Primate Anatomy
An Introduction

THIRD EDITION

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To all those in the world who love peace and the truth
To my family—Elwyn, Cornelia, Verne, Erik, Erin,
and David Brenton
And to my many friends, who have always supported me

Carl Vogt, Marmoset, 1867.

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Foreword to the Second Edition

It is a pleasure and an honor to be asked to write the foreword to the second edition of *Primate Anatomy: An Introduction* by Friderun Ankel-Simons, a dear friend for nearly thirty years.

Anyone attempting to survey the comparative anatomy of primates has my highest respect for a task that can only be described as daunting, if not impossible. Since introductory books on the anatomy of the best known species, *Homo sapiens*, fill hundreds of pages a volume, the goal of covering all 250 or so living species in a few hundred pages requires tremendous research in an arcane literature written in many languages and then draconian summarization. However, any attempt at balance is further undermined by the fact that the anatomy of many species is virtually unknown and for others the coverage is very uneven. We can only hope that many of these poorly known species can be studied before they become extinct.

Yet these gaps in the primary literature only emphasize the need for a general book on this subject. Students of both living and fossil primates, indeed anyone interested in understanding ourselves, in our biological context, need a book that summarizes what is known of primate anatomy in a readily accessible form. The longtime classic, Le Gros Clark's 1963 *Antecedents of Man*, has long been out of print and Dr. Ankel-Simons's first edition is nineteen years old now.

Other attempts to cover this material such as the largely unavailable *Primatologia, Handbook of Primatology*, are far too specialized for student readers, as are the many edited books and papers on specialized topics.

In writing this book, Dr. Ankel-Simons brings an impressive set of credentials and diverse experiences. Originally trained as a marine biologist, she has the biologist's ability to see humans and other primates in the context of the whole animal kingdom. However, she subsequently received her primatological training at the Anthropological Institute of Zürich, Switzerland, under the tutelage of the great Adolph Schultz, who contributed more to our knowledge of primate skeletal anatomy than anyone before or since. She taught primatology for seven years at

the institute of anthropology in Zürich, and in recent decades has held positions at Yale University, Brown University, Duke University, and the Duke Primate Center, and gained considerable knowledge about both living and fossil primates through research in Egypt and Madagascar.

In this new edition, Dr. Ankel-Simons has brought all of her experience to bear and produced a worthy successor to her first edition and a book that will be valued by students and professionals for many years.

John G. Fleagle
Department of Anatomical Sciences
State University of New York at Stony Brook

Preface

> *"Whatever my hearers might do, I myself always learned sometimes by lecturing. And to those who have experience of what a heart-breaking business teaching is—how much the can't-learns and won't-learns and don't-learns predominate over the do-learns—*(sic) *will understand the comfort of that reflection."*
>
> Thomas Henry Huxley (1896)

We humans are classified together with our closest relatives among living things: Lemurs, lorises, galagos and tarsiers, monkeys of the New and Old Worlds, lesser apes or gibbons, greater apes, and humans are all members of the mammal order Primates. The biological science studying humans together with their mammalian relatives is called **primatology**.

Primatology really only exists because mankind has a unique place within the order Primates. No human would pay any more attention to this order of mammals than to any other group of living creatures were it not for our unique interest in understanding our own place in biological nature.

It has been a long time since biologists drew their phylogenetic trees by hand and the results looked like the real thing. Ernst Haeckel's tree (1874) is a beautiful example (Figure 1). Today such "trees"—now also known as cladograms—are constructed by computers and look like stick figures. They are far removed from reality.

Whether we have made much progress since real trees depicted phylogenetic concepts is an important question that we should never forget to keep asking ourselves. Somehow it seems important that we keep in mind that phylogenetic trees used to be real, not abstract. Today, primatology should endeavor to stay close to the biological nature of all primates, humans included. Cladistic stick "trees" are unnatural for various reasons. Biochemical particles such as DNA molecules are infinitely tiny and not alive when they are studied. These modern entities are far removed from the reality and the magic of real life, the magic of real trees, and the magical beauty of the diademed Sifaka, whose likeness is on the cover of this volume. So let us not neglect nature's reality. Let us always

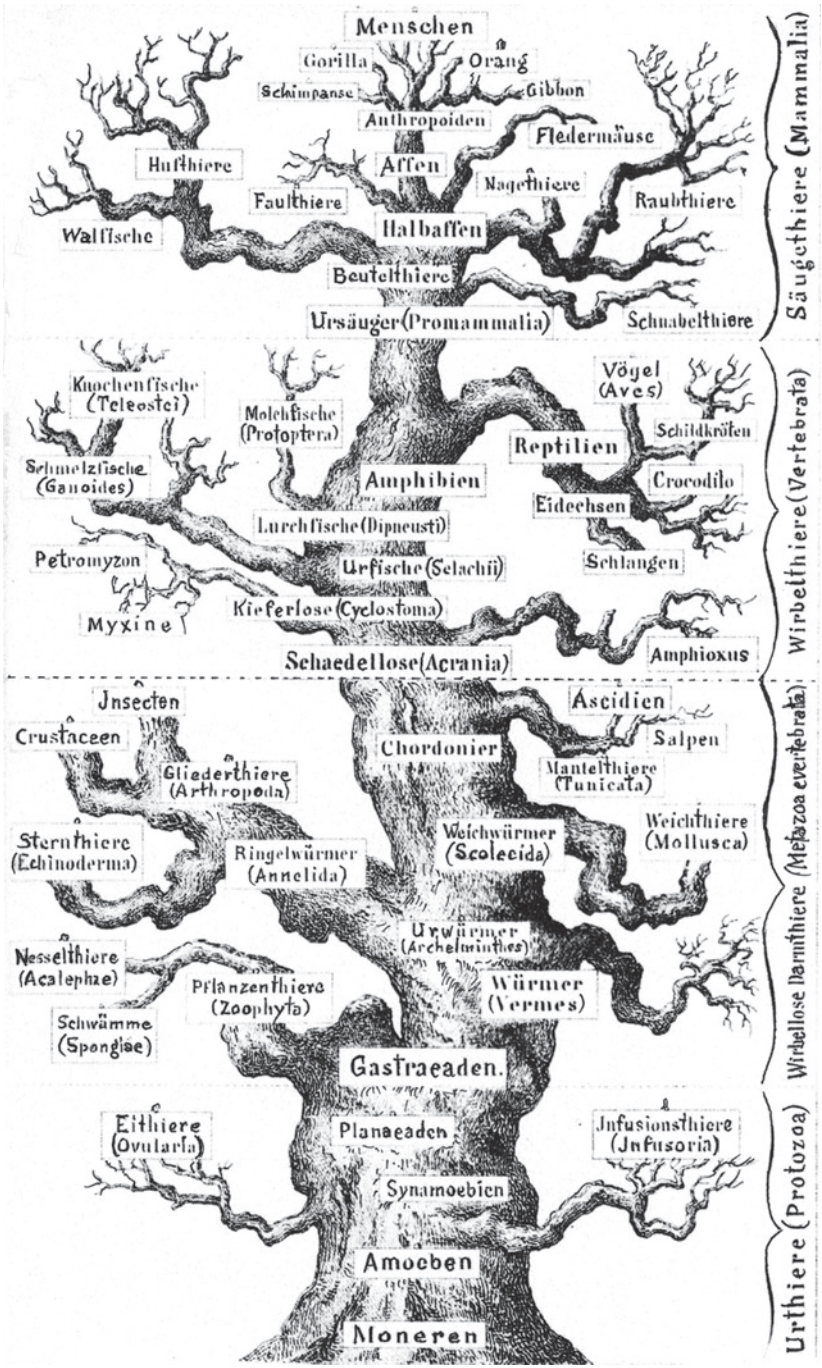

Figure 1 An ancient amazing tree, depicting human phylogeny at the time, hand drawn by Ernst Haeckel, 1874.

remember that we are biologists who are studying living things and that we should have respect for nature.

In the following chapters I shall attempt to guide the reader through the basics of knowledge that any student of our closest relatives, the primates, must grasp to become a primatologist.

The book opens with a taxonomic list of extant primates. The list presented here does not and cannot represent absolute truth as carved in stone. Taxonomic concepts are constantly in flux, partly because new species, even new primates, are being discovered and newly described. Often new insights into relationships between genera and species can change taxonomic assignments (e.g., the placement of the enigmatic South American monkey genus *Callimico* with either callithrichids or cebids). Nevertheless, it is important that discussions of extant primate groups be placed into a clear framework of relationships and names to prevent confusion. Taxonomic changes should be introduced only when they have become properly established and are obviously reasonable: Scientific dialogues are useful only when they use the same terminology. In 2001 the excellent volume on primate taxonomy by Colin Groves was published and has become the fundamental source for any discussion about primate relationships. But since then many changes of assignments have been suggested. Taxonomy continues to be a lively topic. There has been much rearranging of systematic assignments and naming of new taxa since January 2000, when the second edition of *Primate Anatomy: An Introduction* was published.

Chapter 2 introduces the reader to perpetual complications of taxonomic procedures, explaining the puzzling, but widely used, cladistic terminology (as it originated from the work of Willi Hennig (1966).

In Chapter 3 the reader will find an outline of the history and objectives of primatology. A definition of the order Primates is undertaken. Chapter 4 surveys the living primates, briefly describing and characterizing the biology and distinguishing characters of each primate genus. In Chapter 5 the anatomical details of the skull are reviewed, and Chapter 6 takes up the morphological and developmental characteristics of the brain. Chapter 7 presents the developmental and functional morphology of teeth. The postcranial skeleton together with the role of musculature and the variation of primate locomotion are detailed in Chapter 8.

Chapter 9 deals with the senses and their genetics: nose and olfaction, the oral cavity, the tongue, and the function of taste. Since the last edition of *Primate Anatomy: An Introduction* was published, great inroads have been made in understanding of function and importance of olfactory signals (Wyatt, 2003). Also, the auditory region and hearing as well as eye and eyesight are profiled in this chapter. Particularly the new understanding about function and perfection of vision among primates and their genetic manifestation have had great bearing on the need to totally revise the section on vision. Here I would like to especially

thank Pat Wright, Patrick O'Connor, Tab Rasmussen, and James Pettigrew for many helpful interactions. Later in this chapter, diarhythms and biochronology are discussed. Next, the importance of diet and nutrition and the function and differences of the primate intestinal tract are the focus. The sense and sensibility of touch conclude Chapter 9.

In Chapter 10 the nature and role of placentation and early development in primates are presented. Placentation, reproductive organs, reproduction, growth, and development are detailed in Chapter 11. Chapter 12 deals with chromosomes and blood groups of primates, and Chapter 13 again offers a survey of new developments in molecular primatology, molecular clocks, the role of mitochondrial DNA, and problems of attempting to understand phylogeny using molecular data. Chapter 14 represents one of the first endeavors to summarize the vast new world of primate genomics. A short concluding chapter provides the reader with an overview of the state of primatology and humanity today and peers into their precarious future. A bibliography and an index of important terms conclude the volume.

I shall now tell the story of *Primate Anatomy: An Introduction* and how it came about. It is a tale with some intriguing and totally unpredictable convolutions and detours.

After I had taught "all about primates" for more than seven years at the University of Zürich, I decided to compile and consolidate as much primatological information as possible and to make it easily accessible. The result was the first German language *Introduction to Primatology* (Ankel, 1970). Then and now much of what I have learned and know about primates came from the never-ending and enjoyable dialogue with my students, first in Europe, and later in the United States. This exchange still continues. Even today much crucial information about living primates remains scattered randomly in professional journals and specialized books. Access is therefore often too burdensome and costly for teachers and students alike. Even though much information is now available on the Internet, scientific volumes and journals have become forbiddingly expensive. When I started to assemble the information that I had gathered over years of teaching, no survey of living primates was available in German. A year after publication of the small volume *Einführung in die Primatenkunde*, I came to the United States and was asked if my German *Introduction to Primatology* might be translated into English. There was no English textbook like it dealing with the basics of primatology. After lengthy negotiations about a possible translation, it became evident that a new and more detailed and up-to-date book would be the better solution. After signing a contract with the College Division of Macmillan Publishers in New York, I set to work. The textbook was scheduled to be published in the Macmillan Series in Physical Anthropology. Soon, however, the progress of this endeavor was slowed by such important events as marriage and the births of two children. Inasmuch as I am convinced

that infant human primates need the devoted and undistracted attention of a mother, time to write a book about primates took a backseat to providing a solid and functional family life for a while. Yet finally the first edition of the book that, by necessity, was produced in an on-and-off fashion was published in 1983. However, an unanticipated and bizarre development caused the book's premature demise.

The Macmillan press had encountered serious financial problems in the early 1980s and, in November 1988, after an extended financial struggle, was sold to Robert Maxwell, a British tabloid tycoon. Allegedly Maxwell paid $2.6 billion for that prestigious New York publishing house, Macmillan, even though not a penny of the price came from his own fortune. It was all borrowed money (Thomas and Dillon, 2002).

One of the first of Maxwell's publishing decisions was to close the Macmillan College Division, and the book, among other volumes in the series, landed in secondhand bookstores. College textbooks were of no particular interest to Maxwell. And before long Robert Maxwell drowned mysteriously: He allegedly fell off his yacht while sailing alone. Soon it became known that he had also been drowning in financial problems at the time.

The impact of this drama was to thrust the book out of print.

For several years and with chagrin I accepted as fact that my primate book had been terminated, and other interests took over. After a time, however, I began to receive urgent and increasingly frequent requests from colleges and universities to give permission for duplication of the book. Many colleagues and students voiced their hope that I would rewrite and publish a second edition.

In 1994, with the never-tiring encouragement of my husband, Elwyn L. Simons, and friends and colleagues, I decided to find out whether any publisher would be interested in publishing a new, totally rewritten and expanded version of the 1983 primate book. Thanks to the efforts and assistance of Dr. Charles Crumly and the inspiring reassurance and support of my dear friend Tab Rasmussen, I was able to sign a contract with Academic Press.

The process of rewriting the book began. My only good excuse for any delay was the fact that this book has been entirely a one-woman endeavor: Text, ideas, almost all illustrations, as well as the typing have been produced by me alone. Any author could spend an entire lifetime writing a textbook about our intriguing and fascinating relatives, the primates. There is constantly something new, exciting, and different that could be included. But every author must find the right moment when it is time to say it is done. This time has now arrived for the third edition.

I hope that all those who teach primatology with the help of this book will achieve teacher-student relationships of mutual respect, that is, of the love for teaching and learning together. Teaching and learning, even though not always

easy, should be a mutually rewarding and inspiring adventure. I have all too often encountered university, college, and high school teachers whose uncaring arrogance hurt and permanently destroyed their outstanding students' interest and inquisitiveness.

Though I do claim this book for my very own production and as I am taking responsibility for all of it, many others helped the project forward. My family, many friends, and many colleagues, including many of my students, all in some way or another aided and supported this work. Much of the initial impetus came from my students in Switzerland, in Germany, at Yale and Brown Universities, as well as at Duke University. My students have inspired me in much of what I have to say today. I cannot possibly name them all.

A large group of living primates, human and non-human alike, have obliviously provided me with insights and many opportunities to learn. These individuals have taught me most of what I know. Among much else they have shown me that their lives are above and beyond much of what is written about them in scientific publications. I often feel (and have also told my students) how it is a shame that non-human primates are unable to read all the papers and books written about them. Were they able to read about the things that they are supposed to be doing, they would well understand how they all too often do not conform to the tales that are written about their way of life. Perhaps they would feel indignant. I hope that I have not betrayed their anonymous trust and that I have portrayed them properly.

We humans must now fear for the primates' chances to survive the unstoppable, all-consuming tidal wave of human population increase. As the one abundant species of primates rapidly overcrowds, mindlessly exploits, and overwhelms our planet, the non-human primates and many other living things are vanishing rapidly.

As things stand now there are too many of us humans, and we are destroying our closest relatives rapidly, just as we crowd out their habitats. We humans appear to be helpless, unable to deal with this cataclysmic dilemma. Even though we believe that we ourselves are the superior beings on Earth, we are proving to be ultimately destructive, unable to learn from experience, unable to properly plan for the future, and totally lacking respect for Mother Nature's creations. It makes me wonder whether humans ever will be able to live up to their taxonomic name: *Homo sapiens*. The Latin word "*sapiens*" means wise, but are we wise enough to prevent our own destruction?

No matter what the future of humankind may be, I offer my deeply felt gratitude to many humans, friends, and colleagues alike.

Foremost, I would like to thank my family, Elwyn, Cornelia, Erik, and Verne, for their never-ending support, encouragement, patience, help, understanding, and love. Tab Rasmussen, Patricia C. Wright, and Terry Maltsberger should be singled out, for they have been more than understanding friends. Tab is a most inspired and inspiring force behind many fruitful professional discussions; he

has provided incentive, advice, constructive criticism, and ideas all along. Terry Maltsberger has scampered untiringly around zoos, helping to obtain good photographs of primates for this book. Like Elwyn, Terry has been immensely helpful with encouragement and straightening out the sometimes confounding intricacies of the English language, which, after all, is only my second language. (I am getting better at this.)

At times it can be truly vexing to write in a language one did not speak while growing up. Our son Verne told me about the Danish comedian Victor Borge, who concisely expressed it by stating: "English is not my language. I am just trying to use it."

The number of those who have assisted me in various ways is increasing. I would like to mention by name John M. Allman, David Anderson, Summer Arrigo-Nelson, Edilio Nacimento Becerra, Diane Brockman, Anne Burroughs, Jennifer Campbell, Anita Christen, Anja Deppe, Luke Dollar, John Fleagle, Jörg Ganshorn, Phil Gingerich, Ken Glander, Laurie Godfrey, David Haring, Mitchell Irvin, Karen Issler, Jukka Jernvall, Chris Kirk, Jeffrey Laitman, Coleen McCann, Russel Nord, Theresa Pope, Leila Porter, Tab Rasmussen, Marcello Rosa, James Rossie, Marcello Sánchez-Villagra, Erik Seiffert, Verne Simons, Timothy Smith, Tom Struhsaker, Michael Stuart, Linda Taylor, Donald Usery, and Priscilla Watson for their generous help with hard-to-find literature, information, or photographs. Carol Holman kindly donated the elusive volume about the "Creatures of the Dark." Tristram Wyatt also helped with insight and advice, and each has contributed in special ways and deserves my special gratitude. John Fleagle wrote the thoughtful foreword to the second edition.

Kathleen Caron did a terrific job straightening out details of molecular and cell biology. Dieter Glaser thoroughly inspected and improved the chapters on olfaction and taste. Ralph Holloway critiqued and checked the chapter on the brain for correctness. For the second edition, Charles Crumly proffered a challenge that I happily lived up to: namely to include a chapter on molecular primatology.

Jukka Jernvall suggested that the third edition must have a chapter on primate genomics, a very complex issue that I hope to have dealt with successfully. Special thanks go to Patrick O'Connor—who took on the tiring task of reading and improving the vision chapter. James Pettigrew also provided important insights and information about vision. Timothy Smith spent much time discussing olfaction and the vomeronasal organ with me and did not hesitate to share published and as yet unpublished data and figures. Patricia C. Wright played a particularly important role during the process of putting this volume together—she generously contributed her knowledge, improving the new chapters about the primate senses. Pat also provided much new data and knowledge about Madagascar and New World primates and always is ready with much thought and much appreciated encouragement.

Just when I thought I had finished the task, suddenly and out of the blue, Richard Tenaza refreshed long-forgotten memories about the fact that primates

have a third, nictitating membrane. Thank you, Richard Tenaza, for this important message that prompted me to go back and write yet another paragraph.

Finally, I would particularly like to express my gratitude to the editorial staff of Elsevier. To David Cella and Nancy Maragioglio, who approached me about the possibility of preparing a third edition of *Primate Anatomy: An Introduction*. To Kelly Sonnack, who authenticated my contract. To Tamsin Leonard, who met with me in Oxford; to Sarah Hajduk and Rogue Shindler, who both provided valuable editorial assistance; and last but not least, especially to Julie Louis from Graphic World, who never tired to provide excellent editorial advice and to take care of last-minute changes and brainstorms. My heartfelt thanks go to you all for your help, patience, excellent advice, and support: I could not have done it without you.

And finally here is the much improved third edition. Preparing this new edition I have learned uncountable new facts, and I hope that this is now reflected in the third edition of *Primate Anatomy: An Introduction*.

As all authors endeavor to profess, all and every mistake in this book should be blamed on me and me alone. This is my book, I am proud of it, and I will gladly take responsibility for it all.

Friderun Ankel-Simons
Durham, September 2006

Figure 2 The aye-aye (*Daubentonia madagascariensis*), the most remarkable of primates, from the 1863 monograph by Sir Richard Owen.

Preface to the First Edition

Many people give various kinds of help to an author during the preparation of a book. Such aid—both explicit and implicit—deserves the author's thanks.

First, I thank my students, whose inquisitive questions have always been an invaluable stimulus that has taught me more than many teachers have.

Furthermore, my gratitude goes to all those colleagues who assisted me in various ways and especially to those who read and contributed their criticism to parts of the book, namely Fredericka Oakley, Matt Cartmill, Bert Covert, Dieter Glaser, Andy Hamilton, David Pilbeam, Montrose Moses, Patricia Poorman, Len Radinsky, and Ian Tattersall. Rich Kay also helped with some library problems. My husband, Elwyn Simons, edited the manuscript and added much invaluable knowledge and advice. Ruth Nix was helpful with editorial matters.

I am also very grateful to all those who contributed photographs: Alison Richard, Ken Glander, Dieter Glaser, Christian Schmidt, Michael Stuart, and Heinrich Sprankel.

Last, my dear friend Elsa Dubois gave me support in so many ways that a very special word of thanks goes to her.

One final word about the scope of this book seems appropriate here. Because both the primate fossil record and the details of behavior of living primates have already been covered by Elwyn Simons and Alison Jolly in their respective contributions to the Macmillan Series in Physical Anthropology, no attempt is made here to duplicate any of the information included in their two volumes.

F.A.S.
New Haven, 1983

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Chapter 1

Taxonomic List of Extant Primates

New Developments
List of Extant Primates

NEW DEVELOPMENTS

The order Primates is one of the most diversified groups of living mammals, ranging from lemurs to humans. Members of the order have always been the focus of human curiosity, and many primates are astonishingly similar, both behaviorally and anatomically, to human beings, the most successful and progressive species of the order: *Homo sapiens*.

To become familiar with the wide variety and diversity of primates, it is helpful to look over the following list of taxonomic names. The rationale of beginning this book with a comprehensive list of all living primates is that an introduction to the particular taxonomic place and common name of each species will enable the reader to understand more readily the subsequent chapters. Naturally, it takes patience to become familiar with all of the primate groups, and this knowledge will only improve gradually and with time. One should become acquainted, but there is no need to memorize the list of names. These names will fall into place with increased knowledge of and interest in the primates and their characteristics.

It must be kept in mind, however, that taxonomic assignments are subject to constant change, new discovery, and discussion. The following list is the foundation and necessary frame of reference for informed discussion about primates. New discoveries can either change a taxonomic placement of known animals through new insights or add newly discovered species that were hitherto unknown to science. The astonishing increase of species in many genera can be credited to two factors: the increase of the number of primatologists in the field

worldwide who find hitherto unknown taxa and the proliferation of new assignments by primatologists who stay home and increase and change the number of species by desktop contemplations. The recent proliferation of many new species from Madagascar is nothing short of astonishing, although all too often these discoveries appear to be based more on the enthusiasm of the "discoverers" than on unambiguous morphological, genetic, and behavioral distinctions. Surprisingly however, even among living primates, true new species are still occasionally being described. For example, a new species of macaque from northern India, *Macaca munzala,* was described in 2005 (Sinha et al.). A new species from Tanzania was described as *Lophocebus kipunji* in 2005 (Jones et al.), but was reassigned to a new genus, *Rungwecebus,* by Davenport et al. (2006). This shows that some species are truly new, whereas others may either be valid or produced by excessive redefinitions, rearrangements, new rankings, and splits of formerly known taxa.

Patricia Wright and Elwyn Simons have been working in Madagascar since 1981, actively promoting conservation of the rare and endangered lemurs for the future. Both were crucially involved in opening up the magic island for international research and were soon followed by myriad others. Because of this, there can be no doubt that our knowledge about Malagasy lemurs in particular and Madagascar's natural history in general have vastly increased since that time.

The following lineup of living primates is based on the taxonomy of Simons (1972), which has been brought up to the knowledge of 1999 with the help of Patricia Wright and Elwyn Simons for prosimians, Thomas Struhsaker for colobines, and Leslie Digby for callithrichids. The list has been amended for this edition using the texts by Groves (2001) and Geissmann (2003) for all primates, Grubb et al. (2003) for African primates, Brandon-Jones et al. (2004) for Asian primates, and Wright et al. (2003) for genus *Tarsius.* Unlike Grubb et al. (2003), we are not dealing with subspecies in our lineup of living primates. The taxonomy and phylogeny of the subtribe Papionina has long been under discussion (Jolly, 2003). It appears that now the puzzle surrounding the baboons has been solved to some extent by a very interesting and thorough evaluation of cranial allometry, phylogeny, geographic distribution, and systematics of the papionins. The information has been evaluated with the help of geometric morphometric analysis landmark data and resulted in the confirmation of three genera: *Mandrillus* with two species, *Theropithecus* with one species, and *Papio* with one species, *P. hamadryas*, that has six subspecies (Frost et al., 2003). We are not listing subspecies because the taxonomic list of all primates would be too long and cumbersome for this chapter. Also the postcranial morphology and dentition of the papionins has been evaluated to reassess molecular evidence that had separated terrestrial mangabeys (genus *Cercocebus*) together with genus *Mandrillus* from

the arboreal mangabeys (genus *Lophocebus*) together with genus *Papio*. Fleagle and McGraw (2002) have established that postcranial and dental characters support a previous molecular assignment.

Additional sources for the following lineup have been Mittermeier et al. (1994) for lemurs, Rowe (1996) for all primates, Gautier-Hion et al. (1988) for the African guenons (genus *Cercopithecus*), Davies and Oates (1994) for colobine monkeys, and Baer et al. (1994) for new taxonomic insights concerning the South American owl monkey *Aotus*.

The book dealing with all extant primates (Rowe, 1996) provides detailed information about each species and is illustrated by excellent photographs. These various resources have all helped to complete the following taxonomic lineup of living primates. Their geographic distribution is shown in Figure 1.1.

Many subspecies of Malagasy lemurs and other primates have been elevated to species level (Rasolooarison et al., 2000; Groves, 2001; Brandon-Jones 2004; Thalmann and Geissmann, 2000, 2005). The "new" species are included in the lineup, although the justification for such changes in taxonomic ranking remains under discussion. New and formerly unfamiliar names are used in publications and therefore they are listed here.

LIST OF EXTANT PRIMATES

Suborder Prosimii (Illiger, 1811)
Infraorder Lemuriformes (Gregory, 1915)
Superfamily Lemuroidea (Mivart, 1864)
Family Cheirogaleidae (Gray, 1873)
Subfamily Cheirogaleinae (Gray, 1873)

Cheirogaleus (E. Geoffroy Saint-Hilaire, 1812) Dwarf Lemurs	*Cheirogaleus major*
	Cheirogaleus medius
	Cheirogaleus crossleyi
	Cheirogaleus minusculus
	Cheirogaleus ravus
	Cheirogaleus sibreei
Microcebus (E. Geoffroy Saint-Hilaire, 1834) Mouse Lemurs	*Microcebus murinus*
	Microcebus rufus
	Microcebus myoxinus
	Microcebus ravelobensis
	Microcebus berthae
	Microcebus griseorufus
	Microcebus sambiranensis
	Microcebus tavaratra

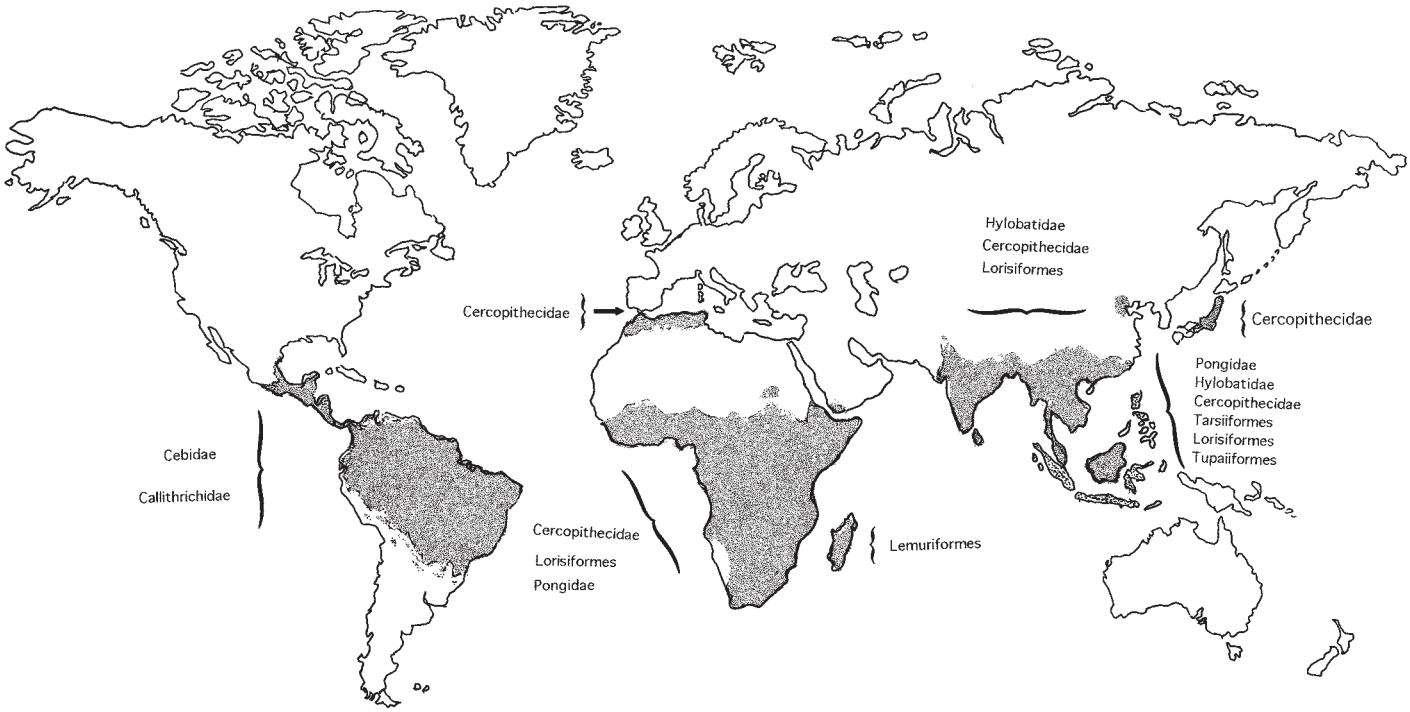

Figure 1.1 Worldwide distribution of primates: not unlike body weight data, animal distribution maps are subject to constant change resulting from human impact, newly confirmed sightings, and other unpredictable factors.

	Microcebus simmonsi
	Microcebus lehilahytsara[1]
Mirza (Gray, 1870)	*Mirza coquereli*
Coquerel's Dwarf Lemur	*Mirza zaza*[1]
Allocebus (Petter-Rousseaux and Petter, 1967) Hairy-eared Dwarf Lemurs	*Allocebus trichotis*
Subfamily Phanerinae (Rumpler, 1974)	
Phaner (Gray, 1870)	*Phaner furcifer*
Fork-marked Mouse	*Phaner pallescens*
Lemurs	*Phaner parienti*
	Phaner electromontis
Family Lemuridae (Gray, 1821)	
Subfamily Lepilemurinae[2] (Gray, 1870)	
Lepilemur (I. Geoffroy	*Lepilemur mustelinus*
Saint-Hilaire, 1851)	*Lepilemur leucopus*
Sportive or Weasel	*Lepilemur dorsalis*
Lemurs	*Lepilemur ruficaudatus*
	Lepilemur edwardsi
	Lepilemur microdon
	Lepilemur septentrionalis
	Lepilemur seali
	Lepilemur mitsinjonensis
Hapalemur (I. Geoffroy	*Hapalemur griseus*
Saint-Hilaire, 1851)	*Hapalemur occidentalis*
Gentle Lemurs	*Hapalemur aureus*
	Hapalemur aloatrensis
	Hapalemur (Prolemur) simus
Varecia (Gray, 1863)	*Varecia variegata*
Ruffed Lemurs	*Varecia rubra*
Eulemur[3] (Simons and	*Eulemur fulvus*
Rumpler, 1988) Lemurs	*Eulemur macaco*
	Eulemur coronatus

[1]New species described by Kappeler et al., 2005.

[2]Rumpler (1975) separates from Lemuridae the genus *Lepilemur* as a fifth family, Lepilemuridae. *Lepilemur* is now listed by some in the family of subfossil *Megaladapis* with two subfamilies: the subfossils in Megaladapinae and the living species in Lepilemurinae (Mittermeier et al., 1994; Shoshani et al., 1996). *Several new species have been announced, their description has not yet been published.

[3]*Eulemur:* new generic name for species of *Lemur* other than *Lemur catta*. C.R. Acad. Science Paris, Ser. 3, 307:547–551. (Not *Petterus* because Groves and Eaglen 1988 was published *after* Simons and Rumpler, 1988).

	Eulemur rubiventer
	Eulemur mongoz
	Eulemur sanfordi
	Eulemur albifrons
	Eulemur rufus
	Eulemur collaris
	Eulemur albocollaris
	Eulemur coronatus
Lemur (Linnaeus, 1758) Ring-tailed Lemurs	*Lemur catta*
Family Indriidae (Burnett, 1828)	
Subfamily Indrinae (Burnett, 1828)	
Indri (E. Geoffroy Saint-Hilaire and Cuvier, 1796) Indris	*Indri indri*
Propithecus (Bennett, 1832) Sifakas	*Propithecus verreauxi*
	Propithecus tattersalli
	Propithecus diadema
	Propithecus edwardsi
	Propithecus perrieri
	Propithecus coquereli
	Propithecus deckenii
	Propithecus candidus
Avahi[4] (Jourdan, 1834) Avahis or Woolly Lemurs	*Avahi laniger*
	Avahi occidentalis
	Avahi unicolor
Family Daubentoniidae (Gray, 1863)	
Daubentonia (E. Geoffroy Saint-Hilaire, 1795) Aye Ayes	*Daubentonia madagascariensis*
Infraorder Lorisiformes (Gregory, 1915)	
Superfamily Lorisoidea (Gray, 1821)	
Family Lorisidae[5]	
Subfamily Lorisinae	
Loris (E. Geoffroy Saint-Hilaire, 1796) Slender Loris	*Loris tardigradus*
	Loris lyddekkerianus

[4]A new *Avahi* species was recently named, *A. cleesei* (Thalmann and Geissmann, 2005) that has been based solely on geography, fur coloration, and video and audiotape data.

[5]In 1987, P. Jenkins pointed out that the family name "Lorisidae" was preceded in time by "Loridae" (Gray, 1921). However, J.H. Schwartz et al. (1998) submitted an appeal to suppress "Loridae" in favor of "Lorisidae." "Lorisidae" has been reinstated and is used in this text.

Nycticebus (E. Geoffroy Saint-Hilaire, 1812) Slow Loris	*Nycticebus bengalensis*
	Nycticebus coucang
	Nycticebus pygmaeus
	Nycticebus menagensis[6]
Perodicticus (Bennett, 1831) Pottos	*Perodicticus potto*
Pseudopotto (Schwartz, 1996)	*Pseudopotto martini*
Arctocebus (Gray, 1863) Angwantibo or Golden Potto	*Arctocebus calabarensi*
	Arctocebus aureus
Subfamily Galaginae[7] (Mivart, 1864)	
Galago (Geoffroy Saint-Hilaire, 1796) Bushbabies	*Galago senegalensis*
	Galago moholi
	Galago cameronensis
	Galago gabonensis
	Galago gallarum
	Galago matchiei
	Galago zanzibaricus
	Galago granti
	Galago murinus
(Galagoides) (Smith, 1833) Dwarf Bushbabies	*Galago (Galagoides, Hemigalago) thomasi*
	Galago (Galagoides, Hemigalago) medius
	Galago (Galagoides, Hemigalago) demidovii
	Galago (Galagoides) nyasae
	Galago (Galagoides) orinus
	Galago (Galagoides) rondoensis
	Galago (Galagoides) alleni
	Galago (Galagoides) udzungwensis
(Otolemur) (Coquerel, 1859) Greater Bushbabies	*Galago (Otolemur) garnettii*
	Galago (Otolemur) crassicaudatus
	Galago (Otolemur) monteiri
(Euoticus) (Gray, 1863) Needle-clawed Bushbabies	*Galago (Euoticus) elegantulus*
	Galago (Euoticus) inustus
	Galago (Euoticus) pallidus

[6]Regarded to be a subspecies of *N. coucang* by Brandon-Jones et al. (2004).

