. . . . . 117. ***H. calandrella***

158 (130). The majority of fully grown macrogametocytes are characterised by two loosely aggregated clumps of pigment granules; each of the clumps is located near the end of macrogametocytes (Fig. 57, *47*); however, macrogametocytes with randomly

scattered pigment granules are also present. The size of the nucleus in microgametocytes does not exceed that of the nucleus in macrogametocytes.

. . . . . 126. ***H. payevskyi***

159 (128). The nucleus in fully grown macrogametocytes is strictly terminal in position (Fig. 57, *45*).

. . . . . 31. ***H. orioli***

160 (90). Fully grown gametocytes of roundish (discoid) form (Fig. 57, *21*, *27*) are present.

161 (162). The average length of fully grown gametocytes is less than 6 μm, and the average length of the nucleus of fully grown macrogametocytes is less than 2 μm.

. . . . . 90. ***H. souzalopesi***

162 (161). The average length of fully grown gametocytes is 6 μm or greater, and the average length of the nucleus of fully grown macrogametocytes is greater than 2 μm.

. . . . . 100. ***H. parus***

163 (91). Fully grown macro- and (or) microgametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*, *20*, *56*, *58*), are present.

164 (169). Medium grown macrogametocytes, which do not touch the nucleus of erythrocytes along their entire margin (Fig. 57, *54*), are present.

165 (168). Fully grown macrogametocytes completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*, *20*, *56*, *58*), and fully grown microgametocytes usually do not. Fully grown microgametocytes completely encircling the nucleus of erythrocytes are absent or uncommon.

166 (167). Medium grown microgametocytes, which do not touch the nucleus of infected erythrocytes, are present. Fully grown microgametocytes usually displace the nucleus of erythrocytes laterally. The average NDR is 0.5 or less. Pigment granules in macro- and microgametocytes are of small (<0.5 μm) size.

. . . . . 114. ***H. pittae***

167 (166). Medium grown microgametocytes, which do not touch the nucleus of infected erythrocytes, are absent. Fully grown microgametocytes usually do not displace or only slightly displace the nucleus of erythrocytes laterally. The average NDR is greater than 0.5. Pigment granules in macro- and microgametocytes are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size.

. . . . . 1. ***H. danilewskii***

168 (165). Fully grown macro- and microgametocytes completely encircle the nucleus of infected erythrocytes. Fully grown microgametocytes, completely encircling the nucleus of erythrocytes, are common.

. . . . . 87. ***H. circumnuclearis***

169 (164). Medium grown macrogametocytes, which do not touch the nucleus of infected erythrocytes along their entire margin (Fig. 57, *54*), are absent.

170 (175). The nucleus of macrogametocytes is usually subterminal in position and, as a rule, does not adhere to the nucleus of infected erythrocytes (Fig. 57, *55*, *56*).

171 (176). The average number of pigment granules in fully grown gametocytes is less than 18.

172 (179). Growing gametocytes, whose pellicle in the centre does not extend to the envelope of infected erythrocytes causing a 'dip' and giving a dumbbell-like appearance (Fig. 57, *44*, *55*), are present. Rod-like large (1.0 to 1.5 μm) pigment granules are absent in fully grown gametocytes.

173 (174). Fully grown macrogametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*, *56*), are present.

. . . . . 98. ***H. belopolskyi***

174 (173). Fully grown macrogametocytes, which completely encircle the nucleus of infected erythrocytes, are absent.

. . . . . 12. ***H. ptilotis***

175 (170). The nucleus of macrogametocytes is in a median position and, as a rule, is closely appressed to the nucleus of infected erythrocytes (Fig. 57, *57*, *58*).
. . . . . 37. ***H. lanii***

176 (171). The average number of pigment granules in fully grown gametocytes is greater than 18.

177 (178). Macrogametocytes contain numerous (usually not less than five) small vacuoles.
. . . . . 111. ***H. nipponensis***

178 (177). Macrogametocytes do not contain or contain only a few vacuoles.
. . . . . 54. ***H. globulosus***

179 (172). Growing gametocytes, whose pellicle in the centre does not extend to the envelope of infected erythrocytes causing a 'dip' and giving a dumbbell-like appearance (Fig. 57, *44*, *55*), are absent. Rod-like large (1.0 to 1.5 μm) pigment granules are present in fully grown gametocytes.
. . . . . 120. ***H. magnus***

180 (92). Fully grown gametocytes, which markedly displace the nucleus of infected erythrocytes toward one pole of erythrocytes (Fig. 57, *13*, *15*, *17*, *34*) and finally enucleate the erythrocytes (Fig. 57, *14*, *35*), are present.

181 (182). Growing gametocytes are closely appressed to the nucleus of infected erythrocytes. The average width of fully grown gametocytes is greater than 4.5 μm. Infected erythrocytes are significantly hypertrophied in width but unchanged in length in comparison to uninfected ones.
. . . . . 91. ***H. tartakovskyi***

182 (181). Growing gametocytes, which do not touch the nucleus of infected erythrocytes (Fig. 57, *59*), are present. The average width of fully grown gametocytes is 4.5 μm or less. Infected erythrocytes are significantly hypertrophied in length but unchanged in width in comparison to uninfected ones.
. . . . . 116. ***H. uraeginthus***

183 (93). Fully grown gametocytes, which are closely appressed to the nucleus of infected erythrocytes but do not touch the envelope of the erythrocytes along their entire margin (Fig. 57, *60–64*), are present.

184 (185). Dumbbell-shaped gametocytes with highly constricted central portion and clearly thickened ends of the parasites (Fig. 57, *60*, *64*) are present.
. . . . . 95. ***H. philippinensis***

185 (184). Dumbbell-shaped gametocytes with highly constricted central portion and clearly thickened ends of the parasites (Fig. 57, *60*, *64*) are absent.

186 (187). Macro- and microgametocytes are easily distinguished on the basis of the intensity of staining of the cytoplasm. The outline of gametocytes is even. Pigment granules in macrogametocytes frequently aggregate in well regulated groups which are rosette-like, fan-like, star-like, or have other forms (Fig. 57, *61*).
. . . . . 105. ***H. nucleophilus***

187 (186). Macro- and microgametocytes are poorly distinguished on the basis of the intensity of staining of the cytoplasm. The outline of gametocytes varies from highly ameboid to even (Fig. 57, *62*, *63*). Pigment granules in macrogametocytes do not aggregate in well regulated groups, which are rosette-like, fan-like, star-like, or have other forms (Fig. 57, *61*), but are randomly scattered throughout the cytoplasm (Fig. 57, *62*, *63*).
. . . . . 113. ***H. pallidus***

188 (94). Medium grown macrogametocytes, which are closely appressed to the nucleus of infected erythrocytes but do not touch the envelope of the erythrocytes along their entire margin (Fig. 57, *60*, *63*, *64*), are present.

189 (196). Dumbbell-shaped gametocytes (Fig. 57, *60*, *64*) are present.

190 (194). The average number of pigment granules in macrogametocytes is less than 20.

191 (195). The average number of pigment granules in gametocytes is less than 15. Medium size (0.5 to 1.0 μm) pigment granules are present in the gametocytes.

192 (193). Dumbbell-shaped gametocytes (Fig. 57, *64*), which do not touch the envelope of infected erythrocytes, represent less than one-third of the total number of growing gametocytes. Dumbbell-shaped microgametocytes are not characteristic. Fully grown macro- and microgametocytes fill the infected erythrocytes up to their poles (Fig. 57, *44*).
. . . . . 43. ***H. quiscalus***

193 (192). Dumbbell-shaped gametocytes (Fig. 57, *60*), which do not touch the envelope of infected erythrocytes, represent more than one-third of the total number of growing gametocytes. Dumbbell-shaped microgametocytes are common. Fully grown macro- and microgametocytes usually do not fill the infected erythrocytes up to their poles.
. . . . . 110. ***H. monarchus***

194 (190). The average number of pigment granules in macrogametocytes is greater than 20.
. . . . . 122. ***H. neseri***

195 (191). The average number of pigment granules in gametocytes is 15 or more. Medium size (0.5 to 1.0 μm) pigment granules are absent in the gametocytes.
. . . . . 20. ***H. aegithinae***

196 (189). Dumbbell-shaped gametocytes (Fig. 57, *60*, *64*) are absent.

197 (203). Growing gametocytes, which are more than 10 μm long, are slender snake-like, and do not touch the nucleus and the envelope of infected erythrocytes (Fig. 57, *65*), are absent.

198 (204). Medium grown gametocytes with a highly ameboid or clearly wavy outline (Fig. 57, *66*) are absent.

199 (207). Fully grown macro- and (or) microgametocytes fill the infected erythrocytes up their poles. Medium size (0.5 to 1.0 μm) pigment granules are present in gametocytes.

200 (208). Fully grown gametocytes displace the nucleus of infected erythrocytes laterally. The average NDR is less than 0.7.

201 (202). Rod-like large (1.0 to 1.5 μm) pigment granules are present in fully grown gametocytes.
. . . . . 53. ***H. sequeirae***

202 (201). Rod-like large (1.0 to 1.5 μm) pigment granules are absent in fully grown gametocytes.
. . . . . 32. ***H. otocompsae***

203 (197). Growing gametocytes, which are longer than 10 μm, are slender snake-like, and do not touch the nucleus and the envelope of infected erythrocytes (Fig. 57, *65*), are common.
. . . . . 94. ***H. furnarius***

204 (198). Medium grown gametocytes with a highly ameboid or clearly wavy outline (Fig. 57, *66*) are common.

205 (206). Pigment granules in fully grown gametocytes tend to aggregate into compact masses (Fig. 57, *67*). The average number of pigment granules in gametocytes is less than seven.
. . . . . 121. ***H. minutus***

206 (205). Pigment granules in gametocytes are not aggregated into compact masses (Fig. 57, *67*). The average number of pigment granules in gametocytes is greater than seven.
. . . . . 125. ***H. kairullaevi***

207 (199). Fully grown macro- and microgametocytes do not fill the infected erythrocytes up to their poles (Fig. 57, *68*). Medium size (0.5 to 1.0 μm) pigment granules are absent in gametocytes.
. . . . . 112. ***H. pachycephalus***

208 (200). Fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally. The average NDR is 0.7 or greater.

209 (210). Rod-like large (1.0 to 1.5 μm) pigment granules are present in fully grown gametocytes. . . . . 93. ***H. formicarius***

210 (209). Rod-like large (1.0 to 1.5 μm) pigment granules are absent in fully grown gametocytes.
. . . . . 46. ***H. sanguinis***

211 (95). Medium grown gametocytes, which are closely appressed to the envelope of infected erythrocytes but do not touch the nucleus of the erythrocytes along their entire margin (Fig. 57, *69*), are present.

212 (213). Pigment granules in macrogametocytes tend to aggregate into one loose group (Fig. 57, *70*). The nucleus of macrogametocytes is in a subterminal position (Fig. 57, *70*). The nucleus of infected erythrocytes is not displaced or slightly displaced laterally. The average NDR is greater than 0.7.
. . . . . 83. ***H. cublae***

213 (212). Pigment granules in macrogametocytes tend not to aggregate in one group. The nucleus in macrogametocytes is in a median or submedian position (Fig. 57, *71*). The nucleus of infected erythrocytes is markedly displaced laterally. The average NDR is less than 0.7.
. . . . . 109. ***H. eurylaimus***

214 (1m). Vertebrate hosts: P i c i f o r m e s.

215 (223). Fully grown gametocytes do not completely encircle the nucleus of erythrocytes.

216 (224). Fully grown gametocytes do not enucleate the infected erythrocytes.

217 (229). The average width of fully grown gametocytes is greater than 2 μm.

218 (230). The average number of pigment granules in macro- and microgametocytes does not differ significantly.

219 (222). The average length of fully grown gametocytes is less than 18 μm.

220 (221). Fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally. The average NDR is 0.4 or less. The average number of pigment granules in gametocytes is less than 15.
. . . . . 50. ***H. borgesi***

221 (220). Fully grown gametocytes slightly displace the nucleus of infected erythrocytes laterally. The average NDR is greater than 0.4. The average number of pigment granules in gametocytes is greater than 15.
. . . . . 47. ***H. xantholaemae***

222 (219). The average length of fully grown gametocytes is greater than 18 μm. Growing gametocytes, which do not touch the nucleus and the envelope of infected erythrocytes (Fig. 57, *72*), are present.
. . . . . 78. ***H. cornuata***

223 (215). Fully grown gametocytes completely encircle the nucleus of infected erythrocytes (Fig. 57, *7*).
. . . . . 41. ***H. velans***

224 (216). Fully grown gametocytes, which enucleate the infected erythrocytes (Fig. 57, *14*), are present.

225 (228). The average number of pigment granules in gametocytes is less than 25.

226 (227). Infected erythrocytes are hypertrophied on average approximately 10% in length in comparison to uninfected ones.
. . . . . 63. ***H. bennetti***

227 (226). Infected erythrocytes on average do not change significantly in length in comparison to uninfected ones.
. . . . . 86. ***H. bucconis***

228 (225). The average number of pigment granules in gametocytes is greater than 25.
. . . . . 35. ***H. thereicerycis***

229 (217). The average width of fully grown gametocytes is less than 2 μm. Fully grown gametocytes are clearly dumbbell-like or bilobed in shape (Fig. 57, *73*).
. . . . . 77. ***H. bilobata***

230 (218). The average number of pigment granules in macrogametocytes is approximately two times greater than in microgametocytes.
. . . . . 89. ***H. indicator***

231 (1n). Vertebrate hosts: P s i t t a c i f o r m e s.

232 (233). Fully grown gametocytes encircle the nucleus of infected erythrocytes completely and occupy all available cytoplasmic space in the erythrocytes (Fig. 57, *7*). The average number of pigment granules in gametocytes is greater than 15.
. . . . . 44. ***H. handai***

233 (232). Fully grown gametocytes do not encircle the nucleus of infected erythrocytes completely and do not occupy all available cytoplasmic space in the erythrocytes (Fig. 57, *33*). The average number of pigment granules in gametocytes is less than 15.
. . . . . 123. ***H. psittaci***

234 (1p). Vertebrate hosts: S t r i g i f o r m e s.

235 (236). Gametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *9*, *28*) or almost completely encircle it, are present and represent over 90% of the total number of the mature gametocytes. Fully grown gametocytes do not displace or slightly displace the nucleus of erythrocytes laterally. The average NDR is greater than 0.7.
. . . . . 4. ***H. noctuae***

236 (235). Gametocytes, which completely encircle the nucleus of infected erythrocytes (Fig. 57, *9*, *28*) or almost completely encircle it, are absent or appear occasionally and, if present, they are less than 5% of the total number of mature gametocytes. Fully grown gametocytes markedly displace the nucleus of erythrocytes laterally. The average NDR is less than 0.7.
. . . . . 14. ***H. syrnii***

237 (1r). Vertebrate hosts: T r o g o n i f o r m e s. One species has so far been described.
. . . . . 106. ***H. trogonis***

238 (1s). Vertebrate hosts: P e l e c a n i f o r m e s. One species has so far been described.
. . . . . See Appendix 2: ***H. iwa***

1. **Haemoproteus (Parahaemoproteus) danilewskii** Kruse, 1890

Haemoproteus danilewskii Kruse, 1890: 370. – *Laverania danilewskyi* Grassi and Feletti, 1890b: 4 (partim, nom. praeocc., non Kruse, 1890). – *Haemoproteus corvi* Bhatia, 1938: 218, Fig. 107. – *H. danilewskii* var. *cairogensis* Mohammed, 1958: 186, Pl. 7, Fig. 1–15. – *H. danilewskii*: Levine and Campbell, 1971: 477 (=*H. corvi*); Bishop and Bennett, 1990: 2252 (=*Laverania danilewskyi*).

T y p e v e r t e b r a t e h o s t. *Corvus corone* L. (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. Some species of the Passeriformes (Table 16).
V e c t o r s. *Culicoides crepuscularis*, *C. downesi* (Diptera: Ceratopogonidae).
T y p e l o c a l i t y. Naples, Italy.
D i s t r i b u t i o n. The Holarctic, Ethiopian, and Oriental zoogeographical regions. Relatively rare parasite. Has a patchy distribution.
T y p e m a t e r i a l. Paraneohapantotypes (No. 14239, 97138, 97139, *Corvus corone*, 1949, Cairo, Egypt, A.H.H. Mohammed) are deposited in IRCAH. *Plasmodium* (*Haemamoeba*) sp. is present in the type material.

Preparations of haemoproteids (blood stages, exoerythrocytic meronts), which are included in the collection of Professor P.C.C. Garnham (Garnham and Duggan, 1986) under the name *H. danilewskyi* Kruse, 1890, contain *H. balmorali*.

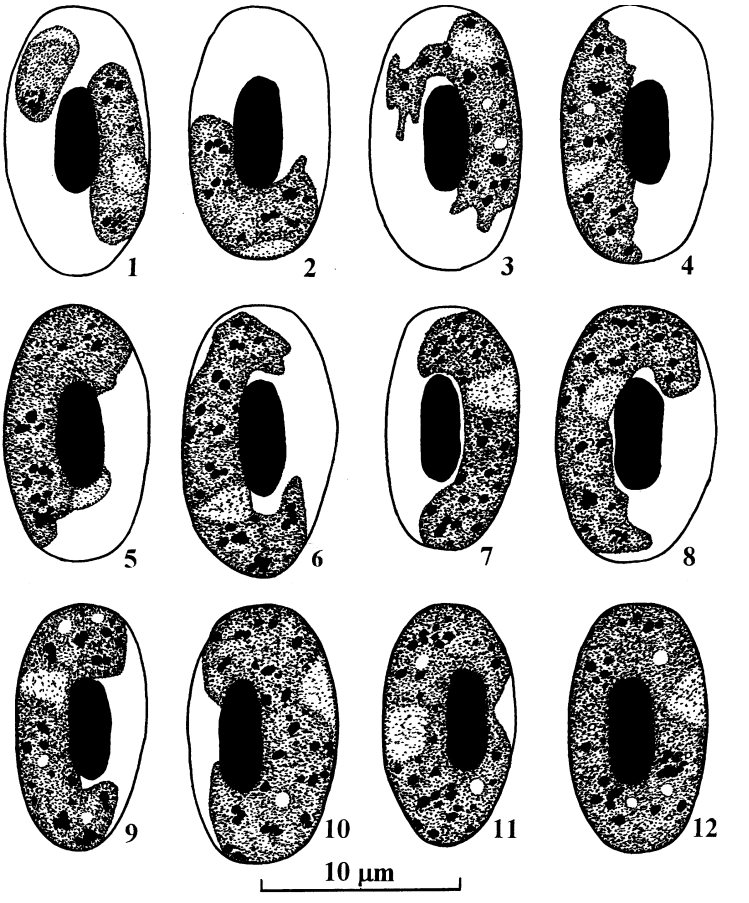

Figure 58 Gametocytes of *Haemoproteus danilewskii* from the blood of *Corvus corone: 1, 2* – young; *3–12* – macrogametocytes.

Table 16 List of vertebrate hosts of *Haemoproteus danilewskii.*

Aphelocoma coerulescens	*C. macrorhynchos*	*Garrulus glandarius*
Corvus brachyrhynchos	*C. monedula*	*Nucifraga caryocatactes*
C. capensis	*C. ossifragus*	*Psilorhinus morio*
C. corax	*C. splendens*	
C. frugilegus	*Dendrocitta vagabunda*	

Etymology. This species is named in honour of Professor V.Ya. Danilewsky who discovered bird haemosporidian parasites and created the comparative blood parasitology of vertebrates.

Main diagnostic characters. A parasite of species of the Passeriformes whose fully grown macrogametocytes completely encircle the nucleus of erythrocyte, but this is not characteristic of microgametocytes. Medium grown macrogametocytes, which do not touch the nucleus of infected erythrocytes, are present. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, roundish and oval, vary from 18 to 30.

Table 17 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. danilewskii* (modified from Bishop and Bennett, 1990c)				*H. passeris* (according to Valkiūnas and Iezhova, 1992b)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	60				31			
Length		–	12.4	1.1		10.8–13.6	12.1	0.8
Width		–	6.8	0.5		5.6–7.1	6.4	0.6
Length of nucleus		–	4.9	0.6		5.2–6.4	5.7	0.4
Width of nucleus		–	1.9	0.3		1.7–2.7	2.3	0.2
Erythrocyte parasitized by macrogametocyte	60				31			
Length		–	13.0	0.8		12.1–15.0	13.0	0.8
Width		–	7.3	0.5		5.8–7.3	6.4	0.6
Length of nucleus		–	4.7	0.5		4.8–6.7	5.8	0.4
Width of nucleus		–	2.0	0.2		1.9–2.7	2.2	0.2
Erythrocyte parasitized by microgametocyte	35				31			
Length		–	12.9	0.8		12.4–14.2	13.1	0.8
Width		–	7.5	0.6		5.8–7.2	7.0	0.6
Length of nucleus		–	4.6	0.5		5.3–6.5	5.8	0.4
Width of nucleus		–	2.0	0.3		1.8–2.5	2.2	0.2
Macrogametocyte	60							
Length		–	19.4	3.4	31	10.8–14.4	12.7	1.0
Width		–	3.2	0.5	31	2.0–2.9	2.5	0.1
Length of nucleus		–	2.9	0.5	31	1.9–2.9	2.4	0.2
Width of nucleus		–	1.9	0.4	31	1.0–2.3	1.7	0.2
NDR		–	0.8	0.2	50	0.5–1.0	0.8	0.1
No. of pigment granules		18–30	23.4	4.2	31	8–14	10.6	1.7
Microgametocyte	35							
Length		–	17.4	2.3	31	12.4–15.5	14.3	1.2
Width		–	3.4	0.5	31	2.0–3.0	2.4	0.2
Length of nucleus		–	6.3	0.8	31	7.4–9.8	8.3	0.4
Width of nucleus		–	2.8	0.4	31	2.0–3.0	2.4	0.2
NDR		–	0.8	0.1	50	0.5–1.0	0.8	0.2
No. of pigment granules		17–36	27.6	2.9	31	7–14	9.0	1.9

Note: All sizes are given in micrometres.

Development in vertebrate host

Young gametocytes (Fig. 58, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes frequently extend along the nucleus of erythrocytes occupying a position asymmetrical to the erythrocyte nucleus (Fig. 58, *2*); a few small clear vacuoles are usually present in cytoplasm; the outline is usually even but sometimes ameboid (Fig. 58, *2*).

Macrogametocytes (Fig. 58, *3–12*; Pl. II, *1*; Table 17). The cytoplasm, which has a finely granular appearance, frequently contains a few clear small vacuoles; gametocytes

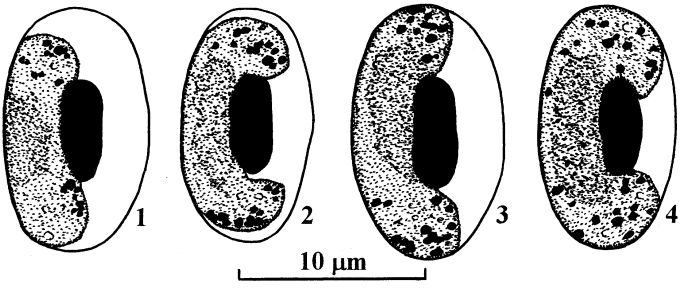

Figure 59 Microgametocytes of *Haemoproteus danilewskii* from the blood of *Corvus corone.*

grow around the nucleus of erythrocytes, they do not displace or only slightly displace the nucleus laterally but encircle it completely and finally occupy all available cytoplasmic space in the erythrocytes (Fig. 58, *12*); growing gametocytes are closely appressed to the envelope of erythrocytes but sometimes do not touch the nucleus of erythrocytes (Fig. 58, *7*, *8*); fully grown gametocytes are closely appressed both to the nucleus and the envelope of erythrocytes (Fig. 58, *10–12*); the parasite nucleus is compact, variable in form and in position but more frequently occupies a median or submedian position (Fig. 58, *7–12*); pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 59). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; at all stages of development, gametocytes are closely appressed both to the nucleus and the envelope of erythrocytes; fully grown gametocytes do not encircle the nucleus of erythrocyte completely; the outline is even; other characters are as for macrogametocytes.

Development in vectors has not been studied in detail. The limited experimental data (Fallis and Bennett, 1961a, 1961b) show that the development is completed in biting midges *Culicoides crepuscularis* and *C. downesi*.

Comments. Frequently, the name *H. danilewskii* (=*H. danilewskyi*) was used by many authors for haemoproteids recorded in various birds, without comparing the morphology of the parasites. It is certain that many species of the haemoproteids were mentioned in the literature under the name *H. danilewskii*. That is why only well described and (or) illustrated records are included in Table 16.

Among the haemoproteids of birds belonging to the Passeriformes, *H. danilewskii* is especially similar to *H. circumnuclearis* and *H. pittae. Haemoproteus danilewskii* can be distinguished from *H. circumnuclearis* primarily on the basis of the morphology of its microgametocytes, and from *H. pittae*, on the basis of the morphology of its microgametocytes and the presence of medium size (0.5 to 1.0 μm) pigment granules in its gametocytes.

2. **Haemoproteus (Parahaemoproteus) passeris** Kruse, 1890

Haemoproteus passeris Kruse, 1890: 370. – *Laverania danilewskyi* Grassi and Feletti, 1890b: 4 (partim, nom. praeocc., non Kruse, 1890). – *Haemoproteus gymnorhidis* Mello, 1935b: 474. – *H. granulosum* Rey Vila, 1945: 150, Fig. 14. – *H. wenyoni* Sergent and Sergent, 1948: 395, Figs. (nom.

praeocc., non Mello, Sa, Souza, Dias and Noronha, 1916). – *H. danilewskii* var. *urbanensis* Sachs, 1953: 221, Fig. 5, 6. – *H. passeris*: Levine and Campbell, 1971: 478 (*H. danilewskii* var. *urbanensis*, *H. granulosum*, *H. wenyoni* Ser. and Ser.). – *H. zasukhini* Burtikashvili, 1973: 697, Fig. – *H. passeris*: Peirce, 1976: 410 (=*Laverania danilewskyi*, partim); Bennett and Peirce, 1991: 8 (=*H. gymnorhidis*, *H. zasukhini*).

Type vertebrate host. *Passer hispaniolensis* (Temm.) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 18).
Type locality. Naples, Italy.
Distribution. This parasite has been recorded in all zoogeographical regions except the Antarctic.
Type material. Neohapantotypes (No. 975, *Passer domesticus*, 16.05.1964, Weybridge, Surrey, England, M.A. Peirce; No. 976, 26.05.1964, other data are as for No. 975) are deposited in CPG. On slide No. 976, *Plasmodium relictum* is also present. The neohapantotype suggested by Bennett and Peirce (1991) is invalid because it was designated later. Paraneohapantotypes [No. 68927(I), 68927(II), 25.06.1973; No. 68926(I–VI), 68928, 12.06.1973, other data are as for the neohapantotypes; No. 108459, 12.05.1972, Ascot, England, other data are as for the neohapantotypes] are deposited in IRCAH. Additionally, Bennett and Peirce (1991) suggested as paraneohapantotypes a series of blood films which were collected from nontype hosts (*Passer griseus*, *P. luteus*, *P. melanurus*, *Petronia superciliaris*) far beyond the type locality (the Ethiopian zoogeographical region). These paraneohapantotypes are invalid because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985).
Etymology. The specific name is derived from the generic name of the type host, *Passer*.

Table 18 List of vertebrate hosts of *Haemoproteus passeris* (modified from Bennett and Peirce, 1991).

Passer flaveolus	*P. luteus*	*P. superciliaris*
P. griseus	*P. melanurus*	*P. xanthocollis*
P. domesticus	*P. montanus*	*Philetairus socius*
P. iagoensis	*P. rutilans*	*Plocepasser mahali*
P. indicus	*Petronia petronia*	*Sporopipes squamifrons*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Medium and fully grown gametocytes adhere to the nucleus and the envelope of erythrocytes. Dumbbell-shaped gametocytes predominate among growing macrogametocytes. Fully grown gametocytes are closely appressed to the nucleus and the envelope of erythrocytes, they fill the erythrocytes up to their poles and slightly displace their nucleus laterally. A considerable number of young gametocytes are closely appressed to the envelope of erythrocytes and grow toward the nucleus of erythrocytes. Pigment granules are usually of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size. There are about ten of them on average. A species identified with difficulty which can be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes only on the basis of a detailed analysis of a set of characters.

Development in vertebrate host
Exoerythrocytic development has been insufficiently investigated (Wenyon, 1926; Burtikashvili, 1973, 1978; Peirce, 1976). Two types of meronts (small and megalomeronts) were recorded. The small meronts were seen in the lungs and liver, and their size in these organs

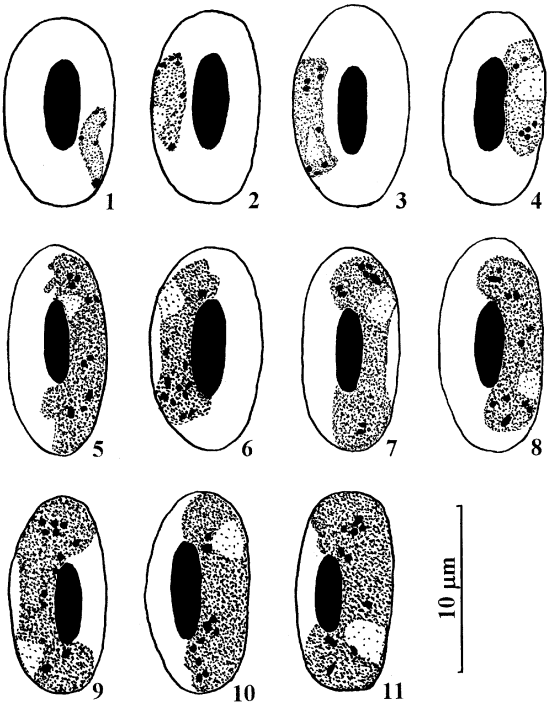

Figure 60 Gametocytes of *Haemoproteus passeris* from the blood of *Passer domesticus: 1–4* – young; *5–11* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992b).

was 12.9×9.5 and 14.6×10.3 μm, respectively. The megalomeronts, whose diameter is up to 220 μm, were found in the lungs, liver, spleen, and kidneys of sparrows in India and Georgia. The sequence and peculiarities of the development of the small meronts and megalomeronts are unknown. Moreover, strictly speaking, it should be proved that the recorded meronts belong to *H. passeris* because they were found in naturally infected birds. Thus, a possibility of latent mixed infections with other parasites should be kept in mind.

Young gametocytes (Fig. 60, *1–4*). The earliest forms can be seen anywhere in infected erythrocytes, variable in form; the outline varies from even to slightly ameboid; a highly ameboid outline is not characteristic; as the parasite develops, gametocytes adhere to the envelop of the erythrocytes and extend in length and width (Fig. 60, *2–4*); the growth of gametocytes from the envelope toward the nucleus of erythrocytes is a characteristic feature of *H. passeris* which has been recorded in different blood films in 20 to 100% of young gametocytes. However, it should be noted that some young gametocytes also adhere to the nucleus of erythrocytes and grow from the nucleus toward the envelope of erythrocytes.

Macrogametocytes (Fig. 60, *5–11*; Table 17). The cytoplasm is homogeneous in appearance; gametocytes grow around the nucleus of erythrocytes, they slightly displace the nucleus laterally but never encircle it completely; gametocytes adhere both to the nucleus and the envelope of erythrocytes; the central part of the pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 60, *6*, *7*, *9*); the dumbbell-shaped forms predominate among growing gametocytes, however, the gametocytes without the 'dip' are also common

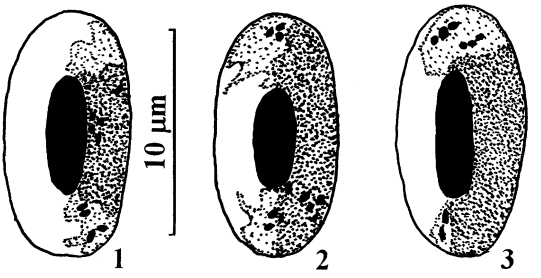

Figure 61 Microgametocytes of *Haemoproteus passeris* from the blood of *Passer domesticus* (modified from Valkiūnas and Iezhova, 1992b).

(Fig. 60, *5*, *8*); fully grown gametocytes lose the dumbbell-like shape, they are closely appressed both to the nucleus and the envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 60, *10*, *11*); the outline is usually even (Fig. 60, *7–9*), but sometimes wavy (Fig. 60, *6*, *10*, *11*) and ameboid (Fig. 60, *5*); the nucleus of gametocytes is compact, variable in form, subterminal in position; pigment granules are usually roundish but sometimes oval and occasionally rod-like, of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 61). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; microgametocytes with a highly ameboid outline are more numerous than macrogametocytes; dumbbell-shaped growing forms are much rare than among macrogametocytes; other characters are as for macrogametocytes.

Comments. *Haemoproteus passeris* is especially similar to *H. queleae* among haemoproteids of birds belonging to the Passeriformes. *Haemoproteus passeris* can be distinguished from the latter species primarily on the basis of its greater average NDR and smaller number of pigment granules in gametocytes. During identification of these species, attention should be paid to the above mentioned characters because the range of their vertebrate hosts partly overlaps. It should be also mentioned that the growth of young gametocytes of *H. passeris* is not strictly accompanied with the adherence to the nucleus of erythrocytes. A considerable number of young gametocytes of this parasite are closely appressed to the envelope of erythrocytes and they grow toward the nucleus of erythrocytes (Fig. 60, *1–3*). This character helps to distinguish *H. passeris* from similar species of passerine haemoproteids like *H. coatneyi* and *H. vireonis*.

3. **Haemoproteus (Parahaemoproteus) alaudae** Celli and Sanfelice, 1891

Haemoproteus alaudae Celli and Sanfelice, 1891: 583 (partim).

Type vertebrate host. *Alauda arvensis* L. (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 19).
Type locality. Northern Italy.
Distribution. The Holarctic, Ethiopian, and Oriental zoogeographical regions.
Type material was not designated in the original description. Neotypes designated by Bennett and Peirce (1990c) are invalid because they came from nontype hosts (*Alaemon alaudipes, Eremopterix signata*, *Galerida cristata*, *G. deva*) investigated far beyond the type locality (Kenya, Iraq), and

they contradict Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). A series of additional slides is deposited in IRCAH.

Etymology. The specific name is derived from the generic name of the type host, *Alauda*.

Table 19 List of vertebrate hosts of *Haemoproteus alaudae* (modified from Bennett and Peirce, 1990c).

Alaemon alaudipes	*E. signata*	*Mirafra africana*
Calandrella cinerea	*Galerida cristata*	*M. cheniana*
Eremophila alpestris	*G. deva*	
Eremopterix grisea	*Melanocorypha bimaculata*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle the nucleus completely. Medium and fully grown gametocytes are appressed to the nucleus and the envelope of erythrocytes. Dumbbell-shaped gametocytes are absent. Fully grown gametocytes fill the erythrocytes up to their poles. The nucleus of macrogametocytes is not located close to the nucleus of infected erythrocytes. Pigment granules are of small (<0.5 μm) size, frequently dust-like in appearance and ill-defined, about ten per gametocyte on average.

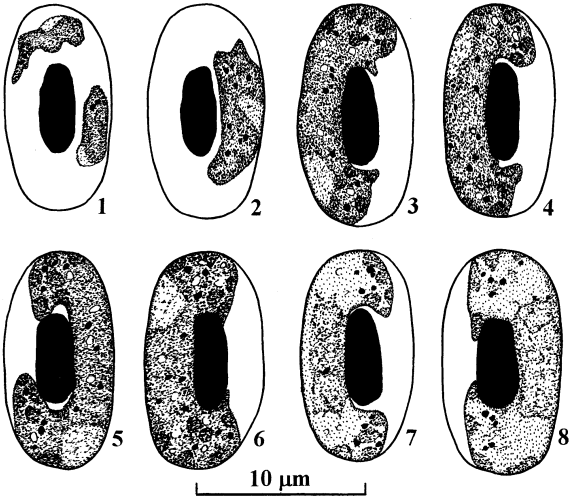

Figure 62 Gametocytes of *Haemoproteus alaudae* from the blood of *Eremopterix signata: 1*, *2* – young; *3–6* – macrogametocytes; *7*, *8* – microgametocytes.

Development in vertebrate host

Young gametocytes (Fig. 62, *1, 2*). The earliest forms can be seen anywhere in infected erythrocytes (Fig. 62, *1*); as the parasite develops, gametocytes extend longitudinally along the erythrocyte nucleus (Fig. 62, *2*) to which they finally adhere; the outline is even or wavy.

Macrogametocytes (Fig. 62, *3–6*; Table 20). The cytoplasm is granular in appearance, contains numerous small vacuoles; valutin granules are usually present, they are numerous and obscuring the pigment granules; gametocytes grow around the nucleus of erythrocytes,

Table 20 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. alaudae* (modified from Bennett and Peirce, 1990c)			*H. noctuae* (according to Valkiūnas and Iezhova, 1989)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	50			33			
Length		12.0	1.1		11.2–15.1	13.7	0.6
Width		6.4	0.6		6.8–8.8	7.3	0.2
Length of nucleus		5.4	0.6		4.2–7.0	5.2	0.1
Width of nucleus		2.0	0.3		2.1–3.0	2.4	0.1
Erythrocyte parasitized by macrogametocyte	70			35			
Length		13.1	1.3		12.7–16.6	14.4	0.4
Width		6.6	0.5		6.3–8.8	7.0	0.2
Length of nucleus		5.3	0.7		3.8–6.9	4.7	0.2
Width of nucleus		2.0	0.3		1.6–2.4	1.9	0.1
Erythrocyte parasitized by microgametocyte	10			37			
Length		12.4	0.8		11.9–16.2	14.0	0.3
Width		6.6	0.4		6.2–8.6	6.8	0.1
Length of nucleus		5.1	0.5		3.9–6.5	4.8	0.1
Width of nucleus		2.1	0.3		1.5–2.7	2.0	0.1
Macrogametocyte	70			34			
Length		16.9	2.2		14.8–23.9	18.1	1.4
Width		2.9	0.5		2.1–3.3	2.8	0.4
Length of nucleus		3.0	0.6		1.9–3.8	3.0	0.2
Width of nucleus		2.2	0.4		1.4–2.5	1.9	0.1
NDR		0.8	0.1		0.8–1.1	0.9	0.1
No. of pigment granules		10.0	1.3		15–39	29.0	2.2
Microgametocyte	10			33			
Length		17.3	1.5		12.8–22.9	18.0	1.7
Width		2.7	0.3		1.8–3.0	2.2	0.3
Length of nucleus		5.9	0.5		8.7–13.1	10.0	0.6
Width of nucleus		2.6	0.6		1.6–3.0	2.0	0.1
NDR		0.8	0.1		0.7–1.1	0.9	0.1
No. of pigment granules		9.7	1.5		11–30	21.0	1.9

Note: All sizes are given in micrometres.

they do not displace or slightly displace the nucleus laterally and do not encircle it completely; gametocytes adhere to the nucleus and the envelope of erythrocytes and fill the erythrocytes up to their poles; growing gametocytes frequently contain clear invaginations of the pellicle near the poles of the nucleus of erythrocytes (Fig. 62, *4, 5*), and these invaginations disappear in fully grown parasites (Fig. 62, *6*); dumbbell-shaped gametocytes are absent; the outline of fully grown parasites is even; the parasite nucleus is compact, variable in form, subterminal in position, never located close to the nucleus of infected erythrocyte;

pigment granules are small (<0.5 μm), frequently dust-like in appearance and ill-defined, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 62, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Small (<0.5 μm) and not numerous (on average about ten) pigment granules are main distinctive characters of gametocytes of *H. alaudae.* On the basis of these characters, *H. alaudae* can be distinguished from many other species of haemoproteids parasitizing birds belonging to the Passeriformes. It should be noted that compact granules of valutin are frequently present in gametocytes of *H. alaudae.* They obscure pigment granules and may sometimes be mistakenly identified as true pigment.

According to the morphology of pigment granules, *H. alaudae* is closely similar to *H. dicaeus*. Gametocytes of *Haemoproteus alaudae* can be clearly distinguished from the latter species on the basis of (i) fewer pigment granules, (ii) the mode of growth in the infected erythrocyte, and (iii) significantly greater NDR. *Haemoproteus alaudae* is also similar to *H. calandrellae*, and it can be readily distinguished from the latter parasite on the basis of (i) the position of nucleus in its macrogametocytes, (ii) its significantly greater NDR, and (iii) the absence of medium size (0.5 to 1.0 μm) pigment granules.

4. **Haemoproteus (Parahaemoproteus) noctuae** Celli and Sanfelice, 1891

Haemoproteus noctuae Celli and Sanfelice, 1891: 583, Pl. 6, Fig. 22–35 (partim). – *H. bramae* Mello, 1935b: 474. – *H. glaucidii* Mello, 1935b: 473 (partim). – *H. noctuae* var. *cellii* Coatney and Roudabush, 1937: 1007, Pl. 1, Fig. 1, 2. – *H. noctuae* var. *nebraskensis* Coatney and Roudabush, 1937: 1008, Pl. 1, Fig. 3, 4. – *H. cellii*: Mohammed, 1958: 204 (emend. pro var. *cellii*). – *H. nebraskensis*: Levine and Campbell, 1971: 476 (emend. pro var. *nebraskensis*). – *H. noctuae*: Bishop and Bennett, 1989: 2676 (=*H. bramae*, *H. glaucidii* partim, *H. nebraskensis*, *H. cellii* partim). – *H. tytoni* Bishop and Bennett, 1989: 2682, Fig. 11, 12. – *H. noctuae*: Valkiūnas, 1997: 166 (= *H. tytoni*).

Type vertebrate host. *Athene noctua* (Scopoli) (Strigiformes).
Additional vertebrate hosts. Numerous species of the Strigiformes belonging to the families Strigidae and Tytonidae (over 30 species).
Type locality. Environs of Rome, Italy.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic. There are no records beyond the North Polar Circle. The prevalence of infection is especially high in the Holarctic where numerous strigiform bird populations are infected up to 90 to 100%.
Type material was not designated in the original description. Bishop and Bennett (1989) designated neotypes which came from nontype hosts (*Strix aluco*, *Ninox philippensis*) investigated far beyond the type locality (England, Philippine Islands). These neotypes are invalid because they contradict Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). A series of good additional blood films is deposited in IRCAH and CDVA.
Etymology. The specific name is derived from the specific name of the type host, *noctua.*

Main diagnostic characters. A parasite of species of the Strigiformes whose gametocytes grow around the nucleus of infected erythrocytes, they do not displace or only slightly displace the nucleus laterally, but finally completely encircle the nucleus.

Development in vertebrate host
Young gametocytes (Fig. 63, *1, 2*). The earliest forms can be seen anywhere in infected erythrocytes, roundish or oval in form; the outline is usually even but sometimes slightly

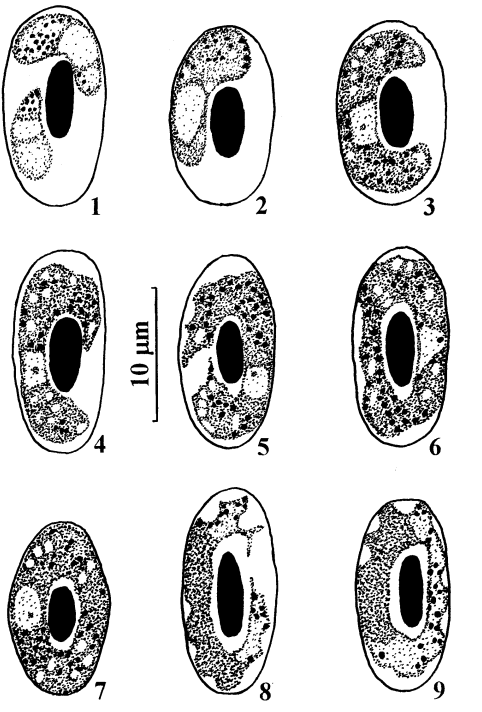

Figure 63 Gametocytes of *Haemoproteus noctuae* from the blood of *Asio otus:*
1, *2* – young; *3–7* – macrogametocytes; *8*, *9* – microgametocytes (modified from Valkiūnas and Iezhova, 1989).

ameboid; as the parasite develops, gametocytes extend around the erythrocyte nucleus, not touching it and not displacing it laterally; some growing gametocytes are also seen not touching the envelope of erythrocytes; horseshoe-like gametocytes, assuming a polar position in erythrocytes (Fig. 63, *1*), are common.

Macrogametocytes (Fig. 63, *3–7*; Table 20). The cytoplasm is homogeneous in appearance, usually contains vacuoles; gametocytes grow around the nucleus of erythrocytes, and they do not displace or only slightly displace the nucleus laterally; fully grown gametocytes completely encircle the erythrocyte nucleus (Fig. 63, *6, 7*); gametocytes, completely encircling the erythrocyte nucleus or nearly completely encircling it (Fig. 63, *4–7*), represent over 90% of the total number of mature gametocytes; gametocytes usually do not touch the nucleus of erythrocytes (Fig. 63, *3–7*) and sometimes they also do not touch the envelope of erythrocytes thus forming a more or less evident unfilled space (a 'cleft') (Fig. 63, *4*); the 'cleft' between the parasite and the erythrocyte envelope is less evident than the 'cleft' between the parasite and the erythrocyte nucleus; the 'cleft' between the parasite and the erythrocyte envelope, if present, is frequently interrupted (Fig. 63, *6*); the outline of gametocytes varies from even (Fig. 63, *3*) to highly ameboid (Fig. 63, *5*); the parasite nucleus is compact, variable in form, median or submedian in position and contains a clear chromatin clump; pigment granules are usually roundish, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 63, *8*, *9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; parasites with a highly ameboid and wavy

outline predominate; the 'cleft' between the parasite and the nucleus of erythrocyte is more evident and vacuoles in the cytoplasm are not as frequently seen as in macrogametocytes; other characters are as for macrogametocytes.

Comments. The variability of outline of gametocytes of *H. noctuae* has been frequently recorded (Coatney and Roudabush, 1937; Mohammed, 1958; Bishop and Bennett, 1989). In this connection, the following observation is of theoretical interest (Valkiūnas and Iezhova, 1989). *Haemoproteus noctuae* gametocytes with an even outline were frequently recorded among both macrogametocytes and microgametocytes in *Asio otus* during migration on the Baltic Sea coast. In owls during migration in the foothills of the Western Tien Shan (*Asio otus*, *Otus scops*) and during the breeding period in the delta of the Amu Darya River (*Athene noctua*), parasites with an even outline were rarely recorded only among macrogametocytes, and microgametocytes were seen being more or less ameboid in outline. In other words, the proportion of gametocytes with even and ameboid outlines is different in the same species (*Asio otus*) in the two above mentioned distant regions, and the proportion is similar in different bird species (*Asio otus*, *Otus scops*, *Athene noctua*) within the same geographical region. This confirms a geographical variability of the outline of the *H. noctuae* gametocytes rather than host-dependent variability.

Gametocytes of *H. tytoni* are morphologically identical to gametocytes of *H. noctuae*. The name *H. tytoni* was created for *noctuae*-like haemoproteids parasitizing strigiform birds belonging to the Tytonidae. Until the family level of specificity of *H. tytoni* is proved experimentally, this name is considered to be a junior synonym of *H. noctuae* (Valkiūnas, 1997).

5. **Haemoproteus (Parahaemoproteus) fringillae** (Labbé, 1894)

Halteridium fringillae Labbé, 1894: 157, Pl. 8, Fig. 1–24 (partim). – *Haemoproteus mazzai* Parodi and Niño, 1927: 359, Pl. 1, 2, Microphotograph (partim.). – *H. fringillae*: Coatney, 1936: 88. – *H. hedymelis* Coatney and Roudabush, 1937: 1008, Pl. 1, Fig. 5, 6. – *H. chloriis* Covaleda Ortega and Gállego Berenguer, 1950: 165, Pl. 4, Fig. 1–20. – *H. serini* Levine and Campbell, 1971: 478. – *H. fringillae*: Peirce, 1984e: 565 (=*H. chloriis*); Valkiūnas, 1997: 168 (= *H. hedymelis, H. mazzai, H. serini*).

Type vertebrate host. *Fringilla coelebs* L. (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 21).
Vectors. *Culicoides crepuscularis*, *C. impunctatus*, *C. sphagnumensis, C. stilobezzioides*, (Diptera: Ceratopogonidae). Previously (Glukhova and Valkiūnas, 1993; Valkiūnas, 1997), *C. impunctatus* was thought to belong to a closely related species *C. delta*, which also belongs to the *C. impunctatus* group (Glukhova, 1989). According to current knowledge, *C. delta* should be excluded from the list of vectors of this parasite.
Type locality. France.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Australian and Antarctic.
Type material. Neohapantotype (No. 92411, *Fringilla coelebs*, 28.06.1981, Bramley, Hants., United Kingdom, M.A. Peirce) and paraneohapantotypes (No. 67603, 21.05.1975, Prague, Czechoslovakia, J. Kučera; No. 58131, the date is unknown, Portugal, C. Mead, other data are as for the neohapantotype) are deposited in IRCAH. A series of additional slides of gametocytes, gametes, zygotes and ookinetes is deposited in CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Fringilla*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes, they slightly displace the

nucleus laterally and never encircle it completely. Gametocytes adhere to the nucleus and the envelope of erythrocytes. Dumbbell-shaped gametocytes predominate among growing macrogametocytes and are usually not present among microgametocytes. Fully grown macrogametocytes often do not fill the erythrocytes up to their poles. Pigment granules are usually of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size; their average number is about 14 per gametocyte. A species difficult to identify; can be distinguished from the close species of haemoproteids of birds belonging to the Passeriformes only on the basis of a detailed analysis of a set of characters.

Table 21 List of vertebrate hosts of *Haemoproteus fringillae.*

Acanthis cannabina	*Emberiza citrinella*	*P. ludovicianus*
A. flammea	*E. hortulana*	*Pyrrhula pyrrhula*
Carduelis carduelis	*Fringilla montifringilla*	*Serinus canaria*
Carpodacus erythrinus	*Melospiza georgiana*	*Spinus spinus*
Chloris chloris	*M. melodia*	
Coccothraustes coccothraustes	*Pheucticus aureoventris*	

Note: See 'Comments'.

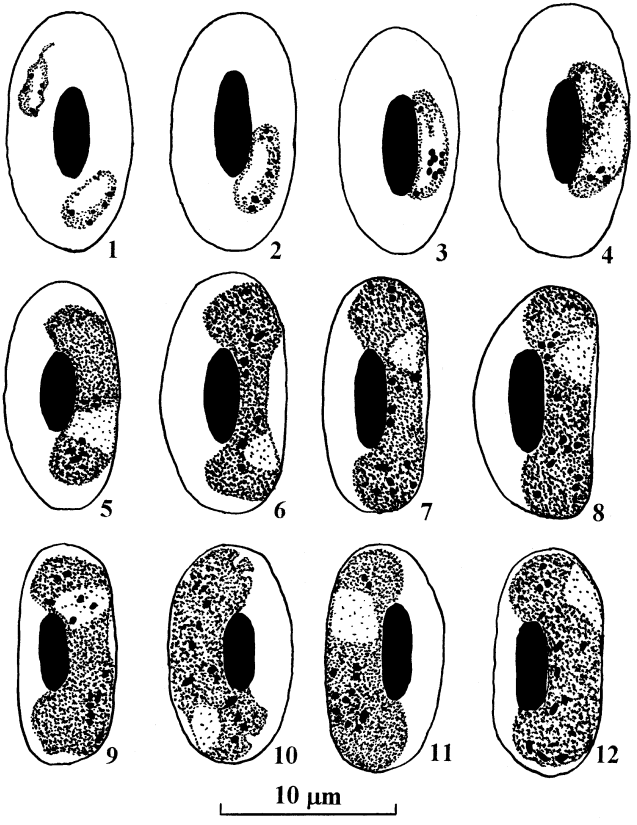

Figure 64 Gametocytes of *Haemoproteus fringillae* from the blood of *Fringilla coelebs: 1–4* – young; *5–12* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992b).

Table 22 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. (according to Valkiūnas and Iezhova, 1992b).

Feature	*H. fringillae*				*H. majoris*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	31				31			
Length		10.8–12.7	11.8	0.6		10.6–12.0	11.3	0.6
Width		5.7–6.8	6.4	0.2		5.8–6.9	6.1	0.2
Length of nucleus		4.6–6.1	5.5	0.4		4.6–5.9	5.5	0.2
Width of nucleus		2.0–3.1	2.5	0.2		1.8–2.7	2.2	0.2
Erythrocyte parasitized by macrogametocyte	31				31			
Length		12.3–14.4	12.9	0.8		10.4–12.6	11.7	0.6
Width		5.2–7.1	6.1	0.3		5.2–6.5	5.5	0.4
Length of nucleus		4.4–6.2	5.3	0.3		4.8–6.0	5.3	0.2
Width of nucleus		2.0–3.1	2.4	0.2		1.8–2.5	2.2	0.1
Erythrocyte parasitized by microgametocyte	31				31			
Length		11.2–14.6	12.6	0.8		10.9–13.2	12.2	0.7
Width		4.9–7.5	6.1	0.4		5.0–5.8	5.5	0.2
Length of nucleus		4.7–6.7	5.4	0.4		4.7–6.1	5.3	0.2
Width of nucleus		1.7–2.8	2.4	0.2		1.9–2.8	2.3	0.1
Macrogametocyte	31							
Length		10.7–11.8	11.2	0.4	31	10.8–14.6	12.8	0.8
Width		1.1–2.4	1.7	0.2	31	1.8–3.2	2.5	0.4
Length of nucleus		1.9–3.6	2.6	0.4	31	1.8–3.4	2.6	0.2
Width of nucleus		0.9–2.5	1.8	0.2	31	1.0–2.5	1.8	0.2
NDR		0.4–0.9	0.6	0.1	50	0.2–0.8	0.4	0.1
No. of pigment granules		8–18	14.1	1.6	31	8–14	10.5	0.8
Microgametocyte	31							
Length		10.8–13.2	11.6	0.6	31	10.3–14.0	12.7	0.7
Width		1.5–2.6	2.1	0.2	31	1.8–3.0	2.4	0.3
Length of nucleus		6.3–8.6	7.6	0.4	31	5.6–8.6	6.8	0.4
Width of nucleus		1.5–2.6	2.1	0.2	31	1.8–3.0	2.4	0.3
NDR		0.4–0.9	0.7	0.2	55	0.2–0.8	0.4	0.1
No. of pigment granules		8–18	13.4	1.6	31	8–14	10.0	0.8

Note: All sizes are given in micrometres.

Development in vertebrate host

Young gametocytes (Fig. 64, *1–4*). The earliest forms are usually seen in a polar position in infected erythrocytes lying free in the cytoplasm (Fig. 64, *1*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 64, *2*) and extend longitudinally along the nucleus (Fig. 64, *2*, *3*); gametocytes grow both in length and in width and completely fill the space between the envelope and the nucleus of erythrocytes (Fig. 64, *4*); the outline is usually even (Fig. 64, *1–4*) but sometimes ameboid (Fig. 64, *1*).

Macrogametocytes (Fig. 64, *5–12*; Table 22). The cytoplasm is heterogeneous in appearance; valutin granules are occasionally present; gametocytes grow along the nucleus

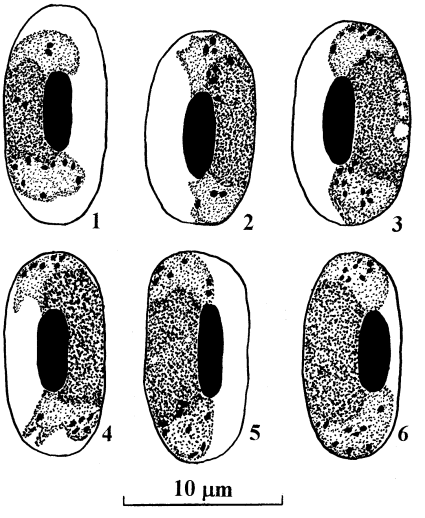

Figure 65 Microgametocytes of *Haemoproteus fringillae* from the blood of *Fringilla coelebs* (modified from Valkiūnas and Iezhova, 1992b).

of erythrocytes, they slightly enclose the nucleus with their ends but do not encircle the nucleus completely; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a clear dumbbell-like appearance (Fig. 64, *6*, *7*); the dumbbell-shaped forms usually predominate among growing gametocytes; as the parasite develops, the 'dip' decreases in size and the dumbbell-shaped gametocytes disappear (Fig. 64, *7–12*); fully grown gametocytes frequently do not fill the erythrocytes up to their poles where a more or less pronounced unfilled space is frequently present (Fig. 64, *9–12*), and this is a characteristic feature of the growth of macrogametocytes of *H. fringillae*; the outline is even (Fig. 64, *8*, *11*, *12*) or angular (Fig. 64, *6*, *7*, *9*), sometimes ameboid (Fig. 64, *10*); growing gametocytes usually do not displace the nucleus of erythrocytes laterally; however, the fully grown forms markedly displace it (Fig. 64, *12*); the parasite nucleus is compact, variable in form, frequently triangular, subterminal in position; pigment granules are usually roundish, of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, randomly scattered throughout the cytoplasm; gametocytes often markedly influence the infected erythrocyte, causing its deformation (Fig. 64, *8*) and atrophy in width (Fig. 64, *9*).

Microgametocytes (Fig. 65). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters. They also differ from the macrogametocytes, first of all, by (i) a more frequently seen and more pronounced ameboid outline (Fig. 65, *2*, *4*), (ii) the absence of dumbbell-shaped forms (Fig. 65, *1–6*), and (iii) completely occupied poles of infected erythrocytes (Fig. 65, *5*, *6*). Incidentally, several large vacuoles can be seen near the pellicle in front of the envelope of erythrocytes (Fig. 65, *3*). A linear combination of these vacuoles may be similar in form to the 'dip' recorded in macrogametocytes. Other characters are as for macrogametocytes.

Development in vector has been insufficiently investigated. Sporogony is completed in the biting midges *Culicoides crepuscularis*, *C. impunctatus*, *C. sphagnumensis C. stilobezzioides* (Fallis and Bennett, 1961a, 1961b; Valkiūnas, 1997).

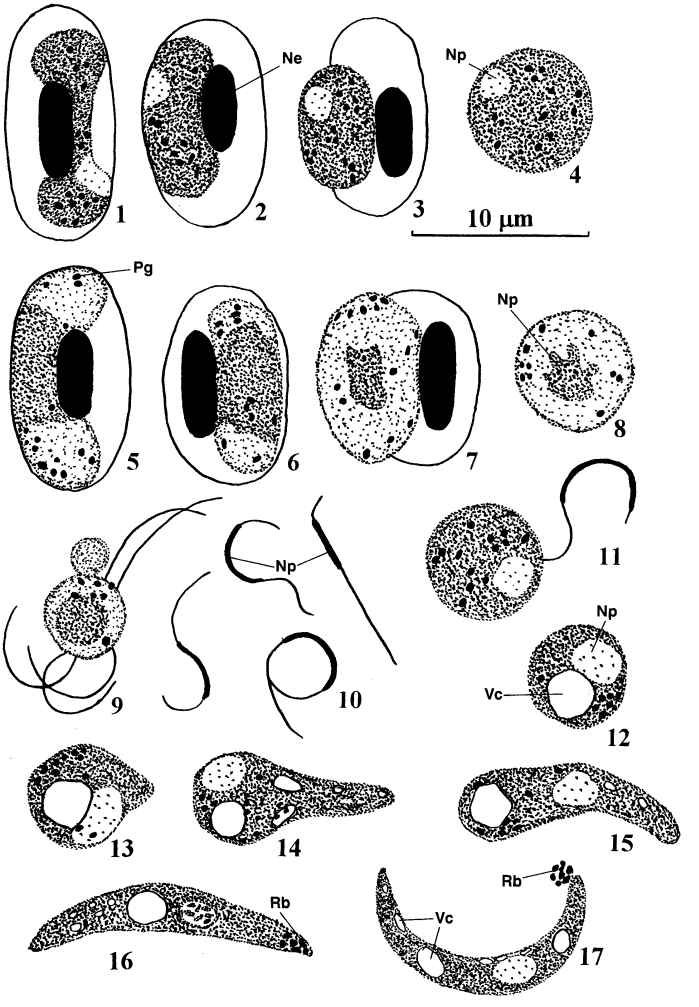

Figure 66 *Haemoproteus fringillae* gametogenesis, zygote and ookinete development *in vitro*: *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Fringilla coelebs* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14*, *15* – medium differentiated ookinete; *16*, *17* – ookinete with a residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1993a).

The gametogenesis, development of zygote and ookinete *in vitro* under a light microscope at temperature 18 to 20°C were studied by Valkiūnas and Iezhova (1993a, 1994). The data on the rate of this process are given in Table 23. Within 5 min after exposure of infected blood to the air (EBA), exflagellation (Fig. 66, *9*) and fertilization of macrogametes (Fig. 66, *11*) were recorded. It should be noted that a residual body, which frequently has a spherical outgrowth, develops during the exflagellation (Fig. 66, *9*). The role of the outgrowth is unclear. Incidentally, the exflagellation takes place inside the

Table 23 Gametogenesis, zygote and ookinete development *in vitro* of four species of *Haemoproteus* (modified from Valkiūnas and Iezhova, 1993a).

Stage of development	Time after exposure of blood with mature gametocytes to air																									
	s	min													h											
	30	1	2	4	5	6	8	10	15	20	30	35	45	1	1.5	2	3	4	6	8	9	12	24	36	48	60
Rounded up gametocyte, *2*, *6–7*	–	■	■	■		■		■	■		■		■	■	■	■	–		–	–						
	–	♦	♦	♦		♦	♦	♦	♦		♦		♦	♦	♦	♦	–	–				♦	♦	♦	–	–
					●			●		●		●		●			●		–		–	–	–			
	▲	▲	▲	▲		▲		▲	▲		▲		▲	▲	▲	▲	▲									
Gametocyte leave the infected erythrocyte, *3*	–	–	■	■		■		■	■		■		■	■	■	–	–		–	–						
	–	–	♦	♦		♦	♦	♦	♦		♦		♦	♦	♦	–	–	–				♦	♦	–	–	–
					●			●		●		●		●			●		–		–	–	–			
	▲	▲	▲	▲		▲		▲	▲		▲		▲	▲	▲	▲	▲									
Macro-gamete, *4*	–	–	■	■		■		■	■		■		■	■	■	■	■		■	■						
	–	–	♦	♦		♦	♦	♦	♦		♦		♦	♦	♦	♦	♦	♦				♦	♦	♦	–	–
					●			●		●		●		●			●		●		●	●	–			
	▲	▲	▲	▲		▲		▲	▲		▲		▲	▲	▲	▲	▲									
Exfla-gellation, *9*	–	–	–	■		■		■	■		■		■	■	■	–	–		–	–						
	–	–	–	♦		♦	♦	♦	–		–		–	–	–	–	–	–				–	–	–	–	–
					●			●		●		●		●			–		–		–	–	–			
	–	▲	▲	▲		▲		▲	▲		▲		–	▲	▲	–	▲									
Micro-gamete, *10*	–	–	–	■		■		■	■		■		■	■	■	■	■		■	■						
	–	–	–	♦		♦	♦	♦	♦		♦		♦	♦	♦	♦	♦	♦				♦	♦	–	–	–
					●			●		●		●		●			●		●		●	●	–			
	–	▲	▲	▲		▲		▲	▲		▲		▲	▲	▲	▲	▲									
Fertilization, *11*	–	–	–	–		■		■	■		■		■	■	■	–	■		■	–						
	–	–	–	♦		♦	♦	♦	♦		♦		♦	♦	♦	–	–	♦				–	–	–	–	–
					●			●		●		●		●			●		–		–	–	–			
	–	–	–	–		▲		▲	▲		▲		▲	–	–	–	▲									
Zygote, *12*	–	–	–	–		■		■	■		■		■	■	■	■	■		■	■						
	–	–	–	♦		♦	♦	♦	♦		♦		♦	♦	♦	♦	♦	♦				♦	♦	♦	–	–
					–			●		●		●		●			●		●		●	●	●			
	–	–	–	–		▲		▲	▲		▲		▲	▲	▲	▲	▲									
Initial stage of differen-tiation of ookinete, *13*	–	–	–	–		–		–	–		–		–	–	■	■	■		■	–						
	–	–	–	–		–	–	–	–		–		–	–	–	–	–	–				♦	♦	–	–	♦
					–			–		–		–		–			●		●		●	●	●			
	–	–	–	–		–		–	–		▲		▲	▲	▲	▲	▲									
Medium differentiated ookinete, *14*	–	–	–	–		–		–	–		–		–	–	–	–	■		■	■						
	–	–	–	–		–	–	–	–		–		–	–	–	–	–	–				♦	♦	♦	♦	♦
					–			–		–		–		–			–		●		●	●	●			
	–	–	–	–		–		–	–		▲		▲	▲	▲	▲	▲									
Ookinete with the residual body, *15*	–	–	–	–		–		–	–		–		–	–	–	–	–		■	■						
	–	–	–	–		–	–	–	–		–		–	–	–	–	–	–					–	–	♦	♦	♦
					–			–		–		–		–			–		●		●	●	●			
	–	–	–	–		–		–	–		▲		▲	–	–	–	–									

Table 23 (continued).

Stage of development	Time after exposure of blood with mature gametocytes to air																								
	s	min												h											
	30	1	2	4	5	6	8	10	15	20	30	35	45	1	1.5	2	3	4	6	8	9	12	24	36	48	60
Ookinete without the residual body, *16*	–	–	–	–		–		–	–		–		–	–	–	–	–		–	–						
	–	–	–	–		–	–	–	–		–		–	–	–	–	–	–					–	–	–	♦	♦
					–			–		–		–		–			–		–		–	–	–			
	–	–	–	–		–		–	–		–		▲	▲	▲	▲	▲									

Note: Numbers in the column 'Stage of development' correspond to the stages shown in Fig. 163. Species of haemoproteids: ■ – *Haemoproteus belopolskyi*, ♦ – *H. tartakovskyi*, ● – *H. fringillae*, ▲ – *H. pallidus*; '–' – time when parasite at the certain stage was not seen; absence of the symbols – time when the development of parasite was not studied.

erythrocytes (Fig. 67) which is an abnormal process. The first zygotes were seen 10 min after EBA (Fig. 66, *12*). They can be readily distinguished from macrogametes by the presence of one large 'vacuole' in their cytoplasm. The initial stages of ookinete differentiation were seen approximately 3 h since the first zygotes had appeared. At this time, a short blunt outgrowth appeared in the centre of the parasite (Fig. 66, *13*). This outgrowth extended, and the developing ookinete took a pear-like or skittle-like shape (Fig. 66, *14*). As the ookinete developed, this outgrowth extended markedly and formed the anterior or

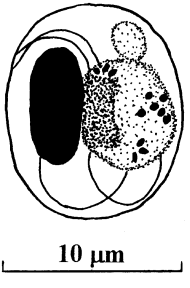

Figure 67 Exflagellation of *Haemoproteus fringillae* inside of infected erythrocyte (modified from Valkiūnas and Iezhova, 1993a).

apical end of the ookinete. Accumulation of pigment granules was recorded at the opposite end of the medium differentiated ookinetes (Fig. 66, *15*). In fully grown ookinetes, the pigment and adjacent part of cytoplasm are eliminated as a residual body (Pl. III, *2*). It should be noted that the residual body is not clearly defined in developing ookinetes, and it can be recognized mainly by the accumulation of pigment granules (Fig. 66, *16*). At all stages of development, one or several clear large 'vacuoles' are present in ookinete (Fig. 66, *13–17*; Pl. III, *2*). This is a distinctive character of this species. Ookinetes with residual body were seen approximately 6 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 24.

P a t h o g e n i c i t y. Clinical signs of illness are not recorded in naturally infected wild birds who were kept in laboratory conditions. At the peak of parasitemia, the decrease in the body mass and the lowering of locomotive activity of young *Fringilla coelebs* have been recorded (Valkiūnas, 1991). In field conditions, this means the decrease of the ability to compete and leads to the increased probability for elimination of the infected specimens (for details, see p. 97).

Table 24 Morphometric parameters of gametes and ookinetes of four species of *Haemoproteus* (according to Valkiūnas and Iezhova, 1993a).

Feature	*H. belopolskyi*				*H. tartakovskyi*				*H. fringillae*				*H. pallidus*			
	n	lim	$\overline{X}$	$m\bar{x}$	*n*	lim	$\overline{X}$	$m\bar{x}$	*n*	lim	$\overline{X}$	$m\bar{x}$	*n*	lim	$\overline{X}$	$m\bar{x}$
Macrogamete	31				20				12				12			
Length		5.9–7.7	6.6	0.2		6.3–7.4	6.6	0.1		5.9–6.9	6.3	0.4		5.5–6.7	6.3	0.3
Width		5.1–7.4	6.0	0.4		5.0–6.4	6.0	0.2		5.5–6.4	6.0	0.2		5.4–6.5	6.0	0.2
Microgamete	11				20				12				12			
Length		11.1–14.1	12.4	0.7		11.4–14.4	12.8	0.2		9.9–15.1	13.1	0.4		7.9–10	8.8	0.3
Width		0.6–0.8	0.7	0.1		0.5–0.7	0.6	0.03		0.6–0.9	0.7	0.1		0.6–0.8	0.7	0.04
Ookinete	6				8				12				12			
Length		14.6–16.3	15.6	0.7		16.4–19.8	18.0	0.5		12.6–16.2	14.6	0.6		8.6–9.9	9.2	0.3
Width		2.0–2.3	2.2	0.1		2.1–2.8	2.6	0.2		2.0–3.2	2.5	0.2		3.0–3.4	3.2	0.3

Note: All sizes are given in micrometres.

S p e c i f i c i t y. *Haemoproteus fringillae* isolated from *Emberiza citrinella* (Passeriformes: Emberizidae), completes its development in the biting midge *Culicoides impunctatus*. Sporozoites, isolated from this vector, induce the infection and development of viable gametocytes in *Fringilla coelebs* (Fringillidae) (Valkiūnas, 1997).

C o m m e n t s. *Haemoproteus fringillae* belongs to the group of species whose identification is difficult, and it can be distinguished from the similar species of haemoproteids only on the basis of a detailed analysis of numerous characters of gametocytes and their host cells. To do this, good quality blood films containing all the main stages of the development of gametocytes are required. It should be noted that, during the identification of *H. fringillae*, attention should be paid first of all to (i) the differences in morphology of macro- and microgametocytes, and (ii) the simultaneous presence of gametocytes shown in Fig. 64, *6*, *9*, *12* in the blood films.

Haemoproteus chloriis was first noted among synonyms of *H. fringillae* by Peirce (1984e). That paper also gives the argumentation of the synonymy. The morphology of gametocytes of *H. chloriis* in the blood of type vertebrate host *Chloris chloris* as well as gametogenesis, zygote and ookinete development of this parasite *in vitro* were studied by Valkiūnas (1997). The investigated stages of development of *H. chloriis* are identical to these in *H. fringillae*. These facts give grounds to support the above mentioned position of M.A. Peirce and to consider *H. chloriis* as a junior synonym of *H. fringillae*.

The status of *H. serini* as a synonym of *H. chloriis* was substantiated by Burry-Caines and Bennett (1992). After the synonymy of *H. chloriis* with *H. fringillae,* the specific name *H. serini* becomes a junior synonym of *H. fringillae* (Valkiūnas, 1997).

Burry-Caines and Bennett (1992) redescribed *H. mazzai* and designated the neotype material. Analysis of the neotypes has shown the identity of gametocytes of *H. fringillae* and *H. mazzai*. Furthermore, haemoproteids isolated from species of the Emberizidae (hosts of *H. mazzai*) successfully develop in species of the Fringillidae (common hosts of *H. fringillae*) (see the paragraph 'Specificity'). These facts give grounds for declaring *H. mazzai* to be a junior synonym of *H. fringillae* (Valkiūnas, 1997).

The status of *H. hedymelis* as a synonym of *H. mazzai* (=*H. fringillae*) was substantiated by Burry-Caines and Bennett (1992). After synonymy of *H. mazzai* with *H. fringillae,* the specific name *H. hedymelis* becomes a junior synonym of *H. fringillae* (Valkiūnas, 1997).

The specific name *H. fringillae* was previously often used by numerous authors for haemoproteids parasitizing various passerine birds without comparison of the morphology of the parasites. As a result, the range of vertebrate hosts of this species has been artificially extended (Bennett *et al*.,

1982b; Bishop and Bennett, 1992). It is certain that numerous species of the haemoproteids have been mentioned under the name *H. fringillae* in the literature, and the list of the vertebrate hosts of this parasite should be revised. That is why only well described and (or) illustrated records were included in Table 21.

Khan and Fallis (1969) recorded exoerythrocytic meronts in *Zonotrichia albicollis* and described them under the name *H. fringillae*. Burry-Caines and Bennett (1992) showed that these meronts belong to *H. coatneyi.* It is important to note that the range of hosts of *H. coatneyi* and *H. fringillae* partly overlaps, and it is not easy to distinguish *H. coatneyi* from *H. fringillae* in naturally infected birds. During the identification of these species, attention should be paid first of all to the following characters. The fully grown gametocytes of *H. coatneyi* fill the infected erythrocytes up to their poles, and the dumbbell-shaped forms are common among its growing microgametocytes. Both features are not characteristic of *H. fringillae.*

6. **Haemoproteus (Parahaemoproteus) majoris** (Laveran, 1902)

Haemamoeba majoris Laveran, 1902: 1122, Fig. 2 (partim). – *Haemoproteus majoris:* Sambon, 1908: 246. – *H. machlolophi* Mello, 1935a: 354. – *H. majoris*: Peirce, 1981a: 151 (=*H. machlolophi*).

Type vertebrate host. *Parus major* L. (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 25).
Type locality. Metz, France.
Distribution. The Holarctic, Ethiopian, and Oriental zoogeographical regions.
Type material. Neohapantotype (No. G436558, *Parus major*, 09.05.1972, Silwood Park, Berkshire, England, M.A. Peirce) is deposited in IRCAH. A series of good additional slides of gametocytes is in IRCAH, CDVA; and slides of gametes, zygotes and ookinetes are in CDVA.
Etymology. The specific name is derived from the specific name of the type host, *major*.

Table 25 List of vertebrate hosts of *Haemoproteus majoris* (modified from Valkiūnas and Iezhova, 1992b).

Parus ater	*P. carolinensis*	*P. palustris*	*P. trochiloides*	*S. borin*
P. bicolor	*P. cristatus*	*P. xanthogenys*	*P. trochilus*	*S. communis*
P. caeruleus	*P. montanus*	*Phylloscopus sibilatrix*	*Sylvia atricapilla*	

Note: See also 'Comment.'

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes, but do not encircle it completely. Gametocytes adhere to the nucleus and the envelope of erythrocytes. Dumbbell-shaped gametocytes are present among macrogametocytes, and they represent over 10% of the total number of the growing macrogametocytes. Pigment granules are usually roundish in form, of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, with about 10 per gametocyte on average. A species difficult for identification; can be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes only on the basis of a detailed analysis of a set of characters.

Development in vertebrate host
Young gametocytes (Fig. 68, *1–3*). The earliest forms are frequently seen in a polar position in infected erythrocytes, usually roundish or oval in shape (Fig. 68, *1*); growing

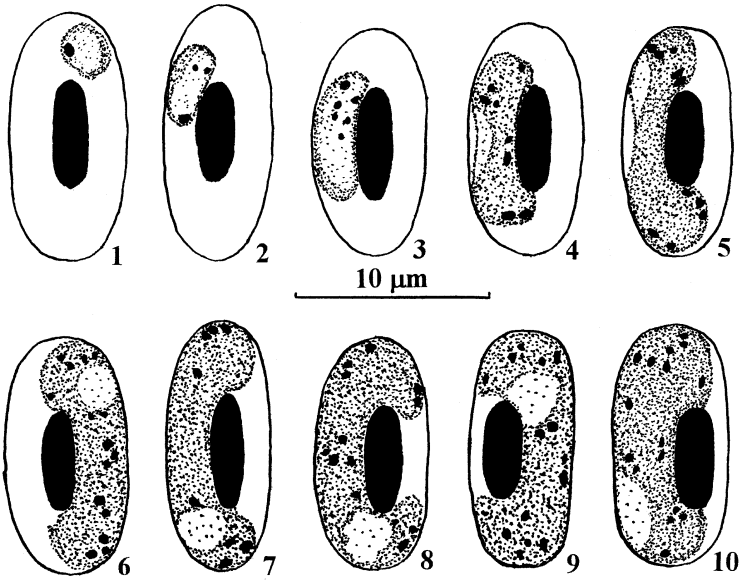

Figure 68 Gametocytes of *Haemoproteus majoris* from the blood of *Parus major: 1–3* – young; *4–10* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992b).

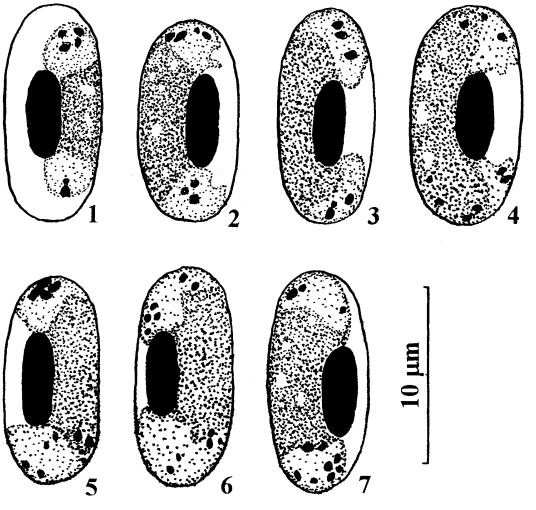

Figure 69 Microgametocytes of *Haemoproteus majoris* from the blood of *Parus major* (modified from Valkiūnas and Iezhova, 1992b).

gametocytes adhere to the nucleus of erythrocytes and extend along the nucleus; their growth in length is accompanied with relatively rapid growth in width, and, as a result, even young gametocytes completely fill the space between the nucleus and the envelope of erythrocytes (Fig. 68, *3*) and slightly displace the erythrocyte nucleus; the outline is usually even.

Table 26 Gametogenesis, zygote and ookinete development *in vitro* of three species of *Haemoproteus* (modified from Valkiūnas and Iezhova, 1994).

Stage of development	Time after exposure of blood with mature gametocytes to air													
	min							h						
	1	3	5	10	15	30	45	1	1.5	3	6	12	24	48
Rounded up gametocyte, *2, 6*	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	♦				
Gametocyte leave the infected erythrocyte, *3, 7*	♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	♦				
Macrogamete, *4*	♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦				
Exflagellation, *9*	♦	● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	● ♦	● ♦	♦	♦				
Microgamete, *10*	♦	● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	● ♦	● ♦	● ♦					
Fertilization, *11*			■ ●	■ ●	■ ●	■ ● ♦	♦	♦	♦					
Zygote, *12*			■ ●	■ ●	■ ●	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦	■ ● ♦
Initial stage of differentiation of ookinete, *13*							■	■	■	■ ●	■ ● ♦	● ♦	● ♦	● ♦
Medium differentiated ookinete, *14*									■	■	■ ● ♦	■ ● ♦	● ♦	● ♦
Ookinete with the residual body, *15*											■ ●	■ ●	● ♦	● ♦
Ookinete without the residual body, *16*											■	■		● ♦

Note: Numbers in the column "Stage of development" correspond to the stages shown in Fig. 7. Species of haemoproteids: ■ – *Haemoproteus majoris*, ● – *H. balmorali*, ♦ – *H. dolniki*, absence of the symbols — time when a parasite at the certain stage of development was not recorded.

Macrogametocytes (Fig. 68, *4–10*; Table 22). The cytoplasm is homogeneous in appearance; valutin granules are usually absent; gametocytes grow around the nucleus of erythrocytes, enclose the nucleus with their ends, but do not encircle it completely; gametocytes adhere to the nucleus and the envelope of erythrocytes; the central part of the pellicle

of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 68, *4*); this 'dip' persists in medium grown forms (Fig. 68, *5*), but subsequently disappears (Fig. 68, *6*); the dumbbell-shaped forms (Fig. 68, *5*) are over 10% of the total number of growing gametocytes; fully grown gametocytes are closely appressed to the nucleus and the envelope of erythrocytes, and fill the erythrocytes up to their poles (Fig. 68, *8–10*); the outline is usually even; the parasite nucleus is compact, variable in form, frequently roundish, subterminal in position; pigment granules are usually roundish, sometimes oval or rod-like, usually of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 69). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; gametocytes with an ameboid outline are present (Fig. 69, *2*, *4*), and they are more numerous than among macrogametocytes; vacuole-like structures have been seen in the zone of the parasite nucleus (Fig. 69, *1*, *2*, *4*, *7*); other characters are as for macrogametocytes.

Development in vector has not been investigated. The gametogenesis, development of zygote and ookinete *in vitro* under the light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1994). The data on the rate of this process are given in Table 26. Within 1 to 3 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave their host cells (Fig. 7, *3*, *4*, *7*, *8*). At approximately the same time, free macrogametes appear (Fig. 7, *4*). Exflagellation (Fig. 7, *9*), free microgametes (Fig. 7, *10*), fertilization of macrogametes (Fig. 7, *11*) and zygotes (Fig. 7, *12*) were seen 5 min after EBA. Zygotes are morphologically identical to macrogametes. The initial stages of ookinete differentiation were seen 45 min after EBA. At this time, a long thin finger-like outgrowth appears, located tangentially to the main body of the parasite (Fig. 7, *13*). As the ookinete develops, this outgrowth extends markedly and forms the anterior or apical end of the ookinete. On the opposite end of the medium differentiated ookinetes, the accumulation of pigment granules is recorded (Fig. 7, *14*). In fully grown ookinetes, the pigment and adjacent part of the cytoplasm are eliminating as a residual body (Fig. 7, *15*). At the late stages of ookinete development, large 'vacuoles' appear in the cytoplasm (Fig. 7, *15*, *16*). Fully developed ookinetes are elongated worm-like bodies (Fig. 7, *16*). Ookinetes with the residual body and mature ookinetes appear 6 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 27.

Table 27 Morphometric parameters of gametes and ookinetes of three species of *Haemoproteus* (according to Valkiūnas and Iezhova, 1994).

Feature	*H. balmorali*				*H. dolniki*				*H. majoris*			
	n	lim	$\overline{X}$	$m\bar{x}$	*n*	lim	$\overline{X}$	$m\bar{x}$	*n*	lim	$\overline{X}$	$m\bar{x}$
Macrogamete	15				15				15			
Length		6.2–7.7	6.7	0.2		6.0–7.4	6.6	0.3		5.7–7.7	6.7	0.3
Width		4.9–7.1	6.0	0.4		5.2–6.5	5.8	0.2		5.2–6.1	5.6	0.1
Microgamete	15				15				15			
Length		10.6–14.3	12.9	0.6		11.1–14.2	13.0	0.5		11.2–17.2	13.5	1.1
Width		0.4–0.6	0.5	0.04		0.4–0.6	0.5	0.03		0.4–0.6	0.5	0.04
Ookinete	15				4				15			
Length		12.0–18.6	14.7	1.0		13.7–18.5	15.1	3.2		13.4–15.3	13.3	2.8
Width		2.2–2.9	2.6	0.1		3.0–3.9	3.4	0.5		2.1–3.2	2.7	0.2

Note: All sizes are given in micrometres.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. majoris* is especially similar to *H. balmorali* and *H. queleae*. The shape of the earliest gametocytes of *H. balmorali* is clearly elongated and rod-like, and numerous valutin granules are always present in growing and fully grown gametocytes. These features are not characteristic of *H. majoris*. It should be also noted that one large clear vacuole is present in zygotes of *H. balmorali,* but not in zygotes of *H. majoris*. Fully grown gametocytes of *H. majoris* can be distinguished from *H. queleae* primarily on the basis of significantly smaller number of pigment granules in its gametocytes.

Analysis of the mitochondrial DNA of *H. majoris* (Bensch *et al*., 2000) provided evidence that a similar parasite also develops in birds of the family Sylviidae. It is probable that *H. sylvae* may be, in part, a synonym of *H. majoris.* Further investigations are needed to solve this taxonomic question.

7. **Haemoproteus (Parahaemoproteus) crumenium** (Hirst, 1905)

Halteridium crumenium Hirst, 1905: 297. – *Haemoproteus crumenium*: Coatney, 1936: 88. – *H. brodkorbi* Forrester, Greiner, Bennett and Kigave, 1977: 1269, Fig. 1–7. – *H. crumenium*: Peirce, 1987: 677 (=*H. brodkorbi*).

Type vertebrate host. *Leptoptilus crumeniferus* (Lesson) (Ciconiiformes).
Additional vertebrate host. *Mycteria americana* (Ciconiiformes).
Type locality was not designated in the original description. Neotype locality is Nairobi, Kenya (Peirce and Cooper, 1977).
Distribution has not been investigated. This parasite has been recorded in the Ethiopian zoogeographical region and in the Nearctic. It is likely that the range is wider.
Type material. Neohapantotype (No. 67225, *Leptoptilus crumeniferus,* 1972, Nairobi, Kenya, J.E. Cooper) is deposited in IRCAH. Paraneohapantotype (data are as for the neohapantotype) is deposited in WMCL.
Etymology. The specific name was derived from the specific name of the type host, *crumeniferus.*

Main diagnostic characters. A parasite of species of the Ciconiiformes whose gametocytes grow along the nucleus of infected erythrocytes, they fill the erythrocytes up to their poles, slightly enclose the nucleus with their ends, but do not encircle the nucleus completely. Growing gametocytes, which do not touch the nucleus of infected erythrocytes, are present. The nucleus of macrogametocyte adhere to the parasite pellicle from the side of erythrocyte nucleus (Fig. 70, *4*). The average number of pigment granules in macrogametocytes is about 20, and it is approximately 1.5 to 2 times less in microgametocytes.

Development in vertebrate host
The description of gametocytes is based on Peirce and Cooper (1977), and it includes new data.

Young gametocytes (Fig. 70, *1*) are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes, and they are closely appressed to the envelope of erythrocytes; gametocytes, which do not touch the nucleus of erythrocytes, are present; the outline is usually even, but sometimes also wavy.

Macrogametocytes (Fig. 70, *2–5*, *7*). The cytoplasm is granular in appearance, frequently contains several clear vacuoles; valutin granules are usually present; gametocytes

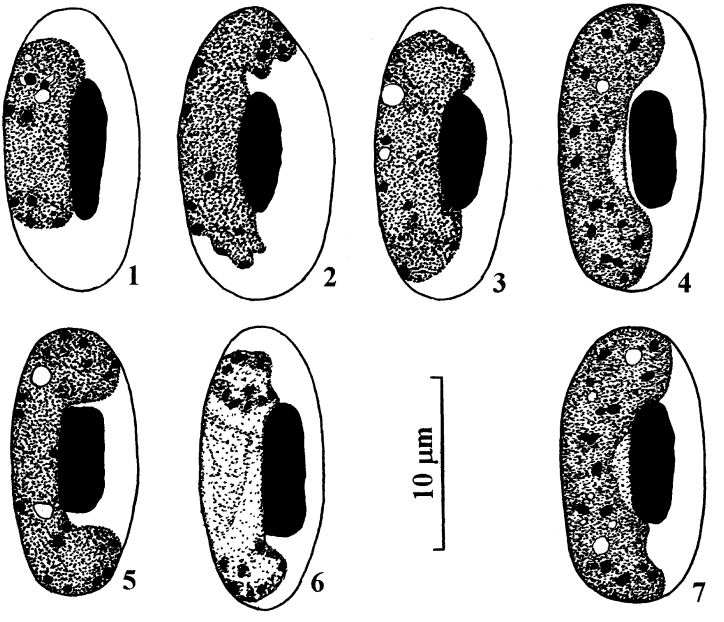

Figure 70 Gametocytes of *Haemoproteus crumenium* from the blood of *Leptoptilus crumeniferus: 1* – young; *2–5*, *7* – macrogametocytes; *6* – microgametocyte (*1–3*, *5*, *6* are modified from Peirce and Cooper, 1977).

grow along the nucleus of erythrocytes, they slightly enclose the nucleus with their ends and never encircle it completely; growing gametocytes frequently do not touch the nucleus of erythrocyte (Fig. 70, *4*); fully grown gametocytes fill the erythrocytes up to their poles (Fig. 70, *7*), and are closely appressed to the nucleus and the envelope of erythrocytes (Fig. 70, *7*); the outline of growing gametocytes is usually even, sometimes wavy (Fig. 70, *2*), and the outline of fully grown forms is even; the parasite nucleus is compact, variable in form, frequently ribbon-like in shape, median or submedian in position, closely appressed to the pellicle of gametocyte from the side of the erythrocyte nucleus (Fig. 70, *4*, *7*); pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, vary from 9 to 33 (on average 18 per parasite); the size of uninfected erythrocytes ($n = 25$) is 12.0 to 18.9 by 6.9 to 9.5 (on average 15.5×7.9) μm, and the size of infected ones ($n = 25$) is 13.8 to 18.9 by 6.9 to 9.5 (on average 16.6×8.3) μm; the nucleus of infected erythrocytes is slightly displaced laterally, NDR is about 0.5.

Microgametocytes (Fig. 70, *6*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules are slightly larger than in macrogametocytes but do not exceed 1.0 μm; the number of pigment granules varies from 4 to 18 (on average 11.3 per parasite); other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Ciconiiformes, *H. crumenium* is especially similar to *H. plataleae*. It can be distinguished from the latter species primarily on the basis of (i) the smaller number of pigment granules in its gametocytes and (ii) the position of the nucleus in its macrogametocytes.

8. **Haemoproteus (Parahaemoproteus) hirundinis** (Sergent and Sergent, 1905)

Haemamoeba danilewskyi var. *hirundinis* Sergent and Sergent, 1905: 57, Fig. – *Haemoproteus hirundinis*: Levine and Campbell, 1971: 477 (emend. pro var. *hirundinis*). – *H. prognei* Coatney and Roudabush, 1937: 1010, Pl. 1, Fig. 11, 12. – *H. hirundinis*: Valkiūnas and Iezhova, 1992b: 75 (=*H. prognei*).

Type vertebrate host. *Hirundo* sp. (the type host was identified only to the generic level in the original description) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 28).
Type locality. Algeria.
Distribution. The Holarctic, Ethiopian and Oriental zoogeographical regions.
Type material has never been designated. The designation of neotype material and neotype host is required. These may be parasites of a species of swallow from Algeria. A series of additional slides is deposited in IRCAH and CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Hirundo*.

Table 28 List of vertebrate hosts of *Haemoproteus hirundinis* (modified from Valkiūnas and Iezhova, 1992b).

Delichon urbica	*H. rustica*	*Progne subis*
Hirundo abyssinica	*H. spilodera*	*Riparia paludicola*
H. daurica	*Phaeoprogne tapera*	*R. riparia*

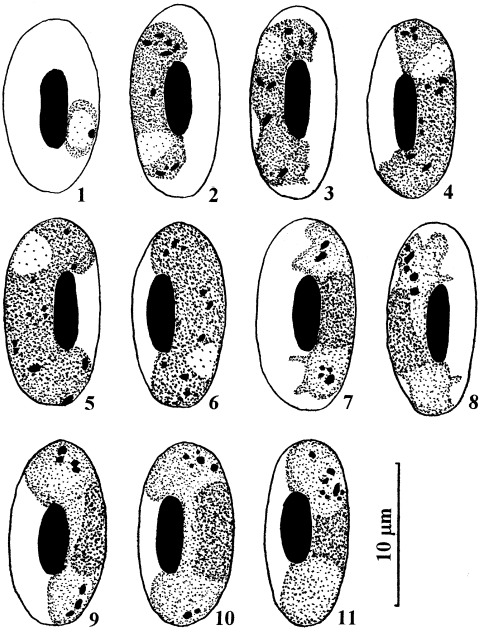

Figure 71 Gametocytes of *Haemoproteus hirundinis* from the blood of *Delichon urbica:* *1* – young; *2–6* – macrogametocytes; *7–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1992b).

Table 29 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. hirundinis* (according to Valkiūnas and Iezhova, 1992b)				*H. porzanae* (modified from Bennett, 1980)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				10		
Length		10.2–12.4	11.4	0.5		11.8	0.3
Width		5.2–6.9	6.2	0.3		6.5	0.4
Length of nucleus		5.0–6.1	5.5	0.2		5.3	0.3
Width of nucleus		1.9–2.6	2.2	0.1		2.1	0.1
Erythrocyte parasitized by macrogametocyte	31				26		
Length		11.3–13.2	12.4	0.6		11.9	0.6
Width		5.0–7.1	6.0	0.4		6.2	0.6
Length of nucleus		4.7–6.7	5.7	0.2		5.6	0.6
Width of nucleus		1.6–2.5	2.1	0.1		2.0	0.2
Erythrocyte parasitized by microgametocyte	31				10		
Length		10.8–13.2	12.3	0.7		11.5	0.5
Width		5.0–7.1	6.4	0.4		6.0	0.8
Length of nucleus		5.1–6.9	5.8	0.2		5.5	0.4
Width of nucleus		1.6–2.6	2.2	0.2		1.9	0.2
Macrogametocyte	31				26		
Length		10.3–15.5	13.1	0.8		13.7	1.0
Width		2.2–3.4	2.8	0.2		1.7	0.7
Length of nucleus		2.2–3.4	2.8	0.2		2.1	0.3
Width of nucleus		1.3–2.6	2.1	0.2		1.7	0.4
NDR		0.4–0.9	0.7	0.1		0.7	–
No. of pigment granules		6–12	9.5	1.1		9.9	1.9
Microgametocyte	31				10		
Length		11.2–15.0	12.8	0.7		12.3	0.9
Width		2.4–4.0	2.9	0.4		1.9	0.5
Length of nucleus		4.9–7.7	6.2	0.5		4.8	0.6
Width of nucleus		2.4–4.0	2.9	0.3		1.8	0.4
NDR		0.1–0.9	0.7	0.1		0.6	–
No. of pigment granules		5–12	8.0	1.4		8.6	1.8

Note: All sizes are given in micrometres.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes, but do not encircle it completely. Medium and fully grown gametocytes adhere to the nucleus and the envelope of erythrocytes. Dumbbell-shaped gametocytes are absent or they represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes fill the erythrocytes up to their poles. Pigment granules vary from small (<0.5 μm) to large (1.0 to 1.5 μm), with about nine per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 71, *1*). The earliest forms are usually seen located in a lateral position to the erythrocyte nucleus, roundish or oval in form; the outline is usually even; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend along the nucleus, completely filling the space between the envelope and nucleus of erythrocytes (Fig. 71, *1*).

Macrogametocytes (Fig. 71, *2–6*; Table 29). The cytoplasm is homogeneous in appearance; gametocytes grow around the nucleus of erythrocytes, they slightly enclose the nucleus with their ends but never encircle it completely; gametocytes adhere to the nucleus and the envelope of erythrocytes; the central part of the pellicle of some growing gametocytes sometimes does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 71, *3*), however, the dumbbell-shaped forms are uncommon, and represent less than 10% of the total number of growing gametocytes; fully grown gametocytes are closely appressed both to the nucleus and the envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 71, *4–6*); the outline is usually even (Fig. 71, *5*, *6*) and sometimes wavy (Fig. 71, *3*, *4*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are randomly scattered throughout the cytoplasm, they vary from small (<0.5 μm) and medium (0.5 to 1.0 μm) to large (1.0 to 1.5 μm), and this is one of the most characteristic features of this parasite. It should be noted that large pigment granules are present not in all fully grown gametocytes and medium-size pigment granules predominate.

Microgametocytes (Fig. 71, *7–11*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline of growing forms is more ameboid than in macrogametocytes (Fig. 71, *7*, *8*); other characters are as for macrogametocytes.

Comments. In 1 of 11 investigated swallows in Algeria, the Sergent brothers (Sergent and Sergent, 1905) recorded gametocytes of haemoproteids which were briefly described under the name *Haemamoeba danilewskyi* var. *hirundinis*. The infected bird was identified only up to the generic level, *Hirundo* sp. The original description is accompanied with an illustration of one macrogametocyte. Levine and Campbell (1971) raised this variety up to the specific level and related it to the genus *Haemoproteus*. According to the illustration in the original description, *H. hirundinis* is characterized by the following main characters. First, macrogametocyte lies free in the cytoplasm and does not touch the nucleus and the envelope of infected erythrocyte. Second, the nucleus of macrogametocyte is submedian in position. Third, the number of pigment granules is about seven to ten in the gametocyte, and the size of the pigment granules in the same gametocyte varies from small to large. In spite of numerous records of *H. hirundinis* in swallows in the literature, the parasite was redescribed only recently (Valkiūnas and Iezhova, 1992b). Having in their disposal the ample materials of the International Reference Centre for Avian Haematozoa, White and Bennett (1978) prepared a review on the haemoproteids of birds belonging to the Hirundinidae, but concerning *H. hirundinis,* they limited themselves in giving the reference of the brief original paper by the Sergents (Sergent and Sergent, 1905). It is important to note that the first two characters of *H. hirundinis* mentioned above are not usually seen in haemoproteids of swallows. In general, the position when fully grown gametocytes do not touch the nucleus and the envelope of erythrocytes, is not characteristic of haemoproteids of passerine birds. Most probably, the position of the gametocyte of *H. hirundinis* in the erythrocyte was shown inaccurately in the original description (Sergent and Sergent, 1905), but in accordance with the tradition which was common among the early authors. Similar inaccurate details are present in original descriptions of *H. danilewskii*, *H. alaudae*, *H. fringillae*, *H. lanii* (Kruse, 1890; Celli and Sanfelice, 1891; Labbé, 1894; Mello, 1936) and other species. Thus, based on our investigation of collection materials and evidence presented above, the fully grown gametocytes, which do not touch the nucleus and the envelope of erythrocytes, should be

excluded from the definition of *H. hirundinis*. Furthermore, the position of the nucleus in macrogametocytes can vary, and it is difficult to generalize the position on the basis of illustration of one gametocyte. The median position of the nucleus in macrogametocytes has never been recorded in haemoproteids of swallows since the description of *H. hirundinis*, and this is also a basis to exclude this character from the species definition. The marked variability of the size of pigment granules has been frequently recorded in *H. hirundinis*, and this character should be considered to be the most useful for the identification of this parasite.

White and Bennett (1978) analysed the status of *H. chelidonis* Franchini, 1922, which was described from the blood of the swallow *Delichon* (=*Chelidon*) *urbica*, and they declared it to be a *species inquirenda*.

Coatney and Roudabush (1937) described *H. prognei* from the blood of the swallow *Progne subis* in detail. These authors published illustrations of macro- and microgametocyte and noted that *H. prognei* is especially similar to *H. hirundinis*, but it can be distinguished from the latter species on the basis of (i) the close adherence of its gametocytes to the nucleus of erythrocytes, (ii) the subterminal position of nucleus in macrogametocyte, and (iii) the pronounced tendency of gametocytes to grow around the erythrocyte nucleus. As it was shown above, all these features are characteristic of both *H. prognei* and *H. hirundinis.* Furthermore, the morphometric parameters of gametocytes in the original description of *H. prognei* (Coatney and Roudabush, 1937) and in our investigation on *H. hirundinis* (Table 29) coincide. The shape and dimensions of pigment granules in the original description of *H. hirundinis* (Sergent and Sergent, 1905), *H. prognei* (Coatney and Roudabush, 1937), and in our material on *H. hirundinis* (Fig. 71) are identical. Thus, gametocytes of *H. prognei* have no major differences from *H. hirundinis*, and the name *H. prognei* should be considered to be a junior synonym of *H. hirundinis*.

9. **Haemoproteus (Parahaemoproteus) porzanae** (Galli-Valerio, 1907)

Halteridium porzanae Galli-Valerio, 1907: 223. – *Haemoproteus porzanae*: Coatney, 1936: 89.

Type vertebrate host. *Porzana pusilla* (Pallas) (Gruiformes).
Additional vertebrate hosts. *Gallinula chloropus*, *Porzana porzana*, *Rallus pectoralis* (Gruiformes).
Type locality. Kairouan, Tunisia.
Distribution. This parasite has been recorded in the Palearctic and New Guinea.
Type material was not designated in the original description of this species. The parasite was redescribed by Bennett (1980) on the basis of slide No. 276, *Rallus pectoralis*, 23.09.1968, New Guinea, E. Mann, IRCAH. This slide does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985), and it cannot be used as a neohapantotype. Valid neotype material should be designated. Some additional slides are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Porzana.*

Main diagnostic characters. A parasite of species of the Gruiformes whose fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally and only slightly enclose the nucleus with their ends. Growing gametocytes are often dumbbell-shaped and do not touch the envelope of erythrocytes along their entire margin. The average number of pigment granules is about ten per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 72, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; they adhere to the nucleus of erythrocytes and extend longitudinally

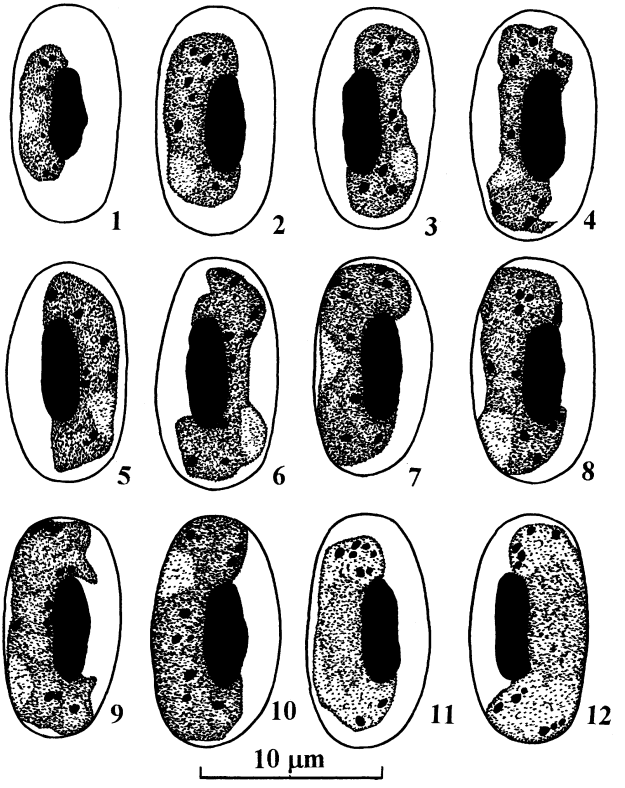

Figure 72 Gametocytes of *Haemoproteus porzanae* from the blood of *Rallus pectoralis:* *1* – young; *2–10* – macrogametocytes; *11*, *12* – microgametocytes.

along the nucleus not touching the envelope of erythrocytes; the outline is even or slightly ameboid.

Macrogametocytes (Fig. 72, *2–10*; Table 29). The cytoplasm is finely granular in appearance, usually lacking vacuoles; gametocytes grow around the nucleus of erythrocytes, they slightly enclose the nucleus with their ends and slightly displace the nucleus laterally but do not encircle it completely; gametocytes are closely appressed to the nucleus of erythrocytes; dumbbell-shaped forms are common (Fig. 72, *3*, *4*, *6*, *8*); medium grown parasites usually do not touch the envelope of erythrocytes along their entire margin (Fig. 72, *2–6*); as the parasite develops, the ends of gametocytes touch the erythrocyte envelope (Fig. 72, *7, 8*), but the central part of their pellicle frequently does not extend to the erythrocyte envelope, causing a 'dip' (Fig. 72, *7–9*), which disappears in fully grown gametocytes; fully grown parasites are closely appressed to the nucleus and the envelope of erythrocytes (Fig. 72, *10*); the outline varies from even (Fig. 72, *7*, *10*) to wavy (Fig. 72, *6*) and ameboid (Fig. 72, *4*, *9*); the parasite nucleus is compact, of small size (see Table 29), usually subterminal in position; pigment granules are usually roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 72, *11*, *12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; other features are as for macrogametocytes.

10. **Haemoproteus (Parahaemoproteus) nettionis** (Johnston and Cleland, 1909)

Halteridium nettionis Johnston and Cleland, 1909: 503, Pl. 48, Fig. 15–17 (partim). – *Haemoproteus nettionis*: Coatney, 1936: 89. – *H. anatis* Haiba, 1946: 209. – *H. hermani* Haiba, 1948: 91. – *H. nettionis*: Herman, 1954: 38 (=*H. anatis*, *H. hermani*). – *H. eulabeiae* Shakhmatov, Balasanova and Pustovaya, 1974: 72, Fig. – *H. anseris* Yakunin and Zhazyltaev, 1977: 133, Fig. 2. – *H. nettionis*: Valkiūnas, 1986b: 54 (=*H. anseris*, *H. eulabeiae*). – *H. gabaldoni* Bennett, 1993a: 120, Fig. 1–7. – *H. nettionis*: Valkiūnas, 1997: 181 (= *H. gabaldoni*).

Type vertebrate host. *Anas castanea* (Eyton) (Anseriformes).
Additional vertebrate hosts. Numerous species of the Anseriformes (over 50 species).
Vector. *Culicoides downesi* (Diptera: Ceratopogonidae).
Type locality. New South Wales, Australia.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic. There are no records beyond the North Polar Circle. The prevalence of infection is especially high in the temperate region of the Holarctic.
Type material. Hapantotype (Z-87, *Anas castanea,* 1907, New South Wales, Australia, F. Tidswell) is deposited in ANMS. A series of additional slides is in ANMS and IRCAH.
Etymology. The specific name is derived from the generic name *Nettion* to which the type host was formerly attributed.

Main diagnostic characters. A parasite of species of the Anseriformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally; they enclose the nucleus with their ends but do not encircle it completely.

Development in vertebrate host

The fate of sporozoites, inoculated into the blood stream, and the number of generations of exoerythrocytic meronts, are unknown. The meronts have been recorded in experimentally infected domestic ducks (*Cairina moschata*) and in naturally infected wild ducks (*Aix sponsa*) in the endothelial cells of blood vessels in lungs, heart, and spleen. They were especially numerous in the lungs (Sibley and Werner, 1984). Mature meronts are usually oval. Cytomeres were not seen. The meronts (n = 50) vary from 6 to 30 μm in length, and from 3 to 10 μm in width. Merozoites are roundish in form, and vary from 0.6 to 1.1 μm in diameter.

The prepatent period varies from 14 to 21 days, usually 16 days (Fallis and Wood, 1957; Sibley and Werner, 1984). Parasitemia increases rapidly, and it reaches a peak two or three days after the appearance of merozoites in the blood. Mature gametocytes appear on the fourth to sixth day of the parasitemia. This coincides with a decrease of the parasitemia which subsequently fluctuates at a level of about 1 parasite per 1000 erythrocytes or less during several months (the period of the observation).

Spring relapse is clearly evident, and it is synchronized with the breeding period of birds.

Young gametocytes (Fig. 73, *1*, *2*). The earliest forms are frequently seen in a polar position in infected erythrocytes, usually roundish or oval in shape; the outline is even or wavy (Fig. 73, *1*); as the parasite develops, gametocytes adhere to the envelope of erythrocytes and extend longitudinally along the erythrocyte nucleus, not touching the nucleus, so that a more or less evident unfilled space (a ‘cleft’) is usually present between the parasite and the erythrocyte nucleus (Fig. 73, *2*).

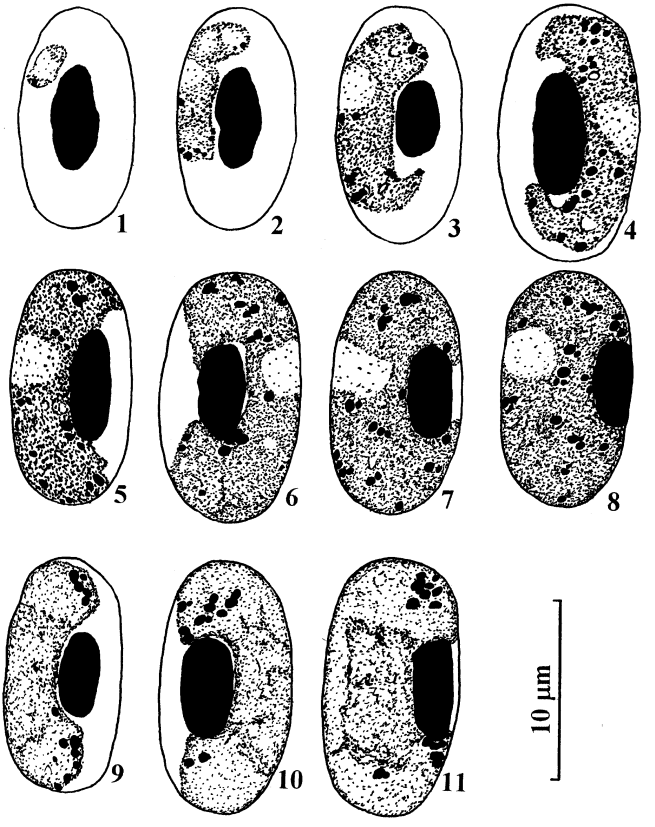

Figure 73 Gametocytes of *Haemoproteus nettionis* from the blood of *Anas querquedula:* *1*, *2* – young; *3–8* – macrogametocytes; *9–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1992b).

Macrogametocytes (Fig. 73, *3–8*; Table 30). The cytoplasm is homogeneous in appearance, sometimes containing several small vacuoles; numerous valutin granules are present in some blood films; gametocytes grow around the nucleus of erythrocytes but do not encircle it completely, they enclose the nucleus with their ends, fill the erythrocytes up to their poles, and markedly displace the erythrocyte nucleus laterally, frequently to the periphery of the host cells (Fig. 73, *7*, *8*); some medium grown parasites do not touch the erythrocyte nucleus (Fig. 73, *3*, *6*), but fully grown forms are closely appressed both to the nucleus and the envelope of erythrocytes (Fig. 73, *7, 8*); the outline is even (Fig. 73, *6*, *7*) or slightly wavy (Fig. 73, *4*, *5*); the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 µm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length and width in comparison to uninfected ones.

Microgametocytes (Fig. 73, *9–11*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has been studied only fragmentarily (Fallis and Wood, 1957). Ookinetes were seen in midgut of the vector 36 h after feeding on infected birds.

Table 30 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. nettionis*				*H. orizivorae* (modified from Bennett and Peirce, 1991)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				65		
Length		10.9–14.1	12.0	0.8		12.4	0.8
Width		5.2–6.9	6.4	0.3		6.3	0.6
Length of nucleus		4.2–6.9	5.7	0.5		5.6	0.5
Width of nucleus		1.4–2.9	2.1	0.2		1.9	0.2
Erythrocyte parasitized by macrogametocyte	31				65		
Length		11.3–15.0	13.4	0.8		13.1	1.0
Width		4.6–8.2	7.7	0.5		6.6	0.5
Length of nucleus		4.0–6.2	5.6	0.6		5.4	0.8
Width of nucleus		1.6–2.9	2.2	0.2		2.0	0.3
Erythrocyte parasitized by microgametocyte	31				10		
Length		11.1–14.8	13.2	0.8		13.7	1.3
Width		4.7–8.0	7.2	0.5		6.6	0.7
Length of nucleus		4.1–6.4	5.8	0.5		5.6	0.5
Width of nucleus		1.7–2.6	2.1	0.2		2.2	0.2
Macrogametocyte	31				65		
Length		14.2–17.8	15.7	1.4		14.2	1.1
Width		2.5–5.1	4.2	0.4		3.6	0.6
Length of nucleus		1.4–4.8	3.0	0.1		3.2	0.5
Width of nucleus		1.0–4.0	2.4	0.1		2.5	0.4
NDR		0.0–0.6	0.3	0.1		0.4	0.2
No. of pigment granules		12–30	22.0	2.4		25.4	2.2
Microgametocyte	31				20		
Length		13.4–17.0	15.2	1.1		15.3	1.9
Width		2.3–5.2	4.0	0.5		3.2	0.5
Length of nucleus		–	–	–		6.2	0.8
Width of nucleus		–	–	–		2.5	0.3
NDR		0.0–0.6	0.3	0.1		0.5	0.3
No. of pigment granules		11–27	17.2	1.8		23.0	1.9

Note: All sizes are given in micrometres.

They are worm-like, containing a large nucleus, numerous ‘vacuoles’ and lacking pigment granules. Oocysts were found in the wall of the midgut of vector approximately four days after the ingestion of gametocytes. They vary from 10 to 14 μm in diameter. Sporozoites were recorded in the salivary glands of the vector on the tenth day after ingestion of gametocytes. However, most probably, the development of the parasite completes more rapidly.

P a t h o g e n i c i t y. Clinical signs of illness were not recorded in experimentally and naturally infected domestic and wild birds. During the development of meronts in internal organs, a heavy infiltration of lymphocytes and granulocytes as well as activation of

macrophages have been recorded. During heavy parasitemia, anaemia may develop. It is likely that the parasite is not dangerous for domestic birds kept in good condition. Pathogenicity for wild birds should be tested in particular because even a negligible decrease of competitiveness can cause elimination of heavily infected specimens during critical periods of their life due to strong competition in nature.

Comments. Bennett (1993a) described haemoproteids recorded in *Cairina moschata* from Venezuela under the name *H. gabaldoni*. Gametocytes of this parasite differ from gametocytes of *H. nettionis* only by numerous valutin granules. It should be noted that this character is variable, and it cannot be a basis for the description of new species. In some blood films deposited in the collection of the author, the valutin granules are also numerous in the gametocytes of *H. nettionis*. *Haemoproteus gabaldoni* should be declared to be a junior synonym of *H. nettionis* (Valkiūnas, 1997).

11. **Haemoproteus (Parahaemoproteus) orizivorae** Anschütz, 1909

Haemoproteus orizivorae Anschütz, 1909: 654, Pl. 1, 2, (partim). – *H. paddae* Brumpt, 1935c: 967, Fig. 19–24. – *H. garnhami* Grewal, 1964: 24, Fig. 1, A–M. – *H. orizivorae*: Levine and Campbell, 1971: 478 (=*H. paddae*); Peirce, 1976: 411 (=*H. garnhami*). – *H. lonchuri* Bandyopadhyay and Haldar, 1988: 293, Fig. 2–5. – *H. orizivorae*: Bennett and Peirce, 1991: 18 (=*H. lonchuri*).

Type vertebrate host. *Lonchura oryzivora* (L.) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 31).
Type locality. This parasite was described on the basis of the material from the blood of an imported bird, and the exact type locality is unknown. Neotype locality is West Java, Indonesia.
Distribution. The Oriental and Ethiopian zoogeographical regions, the Southern Palearctic.
Type material. Neohapantotype (No. 40878, *L. oryzivora*, 27.05.1968, West Java, Indonesia, H.E. McClure) and paraneohapantotypes (No. 40848, *L. malabarica*, 15.11.1970, Gujarat State, India, H.E. McClure; No. 40851, 16.11.1970, other data are as for No. 40848; No. 12132, *L. punctulata*, 21.09.1964, Bangkok, Thailand, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the specific name of the type host, *oryzivora.* In the original description (Anschütz, 1909), the name of this species is given in two different spellings, *orizivorae* and *oryzivorae*. Traditionally, the former name is used as a valid name, and the latter is attributed to the category of *lapsus calami*.

Table 31 List of vertebrate hosts of *Haemoproteus orizivorae* (modified from Bennett and Peirce, 1991).

Erythrura papuana	*L. kelaarti*	*Pyrenestes ostrinus*
E. prasina	*L. leucogastra*	*Pytilia afra*
Estrilda astrild	*L. leucogastroides*	*P. melba*
E. atricapilla	*L. malabarica*	*Spermophaga haematina*
Lonchura bicolor	*L. malacca*	*Uraeginthus angolensis*
L. cucullata	*L. punctulata*	
L. fuscans	*L. striata*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Medium and fully grown gametocytes adhere to the nucleus and the envelope of

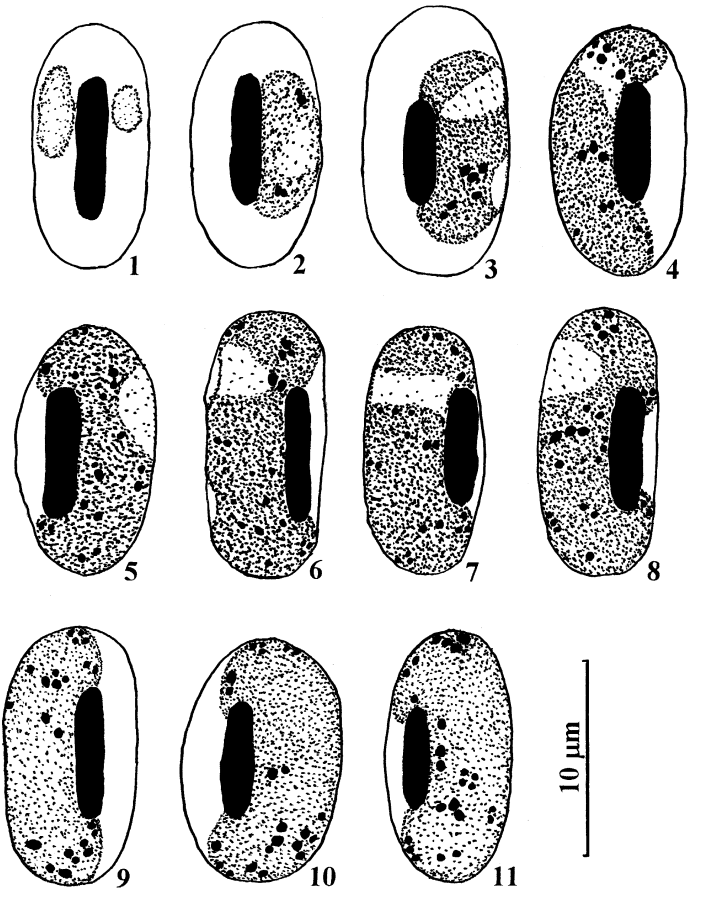

Figure 74 Gametocytes of *Haemoproteus orizivorae* from the blood of *Lonchura punctulata: 1*, *2* – young; *3–8* – macrogametocytes; *9–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1992b).

erythrocytes. Dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes fill the erythrocytes up to their poles. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, their average number is greater than 20 per gametocyte.

Development in vertebrate host

Exoerythrocytic meronts were recorded in the brain, lungs, and bone marrow of the type host (Anschütz, 1909). Details of merogony are unknown. Moreover, there is no convincing evidence that these meronts belong to *H. orizivorae*, because the parasite was found in naturally infected birds.

Young gametocytes (Fig. 74, *1*, *2*). The earliest forms are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the erythrocyte nucleus and adhere to the nucleus and the envelope of erythrocytes; the outline is even.

Macrogametocytes (Fig. 74, *3–8*; Table 30). The cytoplasm is granular in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, they displace the nucleus laterally, sometimes to the periphery of the host cells (Fig. 74, *7*, *8*), but do not encircle the nucleus completely; gametocytes adhere to the nucleus and the envelope of erythrocytes; dumbbell-shaped gametocytes are usually not present or, if they appear occasionally, they represent less than 10% of the total number of the growing gametocytes; gametocytes fill the erythrocytes up to their poles (Fig. 74, *4–8*); the outline is even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 74, *9–11*). The general configuration and other features are as for macrogametocyte with the usual sexual dimorphic characters.

Comments. *Haemoproteus orizivorae* is a species which is difficult to identify, and can only be distinguished from similar species of haemoproteids of birds belonging to the Passeriformes on the basis of a detailed analysis of a set of characters of gametocytes and their host cells. The range of vertebrate hosts of this parasite has been artificially extended because the specific name *orizivorae* was frequently used by many authors for a complex of species parasitizing passeriform birds (Bennett *et al*., 1982b; Bennett and Peirce, 1991). That is why only well described and (or) illustrated host records are included in Table 31.

Among the haemoproteids of birds belonging to the Passeriformes, *H. orizivorae* is especially similar to *H. anthi*, *H. pastoris*, and *H. tyranni*. It can be distinguished from the species mentioned above, particularly, on the basis of more numerous pigment granules in its gametocytes.

12. **Haemoproteus (Parahaemoproteus) ptilotis** (Cleland and Johnston, 1909)

Halteridium ptilotis Cleland and Johnston, 1909: 77, Pl. 1, Fig. 1–15. – *H. philemon* Cleland and Johnston, 1909: 81, Pl. 1, Fig. 16–25. – *H. meliornis* Cleland and Johnston, 1909: 90, Pl. 2, Fig. 1–15. – *Haemoproteus ptilotis*: Coatney, 1936: 89. – *H. philemon*: Coatney, 1936: 89. – *H. meliornis:* Coatney, 1936: 89. – *H. clelandi* Laird and Laird, 1959: 223, Pl. 1, Fig. 14–19. – *H. ptilotis*: Bennett *et al*., 1994b: 15, Fig. 1, A, B (= *H. meliornis, H. philemon*); Valkiūnas, 1997: 185 (=*H. clelandi*).

Type vertebrate host. *Meliphaga chrysops* (Latham) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 32).
Type locality. Hawkesbury River, Milson Island, Australia.
Distribution. The Australian zoogeographical region.
Type material. Hapantotype, designated in the original description, is deposited in the Australian National Museum, Sydney, but it has faded stain and disintegrated erythrocytes, and no parasites were seen anywhere in the blood film by Bennett *et al*. (1994b). Thus, the hapantotype should be declared as useless. The situation is the same with the type material of synonyms of this species. Neotypes should be designated. Bennett *et al*. (1994b) redescribed *H. ptilotis* on the basis of the material which came from the nontype host, *Manorina melanocephala*. This material does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985) and cannot be used as the neotype.
Etymology. The specific name is derived from the generic name *Ptilotis* to which the type host was formerly attributed.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes and displace the nucleus

Table 32 List of vertebrate hosts of *Haemoproteus ptilotis.*

Manorina melanocephala	*M. penicillata*	*Myzomela cardinalis*
Meliphaga fusca	*M. plumula*	*Philemon corniculatus*
M. melanops	*M. virescens*	*Phylidonyris novaehollandiae*

laterally. Fully grown microgametocytes can completely encircle the erythrocyte nucleus, and this was not recorded for macrogametocytes. The nucleus of macrogametocytes is usually subterminal in position and, as a rule, it does not adhere to the nucleus of infected erythrocytes. The average number of pigment granules in gametocytes is less than 12.

Development in vertebrate host

Macrogametocytes (Fig. 75, *1–3*; Table 33). The cytoplasm stains blue, is homogeneous in appearance, contains small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, they enclose the nucleus with their ends, displace the nucleus laterally but do not encircle it completely; gametocytes adhere to the nucleus and the envelope of erythrocytes; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 75, *2*); fully grown gametocytes fill the erythrocytes up to their poles, and they are closely appressed both to the nucleus and the envelope of the erythrocytes; the outline of fully grown gametocytes is even, but ameboid outgrowths are seen in some growing gametocytes (Fig. 75, *1*); the parasite nucleus is compact, variable in form, usually subterminal (Fig. 75, *2*, *3*) but sometimes submedian (Fig. 75, *1*) in position; it usually does not adhere to the nucleus of erythrocytes; the most typical nucleus in form and position is shown in Fig. 75, *2*; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 75, *4–6*). Fully grown gametocytes markedly displace the nucleus of erythrocytes laterally (Fig. 75, *5*) and they can also completely encircle the

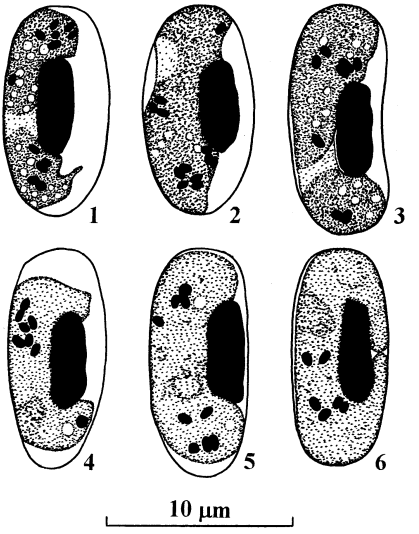

Figure 75 Gametocytes of *Haemoproteus ptilotis* from the blood of *Myzomela cardinalis: 1–3* – macrogametocytes; *4–6* – microgametocytes (modified from Laird and Laird, 1959).

Table 33 Morphometric parameters of gametocytes and host cells of *Haemoproteus ptilotis* (modified from Laird and Laird, 1959) (n = 50).

Feature	lim	$\overline{X}$
Uninfected erythrocyte		
Length	9.0–11.6	10.6
Width	4.3–5.7	5.0
Parasitized erythrocyte		
Length	11.0–12.9	11.9
Width	5.3–6.3	5.7
Macrogametocyte		
Length	11.3–14.6	13.4
Width	1.7–3.3	2.7
No. of pigment granules	6–13	9.0
Microgametocyte		
Length	10.9–20.0	12.4
Width	1.7–2.9	2.2
No. of pigment granules	5–10	7.0

Note: All sizes are given in micrometres. The table is adjusted to the data published by Laird and Laird (1959).

nucleus (Fig. 75, *6*); valutin granules may be present; other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The description of *H. ptilotis* here is based on the material by Laird and Laird (1959) from the blood of *Myzomela cardinalis* (Passeriformes: Meliphagidae), some slight modifications were also introduced according to Bennett *et al*. (1994b) and Mackerras and Mackerras (1960). It should be noted that the morphology of this parasite in the type host has not been investigated in detail. Gametocytes described in the above mentioned papers are similar, and some recorded minor differences in their morphology can be attributed to host and (or) geographical variation which has been poorly investigated in bird haemoproteids. Investigation into the morphology of this parasite in the type host is required to specify the main diagnostic characters of *H. ptilotis.*

Among the haemoproteids of birds belonging to the Passeriformes, *H. ptilotis* is especially similar to *H. belopolskyi*. It can be distinguished from the latter species, particularly, on the basis of the morphology of its macrogametocytes.

13. **Haemoproteus (Parahaemoproteus) mansoni** Castellani and Chalmers, 1910

Haemoproteus mansoni Castellani and Chalmers, 1910: 235, Fig. 55. – *H. canachites* Fallis and Bennett, 1960: 456, Fig. 1–9. – *H. meleagridis* Levine, 1961: 274. – *H. mansoni*: White and Bennett, 1979: 1465 (=*H. canachites*); Valkiūnas, 1997: 187 (=*H. meleagridis*).

Type vertebrate host. *Lagopus scoticus* (Latham) (Galliformes).
Additional vertebrate hosts. Numerous species of the Galliformes (Table 34).
Vectors. *Culicoides arboricola*, *C. edeni*, *C. haematopotus*, *C. hinmani*, *C. knowltoni*,

C. sphagnumensis (Diptera: Ceratopogonidae).

Type locality. Aberdeenshire, Scotland, UK.

Distribution. The Holarctic. Together with birds, this parasite was introduced in several localities outside the Holarctic, and as a result, small local nidi of the infection appeared, but they are rare.

Type material. Neohapantotype (No. 62537, *Lagopus scoticus,* September 1977, Aberdeenshire, Scotland, L. Wilson and G. Wilson) is deposited in IRCAH.

Etymology. This species is named in honour of Lord Patrick Manson who produced blood films for the description of this haemoproteid.

Table 34 List of vertebrate hosts of *Haemoproteus mansoni.*

Alectoris chukar	*Dendragapus obscurus*	*Tetrao urogallus*
A. graeca	*Lagopus lagopus*	*Tetrastes bonasia*
Bonasa umbellus	*Lyrurus tetrix*	*Tympanuchus phasianellus*
Canachites canadensis	*Meleagris gallopavo*	
Centrocercus urophasianus	*Phasianus colchicus*	

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes completely encircle the nucleus of infected erythrocytes and occupy all available cytoplasmic space in the erythrocytes. The average number of pigment granules is about 20 per macrogametocyte.

Development in vertebrate host

The exoerythrocytic merogony was studied in detail by Atkinson *et al*. (1986, 1988b) in experimentally infected domestic turkey poults.

Sporozoites, inoculated into the blood stream by vector, initiate the development of exoerythrocytic meronts. The majority of the meronts develop in skeletal muscle. However, some of the meronts were also recorded in cardiac muscle and in the spleen. The meronts develop in the capillary endothelial cells and in myofibroblasts. They were also recorded in reticular cells of the spleen. The meronts were not seen in liver, lungs, brain, kidney, bone marrow from femur, gizzard, duodenum, pancreas, and cecum. Most of the above mentioned organs, especially lungs and brain, are highly vascular. This suggests a specific requirement for myofibroblasts or their associated physiological environment during the development of the meronts.

During the process of merogony, at least two generations of meronts occur (Fig. 1). Sporozoites initiate a primary merogony in the capillary endothelial cells and myofibroblasts of the skeletal muscle. The uninuclear growing trophozoites, which are up to 3 μm in diameter, were recorded in the capillary endothelial cells of pectoral muscle on the third day post infection (DPI) with sporozoites. The growth and maturation of the first generation of meronts takes between 5 and 8 DPI. The meronts vary from 12 to 20 μm in diameter. It is important to note that the nucleus of infected cells is not hypertrophied. The cytoplasm of growing meronts is granular in appearance and basophilic. Mature meronts are packed with elongated slender merozoites which are 5 to 6 μm long and 1 μm wide (Fig. 5, *1*). The capsule-like structures and immune cell infiltrates were not recorded around the meronts of the first generation.

The elongated merozoites of the first generation initiate secondary merogony, i.e. megalomeronts in skeletal and cardiac muscle and meronts in reticular cells of the spleen.

Initial stages of the development of megalomeronts were recorded in the capillary endothelial cells of skeletal muscle on 8 DPI. The developing megalomeronts were seen

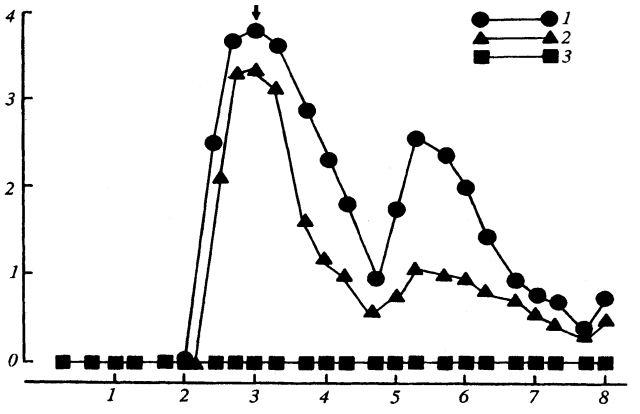

Figure 76 Average parasitemia of *Haemoproteus mansoni* in turkey poults infected with high dose (*1*) and low dose (*2*) of sporozoites, and in control birds (*3*):
The arrow indicates the crisis of parasitemia. Parasitemia, LOG_{10} (parasitemia + 1), is shown on the ordinate; time (weeks) post infection are shown on the abscissa (modified from Atkinson *et al*., 1988b).

both inside and between of the muscle fibres. As the parasite develops, a clear capsule-like hyaline wall appears around the megalomeront. During the development of the megalomeronts, numerous roundish cytomeres are formed (Fig. 5, *2*) which subsequently divide into smaller parts. Merozoites develop as buds from cytomeres (Fig. 5, *3*). Mature megalomeronts are fusiform bodies up to 456 μm long, and they vary from 30 to 150 μm in width. The nucleus of host cells is not hypertrophied. The megalomeronts are packed with numerous roundish merozoites which are about 1 μm in diameter (Fig. 5, *4*). Each merozoite possesses a small nucleus and a relatively large vacuole. The merozoites penetrate into erythrocytes and initiate the development of gametocytes.

In one bird that died on 19 DPI, meronts were recorded in the spleen. Atkinson *et al*. (1988b) believe that these meronts are responsible for relapse and maintenance of chronic parasitemia. These meronts develop in the reticular cells whose nuclei are not hypertrophied. Unlike megalomeronts, the capsule-like wall does not develop around the meronts in the spleen. The diameter of the meronts does not exceed 15 μm. According to the morphology of developing merozoites, the spleen meronts can be separated into two groups. First, a small part of the meronts contains elongated slender merozoites which are similar to merozoites developing in the meronts of the first generation. Second, the majority of the spleen meronts contain roundish merozoites which are identical to merozoites developing in the megalomeronts.

The prepatent period in turkey poults infected intraperitoneally with sporozoites is 17 days (Atkinson *et al.*, 1988b), and it is 14 days in *Bonasa umbellus* infected subcutaneously with sporozoites of the parasite isolated from *Canachites canadensis* (Fallis and Bennett, 1960).

Parasitemia grows quickly (Atkinson, 1986), and the intensity of infection at the peak of the parasitemia differs in different vertebrate hosts infected with the same dose of sporozoites. After intraperitoneal inoculation of $5 \cdot 10^3$ sporozoites of the parasite isolated from turkeys, the parasitemia reached the peak on 22 DPI (22 gametocytes per 1000 erythrocytes) in *Meleagris gallopavo,* on 17 DPI (16/1000) in *Alectoris chukar*, and on 20

DPI (2/1000) in *Phasianus colchicus*. A high parasitemia persists from 5 to 14 days, and later decreases rapidly.

Table 35 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. mansoni*				*H. syrnii*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	32				31			
Length		11.1–13.8	12.1	0.8		11.4–15.0	13.4	0.7
Width		5.3–7.4	6.7	0.5		6.3–8.6	7.4	0.2
Length of nucleus		4.4–6.2	5.3	0.4		4.0–7.7	5.3	0.1
Width of nucleus		2.0–3.3	2.6	0.3		2.0–3.5	2.5	0.1
Erythrocyte parasitized by macrogametocyte	40				24			
Length		11.9–15.2	14.0	1.0		11.9–16.0	14.0	0.9
Width		6.0–7.9	6.9	0.5		6.4–8.8	7.3	0.4
Length of nucleus		3.2–5.8	4.3	0.4		3.0–6.1	4.4	0.2
Width of nucleus		2.1–3.8	2.6	0.4		2.0–3.4	2.2	0.1
Erythrocyte parasitized by microgametocyte	22				17			
Length		11.8–14.7	13.7	0.8		11.9–16.4	14.2	0.8
Width		5.8–7.7	6.9	0.4		6.4–9.0	6.9	0.5
Length of nucleus		2.8–5.9	4.5	0.4		4.0–6.4	5.0	0.2
Width of nucleus		2.0–3.6	2.4	0.2		1.4–2.6	2.0	0.1
Macrogametocyte					24			
Length	40	14.8–24.4	22.1	2.8		12.4–18.8	15.0	1.1
Width	40	2.4–3.9	3.0	0.4		2.7–4.8	3.8	0.4
Length of nucleus	40	1.7–4.3	3.0	0.5		2.1–4.1	3.3	0.3
Width of nucleus	40	1.5–2.6	2.1	0.3		1.0–3.0	2.0	0.2
NDR	40	0.4–1.0	0.7	0.2		0.2–0.7	0.5	0.1
No. of pigment granules	66	16–40	23.5	3.5		13–26	18.6	3.3
Microgametocyte	22				17			
Length		15.0–25.0	21.8	2.4		12.0–16.9	13.8	1.0
Width		2.2–3.9	2.8	0.5		2.7–4.6	3.7	0.5
Length of nucleus		4.3–8.9	7.0	0.7		5.5–11.1	8.0	0.4
Width of nucleus		2.2–3.0	2.4	0.2		1.6–4.2	3.1	0.2
NDR		0.3–1.0	0.7	0.2		0.2–0.6	0.4	0.1
No. of pigment granules		10–32	15.6	4.4		11–22	15.1	2.9

Note: All sizes are given in micrometres.

Parasitemia in turkey poults infected with a low dose (about $4 \cdot 10^3$) and a high dose (about $58 \cdot 10^3$) of sporozoites developed synchronously (Fig. 76). The parasitemia reached its peak on 21 DPI. At this time, the maximum parasitemia reached 200 gametocytes per 1000 erythrocytes in turkeys infected with a low dose of sporozoites, and it was 700/1000 in turkeys infected with a high dose of sporozoites. At the peak of parasitemia, a multiple infection of one erythrocyte with up to six young gametocytes was recorded. During the

next week, the parasitemia decreased rapidly. The second, lower peak of parasitemia, was recorded on 38 DPI. A few gametocytes (<1 per 1000 erythrocytes) were found in the blood of infected turkeys up to eight weeks, which was the period of the observation.

The morphology of gametocytes and the peculiarities of their influence on infected erythrocytes are similar during the development of the parasite in different vertebrate hosts (White and Bennett, 1979; Greiner and Forrester, 1980; Atkinson, 1986; Bennett and Peirce, 1989).

Young gametocytes (Fig. 6, *1–3*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently they are recorded in a polar position (Fig. 6, *1*, *2*); as the parasite develops, gametocytes take a lateral position to the erythrocyte nucleus and usually do not touch the nucleus (Fig. 6, *3*); the outline is usually even, but sometimes also ameboid.

Macrogametocytes (Fig. 6, *4–10*; Table 35). The cytoplasm is homogeneous in appearance, usually contains a few small vacuoles; valutin granules are frequently present; gametocytes grow around the nucleus of infected erythrocytes slightly displacing it laterally; growing gametocytes are closely appressed to the envelope of erythrocytes but frequently do not touch the nucleus of erythrocytes, and as a result, a more or less evident unfilled space (a 'cleft') is usually present between the gametocyte and erythrocyte nucleus (Fig. 6, *5*, *7*) which subsequently disappears (Fig. 6, *8*); fully grown gametocytes completely encircle the nucleus of erythrocytes and occupy all available cytoplasmic space in the host cells (Fig. 6, *9*, *10*); the outline is usually even, sometimes wavy or slightly ameboid; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are of medium (0.5 to 1.0 μm) and small (<0.5 μm) size, randomly scattered throughout the cytoplasm, frequently obscured by valutin granules; infected erythrocytes in comparison to uninfected ones are hypertrophied, and their nucleus is atrophied in length.

Microgametocytes (Fig. 6, *11*, *12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules are less numerous than in macrogametocytes; other characters are as for macrogametocytes.

Relapses are well pronounced in the spring–summer season, and they are clearly synchronized with the bird breeding period. The relapse dependent parasitemia in *Dendragapus obscurus* persists for at least four months (Allan and Mahrt, 1989).

Development in vector

Fallis and Bennett (1960) investigated the development of the parasite, isolated from *Canachites canadensis*, in the biting midge *Culicoides sphagnumensis* at room temperature.

Exflagellation was recorded in the midgut of the vector within 3 min after a blood meal. The process of gametogenesis is asynchronous, and the exflagellation is still available in the midgut 20 min post infection. Zygotes were seen in the midgut 12 h post infection. Their cytoplasm stains blue, contains no or only a few small vacuoles. The zygotes vary from 4 to 7 (on average 5.5) μm in diameter (n = 11). At the same time, the initial stages of differentiation of ookinetes were recorded, and a long finger-like outgrowth appears (Fig. 8, *1*). This outgrowth extends, and the worm-like ookinete develops (Fig. 8, *2*). The cytoplasm of ookinete stains slightly paler than in the zygote. The ookinetes possess a nucleus with clear chromatin clumps and large 'vacuoles.' Pigment granules are located at the distal end of the differentiating ookinete. In fully grown ookinetes, the pigment and adjacent part of cytoplasm are eliminated as a residual body. Mature ookinetes contain no or only a few pigment granules (Fig. 8, *2*).

Initial stages of differentiation of oocysts were recorded in the wall of the midgut on

4 DPI. At this time, the majority of oocysts are filled up with a homogeneous mass (Fig. 8, *3*), and only a few of them were observed to be at the stage of initial differentiation of sporozoites (Fig. 8, *4*). On 5 DPI, the differentiation of sporozoites was seen in the majority of oocysts. On 6 DPI, the fully differentiated sporozoites were recorded in numerous oocysts. The sporozoites are arranged in a fan-like way and are in contact with the residual body of the oocysts (Fig. 8, *5*). At this time, oocysts vary from 8 to 11 (on average 9.5) μm in diameter, and their residual body varies from 3 to 4 μm in diameter ($n = 30$). A few pigment granules were seen in some residual bodies. Each oocyst contains 20 to 30 sporozoites. On 7 DPI, motile sporozoites were seen to be randomly located in the oocysts (Fig. 8, *6*), and they were recorded for the first time also in the salivary glands of the vector. On 8 DPI, only the residual bodies and (or) residual bodies and several (from two to six) sporozoites were seen in the majority of oocysts. At this time, the residual bodies vary from 3 to 4 (on average 3.2) μm in diameter ($n = 10$). Sporozoites gradually escape from oocysts. Live (unfixed) sporozoites in the salivary glands vary from 11 to 15 μm in length ($n = 15$). *In vitro*, sporozoites demonstrate disorderly movement back and forth, and the speed of their movement is significantly higher than in ookinetes and lower than in microgametes. The ends of sporozoites are equally slightly pointed (Fig. 8, *7*).

The morphological peculiarities of the development of the parasite, isolated from turkeys, in the biting midge *Culicoides edeni* are similar to those described above (Atkinson *et al*., 1983; Atkinson, 1991a). Sporogony is completed mainly five to six days after engorging of the flies on an infected turkey, but a few mature oocysts were recorded even on 3 DPI. Mature oocysts contain approximately 50 sporozoites. In *C. baueri*, *C. nanus*, *C. paraensis*, and *C. scanloni,* the parasite develops only up to the oocyst stage and, after this, degenerates (Atkinson, 1991b).

P a t h o g e n i c i t y. It has been proved experimentally that the parasite is pathogenic to domestic turkeys (Atkinson *et al*., 1988b). During heavy infection, an acute disease develops and some of the infected birds die. Reduction in growth has been recorded in surviving turkey poults.

In high-dose infection (about $58 \cdot 10^3$ sporozoites), the first clinical signs were recorded on 7 DPI. The birds were lethargic with slightly drooped wings, ruffled feathers, and partially or completely closed eyes. Between 7 and 14 DPI, a mild diarrhoea developed that produced a 'pasty' vent. By 15 DPI, most of these birds exhibited lameness in one or both legs, severe depression, emaciation, dehydration, and anorexia. Between two and five days after appearance of gametocytes in the blood, i.e., between 19 and 22 DPI, some of the birds died. The birds who survive the crisis of the parasitemia recorded on 21 to 22 DPI usually recover. In spite of the destruction of about 50% of erythrocytes at the peak of parasitemia, anaemia was not recorded in infected birds.

After the infection with a very high dose (about $17 \cdot 10^4$) of sporozoites, the development of the first generation meronts is accompanied with extensive inflammatory reaction and necrosis of isolated muscle fibres and even entire bundles of as many as five to ten adjacent myofibres. Reasons for the necrosis are unknown. The necrosis may have been due to (i) the release of toxins by developing parasites, (ii) the interference with the local circulation, or (iii) the destruction of host cells during the release of the first generation merozoites. As lesions did not occur around the developing meronts, it seems likely that the tissue destruction may have resulted from the rupture of host cells and the ensuing inflammatory reaction during the release of the merozoites. Regeneration of myofibroblasts was recorded on 8 DPI, and was quick. After the infection with a lower dose (about $6 \cdot 10^4$) of sporozoites, the necrosis in skeletal muscle was much less evident.

Especially acute pathological changes were recorded in skeletal muscle due to the development of megalomeronts. Maturation and rupture of megalomeronts are accompanied with necrosis of adjacent myofibres, acute inflammatory reaction with mixed inflammatory infiltrates composed of macrophages, heterophils, plasma cells, and erythrocytes. Local haemorrhages in skeletal muscle may be seen with the naked eye. Activation of secondary bacterial (*Salmonella*) and fungous (*Aspergillus*) infections was recorded in dead birds. Necrotic muscle fibres with calcificates and degenerating megalomeronts were seen up to the eighth week post infection, which was the period of the experimental observations, but clinical signs of the infection were not recorded at this time.

To estimate the pathogenicity of this parasite for wild birds, special ecological testing should be done. The results of experimental and field investigations indicate the negative influence of the parasite on free-living birds (Atkinson, 1991b). The lowering of locomotive activity is obvious in experimentally infected birds. This may play a dramatic role for infected individuals in the wild because this leads to the lowering of ability to compete in comparison to uninfected hosts. Atkinson and Forrester (1987) recorded the death of a naturally infected wild turkey in captivity soon after its capture. The bird was so sick that it was captured by hand in the wild. Numerous intramuscular megalomeronts were recorded after the microscopic examination. While the precise cause of death of this bird could not be determined because of the mixed infection with several other parasites, the most prominent lessons were associated with the megalomeronts. It is likely that, in this case, a combination of at least two factors caused the death, i.e., the weakening of the organism by the parasite infections and the stress due to captivity

S p e c i f i c i t y has been insufficiently investigated. The parasite, isolated from *Meleagris gallopavo* (Meleagrididae), completes its development in *Alectoris chukar* and *Phasianus colchicus* (Phasianidae), but not in the domestic chicken *Gallus gallus* (Phasianidae) and *Numida meleagris* (Numididae) (Atkinson, 1986).

C o m m e n t s. The status of *H. meleagridis*, which is declared to be a junior synonym of *H. mansoni,* is the most debatable thesis of this species essay. The latter species was originally described from galliform birds of the family Tetraonidae. Development of the parasite in turkeys, where it is known under the name *H. meleagridis,* has been investigated much better than *H. mansoni* in tetraonids. That is why this synonymy cannot be estimated unanimously by specialists. However, keeping in mind the facts accumulated by science as well as the principles of identification of species of haemoproteids analyzed above (see p. 69), the status of the name *H. meleagridis* should be changed. The main arguments for this decision are given below. First, the morphology of gametocytes and their host cells in tetraonid (*H. mansoni*), phasianid and meleagridid (*H. meleagridis*) birds is identical for all main diagnostic characters (White and Bennett, 1979; Greiner and Forrester, 1980; Atkinson, 1986; Bennett and Peirce, 1989; Valkiūnas, 1997). Second, it was proved experimentally that the parasite, which was isolated from *Meleagris gallopavo* (Meleagrididae), completes the development in *Alectoris chukar* and *Phasianus colchicus* (Phasianidae), i.e., it infects galliform birds belonging to different families (Atkinson, 1986). This fact eliminates theoretical obstacles to use the name *H. mansoni* for the identical haemoproteids developing in galliform birds of various families. It should be noted that the host range of *H. mansoni* cannot be finally defined now. For example, Atkinson (1986) did not succeed in experimental transmission of the parasite, which was isolated from the turkey *Meleagris gallopavo* (Meleagrididae), to the domestic chicken *Gallus gallus* (Phasianidae) and the guinea-fowl *Numida meleagris* (Numididae). Furthermore, the ability of the parasite of tetraonid birds to develop in meleagridid and phasianid birds should be also tested experimentally. However, the data on the ability of the same parasite to develop in birds belonging to different families of galliform birds, given above, are of theoretical priority. That is why, until it has

been disproved experimentally, it is logical to attribute the morphologically identical parasites of meleagridid, phasianid, and tetraonid birds to the same species, *H. mansoni*. The taxonomic status (family or subfamily) of tetraonid, phasianid, meleagridid, and numidid birds in the order Galliformes has not been finally specified (Potapov, 1992). However, this cannot influence the above argumentation significantly. Third, the areas and habitats of turkeys (the host of *H. meleagridis*) and some tetraonid birds (for example, *Bonasa umbellus,* the host of *H. mansoni*) overlap. Thus, the parasite exchange is theoretically possible between these two bird groups. Therefore, based on our observations and other evidence presented above, it is preferable to consider the name *H. meleagridis* to be the junior synonym of *H. mansoni*. For the final solution of this question, it would be helpful (i) to investigate the merogony of the parasite in tetraonid birds, (ii) to test the ability of haemoproteids of tetraonids to develop in phasianid and meleagridid birds at the locality where the areas of these hosts overlap, and (iii) to investigate taxonomic characters in the DNA of parasites.

14. **Haemoproteus (Parahaemoproteus) syrnii** (Mayer, 1910)

Halteridium syrnii Mayer, 1910: 202, Fig. 1, 2. – *Haemoproteus glaucidii* Mello, 1935b: 473 (partim). – *H. syrnii*: Coatney, 1936: 89. – *H. multiparasitans* Covaleda Ortega and Gállego Berenguer, 1950: 167, Pl. 5, Fig. 1–22. – *H. cellii* var. *aegyptius* Mohammed, 1958: 197, Pl. 8, Fig. 1–20. – *H. aegyptius*: Levine and Campbell, 1971: 476 (emend. pro var. *aegyptius*). – *H. phodili* Bishop and Bennett, 1989: 2682, Fig. 9, 10. – *H. syrnii*: Bishop and Bennett, 1989: 2680, Fig. 6–8 (=*H. glaucidii* partim, *H. multiparasitans*, *H. aegyptius*); Valkiūnas, 1997: 191 (= *H. phodili*).

Type vertebrate host. *Strix aluco* (L.) (Strigiformes).
Additional vertebrate hosts. Numerous strigiform birds of the families Strigidae and Tytonidae (over 30 species).
Type locality. Precise locality is unknown. Lübeck, Germany or Vienna, Austria.
Distribution. This parasite has been recorded in all zoogeographical regions, except Australia and the Antarctic. Most probably, it is cosmopolitan. There is no transmission beyond the North Polar Circle. Particularly numerous records are from strigiform birds in tropics and subtropics, but the parasite is relatively rare in the Holarctic where it is patchy in distribution.
Type material was not designated in the original description of this species. Bishop and Bennett (1989) designated neotypes which came from nontype hosts (*Strix varia*, *Otus scops*, *Bubo bubo*) investigated far beyond the type locality (the Nearctic, the Oriental zoogeographical region). These neotypes are invalid because they contradict Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). A series of additional slides is deposited in IRCAH and CDVA.
Etymology. The specific name is derived from the generic name *Syrnium* to which the type host was formerly attributed.

Main diagnostic characters. A parasite of species of the Strigiformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally; they slightly enclose the nucleus with their ends, but as a rule, do not encircle it completely.

Development in vertebrate host
Young gametocytes (Fig. 77, *1–3*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently, they are recorded in a position lateral to the erythrocyte nucleus (Fig. 77, *1*); as the parasite develops, gametocytes usually take a lateral position to the erythrocyte nucleus (Fig. 77, *2*, *3*) and they slightly displace the nucleus laterally; the outline is usually even, but sometimes ameboid; gametocytes, which adhere to the nucleus and the envelop of erythrocytes (Fig. 77, *2*), are present.

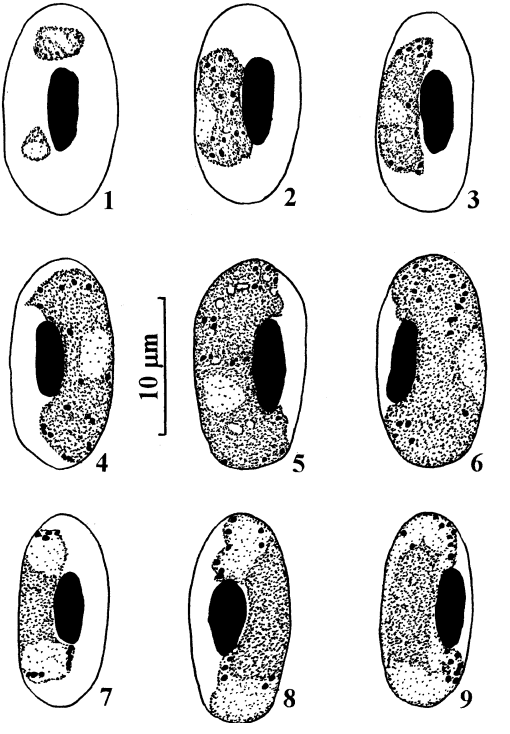

Figure 77 Gametocytes of *Haemoproteus syrnii* from the blood of *Strix uralensis:*
1–3 – young; *4–6* – macrogametocytes; *7–9* – microgametocytes. Valutin granules are omitted.

Macrogametocytes (Fig. 77, *4–6*; Table 35). The cytoplasm is finely granular in appearance, contains a few small vacuoles; valutin granules are frequently present, they are compact, large, and obscure the pigment granules; gametocytes grow along the nucleus of erythrocytes, they markedly displace the nucleus laterally, slightly enclose the nucleus with their ends and, as a rule, do not encircle it completely; if occasionally present during heavy parasitemia, the gametocytes either nearly completely or completely encircling the nucleus of erythrocytes represent less than 5% of the total number of mature gametocytes; gametocytes are usually closely appressed to the envelope of erythrocytes, but frequently a more or less evident unfilled space (a 'cleft') is present between the growing gametocyte and the nucleus of the erythrocyte (Fig. 77, *3*); this 'cleft' disappears in fully grown forms (Fig. 77, *5, 6*); the outline is usually even or slightly wavy (Fig. 77, *5*, *6*), sometimes ameboid (Fig. 77, *4*); the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are usually roundish, of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 77, *7–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; parasites, not touching the erythrocyte nucleus (Fig. 77, *8*), are more numerous among microgametocytes than among macrogametocytes; other characters are as for macrogametocytes.

C o m m e n t s. Growing gametocytes of *H. syrnii* are similar to those of *H. noctuae*. These species can be readily distinguished on the basis of the morphology of their fully grown gametocytes. In

H. syrnii, the gametocytes are bean-shaped, they markedly displace the erythrocyte nucleus laterally and, as a rule, do not encircle the nucleus completely (Fig. 77, *4–6*). In *H. noctuae,* the gametocytes are circumnuclear, and they do not displace or only slightly displace the nucleus laterally (Fig. 63, *6*, *7*, *9*). In addition, valutin granules in gametocytes of *H. syrnii* are numerous, large, and prominent, and this is not characteristic of *H. noctuae.*

With the aim to distinguish the *syrnii*-like gametocytes developing in strigiform birds of the family Tytonidae, Bishop and Bennett (1989) described *H. phodili.* Gametocytes of *H. phodili* are morphologically identical to gametocytes of *H. syrnii*. The main morphometric parameters of gametocytes and their host cells in *H. phodili* and *H. syrnii* overlap, except for the width of the nucleus of microgametocytes. The latter character is variable and depends on the quality of staining the slides and, taken separately, it cannot be a basis to describe a new species. *Haemoproteus phodili* was described mainly on the basis of the theoretically poorly based assumption that the species of haemoproteids cannot be transmitted among birds of different families belonging to the same order (for details, see p. 69). Until the family level of specificity of *H. phodili* is proved experimentally, this name is considered to be a junior synonym of *H. syrnii* (Valkiūnas, 1997).

It should be noted that the range of vertebrate hosts of *H. syrnii* and *H. noctuae* is similar. However, the former species has not been as frequently recorded in the Holarctic as the latter one. For example, during migration on the Baltic Sea coast, *H. syrnii* was not recorded in more than 300 specimens of *Asio otus*, but the prevalence of *H. noctuae* infection in this bird varied from 55 to 100% in different years (Valkiūnas, 1997). However, it is important to mention that *H. syrnii* predominates in some populations of *Strix aluco* in England (A. Anwar, personal communication). According to current knowledge, *H. syrnii* is especially common in tropical species of Strigiformes.

15. **Haemoproteus (Parahaemoproteus) queleae** (Marullaz, 1912)

Haemamoeba queleae Marullaz, 1912: 326, Fig. 1–3 (partim). – *Haemoproteus queleae*: Coatney, 1936: 89 (*H. quelae*); Bennett and Peirce, 1991: 13 (*H. quelea*).

Type vertebrate host. *Quelea erythrops* (Hartlaub) (Passeriformes).
Additional vertebrate hosts. Numerous species of the Passeriformes, mainly of the families Ploceidae and Estrildidae (over 30 species).
Type locality. San Thomé, former Republic of Equatorial Guinea (equatorial Africa).
Distribution. The Ethiopian and Oriental zoogeographical regions.
Type material. Neohapantotype (No. 24656, *Quelea erythrops*, 08.04.1971, Enteble, Uganda, N.A. Okia) and paraneohapantotypes (No. 103825, *Ploceus capensis*, 25.12.1988, Vlakfontein, South Africa, R.A. Earlé; No. 103279, *P. velatus*, 01.09.1988, Glen, South Africa, R.A. Earlé; No. 24532, *P. weynsi*, 16.06.1971, Enteble, Uganda, N.A. Okia; No. 24561, other data are as for the previous slide) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Quelea.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes, they markedly displace the nucleus laterally but do not encircle it completely. Dumbbell-shaped macrogametocytes are present, and they represent more than 10% of the total number of the growing gametocytes. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes, and fill the erythrocytes up to their poles. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about 18 per gametocyte on average. A species difficult to identify; can only be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes on the basis of a detailed analysis of a set of characters.

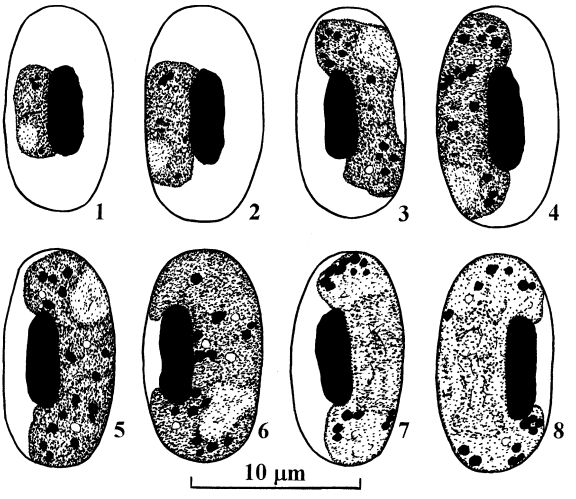

Figure 78 Gametocytes of *Haemoproteus queleae* from the blood of *Quelea erythrops:* *1*, *2* – young; *3–6* – macrogametocytes; *7*, *8* – microgametocytes.

Development in vertebrate host

Young gametocytes (Fig. 78, *1*, *2*). The earliest forms are usually seen in a position lateral to the nucleus of infected erythrocytes; variable in shape, but frequently oval; as the parasite develops, gametocytes adhere to the erythrocyte nucleus (Fig. 78, *1*) and extend longitudinally along the nucleus being also closely appressed to the erythrocyte envelope (Fig. 78, *2*); the outline is even.

Macrogametocytes (Fig. 78, *3–6*; Table 36). The cytoplasm is granular in appearance, usually contains a few small vacuoles; valutin granules are occasionally present; gametocytes grow around the nucleus of infected erythrocytes, they markedly displace the nucleus laterally but do not encircle it completely; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 78, *3*); the dumbbell-shaped forms represent more than 10% of the total number of the growing gametocytes; fully grown gametocytes lose the dumbbell-like shape, and they are closely appressed to both the nucleus and the envelope of erythrocytes, and fill the erythrocytes up to their poles (Fig. 78, *5*, *6*); the outline is usually even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 78, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Haemoproteus queleae* is especially similar to *H. passeris*. It can be distinguished from the latter species on the basis of more numerous pigment granules in its gametocytes and a smaller average NDR. During the identification of *H. queleae* and *H. passeris*, attention should be paid to the above mentioned characters because the ranges of their vertebrate hosts overlap in part. Among haemoproteids of birds belonging to the Passeriformes, *H. queleae* is also similar to *H. majoris* and *H. balmorali*. The earliest gametocytes of *H. balmorali* are elongated, rod-like, and its growing and fully grown gametocytes possess numerous valutin granules. These features are not characteristic of *H. queleae.* Gametocytes of *H. majoris* possess a significantly smaller number of pigment granules than gametocytes of *H. queleae.*

Table 36 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. queleae* (modified from Bennett and Peirce, 1991)				*H. wenyoni* (modified from Bennett *et al.*, 1991b)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	95				65		
Length		–	11.6	0.9		12.4	0.8
Width		–	6.2	0.5		6.5	0.6
Length of nucleus		–	5.0	0.6		5.4	0.5
Width of nucleus		–	1.8	0.2		1.8	0.3
Erythrocyte parasitized by macrogametocyte	95				65		
Length		–	12.3	0.7		13.3	0.8
Width		–	6.2	0.6		6.7	0.6
Length of nucleus		–	5.0	0.5		5.4	0.6
Width of nucleus		–	1.9	0.4		1.9	0.2
Erythrocyte parasitized by microgametocyte	30				20		
Length		–	12.3	0.9		13.3	0.7
Width		–	6.2	0.5		6.8	0.6
Length of nucleus		–	4.9	0.5		5.3	0.7
Width of nucleus		–	1.9	0.2		1.9	0.3
Macrogametocyte	95				65		
Length		–	13.2	1.2		15.7	2.1
Width		–	3.1	0.6		2.9	0.5
Length of nucleus		–	3.1	0.4		3.1	0.8
Width of nucleus		–	2.3	0.4		2.0	0.4
NDR		0.2–0.8	0.4	0.2		0.8	0.2
No. of pigment granules			18.0	2.3		23.5	2.8
Microgametocyte	30				20		
Length		–	13.6	1.5		15.7	1.7
Width		–	2.8	0.4		3.0	0.5
Length of nucleus		–	6.1	0.9		7.3	1.0
Width of nucleus		–	2.3	0.3		2.9	0.5
NDR		0.3–0.8	0.4	0.2		0.8	0.1
No. of pigment granules		–	18.0	1.9		20.0	3.6

Note: All sizes are given in micrometres.

16. **Haemoproteus (Parahaemoproteus) wenyoni** Mello, Sa, Sousa, Dias and Noronha, 1916

Haemoproteus wenyoni Mello, Sa, Sousa, Dias and Noronha, 1916: 187, Pl. 1 (partim).

Type vertebrate host. *Orthotomus sutorius* (Pennant) (Passeriformes).
Additional vertebrate host. Species of the Passeriformes, mainly belonging to the Sylviidae (about 20 species).

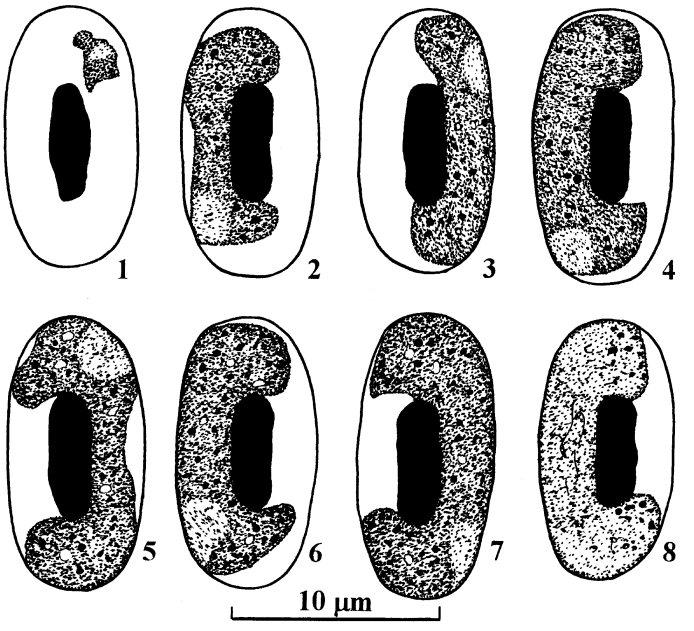

Figure 79 Gametocytes of *Haemoproteus wenyoni* from the blood of *Orthotomus sutorius:* *1* – young; *2–7* – macrogametocytes; *8* – microgametocyte.

Type locality. Nova Goa, India.

Distribution. This parasite has been recorded in all zoogeographical regions, except the Australian and Antarctic. In the Palearctic, this species has been rarely recorded.

Type material. Neohapantotype (No. 41446, *Orthotomus sutorius*, 13.07.1970, Gujarat, India, H.E. McClure) is deposited in IRCAH. Paraneohapantotypes designated by Bennett *et al*. (1991b), are invalid because they came from nontype hosts (*Acrocephalus aedon*, *A. arundinaceus*, *A. dumetorum*) [see Article 75(d)(5) of the International Code of Zoological Nomenclature, 1985].

Etymology. This species is named in honour of the famous protozoologist Professor C.M. Wenyon.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes, they do not displace or only slightly displace the nucleus laterally and do not encircle it completely. Gametocytes adhere to the nucleus and the envelope of erythrocytes. Dumbbell-shaped gametocytes are present, and they represent more than 10% of the total number of the growing gametocytes. Pigment granules are small (<0.5 μm), about 20 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 79, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the erythrocyte nucleus and extend longitudinally along it; the outline of the earliest forms is more or less ameboid (Fig. 79, *1*), and is usually even in more advanced forms.

Macrogametocytes (Fig. 79, *2–7*; Table 36). The cytoplasm is granular in appearance, usually contains a few small vacuoles; valutin granules are present in some blood films; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or only

slightly displace the nucleus laterally, enclose the nucleus with their ends but do not encircle it completely; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 79, *2*, *5*); the dumbbell-shaped forms represent more than 10% of the total number of the growing gametocytes; fully grown parasites lose the dumbbell-like shape, and they are closely appressed to both the nucleus and the envelope of erythrocytes, and fill the erythrocytes up to their poles (Fig. 79, *7*); the outline is usually even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are small (<0.5 μm), frequently dust-like in appearance, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 79, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. wenyoni* is especially similar to *H. belopolskyi*. It can be distinguished from the latter species on the basis of the size and number of pigment granules in its gametocytes.

17. **Haemoproteus (Parahaemoproteus) tinnunculi** Wasielewski and Wülker, 1918

Haemoproteus danilewskyi var. *tinnunculi* Wasielewski and Wülker, 1918: 89, Pl. 1–5 (partim). – *H. tinnunculi*: Brumpt, 1935a: 150 (emend. pro var. *tinnunculi*). – *H. cerchneisi* Bhatia, 1938: 212. – *H. tinnunculi*: Valkiūnas and Iezhova, 1989: 57 (=*H. cerchneisi*).

Type vertebrate host. *Falco tinnunculus* L. (Falconiformes).
Additional vertebrate hosts. Some species of the Falconiformes (Table 37).
Type locality. Germany.
Distribution. The Holarctic, Ethiopian, and Oriental zoogeographical regions. See also Appendix 2.
Type material was not designated in the original description of this species. Peirce *et al.* (1990) suggested a series of blood films collected from nontype hosts (*Falco columbarius*, *F. sparverius*) far beyond the type locality (the Nearctic) as neotypes. These neotypes are invalid because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). The designation of the neotypes is required. A series of additional slides is deposited in IRCAH, CDVA.
Etymology. The specific name is derived from the specific name of the type host, *tinnunculus.*

Table 37 List of vertebrate hosts of *Haemoproteus tinnunculi.*

Caracara plancus	*F. naumanni*	*F. sparverius*
Falco biarmicus	*F. newtoni*	*F. subbuteo*
F. cherrug	*F. peregrinus*	*Polihierax insignis*
F. columbarius	*F. rupicoloides*	

Note: See also Appendix 2.

Main diagnostic characters. A parasite of species of the Falconiformes whose gametocytes grow around the nucleus of infected erythrocytes, they can completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes.

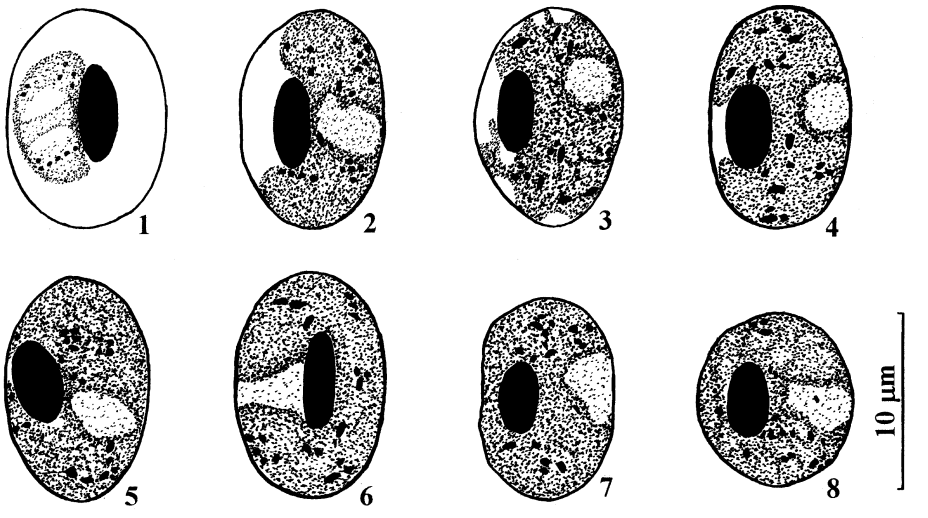

Figure 80 Macrogametocytes of *Haemoproteus tinnunculi* from the blood of *Falco tinnunculus:*
1 – young; *2–8* – mature (modified from Valkiūnas and Iezhova, 1989).

Development in vertebrate host

Young gametocytes (Figs. 80, *1*; 81, *1*). The earliest forms can be seen anywhere in infected erythrocytes; they are roundish or oval; the outline is even; as the parasite develops, gametocytes adhere to the nucleus of erythrocyte in its lateral part; at the beginning, they grow both in length and in width at approximately the same speed. The intensive growth in width leads to the lateral displacement of the nucleus of erythrocytes and to the hypertrophy of the erythrocytes in width even at the early stages of the development, which is a characteristic feature of this species.

Macrogametocytes (Fig. 80, *2–8*; Table 38). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles. A clear tendency to intensive growth not only in length but also in width, recorded for young gametocytes, is also evident in mature parasites. As a result, the nucleus of infected erythrocytes is markedly displaced laterally, and infected erythrocytes are hypertrophied in width in comparison to uninfected erythrocytes. The typical shape of fully grown gametocytes is shown in Fig. 80, *4*, *5*. Gametocytes grow around the nucleus of erythrocytes. Fully grown gametocytes occupy all or nearly all available cytoplasmic space in erythrocytes, and they can completely encircle the nucleus. In the latter case, the ends of the parasite merge together, and they push the erythrocyte nucleus towards the centre of erythrocyte (Fig. 80, *6*, *7*). This leads to the secondary increase of the NDR. Some circumnuclear gametocytes cause marked deformation of the infected erythrocytes giving a spherical shape (Fig. 80, *8*). Gametocytes usually touch the nucleus of erythrocytes, and they are closely appressed to their envelope. Sometimes, however, the growing gametocytes do not touch the erythrocyte nucleus and, as a result, a more or less evident unfilled space (a 'cleft') can be present between the gametocyte and the nucleus of erythrocyte. This 'cleft' has never been seen in the circumnuclear forms. The outline of gametocytes is usually even, but sometimes ameboid (Fig. 80, *3*). The parasite nucleus is compact, variable in shape, usually median or submedian, but sometimes subterminal in position; it can be located freely in the

Table 38 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. tinnunculi* (according to Valkiūnas and Iezhova, 1989)				*H. lophortyx* (modified from Bennett and Peirce, 1989)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				35		
Length		10.7–13.7	12.6	0.6		12.3	0.8
Width		6.0–8.2	7.2	0.4		6.8	0.5
Length of nucleus		4.9–7.3	6.2	0.4		5.6	0.6
Width of nucleus		1.9–3.2	2.6	0.2		2.0	0.3
Erythrocyte parasitized by macrogametocyte	31				35		
Length		10.8–14.0	12.6	0.5		13.2	0.8
Width		6.8–8.6	7.8	0.4		7.7	0.8
Length of nucleus		4.3–6.4	5.3	0.4		5.2	0.5
Width of nucleus		1.8–2.5	2.2	0.2		2.0	0.2
Erythrocyte parasitized by microgametocyte	31						
Length		11.2–14.6	12.8	0.6	–	–	–
Width		6.5–8.6	7.8	0.4	–	–	–
Length of nucleus		4.6–6.5	5.7	0.2	–	–	–
Width of nucleus		1.4–2.6	2.0	0.2	–	–	–
Macrogametocyte	31				35		
Length		14.1–22.0	18.2	1.4		24.4	1.6
Width		2.5–4.9	3.9	0.4		3.1	0.4
Length of nucleus		2.6–4.3	3.3	0.2		3.9	0.7
Width of nucleus		1.7–3.2	2.5	0.2		2.2	0.3
NDR		0.2–0.8	0.5	0.1		0.9	0.1
No. of pigment granules		16–32	22.7	2.4		22.6	2.4
Microgametocyte	31						
Length		12.7–20.3	16.8	1.2	–	–	–
Width		3.2–4.5	4.0	0.2	–	–	–
Length of nucleus		7.2–10.9	8.7	0.4	–	–	–
Width of nucleus		2.5–4.5	4.0	0.2	–	–	–
NDR		0.5–0.9	0.7	0.1	–	–	–
No. of pigment granules		13–22	17.4	2.8	–	–	–

Note: All sizes are given in micrometres.

cytoplasm not touching the parasite pellicle (Fig. 80, *3*, *5*). Pigment granules are usually roundish or oval but sometimes rod-like, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm. Infected erythrocytes are slightly hypertrophied in width, and their nuclei are atrophied in length and width.

Microgametocytes (Fig. 81). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; gametocytes with an ameboid outline are seen more frequently, and the ameboid shape is more marked than in macrogametocytes; other characters are as for macrogametocytes.

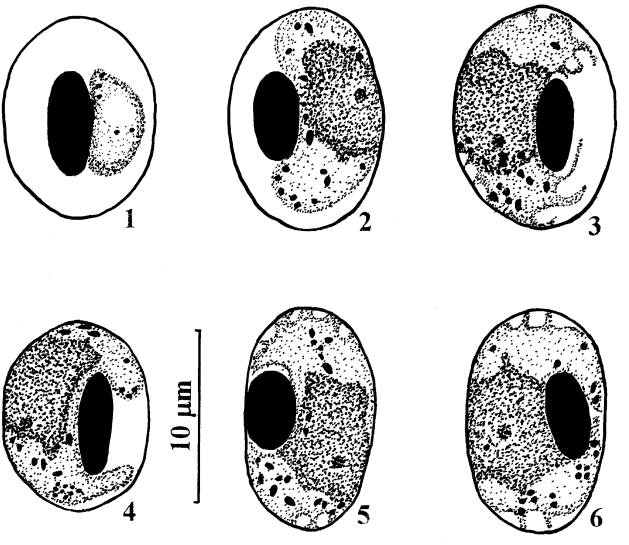

Figure 81 Microgametocytes of *Haemoproteus tinnunculi* from the blood of *Falco tinnunculus: 1* – young; *2–6* – mature (modified from Valkiūnas and Iezhova, 1989).

Pathogenicity has not been investigated. A negative correlation has been recorded between the parasitemia and body mass of females in *Falco sparverius* (Apanius and Kirkpatrick, 1988).

Comments. Gametocytes of *H. tinnunculi*, completely encircling the nucleus of erythrocyte, are an important character of this species. They were recorded by Wasielewski and Wülker (1918), Mohammed (1958), and Maloney *et al.* (1984). The circumnuclear gametocytes of *H. tinnunculi* were described in detail and included in the definition of this species by Valkiūnas and Iezhova (1989). It is important to note that circumnuclear gametocytes appear at the later stages of development in the blood, while they are not always found in naturally infected birds investigated only once in field conditions.

18. **Haemoproteus (Parahaemoproteus) lophortyx** O'Roke, 1929

Haemoproteus lophortyx O'Roke, 1929b: 432.

Type vertebrate host. *Lophortyx (=Callipepla) californica* (Shaw) (Galliformes).
Additional vertebrate hosts. *Callipepla squamata*, *Colinus virginianus*, *Coturnix chinensis*, *C. coturnix*, *Lophortyx gambelli*, *Oreortyx picta* (Galliformes).
Vector. Unknown (see 'Comments').
Type locality. California, USA.
Distribution. This parasite has been recorded in the Holarctic and in the Ethiopian zoogeographical region.
Type material. Neohapantotype (No. 43403, *Lophortyx californica*, June 1942, California, USA, C.M. Herman) is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Lophortyx.*

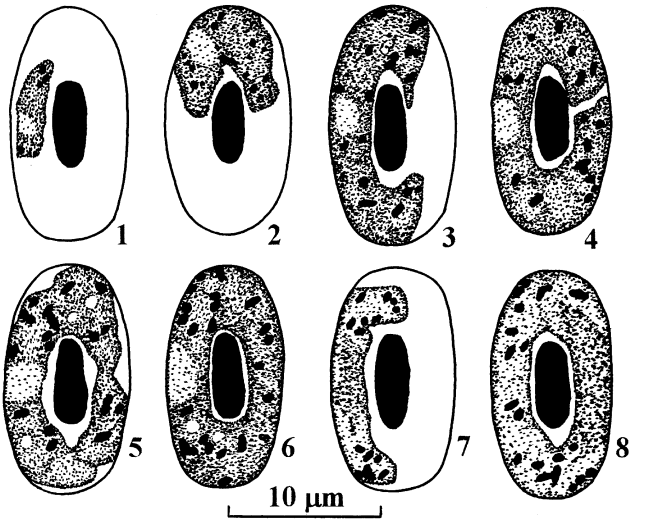

Figure 82 Gametocytes of *Haemoproteus lophortyx* from the blood of *Lophortyx californica: 1*, *2* – young; *3–6* – macrogametocytes; *7*, *8* – microgametocytes.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes completely encircle the nucleus of infected erythrocytes, but do not occupy all available cytoplasmic space in the erythrocytes. A more or less evident unfilled space (a 'cleft') is present between the fully grown gametocyte and the nucleus of erythrocyte. The average number of pigment granules is about 20 per macrogametocyte.

Development in vertebrate host

Young gametocytes (Fig. 82, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes are more frequently seen in a lateral position to the nucleus of erythrocytes (Fig. 82, *1*), but sometimes they also take a polar (Fig. 82, *2*) position in the host cells; growing gametocytes do not touch the nucleus of erythrocyte (Fig. 82, *2*); the outline is even or slightly wavy.

Macrogametocytes (Fig. 82, *3–6*; Table 38). The cytoplasm is finely granular in appearance, sometimes contains a few small vacuoles; valutin granules are seen in some blood films and, when present, obscure the pigment granules; gametocytes grow around the nucleus of infected erythrocytes, and they do not displace the nucleus laterally (Fig. 82, *3*, *4*); fully grown gametocytes encircle the nucleus of erythrocytes completely but do not occupy all available cytoplasmic space in the host cells, so that a more or less evident unfilled space (a 'cleft') is present between fully grown gametocyte and the nucleus of erythrocyte (Fig. 82, *5*, *6*); the outline of the growing gametocytes varies from even to wavy and even ameboid; the parasite nucleus is compact, variable in shape, median or submedian in position; pigment granules are roundish, oval, or sometimes rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are slightly hypertrophied in length and width in comparison to uninfected ones.

Microgametocytes (Fig. 82, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has not been investigated. The gametogenesis, fertilization of macrogametes and development of ookinetes were studied by O'Roke (1929a, 1930b, 1932) *in vitro* at room temperature. Within several minutes after exposure of infected blood to air, mature gametocytes become round and escape from the erythrocytes. At this time, the first microgametes were seen. During the fertilization, a microgamete entirely penetrates into the macrogamete. The process of fertilization does not take more than 15 s. The zygote has been seen outwardly unchanged for about 20 min, and after that, it starts to elongate and an ookinete develops. A great part of pigment concentrates at the posterior end of the ookinete. The pigment eliminates together with a residual body. Fully differentiated ookinetes were seen 45 to 50 min after exposure of blood with mature gametocytes to air.

Comments. Among the haemoproteids of birds belonging to the Galliformes, *H. lophortyx* is especially similar to *H. stableri* and *H. mansoni*. *Haemoproteus lophortyx* can be distinguished from *H. stableri* primarily on the basis of more numerous pigment granules in its gametocytes, and from *H. mansoni*, on the basis of the 'cleft' which is present between its fully grown gametocytes and the nucleus of erythrocytes.

O'Roke (1930b, 1932) and Tarshis (1955) believe that hippoboscid flies (the family Hippoboscidae: *Lynchia hirsuta* and *Stilbometopa impressa*) are vectors of *H. lophortyx*. This should be tested again because biting midges (the family Ceratopogonidae) were not taken into consideration as possible vectors in their field experiments. The experimental birds were not protected from the ceratopogonids. The unusually long prepatent period recorded by the authors cited above (over 100 days) may be due to the penetration of the ceratopogonids, which are known to be the vectors of haemoproteids of galliform birds, into cages with the experimental birds (Bennett and Peirce, 1989; Atkinson, 1991b). See also Appendix 2, p. 868.

19. **Haemoproteus (Parahaemoproteus) scolopaci** Galli-Valerio, 1929

Haemoproteus scolopaci Galli-Valerio, 1929: 57.

Type vertebrate host. *Scolopax rusticola* L. (Charadriiformes).
Additional vertebrate hosts. Some species of the Charadriiformes (Table 39).
Type locality. Lausanne, Switzerland.
Distribution. This parasite has been recorded in the Palearctic and in the Oriental zoogeographical region.
Type material was not designated in the original description. Bennett (1979) redescribed this species on the basis of material obtained from *Scolopax rusticola* and some other charadriiform birds far beyond the type locality (Thailand, Philippine Islands). This material does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of neotypes is required. A series of additional slides is deposited in IRCAH and CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Scolopax*.

Table 39 List of vertebrate hosts of *Haemoproteus scolopaci*.

Actitis hypoleucos	*Gallinago gallinago*	*Tringa glareola*
Calidris minuta	*G. megala*	*T. ochropus*
C. minutilla	*G. stenura*	*T. stagnatilis*
C. pusilla	*Heteroscelus incanus*	*T. totanus*
Charadrius alexandrinus	*Numenius phaeopus*	*Xenus cinereus*
C. dubius	*Phalaropus lobatus*	

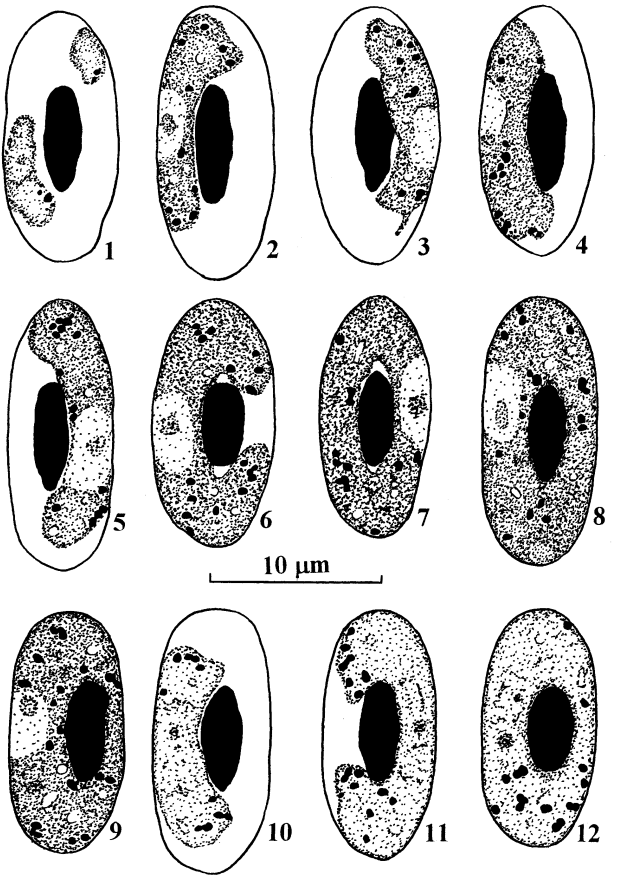

Figure 83 Gametocytes of *Haemoproteus scolopaci* from the blood of *Scolopax rusticola:* *1* – young; *2–9* – macrogametocytes; *10–12* – microgametocytes (according to Valkiūnas and Iezhova, 1992c).

Main diagnostic characters. A parasite of species of the Charadriiformes whose gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends and can completely encircle it and occupy all available cytoplasmic space in the host cells. The maximum number of pigment granules in gametocytes is less than 30.

Development in vertebrate host

Young gametocytes (Fig. 83, *1*). The earliest forms are frequently seen in a polar position in infected erythrocytes, oval or roundish in shape; as the parasite develops, gametocytes adhere to the envelope of erythrocytes and extend longitudinally along the erythrocyte nucleus, not displacing or only slightly displacing the nucleus laterally and usually not touching it; the outline is even or slightly wavy (Fig. 83, *1*).

Macrogametocytes (Fig. 83, *2–9*; Table 40). The cytoplasm is homogeneous in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes not displacing or only slightly displacing it laterally; a more or less evident unfilled space (a ‘cleft’) is usually observed between the growing gametocyte and

Table 40 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. scolopaci*				*H. aegithinae* (modified from Bennett and Peirce, 1990c)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	35				25		
Length		11.2–14.4	12.7	0.7		12.4	0.8
Width		5.4–7.4	6.6	0.4		7.0	0.4
Length of nucleus		5.0–6.7	5.9	0.2		5.8	0.6
Width of nucleus		1.5–2.7	2.2	0.1		2.2	0.3
Erythrocyte parasitized by macrogametocyte	16				40		
Length		12.0–16.1	14.1	0.8		13.2	0.8
Width		5.6–7.3	6.8	0.3		7.3	0.6
Length of nucleus		5.2–6.6	5.4	0.2		5.7	0.6
Width of nucleus		1.7–2.5	1.9	0.1		2.2	0.2
Erythrocyte parasitized by microgametocyte	14				10		
Length		11.8–15.9	13.8	0.7		12.7	2.8
Width		5.4–7.2	6.6	0.3		7.2	0.5
Length of nucleus		5.2–6.6	5.6	0.2		5.8	0.5
Width of nucleus		1.7–2.7	2.0	0.1		2.0	0.4
Macrogametocyte	16				40		
Length		17.3–26.1	21.1	1.4		15.1	1.3
Width		1.9–3.2	2.6	0.4		2.7	1.6
Length of nucleus		3.2–6.0	4.5	0.3		2.5	0.6
Width of nucleus		1.5–3.0	2.0	0.1		1.5	0.4
NDR		0.6–1.0	0.7	0.1		0.8	0.1
No. of pigment granules		14–24	17.8	2.4		16.4	1.5
Microgametocyte	14				10		
Length		15.0–23.2	20.8	1.1		12.3	4.7
Width		2.0–3.1	2.9	0.3		2.8	0.3
Length of nucleus		5.4–10.7	8.6	0.4		5.6	0.4
Width of nucleus		2.0–3.0	2.1	0.1		2.7	0.3
NDR		0.6–1.0	0.7	0.1		0.8	0.1
No. of pigment granules		12–23	16.6	2.0		18.4	2.1

Note: All sizes are given in micrometres.

the nucleus of erythrocyte (Fig. 83, *2, 3*, *5*); a small more or less evident unfilled space is also frequently present between the poles of the nucleus of erythrocyte and growing gametocyte (Fig. 83, *6*, *7*); fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes, and they finally can completely encircle the erythrocyte nucleus and occupy all available cytoplasmic space in the erythrocytes (Fig. 83, *8*, *9*); the outline of growing gametocytes varies from even (Fig. 83, *2, 5*) to wavy and ameboid (Fig. 83, *3*), and it is usually even in advanced forms (Fig. 83, *6*); the parasite nucleus is compact,

usually oval or roundish, median or submedian in position, contains a clear nucleolus (Fig. 83, *5–9*); pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 83, *10–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules tend to gather at the ends in growing gametocytes, but are randomly scattered in the zone lacking the nucleus in fully grown gametocytes; other characters are as for macrogametocytes.

Comments. Gametocytes of *H. scolopaci,* completely encircling the nucleus of erythrocytes, were described by Valkiūnas and Iezhova (1992c) from the type vertebrate host caught on the Curonian Spit in the Baltic Sea during the autumnal migration. These gametocytes had not been seen in *H. scolopaci* before (Bennett, 1979). A clearly evident tendency of gametocytes to grow around the nucleus of erythrocytes up to its complete encircling is an important character of *H. scolopaci*.

20. **Haemoproteus (Parahaemoproteus) aegithinae** Mello, 1935

Haemoproteus aegithinae Mello, 1935b: 471.

Type vertebrate host. *Aegithina tiphia* (L.) (Passeriformes).
Additional vertebrate hosts. *Chloropsis aurifrons* and *C. cyanopogon* (Passeriformes).
Type locality. Nagoa, India.
Distribution. The Oriental zoogeographical region.
Type material. Neohapantotype (No. 37408, *Aegithina tiphia*, 24.07.1969, Maharashra State, India, H.E. McClure) and paraneohapantotype (No. 11727, *Chloropsis aurifrons*, 14.05.1964, Chiang Mai, Thailand, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Aegithina.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed to the envelope of erythrocytes and fill the erythrocytes up to their poles. Dumbbell-shaped growing gametocytes are present. Pigment granules are of small (<0.5 μm) size, about 16 to 18 per gametocyte on average.

Development in vertebrate host
Young gametocytes (Fig. 84, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus not touching the envelope of erythrocytes; the outline is even or slightly ameboid.

Macrogametocytes (Fig. 84, *2–9*; Table 40). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are not seen; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or slightly displace the nucleus laterally and never encircle it completely; medium grown gametocytes usually do not touch the envelope of erythrocytes along their entire margin (Fig. 84, *2–6*); dumbbell-shaped gametocytes are present (Fig. 84, *5*, *7*); fully grown

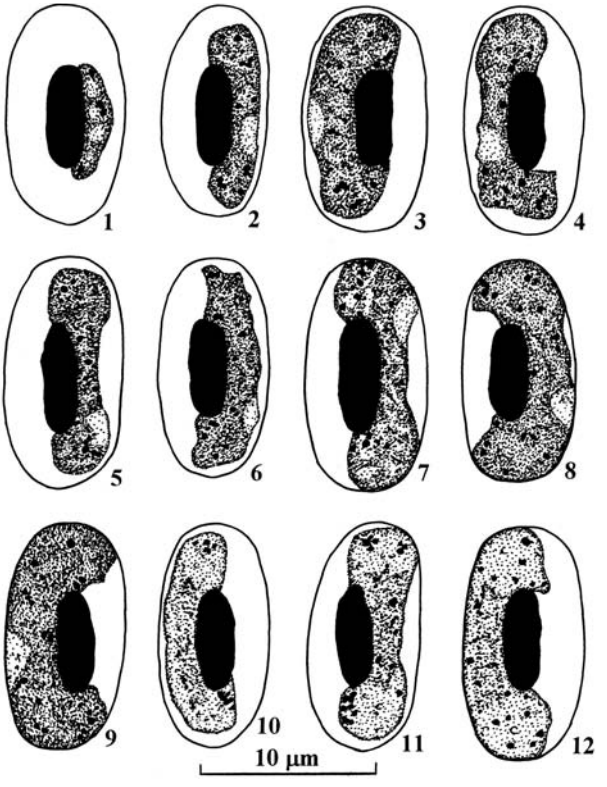

Figure 84 Gametocytes of *Haemoproteus aegithinae* from the blood of *Aegithina tiphia: 1*– young; *2–9* – macrogametocytes; *10–12* – microgametocytes.

gametocytes are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 84, *9*); the outline is usually even, but sometimes wavy or slightly ameboid (Fig. 84, *4*, *6*); the parasite nucleus is compact, variable in form and in position, but most frequently seen in a subterminal position; pigment granules are roundish, of small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 84, *10–12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among haemoproteids of birds belonging to the Passeriformes, *H. aegithinae* is especially similar to *H. monarchus* and *H. quiscalus*. It can be distinguished from the two latter species on the basis of (i) more numerous pigment granules, and (ii) the smaller size of the pigment granules in its gametocytes.

21. **Haemoproteus (Parahaemoproteus) anthi** Mello, 1935

Haemoproteus anthi Mello, 1935b: 474.

T y p e v e r t e b r a t e h o s t. *Anthus novaeseelandiae* (Gmelin) (Passeriformes).

Additional vertebrate hosts. Some species of the Passeriformes (Table 41).
Type locality. Goa, India.
Distribution. The Palearctic, the Ethiopian, and Oriental zoogeographical regions.
Type material. Neohapantotype (No. 11337, *Anthus hodgsoni*, 19.04.1968, Maharashtra State, India, H.E. McClure) is deposited in IRCAH. Paraneohapantotypes designated by Bennett and Peirce (1990c) are invalid because they came from nontype hosts (*Motacilla alba*, *M. capensis*, *M. cinerea*) investigated far beyond the type locality [see Article 75(d)(5), International Code of Zoological Nomenclature, 1985].
Etymology. The specific name is derived from the generic name of the type host, *Anthus*.

Table 41 List of vertebrate hosts of *Haemoproteus anthi.*

Anthus campestris	*A. trivialis*	*M. cinerea*
A. hodgsoni	*Dendronanthus indicus*	*M. flava*
A. leucophrys	*Motacilla alba*	
A. spinoletta	*M. capensis*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes; they displace the nucleus laterally but do not encircle it completely. Medium and fully grown gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent, or they represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes fill the erythrocytes up to their poles. The outline of growing gametocytes varies from even to ameboid but growing gametocytes with a highly ameboid outline are rare and represent less than 10% of the total number of the growing gametocytes. The nucleus in fully grown macrogametocytes is subterminal in position, and it is not located close to the nucleus of infected erythrocytes. Pigment granules are of medium (0.5 to 1.0 μm) or small (< 0.5 μm) size, about 10 per gametocyte on average. This is a species difficult to identify and can only be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes on the basis of a detailed analysis of a set of characters.

Development in vertebrate host

Young gametocytes (Fig. 85, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus (Fig. 85, *1*); advanced gametocytes fill up the space between the nucleus and envelope of erythrocytes (Fig. 85, *2*); the outline is even.

Macrogametocytes (Fig. 85, *3–7*; Table 42). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles; valutin granules are not seen; gametocytes grow along the nucleus of infected erythrocytes, they slightly enclose the nucleus with their ends, displace the nucleus laterally, fill the erythrocytes up to their poles but never encircle the erythrocyte nucleus completely (Fig. 85, *6*, *7*); dumbbell-shaped gametocytes are absent or they represent less than 10% of the total number of growing gametocytes; the outline is even (Fig. 85, *4*, *6*, *7*) or wavy (Fig. 85, *5*), sometimes ameboid; the number of gametocytes with a highly ameboid outline is less than 10% of the total number of growing gametocytes; it should be noted that growing gametocytes usually are not located in the polar position asymmetrically to the nucleus of erythrocyte; the parasite nucleus is variable in form, subterminal in position (Fig. 85, *5–7*), it is not located close to the nucleus of infected erythrocytes; pigment granules are usually roundish or oval,

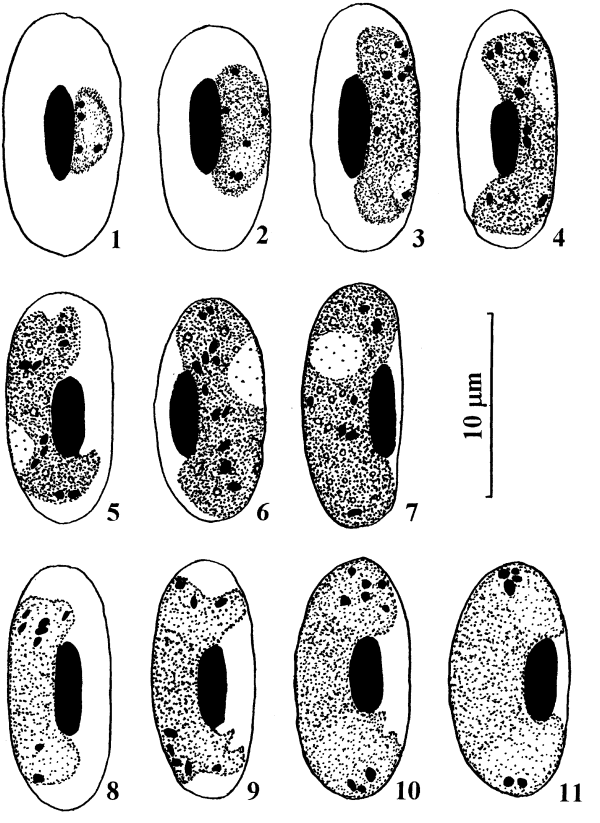

Figure 85 Gametocytes of *Haemoproteus anthi* from the blood of *Anthus trivialis: 1*, *2* – young; *3–7* – macrogametocytes; *8–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1992c).

sometimes rod-like, usually of medium (0.5 to 1.0 μm) and small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 85, *8–11*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. During identification of *H. anthi,* attention should be paid first of all to the following characters. (i) Gametocytes of this parasite are usually closely appressed to the envelope of erythrocytes and, as a result, dumbbell-shaped gametocytes are absent or, if they appear occasionally, they represent less than 10% of the total number of growing gametocytes. (ii) Fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally and fill the erythrocytes up to their poles. By the two above mentioned characters, *H. anthi* is similar to *H. orizivorae* and can be distinguished from the latter species on the basis of its smaller number of pigment granules. *Haemoproteus anthi* has been frequently recorded in mixed infection with *H. motacillae*. The latter parasite has numerous dumbbell-shaped growing gametocytes, and its fully grown gametocytes possess large (1.0 to 1.5 μm) pigment granules. Both of these features are not characteristic of *H. anthi*.

Haemoproteus anthi is also similar to *H. pastoris*, and can be distinguished from the latter species mainly on the basis of a more even outline of its growing gametocytes. The taxonomic status of this character is questionable. It should be noted that additional investigation into *H. anthi* and

Table 42 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. anthi* (modified from Bennett and Peirce, 1990c)				*H. antigonis* (modified from Bennett *et al.*, 1975a)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	45				50		
Length		–	12.1	0.8		13.7	1.0
Width		–	6.3	0.7		7.5	0.5
Length of nucleus		–	5.2	0.5		6.1	0.6
Width of nucleus		–	1.9	0.2		2.8	0.3
Erythrocyte parasitized by macrogametocyte	55				50		
Length		–	12.7	1.1		13.6	1.2
Width		–	6.5	0.6		8.5	1.1
Length of nucleus		–	5.1	0.5		5.9	0.8
Width of nucleus		–	1.8	0.3		2.4	0.4
Erythrocyte parasitized by microgametocyte	10						
Length		–	13.5	0.7	–	–	–
Width		–	6.9	1.0	–	–	–
Length of nucleus		–	5.0	0.5	–	–	–
Width of nucleus		–	2.1	0.2	–	–	–
Macrogametocyte	55				50		
Length		–	15.6	2.0		13.0	1.2
Width		–	3.2	0.5		4.8	1.1
Length of nucleus		–	3.0	0.5		3.6	0.9
Width of nucleus		–	2.1	0.4		3.4	1.1
NDR		0.3–0.7*	0.5	0.1		0.4	–
No. of pigment granules		7–13*	10.7	1.5		19.3	4.0
Microgametocyte	10						
Length		–	15.3	1.6	–	–	–
Width		–	3.5	1.8	–	–	–
Length of nucleus		–	6.1	0.9	–	–	–
Width of nucleus		–	2.8	0.5	–	–	–
NDR		0.3–0.8*	0.6	0.1	–	–	–
No. of pigment granules		5–13*	11.8	2.0	–	–	–

Note: All sizes are given in micrometres. The asterisk marks parameters at $n = 33$.

H. pastoris and detailed comparison of these species, including the experimental transmission and DNA studies, are required. It is possible that *H. pastoris* can be a junior synonym of *H. anthi*.

22. **Haemoproteus (Parahaemoproteus) antigonis** Mello, 1935

Haemoproteus antigonis Mello, 1935b: 471. – *H. tendeiroi* Travassos Santos Dias, 1953: 84, Pl. 2, Fig. 27–29. – *H. antigonis*: Valkiūnas, 1997: 205 (=*H. tendeiroi*).

Type vertebrate host. *Anthropoides virgo* (L.) (Gruiformes).
Additional vertebrate hosts. Some species of the Gruiformes (Table 43).
Type locality. Junagad, India.
Distribution. The Holarctic, Ethiopian, and Oriental zoogeographical regions.
Type material was not designated in the original description. Bennett *et al.* (1975a) designated neotypes which came from a nontype host (*Grus canadensis*) investigated far beyond the type locality (Florida, USA). These neotypes are invalid because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). The designation of neotypes is required. A series of additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name *Antigone* to which the type host was formerly attributed.

Table 43 List of vertebrate hosts of *Haemoproteus antigonis*.

Ardeotis kori	*Eupodotis cafra*	*Grus canadensis*
Balearica pavonina	*E. senegalensis*	*Lissotis melanogaster*
Bugeranus carunculatus	*E. vigorsii*	*Neotis ludwigii*

Main diagnostic characters. A parasite of species of the Gruiformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally, slightly enclosing the nucleus with their ends, but never encircling it completely. The average number of pigment granules is about 20 per macrogametocyte. The average NDR is 0.5 or less.

Development in vertebrate host
Young gametocytes usually take a position lateral to the nucleus of infected erythrocytes and extend longitudinally along the nucleus; growing gametocytes frequently do not touch the nucleus of infected erythrocyte forming a clear more or less evident 'cleft;' the outline is even or wavy.

Macrogametocytes (Fig. 86, *1*, *3–5*; Table 42). The cytoplasm is coarsely granular in appearance, sometimes contains a few small vacuoles; prominent valutin granules were seen in some blood films; gametocytes grow along the nucleus of infected erythrocytes; they markedly displace the nucleus laterally, slightly enclose it with their ends and never encircle it completely; gametocytes are closely appressed to the envelope of erythrocytes; growing gametocytes frequently do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is frequently present between the gametocyte and the erythrocyte nucleus (Fig. 86, *1*, *3*, *5*); this 'cleft' disappears in fully grown gametocytes (Fig. 86, *4*); the outline is usually even; the parasite nucleus is compact, variable in form, frequently roundish, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 86, *2*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The morphology of gametocytes of *H. tendeiroi* and the peculiarities of their influence on infected erythrocytes are identical to *H. antigonis*. Bennett *et al.* (1975a) consider *H. tendeiroi* to be a distinct species only because this parasite develops in gruiform birds of the family Otididae, and *H. antigonis* was originally described from the gruiform birds of the family Gruidae. As discussed above in detail (see p. 69), according to current knowledge, the fact of the record of morphologically identical haemoproteids in birds belonging to different families of the same order cannot be a basis for the description of a new species. That is why *H. tendeiroi* was declared to be a junior synonym of *H. antigonis* (Valkiūnas, 1997).

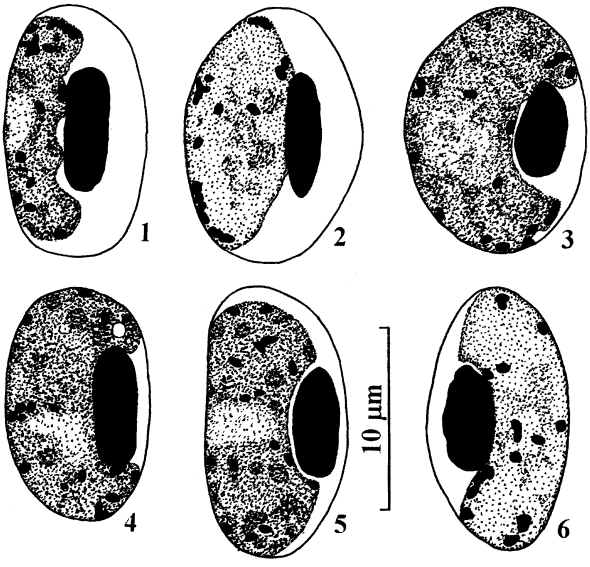

Figure 86 Gametocytes of *Haemoproteus antigonis* from the blood of *Grus canadensis* (*2*, *3*, *6*) and *Lissotis melanogaster* (*1*, *4*, *5*): *1*, *3–5* – macrogametocytes; *2*, *6* – microgametocytes (modified from Bennett *et al*., 1975a).

Among the haemoproteids of birds belonging to the Gruiformes, *H. antigonis* is especially similar to *H. gallinulae*. It can be distinguished from the latter species on the basis of a smaller number of pigment granules in its gametocytes.

23. **Haemoproteus (Parahaemoproteus) beckeri** Roudabush and Coatney, 1935

Haemoproteus beckeri Roudabush and Coatney 1935: 1, Fig. 1, 2.

Type vertebrate host. *Toxostoma rufum* (L.) (Passeriformes).
Additional vertebrate hosts. *Dumetella carolinensis* and *Mimus polyglottos* (Passeriformes).
Type locality. Peru, Nebraska, USA.
Distribution. This species has been recorded only in the Nearctic so far.
Type material. Hapantotype (No. 45242, *Toxostoma rufum*, September 1934, Peru, Nebraska, USA, G.R. Coatney) is deposited in IRCAH.
Etymology. This haemoproteid is named in honour of Dr. Elery R. Becker, the friend and teacher of the authors of the specific name.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends but never encircle it completely. Medium and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent or they represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes do not fill the erythrocytes up to their poles. Pigment granules are of large (1.0 to 1.5 μm) and medium (0.5 to 1.0 μm) size, rod-like or oval, about ten per gametocyte on average. Infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

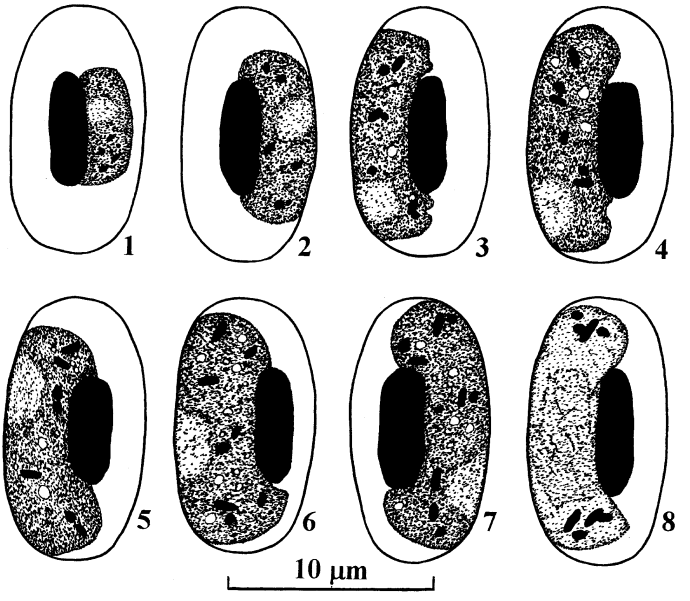

Figure 87 Gametocytes of *Haemoproteus beckeri* from the blood of *Toxostoma rufum: 1*, *2* – young; *3–7* – macrogametocytes; *8* – microgametocyte.

Development in vertebrate host

Young gametocytes (Fig. 87, *1*, *2*). The earliest forms are usually seen located in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the erythrocyte nucleus and extend longitudinally being closely appressed to the envelope of erythrocytes; the outline is usually even.

Macrogametocytes (Fig. 87, *3–7*; Table 44). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; gametocytes grow along the nucleus of infected erythrocytes, they displace the nucleus laterally and slightly enclose it with their ends but never encircle it completely; some fully grown gametocytes markedly displace the erythrocyte nucleus laterally, sometimes to the envelope of erythrocytes; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are absent or, if they appear occasionally, they represent less than 10% of the total number of growing gametocytes; fully grown gametocytes do not fill the erythrocytes up to their poles (Fig. 87, *5–7*); the outline is usually even; the parasite nucleus is compact, variable in form and position, but is most frequently observed in a subterminal position, and has never been recorded in a terminal position; pigment granules are usually rod-like or oval, sometimes roundish, of large (1.0 to 1.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes and their nuclei are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 87, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. beckeri* is especially similar to *H. fallisi* and *H. africanus*. It can be readily distinguished from the two latter species on the basis of the presence of large (1.0 to 1.5 μm), rod-like pigment granules in its gametocytes.

Table 44 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. beckeri* (modified from Roudabush and Coatney, 1935; Bennett *et al.*, 1987)				*H. coraciae*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	25				33			
Length		–	11.3	0.8		11.0–14.7	12.0	0.9
Width		–	6.5	0.6		5.9–9.0	7.2	0.8
Length of nucleus		–	5.2	0.5		5.2–7.0	6.0	0.7
Width of nucleus		–	1.8	0.2		2.2–3.2	2.4	0.4
Erythrocyte parasitized by macrogametocyte	25				37			
Length		–	13.0	0.7		11.8–15.9	13.4	0.8
Width		–	6.6	0.6		6.2–8.8	7.4	0.8
Length of nucleus		–	6.1	0.4		5.0–6.6	5.9	0.5
Width of nucleus		–	2.0	0.2		2.2–3.3	2.7	0.5
Erythrocyte parasitized by microgametocyte	10				24			
Length		–	13.0	1.1		11.4–15.2	13.8	1.0
Width		–	6.9	0.4		5.7–8.7	7.8	0.5
Length of nucleus		–	6.0	0.4		5.4–6.0	5.8	0.5
Width of nucleus		–	2.0	0.3		2.4–3.4	2.6	0.3
Macrogametocyte	25				37			
Length		–	13.6	0.9		11.0–16.2	14.8	1.3
Width		2.4–4.0*	3.5	0.6		2.3–3.2	2.9	0.7
Length of nucleus		–	2.9	0.6		2.0–3.3	2.3	0.3
Width of nucleus		–	2.0	0.3		1.1–3.0	1.4	0.4
NDR		–	0.5	0.2		0.3–0.9	0.7	0.2
No. of pigment granules		4–11*	8.9	1.0		7–16	10.2	1.8
Microgametocyte	10				24			
Length		–	13.3	1.5		11.2–19.4	16.8	1.4
Width		2.6–4.6*	3.6	0.6		2.3–3.2	2.5	0.3
Length of nucleus		–	5.4	0.5		5.2–9.2	7.3	1.2
Width of nucleus		–	2.7	0.4		2.3–3.0	2.4	0.9
NDR		–	0.6	0.2		0.6–1.0	0.8	0.2
No. of pigment granules		5–12*	9.8	1.1		5–15	10.7	1.4

Note: All sizes are given in micrometres. The asterisk marks the parameters when the number of measured cells (*n*) is unknown.

24. **Haemoproteus (Parahaemoproteus) centropi** Mello, 1935

Haemoproteus centropi Mello, 1935b: 471. – *H. froilanoi* Tendeiro, 1947: 292, Fig. 36–40. – *H. centropi*: Peirce, 1977: 59 (=*H. froilanoi*).

Type vertebrate host. *Centropus sinensis* (Stephens) (Cuculiformes).
Additional vertebrate hosts. Some species of the Cuculiformes (Table 45).
Type locality. Diu, India.
Distribution has not been investigated. It is likely that the distribution is limited to the tropical and subtropical regions.
Type material was not designated in the original description. Neohapantotypes designated by Garnham and Duggan (1986) and deposited in the collection of Professor P.C.C. Garnham, the British Museum (Natural History), are invalid because they came from a nontype host (*Clamator jacobinus*) investigated far beyond the type locality (the Ethiopian zoogeographical region). This material does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). The neotypes should be designated. A series of additional slides is deposited in CPG and IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Centropus.*

Table 45 List of vertebrate hosts of *Haemoproteus centropi.*

Centropus milo	*Clamator jacobinus*
C. senegalensis	*C. levaillantii*
C. superciliosus	*Crotophaga sulcirostris*
C. toulou	

Main diagnostic characters. A parasite of species of the Cuculiformes whose gametocytes grow around the nucleus of infected erythrocytes; they displace the nucleus laterally, slightly enclose it with their ends but do not encircle it completely. Pigment granules in fully grown gametocytes tend to aggregate into large compact masses or loosely aggregated clumps. The ends of the gametocytes are rounded.

Development in vertebrate host
The morphometric parameters are given according to Peirce (1977).

Young gametocytes (Fig. 88, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; the outline is even.

Macrogametocytes (Fig. 88, *2*, *3*, *5*, *7–9*). The cytoplasm is finely granular in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, they displace the nucleus laterally, slightly enclose it with their ends but do not encircle it completely; the average NDR is 0.5; growing gametocytes are closely appressed to the envelope of erythrocytes but frequently do not touch the erythrocyte nucleus so that a more or less evident unfilled space (a 'cleft') is usually present between the gametocyte and the erythrocyte nucleus (Fig. 88, *7*, *8*); growing gametocytes frequently take an asymmetrical position to the nucleus of erythrocytes (Fig. 88, *8*); fully grown gametocytes fill the erythrocytes up to their poles (Fig. 88, *5*), and are closely appressed to the nucleus and envelope of erythrocytes; the ends of the gametocytes are more or less rounded; the outline is usually even; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, and in fully grown gametocytes, they tend to aggregate into large compact masses or loosely aggregated clumps (Fig. 88, *5*); the number of the pigment granules varies from 8 to 24 (on average 14.3 per gametocyte); infected erythrocytes are slightly hypertrophied in length and width in comparison to uninfected ones. Uninfected erythrocytes vary from 11.2 to 14.6 (on average 12.4) μm in length, and from 5.2 to 7.7 (on average 6.6) μm in width. The same parameters for parasitized erythrocytes are from 11.2 to 16.3 (on average 13.8) μm and from 6.0 to 9.5 (on average 7.7) μm, respectively.

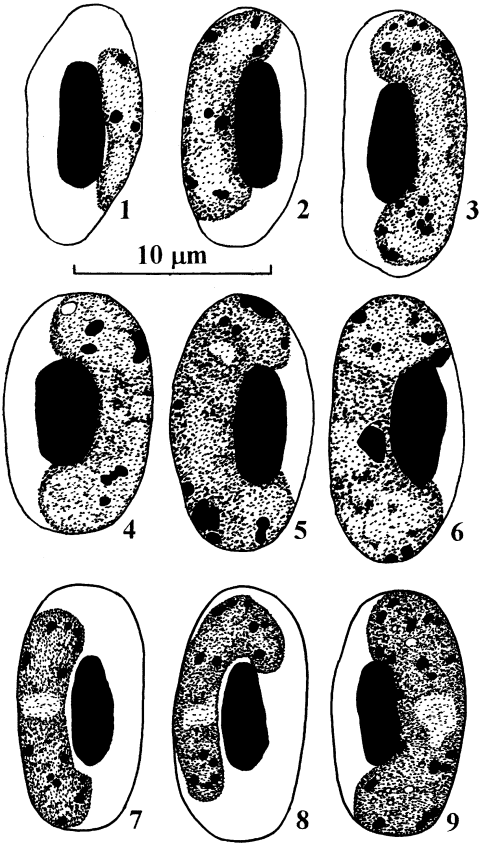

Figure 88 Gametocytes of *Haemoproteus centropi* from the blood of *Clamator jacobinus:* *1* – young; *2*, *3*, *5*, *7–9* – macrogametocytes; *4*, *6* – microgametocytes (*1–6* are modified from Peirce, 1977).

Microgametocytes (Fig. 88, *4*, *6*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the number of pigment granules varies from 5 to 25 (on average 16.3 per gametocyte); other characters are as for macrogametocytes.

25. **Haemoproteus (Parahaemoproteus) coraciae** Mello and Afonso, 1935

Haemoproteus coraciae benghalensis Mello and Afonso, 1935: 68, Pl. 1. – *H. coraciae*: Bhatia, 1938: 217, Fig. 106 (=*H. coraciae benghalensis*). – *H. coraciae* Vallés, 1938: 310, Fig. A (nom. praeocc., non Mello and Afonso, 1935). – *H. cruzferreirae* Tendeiro, 1947: 308, Fig. 51–55 (*H. cruz-ferreirae*). – *H. fontesi* Tendeiro, 1947: 299, Fig. 46–50. – *H. fontesi* var. *cyanogasteri* Tendeiro, 1947: 299. – *H. velascoi* Tendeiro, 1947: 298, Fig. 41–45. – *H. coraciae*: Bishop and Bennett, 1986: 1860 (=*H. coraciae* Vallés, *H. cruzferreirae*, *H. fontesi*, *H. fontesi* var. *cyanogasteri*, *H. velascoi*).

Type vertebrate host. *Coracias benghalensis* (L.) (Coraciiformes).
Additional vertebrate hosts. Some species of the Coraciiformes (Table 46).
Type locality. Goa, India.
Distribution. The Oriental and Ethiopian zoogeographical regions, the South and Central Palearctic.
Type material. Neohapantotype (No. 87992, *Coracias benghalensis*, 13.02.1979, Hyderabad, Andhra Pradesh, India, H.E. McClure) and paraneohapantotypes (No. 46088, *Coracias naevia*, 15.03.1976, Dakar, Senegal, J. Blancou; No. 46089, 1975, other data are as for No. 46088; No. 92132, *C. caudata*, 25.06.1980, Balmoral, Zambia, M.A. Peirce) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Coracias*.

Table 46 List of vertebrate hosts of *Haemoproteus coraciae.*

Coracias abyssinica	*C. naevia*
C. caudata	*C. spatulata*
C. cyanogaster	*Eurystomus glaucurus*
C. garrulus	*E. orientalis*

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes slightly displace the nucleus of infected erythrocytes laterally and enclose it with their ends. Microgametocytes can completely encircle the nucleus of erythrocytes. Growing gametocytes with a highly ameboid outline are present. Dumbbell-shaped growing gametocytes are present. The average number of pigment granules in gametocytes is less than 15. The average width of gametocytes is less than 4 μm.

Development in vertebrate host
Young gametocytes (Fig. 89, *1*, *2*). The early forms are usually seen in a lateral position to the nucleus of erythrocytes, frequently banana-like (Fig. 89, *1*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline varies from even (Fig. 89, *1*) to ameboid (Fig. 89, *2*).

Macrogametocytes (Fig. 89, *3–7*; Table 44). The cytoplasm is finely granular in appearance, usually contains valutin granules; gametocytes grow around the nucleus of erythrocytes, they enclose the nucleus with their ends but do not encircle it completely; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 89, *4*, *5*), however, the forms without the 'dip' are also present (Fig. 89, *3*); fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes, and they frequently do not fill the erythrocytes up to their poles (Fig. 89, *6*, *7*); the outline of growing forms is even (Fig. 89, *3*), wavy (Fig. 89, *4*), or ameboid (Fig. 89, *5*), and it is usually even in full grown gametocytes; the parasite nucleus is compact, variable in form but frequently roundish or oval, median in position; pigment granules are roundish or oval but sometimes rod-like, of medium (0.5 to 1.0 μm) and small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 89, *8–11*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline is more ameboid (Fig. 89, *8*, *9*) than in macrogametocytes; circumnuclear fully grown microgametocytes are seen (Fig. 89, *11*) but are not common; other characters are as for macrogametocytes.

Comments. The morphology of gametocytes of *H. coraciae* from the blood of *Coracias garrulus* and *C. benghalensis* is nearly identical (Bishop and Bennett, 1986; Valkiūnas and Iezhova, 1990b).

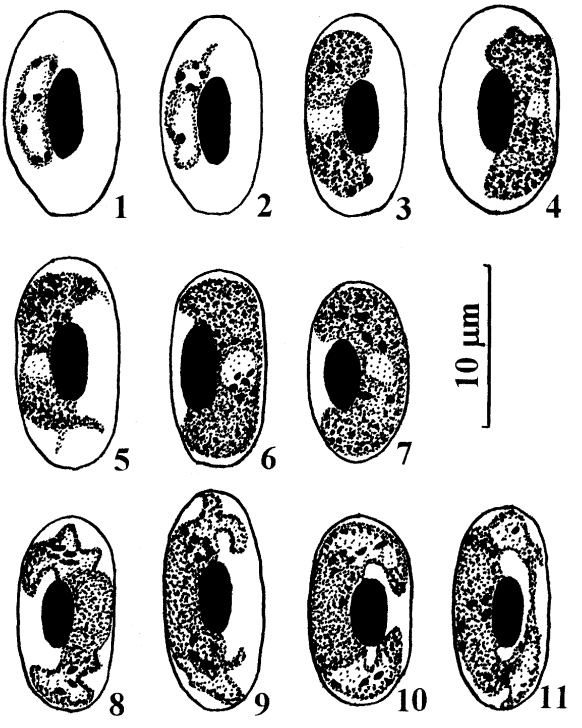

Figure 89 Gametocytes of *Haemoproteus coraciae* from the blood of *Coracias garrulus: 1*, *2* – young; *3–7* – macrogametocytes; *8–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1990b).

It should be noted that the circumnuclear microgametocytes (Fig. 89, *11*) have been recorded only in *C. garrulus* so far. They were seen in numerous blood films together with the gametocytes typical of *H. coraciae* (Fig. 89, *10*).

Among the haemoproteids of birds belonging to the Coraciiformes, *H. coraciae* is especially similar to *H. meropis*. It can be distinguished from the latter species, particularly on the basis of (i) the ameboid outline of its growing gametocytes and (ii) the clearly defined tendency in fully grown gametocytes to grow around the nucleus of the erythrocytes up to the complete encircling of the nucleus by microgametocytes.

A record of *H. coraciae* in *Merops apiaster* (Meropidae) (Kairullaev and Yakunin, 1982) should be validated because the record of this parasite in an unusual host was not accompanied with any description or illustrations.

Musaev and Zeiniev (1992) described *Haemoproteus hachmasensis* from the blood of *Coracias garrulus* in Azerbaijan. The description includes several contradictory points. First, round gametocytes located free in the plasma were recorded. This is not characteristic of species belonging to the 'enucleator' group to which *H. hachmasensis* was originally attributed. This also shows that the gametocytes in the original material are influenced by the onset of gametogenesis, and thus they cannot be used for morphological comparison with other haemoproteid species. Second, the gametocytes shown in microphotographs in the original description, are similar to gametocytes of *H. coraciae* in their shape, form, and number of pigment granules. The latter character is especially obvious in the gametocytes lacking valutin granules. It is likely that *H. coraciae* parasitize *C. garrulus* in Azerbaijan. Until additional material is present, the *H. hachmasensis* is declared to be a *species inquirenda*.

26. **Haemoproteus (Parahaemoproteus) dicruri** Mello, 1935

Haemoproteus dicruri Mello, 1935b: 473.

Type vertebrate host. *Dicrurus macrocercus* (Vieil.) (Passeriformes).
Additional vertebrate host. *Dicrurus adsimilis* (Passeriformes).
Type locality. Pragana, India.
Distribution. The Oriental and Ethiopian zoogeographical regions.
Type material was not designated in the original description, and neotypes have not been designated as yet. The blood films used by Peirce (1984g) for redescription of this species are not suitable for the neotypes because they were collected from a nontype host (*Dicrurus adsimilis*) investigated far beyond the type locality (the Ethiopian zoogeographical region). A series of additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Dicrurus.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Medium and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes were not seen. Fully grown gametocytes fill the erythrocytes up to their poles. The nucleus in fully grown macrogametocytes is usually median or submedian and, as a rule, is not close to the nucleus of infected erythrocytes. The pigment granules are of medium (0.5 to 1.0 μm) size, about 15 per gametocyte on average. One large (about 1.5 μm in diameter) pigment granule is present in some microgametocytes.

Development in vertebrate host
The description of gametocytes is given according to Peirce (1984g) with slight modifications.

Young gametocytes are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere both to the nucleus and envelope of erythrocytes and extend longitudinally along the nucleus; the outline is even.

Macrogametocytes (Fig. 90, *1*, *2*). The cytoplasm stains very pale blue, vacuoles and valutin granules are not characteristic; gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the nucleus laterally but do not encircle it completely; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, and the dumbbell-like forms were not seen; fully grown gametocytes fill the erythrocytes up to their poles; the outline is even; the parasite nucleus stains pale pink and is frequently difficult to distinguish, variable in form, usually median or submedian in position; it usually is not located close to the nucleus of infected erythrocytes; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, usually randomly scattered throughout the cytoplasm, their number varies from 11 to 18 (on average 14.7); infected erythrocytes are slightly hypertrophied in comparison to uninfected ones. The size of uninfected erythrocytes ($n = 20$) is 9.9 to 12.4 by 5.4 to 7.1 (on average 11.2×6.4) μm, and that of infected erythrocytes ($n = 20$) is 10.7 to 13.3 by 6.2 to 7.7 (on average 12.5×6.8) μm.

Microgametocytes (Fig. 90, *3*, *4*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the cytoplasm is colourless and the nucleus is so pale that it is indiscernible; only the presence of pigment granules indicates that the parasite is in the erythrocyte; a large (about 1.5 μm in diameter) distinct roundish pigment granule is present in some gametocytes (Fig. 90, *4*); other characters are as for macrogametocytes.

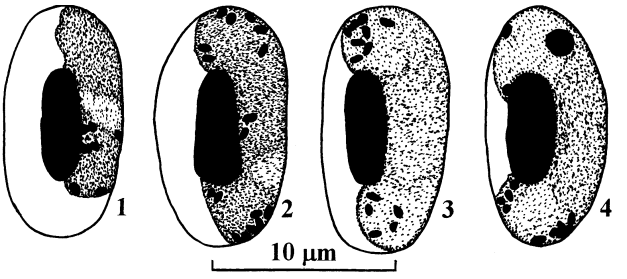

Figure 90 Gametocytes of *Haemoproteus dicruri* from the blood of *Dicrurus adsimilis: 1*, *2* – macrogametocytes; *3*, *4* – microgametocytes (modified from Peirce, 1984g).

Comments. *Haemoproteus dicruri* is an insufficiently investigated species. It can be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes mainly on the basis of the presence of one large pigment granule in some microgametocytes (Fig. 90, *4*). It should be noted that it is not clear whether or not this granule is typical of the parasite and how frequently it develops in microgametocytes. Additional material is required to answer these questions.

27. **Haemoproteus (Parahaemoproteus) elani** Mello, 1935

Haemoproteus elani Mello, 1935b: 472. – *H. figueiredoi* Travassos Santos Dias, 1953: 66, Pl. 1, Fig. 2–5, Microphotograph (Fig. 1). – *H. elani*: Peirce *et al.*, 1990: 1096 (=*H. figueiredoi*).

Type vertebrate host. *Elanus caeruleus* (Desfontaines) (Falconiformes).
Additional vertebrate hosts. Some species of the Falconiformes (Table 47).
Type locality. Daman, India.
Distribution. The Holarctic, Ethiopian, and Oriental zoogeographical regions. So far, this parasite has rarely been recorded in the Palearctic.
Type material was not designated in the original description. Peirce *et al.* (1990) designated neotypes which came from nontype hosts (*Buteo lineatus*, *Accipiter cooperii*, *Aquila rapax*) investigated far beyond the type locality (Nearctic and Ethiopian zoogeographical region). These neotypes are invalid because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of neotypes is required. A series of additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Elanus*.

Table 47 List of vertebrate hosts of *Haemoproteus elani.*

Accipiter cooperii	*Aegypius tracheliotus*	*Circaetus gallicus*
A. gentilis	*Aquila rapax*	*Gyps africanus*
A. melanoleucus	*Buteo jamaicensis*	*Hieraaetus fasciatus*
A. nisus	*B. lagopus*	
A. striatus	*B. lineatus*	

Note: Peirce *et al.* (1990) declared *H. buteonis* to be a junior synonym of *H. elani* and united the hosts of these species. Only the bird species with well described and (or) illustrated records of *H. elani* are included in this table, and the hosts of *H. buteonis* are given separately.

Main diagnostic characters. A parasite of species of the Falconiformes whose fully grown gametocytes displace the nucleus of infected erythrocytes laterally, slightly enclose it with their ends and never encircle it completely. Mature gametocytes, which do not touch the nucleus of erythrocytes or touch the nucleus only at some points, are common.

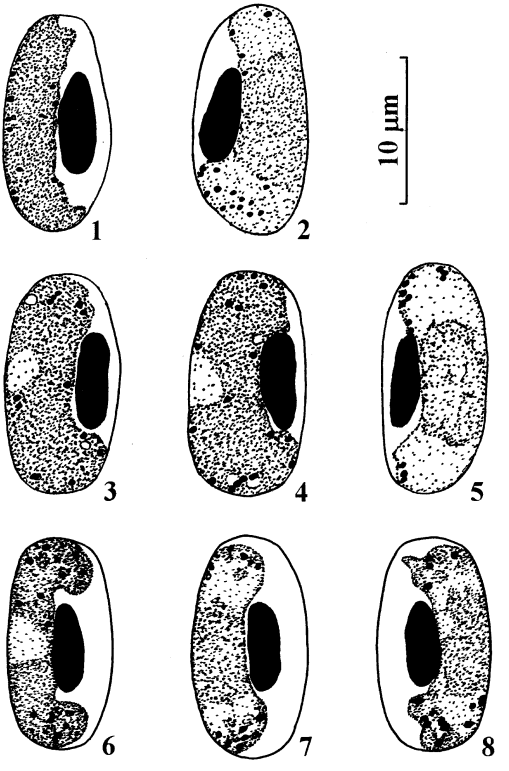

Figure 91 Gametocytes of *Haemoproteus elani* from the blood of *Buteo lineatus* (*1*, *2*, *6*–*8*) and *Accipiter gentilis* (*3*–*5*):
1, *3*, *4*, *6* – macrogametocytes; *2*, *5*, *7*, *8* – microgametocytes (*1*, *2* are modified from Peirce *et al*., 1990).

Development in vertebrate host

Young gametocytes. The earliest forms can be seen anywhere in infected erythrocytes, roundish or oval; the outline is usually even; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes, and they usually take a position lateral to the nucleus and do not touch the nucleus; however, forms which adhere to the erythrocyte nucleus are also present.

Macrogametocytes (Fig. 91, *1*, *3*, *4*, *6*; Table 48). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are present in some blood films, and, when present, they are usually compact, numerous, and obscure the pigment granules; gametocytes grow along the nucleus of infected erythrocytes; they displace the nucleus laterally, only slightly enclose it with their ends, and never encircle it completely; the outline is usually even or slightly wavy, the ameboid outline is not characteristic but has been seen occasionally; gametocytes are characterized by the variable contact with the nucleus of erythrocytes: together with gametocytes which adhere to the nucleus of erythrocytes (Fig. 91, *6*), gametocytes which do not touch the nucleus (Fig. 91, *3*) or touch it only in some points (Fig. 91, *1*, *4*), are common; fully grown gametocytes fill the erythrocytes up to their poles (Fig. 91, *4*); the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish or oval, usually of

Table 48 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. elani* (modififed from Peirce *et al.*, 1990)			*H. gallinulae* (modififed from Bennett, 1980)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	25			40		
Length		15.3	0.8		12.5	0.8
Width		7.7	0.5		7.7	0.6
Length of nucleus		6.5	0.5		5.6	0.6
Width of nucleus		3.1	0.3		2.4	0.3
Erythrocyte parasitized by macrogametocyte	25			41		
Length		15.9	1.7		13.0	0.8
Width		7.6	0.9		8.1	0.5
Length of nucleus		5.5	0.6		5.0	0.8
Width of nucleus		3.2	0.2		2.4	0.3
Erythrocyte parasitized by microgametocyte	25			18		
Length		16.2	0.9		12.5	0.8
Width		7.7	0.6		8.5	0.5
Length of nucleus		5.7	0.5		5.2	0.5
Width of nucleus		2.9	0.3		2.3	0.6
Macrogametocyte	25					
Length		16.0	1.8	–	–	–
Width		3.1	0.4	–	–	–
Length of nucleus		3.0	0.7	41	3.1	0.5
Width of nucleus		1.9	0.4	41	2.2	0.4
NDR		0.6	0.3	41	0.7	–
No. of pigment granules		15.1	1.4	41	32.3	3.5
Microgametocyte	25			18		
Length		16.4	1.3		19.7	2.3
Width		3.3	0.5		3.7	0.5
Length of nucleus		8.1	1.2		4.7	1.0
Width of nucleus		3.3	0.5		2.5	0.4
NDR		0.6	0.2		0.7	–
No. of pigment granules		15.0	1.8		32.3	3.2

Note: All sizes are given in micrometres.

small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 91, *2*, *5*, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; ameboid forms (Fig. 91, *8*) are more frequently seen than among macrogametocytes; other characters are as for macrogametocytes.

Comments. Two species of haemoproteids, whose gametocytes displace the nucleus of erythrocytes laterally and do not encircle the nucleus completely, parasitize falconiform birds. They

are *H. elani* and *H. buteonis*. A detailed analysis of the morphology of their gametocytes revealed some differences which form the basis for differentiation of these species (see 'Comments' to *H. buteonis*). Peirce *et al.* (1990) disregarded these differences and synonymized *H. buteonis* with *H. elani*. They believe that the gametocytes of the latter species are highly pleomorphic, and the characters of *H. elani* gametocyte overlap those of *H. buteonis*. However, slides with a pure infection of *H. buteonis* and *H. elani* are present; this contradicts the opinion mentioned above about the pleomorphism of the gametocytes of *H. elani*. Until the variability of gametocytes of these haemoproteids is studied experimentally, it is reasonable to consider *H. buteonis* as a distinct species.

28. **Haemoproteus (Parahaemoproteus) gallinulae** Mello, 1935

Haemoproteus gallinulae Mello, 1935b: 469. – *H. fulicae* Fonseca, 1938: 315, Fig. 1–9. – *H. gallinulae*: Bennett, 1980: 321 (=*H. fulicae*).

Type vertebrate host. *Gallinula chloropus* (L.) (Gruiformes).
Additional vertebrate hosts. Some species of the Gruiformes (Table 49).
Type locality. Carambolim Lake, Department of Ilhas Goa, India.
Distribution. The Holarctic, Ethiopian, and Oriental zoogeographical regions.
Type material was not designated in the original description. Designation of neotypes is required. The slides used for the redescription of this species (Bennett, 1980; Sacchi and Prigioni, 1986) are not suitable to be designated as the neotypes because they came from nontype hosts investigated far beyond the type locality and thus do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). A series of additional slides is deposited in IRCAH and CDSA.
Etymology. The specific name is derived from the generic name of the type host, *Gallinula.*

Table 49 List of vertebrate hosts of *Haemoproteus gallinulae* (modified from Bennett, 1980).

Amaurornis flavirostris	*Porphyrio porphyrio*	*R. fasciata*
A. phoenicurus	*Porzana fusca*	*Rallus aquaticus*
Fulica americana	*Rallina eurizonoides*	

Main diagnostic characters. A parasite of species of the Gruiformes whose fully grown gametocytes slightly enclose the nucleus of infected erythrocytes with their ends, slightly displace the nucleus laterally but do not encircle it completely. The average number of pigment granules is greater than 25 per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 92, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend along the erythrocyte nucleus; they are frequently located asymmetrically to the nucleus; the outline is usually even.

Macrogametocytes (Fig. 92, *3–6*; Table 48). The cytoplasm is granular in appearance; gametocytes grow around the nucleus of infected erythrocytes, they slightly enclose the nucleus with their ends, displace the nucleus laterally but do not encircle it completely; growing gametocytes frequently take an asymmetrical position to the nucleus of erythrocytes (Fig. 92, *4*) and they frequently do not touch the nucleus, forming a more or less

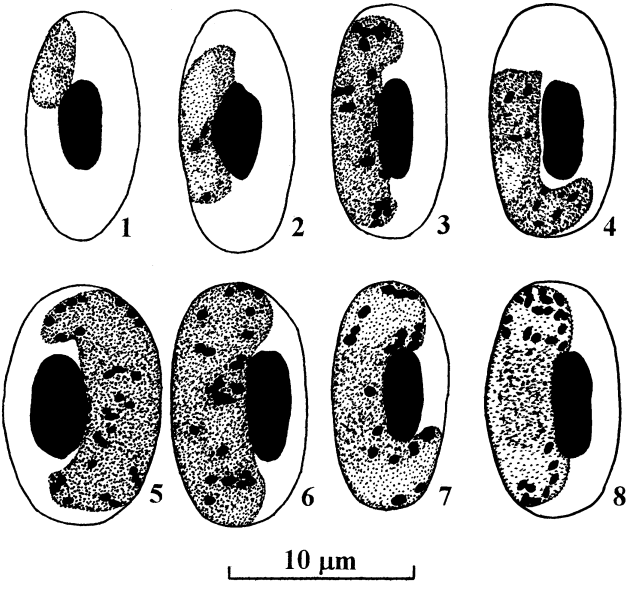

Figure 92 Gametocytes of *Haemoproteus gallinulae* from the blood of *Gallinula chloropus* (*1–4*, *7*, *8*) and *Rallina eurizonoides* (*5*, *6*): *1*, *2* – young; *3–6* – macrogametocytes; *7*, *8* – microgametocytes (*1–3*, *7* are modified from Sacchi and Prigioni, 1986; and *5*, *6* are modified from Bennett, 1980).

evident unfilled space (a 'cleft') between the gametocyte and the erythrocyte nucleus (Fig. 92, *4*); however, growing gametocytes, which touch both the nucleus and the envelope of erythrocytes, are also present (Fig. 92, *3*); medium grown gametocytes, which do not touch the nucleus of erythrocytes, are present; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 92, *6*), and they fill the erythrocytes up to their poles; the outline is usually even; the parasite nucleus is compact, usually roundish or oval, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 92, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Gruiformes, *H. gallinulae* is especially similar to *H. antigonis*. It can be distinguished from the latter species, particularly, on the basis of having more numerous pigment granules in its gametocytes.

29. **Haemoproteus (Parahaemoproteus) halcyonis** Mello, 1935

Haemoproteus halcyonis Mello, 1935b: 474. – *H. ecae* Tendeiro, 1947: 293, Fig. 31–35 (*H. eçae*). – *H. halcyonis*: Bennett and Campbell, 1973: 339 (=*H. ecae*).

T y p e v e r t e b r a t e h o s t. *Halcyon smyrnensis* (L.) (Coraciiformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. Some species of the Coraciiformes (Table 50).

Type locality. Canacona, India.

Distribution. The Oriental and Ethiopian zoogeographical regions, South and Central Palearctic.

Type material was not designated in the original description. The neotypes designated by Bennett and Campbell (1973) are invalid because they came from a nontype host (*Halcyon chloris*) investigated far beyond the type locality (Malaysia) [see Article 75(d)(5) of the International Code of Zoological Nomenclature, 1985]. Designation of neotypes is required. A series of additional slides is deposited in IRCAH.

Etymology. The specific name is derived from the generic name of the type host, *Halcyon.*

Table 50 List of vertebrate hosts of *Haemoproteus halcyonis* (modified from Bennett and Campbell, 1973).

Alcedo atthis	*H. concreta*	*Ispidina picta*
A. cristata	*H. coromanda*	*Lacedo pulchella*
Ceryle rudis	*H. leucopygia*	*Pelargopsis capensis*
Ceyx erithacus	*H. lindsayi*	*Tanysiptera galatea*
C. rufidorsum	*H. pileata*	
Halcyon chloris	*H. senegalensis*	

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally and only slightly enclose the nucleus with their ends. Fully grown gametocytes which do not touch the nucleus of erythrocytes are common. The average number of pigment granules is greater than 15 per gametocyte. The average width of gametocytes is greater than 4 μm.

Development in vertebrate host

Young gametocytes (Fig. 93, *1*). The earliest forms are frequently seen in a polar or subpolar position in infected erythrocytes; as the parasite develops, gametocytes extend along the nucleus of erythrocytes, frequently taking an asymmetrical position to the nucleus (Fig. 93, *1*) and slightly displacing the nucleus laterally; growing gametocytes usually do not touch the nucleus of erythrocytes; the outline is usually even.

Macrogametocytes (Fig. 93, *4*, Table 51). The cytoplasm stains from blue to rose which is uncommon among bird haemoproteids; it is granular in appearance, frequently contains small vacuoles; gametocytes grow around the nucleus of erythrocytes, they slightly enclose the nucleus with their ends, markedly displace the nucleus laterally but do not encircle it completely; gametocytes, which do not touch the nucleus of erythrocytes and thus form a more or less unfilled space (a 'cleft') between the gametocyte

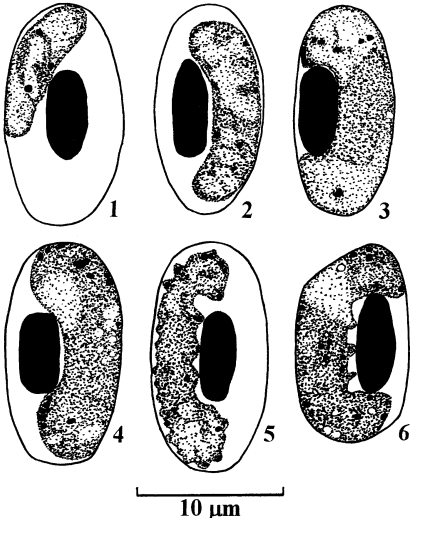

Figure 93 Gametocytes of *Haemoproteus halcyonis* from the blood of *Halcyon chloris:*
1 – young; *2*, *3* – microgametocytes; *4–6* – macrogametocytes (modified from Bennett and Campbell, 1973).

Table 51 Morphometric parameters of gametocytes and host cells of *Haemoproteus halcyonis* ($n = 10$) (modified from Bennett and Campbell, 1973).

Feature	$\overline{X}$	*SD*
Uninfected erythrocyte		
Length	14.2	0.9
Width	7.8	0.6
Length of nucleus	6.9	0.5
Width of nucleus	2.8	0.3
Parasitized erythrocyte		
Length	14.5	0.9
Width	8.0	0.7
Length of nucleus	5.9	0.4
Width of nucleus	2.5	0.3
Gametocyte		
Length	14.4	0.8
Width	4.3	0.7
NDR	0.4	–
No. of pigment granules	24.4	9.4

Note: All sizes are given in micrometres.

and the nucleus of erythrocyte (Fig. 93, *4*), are common and they are found even among the fully grown gametocytes; fully grown gametocytes fill the erythrocytes up to their poles; the parasite nucleus is variable in shape and position; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 93, *2*, *3*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. It should be noted that gametocytes with a highly ameboid outline of unusual shape (Fig. 93, *5*, *6*) are found in the blood films which were the basis for the redescription of this species. The number of such gametocytes is up to 10% of the total number of gametocytes in the films. Bennett and Campbell (1973) believe that these gametocytes are not characteristic of *H. halcyonis*, and they consider their highly ameboid outline to be an artefact. This question needs additional investigation.

Among the haemoproteids of birds belonging to the Coraciiformes, *H. halcyonis* is especially similar to *H. eurystomae* and *H. manwelli*. Mature gametocytes of *H. halcyonis* frequently do not touch the nucleus of erythrocytes, and this is not characteristic of *H. eurystomae*. *Haemoproteus halcyonis* can be distinguished from *H. manwelli* initially on the basis of more numerous pigment granules in its gametocytes.

30. **Haemoproteus (Parahaemoproteus) herodiadis** Mello, 1935

Haemoproteus herodiadis Mello, 1935a: 351. – *H. herodiadis* var. *mathislegeri* Mohammed, 1958: 223, Pl. 10, Fig. 1–17 (var. *mathis-legeri*). – *H. mathislegeri*: Levine and Campbell, 1971: 477 (emend. pro var. *mathis-legeri*). – *H. herodiadis*: Valkiūnas, 1997: 215 (= *H. herodiadis* var. *mathis-legeri*, *H. mathislegeri*).

Type vertebrate host. *Egretta intermedia* (Wagler) (Ciconiiformes).
Additional vertebrate hosts. Some species of the Ciconiiformes (Table 52).
Type locality. Carambolim Lake, Department of Ilhas Goa, India.
Distribution has been insufficiently investigated. This parasite has been recorded in the Holarctic and Oriental zoogeographical region.
Type material has never been designated.
Etymology. The specific name is derived from the generic name *Herodias* to which the type host was formerly attributed.

Table 52 List of vertebrate hosts of *Haemoproteus herodiadis.*

Ardea herodias	*I. sinensis*
Dupetor flavicollis	*Nyctanassa violacea*
Egretta thula	*Nycticorax nycticorax*
Ixobrychus minutus	

Main diagnostic characters. A parasite of species of the Ciconiiformes whose fully grown gametocytes do not displace or only slightly displace the nucleus of infected erythrocytes laterally; they never encircle the nucleus completely and do not fill the erythrocytes up to their poles. The outline of gametocytes is even. Pigment granules are of small (<0.5 μm) size, dust-like in appearance. The average number of pigment granules is about ten per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 94, *1*) are usually seen in a position lateral to the nucleus of infected erythrocytes, but sometimes they also take a polar position in the host cells; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes, and usually they do not touch the nucleus; the outline is even.

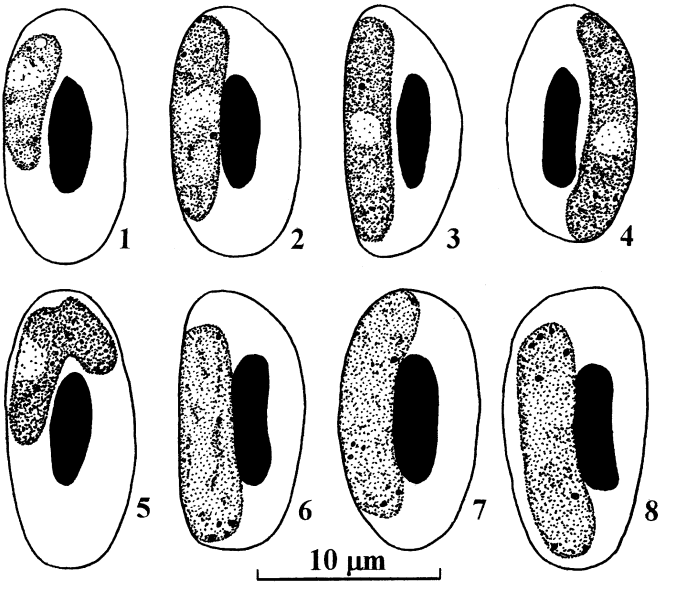

Figure 94 Gametocytes of *Haemoproteus herodiadis* from the blood of *Ixobrychus minutus:*
1 – young; *2–5* – macrogametocytes, *6–8* – microgametocytes (modified from Mohammed, 1958).

Table 53 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. herodiadis* (modififed from Mohammed, 1958)		*H. orioli* (according to Valkiūnas, 1990)			
	lim	$\overline{X}$	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte			31			
Length	–	13.2		9.5–13.0	11.8	0.6
Width	–	7.0		5.3–7.2	6.3	0.2
Length of nucleus	–	6.2		4.0–6.7	5.2	0.3
Width of nucleus	–	2.3		1.6–2.8	2.2	0.1
Erythrocyte parasitized by macrogametocyte			18			
Length	–	14.2		10.4–14.8	12.4	0.6
Width	–	6.8		5.1–7.9	6.8	0.4
Length of nucleus	–	–		4.6–6.6	5.7	0.4
Width of nucleus	–	–		1.6–2.7	2.2	0.1
Erythrocyte parasitized by microgametocyte			15			
Length	–	14.1		10.0–13.9	12.2	0.6
Width	–	7.0		5.1–7.7	6.6	0.3
Length of nucleus	–	–		4.8–6.5	5.3	0.3
Width of nucleus	–	–		1.6–2.9	2.4	0.1
Macrogametocyte						
Length	9.0–14.5	11.3	18	11.4–15.4	12.2	0.7
Width	1.8–3.0	2.5	18	2.0–3.6	3.0	0.2
Length of nucleus	1.3–3.3	2.4	18	1.8–4.4	2.7	0.4
Width of nucleus	1.0–2.5	1.7	18	0.4–2.1	1.3	0.4
NDR	0.7–1.0	–	18	0.6–1.0	0.8	0.1
No. of pigment granules	6–16	10.7	33	15–27	19.2	2.4
Microgametocyte						
Length	9.0–13.0	10.7	15	10.2–13.0	11.4	0.6
Width	2.0–4.8	2.8	15	2.2–3.2	2.6	0.2
NDR	0.6–0.9	–	15	0.7–1.0	0.9	0.1
No. of pigment granules	5–15	8.5	33	10–19	14.4	1.4

Note: All sizes are given in micrometres. NDR for *H. herodiadis* is calculated from the scale illustrations in the book by Mohammed (1958).

Macrogametocytes (Fig. 94, *2–5*, Table 53). The cytoplasm is finely granular in appearance, frequently contains a few small poorly visible vacuoles; gametocytes grow along the nucleus of erythrocytes, usually they do not enclose the nucleus with their ends and never encircle it completely; approximately 95% of gametocytes adhere to the envelope of erythrocytes (Fig. 94, *3*, *4*), and only about 25% of the gametocytes adhere to the nucleus of erythrocytes (Fig. 94, *2*); the outline is even; fully grown gametocytes do not fill the erythrocytes up to their poles; the parasite nucleus is variable in form and is usually median or submedian in position; pigment granules are small (<0.5 μm), dust-like in

appearance and thus are difficult to be observed and calculated; they are randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 94, *6–8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules look slightly larger than in macrogametocytes; however, they do not exceed 0.5 μm in diameter; approximately 75% of gametocytes adhere to the envelope of erythrocytes (Fig. 94, *6*, *7*), and about 60% of gametocytes adhere to the nucleus of erythrocytes (Fig. 94, *6–8*); other characters are as for macrogametocytes.

Comments. Mohammed (1958) described in detail and published excellent illustrations of this parasite which was found in *Ixobrychus minutus* from Egypt. He thought that the recorded haemoproteid belonged to the species *H. herodiadis*, but he noted that it slightly differed from the original description by the shape of its gametocytes and by the form and distribution of the pigment granules in the gametocytes. That is why he described the new variety, *H. herodiadis* var. *mathislegeri*. Levine and Campbell (1971) raised this variety to the species level. It should be noted that the original description of *H. herodiadis* is incomplete, schematic, and based on the material from dead (shot) birds (Mello, 1935a). This explains some differences in the shape of gametocytes recorded by Mello (1935a, 1936) and Mohammed (1958). *Haemoproteus mathislegeri* should be regarded as a synonym of *H. herodiadis*.

31. **Haemoproteus (Parahaemoproteus) orioli** Mello, 1935

Haemoproteus orioli Mello, 1935b: 469. – *H. pintoi* Tendeiro, 1947: 327, Fig. 61–63. – *H. orioli*: Peirce, 1984f: 785 (=*H. pintoi*).

Type vertebrate host. *Oriolus oriolus* (L.) (Passeriformes).
Additional vertebrate host. *Oriolus auratus* (Passeriformes).
Type locality. Nova Goa, India.
Distribution. The Palearctic and the Ethiopian and Oriental zoogeographical regions.
Type material has never been designated. A series of additional slides is deposited in IRCAH and CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Oriolus*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Medium grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent or represent less than 10% of the total number of growing gametocytes. Pigment granules are roundish in form, of small (<0.5 μm) size, about 20 per macrogametocyte and 15 per microgametocyte on average. The nucleus in fully grown macrogametocytes is terminal in position.

Development in vertebrate host
Young gametocytes (Fig. 95, *1–4*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes, they extend longitudinally along the nucleus, and then adhere to the envelope of erythrocytes (Fig. 95, *2, 3*); the parasite nucleus can be seen located anywhere in the gametocytes including the terminal position (Fig. 95, *1–4*); the latter position of the nucleus is a characteristic feature of this species; the outline is even or wavy.

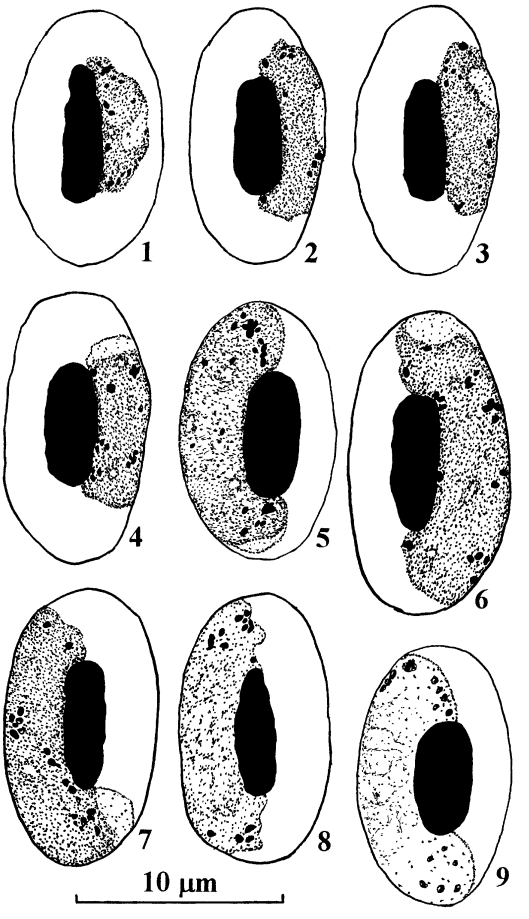

Figure 95 Gametocytes of *Haemoproteus orioli* from the blood of *Oriolus oriolus:* *1–4* – young; *5–7* – macrogametocytes; *8, 9* – microgametocytes.

Macrogametocytes (Fig. 95, *5–7*; Table 53). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes; they slightly enclose the nucleus with their ends and slightly displace the nucleus laterally but never encircle it completely; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are absent or represent less than 10% of the total number of growing gametocytes; the outline is usually even (Fig. 95, *5*) or slightly wavy (Fig. 95, *6*, *7*); the parasite nucleus is strictly terminal in position in fully grown gametocytes, it is band-like (Fig. 95, *5*), cap-like (Fig. 96, *6*), or cork-like (Fig. 95, *7*) in form; pigment granules are usually roundish, of small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 95, *8*, *9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is diffuse and ill-defined but is never less than 6.0 μm in length; an irregular and wavy outline (Fig. 95, *8*) is more evident and more frequently seen than among macrogametocytes; other characters are as for macrogametocytes.

Comments. During the identification of *H. orioli*, attention should be paid, first of all, to (i) the small (<0.5 μm) size, numerous pigment granules in gametocytes and (ii) the terminal position of the nucleus in macrogametocytes.

32. **Haemoproteus (Parahaemoproteus) otocompsae** Mello, 1935

Haemoproteus otocompsae Mello, 1935b: 473.

Type vertebrate host. *Pycnonotus jocosus* (L.) (Passeriformes).
Additional vertebrate host. Some species of the Passeriformes (Table 54).
Type locality. Malim (Baedez), India.
Distribution. The South Palearctic, the Oriental and Ethiopian zoogeographical regions.
Type material. Neohapantotype (No. 42195, *Pycnonotus luteolus*, 18.01.1971, Point Calimere, Tamil Nadu, India, H.E. McClure) and paraneohapantotypes [No. 8612, *Hypsipetes criniger*, 05.10.1962, Subang, Selangor, Federation of Malaysia, H.E. McClure; No. 42286, *Pycnonotus goiavier*, 11.04.1966, Maloh, Siaton, Negros Oriental, Republic of the Philippines, H.E. McClure; No. 2108, *P. leucogenys*, 1968, Bandar Abbas, Iran, coll. Jahangirhejad; No. 12363, *P. melanicterus*, 07.12.1967, Sakaerat, Pakthong Chai, Nakhon Ratchasina (Korat), Thailand, H.E. McClure] are deposited in IRCAH.
Etymology. The specific name is derived from the generic name *Otocompsa* to which the type host was formerly attributed.

Table 54 List of vertebrate hosts of *Haemoproteus otocompsae* (modified from Rahal *et al.*, 1987).

Andropadus virens	*Pycnonotus atriceps*	*P. luteolus*
Criniger bres	*P. barbatus*	*P. melanicterus*
C. ochraceus	*P. blanfordi*	*P. nigricans*
C. pallidus	*P. brunneus*	*P. plumosus*
Hypsipetes criniger	*P. cafer*	*P. simplex*
H. madagascariensis	*P. flavescens*	*P. xanthopygos*
H. propinquus	*P. goiavier*	
Phyllastrephus terrestris	*P. leucogenys*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes do not touch the envelope of erythrocytes along their entire margin. Fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles. The outline of gametocytes is even. Dumbbell-shaped gametocytes are absent. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about ten per gametocyte on average.

Development in vertebrate host
Young gametocytes (Fig. 96, *1*) are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus and extend longitudinally along it not touching the envelope of erythrocytes which is a characteristic feature of this species; the outline is usually even.

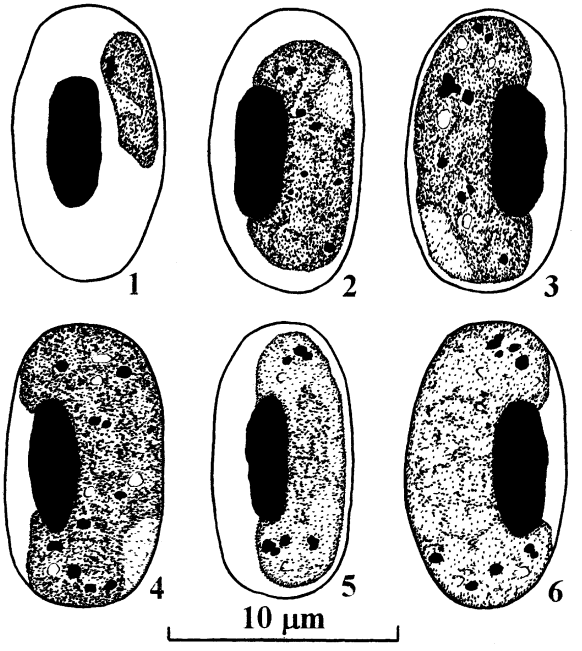

Figure 96 Gametocytes of *Haemoproteus otocompsae* from the blood of *Pycnonotus luteolus: 1* – young; *2–4* – macrogametocytes; *5*, *6* – microgametocytes.

Macrogametocytes (Fig. 96, *2–4*; Table 55). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes, they displace the nucleus laterally but do not encircle it completely; medium grown gametocytes do not touch the envelope of erythrocytes along their entire margin (Fig. 96, *2*, *3*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes and they fill the erythrocytes up to their poles (Fig. 96, *4*); dumbbell-shaped gametocytes are absent; the outline is usually even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are usually roundish, sometimes oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 96, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. otocompsae* is most similar to *H. sanguinis*. Moreover, these two species parasitize the same type host, and the range of their other vertebrate hosts also overlaps in part. *Haemoproteus otocompsae* can be distinguished from *H. sanguinis* primarily on the basis of fewer pigment granules in its gametocytes and greater lateral displacement of the erythrocyte nucleus. Additional investigation into these two species of haemoproteids is necessary. The similarity of gametocytes of these two species is so close that it is possible that *H. sanguinis* may be a synonym of *H. otocompsae.*

Haemoproteus otocompsae is also similar to *H. formicarius* and *H. sequeirae*. It can be distinguished from the latter two species primarily on the basis of the lack of large (1.0 to 1.5 μm) size, rod-like pigment granules in its gametocytes.

Table 55 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. otocompsae* (modified from Rahal *et al.*, 1987)			*H. pastoris* (modified from Bishop and Bennett, 1990)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	55			175		
Length		11.7	0.5		11.5	0.9
Width		6.6	0.4		6.8	0.6
Length of nucleus		6.0	0.6		5.7	0.5
Width of nucleus		2.5	0.3		2.6	0.3
Erythrocyte parasitized by macrogametocyte	55			175		
Length		12.5	0.8		12.8	0.9
Width		6.6	0.7		6.9	0.6
Length of nucleus		5.7	0.6		5.9	0.5
Width of nucleus		2.3	0.3		2.5	0.3
Erythrocyte parasitized by microgametocyte	55			60		
Length		12.7	0.8		13.0	0.8
Width		6.8	0.7		7.1	0.7
Length of nucleus		5.8	0.6		6.0	0.5
Width of nucleus		2.3	0.2		2.6	0.3
Macrogametocyte				175		
Length	55	16.7	1.9		13.5	1.4
Width	55	3.3	0.7		2.8	0.7
Length of nucleus	55	3.4	0.8		2.5	0.6
Width of nucleus	55	2.4	0.6		1.8	0.4
NDR	55	0.5	0.2		0.7	0.2
No. of pigment granules	44	9.6	5.1		11.5	4.3
Microgametocyte				60		
Length	55	17.5	2.2		14.3	1.3
Width	55	3.3	0.7		3.0	0.7
Length of nucleus	7	5.5	2.3		7.5	1.5
Width of nucleus	7	2.7	0.6		2.7	0.5
NDR	55	0.6	0.2		0.7	0.2
No. of pigment granules	42	10.7	4.2		11.1	4.2

Note: All sizes are given in micrometres.

33. **Haemoproteus (Parahaemoproteus) pastoris** Mello, 1935

Haemoproteus pastoris Mello, 1935b: 470. – *H. sturni* Mello, 1935b: 473. – *H. morneti* Tendeiro, 1947: 322, Fig. 69, 70. – *H. morneti orientalis* Travassos Santos Dias, 1953: 82, Pl. 2, Fig. 24, 25. – *H. pastoris*: Bishop and Bennett, 1990: 2255 (=*H. morneti*, *H. morneti orientalis*, *H. sturni*).

Type vertebrate host. *Sturnus roseus* (L.) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 56).
Type locality. Pragana, India.
Distribution. The Palearctic and the Ethiopian and Oriental zoogeographical regions.
Type material was not designated in the original description. The neotypes designated by Bishop and Bennett (1990) are invalid because they came from nontype hosts (*Ampeliceps coronatus*, *Aplonis metallica*, *Creatophora cinerea*, *Sarcops calvus*) investigated far beyond the type locality (the South Africa, the Philippine Islands, New Guinea, Thailand). This material contradicts Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). A series of additional slides is deposited in IRCAH; slides from the type host are deposited in CDVA.
Etymology. The specific name is derived from the generic name *Pastor* to which the type host was formerly attributed.

Table 56 List of vertebrate hosts of *Haemoproteus pastoris* (modified from Bishop and Bennett, 1990).

Acridotheres cristatellus	*Creatophora cinerea*	*Sarcops calvus*
A. fuscus	*Gracula religiosa*	*Sturnus burmannicus*
A. javanicus	*Lamprotornis chalybaeus*	*S. contra*
A. tristis	*L. chloropterus*	*S. malabaricus*
Ampeliceps coronatus	*L. corruscus*	*S. melanopterus*
Aplonis brunneicapillus	*L. nitens*	*S. nigricollis*
A. grandis	*L. purpureus*	*S. pagodarum*
A. metallica	*Mino dumontii*	*S. sinensis*
A. panayensis	*Onychognathus morio*	*S. vulgaris*
Cinnyricinclus leucogaster	*O. walleri*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes; they fill the erythrocytes up to their poles but do not encircle the nucleus of erythrocytes completely. Medium and fully grown gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent or represent less than 10% of the total number of growing gametocytes. The outline of gametocytes varies from even to highly ameboid; growing macrogametocytes with a highly ameboid outline are common. The nucleus in fully grown macrogametocytes usually occupies a subterminal position, and it is not located close to the nucleus of infected erythrocytes. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about 11 per gametocyte on average. A species difficult to identify; can be distinguished from the close species of haemoproteids of birds belonging to the Passeriformes only on the basis of a detailed analysis of a set of characters.

Development in vertebrate host
Young gametocytes (Fig. 97, *1, 2*). The earliest forms can be seen anywhere in the infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 97, *1*) and extend longitudinally, usually being closely appressed to the envelope of erythrocytes (Fig. 97, *2*); the outline is usually even (Fig. 97, *2*).

Macrogametocytes (Fig. 97, *3–8*; Table 55). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes; they enclose the nucleus with their ends but do not encircle it completely; growing gametocytes usually adhere to the nucleus and envelope of erythrocytes

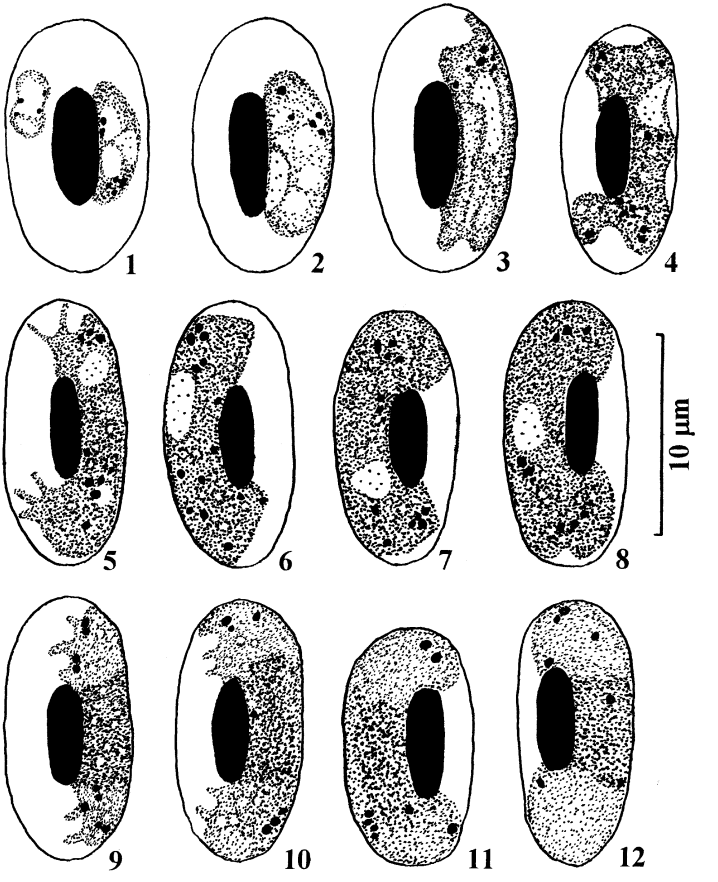

Figure 97 Gametocytes of *Haemoproteus pastoris* from the blood of *Sturnus roseus:* *1*, *2* – young; *3–8* – macrogametocytes; *9–12* – microgametocytes (modified from Valkiūnas and Iezhova, 1993b).

(Fig. 97, *3*) but, occasionally, the central part of the pellicle of the growing gametocytes does not extend to the erythrocyte envelope, causing a more or less evident 'dip' and giving a dumbbell-like appearance (Fig. 97, *4*); however, the dumbbell-shaped gametocytes are not characteristic of this species, and, if present, they represent less than 10% of the total number of growing gametocytes; the position of growing gametocytes at the pole of infected erythrocytes asymmetrically to the nucleus of erythrocytes is not characteristic; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes and they fill the erythrocytes up to their poles; the outline of growing gametocytes varies from even (Fig. 97, *6*) to highly ameboid (Fig. 97, *5*), and is usually even in fully grown forms (Fig. 97, *7*, *8*); highly ameboid gametocytes (Fig. 97, *5*) usually represent more than 10% of the total number of growing gametocytes; the parasite nucleus is compact, variable in form, usually subterminal in position (Fig. 97, *5*, *7*), but occasionally seen even in the median position (Fig. 97, *8*); it is never located close to the nucleus of infected erythrocytes; pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 97, *9–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the dumbbell-shaped gametocytes are not seen, and the ameboid outline is more frequently present than in macrogametocytes; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. pastoris* is especially similar to *H. anthi*. It can be distinguished from the latter species mainly on the basis of more evident ameboid outline of its gametocytes (see also 'Comments' to *H. anthi*).

34. **Haemoproteus (Parahaemoproteus) plataleae** Mello, 1935

Haemoproteus plataleae Mello, 1935b: 471. – *H. galatheae* Laird and Laird, 1959: 220, Pl. 1, Fig. 4–13. – *H. plataleae*: Bennett *et al.*, 1975b: 635 (=*H. galatheae*). – *H. peircei* Forrester, Greiner, Bennett and Kigave, 1977: 1272, Fig. 8. – *H. plataleae*: Valkiūnas, 1997: 221 (=*H. peircei*).

Type vertebrate host. *Platalea leucorodia* L. (Ciconiiformes).
Additional vertebrate hosts. Some species of the Ciconiiformes (Table 57).
Type locality. Diu, India.
Distribution. Cosmopolitan in tropics, subtropics, and temperate region, but it is spotty in distribution.
Type material. Does not exist (Bennett *et al.*, 1975b). Designation of neotypes is required.
Etymology. The specific name is derived from the generic name of the type host, *Platalea.*

Table 57 List of vertebrate hosts of *Haemoproteus plataleae.*

Ephippiorhynchus senegalensis	*Mycteria ibis*
Eudocimus albus	*Plegadis falcinellus*
E. ruber	*Pseudibis papillosa*
Leptoptilus crumeniferus	*Threskiornis molucca*

Main diagnostic characters. A parasite of species of the Ciconiiformes whose fully grown gametocytes usually markedly displace the nucleus of infected erythrocytes laterally and usually do not encircle it completely, but the forms encircling the nucleus completely are sometimes present but they are uncommon. The average number of pigment granules in macrogametocytes is greater than 25, and is approximately half as many in microgametocytes.

Development in vertebrate host
Young gametocytes (Fig. 98, *1*, *2*). The earliest forms can be seen anywhere in the infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes not touching the nucleus; the outline is usually even, but sometimes slightly ameboid.

Macrogametocytes (Fig. 98, *3–6*; Table 58). The cytoplasm is coarsely granular in appearance, usually contains several small vacuoles; occasionally, a large clear vacuole, which is up to 2 μm in diameter, is seen in the cytoplasm (Fig. 98, *3*); gametocytes grow around the nucleus of erythrocytes and they fill the erythrocytes up to their poles; growing gametocytes usually do not touch the nucleus of erythrocytes, and, as a result, a more or

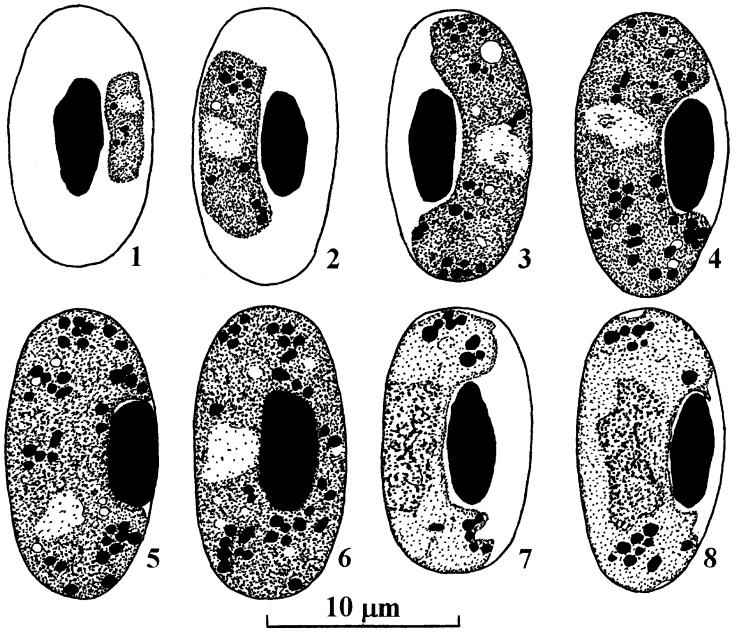

Figure 98 Gametocytes of *Haemoproteus plataleae* from the blood of *Platalea leucorodia:* *1*, *2* – young; *3*–*6* – macrogametocytes; *7*, *8* – microgametocytes.

less evident unfilled space (a 'cleft') is frequently present between the gametocyte and erythrocyte nucleus (Fig. 98, *3*, *4*); this 'cleft' disappears in fully grown gametocytes (Fig. 98, *5*). Two types of gametocytes develop. First, the gametocytes, which markedly displace the erythrocyte nucleus laterally, but do not encircle it completely (Fig. 98, *4*, *5*), are especially common. Second, the gametocytes which completely encircle the erythrocyte nucleus and occupy all available cytoplasmic space in the host cells (Fig. 98, *6*), are also present, but they are much rare than the gametocytes of the first type. The parasite nucleus is variable in form, usually median or submedian in position, frequently lies free in the cytoplasm and does not touch the pellicle of gametocytes (Fig. 98, *3*–*5*). Pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm. Infected erythrocytes are slightly hypertrophied in length and width in comparison to uninfected ones.

Microgametocytes (Fig. 98, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the ameboid outline is more evident and seen more frequently than in macrogametocytes; the number of pigment granules is approximately half as many as in macrogametocytes; the circumnuclear forms are extremely rare; other characters are as for macrogametocytes.

C o m m e n t s. The main morphological characters of gametocytes of *H. peircei* and *H. plataleae* coincide. In the original description of *H. peircei*, the circumnuclear gametocytes were noted among the main diagnostic characters of this species (Forrester *et al.*, 1977). However, such gametocytes are also present in *H. plataleae* infections (Laird and Laird, 1959; Bennett *et al.*, 1975b; our data). *Haemoproteus peircei* was described mainly with the aim to distinguish the parasite, which develops in ciconiiform birds of the family Ciconiidae, but has gametocytes identical to *H. plataleae*.

Table 58 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. plataleae*				*H. thereicerycis* (modified from Bennett and Nandi, 1981)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	33				30		
Length		11.2–14.8	13.0	0.6		14.2	1.0
Width		6.0–7.9	7.2	0.4		7.9	0.5
Length of nucleus		5.6–7.7	6.4	0.2		6.5	0.7
Width of nucleus		2.0–3.8	3.0	0.1		2.5	0.4
Erythrocyte parasitized by macrogametocyte	15				50		
Length		12.8–15.8	14.8	0.8		15.9	1.1
Width		6.6–9.1	7.8	0.4		8.4	0.8
Length of nucleus		5.2–7.2	6.1	0.2		6.0	0.8
Width of nucleus		1.7–3.0	2.6	0.1		2.8	0.4
Erythrocyte parasitized by microgametocyte	14				15		
Length		12.2–16.2	14.8	0.8		15.5	1.1
Width		6.4–8.8	7.7	0.4		8.3	0.6
Length of nucleus		5.4–7.0	6.0	0.3		6.1	0.6
Width of nucleus		1.8–3.2	2.7	0.1		2.8	0.2
Macrogametocyte	15				50		
Length		15.0–17.4	16.3	1.4		16.3	1.8
Width		3.2–5.8	4.6	0.4		4.9	0.9
Length of nucleus		1.8–4.3	3.2	0.4		4.1	0.5
Width of nucleus		1.5–2.6	2.1	0.1		2.7	0.5
NDR		0.0–0.4	0.2	0.2		–	–
No. of pigment granules		20–41	36.1	4.4		31.3	2.9
Microgametocyte	14				15		
Length		14.8–17.3	16.6	1.5		17.2	2.2
Width		2.8–5.3	4.7	0.4		4.8	0.9
Length of nucleus		5.8–8.0	6.5	0.5		5.6	0.8
Width of nucleus		2.1–3.5	2.6	0.2		3.6	0.6
NDR		0.1–0.6	0.2	0.2		–	–
No. of pigment granules		12–28	16.9	3.1		30.1	2.9

Note: All sizes are given in micrometres. The length of gametocytes of *H. plataleae* is given for the forms which do not encircle the nucleus of infected erythrocyte completely.

Haemoproteus plataleae is originally described from the ciconiiform birds belonging to the Threskiornithidae. In other words, *H. peircei* was considered to be a distinct species mainly on the basis of the family specificity device which was formerly attributed to bird haemoproteids. Above, we discussed in detail (see the General Section, p. 69) that the fact of the registration of morphologically identical gametocytes in birds belonging to different families of the same order is not enough for the description of new species of haemoproteids. Until the family level of specificity of *H. peircei* is proved experimentally, this name is considered to be a junior synonym of *H. plataleae*.

It should be noted that the average number of pigment granules in gametocytes of *H. plataleae* varies noticeably in different vertebrate hosts. The number recorded was found to vary from 29 to 45 in macrogametocytes, and from 16.4 to 23 in microgametocytes (Laird and Laird, 1959; Bennett *et al.*, 1975b; Forrester *et al.*, 1977; Sacchi *et al.*, 1992; our data). However, one clear regularity can be pointed out. The average number of pigment granules in macrogametocytes is always high (>25), and is approximately half as many in microgametocytes as in macrogametocytes.

Among the haemoproteids of birds belonging to the Ciconiiformes, *H. plataleae* is especially similar to *H. crumenium*. It can be distinguished from the latter species, first of all, on the basis of (i) the position of the nucleus in its macrogametocytes, (ii) there being more numerous pigment granules in gametocytes, and (iii) a smaller average NDR.

35. **Haemoproteus (Parahaemoproteus) thereicerycis** Mello, 1935

Haemoproteus thereicerycis Mello, 1935b: 470. – *H. thereicerycis* var. *zeylonica* Mello, 1935b: 471. – *H. thereicerycis*: Bennett and Nandi, 1981: 2064 (=*H. thereicerycis* var. *zeylonica*).

Type vertebrate host. *Megalaima zeylanica* (Gmelin) (Piciformes).
Additional vertebrate hosts. Some species of the Piciformes (Table 59).
Type locality. Corlim, Nova Goa, India.
Distribution. The Oriental and Ethiopian zoogeographical regions.
Type material. Neohapantotype (No. 37133, *Megalaima zeylanica*, 13.04.1971, Andhra Pradesh, India, H.E. McClure) and paraneohapantotypes (No. 11119, *M. faiostricta*, 14.01.1965, Chiang-mei, Thailand, H.E. McClure; No. 11502, *M. virens*, 11.09.1965, Chiang-mei, Thailand, H.E. McClure; No. 11641, *M. zeylanica*, 12.05.1964, Chiang-mei, Thailand, H.E. McClure; No. 37083, *M. asiatica*, 06.10.1968, West Bhutan, H.E. McClure; No. 37086, 07.10.1968, *M. asiatica*, West Bhutan, H.E. McClure; No. 37126, *M. viridis*, 10.04.1971, Maharashtra State, India, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name *Thereiceryx* to which the type host was formerly attributed.

Table 59 List of vertebrate hosts of *Haemoproteus thereicerycis* (modified from Bennett and Nandi, 1981).

Gymnobucco calvus	*M. franklinii*	*Trachyphonus darnaudii*
Lybius dubius	*M. haemacephala*	*T. erythrocephalus*
L. leucomelas	*M. virens*	*T. purpuratus*
Megalaima asiatica	*M. viridis*	*T. vaillantii*
M. chrysopogon	*Pogoniulus bilineatus*	
M. faiostricta	*Psilopogon pyrolophus*	

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes; they can enucleate the host cells. The average number of pigment granules is about 30 per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 99, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes not touching the nucleus; the outline is even.

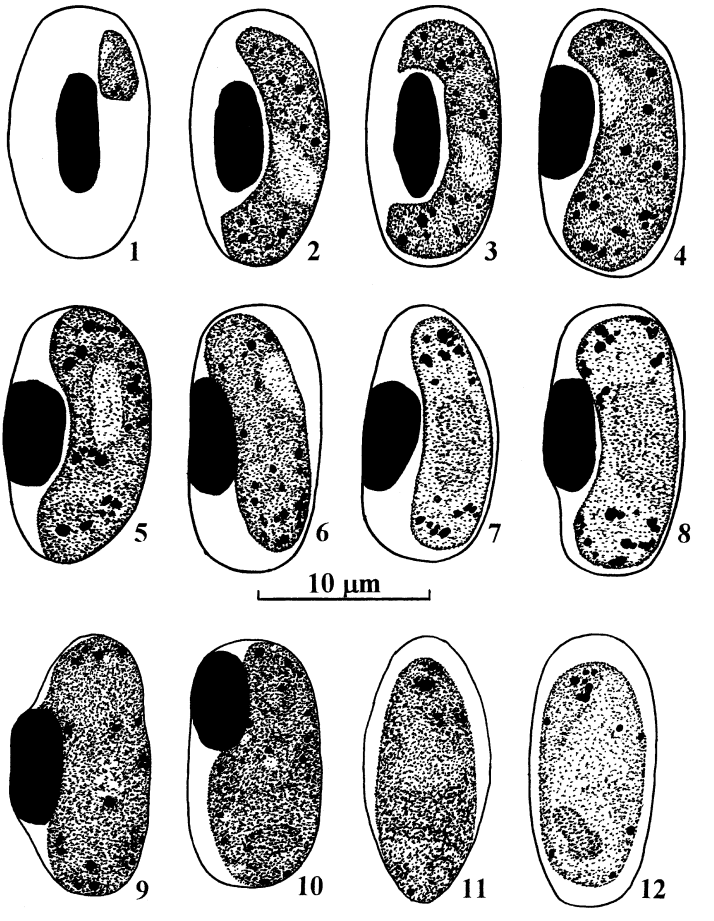

Figure 99 Gametocytes of *Haemoproteus thereicerycis* from the blood of *Megalaima zeylanica: 1* – young; *2–6*, *9–11* – macrogametocytes; *7*, *8*, *12* – microgametocytes (*9–12* are modified from Bennett and Nandi, 1981).

Macrogametocytes (Fig. 99, *2–6*, *9–11*; Table 58). The cytoplasm is granular in appearance, usually lacking vacuoles; growing gametocytes do not touch the nucleus of erythrocytes (Fig. 99, *2–4*), and some of them do not touch the envelope of erythrocytes either (Fig. 99, *4*); gametocytes markedly displace the nucleus of erythrocytes (Fig. 99, *6*, *9*, *10*), and fully grown forms can enucleate the erythrocytes (Fig. 99, *11*); gametocytes in the enucleated erythrocytes are uncommon in the type material, and forms shown in Fig. 99, *6*, *10* predominate; gametocytes in the enucleated host cells are shaped like elongated ellipses (Fig. 99, *11*); the enucleated erythrocytes maintain a solid envelope (Fig. 99, *11*); the outline of gametocytes is even; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are usually roundish, sometimes oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are slightly hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 99, *7*, *8*, *12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

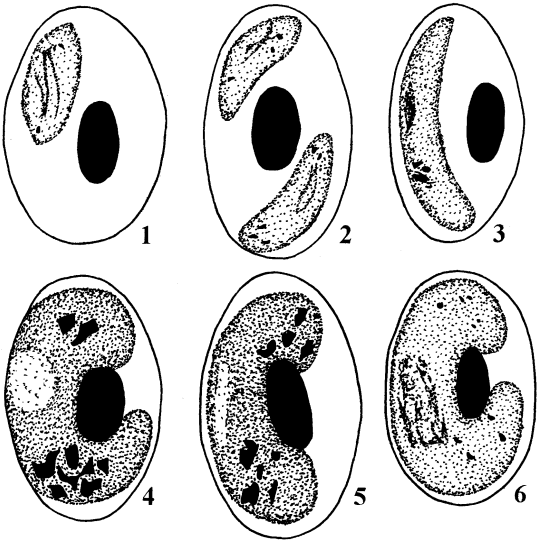

Figure 100 Gametocytes of *Haemoproteus upupae* from the blood of *Upupa epops:*
1, *2* – young; *3–5* – macrogametocytes; *6* – microgametocyte (modified from Mello, 1937).

Comments. Among the haemoproteids of birds belonging to the Piciformes, *H. thereicerycis* is especially similar to *H. bennetti* and *H. bucconis*. It can be distinguished from the latter two species, particularly, on the basis of having more numerous pigment granules in its gametocytes.

Gametocytes, which enucleate the infected erythrocytes, are rare in the type material, and they represent less than 5% of the total number of mature gametocytes.

36. **Haemoproteus (Parahaemoproteus) upupae** Mello, 1935

Haemoproteus upupae Mello, 1935b: 472.

Type vertebrate host. *Upupa epops* L. (Coraciiformes).
Type locality. Daman, India.
Distribution has been insufficiently investigated. This parasite has been recorded in India and in the South Palearctic so far.
Type material has never been designated.
Etymology. The specific name is derived from the generic name of the type host, *Upupa*.

Main diagnostic characters. A parasite of species of the Coraciiformes whose gametocytes grow around the nucleus of infected erythrocytes; they do not displace or slightly displace the nucleus. The shape and size of pigment granules in macro- and microgametocytes are clearly different.

Development in vertebrate host
Young gametocytes (Fig. 100, *1, 2*) can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes not touching the nucleus; the outline is even.

Macrogametocytes (Fig. 100, *3*–*5*) grow around the nucleus of infected erythrocytes, and they markedly enclose the nucleus with their ends; growing gametocytes do not touch the nucleus of erythrocytes (Fig. 100, *3*); fully grown gametocytes are closely appressed to the nucleus of erythrocytes but do not displace or only slightly displace the nucleus laterally; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are aggregated into large masses at the ends of gametocyte (Fig. 100, *4*, *5*).

Microgametocytes (Fig. 100, *6*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules are of small size and frequently dust-like appearance, and have not been recorded to be aggregated into large masses. Other characters are as for macrogametocytes.

Comments. Mello (1935b) briefly described and later (Mello, 1937) published illustrations of gametocytes of *H. upupae* from *Upupa epops* in India. Subsequently, the parasite has been rarely recorded. A detailed redescription of this species is still absent. This parasite was not recorded in the type host investigated by the author during the spring–summer periods in the southern Kazakhstan, Middle Asia (42 birds were examined) and in the Baltic region (107 birds). In addition, haemoproteids were not reported in *Upupa epops* from Western Europe (Peirce, 1981b). It is likely that *H. upupae* has a spotty distribution.

The data on the morphology of gametocytes of *H. upupae* given above, are modified from the paper by Mello (1937). During the identification of this species, attention should be paid to the differences in the morphology of pigment granules in macro- and microgametocytes. This character was recorded in the original description of this parasite. It should be noted, however, that in the illustrations in the paper by Mello (1937), the fully grown gametocytes do not touch the envelope of erythrocytes (Fig. 100, *5*, *6*). Most probably, this feature, which is important for the identification of haemoproteid species, is not characteristic of *H. upupae*, but it can be explained by a manner of illustration of the gametocyte used by Mello (1937). In the latter paper, the gametocytes, which do not touch the envelope of erythrocytes, are also shown in the illustrations of such well investigated species as *H. anthi*, *H. orioli*, *H. pastoris*, and others, but such position in the erythrocytes is not characteristic of these species. It is also possible that the differences in the morphology of the pigment granules in macro- and microgametocytes recorded above may not exist or may be due to valutin granules which are common in some species of haemoproteids. Thus, the redescription of *H. upupae* and designation of its neotype material are essential.

37. **Haemoproteus (Parahaemoproteus) lanii** Mello, 1936

Haemoproteus lanii Mello, 1936: 103, Pl. 1, Fig. 2. – *H. lanii* var. *nucleophilus* Mohammed, 1958: 217, Pl. 9, Fig. 13–28. – *H. lanii*: Bennett *et al.*, 1990: 195 (=*H. lanii* var. *nucleophilus*).

Type vertebrate host. *Lanius schach* L. (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 60).
Vector. *Culicoides impunctatus* (Diptera: Ceratopogonidae) (Valkiūnas and Iezhova, 2004).
Type locality. Pondá, India.
Distribution. The Palearctic and the Ethiopian and Oriental zoogeographical regions.
Type material. Neohapantotype (No. 41809, *Lanius schach*, 13.09.1970, Gujarat, India. H.E. McClure) is deposited in IRCAH. A series of good additional slides of gametocytes is deposited in IRCAH and CDVA; gametes, zygotes, and ookinetes are in CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Lanius*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes and sometimes completely

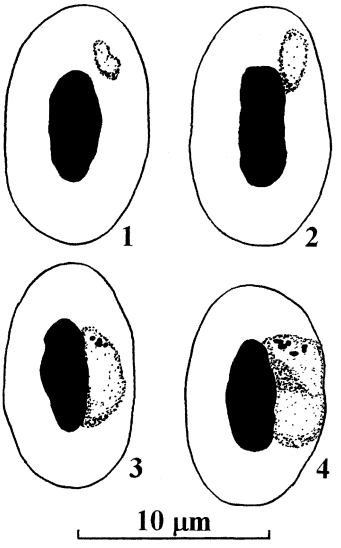

Figure 101 Young gametocytes of *Haemoproteus lanii* from the blood of *Lanius collurio.*

Table 60 List of vertebrate hosts of *Haemoproteus lanii* (modified from Valkiūnas, 1990).

Lanius bucephalus	*L. excubitor*	*L. tephronotus*
L. collaris	*L. isabellinus*	*L. tigrinus*
L. collurio	*L. minor*	*L. validirostris*
L. collurioides	*L. nubicus*	*L. vittatus*
L. cristatus	*L. senator*	

Note: Fringilla coelebs was included in the list of vertebrate hosts of *H. lanii* (Valkiūnas, 1985a) erroneously.

encircle the nucleus. Medium grown gametocytes are closely appressed to the nucleus of infected erythrocytes. The nucleus of macrogametocyte is in a median position and is usually closely appressed to the nucleus of erythrocyte. Pigment granules are of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size.

Development in vertebrate host

Young gametocytes (Fig. 101). The earliest forms are usually seen in polar or subpolar position in infected erythrocytes (Fig. 101, *1*); as the parasite develops, gametocytes adhere to the erythrocyte nucleus usually near the pole of the nucleus (Fig. 101, *2*) and then extend longitudinally along the nucleus finally taking a typical lateral position to the nucleus (Fig. 101, *3*); gametocytes, whose length is approximately equal to the length of the erythrocyte nucleus, are usually closely appressed both to the nucleus and envelope of erythrocytes (Fig. 101, *4*); the outline of gametocytes is usually even.

Macrogametocytes (Fig. 102; Table 61). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes, markedly enclose the nucleus with their ends, and can completely encircle the nucleus and occupy all available cytoplasmic space in erythrocytes (Fig. 102, *6–8*); the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 102, *1–3*); as the parasite develops, this 'dip' decreases in size, is usually located asymmetrically

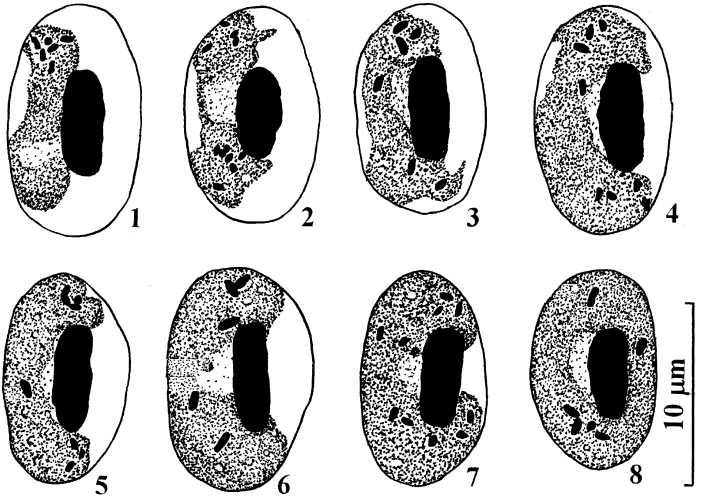

Figure 102 Macrogametocytes of *Haemoproteus lanii* from the blood of *Lanius collurio.*

(Fig. 102, *4*) to the gametocyte, and finally disappears in fully grown gametocyte (Fig. 102, *6–8*); the outline of growing gametocytes is usually more or less ameboid (Fig. 102, *2*, *3*) or wavy (Fig. 102, *4*, *5*), sometimes even (Fig. 102, *1*); mature gametocytes are usually even in outline (Fig. 102, *6–8*); the parasite nucleus is variable in form, frequently band-like, median in position and, as a rule, closely appressed to the nucleus of erythrocytes; a nucleolus is evident in well stained macrogametocytes (Fig. 102, *7*); pigment granules are of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, roundish, oval, or rod-like, randomly scattered throughout the cytoplasm.

Table 61 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. lanii* (according to Valkiūnas, 1990)				*H. rileyi* (modified from Bennett and Peirce, 1989)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				47		
Length		11.2–12.9	12.0	0.6		12.8	1.3
Width		6.0–7.6	6.8	0.4		7.2	0.6
Length of nucleus		5.2–7.1	5.9	0.2		5.5	0.8
Width of nucleus		1.9–3.4	2.5	0.1		2.0	0.3
Erythrocyte parasitized by macrogametocyte	31				47		
Length		10.3–12.0	11.2	0.6		13.0	1.5
Width		5.5–8.0	6.6	0.4		7.8	1.1
Length of nucleus		4.5–6.2	5.4	0.1		5.0	0.6
Width of nucleus		1.8–2.6	2.1	0.1		2.2	0.4
Erythrocyte parasitized by microgametocyte	31				13		
Length		10.5–13.6	11.7	0.7		14.3	0.7

Table 61 (continued).

Feature	*H. lanii* (according to Valkiūnas, 1990)				*H. rileyi* (modified from Bennett and Peirce, 1989)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Width		5.7–8.2	6.9	0.4		7.3	0.7
Length of nucleus		4.9–6.1	5.5	0.1		5.5	0.8
Width of nucleus		1.9–3.2	2.2	0.1		2.2	0.3
Macrogametocyte	31				47		
Length		12.2–20.0	15.9	2.7		14.1	2.1
Width		2.1–3.9	2.9	0.2		3.1	0.6
Length of nucleus		1.6–3.7	2.7	0.2		2.6	0.5
Width of nucleus		0.9–2.8	1.5	0.2		1.8	0.4
NDR		0.4–1.0	0.7	0.2		0.7	0.2
No. of pigment granules		3–11	6.8	1.0		10.9	2.3
Microgametocyte	37				13		
Length		13.1–16.3	14.8	1.4		16.4	1.6
Width		2.3–4.3	3.0	0.4		2.9	0.3
Length of nucleus		5.0–8.8	6.4	0.4		7.1	0.8
Width of nucleus		2.1–4.6	3.1	0.2		2.1	0.3
NDR		0.3–1.0	0.7	0.2		0.8	0.1
No. of pigment granules		4–10	7.2	0.8		11.5	1.8

Note: All sizes are given in micrometres.

Microgametocytes (Fig. 103). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector

Sporonogy is completed in the biting midge *Culicoides impunctatus* (Valkiūnas and Iezhova, 2004). Gametogenesis, development of zygote and ookinete *in vitro* under a light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1995). Data on the rate of this process are given in Table 62. Within 1 min after exposure of infected blood to air (EBA), mature gametocytes become round and escape from erythrocytes (Fig. 104, *2*, *3*, *6*, *7*). It should be noted that the aggregation of the pigment into solid masses was frequently

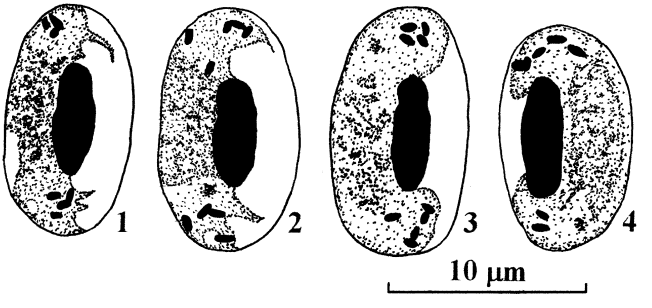

Figure 103 Microgametocytes of *Haemoproteus lanii* from the blood of *Lanius collurio.*

Table 62 Gametogenesis, zygote, and ookinete formation of *Haemoproteus lanii* and *H. minutus in vitro* (modified from Valkiūnas and Iezhova, 1995).

Stage of development	Time after exposure of blood with mature gametocytes to air													
	min							h						
	1	3	5	10	15	30	45	1	1.5	3	6	12	24	48
Rounded up gametocyte, *2, 6*	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■
Gametocyte leave the infected erythrocyte, *3, 7*	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■
Macrogamete, *4*	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■
Exflagellation, *9*	■	■	● ■	■	●	●	● ■			● ■				
Microgamete, *10*			■	■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	■	● ■
Fertilization, *11*				■	● ■	● ■	● ■	● ■			■			
Zygote, *12*				■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■	● ■
Initial stage of differentiation of ookinete, *13*							●	● ■	● ■	● ■	● ■	● ■	● ■	● ■
Medium differentiated ookinete, *14*							●	●	● ■	■	● ■	● ■	● ■	■
Ookinete with the residual body, *15*							●	●	●	■	● ■	●	● ■	■
Ookinete without the residual body, *16*									●	● ■	● ■	●	■	■

Note: Numbers in the column 'Stage of development' correspond to the stages shown in Figs. 104 and 205. Species of haemoproteids: ● – *Haemoproteus minutus*, ■ – *H. lanii*, absence of the symbols – time when the parasite at the certain stage of development was not recorded.

seen in the rounded up macrogametocytes (Fig. 104, *3*). At approximately the same time, exflagellation was recorded (Fig. 104, *9*) and macrogametes appeared (Fig. 104, *4*). Free microgametes (Fig. 104, *10*) were seen 5 min after EBA, and fertilization of macrogametes (Fig. 104, *11*) and first zygotes (Fig. 104, *12*) were seen 10 min after EBA. Zygotes can be distinguished from macrogametes on the basis of the presence of a clear nucleolus in their nucleus (Fig. 104, *12*), which was not seen in the nucleus of macrogametes under a light microscope (Fig. 104, *4*, *11*). The initial stages of ookinete differentiation were seen approximately 1 h after EBA. At this time, a long finger-like outgrowth located tangentionally to the main body of the differentiating ookinete (Fig. 104, *13*), appears. As the ookinete develops, this outgrowth extends markedly and forms the anterior or apical end of the ookinete. An accumulation of pigment granules was recorded on the opposite end of the medium-differentiated ookinete (Fig. 104, *14*). In fully grown ookinete, the pigment aggregates into a huge solid mass at the distal end of the parasite, and finally separates from the ookinete together with a residual body (Fig. 104, *15*). The pigment granules were not seen in fully

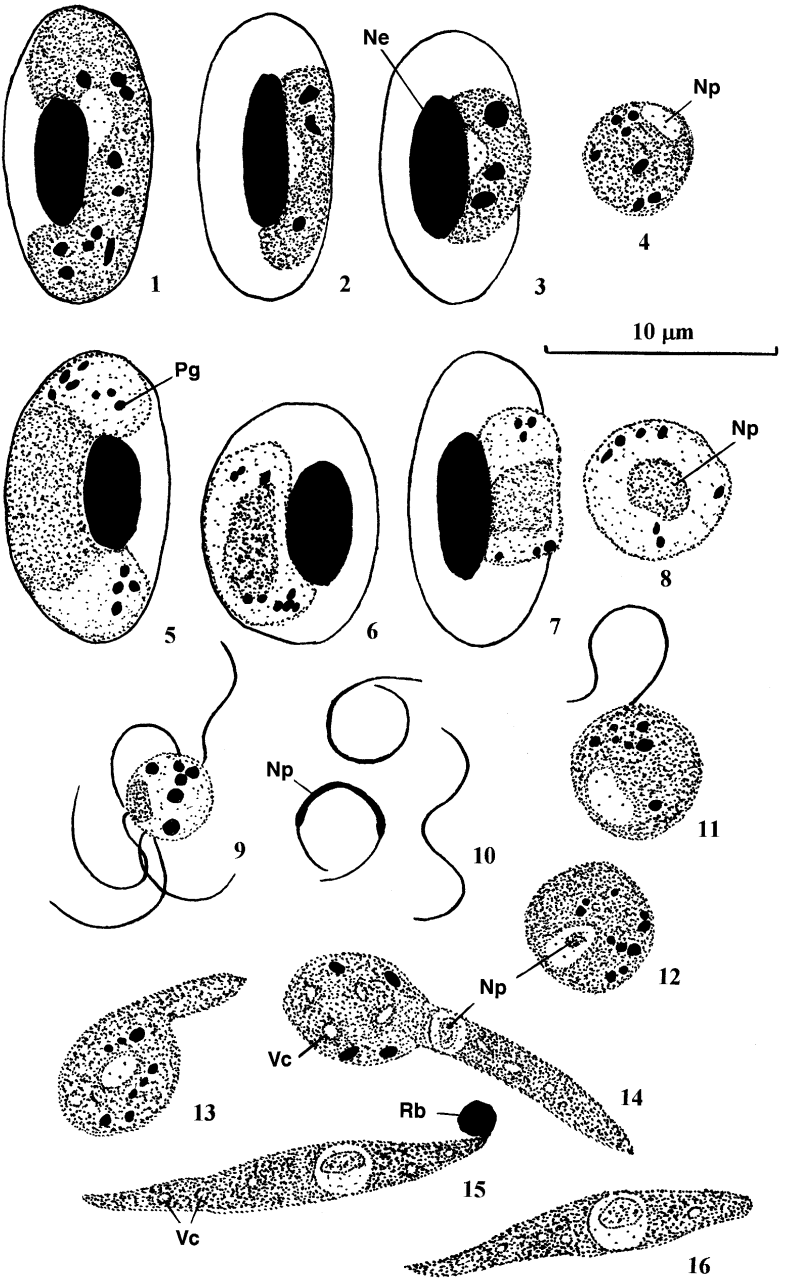

Figure 104 *Haemoproteus lanii* gametogenesis, zygote and ookinete development *in vitro*: *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Lanius collurio* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14* – medium differentiated ookinete; *15* – ookinete with a residual body; *16* – ookinete without a residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1995).

Table 63 Morphometric parameters of gametes and ookinetes of two species of *Haemoproteus* (according to Valkiūnas and Iezhova, 1995).

Feature	*H. minutus*				*H. lanii*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogamete	31				31			
Length		4.0–6.6	5.4	0.3		4.4–6.0	5.3	0.2
Width		3.9–5.9	4.5	0.2		4.1–5.6	4.8	0.1
Microgamete	10				10			
Length		6.7–11.3	9.5	1.1		10.6–12.4	11.8	0.4
Width		0.5–0.9	0.7	0.1		0.7–0.9	0.8	0.1
Ookinete	31				41			
Length		7.2–10.1	8.3	0.3		13.8–18.4	16.2	0.4
Width		2.1–3.6	2.8	0.1		1.7–2.6	2.2	0.1

Note: All sizes are given in micrometres.

differentiated ookinetes (Fig. 104, *16*). At all stages of ookinete development, a few small 'vacuoles' are present in the cytoplasm and its nucleus contains a clear nucleolus (Fig. 104, *13–16*). Mature ookinetes are elongated worm-like bodies (Fig. 104, *16*). Ookinetes with the residual body (Fig. 104, *15*) and forms without the residual body (Fig. 104, *16*) were recorded 3 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 63.

C o m m e n t s. *Haemoproteus lanii* was originally briefly described from the blood of *Lanius schach erythronotus* in India. The original material was collected from a dead (shot) bird, and the changes of gametocytes due to the onset of gametogenesis are obvious in illustrations in the original description (Mello, 1936). However, the close adherence of the nucleus of the macrogametocyte to the nucleus of the infected erythrocyte, which is the important diagnostic character of *H. lanii*, is well illustrated in the original description. Other characters of this species are quite variable. For example, the dumbbell-shaped growing gametocytes were recorded only by Valkiūnas (1990). Additionally, the ameboid outline of the growing gametocytes has also been rarely recorded, but in some illustrations which are available in the literature, this character is evident (Mohammed, 1958; Burtikashvili, 1978). The number of pigment granules in gametocytes also varies in the records of different authors. According to our data (Table 61), the number of pigment granules in macrogametocytes varies from 3 to 11 (on average 6.8). On the illustrations in the original description, the average number of pigment granules in macrogametocytes is also approximately seven (Mello, 1936). According to Mohammed (1958), the number of pigment granules varies from 5 to 17 (on average 9.8), and according to Bennett *et al.* (1990), it is about 12 on average. It should be also noted that gametocytes of *H. lanii*, which completely encircle the nucleus of erythrocytes (Fig. 102, *8*), were rarely seen (Valkiūnas, 1990). These forms appear only at the late stages of development in the blood, and they are not always present in naturally infected birds which are investigated occasionally.

38. **Haemoproteus (Parahaemoproteus) rileyi** Malkani, 1936

Haemoproteus rileyi Malkani, 1936: 155, Pl. 4. – *H. bambusicolae* Manwell, Allen and Kuntz, 1976: 572, Fig. 1–8. – *H. rileyi*: Bennett and Peirce, 1989: 1559, Fig. 3–5 (=*H. bambusicolae*).

Type vertebrate host. *Pavo cristatus* L. (Galliformes).
Additional vertebrate hosts. Some species of the Galliformes (Table 64).
Type locality. Patna, India.
Distribution. The Oriental zoogeographical regions and adjacent regions of the South Palearctic, the Ethiopian zoogeographical region.
Type material. Hapantotype (No. 924, *Pavo cristatus*, 29.07.1935, Patna, India, P.G. Malkani) is deposited in CPW. A series of additional slides is deposited in IRCAH.
Etymology was not specified in the original description.

Table 64 List of vertebrate hosts of *Haemoproteus ryleyi* (modified from Bennett and Peirce, 1989).

Argusianus argus	*Francolinus bicalcaratus*	*Lophura bulweri*
Bambusicola thoracica	*Galloperdix spadicea*	*Pavo muticus*
Coturnix coturnix	*Gallus gallus*	*Polyptectron* sp.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes have an even outline; they displace the nucleus of infected erythrocytes laterally but do not encircle it completely. The average number of pigment granules is about ten per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 105, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes take a lateral position to the erythrocyte nucleus; the outline usually varies from ameboid to wavy.

Macrogametocytes (Fig. 105, *2*, *3*; Table 61). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles; valutin granules usually present and they are numerous in some blood films; gametocytes grow around the nucleus of erythrocytes; they slightly enclose the nucleus with their ends and do not encircle it completely; fully grown gametocytes fill the erythrocytes up to their poles, displace the nucleus of erythrocytes laterally, and are closely appressed to the nucleus and envelope of erythrocytes (Fig. 105, *3*); the outline of growing gametocytes is usually ameboid or wavy (Fig. 105, *2*), and is even in fully grown forms (Fig. 105, *3*); the parasite nucleus is compact, variable in form, usually submedian in position, but sometimes also seen in subterminal position (Fig. 105, *2*); pigment granules are of medium (0.5 to 1.0 μm) size, oval

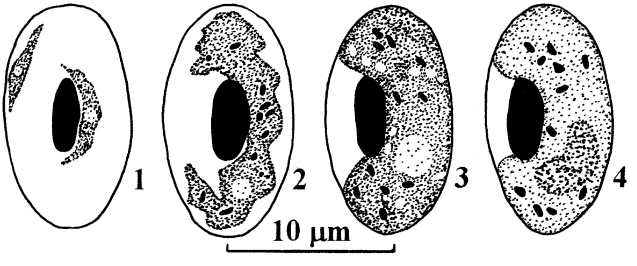

Figure 105 Gametocytes of *Haemoproteus rileyi* from the blood of *Pavo cristatus* (*1*) and *P. muticus* (*2–4*):
1 – young; *2*, *3* – macrogametocytes; *4* – microgametocyte (*1* is modified from Malkani, 1936, and *2–4* are modified from Bennett and Peirce, 1989).

and roundish, usually randomly scattered throughout the cytoplasm, but sometimes are seen gathered into small loose groups.

Microgametocytes (Fig. 105, *4*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Malkani (1936) described *H. rileyi* briefly from a sick *Pavo cristatus* and published only the illustrations of young gametocytes. He thought that the parasite caused the death of the infected bird. It is difficult to identify this species only on the basis of the data presented in the original description. Fortunately, the hapantotype is available. Bennett and Peirce (1989) redescribed this species on the basis of the hapantotype, and they synonymized *H. santosdiasi* Son, 1960, *H. chapini* Berghe, Chardome and Peel, 1958, and *H. ammoperdix* Subkhonov, 1980 with *H. rileyi*. It is difficult to agree with this synonymy for the following reasons. First, the original descriptions of *H. santosdiasi* and *H. chapini* are based on the material markedly influenced by the onset of gametogenesis (Berghe *et al.*, 1958; Son, 1960), and thus cannot be used for morphological comparison with other species of haemoproteids. In other words, it is difficult to identify these species with confidence. Additional material from type hosts and from type localities is required to solve this question. It is important to note that *H. santosdiasi* parasitize the domestic chicken in Africa, and investigation into this parasite would be of some practical significance. Before the additional material is available, *H. santosdiasi* and *H. chapini* are declared to be *species inquirendae*. Second, Subkhonov (1980) briefly described *H. ammoperdix* and published the illustrations of two gametocytes. The original description is brief, but *H. ammoperdix* can be distinguished from *H. rileyi* on the basis of its more numerous pigment granules, whose number varies from 17 to 33 in its gametocytes. Bennett and Peirce (1989) also noted this difference, but they believed that Subkhonov (1980) made a mistake during the calculation of the pigment granules; according to their calculations, the gametocytes in the original illustrations possess from 8 to 16 pigment granules. The analysis of the original description shows that the pigment granules in the schematic illustrations are depicted as cross-hatched and noncross-hatched bodies, and their number in two gametocytes is at least 17 and 28, respectively. Before additional material is available, *H. ammoperdix* should be considered a distinct species.

Bennett and Peirce (1989) declared *H. gallinarum* Yakunin and Zhazyltaev, 1977 as a *nomen nudum*. The original description of *H. gallinarum* contains a brief description, and is accompanied with a microphotograph (Yakunin and Zhazyltaev, 1977). This name corresponds to Article 13(a) of the International Code of Zoological Nomenclature (1985), and cannot be declared as the *nomen nudum*. However, the original description is incomplete and so schematic that species identification is impossible. This parasite develops in the domestic chicken, and is close to *H. santosdiasi*. Additional material is required to resolve the question on the validity of *H. gallinarum* which is declared here as a *species inquirenda*.

39. **Haemoproteus (Parahaemoproteus) fuscae** Mello and Fonseca, 1937

Haemoproteus halcyonis fuscae Mello and Fonseca, 1937: 216, Figs. – *H. fusca* Bennett and Campbell, 1973: 342, Fig. 13, 14. – *H. fuscae*: Valkiūnas, 1997: 231 (=*H. fusca*).

T y p e v e r t e b r a t e h o s t. *Halcyon smyrnensis* (L.) (Coraciiformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. Some species of the Coraciiformes (Table 65).
T y p e l o c a l i t y. Santo Estevam, India.
D i s t r i b u t i o n. The Oriental and Ethiopian zoogeographical regions, the South and Central Palearctic.
T y p e m a t e r i a l was not designated in the original description. The type material of *H. fusca* Bennett and Campbell, 1973 cannot be used as neotypes of *H. fuscae* Mello and Fonseca, 1937

because it does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of neotypes is required.

Etymology. The specific name is derived from the subspecific name of the type host, *Halcyon smyrnensis fusca*.

Table 65 List of vertebrate hosts of *Haemoproteus fuscae* (modified from Bennett and Campbell, 1973).

Alcedo atthis	*H. concreta*	*H. senegalensis*
Ceyx erithacus	*H. coromanda*	*Lacedo pulchella*
C. rufidorsum	*H. lindsayi*	*Tanysiptera galatea*
Halcyon albiventris	*H. pileata*	
H. chloris	*H. sancta*	

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally; they grow around the nucleus of erythrocytes and, finally, completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes. The average number of pigment granules in gametocytes is greater than 20.

Development in vertebrate host

Young gametocytes (Fig. 106, *1*, *2*, *7*). The earliest forms can be seen anywhere in infected erythrocytes, and they are frequently recorded in a polar position; as the parasite develops, gametocytes extend along the nucleus of erythrocytes, frequently taking a comma-like shape and an asymmetrical position to the erythrocyte nucleus (Fig. 106, *2*).

Macrogametocytes (Fig. 106, *3*, *4*, *8*; Table 66). The cytoplasm is granular in appearance; gametocytes grow around the nucleus of erythrocytes, they markedly enclose the

Table 66 Morphometric parameters of gametocytes and host cells of *Haemoproteus fuscae* (modified from Bennett and Campbell, 1973).

Feature	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	10			
Length		–	13.7	0.8
Width		–	7.7	0.4
Length of nucleus		–	6.8	0.4
Width of nucleus		–	2.8	0.3
Parasitized erythrocyte	10			
Length		–	15.5	1.2
Width		–	7.7	0.8
Length of nucleus		–	6.0	0.6
Width of nucleus		–	2.6	0.3
Gametocyte	3			
Length		22.0–25.0	23.8	–
Width		2.3–2.9	2.7	–
NDR	8	–	0.9	–
No. of pigment granules	8	–	33.8	8.0

Note: All sizes are given in micrometres. The length and width of gametocytes are calculated from the scale drawings.

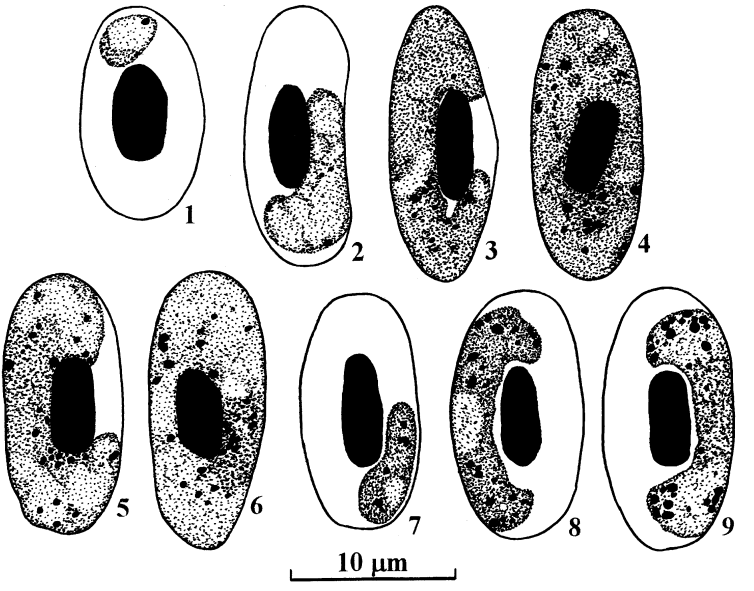

Figure 106 Gametocytes of *Haemoproteus fuscae* from the blood of *Halcyon chloris:* *1*, *2*, *7* – young; *3*, *4*, *8* – macrogametocytes; *5*, *6*, *9* – microgametocytes (*1–6* are modified from Bennett and Campbell, 1973).

nucleus with their ends and finally completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes, but do not displace or only slightly displace the nucleus of erythrocytes laterally; growing gametocytes frequently do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is usually available between the parasite and the nucleus of erythrocyte (Fig. 106, *7*, *8*); this 'cleft' disappears in fully grown forms; mature gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 106, *3, 4*); the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 106, *5*, *6*, *9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Mello and Fonseca (1937) described *Haemoproteus halcyonis fuscae* from the blood of *Halcyon smyrnensis fusca*. Bennett and Campbell (1973) showed that *H. halcyonis fuscae* is clearly separable from *H. halcyonis* on the basis of the morphology of its gametocytes. Thus, *H. halcyonis fuscae* should be considered as a distinct species. According to the principle of priority [Article 23(a)(c)] and the rule of changes in rank or combination [Article 50(c)(i)] of the International Code of Zoological Nomenclature (1985), this new species should be named *H. fuscae* Mello and Fonseca, 1937. In some papers (Bhatia, 1938; Levine and Campbell, 1971), the original trinominal name *Haemoproteus halcyonis fuscae* was changed into infrasubspecific name *H. halcyonis* var. *fuscae*. Bennett and Campbell (1973) accepted this action because, according to their opinion, the trinomen *H. halcyonis fuscae* was used inadvertently in the original description. That is why Bennett and Campbell (1973) suggested a new name for this species, *H. fusca* Bennett and Campbell, 1973. However, this contradicts Article 45(g) of the International Code of Zoological Nomenclature (1985),

according to which the name *fuscae* is available irrespectively of 'a variety' or 'a subspecies' it was attributed to by Mello and Fonseca (1937), because (i) this name was published before 1961 and (ii) the infrasubspecific rank was not meant for this name in the original description. As this parasite is a distinct species, it should be named *H. fuscae* Mello and Fonseca, 1937. In this connection, the name *H. fusca* Bennett and Campbell, 1973 should be declared a junior synonym of *H. fuscae*. It is necessary to note that, according to Article 58 of the International Code of Zoological Nomenclature (1985), the names *fuscae* and *fusca* are not homonyms.

Haemoproteus fuscae can be readily distinguished from the haemoproteids of birds belonging to the Coraciiformes, particularly, on the basis of its (i) circumnuclear fully grown gametocytes and (ii) numerous pigment granules in gametocytes.

40. **Haemoproteus (Parahaemoproteus) picae** Coatney and Roudabush, 1937

Haemoproteus picae Coatney and Roudabush, 1937: 1012, Fig. 13–16.

Type vertebrate host. *Pica pica* L. (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 67).
Type locality. Peru, Nebraska, USA.
Distribution. The Holarctic.
Type material was not designated in the original description. The neotypes designated by Bishop and Bennett (1990) are invalid because they came from nontype hosts (*Corvus brachyrhynchos*, *Perisoreus canadensis*) investigated beyond the type locality (Canada) [see Article 75(d)(5) of the International Code of Zoological Nomenclature, 1985]. Designation of neotypes is required. A series of good additional slides is deposited in IRCAH and CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Pica.*

Table 67 List of vertebrate hosts of *Haemoproteus picae* (modified from Bishop and Bennett, 1990).

Aphelocoma coerulescens	*Cyanocitta cristata*	*Garrulus glandarius*
Corvus brachyrhynchos	*Dendrocitta formosae*	*Perisoreus canadensis*
C. corax	*D. occipitalis*	*Psilorhinus morio*
C. ossifragus	*D. vagabunda*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes predominate among the growing macrogametocytes. Gametocytes with a highly ameboid outline do not predominate among growing macrogametocytes. Large (1.0 to 1.5 μm) in size and rod-like in form pigment granules are present usually only in fully grown gametocytes, and they do not predominate. The average number of pigment granules is about 12 per gametocyte. A species difficult to identify; can be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes only on the basis of a detailed analysis of a set of characters.

Development in vertebrate host
Young gametocytes (Fig. 107, *1–3*). The earliest forms can be seen anywhere in infected erythrocytes; variable in shape; the outline is usually even (Fig. 107, *1*); as the parasite

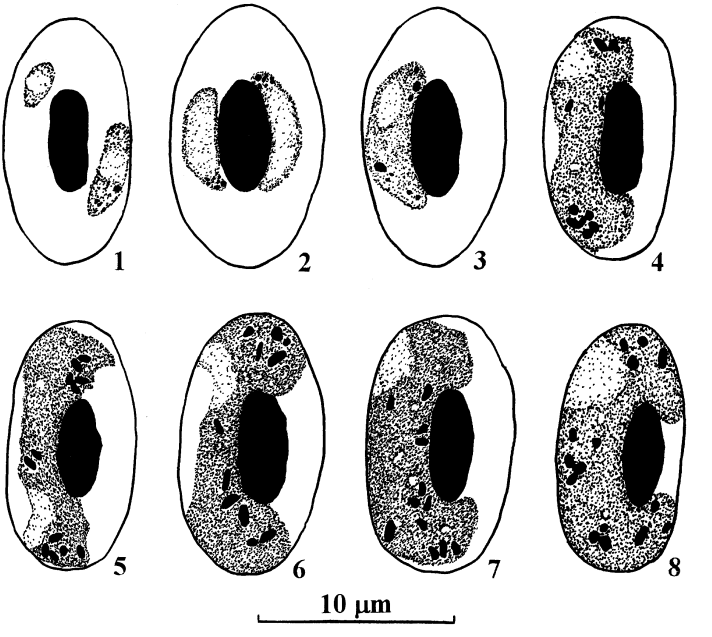

Figure 107 Gametocytes of *Haemoproteus picae* from the blood of *Pica pica:* *1–3* – young; *4–8* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992b).

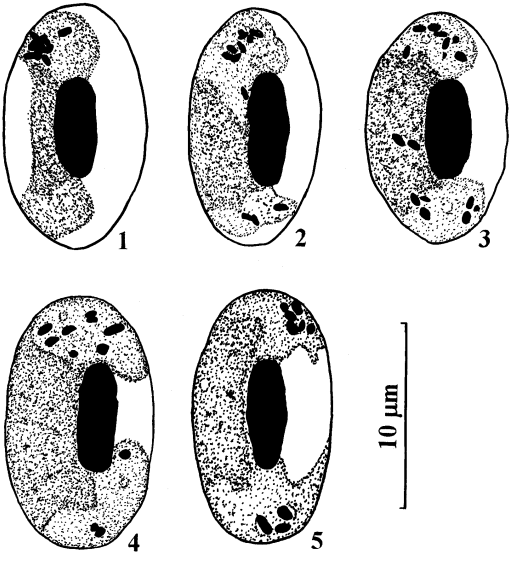

Figure 108 Microgametocytes of *Haemoproteus picae* from the blood of *Pica pica* (modified from Valkiūnas and Iezhova, 1992b).

develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus, frequently taking a crescent-like shape (Fig. 107, *2*, *3*).

Table 68 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. picae* (according to Valkiūnas and Iezhova, 1992b)				*H. velans* (modified from Coatney and Roudabush, 1937; Greiner *et al.,* 1977)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	31				10			
Length		10.2–13.9	12.0	0.8		–	13.0	0.7
Width		5.0–7.7	6.8	0.4		–	7.2	0.3
Length of nucleus		4.4–8.0	5.4	0.4		–	–	–
Width of nucleus		1.7–3.2	2.4	0.1		–	–	–
Erythrocyte parasitized by macrogametocyte	31							
Length		10.0–14.4	12.4	0.8	–	–	–	–
Width		4.9–7.3	6.6	0.4	–	–	–	–
Length of nucleus		5.3–7.8	5.6	0.3	–	–	–	–
Width of nucleus		1.8–3.0	2.2	0.2	–	–	–	–
Erythrocyte parasitized by microgametocyte	31							
Length		11.0–14.6	12.3	0.8	–	–	–	–
Width		5.4–7.4	6.6	0.3	–	–	–	–
Length of nucleus		5.0–7.2	5.6	0.3	–	–	–	–
Width of nucleus		2.0–3.1	2.5	0.2	–	–	–	–
Macrogametocyte	31				15			
Length		12.4–17.2	14.6	0.8		–	24.4	3.4
Width		2.0–3.9	3.1	0.4		–	2.9	0.4
Length of nucleus		0.6–4.0	3.0	0.7		–	3.0	0.2
Width of nucleus		1.2–3.1	2.3	0.4		–	2.3	0.3
NDR		0.3–0.9	0.7	0.1		–	0.7	–
No. of pigment granules		8–18	12.2	1.8		–	18.0	5.1
Microgametocyte	31							
Length		13.3–20.2	15.4	1.0	–	22.4–27.9	24.8	–
Width		2.4–4.4	3.2	0.4	–	1.9–3.2	2.8	–
Length of nucleus		5.3–10.2	7.8	0.8	–	–	–	–
Width of nucleus		2.4–4.4	3.2	0.4	–	–	–	–
NDR		0.5–0.9	0.8	0.1	–	–	–	–
No. of pigment granules		8–16	11.8	1.4	–	–	21.0	–

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 107, *4–8*; Table 68). The cytoplasm is finely granular in appearance, sometimes contains a few small vacuoles; valutin granules were seen in some blood films; gametocytes grow around the nucleus of erythrocytes, they slightly displace the nucleus laterally but do not encircle it completely; medium and fully grown gametocytes fill the erythrocytes up to their poles (Fig. 107, *6*, *8*); the central part of the pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 107, *4–6*); the dumbbell-shaped gametocytes predominate among the growing gametocytes; fully grown gametocytes lose the dumbbell

shape, and they are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 107, *7*, *8*); the outline of medium grown gametocytes is usually angular (Fig. 107, *4*) or slightly ameboid (Fig. 107, *5*), sometimes even (Fig. 107, *6*), and is usually even in fully grown gametocytes (Fig. 107, *7*, *8*); the parasite nucleus is variable in form, frequently triangular, subterminal in position; pigment granules are of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, roundish, oval, and rod-like, randomly scattered throughout the cytoplasm. It should be noted that medium-size, roundish pigment granules predominate in the gametocytes; rod-like pigment granules are not so frequently seen, and they appear usually only in fully grown gametocytes.

Microgametocytes (Fig. 108). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; gametocytes with a highly ameboid outline are frequently seen (Fig. 108, *5*); dumbbell-shaped gametocytes are less numerous than among macrogametocytes; other characters are as for macrogametocytes.

Comments. *Haemoproteus picae* is a common parasite in the Holarctic, and the morphology of its gametocytes in different vertebrate hosts from the Nearctic and Palearctic is surprisingly similar (Coatney and Roudabush, 1937; Bishop and Bennett, 1990; Valkiūnas and Iezhova, 1992b).

Among the haemoproteids of birds belonging to the Passeriformes, *H. picae* is especially similar to *H. killangoi* and *H. motacillae*. During the identification of these species, attention should first of all be paid to the morphology of pigment granules in their gametocytes. In fully grown gametocytes of *H. killangoi* and *H. motacillae*, large (1.0 to 1.5 μm) rod-like pigment granules clearly predominate. Such pigment granules are also present in gametocytes of *H. picae,* but do not predominate, and medium-size (0.5 to 1.0 μm), roundish pigment granules are more numerous. In addition, growing gametocytes of *H. killangoi* are usually highly ameboid in outline, which is not characteristic of *H. picae*.

It should be noted that gametocytes nearly encircling the nucleus of erythrocytes (Fig. 107, *8*) are numerous in the material investigated by the author. Thus, it is likely that circumnuclear forms may appear occasionally, but they have not been recorded in *H. picae* so far.

41. **Haemoproteus (Parahaemoproteus) velans** Coatney and Roudabush, 1937

Haemoproteus velans Coatney and Roudabush, 1937: 1009, Pl. 1, Fig. 7–10.

Type vertebrate host. *Colaptes auratus* (L.) (Piciformes).
Additional vertebrate hosts. Some species of the Piciformes (Table 69).
Vectors. *Culicoides sphagnumensis*, *C. stilobezzioides* (Diptera: Ceratopogonidae).
Type locality. Nebraska, USA.
Distribution. This parasite has been recorded in the Nearctic and in the Oriental zoogeographical region. A record of the parasite in the palearctic *Jynx torquilla* during wintering in India (Greiner *et al.*, 1977) indicates the possibility of introduction of the infection into the Palearctic together with migratory birds.
Type material. Hapantotype (No. 45241, *Colaptes auratus*, Nebraska, USA, G.R. Coatney) is deposited in IRCAH.
Etymology was not specified in the original description.

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes slightly displace the nucleus of infected erythrocytes laterally; they markedly enclose the nucleus with their ends and finally completely encircle it and occupy all available cytoplasmic space in the erythrocytes.

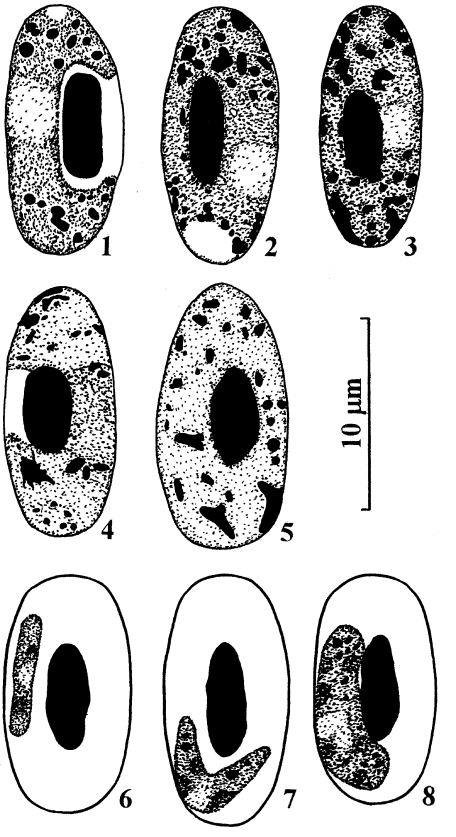

Figure 109 Gametocytes of *Haemoproteus velans* from the blood of *Colaptes auratus:* *1–3* – macrogametocytes; *4*, *5* – microgametocytes; *6–8* – young (*1*, *2*, *4*, *5* are modified from Coatney and Roudabush, 1937; and *3* is modified from Greiner *et al*., 1977).

Development in vertebrate host

Young gametocytes (Fig. 109, *6–8*) can be seen anywhere in infected erythrocytes; they are frequently rod-like (Fig. 109, *6*) or horseshoe-like (Fig. 109, *7*); as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes, they are usually closely appressed to the envelope of erythrocytes but frequently do not touch or only just touch the nucleus of erythrocytes (Fig. 109, *8*); valutin granules are numerous, obscuring the pigment granules; the outline is usually even.

Macrogametocytes (Fig. 109, *1–3*; Table 68). The cytoplasm contains numerous compact granules of valutin; gametocytes grow around the nucleus of erythrocytes, they

Table 69 List of vertebrate hosts of *Haemoproteus velans* (modified from Greiner *et al.*, 1977).

Chrysocolaptes lucidus	*P. chlorolophus*
Dendrocopos mahrattensis	*P. flavinucha*
Jynx torquilla	*P. vittatus*
Picus canus	*Sphyrapicus varius*

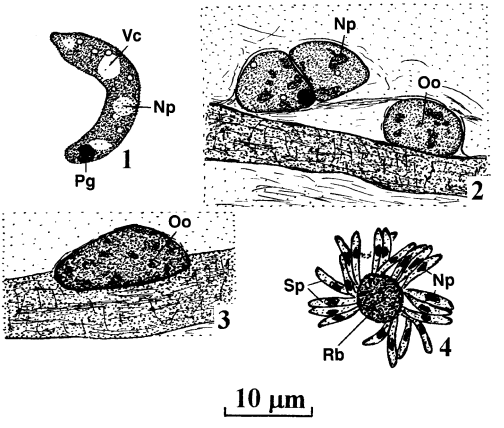

Figure 110 *Haemoproteus velans* in the biting midge *Culicoides* sp.:
1 – ookinete; 2 – young oocysts in midgut of the vector 48 h after the ingestion of gametocytes; *3* – oocyst with divided chromatin from midgut of the vector 60 h after the ingestion of gametocytes; *4* – almost mature oocyst from midgut of the vector 96 h after the ingestion of gametocytes (the capsule of the oocyst is omitted); Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Sp – sporozoite; Oo – oocyst; Vc – 'vacuole' (modified from Khan and Fallis, 1971a).

markedly enclose the nucleus with their ends and finally completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes (Fig. 109, *3*); growing gametocytes are frequently with a clear 'dip,' which resembles a vacuole and is located near the pole of infected erythrocytes (Fig. 109, *1*, *2*); growing gametocytes sometimes do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is present between the parasite and the erythrocyte nucleus (Fig. 109, *1*); this 'cleft' disappears in fully grown gametocytes; the parasite nucleus is compact, usually roundish or oval, median or submedian in position; pigment granules are randomly scattered throughout the cytoplasm; they are difficult to see and to calculate because of numerous valutin granules which are always present in the cytoplasm; infected erythrocytes are hypertrophied approximately 10% in length in comparison to uninfected ones.

Microgametocytes (Fig. 109, *4*, *5*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; growing gametocytes are usually closely appressed to the erythrocyte nucleus; other characters are as for macrogametocytes.

Development in vector

Gametogenesis, development of ookinete and sporogony were studied by Khan and Fallis (1971a) in experimentally infected biting midges. Sporogony is completed in *Culicoides stilobezzioides* and *C. sphagnumensis* within 96 h at 20°C. Exflagellation of microgametocytes occurred 2 to 5 min after exposure of infected blood to air. Each microgametocyte produces up to eight snake-like elongated microgametes. According to Desser (1972a), the microgametes are approximately 11 μm long and 1 μm wide. Macrogametes are roundish, possess a compact nucleus, pigment granules and vacuoles. Ookinetes were seen in the midgut of the vectors between 12 and 72 h after the ingestion of gametocytes. The ookinetes are worm-like bodies, possess a compact nucleus and several large and small 'vacuoles' (Fig. 110, *1*). Pigment granules are seen in clumps on the distal end of the ookinete. Young oocysts were recorded in the midgut of the vector 48 h after the ingestion

of gametocytes (Fig. 110, *2*, *3*). They are approximately 7 μm in diameter and contain pigment granules. After 72 h, the chromatin in some oocysts was located peripherally, and the initial stage of the development of sporozoites was recorded. Mature oocysts were observed after 96 h. They are up to 12 μm in diameter and contain less than 50 sporozoites that arose from a single germinative centre (Fig. 110, *4*). Sporozoites were seen in the salivary glands of the vectors 96 h after the ingestion of gametocytes. The sporozoites vary (n = 25) from 7 to 11 (on average 9) μm in length, and from 1 to 2 (on average 2) μm in width. Few oocysts, if at all, were seen in the vectors dissected five days after the ingestion of gametocytes.

C o m m e n t s. The number of pigment granules in gametocytes of *H. velans* varies remarkably in different vertebrate hosts. The minimum number of pigment granules was recorded from *Jynx torquilla* (16.0±4.6), and the maximum, from *Dendrocopos mahrattensis* (34±4.6). Greiner *et al.*

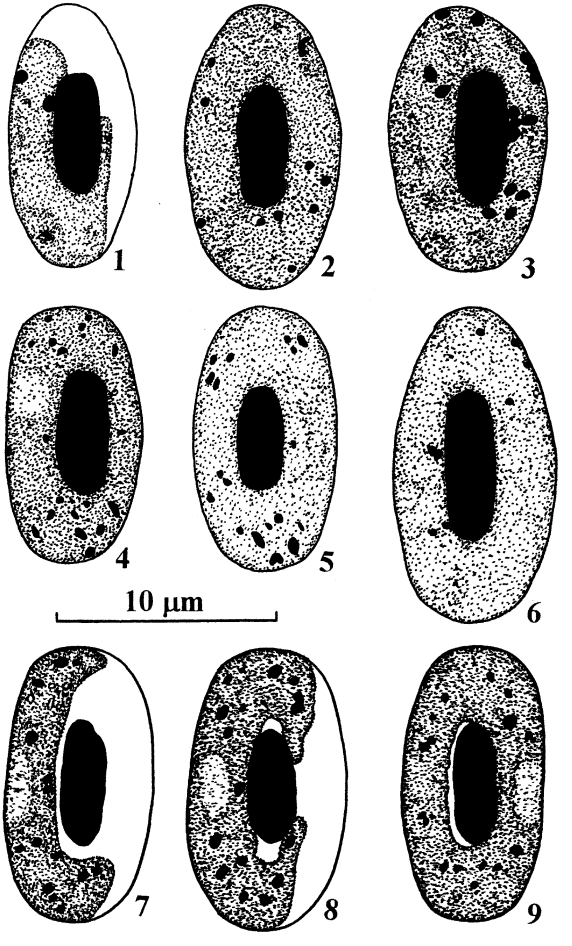

Figure 111 Gametocytes of *Haemoproteus archilochus* from the blood of *Archilochus colubris* (*1–6*) and *Selasphorus rufus* (*7–9*):
1–4, *7–9* – macrogametocytes; *5*, *6* – microgametocytes (*1–3*, *6* are modified from White *et al*., 1979; and *4*, *5* are modified from Coatney and West, 1938).

(1977) believe that this variation is due to the peculiarities of the development of *H. velans* in different hosts. However, this explanation seems unlikely because such a pronounced variation in the number of pigment granules is usually not characteristic of bird haemoproteids. It should be noted that valutin granules, which are numerous in gametocytes of *H. velans*, markedly obscure the pigment, and this can cause an error in counting pigment granules. For example, valutin granules are so numerous in the hapantotype that counting the pigment granules in this film is hardly possible. This may be the explanation of the differences in the number of pigment granules recorded by different authors. However, it should be also noted that the description of gametocytes in the paper by Greiner *et al.* (1977) does not include a detailed comparison of the gametocytes which develop in different vertebrate hosts. It is possible that at least two species of haemoproteids with circumnuclear gametocytes are described under the name *H. velans.* Further study is required to solve this question.

The data on the transformation of macrogametocytes of *H. velans* during gametogenesis into a macrogamete and a residual body (Desser, 1972a) should be tested. The development of the residual body during the macrogametogenesis is not characteristic of species of the subgenus *Parahaemoproteus,* and it was not recorded in *H. velans* by Khan and Fallis (1971a).

42. **Haemoproteus (Parahaemoproteus) archilochus** Coatney and West, 1938

Haemoproteus archilochus Coatney and West, 1938: 601, Pl. 1, Fig. 1, 2.

Type vertebrate host. *Archilochus colubris* (L.) (Apodiformes).
Additional vertebrate hosts. Some species of the Apodiformes (Table 70).
Type locality. Peru, Nebraska, USA.
Distribution. The Nearctic and the Neotropical zoogeographical region in the range of distribution of vertebrate hosts.
Type material. Hapantotype (No. 45249, *Archilochus colubris*, 21.06.1937, Peru, Nebraska, USA, G.R.Coatney) is deposited in IRCAH. A series of good additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Archilochus*.

Main diagnostic characters. A parasite of species of the Apodiformes whose fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally; they completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes.

Development in vertebrate host
Young gametocytes. The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes; they usually adhere to the envelope of erythrocytes but do not touch their nucleus; the outline is usually even.

Table 70 List of vertebrate hosts of *Haemoproteus archilochus* (modified from White *et al.*, 1979).

Amazilia amabilis	*Archilochus alexandri*	*Glaucis hirsuta*
A. edward	*Chalybura buffonii*	*Phaeochroa cuvierii*
A. tzacatl	*Damophila julie*	*Phaethornis anthophilus*
Anthracothorax nigricollis	*Eutoxeres aquila*	*Selasphorus rufus*

Table 71 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. archilochus* (modified from White *et al.*, 1979)			*H. quiscalus* (modified from Burry-Caines and Bennett, 1992)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	95			95			
Length		11.6	–		–	11.7	0.7
Width		5.7	0.4		–	6.7	0.6
Length of nucleus		4.9	0.4		–	5.3	0.5
Width of nucleus		2.2	0.3		–	2.3	0.3
Erythrocyte parasitized by macrogametocyte	90			95			
Length		12.1	0.8		–	12.7	0.8
Width		6.4	0.7		–	6.7	0.6
Length of nucleus		5.0	0.5		–	5.1	0.6
Width of nucleus		2.1	0.3		–	2.4	0.4
Erythrocyte parasitized by microgametocyte	70						
Length		12.2	0.7		–	–	–
Width		6.6	0.6		–	–	–
Length of nucleus		5.0	0.4		–	–	–
Width of nucleus		2.2	0.2		–	–	–
Macrogametocyte	90			95			
Length		22.1	1.3		–	15.1	1.7
Width		2.3	0.5		–	2.5	0.5
Length of nucleus		3.9	0.9		–	2.2	0.7
Width of nucleus		2.0	0.4		–	2.1	0.4
NDR		0.9	0.1		–	0.8	0.1
No. of pigment granules		16.7	4.9		5–24	12.2	3.1
Microgametocyte	70						
Length		22.1	1.6		–	–	–
Width		2.4	0.5		–	–	–
NDR		0.9	0.1		–	–	–
No. of pigment granules		14.5	4.0		–	–	–

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 111, *1–4*, *7–9*; Table 71). The cytoplasm is homogeneous in appearance, usually lacking vacuoles; valutin granules are not characteristic; gametocytes grow around the nucleus of erythrocytes, they do not displace or slightly displace the nucleus laterally and are closely appressed to the erythrocyte envelope; growing gametocytes frequently do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is usually present between the parasite and the erythrocyte nucleus (Fig. 111, *7*, *9*); the outline of growing gametocytes is usually even or slightly wavy; fully grown gametocytes are closely appressed to the nucleus of erythrocytes, and they completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes (Fig. 111, *2–4*); the parasite nucleus is compact, usually roundish or oval,

median or submedian in position; pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, vary from 6 to 23, are randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 111, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Gametocytes of *H. archilochus* demonstrate a marked tendency to encircle the nucleus of erythrocytes completely. The circumnuclear forms, which occupy all available cytoplasmic space in infected erythrocytes, are numerous in the hapantotype and on a series of additional slides deposited in the IRCAH. During the identification of this species, attention should be paid to this character.

43. **Haemoproteus (Parahaemoproteus) quiscalus** Coatney and West, 1938

Haemoproteus quiscalus Coatney and West, 1938: 602, Pl. 1, Fig. 3, 4.

Type vertebrate host. *Quiscalus quiscula* (L.) (Passeriformes).
Additional vertebrate hosts. *Agelaius phoeniceus*, *Cacicus cela*, *Icterus galbula*, *I. spurius*, *Molothrus ater*, *Quiscalus major* (Passeriformes).
Type locality. Peru, Nebraska, USA.
Distribution. The Nearctic and the Neotropical zoogeographical region.
Type material. Hapantotype [No. 45247(I), *Quiscalus quiscula*, 22.06.1937, Peru, Nebraska, G.R. Coatney] and parahapantotype [No. 45247(II), other data are as for the hapantotype] are deposited in IRCAH. A series of good additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Quiscalus*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed to the envelope of erythrocyte and they fill the erythrocytes up to their poles. Dumbbell-shaped growing gametocytes are present. The outline of gametocytes is even. The nucleus of macrogametocytes is terminal or subterminal in position. The average number of pigment granules in gametocytes is between 5 and 15.

Development in vertebrate host

Young gametocytes (Fig. 112, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend along it. At this stage of development, gametocytes usually touch the envelope of the erythrocytes (Fig. 112, *2*). The outline is usually even or slightly wavy.

Macrogametocytes (Fig. 112, *3–8*; Table 71). The cytoplasm is finely granular in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus of erythrocyte, they do not displace or only slightly displace the nucleus laterally and do not encircle it completely; growing gametocytes markedly extend around the nucleus of erythrocytes but do not fill the erythrocytes up to their poles (Fig. 112, *4*) which is a

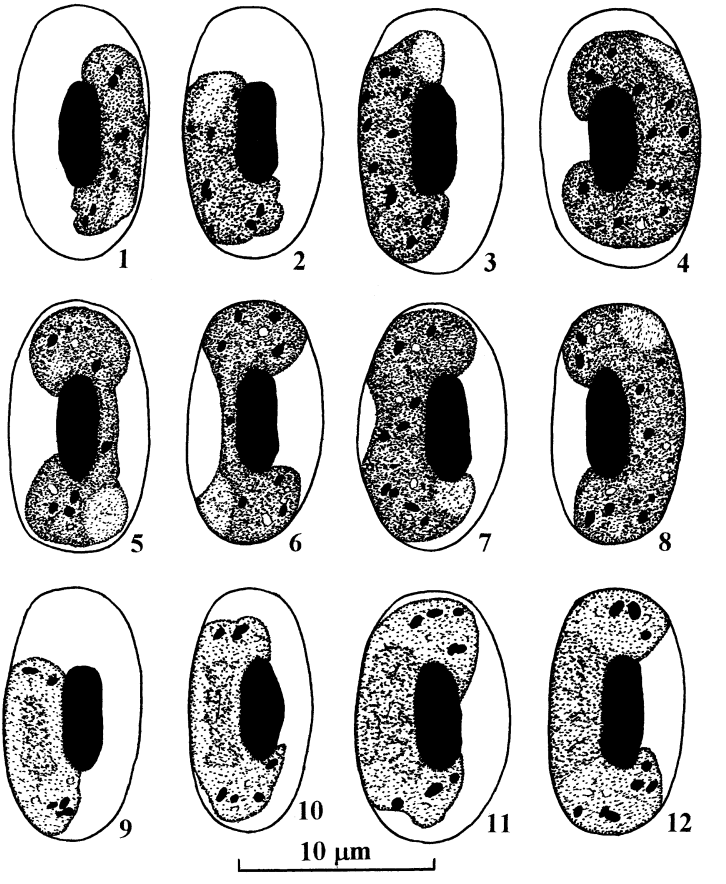

Figure 112 Gametocytes of *Haemoproteus quiscalus* from the blood of *Quiscalus quiscula:* *1*, *2* – young; *3–8* – macrogametocytes; *9–12* – microgametocytes.

characteristic feature of this species; as the parasite develops, the dumbbell-shaped gametocytes appear (Fig. 112, *5–7*), and the gametocytes, which do not touch the envelope of erythrocytes along their entire margin (Fig. 112, *5*), are present among them. However, it should be mentioned that the gametocytes shown in Fig. 112, *5* do not predominate in the type material; they do not exceed 30% of the total number of growing gametocytes, and they are usually even less numerous. Fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocyte up to their poles (Fig. 112, *8*). The outline of gametocytes is usually even. The parasite nucleus is compact, variable in form, but frequently roundish or oval in shape, terminal or subterminal in position (Fig. 112, *3*, *7*, *8*). Pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 112, *9–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; dumbbell-shaped gametocytes as well as medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are not characteristic; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. quiscalus* is especially similar to *H. monarchus*. It can be distinguished from the latter species, particularly on the basis of its numerous medium grown gametocytes markedly extending around the erythrocyte nucleus (see Fig. 112, *4*). Medium grown gametocytes of such shape are not characteristic of *H. monarchus*. In addition, the medium grown gametocytes shown in Fig. 112, *5* are not numerous in *H. quiscalus*, and are always numerous in *H. monarchus.* Furthermore, fully grown gametocytes of *H. quiscalus* fill the infected erythrocytes up to their poles (Fig. 112, *8*); this is not characteristic of *H. monarchus*.

44. **Haemoproteus (Parahaemoproteus) handai** Maqsood, 1943

Haemoproteus handai Maqsood, 1943: 111, Pl. 5, Fig. 1–12. – *Parahaemoproteus desseri* Miltgen, Landau, Ratanaworabhan and Yenbutra, 1981: 123, Pl. 1, 2. – *Haemoproteus handai*: Bennett and Peirce, 1986: 771 (=*Parahaemoproteus desseri, Haemoproteus desseri*).

Type vertebrate host. *Psittacula cyanocephala* (L.) (Psittaciformes).
Additional vertebrate hosts. Some species of the Psittaciformes (Table 72).
Vectors. The natural vectors are unknown. Sporogony is completed in experimentally infected biting midges *Culicoides nubeculosus* (Diptera: Ceratopogonidae).
Type locality. Zoological Gardens, Lahore, Pakistan.
Distribution. The Australian, Oriental, Ethiopian, and Neotropical zoogeographical regions. Records from the Old World are especially numerous. Infected parrots were also imported into the Palearctic, where transmission has not been recorded.
Type material. Neohapantotype (No. 58087, *Psittacula cyanocephala*, January 1975, this bird was imported into the United Kingdom from India, M.A. Peirce) is deposited in IRCAH. A series of additional slides is deposited in IRCAH. Paraneohapantotypes designated by Bennett and Peirce (1986) are invalid because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985).
Etymology. This species was named in honour of Professor B.N. Handa (Punjab Veterinary College, Lahore, Pakistan).

Table 72 List of vertebrate hosts of *Haemoproteus handai* (modified from Bennett and Peirce, 1986).

Amazona amazonica	*C. sulphurea*	*Prioniturus discurus*
Ara ararauna	*Chalcopsitta cardinalis*	*Psittacula krameri*
Aratinga pertinax	*Geoffroyus heteroclitus*	*P. roseata*
Bolbopsittacus lunulatus	*Loriculus vernalis*	*Psittrichas fulgidus*
Cacatua alba	*Melopsittacus undulatus*	*Tanygnathus lucionensis*
C. moluccensis	*Pionus menstruus*	*Trichoglossus haematodus*

Main diagnostic characters. A parasite of species of the Psittaciformes whose fully grown gametocytes completely encircle the nucleus of infected erythrocytes and occupy all available cytoplasmic space in the erythrocytes. The average number of pigment granules is about 20 per gametocyte.

Development in vertebrate host
Exoerythrocytic meronts (megalomeronts) are seen in the muscle fibres in the heart, tongue, hip, and in pectoral muscle (Miltgen *et al.*, 1981). They are especially numerous in the pectoral muscle. The megalomeronts are elongated bodies up to 900 μm long. The

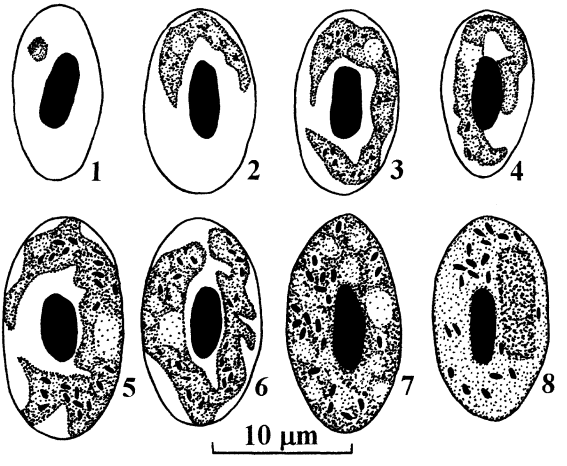

Figure 113 Gametocytes of *Haemoproteus handai* from the blood of *Psittacula roseata* (*1*, *4*) and *P. cyanocephala* (*2*, *3*, *5–8*):
1, *2* – young; *3–7* – macrogametocytes; *8* – microgametocyte (*1*, *4* are modified from Miltgen *et al*., 1981; and *2*, *3*, *5–8* are modified from Bennett and Peirce, 1989).

developing megalomeronts possess basophilic cytoplasm, pseudosepta, and numerous roundish, oval or sometimes rod-like nuclei.

Young gametocytes (Fig. 113, *1*, *2*) can be seen anywhere in infected erythrocytes; growing gametocytes are elegant snake-like bodies; the outline is usually wavy or ameboid; as the parasite develops, gametocytes markedly extend around the nucleus of erythrocytes usually not touching the nucleus and envelope of the erythrocytes (Fig. 113, *2*).

Macrogametocytes (Fig. 113, *3–7*; Table 73). The cytoplasm is granular in appearance; gametocytes grow around the nucleus of erythrocytes and finally completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes; fully grown forms are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 113, *7*); the parasite nucleus is variable in shape, median or submedian in position; pigment granules are roundish, oval, or rod-like, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 113, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

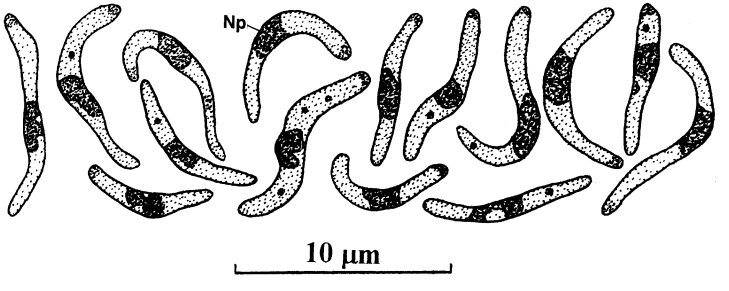

Figure 114 Sporozoites of *Haemoproteus handai:*
Np – nucleus of parasite (modified from Miltgen *et al*., 1981).

Table 73 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. handai* (modified from Bennett and Peirce, 1986)			*H. meropis*			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	75			33			
Length		12.5	0.8		11.0–14.7	11.8	0.9
Width		7.1	0.8		5.8–9.0	7.4	0.4
Length of nucleus		5.6	0.6		5.2–7.1	6.2	0.6
Width of nucleus		2.2	0.3		2.0–2.7	2.2	0.2
Erythrocyte parasitized by macrogametocyte	77			17			
Length		14.0	1.2		11.7–15.5	13.4	1.0
Width		7.8	0.8		5.9–8.7	7.2	0.5
Length of nucleus		5.4	0.6		5.1–6.6	5.5	0.5
Width of nucleus		2.2	0.4		2.0–3.4	2.4	0.4
Erythrocyte parasitized by microgametocyte	15			20			
Length		13.2	1.3		10.9–14.9	12.9	0.8
Width		7.5	0.8		6.2–8.9	7.7	0.4
Length of nucleus		5.5	0.5		5.0–7.7	5.6	0.4
Width of nucleus		2.4	0.5		2.0–2.9	2.1	0.3
Macrogametocyte	77			17			
Length		25.3	1.8		11.8–15.7	13.4	1.1
Width		3.1	0.6		2.7–3.6	3.0	0.4
Length of nucleus		3.5	0.7		1.7–3.2	2.7	0.3
Width of nucleus		2.2	0.4		0.7–2.4	1.6	0.2
NDR		0.9	0.1		0.5–1.0	0.7	0.1
No. of pigment granules		20.8	1.8		8–17	14.1	1.7
Microgametocyte	15			20			
Length		24.2	2.3		11.5–14.4	12.8	1.0
Width		2.9	0.6		2.9–3.8	3.3	0.5
Length of nucleus		6.1	1.3		5.6–9.0	7.5	0.6
Width of nucleus		2.7	0.8		2.7–3.8	3.0	0.4
NDR		0.9	0.1		0.5–0.8	0.6	0.1
No of pigment granules		20.5	1.7		7–15	12.9	1.1

Note: All sizes are given in micrometres.

Development in vector

Sporogony is completed and infective sporozoites develop in the laboratory bred biting midges *Culicoides nubeculosus* (Miltgen *et al.*, 1981). At 26°C, oocysts were recorded in the midgut of the midges on the third day after ingestion of gametocytes. The oocysts vary from 6 to 9 μm in diameter. The mature oocysts were seen on the fifth day, and they were about 12 μm in diameter and contained fewer than 20 sporozoites. Mature sporozoites in fixed and stained smears vary from 6 to 11 μm in length, and from 0.5 to 0.8 μm in width. The apical end of the sporozoites is more intensively stained than the distal one (Fig. 114).

Up to three small inclusions are frequently seen in cytoplasm of the sporozoites. The nucleus of the sporozoites is median in position and up to 2 μm long.

Pathogenicity. It is possible that this parasite may cause the death of heavily infected parrots (Maqsood, 1943).

Comments. *Haemoproteus handai* is especially close to *H. psittaci*. It can be distinguished from the latter species, particularly, on the basis of more numerous and smaller pigment granules in its gametocytes.

45. **Haemoproteus (Parahaemoproteus) meropis** Zargar, 1945

Haemoproteus meropi Zargar, 1945: 125, Fig. A. – *H. meropis*: Bennett, 1978: 1722 (emend. pro *meropi*).

Type vertebrate host. *Merops orientalis* Latham (Coraciiformes).
Additional vertebrate hosts. Some species of the Coraciiformes (Table 74).
Type locality. Nagpur, India.
Distribution. The Oriental and Ethiopian zoogeographical regions, the South and Central Palearctic.
Type material was not designated in the original description. Bennett (1978) redescribed this species on the basis of material which came from nontype hosts investigated far beyond the type locality (Malaysia, Uganda). This material cannot be designated as a neotype because it does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of the neotype material is required, and it may be the blood films from *Merops orientalis* in India (Nandi and Mandal, 1977).
Etymology. The specific name is derived from the generic name of the type host, *Merops.*

Table 74 List of vertebrate hosts of *Haemoproteus meropis*.

Merops albicollis	*M. leschenaulti*
M. apiaster	*M. superciliosus*
M. bulocki	*M. viridis*
M. gularis	

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes slightly displace the nucleus of infected erythrocytes laterally and only slightly enclose it with their ends. A highly ameboid outline is not characteristic of growing gametocytes. The average number of pigment granules is about 14 per gametocyte. The average width of the fully grown gametocytes is less than 4 μm. The average NDR is greater than 0.5.

Development in vertebrate host
Young gametocytes (Fig. 115, *3*) are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the erythrocyte nucleus and extend longitudinally along it; the outline is usually even or slightly ameboid.

Macrogametocytes (Fig. 115, *1*, *2*, *4*; Table 73). The cytoplasm is finely granular in appearance, sometimes contains valutin granules; gametocytes grow along the nucleus of erythrocytes, slightly displacing it, and only slightly enclosing the nucleus with their ends (Fig. 115, *1, 4*); gametocytes are closely appressed both to the nucleus and envelope of

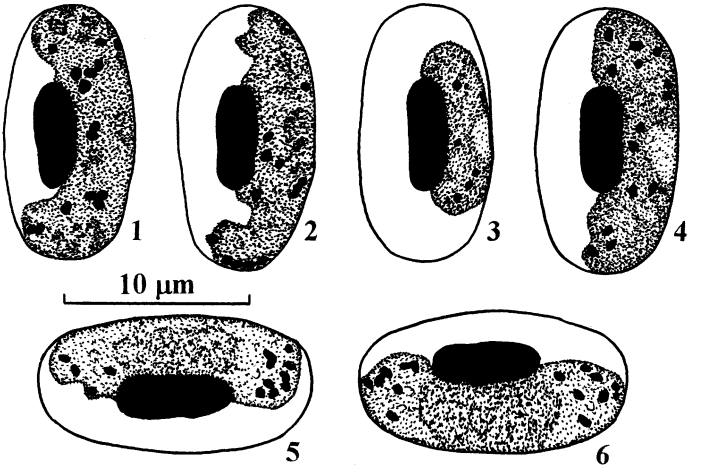

Figure 115 Gametocytes of *Haemoproteus meropis* from the blood of *Merops orientalis:* *1*, *2*, *4* – macrogametocytes; *3* – young; *5*, *6* – microgametocytes (*1*, *2* are modified from Bennett, 1978).

erythrocytes; the outline is usually even (Fig. 115, *1*) or slightly ameboid (Fig. 115, *2*); the parasite nucleus is variable in form, frequently roundish or oval, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 115, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Fully grown gametocytes of *H. meropis* are similar to medium grown gametocytes of *H. gavrilovi*. They can be distinguished from the developing gametocytes of the latter species, in the first instance, on the basis of their more numerous pigment granules. Fully grown gametocytes of *H. meropis* and *H. gavrilovi* are obviously different.

Haemoproteus meropis is especially similar to *H. coraciae*. During the identification of these species, attention should be paid, first of all, to the outline of growing gametocytes and to the size of the fully grown gametocytes. The highly ameboid outline in growing gametocytes, and fully grown gametocytes markedly enclosing the nucleus of erythrocytes with their ends, are common features of *H. coraciae,* where they are not characteristic of *H. meropis*.

46. **Haemoproteus (Parahaemoproteus) sanguinis** Chakravarty and Kar, 1945

Haemoproteus sanguinis Chakravarty and Kar, 1945a: 37, Fig. 1–6.

T y p e v e r t e b r a t e h o s t. *Pycnonotus jocosus* (L.) (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. Numerous species of the Passeriformes, mainly belonging to the Pycnonotidae (over 30 species).
T y p e l o c a l i t y. Calcutta, Bengal, India.

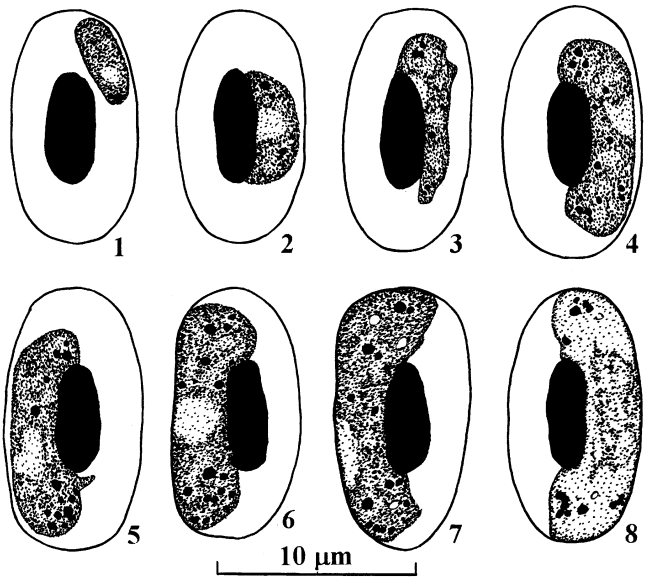

Figure 116 Gametocytes of *Haemoproteus sanguinis* from the blood of *Pycnonotus luteolus: 1–3* – young; *4–7* – macrogametocytes; *8* – microgametocyte.

Distribution. The Oriental and Ethiopian zoogeographical regions.
Type material. Neohapantotype (No. 42183, *Pycnonotus luteolus*, 28.12.1970, Point Calimere, Tamil Nadu, India, H.E. McClure) and paraneohapantotypes (No. 28389, *Pycnonotus barbatus*, 20.01.1972, Lunyo, Uganda, coll. Okia; No. 9829, *P. blanfordi*, 06.01.1965, Nonthaburi, Thailand, H.E. McClure; No. 42249, *P. goiavier*, 28.11.1965, Candugay, Siaton, Negros Oriental, Republic of the Philippines, H.E. McClure; No. 10751, *P. sinensis*, 08.12.1966, Mong Tseng Peninsula, Hong Kong, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the Latin word 'sanguis' (blood).

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow along the erythrocyte nucleus and do not encircle it completely; medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed both to the nucleus and envelope of the erythrocytes and they fill the erythrocytes up to their poles. Dumbbell-shaped gametocytes are absent. The outline of gametocytes is usually even. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about 15 per gametocyte on average. The average NDR is 0.7 or greater.

Development in vertebrate host
Young gametocytes (Fig. 116, *1–3*). The earliest forms are usually seen in a polar or subpolar position in the infected erythrocytes (Fig. 116, *1*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus not touching the envelope of erythrocytes (Fig. 116, *2*, *3*); the outline is even or slightly wavy.

Macrogametocytes (Fig. 116, *4–7*; Table 75). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; gametocytes grow along the nucleus of

Table 75 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. sanguinis* (modified from Rahal *et al.*, 1987)			*H. xantholaemae* (modified from Bennett and Nandi, 1981)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	55			25		
Length		11.7	0.6		13.5	0.9
Width		6.4	0.4		7.7	0.5
Length of nucleus		5.6	0.3		6.3	0.7
Width of nucleus		2.5	0.3		2.6	0.3
Erythrocyte parasitized by macrogametocyte	55			30		
Length		12.7	0.7		14.7	1.0
Width		6.4	0.6		8.2	0.8
Length of nucleus		5.4	0.4		6.2	0.6
Width of nucleus		2.2	0.3		2.5	0.3
Erythrocyte parasitized by microgametocyte	55			15		
Length		12.8	0.6		14.2	0.7
Width		6.6	0.5		7.6	0.6
Length of nucleus		5.5	0.3		6.1	0.4
Width of nucleus		2.2	0.3		2.5	0.3
Macrogametocyte				30		
Length	55	13.8	1.3		13.7	2.6
Width	55	2.4	0.3		3.6	0.6
Length of nucleus	35	2.9	0.6		4.0	0.7
Width of nucleus	35	1.5	0.5		2.3	0.5
NDR	55	0.8	0.1		0.6	–
No. of pigment granules	45	15.4	5.4		19.4	2.6
Microgametocyte				15		
Length	55	14.5	1.3		13.4	1.0
Width	55	2.6	0.4		3.2	0.5
Length of nucleus	1	5.9	–		6.3	1.2
Width of nucleus	1	2.2	–		2.3	0.3
NDR	55	0.8	0.1		0.6	–
No. of pigment granules	49	14.8	4.7		18.6	1.7

Note: All sizes are given in micrometres.

infected erythrocytes and do not encircle it completely; they do not displace or only slightly displace the erythrocyte nucleus laterally; medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present (Fig. 116, *4*, *5*); fully grown gametocytes are closely appressed both to the nucleus and envelope of the erythrocytes and they fill the erythrocytes up to their poles (Fig. 116, *7*); dumbbell-shaped gametocytes are absent; the outline is usually even or slightly ameboid (Fig. 116, *5*); the parasite nucleus is variable in form, median or submedian in position; pigment granules are usually roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 116, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. sanguinis* is similar to *H. formicarius* and *H. sequeirae*. It can be distinguished from the latter two species, particularly on the basis of the shape and size of pigment granules in its gametocytes. See also 'Comments' to *H. otocompsae*.

47. **Haemoproteus (Parahaemoproteus) xantholaemae** Zargar, 1945

Haemoproteus xantholaemi Zargar, 1945: 125, Fig. B. – *H. xantholaemae*: Levine and Campbell, 1971: 480 (emend. pro *xantholaemi*).

Type vertebrate host. *Megalaima haemacephala* (Müller) (Piciformes).
Additional vertebrate hosts. Some species of the Piciformes (Table 76).
Type locality. Reserve forest, Telinkhery, Nagpur, India.
Distribution. The Ethiopian and Oriental zoogeographical regions.
Type material. Neohapantotype (No. 37102, *Megalaima haemacephala*, 24.07.1969, Maharashtra State, India, H.E. McClure) and paraneohapantotypes (No. 3026, *M. franklinii*, 05.03.1961, Mt. Brinchang, Malaya, H.E. McClure; No. 37126, *M. viridis*, 10.04.1971, Maharashtra State, India, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name *Xantholaema* to which the type host was formerly attributed.

Table 76 List of vertebrate hosts of *Haemoproteus xantholaemae* (modified from Bennett and Nandi, 1981).

Megalaima asiatica	*M. viridis*
M. faiostricta	*M. zeylanica*
M. franklinii	*Trachyphonus vaillantii*
M. virens	

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes slightly displace the nucleus of infected erythrocytes laterally; they slightly enclose the nucleus with their ends but do not encircle it completely. Growing gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelope of the erythrocytes. The average number of pigment granules is about 20 per gametocyte. The average width of fully grown gametocytes is greater than 2 μm; the average length, less than 18 μm. The average NDR is 0.5 or greater.

Development in vertebrate host
Young gametocytes (Fig. 117, *5*, *6*) are usually seen in a position lateral to the nucleus of infected erythrocytes; they are of rod-like form; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes but do not touch the envelope of the host cells; the outline is even.

Macrogametocytes (Fig. 117, *1*, *4*; Table 75). The cytoplasm is finely granular in appearance; gametocytes grow along the nucleus of infected erythrocytes; they slightly displace the nucleus laterally and slightly enclose it with their ends but do not encircle the

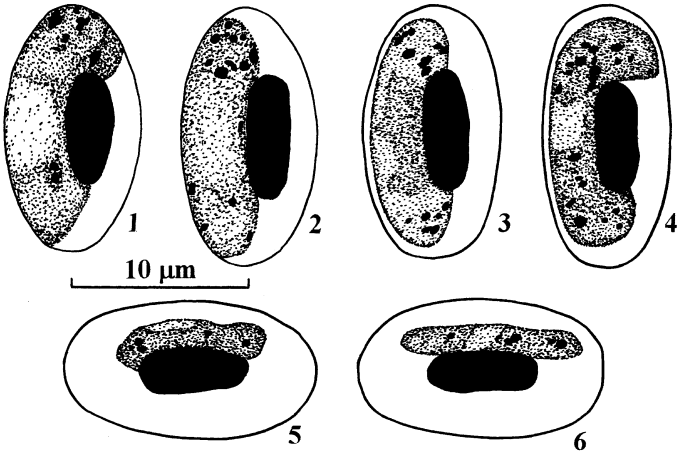

Figure 117 Gametocytes of *Haemoproteus xantholaemae* from the blood of *Megalaima haemacephala:*
1, *4* – macrogametocytes; *2*, *3* – microgametocytes; *5*, *6* – young (*1*, *2* are modified from Bennett and Nandi, 1981).

nucleus completely; growing gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelope of the host cells along their entire margin (Fig. 117, *4*) which is a characteristic feature of this species; fully grown gametocytes are appressed both to the nucleus and envelope of the erythrocytes (Fig. 117, *1*); the outline is usually even; the parasite nucleus is variable in form, frequently roundish or oval, median or submedian in position; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, usually randomly scattered throughout the cytoplasm, but sometimes also seen gathered into loose groups.

Microgametocytes (Fig. 117, *2*, *3*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Piciformes, *H. xantholaemae* is especially similar to *H. borgesi*. It can be distinguished from the latter species, first of all, on the basis of its (i) more numerous pigment granules in gametocytes, (ii) greater average NDR, and (iii) the position of the nucleus in macrogametocytes.

48. **Haemoproteus (Parahaemoproteus) zosteropis** Chakravarty and Kar, 1945

Haemoproteus zosteropsi Chakravarty and Kar, 1945b: 64, Pl. 4, Fig. 1–6. – *H. johnstoni* Laid and Laird, 1959: 225, Pl. 2, Fig. 20–27. – *H. zosteropis*: Bennett and Peirce, 1981: 1155 (emend. pro *zosteropsi*; = *H. johnstoni*).

Type vertebrate host. *Zosterops palpebrosa* (Temm.) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 77).
Type locality. Calcutta, India.

D i s t r i b u t i o n. The South-East Palearctic, the Australian, Oriental and Ethiopian zoogeographical regions.

T y p e m a t e r i a l. Neohapantotype (No. 37233, *Zosterops palpebrosa*, 11.05.1970, Madras, India, H.E. McClure) and paraneohapantotypes (No. 37238, 30.07.1969, Maharashtra, India, other data are as for the neohapantotype; No. 37244, 01.08.1969, other data are as for No. 37238) are deposited in IRCAH. Other neotypes designated by Bennett and Peirce (1981) are invalid because they contradict Article 75(d)(5) of the International Code of Zoological Nomenclature (1985).

E t y m o l o g y. The specific name is derived from the generic name of the type host, *Zosterops*.

Table 77 List of vertebrate hosts of *Haemoproteus zosteropis* (modified from Bennett and Peirce, 1981).

Woodfordia superciliosa	*Z. japonica*	*Z. rennelliana*
Zosterops abyssinica	*Z. montana*	*Z. senegalensis*
Z. borbonica	*Z. nigrorum*	*Z. virens*
Z. erythropleura	*Z. novaeguineae*	
Z. everetti	*Z. pallida*	

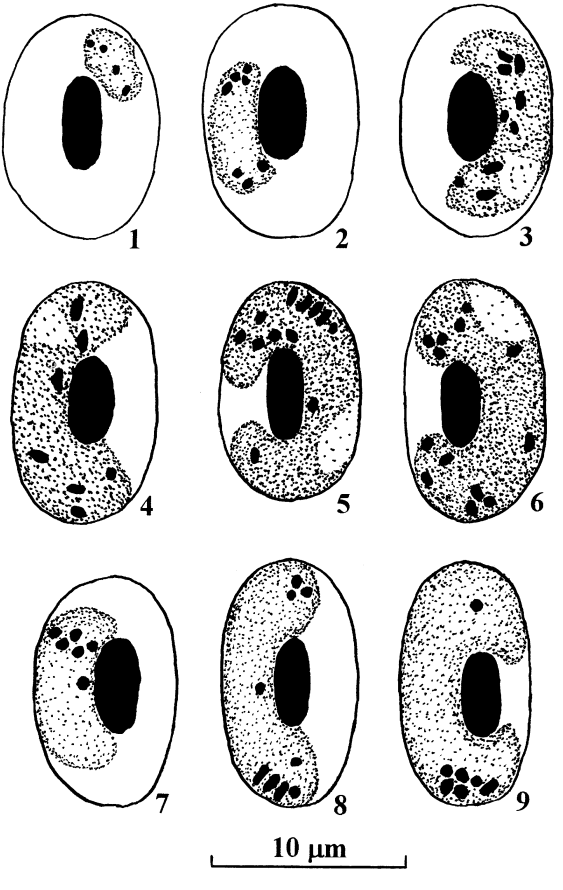

Figure 118 Gametocytes of *Haemoproteus zosteropis* from the blood of *Zosterops palpebrosa: 1*, *2* – young; *3–6* – macrogametocytes; *7–9* – microgametocytes.

Table 78 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. zosteropis* (modified from Bennett and Peirce, 1981)				*H. borgesi* (modified from Greiner *et al.*, 1977)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	45				10		
Length		–	12.0	0.8		11.9	1.0
Width		–	6.8	0.5		6.8	0.4
Length of nucleus		–	5.3	0.3		–	–
Width of nucleus		–	2.2	0.3		–	–
Erythrocyte parasitized by macrogametocyte	45						
Length		–	13.0	1.0		–	–
Width		–	7.3	0.6		–	–
Length of nucleus		–	5.2	0.6		–	–
Width of nucleus		–	2.2	0.3		–	–
Erythrocyte parasitized by microgametocyte	20						
Length		–	13.3	0.9		–	–
Width		–	7.1	0.5		–	–
Length of nucleus		–	5.4	0.5		–	–
Width of nucleus		–	2.3	0.3		–	–
Macrogametocyte	45				15		
Length		–	15.8	1.8		13.2	0.9
Width		–	3.0	0.6		4.0	0.7
Length of nucleus		–	2.1	0.5		3.0	0.3
Width of nucleus		–	1.5	0.4		2.3	0.3
NDR		–	0.8	–		0.04	–
No. of pigment granules		6–19	15.0	2.0		12.0	1.2
Microgametocyte	20				15		
Length		–	15.0	0.9		13.2	1.6
Width		–	2.9	0.7		3.5	0.8
Length of nucleus		–	3.8	0.8		–	–
Width of nucleus		–	2.1	0.5		–	–
NDR		–	0.8	–		0.3	–
No. of pigment granules		6–18	14.0	1.9		10.0	1.4

Note: All sizes are given in micrometres.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Medium and fully grown gametocytes are closely appressed both to the nucleus and the envelope of erythrocytes; they fill the erythrocytes up to their poles. The ends of medium grown gametocytes are rounded. Dumbbell-shaped gametocytes are absent or represent less than 10% of the total number of growing gametocytes. The nucleus in macrogametocytes is subterminal in position. Pigment granules are roundish, oval, and rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, about 15 per gametocyte on average. Large pigment granules are rod-like, but never roundish.

Development in vertebrate host

Young gametocytes (Fig. 118, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 118, *2*), they extend longitudinally along the nucleus, and later also adhere to the envelope of the erythrocytes; the outline is even.

Macrogametocytes (Fig. 118, *3–6*; Table 78). The cytoplasm is finely granular in appearance; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or slightly displace the nucleus laterally and do not encircle it completely; medium and fully grown gametocytes fill the erythrocytes up to their poles (Fig. 118, *4–6*), and they are closely appressed both to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are absent or represent less than 10% of the total number of growing gametocytes; the outline is even; the parasite nucleus is compact, frequently roundish or oval in form, subterminal in position; pigment granules are oval, rod-like, and roundish, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm. It should be noted that large pigment granules are rod-like, but never roundish.

Microgametocytes (Fig. 118, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Haemoproteus zosteropis* has been frequently recorded in mixed infection with *H. killangoi*. These species can be distinguished, first of all, on the basis of the number of pigment granules in their gametocytes. In addition, numerous dumbbell-shaped gametocytes with a highly ameboid outline are common in *H. killangoi*, but they are not characteristic of *H. zosteropis*.

Among the haemoproteids of birds belonging to the Passeriformes, *H. zosteropis* is especially similar to *H. bubalornis*. It can be distinguished from the latter species primarily on the basis of the morphology of its medium grown gametocytes (see 'Comments' to *H. bubalornis*).

49. **Haemoproteus (Parahaemoproteus) pelouroi** Tendeiro, 1946

Haemoproteus pelouroi Tendeiro, 1946 (according to Tendeiro, 1947: 314, Fig. 56–60).

Type vertebrate host. *Bostrychia hagedash* (Latham) (Ciconiiformes).
Additional vertebrate host. *Threskiornis aethiopicus* (Ciconiiformes).
Type locality. Former Portuguese Guinea (West Africa).
Distribution. The Ethiopian zoogeographical region.
Type material. Neohapantotype (No. 105452, *Bostrychia hagedash*, Jonglei, Sudan, M.A. Peirce) is deposited in IRCAH.
Etymology. This species is named in honour of pathoanatomist Dr. Trasmontano Pelouro who died prematurely.

Main diagnostic characters. A parasite of species of the Ciconiiformes whose fully grown gametocytes are elongated and slender, and more or less ameboid in outline. Gametocytes do not displace the nucleus of infected erythrocytes laterally and usually do not touch the nucleus; they never fill the erythrocytes up to their poles and never enclose the nucleus of erythrocytes completely. Pigment granules are roundish and oval, usually of medium (0.5 to 1.0 μm) size, about ten or less per gametocyte on average. The average NDR is about unity.

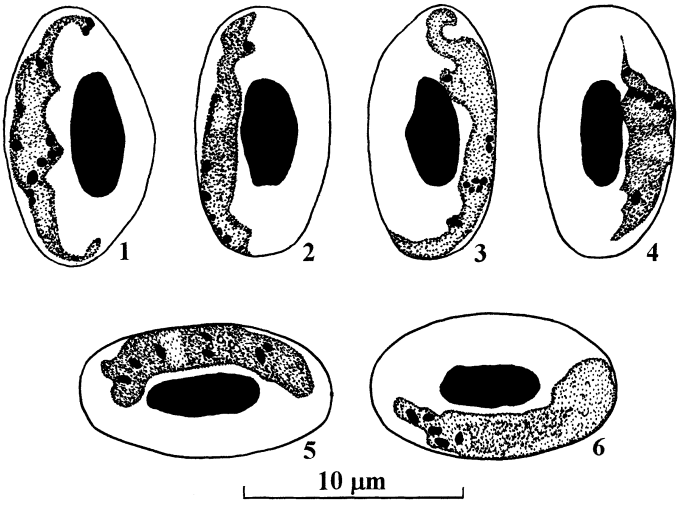

Figure 119 Gametocytes of *Haemoproteus pelouroi* from the blood of *Bostrychia hagedash: 1*, *2*, *4*, *5* – macrogametocytes; *3*, *6* – microgametocytes (*1–3* are modified from Tendeiro, 1947).

Development in vertebrate host

Young gametocytes are usually seen in a position lateral to the nucleus of infected erythrocytes, and they do not touch the nucleus; the outline is more or less ameboid.

Macrogametocytes (Fig. 119, *1*, *2*, *4*, *5*). The cytoplasm is homogeneous in appearance; gametocytes are elongated and slender, they grow along the nucleus of infected erythrocytes and do not displace or only slightly displace the nucleus laterally; NDR is about unity; gametocytes usually adhere to the envelope of erythrocytes but do not touch the erythrocyte nucleus and, as a result, a more or less evident unfilled space (a 'cleft') is usually present between the parasite and the erythrocyte nucleus (Fig. 119, *4*, *5*); the outline is usually ameboid or wavy; the parasite nucleus is variable in form, median or submedian in position; pigment granules are roundish or oval, usually of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; they vary from 5 to 14 (usually about 10). Fully grown gametocytes vary from 11 to 14 μm in length, and from 0.5 to 2.3 μm in width (Bennett *et al.*, 1975b). Infected erythrocytes are not changed significantly in comparison to uninfected erythrocytes.

Microgametocytes (Fig. 119, *3*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

50. **Haemoproteus (Parahaemoproteus) borgesi** Tendeiro, 1947

Haemoproteus borgesi Tendeiro, 1947: 289, Fig. 26–30.

Type vertebrate host. *Campethera punctuligera* (Wagler) (Piciformes).
Additional vertebrate hosts. Some species of the Piciformes (Table 79).
Type locality. Former Portuguese Guinea (West Africa).

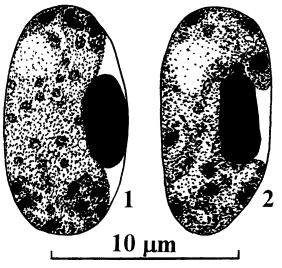

Figure 120 Macrogametocytes of *Haemoproteus borgesi* from the blood of *Picus vittatus* (modified from Greiner *et al*., 1977).

Distribution. The Oriental, Ethiopian, and Neotropical zoogeographical regions. A record of *H. borgesi* in the palearctic *Jynx torquilla* during wintering in India (Nandi and Mandal, 1978) confirms the possibility of the introduction of this haemoproteid to the Palearctic by migratory birds.
Type material was not designated in the original description. Greiner *et al.* (1977) suggested as neotypes the materials which came from a nontype host (*Picus vittatus*) investigated far beyond the type locality (Malaysia). These materials cannot be used as neotypes because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Several additional slides (No. 3126, 86730, low parasitemia, fading staining) are deposited in IRCAH.
Etymology. This species is named in honour of Portuguese parasitologist, Professor Ildefonso Borges.

Table 79 List of vertebrate hosts of *Haemoproteus borgesi.*

Celeus flavescens	*Picus canus*
Dendrocopos mahrattensis	*P. chlorolophus*
Jynx torquilla	*P. flavinucha*
Piculus aurulentus	*P. vittatus*

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally; they enclose the nucleus with their ends, but do not encircle it completely. The average number of pigment granules is about ten per gametocyte. The average length of fully grown gametocytes is less than 18 μm, and the average width, greater than 2 μm. The average NDR is less than 0.5.

Development in vertebrate host
Macrogametocytes (Fig. 120, *1*, *2*; Table 78). The cytoplasm contains small vacuoles and large compact valutin granules; gametocytes markedly displace the nucleus of infected erythrocytes laterally; they enclose the nucleus with their ends, but do not encircle it completely; fully grown gametocytes occupy nearly all available cytoplasmic space in the erythrocytes (Fig. 120, *1*, *2*), and they are closely appressed both to the nucleus and envelope of the erythrocytes; the outline is even; the parasite nucleus is variable in form, subterminal in position; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, obscured by valutin granules; infected erythrocytes are slightly hypertrophied in length (about 4%) and atrophied in width (about 6%) in comparison to uninfected ones.

Microgametocytes. The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; infected erythrocytes are slightly hypertrophied in length (about 7%) and atrophied in width (about 8%) in comparison to uninfected ones; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Piciformes, *H. borgesi* is especially similar to *H. xantholaemae*. It can be distinguished from the latter species primarily on the basis of its (i) smaller number of pigment granules in gametocytes, (ii) smaller average NDR, and (iii) the position of nucleus in macrogametocytes.

The blood film (No. 3126, IRCAH), which was the basis for redescription of *H. borgesi* in the paper by Greiner *et al.* (1977), is fading, and possesses a low parasitemia. New material is required for a more detailed investigation of this species.

51. **Haemoproteus (Parahaemoproteus) buteonis** Wingstrand, 1947

Haemoproteus buteonis Wingstrand, 1947: 15, Fig. 7.

Type vertebrate host. *Buteo buteo* (L.) (Falconiformes).
Additional vertebrate hosts. Some species of the Falconiformes (Table 80).
Type locality. Falsterbo, Skåne, Switzerland.
Distribution. This parasite has been recorded only in the Holarctic so far. It has been more frequently found in the Palearctic where the prevalence of infection usually does not exceed 10% during the warm season of the year.
Type material has never been designated. Designation of neotypes is required. Additional slides are deposited in CDVA.
Etymology. The specific name is derived from the generic name of the type host, *Buteo.*

Table 80 List of vertebrate hosts of *Haemoproteus buteonis.*

Accipiter cooperii	*B. rufinus*
A. nisus	*Circus aeruginosus*
Aquila nipalensis	*Pernis apivorus*
Buteo platypterus	*P. ptilorhynchus*

Main diagnostic characters. A parasite of species of the Falconiformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they enclose the nucleus with their ends but do not encircle it completely. Fully grown gametocytes do not fill the erythrocytes up to their poles where unfilled space is available.

Development in vertebrate host

Young gametocytes (Fig. 121, *1, 2*). The earliest forms can be seen anywhere in infected erythrocytes, are roundish or oval, usually even in outline; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes, extend longitudinally along the nucleus and displace it laterally.

Macrogametocytes (Fig. 121, *3–6*; Table 81). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are frequently present and usually concentrate along the periphery of the parasite; gametocytes grow around the nucleus of erythrocytes, enclose the nucleus with their ends and displace the nucleus laterally, but never encircle it completely; gametocytes are closely appressed to the nucleus of erythrocytes; growing gametocytes usually do not touch the envelope of erythrocytes and, as a result, a clear more or less evident unfilled space (a 'cleft') is frequently available between the gametocyte and the erythrocyte envelope (Fig. 121, *2–4*); fully grown gametocytes do not fill the erythrocytes up to their poles (Fig. 121, *6*); the close

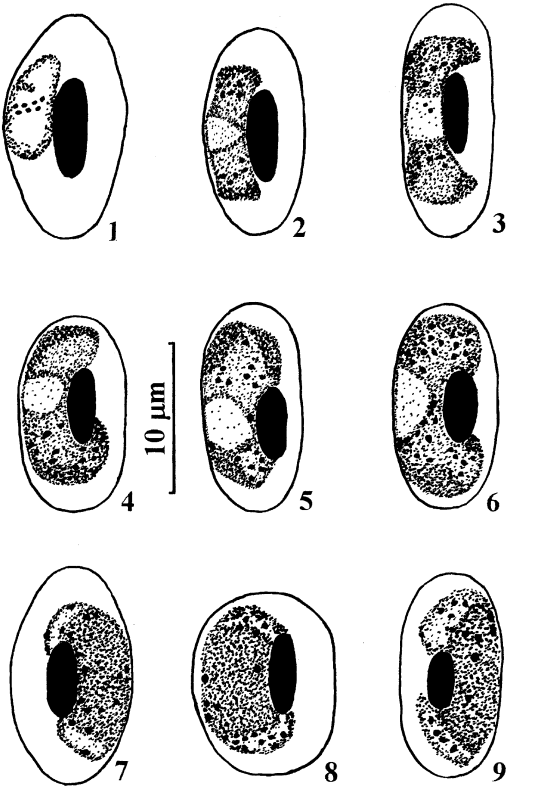

Figure 121 Gametocytes of *Haemoproteus buteonis* from the blood of *Accipiter nisus:* *1*, *2* – young; *3–6* – macrogametocytes; *7–9* – microgametocytes (modified from Valkiūnas and Iezhova, 1989).

adherence of gametocytes to the nucleus of erythrocytes but not to the envelope of the erythrocytes, as well as not filled up the poles of erythrocytes by fully grown gametocytes, are the characteristic features of this species; fully grown gametocytes do not occupy all available cytoplasmic space in the erythrocytes; the outline is even or angular (Fig. 121, *5*), and ends of the gametocytes frequently pointed (Fig. 121, *3*), an ameboid outline is not characteristic; the parasite nucleus is variable in form, median or submedian in position; pigment granules are roundish or oval, of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 121, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. The presence and amount of valutin in gametocytes of the majority of haemoproteid species are variable characters. Taken separately, as a rule, these characters cannot be used for the identification of *H. buteonis* and other species.

Peirce *et al.* (1990) synonymized *H. buteonis* with *H. elani* because, in their opinion, the illustrations of gametocytes of *H. buteonis* in the original description are very similar to *H. elani*. Actually, the gametocytes of these two species have similarities. However, detailed analysis also reveals some clear differences. First, gametocytes of *H. buteonis* are always closely appressed to

Table 81 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. buteonis* (according to Valkiūnas and Iezhova, 1989)				*H. pratasi* (modified from Bennett and Peirce, 1989)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	22				40		
Length		11.3–15.0	14.1	0.6		14.3	1.3
Width		6.0–9.3	7.1	0.4		7.2	0.7
Length of nucleus		4.9–7.5	6.0	0.2		4.9	0.4
Width of nucleus		2.0–3.4	2.3	0.1		2.2	0.3
Erythrocyte parasitized by macrogametocyte	24				40		
Length		11.7–16.1	14.9	0.4		14.5	1.2
Width		6.1–9.7	7.5	0.2		7.5	0.7
Length of nucleus		3.6–6.7	5.3	0.4		5.1	0.8
Width of nucleus		1.6–2.5	2.0	0.1		2.3	0.3
Erythrocyte parasitized by microgametocyte	17				15		
Length		11.8–15.7	13.4	0.6		14.3	1.1
Width		5.8–9.9	7.1	0.4		7.7	0.8
Length of nucleus		3.4–6.0	4.8	0.4		5.1	0.5
Width of nucleus		1.7–2.6	2.0	0.1		2.2	0.3
Macrogametocyte	24				40		
Length		11.1–20.5	15.1	0.8		14.7	1.7
Width		2.4–3.9	3.3	0.4		3.9	0.8
Length of nucleus		2.2–4.9	3.4	0.2		3.0	0.5
Width of nucleus		1.3–2.9	2.2	0.2		1.9	0.4
NDR		0.3–0.8	0.5	0.1		0.5	0.2
No. of pigment granules		8–17	11.5	1.8		19.3	2.3
Microgametocyte	17				15		
Length		10.2–18.1	13.9	0.8		15.3	1.5
Width		2.4–4.7	3.3	0.4		4.0	0.7
Length of nucleus		6.1–10.2	7.2	0.8		5.6	0.9
Width of nucleus		2.2–4.1	3.1	0.4		2.6	0.3
NDR		0.4–0.8	0.6	0.1		0.6	0.2
No. of pigment granules		8–16	11.0	1.6		18.6	2.4

Note: All sizes are given in micrometres.

the nucleus of infected erythrocytes, and this is not characteristic of *H. elani*. Second, fully grown gametocytes of *H. elani* fill the erythrocytes up to their poles, and this is not characteristic of *H. buteonis* (see Fig. 121, *6, 9*). Third, gametocytes of *H. elani* are always closely appressed to the envelope of erythrocytes, but gametocytes of *H. buteonis* frequently do not. *Haemoproteus buteonis* should be considered a distinct species (see also ‘Comments’ to *H. elani*).

52. **Haemoproteus (Parahaemoproteus) pratasi** Tendeiro, 1947

Haemoproteus pratasi Tendeiro, 1947: 326, Fig. 66–68. – *H. silvai* Son, 1960: 776, Pl. 1, Fig. 2, 3, 5, 6, Pl. 3, Fig. 8–11, Pl. 5, Fig. 1, 3–5, Pl. 6, Fig. 8, 9. – *H. pratasi*: Bennett and Peirce, 1989: 1562 (=*H. silvai*).

Type vertebrate host. *Numida meleagris* (L.) (Galliformes).
Additional vertebrate host. *Guttera edouardi* (Galliformes).
Type locality. Former Portuguese Guinea (West Africa).
Distribution. The Ethiopian zoogeographical region.
Type material. Neohapantotype (No. 36762, *Numida meleagris*, 19.07.1952, Kundelungu, Democratic Republic of Congo, M. Lips) is deposited in IRCAH.
Etymology. This species is named in honour of Dr. Abel Pratas, who was the leader of the veterinary service in Angola for a long period.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes displace the nucleus of infected erythrocytes laterally; they enclose the nucleus with their ends, but do not encircle it completely. Dumbbell-shaped gametocytes are absent. The outline of fully grown gametocytes is even. The average number of pigment granules is about 20 per gametocyte. The average NDR is less than 0.7.

Development in vertebrate host

Young gametocytes (Fig. 122, *4*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes and they usually do not touch the nucleus and envelope of erythrocytes (Fig. 122, *4*); the outline varies from even to wavy and highly ameboid.

Macrogametocytes (Fig. 122, *1*, *2*; Table 81). The cytoplasm is homogeneous in appearance, frequently contains vacuoles; gametocytes grow around the nucleus of erythrocytes, they markedly enclose the nucleus with their ends, displace the nucleus

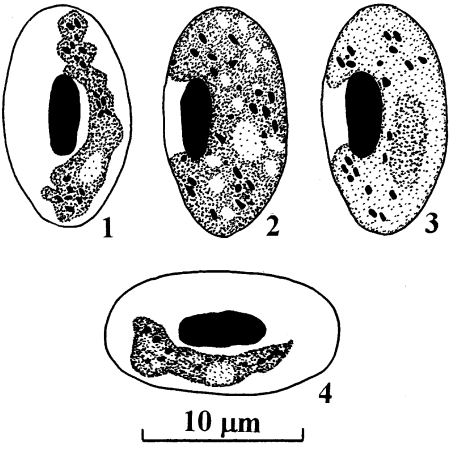

Figure 122 Gametocytes of *Haemoproteus pratasi* from the blood of *Numida meleagris:*
1, *2* – macrogametocytes; *3* – microgametocyte; *4* – young; (*1–3* are modified from Bennett and Peirce, 1989).

laterally but do not encircle it completely; growing gametocytes frequently lie free in the cytoplasm and do not touch the nucleus and envelope of erythrocytes (Fig. 122, *1*); dumbbell-shaped gametocytes are absent; fully grown gametocytes fill the erythrocytes up to their poles and are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 122, *2*); the outline of mature gametocytes is usually even; the parasite nucleus is variable in form, frequently roundish or oval, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 122, *3*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

53. **Haemoproteus (Parahaemoproteus) sequeirae** Tendeiro, 1947

Haemoproteus sequeirae Tendeiro, 1947: 304, Fig. 64, 65.

Type vertebrate host. *Nectarinia coccinigaster* (Latham) (Passeriformes).
Additional vertebrate hosts. *Anthreptes malacensis* (Passeriformes). The range of the additional hosts (Bennett *et al.*, 1985; Bishop and Bennett, 1992) should be defined more precisely because at least two species of haemoproteids are present in the blood films which were the basis for the redescription of *H. sequeirae* (see 'Type material').
Type locality. Former Portuguese Guinea (West Africa).
Distribution. This parasite has been recorded in West Africa and Malaysia. It is likely that it is common in the Ethiopian and Oriental zoogeographical regions.
Type material was not designated in the original description. Two species of haemoproteids

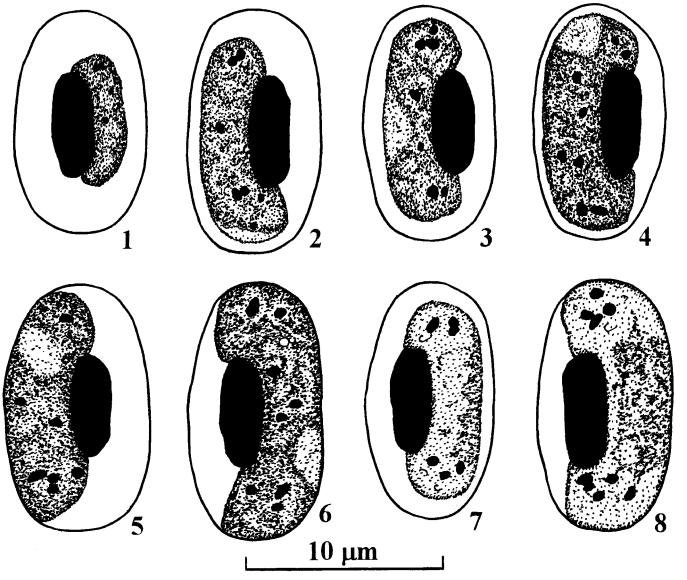

Figure 123 Gametocytes of *Haemoproteus sequeirae* from the blood of *Anthrepetes malacensis: 1* – young; *2–6* – macrogametocytes; *7*, *8* – microgametocytes.

are present in neotypes designated by Bennett *et al.* (1985). The neohapantotype slide No. 17978 contains numerous gametocytes with a highly ameboid outline, and dumbbell-shaped forms are common among them, but medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin (Fig. 123, *4*), are not found in this blood film. In other words, the neohapantotype contains the parasite whose gametocytes are different from the original description (Tendeiro, 1947), and this parasite cannot be attributed to *H. sequeirae*. Thus, the neohapantotype No. 17978 should be dismissed. Paraneohapantotypes No. 5808, A, B, C, E, F, G, H, which were designated together with the neohapantotype, are of good quality, and they contain gametocytes of *H. sequeirae*. The description of the parasite, which is given below, is based on the slides No. 5808, A, B, C. However, the paraneohapantotypes came from a nontype host (*Anthrepetes malacensis*) investigated far beyond the type locality (Malaysia) and thus, they are invalid as a neotype material because they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of neotypes is required.

Etymology. This species is named in honour of Professor Fontoura de Sequeira.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed to the envelope of erythrocytes, and they fill the erythrocytes up to their poles. Dumbbell-shaped gametocytes are absent. The outline of gametocytes is even. Pigment granules are roundish, oval, and rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, about eight per gametocyte on average. The average NDR is less than 0.7.

Development in vertebrate host

Young gametocytes (Fig. 123, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend along the nucleus not touching the envelope of erythrocytes; the outline is even.

Macrogametocytes (Fig. 123, *2–6*). The cytoplasm is finely granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes; they slightly displace the nucleus laterally but never encircle it completely; medium grown gametocytes are closely appressed to the nucleus of erythrocytes but usually do not touch the envelope of erythrocytes along their entire margin (Fig. 123, *2–4*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, and they fill the erythrocytes up to their poles (Fig. 123, *6*); dumbbell-shaped gametocytes are not present; the outline is usually even or slightly wavy; the parasite nucleus is variable in form and in position, but is most frequently seen in a subterminal position; pigment granules are roundish, oval and rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm; the number of pigment granules ($n = 20$) varies from 4 to 12 (on average 7.2±0.8 per gametocyte); the average length of gametocytes is 13 μm, and the average width 3 μm; the average NDR is about 0.5.

Microgametocytes (Fig. 123, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Bennett *et al.* (1985) have carried out an extensive morphometric analysis of gametocytes which are present in the type material designated by these authors. According to our observations, this analysis is based on two different species of haemoproteids (see 'Type material').

That is why the morphometric data mentioned above were not used here for the description of *H. sequeirae.*

Among the haemoproteids of birds belonging to the Passeriformes, *H. sequeirae* is especially similar to *H. formicarius*. Fully grown macrogametocytes of *H. sequeirae* fill the erythrocytes up to their poles; this character was not seen in macrogametocytes of *H. formicarius*. Furthermore, the average number of pigment granules in gametocytes *H. sequeirae* is approximately half as many as in *H. formicarius*.

Haemoproteus sequeirae is also similar to *H. sanguinis* and *H. otocompsae.* It can be distinguished from the two latter species primarily on the basis of the larger size of the pigment granules in its gametocytes.

54. **Haemoproteus (Parahaemoproteus) globulosus** Covaleda Ortega and Gállego Berenguer, 1950

Haemoproteus globulosus Covaleda Ortega and Gállego Berenguer, 1950: 163, Pl. 3, Fig. 1–16.

Type vertebrate host. *Carduelis carduelis* (L.) (Passeriformes).
Type locality. Granada, Spain.
Distribution has not been investigated. This parasite has so far been recorded only in the type locality.
Type material has never been designated.
Etymology. The specific name reflects the globe-like shape of its fully grown gametocytes and their host cells.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes and finally completely

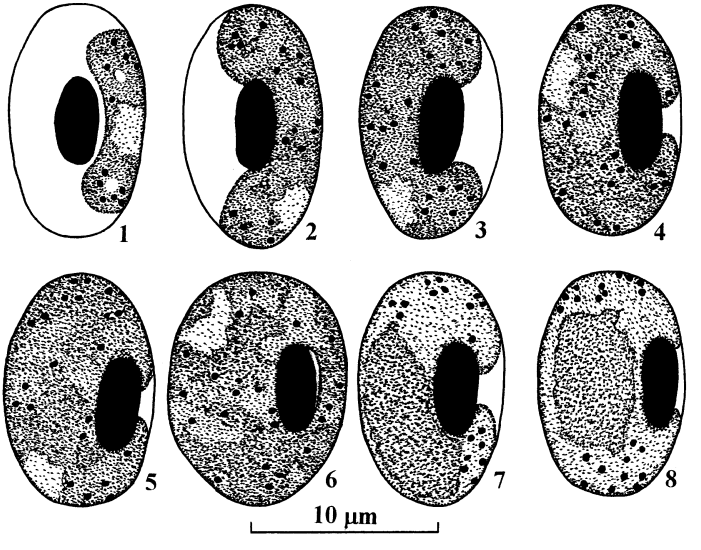

Figure 124 Gametocytes of *Haemoproteus globulosus* from the blood of *Carduelis carduelis: 1* – young; *2–6* – macrogametocytes; *7*, *8* – microgametocytes (modified from Covaleda Ortega and Gállego Berenguer, 1950).

enclose the nucleus. Gametocytes do not possess, or possess only a few, vacuoles. Medium grown and fully grown gametocytes are closely appressed both to the nucleus and envelope of infected erythrocytes. Pigment granules are of small (<0.5 μm) size, and their average number in gametocytes is greater than 18 but less than 30.

Development in vertebrate host

The description of gametocytes, which is given below, is modified from the original description of this species (Covaleda Ortega and Gállego Berenguer, 1950).

Young gametocytes (Fig. 124, *1*) are seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus; the outline is even.

Macrogametocytes (Fig. 124, *2–6*) grow around the nucleus of erythrocytes and finally completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, they do not possess, or possess a few, vacuoles; the outline is even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are small (<0.5 μm), randomly scattered throughout the cytoplasm, vary from 18 to 25 (usually 22 to 24).

Microgametocytes (Fig. 124, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the number of pigment granules varies from 17 to 22 (usually 18 to 19); other characters are as for macrogametocytes.

Comments. According to current knowledge, the gametocytes completely encircling the nucleus of erythrocytes, and the numerous small pigment granules in the gametocytes, are the main diagnostic characters of *H. globulosus*.

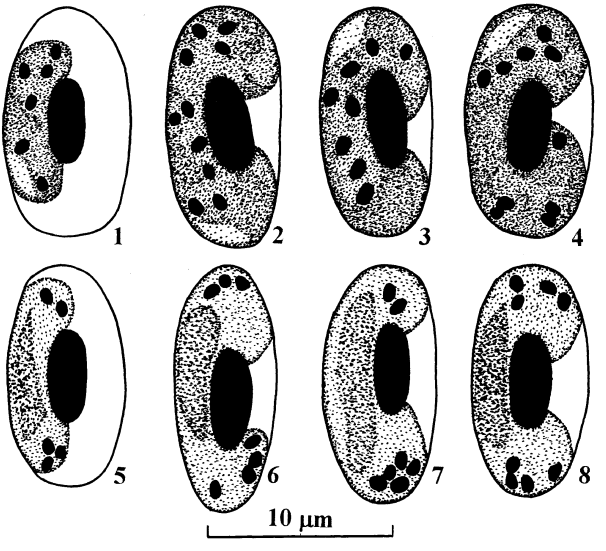

Figure 125 Gametocytes of *Haemoproteus macropigmentatus* from the blood of *Carduelis carduelis:*
1 – young; *2–4* – macrogametocytes; *5–8* – microgametocytes (modified from Covaleda Ortega and Gállego Berenguer, 1950).

Burry-Caines and Bennett (1992) believe that the original description of *H. globulosus* is based on the material from dead birds, and they think that the presence of globe-like gametocytes in the original description is due to the onset of gametogenesis. Based on this argument, Burry-Caines and Bennett (1992) synonymized *H. globulosus* with *H. chloriis* (=*H. fringillae*). Some signs of the onset of gametogenesis are indeed available in the illustrations of gametocytes in the original description of *H. globulosus* (Covaleda Ortega and Gállego Berenguer, 1950). As a result, the globe-like shape of infected erythrocytes (Fig. 124, *6*) is, most probably, connected with the process of rounding up because of the onset of gametogenesis. Thus, at present this character cannot be recommended for characterization of *H. globulosus*. However, such important characters of this species as the number and size of pigment granules in gametocytes, and the presence of circumnuclear gametocytes, are not connected with the onset of gametogenesis. Based on these characters, *H. globulosus* can be easily distinguished from *H. fringillae* and the majority of other species of haemoproteids of birds belonging to the Passeriformes.

It should be noted that *H. globulosus* has been recorded only once, and the redescription of this parasite is required. Among the haemoproteids of birds belonging to the Passeriformes, *H. globulosus* is especially similar to *H. nipponensis*. It can be distinguished from the latter species primarily on the basis of the peculiarities of vacuolization of cytoplasm in macrogametocytes. However, the taxonomic value of this character is questionable.

55. **Haemoproteus (Parahaemoproteus) macropigmentatus** Covaleda Ortega and Gállego Berenguer, 1950

Haemoproteus macropigmentatus Covaleda Ortega and Gállego Berenguer, 1950: 162, Pl. 2, Fig. 15–24.

Type vertebrate host. *Carduelis carduelis* (L.) (Passeriformes).
Additional vertebrate host. *Acanthis flammea, Serinus gularis* (Passeriformes).
Type locality. Granada, Spain.
Distribution has not been investigated. This parasite has been recorded in the type locality, in South Africa and Canada.
Type material has never been designated.
Etymology. The specific name reflects the large size of pigment granules in gametocytes.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends but do not encircle it completely. Medium grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes have not been recorded. Pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, less than 12 per gametocyte on average. Roundish and large (1.0 to 1.5 μm) pigment granules are present.

Development in vertebrate host

The description of gametocytes, which is given below, is modified from the original description of this species (Covaleda Ortega and Gállego Berenguer, 1950).

Young gametocytes (Fig. 125, *1*) are seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus and adhere both to the nucleus and the envelope of erythrocytes; the outline is even; the pigment granules reach a large size even in growing gametocytes.

Macrogametocytes (Fig. 125, *2–4*) grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends but do not encircle it completely; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, and they fill the erythrocytes up to their poles; dumbbell-shaped gametocytes have not been recorded; the outline is even; the parasite nucleus is subterminal in position, varies from 2.5 to 3.0 μm in length, and from 1.0 to 1.5 μm in width; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm, vary usually from 7 to 11; the nucleus of infected erythrocytes is slightly rotated with respect to the normal axis (Fig. 125, *2*, *4*).

Microgametocytes (Fig. 125, *5–8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules usually vary from six to nine; other characters are as for macrogametocytes.

Comments. According to current knowledge, the gametocytes markedly encircling the nucleus of erythrocytes and the large pear-like pigment granules in gametocytes are main diagnostic characters of *H. macropigmentatus*.

Burry-Caines and Bennett (1992) believe that compact valutin granules were mixed up with the pigment granules in the original description of *H. macropigmentatus*, and they synonymized *H. macropigmentatus* with *H. chloriis* (=*H. fringillae*). It is difficult to agree with this for the following reasons. First, compact pear-like valutin granules are not characteristic of haemoproteids of passeriform birds. Furthermore, valutin granules have been only occasionally recorded in gametocytes of haemoproteids in birds of the family Fringillidae, to which the type host of *H. macropigmentatus* belongs (Burry-Caines and Bennett, 1992). Second, the original description of *H. macropigmentatus* is quite complete, and it contains good illustrations (Covaleda Ortega and Gállego Berenguer, 1950). In addition, several other species of haemoproteids are also described in the same paper, and the morphology of pigment granules is stressed repeatedly, especially in the illustrations. It seems unlikely that only valutin granules were shown in the illustrations of *H. macropigmentatus*, and the pigment granules are completely missed. Gametocytes of *H. macropigmentatus* have several distinctive characteristics, and, at present, it is logical to consider this parasite as a distinct species. The redescription of the parasite is required. It should be noted that this parasite was recorded in South Africa and Canada (Earlé *et al.*, 1991a; Bennett *et al.*, 1992a; Seutin, 1994).

56. **Haemoproteus (Parahaemoproteus) montezi** Travassos Santos Dias, 1953

Haemoproteus montezi Travassos Santos Dias, 1953: 75, Pl. 1, Fig. 16, Pl. 2, Fig. 17–19.

Type vertebrate host. *Tauraco porphyreolophus* (Vigors) (Musophagiformes).
Additional vertebrate hosts. *Corythaixoides concolor*, *Musophaga violacea*, *Tauraco hartlaubi*, *T. livingstonii* (Musophagiformes).
Type locality. Mozambique, Africa.
Distribution. The Ethiopian zoogeographical region.
Type material. Neohapantotype (No. 39042a, *Tauraco hartlaubi*, March 1939, Kabete, Kenya, C.M. Herman) and paraneohapantotypes (No. 39042b, other data are as for the neohapantotype; No. 36767, *T. livingstonii*, 21.02.1956, Lumumbashi, Zaire, M. Lips) are deposited in IRCAH.
Etymology. This species is named in honour of Caetano de Carvalho Montez.

Main diagnostic characters. A parasite of species of the Musophagiformes whose fully grown gametocytes only slightly enclose the nucleus of infected erythrocytes,

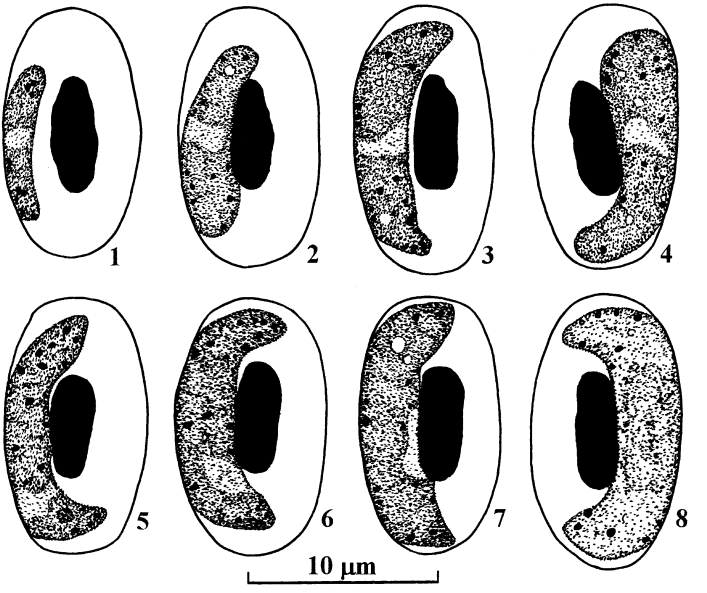

Figure 126 Gametocytes of *Haemoproteus montezi* from the blood of *Tauraco hartlaubi:* *1* – young; *2–7* – macrogametocytes; *8* – microgametocyte.

and they tend to displace the nucleus longitudinally slightly toward one pole of the erythrocytes. The ends of gametocytes are usually more or less narrowed.

Development in vertebrate host

Young gametocytes (Fig. 126, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus; they are usually seen in a position lateral to the erythrocyte nucleus; growing gametocytes usually adhere to the envelope of erythrocytes but do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is usually available between the parasite and the erythrocyte nucleus (Fig. 126, *1*); the outline is even.

Macrogametocytes (Fig. 126, *2–7*; Table 82). The cytoplasm is granular in appearance, frequently contains small clear vacuoles; valutin granules are usually present and gather at the ends of the parasite; gametocytes only slightly enclose the nucleus of infected erythrocytes and never encircle it completely; the erythrocyte nucleus is not displaced or only slightly displaced laterally; however, gametocytes tend to displace the erythrocyte nucleus longitudinally slightly toward one pole of erythrocytes (Fig. 126, *3*, *6*), with the parasite frequently looping over one end of the erythrocyte nucleus but not the other, presenting an asymmetric form (Fig. 126, *4*, *5*) (both features mentioned are rare characters for bird haemoproteids); the ends of the gametocytes are usually more or less narrowed; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 126, *7*) but growing forms, not touching the nucleus of erythrocytes (Fig. 126, *3*) or only slightly touching the nucleus (Fig. 126, *5*), are common; the outline is even; the parasite nucleus is compact, variable in form and position, but most frequently seen in a median or submedian position (Fig. 126, *2–7*); pigment granules are roundish, of small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 126, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

57. **Haemoproteus (Parahaemoproteus) enucleator** Bennett, Okia, Ashford and Campbell, 1972

Haemoproteus enucleator Bennett, Okia, Ashford and Campbell, 1972: 1143, Fig. 1–7.

Type vertebrate host. *Ispidina picta* (Bodd.) (Coraciiformes).
Type locality. Entebbe, Uganda.
Distribution. The Ethiopian zoogeographical region.
Type material. Hapantotype (No. IB 1, *Ispidina picta*, 29.10.1971, Entebbe, Uganda, N.O. Okia) and parahapantotypes (4 blood smears from the type host in Uganda) are deposited in IRCAH.
Etymology. The specific name reflects the ability of gametocytes to enucleate infected erythrocytes.

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes enucleate infected erythrocytes. The outline of gametocytes is even. The average number of pigment granules is about 15 per gametocyte. Infected erythrocytes are significantly hypertrophied in length but unchanged in width in comparison to uninfected ones.

Development in vertebrate host
Young gametocytes (Fig. 127, *1*, *2*; Table 83). The earliest forms can be seen anywhere in infected erythrocytes and are frequently recorded in a polar or subpolar position in the erythrocytes (Fig. 127, *1*); as the parasite develops, gametocytes extend along the nucleus

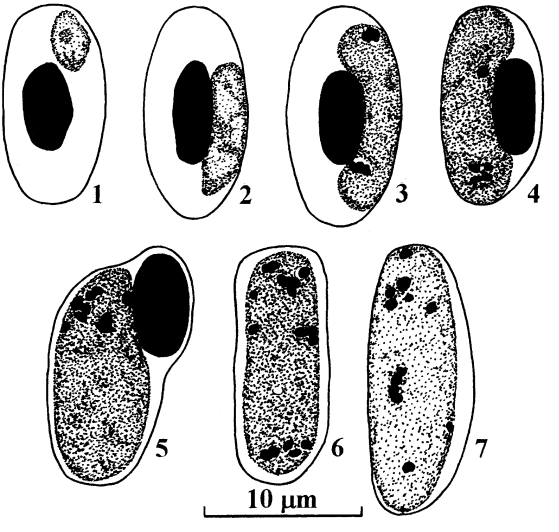

Figure 127 Gametocytes of *Haemoproteus enucleator* from the blood of *Ispidina picta:*
1, *2* – young; *3–6* – macrogametocytes; *7* – microgametocyte (modified from Bennett *et al*., 1972).

Table 82 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. montezi* (modified from Bennett and Peirce, 1990a)			*H. fallisi* (modified from Bennett *et al.*, 1991b)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	35			240		
Length		13.4	0.8		12.2	0.8
Width		7.4	0.6		6.2	0.3
Length of nucleus		6.0	0.8		5.1	0.6
Width of nucleus		2.2	0.3		1.8	0.2
Erythrocyte parasitized by macrogametocyte	35			25		
Length		13.5	1.2		12.9	0.6
Width		7.6	0.6		6.4	0.4
Length of nucleus		6.0	0.6		4.9	0.5
Width of nucleus		2.3	0.3		2.0	0.2
Erythrocyte parasitized by microgametocyte	10			14		
Length		14.0	1.0		13.0	1.0
Width		8.1	0.7		6.4	0.6
Length of nucleus		6.1	0.5		5.0	0.6
Width of nucleus		2.3	0.3		2.0	0.3
Macrogametocyte	35			25		
Length		14.2	1.5		11.8	1.2
Width		3.4	0.6		2.6	0.3
Length of nucleus		3.2	0.8		2.5	0.6
Width of nucleus		2.1	0.5		1.9	0.3
NDR		0.8	0.2		0.8	0.1
No. of pigment granules		16.3	1.5		13.4	1.5
Microgametocyte	10			14		
Length		14.2	1.1		13.0	1.3
Width		3.5	0.5		2.6	0.3
Length of nucleus		6.3	1.0		6.7	1.0
Width of nucleus		3.3	0.5		2.0	0.4
NDR		0.8	0.2		0.8	0.1
No. of pigment granules		16.5	2.0		13.2	1.5

Note: All sizes are given in micrometres.

of erythrocytes, and at this stage, they are closely appressed to the nucleus and envelope of the erythrocytes (Fig. 127, *2*); the outline is even; pigment granules in the largest gametocytes are occasionally clumped.

Macrogametocytes (Fig. 127, *3–6*; Table 83). The cytoplasm is homogeneous in appearance, usually lacking vacuoles; growing gametocytes markedly displace the nucleus of erythrocytes laterally (Fig. 127, *4*) and then toward one pole of the erythrocytes (Fig. 127, *5*), and finally they eliminate the nucleus from infected cells (Fig. 127, *6*); fully grown gametocytes are cigar-shaped bodies extending within an elongated erythrocytic

Table 83 Morphometric parameters of gametocytes and host cells of *Haemoproteus enucleator* (n = 50) (modified from Bennett *et al.*, 1972).

Feature	lim	$\overline{X}$	*SD*
Uninfected erythrocyte			
Length	–	13.6	0.8
Width	–	7.2	0.6
Parasitized erythrocyte			
Length	–	16.4	1.4
Width	–	7.4	1.2
Gametocyte			
Length	–	14.2	1.4
Width	–	4.8	0.5
No. of pigment granules	12–17	14.8	3.0

Note: All sizes are given in micrometres.

remnant; they usually lie free in the cytoplasm and do not touch the envelope of erythrocytes (Fig. 127, *6*); the outline is even; the parasite nucleus markedly varies in shape and position; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm or aggregated in loose clumps; infected erythrocytes are markedly hypertrophied in length (20 to 25%) and statistically unchanged in width in comparison to uninfected ones.

Microgametocytes (Fig. 127, *7*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Coraciiformes, *H. enucleator* is especially similar to *H. gavrilovi* and *H. lairdi*. It can be distinguished from *H. gavrilovi*, particularly, on the basis of having more numerous pigment granules in its gametocytes. Gametocytes of *H. lairdi* induce marked atrophy of infected erythrocytes in width, and this is not characteristic of *H. enucleator*.

58. **Haemoproteus (Parahaemoproteus) fallisi** Bennett and Campbell, 1972

Haemoproteus fallisi Bennett and Campbell, 1972: 1271, Fig. 1–6. – *H. rhipiduris* Bennett, Bishop and Peirce, 1991b: 31, Fig. 13, 14. – *H. fallisi*: Valkiūnas, 1997: 259 (=*H. rhipiduris*).

Type vertebrate host. *Turdus migratorius* (L.) (Passeriformes).
Additional vertebrate hosts. Numerous species of the Passeriformes, mainly belonging to the Turdidae (over 50 species).
Type locality. St. John's, Newfoundland, Canada.
Distribution. The Holarctic, the Neotropical, Ethiopian, and Oriental zoogeographical regions. It is likely that this parasite is cosmopolitan in distribution.
Type material. Hapantotype (No. 21819, *Turdus migratorius*, 10.06.1971, St. John's, Newfoundland, G.F. Bennett) and parahapantotypes (other data are as for the hapantotype) are deposited in IRCAH.

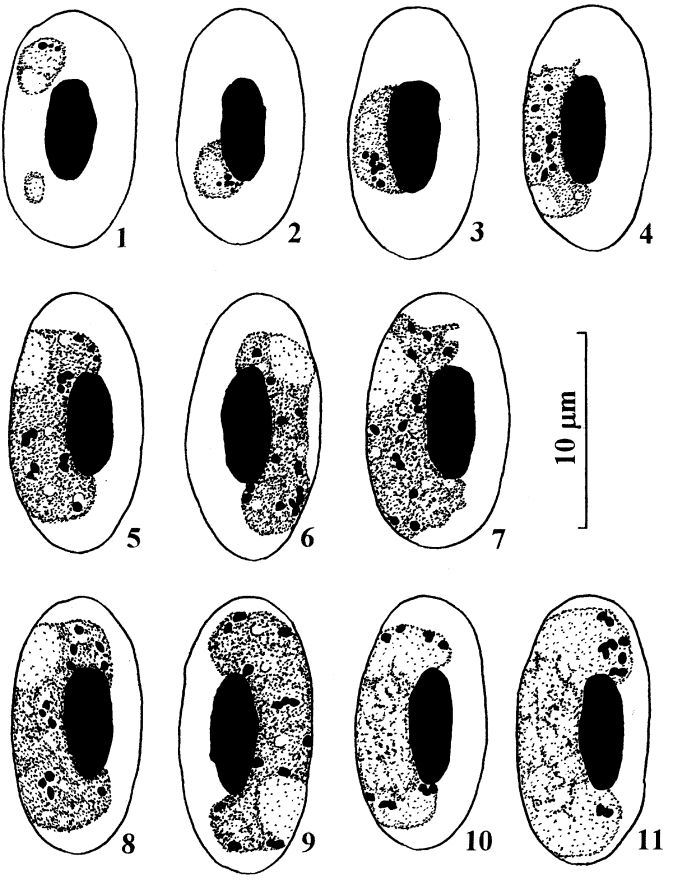

Figure 128 Gametocytes of *Haemoproteus fallisi* from the blood of *Turdus pilaris:* *1–4* – young; *5–9* – macrogametocytes; *10*, *11* – microgametocytes (modified from Valkiūnas and Iezhova, 1992c).

Etymology. This species is named in honour of Professor A. Murray Fallis in recognition of his contribution to the field of avian blood parasitology.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes and never encircle the nucleus completely. Medium and fully grown gametocytes adhere both to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent or represent less than 10% of the total number of growing gametocytes. The nucleus in fully grown gametocytes is subterminal in position. Fully grown gametocytes do not fill the erythrocytes up to their poles. Pigment granules are of medium (0.5 to 1.0 µm) and sometimes small (<0.5 µm) size, about 13 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 128, *1–4*). The earliest forms are frequently seen in a polar or subpolar position in infected erythrocytes lying free in the cytoplasm (Fig. 128, *1*); as the

parasite develops, gametocytes adhere to the nucleus of erythrocytes usually at its terminal part (Fig. 128, *2*), and then extend along the nucleus longitudinally (Fig. 128, *3*); the outline of the earliest forms is even (Fig. 128, *1–3*), and the advanced gametocytes are both even and ameboid (Fig. 128, *4*) in outline.

Macrogametocytes (Fig. 128, *5–9*; Table 82). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles; valutin granules are not characteristic; gametocytes grow along the nucleus of erythrocytes and never encircle the nucleus completely, as a rule, they are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 128, *5*, *7–9*); however, occasionally the central part of the pellicle of growing gametocytes does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 128, *6*); if present, the dumbbell-shaped gametocytes represent less than 10% of the total number of growing gametocytes; gametocytes shown in Fig. 128, *5*, *9* are especially characteristic of this species; fully grown gametocytes do not fill the erythrocytes up to their poles (Fig. 128, *5–9*); the outline is even (Fig. 128, *5*, *6*) or angular (Fig. 128, *9*), sometimes ameboid (Fig. 128, *7*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are usually roundish, but sometimes oval, of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 128, *10*, *11*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. It should be noted that gametocytes of *H. fallisi* are small in size. Fully grown gametocytes do not fill erythrocytes up to their poles (Fig. 128, *8*, *9*). This character should be kept in mind in the identification of this species. Among the haemoproteids of birds belonging to the Passeriformes, *H. fallisi* is especially similar to *H. africanus* and *H. beckeri*, and can be distinguished from *H. africanus,* particularly, on the basis of subterminal position of nucleus in its macrogametocytes. Gametocytes of *H. beckeri* possess large (1.0 to 1.5 μm), rod-like pigment granules, but those of *H. fallisi* do not.

Bennett *et al.* (1991b) described *H. rhipiduris* as a distinct species mainly on the basis that this parasite was recorded in passerine birds of the subfamily Rhipidurinae. According to the original description, the morphology of gametocytes of this parasite and peculiarities of their influence on infected erythrocytes are the same as for *H. fallisi*. The hapantotype is fading and contain low parasitemia. Investigation of the hapantotype showed that gametocytes of *H. rhipiduris* are identical to gametocytes of *H. fallisi*. Taken separately, the record of *H. rhipiduris* in the passerine birds belonging to the subfamily Rhipidurinae provides insufficient data for the description of new species (see the General Section, p. 69). Thus, before additional information is available, *H. rhipiduris* should be considered as a junior synonym of *H. fallisi*.

59. **Haemoproteus (Parahaemoproteus) larae** Yakunin, 1972

Haemoproteus larae Yakunin, 1972: 72. – *H. lari*: Levine, 1985: 361 (emend. pro *larae*).

T y p e v e r t e b r a t e h o s t. *Larus ridibundus* (L.) (Charadriiformes).
A d d i t i o n a l v e r t e b r a t e h o s t. *Larus argentatus*, *L. audouinii, L. cachinnans, L. fuscus*, *Sterna albifrons*, *S. hirundo* (Charadriiformes).
T y p e l o c a l i t y was not specified in the original description in detail. It is South-East Kazakhstan.
D i s t r i b u t i o n. So far, this parasite has been recorded in the Palearctic and in the Ethiopian zoogeographical region.

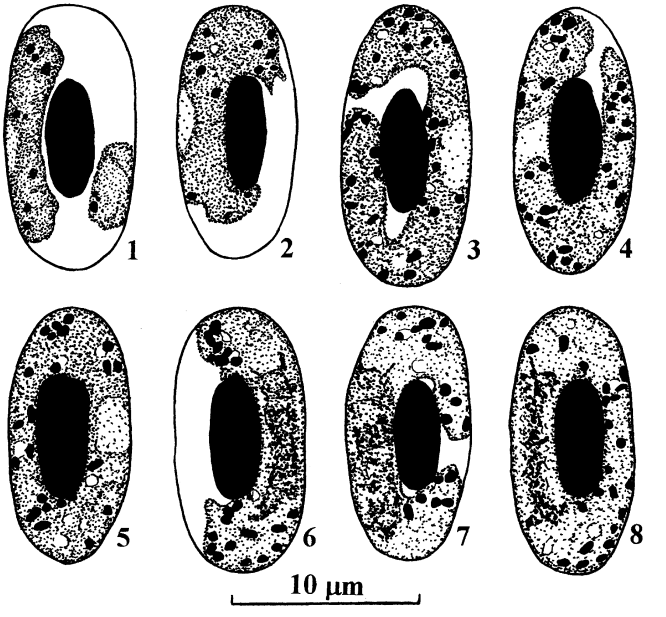

Figure 129 Gametocytes of *Haemoproteus larae* from the blood of *Larus ridibundus:* *1* – young; *2–5* – macrogametocytes; *6–8* – microgametocytes.

Type material was not designated in the original description. Peirce (1981c) redescribed this species on the basis of material which came from *Larus fuscus* investigated in England. This material cannot be used as a neotype because it does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of neotypes is required. A series of additional slides is deposited in IRCAH, and slide No. 86293 is of especially good quality among them.
Etymology. The specific name is derived from the generic name of the type host, *Larus*.

Main diagnostic characters. A parasite of species of the Charadriiformes whose gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends and finally completely encircle it and occupy all available cytoplasmic space in the erythrocytes. The maximum number of pigment granules in macrogametocytes is greater than 30.

Development in vertebrate host
Young gametocytes (Fig. 129, *1*). The earliest forms can be seen anywhere in infected erythrocytes, are oval or roundish; as the parasite develops, gametocytes extend longitudinally along the nucleus; they usually touch both the nucleus and envelope of erythrocytes, but forms which do not touch the erythrocyte nucleus are also present (Fig. 129, *1*); the outline is even or wavy, but occasionally slightly ameboid.

Macrogametocytes (Fig. 129, *2–5*; Table 84). The cytoplasm is homogeneous or slightly granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes and do not displace or only slightly displace the nucleus laterally; they markedly enclose the nucleus with their ends (Fig. 129, *3*) and finally completely encircle it and occupy all available cytoplasmic space in the erythrocytes (Fig. 129, *5*); the outline is usually even, but sometimes wavy or slightly ameboid; the

Table 84 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. larae*				*H. balearicae* (modified from Peirce, 1973; Bennett *et al.*, 1975a)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	33				40			
Length		10.2–14.9	13.2	0.7		–	15.3	1.0
Width		5.7–7.7	7.0	0.5		–	7.0	0.5
Length of nucleus		5.0–7.1	6.1	0.2		–	7.5	0.6
Width of nucleus		1.7–3.4	2.9	0.2		–	2.8	0.3
Erythrocyte parasitized by macrogametocyte	33				40			
Length		11.8–16.1	13.9	0.8		–	15.4	1.0
Width		6.0–7.8	6.8	0.3		–	7.0	0.7
Length of nucleus		5.4–6.9	6.1	0.2		–	7.3	0.6
Width of nucleus		2.2–3.4	3.0	0.1		–	2.5	0.2
Erythrocyte parasitized by microgametocyte	14							
Length		11.7–15.5	13.7	0.9	–	–	–	–
Width		5.9–7.2	6.6	0.4	–	–	–	–
Length of nucleus		5.3–7.0	6.0	0.3	–	–	–	–
Width of nucleus		2.2–3.3	2.8	0.2	–	–	–	–
Macrogametocyte	33				40			
Length		19.9–26.0	23.7	1.8		–	12.0	1.3
Width		1.8–3.0	2.4	0.3		2.0–4.0	–	–
Length of nucleus		1.5–5.0	3.7	0.2		2.0–3.0	–	–
Width of nucleus		1.0–2.2	1.8	0.1		1.0–2.0	–	–
NDR		0.7–1.0	0.9	0.1		–	0.9	–
No. of pigment granules		17–34	25.5	2.7		3–13	7.6	1.9
Microgametocyte	14							
Length		15.2–25.1	23.1	1.4	–	–	–	–
Width		2.1–3.0	2.6	0.3	–	–	–	–
Length of nucleus		6.0–8.7	7.5	0.5	–	–	–	–
Width of nucleus		1.3–2.6	1.8	0.2	–	–	–	–
NDR		0.7–1.0	0.8	0.1	–	–	–	–
No. of pigment granules		14–28	20.0	2.1	–	–	–	–

Note: All sizes are given in micrometres.

parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 129, *6–8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; circumnuclear forms (Fig. 129, *8*) are more rare than for macrogametocytes; other characters are as for macrogametocytes.

C o m m e n t s. Levine (1985) corrected the specific name *larae* to *lari.* This action is an 'unjustified emendation' [see Articles 32(d), and 33(b) of the International Code of Zoological Nomenclature, 1985].

60. **Haemoproteus (Parahaemoproteus) balearicae** Peirce, 1973

Haemoproteus balearicae Peirce, 1973: 469, Fig. 1–28.

Type vertebrate host. *Balearica pavonina* (L.) (Gruiformes).
Additional vertebrate hosts. *Balearica regulorum*, *Bugeranus carunculatus* (Gruiformes).
Type locality. Surrey, England. This parasite was isolated from a bird imported from West Africa.
Distribution has been insufficiently investigated. This parasite has been recorded mainly in birds imported into Europe and North America so far. The transmission takes place in the Ethiopian zoogeographical region.
Type material. Hapantotype (No. 29812, *Balearica pavonina*, Surrey, England, M.A. Peirce) and parahapantotypes (data as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Balearica.*

Main diagnostic characters. A parasite of species of the Gruiformes whose fully grown gametocytes are elongated and slender, ameboid in outline. Gametocytes only negligibly (if at all) enclose the nucleus of erythrocytes with their ends and do not displace the nucleus laterally. The average number of pigment granules in gametocytes is less than 12.

Development in vertebrate host
Exoerythrocytic meronts were recorded in the lungs of naturally infected *Balearica pavonina* (Peirce, 1973). The majority of them were roundish or oval, but the largest forms were frequently intricate (branchy) in configuration. The largest meronts were up to 58 μm long, and up to 23 μm wide. The development of cytomeres was not recorded. Mature meronts contain numerous roundish merozoites about 1 μm in diameter.

Young gametocytes (Fig. 130, *6*, *7*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently they take a polar or subpolar position in the host

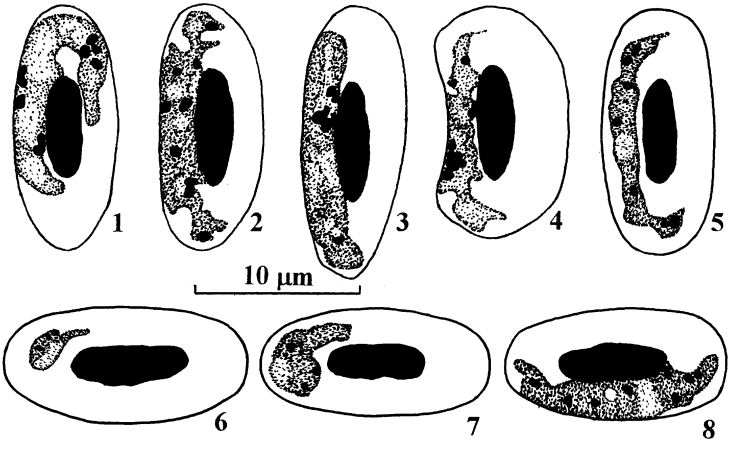

Figure 130 Gametocytes of *Haemoproteus balearicae* from the blood of *Balearica pavonina: 1*, *4* – microgametocytes; *2*, *3*, *5*, *8* – macrogametocytes; *6*, *7* – young (*1–4* are modified from Bennett *et al*., 1975).

cells; gametocytes, which are polar in position, are frequently comma-like with one prominent ameboid outgrowth (Fig. 130, *6, 7*); U-shaped gametocytes, which take a polar position in erythrocytes, are common; as the parasite develops, the majority of gametocytes extend longitudinally along the nucleus of erythrocytes and take a position lateral to the erythrocyte nucleus.

Macrogametocytes (Fig. 130, *2*, *3*, *5*, *8*; Table 84). The cytoplasm is heterogeneous in appearance, sometimes contains a few small clear vacuoles; gametocytes grow along the nucleus of erythrocytes; they only negligibly (if at all) enclose the nucleus with their ends and do not displace the nucleus laterally; fully grown gametocytes are usually closely appressed both to the nucleus and envelope of erythrocytes, but growing forms can locate free in the cytoplasm, they do not touch the nucleus and envelope of erythrocytes (Fig. 130, *5*); among the growing gametocytes, forms touching the erythrocyte envelop but not touching the erythrocyte nucleus (Fig. 30, *4*), are dominant; the outline is usually highly ameboid or wavy, but some fully grown gametocytes lose their ameboid outline and it becomes even (Fig. 130, *3*); the parasite nucleus is compact, relatively small for bird haemoproteids (Fig. 130, *5*, *8*), variable both in form and position, but most frequently seen in a median or submedian position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, usually randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 130, *1*, *4*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters. It should be noted that

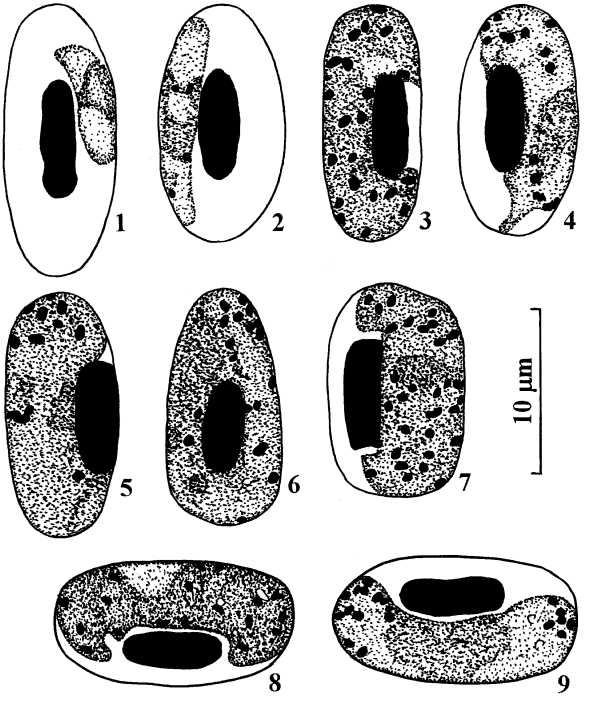

Figure 131 Gametocytes of *Haemoproteus caprimulgi* from the blood of *Chordeiles minor* (*1–5*, *7–9*) and *Eurostopodus macrotis* (*6*):
1, *2* – young; *3*, *5–8* – macrogametocytes; *4*, *9* – microgametocytes (*1–7* are modified from Williams *et al*., 1975).

the parasite nucleus is diffuse and has no visible boundaries; it concentrates close to the outer periphery of the parasite.

61. **Haemoproteus (Parahaemoproteus) caprimulgi** Williams, Bennett and Mahrt, 1975

Haemoproteus caprimulgi Williams, Bennett and Mahrt, 1975: 917, Fig. 1–6.

Type vertebrate host. *Chordeiles minor* (Forster) (Caprimulgiformes).
Additional vertebrate hosts. *Caprimulgus europaeus*, *Eurostopodus macrotis*, *E. temminckii* (Caprimulgiformes).
Type locality. Comox Burn, 18 km west of Courtenay, Vancouver Island, British Columbia, Canada.
Distribution. This parasite has been recorded in the Holarctic and in the Oriental zoogeographical region so far, and it is clearly spotty in distribution. The parasite is rare in the Palearctic. It is likely that the transmission also takes place in the Ethiopian zoogeographical region where the haemoproteids, identified up to the generic level, have been recorded in caprimulgiform birds.
Type material. Hapantotype (No. 39147, *Chordeiles minor*, 24.08.1974, Comox Burn, Vancouver Island, British Columbia, Canada, N.A. Williams) and parahapantotypes (No. 2649, *Eurostopodus temminckii*, 26.12.1962, Subang, Malaysia, M. Laird; No. 2763, *E. macrotis*, 10.03.1962, Subang, Malaysia, M. Laird; No. 9396, *E. macrotis*, 03.03.1965, Palawan, Philippines, coll. Kuntz; No. 10513, *E. macrotis*, 05.11.1964, Mindaro, Philippines, H.E. McClure) are deposited in IRCAH. Parahapantotype (UOA No. 8720, 14.08.1973, other data are as for the hapantotype) is deposited in UAPRC.
Etymology. The specific name is derived from the family name Caprimulgidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Caprimulgiformes with pleomorphic gametocytes. Fully grown gametocytes usually more or less enclose the nucleus of infected erythrocytes with their ends and markedly displace the nucleus laterally, but do not encircle it completely. However, sometimes the gametocytes also completely encircle the nucleus of erythrocytes and occupy all available cytoplasmic space in the host cells. The average number of pigment granules is about 20 per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 131, *1*, *2*) are usually seen located in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the erythrocyte nucleus, and frequently they do not touch the nucleus or touch it only slightly in one or several points (Fig. 131, *1, 2*); the outline is usually even.

Macrogametocytes (Fig. 131, *3*, *5–8*; Table 85). The cytoplasm is homogeneous in appearance. Gametocytes are pleomorphic; two main forms of gametocytes have been recorded. First, the majority of gametocytes markedly displace the nucleus of erythrocytes laterally, frequently to the periphery of the host cells (Fig. 131, *5*); they more or less enclose the erythrocyte nucleus with their ends but do not encircle it completely (Fig. 131, *3*, *5*, *7*). Second, some gametocytes grow around the nucleus of erythrocytes not displacing or only slightly displacing the nucleus laterally; they finally completely encircle the nucleus of erythrocytes and occupy all available cytoplasmic space in the host cells (Fig. 131, *6*). Fully grown gametocytes of both forms mentioned above are closely appressed to the nucleus

Table 85 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. caprimulgi*				*H. telfordi* (modified from Bennett *et al.*, 1975a)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	40				20		
Length		11.4–16.8	13.6	0.6		12.5	1.0
Width		5.6–7.6	7.1	0.4		7.1	0.5
Length of nucleus		5.0–7.7	6.3	0.3		5.6	0.9
Width of nucleus		2.0–2.8	2.1	0.1		2.2	0.2
Erythrocyte parasitized by macrogametocyte	17				20		
Length		11.8–16.4	14.7	0.8		13.7	0.9
Width		5.9–8.6	6.8	0.4		7.2	0.6
Length of nucleus		5.4–7.0	5.9	0.4		4.9	0.6
Width of nucleus		1.8–2.7	2.0	0.1		2.3	0.3
Macrogametocyte	17				20		
Length		13.0–17.7	15.0	1.5		22.8	2.4
Width		2.7–5.0	3.8	0.4		2.4	0.1
Length of nucleus		2.2–4.5	3.4	0.4		2.7	0.6
Width of nucleus		1.8–2.7	2.2	0.1		2.2	0.5
NDR		0.0–0.7	0.4	0.1		1.0	0.2
No. of pigment granules		16–32	21.4	2.4		16.9	1.8

Note: All sizes are given in micrometres. Gametocytes, which are similar to those shown in Fig. 131, *3*, *5*, *8*, were used to measure *H. caprimulgi*.

and envelope of erythrocytes. Growing gametocytes frequently do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is evident between the parasite and the erythrocyte nucleus (Fig. 131, *8*); this 'cleft' disappears in fully grown gametocytes. The outline of gametocytes is usually even, but sometimes also slightly ameboid (Fig. 131, *4*). The parasite nucleus is variable in shape, median or submedian in position (Fig. 131, *8*). Pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 131, *4*, *9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Haemoproteus caprimulgi* is only one species of haemoproteids which has been described in caprimulgiform birds so far.

62. **Haemoproteus (Parahaemoproteus) telfordi** Bennett, Forrester, Greiner and Campbell, 1975

Haemoproteus telfordi Bennett, Forrester, Greiner and Campbell, 1975a: 77, Fig. 9–11.

Type vertebrate host. *Eupodotis melanogaster* (Ruppell) (Gruiformes).
Additional vertebrate hosts. *Ardeotis kori*, *Chlamydotis undulata* (Gruiformes).

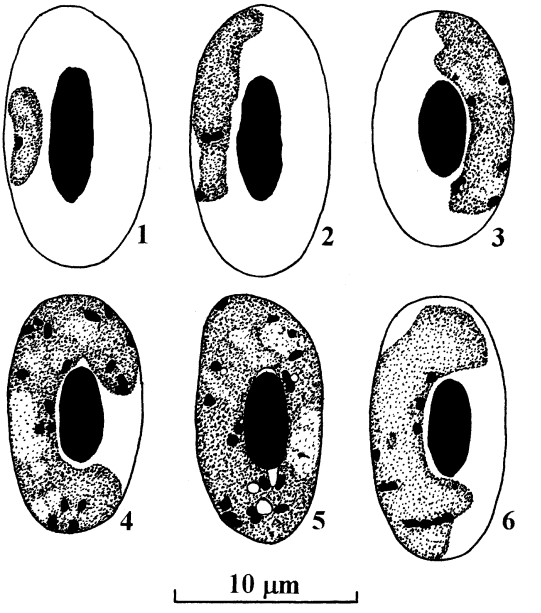

Figure 132 Gametocytes of *Haemoproteus telfordi* from the blood of *Eupodotis melanogaster: 1* – young; *2–5* – macrogametocytes; *6* – microgametocyte (modified from Bennett *et al*., 1975a).

Type locality. Kundelungu, 200 km from Lubumbashi (Elizabethville), Katanga Province, Zaire.

Distribution. The Ethiopian zoogeographical region. So far, this parasite has been recorded mainly in birds imported from Africa and kept in zoological gardens. It is likely that the range of distribution of this parasite is wider than the Ethiopian zoogeographical region.

Type material. Hapantotype (No. 36165, *Eupodotis melanogaster*, 14.12.1952, Zaire, coll. Lips) and parahapantotype (No. 36164, other data are as for the hapantotype) are deposited in IRCAH.

Etymology. This species is named in honour of Dr. Sam R. Telford in recognition of his contribution to the fields of reptilian and avian blood parasitology.

Main diagnostic characters. A parasite of species of the Gruiformes whose fully grown gametocytes completely encircle the nucleus of infected erythrocytes but do not displace or only slightly displace it laterally. The average number of pigment granules is about 17 per macrogametocyte.

Development in vertebrate host

Young gametocytes (Fig. 132, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes and are closely appressed to the envelope of erythrocytes but usually do not touch their nucleus; the outline is even or slightly wavy.

Macrogametocytes (Fig. 132, *2–5*; Table 85). The cytoplasm is finely granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of erythrocytes; they do not displace or only slightly displace the nucleus of erythrocytes laterally; growing gametocytes are closely appressed to the erythrocyte

envelope but usually do not touch the erythrocyte nucleus and, as a result, a more or less evident unfilled space (a 'cleft') is available between the parasite and the erythrocyte nucleus (Fig. 132, *2–4*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; they completely encircle the nucleus and occupy all available cytoplasmic space in the erythrocytes (Fig. 132, *5*); the outline is even or wavy; the parasite nucleus is compact, frequently roundish or oval, median or submedian in position; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 132, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

63. **Haemoproteus (Parahaemoproteus) bennetti** Greiner, Mandal and Nandi, 1977

Haemoproteus bennetti Greiner, Mandal and Nandi, 1977: 654, Fig. 5–8.

Type vertebrate host. *Picus flavinucha* Gould (Piciformes).
Additional vertebrate host. *Picus erythropygius* (Piciformes).
Type locality. Darjeeling W.B., India.
Distribution. The Oriental zoogeographical region.
Type material. Hapantotype (No. Pt. 1843, *Picus flavinucha*, 13.07.1974, Sukua, Darjeeling W.B., India) is deposited in NZCC. Parahapantotypes (No. 37620, 37621, *P. erythropygius*, Central Thailand) are deposited in IRCAH.
Etymology. This species was named in honour of Professor Gordon F. Bennett who was head of the International Reference Centre for Avian Haematozoa (IRCAH), in recognition of his contribution to the field of avian blood parasitology.

Table 86 Morphometric parameters of gametocytes and host cells of *Haemoproteus bennetti* (modified from Greiner *et al.*, 1977).

Feature	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	10		
Length		13.7	0.8
Width		7.6	0.6
Macrogametocyte	15		
Length		12.7	1.0
Width		4.4	0.4
Length of nucleus		3.3	0.4
Width of nucleus		2.7	0.4
No. of pigment granules		20.0	2.5
Microgametocyte	15		
Length		12.9	0.8
Width		4.4	0.5
No. of pigment granules		20.0	2.7

Note: All sizes are given in micrometres.

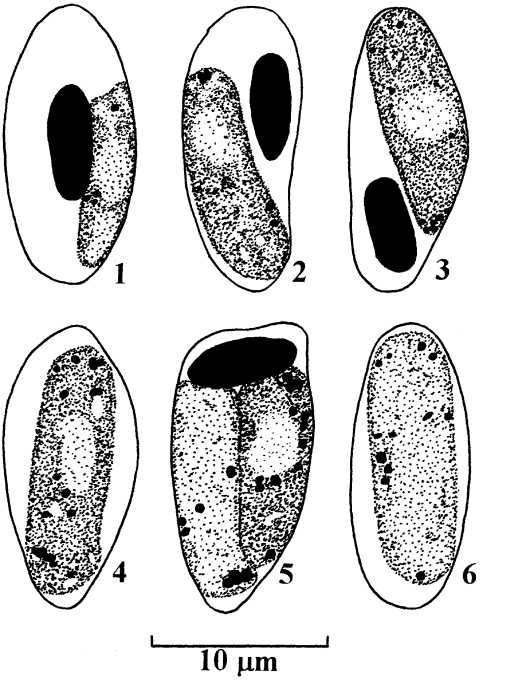

Figure 133 Gametocytes of *Haemoproteus bennetti* from the blood of *Picus flavinucha:* *1* – young; *2–4* – macrogametocytes; *5* – macrogametocyte and microgametocyte in the same erythrocyte; 6 – microgametocyte (modified from Greiner *et al*., 1977).

Main diagnostic characters. A parasite of species of the Piciformes whose gametocytes markedly displace the nucleus of infected erythrocytes and finally enucleate the host cells. The average number of pigment granules is about 20 per gametocyte. Infected erythrocytes are hypertrophied approximately 10% in length on average in comparison to uninfected ones.

Development in vertebrate host

Young gametocytes (Fig. 133, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; the outline is even.

Macrogametocytes (Fig. 133, *2–5*; Table 86). The cytoplasm is finely granular in appearance, frequently contains a few small vacuoles; valutin granules are not seen; growing gametocytes markedly displace the nucleus of erythrocytes toward one pole (Fig. 133, *2*, *3*, *5*), and finally enucleate the host cells (Fig. 133, *4*); fully grown gametocytes are elongated cigar-shaped bodies; they extend within an elongated erythrocytic remnant consisting of the cytoplasm and envelope of the erythrocytes; the outline is even; the parasite nucleus is compact, variable in shape, frequently roundish or oval, usually median or submedian in position; pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length (10%) and width (5%) in comparison to uninfected erythrocytes.

Microgametocytes (Fig. 133, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

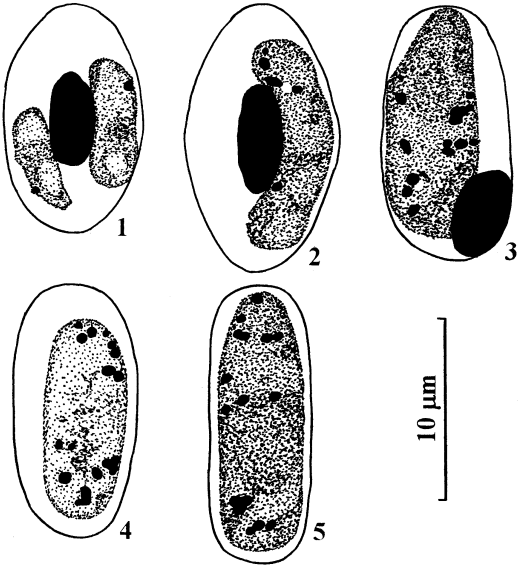

Figure 134 Gametocytes of *Haemoproteus lairdi* from the blood of *Merops variegatus:* *1* – young; *2*, *3*, *5* – macrogametocytes; *4* – microgametocyte (modified from Bennett, 1978).

Comments. During the infection of *H. bennetti*, the percentage of enucleated erythrocytes depends on the number of fully grown gametocytes in the blood or, in other words, on the stage of parasitemia. The original description is based on the blood films where the percentage of the enucleated erythrocytes varies from 1 to 40% (Greiner *et al.*, 1977).

Among the haemoproteids of birds belonging to the Piciformes, *H. bennetti* is especially similar to *H. bucconis* and *H. thereicerycis*. It can be distinguished from *H. thereicerycis* primarily on the basis of a smaller number of pigment granules in its gametocytes. *Haemoproteus bennetti* induces hypertrophy of infected erythrocytes in length, and this is not characteristic of *H. bucconis*. However, it should be noted that the taxonomic value of the latter character is questionable.

64. **Haemoproteus (Parahaemoproteus) lairdi** Bennett, 1978

Haemoproteus lairdi Bennett, 1978: 1724, Fig. 3–6.

Type vertebrate host. *Merops variegatus* (Vieil.) (Coraciiformes).
Type locality. Entebbe, Uganda.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 40683, *Merops variegatus*, 17.01.1974, Entebbe, Uganda, A.B.C. Killango) is deposited in IRCAH.
Etymology. This species is named in honour of Professor Marshall Laird, who was the organizer and first director of the International Reference Centre for Avian Haematozoa (IRCAH), in recognition of his contribution to the field of avian blood parasitology.

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes enucleate infected erythrocytes; they do not possess large (>1 μm

Table 87 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. (modified from Bennett, 1978).

Feature	*H. lairdi*			*H. manwelli*		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	20			40		
Length		12.6	0.6		12.0	0.9
Width		7.3	0.5		6.8	0.6
Length of nucleus		5.9	0.6		5.7	0.6
Width of nucleus		2.6	0.5		2.1	0.5
Parasitized erythrocyte	20			40		
Length		14.1	1.0		12.5	1.0
Width		5.7	0.8		6.9	0.9
Length of nucleus		–	–		4.7	0.5
Width of nucleus		–	–		2.1	0.3
Gametocyte	20			40		
Length		12.7	1.0		12.5	1.0
Width		4.5	0.5		4.4	0.8
Length of nucleus		3.1	0.5		3.0	0.5
Width of nucleus		2.2	0.5		2.4	1.1
NDR		–	–		0.1	–
No. of pigment granules		17.0	2.2		10.0	1.5

Note: All sizes are given in micrometres.

in diameter) vacuoles. The outline of gametocytes is even. The average number of pigment granules is about 17 per gametocyte. Infected erythrocytes are significantly hypertrophied in length and atrophied in width in comparison to uninfected ones.

Development in vertebrate host

Young gametocytes (Fig. 134, *1*). The earliest forms can be seen located everywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus displacing it laterally; the outline is even.

Macrogametocytes (Fig. 134, *2*, *3*, *5*; Table 87). The cytoplasm is finely granular in appearance, usually does not contain or contains only a few small vacuoles; growing gametocytes markedly displace the nucleus of erythrocytes toward one pole, and finally enucleate the host cell (Fig. 134, *5*); fully grown gametocytes are cigar-shaped bodies extending within the erythrocytic remnant; they lie free in the cytoplasm and usually do not touch the envelope of the erythrocytes (Fig. 134, *5*); the outline is even; the parasite nucleus is compact, usually roundish or oval in shape, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length (12%) and atrophied in width (22%) in comparison to uninfected ones.

Microgametocytes (Fig. 134, *4*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Coraciiformes, *H. lairdi* is especially similar to *H. gavrilovi* and *H. enucleator*. It can be distinguished from *H. gavrilovi* primarily on the basis of more numerous pigment granules in its gametocytes. Fully grown gametocytes of *H. lairdi* markedly atrophy infected erythrocytes in width, and this is not characteristic of *H. enucleator*.

65. **Haemoproteus (Parahaemoproteus) manwelli** Bennett, 1978

Haemoproteus manwelli Bennett, 1978: 1722, Fig. 1.

T y p e v e r t e b r a t e h o s t. *Merops orientalis* Latham (Coraciiformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. *Merops viridis* (Coraciiformes).
T y p e l o c a l i t y. Maharashtra, India.
D i s t r i b u t i o n. The Oriental zoogeographical region.
T y p e m a t e r i a l. Hapantotype (No. 37177, *Merops orientalis*, 26.02.1969, Maharashtra State, India, H.E. McClure) and parahapantotypes (No. 37174, *M. orientalis*, 12.05.1967, Chiengmai, Thailand, H.E. McClure; No. 37200, *M. viridis*, 14.06.1967, Subang, Malaysia, H.E. McClure) are deposited in IRCAH.
E t y m o l o g y. This species is named in honour of Dr. Reginald D. Manwell in recognition of his contribution to the field of avian blood parasitology.

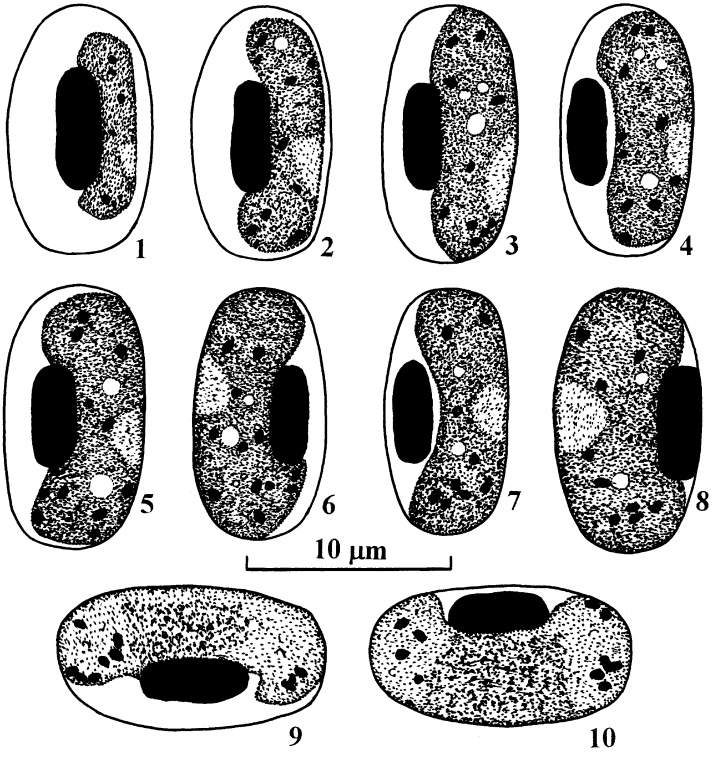

Figure 135 Gametocytes of *Haemoproteus manwelli* from the blood of *Merops orientalis:* *1* – young; *2–8* – macrogametocytes; *9*, *10* – microgametocytes.

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally, but do not enucleate the erythrocytes. The average number of pigment granules in gametocytes is less than 15. The average width of fully grown gametocytes is greater than 4 μm. The average NDR is less than 0.5.

Development in vertebrate host

Young gametocytes (Fig. 135, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline is even.

Macrogametocytes (Fig. 135, *2–8*; Table 87). The cytoplasm is granular in appearance, frequently contains several clear vacuoles; gametocytes grow along the nucleus of erythrocytes; they markedly displace the nucleus laterally, frequently to the periphery of the host cell (Fig. 135, *8*), but only slightly enclose it with their ends (Fig. 135, *5, 6*) and never encircle it completely; growing gametocytes, which do not touch the nucleus of erythrocytes along their entire margin (Fig. 135, *4*, *7*), are present; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 135, *8*), and they do not enucleate the infected erythrocytes; the outline is usually even; the parasite nucleus is variable in shape, frequently roundish or oval, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 135, *9*, *10*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of the Coraciiformes, *H. manwelli* is especially similar to *H. eurystomae* and *H. halcyonis*. It can be distinguished from the two latter species primarily on the basis of a smaller number of pigment granules in its gametocytes.