[7]In 1996, J.H. Schwartz described a new genus and species "*Pseudopotto*" based on a "virtually complete skeleton and adult dentition" and one partial "skull, mandible and mixed dentition" skeletal museum specimens. The names of genera *Galagoides*, *Otolemur*, and *Euoticus* are listed in parenthesis although they have been declared invalid and unwarranted (Nash et al., 1989). I follow this suggestion and use the genus designation *Galago* for all bushbabies.

Suborder Tarsiiformes (Gregory, 1915)
Family Tarsiidae (Gray, 1825)

Tarsius (Storr, 1780)	*Tarsius syrichta*
Tarsiers	*Tarsius bancanus*
	Tarsius spectrum
	Tarsius pumilus
	Tarsius dianae
	Tarsius pelengensis
	Tarsius sangirensis

Suborder Anthropoidea (Mivart, 1864)
Infraorder Platyrrhini—New World Monkeys
Superfamily Ceboidea (Simpson, 1931)
Family Cebidae (Swainson, 1835)
Subfamily Aotinae (Elliot, 1913)

Aotus[8] (Illiger, 1811)	*Aotus trivirgatus*
Night Monkeys	*Aotus vociferans*
	Aotus miconax
	Aotus nancymaae
	Aotus nigriceps
	Aotus azarae
	Aotus infulatus
	Aotus lemurinus
	Aotus hershkovitzi

Subfamily Callicebinae (Hershkovitz, 1977)

Callicebus (Thomas, 1903)	*Callicebus personatus*
Titi Monkeys[9]	*Callicebus torquatus*
	Callicebus moloch
	Callicebus modestus
	Callicebus donacophilus
	Callicebus pallescens
	Callicebus olallae
	Callicebus oennanthe
	Callicebus cinerascens
	Callicebus hoffmannsi
	Callicebus baptista
	Callicebus brunneus

[8]Genus *Aotus* was subdivided by Hershkovitz in 1983 into two species groups with a total of nine species. A careful study of taxonomy and distribution of genus *Aotus* by S.M. Ford in 1994 reduced the number of species to between five to seven, which are recorded here.

[9]In 2002, a Taxonomic review of the Titi monkeys, Genus *Callicebus,* was published (van Roosmalen et al., 2002).

	Callicebus cupreus
	Callicebus ornatus
	Callicebus coimbrai
	Callicebus medemi
	Callicebus bernhardi
	Callicebus melanochir
	Callicebus stephennashi
	Callicebus aureipalatti
	(perhaps a subspecies of *Callicebus personatus*) *Callicebus barbarabrownae*
Subfamily Pitheciinae (Mivart, 1865)	
Cacajao (Lesson, 1840)	*Cacajao melanocephalus*
Uakaris	*Cacajao calvus*
Pithecia[10] (Desmarest, 1804) Sakis	*Pithecia pithecia*
	Pithecia irrorata
	Pithecia aequatorialis
	Pithecia albicans
	Pithecia monacha
Chiropotes[11] (Lesson, 1840)	*Chiropotes satanas*
Bearded Sakis	*Chiropotes albinasus*
Subfamily Alouattinae (Hershkovitz, 1977)	
Alouatta (Lacépède, 1799)	*Alouatta belzebul*
Howler (also Howling)	*Alouatta seniculus*
Monkeys	*Alouatta caraya*
	Alouatta fusca
	Alouatta palliata
	Alouatta villosa
	Alouatta pigra
	Alouatta coibensis
	Alouatta macconnelli
	Alouatta sara
	Alouatta nigerrima
	Alouatta guariba
Subfamily Cebinae (Erxleben, 1777)	
Cebus (Erxleben, 1777)	*Cebus apella*
Capuchin Monkeys	*Cebus capucinus*
	Cebus albifrons[12]
	Cebus nigritus

[10]Hershkovitz (1979, 1987) established five species of genus *Pithecia*.

[11]There are two species of *Chiropotes* according to Hershkovitz (1985).

[12]Defler and Hernández-Camacho (2002) discussed *C. albifrons albifrons* subspecies assignments.

	Cebus olivaceus
	Cebus kaapori
	Cebus libidinous
	Cebus xanthosternos
Saimiri (Voigt, 1831)	*Saimiri sciureus*
Squirrel Monkeys	*Saimiri oerstedti*
	Samiri ustus
	Saimiri boliviensis
	Saimiri vanzolinii
Subfamily Atelinae (Gray, 1825)	
Ateles (Geoffroy	*Ateles paniscus*
Saint-Hilaire, 1806)	*Ateles belzebuth*
Spider Monkeys	*Ateles fusciceps*
	Ateles geoffroyi
	Ateles chamek
	Ateles hybridus
	Ateles marginatus
Brachyteles (Spix, 1823)	*Brachyteles arachnoids*
Woolly Spider Monkeys	*Brachyteles hypoxanthus*
Lagothrix (Geoffroy	*Lagothrix lagothricha*
Saint-Hilaire, 1812)	*Lagothrix cana*
Woolly Monkeys	*Lagothrix lugens*
	Lagothrix poeppigii
Oreonax (Thomas, 1927)	*Oreonax flavicauda*
Yellow-tailed Woolly Monkey	
Family Callitrichidae[13] (Thomas, 1903)	
Subfamily Callitrichinae (Gray, 1821)	
Callimico (Ribeiro, 1912)	*Callimico goeldii*
Goeldi's Marmoset	
Callithrix (Erxleben, 1777)	*Callithrix jacchus*
Shorts-tusked	*Callithrix argentata*
Marmosets or Titis	*Callithrix humeralifer*
	Callithrix saterei
	Callithrix kuhlii
	Callithrix geoffroyi
	Callithrix penicillata
	Callithrix flaviceps
	Callithrix aurita
	Callithrix leucippe

[13]Surprisingly, Callitrichidae and Callitrichinae are also often spelled Callithrichidae and Callithrichinae.

	Callithrix emiliae
	Callithrix (Mico) nigriceps
	Callithrix (Mico) marcai
	Callithrix (Mico) melanura
	Callithrix (Mico) humeralifera
	Callithrix (Mico) mauesi
	Callithrix (Mico) chrysoleuca
	Callithrix (Mico) intermedia
	Callithrix (Mico) humilis
	Callithrix (Mico) manicorensis
Cebuella (Gray, 1866) Pygmy Marmosets	*Cebuella pygmaea*
Saguinus (Hoffmannsegg, 1807) Long-tusked Marmosets or Tamarins	*Saguinus fuscicollis*
	Saguinus bicolor
	Saguinus niger
	Saguinus leucopus
	Saguinus inustus
	Saguinus midas
	Saguinus imperator
	Saguinus mystax
	Saguinus labiatus
	Saguinus tripartites
	Saguinus nigricollis
	Saguinus graellsi
	Saguinus melanoleucus
	Saguinus tripartitus
	Saguinus pileatus
	Saguinus labiatus
	Saguinus martinsi
	Saguinus oedipus[14]
	Saguinus geoffroyi[14]
Leontopithecus (Lesson, 1840) Lion Tamarins	*Leontopithecus rosalia*
	Leontopithecus chrysomelas
	Leontopithecus chrysopygus
	Leontopithecus caissara

Infraorder Catarrhini—Old World Monkeys
Superfamily Cercopithecoidea (Gray, 1821)
Family Cercopithecidae (Gray, 1821)[15]

[14]Regarded to be genus *Oedipomidas* by some.

[15]Several species of *Cercopithecus* have been assigned to the "super genus" *Chlorocebus* (Vervets), and the genus is in need of revision (Groves, 2001). I continue to use genus *Cercopithecus* here.

Subfamily Cercopithecinae (Gray, 1821)

Cercopithecus (Linnaeus, 1758) Guenons	*Cercopithecus aethiops*
	Cercopithecus albogularis
	Cercopithecus ascanius
	Cercopithecus campbelli
	Cercopithecus cephus
	Cercopithecus cynosurus
	Cercopithecus denti
	Cercopithecus diana
	Cercopithecus dryas
	Cercopithecus erythrogaster
	Cercopithecus erythrotis
	Cercopithecus hamlyni
	Cercopithecus lhoesti
	Cercopithecus neglectus
	Cercopithecus nictitans
	Cercopithecus mitis
	Cercopithecus mona
	Cercopithecus petaurista
	Cercopithecus pogonias
	Cercopithecus preussi
	Cercopithecus pygerythrus
	Cercopithecus sabaeus
	Cercopithecus salongo
	Cercopithecus solatus
	Cercopithecus tantalus
	Cercopithecus wolfi
Allenopithecus Allen's Monkey	*Allenopithecus nigriviridus*
Miopithecus (Geoffroy Saint-Hilaire, 1842) Talapoin Monkey	*Miopithecus talapoin*
Erythrocebus (Trouessart, 1897) Patas Monkey	*Erythrocebus patas*
Macaca (Lacépède, 1799) Macaques	*Macaca mulatta*
	Macaca fascicularis
	Macaca maura
	Macaca fuscata
	Macaca speciosa
	Macaca sinica
	Macaca silenus
	Macaca nemestrina

	Macaca tonkeana
	Macaca ochreata
	Macaca radiata
	Macaca assamensis
	Macaca thibetana
	Macaca arctoides
	Macaca cyclopis
	Macaca hecki
	Macaca leonina
	Macaca nigra
	Macaca nigrescense
	Macaca sylvanus
	Macaca pagensis
	Macaca munzala
Cercocebus (E. Geoffroy Saint-Hilaire, 1812) [*Lophocebus*[16] (Palmer, 1903)] Mangabeys	*Cercocebus torquatus*
	Cercocebus galeritus
	Cercocebus atys
	Cercocebus (Lophocebus) aterrimus
	Cercocebus (Lophocebus) albigena
Rungwecebus (Davenport et al., 2006) Highland Mangabey	*Rungwecebus (Lophocebus) kipunji*
Papio (Erxleben, 1777) Baboons	*Papio hamadryas*
	Papio anubis
	Papio cynocephalus
	Papio papio
	Papio ursinus
Mandrillus (Ritgen, 1824) Drills, Mandrills	*Mandrillus sphinx*
	Mandrillus leucophaeus
Theropithecus (I. Geoffroy Saint-Hilaire, 1843) Gelada Baboon	*Theropithecus gelada*
Subfamily Colobinae (Jerdon, 1867)	
Colobus (Illiger, 1811) Black and White Colobus Monkeys, Guerezas	*Colobus polykomos*
	Colobus guereza
	Colobus satanus
	Colobus angolensis
	Colobus vellerosus

[16]A new species of *Lophocebus*, *L. kipunji* (Jones et al., 2005) made news in 2005, but has since been reassigned to its own genus: *Rungwecebus kipunji* (Davenport et al., 2006).

Colobus[17] (*Piliocolobus*) (Rochebrune, 1877) Red Colobus Monkeys	*Colobus (Piliocolobus) badius* *Colobus (Piliocolobus) pennantii* *Colobus (Piliocolobus) rufomitratus* *Colobus (Piliocolobus) gordonorum* *Colobus (Piliocolobus) kirkii*
Procolobus (*Procolobus*) (Rochebrune, 1877) Olive Colobus Monkey	*Procolobus verus*
Presbytis (Eschscholtz, 1821) Langurs, Leaf Monkeys	*Presbytis femoralis* *Presbytis thomasi* *Presbytis melalophos* *Presbytis comata* *Presbytis hosei* *Presbytis potenziani* *Presbytis rubicunda* *Presbytis frontata* *Presbytis federicae* *Presbytis siamensis* *Presbytis natunae*
Semnopithecus (Desmarest, 1822) Hanuman Langur	*Semnopithecus entellus* *Semnopithecus johnii* *Semnopithecus vetulus*
Trachypithecus (Reichenbach, 1862) Brow-ridged Langurs	*Trachypithecus barbei* *Trachypithecus delacouri* *Trachypithecus geei* *Trachypithecus pileatus* *Trachypithecus phayrei* *Trachypithecus francoisi* *Trachypithecus cristatus* *Trachypithecus auratus* *Trachypithecus johnii* *Trachypithecus laotum* *Trachypithecus obscurus* *Trachypithecus poliocephalus* *Trachypithecus villosus*
Pygathrix (E. Geoffroy Saint-Hilaire, 1812) Douc Langurs	*Pygathrix nemaeus* *Pygathrix nigripes*

[17]The following species are regarded as subspecies of *Colobus (Piliocolobus) badius* by some authors.

Rhinopithecus (Milne-Edwards, 1872) Snub-nosed Langurs	*Rhinopithecus roxellana*
	Rhinopithecus avunculus
	Rhinopithecus bieti
	Rhinopithecus brelichi
Simias (Miller, 1903) Pigtailed Langur	*Simias concolor*
Nasalis (E. Geoffroy Saint-Hilaire, 1812) Proboscis Monkey	*Nasalis larvatus*

Superfamily Hominoidea (Simpson, 1931)

Family Hylobatidae (Gray, 1877)

Bunopithecus[18] (Matthew and Granger, 1923)	*Bunopithecus hoolok*
Hylobates (Illiger, 1811) Gibbons, Lesser Apes	*Hylobates lar*
	Hylobates agilis
	Hylobates moloch
	Hylobates klossii
	Hylobates pileatus
	Hylobates muelleri
Nomascus (Miller, 1933)	*Nomascus concolor*
	Nomascus leucogenys
	Nomascus gabriellae
Symphalangus[19] (Gloger, 1841) Siamang	*Symphalangus syndactylus*

Family Pongidae[20] (Elliot, 1913) **Great Apes**

Pongo (Lacépède, 1799) Orangutans	*Pongo pygmaeus*
	Pongo abelii
Pan (Oken, 1816) Chimpanzees and Bonobos	*Pan troglodytes*
	Pan paniscus
Gorilla (Geoffroy Saint-Hilaire, 1852) Gorillas	*Gorilla gorilla*
Homo (Linnaeus, 1758) Modern Humans	*Homo sapiens*

[18]Genus *Hylobates* has been subdivided into genera *Bunopithecus*, *Hylobates*, and *Nomascus* (Geissmann, 2003; Brandon-Jones et al., 2004).

[19]Genus *Symphalangus* is now regarded to be a subgenus of *Hylobates* by some.

[20]An alternative taxonomy puts Pongidae into superfamily Pongoidea and our own family, Hominidae, into superfamily Hominoidea.

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Chapter 2

Taxonomy

Hierarchical Classification
Population Biology and Classification
Traditional (or Evolutionary) Classification
Numerical (or Phenetic) Taxonomy
Cladistics
Misunderstandings in Primate Classification
The Tarsier Conundrum

Human minds are constantly trying to rank or sort out all that surrounds them. Animate as well as inanimate objects are always consciously or unconsciously classified. Humans among themselves are also constantly judged and sorted—within and between groups—and consequently we could say that appraising others and the world around us is part of the human condition. Thus, it appears that human beings have classifying minds. Classification involves all aspects of daily life, even though it is disguised by different names: decision making, selection, planning, pigeonholing, discriminating, and judging are some of the terms that describe classifying endeavors.

Looking back into our past, it appears that classification may have already begun when humans first started to reason. During early human history, and even in prehistoric times, we can find rock and cave art that document how human beings perceive themselves in comparison to animals.

One of the first works to have put classification of the animal world in print is Aristotle's *Historia Animalium* (384–322 B.C.). This early written attempt of animal classification appears to be based on real insight and knowledge concerning the animated world (Mayr, 1982). In fact, Aristotle was the first great natural historian, and his history of the animals was only the beginning of more or less elaborate attempts by early scientists to classify both animals and plants scientifically. These initial efforts to classify nature were purely comparative and based on morphology. Numerous natural history collections were established in Europe during the late fourteenth century when explorers traveled farther than

ever before and returned with strange plants and animals, including shells, dried plants, feathers, skeletons, and skins quite unlike those to be found in their native lands.

The fascination with nature prevalent at this time led to a rapid increase in knowledge about the biotic diversity of the world around us. Attempts to classify nature finally culminated in the *Systema Naturae* (1758, 10th edition) by the Swedish botanist Carolus Linnaeus (1707–78). He created the system of binomial nomenclature for all animals and plants using Latin names for genus and species. His basic binomial methodology of genus and species assignment still prevails.

The goal of science is to find evidence for observable facts—any test of validity must be repeatable. However, this evidence is subject to constant revision as knowledge grows. In biology, we must be content with the immutable certainty that phenomena and evolutionary conclusions cannot be as indisputable as physical or mathematical proofs. Biology is innately unorganized and inherently variable. This does not mean, however, that biological rules can be doubted. The notions of intelligent design and creation clearly reside beyond scientific knowledge and simply belong in the realm of naive and undisputed faith.

The all-encompassing realm of animal life is Linnaeus's highest category: the kingdom Animalia. Within the kingdom, all animals with axial skeletons are categorized in phylum Chordata. The next entity is the class Mammalia, including all mammals. Within mammals, a further step down is the order Primates, including prosimians, tarsiers, monkeys, apes, and humans. All primates are then grouped into families, each of which contains closely related genera and, finally, species. In this system, the genus name (equivalent to the family name) is a Latin (or latinized Greek) name in the nominative singular. The genus name determines a group of similar organisms. The genus then is further divided into species. Species are groups of animals or plants that are able to reproduce sexually with each other and produce fully fertile offspring. Species are assigned the second name that is not capitalized and is usually an adjective that agrees grammatically with the genus name (e.g., *Homo sapiens,* where *Homo* is the Latin name for humans and *sapiens* means intelligent; *Pan troglodytes* for the chimpanzee, where *Pan* is the Latin name for the mythical God of the forest and *troglodytes* is Greek for cave dweller). Both genus (plural of genus = genera) and species (plural = species) names are usually printed in italics (or underlined). For example, the name for the common chimpanzee is genus *Pan* and species *troglodytes* = *Pan troglodytes;* the binomial name for the common macaque is *Macaca mulatta*. Linnaeus's system is still in use today, almost 240 years after it was created. Linnaeus's system used morphological characteristics for his classification and assumed that species and genera were unchangeable. Thus, his system was purely a typological classification lacking any other implications such as questions about relatedness. If a species is named for a person, the annotation should end with

"i," as, for example, *Propithecus tattersalli*, a species of lemur that was named as recently as 1988 (Simons, 1988).

It was Charles Darwin who not only recognized but also published the important insight that the abundance of living forms has evolved throughout time in his *Origin of Species*. In the introduction to the third edition (1861, p. 3), Darwin stated:

> In considering the Origin of Species, it is quite conceivable that a naturalist, reflecting on the mutual affinities of organic beings, on their embryological relations, their geographical distribution, geological succession, and other such facts, might come to the conclusion that each species had not been independently created, but had descended, like varieties, from other species.

Darwin pointed out how variability is of crucial importance for the modification of species throughout long periods of time. He concluded, based on his observations, that all living organisms must be descended from a common ancestor and that all living things are connected to each other through time by genealogical relationships. Thus, it was Darwin who first made it clear that all classification of living organisms is hierarchical and therefore should be genealogical.

HIERARCHICAL CLASSIFICATION

Ultimately the essence of classification is to order all living things into groups that not only resemble each other but are also related to each other by evolution through time. This ordering allows scientists in all fields to communicate effectively with one another about the natural world in which we all live. Classification methodology should be stable to support widespread understanding and not confusion.

Linnaeus only recognized the kingdoms of Animalia and Plantae. In a now commonly used system, all known living organisms are grouped into five kingdoms: Monera, Protista, Fungi, Plantae, and Animalia. These kingdoms are ordered into smaller categories (in descending order), namely, into phyla (singular = phylum), classes, orders, families, genera, and species. Species that are defined according to similarity are called morphological species.

For example, the place of one primate species in the realm of classification within the animal kingdom is as follows:

The chimpanzee *Pan troglodytes* is classified in the

Kingdom	Animalia
Phylum	Chordata
Class	Mammalia
Order	Primates

Family	Hominoidea
Genus	*Pan*
Species	*troglodytes*

Classification of all organisms is structured in such a hierarchical way, putting groups of similar organisms within higher groups of less similar organisms and so on. All of these categories just described have also been subdivided into various further, more detailed groups with the help of the prefixes "sub-" or "super-."

During the 100 years following Linnaeus's initial classification and the publication of Darwin's theory of evolution, there was much written and philosophized about the astonishing wealth of plants and animals on Earth. Early on, humans were able to grasp the fact that there seems to be a gradient of morphological and organismal complication within the plant and animal kingdoms. Many attempts were made to explain this fact. Only during the end of the nineteenth and the first half of the twentieth centuries did it become increasingly clear that today's biological complexity is the result of change through time (evolutionary change). This understanding led to the conclusion that classification should also incorporate information about evolutionary descent. Thus, systematics took on the added dimension of evolutionary systematics or phylogeny.

POPULATION BIOLOGY AND CLASSIFICATION

In the first half of the twentieth century, scientists began to understand that the species definition had to be formalized to include dynamic biological facts about relatedness. The term "species" took on the interpretation of "population" or a group of organisms of the same kind. In 1963, Ernst Mayr defined the term "species" functionally as a reproductive unit and thus profoundly changed the insight of biologists in regard to the true meaning of taxonomy (see also Groves, 2001, pp. 26–27). Ernst Mayr's definition of the biological species is as follows: "A species is a group of interbreeding natural populations that is reproductively isolated from other such groups."

There are many other species concepts, such as the morphological or typological species concept that pertains to fossils but cannot be easily defined because of the factor of time that is involved in the definition of a fossil species. Today the taxonomic grouping of organisms is supported by morphological, structural, behavioral, and biochemical similarity. Similarities between organisms that are based solely on their life in the same environment—such as the shape of fish and sea mammals or birds and bats—are not decisive classificatory factors. Fish and dolphins are not very closely related, nor are birds and bats. Even though the lifestyle and basic shape of fish and dolphins are similar, their ancestors were

very different. These two forms live in the same aquatic environment, but their superficial similarity of appearance is "homoplastic" (or analogous)—caused by living in the same substrate and not by a close evolutionary relationship. On the other hand, the skeletons of the forelimbs of bats and of primates are made up of the same bones and are homologous to each other. Although functionally vastly different, their forelimb bones are similar because of common ancestry. Homology is one of the significant criteria on which classification ideally should be based.

Today classification is a field so vast that it is not possible here even to scratch the surface of all the publications that concern it or even to mention all the books and articles that have dealt with it. Classification, in one sense, has also caused much difficulty, because it unfortunately and inevitably leads some to discrimination, and ultimately racism. Classification in the field of biology is no less controversial than it is in everyday life.

There can be no doubt that ever since Darwin's time, all evolutionary biologists have recognized the crucial importance of phylogeny—the evolutionary history or line of an organism's descent—in classification. Even those biologists who have rejected phylogeny as the basis for classification, such as pheneticists and to a degree also cladists, did so because they decided that phylogeny was impossible to know with certainty and was therefore useless. One of the key problems of classification is that geological lines of descent can only be factual to a certain degree, and therefore other equally logical classifications of groups of organisms in a phylogeny are often proposed.

At present, we recognize three discrete methodologies of classification: traditional (or evolutionary) classification, numerical (or phenetic) taxonomy, and cladistics. (For in-depth discussions, see Cartmill, 1981; Mayr, 1982; Mayr and Ashlock, 1991; Groves, 2001.)

Traditional (or Evolutionary) Classification

This kind of classification begins with the assessment of overall morphological similarity between organisms. Similarities are tested for patterns of homologies in living organisms and, if possible, are compared with fossil forms. Criteria concerning ontogenetic development, cell biology or biochemistry, physiology, and behavior can also be of importance. As many factors as possible should go into such a classification. Similarities within groups of organisms that are classified together—for example, "prosimians" or "insectivores"—are also evaluated in regard to their phylogenetic or evolutionary relationship when attempts are made to link them with each other. Such relationships among organisms are often portrayed with the help of phylogenetic trees. Phylogenetic trees visually illustrate ancestor–descendant relationships as well as the passage of time involved in the evolution of taxa (a taxon [plural = taxa] being a natural unit of organisms that are grouped together and given a common name because

they do have a number of characteristics in common). It must be stressed that phylogenetic trees do not represent classification, because phylogenetic trees are striving to present visually purported lines of descent. In contrast, classification only attempts to group organisms according to characteristics they have in common. Knowledge about, and considerable experience with, a particular group of organisms is an essential prerequisite for any construction of a valid classification because of the great complexity of factors that come into play. An ideal system also includes information about the evolutionary relationship between the classified organisms. This kind of traditional or evolutionary classification has been criticized because it relies on individual experience and observation by researchers and can thus be biased.

In the 1940s and 1950s, biologists increasingly began to realize the need for better and more exacting methods of classification. Specifically, classificatory methods that might be considered unbiased, repeatable, and indisputably correct were sought. This endeavor led to the proposal of two new methodologies: numerical (or phenetic) taxonomy and cladistics.

Numerical (or Phenetic) Taxonomy

Developed and refined during the first half of the twentieth century, numerical taxonomy essentially depends on equal weighting of all phenetic (that is, visible; Greek *pheno* = "making visible," "to show") characters (as many as possible) and it totally rejects phylogenetic implications because phylogenetic events are considered to be scientifically unverifiable (Sneath and Sokal, 1976; Sokal, 1974). This means that all characters evaluated are of equal importance. This method claims to be strictly objective. Numerical or phenetic taxonomy is not new, but has been accelerated in its development by the rapidly increasing availability of refined computer technology as well as the availability of biochemical sequence data of living organisms. Computer programs that cluster taxa together based on quantitative measures of overall similarity can quickly produce multiple variants of assumed relationships that are based on numerical character data. These methods claim to be simple and repeatable. They do not require any previous knowledge of a taxon that is classified. Numerical phenetics has not been used much in primatology recently except in applications for DNA sequence data. The cluster methods used have traditionally been modified to link taxa because of certain nucleotides they share. (For detailed discussions, see Mayr and Ashlock, 1991.)

Cladistics

During the last years of World War II, a young scientist, Willi Hennig, in war-torn Germany struggled with classification problems involving the insects

with which he was working. His struggle was intense because he was somewhat isolated. Most of his peers and teachers were gone, involved in the war and unavailable for helpful discussions. His endeavors cumulated in the 1950 publication of a book in which he presented his theoretical ideas and a new terminology of phylogenetic systematics. In 1966, a variation, not an exact translation, of Hennig's original book and ideas about phylogenetic systematics was published in the United States, where his method of classification soon became fashionable. Hennegian classification techniques and Hennig's new and cumbersome terminology are taught everywhere. The taxonomic method of cladistics is based on the same overall claim for objectivity as numerical phenetic classification. What makes the cladistic method different is the assumption that phylogeny occurs only by means of dichotomies: a parent taxon splits into two sister taxa, and the parent taxon ceases to exist after the split—an assumption that some have called absurd (Cartmill, 1981). The determination of a dichotomy should, according to Hennig, be based solely on the common possession of uniquely derived characters (called "synapomorphies" by Hennig). Such classifications are only workable for the evaluation of few characters at a time; otherwise, they become overwhelmingly complex.

All classification schemes have to be based on the different information value contained in morphological, behavioral, or molecular characters. Characters are the basis for any and every biological taxonomy and have to be chosen by the researcher. Cladistic systematics requires overly simplified recording of characters. Most variable morphological features are reduced to two or more so-called character states. These character states are coded as "0," "1," or "2," although "multistate" characters are sometimes allowed. Thus, cladistic systematics is a labor-intensive recording of numerous characters, which—especially where fossils are concerned—are often numerical measurements. These characters have to be appraised as to their systematic value and are "weighted" according to their intrinsic meaning for subsequent systematic evaluation. Weighting of characters is also practiced in traditional taxonomy because characters defining organisms are not all of equal value. The evaluation of as many characters as possible results in long lists of weighted characters and computer-generated treelike diagrams. All cladistic "trees" are essentially digital,[1] with a parental taxonomic unit splitting into two offspring taxa (also called "sister" or "sibling" groups). Even multiple splitting patterns must be reduced to dichotomies in strict cladistic analyses (Nelson and Platnik, 1980). Finding the most parsimonious tree for large data sets is a complicated mathematical operation. There are many possible trees for any one data set; the most commonly used criterion for selecting the "best" tree is

[1]Digital is derived from the Latin word *digit*, meaning "finger." A digit can be a single character in a system of numbers. Digital systems (e.g., computers) are composed of discrete binary codes (*binary* means "consisting of two"), such as 0 and 1.

so-called evolutionary parsimony. In turn, the most parsimonious tree is the one that requires the fewest "evolutionary" steps for all characters. The artificial construction of cladograms is based on computer programs, and all computers are based on using only digital systems: cladistic systematics is ultimately codependent on the increasing development of computer capabilities (Kay and Williams, 1994). Hennig believed that such cladograms represent the phylogeny of the taxon that is evaluated. Later cladists have realized that these cladograms are actually diagrams showing only character distribution, not evolutionary, time-dependent history of a taxon or of taxa. There can be no doubt that composition of various types of computer-generated phylogenetic relationship "trees" has only been possible because of the rapid development of sophisticated computer software and technology. No one would be able to evaluate cladistic character data the old-fashioned way, and no one would draw angular trees without this advanced technology. There is the inherent danger that technology has actually separated the reality of living things such as primates and the complexities of natural history far away from the process of hands-on scientific assessment and life.

Cladistic Terminology

It is appropriate here to add a list of words with explanations of their derivation. (For a detailed list of taxonomic terminology, see also Mayr and Ashlock, 1991.) These terms are frequently used in taxonomic writing:

Analogy: similarity due only to function, *not* ancestry (compare homology)
Ancestral: a character that is not derived (formerly "unspecialized, primitive")
Apo-: Greek prefix for "away from," "down from," "since," "through," "because"
Apomorphic: a more specialized state of a homologous character within a group
Aut-: Greek *autos*, "self," "own," "immediate," "personal"
Autapomorphic: an apomorphic character found in only one of two sister groups
Clad-: Greek *klados*, "branch," "twig"
Clade: a homogenous (monophyletic) line of descent
Derived: pertaining to characters arising during the history of a group and not included in its primitive ancestors (formerly "specialized")
Holo-: Greek *holos*, "total," "whole," "complete"
Holophyletic: pertaining to a group that consists of all the descendants of its most recent common ancestor (= monophyly of cladists)
Homo-: Greek *homoios*, "alike," "similar," "in common"
Homology: correspondence in type of structure and ancestry (Greek *logos*, "speech," "talk," "word," "expression," "reason," "agreement," "same," "identical")

Homoplasy: characters occurring in one or more taxa through convergence, parallelism, convergence or reversal
Morph-: Greek *morphae*, "form," "shape," "appearance"
Phyl-: Greek *phylon*, "family," "stem," "genus"
Phylogeny: the inferred lines of descent of a group of organisms, including a reconstruction of the common ancestor and the amount of divergence (anagenesis) of the various branches; "the science of the changes of form through which the phyla or organic lineages pass through the entire time of their discrete existence" (Haeckel, 1866).
Phylum: = Greek phylon: family, stem, group, people
-Plas, -plasy: Greek for shaping, creating
Plesio-: = Greek *plesios*, "near," "neighboring," "adjoining"
Plesiomorphic: ancestral, primitive character state
Primitive: pertaining to the earliest members of a given group; sharing characters of the ancestral group
Syn- or Sym-: = Greek *sym* before b, m, and p, "together," "with," "alike," "at the same time," "all together," "united"
Symplesiomorphic: ancestral characters shared by different taxa

Hennig (1950) coined several new pseudo Greek terms for characters that are used to define taxa. He named ancestral characters, or characters that are inherited from a common ancestor, **plesiomorphic.**

Characters that were evident before an ancestral taxon split into two new taxa that contain this ancestral character are called **symplesiomorphic.**

The word "derived" was transformed into **apomorphic.** Thus, characters that uniquely originated in a close common ancestor and are exclusively shared by all direct descendants of this ancestor or "shared derived characters" are called **synapomorphic** characters in Hennegian terminology. One of the problems however, is that it is difficult to determine with any degree of certainty which shared characters are plesiomorphic and which are synapomorphic. Even more complicated is the task of separating shared derived features that are due to common heritage from those that represent evolutionary convergence. For example, in primates, it is not easy to decide whether the fact that Old World and New World primates have three molars in common is based on a common heritage or on evolutionary convergence because of similarity in diet.

Apart from such problems, cladistic theory of classification is orderly because it is based on the simple postulation that it must reflect dichotomous branching on any evolutionary tree. Of course, it is also bound to simple dichotomies because of the dichotomous nature of digital computers.

Characters that newly appear exclusively in any one taxon are called **autapomorphic.**

Among primate taxa cladistic evaluations are usually based on traditionally delimited groups and frequently result in multiple cladograms that vary only in small details. This is the case because cladograms are computer generated linear graphic designs depicting hypothetical modes in which taxa might be related to each other. In a dichotomous cladogram the two groups that derived from the common ancestor each are called a "sister group"[2] (Mayr and Ashlock, 1991).

The diverse abundance of the world's living organisms is the result of adaptation. All organisms are well adapted to live and reproduce successfully in a particular ecological niche (a "niche" being the part of the environment that provides a species with the multidimensional resources for its successful existence).

Adaptations in different organisms can be homologous, that is, characters that have been inherited from an equivalent structure or feature found in the nearest common ancestor. A homologous structure, for example, is the pelvic girdle of both chimpanzees and humans. Often the term "analogy" is used as if it were the antonym to "homology." An analogy is a similarity that is caused by life in a similar environment and similarity of function such as the streamlined shape of fish and whales. It is not the result of common descent. The term "analogy" has recently been abandoned, however.

As mentioned earlier, cladists assume that the shortest cladogram that used the least number of (evolutionary) steps between character changes to be constructed is the most "parsimonious," or most likely to be correct, cladogram. Both cladograms and parsimonies are computer generated (Kay and Williams, 1994; Mayr and Ashlock, 1991).[3]

A further difficulty for any classification system is the fact that similar characters can be acquired independently by different taxa. This situation is called "homoplasy." According to Mayr and Ashlock (1991), homoplasy (Greek from *homoios-,* which means "the same," "equal"; *plastos-*, which means "formed," "molded") is the possession by different taxa of a character that,

[2]In the French literature, "sister group" has been translated into *groupe frères,* which means "brother group," an amusing difference. The French terminology is said to come from the fact that *groupe* is masculine in French, not feminine as the term is in German (Gingerich, personal communication). Linguistically, this does not make sense as group = *Gruppe* is female in German and a *Bruder Gruppe* ("brother group" in German) and *groupe sœures* ("sister group" in French) are perfectly credible. To make this unusual terminology more appropriate (given that both sexes are included in such groups), I think the term actually should be "sibling group."

[3]The most parsimonious cladogram is constructed by computer programs such as PHYLIP (Phylogeny Inference Package) or PAUP (Phylogenetic Analysis using Parsimony) and Mac Clade (Kay and Williams, 1994). Brady (1983) stated that "the parsimony program as described *has no biological implications* [Brady's emphasis] but is simply a methodological demand of a cladogram" and pointed out that "a cladogram is a hypothesis of hierarchy." Cladograms should not be called phylogenetic trees, because they may misrepresent the actual phylogeny (see also Mayr and Ashlock, 1991).

although it appears similar, is derived by convergence, parallelism, or reversal, but not by inheritance from a common ancestor (see also Panchen, 1994).