Fully grown gametocytes of *H. manwelli* are similar to some medium grown gametocytes of *H. gavrilovi*. At this stage of development, *H. gavrilovi* can be distinguished from *H. manwelli,* particularly, on the basis of the highly ameboid outline of its gametocytes. Fully grown gametocytes of *H. gavrilovi* are clearly distinguished from *H. manwelli.*

66. **Haemoproteus (Parahaemoproteus) ortalidum** Gabaldon and Ulloa, 1978

Haemoproteus rotundus ortalidum Gabaldon and Ulloa, 1978: 173, Fig. 1–20. – *H. ortalidum*: Bennett *et al.*, 1982a: 3106 (emend. pro *H. rotundus ortalidum*).

Type vertebrate host. *Ortalis ruficauda* (Jardine) (Galliformes).
Additional vertebrate host. *Penelope purpurascens* (Galliformes).
Type locality. Jácura, Falcón, Venezuela.
Distribution. The Neotropical zoogeographical region.
Type material. Hapantotype (data of the label is unknown) is deposited in Mata de Caña, Guanarito, Portuguesa, Venezuela. Part of parahapantotypes (numbers of slides and data of labels are unknown) is deposited in CPGA. Part of parahapantotypes (*Ortalis ruficauda*, all the slides are collected by A. Gabaldon and G. Ulloa, Venezuela: No. 86256, Jácura, Falcón, 06.12.1973; No. 86267, Negro Primero, 14.11.1974; No. 86277, Sanare, Lara, 06.06.1975; No. 86282, Irapa, Sucre, 28.05.1977; No. 86285, Mario Bricene Iragorry, Aragua, 20.01.1979) is deposited in IRCAH.

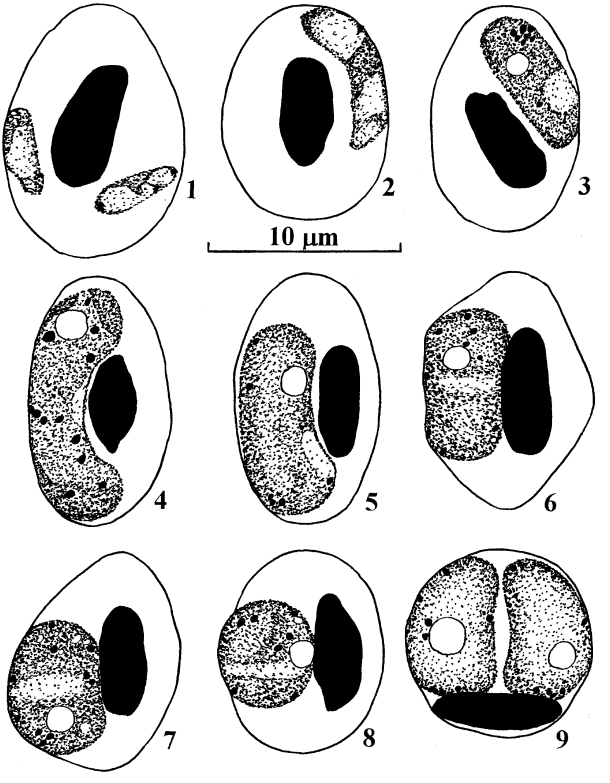

Figure 136 Gametocytes of *Haemoproteus ortalidum* from the blood of *Ortalis ruficauda: 1–3* – young; *4–8* – macrogametocytes; *9* – two microgametocytes in the same erythrocyte (modified from Bennett *et al*., 1982a).

Etymology. The specific name is derived from the generic name of the type host, *Ortalis.*

Main diagnostic characters. A parasite of species of the Galliformes with two types of gametocytes, elongated (usually cylindrical or cigar-like) and roundish (discoid). A large (about 1 to 3 μm in diameter) clear vacuole is present in the majority of macrogametocytes.

Development in vertebrate host

Young gametocytes (Fig. 136, *1–3*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes take a rod-like shape (Fig. 136, *1*), and then extend longitudinally (Fig. 136, *2*); as a rule, the largest forms possess one clear vacuole (Fig. 136, *3*); the outline varies from even to slightly ameboid.

Macrogametocytes (Fig. 136, *4–8*; Table 88). Two types of gametocytes develop, elongated and roundish (discoid) in shape. Additionally, numerous intermediate forms between the two main types mentioned above, are present. During development, young gametocytes are first elongated taking a halteridian, cylindrical, or cigar-like shape, and mature forms finally round up. In slides, either elongated gametocytes (an early stage of parasitemia) or roundish gametocytes (a late stage of the parasitemia) usually predominate.

Table 88 Morphometric parameters of gametocytes and host cells of *Haemoproteus ortalidum* (modified from Bennett *et al.*, 1982a).

Feature	Roundish gametocytes			Elongated gametocytes		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	100					
Length		13.8	0.8	–	–	–
Width		7.3	0.4	–	–	–
Length of nucleus		5.9	0.6	–	–	–
Width of nucleus		2.3	0.3	–	–	–
Erythrocyte parasitized by macrogametocyte	55			50		
Length		11.7	0.8		13.0	1.0
Width		8.5	0.8		7.9	0.7
Length of nucleus		5.4	0.5		5.6	0.8
Width of nucleus		2.2	0.3		2.2	0.4
Erythrocyte parasitized by microgametocyte	40			40		
Length		11.9	0.9		13.0	0.9
Width		9.2	1.1		8.0	0.5
Length of nucleus		5.4	0.6		5.5	0.5
Width of nucleus		2.2	0.3		2.2	0.3
Macrogametocyte	55			50		
Length		6.8	0.8		10.8	1.0
Width		5.7	0.5		3.7	0.4
Length of nucleus		2.5	0.5		2.8	0.6
Width of nucleus		1.8	0.4		1.9	0.3
NDR		–	–		0.5	–
No. of pigment granules		11.3	1.0		12.0	1.5
Microgametocyte	40			40		
Length		7.4	0.6		11.2	1.2
Width		6.3	0.5		3.4	0.4
Length of nucleus		5.0	1.0		6.0	0.6
Width of nucleus		3.3	0.7		3.1	1.0
NDR		–	–		0.6	–
No. of pigment granules		11.1	1.5		11.4	1.4

Note: All sizes are given in micrometres.

Elongated gametocytes (Fig. 136, *4–6*; Table 88). The cytoplasm is homogeneous in appearance, as a rule, containing one large (from 1 to 3 μm in diameter), roundish clear vacuole which markedly varies in position; gametocytes are usually cylindrical (Fig. 136, *6*) or cigar-like (Fig. 136, *5*), but sometimes clearly halteridian (Fig. 136, *4*); gametocytes usually do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is frequently available between the parasite and the erythrocyte nucleus (Fig. 136, *4*, *5*); the outline is even; the parasite nucleus is compact, variable in form, usually median or submedian in position, but sometimes also seen in a subterminal

Table 89 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. stellaris* (modified from White and Bennett, 1978)			*H. contortus* (modified from Bennett, 1979)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocytes	30			10		
Length		11.3	0.5		13.0	0.5
Width		6.2	0.4		7.3	0.7
Length of nucleus		5.1	0.3		6.1	0.6
Width of nucleus		2.5	0.1		2.1	0.2
Erythrocyte parasitized by macrogametocyte				30		
Length	4	13.0	0.6		14.5	1.0
Width	4	6.4	0.5		7.6	0.5
Length of nucleus	32	5.4	0.5		5.7	0.6
Width of nucleus	32	2.3	0.3		2.0	0.2
Erythrocyte parasitized by microgametocyte				10		
Length	1	12.0	–		13.9	1.3
Width	1	7.0	–		7.7	0.8
Length of nucleus	31	5.4	0.4		5.9	0.5
Width of nucleus	31	2.5	0.4		2.0	0.3
Macrogametocyte				30		
Length	32	13.6	1.2		25.2	4.3
Width	32	2.2	0.5		2.3	0.4
Length of nucleus	13	2.9	0.7		3.6	0.5
Width of nucleus	13	1.8	0.4		2.0	0.4
NDR	4	0.8	0.2		0.9	–
No. of pigment granules	32	2.0	0.7		24.1	2.9
Microgametocyte				10		
Length	31	14.2	1.3		24.3	2.2
Width	31	2.4	0.4		2.4	0.4
Length of nucleus	8	4.9	0.7		6.5	1.0
Width of nucleus	8	2.3	0.4		2.2	0.2
NDR	1	1.0	–		1.0	–
No. of pigment granules	31	2.2	0.8		25.0	4.0

Note: All sizes are given in micrometres.

position; pigment granules are roundish or slightly oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are usually not deformed, but their nucleus is displaced laterally.

Roundish gametocytes (Fig. 136, *7*, *8*; Table 88). The cytoplasm looks like in the elongated forms, and the vacuole is also present; the outline is even; the parasite nucleus is variable in form and position; pigment granules look like in the elongated forms; gametocytes markedly deform infected erythrocytes and displace their nuclei.

The percentage of roundish gametocytes in different blood films varies from 4 to 60% of the total number of gametocytes.

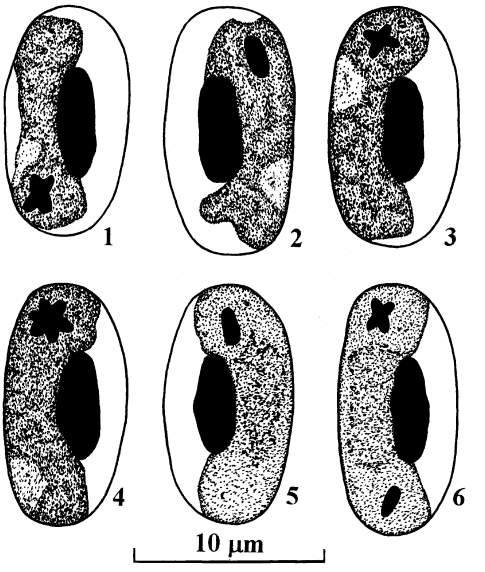

Figure 137 Gametocytes of *Haemoproteus stellaris* from the blood of *Hirundo griseopyga: 1–4* – macrogametocytes; *5*, *6* – microgametocytes.

Microgametocytes (Fig. 136, *9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the vacuole is not seen in some gametocytes; other characters are as for macrogametocytes.

Comments. *Haemoproteus ortalidum* is characterized by a feature rare for bird haemoproteids, i.e., its growing gametocytes are elongated, and fully grown gametocytes are roundish (discoid). It should be noted that roundish gametocytes develop in all species of haemosporidian parasites after exposure of infected blood with mature gametocytes to air due to the onset of gametogenesis. However, the roundish gametocytes of *H. ortalidum* develop in the organism of live birds.

On the possible origin of the vacuole recorded in gametocytes of *H. ortalidum*, see 'Comments' to *H. trogonis.*

67. **Haemoproteus (Parahaemoproteus) stellaris** White and Bennett, 1978

Haemoproteus stellaris White and Bennett, 1978: 2114, Fig. 3–6.

Type vertebrate host. *Hirundo griseopyga* Sundevall (Passeriformes).
Type locality. Kasenyi, Uganda.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 46258, *Hirundo griseopyga*, 11.03.1976, Kasenyi, Uganda, A.B.C. Killango) and parahapantotype (No. 46287, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name reflects the particular stellar-like position of the pigment granules in gametocytes.

Main diagnostic characters. A parasite of species of the Passeriformes whose fully grown gametocytes possess a few (two on average) gigantic (>1.5 μm) rod-like pigment granules; the pigment granules are usually aggregated in stellar-like clumps.

Development in vertebrate host

Young gametocytes. The earliest forms were not seen in the type material; as the parasite develops, gametocytes adhere to the nucleus of infected erythrocytes and extend longitudinally along the nucleus; the outline is even.

Macrogametocytes (Fig. 137, *1–4*; Table 89). The cytoplasm is homogeneous in appearance, it usually lacks vacuoles and valutin granules; gametocytes grow along the nucleus of erythrocytes, they slightly enclose the nucleus with their ends and slightly (if at all) displace the nucleus laterally but do not encircle it completely; gametocytes adhere to the nucleus and envelope of erythrocytes; the central part of the pellicle of growing gametocytes frequently does not extend to the envelope of erythrocytes, causing a 'dip' and giving a dumbbell-like appearance (Fig. 137, *1*); the dumbbell-shaped gametocytes represent more than 10% of the total number of growing gametocytes; fully grown gametocytes lose the dumbbell-like shape and they are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 137, *4*); the outline of growing gametocytes is even (Fig. 137, *3*) or wavy (Fig. 137, *2*), and is usually even (Fig. 137, *4*) in fully grown forms; the parasite nucleus is variable in shape, subterminal in position; pigment granules are gigantic (on average 1.9 μm long and 0.6 μm wide), rod-like, usually aggregated in stellar-like clumps near the ends of gametocytes (Fig. 137, *1*, *3*, *4*); infected erythrocytes are significantly hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 137, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The gigantic size of the pigment granules in gametocytes of *H. stellaris* is a unique character among the bird haemoproteids.

68. **Haemoproteus (Parahaemoproteus) contortus** Bennett, 1979

Haemoproteus contortus Bennett, 1979: 902, Fig. 4–6.

Type vertebrate host. *Numenius phaeopus* (L.) (Charadriiformes).
Additional vertebrate hosts. *Actitis hypoleucos*, *Gallinago megala*, *Tringa glareola*, *Xenus cinereus* (Charadriiformes).
Type locality. Batangas, Philippine Islands.
Distribution. This parasite has so far been recorded only on the Philippine Islands.
Type material. Hapantotype (No. 11760, *Numenius phaeopus*, 17.09.1964, Calatagan, Batangas, Philippine Islands, H.E. McClure) and parahapantotype (No. 37389, *Tringa glareola*, 26.02.1966, Palawan, Philippine Islands, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the Latin word 'contortus,' and it reflects the contorted shape of gametocytes of this parasite.

Main diagnostic characters. A parasite of species of the Charadriiformes whose fully grown gametocytes are elongated and slender; they grow around the nucleus

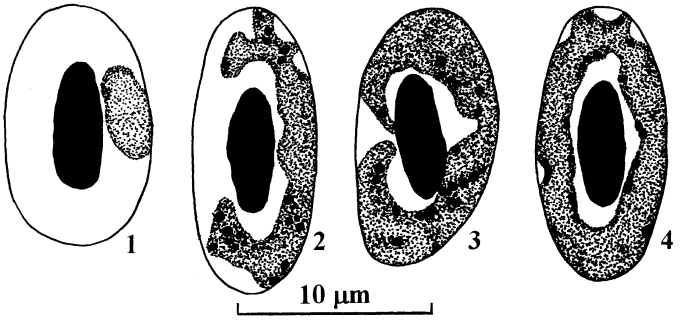

Figure 138 Gametocytes of *Haemoproteus contortus* from the blood of *Numenius phaeopus: 1* – young; *2–4* – macrogametocytes (modified from Bennett, 1979).

of infected erythrocytes and completely encircle the nucleus but do not occupy all available cytoplasmic space in the host cells. The fully grown gametocytes do not touch the nucleus of erythrocytes, and a clear more or less evident unfilled space (a 'cleft') is available between the parasite and the erythrocyte nucleus.

Development in vertebrate host

Young gametocytes (Fig. 138, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; the outline is even.

Macrogametocytes (Fig. 138, *2–4*; Table 89). The cytoplasm is finely granular in appearance; gametocytes grow around the nucleus of erythrocytes and finally completely encircle the nucleus but do not occupy all available cytoplasmic space in the host cells; the nucleus of infected erythrocytes is usually not displaced laterally; fully grown gametocytes do not touch the nucleus of erythrocytes and, as a result, a clear more or less evident unfilled space (a 'cleft') is available between the parasite and the erythrocyte nucleus (Fig. 138, *2–4*) which is a characteristic feature of this species; gametocytes are slender and wriggled in shape, the outline is more or less wavy, but sometimes ameboid; the parasite nucleus is compact, usually roundish or oval, median or submedian in position; the width of the parasite nucleus frequently overlaps the width of gametocyte; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes. The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

69. **Haemoproteus (Parahaemoproteus) janovyi** Greiner and Mundy, 1979

Haemoproteus janovyi Greiner and Mundy, 1979: 148, Fig. 1, 2.

Type vertebrate host. *Gyps africanus* Salvadori (Falconiformes).
Additional vertebrate hosts. *Melierax canorus*, *Necrosyrtes monachus*, *Torgos tracheliotus, Trigonoceps occipitalis* (Falconiformes).
Type locality. Sengwa Wildlife Research Area, Zimbabwe (17°30′–18°15′ S, 27°40′–28°20′ E).
Distribution. South Africa.

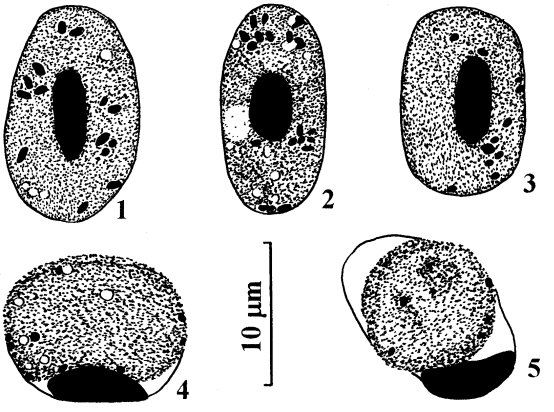

Figure 139 Gametocytes of *Haemoproteus janovyi* from the blood of *Gyps africanus:* *1*, *2*, *4*, *5* – macrogametocytes; *3* – microgametocyte. All gametocytes are from the blood of living birds, and thus they are not under the onset of gametogenesis (*1*, *3*, *4*, *5* are modified from Peirce *et al*., 1990; and *2* is modified from Greiner and Mundy, 1979).

Type material. Hapantotype (No. 59056, *Gyps africanus*, 08.07.1974, Sengwa Wildlife Research Area, Zimbabwe, P.J. Mundy) and parahapantotypes (No. 58952, 59046, 59205, 59004, 59030, *G. africanus*, 1974–1975, Zimbabwe, P.J. Mundy) are deposited in IRCAH.
Etymology. This species is named in honour of American zoologist Professor John Janovy.

Main diagnostic characters. A parasite of species of the Falconiformes with highly pleomorphic gametocytes. Fully grown gametocytes either do not displace the nucleus of infected erythrocytes laterally and completely encircle it, occupying all available cytoplasmic space in the erythrocytes, or markedly displace the nucleus and take a roundish (discoid) shape.

Development in vertebrate host

Young gametocytes. The earliest forms are usually seen in a lateral position to the nucleus of infected erythrocytes; the outline is usually even, but occasionally with ameboid ends.

Macrogametocytes (Fig. 139, *1*, *2*, *4*, *5*; Table 90). The cytoplasm is finely granular in appearance, usually contains a few small vacuoles; stains red with Giemsa's stain which is unusual for haemoproteids; valutin granules are not seen. Two types of fully grown gametocytes develop. First, gametocytes, completely encircling the nucleus of erythrocytes and occupying all available cytoplasmic space in the host cells but not displacing or only slightly displacing the nucleus of erythrocytes laterally (Fig. 139, *1*, *2*), are dominant; they are closely appressed both to the nucleus and envelope of erythrocytes. Second, gametocytes, markedly displacing the nucleus of erythrocytes and taking a roundish (discoid) shape (Fig. 139, *4*, *5*), are also present, and are seen mainly in juvenile birds. The outline of gametocytes is even. The parasite nucleus is compact, stains bright red with Giemsa's stain, median or submedian in position. Pigment granules are roundish or oval, of medium (0.5 to 1.0 µm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 139, *3*). The general configuration is as for macrogametocytes; the cytoplasm stains similar to macrogametocytes with Giemsa's stain which is an unusual character for haemoproteids; the nucleus is diffuse and ill-defined, usually precluding measurement; other characters are as for macrogametocytes.

Table 90 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. janovyi* (modified from Peirce *et al.*, 1990)			*H. rotator* (modified from Bennett, 1979)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	25			20		
Length		14.4	0.9		11.8	0.6
Width		8.2	0.5		6.6	0.5
Length of nucleus		6.7	0.6		5.3	0.6
Width of nucleus		2.7	0.5		2.2	0.2
Erythrocyte parasitized by macrogametocyte	25			30		
Length		15.5	1.2		12.9	0.7
Width		8.4	0.9		6.8	0.6
Length of nucleus		6.3	0.4		4.6	0.4
Width of nucleus		2.3	0.3		2.1	0.9
Erythrocyte parasitized by microgametocyte	20			8		
Length		14.8	1.1		12.3	0.8
Width		8.1	0.7		7.0	0.5
Length of nucleus		6.1	0.6		4.7	0.5
Width of nucleus		2.3	0.3		2.4	0.3
Macrogametocyte	25			30		
Length		27.3	2.4		20.1	2.0
Width		3.0	0.5		2.8	0.6
Length of nucleus		3.9	1.4		3.3	0.5
Width of nucleus		1.1	0.4		2.4	0.4
NDR		1.0	0.1		–	–
No. of pigment granules		16.3	2.7		22.6	2.4
Microgametocyte	20			8		
Length		25.1	1.7		18.6	1.6
Width		3.4	0.6		2.7	0.7
Length of nucleus		–	–		6.1	1.5
Width of nucleus		–	–		2.6	0.6
NDR		0.9	0.1		–	–
No. of pigment granules		15.6	2.2		22.0	3.4

Note: All sizes are given in micrometres.

C o m m e n t s. Circumnuclear gametocytes of *H. janovyi* are similar to the circumnuclear forms of *H. nisi* and *H. tinnunculi*. The two latter species are common parasites of the falconiform birds. *Haemoproteus janovyi* can be distinguished from *H. nisi* and *H. tinnunculi* primarily on the basis of (i) its roundish (discoid) gametocytes, and (ii) the similar staining of macro- and microgametocytes. Furthermore, fully grown gametocytes of *H. janovyi* are closely appressed to the nucleus of erythrocytes, and this is not characteristic of *H. nisi*.

Haemoproteus janovyi is a common parasite in African vultures. This parasite was recorded in all investigated regions in Zimbabwe. The prevalence of infection in vultures from different regions varies from 6.1 to 48.6% (Greiner and Mundy, 1975).

70. **Haemoproteus (Parahaemoproteus) rotator** Bennett, 1979

Haemoproteus rotator Bennett, 1979: 905, Fig. 7–9.

Type vertebrate host. *Gallinago stenura* (Bonaparte) (Charadriiformes).
Type locality. Palawan, Philippine Islands.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 9343, *Gallinago stenura*, 12.09.1965, Palawan, Philippine Islands, H.E. McClure) is deposited in IRCAH.
Etymology. The specific name reflects the unique character of this parasite to rotate the nucleus of infected erythrocytes up to 90° to the normal axis.

Main diagnostic characters. A parasite of species of the Charadriiformes whose fully grown gametocytes rotate the nucleus of infected erythrocytes 45 to 90° to the normal axis.

Development in vertebrate host
Young gametocytes (Fig. 140, *1*) can be seen anywhere in infected erythrocytes; the outline is even.

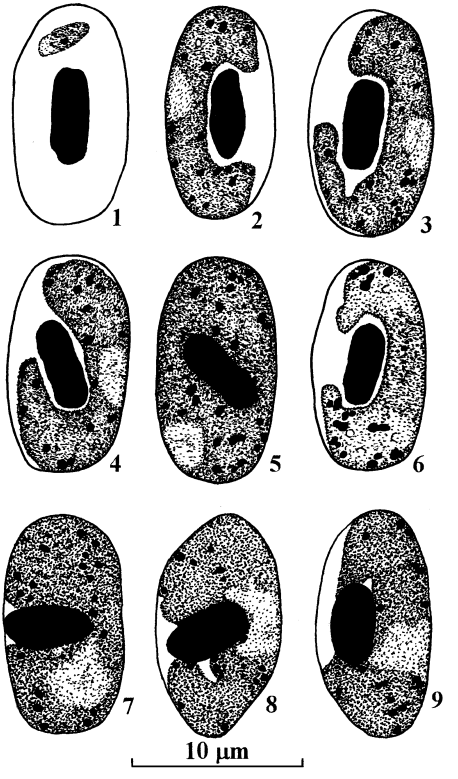

Figure 140 Gametocytes of *Haemoproteus rotator* from the blood of *Gallinago stenura:*
1 – young; *2–5*, *7–9* – macrogametocytes; *6* – microgametocyte (*7–9* are modified from Bennett *et al*., 1979).

Macrogametocytes (Fig. 140, *2–5*, *7–9*; Table 90). The cytoplasm is coarsely granular in appearance; gametocytes grow around the nucleus of infected erythrocytes, and finally they can completely encircle the nucleus and occupy all available cytoplasmic space in the host cells (Fig. 140, *5*); growing gametocytes are closely appressed to the envelope of erythrocytes, but do not touch the erythrocyte nucleus and, as a result, a more or less evident unfilled space (a 'cleft') is available between the parasite and the erythrocyte nucleus (Fig. 140, *2–4*); this 'cleft' disappears in fully grown gametocytes; the outline is even or slightly wavy (Fig. 140, *3*); the parasite nucleus is compact, variable in form, usually median or submedian in position; pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; gametocytes frequently rotate the nucleus of erythrocytes 45 to 90° to the normal axis (Fig. 140, *4*, *5*, *7*, *8*) which is a rare character for bird haemoproteids; however, gametocytes which do not rotate the erythrocyte nucleus and displace it laterally (Fig. 140, *9*), are also available; NDR is difficult to calculate because of the erythrocyte nucleus rotation; the nucleus of infected erythrocytes is atrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 140, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

71. **Haemoproteus (Parahaemoproteus) stableri** White and Bennett, 1979

Haemoproteus stableri White and Bennett, 1979: 1470, Fig. 3–5.

Type vertebrate host. *Bonasa umbellus* (L.) (Galliformes).
Type locality. West Fork, Montana, USA.
Distribution. This parasite has been recorded only in the type locality so far.
Type material. Hapantotype (No. 31507, *Bonasa umbellus*, 17.06.1967, West Fork, Montana, USA, G.W. Clark) and parahapantotype (No. 31508, 25.06.1967, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. This species is named in honour of Dr. Robert Stabler in recognition of his contribution to the field of avian blood parasitology.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes completely encircle the nucleus of infected erythrocytes but do not occupy all available cytoplasmic space in the erythrocytes. A more or less evident

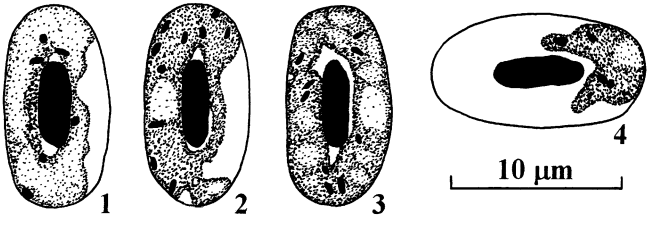

Figure 141 Gametocytes of *Haemoproteus stableri* from the blood of *Bonasa umbellus:*
1 – microgametocyte; *2*, *3* – macrogametocytes; *4* – young (*1*, *2* are modified from White and Bennett, 1979, and *3* is modified from Bennett and Peirce, 1989).

Table 91 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. stableri* (modified from White and Bennett, 1979)			*H. trochili* (modified from White *et al.*, 1979)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	25			25		
Length		11.9	0.5		11.3	0.6
Width		7.1	0.3		6.5	0.6
Length of nucleus		5.0	0.5		5.1	0.3
Width of nucleus		2.3	0.3		2.2	0.3
Erythrocyte parasitized by macrogametocyte	25			26		
Length		12.8	0.8		12.2	0.8
Width		7.3	0.5		6.2	0.5
Length of nucleus		4.6	0.6		4.8	0.4
Width of nucleus		2.0	0.2		2.0	0.3
Erythrocyte parasitized by microgametocyte	25					
Length		13.1	0.6	10	12.1	0.4
Width		7.4	0.7	10	6.4	0.5
Length of nucleus		4.8	0.7	25	4.9	0.6
Width of nucleus		2.2	0.3	25	2.1	0.3
Macrogametocyte						
Length	25	22.1	1.8	40	12.2	1.1
Width	25	2.8	0.4	40	2.3	0.5
Length of nucleus	25	3.5	0.9	40	3.9	1.4
Width of nucleus	25	2.1	0.4	40	1.8	1.0
NDR	25	0.9	0.1	26	0.8	0.2
No. of pigment granules	23	10.4	5.0	40	11.3	1.4
Microgametocyte						
Length	25	19.5	2.8	25	12.3	1.4
Width	25	3.0	0.5	25	2.4	0.6
Length of nucleus	2	4.0	–	–	–	–
Width of nucleus	2	2.0	–	–	–	–
NDR	25	0.8	0.2	10	0.8	0.2
No. of pigment granules	25	7.5	4.5	25	10.0	1.6

Note: All sizes are given in micrometres.

unfilled space (a 'cleft') is available between the fully grown gametocyte and the nucleus of erythrocytes. The average number of pigment granules is about ten per gametocyte.

Development in vertebrate host

Young gametocytes (Fig. 141, *4*) can be seen anywhere in infected erythrocytes, and are frequently present in a polar position where the gametocytes take U-like shape (Fig. 141, *4*); as a rule, growing gametocytes do not touch the nucleus of erythrocytes; the outline is usually more or less wavy or ameboid.

Macrogametocytes (Fig. 141, *2*, *3*; Table 91). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are seen in some blood films; gametocytes grow around the nucleus of infected erythrocytes, they do not displace or only slightly displace it laterally and usually do not touch it so that a more or less evident unfilled space (a 'cleft') is available between the fully grown parasite and the nucleus of erythrocytes (Fig. 141, *3*); fully grown gametocytes encircle the nucleus of erythrocytes completely but do not occupy all available cytoplasmic space in the host cells (Fig. 141, *2, 3*); the outline is ameboid or wavy, and this is especially evident in growing gametocytes; the parasite nucleus is compact, usually roundish or oval, median or submedian in position; pigment granules are usually oval or rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 141, *1*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Galliformes, *H. stableri* is especially similar to *H. mansoni* and *H. lophortyx*. It can be distinguished from the latter two species, particularly, on the basis of the smaller number and larger size of pigment granules in its gametocytes.

72. **Haemoproteus (Parahaemoproteus) trochili** White, Bennett and Williams, 1979

Haemoproteus trochili White, Bennett and Williams, 1979: 911, Fig. 3, 4.

Type vertebrate host. *Eutoxeres aquila* (Bourcier) (Apodiformes).
Additional vertebrate hosts. *Colibri serrirostris*, *Phaethornis guy* (Apodiformes).
Type locality. Rio Zabaletas, Colombia.
Distribution. The Neotropical zoogeographical region.
Type material. Hapantotype (No. 25952, *Eutoxeres aquila*, May–July, 1971, Rio Zabaletas, Colombia, coll. Borrero) is deposited in IRCAH. Parahapantotype (No. is unknown, *Phaethornis guy*, 19.09.1976, Panama, coll. Souza) is deposited in GML.
Etymology. The specific name is derived from the family name Trochilidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Apodiformes whose fully grown gametocytes only slightly enclose the nucleus of infected erythrocytes with their ends and do not displace or only slightly displace the nucleus laterally. Medium and fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent. The average number of pigment granules is about ten per gametocyte.

Development in vertebrate host
Young gametocytes are usually seen in a lateral position to the nucleus of infected erythrocytes.

Macrogametocytes (Fig. 142, *1*, *3*, *4*; Table 91). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are not seen; gametocytes grow along the nucleus of infected erythrocytes, they slightly enclose the nucleus with their ends and do not displace or only slightly displace it laterally; medium and fully

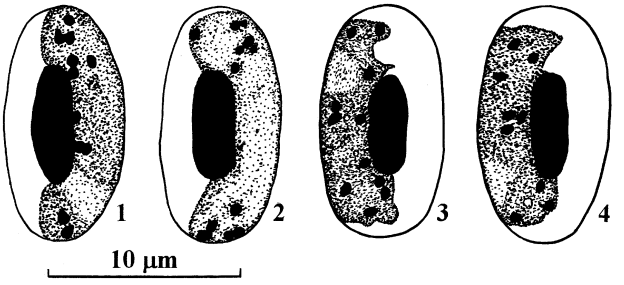

Figure 142 Gametocytes of *Haemoproteus trochili* from the blood of *Eutoxeres aquila:* *1*, *3*, *4* – macrogametocytes, *2* – microgametocyte (*1*, *2* are modified from White *et al*., 1979).

grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are absent; the outline of growing gametocytes varies from even to ameboid (Fig. 142, *3*) and is even in fully grown gametocytes (Fig. 142, *1*); the parasite nucleus is compact, variable in form, subterminal in position (Fig. 142, *3*, *4*); pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; fully grown gametocytes are small (Fig. 142, *1*, *3*, *4*), about 12 μm in length on average (see Table 91).

Microgametocytes (Fig. 142, *2*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The original description of this species (White *et al.*, 1979) is brief, and the intensity of parasitemia in the hapantotype is low. Additional material is required for more detailed investigation of this parasite.

Among the haemoproteids of birds belonging to the Apodiformes, *H. trochili* is especially similar to *H. apodus*. The latter species is characterized by the presence of (i) the large-size (1.0 to 1.5 μm) pigment granules in gametocytes and (ii) the dumbbell-shaped growing gametocytes which do not touch the envelope of erythrocytes. Both these features are not characteristic of *H. trochili*.

73. **Haemoproteus (Parahaemoproteus) witti** White, Bennett and Williams, 1979

Haemoproteus witti White, Bennett and Williams, 1979: 912, Fig. 5, 6.

Type vertebrate host. *Trochilus polytmus* L. (Apodiformes).
Type locality. Greenhills, Jamaica.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 62876, *Trochilus polytmus*, 08.04.1978, Greenhills, Jamaica, H. Witt) is deposited in IRCAH.
Etymology. This species is named in honour of Dr. Hans Witt, who prepared the hapantotype blood smear for description of this species and made a major contribution to the collection of material on blood parasites of Jamaican birds.

Main diagnostic characters. A parasite of species of the Apodiformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally

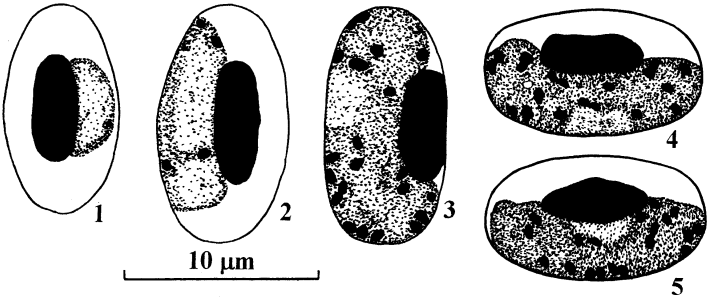

Figure 143 Gametocytes of *Haemoproteus witti* from the blood of *Trochilus polytmus: 1*, *2* – young; *3–5* – macrogametocytes (*1–3* are modified from White *et al*., 1979).

and only slightly enclose the nucleus with their ends. The outline of growing and fully grown gametocytes is even. The parasite nucleus is median or submedian in position. The average number of pigment granules is about 25 per gametocyte.

Development in vertebrate host

Young gametocytes (Fig. 143, *1*, *2*) are usually seen in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 143, *1*) and extend longitudinally along it, they are closely appressed both to the nucleus and envelope of the erythrocytes (Fig. 143, *2*); the outline is even.

Macrogametocytes (Fig. 143, *3–5*; Table 92). The cytoplasm is homogeneous in appearance, usually lacking vacuoles; valutin granules are not characteristic; gametocytes grow along the nucleus of infected erythrocytes; they markedly displace the nucleus laterally and only slightly enclose it with their ends; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; the outline is even; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes. The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Apodiformes, *H. witti* is especially similar to *H. trochili*. It can be distinguished from the latter species primarily on the basis of (i) its smaller NDR, (ii) more numerous pigment granules in gametocytes, and (iii) the median position of nucleus in macrogametocytes.

74. **Haemoproteus (Parahaemoproteus) abdusalomovi** Subkhonov, 1980

Haemoproteus abdusalomovi Subkhonov, 1980: 46, Fig. 2V.

Type vertebrate host. *Glareola pratincola* (L.) (Charadriiformes).
Type locality. The Vakshskaya Valley, Tadzhikistan.
Distribution. This parasite has been recorded in Tadzhikistan and on the eastern coast of the Aral Sea.

Table 92 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. witti* (modified from White *et al.*, 1979)			*H. bilobata* (modified from Bennett and Nandi, 1981)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	15			35		
Length		11.0	0.5		14.8	0.8
Width		5.8	0.3		8.0	0.6
Length of nucleus		5.6	0.2		6.3	0.9
Width of nucleus		2.5	0.3		2.6	0.4
Erythrocyte parasitized by macrogametocyte	15			45		
Length		11.5	0.6		15.6	1.2
Width		6.6	0.6		7.5	0.5
Length of nucleus		5.6	0.3		4.6	0.8
Width of nucleus		2.6	0.3		2.6	0.5
Erythrocyte parasitized by microgametocyte				25		
Length	14	11.7	1.1		16.2	0.8
Width	14	5.4	2.4		7.7	0.6
Length of nucleus	15	5.6	0.3		5.2	0.8
Width of nucleus	15	2.5	0.4		2.6	0.4
Macrogametocyte	15			45		
Length		14.1	1.2		13.1	1.1
Width		3.3	0.5		0.8	0.4
Length of nucleus		3.1	0.5		3.2	0.6
Width of nucleus		2.5	0.5		2.4	0.6
NDR		0.4	0.2		1.0	–
No. of pigment granules		24.1	4.9		16.9	2.0
Microgametocyte				25		
Length	15	14.7	1.5		14.1	0.7
Width	15	3.3	0.4		0.9	0.5
Length of nucleus	2	6.3	1.1		4.1	0.7
Width of nucleus	2	3.5	0.7		3.4	0.5
NDR	15	0.3	0.2		0.9	–
No. of pigment granules	15	24.7	3.7		15.8	1.8

Note: All sizes are given in micrometres.

Type material. Does not exist.
Etymology. This species is named in honour of Tadzhik ornithologist Dr. I.A. Abdusalomov.

Main diagnostic characters. A parasite of species of the Charadriiformes whose fully grown gametocytes markedly enclose the nucleus of infected erythrocytes with their ends but do not encircle it completely; they possess large-size (1.0 to 1.5 μm) pigment granules.

Development in vertebrate host
Macrogametocytes (Fig. 144) grow around the nucleus of infected erythrocytes, they markedly enclose the nucleus with their ends but do not encircle it completely; gametocytes

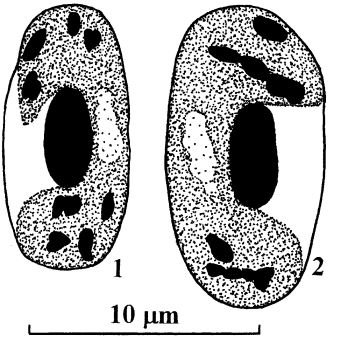

Figure 144 Macrogametocytes of *Haemoproteus abdusalomovi* from the blood of *Glareola pratincola* (modified from Subkhonov, 1980).

do not displace or only slightly displace the nucleus of erythrocytes laterally; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; the outline is even; the parasite nucleus is median in position. According to the illustrations in the original description, pigment granules are of large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm. Their number varies from 11 to 24. According to Subkhonov (1980), gametocytes vary from 10 to 11.5 μm in length, and from 2.2 to 2.7 μm in width. However, larger gametocytes are shown in the illustrations in the original description.

Comments. The original description (Subkhonov, 1980) contain incomplete information about this parasite. According to the personal communication of Professor M.V. Krylov, the type material is lost. Designation of neotype material and redescription of this parasite are required. Based on the original description, *H. abdusalomovi* can be distinguished from the other species of haemoproteids parasitizing charadriiform birds primarily on the basis of the presence of large pigment granules in its gametocytes.

75. **Haemoproteus (Parahaemoproteus) ammoperdix** Subkhonov, 1980

Haemoproteus ammoperdix Subkhonov, 1980: 46, Fig. 2B.

Type vertebrate host. *Ammoperdix griseogularis* (Brandt) (Galliformes).
Type locality. The Vakshskaya Valley, Tadzhikistan.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Does not exist.
Etymology. The specific name is derived from the generic name of the type host, *Ammoperdix*.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes grow around the nucleus of infected erythrocytes and do not displace or only slightly displace it laterally. Gametocytes slightly enclose the nucleus with their ends but do not encircle it completely. The outline of gametocytes is even. The maximum number of pigment granules in gametocytes is greater than 20.

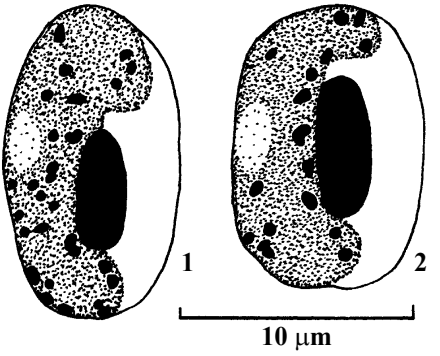

Figure 145 Macrogametocytes of *Haemoproteus ammoperdix* from the blood of *Ammoperdix griseogularis* (modified from Subkhonov, 1980).

Development in vertebrate host

Macrogametocytes (Fig. 145). The cytoplasm is homogeneous in appearance; gametocytes grow around the nucleus of infected erythrocytes and do not displace or only slightly displace it laterally; they slightly enclose the nucleus with their ends but do not encircle it completely; fully grown gametocytes fill the erythrocytes up to their poles, and they are closely appressed both to the nucleus and envelope of erythrocytes; the outline is even; the parasite nucleus is median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, vary from 17 to 33 in number; the average size of gametocytes (n = 10) is 13.7 μm in length and 3.8 μm in width.

Comments. Subkhonov (1980) described this parasite briefly and published illustrations of two macrogametocytes (Fig. 145). According to the personal communication of Professor M.V. Krylov, the type material is lost. Designation of neotype material and redescription of this parasite are required. The available information about this parasite is incomplete, and it is based only on the data which are given in the original description. According to the data available, *H. ammoperdix* can be distinguished from other species of haemoproteids of galliform birds on the basis of the morphology of its gametocytes. Fully grown gametocytes of this parasite possess numerous pigment granules, they do not displace or only slightly displace the nucleus of erythrocytes laterally and do not encircle the nucleus completely.

Among the haemoproteids of birds belonging to the Galliformes, *H. ammoperdix* is especially similar to *H. pratasi*. It can be distinguished from the latter species primarily on the basis of slight (if at all) lateral displacement of erythrocyte nucleus by its gametocytes. According to the illustrations in the original description (Subkhonov, 1980), NDR is 0.8 and 0.9 in erythrocytes parasitized by macrogametocytes of *H. ammoperdix.* The same parameter in *H. pratasi* is 0.5±0.2. Gametocytes of *H. ammoperdix* are also similar to medium grown gametocytes of *H. mansoni*. However, fully grown gametocytes of *H. mansoni* completely encircle the nucleus of infected erythrocytes and occupy all available cytoplasmic space in the erythrocytes. These characters were not recorded for *H. ammoperdix*. It should be noted that the intensity of parasitemia in blood films which were a basis for description of *H. ammoperdix*, was up to 14 gametocytes per 1000 erythrocytes (Subkhonov, 1980). It seems unlikely that the circumnuclear gametocytes were overlooked by Subkhonov (1980) at such high parasitemia if they had been present in the blood films.

Bennett and Peirce (1989) declared *H. ammoperdix* as a junior synonym of *H. rileyi*. However, it is difficult to agree with this synonymy (see 'Comments' to *H. rileyi*).

76. **Haemoproteus (Parahaemoproteus) megapodius** Nandi and Mandal, 1980

Haemoproteus megapodius Nandi and Mandal, 1980: 51, Fig. 1–6.

Type vertebrate host. *Megapodius freycinet* (Gaimard) (Galliformes).
Type locality. Twenty-four km Post on North-South Road, Southwest of Campbell Bay, Great Nicobar Island, India.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. Pt. 1924, *Megapodius freycinet*, 09.04.1977, Campbell Bay, Great Nicobar Island, India, S.S. Saha) and parahapantotypes (No. Pt. 1925, Pt. 1926, other data are as for the hapantotype) are deposited in NZCC.
Etymology. The specific name is derived from the generic name of the type host, *Megapodius*.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes are even in outline; they displace the nucleus of infected erythrocytes laterally but do not encircle it completely. Dumbbell-shaped gametocytes are present. The average number of pigment granules is about 20 per gametocyte.

Development in vertebrate host
Young gametocytes take a position lateral to the nucleus of infected erythrocytes; the outline is even.

Macrogametocytes (Table 93). The cytoplasm is granular in appearance, contains vacuoles, stains irregularly, and is more intensively stained on the periphery of the parasites; valutin granules are not characteristic; fully grown gametocytes slightly displace the nucleus of infected erythrocytes laterally and enclose it with their ends, but do not encircle

Table 93 Morphometric parameters of gametocytes and host cells of *Haemoproteus megapodius* (modified from Nandi and Mandal, 1980).

Feature	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	15		
Length		13.3	0.8
Width		7.7	0.5
Length of nucleus		6.3	0.5
Width of nucleus		2.3	0.1
Macrogametocyte	15		
Length		14.3	1.5
Width		1.9	0.4
Length of nucleus		1.5	0.01
Width of nucleus		1.0	0.01
NDR		0.7	–
No. of pigment granules		21.0	2.2
Microgametocyte	10		
Length		10.5	0.3
Width		3.3	0.7
NDR		0.6	0.1
No. of pigment granules		20.0	1.6

Note: All sizes are given in micrometres.

the nucleus completely; the central part of the pellicle of some growing gametocytes does not extend to the erythrocyte envelope causing a 'dip' and giving a dumbbell-like appearance; some gametocytes rotate the erythrocyte nucleus up to 90° to the normal axis; fully grown gametocytes are even in outline, the parasite nucleus is roundish, subterminal in position; pigment granules are randomly scattered throughout the cytoplasm; infected erythrocytes are not changed significantly in length and width in comparison to uninfected ones, and the nucleus of infected erythrocytes is significantly atrophied in length but unchanged in width.

Microgametocytes. The general configuration is as for macrogametocytes with usual sexual dimorphic characters; the cytoplasm stains pale; microgametocytes are shorter and thicker than macrogametocytes (Table 93); other characters are as for macrogametocytes.

Comments. The author did not manage to obtain the type material for examination. The data about *H. megapodius* presented above are mainly based on the original description which is brief and does not contain sufficiently clear microphotographs (Nandi and Mandal, 1980). The redescription of this parasite is necessary to clarify its main diagnostic characters. During the identification of *H. megapodius*, attention should be paid to the dumbbell-shaped growing gametocytes. According to the original description (Nandi and Mandal, 1980), *H. megapodius* is similar to *H. fringillae* due to the dumbbell-like appearance of its gametocytes. It should be mentioned that the dumbbell-shaped gametocytes are absent in other species of haemoproteids parasitizing galliform birds.

77. **Haemoproteus (Parahaemoproteus) bilobata** Bennett and Nandi, 1981

Haemoproteus bilobata Bennett and Nandi, 1981: 2069, Fig. 10–12.

Type vertebrate host. *Psilopogon pyrolophus* (Müller) (Piciformes).
Additional vertebrate hosts. *Megalaima asiatica*, *M. zeylanica* (Piciformes).
Type locality. Mt. Brinchang, Malaya.
Distribution. The Oriental zoogeographical region.
Type material. Hapantotype (No. 3074, *Psilopogon pyrolophus*, 02.09.1960, Mt. Brinchang, Malaya, H.E. McClure) and parahapantotypes (No. 11641, *Megalaima zeylanica*, 12.05.1964; Chiangmei, Thailand; No. 37082, *M. asiatica*, 06.10.1968, West Bhutan, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name reflects the markedly bilobated shape of fully grown gametocytes.

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes are markedly bilobated in shape (Fig. 146, *6*). Gametocytes are closely appressed to the nucleus of infected erythrocytes but do not touch the envelope of the erythrocyte along their entire margin. The average width of fully grown gametocytes is less than 2 μm.

Development in vertebrate host
Young gametocytes (Fig. 146, *1*, *2*). The earliest forms are usually seen in a lateral or subpolar position in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; at this stage of development, dumbbell-shaped forms were not seen; the outline is even.

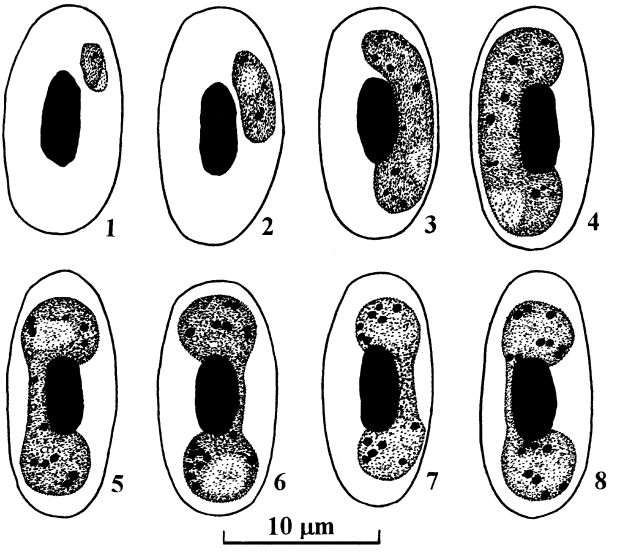

Figure 146 Gametocytes of *Haemoproteus bilobata* from the blood of *Psilopogon pyrolophus: 1*, *2* – young; *3–6* – macrogametocytes; *7*, *8* – microgametocytes.

Macrogametocytes (Fig. 146, *3–6*; Table 92). The cytoplasm is finely granular in appearance, stains pale blue or even rose, which is a rare character for avian haemoproteids; gametocytes grow around the nucleus of infected erythrocytes, are closely appressed to the nucleus of erythrocytes but do not touch the envelope of erythrocytes along their entire margin, and a clear more or less evident unfilled space (a 'cleft') is available between the parasite and the erythrocyte envelope (Fig. 146, *4–6*); gametocytes do not fill the erythrocytes up to their poles; fully grown gametocytes are markedly bilobated in shape with the ends of parasite being spherical in form and connected by a narrow band of cytoplasm (Fig. 146, *6*); gametocytes take the markedly bilobated shape only at the latest stages of development, and growing forms are of halteridian shape typical of haemoproteids (Fig. 146, *3, 4*); the outline is even; the parasite nucleus is compact, roundish or oval, subterminal in position (Fig. 146, *5*, *6*); pigment granules are usually roundish, of medium (0.5 to 1.0 μm) size; they are randomly scattered throughout the cytoplasm in growing gametocytes but are aggregated in the lobular parts of fully grown gametocytes and are absent in the middle part of the gametocytes (Fig. 146, *6*), which is a rare character for haemoproteids; the nucleus of infected erythrocytes usually is not displaced laterally, but sometimes is rotated up to 90° to the normal axis; the nucleus of infected erythrocytes is significantly atrophied in length in comparison to uninfected ones (Table 92).

Microgametocytes (Fig. 146, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is relatively compact in comparison to other species of haemoproteids, which is a rare character for bird haemoproteids; some nuclei of infected erythrocytes are rotated up to 45° to the normal axis; other characters are as for macrogametocytes.

C o m m e n t s. The rotation of nucleus of infected erythrocytes by gametocytes was occasionally seen in the type material. The diagnostic use of this character is not clear.

78. **Haemoproteus (Parahaemoproteus) cornuata** Bennett and Nandi, 1981

Haemoproteus cornuata Bennett and Nandi, 1981: 2068, Fig. 8, 9.

Type vertebrate host. *Megalaima asiatica* (Latham) (Piciformes).
Additional vertebrate hosts. *Lybius leucomelas*, *Megalaima franklinii*, *M. viridis*, *M. zeylanica*, *Trachyphonus vaillantii* (Piciformes).
Type locality. West Bhutan.
Distribution. The Oriental and Ethiopian zoogeographical region.
Type material. Hapantotype (No. 37082, *Megalaima asiatica*, 06.10.1968, West Bhutan, H.E. McClure) and parahapantotype (No. 37118, *M. viridis*, 26.04.1969, Maharashtra State, India, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name reflects the horn-like appearance of the ends of gametocytes of this parasite (Fig. 147, *5*).

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes markedly enclose the nucleus of infected erythrocytes with their ends but do not encircle the nucleus completely. The ends of gametocytes are pointed and frequently form a pair of 'horns' (Fig. 147, *5*, *8*). Medium grown gametocytes, which do not touch the nucleus of erythrocytes, are present. The average number of pigment granules is about 30 per gametocyte. The average length of fully grown gametocytes is greater than 18 μm.

Development in vertebrate host
Young gametocytes (Fig. 147, *1*) are usually seen in a position lateral to the nucleus of infected erythrocytes, they are elongated rod-like and usually do not touch either the nucleus or envelope of erythrocytes; the outline is even.

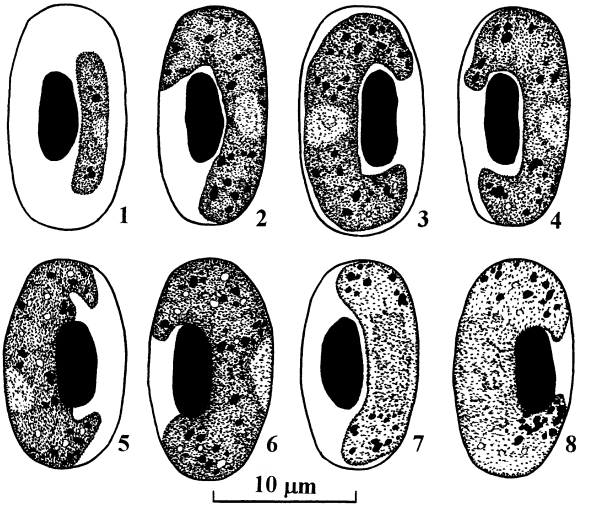

Figure 147 Gametocytes of *Haemoproteus cornuata* from the blood of *Megalaima asiatica:* *1* – young; *2–6* – macrogametocytes; *7*, *8* – microgametocytes.

Table 94 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. cornuata* (modified from Bennett and Nandi, 1981)			*H. killangoi* (modified from Bennett and Peirce, 1981)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	15			30		
Length		14.1	1.0		11.4	2.1
Width		8.3	0.5		6.1	2.3
Length of nucleus		6.1	1.5		5.6	0.4
Width of nucleus		2.7	0.6		2.3	0.3
Erythrocyte parasitized by macrogametocyte	30			30		
Length		15.6	1.1		12.3	0.8
Width		8.6	0.6		7.0	0.6
Length of nucleus		6.0	0.7		5.4	0.4
Width of nucleus		2.6	0.2		2.2	0.4
Erythrocyte parasitized by microgametocyte	10			20		
Length		16.2	0.9		12.0	0.8
Width		8.6	0.6		6.8	0.7
Length of nucleus		6.3	0.6		5.2	0.5
Width of nucleus		2.6	0.2		2.2	0.3
Macrogametocyte	30			30		
Length		21.9	2.3		12.8	1.5
Width		4.3	0.6		1.4	0.6
Length of nucleus		3.5	0.8		2.0	0.4
Width of nucleus		2.3	0.4		1.4	0.5
NDR		0.5	–		1.0	–
No. of pigment granules		28.2	6.4		8.9	1.8
Microgametocyte	10			20		
Length		24.5	2.2		12.4	1.3
Width		4.1	0.4		1.5	0.5
Length of nucleus		4.9	1.1		5.9	1.8
Width of nucleus		3.0	0.4		1.4	0.4
NDR		0.6	–		1.0	–
No. of pigment granules		28.4	2.5		8.6	2.2

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 147, *2–6*; Table 94). The cytoplasm is coarsely granular in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends but do not encircle it completely; ends of gametocytes are frequently pointed and look like 'horns' due to more or less symmetrical invaginations of the parasite pellicle near the poles of nucleus of erythrocytes (Fig. 147, *5*); growing gametocytes do not touch the nucleus of erythrocytes and usually adhere to the envelope of erythrocytes (Fig. 147, *2*, *4*); gametocytes, which lie free in the cytoplasm and do not touch either the nucleus or envelope of

erythrocytes (Fig. 147, *3*), are present; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 147, *5*, *6*); the outline is even; the parasite nucleus is compact, variable in form, frequently oval, median or submedian in position; pigment granules are usually roundish, sometimes oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 147, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Piciformes, *H. cornuata* is especially similar to *H.velans* and *H.indicator*. Fully grown gametocytes of *H.cornuata* are similar to medium grown gametocytes of *H. velans*. However, circumnuclear gametocytes were not recorded in *H. cornuata* but are common in *H. velans*. *Haemoproteus cornuata* can be distinguished from *H. indicator* primarily on the basis of (i) its smaller number of pigment granules in macrogametocytes, and (ii) there being approximately the same number of pigment granules in macro- and microgametocytes.

79. **Haemoproteus (Parahaemoproteus) killangoi** Bennett and Peirce, 1981

Haemoproteus killangoi Bennett and Peirce, 1981: 1158, Fig. 3, 4.

Type vertebrate host. *Zosterops senegalensis* Bonaparte (Passeriformes).
Additional vertebrate hosts. *Zosterops abyssinica*, *Z. maderaspatana*, *Z. pallida*, *Z. palpebrosa* (Passeriformes). Haemoproteids from *Hippolais icterina* and *Muscicapa striata* were attributed to *H. killangoi* erroneously (Valkiūnas, 1985a).
Type material. Zika Forest, Uganda.
Distribution. The Ethiopian and Oriental zoogeographical regions.
Type material. Hapantotype (No. 44999, *Zosterops senegalensis*, 08.10.1975, Zika Forest, Uganda, A.B.C. Killango) and parahapantotypes (No. 44998, other data are as for the hapantotype; No. 28153, 23.02.1972, Entebbe, Uganda, N.O. Okia, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. This species is named in honour of Dr. A.B.C. Killango, who collected the type material for the description of this species.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes with a highly ameboid outline predominate among growing gametocytes. Fully grown gametocytes do not displace the nucleus of erythrocytes laterally. Pigment granules are usually of large (1.0 to 1.5 μm) size, rod-like, about eight per gametocyte on average. Large rod-like pigment granules predominate in medium grown gametocytes.

Development in vertebrate host
Young gametocytes (Fig. 148, *1*) are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline varies from even to slightly ameboid.

Macrogametocytes (Fig. 148, *2–4*; Table 94). The cytoplasm is finely granular in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus

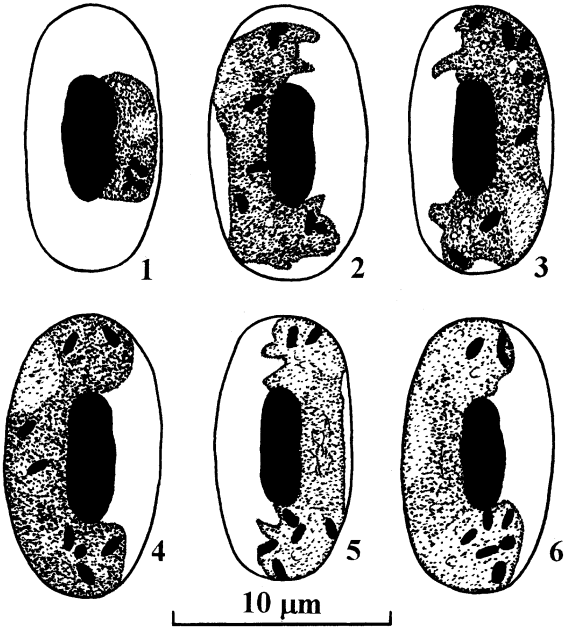

Figure 148 Gametocytes of *Haemoproteus killangoi* from the blood of *Zosterops senegalensis: 1* – young; *2–4* – macrogametocytes; *5*, *6* – microgametocytes.

of infected erythrocytes, and they do not displace the nucleus laterally and do not encircle it completely; medium and fully grown gametocytes fill the erythrocytes up to their poles (Fig. 148, *3*, *4*); gametocytes adhere to the nucleus and envelope of erythrocytes; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 148, *2*, *3*); the dumbbell-shaped gametocytes predominate among the growing gametocytes; fully grown gametocytes lose the dumbbell-like shape, and they are closely appressed to the nucleus and envelope of erythrocytes (Fig. 148, *4*); the outline of growing gametocytes is usually highly ameboid (Fig. 148, *2*, *3*), and is even in fully grown forms (Fig. 148, *4*); the parasite nucleus is compact, variable in form and subterminal in position; pigment granules are frequently rod-like, but sometimes roundish, usually of large (1.0 to 1.5 μm) but sometimes also of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm. It should be noted that large (1.0 to 1.5 μm) rod-like pigment granules appear in growing gametocytes and predominate in medium grown gametocytes (Fig. 148, *2*,*3*); in fully grown gametocytes, large (1.0 to 1.5 μm) rod-like pigment granules clearly predominate (Fig. 148, *4*).

Microgametocytes (Fig. 148, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Haemoproteus killangoi* has been frequently recorded in mixed infection with *H. zosteropis*, and both these parasites are common in passerine birds of the family Zosteropidae. Growing gametocytes of *H. killangoi* and *H. zosteropis* can be easily distinguished, but fully grown parasites are similar. If the young gametocytes are absent in the blood, attention should be, first of all, paid to the number of pigment granules in fully grown gametocytes. The fully grown gametocytes of *H. killangoi* possess a smaller number of pigment granules than gametocytes of *H. zosteropis*.

Among the haemoproteids of birds belonging to the Passeriformes, *H. killangoi* is especially similar to *H. motacillae* and *H. picae*. It can be distinguished from the latter two species primarily on the basis of the highly ameboid outline of its growing macrogametocytes. Furthermore, in *H. killangoi*, large (1.0 to 1.5 μm), rod-like pigment granules appear in young gametocytes and predominate in medium grown forms. These characters are not characteristic of both *H. motacillae* and *H. picae*.

80. **Haemoproteus (Parahaemoproteus) cracidarum** Bennett, Gabaldon and Ulloa, 1982

Haemoproteus cracidarum Bennett, Gabaldon and Ulloa, 1982a: 3109, Fig. 9–14.

Type vertebrate host. *Ortalis ruficauda* Jardine (Galliformes).
Additional vertebrate host. *Penelope purpurascens* (Galliformes).
Type locality. San Juan de los Morros, Guarico, Venezuela.
Distribution. The Neotropical zoogeographical region.
Type material. Hapantotype (No. 82641, *Ortalis ruficauda*, 20.12.1972, San Juan de los Morros, Guarico, A. Gabaldon, G. Ulloa) and parahapantotypes (No. 86243, 19.05.1975, Cabure, Falcón; No. 86244, 05.06.1973, Acuriqua, Falcón; No. 86253, 15.10.1973, Miranda, Trujillo;

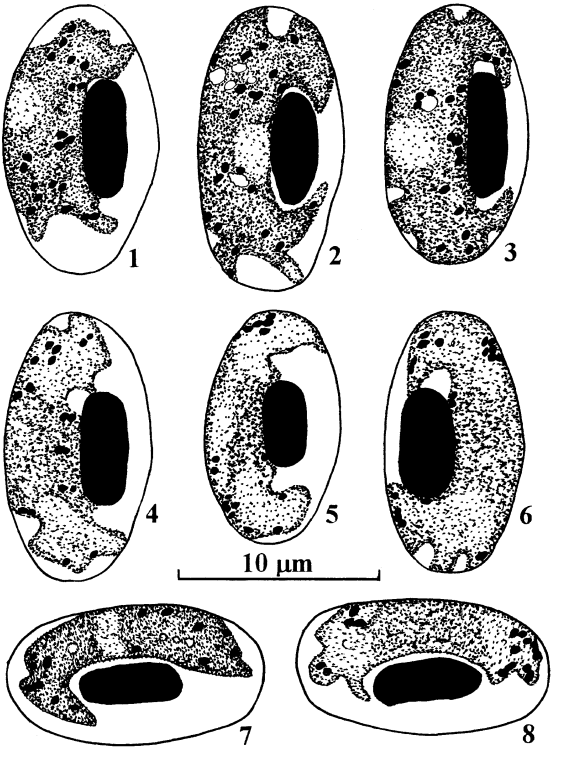

Figure 149 Gametocytes of *Haemoproteus cracidarum* from the blood of *Ortalis ruficauda*: *1–3*, *7* – macrogametocytes; *4–6*, *8* – microgametocytes (*1–6* are modified from Bennett *et al*., 1982a).

Table 95 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. cracidarum* (modified from Bennett *et al.*, 1982a)			*H. nisi* (according to Valkiūnas and Iezhova, 1989)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	100			31			
Length		13.0	0.8		12.2–13.9	13.0	0.6
Width		7.3	0.4		6.7–8.0	7.4	0.4
Length of nucleus		5.9	0.6		6.0–7.7	6.9	0.2
Width of nucleus		2.3	0.3		2.3–3.3	2.7	0.1
Erythrocyte parasitized by macrogametocyte	50			31			
Length		13.6	0.5		11.7–15.7	13.9	0.6
Width		7.8	0.4		6.5–8.8	7.7	0.4
Length of nucleus		5.1	0.4		5.1–7.3	6.3	0.2
Width of nucleus		2.3	0.3		2.0–2.9	2.4	0.1
Erythrocyte parasitized by microgametocyte	20			31			
Length		13.4	0.7		12.9–15.0	14.0	0.5
Width		7.5	0.4		7.1–9.6	7.9	0.4
Length of nucleus		5.4	0.6		5.2–7.2	6.2	0.2
Width of nucleus		2.1	0.1		2.0–3.2	2.5	0.1
Macrogametocyte	50			31			
Length		19.9	1.9		16.9–23.5	19.6	1.6
Width		4.2	0.4		2.3–3.4	2.8	0.4
Length of nucleus		3.1	0.5		2.8–4.6	3.4	0.3
Width of nucleus		2.5	0.4		2.0–3.3	2.6	0.2
NDR		0.5	–		0.8–1.1	0.9	0.1
No. of pigment granules		22.5	2.0		9–20	14.0	2.4
Microgametocyte	20			31			
Length		18.3	1.7		16.9–23.0	20.1	1.8
Width		4.3	0.3		2.3–3.4	3.0	0.3
Length of nucleus		5.1	0.8		7.5–18.0	10.8	1.2
Width of nucleus		2.8	0.4		2.3–3.4	3.0	0.2
NDR		0.4	–		0.7–1.1	0.9	0.1
No. of pigment granules		19.4	0.9		9–25	12.7	2.6

Note: All sizes are given in micrometres.

No. 86283, 26.08.1977, El Paujil, Sucre, other data for all above mentioned slides are as for the hapantotype) are deposited in IRCAH.

Etymology. The specific name is derived from the name of the family Cracidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Galliformes whose fully grown gametocytes are highly ameboid in outline; they displace the nucleus of infected erythrocytes laterally, enclose the nucleus with their ends, but do not encircle it completely. The average number of pigment granules is about 20 per gametocyte.

Development in vertebrate host

Young gametocytes. The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes usually take a position lateral to the nucleus of erythrocytes and they frequently do not touch the nucleus; the outline is usually ameboid.

Macrogametocytes (Fig. 149, *1–3*, *7*; Table 95). The cytoplasm is heterogeneous in appearance, frequently contains several small vacuoles; valutin granules are generally present and gather at the ends of gametocytes; gametocytes grow around the nucleus of infected erythrocytes; medium grown gametocytes, which do not touch the nucleus of erythrocytes (Fig. 149, *7*), are present; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes, and a clear unfilled space appears between the ends of the gametocytes and the poles of nucleus of erythrocytes (Fig. 149, *2*, *3*), which subsequently disappears; one or several clear 'dips,' which look like vacuoles, are frequently seen between the gametocyte and the envelope of erythrocytes, and these 'dips' are especially pronounced near the poles of the erythrocytes (Fig. 149, *2*, *3*, *6*); fully grown gametocytes fill the erythrocytes up to their poles, they displace the nucleus of erythrocytes laterally, enclose the nucleus with their ends but do not encircle it completely (Fig. 149, *2*, *3*); growing and fully grown gametocytes are highly ameboid in outline; the parasite nucleus is compact, frequently roundish in form and median or submedian in position; pigment granules are roundish or slightly oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 149, *4–6, 8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Galliformes, *H. cracidarum* is especially similar to *H. pratasi* and *H. rileyi*. It can be distinguished from the latter two species primarily on the basis of the highly ameboid outline of its fully grown gametocytes.

81. **Haemoproteus (Parahaemoproteus) nisi** Peirce and Marquiss, 1983

Haemoproteus nisi Peirce and Marquiss, 1983: 816, Fig. 1–6.

Type vertebrate host. *Accipiter nisus* (L.) (Falconiformes).

Additional vertebrate hosts. Some species of the Falconiformes (Table 96).

Type locality. Dumfriesshire, Scotland, UK.

Distribution. The Holarctic, and the Ethiopian and Oriental zoogeographical regions. A common parasite in the Palearctic where the prevalence of infection significantly increases from the north-western part toward the south-eastern part of the range of the type vertebrate host (Valkiūnas and Iezhova, 1990a).

Type material. Hapantotype (No. 91084, *Accipiter nisus,* 04.09.1979, Bellholm, Dumfries, Scotland, M.A. Peirce) and parahapantotypes (No. 91081-91083, 1980, other data are as for the hapantotype) are deposited in IRCAH. A series of additional slides is deposited in CDVA.

Etymology. The specific name is derived from the specific name of the type host, *nisus*.

Main diagnostic characters. A parasite of species of the Falconiformes whose fully grown gametocytes grow around the nucleus of infected erythrocytes and can completely encircle the nucleus; they do not displace the nucleus laterally and do not occupy

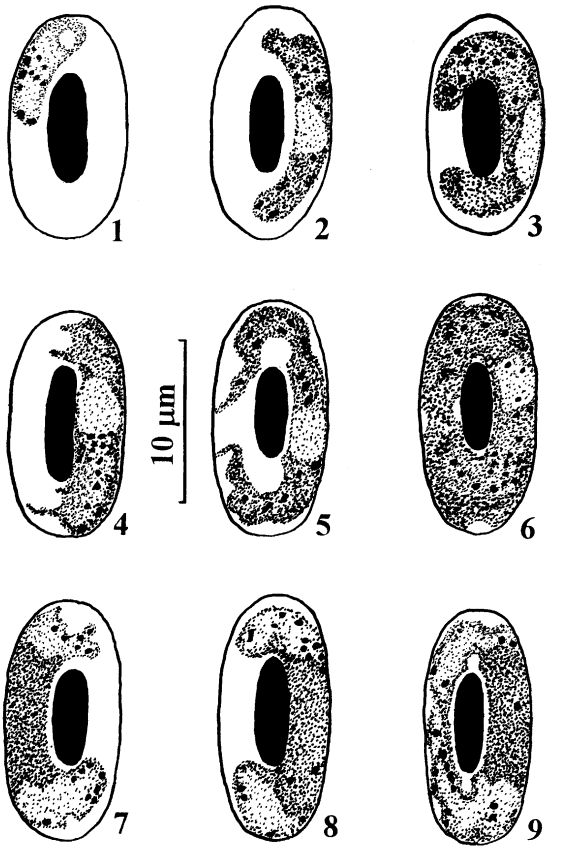

Figure 150 Gametocytes of *Haemoproteus nisi* from the blood of *Accipiter nisus:*
1 – young; *2–6* – macrogametocytes; *7–9* – microgametocytes (modified from Valkiūnas and Iezhova, 1989).

all available cytoplasmic space in the erythrocytes. The majority of gametocytes are without finger-like ameboid outgrowths. Over 50% of mature gametocytes do not touch the nucleus of infected erythrocytes.

Development in vertebrate host

Young gametocytes (Fig. 150, *1*). The earliest forms can be seen anywhere in infected erythrocytes; they are roundish or oval; as the parasite develops, gametocytes markedly extend longitudinally along the nucleus of erythrocytes, and they do not displace the nucleus laterally; growing gametocytes adhere to the envelope of erythrocytes but usually do not touch the erythrocyte nucleus; the outline is usually even, but sometimes wavy or slightly ameboid.

Macrogametocytes (Fig. 150, *2–6*; Table 95). The cytoplasm is granular in appearance, frequently contains a few small vacuoles, stains irregularly; valutin granules are generally present, obscuring the pigment granules; gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends and finally completely encircle it but do not occupy all available cytoplasmic space in the host cells; a

Table 96 List of vertebrate hosts of *Haemoproteus nisi*.

Accipiter cooperi	*Aquila clanga*	*C. cyaneus*
A. soloensis	*A. wahlbergi*	*C. macrourus*
A. striatus	*Butastur indicus*	*C. pygargus*
A. tachiro	*Buteo buteo*	*Melierax metabates*
A. trivirgatus	*B. jamaicensis*	*Milvus migrans*
A. virgatus	*Circus aeruginosus*	

more or less evident unfilled space is available around the nucleus of erythrocytes and gametocytes (Fig. 150, *5, 6*); the central part of the growing gametocytes is closely appressed to the erythrocyte envelope, but the ends of the gametocytes are not (Fig. 150, *3, 5*); gametocytes usually do not touch the nucleus of erythrocytes or touch the nucleus only slightly, and, as a result, a more or less evident unfilled space (a 'cleft') is frequently available between the parasite and the erythrocyte nucleus (Fig. 150, *5*, *6*); however, gametocytes touching the erythrocyte nucleus (Fig. 150, *4*) are also present; the outline varies from even (Fig. 150, *3*) and wavy (Fig. 150, *5*) to highly ameboid (Fig. 150, *4*); gametocytes especially common in shape and outline are shown in Fig. 150, *5*; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are usually roundish, sometimes oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; gametocytes do not displace or only slightly displace the nucleus of infected erythrocytes laterally.

Microgametocytes (Fig. 150, *7–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline is usually even (Fig. 150, *8*), and if ameboid outgrowths are present, they look like thick outgrowths at the ends of gametocytes (Fig. 150, *7*); other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Falconiformes, *H. nisi* is especially similar to *H. brachiatus* and *H. janovyi* (see 'Comments' to these species).

82. **Haemoproteus (Parahaemoproteus) balmorali** Peirce, 1984

Haemoproteus balmorali Peirce, 1984b: 123, Fig. 1–3. – *H. bacillaris* Valkiūnas and Iezhova, 1991: 216, Fig. 3. – *H. balmorali*: Peirce and Bennett, 1993: 505 (=*H. bacillaris*).

T y p e v e r t e b r a t e h o s t. *Muscicapa striata* (Pall.) (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. Numerous species of the Passeriformes belonging to the Muscicapidae and Turdidae (over 40 species).
V e c t o r s. Sporogony is completed and sporozoites appear in the salivary glands of experimentally infected *Culicoides impunctatus* (Valkiūnas *et al.*, 2002b).
T y p e l o c a l i t y. Balmoral, Zambia.
D i s t r i b u t i o n. The Palearctic and the Ethiopian and Oriental zoogeographical regions.
T y p e m a t e r i a l. Hapantotype (No. 91702, *Muscicapa striata,* 23.11.1980, Balmoral, Zambia, M.A. Peirce) and parahapantotype (No. 91701, *Malaenornis pammelaina*, 15.03.1981, other data are as for the hapantotype) are deposited in IRCAH. A series of additional slides of gametocytes, gametes, zygotes, and ookinetes is deposited in CDVA.
E t y m o l o g y. The specific name is derived from the name of the type locality, Balmoral.

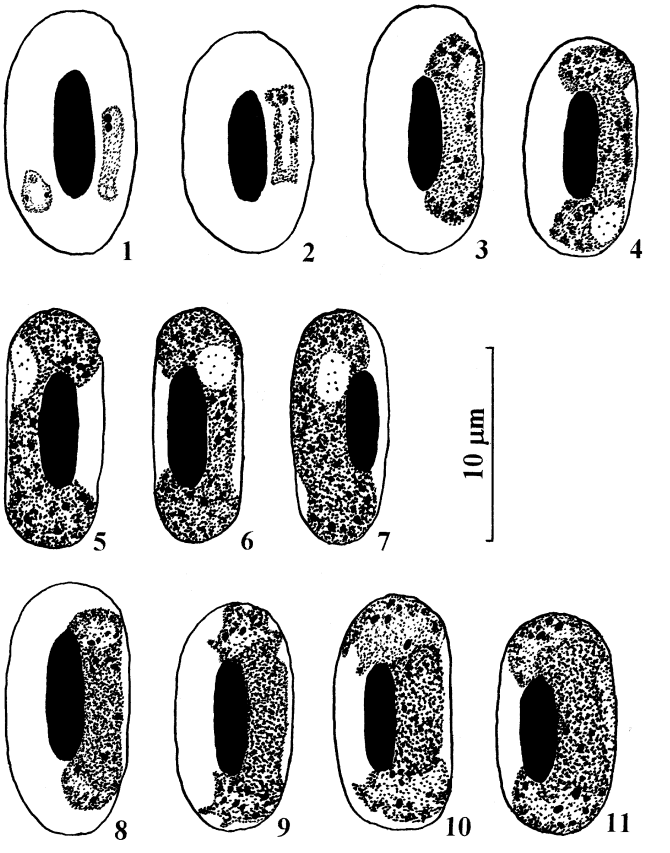

Figure 151 Gametocytes of *Haemoproteus balmorali* from the blood of *Muscicapa striata:* *1*, *2* – young; *3–7* – macrogametocytes; *8–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1991).

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes; they fill the erythrocytes up to their poles but do not encircle the nucleus of erythrocytes completely. Young gametocytes are usually clearly elongated rod-like. The cytoplasm of gametocytes contains numerous valutin granules. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped forms predominate among the growing gametocytes. Fully grown gametocytes displace the nucleus of erythrocytes laterally. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about 15 per gametocyte on average. The average NDR is 0.5 or less.

Development in vertebrate host

Young gametocytes (Fig. 151, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes take an elongated rod-like shape and are usually located in a lateral position to the nucleus of erythrocytes (Fig. 151, *1*,*2*); advanced gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline varies from even to ameboid.

Table 97 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. balmorali*				*H. cublae* (modified from Bennett *et al.*, 1990)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				15		
Length		10.0–12.6	11.3	0.6		12.2	0.5
Width		5.8–7.1	6.6	0.3		6.5	0.5
Length of nucleus		4.8–6.6	5.8	0.2		5.3	0.4
Width of nucleus		2.1–2.8	2.4	0.1		1.8	0.2
Erythrocyte parasitized by macrogametocyte	31				15		
Length		11.0–13.2	12.1	0.6		13.0	0.6
Width		4.7–6.5	5.8	0.2		6.9	0.6
Length of nucleus		5.0–6.7	5.9	0.2		6.0	0.6
Width of nucleus		1.8–2.7	2.1	0.1		1.9	0.2
Erythrocyte parasitized by microgametocyte	31				10		
Length		11.6–13.3	12.2	0.5		13.6	1.0
Width		5.2–6.9	6.7	0.3		6.9	0.7
Length of nucleus		5.2–6.6	6.1	0.1		6.0	0.5
Width of nucleus		1.8–2.6	2.2	0.1		2.0	0.2
Macrogametocyte	48				15		
Length		11.0–16.4	15.0	0.8		12.7	1.2
Width		1.6–3.7	3.0	0.4		2.9	0.5
Length of nucleus		2.2–4.0	2.9	0.3		2.6	0.5
Width of nucleus		1.3–3.2	2.2	0.2		1.8	0.4
NDR		0.2–1.0	0.4	0.2		0.9	0.1
No. of pigment granules		13–24	15.5	1.6		16.7	1.3
Microgametocyte	31				10		
Length		11.6–17.0	15.4	1.0		13.5	0.7
Width		1.6–3.5	2.9	0.6		2.9	0.4
Length of nucleus		7.0–9.2	8.0	0.6		5.9	0.5
Width of nucleus		1.6–3.0	2.2	0.2		2.3	0.4
NDR		0.2–1.0	0.5	0.1		0.8	0.1
No. of pigment granules		10–21	13.0	1.8		17.3	1.6

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 151, *3–7*; Table 97). The cytoplasm is heterogeneous in appearance, contains numerous valutin granules which markedly obscure the pigment granules; gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely; gametocytes are closely appressed to the nucleus of erythrocytes and they also adhere to the envelope of erythrocytes; however, the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 151, *4–6*); dumbbell-shaped forms predominate among the growing gametocytes; fully grown gametocytes are closely appressed

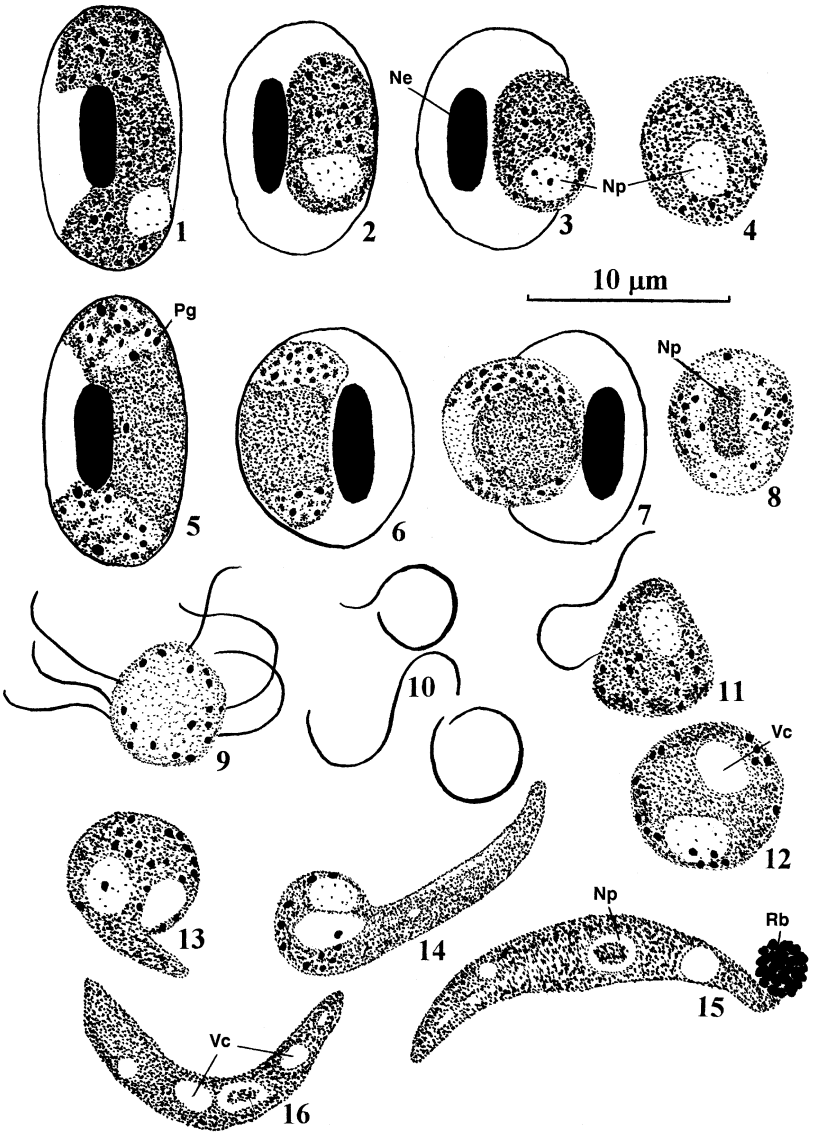

Figure 152 *Haemoproteus balmorali* gametogenesis, zygote and ookinete development *in vitro*: *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Ficedula hypoleuca* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14* – medium differentiated ookinete; *15* – ookinete with a residual body; *16* – fully differentiated ookinete; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1994).

both to the nucleus and envelope of erythrocytes, and fill the erythrocytes up to their poles; the outline is even or slightly ameboid; the parasite nucleus is variable in form, subterminal in position; a parasite nucleus typical in form and position is shown in Fig. 151, *5*; pigment

granules are usually roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; they are difficult to see and count because of heterogeneous cytoplasm and numerous valutin granules.

Microgametocytes (Fig. 151, *8–11*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters. Numerous valutin granules are aggregated at the ends of gametocytes and, as a result, the ends stain more intensively than the central part of gametocytes. This peculiarity of staining is a characteristic feature of this species, but it is difficult to illustrate in black and white illustrations. The outline is more ameboid than in macrogametocytes. Other characters are as for macrogametocytes.

Development in vector

Sporogony is completed in the experimentally infected biting midge *Culicoides impunctatus* (Valkiūnas *et al*., 2002b). Gametogenesis, development of zygote and ookinete *in vitro* under a light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1994). The data on the rate of this process are given in Table 26. Within 1 to 3 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave the infected erythrocytes (Fig. 152, *2*, *3*, *7, 8*). At approximately the same time, macrogametes appear (Fig. 152, *4*), exflagellation takes place (Fig. 152, *9*) and free microgametes are seen (Fig. 152, *10*). Fertilization of macrogametes (Fig. 152, *11*) and first zygotes (Fig. 152, *12*) were recorded 5 min after EBA. Zygotes can be readily distinguished from macrogametes on the basis of a large clear 'vacuole' which is present in their cytoplasm (Fig. 152, *12*). The initial stages of ookinete differentiation were seen 3 h after EBA. At this time, a long finger-like outgrowth develops, located tangentially to the main body of the parasite (Fig. 152, *13*). As the ookinete develops, this outgrowth extends markedly and forms the anterior or apical end of the ookinete. Accumulation of pigment granules was recorded at the opposite end of the medium differentiated ookinetes (Fig. 152, *14*). In fully grown ookinetes, the pigment and adjacent part of the cytoplasm are eliminating as a large residual body (Fig. 152, *15*). It should be noted that large 'vacuoles' present at all stages of differentiation of ookinetes (Fig. 152, *13–16*). Mature ookinetes are elongated worm-like bodies (Fig. 152, *16*). The ookinetes with a residual body were seen approximately 6 h after EBA, and fully differentiated ookinetes without the residual body were recorded only 48 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 27.

It is important to note that the gametogenesis, development of zygote and ookinete *in vitro* of *H. balmorali*, which was isolated from the blood of *Ficedula hypoleuca* (Muscicapidae) and *Saxicola rubetra* (Turdidae) coincide in detail. This shows that the same species of haemoproteids parasitize these birds.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. balmorali* is especially similar to *H. attenuatus*. It can be distinguished from this species primarily on the basis of (i) its marked lateral displacement of erythrocyte nucleus by gametocytes, (ii) the greater width of gametocytes, and (iii) the lack of 'attenuated' growing microgametocytes (see Fig. 170, *9*, *10*). During the identification of *H. balmorali* and *H. attenuatus*, attention should be paid to the above mentioned characters because both species develop in the same vertebrate host, *Erithacus rubecula*. Furthermore, *H. balmorali* is also similar to *H. majoris* and *H. queleae*. It can be distinguished from the latter two species primarily on the basis of (i) its elongated rod-like shape of young gametocytes, and (ii) the numerous valutin granules in growing and fully grown gametocytes.

It was noted in the original description of *H. balmorali* (Peirce, 1984b) that this parasite develops in passerine birds of the families Turdidae and Muscicapidae. Bennett *et al.* (1991b) reduced the range of the vertebrate hosts of *H. balmorali* only to the Old World flycatchers. However, both the Old World flycatchers and thrushes were later recognised again as hosts of *H. balmorali* (Peirce

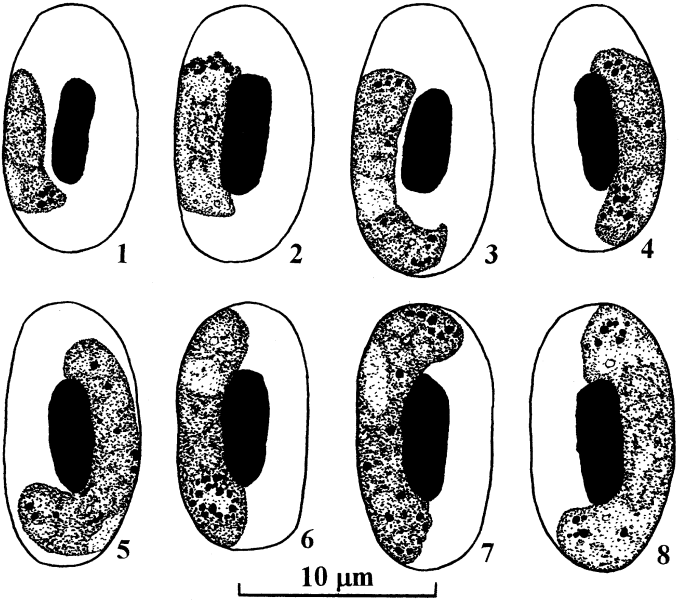

Figure 153 Gametocytes of *Haemoproteus cublae* from the blood of *Dryoscopus cubla: 1*, *2* – young; *3–7* – macrogametocytes; *8* – microgametocyte.

and Bennett, 1993). The results of our investigation also show that *H. balmorali* develops in some birds of the families Turdidae and Muscicapidae. Identical gametocytes develop in the blood of birds belonging to these families, and the development *in vitro* of the parasite, which was isolated from the blood of turdid and muscicapid birds, coincides in details.

83. **Haemoproteus (Parahaemoproteus) cublae** Peirce, 1984

Haemoproteus cublae Peirce, 1984c: 219, Fig.

Type vertebrate host. *Dryoscopus cubla* (Shaw) (Passeriformes).
Additional vertebrate hosts. *Laniarius barbarus*, *L. ferrugineus*, *Malaconotus olivaceus*, *M. sulfureopectus*, *Tchagra minuta* (Passeriformes).
Type locality. Balmoral (15°33′ S, 28°12′ E), Zambia.
Distribution. The Ethiopian zoogeographical region.
Type material. Hapantotype (No. 91700, *Dryoscopus cubla,* 07.03.1981, Balmoral, Zambia, M.A. Peirce) and parahapantotype (No. 46918, *Laniarius barbarus*, 15.01.1970, Queen Elizabeth National Park, Uganda, M.A. Peirce) are deposited in IRCAH. Gametocytes of *Leucocytozoon* sp. are present in the hapantotype.
Etymology. The specific name is derived from the specific name of the type host, *cubla*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely and do not displace or only slightly displace the nucleus laterally. Growing gametocytes are closely appressed to the envelope of erythrocytes. Medium grown gametocytes, which do not touch the nucleus of erythrocytes along their entire margin, are present. Fully

grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes. The average number of pigment granules is about 17 per gametocyte. Pigment granules in macrogametocytes tend to aggregate into one loose group. The average NDR is greater than 0.7.

Development in vertebrate host

Young gametocytes (Fig. 153, *1*, *2*) are usually seen in a lateral position to the nucleus of infected erythrocytes; growing gametocytes are usually closely appressed to the envelope of erythrocytes but do not touch their nucleus (Fig. 153, *1*), however, gametocytes adhering to the nucleus of erythrocytes are also seen (Fig. 153, *2*); the outline is even or slightly ameboid.

Macrogametocytes (Fig. 153, *3–7*; Table 97). The cytoplasm is finely granular in appearance, sometimes contains valutin granules and a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, and they do not displace or only slightly displace the nucleus laterally and do not encircle it completely; some gametocytes rotate the nucleus of erythrocytes 15° to the normal axis; gametocytes are closely appressed to the envelope of erythrocytes; medium grown gametocytes, which do not touch the nucleus of erythrocytes (Fig. 153, *3*), are present; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 153, *6*, *7*), and they fill the erythrocytes up to their poles (Fig. 153, *7*); the outline is even; the parasite nucleus is variable in form, relatively small (see Table 97), subterminal in position; pigment granules are roundish, of small size (<0.5 μm), randomly scattered throughout the cytoplasm and tend to aggregate into one loose group (Fig. 153, *6*).

Microgametocytes (Fig. 153, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules do not tend to aggregate into one loose group, and are usually located at the ends of gametocytes; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. cublae* is especially similar to *H. eurylaimus*. It can be distinguished from the latter species primarily on the basis of (i) a slight lateral displacement of erythrocytes' nuclei by their gametocytes, and (ii) a tendency of the pigment granules in macrogametocytes to be aggregated into one loose group.

84. **Haemoproteus (Parahaemoproteus) greineri** Bennett, Turner and Whiteway, 1984

Haemoproteus greineri Bennett, Turner and Whiteway, 1984: 2290, Fig. 1, 2.

Type vertebrate host. *Anas crecca* L. (Anseriformes).
Additional vertebrate hosts. Some species of the Anseriformes (Table 98).
Type locality. Hughes Lake, Alberta, Canada.
Distribution. This parasite has so far been recorded only in the Holarctic. It is likely that the range is larger. The transmission ceases beyond the North Polar Circle.
Type material. Hapantotype (No. 94872, *Anas crecca,* 16.08.1983, Hughes Lake, Alberta, Canada, B. Turner) and parahapantotypes (No. 94593, 94718, 94828, 94623, 94674, *A. platyrhynchos*, 08.1983, Alberta, Canada, B. Turner; No. 94781, *A. discors*, other data are as for No. 94593; No. 94739, *A. acuta,* other data are as for No. 94593) are deposited in IRCAH.

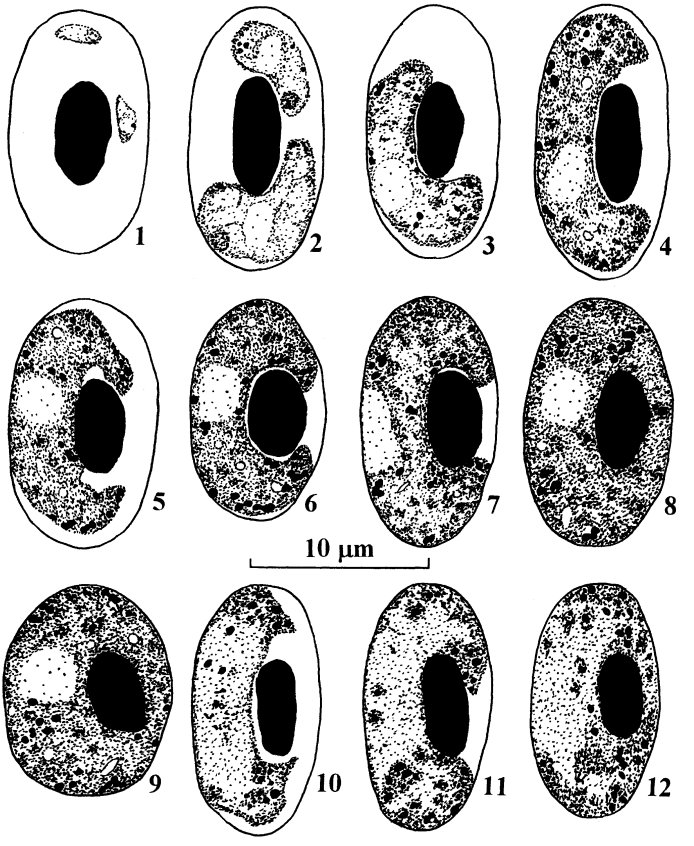

Figure 154 Gametocytes of *Haemoproteus greineri* from the blood of *Anas clypeata: 1*, *2* – young; *3–9* – macrogametocytes; *10–12* – microgametocytes (modified from Valkiūnas and Iezhova, 1992c).

Etymology. This species is named in honour of Dr. Ellis C. Greiner in recognition of his contribution to the field of avian blood parasitology.

Main diagnostic characters. A parasite of species of the Anseriformes whose fully grown gametocytes completely encircle the nucleus of infected erythrocytes and occupy all available cytoplasmic space in the host cells.

Development in vertebrate host

Young gametocytes (Fig. 154, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes (Fig. 154, *1*), but more advanced forms are usually seen in a polar position in

Table 98 List of vertebrate hosts of *Haemoproteus greineri*.

Aix sponsa	*A. discors*	*Cygnus buccinator*
Anas acuta	*A. platyrhynchos*	*C. olor*
A. americana	*A.rubripes*	*Mergus merganser*
A. clypeata	*Anser caerulescens*	

the host cells (Fig. 154, *2*); as the parasite develops, gametocytes extend longitudinally, frequently taking a position asymmetrical to the erythrocyte nucleus (Fig. 154, *2*) which is a characteristic feature of this species; gametocytes adhere to the envelop of erythrocytes but usually do not touch the erythrocyte nucleus.

Macrogametocytes (Fig. 154, *3–9*; Table 99). The cytoplasm is homogeneous in appearance, usually contains a few small vacuoles; valutin granules usually present and numerous, they obscure the pigment granules; gametocytes grow around the nucleus of infected erythrocytes; they displace the nucleus laterally and finally completely encircle the nucleus and occupy all available cytoplasmic space in the host cells (Fig. 154, *8*); growing gametocytes frequently do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') is available between the parasite and the nucleus of erythrocytes (Fig. 154, *4*, *6*, *7*) which subsequently disappears (Fig. 154, *8*, *9*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 154, *8*, *9*); the outline is usually even but sometimes wavy; the parasite nucleus is compact, variable in form, usually median or submedian in position, lies free in the cytoplasm (Fig. 154, *4–6, 8, 9*) or adheres to the pellicle of gametocytes (Fig. 154, *7*); pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; fully grown gametocytes markedly deform infected erythrocytes which sometimes take a roundish shape (Fig. 154, *9*).

Microgametocytes (Fig. 154, *10–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline is sometimes slightly ameboid (Fig. 154, *10*); other characters are as for macrogametocytes.

Comments. After the examination of the type material and a series of additional slides, the author of this book formed the impression that *H. greineri* may be a synonym of *H. nettionis*. First, *H. greineri* has been more frequently seen in mixed infection with *H. nettionis* than in the pure infection. The same fact was also noted by Pung *et al.* (1997). Second, growing gametocytes of *H. greineri* and *H. nettionis* are identical. Third, differences in the number of pigment granules in gametocytes of *H. greineri* and *H. nettionis* may be because of difficulties of their calculation due to numerous valutin granules which markedly obscure the pigment granules. It should be noted that the circumnuclear gametocytes, which are the main distinctive character of *H. greineri*, were recorded by Fallis and Wood (1957) in ducks experimentally infected with *H. nettionis.* Thus, it is possible that *H. nettionis* is a pleomorphic species with both halteridian and circumnuclear fully grown gametocytes, and *H. greineri* may be a synonym of *H. nettionis*. Further investigations are required to resolve this question.

85. **Haemoproteus (Parahaemoproteus) apodus** Bennett, Caines and Whiteway, 1986

Haemoproteus apodus Bennett, Caines and Whiteway, 1986a: 766, Fig. 1, 2.

Type vertebrate host. *Chaetura andrei* Berlepsch et Hartert (Apodiformes).
Type locality. Guaratuba (23°45′ S, 45°55′ W), São Paulo State, Brazil.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 69702, *Chaetura andrei,* 26.10.1972, Guaratuba, São Paulo State, Brazil, O. de Souza Lopes) is deposited in IRCAH.
Etymology. The specific name is derived from the name of the family Apodidae to which the type host belongs.

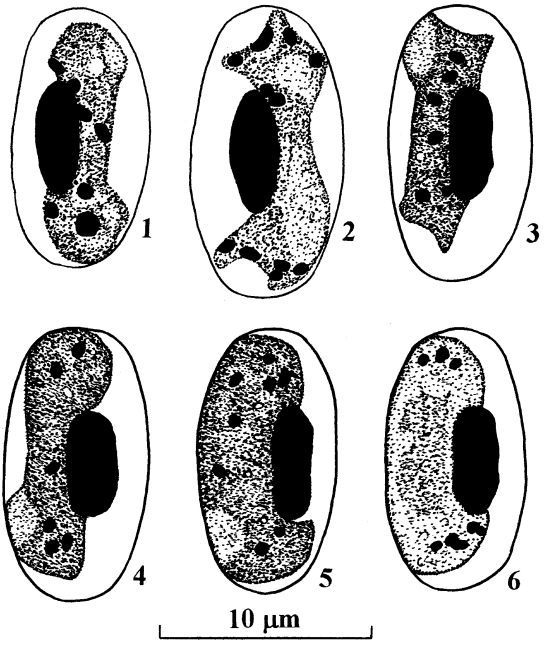

Figure 155 Gametocytes of *Haemoproteus apodus* from the blood of *Chaetura andrei:* *1*, *3–5* – macrogametocytes; *2*, *6* – microgametocytes (*1*, *2* are modified from Bennett *et al*., 1986a).

Main diagnostic characters. A parasite of species of the Apodiformes whose fully grown gametocytes only slightly enclose the nucleus of infected erythrocytes with their ends; they slightly displace the nucleus laterally and do not encircle it completely. Growing dumbbell-shaped gametocytes are present. The average number of pigment granules is about ten per gametocyte.

Development in vertebrate host

Young gametocytes take a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline varies from even to angular and ameboid.

Macrogametocytes (Fig. 155, *1*, *3–5*; Table 99). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are not seen; gametocytes grow along the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends and slightly displace it laterally but never encircle it completely; growing gametocytes are closely appressed to the nucleus of erythrocytes and usually adhere to the erythrocyte envelope; occasionally, gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are also seen, but gametocytes, adhering to the erythrocyte envelope with only one end, are more frequently recorded (Fig. 155, *1*, *3*); the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 155, *1*, *4*); the outline of growing gametocytes varies from even (Fig. 155, *1*, *4*) to angular (Fig. 155, *3*) and ameboid (Fig. 155, *2*); fully grown gametocytes are even in outline, they are closely appressed both to the nucleus and envelope of erythrocytes, but do not fill the

Table 99 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. greineri*				*H. apodus* (modified from Bennett *et al.*, 1986a)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				25		
Length		10.3–13.1	12.2	0.7		12.2	0.6
Width		5.9–6.9	6.1	0.4		6.4	0.4
Length of nucleus		4.2–6.1	5.3	0.3		5.3	0.6
Width of nucleus		1.7–2.6	2.2	0.2		2.1	0.2
Erythrocyte parasitized by macrogametocyte	31				25		
Length		10.4–14.7	13.0	0.8		12.1	0.8
Width		6.2–7.9	7.0	0.5		6.1	0.6
Length of nucleus		4.1–6.6	5.6	0.3		5.0	0.4
Width of nucleus		1.7–2.8	2.2	0.1		1.9	0.2
Erythrocyte parasitized by microgametocyte	31				15		
Length		10.8–14.9	13.1	0.8		12.1	0.7
Width		6.4–8.2	7.1	0.5		6.2	0.3
Length of nucleus		3.8–6.4	5.7	0.2		5.4	0.6
Width of nucleus		1.4–3.1	2.4	0.1		2.0	0.2
Macrogametocyte	31				25		
Length		15.4–24.8	20.1	1.8		13.6	1.4
Width		2.7–3.9	3.3	0.4		3.2	0.6
Length of nucleus		1.4–5.2	3.1	0.2		2.8	0.4
Width of nucleus		1.1–4.3	2.3	0.1		2.1	0.4
NDR		0.3–0.9	0.6	0.2		0.4	0.2
No. of pigment granules		17–33	27.0	3.4		11.5	0.7
Microgametocyte	31				15		
Length		14.4–22.7	20.8	1.6		14.9	1.1
Width		2.0–3.7	3.1	0.3		2.9	0.4
Length of nucleus		–	–	–		6.9	1.0
Width of nucleus		–	–	–		2.1	0.3
NDR		0.3–0.9	0.5	0.1		0.5	0.2
No. of pigment granules		15–34	25.2	3.8		10.7	1.2

Note: All sizes are given in micrometres.

the erythrocytes up to their poles (Fig. 155, *5*); the parasite nucleus is compact, variable in form, relatively small, subterminal in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) but sometimes large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 155, *2*, *6*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules can be aggregated into large (about 1.0 to 1.5 μm in diameter) dense clumps at the ends of gametocytes; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Apodiformes, *H. apodus* is especially similar to *H. trochili*. It can be distinguished from the latter species primarily on the basis of (i) the dumbbell-like shape of its growing gametocytes which do not touch the envelope of erythrocytes, and (ii) the presence of pigment granules of large (1.0 to 1.5 μm) size in some gametocytes.

86. **Haemoproteus (Parahaemoproteus) bucconis** Bennett, Caines and Whiteway, 1986

Haemoproteus bucconis Bennett, Caines and Whiteway, 1986a: 766, Fig. 3–6.

Type vertebrate host. *Nystalus chacuru* (Vieil.) (Piciformes).
Additional vertebrate host. *Hypnelus ruficollis* (Piciformes).
Type locality. Itapetininga (23°40′ S, 48°05′ W), São Paulo State, Brazil.
Distribution. The Neotropical zoogeographical region.
Type material. Hapantotype (No. 86062, *Nystalus chacuru,* 11.09.1975, Itapetininga, São Paulo State, Brazil, O. de Souza Lopes) is deposited in IRCAH.
Etymology. The specific name is derived from the name of the family Bucconidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes and finally enucleate the host cells. The average number of pigment granules is about 20 per gametocyte. Infected erythrocytes are not hypertrophied in length in comparison to uninfected ones.

Development in vertebrate host
Young gametocytes are usually seen in a position lateral to the nucleus of infected erythrocytes.

Macrogametocytes (Fig. 156, *1*, *2*; Table 100). The cytoplasm is finely granular in appearance, pale stained; frequently (up to 50% of gametocytes) one or both ends of gametocytes are stained more pale than their central part and, as a result, the parasite appears to possess large vacuoles at the ends (Fig. 156, *1*); gametocytes markedly displace

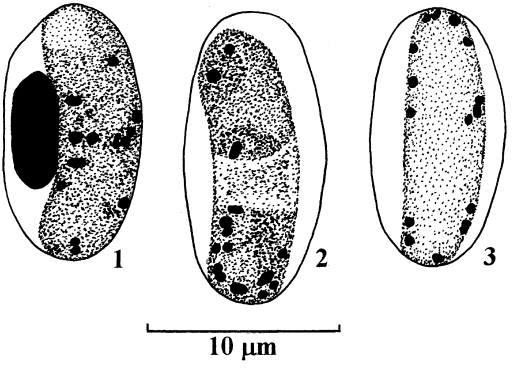

Figure 156 Gametocytes of *Haemoproteus bucconis* from the blood of *Nystalus chacuru: 1*, *2* – macrogametocytes; *3* – microgametocyte (modified from Bennett *et al*., 1986a).

Table 100 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. bucconis* (modified from Bennett *et al.*, 1986a)			*H. circumnuclearis* (modified from Bennett *et al.*, 1986b)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	25			30		
Length		13.9	1.0		12.3	0.7
Width		7.5	0.4		6.5	0.4
Length of nucleus		5.4	0.5		5.1	0.4
Width of nucleus		2.1	0.2		2.0	0.2
Erythrocyte parasitized by macrogametocyte	30			30		
Length		14.0	0.9		13.7	0.6
Width		7.5	0.4		6.7	0.4
Length of nucleus		5.8	0.5		4.8	0.5
Width of nucleus		2.2	0.4		2.0	0.2
Erythrocyte parasitized by microgametocyte	15			15		
Length		14.1	0.7		13.0	0.8
Width		8.5	1.1		7.2	0.4
Length of nucleus		5.6	0.4		4.6	0.5
Width of nucleus		2.2	0.4		1.9	0.2
Macrogametocyte	30			30		
Length		13.1	1.0		22.6	1.3
Width		4.3	0.5		2.4	0.4
Length of nucleus		3.0	0.6		3.9	0.7
Width of nucleus		2.0	0.5		1.9	0.3
NDR		–	–		1.0	–
No. of pigment granules		21.0	2.1		19.5	2.2
Microgametocyte	15			15		
Length		13.3	0.8		22.2	1.4
Width		4.7	0.6		2.8	0.3
Length of nucleus		5.6	0.7		6.0	1.4
Width of nucleus		2.7	0.5		2.7	0.6
NDR		–	–		1.0	–
No. of pigment granules		22.7	2.8		19.3	2.0

Note: All sizes are given in micrometres.

the nucleus of infected erythrocytes laterally or to one pole and finally enucleate the host cells; fully grown gametocytes look like cigar-shaped bodies lying free within the erythrocytic remnant and usually do not touch the erythrocyte envelope with their lateral parts (Fig. 156, *2*); the outline is even; the parasite nucleus is compact, usually roundish or oval, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are not changed significantly in length and width in comparison to uninfected ones.

Microgametocytes (Fig. 156, *3*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Piciformes, *H. bucconis* is particularly similar to *H. bennetti* and *H. thereicerycis*. It can be distinguished from *H. thereicerycis* primarily on the basis of a smaller number of pigment granules in its gametocytes. Gametocytes of *H. bennetti* cause hypertrophy of infected erythrocytes in length, but gametocytes of *H. bucconis* do not. However, it should be noted that the taxonomic value of the latter character is questionable. It is possible that *H. bucconis* may be a synonym of *H. bennetti*. Further investigation into these parasites is required. Unfortunately, the hapantotype of *H. bucconis* is fading and the parasitemia is low in this blood film. Additional material is required for more detailed investigation of the morphology of gametocytes of *H. bucconis*.

87. **Haemoproteus (Parahaemoproteus) circumnuclearis** Bennett, Caines and Whiteway, 1986

Haemoproteus circumnuclearis Bennett, Caines and Whiteway, 1986b: 774, Fig. 1, 2.

T y p e v e r t e b r a t e h o s t. *Mionectes olivaceus* Lawrence (Passeriformes).
T y p e l o c a l i t y. Rio Verde (1120 m), Valle, Colombia.
D i s t r i b u t i o n. This parasite has so far been recorded only in the type locality.
T y p e m a t e r i a l. Hapantotype (No. 31170, *Mionectes olivaceus,* May 1972, Rio Verde, Valle, Colombia, coll. Borrero) is deposited in IRCAH.
E t y m o l o g y. The specific name reflects the circumnuclear shape of fully grown gametocytes of this parasite.

M a i n d i a g n o s t i c c h a r a c t e r s. A parasite of species of the Passeriformes whose fully grown gametocytes do not displace the nucleus of infected erythrocytes laterally but

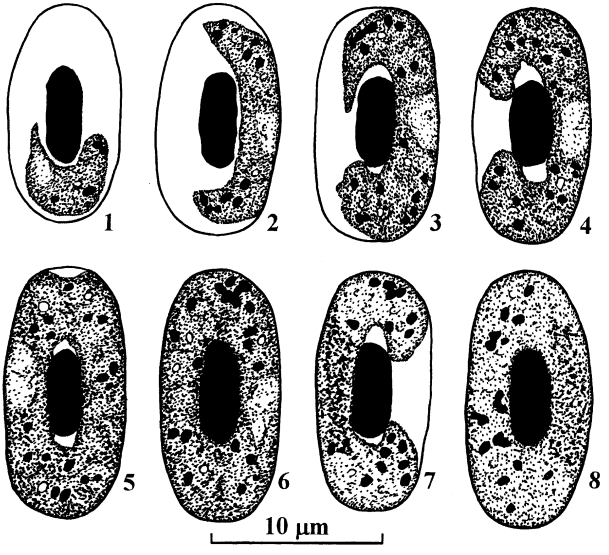

Figure 157 Gametocytes of *Haemoproteus circumnuclearis* from the blood of *Mionectes olivaceus:*
1 – young; *2–6* – macrogametocytes; *7*, *8* – microgametocytes.

completely encircle the nucleus and occupy all available cytoplasmic space in the host cells. Medium grown gametocytes, which do not touch the nucleus of erythrocytes along their entire margin, are present. The average number of pigment granules is about 20 per gametocyte.

Development in vertebrate host

Young gametocytes (Fig. 157, *1*). The earliest forms can be seen anywhere in the infected erythrocytes; as the parasites develop, they frequently take a horseshoe shape and are located in a polar position in erythrocytes (Fig. 157, *1*).

Macrogametocytes (Fig. 157, *2–6*; Table 100). The cytoplasm is finely granular in appearance, contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they do not displace the nucleus laterally, but finally completely encircle it and occupy all available cytoplasmic space in the host cells; growing gametocytes are closely appressed to the erythrocyte envelope but usually do not touch the erythrocyte nucleus; medium grown gametocytes, which do not touch the erythrocyte nucleus along their entire margin (Fig. 157, *2*), are common; advanced gametocytes adhere to the erythrocyte nucleus with their lateral part but still do not touch the poles of the erythrocytes where a clear more or less evident unfilled space is available (Fig. 157, *3–5*); fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes (Fig. 157, *6*); the parasite nucleus is variable in form, median or submedian in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 157, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. circumnuclearis* is particularly similar to *H. danilewskii* and *H. pittae*. It can be distinguished from the latter two species primarily on the basis of the morphology of its microgametocytes.

88. **Haemoproteus (Parahaemoproteus) eurystomae** Bishop and Bennett, 1986

Haemoproteus eurystomae Bishop and Bennett, 1986: 1862, Fig. 7, 8.

Type vertebrate host. *Eurystomus orientalis* (L.) (Coraciiformes).
Additional vertebrate hosts. *Coracias benghalensis*, *Eurystomus glaucurus* (Coraciiformes).
Type locality. Rantau Panjang, Malaysia.
Distribution. The Oriental and Ethiopian zoogeographical regions.
Type material. Hapantotype (No. 3014, *Eurystomus orientalis*, 01.12.1961, Rantau Panjang, Malaysia, H.E. McClure) and parahapantotype (No. 37158, *E. orientalis,* 10.05.1965, Kabigaan, Aborlan, Palawan Island, Philippines, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Eurystomus*.

Main diagnostic characters. A parasite of species of the Coraciiformes whose fully grown gametocytes slightly enclose the nucleus of infected erythrocytes with their ends and displace the nucleus laterally; they are closely appressed to the nucleus and envelope of erythrocytes. The average number of pigment granules in gametocytes is greater than 15. The average width of gametocytes is greater than 4 μm. The average NDR is 0.5 or less.

Table 101 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. eurystomae* (modified from Bishop and Bennett, 1986)			*H. indicator* (modified from Bennett *et al*., 1986a)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	45			25		
Length		13.8	0.8		13.6	0.7
Width		7.7	0.7		7.4	0.4
Length of nucleus		6.9	0.5		6.1	0.4
Width of nucleus		2.8	0.3		2.1	0.3
Erythrocyte parasitized by macrogametocyte	40			30		
Length		14.0	1.5		14.0	1.3
Width		8.5	0.9		8.3	0.9
Length of nucleus		6.6	0.6		5.3	0.5
Width of nucleus		2.6	0.2		2.2	0.4
Erythrocyte parasitized by microgametocyte	20			15		
Length		13.9	1.6		13.7	1.5
Width		8.2	1.4		8.2	0.9
Length of nucleus		6.7	0.6		5.5	0.4
Width of nucleus		2.7	0.4		2.2	0.2
Macrogametocyte	40			30		
Length		15.8	1.6		19.6	1.5
Width		4.3	0.7		5.0	1.0
Length of nucleus		3.1	0.6		4.0	0.5
Width of nucleus		2.0	0.5		2.9	0.5
NDR		0.5	0.2		0.5	0.2
No. of pigment granules		22.9	3.7		42.3	3.1
Microgametocyte	20			15		
Length		16.3	1.7		19.6	1.5
Width		4.2	0.6		4.8	1.0
Length of nucleus		8.0	2.2		6.8	1.2
Width of nucleus		3.3	0.5		3.2	0.6
NDR		0.5	0.2		0.5	0.2
No. of pigment granules		23.4	3.8		24.0	2.7

Note: All sizes are given in micrometres.

Development in vertebrate host

Young gametocytes are usually seen in a lateral position to the nucleus of infected erythrocytes, they do not touch the nucleus of erythrocytes; the outline is usually even.

Macrogametocytes (Fig. 158, *1*, *3*, *4*; Table 101). The cytoplasm is coarsely granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends and displace it laterally; growing gametocytes are appressed to the envelope of erythrocytes but frequently do not touch the nucleus of erythrocytes and, as a result, a more or less evident

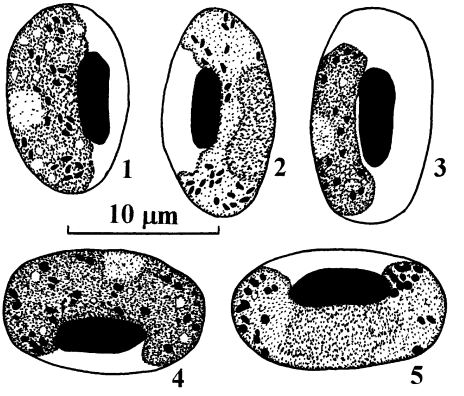

Figure 158 Gametocytes of *Haemoproteus eurystomae* from the blood of *Eurystomus orientalis: 1*, *3*, *4* – macrogametocytes; *2*, *5* – microgametocytes (*1*, *2* are modified from Bishop and Bennett, 1986).

unfilled space (a 'cleft') frequently present between the parasite and the erythrocyte nucleus (Fig. 158, *3*); this 'cleft' disappears in fully grown forms; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; the outline is even or slightly wavy (Fig. 158, *2*); the parasite nucleus is compact, frequently roundish, median or submedian in position; pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 158, *2*, *5*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Coraciiformes, *H. eurystomae* is especially similar to *H. halcyonis* and *H. manwelli*. It can be distinguished from *H. manwelli* primarily on the basis of more numerous pigment granules in its gametocytes. Fully grown gametocytes of *H. eurystomae* are closely appressed to the nucleus of infected erythrocytes, but full grown gametocytes of *H. halcyonis* frequently are not.

89. **Haemoproteus (Parahaemoproteus) indicator** Bennett, Caines and Whiteway, 1986

Haemoproteus indicator Bennett, Caines and Whiteway, 1986a: 769, Fig. 7– 9.

Type vertebrate host. *Indicator indicator* (Sparrman) (Piciformes).
Type locality. Zika Forest, Uganda.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 28203, *Indicator indicator,* 14.01.1972, Zika Forest, Uganda, N. Okia) is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Indicator*.

Main diagnostic characters. A parasite of species of the Piciformes whose fully grown gametocytes displace the nucleus of infected erythrocytes laterally, markedly

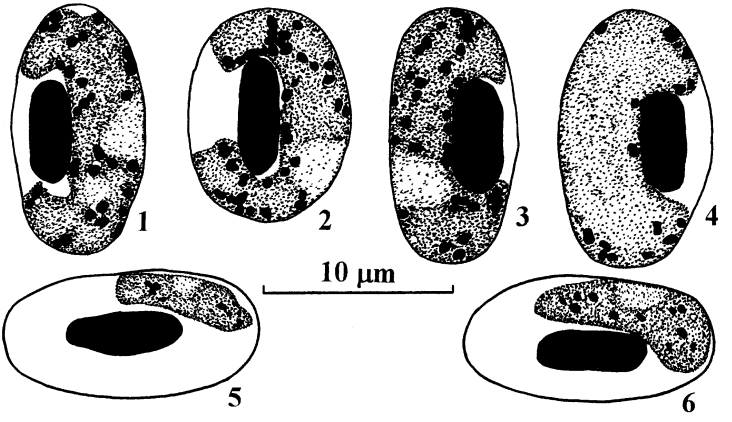

Figure 159 Gametocytes of *Haemoproteus indicator* from the blood of *Indicator indicator: 1–3* – macrogametocytes; *4* – microgametocyte; *5*, *6* – young (*1–4* are modified from Bennett *et al*., 1986a).

enclose the nucleus with their ends but do not encircle it completely. The average number of pigment granules in macrogametocytes is approximately half as many as in microgametocytes.

Development in vertebrate host

Young gametocytes (Fig. 159, *5*, *6*). The earliest forms can be seen anywhere in the infected erythrocytes but more frequently in a polar position in the host cells; as the parasite develops, gametocytes extend longitudinally along the nucleus and they frequently do not touch the nucleus; comma-like forms, which are located in a polar position, are common (Fig. 159, *6*); the outline is even.

Macrogametocytes (Fig. 159, *1–3*; Table 101). The cytoplasm is coarsely granular in appearance; gametocytes grow around the nucleus of infected erythrocytes; they displace the nucleus laterally and markedly enclose it with their ends but do not encircle it completely; gametocytes are closely appressed to the envelope of erythrocytes (Fig. 159, *1*, *3*), however, the growing forms frequently do not touch the erythrocyte nucleus forming a more or less evident unfilled space (a 'cleft') between the parasite and the erythrocyte nucleus (Fig. 159, *2*); this 'cleft' subsequently disappears; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 159, *3*); the parasite nucleus varies in form and position, but more frequently is seen in a median or submedian position; pigment granules are usually roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, about 40 per gametocyte on average which is a rare character for haemoproteids.

Microgametocytes (Fig. 159, *4*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is diffuse and ill-defined; the average number of pigment granules is approximately half as many as in macrogametocytes; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Piciformes, *H. indicator* is especially similar to *H. cornuata.* It can be distinguished from the latter species primarily on the basis of the clearly different average number of pigment granules in its macro- and microgametocytes.

90. **Haemoproteus (Parahaemoproteus) souzalopesi** Bennett, Caines and Whiteway, 1986

Haemoproteus souzalopesi Bennett, Caines and Whiteway, 1986b: 774, Fig. 3, 4.

Type vertebrate host. *Cnemotriccus fuscatus* (Wied) (Passeriformes).
Additional vertebrate hosts. *Empidonax euleri*, *Myiozetetes coyanensis* (Passeriformes).
Type locality. Guaratuba (23°40′ S, 45°55′ W), São Paulo State, Brazil.
Distribution. The Neotropical zoogeographical region. The information about records in the Nearctic (Bennett *et al.*, 1986b) should be confirmed.
Type material. Hapantotype (No. 83024, *Cnemotriccus fuscatus,* 21.10.1969, Guaratuba, São Paulo State, Brazil, O. de Souza Lopes) is deposited in IRCAH.
Etymology. This species is named in honour of Dr. Oscar de Souza Lopes in recognition of his contribution to the field of avian blood parasitology in Brazil.

Main diagnostic characters. A parasite of species of the Passeriformes with roundish (discoid) in shape fully grown gametocytes which markedly deform infected erythrocytes, displace their nuclei, and finally can enucleate the host cells. The average length of fully grown gametocytes is less than 6 μm. The average length of the nucleus of fully grown macrogametocytes is less than 2 μm.

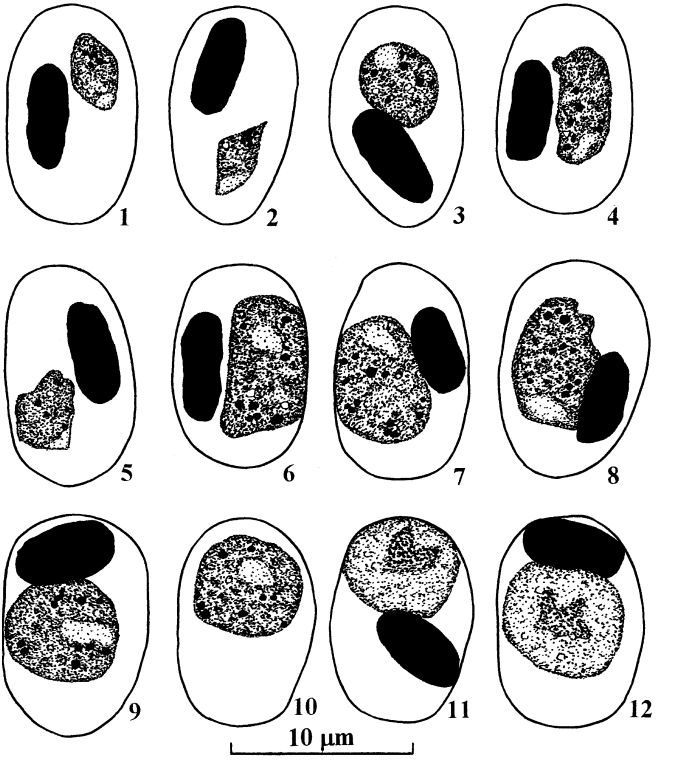

Figure 160 Gametocytes of *Haemoproteus souzalopesi* from the blood of *Cnemotriccus fuscatus: 1–5* – young; *6–10* – macrogametocytes; *11*, *12* – microgametocytes.

Table 102 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. souzalopesi* (modified from Bennett *et al.*, 1986b)			*H. tartakovskyi* (modified from Valkiūnas, 1990)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	20			31			
Length		11.7	0.7		10.5–12.6	11.7	0.6
Width		6.9	0.5		6.1–7.7	7.0	0.4
Length of nucleus		5.6	0.3		5.2–6.5	5.8	0.2
Width of nucleus		2.0	0.1		2.2–3.4	2.7	0.1
Erythrocyte parasitized by macrogametocyte	30			31			
Length		10.6	0.8		11.4–13.5	12.3	0.6
Width		7.5	0.9		5.7–9.9	8.1	0.3
Length of nucleus		5.2	0.4		5.0–6.4	5.6	0.2
Width of nucleus		2.6	0.3		2.1–3.4	2.6	0.1
Erythrocyte parasitized by microgametocyte	20			31			
Length		10.9	1.1		11.1–14.0	12.6	0.6
Width		7.5	0.5		6.4–9.3	7.7	0.4
Length of nucleus		5.0	0.5		5.2–6.3	5.7	0.1
Width of nucleus		2.4	0.4		2.1–3.3	2.6	0.1
Macrogametocyte	30			31			
Length		5.4	0.3		11.0–13.8	12.3	0.5
Width		4.8	0.4		3.4–7.4	5.3	0.4
Length of nucleus		1.8	0.3		2.2–3.9	3.3	0.2
Width of nucleus		1.5	0.2		1.7–2.8	1.8	0.1
No. of pigment granules		12.7	1.6		11–22	16.0	1.8
Microgametocyte	20			31			
Length		5.7	0.6		10.7–14.2	12.0	0.8
Width		5.1	0.5		3.0–7.0	5.2	0.6
Length of nucleus		2.7	0.4		5.4–9.6	7.0	0.6
Width of nucleus		2.2	0.3		3.4–7.0	5.2	0.4
No. of pigment granules		12.4	1.2		7–20	14.2	1.5

Note: All sizes are given in micrometres.

Development in vertebrate host

Young gametocytes (Fig. 160, *1–5*). The earliest forms can be seen anywhere in the infected erythrocytes, but more frequently they were recorded in a subpolar position in the host cells; growing gametocytes markedly vary in shape (Fig. 160, *1–5*); the outline varies from even to angular and wavy; the multiple infection of one erythrocyte with several gametocytes is common in the hapantotype.

Macrogametocytes (Fig. 160, *6–10*; Table 102). The cytoplasm is finely granular in appearance, usually lacking vacuoles; growing gametocytes markedly vary in form (Fig. 160, *6–8*), but fully grown gametocytes are usually roundish in shape (Fig. 160, *9*, *10*); the outline is usually even, sometimes wavy (Fig. 160, *8*); the parasite nucleus is variable in

form and in position; pigment granules are roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; gametocytes cause marked deformation of infected erythrocytes, and they markedly displace the erythrocyte nucleus and finally can enucleate the host cells. In the hapantotype, the enucleated cells represent approximately 3 to 5% of the total number of infected erythrocytes.

Microgametocytes (Fig. 160, *11*, *12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is compact, relatively small in size (Table 102), usually lobular in appearance (Fig. 160, *11*, *12*); other characters are as for macrogametocytes.

Comments. Gametocytes of *H. souzalopesi* are similar to gametocytes of malaria parasites belonging to the subgenus *Haemamoeba*. Parasitemia is high in the hapantotype. Approximately 10% of erythrocytes are parasitized. Furthermore, numerous young gametocytes are present in this blood film, but meronts are absent. Thus, this parasite belongs to the genus *Haemoproteus*.

Among the haemoproteids of birds belonging to the Passeriformes, *H. souzalopesi* is especially similar to *H. parus*. It can be distinguished from the latter species primarily on the basis of the smaller size of its fully grown gametocytes. In addition, the nucleolus was not seen in macrogametocytes of *H. souzalopesi*, but it is distinct in *H. parus*. However, the diagnostic value of this character is unclear. It should be noted that the hapantotype is slightly fading. It is possible that the nucleolus was not seen in the nucleus of macrogametocytes of *H. souzalopesi* for this reason.

91. **Haemoproteus (Parahaemoproteus) tartakovskyi** Valkiūnas, 1986

Haemoproteus tartakovskyi Valkiūnas, 1986c: 307, Fig. 1, 2.

Type vertebrate host. *Loxia curvirostra* L. (Passeriformes).
Additional vertebrate hosts. *Coccothraustes coccothraustes, Spinus spinus* (Passeriformes).
Vectors. Sporogony is completed and sporozoites appear in the salivary glands of experimentally infected biting midges *Culicoides impunctatus* (Valkiūnas *et al.*, 2002b).
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E).
Distribution. The Palearctic.
Type material. Hapantotype (No. 285.82, *Loxia curvirostra,* 01.07.1982, the Curonian Spit, G. Valkiūnas) and parahapantotypes are deposited in CDVA. Parahapantotype (No. G462502, other data are as for the hapantotype) is in IRCAH. A series of additional slides of gametocytes, gametes, zygotes and ookinetes is deposited in CDVA.
Etymology. This species is named in honour of Professor M.G. Tartakovsky, St. Petersburg, Russia, who first recorded haemoproteids in *L. curvirostra*, in recognition of his contribution to the field of avian blood parasitology in the beginning of the 20th century.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes markedly displace the nucleus of infected erythrocytes and finally can enucleate the host cells. The average width of fully grown gametocytes is greater than 4.5 μm. Infected erythrocytes are significantly hypertrophied in width but unchanged in length.

Development in vertebrate host
Young gametocytes (Fig. 161, *1*, *2*). The earliest forms can be seen anywhere in the infected erythrocytes; they are oval or roundish; as the parasite develops, gametocytes adhere to

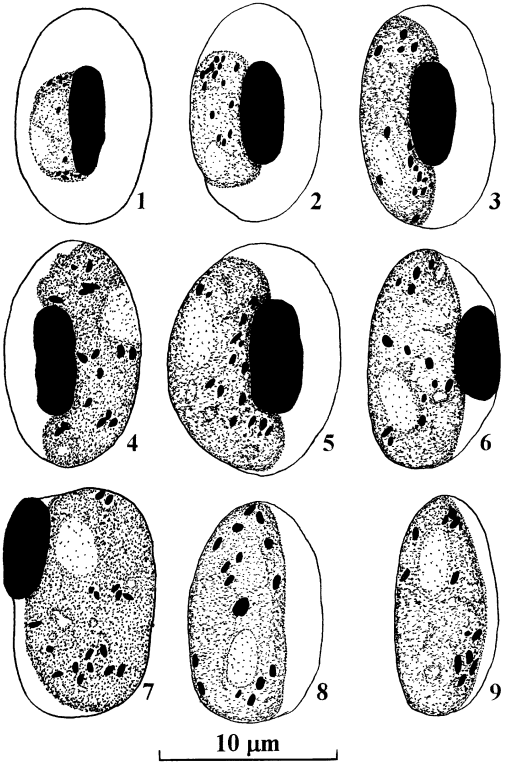

Figure 161 Gametocytes of *Haemoproteus tartakovskyi* from the blood of *Loxia curvirostra: 1*, *2* – young; *3–9* – macrogametocytes (modified from Valkiūnas, 1990).

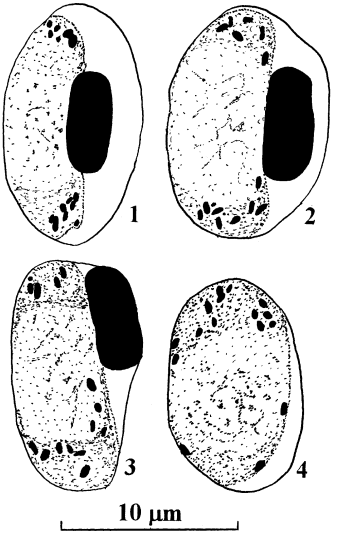

Figure 162 Microgametocytes of *Haemoproteus tartakovskyi* from the blood of *Loxia curvirostra* (modified from Valkiūnas, 1990).

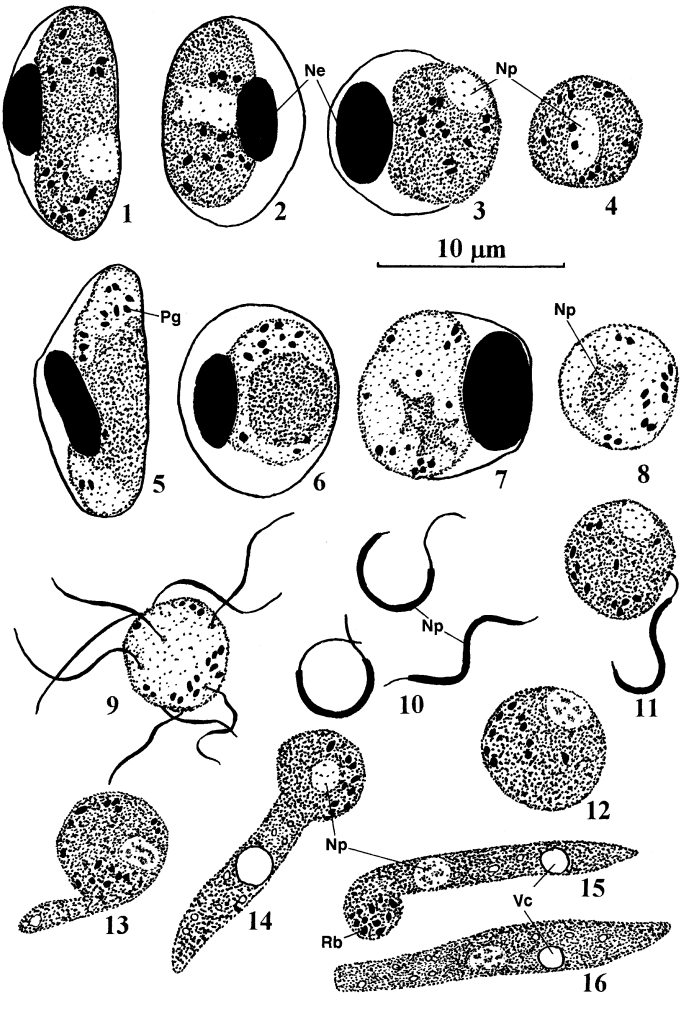

Figure 163 *Haemoproteus tartakovskyi* gametogenesis, zygote and ookinete development *in vitro: 1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Loxia curvirostra* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14* – medium differentiated ookinete; *15* – ookinete with a residual body; *16* – fully differentiated ookinete without the residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1993a).

the nucleus of erythrocytes and extend longitudinally along the nucleus (Fig. 161, *1*); advanced gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 161, *2*); the outline is usually even.

Macrogametocytes (Fig. 161, *3–9*; Table 102). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; growing gametocytes slightly enclose the nucleus of erythrocytes with their ends, and they are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 161, *3, 4*); gametocytes markedly displace the

nucleus of erythrocytes first laterally and then toward one pole of erythrocytes (Fig. 161, *6, 7*); finally, they can even enucleate the host cells (Fig. 161, *8*, *9*); gametocytes, which lie in the enucleated erythrocytes, look like elongated bodies which touch the erythrocyte envelope with one side but not with the other side (Fig. 161, *8*, *9*); the parasite nucleus is variable in form, frequently oval or ellipsoid, subterminal in position, and frequently lies free in the cytoplasm and does not touch the pellicle of parasites; the longitudinal axis of the oval parasite nucleus usually more or less coincides with the longitudinal axis of the gametocytes (Fig. 161, *3*, *5–9*); the (typical in form and position) nuclei of fully grown gametocytes are shown in Fig. 161, *6, 9*; in growing gametocytes, the nuclei frequently adhere to the parasite pellicle (Fig. 161, *4*); pigment granules are oval and roundish, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied approximately 15% in width in comparison to uninfected ones; in the hapantotype, the gametocytes in enucleated cells represent less than 1% of the total number of infected erythrocytes, but the marked displacement of the nucleus of infected erythrocytes (Fig. 161, *5–7*) is distinct.

Microgametocytes (Fig. 162). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus contains clear thread-like clots of chromatin; other characters are as for macrogametocytes.

Development in vector

Sporogony is completed in the experimentally infected biting midges *Culicoides impunctatus* (Valkiūnas *et al.*, 2002b). The gametogenesis, development of zygote and ookinete *in vitro* under a light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1993a). The data on the rate of this process are given in Table 23. Within 1 or 2 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave the erythrocytes (Fig. 163, *2–4*, *6–8*). Exflagellation was recorded approximately 4 min after EBA (Fig. 163, *9*). At approximately the same time, free microgametes (Fig. 163, *10*), fertilization of macrogametes (Fig. 163, *11*), and first zygotes (Fig. 163, *12*) were seen. Zygotes are morphologically identical to macrogametes. Ookinetes develop slowly. The initial stages of ookinetes differentiation were recorded approximately 12 h after the first zygotes appeared. At this time, a long finger-like outgrowth appears, located tangentially to the main body of the parasite (Fig. 163, *13*). As the ookinete develops, this outgrowth extends markedly and forms the anterior or apical end of the ookinete. An accumulation of pigment granules was recorded at the opposite end of the medium-differentiated ookinete (Fig. 163, *14*). In the fully grown ookinete, the pigment and the adjacent part of cytoplasm are eliminated as a residual body. It should be noted that the residual body in ookinetes of *H. tartakovskyi* is frequently located asymmetrically to the longitudinal axis of the parasite (Fig. 163, *15*). At the stage of medium differentiation of ookinetes, one or several large clear 'vacuoles' appear in the cytoplasm, and they persist in the fully grown ookinetes (Fig. 163, *14–16*). Ookinetes with a residual body were seen approximately 36 h after EBA, and fully differentiated ookinetes without the residual body were recorded 48 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 24.

Comments. The marked displacement of the nucleus of erythrocytes up to complete enucleation of the infected cells is the main distinctive character of *H. tartakovskyi*. In all blood films, which are available in the author's collection, gametocytes in enucleated cells are rare or absent, but gametocytes shown in Fig. 161, *5–7* and Fig. 162, *1–3* are common and they should be regarded as typical forms for this species. The process of enucleation of erythrocytes takes place at the latest stages of

the development in the blood, and thus the gametocytes in enucleated host cells are not always present in naturally infected birds.

Among the haemoproteids of birds belonging to the Passeriformes, *H. tartakovskyi* is especially close to *H. uraeginthus*. It can be easily distinguished from the latter species primarily on the basis of (i) the mode of growth of its young gametocytes which are closely appressed to the nucleus of erythrocytes and (ii) the shape of its fully grown gametocytes.

Burry-Caines and Bennett (1992) declared all haemoproteids, which were formerly described in passerine birds of the subfamily Carduelinae, as synonyms of *H. chloriis*, and such distinct parasites as *H. globulosus, H. macropigmentatus, H. tartakovskyi,* and others are among them. The authors believe that the marked displacement of the nucleus of infected erythrocytes is not a diagnostic character of *H. tartakovskyi*, but it is a result of multiple infection of one erythrocyte with several gametocytes. It is difficult to agree because the marked influence of gametocytes of *H. tartakovskyi* on the nucleus of erythrocytes was frequently recorded when only one gametocyte develops in erythrocytes. The gametocytes which are shown in Fig. 161, *6* and Fig. 162, *2* are common in the type material, and it is difficult to attribute the presence of such cells to artefacts, as Burry-Caines and Bennett (1992) suggested. It should be noted here that *H. tartakovskyi* can be easily distinguished from *H. chloriis* (=*H. fringillae*) also on the basis of the morphology of its zygotes and developing ookinetes as well as on the basis of the rate of development of its ookinetes *in vitro* (Figs. 66 and 163; Table 23). Thus, based on our observations and the other evidence presented above, *H. tartakovskyi* is considered to be a distinct species.

92. **Haemoproteus (Parahaemoproteus) tyranni** Bennett, Caines and Whiteway, 1986

Haemoproteus tyranni Bennett, Caines and Whiteway, 1986b: 777, Fig. 5, 6.

Type vertebrate host. *Tyrannus tyrannus* (L.) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 103).
Type locality. Missaquash Marsh, New Brunswick, Canada.
Distribution. The Neotropical zoogeographical region and the Nearctic.
Type material. Hapantotype (No. 28613, *Tyrannus tyrannus,* 03.07.1972, Missaquash Marsh, New Brunswick, Canada, G.F. Bennett) and parahapantotypes (No. 38468, *Empidonax trailii,* 11.06.1974, Jolicure, New Brunswick, Canada, G.F. Bennett; No. 39289, 13.06.1974; other data are as for No. 38468; No. 75772, *Tyrannus melancholicus,* 12.02.1971, Guaratuba, São Paulo State, Brazil, O. de Souza Lopes) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Tyrannus.*

Table 103 List of vertebrate hosts of *Haemoproteus tyranni* (modified from Bennett *et al.*, 1986b).

Capsiempis flaveola	*Myiarchus crinitus*
Empidonax flaviventris	*Phyllomyias fasciatus*
E. traillii	*Platyrinchus mystaceus*
E. varius	*Tyrannus melancholicus*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle the nucleus completely. Growing gametocytes frequently take a polar position in infected erythrocytes and locate asymmetrically to the nucleus of erythrocytes. Medium and fully

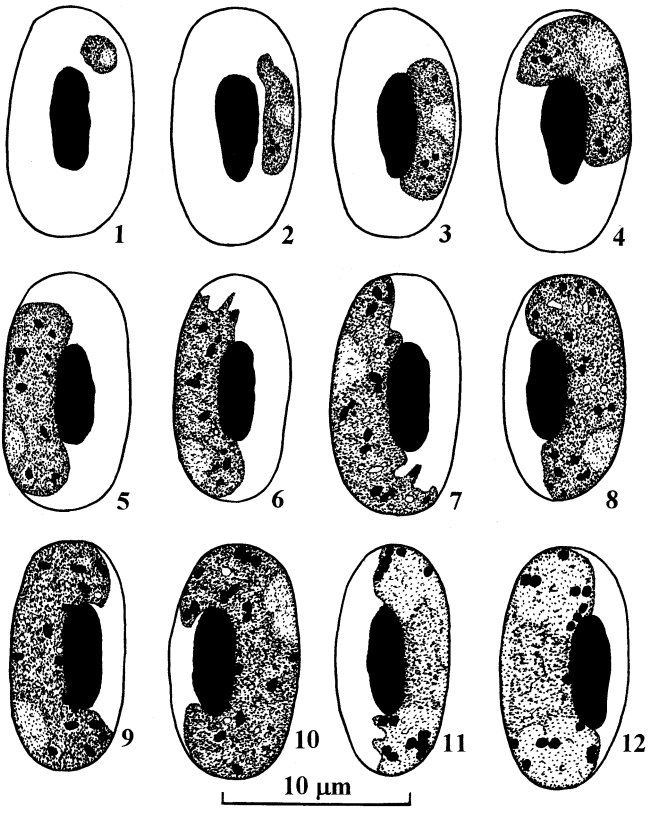

Figure 164 Gametocytes of *Haemoproteus tyranni* from the blood of *Tyrannus tyrannus:* *1–4* – young; *5–10* – macrogametocytes; *11*, *12* – microgametocytes.

grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes fill the erythrocytes up to their poles. The outline of growing gametocytes varies from even to highly ameboid, and it is usually even in fully grown gametocytes. Pigment granules are of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, about 17 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 164, *1–4*). The earliest forms can be seen anywhere in the infected erythrocytes; as the parasite develops, gametocytes extend longitudinally and usually take a lateral position to the erythrocyte nucleus (Fig. 164, *2*); they adhere to the nucleus and then also adhere to the envelope of erythrocytes (Fig. 164, *3, 4*); advanced gametocytes are frequently seen in a polar position in erythrocytes lying asymmetrically to the host cell nucleus (Fig. 164, *4*); the outline is even or slightly ameboid.

Macrogametocytes (Fig. 164, *5–10*; Table 104). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the nucleus laterally but do not encircle it completely; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes;

Table 104 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. tyranni* (modified from Bennett *et al.*, 1986b)			*H. formicarius* (modified from Bennett *et al.*, 1987)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	70			25		
Length		11.8	0.8		11.1	0.8
Width		6.7	0.4		6.5	0.4
Length of nucleus		5.3	0.5		5.1	0.7
Width of nucleus		2.0	0.2		2.1	0.3
Erythrocyte parasitized by macrogametocyte	70			25		
Length		12.4	0.7		12.4	1.2
Width		6.6	0.5		6.0	0.5
Length of nucleus		5.2	0.4		5.0	0.7
Width of nucleus		1.9	0.2		1.9	0.2
Erythrocyte parasitized by microgametocyte	10			10		
Length		12.5	0.4		12.3	0.8
Width		6.8	0.5		6.0	0.4
Length of nucleus		5.4	0.3		4.7	0.5
Width of nucleus		1.8	0.1		2.0	0.2
Macrogametocyte	70			25		
Length		14.6	1.7		12.5	1.4
Width		3.2	0.4		2.4	0.4
Length of nucleus		2.8	0.3		2.0	0.4
Width of nucleus		2.1	0.4		1.3	0.3
NDR		0.6	0.2		0.8	0.2
No. of pigment granules		17.0	1.8		13.4	1.5
Microgametocyte	10			10		
Length		14.5	0.9		13.2	1.3
Width		3.4	0.3		2.4	0.4
Length of nucleus		4.8	0.8		5.0	0.8
Width of nucleus		2.7	0.4		1.7	0.3
NDR		0.7	0.2		0.7	0.2
No. of pigment granules		16.6	1.4		15.6	1.6

Note: All sizes are given in micrometres.

dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes; fully grown gametocytes fill the erythrocytes up to their poles (Fig. 164, *9*, *10*); the outline of growing gametocytes varies from highly ameboid (Fig. 164, *6*, *7*) to even (Fig. 164, *5*, *8*), and is usually even in fully grown forms (Fig. 164, *9*, *10*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish or oval, sometimes rod-like, of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 164, *11*, *12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. tyranni* is especially similar to *H. anthi* and *H. pastoris*. It can be distinguished from the latter species primarily on the basis of more numerous pigment granules in its gametocytes. Additionally, growing gametocytes of *H. tyranni* frequently take a polar position in erythrocytes and are located asymmetrically to its nucleus (Fig. 164, *4*); this is not characteristic of *H. anthi* and *H. pastoris*.

93. **Haemoproteus (Parahaemoproteus) formicarius** Bennett, Caines and Woodworth-Lynas, 1987

Haemoproteus formicarius Bennett, Caines and Woodworth-Lynas, 1987: 317, Fig. 1–4.

T y p e v e r t e b r a t e h o s t. *Dysithamnus mentalis* (Temm.) (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. *Hylopezus ochroleucus, Pyriglena leucoptera* (Passeriformes).
T y p e l o c a l i t y. Itapetininga, Brazil.
D i s t r i b u t i o n. The Neotropical zoogeographical region.
T y p e m a t e r i a l. Hapantotype (No. 44614, *Dysithamnus mentalis,* 31.03.1972, Guaratuba, São Paulo State, Brazil, O. de Souza Lopes) and parahapantotype (No. 44532, *Pyriglena leucoptera,* 13.05.1972, Casa Grande, São Paulo State, Brazil, O. de Souza Lopes) are deposited in IRCAH. Small *Trypanosoma* sp. is present in the hapantotype.
E t y m o l o g y. The specific name is derived from the name of the family Formicariidae to which the type host belongs.

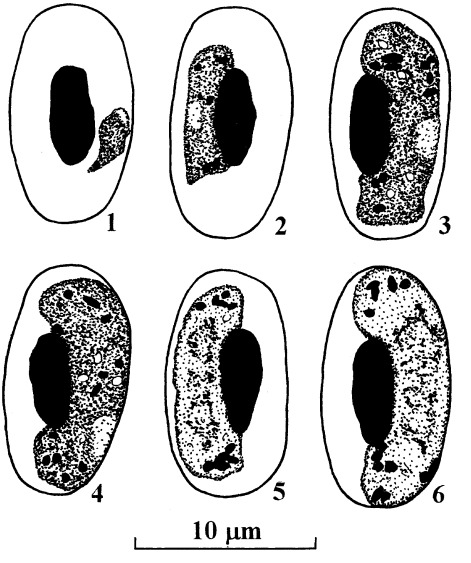

Figure 165 Gametocytes of *Haemoproteus formicarius* from the blood of *Dysithamnus mentalis: 1*, *2* – young; *3, 4* – macrogametocytes; *5*, *6* – microgametocytes.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed to the envelope of erythrocytes. Dumbbell-shaped gametocytes are absent. The outline of gametocytes is even or angular. Large (1.0 to 1.5 μm) rod-like pigment granules are present in fully grown gametocytes. The average number of pigment granules in gametocytes is greater than 10 but less than 18. The average NDR is 0.7 or greater.

Development in vertebrate host

Young gametocytes (Fig. 165, *1*, *2*) are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus not touching the envelope of erythrocytes (Fig. 165, *2*); the outline of the earliest forms varies from even to slightly ameboid (Fig. 165, *1*), and is usually even in more advanced forms.

Macrogametocytes (Fig. 165, *3*, *4*; Table 104). The cytoplasm is granular in appearance, contains a few small vacuoles; gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus slightly displacing it laterally but not encircling it completely; medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin (Fig. 165, *3*), are present; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes but frequently do not fill the erythrocytes up to their poles (Fig. 165, *4*); the outline is even; the parasite nucleus is compact, relatively small (see Table 104), variable in form and in position; pigment granules are of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, roundish, oval, and rod-like, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 165, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. formicarius* is very similar to *H. sanguinis*. It can be distinguished from the latter species primarily on the basis of the shape and size of the pigment granules in its gametocytes. *Haemoproteus formicarius* is also similar to *H. sequeirae.* Fully grown gametocytes of *H. sequeirae* fill the erythrocytes up to their poles but the fully grown gametocytes of *H. formicarius* frequently do not. In addition, the average number of pigment granules in gametocytes of *H. formicarius* is approximately half as many as in gametocytes of *H. sequeirae.*

94. **Haemoproteus (Parahaemoproteus) furnarius** Bennett, Caines and Woodworth-Lynas, 1987

Haemoproteus furnarius Bennett, Caines and Woodworth-Lynas, 1987: 318, Fig. 5–8.

Type vertebrate host. *Automolus leucophthalmus* (Wied) (Passeriformes).
Additional vertebrate hosts. *Lochmias nematura, Philydor atricapillus* (Passeriformes).
Type locality. Itapetininga, Brazil.
Distribution. The Neotropical zoogeographical region.
Type material. Hapantotype (No. 84353, *Automolus leucophthalmus,* 11.09.1967, Itapetininga, São Paulo State, Brazil, O. de Souza Lopes) is deposited in IRCAH.

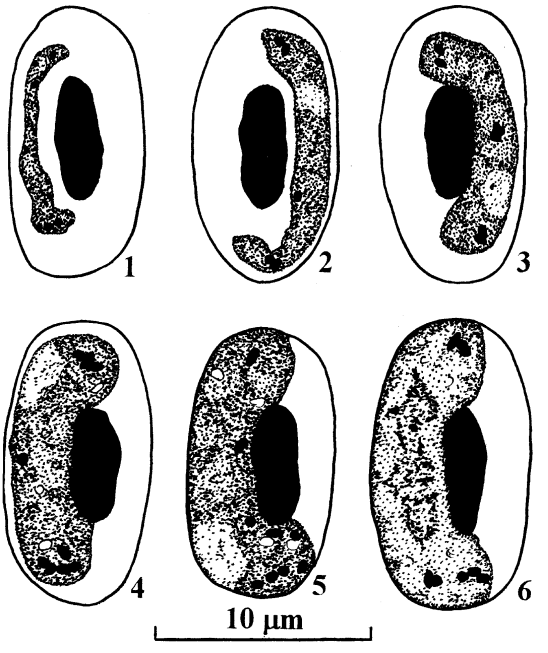

Figure 166 Gametocytes of *Haemoproteus furnarius* from the blood of *Automolus leucophthalmus:*
1 – young; *2–5* – macrogametocytes; *6* – microgametocyte.

Etymology. The specific name is derived from the name of the bird family Furnariidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Growing gametocytes, which are over 10 μm long, slender, snake-like, and do not touch the nucleus and envelope of erythrocytes, are common. Medium grown gametocytes are closely appressed to the nucleus of erythrocytes but do not touch their envelope along their entire margin. Dumbbell-shaped gametocytes are absent. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. The outline of gametocytes is even. The average number of pigment granules is about 10 per gametocyte.

Development in vertebrate host

Young gametocytes (Fig. 166, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; slender snake-like parasites, which do not touch the nucleus and envelope of erythrocytes, are common (Fig. 166, *1*); the outline is even or slightly wavy.

Macrogametocytes (Fig. 166, *2–5*; Table 105). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the nucleus laterally but do not encircle it completely; slender snake-like growing gametocytes, which do not touch both the nucleus and envelope of erythrocytes (Fig. 166, *2*), are common; as the parasite

Table 105 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. furnarius* (modified from Bennett *et al.*, 1987)			*H. philippinensis* (modified from Rahal *et al.*, 1987)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	20			55		
Length		11.4	0.7		12.0	0.6
Width		6.4	0.3		6.6	0.4
Length of nucleus		5.3	0.4		5.6	0.3
Width of nucleus		1.9	0.3		2.5	0.3
Erythrocyte parasitized by macrogametocyte	15			55		
Length		12.4	0.7		13.8	0.9
Width		7.1	0.4		6.5	0.5
Length of nucleus		5.6	0.4		5.4	0.4
Width of nucleus		1.9	0.3		2.5	0.3
Erythrocyte parasitized by microgametocyte	10			55		
Length		12.4	0.8		13.9	0.8
Width		7.1	0.5		6.4	0.5
Length of nucleus		5.6	0.5		5.5	0.5
Width of nucleus		1.9	0.3		2.4	0.3
Macrogametocyte	15					
Length		12.9	0.9	55	13.6	1.4
Width		3.2	0.5	55	1.4	0.6
Length of nucleus		2.7	0.4	45	2.8	0.8
Width of nucleus		1.9	0.4	45	1.6	0.5
NDR		0.7	0.1	55	0.8	0.2
No. of pigment granules		10.1	0.9	39	7.6	2.4
Microgametocyte	10					
Length		12.9	1.2	55	13.9	1.2
Width		3.1	0.5	55	1.5	0.5
Length of nucleus		4.6	0.7	5	3.4	2.2
Width of nucleus		2.0	0.4	5	1.4	0.3
NDR		0.8	0.3	55	0.9	0.2
No. of pigment granules		9.7	1.1	42	8.8	2.3

Note: All sizes are given in micrometres.

develops, gametocytes adhere to the nucleus of erythrocytes but still do not touch their envelope (Fig. 166, *3*); dumbbell-shaped gametocytes are absent; medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin (Fig. 166, *4*), are present; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, and they fill the host cells up to their poles (Fig. 166, *5*); the outline is even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish, oval and rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 166, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. furnarius* is particularly similar to *H. formicarius* and *H. otocompsae*. It can be distinguished from the latter two species primarily on the basis of its slender snake-like growing gametocytes (Fig. 166, *1*, *2*).

95. **Haemoproteus (Parahaemoproteus) philippinensis** Rahal, Bishop and Bennett, 1987

Haemoproteus philippinensis Rahal, Bishop and Bennett, 1987: 327, Fig. 9–12.

Type vertebrate host. *Hypsipetes flavala* (Blyth) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 106).
Type locality. Mount Brinchang, Pahang, Federation of Malaysia.
Distribution. The South Palearctic, the Oriental and Ethiopian zoogeographical regions.
Type material. Hapantotype (No. 8794, *Hypsipetes flavala,* 21.03.1962, Mount Brinchang, Pahang, Federation of Malaysia, H.E. McClure) and parahapantotypes [No. 42100, *H. amaurotis,* 20.10.1969, Tsunoshima, Yamaguchi Prefecture, Japan; No. 42102, 01.05.1969, Lanyu (Orchid Island), Taiwan, other data are as for No. 42100; No. 11765, *H. philippinus*, 18.08.1964, Camp Lookout, Valencia, Negros Oriental, Republic of Philippines; No. 42126, *H. madagascariensis*, 11.04.1971, Maharashtra, India; No. 9891, *Pycnonotus melanicterus*, 14.01.1965, Phunamtok, Saraburi, Thailand. All the parahapantotypes were collected by H.E. McClure] are deposited in IRCAH.
Etymology. The specific name is derived from the name of the locality (Philippines) where the parasite has been especially frequently recorded.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelope of erythrocytes along their entire margin. Dumbbell-shaped gametocytes with marked spherical thickenings at their ends are present. The average number of pigment granules in gametocytes is less than 12.

Development in vertebrate host
Young gametocytes (Fig. 167, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline is even.

Macrogametocytes (Fig. 167, *2–6*; Table 105). The cytoplasm is coarsely granular in appearance, usually contains a few small vacuoles; valutin granules are usually absent; gametocytes grow around the nucleus of infected erythrocytes, they do not displace or only slightly displace the nucleus laterally, enclose it with their ends but do not encircle it completely; gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelope of erythrocytes along their entire margin (Fig. 167, *2–6*); dumbbell-shaped gametocytes with marked spherical thickenings at their ends are present (Fig. 167, *4, 5*); gametocytes do not fill the erythrocytes up to their poles (Fig. 167, *5, 6*); the outline is even; the parasite nucleus is variable in form, subterminal in position; pigment granules are

Table 106 List of vertebrate hosts of *Haemoproteus philippinensis* (modified from Rahal *et al.*, 1987).

Criniger bres	*H. propinquus*	*P. finlaysoni*
C. ochraceus	*H. siquijorensis*	*P. flavescens*
C. pallidus	*Pycnonotus atriceps*	*P. goiavier*
Hypsipetes amaurotis	*P. barbatus*	*P. jocosus*
H. charlottae	*P. blanfordi*	*P. melanicterus*
H. madagascariensis	*P. brunneus*	*P. simplex*
H. mcclellandii	*P. cafer*	
H. philippinus	*P. erythropthalmos*	

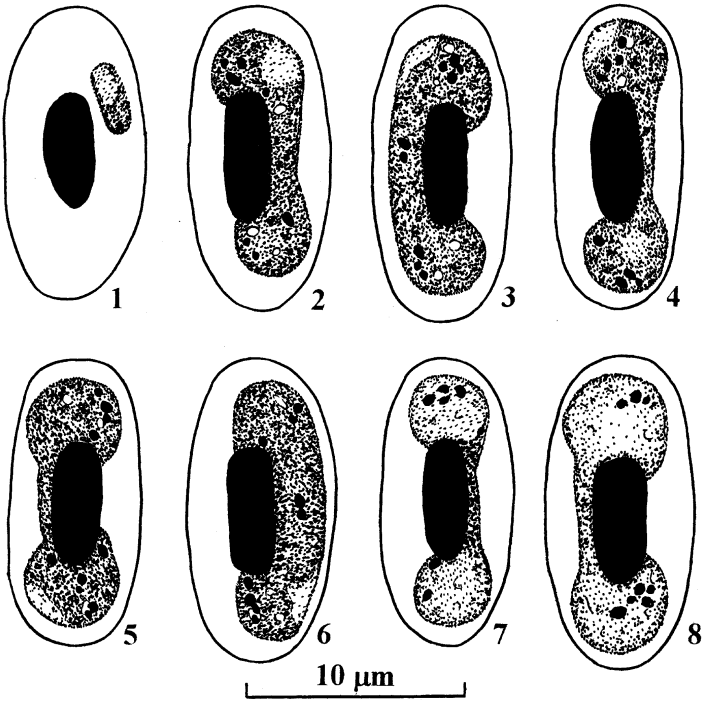

Figure 167 Gametocytes of *Haemoproteus philippinensis* from the blood of *Hypsipetes flavala: 1* – young; *2–6* – macrogametocytes; *7*, *8* – microgametocytes.

roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are significantly hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 167, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. philippinensis* is especially similar to *H. nucleophilus*. It can be distinguished from the latter species primarily on the basis of its dumbbell-shaped gametocytes which are absent in *H. nucleophilus*.

96. **Haemoproteus (Parahaemoproteus) vireonis** Bennett, Caines and Woodworth-Lynas, 1987

Haemoproteus vireonis Bennett, Caines and Woodworth-Lynas, 1987: 320, Fig. 13–16.

Type vertebrate host. *Vireo olivaceus* (L.) (Passeriformes).
Additional vertebrate hosts. *Vireo altiloquus*, *V. flavifrons*, *V. gilvus*, *V. griseus*, *V. philadelphicus* (Passeriformes).
Type locality. Itapetininga, Brazil.
Distribution. The Nearctic and the Neotropical zoogeographical region.
Type material. Hapantotype (No. 83108, *Vireo olivaceus,* 31.10.1969, Itapetininga, Brazil, O. de Souza Lopes) and parahapantotypes (No. 82659, *V. olivaceus,* 14.10.1971, Guaratuba, Brazil, O. de Souza Lopes; No. 57527, *V. altiloquus*, 10.04.1977, Malvern, Jamaica, H. Witt; No. 59711, 01.05.1977, other data are as for No. 57527; No. 38438, *V. olivaceus*, 10.06.1974, Jolicure, New Brunswick, Canada, G.F. Bennett; No. 58716, *V. gilvus*, 18.11.1976, Las Minas, El Salvador, coll. Winchell) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Vireo.*

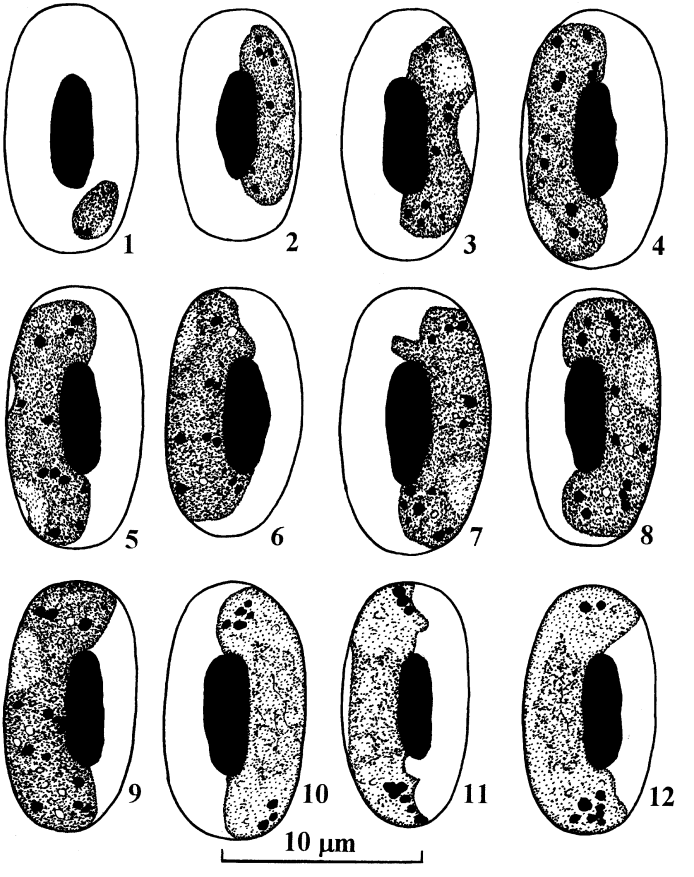

Figure 168 Gametocytes of *Haemoproteus vireonis* from the blood of *Vireo olivaceus:* *1* – young; *2–9* – macrogametocytes; *10–12* – microgametocytes.

Table 107 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. vireonis* (modified from Bennett *et al.*, 1987)			*H. attenuatus*			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	85			27			
Length		12.0	0.8		12.5–14.7	13.4	0.6
Width		6.4	0.5		6.1–7.4	6.8	0.4
Length of nucleus		5.5	0.5		5.4–6.8	6.0	0.3
Width of nucleus		2.0	0.3		2.5–3.0	2.8	0.1
Erythrocyte parasitized by macrogametocyte	95			39			
Length		12.6	0.9		12.8–15.3	13.9	0.6
Width		6.7	0.5		6.0–7.3	6.5	0.4
Length of nucleus		5.2	0.5		5.7–7.2	6.2	0.4
Width of nucleus		2.0	0.3		2.2–2.9	2.6	0.2
Erythrocyte parasitized by microgametocyte	35			31			
Length		12.5	1.0		12.4–15.5	13.3	0.6
Width		6.7	0.7		5.8–7.1	6.3	0.4
Length of nucleus		5.4	0.7		5.5–7.1	6.1	0.3
Width of nucleus		2.1	0.3		2.2–2.8	2.6	0.2
Macrogametocyte	95			52			
Length		13.5	2.1		11.5–19.5	15.8	1.4
Width		3.1	1.4		1.2–2.8	2.1	0.6
Length of nucleus		2.9	0.7		1.4–4.1	2.8	0.8
Width of nucleus		1.8	0.4		1.1–3.4	2.1	0.6
NDR		0.8	0.1		0.9–1.3	1.1	0.1
No. of pigment granules		12.3	2.1		11–26	17.9	1.8
Microgametocyte	35			44			
Length		14.7	2.2		10.5–18.4	15.0	1.2
Width		2.8	0.6		0.4–2.6	1.4	0.7
Length of nucleus		5.6	1.0		4.0–9.8	7.0	1.2
Width of nucleus		2.3	0.4		0.4–2.2	1.4	0.8
NDR		0.8	0.2		1.0–1.4	1.1	0.1
No. of pigment granules		11.7	1.9		10–22	14.0	1.6

Note: All sizes are given in micrometres.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes and do not encircle the nucleus completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are present; they represent more than 10% of the total number of growing gametocytes. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about 12 per gametocyte on average. A species difficult to identify; can be distinguished from the similar species of haemoproteids of passeriform birds only on the basis of a detailed analysis of a set of characters (see the description of gametocytes).

Development in vertebrate host

Young gametocytes (Fig. 168, *1*). The earliest forms can be seen anywhere in the infected erythrocytes, but later they usually take a position lateral to the nucleus of erythrocytes; as the parasite develops, gametocytes adhere to the erythrocyte nucleus and extend longitudinally along the nucleus; the outline is usually even.

Macrogametocytes (Fig. 168, *2–9*; Table 107). The cytoplasm is granular in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, they do not displace or only slightly displace the nucleus laterally and do not encircle it completely; gametocytes adhere to the nucleus and envelope of erythrocytes; the central part of pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 168, *3*, *4*); the dumbbell shaped gametocytes represent more than 10% of the total number of growing gametocytes; fully grown gametocytes lose the dumbbell shape, they are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 168, *9*); the outline of gametocytes is even or slightly wavy, sometimes slightly ameboid (Fig. 168, *7*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm. It should be noted that small and medium size pigment granules occur with approximately the same frequency in fully grown gametocytes. The maximum NDR does not exceed unity.

Microgametocytes (Fig. 168, *10–12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. vireonis* is especially similar to *H. coatneyi*. It can be distinguished from the latter species mainly on the basis of the same frequency of occurrence of small (<0.5 μm) and medium (0.5 to 1.0 μm) pigment granules in its fully grown gametocytes. In the fully grown gametocytes of *H. coatneyi*, medium-size (0.5 to 1.0 μm) pigment granules clearly predominate. However, the taxonomic value of this character is questionable. It is possible that *H. coatneyi* may be a synonym of *H. vireonis*. Further investigation into these parasites is required to solve this question.

97. **Haemoproteus (Parahaemoproteus) attenuatus** Valkiūnas, 1989

Haemoproteus attenuatus Valkiūnas, 1989e: 133, Fig. 2.

Type vertebrate host. *Erithacus rubecula* (L.) (Passeriformes).
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E).
Distribution. This parasite has so far been recorded only in the Palearctic.
Type material. Hapantotype (No. 89.82, *Erithacus rubecula,* 23.04.1982, the Curonian Spit, G. Valkiūnas) is deposited in CDVA. Parahapantotype (No. G462477, 24.04.1982, other data are as for the hapantotype) is deposited in IRCAH.
Etymology. The specific name reflects the minute (attenuated) width of the growing gametocytes of this parasite.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped

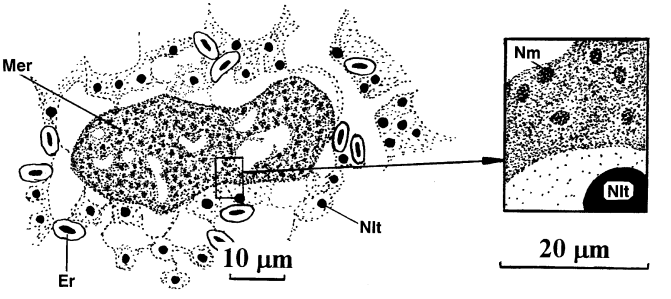

Figure 169 Exoerythrocytic meront of *Haemoproteus attenuatus* in the lungs of *Erithacus rubecula:*
Er – erythrocyte; Mer – meront; Nlt – nucleus of cell of the lung tissue; Nm– nucleus of developing merozoite. Enlarged fragment of the meront with adjacent part of the lung tissue is shown on the right (modified from Iezhova, 1994).

gametocytes predominate among growing gametocytes. Attenuated medium grown microgametocytes, whose width is less than 1 μm, are present. The maximum value of NDR is greater than unity.

Development in vertebrate host

Exoerythrocytic meronts were found in the lungs and spleen of naturally infected *Erithacus rubecula* during the period of spring relapse (Fig. 169; Pl. I, *1*). The meronts were not seen in other internal organs or in skeletal muscles in this bird (Iezhova, 1994). The meronts are variable in form, frequently branched in shape, and sometimes possess vacuoles. Mature meronts vary from 27 to 74 (on average 45) μm in length, and from 13 to 30 (on average 20) μm in width. They possess a homogeneous mass of uninuclear merozoites that are approximately 1 μm in diameter.

Young gametocytes (Fig. 170, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes markedly extend longitudinally and usually take a position lateral to the nucleus of erythrocytes; at this stage of development gametocytes are slender elongated bodies (Fig. 170, *1*), they are frequently clearly rod-like; growing gametocytes adhere to the nucleus of erythrocytes end extend along the nucleus; the outline is usually more or less ameboid.

Macrogametocytes (Fig. 170, *2–8*; Table 107). The cytoplasm is granular in appearance, frequently contains a few small vacuoles, stains irregularly (intensively stained parts alternate with less intensively stained parts); valutin granules are usually present and, if present, they are numerous and obscure the pigment granules; gametocytes grow around the nucleus of infected erythrocytes, they fill the erythrocytes up to their poles but do not encircle the erythrocyte nucleus completely; gametocytes adhere to the nucleus and envelope of erythrocytes; the central part of the pellicle of the growing gametocytes usually does not extend to the erythrocyte envelope, causing a clear 'dip' and giving a dumbbell-like appearance (Fig. 170, *3, 4*); the dumbbell-shaped gametocytes predominate among the growing gametocytes, are attenuated in width with marked dumbbell-like swellings at the ends (Fig. 170, *3–6*); fully grown gametocytes lose the dumbbell-like shape (Fig. 170, *7*), and are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 170, *8*); the outline of growing gametocytes is usually ameboid (Fig. 170, *3*, *4*, *6*), but sometimes even (Fig. 170, *5*), and fully grown gametocytes are usually even in outline (Fig. 170, *8*);

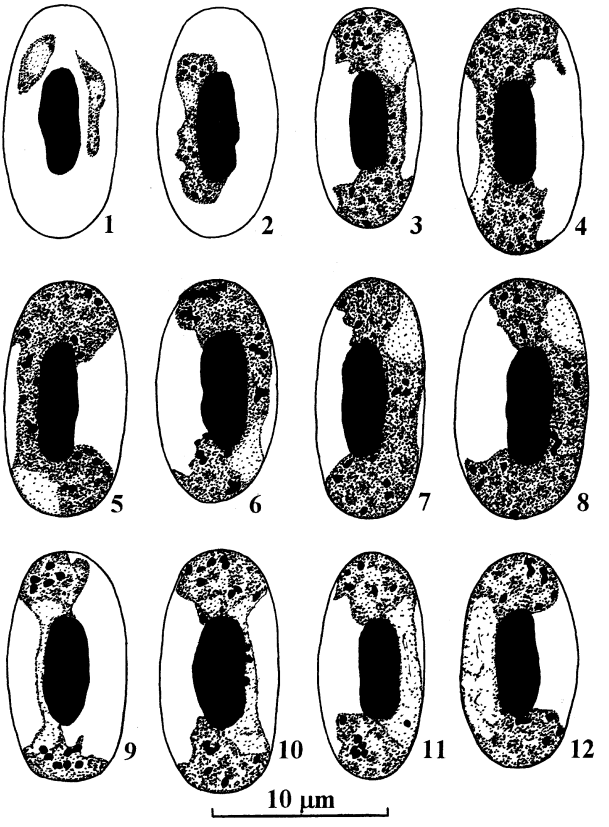

Figure 170 Gametocytes of *Haemoproteus attenuatus* from the blood of *Erithacus rubecula: 1* – young; *2–8* – macrogametocytes; *9–12* – microgametocytes.

the parasite nucleus is variable in form, subterminal in position; a parasite nucleus typical in form and position is shown in Fig. 170, *5, 6, 8*; pigment granules are usually roundish, sometimes oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; nucleus of infected erythrocytes is not displaced laterally, and it is even seen to be pulled into the gametocytes and, as a result, the maximum value of NDR is greater than unity, which is a rare character of haemoproteids.

Microgametocytes (Fig. 170, *9–12*; Table 107). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; growing gametocytes are extremely attenuated in width (Fig. 170, *9*, *10*), and the growing dumbbell-shaped forms are frequently less than 1 μm in width; other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. attenuatus* is especially similar to *H. balmorali*. It can be distinguished from the latter species primarily on the basis of (i) its markedly attenuated dumbbell-shaped gametocytes, and (ii) its greater NDR. It should be noted that the gametocytes shown in Fig. 170, *9*, *10* are absent in *H. balmorali*.

Bennett *et al.* (1991b) thought that only one species of haemoproteids, i.e., *H. fallisi*, parasitize passerine birds of the family Turdidae, and they declared *H. attenuatus* as a junior synonym of *H. fallisi*. Subsequently, however, Peirce and Bennett (1993) noted that *H. balmorali* also develops

in turdid birds. The main differences between *H. balmorali* and *H. attenuatus* are given above. *Haemoproteus attenuatus* can be easily distinguished from *H. fallisi.* Medium and fully grown gametocytes of *H. attenuatus* always fill the infected erythrocytes up to their poles, and this is not characteristic of *H. fallisi*. In addition, growing gametocytes of *H. attenuatus* are frequently highly ameboid in outline and markedly attenuated in width, and they frequently pull the infected erythrocyte nucleus into the gametocytes. All these features are not characteristic of *H. fallisi*.

98. **Haemoproteus (Parahaemoproteus) belopolskyi** Valkiūnas, 1989

Haemoproteus belopolskyi Valkiūnas, 1989e: 130, Fig. 1. – *H. sylvae* Bennett, Bishop and Peirce, 1991b: 35. – *H. belopolskyi*: Valkiūnas, 1997: 315 (=*H. sylvae*).

Type vertebrate host. *Hippolais icterina* (Vieil.) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 108).
Vector. *Culicoides impunctatus* (Diptera: Ceratopogonidae). Previously (Glukhova and Valkiūnas, 1993; Valkiūnas, 1997), this biting midge was thought to belong to a closely related species *C. delta*, which also belongs to the *C. impunctatus* group (Glukhova, 1989). Thus, *C. delta* should be excluded from the list of vectors of this parasite according to current knowledge.
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E).
Distribution. The Palearctic and the Ethiopian and Oriental zoogeographical regions.
Type material. Hapantotype (No. 435.85p, *Hippolais icterina,* 27.05.1985, the Curonian Spit, G. Valkiūnas) and parahapantotypes (No. 303.85p, 379.85p, 455.85p, 527.85p, 528.85p, 23–29.05.1985, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462478, other data are as for other parahapantotypes) is deposited in IRCAH. A series of slides of gametes, zygotes, and ookinetes is deposited in CDVA.
Etymology. This species is named in honour of ornithologist Professor Lev O. Belopolsky, St. Petersburg, Russia, the founding Director of the Biological Station, Russian Academy of Sciences, on the Curonian Spit in the Baltic Sea, who was the author's first teacher in ornithology.

Table 108 List of vertebrate hosts of *Haemoproteus belopolskyi.*

Acrocephalus aedon	*Hippolais caligata*	*S. borin*
A. arundinaceus	*H. olivetorum*	*S. communis*
A. baeticatus	*Parisoma layardi*	*S. curruca*
A. dumetorum	*P. subcaeruleum*	*S. nisoria*
A. palustris	*Phylloscopus collybita*	*Sylvietta rufescens*
A. scirpaceus	*P. trochilus*	
A. schoenobaenus	*Prinia flaviventris*	
Eremomela icteropygialis	*Sylvia atricapilla*	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends and finally can completely encircle the nucleus, but the circumnuclear forms are not numerous. Medium grown gametocytes adhere to the nucleus and envelope of infected erythrocytes. Dumbbell-shaped growing gametocytes are common. Pigment granules are of medium size (0.5 to 1.0 μm). The average number of pigment granules in gametocytes varies during development in different vertebrate hosts, but is usually between 5 and 15.

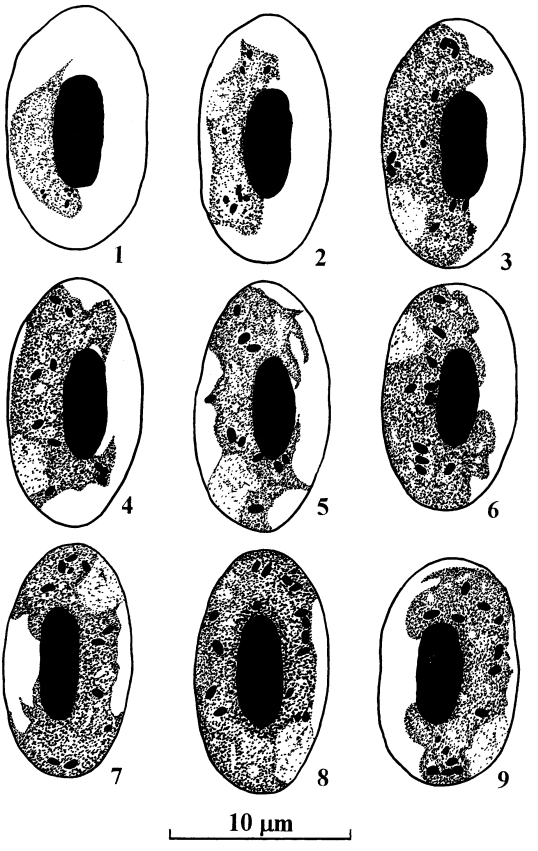

Figure 171 Gametocytes of *Haemoproteus belopolskyi* from the blood of *Hippolais icterina:* *1* – young; *2–9* – macrogametocytes.

Development in vertebrate host

Young gametocytes (Fig. 171, *1*). The earliest forms can be seen anywhere in the infected erythrocytes, roundish or oval; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline varies from even to ameboid.

Macrogametocytes (Fig. 171, *2–9*; Table 109). The cytoplasm is homogeneous in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, markedly enclose the nucleus with their ends (Fig. 171, *6, 7*) and can finally completely encircle the nucleus (Fig. 171, *8*); the circumnuclear gametocytes appear only at the final stages of development in the blood, are never numerous and not always seen in naturally infected birds; gametocytes adhere to the nucleus and envelope of erythrocytes; the central part of the pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 171, *4*, *5*, *7–9*); dumbbell-shaped gametocytes predominate among the growing gametocytes; the outline markedly varies from even to highly ameboid (Fig. 171, *4, 5*); the parasite nucleus is compact, variable in form, subterminal in position and is always located close to the envelope of erythrocytes; a parasite nucleus typical in form and position is

Table 109 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. belopolskyi* (according to Valkiūnas, 1990)				*H. brachiatus* (according to Valkiūnas and Iezhova, 1989)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	27				31			
Length		10.2–13.4	12.0	0.8		11.4–14.4	12.7	0.6
Width		6.1–7.9	6.8	0.4		5.7–7.7	6.8	0.4
Length of nucleus		5.6–6.4	6.0	0.3		5.3–7.1	6.2	0.3
Width of nucleus		2.0–2.8	2.4	0.1		1.9–2.9	2.3	0.1
Erythrocyte parasitized by macrogametocyte	39				31			
Length		10.6–13.6	12.3	0.4		13.6–15.8	14.1	0.6
Width		6.5–7.8	7.1	0.2		5.8–7.7	7.2	0.4
Length of nucleus		4.9–6.8	5.7	0.3		5.2–7.1	5.9	0.2
Width of nucleus		1.9–2.8	2.3	0.2		1.7–2.5	2.1	0.1
Erythrocyte parasitized by microgametocyte	31				31			
Length		10.4–13.2	12.2	0.5		13.8–16.2	14.7	0.7
Width		6.3–8.1	7.4	0.4		6.9–8.1	7.5	0.4
Length of nucleus		4.9–6.6	5.3	0.4		5.3–7.3	6.2	0.2
Width of nucleus		1.8–2.9	2.3	0.3		1.6–2.5	2.1	0.1
Macrogametocyte	39				31			
Length		14.3–26.1	20.4	2.7		13.9–20.3	17.0	1.2
Width		1.2–3.4	2.4	0.6		2.2–3.6	3.0	0.4
Length of nucleus		2.2–4.1	3.4	0.5		2.3–3.9	3.2	0.2
Width of nucleus		1.8–2.5	2.1	0.2		1.7–3.4	2.4	0.2
NDR		0.8–1.0	0.9	0.1		0.5–1.1	0.7	0.1
No. of pigment granules		6–17	10.8	0.8		10–27	18.7	2.0
Microgametocyte	31				31			
Length		14.0–25.7	20.2	2.0		15.1–19.9	17.1	1.3
Width		1.4–3.1	2.2	0.3		2.8–4.1	3.2	0.4
Length of nucleus		6.4–13.0	8.8	1.2		5.2–9.7	7.8	1.0
Width of nucleus		1.4–3.1	2.2	0.2		2.8–4.1	3.2	0.2
NDR		1.0–0.8	0.9	0.1		0.5–1.0	0.8	0.1
No. of pigment granules		5–17	10.4	0.7		11–21	16.8	2.7

Note: All sizes are given in micrometres.

shown in Fig. 171, *7, 9*; pigment granules are oval and roundish, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 172; Pl. II, *2*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline is less ameboid and dumbbell-shaped gametocytes are less frequently seen than in macrogametocytes; occasionally, pigment granules are seen inside the parasite nucleus (Fig. 172, *2*); other characters are as for macrogametocytes.

Development in vector has not been studied in detail. Sporogony is completed and sporozoites infective to birds develop in the biting midge *Culicoides impunctatus.*

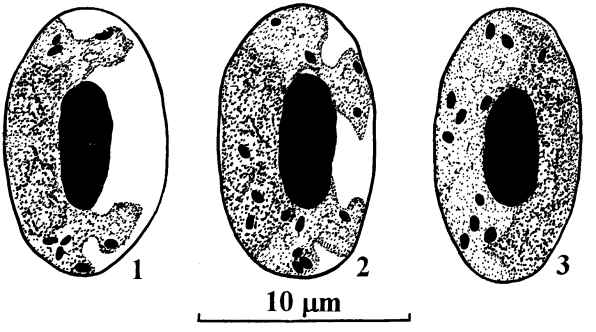

Figure 172 Microgametocytes of *Haemoproteus belopolskyi* from the blood of *Hippolais icterina.*

Gametogenesis, development of zygote and ookinete *in vitro* were studied under the light microscope at 18 to 20°C by Valkiūnas and Iezhova (1993a). The data on the rate of this process are given in Table 23. Within 1 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave the infected erythrocytes (Fig. 173, *3*, *4*, *7*, *8*). Exflagellation was recorded approximately 4 min after EBA (Fig. 173, *10*; Pl. III, *1*). At approximately the same time, free microgametes appear (Fig. 173, *11*), and slightly later, fertilization of macrogametes (Fig. 173, *12*; Pl. III, *3*) and first zygotes (Fig. 173, *13*) were seen. The cytoplasm of zygotes of *H. belopolskyi* stains darker than in macrogametes (Fig. 173, *9*, *13*). The initial stages of ookinete differentiation were seen approximately 1.5 h after the first zygotes appeared. At this time, a long finger-like outgrowth, located tangentially to the main body of the parasite, appears (Fig. 173, *14*). As the ookinete develops, this outgrowth extends markedly and forms the anterior or apical end of the ookinete. At the opposite end of the medium-differentiated ookinete, the accumulation of pigment granules was recorded (Fig. 173, *15*). In fully grown ookinetes, the pigment and adjacent part of cytoplasm are eliminated as a residual body. It should be noted that, in most ookinetes, the compact residual body looks like a smooth continuation of the main body of the ookinetes (Fig. 173, *16*). One or several small 'vacuoles' appear in the cytoplasm of medium differentiated ookinetes, and the 'vacuoles' persist in fully grown ookinetes (Fig. 173, *15*, *16*). The ookinetes with a residual body develop approximately 6 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 24.

C o m m e n t s. Bennett *et al.* (1991b) redescribed *H. belopolskyi* on the basis of the material which came from a nontype host, *Sylvia atricapilla*. In general, their data on the morphology of this parasite coincide with the original description (Valkiūnas, 1989e), except for the average number of pigment granules which reached 17 in gametocytes developed in *S. atricapilla*, and it was about 11 in gametocytes developed in the type host, *Hippolais icterina*. The number of pigment granules varies during the development of this parasite in different vertebrate hosts. It should be also noted that the number of gametocytes with an ameboid outline is also variable in different vertebrate hosts, and it was recorded to be the greatest during the development of the parasite in the type host.

Bennett *et al.* (1991b) described *H. sylvae* from the blood of *Parisoma subcaeruleum* from South Africa. Gametocytes of this parasite grow around the nucleus of infected erythrocytes, markedly enclose the nucleus with their ends, and possess about 10 pigment granules on average. These gametocytes are similar to growing gametocytes of *H. belopolskyi* from the blood of the type host, *Hippolais icterina.* Circumnuclear gametocytes were not recorded in *H. sylvae*, and this is the main difference between *H. belopolskyi* and *H. sylvae.* It should be noted that the circumnuclear gametocytes of *H. belopolskyi* have been recorded only in blood films where fully grown gametocytes

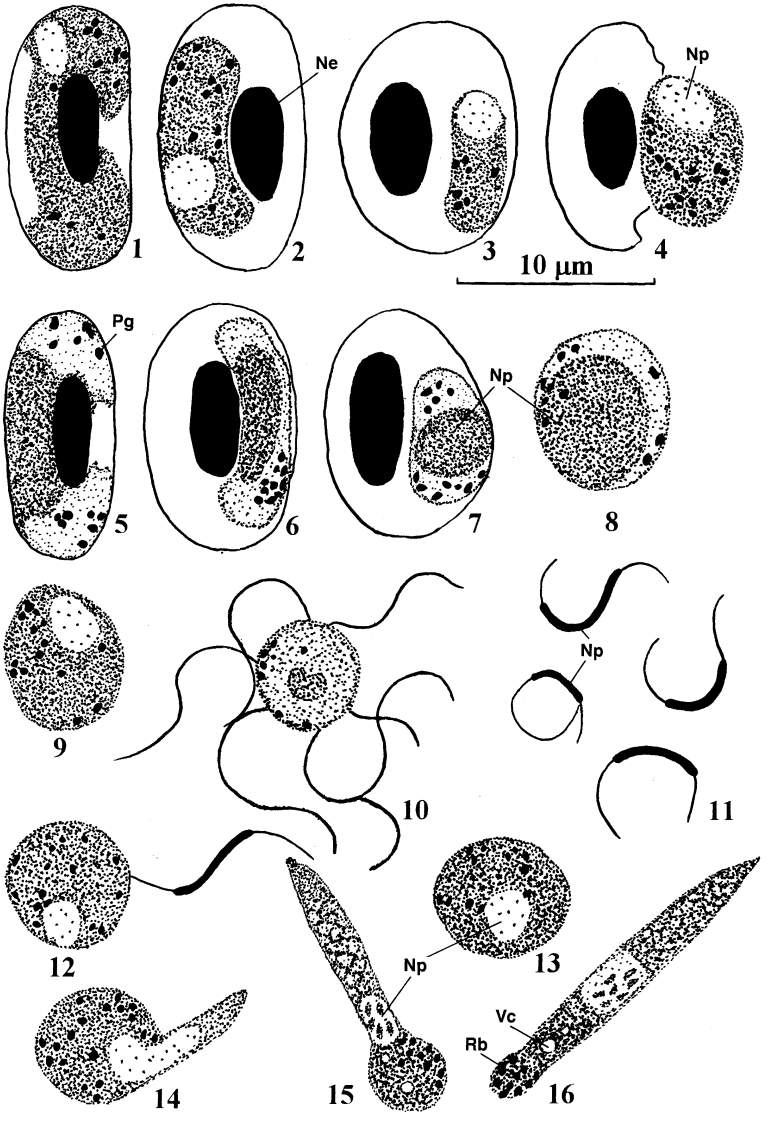

Figure 173 *Haemoproteus belopolskyi* gametogenesis, zygote and ookinete development *in vitro: 1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Hippolais icterina* before the onset of gametogenesis; *2–4* – rounded up macrogametocyte; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – macrogamete; *10* – exflagellation of microgametes; *11* – microgametes; *12* – fertilization of macrogamete; *13* – zygote; *14* – initial stage of differentiation of ookinete; *15* – medium differentiated ookinete; *16* – ookinete with a residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc –'vacuole' (modified from Valkiūnas and Iezhova, 1993a).

predominate and, in early parasitemia, they are absent. Other characters of *H. sylvae* and *H. belopolskyi* overlap. The range of vertebrate hosts, and the areas of distribution of these two parasites overlap, too. The investigation of the type material of the both species showed that, most probably, the original description of *H. sylvae* is based mainly on not fully grown gametocytes of *H. belopolskyi*.

Haemoproteus sylvae should be considered as a junior synonym of *H. belopolskyi* before additional data on the morphology, geographical and host-dependent variability, and other biological characters of *H. sylvae* and *H. belopolskyi* are present (see also 'Comments' to *H. majoris*).

Among the haemoproteids of birds belonging to the Passeriformes, *H. belopolskyi* is especially similar to *H. ptilotis*. It can be distinguished from the latter species primarily on the basis of the morphology of its macrogametocytes.

The range of vertebrate hosts of *H. belopolskyi* (Table 108) needs to be specified by means of (i) the detailed study of the morphology of gametocytes which develop in different species of birds and (ii) the application of taxonomic characters in the DNA of parasites.

99. **Haemoproteus (Parahaemoproteus) brachiatus** Valkiūnas and Iezhova, 1989

Haemoproteus brachiatus Valkiūnas and Iezhova, 1989: 61, Fig. 6.

Type vertebrate host. *Falco tinnunculus* L. (Falconiformes).
Additional vertebrate host. *Falco columbarius, F. naumanni, F. sparverius, F. subbuteo* (Falconiformes).
Type locality. The Chokpak Ornithological Station located in the foothills of the Western Tien Shan, approximately 80 km south-west of Djambul, Southern Kazakhstan.
Distribution. This parasite has so far been recorded only in the Holarctic. However, it is likely that it has a larger range of distribution.
Type material. Hapantotype (No. 3706.87 Az, *Falco tinnunculus,* 07.10.1987, Southern Kazakhstan, G. Valkiūnas) and parahapantotypes (No. 1480-1482.86 Az, 2586-2588.87 Az, 2644-2646.87 Az, 3028-3030.87 Az, 3585-3587.87 Az, 3626-3628.87 Az, 3629-3631.87 Az, 3705.87 Az, 4273-4275.87 Az, 1986-1987, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462480, other data are as for the hapantotype) is deposited in IRCAH.
Etymology. The specific name reflects the highly ameboid outline of gametocytes of this parasite.

Main diagnostic characters. A parasite of species of the Falconiformes whose gametocytes grow around the nucleus of infected erythrocytes and do not displace or slightly displace the nucleus laterally. Fully grown gametocytes nearly completely or even completely encircle the nucleus of the erythrocytes. Gametocytes are highly ameboid in outline with marked finger-like or horn-like outgrowths. Over 50% of mature gametocytes are closely appressed to the nucleus of infected erythrocytes.

Development in vertebrate host
Young gametocytes (Fig. 174, *1*) can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend along the nucleus of infected erythrocytes, and they usually touch the envelope and nucleus of the erythrocytes; gametocytes markedly vary in shape and outline, and are frequently lobulated in shape with one or several marked ameboid outgrowths (Fig. 174, *1*).

Macrogametocytes (Fig. 174, *2–6*; Table 109). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles; valutin granules are not seen; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or only slightly displace the nucleus laterally; gametocytes usually adhere to the envelope of erythrocytes,

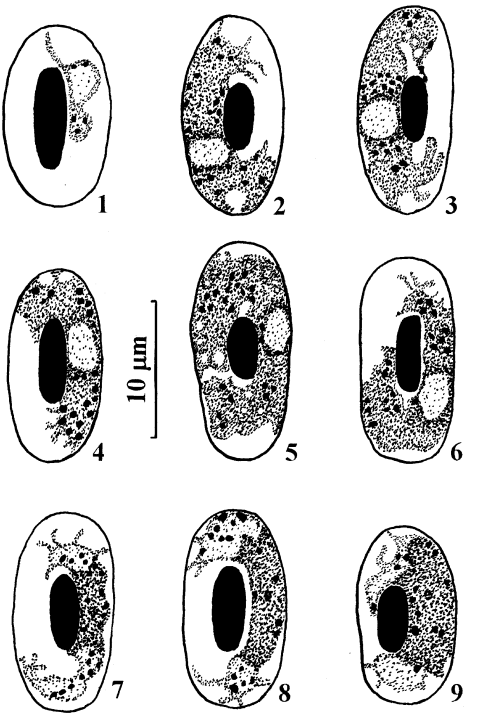

Figure 174 Gametocytes of *Haemoproteus brachiatus* from the blood of *Falco tinnunculus:* *1* – young; *2–6* – macrogametocytes; *7–9* – microgametocytes (modified from Valkiūnas and Iezhova, 1989).

but this contact is sometimes more or less interrupted in gametocytes with a wavy outline (Fig. 174, *3*); gametocytes frequently adhere to the nucleus of erythrocytes (Fig. 174, *2–5*); gametocytes, which do not touch the nucleus of erythrocytes and thus form a more or less evident unfilled space (a 'cleft') between the parasite and erythrocyte nucleus (Fig. 174, *6*), represent 27.1±7.8% of the total number of gametocytes in the type material; growing gametocytes shown in Fig. 174, *3* are especially common; fully grown gametocytes markedly enclose the nucleus of erythrocytes with their ends, and they can completely encircle the nucleus but do not occupy all available cytoplasmic space in the host cells (Fig. 174, *5*); the outline is usually highly ameboid with numerous marked finger-like or horn-like outgrowths which markedly vary in form and length; the parasite nucleus is compact, usually roundish or oval, median or submedian in position; pigment granules are usually roundish, sometimes oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 174, *7–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus possesses clear clumps of chromatin; pigment granules are frequently seen inside the parasite nucleus (Fig. 174, *7–9*); other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Falconiformes, *H. brachiatus* is especially similar to *H. nisi*. These two parasites can be distinguished primarily on the basis of the

following characters. First, in *H. nisi*, gametocytes, which do not touch the nucleus of erythrocytes and, thus, form a more or less evident 'cleft' between the parasite and the erythrocyte nucleus (Fig. 150, *5*, *7*), clearly predominate, and they represent over 80% of the total number of gametocytes. In *H. brachiatus* such gametocytes are also present but they are much less numerous, never predominate and represent less than 40% of the total number of gametocytes. Second, the average number of pigment granules in gametocytes of *H. nisi* is less than in gametocytes of *H. brachiatus*. Third, gametocytes of *H. brachiatus* are highly ameboid in outline with marked finger-like or horn-like outgrowths (Fig. 174), and gametocytes with an even outline were not seen in the type material of this species. A highly ameboid outline in gametocytes of *H. nisi* is also sometimes present (Fig. 150, *4*) but is rare. Most gametocytes of *H. nisi* are even or more or less wavy in outline as is shown in Fig. 150, *5*.

100. **Haemoproteus (Parahaemoproteus) parus** Bennett, 1989

Haemoproteus parus Bennett, 1989b: 2685, Fig. 1–6.

Type vertebrate host. *Parus bicolor* L. (Passeriformes).
Type locality. University Park, Pennsylvania, USA.
Distribution. This parasite has been recorded only in the type locality.
Type material. Hapantotype (No. 102470a, *Parus bicolor,* 21.04.1965, University Park, Pennsylvania, USA, coll. Davis) and parahapantotypes (No. 102470b, 11.05.1965 and No. 102471, 13.06.1965, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Parus.*

Main diagnostic characters. A parasite of species of the Passeriformes whose fully grown gametocytes are roundish (discoid) in form, they markedly deform infected erythrocytes, markedly displace their nuclei, and can even enucleate the host cells. The average length of the fully grown gametocytes is 6 μm or greater. The average length of the nucleus of fully grown gametocytes is greater than 2 μm.

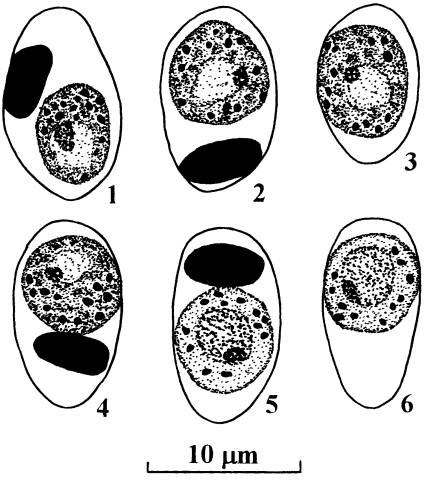

Figure 175 Gametocytes of *Haemoproteus parus* from the blood of *Parus bicolor:* *1–4* – macrogametocytes; *5*, *6* – microgametocytes (modified from Bennett, 1989b).

Table 110 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. (modified from Bennett, 1989b).

Feature	*H. parus*			*H. sittae*			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	35			15			
Length		11.9	1.0		–	11.2	1.0
Width		6.0	0.1		–	6.2	0.4
Length of nucleus		5.6	0.6		–	4.8	0.5
Width of nucleus		1.9	0.2		–	1.9	0.2
Erythrocyte parasitized by macrogametocyte	35			25			
Length		10.6	1.0		–	11.8	0.7
Width		7.2	0.8		–	5.9	0.9
Length of nucleus		5.0	0.6		–	4.7	0.4
Width of nucleus		2.3	0.3		–	2.0	0.2
Macrogametocyte	35			25			
Length		6.6	0.8		–	13.8	1.0
Width		5.5	0.6		–	2.3	0.5
Length of nucleus		3.1	0.7		–	3.0	0.4
Width of nucleus		2.2	0.6		–	1.7	0.3
NDR		–	–		0.5–1.3	0.7	0.2
No. of pigment granules		13.0	2.4		–	13.4	1.6
Microgametocyte	20						
Length		6.6	0.6	10	–	14.4	1.4
Width		6.1	0.6	10	–	2.6	0.7
Length of nucleus		3.9	0.8	10	–	4.9	1.3
Width of nucleus		3.0	0.6	10	–	2.6	0.5
NDR		–	–	25	0.4–1.0	0.6	0.2
No. of pigment granules		12.0	2.0	10	–	13.0	1.2

Note: All sizes are given in micrometres.

Development in vertebrate host

Young gametocytes are not present in the type material.

Macrogametocytes (Fig. 175, *1–4*; Table 110). The cytoplasm is coarsely granular in appearance, contains valutin granules; fully grown gametocytes are roundish (discoid); the outline is even; the parasite nucleus is variable in form, the nucleolus is well seen; pigment granules are roundish or irregular, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; gametocytes markedly deform the infected erythrocytes, markedly displace their nuclei (Fig. 175, *1, 2*), and can even enucleate the host cells (Fig. 175, *3*); the enucleated erythrocytes represent approximately 30% of the total number of infected erythrocytes with fully grown gametocytes.

Microgametocytes (Fig. 175, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The intensity of parasitemia is low in the type material of *H. parus.* After approximately one hour of examination, the author found only nine gametocytes of the parasite. It is possible

that a malaria parasite belonging to the subgenus *Haemamoeba* was described under the name *H. parus*. Gametocytes of *H. parus* are identical to roundish (discoid) gametocytes of most species of the subgenus *Haemamoeba*, for example, *Plasmodium (Haemamoeba) relictum* (see Fig. 12*, 10, 11, 13*). Avian *Plasmodium* species of the subgenus *Haemamoeba* are the most common parasites found particularly in passerines all over the world. Bennett (1989b) believed that the gametocytes described are not gametocytes of *Plasmodium* spp. because erythrocytic meronts were not recorded. The author has not seen meronts in the type material either. However, at low natural infections, malaria meronts are frequently either absent or rare and easy to overlook in blood films. Descriptions of new species of bird haemoproteids with discoid gametocytes from blood films with low parasitemia should be discouraged. Thus, the validity of the name *H. parus* is questionable. Additional material is required to solve this question. It should be noted that discoid gametocytes are not typical of haemoproteids parasitizing the Holarctic birds.

During the identification of *H. parus*, which was recorded in *Parus xanthogenys* in India, Bennett (1989b) noted that only four roundish (discoid) gametocytes were found in the blood films. As shown before, the roundish gametocytes of most species of malaria parasites of the subgenus *Haemamoeba* are similar to the roundish gametocytes of *H. parus*, and it is difficult to find malaria meronts in blood at low natural infections by blood film microscopy. Avian malaria parasites are common in India (Nandi, 1984). Thus, based on the evidence presented above, it is difficult to accept G.F. Bennett's identification of several roundish gametocytes recorded in *Parus xanthogenys* as *H. parus*, and *Parus xanthogenys* is not mentioned here as an additional vertebrate host of *H. parus*.

Among the haemoproteids of birds belonging to the Passeriformes, *H. parus* is especially similar to *H. souzalopesi*. It can be distinguished from the latter species primarily on the basis of the slightly larger size of its gametocytes.

101. **Haemoproteus (Parahaemoproteus) sittae** Bennett, 1989

Haemoproteus sittae Bennett, 1989b: 2687, Fig. 7, 8.

Type vertebrate host. *Sitta carolinensis* Latham (Passeriformes).
Additional vertebrate hosts. *Sitta azurea*, *S. castanea*, *S. europaea* (Passeriformes).
Type locality. University Park, Pennsylvania, USA.
Distribution. The Holarctic and Oriental zoogeographical regions.
Type material. Hapantotype (No. 100443, *Sitta carolinensis,* 06.10.1964, University Park, Pennsylvania, USA, coll. Davis) and parahapantotype (No. 37036, *S. castanea*, 06.10.1968, West Bhutan, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Sitta*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are present, and they predominate among the growing macrogametocytes. Growing macrogametocytes frequently pull the nucleus of infected erythrocytes inside the gametocytes and, as a result, the maximum value of NDR in erythrocytes parasitized by macrogametocytes exceeds unity. The maximum NDR during the development of microgametocytes does not exceed unity. Fully grown gametocytes do not displace or only slightly displace the nucleus of erythrocytes laterally. Pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, about 13 per gametocyte on average. A species difficult to identify; can be distinguished from the similar species of haemoproteids of birds belonging to the Passeriformes only on the basis of a detailed analysis of a set of characters.

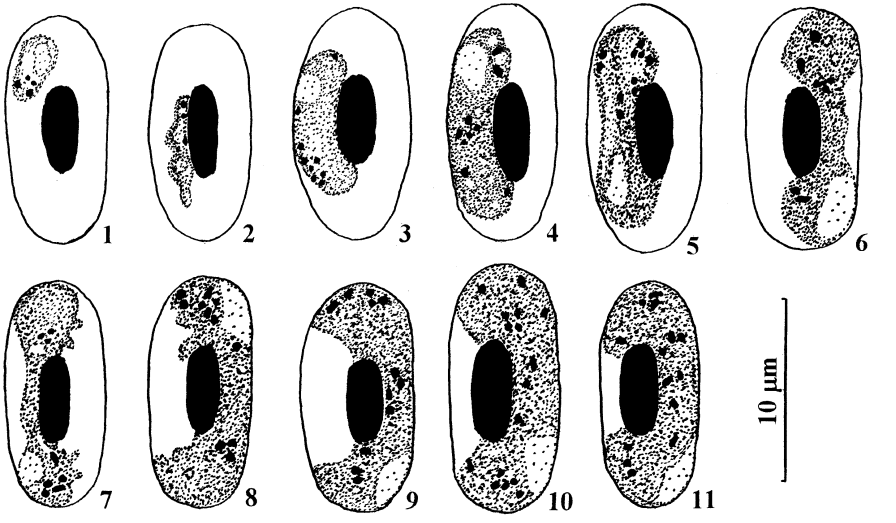

Figure 176 Gametocytes of *Haemoproteus sittae* from the blood of *Sitta europaea: 1–3* – young; *4–11* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992c).

Development in vertebrate host

Young gametocytes (Fig. 176, *1–3*). The earliest forms are usually seen in a polar position in infected erythrocytes, and they lie free in the cytoplasm (Fig. 176, *1*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus. At this stage of development, gametocytes frequently are wavy in outline (Fig. 176, *2*). Advanced gametocytes adhere to the envelope of erythrocytes (Fig. 176, *3*). The outline of young macrogametocytes is usually even (Fig. 176, *3*), but is frequently wavy or ameboid in young microgametocytes (Fig. 177, *1*).

Macrogametocytes (Fig. 176, *4–11*; Table 110). The cytoplasm is homogeneous in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends, fill the erythrocytes up to their poles, but do not encircle the nucleus of the erythrocytes completely; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 176, *5–7*); the dumbbell-shaped parasites predominate among the growing gametocytes; fully grown gametocytes lose the dumbbell-like shape, and they are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 176, *8–11*); growing gametocytes frequently pull the nucleus of infected erythrocytes inside the gametocytes and, as a result, the maximum value of NDR exceeds unity (Fig. 176, *8, 9*; Table 110); fully grown gametocytes do not displace or only slightly displace the nucleus of infected erythrocytes laterally (Fig. 176, *10, 11*); the outline of growing gametocytes varies from even (Fig. 176, *5*, *6*) to ameboid (Fig. 176, *7*, *8*) and is usually even in fully grown gametocytes (Fig. 176, *11*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish or oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 177). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the dumbbell-shaped parasites (Fig. 177, *3*) are

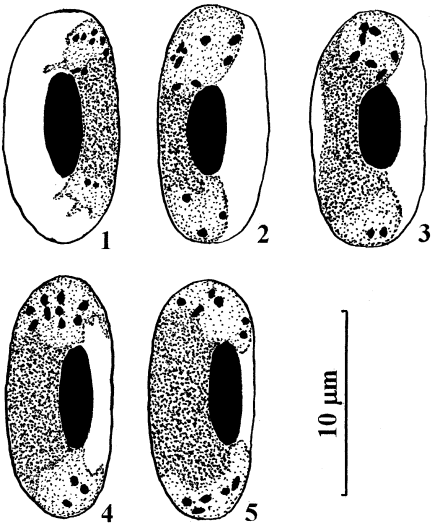

Figure 177 Microgametocytes of *Haemoproteus sittae* from the blood of *Sitta europaea* (modified from Valkiūnas and Iezhova, 1992c).

more rarely seen than for macrogametocytes; gametocytes, which pull the erythrocyte nucleus inside the parasite, are not seen; the maximum value of NDR does not exceed unity; other characters are as for macrogametocytes.

Comments. *Haemoproteus sittae* is a species difficult to identify. This parasite is especially similar to *H. dolniki*. It can be distinguished from the latter species primarily on the basis of (i) its numerous young gametocytes with a wavy outline (Fig. 176, *2*) and (ii) the absence of microgametocytes which pull the erythrocyte nucleus inside the parasite (see Fig. 200, 6).

In the original description (Bennett, 1989b), mainly rod-like pigment granules were shown in the figures of gametocytes of *H. sittae*. However, such pigment granules were rare (if seen at all) in the type material and in a series of additional examined blood films from *Sittae europaea*. Roundish and oval pigment granules predominate in gametocytes of *H. sittae.*

102. **Haemoproteus (Parahaemoproteus) dicaeus** Bennett and Bishop, 1990

Haemoproteus dicaeus Bennett and Bishop, 1990b: 160, Fig. 1, 2.

Type vertebrate host. *Prionochilus percussus* (Temm. et Laugier) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 111).
Type locality. Subang, Malaysia.
Distribution. The Oriental zoogeographical region.
Type material. Hapantotype (No. 5712, *Prionochilus percussus,* 25.04.1962, Subang, Malaysia, H.E. McClure) and parahapantotypes (No. 12325, *Dicaeum cruentatum*, 23.12.1966, Bangphra, Thailand, H.E. McClure; No. 37641, *D. australe*, 25.06.1965, Luzon, Philippine Islands, H.E. McClure) are deposited in IRCAH.

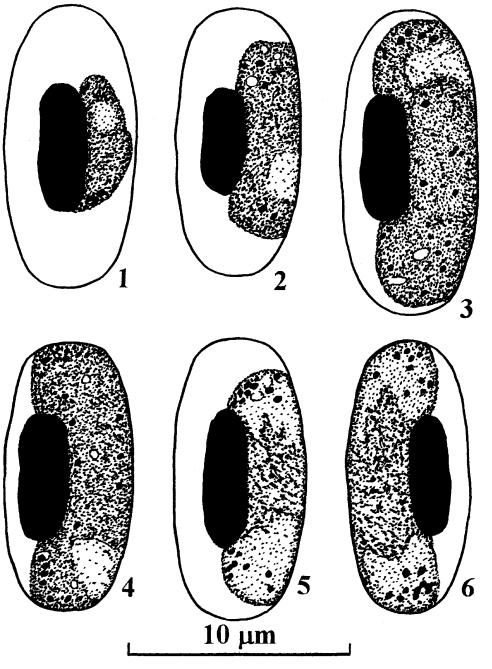

Figure 178 Gametocytes of *Haemoproteus dicaeus* from the blood of *Prionochilus percussus: 1* – young; *2–4* – macrogametocytes; *5*, *6* – microgametocytes.

Etymology. The specific name is derived from the name of the family Dicaeidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes; they displace the nucleus laterally but do not encircle it completely. Medium and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are not seen. Fully grown gametocytes fill the erythrocytes up to their poles. Pigment granules are of small (<0.5 μm) size, about 16 per gametocyte on average. The average NDR is 0.6 or less.

Development in vertebrate host

Young gametocytes (Fig. 178, *1*) are usually seen in a position lateral to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes, they extend longitudinally along it and then adhere to the envelope of erythrocytes; the outline is even.

Table 111 List of vertebrate hosts of *Haemoproteus dicaeus* (according to Bennett and Bishop, 1990b).

Dicaeum australe	*D. trigonostigma*
D. cruentatum	*Prionochilus maculatus*
D. erythrorhynchos	*P. plateni*

Table 112 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. dicaeus* (modified from Bennett and Bishop, 1990b)			*H. gavrilovi* (according to Valkiūnas and Iezhova, 1990b)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	55			31			
Length		11.9	1.0		12.8–14.8	13.6	0.4
Width		6.3	0.7		6.1–7.6	6.7	0.3
Length of nucleus		5.1	0.6		5.3–7.2	6.2	0.2
Width of nucleus		1.8	0.2		1.6–2.8	2.1	0.1
Erythrocyte parasitized by macrogametocyte	55			31			
Length		12.4	0.8		14.7–17.2	15.7	0.5
Width		5.6	0.5		5.2–7.1	6.1	0.3
Length of nucleus		5.2	0.7		4.3–6.1	5.4	0.2
Width of nucleus		1.9	0.3		1.7–2.5	2.2	0.1
Erythrocyte parasitized by microgametocyte	15			31			
Length		12.5	0.7		12.6–17.5	15.9	0.6
Width		6.0	0.6		5.0–7.1	6.2	0.4
Length of nucleus		6.0	0.7		4.7–6.2	5.7	0.2
Width of nucleus		1.9	0.2		1.7–2.7	2.2	0.1
Macrogametocyte	55			31			
Length		12.5	0.8		14.4–17.2	15.6	0.6
Width		3.1	0.5		2.8–4.2	3.6	0.4
Length of nucleus		2.7	0.6		2.1–3.3	2.7	0.2
Width of nucleus		2.2	0.4		1.2–2.7	2.0	0.1
NDR		0.4	0.2		0.0–0.6	0.2	0.1
No. of pigment granules		16.1	1.8		7–11	8.8	1.2
Microgametocyte	15			31			
Length		12.7	1.0		13.9–17.5	15.7	0.6
Width		3.6	0.4		2.8–4.0	3.3	0.4
Length of nucleus		7.6	0.6		–	–	–
Width of nucleus		2.7	0.3		2.8–4.0	3.3	0.2
NDR		0.3	0.1		0.0–0.7	0.4	0.1
No. of pigment granules		16.7	1.0		6–12	8.5	1.4

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 178, *2–4*; Table 112). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; gametocytes grow along the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends and displace it laterally but do not encircle the nucleus completely; gametocytes are closely appressed to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes were not seen; fully grown gametocytes fill the erythrocytes up to their poles (Fig. 178, *4*); the outline is usually even; the parasite nucleus is compact, variable in form, subterminal in position;

pigment granules are of small (<0.5 μm) size, frequently dust-like in appearance and ill-defined, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 178, *5*, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Numerous small pigment granules in gametocytes are the main diagnostic characters of *H. dicaeus*. This species is especially similar to *H. alaudae* and *H. calandrellae*. *Haemoproteus dicaeus* can be distinguished from *H. alaudae* primarily on the basis of (i) its more numerous pigment granules in gametocytes, (ii) the type of growth in infected erythrocytes (fully grown gametocytes of *H. alaudae* markedly enclose the nucleus of erythrocytes with their ends), and (iii) its smaller average NDR. *Haemoproteus dicaeus* can be distinguished from *H. calandrellae,* particularly, on the basis of (i) its subterminal position of nucleus in macrogametocytes and (ii) the absence of pigment granules of medium (0.5 to 1.0 μm) size in gametocytes.

103. **Haemoproteus (Parahaemoproteus) gavrilovi** Valkiūnas and Iezhova, 1990

Haemoproteus gavrilovi Valkiūnas and Iezhova, 1990b: 99, Fig. 6, 7.

Type vertebrate host. *Merops apiaster* L. (Coraciiformes).
Type locality. The Chokpak Ornithological Station located in the foothills of the Western Tien Shan, approximately 80 km south-west of Djambul, Southern Kazakhstan.
Distribution. This parasite has been recorded only in the Palearctic. It is likely that the range is wider.

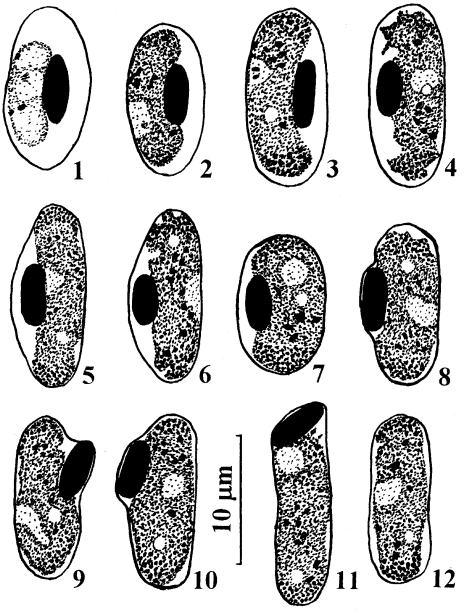

Figure 179 Gametocytes of *Haemoproteus gavrilovi* from the blood of *Merops apiaster: 1* – young; *2–12* – macrogametocytes (modified from Valkiūnas and Iezhova, 1990b).

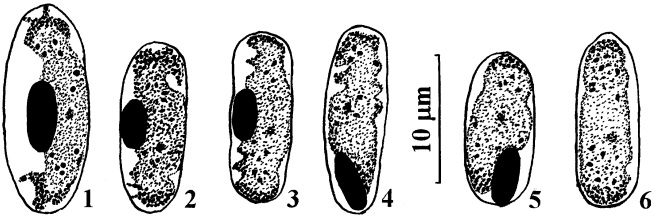

Figure 180 Microgametocytes of *Haemoproteus gavrilovi* from the blood of *Merops apiaster* (modified from Valkiūnas and Iezhova, 1990b).

Type material. Hapantotype (No. 2399.87 Az, *Merops apiaster,* 16.09.1987, Southern Kazakhstan, G. Valkiūnas) and parahapantotypes (No. 2198-2199.87 Az, 2398.87 Az, 2400-2401.87 Az, 2571.87 Az, 14-19.09.1987, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462490, 19.09.1987, other data are as for the hapantotype) is deposited in IRCAH.

Etymology. This species is named in honour of ornithologist Professor Eduard I. Gavrilov, who contributed to the mass investigation into blood parasites of birds in Kazakhstan. He also kindly supported the investigation by the author in South Kazakhstan during which the type material was collected.

Main diagnostic characters. A parasite of species of the Coraciiformes whose gametocytes markedly displace the nucleus of infected erythrocytes laterally and then toward one pole of the erythrocytes, and they can even finally enucleate the host cells. Macrogametocytes frequently possess one large (average diameter is greater than 1 μm) vacuole. The outline of macrogametocytes varies from even to ameboid, and the outline of microgametocytes is usually ameboid. The average number of pigment granules in gametocytes is less than 11. Infected erythrocytes are significantly hypertrophied in length in comparison to uninfected ones, and their nuclei are atrophied in length.

Development in vertebrate host

Young gametocytes (Fig. 179, *1*). The earliest forms are absent in the type material; as the parasite develops, gametocytes usually take a lateral position to the nucleus of infected erythrocytes, and they adhere to the nucleus and envelope of the erythrocytes (Fig. 179, *1*); gametocytes slightly displace the nucleus of erythrocytes laterally; the outline is usually even.

Macrogametocytes (Fig. 179, *2–12*; Pl. II, *3*; Table 112). The cytoplasm is granular in appearance, frequently contains valutin granules which are usually located at the ends of gametocytes and obscure the pigment granules; a large clear vacuole, which is on average 1.3±0.1 μm in diameter, is usually present in the cytoplasm, and this is a characteristic feature of this species; gametocytes adhere to the nucleus and envelope of erythrocytes, but the contact of the gametocytes with the erythrocyte envelope partly varies in parasites with an irregular outer edge (Fig. 179, *4*, *5*, *8*); the outline of gametocytes varies from even (Fig. 179, *3*, *7*) to slightly ameboid (Fig. 179, *8*, *9*, *12*) and ameboid (Fig. 179, *4*, *6*); the parasite nucleus is compact, variable in form and position; pigment granules are roundish and oval, usually of small (<0.5 μm) but sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; gametocytes markedly displace the nucleus of infected erythrocytes first laterally (Fig. 179, *5–8*) and then toward one pole (Fig. 179, *9–11*;

Pl. II, *3*), and finally they can even enucleate the host cells (Fig. 179, *12*); gametocytes in the enucleated erythrocytes are cigar-shaped bodies lying inside the erythrocytic remnant, they are not numerous in the type material, but the forms shown in Fig. 179, *8–11* are common; infected erythrocytes are significantly hypertrophied in length in comparison to uninfected ones, and their nuclei are atrophied in length.

Microgametocytes (Fig. 180). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is diffuse and ill-defined; gametocytes with a highly ameboid outline predominate (Fig. 180, *1–4*); the large vacuole is not seen in the cytoplasm; other characters are as for macrogametocytes.

Comments. In the hapantotype, the large clear vacuole is present in each macrogametocyte of *H. gavrilovi*. In the parahapantotypes, the number of macrogametocytes with this vacuole varies, but the vacuole is always present in some macrogametocytes in all the parahapantotypes. It is likely that this vacuole appears at a certain stage of the development of macrogametocytes (see also 'Comments' to *H. trogonis*).

Among the haemoproteids of birds belonging to the Coraciiformes, *H. gavrilovi* is similar to *H. enucleator* and *H. lairdi*. It can be distinguished from the latter two species, particularly on the basis of a smaller number of pigment granules in its gametocytes. Additionally, *H. gavrilovi* can be also distinguished from *H. lairdi* on the basis of (i) the large clear vacuole which is frequently present in its gametocytes, and (ii) the size of its gametocytes which are larger in length and smaller in width.

Medium grown gametocytes of *H. gavrilovi* (Figs. 179, *4*; 180, *1*) are similar to fully grown gametocytes of *H. meropis*. Both parasites develop in the same host, *Merops apiaster*. Fully grown gametocytes of these species are clearly different. It is important to note that *H. gavrilovi* can be distinguished from *H. meropis* primarily on the basis of (i) a smaller number of pigment granules in its gametocytes and (ii) the peculiarities of the influence on the nucleus of infected erythrocytes (gametocytes of *H. meropis* only slightly displace the nucleus of erythrocytes laterally, but gametocytes of *H. gavrilovi* markedly displace the nucleus and they can even enucleate the host cells).

Some gametocytes of *H. gavrilovi* (Fig. 179, *7*) are similar to gametocytes of *H. manwelli*. Gametocytes of both species possess clear vacuoles in the cytoplasm. *Haemoproteus gavrilovi* can be distinguished from *H. manwelli* primarily on the basis of (i) the different mode of growth of its gametocytes in the erythrocytes (gametocytes of *H. manwelli* do not displace the nucleus toward one pole of erythrocytes and they do not enucleate the infected erythrocytes), (ii) the ameboid outline of gametocytes, especially in microgametocytes, and (iii) significantly longer gametocytes.

In South Kazakhstan, *H. gavrilovi* has been recorded only in adults of *Merops apiaster* which accomplished at least one seasonal migration. This parasite was not seen in over 300 juvenile birds during the autumnal migration. Thus, it is likely that seasonal migrations in the Ethiopian zoogeographical region play an important role in the infection of *M. apiaster* with *H. gavrilovi.* It is still unclear if the transmission of this parasite also takes place in the Palearctic.

104. **Haemoproteus (Parahaemoproteus) motacillae** Bennett and Peirce, 1990

Haemoproteus motacillae Bennett and Peirce, 1990c: 945, Fig. 8–10.

Type vertebrate host. *Motacilla flava* L. (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 113).
Type locality. Entebbe, Uganda.
Distribution. The Palearctic and the Ethiopian and Oriental zoogeographical regions.

Type material. Hapantotype (No. 28183, *Motacilla flava,* 30.12.1971, Entebbe, Uganda, N. Okia) and parahapantotypes (No. 25240, 29.10.1971, other data are as for the hapantotype; No. 40420, *M. alba*, 20.12.1969, Rajastham, India, H.E. McClure; No. 12568 *Dendronanthus indicus*, 20.10.1966, Bangphra, Tailand, H.E. McClure) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Motacilla.*

Table 113 List of vertebrate hosts of *Haemoproteus motacillae*.

Anthus campestris	*Dendronanthus indicus*
A. hodgsoni	*Motacilla alba*
A. trivialis	

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of the erythrocytes. Dumbbell-shaped gametocytes are present, and they predominate in growing macrogametocytes. Gametocytes with a highly ameboid outline do not predominate in growing macrogametocytes.

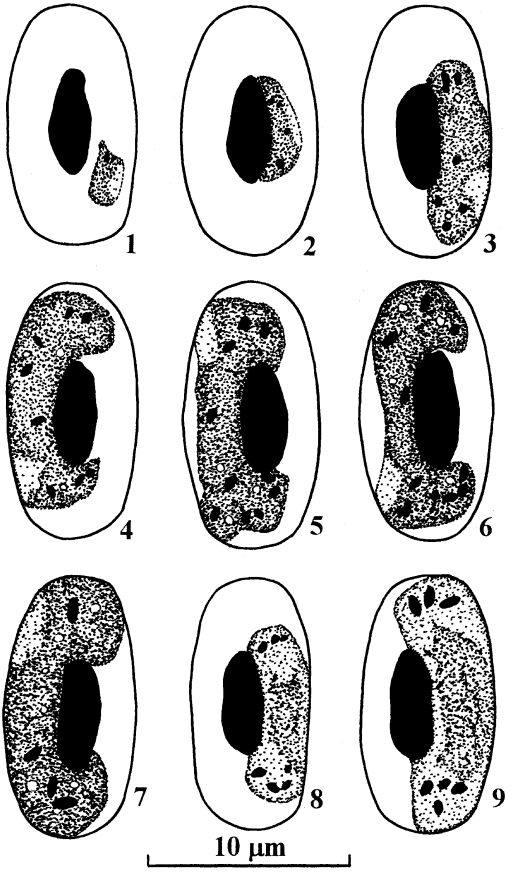

Figure 181 Gametocytes of *Haemoproteus motacillae* from the blood of *Motacilla flava: 1*, *2* – young; *3*–*7* – macrogametocytes; *8*, *9* – microgametocytes.

Table 114 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. motacillae* (modified from Bennett and Peirce, 1990c)				*H. nucleophilus* (modified from Bennett and Bishop 1990b)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	70				32		
Length		–	11.7	0.7		11.9	0.6
Width		–	6.4	0.6		6.4	0.4
Length of nucleus		–	4.9	0.5		5.2	0.6
Width of nucleus		–	1.9	0.2		1.8	0.3
Erythrocyte parasitized by macrogametocyte	70				32		
Length		–	12.5	0.8		13.0	1.0
Width		–	6.5	0.6		6.7	0.5
Length of nucleus		–	4.8	0.4		5.0	0.7
Width of nucleus		–	2.0	0.3		1.9	0.3
Erythrocyte parasitized by microgametocyte	20				15		
Length		–	13.0	0.8		12.5	0.7
Width		–	6.6	0.5		6.5	0.5
Length of nucleus		–	4.9	0.5		4.8	0.5
Width of nucleus		–	2.0	0.3		2.0	0.2
Macrogametocyte					32		
Length	70	–	12.7	1.3		12.2	1.0
Width	70	–	1.9	0.5		2.6	0.3
Length of nucleus	70	–	2.4	0.5		2.6	0.4
Width of nucleus	70	–	1.7	0.3		2.0	0.4
NDR	70	–	0.8	0.1		0.7	0.1
No. of pigment granules	31	4–15	10.3	1.1		8.5	1.3
Microgametocyte					15		
Length	20	–	13.6	1.1		11.6	1.1
Width	20	–	2.0	0.6		2.3	0.3
Length of nucleus	20	–	6.6	0.7		8.1	1.4
Width of nucleus	20	–	1.7	0.3		2.1	0.3
NDR	20	–	0.8	0.1		0.8	0.1
No. of pigment granules	31	4–14	10.8	1.0		7.3	0.9

Note: All sizes are given in micrometres.

Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes, and fill the erythrocytes up to their poles. Rod-like large (1.0 to 1.5 μm) pigment granules appear in medium grown gametocytes and predominate in fully grown gametocytes.

Development in vertebrate host

Young gametocytes (Fig. 181, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 181, *2*), extend longitudinally along the nucleus and then usually adhere to the envelope of the erythrocytes; the outline is usually even, but sometimes also slightly ameboid.

Macrogametocytes (Fig. 181, *3–7*; Table 114). The cytoplasm is finely granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, slightly displace the nucleus laterally but do not encircle it completely; gametocytes adhere to the nucleus and envelope of erythrocytes; however, the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 181, *5, 6*); the dumbbell-shaped gametocytes predominate among the growing gametocytes but subsequently disappear; fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, and they fill the erythrocytes up to their poles (Fig. 181, *7*); the outline of growing gametocytes is even or wavy, sometimes slightly ameboid, and is even in fully grown gametocytes; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are rod-like and oval, sometimes roundish, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm. It should be noted that rod-like large (1.0 to 1.5 μm) pigment granules appear in medium grown gametocytes but are rare; roundish or oval, medium (0.5 to 1.0 μm) pigment granules (Fig. 181, *5, 6*) predominate. In fully grown gametocytes, rod-like large (1.0 to 1.5 μm) pigment granules (Fig. 181, *7*) predominate.

Microgametocytes (Fig. 181, *8*, *9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; dumbbell-shaped growing gametocytes are less frequently seen than for macrogametocytes; other characters are as for macrogametocytes.

Comments. The description of gametocytes of *H. motacillae* is given here on the basis of investigation of the hapantotype. Our data coincide with the original description (Bennett and Peirce, 1990c), except for the number of pigment granules. According to our calculations based on the hapantotype slide, the number of pigment granules in gametocytes of *H. motacillae* is less than noted in the original description (approximately 10 per macrogametocyte compared with approximately 15 in the original description) (see Table 114). In addition, rod-like large (1.0 to 1.5 μm) pigment granules were recorded in gametocytes (Fig. 181, *7*, *9*) for the first time, and this is a valuable diagnostic character of this species.

Haemoproteus motacillae is similar to *H. anthi*. It can be distinguished from the latter species, particularly on the basis of (i) numerous dumbbell-shaped growing gametocytes, (ii) rod-like large pigment granules in gametocytes, and (iii) a greater average NDR. During the identification of these species, attention should be paid to the above mentioned characters because *H. motacillae* and *H. anthi* have been frequently recorded in mixed infections.

Among the haemoproteids of birds belonging to the Passeriformes, *H. motacillae* is especially similar to *H. killangoi* and *H. picae.* Growing gametocytes of *H. killangoi* are usually highly ameboid in outline, and rod-like large (1.0 to 1.5 μm) pigment granules predominate in them. These features are not characteristic of *H. motacillae*. In fully grown gametocytes of *H. motacillae*, rod-like large (1.0 to 1.5 μm) pigment granules predominate, and this is not characteristic of *H. picae.*

105. **Haemoproteus (Parahaemoproteus) nucleophilus** Bennett and Bishop, 1990

Haemoproteus nucleophilus Bennett and Bishop, 1990b: 162, Fig. 3, 4.

Type vertebrate host. *Melanocharis nigra* (Lesson) (Passeriformes).
Additional vertebrate hosts. *Dicaeum aeneum*, *D. australe* (Passeriformes).

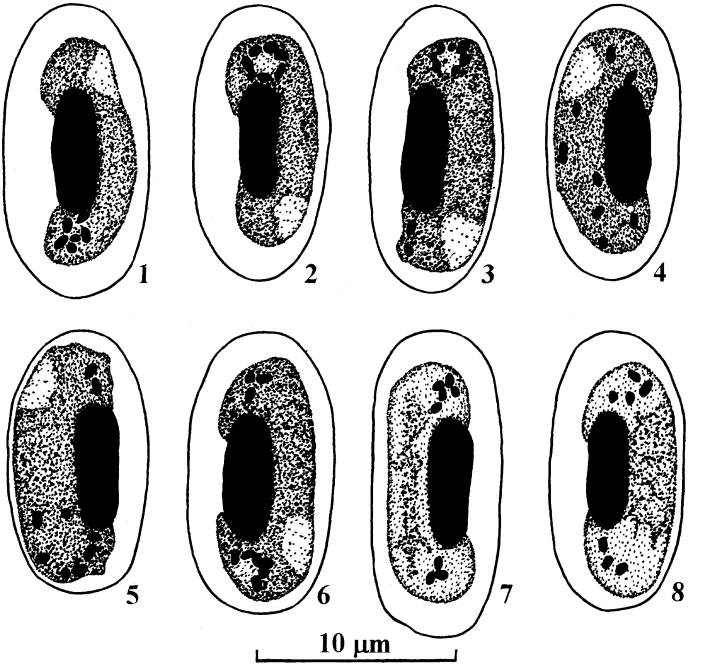

Figure 182 Gametocytes of *Haemoproteus nucleophilus* from the blood of *Melanocharis nigra: 1–6* – macrogametocytes; *7*, *8* – microgametocytes.

Type locality. L. Kopiago, Southern Highlands, Papua, New Guinea.
Distribution. This parasite has so far been recorded in New Guinea and on the Solomon Islands and Philippine Islands.
Type material. Hapantotype (No. 292, *Melanocharis nigra,* 04.11.1968, L. Kopiago, Southern Highlands, Papua, New Guinea, E. Mann) and parahapantotype (No. 61362, *Dicaeum aeneum*, 12.08.1944, Guadalcanal, Solomon Islands, C.M. Herman) are deposited in IRCAH.
Etymology. The specific name reflects the close adherence of gametocytes of the parasite to the nucleus of infected erythrocytes.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle the nucleus completely. Gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelope of the erythrocytes along their entire margin. Pigment granules in macrogametocytes are frequently aggregated in well regulated groups which are of rosette-like, fan-like, star-like or another form. The average number of pigment granules is about eight per gametocyte.

Development in vertebrate host
Young gametocytes are usually seen in a position lateral to the nucleus of infected erythrocytes, and they are closely appressed to the nucleus; the outline is even.

Macrogametocytes (Fig. 182, *1–6*; Table 114). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules usually absent; gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the

nucleus laterally and markedly enclose it but do not encircle the nucleus completely; gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelope of erythrocyte along their entire margin (Fig. 182, *1–6*); dumbbell-shaped gametocytes (with thickenings at the ends) are absent; even fully grown gametocytes do not extend to the envelope of erythrocytes and do not fill the erythrocytes up to their poles (Fig. 182, *5, 6*); the outline is even; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, frequently aggregated in well regulated groups which are of rosette-like, fan-like, star-like, or another form; these groups of pigment granules are usually seen at the end lacking the nucleus (Fig. 182, *1–3*) but there are exceptions (Fig. 182, *6*); in some gametocytes, pigment granules are randomly scattered throughout the cytoplasm (Fig. 182, *4*).

Microgametocytes (Fig. 182, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; well regulated groups of pigment granules are less frequently seen than for macrogametocytes; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. nucleophilus* is especially similar to *H. philippinensis*. It can be distinguished from the latter species primarily on the basis of (i) well regulated groups of pigment granules in its gametocyte and (ii) the absence of dumbbell-shaped gametocytes.

106. **Haemoproteus (Parahaemoproteus) trogonis** Bennett and Peirce, 1990

Haemoproteus trogonis Bennett and Peirce, 1990a: 2465, Fig. 3, 4.

Type vertebrate host. *Harpactes duvaucelli* (Temm.) (Trogoniformes).
Additional vertebrate hosts. *Harpactes ardens*, *H. erythrocephalus*, *H. oreskios*, *Trogon clathratus*, *T. rufus*, *T. violaceus* (Trogoniformes).
Type locality. Subang, Malaysia.
Distribution. This parasite has so far been recorded in the Oriental and Neotropical zoogeographical regions.
Type material. Hapantotype (No. 2749, *Harpactes duvaucelli,* 05.04.1962, Subang, Malaysia, H.E. McClure) and parahapantotype (No. 9397, *H. ardens*, 09.04.1965, Philippine Islands, R. Kuntz) are deposited in IRCAH.
Etymology. The specific name is derived from the name of the family Trogonidae to which the type vertebrate host belongs.

Main diagnostic characters. A parasite of species of the Trogoniformes whose fully grown gametocytes grow along the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends but do not encircle it completely. A clear discrete vacuole is frequently present near the nucleus of macrogametocytes. The NDR varies from 0 to 0.9.

Development in vertebrate host
Young gametocytes (Fig. 183, *3*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend along the nucleus of

Table 115 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. trogonis* (modified from Bennett and Peirce, 1990a)				*H. africanus* (modified from Bennett and Peirce, 1991)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	20				60		
Length		–	13.0	1.0		12.7	0.8
Width		–	7.6	0.6		6.4	0.5
Length of nucleus		–	5.6	0.5		5.5	0.5
Width of nucleus		–	2.2	0.4		1.9	0.2
Erythrocyte parasitized by macrogametocyte	15				60		
Length		–	13.5	1.8		12.8	0.8
Width		–	7.6	0.7		6.1	0.5
Length of nucleus		–	6.0	0.7		5.3	0.6
Width of nucleus		–	2.3	0.4		2.0	0.2
Erythrocyte parasitized by microgametocyte	10				15		
Length		–	14.4	1.0		13.1	0.6
Width		–	7.5	0.6		6.3	0.2
Length of nucleus		–	5.7	0.7		5.5	0.4
Width of nucleus		–	2.3	0.2		2.0	0.1
Macrogametocyte	15	–			60		
Length		–	15.3	2.0		13.9	1.4
Width		–	4.0	0.7		3.3	0.5
Length of nucleus		–	3.1	0.6		3.1	0.6
Width of nucleus		–	2.3	0.5		2.3	0.5
NDR		0.0–0.9	0.5	0.2		0.5	0.2
No. of pigment granules		–	11.0	1.0		11.9	2.4
Microgametocyte	10				15		
Length		–	16.0	1.5		14.3	1.3
Width		–	3.7	0.7		3.5	0.3
Length of nucleus		–	6.5	0.8		6.5	0.7
Width of nucleus		–	2.6	0.7		2.7	0.2
NDR		–	0.6	0.3		0.4	0.1
No. of pigment granules		–	11.3	1.6		11.3	1.3

Note: All sizes are given in micrometres.

erythrocytes, they usually do not touch the nucleus and frequently take a subpolar position in the host cells (Fig. 183, *3*); the outline is even or slightly ameboid.

Macrogametocytes (Fig. 183, *1*, *4*; Table 115). The cytoplasm is coarsely granular in appearance, contains compact valutin granules which tend to gather at the ends of gametocytes; a clear discrete vacuole is frequently situated near the nucleus of macrogametocyte and is usually closely appressed to the nucleus (Fig. 183, *4*); this vacuole is present in approximately 70% of gametocytes in the type material; gametocytes grow along the nucleus of infected erythrocytes, they slightly enclose the nucleus with their ends but do

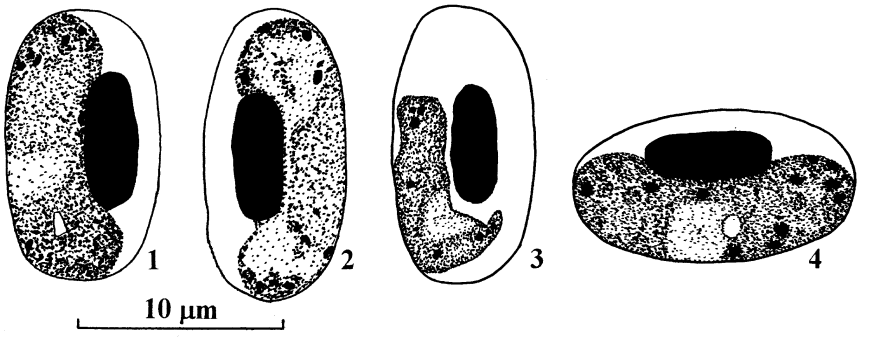

Figure 183 Gametocytes of *Haemoproteus trogonis* from the blood of *Harpactes duvaucelli:* *1*, *4* – macrogametocytes; *2* – microgametocyte; *3* – young (*1*, *2* are modified from Bennett and Peirce, 1990a).

not encircle it completely; the NDR varies markedly (from 0 to 0.9); fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes; the parasite nucleus is compact, frequently roundish, median or submedian in position; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 183, *2*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; a clear vacuole, which is frequently present in macrogametocytes near the parasite nucleus, is not seen in microgametocytes; other characters are as for macrogametocytes.

Comments. The original description of *H. trogonis* is brief (Bennett and Peirce, 1990a), and parasitemia is low in the type material. Additional material is required for more detailed investigation into the morphology of gametocytes of this parasite. During the identification of this species, attention should be paid to the clear vacuole which locates near the nucleus of macrogametocytes and is frequently closely appressed to the parasite nucleus (Fig. 183, *4*). A similar vacuole also occurs in gametocytes of *H. gavrilovi*, *H. ortalidum* and some other species of haemoproteids. However, only in *H. trogonis* this vacuole is clearly nucleophilic. The origin of this vacuole is unclear. It is likely that the vacuole is homologous to the 'vacuoles' in zygotes and ookinetes of haemoproteids and contains energetic materials (proteolipides).

107. **Haemoproteus (Parahaemoproteus) africanus** Bennett and Peirce, 1991

Haemoproteus africanus Bennett and Peirce, 1991: 15, Fig. 11, 12.

Type vertebrate host. *Mandingoa nitidula* (Hartlaub) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 116).
Type locality. Amani, Tanzania.
Distribution. The Ethiopian zoogeographical region.
Type material. Hapantotype (No. 19191, *Mandingoa nitidula,* 18.11.1970, Amani, Tanzania, W.J. Crans) and parahapantotypes (No. 17973, October 1970, other data are as for the hapantotype;

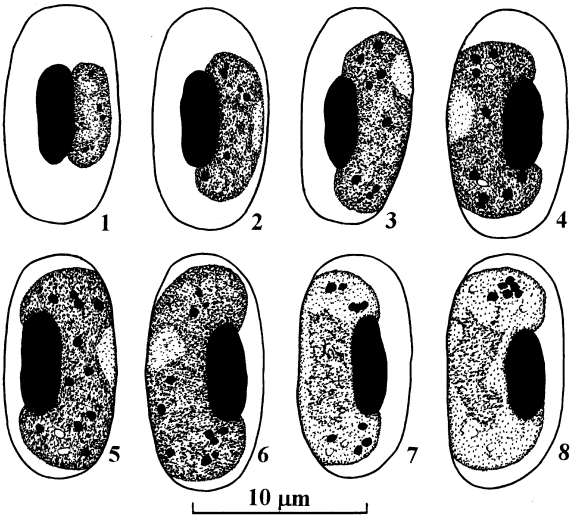

Figure 184 Gametocytes of *Haemoproteus africanus* from the blood of *Mandingoa nitidula:* *1* – young; *2–6* – macrogametocytes; *7*, *8* – microgametocytes.

No. 43257, *Lonchura cucullata*, 11.07.1974, Bugabo, Uganda, A.B.C. Killango; No. 46385, *Lagonosticta rubricata*, 30.12.1975, Kisubi, Uganda, A.B.C. Killango) are deposited in IRCAH.

Etymology. The specific name reflects the territory (Africa) where this parasite is widely distributed.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Medium and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes markedly enclose the nucleus of erythrocytes with their ends but do not fill the erythrocytes up to their poles. The nucleus of macrogametocytes is median or submedian in position. Pigment granules are of medium (0.5 to 1.0 μm) or sometimes small (<0.5 μm) size, about 11 per gametocyte on average.

Table 116 List of vertebrate hosts of *Haemoproteus africanus* (modified from Bennett and Peirce, 1991).

Estrilda atricapilla	*L. senegala*	*Pytilia afra*
E. erythronotos	*Lonchura bicolor*	*P. melba*
E. paludicola	*L. cucullata*	*Uraeginthus angolensis*
Lagonosticta rubricata	*Ploceus velatus*	*U. bengalus*
L. rufopicta	*Pyrenestes ostrinus*	*U. granatina*

Development in vertebrate host

Young gametocytes (Fig. 184, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline is even.

Macrogametocytes (Fig. 184, *2–6*; Table 115). The cytoplasm is granular in appearance, sometimes contains a few small vacuoles; valutin granules usually absent; gametocytes grow around the nucleus of infected erythrocytes; they displace the nucleus laterally but do not encircle it completely; medium and fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 184, *3–6*); fully grown gametocytes markedly enclose the nucleus of erythrocytes with their ends but do not fill the erythrocytes up to their poles (Fig. 184, *5*, *6*); dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes; the out- line is usually even; the parasite nucleus is compact, variable in form, median or submedian in position (Fig. 184, *5*), and the median position of the nucleus is a good diagnostic character of this species; pigment granules are roundish or oval, usually of medium (0.5 to 1.0 μm), but sometimes also small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 184, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. africanus* is especially similar to *H. beckeri* and *H. fallisi*. It can be distinguished from *H. fallisi* primarily on the basis of median position of the nucleus in its macrogametocytes. Rod-like large (1.0 to 1.5 μm) pigment granules are present in gametocytes of *H. beckeri*, but do not occur in gametocytes of *H. africanus.*

108. **Haemoproteus (Parahaemoproteus) bubalornis** Bennett and Peirce, 1991

Haemoproteus bubalornis Bennett and Peirce, 1991: 14, Fig. 8–10.

Type vertebrate host. *Bubalornis albirostris* (Vieil.) (Passeriformes).
Additional vertebrate hosts. *Bubalornis niger*, *Dinemellia dinemelli* (Passeriformes).
Type locality. Ngulia, Kenya.
Distribution. The Ethiopian zoogeographical region.
Type material. Hapantotype (No. 46747, *Bubalornis albirostris,* 10.12.1974, Ngulia, Kenya, M.A. Peirce) and parahapantotypes (No. 108460, *B. niger*, 04.12.1989, Luipersjoek, Republic of South Africa, W. Neser; No. 108461, 05.12.1989, other data are as for No. 108460) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Bubalornis*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocyte, they markedly enclose the nucleus with their ends but do not encircle it completely. Medium and fully grown gametocytes are closely appressed to both the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes. Medium grown gametocytes frequently with pointed ends; the gametocytes markedly enclose the nucleus of erythrocytes with their ends but do not fill the erythrocytes up to their poles. Fully grown gametocytes fill the erythrocytes up to their poles. Pigment granules are roundish, oval and rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, about eight per gametocyte on average. Large pigment granules are rod-like but never roundish.

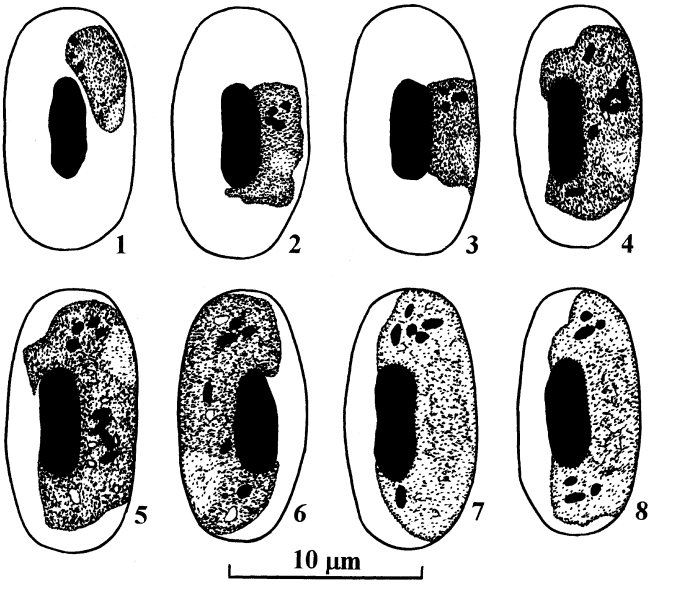

Figure 185 Gametocytes of *Haemoproteus bubalornis* from the blood of *Bubalornis albirostris: 1–3* – young; *4–6* – macrogametocytes; *7*, *8* – microgametocytes.

Development in vertebrate host

Young gametocytes (Fig. 185, *1–3*). The earliest forms can be seen located anywhere in infected erythrocytes; as the parasite develops, gametocytes extend longitudinally along the nucleus of erythrocytes and then adhere to the nucleus (Fig. 185, *2*) and envelope of erythrocytes (Fig. 185, *3*); the outline is usually even or wavy, but sometimes also slightly ameboid.

Macrogametocytes (Fig. 185, *4–6*; Table 117). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; valutin granules are not seen; gametocytes grow around the nucleus of infected erythrocytes, markedly enclose the nucleus with their ends but do not encircle it completely; medium grown gametocytes with pointed ends, which markedly enclose the nucleus of erythrocytes but do not fill the erythrocytes up to their poles (Fig. 185, *4*, *5*), are common and are characteristic of this species; gametocytes are closely appressed both to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are not present or represent less than 10% of the total number of growing gametocytes; fully grown gametocytes usually fill the erythrocytes up to their poles; the outline is even or slightly wavy; the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish, oval, and rod-like, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, randomly scattered throughout the cytoplasm. It is important to note that large pigment granules are rod-like and never roundish.

Microgametocytes (Fig. 185, *7*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. bubalornis* is especially similar to *H. zosteropis*. Medium grown gametocytes of *H. bubalornis* frequently with pointed ends, which markedly enclose the nucleus of erythrocytes, and they do not fill the erythrocytes up to their poles (Fig. 185, *4*, *5*). Such gametocytes are not characteristic of *H. zosteropis*.

Table 117 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. bubalornis* (modified from Bennett and Peirce, 1991)			*H. eurylaimus* (modified from Bennett *et al.*, 1991a)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	45			45		
Length		12.3	0.9		12.4	1.0
Width		6.6	0.5		6.8	0.5
Length of nucleus		5.2	0.5		5.5	0.8
Width of nucleus		1.8	0.2		2.0	0.2
Erythrocyte parasitized by macrogametocyte	45			45		
Length		13.5	1.0		13.1	0.8
Width		7.0	0.6		6.7	0.5
Length of nucleus		5.4	0.7		5.1	0.6
Width of nucleus		2.1	0.3		2.3	0.3
Erythrocyte parasitized by microgametocyte	20			10		
Length		13.5	1.0		12.6	0.9
Width		6.9	0.4		6.6	0.4
Length of nucleus		5.5	0.8		5.3	0.4
Width of nucleus		2.0	0.3		2.3	0.2
Macrogametocyte	45			45		
Length		14.1	1.1		14.7	1.5
Width		3.3	0.5		3.3	0.9
Length of nucleus		2.8	0.5		2.8	0.5
Width of nucleus		2.0	0.4		2.1	0.3
NDR		0.7	0.2		0.4	0.2
No. of pigment granules		8.4	1.4		27.1	3.6
Microgametocyte	20			10		
Length		14.1	1.3		14.9	1.6
Width		3.4	0.5		3.2	0.6
Length of nucleus		6.5	1.1		6.7	1.2
Width of nucleus		2.4	0.2		2.3	0.4
NDR		0.7	0.2		0.6	0.2
No. of pigment granules		8.9	1.9		21.8	2.5

Note: All sizes are given in micrometres.

109. **Haemoproteus (Parahaemoproteus) eurylaimus** Bennett, Bishop and Peirce, 1991

Haemoproteus eurylaimus Bennett, Bishop and Peirce, 1991a: 112, Fig. 1–3.

Type vertebrate host. *Serilophus lunatus* (Gould) (Passeriformes).
Additional vertebrate hosts. *Eurylaimus javanicus*, *E. ochromalus*, *Psarisomus dalhousiae* (Passeriformes).

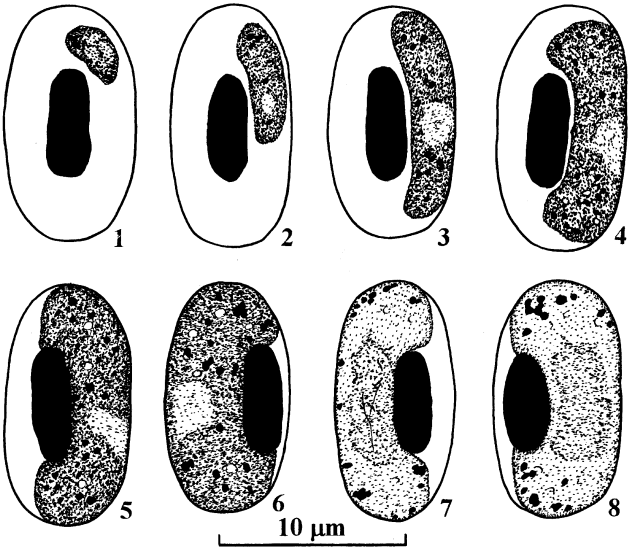

Figure 186 Gametocytes of *Haemoproteus eurylaimus* from the blood of *Serilophus lunatus: 1–2* – young; *3–6* – macrogametocytes; *7*, *8* – microgametocytes.

Type locality. Chieng-mai, Thailand.
Distribution has not been investigated in detail. This parasite has so far been recorded in the Oriental zoogeographical region.
Type material. Hapantotype (No. 11201, *Serilophus lunatus,* 10.12.1964, Chieng-mai, Thailand, H.E. McClure) and parahapantotypes (No. 11200, data as for the hapantotype; No. 37024, *Psarisomus dalhousiae*, 10.03.1970, Doi Pui, Thailand, H.E. McClure) are deposited in IRCAH. Gametocytes of *Leucocytozoon* sp. are present in the hapantotype.
Etymology. The specific name is derived from the family name Eurylaimidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes; they do not encircle the nucleus completely. Medium grown gametocytes are closely appressed to the envelope of erythrocytes but do not touch the nucleus of erythrocytes along their entire margin. Fully grown gametocytes are closely appressed to both the nucleus and envelope of erythrocytes. The nucleus of infected erythrocytes is markedly displaced laterally (the average NDR is less than 0.7). The average number of pigment granules is about 27 in macrogametocytes, and about 22 in microgametocytes.

Development in vertebrate host
Young gametocytes (Fig. 186, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently in a subpolar position; as the parasite develops, gametocytes adhere to the envelope of erythrocytes and extend longitudinally along the erythrocyte nucleus, and they do not touch the nucleus; the outline is even.

Macrogametocytes (Fig. 186, *3–6*; Table 117). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; gametocytes grow along the nucleus of infected erythrocytes, markedly displace the nucleus laterally but do not encircle it

completely; medium grown gametocytes are closely appressed to the envelope of erythrocytes but do not touch the erythrocyte nucleus along their entire margin and, as a result, a more or less evident unfilled space (a 'cleft') is usually present between the parasite and the nucleus of erythrocytes (Fig. 186, *3*, *4*); fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes and they fill the erythrocytes up to their poles (Fig. 186, *5*, *6*); the outline of gametocytes is usually even; the parasite nucleus is compact, variable in form, median or submedian in position; pigment granules are roundish or oval, of small (<0.5 μm) size, numerous (see Table 117), randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 186, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules tend to gather along the periphery of gametocytes (Fig. 186, *7*), and are frequently clumped in loose groups (Fig. 186, *8*); other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. eurylaimus* is especially similar to *H. cublae*. It can be distinguished from the latter species primarily on the basis of (i) the marked lateral displacement of nucleus by its gametocytes and (ii) randomly scattered pigment granules in its macrogametocytes.

110. **Haemoproteus (Parahaemoproteus) monarchus** Bennett, Bishop and Peirce, 1991

Haemoproteus monarchus Bennett, Bishop and Peirce, 1991b: 25, Fig. 1–3.

T y p e v e r t e b r a t e h o s t. *Monarcha cinerascens* (Temm.) (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. *Hypothymis azurea*, *Terpsiphone atrocaudata*, *T. cinnamomea*, *T. cyanescens*, *T. paradisi*, *T. rufiventer*, *T. viridis* (Passeriformes).
T y p e l o c a l i t y. Bagabad Island, New Guinea.
D i s t r i b u t i o n. The Oriental and Ethiopian zoogeographical regions and adjacent territories of the Palearctic.
T y p e m a t e r i a l. Hapantotype (No. 12245, *Monarcha cinerascens,* 15.06.1969, Bagabad Island, Madang, Papua and New Guinea, E. Mann) and parahapantotypes (No. 4924, *Terpsiphone paradisi*, 29.08.1962, Subang, Malaysia, H.E. McClure; No. 4926, 05.12.1962, other data are as for No. 4924) are deposited in IRCAH.
E t y m o l o g y. The specific name is derived from the generic name of the type host, *Monarcha*.

M a i n d i a g n o s t i c c h a r a c t e r s. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are common. Growing dumbbell-shaped gametocytes are common, and the dumbbell-shaped forms, which do not touch the envelope of erythrocytes along their entire margin, are also common and they represent more than one third of the total number of growing gametocytes. Fully grown gametocytes are closely appressed to the envelope of erythrocytes but usually do not fill the erythrocytes up to their poles. The outline of gametocytes is even. The nucleus of macrogametocytes is terminal or close to terminal in position. The average number of pigment granules is about nine per gametocyte.

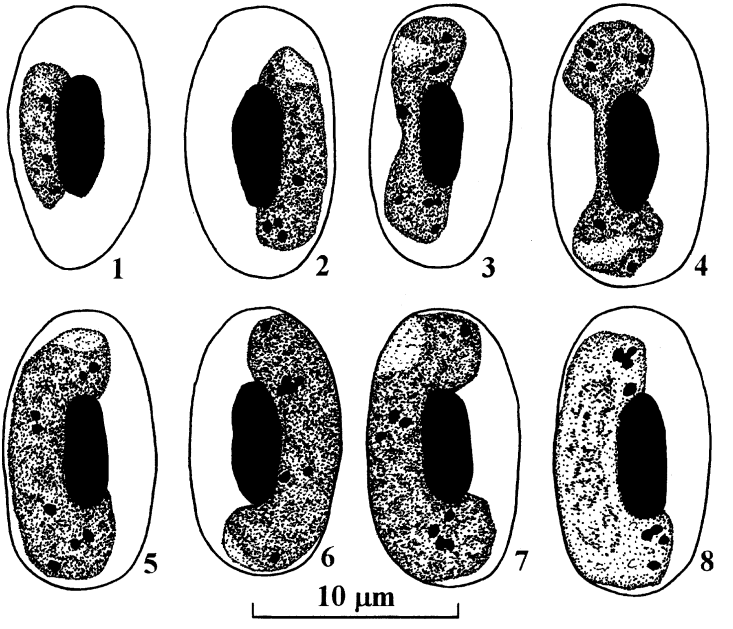

Figure 187 Gametocytes of *Haemoproteus monarchus* from the blood of *Monarcha cinerascens:* *1* – young; *2–7* – macrogametocytes; *8* – microgametocyte.

Development in vertebrate host

Young gametocytes (Fig. 187, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus, and they do not touch the envelope of erythrocytes; the outline is even.

Macrogametocytes (Fig. 187, *2–7*; Table 118). The cytoplasm is finely granular in appearance, usually lacking vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or only slightly displace the nucleus laterally and do not encircle it completely; growing gametocytes usually do not touch the envelope of erythrocytes along their entire margin and they do not fill the erythrocytes up to their poles (Fig. 187, *2–5*); dumbbell-shaped gametocytes are common among growing parasites, and over 30% of the gametocytes do not touch the envelope of erythrocytes along their entire margin (Fig. 187, *3*, *4*); fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes but frequently do not fill the erythrocytes up to their poles (Fig. 187, *6*, *7*); the parasite nucleus is compact, variable in form, terminal or close to terminal in position (Fig. 187, *4–7*); pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 187, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. monarchus* is especially similar to *H. quiscalus*. The main differences between these species are summarised in 'Comments' to *H. quiscalus*. *Haemoproteus monarchus* is also similar to *H. aegithinae*. It can be distinguished from the latter species primarily on the basis of the smaller number and larger size of pigment granules in its gametocytes.

Table 118 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. (modified from Bennett *et al.*, 1991b).

Feature	*H. monarchus*			*H. nipponensis*		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	35			45		
Length		12.2	1.2		12.2	0.6
Width		6.6	0.6		6.9	0.5
Length of nucleus		5.5	0.8		5.5	0.6
Width of nucleus		2.0	0.3		2.0	0.2
Erythrocyte parasitized by macrogametocyte	35			45		
Length		12.7	1.2		13.0	0.7
Width		6.8	0.5		7.2	0.6
Length of nucleus		4.9	0.6		5.3	0.5
Width of nucleus		1.9	0.2		2.1	0.3
Erythrocyte parasitized by microgametocyte	10			20		
Length		13.1	0.6		12.7	0.8
Width		6.8	0.5		7.4	0.6
Length of nucleus		5.1	0.6		5.6	1.2
Width of nucleus		1.7	0.3		2.2	0.3
Macrogametocyte	35			45		
Length		12.9	1.5		18.2	2.3
Width		2.4	0.5		3.6	0.6
Length of nucleus		2.8	0.5		3.1	0.6
Width of nucleus		1.6	0.4		2.3	0.4
NDR		0.9	0.2		0.6	0.2
No. of pigment granules		8.9	1.5		27.6	2.5
Microgametocyte	10			20		
Length		12.7	1.1		17.8	2.4
Width		2.9	0.6		3.6	0.4
Length of nucleus		5.6	0.6		7.0	1.2
Width of nucleus		2.3	0.5		3.0	0.4
NDR		0.9	0.2		0.6	0.1
No. of pigment granules		9.6	1.1		28.9	1.7

Note: All sizes are given in micrometres.

111. **Haemoproteus (Parahaemoproteus) nipponensis** Bennett, Bishop and Peirce, 1991

Haemoproteus nipponensis Bennett, Bishop and Peirce, 1991b: 30, Fig. 7–9.

Type vertebrate host. *Cyanoptila cyanomelana* (Temm.) (Passeriformes).
Additional vertebrate hosts. *Culicicapa ceylonensis*, *Melaenornis silens* (Passeriformes).

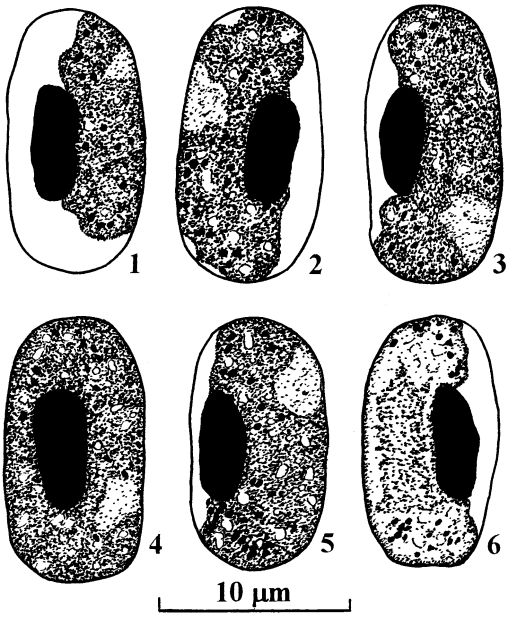

Figure 188 Gametocytes of *Haemoproteus nipponensis* from the blood of *Cyanoptila cyanomelana:*
1–5 – macrogametocytes; *6* – microgametocyte.

Type locality. Tsunoshima, Japan.
Distribution has been insufficiently investigated. This parasite has been recorded in Japan and South Africa.
Type material. Hapantotype (No. 10299, *Cyanoptila cyanomelana,* 03.05.1965, Tsunoshima, Japan, H.E. McClure) and parahapantotypes (No. 38607, 19.10.1965 and No. 38608, 08.05.1966, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name reflects the type locality (Nipponese).

Main diagnostic characters. A parasite of species of the Passeriformes with pleomorphic gametocytes. Some gametocytes enclose the nucleus of infected erythrocytes with their ends and they can completely encircle the nucleus. However, the majority of fully grown gametocytes markedly displace the nucleus of erythrocytes laterally and do not encircle it completely. The cytoplasm of gametocytes is highly vacuolated. Pigment granules are of small (<0.5 μm) size, more than 20 per gametocyte on average.

Development in vertebrate host
Young gametocytes are usually seen in a position lateral to the nucleus of infected erythrocytes; the outline is even or wavy.

Macrogametocytes (Fig. 188, *1–5*; Table 118). The cytoplasm is coarsely granular in appearance, contains numerous (usually not less than five) small vacuoles; valutin granules are frequently present; gametocytes grow around the nucleus of infected erythrocytes. Two types of gametocytes develop. First, gametocytes, which markedly displace the nucleus of infected erythrocytes laterally and do not encircle it completely (Fig. 188, *2*, *3*, *5*), predominate in the type material. Second, gametocytes, which do not displace or slightly displace

the nucleus of erythrocytes laterally but encircle it completely and occupy all available cytoplasmic space in the erythrocytes (Fig. 188, *4*), also occur but are much rarer than gametocytes of the first type. Gametocytes of both types are closely appressed to the nucleus and envelope of erythrocytes and they fill the erythrocytes up to their poles. The outline of gametocytes is usually even. The parasite nucleus is compact, variable in form, subterminal in position; it adheres to the parasite pellicle close to the erythrocyte envelope (Fig. 188, *3*, *5*). Pigment granules are numerous (see Table 118), of small size (<0.5 μm), randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 188, *6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. During the identification of *H. nipponensis*, attention should be paid first of all to (i) the numerous small pigment granules and (ii) the highly vacuolated cytoplasm in its gametocytes. Gametocytes, which completely encircle the nucleus of erythrocytes, are rare in the type material. It should be noted that the parahapantotype slides are poorly stained, and thus they can hardly be recommended for additional investigation into the parasite morphology.

Among the haemoproteids of birds belonging to the Passeriformes, *H. nipponensis* is especially similar to *H. globulosus*. It can be distinguished from the latter species primarily on the basis of the highly vacuolated cytoplasm of its gametocytes. However, the taxonomic value of this character is questionable.

112. **Haemoproteus (Parahaemoproteus) pachycephalus** Bennett, Bishop and Peirce, 1991

Haemoproteus pachycephalus Bennett, Bishop and Peirce, 1991b: 31, Fig. 10–12.

T y p e v e r t e b r a t e h o s t. *Pachycephala pectoralis* (Latham) (Passeriformes).

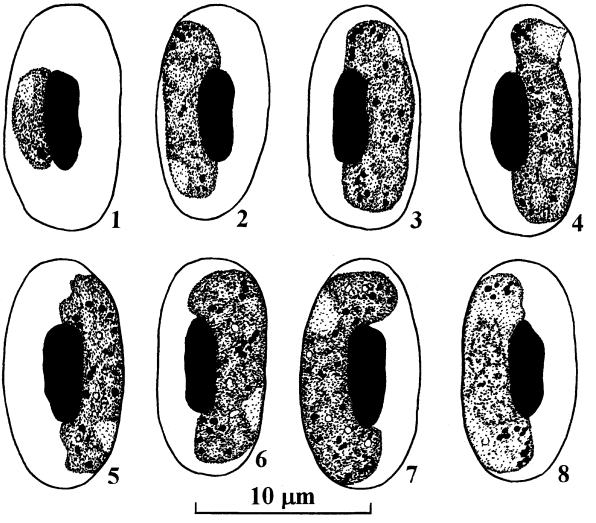

Figure 189 Gametocytes of *Haemoproteus pachycephalus* from the blood of *Pachycephala pectoralis:*
1 – young; *2–7* – macrogametocytes; *8* – microgametocyte.

Table 119 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. pachycephalus* (modified from Bennett *et al.*, 1991b)			*H. pallidus* (according to Valkiūnas and Iezhova, 1991)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	45			31			
Length		12.5	1.2		11.7–13.8	12.5	0.6
Width		6.3	0.5		5.8–7.1	6.5	0.3
Length of nucleus		5.6	0.6		5.2–6.7	5.7	0.2
Width of nucleus		1.8	0.3		2.0–2.8	2.3	0.1
Erythrocyte parasitized by macrogametocyte	45			31			
Length		12.7	0.6		12.0–15.0	13.5	0.6
Width		6.5	0.4		5.2–6.7	6.0	0.4
Length of nucleus		5.2	0.5		4.8–6.3	5.8	0.2
Width of nucleus		1.9	0.2		1.8–2.6	2.2	0.1
Erythrocyte parasitized by microgametocyte	10			31			
Length		12.2	0.6		12.4–14.9	13.5	0.5
Width		7.0	0.3		5.6–7.2	6.3	0.3
Length of nucleus		5.1	0.3		4.9–6.6	5.9	0.2
Width of nucleus		1.9	0.2		1.8–2.5	2.2	0.1
Macrogametocyte	45			31			
Length		12.5	1.7		12.4–15.3	13.7	0.6
Width		3.0	0.3		1.6–2.3	2.0	0.2
Length of nucleus		2.8	0.5		2.0–4.7	3.1	0.4
Width of nucleus		1.9	0.4		0.4–2.4	0.9	0.2
NDR		0.7	0.1		0.5–1.0	0.7	0.1
No. of pigment granules		19.8	1.8		6–15	10.3	1.2
Microgametocyte	10			31			
Length		11.6	0.9		13.3–16.2	14.7	0.6
Width		3.6	0.4		1.3–2.7	2.0	0.2
Length of nucleus		5.9	0.4		4.5–10.3	8.3	0.8
Width of nucleus		1.9	0.1		0.8–2.3	1.6	0.2
NDR		0.7	0.1		0.4–0.9	0.7	0.1
No. of pigment granules		18.8	1.4		5–15	11.1	1.4

Note: All sizes are given in micrometres.

Additional vertebrate hosts. *Pachycephala cinerea*, *P. philippinensis*, *P. rufiventris* (Passeriformes).

Type locality. Mindanao, Philippine Islands.

Distribution. This parasite has so far been recorded on the Philippine Islands and in New Guinea.

Type material. Hapantotype (No. 9544, *Pachycephala pectoralis,* 11.05.1965, Mindanao, Philippine Islands, R.E. Kuntz) and parahapantotypes (No. 9540, 9542, 10.05.1965, other data are as for the hapantotype) are deposited in IRCAH.

Etymology. The specific name is derived from the generic name of the type host, *Pachycephala.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow along the nucleus and do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes but do not fill the erythrocytes up to their poles. Dumbbell-shaped gametocytes are absent. Pigment granules are of small (<0.5 μm) size, about 20 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 189, *1*) are usually seen in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus, usually not touching the envelope of erythrocytes; the outline is even.

Macrogametocytes (Fig. 189, *2–7*; Table 119). The cytoplasm is granular in appearance, frequently contains a few small vacuoles; valutin granules are not characteristic; gametocytes grow along the nucleus of infected erythrocytes, are closely appressed to the nucleus of erythrocytes, slightly displace the nucleus laterally but do not encircle it completely; medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin (Fig. 189, *3*), are present; dumbbell-shaped gametocytes do not occur; fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes but do not fill the erythrocytes up to their poles (Fig. 189, *7*); the outline is even or slightly wavy (Fig. 189, *5–7*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish, of small size (<0.5 μm), randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 189, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. During the identification of *H. pachycephalus*, attention should be first of all paid to (i) the small size of fully grown gametocytes which do not fill the erythrocytes up to their poles, (ii) the presence of medium grown gametocytes which do not touch the envelope of erythrocytes along their entire margin, and (iii) numerous small pigment granules in gametocytes.

113. **Haemoproteus (Parahaemoproteus) pallidus** Valkiūnas and Iezhova, 1991

Haemoproteus pallidus Valkiūnas and Iezhova, 1991: 212, Fig. 1, 2.

Type vertebrate host. *Ficedula hypoleuca* (Pallas) (Passeriformes).
Additional vertebrate hosts. *Ficedula albicollis, Muscicapa parva, M. striata* (Passeriformes).
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E).
Distribution has been insufficiently investigated. This parasite has so far been recorded in the Palearctic and in the Ethiopian zoogeographical region.
Type material. Hapantotype (No. 963.89 Cos, *Ficedula hypoleuca,* 12.05.1989, the Curonian Spit, G. Valkiūnas) and parahapantotypes (No. 964.89 Cos; 1659,1660.89 Cos, 15.05.1989; 1671-1672.89 Cos, 18.05.1989; 1725-1726.89 Cos, 24.05.1989; 2161.89 Cos, 23.05.1989, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G460617, 23.05.1989,

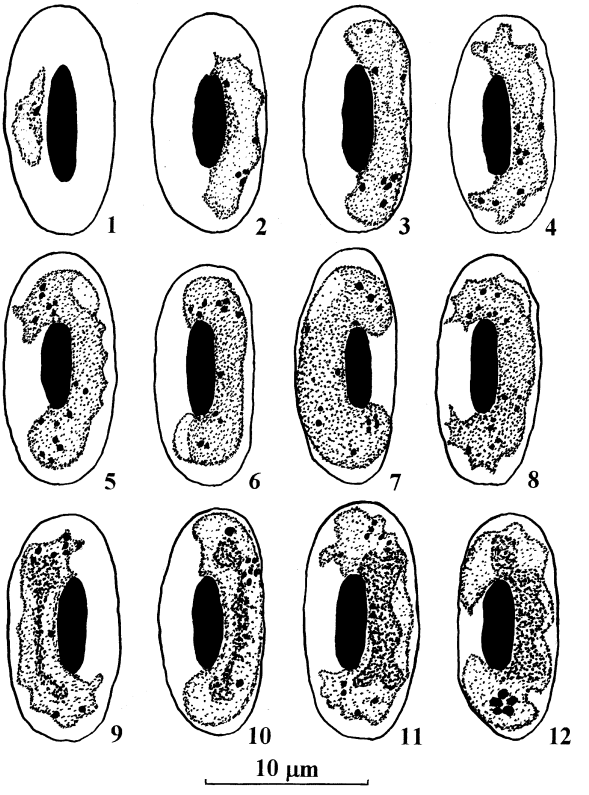

Figure 190 Gametocytes of *Haemoproteus pallidus* from the blood of *Ficedula hypoleuca: 1*, *2* – young; *3–8* – macrogametocytes; *9–12* – microgametocytes (modified from Valkiūnas and Iezhova, 1991).

other data are as for the hapantotype) is deposited in IRCAH. A series of slides of gametes, zygotes and ookinetes is deposited in CDVA.

Etymology. The specific name reflects the pale staining of gametocytes of this parasite.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes are closely appressed to the nucleus of erythrocytes but frequently do not touch the envelope of erythrocytes along their entire margin. Dumbbell-shaped gametocytes are absent. Gametocytes with an ameboid outline predominate. The cytoplasm of gametocytes stains exceptionally pale; macro- and microgametocytes are poorly distinguishable on the basis of the intensity of staining the cytoplasm.

Development in vertebrate host

Multiple infection of one erythrocyte with several gametocytes is characteristic of *H. pallidus*. It was recorded even at the low parasitemia (about 1 gametocyte per 1000 erythrocytes).

Young gametocytes (Figs. 190, *1*, *2*; 191, *1–3*) are markedly variable in form. The outline of growing gametocytes varies from wavy to highly ameboid (Figs. 190, *1*, *2*; 191,

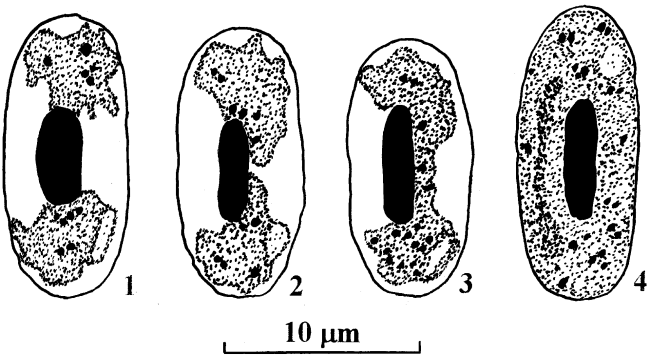

Figure 191 Peculiarities of the development of *Haemoproteus pallidus* gametocytes during the double infection of the same erythrocyte:
1, *2* – initial stages of the development, each gametocyte obtains a polar position in the infected erythrocyte; *3* – growing gametocytes merged together; *4* – mature macrogametocyte (on the right) and microgametocyte (on the left) in the same erythrocyte (modified from Valkiūnas and Iezhova, 1991).

1). Two types of development have been recorded. The first type of development (see Fig. 190) was particularly frequently seen. It takes place when only one gametocyte is present in the infected erythrocyte. In this case, the gametocytes take a position lateral to the nucleus of erythrocytes; they extend longitudinally along the nucleus (Fig. 190, *1*) and then adhere to the nucleus and grow around the nucleus (Fig. 190, *2*). The second type of development (see Fig. 191) takes place when several (usually two) gametocytes are present in one erythrocyte. In this case, each young gametocyte usually takes a polar position in the erythrocytes (Fig. 191, *1*). As the parasite develops, the gametocytes adhere to the nucleus of erythrocytes and then grow toward each other (Fig. 191, *2*). When the gametocytes come into contact with each other, they merge together (Fig. 191, *3*). Subsequently, the boundary between the gametocytes becomes invisible, and they look like one cell (Fig. 191, *3*). During these types of development, gametocytes are closely appressed to the nucleus of erythrocytes but do not touch the envelop of erythrocytes along their entire margin and, as a result, a more or less evident unfilled space (a 'cleft') is available between the parasite and the envelope of erythrocytes. However, in the second type of development, a clear 'dip' develops at the place where two gametocytes merge (Fig. 191, *3*), and this 'dip' gives a dumbbell-like appearance. The true dumbbell-shaped gametocytes do not develop during the first type of the development when only one gametocyte is present in erythrocytes (Fig. 190, *2*). In addition, in the second type of development, gametocytes can occupy all available cytoplasmic space in the erythrocytes (Fig. 191, *4*), and this has never been recorded during the first type of development.

Macrogametocytes (Fig. 190, *3–8*; Table 119). The cytoplasm is homogeneous in appearance, stains pale blue which clearly distinguishes *H. pallidus* from many other species of bird haemoproteids; gametocytes are closely appressed to the nucleus of erythrocytes, they grow around the nucleus, markedly enclose the nucleus with their ends but do not encircle it completely; gametocytes frequently do not touch the envelope of erythrocytes along their entire margin and, as a result, a more or less evident irregular 'cleft' often occurs between the parasite and the envelope of erythrocytes (Fig. 190, *3–8*); fully grown gametocytes slightly displace the nucleus of erythrocytes laterally and do not

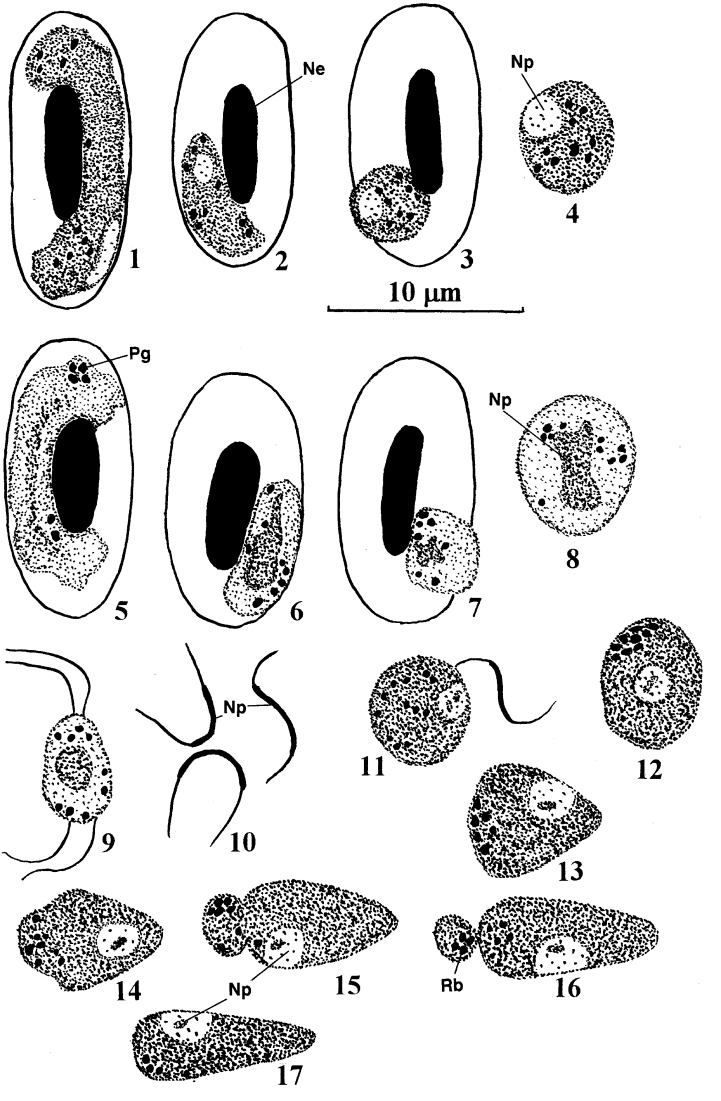

Figure 192 *Haemoproteus pallidus* gametogenesis, zygote and ookinete development *in vitro:* *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Ficedula hypoleuca* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14*, *15* – medium differentiated ookinete; *16* – ookinete with a residual body; *17* – ookinete without the residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body (modified from Valkiūnas and Iezhova, 1993a).

fill the erythrocytes up to their poles; the outline is usually more or less ameboid (Fig. 190, *4*, *5*, *8*) or wavy (Fig. 190, *3*) but sometimes also even (Fig. 190, *6*, *7*); both a macro- and microgametocyte can be present in the same infected erythrocyte, and they are easily distinguishable primarily on the basis of different morphology of their nuclei (Fig. 191, *4*);

the parasite nucleus stains pale rose, usually subterminal but sometimes terminal (Fig. 190, *6*) in position, frequently band-like (Fig. 190, *6*, *8*), sometimes oval (Figs. 190, *5*, *7*; 191, *4*); a parasite nucleus typical in form and position is shown in Fig. 190, *8*; pigment granules are usually roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 190, *9–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; micro- and macrogametocytes are poorly distinguishable on the basis of the intensity of staining of their cytoplasm; the parasite nucleus is diffuse, but it can be more compact in some gametocytes than in others (cf. Figs. 190, *9*, *10* and 190, *11, 12*); pigment granules can be in loosely aggregated clumps (Fig. 190, *12*) and, if so, the granules decrease in number but increase in size; other characters are as for macrogametocytes.

Development in vector has not been investigated. Gametogenesis, development of zygote and ookinete *in vitro* under the light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1993a). The data on the rate of this process are given in Table 23. Within 1 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave erythrocytes (Fig. 192, *2–4*; *6–8*). At the same time, exflagellation (Fig. 192, *9*) and free microgametes (Fig. 192, *10*) were seen. The fertilization of macrogametes (Fig. 192, *11*) and first zygotes (Fig. 192, *12*) were recorded 6 min after EBA. Pigment granules in the zygotes tend to aggregate in a loose clump, and a nucleolus is clearly seen in the zygotes (Fig. 192, *12*). Both these features are not characteristic of macrogametes (Fig. 192, *4*), and they can be readily distinguished from zygotes on the basis of the above mentioned characters. Ookinetes develop quickly. The initial stages of differentiation of ookinetes were seen approximately 30 min after EBA. Ookinetes develop without forming any clearly defined outgrowths. The differentiating ookinetes take a triangular shape (Fig. 192, *13*). On one side of this 'triangle,' pigment granules accumulate and the opposite end extends, and it forms an apical end of the ookinete (Fig. 192, *14–16*). A clearly defined residual body develops at the place of accumulation of the pigment granules (Fig. 192, *15*, *16*). As the ookinete develops, the residual body takes a spherical shape and finally separates from the ookinete (Fig. 192, *16*). Fully differentiated ookinetes are carrot-like in form; they frequently possess a few pigment granules (Fig. 192, *17*). A clear nucleolus was seen in the nucleus of the ookinete. Vacuoles were not recorded in ookinetes at all stages of differentiation of the parasite (Fig. 192, *13–17*). Fully differentiated ookinetes without the residual body (Fig. 192, *17*) were seen 45 min after EBA. The morphometric parameters of gametes and ookinetes are given in Table 24.

Comments. The intensity of staining of gametocyte cytoplasm markedly depends on the conditions of staining. Taken separately, this character cannot be used for the identification of species of haemoproteids. However, in combination with other characters, the pale staining of cytoplasm of gametocytes is a distinctive character of *H. pallidus*, and this has been reflected in the species name. In the same conditions, gametocytes of *H. pallidus* stain much paler than gametocytes of many other species of bird haemoproteids. This is especially evident when two species of haemoproteids are present in the same blood film. The blood smears from *Muscicapa striata* (No. 2241-2243.89 Cos) and *Ficedula hypoleuca* (No. 2825.89 Cos, 3027, 3028.89 Cos, 3491, 3492.89 Cos) with mixed infection of *H. pallidus* and *H. balmorali* are deposited in CDVA.

114. **Haemoproteus (Parahaemoproteus) pittae** Bennett, Bishop and Peirce, 1991

Haemoproteus pittae Bennett, Bishop and Peirce, 1991a: 114, Fig. 4–9.

Type vertebrate host. *Pitta arcuata* (Gould) (Passeriformes).
Additional vertebrate hosts. *Pitta erythrogaster*, *P. moluccensis*, *P. sordida* (Passeriformes).
Type locality. Borneo.
Distribution. The Oriental zoogeographical region.
Type material. Hapantotype (No. 9447a, *Pitta arcuata,* 12.05.1962, Borneo, R.E. Kuntz) and parahapantotype (No. 9447b, 13.05.1962, other data are as for the hapantotype) are deposited in IRCAH.

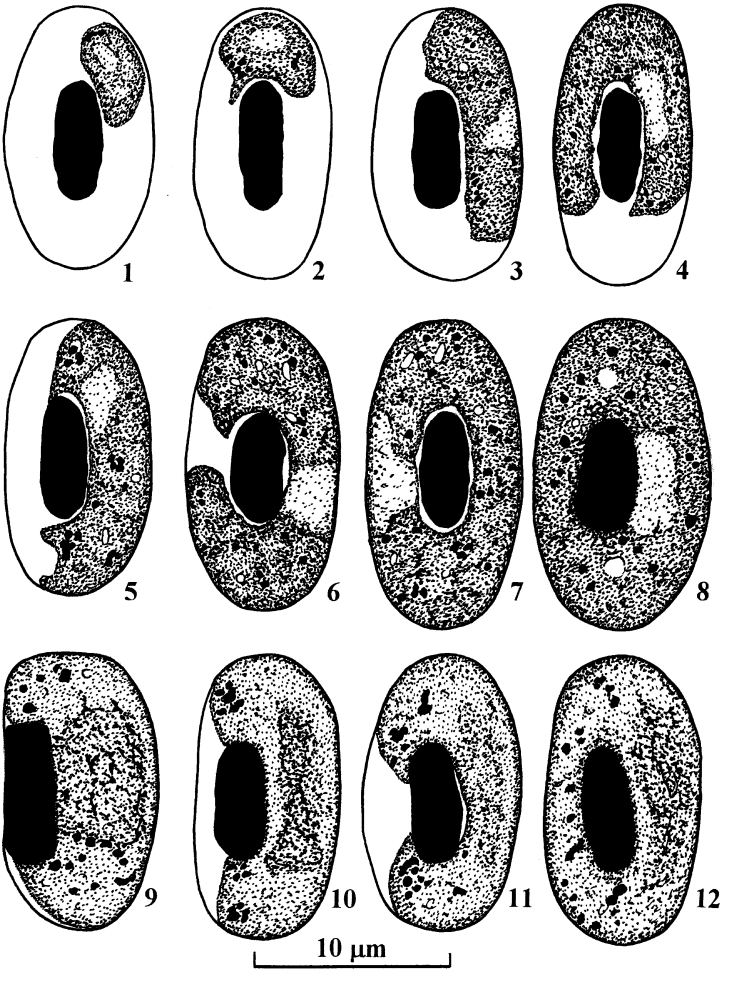

Figure 193 Gametocytes of *Haemoproteus pittae* from the blood of *Pitta arcuata: 1*, *2* – young; *3–8* – macrogametocytes; *9–12* – microgametocytes.

Table 120 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. pittae* (modified from Bennett *et al.*, 1991a)			*H. timalus* (modified from Bennett *et al.*, 1991b)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	40			85		
Length		13.3	0.9		11.6	0.6
Width		7.5	0.5		6.6	0.5
Length of nucleus		6.0	0.6		5.0	0.3
Width of nucleus		2.3	0.3		2.4	0.2
Erythrocyte parasitized by macrogametocyte	40			85		
Length		14.7	1.5		12.7	0.7
Width		8.3	0.6		6.4	0.6
Length of nucleus		6.1	0.7		4.8	0.4
Width of nucleus		2.4	0.3		2.2	0.3
Erythrocyte parasitized by microgametocyte	15			40		
Length		14.0	0.9		12.8	0.7
Width		7.8	0.6		6.4	0.5
Length of nucleus		5.8	0.4		4.9	0.4
Width of nucleus		2.4	0.5		2.3	0.3
Macrogametocyte	40			85		
Length		26.9	2.1		12.5	1.0
Width		3.6	0.6		2.2	0.5
Length of nucleus		4.8	1.1		2.6	0.4
Width of nucleus		3.1	0.6		2.0	0.4
NDR		0.8	0.1		0.8	0.2
No. of pigment granules		20.8	1.9		11.3	2.2
Microgametocyte	15			40		
Length		16.6	1.9		13.4	1.7
Width		4.1	0.5		2.5	0.5
Length of nucleus		7.9	0.7		6.9	0.8
Width of nucleus		3.1	0.4		2.3	0.4
NDR		0.4	0.2		0.8	0.1
No. of pigment granules		19.3	1.8		10.9	2.2

Note: All sizes are given in micrometres.

Etymology. The specific name is derived from the generic name of the type host, *Pitta.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes markedly enclose the nucleus of infected erythrocytes with their ends and can completely encircle the nucleus. The majority of fully grown microgametocytes markedly displace the nucleus of erythrocytes laterally and do not encircle the nucleus completely, however, the circumnuclear forms also occur. The growing gametocytes are closely appressed to the envelope of erythrocytes but do not touch the nucleus of erythrocytes. Pigment granules are of small (<0.5 μm) size, about 20 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 193, *1*, *2*). The earliest forms are usually seen in a polar or subpolar position in infected erythrocytes, and they do not touch the nucleus of erythrocytes; the outline is even or slightly ameboid (Fig. 193, *2*).

Macrogametocytes (Fig. 193, *3–8*; Table 120). The cytoplasm is homogeneous in appearance, usually contains a few small vacuoles; in addition, a few (usually one or two) clear large (about 1.0 μm in diameter and even larger) vacuoles are seen in some gametocytes (Fig. 193, *8*); valutin granules are not seen; growing gametocytes are closely appressed to the envelope of erythrocytes but do not touch the nucleus of erythrocytes (Fig. 193, *3–7*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes (Fig. 193, *8*). Two types of gametocytes develop. First, the majority of gametocytes (usually over 90%) grow around the nucleus of infected erythrocytes; they usually do not displace or only slightly displace the nucleus laterally but finally completely encircle the nucleus and occupy all available cytoplasmic space in the host cells (Fig. 193, *6–8*). Second, some gametocytes (usually less than 10%) markedly displace the nucleus of erythrocytes laterally but do not encircle it completely. In addition, gametocytes which had escaped from the erythrocytes and were lying free in the plasma were occasionally seen. They are of irregular band-like form. The outline of gametocytes of all the types is usually even, but sometimes also slightly ameboid (Fig. 193, *5*). The parasite nucleus is compact, variable in form, large (see Table 120), usually median or submedian in position. Pigment granules are usually roundish, of small (<0.5 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 193, *9–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the cytoplasm stains relatively pale even for microgametocytes; gametocytes, which markedly displace the nucleus of erythrocytes laterally but do not encircle it completely (Fig. 193, *9*, *10*), are clearly predominant, however, circumnuclear forms are also seen (Fig. 193, *12*); medium grown gametocytes, which do not touch the nucleus of erythrocytes (Fig. 193, *11*), occur; other characters are as for macrogametocytes.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. pittae* is especially similar to *H. circumnuclearis* and *H. danilewskii*. It can be distinguished from the latter two species primarily on the basis of the morphology of its microgametocytes.

115. **Haemoproteus (Parahaemoproteus) timalus** Bennett, Bishop and Peirce, 1991

Haemoproteus timalus Bennett, Bishop and Peirce, 1991b: 39, Fig. 24–27.

Type vertebrate host. *Turdoides rubiginosus* (Ruppell) (Passeriformes).

Additional vertebrate hosts. *Garrulax erythrocephalus*, *G. mitratus*, *Heterophasia melanoleuca*, *Leiothrix argentauris*, *Turdoides jardineii* (Passeriformes).

Bennett *et al.* (1991b) believe that all records for haemoproteids listed for 43 species of timaliine birds (see Bennett *et al.*, 1982b) can be referred to *H. timalus*. This hypothesis should be tested.

Type locality. South Horr, Kenya.

Distribution. The Ethiopian and Oriental zoogeographical regions.

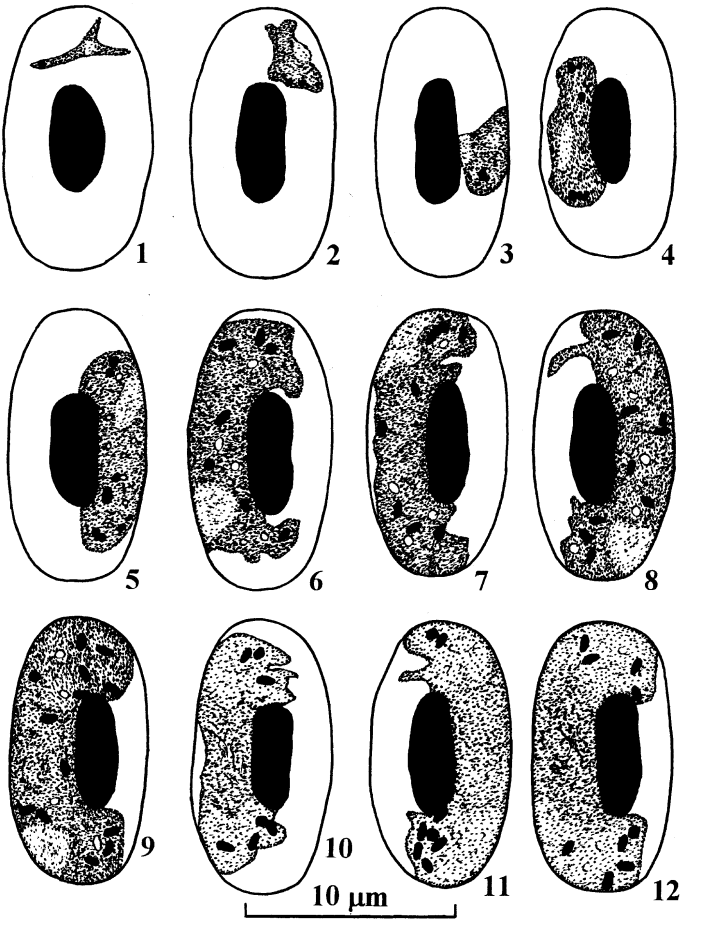

Figure 194 Gametocytes of *Haemoproteus timalus* from the blood of *Turdoides rubiginosus: 1–4* – young; *5–9* – macrogametocytes; *10–12* – microgametocytes.

Type material. Hapantotype (No. 46912, *Turdoides rubiginosus,* 24.09.1969, South Horr, Kenya, M.A. Peirce) and parahapantotypes (No. 4060, *Garrulax mitratus*, 24.11.1961, Mt. Brinchang, Malaysia, H.E. McClure; No. 4062, 06.02.1959, other data are as for the No. 4060; No. 10046, *Heterophasia melanoleuca*, 02.11.1965, Chiang-mai, Thailand, H.E. McClure) are deposited in IRCAH.

Etymology. The specific name is derived from the name of the family Timaliidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Earliest gametocytes are highly ameboid in outline. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are present and represent more than 10% of the total number of growing gametocytes but do not predominate. Fully grown gametocytes fill infected erythrocytes up to their poles. Pigment granules are usually oval or even rod-like, of medium (0.5 to 1.0 μm) size, about 11 per gametocyte on

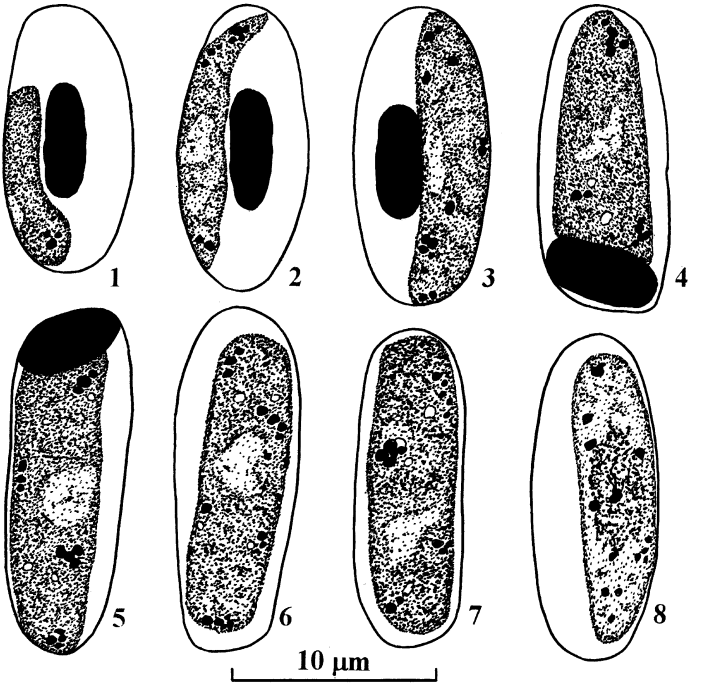

Figure 195 Gametocytes of *Haemoproteus uraeginthus* from the blood of *Uraeginthus bengalus: 1* – young; *2–7* – macrogametocytes; *8* – microgametocyte.

average. The average NDR is about 0.8; the maximum NDR does not exceed unity. A species difficult to identify; can be distinguished from the close species of haemoproteids of passeriform birds only on the basis of a detailed analysis of a complex of characters.

Development in vertebrate host

Young gametocytes (Fig. 194, *1–4*). The earliest forms are frequently seen in a polar position in infected erythrocytes, usually highly ameboid in outline (Fig. 194, *1*, *2*); as the parasite develops, gametocytes take a position lateral to the nucleus of erythrocytes, they adhere to the nucleus and extend longitudinally along it (Fig. 194, *4*).

Macrogametocytes (Fig. 194, *5–9*; Table 120). The cytoplasm is granular in appearance, usually contains a few small vacuoles; valutin granules are sometimes present and tend to gather at the ends of gametocytes; gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the nucleus laterally but do not encircle it completely; medium and fully grown gametocytes adhere to the nucleus and envelope of erythrocytes, and the fully grown gametocytes fill the erythrocytes up to their poles (Fig. 194, *9*); the central part of the pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 194, *7*); the dumbbell-shaped gametocytes represent more than 10% of the total number of growing gametocytes but do not predominate; full grown gametocytes lose the dumbbell-like shape and are closely appressed to the nucleus and envelope of erythrocytes (Fig. 194, *9*); the outline of growing gametocytes varies from even (Fig. 194, *5*) to highly ameboid (Fig. 194, *8*), and is usually even in fully grown gametocytes (Fig. 194, *9*); the parasite nucleus is

compact, variable in form, subterminal in position; pigment granules are usually oval or even rod-like, sometimes roundish, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 194, *10–12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. During the identification of this species, attention should be paid primarily to the highly ameboid outline of the earliest gametocytes. On the basis of this character, *H. timalus* can be distinguished from such similar species of haemoproteids of birds belonging to the Passeriformes as *H. coatneyi*, *H. passeris,* and *H. vireonis*.

116. **Haemoproteus (Parahaemoproteus) uraeginthus** Bennett and Peirce, 1991

Haemoproteus uraeginthus Bennett and Peirce, 1991: 20, Fig. 16–20.

Type vertebrate host. *Uraeginthus bengalus* (L.) (Passeriformes).
Type locality. N'Djamena, Chad, Africa.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 42800a, *Uraeginthus bengalus*, 27.06.1973, N'Djamena, Chad, P.M. Troncy) and parahapantotype (No. 42800b, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Uraeginthus.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes markedly displace the nucleus of infected erythrocytes and finally enucleate the host cells. Growing gametocytes, which do not touch the nucleus of erythrocytes, are present. The average width of fully grown gametocytes is 4.5 μm or less. Infected erythrocytes are significantly hypertrophied in length but unchanged in width in comparison to uninfected ones.

Development in vertebrate host

Young gametocytes (Fig. 195, *1*). The earliest forms can be seen anywhere in infected erythrocytes; as the parasite develops, gametocytes extend along the nucleus of erythrocytes and take a position lateral to the nucleus, they are closely appressed to the envelope of erythrocytes but do not touch the erythrocyte nucleus (Fig. 195, *1*); the outline is usually even.

Macrogametocytes (Fig. 195, *2–7*; Table 121). The cytoplasm is finely granular in appearance, usually contains a few small vacuoles; valutin granules are not seen; growing gametocytes are appressed to the envelope of erythrocytes but frequently do not touch the nucleus of erythrocytes (Fig. 195, *2*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 195, *3*), then markedly displace the nucleus towards one pole of the erythrocytes (Fig. 195, *4*, *5*) and finally enucleate the host cells (Fig. 195, *6*, *7*); fully grown gametocytes are cigar-shaped bodies extending within the erythrocytic remnant; they are frequently located closer to one side of the erythrocyte than to the other (Fig. 195, *6*, *8*); the outline is usually even; the parasite nucleus is variable in form, frequently roundish or oval, usually median or submedian in position; pigment granules are usually

Table 121 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. uraeginthus* (modified from Bennett and Peirce, 1991)			*H. calandrellae* (according to Valkiūnas and Iezhova, 1992c)			
	n	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	40			31			
Length		13.0	0.7		9.5–11.7	10.4	0.6
Width		6.4	0.5		5.2–6.7	6.0	0.2
Length of nucleus		5.9	0.6		4.0–5.8	4.9	0.1
Width of nucleus		1.9	0.2		1.6–2.4	2.1	0.1
Erythrocyte parasitized by macrogametocyte	40			31			
Length		16.5	1.0		10.9–12.4	11.4	0.6
Width		6.2	0.8		5.2–6.8	6.0	0.3
Length of nucleus		–	–		4.6–5.8	5.0	0.2
Width of nucleus		–	–		1.7–2.6	2.1	0.1
Erythrocyte parasitized by microgametocytes	15			31			
Length		15.3	1.6		10.8–12.6	11.6	0.6
Width		6.0	0.7		5.3–6.5	5.9	0.4
Length of nucleus		–	–		4.3–5.8	5.1	0.1
Width of nucleus		–	–		1.7–2.4	2.1	0.1
Macrogametocyte	40			31			
Length		14.5	1.0		10.8–12.4	11.4	0.4
Width		4.0	0.5		2.4–3.8	3.1	0.2
Length of nucleus		3.3	0.5		1.3–5.0	3.3	0.6
Width of nucleus		2.3	0.4		0.9–2.7	1.4	0.2
NDR		–	–		0.2–0.8	0.5	0.1
No. of pigment granules		16.7	1.9		10–20	15.8	2.1
Microgametocyte	15			31			
Length		13.4	1.3		10.3–13.1	11.9	0.5
Width		4.4	0.5		2.4–3.4	3.0	0.2
Length of nucleus		5.0	0.7		4.3–6.5	5.2	0.3
Width of nucleus		2.6	0.4		1.1–3.5	2.8	0.4
NDR		–	–		0.4–0.8	0.5	0.1
No. of pigment granules		15.0	1.4		8–23	15.7	2.2

Note: All sizes are given in micrometres.

roundish, of small (<0.5 μm) size, randomly scattered throughout the cytoplasm. Infected erythrocytes are significantly hypertrophied in length but unchanged in width in comparison to uninfected ones.

Microgametocytes (Fig. 195, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters; pigment granules frequently randomly scattered throughout the cytoplasm which is a rare character for microgametocytes of haemoproteids.

Comments. Among the haemoproteids of birds belonging to the Passeriformes, *H. uraeginthus* is close to *H. tartakovskyi*. It can be easily distinguished from the latter species primarily on the basis of (i) the mode of growth of its young gametocytes which frequently do not touch the nucleus of infected erythrocytes and (ii) the shape of the fully grown gametocytes.

Gametocytes of *H. uraeginthus* in enucleated host cells are common in the type material.

117. **Haemoproteus (Parahaemoproteus) calandrellae** Valkiūnas and Iezhova, 1992

Haemoproteus calandrellae Valkiūnas and Iezhova, 1992c: 62, Fig. 6.

Type vertebrate host. *Calandrella rufescens* (Vieil.) (Passeriformes).
Type locality. The western shore of the Lake Karateren (approximately 30 km north of the settlement Tachta Kupir), Karakalpakiya, Uzbekistan.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 1418.88 Az, *Calandrella rufescens*, 25.05.1988, Karakalpakiya, G. Valkiūnas) and parahapantotypes (No. 1415-1417.88 Az, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462483, other data are as for the hapantotype) is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Calandrella.*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends and do not encircle it completely. Medium and fully grown gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes do not occur or represent less than 10% of the total number of growing gametocytes. Fully grown gametocytes fill the erythrocytes up to their poles. The nucleus of macrogametocytes is median or submedian in position and is usually located close to the erythrocyte nucleus. Pigment granules are of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, about 15 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 196, *1*, *2*, *8*). The earliest forms can be seen anywhere in infected erythrocytes, usually oval in form (Fig. 196, *1*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 196, *2*) and extend longitudinally along the nucleus completely filling the space between the nucleus and envelope of erythrocytes (Fig. 196, *2*); the outline is even.

Macrogametocytes (Fig. 196, *3–7*; Table 121). The cytoplasm is homogeneous in appearance, usually lacks vacuoles, contains valutin granules; gametocytes grow along the nucleus of infected erythrocytes; they slightly enclose the nucleus with their ends and do not encircle it completely; gametocytes are closely appressed to the nucleus and envelope of erythrocytes (Fig. 196, *3–7*); fully grown gametocytes fill the erythrocytes up to their poles (Fig. 196, *5–7*); dumbbell-shaped gametocytes do not occur or represent less than 10% of the total number of growing gametocytes; the outline is usually even (Fig. 196, *5*, *7*) but sometimes also wavy (Fig. 196, *6*); the parasite nucleus is compact, variable in form, frequently band-like (Fig. 196, *5*, *7*), median or submedian in position and is usually located close to the nucleus of erythrocytes (Fig. 196, *5–7*); pigment granules are usually

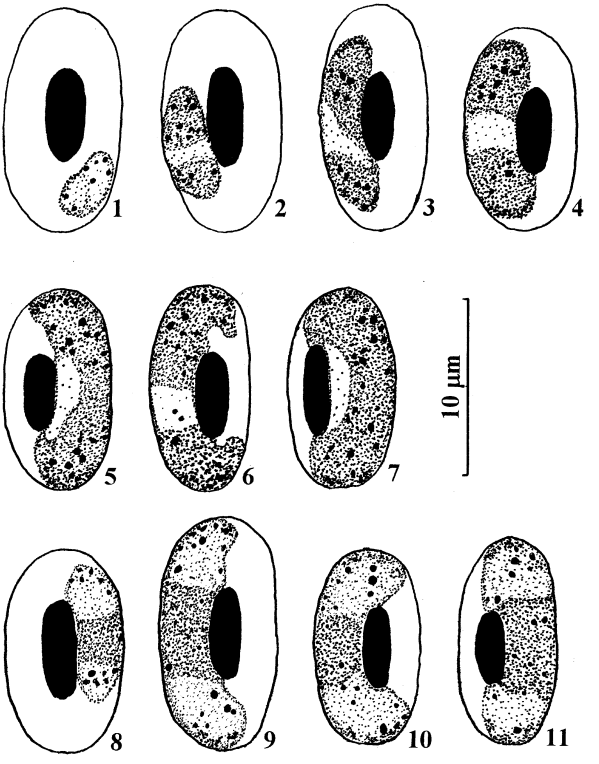

Figure 196 Gametocytes of *Haemoproteus calandrellae* from the blood of *Calandrella rufescens: 1*, *2*, *8* – young; *3–7* – macrogametocytes; *9–11* – microgametocytes (modified from Valkiūnas and Iezhova, 1992c).

roundish, of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 196, *9–11*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. calandrellae* is especially similar to *H. alaudae* and *H. dicaeus*. It can be distinguished from the latter two species primarily on the basis of (i) the median position of nucleus in its macrogametocytes, and (ii) the presence of medium-size (0.5 to 1.0 μm) pigment granules in its gametocytes. In addition, the close adherence of the nucleus of macrogametocytes to the nucleus of erythrocytes (Fig. 196, *5*, *7*) is a distinctive characteristic of this species.

118. **Haemoproteus (Parahaemoproteus) coatneyi** Burry-Caines and Bennett, 1992

Haemoproteus coatneyi Burry-Caines and Bennett, 1992: 1155, Fig. 15–19. – *H. coereba* Burry-Caines and Bennett, 1992: 1155, Fig. 13, 14. – *H. paruli* Burry-Caines and Bennett, 1992: 1157, Fig.

24, 25. – *H. thraupi* Burry-Caines and Bennett, 1992: 1158, Fig. 26–29. – *H. coatneyi*: Valkiūnas, 1997: 349 (=*H. coereba*, *H. paruli*, *H. thraupi*).

Type vertebrate host. *Zonotrichia albicollis* (Gmelin) (Passeriformes).
Additional vertebrate hosts. Some species of the Passeriformes (Table 122).
Type locality. Gander, Newfoundland, Canada.
Distribution. The Holarctic and the Neotropical zoogeographical region.
Type material. Hapantotype (No. 79654, *Zonotrichia albicollis*, 18.08.1979, Gander, Newfoundland, Canada, J. Caines) and parahapantotypes (No. 30671, *Passerella iliaca,* 14.06.1972; Pickavance, Creek, Newfoundland; No. 46137, *Zonotrichia capensis,* 28.04.1973, Arica, Chile, R.W. McFarlane; No. 76654, *Z. capensis*, 03.04.1969, Itapetininga, Brazil, O. Souza Lopes; No. 97246, *Z. capensis*, 04.09.1980, Merida, Venezuela, A. Gabaldon; No. 97846, *Z. albicollis*, 05.05.1985, Mercer County, New Jersey, C. Kirkpatrick; No. 113646, *Passerella iliaca,* 30.09.1989, Point Reyes Peninsula, California, P. Super) are deposited in IRCAH. Gametocytes of *Leucocytozoon* sp. are present in the parahapantotype No. 30671.
Etymology. This species is named in honour of Professor G. Robert Coatney in recognition of his contribution to the field of avian blood parasitology.

Table 122 List of vertebrate hosts of *Haemoproteus coatneyi*.

Atlapetes gutturalis	*E. bruniceps*	*Tangara chilensis*
A. brunneinucha	*E. hortulana*	*Thraupis sayaca*
Coereba flaveola	*Melozone leucotis*	*Vermivora celata*
Dacnis cayana	*Passerella iliaca*	*Zonotrichia capensis*
Dendroica coronata	*Piranga rubra*	*Wilsonia citrina*
D. petechia	*Seiurus aurocapillus*	
Emberiza citrinella	*S. noveboracensis*	

Main diagnostic characters. A parasite of species of the passeriform birds whose gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the nucleus laterally but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are present and represent more than 10% of the total number of growing gametocytes. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles. Pigment granules are usually of medium (0.5 to 1.0 μm) and sometimes small (<0.5 μm) size, about 11 per gametocyte on average. A species difficult to identify; can be distinguished from the similar species of haemoproteids of passeriform birds only on the basis of a detailed analysis of a complex of characters (see the description of gametocytes below).

Development in vertebrate host
Exoerythrocytic merogony was studied by Khan and Fallis (1969) in *Zonotrichia albicollis*. The meronts were found in endothelial cells in the lungs, heart, liver, spleen, caecum, and kidneys. They were especially frequently seen in the lungs and heart. The meronts markedly vary in shape. In the lungs, the meronts are usually oval or irregular (frequently elongated and worm-like) (Fig. 197, *1–3*) and their size is up to 75×15 μm. In the cardiac muscle, worm-like meronts are especially common (Fig. 197, *4*). Cytometes were not seen. The nucleus of some parasitized host cells was discernible near the developing meronts as a small cap at one end of the cell. Mature merozoites are up to 2 μm in diameter.

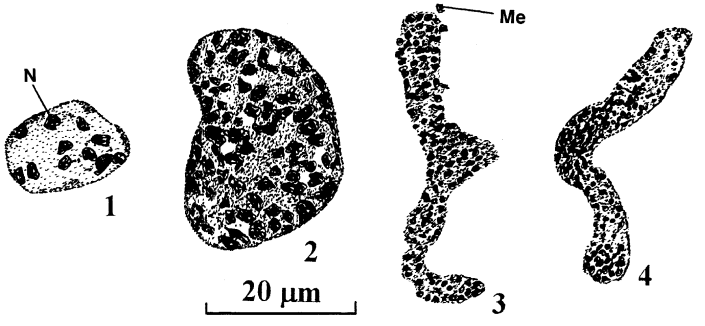

Figure 197 Exoerythrocytic meronts of *Haemoproteus coatneyi* from *Zonotrichia albicollis: 1*, *2* – growing meronts in lungs; *3* – mature meront in lungs; *4* – mature meront in heart; Me – merozoite; N– nucleus (modified from Khan and Fallis, 1969).

Young gametocytes (Fig. 198, *1*). The earliest forms can be seen located anywhere in infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes (Fig. 198, *1*) and extend longitudinally along the nucleus; the outline is usually even.

Macrogametocytes (Fig. 198, *2–7*; Table 123). The cytoplasm is finely granular in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or only slightly displace the nucleus laterally and do not encircle it completely; the maximum NDR does not exceed unity; gametocytes

Table 123 Morphometric parameters of gametocytes and host cells of *Haemoproteus coatneyi* (modified from Burry-Caines and Bennett, 1992).

Feature	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	135			
Length		–	11.9	0.8
Width		–	6.2	0.6
Length of nucleus		–	5.5	0.5
Width of nucleus		–	2.4	0.3
Parasitized erythrocyte	150			
Length		–	12.3	0.9
Width		–	6.2	0.7
Length of nucleus		–	5.4	0.5
Width of nucleus		–	2.3	0.4
Macrogametocyte	150			
Length		–	16.5	3.4
Width		–	2.0	0.9
Length of nucleus		–	2.4	0.6
Width of nucleus		–	2.1	0.5
NDR		0.5–1.0*	0.8	0.2
No. of pigment granules		7–20*	11.6	2.9

Note: All sizes are given in micrometres. The asterisk marks the parameters which were calculated at $n = 31$.

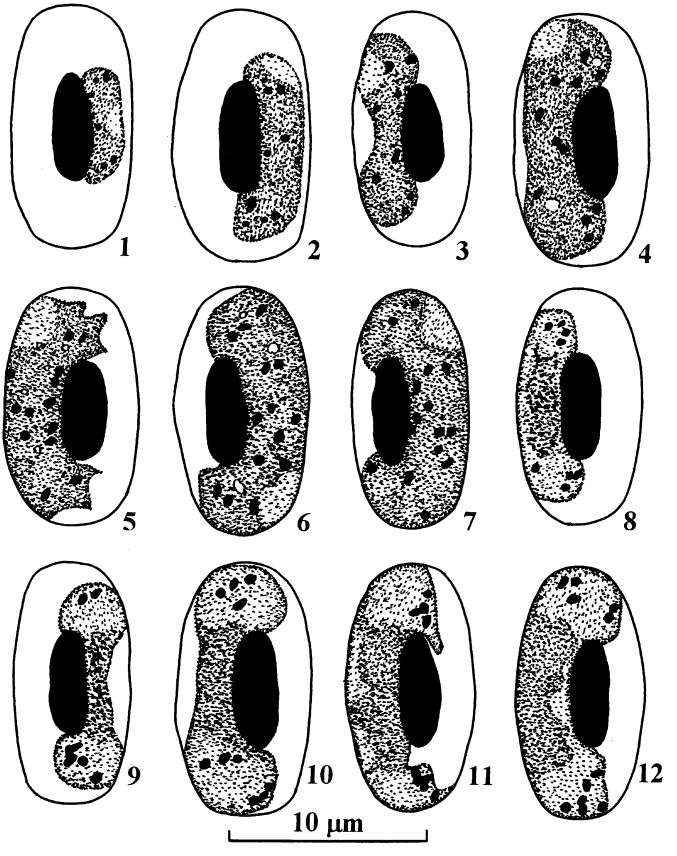

Figure 198 Gametocytes of *Haemoproteus coatneyi* from the blood of *Zonotrichia albicollis:* *1* – young; *2–7* – macrogametocytes; *8–12* – microgametocytes.

adhere to the nucleus and envelope of erythrocytes; the central part of the pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a dumbbell-like appearance (Fig. 198, *3*, *4*); the dumbbell-shaped gametocytes represent more than 10% of the total number of growing gametocytes; fully grown gametocytes lose the dumbbell-like shape, and are closely appressed to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 198, *6*, *7*); the outline is usually even (Fig. 198, *4*, *6*, *7*), but sometimes also ameboid (Fig. 198, *5*); the parasite nucleus is compact, variable in form, subterminal in position; pigment granules are roundish and oval, usually of medium (0.5 to 1.0 μm) but sometimes also small (<0.5 μm) size, randomly scattered throughout the cytoplasm. It should be noted that small pigment granules are common in fully grown gametocytes.

Microgametocytes (Fig. 198, *8–12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. coatneyi* is especially similar to *H. vireonis*. Medium-size (0.5 to 1.0 μm) pigment granules clearly predominate in gametocytes of *H. coatneyi*. In gametocytes of *H. vireonis*, medium (0.5 to 1.0 μm) and small

(<0.5 μm) pigment granules are seen with approximately the same frequency. It should be noted that the taxonomic value of this difference is unclear. Additional investigation of both parasites and a more detailed comparison of these species are required. It is possible that *H. coatneyi* can be a synonym of *H. vireonis.*

Haemoproteus coatneyi should be also distinguished from *H. fringillae* and *H. dolniki*. It is important to note that the range of hosts of *H. coatneyi* and *H. fringillae* partly overlaps. Fully grown gametocytes of *H. coatneyi* fill the infected erythrocytes up to their poles, and dumbbell-shaped forms are common among its growing microgametocytes. Both these features are not characteristic of *H. fringillae.* Gametocytes of *H. dolniki* pull the nucleus of infected erythrocytes inside and, as a result, the maximum value of NDR exceeds unity. This character was not recorded in *H. coatneyi.*

Khan and Fallis (1969) described the exoerythrocytic meronts from *Zonotrichia albicollis* which they attributed to *H. fringillae*. However, Burry-Caines and Bennett (1992) showed that these meronts belong to *H. coatneyi.*

Burry-Caines and Bennett (1992) described *H. coereba*, *H. paruli*, and *H. thraupi* on the basis of the morphology of gametocytes and their host cells. According to the original description, these parasites are identical to *H. coatneyi*, and they were considered to be distinct species mainly because these parasites were recorded in emberizid birds (the family Emberizidae) of different subfamilies. As shown in the General Section, such a method of description of new species of bird haemoproteids should be discouraged (see p. 69). Investigation of type material of *H. coereba*, *H. paruli*, *H. thraupi*, and *H. coatneyi* showed that their gametocytes are indistinguishable. Thus, based on our observations and other evidence presented above, *H. coereba*, *H. paruli*, and *H. thraupi* should be declared junior synonyms of *H. coatneyi*. Description of taxonomic characters in DNA of the parasites is needed to understand fully the validity of these haemoproteids.

119. **Haemoproteus (Parahaemoproteus) dolniki** Valkiūnas and Iezhova, 1992

Haemoproteus dolniki Valkiūnas and Iezhova, 1992a: 10, Fig. 4, 5.

Type vertebrate host. *Fringilla coelebs* L. (Passeriformes).
Vector. Sporogony is completed and sporozoites appear in the salivary glands of experimentally infected biting midge *Culicoides impunctatus* (Diptera: Ceratopogonidae) (Valkiūnas *et al.*, 2002b).
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E).
Distribution. This parasite has so far been recorded in the Palearctic.
Type material. Hapantotype (No. 1178.90 Cos, *Fringilla coelebs*, 11.07.1990, the Curonian Spit, G. Valkiūnas) and parahapantotypes (No. 1175.90 Cos, 1176.90 Cos; 261.87 Cos, 262.87 Cos, 26.07.1987, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462488, other data are as for the hapantotype) is in IRCAH. A series of additional slides of gametes, zygotes, and ookinetes is deposited in CDVA.
Etymology. This species is named in honour of ornithologist Professor Victor R. Dolnik, St. Petersburg, Russia, Director of the Biological Station of the Zoological Institute on the Curonian Spit where the type material was collected, in memory of the long period of collaboration during field work on the Curonian Spit.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it completely. Gametocytes adhere to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes predominate among the growing gametocytes. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes, and they fill the erythrocytes

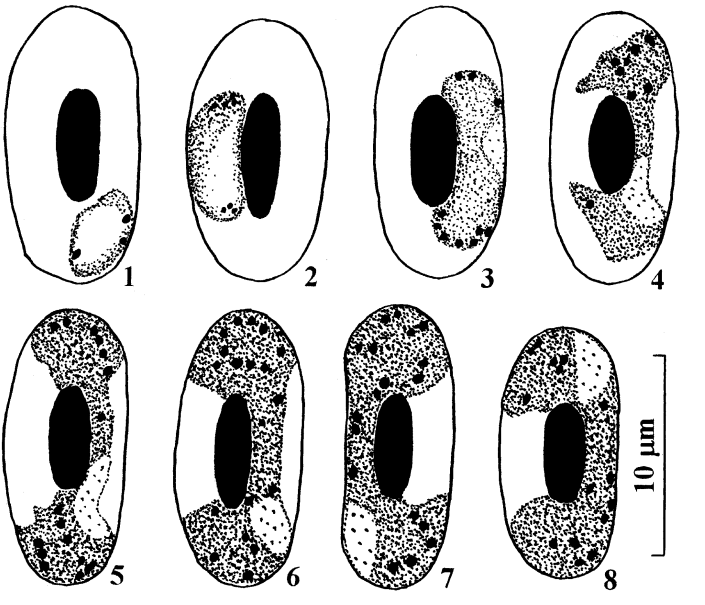

Figure 199 Gametocytes of *Haemoproteus dolniki* from the blood of *Fringilla coelebs: 1*, *2* – young; *3–8* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992a).

up to their poles. Gametocytes frequently pull the nucleus of erythrocytes inside and, as a result, the maximum value of NDR exceeds unity. Pigment granules are of medium (0.5 to 1.0 μm) size, about 12 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 199, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently they take a polar position in the erythrocytes (Fig. 199, *1*); they are oval or roundish; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus (Fig. 199, *2*); gametocytes do not displace the nucleus of erythrocytes laterally, and they adhere to the nucleus and envelope of erythrocytes (Fig. 199, *2*); the outline is usually even.

Macrogametocytes (Fig. 199, *3–8*; Table 124). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are not seen; gametocytes grow around the nucleus of infected erythrocytes; they markedly enclose the nucleus with their ends but do not encircle it completely; gametocytes adhere to the nucleus and envelope of erythrocytes; however, the central part of the pellicle of the growing gametocytes frequently does not extend to the erythrocyte envelope, causing a 'dip' and giving a clear dumbbell-like appearance (Fig. 199, *4–6*); dumbbell-shaped gametocytes predominate among the growing gametocytes; fully grown gametocytes lose the dumbbell-like shape, and are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 199, *7*, *8*); gametocytes do not displace or slightly displace the nucleus of erythrocytes laterally, and they frequently pull the nucleus inside (Fig. 199, *7*); as a result, the maximum NDR exceeds unity (see Table 124) which is a rare character of bird haemoproteids; the outline is usually even (Fig. 199, *6*, *7*), but sometimes ameboid (Fig. 199, *5*); the parasite nucleus is compact, variable in form, subterminal in

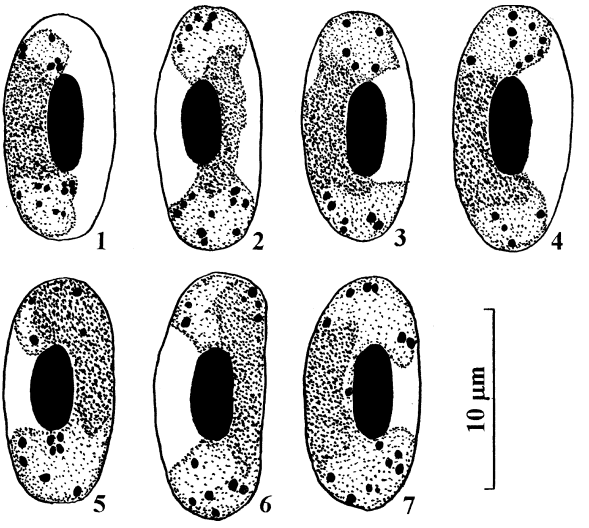

Figure 200 Microgametocytes of *Haemoproteus dolniki* from the blood of *Fringilla coelebs* (modified from Valkiūnas and Iezhova, 1992a).

position; pigment granules are usually roundish, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 200). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the dumbbell-shaped gametocytes are less frequently seen than among macrogametocytes; other characters are as for macrogametocytes.

Development in vector

Sporogony is completed in experimentally infected biting midges *Culicoides impunctatus* (Valkiūnas *et al.*, 2002b). Gametogenesis and development of zygote and ookinete *in vitro* under the light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1994). The data on the rate of this process are given in Table 26. Within 1 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave the infected erythrocytes (Fig. 201, *2*, *3*, 6, *7*). At approximately the same time, exflagellation (Fig. 201, *9*), free microgametes (Fig. 201, *10*), and macrogametes (Fig. 201, *4*) were seen. It is necessary to note that a spherical outgrowth, which looks like a residual body, sometimes develops during the exflagellation, and the role of the outgrowth is unclear. The fertilization of macrogametes (Fig. 201, *11*) and first zygotes (Fig. 201, *12*) were recorded only 30 min after EBA. The zygotes are morphologically identical to macrogametes. The initial stages of ookinete differentiation were seen approximately 6 h after EBA. At this time, a long finger-like outgrowth appears, located tangentially to the main body of the parasite (Fig. 201, *13*). As the ookinete develops, this outgrowth markedly extends and forms the anterior or apical end of the ookinete. On the opposite end of the medium differentiated ookinete, the accumulation of pigment granules was recorded (Fig. 201, *14*). In the fully grown ookinete, the pigment and adjacent part of cytoplasm are eliminated as a residual body (Fig. 201, *15*). At the stage of the medium differentiated ookinete, several large clear 'vacuoles' appear in the cytoplasm, and they persist in fully differentiated ookinetes (Fig. 201, *15*, *16*). The mature ookinetes look like elongated worm-like bodies (Fig. 201, *16*). Ookinetes with the residual body were seen approximately 24 h after EBA, and

Table 124 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. ($n = 31$) (according to Valkiūnas and Iezhova, 1992a).

Feature	*H. dolniki*			*H. magnus*		
	lim	$\overline{X}$	*SD*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte						
Length	11.5–13.2	12.4	0.4	10.6–12.8	11.6	0.6
Width	5.4–7.0	6.1	0.3	5.7–6.8	6.1	0.3
Length of nucleus	5.0–6.3	5.7	0.2	4.7–6.3	5.3	0.2
Width of nucleus	2.2–2.9	2.5	0.1	2.2–2.8	2.5	0.1
Erythrocyte parasitized by macrogametocyte						
Length	11.5–13.7	12.8	0.6	11.8–13.7	12.6	0.6
Width	5.0–6.6	5.7	0.4	5.3–6.9	5.8	0.4
Length of nucleus	4.6–5.9	5.3	0.2	4.4–5.4	5.1	0.2
Width of nucleus	1.7–2.8	2.4	0.1	2.2–2.9	2.5	0.1
Erythrocyte parasitized by microgametocyte						
Length	11.9–13.2	12.6	0.6	11.5–13.5	12.6	0.5
Width	5.1–7.0	6.0	0.3	5.2–6.9	6.2	0.4
Length of nucleus	4.5–6.0	5.4	0.4	4.7–6.0	5.3	0.2
Width of nucleus	2.1–3.1	2.5	0.2	2.2–3.2	2.6	0.1
Macrogametocyte						
Length	13.0–15.6	14.5	0.8	14.7–18.0	16.5	0.7
Width	0.9–2.5	1.4	0.6	1.6–2.9	2.1	0.4
Length of nucleus	2.2–4.2	2.9	0.4	2.1–3.2	2.7	0.2
Width of nucleus	1.1–3.3	2.0	0.4	1.3–2.7	1.8	0.2
NDR	0.5–1.2	0.8	0.1	0.4–1.0	0.8	0.1
No. of pigment granules	10–15	12.4	1.9	6–14	9.8	1.3
Microgametocyte						
Length	12.2–16.2	14.6	0.9	14.7–19.4	16.5	0.8
Width	1.5–2.8	2.1	0.3	1.7–3.1	2.4	0.4
Length of nucleus	7.6–10.3	8.9	0.4	6.5–10.3	8.2	0.2
Width of nucleus	1.5–2.8	2.1	0.2	1.2–2.7	1.8	0.1
NDR	0.6–1.1	0.8	0.1	0.5–1.0	0.8	0.1
No. of pigment granules	9–19	12.7	2.2	6–13	8.7	1.1

Note: All sizes are given in micrometres.

ookinetes without the residual body were recorded 48 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 27.

C o m m e n t s. During the identification of species, *H. dolniki* should be, first of all, distinguished from *H. fringillae*. Both these haemoproteids parasitize the same host, *Fringilla coelebs*, and are frequently seen in a mixed infection. *Haemoproteus dolniki* can be distinguished from *H. fringillae* primarily on the basis of (i) its significantly greater maximum value of the NDR, and (ii) markedly filled up poles of infected erythrocytes by fully grown gametocytes.

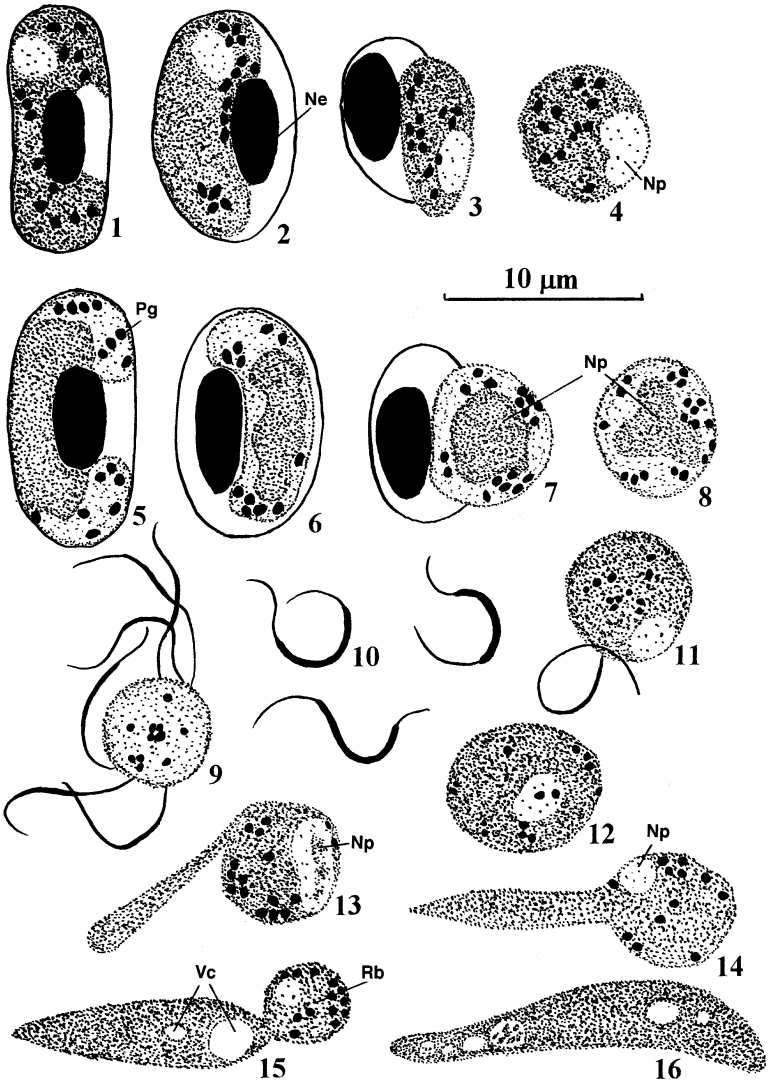

Figure 201 *Haemoproteus dolniki* gametogenesis, zygote, and ookinete development *in vitro:* *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Fringilla coelebs* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14* – medium differentiated ookinete; *15* – ookinete with a residual body; *16* – ookinete without the residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1994).

Macrogametocytes of *H. dolniki* are similar to macrogametocytes of *H. attenuatus* and *H. sittae* in the manner of their influence on the nucleus of infected erythrocytes (the macrogametocytes of all these species pull the nucleus inside and, as a result, the maximum value of the NDR exceeds unity). However, the morphology of microgametocytes and the peculiarities of their influence on infected erythrocytes as well as the morphology of young gametocytes are clearly different in all above

mentioned species. *Haemoproteus dolniki* is also similar to *H. coatneyi*. It can be distinguished from the latter species, particularly on the basis of the greater maximum value of the NDR during the development of its gametocytes.

120. **Haemoproteus (Parahaemoproteus) magnus** Valkiūnas and Iezhova, 1992

Haemoproteus magnus Valkiūnas and Iezhova, 1992a: 9, Fig. 3.

Type vertebrate host. *Fringilla coelebs* L. (Passeriformes).
Additional vertebrate host. *Carpodacus erythrinus* (Passeriformes).
Type locality. The Curonian Spit in the Baltic Sea (55°05′N, 20°44′ E).
Distribution. The Palearctic.
Type material. Hapantotype (No. 2480.89 Cos, *Fringilla coelebs*, the Curonian Spit, 25.05.1989, G. Valkiūnas) and parahapantotypes (No. 2479.89 Cos, 25.05.1989; 1374.85p, 06.06.1985, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462493, other data are as for the hapantotype) is deposited in IRCAH.

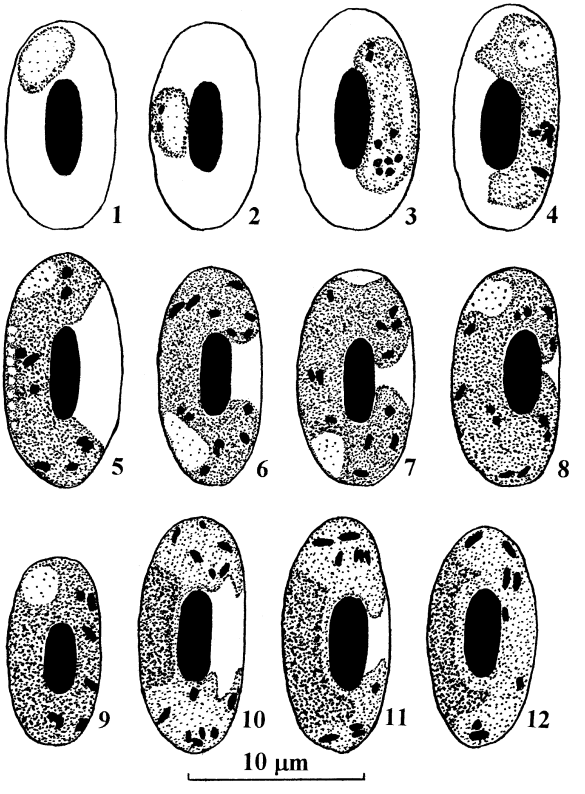

Figure 202 Gametocytes of *Haemoproteus magnus* from the blood of *Fringilla coelebs:* *1*, *2* – young; *3–9* – macrogametocytes; *10–12* – microgametocytes (modified from Valkiūnas and Iezhova, 1992a).

Etymology. The specific name reflects the large size of gametocytes and their pigment granules.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow around the nucleus of infected erythrocytes and can completely encircle the nucleus. Medium and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes do not occur. Rod-like large (1.0 to 1.5 μm) pigment granules are present in gametocytes.

Development in vertebrate host

Young gametocytes (Fig. 202, *1*, *2*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently they take a polar position in the host cells (Fig. 202, *1*); they are oval or roundish; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes at its lateral side (Fig. 202, *2*) and extend longitudinally along the nucleus completely filling the space between the envelope and nucleus of erythrocytes; the outline is usually even.

Macrogametocytes (Fig. 202, *3–9*; Table 124). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are not seen; gametocytes grow around the nucleus of infected erythrocytes, they markedly enclose the nucleus with their ends (Fig. 202, *5–8*) and can finally completely encircle the nucleus and occupy all available cytoplasmic space in the host cells (Fig. 202, *9*); numerous small vacuoles, which are located close to the erythrocyte envelope, are seen in some growing gametocytes (Fig. 202, *5*); medium and fully grown gametocytes fill infected erythrocytes up to their poles and they are closely appressed both to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are not seen; the outline is usually even; the parasite nucleus is compact, variable in form, frequently roundish (Fig. 202, *4, 9*), subterminal in position and is located close to the erythrocyte envelope; pigment granules are roundish, oval and rod-like, of large (1.0 to 1.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; rod-like large (1.0 to 1.5 μm) pigment granules clearly predominate in fully grown gametocytes.

Microgametocytes (Fig. 202, *10–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline is sometimes ameboid (Fig. 202, *10*); other characters are as for macrogametocytes.

Comments. *Haemoproteus magnus* is a relatively rare parasite of *Fringilla coelebs* in the type locality. The prevalence of infection in this bird does not exceed 5% during the breeding period. During the identification of this species, attention should be paid, first of all, to rod-like large (1.0 to 1.5 μm) pigment granules in its mature gametocytes. On the basis of this character, *H. magnus* can be easily distinguished from *H. fringillae* and *H. dolniki* which also parasitize the same bird, *F. coelebs.*

121. **Haemoproteus (Parahaemoproteus) minutus** Valkiūnas and Iezhova, 1992

Haemoproteus minutus Valkiūnas and Iezhova, 1992a: 5, Fig. 1, 2.

Type vertebrate host. *Turdus merula* L. (Passeriformes).
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E).

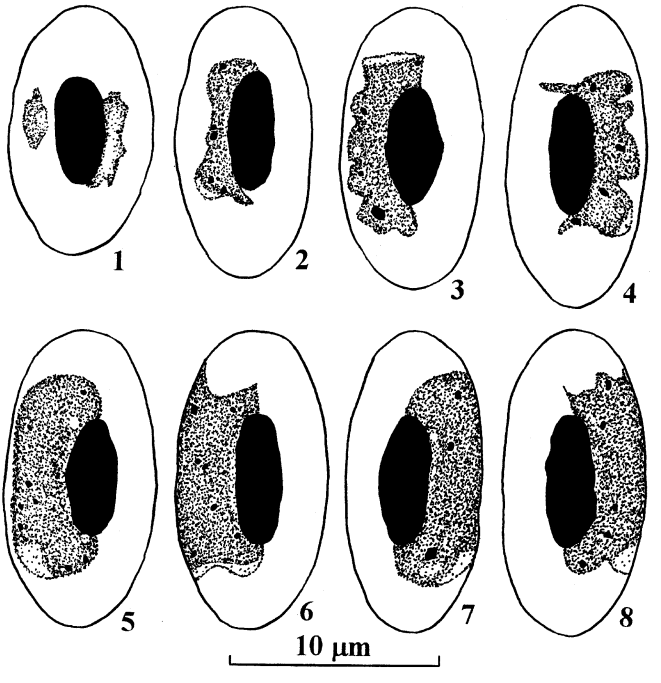

Figure 203 Gametocytes of *Haemoproteus minutus* from the blood of *Turdus merula:* *1*– young; *2*–*8* – macrogametocytes (modified from Valkiūnas and Iezhova, 1992a).

Distribution. The Palearctic.

Type material. Hapantotype (No. 245.85p, *Turdus merula*, 20.05.1985, the Curonian Spit, G. Valkiūnas) and parahapantotypes (No. 1581-1584.89 Cos, 2095-2096.89 Cos, 2098.89 Cos, 2165-2167.89 Cos, 18-24.05.1989, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462496, other data are as for the hapantotype) is deposited in IRCAH. A series of additional slides of gametes, zygotes, and ookinetes is deposited in CDVA.

Etymology. The specific name reflects the minute size of gametocytes of this parasite.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes and only slightly enclose the nucleus with their ends. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present, and gametocytes with a highly ameboid or clearly wavy outline are common among them. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes but do not fill the erythrocytes up to their poles. Dumbbell-shaped gametocytes are absent. Pigment granules tend to aggregate into compact masses. The average number of pigment granules is about five per gametocyte.

Development in vertebrate host

Young gametocytes (Fig. 203, *1*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently recorded in a lateral position to the nucleus of infected erythrocytes; as the parasite develops, gametocytes adhere to the nucleus of erythrocytes and extend longitudinally along the nucleus; the outline is usually irregular (Fig. 203, *1*).

Table 125 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. minutus* (according to Valkiūnas and Iezhova, 1992a)				*H. neseri* (modified from Bennett and Earlé, 1992)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	33				15		
Length		11.1–14.0	12.3	0.6		12.0	1.0
Width		5.8–7.1	6.4	0.3		7.3	0.4
Length of nucleus		4.9–6.6	5.7	0.2		5.4	0.6
Width of nucleus		2.4–3.2	2.8	0.1		2.4	0.3
Erythrocyte parasitized by macrogametocyte	31				25		
Length		12.2–15.1	13.6	0.7		13.6	0.9
Width		5.6–7.1	6.4	0.4		7.6	0.7
Length of nucleus		4.9–6.2	5.7	0.2		5.0	0.6
Width of nucleus		2.2–3.0	2.5	0.1		2.3	0.3
Erythrocyte parasitized by microgametocyte	31				–		
Length		12.2–16.8	14.0	0.8		–	–
Width		5.0–6.9	6.3	0.4		–	–
Length of nucleus		5.1–6.7	5.8	0.2		–	–
Width of nucleus		2.1–3.0	2.6	0.1		–	–
Macrogametocyte					25		
Length	33	7.6–12.4	10.2	0.8		13.3	0.8
Width	33	1.2–3.6	2.4	0.6		2.2	0.6
Length of nucleus	33	0.8–3.6	2.0	0.4		2.5	0.5
Width of nucleus	33	0.3–1.6	0.6	0.4		2.1	0.4
NDR	33	0.6–1.0	0.8	0.1		0.7	0.1
No. of pigment granules	64	1–10	4.5	1.8		30.0	3.7
Microgametocyte							
Length	31	8.8–14.0	11.0	0.8		–	–
Width	31	1.6–3.2	2.4	0.4		–	–
NDR	31	0.6–0.9	0.8	0.1		–	–
No. of pigment granules	73	1–10	5.0	2.0	15	26.0	2.1

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 203, *2–8*; Table 125). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles, stains pale and, on the basis of staining, macrogametocytes are similar to microgametocytes, which is a rare character for bird haemoproteids; gametocytes grow along the nucleus of infected erythrocytes; they only slightly enclose the nucleus with their ends and slightly (if at all) displace the nucleus laterally; gametocytes adhere to the nucleus of erythrocytes, but the growing gametocytes do not touch the envelope of erythrocytes along their entire margin and, as a result, a clear, more or less evident unfilled space (a 'cleft') is available between the parasite and the envelope of erythrocytes (Fig. 203, *2–5*); this 'cleft' disappears at the final stages of gametocyte development, and fully grown gametocytes are closely appressed to the nucleus and

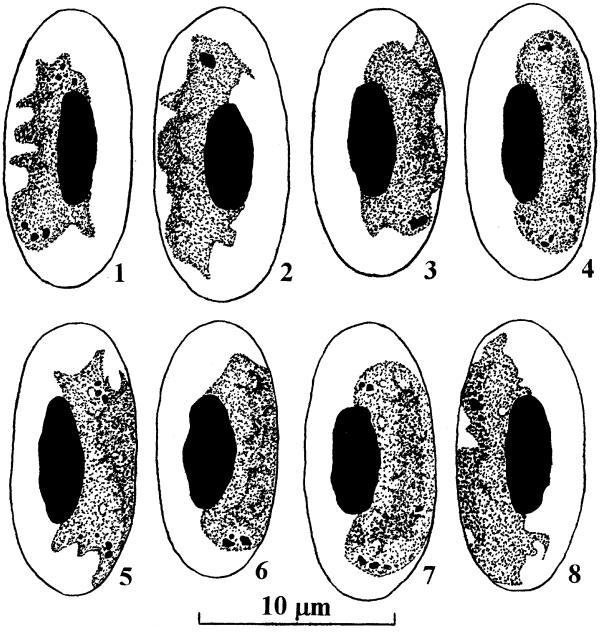

Figure 204 Microgametocytes of *Haemoproteus minutus* from the blood of *Turdus merula* (modified from Valkiūnas and Iezhova, 1992a).

envelope of erythrocytes (Fig. 203, *6–8*); the outline varies markedly from highly ameboid (Fig. 203, *4*, *8*) to even (Fig. 203, *5*, *7*), but gametocytes with an ameboid outline usually predominate; fully grown gametocyte are small (see Table 125) and never fill the erythrocytes up to their poles; the parasite nucleus is compact, small, variable in form, and frequently more or less elongated (Fig. 203, *3, 4*, *6*), varies from median to terminal in position; pigment granules are roundish and oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, and they tend to aggregate into one or several large masses (Fig. 203, *3*, *7*); infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 204). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is diffuse and ill-defined, and chromatin frequently concentrates along the outer periphery of gametocytes (Fig. 204, *1*, *2*); gametocytes with an ameboid outline predominate (Fig. 204, *1–3*, *5*, *8*); other characters are as for macrogametocytes.

Development in vector has not been investigated. Gametogenesis, development of zygote and ookinete *in vitro* under the light microscope at 18 to 20°C were studied by Valkiūnas and Iezhova (1995). The data on the rate of this process are given in Table 62. Within 1 min after exposure of infected blood to air (EBA), mature gametocytes round up and leave erythrocytes (Fig. 205, *2*, *3*, *6*, *7*). The cytoplasm of macrogametes usually contains several clear vacuoles (Fig. 205, *4*), and the nucleus of macrogametes possesses a clear clump of chromatin (Fig. 205, *4*, *11*). Exflagellation (Fig. 205, *9*) was seen approximately 5 min after EBA, and free microgametes (Fig. 205, *10*), fertilization of macrogametes (Fig. 205, *11*) and zygotes (Fig. 205, *12*) were recorded 15 min after EBA.

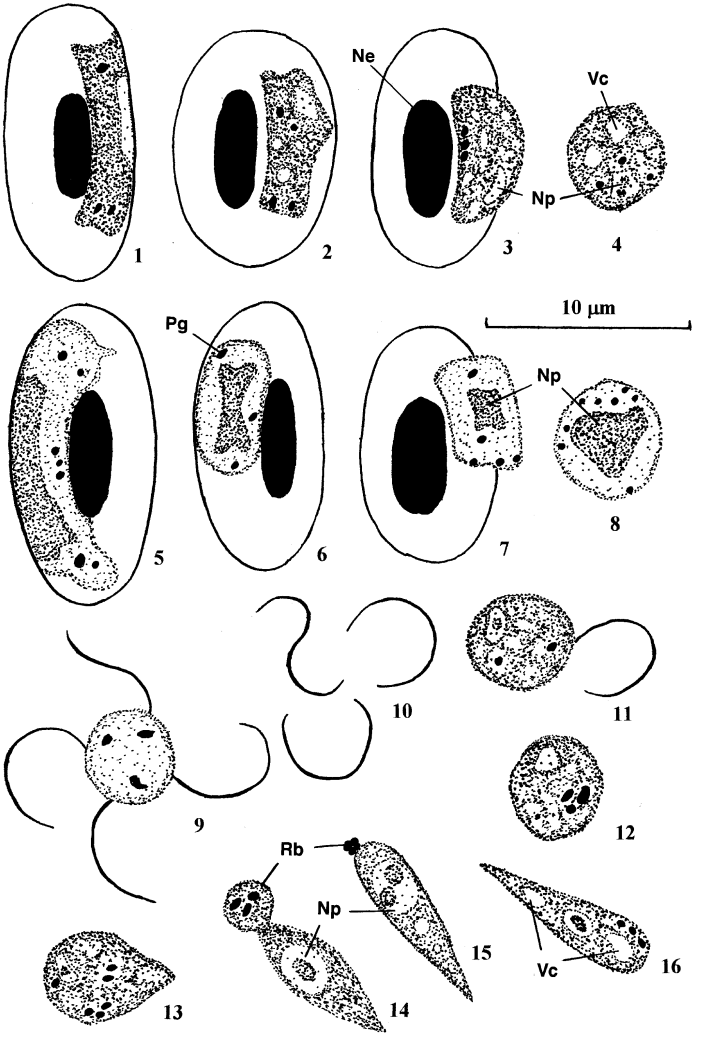

Figure 205 *Haemoproteus minutus* gametogenesis, zygote and ookinete development *in vitro:* *1*, *5* – mature macrogametocyte (*1*) and microgametocyte (*5*) in the blood of *Turdus merula* before the onset of gametogenesis; *2*, *3* – rounded up macrogametocyte; *4* – macrogamete; *6*, *7* – rounded up microgametocyte; *8* – free microgametocyte; *9* – exflagellation of microgametes; *10* – microgametes; *11* – fertilization of macrogamete; *12* – zygote; *13* – initial stage of differentiation of ookinete; *14* – medium differentiated ookinete; *15* – ookinete with a residual body; *16* – ookinete without the residual body; Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – 'vacuole' (modified from Valkiūnas and Iezhova, 1995).

Morphologically zygotes are similar to macrogametes. The initial stages of ookinete differentiation were seen 45 min after EBA. At this time, a short pointed outgrowth appears, it extends and forms the anterior or apical end of the ookinete (Fig. 205, *13*). A clear large spherical residual body develops on the opposite end of the ookinete. It possesses pigment granules and some cytoplasm (Fig. 205, *14*). As the ookinete develops, the residual body decreases in size, and finally becomes a compact minute clump of

pigment granules (Fig. 205, *15*). Fully differentiated ookinetes are carrot-like in shape (Fig. 205, *16*). It is important to note that the shape of the ookinetes *in vitro* is relatively constant. The ookinetes vary only slightly in shape, which is a rare character for bird haemoproteids during their *in vitro* development. Several clear 'vacuoles' are usually present in fully differentiated ookinetes, and a few pigment granules are also seen sometimes (Fig. 205, *15*, *16*). Ookinetes develop quickly. The ookinetes with a residual body were seen approximately 45 min after EBA, and the ookinetes without the residual body were recorded 1.5 h after EBA. The morphometric parameters of gametes and ookinetes are given in Table 63.

Comments. *Haemoproteus minutus* is similar to *H. fallisi* in the small size of its fully grown gametocytes. However, *H. minutus* can be easily distinguished from *H. fallisi* primarily on the basis of (i) the smaller number of pigment granules in its gametocytes, (ii) the smaller size of nucleus in macrogametocytes, and (iii) the frequently seen ameboid outline in growing gametocytes. It should be noted that medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin (Fig. 203, *5*) and the gametocytes with highly wavy outer edge (Figs. 203, *3*, *4*; 204, *1*, *2*), are common in *H. minutus*, but they were never seen in *H. fallisi.*

122. **Haemoproteus (Parahaemoproteus) neseri** Bennett and Earlé, 1992

Haemoproteus neseri Bennett and Earlé, 1992: 115, Fig. 5–8.

Type vertebrate host. *Cossypha dichroa* (Gmelin) (Passeriformes).
Type locality. Louis Trichardt, Transvaal, Republic of South Africa.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 118556, *Cossypha dichroa*, 22.11.1990, Louis Trichardt, Republic of South Africa, W. Neser) is deposited in IRCAH.
Etymology. This species is named in honour of Mr. Walter Neser, who collected the type material for the description of this haemoproteid.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes are closely appressed to the nucleus of infected erythrocytes; they grow around the nucleus but do not encircle it completely. Medium grown gametocytes, which do not touch the envelope of erythrocytes along their entire margin, are present. Fully grown gametocytes are closely appressed to both the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles. Dumbbell-shaped growing gametocytes are present. The outline of gametocytes is even. The average number of pigment granules is about 30 per macrogametocyte.

Development in vertebrate host

Young gametocytes are usually seen in a position lateral to the nucleus of infected erythrocytes; they adhere to the nucleus and extend longitudinally along it, not touching the envelope of the erythrocytes; the outline is even.

Macrogametocytes (Fig. 206, *1–5*; Table 125). The cytoplasm is granular in appearance, usually contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they slightly displace the nucleus laterally and enclose it with their ends, but do not encircle it completely; growing gametocytes are usually clearly dumbbell-like (Fig. 206, *1–3*); medium grown gametocytes usually do not touch the

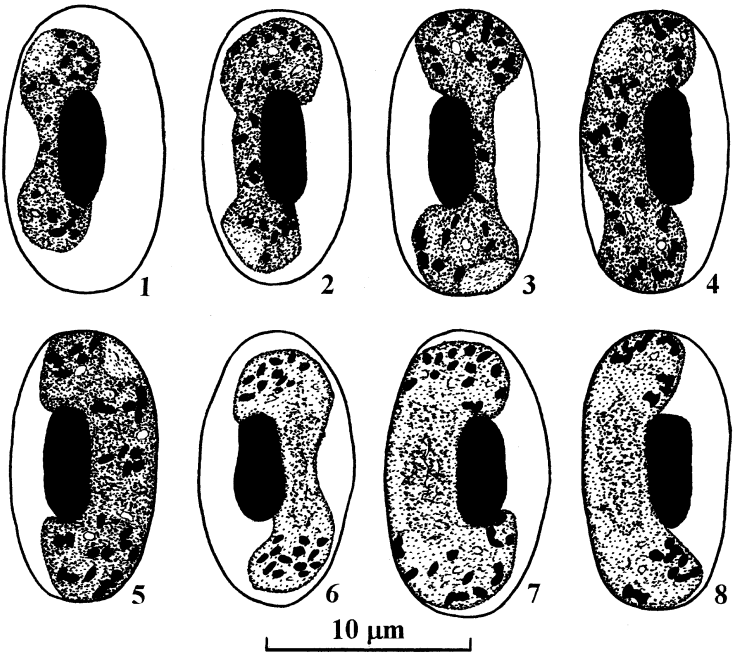

Figure 206 Gametocytes of *Haemoproteus neseri* from the blood of *Cossypha dichroa: 1–5* – macrogametocytes; *6–8* – microgametocytes.

envelope of erythrocytes along their entire margin (Fig. 206, *1*, *2*); fully grown gametocytes gradually lose the dumbbell-like shape (Fig. 206, *4*), and finally they closely appress both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 206, *5*); the outline is usually even; the parasite nucleus is compact, variable in form, subterminal or even terminal in position; pigment granules are roundish and oval, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 206, *6–8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the average number of pigment granules is slightly less than in macrogametocytes (see Table 125); other characters are as for macrogametocytes.

C o m m e n t s. *Haemoproteus neseri* can be easily distinguished from other haemoproteids of birds belonging to the Passeriformes primarily on the basis of (i) numerous pigment granules in its gametocytes, and (ii) numerous medium grown dumbbell-shaped gametocytes which do not touch the envelope of erythrocytes along their entire margin (Fig. 206, *2*, *6*).

123. **Haemoproteus (Parahaemoproteus) psittaci** Bennett and Peirce, 1992

Haemoproteus psittaci Bennett and Peirce, 1992a: 21, Fig. 1–5.

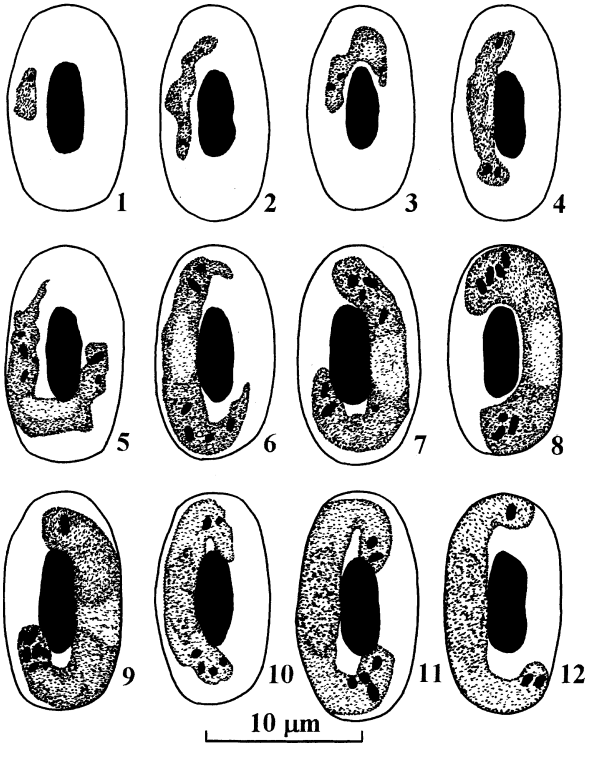

Figure 207 Gametocytes of *Haemoproteus psittaci* from the blood of *Psittacus erithacus:* *1–3* – young; *4–9* – macrogametocytes; *10–12* – microgametocytes.

Type vertebrate host. *Psittacus erithacus* L. (Psittaciformes).
Type locality. Wickford, Essex, UK. This parasite was found in a bird imported from Africa and kept in captivity.
Distribution has not been investigated.
Type material. Hapantotype (No. 115711, *Psittacus erithacus*, 03.06.1991, Wickford, Essex, UK, M.A. Peirce) and parahapantotype (No. 115712, other data are as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type host, *Psittacus*.

Main diagnostic characters. A parasite of species of the Psittaciformes whose fully grown gametocytes enclose the nucleus of infected erythrocytes with their ends but do not encircle it completely. The average number of pigment granules is about 10 per gametocyte.

Development in vertebrate host
Young gametocytes (Fig. 207, *1–3*) can be seen anywhere in infected erythrocytes, frequently they take a polar position in the host cells (Fig. 207, *3*); growing gametocytes are elongated slender snake-like bodies with a wavy or ameboid outline, usually lying free in the cytoplasm and not touching either the nucleus or envelope of erythrocytes (Fig. 207, *1–3*); as the parasite develops, advanced gametocytes frequently adhere to the nucleus of erythrocytes, their outline is less ameboid than for the earliest gametocytes (Fig. 207, *4*).

Table 126 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. psittaci* (modified from Bennett and Peirce, 1992a)			*H. undulatus* (modified from Bennett and Earlé, 1992)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	35			15		
Length		12.3	0.5		13.7	0.9
Width		7.0	0.6		6.9	0.6
Length of nucleus		5.9	0.5		6.5	0.6
Width of nucleus		2.4	0.2		2.4	0.2
Erythrocyte parasitized by macrogametocyte	35			25		
Length		13.8	1.0		14.5	0.8
Width		7.9	0.6		7.5	0.6
Length of nucleus		6.1	0.7		6.3	0.5
Width of nucleus		2.8	0.3		2.6	0.3
Erythrocyte parasitized by microgametocyte	10			–		
Length		13.9	1.8		–	–
Width		8.4	0.4		–	–
Length of nucleus		5.8	0.7		–	–
Width of nucleus		2.7	0.1		–	–
Macrogametocyte	35			25		
Length		15.7	1.4		22.2	3.2
Width		2.6	0.3		1.4	0.4
Length of nucleus		3.4	0.5		2.7	0.6
Width of nucleus		2.2	0.4		1.5	0.3
NDR		0.8	0.1		0.9	0.1
No. of pigment granules		9.6	1.3		23.0	2.0
Microgametocyte	10			–		
Length		17.0	3.4		–	–
Width		3.1	0.5		–	–
Length of nucleus		6.2	0.9		–	–
Width of nucleus		2.6	0.4		–	–
NDR		0.7	0.1		–	–
No. of pigment granules		11.4	1.2		–	–

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 207, *4–9*; Table 126). The cytoplasm is granular in appearance, sometimes contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes; they do not displace or only slightly displace the nucleus laterally, enclose the nucleus with their ends but do not encircle it completely; growing gametocytes usually adhere to the nucleus of erythrocytes but do not touch the envelope of erythrocytes along their entire margin (Fig. 207, *6*, *7*); however, gametocytes adhering to the erythrocyte envelope but not touching the erythrocytes nucleus (Fig. 207, *8*) are also sometimes seen; fully grown gametocytes are closely appressed both to the nucleus and envelope of

erythrocytes (Fig. 207, *9*); the outline varies from even to slightly wavy or slightly ameboid in growing gametocytes (Fig. 207, *5–7*), and it is usually even in fully grown gametocytes (Fig. 207, *9*); the parasite nucleus is compact, variable in form, frequently oval in shape, median or submedian in position; pigment granules are roundish, oval, and rod-like in form, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, usually located at the ends of gametocytes and are not scattered throughout the cytoplasm (Fig. 207, *7–9*) which is a rare character for macrogametocytes of bird haemoproteids; infected erythrocytes are slightly hypertrophied in length and width in comparison to uninfected ones.

Microgametocytes (Fig. 207, *10–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; microgametocytes with an ameboid outline are more frequently seen than among macrogametocytes; the parasite nucleus is relatively compact for microgametocytes (Fig. 207, *10–12*); other characters are as for macrogametocytes.

Comments. *Haemoproteus psittaci* is especially similar to *H. handai*. It can be distinguished from the latter species primarily on the basis of smaller number and larger size of pigment granules in its gametocytes.

124. **Haemoproteus (Parahaemoproteus) undulatus** Bennett and Earlé, 1992

Haemoproteus undulatus Bennett and Earlé, 1992: 115, Fig. 1–4.

Type vertebrate host. *Colius indicus* (Latham) (Coliiformes).
Type locality. Kruger National Park, Republic of South Africa.
Distribution. This parasite has so far been recorded only in the type locality.
Type material. Hapantotype (No. 118217, *Colius indicus*, 19.04.1991, Kruger National Park, Republic of South Africa, coll. Chadwick) is deposited in IRCAH.
Etymology. The specific name reflects the undulated outline of the gametocytes of this parasite.

Main diagnostic characters. A parasite of species of the Coliiformes whose gametocytes are wavy (undulated) or ameboid in outline, they grow around the nucleus of infected erythrocytes and markedly enclose it with their ends, but do not displace or only slightly displace the nucleus laterally. Growing gametocytes are usually appressed to the envelope of erythrocytes but do not touch the nucleus of the erythrocytes along their entire margin.

Development in vertebrate host

Young gametocytes. The earliest forms are not seen in the type material; advanced forms can be seen anywhere in infected erythrocytes, they frequently take a polar position in the host cells; as the parasite develops, gametocytes adhere to the envelope of erythrocytes and extend along the erythrocyte nucleus not touching it; the outline is usually wavy or ameboid.

Macrogametocytes (Fig. 208, *1–6*; Table 126). The cytoplasm is finely granular in appearance, frequently contains a few small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, they markedly enclose the nucleus with their ends but do not displace or only slightly displace the nucleus laterally (Fig. 208, *5*, *6*); advanced

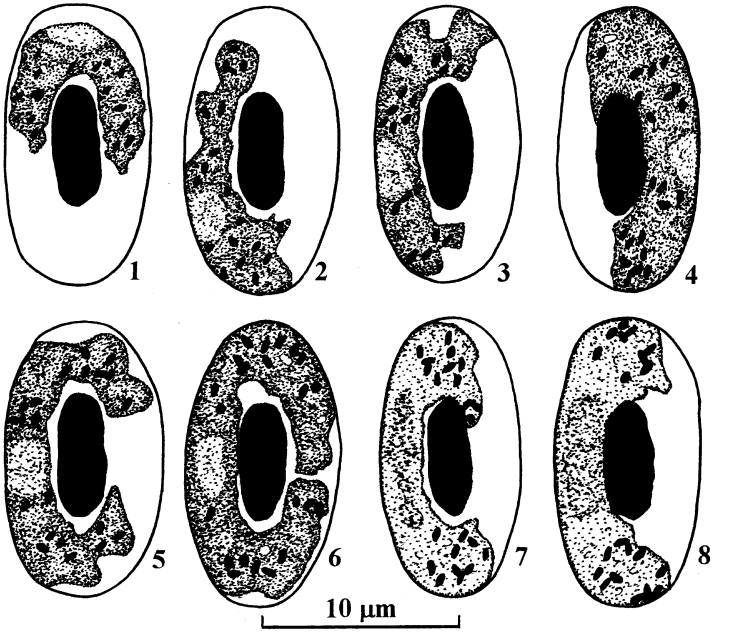

Figure 208 Gametocytes of *Haemoproteus undulatus* from the blood of *Colius indicus: 1–6* – macrogametocytes; *7*, *8* – microgametocytes.

gametocytes are closely appressed to the envelope of erythrocytes but usually do not touch the nucleus of erythrocytes along their entire margin and, as a result, a clear more or less evident unfilled space (a 'cleft') is available between the parasite and the nucleus of erythrocytes (Fig. 208, *2*, *3, 5, 6*); however, gametocytes adhering to the nucleus of erythrocytes (Fig. 208, *4*) also occur, but are rare; the outline is usually wavy (undulated) or ameboid; the parasite nucleus is compact, frequently oval, median or submedian in position; pigment granules are oval or roundish, of medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 208, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; fully grown gametocytes adhere to the nucleus of erythrocytes (Fig. 208, *8*); other characters are as for macrogametocytes.

C o m m e n t s. It should be noted that gametocytes which nearly completely encircle the nucleus of infected erythrocytes (Fig. 208, *6*) are common in the hapantotype. Thus, it is possible that circumnuclear gametocytes may develop, but they have not been found so far.

Haemoproteus undulatus is the only species of haemoproteids which has so far been described in birds of the order Coliiformes.

125. **Haemoproteus (Parahaemoproteus) kairullaevi** Valkiūnas and Iezhova, 1993

Haemoproteus kairullaevi Valkiūnas and Iezhova, 1993b: 141, Fig. 1, 2.

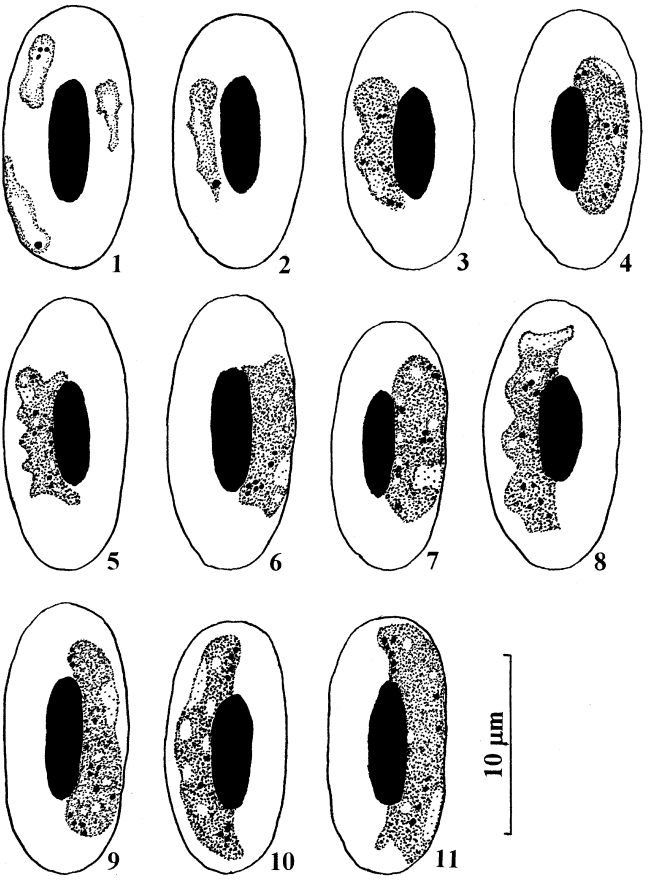

Figure 209 Gametocytes of *Haemoproteus kairullaevi* from the blood of *Acridotheres tristis: 1–3* – young; *4–11* – macrogametocytes (modified from Valkiūnas and Iezhova, 1993b).

Type vertebrate host. *Acridotheres tristis* (L.) (Passeriformes).
Type locality. The settlement Visokoye located in the foothills of the Western Tien Shan, approximately 90 km south-west of Djambul, Southern Kazakhstan.
Distribution. This parasite has so far been recorded only from Southern Kazakhstan, where it is common.
Type material. Hapantotype (No. 3197.86 Az, *Acridotheres tristis*, 11.05.1986, Southern Kazakhstan, G. Valkiūnas) and parahapantotypes (No. 3165, 3166.86 Az, 3189, 3190.86 Az, 3250-3252.86 Az, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (No. G462491, other data are as for the hapantotype) is deposited in IRCAH.
Etymology. This species is named in honour of Dr. Kenesbay K. Kairullaev, Alma-Ata, Kazakhstan, for his research activities into blood parasites of birds in Kazakhstan.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes; they do not displace or only slightly displace the nucleus laterally and do not encircle it completely. Medium grown gametocytes, which are closely appressed to the nucleus of erythrocytes but do not touch the envelope of erythrocytes along their entire margin, are present, and forms with either

Table 127 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. ($n = 31$).

Feature	*H. kairullaevi* (according to Valkiūnas and Iezhova, 1993b)			*H. payevskyi* (according to Valkiūnas *et al.*, 1994)		
	lim	$\overline{X}$	*SD*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte						
Length	10.3–12.9	11.7	0.6	10.3–12.7	11.7	0.5
Width	6.3–7.8	7.2	0.2	6.1–7.4	6.7	0.3
Length of nucleus	5.2–6.5	5.8	0.2	5.2–6.0	5.5	0.2
Width of nucleus	2.2–3.0	2.6	0.1	1.8–2.6	2.2	0.2
Erythrocyte parasitized by macrogametocyte						
Length	11.3–14.8	13.4	0.7	10.8–12.9	11.9	0.6
Width	6.1–8.0	7.0	0.4	5.8–7.4	6.7	0.2
Length of nucleus	4.4–7.0	6.2	0.4	4.6–6.4	5.2	0.2
Width of nucleus	2.2–3.0	2.5	0.1	1.9–2.8	2.2	0.1
Erythrocyte parasitized by microgametocyte						
Length	12.4–14.4	13.4	0.8	10.9–12.7	12.0	0.6
Width	5.7–7.8	7.1	0.3	6.1–7.3	6.7	0.2
Length of nucleus	5.4–6.7	6.1	0.2	4.6–6.2	5.4	0.2
Width of nucleus	1.9–2.9	2.4	0.1	1.8–2.7	2.2	0.2
Macrogametocyte						
Length	9.8–12.7	11.3	0.6	9.8–12.0	10.5	0.4
Width	1.7–2.9	2.4	0.2	2.4–3.4	2.9	0.4
Length of nucleus	1.4–3.1	2.1	0.3	1.8–3.9	3.0	0.4
Width of nucleus	0.9–1.7	1.3	0.1	1.1–2.6	1.7	0.2
NDR	0.8–1.0	0.9	0.1	0.6–0.9	0.8	0.1
No. of pigment granules	5–16	9.5	1.2	9–18	12.0	1.8
Microgametocyte						
Length	10.5–14.1	11.8	0.7	9.2–10.8	9.8	0.3
Width	1.7–3.2	2.7	0.2	2.6–4.0	3.1	0.2
Length of nucleus	–	–	–	1.4–2.8	2.0	0.2
Width of nucleus	–	–	–	0.8–1.7	1.3	0.2
NDR	0.7–1.1	0.9	0.1	0.5–0.9	0.7	0.1
No. of pigment granules	5–14	8.7	1.0	8–15	10.7	1.4

Note: All sizes are given in micrometres.

a highly ameboid or a clearly wavy outline are common among them. Fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes. Dumbbell-shaped gametocytes are absent. Pigment granules are of small (<0.5 μm) size, about 10 per gametocyte on average.

Development in vertebrate host

Young gametocytes (Fig. 209, *1–3*). The earliest forms can be seen anywhere in infected erythrocytes; they are frequently elongated (Fig. 209, *1*); as the parasite develops,

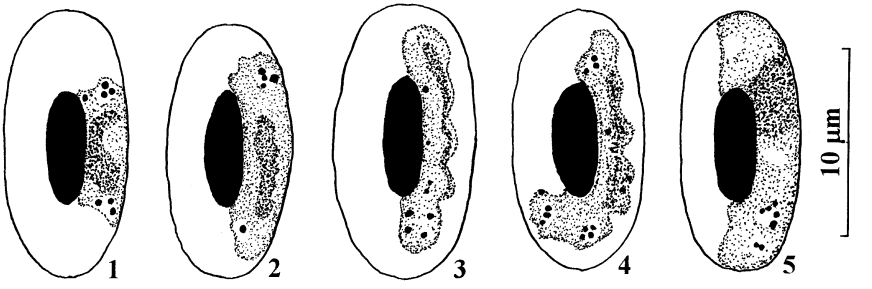

Figure 210 Microgametocytes of *Haemoproteus kairullaevi* from the blood of *Acridotheres tristis* (modified from Valkiūnas and Iezhova, 1993b).

gametocytes extend along the nucleus of erythrocytes (Fig. 209, *2*) and adhere to the nucleus (Fig. 209, *3*); the outline is usually irregular; multiple infection of the same erythrocyte with several gametocytes (Fig. 209, *1*) is common even at low parasitemia.

Macrogametocytes (Fig. 209, *4–11*; Table 127). The cytoplasm is homogeneous in appearance, contains small vacuoles; gametocytes grow along the nucleus of infected erythrocytes; they do not displace or only slightly displace the nucleus laterally and do not encircle it completely; growing gametocytes are closely appressed to the nucleus of erythrocytes but usually do not touch the envelope of erythrocytes along their entire margin (Fig. 209, *8, 9, 10*), and forms with a highly ameboid or clearly wavy outline (Fig. 209, *5*, *8*) are common among them; some growing gametocytes adhere to both the nucleus and envelope of erythrocytes (Fig. 209, *6*, *7*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes but usually do not fill the erythrocytes up to their poles (Fig. 209, *11*); the outline varies markedly from even (Fig. 209, *7*, *9*, *10*) to slightly ameboid (Fig. 209, *6*, *11*) and clearly wavy (Fig. 209, *5*, *8*); the highly wavy (undulated) outline of growing gametocytes (Fig. 209, *5*, *8*) is a characteristic feature of this species; the parasite nucleus is small (see Table 127), usually elongated, varies from subterminal to terminal in position; the most typical parasite nucleus in form and position is shown in Fig. 209, *4*; pigment granules are roundish, of small (<0.5 μm) size, randomly scattered throughout the cytoplasm; infected erythrocytes are hypertrophied in length in comparison to uninfected ones.

Microgametocytes (Fig. 210). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is diffuse and ill-defined, and chromatin concentrates along the outer edge of the parasite in undulated gametocytes (Fig. 210, *3*, *4*); fully grown gametocytes fill erythrocytes up to their poles (Fig. 210, *5*); other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Passeriformes, *H. kairullaevi* is especially similar to *H. pallidus* and *H. minutus*. It can be distinguished from *H. pallidus* primarily on the basis of (i) its numerous gametocytes which adhere to the envelope of erythrocytes (Figs. 209, *6*, *7*; 210, *1*, *2*, *5*) and (ii) clear differences in staining of its macro- and microgametes, and from *H. minutus*, on the basis of more numerous pigment granules in its gametocytes.

Haemoproteus kairullaevi is a common parasite of *Acridotheres tristis* in Southern Kazakhstan. In the type locality, the prevalence of infection reached 60.0% (95% confidence limit is 44.3–74.3) in May 1986.

126. **Haemoproteus (Parahaemoproteus) payevskyi** Valkiūnas, Iezhova and Chernetsov, 1994

Haemoproteus payevskyi Valkiūnas, Iezhova and Chernetsov, 1994: 469, Fig.

Type vertebrate host. *Acrocephalus scirpaceus* (Hermann) (Passeriformes).
Additional vertebrate hosts. *Acrocephalus arundinaceus, A. dumetorum, A. palustris.*
Type locality. The Curonian Spit in the Baltic Sea (55°05′ N, 20°44′ E). The infected birds were caught in the reeds in the grounds of the Biological Station, in Rybachy village.
Distribution. This parasite has so far been recorded in the Palearctic and in the Ethiopian zoogeographical region.
Type material. Hapantotype (No. 884.92 Cos, *Acrocephalus scirpaceus*, 12.07.1992, the Curonian Spit, N.S. Chernetsov) and parahapantotypes (No. 803.92 Cos, 815, 816.92 Cos, 837–838.92 Cos, 883.92 Cos, 903–904.92 Cos, 10.06–21.07.1992, other data are as for the hapantotype) are deposited in CDVA. Parahapantotype (G462373, other data are as for the hapantotype) is deposited in IRCAH.
Etymology. This species is named in honour of ornithologist Professor Vladimir A. Payevsky, St. Petersburg, Russia, in memory of the long period of collaboration during field work on the Curonian Spit.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes grow along the nucleus of infected erythrocytes; they slightly displace the nucleus laterally and do not encircle it completely. Medium and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes, and they usually do not fill the erythrocytes up to their poles. Dumbbell-shaped gametocytes are absent. The nucleus in macrogametocytes is usually median in position. The size of the nucleus of microgametocytes does not exceed that of the nucleus of macrogametocytes, which is an important diagnostic character of this species. The majority of fully grown macrogametocytes contain two loosely aggregated clumps of pigment granules, and each of the clumps is located near the end of the macrogametocytes. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, about 12 per gametocyte on average.

Development in vertebrate host

Description of gametocytes from the type vertebrate host is given below.

Young gametocytes (Fig. 211, *1*, *2*). The earliest forms are usually seen in a position lateral to the nucleus of infected erythrocytes, are roundish or oval (Fig. 211, *1*); as the parasite develops, gametocytes adhere to the nucleus of erythrocytes; they extend longitudinally along the nucleus, slightly displace the nucleus laterally and adhere to the envelope of erythrocytes (Fig. 211, *2*); the outline is even.

Macrogametocytes (Fig. 211, *3–6*; Table 127). The cytoplasm is homogeneous in appearance, usually lacking vacuoles; gametocytes grow along the nucleus of infected erythrocytes, they slightly displace the nucleus laterally and do not encircle it completely; gametocytes are closely appressed to the nucleus and envelope of erythrocytes; dumbbell-shaped gametocytes are absent; fully grown gametocytes are of small size (see Table 127) and usually do not fill the erythrocytes up to their poles (Fig. 211, *5*, *6*), which is a characteristic feature of this species; it should be noted that some gametocytes take an asymmetrical position to the nucleus of erythrocytes (Fig. 211, *4*) and, in this case, one end of gametocytes can touch a pole of erythrocytes (see also ‘Comments’); the parasite nucleus is compact, frequently oval, usually median (Fig. 211, *4–6*) but sometimes submedian in

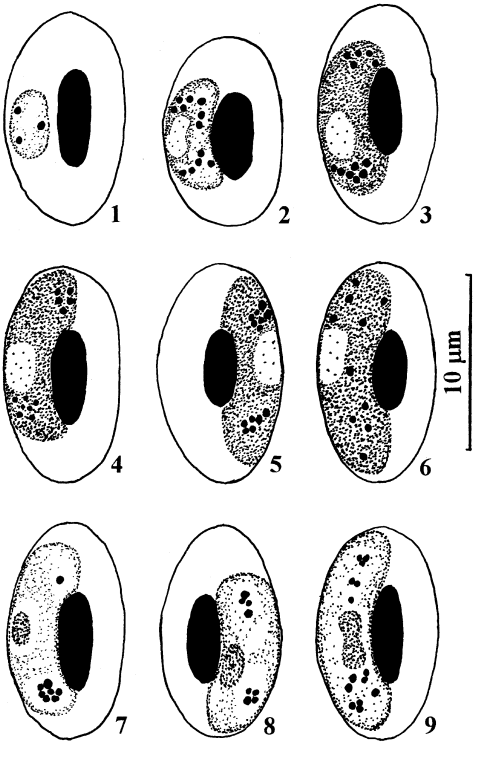

Figure 211 Gametocytes of *Haemoproteus payevskyi* from the blood of *Acrocephalus scirpaceus: 1*, *2* – young; *3–6* – macrogametocytes; *7–9* – microgametocytes (modified from Valkiūnas *et al.*, 1994).

position (Fig. 211, *3*); a parasite nucleus typical in form and shape is shown in Fig. 211, *5*; pigment granules are roundish, usually of small (<0.5 μm) but sometimes medium (0.5 to 1.0 μm) size, usually aggregated in more or less evident loose clumps (Fig. 211, *3–5*), but sometimes also randomly scattered throughout the cytoplasm (Fig. 211, *6*); the majority of fully grown gametocytes have two loosely aggregated clumps of pigment granules (Fig. 211, *5*) and each of the clumps is located near the end of the gametocytes, which is an unusual location for pigment granules in macrogametocytes of bird haemoproteids; in the hapantotype, pigment granules are clumped at the ends in 65% (95% confidence limit is 52.6–72.8) of gametocytes.

Microgametocytes (Fig. 211, *7–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; however, the nucleus of microgametocytes is relatively small (see Table 127) and compact; the size of the nucleus of microgametocytes does not exceed that of the nucleus of macrogametocytes which is a rare feature for bird haemoproteids; other characters are as for macrogametocytes.

Comments. *Haemoproteus payevskyi* can be easily distinguished from the other species of haemoproteids parasitizing the passeriform birds on the basis of several unique characters of its gametocytes. Among these characters, (i) the aggregation of pigment granules into loose clumps at the ends of gametocytes, (ii) the median position of nucleus in macrogametocytes, and (iii) compact small nucleus in microgametocytes, should be pointed out first of all.

It should be noted that the size of fully grown gametocytes varies in different avian hosts. The gametocytes, which fill the infected erythrocytes slightly up to their poles, were sometimes seen in additional vertebrate hosts. However, other diagnostic characters of this parasite are quite stable during its development in different species of birds.

It is probable that transmission of *H. payevskyi* takes place only in Africa. In the Palearctic, this parasite is common in adult birds after their arrival from the wintering ground, but has never been recorded in juvenile birds.

2. Subgenus **HAEMOPROTEUS** Kruse, 1890

Haemoproteus Kruse, 1890: 370 (pro gen.).

Type species. *Haemoproteus columbae* Kruse, 1890, according to the subsequent designation (Bennett *et al.*, 1965).

Vertebrate hosts are birds of the order Columbiformes. Sporogony takes place in hippoboscid flies (Hippoboscidae). Exflagellation does not occur at temperatures below 20°C. The diameter of fully grown oocysts is greater than 20 μm. Several germinative centres and more than 100 sporozoites develop in the oocysts. The average length of sporozoites is less than 10 μm. One end of the sporozoites is more pointed than the other.

KEY TO THE SPECIES

1(7). Fully grown gametocytes do not markedly deform infected erythrocytes. The average width of fully grown gametocytes is less than 5 μm.

2(8). Pigment granules in fully grown microgametocytes are not aggregated into large (over 1 μm in diameter) compact masses (Fig. 57, *74*).

3(9). The nucleus in macrogametocytes is median or submedian in position. Fully grown gametocytes, which do not touch the envelope of erythrocytes (Fig. 57, *75*), are absent.

4(10). Fully grown gametocytes do not displace or slightly displace the nucleus of infected erythrocytes laterally. The average NDR is greater than 0.5.

5(6). The maximum length of fully grown gametocytes is greater than 15 μm.
. . . . . 130. ***H. palumbis***

6 (5). The maximum length of fully grown gametocytes is less than 15 μm.
. . . . . 131. ***H. krylovi***

7(1). Fully grown gametocytes markedly deform infected erythrocytes. The average width of fully grown gametocytes is greater than 5 μm.
. . . . . 128. ***H. sacharovi***

8(2). Pigment granules in fully grown microgametocytes are aggregated into large (over 1 μm in diameter) compact masses (Fig. 57, *74*). The average number of pigment granules in microgametocytes is approximately half as many as in macrogametocytes.
. . . . . 127. ***H. columbae***

9(3). The nucleus in macrogametocytes is subterminal in position. Fully grown gametocytes, which do not touch the envelope of infected erythrocytes (Fig. 57, *75*), are present.
. . . . . 132. ***H. pteroclis***

10(4). Fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally. The average NDR is equal to 0.5 or less. The average number of pigment granules in macro- and microgametocytes does not differ significantly.
. . . . . 129. ***H. turtur***

127. **Haemoproteus (Haemoproteus) columbae** Kruse, 1890

Haemoproteus columbae Kruse, 1890: 370. – *Laverania danilewskyi* Grassi and Feletti, 1890b: 4 (partim, nom. praeocc., non Kruse, 1890). – *Haemoproteus maccallumi* Novy and MacNeal, 1904a: 933 (partim). – *Haemamoeba melopeliae* Laveran and Pettit, 1909: 954, Fig. 1–13 (partim). – *Haemoproteus melopeliae*: Coatney, 1936: 89 (partim). – *H. turtur* Covaleda Ortega and Gállego Berenguer, 1950: 169, Pl. 6, Fig. 1–20 (partim). – *H. columbae*: Peirce, 1976: 410 (=*Laverania danilewskyi*, partim); Bennett and Peirce, 1990b: 313 (=*H. maccallumi*, partim; *H. melopeliae*, partim; *H. turtur*, partim).

Type vertebrate host. *Columba livia* Gmelin (Columbiformes).
Additional vertebrate hosts. Numerous species of the Columbiformes (Table 128).
Vectors. *Microlynchia pusilla*, *Pseudolynchia brunnea*, *P. canariensis* (=*Lynchia capensis*, *L. lividicolor*, *L. maura*) (Diptera: Hippoboscidae).
Type locality. Naples, Italy.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic. It is especially prevalent in the tropics and subtropics. In the Holarctic, the prevalence of infection markedly decreases from the southern to the northern latitudes. This parasite was not found by the author in 116 specimens of *Columba livia* from the environs of St. Petersburg. It was not recorded in *C. livia* from England (Baker, 1975).
Type material was not designated in the original description. The neotypes should be designated. A series of additional slides is deposited in IRCAH and CDVA. The slide with sporozoites (No. 966, *Pseudolynchia canariensis*, other data are absent) is deposited in CPG.
Etymology. The specific name is derived from the generic name of the type host, *Columba.*

Table 128 List of vertebrate hosts of *Haemoproteus columbae* (modified from Garnham, 1966; Valkiūnas and Iezhova, 1990b).

Claravis pretiosa	*Gallicolumba luzonica*	*S. picturata*
Columba cayennensis	*Geotrygon montana*	*S. semitorquata*
C. eversmanni	*Macropygia nigrirostris*	*S. senegalensis*
C. fasciata	*M. phasianella*	*S. turtur*
C. flavirostris	*Oena capensis*	*S. vinacea*
C. guinea	*Phapitreron leucotis*	*Treron calva*
C. leucocephala	*Ptilinopus superbus*	*Turtur abyssinicus*
C. oenas	*P. viridis*	*T. chalcospilos*
C. rupestris	*Scardafella squammata*	*T. tympanistria*
Columbina cruziana	*Streptopelia capicola*	*Zenaida asiatica*
C. passerina	*S. chinensis*	*Z. auriculata*
C. talpacoti	*S. decaocto*	*Z. aurita*
Ducula pistrinaria	*S. decipiens*	*Z. macroura*
D. rubricera	*S. orientalis*	

Main diagnostic characters. A parasite of species of the Columbiformes whose fully grown gametocytes markedly displace the nucleus of infected erythrocytes laterally, slightly enclose the nucleus with their ends but do not encircle it completely. Infected erythrocytes are not deformed markedly. Pigment granules tend to aggregate into large compact masses which frequently exceed 1 μm in diameter in microgametocytes. The average number of pigment granules in macrogametocytes is approximately half as many as in microgametocytes. The nucleus in macrogametocytes is median or submedian in position.

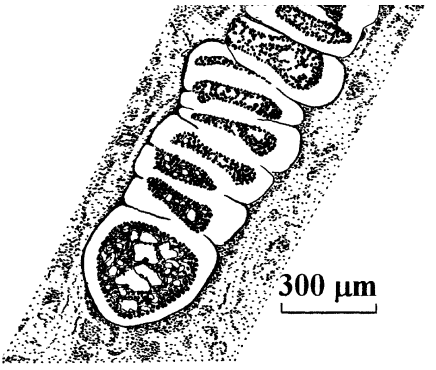

Figure 212 Multilocular megalomeront of *Haemoproteus* sp. in the skeletal muscle of *Gallicolumba luzonica* (modified from Earlé *et al*., 1993).

Development in vertebrate host

Exoerythrocytic merogony has been studied by numerous authors (Aragão, 1908; Acton and Knowles, 1914; Huff, 1942; Mohammed, 1958, 1967; Ahmed and Mohammed, 1977; Linxian *et al.*, 1989; Earlé *et al.*, 1993), but it is still insufficiently investigated. The meronts were especially frequently recorded in the lungs. In heavily infected nestlings, the meronts are sometimes seen in the liver and spleen, but they are rare.

The question about the host cells for the exoerythrocytic meronts has not been finally resolved. The most common opinion is that which came from Aragão (1908) and was supported by Wenyon (1926) and Garnham (1966). According to this view, the meronts initiate development in the endothelial cells of blood vessels. However, there are also data about the development of the meronts in mononuclear leukocytes and macrophages in the lungs (Aragão, 1908; Mohammed, 1967). In addition, the hypothesis about the development of the meronts in the endothelial cells of blood vessels was not finally confirmed by Acton and Knowles (1914), Mohammed (1967), or Ahmed and Mohammed (1977). Linxian *et al.* (1989) saw the development of oval meronts in mononuclear leukocytes in lungs of birds on the eighth day after the experimental infection. However, later (on the 14th day after infection), different stages of the development of meronts were recorded in the endothelial cells of the capillaries in the lungs.

The size of the exoerythrocytic meronts varies markedly. The largest worm-like meronts usually do not exceed 100 μm in length. Large meronts can block up the capillaries of the lung alveoles. The size of meronts is not a measure of their maturity. Growing worm-like meronts were described which were up to 60 μm long. However, some small mature meronts, which were about 20 μm long and 10 μm wide, were also seen and they were packed with completely developed merozoites.

The shape of the exoerythrocytic meronts varies markedly. Worm-like or irregular meronts, extending along the capillaries of the alveoles, are especially common (Fig. 4, *1–3*). They are frequently V-like (Fig. 4, *1*) or lobular (Fig. 4, *3*). The process of merogony can be asynchronous in different lobules of the same meront. Both roundish and oval meronts have been also described. In some roundish meronts, the nuclei are located along the periphery of the parasite (Fig. 4, *4*) as is frequently seen in meronts of *H. palumbis*. Some meronts possess small clear vacuoles (Fig. 4, *1*, *5*, *6*). The number of vacuoles is usually less than 10, and they vary from 0.5 to 2.5 μm in diameter. Cytomeres develop in meronts

(Fig. 4, *8*, *9*).† Both mature and immature meronts were not enclosed in a thick envelope, and thick-walled structures are not seen around the meronts.

Mature meronts rupture and release hundreds of merozoites which are of two types. First, the majority of mature meronts contain small (about 1 μm in diameter) roundish merozoites (Fig. 4, *6*). The size and shape of these merozoites are identical to the merozoites that invade erythrocytes. It is likely that these merozoites initiate development of gametocytes. Second, some mature meronts contain merozoites which are irregular in shape and approximately twice as large as the roundish merozoites of the first type (Fig. 4, *7*). The role of the irregular-shape merozoites in the life cycle of the parasite is unclear. It is possible that they induce the development of subsequent generations of exoerythrocytic meronts.

Megalomeronts, which are clearly different from the above described meronts, were found in two naturally infected doves *Gallicolumba luzonica* which were kept in the same aviary in South Africa and died in captivity (Earlé *et al.*, 1993). Heavy parasitemia of gametocytes, which were similar to gametocytes of *H. columbae*, was recorded in the blood of these birds. Thus, it is possible that both gametocytes and megalomeronts belong to the same species, *H. columbae*. The megalomeronts are similar to the megalomeronts of *H. mansoni* (=*H. meleagridis*) (Atkinson *et al.*, 1986; Atkinson and Forrester, 1987). They are of two types. First, the megalomeronts that are surrounded with a thin wall. They developed in the skeletal muscle, lungs, liver, kidneys, and proventriculus. Second, the megalomeronts that are surrounded with a thick wall. They developed in the skeletal muscle, heart, and gizzard. The thick-walled megalomeronts are frequently multilocular and septate (Fig. 212). The septa resembled the outer wall of the megalomeront. Large megalomeronts in the skeletal muscle exceeded 1000 μm in length and 500 μm in width. They can be seen with a naked eye and are usually located within the lumina of the blood vessels. It seems likely that the meronts initiate the development in the endothelial cells of the capillaries and, as the parasite develops, they break out of the host cells and lie loose in the lumen of the blood vessels. The rupture of megalomeronts causes necrosis of the adjacent tissues. Earlé *et al.* (1993) believe that the exoerythrocytic merogony in this bird species comprises at least two generations of meronts. One generation develops in a wide range of tissues, and the other generation develops in muscles. The discovery of megalomeronts in *Gallicolumba luzonica* is of major importance for future investigations of the life cycle of *H. columbae*. Several questions arise. First, it was not proved experimentally that gametocytes and megalomeronts found in the naturally infected birds belong to the same species of haemoproteids. This looks likely theoretically but needs to be proved. Second, if this parasite belongs to the subgenus *Haemoproteus*, it should be proved that this is *H. columbae*. Megalomeronts were formerly not seen in birds experimentally infected with *H. columbae.* Third, if the parasite is *H. columbae*, it is important to know how typical the megalomeronts are for this species. It should be noted here that megalomeronts of *Leucocytozoon simondi* do not develop in all vertebrate hosts (see p. 790).

The prepatent period varies from 22 to 38 days (on average about 30 days). The data about the shorter prepatent period (Rendtorff *et al.*, 1949) were not proved experimentally. Exoerythrocytic merogony is completed quickly, and the meronts were not seen during a long chronic period of infection. Relapses occur; this shows that the parasite persists in the infected birds. However, the stages responsible for the long persistence have not been

† After fixation of the material with Zenker-formol, numerous clefts, which are similar to cytomeres, are seen in growing meronts. This is an artefact of the fixation. These clefts are not observed in preparations fixed in Bouin's and Carnoy's fluids.

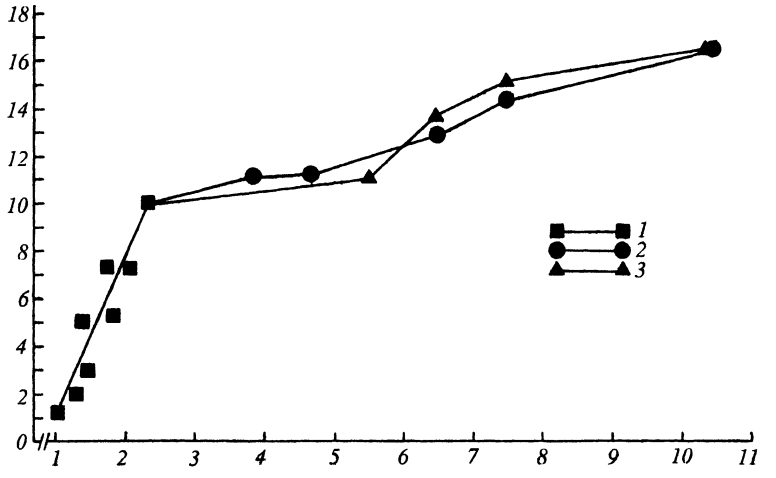

Figure 213 Growth rate of gametocytes of *Haemoproteus columbae:*
1 – young undifferentiated gametocytes; *2* – macrogametocytes; *3* – microgametocytes. Length of gametocytes is shown on the ordinate, μm; days of the parasitemia are shown on the abscissa (modified from Ahmed and Mohammed, 1978b).

investigated. The difficulties in finding these stages during the long chronic period of infection show that it may be small hypnozoite-like stages which require immunofluorescence methods for their investigation.

Mature macrogametocytes, i.e., ready for gametogenesis, appear in the blood 68 h after merozoites invade erythrocytes, and mature microgametocytes, 116 h after the merozoites invade the host cells (Ahmed and Mohammed, 1978b). At this time, the gametocytes are approximately 11 μm long (Fig. 213). The gametocytes grow until the 11th day when they reach their maximum size.

Young gametocytes. The earliest forms can be seen anywhere in infected erythrocytes, are usually oval, but sometimes irregular in shape; as the parasite develops, gametocytes take a position lateral to the nucleus of erythrocytes and extend longitudinally not touching the nucleus; growing gametocytes adhere to the envelope of erythrocytes; the outline is usually even but sometimes irregular; multiple infection of the same erythrocyte with several (up to 15) gametocytes is common during the primary parasitemia, but usually not more than two gametocytes reach maturity; multiple infection is uncommon during the relapsed parasitemia.

Macrogametocytes (Fig. 214, *1–5*; Table 129). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; valutin granules are present in some blood films; gametocytes grow along the nucleus of infected erythrocytes; they markedly displace the nucleus laterally, frequently to the erythrocyte envelope (Fig. 214, *5*), and never encircle it completely; growing gametocytes are closely appressed to the envelope of erythrocytes but do not touch the nucleus of erythrocytes; as a result, a more or less evident unfilled space (a 'cleft') is available between the parasite and the erythrocyte nucleus (Fig. 214, *1, 2, 4*); as the parasite develops, this 'cleft' disappears (Fig. 214, *3*); fully grown gametocytes are closely appressed both to the nucleus and envelope of the erythrocytes and fill the erythrocytes up to their poles (Fig. 214, *5*); the outline is even (Fig. 214, *4*) or wavy (Fig. 214, *2*, *3*, *5*); the parasite nucleus is compact, variable in form, frequently oval or

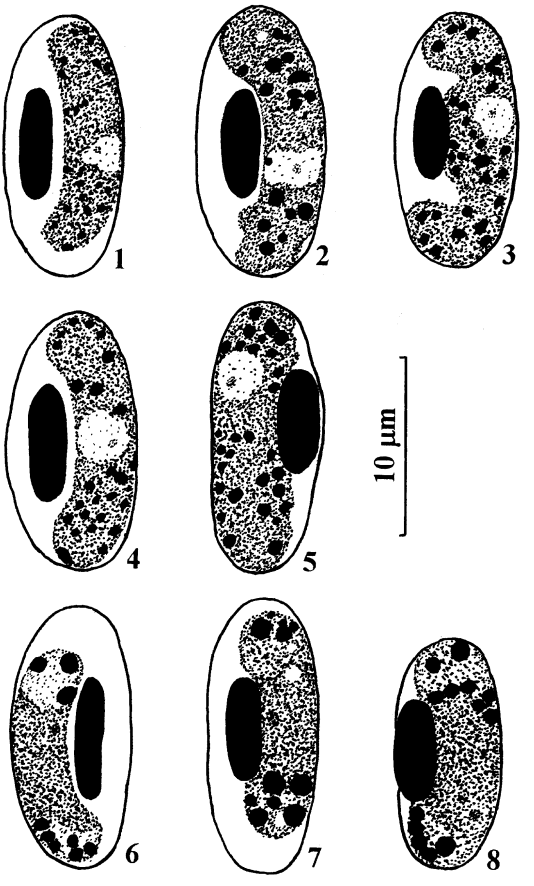

Figure 214 Gametocytes of *Haemoproteus columbae* from the blood of *Columba livia:* *1–5* – macrogametocytes; *6–8* – microgametocytes (modified from Valkiūnas and Iezhova, 1990b).

roundish, usually median or submedian in position and possesses a clump of chromatin; pigment granules are roundish, of medium (0.5 to 1.0 μm) and large (1.0 to 1.5 μm) size, frequently aggregated into large compact masses (Fig. 214, *2, 5*), randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 214, *6–8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules tend to aggregate into large (over 1 μm in diameter) compact masses and, as a result, the granules are larger and their number approximately half as many as in macrogametocytes; other characters are as for macrogametocytes.

The aggregation of pigment into large compact masses in gametocytes is a distinctive character of *H. columbae.* This aggregation takes place during the final stages of development in the blood. It has not always been recorded in naturally infected birds investigated only once (Roudabush and Coatney, 1935; Ahmed and Mohammed, 1978b; Valkiūnas and Iezhova, 1990b).

The dynamics of parasitemia, relapses, and some peculiarities of immunity were investigated by Ahmed and Mohammed (1978a) in experimentally infected *Columba livia.*

Table 129 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp.

Feature	*H. columbae* (according to Valkiūnas and Iezhova, 1990b)				*H. sacharovi* (modified from Bennett and Peirce, 1990b)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Uninfected erythrocyte	31				55		
Length		12.8–14.7	13.7	0.8		13.2	1.3
Width		6.4–7.7	7.0	0.4		7.1	0.6
Length of nucleus		6.2–7.7	6.7	0.1		5.8	0.6
Width of nucleus		2.1–2.9	2.4	0.1		2.1	0.3
Erythrocyte parasitized by macrogametocyte	31				55		
Length		13.8–16.0	15.0	0.7		16.0	0.9
Width		6.0–7.9	7.1	0.3		9.3	1.7
Length of nucleus		6.0–7.4	6.5	0.2		10.0	1.4
Width of nucleus		1.7–2.7	2.3	0.1		2.5	0.4
Erythrocyte parasitized by microgametocyte	31				14		
Length		12.9–15.9	14.4	0.8		16.2	1.0
Width		5.3–7.8	6.9	0.4		8.9	1.4
Length of nucleus		5.5–7.4	6.5	0.1		10.2	1.0
Width of nucleus		2.1–2.6	2.3	0.1		2.7	0.5
Macrogametocyte	31				55		
Length		13.4–16.7	14.8	0.9		16.0	0.9
Width		3.0–4.2	3.4	0.3		8.2	1.6
Length of nucleus		2.1–3.6	2.9	0.1		3.9	0.7
Width of nucleus		1.5–3.4	2.3	0.1		2.4	0.5
NDR		0.0–0.7	0.5	0.1		–	–
No. of pigment granules		16–36	27.8	2.6		–	–
Microgametocyte	31				14		
Length		11.6–15.5	13.3	0.6		16.2	1.0
Width		2.6–4.3	3.6	0.2		8.2	1.4
Length of nucleus		–	–	–		7.8	0.8
Width of nucleus		2.6–4.3	3.6	0.1		4.7	1.0
NDR		0.0–0.9	0.5	0.1		–	–
No. of pigment granules		5–18	10.7	1.8		–	–

Note: All sizes are given in micrometres.

The dynamics of parasitemia is shown in Fig. 215. Acute parasitemia lasts from 9 to 20 days in different hosts, and it decreases rapidly during the crisis. The level of parasitemia during the chronic period of infection usually does not exceed 1 gametocyte per 1000 erythrocytes. The duration of the chronic parasitemia varies markedly in different hosts. Chronic infection frequently turns to latent infection, and gametocytes disappear from the blood. The duration of initial parasitemia varies from 15 to 70 days in different hosts. It should be noted that the mode of bird infection (fly bite, intramuscular, intravenous, and intraperitoneal inoculation of sporozoites) influences the dynamics of the parasitemia (Fig. 215).

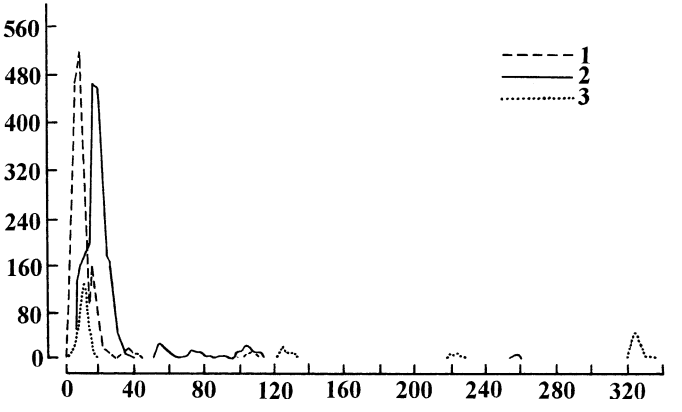

Figure 215 Dynamics of parasitemia of *Haemoproteus columbae* in experimentally infected *Columba livia* after different modes of infection:
1, *2* – intramuscular inoculation of sporozoites; *3* – fly bite. The intensity of parasitemia (number of gametocytes per 1000 erythrocytes) is shown on the ordinate, days of the parasitemia are shown on the abscissa (modified from Ahmed and Mohammed, 1978a).

A significant fluctuation of the number of gametocytes in the blood of birds during the 24-hour period was not recorded. It is likely that this is an adaptation to the mode of life of the vectors. Hippoboscid flies spend a great part of the day on birds and thus they can take a blood meal at any time.

During chronic infection, birds acquired immunity (premunition), whereas birds which had recovered from previous infections were susceptible to reinfection.

Relapses do not depend on the mode of infection of experimental birds. There is no periodicity of relapse occurrence, nor any correlation between the frequency of relapses and the intensity of the initial infection. In the Egyptian strain, the relapses were not influenced by seasonal changes. The mechanism of relapses has not been investigated in detail.

Development in vector has been studied by numerous authors (Sergent and Sergent, 1906; Aragão, 1908; Adie, 1915; Wenyon, 1926; Huff, 1932b; Coatney, 1933; Mohammed, 1958; Baker, 1968; Linxian *et al.*, 1989). Gametogenesis is especially quickly initiated at a temperature close to the temperature of the birds' body. The exflagellation was

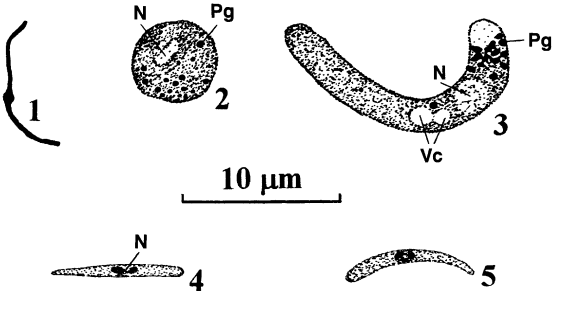

Figure 216 *Haemoproteus columbae:*
1 – microgamete; *2* – macrogamete; *3* – ookinete; *4*, *5* – sporozoites; N – nucleus; Pg – pigment granule; Vc – 'vacuole' (*1–3* are modified from Mohammed, 1958).

recorded *in vitro* at 28°C approximately 7 min after exposure of the blood with mature gametocytes to air (EBA), and it was seen 2.5 min after EBA at 32 to 35°C. Microgametes are elongated bodies typical of haemosporidian parasites (Fig. 216, *1*). Zygotes lack large vacuoles (Fig. 216, *2*). Ookinetes are elongated worm-like bodies. They possess pigment granules and large 'vacuoles' (Fig. 216, *3*). Fully grown ookinetes are up to 23 to 25 μm long. The initial stages of the development of oocysts were recorded on the fourth day after ingestion of gametocytes by the vector. Several germinative centres develop in each oocyst. Sporozoites germinate in these centres. Fully grown oocysts are about 35 to 40 μm in diameter or even larger. Several hundreds of sporozoites develop in each oocyst. The sporozoites are elongated bodies with one end more pointed than the other (Fig. 216, *4*, *5*). They usually vary from 6.0 to 11.0 (most frequently 8) μm in length and about 1 μm in width. The average length of sporozoites does not exceed 10 μm.

When *Pseudolynchia canariensis* is kept on infected birds, sporogony is completed within nine to ten days. This hippoboscid fly is slightly susceptible to the infection. However, according to current knowledge, it is the main vector of *H. columbae* among the vectors which have been recorded so far. The sporozoites were found in approximately 10% of the flies which ingested mature gametocytes. The sporozoites do not develop in *Ornithomyia avicularia* but oocysts were seen (Mohammed, 1958; Baker, 1968). The oocysts and sporozoites developed in *Columbicola columbae*, however it was not proved that they belong to *H. columbae* (Linxian *et al.*, 1989).

P a t h o g e n i c i t y has been insufficiently investigated. Over 50% of erythrocytes are frequently parasitized at the height of parasitemia, and a marked enlargement of the liver and spleen was recorded. Garnham (1966) believed that the parasite should be pathogenic for birds. However, the clinical signs of illness do not always occur even during heavy infections (Ahmed and Mohammed, 1978a). The signs of illness (refusal of food, lethargy, anaemia) have rarely been recorded (Coatney, 1933; Levine, 1961; Markus and Oosthuizen, 1972). It should be noted that there are data that the parasite can cause the death of infected doves in South Africa (Earlé *et al.*, 1993), and this should be tested experimentally (see p. 569).

S p e c i f i c i t y has been insufficiently investigated. It was proved experimentally that *H. columbae* does not complete its development in *Columba palumbus* (Baker, 1966a). It is unknown at what stage the development interrupts in this bird. The information that the parasite does not complete development in *Zenaida macroura* should be tested because it is based on a single experimental observation (Coatney, 1933). *Haemoproteus columbae* was successfully transmitted experimentally to *Streptopelia senegalensis* and *S. turtur* (Rashdan, 1998a). Investigations of J.R. Baker (summarized in Baker, 1975) provide the basis for thinking that the range of vertebrate hosts of *H. columbae* is not as wide as recorded in the literature (see Bennett and Peirce, 1990b). That is why the list of vertebrate hosts of this parasite (Table 128) should be used with caution.

C o m m e n t s. Celli and Sanfelice (1891) were the first to publish a detailed description of gametocytes of *H. columbae.* However, they are not the authors of the specific name *H. columbae* as was thought by numerous early investigators.

Bennett and Peirce (1990b) published a combined redescription of *H. columbae*. Under this name, they united all species of haemoproteids of birds belonging to the Columbidae, except *H. sacharovi*. As a result, the range of morphological characters of *H. columbae* increased. The objections on the synonymy of *H. palumbis* and *H. turtur* (partim) with *H. columbae* are summarized in 'Comments' to these species. It should only be noted that Bennett and Peirce (1990b) consider the large compact masses of a substance in cytoplasm of gametocytes (Fig. 214) as valutin granules but

not pigment granules. If one accepts this view, it should be also accepted that true pigment granules are absent in gametocytes because they were never seen in the gametocytes with 'the compact masses of the substance.' This is especially evident for microgametocytes. The author of this book thinks that these 'compact masses' are the aggregation of pigment, and it is conceivable that the valutin may also be a part of these masses. However, it is unlikely that these 'compact masses' completely conceal the true pigment. Further investigations are required to solve this question.

During the identification of *H. columbae* attention should be paid, first of all, to (i) the aggregation of pigment granules into large compact masses in fully grown gametocytes (especially in microgametocytes), and (ii) the clear differences in the number of pigment granules in macro- and microgametocytes. These features are not characteristic of *H. turtur* which is especially close to *H. columbae*.

Haemoproteus piresi was described from the blood of *Columba livia* on the basis of material in which gametocytes are rounded up due to the onset of gametogenesis (Son, 1960). Based on the original description, the species identification can be only speculative. *Haemoproteus piresi* is considered to be a *nomen dubium.* It should be noted that Bennett and Peirce (1990b) declared *H. piresi* to be a synonym of *H. columbae*.

128. **Haemoproteus (Haemoproteus) sacharovi** Novy and MacNeal, 1904

Haemoproteus sacharovi Novy and MacNeal, 1904a: 933. – *H. maccallumi* Novy and MacNeal, 1904a: 933 (partim). – *Haemamoeba melopeliae* Laveran and Pettit, 1909: 954, Fig. 1–13 (partim). – *Haemoproteus melopeliae*: Coatney, 1936: 89 (partim). – *H. sacharovi*: Bennett and Peirce, 1990b: 313 (=*H. maccallumi,* partim; *H. melopeliae,* partim).

Type vertebrate host. *Zenaida macroura* (L.) (Columbiformes).
Additional vertebrate hosts. Some species of the Columbiformes (Table 130).
Vector. *Pseudolynchia canariensis* (=*P. maura*) (Diptera: Hippoboscidae).
Type locality. Michigan, USA.
Distribution. The Nearctic and the Neotropical, Ethiopian and Oriental zoogeographical regions, Southern Palearctic. This parasite is common in tropics and subtropics. No records from Australia so far.
Type material. Neohapantotype (No. 45236A, *Zenaida macroura*, 11.08.1938, Peru, Nebraska, USA, G.R. Coatney) and paraneohapantotypes (No. 45236B, 12.08.1938, other data are as for the neohapantotype; No. 103700, August 1970, Lincoln, Nebraska, E.C. Greiner, other data are as for the neohapantotype) are deposited in IRCAH.
Etymology. This species is named in honour of Dr. N.A. Sakharoff in recognition of his contribution to the field of avian blood parasitology.

Table 130 List of vertebrate hosts of *Haemoproteus sacharovi* (according to Bennett and Peirce, 1990b).

Columba fasciata	*Macropygia phasianella*
C. guinea	*Streptopelia chinensis*
C. livia	*S. senegalensis*
Columbina passerina	*Treron vernans*
C. talpacoti	*Zenaida asiatica*

Main diagnostic characters. A parasite of species of the Columbiformes whose fully grown gametocytes are highly pleomorphic, they are outwardly similar to gametocytes

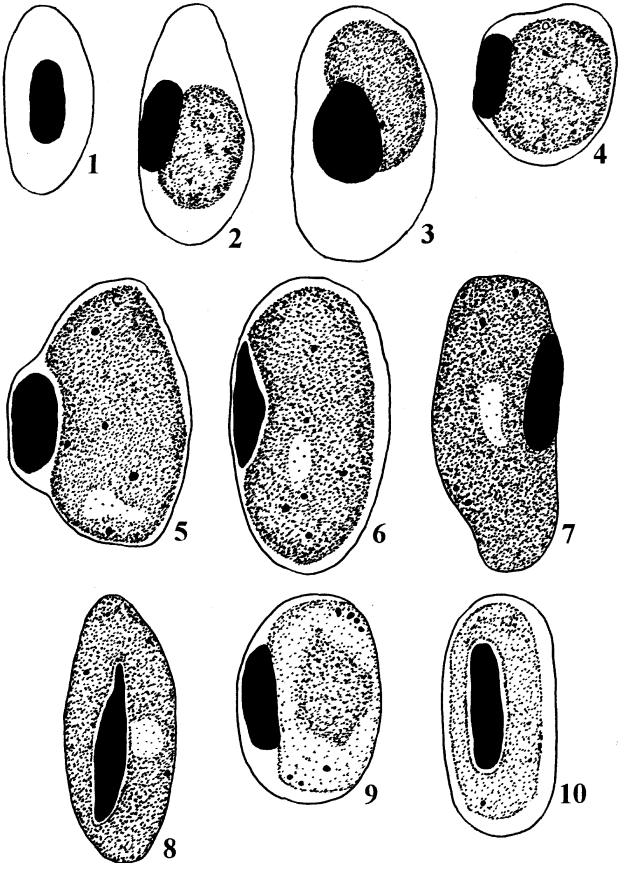

Figure 217 *Haemoproteus sacharovi* from the blood of *Zenaida macroura:*
1 – uninfected erythrocyte; *2*, *3* – young gametocytes; *4–8* – macrogametocytes; *9*, *10* – microgametocytes (*1–7*, *9* are modified from Huff, 1932b; *8*, *10* are modified from Coatney and Roudabush, 1937).

of *Leucocytozoon* spp. and cause marked deformation of infected erythrocytes. The average width of fully grown gametocytes is greater than 5 μm.

Development in vertebrate host

Exoerythrocytic merogony has not been investigated. In naturally infected *Zenaida macroura*, the exoerythrocytic meronts were not found in the liver, lungs, kidney, spleen, heart, or brain. However, oval and roundish thick-walled megalomeronts were revealed in the gizzard (Farmer, 1964). The exact dimensions of the megalomeronts were not given in the original description, but they are large and can be seen with a naked eye on the surface of the gizzard. It is likely that these megalomeronts belong to *H. sacharovi*, but this should be tested.

Young gametocytes (Fig. 217, *2*, *3*). The earliest forms can be seen anywhere in infected erythrocytes, but more frequently take a lateral position to the nucleus of infected erythrocytes; are roundish, oval, or irregular; the outline is even; growing gametocytes deform erythrocytes and markedly displace their nuclei laterally.

Macrogametocytes (Fig. 217, *4–8*; Table 129). The cytoplasm is finely granular in appearance, contains small valutin granules which obscure the pigment granules; gametocytes are highly pleomorphic; they markedly displace the nucleus of infected erythrocytes laterally, frequently to the periphery of the host cells, and usually occupy all available cytoplasmic space in erythrocytes (Fig. 217, 5–7); sometimes gametocytes encircle the nucleus of erythrocytes completely (Fig. 217, *8*) or even enucleate the host cells; fully grown gametocytes are outwardly similar to gametocytes of *Leucocytozoon* spp.; the outline is even; the parasite nucleus is variable in form and position, the nucleolus usually well defined; pigment granules are of small (<0.5 μm) size, dust-like, randomly scattered throughout the cytoplasm, markedly obscured by valutin granules and difficult to count; the maximum number of the pigment granules does not exceed 12, but is usually less; the average number of the pigment granules does not exceed 10; infected erythrocytes are markedly deformed in comparison to uninfected ones, and are markedly hypertrophied in length and (or) width; the nucleus of infected erythrocytes is also markedly hypertrophied in length (Table 129).

Microgametocytes (Fig. 217, *9*, *10*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has not been investigated in detail. Infectious sporozoites develop in the hippoboscid fly *Pseudolynchia canariensis* (=*P. maura*). The duration of sporogony is not more than eight days (Huff, 1932b).

Pathogenicity is insufficiently investigated. Clinical signs of illness are usually not seen in naturally infected birds. The liver is enlarged. The spleen is also enlarged, swollen, fragile, and dense purplish-black in colour (Becker *et al.*, 1956; Farmer, 1964).

Specificity. By fly bite, this parasite was transmitted from *Zenaida macroura* to *Columba livia* (Huff, 1932b).

Comments. *Haemoproteus sacharovi* is a unique species among bird haemoproteids. Gametocytes of this parasite are outwardly similar to gametocytes of *Leucocytozoon* spp., and can even be confused with leucocytozoids. This character of the species was noted in the brief original description (Novy and MacNeal, 1904a). It should be noted that the average width of fully grown gametocytes is approximately twice as large as in all other species of bird haemoproteids. Species identification is not difficult.

129. **Haemoproteus (Haemoproteus) turtur** Covaleda Ortega and Gállego Berenguer, 1950

Haemoproteus turtur Covaleda Ortega and Gállego Berenguer, 1950: 169, Pl. 6, Fig. 1–20 (partim).

Type vertebrate host. *Streptopelia turtur* (L.) (Columbiformes).
Additional vertebrate hosts. *Columba livia, Streptopelia orientalis, S. senegalensis* (Columbiformes).
Vector. *Pseudolynchia canariensis* (Diptera: Hippoboscidae) (Rashdan, 1998b).
Type locality. Granada, Spain.
Distribution. This parasite has only been recorded in the Palearctic.
Type material was not designated in the original description. The designation of neotypes is required. A series of additional slides is deposited in CDVA.

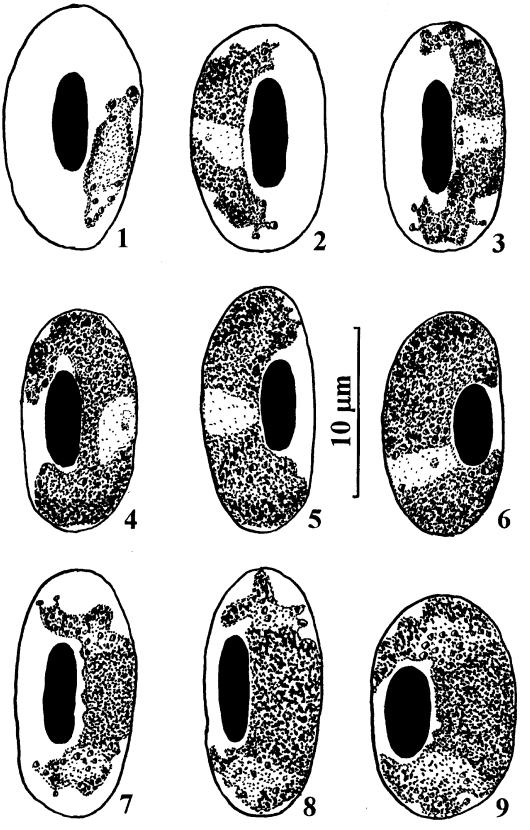

Figure 218 Gametocytes of *Haemoproteus turtur* from the blood of *Streptopelia turtur:* *1* – young; *2–6* – macrogametocytes; *7–9* – microgametocytes (modified from Valkiūnas and Iezhova, 1990b).

Etymology. The specific name is derived from the specific name of the type host, *turtur*.

Main diagnostic characters. A parasite of species of the Columbiformes whose fully grown gametocytes usually do not touch the nucleus of infected erythrocytes; they grow around the nucleus and markedly displace it laterally. Pigment granules are of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size. The average number of pigment granules in macro- and microgametocytes does not differ significantly. The average width of fully grown gametocytes is less than 5 μm. Nucleus in macrogametocytes is median or submedian in position. Infected erythrocytes are not deformed markedly in comparison to uninfected ones.

Development in vertebrate host

Young gametocytes (Fig. 218, *1*). The earliest forms can be seen anywhere in infected erythrocytes, are markedly variable in shape; valutin granules usually present; as the parasite develops, gametocytes extend along the nucleus of erythrocytes, do not touch the nucleus but usually adhere to the envelope of erythrocytes; the outline is usually ameboid or irregular (Fig. 218, *1*).

Table 131 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. (according to Valkiūnas and Iezhova, 1990b) ($n = 31$).

Feature	*H. turtur*			*H. palumbis*		
	lim	$\overline{X}$	*SD*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte						
Length	12.0–14.8	13.2	0.6	11.2–13.8	12.4	0.6
Width	5.4–7.7	6.9	0.4	7.1–8.6	8.1	0.3
Length of nucleus	5.6–7.0	6.4	0.2	5.0–7.4	6.4	0.2
Width of nucleus	1.8–2.8	2.4	0.2	2.2–3.0	2.6	0.1
Erythrocyte parasitized by macrogametocyte						
Length	12.7–14.8	13.8	0.6	13.4–16.3	14.7	0.8
Width	5.6–7.8	6.5	0.4	6.9–8.9	8.0	0.4
Length of nucleus	4.9–6.7	5.8	0.2	4.8–7.1	5.9	0.2
Width of nucleus	1.8–2.6	2.2	0.2	2.0–2.9	2.5	0.1
Erythrocyte parasitized by microgametocyte						
Length	11.8–15.4	13.9	0.8	12.8–16.3	15.0	0.8
Width	6.2–7.7	7.0	0.4	7.0–8.6	8.0	0.2
Length of nucleus	5.2–6.7	5.8	0.2	4.8–7.3	6.1	0.1
Width of nucleus	1.8–2.7	2.3	0.2	2.0–2.9	2.5	0.1
Macrogametocyte						
Length	12.1–21.1	15.7	1.4	14.6–18.7	16.6	0.7
Width	3.0–4.2	3.7	0.4	2.8–4.0	3.2	0.2
Length of nucleus	2.6–3.8	3.2	0.2	2.6–4.0	3.2	0.2
Width of nucleus	2.2–3.7	2.7	0.1	1.7–3.5	2.7	0.1
NDR	0.0–0.8	0.3	0.2	0.6–1.0	0.8	0.1
No. of pigment granules	15–29	19.9	2.5	15–38	21.3	2.0
Microgametocyte						
Length	13.8–22.8	17.9	1.2	14.8–19.8	16.9	0.6
Width	3.1–4.2	3.6	0.2	2.7–3.8	3.3	0.1
Width of nucleus	3.1–4.2	3.6	0.2	2.7–3.8	3.3	0.1
NDR	0.0–0.8	0.5	0.1	0.7–1.0	0.9	0.1
No. of pigment granules	11–30	21.0	1.9	12–20	14.3	1.4

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 218, *2–6*; Table 131). The cytoplasm is granular in appearance, contains numerous small valutin granules which usually gather along the periphery of gametocytes; the valutin granules are similar to pigment granules in size and shape and markedly obscure the pigment granules; gametocytes grow around the nucleus of infected erythrocytes, markedly displace the nucleus laterally and enclose it with their ends but do not encircle the nucleus completely; gametocytes are closely appressed to the envelope of erythrocytes but usually do not touch the nucleus of erythrocytes and, as a result, a more or less evident unfilled space (a 'cleft') frequently occurs between the parasite and the nucleus of erythrocytes (Fig. 218, *2–6*); in fully grown gametocytes, this 'cleft' is less evident

(Fig. 218, *5, 6*) than in growing forms (Fig. 218, *2*); the outline is usually highly ameboid in growing gametocytes (Fig. 218, *2*, *3*); fully grown gametocytes lose the highly ameboid outline, and their outline varies from slightly ameboid to even (Fig. 218, *4–6*); the parasite nucleus is compact, variable in shape, median or submedian in position; pigment granules are roundish, usually of small (<0.5 μm) but sometimes also medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 218, *7–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the outline is even more ameboid than for macrogametocytes; other characters are as for macrogametocytes.

C o m m e n t s. Among the haemoproteids of birds belonging to the Columbiformes, *H. turtur* is especially similar to *H. columbae* and *H. palumbis*. Growing gametocytes of these species are especially similar, but they can be distinguished on the basis of fully grown gametocytes. Morphologically, gametocytes of *H. turtur* take an intermediate position between *H. columbae* and *H. palumbis*. Gametocytes of *H. turtur* markedly displace the nucleus of infected erythrocytes laterally (a character of *H. columbae*) and they are highly ameboid in outline and possess small (<0.5 μm) or medium (0.5 to 1.0 μm) size pigment granules (characters of *H. palumbis*). The characters mentioned are important to differentiate *H. columbae*, *H. palumbis*, and *H. turtur*, but they were not pointed out in the original descriptions (Kruse, 1890; Covaleda Ortega and Gállego Berenguer, 1950; Baker, 1966b). These characteristics should be added to the species definitions.

The analysis of the original description (Covaleda Ortega and Gállego Berenguer, 1950) shows that two species of haemoproteids were described under the name *H. turtur*, i.e., *H. columbae* and *H. turtur*. According to the author's opinion, gametocytes with large aggregations of pigment should be attributed to *H. columbae*, and gametocytes lacking the large aggregations of pigment, to *H. turtur*. To reach this conclusion, the author investigated a large collection which contains numerous blood films with a pure infection of *H. turtur*. Fully grown gametocytes of *H. turtur* can be distinguished from *H. columbae*. Bennett and Peirce (1990b) declared *H. turtur* to be a synonym of *H. columbae*, and, in the redescription of *H. columbae*, they combined the characters of all the species of haemoproteids (except *H. sacharovi*) which have been described in columbid birds so far (see also 'Comments' to *H. columbae*). However, the collection material which the author has investigated does not conform to this hypothesis. *Haemoproteus turtur* (a common parasite of *Streptopelia orientalis* and *S. turtur* in the author's collection) can be distinguished from *H. columbae* (a common parasite of *Columba livia*) primarily on the basis of (i) the approximately equal number of pigment granules in its macro- and microgametocytes, and (ii) the lack of large aggregations of pigment granules in its gametocytes. Based on our observations and the other evidence presented above, *H. turtur* is considered as a distinct species. However, it should be noted that there are numerous similarities between gametocytes of *H. turtur* and *H. columbae*, and there is no information about the geographical or host-dependent variation of the morphology of these parasites. Further studies are required to solve the question on the validity of *H. turtur.* It is important to note that attempts to transmit *H. turtur* to *C. livia* were unsuccessful (Rashdan, 1998b).

Numerous records of *H. turtur* in the columbiform birds are available in the literature. However, most of them concern *H. columbae* recorded under the name *H. turtur*. The range of vertebrate hosts of *H. turtur* has not been investigated. That is why only the birds, in which gametocytes clearly fitting for the description of *H. turtur* were recorded, are included in the list of vertebrate hosts of this parasite.

130. **Haemoproteus (Haemoproteus) palumbis** Baker, 1966

Haemoproteus palumbis Baker, 1966b: 518, Fig. 1–9.

Type vertebrate host. *Columba palumbus* L. (Columbiformes).
Vectors. *Ornithomyia avicularia*, *Pseudolynchia canariensis* (Diptera: Hippoboscidae).
Type locality. South-eastern Britain.
Distribution. The Palearctic (within the range of *Columba palumbus*).
Type material. Hapantotypes (*exoerythrocytic meronts*: No. 974, *Columba palumbus*, lungs, South-eastern Britain, J.R. Baker; *blood stages*: No. 969, 970, other data are as for No. 974; *oocysts* and *sporozoites*: No. 971-973, *Ornithomyia avicularia*, other data are as for No. 974) are deposited in CPG.
Etymology. The specific name is derived from the Latin feminine noun *palumbes*, meaning wood-pigeon.

Main diagnostic characters. A parasite of species of the Columbiformes whose fully grown gametocytes are closely appressed to the nucleus and envelope of infected erythrocytes; they enclose the nucleus of erythrocytes with their ends but do not encircle it completely and do not displace or only slightly displace the nucleus laterally. Pigment

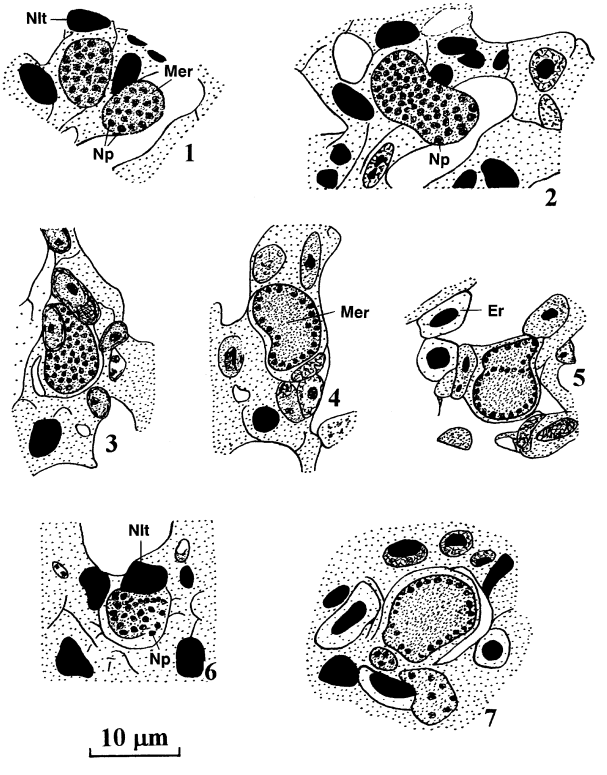

Figure 219 Exoerythrocytic meronts (*1–7*) of *Haemoproteus palumbis* from the lungs of *Columba palumbus:*
Er – erythrocyte; Mer – meront; Nlt – nucleus of cell of the lung tissue; Np – nucleus of parasite (modified from Baker, 1966b). Explanations are given in the text.

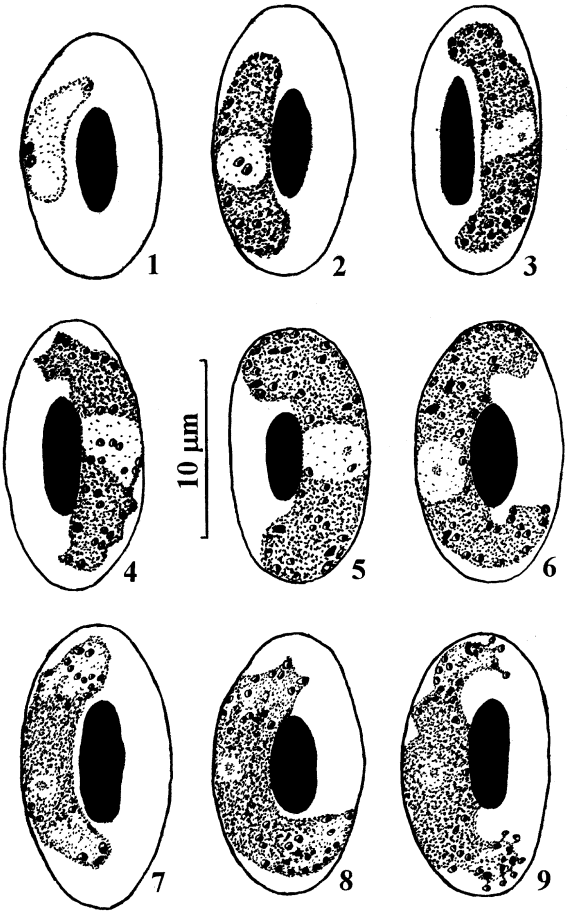

Figure 220 Gametocytes of *Haemoproteus palumbis* from the blood of *Columba palumbus:* *1* – young; *2–6* – macrogametocytes; *7–9* – microgametocytes (modified from Valkiūnas and Iezhova, 1990b).

granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size. The maximum length of fully grown gametocytes is greater than 15 μm. The average width of fully grown gametocytes is less than 5 μm. The nucleus in macrogametocytes is median or submedian in position. Infected erythrocytes are not deformed markedly in comparison to uninfected ones.

Development in vertebrate host

Exoerythrocytic merogony was studied by Baker (1966b) in naturally infected nestlings of *Columba palumbus*. The meronts are seen in the lungs and heart. They were not found in the spleen, kidney, liver, brain, or bone marrow. The meronts appeared to be inside the endothelial cells. In the histological sections, they are oval in shape (Fig. 219). Elongated worm-like meronts, which are common in *H. columbae*, were not recorded for *H. palumbis*. The meronts are about 14 μm long and 7 μm wide. The nuclei are located along the periphery in some meronts (Fig. 219, *4*, *5*, *7*). The prepatent period is about 14 days after infection with sporozoites.

Young gametocytes (Fig. 220, *1*). The earliest forms can be seen anywhere in infected erythrocytes, are variable in shape; the outline varies from even to ameboid; growing gametocytes frequently take a subpolar position in erythrocytes; advanced gametocytes adhere to the envelope of erythrocytes and extend longitudinally along the nucleus of erythrocytes not touching the nucleus (Fig. 220, *1*).

Macrogametocytes (Fig. 220, *2–6*; Table 131). The cytoplasm is homogeneous in appearance, usually contains valutin granules; gametocytes grow around the nucleus of infected erythrocytes, they enclose the nucleus with their ends and slightly (if at all) displace it laterally but do not encircle the nucleus completely; growing gametocytes touch the envelope of erythrocytes but do not touch the nucleus of erythrocytes and, as a result, a clear more or less evident unfilled space (a 'cleft') is available between the growing parasite and the nucleus of erythrocytes (Fig. 220, *2, 3*); as the parasite develops, this 'cleft' disappears, and fully grown gametocytes are closely appressed to the nucleus and envelope of erythrocytes (Fig. 220, *4–6*) and they fill the erythrocytes up to their poles (Fig. 220, *5*); the outline is usually even (Fig. 220, *5*) or slightly wavy (Fig. 220, *6*), but sometimes also slightly ameboid or irregular (Fig. 220, *4*); the parasite nucleus is compact, variable in form, median or submedian in position, possesses a compact clump of chromatin (Fig. 220, *6*); pigment granules are roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 220, *7–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; an ameboid outline is more evident (Fig. 220, *9*) and more often seen than in macrogametocytes; other characters are as for macrogametocytes.

Macrogametocytes reach their maximum size on the sixth day of parasitemia, and microgametocytes, on the fifth day. The parasite can persist in infected birds at least two years (Baker, 1963).

Development in vector was studied by Baker (1957, 1963, 1966a, 1966b). For successful exflagellation, a relatively high temperature is required. Eflagellation is not initiated at 21 or 22°C. The exflagellation was seen 10 to 12 min after exposure of the blood with mature gametocytes to air (EBA) at 23 to 28°C, 3.5 to 5 min after EBA at 30°C, and 3 min after EBA and even earlier at 32 to 37°C. It is likely that a temperature close to the temperature of bird's body is optimal for the development of gametes. This should be regarded as an adaptation of the parasite to the mode of life of the vectors (hippoboscid flies) which spend a great part of their life on birds. The peculiarities of gametogenesis and the development of zygote and ookinete are not investigated in detail. *In vitro* at 35°C, fully differentiated ookinetes were seen 3.5 h after EBA (Fig. 9, *1–3*). The ookinetes possess large 'vacuoles' and pigment granules which gather at the distal end of the parasite. However, the pigment granules were seen not in all ookinetes. The ookinetes vary from 15 to 16 μm in length, and from 2 to 3 μm in width. The oocysts are large and can be easily seen on the surface of the isolated midgut. Pigment granules are frequently recorded in the oocysts. Several germinative centres appear in the developing oocysts, and sporozoites germinate in these centres. Mature oocysts vary from 32 to 75 (on average 36) μm in diameter. Sporozoites look like elongated bodies with one end pointed more than the other (Fig. 9, *4–10*). They vary ($n = 20$) from 6 to 11 (on average 8.7) μm in length, and from 0.8 to 1.0 (on average 0.8) μm in width. Sporogony is completed within 6.5 to 7 days at a temperature close to the temperature of bird's body (35 to 40°C). The hippoboscid fly *Ornithomyia avicularia* can be easily infected. Infectious sporozoites developed in approximately 90% of the experimentally infected flies. *Pseudolynchia canariensis* is much less susceptible.

Specificity. The available experimental data (see Baker, 1975) shows that *H. palumbis* is a highly specific species that does not complete development in *Columba livia*.

Comments. The comparison of the morphology of *H. palumbis* and *H. columbae* based on a series of good blood films from the type vertebrate hosts (Valkiūnas and Iezhova, 1990b) as well as the investigation of the type material showed that gametocytes of these species can be distinguished from each other. *Haemoproteus palumbis* can be distinguished from *H. columbae* primarily on the basis of (i) peculiarities of the influence of its fully grown gametocytes on the nucleus of infected erythrocytes, (ii) the outline of the microgametocytes, and (iii) the absence of large aggregations of pigment granules in gametocytes. It should be mentioned that Baker (1966b) also noted some differences in the morphology of gametocytes of these species. He showed that gametocytes of *H. palumbis* are longer and more narrow than gametocytes of *H. columbae*. This was confirmed by Valkiūnas and Iezhova (1990b) on the basis of the investigation of a large collection material. These characters were not previously considered to be important diagnostic features of *H. palumbis*. It should be noted that the conclusion on the differences in morphology of gametocytes of *H. palumbis* and *H. columbae* is of theoretical significance. On the one hand, it strengthens the diagnostic status of the morphological characters during the identification of haemoproteid species and, on the other hand, it shows that the commonly held opinion about the identical morphology of gametocytes of these species is not correct. From this point of view, the unsuccessful experimental transmission of *H. palumbis* to *Columba livia* and *H. columbae* to *C. palumbus* (see Baker, 1975) supports the morphological data. The morphological characters of gametocytes and their host cells can be used to identify species of haemoproteids parasitizing the relative bird species. A detailed analysis of a set of characters is required for this work.

Bennett and Peirce (1990b) declared *H. palumbis* to be a junior synonym of *H. columbae*. They doubted the experimental data (Baker, 1966b) about the absence of transmission of *H. palumbis* to *Columba livia*. These authors believed that the flies *Ornithomyia avicularia* did not feed on the *C. livia* and hence, in J.R. Baker's experiments, the transmission did not occur due to distinct host preferences of the hippoboscid flies. Putting off the interesting and poorly investigated problem about the host specificity of the vectors of bird haemosporidian parasites, it should be noted that Baker (1966a) infected birds by the syringe inoculation of sporozoites. During this experiment, *C. palumbus* was successfully infected with *H. palumbis*, but *C. livia* was not. In this case, the vector feeding preferences cannot influence the results of the experiment. Baker (1966a, 1966b) proved that haemoproteids of *C. palumbus* do not develop in *C. livia*, and vice versa. In addition, *H. palumbis* can be distinguished from *H. columbae* on the basis of its more rapid sporogony (7 days compared with 10) and shorter prepatent period (two weeks compared with three). Thus, based on our observations and other evidence presented above, *H. palumbis* is considered to be a distinct species.

Haemoproteus palumbis is a common parasite of *C. palumbus*. The prevalence of infection of young birds exceeds 50% (95% confidence limit is 44.8–64.1) in England during the warm period of the year. It is interesting to note that *H. columbae* was not recorded in *C. livia* in England (Baker, 1975), and this also supports the validity of *H. palumbis*. Up to 100% of adult *C. palumbus* were found by the author to be infected with this parasite in South Kazakhstan.

131. **Haemoproteus (Haemoproteus) krylovi** Subkhonov, 1980

Haemoproteus krylovi Subkhonov, 1980: 46, Fig. 2A.

Type vertebrate host. *Pterocles orientalis* (L.) (Columbiformes).
Type locality. The Vakshskaya Valley, Tadzhikistan.

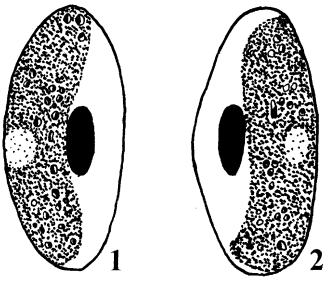

Figure 221 Macrogametocytes of *Haemoproteus krylovi* from the blood of *Pterocles orientalis* (modified from Valkiūnas and Iezhova, 1990b).

Distribution. This parasite has so far been recorded only in the type locality.
Type material does not exist.
Etymology. This species is named in honour of Professor Mstislav V. Krylov, St. Petersburg, Russia, in recognition of his contribution to the field of blood parasites of vertebrates.

Main diagnostic characters. A parasite of species of the Columbiformes whose gametocytes are even in outline, they adhere to the envelope of infected erythrocytes, slightly displace the nucleus of erythrocytes laterally but do not encircle it completely. The nucleus of macrogametocytes is median in position. Pigment granules are not aggregated into large compact masses. The maximum length of fully grown gametocytes is less than 15 μm. The average width of fully grown gametocytes is less than 5 μm. Infected erythrocytes are not deformed markedly in comparison to uninfected ones.

Development in vertebrate host
Macrogametocytes (Fig. 221, *1*, *2*). The cytoplasm stains pale-blue; valutin granules have not been not recorded; gametocytes extend along the nucleus of infected erythrocytes, they slightly displace the nucleus laterally and take a bean-like shape (Fig. 221, *1*, *2*); gametocytes are closely appressed to the envelope of erythrocytes and they slightly touch the erythrocyte nucleus (Fig. 221, *1*, *2*); the outline is even; the parasite nucleus is roundish in form and median in position; pigment granules are not aggregated into large compact masses, they are randomly scattered throughout the cytoplasm, vary from 20 to 25 in number; gametocytes vary from 10.0 to 10.3 μm in length and from 2.4 to 2.6 μm in width.

Microgametocytes were not described in the original description.

Comments. The original description of *H. krylovi* is incomplete and the type material is lost. The information on this species is solely based on the original description. The redescription of this parasite and designation of neotype material are required. *Haemoproteus krylovi* is especially close to *H. pteroclis*. The latter species was described from *Pterocles alchata* in Northern Iraq. According to the original description (Shamsuddin and Mohammad, 1980), gametocytes of *H. pteroclis* do not touch the envelope of erythrocytes, and the nucleus in its macrogametocytes is subterminal in position. These features are not characteristic of *H. krylovi*. However, it should be noted once again, that the original descriptions of both parasites are incomplete, and thus the validity of *H. krylovi* and *H. pteroclis* is unclear. New material from the type hosts is required to solve this question.

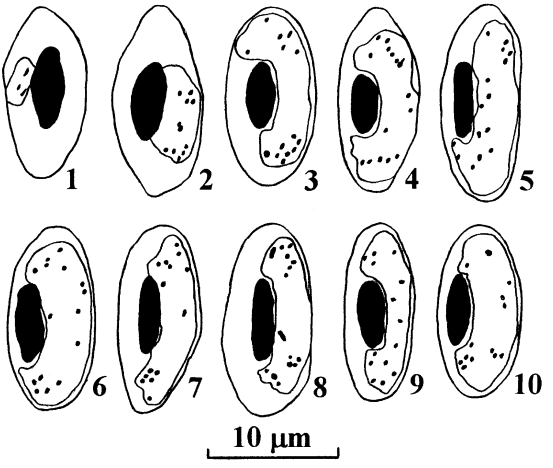

Figure 222 Gametocytes of *Haemoproteus pteroclis* from the blood of *Pterocles alchata:* *1*, *2* – young; *3–6* – macrogametocytes; *7–10* – microgametocytes (modified from Shamsuddin and Mohammad, 1980).

132. **Haemoproteus (Haemoproteus) pteroclis** Shamsuddin and Mohammad, 1980

Haemoproteus pteroclis Shamsuddin and Mohammad, 1980: 124, Fig. 5–16, 53–56, Table 3.

Type vertebrate host. *Pterocles alchata* (L.) (Columbiformes).
Type locality. Sinjar, Northern Iraq.
Distribution. This parasite has been recorded only in the type locality.
Type material. Hapantotype (No. is unknown, *Pterocles alchata*, 12.06.1978, Sinjar, Northern Iraq) is deposited in NHRCB.
Etymology. The specific name is derived from the generic name of the type host, *Pterocles*.

Main diagnostic characters. A parasite of species of the Columbiformes whose gametocytes are wavy or ameboid in outline, slightly enclose the nucleus of infected erythrocytes with their ends and displace the nucleus laterally. Fully grown gametocytes, which do not touch the envelope of erythrocytes, are present. The nucleus in macrogametocytes is subterminal in position. Pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size. The average width of fully grown gametocytes is less than 5 μm. Infected erythrocytes are not deformed markedly in comparison to uninfected ones.

Development in vertebrate host
Young gametocytes (Fig. 222, *1*, *2*) usually take a lateral position to the nucleus of infected erythrocytes, but they were sometimes also seen in a polar position in the host cells.

Macrogametocytes (Fig. 222, *3–6*; Table 132). The cytoplasm is finely granular in appearance, contains vacuoles; gametocytes grow around the nucleus of infected erythrocytes, slightly enclose the nucleus with their ends, displace it laterally but do not encircle the nucleus completely; frequently one end of gametocytes encircles the nucleus more than

Table 132 Morphometric parameters of gametocytes and host cells of *Haemoproteus pteroclis* (modified from Shamsuddin and Mohammad, 1980) ($n = 10$).

Feature	lim	$\overline{X}$	*SD*
Uninfected erythrocyte			
Length	–	12.6	0.4
Width	–	6.6	0.4
Length of nucleus	–	5.2	0.7
Width of nucleus	–	2.4	0.5
Erythrocyte parasitized by macrogametocyte			
Length	–	14.3	0.9
Width	–	6.5	0.5
Erythrocyte parasitized by microgametocyte			
Length	–	13.7	0.8
Width	–	6.9	0.9
Macrogametocyte			
Length	–	11.9	1.0
Width	–	2.9	0.4
Length of nucleus	2.7–3.0	–	–
Width of nucleus	1.5–2.0	–	–
NDR	–	0.4	0.2
No. of pigment granules	11–22	16.0	3.0
Microgametocyte			
Length	–	12.0	1.2
Width	–	3.2	0.8
NDR	–	0.5	0.2
No. of pigment granules	–	15.6	2.6

Note: All sizes are given in micrometres.

the other end (Fig. 222, *3*, *5*); gametocytes frequently lie free in the cytoplasm, and they usually do not touch the envelope and the nucleus of erythrocytes (Fig. 222, *3, 5*); the outline is usually more or less wavy or ameboid; the parasite nucleus is roundish, subterminal in position; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 222, *7–10*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; vacuoles are rarely seen; other characters are as for macrogametocytes.

Comments. *Haemoproteus pteroclis* can be distinguished from other species of haemoproteids of birds belonging to the Columbiformes on the basis of the subterminal position of the nucleus in its macrogametocytes. This character was noted in the text but not in the illustrations in the original description (Shamsuddin and Mohammad, 1980). The nucleus of macrogametocytes of other similar species of haemoproteids, parasitizing columbiform birds, is median or submedian in position.

Haemoproteus pteroclis is especially close to *H. krylovi.* It can be distinguished from the latter species on the basis of several characters (see 'Comments' to *H. krylovi*).

In the type locality, *H. pteroclis* was found in 3 of 17 investigated *Pterocles alchata.*

II. Family **PLASMODIIDAE** Mesnil, 1903

Type genus. *Plasmodium* Marchiafava and Celli, 1885.

Merogony takes place in cells of fixed tissues and blood cells of vertebrate hosts. Malarial pigment (hemozoin) is present in meronts, which develop in blood cells, and in gametocytes; during the development in immature erythrocytes, it can be absent in some species. Sexual process and sporogony take place in mosquitoes (Diptera: Culicidae), sand flies (Phlebotomidae), and biting midges (Ceratopogonidae).

This family contains one genus, *Plasmodium.*

1. Genus **Plasmodium** Marchiafava and Celli, 1885

Plasmodium Marchiafava and Celli, 1885: 791. – *Haemamoeba* Grassi and Feletti, 1890b: 6 (partim). – *Laverania* Grassi and Feletti, 1890b: 6 (partim). – *Proteosoma* Labbé, 1894: 142. – *Haemosporidium* Lewkowicz, 1897: 132. – *Haemomenas* Ross, 1899: 324. – *Plasmodium*: Castellani and Chalmers, 1910: 289 (=*Haemamoeba*, *Haemosporidium*, *Laverania*, *Proteosoma*); Brumpt, 1913: 94 (=*Haemomenas*).

Type species. *Plasmodium malariae* (Grassi and Feletti, 1892), according to subsequent designation (Garnham, 1966). A parasite of *Homo sapiens*.

Characteristics of the family. Representatives of five subgenera parasitize birds.

KEY TO THE SUBGENERA

1 (4). Roundish fully grown gametocytes are present.

2 (3). Size of fully grown gametocytes and erythrocytic meronts markedly exceeds that of the nuclei of infected erythrocytes. Pedunculated oocysts are absent.
. . . . . 1. ***Haemamoeba***

3 (2). Size of fully grown gametocytes and erythrocytic meronts does not exceed that of the nuclei of infected erythrocytes. Pedunculated oocysts are present.
. . . . . 4. ***Bennettinia***

4 (1). Roundish fully grown gametocytes are absent. The gametocytes are elongated.

5 (8). Erythrocytic meronts contain plentiful cytoplasm. Fully grown erythrocytic meronts, whose size markedly exceeds that of the nuclei of infected erythrocytes, are present.

6 (7). Exoerythrocytic merogony in cells of the haemopoietic system is absent. Meronts in cells – precursors of erythrocytes are absent in the peripheral blood.
. . . . . 2. ***Giovannolaia***

7 (6). Exoerythrocytic merogony in cells of the haemopoietic system is present. Meronts in cells – precursors of erythrocytes are present in the peripheral blood in some species.
. . . . . 5. ***Huffia***

8 (5). Erythrocytic meronts contain scanty cytoplasm. Size of fully grown erythrocytic meronts does not usually exceed or sometimes only slightly exceed that of the nuclei of infected erythrocytes.
. . . . . 3. ***Novyella***

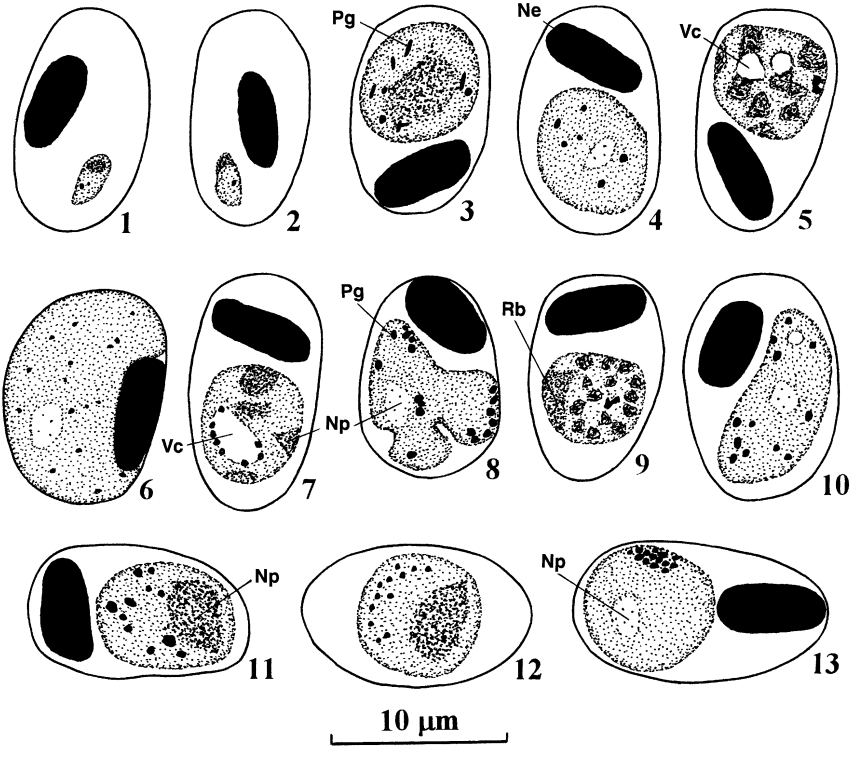

Figure 223 Main morphological peculiarities of the structure of the erythrocytic stages of malaria parasites of the subgenus *Haemamoeba*, which are used for identification of the species:
Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Rb – residual body; Vc – vacuole. Explanations are given in the text.

1. Subgenus **HAEMAMOEBA** Grassi and Feletti, 1890

Haemamoeba Grassi and Feletti, 1890b: 6 (pro gen., partim).

Type species. *Plasmodium relictum* (Grassi and Feletti, 1891), according to subsequent designation (Corradetti *et al.*, 1963a).

Erythrocytic meronts contain plentiful cytoplasm. The size of fully grown erythrocytic meronts exceeds that of the nuclei of infected erythrocytes. Fully grown gametocytes are roundish, oval or of irregular form, and their size markedly exceeds that of the nuclei of infected erythrocytes. Exoerythrocytic merogony takes place in cells of the reticuloendothelial system. Pedunculated oocysts are absent.

KEY TO THE SPECIES

1 (8). Pigment granules in gametocytes are roundish or oval in form (Fig. 223, *4*). Rod-like pigment granules (Fig. 223, *3*) are absent.

2 (9). Large (>1 μm in diameter) vacuoles (Fig. 223, *5*) are absent in erythrocytic meronts.

3 (16). The maximum number of merozoites in erythrocytic meronts is greater than 16.

4 (17). Pigment granules in gametocytes are randomly scattered throughout the cytoplasm (Fig. 223, *4*, *6*).

5 (18). Without multiple infection of one host cell, young trophozoites do not displace or only slightly displace the nuclei of infected erythrocytes (Fig. 223, *2*). Fully grown gametocytes can occupy all available cytoplasmic space in infected erythrocytes (Fig. 223, *6*). The length of the largest gametocytes exceeds 10 μm.

6 (7). Periodicity of erythrocytic merogony is 36 h. The parasite develops in domestic chickens. In nature, transmission does not take place outside the Oriental zoogeographical region.

. . . . . 4. ***P. gallinaceum***

7 (6). Periodicity of erythrocytic merogony is 24 h. The parasite does not develop in domestic chickens. In nature, transmission is present outside the Oriental zoogeographical region.

. . . . . 10. ***P. coturnixi***

8 (1). Pigment granules in gametocytes are roundish, oval, and rod-like (Fig. 223, *3*) in form. The rod-like pigment granules are especially frequently seen in microgametocytes and are not common in macrogametocytes

. . . . . 3. ***P. cathemerium***

9 (2). Large-size (>1 μm in diameter) vacuoles (Fig. 223, *5*) are present in erythrocytic meronts.

10 (14). One or several large vacuoles, which do not exceed 2 μm in diameter, are present in growing erythrocytic meronts (Fig. 223, *5*). Pigment granules do not gather around these vacuoles. Lobulated gametocytes (Fig. 223, *8*) are absent.

11 (15). A residual body (Fig. 223, *9*) is absent in mature erythrocytic meronts. Oval-elongated gametocytes, which are over 10 μm in length (Fig. 223, *10*), are absent.