Another increasingly obvious problem for classification is that of human communication. Only in the last decade of the twentieth century was a book published (Hall, 1994) that dealt exclusively with the interpretation of the ancient term homology. Over time, the information content of words such as "homology" has become vast, and the application of new meanings by different scholars has led to ambiguity and incongruent connotations. A term's meaning is often complicated, therefore, by new and different interpretations and applications that are attached to it. Changing the original meaning of an initially simple and easily understood idiom causes misunderstanding and incompatibility in scientific procedure. It also leads to miscomprehension between various scientific "schools." Both terminology and classification should therefore be changed only when absolutely necessary. They are the basis for communication among scientists, much as spoken and written language is among people more generally. Frequent changes or endeavors to communicate in foreign tongues make mutual understanding difficult, if not impossible. In 1972, a scientist from New Zealand attempted to revamp the nomenclature concerning dental characteristics in an article titled "A New Terminology for Mammalian Teeth" (Every, 1972). This intellectual exercise was doomed from the start because of its hopelessly complex terms, which were based on the functional aspect of teeth and called "Thegosis" (from Greek *thego* for "sharpen"), "a phylogenetically derived behavior that sharpens a tooth by grinding it violently against another." Every's new terminology was far too complicated, with terms such as "Stego-alpha-scissorio-tetrakididrepanon (= a morphological and functional unit made up of two adjacent teeth).

MISUNDERSTANDINGS IN PRIMATE CLASSIFICATION

One example of the considerable confusion concerning classification is evident in the incongruent interpretation of similarities among higher primates—namely, pongids and humans. Recent attempted changes and differences in the meaning of the extant family Hominidae (even without the inclusion of any fossil forms) have caused confusion and misunderstanding. The three genera of great apes (genera *Pongo, Gorilla, Pan*) have commonly been grouped in the taxonomic family Pongidae and all humans (genus *Homo*) in the family Hominidae. Already in 1863, Huxley recognized that humans are most closely related to the African great apes, to the exclusion of the Asian Orangutans genus *Pongo;* this fact was then carefully documented by Gregory (1934). Humans were habitually classified in their own family Hominidae because there is a fundamental degree of difference in the adaptive features of humans and great apes.

New findings about the molecular similarity between African apes and humans by cladistic classifiers gave rise to a new classification that included the African great apes (*Gorilla* and *Pan*) in the family Hominidae. This was done because, for cladists, the adaptive divergence of humans from apes and the shared primitive features among African apes are unimportant because cladist terminology is based exclusively on the sequence of evolutionary (digital) branching, as noted earlier. Hennegian molecular cladists were totally committed to this system, and thus they could not accept the proper classification as prosposed by Gregory. This situation changed the formerly clear-cut and well-understood meaning of the terms "pongid" and "hominid," leaving the family Pongidae to refer only to the Asian great apes genus *Pongo.*

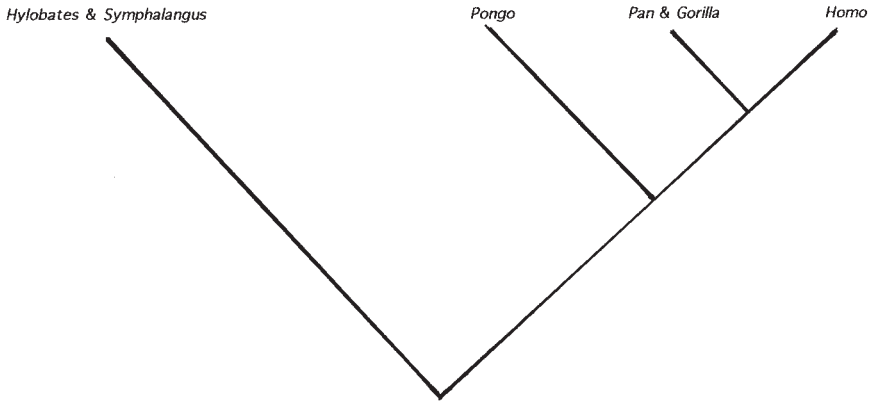
Followers of cladistic (also called phylogentic) systematics demand that classification reflect phylogeny. This conflicts with evolutionary systematics in which classification closely reflects phylogeny but also "the practical needs of discussion and communication" (Simpson, 1963, p. 25). Evolutionary classification recognizes the fact that rates of evolution vary and includes this notion in its classificatory schema. A noteworthy example is the classification of the hominoid primates—lesser and great apes and humans. One view of the evolutionary relationship of these forms is shown in the cladogram/phylogeny in Figure 2.1A. In contrast, Figure 2.1B illustrates the point that *Homo* has undergone more evolutionary change than have the African apes since their lineages diverged. At the time, Simpson placed all African apes in genus *Pan*. He stressed that "placing all African apes in *Pan* permits classification to express the clear fact that they are much more closely related to each other than to any species of other genera." Cladistic/phylogentic classification would ignore the information as Simpson saw it (and as is illustrated in Figure 2.1B). It would tabulate the relationships something like this:

1. Hominoidea
  2. Hylobatidae
    3. Hylobatinae
      4. *Hylobates, Symphalangus*
  2. Pongidae
    3. Pongoinae
      4. *Pongo*
    3. Paninae
      4. *Pan gorilla, Pan troglodytes, and paniscus*
      4. *Homo*

This classification does not tell us that *Homo* and the African great apes are more closely related than *Homo* and *Pongo* or that the African apes and *Pongo* are morphologically and adaptively more similar to one another than both are to *Homo.* This view has recently been strengthened by new insights into the

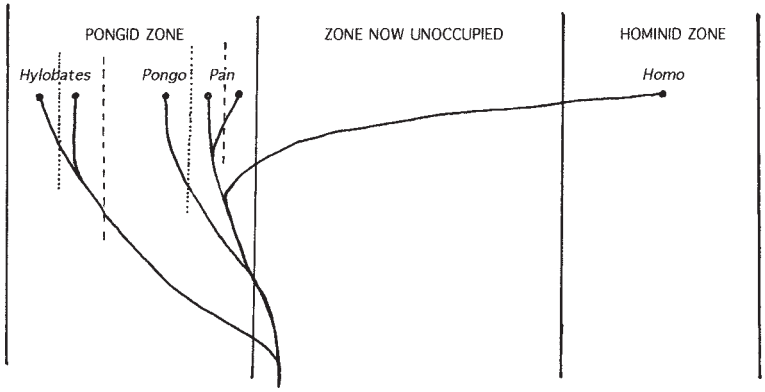
A

PHYLOGENETIC RELATIONSHIP OF EXTANT HOMINOIDS



B

ADAPTIVE AND STRUCTURAL-FUNCTIONAL ZONES



From Simpson (1963): "Dendrogram of possible affinities of recent hominoids in relationship to their radiation into adaptive-structural-functional zones. The two major adaptive zones are bordered by solid lines. Pongid radiation into sub- and sub-sub-zones is schematically suggested by broken and dotted lines. A dendrogram of this sort has no time dimension and does not indicate lineages, and it is probable that divergences of lines showing affinities are topologically similar to the phylogenetic lineage pattern."

Figure 2.1 Contrasting phylogenetic relationships of hominoids: the cladogram in Figure 2.1A fails to show that the African great apes and *Pongo* are more closely related to one another, both structurally and adaptively, than either is to *Homo sapiens*. Figure 2.1B is a phylogenetic tree that illustrates the evolutionary relationships of hominoids according to their adaptive similarities.

molecular biology of great apes and humans. It turns out that biochemically, it is genus *Pan* that is more similar to humans than *Pongo,* whereas the molecular relationships among *Homo*, *Pan*, and *Gorilla* are still unresolved. In contrast, the classification of extant primates used in this book remains conservative:

1. Hominoidea
  2. Hylobatidae
    3. *Hylobates*, *Symphalangus*
  2. Pongidae
    3. *Pongo*, *Pan, Gorilla*
  2. Hominidae
    3. *Homo*

A similar problem has become apparent concerning the term "anthropoids" (Williams and Kay, 1995; Wyss and Flynn, 1995), which has various meanings attached to it by different authors. Such inconsistencies preferably should be avoided.

An even more extreme classificatory scheme that is based on selective genetic information has recently been proposed (Wildman et al., 2003). According to this taxonomy, the two species of chimpanzees, *Pan troglodytes* and *Pan paniscus,* belong in genus *Homo,* which thus looks like this: *Homo troglodytes*, *H. paniscus,* and *H. sapiens*. This proposal is based on the alleged discovery of almost identical DNA structures between the two genera. What the authors did not consider is the startling fact that if their taxonomic rankings were correct, viable hybrids between the three species would have to be possible—which is unlikely at best. Also there are now other studies that came to the conclusion that the degree of genomic difference between genera *Homo* and *Pan* is much greater than Wildman and colleagues (2003) claimed (see also Chapter 14).

A recent review, "Evolutionary [classical] Taxonomy versus Cladism" (P.A. Williams, 1995), clearly shows the inherent problems of any classification system. The author stated (p. 762), "No matter how rigorous their logic, taxonomists need to have wide experience with a group of organisms to make a sound taxonomic judgment." All this confusion about taxonomy and classification is caused by the fact that nature is not the result of a rational and orderly plan, but the result of undirected, irrational evolution. Mother Nature is not "parsimonious."

There is one true phylogeny for life on Earth, and there is also one for the order Primates. The exact details of these phylogenies are difficult to determine. For any one phylogeny, even the correct one, there are many possible classifications. The pursuit of establishing a correct phylogeny is a goal of biological science. The practice of classification necessarily remains an art that requires in-depth knowledge of the animals being classified. It turns out that even the most "parsimonious" classification is hampered by the fact that none of the classificatory methods we know today are totally objective and unbiased by the choices of the

scientists who create them. Misunderstandings in science are often caused by the fact that although humans are able to speak and hear, to listen, write, and read, they often fail to communicate.

Finally, there are three terms we need to know when dealing with various aspects of taxonomy because this terminology is used by taxonomists. In this phraseology, descriptive taxonomy is called **alpha taxonomy;** it deals with those aspects of taxonomy that describe and designate species, typically by using morphological characteristics. The term **beta taxonomy** is used for taxonomic endeavors that arrange species into hierarchical systems of higher categories. The third term is **gamma taxonomy,** and it covers those studies of taxonomy that are dealing with intraspecific populations and phylogenetic trends.

THE TARSIER CONUNDRUM

The external nose in extant primates has been the basis for a classification scheme that started with a publication by Pocock in 1918; Pocock pointed out that prosimian primates have a rhinarium (see also the section in Chapter 9, "Nose and Olfaction"), whereas tarsiers and simian primates (or anthropoids according to yet another classificatory scheme; Simpson, 1945) do not. In the meantime, various primates have been grouped together in modern cladistic arrangements for many reasons, but most obviously according to the presence or lack of a wet nose: the suborder Strepsirrhini (the lowly, wet-nosed prosimians) versus the suborder Haplorhini (combining dry-nosed anthropoids and tarsiers). Yet the two taxa combined in Haplorhini are incongruent behaviorally, morphologically, and functionally. Taxonomic issues become complicated when phylogenetic relationships, fossils, and time frames are added into this taxonomic equation.

Only a single example of what using such incongruent classification leads to will be mentioned here. It is the grouping of genus *Tarsius* with the New World monkey genus *Aotus,* the only extant night monkey, under the category of "nocturnal haplorhines" (Martin and Ross, 2005, p. 12, and many others. See also the section in Chapter 9 on eyes and vision). It is true that these two genera have enlarged eyes because they are both nocturnal, but no further visual synapomorphies between them can be established, for they are different in other aspects of their vision. This lumping together of two anatomically and functionally disparate primates does not result in improved understanding of primate vision or of their taxonomic relationship.

Among extant primates, the separation into the two nose-based groups has caused considerable confusion. With molecular considerations applied to the problem, the situation has been clarified to some extent, placing lemurs and lorises in one category, tarsiers by themselves, and monkeys, apes, and humans

in another category, although the members of the final grouping appear to have split from each other in a trichotomy long ago, and this distant trichotomy cannot reliably be resolved (Yoder, 2003). This also means that tarsiers cannot be compellingly shown to have shared much, if any, common ancestry with either of the other two primate groups; therefore, they probably should stand alone taxonomically. The joint possession of SINE markers of all "haplorhines" (Schmitz and Zischler, 2004) does not necessarily bring tarsiers and anthropoids any closer in phylogenetic separation time: the evaluation of molecular data, such as SINE markers, is still in its infancy and subject to much disagreement (Schmitz et al., 2002). Schmitz et al. (2005) reported that "Three of the 118 markers investigated proved to support the sister taxon relationship between Tarsioidea and Anthropoidea while the remaining markers provided no relevant information on the split in question" (p. 783).

As for morphological similarities between tarsiers and either one of the other two groups, resemblances to both can be found. Again, the issue in deciding whether prosimians or anthropoids is more similar to tarsiers cannot be unequivocally disentangled. However, the dogma of the nose-based cladistic grouping (Strepsirrhini vs. Haplorhini) has become widely accepted among New World primatologists. Therefore, the following statement is surprising:

> In a cladistic classification (i.e., one *designed* to provide a direct reflection of *inferred* phylogenetic relationship), lemurs and lorises are hence allocated to the suborder Strepsirrhini, while tarsiers and simians are allocated to the suborder Haplorhini. *Regardless of the choice of classification,* which is a matter of continuing controversy, in some contexts it is *convenient* to distinguish between prosimians and simians in discussing primate features, whereas in others *it is useful* to contrast strepsirrhines with haplorhines. (Martin and Ross, 2005, p. 2; emphasis mine)

Here is frank admission that some believe it is acceptable to pick and choose freely between taxonomic systems to underpin a preconceived outcome. This clearly contradicts adherence to a stable taxonomy and to an unbiased approach to either alternative.

Unfortunately, some students of primatology have been indoctrinated by misleading statements such as, "tarsiers are nothing but little monkeys." If such students begin their scientific endeavors assuming that the strepsirrhine–haplorhine dichotomy is fact, they may continue to be blinded by the preconception that tarsiers and anthropoids share much in common morphologically, functionally, and biochemically. Starting with such an assumption can bias the outcome of a study.

Chapter 3

A History and Objectives of Primatology

The State of Affairs
History
Primatology as a Branch of Biology
The Future of Primatology
Retrospection and Prediction
Definition of Order Primates

THE STATE OF AFFAIRS

The science of primatology is concerned with the study of those mammals that are most closely related to human beings. Humans, being the most successful and erudite of all mammals, have been fascinated by the challenge of discovering their own place in the complicated realm of nature ever since they began to reason. Our closest mammal relatives constitute the order Primates, which includes four main living groups: prosimians, monkeys of the Old and New Worlds, greater and lesser apes, and humans. Some more distantly related forms such as the tree shrews, colugos, elephant shrews, and opossums may belong in separate mammal orders but are also of comparative interest. Today primatology has blossomed into an important subdiscipline of biology and has developed different focal points such as the study of primate morphology, history, and function as well as primate social behavior and molecular primatology.

Primatology as a distinctive field within biology did not exist until the second half of the 1950s. Despite the fact that magnificent monographs such as those of Owens and Peters on the aye aye had been published in the middle of the ninetieth century, knowledge about primates in general was sparse before the twentieth century.

Even though humans have always been spellbound by their close relatives, the monkeys and the apes, these were regarded for a long time as curiosities rather than our kin, and that learning about them would help us to better understand ourselves. Primates dressed in human attire, such as the organ churning, highly intelligent South American monkey, the capuchin, have played a great part in our history as subjects of amusement and even as pets.

The thought processes leading to the development of primatology took root when Darwin's theory of evolution by natural selection was first applied by Thomas Henry Huxley (1825–95) to interpret the comparative biology of humans and apes. In his 1863 essay, "Man's Place in Nature," Huxley first dealt with many of the topics that have remained important in primatology up to the present day. Such topics include the position of human beings among the other primates and the question of our descent from animals that were of simpler and different grades of organization. He stated without hesitation that human beings had evolved from other animals. Huxley was also one of the first to show in great detail that humans were most closely related to the African apes.

For those who engage in research on the primates, primatology has never seemed more relevant than at present. Arising from diverse beginnings, its subdisciplines are becoming more closely integrated. As many more precise evaluations and data about primates are published, the subject is making increasing contributions to biological studies. With the added recognition of problems related to endeavors of conservation of extant primate species, rapidly encroaching human overpopulation, and the fast expanding demands on the world's environments and natural resources by the multitude of human beings, primatology has become a cutting-edge scientific discipline that provides an information base for strategies that are aimed to protect our planet from environmental disasters. Religious disagreements, human hatred, hunger and preemptive wars are turning this planet into a world of vanishing hope for all primates.

Within the biological sciences, primatology is closest to physical—or biological—anthropology and human biology, disciplines that are specifically concerned with analysis of our own species, *Homo sapiens*—the only species capable of seeking a certain degree of self-understanding.

Despite centuries of developing human self-interest, many aspects of human biology and primatology have only recently been explored. As disciplines concerned mainly with one species, *Homo sapiens*, anthropology and cognition have a unique coincidence of subject and object, but most physical anthropologists also study nonhuman primates as analogs to ourselves. Humans are still fascinated by their near relatives; we continue to be amused, even shocked, by the many parallels between primates and ourselves. There is one big difference between humans and all the other primates: only humans have religion, with all the disturbing consequences it can cause.

HISTORY

One could compile a lengthy account of references to primates in literature, but here a brief outline must suffice. In the fourth century B.C., the philosopher Aristotle (384–322 B.C.), in his *Historia animalium*, initially divided monkeys into three main groups: 1) the *pithekoi*, forms with reduced tails; 2) the *keboi*, forms with long tails; and 3) the *kynokephaloi*, dog-headed forms, namely, the baboons. Pliny the Elder (circa 23–79 A.D.), in his *Natural History*, observed that the primates are much like humans. Later, Galen of Pergamon (c. 130–200) dissected both monkeys and apes and pointed out that they closely resembled humans in their bony skeletons and in their intestinal, muscular, nervous, and vascular systems. He wisely admonished his students to study the primates to gain a better understanding of human anatomy.

Marco Polo (?1254–?1324), who traveled widely in the Orient in the thirteenth century, described strange, small, humanlike creatures. This was perhaps the first reference to gibbons. From Marco Polo's time on, scholars in Europe showed an increasing interest in the natural world. By the sixteenth century, Konrad von Gesner (1516–65) in Switzerland reviewed all he could find about primates for his *Natural History*. This outstanding early work reflects, together with a certain credulousness and the superstition characteristic of those times, the inception of ecstatic feelings about the wonders of the natural world. In 1699, an English scholar, Edward Tyson, published the first study of the anatomy of an ape, basing his work on the body of a "pygmy" from Angola that was later understood to be that of a young chimpanzee. Despite its early date, this study was remarkably accurate. In the 300 years after this study, many descriptions of monkeys and apes were published in Europe. Their authors included the well-known natural historians Johann Friedrich Blumenbach, Georges Buffon, Georges Cuvier, Johann Christian Polycarp Erxleben, Johann Karl Wilhelm Illiger, Richard Owen, Thomas Pennant, and Étienne Geoffrey Saint-Hilaire, all of whom added significantly to knowledge of primates.

Attempts to organize the taxonomy of primates began in Sweden in 1758 when the naturalist Linnaeus published a remarkable work. This was the tenth edition of his famous book, *Systema Naturae*, in which he named one of the orders of mammals Primates. In this order, he placed, together with humans, a genus of ape, of monkey, of lemur, and of bat. Twenty-three years before this publication, in the first edition of *Systema Naturae*, he had already grouped humans, apes, and monkeys together, as well as (with unintentional humor) the sloths. These he had ranked together in one group, the "anthropomorphic" or humanlike creatures. Amazingly, it turns out that several of the large, subfossil lemurs from Madagascar have been called "sloth lemurs" because of their astonishing morphological similarity with sloths (E.L. Simons et al., 1992; Jungers et al., 1997). For his objective, Linnaeus systematically ranked animals only according to their

obvious, overall similarities and drew no conclusions about a place in nature for humans. Nevertheless, his bold step in uniting humans with animals caused much protest, and others soon began to reassert the uniqueness of humans by separating them as distantly as possible from all other living organisms.

Thus, Johann Friedrich Blumenbach, in 1719, separated humans from an embarrassingly close relationship to apes by creating two orders. One was the order Bimana (meaning two handed) for humans and a second the order Quadrumana (meaning four handed) for all remaining primates. The same distinction was made by Baron Cuvier nine years later, and the use of these two terms persisted for nearly 100 years thereafter. Differing with this usage, Illiger (1811) took as the central concept of his systematics the uprightness of humans and established for them the order Erecta. Owen (1863) believed that the difference between humans and the other primates was great enough to create a much higher category in the animal kingdom for humankind. He coined for humans the subclass Archencephala, those with the most advanced kind of brains.

Beginning in 1859, Darwin brought a fresh point of view to the discussion of our relationship to other animals. For him, the similarities between different kinds of organisms were due neither to design nor to chance. He recognized that the relationships of living things to each other showed that the similarities among animals are due to common descent. Darwin thereby made a critical push toward a new kind of biological thinking, although he avoided, at that time, the implications of natural selection as the basis for the origin of *Homo sapiens*.

A few years later Thomas Henry Huxley (1863) took his significant step of showing the close relationship between humans and African apes in his article *"Man's Place in Nature."* Finally, Charles Darwin (1861/1871) himself, in *The Descent of Man*, made an elaborate study comparing human and animal. From then on, many scientists throughout the last decades of the nineteenth century and during the early part of the twentieth century dealt with the close ties between humans and the other primates as the full impact of the biological nature of humans became evident. Together, these publications have shown that primatology provides a necessary background for understanding the main stages of human evolution.

Because of the identity of subject and object, a high level of subjectivity characterizes much that has been done in anthropology, and this has been intruded into the study of our species. Primatology as a whole provides new and better sources of more objective information that should help to clarify some of the phases of understanding human evolution that have been controversial in the past. Consequently, it is hoped that *Homo sapiens* may be dealt with more objectively if it is recognized as merely one species of the order Primates.

PRIMATOLOGY AS A BRANCH OF BIOLOGY

Biology is essentially a comparative science. The relationships of organisms to one to another, their similarities and their distinctions, are the bases of contrast. In and of itself, a single biological object has no context. Because it is impossible to avoid recognizing the many similarities between humans and apes, the study of humans as not different from primates gains both strength and objectivity in a comparative approach. Were it not for the uniqueness of humans in the natural world, there would be less importance to primatology; there would be no more interest in this particular mammalian order than in the others. Some other orders are more diverse than Primates—Rodentia, Chiroptera, Artiodactyla—and each mammalian order has evolved its own distinctive specializations, such as the flight of bats. As many of the strengths of present-day physical anthropology are derived from primatology, primatology in turn is dependent on understanding other animals, especially other nonprimate mammals. Thus, primatology cannot be taken as an entirely self-contained field.

In considering more recent advances in primatology, one thinks automatically of such leading scientists in the field as the English anatomist Sir Wilfrid Le Gros Clark or of Adolph Hans Schultz of Zürich, both of whom, from early in the twentieth century, began publishing a series of fundamental contributions to primatology.[1]

Wilfrid Edward Le Gros Clark (1896–1971) was a young physician and officer in the English army when he was sent to Borneo. There, in his spare time, he focused his interest on the study of human biology, primates in general and tree shrews, as well as tarsiers in particular. His keen curiosity and knowledge laid the foundation for a prominent career in anatomy and primatology after his return to Great Britain. He published detailed studies about the tree shrews and was appointed professor of anatomy at Oxford University in 1934. His thoughts and books about human and primate evolution became the leading texts for generations of biological anthropologists and still have great applicability to the formulation of theories of primate and human evolution. These influential books are as follows: *Early Forerunners of Man* (1934), *History of the Primates* (1949), *Antecedents of Man* (1959), and *Man-apes or Ape-men?* (1967). He was also one of the leading scientists who discovered and exposed the "Piltdown Man" forgery.[2]

[1]A book about A.H. Schultz that was published in 2004 by Chaoui fails on two levels. The author sadly misrepresents the complex personality of a scholar who arguably was the most preeminent primatologist of his time. Also, Chaoui unfortunately mangles the intricate complexities of the German language.

[2]In 1912, a sensational announcement proclaimed that a Paleolithic human skull and mandible had been discovered in a fossil-bearing quarry near Piltdown, England (Dawson and Smith Woodward, 1912). This find immediately caused much controversy, and 40 years later was revealed to be a hoax by John S. Weiner, Kenneth P. Oakley, and Wilfrid E. Le Gros Clark (1953; Weiner, Introduction and Afterword by Springer, 2003).

Five years older than Le Gros Clark, the young Swiss anthropologist Adolph Hans Schultz (1891–1976) went to the New World in 1925, where he was appointed professor of anatomy at Johns Hopkins University in Baltimore. During his tenure there (1925–51) he launched many expeditions to far-flung corners of the world to study and collect living primates. Schultz assembled an impressive collection of primate skulls and skeletons, as well as primate fetuses. He was especially intrigued by the variability of living primates and published many scientific reports that document primate morphology in comparison with the anatomy of modern humans. In 1951, Schultz returned to Zürich, Switzerland, to take over the directorship of the Institute of Anthropology at the university there. He brought a sizable collection of primate skeletons and soft tissues that he had collected while at Johns Hopkins with his own personal funding. Schultz established one of the most extensive primate collections at the institute in Zürich and added to this collection during his lifetime. He published a host of scientific papers about extant primates that are still fundamental resources of information about measurements and details of primate morphology for today's students.

Early on it was believed that individual monkeys within a species were very much alike, if not identical, to each other. Thus, it was not considered incorrect to generalize from findings based on one or two individual monkeys to the whole species. Now we know that the high degree of present human structural and behavioral variability extends not only to other primate species but to nonprimates as well. This fact was initially documented thoroughly and extensively by the father of primatology, Adolph Hans Schultz. The significance of variability in morphological studies was taught at Johns Hopkins under Schultz's tutelage and in Zürich to the extent that young students of zoology who took his courses in primatology tended to protest against the focus on variability. These students were still being taught in other classes that all animals belonging to one species were morphologically identical to each other, which appeared to be a much simpler concept. We now know that organismal individuality is also expressed in the uniqueness of every creature's DNA. Today this fact is widely applied in forensic investigations.

It is clear that because of the high individual variability of primates, we have a rich source of possible error in the interpretation of fossil primates. By understanding the range of variation found within and between species of related living primates, we can avoid this error. This knowledge of variability has become a principal basis for the latest taxonomic revisions of fossil finds. In general, such revisions suggest grouping of fossils that previously had separate names, and this in turn makes the picture of primate evolutionary history easier to grasp.

In retrospect it becomes evident that the term "primatology" seems to have been first used in print as recently as 1941 by T.C. Ruch. Even though a comprehensive focus on primates is a comparatively recent scientific development,

the literature in this field has been expanding rapidly since the late 1950s. Now, more than 40 years have passed since the introduction of *Folia Primatologica*, the first regularly published journal reporting research on primates, and it is still going strong. In the meantime, numerous other scientific magazines such as the *International Journal of Primatology* and the *American Journal of Primatology* have joined the primatologists' printed forum. Universities all over the world have initiated educational programs in primatology, and numerous students focus their life goal on the study of primates. In 1968, the International Society of Primatology had its first meeting at the University of Gießen in Germany and was soon followed by other national and international societies of primatology.

The recognition that humans are unique in many ways but at the same time nothing but a mammal biologically is as ancient as Linnaeus's (1758) decision to classify humans among primates. This biological character of our animal nature has never again been seriously questioned. Great thinkers and naturalists had already early documented the similarities between primates and humans. Anthropologists and paleontologists, making use of the analogies to be drawn from the study of extant primates, have endeavored to reconstruct the natural history of humans and primates.

This history often has had to be interpreted from meager evidence. The last decade, however, has yielded many new fossil finds that now allow more detailed insights into primate and human evolution. Primate paleontological, behavioral, and molecular research continue to provide important kinds of clues to this particular type of study. The late development of this field is indicated by the fact that one of the first academic courses in primatology was taught by Elwyn L. Simons as recently as 1959. Elwyn Simons is also credited to be the mastermind of a new field in science: paleoprimatology (Fleagle and Kay, 1994). The field of primatology covers not only the study of primates but ultimately focuses on the human quest to gain an ever-increasing understanding of the most influential of extant primates, *Homo sapiens*, ourselves.

THE FUTURE OF PRIMATOLOGY

The field of primatology covers such varied research areas as anatomy, locomotor behavior and morphology, typology and variation, cell and molecular biology, and genomics as well as primate and hominid paleontology, growth and development, social behavior, taxonomy, reproductive biology and conservation. For example, one major scope within primatology centers on the interpretation of body form and function. Form and function are closely interrelated in the morphology of bones and teeth. By studying the movements of living primates, we can begin to identify the relationship between morphology and function in these mammals. With caution, and within limits, such functional interpretations

can (by analogy) be applied to fossil forms to reconstruct the function of extinct animals. This can only be done effectively when we know as much as possible about the lifestyle of present-day species. In fact, even today it would be an exaggeration to imply that we know well the biology of most living primates, but nonetheless the groundwork has been laid. Fundamental studies on the locomotor behavior of living primates are now being undertaken in increasing numbers and with advancing precision. Modern video and biomechanical technology has made possible more intricate insights into locomotor behavior. The discussion of terminology for basic primate locomotor types continues unabated. This is the case because extant primates exhibit a wide variety of habitat uses and locomotor behaviors. For example, it long seemed impossible to reconstruct with confidence the locomotor behavior of earliest hominids. Now, with new comparative knowledge gained from other living primates and from modern humans we can approach the problem with increasing confidence. There has been a lengthy debate about whether the ancestors of humans, before they became true upright walkers, were brachiators living in the forest canopy or, alternatively, whether they were quadrupedal branch runners and climbers. From fossil finds and comparative studies made in recent years, we have now gained increasing clarification about these alternatives. The supposition that wild gorillas and chimpanzees were brachiators (resembling the small Asiatic gibbons) persisted for a long time in the literature without verification from field observations. In the meantime, long-term field observations have shown that gorillas virtually never move by means of arm swinging and that chimpanzees, as adults, rarely arm swing during locomotion.

Comparative research on a broad range of primates has shown that we are not only very different from other primates in aspects such as bodily proportions and the construction of skull and face but also in our complex way of life. However, biochemical findings of the last few years have indicated great similarities between humans and the African apes, especially the chimpanzee. The intrinsic complexity of a single individual increases as the structural and behavioral organization of animals becomes more advanced. This is especially true for monkeys and apes.

The course of human evolution is now documented by an ever-increasing number of fossils, and there will surely be collections of many more if the search for human forerunners can be continued. The rough outline of the successive phases in the history of humans during the last 3 million years can now be drawn with general agreement. Recent finds appear to have doubled this age to 4 million for the earliest *Australopithecus*, but the period from 2 to 4 million years ago is still not clearly understood. *Australopithecus* has a skull that is outwardly more reminiscent of the apes than that of modern humans, but the teeth are not apelike. There is definite evidence that by about 3.5 million years ago at least, some hominids had already achieved an upright gait.

RETROSPECTION AND PREDICTION

Darwin and some of his contemporaries already recognized that humans and apes were close relatives. Recent research has shown that this resemblance is further evident when one examines the microstructures of these primates. Today a close relationship between humans and apes is reinforced by the most modern methods of cytology, serology, genetics, and molecular biology. It is clear that many characteristics of the human organism differ only quantitatively from other primates. It is, therefore, more the exaggeration of certain characteristics in humans rather than qualitative differences that makes us distinct.

A hypothesis of the Dutch scientist Louis Bolk, who in 1926 suggested that humans are nothing but apes who have retained infant proportions into adult stages, has received broad circulation and regularly resurfaces in formulations of scientific ideas. This speculation that originated with Bolk is fascinating only at first glance. Examples of slow development in the ontogeny of humans, which would substantiate Bolk's theory, can easily be found; for example, the late fusion of the sutures between the bones of the brain case. It is also easy to find examples of speeding up rather than slowing down in human embryonic development, such as the early fusion of the elements of the sternum. When one has the advantage of knowing the developmental history of a broad spectrum of different primates, it becomes obvious that the developmental differences between humans and the other primates are achieved by a combination of speeding up (acceleration) and slowing down (retardation). New research on comparative behavior and cognition of primates, both in adult societies and during the individual's behavioral growth, has changed our thinking. The dependency of the offspring on the mother up to puberty was thought to be unique to humans. Now we know that here, too, we have only differences of degree between humans, apes, and monkeys. Newborn apes show as much need (but for a shorter period) for the mother's care as humans do. Although juvenile development, the learning period, the onset of puberty, and the following phases of life are definitely shorter in apes than in modern humans, all follow the same fundamental sequence. Even newborn monkeys, which are more self-sufficient than infant humans or apes, cannot survive on their own in the wild without the mother—and without the whole troop in many cases. Because young monkeys have much to learn and because, within the troop, experiences are passed from generation to generation by example, we see here the beginning of different traditions varying from troop to troop within the same species.

Young monkeys must practice activities that will be important for their integration into adult social life. During play they come to understand their physical abilities. They learn how to defend themselves, how to help themselves in difficult circumstances, and how to escape. Juveniles isolated from their mothers and from the group do not develop the proper behavioral repertoire for

social integration. Such monkeys cannot later develop the capacity for complex social interactions with con specifics.

Thus, the mother and her care are very important during the first stages of life. After this, play with other infants is necessary for later behavioral development. Such findings are important to understanding human behavior and in all attempts to reconstruct possible early human or prehuman behavior. Nevertheless, it is simplistic to suppose that behavioral observations on the nonhuman primates can be used directly to infer the early behavior of humans. Play in monkeys, in human children, or among human ancestors may have, or have had, somewhat different functions. However, using the cladistic view, if play behavior does occur in most primates, it likely occurred in their common ancestor.

Thus, comparative research among primates can demonstrate that human ontogeny after birth indeed has a certain uniqueness. All phases of life—childhood, youth, adulthood, and old age—are absolutely longer in humans than in any other present-day primate. The difference of *Homo sapiens* here is particularly marked in the later maturation of individuals together with the continued accumulation of individual wisdom and knowledge, a process on which much of human civilization depends. This long period of old age is a new development in organic evolution. We all know that the human life span long outlasts the reproductive period, and in fact much of what it means to be human depends on this particular component of human existence.

The living primates provide us with a range of adaptive diversity that by analogy allows us to speculate on the adaptive nature of our ancestors. Thus, the combined field and laboratory studies of primate behavior and adaptations enable us to learn more about our relatives the primates and to enrich understanding of ourselves and our origins.

Primatology has many practical applications. For example, a whole series of biomedical questions have been considered and a variety of medicines and medical procedures were developed through the study of captive primates. Extensive laboratory analysis of primates, especially monkeys, has been devoted to the study of nutrition, infectious diseases, deficiencies of the heart and circulatory system, arteriosclerosis, Alzheimer's disease, diabetes, and cancer. Not the least of their contribution was the involvement of nonhuman primates in the initial stages of space exploration. Thus, our relatives, the nonhuman primates, have been and still are invaluable acolytes in the endeavor to improve human life and self-understanding. In this context we must not forget that judicious care has to be taken to protect our closest relatives from extinction. We must be the guardians of our world, not those who exploit it into oblivion.

Primatologists increasingly raise their voices in warning that the wild populations of many primates are under imminent threat of abolition. Because the survival of our planet's ecosystems is a human responsibility, we must ensure the future of all living organisms and not just our uniquely successful own kind. If lemurs, lorises, tarsiers, monkeys, and apes all should become extinct, we will

not only lose the chance to understand further the pathway through which we ourselves arose, we will also turn our world into a bleak and desolate place. Even though natural extinction is not an uncommon event, we alone can avoid being the cause of animal extinction.

Development of primatology in the last 50 years has not only produced new comparative insights but has also shown that there are still many aspects of primate history and biology about which we know very little. Consequently, beyond present understanding, broad topics open up for future research and improved understanding. Primatology today is a vigorous and important science. A distinct separation between ourselves and the most closely related nonhuman primates does not exist. Yet *Homo sapiens* stands out as much more than an animal: our species alone exhibits the ability to reason and speak, to write and read, to plan for the future, and to produce civilization, culture, science, and religion. We are also the only primate that has put into jeopardy the future of its own species as well as that of other living things. Human overpopulation may ultimately lead to the destruction of our own living sphere, and consequently to the end of humanity.

Although in biology, evolutionary processes are usually complex and influenced by multiple factors, it appears that there are now two powerful and crucial trends at work on our planet. One is the ever-increasing population of the human species. Humans are a major force that make a plethora of demands on Earth's resources. Glaciers are melting, and temperatures are rising. On the other hand, the human mind has evolved to be able to recognize that we must try to protect the biotic diversity as well as the abiotic components of Earth's environments, such as water, minerals, metals, and energy, from destruction.

Between these two factors—which are mutually irreconcilable—there is an evolutionary conflict in progress, and it is questionable whether the defense of Earth's resources can be sustained under the multifaceted human onslaught. The crucial question, one that will only be answered with time, is whether it will be possible to put the defensibility factor to work soon enough to prevent the extreme outcome of this contest: disappearance of many or most of Earth's biotic and abiotic resources and, ultimately, total self-destruction of the human species.

There is no doubt in my mind that Earth will be just fine without humans, and evolution will restart itself for a new, most likely different and exiting evolutionary adventure in the millions of years to come.

But we won't be around to study it.

DEFINITION OF ORDER PRIMATES

The Linnaean order Primates has no doubt stimulated more scholarly and popular interest than has any other major group of mammals. These vertebrates have a long history. Ostensibly, they first appeared in the form of the late

Cretaceous genus *Purgatorius*, a genus that was described by a single tooth (Van Valen and Sloan, 1965; K.D. Rose, 1995). In addition to the interest arising from the fact that humans are ranked in this mammalian order is the diversity of the group, which includes 61 extant genera with 252 species compared with more than 200 fossil genera—218 according to Shoshani et al. (1996)—containing 405 species. This living diversity makes it the seventh most populous order of mammals in terms of generic groups; the orders Marsupialia, Insectivora, Chiroptera, Rodentia, Carnivora, and Artiodactyla have more genera than the order Primates. The great generic diversity among primates is emphasized by the high variety of locomotor and social systems, and both systems probably show greater variation within the order than can be found within any other major mammalian group. Adding to this entire series of living forms that provide a sequence of grades of organization (roughly approximating a scale or ladder of nature) are the great variety of fossil genera. There are at least twice as many fossil genera as there are living genera. The number is now over 120 and rising every year with the description of new discoveries from the distant past.

A delineation of the order is difficult because many of the characterizing features are not unique to primates (for detailed discussion, see Martin, 1990). Rather, the definition of the order Primates depends on a shared combination of traits, any one of which can be found independently in other mammalian orders.

Primates can be defined as placental mammals having orbits encircled with bone, clavicles, and flat nails on at least some digits. The brain tends to be large relative to body size and shows a posterior lobe and triradiate calcarine sulcus (situated posterior on the internal aspect of the occipital area of both cerebral hemispheres and said to be typical for most primates) as well as a sylvian fissures (also typical for primates, situated on the outside of the hemispheres and separating the frontal lobe from the temporal lobe). Typically, in primates there are single offspring and two pectoral (in contrast to abdominal) mammae, but the number of bilaterally paired mammal glands has been recorded to be dependent on the regular number of offspring in a litter (Schultz, 1948; Gilbert, 1986). The innermost digits on the extremities are opposable. Males have a pendulous penis and scrotal testes (compared with scrotum and testes being attached to the lower abdomen or positioned inside the abdomen). All primates have a large caecum. Their cheek teeth tend to be simple and low crowned, often with secondary development of surface wrinkling and upper molar hypocones (Hunter and Jernvall, 1995).

The order Primates has two suborders: Prosimii, the prosimians or premonkeys, and Anthropoidea, anthropoids (or more correctly anthropoideans)—higher primates, including Old and New World monkeys, apes, and humans (Kay and Williams, 1994; Williams and Kay, 1995; Wyss and Flynn, 1995).

Besides these two suborders of the mammalian order Primates, there is another group of mammals, the tree shrews or tupaias (family Tupaiidae), that many authorities (Simpson, 1945; Martin, 1990) formerly classified in Primates. Present evidence—although ambiguous—places them as a generalized side branch of insectivores or as order Scandentia. It is a reflection of the taxonomic uncertainty that has created an order separate from Primates for the tree shrews. They have been removed from the order Primates because they seem to be rather different from primates in having high reproductive rates and because it was unclear which mammals were their closest ancestors. Despite the trend to classify tree shrews apart from the order Primates (see Hill, 1953; Van Valen, 1965), little work has been conducted to justify that they are actually closer to other Insectivora, for which the principal subdivisions have long been separate, at least since the Cretaceous period. Even if tree shrews are considered to belong to an order separate from primates, they do indicate fairly closely what we think the Cretaceous forebears of primates looked like. Hence, primatologists have often kept and studied tree shrews together with primate colonies. For these reasons, tree shrews are included in this book, together with our survey of living prosimian primates. For those who wish to consider this question further, see Luckett (1980) and Martin (1990). Despite extensive analysis by many authors, the question of whether to exclude the tupaiids from the order Primates has still not been resolved (Rose, 1995). The three mammalian groups reviewed here can be defined as follows:

1. **Tupaiiformes.** An infraorder (or order) resembling primates in the possession of a number of characteristics, such as having a relatively large braincase, eye sockets rimmed by a circle of bone, and males possessing a pendulous penis. Tupaiids differ from primates in lacking flat nails on any digits, all of which are clawed with the large toe aligned with the other digits; they also differ in having the bony floor of the middle ear composed of a different bone from that which encloses the inner ear. Lastly, they have either premolar-like upper canines or none.

2. **Prosimii.** A suborder of primates differing from tree shrews and other nonprimates because they have a petrosal bulla of the ear, typically a higher degree of orbital frontality, and flat nails on some or most of the digits. Hind limbs are usually considerably longer than forelimbs. Prosimii differ from Anthropoidea because they have no postorbital closure, but a postorbital bar; no fusion of the metopic suture between frontal bones; and no symphyseal suture between the two parts of the mandibles; these are sutures where closure either does not occur or appears late in individual development. Prosimii are also different because they typically have procumbent lower incisors (or toothcombs) and at least one toilet claw on the hind foot.

3. **Anthropoidea.**[3] A suborder of primates in which eye sockets are closed from behind by bony plates and in which there is midline fusion of the two halves of the mandible and in the forehead of the primitively dual frontal bones into single bones (mandible and frontal). The auditory region is characterized by loss of the stapedial artery, a branch of the carotid artery supplying blood to the brain, and its replacement by a large promontory artery.

[3]The term "Anthropoidea" was first introduced by Mivart (1864), who thus contrasted all higher primates "Anthropoidea" to all lower primates "Lemuroidea." When "Anthropoidea" was elevated to the rank of "suborder" that in turn contained the two superfamilies Ceboidea and Cercopithecoidea, a linguistic quandary was created: the name of any taxonomic group ending with "-oidea" used to indicate a superfamily. The now widely accepted use of "suborder" Anthropoidea with two superfamilies, Ceboidea and Cercopithecoidea, all three ending with the suffix "-oidea," is somewhat perplexing, but adopted in this text: in English taxonomy all rankings above superfamilies may be assigned any suffix.

Chapter 4

Survey of Living Primates

Survey of Living Scandentia and Prosimii
Infraorder Tupaiiformes (Schultz, 1953)
Infraorder Prosimii
Infraorder Lemuriformes (Gregory, 1915)
Infraorder Lorisiformes (Gregory, 1915)
Infraorder Tarsiiformes (Gregory, 1915)
Survey of Living Anthropoidea
Infraorder Platyrrhini—New World Monkeys
Infraorder Catarrhini—Old World Monkeys

Any researcher's account about primates, morphological and behavioral, largely depends on the reports by other primatologists. Unfortunately, such communications are frequently based on scanty observations or secondhand information. The following discussions therefore should be regarded as tentative and not always reliable. Examples of such misrepresentation are the stories about the elusive South American species *Callimico goeldii*. Recent long-term observations in the natural habitat have shown that the information previously believed to be true could not be corroborated in the field. *Callimico goeldii* does not habitually locomote in an upright leaping manner (although it occasionally will do so), nor does this small primate live in or prefer bamboo forests (Christen and Geissmann, 1994, contradicting statements in, e.g., Fleagle, 1988; but see also Garber et al., 2005).

One of the most recent discoveries and descriptions of new anthropoid species is that of *Macaca munzala* from northern India (Sinha et al., 2005; see Figure 4.1) and *Rungwecebus kipunji* from Tanzania (Davenport et al., 2006).

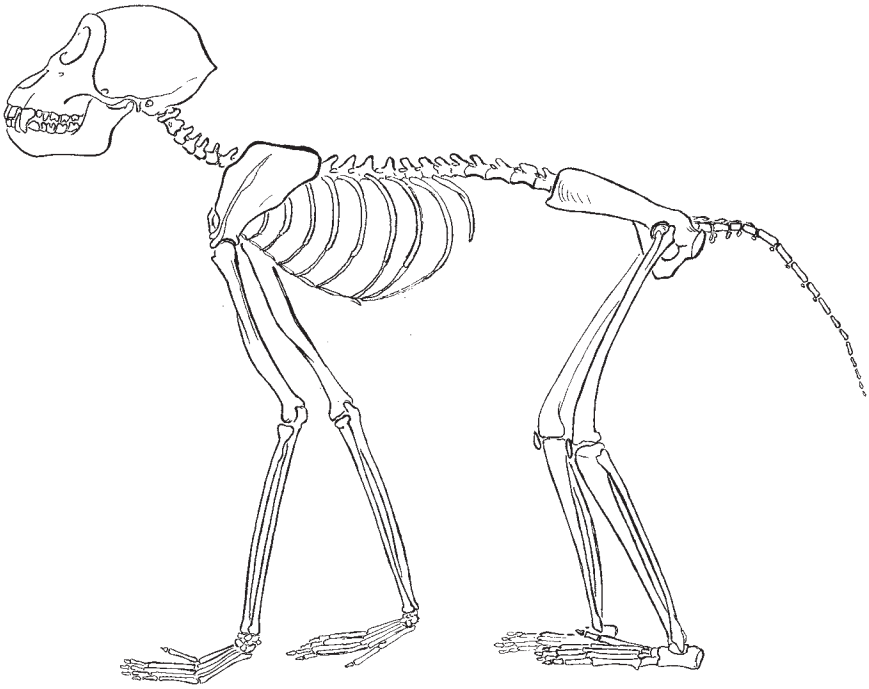


Figure 4.1 Skeleton of *Macaca mulatta*.

SURVEY OF LIVING SCANDENTIA AND PROSIMII

INFRAORDER TUPAIIFORMES (SCHULTZ, 1953)

Family Tupaiidae (Mivart, 1886)	
Subfamily Ptilocercinae (Lyon, 1913)	
Ptilocercus (Gray, 1848)	*Ptilocercus lowii*
Subfamily Tupaiinae Lyon 1913	
Tupaia (Raffles, 1821)	*Tupaia glis*
	Tupaia nicobarica
	Tupaia splendidula
	Tupaia javanica
	Tupaia gracilis
	Tupaia picta
	Tupaia dorsalis
Subgenus *Lynogale* (Conisbee, 1953)	*Tupaia (Lynogale) montana*

	Tupaia (Lynogale) minor
	Tupaia (Lynogale) tana
	Tupaia (Lynogale) palawanensis
Anathana (Lyon, 1913)	*Anathana ellioti*
Dendrogale (Gray, 1848)	*Dendrogale murina*
	Dendrogale melanura
Urogale (Mearns, 1905)	*Urogale everetti*

As we have already seen in Chapter 3, this group of relatively unspecialized arboreal placental animals may well give us a general impression of what the earliest forerunners of the primates were like, and therefore they are of considerable interest to primatologists regardless of the order in which they are placed. The lengthy debate about whether these animals should be placed with Insectivora or Primates (see Luckett, 1980; Olson et al., 2004) demonstrates that they occupy a broad transitional position between certain members of these two orders. The intermediate anatomical characteristics of Tupaiidae certainly suggest that this type of mammal and the primates were interrelated in origin.

A first impression of the behavior of these small animals is one of intense nervous tension. They show considerable size range from species to species, and their general body form differs from any prosimians. Tupaias look more like squirrels than lemurs, except that their long and somewhat pointed snout resembles the latter. The subfamily Tupaiidae contains two subfamilies, Tupaiinae and Ptilocercinae.

The subfamily Ptilocercinae contains one genus, *Ptilocercus*, with a single species, *Ptilocercus lowii* (Sargis, 2002). This monotypic species occurs in the tropical rain forests of northern Borneo, the island of Bangka, the south Moluccas, and northern Sumatra as well as in nearby outlying islands. The species' common name is the pen-tailed tree shrew. It is a small-bodied form (body and head length 12–15 cm, tail length 16–18 cm).[1] The forearms are relatively long, averaging about four-fifths of leg length. The intermembral index for *Ptilocercus* averages 80. The intermembral indices are determined thus:

$$\frac{\text{humerus} + \text{radius} \times 100}{\text{femur} + \text{tibia}}$$

Using this index, one can see that animals with forelimbs and hind limbs of equal length score 100, indices smaller than 100 reflect longer hind limbs than forelimbs, and numbers above 100 indicate proportionally long forelimbs. See Figures 4.2 and 4.3 for comparisons of limb proportions.

The tail is tufted on the sides of the distal third, or that away from the body. This tuft is flat and gives the impression of a feather. In the proximal region, the

[1]Body size is the head plus body length if not otherwise indicated.

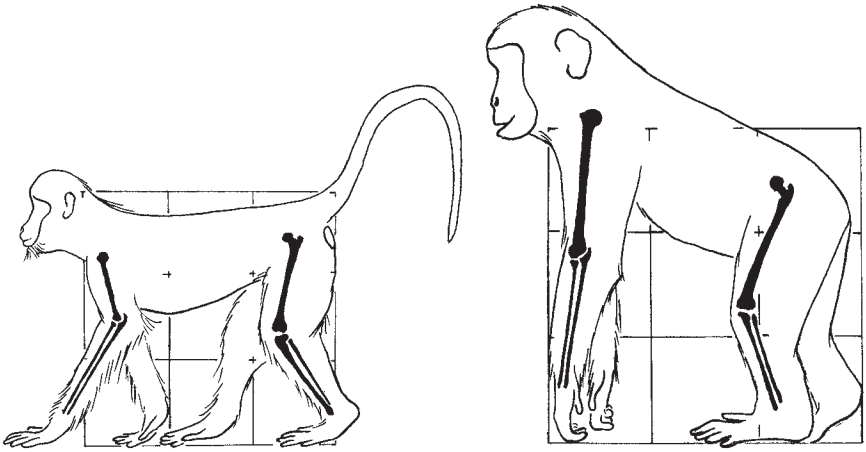


Figure 4.2 Comparing the limb proportions of *Macaca* with *Pan*.

two-thirds near the body, the tail is sparsely haired. Moreover, the bare part is scaled, and each scale is followed by three short hairs. The large, mobile, and divergent ears are unlike those of the Tupaiinae in form and are relatively large for an animal its size.

In many characteristics *Ptilocercus* stands even closer to a hypothetical basal placental than do the tupaiines in appearance and behavior. "Pen-tails" are crepuscular (active at dawn and dusk) and nocturnal (active at night), and like tupaiines they inhabit the lower canopy of the forest. Their eyes are relatively larger and more frontally oriented than in Tupaiinae; the snout is somewhat shorter. These mammals have been said to feed primarily on insects and occasionally on small lizards. *Ptilocercus lowii* builds nests in tree holes or in the forks of branches.

The subfamily Tupaiinae contains four genera. All four genera are active during the day (or diurnal): ***Anathana***—the Indian tree shrew has only one species, *A. ellioti*. It is 175 to 200 mm long with the tail measuring 160 to 190 mm. *Anathana* is found on the Indian subcontinent south of the Ganges River. Its back is spotted brown and yellow with a reddish hue. The underside is whitish or buff. A light-colored shoulder stripe is present. It has comparatively large, haired ears. It forages for insects and digs worms. It appears to be largely solitary. Genus ***Dendrogale,*** the small smooth-tailed tree shrew, has two species. *D. murina* is found in eastern Thailand, Cambodia, and southern Vietnam. *D. melanura* occurs on the island of Borneo. Head plus body length varies between 100 and 150 mm, and the length of the tail between 90 and 145 mm. *D. murina* is light in color and has facial markings: a black line that extends from the base of the whiskers over

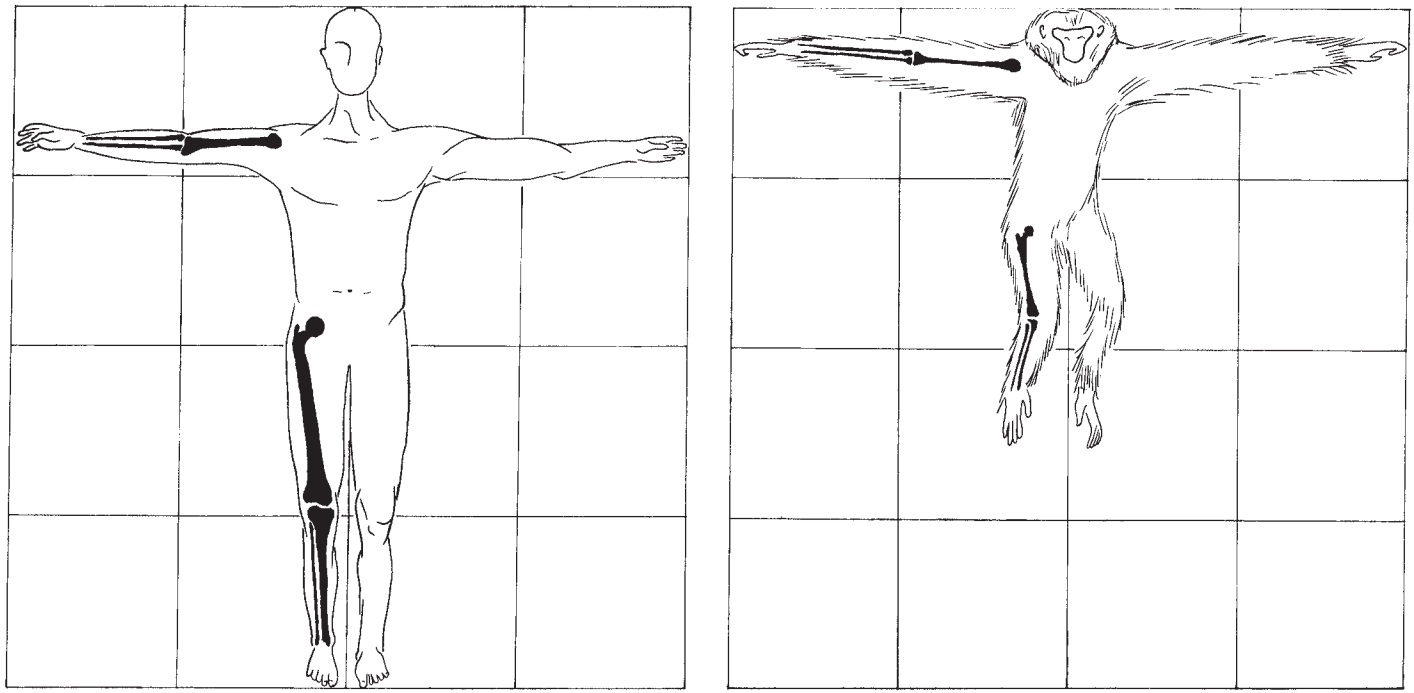


Figure 4.3 Comparing the limb proportions of *Hylobates* with *Homo*.

the eye region to the ear, and buff-colored lines above and below the ear. Its back is black to brown, and the under parts and inner aspects of the limbs are buff colored. *D. melanura* is dark overall with a dark orange hue. The undersides are light brown. This is the smallest member of the family Tupaiinae and has a short-haired, round tail. *Dendrogale* is the most arboreal of the genera. It roams in areas that are 900 to 1500 m high. Genus ***Urogale***—the Philippine tree shrew, has only one species, *U. everetti*. It is found on the Philippine islands of Mindanao, Dinagat, and Siargao. It is 170 to 220 mm in length with a tail length between 115 to 175 mm. It is the largest of the tree shrews. The back is brown and the underside orange red, being lighter in the chest region. There is often an orange shoulder stripe. It has an elongated, rather pointed snout and an even-haired, round tail. Its second pair of incisors is enlarged and canine shaped. The best documented genus, ***Tupaia,*** the tree shrew, has 11 species (but see also Olson et al., 2004) that have been assigned to two subgenera. Four species were formerly assigned to subgenus *Lynogale* (see also Martin, 1984). Species of genus *Tupaia* occur from eastern Nepal to southeastern China and the Malay Peninsula; on the islands of Hainan, Sumatra, Java, and Borneo; and on many of the small islands in the region. In this genus the body size ranges from 140 to 230 mm, and the length varies between 100 and 300 mm. Its tail is bushy, but the body is overall less densely haired than the other genera. Its back is dark, often almost olive-colored reddish, brown, or black. The underside is lighter than the back. The tail is rather bushy but naked on the underside. The general appearance is similar to squirrels, although the snout is generally more pointed. In fact, the Malay word *tupai* means "squirrel." The eyes are relatively large, and the snout has a glandular rhinarium or wet skin, as in the dog or cat. Their ears are immobile and lie flat against the head, having a shape and general outline that rather closely resembles that of humans. In *Tupaia,* the hind limbs are slightly longer than the forelimbs, and the intermembral index falls around 73, much lower than in *Ptilocercus.* All fingers and toes of tree shrews have curved and pointed claws. Tupaias appear to have greater dexterity in holding food items than do squirrels. The elongated and narrowing skull of the tree shrew, its laterally directed but comparatively big eyes, its long bushy tail, its nearly equal limb length (legs are somewhat longer than arms), and the rapidity of its nervous movements combine to give the impression that these animals are more primitive than true primates. Tree shrews seem to live in pairs and are known to have a high level of intraspecific aggression. They sleep in nests that they build in tree holes and other suitable places, and the young are born and raised in these nests. In contrast to most primate species, tree shrews have multiple births or litters, and the young are left in a nest. Tupaias are more active during the morning hours and the early evening than during the middle of the day. Tree shrews occasionally eat seeds, fruit, and shoots, but more often insects, insect larvae, small lizards, birds and birds' eggs, and even snails; in other words, they are omnivorous.

Infraorder Prosimii

Included in the suborder Prosimii are four extant families from Madagascar—Cheirogaleidae, Lemuridae, Indriidae, Daubentoniidae—and two families from Africa and Asia—the Asian and African Lorisidae. Subfamilies include Lorisinae and Galaginae and the Asian Tarsiidae, although some regard the Tarsiidae to be Haplorhines and thus include them in Anthropoidea.

Compared with the other primate suborder Anthropoidea (including all the monkeys, lesser and great apes, and humans), many extant Prosimii (or lower primates) are in general smaller, simpler, and less advanced animals. Relative to body size, the brain of all prosimians is comparatively small, and many of the prosimians do not look like monkeys but more like primitive mammals. Among primates the intermembral index is an invaluable measure of the very heterogeneous activities. The long skeletal elements of the limbs have widely differing proportions in primates. These proportions express primary differences in the mode of locomotion. In quadrupedal running and climbing species, the forelimbs and hind limbs are close in proportion, with the arms usually being somewhat shorter than the legs. In predominantly leaping primates and in bipedal humans, the legs are much longer than the arms. In primates that predominantly use their forearms to locomote through the forest, the arms are longer than the legs. These differences are expressed in the intermembral index mentioned earlier. This index expresses total length of humerus plus radius as percentage of total length of femur plus tibia. Thus, the index is low in primates with long hind legs, cluster variously near 100 in quadrupeds, and exceed 100 considerably in primates that frequently use their forearms as means of locomotion.

There are 32 species belonging to four of the prosimian families that live on the island continent of Madagascar and in the Comoro archipelago (there are only two species of genus *Eulemur,* or true lemurs, *Eulemur fulvus fulvus* and *Eulemur mongoz*), where they are the dominant endemic mammals occupying many niches. No higher primates (with the exception of humans) are known to have reached Madagascar to compete with the Malagasy lemurs. Many of these Madagascan lower primates are diurnal or crepuscular. Species of the genera *Cheirogaleus, Microcebus, Mirza, Allocebus, Phaner, Lepilemur, Avahi,* and *Daubentonia* are, however, nocturnal. A new term for a biorhythmic activity pattern, in addition to the tried and true terms "nocturnal," "diurnal," "circadian," and "crepuscular," is "cathemeral" (see also Chapter 9), used to describe some of the diurnal lemurs.

Another prosimian family, the Lorisidae, with two subfamilies, developed on two continents. It contains two African (*Perodicticus* and *Arctocebus*) and two Asian (*Nycticebus* and *Loris*) genera. The other subfamily of family Lorisidae, the Galaginae or bushbabies, are spread widely across equatorial Africa and includes one or more genera. The family Tarsiidae is restricted to several Asian islands. Both families are exclusively nocturnal or crepuscular.

All prosimians have pointed muzzles of varying degrees. Their eye sockets are rotated forward and are nearer to each other than are those of Tupaiidae or most nonprimate mammals. In animals that have their eyes on either side of the head, the two fields of vision are totally different and overlap little, if at all. In living *Tupaia* the angle between the visual axes of both eyes is still 140 degrees, whereas among lower primates this angle is reduced to 70 or 60 degrees. Thus, in *Tupaia* partial binocular vision appears to be possible, but this requires a reduction of the total area seen at one time. A binocular field of vision is key to stereoscopic vision and is necessary for estimating distances in three-dimensional space. The characteristic of forward-directed eyes is sometimes called "orbital frontality." This latter evolutionary achievement is important for a successful life in a three-dimensional arboreal habitat—the basic primate environment. Cartmill (1972), however, presented the case that frontality initially evolved mainly to facilitate precision in food catching and gathering.

Like all other primates, prosimians have highly grooved and ridged tactile skin on the palmar and plantar aspect of hands and feet (called "dermatoglyphics"—fingerprints or dermal rugosities). Prosimians, with the exception of the aye-aye *(Daubentonia)*, have nails on most toes and all fingers. The aye-aye, in contrast, has claws on its fingers and toes except on the great toe or hallux, where it has a nail. All the other Malagasy prosimians have a claw only on the second toe, the so-called toilet-claw because it is used for scratching and grooming. This claw pattern also holds for all the non-Malagasy lower primates except for *Tarsius,* whose second and third toes are clawed for grooming. All the lower primates have a widely abducted first toe, the hallux; this is one of the basic primate adaptations for grasping. The feet of lower primates are typically five fingered. In all the lower primates except *Tarsius,* the area around the nose and lip is covered by a moist skin, the rhinarium. The rhinarium is a "close-up" touch sense organ found in most other nonprimate mammals. *Tarsius* has a peculiar glandular tissue in the area around the snout, both between the nose and on the lower lip, but it lacks true lips, which are found on higher primates. The rhinarium is perhaps the most modified in galagos and mouse lemurs *(Microcebus)* and is lost among the higher primates and in a different way in *Tarsius.* In prosimians the tail is reduced in the Malagasy genus *Indri* and in the African and Asian Lorises, but not in *Galago.* All of the extant lower primates are basically arboreal; only one of the surviving lemurs, *Lemur catta,* has adopted partial terrestrial patterns, but several possibly terrestrial subfossil lemurs are known.

Two subfamilies were once thought to belong in Lemuridae: the Lemurinae and the Cheirogaleinae. Rumpler (1974) revised the classification of Lemuroidea. He raised Cheirogaleinae to the rank of a family as Cheirogaleidae with two subfamilies Cheirogaleinae and Phanerinae. Cheirogaleine contains the genera *Microcebus, Cheirogaleus,* and *Allocebus.* Phanerinae only has one genus, *Phaner.*

INFRAORDER LEMURIFORMES[2] (GREGORY, 1915)

Superfamily Lemuroidea (Mivart, 1864)
Family Cheirogaleidae (Gray, 1873)
Subfamily Cheirogaleinae (Gray, 1873)

Cheirogaleus (E. Geoffroy Saint-Hilaire, 1812) Dwarf Lemurs	*Cheirogaleus major*
	Cheirogaleus medius
	Cheirogaleus crossleyi
	Cheirogaleus minusculus
	Cheirogaleus ravus
	Cheirogaleus sibreei

Genus *Cheirogaleus,* dwarf lemurs, contains six species at present (revised by Groves, 2000). Members of this genus are found throughout the coastal forests of Madagascar. They roam in the lower strata of the foliage. Dwarf lemurs are nocturnal with large eyes and are somewhat larger than mouse lemurs but smaller than the gentle lemurs (genus *Hapalemur*). Their body length measures between 19 and 27 cm, and tail length is between 16 and 17 cm. The shape of the head appears rather globular compared with the elongate, foxlike head of lemurs, but the muzzle is somewhat more pointed than that of *Hapalemur* species. The ears are comparatively small and membranous, not haired. Dwarf lemurs are quadrupedal. Their hind limbs are somewhat longer than their forelimbs but not as elongated as in *Lepilemur* or the Indriids. The intermembral index of cheirogaleids averages around 71. Interestingly, the grip of the hand in these small prosimians resembles that of South American monkeys: objects are picked up and small branches grasped between the second and third fingers, not between the index finger and thumb as in other primates. The nails of cheirogaleids are somewhat keeled and pointed. The dwarf lemur has periods of inactivity or torpor during the winter season. This period usually lasts between four to five months. The tail in dwarf lemurs serves as an area for fat storage that fluctuates seasonally, most of the fat being absorbed during the period of greatest food scarcity. The six species of this genus are reported to live solitary or in pairs, as seems to be the case for all strictly nocturnal prosimians. These lemurs use

[2]Much more is now known about this infraorder today compared with the first edition of this volume, published in 1983. Madagascar was reopened for international research through the diplomatic efforts of Dr. Elwyn L. Simons, director of the Duke Primate Center at that time. Simons was able to forge an agreement with the government of Madagascar in 1981, which allowed scientists from all over the world to enter Madagascar once again to conduct extensive research after years of stasis. Because of political issues, only a few selected researchers had been able to do research in Madagascar during the 1960s and 1970s. In the 1980s, the Duke University Primate Center, under Simons's direction, was also able to import some of the rarest prosimian species for research. Research on prosimians in the field and in captivity has been extraordinarily productive since 1981. The chapter on Lemuriformes has increased accordingly between the editions.

fecal and scent marking activities to mark their home range or territory. Dwarf lemurs nest in tree holes and often sleep together in these nests in a curled up position; their diet consists primarily of fruits, flowers, and perhaps gums, and they appear to play a part in pollinating certain food plants (Wright and Martin, 1995).

Microcebus (E. Geoffroy Saint-Hilaire, 1834) Mouse Lemurs	*Microcebus murinus*
	Microcebus rufus
	Microcebus myoxinus
	Microcebus ravelobensis
	Microcebus berthae
	Microcebus griseorufus
	Microcebus sambiranensis
	Microcebus tavaratra
	Microcebus simmonsi
	Microcebus mittermieri
	Microcebus jollyae[3]
	Microcebus lehilahytsara[3]

Genus *Microcebus*, the mouse lemur (Figure 4.4), has increased to 12 species (Rasolooarison et al., 2000; Louis et al., 2006). Mouse lemurs are small, no bigger than about 27 cm, tail included. One of the most recently described species, *M. lehilahytsara*, is truly tiny, only approximately 9 cm (head + body) long (Kappeler et al., 2005). They are nocturnal and omnivorous, although they appear to prefer insects, particularly beetles, to which they add fruit, flowers and their buds, and tender leaves. The gray mouse lemur is said to indulge in such delicacies such as sap and gum from various trees, secretions from insect larvae, and even small vertebrates such as chameleons and other small reptiles. *M. myoxinus* has been regarded as the smallest of all primates and weighs just about 1 ounce. This species, rediscovered in 1992, had been confused with *M. murinus* for a long time; it had been known to science, however, having been described by Wilhelm Peters in 1842. Members of genus *Microcebus* are abundant in all forests of the east and west coasts of Madagascar. In 1982, Tattersall recognized another genus of mouse lemurs named *Mirza coquereli.* According to Tattersall, Coquerel's dwarf lemur was described in 1867 by Grandidier as *Cheirogaleus coquereli* but was also known as *Microcebus coquereli.* Details of its dentition as well as its locomotion are said to be more similar to mouse lemurs than to members of genus *Cheirogaleus*, the dwarf lemurs. Tattersall asserted that it fits best in a separate genus *Mirza* together with the mouse lemurs (genus *Microcebus*), although these lemurs are considerably smaller.

[3]New species described by Louis et al., 2006, and Kappeler et al., 2005, respectively.

Figure 4.4 *Microcebus murinus*, the gray mouse lemur. Photo courtesy of Michael D. Stuart. From Ankel-Simons, 1983.

Mirza (Gray, 1870) Coquerel's Mouse Lemur, Giant Mouse Lemur	*Mirza coquereli* *Mirza zaza*[4]

Mirza coquereli, Coquerel's mouse lemur, is medium sized, omnivorous, and nocturnal. Its body is 20 cm, and its tail is 33 cm long. It has comparatively large, hairless ears and a round, haired, bushy tail. Locomotion is quadrupedal and rapid. It occurs in two isolated areas on the east coast of Madagascar. It spends the daytime hours sleeping in a globular nest above ground, roaming and predominantly solitary at night. They feed on a wide variety of food items ranging from fruit to arachnoids and vertebrates such as lizards and frogs and

[4]Newly described by Kappeler et al., 2005.

anything that they can catch (Patricia C. Wright, personal communication, January, 2006; Pagés, 1980).

The new *M. zaza* (the northern giant mouse lemur) species from northern Madagascar is somewhat smaller than *M. coquereli*. It differs from other mouse lemurs in that it sleeps in groups that include several adult males, whereas other mouse lemur males appear to inhabit their own nests (Kappeler et al., 2005).

Allocebus (Petter-Rousseaux and Petter, 1967) Hairy-eared Dwarf Lemurs	*Allocebus trichotis*

The one species of genus *Allocebus* was a mystery lemur until 1989 because only four museum specimens were known to science (Mittermeier et al., 1994). One other specimen was captured in 1965. At the end of the 1980s, *A. trichotis* was rediscovered alive and well in northwestern Madagascar (Meier and Albignac, 1991), although it is very rare. It is now regarded as highly endangered and exists only in a restricted area of coastal northwestern rain forest. It is a small, nocturnal animal measuring about 14 cm in body length with a 17-cm tail. Its head is uniquely adorned with long hairs around the ears. It might be a nectar feeder because it reportedly has an unusually long tongue. It is said to store fat deposits not only in its long round and hairy tail but all over its body at the beginning of the Madagascar winter. Locals report that it cannot be detected at all during the months of May through September and therefore may be hibernating.

Subfamily Phanerinae Rumpler 1974

Phaner (Gray, 1870) Fork-marked Mouse Lemurs	*Phaner furcifer* *Phaner pallescens* *Phaner parienti* *Phaner electromontis*

Phanerinae with one genus, *Phaner,* and four species are found widely throughout the western rain forest of Madagascar. The fork-marked dwarf lemur *(P. furcifer)* is about the same size as the greater dwarf lemur *(C. major)* and somewhat larger than the fat-tailed dwarf lemur *(C. medius)*. Its body plus head length measures 23 to 29 cm, and the tail is 29 to 36 cm long. This species has a dark ring around each eye. The eyes are set within in a dark stripe that continues upward to the middle of the top of the head where the dark stripes merge into one black median stripe that progresses down the back, tapering off and ending above the hind legs. This Y-shaped marking gives the animals their common name. In this species the snout is relatively blunt, and the eyes are large as the animals are nocturnal. With *Phaner* the ears are considerably larger than those of the two cheirogaleid species and differ also because they are more pointed. In *Phaner,* the nails are more strongly keeled and pointed than in *Cheirogaleus* and are comparable to the nails of *Euoticus elegantulus,* the needle-clawed African

bushbaby (Petter et al., 1971, 1977). Taking into account anatomical differences, differences in coloration, and geographical isolation, Groves and Tattersall (1991) recognized four subspecies. Fork-marked Lemurs live alone or in pairs. Sometimes larger groups congregate, but whether this is for feeding or breeding is not clear. They run and leap quadrupedally and are very vocal, frequently emitting loud cries that are thought to be territorial. The intermembral index is lower than in dwarf lemurs, around 67. Gum from trees seems to be a staple in their diet, but sap, flowers, and their buds and insects are also part of their menu. They also have been observed eagerly licking up sticky liquids of insect larvae (Homoptera and Coleoptera). Their dentition is characterized by a comparatively long toothcomb comprising incisors and canines in the mandibular dentition that are tightly oppressed. Uniquely enlarged canines and first premolars that are separated by a gap characterize the maxillary dentition. Fork-marked dwarf lemurs use their toothcomb frequently to sever the bark of trees, which brings about the flow of edible juices.