12 (13). Pigment granules in fully grown gametocytes are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size. The medium size pigment granules are numerous (Fig. 223, *11*). Phanerozoites develop mainly in the spleen; they contain 300 and more merozoites. Phanerozoites do not develop in the brain.

. . . . . 7. ***P. giovannolai***

13 (12). Pigment granules in fully grown gametocytes are of small (<0.5 μm) size (Fig. 223, *12*). Medium size (0.5 to 1.0 μm) pigment granules (Fig. 223, *11*) are not characteristic. Phanerozoites develop in numerous organs, and they contain less than 300 merozoites. Phanerozoites develop in the brain.

. . . . . 5. ***P. matutinum***

14 (10). One large (>2 μm in diameter) vacuole is present in growing erythrocytic meronts (Fig. 223, *7*). Pigment granules gather around this vacuole. Lobulated gametocytes (Fig. 223, *8*) are present.

. . . . . 9. ***P. tejerai***

15 (11). A residual body (Fig. 223, *9*) is present in mature erythrocytic meronts. Oval-elongated gametocytes, which are over 10 μm in length (Fig. 223, *10*), are present.

. . . . . 8. ***P. griffithsi***

16 (3). The maximum number of merozoites in erythrocytic meronts is less than 16.

. . . . . 2. ***P. subpraecox***

17 (4). Pigment granules in gametocytes clearly tend to be clumped into a spot (Fig. 223, *13*) and can be aggregated into a solid mass of pigment.

. . . . . 6. ***P. lutzi***

18 (5). Without multiple infection of one host cell, young trophozoites markedly displace the nuclei of infected erythrocytes (Fig. 223, *1*). Fully grown gametocytes do not occupy all available cytoplasmic space in infected erythrocytes (Fig. 223, *4*). The length of the largest gametocytes does not exceed 10 μm.

. . . . . 1. ***P. relictum***

1. **Plasmodium (Haemamoeba) relictum** (Grassi and Feletti, 1891)

Haemamoeba relicta Grassi and Feletti, 1891: 465. – *Haemoproteus alaudae* Celli and Sanfelice, 1891: 583 (partim). – *Proteosoma grassii* Labbé, 1894: 157, Pl. 9, Fig. 1–31. – *Haemamoeba majoris* Laveran, 1902: 1122, Fig. 4 (partim). – *Plasmodium relictum*: Novy and MacNeal, 1904b: 1145 (emend. pro *Haemamoeba relicta*). – *P. majoris*: Lühe, 1906: 224. – *P. passeris* Johnston and Cleland, 1909: 505, Pl. 48, Fig. 19–24. – *Proteosoma biziurae* Gilruth, Sweet and Dodd, 1910: 231, Pl. 28, Fig. 1–15. – *Plasmodium inconstans* Hartman, 1927: 3, Pl. 2, Fig. 23–30. – *P. maior* Raffaele, 1930: 215, Fig. 13–21. – *P. capistrani* Russell, 1932: 271, Pl. 1, Fig. 1–8, Pl. 2, Fig. 1, 2. – *P. chloropsidis* Mello, 1935a: 355. – *P. paddae* Brumpt, 1935c: 968, Fig. 1–18. – *P. relictum*: Manwell, 1935c: 428 (=*P. capistrani*). – *P. biziurae*: Coatney and Roudabush, 1936: 338. – *P. grassii*: Coatney and Roudabush, 1936: 339. – *P. relictum*: Hewitt, 1940: 52 [=*P. grassii*, *P. inconstans*, *P. maior* (*P. major*), *P. passeris*]. – *P. praecox* var. *muniae* Das Gupta and Siddons, 1941: 150, Pl. 9, Fig. 1–16. – *P. relictum* var. *spheniscidae* Fantham and Porter, 1944: 279. – *P. ploceii* Chakravarty and Kar, 1945b: 66, Pl. 4, Fig. 7–13. – *P. pericrocoti* Chakravarty and Kar, 1945b: 67, Pl. 4, Fig. 14–21. – *P. relictum*: Herman, 1951: 280 (=*P. biziurae*). – *P. relictum*: Laird, 1952: 585 (=*P. relictum* var. *spheniscidae*). – *P. alaudae*: Garnham, 1966: 544. – *P. muniae*: Garnham, 1966: 544 (*P. munia*). – *P. relictum*: Garnham, 1966: 544 (=*P. alaudae*, *P. chloropsidis*, *P. paddae*, *P. muniae*, *P. ploceii*, *P. pericrocoti*). – *P. relictum biziurae*: Garnham, 1966: 545 (emend. pro *Proteosoma biziurae*). – *P. relictum capistranoae*: Garnham, 1966: 546 (emend. pro *P. capistrani*). – *P. relictum spheniscidae*: Garnham, 1966: 547 (emend. pro var. *spheniscidae*). – *P. relictum*: Valkiūnas, 1997: 383 (=*Haemamoeba majoris*, partim; *Plasmodium majoris*, *P. relictum biziurae*, *P. relictum capistranoae*, *P. relictum spheniscidae*).

Type vertebrate host. *Passer hispaniolensis* (Temm.) (Passeriformes).

Additional vertebrate hosts. Numerous species of birds of the orders Anseriformes, Charadriiformes, Ciconiiformes, Columbiformes, Coraciiformes, Falconiformes, Galliformes, Piciformes, Psittaciformes, Sphenisciformes, and some others but particularly of the Passeriformes (more than 310 species total).

Vectors. Numerous species of mosquitoes (Diptera: Culicidae) (Table 133).

Type locality. Catania, Sicily.

Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic.

Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 230–234, first passage from *Passer hispaniolensis* to canary through *Culex pipiens*; *blood stages*: No. 225, *Passer hispaniolensis*, January 1969, Catania, A. Corradetti; *sporogonic stages*: No. 226–228, oocysts and sporozoites from *Culex pipiens*) are deposited in CPG.

Main diagnostic characters. Without multiple infection of one host cell, young trophozoites usually markedly displace the nuclei of infected erythrocytes and deform the erythrocytes. Fully grown erythrocytic meronts and gametocytes occupy more than half of the cytoplasmic space in the infected erythrocytes but do not occupy all available cytoplasmic space in the erythrocytes. The number of merozoites in erythrocytic meronts markedly varies in different strains (from 6 to 32) but is more often between 10 and 24. Pigment granules in gametocytes are roundish, sometimes oval, usually randomly scattered throughout the cytoplasm. Large (>1 μm in diameter) vacuoles are absent either in exoerythrocytic or erythrocytic meronts. The length of fully grown gametocytes does not exceed 10 μm. Periodicity of erythrocytic merogony is between 30 to 36 h. Passerine birds are good hosts.

Table 133 List of vectors of *Plasmodium relictum* (modified from Garnham, 1966).

Aedes aegypti	*A. quadrimaculatus*	*C. salinarius*
A. communis	*A. subpictus*	*C. stigmatosoma*
A. concolor	*Culex apicalis*	*C. tarsalis*
A. dorsalis	*C. bitaeniorhynchus*	*C. territans*
A. mariae	*C. fuscanus*	*C. theileri*
A. vexans	*C. gelidus*	*C. whitmorei*
Anopheles albimanus	*C. hortensis*	*Culiseta annulata*
A. crucians	*C. pipiens*	*C. longiareolata*
A. freeborni	*C. quinquefasciatus*	

Development in vertebrate host

Localization of exoerythrocytic meronts of the first generation depends on the mode of infection. After inoculation of sporozoites into the skin, the primary exoerythrocytic merogony initiates in macrophages and fibroblasts in the skin. In this case, merogony develops as in *P. cathemerium* and is not described here. Under a more natural intravenous infection, the primary exoerythrocytic meronts develop in lymphoid-macrophage cells in internal organs. The description of the exoerythrocytic development in canary of the strain, which was isolated from the type vertebrate host at the type locality, is given below (Corradetti *et al.*, 1970).

Primary exoerythrocytic meronts (Fig. 13, *1*, *2*) develop in reticuloendothelial cells in numerous organs. Cryptozoites appeared in the liver especially quickly (48 h after infection with sporozoites) and then (60 h after the infection) they were seen in the spleen. Much later (120 h after the infection), metacryptozoites were found in the lungs, bone marrow, and brain. Between 144 and 192 h after the infection, metacryptozoites are seen in the kidneys and heart. It should be noted that the primary exoerythrocytic meronts are most frequently seen in the liver and spleen, and only a few of them are sometimes recorded in the brain.

Secondary exoerythrocytic meronts (Fig. 14) are seen in endothelial cells of capillaries of the brain in canaries which died after inoculation of infected blood with mature erythrocytic meronts. Phanerozoites could not be found before the 18th day after the inoculation. Between the 18th and 64th days postinfection, they are seen regularly in the cerebral capillaries. A few phanerozoites were also observed in the liver but not in other organs.

In all organs, except the brain, exoerythrocytic meronts look like roundish or oval bodies (Fig. 13, *1*, *2*). Elongated worm-like meronts develop in the brain (Fig. 13, *3*; 14, *2–4*). The maximum length of exoerythrocytic meronts in all organs does not exceed 120 μm, and they contain not more than 180 merozoites. However, the meronts are usually smaller. The cytoplasm of the growing meronts stains bright blue, lacking vacuoles. Oval or slightly elongated merozoites develop in exoerythrocytic meronts.

The prepatent period does not exceed 120 h after infection with sporozoites. Experiments show that subinoculation of blood from a canary infected with sporozoites 65 h before leads to parasitemia in the new hosts (Raffaele, 1936; Sergent and Sergent, 1952). Parasites are not seen in erythrocytes at this time, however, and the true prepatent period is longer. Merozoites from primary exoerythrocytic meronts are present in the blood 65 h after infection with sporozoites, and it is likely that they are responsible for the infection in the subinoculated birds (Garnham, 1980).

Erythrocytic merogony is only slightly synchronized and, thus, its periodicity is hard to determine. Usually, a cycle of erythrocytic merogony is completed within 30 to 36 h.

Mature erythrocytic meronts usually rupture in the morning. Gametocytes appear in the blood together with trophozoites.

An increased parasitemia is usually recorded for less than a 30-day period. Then, the infection turns into a chronic stage, and only a few parasites can be seen in the blood during three to four subsequent months.

Once infected birds, who survive the acute stage of the infection, usually remain infected for all their lives.

Trophozoites (Fig. 12, *1*, *2*) are seen in mature and polychromatic erythrocytes; earliest parasites are roundish or oval, but sometimes are also of irregular shape; the outline is usually even, occasionally slightly ameboid; growing trophozoites look like solid bodies with a relatively large nucleus; a 'ring' stage is not characteristic; as the parasite develops, the amount of cytoplasm increases, and a pigment granule appears quite early, located close to the edge of the parasite; one or several small vacuoles are present in the cytoplasm of some growing trophozoites; fully grown trophozoites possess several minute, dark-gold or brown pigment granules; the outline of fully grown trophozoites is usually even or irregular, sometimes slightly ameboid; the nuclei of infected erythrocytes are displaced, and the erythrocytes are usually more or less deformed even at the early stages of development of trophozoites (Fig. 12, *2*); multiple infection of the same erythrocyte with several parasites is common during a heavy parasitemia.

Erythrocytic meronts (Fig. 12, *3–9*) are usually seen in mature erythrocytes; they are roundish or oval, sometimes of irregular shape (Fig. 12, *5*), and possess plentiful cytoplasm; the meronts markedly displace the nuclei of infected erythrocytes, deform the erythrocytes and can even enucleate the host cells (Fig. 12, *8*); as the parasite matures, its nuclei decrease in size and are usually located randomly (Fig. 12, *6–8*); pigment granules are black, usually clumped into a spot, sometimes into several (not more than three) spots which vary in position; pigment granules can also be aggregated into one or several solid masses (Fig. 12, *6*); the number of merozoites in mature meronts varies from 6 to 32 in different strains, but most frequently it ranges from 10 to 24; fully grown meronts occupy more than half of the cytoplasmic space in infected erythrocytes but do not occupy all available cytoplasmic space in the erythrocytes.

Macrogametocytes (Fig. 12, *10–14*) are usually seen in mature erythrocytes; they are roundish or oval, sometimes of irregular (Fig. 12, *12*) shape; gametocytes markedly displace the nuclei of infected erythrocytes, deform the erythrocytes and can even enucleate the host cells (Fig. 12, *11*); the cytoplasm sometimes contains a few small (<1 μm in diameter) vacuoles; the parasite nucleus is compact, variable in form and position; the nucleolus is usually well seen (Fig. 12, *14*); pigment granules are usually roundish, sometimes oval, dark-brown or black; usually of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, markedly vary in number but are usually less than 30; sometimes pigment granules are seen in a loose clump near the edge of gametocytes, but in general this is not characteristic of this species; fully grown gametocytes occupy more than half of the cytoplasmic space in the infected erythrocytes; fully grown gametocytes (n = 10) vary from 6.4 to 7.2 (on average 6.9±0.3) μm in diameter (Corradetti *et al.*, 1970).

Microgametocytes (Fig. 12, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Relapses are well pronounced in infected birds at the temperate latitudes in spring. As a result, parasitemia increases during the spring period (Applegate and Beaudoin, 1969; Applegate, 1970, 1971). It should be noted that gametocytes are significantly more

infectious to vectors during the spring relapse period than during the autumnal chronic stage of infection. This is ecologically important in reestablishing the transmission of the parasite. It is likely that relapses are initiated by persisting secondary exoerythrocytic meronts whose localization has been still insufficiently investigated. Spring relapse is synchronized with the season and does not depend on individual dates of the initial infection of birds. It was shown experimentally that the increase of the level of corticosterone in the blood is one of the factors which stimulate the relapse in birds (Applegate, 1970).

Development in vector of the strain, isolated from the type vertebrate host at the type locality, was studied by Corradetti *et al.* (1970). *Culex pipiens* was used as a vector. The mosquitoes were fed on infected canaries and then were maintained at temperature of 22 to 25°C and relative humidity of 65 to 80%. In these conditions, 100% of the mosquitoes became infected. Ookinetes are seen in the midgut of mosquitoes 24 to 48 h after ingestion of mature gametocytes. Ookinetes are elongated worm-like bodies which possess a prominent centrally located nucleus, large 'vacuoles' and numerous pigment granules (Fig. 13, *4*, *5*). They vary ($n = 20$) from 14.3 to 18.6 (on average 16.4±1.2) μm in length and from 2.1 to 3.6 (on average 2.9±0.6) μm in width in preparations fixed with methanol. The earliest oocysts are seen in the midgut of the vector on the fourth day after ingestion of gametocytes. They became mature on the sixth day post infection. The sporogony is not synchronized, and some oocysts are seen in the midgut until the 15th day. After fixation in Carnoy's fluid, fully grown oocysts vary ($n = 24$) from 32.9 to 42.9 (on average 38.0) μm in diameter. The oocysts possess pigment granules whose number does not exceed 12. The pigment granules are usually in a loosely aggregated clump whose position varies (Fig. 13, *6–9*). Sporozoites are seen in the salivary glands of the vector on the seventh day after the ingestion of gametocytes, and they were recorded up to the 22nd day. They look like elongated spindle-shaped bodies with a prominent, more or less centrally located, nucleus (Fig. 13, *10–12*). They vary ($n = 24$) from 10.1 to 15.7 (on average 13.7±1.5) μm in length and from 1.1 to 1.4 (on average 1.4±0.1) μm, in width in preparations fixed with methanol. Sporogony is interrupted and the infection is sterilized if mosquitoes are maintained after the infection at a temperature of 12°C for three days. Once infected, mosquitoes do not acquire immunity to the reinfection (Garnham, 1966).

Pathogenicity. *Plasmodium relictum* is a pathogenic parasite, and the highly virulent strains have been isolated. Mortality of canaries is high (usually more than 50%). During the crisis (usually in the second week after infection), the birds look unhealthy with ruffled plumage, drooped head, and clearly evident anaemia. At autopsy, the liver and spleen are markedly enlarged and contain the malarial pigment. The volume of the spleen in heavily infected birds can be 20 times its normal volume. The severity of the disease is usually directly proportional to the intensity of the acute parasitemia.

Plasmodium relictum and its vector *Culex quinquefasciatus* were introduced on the Hawaiian Islands where malaria in birds was formerly absent (van Riper *et al.*, 1982; van Riper, 1991). As a result of this introduction, epizooties appeared among native Hawaiian birds, and they contributed to the decrease of densities of native bird populations and even to the disappearance of some endemic bird species (see p. 93). Presently, the native Hawaiian birds are more numerous on the territories where the vectors of *P. relictum* are absent or not numerous (high-elevation forests, dry forests).

Plasmodium relictum is an important agent of diseases of birds in zoos (Cranfield *et al.*, 1990). Numerous outbreaks of malaria have been reported in penguins and other birds all over the world. For example, the outbreak of malaria caused a significant mortality in

the Blank Park Zoo in Des Moines, Iowa (USA) (Fix *et al.*, 1988). About 60% of the Magellanic penguins *Spheniscus magellanicus* were infected and approximately 80% of them died. The birds became weak and inactive and died after two days. A marked enlargement of the spleen and liver, as well as a pulmonary edema, were recorded at the postmortem examination. A cardiomegaly with dark green pericardial effusion was also seen in some birds. Numerous exoerythrocytic meronts were found in the endothelial cells of capillaries and in the macrophages in the spleen, liver, lungs, heart, and kidneys. The inflammatory response included numerous lymphocytes and plasma cells with fewer numbers of heterophils and macrophages. It is likely that endothelial damage plays a prominent role in parenchymal organ dysfunction and failure. This failure results in the death of infected birds. Additionally, pulmonary edema and macrophage infiltrates lead to respiratory failure.

Plasmodium relictum is pathogenic for wild free-living birds, and epizooties in game birds due to this parasite have been described. The acute outbreak of malaria in partridges *Perdix perdix*, which were imported from Hungary to the endemic territory in France, is an example (Garnham, 1966). However, the role of this parasite in long-existing natural ecosystems has been still insufficiently investigated. It is important to note that the parasite does not act as the pyrogenic agent (Hayworth *et al.*, 1987). Significant decreases of both O_2 assimilation and body temperature are recorded in experimentally infected canaries at the peak of parasitemia. It looks likely that the parasite can be dangerous even for adapted hosts due to a decreased ability for thermoregulation and the O_2 assimilation in the tissues when the peak of parasitemia coincides with a thermally stressful time, i.e., at critical periods of the birds' life.

S p e c i f i c i t y. *Plasmodium relictum* has a huge range of vertebrate hosts, including numerous representatives of many bird orders (see 'Additional vertebrate hosts'). This is the first bird malaria parasite by the frequency of occurrence. Canary is a good experimental host. Domestic chickens, ducklings, and pigeons can be infected experimentally. It is important to note that owls (the order Strigiformes) were not infected experimentally.

S u b s p e c i e s of *P. relictum* have been insufficiently investigated, and they are characterized only by some negligible traits. These differences are based mainly on the morphology of blood stages. However, the morphology alters in abnormal hosts. For example, even elongated gametocytes can develop in experimentally infected chickens (Garnham, 1966). Diagnostic characters of all subspecies of *P. relictum*, which have been described so far, are often significantly narrower than the differences of some strains and geographical isolates. Unfortunately, type material for most of the subspecies is absent. Thus, based on the evidence presented above, subspecies of *P. relictum* are not considered here, but they are given in the list of synonyms of *P. relictum*. Further investigation into subspecies of *P. relictum* is required.

C o m m e n t s. *Plasmodium relictum* is the most common and widely distributed avian malaria parasite. At the end of the 19th century and the beginning of the 20th century, numerous species of malaria parasites of the subgenus *Haemamoeba* and some other subgenera were described or mentioned in the literature as *P. relictum* or *P. praecox*. As it was proved by Garnham (1966), the specific name *P. praecox* is invalid. Additionally, some strains of *P. relictum* are clearly different on their biological features. These facts, on the one hand, explain the existence of contradictory data on the development of *P. relictum* in the literature (the periodicity of erythrocytic merogony, the rate of maturation and the size of exoerythrocytic meronts, the number of merozoites in erythrocytic meronts, the rate of sporogony, etc.) and, on the other hand, make it difficult to prepare a correct and complete list of vertebrate hosts of this parasite. That is why the data, which are mainly based on the

development in canary of the parasite isolated from the type vertebrate host (*Passer hispaniolensis*) at the type locality (Sicily), are given in this species essay.

During the identification of *P. relictum* and the similar species of the subgenus *Haemamoeba*, attention should, first of all, be paid to the following characters. First, both exoerythrocytic and erythrocytic meronts of this parasite possess no large (>1 μm in diameter) vacuoles. Second, pigment granules in gametocytes are usually roundish and only sometimes oval, but never rod-like. Thirdly, the periodicity of erythrocytic merogony is more than 24 h. Fourthly, the brain is not the main place of localization of primary exoerythrocytic meronts.

According to the original description (Bennett *et al.*, 1995a), *Haemoproteus mcleani* is the haemoproteid of the passeriform birds with discoid (round to slightly oval) gametocytes causing major distortion of the host erythrocytes and displacement of their nuclei. All these characters were observed in the hapantotype. Besides, numerous growing erythrocytic meronts of *Plasmodium (Haemamoeba)* sp. are also present in this blood film. The meronts are round, oval, or of irregular form and possess plentiful cytoplasm. The majority of them are growing, but a few segmenters were also seen containing up to 16 merozoites. A malaria parasite, which belongs to *Plasmodium (Haemamoeba) relictum* group, is present in this blood film. The discoid gametocytes of *H. mcleani*, described by Bennett *et al.* (1995a), are identical to the gametocytes of this malaria parasite. Furthermore, only one type of discoid gametocytes, which are identical to gametocytes of *P. relictum*, is seen in the hapantotype. This blood film is pale-stained, and the nuclei of the meronts are not well seen. Gametocytes of haemoproteids are likely to be absent in this blood film, and the infection of the malaria parasite (both gametocytes and erythrocytic meronts) was described by Bennett *et al.* as a haemoproteid infection under the new name *H. mcleani*. It is probable that *H. mcleani* is an erroneously identified species, and the specific name *H. mcleani* can be a synonym of *P. relictum*. Additional information is required to answer this question. Only one type preparation was designated in the original description, and it is also possible that the hapantotype was mislabelled. Until additional information is available, *H. mcleani* has been declared to be a *species inquirenda* (Valkiūnas and Iezhova, 2000).

2. **Plasmodium (Haemamoeba) subpraecox** (Grassi and Feletti, 1892)

Haemamoeba subpraecox Grassi and Feletti, 1892: 29, Fig. 8, 9. – *Plasmodium wasielewskii* Brumpt, 1910: 84. – *P. subpraecox*: Raffaele, 1931: 684. – *P. subpraecox*: Garnham, 1966: 551 (=*P. wasielewskii*).

Type vertebrate host. *Athene noctua* (Scopoli) (Strigiformes).
Additional vertebrate hosts. Some species of birds (Table 134).
Vector. *Culex pipiens* (Diptera: Culicidae).
Type locality. Italy.
Distribution. This parasite has been recorded mainly in the Holarctic. It was once found in South China. The geographical range is unclear.
Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 221, *Athene noctua*, brain, 7.10.1968, Roman Campagna; *blood stages*: No. 218, other data as for the No. 221) are deposited in CPG. A series of good additional slides of blood stages and sporogonic stages of the Egyptian strain is deposited in CPG.
Etymology. The specific name reflects the similarity of blood stages of this parasite with those of *P. praecox* (*P. relictum* according to present knowledge).

Table 134 List of vertebrate hosts of *Plasmodium subpraecox*.

Alauda arvensis	*Otus asio*
Asio flammeus	*Strix aluco*
Nyctea scandiaca	*Zosterops cinerea*

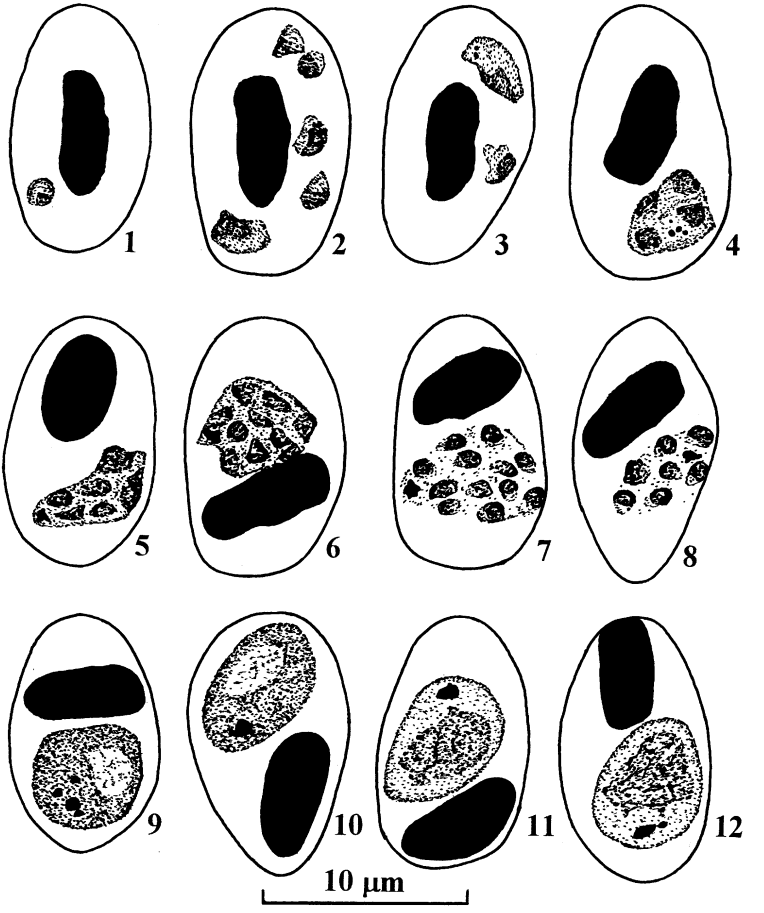

Figure 224 *Plasmodium subpraecox* from the blood of *Athene noctua:*
1–3 – trophozoites; *4–8* – erythrocytic meronts; *9*, *10* – macrogametocytes; *11*, *12* – microgametocytes.

Main diagnostic characters (during development in the natural hosts, owls). Fully grown erythrocytic meronts and gametocytes occupy not more than half of cytoplasmic space in infected erythrocytes. Large (>1 μm in diameter) vacuoles are absent in erythrocytic meronts. Pigment granules in gametocytes are roundish, and tend to be clumped into a spot and can be aggregated into a solid mass of pigment. Mature erythrocytic meronts contain 5 to 12 merozoites.

The development of this parasite in vertebrate hosts and in the vector was studied mainly up to the middle of the 20th century. The results of these investigations were generalised by Garnham (1966). They are added on the basis of reexamination of the collection materials and some literature data and given in the text below.

Development in vertebrate host

Repeated attempts to find exoerythrocytic meronts in naturally and experimentally infected birds were usually unsuccessful. The exoerythrocytic meronts (most probably, phanerozoites) were finally found in one naturally infected *Athene noctua* (Garnham and

Duggan, 1986). The parasites develop in the endothelial cells of capillaries in the brain. They are similar to the phanerozoites of *P. relictum* which develop in cerebral endothelium.

Parasitemia in experimentally infected owls increases rapidly, remains at a relatively high level during two or three weeks and then decreases and turns into a chronic stage. The birds which survive acquire premunition. The period of chronic infection lasts for years. Sometimes, a sudden marked increase of parasitemia takes place. Erythrocytic merogony is synchronized, and a cycle of the erythrocytic merogony is about 24 h.

The description of blood stages from naturally infected type vertebrate hosts is given below.

Trophozoites (Fig. 224, *1–3*) are seen in mature and polychromatic erythrocytes; the earliest forms are usually roundish (Fig. 224, *1*); the 'ring' stage is seen occasionally among young trophozoites but is not characteristic in general; as the parasite develops, trophozoites take an irregular shape and their nuclei markedly increase in size (Fig. 224, *2*); vacuoles are usually not seen in the cytoplasm of fully grown trophozoites (Fig. 224, *3*); pigment was observed in large trophozoites as one to three small dark granules; trophozoites usually slightly (if at all) influence infected erythrocytes whose nuclei can be slightly displaced.

Erythrocytic meronts (Fig. 224, *4–8*) are usually seen in mature erythrocytes, but sometimes also in polychromatic erythrocytes; the cytoplasm stains bright blue, plentiful, usually lacking vacuoles; as the parasite develops, the basophility of the cytoplasm decreases; fully grown meronts are roundish, oval, or of irregular form, occupy not more than half of the cytoplasmic space in the infected erythrocytes; nuclei are usually located randomly (Fig. 224, *7*) but occasionally were also seen in rosettes; mature meronts usually contain 5 to 12 (most frequently 8) merozoites; pigment granules are roundish, of small size (<0.5 μm), dark, clearly tend to be clumped into a spot and are frequently seen to be aggregated into a solid mass of pigment (Fig. 224, *7*); meronts markedly displace the nuclei of the infected erythrocytes and can deform the erythrocytes.

Macrogametocytes (Fig. 224, *9*, *10*) are usually seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, usually lacking vacuoles; the earliest gametocytes look like trophozoites; fully grown gametocytes are roundish or oval, occupy not more than half of the cytoplasmic space in the infected erythrocytes; the parasite nucleus is compact, variable in form and position, relatively large (Fig. 224, *10*); pigment granules are roundish, of variable size, tend to be clumped into a spot and can be aggregated into a solid mass of pigment which is near the edge of the parasite (Fig. 224, *10*); fully grown gametocytes deform infected erythrocytes, displace their nuclei and can even enucleate the erythrocytes; fully grown gametocytes are less than 10 μm in diameter.

Microgametocytes (Fig. 224, *11*, *12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules tend to aggregate into a solid mass even more than in macrogametocytes; other characters are as for macrogametocytes.

Development in vector

Exflagellation of the Egyptian strain in mosquito *Culex pipiens fatigans* was seen 22 min after the ingestion of gametocytes at temperature of 27 to 28°C. Microgametes reach 16 μm in length. Ookinetes look like elongated worm-like bodies with one end pointed more than the other. They possess a large compact nucleus and numerous pigment granules. The cytoplasm is more intensively stained along the periphery of the ookinetes. Ookinetes are about 17 to 20 μm in length. On the seventh day after ingestion of the gametocytes, oocysts reach

approximately 30 μm in diameter. Pigment granules in growing oocysts are accumulated into a single conspicuous mass. Mature oocysts were seen on the 13th day after ingestion of the gametocytes, and they reach approximately 40 μm in diameter. The sporozoites are about 14 μm in length in fresh preparations and vary from 11 to 12 μm in preparations fixed with methanol.

Development of the Italian strain of the parasite in *Culex pipiens* is completed 15 to 16 days after the ingestion of gametocytes at a temperature of 22°C.

Pathogenicity has been insufficiently investigated. Experimentally infected birds usually survive and acquire premunition. The virulence of the parasite for canaries gradually increases with the number of passages.

Specificity. The range of natural vertebrate hosts has been insufficiently investigated. The parasite develops in canaries but not in domestic chickens, pigeon *Passer domesticus* and kestrel *Falco tinnunculus.*

Comments. The morphology of blood stages of *P. subpraecox* during its development in canaries markedly differs from that in owls. In experimentally infected canaries, *P. subpraecox* is more similar to *P. relictum*, i.e., the parasite increases in size, the number of merozoites in erythrocytic meronts augments up to 12 to 18, pigment is more plentiful and is usually found in discrete granules which not so clearly tend to aggregate into a solid mass. Even elongated gametocytes are seen in the canaries (Garnham, 1966). After inoculation of infected blood from canary back to owl, the morphological characters, which are typical of the parasite in the type vertebrate host, are reestablished again. It is possible that *P. subpraecox* evolved due to the adaptation for development in owls not long ago, and it did not yet obtain stability. As mentioned above, the experimental attempts to infect owls with *P. relictum* were not successful.

Plasmodium subpraecox can be distinguished from other species of the subgenus *Haemamoeba*, first of all, on the basis of the small size of its mature erythrocytic meronts and gametocytes. During development in owls, these characters are well evident. The metamorphosis of blood stages after subinoculation into canaries can also be used as a laboratory test to distinguish *P. subpraecox* from the close species of the *Haemamoeba.*

3. **Plasmodium (Haemamoeba) cathemerium** Hartman, 1927

Plasmodium cathemerium Hartman, 1927: 2, Pl. 1, Fig. 13–16, Pl. 2, Fig. 17–22. – *P. centropi* Mello, 1936: 98 (partim). – *P. cathemerium*: Valkiūnas, 1997: 338 (=*P. centropi*, partim).

Type vertebrate host. *Passer domesticus* (L.) (Passeriformes).
Additional vertebrate hosts. Numerous birds (about 50 species) of several avian orders, but mainly of the Passeriformes.
Vectors. The natural vectors are unknown. Sporogony is completed in numerous species of experimentally infected mosquitoes (Table 135).
Type locality. Baltimore, USA.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Australian and Antarctic. It has been frequently found in the Holarctic.
Type material. Neohapantotypes (No. 237, 238, *Serinus canaria*, Roman Campagna strain from *Passer domesticus*, 1941, A. Corradetti) are deposited in CPG. A series of good additional slides, including exoerythrocytic meronts, is deposited in CPG.

Main diagnostic characters. Fully grown gametocytes possess elongated rod-like pigment granules with pointed ends; these pigment granules are especially common in microgametocytes but are not present in all macrogametocytes.

Table 135 List of experimental vectors of *Plasmodium cathemerium* (modified from Garnham, 1966).

Aedes aegypti	*A. strodei*	*C. territans*
A. cantator	*Culex bitaeniorhynchus*	*C. tritaeniorhynchus*
A. geniculatus	*C. fuscanus*	*Culiseta melaneum*
A. sollicitans	*C. pipiens*	*C. morsitans*
Anopheles norestensis	*C. salinarius*	*Psorophora ferox*
A. quadrimaculatus	*C. tarsalis*	

Plasmodium cathemerium was widely used as a model species in investigations of malaria before the discovery of *P. gallinaceum*. The main information about *P. cathemerium* was received before the 1950s. This information was generalised by Garnham (1966). The results of these early investigations are modified in light of current knowledge on the basis of a reexamination of the collection materials and the literature data, and are given in the text below.

Development in vertebrate host

The exoerythrocytic development is similar to *P. relictum*. Sporozoites initiate the first generation of primary exoerythrocytic meronts, called cryptozoites. Localization of the cryptozoites depends on the mode of infection. After intravenous inoculation of sporozoites, which is the mode of infection similar to the natural one, cryptozoites initiate the development in the Kupffer cells of the liver and in the lymphoid-macrophage cells of the spleen, bone marrow, and probably in some other organs. After inoculation of sporozoites into the skin, cryptozoites initiate development in macrophages and fibroblasts of the skin at the place of their inoculation. Cryptozoites develop rapidly. Uninuclear parasites are seen in macrophages 16 h after inoculation of sporozoites into the skin, and the fission of nucleus is seen soon after that. The first mature cryptozoites, which contain about 30 nuclei, were observed approximately 30 h after the infection. They look like roundish or oval bodies about 10 to 20 μm in diameter (Fig. 225, *1*). Cryptozoites produce egg-like merozoites which initiate the development of the second generation of primary exoerythrocytic meronts, the metacryptozoites. Metacryptozoites reach their maturity approximately 60 to 72 h after infection with sporozoites, and produce less than 100 merozoites. The morphology of cryptozoites and metacryptozoites, as well as the morphology of their merozoites, are similar.

Part of merozoites, from metacryptozoites, initiate the development of blood stages. The other part of merozoites from metacryptozoites initiate the development of subsequent generations of metacryptozoites which are found seven to nine days after the infection with sporozoites. Only after this period, do the secondary exoerythrocytic meronts (phanerozoites) appear in the endothelial cells of capillaries in the brain, lungs, and numerous other organs (Fig. 225, *2*–*5*). The nucleus of the host cells of phanerozoites is enlarged, and the enucleated host cells were also seen. In the brain, phanerozoites are elongated, and are frequently located close to each other. As a result, the boundaries between the phanerozoites frequently cannot be distinguished and, thus, it is difficult to calculate the exact number of merozoites in the meronts. Phanerozoites can block up the brain capillaries (Fig. 225, *4*, *5*). Morphology of phanerozoites, which develop in the lungs and other organs, is similar to the morphology of primary exoerythrocytic meronts, but the phanerozoites are larger and contain a greater number of merozoites (Fig. 225, *2*, *3*). Over 100 merozoites usually develop in phanerozoites.

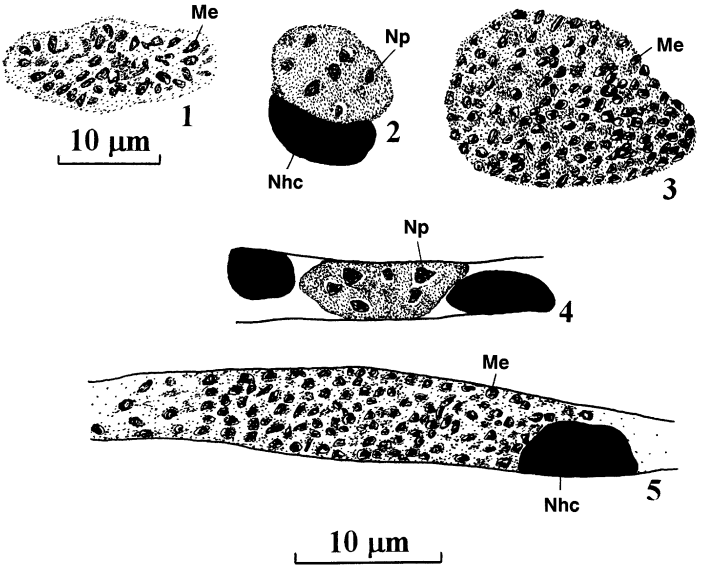

Figure 225 Exoerythrocytic meronts of *Plasmodium cathemerium:*
1 – mature cryptozoite; *2–5* – phanerozoites from *Fringilla coelebs:* immature (*2*) and mature (*3*) parasites in lungs, immature (*4*) and mature (*5*) parasites in brain; Me – merozoite; Nhs – nucleus of host cell; Np – nucleus of parasite (*1* is modified from Garnham, 1966).

Secondary exoerythrocytic merogony of most of the strains can be easily initiated by merozoites from erythrocytic meronts.

The prepatent period is no longer than 72 h after the infection with sporozoites. Gametocytes appear in the blood together with asexual stages, but they mature more slowly than the asexual stages. In the beginning of the patency, the intensity of parasitemia is low, but it increases dramatically after the maturation of phanerozoites. Up to 50% of erythrocytes can be parasitized at the peak of parasitemia. The high parasitemia maintains approximately for one week, and then it decreases rapidly and turns into a chronic stage. Only a few parasites can be seen in the blood during the long-term chronic parasitemia. Erythrocytic merogony is clearly synchronized. The cycle of the erythrocytic merogony is 24 h. The majority of mature erythrocytic meronts rupture in the evening (between 18 and 22 h). The vitality of gametocytes decreases during the acute stage of parasitemia. The ability of the parasite to produce gametocytes also decreased as the number of blood passages increased, but this ability can be restored after passages through mosquitoes.

Trophozoites (Fig. 226, *1–3*) are seen in mature and polychromatic erythrocytes; the earliest forms look like compact bodies with a nucleus and lacking vacuoles; the 'ring' stage is not characteristic; as the parasite develops, trophozoites take an oval or slightly elongated form, and they are frequently seen in a subpolar position in infected erythrocytes (Fig. 226, *3*); the outline is usually even; fully grown trophozoites can displace the nucleus of erythrocytes (Fig. 226, *3*), and this is especially evident during multiple infection of a host cell.

Erythrocytic meronts (Fig. 226, *4–10*) are seen in mature and polychromatic erythrocytes; the cytoplasm usually lacks vacuoles; the nuclei are located near the periphery in young meronts (Fig. 226, *4*, *5*) and are randomly located in fully grown meronts (Fig. 226,

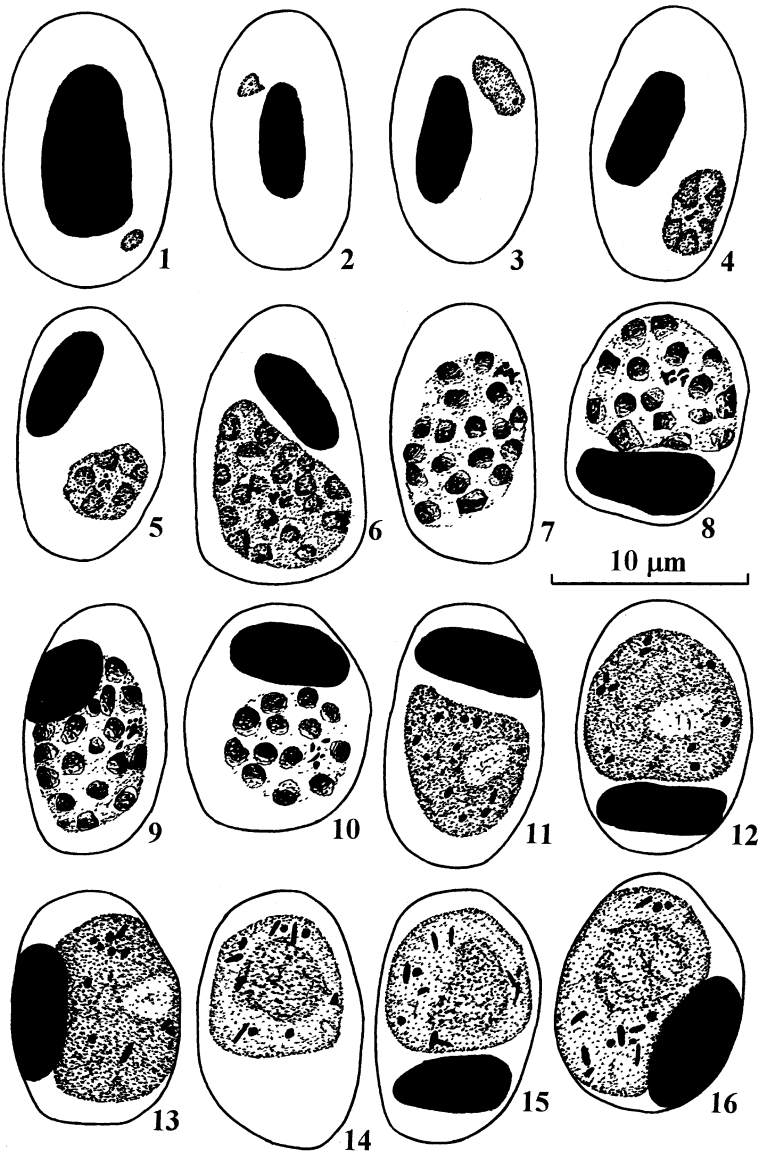

Figure 226 *Plasmodium cathemerium* from the blood of *Serinus canaria:*
1–3 – trophozoites; *4–10* – erythrocytic meronts; *11–13* – macrogametocytes; *14–16* – microgametocytes.

6); fully grown meronts are roundish, oval, or irregular in form, they occupy more than half of the cytoplasmic space in the infected erythrocytes; mature meronts contain 6 to 24 (on average 16) merozoites; pigment granules are roundish or oval, usually of small size (<0.5 μm), brown, and clumped into a spot; meronts markedly deform the infected erythrocytes, they markedly displace their nuclei and can even enucleate the host cells (Fig. 226, *7*); as a rule, the fully grown meronts are less than 10 μm and are usually about 7 to

8 μm in diameter; mature merozoites are about 1 μm in diameter, they possess a prominent nucleus and a small portion of basophilic cytoplasm (Fig. 226, *10*).

Macrogametocytes (Fig. 226, *11–13*) are usually seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, usually lacks vacuoles; the earliest gametocytes look like trophozoites; fully grown gametocytes are roundish or oval (Fig. 226, *12, 13*), and sometimes of irregular shape (Fig. 226, *11*), they occupy more than half of the cytoplasmic space in the infected erythrocytes; the outline is even; the parasite nucleus is compact, variable in form; the nucleolus is usually well seen; pigment granules are roundish, oval and elongated rod-like, randomly scattered throughout the cytoplasm, vary from 6 to 24 (usually about 12) in number; rod-like pigment granules frequently have pointed ends (Fig. 226, *13*); it is important to note that rod-like pigment granules are always much more rare than roundish granules, and they are not present in all gametocytes (Fig. 226, *12*); gametocytes significantly deform infected erythrocytes, markedly displace their nuclei and can even enucleate the host cells; gametocytes are less than 10 μm in diameter.

Microgametocytes (Fig. 226, *14–16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; rod-like pigment granules are much more frequently seen than in macrogametocytes; other characters are as for macrogametocytes.

Relapses were recorded.

Development in vector

The natural vectors are unknown. The range of experimental vectors is wide (Table 135). Mosquitoes of the genus *Culex* are the best experimental vectors. Sporogony is completed in the mosquitoes of the genus *Anopheles*, but sporozoites are usually not numerous in them. The susceptibility of mosquitoes can be easily changed by their selection. Ookinetes are worm-like bodies up to 15 μm long. They possess a prominent nucleus and pigment granules, and some of the granules are rod-like. The earliest oocysts were seen at a temperature of 28°C 14 h after the ingestion of gametocytes. From the second to sixth day after the infection, the oocysts increase from 11 to 36–48 μm in diameter, and later they usually do not increase in size. Sporogony is completed on the sixth day after the ingestion of gametocytes under optimum conditions. Sporozoites look like elongated crescent-shaped bodies with pointed ends.

Pathogenicity. Canaries frequently die during heavy infections. The virulence of different strains varies markedly. The birds usually die because of acute anaemia and a blockage of the capillaries of the brain and other organs by phanerozoites. At autopsy, the spleen and liver are markedly enlarged in infected birds, and malarial pigment accumulates in these organs. The hyperplasia of lymphoid tissues has been recorded. Birds that survive the acute stage of infection acquire the premunition.

Specificity. The range of vertebrate hosts of *P. cathemerium* is wide and includes representatives of the orders Apodiformes, Caprimulgiformes, Charadriiformes, and some others, but the passeriform birds clearly predominate among them. Canary is a good experimental host. Ducklings can be easily infected by subinoculation of infected blood, and they are also good experimental hosts. However, metacryptozoites do not develop in the ducklings after infection with sporozoites, and the infection is usually blocked up at the stage of cryptozoites. Domestic chickens can be infected with difficulty only by some strains and only transient parasitemia develops; they are poor hosts for *P. cathemerium*.

Comments. During identification of *P. cathemerium*, attention should be paid, first of all, to the elongated rod-like pigment granules in gametocytes. It is important to note that such pigment granules

are not present in all gametocytes, and thus at low parasitemia the identification of species on the basis of this character is not always possible.

The elongated rod-like pigment granules in gametocytes were recorded in the original description of *P. centropi* (Mello, 1936). *Plasmodium centropi* is a synonym of *P. cathemerium*, in part. It is likely that at least two species of malaria parasites were described under the name *P. centropi*, i.e., *P. cathemerium* and *Plasmodium* sp. with elongated gametocytes.

It should be also noted that the morphology of blood stages of *P. cathemerium* during its development in nonpasserine birds (ducklings, chickens) changes markedly. The main morphological changes include the reduced number of merozoites in erythrocytic meronts and the disappearance of rod-like pigment granules in gametocytes. In addition, the parasites tend to displace the nucleus of infected erythrocytes less and tend to grow around the nucleus. However, the main characters of this species are relatively stable during the development in various passeriform birds.

4. **Plasmodium (Haemamoeba) gallinaceum** Brumpt, 1935

Plasmodium gallinaceum Brumpt, 1935b: 783, Fig. 1–18. – *P. metastaticum* Raffaele, 1966: 279. – *P. gallinaceum*: Lowe, 1966: 153 (=*P. metastaticum*).

Type vertebrate host. Domestic chicken *Gallus gallus* L. (Galliformes).
Additional vertebrate hosts. *Gallus gallus* (=*G. bankiva*), *G. sonneratii* (Galliformes).
Vectors. *Mansonia crassipes* (Diptera: Culicidae) is the natural vector. The range of experimental vectors is wide (Table 136).
Type locality. Ceylon.
Distribution. The Oriental zoogeographical region. Occasionally, the parasite has been removed, together with its vertebrate hosts, outside of this region. However, there is no convincing evidence of the natural transmission outside the Oriental zoogeographical region.
Type material. Neohapantotypes (Brumpt strain, passages through *Gallus gallus* and *Aedes aegypti*; *exoerythrocytic meronts*: No. 262, cardiac muscle, 12.12.1957; No. 263, brain, 1936, S.P. James, P. Tate; No. 264, brain, 1936, S.P. James; No. 265, strain is unknown, brain, 13.04.1965; *blood stages*: No. 252–254, 1936; *sporogonic stages*: No. 258, exflagellation; No. 259, ookinetes; No. 260, oocysts, *Aedes aegypti queenslandensis*; No. 261, sporozoites) are deposited in CPG. Paraneohapantotype (No. 255, 10.05.1936, other data as for No. 252) is deposited in CPG.
Etymology. The specific name is derived from the name of the type vertebrate host, *Gallus gallus*.

Main diagnostic characters. Without multiple infection of one host cell, young trophozoites usually do not displace or only slightly displace the nuclei of infected erythrocytes and do not markedly deform the erythrocytes. Fully grown erythrocytic meronts and gametocytes markedly displace the nuclei of erythrocytes and deform the host cells. They can occupy more than half of the cytoplasmic space in the infected erythrocytes and even can occupy all available cytoplasmic space in the erythrocytes. Large (>1 μm in diameter) vacuoles are not present both in exoerythrocytic and erythrocytic meronts. Mature erythrocytic meronts contain 8 to 36 (more often 16 to 20) merozoites. Pigment granules in gametocytes are roundish, randomly scattered throughout the cytoplasm. Largest fully grown gametocytes exceed 10 μm in length. The parasite develops in domestic chickens but not in canary and other passeriform birds. The periodicity of erythrocytic merogony is 36 h. In nature, transmission does not take place outside the Oriental zoogeographical region.

Over 1000 scientific publications deal with *P. gallinaceum*. This species essay was written on the basis of generalizing works by Garnham (1966, 1980) which were

Table 136 List of experimental vectors of *Plasmodium gallinaceum* (modified from Garnham, 1966).

Aedes aegypti	*A. pseudotaeniatus*	*Armigeres annulipalpis*
A. albolateralis	*A. scutellaris*	*A. aureolineatus*
A. albopictus	*A. stimulans*	*A. kuchingensis*
A. atropalpus	*A. stokesi*	*A. magnus*
A. campestris	*A. togoi*	*A. obturbans*
A. canadensis	*A. triseriatus*	*A. subalbatus*
A. cantator	*A. trivittatus*	*Culex mimulloides*
A. chrysolineatus	*A. unilineatus*	*C. pipiens fatigans*
A. geniculatus	*A. vexans*	*C. salinarius*
A. jamesi	*A. vittatus*	*C. tarsalis*
A. japonicus	*Anopheles freeborni*	*Culiseta inornata*
A. lepidus	*A. pulcherrimus*	*Mansonia albimanus*
A. pallirostris	*A. quadrimaculatus*	*M. perturbans*
A. pseudoalbopictus	*A. sacharovi*	

supplemented on the basis of the investigation of the collection material and new literature. Papers of the early authors were also studied and considered.

Development in vertebrate host

Sporozoites initiate the development of the first generation of primary exoerythrocytic meronts, the cryptozoites, which develop in reticuloendothelial cells. They are frequently seen in macrophages in the skin (Fig. 227, *2*) but were also found in other organs. Cryptozoites look like roundish or oval bodies, and the growing parasites usually possess small vacuoles. Multiple infection of the same host cell with several cryptozoites is common. Cryptozoites mature approximately 40 h after the infection. They possess a prominent residual body (Fig. 227, *3*). Approximately 50 to 200 elongated merozoites develop in cryptozoites (Fig. 227, *4*). Since the maturity of cryptozoites, the blood is infective for experimental birds who can be infected by blood subinoculation, but parasites are still absent in erythrocytes. Merozoites from cryptozoites are distributed via the blood stream, invade cells of the reticuloendothelium (mainly macrophages) in numerous organs and initiate development of the second generation of primary exoerythrocytic meronts, the metacryptozoites. It should be noted that metacryptozoites were never seen in the brain or bone marrow. Metacryptozoites mature approximately 70 to 75 h after infection with sporozoites. The morphology of cryptozoites and metacryptozoites, as well as merozoites, which develop in these meronts, is similar (Fig. 227, *3–6*). An important biological difference between them is that merozoites from metacryptozoites can invade erythrocytes but merozoites from cryptozoites cannot develop in the erythrocytes.

Part of merozoites from metacryptozoites initiate the secondary exoerythrocytic merogony (phanerozoites), while the other part of the merozoites invade erythrocytes and grow into asexual blood stages and gametocytes. Phanerozoites develop in reticuloendothelial cells in numerous organs (Fig. 227, *7–13*). They appear especially quickly in the cells of lymphoid-macrophage series in the skin, spleen, and lungs. Both the localization and the sequence of appearance of phanerozoites markedly vary depending on strain characteristics, age of birds, intensity of infection, stage of infection, and some other factors. It should be noted that merozoites from erythrocytic meronts also initiate the

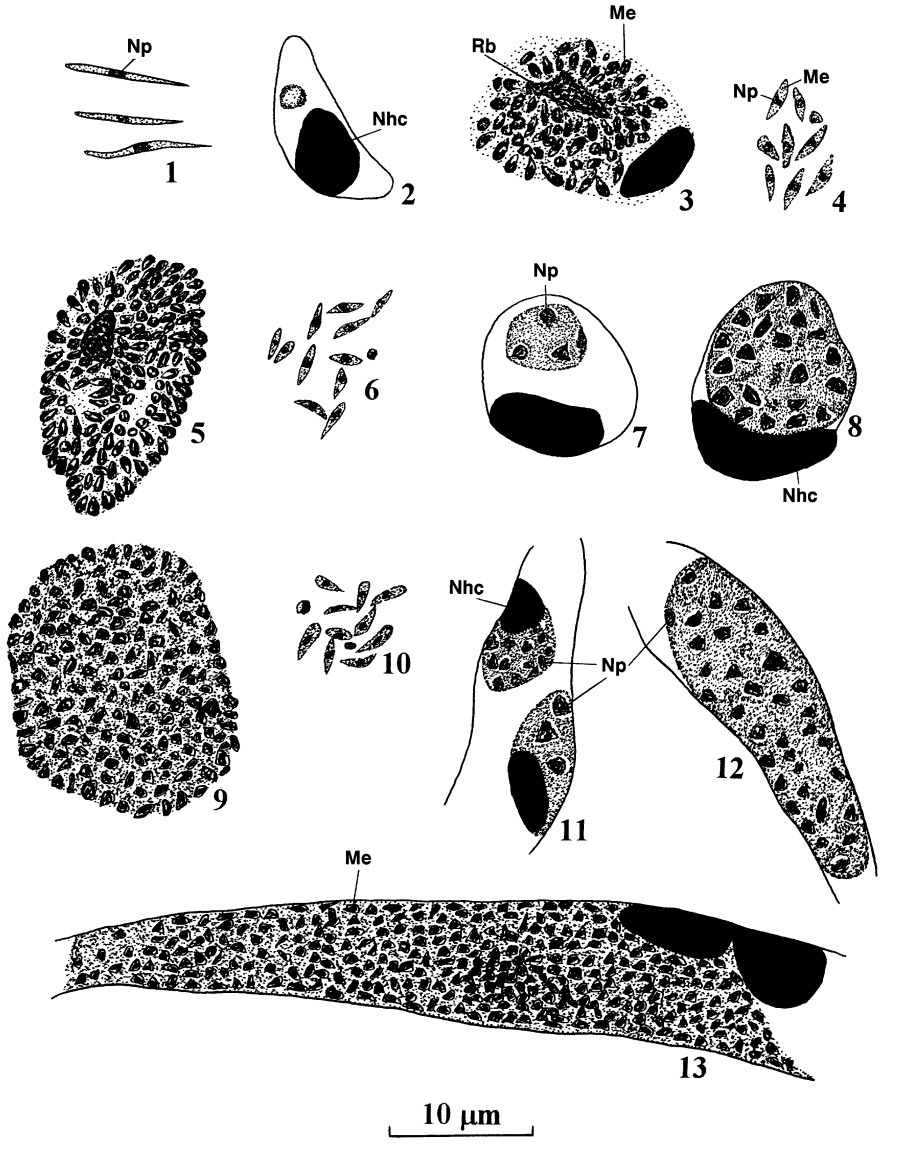

Figure 227 *Plasmodium gallinaceum:*
1 – sporozoites from *Aedes aegypti*; *2*, *3* – cryptozoites in macrophages of the skin: young parasite with two nuclei (*2*) and mature parasite with off-centre located residual body (*3*); *4* – merozoites from cryptozoites; *5* – mature metacryptozoite in lungs (small residual body is located off-centre); *6* – merozoites from metacryptozoites; *7–9* – phanerozoites in liver: immature parasites (*7*, *8*) and mature parasite (*9*); *10* – merozoites from phanerozoites; *11–13* – phanerozoites in capillaries of brain: immature parasites (*11*, *12*) and mature parasite (*13*); Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Rb – residual body. The exoerythrocytic meronts and merozoites are from experimentally infected *Gallus gallus.*

secondary exoerythrocytic merogony, and this complicates the course of the secondary exoerythrocytic development. The mass maturation of the first phanerozoites and the mass

release of merozoites from them take place approximately one week after the infection of birds with sporozoites. At this time, parasitemia increases dramatically, and phanerozoites now appear in the brain, and their number in other organs also increases. Phanerozoites are frequently seen in the lungs, spleen, liver, heart, kidneys, and brain, and they are less frequently recorded in the intestine, pancreas, bone marrow, thymus, testis, and breath muscle.

The morphology of all types of exoerythrocytic meronts, which develop in macrophages, is similar. They look like roundish or oval bodies with basophilic cytoplasm lacking large vacuoles, and they contain numerous nuclei (Fig. 227, *3*, *5*, *7–9*). The size of these meronts usually varies from 10 to 45 μm in diameter. In the growing meronts, a portion of cytoplasm, which adheres to the nuclei, is slightly lighter in colour than the remaining cytoplasm (Fig. 227, *7*, *8*). The morphology of phanerozoites, which develop in the endothelial cells of capillaries and sinusoids, is different (Fig. 227, *11–13*). They are of elongated worm-like form and contain several hundred merozoites. These meronts are usually about 60 μm long and even larger. It should be noted that it is difficult to calculate the correct number of merozoites in the elongated meronts because several parasites can develop in one cell, and the boundaries between the parasites are usually not visible. The analysis of histological sections shows that all types of exoerythrocytic meronts do not possess large (>1 μm in diameter) clear vacuoles. The vacuoles were sometimes seen in smear preparations, and it is likely that they are artefacts. Cytomeres are not seen in exoerythrocytic meronts. Even young meronts displace the nuclei of infected cells, and they can enucleate the host cells.

The morphology of merozoites, which develop in all types of exoerythrocytic meronts, is similar. In the histological sections, they look like oval or elongated bodies and possess a prominent nucleus (Fig. 227, *4*, *6*, *10*). The dimorphism of the merozoites, which was noted by some early authors, most probably is not real. The merozoites invade host cells both actively and passively (during the phagocytosis).

After infection with sporozoites, the exoerythrocytic merogony lasts not more than one month. After infection with blood containing mature erythrocytic meronts, the exoerythrocytic merogony lasts approximately 1.5 months. After this period, reticuloendothelial cells are not acquisitive to infection, and the parasite persists in birds due to a limited erythrocytic merogony.

The prepatent period is 70 to 75 h after the infection with sporozoites. At this time, merozoites from metacryptozoites invade erythrocytes and initiate the development of asexual blood stages and gametocytes. However, these merozoites are only slightly adapted to the development in the blood cells. The intensity of parasitemia during the first week of the infection is usually low. The parasitemia dramatically increases after mass maturation of phanerozoites which takes place approximately one week after infection. At this time, nearly all erythrocytes can be parasitized (Pl. II, *4*). The acute stage of the infection is approximately eight to ten days, and then the parasitemia rapidly decreases in surviving birds. However, a small number of parasites persist in the blood, and they can be found using the method of long-time microscopy of the stained blood films. Recrudescences of the high parasitemia have been recorded.

The erythrocytic merogony is synchronized. A cycle of the merogony is 36 h. The mass maturation and rupture of the erythrocytic meronts take place at midday and midnight on alternate days.

Gametocytes appear in the blood simultaneously with erythrocytic meronts. Merozoites from metacryptozoites, phanerozoites, and erythrocytic meronts initiate the develop-

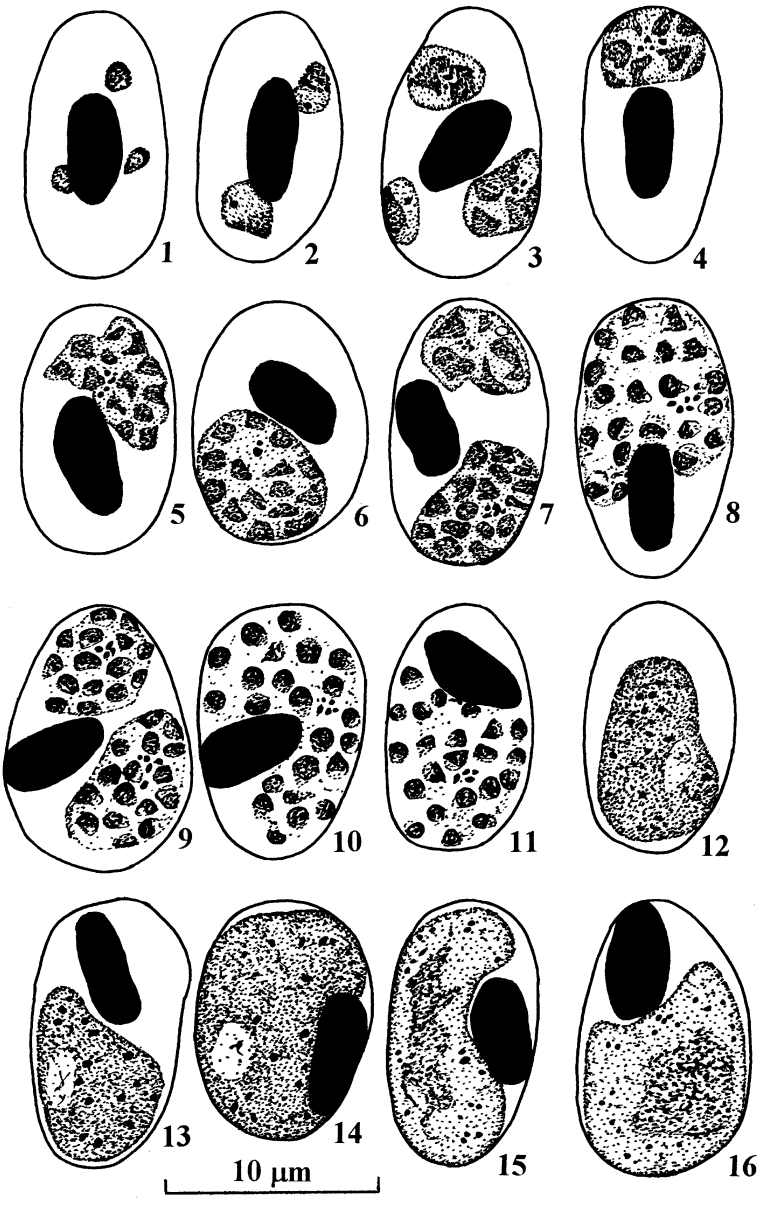

Figure 228 *Plasmodium gallinaceum* from the blood of *Gallus gallus:*
1, *2* – trophozoites; *3–11* – erythrocytic meronts; *12–14* – macrogametocytes; *15*, *16* – microgametocytes.

ment of gametocytes. The number of gametocytes varies markedly during different stages of the parasitemia. However, the gametocytes are always less numerous than erythrocytic meronts. Infectivity of gametocyte for the vector is highest in the beginning of primary parasitemia (before five to seven days), and it decreases later, most probably, due to the immune response.

Trophozoites (Fig. 228, *1*, *2*) are seen in mature and polychromatic erythrocytes; the earliest forms can be seen anywhere in infected erythrocytes, and are roundish or oval in form, sometimes irregular in shape, usually lacking vacuoles (Fig. 228, *1*); the typical 'ring' stage is not characteristic; growing trophozoites are of oval or irregular form, frequently touch the nuclei of erythrocytes (Fig. 228, *2*); the outline is even, and ameboid outgrowths are not seen; the parasite nucleus is large; pigment appears early, and a minute dark pigment granule is clearly seen in the young trophozoites (Fig. 228, *2*); largest trophozoites possess up to five (usually two or three) small pigment granules which are clumped off-centre into a spot; trophozoites only slightly influence infected erythrocytes, they do not deform the host cells and do not displace or only slightly displace their nuclei; however, a multiple infection of the same erythrocyte with several trophozoites is an exception, when infected erythrocytes can be markedly deformed and their nucleus displaced. At the peak of parasitemia, up to 10 trophozoites can be present in the same erythrocyte.

Erythrocytic meronts (Fig. 228, *3–11;* Pl. II, *4*) are seen in mature and polychromatic erythrocytes; the cytoplasm is plentiful, sometimes contains a few minute vacuoles; nuclei are large in growing meronts and can be up to 2.5 μm long; as the parasite develops, the size of the nuclei and the basophility of the cytoplasm markedly decreases; fully grown meronts vary markedly in form depending on their position in the infected erythrocytes; oval, roundish, and irregular meronts are common; nuclei are located randomly in fully grown meronts (Fig. 228, *8–11*); the number of merozoites in mature meronts varies from 8 to 36 (usually 16 to 20); pigment granules are of variable form, small size (<0.5 μm), dark-brown or black colour, not numerous (usually four to six per meront), clumped into a spot frequently close to the centre of meronts; young meronts usually only slightly influence on infected erythrocytes and their nuclei (Fig. 228, *4*, *5*); fully grown meronts markedly deform infected erythrocytes and displace their nuclei; during a multiple infection of the same erythrocyte, the influence of meronts on the host cells is much more evident (Fig. 228, *3*) than for the single infection; mature meronts markedly vary in size, and they occupy more than half of the cytoplasmic space in the infected erythrocytes; the largest meronts can occupy all available cytoplasmic space in the erythrocytes; mature merozoites are about 1 μm in diameter, they possess a prominent nucleus and a small portion of cytoplasm.

Macrogametocytes (Fig. 228, *12–14;* Pl. II, *4*) are seen in mature and polychromatic erythrocytes; the cytoplasm is homogeneous in appearance, usually lacking vacuoles, but occasionally a few small vacuoles are seen; young gametocytes look like trophozoites; fully grown gametocytes markedly vary in form depending on their position in infected erythrocytes, and oval and roundish gametocytes are common; the parasite nucleus is compact, variable in form and position, usually oval in shape, and frequently contains a clump of chromatin; pigment granules are roundish, usually of small (<0.5 μm), sometimes medium (0.5 to 1.0 μm) size, black, randomly scattered throughout the cytoplasm; the number of pigment granules in the type material (n = 34) varies from 8 to 22; fully grown gametocytes markedly deform infected erythrocytes, displace their nuclei and can enucleate the host cells (Fig. 228, *12*); the large gametocytes are more than 10 μm long and can occupy all available cytoplasmic space in the erythrocytes.

Microgametocytes (Fig. 228, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; vacuoles are not seen in the cytoplasm; pigment granules are smaller than in macrogametocytes, sometimes they are dust-like in appearance; the number of pigment granules in the type material (n = 17) varies from 12 to 30; other characters are as for macrogametocytes.

Development in vector

The range of experimental vectors is wide (Table 136). The susceptibility of different species of mosquitoes varies markedly. Representatives of the genera *Aedes* and *Armigeres* are especially susceptible. About 100% of *Aedes aegypti*, which is frequently used in experimental work, usually become infected. The susceptibility of mosquitoes to the infection can be easily changed by their selection. Peculiarities of the development of *P. gallinaceum* in *A. aegypti* at temperature of 24 to 28°C and relative humidity of about 80% are given below.

Gametocytes escaped from infected erythrocytes in the midgut of the vector approximately 7 or 8 min after the mosquito has become engorged. At 37°C, the exflagellation was seen 14 min after the ingestion of gametocytes, and it was recorded 10 min after the ingestion at 24°C. Microgametes look like elongated snake-like bodies with a prominent more or less centrally located nucleus, and they vary from 11 to 15 μm in length in preparations fixed with methanol. Zygotes look like roundish bodies with a compact nucleus and pigment granules. Zygotes are numerous in the midgut of mosquitoes 5 h after ingestion of gametocytes. The earliest stages of differentiation of ookinetes are seen approximately 12 h after the ingestion. Fully differentiated ookinetes are observed approximately 30 h after the infection. They are up to 16 μm in length. Undeformed ookinetes look like banana-like bodies. They possess a large nucleus, one or several large 'vacuoles' and numerous pigment granules. The apical end of ookinetes is slightly pointed, and the distal end is slightly rounded. Ookinetes first enter the midgut epithelial cells, then the space between the epithelial cells and move toward the basal lamina where they develop into oocysts (Torii *et al.*, 1992). The earliest oocysts are seen in the midgut of mosquitoes approximately 48 h after the infection. They are about 8 to 9 μm in diameter and possess a nucleus and numerous pigment granules. The oocysts grow until the ninth day post infection. Fully grown oocysts are usually up to 35 μm in diameter. As oocysts mature, the pigment granules clump into a spot and become obscured. Sporozoites appear in the salivary glands of the vector between the ninth and tenth days after the ingestion of gametocytes (Fig. 227, *1*). In fresh preparations, sporozoites look like slightly bow-shaped bodies about 10 μm in length. They possess a prominent nucleus. In preparations fixed with methanol, the sporozoites usually look like more straight bodies, and they usually do not exceed 9 μm in length. Both ends of sporozoites are pointed, but one end is pointed more than the other end (Fig. 227, *1*). Sporozoites persist in the vector for weeks and even months but their vitality decreases with growing age.

Pathogenicity. Malaria caused by *P. gallinaceum* is distributed in domestic chicken in the tropics of the Oriental zoogeographical region. Jungle fowls (*Gallus gallus*, *G. sonneratii*) are known to be the natural reservoir hosts. Pathogenicity of the parasite for the wild free-living hosts has not been investigated. Signs of illness are not recorded in the Jungle fowls. The disease is severe in all breeds of domestic chicken, and epizooties have been described in imported breeds of chickens on the endemic territories. The mortality rate depends both upon the age of birds and the mode of infection. Chickens of less than 250 g weight usually die, but the older chickens are less affected. Death is rare in adult birds but they also die occasionally. The death rate is much higher after infection with sporozoites than after the subinoculation of blood stages.

Infected birds are lethargic and unable to stand, mucous membranes are pale, feathers are ruffled, diarrhoea is often present. The bird's face and comb become congested. The first wave of death among infected chickens takes place at the peak of parasitemia approximately a week after the infection, and it is caused mainly by mass erythrocyte destruction

and severe anaemia. Numerous phanerozoites develop in the brain of the chickens which managed to survive the primary attack of the parasite. The phanerozoites block up the blood vessels in the brain and, as a result, the birds die with the cerebral signs during the second or third week after the infection. At autopsy, both liver and spleen are enlarged and contain malarial pigment. Fibrosis and marked hypertrophy of the spleen are obvious during the chronic stage of infection. An acute nephrotic syndrome has been recorded in infected birds. It is likely that this syndrome develops due to an antigen-antibody reaction.

Specificity. In nature, the parasite has been recorded only in Jungle fowls. Domestic chickens are the best experimental hosts. Pheasant *Phasianus colchicus* is also a good host. The blood stages develop (but not so well as in the above mentioned birds) in partridge *Perdix perdix*, peacock *Pavo cristatus*, turkey, guinea-fowl, goose, and duck. Domestic pigeon, canary, house sparrow *Passer domesticus*, and other passerine birds are resistant.

Comments. During the identification of this species, attention should be paid, first of all, to the following characters. First, fully grown gametocytes are large in size, frequently exceed 10 μm in length and can occupy all available cytoplasmic space in infected erythrocytes. Second, pigment granules in microgametocytes are slightly smaller in size than in macrogametocytes. Third, the periodicity of erythrocytic merogony is 36 h. Fourth, passerine birds are resistant. It should be also noted that the transmission has not been recorded outside the Oriental zoogeographical region so far.

5. **Plasmodium (Haemamoeba) matutinum** Huff, 1937

Plasmodium relictum matutinum Huff, 1937: 400. – *Plasmodium matutinum*: Corradetti *et al.*, 1960: 340, Fig. 1–8 (emend. pro *P. relictum matutinum*).

Type vertebrate host. *Turdus migratorius* (L.) (Passeriformes).
Additional vertebrate hosts. Some species of birds (Table 137).
Vectors. *Culex pipiens, C. pipiens fatigans, C. stigmatosoma, C. tarsalis* (Diptera: Culicidae).
Type locality. Kansas, Illinois, USA.
Distribution. This parasite has been frequently recorded in the Holarctic. Several records come from Mexico and the Oriental zoogeographical region. It is likely that the geographical range of this parasite is wider than is expected currently.
Type material. Neohapantotypes (*blood stages*: No. 243, 244, *Serinus canaria*, Italian strain, A. Corradetti; *sporogonic stages*: No. 247, micro- and macrogametes, 28.05.1962, A. Corradetti; No. 245, ookinetes *in vivo*, 29.05.1962) and paraneohapantotype (No. 246, other data as for No. 245) are deposited in CPG.
Etymology. The specific name is derived from the Latin word ‘matutinus’ and reflects a character of erythrocytic meronts of the New World strains to rupture in the morning.

Main diagnostic characters. Erythrocytic meronts contain large (up to 2 μm in diameter) vacuoles, and pigment granules do not gather around these vacuoles. Mature

Table 137 List of vertebrate hosts of *Plasmodium matutinum*.

Columba livia	*T. merula*
Hylocichla mustelina	*T. pilaris*
Passer domesticus	*Zenaida macroura*
Turdus iliacus	

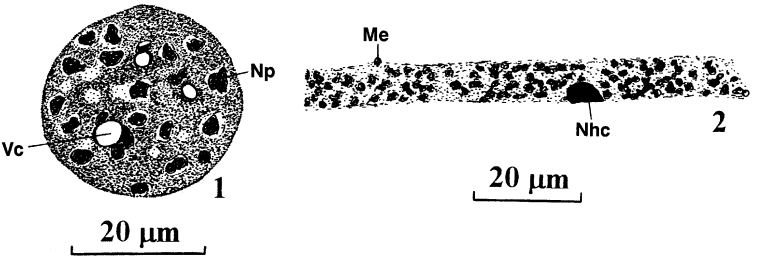

Figure 229 Phanerozoites of *Plasmodium matutinum:*
1 – immature parasite from *Columba livia*; *2* – mature parasite in brain of *Serinus canaria*; Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – vacuole (*1* is modified from Garnham, 1966; *2* is modified from Corradetti *et al*., 1960).

erythrocytic meronts do not possess a residual body, they produce 10 to 24 (usually 14 to 16) merozoites. Fully grown gametocytes are roundish or oval and do not exceed 10 μm in length. Pigment granules in gametocytes are roundish, of small size (<0.5 μm). Phanerozoites develop in numerous organs, and they contain not more than 300 merozoites. Phanerozoites are common in the brain.

Development in vertebrate host has been insufficiently studied (Huff, 1937; Manwell, 1940; Corradetti *et al.*, 1960; Becker, 1961; Garnham, 1966). Primary exoerythrocytic merogony has still not been investigated. Some indirect observations show that the primary exoerythrocytic development involves the sequence of cryptozoites and metacryptozoites in cells of the reticuloendothelial system in the skin and some other organs, typical of other species of the subgenus *Haemamoeba*. Phanerozoites were observed in naturally and experimentally infected birds in reticuloendothelial cells in the brain, liver, spleen, kidneys, bone marrow, lungs, heart muscle, and intestine. During heavy infection, the phanerozoites are also seen in the peripheral blood of pigeons. The sequence of appearance of phanerozoites in the above mentioned organs and the peculiarities of their localization vary depending both on the host species and the strain differences. The Italian strain killed the experimentally infected canaries before the phanerozoites appeared. The use of chemotherapy increases the vitality of canaries, and the phanerozoites then develop. It should be noted that the general peculiarity of the exoerythrocytic merogony for all strains of this parasite is that phanerozoites are numerous in the brain, where they develop in the endothelial cells of capillaries. Domestic pigeon is a good host for experimental investigation of the exoerythrocytic merogony. Numerous phanerozoites develop in various organs of the pigeon two to four weeks after subinoculation of infected blood. Two morphological types of phanerozoites develop, i.e., roundish (sometimes oval) and elongated (worm-like in shape). The roundish phanerozoites (Fig. 229, *1*) are seen in all above mentioned organs. They are up to 30 μm in diameter and sometimes even larger. The growing phanerozoites frequently possess one or several clearly defined large (>1 μm in diameter) vacuoles (Fig. 229, *1*). The worm-like phanerozoites (Fig. 229, *2*) are usually seen in brain capillaries. Mature phanerozoites of both these types contain not more than 300 merozoites, but usually their number is much less.

Erythrocytic merogony is clearly synchronized, and a cycle of the merogony is exactly 24 h. The meronts usually rupture in the morning (between 6 and 10 h in the New World strains, and between 11 and 12 h in the Italian strain). Garnham (1966) believed that the

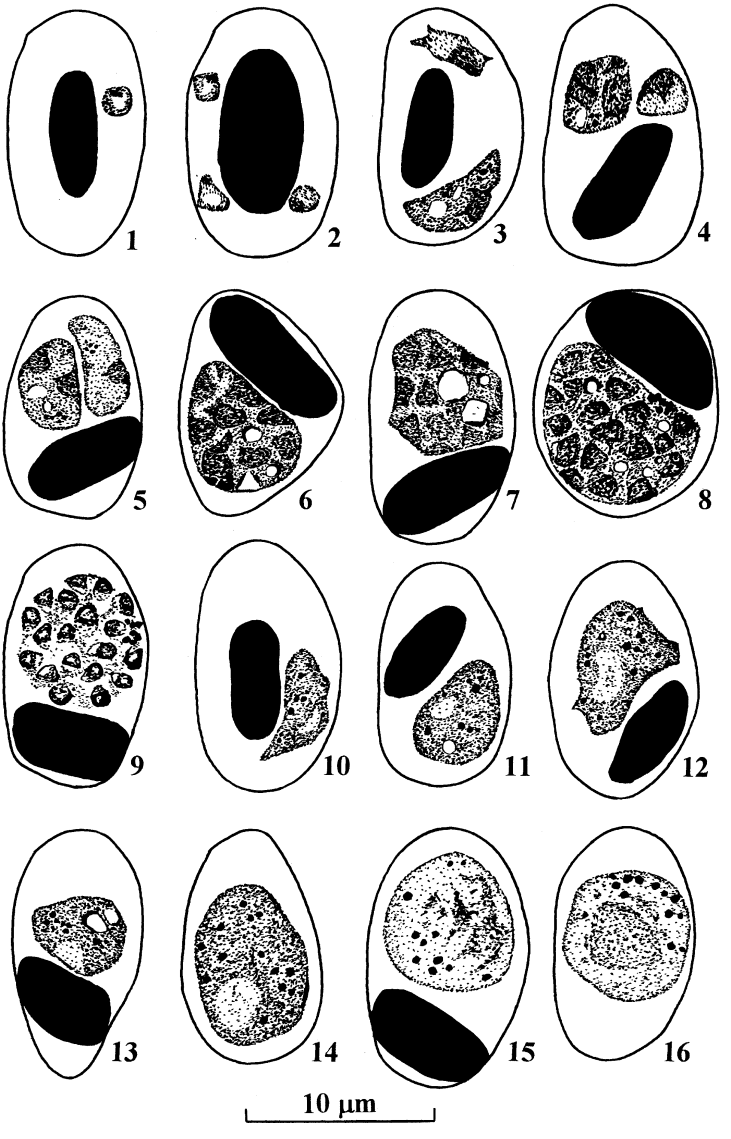

Figure 230 *Plasmodium matutinum* from the blood of *Serinus canaria:*
1–3 – trophozoites; *4–9* – erythrocytic meronts; *10–14* – macrogametocytes; *15*, *16* – microgametocytes.

strain S of *P. relictum*, which was isolated in Russia, belongs to *P. matutinum*. However, erythrocytic meronts of this strain rupture in the evening (Demina, 1959).

Gametocytes are numerous in the peripheral blood, and they appear simultaneously with asexual blood stages.

Trophozoites (Fig. 230, *1–3*) are seen in mature and polychromatic erythrocytes; the earliest trophozoites markedly vary in form, frequently possess a vacuole, and the typical 'ring' stage can be seen but the 'rings' are not numerous; as the parasite develops,

trophozoites take an irregular shape and are now more or less ameboid in outline; fully grown trophozoites (Fig. 230, *3*) are large, they reach the size of the nucleus of infected erythrocyte and possess plentiful basophilic cytoplasm and a large nucleus; one or several vacuoles are frequently seen in the advanced trophozoites; a few pigment granules, which are roundish, of minute size, dark colour and clumped into a spot, are present in fully grown trophozoites; infected erythrocytes are usually not deformed but their nuclei can be slightly displaced, however, trophozoites deform the host cells during the multiple infection of the same cell (Fig. 230, *3*, *4*).

Erythrocytic meronts (Fig. 230, *4–9*) are seen in mature and polychromatic erythrocytes; the cytoplasm is plentiful; growing meronts usually possess clearly defined vacuoles which can be up to 2 μm in diameter (Fig. 230, *7*); as the parasite develops, nuclei markedly decrease in size and vacuoles disappear; fully grown meronts are roundish, oval, or irregular, they occupy more than half of the cytoplasmic space in the infected erythrocytes and contain randomly located nuclei (Fig. 230, *9*); mature meronts contain 10 to 24 (usually 14 to 16) merozoites; pigment granules are of small size (<0.5 μm), usually dark colour, aggregated into a dense clump and, thus, are difficult to calculate; they never gather around the vacuoles; meronts markedly deform infected erythrocytes, they markedly displace their nuclei and even can enucleate the host cells; mature merozoites are roundish, about 1 μm in diameter, possess a prominent nucleus and a small portion of cytoplasm.

Macrogametocytes (Fig. 230, *10–14*) are usually seen in mature erythrocytes, but sometimes develop in polychromatic erythrocytes; the cytoplasm is homogeneous in appearance; young gametocytes are similar to trophozoites but possess pigment granules randomly scattered throughout the cytoplasm; growing gametocytes sometimes possess vacuoles which can be large (Fig. 230, *11*, *13*); fully grown gametocytes are usually roundish or oval, sometimes of irregular shape (Fig. 230, *12*); the parasite nucleus is compact, variable both in form and position; pigment granules are roundish, of small size (<0.5 μm), usually randomly scattered throughout the cytoplasm; their number varies from 3 to 20 (usually 10 to 15); gametocytes markedly deform infected erythrocytes, markedly displace their nuclei and can even enucleate the host cells (Fig. 230, *14*); fully grown gametocytes are of variable size but are not more than 10 μm in length.

Microgametocytes (Fig. 230, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Primary parasitemia increases rapidly. The peak of the parasitemia is usually four to five days after the first parasites appear in erythrocytes and even sooner. Then the parasitemia rapidly decreases, and only a few parasites, which are difficult to found, can be seen in the blood during the long-term chronic stage of infection.

Development in vector has been incompletely investigated (Garnham, 1966). The range of known vectors is restricted to mosquitoes of the genus *Culex*. The susceptibility of these mosquitoes to different strains of the parasite varies considerably. Some peculiarities of the development of the parasite in the mosquitoes at a temperature of 24 to 28°C are given below. Exflagellation was seen *in vitro* 10 to 15 min after exposure of blood with mature gametocytes to air. Microgametes possess a centrally located nucleus, and they are about 15 to 18 μm in length in preparations fixed with methanol. Macrogametes look like roundish bodies with a compact nucleus and numerous pigment granules. Ookinetes were seen in the midgut of the vectors 18 to 24 h after the ingestion of mature gametocytes. The ookinetes look like worm-like bodies about 14 μm in length and possess a large nucleus, several ‘vacuoles,’ and numerous pigment granules. Mature oocysts are observed 10 days

after the infection. They varied from 50 to 80 μm in diameter. The oocyst possesses pigment granules which quickly become clumped into a spot.

Pathogenicity. *Plasmodium matutinum* is a pathogenic parasite but the virulence of different strains is variable. The Italian strain causes the death in canaries between the 5th and 20th days after the inoculation of infected blood. The birds die because of massive parasitemia. Phanerozoites are not seen in the dead birds. At autopsy, both the liver and spleen are enlarged and contain the malarial pigment. The death was not recorded in other experimentally infected hosts except the canaries. The signs of illness were never seen in wild birds. However, the marked increase of parasitemia has been recorded in infected wild birds who were kept in the laboratory, and these birds could even have died during the recrudescences (Corradetti *et al.*, 1960). This probably happens due to stress conditions in the captivity which lead to subsequent decrease in birds' immune status.

Specificity. The range of vertebrate hosts has been insufficiently investigated (Table 137). This parasite has been especially frequently recorded in passerine birds. Canary and domestic pigeon are good experimental hosts. The ducklings of *Cairina moschata* and domestic chickens can also be infected, but they are more difficult to infect and parasitemia is usually no longer than three to four days. The experimental attempts to infect the quail *Coturnix coturnix* available and the Jungle fowl *Gallus gallus* were unsuccessful.

Comments. During the identification of *P. matutinum*, attention should be paid, first of all, to clear large vacuoles which are frequently present in growing erythrocytic meronts. However, it should be noted that the large vacuoles are present not in all erythrocytic meronts and, thus, the meronts typical of *P. matutinum* (see Fig. 230, *6, 7*) can be not found at low parasitemia.

Plasmodium matutinum is especially similar to *P. giovannolai*, and the identification of these species is difficult (see 'Comments' to *P. giovannolai*).

6. **Plasmodium (Haemamoeba) lutzi** Lucena, 1939

Plasmodium lutzi Lucena, 1939: 27, Fig. 1–9. – *P. relictum lutzi*: Garnham, 1966: 549 (emend. pro *P. lutzi*).

Type vertebrate host. *Aramides cajanea cajanea* Müller (Gruiformes).
Type locality. São Paulo State, Brazil.
Distribution. The Neotropical zoogeographical region.
Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 438, *Aramides cajanea*, lungs, 1974, Venezuela, A. Gabaldon; *blood stages*: No. 267, other data as for No. 438) and paraneohapantotype (No. 268, a duplicate of No. 267) are deposited in CPG. Part of paraneohapantotypes is deposited in IRCAH and CPGA.
Etymology. This species is named in honour of Dr. A. Lutz, who was among the first to find this parasite.

Main diagnostic characters. Pigment granules in gametocytes are roundish. Pigment granules in trophozoites, young erythrocytic meronts, and in gametocytes clearly tend to be clumped into a spot which is located near the margin of parasites; they can be aggregated into a solid mass of pigment in fully grown gametocytes. Large (>1 μm in diameter) vacuoles are not present in erythrocytic meronts. Mature erythrocytic meronts contain 6 to 26 (more frequently 10 to 18) merozoites.
Development in vertebrate host was studied by Gabaldon and Ulloa (1976b)

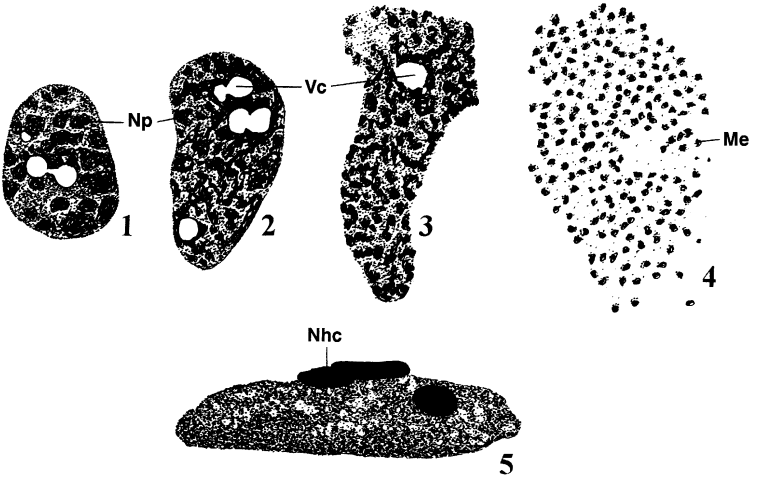

Figure 231 Phanerozoites of *Plasmodium lutzi* from *Aramides cajanea:*
1–3 – growing parasites in kidneys; *4* – mature parasite at the stage of segmentation into separate merozoites in liver; *5* – growing parasite in brain; Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – vacuole (modified from Gabaldon and Ulloa, 1976b).

who redescribed this species. Primary exoerythrocytic merogony has not been investigated. In the type vertebrate host, phanerozoites are especially frequently seen in the liver and kidneys, and are less frequently found in the lungs, spleen, and brain. In all these organs, except the brain, phanerozoites look like roundish or oval bodies with even margins (Fig. 231, *1–3*). In the brain, phanerozoites extend along the capillaries and are elongated (Fig. 231, *5*). Growing phanerozoites possess plentiful basophilic cytoplasm and large nuclei. Several (from one to five) clear vacuoles are frequently seen in the cytoplasm of phanerozoites. Outside the brain, large phanerozoites are up to 36 μm in length and 22 μm in width. Up to 200 merozoites develop in these phanerozoites (Fig. 231, *4*).

The dynamics of primary parasitemia is similar to that in *Plasmodium relictum*. Up to 20% of erythrocytes were parasitized at the peak of parasitemia in the type host. Erythrocytic merogony is only slightly (if at all) synchronized. All blood stages are present simultaneously in the type material.

Trophozoites (Fig. 232, *1–3*) are more frequently seen in polychromatic erythrocytes but are also present in mature erythrocytes; the earliest trophozoites are roundish and were seen anywhere in infected erythrocytes; the 'ring' stage is not characteristic but can be seen occasionally; as the parasite develops, trophozoites usually take an irregular shape and are more frequently seen in a polar or subpolar position in the erythrocytes (Fig. 232, *3*); a small vacuole is sometimes present in the cytoplasm; the parasite nucleus is large; pigment granules are small, dark-brown, usually clumped into a spot which is located near the margin of the parasite (Fig. 232, *3*); infected erythrocytes are deformed and their nuclei are displaced which is especially evident during the infection of the same erythrocyte with several trophozoites.

Erythrocytic meronts (Fig. 232, *4–9*) are seen in polychromatic and mature erythrocytes; vacuoles are usually not observed in the cytoplasm; as the parasite develops, nuclei of meronts markedly decrease in size, and the basophility of the cytoplasm also decreases; meronts are usually roundish or oval, sometimes of irregular shape; the nuclei

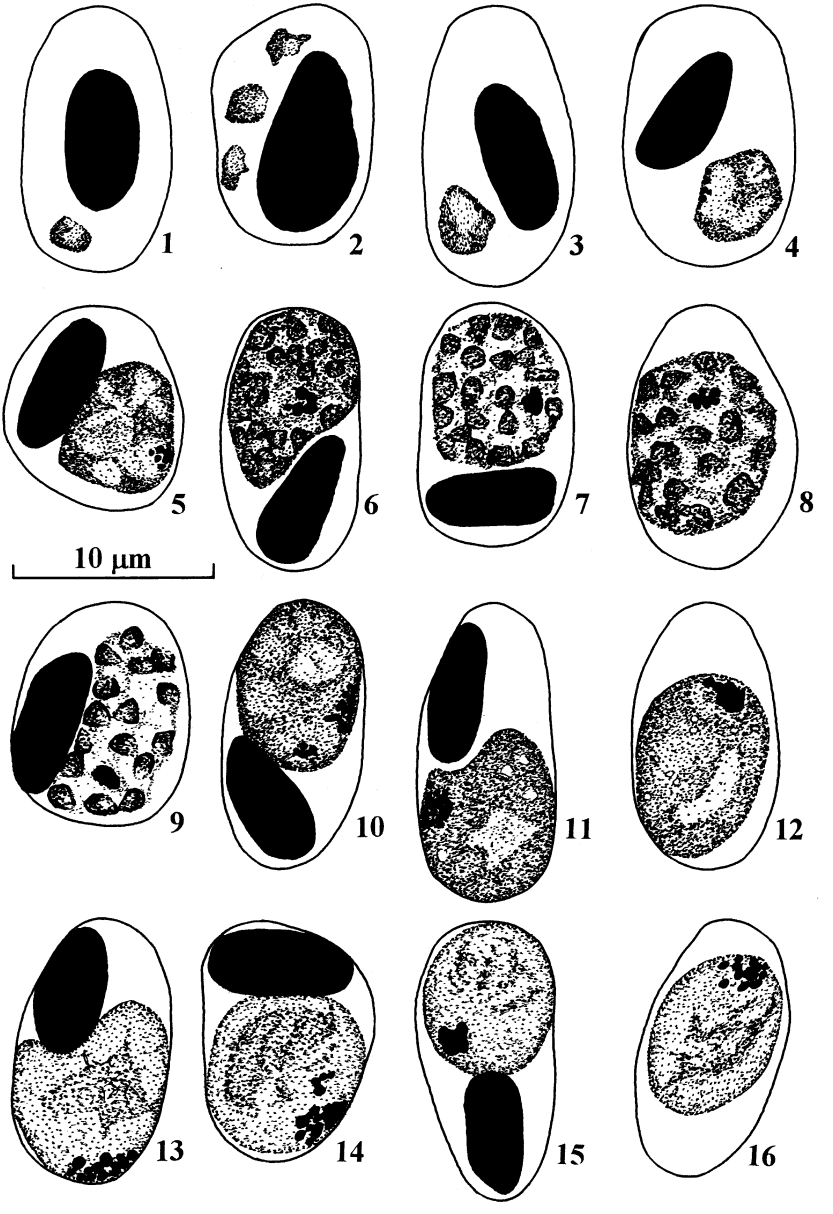

Figure 232 *Plasmodium lutzi* from the blood of *Aramides cajanea:*
1–3 – trophozoites; *4–9* – exoerythrocytic meronts; *10–12* – macrogametocytes; *13–16* – microgametocytes.

are located randomly in fully grown meronts (Fig. 232, *7–9*); mature meronts contain 6 to 26 (usually 10 to 18, on average about 15) merozoites; pigment granules are usually roundish, of small size (<0.5 μm), dark colour, numerous (up to 11); in young meronts, pigment granules clearly tend to be clumped into a spot which is located near a margin of the parasite (Fig. 232, *4*, *5*); in fully grown meronts, pigment granules are seen aggregated

into a large solid mass (Fig. 232, *7*, *9*); meronts deform infected erythrocytes, markedly displace the nuclei of erythrocytes and can even enucleate the host cells (Fig. 232, *8*); fully grown meronts (n = 10) vary from 6.5 to 9.8 (on average 7.6±0.9) μm in length, and from 5.3 to 7.1 (on average 6.4±0.6) μm in width.

Macrogametocytes (Fig. 232, *10–12*) are seen in mature and polychromatic erythrocytes; the cytoplasm is homogeneous in appearance, sometimes possesses small vacuoles; young gametocytes are morphologically identical to trophozoites; fully grown gametocytes are usually roundish or oval, sometimes of irregular shape; the parasite nucleus is compact, of variable form, usually subcentral in position; pigment granules are roundish, usually of small (<0.5 μm), sometimes medium (0.5 to 1.0 μm) size, clearly tend to be clumped into a spot which is located near a margin of the parasite (Fig. 232, *10, 11*), sometimes they are also seen aggregated into a large solid mass of pigment (Fig. 232, *12*); however, it is important to note that gametocytes with pigment granules randomly scattered throughout the cytoplasm (as in *P. relictum* gametocytes) are also present in the type material but are not numerous; the number of pigment granules in gametocytes can be up to 26 but is usually about 15; gametocytes deform the infected erythrocytes, markedly displace their nuclei, and can even enucleate the host cells (Fig. 232, *12*); fully grown gametocytes (n = 10) vary from 6.9 to 9.5 (on average 8.1±0.7) μm in length, and from 5.5 to 7.7 (on average 6.6±0.7) μm in width.

Microgametocytes (Fig. 232, *13–16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters. Gametocytes (n = 10) vary from 6.3 to 8.6 (on average 7.5±0.6) μm in length, and from 5.3 to 7.4 (on average 6.3±0.9) μm in width. Other characters are as for macrogametocytes.

P a t h o g e n i c i t y has not been investigated.

S p e c i f i c i t y. The range of natural hosts is unknown. Attempts to infect canary, domestic chicken, domestic pigeon, and quail *Coturnix coturnix* were unsuccessful.

C o m m e n t s. *Plasmodium lutzi* is especially similar to *P. relictum*. During the identification of *P. lutzi*, attention should be paid, first of all, to the clearly evident tendency of pigment granules in trophozoites, young meronts, and gametocytes to be clumped into a spot near a margin of the parasites. This character is also sometimes seen in *P. relictum* and some other species of the subgenus *Haemamoeba*. However, the aggregation of pigment granules into a spot, which is located close to the margin of the parasite, is the predominant mode of the location of pigment in *P. lutzi*, and this is especially evident in gametocytes. In addition, large vacuoles are frequently present in phanerozoites of *P. lutzi* and they are not characteristic of *P. relictum*. Furthermore, *P. lutzi* does not infect the canary which is a perfect experimental host for *P. relictum*.

7. **Plasmodium (Haemamoeba) giovannolai** Corradetti, Verolini and Neri, 1963

Plasmodium giovannolai Corradetti, Verolini and Neri, 1963b: 11, Pl. 1, Fig. 1–23, Pl. 2, Fig. 1–6, Pl. 3, Fig. 1–14.

T y p e v e r t e b r a t e h o s t. *Turdus merula* (L.) (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s are unknown in nature.
V e c t o r. *Culex pipiens* (Diptera: Culicidae).
T y p e l o c a l i t y. Castelli romani (Provincia di Roma, Lazio, Italy).

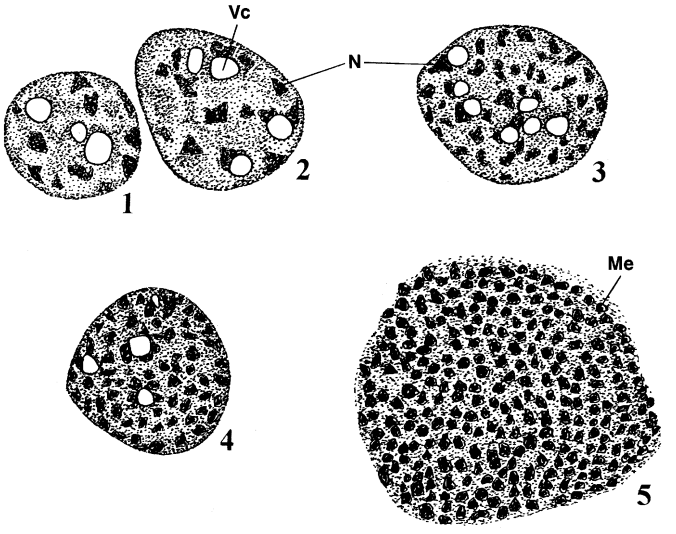

Figure 233 Phanerozoites of *Plasmodium giovannolai* from *Serinus canaria:*
1–4 – growing parasites at different stages of their development; *5* – mature parasite with nearly developed merozoites; Me – merozoite; N – nucleus; Vc – vacuole (modified from Corradetti *et al*., 1963).

Distribution. This parasite has only been recorded in the type locality so far.
Type material. Hapantotypes (*exoerythrocytic meronts*: No. 204, *Serinus canaria*, spleen, A. Corradetti; *blood stages*: No. 200–203, *Serinus canaria*, 24–25.03.1961, A. Corradetti) are deposited in CPG. A blood smear from the type vertebrate host (No. 205, not included into the type series) is deposited in CPG.
Etymology. This species is named in honour of Italian parasitologist Dr. Arnaldo Giovannola in recognition of his contribution to the field of avian malariology. He died tragically at the age of 29.

Main diagnostic characters. Erythrocytic meronts frequently possess large (up to 2 μm in diameter) clear vacuoles, and pigment granules do not gather around these vacuoles. Mature erythrocytic meronts do not possess a residual body; they produce 10 to 30 (more frequently 18) merozoites. Pigment granules in gametocytes are roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size. Phanerozoites develop mainly in the spleen; they can contain 300 and even more merozoites. Phanerozoites do not develop in the brain.

Development in vertebrate host was studied by Italian scientists (Corradetti *et al.*, 1963b, 1963c). Primary exoerythrocytic merogony has not been investigated. Parasites appear in erythrocytes of canaries on the ninth day after infection with sporozoites. Thus, the primary exoerythrocytic merogony is completed no later than eight to nine days after the infection. Phanerozoites developed in canaries both after infection with sporozoites and after subinoculation of infected blood. It is important to note that numerous passages of infected blood (up to 20 and even more) do not reduce the ability of the parasite to produce phanerozoites. Phanerozoites develop in wandering monocytes and macrophages. The spleen is the main place of their localization. A few phanerozoites are seen in the liver and bone marrow, but were never observed in the brain. Phanerozoites are especially numerous

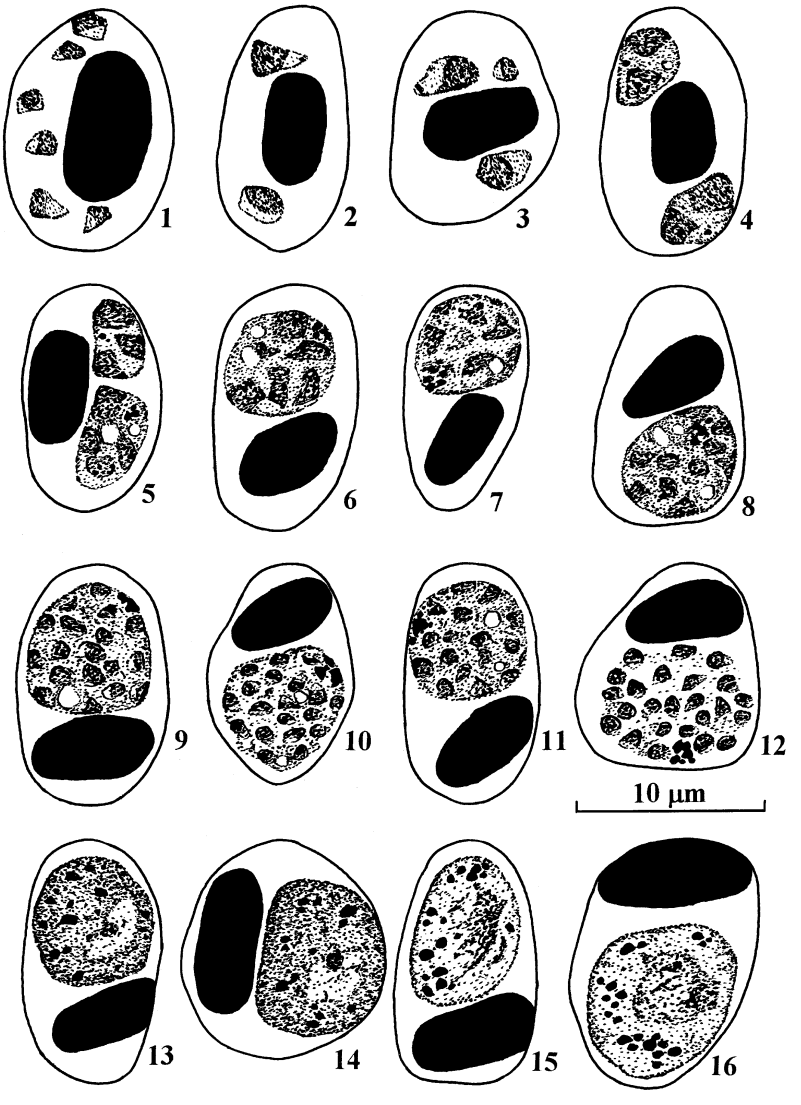

Figure 234 *Plasmodium giovannolai* from the blood of *Serinus canaria:*
1–3 – trophozoites; *4–12* – erythrocytic meronts; *13*, *14* – macrogametocytes; *15*, *16* – microgametocytes.

in experimentally infected canaries at the late stage of the infection than in the early or acute stages. They are usually not seen before the ninth day after the blood-induced infection, and are not numerous at the top of parasitemia, but, later, the number of phanerozoites increases markedly. Phanerozoites are seen in the spleen of canaries a month and even later after the blood-induced infection. Phanerozoites look like roundish or oval bodies. The growing parasites possess basophilic cytoplasm and large nuclei, and clear large vacuoles are frequently seen in the cytoplasm (Fig. 233, *1–3*). The mature phanerozoites are filled up with a homogeneous mass of small (about 1 μm in diameter) merozoites that look like

roundish or slightly oval bodies (Fig. 233, *5*). It was noted in the original description (Corradetti *et al.*, 1963b) that two morphological types of merozoites develop in phanerozoites, i.e., macro- and micromerozoites, and this issue requires additional investigation. Mature phanerozoites vary from 18.0 to 38.4 μm in length, and from 12.0 to 19.2 μm in width. About 300 and even more merozoites were seen in large mature phanerozoites.

The prepatent period in canaries is about eight to nine days after the infection with sporozoites, and it is recorded to be only about three days after the blood-induced infection. The peak of the parasitemia is recorded approximately 23 to 25 days after the infection with sporozoites, and the infected canaries died within several days after the parasitemia reached its peak. After the blood-induced infection, the parasitemia increased much more rapidly, and canaries usually died between the 7th and 30th day after infection.

Erythrocytic merogony is clearly synchronized. The cycle of the merogony is equal to 24 h. Erythrocytic meronts rupture in the morning (usually between 6 and 9 h).

Trophozoites (Fig. 234, *1–3*) are more frequently seen in polychromatic erythrocytes in the type material but they also develop in mature erythrocytes; growing trophozoites are variable in form, frequently irregular in shape, and possess a prominent nucleus and a portion of basophilic cytoplasm; a 'ring' stage is not characteristic; vacuoles were not seen or appeared occasionally in fully grown trophozoites; as the parasite develops, the nucleus markedly increases in size (Fig. 234, *2*, *3*); fully grown trophozoites possess one to three small (<0.5 μm), dark pigment granules which are clumped into a spot; trophozoites slightly displace the nuclei of infected erythrocytes, however, they deform the erythrocytes and displace their nuclei during multiple infection of the same erythrocyte (Fig. 234, *3*).

Erythrocytic meronts (Fig. 234, *4–12*) are seen in polychromatic and mature erythrocytes; the cytoplasm is plentiful, and usually contains prominent vacuoles which appear in young meronts, and they persist until the segmentation of meronts; the vacuoles vary in form and size and frequently exceed 1 μm in diameter but never exceed 2 μm; young meronts possess large nuclei (Fig. 234, *4–7*) which markedly decrease in size as the parasites mature (Fig. 234, *8–11*); basophility of cytoplasm also markedly decreases in mature meronts; fully grown meronts occupy more than half of the cytoplasmic space in the infected erythrocytes, and they are roundish or oval with randomly located nuclei; mature meronts contain 10 to 30 (most frequently 18) merozoites which are about 1 μm in diameter; pigment granules are of small size (<0.5 μm), dark, clumped into a spot and can be aggregated into one or several solid masses (Fig. 234, *10*); they never gather around the vacuoles; meronts markedly deform infected erythrocytes (Fig. 234, *10*, *12*), significantly displace their nuclei and can even enucleate the host cells.

Macrogametocytes (Fig. 234, *13*, *14*) are seen in polychromatic and mature erythrocytes; the cytoplasm is homogeneous in appearance, usually lacking vacuoles; young gametocytes are similar to trophozoites; fully grown gametocytes occupy more than half of the cytoplasmic space in the infected erythrocytes, and they are roundish or oval in form; the parasite nucleus is compact, relatively large, possesses a well defined nucleolus (Fig. 234, *13*, *14*); pigment granules are roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, vary (n = 14) from 8 to 23 (usually 12 to 15), randomly scattered throughout the cytoplasm; gametocytes deform infected erythrocytes and displace their nuclei; fully grown gametocytes do not exceed 10 μm in length.

Microgametocytes (Fig. 234, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment is more plentiful than in macrogametocytes; other characters are as for macrogametocytes.

Development in vector has not been studied in detail. The mosquito *Culex pipiens* can be easily infected. Sporozoites are seen in the salivary glands of the mosquito six to eight days after the ingestion of gametocytes (Corradetti *et al.*, 1963b).

Pathogenicity has been insufficiently investigated. Canaries die within a month after experimental infection.

Specificity. The range of natural hosts is unknown. Canary is a good experimental host.

Comments. Identification of *P. giovannolai* solely on the basis of blood smears is difficult, and probably even impossible at low natural infection. This parasite is especially similar to *P. matutinum*. During the identification of these species in subinoculated canaries the attention should be paid, first of all, to the following characters. First, vacuoles in trophozoites of *P. giovannolai* are not seen or appeared occasionally, but they are frequently present in trophozoites of *P. matutinum*. Second, vacuoles in young erythrocytic meronts of *P. giovannolai* are not so clearly defined and less frequently seen than in young meronts of *P. matutinum*. Third, pigment in gametocytes of *P. giovannolai* is more prominent than in gametocytes of *P. matutinum* (cf. Figs. 230, *14–16* and 234, *13–16*). However, the above mentioned features cannot be attributed to the group of good diagnostic characters, and they can be estimated only at high parasitemia in well prepared blood films. Phanerozoites of *P. giovannolai* develop nearly exclusively in the spleen (they were never seen in the brain), and they contain numerous (300 and even more) merozoites. These characters were noted among the main distinctive features of *P. giovannolai* in the original description. Phanerozoites of *P. matutinum* develop in numerous organs, including the brain, and this is the main difference between these species. However, the number of merozoites, which develop in the phanerozoites of *P. matutinum*, is also large (close to 300) and, thus, it is difficult to distinguish these species on the basis of the number of merozoites in their phanerozoites. Further investigation of *P. giovannolai* is required. It is possible that *P. giovannolai* can be a subspecies of *P. matutinum*.

8. **Plasmodium (Haemamoeba) griffithsi** Garnham, 1966

Plasmodium griffithsi Garnham, 1966: 619, Pl. 49, Fig. 12–19.

Type vertebrate host. *Meleagris gallopavo* L. (Galliformes).
Additional vertebrate hosts. Unknown.
Type locality. Rangoon, Burma.
Distribution. This parasite has been recorded only in the type locality.
Type material. Hapantotype (No. 249–251, *Meleagris gallopavo*, 1961, Rangoon, Burma, R.B. Griffiths) is deposited in CPG.
Etymology. This species is named in honour of Dr. R.B. Griffiths, who discovered the parasite in turkeys.

Main diagnostic characters. Erythrocytic meronts frequently possess large (up to 2 μm in diameter) vacuoles; pigment granules do not gather around these vacuoles. Mature erythrocytic meronts contain a large residual body; they produce 16 to 20 (on average 18) merozoites. Gametocytes, which are oval-elongated (Fig. 235, *13*, *15*), are present; they can be larger than 10 μm in length. Pigment granules in gametocytes are roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size.

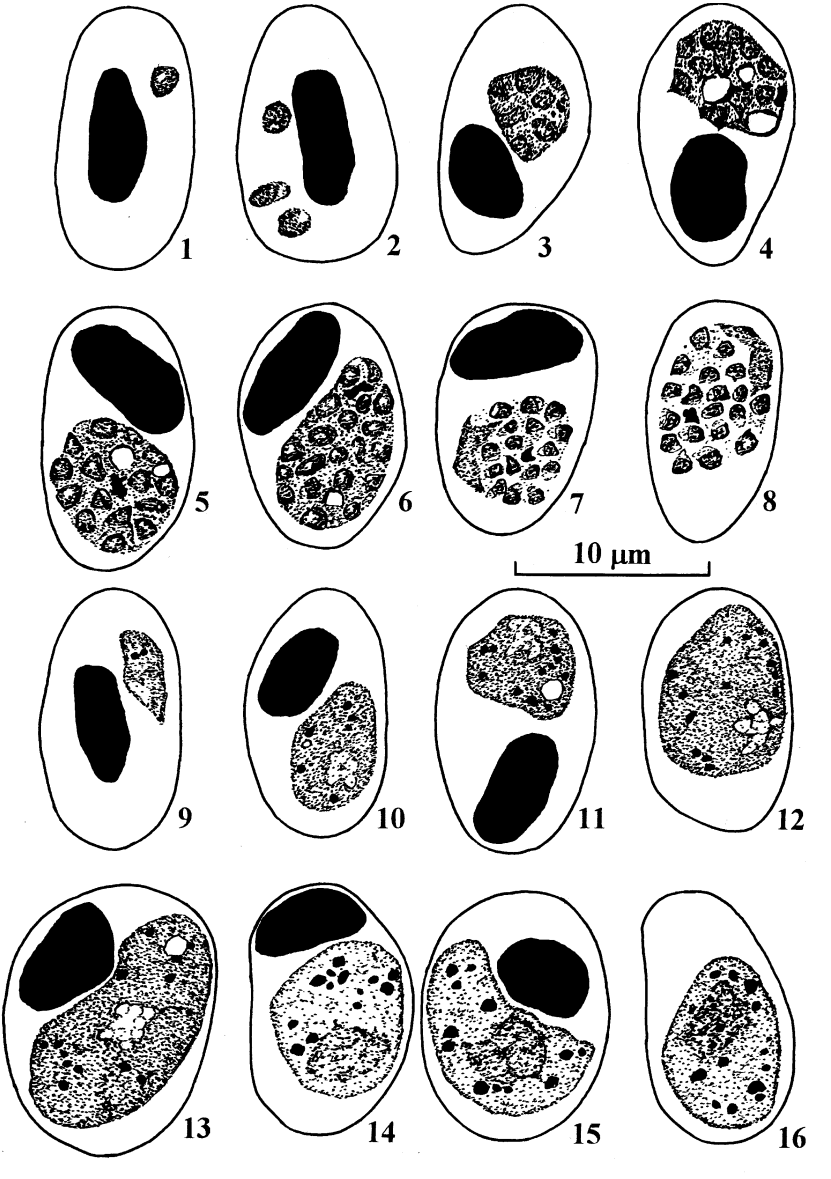

Figure 235 *Plasmodium griffithsi* from the blood of *Meleagris gallopavo:*
1, *2* – trophozoites; *3–8* – erythrocytic meronts; *9–13* – macrogametocytes; *14–16* – microgametocytes.

Development in vertebrate host

Exoerythrocytic merogony, periodicity, and development in vector have not been investigated.

Trophozoites (Fig. 235, *1*, *2*) are seen in mature, sometimes in polychromatic erythrocytes; growing parasites are roundish or oval solid bodies with a large nucleus; the 'ring' stage is not characteristic; advanced parasites possess a few small, dark pigment

granules; trophozoites only slightly influence infected erythrocytes whose nuclei can be slightly displaced (Fig. 235, *2*).

Erythrocytic meronts (Fig. 235, *3–8*) are seen in mature erythrocytes; one or several (up to 4) clear vacuoles are frequently present in the cytoplasm; the vacuoles vary in size and the largest of them are up to 2 μm in diameter; the vacuoles are especially evident and common in medium grown meronts whose size exceeds that of the nuclei of infected erythrocytes (Fig. 235, *4*); as the parasite develops, nuclei and vacuoles markedly decrease in size (Fig. 235, *6*) and basophility of cytoplasm also decreases; vacuoles are absent in mature meronts (Fig. 235, *7*); fully grown meronts usually are roundish or oval in form, sometimes irregular in shape, they possess randomly located nuclei; mature meronts contain 16 to 20 (on average 18) merozoites; a large amorphous residual body is present in mature meronts, and it locates near the edge of the parasite (Fig. 235, *7*, *8*); pigment granules are roundish, of small size (<0.5 μm), clumped into a spot or aggregated into a solid mass of pigment (Fig. 235, *6–8*); fully grown meronts usually occupy more than half of the cytoplasmic space in the infected erythrocytes, they markedly deform the erythrocytes, displace their nuclei and even can enucleate the host cells (Fig. 235, *8*).

Macrogametocytes (Fig. 235, *9–13*) are seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, frequently contains one or several clear vacuoles which do not exceed 1 μm in diameter (Fig. 235, *11*); young gametocytes are slightly elongated (Fig. 235, *9*), they are similar to trophozoites; fully grown gametocytes are roundish, oval, and oval-elongated (Fig. 235, *12, 13*); the parasite nucleus is variable in form and position, relatively small (Fig. 235, *13*); pigment granules are roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; the number of pigment granules in the type material varies (n = 19) from 6 to 19 (more often about 13); gametocytes markedly deform infected erythrocytes, they markedly displace their nuclei and even can enucleate the host cells (Fig. 235, *12*); the oval-elongated gametocytes usually exceed 10 μm in length.

Microgametocytes (Fig. 235, *14–16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment is more plentiful and the pigment granules look a bit lighter in colour than in macrogametocytes; other characters are as for macrogametocytes.

Comments. *Plasmodium griffithsi* can be distinguished from other species of the subgenus *Haemamoeba*, first of all, on the basis of its (i) oval-elongated fully grown gametocytes (Fig. 235, *13*, *15*) and (ii) the large amorphous residual body in mature erythrocytic meronts (Fig. 235, *7*, *8*). Both these characters are seen during development of the parasite in turkeys. It should be noted that the latter character is unique for avian malaria parasites.

9. **Plasmodium (Haemamoeba) tejerai** Gabaldon and Ulloa, 1977

Plasmodium tejerai Gabaldon and Ulloa, 1977: 271, Fig. 1–131.

Type vertebrate host. *Meleagris gallopavo* L. (Galliformes).
Additional vertebrate hosts. Natural hosts are unknown. *Anas platyrhynchos*, *Anser anser*, *Columba livia*, *Coturnix coturnix*, *Dendrocygna autumnalis*, *Gallus gallus* and *Numida meleagris* were infected experimentally.
Type locality. Santa Inés, municipio Miranda, Trujillo, Venezuela.

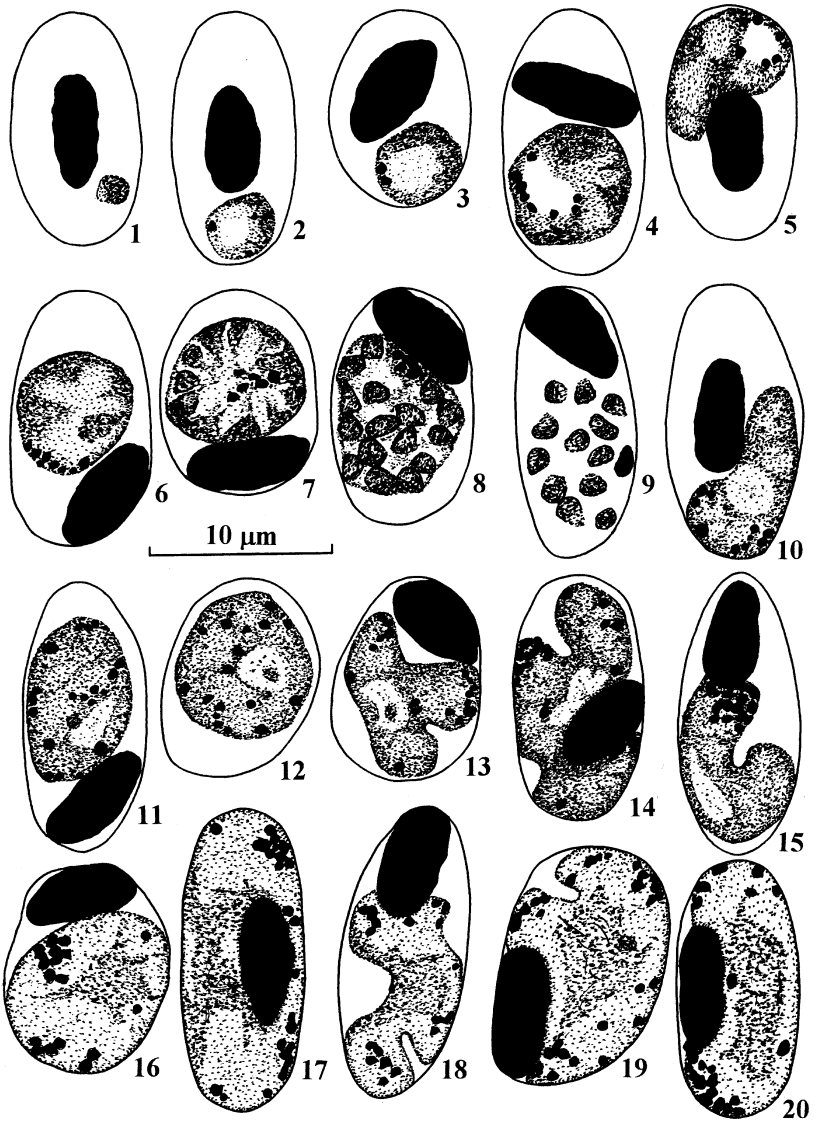

Figure 236 *Plasmodium tejerai* from the blood of *Meleagris gallopavo:*
1–3 – trophozoites; *4–9* – erythrocytic meronts; *10–15* – macrogametocytes; *16–20* – microgametocytes.

Distribution. This parasite has been recorded only in Venezuela so far.
Type material. Hapantotypes are deposited in CPGA; parahapantotype is deposited in IRCAH. It was noted in the original description that part of parahapantotypes was deposed in the CPG (Wellcome Museum of Medical Sciences, London). However, the type material is absent in the CPG.
Etymology. This species is named in honour of Venezuelan parasitologist Dr. Enrique Tejera.

Main diagnostic characters. Fully grown trophozoites and young erythrocytic meronts possess a large (frequently greater than 2 μm in diameter) vacuole, and pigment

granules gather around this vacuole. Erythrocytic meronts produce 8 to 24 (usually 10 to 15) merozoites. Pigment granules in gametocytes are roundish. Lobulated gametocytes are present.

This parasite was studied by Gabaldon and Ulloa (1977) in detail.

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. Phanerozoites are especially frequently seen in the brain, kidney, liver, and spleen, and they are less frequently found in the heart, lungs, and bone marrow. Young phanerozoites possess plentiful cytoplasm and large nuclei. In the brain, phanerozoites extend along the capillaries, and the largest parasites measured up to 80 μm in length and 16 μm in width. They contain up to 200 merozoites. According to the original description, two types of merozoites (macro- and micromerozoites) develop in phanerozoites in the brain. Micromerozoites are about 1 μm in diameter, and macromerozoites are approximately 2 μm in length and 1.5 μm in width. In all other organs, phanerozoites look like roundish or oval bodies. Vacuoles are not seen. The large phanerozoites vary from 34 to 43 μm in length and from 19 to 30 μm in width. They contain approximately 100 to 200 merozoites which are roundish in shape.

At the peak of parasitemia, up to 15% of erythrocytes were parasitized in experimentally infected birds.

Trophozoites (Fig. 236, *1–3*) are seen in polychromatic and mature erythrocytes; earliest parasites are roundish or oval in form; fully grown trophozoites are roundish, even in outline, usually polar or subpolar in position, possess a large (frequently greater than 2 μm in diameter) centrally located vacuole or clear light zone (Fig. 236, *2, 3*); the parasite nucleus is located at one side of trophozoite (Fig. 236, *2*, *3*); pigment granules are roundish, of small size (<0.5 μm), brown colour, their number varies from one to four, and they gather around the vacuole (Fig. 236, *3*); large trophozoites deform infected erythrocytes and displace their nuclei; this is especially evident during the infection of the same erythrocyte with several trophozoites.

Erythrocytic meronts (Fig. 236, *4–9*) are seen in polychromatic and mature erythrocytes; young meronts possess highly basophilic cytoplasm and a large (frequently greater than 2 μm in diameter) clear vacuole (Fig. 236, *4*, *5*); as the parasite develops, the basophility of cytoplasm decreases, the vacuole disappears, a light zone appears in the centre of meront, and the nuclei then are seen located off-centre along the periphery of meronts (Fig. 236, *6*, *7*); nuclei markedly decrease in size in mature meronts; fully grown meronts usually roundish or oval in form, sometimes irregular or even elongated in shape, contain randomly located nuclei; meronts produce 8 to 24 (usually 10 to 15, on average 13.4) merozoites; pigment granules are roundish, usually of small size (<0.5 μm), dark-brown or black; pigment granules gather around the vacuole in young meronts (Fig. 236, *4*, *5*), they are clumped in a loose group after disappearance of the vacuole (Fig. 236, *6*, *7*) and they are then seen clumped into a spot or even aggregated into a solid mass in mature meront (Fig. 236, *8*, *9*); meronts markedly deform infected erythrocytes and displace their nuclei; fully grown roundish and oval meronts vary from 6.4 to 8.7 (on average 7.9) μm in length, and from 5.8 to 7.5 (on average 6.5) μm in width; mature merozoite possesses a prominent nucleus and a small portion of cytoplasm (Fig. 236, *9*); the merozoites usually exceed 1 μm in diameter.

Macrogametocytes (Fig. 236, *10–15*) are seen in mature and polychromatic erythrocytes; fully grown gametocytes markedly vary in form, but roundish and oval gametocytes (Fig. 236, *11*, *12*) predominate; elongated gametocytes (Fig. 236, *10*) and circumnuclear

forms, which occupy all available cytoplasmic space in erythrocytes, are seen; it is important to note that lobulated in shape gametocytes (Fig. 236, *13–15*) develop and their number varies in different vertebrate hosts but they are always present; the parasite nucleus is compact, variable both in form and position, possesses a prominent nucleolus; pigment granules are roundish, of dark colour, small (<0.5 μm) and medium (0.5 to 1.0 μm) size, usually randomly scattered throughout the cytoplasm but also seen in clumps (Fig. 236, *14*, *15*); the number of pigment granules varies from 10 to 47 (usually about 20); gametocytes deform infected erythrocytes, they displace their nuclei and even can enucleate the host cells (Fig. 236, *12*); gametocytes markedly vary in size which depends on their shape; oval gametocytes vary from 9.5 to 13.3 (on average 11.6) μm in length, and from 3.4 to 7.5 (on average 6.0) μm in width.

Microgametocytes (Fig. 236, *16–20*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters; microgametocytes are even more variable in form than macrogametocytes, and their size is a bit larger than for macrogametocytes; the number of pigment granules varies from 16 to 33 (usually about 20); other characters are as for macrogametocytes.

Development in vector has not been investigated, and vectors are still unknown. Exflagellation was seen 8 to 10 min after exposure of blood with mature gametocytes to air at a temperature of 22 to 24°C. Ookinetes were observed in the midgut of the mosquito *Aedes aegypti* between 24 and 27 h after ingestion of gametocytes. Fully grown ookinetes vary from 13.2 to 16.7 μm in length, and from 3.3 to 4.4 μm in width. Nucleus of ookinete measured about 2.8 μm in length and 1.9 μm in width. Pigment granules are present in ookinetes. Oocysts do not develop in the mosquitoes *A. aegypti* and *Culex pipiens fatigans*.

Pathogenicity. Mortality rate among experimentally infected turkey poults, ducklings, and domestic pigeons was recorded to be over 50% after the blood-induced infection.

Specificity. The range of natural hosts has not been investigated. Domestic pigeon, duck and turkey are good experimental hosts. Geese, guinea-fowl, and wood duck *Dendrocygna autumnalis* are also infected experimentally. Domestic chicken and quail *Coturnix coturnix* can be infected with difficulty, but parasitemia is not high and it decreases rapidly. Canary is resistant.

Comments. *Plasmodium tejerai* is characterized by variable-form gametocytes. Roundish and oval in shape gametocytes predominate, and thus this parasite is attributed to the subgenus *Haemamoeba*. Lobulated in shape gametocytes are seen in all experimentally infected hosts, and they are a characteristic feature of this species.

10. **Plasmodium (Haemamoeba) coturnixi** Bano and Abbasi, 1983

Plasmodium coturnixi Bano and Abbasi, 1983: 17, Fig. 1–6.

Type vertebrate host. *Coturnix coturnix* (L.) (Galliformes).
Additional vertebrate hosts. Unknown.
Type locality. Kohat, Pakistan.
Distribution. This parasite has been recorded only in the type locality so far.
Type material was not designated in the original description.

Etymology. The specific name is derived from the name of the type vertebrate host, *Coturnix coturnix*.

Main diagnostic characters. Without multiple infection of one host cell, trophozoites do not displace or only slightly displace the nuclei of infected erythrocytes. Fully grown meronts and gametocytes occupy more than half of the cytoplasmic space in the infected erythrocytes and they even can occupy all available cytoplasmic space in the host cells. Large (>1 μm in diameter) vacuoles are absent in erythrocytic meronts. The maximum number of merozoites in mature erythrocytic meronts is greater than 16. Pigment granules in gametocytes are roundish or oval, randomly scattered throughout the cytoplasm. Length of largest gametocytes exceed 10 μm. Periodicity of erythrocytic merogony is 24 h. Domestic chickens are resistant. Transmission takes place outside the Oriental zoogeographical region.

The description of this species is based on the data which are available from the original description (Bano and Abbasi, 1983).

Development in vertebrate host

Erythrocytic merogony is synchronized. A cycle of erythrocytic merogony is equal to 24 h. The ratio of macro- and microgametocytes in blood-induced infections in first passages is 2:1.

Trophozoites. The earliest trophozoites are irregular in form, usually seen in a polar or subpolar position in infected erythrocytes, and usually do not displace their nuclei; as the parasite develops, trophozoites take a roundish or oval shape; pigment granules are black, of small size, clumped into a spot near the edge of the parasites; pigment was first seen in trophozoites which are up to 2 μm in diameter; fully grown trophozoites can slightly displace the nuclei of infected erythrocytes.

Erythrocytic meronts. Growing meronts are usually ellipsoid in shape; fully grown meronts are roundish or oval with randomly located nuclei; vacuoles were not recorded; mature meronts possess 16 merozoites on average; pigment granules are black, clumped into a spot near the centre of meront; the parasites deform infected erythrocytes, displace their nuclei and can occupy all available cytoplasmic space in the erythrocytes; meronts are 6.3 μm in diameter on average.

Macrogametocytes. Earlier gametocytes are roundish or oval in shape; fully grown gametocytes are roundish, oval, and irregular, can occupy all available cytoplasmic space in erythrocytes; the parasite nucleus is prominent; pigment granules are roundish or oval, randomly scattered throughout the cytoplasm; fully grown gametocytes markedly deform infected erythrocytes and displace their nuclei; the roundish gametocytes are 7.5 μm in diameter on average; according to illustrations in the original description, the largest gametocytes can exceed 10 μm in length.

Microgametocytes. The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters; roundish gametocytes are 7 μm in diameter on average; other characters are as for macrogametocytes.

Specificity. Domestic chickens of the breed Mini Red are resistant.

Comments. The original description of *P. coturnixi* (Bano and Abbasi, 1983) is incomplete and accompanied with not informative illustrations. It was noted in the species definition that *P. coturnixi* is similar to *P. gallinaceum*, and it can be distinguished from the latter species, first of all, on the basis of its (i) a 24-hour cycle of erythrocytic merogony and (ii) the inability to infect domestic chickens. It is interesting to note that *P. coturnixi* was found in quail outside the Oriental zoogeographical

region (in Northern Pakistan). According to current knowledge, the range of *P. gallinaceum* does not extend outside the Oriental region and it is usually restricted to the central and southern parts of the region. This peculiarity of the geographical distribution can be borne in mind during identification of *P. coturnixi* and *P. gallinaceum.* It should be also noted that fully grown gametocytes of *P. coturnixi* can occupy all available cytoplasmic space in infected erythrocytes. This character can be used for identification of *P. coturnixi* and similar species of the subgenus *Haemamoeba. Plasmodium coturnixi* is similar to *P. relictum* but differs from the latter species on the basis of its rapid (24 h compared with 30 to 36 h) and synchronous erythrocytic merogony. However, the redescription and designation of type material are required to prove the validity of *P. coturnixi.*

2. **Subgenus GIOVANNOLAIA** Corradetti, Garnham and Laird, 1963

Giovannolaia Corradetti, Garnham and Laird, 1963a: 3.

Type species. *Plasmodium circumflexum* Kikuth, 1931, according to the original designation.
Etymology. This subgenus is named in honour of Dr. Arnaldo Giovannola, who was the first to attempt a classification of avian malaria parasites.

Erythrocytic meronts contain plentiful cytoplasm. The size of fully grown erythrocytic meronts exceeds that of the nuclei of infected erythrocytes. Fully grown gametocytes are elongated. Exoerythrocytic merogony takes place in cells of the reticuloendothelial system. Pedunculated oocysts are absent.

KEY TO THE SPECIES†

1 (4). The maximum number of merozoites in erythrocytic meronts is greater than 22. Fully grown erythrocytic meronts and gametocytes either completely encircle the nuclei of infected erythrocytes but do not displace or only slightly displace the nuclei laterally (Fig. 237, *6*, *7*) or markedly displace the nuclei of erythrocytes and occupy all available cytoplasmic space in the erythrocytes (Fig. 237, *4*, *5*).

2 (3). Fully grown erythrocytic meronts and gametocytes markedly deform infected erythrocytes which become rounded (Fig. 237, *4*, *5*). Erythrocytic meronts at the stage of segmentation frequently are roundish or close to roundish, markedly displace the nuclei of infected erythrocytes and can occupy all available cytoplasmic space in the erythrocytes (Fig. 237, *4*).

. . . . . 24. ***P. gabaldoni***

3 (2). Fully grown erythrocytic meronts and gametocytes usually slightly influence infected erythrocytes (Fig. 237, *6*, *7*). Infected erythrocytes usually do not became rounded and their nuclei are not displaced or only slightly displaced. Erythrocytic meronts at the stage of segmentation usually grow around the nuclei of erythrocytes and do not displace or only slightly displace the nuclei (Fig. 237, *6*).

. . . . . 12. ***P. circumflexum***

4 (1). The maximum number of merozoites in erythrocytic meronts is less than 22. Fully grown erythrocytic meronts neither encircle the nuclei of infected erythrocytes completely nor occupy all available cytoplasmic space in the erythrocytes.

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† Identification of species of the subgenus *Giovannolaia* is difficult because the range of variation of some important taxonomic characters frequently overlaps. To facilitate the identification, some species of parasites are mentioned twice in this key.

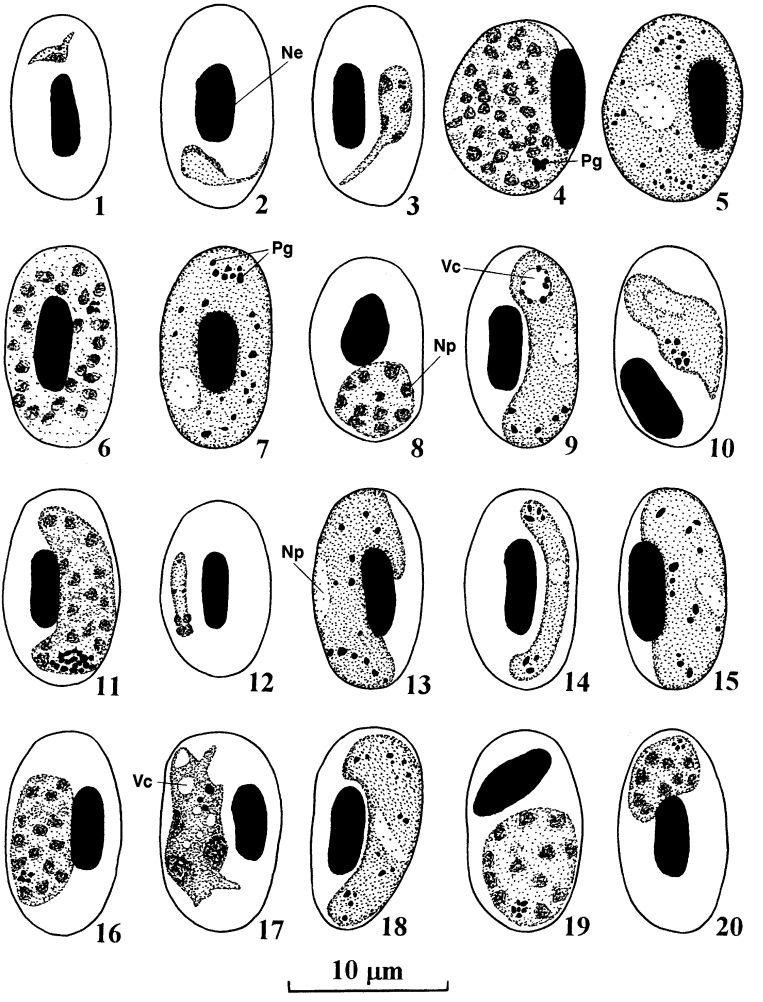

Figure 237 Main morphological peculiarities of the structure of the erythrocytic stages of malaria parasites of the subgenus *Giovannolaia*, which are used for identification of the species:
Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Vc – vacuole. Explanations are given in the text.

5 (20). Large (>1.5 μm in diameter) vacuoles (Fig. 237, *9*) are not present in gametocytes.

6 (22). Fully grown gametocytes do not tend to lie obliquely in infected erythrocytes (Fig. 237, *10*).

7 (21). Erythrocytic meronts can be seen anywhere in infected erythrocytes including a lateral, subpolar, and polar position. If the meronts take mainly a polar or subpolar position in the erythrocytes, they markedly influence the host cells causing their deformation and (or) displacement of their nuclei.

8 (23). Growing erythrocytic meronts do not possess long (>2 μm in length) tail-like or finger-like outgrowths (Fig. 237, *3*).

9 (16). Fully grown erythrocytic meronts are more or less elongated (Fig. 237, *11*, *16*). Roundish erythrocytic meronts (Fig. 237, *8*) are absent.

10 (26). Pigment granules in erythrocytic meronts are not aggregated into large (>1.5 μm in length) clumps which usually locate at one end of the meronts (Fig. 237, *11*).

11 (27). Nuclei are located randomly in erythrocytic meronts, and they do not tend to lean to one end of the meronts (Fig. 237, *12*).

12 (28). Fully grown gametocytes only slightly enclose the nuclei of infected erythrocytes with their ends and they do not encircle the nuclei completely (Fig. 237, *15*, *18*).

13 (29). The cytoplasm of gametocytes is not vacuolated or only slightly vacuolated. The minimum number of merozoites in erythrocytic meronts is less than ten.

14 (15). Fully grown gametocytes are slender and elongated; they do not displace the nuclei of infected erythrocytes (Fig. 237, *14*).

. . . . . 19. ***P. gundersi***

15 (14). Fully grown gametocytes are broad and elongated; they frequently displace the nuclei of infected erythrocytes laterally (Fig. 237, *15*).

. . . . . 23. ***P. octamerium***

16 (9). Roundish fully grown erythrocytic meronts (Fig. 237, *8*, *19*) are present.

17 (30). Maximum number of merozoites in erythrocytic meronts is greater than ten.

18 (19). Fully grown meronts occupy more than half of the cytoplasmic space in the infected erythrocytes. Fully grown gametocytes take a lateral position to the nuclei of erythrocytes (Fig. 237, *18*). Size of pigment granules in macro- and microgametocytes is clearly different.

. . . . . 17. ***P. pinottii***

19 (18). Fully grown meronts occupy less than half of the cytoplasmic space in the infected erythrocytes. Fully grown gametocytes take a lateral, subpolar, and polar position in infected erythrocytes, and U-like gametocytes are present in the polar position in erythrocytes. Size of pigment granules in macro- and microgametocytes is approximately the same.

. . . . . 16. ***P. pedioecetae***

20 (5). Large (>1.5 μm in diameter) vacuoles (Fig. 237, *9*) are present in macrogametocytes. Pigment granules usually gather around these vacuoles. Roundish fully grown erythrocytic meronts (Fig. 237, *8*) are present.

. . . . . 18. ***P. formosanum***

21 (7). Erythrocytic meronts take a polar or subpolar position in infected erythrocytes (Fig. 237, *20*), and their influence on infected erythrocytes is not pronounced.

. . . . . 13. ***P. polare***

22 (6). Fully grown gametocytes tend to lie obliquely in infected erythrocytes and they displace their nuclei toward one pole of the erythrocytes (Fig. 237, *10*). Roundish fully grown erythrocytic meronts (Fig. 237, *8*) are present.

. . . . . 15. ***P. durae***

23 (8). Growing erythrocytic meronts frequently possess long (>2 μm in length) tail-like or finger-like outgrowths (Fig. 237, *3*).

24 (25). Nuclei in mature erythrocytic meronts are usually arranged as fans, rosettes, or more or less pronounced rows.

. . . . . 16. ***P. pedioecetae***

25 (24). Nuclei in mature erythrocytic meronts are usually located randomly and they only occasionally can be arranged as rosettes.

. . . . . 22. ***P. hegneri***

26 (10). Pigment granules in erythrocytic meronts are aggregated into large (>1.5 μm in length) clumps which usually locate at one end of the meronts (Fig. 237, *11*).

. . . . . 20. ***P. anasum***

27 (11). Nuclei tend to lean to one end of the erythrocytic meronts (Fig. 237, *12*).

. . . . . 25. ***P. leanucleus***

28 (12). Fully grown gametocytes markedly enclose the nuclei of infected erythrocytes with their ends (Fig. 237, *13*) and they can completely encircle the nuclei. Trophozoites and growing erythrocytic meronts are highly ameboid in outline (Fig. 237, *1*, *17*).
. . . . . 14. ***P. lophurae***

29 (13). The cytoplasm of gametocytes (especially macrogametocytes) is highly vacuolated. Growing erythrocytic meronts possess small vacuoles. The minimum number of merozoites in erythrocytic meronts is greater than ten.
. . . . . 11. ***P. fallax***

30 (17). The maximum number of merozoites in erythrocytic meronts is less than ten.
. . . . . 21. ***P. garnhami***

11. **Plasmodium (Giovannolaia) fallax** Schwetz, 1930

Plasmodium fallax Schwetz, 1930: 289; Pl. I, Fig. 1–20.

Type vertebrate host. *Ciccaba woodfordii nuchale* (=*Syrnium nuchale*) (Strigiformes).
Additional vertebrate hosts. Some species of birds (Table 138).
Vectors. *Aedes aegypti*, *A. albopictus*, *A. atropalpus*, *A. triseriatus*, *Anopheles quadrimaculatus*, *Culex quinquefasciatus*, *C. tarsalis* (Diptera: Culicidae).
Type locality. Former Belgian Congo.
Distribution. The Ethiopian and Oriental zoogeographical regions and adjacent territories of the Palearctic. This parasite has been also recorded in Central and Northern Palearctic in some birds after their arrival from wintering grounds. However, there is no convincing evidence that the transmission takes place here.
Type material. Hapantotype (No. 337, *Ciccaba woodfordii nuchale*, 1937, Stanleyville, Zaire, J. Schwetz) is deposited in CPG.
Etymology. The specific name reflects the uncertainty of J. Schwetz ('fallacy') during description of this parasite as a new species.

Table 138 List of vertebrate hosts of *Plasmodium fallax*.

Accipiter nisus	*A. wahlbergi*	*Gyps africanus*	*Sylvia borin*
Aquila rapax	*Emberiza tahapisi*	*Numida meleagris*	

Note: Laird (1998) recorded *P. fallax* in four species of strigiform birds in the Asian Tropical Subregion. However, the quality of blood films used to identify species was poor (see Valkiūnas and Peirce, 2000), and the identification needs to be confirmed.

Main diagnostic characters. Growing erythrocytic meronts possess small (usually <1 μm in diameter) vacuoles; they do not produce long (>2 μm in length) tail-like or finger-like outgrowths. Erythrocytic meronts contain randomly located nuclei; they produce 12 to 18 merozoites. Pigment granules in erythrocytic meronts are clumped into a spot which usually does not exceed 1.5 μm in length. The cytoplasm of gametocytes (especially macrogametocytes) is usually highly vacuolated, but large-size (>1.5 μm in diameter) vacuoles are absent. Fully grown erythrocytic meronts and gametocytes are elongated; they take a lateral position to the nuclei of infected erythrocytes and do not displace or only slightly displace the nuclei laterally and never encircle them completely.

Development in vertebrate host

Exoerythrocytic merogony was investigated by C. Huff and co-authors (Huff *et al.*, 1950; Huff, 1957; Huff *et al.*, 1960). Exoerythrocytic meronts were not found in the natural vertebrate hosts (owls and guinea-fowl), but they were observed in numerous species of experimentally infected hosts. However, it should be mentioned that all known exoerythrocytic stages were never seen together in the same species of the host. From this point of view, the available data on the exoerythrocytic merogony of *P. fallax* are still fragmentary. Exoerythrocytic meronts are similar to the meronts of *P. gallinaceum*, but they are smaller in size.

Primary exoerythrocytic merogony easily initiates in domestic pigeon. Cryptozoites develop in the skin at the place of inoculation of sporozoites. They are seen in macrophages, lymphocytes, and fat cells. It should be noted that after intravenous inoculation of sporozoites, cryptozoites develop in reticuloendothelial cells of internal organs. The parasites grow quickly. The uninuclear parasites were observed 24 h after the infection. The mature cryptozoites with a residual body and merozoites, which develop around the body, are seen approximately 40 h after the infection. Each cryptozoite usually produce less than 50 merozoites which look like slightly elongated and slightly curved bodies with prominent nuclei. Metacryptozoites were much more rarely seen than cryptozoites in pigeon and other experimental hosts, and they usually are found in the liver and spleen. Based on the pale staining of their cytoplasm, metacryptozoites look anomalous (degenerative) in comparison to cryptozoites. It is likely that they do not complete the development in the experimental hosts.

Phanerozoites were not seen in experimentally infected domestic pigeon. However, numerous phanerozoites develop in experimentally infected turkey poults in the brain, heart, kidneys, liver, lungs, and spleen. They were found on the 5th day after infection with sporozoites, and between the 12th and the 17th day after the blood-induced infection. After infection with sporozoites, phanerozoites were seen in these organs between the fifth and ninth day, and they gradually disappear then. Phanerozoites, which develop in heart, are up to 40 μm in length and 10 μm in width. Sometimes larger in size parasites, which probably are several compactly located meronts, were seen. Largest phanerozoites contain several hundreds of merozoites. Two types of the merozoites have been described, macromerozoites (>2 μm in length) and micromerozoites (<2 μm in length). The functional role of these two types of merozoites is unknown.

Exoerythrocytic meronts are only occasionally seen in experimentally infected domestic chickens, and they look degenerative. Numerous exoerythrocytic meronts develop in partridge.

Minimum prepatent period is 4 days after experimental infection with sporozoites, but parasites are usually seen microscopically in the blood not earlier than on the 11th day after the infection. Erythrocytic merogony is asynchronous. The intensity of parasitemia markedly varies in different experimental hosts and can be high. A peak of parasitemia is clearly evident in experimentally infected birds. Parasites are not numerous in the blood during a chronic stage of infection.

Trophozoites (Fig. 238, *1–4*) are seen mainly in mature erythrocytes and can be found anywhere in the erythrocytes; earliest trophozoites are roundish, possess a prominent nucleus; the 'ring' stage is not characteristic; as the parasite develops, markedly variable in shape trophozoites appear, and one or several small vacuoles frequently present in the cytoplasm of largest trophozoites (Fig. 238, *4*); growing trophozoites frequently with a clear finger-like outgrowth (Fig. 238, *2*, *3*); the parasite nucleus is relatively large and the

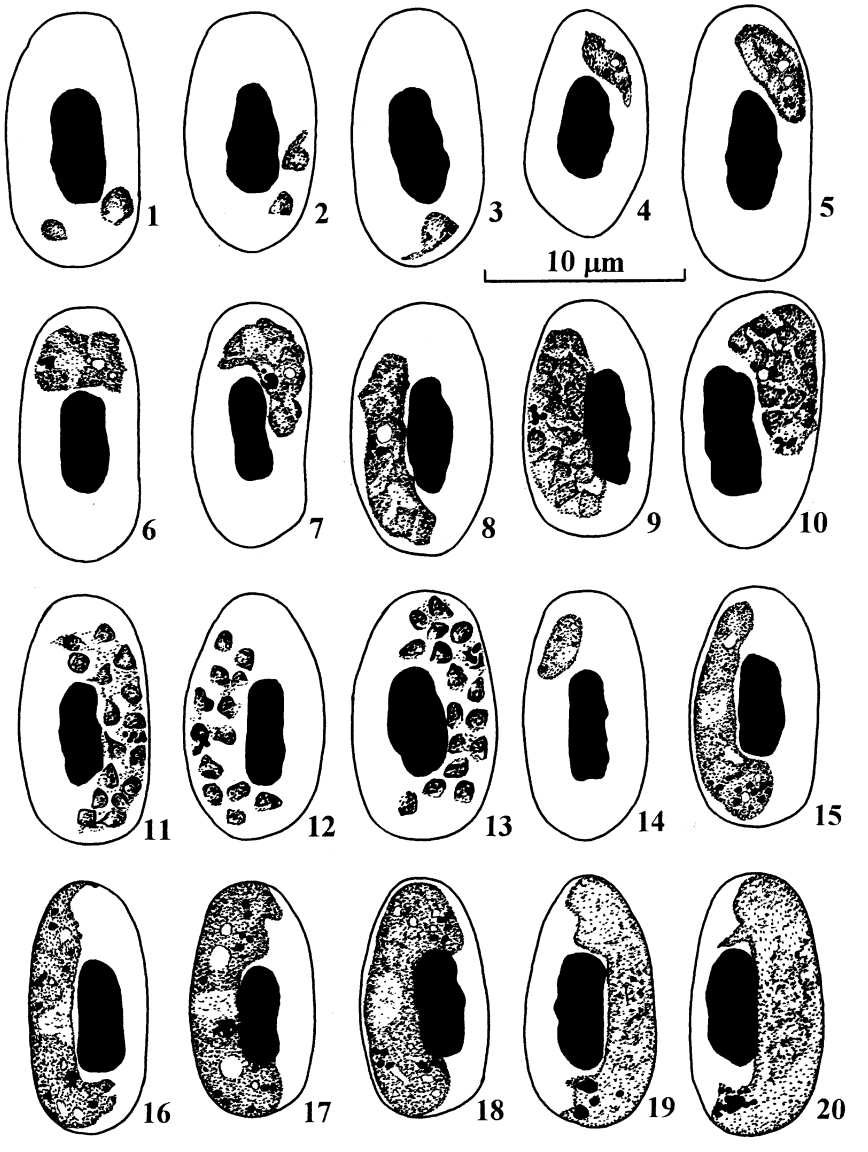

Figure 238 *Plasmodium fallax* from the blood of *Ciccaba woodfordii:*
1–4 – trophozoites; *5–13* – erythrocytic meronts; *14–18* – macrogametocytes; *19*, *20* – microgametocytes.

cytoplasm is plentiful (Fig. 238, *3*); malarial pigment appears in the earliest trophozoites like a minute, light-brown granule (Fig. 238, *1*); fully grown trophozoites are usually elongated in form and irregular in outline (Fig. 238, *4*), they possess up to four small pigment granules clumped into a spot; multiple infection of the same erythrocyte with several parasites is common; trophozoites only slightly (if at all) influence infected erythrocytes.

Erythrocytic meronts (Fig. 238, *5–13*) are seen in mature erythrocytes; young meronts frequently take a polar or subpolar position in infected erythrocytes, possess large nuclei,

plentiful cytoplasm, and one or several small (usually <1 μm in diameter) vacuoles are frequently also present (Fig. 238, *5–7*); nuclei in growing meronts are usually located along the periphery of parasite (Fig. 238, *6–8*); as the parasite develops, meronts extend along the nuclei of infected erythrocytes and then take a lateral position to the nuclei (Fig. 238, *8–10*); nuclei of meronts gradually decrease in size and basophility of cytoplasm also decreases; fully grown meronts are elongated in form and lateral in position to the erythrocyte nuclei, they can slightly enclose the nuclei with their ends but do not encircle them completely (Fig. 238, *11*); nuclei in fully grown meronts are located randomly; mature meronts (Fig. 238, *11–13*) contain 12 to 18 merozoites; pigment granules are light-brown with yellowish shade, clumped in a small (usually <1.5 μm in diameter) focus near the edge of meront; meronts only slightly (if at all) influence infected erythrocytes whose nuclei can be slightly displaced laterally (Fig. 238, *9*, *10*); mature merozoites possess a prominent nucleus and a small portion of cytoplasm.

Macrogametocytes (Fig. 238, *14–18*) are seen in mature erythrocytes; cytoplasm is homogeneous in appearance, usually highly vacuolated, and small valutin granules were frequently seen; prominent (up to 1.5 μm in diameter) vacuoles are present in some gametocytes (Fig. 238, *17*); young gametocytes are elongated in form and variable in outline, they can be easily distinguished from fully grown trophozoites due to pigment granules randomly scattered throughout their cytoplasm (Fig. 238, *14*); fully grown gametocytes are elongated and take a lateral position to the nuclei of erythrocytes, they usually slightly enclose the nuclei with their ends but do not encircle them completely (Fig. 238, *15–18*); the outline varies markedly from even to ameboid (Fig. 238, *16*); the parasite nucleus is compact, relatively small, usually median in position (Fig. 238, *15–18*); pigment granules are usually roundish and small (<0.5 μm), dark-brown, randomly scattered throughout the cytoplasm but also can be aggregated in clumps (Fig. 238, *16*, *17*); the number of pigment granules in fully grown gametocytes varies from 8 to 18; gametocytes only slightly (if at all) influence infected erythrocytes whose nuclei can be slightly displaced laterally (Fig. 238, *18*); fully grown gametocytes do not exceed 16 μm in length.

Microgametocytes (Fig. 238, *19*, *20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules tend to aggregate in solid masses and thus they are less numerous and larger than in macrogametocytes; vacuoles in the cytoplasm are not so frequently seen and the ameboid outline is more frequently recorded than for macrogametocytes; other characters are as for macrogametocytes.

In experimentally infected birds, gametocytes appear in the peripheral blood together with asexual blood stages.

Development in vector has not been investigated in detail. Natural vector is unknown. Sporogony is completed in mosquitoes of the genera *Aedes*, *Culex*, and *Anopheles* (see 'Vectors'). However, *Culex pipiens pipiens* was recorded to be resistant.

Pathogenicity. Pathogenicity of *P. fallax* for natural hosts (owls and guineafowl) has not been investigated in the field conditions. Infection is mild in experimentally infected natural hosts. However, the parasite is pathogenic for many other experimentally infected birds. The virulence increases as the number of blood passages increases. Experimentally infected domestic pigeons, domestic chickens, turkeys, and some other birds frequently die mainly because of high parasitemia and (or) blockage of capillaries in the brain by exoerythrocytic meronts. Development of numerous exoerythrocytic meronts in other organs also contributes to the mortality. Convulsions are seen before death. The survived birds acquire premunition.

Specificity. The range of natural vertebrate hosts is probably wider than is known now (Table 138). Turkey is the best experimental host. Partridge, quail, guinea-fowl, pheasant, domestic pigeon, and goslings can be also easily infected. Ducklings and canaries are susceptible but more difficult to infect than above mentioned birds.

Comments. *Plasmodium fallax* is especially similar to *P. circumflexum*. Meronts and gametocytes of *P. fallax* never encircle the nuclei of infected erythrocytes, but the circumnuclear forms (especially meronts) are common in *P. circumflexum*. Additionally, erythrocytic merogony of *P. fallax* is not synchronized, and all erythrocytic stages are available in the blood at any stage of parasitemia, and this is not characteristic of *P. circumflexum*. Furthermore, *P. fallax* completes sporogony in mosquitoes of the genera *Aedes*, *Culex* (except *C. pipiens*) and *Anopheles* but *P. circumflexum* does not.

Plasmodium fallax has some similarities with *P. rousseloti*. Unfortunately, the original preparations of the latter parasite are lost (Garnham, 1966). According to the original description (Bray, 1964), some meronts of *P. rousseloti* completely encircle the nuclei of infected erythrocytes. *Plasmodium fallax* can be distinguished from *P. rousseloti* on the basis of this character. Blood stages of *P. rousseloti* are similar to *P. circumflexum*, *P. durae*, *P. fallax*, and some other species. Identification of *P. rousseloti* is impossible on the basis of data which are available in the original description. Thus, in the absence of the type material, *P. rousseloti* should be declared a *species inquirenda*.

12. **Plasmodium (Giovannolaia) circumflexum** (Kikuth, 1931)

Proteosoma circumflexum Kikuth, 1931: 405, Fig. 1–7. – *Plasmodium circumflexum*: Coatney and Roudabush, 1936: 339. – *P. heroni* Basu, 1938: 278, Pl. 14, Fig. 1–14. – *P. circumflexum*: Garnham, 1966: 636 (=*P. heroni*).

Type vertebrate host. *Turdus pilaris* L. (Passeriformes).
Additional vertebrate hosts. Numerous species of birds of the orders Anseriformes, Columbiformes, Coraciiformes, Charadriiformes, Falconiformes, Strigiformes, Galliformes, and some others, but particularly of the Passeriformes (over 100 species total).
Vectors. *Culiseta* (=*Theobaldia*) *annulata*, *C. longiareolata*, *C. melaneura*, *C. morsitans*, *Mansonia crassipes* (Diptera: Culicidae).
Type locality. Germany.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic. It is especially common in the Holarctic. A few records are known from the Neotropical and Australian zoogeographical regions.
Type material. Neohapantotype (No. 270, *Serinus canaria*, 1939, Germany, L. Mudrow) is deposited in CPG. A series of good additional slides (blood and sporogonic stages) is deposited in CPG.
Etymology. The specific name reflects the circumnuclear form of fully grown erythrocytic meronts and gametocytes of this parasite.

Main diagnostic characters. Meronts and gametocytes grow around the nuclei of infected erythrocytes and can completely encircle the nuclei. Pigment granules in growing erythrocytic meront are aggregated into a small loose clump near one end of the parasite. Small (<1.0 μm in diameter) vacuoles are frequently present in erythrocytic meronts and gametocytes. Fully grown erythrocytic meronts and gametocytes usually do not deform infected erythrocytes and do not displace or only slightly displace their nuclei laterally. Mature erythrocytic meronts contain 8 to 30 (usually 12 to 20) merozoites.

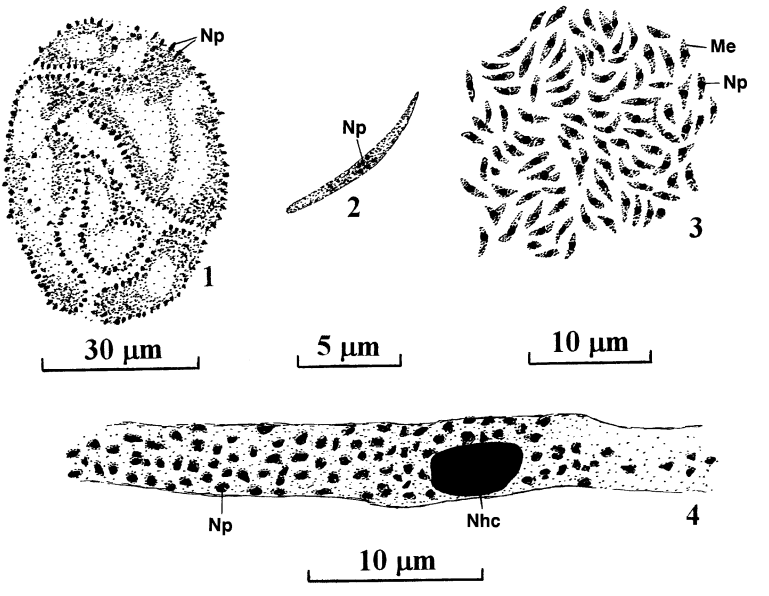

Figure 239 *Plasmodium circumflexum:*
1 – section of oocyst with developing sporozoites; *2* – sporozoite; *3* – a fragment of ruptured phanerozoite with completely developed elongated merozoites; *4* – phanerozoite in the brain of *Serinus canaria*; Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite (modified from Garnham, 1966).

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. Phanerozoites were found in reticuloendothelial cells in sick or dead experimentally infected canaries and turkey poults (Manwell and Goldstein, 1938; Coulston and Manwell, 1941; Paraense, 1952; Corradetti *et al.*, 1964; Huchzermeyer and Vyver, 1991). The phanerozoites were seen in the brain, lungs, liver, spleen, kidneys, and bone marrow. In experimentally infected canaries, phanerozoites were usually seen during the acute stage of parasitemia. In turkeys, they were found during the chronic stage of parasitemia approximately two weeks after the acute stage. Phanerozoites of *P. circumflexum* morphologically are similar to those of *P. gallinaceum*, but they are smaller in size (Fig. 239, *4*). Phanerozoites, which developed in the endothelial cells of capillaries of the brain in turkeys, vary from 17 to 29 μm in length, and from 9 to 19 μm in width. Mature merozoites are elongated with pointed ends and possess a compact centrally located nucleus (Fig. 239, *3*).

The prepatent period in canaries is seven to eight days after both the blood- and sporozoite-induced infections, and can be slightly longer in some other experimental birds (Manwell, 1934b; Herman, 1938a; Huchzermeyer and Vyver, 1991). Primary parasitemia increases quickly. It maintains a high level for approximately a week or slightly longer and then decreases rapidly. A few parasites difficult to find are present in the blood during the chronic parasitemia. The intensity of parasitemia during the same stage of infection markedly varies in different vertebrate hosts.

Erythrocytic merogony is synchronized. However, two groups of strains, with the periodicity close to 24 and 48 h, respectively, have been recorded. Mature erythrocytic meronts rupture usually in the evening.

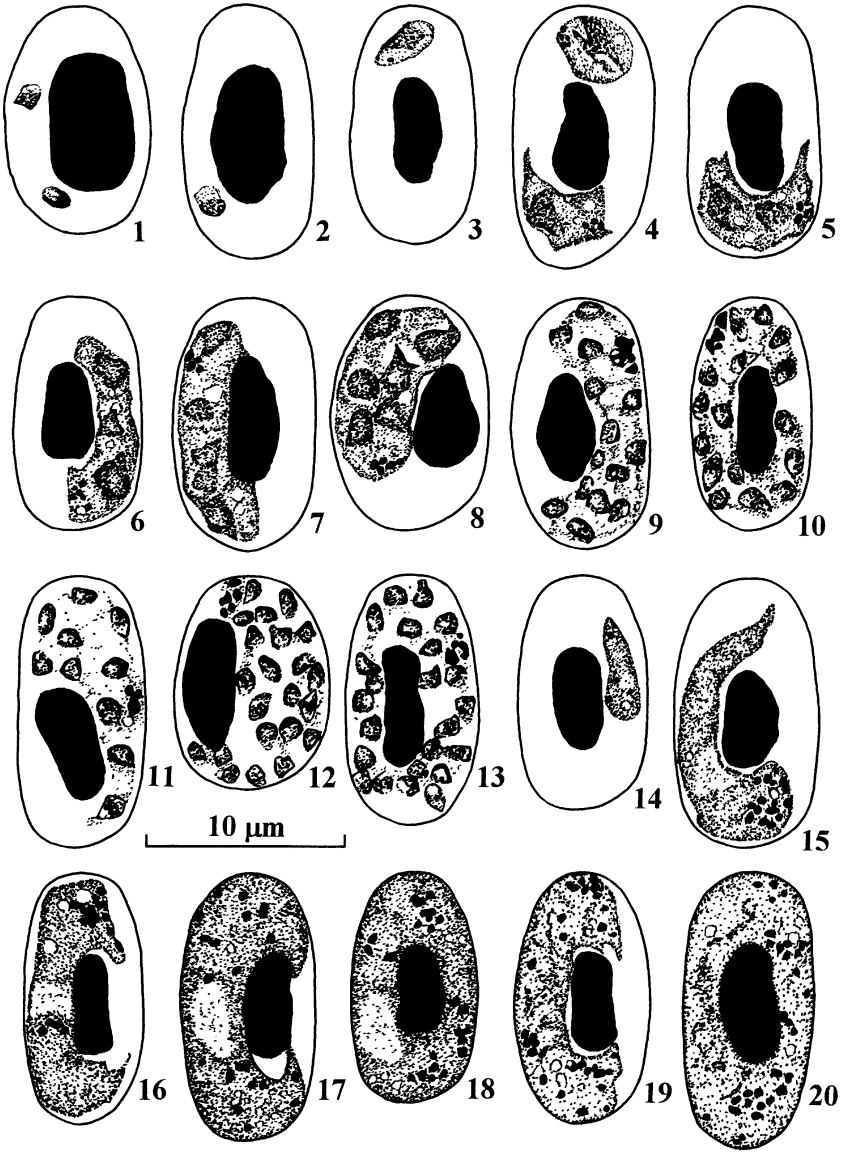

Figure 240 *Plasmodium circumflexum* from the blood of *Serinus canaria:*
1–3 – trophozoites; *4* – a fully grown trophozoite (top) and an earliest binuclear erythrocytic meront (bottom); *5–13* – erythrocytic meronts; *14–18* – macrogametocytes; *19*, *20* – microgametocytes.

Trophozoites (Fig. 240, *1–4*) are seen in polychromatic and mature erythrocytes; earliest trophozoites which are roundish or oval, sometimes of irregular shape, can be seen anywhere in infected erythrocytes; the outline is even; the 'ring' stage is not characteristic; as the parasite develops, nucleus markedly increases in size, plentiful cytoplasm develops and one or several small roundish pigment granules appear (Fig. 240, *2*, *3*); fully grown trophozoites are variable in form, they can be seen anywhere in infected erythrocytes but

more frequently observed in a polar or subpolar position in the host cells; a few minute in size vacuoles are seen in cytoplasm of some largest trophozoites; pigment granules are roundish, of small size (<0.5 μm), dark-brown, clumped into a spot near the edge of parasite (Fig. 240, *4*); the number of pigment granules does not exceed six; trophozoites do not influence or only slightly influence infected erythrocytes; infection of the same erythrocyte with several trophozoites is common at high parasitemia.

Erythrocytic meronts (Fig. 240, *4–13*) are seen in mature and polychromatic erythrocytes; cytoplasm is plentiful, usually possesses small (<1.0 μm in diameter) vacuoles; the vacuoles are sometimes seen even in mature meronts where they are located close to a clump of pigment granules (Fig. 240, *11*); the first fission of nucleus takes place in large meronts which length is close to the length of nuclei of infected erythrocytes (Fig. 240, *4, 5*); nuclei are large in young meronts (Fig. 240, *4–8*) and they markedly decrease in size subsequently; meronts are elongated, they grow around the nuclei of erythrocytes, enclose the nuclei with their ends and can completely encircle the nuclei (Fig. 240, *9*, *10*, *13*); the outline is variable in young meronts and is usually even in advanced parasites; the nuclei are randomly located in fully grown meronts; parasites usually only slightly influence infected erythrocytes whose nuclei are usually not displaced or only slightly displaced laterally (Fig. 240, *9, 10, 13*); mature meronts at the stage of segmentation sometimes are seen to displace the nuclei of erythrocytes and to deform the host cells (Fig. 240, *8*, *11*, *12*) which in general is not characteristic of this species; mature meronts contain 8 to 30 (usually 12 to 20) merozoites, and the average number of merozoites varies in different strains; pigment granules are roundish, of small size (<0.5 μm), variable colour, usually tend to be located close to one end of the parasite, which is especially evident in young meronts (Fig. 240, *4–8*); pigment granules are aggregated into loose clumps in growing meronts and are frequently seen aggregated into one or several solid masses in mature meronts; the solid masses of pigment can be seen anywhere in meronts, including a median position (Fig. 240, *11*), but more often they were seen closer to one end of the parasites (Fig. 240, *9, 10*); fully grown meronts usually exceed 12 μm in length; mature merozoites are usually slightly oval or slightly elongated, possess a prominent nucleus and a small portion of cytoplasm (Fig. 240, *10–13*).

Macrogametocytes (Fig. 240, *14–18*) are usually seen in mature erythrocytes, sometimes in polychromatic erythrocytes; they frequently possess small (<1.0 μm in diameter) vacuoles; gametocytes are elongated and take a lateral position to the nuclei of infected erythrocytes; most gametocytes markedly enclose the nuclei with their ends (Fig. 240, *15–17*) and can completely encircle the nuclei and occupy all available cytoplasmic space in the erythrocytes but do not displace or only slightly displace the nuclei of erythrocytes laterally (Fig. 240, *18*); however, gametocytes markedly displacing the nuclei of erythrocytes laterally, sometimes to the periphery of the host cells, and not encircling them completely were also observed occasionally but are not characteristic of this species; the outline varies from even to ameboid; the parasite nucleus is compact, relatively large (Fig. 240, *17, 18*), usually submedian in position; pigment granules are usually roundish, of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, dark-brown color, usually randomly scattered throughout the cytoplasm, sometimes aggregated into one or several clumps (Fig. 240, *15*, *16*); the number of pigment granules is usually more than 12 but less than 30; gametocytes usually only slightly (if at all) influence infected erythrocytes whose nuclei can be more or less displaced laterally; fully grown gametocytes exceed 16 μm in length.

Microgametocytes (Fig. 240, *19*, *20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; gametocytes, which markedly

displace the nuclei of infected erythrocytes, were not seen; other characters are as for macrogametocytes.

Development in vector was studied by numerous authors (Reichenov, 1932; Herman, 1938c; Corradetti *et al.*, 1964; Niles *et al.*, 1965; Meyer *et al.*, 1974; Meyer and Bennett, 1976). As a rule, sporogony does not complete in mosquitoes of the genera *Aedes*, *Culex*, and *Anopheles.* Sporozoites developed in *Aedes aegypti* and *Mansonia perturbans*, but they were not infectious for vertebrate hosts. The mosquitoes *Culiseta annulata*, *C. longiareolata*, *C. melaneura*, *C. morsitans*, and *Mansonia crassipes* are good vectors. Crewe (1975) noted that sporogony was completed in the mosquito *Aedomyia africana*. However, a mixed infection of *P. circumflexum* and *P. vaughani* was present in birds the mosquitoes were fed on. Thus, it is unclear what species of the malaria parasites completed sporogony in *A. africana*. Exflagellation, development of ookinetes and oocysts are not synchronized. Ookinetes and oocysts at different stages of their development were seen in midgut of experimentally infected mosquitoes. Exflagellation was seen 10 to 40 min after exposure of blood with mature gametocytes to air at a temperature of 20°C and higher. Ookinetes look like elongated bodies with one end pointed more than the other end. The ookinetes are about 16 to 18 μm in length in fresh preparations. They possess a prominent nucleus with a nucleolus, 'vacuoles' and numerous pigment granules aggregated into small clumps, which are randomly scattered throughout the cytoplasm. Ookinetes can penetrate into epithelial cells of the midgut. The earliest oocysts were seen intracellularly. As oocysts develop, the host cells rupture and mature oocysts finally were observed extracellularly. In mosquito *Culiseta annulata* at a temperature of 20 to 23°C, oocysts increase from 13 to 28 μm in diameter between the fourth and seventh day after ingestion of gametocytes. Numerous germinative centres, from which sporozoites are budding off, develop in growing oocysts (Fig. 239, *1*). Mature oocysts were seen on the 12th day after the infection. They measured up to 60 μm in diameter. At the same time, sporozoites were recorded in the salivary glands. Sporogony is completed more quickly in the mosquito *C. morsitans* (Pl. III, *5*). In this case, sporozoites were first seen in the salivary glands on the eighth day after infection, but the differentiating oocysts were seen as long as up to the 16th day after the infection. Sporozoites persist in the salivary glands at least up to six weeks. They look like elongated spindle-shaped bodies with one end pointed more than the other end (Fig. 239, *2*). Nucleus locates near the centre of sporozoites; it possesses several clear clumps of chromatin. The sporozoites are about 8 to 9 μm in length in preparations fixed with methanol.

Three chromosomes were seen during nuclear fission in young oocysts. Thus the karyotype of the species is $2n = 6$.

Pathogenicity. All strains of *P. circumflexum* cause heavy disease in canaries with mortality rate ranging from 25 to 100%. Moreover, the canaries can die during relapses.

The strain, isolated from wild guinea-fowls in South Africa, causes a severe disease in juvenile turkeys (Huchzermeyer and Vyver, 1991). Diseased birds are lethargic and unable to stand. Mucous membranes are pale. The birds die at the peak of parasitemia because of severe anaemia. Watery blood, moderate to severe icterus, severe spleenomegaly, slightly enlarged liver, microscopical changes in cardiac muscle were recorded in birds which died at the peak of parasitemia. The second phase of mortality takes place between the 7th and the 18th (usually around the 14th) day after decrease of the parasitemia due to cerebral malaria which is caused by blockage of brain capillaries with phanerozoites. Severe

spleenomegaly, numerous phanerozoites in the brain and some other organs, multifocal interstitial myocarditis were recorded in birds which died at the second phase of mortality. The Kupffer cells in the liver and the red pulp of the spleen of birds, which died during the first and the second phases of mortality, contained much dark-brown pigment. Birds that survived acquired premunition.

The death has been rarely recorded among other experimentally infected birds. Peculiarities of the pathogenic influence on free-living hosts at the natural conditions have not been investigated.

Specificity. *Plasmodium circumflexum* is one of the most common parasites of the subgenus *Giovannolaia*. It has been reported in numerous bird species belonging to several orders (see 'Additional vertebrate hosts'). Canary is a good experimental host for all tested strains. The strain, isolated from wild guinea-fowls in South Africa, develops well in juvenile turkeys. Ducklings and domestic chickens can be infected with difficulty by some strains. Domestic pigeon, partridge *Perdix perdix*, bobwhite *Colinus virginianus*, pheasant *Phasianus colchicus*, and Japanese quail were infected experimentally. The susceptibility of birds to different strains is variable.

Comments. During identification of *P. circumflexum* in blood smears, attention should be paid to the clear tendency of erythrocytic meronts and gametocytes to grow around the nuclei of infected erythrocytes. These blood stages usually do not displace the nuclei of infected erythrocytes laterally but can completely encircle the nuclei. Additionally, location of pigment granules near one end of growing erythrocytic meronts is also a characteristic feature of this species. During testing of biological characters, it should be taken into account that the parasite do not develop or poorly develop in ducklings. Moreover, all known vectors of the parasite are mosquitoes of the genera *Culiseta* and *Mansonia*.

It is important to note that *P. circumflexum* has a huge range of vertebrate hosts, and biological characters of different strains vary markedly. It is impossible to exclude at present that several species of malaria parasites with similar blood stages have been described under the name *P. circumflexum*. This hypothesis should be attributed, first of all, to the two groups of strains with periodicity of erythrocytic merogony close to 24 h (Reichenov, 1932; Paraense, 1952; Crewe, 1975) on the one hand and to 48 h (Herman, 1938a; Laird and Lari, 1958; Huchzermeyer and Vyver, 1991) on the other hand. Further investigation is required to solve this question.

Blood stages of *P. heroni* are similar to *P. circumflexum*. Additionally, as *P. circumflexum*, *P. heroni* does not complete the development in mosquitoes of the genera *Aedes*, *Anopheles*, and *Culex* (Basu, 1938). *Plasmodium heroni* is considered to be a junior synonym of *P. circumflexum*. The idea of this synonymy was discussed by Garnham (1966) who also noted some similarities between *P. heroni* and *P. fallax*. However, according to the original description (Basu, 1938), erythrocytic meronts of *P. heroni* contain up to 26 merozoites and they can completely encircle the nuclei of infected erythrocytes, and its gametocytes do not possess clearly defined vacuoles. Furthermore, this parasite developed only up to the stage of oocyst in mosquito *Culex pipiens fatigans*. Based on the above mentioned characters, *P. heroni* is more similar to *P. circumflexum* than to *P. fallax*.

13. **Plasmodium (Giovannolaia) polare** Manwell, 1934

Plasmodium polare Manwell, 1934a: 334.

Type vertebrate host. *Hirundo pyrrhonota* Vieil. (=*Petrochelidon pyrrhonota*) (Passeriformes).
Additional vertebrate hosts. Numerous species of birds (Table 139).
Vectors. *Culiseta longiareolata*, *C. morsitans* (Diptera: Culicidae).

Table 139 List of vertebrate hosts of *Plasmodium polare*.

Agelaius phoeniceus	*Grus canadensis*	*Pycnonotus jocosus*
Anas discors	*Haliaeetus leucocephalus*	*Thamnophilus aethiops*
A. platyrhynchos	*Hirundo cucullata*	*Turdus migratorius*
Chordeiles minor	*Icteria virens*	*Tympanuchus phasianellus*
Dendrocygna viduata	*Nothura maculosa*	*Zenaida macroura*
Emberiza citrinella	*Parus atricapillus*	*Zonotrichia albicollis*
Falco tinnunculus	*Passer domesticus*	
Francolinus pondicerianus	*Piranga rubra*	

Note: Laird (1998) published 17 additional host records of *P. polare* in the Asian Tropical Subregion. However, the quality of slides, which were used for species identification, was poor (see Valkiūnas and Peirce, 2000), and the identification needs to be confirmed.

Type locality. Syracuse, USA.

Distribution. This parasite has been recorded in all zoogeographical regions except the Australian and Antarctic. It has been especially frequently recorded in the central and southern territories of the Holarctic so far.

Type material was not designated in the original description of this species. Garnham and Duggan (1986) designated neotypes from the material which came from the nontype vertebrate host (*Falco tinnunculus*, order Falconiformes) sampled far beyond the type locality (Sicily). This material is invalid because it contradicts Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of valid neotypes is required. A series of good slides of exoerythrocytic meronts, blood stages and sporogonic stages is deposited in CPG.

Etymology. The specific name reflects an important character of asexual blood stages of this parasite, i.e., their polar or subpolar position in infected erythrocytes.

Main diagnostic characters. The great majority of erythrocytic meronts take a polar or subpolar position in infected erythrocytes, and they occupy less than half of the cytoplasmic space in host cells. Mature erythrocytic meronts contain 6 to 16 merozoites. Gametocytes take a lateral position to the nuclei of infected erythrocytes; they usually do not possess vacuoles. The blood stages usually do not influence or only slightly influence infected erythrocytes.

Development in vertebrate host has been fragmentarily investigated (Manwell, 1936; Corradetti and Scanga, 1965; Garnham, 1966; Ayala and Varela, 1975; Greiner *et al.*, 1981; Telford *et al.*, 1994). Exoerythrocytic meronts were usually not seen in naturally and experimentally infected birds. It is likely that phanerozoites do not develop in canaries after blood-induced infection. A few primary exoerythrocytic meronts were seen in spleen of canaries after experimental infection with sporozoites. They look like roundish or oval bodies containing about 50 small merozoites.

The prepatent period is long, and it can be two or three months after intravenous inoculation of high doses of infected blood. The peak of primary parasitemia is not pronounced. Parasitemia always is low, and it can persist for years. Erythrocytic merogony is slightly synchronized. It is likely that a cycle of the merogony is close to 24 h.

Relapses and recrudescences were not recorded.

Trophozoites (Fig. 241, *1*, *2*) are usually seen in mature erythrocytes, sometimes in polychromatic erythrocytes; earliest trophozoites are variable in form, usually possess a more or less evident vacuole, they can be seen anywhere in infected erythrocytes; the 'ring' stage was seen (Fig. 241, *1*); as the parasite develops, trophozoites take an irregular form

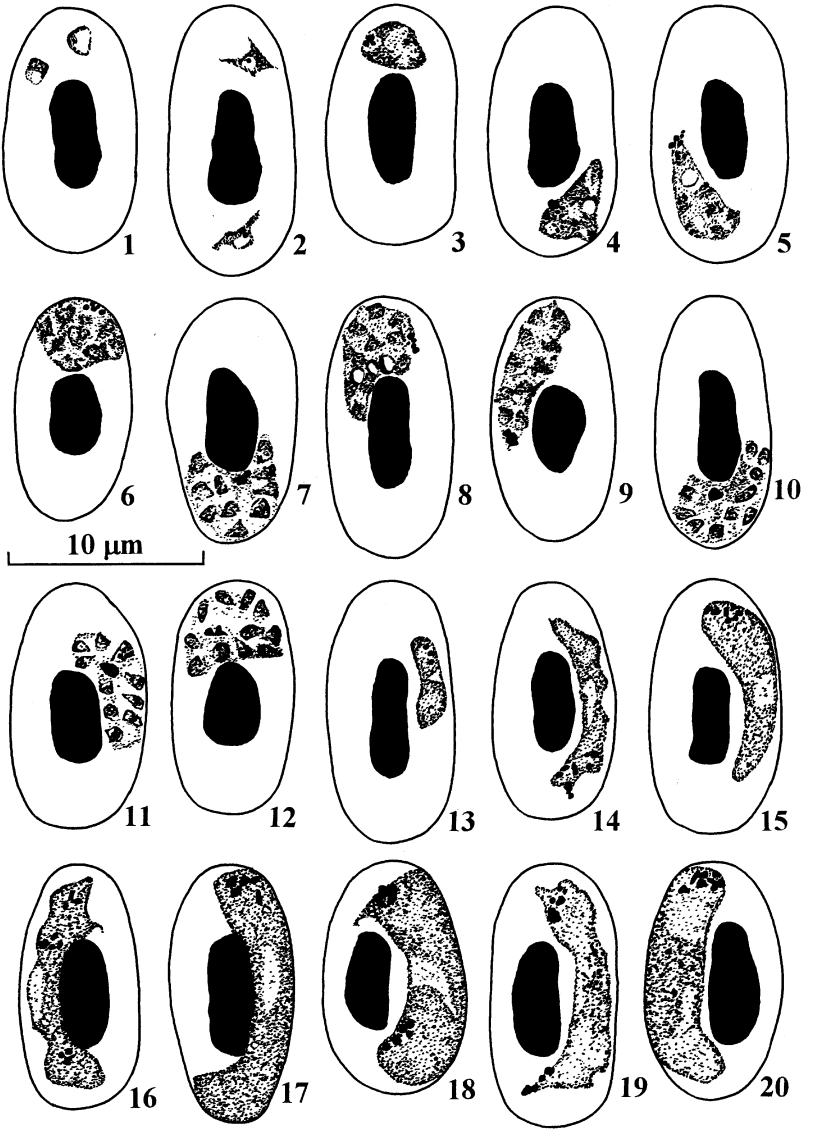

Figure 241 *Plasmodium polare* from the blood of *Serinus canaria* and *Falco tinnunculus: 1*, *2* – trophozoites; *3–12* – erythrocytic meronts; *13–18* – macrogametocytes; *19*, *20* – microgametocytes.

with ameboid outgrowths and are now usually seen in a polar or subpolar position in the erythrocytes (Fig. 241, *2*); one roundish, small-size (<0.5 μm), brown-colour pigment granule is usually present in trophozoite; trophozoites do not influence infected erythrocytes.

Erythrocytic meronts (Fig. 241, *3–12*) are seen mainly in mature erythrocytes; cytoplasm is plentiful, frequently possesses one or several small (usually <1.0 μm in diameter) vacuoles (Fig. 241, *4, 5, 8*); meronts markedly vary in form (Fig. 241, *6–12*); the great majority of meronts take a polar or subpolar position in infected erythrocytes, frequently

do not touch the nuclei of the host cells; nuclei in fully grown meronts are usually located randomly, but sometimes were also seen to be arranged as rosettes (Fig. 241, *12*); mature meronts contain 6 to 16 merozoites; pigment granules are small, not numerous, brown or black, clumped into a spot and can be aggregated into a solid mass of pigment (Fig. 241, *10*); meronts usually do not influence or only slightly influence infected erythrocytes; the size of meronts varies in different vertebrate hosts but fully grown parasites always occupy less than half of the cytoplasmic space in infected erythrocytes.

Macrogametocytes (Fig. 241, *13–18*) are seen in mature erythrocytes; cytoplasm is homogeneous in appearance, usually lacking vacuoles; gametocytes are elongated in form and variable in outline, they take a lateral position to the nuclei of infected erythrocytes and grow along the nuclei; largest gametocytes can slightly enclose the nuclei of erythrocytes with their ends (Fig. 241, *17*) but never encircle the nuclei completely; the parasite nucleus is of variable form, small size (Fig. 241, *15–17*), usually median position; pigment granules are usually roundish, sometimes of oval and irregular shape, usually of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, frequently clumped into a spot or in several more or less loose groups or even solid masses but can also be randomly scattered throughout the cytoplasm; the number of pigment granules usually varies from 4 to 14, most frequently about 8; gametocytes usually do not influence or only slightly influence infected erythrocytes whose nuclei can be slightly displaced laterally; the size of gametocytes varies during the development in different vertebrate hosts; fully grown gametocytes are most frequently about 10 to 14 μm in length, however shorter and longer gametocytes were also observed.

Microgametocytes (Fig. 241, *19*, *20*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

D e v e l o p m e n t i n v e c t o r has not been investigated in detail. Exflagellation was seen only 40 min after exposure of the blood with mature gametocytes to air. The parasite does not complete the development in the mosquito *Culex pipiens*. Sporozoites developed in the mosquito *Mansonia perturbans*. However, it is unknown if these sporozoites are infectious to birds. The mosquitoes *Culiseta longiareolata* and *C. morsitans* are good vectors. Sporozoites were recorded in the salivary glands of *C. longiareolata* on the 17th day after ingestion of mature gametocytes at a temperature of 26°C. In the mosquitoes *C. morsitans* maintained at 23°C, oocysts vary from 10 to 23 (on average 17) μm in diameter on the fifth day after infection. The oocysts possess pigment granules clumped into a spot (Corradetti and Scanga, 1965, 1968; Meyer and Bennett, 1976).

P a t h o g e n i c i t y has been insufficiently investigated. Mortality was not recorded among experimentally infected canaries. The role of this parasite in natural bird populations is unclear.

S p e c i f i c i t y. The range of natural vertebrate hosts is relatively wide (Table 139). Canary can be infected but is not a good experimental host. *Coturnix coturnix* and *Colinus virginianus* (Galliformes) were refractive after subinoculation of blood from the naturally infected type vertebrate host, cliff swallow *Petrochelidon pyrrhonota* (Stabler and Kitzmiller, 1976).

C o m m e n t s. During identification of *P. polare*, the attention should be paid, first of all, on small size of erythrocytic meronts, the great majority of which take a polar or subpolar position in infected erythrocytes and do not influence or only slightly influence the host cells.

14. **Plasmodium (Giovannolaia) lophurae** Coggeshall, 1938

Plasmodium lophurae Coggeshall, 1938: 616, Pl. 1, Fig. 1–9.

Type vertebrate host. *Lophura igniti igniti* (Shaw and Nodd) (Galliformes).
Additional vertebrate hosts. *Geopelia striata*, *Lophura erythropthalma*, and *Meleagris gallopavo* (see also 'Specificity' in the text below).
Vectors. *Aedes albopictus* (Diptera: Culicidae). Sporozoites develop in mosquitoes *Aedes aegypti*, *A. atropalpus*, *Anopheles quadrimaculatus*, and *Culex restuans*.
Type locality. Probably, Borneo. This parasite was isolated from a bird in the New York Zoological Gardens.
Distribution. The Oriental zoogeographical region.
Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 335, the smear from tissue culture of the brain of a turkey embryo; No. 336, turkey, a histological section of the brain; *blood stages*: No. 332, domestic chicken subinoculated from the original stock, 24.03.1938; No. 333, duckling, other data are not available; No. 334, duckling, June 1975, W. Trager) are deposited in CPG.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Lophura*.

Main diagnostic characters. Trophozoites and young erythrocytic meronts are highly ameboid in outline with vacuolated cytoplasm; they do not produce long (>2 μm in length) tail-like or finger-like outgrowths and can be seen anywhere in infected erythrocytes. Erythrocytic meronts and gametocyte are elongated, do not influence or only slightly influence infected erythrocytes. Erythrocytic meronts contain randomly located nuclei, and pigment granules are usually clumped into one or two small spots or aggregated into a solid mass. Mature erythrocytic meronts contain 8 to 18 merozoites. Fully grown meronts do not encircle the nuclei of erythrocytes completely but the fully grown gametocytes can do so. Gametocytes usually take a lateral position to the nuclei of infected erythrocytes, and do not possess large (>1.5 μm in diameter) vacuoles.

Development in vertebrate host

Exoerythrocytic merogony was investigated in experimentally infected domestic chickens, ducklings, turkey poults and some other birds (Huff *et al.*, 1947; Tonkin and Hawking, 1947; Huff, 1957; Garnham, 1966). Morphology of the exoerythrocytic meronts is similar to *P. gallinaceum*. Cryptozoites develop in various cells of the lymphoid-macrophage series at the place of inoculation of sporozoites in the skin. They were frequently seen in lymphocytes, macrophages, fibroblasts, and some other cells. The earliest cryptozoites are roundish and possess clear vacuoles. As the parasite develops, the vacuolization of the cytoplasm increases. Mature cryptozoites were observed 48 to 60 h after inoculation of sporozoites. They contain small number (usually less than 50), slightly elongated merozoites. After rupture of cryptozoites, the blood is infectious for experimental birds. Metacryptozoites develop in lymphocytes, macrophages, and fibroblasts not only in the skin, but also in internal organs. Numerous metacryptozoites were seen in the brain. First metacryptozoites mature 72 h after the rupture of cryptozoites. They contain about 100 elongated merozoites. Aberrant meronts were recorded during the primary exoerythrocytic merogony. They were especially common in ducklings. In such meronts, cytoplasm was eosinophilic in shade and contained vague inclusions, and smaller-size merozoites developed.

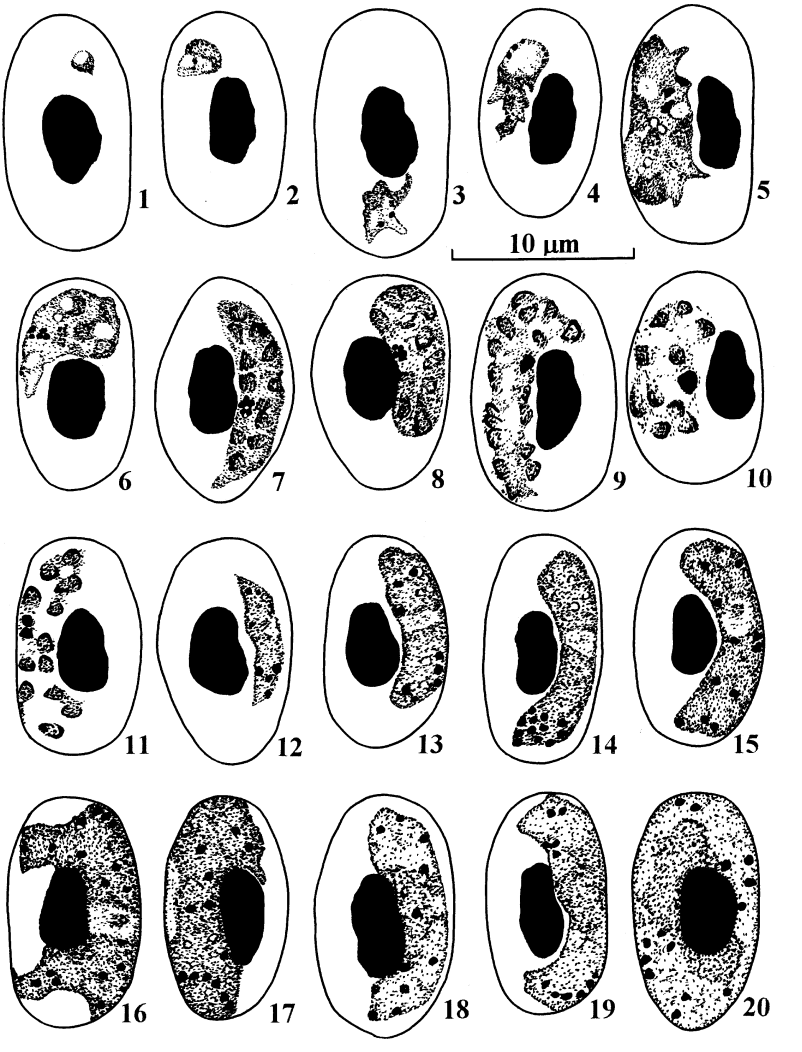

Figure 242 *Plasmodium lophurae* from the blood of *Gallus gallus:*
1–4 – trophozoites; *5–11* – erythrocytic meronts; *12–17* – macrogametocytes; *18–20* – microgametocytes.

Phanerozoites were not recorded in chickens, and they were rarely seen in ducklings. They are especially frequently observed in turkeys and guinea-fowls. The rate of development of phanerozoites differs in sporozoite-induced and blood-induced infections. The parasites were found in reticuloendothelial cells of internal organs of turkey poults six days after intravenous inoculation of sporozoites. They were especially numerous in the brain and were also frequently seen in the heart, renal glomeruly, and adrenal cortex. The parasites were also sometimes seen in the spleen, lungs, and sympathetic ganglia. They look like sausage-shaped bodies extended along the capillaries. Cytomeres are not seen, and the amount of cytoplasm and number of nuclei vary markedly in different phanerozoites. In blood-induced infection, phanerozoites usually appear not earlier than on the 11th day and

were seen for about a week after that. The parasites develop in endothelial cells of capillaries. They appear especially quickly in the brain, lungs, and spleen, and, a bit later, they were seen in the kidneys, liver, heart, and thyroid.

The prepatent period does not exceed five days. The dynamics of primary parasitemia markedly varies in different vertebrate hosts. In young domestic chickens, the parasitemia increases rapidly, maintains on the high level for about one to two weeks and then decreases and turns into a chronic stage. The blood of the chickens is infectious to experimental birds at least for 11 months. The parasitemia usually does not exceed 10% of infected erythrocytes in the experimentally infected chickens. However, strains which parasitize about 70% of erythrocytes have been selected. In adult chickens, the peak of parasitemia is only slightly evident, and infection quickly turns into the chronic stage. In ducklings and in adult ducks, a heavy parasitemia develops, and up to 100% of erythrocytes can be parasitized at the top of the parasitemia. The ducks usually die.

Erythrocytic merogony is slightly synchronized. It is likely that a cycle of the merogony is close to 24 h in the majority of tested experimental hosts. A 36 h periodicity has been much rarely recorded. The meronts rupture in the evening (around 18 h).

Blood stages usually develop in mature erythrocytes, but they were also frequently seen in polychromatic erythrocytes in ducks.

Trophozoites (Fig. 242, *1–4*). The earliest trophozoites are roundish, possess a more or less evident vacuole; as the parasite develops, trophozoites take a highly ameboid form and the vacuoles increase in size (Fig. 242, *3, 4*); the parasite nucleus is large and the cytoplasm is plentiful; pigment appear early (see Fig. 242, *2*) as one or two granules which are roundish, small and dark-brown; up to six small pigment granules can be seen in fully grown trophozoites (Fig. 242, *4*); trophozoites do not influence or only slightly influence infected erythrocytes.

Erythrocytic meronts (Fig. 242, *5–11*). Young meronts possess large nuclei, plentiful cytoplasm, and vacuoles are frequently seen in the cytoplasm (Fig. 242, *5*, *6*); the meronts can be seen anywhere in infected erythrocytes; as the parasite develops, nuclei decrease in size and basophility of cytoplasm also decreases; fully grown meronts are usually elongated, can be seen anywhere in infected erythrocytes, but more frequently are seen in a lateral position to the nuclei of erythrocytes (Fig. 242, *7–11*); nuclei are usually located randomly in fully grown meronts but they also frequently locate along the periphery of the parasites (Fig. 242, *7, 9*); mature meronts contain 8 to 18 merozoites; pigment granules are of small size (<0.5 μm), dark-brown colour, clumped into one or two small spots (Fig. 242, *6–8*) and frequently aggregated into a solid mass of pigment in mature meronts (Fig. 242, *10*, *11*); meronts usually do not deform infected erythrocytes but can displace their nuclei laterally (Fig. 242, *10*); mature meronts do not exceed 16 μm in length; mature merozoite look like a roundish body with a compact nucleus and a small portion of cytoplasm.

Macrogametocytes (Fig. 242, *12–17*). The cytoplasm is homogeneous in appearance, sometimes contains a few small vacuoles; gametocytes are elongated in form and variable in outline, they usually are seen in a lateral position to the nuclei of infected erythrocytes; fully grown gametocytes enclose the nuclei with their ends and can completely encircle the nuclei; the parasite nucleus is compact, usually median in position; pigment granules are usually roundish, sometimes of oval shape, usually of small size (<0.5 μm), randomly scattered throughout the cytoplasm but sometimes aggregated in one or several loose clumps (Fig. 242, *14*), their number varies from 7 to 20; gametocytes only slightly influence infected erythrocytes whose nuclei can be displaced laterally.

Microgametocytes (Fig. 242, *18–20*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector

Plasmodium lophurae was isolated from its natural hosts only once. After numerous blood passages in laboratory hosts, the strain lost the ability to produce gametocytes. Thus, the data on sporogony of *P. lophurae* are restricted to the experiments which were carried out with the 'young' strain (Coggeshall, 1938; Huff, 1940; Laird, 1941; Jeffery, 1944; Garnham, 1966). The parasite does not develop in mosquito *Anopheles punctipennis*. Initial stages of development of oocysts were seen in *Culex pipiens*. Sporozoites developed in *Aedes aegypti*, *A. albopictus*, *A. atropalpus*, *Anopheles quadrimaculatus*, and *Culex restuans*. The mosquito *Aedes albopictus* transmitted the infection to experimental hosts by bite. In the mosquito *Aedes aegypti* maintained at a temperature of 28°C, the oocysts increase from 18 to 38 μm in diameter between the fifth and seventh days after ingestion of mature gametocytes. It is important to note that the oocysts do not grow at temperatures below 28°C. Sporogony is completed in 11 days. In mosquito *A. albopictus*, sporozoites were seen in the salivary glands six or seven days after infection at 30°C. However, the rapid development is accompanied by the loss of viability of the sporozoites. The sporozoites were not seen in the salivary glands of *A. albopictus* until the 11th day after the infection if the mosquitoes were maintained at the room temperature.

Pathogenicity. More or less evident clinical signs of the *lophurae*-malaria have been recorded in domestic chickens, ducks, turkeys, guinea-fowls, and some other birds. The disease is especially severe in ducks, and the mortality rate is high not only among ducklings, but also among adult ducks. Parasitemia can be up to 100% of erythrocytes in ducks. The mortality rate is much lower among adult birds of other species. The infected birds usually die due to blockage of capillaries of the brain with exoerythrocytic meronts and severe anaemia. The clinical signs are especially pronounced in ducklings who became lethargic and unsteady, feathers are ruffled; the birds refuse food and finally die in convulsions because of the cerebral malaria. The acute anaemia develop during heavy parasitemia, and this can be the main cause of death in some infections. Spleen is markedly enlarged. The survived birds acquire premunition.

Specificity. The range of natural hosts has not been investigated. There are some doubtful records in naturally infected nonmigrant birds in the Holarctic. However, *P. lophurae* require a high amount of heat to be able to develop in vectors, so natural transmission in the Holarctic, especially in its central and northern parts, is questionable.

Domestic chickens, ducklings of all breeds, turkey poults, and guinea-fowl are good experimental hosts. Numerous species of pheasants as well as goslings, domestic pigeon, and coot *Fulica atra* were also successfully infected. Canary infects with difficulty.

It should be noted that *P. lophurae* is the sole species among bird malaria parasites which was successfully adapted to mice (McGhee, 1951, 1956). Moreover, the strains which developed not only in juvenile but also in adult mice were selected. Thus, the composition of experimental hosts of *P. lophurae* is unique.

Comments. During identification of *P. lophurae*, the attention should be, first of all, paid on the following characters. First, erythrocytic merogony is only slightly synchronized and thus all blood stages can be found simultaneously at any stage of parasitemia. Second, trophozoites and young meronts usually are highly ameboid in outline and their cytoplasm is vacuolated. Third, fully grown erythrocytic meronts never encircle the nuclei of infected erythrocytes completely but gametocyte

can do so. Furthermore, *P. lophurae* can be distinguished from all known species of the subgenus *Giovannolaia* on the basis of its wide range of experimental vertebrate hosts.

15. **Plasmodium (Giovannolaia) durae** Herman, 1941

Plasmodium durae Herman, 1941: 23, Pl. 1, Fig. 1–9.

Type vertebrate host. *Meleagris gallopavo* L. (Galliformes).
Additional vertebrate hosts. *Francolinus leucoscepus*, *F. levaillantii*, *F. swainsonii*, *Numida meleagris*, *Pavo cristatus* (Galliformes).
Vectors. *Culex antennatus, C. pipiens fatigans*, *C. univittatus* (Diptera: Culicidae).
Type locality. Langata, near Nairobi, Kenya.
Distribution. The Ethiopian zoogeographical region.
Type material. Neohapantotypes (*exoerythrocytic meronts* in *Meleagris gallopavo*: No. 303, spleen section; No. 304, cerebellum section; No. 305, brain smear; *blood stages*: No. 292, 293, Kenya strain subinoculated in *M. gallopavo*; *sporogonic stages*: No. 299, *Culex pipiens fatigans*, oocysts on the seventh day after infection; No. 300, *C. p. fatigans*, oocysts on the 10th day after infection; No. 301, *C. p. fatigans*, sporozoites; No. 302, *C. antennatus*, sporozoites) are deposited in CPG.
Etymology. This species is named in honour of Mrs. Deking Dura, who contributed material, which served as the source of the original description, from her farm in Kenya.

Main diagnostic characters. Fully grown erythrocytic meronts are roundish or oval, do not occupy all available cytoplasmic space in infected erythrocytes and produce from 4 to 14 (usually 8 to 12) merozoites. Fully grown gametocytes are elongated, usually lacking vacuoles; they tend to lie obliquely in infected erythrocytes.

Development in vertebrate host has been incompletely studied (Purchase, 1942; Simpson, 1944; Laird, 1978; Garnham, 1980; Huchzermeyer, 1993a, 1993b). Primary exoerythrocytic merogony has not been investigated. Phanerozoites were recorded both in the dead naturally infected turkeys and the experimentally infected turkeys after blood-induced infections. Morphology of phanerozoites is similar to *P. gallinaceum*. The parasites develop in reticuloendothelial cells. They are especially numerous in the brain, including cerebellum, and they were also observed in the lungs, liver, and spleen. Phanerozoites are especially frequently recorded between the 15th and 30th days after inoculation of infected blood. They were not found during the first week after the blood-induced infection, and they usually were absent two months after the infection. However, phanerozoites were seen during the chronic stage of infection in turkeys infected with the South African strain. Phanerozoites cause the broadening of brain capillaries, and they finally block up the capillaries.

The prepatent period in turkeys varies from 3 to 18 days after intravenous blood-induced infection, and from 12 to 40 days after the intramuscular inoculation of infected blood. Initial parasitemia is usually high. The high parasitemia is present for about two or three weeks, and then the infection turns into a chronic stage. Erythrocytic merogony is synchronized. A cycle of merogony is close to 24 h. The meronts rupture in the morning.

Trophozoites (Fig. 243, *1–4*) develop in mature erythrocytes; earliest trophozoites are of variable form, are seen anywhere in infected erythrocytes; the ‘ring’ stage is not characteristic; as the parasite develops, trophozoites take an irregular form, ameboid

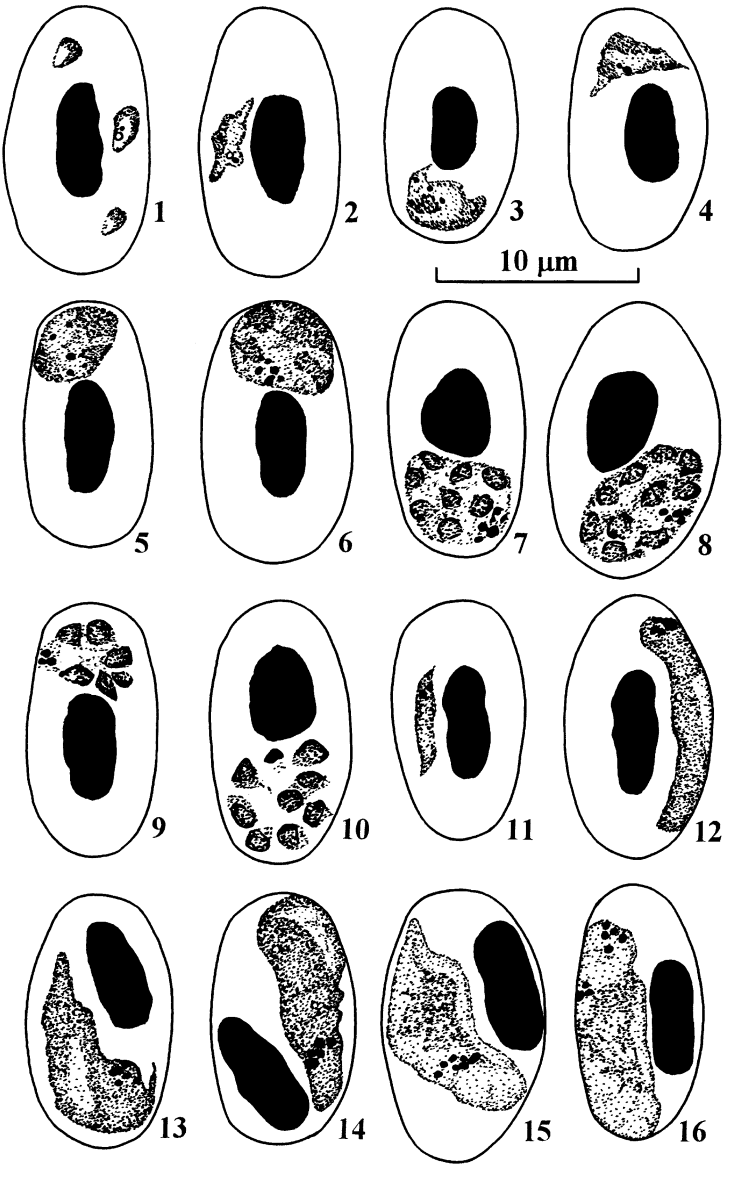

Figure 243 *Plasmodium durae* from the blood of *Meleagris gallopavo:*
1–4 – trophozoites; *5–10* – erythrocytic meronts; *11–14* – macrogametocytes; *15, 16* – microgametocytes.

outgrowths appear, and they are now usually seen in a polar or subpolar position in the erythrocytes not touching their nuclei (Fig. 243, *3*, *4*); a minute greenish-shade, round-form refractive globule was observed in some trophozoites (Fig. 243, *1*, *2*); pigment appears early in young trophozoites as a minute round-form, brown-colour granule (Fig. 243, *1*); fully grown trophozoites contain up to four small (<0.5 μm) dark-brown pigment granules; trophozoites usually do not influence infected erythrocytes.

Erythrocytic meronts (Fig. 243, *5–10*) are seen in mature erythrocytes; cytoplasm is plentiful in young meronts (Fig. 243, *5*, *6*) but nearly invisible in mature meronts (Fig. 243, *9*); nuclei markedly decrease in size as the parasite matures; fully grown meronts are roundish or oval, occupy no more than half of the cytoplasmic space in the infected erythrocytes; nuclei are usually located randomly or arranged as rosettes in fully grown meronts but were also seen arranged as fans; mature meronts contain 4 to 14 (more frequently 8 to 12) merozoites; meronts usually produce eight merozoites during the development in turkeys; pigment granules are roundish, of markedly variable size but usually do not exceed 0.5 μm in diameter, of black colour, were seen scattered in some young meronts (Fig. 243, *5*) and clumped into a spot in advanced parasites (Fig. 243, *7–9*) and even aggregated into a solid mass in mature meronts (Fig. 243, *10*); the number of pigment granules varies from one to eight (usually three to five); meronts are usually seen in a polar or subpolar position in infected erythrocytes, usually they do not influence or only slightly influence the host cells whose nuclei can be slightly displaced (Fig. 243, *8*, *10*).

Macrogametocytes (Fig. 243, *11–14*) are seen in mature erythrocytes, are elongated and of variable outline; the cytoplasm is homogeneous in appearance, usually lacking vacuoles; growing gametocytes are usually seen in a lateral position to the nuclei of infected erythrocytes (Fig. 243, *11, 12*); as the parasite develops, gametocytes tend to lie obliquely in the host cells (Fig. 243, *13*, *14*) but some fully grown gametocytes were also observed in a lateral position to the nuclei of erythrocytes; fully grown gametocytes are usually irregular in outline (Fig. 243, *13*, *14*); oval gametocytes sometimes appear; the parasite nucleus is usually oval or ribbon-like, variable in position; pigment granules are roundish, black, usually of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, usually clumped into a spot (Fig. 243, *12–14*), sometimes clumped in two small spots; their number varies from 3 to 12; fully grown gametocytes do not deform infected erythrocytes but frequently displace their nuclei either laterally or toward one pole (Fig. 243, *13*, *14*); gametocytes do not exceed 13 μm in length.

Microgametocytes (Fig. 243, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has not been investigated in detail. *Culex antennatus* is the natural vector. Sporogony is completed in mosquitoes *Culex pipiens fatigans* and *C. univittatus*. Sporozoites are about 12 to 15 μm in length.

Pathogenicity. *Plasmodium durae* causes lethal epizooties in domestic turkeys in Africa (Purchase, 1942; Garnham, 1980; Huchzermeyer, 1993b). Virulence of different strains varies markedly. In Central Africa, mortality in juvenile turkeys was recorded to be up to 86%, but some strains do not cause severe death in turkeys in South Africa. The virulence increases with serial of blood passages. The disease is especially severe and rapid in young poults. In older birds, the infection usually quickly turns into a chronic stage, and the birds usually survive. However, even adult birds can sometimes die. In blood-induced infections, the mortality markedly depends on the dose of the inoculum and the age of birds. All three-week-old or younger poults died between the 18th and 22nd days after subinoculation of approximately two million parasites. However, the mortality does not exceed 30% in birds between the third and sixth weeks in age. Clinical signs of infection were seen in young turkey poults usually only before the death mainly as convulsions and paralysis. Deceased older birds were lethargic with ruffled feathers; they stand with a difficulty, and rest with their heads on the ground; legs are oedematous, eyelids drooped; the birds refuse food, and inflammation of the wattles and diarrhoea were recorded in some birds. Anaemia develops at high parasitemia. The convulsions were also seen in some

heavily infected older birds. In adult birds, the infection usually becomes chronic, and the signs of disease gradually disappear. Blockage of brain capillaries by phanerozoites is the main cause of death. At autopsy, enlargement of the spleen, deposition of malarial pigment in the spleen, liver, and kidneys, fibrosis in the kidneys and cirrhosis of liver were recorded.

Specificity. According to current knowledge, the range of natural vertebrate hosts is limited to several bird species (see 'Additional vertebrate hosts'). Domestic chickens can be infected with difficulty but the infection is transient in duration and no signs of illness were seen. Ducklings can be infected only by some strains. Canary and domestic pigeon are resistant. Some south African strains produce low and transient experimental infections in Japanese quail and high, long-lasting parasitemias in pheasant *Chrysolophus amherstiae.*

Comments. *Plasmodium durae* can be distinguished from other species of malaria parasites of the subgenus *Giovannolaia*, first of all, on the basis of its (i) roundish fully grown erythrocytic meronts and (ii) elongated gametocytes which tend to lie obliquely in the infected erythrocytes. See also 'Comments' to *P. hermani.*

16. **Plasmodium (Giovannolaia) pedioecetae** Shillinger, 1942

Plasmodium pedioecetae Shillinger, 1942: 1217. – *P. pedioecetii*: Stabler *et al.*, 1973: 395 (emend. pro *pedioecetae*).

Type vertebrate host. *Tympanuchus (=Pedioecetes) phasianellus* (L.) (Galliformes).
Additional vertebrate hosts. Some species of birds (Table 140).
Type locality. North Dakota, USA.
Distribution. This parasite has been recorded in the Nearctic and in the Neotropical zoogeographical region so far.
Type material. Neohapantotypes (No. 347, 348, *Perdix perdix*, R.M. Stabler) are deposited in CPG.
Etymology. The specific name is derived from the generic name *Pedioecetes* to which the type vertebrate host was formerly attributed. Stabler *et al.* (1973) noted that the name *pedioecetii* would be better for this species, and they changed the original spelling of the name *pedioecetae*. However, this action is an unjustified emendation [Article 33(b)(ii)(iii) of the International Code of Zoological Nomenclature, 1985].

Table 140 List of vertebrate hosts of *Plasmodium pedioecetae* (modified from Stabler and Kitzmiller, 1976).

Alectoris chukar	*Dendragapus obscurus*	*Perdix perdix*
Centrocercus urophasianus	*Lophortyx gambelii*	*Serinus canaria*
Colinus virginianus	*Nothura darwinii*	*Tympanuchus cupido*
Coturnix coturnix	*Oreortyx picta*	

Main diagnostic characters. Trophozoites and growing erythrocytic meronts are ameboid in outline. Growing erythrocytic meronts frequently possess long (>2 μm in length) tail-like or finger-like outgrowths. Roundish fully grown erythrocytic meronts are present. Fully grown meronts occupy less than half of the cytoplasmic space in infected erythrocytes, they contain 8 to 22 (usually 8 to 12) merozoites. Most meronts are located

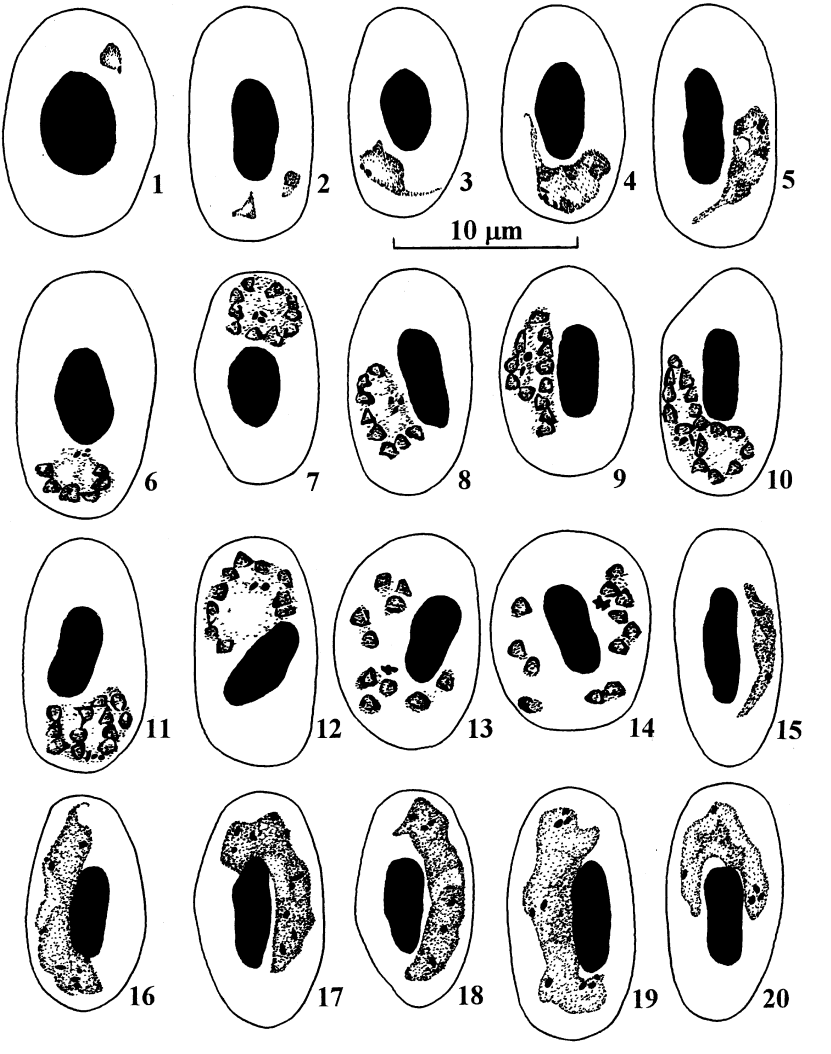

Figure 244 *Plasmodium pedioecetae* from the blood of *Perdix perdix:*
1–3 – trophozoites; *4–14* – erythrocytic meronts; *15–18* – macrogametocytes; *19, 20* – microgametocytes.

in a polar or subpolar position in infected erythrocytes, do not touch the nuclei of erythrocytes but usually more or less displace the nuclei as the parasites mature. Nuclei in mature erythrocytic meronts are usually arranged as fans, rosettes, or more or less pronounced rows. Mature gametocytes can be seen anywhere in infected erythrocytes but do not lie obliquely in the host cells, usually possess no vacuoles.

Development in vertebrate host

Exoerythrocytic merogony has not been investigated. Erythrocytic merogony is not synchronized, but the majority of mature meronts were recorded to rupture in the morning before noon (Stabler and Kitzmiller, 1976).

Trophozoites (Fig. 244, *1–3*) are seen in mature and polychromatic erythrocytes; earliest trophozoites can be seen anywhere in infected erythrocytes; the 'ring' stage was seen; as the parasite develops, trophozoites take an irregular form and ameboid outgrowths appear, and they are now more frequently seen in a polar or subpolar position in infected erythrocytes (Fig. 244, *2*, *3*); a large vacuole and a long (>2 μm in length) tail-like or finger-like growth were frequently seen in advanced trophozoite (Fig. 244, *3*); nucleus relatively large (Fig. 244, *2, 3*); pigment appears in earliest trophozoites as a minute round, brown-colour granule (Fig. 244, *1*, *2*), and largest trophozoites possess up to two minute-size pigment granules located close to each other (Fig. 244, *3*); the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 244, *4–14*) are usually seen in mature erythrocytes but sometimes also found in polychromatic erythrocytes; cytoplasm is plentiful in young meronts (Fig. 244, *3–5*) but nearly invisible in mature parasites (Fig. 244, *6–12*); growing meront frequently possesses a long (>2 μm in length) tail-like or finger-like outgrowth (Fig. 244, *4*, *5*) which disappears as the parasite matures; fully grown meronts are variable in form but the roundish and oval in shape meronts (Fig. 244, *7*, *8*, *11*, *12*) predominate; nuclei tend to locate along the periphery in young meronts (Fig. 244, *4, 5*); the nuclei are usually arranged as rosettes (Fig. 244, *7*), fans (Fig. 244, *6*), or more or less pronounced rows (Fig. 244, *9*, *11*) in fully grown meronts, but they were also observed to be located randomly in some meronts; mature meronts contain 8 to 22 (usually 8 to 12) merozoites which are about 1 μm in diameter; pigment granules are usually of small size (<0.5 μm), not numerous, clumped into a spot; most meronts are in a polar or subpolar position in infected erythrocytes and they usually do not touch the nuclei of erythrocytes; fully grown meronts slightly displace the nuclei of erythrocytes and frequently more or less rotate the nuclei to the normal axis (Fig. 244, *11*, *12*); merozoites were seen to persist in the erythrocytes for some time after segmentation of meronts, and the host cells with completely developed merozoites usually are deformed and even rounded (Fig. 244, *13*, *14*); due to variability of form of meronts, their size also varies markedly; fully grown meronts occupy less than half of the cytoplasmic space in the infected erythrocytes.

Macrogametocytes (Fig. 244, *15–18*) are usually seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, usually lacking vacuoles; gametocytes are variable in form, outline, and position in infected erythrocytes; ameboid outgrowths were seen (Fig. 244, *16*, *18*); fully grown gametocytes can be seen anywhere in infected erythrocytes, they more frequently take a lateral position to the nuclei of erythrocytes (Fig. 244, *16*, *18*) but were also common in a subpolar-lateral position (Fig. 244, *17*) and were even observed in a polar position; the parasite nucleus is compact, small (see Fig. 244, *17*, *18*), usually median in position; pigment granules are usually roundish, of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, usually randomly scattered throughout the cytoplasm, their number varies (n = 28) from 3 to 11 (most frequently 8); gametocytes only slightly (if at all) influence infected erythrocytes whose nuclei can be slightly displaced laterally; fully grown gametocytes (n = 78) are on average 9.8 μm in length and 2.2 μm in width.

Microgametocytes (Fig. 244, *19*, *20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; they were more frequently seen in subpolar and polar position in infected erythrocytes (Fig. 244, *20*) than macrogametocytes; other characters are as for macrogametocytes.

P a t h o g e n i c i t y has not been investigated. Infected males of *Centrocercus urophasianus* were recorded to have significantly lower reproductive success than noninfected males (Boyce, 1990; Johnson and Boyce, 1991).

Specificity. *Plasmodium pedioecetae* has been found in nature mainly in birds of the order Galliformes (Table 140). Partridge *Alectoris chukar*, bobwhite *Colinus virginianus*, quail *Coturnix coturnix*, and canary were infected experimentally by subinoculation of infected blood, but ducklings of *Cairina moschata*, domestic pigeon, pheasant *Phasianus colchicus*, and falcon *Falco sparverius* were resistant.

Comments. Blood stages of *P. pedioecetae* are especially similar to *P. polare*. During identification of these species, the attention should be paid, first of all, on the following characters. First, mature meronts of *P. pedioecetae* frequently rotate the nuclei of infected erythrocytes which is not characteristic of *P. polare*. Second, long tail-like or finger-like outgrowths were usually not seen in young erythrocytic meronts of *P. polare*, but they are common in *P. pedioecetae*. Third, location of pigment granules in gametocytes of these specie is different (cf. Figs. 241, *14–20* and 244, *16–20*). Furthermore, bobwhite *Colinus virginianus* and quail *Coturnix coturnix* were resistant to *P. polare* but highly susceptible to *P. pedioecetae* after blood-induced infection (Stabler and Kitzmiller, 1976).

17. **Plasmodium (Giovannolaia) pinottii** Muniz and Soares, 1954

Plasmodium pinottii Muniz and Soares, 1954: 616.

Type vertebrate host. *Ramphastos toco* (Müller) (Piciformes).
Additional vertebrate hosts. Some species of birds (Table 141).
Type locality. Brazil.
Distribution. From wild birds, this parasite was isolated only once in Brazil. A few records, which came outside the Neotropical zoogeographical region, should be tested.
Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 326–329, *Columba livia*, brain; *blood stages*: No. 323, 324, *C. livia*, strain passaged for 10 years) are deposited in CPG. A series of additional slides is deposited in CPG and IOCB.
Etymology. This species is named in honour of Brazilian malariologist Dr. Mário Pinotti.

Main diagnostic characters. Growing erythrocytic meronts do not possess long tail-like or finger like outgrowths. Fully grown erythrocytic meronts are roundish, oval, or slightly elongated; they can be seen anywhere in infected erythrocytes, displace the nuclei of infected erythrocytes, frequently occupy more than half of the cytoplasmic space in the infected erythrocytes but never occupy all available cytoplasmic space in the host cells. Mature erythrocytic meronts contain 6 to 18 merozoites. Gametocytes do not possess large

Table 141 List of natural and experimental vertebrate hosts of *Plasmodium pinottii* (modified from Muniz and Soares, 1954).

**Anas boschas*	**C. monedula*	**Passer domesticus*
**A. platyrhynchos*	*Euneornix campestris*	**Serinus canaria*
**Aramides* sp.	**Gallus gallus*	*Tiaris bicolor*
Coereba flaveola	**Geothlypis aequinoctialis*	*Turdus migratorius*
**Columba livia*	*Loxipasser anoxanthus*	**Volatinia jacarina*
**Corvus frugilegus*	**Meleagris gallopavo*	**Zonotrichia capensis*

Note: The birds infected experimentally by subinoculation of infected blood are marked with an asterisk.

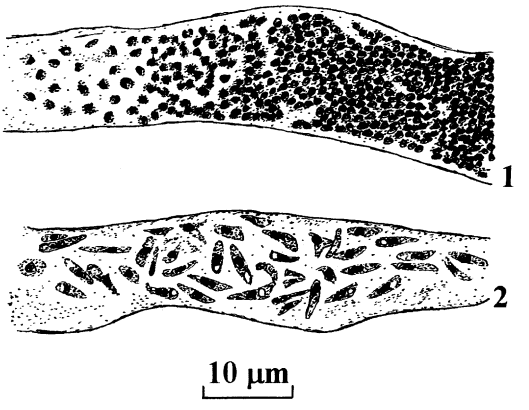

Figure 245 Mature phanerozoites of *Plasmodium pinottii* with micromerozoites (*1*) and macromerozoites (*2*) in a smear of brain of *Columba livia* (modified from Garnham, 1966).

(>1.5 μm in diameter) vacuoles, they take a lateral position to the nuclei of infected erythrocytes and usually do not displace or slightly displace the nuclei. Pigment granules in macro- and microgametocytes are clearly different in size.

Development in vertebrate host has been insufficiently studied (Muniz and Soares, 1954; Garnham, 1966). Primary exoerythrocytic merogony has not been investigated. Phanerozoites develop in endothelial cells of capillaries in the brain. They were especially frequently seen in experimentally infected domestic pigeons, but only occasionally observed in canaries. Phanerozoites were seen in the brain of pigeons between the 18th and 24th days after blood-induced infection, and subsequently were found much more rarely. The majority of subinoculated pigeons died before the appearance of phanerozoites in the brain because of high parasitemia. Phanerozoites were recorded in pigeons with parasitemia suppressed by chemotherapy. Growing phanerozoites look like roundish or elongated bodies which displace the nuclei of host cells. They were seen located both singly and in groups. Up to 25 large (about 2 μm in diameter) roundish nuclei were seen in young phanerozoites which reached approximately 10 μm in length. The nuclei are surrounded with a thin band of light in colour cytoplasm. Some growing meronts possess roundish vacuoles. Mature phanerozoites measured up to 70 μm in length and 10 μm in width. They extend along capillaries and usually look like sausage-shaped bodies, but V-shaped parasites were also seen in bifurcated vessels. Two types of merozoites develop in phanerozoites, i.e., micro- and macromerozoites. The micromerozoites were especially frequently seen. They look like roundish bodies about 1.3 μm in diameter, and they possess a prominent nucleus and a small portion of cytoplasm (Fig. 245, *1*). The macromerozoites were much rarely seen than micromerozoites. They look like slightly curved elongated bodies with one end more pointed than the other end (Fig. 245, *2*). The macromerozoites possess cytoplasm, which is granular in appearance, and a prominent centrally located nucleus. A minute clearly defined roundish vacuole was seen in some macromerozoites. Macromerozoites are about 5 μm in length and 1.5 μm in width.

The prepatent period does not exceed three to four days after intravenous blood-induced infection. Initial parasitemia increases rapidly and reaches its peak seven to eight days after the infection. After the crisis, the parasitemia rapidly decreases and

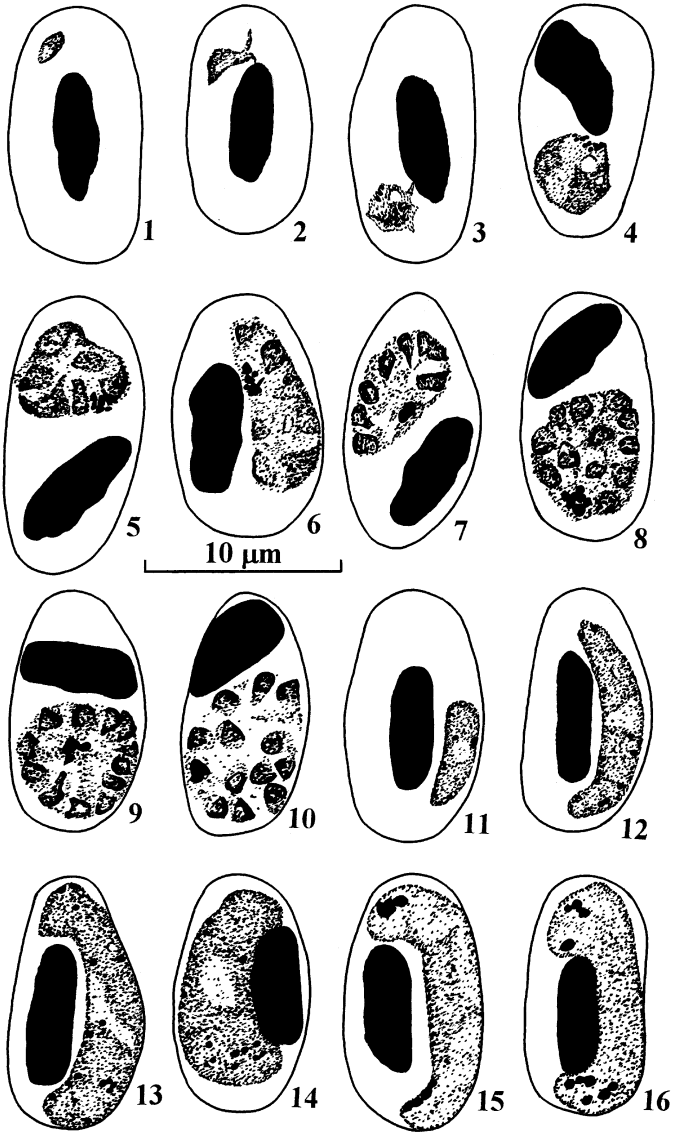

Figure 246 *Plasmodium pinottii* from the blood of *Columba livia:*
1–3 – trophozoites; *4–10* – erythrocytic meronts; *11–14* – macrogametocytes; *15*, *16* – microgametocytes.

parasites disappear from the blood in survived birds. Adult pigeons and domestic chickens at the age up to three days usually die at the top of parasitemia. A cycle of erythrocytic merogony is close to 24 h.

Trophozoites (Fig. 246, *1–3*) are seen in mature and polychromatic erythrocytes; earliest trophozoites are oval (Fig. 246, *1*); as the parasite develops, they take an irregular form, and ameboid outgrowths are frequently seen (Fig. 246, *2*); the 'ring' stage is not characteristic; fully grown trophozoites possess plentiful cytoplasm, a large nucleus, and a small-size vacuole was frequently seen in the cytoplasm (Fig. 246, *3*); pigment granules are

of minute size, dark colour, clumped into a spot near the edge of trophozoites; some trophozoites slightly displace the nuclei of infected erythrocytes (Fig. 246, *3*).

Erythrocytic meronts (Fig. 246, *4–10*) are seen in mature and polychromatic erythrocytes; the cytoplasm is plentiful, and small vacuoles are usually present in young meronts (Fig. 246, *4*); nuclei are large in growing meronts (Fig. 246, *4*, *5*) and markedly decrease in size as the parasite matures; during the development in pigeon, fully grown meronts are roundish, oval, or sometimes slightly elongated; elongated meronts were more numerous during the development in the type vertebrate host (toucan) than in pigeon; nuclei usually are located randomly or arranged as rosettes in fully grown meronts, sometimes they were also seen arranged as fans; mature meronts contain 6 to 18 (usually 8 to 12) merozoites; pigment granules are of small size (<0.5 μm), numerous, brown or black, sometimes with golden shade, clumped into a spot near edge in growing meronts (Fig. 246, *4–6*) and can be aggregated into a solid mass in mature meronts (Fig. 246, *7*, *9*, *10*); meronts can be seen anywhere in infected erythrocytes and usually do not touch the nuclei of erythrocytes; during development in pigeon, the meronts are more frequently seen in a polar or subpolar position in erythrocytes, and they markedly displace the nuclei of erythrocytes (Fig. 246, *5*, *7–10*); meronts located laterally to the nuclei of erythrocytes also displace the nuclei but not so markedly (Fig. 246, *6*); infected erythrocytes can be deformed (Fig. 246, *7*); fully grown meronts occupy more than half of the cytoplasmic space in the infected erythrocytes.

Macrogametocytes (Fig. 246, *11–14*). The parasite was isolated only once. The strain quickly lost the ability to produce gametocytes which can be found in a small number only in preparations from the early passages. The cytoplasm is homogeneous in appearance; vacuoles are not seen; gametocytes are elongated and usually even in outline; as the parasite develops, they take a lateral position to the nuclei of infected erythrocytes, slightly enclose the nuclei with their ends but do not encircle them completely; the parasite nucleus is compact, of variable form, median or submedian position; pigment granules are of small size (<0.5 μm), randomly scattered throughout the cytoplasm, about 12 in number; gametocytes usually slightly influence infected erythrocytes whose nuclei can be more or less displaced laterally (Fig. 246, *13*, *14*).

Microgametocytes (Fig. 246, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules are larger than in macrogametocytes, and medium-size (0.5 to 1.0 μm) granules were frequently seen; pigment granules can be aggregated into solid clumps (Fig. 246, *15*); other characters are as for macrogametocytes.

Relapses were not recorded.

D e v e l o p m e n t i n v e c t o r has not been investigated because the strain rapidly lost the ability to produce a sufficient number of gametocytes for experimental work.

P a t h o g e n i c i t y. The type vertebrate host (toucan) and most other species of wild birds, who were subinoculated with infected blood (see Table 141), usually do not exhibit clinical signs of illness and recovered rapidly. However, the decease is more severe in rooks and jackdaws which sometimes even die. It is interesting to note that no chronic infection was found in birds that recovered, and Garnham (1966) believed that a state of true immunity can develop. Adult domestic pigeons and domestic chickens at the age up to three days develop severe malaria and frequently die seven to nine days after the blood-induced infection with the mortality rate up to 90%. High parasitemia is the main cause of death. Older chickens are less susceptible, and adult hens are resistant. The disease can be severe in canaries, and some of the birds die approximately 20 days after parasites appear in the blood (Muniz and Soares, 1954; Garnham, 1966).

Specificity. *Plasmodium pinottii* has a wide range of vertebrate hosts. Numerous species of birds were infected experimentally (Table 141). Attempts to infect the lizard *Tupinambis teguixin* and laboratory mice with the strain isolated from toucan were not successful.

Comments. Both the elongated erythrocytic meronts, which were most frequently seen in toucan, and the gametocytes of *P. pinottii* are especially similar to *P. fallax*. However, numerous roundish erythrocytic meronts develop in all experimental hosts of *P. pinottii*, and this is not characteristic of *P. fallax*.

The Brazilian strain of this parasite has been lost.

18. **Plasmodium (Giovannolaia) formosanum** Manwell, 1962

Plasmodium formosanum Manwell, 1962: 401, Fig. 1–9.

Type vertebrate host. *Arborophila crudigularis* (Swinhoe) (Galliformes).
Additional vertebrate hosts. *Amaurornis phoenicurus*, *Arborophila gingica*.
Type locality. Nan Tou Hsien, Taiwan, China.
Distribution. This parasite has been found on Taiwan and in Guangdong province (China).
Type material. Hapantotype (*Arborophila crudigularis*, Taiwan, R.E. Kuntz) is deposited in CPM. Parahapantotype (No. 330, other data as for the hapantotype) is deposited in CPG.
Etymology. The specific name is derived from one of the names of the type locality (Formosa).

Main diagnostic characters. Fully grown erythrocytic meronts are roundish, are usually located in a polar position in infected erythrocytes and do not displace or only slightly displace the nuclei of erythrocytes. Mature erythrocytic meronts contain 5 to 16 (usually 8 or 10) merozoites. Large (>1.5 μm in diameter) clear vacuoles are often present in macrogametocytes. Pigment granules frequently gather around these vacuoles.

Development in vertebrate host

Limited data (He and Huang, 1990) show that the prepatent period is short (five days) after blood-induced infection. Synchronization of erythrocytic merogony is low. All blood stages are present in the type preparations. A cycle of erythrocytic merogony was said to be about 48 h (He and Huang, 1990).

Trophozoites (Fig. 247, *1–3*) are seen in mature erythrocytes; earliest trophozoites are seen anywhere in infected erythrocytes, are of small size, possess a prominent nucleus and a small portion of cytoplasm (Fig. 247, *1*); the typical 'ring' stage is not characteristic; as the parasite develops, trophozoites take an irregular form and ameboid outgrowths appear, and now they more frequently locate in a polar or subpolar position in the erythrocytes (Fig. 247, *2*, *3*); pigment appear early as a minute granule (Fig. 247, *2*); fully grown trophozoite possesses a large nucleus, plentiful cytoplasm and several pigment granules which are small (<0.5 μm) and dark-brown (Fig. 247, *3*); the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 247, *4–10*) are seen in mature erythrocytes; growing parasites possess the plentiful cytoplasm; vacuoles are not seen; nuclei only slightly decrease in size as the parasite matures (Fig. 247, *4–6*); fully grown meronts are roundish

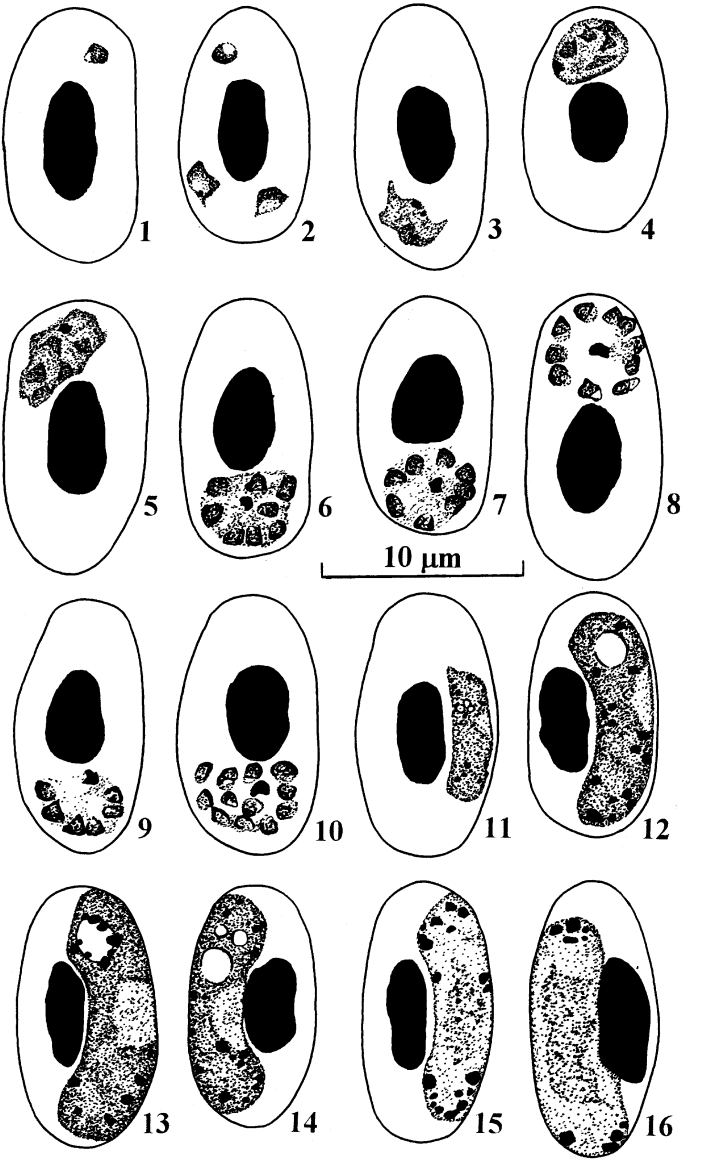

Figure 247 *Plasmodium formosanum* from the blood of *Arborophila crudigularis:* *1–3* – trophozoites; *4–10* – erythrocytic meronts; *11–14* – macrogametocytes; *15*, *16* – microgametocytes.

or oval; nuclei are arranged usually as rosettes (Fig. 247, *6–8*) or sometimes also as fans (Fig. 247, *9*) or distributed randomly (Fig. 247, *10*) in fully grown meronts; mature parasites contain 5 to 16 (usually 8 or 10) merozoites; pigment granules are usually aggregated into a solid mass which is dark-brown and is located near the centre of parasite (Fig. 247, *6–8*, *10*); meronts usually seen in a polar position in infected erythrocytes and they, as a rule, do not touch the nuclei of erythrocytes; parasites do not influence or only

slightly influence infected erythrocytes whose nuclei can be slightly displaced; meronts do not exceed 6 μm in diameter.

Macrogametocytes (Fig. 247, *11–14*) are seen in mature erythrocytes; gametocytes are elongated, usually even in outline; the cytoplasm is homogeneous in appearance; young gametocytes possess several minute vacuoles (Fig. 247, *11*); fully grown gametocyte frequently contain one clearly defined, large (about 1 or 2 μm in diameter and even larger) vacuole which is subterminal in position (Fig. 247, *12–14*), and several small vacuoles were also seen in some gametocytes (Fig. 247, *14*); gametocytes take a lateral position to the nuclei of infected erythrocytes and only slightly enclose the nuclei with their ends; the majority of gametocytes do not touch the nuclei of erythrocytes (Fig. 247, *12*, *13*); the parasite nucleus is compact, large (see Fig. 247, *13*, *14*), median in position; pigment granules are roundish and irregular, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm and also frequently gathered around the large vacuoles and were even seen inside the vacuoles (Fig. 247, *13*); the number of pigment granules varies from 15 to 25; gametocytes only slightly influence infected erythrocytes whose nuclei are more or less displaced laterally; gametocytes (n = 14) vary from 8.7 to 14.0 (on average 11.5±0.3) μm in length and from 2.3 to 4.0 (on average 3.2±0.3) μm in width.

Microgametocytes (Fig. 247, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the large vacuoles are not seen; other characters are as for macrogametocytes.

Development in vector has not been investigated. Oocysts did not develop in mosquitoes *Aedes albopictus* and *Culex pipiens fatigans* (He and Huang, 1990).

Specificity. Attempts to infect domestic pigeons and ducklings by subinoculation of infected blood were not successful (He and Huang, 1990).

Comments. *Plasmodium formosanum* can be distinguished from other species of malaria parasites of birds, first of all, on the basis of the large vacuoles which frequently present in its macrogametocytes. Small rosette-like erythrocytic meronts are also a good character of this species.

Plasmodium formosanum is similar to the malaria parasites of the subgenus *Novyella*. It can be distinguished from the species of *Novyella*, first of all, on the basis of (i) plentiful cytoplasm in its fully grown trophozoites and growing erythrocytic meronts and (ii) more numerous merozoites in the erythrocytic meronts. The erythrocytic meronts of *P. formosanum* frequently contain 10 merozoites.

19. **Plasmodium (Giovannolaia) gundersi** (Bray, 1962)

Haemamoeba gundersi Bray, 1962: 206, Fig. 1, 2. – *Plasmodium gundersi*: Garnham, 1966: 657.

Type vertebrate host. *Ciccaba woodfordii* (Smith) (Strigiformes).
Additional vertebrate host. *Arborophila gingica*.
Type locality. Harbel, Marshall Territory, Liberia.
Distribution. This parasite has been recorded in Liberia and in Guangdong province (China).
Type material has been never designated.
Etymology. This species is named in honour of Dr. A.E. Gunders.

Main diagnostic characters. Growing erythrocytic meronts can be seen anywhere in infected erythrocytes and do not possess any long outgrowths. Fully grown

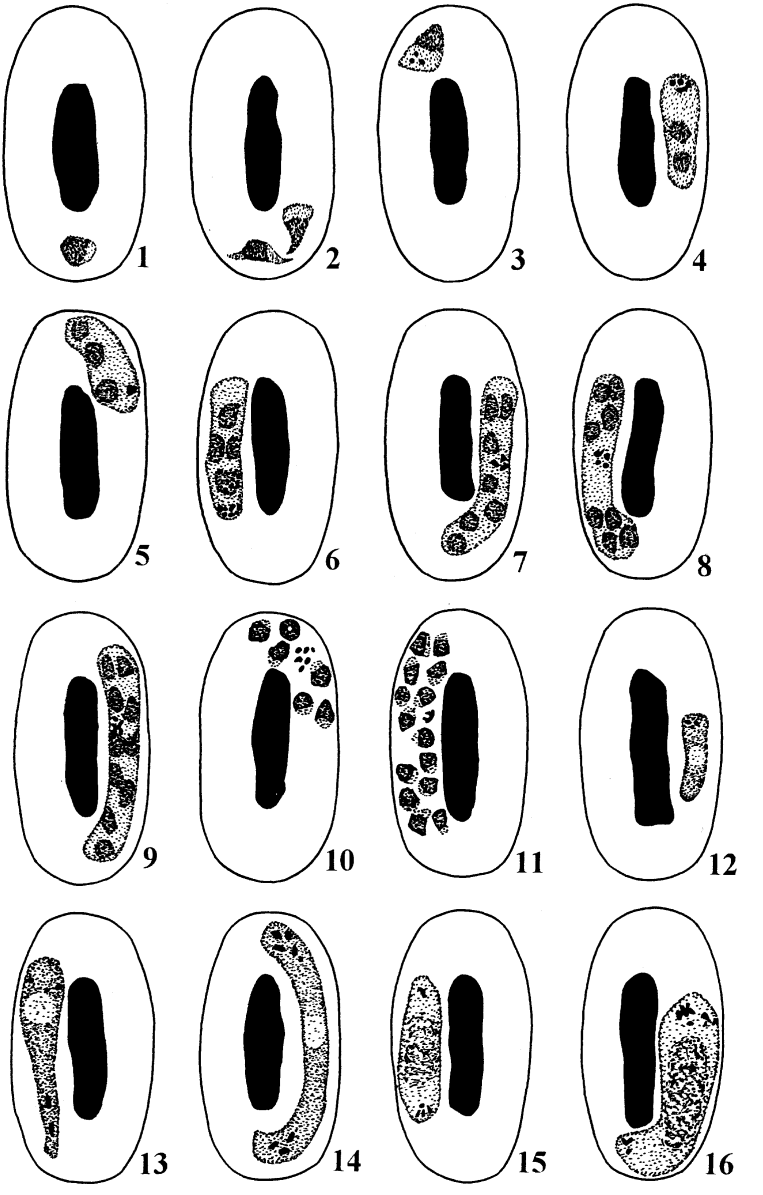

Figure 248 *Plasmodium gundersi* from the blood of *Ciccaba woodfordii:*
1–3 – trophozoites; *4–11* – erythrocytic meronts; *12–14* – macrogametocytes; *15*, *16* – microgametocytes (modified from Bray, 1962).

erythrocytic meronts and gametocytes are slender and elongated, their cytoplasm is not vacuolated; they take a lateral position to the nuclei of infected erythrocytes and neither encircle the nuclei completely nor displace them. Erythrocytic meronts possess randomly located nuclei, and pigment granules are clumped into a small group. Mature erythrocytic meronts contain 6 to 14 merozoites.

Development in vertebrate host

The prepatent period in canaries is 17 days after the subinoculation of infected blood from naturally infected *Arborophila gingica*. Periodicity of erythrocytic merogony appears to be 24 h (Huang and Huang, 1992).

Trophozoites (Fig. 248, *1–3*) are seen in mature erythrocytes; earliest trophozoites can be seen anywhere in the erythrocytes, and each trophozoite possesses a prominent nucleus and a small portion of cytoplasm; as the parasite develops, trophozoites take an irregular form, ameboid outgrowths appear, and they are now more frequently seen in a polar or subpolar position in infected erythrocytes (Fig. 248, *2*, *3*); pigment granules appear in advanced trophozoites, are small, dark-brown, their number varies from two to five; they are clumped into a spot; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 248, *4–11*) are seen in mature erythrocytes; the cytoplasm is plentiful; vacuoles are not seen; nuclei are prominent, located randomly; the outline is even; meronts are elongated and slender from the earliest stages of their development (Fig. 248, *4–9*); young meronts can be seen anywhere in infected erythrocytes (Fig. 248, *4*, *5*) but fully grown parasites are usually seen in a lateral position to the nuclei of erythrocytes (Fig. 248, *9*, *11*); mature meronts contain 6 to 14 (more frequently 8 or 10) merozoites; pigment granules are small, dark-brown, their number varies from three to five, they are clumped in a small group located near one end of the growing meronts (Fig. 248, *4–6*) and observed in a median position in advanced parasites (Fig. 248, *7–11*); meronts do not touch the nuclei of infected erythrocytes, and their influence on the host cells is not pronounced; mature merozoite possesses a prominent nucleus and a small portion of cytoplasm (Fig. 248, *10*, *11*).

Macrogametocytes (Fig. 248, *12–14*) are seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, vacuoles are not seen; the outline is even; gametocytes are elongated and slender from the earliest stages of development (Fig. 248, *12–14*) and were usually recorded in a lateral position to the nucleus of infected erythrocytes; the parasite nucleus is compact, small (see Fig. 248, *14*), median or submedian in position; pigment granules are not numerous, of variable size, relatively large in fully grown gametocytes (Fig. 248, *13*, *14*); gametocytes do not influence infected erythrocytes.

Microgametocytes (Fig. 248, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; some gametocytes were recorded in polar-lateral position in infected erythrocytes (Fig. 248, *16*); fully grown microgametocytes are shorter and wider than macrogametocytes; pigment granules are of smaller size and aggregated in more compact groups than in macrogametocytes; other characters are as for macrogametocytes.

Pathogenicity. The strain, isolated in China from *Arborophila gingica*, is lethal for canaries (Huang and Huang, 1992).

Specificity. In nature, this parasite was recorded in strigiform and galliform birds. The Chinese strain develops in canary (Huang and Huang, 1992).

Comments. Blood stages of *P. gundersi* are similar to *P. fallax*. Erythrocytic meronts and gametocytes of *P. gundersi* are much more slender than the same stages of *P. fallax*. In addition, vacuoles were not seen in erythrocytic meronts and gametocytes of *P. gundersi* but are common in *P. fallax*. Furthermore, erythrocytic meronts of *P. fallax* contain more merozoites on average, and their gametocytes have a greater number of pigment granules which are of larger size than in *P. gundersi*.

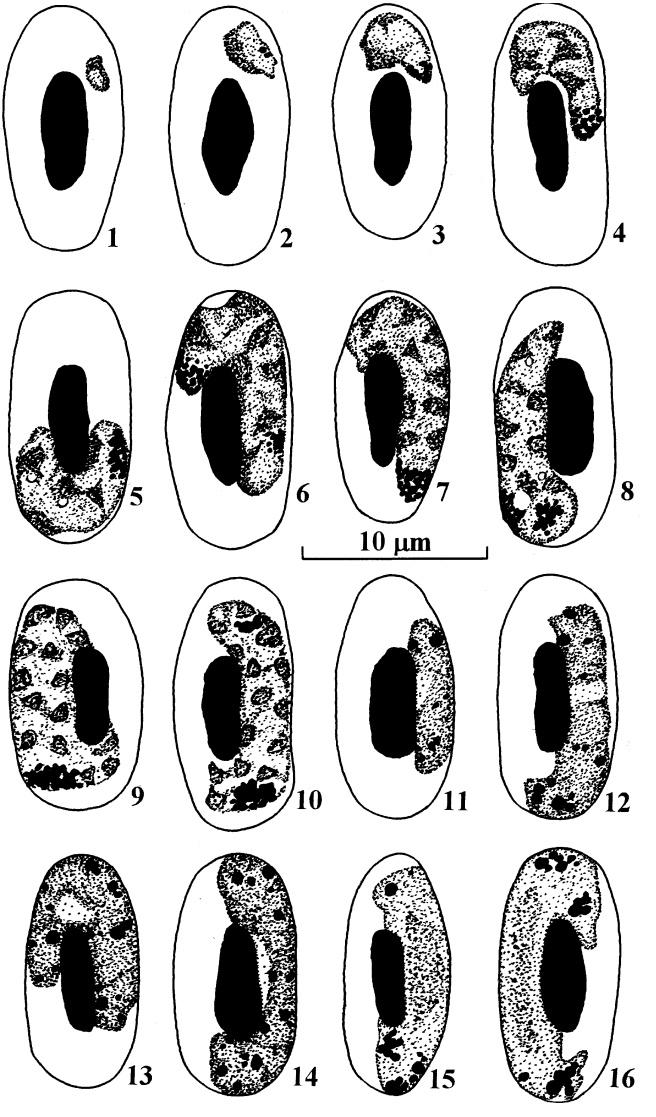

Figure 249 *Plasmodium anasum* from the blood of *Anas clypeata:*
1, *2* – trophozoites; *3–10* – erythrocytic meronts; *11–14* – macrogametocytes; *15, 16* – microgametocytes.

20. **Plasmodium (Giovannolaia) anasum** Manwell and Kuntz, 1965

Plasmodium anasum Manwell and Kuntz, 1965: 103, Fig. 1–20.

Type vertebrate host. *Anas clypeata* L. (Anseriformes).
Type locality. Lin-pien Ping-tung Hsien, Taiwan, China.

Distribution. This parasite has been recorded only in the type locality so far.
Type material. Hapantotype (No. PF 10103, *Anas clypeata*, Taiwan, R.E. Kuntz) is deposited in USNPC. Parahapantotype (No. 331, other data as for the hapantotype) is deposited in CPG.
Etymology. The specific name is derived from the generic name of the type host, *Anas*.

Main diagnostic characters. Growing erythrocytic meronts frequently are polar or subpolar in position and U-like in form; they do not produce long tail-like or finger-like outgrowths. Fully grown erythrocytic meronts are elongated and can be seen anywhere in infected erythrocytes; they do not encircle the nuclei of infected erythrocytes completely and do not occupy all available cytoplasmic space in the erythrocytes. Mature erythrocytic meronts contain 12 to 18 (on average 15) merozoites. Gametocytes are elongated and take a lateral or polar position in infected erythrocytes; they usually lack vacuoles. Pigment granules in erythrocytic meronts are numerous; they are frequently aggregated into large (>1.5 μm in length) clumps usually located at one end of the meronts.

Development in vertebrate host
Trophozoites (Fig. 249, *1*, *2*) are seen in mature erythrocytes; earliest trophozoites are variable in form and position, possess a more or less evident vacuole (Fig. 249, *1*); the typical 'ring' stage is not characteristic; the outline is usually irregular but ameboid outgrowths were only occasionally seen; as the parasite develops, trophozoites usually take a polar or subpolar position in infected erythrocytes (Fig. 249, *2*), and each possesses plentiful cytoplasm and a large nucleus; pigment appears in the earliest trophozoites, and the fully grown trophozoites possess two to five pigment granules which are of minute size, roundish and dark-brown; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 249, *3–10*) are seen in mature erythrocytes; the cytoplasm is plentiful, sometimes possesses a few small or sometimes medium-size clear vacuoles (Fig. 249, *5*, *8*); meronts are elongated; young parasites are usually seen in a polar or subpolar position in infected erythrocytes (Fig. 249, *3*); as the parasite develops, meronts keep the polar position, extend along the nuclei of erythrocytes and usually take a U-like form (Fig. 249, *4–6*); fully grown meronts are usually seen in a lateral position to the nuclei of infected erythrocytes (Fig. 249, *8–10*), possess randomly located nuclei; mature meronts contain 12 to 18 (on average 15) merozoites; pigment granules are roundish, of small size (<0.5 μm), numerous, usually aggregated into one or two large (frequently >1.5 μm in length) clumps located at one end of the meronts; pigment granules are difficult to count because of their dense clumping; fully grown meronts are usually closely appressed to the nuclei of infected erythrocytes and can slightly enclose the nuclei with their ends (Fig. 249, *9*); meronts at the stage of segmentation into merozoites were not seen in the type material; it is likely that the segmentation of meronts rapidly leads to the rupture of host cells; meronts only slightly influence infected erythrocytes whose nuclei can be more or less displaced laterally (Fig. 249, *8*, *9*).

Macrogametocytes (Fig. 249, *11–14*) are seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, usually lacks vacuoles; from the earliest stages of development, gametocytes are elongated and are usually seen in a lateral position to the nuclei of infected erythrocytes (Fig. 249, *11*), but some gametocytes were also seen in a polar position in the host cells and were of U-like form (Fig. 249, *13*); fully grown gametocytes markedly enclose the nuclei of infected erythrocytes with their ends, and some of them were occasionally seen nearly completely encircling the nuclei; the outline is usually even, sometimes slightly ameboid; the parasite nucleus is compact, of variable form, small (see

Fig. 249, *12*, *13*), median in position; pigment is plentiful even in young gametocytes; the pigment granules are roundish and irregular, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, vary from 9 to 19 (on average 14); gametocytes usually do not influence or only slightly influence infected erythrocytes whose nuclei can be slightly displaced laterally.

Microgametocytes (Fig. 249, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters. A few microgametocytes were seen in the type material, and all of them have prominent clumps of pigment granules at their ends.

Comments. Only blood stages of *P. anasum* have been investigated so far. During identification of this species, attention should be paid, first of all, to the following characters. First, growing erythrocytic meronts are frequently polar in position in infected erythrocytes, and U-like parasites are common. Second, pigment is plentiful both in erythrocytic meronts and gametocytes. Third, pigment granules in erythrocytic meronts are aggregated into large (>1.5 μm in length) clumps which are usually located at one end of the meronts. Fourth, relatively large-size pigment granules are present in gametocytes (see Fig. 249, *13–16*).

21. **Plasmodium (Giovannolaia) garnhami** Guindy, Hoogstraal and Mohammed, 1965

Plasmodium garnhami Guindy, Hoogstraal and Mohammed, 1965: 280, Fig. 1–24.

Type vertebrate host. *Upupa epops major* Brehm (Coraciiformes).
Additional vertebrate hosts. Unknown.
Vector. *Culex pipiens molestus* (Diptera: Culicidae).
Type locality. Imbaba District, Giza Province, Egypt.
Distribution. The Southern Palearctic and the Ethiopian zoogeographical region.
Type material. Hapantotypes (*blood stages*: No. 315–317, *Upupa epops major*, 1965, Egypt; *exoerythrocytic stages*: No. 318–320, 322, histological sections and smears of liver, sporozoite-induced infection, other data as for No. 315) and parahapantotype (No. 321, a duplicate of No. 320) are deposited in CPG.
Etymology. This species is named in honour of Professor P.C.C. Garnham in recognition of his outstanding contribution to the field of malariology.

Main diagnostic characters. Growing erythrocytic meronts do not possess long tail-like or finger-like outgrowths. Fully grown erythrocytic meronts are roundish or irregular in form, they are usually polar or subpolar in position in infected erythrocytes, displace the nuclei of erythrocytes but never occupy all available cytoplasmic space in the erythrocytes. Mature erythrocytic meronts contain six to eight merozoites. Growing gametocytes are slender and irregular in outline. Fully grown gametocytes are sausage-like in form, they take a lateral position to the nuclei of infected erythrocytes and do not possess large (>1.5 μm in diameter) vacuoles.

Development in vertebrate host

Exoerythrocytic merogony was investigated in the experimentally infected young hoopoes *Upupa epops major* (Guindy *et al.*, 1965; Garnham, 1966). Numerous primary exoerythrocytic meronts were found in the Kupffer cells of the liver six to seven days after

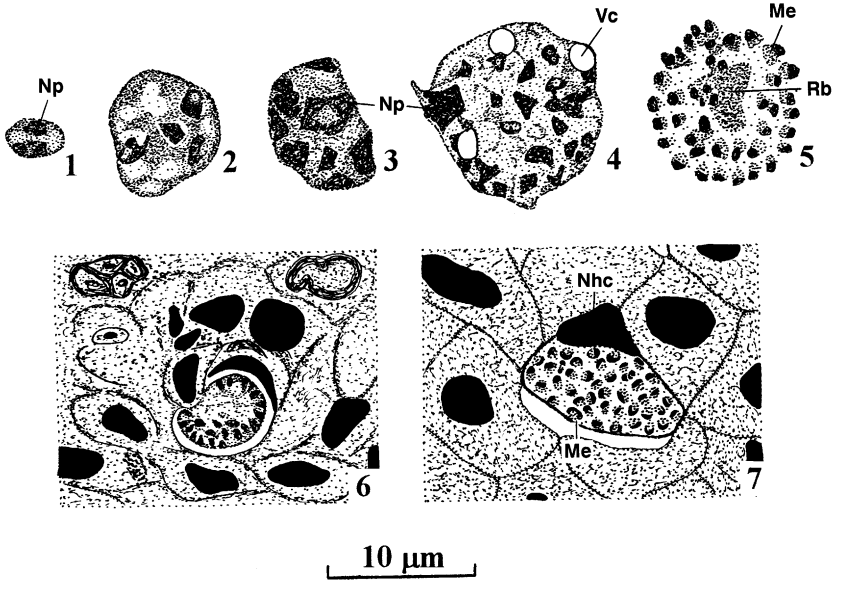

Figure 250 Exoerythrocytic meronts of *Plasmodium garnhami* in smears (*1–5*) and histological sections (*6*, *7*) of the liver and spleen of *Upupa epops:*
1–4 – young meronts; *5–7* – mature meronts with merozoites; Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Rb – residual body; Vc – vacuole (modified from Guindy *et al*., 1965).

experimental infection with sporozoites. They were not seen in other organs. On the sixth day, the cryptozoites were seen to possess highly vacuolated cytoplasm and up to 100 nuclei. At the same time, meronts with three or four nuclei were also observed. It is likely that they are metacryptozoites. Numerous mature meronts were seen in the liver on the seventh day after the infection. They are about 15 to 20 μm in diameter and contain up to 200 small merozoites (Pl. I, *2*). Phanerozoites were found in the spleen and liver of young hoopoes infected experimentally by subinoculation of the blood from infected adult birds (Fig. 250). They were not seen in other organs. Phanerozoites develop in reticuloendothelial cells. They were recorded in the Kupffer cells of the liver and in the endothelial cells of sinuses in the spleen. The earliest binuclear parasites measured up to 4.4 μm in diameter (Fig. 250, *1*). Phanerozoites, which measured about 10 μm in diameter, possess a plentiful basophilic cytoplasm and large nuclei (Fig. 250, *2*, *3*). Large vacuoles were seen in growing phanerozoites (Fig. 250, *4*). Mature phanerozoites contain 26 to 44 merozoites and a centrally located residual body (Fig. 250, *5*). Nuclei of their host cells are not hypertrophied (Fig. 250, *6*, *7*). Largest observed mature phanerozoites measured up to 13.5 μm in diameter.

The prepatent period in young hoopoes is seven days after experimental infection with sporozoites, and five or six days after the blood-induced infection. Mature erythrocytic meronts were observed 48 h after appearance of first trophozoites in the blood. Gametocytes were seen in the blood approximately four or five days after initiation of the asexual parasitemia. Parasitemia was low in naturally infected birds, and mainly gametocytes were seen in the birds. However, it was high in the blood induced infections.

Trophozoites (Fig. 251, *1–3*) are seen in mature and polychromatic erythrocytes; earliest trophozoites are variable both in form and position, and each possesses a prominent

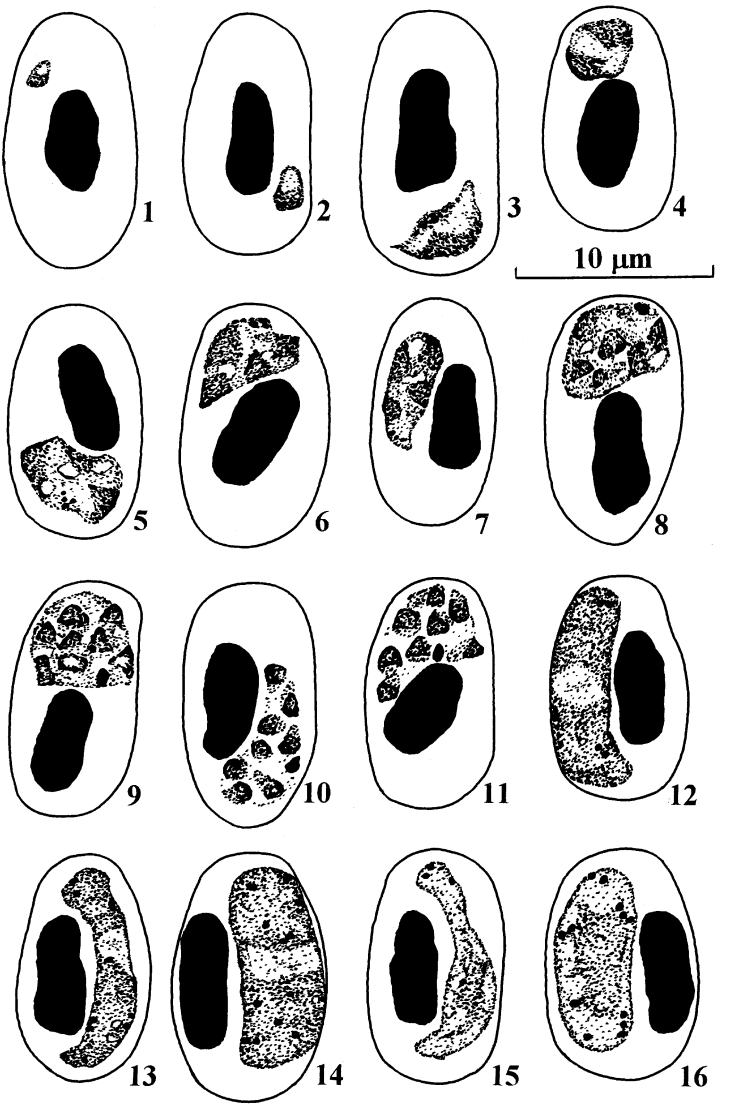

Figure 251 *Plasmodium garnhami* from the blood of *Upupa epops:*
1–3 – trophozoites; *4–11* – erythrocytic meronts; *12–14* – macrogametocytes; *15*, *16* – microgametocytes.

nucleus and a small vacuole (Fig. 251, *1*); the outline is usually even; fully grown trophozoites (Fig. 251, *3*) are usually seen in a polar position in infected erythrocytes, and each possesses a large nucleus and plentiful cytoplasm; pigment appears in early trophozoites, and a few minute pigment granules are present in fully grown parasites; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 251, *4–11*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; cytoplasm is plentiful, frequently possesses one or several small variable-form vacuoles (Fig. 251, *5–9*); nuclei are large in young

meronts (Fig. 251, *4–6*) and markedly decrease in size as the parasite matures (Fig. 251, *10*, *11*); meronts are of variable form, and roundish, oval, irregular, and even slightly elongated parasites were seen; the majority of fully grown meronts are roundish or of irregular form, usually seen in a polar or subpolar position in infected erythrocytes and possessing randomly located nuclei (Fig. 251, *8–11*); mature parasites contain six to eight (usually eight) merozoites; pigment granules are usually clumped into a spot in growing meronts (Fig. 251, *6*) and frequently aggregated into a solid irregular-form mass in fully grown parasites (Fig. 251, *9–11*); pigment granules are dark-brown with golden shade on the periphery; meronts usually do not touch the nuclei of erythrocytes, they usually do not markedly deform the host cells but more or less displace their nuclei; largest fully grown meronts measured up to 9 μm in length; mature merozoite possesses a prominent nucleus and a prominent portion of cytoplasm (Fig. 251, *11*).

Macrogametocytes (Fig. 251, *12–14*) are usually seen in mature erythrocytes; the cytoplasm is heterogeneous in appearance, frequently possesses a few small vacuoles; gametocytes are elongated and are usually observed in a lateral position to the nuclei of infected erythrocytes; growing gametocytes are slender and irregular in form with one end usually narrower than the other (Fig. 251, *13*, *15*); fully grown gametocytes are of broad sausage-like form with an even outline, usually do not touch the nuclei of erythrocytes (Fig. 251, *12*, *14*); the parasite nucleus is compact, of variable form, large (see Fig. 251, *14*), median or submedian in position; pigment granules are roundish, of small size (<0.5 μm), randomly scattered throughout the cytoplasm, their number varies (n = 28) from 2 to 15 (usually 9); fully grown gametocytes displace the nuclei of infected erythrocytes laterally, vary from 8.8 to 12.0 (on average 10.2) μm in length and from 2.5 to 4.0 (on average 3.0) μm in width.

Microgametocytes (Fig. 251, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has not been investigated in detail. Sporogony is completed in mosquito *Culex pipiens molestus* (Garnham, 1966). At temperature 27°C, oocysts measured about 12 μm in diameter on the fifth day after infection and contained several short rods of pigment in a random distribution. The oocysts reached on average 16 μm in diameter on the eighth day after infection and measured about 18 μm on the ninth day. Sporozoites were found in the salivary glands on the 13th day after infection and measured 9 to 13 μm in length. The sporozoites were infectious for hoopoes.

Pathogenicity. Young hoopoes died nine to ten days after experimental subinoculation of blood from naturally infected adult hoopoes. It is likely that high parasitemia is the main cause of the death (Guindy *et al.*, 1965).

Specificity. Attempts to infect canaries and ducklings by subinoculation of infected blood were not successful. Splenectomized domestic pigeons, domestic chickens, and a jackdaw *Corvus monedula* were not susceptible (Garnham, 1966).

Comments. *Plasmodium garnhami* is similar to *P. polare* and *P. elongatum*. It can be distinguished from *P. polare*, first of all, on the basis of a smaller number of merozoites in its erythrocytic meronts, and from *P. elongatum*, on the basis of broad sausage-like form of its fully grown gametocytes. It should be mentioned also that pigment in gametocytes *P. garnhami* is not so plentiful as in gametocytes both of *P. polare* and *P. elongatum*.

Erythrocytic meronts of *P. garnhami* produce not more than eight merozoites, and thus this parasite is close to species of the subgenus *Novyella.* However, trophozoites and erythrocytic meronts of *P. garnhami* possess plentiful cytoplasm, and the size of its fully grown erythrocytic meronts frequently exceeds that of the nuclei of infected erythrocytes. It should be also noted that mature

erythrocytic merozoites of *P. garnhami* possess both prominent nuclei and cytoplasm. These characters are well pronounced in the type material of *P. garnhami*, and help to distinguish this parasite from the species of *Novyella.*

It is worth noting that, in the type locality, *P. garnhami* was found in 16.7% (95% confidence limit is 11.5–22.6) of adult hoopoes, but the parasite was not seen in 198 investigated juvenile hoopoes. A single infection was found in 28 *Upupa epops* sampled in Ethiopia (Ashford *et al.*, 1976).

22. **Plasmodium (Giovannolaia) hegneri** Manwell and Kuntz, 1966

Plasmodium hegneri Manwell and Kuntz, 1966: 439, Fig. 1–25.

Type vertebrate host. *Anas crecca* L. (Anseriformes).
Additional vertebrate hosts. Unknown.
Type locality. Lo-tung, I-lan Hsien, Taiwan.
Distribution. This parasite has been recorded only in the type locality.
Type material was not designated in the original description. Preparations of the type series are deposited in CPM and IRCAH.
Etymology. This species is named in honour of Dr. Robert Hegner in recognition of his contribution to the field of avian malaria parasites.

Main diagnostic characters. Trophozoites possess a large vacuole. Growing erythrocytic meronts frequently possess long (>2 μm in length) tail-like or finger-like outgrowths. Fully grown meronts are usually roundish or oval, more frequently take a polar or subpolar position in infected erythrocytes, slightly displace the nuclei of erythrocytes and never occupy all available cytoplasmic space in the erythrocytes. Nuclei are located randomly in erythrocytic meronts which produce 9 to 19 merozoites. Growing gametocytes frequently take a polar-lateral position in infected erythrocytes (Fig. 252, *13*, *16*), and fully grown gametocytes take a lateral position to the nuclei of infected erythrocytes. Gametocytes do not possess large (>1.5 μm in diameter) vacuoles.

Development in vertebrate host
Exoerythrocytic merogony has not been investigated. Erythrocytic merogony is not synchronized. All blood stages are present in the type material simultaneously.

Trophozoites (Fig. 252, *1–3*) are seen in mature erythrocytes; earliest trophozoites can be seen anywhere in infected erythrocytes; the 'ring' stage was observed; advanced trophozoites are roundish or oval, more frequently seen in a polar or subpolar position in infected erythrocytes, they adhere to the nuclei of erythrocytes; each trophozoite usually possesses a large vacuole (Fig. 252, *2*, *3*); the outline is even; the parasite nucleus is large; a few small pigment granules present in fully grown trophozoites; the influence of trophozoites on infected erythrocytes is not pronounced

Erythrocytic meronts (Fig. 252, *4–12*) are seen in mature erythrocytes; cytoplasm is plentiful; young meronts are usually seen in a polar or subpolar position in infected erythrocytes, they possess large nuclei, one or several centrally located vacuoles and frequently produce one long (>2 μm in length) tail-like or finger-like outgrowth (Fig. 252, *6, 7*); as the parasite develops, the vacuolization of the cytoplasm and size of the nuclei gradually decrease; fully grown meronts can be seen anywhere in infected erythrocytes but they are still more frequently observed in a polar or subpolar position in the erythrocytes; fully

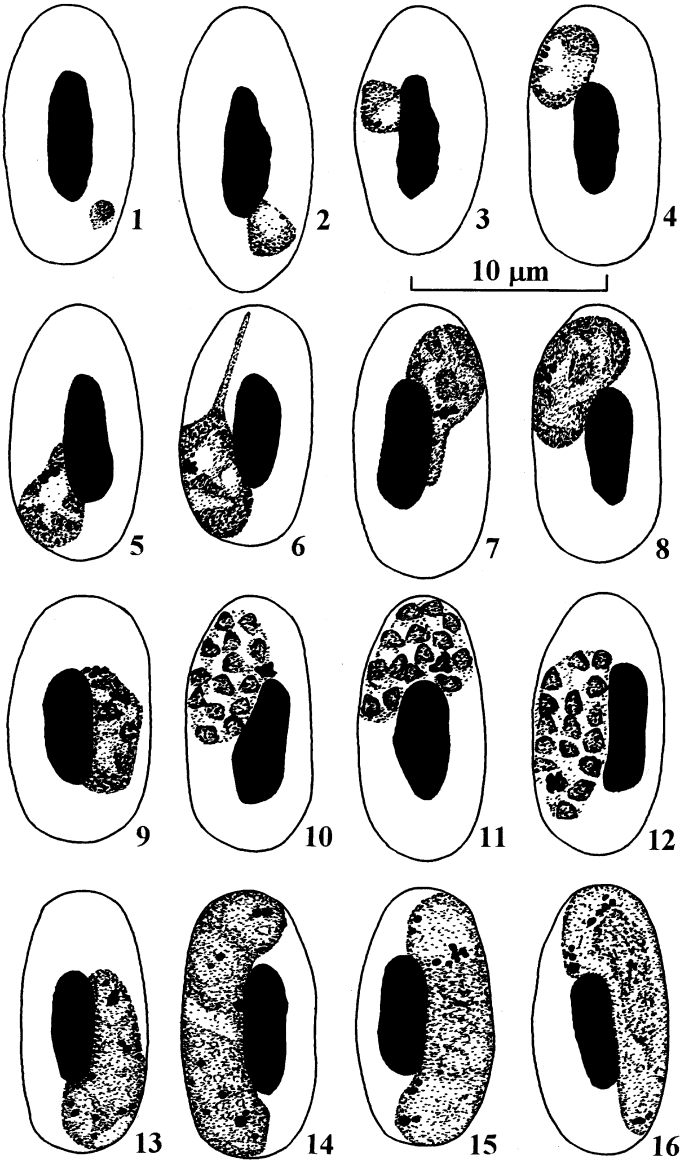

Figure 252 *Plasmodium hegneri* from the blood of *Anas crecca:*
1–3 – trophozoites; *4–12* – erythrocytic meronts; *13*, *14* – macrogametocytes; *15*, *16* – microgametocytes.

grown parasites are usually roundish or oval, but irregular (Fig. 252, *11*) and slightly elongated (Fig. 252, *12*) parasites were also seen; nuclei are usually located randomly in fully grown meronts and were only occasionally seen arranged as rosettes; mature meronts contain 9 to 19 (on average about 14) merozoites; pigment granules are clumped into a spot, are black; meronts are usually closely appressed to the nuclei of erythrocytes, they only slightly influence infected erythrocytes which nuclei can be slightly displaced.

Macrogametocytes (Fig. 252, *13*, *14*) are seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, usually lacks vacuoles; gametocytes are elongated and of variable outline from the earliest stages of their development; growing gametocytes are frequently located asymmetrically (in a polar-lateral position) to the nuclei of infected erythrocytes (Fig. 252, *13*); fully grown gametocytes are broad and take a lateral position to the nuclei of erythrocytes, slightly enclose the nuclei with their ends but do not encircle them completely (Fig. 252, *14*); the parasite nucleus is compact, of variable form and position; pigment granules are usually roundish and small (<0.5 μm), sometimes of medium size (0.5 to 1.0 μm), randomly scattered throughout the cytoplasm, averaging about 12 per gametocyte; gametocytes do not influence or only slightly influence infected erythrocytes whose nuclei can be slightly displaced laterally.

Microgametocytes (Fig. 252, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Plasmodium hegneri* was discovered in the naturally infected teal *Anas crecca*. Only blood stages of this parasite have been described so far. *Plasmodium hegneri* is especially similar to *P. fallax*. It can be distinguished from the latter species, first of all, on the basis of (i) presence of a large vacuole in its trophozoites, (ii) a long tail-like or finger-like outgrowth which was frequently seen in its young erythrocytic meronts, (iii) numerous roundish fully grown erythrocytic meronts which locate in a polar or subpolar position in infected erythrocytes, and (iv) absence of prominent vacuoles in gametocytes. It should be mentioned that ducklings are susceptible to *P. fallax*, and they were experimentally infected with this parasite. However, the mentioned above four morphological characters of *P. hegneri* were not observed in ducklings experimentally infected with *P. fallax*. Thus, it looks likely that *P. hegneri* is a distinct species. Further studies are required to prove the validity of *P. hegneri.*

23. **Plasmodium (Giovannolaia) octamerium** Manwell, 1968

Plasmodium octamerium Manwell, 1968: 681, Pl. I, Fig. 1–24, Pl. II, Fig. 1–5.

Type vertebrate host. *Vidua macroura* (Pallas) (Passeriformes).
Additional vertebrate hosts. Some species of birds (Table 142).
Type locality. The range of the type vertebrate host is in Africa. This parasite was isolated from one female of tiny African finch *V. macroura* purchased in a pet shop. The locality where this bird acquired the infection is unknown.
Distribution has not been investigated.
Type material was not designated in the original description. Neohapantotypes [*blood stages*: No. 645, 646, starling (scientific name is not given), R.D. Manwell; *exoerythrocytic meronts*: No. 647, *Alectoris chukar*, phanerozoites, brain smear, R.D. Manwell] are deposited in CPG.
Etymology. The specific name reflects an important character of erythrocytic meronts to produce mainly eight merozoites.

Main diagnostic characters. Growing erythrocytic meronts do not possess long tail-like or finger-like outgrowths. Fully grown erythrocytic meronts are elongated, possess randomly located nuclei and pigment granules clumped in a small focus; they usually take a lateral position to the nuclei of infected erythrocytes and never encircle the nuclei completely. Both erythrocytic meronts and gametocytes either do not possess or possess a few small vacuoles. Mature erythrocytic meronts produce 6 to 16 (usually 8) merozoites.

Table 142 List of natural and experimental vertebrate hosts of *Plasmodium octamerium* (modified from Manwell, 1968).

**Alectoris chukar*	**E. troglodytes*	*P. melanurus*
**Anas platyrhynchos*	*Euplectes macrourus*	**Serinus canaria*
**Auripasser luteus*	**Gallus gallus*	**S. mozambicus*
**Colinus virginianus*	*Lamprotornis chalybaeus*	**Spizella arborea*
**Columba livia*	**Melospiza melodia*	**Streptopelia risoria*
Estrilda astrild	**Munia acuticauda*	**Taeniopygia castanotis*
**E. melpoda*	**M. atricapilla*	
E. paludicola	*Passer domesticus*	

Note: The bird species infected experimentally by the subinoculation of infected blood are marked with an asterisk.

Fully grown gametocytes are broad and elongated; they take a lateral position to the nuclei of infected erythrocytes and frequently displace the nuclei laterally but never encircle them completely.

Development in vertebrate host was studied by Manwell (1968). Primary exoerythrocytic merogony has not been investigated. Phanerozoites were found in reticuloendothelial cells of the brain and in heart blood of chukar *Alectoris chukar* after experimental blood-induced infection. Phanerozoites were not observed in canaries and other experimentally infected birds. In the brain, phanerozoites look like elongated sausage-shaped bodies overfilled with small-size merozoites (Fig. 253, *1;* Pl. I, *3*). The merozoites are so closely packed that their certain size and number are difficult to estimate.

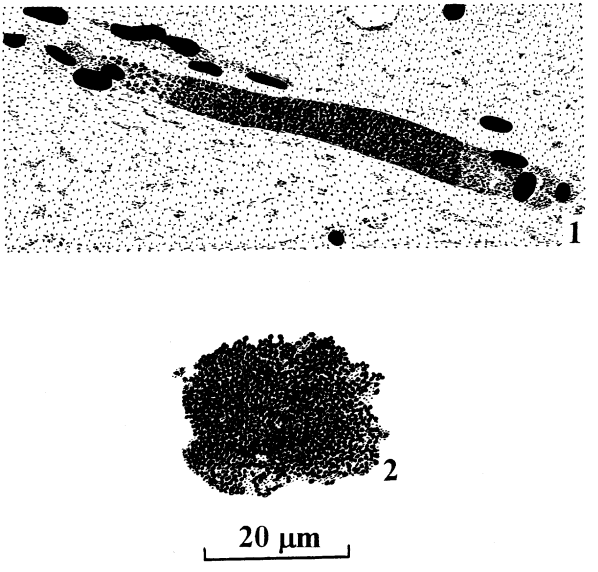

Figure 253 Mature phanerozoites of *Plasmodium octamerium* from *Alectoris chukar:*
1 – elongated parasite in brain; *2* – roundish parasite from the heart blood (modified from Manwell, 1968).

The largest phanerozoites contain about 1000 merozoites. In the heart blood, smaller-size roundish phanerozoites were observed. They are variable in size and contain approximately from 50 to 300 merozoites (Fig. 253, *2*). Phanerozoites are numerous in the brain of the chukar and can block up the brain capillaries.

The prepatent period varies markedly from two days to three weeks depending on dose of subinoculated infected blood, mode of the subinoculation and species of host. Usually, the prepatent period is about one week. Peak of the primary parasitemia is pronounced, and it was recorded approximately one week after appearance of first parasites in the blood cells. The parasitemia rarely exceeds 10% of erythrocytes, and it is usually much less (about 1 or 2%). After the crisis, the parasitemia decreases gradually, and a few parasites are present in the blood during a chronic stage of infection. Erythrocytic merogony is only slightly (if at all) synchronized. A cycle of the merogony looks to be close to 24 h.

Trophozoites (Fig. 254, *1–4*) are seen in mature and polychromatic erythrocytes; the earliest trophozoites are roundish; the 'ring' stage is frequently seen; as the parasite develops, trophozoites take an irregular form and small ameboid outgrowths are frequently seen (Fig. 254, *3*, *4*); fully grown trophozoites are more or less elongated and large, were more frequently seen in a polar or subpolar position in infected erythrocytes and each possesses plentiful cytoplasm and a large nucleus (Fig. 254, *4*); pigment granules appear in early trophozoites (Fig. 254, *3*) as one or two minute-size granules which are brownish with golden shade; fully grown trophozoites usually possess up to four small-size (<0.5 μm) pigment granules usually clumped into a spot.

Erythrocytic meronts (Fig. 254, *5–12*) are seen in mature and polychromatic erythrocytes; cytoplasm is plentiful, usually lacking vacuoles; young meronts possess large nuclei (Fig. 254, *5–7*), the parasites are usually elongated, frequently seen in a polar or subpolar position in infected erythrocytes where they can take a U-like shape (Fig. 254, *6*); as the parasite develops, both the basophility of the cytoplasm and the size of the nuclei markedly decrease; fully grown meronts are elongated, take a lateral position to the nuclei of infected erythrocytes and never encircle the nuclei completely; nuclei were frequently seen arranged in a more or less evident line in fully grown meronts and often lie in a series of pairs (Fig. 254, *10*, *11*); fully grown meronts usually contain 6 to 12 merozoites, and about 50% of meronts contained 8 merozoites in different vertebrate hosts; however, the number of merozoites varies in different hosts, and up to 24 merozoites were occasionally seen; it is likely that the high number of merozoites (>12) is a result of infection of the same erythrocyte with several (usually two) meronts; pigment granules are roundish, of small size (<0.5 μm), their number is usually less than six, are clumped into a spot in advanced meronts (Fig. 254, *6–12*) but were also seen to be scattered throughout the cytoplasm or aggregated into a loose group in the earliest parasites (Fig. 254, *5*); meronts only slightly influence infected erythrocytes whose nuclei can be displaced laterally (Fig. 254, *11*); fully grown meronts do not exceed 14 μm in length; a mature merozoite possesses a prominent nucleus and a small portion of cytoplasm (Fig. 254, *12*).

Macrogametocytes (Fig. 254, *13–15*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; cytoplasm is homogeneous in appearance, usually lacking vacuoles; gametocytes are elongated and variable in outline from the earliest stages of development but clearly pronounced ameboid outgrowths are not characteristic; fully grown gametocytes take a lateral position to the nuclei of infected erythrocytes, can slightly enclose the nuclei with their ends but never encircle them completely; the parasite nucleus is compact, small (see Fig. 254, *13–15*), usually median in position; pigment granules are roundish or of irregular form, usually of small (<0.5 μm), sometimes

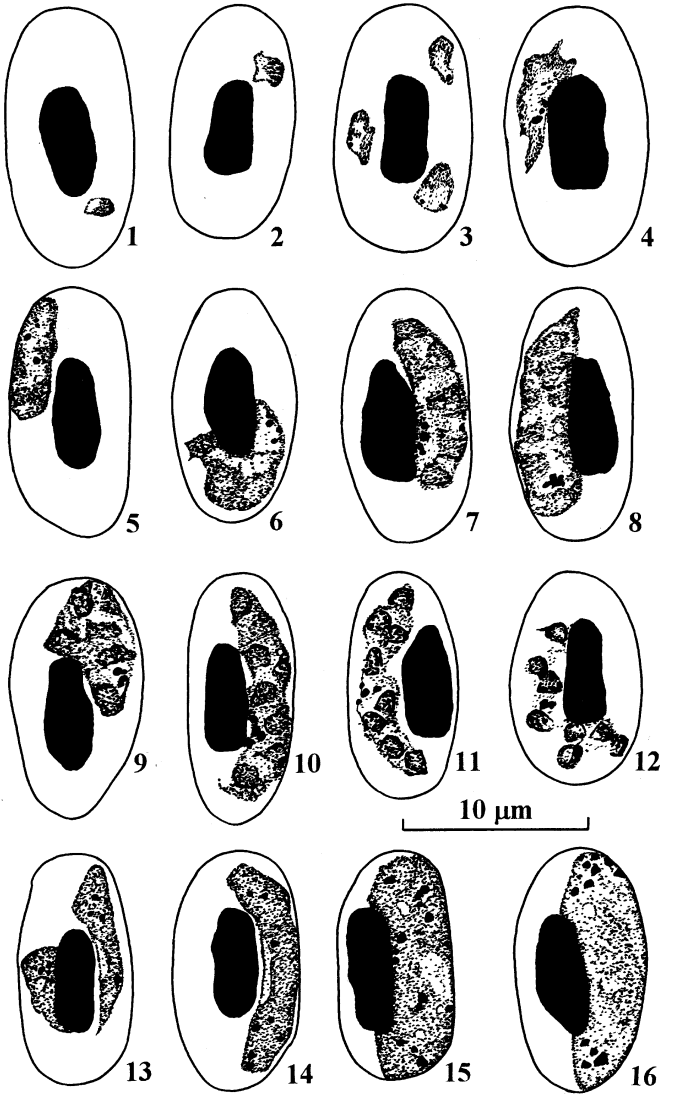

Figure 254 *Plasmodium octamerium* from the blood of *Sturnus* sp.:
1–4 – trophozoites; *5–12* – erythrocytic meronts; *13–15* – macrogametocytes; *16* – microgametocyte.

medium (0.5 to 1.0 μm) size, usually randomly scattered throughout the cytoplasm; the number of pigment granules in the type material varies from 6 to 18 (more frequently 10 to 14); gametocytes only slightly influence infected erythrocytes whose nuclei can be more or less displaced laterally (Fig. 254, *15*).

Microgametocytes (Fig. 254, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment can be aggregated into solid masses; other characters are as for macrogametocytes.

Relapses were not observed.

P a t h o g e n i c i t y. In the experimentally infected birds (see Table 142), the mortality was recorded only among chukars. Numerous phanerozoites, which block up capillaries, developed in the brain of the chukars. As a result, these birds died because of cerebral malaria. At autopsy, the markedly enlarged spleen was recorded.

S p e c i f i c i t y. Sixteen species of birds were infected experimentally by subinoculation of infected blood (Table 142). Chukar and canary are good experimental hosts. Domestic pigeon, domestic chickens, and ducklings are also susceptible. Day-old chickens are readily infected, but parasitemia is low and lasts only a few days. Older chickens are less susceptible.

C o m m e n t s. *Plasmodium octamerium* is a species difficult for identification. It can be distinguished only after analysis of morphology of all blood stages. It is difficult to identify this parasite in the blood films from naturally infected birds with low parasitemia. *Plasmodium octamerium* is especially similar to *P. fallax*. It can be distinguished from the latter species, first of all, on the basis of (i) smaller number of merozoites in its erythrocytic meronts and (ii) absence of highly vacuolated gametocytes.

It was noted in the original description of *P. octamerium* (Manwell, 1968) that this parasite is similar to species of the subgenus *Novyella* from the point of view of the morphology of its blood stages. *Plasmodium octamerium* was attributed to the subgenus *Novyella* in the collection of malaria parasites of Prof. P.C.C. Garnham (Garnham and Duggan, 1986). However, after examination of the type material, the author attributed *P. octamerium* to the subgenus *Giovannolaia* as Manwell (1968) did originally. The cytoplasm is plentiful and nuclei are large in erythrocytic meronts of *P. octamerium*. Additionally, each mature erythrocytic merozoite possesses a prominent nucleus and a clearly visible portion of cytoplasm. *Plasmodium octamerium* can be readily distinguished from most species of the *Novyella* on the basis of these characters. Strictly speaking, *P. octamerium* belong to a group of species (together at least with *P. dissanaikei*) which subgeneric position is especially difficult to specify, especially at low parasitemia.

24. **Plasmodium (Giovannolaia) gabaldoni** Garnham, 1977

Plasmodium gabaldoni Garnham, 1977: 124, Fig. 1–19.

T y p e v e r t e b r a t e h o s t. *Columba livia* Gmelin (Columbiformes).
A d d i t i o n a l v e r t e b r a t e h o s t. *Cairina moschata* (Anseriformes).
T y p e l o c a l i t y. Villa Brunzal, Portuguesa State, Venezuela.
D i s t r i b u t i o n. This parasite has been recorded only in Venezuela so far.
T y p e m a t e r i a l. Hapantotypes (*blood stages*: No. 280, 281, *Cairina moschata*, passage from *Columba livia*, 2.10.1973; No. 282, 20.08.1974 and No. 286, 21.08.1974, other data are as for No. 280; *exoerythrocytic meronts*: No. 290, brain, *Columba livia*, passage from *Cairina moschata*, 15.05.1975; No. 291, spleen, 17.05.1975, other data are as for No. 290; *exflagellation*: No. 287, 12 min, August 1974; No. 288, 15 min, 15.07.1975; No. 298, 16 min) and parahapantotype (No. 283, a duplicate of No. 282) are deposited in CPG. Part of parahapantotypes is deposited in CPGA.
E t y m o l o g y. This species is named in honour of prominent Venezuelan malariologist Professor Arnoldo Gabaldon.

M a i n d i a g n o s t i c c h a r a c t e r s. Erythrocytic meronts and gametocytes are large and clearly tend to grow around the nuclei of infected erythrocytes. Polychromatic erythrocytes are common host cells of blood stages. Fully grown meronts markedly displace the nuclei of infected erythrocytes and frequently occupy all available cytoplasmic space in the

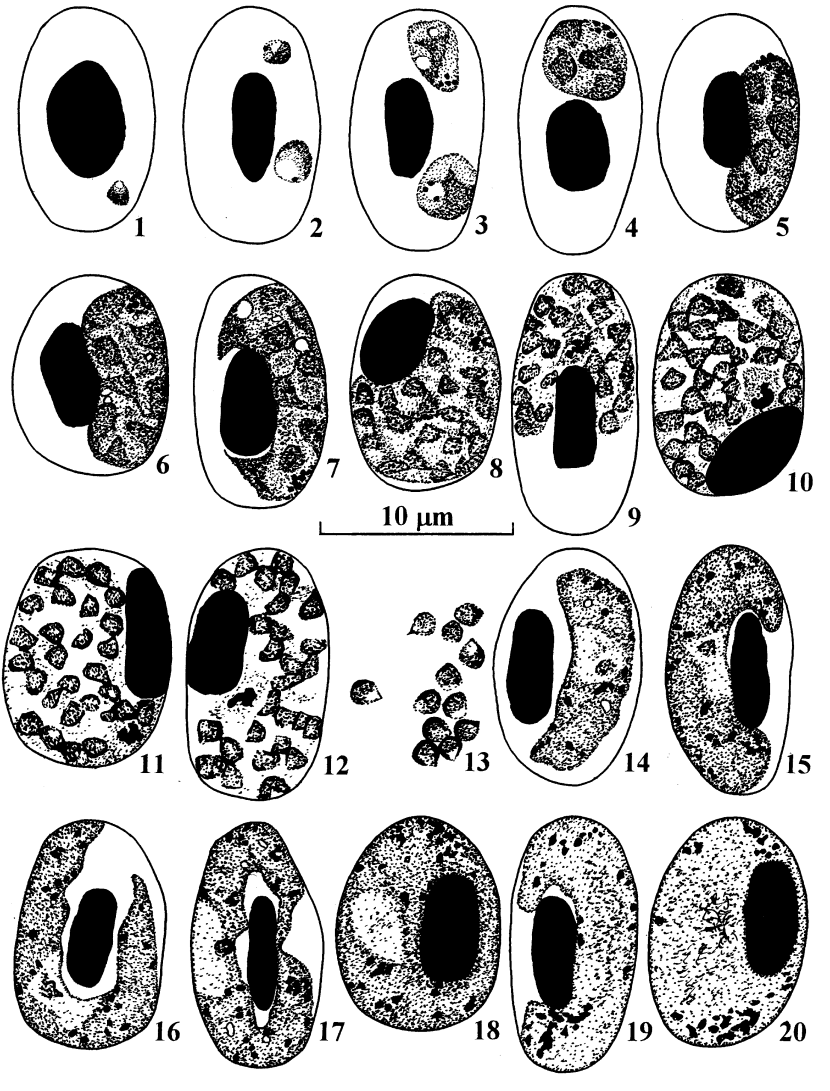

Figure 255 *Plasmodium gabaldoni* from the blood of *Cairina moschata:*
1–3 – trophozoites; *4–12* – erythrocytic meronts; *13* – merozoites from erythrocytic meronts; *14–18* – macrogametocytes; *19*, *20* – microgametocytes.

erythrocytes. Gametocytes markedly enclose the nuclei of erythrocytes with their ends and can completely encircle the nuclei. Fully grown erythrocytic meronts and gametocytes markedly deform infected erythrocytes which become rounded. Mature erythrocytic meronts contain 12 to 36 (most frequently 24) merozoites. Fully grown gametocytes possess more than 30 pigment granules.

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. Secondary exoerythrocytic merogony was described by Garnham (1977). Phanerozoites were found in domestic

pigeons and ducklings infected experimentally by subinoculation of infected blood. Phanerozoites were more numerous in the pigeons than in ducklings. The parasites were especially common in the brain of infected pigeons after subinoculation with the duckling strain. Phanerozoites were less frequently seen in the liver, spleen, and bone marrow. A few phanerozoites were observed in the lungs and kidneys. In the brain, phanerozoites look like large sausage-shaped bodies with basophilic cytoplasm and numerous nuclei. They can block up the brain capillaries. Large parasites in the brain measured up to 45 μm in length and 10 μm in width. Additionally, smaller roundish phanerozoites, which looked to lie extracellularly, were also seen in smears of other internal organs.

Erythrocytic merogony is synchronized. A cycle of merogony is about 24 h. The majority of mature erythrocytic meronts rupture around the midday. The parasite gradually loses the ability to produce gametocytes as the number of blood passages in ducklings increases.

Trophozoites (Fig. 255, *1–3*) are seen in mature and polychromatic erythrocytes, and the latter are common host cells; earliest trophozoites can be seen anywhere in infected erythrocytes, they are roundish, each possesses a large nucleus and a more or less evident vacuole (Fig. 255, *1*, *2*); as the parasite develops, some trophozoites elongate and a few (from one to three) small vacuoles are seen in their cytoplasm (Fig. 255, *3*); pigment appears in early trophozoites (Fig. 255, *2*) as a minute dark-brown granule, and up to five small-size (<0.5 μm) pigment granules, which are clumped into a spot, are seen in fully grown trophozoites; pigment granules are also seen gathered around a vacuole in some parasites (Fig. 255, *3*); trophozoites usually do not touch the nuclei of infected erythrocytes and do not markedly influence infected erythrocytes; infection of the same erythrocyte with several trophozoites is common at high parasitemia.

Erythrocytic meronts (Fig. 255, *4–12*) are seen in mature and polychromatic erythrocytes, and the latter are common host cells; the cytoplasm is highly basophilic, sometimes possesses a few small vacuoles (Fig. 255, *7*); the nuclei are large and the cytoplasm is plentiful in young meronts (Fig. 255, *4–6*); the nuclei markedly decrease in size as the parasite matures (Fig. 255, *8*, *9*) and the basophility of the cytoplasm decreases also; growing meronts are usually elongated, take a lateral position to the nuclei of infected erythrocytes and enclose the nuclei with their ends (Fig. 255, *5–7*); U-like meronts sometimes were seen in a polar position in erythrocytes (Fig. 255, *9*); fully grown meronts can occupy all available cytoplasmic space in infected erythrocytes, are roundish, of irregular form (Fig. 255, *10*, *11*) or elongated (Fig. 255, *12*); the nuclei are located randomly in meronts; mature meronts contain 12 to 36 (usually 24) merozoites; pigment granules are of small size (<0.5 μm), numerous, clumped into a spot and can be aggregated into a solid mass in mature parasites (Fig. 255, *10–12*); the exact number of pigment granules is difficult to count because of their compact clumping and obscuring by the nuclei or merozoites; a portion of cytoplasm, which resembles a diffuse residual body, was seen around the clump of pigment in segmenters (Fig. 255, *10–12*); meronts displace the nuclei of infected erythrocytes and deform the erythrocytes which frequently become rounded (Fig. 255, *11*); multiple infection of the same erythrocyte with several (up to three) meronts was seen at high parasitemia; mature merozoites are approximately 1.5 μm in diameter, are roundish, and each possesses a prominent nucleus and a portion of basophilic cytoplasm; a more or less evident minute lanceolated outgrowth can be seen in some mature merozoites (Fig. 255, *13*).

Macrogametocytes (Fig. 255, *14–18*) are seen in mature and polychromatic erythrocytes; cytoplasm is highly basophilic, frequently possesses a few small vacuoles;

gametocytes are elongated and variable in outline from the earliest stages of development, markedly enclose the nuclei of infected erythrocytes with their ends and can completely encircle the nuclei and occupy all available cytoplasmic space in the erythrocytes (Fig. 255, *17*, *18*); the parasite nucleus is compact, large, median in position; a nucleolus is usually well seen (Fig. 255, *14–17*); pigment granules are usually roundish, dark-brown or black, usually of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; the number of pigment granules in fully grown gametocytes frequently exceeds 30; gametocytes usually displace the nuclei of erythrocytes and deform the erythrocytes which frequently become rounded (Fig. 255, *18*).

Microgametocytes (Fig. 255, *19*, *20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is extremely diffuse and its boundaries are ill-defined; the majority of pigment granules are gathered near the ends of gametocytes; other characters are as for macrogametocytes.

Development in vector has been incompletely investigated. Exflagellation was seen 8 min after exposure of infected blood with mature gametocytes to air at a temperature of 20 to 25°C. Microgametes are about 16 to 18 μm in length. The nucleus of microgamete is off-centre in position. Ookinetes were observed in the midgut of mosquitoes *Aedes aegypti* and *Culex pipiens* approximately 16 to 17 h after blood meal on the infected ducklings. The ookinetes look like curved C-like bodies. They possess a prominent nucleus, and pigment granules were seen at both sides of the nucleus. The ookinetes vary from 11 to 15 μm in length and from 2 to 4 μm in width. Other sporogonic stages have not been described as yet.

Pathogenicity. Domestic pigeons and ducklings usually die 7 to 12 days after the blood-induced infection. The virulence of the parasite increases in successive blood passages.

Specificity. Domestic pigeon and ducklings are good experimental hosts. After numerous passages, the parasite was adapted to canary which, however, can be infected with difficulty.

Comments. Blood stages of *P. gabaldoni* are especially similar to *P. anasum* and *P. circumflexum*. *Plasmodium gabaldoni* can be distinguished from *P. anasum*, first of all, on the basis of its (i) well pronounced ability to develop in immature erythrocytes and (ii) large size of erythrocytic meronts and gametocytes which frequently markedly deform infected erythrocytes. Additionally, pigment granules in erythrocytic meronts of *P. anasum* clearly tend to gather into large (>1.5 μm in length) clumps near one end of the parasites, but this is not characteristic of *P. gabaldoni*. It is difficult to distinguish *P. gabaldoni* and *P. circumflexum* solely on the basis of their blood stages. It is important to note that meronts and gametocytes of *P. gabaldoni* much markedly influence infected erythrocytes than the same stages of *P. circumflexum*. Additionally, mature erythrocytic merozoites of *P. circumflexum* are usually slightly elongated but are roundish in *P. gabaldoni.* It should be also noted that *P. circumflexum* do not develop or only poorly develop in ducklings whose are excellent experimental hosts of *P. gabaldoni.* On the contrary, the canary is a good experimental host of *P. circumflexum* but not of *P. gabaldoni.*

25. **Plasmodium (Giovannolaia) leanucleus** Huang, 1991

Plasmodium leanucleus Huang, 1991: 262, Fig. 1, 2.

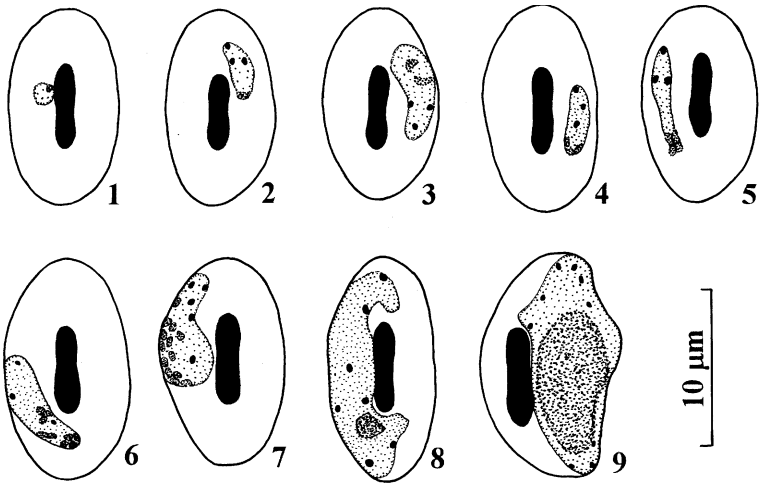

Figure 256 *Plasmodium leanucleus* from the blood of *Passer domesticus:* *1*, *2* – trophozoites; *3–7* – erythrocytic meronts; *8* – macrogametocyte; *9* – microgametocyte (modified from Huang, 1991).

Type vertebrate host. *Passer domesticus* (L.) (Passeriformes).
Additional vertebrate host. *Pycnonotus jocosus* (Passeriformes).
Type locality. Suburb of Guangzhou, China.
Distribution. This parasite has been recorded only in the type locality so far.
Type material. A hapantotype is deposited in DBZU.
Etymology. The specific name reflects a peculiarity of morphology of erythrocytic meronts and gametocytes whose nuclei tend to lean to one end of the parasites.

Main diagnostic characters. Growing erythrocytic meronts do not possess long tail-like or finger-like outgrowths. Erythrocytic meronts are elongated, possess a few pigment granules; the meronts only slightly exceed the nuclei of infected erythrocytes in length and can be seen anywhere in the erythrocytes. The nuclei in erythrocytic meronts and the nuclei in macrogametocytes tend to lean to one end of the parasites. Mature erythrocytic meronts contain 6 to 14 merozoites. Gametocytes take a lateral position to the nuclei of infected erythrocytes; they do not possess large (>1.5 μm in diameter) vacuoles and only slightly enclose the nuclei of erythrocytes with their ends.

Development in vertebrate host
Exoerythrocytic merogony has not been investigated. Erythrocytic merogony is synchronized. A cycle of the merogony appears to be 24 h (Huang, 1991).

Trophozoites (Fig. 256, *1*, *2*). The earliest trophozoites are roundish (Fig. 256, *1*); as the parasite develops, the trophozoite elongates, and its nucleus takes a terminal position (Fig. 256, *2*); pigment granules are oval, small, black, their number is up to three; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 256, *3–7*) are seen in mature erythrocytes; they are elongated and possess plentiful cytoplasm from the earliest stages of development; meronts either take a lateral position to the nuclei of infected erythrocytes (Fig. 256, *3–5*) or are slightly displaced toward one pole of the erythrocytes (Fig. 256, *6*, *7*); mature meronts only

slightly exceed the nuclei of infected erythrocytes in length, contain 6 to 14 merozoites; the outline is even; nuclei tend to lean to one end of the parasites, and this character is especially evident in growing meronts (Fig. 256, *3–6*); pigment granules are oval, small, black, their number varies from three to five; the influence of meronts on infected erythrocytes is not pronounced.

Macrogametocytes (Fig. 256, *8*) are seen in mature erythrocytes; they are elongated and lateral in position to the nuclei of infected erythrocytes; gametocytes only slightly enclose the nuclei of erythrocytes with their ends; the parasite nucleus is subterminal in position; pigment granules are oval, black, randomly scattered throughout the cytoplasm, their number varies from six to nine; the influence of gametocytes on infected erythrocytes is not pronounced.

Microgametocytes (Fig. 256, *9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; gametocytes can slightly displace the nuclei of infected erythrocytes (Fig. 256, *9*); other characters are as for macrogametocytes.

D e v e l o p m e n t i n v e c t o r has been incompletely investigated. Growing oocysts with

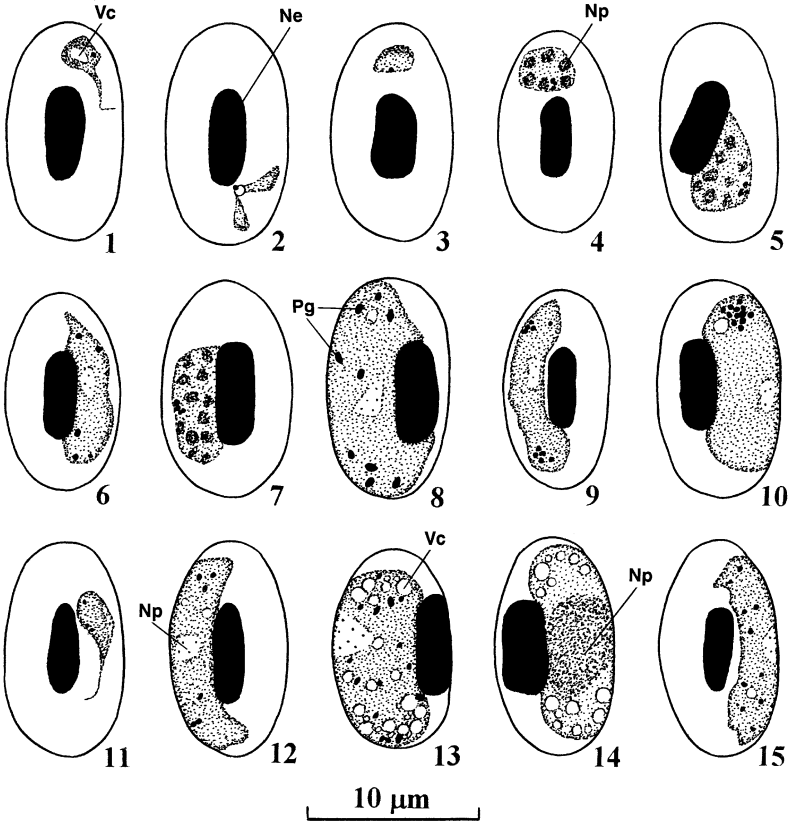

Figure 257 Main morphological peculiarities of the structure of the erythrocytic stages of malaria parasites of the subgenus *Novyella*, which are used for identification of species:
Ne – nucleus of erythrocyte; Np – nucleus of parasite; Pg – pigment granule; Vc – vacuole. Explanations are given in the text.

numerous round sporoblasts were observed approximately in 30% of mosquitoes *Culex pipiens* after blood meal on the heavily infected house sparrow *Passer domesticus*. The susceptibility of mosquitoes *Anopheles dirus* was said to be much lower (Huang, 1991).

C o m m e n t s. Erythrocytic meronts of *P. leanucleus* are of small size and contain not numerous merozoites. On the basis of these characters, *P. leanucleus* is similar to some species of the subgenus *Novyella*. However, the cytoplasm is plentiful in erythrocytic meronts of this parasite. On the basis on the latter character, *P. leanucleus* belongs to the subgenus *Giovannolaia.* According to the original description, *P. leanucleus* can be distinguished from other species of the *Giovannolaia*, first of all, on the basis of terminal and subterminal position of the nuclei in its erythrocytic meronts. However, it should be noted that the morphology of *P. leanucleus* has not been investigated in other experimental hosts, and the exoerythrocytic merogony and complete sporogonic development have not been studied either. Additional experimental data are required to prove the validity of *P. leanucleus.*

3. **Subgenus NOVYELLA** Corradetti, Garnham and Laird, 1963

Novyella Corradetti, Garnham and Laird, 1963a: 3.

T y p e s p e c i e s. *Plasmodium vaughani* Novy and MacNeal, 1904, according to the original designation.

E t y m o l o g y. This subgenus is named in honour of Dr. F.G. Novy who together with W.J. MacNeal described its type species, *P. vaughani*.

Erythrocytic meronts contain scanty cytoplasm. The size of fully grown erythrocytic meronts does not exceed or only slightly exceed that of the nuclei of infected erythrocytes. Fully grown gametocytes are elongated. Exoerythrocytic merogony takes place in cells of the reticuloendothelial system. Pedunculated oocysts are absent.

KEY TO THE SPECIES[†]

1 (8). The maximum number of merozoites in erythrocytic meronts is greater than four.

2 (11). Erythrocytic meronts and (or) gametocytes, which do not touch the nuclei of infected erythrocytes (Fig. 257, *4*, *9*, *15*), are present.

3 (14). Trophozoites do not possess clearly defined long outgrowths (Fig. 257, *1*); if ameboid outgrowths are present, they do not exceed the main body of the trophozoites in length.

4 (5). The maximum number of merozoites in erythrocytic meronts is greater than eight. Young gametocytes frequently possess one long thread-like outgrowth (Fig. 257, *11*).
. . . . . 31. ***P. dissanaikei***

5 (4). Maximum number of merozoites in erythrocytic meronts is equal to eight. Young gametocytes do not possess long thread-like outgrowths.

6 (7). The number of merozoites in erythrocytic meronts is relatively stable. Over 90% of the meronts contain six merozoites.
. . . . . 29. ***P. hexamerium***

7 (6). The number of merozoites in erythrocytic meronts is variable, but more frequently is equal to four or six.
. . . . . 26. ***P. vaughani***

[†] See also Appendix 2 for *Plasmodium forresteri*.

8 (1). Maximum number of merozoites in erythrocytic meronts is equal to four.

9 (10). Binuclear erythrocytic meronts frequently take a bilobular ('bow-tie') form (Fig. 257, *2*). Vacuoles are either not present in the cytoplasm of fully grown gametocytes or only a few of them can be present (Fig. 257, *12*, *15*). Fully grown gametocytes do not displace or only slightly displace the nuclei of infected erythrocytes laterally (Fig. 257, *9*, *12*, *15*). The maximum width of fully grown gametocytes is less than 3 μm.

. . . . . 28. ***P. rouxi***

10 (9). Binuclear erythrocytic meronts do not take a bilobular ('bow-tie') form (Fig. 257, *2*). Numerous clear vacuoles are present in the cytoplasm of fully grown gametocytes; the vacuoles tend to gather at the ends of the gametocytes (Fig. 257, *13*, *14*). Fully grown gametocytes markedly displace the nuclei of infected erythrocytes laterally (Fig. 257, *13*, *14*). The maximum width of fully grown gametocytes is greater than 3 μm.

. . . . . 33. ***P. bertii***

11 (2). Erythrocytic meronts and gametocytes are closely appressed to the nuclei of infected erythrocytes, and this contact does not break down as the parasites develop (Fig. 257, *5*–*8*).

12 (13). Fully grown erythrocytic meronts can markedly displace the nuclei of infected erythrocytes (Fig. 257, *5*). Fully grown gametocytes do not displace the nuclei of infected erythrocytes (Fig. 257, *6*). The average length of fully grown gametocytes is usually less than 10 μm. Phanerozoites are absent in the peripheral blood.

. . . . . 30. ***P. nucleophilum***

13 (12). Fully grown erythrocytic meronts do not displace or only slightly displace the nuclei of infected erythrocytes (Fig. 257, *7*). Fully grown gametocytes markedly displace the nuclei of infected erythrocytes laterally (Fig. 257, *8*). The average length of fully grown gametocytes is greater than 10 μm. Phanerozoites can be present in the peripheral blood.

. . . . . 32. ***P. paranucleophilum***

14 (3). Trophozoites frequently possess one long clearly defined thread-like or tail-like outgrowth which can exceed the main body of the trophozoites in length (Fig. 257, *1*).

15 (16). A large (>1 μm in length) refractive vacuole is present in trophozoites (Fig. 257, *1*). The number of merozoites in erythrocytic meronts is relatively stable; approximately 95% of the meronts contain five merozoites. Pigment granules in gametocytes either randomly scattered throughout the cytoplasm or clumped into several small groups (Fig. 257, *9*).

. . . . . 34. ***P. kempi***

16 (15). A large (>1 μm in length) refractive vacuole (Fig. 257, *1*) is absent in trophozoites, but a small (<1 μm in diameter) vacuole sometimes present. The number of merozoites in erythrocytic meronts is variable but most frequently is equal to eight. Pigment granules in gametocytes frequently are clumped into a spot near one end of the gametocytes (Fig. 257, *10*).

. . . . . 27. ***P. columbae***

26. **Plasmodium (Novyella) vaughani** Novy and MacNeal, 1904

Plasmodium vaughani Novy and MacNeal, 1904a: 932. – *P. vaughani* Novy and MacNeal, 1905: 23 (nom. praeocc., Novy and MacNeal, 1904). – *Haemamoeba tenuis* Laveran and Marullaz, 1914: 22. – *Proteosoma tumbayaensis* Mazza and Fiora, 1930: 993. – *Plasmodium tenuis*: Manwell, 1935b: 184 (*P. tenue*). – *P. tumbayaensis*: Coatney and Roudabush, 1936: 340. – *P. vaughani*: Garnham, 1966: 688 (=*P. tumbayaensis*). – *P. merulae*: Corradetti and Scanga, 1973: 346 (emend. pro *P. vaughani merulae*). – *P. vaughani*: Valkiūnas, 1997: 446 (=*P. merulae*).

Type vertebrate host. *Turdus migratorius* (L.) (Passeriformes).

Additional vertebrate hosts. Numerous species of birds of the orders Anseriformes,

Apodiformes, Charadriiformes, Columbiformes, Coraciiformes, Cuculiformes, Piciformes, and some others but particularly of the Passeriformes (over 240 species total). Canary is a good experimental host for the nominal subspecies.

Vectors. The susceptibility of mosquitoes to different strains and subspecies of *P. vaughani* varies markedly. The majority of them do not develop in mosquitoes of the genera *Aedes*, *Anopheles*, and *Culex* (Manwell, 1947; Huff, 1955, 1965; Dissanaike *et al.*, 1963; Crewe, 1975; Williams and Bennett, 1978). A strain of the nominal subspecies, which was isolated from *Agelaius phoeniceus*, completes sporogony in mosquito *Culiseta morsitans* (Williams and Bennett, 1978), and subspecies *P. vaughani merulae*, in *Culex pipiens* (Corradetti and Scanga, 1972).

Type locality. Ann Arbor, Michigan, USA.

Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic.

Type material. Neohapantotype [No. 635, *Turdus* (= *Planesticus*) *migratorius*, 1935, USA, R.D. Manwell] is deposited in CPG.

Etymology. This species is named in honour of Dr. Vaughan.

Main diagnostic characters. Growing trophozoites are ameboid in outline and they do not contain clearly defined vacuoles. Ameboid outgrowths of trophozoites do not exceed the main body of the trophozoites in length. Erythrocytic meronts and gametocytes, which do not touch the nuclei of infected erythrocytes, are common. The number of merozoites in mature erythrocytic meronts varies from four to eight, but more frequently is equal to four or six. Young gametocytes do not possess long thread-like outgrowths. Canary is susceptible not to all subspecies.

Development in vertebrate host

Primary exoerythrocytic merogony has been insufficiently investigated. Garnham (1966) noted that exoerythrocytic meronts, which were sometimes observed in internal organs of birds and described under the name *P. vaughani* (see Manwell, 1947; Laird, 1953), can belong to other species of malaria parasites (probably to *P. relictum* or *P. elongatum*).

Nelson (1966) succeeded to infect domestic pigeon with the Ceylon strain of *P. vaughani* isolated from myna *Acridotheres tristis* and passaged through the canary. Not numerous exoerythrocytic meronts were recorded in macrophages in lungs, bone marrow, liver, spleen, and kidneys, but they were absent from the brain. These meronts were up 20 to 25 μm in diameter, and they contained up to 70 to 80 merozoites. After examination of this material, Garnham (1966) noted that nuclei were large in the growing exoerythrocytic meronts especially in comparison to the size of the nuclei of erythrocytic meronts.

Exoerythrocytic meronts of *P. vaughani merulae* were found in blackbird *Turdus merula* in macrophages in the liver, spleen, kidneys, bone marrow, lungs, and brain 7 to 11 days after the infection with sporozoites isolated from *Culex pipiens* (Corradetti and Scanga, 1972). The meronts were especially numerous in the liver and spleen. They were also seen on the 27th day after the infection with sporozoites, and it is likely that they persist even for a longer period. The number of nuclei in the majority of mature meronts does not exceed 70, but sometimes it was recorded to be up to 100 to 130.

Both the number of generations and the sequence of the exoerythrocytic merogony are unknown.

The prepatent period in canaries is long and varies in different infected individuals after blood-induced infection (Manwell, 1935b; Corradetti and Scanga, 1973; Crewe, 1975). The parasites can appear in the blood cells of canaries only six to seven weeks after intramuscular subinoculation of infected blood. The prepatent period is usually about one

week after the intravenous infection, but it sometimes also extends up to six weeks. The prepatent period was recorded to be 12 days in juveniles *Agelaius phoeniceus* after infection with sporozoites which developed in the mosquito *Culiseta morsitans* (Williams and Bennett, 1978). The similar results were obtained when *Turdus merula* was infected with sporozoites of *P. vaughani merulae* developed in the mosquito *Culex pipiens*. The parasites appeared in the peripheral blood on the 11th day after the inoculation of sporozoites (Corradetti and Scanga, 1972).

Erythrocytic merogony is not synchronized. As a result, all blood stages can be seen at any stage of parasitemia. Usually a cycle of merogony is completed in 24 to 26 h. Gametocytes appear in the peripheral blood together with trophozoites. The number of parasites in the blood increases and then decreases slowly. The peak of primary parasitemia is only slightly evident. The parasitemia lasts for months, and it was recorded to be present up to 450 days (the period of observation) in some experimentally infected canaries (Manwell, 1935b; Corradetti and Scanga, 1972; Crewe, 1975).

Trophozoites (Fig. 15, *1–3*) are seen in mature and polychromatic erythrocytes; growing trophozoites are variable in form, frequently more or less irregular or ameboid in outline, and can produce one short clear outgrowth which does not exceed the main body of the trophozoites (Fig. 15, *2*, *3*); the 'ring' stage is not characteristic, but the ring-like parasites were occasionally seen among youngest trophozoites (Fig. 15, *1*); the parasite nucleus is small; fully grown trophozoites usually possess one or sometimes two minute-size pigment granules; largest trophozoites sometimes possess one roundish colourless refractive globule; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 15, *4–13*) are seen in mature and polychromatic erythrocytes; the cytoplasm is scanty, stains pale blue and becomes poorly visible or even invisible in fully grown meronts; nuclei markedly decrease in size as the parasite matures; fully grown meronts are roundish, quadrangular, oval, fan-like, or of irregular form; nuclei are arranged as rosettes, fans, or are located randomly in fully grown meronts; mature meronts contain four to eight (more frequently four or six) merozoites; one clearly defined round refractive colourless globule is frequently seen in meronts (Fig. 15, *4*, *6–9*), and it is usually located close to a clump of pigment granules; this globule can be present even in some segmenters (Fig. 15, *13*); pigment granules are usually roundish, markedly variable in size but usually do not exceed 0.5 μm in diameter, their number varies from one to three and they are black or dark-brown; two pigment granules clearly different in size were especially frequently observed in meronts (Fig. 15, *10*), and the larger granule is more refractive than the smaller one; meronts usually do not touch the nuclei of infected erythrocytes and can be seen anywhere in the erythrocytes but more frequently take a polar or subpolar position in the host cells; the influence of meronts on infected erythrocytes is not pronounced; fully grown meronts ($n = 37$) vary from 2.3 to 5.4 (on average 3.0±0.6) μm in length, and from 1.5 to 4.4 (on average 2.0±0.2) μm in width; mature merozoites usually do not exceed 1 μm in diameter, and their cytoplasm is usually invisible (Fig. 15, *13*).

Macrogametocytes (Fig. 15, *14–17*) are usually seen in mature erythrocytes; the cytoplasm is homogeneous in appearance, frequently possesses a few small clear vacuoles (Fig. 15, *15–17*); gametocytes are of elongated form and variable outline from the earliest stages of their development; fully grown gametocytes usually take a lateral position to the nuclei of infected erythrocytes; the parasite nucleus is compact, variable in form, stains pale, usually median in position; pigment granules are usually roundish, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; the number of pigment granules varies markedly from 2 to 24 in different strains but more frequently

is about ten; the size of pigment granules usually increases as their number decreases and vice versa; the influence of gametocytes on infected erythrocytes is not pronounced; gametocytes (n = 34) vary from 8.0 to 13.7 (on average 11.8±0.6) μm in length, and from 1.2 to 2.8 (on average 1.8±0.2) μm in width.

Microgametocytes (Fig. 15, *18–20*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Relapses and recrudescences were recorded in experimentally infected canaries, and they frequently are accompanied with higher parasitemia than during the primary infection. Stages, which are responsible for the relapses, are unknown.

Development in vector has been incompletely investigated. The North American strain, which was isolated from *Agelaius phoeniceus*, does not develop in mosquitoes of the genera *Aedes*, *Anopheles*, and *Culex*. This strain completes the sporogony in the mosquito *Culiseta morsitans* (Williams and Bennett, 1978). Oocysts were seen in the midgut of the mosquito from the 2nd to 14th day after the ingestion of mature gametocytes. Sporozoites were especially numerous in the middle lobes of the salivary glands.

A few sporozoites were seen in the salivary glands in several specimens of the mosquitoes *Mansonia perturbans* which fed on infected birds (Williams and Bennett, 1978). However the role of this mosquito in transmission of the parasite is unclear.

The subspecies *P. vaughani merulae* completes sporogony in the mosquito *Culex pipiens* (Corradetti and Scanga, 1972).

Pathogenicity has been insufficiently investigated, and there is no convincing information about the pathology in vertebrate hosts. Naturally and experimentally infected wild birds, who were maintained at the laboratory, do not exhibit any signs of illness. Mortality usually was not recorded among experimentally infected canaries.

Specificity. *Plasmodium vaughani* is one of the most common bird malaria parasites which is second only to *P. relictum* in the frequency of occurrence. This species has a wide range of vertebrate hosts including representative of several bird orders but is particularly common in passerines. However, the specificity of different strains and subspecies is different. The nominal subspecies develops in canary. *Plasmodium vaughani tenuis* acquire the ability to develop in the canary only after passage through hybrids of *Carduelis carduelis* and *Serinus canaria*. *Plasmodium vaughani merulae* do not develop either in the canary or in *Leiothrix lutea* which is the type vertebrate host of *P. vaughani tenuis* (Corradetti and Scanga, 1973). The nominal subspecies develops in domestic pigeon but not in ducklings and turkey poults (Manwell, 1952; Nelson, 1966).

Crewe (1975) isolated two strains of *P. vaughani* from *Streptopelia senegalensis* and *Ploceus cucullatus*, respectively, near Ibadan (Nigeria). The morphology of blood stages of these strains was identical. However, the strain isolated from *S. senegalensis* did not develop in canary which was shown to be the excellent experimental host of the strain isolated from *P. cucullatus*.

Subspecies

1. **Plasmodium vaughani vaughani** Novy and MacNeal, 1904

Plasmodium vaughani Novy and MacNeal, 1904a: 932. – *P. vaughani vaughani*: Valkiūnas, 1997: 447 (emend. pro *P. vaughani*).

Type vertebrate host. *Turdus migratorius* (L.) (Passeriformes).
Vector. *Culiseta morsitans* (Diptera: Culicidae).
Type locality. Ann Arbor, Michigan, USA.
Distribution has been insufficiently investigated. Transmission takes place in the North America and in Europe. It is likely that this subspecies is cosmopolitan in the distribution but restricted to a limited number of vertebrate hosts. The range of the hosts has not been investigated.
Type material. The neohapantotype of *P. vaughani* is the hapantotype for this subspecies.

Main diagnostic characters. The same as for *P. vaughani*. The parasite develops in canary but does not complete sporogony in the mosquito *Culex pipiens*.

2. **Plasmodium vaughani tenuis** (Laveran and Marullaz, 1914)

Haemamoeba tenuis Laveran and Marullaz, 1914: 22. – *Plasmodium tenuis*: Manwell, 1935b: 184 (*P. tenue*). – *P. vaughani tenuis*: Corradetti and Scanga, 1973: 348 (*P. vaughani tenue*).

Type vertebrate host. *Leiothrix lutea* (Scopoli) (Passeriformes).
Type locality. Paris (the parasite was isolated from a bird kept in captivity).
Distribution. Far East and, probably, in the range of the type vertebrate host.
Type material. Neohapantotypes (No. 642, 643, 1969, *Leiothrix lutea*, R.D. Manwell) are deposited in CPG.

Main diagnostic characters. The same as for *P. vaughani* (Fig. 258). Canary is not susceptible to the strain isolated from the type vertebrate host but gets susceptible to this strain after its passage through hybrids of *Carduelis carduelis* and *Serinus canaria*. Blackbird *Turdus merula* is resistant to *P. vaughani tenuis.*

3. **Plasmodium vaughani merulae** Corradetti and Scanga, 1972

Plasmodium vaughani merulae Corradetti and Scanga, 1972: 85. – *P. merulae*: Corradetti and Scanga, 1973: 346 (emend pro *P. vaughani merulae*).

Type vertebrate host. *Turdus merula* (L.) (Passeriformes).
Vector. *Culex pipiens* (Diptera: Culicidae).
Type locality. Macerata, Marche, Italy.
Distribution has not been investigated. This parasite has been recorded only in Italy so far.
Type material. Hapantotypes (*exoerythrocytic meronts*: No. 656, *Turdus merula*, smear of liver 264 h after infection with sporozoites; *blood stages*: No. 654, 655, *T. merula*) are deposited in CPG.

Main diagnostic characters. The same as for *P. vaughani*. Canary and *Leiothrix lutea* are not susceptible. Sporogony is completed in mosquito *Culex pipiens*.

Comments. *Plasmodium vaughani* is characterized by (i) its vast geographical and vertebrate host ranges, (ii) the variability of the average number of merozoites in erythrocytic meronts, (iii) different specificity of strains and subspecies both to vertebrate hosts and vectors. It is likely that *P. vaughani* can be at the stage of active differentiation into subspecies or even distinct species.

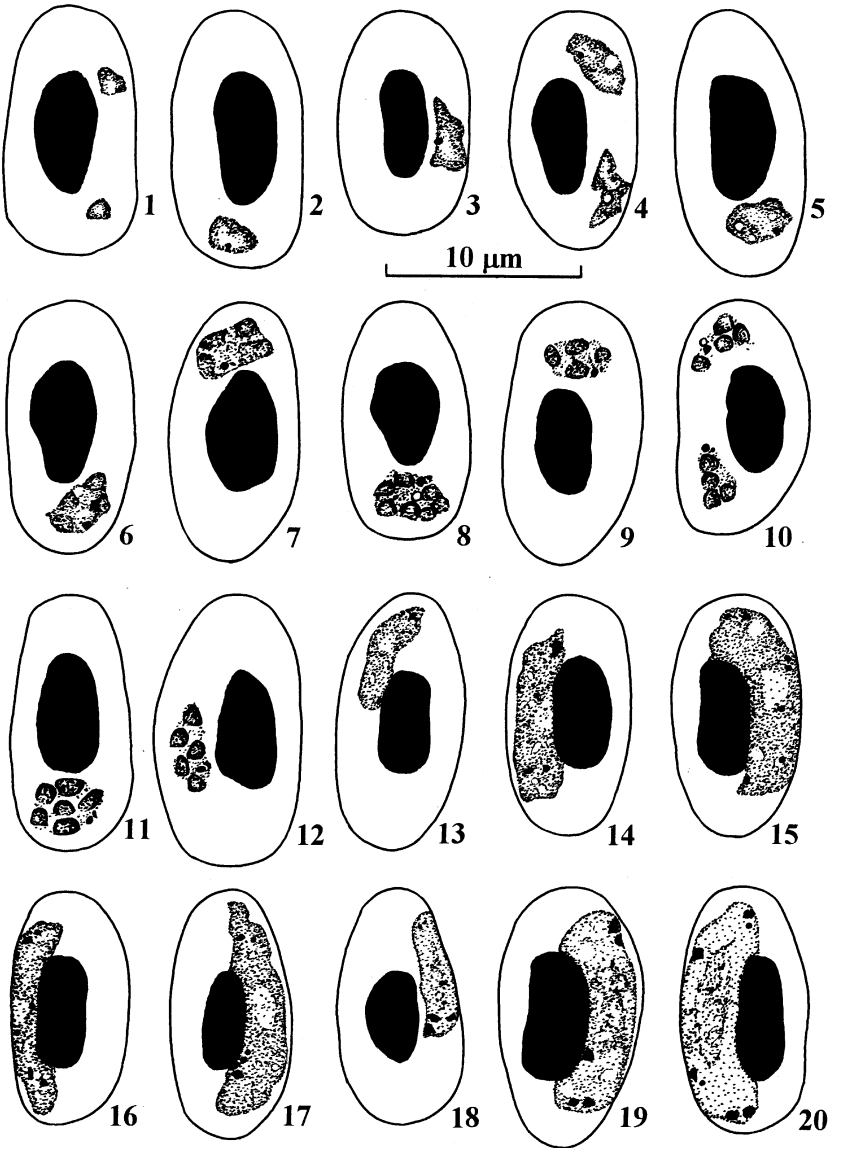

Figure 258 *Plasmodium vaughani tenuis* from the blood of *Leiothrix lutea:*
1–4 – trophozoites; *5–12* – erythrocytic meronts; *13–17* – macrogametocytes; *18–20* – microgametocytes.

Plasmodium vaughani is especially similar to *P. hexamerium*. During identification of these species, the attention should be paid, first of all, on the following characters. First, the number of merozoites in mature erythrocytic meronts of *P. vaughani* is variable but is relatively stable (usually six) in the meronts of *P. hexamerium*. Second, *P. hexamerium* successfully develops in ducklings and turkey poults but this is not characteristic of *P. vaughani*.

Blood stages of *P. vaughani* are also similar to *P. rouxi*. The latter species can be distinguished from *P. vaughani*, first of all, on the basis of (i) its 'bow-tie' binuclear erythrocytic meronts and (ii) smaller maximum number of merozoites (not more than 4) in mature erythrocytic meronts.

27. **Plasmodium (Novyella) columbae** Carini, 1912

Plasmodium columbae Carini, 1912: 398, Fig. 1–5.

Type vertebrate host. Domestic pigeon *Columba livia* Gmelin (Columbiformes).
Additional vertebrate hosts. The natural hosts are unknown (see also 'Specificity').
Type locality. São Paulo, Brazil.
Distribution. This parasite has been found in Brazil and Venezuela so far.
Type material. Neohapantotypes (No. 651–653, *Columba livia*, 1974–1975, Venezuela, A. Gabaldon) are deposited in CPG. Paraneohapantotypes are deposited in IRCAH and CPGA.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Columba*.

Main diagnostic characters. Advanced trophozoites frequently possess one long clearly defined thread-like or tail-like outgrowth which exceeds the main body of the trophozoites in length. Trophozoites sometimes possess a small (<1 μm in diameter) vacuole. Erythrocytic meronts, which do not touch the nuclei of infected erythrocytes, are present. Mature erythrocytic meronts contain four to ten (usually eight) merozoites. Pigment granules in gametocytes are frequently clumped into a spot near one end of the gametocytes. Fully grown gametocytes are small (their maximum length is less than 11 μm) and highly vacuolated.

Development in vertebrate host was studied by Gabaldon and Ulloa (1976a) in experimentally infected domestic pigeons. Exoerythrocytic meronts were not found. The prepatent period usually is about 10 days after subinoculation of infected blood. However, the prepatent period was also recorded to be as long as 76 days in some birds. Periodicity of erythrocytic merogony is only slightly (if at all) evident. The patent stage of infection is long. The chronic parasitemia lasts for a year and even longer.

Trophozoites (Fig. 259, *1–8*) are seen in mature erythrocytes; growing trophozoites are usually seen in a polar or subpolar position in infected erythrocytes, they are of variable form and frequently ameboid outline; trophozoites sometimes possess a small (<1 μm in diameter) vacuole; a roundish refractive colourless globule was seen in numerous growing trophozoites (Fig. 259, *5*, *7*); advanced trophozoites frequently possess one long clearly defined thread-like or tail-like outgrowth which can exceed the main body of the parasites in length (Fig. 259, *7*, *8*); pigment appears in the earliest trophozoites as a minute, brown granule; fully grown trophozoites possess one or two minute pigment granules which are light-brown or brown; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 259, *9–15*) are seen in mature erythrocytes and are not numerous in the peripheral blood; cytoplasm is scanty; fully grown meronts are roundish, oval or sometimes fan-like in form, are usually seen in a polar or subpolar position in infected erythrocytes, and some of them adhere to the nuclei of erythrocytes (Fig. 259, *9*, *10*, *12*, *13*); nuclei are located randomly (Fig. 259, *12*, *15*) or along the periphery (Fig. 259, *14*) in fully grown meronts or sometimes arranged as fans (Fig. 259, *13*); mature meronts contain four to ten (usually eight) merozoites; pigment granules are of variable size but usually do not exceed 0.5 μm in diameter, light-brown or brown, clumped into a spot near the edge of the parasite (Fig. 259, *12–15*); growing meronts frequently adhere to the nuclei of infected erythrocytes (Fig. 259, *9*, *10*) but this contact usually disrupts in advanced meronts (Fig. 259,

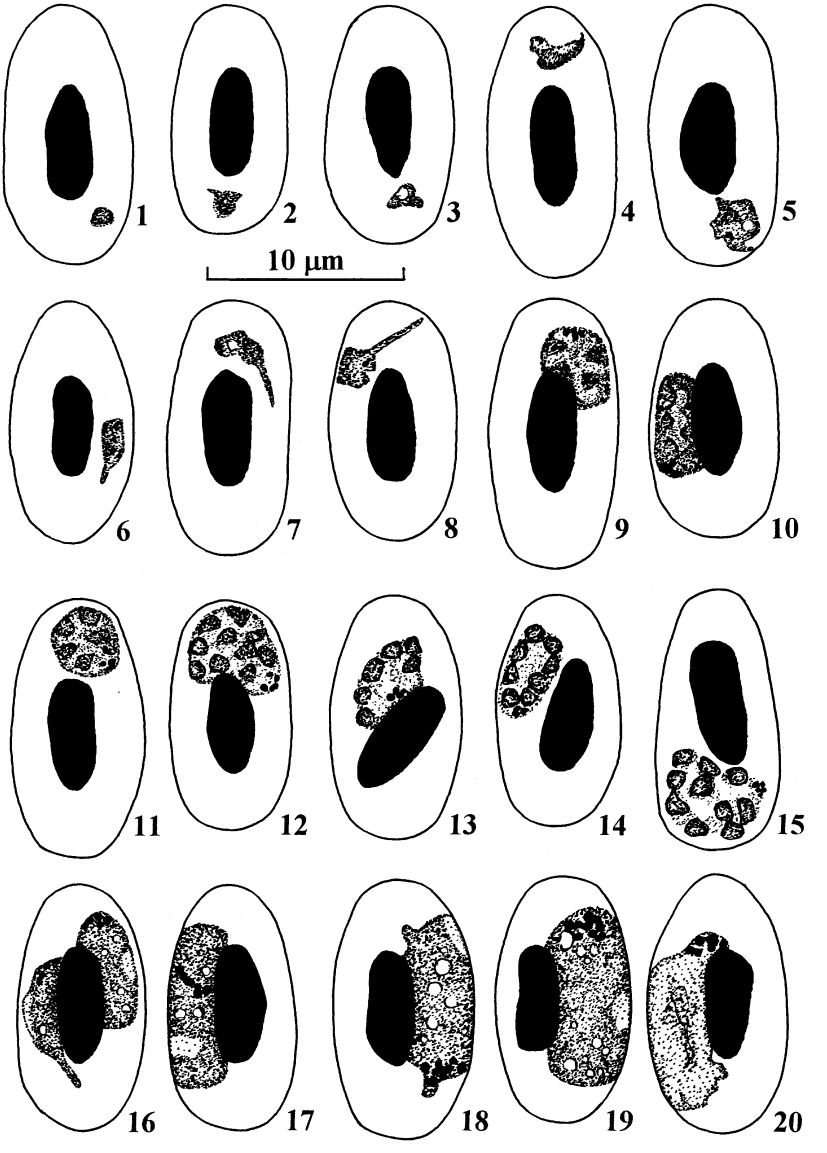

Figure 259 *Plasmodium columbae* from the blood of *Columba livia:*
1–8 – trophozoites; *9–15* – erythrocytic meronts; *16–19* – macrogametocytes; *20* – microgametocyte.

14, *15*); meronts only slightly influence infected erythrocytes whose nuclei can be slightly displaced (Fig. 259, *13–15*).

Macrogametocytes (Fig. 259, *16–19*) are seen in mature erythrocytes and are not numerous in the peripheral blood; cytoplasm possesses numerous (up to 30) small, well evident vacuoles (Fig. 259, *18*, *19*); young gametocytes are elongated, frequently possess one long finger-like outgrowth (Fig. 259, *16*); fully grown gametocytes are elongated, take a lateral position to the nuclei of infected erythrocytes and are closely appressed to the nuclei

but never reach the poles of the host cells; the outline is usually even (Fig. 259, *17*, *19*), sometimes ameboid (Fig. 259, *18*); the parasite nucleus is compact, small (Fig. 259, *16–19*), of variable form and position but more frequently seen in a median position; pigment granules are roundish, of small size (<0.5 μm), usually clumped into a spot near one end of the gametocytes (Fig. 259, *16, 18, 19*), vary from 5 to 15; sometimes two clumps of pigment granules were seen, and each of the clumps was located near the ends of gametocytes; gametocytes only slightly influence infected erythrocytes whose nuclei can be slightly displaced laterally (Fig. 259, *19*); gametocytes are small, do not exceed 11 μm in length.

Microgametocytes (Fig. 259, *20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; vacuoles are not so numerous and not so clearly seen as in macrogametocytes; other characters are as for macrogametocytes.

Development in vector has not been investigated. Exflagellation was seen 10 to 12 min after exposure of the blood with mature gametocytes to air (Gabaldon and Ulloa, 1976a).

Pathogenicity. Pathogenic parasite. The virulence is high in ducklings but low in domestic pigeon.

Specificity. Guinea-fowl is resistant. Quail *Coturnix coturnix* and canary can be infected with difficulty, and they are not good experimental hosts. Domestic pigeons and ducklings of *Cairina moschata* are excellent experimental hosts.

28. **Plasmodium (Novyella) rouxi** Sergent, Sergent and Catanei, 1928

Plasmodium rouxi Sergent, Sergent and Catanei, 1928: 811.

Type vertebrate host. *Passer hispaniolensis* (Temm.) (Passeriformes).
Additional vertebrate hosts. Numerous species of birds of the orders Apodiformes, Galliformes, Gruiformes, Piciformes, and some others, but particularly of the Passeriformes (over 60 species total).
Vectors. *Culex pipiens* is the vector in the type locality. Originally, *P. rouxi* was isolated from this mosquito. Sporogony is completed in experimentally infected *C. tarsalis* and *C. territans*. However, the attempts to infect canaries with sporozoites from these mosquitoes were not successful (Huff, 1932a).
Type locality. Mitidja plains, near Algiers, Algeria.
Distribution. This parasite has been recorded in the Holarctic, Oriental and Ethiopian zoogeographical regions. Especially numerous records came from Africa.
Type material. Neohapantotypes (No. 648, 649, *Serinus canaria*, a passage from *Passer domesticus*, 1951, Cairo, A.H. Mohammed) are deposited in CPG.
Etymology. This species is named in honour of Dr. Roux who was the revered teacher of the authors of the specific name.

Main diagnostic characters. Binuclear erythrocytic meronts frequently take a bilobular ('bow-tie') form. Mature erythrocytic meronts contain four merozoites. The maximum width of fully grown gametocytes is less than 3 μm. Vacuoles are either absent in the cytoplasm of fully grown gametocytes or only a few of them can be present. Macro- and microgametocytes are poorly distinguishable on the basis of sexual dimorphic characters. Gametocytes do not or only slightly displace the nuclei of infected erythrocytes laterally.

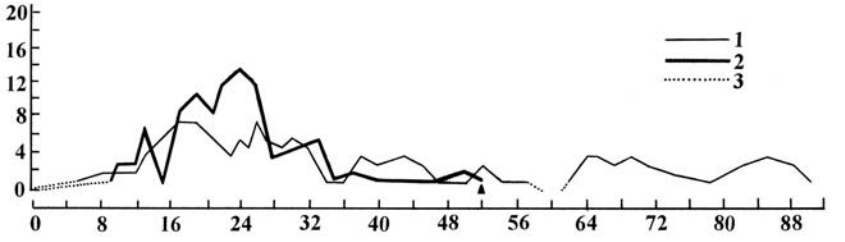

Figure 260 Dynamics of the parasitemia of *Plasmodium rouxi* in two canaries after blood-induced infection:
1, *2* – the third and fourth blood-induced passages of the freshly isolated Egyptian strain through the canary; *3* – intensity of parasitemia < 1 parasite per 1000 erythrocytes. The ordinate is the intensity of parasitemia (the number of parasites per 1000 erythrocytes) and the abscissa is the days of parasitemia. The arrowhead indicates the day of the death of the bird (modified from Mohammed, 1958).

Development in vertebrate host

Exoerythrocytic merogony has not been investigated. Attempts to find the meronts in experimentally infected canaries were not successful. Garnham (1966) believed that this could be a result of the lost ability to produce the exoerythrocytic meronts by the strains which were maintained in canaries for a long period by blood subinoculation. It is possible also that the period of the exoerythrocytic merogony of this parasite is short and confined to a limited period of the infection. Further experimental investigations into the exoerythrocytic merogony are required.

The prepatent period in canaries can be up to eight weeks after experimental peritoneal and intramuscular blood-induced infections, and it is usually about ten days and even less after intravenous inoculation of infected blood. Erythrocytic merogony is not synchronized or only slightly synchronized. All blood stages can be found at any period of the parasitemia. Maturation of the erythrocytic meronts more frequently observed around the midday. A cycle of the merogony usually is close to 24 h.

Primary parasitemia increases and then decreases slowly in the experimentally infected canaries. The peak of parasitemia only slightly evident (Fig. 260). The increased number of parasites was seen in the blood for approximately one to two months. The parasitemia decreases after this, and the infection turns into a chronic stage. During the chronic infection, parasites are regularly seen in the blood, and the intensity of parasitemia is relatively high in comparison to the chronic infection in species of the subgenera *Haemamoeba* and *Giovannolaia*. A few parasites are usually present in the blood of once infected canaries for all of their lives.

Trophozoites (Fig. 261, *1–3*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; earliest trophozoites are small (about 1 μm) (Fig. 261, *1*), cytoplasm is usually not seen; the 'ring' stage is not characteristic; as the parasite develops, trophozoites take an irregular form, and each growing trophozoite usually produces one clearly defined short outgrowth (Fig. 261, *2*, *3*); fully grown trophozoites are variable in outline and possess one or two small (<0.5 μm), dark-brown pigment granules (Fig. 261, *3*); the influence of parasites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 261, *4–14*) are usually seen in mature erythrocytes; cytoplasm is scanty and even invisible in mature meronts; binuclear parasites frequently take a bilobular ('bow-tie') form (Fig. 261, *6*, *7*) which is a characteristic feature of this

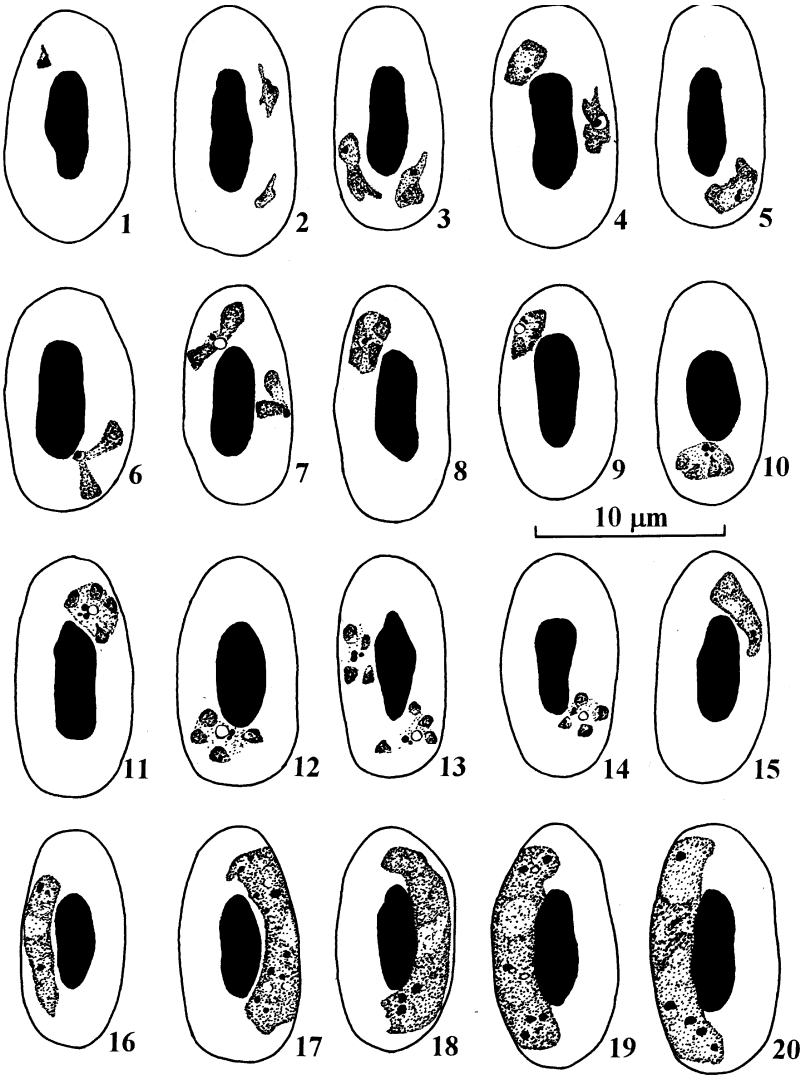

Figure 261 *Plasmodium rouxi* from the blood of *Serinus canaria* and *Oriolus oriolus:* *1–3* – trophozoites; *4–14* – erythrocytic meronts; *15–19* – macrogametocytes; *20* – microgametocyte.

species; nuclei decrease in size as the parasite matures; fully grown meronts are roundish, quadrangular, of oval or fan-like form with nuclei arranged usually as rosettes or fans; mature meronts contain four merozoites; one round globule, which is colourless or of light-turquoise colour and is located close to the pigment granules, is frequently seen (Fig. 261, *7*, *9*, *11–14*); this globule is sometimes seen even in segmenters (Fig. 261, *13, 14*); pigment granules are of variable size but never exceed 0.5 μm in diameter, are not numerous (usually one to three), black or dark brown, clumped into a spot; two different-size pigment granules are most frequently seen; meronts can be seen anywhere in infected erythrocytes but more frequently are seen in a polar or subpolar position in the

erythrocytes, usually do not touch the nuclei of erythrocytes; the influence of parasites on infected erythrocytes is not pronounced; fully grown meronts ($n = 36$) vary from 1.2 to 4.9 (on average 3.0±0.2) μm in length, and from 0.7 to 3.0 (on average 1.8±0.2) μm in width; cytoplasm is invisible in mature merozoites which do not exceed 1 μm in diameter.

Macrogametocytes (Fig. 261, *15–19*) are usually seen in mature erythrocytes; cytoplasm stains pale blue, is homogeneous in appearance, sometimes possesses a few small vacuoles; gametocytes are elongated from the earliest stages of their development (Fig. 261, *15*); the outline is variable but more frequently seen to be even; fully grown gametocytes take a lateral position to the nuclei of infected erythrocytes and usually do not fill the erythrocytes up to their poles (Fig. 261, *17–19*); the parasite nucleus is compact, variable in form, pale stained, usually median in position; pigment granules are roundish, usually of small (<0.5 μm) and sometimes medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, vary from 2 to 14 in different strains but more frequently five to eight pigment granules are present; the size of the pigment granules decreases as their number increases and vice versa; the influence of parasites on infected erythrocytes usually is not pronounced or only slightly pronounced, and nuclei of infected erythrocytes can be slightly displaced laterally; fully grown gametocytes ($n = 28$) vary from 7.0 to 12.0 (on average 10.0±0.3) μm in length and from 1.1 to 2.7 (on average 2.0±0.2) μm in width.

Microgametocytes (Fig. 261, *20*). The general configuration is as for macrogametocytes with sexual dimorphic characters; microgametocytes only slightly differ from macrogametocytes on the basis of the staining reaction of their cytoplasm; the parasite nucleus is relatively compact (Fig. 261, *20*); other characters are as for macrogametocytes.

The number of gametocytes is usually not high and does not exceed 10% of the total number of parasites at any stage of parasitemia. Once infected, canaries maintain the parasite for their whole life. Recrudescences are common but not regularly seen. Relapses were also recorded, but are uncommon.

D e v e l o p m e n t i n v e c t o r has been insufficiently investigated. Sporozoites were observed in the salivary glands of *Culex pipiens* three weeks after ingestion of mature gametocytes. The sporozoites measured about 9 to 10 μm in length and 0.5 to 0.8 μm in width (Garnham, 1966).

P a t h o g e n i c i t y. Pathogenic parasite. The mortality rate is usually high in experimentally infected canaries. However, the clinical signs of infection may not show until the death of the birds. It should be noted that the virulence of different strains is variable, and the strains with low virulence for canaries are also isolated (Garnham, 1966). The sick birds usually huddle on the bottom of cages. The birds die both at the top of primary parasitemia and during recrudescences seen several years after the infection. Among the pathological changes, (i) the decrease of erythrocyte number at the top of parasitemia and (ii) the marked enlargement of the spleen, whose weight can be four times larger in comparison to the control birds, should be pointed out first of all. It is important to note that the number of erythrocytes remains low at least for six weeks after the peak of parasitemia and even longer. In addition, the spleen remains soft even during late chronic infections. The hypertrophy of Kupffer cells in the liver and the hyperplasia of the bone marrow were also recorded during the acute stage of infection.

S p e c i f i c i t y. *Plasmodium rouxi* has a wide range of vertebrate hosts but is particularly common in passerines. It was recorded in naturally infected birds of several orders (see ‘Additional vertebrate hosts’). Attempts to infect domestic chickens were not successful. Canary is the good experimental host.

Comments. Blood stages of *P. rouxi* are especially similar to *P. vaughani* and *P. bertii*. Mature erythrocytic meronts of *P. rouxi* produce maximum 4 merozoites, and bilobular ('bow-tie') binuclear erythrocytic meronts are frequently seen. Both these features are not characteristic of *P. vaughani*. *Plasmodium rouxi* can be distinguished from *P. bertii*, first of all, on the basis of clearly different morphology of their gametocytes (cf. Figs. 261, *15–20* and 267, *14–20*). Additionally, the 'bow-tie' binuclear erythrocytic meronts were not seen in *P. bertii* but they are common in *P. rouxi.*

29. **Plasmodium (Novyella) hexamerium** Huff, 1935

Plasmodium hexamerium Huff, 1935: 276, Fig. 1–16. – *P. oti* Wolfson, 1936: 99, Pl. 1, Fig. 1–16. – *P. hexamerium*: Manwell, 1949b: 563, Pl, Fig. 1–16 (= *P. oti*).

Type vertebrate host. *Sialia sialis sialis* (L.) (Passeriformes).
Additional vertebrate hosts. Numerous species of birds of the orders Columbiformes and Strigiformes but it is particularly common in species of the Passeriformes (over 40 species total).
Type locality. Kansas, Illinois, USA.
Distribution. This parasite is common in the Nearctic and it was recorded in the Neotropical zoogeographical region. There are also a few records from the Old World, but they should be tested.
Type material. Neohapantotypes (No. 629, 630, *Melospiza melodia*, 1952, Syracuse, USA, R.D. Manwell) are deposited in CPG.
Etymology. The specific name reflects the peculiarity of this parasite to produce mainly six merozoites in erythrocytic meronts.

Main diagnostic characters. Trophozoites are ameboid in outline, but their ameboid outgrowths do not exceed the main body of the trophozoites in length. Erythrocytic meronts and gametocytes, which do not touch the nuclei of infected erythrocytes, are common. Mature erythrocytic meronts contain four to eight merozoites but the majority of the meronts (>90%) produce six merozoites. Pigment granules in mature erythrocytic meronts are aggregated into a solid mass. Gametocytes do not possess long thread-like outgrowths. Canary is susceptible not to all strains.

Development in vertebrate host
Primary exoerythrocytic merogony has not been investigated. Phanerozoites were found in endothelial cells of brain capillaries in naturally infected *Vermivora celata* (Manwell, 1951b). Vacuoles are not seen in the cytoplasm of the phanerozoites. Mature phanerozoites contained approximately 40 merozoites. The phanerozoites were not found in canaries subinoculated with heavily infected blood.

The prepatent period in canaries is up to 3 months after intravenous subinoculation of infected blood from the type vertebrate host, but it is only 5 to 12 (on average 9) days after the subinoculation of the strain which was adapted to canaries (Huff, 1935). A peak of parasitemia is only slightly (if at all) pronounced. The primary parasitemia increases and then decreases slowly. A few parasites are seen in the blood of birds for many months, and it is likely that they persist in the blood for the whole life in infected birds.

Erythrocytic merogony is only slightly synchronized. The periodicity has not been clearly determined so far. Mature meronts are especially common in the blood in the morning.

Trophozoites (Fig. 262, *1*, *2*) are seen in mature and polychromatic erythrocytes; growing trophozoites are variable in outline, frequently possess short ameboid outgrowths

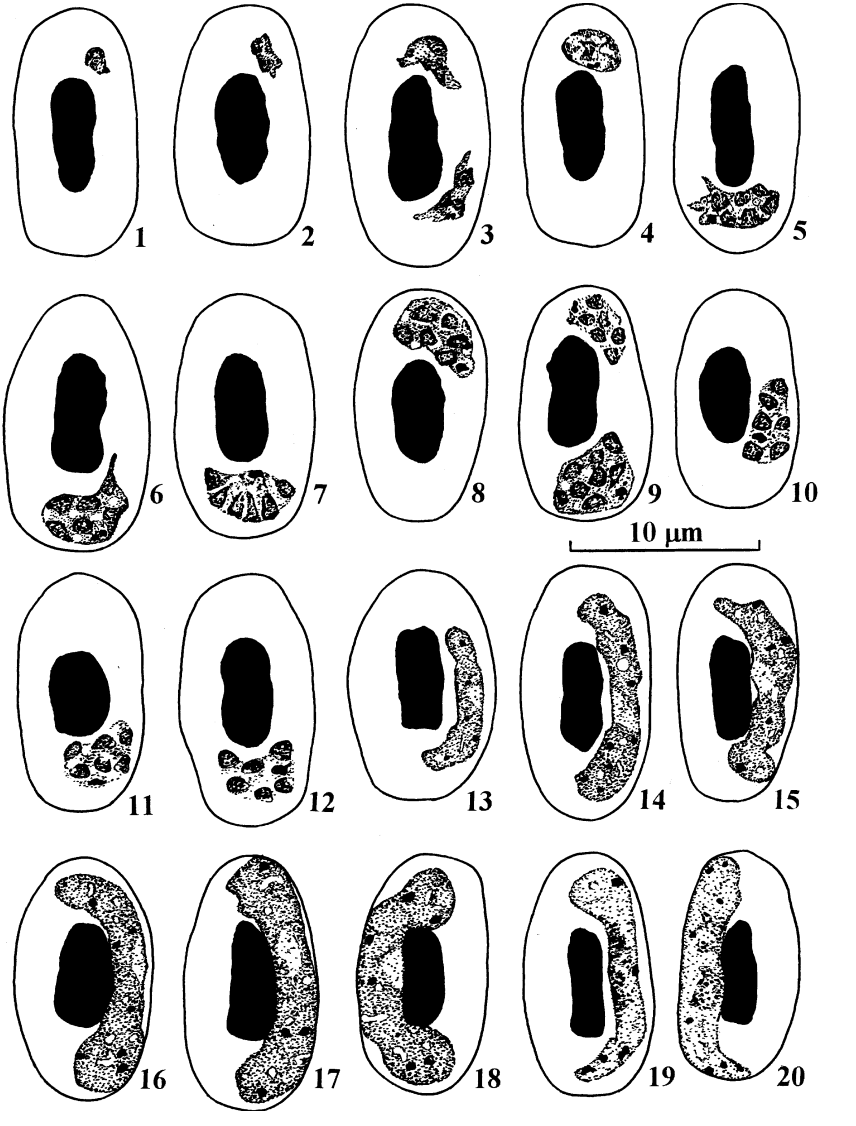

Figure 262 *Plasmodium hexamerium* from the blood of *Melospiza melodia:* *1*, *2* – trophozoites; *3–12* – erythrocytic meronts; *13–18* – macrogametocytes; *19*, *20* – microgametocytes.

which do not exceed the main body of trophozoites in length; the 'ring' stage is not characteristic but it was observed occasionally; the nucleus is of small size, is located close to the edge of trophozoite; fully grown trophozoites usually possess one or two minute-size dark-colour pigment granules; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 262, *3–12*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; cytoplasm is scanty and even invisible in mature meronts (Fig. 262, *11*, *12*); a few minute-size vacuoles are sometimes seen in the

cytoplasm (Fig. 262, *6*, *9*); nuclei decrease in size as the parasite matures; fully grown meronts are usually irregular in form (Fig. 262, *8–11*), sometimes fan-like in shape (Fig. 262, *7*); nuclei are usually located randomly in fully grown meronts but are also sometimes observed to be arranged as fans or rosettes; mature meronts contain four to eight merozoites but the great majority of the meronts (>90%) contain six merozoites; pigment granules are usually aggregated into a solid dark mass which is of medium size (0.5 to 1.0 μm); meronts can be seen anywhere in infected erythrocytes but are more frequently seen in a polar or subpolar position and usually do not touch the nuclei of erythrocytes; the influence on infected erythrocytes usually is not pronounced; fully grown meronts (n = 13) vary from 3.0 to 5.4 (on average 4.0±0.4) μm in length, and from 1.7 to 4.1 (on average 2.6±0.2) μm in width; mature merozoites are roundish or slightly oval with invisible cytoplasm, they do not exceed 1 μm in length.

Macrogametocytes (Fig. 262, *13–18*) are usually seen in mature erythrocytes but occasionally also in polychromatic erythrocytes; the cytoplasm is homogeneous in appearance, frequently possesses a few small vacuoles; gametocytes are elongated from the earliest stages of their development, they take a lateral position to the nuclei of infected erythrocytes; one end of gametocytes frequently is more pointed than the other end (Fig. 262, *15*, *16*); the outline is variable but gametocytes with an even outline are more frequently seen; the parasite nucleus is compact, variable both in form and position, pale stained; pigment granules are roundish or oval, usually of small size (<0.5 μm), randomly scattered throughout the cytoplasm; the number of pigment granules in the neohapantotypes (n = 16) vary from 4 to 11 (most frequently 6); the influence of parasites on infected erythrocytes is not pronounced; fully grown gametocytes (n = 16) vary from 10.8 to 13.1 (on average 11.2±0.3) μm in length, and from 1.1 to 2.8 (on average 1.5±0.3) μm in width.

Microgametocytes (Fig. 262, *19*, *20*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has not been investigated. This parasite does not complete sporogony in *Aedes aegypti*, *A. albopictus*, *Culex pipiens*, and *C. tarsalis*.

Pathogenicity. Virulence is low. Mortality was not recorded among experimentally infected canaries.

Specificity. The range of vertebrate hosts is wide. This parasite has been found in naturally infected birds of the orders Columbiformes and Strigiformes but is particularly common in species of the Passeriformes. Canary is the good experimental host. The parasite can be easily adapted to ducklings and turkey poults.

Comments. Blood stages of *P. hexamerium* are similar to *P. vaughani*. During identification of these species, the attention should be paid, first of all, on the following characters. First, the number of merozoites in erythrocytic meronts of *P. vaughani* varies markedly but is relatively stable in *P. hexamerium*. In the type material of *P. hexamerium*, over 90% of mature erythrocytic meronts contain six merozoites. Second, *P. hexamerium* develops in ducklings and turkey poults, but this is not characteristic of *P. vaughani*. It should be also noted that active transmission of *P. hexamerium* takes place in the New World. A few records of this parasite in the Old World (Levitanskaya and Lysenko, 1952; Huang and Wu, 1990) are questionable. The Palearctic isolates should be tested on the biological characters and compared with those of *P. vaughani* before the parasite is attributed to *P. hexamerium*.

Plasmodium hexamerium is also similar to *P. dissanaikei*. During the identification of these species the attention should be paid, first of all, on (i) the number of merozoites in mature erythrocytic

meronts, (ii) the position of meronts in infected erythrocytes and (iii) the form of young gametocytes (see also 'Comments' to *P. dissanaikei*).

Plasmodium hexamerium should be also distinguished from *P. kempi*. Both these species contain relatively stable number of merozoites in erythrocytic meront, but the meronts of *P. hexamerium* contain usually six merozoites and *P. kempi*, five merozoites.

30. **Plasmodium (Novyella) nucleophilum** Manwell, 1935

Plasmodium nucleophilum Manwell, 1935a: 268, Pl. 1, Fig. 13–24. – *P. huffi* Muniz, Soares and Batista, 1951: 342, Pl. 1, Fig. 1–15 (partim).

Type vertebrate host. *Dumetella carolinensis* L. (Passeriformes).
Additional vertebrate hosts. Numerous species of birds of the orders Anseriformes, Columbiformes, Piciformes and some others, but particularly common in species of the Passeriformes (over 60 species total). Canary is a good experimental host.
Type locality. Syracuse, New York, USA.
Distribution. This parasite has been recorded in all zoogeographical regions, except the Australian and Antarctic.
Type material. Neohapantotypes (No. 640, 641, late passage of the strain, which was isolated from the type vertebrate host, through canary, 1953, USA, R.D. Manwell) are deposited in CPG.
Etymology. The specific name reflects an important character of this parasite, i.e., the close adherence of meronts and gametocytes (nucleophility) to the nuclei of infected erythrocytes.

Main diagnostic characters. Erythrocytic meronts and gametocytes are closely appressed to the nuclei of infected erythrocytes. Mature erythrocytic meronts contain four to nine (usually six to eight) merozoites. The average length of fully grown gametocytes is usually less than 10 μm. Fully grown meronts frequently displace the nuclei of infected erythrocytes but fully grown gametocytes usually do not. Ducklings are susceptible. Phanerozoites are absent in the peripheral blood.

Development in vertebrate host
Primary exoerythrocytic merogony has not been investigated. Phanerozoites are observed in the lungs, spleen, liver, bone marrow, kidneys, and brain of canaries after blood-induced infection (Manwell and Sessler, 1971a). Phanerozoites are especially numerous in the lungs, spleen, and brain where they were seen two weeks after the infection and even earlier. In all above mentioned organs (except the brain), the phanerozoites develop in lymphocytes and are roundish. The parasites possess clear vacuoles. Both nucleus and cytoplasm of the host cells are markedly enlarged. In the brain, phanerozoites develop in endothelial cells of vessels. They are elongated, do not possess vacuoles, and do not induce hypertrophy of the nuclei of infected cells. The number of merozoites in exoerythrocytic meronts varies markedly. In the lungs, the meronts usually contained 40 to 60 merozoites. Phanerozoites were not seen in the peripheral blood.

The prepatent period markedly varies in canaries after blood-induced infection depending on mode of the infection. The parasites appeared in the blood approximately one week or even sooner after the intravenous infection. However, they were observed only on the sixth week and even later after the intramuscular subinoculation of small doses of infected blood. The primary parasitemia increases and than decreases slowly, and it lasts at least several weeks and longer. Erythrocytic merogony is only slightly synchronized. A

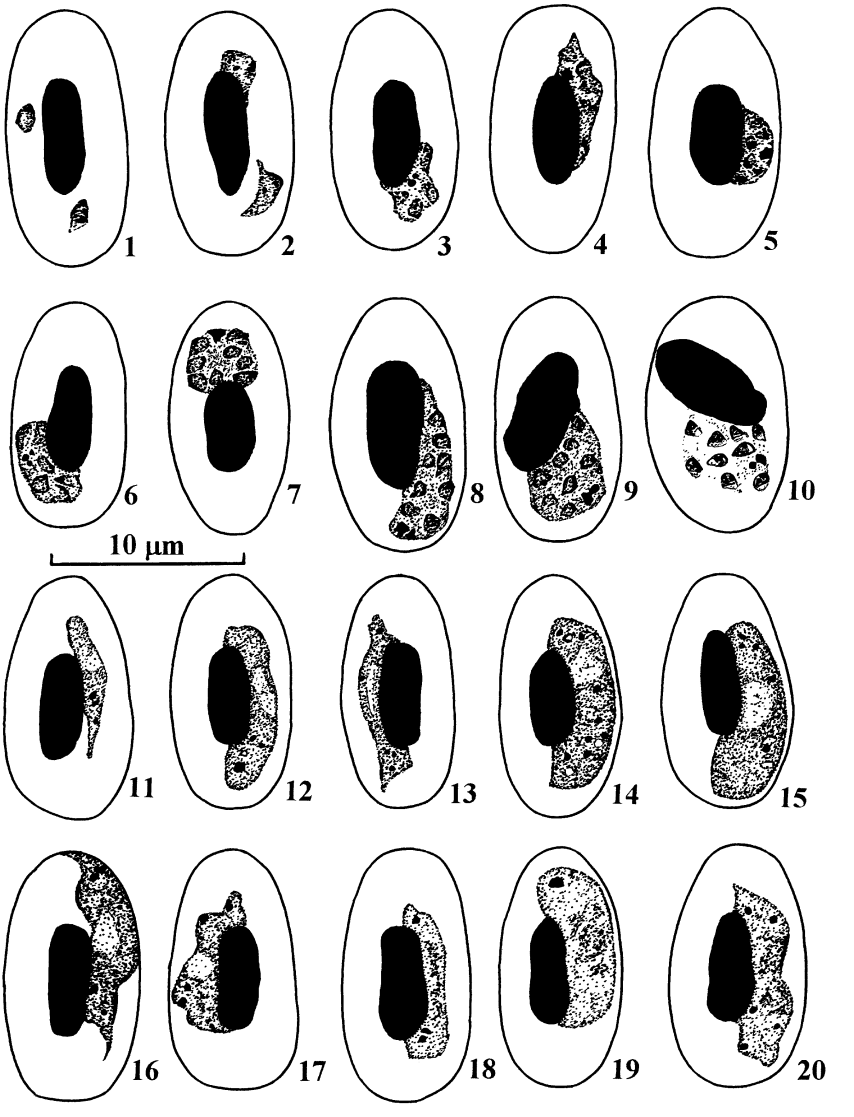

Figure 263 *Plasmodium nucleophilum* from the blood of *Serinus canaria:* *1*, *2* – trophozoites; *3–10* – erythrocytic meronts; *11–17* – macrogametocytes; *18–20* – microgametocytes.

cycle of merogony is close to 24 h. The majority of meronts rupture around the midday or shortly afterward. A few parasites are present in the blood during a chronic stage of infection. Relapses were recorded but are not well pronounced (Manwell, 1935a).

Trophozoites (Fig. 263, *1*, *2*) are seen in mature erythrocytes; the 'ring' stage can be present but the 'rings' are uncommon; growing trophozoites are variable in form but well evident ameboid outgrowths are not characteristic; earliest trophozoites can be seen anywhere in infected erythrocytes; as the parasite develops, trophozoites elongate and one or two minute-size dark pigment granules appear, and trophozoites are now usually seen in

a polar or subpolar position in infected erythrocytes (Fig. 263, *2*); the influence of parasites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 263, *3–10*) are seen in mature erythrocytes; cytoplasm is pale stained and scanty; meronts are closely appressed to the nuclei of infected erythrocytes from the stage of binuclear parasites to their complete maturity and, as a rule, this contact does not disrupt during development of the parasite; young meronts usually adhere to the nuclei of erythrocytes near one of its poles (Fig. 263, *3*); advanced meronts can be found at any position to the nuclei of erythrocytes (Fig. 263, *4–7*) but still more frequently seen in the polar or subpolar position (Fig. 263, *6–9*); fully grown meronts are variable in form, and the roundish, oval, irregular, and even slightly elongated parasites are seen; nuclei are usually located randomly in fully grown meronts; mature meronts contain four to nine (more frequently six to eight) merozoites; up to 12 merozoites were observed occasionally, and this is probably a case of the double infection of the same erythrocyte; pigment granules are of small size, dark colour, only slightly refractive, clumped into a spot, and frequently aggregated into one or two solid masses (Fig. 263, *6–10*); young meronts only slightly (if at all) influence infected erythrocytes, but full grown meronts frequently displace the nuclei of erythrocytes (Fig. 263, *9*, *10*); segmenters (Fig. 263, *10*) were only occasionally seen in the peripheral blood; mature merozoites do not exceed 1 μm in diameter, possess a relatively prominent nucleus, and a minute portion of cytoplasm was sometimes visible (Fig. 263, *10*).

Macrogametocytes (Fig. 263, *11–17*) are seen in mature erythrocytes; vacuoles are usually absent; gametocytes are elongated from the earliest stages of development (Fig. 263, *11*), take a lateral position to the nuclei of infected erythrocytes and are closely appressed to the nuclei (Fig. 263, *12–17*); this contact with the nuclei is not disrupted as the parasites develop; the outline varies from even (Fig. 263, *15*) to irregular (Fig. 263, *17*) and highly ameboid (Fig. 263, *16*); the parasite nucleus is compact, of variable form, pale stained, usually median in position; pigment granules are of small size (<0.5 μm), dark colour, randomly scattered throughout the cytoplasm or clumped in one or several foci and even seen aggregated into solid masses (Fig. 263, *12*, *17*); sometimes pigment granules were also seen aggregated in one solid mass (Fig. 263, *19*); the number of pigment granules ($n = 21$) usually varies from three to ten (most frequently six); fully grown gametocytes ($n = 17$) vary from 7.4 to 12.0 (on average 8.9) μm in length and from 1.0 to 2.8 (on average 2.0) μm in width; the influence of parasites on infected erythrocytes is usually not pronounced.

Microgametocytes (Fig. 263, *18–20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is extremely diffuse and ill-defined; other characters are as for macrogametocytes.

Development in vector has not been investigated and the vector is still unknown. *Culex pipiens* is refractive (Manwell, 1949a).

Pathogenicity. A pathogenic parasite, but the virulence of different strains varies markedly. The nominal subspecies is not lethal for experimentally infected canaries. *Plasmodium nucleophilum toucani* is highly virulent for canaries with the mortality rate up to 75%. It is likely that phanerozoites, which are numerous in the brain and lungs, are the main cause of the death (Manwell, 1935a; Manwell and Sessler, 1971a).

Specificity. The range of natural vertebrate hosts includes representatives of several bird orders (see 'Additional vertebrate hosts'), but the parasite is particularly common in passerines. Canary is a good experimental host. The nominal subspecies easily infects young ducklings. A light parasitemia develops in ducklings and persists up to two

weeks (Manwell and Hatheway, 1943). A light and transient parasitemia develops in domestic chickens (Garnham, 1966).

Subspecies

1. **Plasmodium nucleophilum nucleophilum** Manwell, 1935

Plasmodium nucleophilum Manwell, 1935a: 268, Pl. 1, Fig. 13–24. – *P. nucleophilum nucleophilum*: Valkiūnas, 1997: 458 (emend. pro *P. nucleophilum*).

Type vertebrate host. *Dumetella carolinensis* L. (Passeriformes).
Type locality. Syracuse, New York, USA.
Distribution has been insufficiently investigated. Probably, North America.
Type material. Neohapantotypes of *P. nucleophilum* are hapantotypes of this subspecies.

Main diagnostic characters. The same as for *P. nucleophilum.* A few phanerozoites develop in canaries after blood-induced infection. The parasite is low virulent for canaries.

2. **Plasmodium nucleophilum toucani** Manwell and Sessler, 1971

Plasmodium nucleophilum toucani Manwell and Sessler, 1971a: 574, Fig. 1–15 (partim).

Type vertebrate host. *Ramphastos swainsonii* Gould. (Piciformes).
Type locality. Brazil.
Distribution has been insufficiently investigated. Probably South America.
Type material. Should be designated.

Main diagnostic characters. The same as for *P. nucleophilum*, but young erythrocytic meronts are less nucleophilic. Numerous phanerozoites develop in canaries after blood-induced infection. Virulence is high for canaries.

Comments. *Plasmodium nucleophilum* is especially similar to *P. paranucleophilum*, and it can be distinguished from the latter species, first of all, on the basis of (i) the smaller size of its gametocytes which usually do not displace the nuclei of infected erythrocytes laterally, (ii) the marked enlargement both of the nucleus and the cytoplasm of lymphocytes containing its phanerozoites, and (iii) the absence of phanerozoites in the peripheral blood. Additionally, mature erythrocytic meronts of *P. nucleophilum* frequently displace the nuclei of infected erythrocytes which is not characteristic of *P. paranucleophilum.*

31. **Plasmodium (Novyella) dissanaikei** Jong, 1971

Plasmodium dissanaikei Jong, 1971b: 41, Pl. 1, Fig. 1–16.

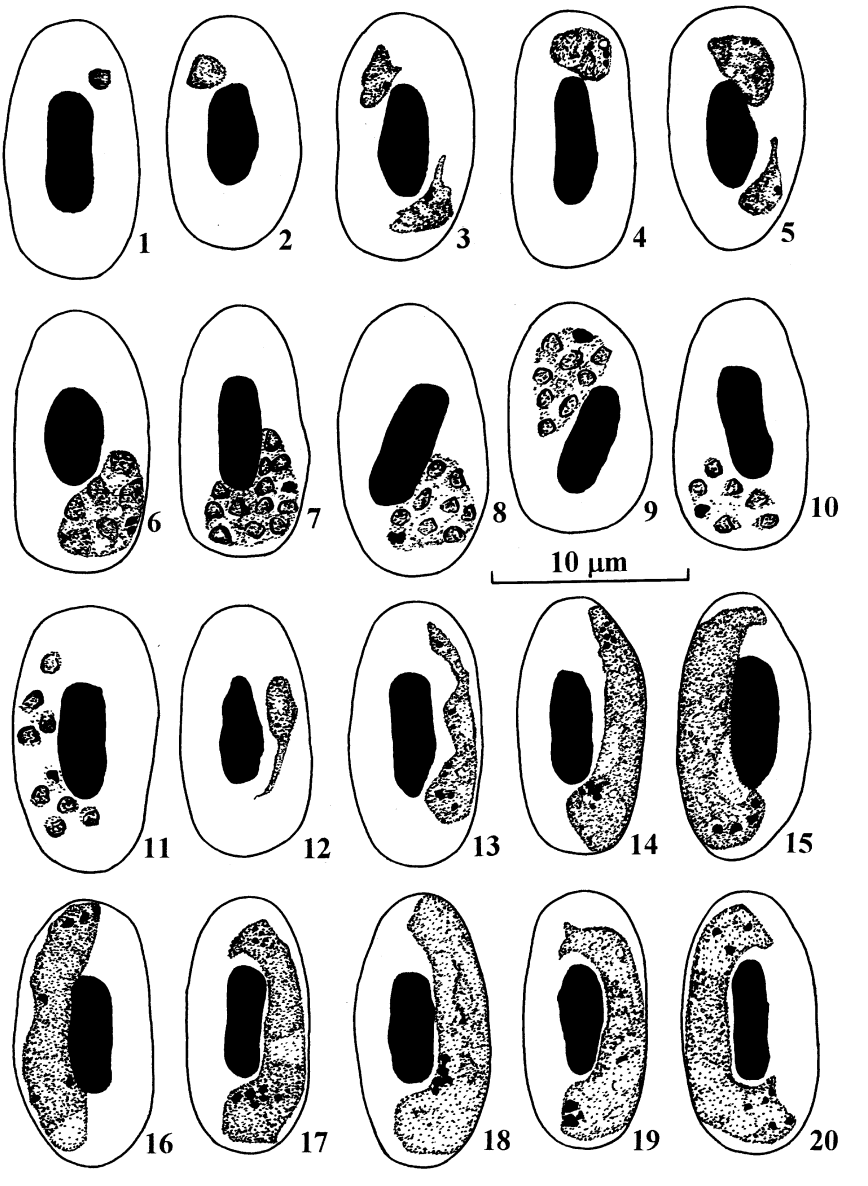

Figure 264 *Plasmodium dissanaikei* from the blood of *Psittacula krameri:*
1–5 – trophozoites; *5–11* – erythrocytic meronts; *12–17* – macrogametocytes; *18–20* – microgametocytes.

Type vertebrate host. *Psittacula krameri manillensis* (Psittaciformes).
Additional vertebrate hosts. There is no convincing evidence about the presence of this parasite in other bird species in nature. Ducklings are good experimental hosts. Canary can be infected with difficulty.
Type locality. Ja-ela, Ceylon.

Distribution. The Oriental zoogeographical region.

Type material. Hapantotypes (No. 631, 632, *Psittacula krameri manillensis*, 1.06.1971, Ja-ela, Ceylon, A.C. Jong) and parahapantotypes (No. 633, 634, the duplicates of No. 632) are deposited in CPG.

Etymology. This species is named in honour of prominent parasitologist A.S. Dissanaike.

Main diagnostic characters. Trophozoites frequently possess ameboid outgrowths which do not exceed the main body of the trophozoites in length. Numerous erythrocytic meronts (about 40%) are closely appressed to the nuclei of infected erythrocytes but the parasites, which do not touch the nuclei, are also common. The majority of growing meronts are polar or subpolar in position in the infected erythrocytes. Mature erythrocytic meronts contain 6 to 12 (most frequently 8) merozoites. Growing gametocytes frequently possess one long thread-like or tail-like outgrowth. Ducklings are good experimental hosts, but canary infects with difficulty.

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. A few phanerozoites were found in smears of the liver of turkey 16 days after blood-induced infection (Jong, 1971b). The parasites probably develop in lymphocytes.

Trophozoites (Fig. 264, *1–5*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; growing trophozoites can be seen anywhere in infected erythrocytes, variable in form, they frequently possess one outgrowth which does not exceed the main body of the trophozoites in length (Fig. 264, *3*, *5*); the 'ring' stage is not characteristic; the parasite nucleus is relatively large; fully grown trophozoites possess one or two minute-size golden-brown pigment granules; one or several minute-size refractive globules, which are colourless and roundish, were seen in some largest trophozoites (Fig. 264, *4*); the influence of parasites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 264, *5–11*) are usually seen in mature erythrocytes; cytoplasm is pale stained, relatively plentiful in comparison to other species of the *Novyella* but less plentiful than most species of the *Giovannolaia*; cytoplasm is poorly seen or even invisible in mature meronts (Fig. 264, *8–10*); vacuoles are not seen; meronts are roundish or irregular in form, usually possess randomly located nuclei, but the nuclei were also sometimes seen arranged as fans in young meronts; mature meronts contain 6 to 12 merozoites, but the great majority of the meronts produce 8 merozoites; segmenters (Fig. 264, *11*) are common in the peripheral blood; pigment granules are clumped into a spot and frequently aggregated into a solid mass which is golden-brown (Fig. 264, *9–11*); meronts usually take a polar or subpolar position in infected erythrocytes; about 40% of meronts are seen to adhere to the nuclei of the erythrocytes in the type material; meronts usually do not deform infected erythrocytes but can displace their nuclei (Fig. 264, *8–10*); fully grown meronts ($n = 14$) before their segmentation into merozoites (Fig. 264, *7–9*) vary from 4.2 to 6.6 (on average 5.5±0.3) μm in length and from 2.4 to 4.8 (on average 3.4±0.3) μm in width.

Macrogametocytes (Fig. 264, *12–17*) are seen in mature erythrocytes; the cytoplasm stains a bit irregularly, and a few small vacuoles are sometimes present; young gametocytes frequently possess one long thread-like or tail-like outgrowth (Fig. 264, *12*); growing gametocytes are elongated and usually of irregular outline (Fig. 264, *13*); fully grown gametocytes are elongated, take a lateral position to the nuclei of infected erythrocytes and can slightly enclose them with their ends (Fig. 264, *15*, *17*); the parasite nucleus is compact, variable in form, pale stained, variable in position but more frequently seen in a median or

submedian position; pigment granules are usually of small size (<0.5 μm), frequently clumped into one or several groups (Fig. 264, *14*) and can be aggregated into solid masses (Fig. 264, *15*, *16*) and, thus, are difficult to count; the influence of the parasites on infected erythrocytes is not pronounced; fully grown gametocytes (n = 17) vary from 12.0 to 14.8 (on average 13.4±0.4) μm in length and from 1.5 to 2.8 (on average 1.9±0.2) μm in width.

Microgametocytes (Fig. 264, *18–20*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

The number of gametocytes is usually 5 to 13% of the total number of parasites in the blood. The parasite loses the ability to produce gametocytes approximately after the seventh blood passage through ducklings. Furthermore, the morphology of blood stages changes slightly as the number of blood passages increases. The erythrocytic meronts increase in size and the parasites, which adhere to the nuclei of infected erythrocytes, were less frequently seen (Jong, 1971b).

Development in vector has not been investigated. The mosquitoes *Aedes aegypti*, *A. togoi*, *Culex gelidus*, *C. pipiens pipiens*, and *C. p. fatigans* are not susceptible. Ookinetes look like banana-like elongated bodies with prominent nuclei, typical for bird malaria parasites, and can possess small 'vacuoles' (Jong, 1971b).

Pathogenicity has not been investigated in the natural vertebrate host. The parasite is pathogenic for experimental hosts. Anaemia develops in heavily infected ducklings. They huddle on the floor of cages, refuse food and look unhealthy with ruffled feathers and drooped eyelids. Experimentally infected ducklings usually survive.

Specificity. Ducklings are good experimental hosts. The parasite develops in turkey poults but not so well as in the ducklings. Domestic pigeon and canary are susceptible, but they were infected with difficulty. Attempts to infect domestic chickens, zebra parakeet *Melopsittacus undulatus*, and quails were not successful.

Comments. *Plasmodium dissanaikei* is especially similar to *P. hexamerium*. Both these species develop in ducklings and turkey poults, but canary is a good experimental host of *P. hexamerium* and poor host of *P. dissanaikei*. The majority of mature erythrocytic meronts of *P. dissanaikei* contain eight merozoites, and usually six merozoites develop in the meronts of *P. hexamerium.* Additionally, (i) meronts of *P. dissanaikei* frequently adhere to the nuclei of infected erythrocytes and (ii) its young gametocytes frequently possess one long thread-like or tail-like outgrowth. Both these features are not characteristic of *P. hexamerium*.

32. **Plasmodium (Novyella) paranucleophilum** Manwell and Sessler, 1971

Plasmodium paranucleophilum Manwell and Sessler, 1971b: 631, Fig. 1–21.

Type vertebrate host. *Tachyphonus* sp. (Passeriformes).
Additional vertebrate hosts are unknown in nature. Canary is a good experimental host.
Type locality. Probably the Northeast Brazil. This parasite was isolated from a bird imported to the USA from South America.
Distribution has not been investigated. This parasite was recorded only in the type locality.
Type material. Hapantotype (passage from the type vertebrate host to canary) is deposited in IRCAH.
Etymology. The specific name reflects the similarity of blood stages of this parasite to *P. nucleophilum*.

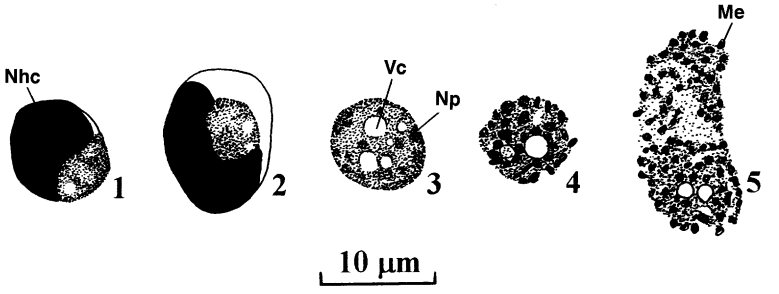

Figure 265 Phanerozoites of *Plasmodium paranucleophilum* from the peripheral blood of *Tachyphorus* sp.:
1, *2* – young parasites in lymphocytes; *3*–*5* – extracellular parasites: young (*3*) and mature (*4*, *5*); Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – vacuole (modified from Manwell and Sessler, 1971b).

Main diagnostic characters. Meronts and gametocytes are closely appressed to the nuclei of infected erythrocytes. Mature erythrocytic meronts usually contain four to eight (most frequently six) merozoites but up to 12 merozoites can be seen occasionally. The average length of fully grown gametocytes is greater than 10 μm. Fully grown erythrocytic meronts do not displace or only slightly displace the nuclei of infected erythrocytes, but fully grown gametocytes markedly displace the nuclei of erythrocytes laterally. Phanerozoites can be present in the peripheral blood.

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. Numerous phanerozoites are observed in the spleen and bone marrow of canaries after blood-induced infection (Manwell and Sessler, 1971b). Numerous phanerozoites are also seen in the peripheral blood. The parasites are only occasionally recorded in other organs where they probably penetrate via the blood stream. Phanerozoites were not found in the brain. The parasites are seen only in lymphocytes (Fig. 265). The host cells are only slightly enlarged probably due to their mechanical deformation by the parasites. The earliest phanerozoites usually locate in an 'indentation' of nucleus of the host cell (Fig. 265, *1*, *2*). The phanerozoites possess prominent vacuoles from the earliest stages of their development up to their complete maturity (Fig. 265, *1*–*5*). The number of merozoites in mature phanerozoites usually varies from 30 to 60. The number of phanerozoites in the peripheral blood was recorded to be markedly variable in different individuals of the same species of the vertebrate host.

The prepatent period varies from one to several weeks in canaries after intravenous blood-induced infection. Primary parasitemia increases and than decreases slowly. The peak of parasitemia is only slightly pronounced. The parasites are frequently seen during a long chronic stage of infection, but the parasitemia is low.

Trophozoites (Fig. 266, *1*) are, as a rule, seen in mature erythrocytes but were occasionally also observed in thrombocytes; the 'ring' stage is not characteristic but the 'rings' were seen occasionally; a small vacuole is frequently present in young trophozoites; growing parasites can be seen anywhere in infected erythrocytes, are variable in outline, sometimes slightly ameboid but the long ameboid outgrowths are not seen; as the parasite develops, trophozoites are more frequently seen in a polar or subpolar position in the erythrocytes; the influence of parasites on infected erythrocytes is not pronounced.

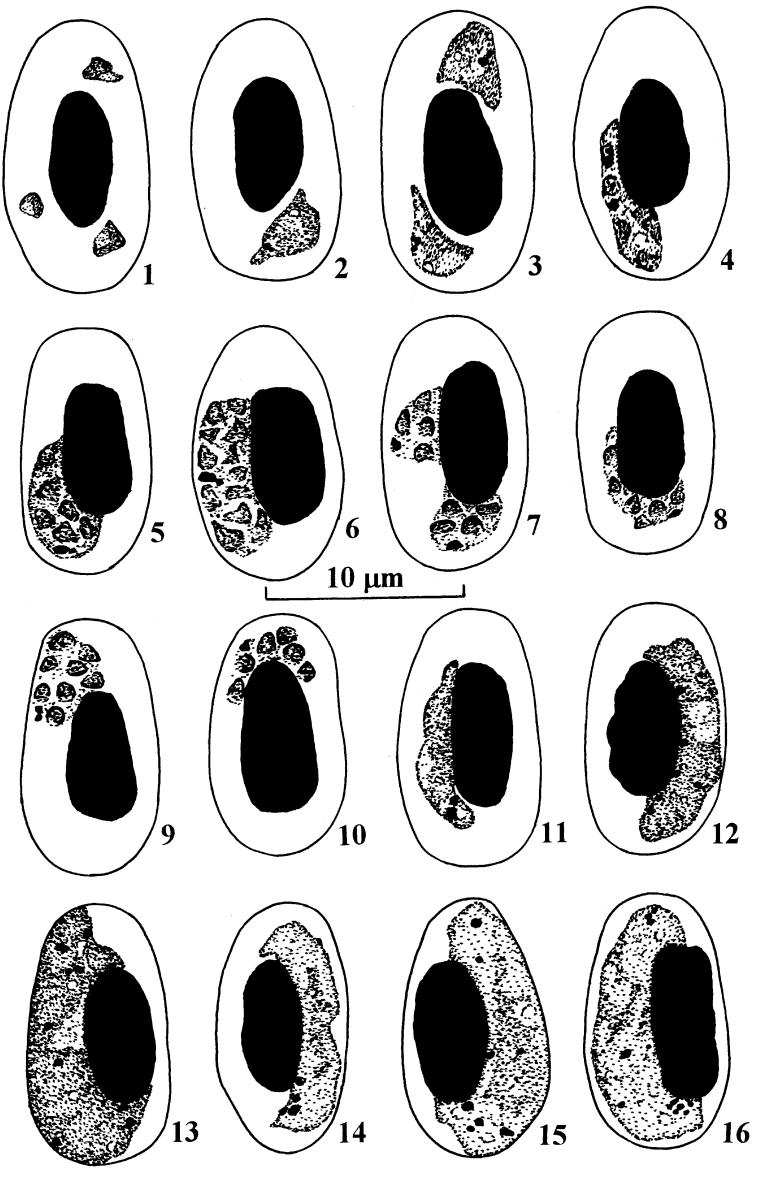

Figure 266 *Plasmodium paranucleophilum* from the blood of *Serinus canaria:*
1 – trophozoites; *2–10* – erythrocytic meronts; *11–13* – macrogametocytes; *14–16* – microgametocytes.

Erythrocytic meronts (Fig. 266, *2–10*) are seen in mature erythrocytes; the cytoplasm is pale stained, quite plentiful in binuclear meronts (Fig. 266, *2, 3*) but markedly decreases in amount as the parasite develops; the earliest meronts are usually seen in a polar or subpolar position in infected erythrocytes (Fig. 266, *2*, *3*) and can touch the nuclei of erythrocytes; multinuclear meronts are closely appressed to the nuclei of infected erythrocytes and this contact is usually not disrupted as the parasite develops; growing and

mature meronts are more frequently seen in a polar or subpolar position in infected erythrocytes (Fig. 266, *4, 5, 7–10*) but can also take a lateral position to the nuclei of the host cells (Fig. 266, *6*); fully grown meronts are of variable form and roundish, elongated and irregular-shape parasites were seen; nuclei are usually located randomly in the meronts; mature parasites usually contain 4 to 8 (most frequently 6) merozoites but up to 12 merozoites were observed occasionally; pigment granules are dark, usually clumped in focus and can be aggregated into one or two solid masses; the influence of parasites on infected erythrocytes is usually not pronounced.

Macrogametocytes (Fig. 266, *11–13*) are seen in mature erythrocytes; cytoplasm stains a bit irregularly, usually lacking vacuoles; from the earliest stages of their development, gametocytes are elongated, take a lateral position to the nuclei of infected erythrocytes, and are closely appressed to the nuclei (Fig. 266, *11*); this contact of gametocytes with the nuclei of the host cells is not disrupted as the parasite develops (Fig. 266, *12–13*); the outline of gametocytes is variable but highly ameboid parasites were not seen; the parasite nucleus is compact, of variable form, pale stained, usually median in position; pigment granules are dark, of small size (<0.5 μm), not numerous, more frequently seen randomly scattered throughout the cytoplasm but can be also clumped into a spot and even aggregated into several solid masses; fully grown gametocytes (n = 6) vary from 11.0 to 14.4 (on average 13.1) μm in length; gametocytes usually do not deform infected erythrocytes but displace their nuclei laterally, frequently markedly (Fig. 266, *13*).

Microgametocytes (Fig. 266, *14–16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is extremely diffuse and ill-defined; other characters are as for macrogametocytes.

It should be noted that gametocytes are not numerous in experimentally infected canaries.

Pathogenicity. Experimentally infected canaries usually survive. Anaemia develops in the heavily infected birds. The spleen is markedly enlarged. The level of hematocrit in infected canaries decreased 1.4 times in comparison to control birds.

Specificity has been insufficiently investigated. Canaries can be easily infected by subinoculation of infected blood. The attempts to infect *Streptopelia risoria* (Columbiformes), *Piranga hepatica*, and *Thraupis palmarum* (Passeriformes) were not successful.

Comments. *Plasmodium paranucleophilum* is especially similar to *P. nucleophilum*. It can be distinguished from the latter species, first of all, on the basis of (i) a larger size of its gametocytes which displace the nuclei of infected erythrocytes laterally, (ii) slight hypertrophy of nuclei and cytoplasm of lymphocytes with its phanerozoites, and (iii) presence of phanerozoites in the peripheral blood. Additionally, mature erythrocytic meronts of *P. nucleophilum* frequently displace the nuclei of infected erythrocytes which is not characteristic of *P. paranucleophilum.*

33. **Plasmodium (Novyella) bertii** Gabaldon and Ulloa, 1981

Plasmodium bertii Gabaldon and Ulloa, 1981: 100, Fig. 1–32.

Type vertebrate host. *Aramides cajanea cajanea* Müller (Gruiformes).
Type locality. Guaquitas, Barinas, Venezuela.
Distribution. This parasite has been recorded only in Venezuela so far.

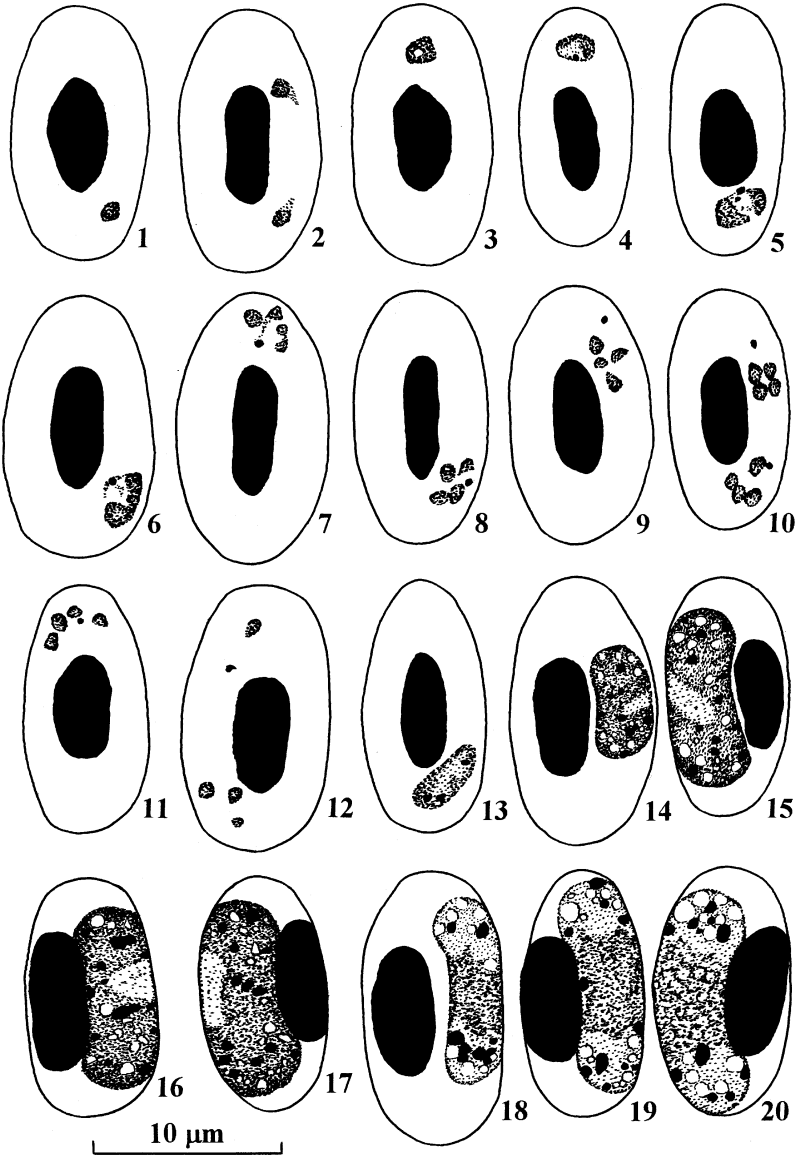

Figure 267 *Plasmodium bertii* from the blood of *Aramides cajanea:*
1–4 – trophozoites; *5–12* – erythrocytic meronts; *13–17* – macrogametocytes; *18–20* – microgametocytes.

Type material. Hapantotype (No. 960, *Aramides cajanea*, 1981, Barinas, Venezuela, A. Gabaldon) is deposited in CPG. Parahapantotypes are deposited in IRCAH and CPGA.
Etymology. This species is named in honour of Venezuelan parasitologist, Dr. Arturo Luis Berti.

Main diagnostic characters. Binuclear erythrocytic meronts do not take a bilobular ('bow-tie') form. Mature erythrocytic meronts contain four merozoites.

Numerous clear vacuoles are present in the cytoplasm of gametocytes; the vacuoles tend to accumulate at the ends of gametocytes. Fully grown gametocytes exceed 3 μm in width, they markedly displace the nuclei of infected erythrocytes. Macro- and microgametocytes are well distinguishable on the basis of sexual dimorphic characters.

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. Phanerozoites were found in smears of the lungs, liver, and spleen in one naturally infected bird which died in captivity with high parasitemia. Phanerozoites were not observed in the brain and bone marrow. The parasites were of oval form with pale stained cytoplasm which possessed small vacuoles. Nuclei decrease in size as the parasite develops. Fully grown phanerozoites contain up to 22 nuclei. Mature phanerozoites, which contained over 18 merozoites, were about 9 μm in length and 6 μm in width.

Periodicity of erythrocytic merogony has not been investigated. All blood stages are present in the peripheral circulation in the morning (Gabaldon and Ulloa, 1981).

Trophozoites (Fig. 267, *1–4*) are seen in mature erythrocytes; cytoplasm is invisible in the earliest trophozoites (Fig. 267, *1*) but is well pronounced in advanced parasites (Fig. 267, *2*); a minute vacuole is frequently seen in the centre of growing trophozoite (Fig. 267, *3*); fully grown trophozoites are roundish or oval, of even outline, possess one or two minute pigment granules which are dark-brown or black (Fig. 267, *4*).

Erythrocytic meronts (Fig. 267, *5–12*) are seen in mature erythrocytes; cytoplasm is pale stained, scanty, and even invisible in fully grown meronts; remnants of the cytoplasm in mature meronts can be seen as variable-form threads or scraps (Fig. 267, *6*, *7*) or are even invisible (Fig. 267, *8–11*); nuclei are usually located close to the edge in binuclear growing meronts (Fig. 267, *5*, *6*) and markedly decrease in size as the parasite matures; binuclear erythrocytic meronts do not take a bilobular ('bow-tie') form; fully grown meronts are roundish, quadrangular, oval, or of fan-like form; the nuclei are arranged as rosettes, fans, or located randomly; mature meronts contain four merozoites; meronts usually do not touch the nuclei of infected erythrocytes and can be seen anywhere in the erythrocytes; pigment granules are usually aggregated into one small (usually <0.5 μm) solid mass (Fig. 267, *6–12*); the influence of parasites on infected erythrocytes is not pronounced; according to the original description, the fully grown meronts vary from 1.9 to 3.6 (on average 2.9±0.2) μm in length and from 1.9 to 2.8 (on average 2.1±0.1) μm in width; mature merozoites do not exceed 1 μm in diameter; cytoplasm is invisible in the merozoites.

Macrogametocytes (Fig. 267, *13–17*) are seen in mature erythrocytes; cytoplasm stains bright blue, and the ends of gametocytes are more intensively stained than their central part; the cytoplasm possesses numerous small vacuoles which tend to accumulate at the ends of gametocytes; fully grown gametocytes are of elongated form, lateral in position to the nuclei of infected erythrocytes, and are closely appressed to the nuclei and do not fill the erythrocytes up to their poles (Fig. 267, *16*, *17*); the parasite nucleus is compact, intensively stained, of variable form, frequently ribbon-like in shape (Fig. 267, *17*), median in position; pigment granules are black, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm and can be aggregated into compact groups and even solid masses (Fig. 267, *16*); the number of pigment granules in the hapantotype varies from 5 to 14 (most frequently 11); fully grown gametocytes usually do not deform infected erythrocytes but markedly displace their nuclei laterally, frequently to the periphery of the host cells (Fig. 267, *16*, *17*); according to the original description,

fully grown gametocytes vary from 8.1 to 10.0 (on average 9.2±0.2) μm in length and from 2.4 to 3.8 (on average 3.0±0.2) μm in width.

Microgametocytes (Fig. 267, *18–20*). The general configuration is as for macrogametocytes with the clearly pronounced sexual dimorphic characters; vacuoles are slightly larger and even more pronounced than in macrogametocytes; fully grown gametocytes vary from 10.0 to 11.4 (on average 10.5±0.2) μm in length and from 1.9 to 3.3 (on average 2.7±0.1) μm in width; other characters are as for macrogametocytes.

Specificity has not been investigated. This parasite has been found only in the type vertebrate host. Attempts to infect one canary, three domestic pigeons, and 11 Peking ducklings were not successful (Gabaldon and Ulloa, 1981).

Comments. Erythrocytic meronts of *P. bertii* are especially similar to *P. rouxi*. These species differ well on the basis of morphology of their gametocytes. Additionally, binuclear erythrocytic meronts of *P. rouxi* frequently take a bilobular ('bow-tie') form which is not characteristic of *P. bertii.*

Plasmodium bertii is a common parasite in the type locality where it was recorded in 13.6% (95% confidence limit is 7.8–21.4) of the sampled type vertebrate hosts.

34. **Plasmodium (Novyella) kempi** Christensen, Barnes and Rowley, 1983

Plasmodium kempi Christensen, Barnes and Rowley, 1983: 209, Fig. 1–18.

Type vertebrate host. *Meleagris gallopavo silvestris* Vieil. (Galliformes).
Additional vertebrate hosts. *Alectoris graeca, Anas platyrhynchos, Anser anser, Colinus virginianus, Numida meleagris, Pavo cristatus*, and *Serinus canaria* were infected experimentally.
Vectors. *Culex pipiens pipiens, C. tarsalis* (Diptera: Culicidae).
Type locality. Stephen State Forest, Lucas County, Iowa, USA.
Distribution has been insufficiently investigated. This parasite has been recorded in Lucas County, Iowa, USA so far.
Type material. Hapantotypes (No. 91085–91088, *Meleagris gallopavo silvestris*) are deposited in IRCAH. Parahapantotype (No. 77457, other data as for the hapantotype) is deposited in USNPC; blood smears are also available in collections of the authors of this species.
Etymology. This species is named in memory of American protozoologist Dr. Russell Kemp, Iowa State University.

Main diagnostic characters. Trophozoites and young erythrocytic meronts possess one large (>1 μm in length) refractive vacuole and frequently produce one clearly defined long thread-like or tail-like outgrowth which can exceed the main body of the parasites in length. Erythrocytic meronts and gametocytes, which do not touch the nuclei of infected erythrocytes, are common. Mature erythrocytic meronts usually are fan-like in form, contain four to eight merozoites, but approximately 95% of the meronts contain five merozoites. Pigment granules in gametocytes either randomly scattered throughout the cytoplasm or clumped into several small groups.

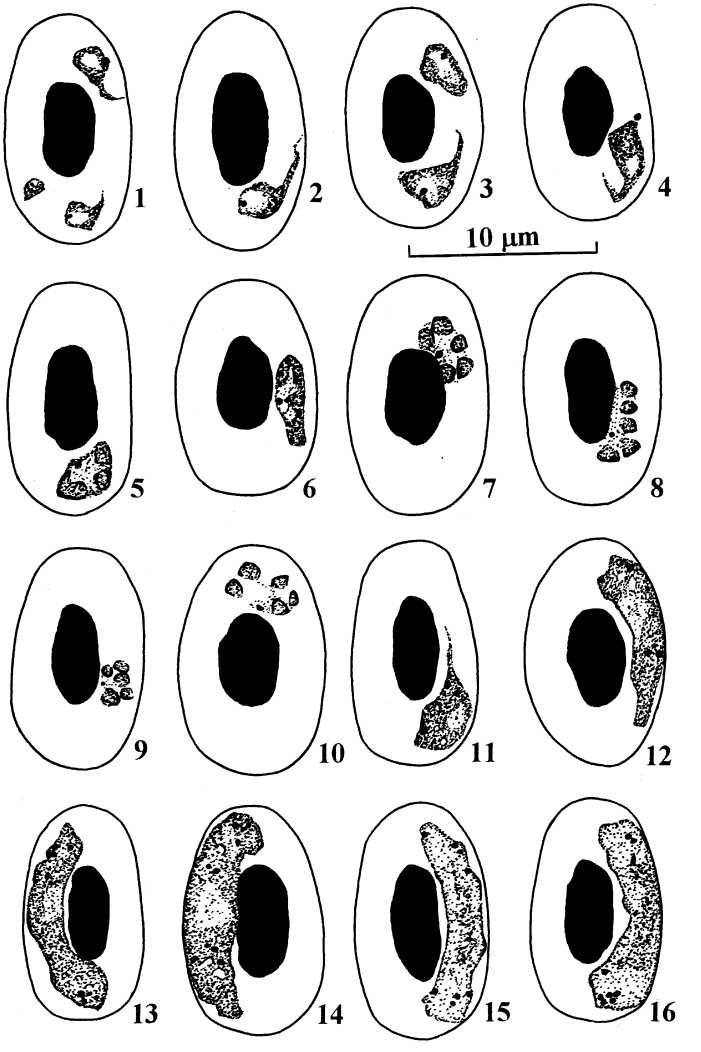

Figure 268 *Plasmodium kempi* from the blood of *Meleagris gallopavo:*
1, *2* – trophozoites; *3–10* – erythrocytic meronts; *11–14* – macrogametocytes; *15*, *16* – microgametocytes.

Development in vertebrate host

Exoerythrocytic merogony has not been investigated. Phanerozoites were not found in the brain, liver, lungs, spleen, kidneys, and bone marrow of turkey poults which had a heavy parasitemia after blood-induced infection (Christensen *et al.*, 1983).

Trophozoites (Fig. 268, *1*, *2*) are seen in mature erythrocytes, are of variable form, contain one large (>1 μm in length) refractive vacuole and frequently possess one clearly defined long thread-like or tail-like outgrowth which can exceed the main body of the parasites in length; fully grown trophozoites usually possess one, sometimes two, dark-colour, minute-size pigment granules; the influence of parasites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 268, *3–10*) are seen in mature erythrocytes; cytoplasm stains pale, scanty, and even invisible in mature meronts; nuclei markedly decrease in size as the parasite matures; young meronts are of variable form, contain a large refractive vacuole and often possess a long thread-like or tail-like outgrowth which can exceed the main body of the parasites in length (Fig. 268, *3*, *4*); as the parasite matures, meronts usually take a more or less evident fan-like form (Fig. 268, *5–10*); nuclei are usually arranged as fans in fully grown meronts; mature meronts contain four to eight merozoites, but the majority of meronts (approximately 95%) contain five merozoites; pigment granule is usually one, of small size (<0.5 μm), black or black-brown; meronts usually do not touch the nuclei of infected erythrocytes and can be seen anywhere in the erythrocytes; the influence of parasites on infected erythrocytes is usually not pronounced; according to the original description, mature meronts (n = 20) vary from 1.8 to 4.0 (on average 2.5) μm in length and from 1.6 to 3.7 (on average 2.6) μm in width; cytoplasm is invisible in mature merozoites which do not exceed 1 μm in diameter.

Macrogametocytes (Fig. 268, *11–14*) are seen in mature erythrocytes; the cytoplasm stains pale, is homogeneous in appearance, sometimes contains a few small vacuoles; young gametocytes are of variable form, frequently possess a long thread-like or tail-like outgrowth (Fig. 268, *11*); fully grown gametocytes are elongated, take a lateral position to the nuclei of infected erythrocytes, and frequently do not touch the nuclei (Fig. 268, *12, 13*); the outline is usually irregular but clearly defined ameboid outgrowths are not characteristic; the parasite nucleus is compact, of variable form, pale stained, usually median in position; pigment granules are roundish, of small size (<0.5 μm), are randomly scattered throughout the cytoplasm, and tend to clump into several small groups of three to five granules (Fig. 268, *12–14*); the number of pigment granules in gametocytes varies from six to ten; the influence of gametocytes on infected erythrocytes is not pronounced; according to the original description, fully grown gametocytes (n = 10) vary from 7.3 to 11.0 (on average 8.9) μm in length and from 1.5 to 2.2 (on average 1.8) μm in width.

Microgametocytes (Fig. 268, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; according to the original description, fully grown gametocytes (n = 10) vary from 7.3 to 9.5 (on average 8.2) μm in length and from 1.3 to 2.2 (on average 1.8) μm in width; other characters are as for macrogametocytes.

Development in vector

Oocysts and sporozoites develop in mosquitoes *Culex pipiens pipiens*, *C. tarsalis*, and *C. restuans*. However, the ability to transmit the infection was proved experimentally only for the former two species. *Culex tarsalis* is the especially effective vector. Approximately 100% of *C. tarsalis* were susceptible. At a temperature of 26.5±1.0°C, sporozoites were observed in the salivary glands of *C. tarsalis* on the sixth day after the ingestion of mature gametocytes, and were recorded on the seventh day in *C. pipiens*. The mosquitoes *Aedes aegypti* and *A. triseriatus* are refractive (Christensen *et al.*, 1983).

Pathogenicity. Slightly virulent parasite. Signs of illness were not seen in experimentally infected birds.

Specificity. The range of experimental vertebrate hosts is wide. Turkey is the type vertebrate host. Mallard ducklings, goslings, chukars *Alectoris graeca*, bobwhites *Colinus virginianus*, guinea-fowls, peacocks *Pavo cristatus*, and canaries were infected experimentally, however, only a transient infection was observed in the ducklings and goslings. Attempts to infect pheasants *Phasianus colchicus*, domestic pigeons, Japanese quails, Leghorn white chickens, and starlings *Sturnus vulgaris* were not successful.

Comments. Blood stages of *P. kempi* are similar to *P. vaughani*. It should be noted that erythrocytic meronts of *P. kempi* are characterized by relatively stable characters and they are much more variable in *P. vaughani.* During identification of *P. kempi*, the attention should be, first of all, paid on (i) the large refractive vacuole which is present in trophozoites and young erythrocytic meronts and (ii) the fan-like mature erythrocytic meronts, which clearly predominate among the erythrocytic meronts and usually contain five merozoites. These features are not characteristic of *P. vaughani*. Additionally, *P. kempi* develops in turkey poults and ducklings but *P. vaughani* do not.

Plasmodium kempi is also similar to *P. hexamerium*. Most erythrocytic meronts of *P. kempi* produce five merozoites, and usually six merozoites develop in the meronts of *P. hexamerium*.

4. **Subgenus BENNETTINIA** Valkiūnas, 1997

Bennettinia Valkiūnas, 1997: 466.

Type species. *Plasmodium juxtanucleare* Versiani and Gomes, 1941, according to the original designation.
Etymology. This subgenus is named in honour of prominent parasitologist, Professor Gordon F. Bennett, who together with M. Warren and W.H. Cheong investigated development of *P. juxtanucleare* in the vertebrate host and in the vector and discovered pedunculated oocysts.

Erythrocytic meronts contain scanty cytoplasm. The size of fully grown erythrocytic meronts does not exceed that of the nuclei of infected erythrocytes. Fully grown gametocytes are roundish, oval, of irregular form, sometimes elongated; their size does not exceed that of the nuclei of infected erythrocytes. Exoerythrocytic merogony takes place in cells of the reticuloendothelial system. Oocysts are pedunculated.

This subgenus includes only one species, *P.* (*B*). *juxtanucleare*.

35. **Plasmodium (Bennettinia) juxtanucleare** Versiani and Gomes, 1941

Plasmodium juxtanucleare Versiani and Gomes, 1941: 233. – *P. japonicum* Ishiguro, 1957: 725, Pl. 44, Fig. 1–6. – *P. juxtanucleare*: Akiba, 1959: 18 (=*P. japonicum*).

Type vertebrate host. Domestic chicken *Gallus gallus* (L.) (Galliformes).
Additional vertebrate hosts. Some species of birds (Table 143).
Vectors. *Culex annulus, C. gelidus, C. pipiens fatigans, C. p. pallens, C. pseudovishnui, C. sitiens*, and *C. tritaeniorhynchus* (Diptera: Culicidae).
Type locality. Western zone of the State of Minas Gerais, Brazil.
Distribution. The Neotropical, Ethiopian and Oriental zoogeographical regions and the South-East Palearctic.
Type material. Neohapantotypes (No. 657, 658, *Gallus gallus*, 1944, Brazil, W.L. Parense) are deposited in CPG.

Table 143 List of vertebrate hosts of *Plasmodium juxtanucleare*.

Bambusicola thoracica	*Gallus lafayettei*
Francolinus africanus	*Meleagris gallopavo*
F. sephaena	*Pavo cristatus*

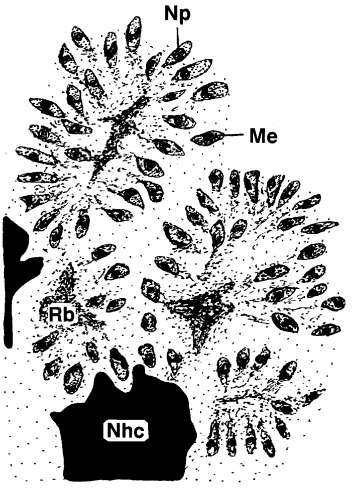

Figure 269 Mature phanerozoites of *Plasmodium juxtanucleare:*
Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Rb – residual body (modified from Garnham, 1966).

Etymology. The specific name reflects a juxtanuclear position of asexual blood stages and young gametocytes of this parasite.

Main diagnostic characters. Erythrocytic meronts are clearly nucleophilic; they produce two to six merozoites. Roundish fully grown gametocytes are common.

Development in vertebrate host

Primary exoerythrocytic merogony has not been investigated. Different strains of the parasite differ in the ability to produce phanerozoites after blood-induced infections, and phanerozoites were not always found in experimentally infected birds. They were recorded in reticuloendothelial cells of the spleen, brain, bone marrow, liver, lungs, kidneys, heart muscle, ovary, and pancreas of experimentally infected domestic chickens. Both the time and sequence of the appearance of phanerozoites in these organs vary markedly after the infection with different strains. Phanerozoites were seen in chickens from the 9th to 155th day after the blood-induced infection (Garnham, 1966). The parasites do not possess vacuoles. They are roundish or oval in all organs except the brain where they slightly extend along the capillaries. However, the brain phanerozoites of *P. juxtanucleare* are not so long as of *P. gallinaceum* (see Fig. 227, *12*, *13*). Mature phanerozoites are about 15 μm in length and contain up to 50 merozoites which are located on the periphery of the phanerozoites. A centrally located residual body is usually seen in mature phanerozoites (Fig. 269).

The prepatent period varies from 4 to 53 and even up to 106 days in different hosts after intravenous blood-induced infection. After infection with sporozoites, the prepatent period varies from 11 to 21 days. Irrespective of the mode of infection, primary parasitemia is characterised by a slightly pronounced peak and a long (several months) chronic stage. Erythrocytic merogony is only slightly synchronized. A cycle of merogony is about 24 h. The majority of meronts rupture in the early morning. Intensity of parasitemia markedly varies in different hosts and can exceed 90% of erythrocytes (Bennett and Warren, 1966; Garnham, 1966).

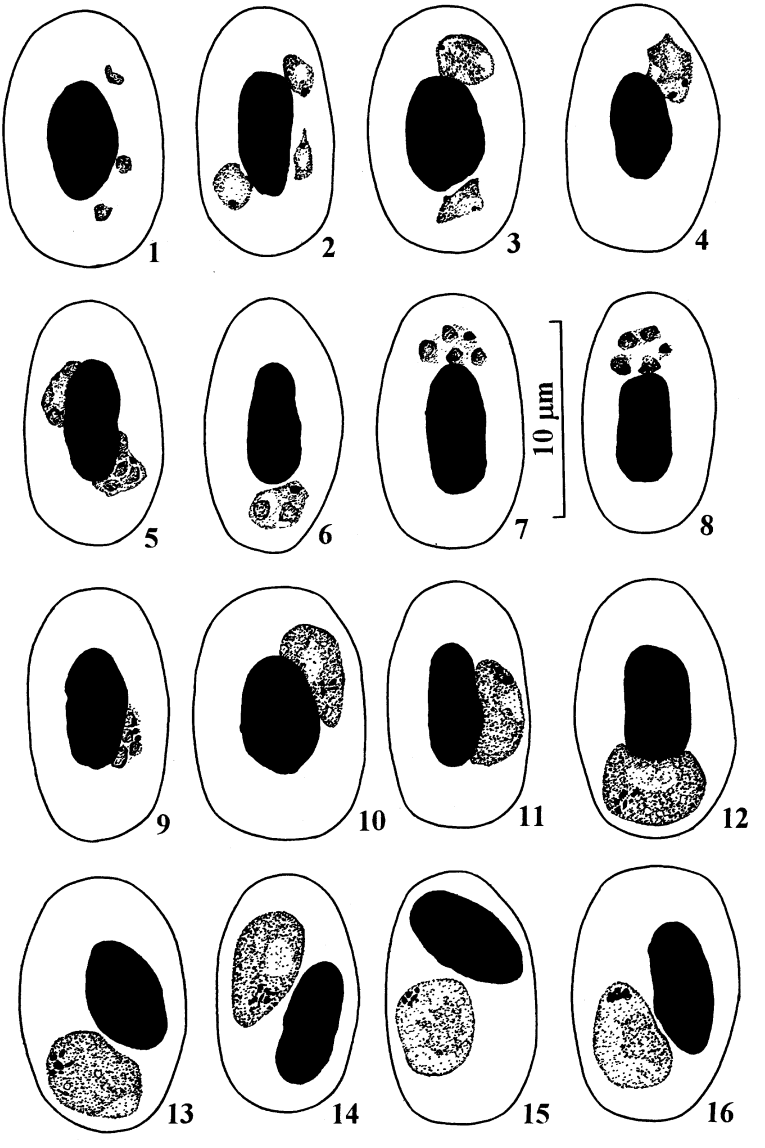

Figure 270 *Plasmodium juxtanucleare* from the blood of *Gallus gallus:*
1, *2* – trophozoites; *3–9* – erythrocytic meronts; *10–14* – macrogametocytes; *15*, *16* – microgametocytes.

Trophozoites (Fig. 270, *1*, *2*) are seen in mature and polychromatic erythrocytes; the earliest trophozoites are of variable form, even or irregular in outline, possess negligible cytoplasm (Fig. 270, *1*); clearly pronounced ameboid outgrowths are not seen; fully grown trophozoites are roundish, oval, or of irregular form, usually adhere to the nuclei of infected erythrocytes, possess one or two minute dark-brown pigment granules (Fig. 270, *2*); a small vacuole is sometimes present in the cytoplasm, but the typical 'ring' stage is not characteristic; infection of the same erythrocyte with several parasites is common during

high parasitemia; the influence of trophozoites on infected erythrocytes is usually not pronounced.

Erythrocytic meronts (Fig. 270, *3–9*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; meronts are difficult to find in the peripheral blood during a chronic stage of infection, because they clearly tend to concentrate in deep circulation of internal organs; the cytoplasm is scanty, pale stained, and sometimes even invisible in mature meronts; meronts are usually closely appressed to the nuclei of infected erythrocytes and most frequently seen in a polar or subpolar position in the erythrocytes; both the close adherence to the nuclei of erythrocytes and the small size of meronts (see Fig. 270, *9*) make the parasites difficult to find at low parasitemia; nuclei markedly decrease in size as the parasite matures; fully grown meronts are roundish or of irregular form with nuclei usually located at the periphery of the parasites (Fig. 270, *7*, *8*); mature meronts contain two to six (more frequently three to five) merozoites; sometimes up to nine merozoites were recorded (Earlé *et al.*, 1991b), which, in general, is not characteristic of this species and can be a result of a multiple infection of the same erythrocytes with several meronts; the multiple infection is common at high parasitemia; up to four minute-size dark-brown pigment granules were seen in meronts; mature parasites usually possess one solid mass of pigment (Fig. 270, *7*, *8*); the influence of parasites on infected erythrocytes is not pronounced; fully grown meronts do not exceed 5 μm in length but usually are much smaller, and their size never exceeds that of the nuclei of infected erythrocytes; the cytoplasm is invisible in mature merozoites which do not exceed 1 μm in diameter.

Macrogametocytes (Fig. 270, *10–14*) are usually seen in mature erythrocytes but sometimes also in polychromatic erythrocytes; the cytoplasm is pale stained, homogeneous in appearance, sometimes contains a few small vacuoles; the outline is usually even or sometimes irregular; young gametocytes are roundish or slightly elongated, frequently adhere to the nuclei of infected erythrocytes (Fig. 270, *10*, *11*), and can be seen anywhere in the erythrocytes; fully grown gametocytes are roundish, oval, of irregular form but sometimes also slightly elongated, more frequently seen in a polar or subpolar position to the nuclei of erythrocytes and do not touch the nuclei; pigment granules are roundish, of small size (<0.5 μm), not numerous (<10), usually clumped into a spot near the edge of parasites (Fig. 270, *12–14*); fully grown gametocytes usually displace the nuclei of infected erythrocytes; the size of gametocytes usually does not exceed that of the nuclei of erythrocytes; gametocytes are less than 7.0 μm in length and less than 5.0 μm in width.

Microgametocytes (Fig. 270, *15*, *16*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Gametocytes are not numerous in the peripheral blood. They are usually less than 14% of the total number of parasites in the blood. It is difficult to find gametocytes during the chronic stage of infection.

Recrudescences and relapses were recorded after spleenectomy, and up to 60% of erythrocytes were observed to be parasitized.

Development in vector

Numerous attempts to initiate sporogony in various species of mosquitoes of the genera *Aedes, Anopheles, Armigeres*, and *Mansonia* were not successful. Development of the Malaysian strain in mosquito *Culex sitiens* was studied by Bennett *et al.* (1966) and Bennett and Warren (1966) at temperature 27°C in detail. It is important to note that gametocytes are more infective to the vector during a chronic stage of infection (after the 30th day of the parasitemia) than in the beginning of parasitemia. Approximately two-third of oocysts

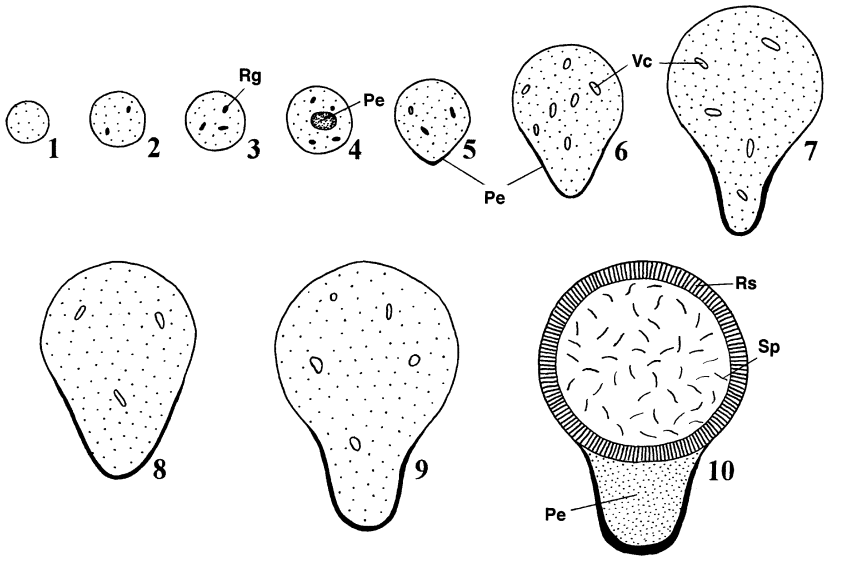

Figure 271 Diagrammatic representation of the development of peduncle in oocysts of *Plasmodium juxtanucleare:*
1–3 – young oocysts from the second to seventh day after the ingestion of gametocytes; *4*, *5* – young oocyst on the seventh day after the ingestion of gametocytes showing the earliest stages of development of peduncle (*4* – a peduncle viewed from above looks like a circle within the oocyst, *5* – a peduncle viewed laterally); *6–9* – pedunculated oocysts on the eighth to tenth days after ingestion of gametocytes viewed from laterally (the wall of peduncle gradually thickens, and randomly distributed vacuoles and refractive granules are present both in oocyst and peduncle); *10* – differentiating oocyst with the region of sporozoitegenesis which looks like a band on the periphery of the oocyst; Pe – peduncle; Rg – refractive granule; Rs – region of sporozoitegenesis; Sp – sporozoite; Vc – vacuole (modified from Bennett *et al*., 1966).

occurred on the posterior half of the midgut of mosquitoes. The earliest oocysts, which do not exceed 6 μm in diameter, were seen on the 1.5 day after ingestion of gametocytes. They possessed a homogeneously looking cytoplasm with no obvious inclusions (Fig. 271, *1*). Oocysts averaged 18 μm in diameter on the seventh day after the infection, and several refractive granules and inclusions were now seen randomly scattered throughout the cytoplasm (Fig. 271, *2*, *3*). A peduncle was seen in oocysts which are 15 μm in diameter and larger, and the oocysts are attached to the midgut by the peduncle (Fig. 271, *4–10*). Viewed from above, the peduncle was clearly seen as a dark ring within the oocyst (Fig. 271, *4*). Viewed laterally, it looks like cone-shaped structure which slightly widened toward the oocyst (Fig. 271, *5–10*). On the 10th day after infection, oocysts averaged approximately 40 μm in diameter. Oocysts with the developing sporozoites ($n = 17$) vary from 75 to 115 μm (on average 89 μm) in diameter. Oocysts are clearly separated from the midgut wall by peduncles. A zone of the sporozoitegenesis looks like a band about 7 μm in width on the periphery of the oocyst. Randomly located sporozoites are seen in the central part of oocysts (Fig. 271, *10*). Sporozoites do not develop in the peduncle and are not seen inside the peduncle. Peduncles ($n = 22$) vary from 20 to 36 (on average 28) μm in length and, from 15 to 27 (on average 18) μm in width in fully differentiated oocysts. The wall of the peduncle appeared to be thicker than the wall of the oocyst (Fig. 271, *5–10*). There is no indication of any separate structures between the cytoplasmic contents of the oocyst and

the peduncle under the light microscope. After the rupture of oocysts and the release of sporozoites, the peduncles were seen to persist on the midgut wall. On the 14th day after infection, all vital oocyst were seen to be at the stage of differentiation of sporozoites. Sporozoites were recorded in the salivary glands of mosquitoes on the 12th day after infection. They look like elongated bodies which (n = 60) vary from 10 to 18 (on average 13) μm in length and from 1 to 2 μm in width. Nucleus is usually seen in the anterior half of the sporozoite.

P a t h o g e n i c i t y. Pathogenic parasite but the virulence of different strains varies markedly (Bennett *et al.*, 1966; Garnham, 1980). The virulence of the Neotropical strains is higher than that of the Asian strains. The death was rarely recorded in domestic chickens in Asia but is common in the Neotropics where the mortality rate can exceed 90%. Furthermore, the Neotropical strains are lethal not only for juvenile chickens but also for adult birds. The chickens usually die in about two months after infection. A few of them can survive for about a year. Birds usually die because of pathological changes induced by phanerozoites in the brain, spleen, and heart. At autopsy, the spleen is markedly enlarged, and it can reach a size of 10 and even more than the control. It is likely that the blockage of brain capillaries and heavy infiltration and inflammatory changes both in the heart muscle and brain are main causes of death. However, the death can be solely because of the severe anaemia during heavy infections. Clinical signs usually appear only shortly before death when birds become weak, move with difficulty, mucous membranes are pale, and diarrhoea is common.

Plasmodium juxtanucleare is not lethal for experimentally infected turkeys.

S p e c i f i c i t y. The range of vertebrate hosts is not wide (Table 143). Turkey poults are susceptible for the majority of strains. Canaries, domestic pigeons, ducklings, guinea-fowls, the house sparrow *Passer domesticus*, and some other passerines are refractive.

C o m m e n t s. *Plasmodium juxtanucleare* can be distinguished from all other species of bird malaria parasites, first of all, on the basis of its roundish small gametocytes. Laird (1998) noted that in the absence of any small round to oval gametocytes, the identification of this parasite in naturally infected birds is questionable. The author agrees.

It is likely that *P. juxtanucleare* originated in the Oriental zoogeographical region where it is widely distributed. The jungle fowls are its natural reservoir hosts. Subsequently, the parasite penetrated into the adjacent South-East Palearctic and in the Ethiopian zoogeographical region. Most probably, it was introduced to the Neotropical region not long ago where highly virulent strains developed.

5. **Subgenus HUFFIA** Corradetti, Garnham and Laird, 1963

Huffia Corradetti, Garnham and Laird, 1963a: 3.

T y p e s p e c i e s. *Plasmodium elongatum* Huff, 1930, according to the original designation.
E t y m o l o g y. This subgenus is named in honour of Dr. Clay G. Huff, who described the type species *P. elongatum*, in recognition of his contribution to the field of avian blood parasitology.

Erythrocytic meronts contain plentiful cytoplasm. Fully grown erythrocytic meronts are variable both in form and size. Fully grown gametocytes are elongated. Exoerythrocytic merogony takes place in cells of the haemopoietic system and in some species also in cells of the reticuloendothelial system. Pedunculated oocysts are absent.

KEY TO THE SPECIES

1 (4). In peripheral blood, trophozoites and erythrocytic meronts develop mainly in young erythrocytes. The maximum number of merozoites in erythrocytic meronts is less than 20.

2 (3). Elongated erythrocytic merozoites are present. Fully grown gametocytes do not displace or only slightly displace the nuclei of infected erythrocytes and do not fill the poles of erythrocytes completely. The maximum width of fully grown gametocytes is less than 3 μm.
.. . . . . 36. ***P. elongatum***

3 (2). Elongated erythrocytic merozoites are absent. Fully grown gametocytes markedly displace the nuclei of infected erythrocytes laterally and they can fill the poles of erythrocytes completely. The maximum width of fully grown gametocytes is greater than 3 μm.
. . . . . 38. ***P. hermani***

4 (1). In peripheral blood, trophozoites and erythrocytic meronts develop mainly in mature erythrocytes. The maximum number of merozoites in erythrocytic meronts is greater than 20.
. . . . . 37. ***P. huffi***

36. **Plasmodium (Huffia) elongatum** Huff, 1930

Plasmodium elongatum Huff, 1930: 388, Fig. 1–13.

Type vertebrate host. *Serinus canaria* (L.) (Passeriformes).
Additional vertebrate hosts. Numerous species of birds of the orders Anseriformes, Falconiformes, Columbiformes, Sphenisciformes, Strigiformes, and some others but particularly of the Passeriformes (over 60 species total).
Vectors. *Culex pipiens* and *C. restuans* are natural vectors. Sporogony is completed in experimentally infected *C. nigripalpus, C. salinarius, C. tarsalis*, and *C. territans* (Diptera: Culicidae).
Type locality. Baltimore, Maryland, USA.
Distribution. This parasite has been found in all zoogeographical regions except the Australian and Antarctic. It has been especially frequently recorded in the Holarctic.
Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 211, *Serinus canaria*, liver, 1966, Udine, Italy, A. Corradetti; *blood stages*: No. 216, 217, other data as for No. 211; *sporogonic stages*: No. 212, 213, *Culex pipiens*, oocysts and sporozoites, other data as for No. 211) are deposited in CPG. A series of good additional slides of exoerythrocytic meronts is deposited in CPG.
Etymology. The specific name reflects the elongated form of gametocytes of this parasite.

Main diagnostic characters. In the peripheral blood, asexual stages develop mainly in young erythrocytes, but gametocytes develop mainly in mature erythrocytes. Mature erythrocytic meronts contain 6 to 12 merozoites which are frequently more or less elongated. Fully grown gametocytes do not displace or only slightly displace the nuclei of infected erythrocytes and they do not fill the poles of erythrocytes completely. The maximum width of fully grown gametocytes is less than 3 μm. Passerine birds are common hosts.

Development in vertebrate host has been investigated in experimentally infected canaries and ducklings (Garnham, 1966; Corradetti *et al.*, 1968). Primary exoerythrocytic merogony has not been studied. Phanerozoites are common in the experimental hosts both after the blood-induced and the sporozoite-induced infections. They develop mainly in cells of the haemopoietic system. Phanerozoites are especially numerous in migrating cells of haemopoietic tissues in bone marrow and also in spleen and liver. They develop in erythroblasts, precursor cells of the erythrocytic series, sometimes in

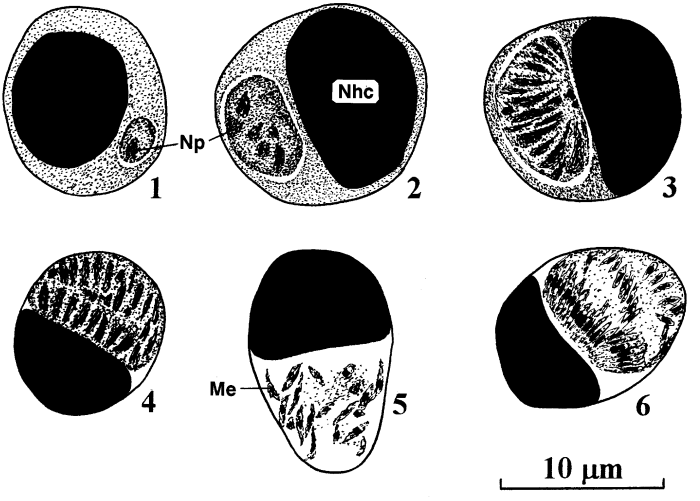

Figure 272 Phanerozoites of *Plasmodium elongatum* in the cells of erythrocytic series of bone marrow of *Serinus canaria:*
1, *2* – young parasites; *3–6* – mature parasites; Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite.

normoblasts and thrombocytes. In adapted vertebrate hosts, phanerozoites usually do not develop or only occasionally appear in cells of the reticuloendothelial system. The size of parasites varies depending on that of the host cells, but they rarely exceed 20 μm in diameter and are usually smaller. Phanerozoites are surrounded with a light band of cytoplasm of host cells, they possess basophilic cytoplasm and compact brightly stained nuclei (Fig. 272, *1–3*). During development in more advanced cells of erythrocytic series, a minute pigment granule sometimes was seen in the phanerozoites (Fig. 272, *3*). Nuclei of infected cells usually slightly deformed and more or less displaced. Some phanerozoites were seen in enucleated host cells which is especially common during heavy infection. In the latter case, the parasites look like extracellular forms. Phanerozoites produce not numerous (usually less than 30) elongated merozoites which contain a centrally located nucleus (Fig. 272, *5*). The merozoites are distributed randomly or arranged as well regulated rows in mature meronts (Fig. 272, *3*, *4*, *6*) which is a characteristic feature of this species. The secondary exoerythrocytic merogony is restricted to the haemopoietic system, and phanerozoites are usually not seen in the peripheral blood.

Enormous number of phanerozoites develop in cells of the reticuloendothelial system when the parasite develops in unusual vertebrate hosts which are not adapted to the parasite. The cape penguin *Spheniscus demersus* is an example (Fleischman *et al.*, 1968). Phanerozoites developed mainly in histiocytes of the lungs, spleen, liver, and heart in the penguins. They were less frequently seen in the kidneys, skeletal muscles, intestine, brain, and bone marrow. The phanerozoites look like roundish or oval bodies about 15 to 20 μm in diameter and contained numerous (100 and even more) merozoites. The merozoites look roundish in smear preparations.

The prepatent period is usually 9 to 12 days after the infection with sporozoites, but was sometimes recorded to be as short as 5 days and even less. The prepatent period is usually about 11 days after blood-induced infection. Primary parasitemia is usually low. It rarely exceeds 10% of erythrocytes but, as a rule, is less than 1%. The parasitemia increases slowly

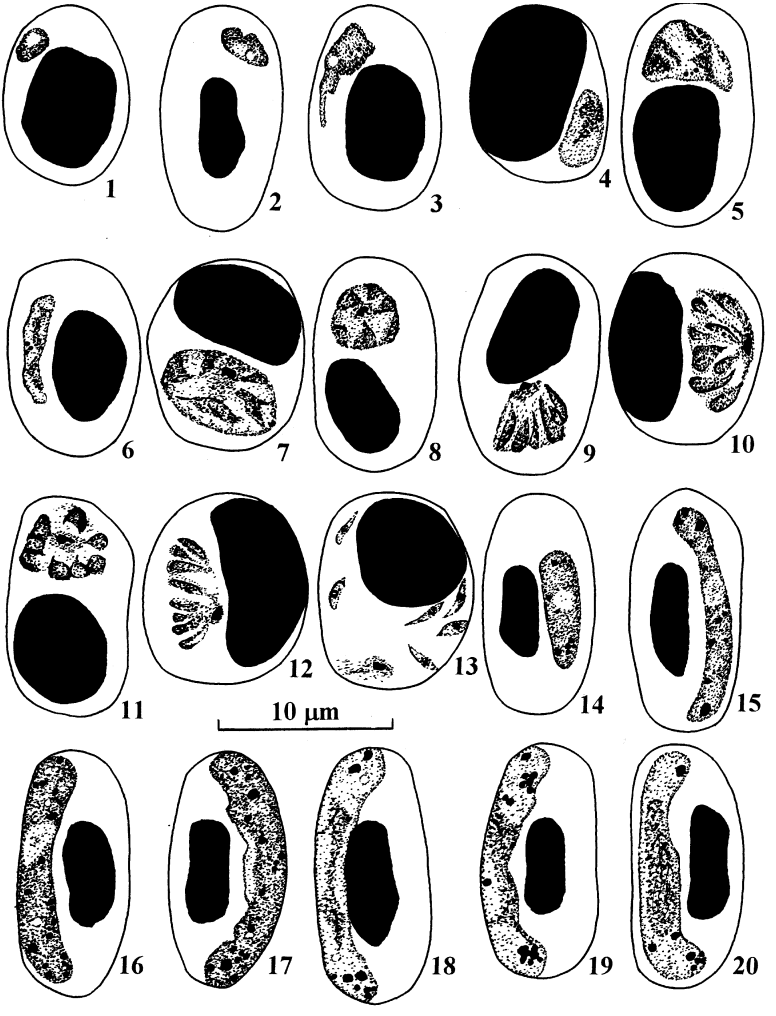

Figure 273 *Plasmodium elongatum* from the blood of *Serinus canaria:*
1–4 – trophozoites; *5–13* – erythrocytic meronts; *14–17* – macrogametocytes; *18–20* – microgametocytes.

(within one to three weeks) and then turns into a chronic stage which lasts for several months. Erythrocytic meronts are always rare in the peripheral blood, and gametocytes predominate. The majority of erythrocytic meronts concentrate in the haemopoietic organs.

Erythrocytic merogony is clearly synchronized. A cycle of merogony is equal to 24 h. The majority of meronts rupture in the morning. The number of gametocytes decreases as the number of blood passages increases, and the laboratory strains can finally lose the ability to produce gametocytes.

Trophozoites (Fig. 273, *1–4*) are seen in all types of erythrocytes but more frequently recorded in young erythrocytes including erythroblasts; earliest trophozoites are roundish or oval, frequently possess a vacuole; the 'ring' stage was seen occasionally; as the parasite develops, trophozoites take an irregular form, ameboid outgrowths appear and are now

usually seen in a polar or subpolar position in infected erythrocytes (Fig. 273, *3*); pigment appears only in the largest trophozoites that develop in advanced erythrocytes; one or two minute pigment granules were usually seen (Fig. 273, *2*, *3*); pigment was not seen in trophozoites that developed in erythroblasts (Fig. 273, *4*); the influence of parasites on infected erythrocytes is usually not pronounced.

Erythrocytic meronts (Fig. 273, *5–13*) are seen in all types of erythrocytes but are predominantly observed in young erythrocytes including erythroblasts; cytoplasm is basophilic, usually lacking vacuoles; nuclei more frequently gather on the periphery in growing meronts (Fig. 273, *5*, *7*, *8*); meronts are of variable form, but roundish and oval parasites are especially common; nuclei in fully grown meronts are more frequently arranged as fans (Fig. 273, *10*, *12*), sometimes as rosettes (Fig. 273, *11*); merozoites were sometimes also seen arranged in a row (Fig. 273, *12*); mature meronts contain 6 to 12 merozoites which are usually more or less elongated with pointed ends (Fig. 273, *13*); roundish merozoites were also seen (Fig. 273, *11*) and were more frequently recorded in unusual vertebrate hosts (for example, in penguins); a clump of pigment and a small-size diffuse residual body was seen in segmenters (Fig. 273, *13*); pigment granules are of small size, black, clumped into a spot and can be aggregated into a small solid mass; meronts deform erythrocytes and displace their nuclei; fully grown meronts usually do not exceed 7 μm in length.

Macrogametocytes (Fig. 273, *14–17*) are seen in mature erythrocytes; cytoplasm is homogeneous in appearance, sometimes contain a few small vacuoles; gametocytes are elongated and slender from the earliest stages of development; young gametocytes can be easily distinguished from trophozoites on the basis of their even outline and more numerous randomly scattered pigment granules (Fig. 273, *14*); fully grown gametocytes are elongated and slender, take a lateral position to the nuclei of infected erythrocytes and do not fill the poles of erythrocytes completely (Fig. 273, *16*, *17*); gametocytes are variable in outline, their ends are usually rounded; the parasite nucleus is compact, of variable form, median or submedian in position; pigment granules are roundish or oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm or clumped into several small groups; the number of pigment granules usually does not exceed 20; gametocytes only slightly influence infected erythrocytes which are hypertrophied in length and their nuclei can be slightly displaced laterally; fully grown gametocytes do not exceed 17 μm in length and 3 μm in width.

Microgametocytes (Fig. 273, *18–20*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules were more frequently seen in clumps than in macrogametocytes and can be aggregated into a solid mass; the outline is more variable than for macrogametocytes; other characters are as for macrogametocytes.

Development in vector

The mosquitoes *Culex pipiens* and *C. restuans* are natural vectors. Sporogony is also completed in *C. nigripalpus*, *C. salinarius*, *C. tarsalis*, and *C. territans*. The mosquitoes of the genera *Aedes* and *Anopheles* are refractive (Raffaele, 1934; Micks, 1949; Huff and Shiroishi, 1962; Beier and Trpis, 1981; Telford *et al.*, 1997). Exflagellation was not seen *in vitro* after exposure of blood with mature gametocytes to air. Furthermore, the exflagellation can be blocked in nonspecific mosquitoes. Sporozoites usually appear in the salivary glands of mosquitos eight to nine days after the ingestion of mature gametocytes at a temperature of 26°C and relative humidity 80 to 86%. However, some strains develop very slowly, and sporozoites were seen in the salivary glands not earlier than the 13th day

after infection. The size of maturing oocyst varies markedly (from 15 to 100 μm in diameter) but it is usually about 40 to 60 μm in diameter. Sporozoites look like slightly curved or straight elongated bodies with centrally located nuclei, one end rounded and the other end pointed. Sporozoites vary from 12 to 14 μm in length in preparations fixed with methanol.

Pathogenicity. Pathogenic parasite. *Plasmodium elongatum* causes lethal epizooties in penguins in zoos all over the world (Fleischman *et al.*, 1968; Herman *et al.*, 1968; Beier and Stoskopf, 1980; Beier and Trpis, 1981; Cranfield *et al.*, 1990; Graczyk *et al.*, 1994a). Wild free-living passerines are common reservoir hosts. The disease in the cape penguin *Spheniscus demersus* manifests itself suddenly and the birds die within several hours after that. Clinical signs of infection are nonspecific; they usually appear only before death. Typically, birds eating well began to look depressive and start vomiting; oxygen deficiency, breath difficulties, and paleness of mucous membranes are evident. Parasites can be not found in the blood, but the number of lymphocytes increases markedly which can be used for the diagnostics of the disease. The birds die mainly because of massive damage of the lungs by phanerozoites which are numerous here. At necropsy, marked subcutaneous, pulmonary and epicardial edema, hydropericardium, markedly enlarged liver and spleen, and marked lymphoreticular proliferation are obvious.

Experimentally infected canaries and young ducklings frequently die. The birds die because of severe anaemia due to massive destruction of stem haemopoietic cells in the bone marrow and other organs and thus resulting disruptions of the haemopoiesis. The level of hematocrit decreases markedly, but the number of parasites in the peripheral blood can be low. Birds, who survive the first two to three weeks of infection, usually recover. Reinfection is possible. The disease is not so severe in experimentally infected wild birds which usually survive, but mortality among them was also recorded. Peculiarities of the influence of this parasite on wild free-living birds in natural ecosystems has not been investigated.

Specificity. The range of natural vertebrate hosts is wide (see 'Additional vertebrate hosts'). The passerines are principal reservoir hosts. Canary and young ducklings are excellent experimental hosts. Older ducks are less susceptible. Goslings are also susceptible but develop light infection, and they do not die. Domestic chickens and turkey poults are refractive.

Comments. Identification of *P. elongatum* in naturally infected birds is usually difficult because of the absence or presence of only a few erythrocytic meronts in the peripheral blood. It should be also noted that elongated erythrocytic merozoites were rarely observed in penguins and some other unusual hosts. Additionally, the variability of the morphology of blood stages of this parasite requires further investigation.

Plasmodium elongatum is especially similar to *P. hermani*. Gametocytes of *P. elongatum* are slender and never fill the poles of infected erythrocytes completely. Additionally, *P. elongatum* develops in passerine birds which are its common vertebrate hosts. These features are not characteristic of *P. hermani.*

37. **Plasmodium (Huffia) huffi** Muniz, Soares and Batista, 1951

Plasmodium huffi Muniz, Soares and Batista, 1951: 342, Pl. 1–5 (partim).

Type vertebrate host. *Ramphastos toco* (Müller) (Piciformes).
Additional vertebrate hosts. Unknown.

Type locality. Brazil.

Distribution. *Plasmodium huffi* was isolated from a toucan *Ramphastos toco* in the Zoological Gardens of Rio de Janeiro. This bird was caught in the State of Goias in the interior Brazil. Subsequently, this parasite has never been found neither in toucans nor in other species of birds. It is likely that both the host range and the geographical range are strictly limited. In fact, such a stenoxenousity is a common phenomenon for the Neotropical faunae of plants and animals but still has not been investigated for the bird haemosporidian parasites.

Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 345, 346, *Ramphastos toco*, bone marrow, 18.04.1950, Zoological Gardens of Rio de Janeiro, J. Muniz; *blood stages*: No. 341–344, 9.02–23.03.1950, other data as for No. 345) are deposited in CPG. *Plasmodium* (*Novyella*) sp. is present in the type material.

Etymology. This species is named in honour of prominent American malariologist Professor Clay G. Huff in recognition of his contribution to the field of avian blood parasitology.

Main diagnostic characters. In the peripheral blood, trophozoites and erythrocytic meronts develop mainly in mature erythrocytes. Mature erythrocytic meronts contain numerous (up to 30) merozoites which are slightly oval or elongated. Fully grown gametocytes displace the nuclei of infected erythrocytes laterally (sometimes to the periphery of the host cells) and fill the poles of erythrocytes completely. The maximum width of fully grown gametocytes is greater than 3 μm. All tested passerine birds were resistant.

Development in vertebrate host was studied in naturally and experimentally infected toucans (Muniz *et al.*, 1951; Huff, 1953; Garnham, 1966). Primary exoerythrocytic merogony has not been investigated. Secondary exoerythrocytic merogony can be easily induced in toucans by subinoculation of infected blood. Phanerozoites were numerous in haemopoietic organs, first of all, in bone marrow and the spleen, both in naturally and experimentally infected birds. The parasites develop mainly in lymphoid cells but also in macrophages, myelocytes, thrombocytes, erythroblasts, and some other relative cells. Although some reticuloendothelial cells were seen to be parasitized (for example, macrophages), the fixed reticuloendothelial cells have been never recorded to be infected, and phanerozoites were not seen in the endothelial cells of capillaries in the brain or other organs. The parasites concentrate in haemopoietic tissues but sometimes can be also found in the peripheral blood. They look like roundish or oval bodies with prominent nuclei and basophilic cytoplasm which frequently contains small vacuoles (Fig. 274). Both the size of phanerozoites and the number of merozoites in the parasites vary markedly depending on the type of their host cells. The smallest-size phanerozoites, which contain up to 10 merozoites, were seen in thrombocytes (Fig. 274, *1*). The largest phanerozoites, which contained about 100 merozoites, were recorded in macrophages (Fig. 274, *7*). Phanerozoites markedly influence the nuclei of host cells which is a characteristic feature of the secondary exoerythrocytic merogony. The nuclei of infected cells are displaced, deformed, and can be even pushed out of the cells. As a result, some phanerozoites in the enucleated cells look to be extracellular which was especially frequently observed during heavy infections. Several parasites were frequently seen in the same host cell (Fig. 274, *5*).

Erythrocytic merogony is synchronized. A cycle of erythrocytic merogony is 48 h. A peak of the primary parasitemia is clearly pronounced. About 20% of erythrocytes can be parasitized at the top of the parasitemia. The parasitemia rapidly decreases in survived birds, and the infection then turns into a chronic stage.

Trophozoites (Fig. 275, *1*, *2*) are usually seen in mature erythrocytes, sometimes in polychromatic erythrocytes; the earliest trophozoites are roundish or oval, usually even in

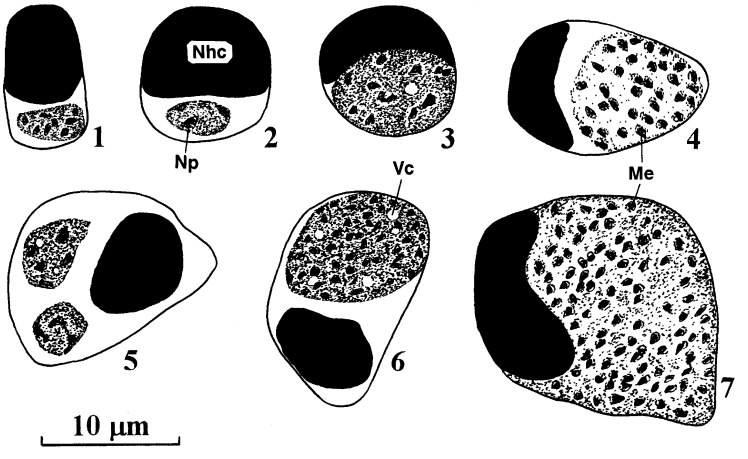

Figure 274 Phanerozoites of *Plasmodium huffi* from the bone marrow of *Ramphastos toco: 1–3*, *5* – young parasites; *4*, *6*, *7* – mature parasites; *1* – parasite in thrombocyte; *2–4* – parasites in lymphocytes; *5–7* – parasites in macrophages; Me – merozoite; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – vacuole.

outline; the 'ring' stage was frequently recorded (Fig. 275, *1*); as the parasite develops, trophozoites take an irregular form and more or less evident ameboid outgrowths appear, and parasites are now more frequently seen in a polar or subpolar position in infected erythrocytes (Fig. 275, *2*); the parasite nucleus is relatively small; fully grown trophozoites usually possess one, sometimes two minute-size light-brown pigment granules; the influence of trophozoites on infected erythrocytes is not pronounced.

Erythrocytic meronts (Fig. 275, *3–8*) are seen in mature erythrocytes; the cytoplasm is basophilic, plentiful, usually lacks vacuoles; fully grown meronts are of variable form, and roundish, oval, elongated, and irregular-shape parasites were seen; meronts are even in outline, possess randomly located nuclei; mature meronts contain numerous merozoites (usually 16 to 30), but the minimum number of merozoites is difficult to determine because of the presence of a mixed infection with *P.* (*Novyella*) sp. in the type material; it is likely that the minimum number of merozoites is about 12; pigment granules are of small size (<0.5 μm), brown, not numerous (less than 10), clumped into a spot in growing meronts (Fig. 275, *4*), and usually aggregated into a prominent solid mass in fully grown parasites (Fig. 275, *5–8*); meronts can be seen anywhere in infected erythrocytes, they usually more or less deform the erythrocytes and slightly displace their nuclei; fully grown meronts markedly vary in size depending on their position in the infected erythrocytes (Fig. 275, *5–8*); mature merozoites vary from slightly oval to slightly elongated (Fig. 275, *8*), possess a prominent nucleus and a portion of cytoplasm.