Family Lemuridae (Gray, 1821)
Subfamily Lepilemurinae (Gray, 1870)[5]

Lepilemur (E. Geoffroy Saint-Hilaire, 1851) Sportive or Weasel Lemurs	*Lepilemur mustelinus*
	Lepilemur leucopus
	Lepilemur dorsalis
	Lepilemur ruficaudatus
	Lepilemur edwardsi
	Lepilemur microdon
	Lepilemur septentrionalis
	Lepilemur seali
	Lepilemur mitsinjonensis

Lepilemur, the sportive lemur (Figure 4.5), has seven species and is widely distributed in all the coastal areas around the island and on the island of Nosy Bé. The extant genus *Lepilemur* (about 1 kg) has recently been taxonomically grouped with the much larger (about 40–80 kg) and very derived, extinct subfossil lemur *Megaladapis* (see footnote 5). The reasoning for this classification is that some cranial and dental features of *Megaladapis* are similar to those of extant *Lepilemur.* We are not adopting this practice here because the difference between the two genera is considerable, not only regarding body size but also in the details of the postcranial anatomy that are related to differences in locomotion. Their similarities may be convergent acquisitions related to a folivorous diet, such as

[5]Two additional species, *L. seali* and *L. mitsinjonensis,* have been distinguished by Edward E. Louis, and their description will be published in the *International Journal of Primatology* in 2006. *Lepilemur* is now listed in the family of subfossil *Megaladapis* with two subfamilies, Megaladapinae and Lepilemurinae, by some (Mittermeier et al., 1994; Shoshani et al., 1996).

Figure 4.5 *Lepilemur leucopus*, the white-footed sportive lemur. Photo courtesy of Diane Brockman. From Ankel-Simons, 2000.

the loss of upper incisors. Sportive lemurs are nocturnal and locomote in an upright leaping manner.

Body length among the species of genus *Lepilemur* varies between 25 and 35 cm and tail length between 25 and 28 cm. Lepilemurs have short muzzles, big eyes, and rounded ears. The hind limbs, are considerably longer than the forelimbs with an intermembral index of around 60. Sportive lemurs usually jump in a vertical position, leaping from one upright support to another. They are adapted to many habitats, including both rain forests and xerophytic (dry) scrub forests. Mainland sportive lemurs usually sleep rolled up into a ball in tree holes, whereas those on Nosy Bé sleep on exposed, thick branches. The difference in sleeping habits has been correlated with the total absence of predators on Nosy Bé. Although sportive lemurs also sleep in exposed locations in Beza Mahafaly where potential predators are present (Patricia C. Wright, personal communication, September, 2005). They are said to be mostly solitary but seem to be concentrated in greater numbers in certain areas. The breeding season is apparently restricted

to the period from May to August. Mothers may carry their youngsters in the mouth. Marking behavior is seldom seen despite the fact that males have scent glands in the scrotal skin. Sportive lemurs emit a variety of loud, mainly territorial calls. Their diet consists of leaves, flowers, bark, and some fruit.

Hapalemur (E. Geoffroy Saint-Hilaire, 1851) Gentle Lemurs	*Hapalemur griseus*
	Hapalemur occidentalis
	Hapalemur aureus
	Hapalemur aloatrensis
	Hapalemur (Prolemur) simus

Members of genus *Hapalemur* (Figures 4.6 and 4.7) have the common names of gentle or bamboo lemurs. The genus has three species, the most widely spread, *Hapalemur griseus* or gray bamboo lemur with three subspecies; the greater bamboo lemur *H. simus;* and the newly discovered golden bamboo lemur,

Figure 4.6 *Hapalemur (Prolemur) aureus*, the golden bamboo lemur. Photo courtesy of Summer J. Arrigo-Nelson.

Figure 4.7 *Hapalemur simus*, the greater bamboo lemur. Photo courtesy of Mitchell T. Irwin.

H. aureus. Gray bamboo lemurs are gray overall; the greater bamboo lemur is darker and more brown than the former and has prominent hair tufts around the ears as well as a shorter face. The golden bamboo lemur has a golden coloration of its fur, especially on the face and no ear tufts.

Subspecies *H. griseus griseus* occurs in the coastal rainforests of the east coast of Madagascar and is the smallest of the diurnal lemurs. Gentle lemurs differ from members of genus *Eulemur* in having shorter snouts and a globular head shape. One of the other subspecies, *H. g. occidentalis* still occurs in two restricted areas on the west coast of Madagascar, one in the north and one in the middle of the coast. It is in the area around lake Alaotra that *H. g. alaotrensis* occurred, but it is becoming increasingly rare. *H. aureus,* the golden bamboo lemur, was only recently discovered and described (Meier et al., 1987). It is larger than *H. griseus* and smaller than *H. simus*. The body length of *H. griseus* measures around 28 cm, and the tail is about 37 cm long. *H. simus,* the greater bamboo lemur weighs more than twice as much when adult (2.4 kg) as the lesser bamboo lemur (700 g to 2.4 kg). New measurements for this very rare species *(H. simus)* from unpublished field data have been kindly provided by Pat C. Wright. These are: Eight-year-old female: body weight: 2.45 kg, tail base to crown body length: 36.3 cm, and tail length: 43 cm. Ten-year-old male: body weight: 2.49 kg, body length: 39.1 cm, and tail length: 44.6 cm. Both animals were captured in September 2004 in Ranomafana,

September being the season when their weights are the lowest. Pat Wright also reports that *H. simus* females have the unusual feature of having four nipples. It has been proposed by some that the genus name for *Hapalemur simus* should be changed to *Prolemur* (Groves, 2001). All bamboo lemurs eat predominantly bamboo including the pith of the giant bamboo *(H. simus)*, and *H. aureus* seems to prefer new bamboo shoots, an occasional fruit, leaves, and grasses such as bamboo grass. Glander et al. (1989) reported levels of cyanide in the bamboo shoots that are the preferred food of the golden bamboo lemur that would kill most other mammals. Wright and Randriamanantena (1989) hypothesized that this adaptation to a poisonous food allows three species of bamboo lemurs (*H. griseus, aureus,* and *simus*) to coexist in the same environment. The two other species do not eat the bamboo with high cyanide content (C.L. Tan, 1999). The golden bamboo lemur is most active during dawn and dusk and also at night. *H. (Prolemur) simus* is among the world's most endangered primates (Konstant et al., 2002), and it appears that *H. aloatrensis* should also be on this list.

Varecia (Gray, 1863)	*Varecia variegata variegata*
Ruffed Lemurs	*Varecia variegata rubra*

The lemur genus *Varecia* (Figure 4.8) has only one extant species and two subspecies, and these prosimians are commonly known as ruffed lemurs. Genus *Varecia* has only recently been resurrected as the genus for the ruffed lemurs (Groves and Eaglen, 1988). They were regarded to belong in genus *Lemur (Lemur varigatus)* before Simons and Rumpler (1988) separated this genus into *Lemur catta* as the only species of true lemurs and *Eulemur* for all other lemur species. The ruffed lemurs are different from the other large lemurs both anatomically and behaviorally. For example, they have a gland for scent marking on the base of the neck. There are two subspecies of *Varecia variegata, V. v. variegata,* the black and white ruffed lemurs and *V. v. rubra*, the red ruffed lemurs. Ruffed lemurs are the largest of the living Lemuridae. Ruffed lemurs are between 50 cm and 60 cm long with long, bushy tails that measure between 55 cm and 65 cm. Ruffed lemurs caught in the wild weigh about 3.5 kg (Patricia C. Wright, personal communication, 1999). The subspecies are about the same size. The black and white ruffed lemurs are striking animals with ears hidden by hair tufts. There are many distribution patterns of the white and black areas of fur. The most extensive representation in pictures of the white and black fur color distribution patterns of *V. v. variegata* have been published in Ceska et al. (1992). Female *Varecia* have three pairs of nipples and, unlike most other primates except the South American Callitrichidae as well as cheirogaleids and galagos, commonly give birth to twins, even triplets. They build nests in which the young offspring are parked when the mothers are foraging. Black and white ruffed lemurs do live in groups, and the females are commonly the dominant animals. These ruffed lemur groups engage in loud, barking chorus vocalizations that are regarded as alarm calls, as well as catlike, long, wailing howls that are presumably territorial

Figure 4.8 *Varecia variegata*, the ruffed lemur. Photo courtesy of Verne Simons. From Ankel-Simons, 2000.

in nature. They live predominantly in an arboreal environment where they deliberately move around in a quadrupedal fashion, occasionally combined with long, horizontal leaps as the substratum requires. Ruffed lemurs are found in patchy areas of the rain forests at low to mid-altitude along the east coast of Madagascar from the Mananara River in the south to the Antainambalana River on the north side of the city Maroantsetra in the north (Mittermeier et al., 1994). Their diet consists predominantly of fruit.

The body of red ruffed lemurs, *Varecia variegata rubra*, is dark rusty orange, with pitch-black face, tail, hands, and feet. The ears are covered with rusty-colored fur tufts that extend into a beardlike ring of hair that is somewhat longer than the body hairs and circles around the face. They have a white patch of fur on the back of their head that extends in varying patterns further backward onto the rump. Some specimens have a white area of fur around the base of the tail and to a varying degree on the hind legs (Ceska et al., 1992). The fur of ruffed lemurs is dense and soft. They, like their cogenerics, move around in trees quadrupedally in a deliberate manner, which is occasionally interrupted by a leap across gaps. Generally, their behavior and lifestyle appear similar to the species'

closest relatives, the black and white ruffed lemurs. They occur only in a few patchy areas of the Masoala Peninsula of northeastern Madagascar (H.J. Simons and Lindsay, 1987).

Eulemur (Simons and Rumpler, 1988)[6] Lemurs	*Eulemur fulvus*
	Eulemur macaco
	Eulemur coronatus
	Eulemur rubiventer
	Eulemur mongoz
	Eulemur sanfordi
	Eulemur albifrons
	Eulemur rufus
	Eulemur collaris
	Eulemur albocollaris
	Eulemur coronatus

The true lemurs, genus *Eulemur*, comprises a varied but closely related group of extant lemurs. Generally speaking the members of the genus are comparatively similar to each other, both morphologically and behaviorally. The genus that formerly had 5 species now has 11 that are generally recognized. It turns out that the new "species" have formerly been regarded to be subspecies. True lemurs are found in forested areas all around the island of Madagascar, on Mayotte Island, and on the Comoro Islands off the northwestern coast of Madagascar. Their size varies between a head plus body length of 38 to 50 cm and a tail length between 45 and 60 cm. They are all arboreal quadrupeds that intersperse their walking and running through the canopy with occasional leaps. They live on a varying diet that includes ripe fruit, leaves, and blossoms; some also eat insects, spiders, and millipedes. Some subspecies appear to tolerate a high degree of tannins and alkaloids (Ganzhorn, 1988).

The most varied species is the brown lemur, *Eulemur fulvus*, with six subspecies. *E. fulvus*, the common brown lemur, occurs in an area northwest of Madagascar and also in rain forest in the middle of the east coast of the island. It also occurs on the Comoros and on Mayotte Island. Some authors recognize yet another subspecies for those on Mayotte and the Comoros, *E. fulvus mayottensis* (Tattersall, 1982), whereas others believe that the lemurs on the Comoros are nothing but the common brown lemur *E. fulvus*, introduced there only recently by humans (Mittermeier et al., 1992). There does not seem to be much of a difference in either morphology or pelage between the two disputed subspecies. All brown lemurs live in groups of variable numbers and composition that can differ within subspecies.

[6]*Eulemur:* new generic name for species of *Lemur* other than *Lemur catta*. *C.R. Acad. Science Paris,* Ser. 3, 307:547–551 (not *Petterus* as Groves and Eaglen, 1988, was published after Simons and Rumpler, 1988).

Members of the subspecies *E. fulvus* are generally grayish brown, with a dark gray to black crown on the head. The cheeks are lighter than the rest of the body as is the short beard that encircles the lower part of the head. The ears are only covered with sparse short hair and, as the face, almost black and quite visible. There is a slightly lighter patch of short fur above each eye. The underparts of the body and limbs are somewhat lighter than the rest of the body and the fur on the tail gets darker towards the tip. Females tend to be somewhat lighter than males, but not to the extent of true sexual dichromatism. The fur is generally short all over the body.

Eulemur rufus (Figure 4.9) males are gray to grayish brown, and the females are reddish brown. Both sexes have light patches over the eyes that are lighter and more obvious than those of *E. fulvus* and topped by reddish patches in males. These reddish patches are the reason for the subspecies' common name red-

Figure 4.9 *Eulemur rufus*, the brown lemur. Photo courtesy of Michael D. Stuart. From Ankel-Simons, 1983.

fronted brown lemur. Only the faces are black, and both sexes have beards that are more prominent than those of *E. fulvus* and longer in males than in females. Red-fronted brown lemurs occur in a rim around much of the island's west coast and a smaller area in the east predominantly between the Mangoro and Manampatrana Rivers.

Eulemur albifrons (Figure 4.10), the white-fronted brown lemur is called white-fronted because the males of this subspecies have a white area of fur longer than the body hair all around their black face. The white fur almost covers up the ears. Whereas females are grayish all over the body including the darker face, the back is reddish rather than gray in male animals, and the entire tail is covered with dark gray hair. They are found in most of the rain forest that still cover the northeast of Madagascar between the Bemarivo River in the north and south toward the Tamatave area.

Eulemur sanfordi only occurs in a very restricted area in the north of Madagascar. This subspecies only differs from the white-fronted subspecies in the appearance of the males. Male Sanfords have longer hair surrounding their heads and faces and are generally lighter in overall coloration than white-fronted lemurs. It has been reported that this subspecies of brown lemurs adds invertebrates to its usual diet of fruit, leaves, and flowers.

Another slight color and fur pattern variation of the brown lemurs is the white-collared brown lemur, *Eulemur albocollaris*. These lemurs occur in a very restricted area in the rain forest adjacent to the coastline in southeastern Madagascar. The males of this subspecies stand out because of their prominent white beards, or collars. Both females and males are very similar overall to the other brown lemurs except that their coats have a more reddish tint than most. The males are somewhat darker in tint than the females.

Eulemur collaris, the collared-brown lemur, occurs in a somewhat larger area south of the white-collared brown lemurs range in the very southeast of the island's rain forests and is mainly discerned from the latter by having off-white to tan collars or beards in the male. Their faces are somewhat darker in both sexes than are those of the white-collared subspecies.

Eulemur macaco has two subspecies, *E. m. macaco* and *E. m. flavifrons*. They are called black lemurs because of a striking sexual color dimorphism: the adult males of the species are black overall, whereas the females are orange brown and much lighter in the hue of their fur. These medium-sized lemurs are about 40 cm in body plus head length, and their tails are about 50 cm long. The overall pattern of their behavior appears to be similar to that of other *Eulemur* species. Members of *Eulemur macaco macaco* can easily be recognized because both sexes have comparatively long hair tufts around their ears, extending all around the neck and framing their faces. The males are totally black, and females have white ear tufts and beards, black faces, and are orange on the top of the body and extremities. Their occurrence is restricted to the island of Nosy Bé off the far northwest of Madagascar and the rain forest on the mainland near to Nosy

Figure 4.10 *Eulemur albifrons*, the white-fronted lemur. Photo courtesy of Michael Stuart. From Ankel-Simons, 1983.

Bé between the Mahavavy River in the north and the Sambirano River in the south. Their eyes are brown.

In contrast to these black lemurs, the blue-eyed black lemurs, *Eulemur macaco flavifrons*, have clear blue to light gray eyes. This is the only primate species that consistently has true blue-gray eye color. They are of the same size as the black lemur. Blue-eyed black lemurs differ from black lemurs in having shorter fur and no tufts or beards around the head; females are slightly lighter in color overall then those of *E. m. macaco.* The blue-eyed black lemur is restricted to small areas adjacent to the area that is occupied by black lemurs south of the Andromalaza River. There may be an area between the two populations in which these two subspecies are interbreeding (Mittermeier et al., 1992).

One of the smaller *Eulemur* species is *Eulemur coronatus*, the crowned lemur. Its head plus body length is about 35 cm, and its tail is generally about 45 cm long. Crowned lemurs exhibit a notable sexual dichromatism. Although both sexes have gray body and tail fur and light faces and undersides of body and limbs, in the male, a striking black triangle occupies the crown of the head and is underlined by a wide, intensely orange rim around the face, pointed toward the nose, that extends sideways toward the ears and down into an orange beard. The female has a faint orange rim above both eyes that fades out backward above the ears; females have no black markings. Crowned lemurs live in a range at the very northern tip of Madagascar but are also found farther to the southeast

(E.L. Simons, personal communication, 1998). Also morphologically diurnal and predominantly active during the day, crowned lemurs variously show activity at night, dawn, or dusk, as many other diurnal lemurs do. Crowned lemurs are, unfortunately, widely used as pets by the Malagasy people.

Eulemur rubiventer, the red-bellied lemur, is medium sized, with its body plus head length not exceeding 40 cm and a tail that is about 50 cm long. Both sexes of this species are reddish brown and have black tails. The male gender is distinguished by having longer hair around the ears and cheeks than females. The males also have reddish brown hair on their bellies, whereas the females are light tan on the underside. They are said to roam the middle to high altitude rain forest on Madagascar's east side from the Tsaratanana Massif in the north to the Andringitra Massif in the south. Male red-bellied lemurs have the strange habit of rubbing their foreheads with oily glandular exudes to the extent that their forehead appears to be covered with a black, shiny bald spot. Similar behavior has been observed in male *E. macaco*. *E. rubriventer* has also been reported as occasionally being active at night as well as during the day. They live in small groups with female leaders (Overdorff, 1991). Overdorff reported that *E. rubriventer* includes millipeds in its diet.

Eulemur mongoz (Figure 4.11) falls into the same size range as the previously described *Eulemur* species, *E. rubriventer*. This species occurs on two of the larger Comoro islands, Moheli and Anjouan, where they were introduced by humans. They are also found in fragmented forests of the northwestern dry

Figure 4.11 *Eulemur mongoz*, the mongoz lemur. Photo courtesy of Michael D. Stuart. From Ankel-Simons, 1983.

deciduous forests of Madagascar. This is another morphologically diurnal *Eulemur* species that has been reported to be active at night.

Lemur (Linnaeus, 1758) *Lemur catta*
Ring-tailed Lemurs

Lemur catta (Figure 4.12), the ring-tailed lemur, is about 43 cm long (body + head length), and its tails are comparatively very long, measuring about 60 cm. Its back is gray to rosy orange, the limbs are a dusty gray, the crown and neck are dark gray, and the underside of the body is white. The face is marked by dark gray triangular patches, tips pointing upward around the eyes, a black, velvety nose, and an almost black caplike area on the top of the head. The ears are white and stick out farther than those of the *Eulemur* species, thus being much more obvious than those of the true lemurs. The tail is marked by alternating black and white rings all the way to the tip, which gives this species its common name. Ringtails have dark glandular areas on the insides of their forearms near the wrists that are hidden under a horny spur in mature males. The two sexes of ringtails are alike with the exception of this morphological difference. These glands on the wrists are used to scent mark the tail by pulling it through between the inside of the forearms that are clasped around it. The animals then spread the scent by flinging their tails into the air. The occurrence of ring-tailed lemurs is restricted to areas southwest of Madagascar where they inhabit many different types of forests, preferably gallery forests along riverbanks. Their diet is predominantly vegetarian and includes bark and sap. The kily tree *(Tamarindus indica)* is reported to be their preferred food source (S.M. O'Connor, 1988). Ring-tailed lemurs are quadrupeds that spend a great part of their time on the ground. They do forage in all forest strata, however, and live in groups of variable numbers. Females are dominant over the males. Newborns are carried under their mother's bellies for the first two weeks of their lives. Ring-tailed lemurs emit catlike alarm calls that distinguish between terrestrial and aerial predators (Sussman, 1991a; Macedonia, 1993). Ring-tailed lemurs are the most well known of lemurs because they are exhibited in zoos and animal colonies all over the world.

Family Indriidae[7] (Burnett, 1828)
Subfamily Indrinae (Burnett, 1828)
Indri (E. Geoffroy Saint-Hilaire and Cuvier, 1796) Indris *Indri indri*

Genus *Indri* is giving its name to the family of Indriidae, which contains only three extant genera: *Indri*, *Propithecus*, and *Avahi*. All genera of this lemur

[7]This spelling was changed to Indridae by P.D. Jenkins (1987); however, the spelling Indriidae has been reinstated (see Schwartz et al., 1998).

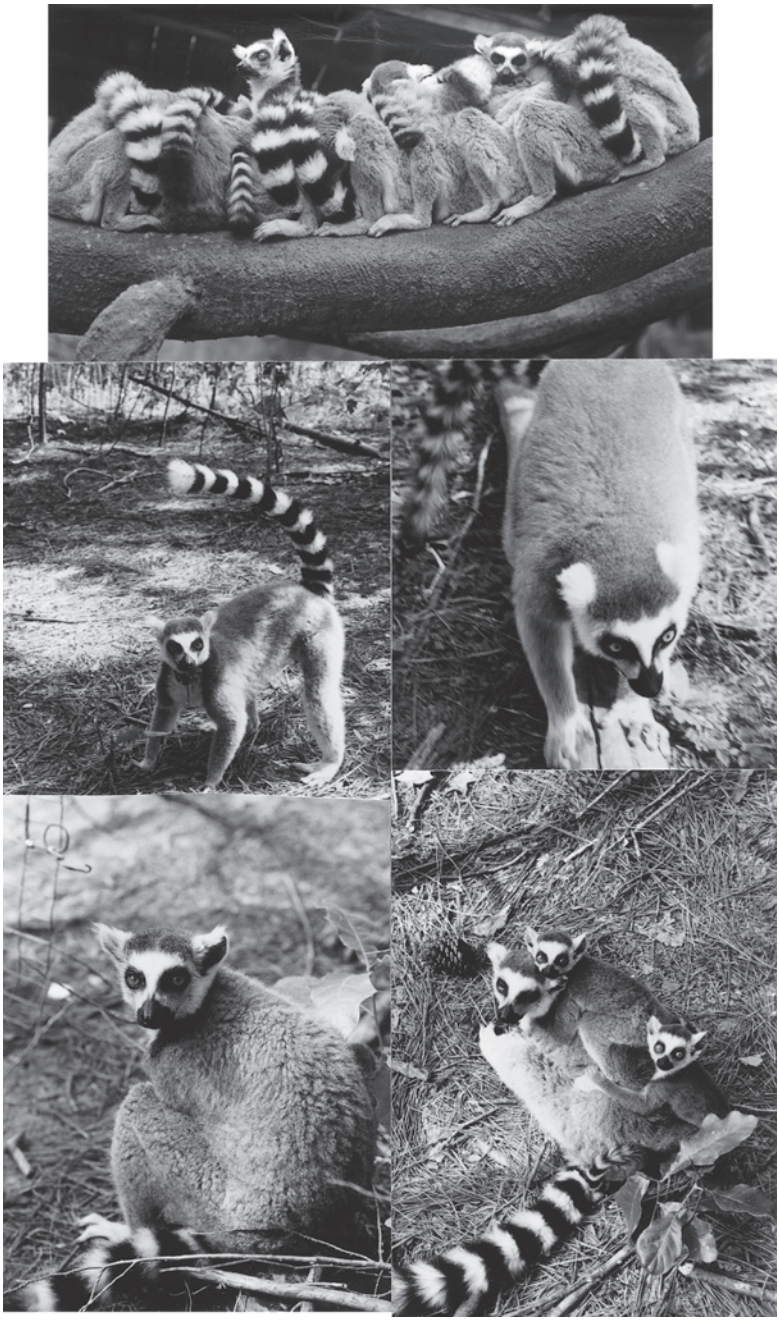


Figure 4.12 *Lemur catta:* "*Lemur* ball," top photo. Photos courtesy of Verne Simons.

family locomote predominantly in an upright fashion, leaping between upright supports. Their hind limbs are considerably longer than their forelimbs with an intermembral index averaging around 62. Indris are among the largest extant lemurids and are distinguished from all other genera of Madagascan prosimians by having very short tails (tail length is about 5 cm).

Genus *Indri* is represented by only one species, *Indri indri*. The strange and exotic *Indri*—or "babakoto" pronounced "babakut"—are regarded as "men" by the Malagasy people whose villages are near where the indri live, and their killing is regarded as murder.

The fur of indris is soft, silky, and predominantly black and white in individually differing combinations and patterns. They have rather large, furry, and tufted ears that are always black; head shape is globular. The face is black but surrounded by a lighter color in some individuals. The black face gives the light-colored eyes a striking, almost staring appearance. The snout is comparatively pointed, more so than that of the members of genus *Propithecus*. The predominantly diurnal *Indri* inhabits the central eastern rain forests of the northern half of Madagascar (Pollock, 1979; Mittermeier et al., 1994; Glessner and Britt, 2005). The *Indri* is one of the largest extant lemurs, having a combined head plus body length of about 70 cm and an average weight of between 10 to 15 kg. Only the diademed sifaka *Propithecus diadema diadema* is close in size to the indri. Although large, they are strictly arboreal, moving around in the same way as do sifakas and avahis. When active, they prefer positions with their body upright; while resting, they prefer to adopt more prone positions on large branches. The indri rise with the sun, but they stop feeding and moving about at about three o'clock in the afternoon. As with the avahis, the digits of hands and feet are webbed. Indri live in family units of two to four individuals. Pollock (1977) has shown that the infrequent, very loud and melodious calls strictly define the territories of each family. These are surely the noisiest of all Malagassy lemurs. Their song can carry for two or three miles so that many travelers have heard their far-reaching songs without ever seeing them. In fact, the name "indri" means "look, there [it is]" in the Merina dialect of the highlands. Indris have a large laryngeal sac in the throat, presumably developed to enhance their vocal skills. They protrude their lips into a trumpet-like extension when calling. The indri feed on foliage, flowers, fruit, and leaf buds, mainly from laurel trees.

Propithecus (Bennett, 1832) Sifakas	*Propithecus verreauxi*
	Propithecus tattersalli
	Propithecus diadema
	Propithecus edwardsi
	Propithecus perrieri
	Propithecus coquereli
	Propithecus deckenii
	Propithecus candidus

Genus *Propithecus,* with the common name "sifaka" or "simponas," are found over most of the areas of Madagascar that are still forested. Eight species are now recognized. Both *P. perrieri* and *P. candidus* are on the 2002 list of the world's most endangered primates (Konstant et al., 2002). The change from three species to eight is because five subspecies have been elevated to species rank (Groves, 2001). Like the indri, the sifaka rarely come to the ground in their natural habitat. Only when they must cross a large barren gap between forested areas do they use terrestrial progression, which in *P. verreauxi* is often a bipedal, upright, rapid, long-distance hopping activity with the arms extended sideways above the head and arms and long tail acting as balancing beams. Sifakas are predominantly arboreal and move in an upright position, propelled by the long and powerful hind extremities between upright supports.

Propithecus verreauxi (Figure 4.13) had two subspecies, *P. v. verreauxi* and *P. v. coquereli* (Figure 4.14). Tattersall (1982) however, distinguished two other

Figure 4.13 *Propithecus verreauxi verreauxi*, Verreaux's sifaka. Photo courtesy of Diane Brockman. From Ankel-Simons, 2000.

Figure 4.14 *Propithecus verreauxi coquereli*, Coquerel's sifaka. From Ankel-Simons, 1983.

subspecies, namely *P. v. deckeni*, and *P. v. coronatus*. Two of these three subspecies now have species rank: *P. coquereli* and *P. deckeni*.

Verreaux's sifaka have soft, dense fur that is predominantly white; the hairless face and insides of the ears as well as the palmar and plantar surface of hands and feet are black. Short white hair covers the back of the comparatively small ears, and a reddish brown hue extends from the top of the head onto the back of the neck. The face is always surrounded by a frame of white hair. Some color variants are found, with certain individuals having varying amounts of grayish hues on their backs or gray backs and dark brown fur on the top of their arms and around their thighs. The eyes are light colored and pronounced by the surrounding black skin of the face. Male animals have a reddish brown gland in front on the base of the neck. Verreaux's sifakas are about 45 to 54 cm long (head plus body length) and weigh about 3.5 kg. Their short-haired tails measure between 50 and 55 cm. The head is round and the snout comparatively wide and short. Their tails are often rolled up forward and toward the body. According to Tattersall (1982), individuals from higher altitudes have longer thicker fur than

those from the lowlands. Sifakas emit a sharp and penetrating call that is bisected by a glottal stop and sounds like "shi-fahk." The native names for Verreaux's sifaka such as "sifak" and "tsibuhak" imitate some of the animals' cries. The diet of Verreaux's sifakas consists principally of leaves, flowers, buds, fruit, bark, and cambium and is highly variable depending on the seasonal change of available food sources (Richard, 1977). Home ranges are comparatively small (Sussman, 1974; Richard and Dewar, 1991). Although it is taboo for the human tribes who live in the same area as the sifakas to kill the animals, they are hunted by others. Sifakas have single births, and infants ride first on their mother's front until they are about three months of age when they move onto the mother's back. They usually become totally independent at about six months (Jolly, 1966). Verreaux's sifaka occurs in the southwestern and southern dry forests of Madagascar. They live in multimale groups of 2 to 12 individuals, and females are dominant over males.

Propithecus coquereli, Coquerel's sifakas are similar in many traits to the Verrauxi sifakas. They do, however, differ from the former subspecies by sometimes having white fur on the nasal area and, in many specimens, by having dark chocolate-brown triangles on top of the arms and legs. They also inhabit distant areas of Madagascar: whereas Verreaux's sifakas live in the south and southwestern dry forests, Coquerel's sifakas are found in the northwest north of Majunga. Two other color variants are recognized by some as two additional subspecies (*P. v. deckeni* [now *P. deckeni*, a species] and *P. v. coronatus;* Mittermeier et al., 1994) as they also differ in their appearance. Both have white bodies, *P. deckeni* with a black face and a white hue on top of its nose, and *P. v. coronatus* differs from the latter subspecies only in its black head. Both occur in northwestern fragmented forests.

Propithecus diadema (photo on the book cover) can be regarded as one of the most striking and beautiful mammal species. The native name "simpoon" for these animals mimics the sound of their calls. Their long, silky fur is gray on the back, hands, and feet, and bright orange on top of arms and legs. The long tail is white, and long white hairs frame the black, naked face. The ears are comparatively small and almost totally hidden in the white hair. The top of the head is adorned by a black triangle with one point of the triangle pointing toward the forehead. Diademed sifakas or simponas rival the indri in size, measuring 52 cm (head plus body) and having tails that are about 47 cm long. They weigh about 5 to 8 kg (Glander and Powzyk, 1998). They inhabit remote areas of the eastern rain forests of Madagascar. They travel in groups of two to nine animals within large home ranges, and their population size is very small. Three subspecies are recognized (Mittermeier et al., 1994), one being almost totally black except for the white underside (*P. d. edwardsi,* weighing 6 kg[8]; Figure 4.15), another being

[8]Weights provided by Patricia C. Wright.

Figure 4.15 *Propithecus edwardsi*. Photos courtesy of Jukka Jernvall.

totally black (*P. d. perrieri*, weighing 5 kg), and the third being totally white, sometimes with silver hues on the top of the head, back, and top of the limbs, except for the black, hairless face (*P. d. candidus;* Tattersall 1982). All subspecies have a varied diet of leaves, fruit, and blossoms. These large, placid, and very visible indrids are unfortunately hunted for food by the natives.

Propithecus tattersalli, the golden-crowned sifaka, occurs in a restricted area in the north east of Madagascar. This species was newly described as recently as 1988 by Simons. The animals are comparatively small with a head plus body length of about 50 cm and the tail measuring 40 cm. Their average weight is 3.5 kg. Unlike the other sifaka species, these animals have protruding, tufted ears, which give their faces and heads a triangular outline, with the tips of the ears and the tip of the muzzle shaping the triangle, unlike the other species, which have round heads. Above the black, hairless face that is surrounded by a narrow ring of golden fur is a dark golden cap. The golden, short-haired fur lies flat over the skin, giving a more sleek impression compared with the fur of the other sifakas. The eyes are golden or orange. The locomotor habits and limb proportions of these upright leapers are similar to those of the other sifakas, as is their predominantly vegetarian diet. They also emit the characteristic explosive "shi-fahk" vocalization. These sifakas are highly endangered.

Avahi (Jourdan, 1834)	*Avahi laniger*
Avahis or Woolly	*Avahi occidentalis*
Lemurs	*Avahi unicolor* (?)
	Avahi cleesei (?)

The third genus of indrids, the *Avahi,* is commonly known as the woolly lemur. There are now four species, whereas formerly there was one, *Avahi laniger* with two subspecies *A. l. laniger* and *A. l. occidentalis.* The three new species are *A. occidentalis, A. unicolor* (Thalmann and Geissmann, 2000), and *A. cleesei* (Thalmann and Geissmann, 2005). *A. occidentalis* was first recognized as a separate species based on karyological differences (Rumpler et al., 1990). Whether *A. unicolor* and *A. cleesei* really are sufficiently differentiated from each other to support species status remains an open question. The first has been elevated to species status from the subspecies *A. l. occidentalis,* whereas the second, *A. unicolor,* has been newly described as different from the other two. The new species are said to be different in fur coloration and separated geographically. No extensive genetic support exists for the species status as yet (but see Adriantompohavana, 2004). Members of genus *Avahi* represent the only nocturnal indrids and, accordingly, have large eyes that make their heads look fairly round. Their ears are small but visible. These small animals are about 32 cm long (head plus body) and have tails that measure circa 28 cm; their weight is reported to be about 1 kg. Their hind limbs, as in the other indrids, are longer and more powerful than the forelimbs as they locomote by upright leaping

motions and postures. Their overall woolly brownish gray fur is accentuated by white patches on the underside of the thighs, forearms, hands, and feet. The tail is a reddish orange hue. The underside of the body is somewhat lighter in color than the backside. They inhabit restricted rain forest areas of the northwest as well as a very small range in the middle of western Madagascar. Woolly lemurs spend the day sleeping in tree holes or thick vegetation. According to Patricia C. Wright, in Ranomafana they never sleep in tree holes but on open branches. Their diet is composed of leaves, buds, and bark, and the animals live in small family groups of only two to four individuals. They vocalize with high-pitched whistles (Ganzhorn et al., 1985).

Family Daubentoniidae Gray 1863

Daubentonia (E. Geoffroy Saint-Hilaire, 1795) Aye-Ayes — *Daubentonia madagascariensis*

Genus *Daubentonia*, the aye-aye, in its own family with only one extant species *Daubentonia madagascariensis* (Figure 4.16) is perhaps the most intriguing of the Malagasy lemurs, if not the most peculiar of all the living primates. It was only during the second half of the 1980s that research began to seriously focus on the aye-aye (Ankel-Simons, 1984). A great abundance of research involving the animal was published in the second half of the nineteenth century and the first decade of the twentieth. Until the 1980s, access to aye-ayes was an extraordinary rarity both in scientific museum collections and in captivity. It was discovered only in the second half of that decade that aye-ayes—although rare and living in low-density populations where they occur—are present in many more locations than was previously thought (Albignac, 1987), along Madagascar's east coast as well as scattered over the entire north of the island. In the meantime, aye-ayes have also been discovered from one area in the Malagasy midwest (Simons, 1993).

In 1994, Feistner and Sterling edited a volume with nineteen contributions entirely dedicated to *D. madagascariensis* and reporting on the history, ethology, reproduction, breeding, development, diet, vocalization, and few aspects of its biochemistry. It is now known that aye ayes are much more widely spread than was previously thought. The fur of the aye-aye has hairs of different length, and some of the longer, coarser hairs, have white tips, especially on the back, giving the dark brown under fur a light hue. Overall the appearance is that of a shaggy animal. The tail is long and bushy and very thick, with long fur. Aye-ayes have a body length measuring about 40 cm, and the tail length exceeds that of the body and is between 55 and 60 cm. Unlike other lemurs, *Daubentonia* has claws on its hands and feet except on the great toe. It is thought that these "claws" are a secondary development from nails. The third digit of the hand is elongated and very thin; it is used by the animal to hook beetle grubs and other insects out of cracks. It is also used to pump liquid from cracked coconuts or eggs by means

Figure 4.16 *Daubentonia madagascariensis*, the aye-aye. Photo courtesy of David Haring. From Ankel-Simons, 2000.

of a rapid pumping motion directly onto the tongue and into the mouth. The hands and feet of *Daubentonia* are large and long compared with those of all other prosimians, and fingers and toes are almost the same length, except for the highly specialized fingers three and four. The dentition of *Daubentonia* is unique among extant primates: it is highly specialized and anteriorly resembles that of rodents. The muzzle is comparatively high and narrow as a result of the narrow front dentition. Perhaps in correlation with enhanced manual dexterity, the brain is relatively larger and more convoluted than the brain of other lemurs. The eyes of the aye-aye, a nocturnal lemur, are big and directed slightly upward and forward. Enormous membranous ears add to the peculiar appearance of the head that is broad, except for the high and narrow snout. All four limbs are comparatively short, the hind limbs shorter than the forelimbs: the intermembral

index is about 70. The activity pattern of the aye-aye is nocturnal and they seem to have rather solitary habits, although they live in territories that overlap each other. They build and sleep separately in large covered, leafy nests. They have single birth, and very unusual for a primate, a pair of inguinal nipples (positioned between the hind legs near the vulva); they place their newborn offspring in covered sleeping nests for approximately 60 days. Their diet has been reported to be a combination of seeds, nectar, fungus, and insect larvae, and the combination of these foods changes according to season (Sterling et al., 1994). Cartmill (1974) proposed that because of its feeding habits, the aye-aye is filling the ecological niche of woodpeckers on the island of Madagascar. (Woodcutting birds like woodpeckers do not exist on Madagascar.) In a letter by the honorable Doctor H. Sandwith, dated January 27, 1859, and addressed to Professor Richard Owen, Sandwith described in great detail how the aye-aye skillfully forages for insect grub in a manner similar to that of a woodpecker (Owen, 1863, p. 38).

Villagers hold aye-ayes in dread and will move away from places where they have been seen. In many areas of Madagascar, meeting an aye-aye means death or bad luck in the family.

Infraorder Lorisiformes (Gregory, 1915)

Superfamily Lorisoidea (Gray, 1821)
Family Lorisidae[9] (Gray, 1821)
Subfamily Lorisinae

The relationships among Lorisines were discussed in great detail by Rasmussen and Nekaris (1998).

Family Lorisidae contains two Asian genera, *Loris* and *Nycticebus*, the former being comparatively slender and the latter having a more stocky build. The family's two African genera, *Arctocebus* and *Perodicticus*, are also divided in one slender genus with two species namely *Arctocebus calabarensis.* Schwartz and Beutel (1995) raised the subspecies *A. c. aureus* to species rank, whereas the other genus and species, *Perodicticus potto*, is similar to the Asian slow loris, being more robust overall than *Arctocebus.* Asiatic *Nycticebus* is comparatively stout.

All members of the lorisine subfamily have so-called retia mirabilia of capillaries in their hands and feet, which provide sustained blood supply to lorises, which can powerfully clamp onto a branch for hours at a time without their extremities getting numb.

[9]In 1987, P. Jenkins pointed out that the family name Lorisidae was preceded in time by Loridae, (Gray, 1821), which, despite Lorisidae having been commonly used, would be the proper assignation for this prosimian family. However, J.H. Schwartz et al. (1998) submitted an appeal to suppress Loridae in favor of Lorisidae. Therefore, Lorisidae is being used in this text.

Loris (E. Geoffroy Saint-Hilaire, 1796) Slender Loris	*Loris tardigradus* *Loris lyddekkerianus*

The genus that gives its name to the family Lorisidae has only two species (Groves, 1998): the slender Loris, *Loris tardigradus* (Figure 4.17), and *L. lydekkerianus*. The results of two long-term field studies of this genus have been published (Nekaris, 1997; Kar Gupta, 1998; Nekaris and Rasmussen, 2003). Slender lorises are restricted in distribution to southern India and Sri Lanka (formerly Ceylon). Their body plus head length varies between 18 and 27 cm, and their tail is very short, as is the case in the three other genera of this family. Fore- and hind limbs are almost equal in length and elongated; the intermembral index averages 91.

Lorises have round heads and round ears that stick out from the head. The large eyes are positioned comparatively close to each other, and the narrow muzzle ends in a snub nose. The eyes are surrounded by dark areas of fur that are narrow below the eyes and extended above the eyes, giving the animals a surprised expression. The Lorises fur is shorter and sparser than in the other Asian lorises, especially on the limbs, thus giving the animal the impression of

Figure 4.17 *Loris tardigradus*, the slender loris. Photo courtesy of Dieter Glaser. From Ankel-Simons, 1983.

being slender and having scrawny arms and legs. Although the fur is not dense, their heels are haired. Habitually, all Lorises usually climb slowly and deliberately, but they can move rapidly when catching prey or attempting to escape from a predator (A.C. Walker, 1969). Slender lorises are arboreal and inhabit tropical rain forests. Individual lorises are said to live solitary. Being nocturnal, they sleep during the day rolled up in crotches between the branches of trees, securing their position with the clasping feet. Lorises appear to have two mating seasons a year, in April–May and in November. Slender lorises usually have single births, but twin births can occur. They urine mark their territories and intensively employ urine washing as is known from all lorisidae.

Nycticebus (E. Geoffroy Saint-Hilaire, 1812) Slow Loris	*Nycticebus coucang* *Nycticebus pygmaeus* *Nycticebus bengalensis* *Nycticebus menagensis*[10]

Members of genus *Nycticebus* are commonly known as slow loris. *Nycticebus*, now with four species, has a wide distribution over the southeast Asian continent and adjacent islands. The animals inhabit the high strata of the tropical rain forest. Slow lorises have a comparatively more bulky appearance than slender lorises. This is particularly true for their extremities. The head is round; the snout appears to be less pointed than in slender lorises. The ears are sparsely haired, somewhat smaller than in slender lorises and hidden in the dense fur. The area around the eyes is dark furred, especially above them. The dark area, however, is less circumscribed than in slender lorises and separated by a whitish stripe that widens and fades out onto the forehead above and widens and extends to the tip of the nose below the eyes. The common species, *N. coucang*, has a body plus head length between 27 and 38 cm. The outer tail is totally reduced: only a short stump is present and is invisible in the dense fur. The other species, *Nycticebus pygmaeus*, is smaller than *N. coucang*. The common name for this species is pygmy loris. Its head plus body lengths is 18 to 21 cm. Its fur is especially dense and woolly. The coloration of the body is grayish brown and dark on the back and lighter on the underside. A dark midline goes from the neck down the back. In *Nycticebus*, the second digit of the hand is reduced in length. The sturdy thumb constitutes one side of a virtual clamp when digits three to five grasp the opposite side of a branch. *Nycticebus* not only has powerful hands but especially powerful grasping feet compared with the hands and feet of the slender loris. In the slow loris, the limbs are nearly equal in length, with an intermembral index averaging 89.

Slow lorises live singly or in pairs. No distinct breeding season has been recorded. They walk deliberately, habitually holding on with three extremities at

[10]Regarded to be a subspecies of *N. coucang* by Brandon-Jones et al. (2004).

a time. They have, however, been described to securely hold on with only their hind feet while raising their body upright to be able to rapidly launch forward and to seize their prey with both hands. Adult male *Nycticebus* are said to be very territorial in the natural habitat. They mark their territories with urine. Vocalization has been described as a low buzzing hiss or growl when they are disturbed by an intruder and as a high-pitched rising contact call and some high whistles by females during estrus. *Nycticebus* habitually have single offspring, but twinning does occur. Both sexes carry the infants, which are occasionally parked clinging to a branch as well. Their diet consists of large mollusks, lizards, birds, small mammals, and fruits.

Perodicticus (Bennett, 1831) Pottos	*Perodicticus potto*
Pseudopotto (Schwartz, 1996)[11]	*Pseudopotto martini*

Pottos—*Perodicticus potto* (Figure 4.18)—inhabit the same general area of tropical rain forests in West Africa as the angwantibo. In addition, their range reaches farther east than that of *Arctocebus*, into the western areas of Uganda and Kenya. In Gabon, Zaire, and Cameroon where they occur in the same forests as genus *Arctocebus*, they are reported to differ from them in that they prefer the higher strata of the forest. The body plus head length of pottos varies between 33 and 42 cm. The tail, although greatly reduced, is longer than in any of the other three genera of lorises and can measure 6 to 8 cm, varying in length from individual to individual; it is always visible.

The overall appearance of pottos is close to that of slow lorises. They are stout and robust in body build and in their extremities; both look somewhat like tiny bears. Fore- and hind limbs of pottos are subequal in length with the hind limbs being somewhat longer than the forelimbs and an intermembral index of 88. The fur of pottos has a more woolly appearance than that of slow lorises and varies in coloration from a grayish brown to a dark brown with much lighter undersides. Both the hands and feet of pottos are powerful and adapted for grasping. Apparently to extend the size of the grasp, the second digit is nearly totally reduced. Thus, the strongly developed thumb is positioned opposite digits three to five of the hand. Hands and feet act like powerful pairs of grasping tongues. All digits and toes are very broad and, except for the second toe, adorned with flat nails as in most prosimians. The second toe carries the grooming claw. The heel is covered with hair, and, as in other lorisines, both wrists and ankles are extraordinarily flexible. The head appears to be globular but slightly flat

[11]In 1996, Schwartz described a new genus and species, *Pseudopotto*, based on a "virtually complete skeleton and adult dentition" and one partial "skull, mandible and mixed dentition" museum specimens. This assignment is not very well documented; there are no observations from the wild and no molecular data to support this new genus and species.

Figure 4.18 *Perodicticus potto*, the potto. From Ankel-Simons, 1983.

lengthwise, with relatively small, rounded ears and the big eyes of a nocturnal prosimian. The eyes of *Perodicticus*, however, are comparatively smaller than those of *Nycticebus*. In *Perodicticus*, the dorsal spines of the lower neck and upper breast vertebrae are much elongated and pointed at their tips. In pottos, these dorsal spines protrude to some extent above the surface of the skin. They are covered by a cornified epithelium, hairless but surrounded by dense fur (see Figure 8.14). Several differing explanations in regard to the function of these spines on the base of the neck in the back have been proposed. A.C. Walker (1970) proposed that this covering skin is highly sensitive to touch and plays an important role in the social behavior of pottos. However, sensory receptors have yet to be reconfirmed within this skin area (Montagna and Yun, 1962). Others

believe that these spines provide a defense mechanism, for example, when pottos forage for food with their head down (Oates, 1984). Pottos are highly territorial. The home ranges of males overlap with those of one or two females, but the animals roam and sleep solitary. Vocalization is made by high-pitched "tsic" noises, whistles, and growling, as well as high-pitched distress calls. Pottos urine mark and males scent mark with their circumgenital glands (Charles-Dominique, 1978). The diet of pottos consists principally of fruit and gum, occasionally augmented by insects and small birds or even bats.

Arctocebus (Gray, 1863)	*Arctocebus calabarensi*
Angwantibo or	*Arctocebus aureus*
Golden Potto	

The slender African loris, *Arctocebus calabarensis* (Figure 4.19) is commonly called angwantibo or golden potto. Two species are now recognized. These animals are restricted to the tropical forest of West Africa from southeastern Nigeria, to southern Congo and western Zaire. They live in the lower forest strata. Angwantibos are somewhat larger than slender lorises; their body plus head length measures between 22 and 27 cm. They do not have a tail. The limbs of *Arctocebus* are slim, and the body is almost cylindrical with an unusual, "blunt" backside, unlike that of any other primate. Hands and feet are dissimilar to those of most other prosimians. The index finger is reduced to two short phalanges,

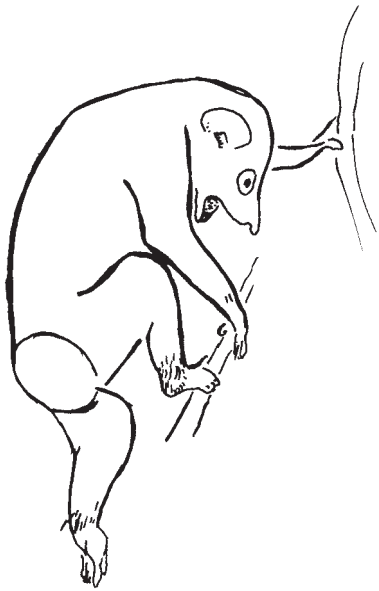


Figure 4.19 Sketch of *Arctocebus calabarensis*, the angwantibo.

amounting to only a slight bump, and the thumb is positioned opposite digits three to five in the hand. Digits four and five are webbed by a skin duplication up to the articulation between the most proximal and the middle phalanges, and the third digit is much shorter than digits four and five. Also toes three through five of the foot are webbed to the same extent as the digits of the hand. The heels are covered with hair, and the second toe is equipped with the characteristic, strongly developed prosimian grooming claw. The head of *Arctocebus* somewhat resembles that of the slender lorises; it is globular with a pointed, narrow muzzle. Its ears are somewhat smaller and slightly compressed sideways and elongated compared with the round ears of genus *Loris.* The eyes are large but comparatively somewhat smaller than those of slow lorises. The locomotion of the angwantibo is more rapid and less deliberate than that of slow lorises and pottos. Their activity period is primarily at night, but they have also been observed moving about during the day. They have a comparatively woolly fur that is longer than that of genus *Loris* and generally has an orange tint, which is especially bright in the species *A. aureus.* The tip of the nose has a light whitish line on it. Their diet consists mainly of insects and about 15% fruit. Angwantibos have been observed to raise up on their hind legs into an upright position to catch flying moths. When frightened, they cling on to a branch rolled up into a furry ball. They appear to be mainly solitary and vocalize to each other with low growls and powerful contact calls (Charles-Dominique, 1977).

Family Galagidae (Mivart, 1864)[12]

There is some disagreement about the question of whether the family Galagidae, commonly known as bushbabies, contains one genus with four subgenera or four different genera. Napier and Napier (1967) differentiated but three subgenera that are assigned to genus *Galago: Galago (Galago)*, the typical galagos with three species; *Galago (Euoticus)*, the needle-clawed galagos with two species; and *Galago (Galagoides)*, the dwarf galagos with one species. In 1986, Meester et al. discussed the different views concerning the assignment of genera and species of the bush babies. Bearder et al. (1995) proposed that the number of nocturnal primate species in general and the number of galago species in particular have been "seriously underestimated." The authors stated that reason for this is that in nocturnal species, mate recognition depends on scent and sound, not on sight as it does in day-living primates or birds. They proposed that "vocal fingerprinting" in the wild makes it possible to propose at least five or six more bushbaby species than previously recognized. In 1996, Shoshani et al. listed four

[12]In 1987, P. Jenkins has pointed out that the family name Galagidae was preceded in time by Galagoninae (Gray, 1825), which, despite Galagidae having been commonly used, would be the proper assignation for this prosimian family. However, J.H. Schwartz et al. (1998) submitted an appeal to suppress Galagoninae in favor of Galagidae. Therefore, Galagidae is used in the current text.

valid genera for bushbabies, *Galago* (bushbabies), *Galagoides* (dwarf bushbabies), *Otolemur* (greater bushbabies), and *Euoticus* (needle-clawed bushbabies). Here we follow the recommendation of Nash et al. (1989) to retain all bushbabies in genus *Galago*.

Galago (E. Geoffroy Saint-Hilaire, 1796) Bushbabies	*Galago senegalensis* *Galago moholi* *Galago cameronensis* *Galago gabonensis* *Galago gallarum* *Galago matchiei* *Galago zanzibaricus* *Galago granti* *Galago murinus*

The home range of all bushbabies including genus *Galago* is the continent of Africa and a few adjacent islands. Bushbabies are nocturnal and therefore all have large, forward-directed eyes. They are characterized by globular heads, and large, membranaceous ears that can be folded down, have cross ridges, and are very mobile; the two ears can move independently. Bushbaby ears are relatively the largest ears of all primates. All bushbabies are upright leapers and often may even rest in an upright position. Their hind limbs are considerably longer than their forelimbs. Among galagos intermembral indices vary between 57 and 64. They reportedly rarely use quadrupedal locomotion.

The two species of genus *Galago* are medium sized, with a body plus head length between 12 and 20 cm and tail length that varies between 18 and 30 cm. The fur is dense, and the long tails are covered with hair and rather bushy. The color is silvery gray to light brown, and the undersides of body and tail are lighter in color than the top. The end phalanges of fingers and toes are covered with disklike pads on the palmar and plantar aspect, and they carry flat nails dorsally, except for the second toe, which is adorned with the characteristic prosimian toilet claw. Galagos are predominantly arboreal and nocturnal.

They inhabit open woodlands and underbrush. Females of *G. moholi* have been reported to build nests. Bushbabies live in small groups, and males appear to be rather territorial. Vocalizations are a distinct clicking sound characteristic for young animals, twittering and barking for long-distance communication, and high-pitched cries that have been identified as alarm calls. Bushbabies appear to be lively and agile animals. They are said to feed on acacia gums and insect prey, young birds, lizards, blossoms, nectar, fruit, and seeds. They occur in many areas south of the Sahara, both in the lowlands and up to mountain heights of about 2000 m. A considerable amount of urine washing occurs, especially in males. This wetting of the palms of hands and feet has been interpreted both as territorial by spreading scent and as a means to achieve a better grip during locomotion

(Harcourt, 1981). Galagos have two births per year and usually one offspring, although twinning does occur.

The following *Galago* species represent the dwarf bushbabies. Members of the species *G. demidovii* are only 10 to 15 cm long, with tails that measure between 15 and 22 cm and are the smallest of bushbabies. They live in the lower, bushy strata of forests in central African gallery forests, flooded areas, and often plantations. They build nests of leaves in which they spend the day sleeping, females together with a young, but only rarely with a male because males habitually sleep alone in their own nests. Their vocalizations are very varied and species characteristic. Allen's dwarf galago is in many respects similar to *G. demidorii* but somewhat larger overall. They are geographically separated from *G. demidovii*; Allen's bushbabies occur in a defined area of west-central Africa north of the area where *G. demidovii* is found, from Niger eastward to Chad around the Congo river and also on the island of Fernando Po. Allen's bushbabies have a head plus body length that varies between 19 and 21 cm, and their tails vary between 23 and 28 cm in length. Whereas Demidoff's bushbaby is grayish brown, the third species, *G. zanzibaricus* is said to be reddish brown. The Zansibar bushbabies are intermediate in size between the two other species, namely measuring 14 to 17 cm in head plus body length with 20 to 23 cm long tails. They are geographically restricted to coastal Kenya, Tanzania, Malawi, the island of Zanzibar, and south into eastern Zimbabwe. They feed on small beetles and moths and some fruit and sap. Dwarf bushbabies have only one offspring per year, which is carried along and hidden in brush by the mother while she forages. All dwarf galagoes are territorial and very agile. Some of them will go to the ground to pick up fallen ripe fruit.

Galagoides (Smith, 1833) Dwarf Bushbabies	*Galago (Galagoides, Hemigalago) thomasi* *Galago (Galagoides, Hemigalago) medius* *Galago (Galagoide, Hemigalago) demidovii* *Galago (Galagoides) nyasae* *Galago (Galagoides) orinus* *Galago (Galagoides) rondoensis* *Galago (Galagoides) alleni* *Galago (Galagoides) udzungwensis*

The largest of the bushbaby genera are known as the greater bushbabies, which covers three species. Although very similar to the other galagoes, these three *Galago (Otolemur)* species are considerably larger than the others. Their length (head plus body) varies between 27 and 47 cm with tails that are 33 to 52 cm long. They occur in Africa south of the equator and north of the Tropic of Capricorn. They inhabit various kinds of forests and savanna-like environments, invade many kinds of plantations, and are found at heights of more than 3500 m in mountainous regions. The greater bushbabies live in family groups. They use

glandular scents and bite marks to mark territories and spend the day sleeping, preferably in tree holes. They often run quadrupedally and wet the plantar surface of their soles with urine, presumably to improve friction in dry areas and seasons. It has been reported that this urine washing decreases when the humidity rises. They do run quadrupedally on the ground, often with the tail held upright in the air. They also have been observed to hop on the ground in a kangaroo style, covering large areas. They emit loud cries when awake that sound similar to the cries of human infants. Reputedly, this is the origin of the common name bushbaby. Some other vocalizations, such as screams, cackles, and clicking noises, are emitted by both infants and adult animals. Greater bushbabies are omnivorous. Their diet includes insects and lizards, small birds and their eggs, insects and their larvae, fruits, berries, nuts, seeds, flower buds, sap, and gum. With two breeding seasons per year, they carry one to three offspring, which are frequently parked in tree holes or nests built by the mother while she is foraging.

Otolemur (Coquerel, 1859)	*Galago (Otolemur) garnettii*
Greater Bushbabies	*Galago (Otolemur) crassicaudatus*
	Galago (Otolemur) monteiri
Galago Euoticus (Gray, 1863)	*Galago (Euoticus) elegantulus*
Needle-clawed Bushbabies	*Galago (Euoticus) inustus*
	Galago (Euoticus) pallidus

These three bushbaby species, *G. elegantulus*, *G. inustus*, and *Galago pallidus*, get their common name, needle-clawed bushbabies, from a unique characteristic of their fingernails on all digits except the thumb and the big toe and the second phalanx of the foot; all other seven end phalanges bear a nail that is adorned by a central ridge that ends in a needlelike point at the finger- and toe tips. The needlelike points on fingers and toes supposedly make it possible for these bushbabies to explore large tree trunks, presumably by digging into the bark with the help of these sharp points. The second toe is also equipped with the prosimian toilet claw like all other prosimians, and the end phalanges of pollex and hallux are simply shaped like nails. *G. inustus* is the smaller of these species with a head plus body length of 16 to 20 cm and a tail length of 20 to 26 cm. Its fur is dark brown, and it has black rings around the eyes. *G. elegantulus* is 18 to 23 cm, and its fur has an orange-brown hue. These species are generally quite similar to each other, except that the ears are comparatively larger in the smaller *G. inustus* than they are in *G. elegantulus*. These nocturnal bushbabies sleep in foliage and hunt during the night for insects and gum that is exuded by trees. *G. elegantulus* is also known as the western needle-clawed galago because it occupies a larger territory than *G. inustus*. The western needle-clawed bushbaby is found in western Africa in the greater Congo river basin. *G. inustus* are only found in a narrow area in the middle of the African continent from Lake Albert in the

Figure 4.20 *Galago garnetti*, Garnett's greater bushbaby. Photo by Michael Sewell, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

north to Lake Tanganyika in the south, which roughly corresponds to the southern extension of the rift valley.

Figure 4.20 is an example of a greater bushbaby, *Galago (Otolemur) garnettii*.

Infraorder Tarsiiformes (Gregory, 1915)

Family Tarsiidae[13] (Gray, 1825)

Tarsius (Starr, 1780) Tarsiers

Tarsius syrichta
Tarsius bancanus
Tarsius spectrum
Tarsius pumilus
Tarsius dianae
Tarsius pelengensis
Tarsius sangirensis

[13]A recent comprehensive volume about genus *Tarsius* is Wright et al. (2003).

Only since the end of the 1980s has it been generally accepted that genus *Tarsius* has four species, not three as formerly thought. The fourth species of *Tarsius*, *T. pumilus*, was only recognized and newly described in 1987 by Musser and Dagosto. In 2006, there were seven tarsier species. In terms of their body size, tarsiers are the smallest major group of prosimians. They live on many islands off Southeast Asia. The geographic distribution of the species is as follows: *T. syrichta* lives on some of the Philippine islands and on Mindanao; *T. bancanus* lives in southeast Sumatra, Borneo, Banka, and also on some other small, adjacent islands; *T. spectrum* lives on Sulawesi (formerly known as Celebes) and some of the small surrounding islands; and *T. pumilus* is found in the mountain regions of the island of Sulawesi. Their body size ranges from 9 to 16 cm, and tail length from 13 to 28 cm. Only the last third or half of the tail is hairy. The tail's hairs are considerably longer than the short fine hairs of the dense fur that covers the body. *T. dianae* has been reported from central Sulawesi. *T. pelengensi* occurs on Peleng island and *T. sangirensis* supposedly occurs exclusively on the island of Sangihe in north Sulawesi. The eyes of tarsiers are relatively the largest of all primate eyes: a single eyeball of a tarsier has a greater volume than does the same animal's brain (Sprankel, 1965). Tarsiers have short trunks and comparatively big, globular heads; short, small snouts; and no wet rhinarium. The ears are membranous, naked, rounded off, and very mobile. The name *Tarsius* is derived from the elongation of the tarsus or heel bones that, among all the primates, are the longest in this genus. These long heels are totally covered with hair.

T. bancanus (Figure 4.21) has a special "friction pad" ventroproximally on the tail, an area used for additional support when the animal clings vertically. Suction cup–like prehensile pads at the tips of the digits are characteristic of tarsiers. The second and third digits of tarsiers have claws; unlike all other prosimians, tarsier feet are adorned with two grooming claws. Tarsiers move about in a vertical leaping and clinging fashion and prefer upright supports. The intermembral index is low, about 56—indeed, this is the lowest intermembral index among all primates. Many tarsiers actually live in bamboo thickets, a perfect environment that provides vertical supports for an animal of the tarsier's size. Tarsiers are, however, also found in the lower, bushlike strata of the tropical rain forest.

Tarsiers live in pairs with one or two offspring of different ages; females are sometimes seen alone with their offspring. As far as is known, tarsiers do not have defined breeding seasons. These small animals have been observed carrying their young in their mouths. Tarsiers are reported to be silent animals except when very young and during mating, when both partners vocalize. Tarsiers establish and defend well-circumscribed territories. They show frequent marking behaviors with their circumanal gland by means of "urine-washing" with their feet and other urine-marking behavior common in prosimians. Grooming is

Figure 4.21 *Tarsius bancanus*, the western tarsier. Photo courtesy of Heinrich Sprankel. From Ankel-Simons, 1983.

Figure 4.22 *Tarsius syrichta* infant.

Table 4.1

Suborder Prosimii

Infraorder Genera	Tupaiiformes *Tupaia*	Lemuriformes *Eulemur*	Lorisiformes Lorisinae	Lorisiformes Galaginae	Tarsiiformes *Tarsius*
Cervical vertebrae	7	7	7	7	7
Thoracic vertebrae: with ribs	12 to 13	12 to 13	15 to 16	13 to 14	14
Thoracic vertebrae: articulation	11 to 12	11 to 12	15 to 15	12 to 13	12
Lumbar vertebrae	6	6 to 7	6 to 7	6	6
Functional lumbar vertebrae	7	7 to 8	6 to 7	6 to 7	8
Sacral vertebrae	3	3	6 to 7	3	3
Caudal vertebrae	25	25 (*Indri:* 10)	7 to 11	25	Up to 30
Length of arms in % of body length	82 Legs longer	106 Legs longer	104 Arms longer	112 Legs longer	148 Legs much longer
Length of legs in % of body length	88	111	91	126	178
Hand length in % of body length	23	29	28	32	55 (very long)
Foot length in % of body length	44	43	36 (short)	65*	91*

Locomotor activity	Climbing with the help of claws, Hallux and pollex not opposable. Digital formula 3-4-2-5-1	Pollex not opposable. Hallux opposable. Tollet claw on second toe. Heel covered with hair. Indriidae are vertical clingers and leapers. Quadrupedal running and climbing. Predominantly arboreal except Lemur catta.	Clasp hands with extreme opposition of the pollex. Second finger much reduced. Clasp feet similar to hands. 4th toe the longest. Second toe much reduced. Toilet claw on second toe.	*Calcaneus and navicular elongated. Specialized leapers. Grasping hand with fourth digit the longest. Disque shaped pads. Foot specialized for jumping and grasping. Toilet claw on second toe.	*Fused tibio-fibula, Calcaneus and navicular much elongated. Extreme leapers. Third digits the longest. Expanded terminal disques. Toilet claws on second and third toes.
Activity pattern	Diurnal/crepuscular	Diurnal, crepuscular. Several genera are nocturnal.	Nocturnal	Nocturnal	Nocturnal

rarely a social activity but mainly self-directed; tarsiers lick and rub their own fur and scratch themselves frequently with the two toilet claws of their feet.

The tarsier diet consists of animal protein. They live on insects and their larvae, small lizards, and nestlings of birds and other small prey. The litter size of tarsiers is one. The young are well-developed at birth, furred with open eyes, and capable of climbing and of making short jumps (Figure 4.22). Tarsiers have the ability to rotate their heads almost 360 degrees, which is possible because of a unique feature of the morphology of their neck vertebrae (Ankel-Simons and Simons, 2003).

The question of whether tarsiers are true prosimians or whether they should be grouped together with the anthropoid primates is at present unsolved and one of the most hotly discussed issues in primatology. In this context, I have decided to regard tarsiers together with the prosimians, because many of the characteristics in extant tarsiers align them with prosimians, not higher primates.

Table 4.1 lists the suborder Prosimii.

SURVEY OF LIVING ANTHROPOIDEA

This suborder includes all monkeys, apes, and humans. The suborder is divided into two infraorders, Catarrhini and Platyrrhini, and these, in turn, contain three subfamilies: Infraorder Platyrrhini, the New World primates covers the subfamily Ceboidea, and infraorder Catarrhini contains two superfamilies of Old World primates, Cercopithecoidea and Hominoidea. The entire group of anthropoid or simian primates appears to be more homogenous than does the suborder Prosimii. These anthropoideans are commonly called simian primates, from an old name for the suborder "Simii"; they can be subdivided into two infraorders. The division is in accordance with their geographic separation into Old and New World higher primates. Additionally, it correlates with a morphological difference of the face that can be easily recognized visually: all South American monkeys have flaring cartilaginous nasal wings and broad septa separating the two nostrils. In Old World monkeys, apes, and humans, these wings are positioned close to each other, and the septum is narrow. The nares of Old World monkeys thus open downward and are placed near each other, and those of the New World monkeys are directed more upward and laterally. From the Greek words *platys* and *cata*, meaning "broad" and "downward," respectively, these two primate suborders are also named *Platyrrhini* and *Catarrhini*, broad-nosed and down-nosed primates. However, characteristics such as the cartilaginous nasal wings and septa are variable and consequently not of high taxonomic value. The terms *platyrrhine* and *catarrhine* are widely used in primatology because they usefully and obviously distinguish between the higher primates of the New and Old Worlds.

Countless discussions have concentrated on general as well as specific problems of primate taxonomy. Thus, it has, for example, been questioned whether it is justifiable to subdivide the suborder Anthropoidea into the Superfamily Ceboidea, the South American monkeys on one side and the superfamilies Cercopithecoidea, the monkeys of the Old World, and Hominoidea, lesser and great apes and humans together on the other. These three superfamilies are groups of very different diversification, and consequently many different ways of dividing them up have been proposed. The same problem arises from a comparison of the two suborders Prosimii and Anthropoidea. Suborder Prosimii exhibits many more adaptive types than do the primates that belong to the suborder Anthropoidea. It is increasingly clear that a group covering Platyrrhini together with Catarrhini cannot be monophyletic.

In 1956, Fiedler based his subdivision of the order Primates on Haeckel's (1866) suborders Prosimiae and Simiae. The correlative terms used by Simpson (1945) are Prosimii, including the superfamilies Tupaiiformes, Lemuriformes, Lorisiformes, and Tarsiiformes, and the Anthropoidea, containing the superfamilies Ceboidea, Cercopithecoidea, and Hominoidea. Most continental European scientists working with primates have generally agreed to follow Fiedler's taxonomy. This is not the case, however, for English-speaking scholars. They usually follow Simpson's 1945 macro classification and, as stated, subdivide the orders into suborders Prosimii (Illiger, 1811) and Anthropoidea (Mivart, 1873). As mentioned earlier, the Tupaiiformes (Scandentia) are no longer included in order Primates. Here I follow the classification according to Simpson as it was modified by Simons (1972). Simons's classification of Primates has also been adopted more recently by Martin (1990; see also Groves, 2001).

This section not only provides information about the morphology of primates briefly described here but also offers some observations about their behavior. Many primate species, however, have never been studied in any detail, and thus observations might be based on unconfirmed casual reports.

Infraorder Platyrrhini—New World Monkeys

Superfamily Ceboidea (Simpson, 1931)

In 1977, Hershkovitz reclassified the New World monkeys—infraorder Platyrrhini. In his classification, the infraorder has one superfamily, Ceboidea, that consists of two families: Cebidae and Callitrichidae. Hershkovitz argued that *Callimico* is neither a cebid nor a callithrichid and therefore should be classified in a family of its own: Callimiconidae. I do not follow his decision in the classificatory scheme used here because it appears that callimicos are much closer to callithrichids than to cebids.

In the following classification, I recognize only two families belonging to Ceboidea—Cebidae and Callitrichidae—with six and one subfamilies, respectively. All Cebidae are discerned from Old World monkeys by having three premolars and three molars in their permanent dentition. This is also the tooth formula for *Callimico goeldii*, although the third molars in this species are minute. I regard Goeldi's marmoset as belonging in the family Callitrichidae; it has the cebid tooth formula and overall morphology of the head and skull on one hand, but the clawlike nails of callithrichids on all fingertips and toes except for the hallux and the postcranial anatomy of marmosets on the other. Members of family Callitrichidae are dentally characterized by having three premolars and two molars. In contrast, all Old World monkeys have two premolars and three molars in their adult dentition.

Family Cebidae (Swainson, 1835)
Subfamily Aotinae[14] (Elliot, 1913)

Aotus (Illiger, 1811) Night Monkeys[15]	*Aotus trivirgatus*
	Aotus vociferans
	Aotus miconax
	Aotus nancymaae
	Aotus nigriceps
	Aotus azarae
	Aotus infulatus
	Aotus lemurinus
	Aotus hershkovitzi

The South American night monkeys, genus *Aotus*, also commonly known as Douroucoulis, are the only representatives of higher primates that are truly nocturnal (nightly active) and have the anatomical features, such as comparatively large eyes, to document this behavioral trait. Although genus *Aotus* was until recently thought to have only one species, *A. trivirgatus* (Figure 4.23), there are now at least seven valid species recognized (Mittermeier et al., 1988) while Groves (2001) lists nine.

Night monkeys are widely spread in the greater Amazon Basin from Panama to Argentina, and the area of their occurrence is bounded by the Orinoco River in the north and the Andes in the west. Night monkeys are found as far south as the Gran Chaco. They are said to occur at altitudes as high as 3200 m (Eisenberg, 1989). Night monkeys live in bonded pairs throughout their life span. The head of

[14]Genus *Aotus* was subdivided by Hershkovitz in 1983 into two species groups with a total of nine species. A careful study of taxonomy and distribution of genus *Aotus* by S.M. Ford in 1994 reduced the number of species to between five to seven, but Groves (2001) listed nine, the number adopted here. See Brandon-Jones and Groves (2002) about neotropical family group names.

[15]A book dealing in detail with the genus *Aotus* is Baer et al. (1994).

Figure 4.23 *Aotus trivirgatus*, the northern gray-necked owl monkey. From Ankel-Simons, 2000.

these long-tailed, medium-sized monkeys (17–24 cm body length, 22–42 cm tail length) is dominated by comparatively large eyes that are typical of nocturnal animals. The head is globular and the face short, and the nostrils are spread apart in the platyrrhine manner. The intrinsic morphology of the eyes affirms, however, that the extant night monkeys' nocturnal activity pattern derived from a diurnal antecedent (P.C. Wright, 1989). The ears are nearly totally hidden in the fur. White spots are seen above the eyes in some species, and these are topped by a black band of fur, which has a triangular extension reaching between the eyes from the middle of the forehead. The body is covered by short, almost woolly, dense fur. The color varies from silver gray to dark gray on the back, and lighter brownish on the underside. The bushy tail is usually longer than the body and not prehensile. The forelimbs are short relative to the hind limbs, and the intermembral index averages 74. Douroucoulis leap and run quadrupedally. They live in pairs together with their offspring in comparatively small territories and vocalize with a variety of calls. The vocalization appears to be correlated with both the territoriality and the nocturnal habits of these monkeys. Their scent-marking and urine-washing behavior may be correlated with territoriality, as it is in many prosimians.

Night monkeys have a glandular area on the underside of the base of the tail. Night monkeys usually have single births. There is no evidence for a restricted

breeding season. The male grooms the female only in the context of sexual activity. Very young animals cling to their mothers. Later the offspring are carried most of the time by the male and possibly by older siblings. The infants only return to their mother to be nursed. During the day, the night monkeys sleep in tree holes of the forest canopy where they live. The diet of night monkeys consists of a combination of fruit, flowers, young leaves, nectar, insects, small mammals, and possibly small birds.