Macrogametocytes (Fig. 275, *9–11*) are seen in mature erythrocytes; vacuoles are uncommon; gametocytes are elongated and of variable outline from the earliest stages of their development; fully grown gametocytes take a lateral position to the nuclei of infected erythrocytes, slightly enclose the nuclei with their ends, displace them laterally, sometimes to the periphery of the host cells, fill the host cells up to their poles but do not encircle their nuclei completely (Fig. 275, *11*); the parasite nucleus is compact, of variable form, brightly stained, usually median in position; pigment granules are of small (<0.5 μm) and medium

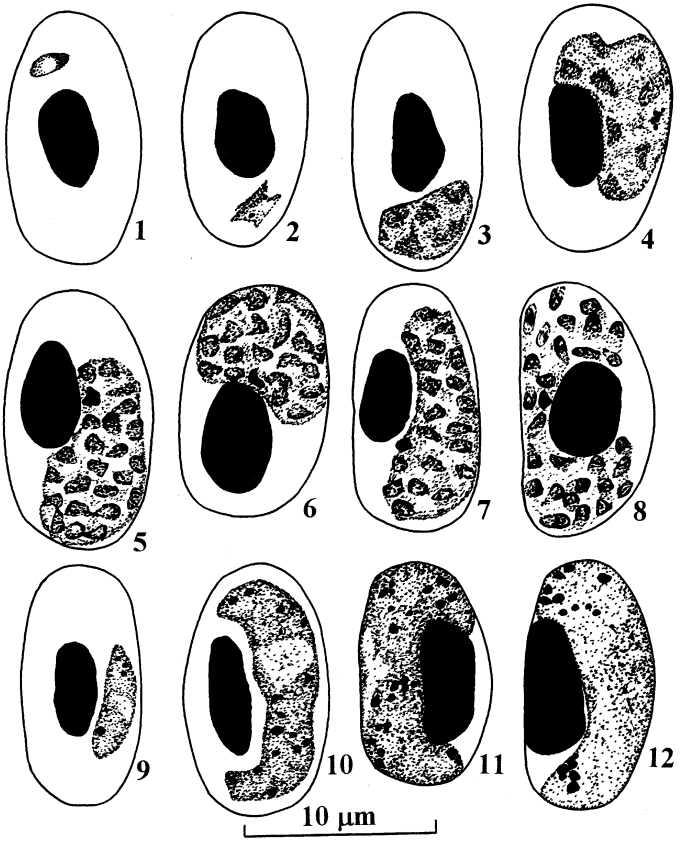

Figure 275 *Plasmodium huffi* from the blood of *Ramphastos toco:*
1, *2* – trophozoites; *3–8* – erythrocytic meronts; *9–11* – macrogametocytes; *12* – microgametocyte.

(0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm; the number of pigment granules (n = 17) varies from 11 to 28 (most frequently 18); fully grown gametocytes are about 15 μm in length and 4 μm in width.

Microgametocytes (Fig. 275, *12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; medium-size (0.5 to 1.0 μm) pigment granules are more frequently seen than in macrogametocytes; other characters are as for macrogametocytes.

P a t h o g e n i c i t y. Heavily infected toucans die.

S p e c i f i c i t y. The range of natural hosts has not been investigated. Attempts to infect canaries, the house sparrow *Passer domesticus*, domestic pigeons, domestic chickens, ducklings and turkey poults by subinoculation of infected blood were not successful. It is likely that *P. huffi* is a parasite with narrow specificity which is in general not characteristic of species of bird *Plasmodium*.

C o m m e n t s. The strain of *P. huffi*, isolated in Brazil in 1950, is lost. Since the original discovery, this parasite has never been found again. *Plasmodium huffi* can be distinguished from other species of the subgenus *Huffia*, first of all, on the basis of numerous merozoites in its erythrocytic meronts.

38. **Plasmodium (Huffia) hermani** Telford and Forrester, 1975

Plasmodium hermani Telford and Forrester, 1975: 326, Fig. 1–12.

Type vertebrate host. *Meleagris gallopavo* L. (Galliformes).
Additional vertebrate hosts. *Colinus virginianus* (Galliformes). The knot *Calidris canutus* (Charadriiformes) was infected experimentally.
Vectors. The mosquitoes *Culex nigripalpus* and *C. salinarius* are natural vectors, and *C. restuans* and *Wyeomyia vanduzeei* are experimental vectors (Diptera: Culicidae).
Type locality. Palmdale, Glade's Country, Florida, USA.
Distribution. This parasite has been recorded in Florida, USA.
Type material. Hapantotypes (*exoerythrocytic meronts*: No. 312, *Meleagris gallopavo*, bone marrow; *blood stages*: No. 306, 311, *M. gallopavo*, 29.12.1972, Palmdale, Florida, D.J. Forrester) and parahapantotypes (No. 307, 308, duplicates of No. 306) are deposited in CPG. Part of parahapantotypes is deposited in IRCAH, and also in the collections of the authors of the specific name.
Etymology. This species is named in honour of Dr. Carlton M. Herman in recognition of his contribution to the field of avian blood parasitology.

Main diagnostic characters. In the peripheral blood, asexual stages develop mainly in young erythrocytes but gametocytes develop mainly in mature erythrocytes. Mature erythrocytic meronts contain 6 to 14 merozoites which are roundish or slightly oval. Fully grown gametocytes markedly displace the nuclei of infected erythrocytes laterally, frequently to the periphery of the host cells, and they can fill the poles of erythrocytes completely. The maximum width of fully grown gametocytes is greater than 3 μm. Passerine birds are usually refractive.

Development in vertebrate host was studied by Telford and Forrester (1975), Forrester and Humphrey (1981), Nayar *et al.* (1982), and Forrester *et al.* (1987). Primary exoerythrocytic meronts were not found. Phanerozoites develop in bone marrow in cells-precursors of erythrocytes and in the erythroblasts. They were frequently observed to lie extracellularly in bone marrow at heavy infections. Phanerozoites were also sometimes recorded in lymphocytes in the peripheral blood. They have never been found in endothelial cells of capillaries in the brain and other organs.

The prepatent period is about 9 to 20 (usually 10 to 12) days after infection with sporozoites. Intensity of primary parasitemia usually does not exceed 6% of erythrocytes. The ability of the parasite to produce gametocytes gradually decreases as the number of blood passages increases.

Trophozoites (Fig. 276, *1*, *2*) are seen in young erythrocytes, including erythroblasts; earliest trophozoites are roundish, each possesses a large nucleus and a small portion of cytoplasm (Fig. 276, *1*); as the parasite develops, trophozoites elongate and cytoplasm increases in amount; the outline is even; vacuoles and pigment granules are not seen; large trophozoites can markedly displace the nuclei of infected erythrocytes (Fig. 276, *2*) which is especially common during infection of the same host cell with several parasites.

Erythrocytic meronts (Fig. 276, *3–10*) are usually seen in young erythrocytes but sometimes also in nearly mature erythrocytes; cytoplasm is pale stained, does not contain vacuoles; meronts are roundish or oval in form and even in outline; nuclei are more

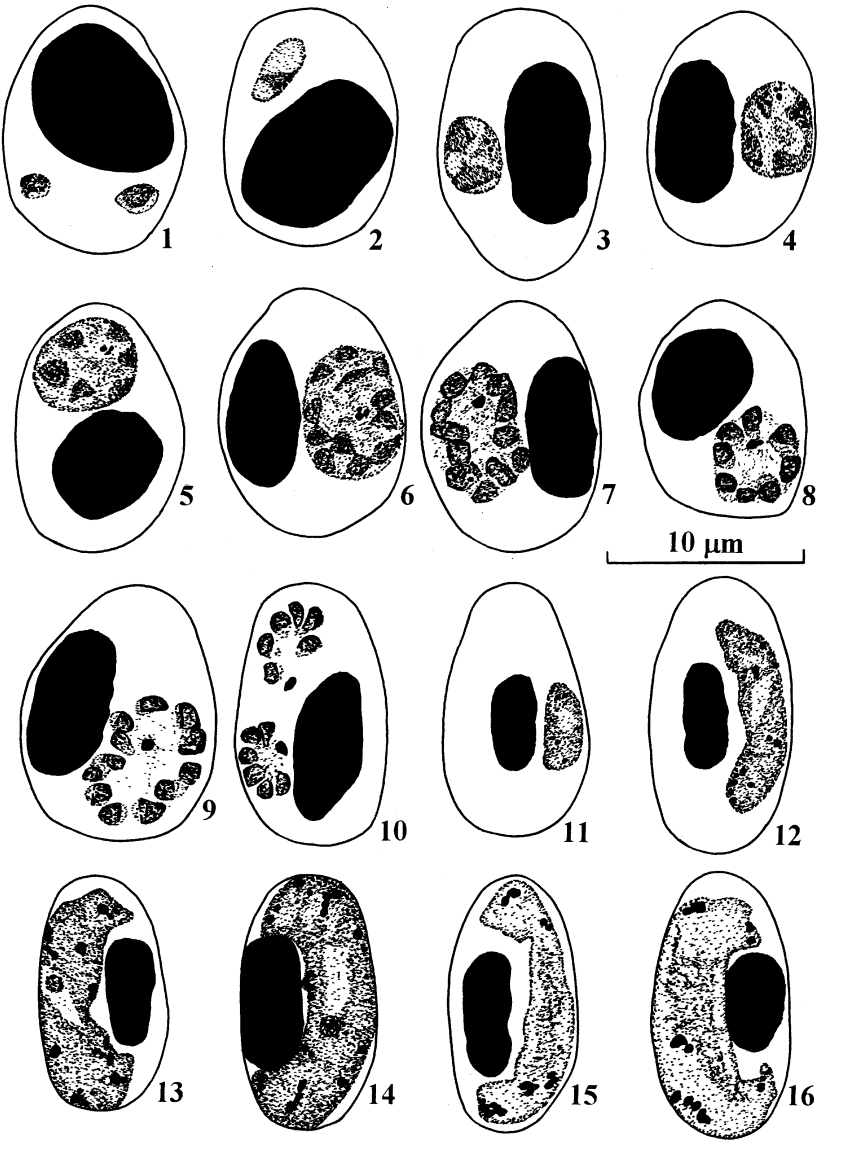

Figure 276 *Plasmodium hermani* from the blood of *Meleagris gallopavo:*
1, *2* – trophozoites; *3–10* – erythrocytic meronts; *11–14* – macrogametocytes; *15*, *16* – microgametocytes.

frequently seen to be located on the periphery of growing meronts and are usually arranged as rosettes (Fig. 276, *8*) or sometimes as fans (Fig. 276, *10*) in fully grown parasites; mature meronts contain 6 to 14 (more frequently 8 to 12) merozoites; pigment appears in young meronts as several minute-size golden-colour granules (Fig. 276, *3–5*); the quantity of pigment in meronts directly depends on the age of infected erythrocytes, and the pigment can be absent in parasites which invade erythroblasts; pigment granules were usually seen to be aggregated into a small golden-brown mass in fully grown parasites (Fig. 276, *8–10*);

meronts can be seen anywhere in infected erythrocytes, they displace their nuclei and can markedly deform the host cells which were sometimes seen to be rounded up (Fig. 276, *8*); fully grown meronts ($n = 51$) vary from 4 to 7 μm in length and from 4 to 7 μm in width; each mature merozoite possesses a prominent nucleus and a portion of cytoplasm.

Macrogametocytes (Fig. 276, *11–14*) are seen in mature erythrocytes; the cytoplasm is basophilic, homogeneous in appearance, usually lacking vacuoles; gametocytes are elongated from the earliest stages of their development (Fig. 276, *11*), usually take a lateral position to the nuclei of infected erythrocytes; the outline is variable, frequently irregular and even ameboid; the parasite nucleus is compact with a well evident nucleolus (Fig. 276, *13, 14*), median or submedian in position; pigment granules are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm, vary from 7 to 30 (more frequently about 15), are usually of golden colour in young gametocytes and dark in mature parasites; infected erythrocytes are usually not deformed but their nuclei are displaced laterally, sometimes to the periphery of the host cells (Fig. 276, *14*); fully grown gametocytes ($n = 25$) vary from 9 to 12 μm in length and from 2 to 4 μm in width.

Microgametocytes (Fig. 276, *15*, *16*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; pigment granules were frequently seen to be clumped into small groups; other characters are as for macrogametocytes.

Development in vector has not been described in detail. The mosquitoes *Culex salinarius* and *C. nigripalpus* are natural vectors, and *C. restuans* and *Wyeomyia vanduzeei* are experimental vectors (Nayar *et al.*, 1982; Nayar and Forrester, 1985). Sporogony is not completed in mosquitoes of the genera *Aedes*, *Mansonia*, and *Anopheles*.

Pathogenicity. Mortality was not recorded among experimentally infected birds.

Specificity. In nature, this parasite has been found in wild turkeys and bobwhites *Colinus virginianus*. The knot *Calidris canutus* was easily infected by subinoculation of infected blood. Goslings of *Anser anser* and canaries can be infected with difficulty but only a transient parasitemia develops. The tested wild passerine birds (*Taeniopygia guttata* and some others) were refractive.

Comments. *Plasmodium hermani* is especially similar to *P. elongatum*. It can be distinguished from the latter species, first of all, on the basis of (i) its much less elongated form of erythrocytic merozoites, (ii) numerous rosette-like erythrocytic meronts, and (iii) thick fully grown gametocytes which frequently markedly displace the nuclei of infected erythrocytes laterally. It should also be noted that *P. hermani* does not develop or poorly develops in passerine birds which are main vertebrate hosts of *P. elongatum*.

Blood stages of *P. hermani* are similar to *P. durae* which also parasitize turkeys. *Plasmodium hermani* can be distinguished from the latter species, first of all, on the basis of (i) the clearly evident preference of its asexual blood stages to develop in young erythrocytes, (ii) the absence of phanerozoites in cells of the reticuloendothelial system, and (iii) its low virulence for turkeys. In addition, fully grown gametocytes of *P. durae* (i) tend to lie obliquely in infected erythrocytes, (ii) displace the nuclei toward one pole of the erythrocytes and (iii) possess one or several clear clumps of pigment granules. These features are not characteristic of *P. hermani.*

III. Family **GARNIIDAE** Lainson, Landau and Shaw, 1971

Type genus. *Garnia* Lainson, Landau and Shaw, 1971. Parasites of reptiles.

Merogony takes place in cells of fixed tissues and blood cells of vertebrate hosts. Malarial pigment (hemozoin) is absent at all stages. Vectors are still unknown.

A representative of the genus *Fallisia* parasitize birds.

1. Genus **FALLISIA** Lainson, Landau and Shaw, 1974

Fallisia Lainson, Landau and Shaw, 1974: 122.

Type species. *Fallisia effusa* Lainson, Landau and Shaw, 1974: 123, according to the original designation. The parasite of reptiles.
Etymology. This genus is named in honour of Professor A. Murray Fallis, in recognition of his contribution to the field of avian blood parasitology.

Characteristics of the family. Merogony in the peripheral blood and the development of gametocytes take place in thrombocytes and leukocytes. Parasites do not develop in cells of the erythrocytic series.

A representative of the subgenus *Plasmodioides* parasitize birds.

1. Subgenus **PLASMODIOIDES** Gabaldon, Ulloa and Zerpa, 1985

Plasmodioides Gabaldon, Ulloa and Zerpa, 1985: 224.

Type species. *Fallisia neotropicalis* Gabaldon, Ulloa and Zerpa, 1985, according to monotypy.
Etymology. The subgeneric name reflects the similarity of the parasites to species of *Plasmodium*.

Characteristics of the genus. Parasites of birds.

One species parasitize birds, *F.* (*P.*) *neotropicalis*.

1. **Fallisia (Plasmodioides) neotropicalis** Gabaldon, Ulloa and Zerpa, 1985

Fallisia neotropicalis Gabaldon, Ulloa and Zerpa, 1985: 224, Fig. 1, a–i′; Fig. 2, a–x.

Type vertebrate host. *Columba livia* Gmelin (Columbiformes).
Additional vertebrate hosts. Some species of birds of the order Ciconiiformes (Table 144).

Table 144 List of vertebrate hosts of *Fallisia neotropicalis* (modified from Gabaldon *et al.*, 1985).

Ajaia ajaja	*Egretta alba*	*Mesembrinibis cayennensis*
Ardea cocoi	*E. thula*	*Nycticorax nycticorax*
A. herodias	*Eudocimus ruber*	*Pilherodius pileatus*
Botaurus pinnatus	*Euxenura maguari*	*Tigrisoma lineatum*
Bubulcus ibis	*Ixobrychus exilis*	

Type locality. El Saman, Villa Bruzual, Portuguesa, Llanos region, Venezuela. Not far from Camaguan, Guarico (220 km) and Mantecal, Apure (200 km).
Distribution. This parasite has been recorded only from the type locality.
Type material. Hapantotype and part of parahapantotypes are deposited in CDGA. Parahapantotype (No. 1025, *Columba livia*, the date is not noted, Venezuela, A. Gabaldon) is deposited in CPG. Part of parahapantotypes is deposited in IRCAH.
Etymology. The specific name is derived from the name of the Neotropical zoogeographical region where this unique bird parasite was discovered.

Main diagnostic characters. A parasite of birds whose blood stages develop mainly in thrombocytes and less frequently in lymphocytes and monocytes. Meronts in blood cells are roundish, sometimes oval or crescent-shaped. Gametocytes are markedly variable in form. Mature meronts in the blood contain 9 to 43 merozoites.

Development in vertebrate host

Merogony in internal organs was easily induced in nestlings of *Columba livia* by subinoculation of the blood with mature meronts (Gabaldon *et al.*, 1985). From this point of view, *F. neotropicalis* is similar to species of the bird *Plasmodium*. Phanerozoites are especially numerous in heavily infected nestlings which died up to the age of one month. They were observed in smears of the brain, heart, lungs, liver, spleen, kidneys, and bone marrow. The host cells in the different organs are mostly reticular cells and histiocytes of the connective tissue. In the brain, phanerozoites develop in endothelial cells of capillaries. They are of an elongated worm-like form. In other organs, phanerozoites are usually roundish or oval, and were only occasionally seen to be slightly elongated. The roundish-shape host cells are about 15 μm in diameter and possess large nuclei. Multiple infection of the same cell with several parasites (up to ten) was frequently observed. During the multiple infection, the nucleus of the host cell becomes lobular or stellate and its branches separate the parasites which lie in the indentations of the nucleus. Growing phanerozoites possess large nuclei, and several clear vacuoles are frequently seen in the cytoplasm. Mature phanerozoites usually contain more than 100 merozoites. Elongated phanerozoites are similar to those described in bird *Plasmodium* spp. During heavy infections, which lead to death of infected birds, phanerozoites can escape to the peripheral blood. They can be easily distinguished from meronts, which develop in blood cells, on the basis of the larger size of their nuclei and the prominent vacuoles which are frequently present in their cytoplasm.

In the peripheral blood, trophozoites, meronts, and gametocytes develop mainly in thrombocytes and less frequently in lymphocytes and monocytes. Occasionally, the earliest parasites were also recorded in granulocytes and reticulocytes. However, mature parasites are not seen in the two latter types of cells.

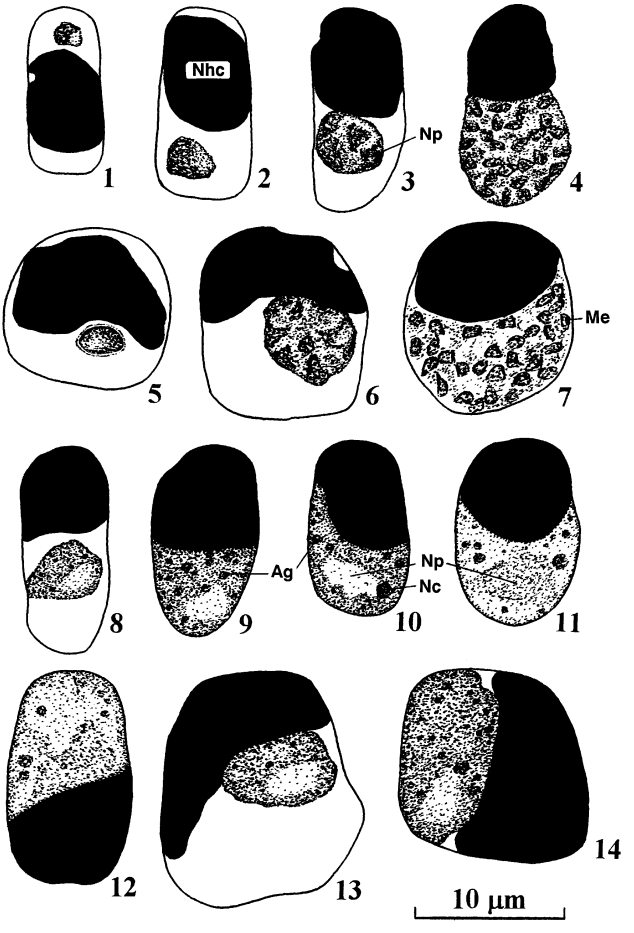

Figure 277 *Fallisia neotropicalis* from the blood of *Columba livia:*
1, *2*, *5* – trophozoites; *3*, *4*, *6*, *7* – meronts in the blood cells; *8–10*, *13*, *14* – macrogametocytes; *11*, *12* – microgametocytes; *1–4*, *8–11* – parasites in thrombocytes; *5–7*, *12–14* – parasites in mononuclear leukocytes; Ag – azurophilic granule; Me – merozoite; Nc – nucleolus; Nhc – nucleus of host cell; Np – nucleus of parasite.

Trophozoites (Fig. 277, *1*, *2*, *5*) are of variable form and even in outline; the cytoplasm is basophilic; the parasite nucleus is prominent; when in thrombocytes, trophozoites usually take a polar position in the infected cells (Fig. 277, *1*, *2*), markedly displace the nuclei of thrombocytes and slightly hypertrophy the host cells as the parasite develops (Fig. 277, *2*); when in mononuclear leucocytes, trophozoites usually lie in a more or less evident 'indentation' of the nucleus of the host cell and are surrounded by a clear light band of the cytoplasm of the host cell (Fig. 277, *5*); fully grown trophozoites markedly displace the nuclei of infected mononuclear leucocytes.

Meronts in blood cells (Fig. 277, *3*, *4*, *6*, *7*) are of variable form and even outline; the cytoplasm is basophilic and plentiful; the nuclei are prominent; as the parasite matures, meronts round up; fully grown nondeformed meronts are usually roundish, sometimes oval or crescent-shaped, contain randomly located nuclei (Fig. 277, *4*, *7*); when in

mononuclear leucocytes, growing parasites frequently lie in an indentation of the nucleus of the cell (Fig. 277, *6*) which is not characteristic of parasites developing in thrombocytes (Fig. 277, *3*); mature meronts usually contain 9 to 23 merozoites, but up to 43 merozoites were occasionally seen in some ruptured meronts; parasites markedly influence infected host cells which are hypertrophied; meronts can occupy all or nearly all available cytoplasmic space in the host cells, they deform their nuclei and displace them usually to the periphery of the cells (Fig. 277, *4*, *7*); fully grown meronts are about 5.7 to 7.7 μm in length and 5.7 to 6.4 μm in width.

Macrogametocytes (Fig. 277, *8–10*, *13*, *14*). The cytoplasm is basophilic, homogeneous in appearance, possesses prominent azurophilic granules which, according to cytochemistry tests (Gabaldon *et al.*, 1985), does not contain valutin; vacuoles are usually absent; gametocytes markedly vary in form depending both on their host cells and their position in the host cells (Fig. 277, *9*, *10*, *14*); the parasite nucleus is compact, variable both in form and position; the prominent nucleolus is usually well seen; gametocytes influence infected cells in the same way as meronts; during infection of the same cell with several gametocytes, the host cells are markedly deformed and can be odd-shaped; fully grown gametocytes vary from 5.5 to 12.7 (on average 8.6±0.4) μm in length and from 5.5 to 7.8 (on average 5.5±0.1) μm in width.

Microgametocytes (Fig. 277, *11*, *12*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

A peak of primary parasitemia is recorded in pigeon nestlings between the second and third weeks after the blood-induced infection (Gabaldon *et al.*, 1985). At the top of parasitemia, more than 50% of thrombocytes can be parasitized, but only about 12% mononuclear leukocytes and 2% of granulocytes were seen to be infected. Granulocytes can probably phagocytize the parasites.

D e v e l o p m e n t i n v e c t o r has not been investigated. There are some indirect data that *Aedeomyia squamipennis* (Diptera: Culicidae) can be a vector (Gabaldon *et al.*, 1985). This hypothesis should be tested. Ookinetes developed in the midgut of experimentally infected mosquito *Anopheles albimanus*. They were observed in smears of the midgut prepared 10 and 16 h after biting an infected pigeon. Ookinetes are similar to those of species of *Plasmodium.* They are worm-like bodies with a prominent nucleus and azurophilic granules. Ookinetes vary from 11.3 to 14.9 μm in length and from 2.8 to 3.2 μm in width.

P a t h o g e n i c i t y has been insufficiently investigated. Heavily infected nestlings of domestic pigeon can die. Four birds of 46 experimentally infected nestlings up to the age of one month died (Gabaldon *et al.*, 1985).

S p e c i f i c i t y. This parasite has a wide range of vertebrate hosts (Table 144) and can infect (at least) representatives of the orders Columbiformes and Ciconiiformes (see also ‘Comments’).

C o m m e n t s. *Fallisia neotropicalis* is a common parasite of ciconiiform birds in the type locality. The prevalence of infection is especially high in nestlings. The type vertebrate host of this parasite (domestic pigeon *Columba livia*) was introduced into the Neotropical region. It is likely that the pigeon acquired the infection secondary from the ciconiiform birds, because the representatives of the genus *Fallisia* are absent in birds in other zoogeographical regions.

It should be noted that parasites similar to *F. neotropicalis* were also found in nestlings of *Polyborus plancus* (Falconiformes) and *Anhinga anhinga* (Pelecaniformes) in Venezuela, but they have

not been identified to the species level so far. However, it is clear that the range of vertebrate hosts of *Fallisia* spp., parasitizing birds, involves representatives of at least several bird orders.

IV. Family **LEUCOCYTOZOIDAE** Fallis and Bennett, 1961

Type genus. *Leucocytozoon* Berestneff, 1904.

Merogony takes place in cells of fixed tissues of vertebrate hosts. No merogony occurs in blood cells. Malarial pigment (hemozoin) is absent at all stages. Sexual process and sporogony take place in simuliid flies (Diptera: Simuliidae) and biting midges (Ceratopogonidae).

Representatives of the genus *Leucocytozoon* parasitize birds.

1. Genus **Leucocytozoon** Berestneff, 1904

Haemamoeba Grassi and Feletti, 1890b: 6 (partim). – *Leucocytozoon* Berestneff, 1904: 376. – *Leucocytozoon*: Sambon: 1908: 246 (=*Haemamoeba*, partim). – *Legerozoon* Mello, 1937: 1440 (footnote). – *Akiba* Bennett, Garnham and Fallis, 1965: 929. – *Leucocytozoon*: Garnham, 1966: 964 (=*Legerozoon*). – *Leucocytozoon*: Hsu *et al.*, 1973: 195 (=*Akiba*).

Type species. *Leucocytozoon danilewskyi* (Ziemann, 1898), according to monotypy.
Etymology. The generic name reflects the ability of some species to develop in leukocytes.

Characteristics of the family. Gametocytes develop in cells of erythrocytic and (or) leukocytic series.

Representatives of two subgenera, *Leucocytozoon* and *Akiba,* parasitize birds.

Comments. After Garnham (1966) and Hsu *et al.* (1973), the authorship of the genus *Leucocytozoon* is attributed to Berestneff (1904) who was the first to publish the binomen *Leucocytozoon danilewskyi* accompanied with illustrations. The problem of the author of the genus *Leucocytozoon* and the type species of this genus was discussed by Valkiūnas (1997, 1999). The International Commission on Zoological Nomenclature was applied to adopt Berestneff (1904) as the author and *Leucocytozoon danilewskyi* as the type species of the genus *Leucocytozoon* (see Valkiūnas, 1999). The positive ruling of the Commission has been received on this issue (see International Commission on Zoological Nomenclature, 2001).

KEY TO THE SUBGENERA

1 (2). Range of vertebrate hosts includes representatives of numerous (no less than 18) orders of birds, including the domestic chicken *Gallus gallus*. Meronts of the first generation develop in hepatocytes. Merozoites of the first generation are roundish or oval; they are less than 3 μm in length. Host cells of gametocytes are roundish and (or) fusiform. Sporogony takes place in simuliid flies (Simuliidae). One end of sporozoites is rounded and the other end is pointed.

. . . . . 1. ***Leucocytozoon***

2 (1). Specific parasite of *Gallus gallus*. Meronts of the first generation do not develop in hepatocytes. Merozoites of the first generation are elongated; they are greater than 3 μm in length. Host cells of gametocytes are roundish. Sporogony takes place in biting midges (Ceratopogonidae). Both ends of sporozoites are pointed.

. . . . . 2. ***Akiba***

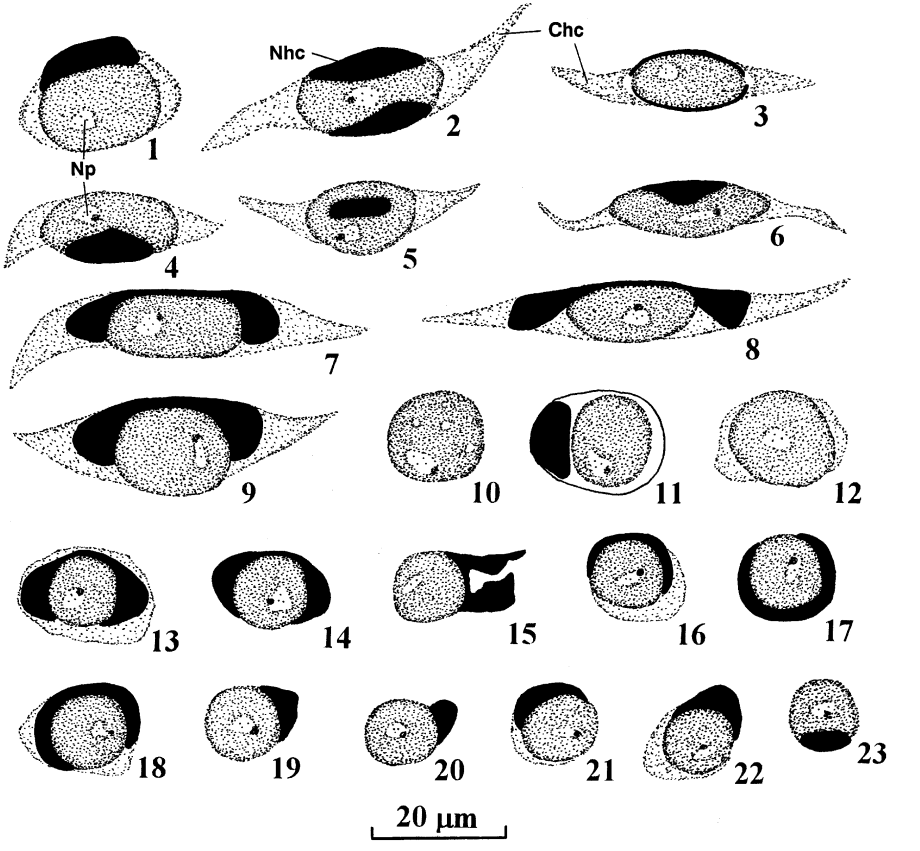

Figure 278 Main morphological peculiarities of the structure of *Leucocytozoon* spp. gametocytes and their host cells, which are used for identification of the species:
Chc – cytoplasm of host cell; Nhc – nucleus of host cell; Np – nucleus of parasite. Explanations are given in the text.

1. Subgenus **LEUCOCYTOZOON** Berestneff, 1904

Leucocytozoon Berestneff, 1904: 376 (pro gen.).

Type species. *Leucocytozoon danilewskyi* (Ziemann, 1898), according to monotypy.

The first generation of exoerythrocytic meronts develops in liver cells (hepatocytes). Merozoites of the first generation are roundish or oval; they are less than 3 μm in length. Meronts of the second generation develop intracellularly. The prepatent period is usually less than ten days after infection with sporozoites (there are several exceptions which need to be tested). Gametocytes develop in cells of erythrocytic series and (or) in mononuclear leukocytes; infected cells are roundish and (or) fusiform. Sporogony takes place in simuliid flies (Diptera: Simuliidae). One end of sporozoites is rounded and the other end is pointed.

KEY TO THE SPECIES[†]

1 (12). Gametocytes in fusiform host cells (Fig. 278, *1–9*) are present.

2 (11). Gametocytes in fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width (Fig. 278, *2–9*), are present.

3 (6). Fusiform host cells, whose nucleus is split into two portions (Fig. 278, *2*) or is uniformly dispersed as a narrow (0.5 to 1.0 μm) band around the circumference of the parasite (Fig. 278, *3*), are present.

4 (5). Nucleus of fusiform host cell is not dispersed along the circumference of the gametocyte; the nucleus is usually split into two more or less symmetrical portions (Fig. 278, *2*).
. . . . . 3. ***L. smithi***

5 (4). Nucleus of fusiform host cell is never split into two more or less symmetrical portions; the nucleus is uniformly dispersed as a narrow (0.5 to 1.0 μm) band around all or nearly all of the circumference of the gametocyte (Fig. 278, *3*).
. . . . . 26. ***L. maccluri***

6 (3). Fusiform host cells, whose nucleus is split into two portions (Fig. 278, *2*) or is uniformly dispersed as a narrow (0.5 to 1.0 μm) band around the circumference of the parasite (Fig. 278, *3*), are absent.

7 (10). Fusiform host cells, whose nuclei extend less than 1/3 of the circumference of gametocytes (Fig. 278, *4–6*), are absent.

8 (9). Nucleus of fusiform host cell looks like a more or less dumbbell-shaped band with clear thickenings at both ends which are closely appressed to the gametocyte (Fig. 278, *7*, *9*).
. . . . . **Group *danilewskyi***
A parasite of the Caprimulgiformes. . . . . 17. ***L. caprimulgi***
A parasite of the Strigiformes. . . . . 1. ***L. danilewskyi***

9 (8). Nucleus of fusiform host cell looks like a more or less dumbbell-shaped band with clear thickenings on both ends which do not adhere to the gametocyte (Fig. 278, *8*).
. . . . . 12. ***L. simondi***

10 (7). Fusiform host cells, whose nuclei extend less than 1/3 of the circumference of the gametocytes (Fig. 278, *4–6*), are present.
. . . . . **Group *neavei***
A parasite of the Charadriiformes. . . . . 23. ***L. sousadiasi***
A parasite of the Coraciiformes, including the Upupidae 18. ***L. eurystomi***
A parasite of the Falconiformes. . . . . 9. ***L. toddi***
A parasite of the Galliformes, excluding the Numididae, Tetraonidae and *Tetraogallus* 7. ***L. macleani***
A parasite of the Galliformes (only the Numididae). . . . . 4. ***L. neavei***
A parasite of the Galliformes (only the Tetraonidae). . . . . 5. ***L. lovati***
A parasite of the Galliformes (only the *Tetraogallus*) . . . . . 24. ***L. cheissini***
A parasite of the Gruiformes . . . . . 25. ***L. grusi***
A parasite of the Passeriformes . . . . . 29. ***L. balmorali***

11 (2). Gametocytes in fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width (Fig. 278, *2–9*), are absent. Length of the spindle-shaped cytoplasmic processes is less than their width (Fig. 278, *1*).
. . . . . 28. ***L. nycticoraxi***

12 (1). Gametocytes in fusiform host cells (Fig. 278, *1–9*) are absent. Gametocytes develop in roundish host cells (Fig. 278, *10–23*).

13 (20). Gametocytes, which enucleate host cells (Fig. 278, *10*), are absent.

[†] See also Appendix 2 for *Leucocytozoon hamiltoni*.

14 (17). Roundish host cells, whose nucleus is more or less dumbbell-shaped with thickenings at both ends (Fig. 278, *13, 14*) or is of a markedly irregular form (can be distorted into filaments) (Fig. 278, *15*), are absent.

15 (16). Roundish host cells, whose nuclei extend more than 1/2 of the circumference of the gametocytes (Fig. 278, *16–18*), are present.

. . . . .	**Group *majoris***
A parasite of the Ciconiiformes	14. ***L. leboeufi***
A parasite of the Coraciiformes, including the Upupidae	30. ***L. nyctyornis***
A parasite of the Galliformes	19. ***L. schoutedeni***
A parasite of the Passeriformes, excluding the Corvidae.	2. ***L. majoris***
A parasite of the Passeriformes (only the Corvidae, excluding the genera *Pica* and *Cyanocitta*)	8. ***L. sakharoffi***
A parasite of the Passeriformes (only the genera *Pica* and *Cyanocitta*)	6. ***L. berestneffi***
A parasite of the Piciformes	31. ***L. squamatus***

16 (15). Roundish host cells, whose nuclei extend more than 1/2 of the circumference of gametocytes (Fig. 278, *16–18*), are absent. Nucleus of host cell usually extends less than 1/2 of the circumference of gametocyte (Fig. 278, *19–23*) or sometimes up to 1/2 of the circumference of the gametocyte.

. . . . .	**Group *fringillinarum***
A parasite of the Caprimulgiformes	17. ***L. caprimulgi***
A parasite of the Charadriiformes	15. ***L. legeri***
A parasite of the Coliiformes	34. ***L. colius***
A parasite of the Columbiformes.	11. ***L. marchouxi***
A parasite of the Coraciiformes, including the Upupidae	32. ***L. communis***
A parasite of the Cuculiformes	20. ***L. centropi***
A parasite of the Musophagiformes	22. ***L. dizini***
A parasite of the Passeriformes, excluding the Corvidae.	10. ***L. fringillinarum***
A parasite of the Sphenisciformes.	27. ***L. tawaki***
A parasite of the Struthioniformes	16. ***L. struthionis***

17 (14). Roundish host cells, whose nuclei are more or less dumbbell-shaped with thickenings at both ends (Fig. 278, *13, 14*) or is of a markedly irregular form (can be distorted into filaments) (Fig. 278, *15*), are present.

18 (19). Nucleus of roundish host cell is more or less dumbbell-shaped with thickenings at both ends; the nucleus extends more than 1/2 of the circumference of the gametocyte (Fig. 278, *13–14*).

. . . . .	13. ***L. dubreuili***

19 (18). Nucleus of roundish host cell is of an irregular form (can be distorted into filaments); the nucleus extends up to 1/2 and less of the circumference of the gametocyte (Fig. 278, *15*).

. . . . .	21. ***L. vandenbrandeni***

20 (13). Gametocytes, which enucleate host cells (Fig. 278, *10*), are present.

. . . . .	33. ***L. bennetti***

Note: Gametocytes in the fusiform host cells in *L. caprimulgi* have been extremely rarely recorded, and gametocytes in roundish host cells predominate. To facilitate the identification of this species, *L. caprimulgi* is mentioned in the key twice.

1. **Leucocytozoon (Leucocytozoon) danilewskyi** (Ziemann, 1898)

Leukocytozoen danilewskyi Ziemann, 1898: 128, Pl. 3, Fig. 29–33. – *Haemamoeba ziemanni* Laveran, 1902: 1124, Fig. 8–10. – *Leucocytozoon danilewskyi*: Berestneff, 1904: 376, Fig. 1–3 (partim). – *Spirochaete ziemanni*: Schaudinn, 1904: 387 (partim). – *Plasmodium ziemanni*: Blanchard, 1905 according to: Sambon, 1908: 325 (partim). – *Leucocytozoon ziemanni*: Lühe, 1906: 171, Fig. 38. – *L. danilewskyi*: Sambon, 1908: 325 (=*Leucocytozoon ziemanni*, *Spirochaete ziemanni*, *Plasmodium ziemanni*). – *L. lutzi* Carini, 1920: 508. – *L. ziemanni* var. *bubonis* Fantham, 1926: 565. – *L. ziemanni* var. *nebraskensis* Coatney and Roudabush, 1937: 1016, Pl. 2, Fig. 3, 4. – *L. bubonis*: Glushchenko, 1963: 6 (emend. pro var. *bubonis*). – *L. danilewskyi*: Hsu *et al.*, 1973: 195 (=*L. ziemanni* var. *bubonis*, *L. ziemanni* var. *nebraskensis*); Fallis *et al.*, 1974: 12 (=*L. lutzi*); Bennett *et al.*, 1975c: 27 (*nomen nudum*); Bennett *et al.*, 1982b: 217 (valid); Valkiūnas, 1988b: 124 (=*L. bubonis*).

Type vertebrate host. *Athene noctua* (Scopoli) (Strigiformes).
Additional vertebrate hosts. Numerous species of the Strigiformes (Table 145).
Vectors. *Simulium aureum*, *S. latipes*, *Prosimulium decemarticulatum* (Diptera: Simuliidae).
Type locality. Crema, the Northern Italy.
Distribution. This parasite has been found in owls in all zoogeographical regions, except the Antarctic. It is common in the Holarctic, and is less frequently recorded in the Ethiopian and Oriental regions. A few records are known in the Neotropical and Australian regions.
Type material. Neohapantotype (No. 92604, *Athene noctua,* 13.10.1977, Woking, Surrey, UK, M.A. Peirce) is deposited in IRCAH. Paraneohapantotypes designated by Bennett *et al.* (1993a) do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985) because they came from nontype vertebrate hosts investigated far beyond the type locality.
Etymology. This species is named in honour of Russian parasitologist and physiologist Professor V.Ya. Danilewsky, who discovered bird haemosporidian parasites and created a basis for the comparative parasitology of blood.

Table 145 List of vertebrate hosts of *Leucocytozoon danilewskyi* (modified from Valkiūnas, 1988b).

Aegolius acadicus	*B. virginianus*	*Strix aluco*
A. funereus	*Ciccaba woodfordii*	*S. occidentalis*
Asio flammeus	*Glaucidium brasilianum*	*S. uralensis*
A. otus	*G. cuculoides*	*S. varia*
Bubo africanus	*Ninox novaeseelandiae*	*Surnia ulula*
B. bubo	*Otus asio*	
B. capensis	*O. scops*	

Main diagnostic characters. A parasite of species of the Strigiformes whose gametocytes develop in roundish and fusiform host cells. Nucleus of fusiform host cells is more or less dumbbell-shaped with clear thickenings at both ends, which are closely appressed to the gametocytes. Gametocytes in fusiform host cells are common in the peripheral blood during the chronic parasitemia and relapses.

Development in vertebrate host was studied by Khan (1975) in the saw-whet owls *Aegolius acadicus* which were infected by experimental inoculation of sporozoites. Four types of exoerythrocytic meronts are recorded: hepatic in parenchymal cells; renal in tubular cells; megalomeronts in endothelial cells lining the blood vessels in the spleen, liver, kidney, heart, intestine, gonads, and bone marrow; small worm-like

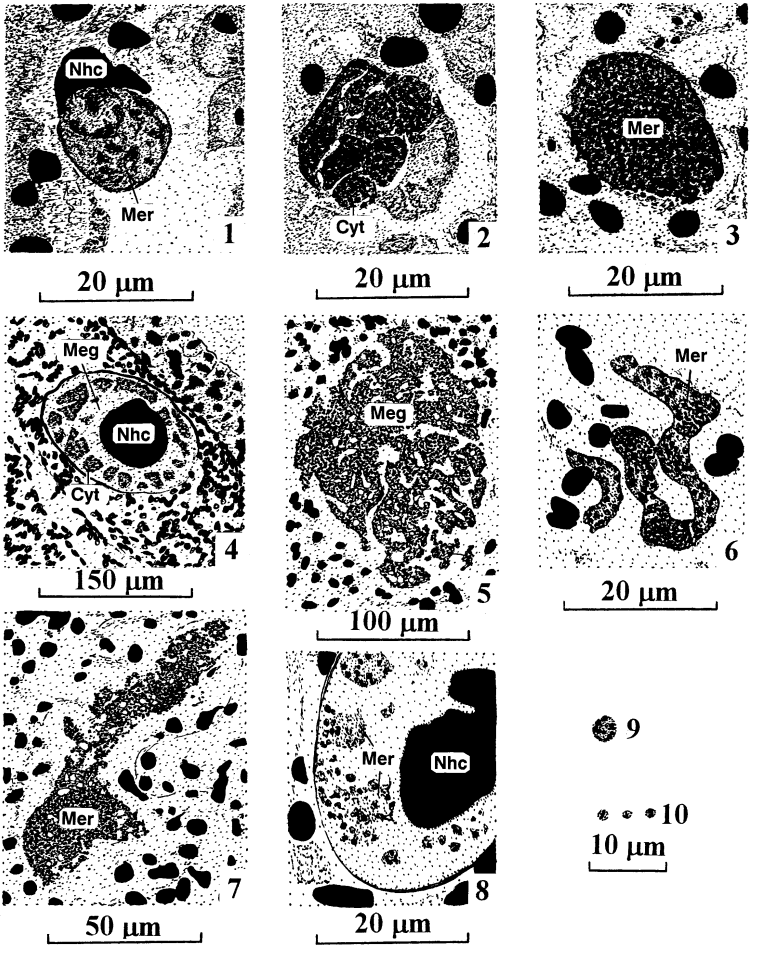

Figure 279 Exoerythrocytic meronts of *Leucocytozoon danilewskyi* from *Aegolius acadicus:* *1–3* – meronts in the liver: *1* – young parasite, *2* – parasite with cytomeres, *3* – mature parasite; *4*, *5* – megalomeronts: *4* – growing parasite in ovarian wall (numerous cytomeres are seen), *5* – mature parasite in spleen; *6* – worm-like in form meront in lungs; *7* – mature meront in kidney; *8* – a fragment of meront which develops in the cuboidal cells of kidney; *9* – syncytium from hepatic meront; *10* – merozoites from hepatic meront; Cyt – cytomere; Meg – megalomeront; Mer – meront; Nhc – nucleus of host cell (modified from Khan, 1975).

meronts in the endothelial cells of the lungs. Meronts were not found in the brain. Peculiarities of the development of these meronts are given in the text below.

Sporozoites, inoculated into the blood stream of birds, invade cells of the liver and kidneys. They initiate the development of the first generation of meronts. The hepatic meronts develop especially rapidly. They develop in the liver parenchymal cells. Nucleus of the host cell is enlarged, is located close to the meront and frequently is of a cap-like form (Fig. 279, *1*). As the parasite develops, cytomeres appear in meronts (Fig. 279, *2*). Mature hepatic meronts are seen four days after infection. They are oval and packed with a homogeneous mass of merozoites (Fig. 279, *3*). Mature hepatic meronts ($n = 20$) are 16 to 21 by

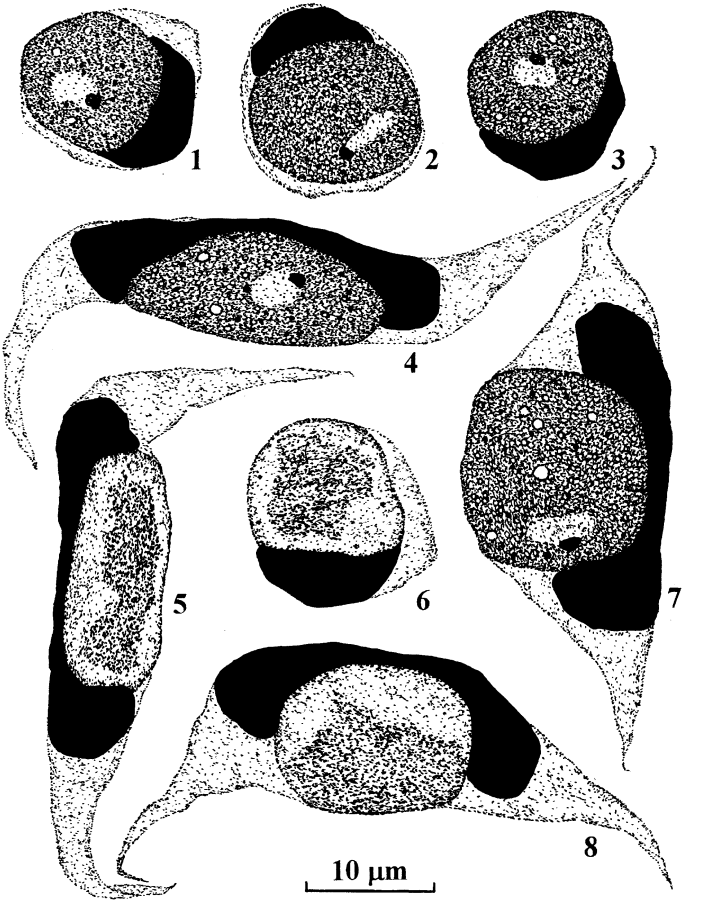

Figure 280 Gametocytes of *Leucocytozoon danilewskyi* from the blood of *Athene noctua: 1–4*, *7* – macrogametocytes; *5*, *6*, *8* – microgametocytes.

16 to 25 (on average 18×20) μm in diameter. They contain up to 2000 merozoites. Merozoites released from these meronts are no more than 2 μm in diameter.

In the kidneys, meronts are more numerous than in the liver (Fig. 279, *7*). They develop in renal tubular cells. As the parasite develops, meronts elongate. The nucleus of the host cell is enlarged and is located laterally to the meront. The renal meronts mature on the sixth day after infection and even earlier. The largest forms are seen to be up to 120 μm in length and 35 μm in width.

Merozoites, which develop in meronts of the first generation, initiate the development of gametocytes in roundish host cells (Fig. 280, *1–3*, *6*). The host cells are polychromatic erythrocytes. The prepatent period is four days after inoculation of sporozoites. Mature gametocytes are seen two days later when the blood starts to be infective for vectors. Thus, gametocytes capable of gametogenesis appear in the blood six days after the infection with sporozoites.

Numerous uninuclear merozoites (Fig. 279, *10*) and 'islands' of hepatic meronts with several nuclei (syncytia) (Fig. 279, *9*) are seen in the liver on the fifth day after infection.

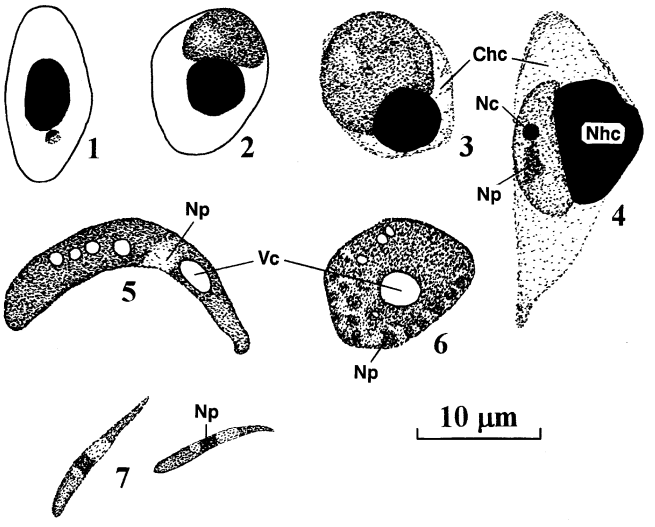

Figure 281 *Leucocytozoon danilewskyi:*
1–4 – initial stages of development of gametocytes in immature erythrocytes [the nucleus of the infected cell is markedly enlarged, and the host cell assumes the cytoplasmic processes at the early stages of the development of gametocyte, (4)]; *5* – ookinete; *6* – young oocyst from the midgut of vector three days after ingestion of gametocytes; *7* – sporozoites from the salivary glands of vector; Chc – cytoplasm of host cell; Nc – nucleolus; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – 'vacuole' (modified from Khan, 1975).

The syncytia are spread via the blood stream to numerous organs. They are phagocytized by reticuloendothelial cells, particularly macrophages, and give rise to megalomeronts. The latter are especially numerous in the spleen and liver. The nucleus of host cell (a 'residual body') is enlarged, and is usually located in the centre of the megalomeront. The nucleus can be located laterally to the parasite in cells with growing megalomeronts. The development of megalomeronts includes the successive stages of splitting up of the parasite into cytomeres with subsequent gradual disintegration of the cytomeres into uninuclear merozoites (Fig. 279, *4*, *5*, *8*). In the spleen, some megalomeronts are seen to be surrounded by a thin envelope of fibrillar structure. Mature megalomeronts, which develop in different organs, are of variable size. For example, in the same experimentally infected owl, their diameter ($n = 20$) is 43 to 56 by 82 to 126 (on average 51×97) μm in the spleen, 21 to 65 by 57 to 82 (on average 45×70) μm in the kidneys, and 29 to 57 by 29 to 64 (on average 35×49) μm in the liver. The largest megalomeronts in owls are recorded to be 110×160 μm in diameter. Mature megalomeronts are seen approximately on the eighth day after the infection with sporozoites. Their development takes approximately three days to complete maturation. Merozoites, which develop in megalomeronts, invade erythroblasts and lymphocytes. These merozoites initiate the development of gametocytes which induce the host cells to elongate, and thus fusiform host cells appear (Figs. 280, *4*, *5*, *7*, *8*; 281, *1–4*). Gametocytes in fusiform cells reach their maximum size about 10 days after the infection with sporozoites, and thus the growth of gametocytes in the fusiform host cells takes place in approximately two days. Enormous number of merozoites is realized after the rupture of megalomeronts, and this leads to the rapid increase of parasitemia. The largest number of gametocytes is observed in smears of internal organs. The peak of parasitemia is recorded

on approximately the tenth day after the infection with sporozoites, and parasitemia rapidly decreases then. It is important to note that gametocytes in fusiform host cells predominate during a chronic parasitemia.

Meronts in the lungs are recorded to be worm-like and resemble the meronts of haemoproteids (Fig. 279, *6*). Their role in the life cycle of the parasites is unclear. The meronts develop in the endothelial cells of capillaries and were recorded on the eighth day after infection. The worm-like meronts vary (n = 20) from 15 to 25 (on average 20) μm in length, and from five to nine (on average 7.5) μm in width.

Intensified haemopoiesis is recorded in the bone marrow of infected birds, and the number of erythroblasts, which are common host cells of gametocytes, increases markedly.

Macrogametocytes (Fig. 280, *1–4*, *7*; Table 146) develop in roundish and fusiform host cells; the cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes in roundish host cells are roundish (Fig. 280, *1–3*), and gametocytes

Table 146 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. danilewskyi* (according to Valkiūnas, 1988b)				*L. smithi* (modified from Bennett *et al.*, 1991c)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	38				15		
Length		11.4–17.4	13.0	1.4		12.7	1.3
Width		10.7–17.2	12.8	1.7		10.6	1.4
Length of nucleus		3.0–5.5	4.1	0.4		3.7	0.5
Width of nucleus		2.2–4.7	3.1	0.6		2.5	0.4
Length of nucleus of host cell		9.2–17.1	13.0	1.9		13.3	2.8
Macrogametocyte in fusiform host cell	38				44		
Length		14.1–22.7	19.4	1.6		24.9	2.3
Width		6.1–13.1	9.1	1.1		8.6	1.7
Length of nucleus		2.4–6.0	5.0	0.8		3.7	0.7
Width of nucleus		1.6–5.0	3.0	0.7		2.2	0.5
Length of nucleus of host cell		24.2–30.3	26.2	3.0		32.3	2.5

Note: All sizes are given in micrometres.

in fusiform host cells vary from roundish to oval and even slightly elongated (Fig. 280, *4*, *7*); the parasite nucleus is variable both in form and position; the nucleolus is prominent and well seen; the nucleus of roundish host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap or sometimes band; it usually extends less than 1/2 of the circumference of the gametocyte (Fig. 280, *1–3*); the nucleus of fusiform host cell is markedly deformed and enlarged, pushed aside, lies peripherally as an elongated dumbbell-shaped structure with clear thickenings at both ends closely appressed to the gametocyte (Fig. 280, *4*, *7*); the cytoplasm of roundish host cells is largely replaced by the gametocytes and sometimes is even invisible (Fig. 280, *3*) but more frequently is present around the gametocytes as a more or less evident and a very pale margin of variable form (Fig. 280, *1*, *2*); the cytoplasm of fusiform host cells forms two pronounced and variable (in form and

length) processes at the ends of gametocytes (Fig. 280, *4*, *7*); fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are common.

Microgametocytes (Fig. 280, *5*, *6*, *8*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Relapses are well pronounced and are clearly synchronized with the breeding period of birds (spring and summer in the Holarctic).

Development in vector was investigated by Khan (1975). Gametocytes both in roundish and fusiform host cells are infective for vectors. Exflagellation initiates *in vitro* within 1 min after exposure of the blood with mature gametocytes to air at room temperature. Ookinetes were observed 8 h after exposure of the blood to air (Fig. 281, *5*). They vary ($n = 20$) from 28 to 41 (on average 35) μm in length, and from 4 to 6 (on average 5) μm in width. *In vivo* at about 21°C, the ookinetes appear approximately at the same time. The ookinetes move to the periphery of the blood meal, penetrate the midgut wall of simuliid flies, round up, and develop into oocysts. The earliest oocysts appear within the wall of the midgut as small roundish or oval bodies, each with a few chromatin portions and an off-centre located 'vacuole' (Fig. 281, *6*). A few oocysts were observed in simuliid flies on the second day after the ingestion of gametocytes. The number of oocysts at the same stage of development markedly increases on the third day, and they vary ($n = 20$) from 10 to 13 (on average 11.5) μm in diameter. Larger-size oocysts were seen between the fourth and fifth days. They now vary ($n = 20$) from 12 to 16 (on average 14) μm in diameter and contain a dark-staining central body with small peripheral buds which are developing sporozoites. At five to seven days, oocysts vary ($n = 20$) from 15 to 18 (on average 16.4) μm in diameter. They contain free sporozoites which are seen in the salivary glands of simuliids from 6 to 27 days after infection. Sporozoites ($n = 20$) vary from 11 to 13 (on average 12) μm in length, and from 1 to 2 (on average 1.4) μm in width. One end of sporozoites is rounded and the other end is pointed (Fig. 281, *7*).

Pathogenicity has not been investigated. Infected females of *Aegolius funereus* are recorded to lay a smaller number of eggs during the years with restricted food resources (Korpimäki *et al.*, 1993).

Comments. The problem of validity of the species name *Leucocytozoon danilewskyi* was discussed by Valkiūnas (1997, 1999). The International Commission on Zoological Nomenclature was applied to adopt *Leucocytozoon danilewskyi* (Ziemann, 1898) as the type species of the genus *Leucocytozoon.* The ruling of the Commission was positive (see International Commission on Zoological Nomenclature, 2001).

Morphology of *L. danilewskyi* gametocytes and their host cells is especially similar to *L. caprimulgi*. It should be noted that gametocytes of *L. danilewskyi* in fusiform host cells in the peripheral blood of naturally infected birds are common, but have been extremely rarely recorded in *L. caprimulgi* infections.

Leucocytozoon danilewskyi is the only species of leucocytozoids that has been described in birds of the order Strigiformes.

2. **Leucocytozoon (Leucocytozoon) majoris** (Laveran, 1902)

Haemamoeba majoris Laveran, 1902: 1122, Fig. 5, 6 (partim). – *Leucocytozoon majoris*: Sambon, 1908: 325. – *Haemamoeba liothricis* Laveran and Marullaz, 1914: 24, Fig. 6–10. – *Leucocytozoon liothricis*: Wenyon, 1926: 1370. – *L. monardi* Rodhain, 1931: 274, Fig. 7 (partim). – *L. phylloscopus*

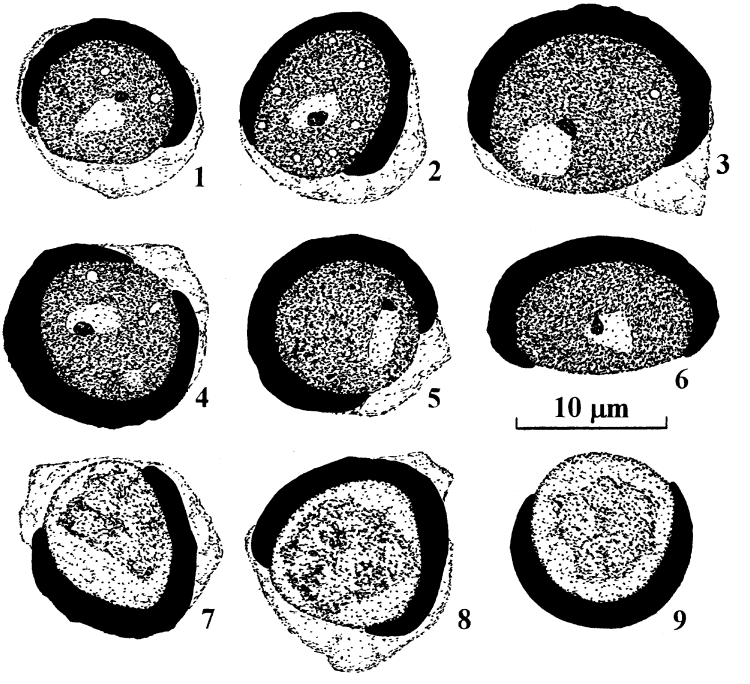

Figure 282 Gametocytes of *Leucocytozoon majoris* from the blood of *Parus caeruleus* and *Parus major:*
1–6 – macrogametocytes; *7–9* – microgametocytes.

Subkhonov, 1980: 45, Fig. 1, B. – *L. shaartusicum* Subkhonov, 1980: 46, Fig. 1, V. – *L. majoris*: Valkiūnas, 1988b: 118, Fig. 3 (=*L. phylloscopus, L. shaartusicum*). – *L. bishopae* Bennett and Peirce, 1992b: 702, Fig. 18–21 (emend. pro *L. bishopi*.). – *L. oriolis* Bennett and Peirce, 1992b: 700, Fig. 15–17. – *L. pittae* Bennett and Peirce, 1992b: 705, Fig. 30–32 (partim). – *L. pycnonoti* Bennett, Earlé and Peirce, 1992c: 245, Fig. 37–41. – *L. underhilli* Bennett, Earlé and Squires-Parsons, 1995a: 6, Fig. 20–23 (syn. nov.). – *L. majoris*: Valkiūnas, 1997: 488 (=*Haemamoeba liothricis*, *Leucocytozoon bishopae*, *L. monardi* partim, *L. oriolis*, *L. pittae* partim, *L. pycnonoti*).

Type vertebrate host. *Parus major* L. (Passeriformes).
Additional vertebrate hosts. Numerous species of the Passeriformes belonging to many families (over 80 species).
Type locality. Metz, France.
Distribution. This parasite has been recorded in all zoogeographical regions except the Neotropical and Antarctic.
Type material. Neohapantotype (No. 64339, *Parus major*, 24.06.1978, Malzeville, France, J. Blancou) is deposited in IRCAH.
Etymology. The specific name is derived from the specific name of the type vertebrate host, *P. major*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is of band-like form and has approximately the same width along all of its length; the nucleus extends more than 1/2 of the circumference of the gametocyte.

Development in vertebrate host

Macrogametocytes (Fig. 282, *1–6*; Table 150) develop in roundish host cells; the cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is variable both in form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed and lies peripherally as a band which, if not distorted, has approximately the same width along all of its length, and usually extends more than 1/2 of the circumference of the gametocyte; the cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 282, *6*) but more frequently is present around the gametocytes as a more or less evident and pale margin of a variable form (Fig. 282, *1–5*).

Microgametocytes (Fig. 282, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon monardi* was formerly considered to be a junior synonym only of *L. fringillinarum*. It is likely that Rodhain (1931) dealt with a mixed infection of *L. fringillinarum* and *L. majoris* during description of *L. monardi* from the blood of *Passer griseus*. In the original description of *L. monardi* (Rodhain, 1931), there is an indication in the text on a cap-like nucleus of the host cell (the character of *L. fringillinarum*) but a band-like nucleus (the character of *L. majoris*) is shown on the illustration. Thus it is preferable to consider *L. monardi* to be a partial junior synonym both for *L. fringillinarum* and *L. majoris*.

Leucocytozoon bishopae, *L. liothricis*, *L. oriolis*, *L. pittae* (partim), *L. pycnonoti*, and *L. underhilli* were described as distinct species mainly because they were found in passerine birds belonging to different families of the Passeriformes (Laveran and Marullaz, 1914; Bennett *et al.*, 1992c; Bennett and Peirce, 1992b; Bennett *et al.*, 1995a). Gametocytes and host cells of these parasites cannot be distinguished from those of *L. majoris*. Specificity of these leucocytozoids has not been investigated, and data on other stages of their development are not available. Based on these facts and bearing in mind the available data on the specificity of leucocytozoids and the main principles of identification of their species presented above (see p. 76), *L. bishopae*, *L. liothricis*, *L. oriolis*, *L. pittae* (partim), *L. pycnonoti*, and *L. underhilli* are considered to be junior synonyms of *L. majoris*.

It was noted in the original description of *L. bishopi* that this species is named in honour of Madonna Bishop (Bennett and Peirce, 1992b). Thus, the specific name *L. bishopi* should be emendated as *L. bishopae* [Articles 31(a)(ii), 32(c)(i) of the International Code of Zoological Nomenclature, 1985].

3. **Leucocytozoon (Leucocytozoon) smithi** (Laveran and Lucet, 1905)

Haemamoeba smithi Laveran and Lucet, 1905: 676, Fig. 1–6. – *Leucocytozoon smithi*: Sambon, 1908: 328. – *L. peaolopesi* Travassos Santos Dias, 1951: 73, Figs. – *L. smithi*: Valkiūnas, 1997: 489 (=*L. peaolopesi*).

Type vertebrate host. *Meleagris gallopavo* L. (Galliformes).
Additional vertebrate hosts. *Francolinus afer*, *F. swainsonii* (Galliformes).
Vectors. *Prosimulium hirtipes*, *Simulium aureum*, *S. congareenarum*, *S. jenningsi*, *S. meridionale*, *S. pictipes*, *S. slossonae*, *S. vittatum* (Diptera: Simuliidae).
Type locality. Loiret, France.
Distribution. Active transmission takes place in Central and North America. This parasite was introduced into the Old World where it was occasionally recorded in Europe (the western record came from France and the eastern one from Ukraine) and more frequently in South Africa.

Type material. Neohapantotype (No. 425549, *Meleagris gallopavo*, 25.08.1970, Lockloosa, Florida, USA, D.J. Forrester) and paraneohapantotypes (No. 42544, 42548, other data are as for the neohapantotype) are deposited in IRCAH.

Etymology. This species is named in honour of Dr. Theodore Smith, who first observed the parasite in turkeys in North America in 1895.

Main diagnostic characters. A parasite of species of the Galliformes whose gametocytes develop in roundish and fusiform host cells. Nucleus of fusiform host cell is usually split into two more or less symmetrical portions which extend on each side of the gametocyte as more or less crescent-like bands.

Development in vertebrate host

Exoerythrocytic merogony takes place in parenchymal cells of the liver. Meronts are not seen in any other organs and tissues. Megalomeronts are absent (Newberne, 1955; Richey and Ware, 1955; Wehr, 1962; Steele and Noblet, 1992). Two generations of meronts develop. Sporozoites invade hepatocytes and initiate the development of the first generation of meronts. Sporozoites are seen in hepatic cells 60 h after their intraperitoneal inoculation. Trophozoites are recorded three days after infection, and meronts are seen three or four days after infection. As meronts develop, cytomeres appear. Meronts of the first generation mature approximately five to six days after infection. They release uninuclear merozoites which are roughly spherical or pear-shaped and about 1 μm in diameter. The merozoites again invade parenchymal liver cells and initiate the development of the second generation of exoerythrocytic meronts. Numerous merozoites are also seen in macrophages in the liver. However, the parasite does not complete the development in these cells (the development is abortive at the stage of trophozoite and young meront). First meronts of the second generation were observed approximately five days after the infection. They are numerous on the sixth day after infection, and mainly complete their development by the seventh day post infection. Under the light microscope, there were no differences in the morphology between infected and noninfected host cells, except the presence of parasites. The size and morphology of first and second generation meronts are similar under the light microscope. However, cytomeres are not seen in meronts of the second generation. Mature meronts ($n = 40$) are 7 to 11 by 14 to 20 (on average 11×14) μm in diameter. Merozoites released from meronts of the second generation invade mononuclear phagocytes (monocytes or lymphocytes) and develop into gametocytes. Gametocytes do not develop in cells of the erythrocytic series and in polymorphonuclear leukocytes (Solis, 1973; Steele and Noblet, 1993).

The prepatent period is less than ten days. Two types of gametocytes develop, i.e., in roundish and fusiform host cells. Young gametocytes in roundish host cells appear in the deep vasculature of the liver, lungs, and spleen seven to ten days after the infection, and they can be present in the peripheral blood. As the parasite develops, the host cells elongate. Mature gametocytes are located in fusiform host cells whose nuclei are usually split into two more or less symmetrical portions; they appear both in the deep vasculature of the internal organs and in the peripheral blood on the 12th day after infection. At this time, gametocytes in roundish host cells are already not observed. It looks likely that gametocytes in roundish host cells in *L. smithi* are young (transitional to elongated) forms which do not take an important part in further development in vector and transmission of the infection (Steele and Noblet, 1993). It is worth noting that the parasite does not destroy the nucleus of host cell during its splitting, and numerous organelles are present in the cytoplasm

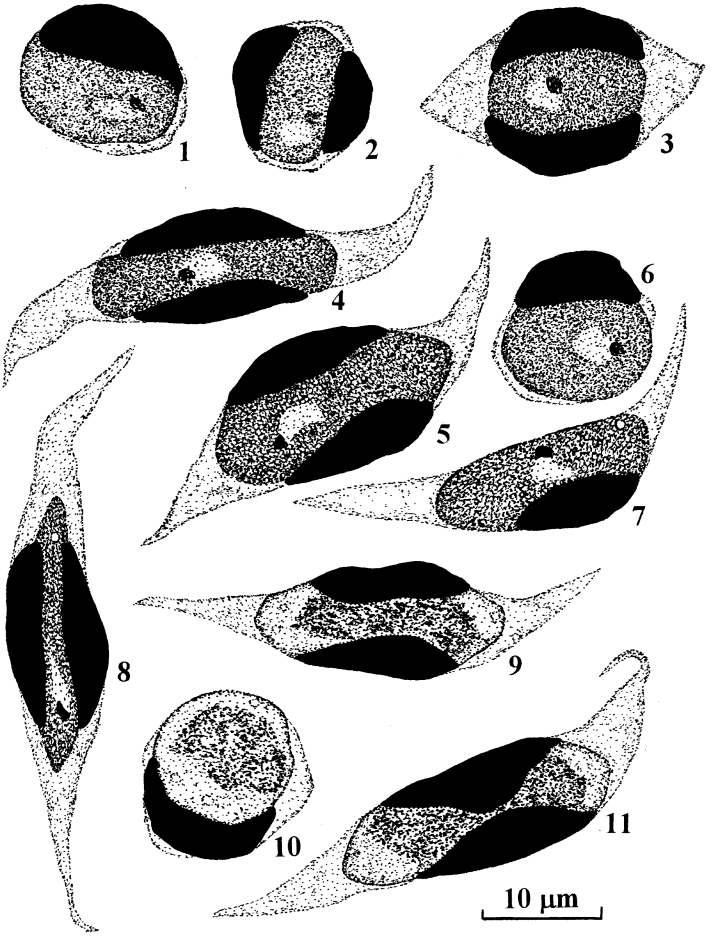

Figure 283 Gametocytes of *Leucocytozoon smithi* from the blood of *Meleagris gallopavo: 1–8* – macrogametocytes; *9–11* – microgametocytes.

of infected cells. These suggest (i) deep adaptation of the parasite to the intracellular development and (ii) the active metabolism in the host cells.

Clear daily variation of parasitemia is recorded. Under natural photoperiod, the peak of gametocytemia was observed from 8 to 20 h, and minimum parasitemia occurred from 22 to 4 h. The period of highest gametocytemia in vertebrate host coincides with the period of maximum activity of the vectors (Noblet and Noblet, 1976). This increases the probability for parasite to infect the vectors and thus contributes to transmission. When turkeys were maintained under continuous light, the number of gametocytes in the blood increased at or near the time of feed availability (Noblet *et al.*, 1980).

In once infected turkeys, which were protected from reinfection, gametocytes were observed up to a 13-month period (the time of observation) (Dick and Rice, 1975). Persistence of *L. smithi* in internal organs of birds is proved experimentally. The sharp increase of gametocytemia in vector-protected birds in captivity after a period, when the parasites were not seen in the blood, testify to the renewal of exoerythrocytic merogony

(Alverson and Noblet, 1977). However, the stages responsible for the long-period persistence and the relapses in birds have not been investigated.

Macrogametocytes (Fig. 283, *1–8*; Table 146) develop in roundish and fusiform host cells; parasites in roundish host cells (Fig. 283, *1*, *2*, *6*) are the earliest stages of development of gametocytes, are present only in the early period of infection; the cytoplasm sometimes contains a few small vacuoles; valutin granules are present; gametocytes in roundish host cells are roundish (Fig. 283, *6*) or oval (Fig. 283, *1, 2*); gametocytes in fusiform host cells are of variable shape; are usually oval (Fig. 283, *3–5*, *7*) but sometimes roundish and even band-like (Fig. 283, *8*); the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of fusiform host cell is usually split into two more or less symmetrical portions which extend on each side of the gametocyte as more or less crescent-like bands (Fig. 283, *3–5*, *8*) but the host cells with not-split nuclei (Fig. 283, *7*) are also present; occasionally, the nucleus of fusiform host cell was also seen to be split into three portions; the cytoplasm of fusiform host cell forms two well evident and variable (both in form and length) processes at the ends of gametocyte (Fig. 283, *4*, *5*, *7*, *8*); fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are common.

Microgametocytes (Fig. 283, *9–11*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector is similar to other species of *Leucocytozoon* (Steele *et al.*, 1992). At temperature of about 20°C, young oocysts were seen in the midgut of simuliid flies approximately on the second day after the ingestion of gametocytes. They were about 7 to 9 μm in diameter. Mature oocysts were observed on the third day after infection. They are about 9 to 15 μm in diameter. Less than 50 sporozoites usually develop in each oocyst. Mature sporozoites are about 10 to 16 μm in length, and 0.7 to 1.0 μm in width. Sporozoites were seen in the salivary glands on the fourth day after infection.

Pathogenicity. *Leucocytozoon smithi* is the agent of a heavy leucocytozoonosis of turkeys. The disease is quick and usually leads to the death of young birds. Dead turkey poults were frequently found beneath the roosts in the morning without showing premonitory symptoms. Within two to three days after the appearance of clinical symptoms, birds either die or start to recover and the disease turns into a chronic stage. Acute leucocytozoonosis is characterized by anorexia, increased thirst, progressive weakness and muscular incoordination, depression, emaciation, drowsiness, respiratory 'rattling,' diarrhoea. If the comatose condition develops, the birds do not usually recover. Heavily affected turkey poults frequently sit on their hocks with the neck extended and the head resting on the ground. The wings droop and the feathers on the neck are erected. Convulsions, which last for several minutes, can precede the death. At the peak of parasitemia, capillaries of internal organs, especially in the lungs and spleen, are frequently blocked up by numerous mature gametocytes. As a result of this, pneumonia develops. Necropsy reveals emaciation, dehydration, congestion in the lungs, liver, and spleen, and enlargement of the spleen and liver (Wehr, 1962; Siccardi *et al.*, 1971).

The economic losses due to the leucocytozoonosis are stipulated not only by the high mortality rate among turkey poults but also by a significant decrease of productivity of adult birds (Jones *et al.*, 1972; Solis, 1973; Forrester *et al.*, 1974).

It should be noted that turkey leucocytozoonosis has been only occasionally recorded in Europe, and there have been no convincing records here since 1961 when the parasite was found in Ukraine. The disease has been more frequently reported in South Africa. It is

common in Central and North America where natural foci of infection occur. The most devastating outbreaks have occurred in the south-eastern states of the USA.

S p e c i f i c i t y. Experimental attempts to infect domestic chickens, quails, partridges, pheasants, and ducklings were unsuccessful (Solis, 1973). See also 'Comments' below.

C o m m e n t s. *Leucocytozoon peaolopesi* was originally described from the galliform bird *Francolinus afer* (the family Phasianidae) (Travassos Santos Dias, 1951). Gametocytes of *L. peaolopesi* and their host cells are indistinguishable from those of *L. smithi*. Other stages of development of *L. peaolopesi* have not been investigated. Thus, bearing in mind the main principles of identification of leucocytozoids presented above (see p. 76), *L. peaolopesi* is considered to be a junior synonym of *L. smithi*. Bennett *et al.* (1991c) believe that *L. peaolopesi* is distinguishable from *L. smithi*, first of all, on the basis of larger size of its fusiform host cells. The length of fusiform host cells of *L. peaolopesi* was recorded to be 51.5 μm on average. However, this character is markedly variable in *L. smithi*. For example, according to Johnson *et al.* (1938), the length of fusiform host cells can be on average 45.8 μm in the peripheral circulation, and even 58.2 μm in smears of internal organs. These sizes are close to the same parameters of *L. peaolopesi*. It should be also noted that dimensions of gametocytes and their fusiform host cells of *L. peaolopesi* on the illustrations in the original description (Travassos Santos Dias, 1951) coincide with the same parameters of *L. smithi.* These facts show that the sizes of gametocytes and their host cells are unreliable characters for identification of *L. smithi* and *L. peaolopesi*. In fact, morphometric parameters of gametocytes of leucocytozoids and their host cells are markedly variable during the development of the same species of parasite in different vertebrate hosts, and thus they cannot be a basis for identification of species. The well known example is *L. toddi* whose morphometric parameters are even more variable than in *L. smithi* (see p. 776).

It is likely that *L. smithi* was introduced to South Africa together with its vertebrate host (turkey) in the second part of the 17th century (Huchzermeyer, 1993a). There, this parasite not only adapted itself to new vectors, which is the basis for maintenance of local foci of infection, but also inhabited new vertebrate hosts (*Francolinus afer*, *F. swainsonii*). This hypothesis is of theoretical significance from the point of view of epidemiology and should be tested.

4. **Leucocytozoon (Leucocytozoon) neavei** (Balfour, 1906)

Haemamoeba neavei Balfour, 1906: 200, Pl. 20. – *Leucocytozoon neavei*: Sambon, 1909: 37. – *L. numidae* Kerandel, 1913: 433, Pl. 6, Fig. 22–29. – *L. costae* Tendeiro, 1947: 323, Fig. 24, 25. – *L. costai*: Bray, 1964: 238 (emend. pro *L. costae*). – *L. neavei*: Hsu *et al.*, 1973: 196 (=*L. numidae*); Fallis *et al.*, 1974: 9 (=*L. costai*).

T y p e v e r t e b r a t e h o s t. *Numida meleagris* (L.) (Galliformes).
A d d i t i o n a l v e r t e b r a t e h o s t. *Guttera pucherani* (Galliformes).
V e c t o r s. *Simulium adersi* and *S. nyasalandicum* (Diptera: Simuliidae)
T y p e l o c a l i t y. Khartoum, Sudan.
D i s t r i b u t i o n. The Ethiopian zoogeographical region.
T y p e m a t e r i a l. Neohapantotype (No. 24496, *Numida meleagris*, 16.08.1971, Handeni, Tanzania, coll. White) is deposited in IRCAH.
E t y m o l o g y. This species is named in honour of Dr. Sheffield Neave.

M a i n d i a g n o s t i c c h a r a c t e r s. A parasite of species of the Galliformes whose gametocytes develop in fusiform host cells. Nucleus of the host cell is of cap-like form or resembles the nucleus of uninfected erythrocyte in shape; the nucleus extends less than 1/3

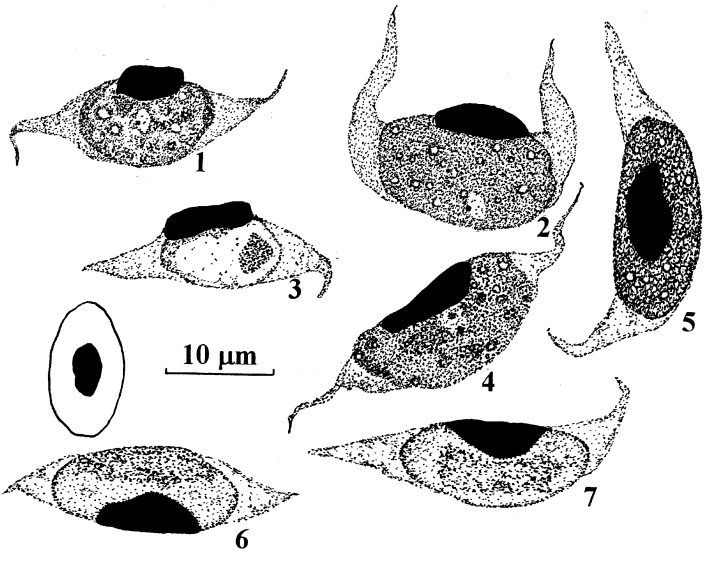

Figure 284 Gametocytes of *Leucocytozoon neavei* from the blood of *Numida meleagris: 1*, *2*, *4*, *5* – macrogametocytes; *3*, *6*, *7* – microgametocytes.

of the circumference of the gametocyte. Currently, this parasite can be identified only in birds of the family Numididae with confidence.

Development in vertebrate host

The prepatent period in guinea-fowl chickens is about 12 days or even less after experimental peritoneal inoculation of sporozoites. It is likely that gametocytes complete development within 48 h. Mature gametocytes appear in the peripheral blood 14 days after infection (Fallis *et al.*, 1973).

Macrogametocytes (Fig. 284, *1*, *2*, *4*, *5*; Table 147) develop in fusiform host cells; the cytoplasm frequently possesses small vacuoles and valutin granules; gametocytes are usually oval, sometimes roundish; the parasite nucleus is both of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is deformed, usually pushed aside and lies peripherally as a cap-like structure (Fig. 284, *2*, *4*) or

Table 147 Morphometric parameters of gametocytes and host cells of *Leucocytozoon neavei* (modified from Bennett *et al.*, 1991c) ($n = 30$).

Feature	$\overline{X}$	*SD*
Macrogametocyte in fusiform host cell		
Length	17.6	2.3
Width	8.5	1.9
Length of nucleus	4.4	1.1
Width of nucleus	2.3	0.5
Length of nucleus of host cell	9.5	1.5

Note: All sizes are given in micrometres.

resembles by its shape the nucleus of uninfected erythrocyte (Fig. 284, *1*); the nucleus extends less than 1/3 of the circumference of gametocyte; occasionally the host cell nucleus can be encircled by the gametocyte (Fig. 284, *5*); the cytoplasm of host cell forms two well evident and variable (both in form and length) processes at the ends of gametocytes; fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are common.

Microgametocytes (Fig. 284, *3*, *6*, *7*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector

Sporogony is completed in the simuliid flies *Simulium adersi* and *S. nyasalandicum* in six or seven days after the ingestion of mature gametocytes at approximately 20°C. Early oocysts are about 13 μm in diameter on the third day after infection. Sporozoites are recorded in the salivary glands of *S. adersi* six to eight days after infection. Live sporozoites are approximately 11 μm in length and 1 μm in width (Fallis *et al.*, 1973).

Pathogenicity. Signs of illness are not recorded in infected guinea-fowls.

Specificity has been insufficiently investigated. Limited observations suggest that *L. neavei* is not transmissible to domestic chickens (Fallis *et al.*, 1973). It is worth noting that the domesticated guinea-fowl *Numida meleagris* is distributed all over the world. However, *Leucocytozoon* species have never been recorded in this bird outside the Ethiopian zoogeographical region. The active transmission of *L. neavei* takes place only in Africa. These zoogeographical data can be regarded as indirect evidence that close species such as *L. lovati* and *L. macleani*, which are common in galliform birds outside Africa, do not develop in the guinea-fowl.

Comments. *Leucocytozoon macleani*, which is close to *L. neavei*, has been frequently recorded in the African representatives of the genus *Francolinus*. Thus, it is of theoretical interest to test a possibility for *L. neavei* to infect birds of this genus.

5. **Leucocytozoon (Leucocytozoon) lovati** Seligman and Sambon, 1907

Leucocytozoon lovati Seligman and Sambon, 1907: 829, Fig. 1, 2. – *L. mansoni* Sambon, 1908: 327. – *L. bonasae* Clarke, 1935: 646, Fig. 1, Pl. 1, Fig. 1, 2. – *L. jakimovi* Oliger, 1940a: 470, Fig.; 1940b: 102. – *L. lovati*: Fallis *et al.*, 1974: 10 (=*L. mansoni*, *L. bonasae*); Bennett *et al.*, 1991c: 1424 (=*L. jakimovi*).

Type vertebrate host. *Lagopus scoticus* L. (Galliformes).
Additional vertebrate hosts. Some species of the family Tetraonidae (Table 148).
Vectors. *Simulium aureum*, *S. croxtoni*, *S. latipes*, *S. quebecense* (Diptera: Simuliidae).
Type locality. Scotland, UK.
Distribution. The Northern and Central Holarctic.
Type material was not designated in the original description. The neotypes suggested by Bennett *et al.* (1991c) do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985) because they came from the nontype vertebrate host. Designation of valid neotypes is required. A series of good additional slides is deposited in IRCAH.
Etymology. This species is named in honour of Lord Lovat, who was Chairman of the Commission upon Grouse Disease in the United Kingdom in the beginning of the 20th century.

Table 148 List of vertebrate hosts of *Leucocytozoon lovati.*

Bonasa umbellus	*D. obscurus*	*Lyrurus tetrix*
Canachites canadensis	*Lagopus lagopus*	*Tetrao urogallus*
Centrocercus urophasianus	*L. leucurus*	*Tetrastes bonasia*
Dendragapus canadensis	*L. mutus*	*Tympanuchus phasianellus*

Main diagnostic characters. A parasite of species of the Galliformes whose gametocytes develop in roundish and fusiform host cells. The nucleus of fusiform host cell is of cap-like form or almond-shaped or resembles the nucleus of uninfected erythrocyte; the nucleus extends less than 1/3 of the circumference of the gametocyte. Currently, this parasite can be identified with confidence only in birds of the family Tetraonidae.

Development in vertebrate host

The exoerythrocytic merogony is only fragmentary investigated in naturally infected birds. Two types of meronts are recorded, the meronts in the liver and the megalomeronts in the kidneys. Merogony was not observed in the other organs.

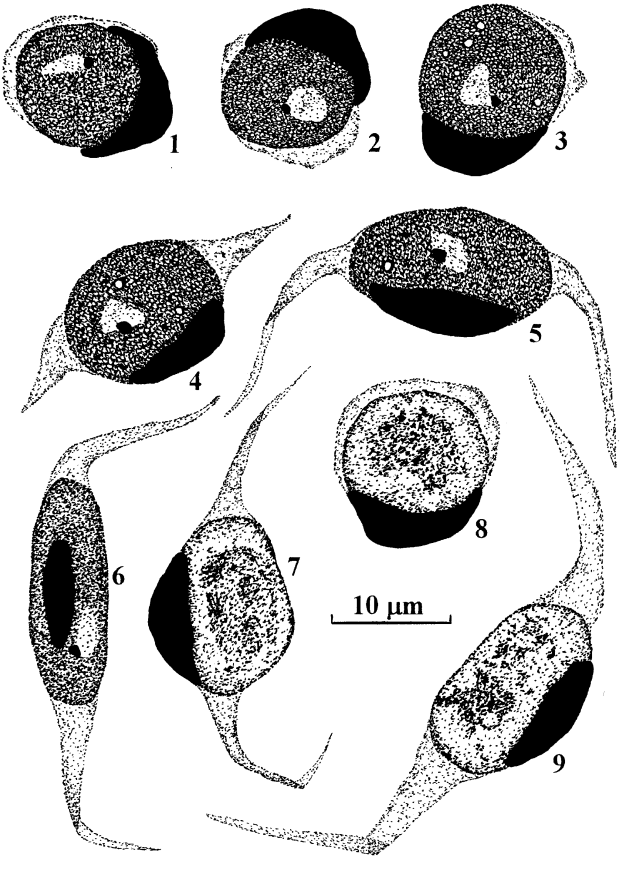

Figure 285 Gametocytes of *Leucocytozoon lovati* from the blood of *Lagopus lagopus: 1–6* – macrogametocytes; *7–9* – microgametocytes.

Small meronts were found in the liver cells of *Bonasa umbellus*, *Lyrurus tetrix*, *Tetrao urogallus*, and *Tetrastes bonasia* (Clarke, 1938; Borg, 1953). The meronts do not exceed 7 μm in diameter in *L. tetrix*, *T. urogallus* and *T. bonasia*, and their influence on the host cells is not pronounced. Mature meronts contain approximately 60 to 80 merozoites which vary from 0.5 to 1.5 μm in diameter. The smallest observed mature hepatic meronts do not exceed 4 μm in diameter. They contain about 30 merozoites. Meronts were seen in the liver of *B. umbellus* from the ten-day age of the birds throughout a year. The meronts were especially frequently recorded and numerous in the beginning of June. Subsequently, the number of hepatic meronts decreased markedly. A few multinuclear parasites, which outwardly resemble cysts and are probably responsible for spring relapses, were observed in the liver of *B. umbellus* between October and April.

Megalomeronts were found only once in the kidneys of *Bonasa umbellus* (Newman, 1970). The megalomeronts most often appeared to be filling the lumens of uriniferous tubules, probably originating in the epithelial cells of the tubules or in macrophages. As the parasite develops, cytomeres appear, and they can develop asynchronously. The nucleus of host cell is markedly deformed and enlarged. A thin sheath of reticulum was often seen to surround the meronts.

The prepatent period is no more than 12 to 13 days after infection with sporozoites (Fallis and Bennett, 1958).

Macrogametocytes (Fig. 285, *1–6*; Table 149) develop in roundish and fusiform host cells; the cytoplasm frequently contains a few small vacuoles; valutin granules are usually present; gametocytes in roundish host cells are roundish or slightly oval (Fig. 285, *1–3*), and gametocytes in fusiform host cells vary from roundish (Fig. 285, *4*) to oval (Fig. 285, *5*) and even elongated (Fig. 285, *6*); the parasite nucleus is variable both in form and position; the nucleolus is prominent and well seen; the nucleus of roundish host cell is pushed aside, deformed, and lies peripherally usually as a more or less evident cap or

Table 149 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. macleani*				*L. lovati* (according to Valkiūnas, 1989a)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish cell	31				31			
Length		10.2–15.8	13.1	1.1		9.5–14.0	11.4	1.1
Width		10.0–15.0	12.0	0.9		8.9–15.5	11.2	1.0
Length of nucleus		2.6–5.4	4.0	0.8		3.3–6.3	4.1	0.4
Width of nucleus		1.0–4.4	3.0	0.8		1.4–4.2	3.1	0.3
Length of nucleus of host cell		8.2–22.2	15.8	3.0		12.0–17.5	14.0	1.0
Macrogametocyte in fusiform host cell	40				10			
Length		12.2–24.4	17.7	1.4		14.1–22.0	17.5	1.4
Width		6.0–15.4	11.0	1.3		6.7–13.1	11.0	0.7
Length of nucleus		2.2–7.0	4.0	0.4		3.2–6.8	4.2	0.3
Width of nucleus		1.4–5.3	3.7	0.4		1.8–4.4	3.6	0.3
Length of nucleus of host cell		8.8–16.8	13.9	1.0		9.8–16.3	13.5	1.5

Note: All sizes are given in micrometres.

sometimes band, extends less than 1/2 of the circumference of gametocyte (Fig. 285, *1–3*); the nucleus of fusiform host cell is slightly enlarged, deformed, usually pushed aside, and lies peripherally as a cap-like or almond-shaped structure (Fig. 285, *4*, *5*) or resembles the nucleus of uninfected erythrocyte by its form; it extends less than 1/3 of the circumference of gametocyte; sometimes, the nucleus of fusiform host cell can be encircled by gametocyte (Fig. 285, *6*); the cytoplasm of roundish host cells is largely replaced by gametocytes, and is sometimes even invisible, but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 285, *1–3*); the cytoplasm of fusiform host cells forms two well evident and variable (both in form and length) processes at the ends of gametocytes (Fig. 285, *4–6*); the processes are frequently markedly attenuated (Fig. 285, *5*, *7*) which is especially frequently recorded in the type vertebrate host; fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are common.

Microgametocytes (Fig. 285, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Gametocytes in roundish and fusiform host cells are frequently present in peripheral blood of naturally infected birds.

Relapses are well evident in a spring–summer period, and are clearly synchronized with a breeding period of birds. The relapsed parasitemia maintains in *Dendragapus obscurus* at least for a three-month period (Allan and Mahrt, 1989).

Development in vector

Exflagellation was recorded within 1 min *in vitro* after exposure of the blood with mature gametocytes to air at room temperature, and ookinetes were seen 4 h later. Ookinetes stained and fixed with methanol ($n = 20$) vary from 24 to 31 (on average 27) μm in length, and from 2 to 4 (on average 3) μm in width (Fallis and Bennett, 1958). The stained and fixed ookinetes, which developed *in vivo*, vary from 18 to 31 (on average 26) μm in length (Fallis and Bennett, 1962). Development of ookinetes in vector is not synchronized. They were still present in midgut of simuliid flies 48 h after the ingestion of gametocytes. Sporogony is completed on the fifth day in *Simulium latipes* at temperature of 16°C (Fallis and Bennett, 1961b). Mature oocysts vary from 8 to 16 (on average 13) μm in diameter. The largest oocysts contain 50 to 100 and even more sporozoites. Small oocysts contain less than 50 sporozoites, and sometimes even less than 30 sporozoites were observed (Fallis and Bennett, 1962).

Pathogenicity has not been investigated. Signs of illness were not recorded both in naturally and experimentally infected birds at low parasitemia (Fallis and Bennett, 1958).

Comments. *Leucocytozoon lovati* is a common parasite of tetraonid birds (the family Tetraonidae) in the Northern and Central Holarctic. By the morphology of gametocytes and their host cells, this parasite is identical to *L. macleani* which parasitizes phasianid birds (the family Phasianidae). It is possible that *L. macleani* can be a synonym or subspecies of *L. lovati*. Further comparative investigations of leucocytozoids of tetraonid and phasianid birds are required to solve the problem of the validity of *L. macleani*. Currently, data on geographical distribution of *L. lovati* and *L. macleani* are the basis for accepting the validity of these species. Active transmission of *L. lovati* takes place at high latitudes of the Northern hemisphere and even beyond the North Polar Circle. The active transmission of *L. macleani* takes place at low latitudes and in the tropics (for more details, see 'Comments' to *L. macleani*). Tetraonid birds originated from more ancient phasianids (Potapov, 1985; 1992). It is likely that the tetraonid birds have gained the leucocytozoids from the

phasianids. The evolution of *L. lovati* is probably related to an adaptation for transmission at severe climatic conditions of the Northern Holarctic. This adaptation can develop simultaneously with the evolution of tetraonid birds. It is interesting to note that the prevalence of infection of tetraonids with *L. lovati* markedly decreases from the northern to the southern latitudes as it takes place in *L. simondi* parasitizing anseriform birds in the Holarctic.

6. **Leucocytozoon (Leucocytozoon) berestneffi** Sambon, 1908

Leucocytozoon berestneffi Sambon, 1908: 325.

Type vertebrate host. *Pica pica* L. (Passeriformes).
Additional vertebrate hosts. *Cyanocitta cristata*, *Pica nuttalli* (Passeriformes).
Vectors. *Prosimulium decemarticulatum*, *Simulium aureum* (Diptera: Simuliidae).
Type locality was not specified in the original description. This species was described on the basis of the literature data of Russian scientists (Sakharoff, 1893; Berestneff, 1904) who collected their material in the environs of Tbilisi (Georgia) and Voronezh (Russia), respectively.
Distribution. This parasite has been recorded only in the Holarctic so far.
Type material has never been designated. A series of good additional slides is deposited in IRCAH and CDVA.
Etymology. This species is named in honour of Russian scientist N.M. Berestneff in recognition of his contribution to the field of avian blood parasitology in the beginning of the 20th century.

Main diagnostic characters. A parasite of species of the Corvidae whose gametocytes develop in roundish host cells. Nucleus of the host cell vary from cap-like to band-like in form, it can extend up to 2/3 and even more of the circumference of the gametocyte. Currently, this parasite can be identified in birds of the genera *Pica* and *Cyanocitta* with confidence.

Development in vertebrate host
The precise fate of sporozoites, inoculated into the blood stream of birds by the vector, is not investigated. Two types of exoerythrocytic meronts have been described.

Meronts of the first type were found and described in naturally infected nestlings and adults of *Pica nuttalli* which were captured in California, USA (Clark, 1965). The meronts were especially frequently observed in the liver, and less frequently seen in the spleen and kidneys. The successive stages of their development are shown in Figs. 286 and 287. The earliest parasites seen in hepatic cells are oval or roundish (Figs. 286, *1*; 287, *1*, *2*). Several such parasites were frequently present in the same host cell (Figs. 286, *1*, *3*, *4*; 287, *1*, *2*). The developing meront is surrounded with a lighter portion of the cytoplasm (Fig. 286, *1*, *3–6*, *8*). As the parasite develops, the number of nuclei increases (Figs. 286, *5–7*; 287, *7–17*). In the advanced meronts, chromatin was seen to be arranged as elongate discrete masses (Figs. 286, *9*; 287, *18–20*). Mature meronts were about 8 to 9 μm in diameter. They contain numerous merozoites (Fig. 286, *10*). The mature meronts rupture, and merozoites first invade the host cell (Fig. 286, *11*), and only then they are released. Thus, the rupture of meronts takes place before the rupture of their host cells. Meronts only slightly (if at all) influence the host cells. The parasite can induce an indentation of the host cell nucleus at the place of their contact (Fig. 286, *3*). Meronts of the first type are not numerous in the internal organs of birds, and pathological changes were not observed in the affected organs.

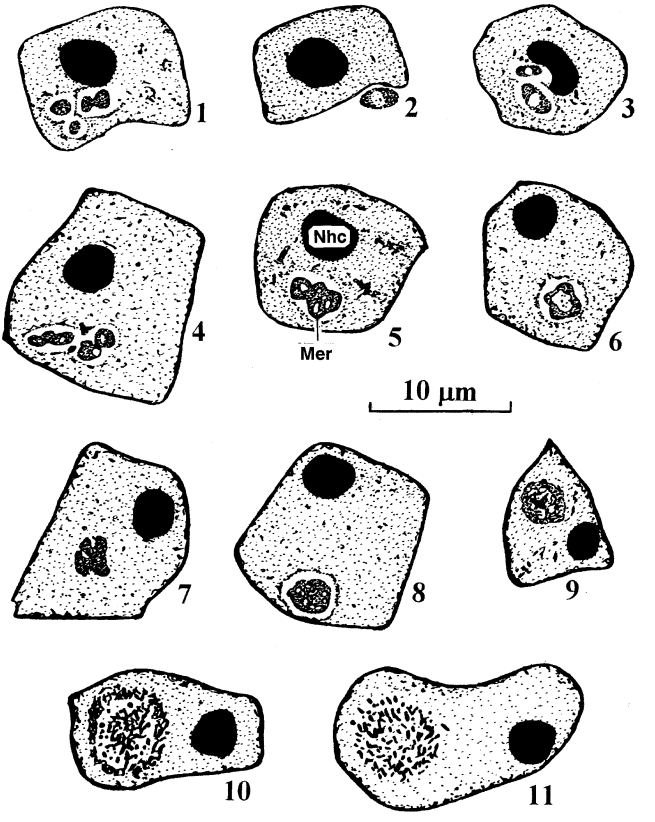

Figure 286 Exoerythrocytic meronts of *Leucocytozoon berestneffi* in hepatic cells of *Pica nuttalli: 1*, *3* – earliest stages of development of parasites; *2* – extracellular parasite; *4–9* – growing parasites at different stages of fission of their nuclei; *10*, *11* – mature parasites; Mer – meront; Nhc – nucleus of host cell (modified from Clark, 1965).

Gametocytes appear in the peripheral blood nine days after exposure of uninfected *Pica nuttalli* in the locality with active transmission of *L. berestneffi*. The prepatent period is unknown precisely but is no longer than nine days.

Meronts of the second type were investigated in experimentally infected *Cyanocitta cristata* which were trapped in Algonquin Park, Canada (Khan and Fallis, 1971b). The meronts were found in the liver, kidneys, and spleen. They were not observed in the lungs, heart, brain, bone marrow, and breast muscle. The earliest parasites are seen in hepatic parenchymal cells three days after experimental infection with sporozoites (Fig. 288, *1*). They contained several irregularly distributed chromatin masses. At the same time, meronts with cytomeres are seen (Fig. 228, *2*). Numerous meronts at different stages of development, including mature forms, were observed four days after inoculation of sporozoites (Fig. 288, *3*). Mature hepatic meronts ($n = 20$) were 16 to 22 by 16 to 24 (on average 18×21) μm. They contain hundreds of merozoites. On the fifth day after infection, the number of meronts decreases, and a few of them were found in the liver 12 h later. In the kidneys, meronts develop in renal tubular cells whose nuclei are enlarged. The meronts were especially numerous 5.5 days after inoculation of sporozoites, i.e., when the number

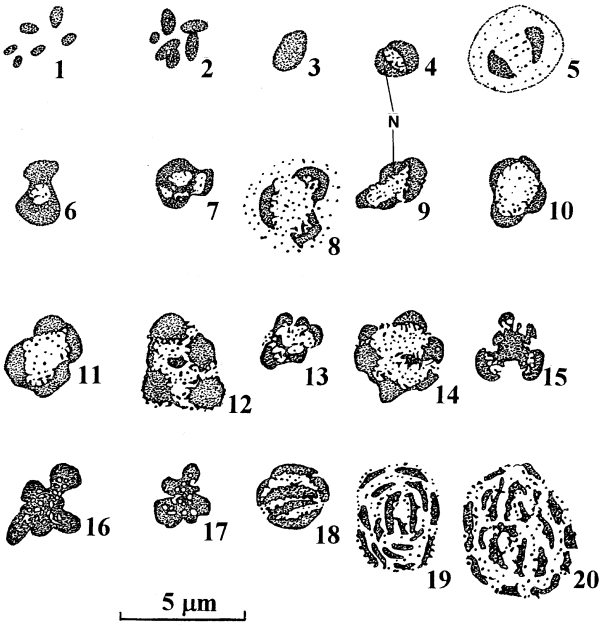

Figure 287 Diagrammatic representation of the development of exoerythrocytic meronts of *Leucocytozoon berestneffi* in hepatic cells of *Pica nuttalli* (host cells are omitted): *1–3* – trophozoites; *4*, *5* – early binuclear meronts; *6–20* – growing meronts at different stages of fission of their nuclei; N – nucleus of parasite (modified from Clark, 1965).

of hepatic meronts decreased markedly. It is possible that merozoites from the hepatic meronts induce merogony in the kidneys. Fully grown renal meronts are of variable form, and frequently curiously shaped (Fig. 288, *4*). They (n = 20) were 15 to 40 by 45 to 130 (on average 28×62) μm in size. One meront, which was seen in the spleen, reached 38×73 μm in diameter.

A few meronts were found in smears of the liver of one adult *Pica pica* sampled on the Curonian Spit in the Baltic Sea. These meronts are identical both in form and size to the hepatic meronts recorded in *Cyanocitta cristata* (Fig. 288, *1–3*).

Young gametocytes appeared in the blood of *Cyanocitta cristata* and *Pica pica* 92 h after experimental infection with sporozoites, and mature gametocytes are seen five to six days after infection. A peak of parasitemia was recorded nine days after infection, and the parasitemia markedly decreases after this (Fig. 289, *c*). The parasitemia was recorded to be especially high in young birds. In adult birds, gametocytes tend to gather in capillaries of internal organs, where they are significantly more numerous than in the peripheral circulation at all seasons of a year (Clark, 1964; Khan and Fallis, 1971b; Valkiūnas, unpublished).

Gametocytes develop in erythrocytes and lymphocytes. The morphology of mature gametocytes, which develop in both types of host cells, is similar. The initial stages of development of gametocytes in lymphocytes were studied by Clark (1965) in detail. The earliest forms seen inside the host cells are about 1 μm in diameter (Fig. 290, *1*, *2*). As the parasite develops, the nucleus of the host cell slightly enlarges, loses its oval contour and usually assumes a kidney-bean shape with the parasite located in the indentation (Fig. 290, *3–5*). As the size of the parasite increases, the intensity of staining of its cytoplasm also

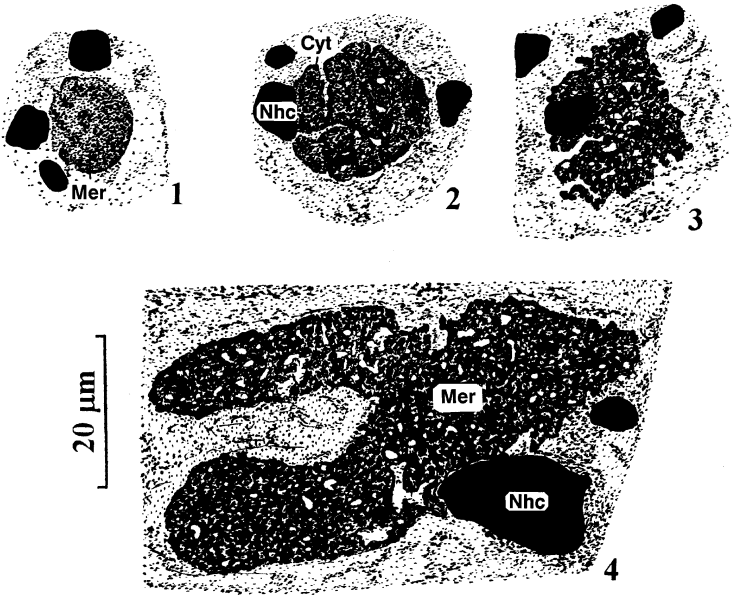

Figure 288 Exoerythrocytic meronts of *Leucocytozoon berestneffi* from *Cyanocitta cristata:*
1–3 – meronts in the liver: *1* – young parasite, *2* – parasite with cytomeres, *3* – mature parasite; *4* – mature renal meront dividing into merozoites; Cyt – cytomere; Mer – meront; Nhc – nucleus of host cell (modified from Khan and Fallis, 1971b).

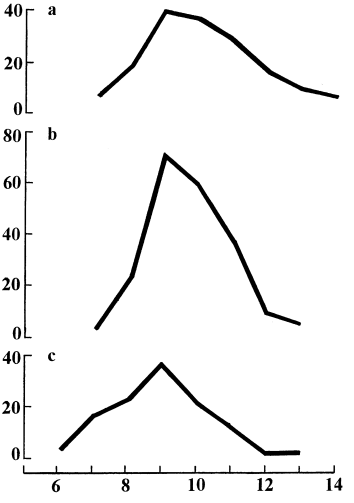

Figure 289 Dynamics of parasitemia of *Leucocytozoon sakharoffi* (*a*, *b*) and *L. berestneffi* (*c*) in birds experimentally infected with sporozoites:
a – *Corvus brachyrhynchos* ($n = 3$) and *C. cornix* ($n = 2$); *b* – *C. corax* ($n = 3$); *c* – *Cyanocitta cristata* ($n = 2$) and *Pica pica* ($n = 3$). The mean intensity of parasitemia (the number of parasites per 1000 erythrocytes) is shown on the ordinate, days after inoculation of sporozoites are shown on the abscissa (modified from Khan and Fallis, 1971b).

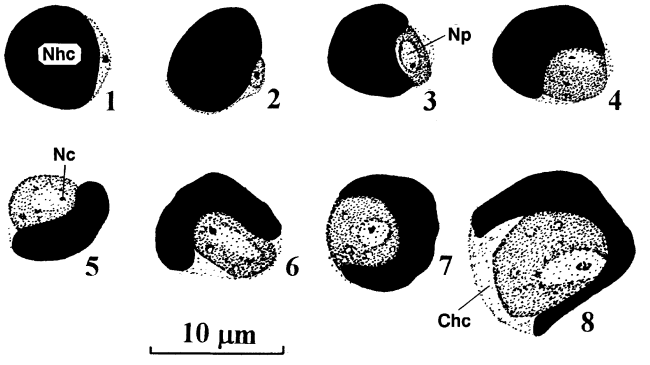

Figure 290 Initial successive stages of the development of gametocytes of *Leucocytozoon berestneffi* in lymphocytes of *Pica nuttalli*:
Chc – cytoplasm of host cell; Nc – nucleolus; Nhc – nucleus of host cell; Np – nucleus of parasite (modified from Clark, 1965). Explanations are given in the text.

increases; the cytoplasm acquires a darker blue colour, and vacuoles appear (Fig. 290, *6–8*). The nucleus of lymphocyte is pushed aside and markedly deformed. The process of development of gametocytes in erythrocytes is accompanied with marked deformation of infected cells and enlargement of their nuclei. The parasite also lies in the indentation of the nucleus of the host cell (Khan and Fallis, 1971b).

Table 150 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp. (according to Valkiūnas, 1988b).

Feature	*L. majoris*				*L. berestneffi*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	11				37			
Length		8.1–13.2	10.9	1.3		7.3–13.4	11.9	0.8
Width		8.2–12.1	10.5	1.3		7.9–14.0	11.4	0.6
Length of nucleus		3.4–6.2	4.2	1.0		1.2–5.4	3.9	0.4
Width of nucleus		1.6–3.2	2.5	0.8		1.1–3.9	2.1	0.3
Length of nucleus of host cell		18.9–34.9	25.3	3.6		–	–	–

Note: All sizes are given in micrometres.

Macrogametocytes (Fig. 291, *1–6*; Table 150) develop in roundish host cells; the cytoplasm frequently contains a few small vacuoles; valutin granules are usually present; gametocytes are roundish or sometimes of slightly oval form; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, markedly deformed, and lies peripherally, is of markedly variable form and can be cap-like (Fig. 291, *3*, *5*, *6*) or band-like (Fig. 291, *1*, *2*, *4*) in shape but never has dumbbell-shaped thickenings at both ends (see Fig. 278, *13, 14* for comparison); the band-shaped host cell nucleus frequently extends more than 2/3 of the gametocyte's circumference (Fig. 291, *1*, *2, 4*); the cytoplasm of host cells is largely replaced by gametocytes,

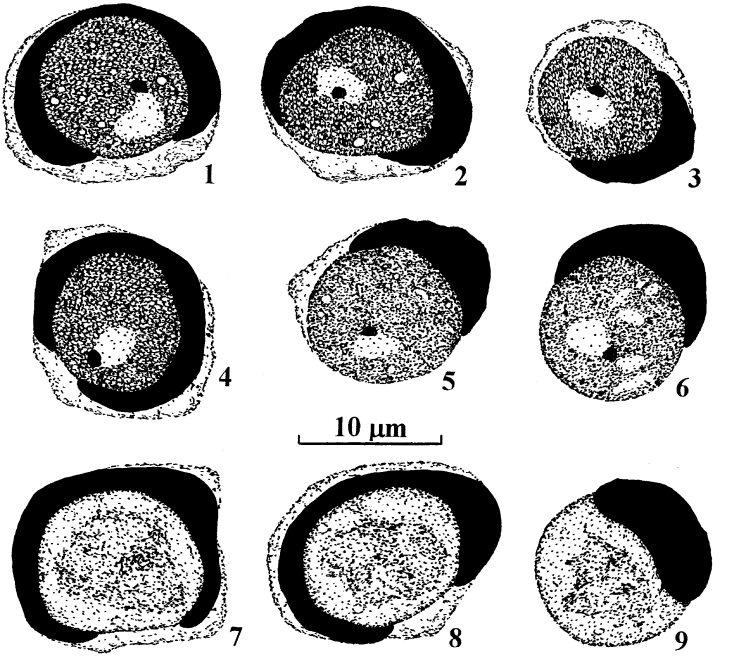

Figure 291 Gametocytes of *Leucocytozoon berestneffi* from the blood of *Pica pica*: *1–6* – macrogametocytes; *7–9* – microgametocytes.

and is sometimes even invisible (Fig. 291, *6*) but more frequently is present around the gametocytes as a more or less evident, pale margin of variable form (Fig. 291, *1–5*).

Microgametocytes (Fig. 291, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Relapses are well evident in spring and summer, and are synchronized with the breeding period of birds.

Development in vector has not been studied in detail. Sporogony is completed and infective sporozoites develop in the simuliid flies *Prosimulium decemarticulatum* and *Simulium aureum* (Khan and Fallis, 1971b).

Specificity has been insufficiently investigated. The parasite, isolated from *Cyanocitta cristata*, does not complete development in *Corvus corax* and *C. brachyrhynchos*, and vice versa (Khan and Fallis, 1971b).

Comments. Bennett and Peirce (1992b) considered *L. berestneffi* to be a junior synonym of *L. sakharoffi*. However, it is difficult to agree with this nomenclature act. Indeed, morphology of gametocytes and their host cells of these two species is identical. Moreover, the available data on exoerythrocytic merogony of *L. berestneffi* and the close species, *L. sakharoffi* are incomplete and even contradictory. Anyhow, according to current knowledge, both the morphology and the location of meronts of these two species differ not more than they differ in each of these species during their development in different vertebrate hosts. Thus, the data both on (i) the exoerythrocytic development and (ii) the morphology of gametocytes and their host cells cannot be used for identification of *L. berestneffi* and *L. sakharoffi*. It should be also noted that exoerythrocytic development of *L. berestneffi* and *L. sakharoffi* has been studied either in naturally infected birds or experimentally infected

birds which, in both cases, were obtained in nature. Under such circumstances, (i) it is difficult to exclude completely an opportunity of mixed infection with two species and, moreover, (ii) the exo-erythrocytic stages of the same species can be studied at different stages of their development. Both these factors can contribute to the above mentioned differences in the exoerythrocytic merogony. Thus, careful and critical analysis of the data available in the literature is required. Exoerythrocytic merogony of leucocytozoids in corvid birds should be studied additionally. However, the results of experimental investigations show that the leucocytozoids of *Cyanocitta cristata* cannot be transmitted to *Corvus corax* and *C. brachyrhynchos*, and vice versa (Khan and Fallis, 1971b). Furthermore, the prepatent period of development of *L. berestneffi* in *C. cristata* is 92 h after infection with sporozoites, and this is 24 h less than in *L. sakharoffi* during its development in *C. corax* and *C. brachyrhynchos*. Thus, based on evidence presented above, it makes sense to admit at present the existence of two distinct species. *Leucocytozoon berestneffi* is proposed to restrict to the corvid birds of the genera *Pica, Cyanocitta,* and *L. sakharoffi,* of the genus *Corvus* and some other bird genera. This proposal (as any other at present) has shortcomings, but it also (i) provides an opportunity to gather information on the distribution of the parasites in different vertebrate hosts taking in mind the experimental data on their specificity and (ii) restricts the introduction of new poor-grounded specific names for naming morphologically identical leucocytozoids parasitizing closely related birds. Further investigations are required to solve the problem on the range of vertebrate hosts of *L. berestneffi* and *L. sakharoffi.*

7. **Leucocytozoon (Leucocytozoon) macleani** Sambon, 1908

Leucocytozoon macleani Sambon, 1908: 328, Fig. – *L. mesnili* Léger and Mathis, 1909: 743, Pl. 19, Fig. 1–7. – *L. sabrazesi* Mathis and Léger, 1910a: 23. – *L. kerandeli* Mathis and Léger, 1911b: 282, Pl. 4, Fig. 9–11. – *L. martini* Mathis and Léger, 1911a: 212. – *L. schuffneri* Prowazek, 1912: 263 (partim). – *L. francolini* Kerandel, 1913: 434, Pl. 6, Fig. 1–21. – *L. macleani*: Bennett *et al.*, 1991c: 1416 (=*L. francolini, L. kerandeli, L. martini, L. mesnili, L. sabrazesi, L. schuffneri*).

Type vertebrate host. *Phasianus colchicus* L. (Galliformes).
Additional vertebrate hosts. Some species of the Phasianidae (Table 151).
Vector. *Simulium metatarsale* (Diptera: Simuliidae).
Type locality was not specified in the original description. Probably England.
Distribution. The Central and Southern Palearctic, the Ethiopian and Oriental zoogeographical regions.
Type material. Neohapantotypes (*Phasianus colchicus,* 1983–1984, Pavia, Northern Italy, L. Sacchi) are deposited in CDSA.
Etymology was not specified in the original description.

Main diagnostic characters. A parasite of species of the Galliformes whose gametocytes develop in roundish and fusiform host cells. The nucleus of fusiform host cell is cap-like in form or resembles the nucleus of uninfected erythrocyte in shape; the nucleus extends less than 1/3 of the circumference of the gametocyte. Currently, this parasite can be identified with confidence only in birds of the family Phasianidae.

Development in vertebrate host
According to the available data (Hong *et al.*, 1990), exoerythrocytic merogony in domestic chicken, infected by inoculation of sporozoites, takes place in hepatic cells. Meronts, containing over 100 merozoites, were observed in the hepatocytes 72 h after infection. It is possible that subsequent generations of meronts also develop in macrophages.

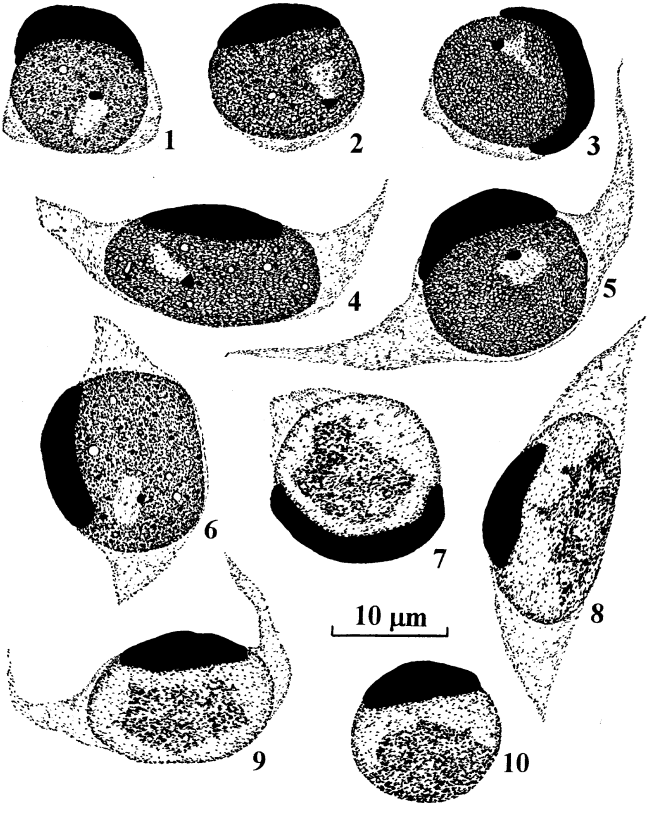

Figure 292 Gametocytes of *Leucocytozoon macleani* from the blood of *Phasianus colchicus*: *1–6* – macrogametocytes; *7–10* – microgametocytes.

Megalomeronts were not found. The prepatent period is about 4.5 days. The peak of parasitemia was recorded 15 to 25 days after the infection.

Exoerythrocytic meronts were also found in the naturally infected *Francolinus leucoscepus* in Kenya (Jong, 1971). They were described under the name *Leucocytozoon neavei*. The parasites were observed only in one bird in the brain and kidneys. In the brain, the meronts located in enlarged capillaries. Endothelial cells adjacent to meronts and the nuclei of infected cells were enlarged. Cytomeres were not seen. Fully grown meronts are roundish or of oval form. They vary from 29 to 45 μm in diameter. In the kidneys, the

Table 151 List of vertebrate hosts of *Leucocytozoon macleani*.

Alectoris barbara	*F. africanus*	*F. sinensis*
A. chukar	*F. ahantensis*	*F. swainsonii*
A. graeca	*F. bicalcaratus*	*Gallus gallus*
Coturnix chinensis	*F. capensis*	*Pavo cristatus*
C. coturnix	*F. leucoscepus*	*Perdix perdix*
Francolinus adspersus	*F. levaillantii*	
F. afer	*F. pondicerianus*	

meronts developed in renal tubular cells, and they were of irregular shape. Mature meronts extend along the capillaries. They were approximately 84 μm in length and 6 μm in width, and contained numerous merozoites.

Macrogametocytes (Fig. 292, *1–6*, Table 149) develop in roundish and fusiform host cells. The morphology of gametocytes and their host cells is the same as for *L. lovati* (see p. 756). However, markedly attenuated cytoplasmic processes (Fig. 285, *7*) have been recorded much more rarely than in *L. lovati*, but occur during the development of the parasite in some vertebrate hosts. The taxonomic value of this character is unclear.

Microgametocytes (Fig. 292, *7–10*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Gametocytes both in roundish and fusiform host cells have been frequently recorded in peripheral circulation of naturally infected birds.

Development in vector

In the natural vector, the simuliid fly *Simulium metatarsale,* the parasite completes the development three to four days after blood meal on infected domestic chicken (Hong *et al.*, 1990). Exflagellation was observed 2 to 5 min after the infection, and ookinete develops 1 h after the infection. Mature oocysts were observed 72 to 84 h after the blood meal. They contain 30 to 50 sporozoites which appear in salivary glands of vector 96 h after the infection.

Exflagellation both *in vitro* and in the mosquito *Aedes aegypti* initiates with difficulty and proceeds slowly (Colley *et al.*, 1974). Under such circumstances, a few microgametes appear approximately 1 h after the exflagellation was induced.

The results of some preliminary observations (Kadyrova *et al.*, 1990) show that the simuliid flies *Tetisimulium alajensis* and *Odagmia ornata* can be potential vectors of the parasite of chukar *Alectoris chukar*.

Pathogenicity. The leucocytozoonosis of domestic chicken, caused by *L. macleani* (=*L. sabrazesi*), has been frequently recorded in South-East Asia (Lee *et al.*, 1969). In other regions, this parasite in domestic chicken is clearly spotty in distribution, and has been much less frequently found. Native breeds of chicken are susceptible but usually show subclinical infection. Chickens of introduced breeds usually show mild infection with clinical symptoms, but they sometimes even die in the course of one to six months. Productivity of birds of introduced breeds decreases, and they sometimes need to be rejected, first of all, because of economic losses in egg production. The clinical signs of infection usually are slight depression, slight pale shrunk comb, greenish droppings, anaemia, gradual emaciation and ruffled feathers, mild decrease of egg production. In severe cases, the loss of appetite and stopped egg production were recorded. The disease is usually not severe, and rapidly turns into a chronic stage. The infected birds can be found all year around in the South-East Asia. On Taiwan, the prevalence of infection was recorded to be the highest from March to September. It is worth noting that this parasite has been rarely found in peripheral circulation of chickens under two months old, but gametocytes are common in the blood of mature birds.

Specificity has been insufficiently investigated. Turkeys and guinea-fowls were not infected when kept in a locality with active transmission of this parasite (Mathis and Léger, 1910d).

Comments. *Leucocytozoon macleani* is especially similar to *L. neavei* and *L. lovati*. *Leucocytozoon macleani* can be distinguished from *L. neavei* on the basis of its gametocytes in roundish host

cells which have not been observed in *L. neavei* so far. However, it should be noted that gametocytes in roundish host cells of *L. macleani* cannot always be found in the peripheral blood of naturally infected birds which are investigated only one time. The investigation of parasitemia in its dynamics is required for the detection of such gametocytes. Gametocytes and their host cells of *L. macleani* are indistinguishable from those of *L. lovati*. Furthermore, life cycles of these species as well as the other stages of their development in different vertebrate hosts are insufficiently investigated, and this precludes a detail comparison of these two parasites. Thus, it is impossible to exclude that *L. macleani* can be a subspecies of *L. lovati*. The data on geographical distribution of these parasites is a basis for accepting their validity at present. *Leucocytozoon macleani* is more restricted to tropics and subtropics, and it also has been recorded in the temperate region where it managed to penetrate sometimes into the zone of coniferous forest. On the contrary, *L. lovati* is actively transmitted at high latitudes on the Northern hemisphere, and it even penetrated beyond the North Polar Circle. Domestic chicken is a good indicator of the geographical distribution of *L. macleani*. This parasite, which was also mentioned as *L. mesnili* and *L. sabrazesi* in the literature, has never been recorded north of the territory of Kazakhstan in the Palearctic. The data on geographical distribution of *L. macleani* can be regarded as quite reliable due to well investigated fauna of parasites of domestic chicken. Based on the above-mentioned facts, it looks preferable at present to consider *L. macleani* to be a distinct species parasitizing birds of the family Phasianidae.

8. **Leucocytozoon (Leucocytozoon) sakharoffi** Sambon, 1908

Leucocytozoon sakharoffi Sambon, 1908: 325. – *L. laverani* França, 1912a: 17. – *L. zuccarellii* Léger, 1913: 522. – *L. sakharoffi*: Coatney and West, 1938: 606 (=*L. zuccarellii*); Bennett and Peirce, 1992b: 695. (=*L. laverani*).

Type vertebrate host. *Corvus corax* L. (Passeriformes).
Additional vertebrate hosts. Some species of corvid birds (Table 152).
Vectors. *Prosimulium decemarticulatum*, *Simulium angustitarse*, *S. aureum*, and *S. latipes* (Diptera: Simuliidae).
Type locality was not specified in the original description. This species was described on the basis of the literature data of Russian scientists (Sakharoff, 1893; Berestneff, 1904), who collected their materials in the environs of Tbilisi (Georgia) and Voronezh (Russia), respectively.
Distribution. Common parasite of corvid birds in the Holarctic. It has been much less frequently recorded in the southern zoogeographical regions. Probably it is cosmopolitan.
Type material. Neohapantotype (No. 986, *Corvus corone*, 6.07.1953, St. Albans Herts, UK, J.R. Baker) is deposited in CPG. Good additional preparations of exoerythrocytic meronts are deposited in CPG, and of gametocytes, in CDVA.
Etymology. This species is named in honour of Russian scientist N. Sakharoff in recognition of his contribution to the field of avian blood parasitology in the beginning of the 20th century.

Main diagnostic characters. A parasite of species of the Corvidae whose gametocytes develop in roundish host cells. Nucleus of the host cell vary from cap-like to

Table 152 List of vertebrate hosts of *Leucocytozoon sakharoffi*.

Corvus brachyrhynchos	*C. monedula*
C. cornix	*C. splendens*
C. corone	*Dendrocitta vagabunda*
C. frugilegus	*Garrulus glandarius*
C. macrorhynchos	*Nucifraga caryocatactes*

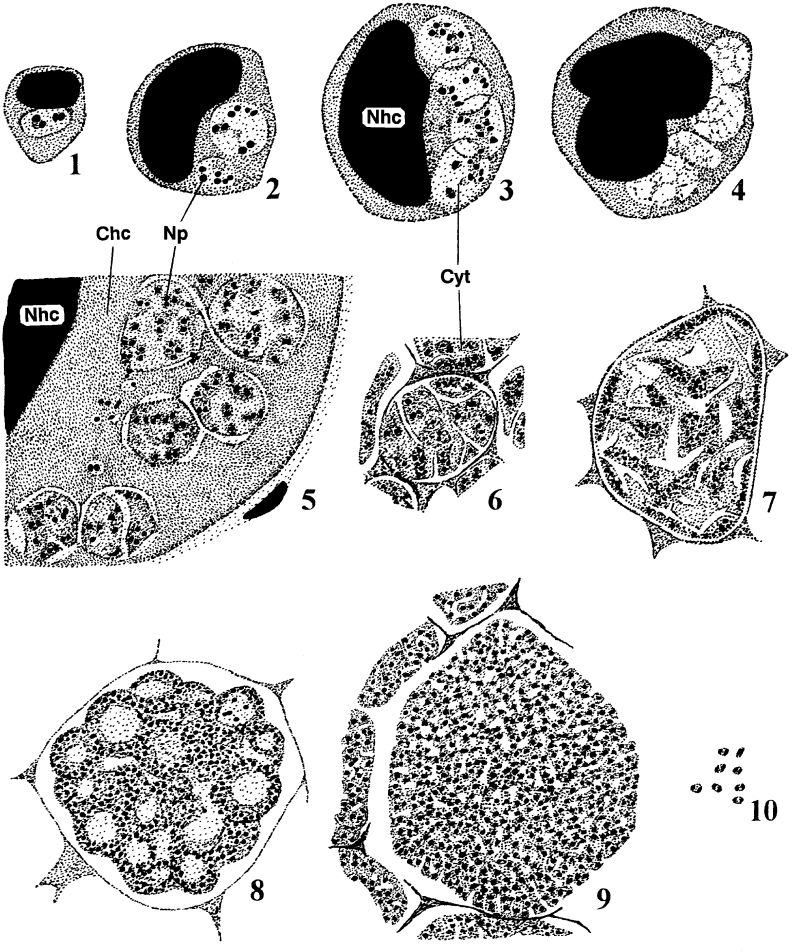

Figure 293 Development of megalomeronts of *Leucocytozoon sakharoffi* in spleen of *Corvus cornix*:
1 – young megalomeront in macrophage; *2–5* – early stages of the development of megalomeront; *6–9* – diagram of successive stages of the development of cytomeres; *10* – merozoites; Cyt – cytomere; Chc – cytoplasm of host cell; Nhc – nucleus of host cell; Np – nucleus of parasite (modified from Wingstrand, 1948). Explanations are given in the text.

band-like in form, it can extend up to 2/3 and even more of the circumference of the gametocyte. This parasite does not develop in corvid birds of the genera *Pica* and *Cyanocitta.*

Development in vertebrate host

The fate of sporozoites, inoculated into blood stream of birds, is unknown precisely. Exoerythrocytic merogony was studied in naturally infected *Corvus cornix* (Wingstrand, 1947, 1948) and *C. frugilegus* in Europe (Baker, 1970, 1971, 1974) and in experimentally infected *C. corax* and *C. brachyrhynchos* in North America (Khan and Fallis, 1971b). The exoerythrocytic merogony has been recorded to have several distinctive features in European and American corvid birds, and thus it is described separately below.

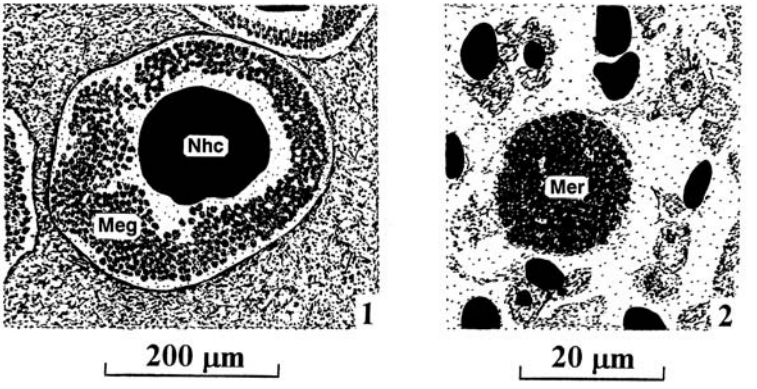

Figure 294 General view of the exoerythrocytic meronts of *Leucocytozoon sakharoffi*: *1* – nearly mature megalomeront with numerous cytomeres in spleen of *Corvus cornix*; *2* – mature hepatic meront dividing into separate merozoites from *Corvus brachyrhynchos*; Meg – megalomeront; Mer – meront; Nhc – nucleus of host cell (*1* is modified from Wingstrand, 1948; *2* is modified from Khan and Fallis, 1971b).

Merogony in European birds of the genus Corvus

It is likely that sporozoites invade parenchymal hepatic cells and initiate development of the first generation of exoerythrocytic meronts. These meronts were found in hepatocytes of *Corvus frugilegus*. They were about 15×18 μm in diameter. Cytomeres were not seen. Probably part of merozoites from the hepatic meronts invade blood cells and initiate development of gametocytes, and other merozoites are spread via blood stream into numerous organs where they are captured by macrophages and initiate development of megalomeronts. This mode of development has not been proved experimentally. However, megalomeronts are extremely numerous in naturally infected young *C. cornix,* and they appear together with gametocytes. This testifies to the presence of merogony, which precede the appearance of megalomeronts, in the infected birds.

Megalomeronts develop in macrophages (Fig. 293, *1*) and were observed in the spleen, liver, pancreas, thyroid glands, hypophysis, and gonads. Megalomeronts are especially numerous in the spleen which is markedly enlarged in infected birds. As the parasite develops, the nucleus of infected macrophage is pushed aside and markedly enlarged, and cytoplasm also markedly increases in amount (Fig. 293, *1–4*). Nucleus of macrophage, which contain mature megalomeront, reaches 190 μm in diameter, and the infected host cells are close to 500 μm in diameter. Mature megalomeronts and their host cells can be seen with a naked eye. Growing megalomeront breaks up into separate parts (cytomeres), each containing several nuclei (Fig. 293, *2–5;* Pl. I, *4*). As cytomeres increase in size, the number of nuclei also increases. Subsequently, each cytomere breaks up into numerous smaller-size bladder-like portions (subcytomeres) with the nuclei gathering on the surface (Fig. 293, *6–8*). Merozoites develop inside cytomeres. As megalomeront develops, the cytomeres are packed with numerous merozoites, and boundaries between the cytomeres disappear gradually (Figs. 293, *9*; 294, *1*). Mature megalomeronts were recorded to be up to 480 μm in diameter. They are packed with a homogeneous mass of merozoites.

Megalomeronts rupture, and released merozoites enter the blood stream. The merozoites look like slightly oval bodies about 1 μm in diameter with two granules of chromatin lying on the poles and giving a bipolar appearance (Fig. 293, *10*). It is likely that

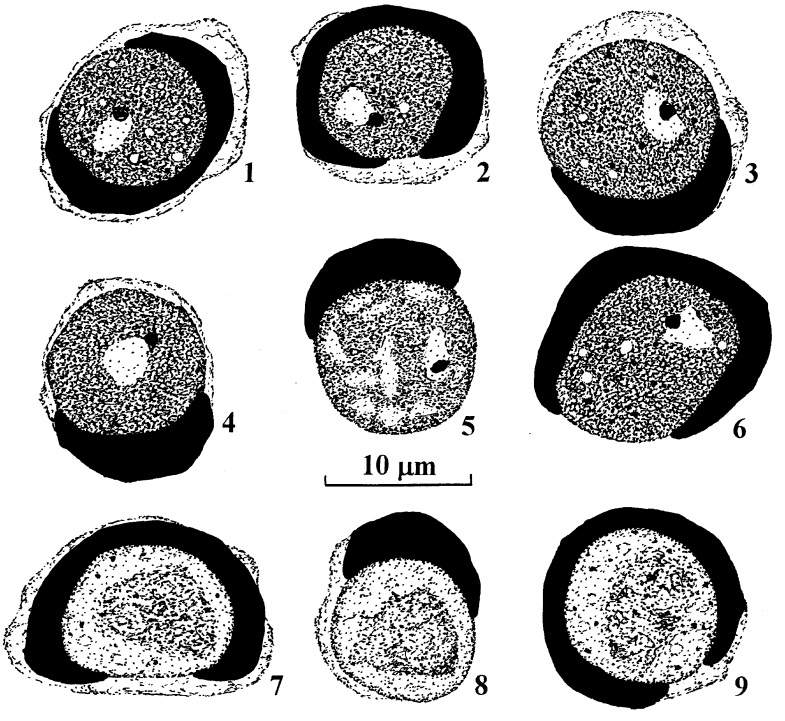

Figure 295 Gametocytes of *Leucocytozoon sakharoffi* from the blood of *Corvus cornix*: *1–6* – macrogametocytes; *7–9* – microgametocytes.

part of these merozoites invade blood cells and initiate development of gametocytes, and other part of merozoites invade cells of the liver and grow into small hepatic meronts which were recorded only in adults of *C. cornix*. The nuclei in mature hepatic meronts are not numerous. These meronts do not induce enlargement of infected cells and are similar to the initial stages of development of hepatic meronts of *L. berestneffi* during its development in *Pica nuttalli* (Clark, 1965). Probably they are responsible for maintenance of chronic parasitemia and relapses.

It should be noted that megalomeronts were found only in nestlings of *C. cornix*. They were not observed in adults of *C. cornix* and in adults and juveniles of *C. frugilegus*. It is likely that megalomeronts develop only in the beginning of primary infection of birds. On the contrary, small hepatic meronts were found only in adults of *C. cornix*.

Merogony in the North American birds of the genus Corvus

Meronts were found in the liver and kidneys of *Corvus corax* and *C. brachyrhynchos* which were infected experimentally by inoculation of sporozoites. The meronts were not observed in the spleen, heart, lungs, pancreas, brain, and bone marrow. Megalomeronts do not develop in these birds. In the liver, meronts were observed 7 or 8 days after infection, and they were already not seen in this organ between 10 and 12 days after the infection. In the kidneys, a few mature meronts were found on the 14th day after the infection. The meronts are not seen in *C. brachyrhynchos* 35 days after infection. It is important to note that gametocytes appear in the blood of birds six days after inoculation of sporozoites. Therefore, it is

probable that meronts, which were recorded from the seventh day after infection, belong to the second generation. However, the first generation of meronts has not been described so far. According to the evidence presented above, these meronts should mature not later than by the sixth day after infection. It looks likely that part of their merozoites initiate development of gametocytes, and the other part of the merozoites induce the secondary merogony in the liver and kidneys as it takes place in *L. dubreuili* infection.

Meronts both in the liver and kidneys induce enlargement of nuclei of host cells. As the parasites develop, cytomeres appear. Mature meronts are packed with a homogeneous mass of merozoites (Fig. 294, *2*). Mature hepatic meronts ($n = 20$) were 14 to 20 by 15 to 24 (on average 16×19) μm in size. The largest observed hepatic meront reached 25×64 μm in size. Mature renal meronts ($n = 20$) were 13 to 19 by 14 to 20 (on average 15×18) μm.

Table 153 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. fringillinarum*				*L. sakharoffi* (according to Bennett and Peirce, 1992b)		
	n	lim	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	44				35		
Length		7.5–17.8	13.1	2.4		12.6	1.3
Width		8.1–16.1	12.4	2.0		10.9	1.0
Length of nucleus		2.3–4.6	3.6	0.8		3.8	0.8
Width of nucleus		1.4–3.7	2.7	0.7		2.5	2.1
Length of nucleus of host cell		6.2–18.1	12.7	2.9		29.8	3.2

Note: All sizes are given in micrometres.

Thus, the morphology of exoerythrocytic meronts, which were described in the North American *Corvus corax* and *C. brachyrhynchos*, is more similar to the morphology of meronts found in European *C. frugilegus*. In all these birds, the observed hepatic meronts are similar in size. The differences include (i) the presence of renal meronts and (ii) the presence of cytomeres in hepatic meronts during the development of the parasite in the North American birds. Megalomeronts have been recorded only in juveniles of *C. cornix* in Europe so far. It is impossible to exclude currently that the process of exoerythrocytic merogony can differ in different vertebrate hosts at different study sites as it takes place during development of *L. simondi* in its adapted and not adapted vertebrate hosts (see p. 790).

The prepatent period is 116 h in *Corvus corax* and *C. brachyrhynchos*, and it is 192 h in *C. frugilegus* after experimental infection with sporozoites (Baker, 1971; Khan and Fallis, 1971b). A peak of parasitemia in *Corvus corax*, *C. cornix*, and *C. brachyrhynchos* was recorded at the ninth day after infection (Fig. 289, *a*, *b*). Maximum intensity of parasitemia in nestlings of *C. cornix* was recorded to be 160 gametocytes per 1000 erythrocytes (Wingstrand, 1948).

Gametocytes develop in erythrocytes and lymphocytes (Wingstrand, 1948; Ramisz, 1962; Khan and Fallis, 1971b).

Macrogametocytes (Fig. 295, *1–6*; Pl. II, *5*; Table 153) develop in roundish host cells. The morphology of gametocytes and their host cells is identical to *L. beresneffi* (see p. 763).

Microgametocytes (Fig. 295, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Relapses are well evident in spring and summer. They are clearly synchronized with the breeding period of birds.

Development in vector

Microgametes vary from 20 to 30 μm in length (Garnham, 1966). Ookinetes were seen in the midgut of simuliid flies up to 72 h after ingestion of mature gametocytes at temperature close to room temperature (Fallis and Bennett, 1961b). They were up to 40 μm in length, and each ookinete possesses a more or less off-centre located nucleus and several large 'vacuoles.' Oocysts only slightly increase in size during their development. Mature oocysts were about 12 μm in diameter. They produce up to 50 sporozoites with one end rounded and other end pointed. Sporozoites of the North American strains were recorded to be on average about 12 μm in length, and the European strain about 9 μm in length (Fallis and Bennett, 1961b; Baker, 1971). First mature oocysts as well as sporozoites in the salivary glands of vectors were seen three to four days after ingestion of gametocytes. Sporogony is not synchronized. A few oocysts were observed in the midgut of vectors 18 days after infection.

Pathogenicity has been insufficiently studied. Young *Corvus cornix* were recorded to die during heavy infections.

Specificity has been insufficiently investigated. The parasite isolated from *Corvus corax* (Corvidae) completes development in *C. brachyrhynchos*, and vice versa. However, both of these isolates failed to complete development in *Cyanocitta cristata* (Corvidae) (Khan and Fallis, 1971b). Attempts of the author to transmit this parasite from *Corvus cornix* to *Pica pica* by inoculation of sporozoites developed in *Simulium* sp. were also unsuccessful, but *Corvus cornix* were easily infected.

Comments. A problem of the validity of *L. sakharoffi* and *L. berestneffi* is considered in 'Comments' to *L. berestneffi*.

9. **Leucocytozoon (Leucocytozoon) toddi** Sambon, 1908

Leucocytozoon toddi Sambon, 1908: 326. – *L. audieri* Laveran and Nattan-Larrier, 1911: 688, Fig. 1–6. – *L. mathisi* França, 1912a: 19. – *L. martyi* Commes, 1918: 33. – *L. circaeti* Sergent and Fabiani, 1922: 480. – *L. laverani* Franchini, 1923: 122, Fig. 1 (nom. praeocc., non França, 1912). – *L. franchini* França, 1927: 16. – *L. mathisi* var. *buteonis* Coatney and Roudabush, 1937: 1017, Pl. 2, Fig. 7, 8. – *L. bacelari* Tendeiro, 1947: 318, Fig. 7, 8. – *L. beaurepairei* Travassos Santos Dias, 1954: 9, Fig. 1. – *L. mathisi*: Hsu *et al.*, 1973: 196 (=*L. mathisi* var. *buteonis*). – *L. toddi*: Greiner and Kocan, 1977: 766, Fig. 1–2, Table 1 (=*L. audieri*, *L. bacelari*, *L. beaurepairei*, *L. circaeti*, *L. franchini*, *L. martyi*, *L. mathisi*). – *L. muratovi* Subkhonov, 1980: 45, Fig. 1, A. – *L. buteonis*: Valkiūnas, 1988b: 127. – *L. toddi*: Valkiūnas, 1988b: 127, Fig. 9 (=*L. buteonis*); Valkiūnas, 1989b: 47, Fig. 1 (=*L. muratovi*).

Type vertebrate host. *Kaupifalco monogrammicus* (Temm.) (Falconiformes).

Additional vertebrate hosts. Numerous species of the Falconiformes (over 50 species).

Type locality. Congo.

Distribution. Common parasite of falconiform birds in the Holarctic where the highest prevalences of infection have been recorded. It was found in the Ethiopian, Oriental, and Neotropical

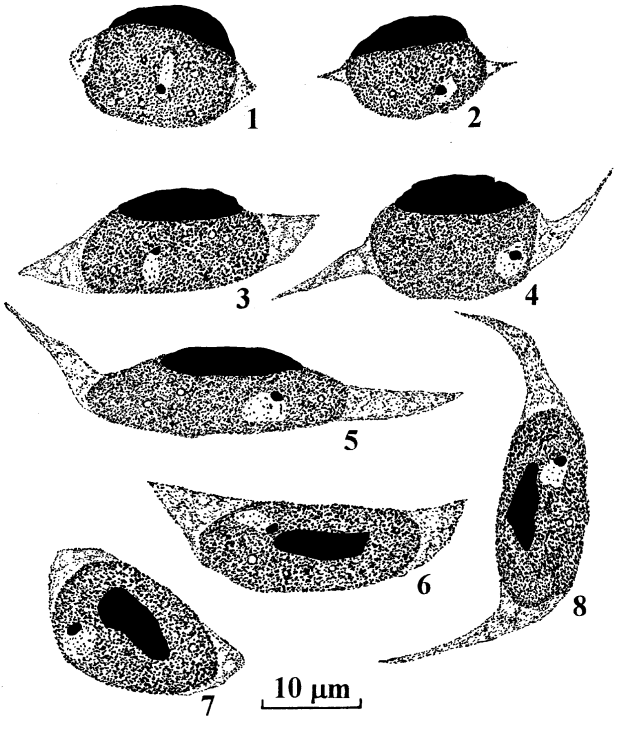

Figure 296 Macrogametocytes and their host cells of different shape of *Leucocytozoon toddi* from the blood of *Accipiter nisus*. Explanations are given in the text.

zoogeographical regions. It is worth noting that this parasite is especially common in birds of the family Accipitridae.

Type material has not been designated. A series of good additional slides is deposited in IRCAH and CDVA.

Etymology. This species is named in honour of Dr. J.L. Todd.

Main diagnostic characters. A parasite of species of the Falconiformes whose gametocytes develop in roundish and fusiform host cells. Gametocytes in roundish host cells are extremely rare, and usually only gametocytes in fusiform host cells are present in the blood. Nucleus of fusiform host cell is of cap-like form or almond-shaped or resembles by its shape the nucleus of uninfected erythrocyte; the nucleus extends less than 1/3 of the circumference of the gametocyte.

Development in vertebrate host

Macrogametocytes (Figs. 296; 297, *1–4*, *6*, *7*; Pl. II, *6*; Table 154) develop in roundish and fusiform host cells; young gametocytes are frequently seen inside young erythrocytes in intensively infected nestlings, and the gametocytes (at least part of them) develop in these cells; the cytoplasm of gametocytes frequently contains valutin granules; vacuoles are not numerous, and they are not always present; gametocytes in roundish host cells are roundish or of oval form (Fig. 297, *4*, *6*, *7*), and gametocytes in fusiform host cells vary from roundish to oval and even elongated (Figs. 296; 297, *1–3*; Pl. II, *6*); the parasite nucleus is

of variable form and position; the nucleolus is prominent and well seen; the nucleus of roundish host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap or sometimes band, usually extends less that 1/2 of the circumference of gametocyte (Fig. 297, *4, 6, 7*); the nucleus of fusiform host cell is deformed and slightly enlarged, usually pushed aside and lies peripherally as a cap-like or almond-shaped structure or resembles by its form the nucleus of uninfected erythrocyte, extends less than 1/3 of the

Table 154 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. toddi* (according to Valkiūnas, 1988b, 1989b)				*L. simondi* (according to Valkiūnas, 1988b)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	17				32			
Length		9.1–13.4	12.0	0.7		7.7–16.2	13.1	0.8
Width		8.6–13.1	11.8	0.8		6.8–15.8	12.0	1.0
Length of nucleus		3.1–5.3	4.4	0.4		2.7–5.1	3.8	0.7
Width of nucleus		1.7–3.8	2.4	0.3		2.2–4.0	2.9	0.8
Length of nucleus of host cell		10.2–20.7	13.6	2.2		7.2–16.9	13.0	2.0
Macrogametocyte in fusiform host cell	22				32			
Length		14.6–30.3	17.6	4.2		13.9–24.4	18.8	2.2
Width		4.8–13.6	8.1	2.0		3.7–13.1	7.2	2.2
Length of nucleus		3.4–7.0	5.3	1.0		2.4–6.8	5.0	1.2
Width of nucleus		3.3–6.1	4.2	0.9		1.8–4.7	3.2	0.9
Length of nucleus of host cell		6.4–18.0	11.4	3.2		31.2–48.5	38.9	4.6

Note: All sizes are given in micrometres.

circumference of gametocyte (Figs. 296, *1–5*; 297, *1, 2*); occasionally the host cell nucleus can be completely enclosed by gametocyte (Figs. 296, *6–8*; 297, *3*); the cytoplasm of roundish host cells is largely replaced by gametocytes, and is sometimes even invisible but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 297, *4*, *6*, *7*); the cytoplasm of fusiform host cells forms well evident and markedly variable (both in form and length) processes at the ends of gametocytes (Figs. 296, *1–8*; 297, *1–3*); fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are common.

Microgametocytes (Fig. 297, *5*, *8–10*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Only gametocytes in fusiform host cells usually have been recorded in *L. toddi*. Gametocytes in roundish host cells have been extremely rarely found. The reason of this is unclear. Valkiūnas (1989b) has investigated the frequency of occurrence of gametocytes in roundish and fusiform host cells in 11 species of the Palearctic falconiform birds during their seasonal migration on the Curonian Spit in the Baltic Sea and in the foothills of Western Tien-Shan (South Kazakhstan). Only gametocytes in fusiform host cells were recorded in 99.6±0.3% of the infected birds. Gametocytes in roundish host cells were found only twice, in one *Accipiter badius* and one *Falco subbuteo*. It is worth noting that gametocytes in

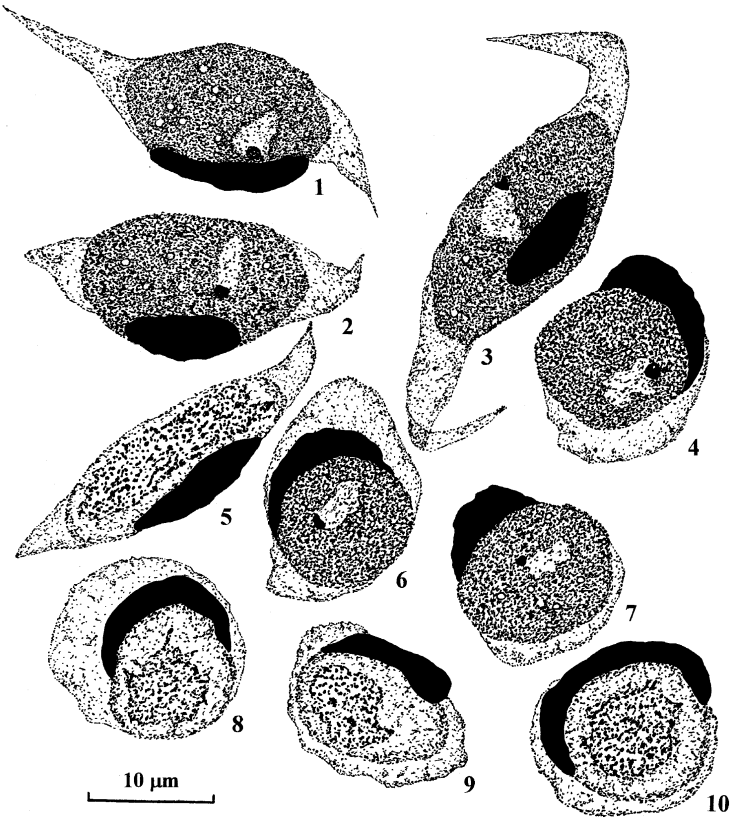

Figure 297 Gametocytes of *Leucocytozoon toddi* from the blood of *Accipiter badius*: *1–4*, *6*, *7* – macrogametocytes; *5*, *8–10* – microgametocytes.

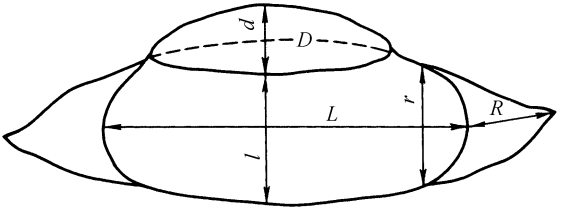

Figure 298 General diagram to measure gametocytes and host cells of *Leucocytozoon toddi*: *L*, *l* – gametocyte; *D*, *d* – nucleus of host cell; *R*, *r* – cytoplasmic processes of host cell. Capital letters denote length and small letters denote width (modified from Valkiūnas and Iezhova, 1990a).

roundish host cells were not observed in the blood of 505 infected *Accipiter nisus* during seasonal migrations. These data are of theoretical interest, as they testify to the rarity of gametocytes in the roundish host cells in the falconiform birds at the late period of infection (in autumn) and in relapsed infections (in spring). Most probably, gametocytes in roundish host cells in *L. toddi* develop only in the beginning of primary parasitemia, and the time of

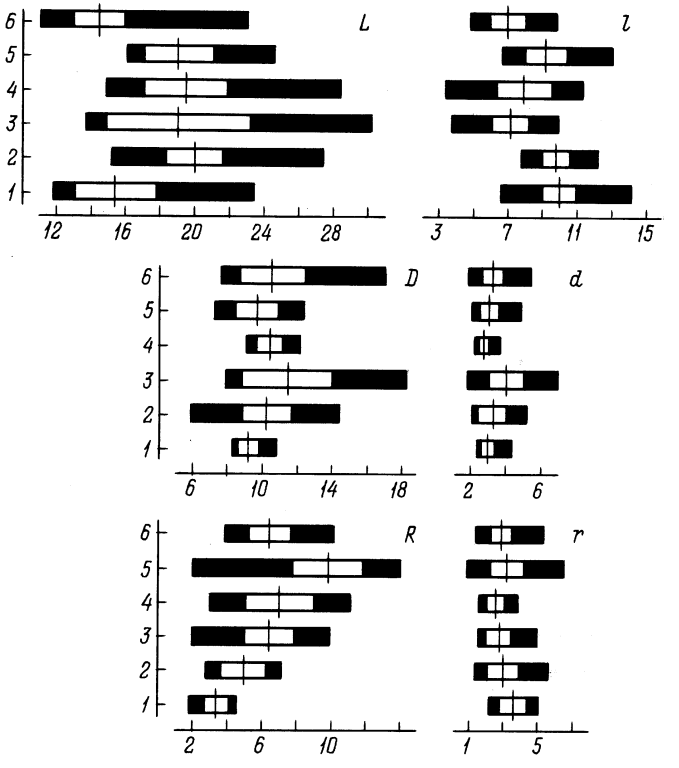

Figure 299 Morphometric features of macrogametocytes and their fusiform host cells of *Leucocytozoon toddi* from *Accipiter nisus* of the West-European (*1–3*) and Indian-Asiatic (*4–6*) directions of migration:
The size, μm, is shown on the abscissa. The central vertical line equals the mean; the white bar represents one standard error, and the black bar represents the limit of variation. Other symbols as in Fig. 298 (modified from Valkiūnas and Iezhova, 1990a).

their existence is short. This conclusion corresponds to the data of Peirce and Marquiss (1983) who observed gametocytes of *L. toddi* in roundish host cells mainly in nestlings.

Gametocytes in fusiform host cells are characterized by markedly variable morphometric characters during their development both in the same and different vertebrate hosts (Greiner and Kocan, 1977; Valkiūnas and Iezhova, 1990a). This is illustrated in Figs. 296, 297, and 299. Morphometric parameters of gametocytes and their host cells are not good characters for identification of *L. toddi.* During identification of this species, the attention should be, first of all, paid on (i) the form of infected host cells and (ii) the form and location of their nuclei.

D e v e l o p m e n t i n v e c t o r has not been investigated in detail. Sporogony is completed in the simuliid flies *Prosimulium decemarticulatum*, *Simulium aureum,* and *S. quebecense* (Diptera: Simuliidae). However, the ability of these flies to transmit the infection has not been proved so far (Bennett *et al.*, 1993a).

P a t h o g e n i c i t y has been insufficiently investigated. Peirce and Marquiss (1983) suggested that *L. toddi* can be a contributing factor to the mortality of chicks of *Accipiter*

nisus in some localities. However, there were no significant differences in mortality rate in infected and uninfected young and adult *A. nisus* in the observation based on recaptures of ringed *A. nisius* in the UK (Ashford *et al.*, 1990, 1991). It should be noted that the primary parasitemia of *L. toddi* is frequently extremely high. Chicks, which acquire primary infection in the nests, have an advantage in comparison to the juvenile birds, which acquire the infection after leaving the nests (but still live near the nest), because the former receive marked support from parents during the heavy stage of infection and the latter do not. So, it is an advantage for the chicks to be infected when they are under the parents. The fate of infected juvenile birds, which acquire primary infection after leaving the nests, is unknown, but this is of principal importance to understand the pathogenic effect of *L. toddi* on free-living populations of *A. nisus.*

C o m m e n t s. The majority of synonyms of *L. toddi* were well grounded by Greiner and Kocan (1977). Valkiūnas (1988b, 1989b) added to this list of synonyms two names, i.e., *L. buteonis* and *L. muratovi*, both of which were introduced in the literature to name morphologically identical to *L. toddi* gametocytes recorded in falconiform birds. Bennett *et al.* (1993a) considered *L. beaurepairei* to be a distinct species. However, the limits of variation of main diagnostic characters of gametocytes and their host cells of *L. beaurepairei* overlap the variation of the same parameters of *L. toddi* (Greiner and Kocan, 1977). Gametocytes and their host cells of these two parasites cannot be distinguished morphologically, and the data on other stages of their development are not available. Based on the evidence presented above and taking in mind the main principles of identification of species of leucocytozoids (see p. 76), *L. beaurepairei* is considered to be a junior synonym of *L. toddi.* However, it should be mentioned that the status of some current synonyms of *L. toddi* can be changed again to the valid rank as additional information on the life cycle and DNA analysis of parasites of falconiform birds will be received. This is especially actual for *L. beaurepairei* and *L. franchini* which were described in birds of the families Sagittariidae and Falconidae, respectively. The remainder synonyms of *L. toddi* were suggested for naming gametocytes in birds of the family Accipitridae, and it is likely that they will remain the status of synonyms in the future.

The life cycle of *L. toddi* has not been investigated yet, in spite of the fact that falconiform birds are favourite objects of investigation of parasitologists. The majority of investigations are restricted to the blood stages of this parasite. Main reasons of this situation the author has found to be as follows. The majority of falconiform birds are rare and protected birds species, and thus their capture and maintenance under laboratory conditions in amounts required for experimental work are of some difficulty. The Holarctic falconiform birds (for example, *Accipiter nisus* and the representatives of the genus *Circus*) are especially numerous. However, the prevalence of *L. toddi* infection in these naturally infected birds is so high that it is a problem to find uninfected birds in natural populations for experimental work. For example, the prevalence of *L. toddi* is more than 94% in the Palearctic *Accipiter nisus,* and more than 73% in birds of the genus *Circus* (Valkiūnas, 1989b). The difficulties (i) to keep a sufficient number of experimental birds under laboratory conditions and (ii) to choose uninfected birds, which can be used for experimental infection, in nature, are the prominent obstacles for investigation of the life cycle of *L. toddi*.

Leucocytozoon toddi is only one species of leucocytozoids which is known at present to parasitize birds of the order Falconiformes.

10. **Leucocytozoon (Leucocytozoon) fringillinarum** Woodcock, 1910

Leucocytozoon fringillinarum Woodcock, 1910: 728, Fig. 19–21, 24–26, 59–62. – *L. brimonti* Mathis and Léger, 1910c: 32. – *L. bouffardi* Léger and Blanchard, 1911: 527. – *L. roubaudi* Mathis and Léger, 1911a: 212. – *L. cambournaci* França, 1912b: 85. – *L. gentili* Léger, 1913: 519. – *L. monardi* Rodhain,

1931: 274 (partim). – *L. chloropsidis* Mello, 1935a: 357. – *L. enriquesi* Mello, 1936: 106. – *L. molpastis* Mello, 1936: 106, Pl. 2, Fig. 1. – *L. fringillinarum*: Bennett and Campbell, 1975: 805, Fig. 2 (bottom), 3, Table 5–7 (=*L. bouffardi*, *L. cambournaci*, *L. gentili*, *L. monardi*, *L. roubaudi*); Peirce, 1984a: 118 (=*L. brimonti*); Valkiūnas, 1988b: 117, Fig. 2 (=*L. molpastis*). – *L. deswardti* Bennett, Earlé and Peirce, 1992c: 242, Fig. 30–32. – *L. dutoiti* Bennett, Earlé and Peirce, 1992c: 236, Fig. 5–9. – *L. icteris* Bennett and Squires-Parsons, 1992: 2010, Fig. 13–17. – *L. parulis* Bennett and Squires-Parsons, 1992: 2011, Fig. 18–21. – *L. pittae* Bennett and Peirce, 1992b: 705, Fig. 29 (partim). – *L. prionopis* Bennett and Earlé, 1992: 117, Fig. 15–19. – *L. thraupis* Bennett and Squires-Parsons, 1992: 2012, Fig. 22–27. – *L. sturni* Bennett, Earlé and Peirce, 1992c: 245, Fig. 42–44. – *L. whitworthi* Bennett and Peirce, 1992b: 698, Fig. 4–8. – *L. timallae* Bennett, Earlé and Peirce, 1993d: 83, Fig. 9–11. – *L. muscicapa* Bennett, Siikamäki, Jokimäki, Hovi and Huhta, 1995b: 35, Fig. 1–5. – *L. fringillinarum*: Valkiūnas, 1997: 508 (=*L. chloropsidis, L. deswardti, L. dutoiti, L. enriquesi, L. icteris, L. muscicapa, L. parulis, L. pittae* partim*, L. prionopis, L. sturni, L. thraupis, L. timallae, L. whitworthi*).

Type vertebrate host. *Fringilla coelebs* L. (Passeriformes).

Additional vertebrate hosts. Numerous species of the Passeriformes (over 200 species).

Vectors. *Cnephia ornithophilia*, *Prosimulium decemarticulatum*, *Simulium aureum*, *S. latipes* and *S. quebecense* (Diptera: Simuliidae).

Type locality. England.

Distribution. This parasite has been recorded in all zoogeographical regions, except the Antarctic. It is especially common in the Holarctic, Ethiopian and Oriental zoogeographical regions. A few records are known from the Neotropical and Australian zoogeographical regions.

Type material. Neohapantotype (No. 98636, *Fringilla coelebs*, 7.07.1968, Rendalen, Norway, A.M. Fallis) and paraneohapantotypes (No. 98639, *F. coelebs*, 5.07.1968, Rendalen, Norway, A.M. Fallis; No. 98575, *F. montifringilla*, 11.07.1968, other data as for No. 98639) are deposited in IRCAH.

Etymology. The specific name is derived from the generic name of the type vertebrate host, *Fringilla*.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is usually of a cap-like form, sometimes band-like in shape; the nucleus usually extends less than 1/2 of the circumference of gametocyte but can sometimes extend up to 1/2 of the circumference of gametocyte.

Development in vertebrate host was investigated in experimentally infected *Quiscalus quiscula* (Khan and Fallis, 1970a). Sporozoites invade cells in the liver and kidneys and initiate the development of the first generation of exoerythrocytic meronts. Part of merozoites from these meronts invades the erythrocytes and develops into gametocytes, and the other part initiates the secondary exoerythrocytic merogony in the liver and kidneys. Meronts were not found in other organs. Some details of the exoerythrocytic development are given below.

In the liver, meronts develop in parenchymal cells. A few of them were observed 42 h after infection with sporozoites, and were more numerous 48 h after infection (Fig. 300, *1*). Cytomeres are well evident in growing hepatic meronts (Fig. 300, *2*). Nuclei tend to be located peripherally in cytomeres. Mature meronts appear 72 h after the infection. They are roundish or of oval form and are packed with a homogeneous mass of merozoites (Fig. 300, *3*). Mature meronts ($n = 20$) were 23 to 41 by 17 to 34 (on average 30 by 27) μm in size. The merogony is nonsynchronized, and growing parasites about 10 μm in diameter were seen at the moment when the first mature meronts appeared. It should be noted that a

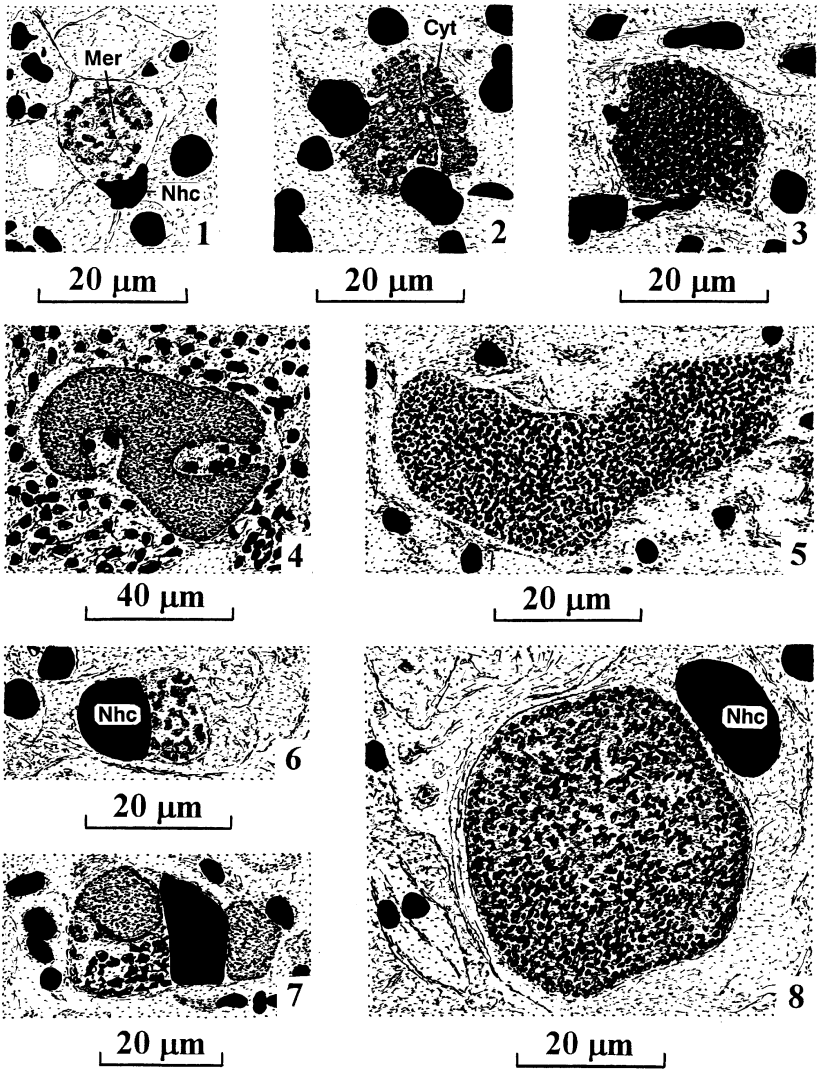

Figure 300 Exoerythrocytic meronts of *Leucocytozoon fringillinarum* from *Quiscalus quiscula*: *1–3* – meronts of the first generation in the liver: *1* – young parasite, *2* – parasite with cytomeres, *3* – mature parasite; *4*, *5* – meronts in kidneys: *4* – growing irregular-shaped parasite, *5* – mature parasite; *6–8* – meronts of the second generation in the liver: *6*, *7* – young parasite in host cell with enlarged nucleus, *8* – mature parasite; Cyt – cytomere; Mer – meront; Nhc – nucleus of host cell (modified from Khan and Fallis, 1970a).

characteristic feature of hepatic meronts of the first generation is that they do not induce significant enlargement of nuclei of the host cells (Fig. 300, *1*). Meronts of the second generation appear in the liver approximately 90 h after infection. They induce marked enlargement of nuclei of parasitized hepatocytes (Fig. 300, *6–8*). Mature hepatic meronts of the second generation were observed seven days after inoculation of sporozoites (Fig. 300, *8*). At the same time, growing meronts were also common. This testifies to the asynchronous

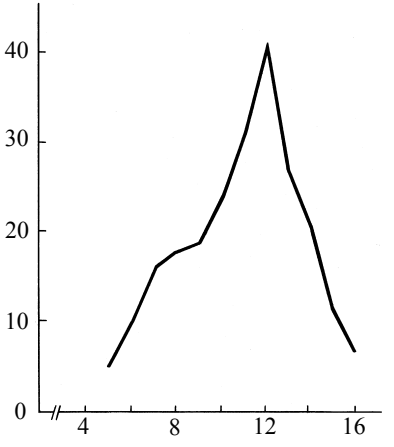

Figure 301 Dynamics of parasitemia of *Leucocytozoon fringillinarum* in *Quiscalus quiscula* and *Fringilla coelebs* experimentally infected with sporozoites:
Mean parasitemia (number of parasites per 1000 erythrocytes) in ten infected birds is shown on the ordinate, days after the inoculation of sporozoites are shown on the abscissa (modified from Khan and Fallis, 1970a; Valkiūnas, 1997).

process of merogony. Mature meronts of the second generation are larger than meronts of the first generation. They are roundish and of oval form and up to 45 μm in diameter.

In the kidneys, meronts are more numerous than in the liver. They develop mainly in proximal tubular cells but sometimes also in cells of distal and collecting tubules. As the parasite develops, cytomeres appear. Nucleus of infected cell is enlarged. Mature renal meronts of the first generation appear 96 h after infection with sporozoites. The majority of these meronts complete their development between 4.5 and 5.5 days after infection. Meronts in the kidneys conform to the convolutions of the tubules in which they locate, and they even were observed to be irregular-shaped (Fig. 300, *4*). They frequently look roundish or of oval form in transverse section (Fig. 300, *5*). Mature renal meronts of the first generation ($n = 20$) were 46 to 120 by 20 to 39 (on average 72×30) μm in size. The second generation of renal meronts follows. Both the morphology and the size of renal meronts of the first and second generation are similar. However, meronts of the second generation are more numerous than those of the first generation. Merogony in the kidneys is not synchronized either, as it is in the liver.

Meronts in the liver and kidneys were observed up to 16 days after inoculation of sporozoites. Subsequently, it is difficult to find them. However, part of parasites persists in the internal organs. A long-term primary parasitemia and well evident spring relapses testify to this.

Merozoites from exoerythrocytic meronts invade polychromatic erythrocyte and grow into gametocytes. Occasionally, small parasites were also seen in lymphocytes, but it is still unclear if they develop in these cells. It is likely that gametocytes also develop in mature erythrocytes as it takes place in *L. dubreuili* infection (Wong and Desser, 1977).

Young gametocytes appear in the peripheral circulation approximately three days after inoculation of sporozoites. This period coincides with the time of maturation of hepatic meronts of the first generation. First mature gametocytes were observed 5.5 days after infection.

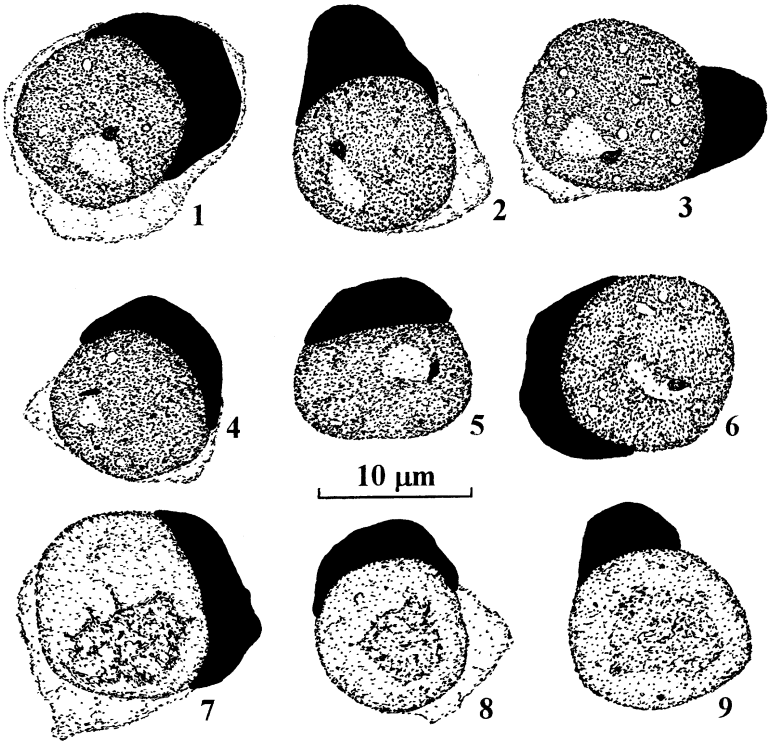

Figure 302 Gametocytes of *Leucocytozoon fringillinarum* from the blood of *Fringilla coelebs*: *1–6* – macrogametocytes; *7–9* – microgametocytes.

Parasitemia markedly increases from the 5th to 12th day after inoculation of sporozoites, and then rapidly decreases (Fig. 301). A low parasitemia was recorded in birds, which were infected once, up to a 10-month period (the period of observation).

Macrogametocytes (Fig. 302, *1–6*; Table 153) develop in roundish host cells; cytoplasm frequently contains small vacuoles; valutin granule are usually present; gametocytes are roundish or of slightly oval form; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed, and lies peripherally usually as a more or less evident cap (Fig. 302, *1–5*), sometimes band-like (Fig. 302, *6*), it usually extends less than 1/2 of the circumference of gametocyte but sometimes can extend up to 1/2 of the circumference; the cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 302, *5*, *6*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 302, *1–4*).

Microgametocytes (Fig. 302, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Relapses are well evident and synchronized with the breeding period of birds.

Development in vector was investigated by Khan and Fallis (1970a) at a temperature of 21°C. Exflagellation was observed in the midgut of simuliid flies 2 to 5 min after ingestion of gametocytes. Ookinetes are present in the midgut between 12 and 108 h after

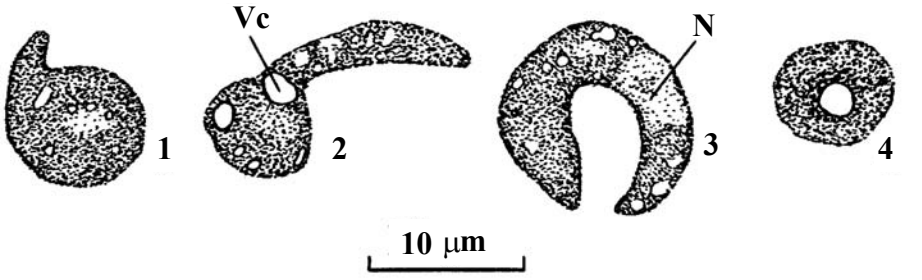

Figure 303 *Leucocytozoon fringillinarum*:
1 – initial stage of the development of ookinete; *2* – medium developed ookinete; *3* – mature ookinete; *4* – young oocyst; N – nucleus; Vc – 'vacuole' (modified from Khan and Fallis, 1970a).

infection. As ookinete develops, a long finger-like outgrowth appears. It extends markedly and forms the anterior or apical end of the ookinete (Fig. 303, *1–3*). Ookinetes (n = 10) vary from 20 to 26 (on average 23) μm in length, and from 2 to 5 (on average 3) μm in width. The earliest oocyst were observed in the midgut wall 36 h after infection (Fig. 303, *4*). They possess a large centrally located 'vacuole.' One germinative centre, from which sporozoites bud off, develop in oocyst. As the parasite develops, oocysts only slightly increase in size. Oocysts (n = 20) vary from 6 to 10 (on average 8) μm in diameter 36 h after ingestion of gametocytes, and mature oocysts (n = 20) vary from 11 to 15 (on average 13) μm in diameter 96 h after the infection. Up to 50 sporozoites, whose form is typical of species of the subgenus *Leucocytozoon*, develop in the oocysts. They (n = 25) vary from 8 to 10 (on average 9) μm in length, and are about 1 μm in width.

P a t h o g e n i c i t y. Signs of illness were not observed in young *Quiscalus quiscula* experimentally infected by inoculation of sporozoites (Khan and Fallis, 1970a). A possible way of pathogenic influence of leucocytozoids on free-living wild birds are discussed in the General Section (see p. 110).

S p e c i f i c i t y has been insufficiently investigated (see p. 77).

C o m m e n t s. Recently, numerous new species of leucocytozoids (for example, *L. deswardti*, *L. dutoiti*, *L. icteris*, *L. parulis*, *L. pittae*, *L. prionopis*, *L. sturni*, *L. thraupis*, *L. timallae*, *L. whitworthi* and others) were described mainly on the basis that they were found in passerine birds belonging to different families or even subfamilies (Bennett and Earlé, 1992; Bennett and Peirce, 1992b; Bennett and Squires-Parsons, 1992; Bennett *et al.*, 1992c, 1993d and others, see p. 79). Gametocytes and their host cells of these parasites are morphologically indistinguishable from *L. fringillinarum*. Specificity of these leucocytozoids is not investigated experimentally, and the data on other stages of their development are also unavailable. It is preferable at present to consider the above mentioned specific names to be junior synonyms of *L. fringillinarum*. This synonymy was grounded in connection with the problem of specificity of leucocytozoids in the General Section in detail (see p. 76). It should be noted that gametocytes of *L. timallae* on average are larger in size than other representatives of the group '*fringillinarum*' (Bennett *et al.*, 1993d). However, as it was discussed above (see pp. 76, 776), sizes of gametocytes of the same species of leucocytozoids vary during its development in different vertebrate hosts. Taken separately, this character cannot be used for description of new species of *Leucocytozoon*.

In the original description of *L. timallae*, the specific name is given in three different spellings, i.e., *L. timallae*, *L. timaliae*, and *L. timaliniae* (Bennett *et al.*, 1993d). The latter two spellings are considered to be a *lapsus calami*.

11. **Leucocytozoon (Leucocytozoon) marchouxi** Mathis and Léger, 1910

Leucocytozoon marchouxi Mathis and Léger, 1910b: 118. – *L. turtur* Covaleda Ortega and Gállego Berenguer, 1946: 215, Pl. 1, Fig. 1–10. – *L. turtur orientalis* Yakunin, 1972: 75, Fig. 4. – *L. marchouxi*: Hsu *et al.*, 1973: 198 (=*L. turtur*); Peirce and Bennett, 1979: 358 (=*L. turtur orientalis*).

Type vertebrate host. *Streptopelia tranquebarica* (Hermann) (Columbiformes).
Additional vertebrate hosts. Some species of the Columbiformes (Table 155).
Type locality. Tonkin (environs of Hanoi, Vietnam).
Distribution. Common parasite of columbiform birds in the Holarctic and Ethiopian zoogeographical regions. It has been less frequently recorded in the Oriental region. In the Neotropics, it has been found only in its Central-American subregion. No records from the South America and Australia so far.
Type material has not been designated. A series of good additional slides is deposited in IRCAH and CDVA.
Etymology. This species is named on honour of Dr. E. Marchoux.

Table 155 List of vertebrate hosts of *Leucocytozoon marchouxi* (modified from Valkiūnas, 1989a).

Columba eversmanni	*Oena capensis*	*S. turtur*
C. fasciata	*Streptopelia capicola*	*Treron sphenura*
C. livia	*S. chinensis*	*Turtur chalcospilos*
C. mayeri	*S. lugens*	*T. tympanistria*
C. oenas	*S. orientalis*	*Zenaida asiatica*
C. palumbus	*S. semitorquata*	*Z. macroura*
Geopelia striata	*S. senegalensis*	

Main diagnostic characters. A parasite of species of the Columbiformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is usually of cap-like form, sometimes of band-like shape; the nucleus usually extends less than 1/2 of the circumference of gametocyte but sometimes also up to 1/2 of the circumference.

Development in vertebrate host

Exoerythrocytic merogony has been insufficiently investigated. Numerous megalomeronts were found by Peirce *et al.* (1997) in one squab *Columba mayeri* which was infected naturally and died at the age of seven weeks old. This bird was aviary bred by domestic Barbary doves *Streptopelia risoria* on Indian Ocean island of Mauritius. Megalomeronts on various stages of their development were observed in the liver, pancreas, heart, spleen, kidneys, and intestine. They were especially numerous in the spleen and were up to 210 μm in diameter. Morphology of megalomeronts and their host cells is similar to those of *L. simondi* in anseriform birds. Further experimental studies are required to understand the role of the megalomeronts in the life cycle of *L. marchouxi*. It is unclear whether megalomeronts develop in all vertebrate hosts or only in some of them as it takes place in *L. simondi* infections (see p. 790). Further investigation into the exoerythrocytic development of this parasite is of theoretical significance.

Young gametocytes were recorded in the peripheral circulation of naturally infected nestlings of *Zenaida macroura* at the age of 14 days. Therefore, as the birds could be infected only after their birth, at least the first generation of exoerythrocytic meronts should

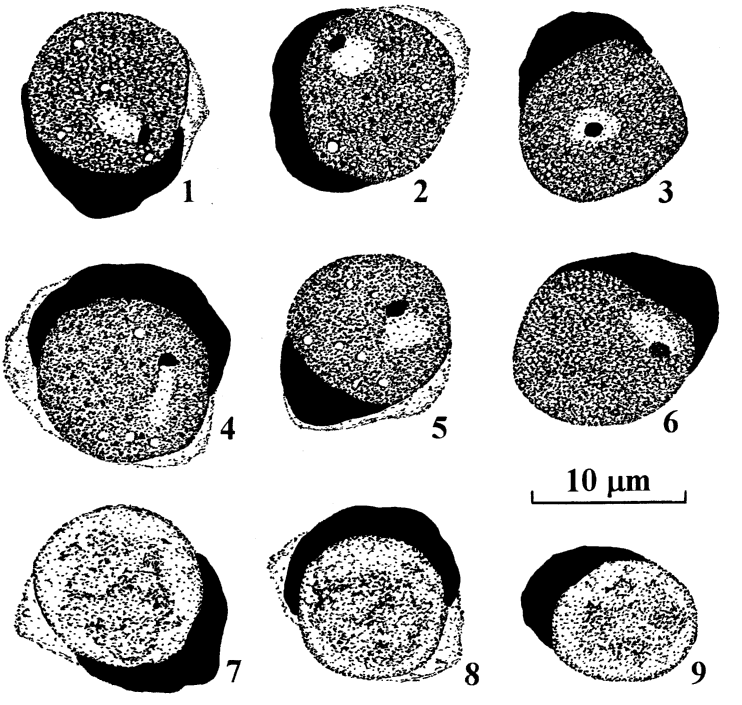

Figure 304 Gametocytes of *Leucocytozoon marchouxi* from the blood of *Streptopelia orientalis*: *1–6* – macrogametocytes; *7–9* – microgametocytes.

mature no later that two weeks after infection. It looks likely that gametocytes develop in mononuclear leukocytes (monocytes and lymphocytes) (Levine, 1954; Peirce *et al.*, 1977).

Macrogametocytes (Fig. 304, *1–6*; Table 156) develop in roundish host cells; the cytoplasm frequently contains a few small vacuoles; valutin granules are usually present; gametocytes are usually roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed,

Table 156 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. marchouxi* (according to Valkiūnas, 1989a)				*L. dubreuili* (according to Valkiūnas, 1988b)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	30				18			
Length		11.7–16.0	13.0	1.1		7.4–14.5	11.1	1.6
Width		8.6–13.9	11.3	1.0		7.7–13.0	10.1	1.7
Length of nucleus		1.7–6.9	4.5	0.4		2.1–4.1	3.2	0.6
Width of nucleus		3.4–6.5	2.1	0.3		1.4–3.9	2.5	0.7
Length of nucleus of host cell		9.1–23.9	19.5	3.2		19.1–34.2	26.7	3.7

Note: All sizes are given in micrometres.

and lies peripherally usually as a more or less evident cap (Fig. 304, *1, 3, 5, 6*) or sometimes band (Fig. 304, *2, 4*), it usually extends less than 1/2 of the circumference of gametocyte (Fig. 304, *1–3, 5,6*) but sometimes also up to 1/2 of the circumference (Fig. 304, *4*); the cytoplasm of host cell is largely replaced by gametocyte, and is sometimes even invisible (Fig. 304, *3*, *6*), but more frequently is present around the gametocyte as a more or less evident and pale margin of variable form (Fig. 304, *1*, *2*, *4*, *5*).

Microgametocytes (Fig. 304, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector has not been investigated. Exflagellation was observed 6 to 10 min after exposure of the blood with mature gametocytes to air at a temperature of 18 to 20°C. Microgametes are about 16 μm in length (Garnham *et al.*, 1967).

Pathogenicity has been insufficiently investigated. In spite of numerous records of *L. marchouxi* in domestic and wild columbiform birds, clinical signs of infection have been rarely observed. Peirce (1984a) investigated one naturally heavily infected *Turtur chalcospilos* in Zambia. The infected bird showed a high parasitemia of *L. marchouxi*, and it was listless with closed eyes and ruffled feathers. The bird did not attempt to fly when approached. It weighed 25% below the normal weight for this species. However, the examination of blood smears also showed a low parasitemia of *Haemoproteus columbae*. It is possible that the disease was associated with the mixed infection. The preliminary observations by Oosthuizen and Markus (1968) show that there can be a direct relation between the mortality of juveniles of *Streptopelia senegalensis* in southern Africa and their infection with *L. marchouxi.* Furthermore, Peirce *et al.* (1997) noted that (i) there was little doubt that *L. marchouxi* was responsible for the death of an aviary bred squab of *Columba mayeri* on island of Mauritius in the Indian Ocean mainly because of numerous megalomeronts which developed in internal organs, and (ii) the parasite possesses a potential threat to the continued recovery of a population of this bird on the island. Further investigations are required to understand the pathogenicity of this parasite for its different vertebrate hosts.

Comments. *Leucocytozoon marchouxi* is only one species of leucocytozoids which is known at present to parasitize birds of the order Columbiformes. This parasite is poorly investigated in spite of the fact that it parasitizes domestic pigeon which is an excellent object for experimental investigations. It is important to note that a record of gametocytes in fusiform host cells, which are similar to those of *L. toddi*, in one young *Columba livia* in Iraq (Shamsuddin and Mohammad, 1980) is of theoretical significance. This case requires further investigation. There are no sufficient data at present to attribute these gametocytes to *L. marchouxi*.

12. **Leucocytozoon (Leucocytozoon) simondi** Mathis and Léger, 1910

Leucocytozoon simondi Mathis and Léger, 1910b: 119. – *L. anatis* Tartakovsky, 1913: 73, Table 1, 2. – *L. anatis* Wickware, 1915: 19, Pl. 2, 3 (nom. praeocc., nonTartakovsky, 1913). – *L. anseris* Knuth and Magdeburg, 1922: 360, Fig. – *L. simondi*: Herman, 1938b: 473 (=*L. anatis* Wickware); Levine and Hanson, 1953: 188 (=*L. anseris*); Valkiūnas, 1986b: 61 (=*L. anatis* Tartakovsky).
Type vertebrate host. *Anas crecca* L. (Anseriformes).
Additional vertebrate hosts. Numerous species of the Anseriformes (Table 157).
Vectors. *Cnephia ornithophilia*, *Simulium anatinum*, *S. fallisi*, *S. innocens*, *S. parnassum*, *S. rendalense*, *S. rugglesi*, *S. venustum*, and *S. vittatum* (Diptera: Simuliidae).
Type locality. Tonkin (environs of Hanoi, Vietnam).

Distribution. Transmission takes place only in the Holarctic. This parasite is especially common in wild anseriform birds in the Northern Holarctic. In the Palearctic, active transmission occurs even beyond the North Polar Circle. The prevalence of infection markedly decreases from northern to southern latitudes. The southern territory, where transmission has been recorded, is north-eastern Mexico. This parasite has also been sometimes recorded in overwintering migrating birds outside the Holarctic where it usually does not complete its cycle of development. The type locality is an example.

Type material was not designated in the original description. Garnham and Duggan (1986) suggested for the neohapantotypes different stages of development which came from nontype vertebrate hosts (*Branta canadensis*, *Anas platyrhynchos*) far beyond the type locality (Canada). This is in contradiction with Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of valid neotypes is required. It should be noted that gametocytes, and their host cells typical of *L. simondi*, are not present in blood film No. 980, which was designated as a neohapantotype of blood stages. This blood film contains numerous gametocytes located in the enucleated host cells. They are similar to gametocytes of *Leucocytozoon (Akiba) caulleryi*. Thus, slide No. 980 should be dismissed as the neohapantotype also for this reason. A series of good additional slides of exoerythrocytic meronts and oocysts is deposited in CPG, and of gametocytes, in IRCAH and CDVA.

Etymology. This species is named in honour of Professor P.L. Simond.

Table 157 List of vertebrate hosts of *Leucocytozoon simondi* (modified from Garnham, 1966; Valkiūnas *et al.*, 1990).

Aix galericulata	*Anser albifrons*	*Clangula hyemalis*
A. sponsa	*A. anser*	*Cygnus buccinator*
Anas acuta	*A. caerulescens*	*C. columbianus*
A. americana	*A. cygnoides*	*C. olor*
A. clypeata	*A. fabalis*	*Lophodytes cucullatus*
A. crecca	*Aythya affinis*	*Melanitta nigra*
A. diazi	*A. americana*	*M. perspicillata*
A. discors	*A. collaris*	*Mergus albellus*
A. falcata	*A. ferina*	*M. merganser*
A. formosa	*A. fuligula*	*M. serrator*
A. penelope	*A. marila*	*Netta rufina*
A. platyrhynchos	*Branta canadensis*	*Oxyura jamaicensis*
A. querquedula	*Bucephala clangula*	*Somateria fischeri*
A. rubripes	*Cairina moschata*	*S. mollissima*
A. strepera	*Chen canagica*	

Note: The ability of *L. simondi* to parasitize *Limnodromus griseus* and *Squatarola squatarola* (Charadriiformes) (Laird and Bennett, 1970), which are unusual vertebrate hosts of this parasite, should be confirmed.

Main diagnostic characters. A parasite of species of the Anseriformes whose gametocytes develop in roundish and fusiform host cells. Nucleus of fusiform host cell looks like a more or less evident dumbbell-shaped band with clear thickenings at both ends which do not adhere to the gametocyte.

Development in vertebrate host

General characteristic of the development of *L. simondi* in birds is given in the General

Section together with the description of the life cycle of leucocytozoids (see p. 36). Some important details of this process are given below.

Development of the parasite was not observed in skin and subcutaneous tissues. This testifies to the absence of quick merogony at the place of inoculation of sporozoites. Viable sporozoites have been recorded in the blood up to 48 h after their inoculation, and were observed in internal organs up to 114 h after infection (Desser, 1967; Khan *et al.*, 1969). The role of such persistence is unclear.

Sporozoites invade parenchymal cells of the liver and initiate hepatic merogony (Fig. 18, 19, *1–3*). Initial stages of development of asexual stages were observed in hepatocytes approximately 48 h after inoculation of sporozoites (Fig. 19, *1*). They are located in distorted cells of hepatic parenchyma and each possesses a small nucleus. These parasites were approximately 6 to 7 μm in diameter. Nucleus of infected hepatocyte is enlarged. Developing meronts contain numerous basophilic cytomeres (Fig. 19, *2*), and each cytomere is usually surrounded with a narrow light-colour portion of cytoplasm. Meronts with numerous basophilic cytomeres, which are surrounded with a prominent portion of intact cytoplasm of the host cells, were also sometimes observed. Mature meronts are roundish or of oval form and about 25 μm in diameter (Fig. 19, *3*). They possess (i) numerous roundish merozoites, which are about 1 μm in diameter, and (ii) small fragments or 'islands' of cytoplasm containing several (two or usually more) nuclei (Desser, 1973). First mature hepatic meronts were observed four days after the infection with sporozoites, and the majority of them are mature and rupture on the fifth day after infection. Numerous merozoites and 'islands' (known as syncytia) are released from the ruptured meronts. During the first five days after infection, meronts were observed only in the liver where merogony is asynchronous, and thus the meronts are present at all stages of development. It is likely that the asynchrony is due to a long-term survival of sporozoites, which can gradually initiate hepatic merogony in the bird.

Part of merozoites from hepatic meronts invade mature and polychromatic erythrocytes and develop into gametocytes whose host cells are roundish (Fig. 20, *4*, *6, 7*). Merozoites were observed inside blood cells in impression smears of the liver 4.5 days after the inoculation of sporozoites. In peripheral circulation, they were seen not earlier than five days after infection. Therefore, the prepatent period is about five days. First mature gametocytes are observed in imprints of the liver seven days after infection and are numerous here eight days after. The other part of merozoites from hepatic meronts probably again invades hepatocytes and initiates secondary merogony in the liver. However, this is difficult to prove because of a long-term survival of sporozoites, which can also gradually initiate hepatic merogony. The number of hepatic meronts decreases after the 6th to 12th day post infection. It is likely that mature meronts present in the liver seven to eight days after the inoculation of sporozoites belong to the first generation of the parasites, and young meronts belong to the second generation.

Syncytia are spread via the blood stream to numerous organs where they are phagocytized by reticuloendothelial cells and develop into megalomeronts five to six days after the inoculation of sporozoites (Fig. 19, *4–7*). Megalomeronts are usually especially numerous in the spleen and lymph nodes, and were much more rarely observed in the brain, heart, pericardium, lungs, trachea, kidneys, liver, skeletal muscles, masticatory, and glandular parts of the stomach, intestine, gonads, bursa of Fabricius. It is likely that syncytia are especially actively phagocytized by macrophages in lymphoid tissues. It should be noted that megalomeronts have been relatively rarely observed in the liver which is the organ of especially extensive phagocytosis in birds. Probably, the local immunity is induced in the

liver during the primary hepatic merogony, and thus syncytia are destroyed in Kupffer cells. Growing megalomeronts, which vary (n = 20) from 20 to 38 (on average 29) μm in diameter, were observed in the spleen six days after the inoculation of sporozoites (Fig. 19, *4*). At the same time, megalomeronts observed in the lymph nodes, the heart and lungs were of similar size but smaller in the brain where they (n = 20) were from 14 to 20 (on average 19) μm in diameter. By the seventh day after infection, megalomeronts increased in size in all organs, and were now (n = 20) 40 to 160 (on average 108) μm in diameter in the spleen and smaller in other organs. First mature megalomeronts were observed in the spleen eight days after infection (Fig. 19, *5*). Megalomeronts are usually roundish or oval. They are slightly elongated and can be even fusiform in the heart because of their compression by the muscle tissue. Nine days after infection, numerous mature megalomeronts with uninuclear merozoites were observed in the spleen. They (n = 40) are now 60 to 189 (on average 145) μm in diameter. Intensity of infection in the spleen and lymph nodes can be extremely high. The parasites are estimated to occupy 3/4 of the mass of an organ (Fig. 19, *7*). The enlargement of the spleen is thus associated with an increase in parasite mass *per se* which has not been recorded in any other haemosporidian infection. On 12th to 15th day after infection, the spleen is still markedly enlarged or it can be even larger than previously but megalomeronts were not found, and this organ was engorged with blood. On the tenth day after infection, the majority of megalomeronts in the spleen, lymph nodes, lungs, heart, and other organs were mature. At the same time, they continued to grow in the brain where they were still relatively small (about 25 to 60 μm in diameter). The majority of megalomeronts disappear by days 12 to 13 after infection leaving haemorrhagic scars. On 14 to 15 days, megalomeronts were observed only in the brain (Fig. 19, *6*). By this time, they nearly completed their development and were 90 to 110 μm in diameter. It should be noted that in a naturally infected wild mallard with unknown age of infection, the majority of megalomeronts were found in the brain, and some parasites were up to 160 to 190 μm in diameter (Karstad, 1965). Mature megalomeronts possess roundish uninuclear merozoites about 1 μm in diameter. The development of megalomeronts is synchronized in different organs, except the brain. The majority of megalomeronts mature and rupture between 9 and 12 days after the inoculation of sporozoites. In the brain, growing megalomeronts were observed 15 days after infection.

The morphology of megalomeronts was studied by Desser and Fallis (1967b) in detail from the earliest stages of their development to maturity in ducks experimentally infected with sporozoites. Syncytia are unable to penetrate host cells. They are phagocytized by reticuloendothelial cells. In six days after infection, morphologically unaltered macrophages were revealed to contain syncytia similar to those seen in liver smears. Syncytia grow rapidly, and they induce a marked enlargement both of the nucleus and the cytoplasm of the host cell. At this stage, the nuclei were randomly scattered throughout the cytoplasm of the parasite. In seven days, phagocytes were observed in the brain to contain two or more discrete masses of the parasite. At this time, megalomeronts in the spleen contained numerous spherical cytomeres with nuclei arranged peripherally, rather than randomly, in the cytoplasm. Cytomeres now were about 6 to 8 μm in diameter. Hypertrophy of the nucleus and cytoplasm of infected cell continues, and the cytoplasm is filled with cytomeres of approximately uniform size. First mature megalomeronts appear eight days after infection. At this time, the host cell ceases to enlarge, and deep clefts and indentations are apparent in the enlarged cytomeres. These clefts subdivide the cytomeres into smaller portions. Subdivision of smaller cytomeres continues until uninuclear merozoites appear. Gaps between merozoites are filled with remnants of cytoplasm of the host cell. Growth of

megalomeronts from their initiation to maturity represents approximately an 8000-fold increase in volume. A markedly enlarged nucleus of the host cell (a 'central body' of megalomeront) probably take part in transportation of nutrient materials inside the parasite. Both the division of the parasite into cytomeres and the peripheral arrangement of nuclei facilitate metabolic and trophic functions. Megalomeronts are surrounded with a collagen-positive capsule which was first observed seven days after infection. The encapsulation is most obvious in the spleen and lymph nodes, and it is the least in the brain and heart. It is likely that the encapsulation consists of the active and passive phases. Fibroblasts frequently seen to lie adjacent to the capsular are probably responsible for the secretion of capsular material. It should be noted that encapsulation is especially evident in organs with a dense reticular network such as the spleen and lymph nodes. Therefore, the encapsulation can be partially a passive process. Under remarkable growth, megalomeronts displace surrounding cells and reticular fibres which become associated with the surface of the expanding sphere and thus take part in formation of the capsular wall. It is likely that the size of mature megalomeronts is related to the size and number of syncytia phagocytized by the host cells. Megalomeronts with cytomeres at distinctly different stages of development were seen, and this testifies to the possibility of some syncytia to be phagocytized at different times.

Part of the merozoites from megalomeronts invade leukocytes and develop into gametocytes whose host cells assume a fusiform shape (Fig. 20, *1–3*, *5*). The merozoites were usually seen in lymphocytes and monocytes but were also occasionally observed in heterophils and eosinophils. However, it is uncertain whether or not the gametocytes mature in the two latter cell types (Desser *et al.*, 1970). It is likely that part of merozoites from megalomeronts also initiates (i) the slowly developing meronts in the liver and other organs and (ii) the megalomeronts which are responsible for maintenance of chronic parasitemia and relapses (Yang, 1971; Yang *et al.*, 1971). Persisting meronts are difficult to find because they are not numerous, and they still are not investigated in detail. In winter, megalomeronts usually were not recorded in birds. Parasitemia is also low (if present at all) this time of the year. This shows that a few megalomeronts mature in winter. The majority of parasites persist at the earliest stages of development which are difficult to reveal. In spring, an active growth and maturation of meronts initiates, and parasitemia increases.

Relapses are well evident in spring. Megalomeronts responsible for relapses were found in the lungs (Desser *et al.*, 1968). They look elongated in the longitudinal sections and roundish in the transverse sections. Their precise location is uncertain. The majority of megalomeronts develop inside the alveolar tissue but some of them were also seen to lie in the lumen of blood vessels. Parasites were about 26×100 μm in diameter in the longitudinal sections, and up to 30 μm in diameter in the transverse sections. The parasites develop in cells with markedly enlarged nuclei. They are surrounded with an obvious capsule-like wall that contains a few reticular cells. The capsule wall is about 1 μm in width. Merozoites develop inside cytomeres. Mature megalomeronts are packed with a homogeneous mass of merozoites. Some tissue reaction occurs around the meronts, and adventitious cells were mainly lymphocytes and endothelial cells but some plasma cells and macrophages were also present. No invasion of megalomeronts was seen, as is common in primary megalomerogony. A single megalomeront was also observed in heart muscle of a duck during the relapse (Pl. I, *5)*. It was 30×50 μm in size. It is likely that the above described megalomeronts are at the stage of waiting for a signal to release merozoites. It should be noted that the 'relapse megalomeronts' were recorded to be elongated in contrast to the characteristically roundish forms seen in primary infections.

Exoerythrocytic merogony of *L. simondi* in ducks in Northern Europe is completed more rapidly than in North America. This is probably due to the strain differences. In experimentally infected ducks in Norway, young gametocytes in the peripheral circulation were recorded four to five days after the inoculation of sporozoites, mature gametocytes in roundish host cells are numerous in six to seven days, and gametocytes in fusiform host cells were recorded already in eight to nine days. Mature megalomeronts in the spleen were observed six days after infection, and this is at least one day earlier than it was recorded in North American ducks. Additionally, some differences in location and size of meronts were also found. Megalomeronts of the Norwegian strain in the kidneys were located in the glomeruli while they were not seen here in the strain originating in North America. Moreover, in the North American strain, hepatic meronts were smaller and megalomeronts larger than in the Norwegian strain (Eide and Fallis, 1972).

It is important to note that the above described sequence of endogenous development, with (i) hepatic meronts followed by megalomeronts and (ii) gametocytes in roundish host cells followed by gametocytes in fusiform host cells, is characteristic of *L. simondi* but was constantly observed only in ducks. In geese, this parasite undergoes either complete or 'partial' endogenous cycle in different localities in North America. During the 'partial' development, hepatic meronts and gametocytes in roundish host cells develop in geese, but megalomeronts and gametocytes in fusiform host cells do not develop (Desser and Ryckman, 1976). This 'partial' endogenous development is accompanied with lowering of parasitemia and virulence of the parasite. Moreover, the parasite finally disappears from infected geese, and relapses were not observed. That the parasite in ducks and geese is the same species was supported experimentally. Experimental ducklings and goslings were infected with the same inoculum derived from the simuliid flies *Simulium rugglesi* which were fed to an infected goose. In ducklings, the parasite followed its normal course of development with the appearance of gametocytes in roundish host cells followed by gametocytes in fusiform host cells, while in the goslings only the gametocytes in roundish host cells appeared. Desser and Ryckman (1976) speculated that *L. simondi* is more adapted for development in ducks in which the parasite follows its complete life cycle accompanied with especially heavy infection. During development of the parasite in geese, the strain differences appear. In geese, the adapted strains follow the complete life cycle, and the nonadapted strains undergo only 'partial' development. This hypothesis was tested experimentally (Desser *et al.*, 1978). Geographical variation both in the pathogenicity and the peculiarities of endogenous development of *L. simondi* was revealed after exposure of goslings of the Canada geese *Branta canadensis maxima* to natural infection of *L. simondi* at different localities in the upper peninsula of Michigan. In some localities, the parasite was recorded to undergo complete development similar to that in ducks, and it was very virulent with a high rate of mortality among the goslings. However, in other localities, it was revealed to undergo 'partial' development and was slightly virulent with no signs of illness observed in the goslings. This experiment shows that the *L. simondi* strains, which markedly differ from one another by the ability to undergo endogenous development in geese, do exist. Desser *et al.* (1978) believe that the parasite usually follows its complete cycle of development in ducks. In localities where transmission of *L. simondi* among ducks takes place (and thus where a 'duck strain' is well established) and where geese have been recently introduced, the parasite undergoes 'partial' development in geese and is slightly virulent for these birds. In localities where breeding sites of ducks and geese have overlapped for many years, the parasite has adapted itself to complete development in geese. In the latter case, the heavy disease, which has been well investigated (Tartakovsky,

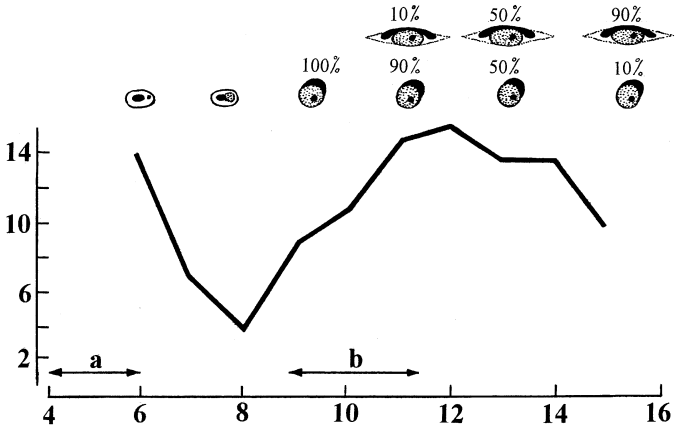

Figure 305 Dynamics of parasitemia of *Leucocytozoon simondi* in ducklings, and the ratio of gametocytes of the parasite in roundish and fusiform host cells in relation to the development of exoerythrocytic meronts:
a, *b* – period of rupture of meronts: *a* – hepatic meronts, *b* – megalomeronts. Mean parasitemia (number of parasites per 1000 erythrocytes) in ten experimentally infected ducklings is shown on the ordinate, days after the inoculation of sporozoites are shown on the abscissa (modified from Desser, 1967).

1913; O'Roke, 1934; Levine and Hanson, 1953; Herman and Bennett, 1976; Desser *et al.*, 1978), develops both in geese and ducks. It is important to note that evidence for (i) the geographical strain differences of endogenous development and (ii) the different mode of development of the same species of *Leucocytozoon* in different vertebrate hosts are of great theoretical significance for future studies of pathogenicity and life cycles of bird haemosporidian parasites.

As is shown in Fig. 305, merozoites from hepatic meronts invade blood cells of the erythrocytic series (mature and polychromatic erythrocytes, erythroblasts) and develop into gametocytes in roundish host cells. The decrease of parasitemia six to eight days after the inoculation of sporozoites is due to retention of developing gametocytes in deep circulation, especially in the liver, where a large number of developing gametocytes in roundish host cells is found. Some mature gametocytes in roundish host cells are present in the peripheral circulation seven to eight days after infection, but the growing gametocytes predominate at this time. In nine to ten days after infection, mainly mature gametocytes in roundish host cells are present in the peripheral blood. Subsequently, their number decreases. In 10 to 12 days after infection, the number of young gametocytes in the peripheral circulation increases, and gametocytes in fusiform host cells appear. The number of gametocytes in the fusiform host cells increases in 12 to 14 days, and then they decrease in number markedly. From the 14th day after infection, the ratio of gametocytes in fusiform and roundish host cells is approximately equal to 9:1. Later, the parasitemia turns into a chronic stage in surviving birds. The peaks of parasitemia recorded on the 6th and 12th day after infection coincide with the time of mass release of merozoites from hepatic meronts and megalomeronts, respectively. A considerable number of growing gametocytes is retained in deep circulation where many of them are destroyed.

Gametocytes both in roundish and fusiform host cells are infective for vectors.

Macrogametocytes (Fig. 20, *1–4*, *6*; Table 154) develop in roundish and fusiform host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present;

gametocytes in roundish host cells usually are roundish (Fig. 20, *4*, *6*), and gametocytes in fusiform host cells vary from roundish to oval and even elongated but more frequently are oval or ellipsoid (Fig. 20, *1–3*); the parasite nucleus is of variable form and position; nucleolus is prominent and well seen; the nucleus of roundish host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap or sometimes band, extends usually less than 1/2 of the circumference of gametocyte (Fig. 20, *4*, *6*); the nucleus of fusiform host cell is markedly deformed and enlarged, pushed aside, and usually lies peripherally as a more or less evident dumbbell-shaped band with clear thickenings at both ends which do not adhere to the gametocyte (Fig. 20, *1–3*); the cytoplasm of roundish host cell is largely replaced by the gametocyte, and can sometimes be even invisible but more often is present around the gametocyte as a more or less evident and pale margin of variable form (Fig. 20, *4*, *6*); the cytoplasm of fusiform host cells forms two well evident and variable (both in form and length) processes at the ends of gametocytes (Fig. 20, *1–3*); fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are clearly dominant.

Microgametocytes (Fig. 20, *5*, *7*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector

General characteristic of development of *L. simondi* in the vector is given in the General Section together with the description of the life cycle of leucocytozoids (see p. 36). Some important details of this process are given below.

As it was mentioned above, large gametocytes, which outwardly look completely developed, appear in the blood of ducks eight days after the inoculation of sporozoites. However, at this time they are not completely mature, and microgametocytes are not able to exflagellate. Mass maturation of gametocytes takes place nine days after infection. The ability of gametocytes to exflagellate does not change between the 9th and 21st day after infection. During this period of time, exflagellation initiates usually within 1 min after exposure of infected blood to air at a temperature of about 30°C. It is important to note that, from the 22nd day after infection, exflagellation initiates later, and it was not recorded after 26 days. In the vertebrate host, there is usually a variation in the length of time when gametocytes capable of exflagellating are present because of the asynchronous exoerythrocytic merogony which leads to the simultaneous presence of different-age gametocytes in the blood. However, it looks likely that each generation of gametocytes is capable of exflagellating for only about five days after they attain maturity. Below 15°C, exflagellation was rarely seen. There is a decrease in the time required for exflagellation as the temperature increases from 15 to 25°C. Between 26 and 40°C, microgametes develop usually within 1 to 1.5 min (Roller and Desser, 1973).

Gametocytes, which develop both in roundish and fusiform host cells, produce gametes. However, both the exflagellation of microgametocytes and the structure of the microgametes produced by gametocytes of these two types were recorded to be different. After escaping from host cells, gametocytes of the former type (Fig. 21) produce microgametes without any major transformation of the main body of gametocyte, evident under the light microscope (Desser, 1970c; Desser *et al.*, 1976). Microgametes fixed with methanol are about 23 μm in length and 1 μm in width. Each microgamete was said to possess two axonemes. Gametocytes, which develop in fusiform host cells, become dumbbell-shaped after escaping from infected cells (Aikawa *et al.*, 1970). Part of this dumbbell contains a nucleus and other organelles, and microgametes develop here. The

other part is a residual body. Microgametes fixed with methanol are about 12 μm in length and 1 μm in width. Each microgamete possesses one axoneme. The presence of two types of exflagellation and the dualism in the structure of microgametes have not been recorded in other haemosporidian parasites, and thus further investigations are required.

Worm-like motile ookinetes were observed in the midgut content of *Simulium rugglesi* 12 h after the ingestion of gametocytes at a temperature of 18°C (Fig. 22, *1*). Ookinetes were about 30 μm in length and 4 μm in width, and each possessed a prominent, more or less off-centre-located nucleus and several large 'vacuoles.' Young oocyst possesses one large well evident 'vacuole' (Fig. 22, *2*). The development of ookinetes and oocysts is not synchronized. Oocysts complete their development within three to five days after infection, and their size increases only slightly. Mature oocysts usually vary from 9 to 14 μm in diameter. Each oocyst produces less than 100 sporozoites (Desser and Fallis, 1967a; Desser, 1972c; Eide and Fallis, 1972).

Sporozoites look like elongated bodies with one end rounded and the other end pointed (Fig. 22, *3*). They are on average about 8 μm in length and 1 μm in width. Sporozoites, which were shorter and thicker, were sometimes also observed in the salivary glands of simuliid flies. These sporozoites were on average about 6 μm in length and 2 μm in width. They are, probably, growing older forms because they were observed mainly at the end of a season of transmission (Desser and Fallis, 1967a; Desser and Wright, 1968).

Leucocytozoon simondi successfully develops both in simuliid flies which prefer to feed mainly on birds (*Simulium rugglesi*) and mammals (*S. venustum*). Moreover, the duration of sporogony is similar in different species of vectors, and it is usually completed three days after the ingestion of mature gametocytes at a temperature of 20°C (Desser and Yang, 1973). It is likely that restrictions for the development of *L. simondi* in different species of simuliid flies are ecological rather than physiological.

P a t h o g e n i c i t y. *Leucocytozoon simondi* is responsible for a severe leucocytozoonosis in domestic and wild anseriform birds. This disease was first investigated in detail by Tartakovsky (1913) in the north-eastern Russia. The Russian scientist discovered the disease to be common in the environs of St. Petersburg, Novgorod and Pskov guberniyas, and in Finland. In spite of the practical significance of these data, the work of M.G. Tartakovsky was overlooked by his contemporaries, and the leucocytozoonosis of anseriform birds was subsequently redescribed in Canada (Wickware, 1915) and Germany (Knuth and Magdeburg, 1922).

Mortality among ducks, geese, and swans because of *L. simondi* infection has been reported by numerous authors. Moreover, in localities with active transmission, the disease is a prominent ecological factor influencing negatively wild anseriform birds and markedly limiting industrial breeding of domestic anseriforms (Tartakovsky, 1913; Wickware, 1915; Knuth and Magdeburg, 1922; O'Roke, 1934; Karstad, 1965; Fallis and Bennett, 1966; Khan and Fallis, 1968; Kocan, 1968; Laird and Bennett, 1970; Herman *et al.*, 1975; Desser and Ryckman, 1976; Mörner and Wahlström, 1983, and others).

It is important to note that leucocytozoonosis in anseriform birds has not been recorded outside the Holarctic. This disease is distributed mainly in the Northern Holarctic (Valkiūnas *et al.*, 1990). In the Nearctic, the disease has been especially frequently recorded between 42° and 58° N latitudes, and in the Palearctic, north of 52° N latitude, and even more toward south in Western Siberia, environs of Lake Baikal, and some regions of the Far East where the density of both simuliid flies and anseriform birds is high.

The disease is especially severe in young birds, but adult birds of some species and breeds also suffer. Domestic birds are more susceptible and the disease is more severe in

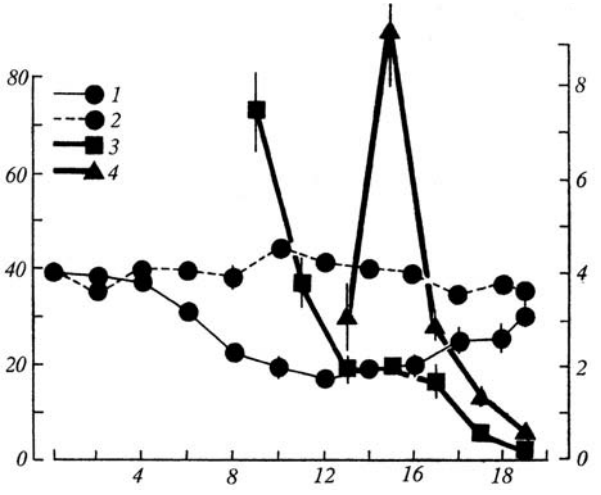

Figure 306 Dynamics of mean percentage hematocrit (*1*, *2*) and gametocytemia (*3*, *4*) in infected with *Leucocytozoon simondi* ducklings ($n = 11$) and noninfected (control, $n = 10$) birds:
1, *2* – groups of birds: *1* – experimental, *2* – control; *3*, *4* – morph of gametocytes: *3* – in roundish host cells, *4* – in fusiform host cells. In the ordinate, there are indicated the mean level of hematocrit, % (on the left) and the mean number of gametocytes, $(\times 10^3)/mm^3$ blood (on the right), and on the abscissa, the days after exposure of birds in the endemic to leucocytozoonosis locality. The bars denote the standard error of the mean; where the bars are absent, the standard errors does not exceed the diameter of the symbol designating the data point (modified from Maley and Desser, 1977).

them than in wild birds. Khan and Fallis (1968) evaluated the effects of *L. simondi* on wild (*Anas rubripes, A. platyrhynchos*) and domestic (*A. boschas*) young and adult ducks which were infected both naturally and experimentally. After continual natural exposure to infected simuliid flies, the highest mortality rate was recorded in immature *A. boschas* (75%), and it was lower in immature *A. platyrhynchos* (40 %) and *A. rubripes* (18%). Similar results were obtained after the inoculation of comparable doses of sporozoites to ducklings of these species; mortality among *A. boschas* was 91%, and it was 58% and 54% among *A. platyrhynchos* and *A. rubripes*, respectively. The highest parasitemias were recorded in wild birds, but the lowest volumes of erythrocytes and thus the most severe anaemia were noticed in domestic birds. The mortality rate among adult *A. boschas* reached 60%, and only a few cases of death were recorded in adult *A. rubripes* and *A. platyrhynchos*. During primary infection and relapses, despite some variations, the highest parasitemia was seen in *A. rubripes*. The latter fact shows that the parasitemia is not necessarily a measure of resistance. Wild birds are much less affected than domestic ones, but the parasitemia is usually much higher in the former. This contributes to the maintenance of the parasite in natural foci of infection.

Symptoms vary markedly depending on bird species, breed, and age. Mortality is especially high in young domestic birds which are usually inactive, weak, depressed, and emaciated. Diarrhoea with green faeces and breath difficulties can be evident. Birds can die in conditions of shock, and convulsions are common before the death. The disease is frequently rapid. A flock can be normal in the morning, ill in the afternoon, and dead the following morning. The surviving birds become stunted in growth. Heavy anaemia and marked damage of tissues in such vital organs as the heart, lungs, liver, spleen, brain, and

others by ruptured megalomeronts are the main causes of high mortality. Numerous inflammatory and necrotic nidi develop at the place of ruptured megalomeronts. At necropsy, an enormous enlargement of the spleen and also a marked enlargement of the liver, necrotic nidi and blockage of blood vessels in numerous organs, infiltration of inflammatory cells around and inside megalomeronts, are evident (Tartakovsky, 1913; Wickware, 1915; O'Roke, 1934; Cowan, 1957; Newberne, 1957; Desser, 1967; Kocan, 1968; Maley and Desser, 1977).

Anaemia is the most marked pathological feature of this disease (Maley and Desser, 1977). In heavily infected birds, the erythrocyte count drops approximately twice or even more compared to the normal level. This drop is not associated with direct destruction of erythrocytes by gametocytes, because the peak of anaemia precedes the peak of parasitemia (Fig. 306). Anaemia begins four days after exposure to natural infection, and this coincides with the time of maturity of hepatic meronts. The highest loss of erythrocytes occurs on the 10th to 12th day after the exposure when megalomeronts mature. The hematocrit level begins to approach the preinfection level gradually soon after the maximum parasitemia on day 15 after exposure when gametocytes in fusiform host cells predominate in the peripheral circulation. The highest mortality of ducklings was recorded at 12 days post exposure when the majority of megalomeronts are ruptured and anaemia reaches its peak. It is important to note that, in addition to physical damage of tissues because of ruptured megalomeronts, a huge amount of alien material is released into the blood circulation, and this can be a reason for severe biochemical trauma.

Anaemia is accompanied with increased osmotic fragility of erythrocytes, and the dynamics of anaemia coincides with that of osmotic fragility of red blood cells (Fig. 307). The increased osmotic fragility of erythrocytes begins after hepatic meronts mature (four to six days after infection), it reaches a peak before the peak of anaemia after the release of merozoites from megalomeronts (9 days after infection), and decreases rapidly thereafter (15 days after infection with sporozoites). It is likely that the marked decrease of erythrocyte counts is due to the presence of the so-called anti-erythrocyte factor which leads to increased osmotic fragility and thus to severe anaemia. Both the increased osmotic fragility of erythrocytes and the anaemia began after maturation of hepatic meronts. Probably, this product is released from these meronts or their host cells (Kocan and Clark, 1966; Desser, 1967; Khan and Fallis, 1968; Kocan, 1968; Desser and Ryckman, 1976). The nature of this factor is still unknown. It was proved experimentally that the serum of acutely infected ducks induces the lysis of erythrocytes from intact birds. Titers of this factor are lower and anaemia is less severe in reinfected birds in comparison to the primarily infected birds. It thus looks likely that the factor is produced by the parasite and does not belong to a group of autoantibodies. This factor can include a parasite product, which is released from meronts, and (or) a material, which is elaborated from the host cells through their mechanical disruption (Kocan, 1968).

Disease was recorded to be especially heavy in ducklings, in which the parasite usually undergoes its complete cycle of exoerythrocytic merogony to form megalomeronts. Mortality is usually associated, although not exclusively, with infection in domestic birds. However, wild birds such as ducks, geese, and swans were also recorded to suffer from the infection (Karstad, 1965; Desser and Ryckman, 1976; Mörner and Wahlström, 1983).

Virulence of different strains for geese varies markedly. The strains, which undergo complete exoerythrocytic merogony, are markedly virulent and frequently cause the death of infected goslings. The clinical signs of illness in goslings are similar to these in ducklings. However, the strains, which undergo only 'partial' development without

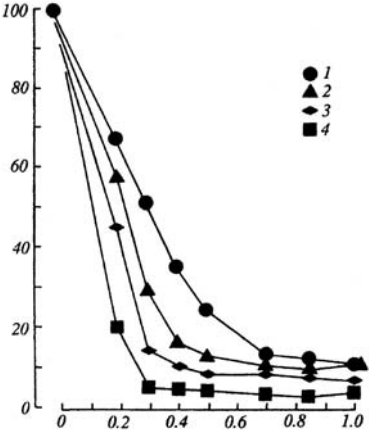

Figure 307 Hemolysis for infected with *Leucocytozoon simondi* (*1–3*) and noninfected (control, *4*) ducklings after dilution of the blood by saline of different concentrations:
1–3 – time after exposure of experimental birds at the endemic for leucocytozoonosis locality, days: *1* – 6 days (sample size, $n = 14$), *2* – 15 days ($n = 10$); *3* – 9 days ($n = 15$). The sample size for control birds is $n = 20$. The level of hemolysis, %, is shown on the ordinate; the saline concentration, %, is shown on the abscissa (modified from Maley and Desser, 1977).

formation of megalomeronts, are relatively benign and do not kill goslings (Herman *et al.*, 1970, 1975; Desser and Ryckman, 1976; Desser *et al.*, 1978). This testifies to the important role of megalomeronts in the pathology of birds.

Reinfection of formerly infected birds is possible, and it was even recorded to be accompanied with mortality (Fallis *et al.*, 1951).

Simuliid flies, which were fed on birds with heavy parasitemia, ether rapidly die in captivity or live less than uninfected flies (Desser and Yang, 1973). This testifies to the pathogenicity of the parasite for vectors.

S p e c i f i c i t y. *Leucocytozoon simondi* is a specific parasite of anseriform birds (see p. 76 for a detailed analysis of the specificity). It successfully develops in ducks, geese, swans, and other species of the Anseriformes (Table 157).

C o m m e n t s. Tartakovsky (1913) published both excellent colour illustrations of the parasite, which was described by him as a new species *L. anatis*, and detailed comments to these illustrations. The species name *L. anatis* Tartakovsky, 1913 corresponds to Article 12 of the International Code of Zoological Nomenclature (1985), and it cannot be considered to be a *nomen nudum* as suggested by Peirce and Bennett (1979), Bennett and Squires-Parsons (1992), Bishop and Bennett (1992). The specific name *L. anatis* Wickware, 1915 is a junior homonym of *L. anatis* Tartakovsky, 1913, and thus should be dismissed.

Leucocytozoon simondi is the only species of leucocytozoids currently known to parasitize birds of the order Anseriformes.

13. **Leucocytozoon (Leucocytozoon) dubreuili** Mathis and Léger, 1911

Leucocytozoon dubreuili Mathis and Léger, 1911b: 317, Pl. 6, Fig. 9–13. – *L. mirandae* França, 1912c: 174. – *L. seabrae* França, 1912c: 175. – *L. francai* Nikitin, 1927: 350. – *L. giovannolai* Travassos

Santos Dias, 1954: 7. – *L. dubreuili*: Fallis *et al.*, 1974: 14 (=*L. francai*, *L. giovannolai*, *L. mirandae*, *L. seabrae*). – *L. zosteropis* Peirce, Cheke and Cheke, 1977: 455, Pl. 4. – *L. dubreuili*: Valkiūnas, 1988b: 115, Fig. 1 (=*L. zosteropis*). – *L. irenae* Bennett and Peirce, 1992b: 700, Fig. 12–14. – *L. nectariniae* Bennett, Earlé and Peirce, 1992c: 240, Fig. 18–22. – *L. dubreuili*: Valkiūnas, 1997: 520 (= *L. irenae, L. nectariniae*).

Type vertebrate host. *Turdus* sp. (Passeriformes). The scientific name of the species is not given in the original description. The French name of the type host is 'Grive.' It is likely that this is *Turdus iliacus* L. investigated during its seasonal migration.
Additional vertebrate hosts. Numerous species of the Passeriformes (over 60 species).
Vectors. *Cnephia ornithophilia*, *Prosimulium decemarticulatum, Simulium aureum, S. latipes* and *S. quebecense* (Diptera: Simuliidae).
Type locality. Tonkin (environs of Hanoi, Vietnam).
Distribution. Common parasite of passeriform birds in the Holarctic, Ethiopian, and Oriental zoogeographical regions. Only a few records came from the Neotropical and Australian regions.
Type material. Neohapantotype (No. 42575, *Turdus iliacus*, 23.01.1963, UK, coll. Threlfall) is deposited in IRCAH.
Etymology. This species is named in honour of Dr. Jouveau-Dubreuil.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is more or less dumbbell-shaped with thickenings at both ends; the nucleus extends more than 1/2 of the circumference of gametocyte.

Development in vertebrate host

According to the results of experimental investigations (Khan and Fallis, 1970a; Wong and Desser, 1978, 1981), a general scheme of the endogenous development is as follows. Sporozoites, inoculated into blood stream of birds, initiate three types of meronts. First, part of sporozoites invades parenchymal cells of the liver and develops into first-generation hepatic meronts. Part of merozoites from these meronts invades erythrocytes and develops into gametocytes. The remaining merozoites induce secondary merogony in the liver and kidneys. Second, part of sporozoites invades cells of renal proximal tubules, and, after a short period, they initiate the development of first-generation meronts in the kidneys. Renal meronts, which are induced both by sporozoites and merozoites from first-generation hepatic meronts, appear approximately at the same time. Merozoites from renal meronts invade erythrocytes and develop into gametocytes. Third, part of sporozoites invades liver parenchymal cells and develops into oocyst-like meronts which produce 'cystozoite-like' merozoites. The latter are normally released during a spring period. Part of these 'cystozoites' invades erythrocytes and develops into gametocytes, and the other part of the parasites develops into subsequent generations of the oocyst-like meronts. It is likely that merozoites from the latter meronts are responsible for a long-term persistence of parasite in the vertebrate host. Some details of endogenous development are given below.