Subfamily Callicebinae (Hershkovitz, 1977) **Titi Monkeys**

Callicebus (Thomas, 1903)

Callicebus personatus
Callicebus torquatus
Callicebus moloch
Callicebus modestus
Callicebus donacophilus
Callicebus pallescens
Callicebus olallae
Callicebus oenanthe
Callicebus cinerascens
Callicebus hoffmannsi
Callicebus baptista
Callicebus brunneus
Callicebus cupreus
Callicebus ornatus
Callicebus coimbrai
Callicebus medemi
Callicebus bernhardi
Callicebus melanochir
Callicebus stephennashi
Callicebus barbarabrownae
(the latter is perhaps a subspecies of *Callicebus personatus*)

Genus *Callicebus*—or the titis—formerly included three species but now is up to 19 or 20 (Groves, 2001). It falls into approximately the same size range as the night monkeys. These monkeys also occur in the Amazon Basin, but in the northeast they do not cross the Rio Negro or the Amazon River. The western limits are the mountain ranges of the Andes. *Callicebus* occur throughout Brazil and range into Paraguay. They prefer low thickets and forest areas near rivers and perhaps are the New World counterpart of African swamp monkeys. The head is globular, a characteristic of all South American monkeys of small body size. The snout is not prominent, the nares are far apart, and the ears are hidden in the coarse fur. The face is only sparsely covered with short hair and appears to be rather flat. A band of either dark or white long hair is seen across the

forehead. The head and body length varies from 24 to 61 cm, and tail length varies from 51 to 73 cm. The tail is not truly prehensile and sometimes ends in a tuft of hair at the tip. Couples are often observed having their tails spirally intertwined while sitting next to each other. The hair of the body fur is long and soft. Coloration varies from a reddish gray to reddish brown, and even black on the back, being lighter in color on the underside. The hind limbs are relatively shorter than the forelimbs and the intermembral index is 73, similar to that of *Aotus* and other Platyrrhine monkeys of similar body size. These animals run and leap in a quadrupedal manner and are agile and fast. *Callicebus* species live in family groups within territories that are comparatively small, well defined (that is, they do not change noticeably over time), and noisily defended against intruders. Titis vocalize frequently, and their chorus reaches far into the distance. In fact, the morphology of the mandibular angle and an enlargement of the hyoid bone are in accordance with the vocal abilities of the titis, and both morphology and function resemble those of the howling monkeys, which are exceptional among primates in having huge hyoid bones and very deep jaw angles to accommodate a large voice box.

Pair bonding between *Callicebus* males and females is said to last over many years. A mated pair or nuclear family spends much time together as a family group; parents have up to three successive generations of their offspring in their group. Young animals are carried by their father or older sibling, except when they change over to the mother to be nursed. Social grooming within the family group is frequent, and copulation between the mated pairs occurs comparatively often during the breeding season. Groups "fight" vocally with loud, prolonged songs and with threatening movements when they meet. Titis are predominantly diurnal animals. They eat flowers and leaves, insects, small birds and their eggs, possibly small mammals, and an occasional fruit.

Subfamily Pitheciinae (Mivart, 1865)

Cacajao (Lesson, 1840) Uakaris	*Cacajao melanocephalus*
	Cacajao calvus

This subfamily contains three genera of medium-sized monkeys all of which are characterized by distinctive hairdos or coloration. ***Cacajao*** is now commonly subdivided into two species, although formerly *C. rubicundus* was also thought to be a valid species (Napier and Napier, 1967) not a subspecies of *C. calvus*, *C. calvus rubicundus*, as it is listed now.

The common name of these monkeys is uakari (pronounced WA-kee-ree). Uakaris only occur in the tropical rain forest and are more restricted in their habitat than the other pithecinae. They occur predominantly in the high treetops of forests along the shore of small rivers or lakes and are said to avoid the riverine forests alongside large streams (Mittermeier and Coimbra-Filho, 1977). Their range is restricted to a small area within the Amazon Basin. Strictly arboreal

these diurnal monkeys never come to the ground. In contrast to the sakis, the fur of the uakaris is long and sparse. Parts of the body, such as the chest are almost naked. *C. calvus* has reddish brown to silvery gray body hair, but the face is bare, and the forehead is completely bald in this species. These bare skin areas are bright raspberry red and give *C. calvus* the strangest appearance among all South American monkeys. They look like a very aged, bald human who is about to have an apoplexy (seizure). In contrast, *C. melanocephalus* has a black face and a hairy forehead, while the extremities and the head are black and the trunk a dark chestnut brown. The snout of uakaris is blunt, and the nostrils are separated by a wide septum. The ears are large, not hidden by fur, and similar to human ears. The narrow slit of the mouth with its somewhat downward-projecting corners gives these monkeys a seemingly glum appearance. The body length of uakaris varies between 36 and 48 cm, and relative to body length, the tails are short, between 15 and 18 cm. Uakaris are the only New World monkeys that have somewhat reduced tail length. Uakaris are said to live in large groups with up to 100 individuals. They are active during the day and move fast in a quadrupedal manner. Not much is known about territoriality and social behavior. The diet combines predominantly fruit with leaves, buds, and seeds and may be devoid of any animal protein.

Pithecia (Desmarest, 1804)[16] Sakis	*Pithecia pithecia* *Pithecia irrorata* *Pithecia aequatorialis* *Pithecia albicans* *Pithecia monacha*

Genus *Pithecia*, which gives the name to the subfamily Pitheciinae, contains five species. The common name of these monkeys is saki. Their geographic range is defined by the Amazon and Orinoko Rivers in the north, and they occur south of these rivers as far as the tropical rain forest extends its reach. The sakis' head is round, and the snout is comparatively short and more or less naked. The nostrils are very far apart. The hair on top of the head gives the impression of having been combed downward in the direction of the face and sides of the head from the head's center. This head-hair pattern gives sakis the anthropomorphic impression of a monk's hood. Accordingly, one species, *P. monachus*, is called the monk saki. The male of *P. pithecia* has a broad band of white hair around the naked, dark face. The ears are barely visible, hidden in the long fur. The body color of both male and female sakis is dark brownish gray. Sakis have long fur and bushy tails. Their body size varies between 30 and 48 cm, the length of the tails between 25 and 55 cm. Their tails are not prehensile. The hind limbs are longer than the forelimbs, and they have an intermembral index of 76.

[16]Hershkovitz (1979, 1987) established five species of genus *Pithecia*.

Pithecia species run quadrupedally and are capable of making long leaps. They have been observed running upright and bipedally on large branches with their arms reaching above their heads. They are predominantly arboreal and diurnal. The diet consists of berries and larger fruits, honey, leaves, flowers, small mammals, bats, and small birds. The two latter are taken out of tree holes or their nests. Sakis usually live in small family groups. All three genera of the subfamily Pitheciinae share a peculiarity of their dentition: their upper and lower incisors are not implanted vertically in the jaws but are set in a forward tilted or procumbent position. Thus, the incisors mainly function as a pair of pincers. Sakis have glandular areas on the throat of unknown function. *Pithecia* is one of the South American monkeys that has only rarely been caught or observed and is seldom seen in zoos. An average of eight sakis are said to live in territories that measure about 30 to 40 km^2, and they have home ranges of about 12 km.

Chiropotes (Lesson, 1840)	*Chiropotes satanas*
Bearded Sakis[17]	*Chiropotes albinasus*

The third genus of the subfamily Pitheciinae is *Chiropotes,* the bearded sakis, has two species, *C. satanas* and *C. albinasus.* Some authors do not separate this genus from *Pithecia.* The geographic range of the bearded sakis appears to center along the Amazon River. However, *C. albinasus* with a light-colored nose, the rest of the body being very dark, has been reported to appear as far south as the Gran Chaco of Argentina. They are called bearded sakis because the beards of *Chiropotes* monkeys strongly contrast to the short hair on the chin of the sakis that belong to genus *Pithecia*. Bearded sakis have moderately long hair that is parted in the middle of the head. The nares are separated from each other by a broad septum and open somewhat upward. The relatively small ears are nearly imperceptible in the fur. *C. albinasus* has a jet black body but yellowish white stiff hair growing on the nose and upper lip; this area is covered with red skin, standing out visibly against the black skin of the rest of the body. The fur on the trunk of bearded sakis is flat and sleek, but the shoulder region and upper arms give the impression of being covered by a bload cape because the fur hair there is long and dense, as is the hair of the head and beard. The tail also appears very thick because of the animals' dense fur. The tail has a blunt tip and does not taper toward its end, as in *Pithecia*. The body size varies between 40 and 46 cm, and the tail length approximates 35 cm. *Chiropotes* move in a quadrupedal manner, and their hind limbs are longer than their forelimbs, with an intermembral index the same as in *Pithecia*, namely, 76. Because bearded sakis are even less commonly seen than members of genus *Pithecia,* there is little information about group size, territoriality, breeding, or social structure. Bearded sakis are said to live in groups of up to 20 individuals. The bearded sakis are active during the

[17]There are two species of *Chiropotes* according to Hershkovitz (1985).

day, and their food is said to consist primarily of fruits, nuts, and seeds, as well as flowers, leaves, and probably insects and small vertebrates.

Subfamily Alouattinae (Hershkovitz, 1977)

Alouatta (Lacépède, 1799)	*Alouatta belzebul*
Howler Monkeys	*Alouatta seniculus*
	Alouatta caraya
	Alouatta fusca
	Alouatta palliata
	Alouatta villosa
	Alouatta pigra
	Alouatta coibensis
	Alouatta macconnelli
	Alouatta sara
	Alouatta nigerrima
	Alouatta guariba

As already stated, most authors separate the howler or howling monkey as a distinct and separate subfamily Alouattinae, with only one genus *Alouatta* (Figure 4.24). This genus now contains 12 species. Howler monkeys are widely distributed over Central and South America east of the Andes, south to the Gran Chaco area, and north into the coastal forest of Mexico with the exception of Yucatan. The faces of howler monkeys are not furry, but their head hair extends far down on the forehead; male howlers have beards. The head of the howlers appears to be somewhat elongated because of the enlarged laryngeal apparatus and the concomitant change of the morphology of the skull and mandible. In addition, the upper part of the breastbone is bifurcated to accommodate the enlargement of the vocal apparatus. The size of the hyoid box is much greater in male howling monkeys than in females. This voice box serves as a remarkable resonating chamber that amplifies the male territorial call, which in turn gives these monkeys their name. The howling chorus of the males can be heard for quite a distance. The internasal septum is comparatively narrow in howler monkeys, and the nasal openings are directed forward even slightly upward. Fur color dimorphism occurs in *A. caraya:* males are black, and females and young of both sexes have olive-colored fur. Howler monkeys are among the largest New World monkeys. Their body size varies from 40 to 70 cm and the long tails measure between 50 and 57 cm. Howler monkeys have truly prehensile tails; the last third of the tail has a well-developed friction pad on the ventral aspect. Fore- and hind limbs are of nearly equal length, and intermembral indices range from 92 to 105.

Howler monkeys are predominantly arboreal animals. They feed in the peripheral branches of trees and often jump from the outer branches of one tree down into those of adjacent trees, having all "five" extremities (namely arms, legs, and prehensile tail) extended in a spread-eagle manner to grasp the small

Figure 4.24 *Alouatta palliata*, the mantled howler monkey. Photo courtesy of Ken Glander. From Ankel-Simons, 2000.

branches below when they are landing. *A. villosa* have been seen to "bridge" gaps between larger branches with their bodies to make passage for others, often young animals. Howlers also have occasionally been observed swimming.

In general, howlers are not very elegant in their movements but proceed in a deliberate climbing way with all four limbs and the tail engaged in the process, often walking quadrupedally on thicker, more or less horizontal branches. Like other cebids, they do not grasp objects between thumb and index finger but between index finger and third finger, a grasping pattern that can frequently be observed in more primitive animals such as the American opossum (Figure 4.25). Howler monkeys are diurnal and have a specialized diet. They are leaf eaters like the Old World colobines but lack the highly specialized sacculated stomach of the latter group. Howlers also eat fruit, flowers, a bird (rarely), rotten wood, and bark. Howlers have often been and are continuously studied in the wild. The

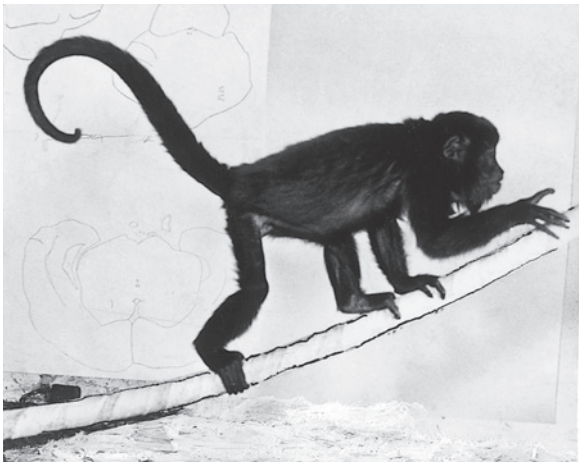


Figure 4.25 Infant howler monkey showing the typical handgrip between second and third fingers. From Ankel-Simons, 2000.

first extensive, long-term modern field study of a primate was a detailed account of their behavior by Carpenter (1934). These primates usually live in moderate-sized groups of 10 to 20 individuals. In addition to defining and defending their territories vocally, the far-reaching howling may also help to locate the position of different groups, and may have other social implications that are little understood (e.g., group coherence). Howlers may also exuberantly shake and tear branches when excited. Hierarchical dominance patterns are present in both adult males and females. Howlers are born throughout all seasons of the year. Single young are the rule, but twinning has also been observed.

Subfamily Cebinae (Erxleben, 1777)

Cebus (Erxleben, 1777)	*Cebus apella*
Capuchin Monkeys	*Cebus capucinus*
	Cebus albifrons
	Cebus nigritus
	Cebus olivaceus
	Cebus kaapori
	Cebus libidinous
	Cebus xanthosternos

The capuchin monkeys, genus *Cebus*, gives its name to the entire superfamily Ceboidea. *C. xanthosternos* is listed as one of the world's most endangered primates (Konstant et al., 2002). There are two kinds of capuchins, the appearance of which differs most noticeably in the arrangement and length of hair on the head. One group constitutes the tufted capuchins, whose elongate hair on top and both

sides of the head forms paired tufts of individually variable size and shape. Tufted capuchins all belong to the species *C. apella*. The three remaining species have dark caps of head hair (similar to those of the "Three Stooges") and no hair tufts. This latter trio of species includes slightly smaller-sized animals than does *Cebus apella*. Members of genus *Cebus* are found in most of the forested areas of Central and South America; they live in mountainous regions up to an altitude of about 7000 feet. Mostly fruit and insects are combined in the diet of these diurnal primates. The body size range from 30 to 60 cm, the tail length also varies between 30 and 60 cm. The tail is functionally prehensile, but it is not equipped with the ventrodistal friction pad of truly prehensile-tailed monkeys. Basically, capuchins are quadrupedal climbers. In this mode of locomotion, the tail is always employed as an additional grasping limb securing their movements. Capuchin monkeys live in groups, reportedly of about 10 to 30 individuals. No defined territoriality rules the life of capuchin monkey groups. They have a wide variety of vocalizations to communicate with each other and are said to have a complicated dominance ranking order. Possibly the unusual vocalization relates to the latter. The sexes cannot easily be recognized in the field, for females have a pendulous clitoris that at a distance resembles the penis. The females give birth during all seasons. Capuchin monkeys can easily be kept in zoos and are known for remarkable manipulative skills and outstanding memories. Capuchin monkeys are the organ-grinder monkeys and historically worked for their keep by doing tricks and collecting money at fairs and in the circus; they are apt tool users (Fragaszy et al., 2004). The astonishing fact of a cross-genus adoption of a marmoset *(Callithrix jacchus)* infant by a capuchin *(Cebus libidinosus)* female in the wild has been observed (Izar et al., 2006). On the other hand, capuchins are also known to kill other primate infants. An adult male tufted capuchin *(Cebus apella)* captured, killed, and partially ingested an infant titi monkey *(Callicebus moloch)*. Here are two very disparate behaviors described for members of the same genus. In this context, it seems important to remember that *Cebus apella* is the most faunivorous species of capuchins (Sampaio and Ferrari, 2005).

Saimiri (Voigt, 1831)	*Saimiri sciureus*
Squirrel Monkeys	*Saimiri oerstedti*
	Saimiri ustus
	Saimiri boliviensis
	Saimiri vanzolinii

Saimiri, the squirrel monkey, is commonly regarded as having two species (*S. sciureus* and *S. oerstedti*), although some do believe that there are five species, as listed here. Squirrel monkeys are widely found in tropical rain forests of South America east of the Andes. These monkeys prefer living in gallery forests or at forest edges. In contrast to the other small-bodied New World monkeys that have rounded heads, species of *Saimiri* have egg-shaped, elongated heads. Squirrel

monkeys' body fur is yellowish tan, mottled with black hair tips; they have a white, masklike area around the eyes, and the snout is usually dark, almost black, whereas the cheeks and ears are almost white. The underside of the body is very light in color. The ears are comparatively large, visible, and often tufted. A wide internasal septum separates the nasal openings on the short and blunt snout. The tail has a tuft of long hair at the tip being black throughout the last quarter. The hair is dense and short all over the body as well as over the length of the long tails. These comparatively small and nervous primates measure between 20 and 40 cm in body length; the tail is longer than the body and varies in length between 35 and 47 cm. The tails of these monkeys are not prehensile and are not actively involved in any grasping activities. *Saimiri* species are the smallest of the Cebidae. The hind limbs are considerably longer than the forelimbs, with an intermembral index averaging about 77. These small cebids are agile and run and leap quadrupedally. Their breeding season is evidently restricted. *Saimiri* are also reported to congregate in large numbers, comprising groups up to 500, but the average troop size is about 40 or 50 monkeys. Saimiris are diurnal, and their diet consists mainly of fruit and insects. Squirrel monkeys are easily kept and bred in captivity and were frequently sold as pets in the past. Like all primates, however, squirrel monkeys do not make good pets because they cannot be house broken, and *Saimiri* that are maintained in captivity are extraordinarily destructive and messy.

Subfamily Atelinae (Gray, 1825)

Ateles (E. Geoffroy Saint-Hilaire, 1806) Spider Monkeys	*Ateles paniscus*
	Ateles belzebuth
	Ateles fusciceps
	Ateles geoffroyi
	Ateles chamek
	Ateles hybridus
	Ateles marginatus

The subfamily Atelinae includes three genera: *Ateles,* the spider monkey; *Brachyteles*, the woolly spider monkey; and *Lagothrix*, the woolly monkey. The genus *Ateles* (Figure 4.26), which gives its name to the subfamily, is divided into seven species. Spider monkeys occur in lowland tropical rain forests of South and Central America and range as far north as Mexico. The heads of spider monkeys are rounded, and the forehead is high, whereas the snout protrudes somewhat but is blunt. The fur is usually dark gray or brownish, and the eyes are surrounded by a white ring, whereas the face is black. The underside of the body is light in color, and the fur is overall scruffy and lacks an undercoat. The wide internasal septum characteristic of New World monkeys separates the nostrils, and the eyes are wide set. The nose and mouth are usually naked. The ears are large and positioned comparatively low on the head; they are hidden in the shaggy head hair in some

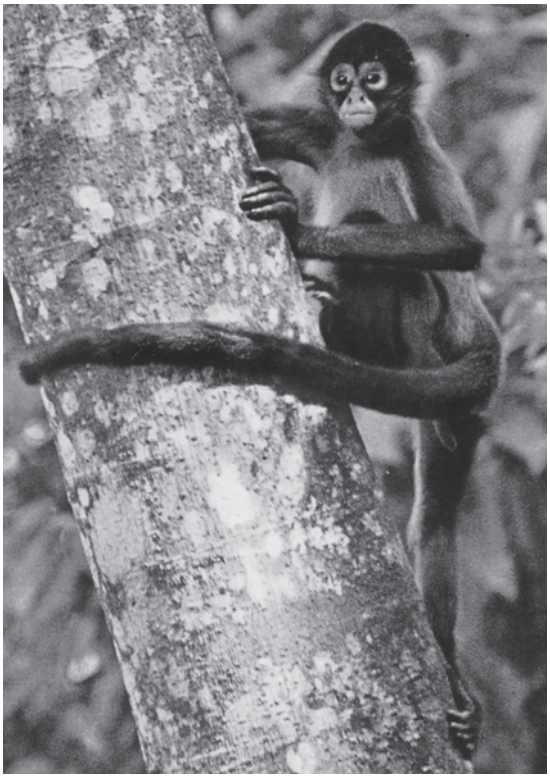


Figure 4.26 *Ateles geoffroyi*, Geoffroy's spider monkey.

species. The fur is variable in color and texture both, within and between species. Species of *Ateles* are the largest South American monkeys, with body length ranging between 35 and 65 cm and the very long prehensile tails ranging between 60 to 90 cm in length. Long, slender limbs and tail combined with a relatively short trunk that has the rounded belly of a leaf eater add to the spiderlike appearance of these monkeys and gave rise to their common name.

Spider monkeys are highly adapted for arboreal life and live in the high canopies of rain forests. They have a long prehensile tail bearing a large friction pad on the ventrodistal third of the tail. They typically move rather deliberately with all five extremities grasping and holding onto branches, and at least two extremities holding on at most times. Sometimes, however, they have been observed to hang by the tip of their tails only while foraging alone. Spider monkeys swing by their arms overhead, hand over hand, comparatively often when they are on the move. As in apes, their forelimbs are longer than their hind limbs, and their intermembral index averages 105. In addition, both the fore- and

hind limbs are comparatively long compared with the length of the trunk. In captivity and in an artificial environment, spider monkeys frequently walk bipedally when on the ground. They also walk bipedally when they move along more horizontal branches that are large in diameter. The thumb is greatly reduced or absent. Spider monkeys live in groups of variable size that average about 20. They rarely descend to the ground; are noisy, emitting bark-like calls; and apparently do not have a defined breeding season; spider monkeys have been seen carrying young during all months. Twinning is rare. Females and males cannot easily be discerned because the clitoris is long and pendulous and resembles the penis. The diet of these diurnal primates consists predominantly of fruit, leaves, seeds, flowers, and their buds. Hierarchies of dominance are not clearly defined. Group size seems to be determined by availability of food.

Brachyteles (Spix, 1823)	*Brachyteles arachnoids*
Woolly Spider Monkeys	*Brachyteles hypoxanthus*

Woolly spider monkeys, genus *Brachyteles* and species *arachnoides,* generally appear to be similar to members of genus *Ateles,* and some primatologists do not regard them as a separate genus. The known differences between the two genera are the woolly character of the fur, the comparatively narrower internasal septum, and the isolated occurrence in a restricted area of forest in southeastern Brazil. Perhaps the most important differences are dental modifications: *Brachyteles* is said to be dentally similar to *Alouatta* in having additional crests on the molars that form a functionally powerful system for grinding leaves. Diet, activity pattern, and most of the known skeletal and nondental anatomical characteristics, however, are like those of genus *Brachyteles hypoxanthus* is on the 2002 list of the world's most endangered primates (Konstant et al., 2002).

Lagothrix (E. Geoffroy	*Lagothrix lagotricha*
Saint-Hilaire, 1812)	*Lagothrix cana*
Woolly Monkeys	*Lagothrix lugens*
	Lagothrix poeppigii
Oreonax (Thomas, 1927)	*Oreonax flavicauda*

Woolly monkeys—genus *Lagothrix*—are given their common name because of their dense, soft, short, woolly fur. *O. flavicauda* occurs only in a very restricted area in western Peru. The genus has now been split into two genera with *L. flavicuada* being reclassified as *O. flavicauda* (Groves, 2001). *O. flavicauda* is on the 2002 list of the world's most endangered primates (Konstant et al., 2002). *L. lagotricha* are found in central Brazil and northward into southern Colombia and Venezuela, as well as throughout the Amazon, Orinoco, and Rio Magdalena River headwaters. They occur in the tropical rain forests and roam into mountainous regions up to 3,000 m. The body length of woolly monkeys varies between 40 and 60 cm and the powerful prehensile tail between 55 and 75 cm. The fur of *L. lagotricha* is dark gray, and *O. flavicauda* has a

yellow tail. Woolly monkeys are skillful in the use of their prehensile tail, which has a friction pad along its ventrodistal third. Their limbs are of almost equal length with an average intermembral index of 98. Like the other New World monkeys with prehensile tails, they usually locomote using all five extremities.

Woolly monkeys are almost exclusively arboreal, and when climbing, the tail continuously keeps in contact with branches, securing the animal. When on the ground they frequently adopt a bipedal posture, and when bipedally standing, the tail is used as a tripod strut. The diet of these diurnal primates combines mainly fruit, nuts, leaves, flowers, flower buds, and insects but will also include small birds, birds' eggs, and small mammals when available. Woolly monkeys live in moderate-sized groups of about 25 individuals and join species of other cebid genera to forage together. Almost nothing is known about a possible breeding season, the monkeys' territoriality, or their social hierarchies.

Family Callitrichidae
Subfamily Callitrichinae (Gray, 1821)
Callimico (Ribeiro, 1912) *Callimico goeldii*
Goeldi's Marmoset

We here consider genus *Callimico* together with family Callitrichidae (Rylands et al., 1995; Pastorini et al., 1998) with only one species *goeldii* (Figure 4.27). Goeldi's marmoset is another rarely observed platyrrhine that is uncommon in captivity. Although customarily called a marmoset, it seems that *Callimico* is different, both morphologically and behaviorally, from the other marmosets. These differences are not enough to justify classification in its own family separate from the callithrichids, however. This monkey lives only in inaccessible, remote areas of the rain forest around the tributaries of the Amazon River in northwestern Brazil, southeastern Peru, and the Patumayo of Colombia. Only at the end of the twentieth century were renewed efforts undertaken to find and study these elusive platyrrhines (Christen, 1999).

The fur of these small monkeys is dense and silky, with rather long hairs. The color is dark brown to almost black, with light, often golden brown hair tips. On the top of the head the long hair forms a hairdo that resembles a dark wig: long and straight on the back and the sides of the head and short and brushlike on top. The body length of *Callimico* averages 20 cm; the tail measures between 25 to 27 cm in length and appears to be rather thin and covered with long, straight hair. These tails are not prehensile. The hind legs of these diurnally active primates are somewhat longer than the forelimbs, and their intermembral index is about 70 to 80. Goeldi's marmosets usually walk, run, and leap quadrupedally, but they are said to also move in a vertical leaping and clinging fashion. Callimicos have claws on all digits of their fingers and toes with the exception of the hallux, being similar in this characteristic to all species of the family Callitrichidae. In contrast, their permanent tooth formula in combination with the morphology of the skull seem to align *Callimico* with the Cebidae. Social groups are small, consisting of a mated

Figure 4.27 *Callimico goeldii*, Goeldi's monkey. Photo courtesy of Edilio Nacimento Becerra.

pair and their offspring. Goeldi's marmosets usually have single birth. They have been observed eating fruits, berries, and occasionally insects.

Callithrix (Erxleben, 1777) Short-tusked Marmosets or Titis	*Callithrix jacchus* *Callithrix argentata* *Callithrix humeralifer* *Callithrix saterei* *Callithrix kuhlii* *Callithrix geoffroyi* *Callithrix penicillata* *Callithrix flaviceps* *Callithrix aurita* *Callithrix leucippe* *Callithrix emiliae* *Callithrix (Mico) nigriceps* *Callithrix (Mico) marcai* *Callithrix (Mico) melanura*

Callithrix (Mico) humeralifera
Callithrix (Mico) mauesi[18]
Callithrix (Mico) chrysoleuca
Callithrix (Mico) intermedia
Callithrix (Mico) humilis
Callithrix (Mico) manicorensis

This subfamily of family Callitrichidae includes the clawed and small-sized New World primates: the marmosets and tamarins. All genera and species of family Callitrichidae have three premolars and two molars in their permanent dentition. Marmosets and genus *Callimico* are unique among higher primates in having claws on all digits except the hallux. These claws are regarded as modified nails, however, and thus are not true claws. Hershkovitz (1977) attributed four genera to this family. Proposed generic names vary strikingly among different authors. Callitrichidae have provided a field day for taxonomists. Generally speaking, it is not at all advisable that scientific names, which are in common use among scientists, continually be changed, nor should groups of primates be split up into unnecessary genera. To give an example of the confusing number of names that have been attributed to two of the main kinds of marmosets, some of the proposed generic names for the genera *Callithrix* and *Saguinus*, and what appears to be the most valuable and concise data about Callitrichidae, can be found in the monograph by Hershkovitz (1977).

Alternate Genus Names Proposed for *Callithrix* and *Saguinus:*

Callithrix	Saguinus
Arctopithecus	*Callithrix*
Hapale	*Cercopithecus*
Jacchus	*Hapale*
Liocephalus	*Hapanella*
Mico	*Jacchus*
Miocoella	*Leontideus*
Midas	*Leontocebus*
Ouistitis	*Leontopithecus*
Sagouin	*Marikina*
Simia	*Midas*
Sylvanus	*Mystax*
	Oedipomidas
	Oedipus
	Saguinus
	Seniocebus
	Simias

[18]Mittermeier (1992). *C. sateri* was reported in 1996 by Mauricio de Almaido Norohona (1996). Since then, *Callithrix* species have proliferated vastly.

Genus *Callithrix*—the marmosets—was originally subdivided into three species: *Callithrix jacchus*, *C. argentata*, and *C. humeralifer* while genus *Saguins* originally had twelve species *(S. fuscicollis*, *S. bicolor*, *S. leucopus*, *S. inustus*, *S. midas*, *S. imperator*, *S. mystax*, *S. labiatus*, *S. tripartitus*, *S. rosalia*, *S. chrysomelas*, and *S. chrysopygus)*. Only in the 1990s (Mittermeier, 1992; Almaido Norohona, 1996) were fourth and fifth species newly discovered and described. Marmosets occur in equatorial rain forests south of the Amazon and range south into the Mato Grosso region. With marmosets, colors of the dense shiny fur are variable as is the hair length. Many of the marmosets have distinctive hair tufts hiding their ears. The head is globular, the snout short and blunt, the forehead low and flat, and marmosets have a typically wide platyrrhine internasal septum. Body size of these primates varies between 18 and 32 cm, and the tail length varies between 24 and 40 cm. The intermembral index of marmosets averages 76. Marmosets live in small social groups consisting of a mated pair and their offspring. Female marmosets predominantly give birth to two offspring, and the male takes a prominent role in carrying and protecting the infants. These agile, diurnal primates have a variable diet consisting of insects, fruit, gum, and sap. *Callithrix* have been seen to gouge bark off trees with their incisors and canines to get to gum and sap. Their lower canines are not longer than the incisors and rather incisiform. The same is true for the lower front dentition of pygmy marmosets, and this dental adaptation seems to facilitate bark and wood chiseling. There is great variance of hair color and arrangement of ear tufts among marmosets. Locomotion is predominantly quadrupedal running, interspersed by leaps and bounds. Their vocalization is high pitched and not very far reaching.

Cebuella (Gray, 1866) *Cebuella pygmaea*
Pygmy Marmosets

Pygmy marmosets, *Cebuella* with only one species *pygmaea* (Figures 4.28 and 4.29), are basically a smaller version of the common marmosets genus *Callithrix*. The pygmy marmoset is the smallest of the South American monkeys and, in fact, the smallest of all living higher primates. *Cebuella* live in the dense tropical rain forest close to the Amazon River. The fur of pygmy marmosets is yellowish brown, mottled with black spots, and almost white on the belly. The overall color impression is grizzled gray, often having a green hue. The tail is faintly cross striped. Comparatively large ears are hidden in the fur. The body of this small species is about 13 cm long, and it has a nonprehensile tail that is close to 20 cm long. These primates weigh between 120 to 190 g when grown, just "a handful" of monkey. Together with *Galago demidovii, Microcebus myoxinus* (note, however, that new and ever tinier species of *Microcebus* are being discovered all the time), and *Tarsius syrichta*, these species are the smallest extant primates. Pygmy marmosets certainly are the smallest anthropoids. They live in family groups, consisting of an adult pair together with their offspring of

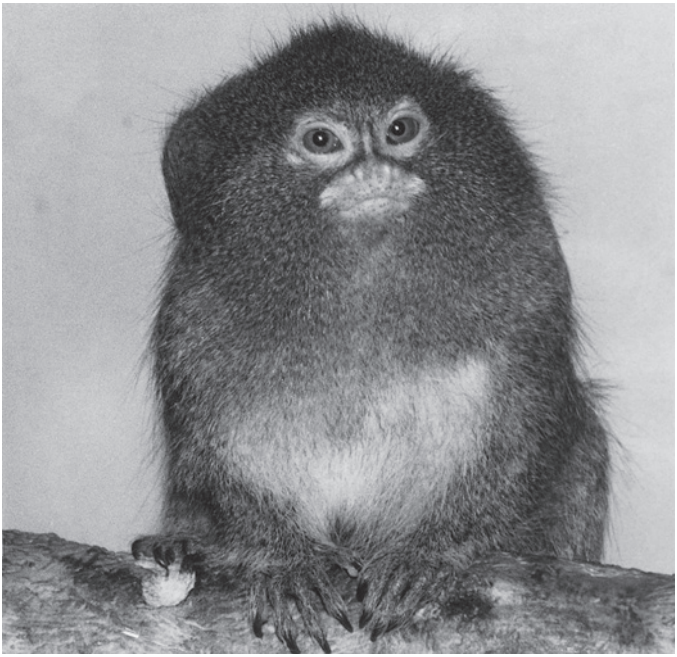


Figure 4.28 *Cebuella pygmaea*, the pygmy marmoset. Photo courtesy of Dieter Glaser. From Ankel-Simons, 2000.

Figure 4.29 *Cebuella pygmaea* family. Photo courtesy of Dieter Glaser. From Ankel-Simons, 1983.

two generations or more. Pygmy marmosets sleep in tree holes; usually they have twin births. As with many callithrichids, infants ride on their parents and on older siblings and often only change over to the mother to nurse during their first three months of life (Christen, 1968). The pygmy marmoset eats gum, sap, insects, arthropods, and fruit. Pygmy marmosets have fairly procumbent incisors and canines, and it has been suggested that this is an adaptation for removing bark to get at tree sap and gum. It also appears that the geographic distribution of the pygmy marmoset is limited by distribution of the trees producing the sap and gum they eat.

The primary locomotor patterns used by these small primates are rapid quadrupedal leaping and running, not unlike the locomotion of squirrels. The vocalization of the pygmy marmosets is a chirp that resembles that of a cricket.

Saguinus (Hoffmannsegg, 1807) Long-tusked Marmosets or Tamarins	*Saguinus fuscicollis* *Saguinus bicolor* *Saguinus niger* *Saguinus leucopus* *Saguinus inustus* *Saguinus midas* *Saguinus imperator* *Saguinus mystax* *Saguinus labiatus* *Saguinus nigricollis* *Saguinus graellsi* *Saguinus melanoleucus* *Saguinus tripartitus* *Saguinus pileatus* *Saguinus labiatus* *Saguinus martinsi* *Saguinus oedipus*[19] *Saguinus geoffroyi*[19]

Tamarins—genus *Saguinus*—are the most common callithrichids, and the group includes at least 12 species. As mentioned earlier, this genus has had as many as 16 names. They inhabit most of the Amazon Basin and the coasts of Colombia and range into southern Central America. The pelage of species that belong to this genus is variable, from white body fur with gray face in *S. fuscicollis* to black body fur with a black nose and a short-haired white mustache in *S. nigricollis.* The emperor tamarin, *S. imperator*, is dark all over except for a long, white mustache that sprouts from a totally white nose and snout. The head

[19]Regarded as genus *Oedipomidas* by some. See also Tagliaro et al., 2005.

of tamarins is long and ovoid with a short, blunt muzzle. Body size ranges between 18 and 31 cm, and the length of their nonprehensile tails varies from 25 to 43 cm. The hind limbs are somewhat longer than the forelimbs, and the locomotor behavior of these frisky primates is a combination of quadrupedal running, walking, and jumping, interspersed with occasional leaps (Fleagle and Mittermeier, 1980). Their intermembral index lies at 75. Tamarins live in dense forests and spend most of their active time in the lower and middle levels. They often spend the night sleeping in tree holes. They live in small social groups, of rarely more than about 20 individuals. Births usually occur seasonally, and twins are typical. The males play an active role in rearing the offspring. The tamarin diet includes tender leaves, gum, sap, fruit, and insects. An occasional bird's egg and small vertebrate can be included in the menu. Unlike the short-tusked marmosets, tamarins have long, lower canines that project much higher than their incisors. Their vocalization resembles the chirp of small birds.