Meronts were not found in the lungs, spleen, heart, brain, and bone marrow. The exo-erythrocytic merogony especially quickly initiates in the liver, where binuclear parasites were observed 42 h after the inoculation of sporozoites. Young meronts contain several masses of chromatin which are randomly scattered throughout the cytoplasm (Fig. 308, *1*). Nucleus of infected cell is pushed aside, enlarged, and can be deformed (cap-like in form). As the parasite develops, well-pronounced cytomeres appear, and nuclei tend to locate peripherally in the cytomeres (Fig. 308, *2*). First mature meronts were found approximately 87 h after infection, and it is likely that they appear even earlier. The parasites are filled up

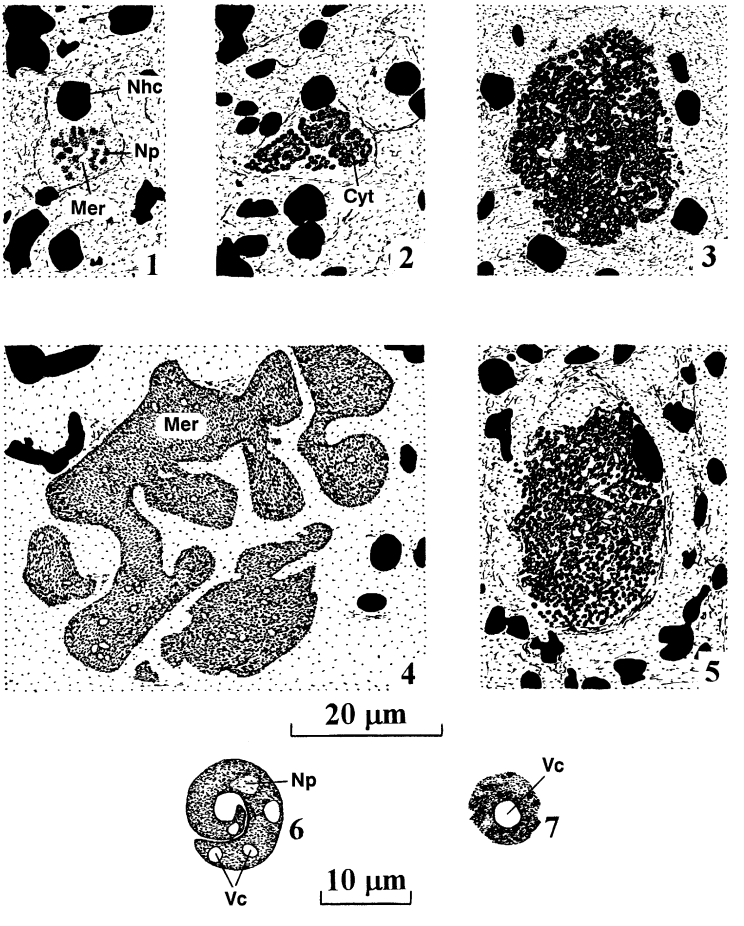

Figure 308 *Leucocytozoon dubreuili:*
Exoerythrocytic meronts from *Turdus migratorius* (*1–5*), ookinete (*6*), and young oocyst (*7*); *1–3* – meronts in the liver: *1* – young parasite, *2* – parasite with cytomeres, *3* – mature parasite dividing into separate merozoites; *4–5* – meronts in kidneys: *4* – growing parasite with cytomeres, *5* – mature parasite; Cyt – cytomere; Mer – meront; Nhc – nucleus of host cell; Np – nucleus of parasite; Vc – 'vacuole' (modified from Khan and Fallis, 1970a).

with a homogeneous mass of sporozoites (Fig. 308, *3*). Nondeformed hepatic meronts are roundish or of oval form. Mature meronts ($n = 20$) were 21 to 40 by 17 to 33 (on average 28×33) μm in size. Second-generation meronts in the liver appear four days after infection, and the majority of them mature by the seventh day. The morphology of meronts of both the first and second generations is similar. Hepatic meronts were recorded up to 11 days after infection. However, they are not numerous after the seventh day.

Sporozoites, which penetrate into the kidneys, are delayed in their development. Renal meronts of the first generation appear approximately at the same time as renal meronts of the second generation, which are induced by merozoites from hepatic meronts. Young meronts are numerous in the kidneys 90 h after infection. As the parasite develops, meronts follow the convolutions of the proximal renal tubules and thus can assume an irregular form

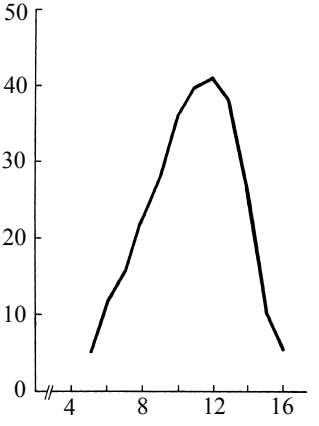

Figure 309 Dynamics of parasitemia of *Leucocytozoon dubreuili* in *Turdus migratorius* and *T. merula* experimentally infected with sporozoites:
Mean parasitemia (number of parasites per 1000 erythrocytes) in ten infected birds is shown on the ordinate, days after the inoculation of sporozoites are shown on the abscissa (modified from Khan and Fallis, 1970a).

(Fig. 308, *4*). Cytomeres develop. First mature meronts appear in the kidneys seven days after infection, but the majority of them complete their development 7.5 to 9 days after the infection. They frequently look roundish or oval in form in cross sections (Fig. 308, *5*). A few meronts were observed in the kidneys 11 days after infection, but some of them were seen up to 42 days.

Oocyst-like meronts are also present in the liver of experimentally infected birds. They contain elongated (cystozoite-like) merozoites. These meronts develop in hepatocytes and, probably, they are persisting stages which are responsible for relapses. However, the certain role of these stages in life cycle of this parasite is unknown. The meronts are about 6×4 μm in size. Merozoites germinate from a single germinative centre as it takes place in oocysts (Wong and Desser, 1981).

First merozoites appear in the peripheral circulation approximately 3.5 days after inoculation of sporozoites. They invade polychromatic and mature erythrocytes and develop into gametocytes which host cells assume a roundish form. Gametocytes do not develop in leukocytes (Wong and Desser, 1981). During heavy primary parasitemia, infection of the same erythrocyte with several (up to six) parasites is common. However, usually only one parasite reaches maturity. Mature (capable of gametogenesis) gametocytes appear six days after infection. The process of maturation of gametocytes takes approximately two or three days. Since the 11th day after infection, the majority of gametocytes are mature in the peripheral blood. Parasitemia markedly increases from the fifth day after the inoculation of sporozoites. It reaches its peak on the 11th day and then decreases rapidly (Fig. 309). A few gametocytes in birds infected only once have been recorded for many years and sometimes even up to 3.5 years (the period of observation). Chronic parasitemia can be maintained due to the activation of the 'oocyst-like' meronts in the liver and (or) renal meronts. Both types of meronts are probably also responsible for relapses. The latter are well-pronounced and synchronized with a breeding period of birds.

Macrogametocytes (Fig. 310, *1–6*; Table 156) develop in roundish host cells; the cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes

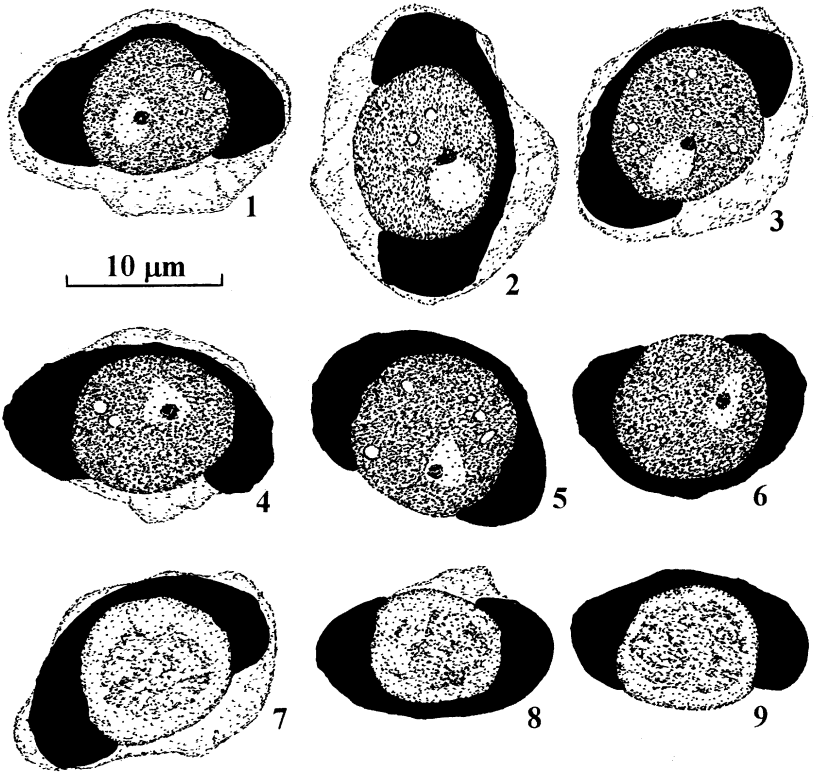

Figure 310 Gametocytes of *Leucocytozoon dubreuili* from the blood of *Turdus philomelos*: *1–6* – macrogametocytes; *7–9* – microgametocytes.

are usually roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, markedly deformed and enlarged, and lies peripherally as a more or less evident dumbbell-shaped structure with thickening at both ends (a bipolar cap), it extends more than 1/2 of the circumference of gametocyte; cytoplasm of host cells is largely replaced by gametocytes, and it is sometimes even invisible (Fig. 310, *5*, *6*) but more frequently present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 310, *1–4*).

Microgametocytes (Fig. 310, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector was investigated by Khan and Fallis (1970a) at a temperature of 21 to 22°C. Exflagellation was observed 2 to 5 min after the ingestion of mature gametocytes by simuliid flies. Ookinetes were seen in the contents of midgut of the flies 12 to 108 h after infection (Fig. 311, *1*). After fixation with methanol, they vary (n = 10) from 22 to 30 (on average 26) μm in length. Ookinete possesses an off-centre-located nucleus and several prominent 'vacuoles.' Ovoid- to spherical-form oocysts at various stages of development were observed in the midgut wall of simuliids dissected 36 to 96 h after the ingestion of gametocytes. A large well-pronounced 'vacuole' and randomly scattered masses of chromatin are evident in young oocyst (Fig. 311, *2*). As oocyst develops, the

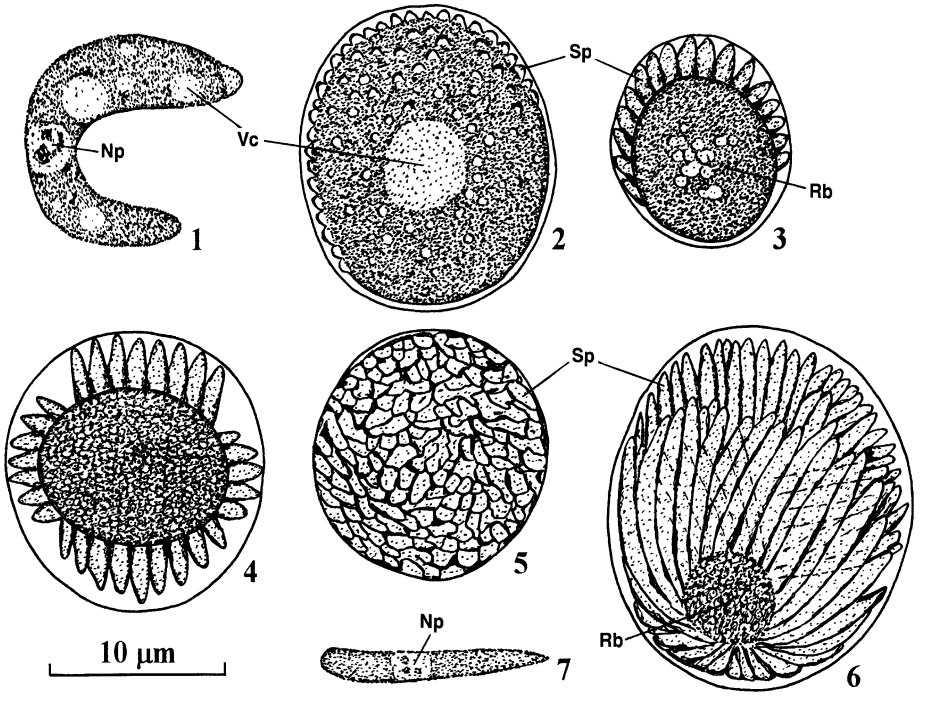

Figure 311 *Leucocytozoon dubreuili*:
1 – ookinete; *2–6* – different stages of the development of oocyst: *2–4* – initial stages of the development of sporozoites which bud from a single germinative centre (a residual mass of cytoplasm); *5, 6* – nearly mature oocyst with numerous sporozoites; *7* – sporozoite; Np – nucleus of parasite; Rb – residual body; Sp – developing sporozoite; Vc – 'vacuole' (modified from Fallis and Bennett, 1962).

'vacuole' decreases in size and finally disappears, and more nuclei are evident and locate at the periphery of the oocyst. The surface of the latter is now formed into small buds (Fig. 311, *2*, *3*), which gradually increase in length to become sporozoites at 72 h after infection. The sporozoites germinate radially from a single germinative centre (Fig. 311, *4*, *6*). They finally leave the residual mass of cytoplasm. Motile sporozoites were seen in some oocysts approximately 90 h after the ingestion of gametocytes. The process of sporogony is not synchronized. Ookinetes, young and mature oocysts are present simultaneously. As oocyst develops, its size increases no more than twice. Mature oocysts vary from 9 to 19 (more frequently 14 to 16) μm in diameter. Largest oocysts contain up to 150 sporozoites (Wong and Desser, 1976). Sporozoites appear in the salivary glands four days after the ingestion of gametocytes. They look like elongated bodies with one end more or less rounded and the other pointed (Fig. 311, *7*). They (n = 10) vary from 7 to 13 (on average 11) μm in length, and about 1 μm in width.

The process of sporogony is similar in different species of vectors which are maintained at similar conditions.

P a t h o g e n i c i t y. Signs of illness have not been recorded in experimentally infected birds at the laboratory conditions. Possible ways of pathogenic influence on wild free-living birds are discussed in the General Section (see p. 110).

S p e c i f i c i t y has been insufficiently investigated (see p. 77).

Comments. *Leucocytozoon irenae* and *L. nectariniae* were described mainly on the basis that they were found in birds belonging to different passeriform families than *L. dubreuili* is originally described (Bennett *et al.*, 1992c; Bennett and Peirce, 1992b). Gametocytes and their host cells both of *Leucocytozoon irenae* and *L. nectariniae* cannot be distinguished morphologically from the same stages of *L. dubreuili*. The specificity of the former two parasites has not been investigated, and the data on stages of their development other than gametocytes are not available at present, either. Therefore, *L. irenae* and *L. nectariniae* are considered to be junior synonyms of *L. dubreuili*. This synonymy is discussed in connection with the problem of specificity of leucocytozoids in the General Section in more detail (see p. 79).

14. **Leucocytozoon (Leucocytozoon) leboeufi** Mathis and Léger, 1911

Leucocytozoon leboeufi Mathis and Léger, 1911a: 212. – *L. ardeae* Rodhain, Pons, Vandenbranden and Bequaert, 1913a: 274, Fig. D. – *L. sanarellii* Babudieri, 1931: 626. – *L. ardeolae* Mello, 1936: 106. – *L. iowense* Coatney, 1938: 336, Pl. 1, Fig. 1, 2. – *L. leboeufi*: Valkiūnas, 1997: 524 (=*L. ardeae, L. ardeolae, L. iowense, L. sanarellii*). – *L. ibisi* Adlard, Peirce and Lederer, 2002: 1265, Fig. 5, 6 (syn. nov., see Appendix 2 for comments).

Type vertebrate host. *Ixobrychus sinensis* (Gmelin) (Ciconiiformes).
Additional vertebrate hosts. Some species of the Ciconiiformes (Table 158).
Type locality. Tonkin (environs of Hanoi, Vietnam).
Distribution. The Holarctic, Ethiopian and Oriental zoogeographical regions.
Type material has not been designated.
Etymology. This species is named in honour of Dr. A. Leboeuf.

Table 158 List of vertebrate hosts of *Leucocytozoon leboeufi*.

Ardea cinerea	*Bubulcus ibis*	*E. thula*
A. goliath	*Butorides virescens*	*Ixobrychus minutus*
A. herodias	*Ciconia ciconia*	*Nycticorax nycticorax*
Ardeola grayii	*Egretta alba*	*Threskiornis molucca*
A. striatus	*E. dimorpha*	
Botaurus stellaris	*E. garzetta*	

Table 159 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. leboeufi*				*L. legeri* (according to Valkiūnas, 1989a)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	25				13			
Length		10.1–18.2	13.1	1.0		8.9–13.3	11.1	0.3
Width		10.0–15.9	12.4	1.2		9.7–11.2	10.8	0.2
Length of nucleus		3.6–6.0	4.9	0.8		2.7–5.0	3.6	0.2
Width of nucleus		1.8–4.5	3.3	0.7		1.3–4.8	2.6	0.2
Length of nucleus of host cell		10.4–31.8	16.9	1.9		4.7–15.5	9.6	2.4

Note: All sizes are given in micrometres.

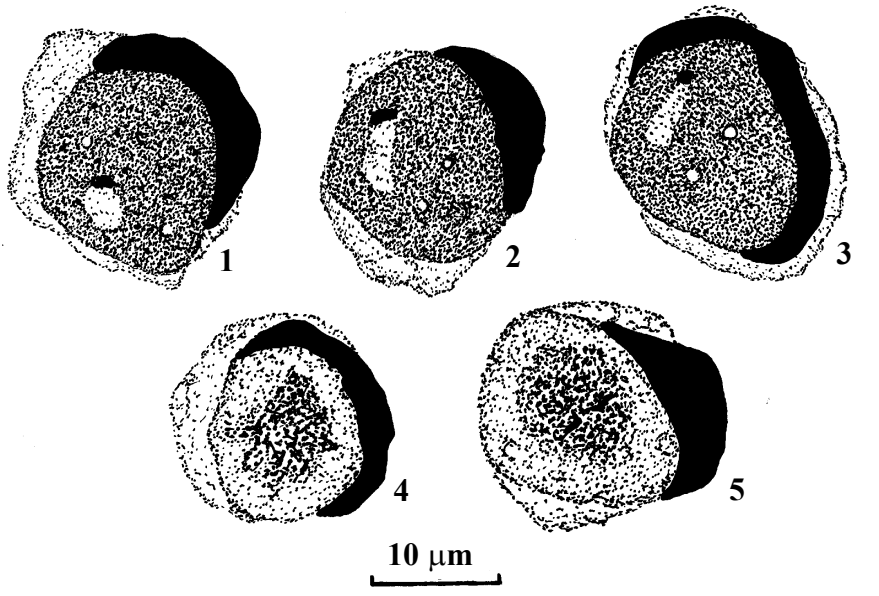

Figure 312 Gametocytes of *Leucocytozoon leboeufi* from the blood of *Ardea cinerea*: *1–3* – macrogametocytes; *4, 5* – microgametocytes.

Main diagnostic characters. A parasite of species of the Ciconiiformes whose gametocytes develop in roundish host cells. Nucleus of the host cell varies from a cap-like to band-like form; the nucleus can extend up to 2/3 of the circumference of the gametocyte.

Development in vertebrate host

Macrogametocytes (Fig. 312, *1–3*; Table 159) develop in roundish host cells; the cytoplasm frequently contain small vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap (Fig. 312, *2*) or band (Fig. 312, *1*, *3*), it extends less than 2/3 of the circumference of gametocyte; the nuclei of host cells, which extend more than 1/2 of the circumference of gametocytes (Fig. 312, *3*), are present; moreover, the host cells, which nuclei nearly completely surround gametocytes, were seen occasionally, and are probably deformed cells appearing during preparation of blood smears; the cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 312, *1–3*).

Microgametocytes (Fig. 312, *4*, *5*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The available data about *L. ardeae*, *L. ardeolae*, *L. iowense*, and *L. sanarellii* are restricted to morphology of gametocytes and their host cells which are indistinguishable from those of *L. leboeufi*. Therefore, bearing in mind the main principles of identification of species of leucocytozoids (see p. 76), it is preferable at present to consider the above mentioned species names to be junior synonyms of *L. leboeufi*.

15. **Leucocytozoon (Leucocytozoon) legeri** França, 1912

Leucocytozoon legeri França, 1912a: 20.

Type vertebrate host. *Scolopax rusticola* L. (Charadriiformes).
Additional vertebrate hosts. Some species of the Charadriiformes (Table 160).
Type locality. Portugal.
Distribution. This parasite has been recorded in the Palearctic. It is likely that the range is markedly wider.
Type material has not been designated. A series of good additional slides is deposited in CDVA.
Etymology. This species is named in honour of prominent parasitologist Professor M. Léger.

Main diagnostic characters. A parasite of species of the Charadriiformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is of a cap-like or band-like form; the nucleus extends less than 1/2 of the circumference of gametocyte.

Table 160 List of vertebrate hosts of *Leucocytozoon legeri*.

Calidris alpina	*Phalaropus lobatus*
C. temminckii	*Tringa stagnatilis*
Gallinago gallinago	*Vanellus vanellus*
G. media	

Development in vertebrate host
Macrogametocytes (Fig. 313, *1–3*; Table 159) develop in roundish host cells; the cytoplasm frequently contains more or less evident vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed, and lies peripherally usually as a more or less evident cap (Fig. 313, *1–3*) or sometimes band, it extends less than 1/2 of the circumference of the gametocyte; the cytoplasm of host cells is largely

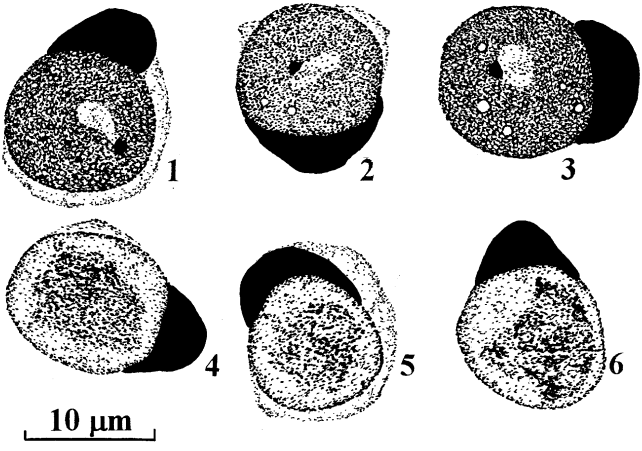

Figure 313 Gametocytes of *Leucocytozoon legeri* from the blood of *Scolopax rusticola*: *1–3* – macrogametocytes; *4–6* – microgametocytes.

replaced by gametocytes, and is sometimes even invisible (Fig. 313, *3*) but more frequently is present around the gametocyte as a more or less evident and pale margin of variable form (Fig. 313, *1*, *2*).

Microgametocytes (Fig. 313, *4–6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon legeri* is a common parasite of *Scolopax rusticola* in the Palearctic where it has been much less frequently recorded in other species of charadriiform birds.

16. **Leucocytozoon (Leucocytozoon) struthionis** Walker, 1912

Leucocytozoon struthionis Walker, 1912: 375, Figs.

Type vertebrate host. *Struthio camelus* L. (Struthioniformes).
Type locality. Cape Province, Middelburg District, South Africa.
Distribution. The Ethiopian zoogeographical region. The majority of records came from South Africa.
Type material. Neohapantotype (No. 104984, *Struthio camelus*, 2.11.1988, Oudsthoorn, South Africa, F.W. Huchzermeyer) and paraneohapantotype (No. 113831, 3.11.1990, G.F. Bennett, other data as for the neohapantotype) are deposited in IRCAH.
Etymology. The specific name is derived from the genetic name of the type vertebrate host, *Struthio*.

Main diagnostic characters. A parasite of species of the Struthioniformes whose gametocytes develop in roundish host cells. The nucleus of the host cell is usually of a cap-like or sometimes band-like form; the nucleus extends less than 1/2 of the circumference of the gametocyte. The cytoplasm is frequently highly vacuolated in fully grown gametocytes.

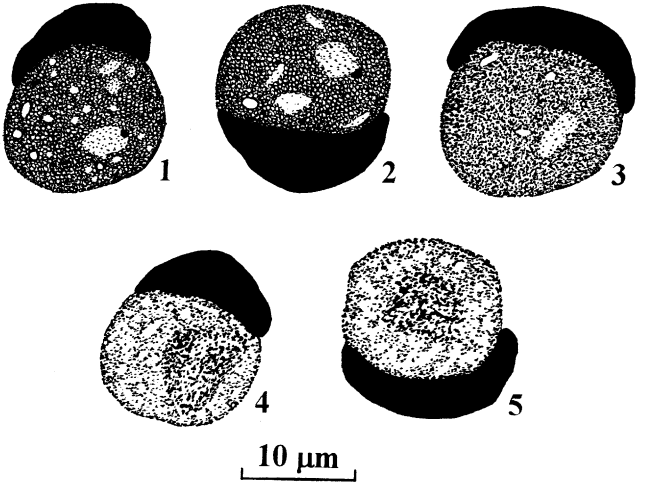

Figure 314 Gametocytes of *Leucocytozoon struthionis* from the blood of *Struthio camelus*: *1–3* – macrogametocytes; *4*, *5* – microgametocytes.

Development in vertebrate host

Macrogametocytes (Fig. 314, *1–3*; Table 161) develop in roundish host cells; the cytoplasm frequently contains vacuoles and is frequently highly vacuolated in fully grown gametocytes (Fig. 314, *1*, *2*); gametocytes are roundish; the parasite nucleus is of variable form and position; the nucleolus is well seen; the nucleus of host cell is pushed aside, deformed, and lies peripherally usually as a more or less evident cap (Fig. 314, *1, 2*) or sometimes a band (Fig. 314, *3*), it extends less than 1/2 of the circumference of the gametocyte; the cytoplasm of host cells is usually largely replaced by gametocytes, and is frequently even invisible around fully grown gametocytes (Fig. 314, *1–3*).

Table 161 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. schoutedeni* (modified from Bennett *et al.*, 1991c)			*L. struthionis* (modified from Bennett *et al.*, 1992d)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	20			23		
Length		13.9	1.3		15.3	2.0
Width		12.0	1.1		12.6	1.4
Length of nucleus		4.2	0.7		5.0	1.1
Width of nucleus		2.9	0.5		2.7	0.6
Length of nucleus of host cell		18.9	2.9		18.6	3.1

Note: All sizes are given in micrometres.

Microgametocytes (Fig. 314, *4*, *5*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the size of microgametocytes is slightly smaller than for macrogametocytes; other characters are as for macrogametocytes.

Microgametocytes are less numerous in peripheral circulation than macrogametocytes.

Pathogenicity. This parasite was discovered in ostrich chicks which were dying massively on farms in South Africa (Walker, 1912, 1913). The disease was recorded only in young birds (up to seven months old). Clinical symptoms were noticed some days before death. Diseased chickens are listless, anorexic, grow weaker with inability to keep up with the rest of the brood when driven; buccal mucous membranes are pale, and skin of body and around eyes is bluish. Loss of condition and stunted growth are obvious in recovered birds.

Comments. It is important to note that *L. struthionis* has been found only in young (about two to seven months old) ostriches, and it has never been recorded in the adults, even on farms were young birds were infected (Walker, 1912, 1913; Bennett *et al.*, 1992d). It looks likely that the ostriches are incidental or abnormal hosts of the parasite which normally develops in other birds. The adult ostriches are insusceptible, and the susceptible young birds lose the infection when they recover and grow older. *Leucocytozoon struthionis* is especially similar to *L. schoutedeni*, which is a common parasite of domestic chicken in southern Africa (Huchzermeyer, 1966; 1993a). It is possible that ostriches acquire the parasite from domestic chickens which are frequently maintained on ostrich ranches. Experimental testing of this hypothesis is of theoretical and practical significance.

Leucocytozoon struthionis is the only species of leucocytozoids known to parasitize birds of the order Struthioniformes.

17. **Leucocytozoon (Leucocytozoon) caprimulgi** Kerandel, 1913

Leucocytozoon caprimulgi Kerandel, 1913: 437, Pl. 6, Fig. 44–50. – *L. podargii* Adlard, Peirce and Lederer, 2002: 1262, Fig. 1–4 (syn. nov., see Appendix 2 for comments).

Type vertebrate host. *Scotornis fossii* (Hartlaub) (Caprimulgiformes).
Additional vertebrate hosts. *Caprimulgus aegyptius*, *C. europaeus*, *C. pectoralis*, and *Podargus strigoides* (Caprimulgiformes).
Type locality. Haute-Sangha, former Belgian Congo.
Distribution. A rare parasite which has been recorded in the Central and South Palearctic, and in the Ethiopian and Australian zoogeographical regions so far. The range has not been investigated with certainty.
Type material was not designated in the original description. The neohapantotype, designated by Bennett *et al.* (1992b), came from a nontype vertebrate host (*Caprimulgus pectoralis*) and thus it does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of valid neotypes is required.
Etymology. The specific name is derived from the generic name *Caprimulgus*, to which the type vertebrate host was formerly attributed.

Main diagnostic characters. A parasite of species of the Caprimulgiformes whose gametocytes develop in roundish and fusiform host cells. Nucleus of the fusiform host cell is of a band-like form and frequently more or less dumbbell-shaped with clear thickenings at both ends which are closely appressed to gametocyte. Gametocytes in fusiform host cells are rare, and have been only occasionally recorded in peripheral circulation during chronic parasitemia and relapses, and gametocytes in roundish host cells clearly predominate.

Table 162 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. caprimulgi* (according to Valkiūnas, 1989a)				*L. eurystomi* (modified from Valkiūnas, 1989a; Bennett *et al.*, 1993c)			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	35				8			
Length		10.0–14.3	11.7	1.1		–	13.4	1.8
Width		9.1–14.8	10.8	0.9		–	11.2	1.3
Length of nucleus		3.0–6.1	4.3	0.6		–	4.5	0.8
Width of nucleus		2.1–3.9	3.1	0.5		–	2.7	0.7
Length of nucleus of host cell		13.0–21.7	16.1	1.9		–	11.1	2.4
Macrogametocyte in fusiform host cell	3				22			
Length		17.4–21.7	–	–		22.6–29.6	25.2	1.3
Width		8.2–9.6	–	–		7.0–12.2	8.1	1.0
Length of nucleus		3.0–4.8	–	–		2.8–6.4	4.1	0.4
Width of nucleus		3.1–4.0	–	–		1.4–5.7	3.5	0.3
Length of nucleus of host cell		19.5–23.0	–	–		18.3–26.0	21.7	2.3

Note: All sizes are given in micrometres.

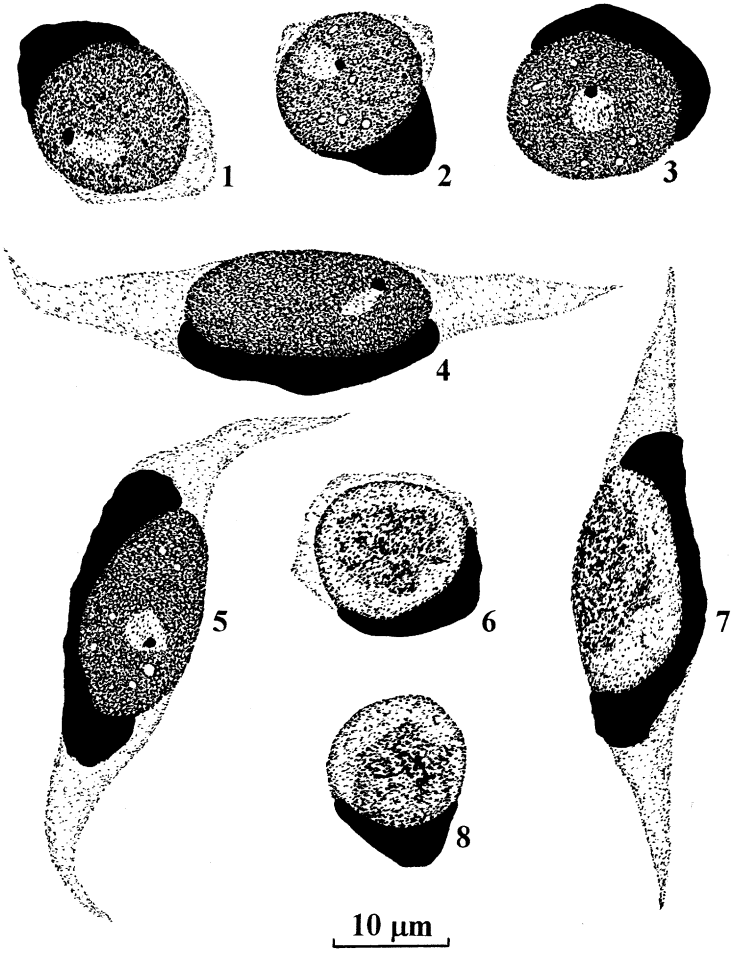

Figure 315 Gametocytes of *Leucocytozoon caprimulgi* from the blood of *Caprimulgus europaeus*: *1–5* – macrogametocytes; *6–8* – microgametocytes.

Development in vertebrate host

Macrogametocytes (Fig. 315, *1–5*; Table 162) develop in roundish and fusiform host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes in roundish host cells are usually roundish (Fig. 315, *1–3*), and gametocytes in fusiform host cells are oval (Fig. 315, *4*, *5*); the parasite nucleus is of variable form and position; nucleolus is prominent and well seen; nucleus of roundish host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap (Fig. 315, *1*, *2*), or sometimes band (Fig. 315, *3*), it can extend up to 1/2 of the circumference of gametocyte but usually less; nucleus of the fusiform host cell is markedly deformed and enlarged, pushed aside, lies peripherally as a long band-like structure (Fig. 315, *4*) which frequently has clear thickenings at both ends, closely appressed to gametocyte (Fig. 315, *5*); cytoplasm of roundish host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 315, *3*) but more frequently present around the gametocytes as a more or less evident

and pale margin of variable form (Fig. 315, *1*, *2*); cytoplasm of fusiform host cells forms two well evident and variable-form and -length processes at the ends of gametocytes (Fig. 315, *4*, *5*); fusiform host cells, whose spindle-shaped cytoplasmic processes in length exceed their width, are present.

Microgametocytes (Fig. 315, *6–8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; microgametocytes, which develop in roundish host cells, are a bit smaller in size than macrogametocytes; other characters are as for macrogametocytes.

It is important to note that gametocytes in fusiform host cells are rare, and they have been only occasionally recorded in the peripheral blood during a chronic parasitemia and relapses. In the majority records, which have been known so far, gametocytes in roundish host cells clearly predominate in the blood.

C o m m e n t s. *Leucocytozoon caprimulgi* is a rare parasite. It was found by the author in 2 of 36 investigated nightjars *Caprimulgus europaeus* during spring migration on the Curonian Spit in the Baltic Sea. Only gametocytes in roundish host cells were observed. This parasite was also recorded by the author only in 6 of over 150 investigated nightjars during autumnal migration in southern Kazakhstan, and a few gametocytes in fusiform host cells were observed only in the blood of a single bird. In eastern and southern Asia, this parasite was not found in 232 investigated caprimulgiform birds (McClure *et al.*, 1978). A few records are known from Africa and Australia. The exclusive rarity of this parasite in caprimulgiform birds shows that they can be incidental or abnormal hosts for the parasite that normally occurs in other avian hosts.

By the morphology of gametocytes and their host cells, *L. caprimulgi* is especially similar to *L. danilewskyi*. The latter species is a common parasite of birds of the order Strigiformes. It is possible that the sporadic records of leucocytozoids in caprimulgiform birds, which are mentioned above, can be the cases of successful incorporation of unusual vertebrate hosts by *L. danilewskyi*, which normally parasitize strigiform birds. In this case, the rarity of occurrence of typical and common for *L. danilewskyi* gametocytes in fusiform host cells in caprimulgiform birds can be explained by the peculiarities of development of this parasite in the unusual hosts as it was recorded for *L. simondi* during its development in some nonadapted hosts (in geese, see p. 790). Testing of this hypothesis is of theoretical significance, and such tests are also important to elucidate the taxonomic status of *L. caprimulgi.* Probably penetration of *L. danilewskyi* into caprimulgiform birds is restricted, at least in part, by the bird's mode of life. Numerous species of caprimulgiform birds prefer to nest and spend a significant part of their time on the ground and (or) inside tree-hollows. In part, this mode of life was shown to protect ecologically birds of blood-sucking simuliid flies (Valkiūnas, 1987c), which are vectors of all currently known parasites of the subgenus *Leucocytozoon*.

Leucocytozoon caprimulgi is the only species of leucocytozoids which has been described in birds of the order Caprimulgiformes.

18. **Leucocytozoon (Leucocytozoon) eurystomi** Kerandel, 1913

Leucocytozoon eurystomi Kerandel, 1913: 438, Pl. 6, Fig. 30–37. – *L. coraciae benghalensis* Mello and Afonso, 1935: 73, Pl. 2. – *L. coraciae*: Bhatia, 1938: 240. – *L. melloi* Bhatia, 1938: 241, Fig. 121. – *L. francae* Tendeiro, 1947: 307, Fig. 14–17. – *L. leitaoi* Tendeiro, 1947: 296, Fig. 18–21. – *L. eurystomi*: Hsu *et al.*, 1973: 196 (=*L. francae*); Bennett *et al.*, 1993c: 79 (=*L. coraciae benghalensis*, *L. coraciae*, *L. leitaoi*, *L. melloi*). – *L. huchzermeyeri* Bennett, Earlé and Squires-Parsons, 1995a: 4, Fig. 15–19 (syn. nov.).

T y p e v e r t e b r a t e h o s t. *Eurystomus gularis* Vieil. (Coraciiformes).

Table 163 List of vertebrate hosts of *Leucocytozoon eurystomi*.

Coracias abyssinica	*C. garrulus*	*Halcyon albiventris*
C. benghalensis	*C. spatulata*	*Merops apiaster*
C. caudata	*Eurystomus glaucurus*	*M. superciliosus*
C. cyanogaster	*E. gularis*	

Additional vertebrate hosts. Some species of the Coraciiformes (Table 163).
Type locality. Haute-Sangha, former Belgian Congo.
Distribution. The Central and South Palearctic, Ethiopian and Oriental zoogeographical regions.
Type material. Neohapantotype, which was designated by Bennett *et al.* (1993c), came from the nontype vertebrate host (*Coracias abyssinica*) and thus does not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of valid neotypes is required. A series of good additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Eurystomus.*

Main diagnostic characters. A parasite of species of the Coraciiformes, whose gametocytes develop in roundish and fusiform host cells. Nucleus of fusiform host cell is usually of an elongated crescent-like form, sometimes band-like shape or resembles the nucleus of uninfected erythrocyte by its form; the nucleus extends less than 1/2 of the circumference of gametocyte. Fusiform host cells, whose nuclei extend less than 1/3 of the circumference of gametocytes, are present.

Development in vertebrate host
Macrogametocytes (Fig. 316, *1–6*; Table 162) develop in roundish and fusiform host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes in roundish host cells are usually roundish (Fig. 316, *1–3*), and gametocytes in fusiform host cells vary from roundish (Fig. 316, *5*) to oval (Fig. 316, *4*) and oval-elongated (Fig. 316, *6*) forms; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of roundish host cell is pushed aside, deformed, and lies peripherally usually as a more or less evident cap (Fig. 316, *1–3*) or sometimes band; it usually extends less than 1/2 of the circumference of gametocyte; nucleus of fusiform host cell is deformed and enlarged, usually pushed aside and lies peripherally as an elongated crescent-like (Fig. 316, *4*, *6*) or sometimes band-like (Fig. 316, *5*) structure or resembles the nucleus of uninfected erythrocyte by its form (Fig. 316, *7*), it extends less than 1/2 of the circumference of gametocyte; fusiform host cells, whose nuclei extend less than 1/3 of the circumference of gametocytes, are present; cytoplasm of roundish host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 316, *3*) but more frequently are present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 316, *1*, *2*); cytoplasm of fusiform host cells forms two well evident and variable-form and -length processes at the ends of gametocytes (Fig. 316, *4–6*); fusiform host cells, whose spindle-shaped cytoplasmic processes in length exceed their width, are common.

Microgametocytes (Fig. 316, *7–11*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon huchzermeyeri* was described mainly on the basis that it was found in coraciiform birds of the family Alcedinidae (Bennett *et al.*, 1995a). Morphology both of gametocytes

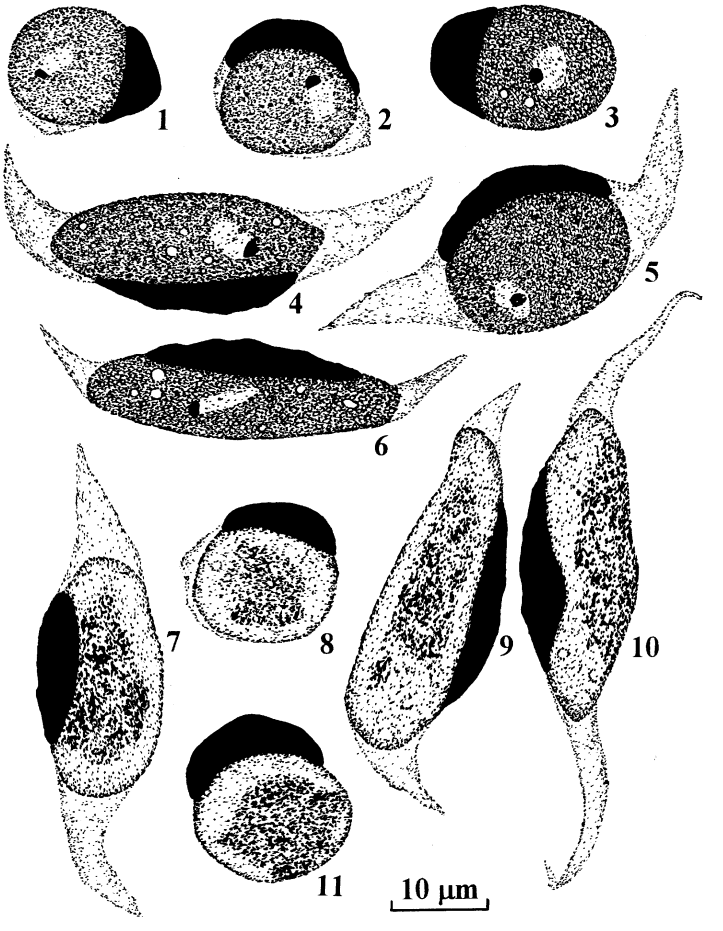

Figure 316 Gametocytes of *Leucocytozoon eurystomi* from the blood of *Coracias abyssinica*: *1–6* – macrogametocytes; *7–11* – microgametocytes.

and their host cells of *L. huchzermeyeri* is identical to this of *L. eurystomi* which is a common parasite of species of the Coraciiformes. Specificity of both these parasites has yet not been investigated experimentally, and the data on other stages of their development, other than gametocytes, are also not available. Based on these facts, and bearing in mind the available data on the specificity of leucocytozoids and main principles of identification of their species, which were discussed above (see p. 76), it is preferable at present to consider *L. huchzermeyeri* to be a junior synonym of *L. eurystomi.*

19. **Leucocytozoon (Leucocytozoon) schoutedeni** Rodhain, Pons, Vandenbranden and Bequaert, 1913

Leucocytozoon schoutedeni Rodhain, Pons, Vandenbranden and Bequaert, 1913b: 160. – *L. andrewsi* Atchley, 1951: 483, Fig. 1–3. – *L. gallinarum* Rousselot, 1953: 40, Fig. 6b. – *L. schoutedeni*: Huchzermeyer, 1966: 323, Pl. 1–2 (=*L. andrewsi*); Bennett *et al.*, 1991c: 1417 (=*L. gallinarum*).

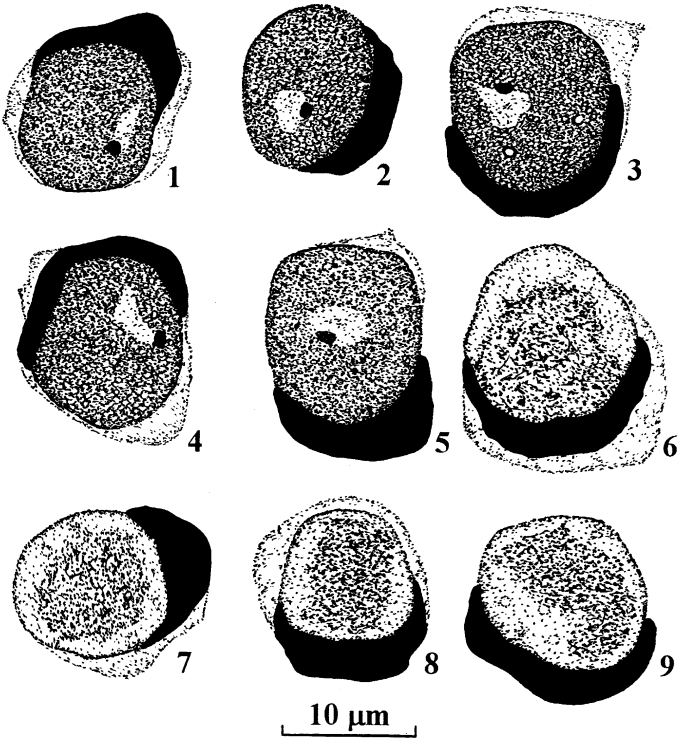

Figure 317 Gametocytes of *Leucocytozoon schoutedeni* from the blood of *Gallus gallus*: *1–5* – macrogametocytes; *6–9* – microgametocytes.

Type vertebrate host. *Gallus gallus* L. (Galliformes).
Additional vertebrate hosts. Unknown.
Vectors. *Simulium adersi*, '*S. impukane*' (according to Fallis *et al.*, 1973), *S. nyasalandicum*, *S. vorax* (Diptera: Simuliidae).
Type locality. Bukama, Lake Upemba, Katanga, former Belgian Congo.
Distribution. This parasite has been especially frequently recorded in the Ethiopian zoogeographical region. It was also found in South-East Asia (Taiwan and other localities) and in the USA (South Carolina).
Type material. Neohapantotype (No. 114488, *Gallus gallus*, 17.02.1971, Amani, Tanzania, A.M. Fallis) is deposited IRCAH. A series of good additional slides is deposited in CPHU, IRCAH, and CDVA.
Etymology. This species is named in honour of Dr. Schouteden.

Main diagnostic characters. A parasite of species of the Galliformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is usually of a band-like form, sometimes cap-like shape; the nucleus usually extends up to 1/2 of the circumference of gametocyte but sometimes more.

Development in vertebrate host
Gametocytes were observed in the peripheral circulation of domestic chickens 10 to 14 days after intraperitoneal inoculation of sporozoites (Fallis *et al.*, 1973).

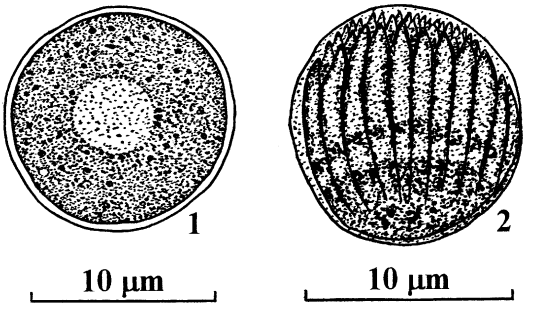

Figure 318 Oocysts of *Leucocytozoon schoutedeni*:
1 – young oocyst 48 h after ingestion of mature gametocytes by vector; *2* – mature oocyst five days after infection of vector (modified from Fallis *et al*., 1973).

Macrogametocytes (Fig. 317, *1–5*; Table 161) develop in roundish host cells; cytoplasm sometimes contains small vacuoles; valutin granules are frequently present; gametocytes are roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed, and lies peripherally usually as a band-like structure, sometimes of a cap-like form, it usually extends up to 1/2 of the circumference of gametocyte but sometimes more; cytoplasm of host cells is largely replaced by gametocytes and is sometimes even invisible (Fig. 317, *2*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 317, *1*, *3–5*).

Microgametocytes (Fig. 317, *6–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Development in vector was investigated at temperature of 20°C (Fallis *et al.*, 1973). Young oocysts are roundish in form. Each oocyst possesses granular cytoplasm and a large centrally located 'vacuole' (Fig. 318, *1*). Development of oocysts is not synchronized. Mature oocysts were observed five to six days after ingestion of gametocytes by simuliid flies (Fig. 318, *2*). A few sporozoites were found in the salivary gland of the flies at the sixth day after infection, and they were numerous here on the seventh day. Approximately 50 to 60 sporozoites develop in each oocyst. As the parasite develops, oocysts only slightly (if at all) increase in size. Young oocysts in the midgut of vector vary on average from 11.3 to 12.1 μm in diameter, and mature oocysts vary from 12.0 to 12.4 μm.

Pathogenicity. Damage caused by this parasite is usually moderate both in the native breeds of chickens and those which are introduced at endemic territories. The infection is characterized by a low and long-term chronic parasitemia (Lee *et al.*, 1969). Affected chickens always show insignificant symptoms, and a mild chronic infection usually develops. The main symptoms are dullness, slightly decreased egg production, greenish droppings, and slight emaciation. If there are no complications, infected chickens recover, and mortality is usually not recorded among them. Diagnostics is based on the observation of gametocytes in the peripheral circulation. It should be noted that the chronic parasitemia was recorded to be up to 390 days and even longer in once infected birds.

Specificity. During a joint maintenance of domestic chickens and guinea-fowl at the locality, where transmission of *L. schoutedeni* takes place, only the domestic chickens were recorded to be infected and the guinea-fowls are not susceptible (Fallis *et al.*, 1973).

Comments. It looks likely that the geographical distribution of *L. schoutedeni* is wider than is believed at present. A possibility of introducing this parasite to new localities, as it took place in South Carolina, USA (Atchley, 1951), should be taken in mind. See also 'Comments' to *L. struthionis*.

20. **Leucocytozoon (Leucocytozoon) centropi** Fantham, 1921

Leucocytozoon centropi Fantham, 1921: 167. – *L. coccyzus* Coatney and West, 1938: 605, Pl. 1, Fig. 9, 10. – *L. centropi*: Bennett *et al.*, 1993b: 74 (=*L. coccyzus*).

Type vertebrate host. *Centropus superciliosus* Hemprich and Ehrenberg (=*C. burchelli*) (Cuculiformes).
Additional vertebrate hosts. Some species of the Cuculiformes (Table 164).
Type locality. Pietermaritzburg, South Africa.
Distribution. This parasite has been recorded in the Nearctic and in the Ethiopian and Oriental zoogeographical regions.
Type material was not designated in the original description. Neotypes, designated by Bennett *et al.* (1993b), came from nontype vertebrate hosts investigated far beyond the type locality, and thus they do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of valid neotypes is required. A series of good additional slides is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Centropus.*

Main diagnostic characters. A parasite of species of the Cuculiformes whose gametocytes develop in roundish host cells. Nucleus of host cell is of cap-like form, sometimes band-like shape; the nucleus extends less than 1/2 of the circumference of the gametocyte.

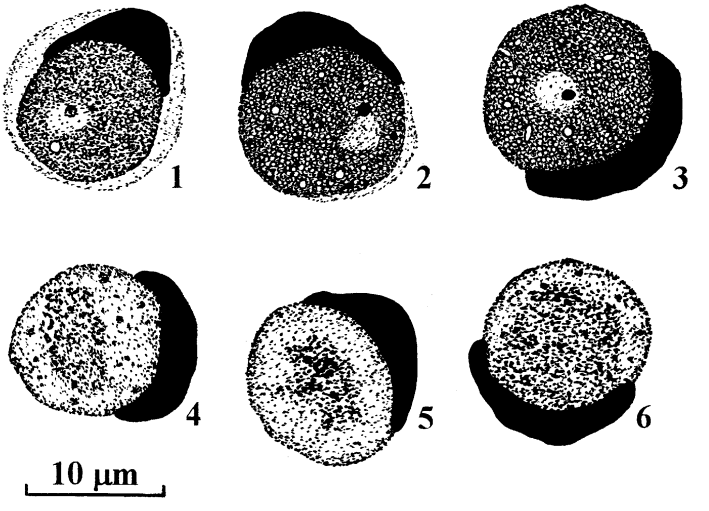

Figure 319 Gametocytes of *Leucocytozoon centropi* from the blood of *Coccyzus americanus*: *1–3* – macrogametocytes; *4–6* – microgametocytes.

Development in vertebrate host

Macrogametocytes (Fig. 319, *1–3*; Table 165) develop in roundish host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is of variable form and position; nucleolus is prominent and usually well seen; nucleus of host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap (Fig. 319, *1, 2*) or sometimes band (Fig. 319, *3*), it extends less than 1/2 of the circumference of gametocyte; cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 319, *3*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 319, *1*, *2*).

Table 164 List of vertebrate hosts of *Leucocytozoon centropi*.

Centropus monachus	*Chrysococcyx caprius*
C. sinensis	*Clamator jacobinus*
C. toulou	*C. levaillantii*
C. viridis	*Coccyzus americanus*

Table 165 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp. (modified from Bennett *et al.*, 1993b) ($n = 45$).

Feature	*L. dizini*		*L. centropi*	
	$\overline{X}$	*SD*	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell				
Length	14.2	2.3	13.5	0.9
Width	11.5	1.5	11.2	1.1
Length of nucleus	4.0	1.1	3.7	0.7
Width of nucleus	2.6	0.6	2.7	0.4
Length of nucleus of host cell	13.1	3.8	15.2	2.3

Note: All sizes are given in micrometres.

Microgametocytes (Fig. 319, *4–6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Nikitina (1983) published a first record of *L. centropi* (=*L. coccyzus*) from the blood of *Cuculus canorus* in the Palearctic. However, reexamination of her material by the author showed that unusually shaped mononuclear leukocytes were identified as gametocytes of *Leucocytozoon* sp., and thus *L. centropi* should be excluded from the fauna of the Palearctic at present.

Leucocytozoon centropi is the only species of leucocytozoids known at present to parasitize birds of the order Cuculiformes.

21. **Leucocytozoon (Leucocytozoon) vandenbrandeni** Rodhain, 1931

Leucocytozoon vandenbrandeni Rodhain, 1931: 276, Fig. 5, 6.

Type vertebrate host. *Anhinga rufa* (Daudin) (Pelecaniformes).
Additional vertebrate host. *Halietor melanoleucos* (Pelecaniformes).
Type locality. Leopoldville, former Belgian Congo.
Distribution has not been investigated. Until now, this parasite has been found in the environs of Leopoldville, Congo and on the Murray River below Mildura, Australia.
Type material has not been designated.
Etymology. This species is named in honour of Dr. F. Vandenbranden.

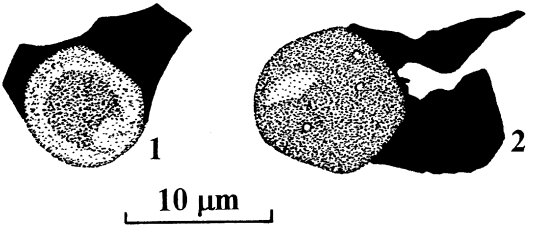

Figure 320 Gametocytes of *Leucocytozoon vandenbrandeni* from the blood of *Anhinga rufa*: *1* – microgametocyte; *2* – macrogametocyte (modified from Rodhain, 1931).

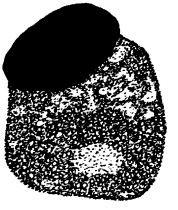

Figure 321 Macrogametocyte of *Leucocytozoon vandenbrandeni* from the blood of *Halietor melanoleucos* (modified from Mackerras and Mackerras, 1960).

Main diagnostic characters. A parasite of species of the Pelecaniformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is markedly deformed, of irregular form (can be distorted into filaments); the nucleus extends up to 1/2 of the circumference of gametocyte.

Development in vertebrate host

Macrogametocytes (Fig. 320, *2*) develop in roundish host cells; cytoplasm contains small vacuoles; the parasite nucleus is of variable form; nucleus of host cell is easily deformed. According to the original description, the nucleus is pushed aside, markedly deformed, and lies peripherally as an irregular-shape structure, and can be distorted into variable-form filaments (Fig. 320, *2*). The nucleus extends up to 1/2 of the circumference of the gametocyte. Fully grown gametocytes are up to 16 μm in diameter.

Microgametocytes (Fig. 320, *1*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; fully grown gametocytes are about 11 to 14 μm in diameter; other characters are as for macrogametocytes.

Comments. According to the original description (Rodhain, 1931), *L. vandenbrandeni* is an uncommon parasite which was found only in one bird in Congo. Subsequently, this parasite has not

been found in Africa. Thus, information about *L. vandenbrandeni* is restricted mainly by the brief information available in the original description. An important peculiarity of this species is a marked fragility of host cell nucleus, which easily deforms and can be distorted into ribbon-like structures or filaments (Fig. 320, *2*). However, because of very limited information about this species, it is still unclear how far this character is typical of *L. vandenbrandeni*. This parasite was recorded for the second time in 6 of 35 investigated cormorants *Halietor melanoleucos* in the South-East of Australia (Mackerras and Mackerras, 1960). It was noted by the Australian authors that the nucleus of host cell was enlarged and compressed into a narrow oval mass which adhere to gametocyte (Fig. 321), but it was not seen to be drawn out into ribbon-like structures or filaments as it was shown in the original description. However, the intensity of infection was low in the Australian material, and the regularities in form of nucleus of host cell were not determined. Further investigation of this character, which is important for species identification, is required.

Leucocytozoon vandenbrandeni is the only species of leucocytozoids which has been described in birds of the order Pelecaniformes.

22. **Leucocytozoon (Leucocytozoon) dizini** Tendeiro, 1947

Leucocytozoon dizini Tendeiro, 1947: 302, Fig. 3, 4.

Type vertebrate host. *Crinifer piscator* (Bodd.) (Musophagiformes).
Additional vertebrate hosts. *Corythaeola cristata*, *Corythaixoides concolor*, *C. leucogaster*, *Musophaga violacea*, *Tauraco corythaix*, and *T. hartlaubi* (Musophagiformes).
Type locality. Former Guiné Portuguesa.
Distribution. The Ethiopian zoogeographical region.
Type material was not designated in the original description. Neotypes, which were designated by Bennett *et al.* (1993b), came from nontype vertebrate hosts (*Corythaixoides concolor*, *C. leucogaster*) and thus do not correspond to Article 75(d)(5) of the International Code of Zoological Nomenclature (1985). Designation of valid neotypes is required. A series of additional slides is deposited in IRCAH.
Etymology. This species is named in honour of Portuguese scientist Dr. Teixeira Dizin.

Main diagnostic characters. A parasite of species of the Musophagiformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is cap-like or sometimes band-like in form; the nucleus extends less than 1/2 of the circumference of the gametocyte.

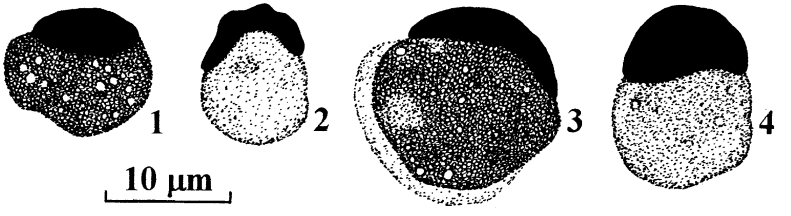

Figure 322 Gametocytes of *Leucocytozoon dizini* from the blood of *Crinifer piscator* (*1*, *2*) and *Corythaixoides leucogaster* (*3*, *4*):
1, *3* – macrogametocytes; *2*, *4* – microgametocytes (*1*, *2* are modified from Tendeiro, 1947; *3*, *4* are modified from Bennett *et al*., 1993b).

Development in vertebrate host

Macrogametocytes (Fig. 322, *1*, *3*; Table 165) develop in roundish host cells; cytoplasm sometimes contains small vacuoles; gametocytes are roundish; the parasite nucleus is of variable form and position; nucleolus was seen not in all gametocytes; nucleus of host cell is pushed aside, deformed and lies peripherally usually as a more or less evident cap or sometimes band, it extends less than 1/2 of the circumference of gametocyte; occasionally the host cell nucleus was also seen to be of bulb-like form or resemble the nucleus of uninfected erythrocyte by its shape (Fig. 322, *1*); cytoplasm of host cell is largely replaced by gametocytes, and is sometimes even invisible (Fig. 322, *1*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 322, *3*).

Microgametocytes (Fig. 322, *2*, *4*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. Morphology of gametocytes and their host cells of *L. dizini* is similar to *L. centropi*. The latter species parasitize the relative birds of the order Cuculiformes. Geographical ranges of vertebrate hosts of these two parasites overlap in Africa. It is likely that *L. dizini* is phylogenetically especially close to *L. centropi*.

Leucocytozoon dizini is only one species of leucocytozoids which has been described in birds of the order Musophagiformes.

23. **Leucocytozoon (Leucocytozoon) sousadiasi** Tendeiro, 1947

Leucocytozoon sousadiasi Tendeiro, 1947: 329, Fig. 22, 23 (*L. sousa-diasi*). – *L. sousadiasi*: Hsu *et al.*, 1973: 196 (emend. pro *L. sousa-diasi*).

Type vertebrate host. *Vanellus tectus* (Bodd.) (Charadriiformes).
Type locality. Former Guiné Portuguesa.
Distribution. This parasite has been recorded only in the type locality so far.
Type material has not been designated.
Etymology. This species is named in honour of Portuguese scientist Dr. Vasco Antunes Sousa Dias.

Main diagnostic characters. A parasite of species of the Charadriiformes whose gametocytes develop in fusiform host cells. Nucleus of the host cell is a cap-like or almond-like in form; the nucleus extends less than 1/3 of the circumference of gametocyte.

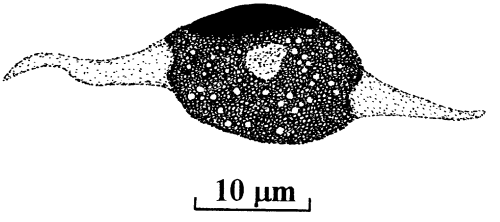

Figure 323 Macrogametocyte of *Leucocytozoon sousadiasi* from the blood of *Vanellus tectus* (modified from Tendeiro, 1947).

Development in vertebrate host

Macrogametocytes (Fig. 323) develop in fusiform host cells; cytoplasm contains small vacuoles; gametocytes are of oval form; nucleus of host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap or is almond-shaped, it extends less than 1/3 of the circumference of gametocyte; cytoplasm of host cell forms two well evident processes of variable form and length at the ends of gametocyte (Fig. 323); host cells, whose spindle-shaped cytoplasmic processes in length exceed their width, are present. Gametocytes vary from 14.0 to 20.9 μm in length, and from 9.1 to 11.6 μm in width. The same parameters for their host cells are 35.8 to 42.8 and 12.6 to 14.0 μm, respectively.

Microgametocytes. The general configuration is as for macrogametocytes with the usual sexual dimorphic character; microgametocytes vary from 23.5 to 25.6 μm in length, and from 6.7 to 9.3 μm in width; the same parameters for their host cells are 31.2 to 48.7 and 9.3 to 10.5 μm, respectively; other characters are as for macrogametocytes.

Comments. *Leucocytozoon sousadiasi* has been found only once (Tendeiro, 1947). Redescription of this species is required. *Leucocytozoon sousadiasi* can be distinguished from *L. legeri*, which also parasitize birds of the order Charadriiformes, on the basis of the fusiform shape of the host cells of its gametocytes.

24. **Leucocytozoon (Leucocytozoon) cheissini** Krylov and Trjapicina, 1965

Leucocytozoon cheissini Krylov and Trjapicina, 1965: 219, Fig.

Type vertebrate host. *Tetraogallus himalayensis* Gray (Galliformes).
Type locality. Central Tadzhikistan, 3000 m above sea level.
Distribution. This parasite has been recorded only in the type locality so far.
Type material was lost.
Etymology. This species is named in honour of Russian protozoologist Professor E.M. Cheissin.

Main diagnostic characters. A parasite of species of the Galliformes whose gametocytes develop in fusiform host cells. Nucleus of host cell resembles the nucleus of uninfected erythrocyte in form; the nucleus is markedly enlarged, extends less than 1/3 of the circumference of gametocyte. Currently, this parasite can be identified with confidence only in birds of the genus *Tetraogallus*.

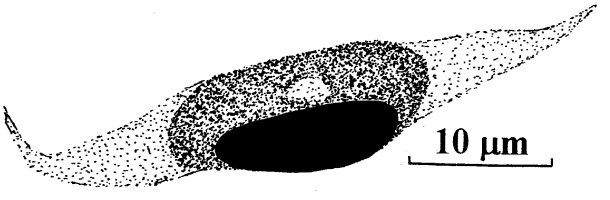

Figure 324 Macrogametocyte of *Leucocytozoon cheissini* from the blood of *Tetraogallus himalayensis* (modified from Valkiūnas, 1989a).

Development in vertebrate host

Macrogametocytes (Fig. 324). According to the original description (Krylov and Trjapicina, 1965), gametocytes are of ellipsoid-like or oval form, and develop in fusiform host cells; the nucleus of the host cell is pushed aside, markedly enlarged, and resembles the nucleus of uninfected erythrocyte by its form; the cytoplasm of the host cell forms two well evident processes of variable form and length at the ends of gametocyte; fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are present. Gametocytes vary from 12.0 to 18.0 μm in length, and from 3.6 to 6.0 μm in width.

Comments. As the type material of *L. cheissini* is lost, more detailed description of this parasite is impossible at present. New material is required for this purpose. This parasite is especially similar to *L. macleani* by the morphology of its gametocytes and their host cells and the range of vertebrate hosts. *Leucocytozoon cheissini* can be distinguished from *L. macleani* mainly on the basis of markedly enlarged nucleus of its host cell containing gametocyte. The taxonomic value of this character is unclear. It should be also noted that *L. cheissini* parasitize birds inhabiting high altitudes (Krylov and Krylova, 1979).

25. **Leucocytozoon (Leucocytozoon) grusi** Bennett, Khan and Campbell 1974

Leucocytozoon grusi Bennett, Khan and Campbell 1974b: 360, Fig. 1–5.

Type vertebrate host. *Grus canadensis* (L.) (Gruiformes).
Additional vertebrate host. *Balearica pavonina* (Gruiformes).
Type locality. Payne's Prairie, Florida, USA.
Distribution has not been investigated. It is known that transmission takes place in Florida, USA. A record of this parasite in one specimen of *Balearica pavonina*, which was imported from Africa, testifies to the transmission in the Old World.
Type material. Hapantotype (primary registration No. is USNM 72637, *Grus canadensis*, June 1973, Florida, D.J. Forrester) and parahapantotype (No. 29789, other data as for the hapantotype) are deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Grus*.

Main diagnostic characters. A parasite of species of the Gruiformes whose gametocytes develop in roundish and fusiform host cells. Nucleus of fusiform host cell is of cap-like or crescent-like form or resembles the nucleus of uninfected erythrocyte by its shape; the nucleus extends less than 1/3 of the circumference of gametocyte.

Development in vertebrate host

Macrogametocytes (Fig. 325, *1–4*; Table 166) develop in roundish and fusiform host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present, and are more numerous and more common in gametocytes which develop in fusiform host cells; gametocytes in roundish host cells are usually roundish or of slightly oval form, and gametocytes in fusiform host cells vary from roundish to oval; the parasite nucleus is of variable form and position; nucleolus is prominent and well seen; nucleus of roundish host

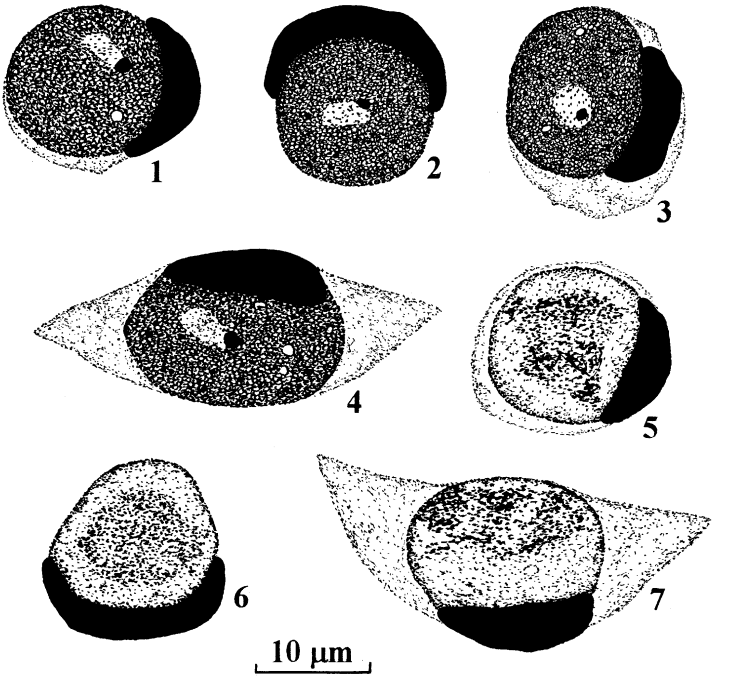

Figure 325 Gametocytes of *Leucocytozoon grusi* from the blood of *Grus canadensis*: *1–4* – macrogametocytes; *5–7* – microgametocytes.

Table 166 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. maccluri* (modified from Bennett *et al.*, 1993d)			*L. grusi* (modified from Bennett *et al.*, 1992b)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	6			20		
Length		10.6	0.6		13.8	1.1
Width		9.1	0.8		11.8	0.9
Length of nucleus		2.8	1.0		4.4	0.9
Width of nucleus		1.9	0.3		2.7	0.6
Length of nucleus of host cell		15.2	3.1		15.7	2.2
Macrogametocyte in fusiform host cell	13			25		
Length		19.6	2.2		14.4	2.0
Width		8.2	1.8		11.5	1.8
Length of nucleus		2.9	0.6		5.0	1.0
Width of nucleus		1.8	0.4		2.8	0.5
Length of nucleus of host cell		45.6	4.3		16.4	2.1

Note: All sizes are given in micrometres.

cell is pushed aside, deformed, and lies peripherally as a more or less evident cap (Fig. 325, *1, 3*) or band (Fig. 325, *2*), it extends less than 1/2 of the circumference of gametocyte; nucleus of fusiform host cell is deformed and usually lies peripherally as a cap-like or crescent-like structure or resembles the nucleus of uninfected erythrocyte by its shape (Fig. 325, *4*), it extends less than 1/3 of the circumference of gametocyte; cytoplasm of roundish host cells is largely replaced by gametocytes, and it is sometimes even invisible (Fig. 325, *2*), but more frequently present around the gametocytes as more or less evident and pale margin of variable form (Fig. 325, *1*, *3*); cytoplasm of fusiform host cells forms two well evident processes of variable form and length at the ends of gametocytes (Fig. 325, *4*); fusiform host cells, the length of whose spindle-shaped cytoplasmic processes exceeds their width, are present.

Microgametocytes (Fig. 325, *5–7*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon grusi* is the only species of leucocytozoids which has been described in birds of the order Gruiformes. See also Appendix 2 about a possible taxonomic relationship between *L. grusi* and *L. otidis* (p. 868).

26. **Leucocytozoon (Leucocytozoon) maccluri** Greiner, 1976

Leucocytozoon maccluri Greiner, 1976: 545, Fig. 1–4. – *L. mcclurei*: Bennett *et al.*, 1993d: 86 (emend. pro *maccluri*).

Type vertebrate host. *Zoothera marginata* Blyth. (Passeriformes).
Additional vertebrate hosts. Unknown.
Type locality. Chiengmai, north-western Thailand.
Distribution. This parasite has been recorded only in the type locality so far.
Type material. Hapantotype (No. 41296, *Zoothera marginata*, 12.03.1970, Chiengmai, Thailand, H.E. McClure) and parahapantotype (No. 11732, 2.05.1964, Chang Kheong, other data as for the hapantotype) are deposited in IRCAH.
Etymology. This species is named in honour of Dr. H. Elliott McClure, who contributed the type specimens as well as a prominent collection of slides, which were collected for the project called the Migratory Animal Pathological Surveys (MAPS), to the International Reference Centre for Avian Haematozoa (IRCAH). Dr. H.E. McClure was a leader of MAPS, and the great part of collection material of bird haemosporidian parasites of eastern and southern Asia, which are available for science at present, were collected under the leadership of this scientist in 1963–1971.

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes develop in roundish and fusiform host cells. The nucleus of the fusiform host cell is uniformly dispersed as a narrow (0.5 to 1.0 μm in width) band around all or nearly all of the circumference of the gametocyte.

Development in vertebrate host
Macrogametocytes (Fig. 326, *1*, *2, 4–6*; Table 166) develop in roundish and fusiform host cells; vacuoles are not seen; valutin granules are present; gametocytes in roundish host cells are roundish, and gametocytes in fusiform host cells are of oval or ellipsoid form; gametocytes in fusiform host cells look flattened (leaf-like) which is an unusual feature for bird leucocytozoids, they were even seen to be bent transversally in stained blood films; the

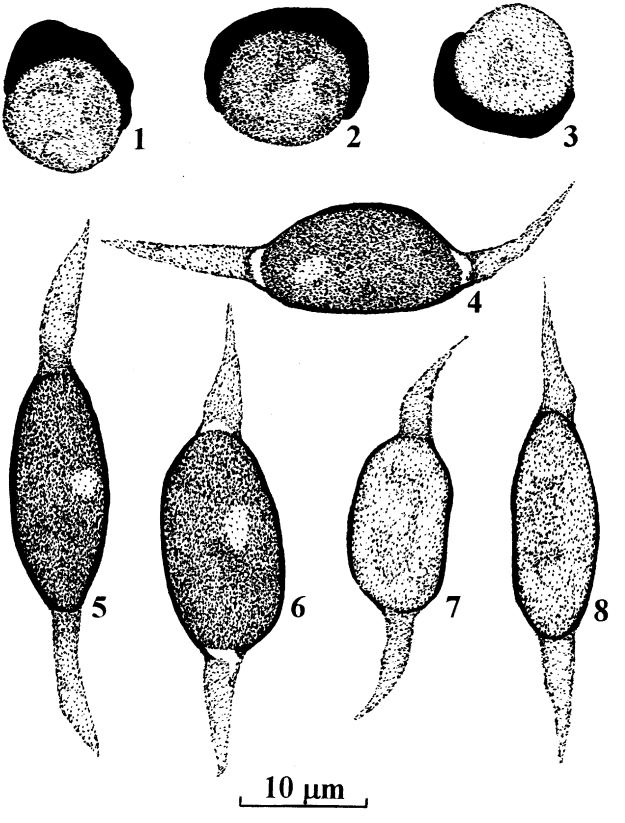

Figure 326 Gametocytes of *Leucocytozoon maccluri* from the blood of *Zoothera marginata*: *1*, *2*, *4–6* – macrogametocytes; *3*, *7*, *8* – microgametocytes (*1*, *2* are modified from Greiner, 1976).

parasite nucleus is of variable form and position; nucleolus is not seen; nucleus of roundish host cell is pushed aside, deformed, and lies peripherally usually as a band or sometimes a cap, can be extended more than 1/2 of the circumference of gametocyte (Fig. 326, *1*, *2*); nucleus of fusiform host cell is uniformly dispersed as a narrow (0.5 to 1.0 μm in width) band around all or nearly all of the circumference of gametocyte (Fig. 326, *4–6*); cytoplasm of roundish host cells is largely replaced by gametocytes, and was recorded even to be invisible (Fig. 326, *1*, *2*); cytoplasm of fusiform host cells forms two well evident processes of variable form and length at the ends of gametocytes (Fig. 326, *4–6*); fusiform host cells, whose spindle-shaped cytoplasmic processes in length exceed their width, are common; clear vacuole-like structures frequently seen adjacent to gametocyte poles close to cytoplasmic processes (Fig. 326, *4*, *6*).

Microgametocytes (Fig. 326, *3*, *7*, *8*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; cytoplasm stains extremely pale; the borderline of nucleus is not evident; gametocytes are a bit smaller in size than macrogametocytes; other characters are as for macrogametocytes.

C o m m e n t s. It was speculated in the original description that gametocytes in roundish host cells can belong not to *L. maccluri* but to *L. fringillinarum* or *L. majoris* (Greiner, 1976). This is possible

theoretically because a mixed infection of the same vertebrate host with several species of leucocytozoids has been descried in wild birds (Bennett and Campbell, 1975; Valkiūnas, 1985b). Taking in mind that *L. maccluri* was found only in two birds, and gametocytes in roundish host cells were observed only in one of them, this problem cannot be solved finally at present. Bennett *et al.* (1993d) attributed gametocytes in roundish host cells to *L. maccluri*. The author reexamined the type material. However, new facts, which can support any of the two above-mentioned hypotheses, were not obtained. It would be incorrect to exclude gametocytes in roundish host cells from the definition of *L. maccluri* at present. Further investigations are required to solve this problem. Anyhow, it is necessary to agree with Greiner (1976) that the unique morphology of fusiform host cells of gametocytes is the main diagnostic character of this species.

It should be noted that the blood films with type specimens of *L. maccluri* are fading. So, it is likely that both the pale staining of nucleus of gametocyte and the invisible nucleolus in macrogametocyte are rather due to the defect of staining than the true characters of this species.

The specific name *L. maccluri* is derived from the male surname 'McClure' by adding to the stem of the latter -i, and this corresponds to Article 31(a)(ii)(Example) of the International Code of Zoological Nomenclature (1985). Furthermore, according to Article 32(c)(i)(ii)(Examples), the name is not an incorrect original spelling solely on the grounds that it was incorrectly transliterated (*maccluri* instead of *mccluri*). Based on the evidence presented above, the emendation of the specific name *L. maccluri* to *L. mcclurei*, which was suggested by Bennett *et al.* (1993d), is an unjustified emendation.

27. **Leucocytozoon (Leucocytozoon) tawaki** Fallis, Bisset and Allison, 1976

Leucocytozoon tawaki Fallis, Bisset and Allison, 1976: 11, Fig. 1–4, 6, 7.

Type vertebrate host. *Eudyptes pachyrhynchus* Gray (Sphenisciformes).
Additional vertebrate hosts. *Eudyptula minor*, *Spheniscus demersus* (Sphenisciformes).
Vectors. *Austrosimulium australense*, *A. dumbletoni*, *A. ungulatum* (Diptera: Simuliidae).
Type locality. Kaikoura, Jackson's Head, South Island, New Zealand.
Distribution. This parasite has been found in New Zealand and South Africa.
Type material. Hapantotype and part of parahapantotypes (*Eudyptes pachyrhynchus*, 11.02.1975, Kaikoura, New Zealand, A.M. Fallis, S.A. Bisset) are deposited in NMNZ. Parahapantotype (No. 40451, 2.02.1975, other data are as for the hapantotype) is deposited in IRCAH.
Etymology. The specific name is derived from 'tawaki,' the Maori name for the type vertebrate host, Fiordland crested penguin *Eudyptes pachyrhynchus*.

Main diagnostic characters. A parasite of species of the Sphenisciformes whose gametocytes develop in roundish host cells. Nucleus of host cell is of cap-like or band-like form; the nucleus extends less than 1/2 of the circumference of gametocyte.

Development in vertebrate host was investigated in naturally infected *Eudyptes pachyrhynchus* (Fallis *et al.*, 1976; Allison *et al.*, 1978). Exoerythrocytic meronts were found in the liver, kidneys, and spleen. Megalomeronts were not observed. In young birds, meronts were recorded in the kidneys and liver, and they were found in the kidneys and spleen in adult penguins. The sequence of development of meronts is unknown precisely. It is likely that sporozoites induce the primary exoerythrocytic merogony in the liver, and meronts in the kidneys and spleen belong to the subsequent generations of

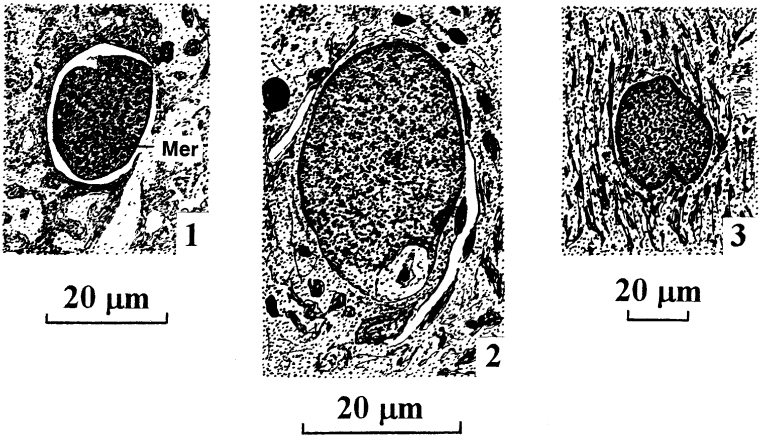

Figure 327 Mature exoerythrocytic meronts of *Leucocytozoon tawaki* from *Eudyptes pachyrhynchus*:
1 – hepatic meront in the liver parenchymal cell of young bird; *2* – meront in proximal renal tubule cell of young bird; *3* – meront in wall of blood vessel in the spleen of adult bird; Mer – meront (modified from Allison *et al*., 1978).

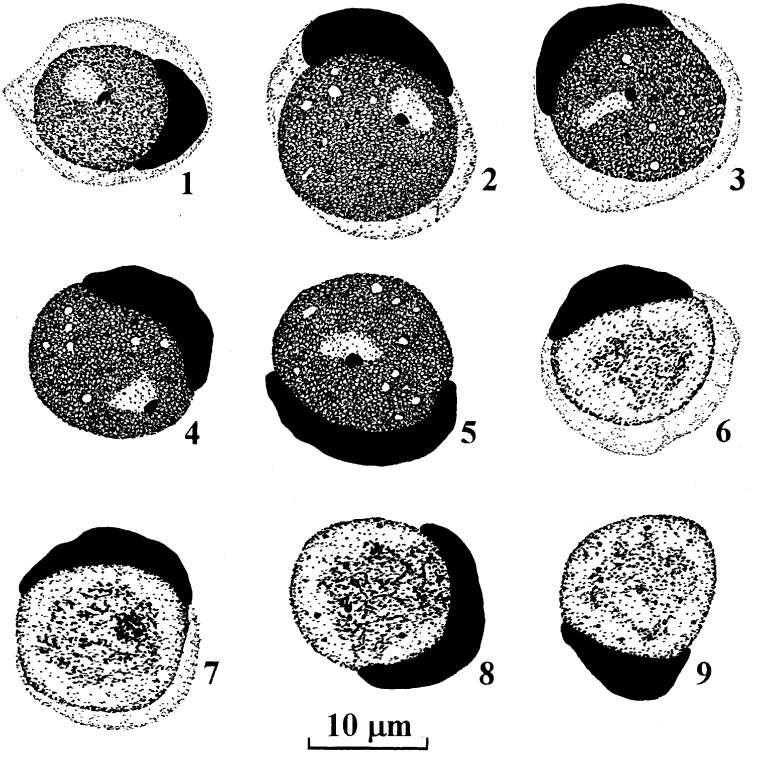

Figure 328 Gametocytes of *Leucocytozoon tawaki* from the blood of *Eudyptes pachyrhynchus*:
1–5 – macrogametocytes; *6–9* – microgametocytes.

merogony. The absence of hepatic meronts in adult birds, which usually have a chronic parasitemia, testifies to this hypothesis.

Hepatic meronts develop in hepatocytes, and they are roundish (Fig. 327, *1*). These meronts ($n = 6$) vary from 17 to 22 μm in their maximum diameter. In the kidneys, meronts develop in proximal renal tubule cells, and they were more numerous here than in the liver. Fully grown renal meronts usually are roundish or oval (Fig. 327, *2*). They were on average ($n = 12$) about 33 μm in maximum diameter, and the larger ovoid parasites were up to 50 μm. In the spleen, meronts develop in endothelium of blood vessels (Fig. 327, *3*). They were not numerous. A single observed mature meront in the spleen was 35×40 μm in size.

Relapses were observed in penguins which came ashore to breed and to moult in New Zealand. The factors responsible for the relapses have not been investigated. There can be a relationship between the breeding and moulting and the relapses because of temporary impairment of birds' immune system due to their weakened condition. Stages responsible for relapses in *L. tawaki* have not been investigated either. Infection of birds of the younger generation takes place two to three weeks after hatching when chicks move from their nest and gather together in creches.

It is likely that gametocytes develop in cells of erythrocytic series. Intensity of parasitemia was recorded to vary from 2 to 132 gametocytes per 10,000 erythrocytes in naturally infected chicks, and from 0.1 to 5 in adults.

Macrogametocytes (Fig. 328, *1–5*; Table 167) develop in roundish host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is of variable form and position; nucleolus is prominent and well seen; nucleus of host cell is pushed aside, deformed and lies peripherally as a more or less evident cap (Fig. 328, *1–4*) or band (Fig. 328, *5*), it extends less than 1/2 of the circumference of gametocyte; cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 328, *4*, *5*), but more frequently present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 328, *1–3*). Fully grown gametocytes in the type vertebrate host vary ($n = 100$) from 10 to 14 (on average 12) μm in diameter.

Microgametocytes (Fig. 328, *6–9*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; fully grown gametocytes in the type vertebrate host vary ($n = 55$) from 9 to 11 (on average 10) μm in diameter; other characters are as for macrogametocytes.

Table 167 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. nyctyornis* (modified from Nandi, 1986a)			*L. tawaki* (modified from Bennett *et al.*, 1992b)		
	n	$\overline{X}$	*SD*	*n*	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	20			60		
Length		10.8	0.9		15.8	1.4
Width		10.3	1.1		13.4	1.1
Length of nucleus		3.2	–		5.6	1.0
Width of nucleus		2.5	–		3.4	0.8
Length of nucleus of host cell		20.0	2.2		18.2	2.3

Note: All sizes are given in micrometres. Gametocytes of *L. tawaki* from both the type vertebrate host and the nontype vertebrate host *Spheniscus demersus* were measured.

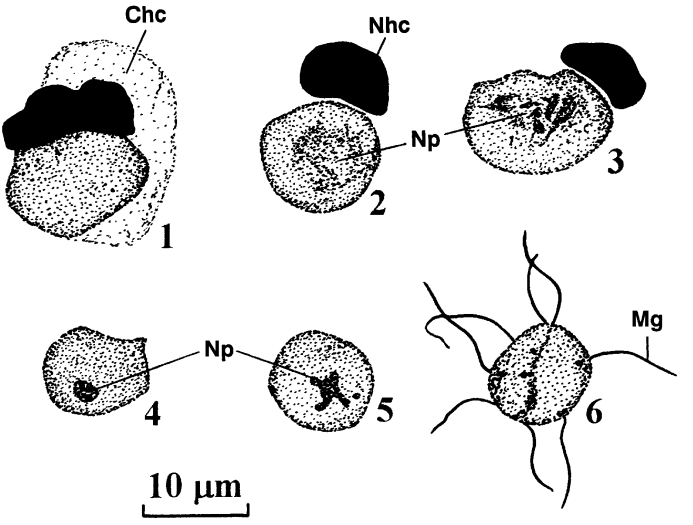

Figure 329 Microgametogenesis of *Leucocytozoon tawaki*:
1 – mature microgametocyte in the peripheral blood of birds before the onset of gametogenesis; *2*, *3* – free of the host cell microgametocyte with adjacent nucleus of the host cell; *4*, *5* – free microgametocyte; *6* – exflagellation of microgametes; Chc – cytoplasm of host cell; Mg – microgamete; Nhc – nucleus of host cell; Np – nucleus of parasite (modified from Desser *et al*., 1976). Description of nuclear changes of microgametocyte is given in the text.

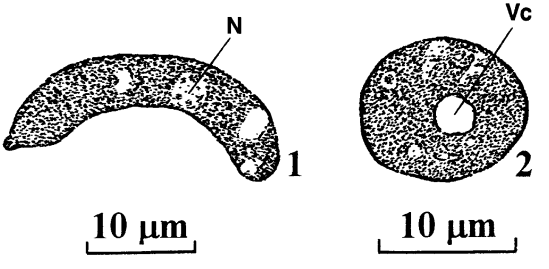

Figure 330 *Leucocytozoon tawaki* from *Austrosimulium ungulatum*:
1 – ookinete in blood meal 12 h after ingestion of gametocytes; *2* – young oocyst from midgut wall 64 h after ingestion of gametocytes; N – nucleus; Vc – 'vacuole' (modified from Fallis *et al*., 1976).

The ratio of macro- and microgametocytes in the peripheral circulation was said to be approximately 1:3. Gametocytes and their host cells are fragile, and are easily deformed during the preparation of blood films.

Development in vector

In vitro, exflagellation was observed soon after exposure of blood with mature gametocytes to air (Desser *et al*., 1976). Nucleus of microgametocytes undergoes rapid changes before exflagellation. Nucleus of intracellular microgametocyte is large and diffuse in blood fixed immediately after withdrawal from the peripheral circulation (Fig. 329, *1*). Several seconds after exposure of blood to air, many gametocytes escape from host cells, whose nuclei lie

adjacent to the parasites (Fig. 329, *2*, *3*). The nuclear chromatin of the parasite assumes a condensed and reticular appearance (Fig. 329, *3*) and soon contracts into a central dense mass (Fig. 329, *4*). At this stage, short flagella begin to emerge from the periphery of the microgametocytes. The chromatin divides (Fig. 329, *5*), and its small portions were observed in the peripheral cytoplasm. Finally, one of them incorporates into each of eight developing microgametes (Fig. 329, *6*). This process can complete in less than 1 min. At the same time, first zygotes appear.

Ookinetes were observed in the midgut of vector 12 to 24 h after ingestion of gametocytes at temperature of 15°C. Each ookinete possesses a prominent nucleus and several clear 'vacuoles' (Fig. 330, *1*). Young oocysts were found in the midgut 24 to 48 h after infection. Each young oocyst possesses a large centrally located 'vacuole' and five to ten prominent chromatin masses (Fig. 330, *2*). At this stage of development, oocysts vary (n = 12) from 11.9 to 14.6 (on average 13.2) μm in their maximum diameter. On the third day after infection, the 'vacuole' is still discernible, and the oocysts contained 20 to 30 chromatin masses located peripherally. At this time, oocysts vary (n = 12) from 14.6 to 17.3 (on average 16.6) μm in their maximum diameter. By the fourth day after infection, the 'vacuole' is no longer apparent in some oocysts and about 50 nuclei lie in the peripheral cytoplasm, and first stages of development of sporozoites were observed. The fourth-day oocysts vary from 15.9 to 18.4 (on average 16.8) μm in their maximum diameter. Maturing and mature oocysts were observed in the midgut five or six days after infection. Sporozoites were observed for the first time in the salivary glands on the sixth day after infection. Less than 100 sporozoites develop in oocysts. The sporozoites look like comma-shaped bodies with a sub-central nucleus, a pink-stained apical (anterior) end, and a minute 'vacuole' posterior to the nucleus. Sporozoites (n = 10) were approximately 9 μm in length, and 1.3 μm in width (Fallis *et al.*, 1976; Allison *et al.*, 1978; Desser and Allison, 1979).

P a t h o g e n i c i t y has been insufficiently investigated. Signs of illness were not observed in naturally infected young and adult penguins. It looks likely that heavy infections might render young chicks more susceptible to secondary infection by other pathogens and more sensitive to stress factors such as inclement weather (Allison *et al.*, 1978). The parasite is pathogenic for simuliid flies. A heavy mortality was observed among flies that fed on a heavily infected bird as compared to flies that fed on a lightly infected penguin.

C o m m e n t s. It is worth noting that infection of chicks of *Eudyptes pachyrhynchus* in New Zealand takes place most probably two to three weeks after hatching, when they move from nests. Before this time, the chicks are well protected mechanically from vectors by male parents which almost totally cover them during the day by the brood pouch. This can contribute to the relatively low influence of the parasites on younger chicks. Mass infection of the younger generation occurs in September–October when chicks move independently and huddle together in groups. By the end of February, nearly all young birds were recorded to be infected. The simuliid fly *Austrosimulium ungulatum* is the main vector.

The high prevalence of *L. tawaki* in *E. pachyrhynchus* in New Zealand is of theoretical interest. In other native birds, leucocytozoids were not found here. Probably the penguins incorporated the parasite from some other migrating or introduced birds.

In South Africa, *L. tawaki* was found in penguin *Spheniscus demersus*, but it is uncommon here. Probably, this bird is an incidental host of the parasite, which normally develops in other avian hosts (Earlé *et al.*, 1992).

Leucocytozoon tawaki is the only species of leucocytozoids which has been described in birds of the order Sphenisciformes.

28. **Leucocytozoon (Leucocytozoon) nycticoraxi** Shamsuddin and Mohammad, 1980

Leucocytozoon nycticoraxi Shamsuddin and Mohammad, 1980: 127, Fig. 27–34, 67.

Type vertebrate host. *Nycticorax nycticorax* L. (Ciconiiformes).
Additional vertebrate host. *Ardea purpurea* (Ciconiiformes).
Type locality. Al-Kahla, South Iraq.
Distribution. This parasite has been found only in the type locality so far.
Type material. Hapantotype (*Nycticorax nycticorax*, 21.01.1978, Al-Kahla, South Iraq) is deposited in NHRCB.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Nycticorax*.

Main diagnostic characters. A parasite of species of the Ciconiiformes whose gametocytes develop in fusiform host cells with only slightly pronounced cytoplasmic processes, which width usually markedly exceed their length. Fusiform host cells, which spindle-shaped cytoplasmic processes in length exceed their width, are absent.

Development in vertebrate host
According to the original description, gametocytes probably develop in mononuclear leukocytes.

Macrogametocytes (Fig. 331, *1–4*; Table 168) develop in fusiform host cells with only slightly (if at all) pronounced cytoplasmic processes, and the width of these processes usually markedly exceeds their length (Fig. 331, *1–4*); gametocytes are roundish or slightly oval; the parasite nucleus is of variable form and position; nucleus of host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap or band, it extends less than 1/2 of the circumference of gametocyte. In the original description, the host cells, whose nuclei extend more than 1/2 of the circumference of gametocyte, were mentioned.

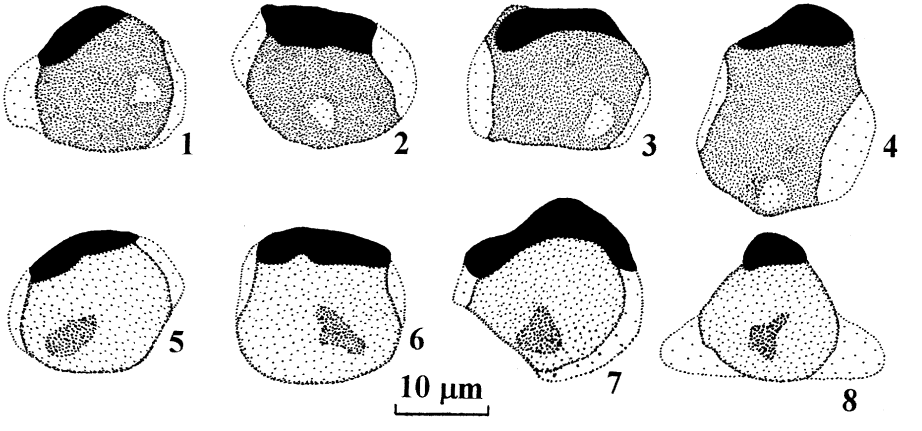

Figure 331 Gametocytes of *Leucocytozoon nycticoraxi* from the blood of *Nycticorax nycticorax*: *1–4* – macrogametocytes; *5–8* – microgametocytes (modified from Shamsuddin and Mohammad, 1980).

Table 168 Morphometric parameters of gametocytes and host cells of *Leucocytozoon nycticoraxi* (modified from Shamsuddin and Mohammad, 1980) ($n = 20$).

Feature	$\overline{X}$	*SD*
Macrogametocyte		
Length	16.1	1.7
Width	10.6	1.6
Length of nucleus	5.9	1.3
Width of nucleus	3.1	0.8
Length of nucleus of host cell	10.1	2.6

Note: All sizes are given in micrometres.

However, the length of nucleus of host cell is shown to be much less at all illustrations in the original description (Fig. 331), and the nucleus is said to be about 10 μm in length on average. It is likely that the nucleus of the host cell extends less than 1/2 of the circumference of gametocyte on average.

Microgametocytes (Fig. 331, *5–8*). The general configuration is as for macrogametocytes with the sexual dimorphic characters. According to the illustrations in the original description, nucleus of gametocytes is relatively compact and small (Fig. 331, *5–8*). Other characters are as for macrogametocytes.

C o m m e n t s. The presence of short and wide cytoplasmic processes in host cells with fully grown gametocytes (Fig. 331) is the main diagnostic character of *L. nycticoraxi.* In some illustrations, which are available in the original description, such processes are well seen (Fig. 331, *8*). Fusiform host cells, which spindle-shaped cytoplasmic processes in length exceed their width, were not recorded for this parasite. Based on other characters, *L. nycticoraxi* is similar to *L. leboeufi*, which also parasitizes birds of the order Ciconiiformes. It is important to note that cytoplasmic processes in host cells of *L. nycticoraxi* are only slightly evident (if at all in some sells). Moreover, according to the illustrations in the original description (Fig. 331), some such 'cytoplasmic processes' are more similar to cytoplasmic remnants, which are frequently observed around gametocytes of *L. leboeufi* in roundish host cells (see Fig. 312, *2*, *5* for comparison), than to the typical cytoplasmic processes, which develop in host cells of numerous other species of leucocytozoids with gametocytes in fusiform host cells (see Fig. 316, *4–7, 9, 10* for comparison). Furthermore, Shamsuddin and Mohammad (1980) noted that the cytoplasmic processes were rarely observed in *L. nycticoraxi*, which was found by these authors in *Ardea purpurea*, and thus this record can be *L. leboeufi*. The analysis of text and illustrations of the original description shows that *L. nycticoraxi* can be a synonym of *L. leboeufi*. Remnants of cytoplasm of host cells around gametocytes of *L. leboeufi* are frequently seen and they, in general, are similar to those recorded in *L. nycticoraxi*. Unfortunately, the hapantotype was not available for the author, and the problem of the validity of *L. nycticoraxi* requires additional investigation.

29. **Leucocytozoon (Leucocytozoon) balmorali** Peirce, 1984

Leucocytozoon balmorali Peirce 1984d: 223, Fig. 1–4. – *L. peircei* Bennett, Earlé and Squires-Parsons, 1995a: 4, Fig. 12–14 (syn. nov.).

T y p e v e r t e b r a t e h o s t. *Dryoscopus cubla* (Shaw) (Passeriformes).
A d d i t i o n a l v e r t e b r a t e h o s t s. Some species of the Passeriformes (Table 169).

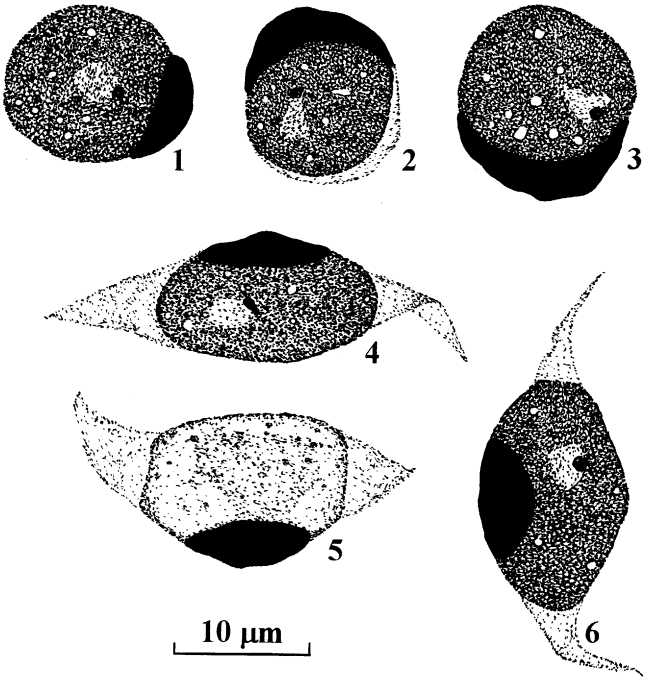

Figure 332 Gametocytes of *Leucocytozoon balmorali* from the blood of *Dryoscopus cubla*: *1–4*, *6* – macrogametocytes; *5* – microgametocyte.

Type locality. Balmoral, Zambia.
Distribution. The Ethiopian zoogeographical region.
Type material. Hapantotype (No. 91780b, *Dryoscopus cubla*, 19.09.1981, Balmoral, Zambia, M.A. Peirce) and parahapantotype (No. 91781, 10.10.1980, other data are as for the hapantotype) are deposited in IRCAH. Parahapantotypes (other data are as for the hapantotype) are deposited in WMCL.
Etymology. The specific name is derived from the name of the type locality, Balmoral.

Table 169 List of vertebrate hosts of *Leucocytozoon balmorali* (modified from Peirce, 1984d).

Malaconotus blanchoti	*Phylloscopus trochilus*
M. olivaceus	*Tchagra australis*
M. sulfureopectus	*T. senegala*
Nilaus afer	*Telephorus zeylonus*

Main diagnostic characters. A parasite of species of the Passeriformes whose gametocytes develop in roundish and fusiform host cells. Nucleus of fusiform host cell is of cap-like form or almond shape or resembles the nucleus of uninfected erythrocyte by its form; the nucleus extends less than 1/3 of the circumference of gametocyte.

Development in vertebrate host
According to the original description (Peirce, 1984d), gametocytes develop in lymphocytes and reticulocytes.

Macrogametocytes (Fig. 332, *1–4, 6*; Table 170) develop in roundish and fusiform host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present; cytoplasm of gametocytes in roundish host cells stains a bit darker than those in fusiform host cells; gametocytes in roundish host cells are roundish (Fig. 332, *1–3*), and gametocytes in fusiform host cells are usually oval (Fig. 332, *4, 6*); the parasite nucleus is of variable form and position; nucleolus is present but not always well seen in pale stained blood films; nucleus of roundish host cell is pushed aside, deformed, and lies peripherally as a more or less evident cap or band, it extends usually less than 1/2 of the circumference of gametocyte (Fig. 332, *1–3*); nucleus of fusiform host cell is deformed, pushed aside, and usually lies peripherally as a cap-like or an almond-like structure or resemble the nucleus of uninfected erythrocyte in form, it extends less than 1/3 of the circumference of gametocyte (Fig. 332, *4*, *6*); cytoplasm of roundish host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 332, *1*, *3*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 332, *2*); the cytoplasm of fusiform host cells forms two well evident processes of variable form and length at the ends of gametocytes (Fig. 332, *4*, *6*); fusiform host cells, whose spindle-shaped cytoplasmic processes in length exceed their width, are common.

Table 170 Morphometric parameters of gametocytes and host cells of *Leucocytozoon balmorali* (modified from Peirce, 1984d).

Feature	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	15			
Length		9.9–15.4	12.8	1.6
Width		8.9–14.0	11.0	1.4
Length of nucleus		2.4–4.7	3.2	0.8
Width of nucleus		1.6–3.9	2.6	0.5
Length of nucleus of host cell		8.6–18.8	13.1	2.7
Macrogametocyte in fusiform host cell	20			
Length		14.5–18.6	15.9	–
Width		9.3–14.3	11.5	–
Length of nucleus of host cell	17	7.9–14.7	9.3	2.5

Note: All sizes are given in micrometres.

Microgametocytes (Fig. 332, *5*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; vacuoles are not seen; microgametocytes in roundish host cells were not observed in the type vertebrate host but were present in *Phylloscopus trochilus.*

In the type vertebrate host, microgametocytes are much more rarely seen in the peripheral blood than macrogametocytes. The ratio of macro- and microgametocytes in fusiform host cells in the type material is 40:1, but much more microgametocytes were seen during the development in *Phylloscopus trochilus.*

Comments. *Leucocytozoon balmorali* is a common parasite in the Ethiopian zoogeographical region. In the type locality, all sampled *Dryoscopus cubla* (11 birds) were infected (Peirce, 1984d).

Due to the presence of gametocytes in fusiform host cells, *L. balmorali* can be easily distinguished from other species of leucocytozoids parasitizing passeriform birds, except *L. maccluri* and *L. hamiltoni*. These species can be easily distinguished on the basis of the morphology of nuclei of their fusiform host cells.

Bennett *et al.* (1995a) described *L. peircei* from *Phylloscopuis trochilus* (Passeriformes) in South Africa. They noted that gametocytes of this parasite develop only in fusiform host cells. These authors pointed out that *L. peircei* is the only species of leucocytozoids with gametocytes in fusiform host cells in birds of the order Passeriformes but they overlooked (see Bennett *et al.*, 1992c) that the identical gametocytes in fusiform host cells also develop in *L. balmorali*, which parasitize passeriforms in the Ethiopian zoogeographical region. Moreover, the reexamination of the type material by the author showed that Bennett *et al.* (1995a) have overlooked gametocytes in roundish host cells, which are present in the hapantotype of *L. peircei* (slide No 125223, IRCAH), and which are also characteristic of *L. balmorali*. Morphology of gametocytes and their host cells both in roundish and fusiform host cells in *L. peircei* is indistinguishable from these of *L. balmorali*. Based on evidence presented above, and bearing in mind the main principles of identification of species of leucocytozoids (see p. 76), it is preferable at present to consider *L. peircei* to be a junior synonym of *L. balmorali*. It should be noted that, during development of this parasite in *Phylloscopuis trochilus*, microgametocytes were frequently seen, but they were uncommon in *Dryoscopus cubla*. The reason for this difference is unknown, and additional investigations are required to solve this question. The ratio of macro- and microgametocytes is not used in the taxonomy of haemosporidian parasites at present, and thus this character cannon be a basis to consider *L. peircei* to be a distinct species.

30. **Leucocytozoon (Leucocytozoon) nyctyornis** Nandi, 1986

Leucocytozoon nyctyornis Nandi, 1986a: 114, Fig. 1–3. – *L. alcedinis* Bennett, Earlé, Peirce and Nandi, 1993c: 75, Fig. 5, 6. – *L. nyctyornis*: Valkiūnas, 1997: 543 (=*L. alcedinis*).

Type vertebrate host. *Nyctyornis athertoni* (Jardine and Selby) (Coraciiformes).
Additional vertebrate hosts. *Halcyon chelicuti*, *H. coromanda*, *H. smyrnensis*, *Merops apiaster* (Coraciiformes).
Type locality. Rani, Kamrup District, Assam, India.
Distribution. The Ethiopian and Oriental zoogeographical regions. In the Palearctic, this parasite has been recorded in southern Kazakhstan.
Type material. Hapantotype (*Nyctyornis athertoni*, Assam, India, N.C. Nandi) is deposited in NZCC.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Nyctyornis*.

Main diagnostic characters. A parasite of species of the Coraciiformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is of band-like form and, if not deformed, it has approximately the same width along all of its length; the nucleus extends about 1/2 and even more of the circumference of gametocyte.

Development in vertebrate host
Macrogametocytes (Fig. 333, *1–3*; Table 167) develop in roundish host cells; cytoplasm frequently contains small vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is of variable form and position; nucleolus is prominent and well seen; nucleus of host cell is pushed aside, deformed, and lies peripherally as a band, which, if not deformed, has approximately the same width along all of its length (Fig. 333,

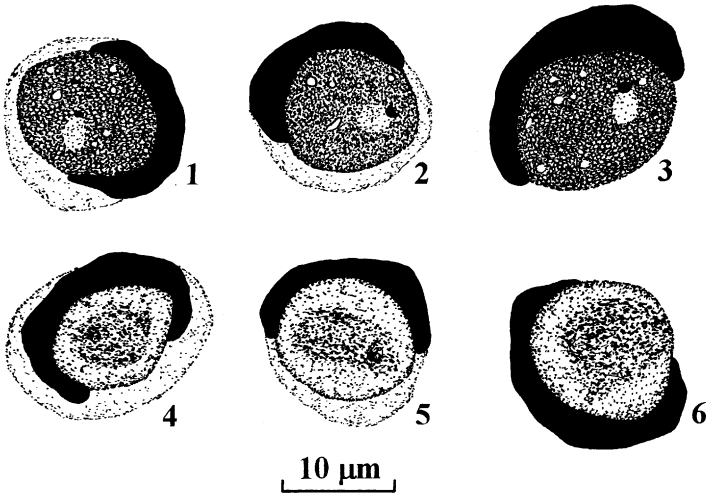

Figure 333 Gametocytes of *Leucocytozoon nyctyornis* from the blood of *Merops apiaster*: *1–3* – macrogametocytes; *4–6* – microgametocytes.

1), it extends usually about 1/2 and even more of the circumference of gametocyte; cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 333, *3*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 333, *1*, *2*).

Microgametocytes (Fig. 333, *4–6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. The available data about this parasite are scanty at present. The original description is based on material from a single infected bird (Nandi, 1986a). A band-like in form host cell nucleus, which extends usually about 1/2 and even more of the circumference of gametocyte, is the main diagnostic character of *L. nyctyornis*. A low parasitemia was found by the author in one *Merops apiaster* in southern Kazakhstan, and the morphology of gametocytes and their host cells of this parasite especially corresponds to those in *L. nyctyornis* (Fig. 333).

Leucocytozoon alcedinis was described mainly on the basis that it was found in coraciiform birds of the family Alcedinidae. Morphology both of gametocytes and their host cells of *L. alcedinis* is indistinguishable from this of *L. nyctyornis*, and data on other stages of development of these two parasites are not available. Based on these facts, and bearing in mind the available data on the specificity of leucocytozoids and the main principles of identification of their species (see p. 76), it is preferable at present to consider *L. alcedinis* to be a junior synonym of *L. nyctyornis*.

31. **Leucocytozoon (Leucocytozoon) squamatus** Nandi, 1986

Leucocytozoon squamatus Nandi, 1986b: 224, Fig. 1. – *L. capitonis* Bennett, Earlé and Peirce, 1993b: 76, Fig. 10–13. – *L. squamatus*: Valkiūnas, 1997: 544 (= *L. capitonis*).

Type vertebrate host. *Picus squamatus* Vigors (Piciformes).
Additional vertebrate hosts. Some species of the Piciformes (Table 171).

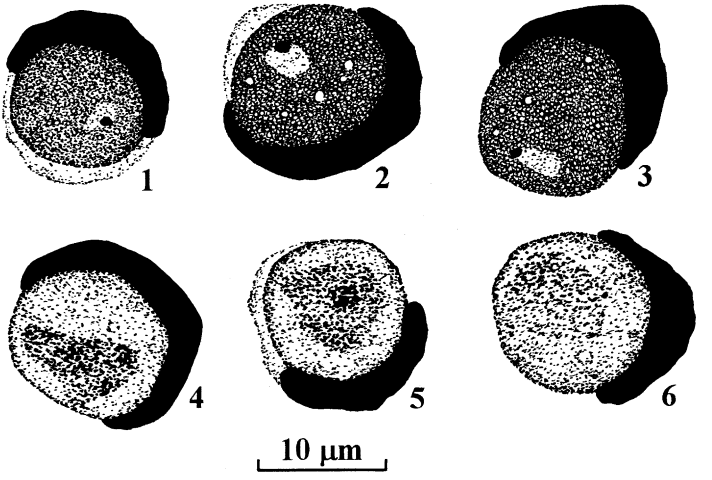

Figure 334 Gametocytes of *Leucocytozoon squamatus* from the blood of *Jynx torquilla*: *1–3* – macrogametocytes; *4–6* – microgametocytes.

Type locality. Patnitop, Uddampur, Jammu and Kashmir State, India.
Distribution. The Holarctic, Ethiopian and Oriental zoogeographical regions.
Type material. Hapantotype (No. Pt 2054, *Picus squamatus squamatus*, Kashmir State, India, N.C. Nandi) is deposited in NZCC.
Etymology. The specific name is derived from the specific name of the type vertebrate host, *P. squamatus.*

Table 171 List of vertebrate hosts of *Leucocytozoon squamatus*.

Colaptes auratus	*Megalaima franklinii*
Geocolaptes olivaceus	*M. viridis*
Jynx ruficollis	*Picus chlorolophus*
J. torquilla	*P. viridis*
Lybius torquatus	*Trachyphonus darnaudii*

Main diagnostic characters. A parasite of species of the Piciformes whose gametocytes develop in roundish host cells. Nucleus of the host cell is of a band-like form with approximately the same width along its entire length, or sometimes cap-like shape; the nucleus can extend more than 1/2 of the circumference of gametocyte.

Development in vertebrate host
According to the original description (Nandi, 1986b), gametocytes develop in cells of erythrocytic series.

Macrogametocytes (Fig. 334, *1–3*; Table 172) develop in roundish host cells; the cytoplasm sometimes contains small vacuoles; valutin granules are usually present; gametocytes are roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is pushed aside, deformed, and lies peripherally usually as a band, which, if not deformed, is of approximately the same width along its entire length, the nucleus can extend more than 1/2 of the

circumference of gametocyte (Fig. 334, *1*, *2*); sometimes cap-like nuclei of host cells were also seen (Fig. 334, *3*); the cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 334, *3*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 334, *1*, *2*).

Table 172 Morphometric parameters of gametocytes and host cells of *Leucocytozoon* spp.

Feature	*L. squamatus*				*L. communis*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell	17							
Length		9.9–14.0	12.0	1.4	34	10.0–15.7	13.1	1.2
Width		10.0–13.2	11.1	1.1	34	11.0–14.4	12.2	1.0
Length of nucleus		1.8–4.9	3.4	0.8	34	3.5–6.0	4.4	0.4
Width of nucleus		1.5–4.0	2.9	0.6	34	1.3–4.3	3.2	0.3
Length of nucleus of host cell		12.2–27.2	22.1	3.8	48	9.2–21.4	15.4	3.2

Note: All sizes are given in micrometres.

Microgametocytes (Fig. 334, *4–6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon capitonis* was described mainly on the basis that it was found in piciform birds of the family Capitonidae. The morphology of both gametocytes and their host cells of *L. capitonis* is indistinguishable from this in *L. squamatus*, and data on other stages of development of these two parasites are not available. Based on these facts, and bearing in mind the available data on the specificity of leucocytozoids and the main principles of identification of their species (see p. 76), it is preferable at present to consider *L. capitonis* to be a junior synonym of *L. squamatus.*

It should be noted that, in spite of the wide geographical range, *L. squamatus* has been extremely rarely recorded in piciform birds, and it is clearly spotty in distribution. In all parts of the range, the prevalence of infection in piciform birds rarely exceeds 2% and usually is even less. This fact shows that birds of the order Piciformes can be incidental hosts of leucocytozoids which only started to incorporate the representatives of this avian order.

Leucocytozoon squamatus is the only species of leucocytozoids which has been described in birds of the order Piciformes.

32. **Leucocytozoon (Leucocytozoon) communi**s Valkiūnas, 1989

Leucocytozoon communis Valkiūnas, 1989a: 85, Fig. 5. – *L. bucerotis* Bennett, Earlé, Peirce and Nandi, 1993c: 77, Fig. 11–14. – *L. dacelo* Bennett, Earlé, Peirce and Nandi, 1993c: 75, Fig. 7–10. – *L. communis*: Valkiūnas, 1997: 545 (=*L. bucerotis, L. dacelo*).

Type vertebrate host. *Upupa epops* L. (Coraciiformes).
Additional vertebrate hosts. Some species of the Coraciiformes (Table 173).
Type locality. The Chokpak Ornithological Station located in the foothills of the Western Tien Shan, approximately 80 km south-west of Djambul, southern Kazakhstan.
Distribution. The Ethiopian, Oriental and Australian zoogeographical regions, and the South and Central Palearctic.

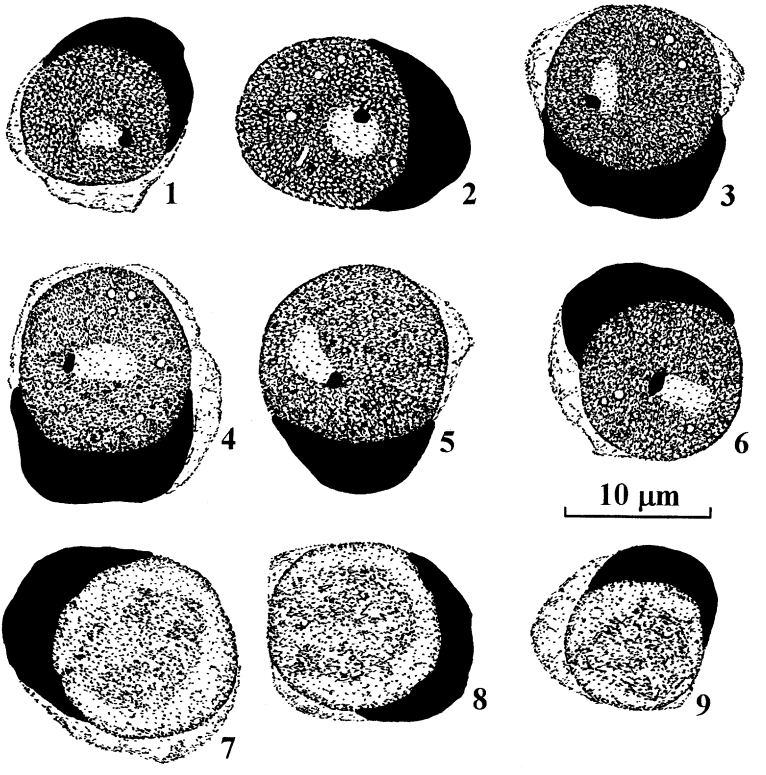

Figure 335 Gametocytes of *Leucocytozoon communis* from the blood of *Upupa epops*: *1–6* – macrogametocytes; *7–9* – microgametocytes.

Type material. Hapantotype (No. 3256.86 Az, *Upupa epops*, 11.05.1986, Southern Kazakhstan, G. Valkiūnas) and parahapantotypes (No. 3255.86 Az, 3257.86 Az, 3258.86 Az, other data are as for the hapantotype) are deposited in CDVA.
Etymology. The specific name is derived from the Latin word 'communis,' and it reflects the morphology of gametocytes and host cells of this parasite, common for leucocytozoids.

Table 173 List of vertebrate hosts of *Leucocytozoon communis*.

Aceros plicatus	*Halcyon concreta*	*Tockus deckeni*
Anthracoceros malayanus	*H. lindsayi*	*T. erythrorhynchus*
Dacelo novaeguineae	*Ispidina picta*	*T. monteiri*

Main diagnostic characters. A parasite of species of the Coraciiformes whose gametocytes develop in roundish host cells. Nucleus of host cell usually is of a cap-like form, sometimes band-like shape; the nucleus extends less than 1/2 of the circumference of gametocyte.

Development in vertebrate host
Macrogametocytes (Fig. 335, *1–6*; Table 172) develop in roundish host cells; cytoplasm sometimes contains small vacuoles; valutin granules are frequently present; gametocytes

are roundish; the parasite nucleus is of variable form and position; nucleolus is prominent and well seen; nucleus of host cell is pushed aside, deformed, and lies peripherally usually as a more or less evident cap, or sometimes a band, it extends less than 1/2 of the circumference of gametocyte; cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 335, *2*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 335, *1, 3, 4–6*).

Microgametocytes (Fig. 335, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon bucerotis* and *L. dacelo* were described mainly on the basis that they were found in coraciiform birds of the families Bucerotidae and Alcedinidae, respectively. The morphology of both gametocytes and their host cells of *L. bucerotis* and *L. dacelo* is indistinguishable from this of *L. communis*, and data on other stages of development of these three parasites are not available. Based on these facts, and taking in mind the available data on the specificity of leucocytozoids and the main principles of identification of their species (see p. 76), it is preferable at present to consider *L. bucerotis* and *L. dacelo* to be a junior synonym of *L. communis.*

33. **Leucocytozoon (Leucocytozoon) bennetti** Valkiūnas, 1993

Leucocytozoon bennetti Valkiūnas, 1993c: 436, Fig. 1–9.

Type vertebrate host. *Coracias garrulus* L. (Coraciiformes).
Type locality. The Chokpak Ornithological Station located in the foothills of the Western Tien Shan, approximately 80 km south-west of Djambul, southern Kazakhstan.
Distribution. This parasite has been found in the southern Palearctic so far, where it is common in the type vertebrate host. It is likely that the geographical range is wider.
Type material. Hapantotype (No. 2309.86 Az, *Coracias garrulus*, 28.04.1986, Southern Kazakhstan, G. Valkiūnas) and parahapantotypes (No. 2099–2101.86 Az, 2294–2296.86 Az, 2311.86 Az, 2513–2514.86 Az, 27.04.–01.05.1986, other data as for the hapantotype) are deposited in CDVA. Parahapantotype (G462980, other data are as for the hapantotype) is deposited in IRCAH. Gametocytes of *Haemoproteus coraciae* are present in the type material.
Etymology. This species is named in honour of Professor Gordon F. Bennett in recognition of his contribution to the study of avian blood parasites.

Main diagnostic characters. A parasite of species of the Coraciiformes whose gametocytes develop in roundish host cells. Nucleus of the host cell takes a cap-like or sometimes band-like form and, as the parasite develops, gametocyte finally enucleate the host cell. Fully grown gametocytes look like roundish naked parasites lying in the plasma. The size of gametocytes in enucleated host cells is significantly smaller than of those lying in host cells still containing the nuclei.

Development in vertebrate host
Young gametocytes (Fig. 336, *1*). The earliest gametocytes were seen in cells of erythrocytic series. A few earliest forms were observed. They are roundish and oval, and closely adhere to the enlarged nucleus of the host cell.

Macrogametocytes (Fig. 336, *2–6*; Table 174) develop in roundish host cells; cytoplasm frequently contains small vacuoles, and gametocytes with highly vacuolated

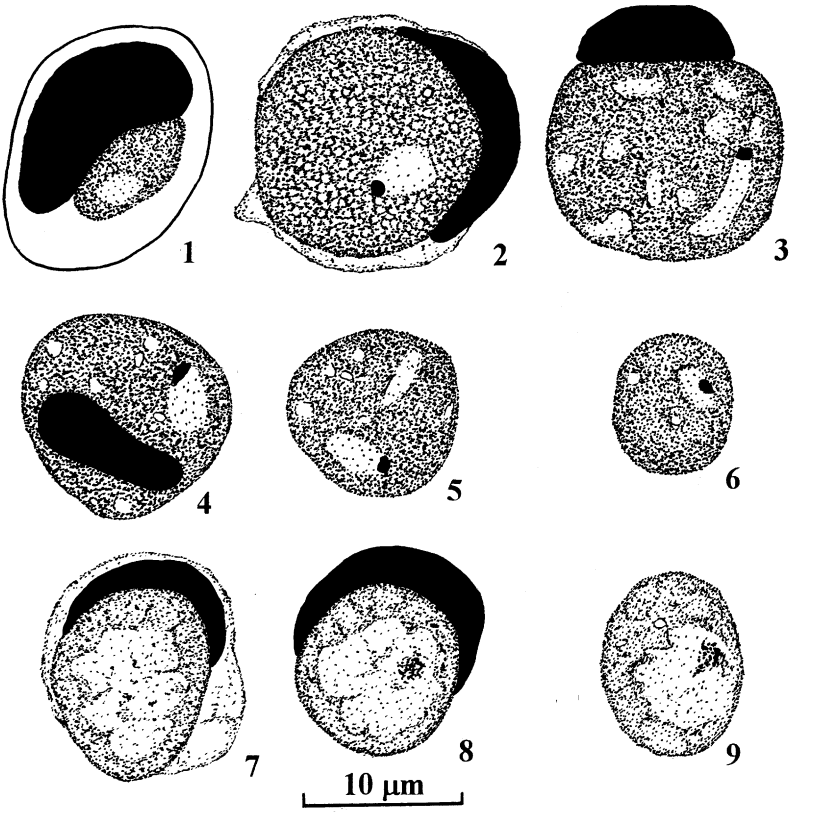

Figure 336 Gametocytes of *Leucocytozoon bennetti* from the blood of *Coracias garrulus*: *1* – young; *2–6* – macrogametocytes; *7–9* – microgametocytes.

cytoplasm were observed (Fig. 336, *3, 5*), but parasites lacking vacuoles or possessing a few vacuoles are also common (Fig. 336, *1, 6*); gametocytes are roundish; the parasite nucleus is of variable form and position; the nucleolus is prominent and well seen; the nucleus of host cell is enlarged, pushed aside, deformed, and lies peripherally as a more or less evident cap or sometimes band, it extends less than 1/2 of the circumference of gametocyte (Fig. 336, *2*); as the parasite develops, a contact of gametocyte with nucleus of host cell is gradually abated (Fig. 336, *3*), and the nuclei encircled by gametocytes (Fig. 336, *4*) were occasionally seen; fully grown gametocytes enucleate host cells (Fig. 336, *5*, *6*); cytoplasm of host cells is usually present around the growing gametocytes as a more or less evident and pale margin of variable form (Fig. 336, *2*) and is invisible in enucleated host cells, and thus fully grown gametocytes look like roundish 'naked' parasites lying in the plasma (Fig. 336, *3–6*); the size of gametocytes in enucleated host cells is significantly smaller than of those lying in host cells still containing the nuclei (Table 174). It is important to note that the enucleation of host cell takes place at the latest stages of development in the blood, and thus the 'naked' parasites are not always present in naturally infected bird. This depends on the stage of parasitemia observed. In the type material, the number of gametocytes in enucleated host cells is markedly variable, and it is up to 80% from the total number of gametocytes in some blood films.

Table 174 Morphometric parameters of gametocytes and host cells of *Leucocytozoon bennetti* (according to Valkiūnas, 1993).

Feature	*n*	lim	$\overline{X}$	*SD*
Macrogametocyte in nonenucleated host cell	40			
Length		10.7–16.0	14.4	1.2
Width		9.1–15.9	13.3	1.0
Length of nucleus		3.4–6.2	4.3	0.6
Width of nucleus		1.1–5.0	3.0	0.4
Macrogametocyte in enucleated host cell	40			
Length		7.8–11.4	9.2	0.8
Width		6.6–11.3	8.1	0.8
Length of nucleus		2.0–4.2	2.8	0.6
Width of nucleus		1.4–3.0	1.7	0.5
Microgametocyte in nonenucleated host cell	31			
Length		10.9–15.2	13.6	1.4
Width		9.5–15.2	12.9	1.2
Length of nucleus		5.7–10.1	8.0	0.4
Width of nucleus		5.0–9.4	7.8	0.4
Microgametocyte in enucleated host cell	25			
Length		7.1–12.4	9.5	1.6
Width		6.3–10.2	8.4	1.2
Length of nucleus		5.7–8.8	6.5	0.7
Width of nucleus		5.0–8.3	6.3	0.5
Length of nucleus of host cell				
Macrogametocyte	40	8.1–20.0	13.4	2.8
Microgametocyte	31	12.5–21.4	14.9	2.4

Note: All sizes are given in micrometres.

Microgametocytes (Fig. 336, *7–9*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters; the total number of microgametocytes in enucleated host cells in different blood films was recorded to be three to six times less than for macrogametocytes in the enucleated cells; a clump of chromatin was frequently seen in the nucleus (Fig. 336, 8, 9); other characters are as for macrogametocytes.

Comments. The presence of gametocytes, which enucleate host cells and look like 'naked' roundish parasites, is the main diagnostic character of *L. bennetti.* On the basis of these features, *L. bennetti* can be easily distinguished from other species of the family Leucocytozoidae, except *L. caulleryi*. Gametocytes of *L. bennetti* can be distinguished from *L. caulleryi*, first of all, on the basis of following characters. First, development of *L. bennetti* gametocyte includes a stage when the nucleus of the host cell assumes a cap-like or band-like form and closely adheres to gametocyte (Fig. 336, *2, 3*). Second, the size of *L. bennetti* gametocytes in enucleated host cells is significantly smaller than of those lying in host cells still containing the nuclei (Table 174). Both these features are not characteristic of *L. caulleryi*.

In the type material, gametocytes in enucleated host cells are common. The presence of such gametocytes cannot be explained by the onset of gametogenesis, because the blood was taken only from the peripheral circulation from live birds and it was quickly air-dried. Gametocytes of *L. bennetti*, which enucleate host cells, develop in birds. Until now, such gametocytes were known only for *L. caulleryi*. It should be noted that there is no data on vitality of gametocytes *L. bennetti* in enucleated host cells. However, it is clear that enucleation of infected cells by gametocytes is a feature which is characteristic not only of *L. caulleryi,* as it was thought formerly. In many respects, *L. caulleryi* is a unique representative of the Leucocytozoidae. Biting midges of the family Ceratopogonidae are its vectors, and it belongs to the separate subgenus *Akiba*. Until the life cycle of *L. bennetti* is investigated, this parasite is attributed to the subgenus *Leucocytozoon* sensu latu as some other species of leucocytozoids.

Leucocytozoon bennetti is a common parasite of *Coracias garrulus* in the southern Kazakhstan during spring migration. The prevalence of infection was recorded to exceed 50%.

34. **Leucocytozoon (Leucocytozoon) colius** Bennett, Earlé, Peirce and Nandi, 1993

Leucocytozoon colius Bennett, Earlé, Peirce and Nandi, 1993c: 75, Fig. 1–4.
Type vertebrate host. *Colius striatus* Gmelin (Coliiformes).
Type locality. Lydenburg, Transvaal, Republic of South Africa.
Distribution. This parasite has been found only in the type locality so far.
Type material. Hapantotype (No. 104891, *Colius striatus*, 18.06.1989, Lydenburg, Transvaal, Republic of South Africa, coll. Swardt) is deposited in IRCAH.
Etymology. The specific name is derived from the generic name of the type vertebrate host, *Colius*.

Main diagnostic characters. A parasite of species of the Coliiformes whose gametocytes develop in roundish host cells. Nucleus of host cell is of a cap-like or band-like form; the nucleus extends less than 1/2 of the circumference of gametocyte.

Development in vertebrate host
Macrogametocytes (Fig. 337, *1–3*; Table 175) develop in roundish host cells; the cytoplasm frequently contains a few vacuoles; gametocytes are roundish; the parasite nucleus is of variable form and position; nucleolus is prominent; nucleus of host cell is

Table 175 Morphometric parameters of gametocytes and host cells of *Leucocytozoon colius* (modified from Bennett *et all.*, 1993c) ($n = 25$).

Feature	$\overline{X}$	*SD*
Macrogametocyte in roundish host cell		
Length	14.1	1.1
Width	11.0	1.4
Length of nucleus	5.9	1.3
Width of nucleus	2.4	0.7
Length of nucleus of host cell	14.5	1.8

Note: All sizes are given in micrometres.

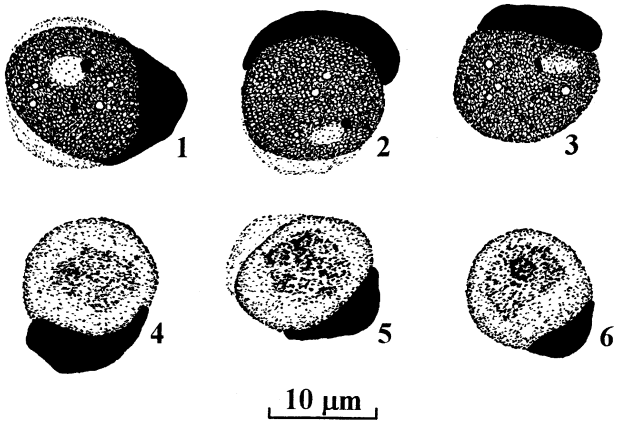

Figure 337 Gametocytes of *Leucocytozoon colius* from the blood of *Colius striatus*: *1–3* – macrogametocytes; *4–6* – microgametocytes.

pushed aside, deformed and lies peripherally as a more or less evident cap or band, it extends less than 1/2 of the circumference of gametocyte; cytoplasm of host cells is largely replaced by gametocytes, and is sometimes even invisible (Fig. 337, *3*) but more frequently is present around the gametocytes as a more or less evident and pale margin of variable form (Fig. 337, *1*, *2*).

Microgametocytes (Fig. 337, *4–6*). The general configuration and other features are as for macrogametocytes with the usual sexual dimorphic characters.

Comments. *Leucocytozoon colius* is the only species of leucocytozoids known at present to parasitize birds of the order Coliiformes.

2. Subgenus **AKIBA** Bennett, Garnham and Fallis, 1965

Akiba Bennett, Garnham and Fallis, 1965: 929 (pro gen.).

Type species. *Leucocytozoon caulleryi* Mathis and Léger, 1909, according to the original designation.

Etymology. This subgenus is named in honour of Japanese parasitologist Dr. Kazuo Akiba, who, together with his colleagues, investigated the life cycle of *L. caulleryi* and discovered that biting midges are vectors of this parasite.

The first generation of exoerythrocytic meronts develops in endothelial cells of capillaries in numerous organs; the meronts do not develop in hepatocytes. Merozoites of the first generation are elongated; they are greater than 3 μm in length. Meronts of the second generation can develop extracellularly. The prepatent period is more than 10 days after infection with sporozoites. Gametocytes develop in cells of erythrocytic series; the host cells are roundish. Sporogony takes place in biting midges (Diptera: Ceratopogonidae). Ends of sporozoites are pointed.

This subgenus includes only one species, *L. caulleryi.*

35. **Leucocytozoon (Akiba) caulleryi** Mathis and Léger, 1909

Leucocytozoon caulleryi Mathis and Léger, 1909: 472. – *L. schuffneri* Prowazek, 1912: 263 (partim). – *L. caulleryi*: Levine, 1961: 280 (=*L. schuffneri*, partim). – *Akiba caulleryi*: Bennett *et al.*, 1965: 929. – *L. caulleryi*: Hsu *et al.*, 1973: 195.

Type vertebrate host. Domestic chicken *Gallus gallus* L. (Galliformes).
Additional vertebrate hosts. Unknown.
Vectors. *Culicoides arakawae*, *C. circumscriptus*, *C. odibilis*, *C. schultzei* (Diptera: Ceratopogonidae).
Type locality. Tonkin (environs of Hanoi, Vietnam).
Distribution. South and South-East Asia. The eastern record came from Japan, and the western one from South Kazakhstan (Akiba, 1970; Kairullaev and Osipov, 1981).
Type material. Neohapantotypes (*exoerythrocytic meronts*: No. 993, *Gallus gallus*, the kidneys, Ceylon, other data are not available; *blood stages*: No. 991, *G. gallus*, 16.06.1959, Ceylon; No. 992, 10.02.1960, other data as for No. 991) are deposited in CPG.
Etymology. This species is named in honour of Dr. Caullery.

Main diagnostic characters. Specific parasite of *Gallus gallus*; gametocytes develop in roundish host cells and finally enucleate the infected cells.

Development in vertebrate host
Sporozoites, inoculated into blood stream of birds by *Culicoides* biting midges, invade the endothelial cells of capillaries in the spleen, lungs, liver, bursa of Fabricius, and probably other organs (Morii and Fukuda, 1992). The sporozoites initiate the development of the first generation of exoerythrocytic meronts which have been found between three and six days after infection. The earliest meronts were observed on the third day after infection. They look like roundish bodies about 15 to 20 μm in diameter; possess basophilic cytoplasm and several irregular-shape nuclei. On the fourth day after infection, the meronts reach up to 25 to 30 μm in diameter, and now contain numerous nuclei. Mature meronts appear between the fifth and sixth day after the inoculation of sporozoites. They vary (n = 22) from 40 to 65 (on average 55.2±6.4) μm in diameter. The nucleus of the host cell is enlarged and displaced (Fig. 338, *1*). The mature meront of the first generation is surrounded with a thin envelope and possesses numerous long and slender merozoites (Fig. 338, *2*). Mature first-generation merozoites (n = 30) are on average 7.1±0.1 μm in length and less than 1 μm in width. These merozoites, in turn, invade endothelial cells of the capillaries of numerous tissues and organs and initiate the development of the second generation of meronts known as megalomeronts because of their large size (Fig. 338, *3–5*). Megalomeronts mature and release the second generation of merozoites 14 to 15 days after infection (Akiba, 1970; Akiba *et al.*, 1971; Morii *et al.*, 1986). An enormous number of merozoites, which are of oval form, about 1.7 μm in length and 1 μm in width, develops in megalomeronts. Merozoites of the second generation invade erythrocytes and grow into gametocytes.

Peculiarities of the development of megalomeronts were studied in experimentally infected chickens in detail (Akiba, 1970; Akiba *et al.*, 1971; Morii *et al.*, 1986). Initial stages of their development were observed on the seventh day after the inoculation of sporozoites. Young parasites were found in the capillary endothelial cells in the brain, bursa of Fabricius, thymus, trachea, bronchus, lungs, heart, liver, spleen, kidneys, pancreas, gullet, masticatory and glandular stomach, crop, duodenum, ovary, testis, skeletal muscle, and numerous other organs and tissues. They were especially numerous in bursa of Fabricius and thymus. At

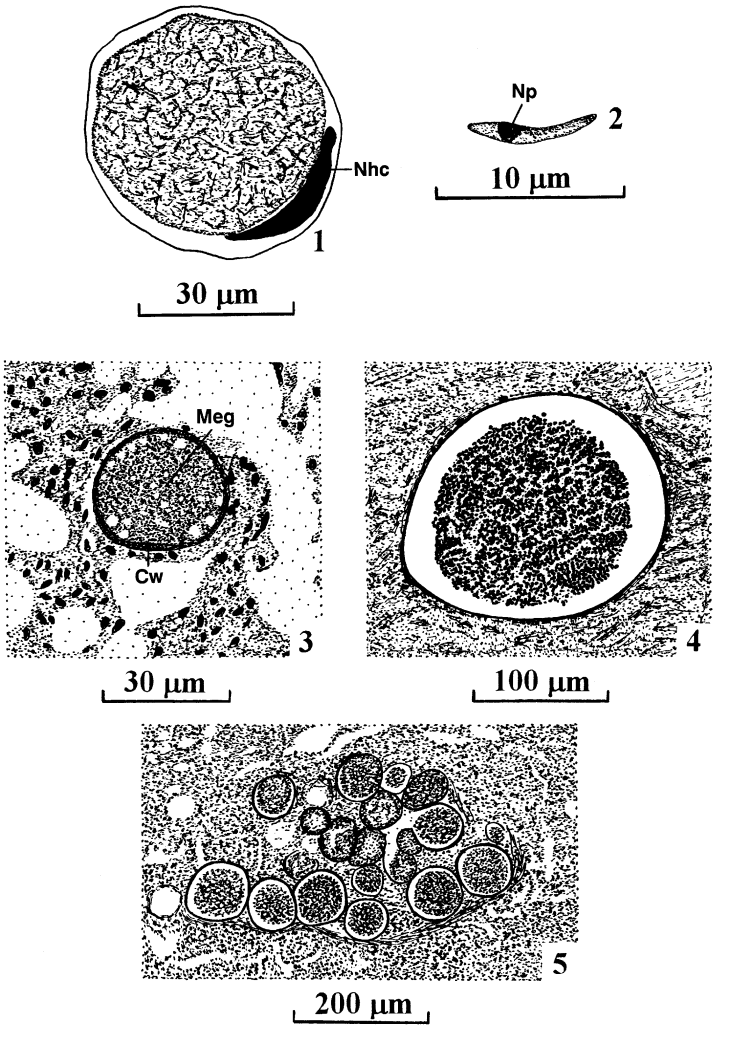

Figure 338 Exoerythrocytic meronts (*1*, *3–5*) and a merozoite (*2*) of *Leucocytozoon caulleryi* from *Gallus gallus*:
1 – mature meront of the first generation in the endothelial cell of the spleen; *2* – long slender merozoite of the first generation in the peripheral blood; *3* – growing megalomeront in the lungs enclosed by a well defined thick capsule-like wall; *4* – mature megalomeront in the heart; *5* – a group of megalomeronts in the lungs; Cw – capsule-like wall; Meg – megalomeront; Nhc – nucleus of the host cell; Np – nucleus of the parasite (*1, 2* are modified from Morii and Fukuda, 1992 and *3–5* are modified from Isobe and Akiba, 1990).

this stage of development, the meronts are intracellular, the nuclear fission is only slightly evident, and the host cell is on average about 15 μm in diameter and its nucleus is approximately 9×11 μm in size. On the eighth day after the inoculation of sporozoites, nuclear fission is well pronounced in megalomeronts. Host cell increases on average to 18 to 24 μm in diameter and its nucleus reaches about 9×13 μm in size. Several (up to 10 to 15) meronts are frequently present in the same infected cell, and this is a distinctive character of

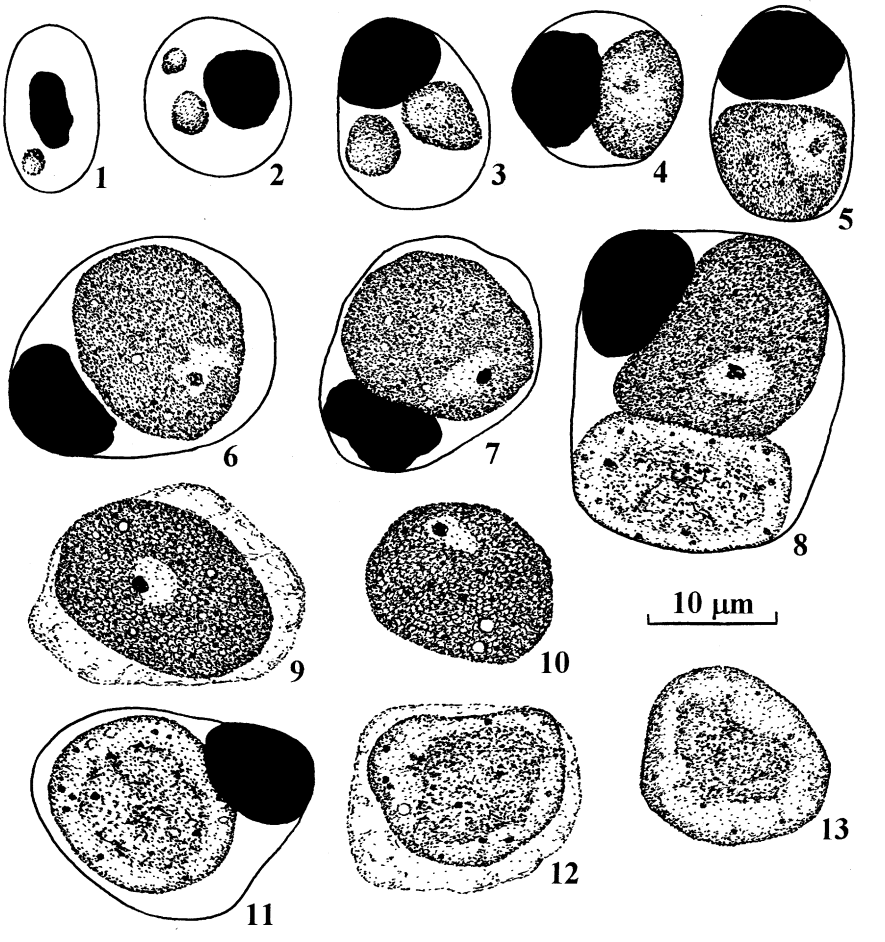

Figure 339 Gametocytes of *Leucocytozoon caulleryi* from the blood of *Gallus gallus*: *1–4* – young; *5–7*, *9*, *10* – macrogametocytes; *8* – macro- and microgametocyte in the same host cell; *11–13* – microgametocytes. Explanations are given in the text.

megalomerogony of *L. caulleryi*. Meronts are about 4 to 11 μm in diameter at this time. Infected cells start to rupture, and growing megalomeronts are released from the host cells. On the ninth day after infection, extracellular meronts are common in numerous organs and tissues. It is interesting to note that they were recorded not only in the visceral organs but also in the eyes and sciatic nerves (Chew, 1968). Megalomeronts rapidly increase in size and are enclosed by a well defined capsular-like thick wall. As the megalomeront develops, cytomeres appear (Morii *et al.*, 1987). Parasites are located solely (Fig. 338, *3*, *4*) and in clusters containing from several to approximately 20 megalomeronts (Fig. 338, *5*). Mature megalomeronts are located extracellularly. They usually vary from 100 to 200 μm in diameter, and often reach 300 μm in diameter. The largest megalomeronts can reach 500 μm in diameter (Omar, 1968). The size of megalomeronts depends on the peculiarities of their location. Solely developing megalomeronts are usually larger than the parasites developing in clusters (Kitaoka *et al.*, 1972). It should be noted that megalomeronts developing in

embryos of experimentally infected chickens are markedly smaller (Takamatsu *et al.*, 1978). They do not exceed 180 μm in diameter and are, on average, about 65 μm in diameter. It is likely that megalomeronts grow faster and reach their largest size at a temperature close to the body temperature of chickens (about 41°C) rather than at temperature of 38°C at which incubation of embryos takes place. This phenomenon is known for the coccidia *Eimeria tenella* (Long, 1970).

The number of megalomeronts depends on the dose of primary inoculated sporozoites but it decreases with the age of chickens. Under the same circumstances, the largest number of megalomeronts developed in youngest chickens (Kitaoka *et al.*, 1972).

The prepatent period is 14 to 15 days after the inoculation of sporozoites (Akiba, 1970; Morii *et al.*, 1986). This period was shown to be strictly fixed, and it does not depend on the dose of inoculated sporozoites (Kitaoka *et al.*, 1972).

Gametocytes (Fig. 339) develop in young and mature erythrocytes. Five stages of gametocyte development have been distinguished (Akiba, 1970).

Stage I. Free merozoites in the blood (still extracellular forms). They are usually ovoid or sometimes oval, and each possesses a nucleus located at the bluntly tapering end of the body.

Stage II (Fig. 339, *1*). The earliest forms in erythroblasts, polychromatic and mature erythrocytes. They are usually roundish, and some of them are ring-shaped. The influence of parasites on infected cells is usually not evident. The size of parasites is very close to that in stage I.

Stage III (Fig. 339, *2–5*). Gametocytes are markedly larger than at stage II. Macro- and microgametocytes are still indistinguishable or poorly distinguishable morphologically under the light microscope. Infected cell and its nucleus are enlarged and deformed. The cytoplasm of gametocytes is homogeneous in appearance. The parasite nucleus is well seen, it possesses a well evident nucleolus. Large gametocytes are about 9 to 11 μm in diameter, and their host cells are about 13 to 15 μm in diameter. At this stage of development, a large number of gametocytes are in deep circulation especially in the lungs, spleen, and bone marrow, and they are less frequently found in the peripheral circulation. Sometimes, gametocytes were observed extracellularly. It is likely that such gametocytes are forms released from ruptured host cells which contained more than two gametocytes.

Stage IV (Fig. 339, *6–8*, *11*). Gametocytes occupy a great part of cytoplasmic space in host cells. Parasites are roundish or oval. Macro- and microgametocytes can be easily distinguished on the basis of usual sexual dimorphic characters. Nucleolus is well seen in macrogametocytes. Gametocytes are about 13 to 16 μm in diameter, and their host cells are approximately 17 to 21 μm in diameter. However, the host cell is much larger during infection of the same cell with several (usually two) parasites (Fig. 339, *8*). Nucleus of the host cell is pushed aside and lies as a compact usually roundish or oval mass located close to the gametocyte; it never assumes a band-like form. Gametocytes can be found in the peripheral blood but are still more numerous in deep circulation.

Stage V (Fig. 339, *9*, *10*, *12, 13*). Fully grown gametocytes are located in enucleated host cells. Gametocytes are similar in form, appearance, and size to those in stage IV. Sometimes they possess small vacuoles. Numerous gametocytes look like naked parasites with invisible cytoplasm of host cell and some lie free in the plasma (Fig. 339, *10*, *13*). Macrogametocytes are about 15 μm in diameter, and microgametocytes are slightly smaller. They can be readily distinguished on the basis of usual sexual dimorphic characters.

In the Japanese strain, parasites of stage I appear from the 14th day after the infection with sporozoites. Gametocytes of stage II were observed at approximately the same time.

Parasites of these two stages are present during the first four or five days of parasitemia. Gametocytes of stage V appear 18 to 19 days after infection with sporozoites. Gametocytemia lasts about eight to nine days. Development of the parasite in birds (from inoculation of sporozoites to disappearance of gametocytes from the peripheral circulation) is completed within 23 days and even faster. In the Taiwanese strain, this process is completed in 26 days (Morii *et al.*, 1986).

Peculiarities of the development of gametocytes and the dynamics of parasitemia do not depend on the species of vector in which sporozoites develop (Morii and Kitaoka, 1968b).

The number of gametocytes in the peripheral blood does not depend on that of secondary inoculated sporozoites. When the number of sporozoites ranging from 5 to 500 was inoculated repeatedly three to five times at one- or two-day intervals, the prepatent period and the severity and duration of parasitemia were influenced only by the number of sporozoites inoculated for the first time, but not by the number of repeated inoculations. Moreover, the secondary inoculations of sporozoites induce no extension of duration of parasitemia or reappearance of parasites (Morii and Kitaoka, 1969).

Chickens can be easily infected by subinoculation of blood containing merozoites, and gametocytes appear in the peripheral blood of these birds. There was no difference in the period of gametocytemia between these birds and chickens infected by inoculation of sporozoites (Morii and Kitaoka, 1969; Akiba, 1970).

Description of a so-called 'atypical' parasitemia for *L. caulleryi* is given below. It was recorded after (i) intravenous injection with such number of sporozoites as presumed to be only one, (ii) inoculation of more than several sporozoites by any route other than the intravenous one, (iii) intravenous injection approximately 100 sporozoites and influenced by the effect of drugs of the pyrimethamine group (Akiba, 1970). In the above mentioned cases of infection, the appearance of gametocytes of stages II and V is retarded, or the duration of appearance of these parasites is shortened. As a result of this, it is difficult or even impossible to observe gametocytes of stage II in chickens of these groups by ordinary microscopy. A similar phenomenon was seen in chickens infected with sporozoites at the age up to seven days (Morii and Kitaoka, 1970).

Normally, gametocytes of stages II and V are present in the peripheral blood. Gametocytes of stages III and IV have been observed much less frequently in the peripheral circulation. They are more numerous in deep circulation in the lungs, spleen, bone marrow, liver, kidneys, and thymus. Multiple infection of the same host cell with three to seven parasites is common. As the parasites develop, such heavily parasitized cells perish gradually, and the released gametocytes are destroyed by macrophages (Akiba, 1970). As a result of this, gametocytes of stage V are less numerous than of stage II. The concentration of infected cells in deep circulation leads to partial lowering both of the probability of mechanical destruction of host cells and the phagocytosis. This can explain the concentration of growing gametocytes of stages III and IV in the deep circulation of visceral organs.

Development of gametocytes *in vitro* was studied by Isobe *et al.* (1984). It was shown that merozoites, which parasitize young (polychromatic) erythrocytes, develop better and faster than those in mature erythrocytes. Some parasites were observed to cease development in mature erythrocytes. It is likely that growing gametocytes need the metabolism met in young erythrocytes.

Relapses, such as in *L. smithi* or *L. simondi* infections, have never been observed in *L. caulleryi* infection (Morii, 1992). A few exoerythrocytic meronts have been detected in

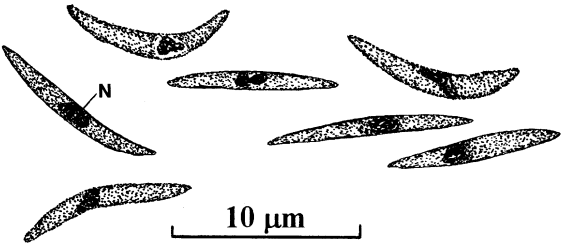

Figure 340 Sporozoites of *Leucocytozoon caulleryi*: N – nucleus.

internal organs of some chickens recovered from infection. However, the role of these meronts in the life cycle of *L. caulleryi* is unclear (Isobe and Akiba, 1986). *Leucocytozoon caulleryi* usually do not survive in the vertebrate host, and this is considered to be the main obstacle to spreading the infection outside its endemic territories in South and South-East Asia. It is likely that (i) the possibility of a round-the-year transmission at low latitudes and (ii) the long (up to 33 days at temperature of 15°C) persistence of vital sporozoites in the salivary glands of vector (Akiba, 1970; Morii and Kitaoka, 1968b) contributes to maintenance of this species in nature.

Development in vector

After ingestion of mature gametocytes by *Culicoides* biting midges, gametes and zygotes rapidly develop in the midgut. Ookinetes were observed 30 to 60 min after the blood meal. Mature ookinetes are about 21 μm in length and 7 μm in width, and each possesses a prominent nucleus and numerous variable-size 'vacuoles.' Ookinetes cross the midgut wall and develop into oocysts. Mature oocysts are usually about 10 μm in diameter, and the largest forms seen are about 14 μm in diameter. Each oocyst contains less than 100 sporozoites. Mature sporozoites are about 10 μm in length and 1.2 μm in width. The ends of sporozoites are more or less pointed, sometimes markedly (Fig. 340). Sporogony is rapid. It is completed in two to three days at a temperature of 25°C after the ingestion of mature gametocytes (Akiba, 1970; Morii, 1992).

Infection in chickens can be initiated by experimental inoculation even of a single sporozoite isolated from the salivary glands of *Culicoides arakawae* three to four days after the ingestion of gametocytes and kept at temperature of 25°C (Morii and Kitaoka, 1969). The inoculation of ten and more of such sporozoites always induces the infection in chickens. However, the birds were not infected after inoculation of about 2000 sporozoites isolated from the salivary glands of the vector two days after the blood meal. Sporozoites, isolated from the salivary glands three days after the ingestion of gametocytes, always induce the infection in chickens (Morii *et al.*, 1984b). Thus, sporozoites are not capable of developing in birds just after their release from oocysts and penetration into the salivary glands. They acquire the ability to initiate the infection in chickens some time (approximately a day) after the penetration into the salivary glands of the vector. Moreover, sporozoites acquire a high degree of infectivity only after penetration into the salivary glands. This was proved in experiments on the development of sporozoites *in vitro* (Morii *et al.*, 1984b). After the blood meal on infected birds, the midgut was isolated from the biting midges *Culicoides arakawae*, and sporogony was studied *in vitro* in two experimental groups when the salivary glands were present and absent. Sporogony is

completed and infective sporozoites develop in both these experiments. However, sporozoites acquired the high infectivity only after penetration into the salivary glands. The infective features of sporozoites are thus more site-dependent than time-dependent.

Infectivity of gametocytes for vector markedly changes in the course of parasitemia (Akiba, 1970). The maximum number of sporozoites developed in biting midges which fed on chickens one or two days before a peak of parasitemia, i.e., approximately on the 19th day after the inoculation of sporozoites into birds. Gametocytes can be capable of developing in the vector even on the first day of parasitemia. Vitality of gametocytes decreases with the advance of parasitemia, and there occurred an exponential decrease in the number of sporozoites developed in *Culicoides arakawae* soon with the advance in the process of infection.

Under the same circumstances, sporogony of the Japanese and Taiwanese strains in *Culicoides arakawae* is similar. The Taiwanese strain successfully developed in the laboratory reared colony of *C. arakawae* from Japan (Morii *et al.*, 1986).

Morii and Kitaoka (1968b) investigated experimentally the influence of temperature on the rate of sporogony and the infectivity of sporozoites. At temperature of 15, 20, 25, and 30°C, sporozoites appear in the salivary glands of the biting midges *Culicoides arakawae* on the sixth, fourth, third, and second day after the ingestion of gametocytes, respectively. At temperature of 12.5°C, the development is suspended at the stage of oocyst. At temperature of 30°C, sporozoites appear in the salivary glands as early as two days after infection. However, chickens are not susceptible to these sporozoites and even to those appearing five days after the blood meal. Sporozoites which developed at temperature of 25°C were always infective for chickens. Furthermore, the largest number of sporozoites developed in the vector at this temperature. It seems likely that a temperature of 25°C is an optimum for sporogony. Infective sporozoites developed in the experimentally infected biting midges which were kept 4 to 19 days at temperature of 20°C and 7 to 33 days at 15°C.

Sporogony of *L. caulleryi* successfully is completed not only in biting midges which prefer to feed on birds such as *Culicoides arakawae*, *C. circumscriptus*, and *C. odibilis* but also in *C. schultzei* which prefer to feed on cattle (Morii *et al.*, 1965).

Development of ovaries in females of *Culicoides arakawae* and sporogony of *L. caulleryi* are strictly synchronized (Morii and Kitaoka, 1968b). At the latest stage of development of ovaries (stage V), sporozoites appear in the salivary glands. This contributes to the effective transmission of the infection to new vertebrate hosts during subsequent blood meals of the vector.

P a t h o g e n i c i t y. Leucocytozoonosis caused by *L. caulleryi* is one of the most important diseases of domestic chicken in South and South-East Asia. Outbreaks of this disease have been reported in numerous countries of this region including India, Malaysia, Philippines, Taiwan, Japan, and others. The leucocytozoonosis started to be a great problem after increased development of poultry industry. In some localities, the prevalence of infection reached 80 to 100% before administration of preventive compounds, and the mortality rate varied from several to about 20% and sometimes reached 70 to 80% and even more among young chicks. The most severe losses usually take place in spring and summer. For example, they were recorded to be especially severe from late April to early June in Taiwan (Lee *et al.*, 1969; Akiba, 1970).

Clinical symptoms of infection vary markedly depending on the breeds and age of chickens, ages, seasons, and complications. Diseased birds are usually weakened, listless, and move with difficulty. Loss of appetite, breath difficulties, greenish watery diarrhoea as

well as pallid combs, wattles, mucousas, and underskin tissues are frequently reported. Before death, cataract-like eye lesions and paralysis of legs can be also evident, and severe anaemia develops because of haemorrhages and destruction of erythrocytes. At autopsy, the liver and spleen are enlarged. The haemorrhages are numerous at the place of ruptured megalomeronts, and can be found all over the body including visceral organs, abdominal cavity, skeletal muscle, and subcutaneous tissue. In fact, this infection is known in some localities as Bangkok haemorrhagic disease. Largest megalomeronts and their clusters can be seen with the naked eye. They block up capillaries and small vessels in numerous organs and tissues (Chew, 1968; Akiba, 1970; Morii, 1992).

Clinical symptoms first appear 12 days after infection with sporozoites. The disease is often so fast that the death of apparently healthy chickens occurs overnight. Chickens of exotic breeds at the age of one month and less often die. Older birds frequently survive, but the stunted growth, lowered or stopped egg production were recorded among them. Native breeds of chickens are much more resistant to infection than introduced ones (Lee *et al.*, 1969; Akiba, 1970; Morii, 1992).

The severity of disease and mortality rate directly depend on the number of initially inoculated sporozoites. The virulence of different strains is variable. The Taiwanese strain of *L. caulleryi* is more virulent than the Japanese one (Morii *et al.*, 1986).

Survived birds show complete resistance to reinfection with sporozoites. The acquired immunity is expressed against the megalomeronts but meronts of the first generation develop (Morii *et al.*, 1989; Morii, 1992).

S p e c i f i c i t y. *Leucocytozoon caulleryi* is a strictly host-specific haemosporidian parasite. Domestic chicken is the only known vertebrate host of this leucocytozoid at present. Such species of galliform birds as *Bambusicola thoracica*, *Chrysolophus pictus*, *Colinus virginianus*, *Coturnix japonica*, *Numida meleagris*, *Phasianus colchicus*, *P. versicolor*, *Syrmaticus soemmerringii*, and *S. reevesi* were not infected experimentally by inoculation of both sporozoites and blood-containing merozoites (Morii and Kitaoka, 1971). Splenectomy and use of immunodepressants do not affect the susceptibility of *Coturnix japonica* to infection.

C o m m e n t s. A few available records of *L. caulleryi* in Africa (Fallis *et al.*, 1973) were not confirmed. Some information about *L. caulleryi* is also available in the General Section (see p. 45).

Until recently, gametocytes enucleating host cells and lying free in the blood plasma were considered to be a unique character of *L. caulleryi.* However, such gametocytes were also found in *L. bennetti* which parasitize *Coracias garrulus*. Besides different vertebrate hosts, *L. caulleryi* and *L. bennetti* can be easily distinguished, first of all, on the basis of the mode of influence of their gametocytes on the nucleus of host cell during its enucleation.

Appendix 1

List of specific names of bird haemosporidians belonging to the categories of *nomen nudum*, *nomen dubium*, *species inquirenda*, *incertae sedis*, and important *lapsus calami* (modified from Levine and Campbell, 1971; Hsu *et al.*, 1973; Bishop and Bennett, 1992 with new data):

Name	Status
1	2
Haemamoeba praecox Grassi and Feletti, 1890a: 300	*nomen nudum*
H. rousseloti Bray, 1964: 269	*species inquirenda*
H. subimmaculata Grassi and Feletti, 1892: 10	*incertae sedis*
Haemoproteus acanthis Musaev and Zeiniev, 1977: 55	*nomen nudum*
H. accipiter Zeiniev, 1975b: 87	*nomen nudum*
H. accipiter Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. aluci Celli and Sanfelice, 1891: 583	*nomen dubium*
H. americaniae Anonymous, 1977: 396	*nomen nudum*
H. asio Zeiniev, 1975b: 87	*nomen nudum*
H. asio Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. asturisdussumieri Mello, 1935b: 469	*incertae sedis*
H. balfouri Sambon, 1909: 37	*nomen nudum*
H. bubonis Celli and Sanfelice, 1891: 583	*nomen dubium*
H. caprimulgi Musaev and Zeiniev, 1977: 55	*nomen nudum*
H. caprimulgus Musaev and Zeiniev, 1977: 57	*nomen nudum*
H. chapini Berghe, Chardome and Peel, 1958: 17	*species inquirenda*
H. chelidonis Franchini, 1922: 13	*incertae sedis*
H. chloris: Burry-Caines and Bennett, 1992: 151; Valkiūnas, 1997: 168.	*lapsus calami*
H. chukari Tartakovsky, 1913: 70	*nomen nudum*
H. circus Yakunin and Zhazyltaev, 1977: 133	*incertae sedis*
H. columbae liviae Tartakovsky, 1913: 70	*nomen nudum*
H. coraciatis Tartakovsky, 1913: 71	*nomen nudum*
H. coturnix Musaev and Zeiniev, 1977: 57	*nomen nudum*
H. cuculus Musaev and Zeiniev, 1977: 56	*nomen nudum*
H. dendragapi Woo, 1964 (according to White and Bennett, 1979: 1470)	*nomen nudum*
H. emberiza: Berson, 1964 (according to Zeiniev, 1975b: 87)	*nomen nudum*, *non Berson, 1964*
H. erythropi Tartakovsky, 1913: 70	*nomen nudum*
H. gallinarum Yakunin and Zhazyltaev, 1977: 133	*species inquirenda*

1	2
Haemoproteus garrulus Zeiniev, 1975b: 87	*nomen nudum*
H. geocichlae (Cleland and Johnston, 1909): 85	*species inquirenda*
H. glandarius Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. glaucidiumi Jörg, 1931: 1153	*nomen dubium*
H. glaucidiumi houssayi Jörg, 1931: 1154	*nomen dubium*
H. hachmasensis Musaev and Zeiniev, 1992: 45	*species inquirenda*
H. hartmanni Babudieri, 1931: 624	*species inquirenda*
H. himalayanus Pal and Dasgupta, 1980: 96	*species inquirenda*
H. houssayi Jörg, 1931: 1153	*nomen dubium*
H. loxiae Tartakovsky, 1913: 71	*nomen nudum*
H. majoris Zeiniev, 1975b: 87	*nomen nudum*
H. majoris Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. mansoni Sambon, 1908: 327	*nomen nudum*
H. mcleani Bennett, Earlé and Squires-Parsons, 1995a: 2	*species inquirenda*
H. meropis Tartakovsky, 1913: 70	*nomen nudum*
H. merulla Zeiniev, 1975b: 87	*nomen nudum*
H. merulla Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. monticola Musaev and Zeiniev, 1977: 54	*nomen nudum*
H. moruony Mello and Braz de Sá, 1916: 734	*nomen dubium*
H. motasillae Zeiniev, 1975b: 87	*nomen nudum*
H. motasillae Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. muscicapa Musaev and Zeiniev, 1977: 56	*nomen nudum*
H. myophonus Musaev and Zeiniev, 1977: 54	*nomen nudum*
H. nascimentoi Tendeiro, 1947: 330	*incertae sedis*
H. oenante Musaev and Zeiniev, 1977: 54	*nomen nudum*
H. otus Musaev and Zeiniev, 1977: 57	*nomen nudum*
H. pastor Musaev and Zeiniev, 1977: 55	*nomen nudum*
H. perdix Musaev and Zeiniev, 1977: 57	*nomen nudum*
H. phoenicurus Musaev and Zeiniev, 1977: 54	*nomen nudum*
H. piresi Son, 1960: 783	*nomen dubium*
H. podicepsi houssayi Jörg, 1931: 1153	*nomen dubium*
H. raymundi Mello and Raimundo, 1934: 97	*nomen dubium*
H. rotundus Oliger, 1952: 411	*nomen nudum*
H. rotundus Oliger, 1956: 329	*species inquirenda*
H. rouxii Novy and MacNeal, 1904a: 933	*incertae sedis*
H. santosdiasi Son, 1960: 783	*species inquirenda*
H. savianae Tendeiro, 1947: 319	*incertae sedis*
H. sittae Zeiniev, 1975b: 87	*nomen nudum*
H. sittae Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. sternae Zeiniev, 1975b: 87	*nomen nudum*
H. sternae Musaev and Zeiniev, 1977: 52	*nomen nudum*
H. sylvia Musaev and Zeiniev, 1977: 56	*nomen nudum*
H. tephrodornis Mello, 1935b: 473	*species inquirenda*
H. vilhenai Travassos Santos Dias, 1953: 86	*nomen dubium*
Leucocytozoon alaudidae Musaev and Zeiniev, 1978: 95	*nomen nudum*

1	2
Leucocytozoon anellobiae (Cleland and Johnston, 1911): 420	*species inquirenda*
L. apiaster Zeiniev, 1975b: 87	*nomen nudum*
L. apiaster Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. circus Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. falco Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. galli Ivanić, 1937a: 12	*incertae sedis*
L. janovyi Kairullaev, 1992: 70	*nomen nudum*
L. lanii Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. minchini Yakunin, 1976: 167	*nomen nudum*
L. motacilla Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. musajevi Zeiniev, 1975b: 87	*nomen nudum*
L. musajevi Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. onqtis Yakunin, 1976: 167	*nomen nudum*
L. oriolus Musaev and Zeiniev, 1978: 96	*nomen nudum*
L. ralli Galli-Valerio, 1930: 216	*species inquirenda*
L. sitta Musaev and Zeiniev, 1978: 95	*nomen nudum*
L. turtur Ulugzadaev, 1982: 366	*nomen nudum*
L. vulgaris Zeiniev, 1975b: 87	*nomen nudum*
L. vulgaris Musaev and Zeiniev, 1978: 96	*nomen nudum*
L. zasukhini Yakunin, 1976: 167	*nomen nudum*
Plasmodium arachnidi Huang, Huang and Jiang, 1995: 352	*species inquirenda*
P. bambusicolai Huang and Huang, 1995: 385	*species inquirenda*
P. conturnixae Sarkar and Ray, 1969: 353	*nomen nudum*
P. corradettii Laird, 1998: 84	*nomen dubium*
P. danilewskyi (Grassi and Feletti, 1890) emend. Castellani and Chalmers, 1910: 297	*incertae sedis*
P. gallinulae Mello, 1935a: 353	*incertae sedis*
P. gambeli Stabler and Kitzmiller, 1969 (according to Bennett *et al.*, 1982b: 104)	*nomen nudum*
P. herodiadis Mello, 1935a: 351	*species inquirenda*
P. holti Stabler, Holt and Ellison, 1965: 49	*nomen nudum*
P. jiangi He and Huang, 1993: 129	*species inquirenda*
P. lagopi Oliger, 1956: 329	*species inquirenda*
P. lairdi Corradetti, Neri, Palmieri, Verolini, Giuliani and Scanga, 1961: 99	*nomen nudum*
P. malariae raupachi Partsvanidze, 1914: 86	*incertae sedis*
P. manwelli Stabler and Datel, 1959: 59	*nomen nudum*
P. noctuae (Celli and Sanfelice, 1891), emend. Bennett *et al.*, 1982b: 223	*species inquirenda*
P. praecox see *Haemamoeba praecox*	
P. rousseloti see *Haemamoeba rousseloti*	
P. spartani Yarrington, Whitehair and Corwin, 1973: 232	*nomen nudum*
P. struthionis Fantham and Porter, 1943: 25	*incertae sedis*
P. venkataramiahii Bhaskar Rao, Devi and Bhaskar Rao, 1977: 194	*nomen nudum*

Note: The authors of the original description and the page, on which the specific name is published for the first time, are given after the specific name. Besides, the subgeneric name of malaria parasites *Garnhamella* Sarkar and Ray, 1969: 353 is a *nomen nudum*.

Appendix 2
Additional information to the Russian edition

Haemoproteus (Parahaemoproteus) bucerotis Bennett, Earlé and Squires-Parsons, 1995

Haemoproteus bucerotis Bennett, Earlé and Squires-Parsons, 1995a: 2, Fig. 1–3.

Type vertebrate host. *Tockus erythrorhynchus* (Temm.) (Coraciiformes).
Type locality. Gaborone, Botswana.
Distribution. This parasite has been recorded only in the type locality so far.
Type material. Hapantotype (No. 6451 New Series, *Tockus erythrorhynchus,* 23.06.1993, Gaborone, Botswana, coll. Herremans) is deposited in IRCAH.
Etymology. The specific name is derived from the name of the family Bucerotidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Coraciiformes whose gametocytes grow around the nucleus of infected erythrocytes, markedly enclosing the nucleus with their ends, displacing it laterally but not encircling it completely. The gametocytes adhere to the nucleus and envelope of the erythrocytes. Growing dumbbell-shaped macrogametocytes are common. The form and size of pigment granules in macro- and microgametocyte are approximately the same. The average number of pigment granules in gametocytes is greater than 15. The average width of fully grown gametocytes is less than 4 μm. The average NDR is greater than 0.5.

Development in vertebrate host
Young gametocytes were not seen in the hapantotype; only forms larger than the erythrocyte nucleus are recorded.

Macrogametocytes (Fig. 341, *1–7*; Table 176). The cytoplasm is granular in appearance, usually contains small vacuoles; gametocytes grow around the nucleus of infected erythrocytes, markedly displacing the nucleus laterally, and enclosing it with their ends but not encircling it completely; gametocytes adhere to the nucleus and envelope of erythrocytes; the central part of the pellicle of growing gametocytes frequently does not extend to the erythrocyte envelope, causing a ‘dip’ and giving a dumbbell-like appearance (Fig. 341, *2, 3, 6*); fully grown gametocytes lose the dumbbell-like shape, are closely appressed both to the nucleus and envelope of erythrocytes and fill the erythrocytes up to their poles (Fig. 341, *5, 7*); the outline is usually even (Fig. 341, *3–5*), but occasionally also slightly wavy (Fig. 341, *1*) or slightly ameboid (Fig. 341, *2*); growing gametocytes with one or both ends ‘cut-like’ (Fig. 341, *3, 4*) are common; the ends of fully grown gametocytes are usually more or less pointed (Fig. 341, *5–7*); the parasite nucleus is compact, of variable form, subterminal in position, and is usually located close to the envelope of erythrocytes (Fig. 341, *4, 5*), but occasionally it is also seen close to the erythrocyte nucleus (Fig. 341, *3*) or even lying free in the cytoplasm (Fig. 341, *6, 7*); pigment granules are usually roundish, but

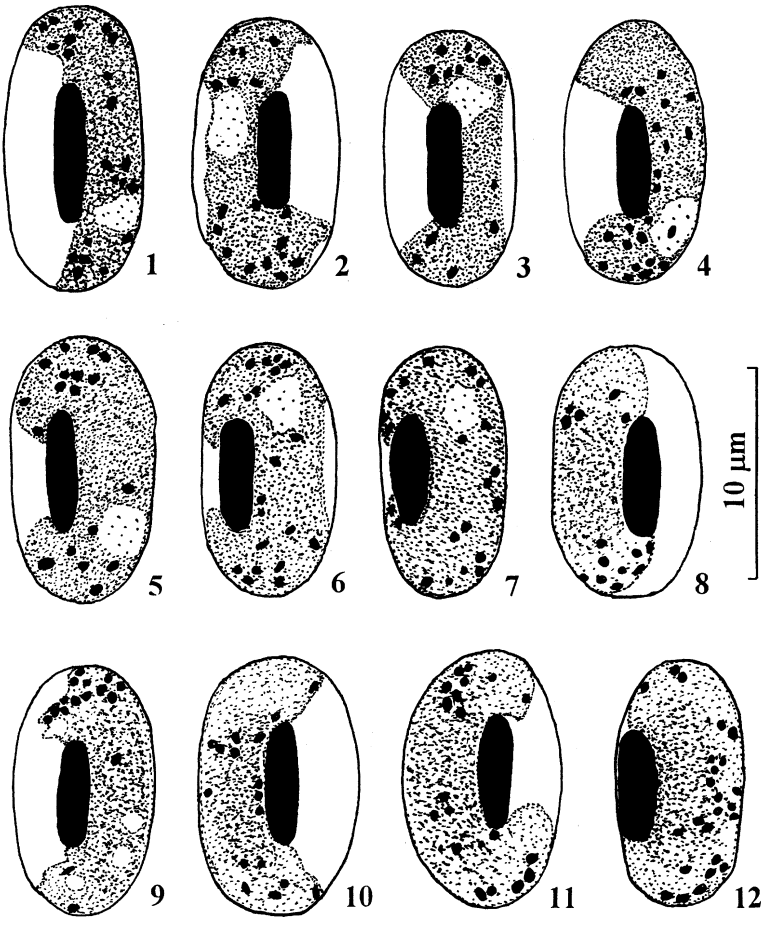

Figure 341 Gametocytes of *Haemoproteus bucerotis* from the blood of *Tockus erythrorhynchus*: *1–7* – macrogametocytes, *8–12* – microgametocytes (according to Valkiūnas and Iezhova, 2000).

occasionally are also oval, of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm.

Microgametocytes (Fig. 341, *8–12*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; large vacuole-like structures are present in some parasites (Fig. 341, *9*); the parasite nucleus is diffuse and ill-defined; microgametocytes with the ameboid outline are more common than macrogametocytes and, when present, the ameboid appearance is more evident (Fig. 341, *9*) than in macrogametocytes; dumbbell-shaped parasites are not seen; other characters are as for macrogametocytes.

C o m m e n t s. Bennett *et al.* (1995a) noted that gametocytes of *H. bucerotis* occasionally completely encircle the erythrocyte nucleus. Such gametocytes were not seen in the hapantotype by Valkiūnas and Iezhova (2000), but the parasites nearly encircling the host cell nucleus (Fig. 341, *6, 7*) are common. Thus, it is possible that the circumnuclear gametocytes may develop occasionally, but are not characteristic of this species.

Table 176 Morphometric parameters of gametocytes and host cells of *Haemoproteus* spp. (according to Valkiūnas and Iezhova, 2000).

Feature	*H. bucerotis*				*H. burhini*			
	n	lim	$\overline{X}$	*SD*	*n*	lim	$\overline{X}$	*SD*
Uninfected erythrocyte	31				31			
Length		10.4–12.6	11.3	0.5		12.3–15.4	13.2	0.7
Width		5.4–6.5	6.0	0.3		6.9–9.3	8.2	0.6
Length of nucleus		5.2–6.5	5.6	0.4		5.3–6.9	6.1	0.4
Width of nucleus		1.6–2.4	1.9	0.2		2.5–3.4	2.9	0.2
Erythrocyte parasitized by macrogametocyte	31				31			
Length		11.1–12.9	12.1	0.5		10.8–13.3	12.4	0.6
Width		5.6–7.6	6.6	0.5		6.0–8.3	7.1	0.5
Length of nucleus		5.1–6.3	5.7	0.3		3.9–5.6	4.9	0.4
Width of nucleus		1.6–2.4	1.9	0.2		2.1–2.9	2.4	0.2
Erythrocyte parasitized by microgametocyte	31				11			
Length		11.4–13.3	12.2	0.5		11.9–14.0	13.0	0.5
Width		5.8–7.4	6.7	0.4		7.0–7.9	7.4	0.3
Length of nucleus		4.8–7.0	5.7	0.5		4.9–5.6	5.1	0.2
Width of nucleus		1.5–2.2	1.9	0.2		2.1–2.7	2.4	0.2
Macrogametocyte	31				31			
Length		13.1–16.6	15.1	0.9		11.7–17.0	14.6	1.1
Width		2.2–3.6	2.8	0.4		2.6–4.7	3.3	0.5
Length of nucleus		2.3–3.8	3.0	0.4		2.1–4.5	3.2	0.6
Width of nucleus		1.5–2.8	2.2	0.4		1.4–3.4	2.5	0.5
NDR		0.4–1.0	0.8	0.1		0.5–0.9	0.7	0.1
Number of pigment granules		11–23	17.8	2.6		12–33	22.7	5.1
Microgametocyte	31				11			
Length		13.5–16.5	14.9	0.8		11.4–15.3	13.4	1.3
Width		2.8–4.3	3.5	0.4		3.1–4.0.	3.7	0.3
Length of nucleus		–	–	–		–	–	–
Width of nucleus		–	–	–		–	–	–
NDR		0.1–0.9	0.6	0.2		0.4–0.8	0.6	0.1
Number of pigment granules		13–24	19.7	2.9	31	14–23	18.7	2.3

Note: All sizes are given in micrometres.

Haemoproteus bucerotis can be easily distinguished from most species of haemoproteids parasitizing the coraciiform birds, except *H. coraciae*, by its numerous dumbbell-shaped growing macrogametocytes (Fig. 341, *2, 3, 6*). This is a distinctive character of *H. bucerotis* (Valkiūnas and Iezhova, 2000). *Haemoproteus bucerotis* can be distinguished from *H. coraciae* primarily on the basis of (i) its numerous pigment granules (about 18 in macrogametocytes on average compared with 10 in *H. coraciae*), (ii) a more smooth outline of gametocytes, and (iii) filled up poles of infected erythrocytes containing fully grown gametocytes.

Haemoproteus (Parahaemoproteus) burhini Bennett, Earlé and Squires-Parsons, 1995

Haemoproteus burhini Bennett, Earlé and Squires-Parsons, 1995a: 2, Fig. 4–6.

Type vertebrate host. *Burhinus capensis* (Lichtenstein) (Charadriiformes).
Type locality. Satara, Kruger National Park, South Africa.
Distribution. This parasite has been recorded only in the type locality so far.
Type material. Hapantotype (No. 6030 New Series, *Burhinus capensis*, 29.04.1993, Kruger National Park, South Africa, coll. Grobler, Whitfield and Oliver) is deposited in IRCAH.
Etymology. The specific name is derived from the name of the family Burhinidae to which the type host belongs.

Main diagnostic characters. A parasite of species of the Charadriiformes whose gametocytes grow around the nucleus of infected erythrocytes but do not encircle it

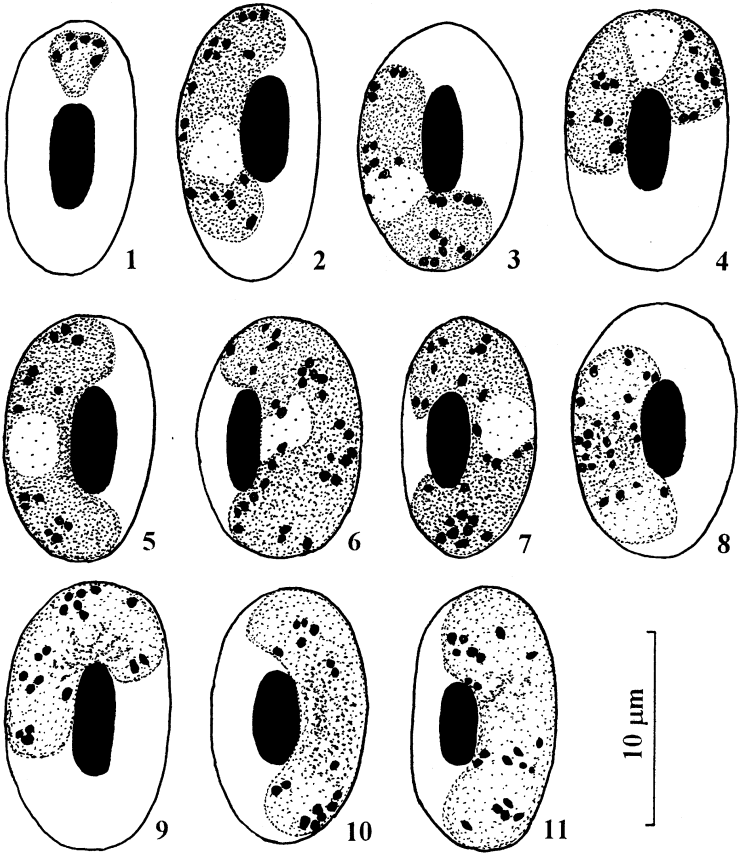

Figure 342 Gametocytes of *Haemoproteus burhini* from the blood of *Burhinus capensis*: *1* – young, *2–7* – macrogametocytes, *8–11* – microgametocytes (according to Valkiūnas and Iezhova, 2000).

completely. Pigment granules in gametocytes are of small (<0.5 μm) and medium (0.5 to 1.0 μm) size, the average number is about 20 per gametocyte.

Development in vertebrate host

Young gametocytes (Fig. 342, *1*). Only four earliest forms were recorded in the hapantotype, and three of them were seen in a polar position in infected erythrocytes; the outline is even.

Macrogametocytes (Fig. 342, *2–7*; Table 176). The cytoplasm is granular in appearance; vacuoles are not seen; gametocytes grow around the nucleus of infected erythrocytes, displacing the nucleus laterally and enclosing it with their ends but not encircling it completely; growing forms, which are located asymmetrically in the erythrocytes (with one end flexing around the erythrocyte nucleus more than another) (Fig. 342, *2–4*), are frequently seen, and are characteristic of this species; growing gametocytes, taking a polar position in the erythrocytes (Fig. 342, *4*), are common; fully grown gametocytes take a lateral position to the nucleus of erythrocytes, are usually closely appressed both to the nucleus and envelope of the erythrocytes and fill the erythrocytes up to their poles (Fig. 342, *6, 7*); the outline is usually even; the parasite nucleus is compact, ovoid or irregular in shape, and usually occupies a median or submedian position; pigment granules are usually roundish but occasionally oval, of small (< 0.5 μm) and medium (0.5 to 1.0 μm) size, randomly scattered throughout the cytoplasm and demonstrate a tendency to be located in pairs (Fig. 342, *3–7*); infected erythrocytes and their nuclei are slightly atrophied in length and width in comparison to uninfected ones.

Microgametocytes (Fig. 342, *8–11*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the parasite nucleus is ill-defined; other characters are as for macrogametocytes.

Comments. *Haemoproteus burhini* is clearly distinguishable from the other species of haemoproteids parasitizing the charadriiform birds on the basis of the following characters. First, fully grown gametocytes of *H. contortus, H. larae*, and *H. scolopaci*, which also parasitize the charadriiform birds, completely encircle the nucleus of infected erythrocytes, but gametocytes of *H. burhini* do not. Second, gametocytes rotating the erythrocyte nucleus 90° to the normal axis (the main feature of *H. rotator*) and gametocytes possessing large (1.0 to 1.5 μm) pigment granules (the main feature of *H. abdusalomovi*), are not present in *H. burhini*. It should be noted that the growing gametocytes, which take asymmetric positions in the erythrocytes (Fig. 342, *3, 4*), are common in the hapantotype, and are characteristic of this species (Valkiūnas and Iezhova, 2000).

It is important to note that, together with the numerous typical gametocytes described above, the hapantotype slide of *H. burhini* contains about 15% of gametocytes which are observed at different stages of rounding up as well as escaping from the host cells and can even be seen free in the plasma (see Valkiūnas and Iezhova, 2000). Furthermore, some gametocytes were seen not to adhere to the nucleus and (or) envelope of the erythrocytes (Fig. 343, *1–3*), and not to fill the erythrocytes up to their poles (Fig. 343, *4*). It seems that the hapantotype slide was not dried quickly in the field, and this induced the changes in the gametocytes due to the onset of gametogenesis. This is a common and well known phenomenon in haemosporidian parasites. If this hypothesis is correct, only the early stages of gametogenesis are present in the hapantotype because there is no evidence of exflagellation, and typical gametocytes, which are not influenced by the gametogenesis (see Fig. 342) are common in this blood film. Unfortunately, at present, only one hapantotype slide of *H. burhini* is available for investigation. It is likely that *H. burhini* is a distinct species, but additional material is required to make sure whether the gametocytes shown in Fig. 343 are typical of this species and the parasite is a pleomorphic one, or these forms have appeared as a result of the onset of the gametogenesis, and thus should be excluded from the species definition.

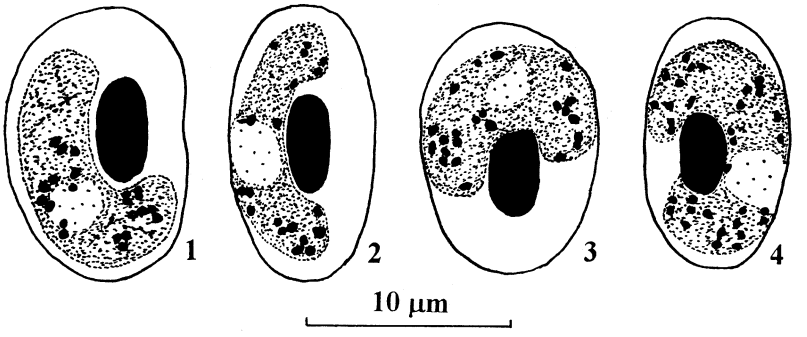

Figure 343 Macrogametocytes of *Haemoproteus burhini*, which are not considered typical for this species, from the blood of *Burhinus capensis*:
1 – gametocyte lying free in the cytoplasm and touching neither the nucleus nor the envelope of the erythrocyte; *2* – gametocyte not touching the nucleus of erythrocyte; *3*, *4* – gametocytes not filling the erythrocytes up to their poles.

Haemoproteus (Parahaemoproteus) iwa Work and Rameyer, 1996

Haemoproteus iwa Work and Rameyer, 1996: 489, Fig. 1.

Type vertebrate host. *Fregata minor* (Gmelin) (Pelecaniformes).
Type locality. Laysan Island, Hawaii, USA (25°46′ N, 171°44′ W).
Distribution. This parasite has been recorded only in Hawaii so far. Unidentified *Haemoproteus* sp. was also recorded in *Fregata minor* and *F. ariel* from Aldabra Atoll in the Indian Ocean. Thus, it is likely that the range of this parasite is wider.
Type material. Hapantotype (*Fregata minor,* 11.11.1993, Laysan Island, Hawaii) and parahapantotypes (32 blood films, March 1994, Laysan Island and Tern Island, Hawaii, other data are as for the hapantotype). The place of deposition of these preparations was not specified in the original description. Parahapantotypes (No. G212808, G212809, G212810, other data are as for the other parahapantotypes) are deposited in IRCAH.
Etymology. The specific name refers to the Hawaiian name for the type vertebrate host (iwa).

Main diagnostic characters. A parasite of species of the Pelecaniformes whose fully grown gametocytes grow along the nucleus of infected erythrocytes and slightly enclose the nucleus with their ends, they displace the nucleus laterally but do not encircle it completely. The nucleus of macrogametocyte is usually median in position. Pigment granules are of small size (< 0.5 μm) and dust-like in appearance.

Development in vertebrate host
Young gametocytes. Only two earliest gametocytes were recorded in the type material. They were roundish and irregular, about 2 μm in diameter and contained from one to four minute pigment granules.

Macrogametocytes (Fig. 344, Table 177). The cytoplasm is finely granular in appearance, frequently containing several clear small vacuoles; a large vacuole can be seen occasionally in some gametocytes; valutin granules are not numerous, red-colour, minute-size, and markedly obscuring pigment granules; gametocytes grow along the nucleus of infected

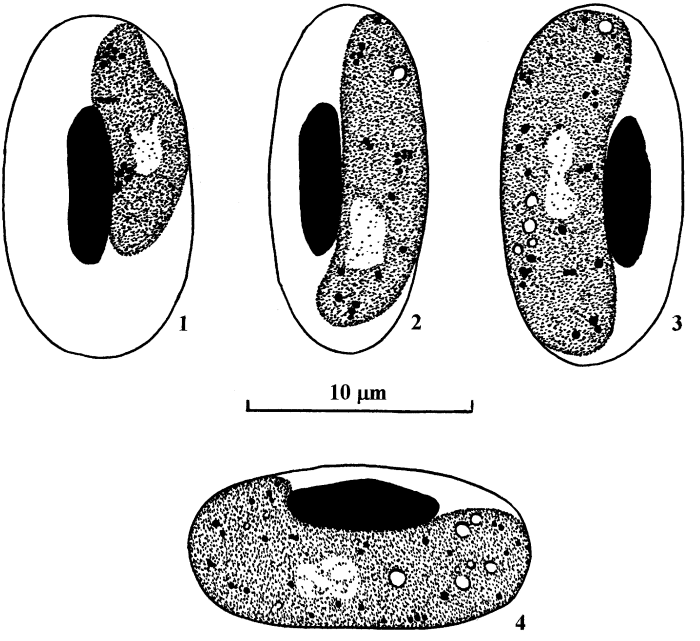

Figure 344 Macrogametocytes of *Haemoproteus iwa* from the blood of *Fregata minor*.

erythrocytes, slightly enclosing the nucleus with their ends but not encircling it completely; growing gametocytes are appressed to the envelope of erythrocytes and also touch the nucleus of erythrocytes, however the contact of gametocytes with the nucleus of erythrocytes is light and the gametocytes are usually seen only slightly touching the nucleus (Fig. 344, *2, 3*); fully grown gametocytes are closely appressed both to the nucleus and envelope of erythrocytes, displace the nucleus of erythrocytes laterally, and fill the erythrocytes up to their poles (Fig. 344, *4*); the outline is even; the parasite nucleus is of variable shape and position, but more frequently it occupies a median or submedian position; pigment granules are roundish, usually of small size (<0.5 μm), and even dust-like in appearance, and thus difficult to calculate; are randomly scattered throughout the cytoplasm; sometimes the pigment granules are seen to be aggregated into solid clumps, and thus, granules of medium size (0.5 to 1.0 μm) occasionally appear (Fig. 344, *3*). An unusually high variation of the number of pigment granules in gametocytes (see Table 177) is probably due to the difficulties of their calculation.

Microgametocytes were not seen in the type material.

C o m m e n t s. *Haemoproteus iwa* is the only species of haemoproteids which has been described in birds of the order Pelecaniformes so far. It is likely that the infection in *F. minor* in Hawaii is of secondary origin from the evolutionary point of view. It is not clear how this parasite appeared in Hawaii and from what bird group this parasite was gained. The vector of *H. iwa* is also unknown. Formerly, haemoproteids were recorded only in *Columba livia* in Hawaii. The hippoboscid flies (the family Hippoboscidae) are the most likely vectors in Hawaii because other groups of blood-sucking dipterans are not present in the type locality of *H. iwa*. Thus, it is possible that this parasite may belong to the subgenus *Haemoproteus* and this hypothesis should be tested. The following peculiarities of the parasitemia recorded in 32 investigated *F. minor* should be noted: (i) the low intensity

Table 177 Morphometric parameters of gametocytes and host cells of *Haemoproteus iwa* (modified from Work and Rameyer, 1996) (*n* varies from 30 to 31).

Feature	lim	$\overline{X}$	*SD*
Uninfected erythrocyte			
Length	13.0–18.5	15.3	1.0
Width	6.0–9.0	7.7	0.7
Length of nucleus	5.5–7.5	6.7	0.6
Width of nucleus	2.0–3.0	2.4	0.3
Parasitized erythrocyte			
Length	14.0–17.5	15.8	0.8
Width	7.0–9.5	7.8	0.6
Length of nucleus	5.5–8.0	6.7	0.6
Width of nucleus	1.5–3.0	2.2	0.4
Macrogametocyte			
Length	8.5–16.0	13.7	1.9
Width	2.5–4.0	3.3	0.5
Length of nucleus	1.5–4.5	2.3	0.7
Width of nucleus	1.0–3.0	1.9	0.4
NDR	0.2–1.0	0.7	0.2
No. of pigment granules	7–32	22.0	6.0

Note: All sizes are given in micrometres.

of parasitemia which varied from one to seven gametocytes per 10,000 erythrocytes (on average 2/10,000), (ii) the absence of microgametocytes, and (iii) the extremely rare earliest gametocytes. In addition, exoerythrocytic meronts were not found in six of the naturally infected *F. minor* investigated. It is also important to note that haemoproteids were not found in Hawaii in other sea birds of the families Procellariidae, Phaethontidae, Sulidae, and Diomedeidae. Further investigation of *H. iwa* in *F. minor* is of theoretical importance for understanding the process of colonization of new vertebrate hosts by haemoproteids.

The parasitemia is low in the type material of *H. iwa.* Only several infected erythrocytes were found by the author after two hours of investigation of the parahapantotypes. Additional material is required for more detailed investigation of this species. The redescription of this parasite is also required.

Plasmodium (Novyella) forresteri Telford, Nayar, Foster and Knight, 1997

Plasmodium forresteri Telford, Nayar, Foster and Knight, 1997: 932, Fig. 1–20.

Type vertebrate host. *Strix varia* Barton (Strigiformes).
Additional vertebrate hosts. *Bubo virginianus, Buteo jamaicensis, B. lineatus, B. platypterus, Haliaeetus leucocephalus, Otus asio* are natural hosts. *Coturnix japonica* and *Anas platyrhynchos* are infected experimentally.
Vector. Natural vector is unknown. Sporogony is completed in *Culex restuans* but the ability of this mosquito to transmit the infection should be proved.

Type locality. Trenton, Gilchrist Country, Florida, USA (29°37′ N, 82°49′ W).
Distribution. This parasite has been recorded in Florida and Georgia, USA.
Type material. Hapantotypes (No. 86925, *Strix varia,* Trenton, Florida, USA) and parahapantotypes (No. 86926, *Buteo jamaicensis*; No. 86927, passage from *B. jamaicensis* to *Coturnix japonica*; No. 86928, passage from *B. jamaicensis* to *Anas platyrhynchos*) are deposited in USNPC. Parahapantotype (No. 114916, other data as for the hapantotype) is deposited in IRCAH.
Etymology. This species is named in honour of Dr. Donald J. Forrester, University of Florida, in recognition of his contribution to wildlife parasitology and wildlife diseases in Florida.

Main diagnostic characters. Mature erythrocytic meronts contain two to six merozoites but the great majority of the meronts produce four merozoites. Vacuoles are either not present in the cytoplasm of fully grown gametocytes or only a few of them can be present. Erythrocytic meronts and gametocytes, which do not touch the nuclei of infected erythrocytes, are common. Gametocytes are slender and of irregular outline, macrogametocytes are often with crenulate margins; gametocytes do not displace or only slightly displace the nuclei of infected erythrocytes laterally.

Development in vertebrate host
Young asexual and sexual blood stages have not yet been described because mixed *Plasmodium* sp. infections are common in both natural and experimental hosts studied (Telford *et al.*, 1997). Additional material is required to complete the investigation into the variability of these blood stages.

Erythrocytic meronts (Fig. 345, *1–6*) are most frequently seen in mature erythrocytes but are also present in polychromatic (nearly mature) erythrocytes; occasionally, the parasites are also seen in thrombocytes; the cytoplasm is scanty but usually visible in mature meronts; the cytoplasm is more plentiful and the nuclei are larger than in *P. rouxi*, and this is especially evident in growing meronts (cf. Fig. 261, *6*, *9* and Fig. 345, *1*, *4*); typical of *P. rouxi* bilobular ('bow-tie') binuclear meronts (see Fig. 261, *6, 7*) were not seen, but similar forms are present (Fig. 345, *1*); the nuclei decrease in size as the meronts mature; fully grown meronts are usually fan-like (Fig. 345, *2, 4, 5*) and more rarely cruciform (Fig. 345, *3*), quadrangular (Fig. 345, *6*) or oval; mature meronts contain two to six merozoites but the great majority of them produce four merozoites with means among host species ranging between 3.5 and 4.5; a few segmenters with two merozoites were observed; there is usually one pigment granule, which is small (<0.5 μm) and dark, and is usually located at the base of the 'fan' (Fig. 345, *1, 2, 4, 5*) or in the centre of cruciform parasites (Fig. 345, *3*); meronts can be seen anywhere in infected erythrocytes but are predominantly observed in a polar or subpolar position in the erythrocytes (Fig. 345, *1–6*), usually they do not touch the nuclei of erythrocytes; the influence of parasites on infected erythrocytes is usually not pronounced, but the host cell nucleus can be slightly displaced (Fig. 345, *4*); fully grown meronts (n = 84) vary from 2.0 to 6.0 μm (mean values among host species are between 3.7 and 4.8 μm) in length and from 1.5 to 4.5 μm (mean values among host species are between 2.5 and 3.4 μm) in width; the cytoplasm is sometimes visible in mature merozoites as a minute portion; merozoites rarely exceed 1 μm in diameter.

Macrogametocytes (Fig. 345, *7–9*) are usually seen in mature erythrocytes; the cytoplasm stains pale-blue, is homogeneous in appearance, and sometimes possesses a few small vacuoles; gametocytes are elongated and slender, usually lie free in the cytoplasm and touch neither the nucleus nor the envelope of infected erythrocytes (Fig. 345, *7*)*;* the forms, which adhere to the nucleus and envelope of the host cell, are also present (Fig. 345, *8*); the outline is variable but is more frequently seen to be more or less irregular or ameboid along one or

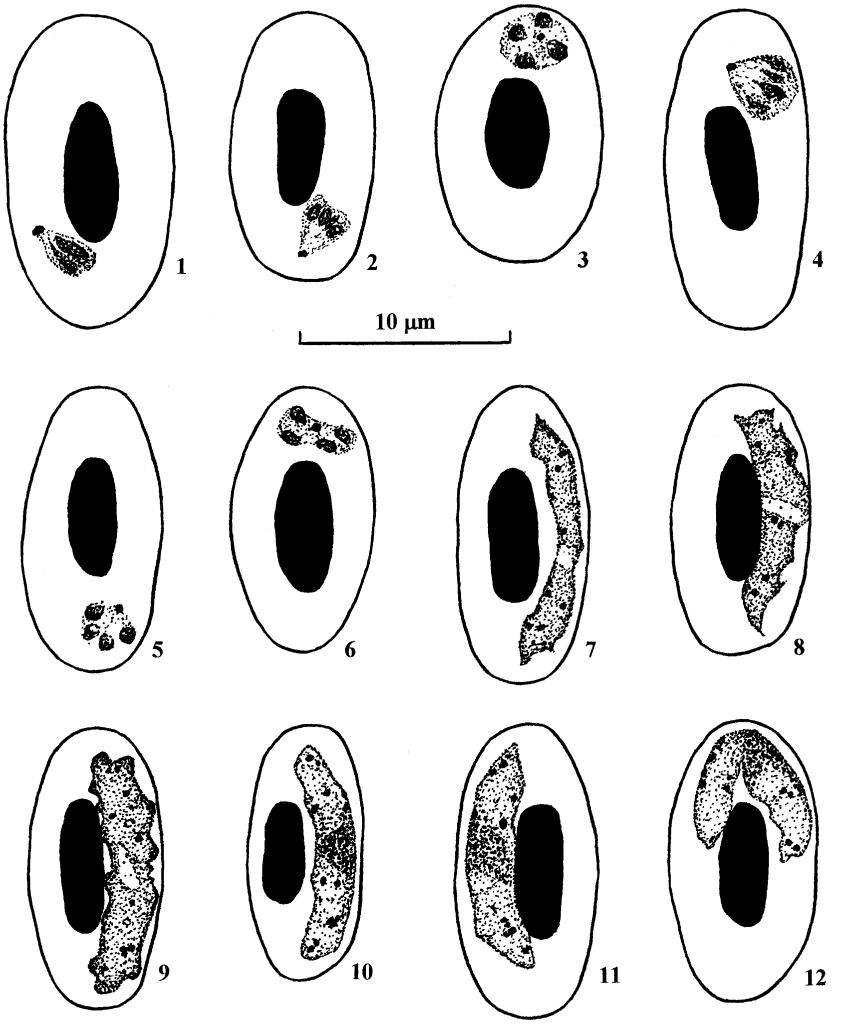

Figure 345 *Plasmodium forresteri* from the blood of *Strix varia*:
1–6 – erythrocytic meronts; *7–9* – macrogametocytes; *10–12* – microgametocytes.

both sides of gametocytes (Fig. 345, *7, 8*) and sometimes is even deeply crenulated (Fig. 345, *9*); the parasite nucleus is compact, of variable form, pale stained, usually median in position; the pigment granules are roundish, usually of small size (<0.5 μm), randomly scattered throughout the cytoplasm but sometimes also clumped into small groups; the number of pigment granules varies from 3 to 19 in different hosts with mean values among hosts species varying from 8.0 to 14.8; fully grown gametocytes usually take a lateral position to the nuclei of infected erythrocytes and do not fill the erythrocytes up to their poles (Fig. 345, *7–9*); sometimes gametocytes are observed in latero-polar or even polar positions to the host cell nucleus; the influence of parasites on infected erythrocytes is not pronounced or only slightly pronounced, and the nuclei of host cells are often slightly displaced laterally; fully grown gametocytes vary from 9 to 15 μm in length (with mean values among host species

varying between 11.5 and 13.1 μm) and from 2.0 to 3.0 μm (occasionally up to 3.5 μm) in width (with mean values among host species varying between 2.0 and 2.4 μm).

Microgametocytes (Fig. 345, *10–12*). The general configuration is as for macrogametocytes with the sexual dimorphic characters; microgametocytes only slightly differ from macrogametocytes on the basis of the staining reaction of their cytoplasm; a smooth outline is more frequently seen than in macrogametocytes, and the outer margins are often smooth in outline; the other characters are as for macrogametocytes.

Development in vector has been insufficiently investigated. Sporogony is completed in the experimentally infected mosquitoes *Culex restuans* (Telford *et al.*, 1997). Sporozoites were observed in the salivary glands on day 12 after the ingestion of gametocytes. However, these sporozoites did not produce any infection in a Pekin duck *Anas platyrhynchos*. It should be noted that Pekin ducks were easily infected by the subinoculation of infected blood. Sporogony is not completed in *Anopheles quadrimaculatus*, *Aedes aegypti, Culex erraticus, C. quinquefasciatus*, and *C. nigripalpus*.

Pathogenicity has not been investigated.

Specificity. Natural vertebrate hosts belong to the orders Strigiformes and Falconiformes. The Japanese quail *Coturnix japonica* (Galliformes) and Pekin duck *Anas platyrhynchos* (Anseriformes) are infected experimentally by the subinoculaton of infected blood from the red-tailed hawk *Buteo jamaicensis* (Falconiformes). The ability to develop in passeriform birds has not been investigated.

Comments. In the original description (Telford *et al.*, 1997), *P. forresteri* was compared in detail with *P. elongatum*. It can be easily distinguished from the latter species on the basis of (i) the smaller number of merozoites in its erythrocytic meronts and (ii) the clear preference of the meronts to develop in mature or nearly mature erythrocytes but never in erythroblasts. Exoerythrocytic merogony of *P. forresteri* has not been investigated. This parasite belongs to the subgenus *Novyella* due to its small erythrocytic meronts and elongated slender gametocytes. Based on the morphology of the blood stages, *P. forresteri* is in an intermediate position between *P. rouxi* and *P. vaughani*. The great majority of erythrocytic meronts of *P. forresteri* produce four merozoites (the character of *P. rouxi*) but the maximum number of merozoites was recorded to be six (the common character of *P. vaughani* which frequently produces four or six merozoites in its erythrocytic meronts but maximum eight). It should be noted that, according to Telford and Forrester (1992) as well as our investigation of the type material, only four merozoites were observed in the erythrocytic meronts of *P. forresteri* during its development in the type vertebrate host, *Strix varia*. Moreover, it was noted in the original description of *P. forresteri* that 'mixed *Plasmodium* infections were common in the natural and experimental hosts studied,' and thus, it is impossible to rule out that the meronts with more than four merozoites can belong to other species of the *Novyella*, first of all, to *P. vaughani* or *P. hexamerium*. Most other morphological and morphometrical characters of *P. vaughani, P. rouxi*, and *P. forresteri,* such as the size of erythrocytic meronts and gametocytes, the number and peculiarities of the location of pigment granules in erythrocytic meronts and gametocytes, the outline of gametocytes and their position in infected erythrocytes, the minor differences in the influence on infected erythrocytes, overlap and may be explained by the host-dependent variability which is a well known and still poorly investigated phenomenon for bird malaria parasites (Manwell, 1952; Garnham, 1966; Valkiūnas and Peirce, 2000). It should be noted that erythrocytic meronts and mature erythrocytic merozoites of *P. forresteri* possess proportionately more plentiful cytoplasm and larger nuclei (especially in the growing parasites) in comparison to the erythrocytic meronts and merozoites of *P. vaughani* and *P. rouxi* during their development in the type vertebrate hosts. However, the degree to which the development in different vertebrate hosts affects these character has been insufficiently studied. It should also be noted that typical 'bow-tie' binuclear erythrocytic meronts were not seen in *P. forresteri*, but they are

common in *P. rouxi* infections in passerines (see Fig. 261, *6, 7*). Further experimental investigation into the behaviour of *P. forresteri* in its vertebrate hosts, first of all, in passerines, is required to support its status. At present, it is impossible to rule out a possibility that *P. forresteri* may be a strain or subspecies of *P. rouxi* or *P. vaughani* which is adapted for development in raptor birds.

Plasmodium forresteri is a common parasite in Florida, USA. The prevalence of infection in its natural vertebrate hosts was shown to reach 4.6% by microscopic examination of blood films and 25% by the method of subinoculation of infected blood (Telford *et al.*, 1997).

Leucocytozoon (Leucocytozoon) hamiltoni Valkiūnas, Iezhova and Mironov, 2002

Leucocytozoon hamiltoni Valkiūnas, Iezhova and Mironov, 2002a: 577, Fig. 2–13.

Type vertebrate host. *Parus bokharensis* Licht. (Passeriformes).
Type locality. Western Kopetdag, about 1500 m above sea level, approximately 40 km east of Kara-Kala, southern Turkmenistan (38°25′ N, 56°45′ E).
Distribution. This parasite has been recorded only in the type locality so far.
Type material. Hapantotype (No. 3079.88 Az., *P. bokharensis*, 3.08.1991, S.V. Mironov) is deposited in CDVA. Light mixed infection with *Trypanosoma avium* and *Haemoproteus majoris* are present in the hapantotype. The material is also available on CD-ROM in the Collection of the Institute of Ecology, Vilnius University, Vilnius, Lithuania.
Etymology. This species was named in honour of the evolutionary biologist Professor William D. Hamilton, University of Oxford, UK, whose ideas on the evolutionary significance of parasitism markedly stimulated the populational research on avian blood parasites at the end of the 20th century.

Main diagnostic characters. Gametocytes develop in fusiform host cells whose nuclei are split into two more or less symmetrical portions, each located at an end of the host cell within its elongated fusiform processes.

Development in vertebrate host
Young gametocytes were not seen in the type material.
Macrogametocytes (Fig. 346, *1, 2, 4*) develop in fusiform host cells, and are ellipsoid.

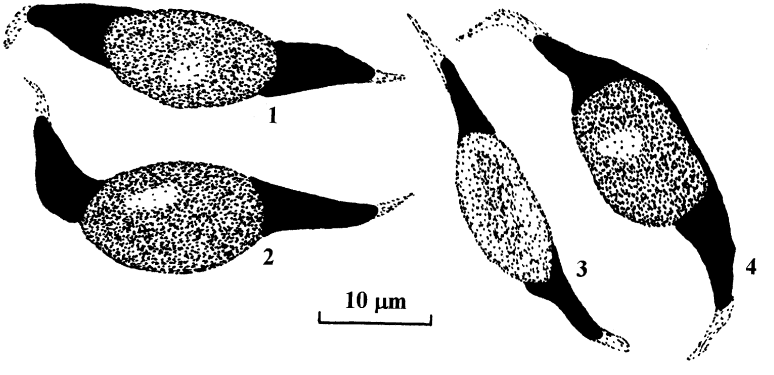

Figure 346 Gametocytes of *Leucocytozoon hamiltoni* from the blood of *Parus bokharensis*: *1*, *2*, *4* – macrogametocytes; *3* – microgametocyte.

The cytoplasm of gametocytes is heterogeneous in appearance, frequently possesses small vacuoles and volutin granules; the parasite nucleus is prominent, of variable shape and position; the cytoplasm of host cell forms two polar processes which are of variable shape and length; the nucleus of the host cell is split into two more or less symmetrical portions, each being located at an end of the host cell within its fusiform processes; each nuclear portion takes the shape of a process, and occupies part or, sometimes, all of each process so that the host cell cytoplasm is either not seen or only a minute portion of it is discernible distal to each portion of the host cell nucleus (Fig. 346, *1, 2*); occasionally, a thin band of host cell nuclear material is present along one side of the gametocyte, connecting both portions of the nucleus (Fig. 346, *4*); gametocytes vary from 12.1 to 19.8 (on average 15.6±2.0) μm in length and from 6.2 to 12.7 (8.9±1.7) μm in width; the gametocyte nucleus varies from 3.2 to 6.3 (4.4±0.7) μm in length and from 1.6 to 4.0 (2.6±0.5) μm in width. The length of the host cell–parasite complex varies from 26.2 to 48.3 (37.8±5.6) μm.

Microgametocytes (Fig. 346, *3*). The general configuration is as for macrogametocytes with the usual sexual dimorphic characters; the microgametocyte nucleus is diffuse and ill-defined; microgametocytes are smaller than macrogametocytes; other characters are as for microgametocytes.

C o m m e n t s. The nature of the host cells was not determined due to the marked influence of the gametocytes on the morphology of infected blood cells and the absence of immature parasites. In the hapantotype, the intensity of infection is 0.1%, and the ratio of macrogametocytes to microgametocytes (n = 100) is 5 : 1.

Comments on some new species of *Plasmodium*: Grès and Landau (1997) reexamined blood stages of *Plasmodium (Giovannolaia) lophurae* from the collection material of L.T. Coggeshall, E. Brumpt, and P.C.C. Garnham and concluded that mixed infections with two other species of malaria parasites were present. These parasites were described under the names *P. (Haemamoeba) coggeshalli* and *P. (Novyella) papernai* on the basis of the morphology of their blood stages. As was discussed earlier (Valkiūnas and Peirce, 2000), the description of avian *Plasmodium* spp. based solely on their blood stages should be discouraged due to the variation of the morphology of the parasites in different vertebrate hosts (see also p. 232 for discussion). The blood stages of *P. coggeshalli* exhibit similarities to *P. (H.) gallinaceum*, *P. (H.) griffithsi*, and *P. (H.) relictum*, and *P. papernai* to *P. (N.) hexamerium*, *P. (N.) dissanaikei*. To be accepted as distinct species, *P. coggeshalli* and *P. papernai* should be supported by a comprehensive package of additional taxonomic data, at least by the data on their periodicity and the peculiarities of their development in different experimental avian hosts.

Comments on an important new host record: Forrester *et al.* (2001) recorded *Haemoproteus tinnunculi* and *Leucocytozoon toddi* in *Milvago chimango* in the Neotropical zoogeographical region (southern Chile), where the transmission of these parasites takes place.

Comments on some new species of *Leucocytozoon*: An article by Adlard *et al.* (2002) describes and names three new species of avian haemosporidian parasites of the genus *Leucocytozoon*, each justified mainly by the family identity of their hosts. Such concept of the description of new species of leucocytozoids was discussed in this book in detail (see p. 76). Especially now that methods are available to describe valid taxonomic characters in

the DNA of parasites in blood films, the previous justification of the use of the host-family specificity concept in the taxonomy of leucocytozoids should be discontinued (for discussion, see Valkiūnas and Ashford, 2002). The parasites described by Adlard *et al.* (2002) are *L. ibisi* (the host is *Threskiornis molucca*, Ciconiiformes), *L. otidis* (*Ardeotis kori*, Gruiformes), and *L. podargii* (*Podargus strigoides*, Caprimulgiformes). The three names are clearly provisional, so are hardly valid. They are likely to be junior synonyms of the earlier-described morphologically similar species. *Leucocytozoon ibisi* and *L. podargii* are indistinguishable from *L. leboeufi* and *L caprimulgi*, respectively. Gametocytes of *L. otidis* in roundish host cells are indistinguishable from the same morph of gametocytes of *L. grusi.* To accept *L. otidis* as a distinct species, it should be proved that this parasite does not produce gametocytes in fusiform host cells. However, it should be noted that some species of leucocytozoids (for example, *L. simondi*) do not produce gametocytes in fusiform host cells during their development in some vertebrate hosts (in geese, see p. 790), but gametocytes in roundish host cells do develop. This also may be the case with *L. grusi* in *Ardeotis kori*.

Important information about a new species of the Garniidae: Lainson (1995) described a new genus and species of garniids, *Progarnia archosauriae*, in the blood of the South American caiman *Caiman crocodilus.* This parasite shares features both of *Fallisia* and *Garnia* spp. R. Lainson believes that this, and the antiquity of the order Crocodilia, suggests that the species of *Progarnia* might be ancestors of reptilian and avian haemosporidian parasites. That is possible. However, because haemosporidian parasites have not been recorded in other species of the order Crocodilia – cosmopolitan in tropics – except the Neotropics, it is not inconceivable that caimans gained this garniid parasite in a secondary way from other Neotropical lizards. That was likely the case with *Fallisia neotropicalis* in birds (see p. 203). Additionally, many species of avian haemosporidian parasites certainly inhabited primitive groups of birds in the secondary way (see p. 199). This way of evolution of haemosporidians cannot be excluded. Further studies are needed to understand the origin of *P. archosauriae.*

Important information about the pathogenicity of avian haemosporidian parasites: *Haemoproteus lophortyx* causes severe recurring outbreaks of haemoproteosis in the captive northern bobwhite quail *Colinus virginianus* in California between the months of May and October (Cardona *et al.,* 2002). The cumulative mortality rate among juvenile birds is over 20%. Numerous megalomeronts develop in the skeletal muscles. They are most numerous in the thigh and back muscles, and are also observed in the leg, abdominal oblique, and breast muscles. The main clinical symptoms of the infection include reluctance to move, ruffled feathers, and prostration. At autopsy, the liver and spleen are enlarged and dark. It is probable that the California quail *Lophortyx* (=*Callipepla*) *californica* is a reservoir host of the infection in the wild. The heavy disease develops in the non-adapted northern bobwhites which are bred in captivity on the endemic territory.

The elevated number of lymphocytes, heterophils, basophils, eosinophils, and monocytes and the decreased packed cell volume in the peripheral blood are recorded in the captive juvenile blue jays *Cyanocitta cristata* experimentally infected with *Haemoproteus* sp. (most likely *H. picae*) (Garvin *et al.,* 2003). Sublethal pathological changes associated with the development of exoerythrocytic meronts are observed in the liver, lungs, and spleen. The meronts were recorded in the pulmonary capillaries of one experimentally infected bird.

Haemoproteus belopolskyi, H. fringillae, and *H. lanii* reduce the survival of their vector, the biting midge *Culicoides impunctatus* (Valkiūnas and Iezhova, 2004). The mortality rate of the experimentally infected flies is highest between the first and second day post infection, indicating possible negative effects of ookinetes and early oocysts on the vector.

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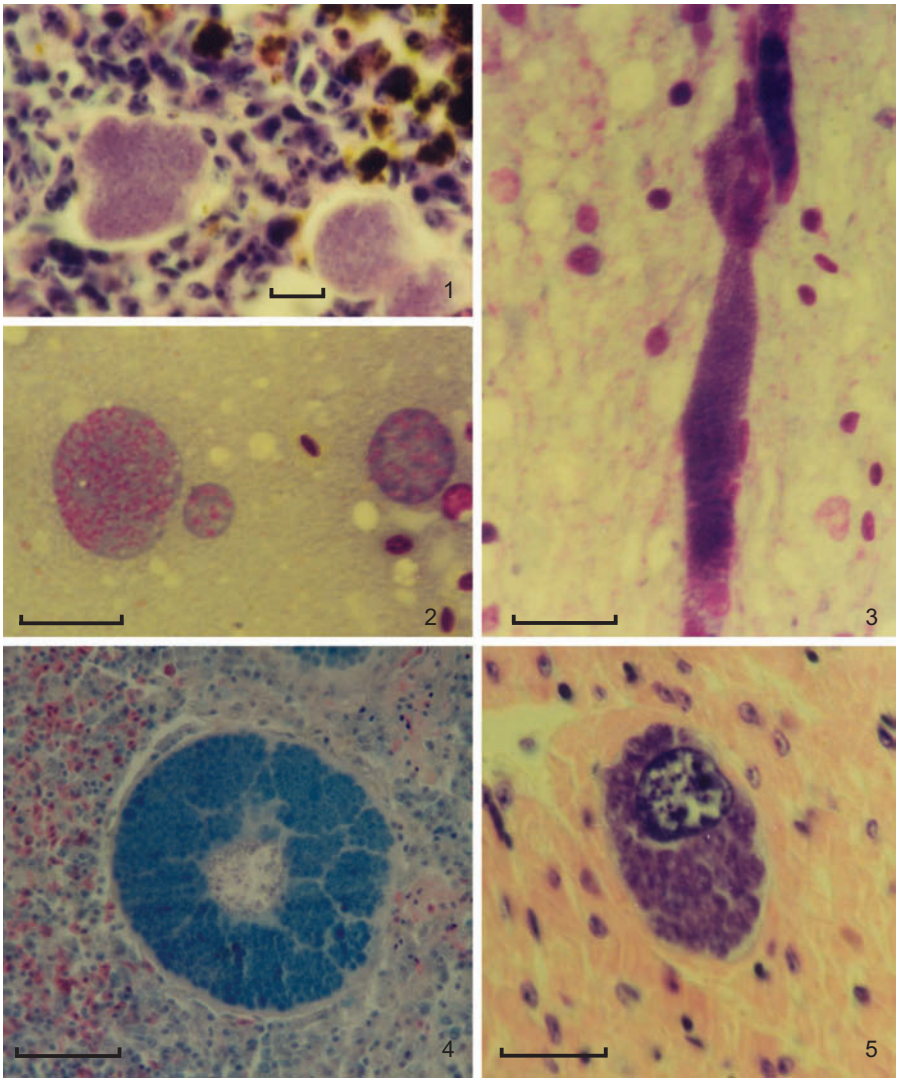

Plate I Exoerythrocytic meronts of bird haemosporidian parasites:
1 – nearly mature meronts of *Haemoproteus attenuatus* in the spleen section of *Erithacus rubecula,* note numerous nuclei of developing merozoites; *2* – three metacryptozoites of *Plasmodium garnhami* at different stages of growth in the liver smear of *Upupa epops*, note a large roundish mature meront with numerous developing merozoites and two smaller growing meronts with prominent nuclei and the plentiful cytoplasm; *3* – mature phanerozoite of *P. octamerium* in the brain smear of *Alectoris chukar*, the meront extends along a brain capillary and is overfilled with numerous completely developed merozoites; *4* – growing megalomeront of *Leucocytozoon sakharoffi* in the spleen section of *Corvus cornix,* note a capsule-like wall, a markedly enlarged centrally located nucleus of the host cell, and numerous developing cytomeres; 5 – growing megalomeront of *L. simondi* in the heart section of *Anas platyrhynchos*, note numerous developing cytomeres located around a markedly enlarged host cell nucleus. Staining: *1–3,* 5 – Giemsa followed by nuclear differentiation methods; *4* – Delafield's hematoxylin followed by eosin-azure II according to Maximow. Scale bars: Fig. *1* = 10 μm, Figs. *2*, *3*, *5* = 20 μm, and Fig. *4* = 50 μm.

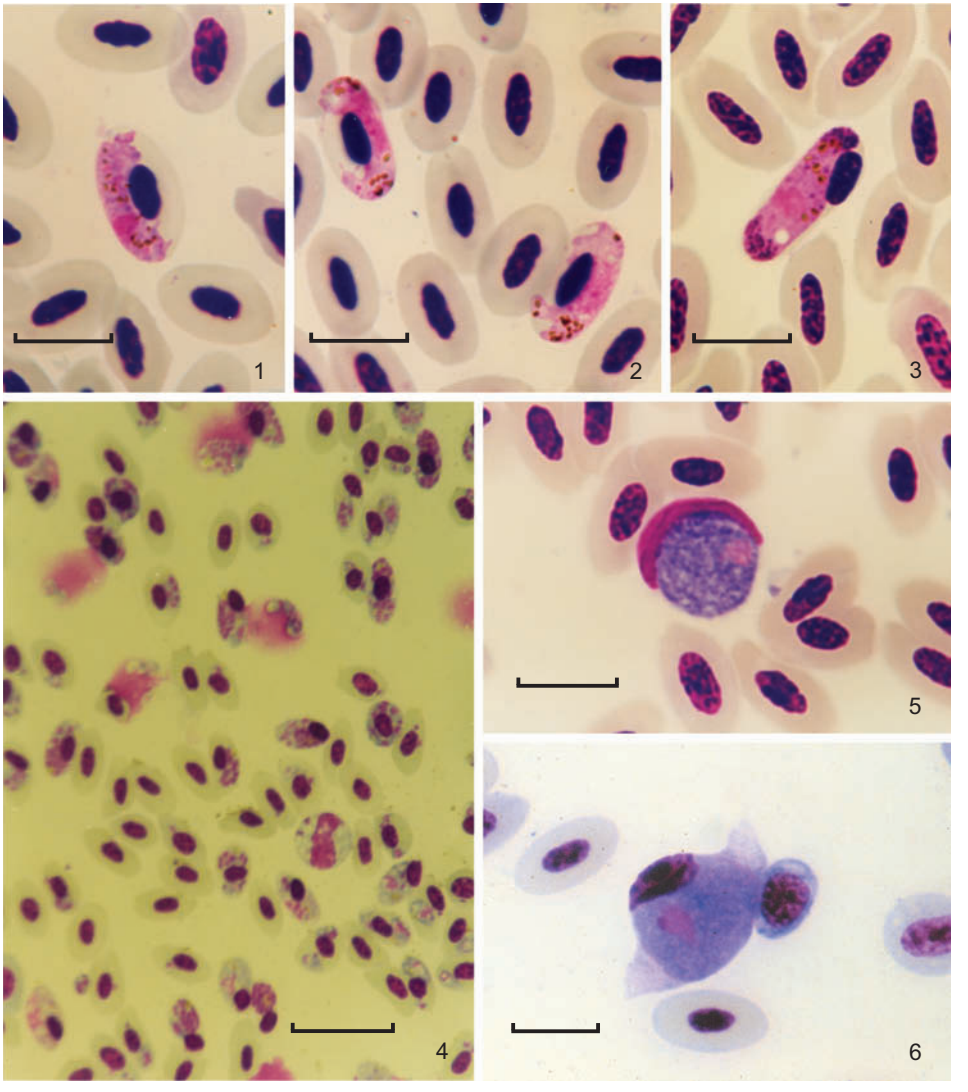

Plate II Blood stages of bird haemosporidian parasites:
1 – growing macrogametocyte of *Haemoproteus danilewskii* from *Corvus corone*, note the ameboid outline of the gametocyte and a prominent compact nucleus which is located off-centre; *2* – two mature microgametocytes of *H. belopolskyi* from *Hippolais icterina*, note the ameboid outline of the gametocytes and the large diffuse centrally located nuclei; *3* – mature macrogametocyte of *H. gavrilovi* from *Merops apiaster*, note the markedly displaced nucleus of the infected erythrocyte, the clumps of valutin granules at the ends of the gametocyte, and a prominent clear vacuole in the cytoplasm of the gametocyte; *4* – heavy infection of *Plasmodium gallinaceum* from domestic chicken, numerous trophozoites, erythrocytic meronts and gametocytes at different stages of growth are present; *5* – macrogametocyte of *L. sakharoffi* in a roundish host cell from *Corvus cornix*, note the band-like host cell nucleus which extends approximately 1/2 of the circumference of the gametocyte; *6* – macrogametocyte of *L. toddi* in a fusiform host cell from *Accipiter nisus*, note the cap-like nucleus of the host cell, the red-stained gametocyte nucleus with a prominent nucleolus and two short cytoplasmic fusiform processes of the host cell. All preparations are Giemsa stained. Scale bars: Figs. *1–3*, *5*, *6* = 10 μm, and Fig. *4* = 20 μm.

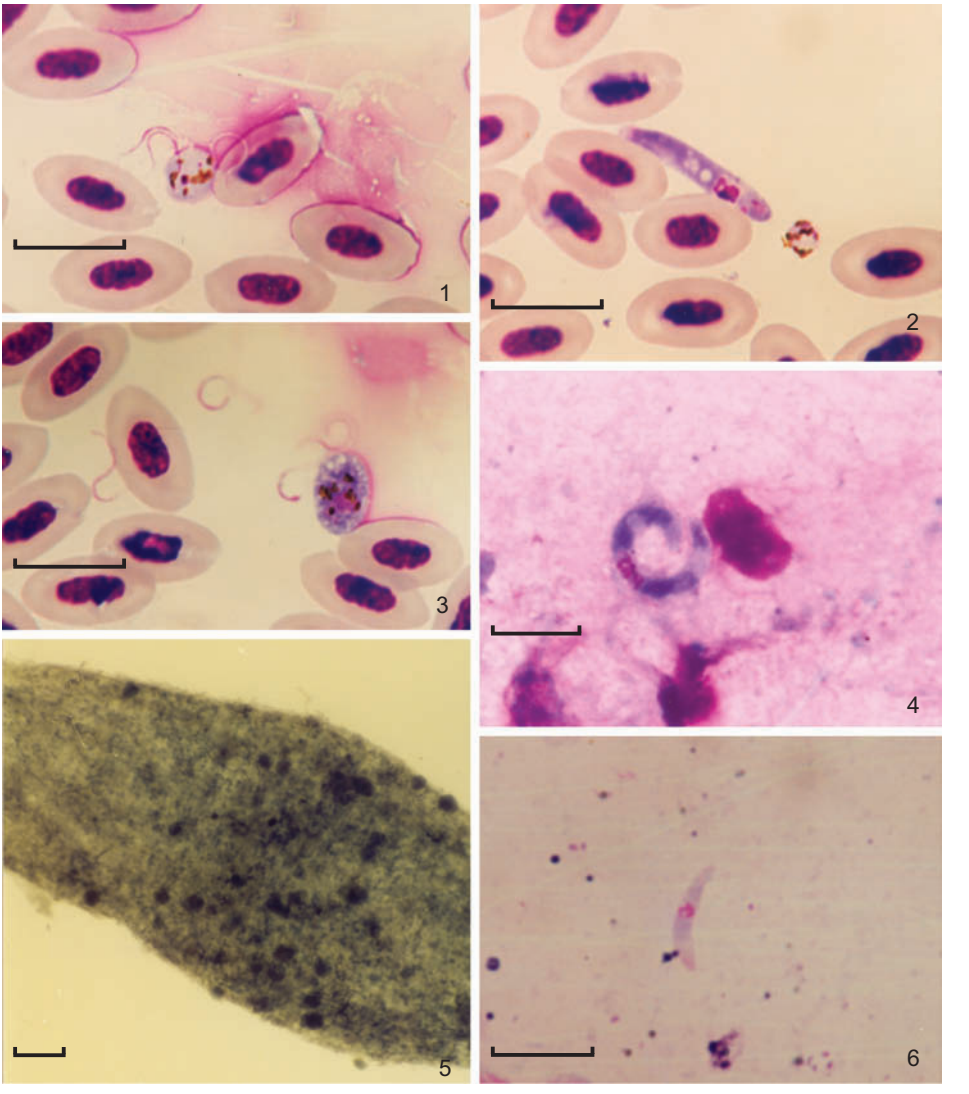

Plate III Vector stages of bird haemosporidian parasites:
1 – exflagellation of *Haemoproteus belopolskyi in vitro*; *2* – mature ookinete of *H. fringillae in vitro*, note a clear large 'vacuole' in the cytoplasm of the parasite and a prominent roundish residual body located near the posterior end of the ookinete; *3* – several elongated microgametes and a roundish macrogamete of *H. belopolskyi in vitro*; *4* – mature ookinete of *H. balmorali* from the midgut of *Culicoides impunctatus*, note two prominent 'vacuoles' in the cytoplasm of the parasite; *5* – midgut of *Culiseta morsitans* with numerous oocysts (dark roundish bodies) of *Plasmodium circumflexum* at different stages of their development including fully grown ones; *6* – sporozoite of *H. fringillae* from the salivary glands of *Culicoides impunctatus*. All preparations are Giemsa stained except *5*, which is mercurochrome. Scale bars: Figs. *1–4*, *6* = 10 μm and Fig. *5* = 100 μm.

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