Figure 4.30 *Leontopithecus rosalia*, golden lion tamarin.

Leontopithecus (Lesson, 1840) Lion Tamarins	*Leontopithecus rosalia* *Leontopithecus chrysomelas* *Leontopithecus chrysopygus* *Leontopithecus caissara*

The last genus of the Callitrichidae, the lion tamarins—*Leontopithecus* (Figure 4.30)—with four species are probably the rarest members of all New World primates and have the depressing honor to be among the world's most critically endangered mammals (*L. caissara* is on the list of the world's most endangered primates; Konstant et al., 2002). This is partly because they inhabit a region of lowland rain forests of Brazil that has the highest human population density. The other reason for these primates to be so highly threatened in their survival is that their appearance is very conspicuous: one species—*L. rosalia*, the golden lion tamarin—is covered with bright golden, long, silky pelage, the other two are black on the back of the body, with one species, *L. chrysomelas*, having a golden lion mane covering its shoulders, and the other, *L. chrysopygus*, a bright golden rump and thighs. The body size of lion tamarins varies between 20 to 34 cm, and their nonprehensile tails are about 32 to 40 cm long. They are the largest extant callithrichids with an intermembral index that averages over 80, a little higher than in the other three genera of this family. Hands and feet of the members of this genus are slender and long, with unusually short thumbs.

Lion tamarins are pair-bonded and usually give birth to twins. As with the other callithrichids, the male predominantly carries the offspring. Births appear to be seasonal. Lion tamarins are diurnal and sleep in hollow trees or tangles of epiphytes. Their diet includes fruit, insects, snails, spiders, bird's eggs, small lizards, and small birds as well as other small vertebrates.

Infraorder Catarrhini—Old World Monkeys

The infraorder contains two superfamilies: Cercopithecoidea and Hominoidea. Within the superfamily Cercopithecoidae and family Cercopithecidae, we recognize two subfamilies: the Cercopithecinae and the Colobinae. Two comprehensive volumes deal with these two subfamilies in some detail: the Cercopithecinae, or guenons, are discussed in *A Primate Radiation, Evolutionary Biology of the African Guenons.* The Colobines are dealt with in *Colobine Monkeys, Their Ecology, Behavior and Evolution*. Species assignment differs considerably according to various authorities on both subfamilies. Details of taxonomy are constantly changing because new research often produces altered viewpoints. All Old World monkeys are included in the superfamily Cercopithecoidea and family Cercopithecidae. They have the same tooth formula, which they also share with the other superfamily of Old World Primates, the Hominoidea.

Species of the subfamily Cercopithecinae have the following characteristics in common: subequal length of their fore- and hind limbs; simple stomachs; variable, omnivorous diets; cheek pouches; and ischial callosities—thick, cornified plates that cover the flattened and expanded ischial portions of the pelvis and jut through the skin. These function as props on which the primates sit (Rose, 1974). Colobines also have ischial callosities, but in contrast to the Cercopithecinae, the Colobinae lack cheek pouches and have sacculated and highly evolved stomachs for their rather restricted diet: Colobines are herbivorous and are predominantly leaf eaters.

Superfamily Cercopithecoidea (Gray, 1821)
Family Cercopithecidae (Gray, 1821)
Subfamily Cercopithecinae (Gray, 1821)

Cercopithecus (Linnaeus, 1758) Guenons	*Cercopithecus aethiops*
	Cercopithecus albogularis
	Cercopithecus ascanius
	Cercopithecus campbelli
	Cercopithecus cephus
	Cercopithecus cynosurus
	Cercopithecus denti
	Cercopithecus diana[20]
	Cercopithecus dryas
	Cercopithecus erythrogaster
	Cercopithecus erythrotis
	Cercopithecus hamlyni
	Cercopithecus lhoesti
	Cercopithecus neglectus
	Cercopithecus nictitans
	Cercopithecus mitis
	Cercopithecus mona
	Cercopithecus petaurista
	Cercopithecus pogonias
	Cercopithecus preussi
	Cercopithecus pygerythrus
	Cercopithecus sabaeus
	Cercopithecus salongo
	Cercopithecus solatus
	Cercopithecus tantalus
	Cercopithecus wolfi

[20]The subspecies *C. diana roloway* is on the most endangered list (Konstant et al., 2002).

Genus *Cercopithecus*, the vervets or guenons, is one of the most diversified genera of all primates (Figures 4.31 and 4.32). At this point in time, 26 species are generally accepted, but many more have been proposed. Guenons are found to be widely distributed throughout sub-Saharan Africa in a variety of environments. There is a high degree of variation in fur thickness, length, and coloration as well as contrasting adornments such as beards, hair tufts, and brightly colored spots. Their faces are distinctively marked; for example, *C. hamlyni*, which are generally dark gray in color, have a characteristic white stripe extending from the root of the nose between the eyes to the upper lip. The snout is less prominent in this genus (it is comparatively short in the closely related genera *Allenopithecus* and *Miopithecus* as well) than in the other genera belonging to this family.

Usually the face is hirsute, except for the immediate area around the eyes, nose, and mouth, where the bare skin can be brightly colored in distinct "face patterns," as can the ears (Kingdon, 1988). The body length of the members of this genus varies between 32 and 65 cm, and the length of their long tails—which are not prehensile—ranges between 48 and 110 cm. The intermembral index typically averages in the mid-80s. Male guenons are usually somewhat larger than females. Their ischial callosities are comparatively small and distinctly separated in the midline. Guenons predominantly locomote quadrupedally. They have diurnal activity rhythms, but there is one species, *C. hamlyni*, that was once

Figure 4.31 *Cercopithecus aethiops*, the green monkey or vervet. From Ankel-Simons, 1983.

Figure 4.32 *Cercopithecus neglectus*, De Brazza's monkey. Photo courtesy of Terry Maltsberger. From Ankel-Simons, 2000.

reported to be nocturnal. Areas covered by daily travels of *Cercopithecus* groups vary in size, but these wanderings appear to be ruled mainly by the distribution and availability of food sources. The ratio of females to males in these groups averages around three females to two males. Relationships of dominance are not elaborate. Social grooming is rare compared with the other genera of cercopithecines. *Cercopithecus* females do not have sexual swellings or change of skin color during estrus. Most of the species lives predominantly on fruit, although *C. ascanius* eats leaves and *C. aethiops* and *C. mitis* are known to

include many insects. The seeds of the fruit that the guenons eat pass through their digestive tract intact and are thus dispersed by the monkeys.

Allenopithecus (Lang, 1923) *Allenopithecus nigriviridis*
Allen's Monkey

The genus ***Allenopithecus*** has only one species, *nigriviridis*, that has the common name Allen's swamp monkey. This species is considered part of the genus *Cercopithecus* by some. Overall the build of the swamp monkey is more heavyset than that of the other guenons. They measure about 45 cm in body length, with tails 50 cm long. Their intermembral index is 84, and their locomotion is predominantly quadrupedal.

In contrast to other guenons, Allen's swamp monkey females have distinct estrous swellings, and in males the scrotal skin is light blue. Allen's swamp monkeys live in swampy areas. They have interdigital webbing from digits two to five. Another feature that distinguishes Allen's swamp monkey from the other guenons is the larger, comparatively square ischial callosities that are connected across the midline in some males. Members of this genus live in the lower strata of the forest in swampy areas restricted to the central area of Zaire and are unusual in that they are good swimmers and know how to dive. They also have an unusual diet; in addition to fruit, nectar, and blossoms, they consume insects, worms, and fish.

Miopithecus (I. Geoffroy Saint-Hilaire, 1842) *Miopithecus talapoin*
Talapoin Monkey,
Dwarf Guenon, or
Mangrove Monkey

The other genus that is now discerned from genus *Cercopithecus* is genus *Miopithecus*, with only one species, *talapoin*. *M. talapoin* has the common names of dwarf guenon, mangrove monkeys, and talapoin monkeys. They are on average the smallest of Old World monkeys. Their body length is only 35 cm, and the tail is close to 53 cm long and their intermembral index is 83. Their locomotion is predominantly quadrupedal. The name "mangrove monkey" is derived from the fact that these guenons never go far away from mangrove and gallery forests near rivers of a rather restricted area of coastal central West Africa. The head of the talapoin appears to be more rounded than the heads of the larger guenons, probably because of its relatively short snout. The diet is a combination of fruit, leaves, and flowers as well as animal prey. They raid bird's nests for eggs, catch flying insects including grasshoppers, eat caterpillars and beetles, and even catch an occasional shrimp.

Erythrocebus (Trouessart, 1897) *Erythrocebus patas*
Patas or Military Monkey

Erythrocebus is another genus of the Cercopithecinae that has been changed back and forth between *Cercopithecus* and *Erythrocebus* and has but one species, *E. patas* (Figure 4.33). Patas monkeys are adapted to ground living and open country and are widely distributed in lowland savannas and wooden steppes south of the Sahara desert. They are active during the day and climb into trees in the evening where they spend the night being safe from large predators. The muzzle of patas monkeys is comparatively long, and the eyes are set close to each other. Adults of both sexes have an angled black stripe above the eyes that offsets the rusty tan skullcap of fur. They have a white mustache and a white area of almost bare skin around the pitch-black nose. Except for these small bare areas that also extend around the eyes where the skin turns dark gray, the face is hairy, and tufts

Figure 4.33 *Erythrocebus patas*, the patas monkey. Photo by Steve Underwood, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

of long hair which is gray on the cheeks and above as well as in front of the ears give the face a broader appearance than it actually is. The body and limbs are of slender build, and the fur is comparatively coarse—rusty tan on the back, and bright off-white on the four legs and the underside of both, body and tail. A mottled gray area of long fur covers the shoulders. The tail fur is smooth.

Male patas monkeys are considerably larger than females, with an average body length of 65 to 88 cm and tails of about the same length. Females are an average of only 50 cm long, with tails also measuring about 50 cm. Their intermembral index averages about 92. During quadrupedal locomotion, the hands are usually held in a digitigrade position. Although all-male groups occur, most patas monkeys live in groups of about 5 to 30 individuals with a single adult male (Gartlan, 1975). The lone adult male patas functions as the guard or sentry of the group. Females are the group leaders and engage in territorial disputes (Chism et al., 1984). The diet of patas monkeys is a combination of vegetarian items and animal prey, including fruit, seeds, insects, lizards, and an occasional bird's egg.

Macaca (Lacépède, 1799)	*Macaca mulatta*
Macaques	*Macaca fascicularis*
	Macaca maura
	Macaca fuscata
	Macaca speciosa
	Macaca sinica
	Macaca silenus
	Macaca nemestrina
	Macaca tonkeana
	Macaca ochreata
	Macaca radiata
	Macaca assamensis
	Macaca thibetana
	Macaca arctoides
	Macaca cyclopis
	Macaca hecki
	Macaca leonina
	Macaca nigra
	Macaca nigrescense
	Macaca sylvanus
	Macaca pagensis
	Macaca munzala

Genus *Macaca* is the most common and geographically widespread of all primate genera. One species, *M. sylvanus*, the "Barbary Ape" or "Barbary macaque," thrives in northern Africa (Algeria and Morocco) and even on the

southernmost tip of western Europe, Gibraltar. Humans introduced this species to the Gibraltar area. The other 21 *Macaca* species—a total of 22 are generally accepted—are spread across many areas of Asia, such as India, north to Afghanistan, Nepal, Burma, Tibet, Thailand, southern China, and as far east and north as Japan. They also occur on many of the Asian islands including Sri Lanka (formerly Ceylon), Taiwan, Sulawesi (formerly Celebes), Borneo, Sumatra, the Philippines, and Formosa (Taiwan), as well as the Japanese islands. Artificial colonies of macaques have been established in the Western Hemisphere. One example is the colony of *M. mulatta* (rhesus monkeys) on Cayo Santiago Island off the coast of Costa Rica. This colony was established in 1938, and the macaques on the island have been under continued scientific observation ever since.

Macaques are adapted to a great variety of environments, and some inhabit areas with occasional snowfall and frost. Others live on seashores and go swimming in the surf. Macaques thrive in tropical rain forests; they hide in rocky, mountainous areas and invade villages, cities, and temple districts where they easily adjust to more civilized environments. Macaque body lengths range between 34 and 70 cm, and the tails of different species show various degrees of reduction from long-tailed forms (*M. fuscata*, *M. sinica*, *M. radiata*, and *M. fascicularis*), to those with medium-long tails (*M. cyclops*, *M. assamensis*, *M. silenus*, *M. mulatta*, *M. tonkeana*, and *M. nemestrina*), to stump-tailed species (*M. thibetana*, *M. maurus*, *M. sylvanus*, *M. ochreata*, and *M. arctoides*). *Macaca nigra* (Figure 4.34) is one of the stump-tailed macaques. Tail length differs not only between but also within species. Limbs are close to each other in length with forelimbs averaging about 90% of the length of hind limbs: the intermembral indices vary between 85 to 95.

Those macaques that live in cold environments have long, dense fur. Considerable sexual dimorphism of body size is evident in all macaque species, and this is also seen in the size of the canine teeth: that is, male macaques are bigger than females and have longer canines than females. Fur color and arrangement vary considerably with the many species, as does the degree and coloration of sexual swellings of female macaques in estrus; these external changes do not occur in females of *M. radiata* and *M. sinica*. In male macaques, a higher intensity of coloration of sexual skin also develops during periods of sexual activity.

Macaques have protruding, blunt muzzles. The internasal septum is often very narrow, and the nasal openings project downward and somewhat laterally. The eyes are typically positioned comparatively near to each other. Cheek pouches enlarge the cheek region and protrude considerably when filled with food. In contrast to females, male macaques have larger tori (brow ridges) above their eyes. The ears of most macaques are pointed at the upper end, forming the so-called Darwinian angle. The face of macaques is almost hairless, but some

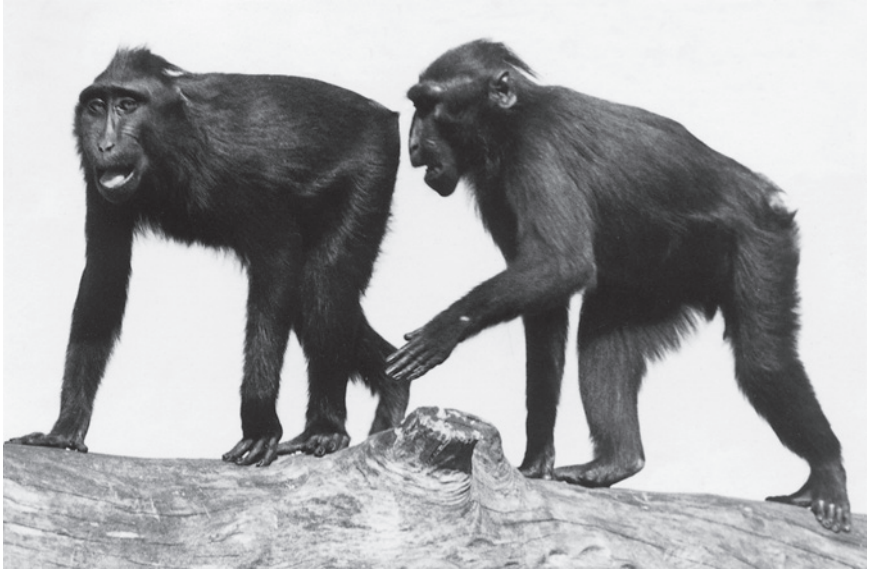


Figure 4.34 *Macaca nigra*, the Celebes or crested black macaque. Photo courtesy of Dieter Glaser. From Ankel-Simons, 2000.

species have patterned arrangements of hair on top of the head. In all macaques but one, *M. maura*, the ischial callosities are separated from each other in the midline. Having an opposable thumb, as do all Old World monkeys, macaques are fully capable of grasping. They frequently engage in mutual grooming, especially in connection with sexual activities but also in mother–child relationships. Relatively short and robust limbs of nearly equal length characterize these monkeys, and the intermembral index averages close to 90. Macaques are predominantly quadrupedal in their locomotion and are capable climbers. They adapt to various environments. The amount of time spent either on the ground or in trees varies inter- and intraspecifically. One species, *M. silenus*—the lion-tailed macaque or wanderoo—prefers arboreal habitats.

Macaques occasionally exhibit a bipedal stance, especially when curious and peering at distant objects. They can walk or run bipedally over some distance across the ground, as do many primates that are partially terrestrial. Much research has been published on macaque behavior. Macaque group sizes are highly variable according to the species concerned, differences in the environment that they inhabit, and other factors. No group contains fewer than two adult males. Group compositions are usually multimale and multifemale except for *M. silenus*, where either one adult male/multifemale or two adult males/multifemales are characteristic. Group size varies normally from 10 up to about 40 individuals of

different ages, and females generally outnumber males. Relations of dominance are clear-cut between adult males in a number of macaque species. Females predominantly appear to maintain matrilineal dominance hierarchies. Macaques apparently do not recognize distinctly circumscribed territories that are defended, and adjacent troops appear to avoid fighting. An interesting exception to this are groups that live in human urban environments. These engage in frequent and serious battles. Sexual behavior, pair-bond relationships, and times of high reproductive activity differ widely among the macaque species. Learning plays an important role in their ability to adapt.

The dietary staple of macaques is any kind of fruit, which can be substituted by almost any available foodstuff. For example, two macaque species include a large amount of crustaceans and mollusks in their diet—clearly a learned skill (*M. fascicularis* and *M. cyclopis* swim and dive to obtain their seafood). Thus, diets in the many members of this genus are variable. One of the macaque species that was considered to belong to its own genus, *M. maura*, was named in 1823 by Cuvier, and, after having changed the name repeatedly, was transferred back to *Cynopithecus niger* by Fiedler (1956)—a name it was given in 1820 by Desmarest—to again be regarded as *M. maura* today (Fooden, 1976), the southern species of Celebes moor macaques. *M. nigra* is recognized as the northern species of Celebes or crested black macaques (Groves, 1993). *M. nigra* and *maura* both have comparatively long faces, almost more similar to baboons than to other macaques in this respect. They have deep grooves on both sides of the long snout. A prominent brow ridge that is continuous above the eye region also resembles baboons rather than the other species of genus *Macaca*. The northern population is characterized by a distinctive tuft of long, straight hair on top and in the center of the head that typifies this species and is missing in the southern Celebes moor macaque. The fur of *M. nigra* is totally black, whereas in *M. maura*, it is dark brown. The intermembral index of both species is 92. The tails are reduced to short stumps. The internasal septa a very narrow, and the nasal openings are slitlike. These monkeys live in forests, and their diet is predominantly fruit.

Mandrillus (Ritgen, 1824)	*Mandrillus sphinx*
Drill, Mandrill	*Mandrillus leucophaeus*

Two of the species that were regarded as belonging to genus *Papio*—species *sphinx* and *leucophaeus*, commonly called mandrill and drill, respectively—have been reassigned (Groves, 1993) to their own genus, *Mandrillus.* Although some authorities believe that this reassignment of the drill and mandrill to genus *Mandrillus* is not warranted, here I treat the two species as species of genus *Mandrillus* and separate from genus *Papio.* The five other baboon species populate most of sub-Saharan Africa and some small areas in central West Africa (Ivory Coast). The northeastern species *P. hamadryas*, the sacred baboon, has a range extending across the Aden Channel of the Red Sea into Arabia, and thus

into the edge of the Asian continent. Two of the species, *Mandrillus sphinx* and *M. leucophaeus*, inhabiting rain forest areas of West Africa (Cameroon, Congo, Equatorial Guinea) are here excluded from genus *Papio* and regarded as belonging to a separate genus *Mandrillus*. These two species live in the rain forest but spend much of their active daytime on the ground. Both drills and mandrills have swollen areas running along each side of the upper part of the snout. These swellings have four to five bright blue parallel ridges on either side of the snout in adult male mandrills. In contrast, the entire nose is bright red. This facial coloration of mandrills is perhaps the most striking of any mammal. White tufts of hair in the cheek region and a yellow beard add to the amazing impression. In both, drills and mandrills, the face is bare around the eyes and on top of the muzzle. Both species have comparatively prominent and large brow ridges. The ears of mandrills are light colored and protrude slightly from the fur, whereas they are hardly visible in drills and are colored black. In contrast, drills have plain black faces, white beards, and white cheek fur. Polychromatic red and blue colors on the perineal region of male drills are presumably comparable, as sexual signals, to the technicolor facial and perineal colors of mandrills. Male mandrills have brightly colored genital regions, showing red, pink, blue, scarlet, and purple hues. Female mandrills and drills do not have these extraordinary skin colorations. The fur of mandrills is thick, coarse, and dark gray. Drills have greenish gray furs, and in both species, the ischial callosities are prominent and pink. Females are smaller than males, and the body length ranges from around 65 to 80 cm, with tail length between 7 and 12 cm. Females show moderate sexual swellings that are not particularly colorful. Forelimbs and hind limbs are almost equal in length, but the forelimbs seem longer and more muscular than the hind limbs. Because these two species have lifestyles that are considerably more arboreal than species of genus *Papio*, their digits are longer than those of typical baboons. They accomplish a functional elongation of their forearms by walking with the hands in a digitigrade position. Although they are closely related to baboons (and may actually be similar enough to be retained in genus *Papio*), drill and mandrill are not typically spoken of as baboons. Drills and mandrills are omnivorous, with fruit as the predominant food.

Papio (Erxleben, 1777) Baboons	*Papio hamadryas* *Papio anubis* *Papio cynocephalus* *Papio papio* *Papio ursinus*

Baboon species—genus *Papio* in the strict sense (Figure 4.35)—have adapted to various habitats ranging from tropical forest to semiarid savannas. The deep and long snout of baboons led to coining the collective noun "cynomorpha"—"doglike animals"—for baboons. Unlike drills and mandrills, the long snout of

Figure 4.35 *Papio cynocephalus*, the yellow baboon. From Ankel-Simons, 1983.

baboons is comparably narrow in the nasal region, and the wide nasal openings point directly forward. The northeastern species *P. hamadryas*, the sacred baboon, has a range extending across the Aden Channel of the Red Sea into Arabia, and thus, into the edge of the Asian continent. In *P. hamadryas*, the tip of the nose is slightly tilted upward, or snub-nosed; their face is naked, as are the ears, which are hidden under long hairs in males. The color of the dense fur varies through grayish, green, yellow, or brownish tones among the various species of *Papio*, and males often have virtual capes of elongated hair around the shoulders that seem to enlarge their appearance. This furry cape is especially well developed in *P. hamadryas*.

Hairs in the cheek region are also often long in male baboons. The body length varies between 50 and 60 cm. Sexual dimorphism in body size of *Papio* is marked; the males are often twice as large as the females. Females have conspicuous sexual swellings of the perineal region when in estrus. Forelimbs and hind limbs are approximately equal in length with the intermembral index ranging close to 100. The tail is of variable length in different species but is generally comparatively longer in baboons than in drills and mandrills. Baboons are terrestrial and regularly walk quadrupedally, placing the hands in a digitigrade position; they frequently adopt a bipedal stance, especially when "lookouts" stare across grassland in search of possible threats. Baboons often sit on their large ischial callosities, which, in *P. papio*, are bright red.

Numerous publications continue to deal with the social behavior of baboons, and these primates are consequently among the best documented series of primate species. Social behavior varies widely within and between species, as does group

size and composition of social groups. Many of these behavioral differences seem to be correlated with variations in the environment. All baboons live in large, mixed groups except for hamadryas baboons, which gather in one male, multifemale "harem" groups. Adult females almost always outnumber males in the troop. The males are the leaders, however, having numerous social functions and responsibilities. Dominance is a crucial factor for baboons of both sexes. Mutual grooming is frequent and makes up a significant fraction of all social activities. Newborn baboons occur throughout the year. Births are, however, especially numerous from October through December in South and East Africa. Baboons usually retire into trees or onto steep, rocky cliffs at dusk and sleep together in large colonies; thus, individuals are relatively safe from predation. At dawn they leave these sleeping quarters for the day's foraging. The diet of baboons includes fruits, nuts, berries, seeds, roots, and an occasional small animal.

Theropithecus (I. Geoffroy Saint-Hilaire, 1843)
Gelada Baboon

Theropithecus gelada

Genus *Theropithecus* (Figure 4.36), with only one species, *T. gelada*, is commonly called gelada baboon or "bleeding heart" baboon. Geladas only occur in a comparatively small mountainous area in Ethiopia. This region is at high altitude, rocky, and devoid of trees or other types of dense vegetation. The snout of these baboon-like monkeys is comparatively shorter from front to back and higher than the muzzle of the *Papio* species. The nasal openings are not situated as far forward at the end of the snout as they are in baboons, and they are somewhat triangular and tilted upward. The end of the snout is rounded, more similar to chimpanzees than baboons. A not very prominent supraorbital torus makes the eyes appear deep set. The fur of geladas is coarse and predominantly dark brown to buff. Males have a long mane, and the tips of the tails are tufted in both sexes. As in the other baboons, the face is naked. The ears are positioned comparatively far back on the head; in male geladas, they are hidden in the long fur, but they are visible in females. Perhaps the most extraordinary feature that characterizes geladas is a more or less triangular, pale pink or red naked skin area on the chest, which is exaggerated in its appearance by surrounding skin knobs in female geladas. This area is the so-called bleeding heart. The skin changes its color from pink to red in females when they come into estrus. Females also have skin knobs around the perineal region, and these enlarge when the females come into heat. Size range in geladas overlaps with that of baboons (body length 50 to 75 cm). The intermembral index is in the 90s, as it is among *Papio* species. Tail length varies between 30 to 50 cm. Females are smaller than males. This dimorphism is, however, less marked in geladas than in common baboons. This is clearly one of the most terrestrially adapted of all the monkeys.

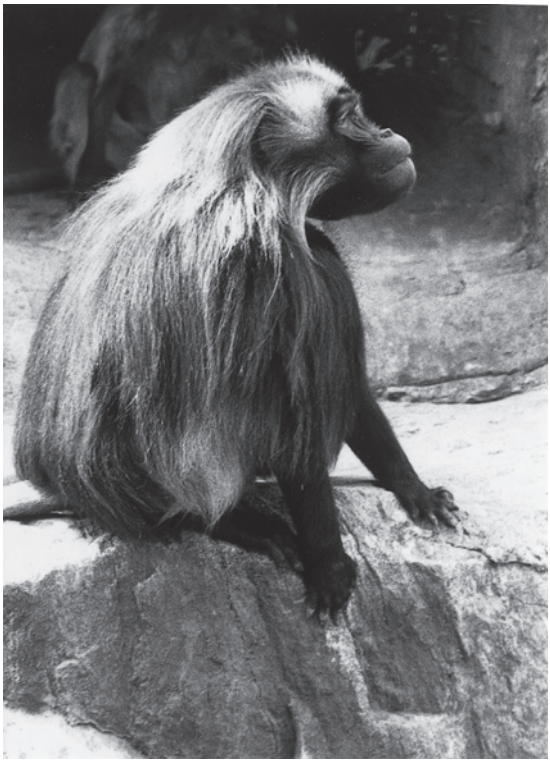


Figure 4.36 *Theropithecus gelada*, the gelada baboon. Photo courtesy of Terry Maltsberger. From Ankel-Simons, 2000.

Geladas live in large groups ranging up to about 400 individuals in certain seasons. These groups are composed of numerous small core units that can consist of one male with four to eight females plus offspring, of groups made up exclusively of subadult males, or of play groups with multiple female and male juveniles. The size of these core units varies from 5 to about 30 individuals. These animals sit most of the day on their well-developed ischial callosities, digging up roots and collecting small food items from the ground, even dragging themselves around in this position. Large groups stay together only when food is abundant. During the dry season, they tend to split up into the core families. Thus, group size and composition are widely influenced by environmental factors.

When traveling long distances in a quadrupedal manner, females and young are kept in the center of the moving herd or more in a wing that is between the group of males and a cliff edge and is thus protected from intruders. In geladas, like other baboons, the lids of the eyes are white and can be exposed by rapid

backward movement of the scalp. This ability, together with other facial expressions such as exposure of the gums and teeth, is important in gelada social interaction. Newborn geladas are abundant during February, March, and April. Terrestrial feeding on grasses, roots, and other small objects has resulted in large cheek teeth and small incisors, a condition reversed in arboreal forest forms like the drill and mandrill.

Cercocebus (E. Geoffroy Saint-Hilaire, 1812) [*Lophocebus* (Palmer, 1903)] Mangabeys	*Cercocebus torquatus* *Cercocebus galeritus*[21] *Cercocebus atys* *Cercocebus (Lophocebus) aterrimus* *Cercocebus (Lophocebus) albigena* *Rungwecebus (Lophocebus) kipunji*[21]

Genus *Cercocebus*—with the common name mangabeys—has either four or five species, depending on the preference of whether *Cercocebus aterrimus* and *C. albigena* should be regarded as belonging to a different genus, *Lophocebus*. The mangabeys are found in rain forests all across tropical central Africa. Two species of these monkeys seem to be attracted to swampy areas and stay predominantly in trees. The other three "true" members of genus *Cercocebus* are more terrestrial in their habits except for feeding and sleeping when they ascend into trees. The head and face of mangabeys appear to be shorter and rounder in outline compared with those of macaques. Hair tufts around the face, contrasting colors, and different "hairdos" are characteristic of mangabeys; they have chalky white areas on the top of or above their eyelids. Mangabeys have naked faces and their nostrils, although typically catarrhine, are directed somewhat laterally. The three *Cercocebus* species have short-haired, coarse fur, and the two other species, *C. albigena* and *C. aterrimus*, have long hairs on their bodies. All mangabeys have well-developed ischial callosities. Mangabeys are elegant and slender monkeys of around 45 to 60 cm body length, with very long tails that vary in length from 64 to 89 cm. The intermembral index is fairly high, around 86, similar to that in genus *Cercopithecus*.

Males tend to be larger than females. *C. albigena* and *C. aterrimus* tend to put their hands into a digitigrade position when walking on the ground. This behavior seems to be much less pronounced in the three other mangabey species. Members of one of these, *C. torquatus*, are known to be predominantly terrestrial and avid swimmers (Malbrant and Maclatchy, 1949). There are only few field observations of this species, all from years ago, and they are contradictory to

[21]Two subspecies of *C. galeritus*, *C. galeritus galeritus* and *C. galeritus sanjei*, as well as *C. atys lunulatus* are on the most endangered primates list (Konstant et al., 2002). A new species from Tanzania originally thought to belong to genus *Lophocebu*s with the species name *kipunji: L. kipunji* (T. Jones et al., 2005) has now been assigned its own, new genus *Rungwecebus kipunji* by Davis et al. (2006).

some extent. Thus, reports suggest both intense vocalization and unusually quiet groups of these mangabeys. Chalmers (1968) reported on the considerable resemblance of mangabeys, baboons, and macaques in vocalization and facial expressions. He considered the black mangabey to be adapted to communicate under poor visibility conditions in the forest; its calls are more common than gestures, but under these conditions, their gestures also show exaggerated movement. Mangabeys move about in groups of 20 to 40 individuals during the day but split up into smaller units (of about 5 individuals) at night. Female mangabeys have only slight color and tumescence changes of their perineal region. All members of this genus have comparatively small ischial callosities. Their predominantly vegetarian diet is said to be composed mostly of fruits and nuts but is occasionally enriched by animal prey.

Subfamily Colobinae (Jerdon, 1867)

Colobus (Illiger, 1811)	*Colobus polykomos*
Black and White	*Colobus guereza*
Colobus Monkeys,	*Colobus satanus*
Guerezas	*Colobus angolensis*
	Colobus vellerosus

Guereza is the common name for species of genus *Colobus* (Figure 4.37), from which the second subfamily of the Cercopithecoidea—Colobinae—takes its name. Species of genus *Colobus* are restricted to Africa. All Colobinae lack the cheek pouches found in Cercopithecinae and differ from the latter in having sacculated stomachs containing bacterial colonies for processing of the cellulose in their highly specialized, vegetarian diet (Kuhn, 1967; Chivers, 1994). Members of genus *Colobus* are characterized by a large larynx; they vocalize in loud and far-reaching choruses. In genus *Colobus* and its two subgenera, the thumbs of their hands are reduced to a small tubercle, and some have no thumbs at all. The other genera of this family—*Presbytis* (leaf-eating monkeys), *Semnopithecus* (langurs), *Trachypithecus* (leaf monkeys), *Pygathrix* (douc langurs), *Rhinopithecus* (snub-nosed monkeys), *Simias* (pig-tailed langur), and *Nasalis* (proboscis monkeys)—are also generally called leaf-eating monkeys and occur in East Asia.

Genus *Colobus* is often subdivided into three subgenera: *Colobus* (with five species), subgenus *Procolobus*, subgenus *Piliocolobus* (also with five species), and subgenus *Procolobus*. Guerezas are widespread throughout the rain forests of Africa south of the Sahara.

All members of genus *Colobus* have three-chambered sacculated stomachs. The females do not have changes of tumescence and color in the perineal region during estrus. Four of the five *Colobus* species have striking black and white fur. Their base fur and body color is black, adorned with long white hairs that form capelike structures along the shoulders, body sides, and tail. The black face is

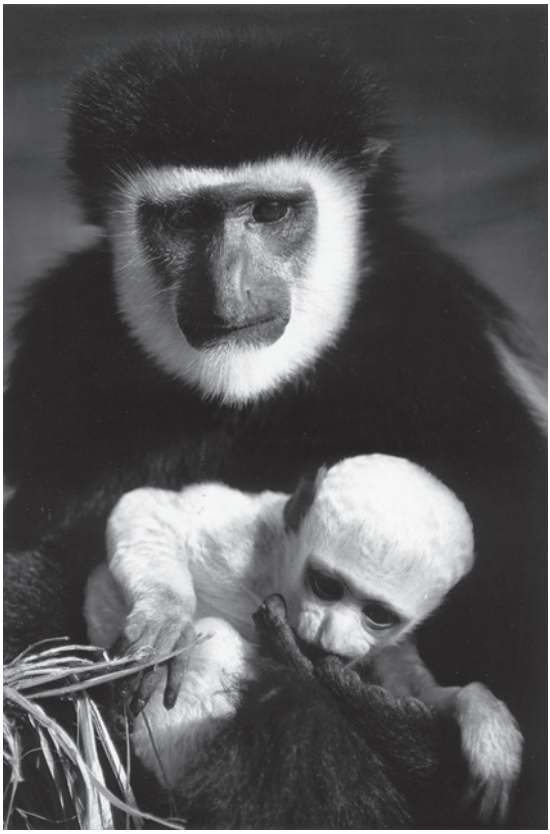


Figure 4.37 *Colobus guereza*, the eastern black and white colobus. Photo by Steve Underwood, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

surrounded by a rosette of white fur; the head cap is black. These combinations of black and white areas vary within and between the four black and white species. The black and white fur of colobus monkeys is highly prized by humans for garments. Only the fur of the black Colobus, *C. satanas*, is black all over. The face is nearly hairless, and the ears are comparatively small. The head of guerezas is more globular than in most species of the cercopithecines, and the snout is not prominent. In two of the larger species, *C. polykomos* and *C. guereza*, the nose protrudes somewhat over the upper lip. There is little sexual dimorphism in size. In body length the five species ranges between 43 and 69 cm. Tail length varies 41 and 89 cm. Usually the tail is longer than the body. The hind limbs of members of this genus are longer than the forelimbs, with an intermembral index

averaging around 80. Colobines are highly arboreal and normally occupy the high levels of the forest canopy. Guereza live in territories that are said to be hotly defended against intruders of the same species. Group numbers average about 15, and no clear-cut dominance hierarchies within these groups have been observed. The fur of newborn guerezas is white. Leaves are the primary food source of guerezas.

Procolobus *(Piliocolobus)* (Rochebrune, 1877) Red Colobus Monkeys	*Procolobus (Piliocolobus) badius*[22] *Procolobus (Piliocolobus) pennantii* *Procolobus (Piliocolobus) rufomitratus*[23] *Procolobus (Piliocolobus) gordonorum* *Procolobus (Piliocolobus) kirkii*

The red colobus monkeys (Figure 4.38) are different from the white and black species in having a sacculated stomach with four chambers and in that females have swelling as well as color changes of the perineal area during estrus. Unlike in guerezas, the larynx is small in species of *Procolobus*.

Procolobus *(Procolobus)* (Rochebrune, 1877) Olive Colobus Monkeys	*Procolobus (Procolobus) verus*

Procolobus verus is much less conspicuous than the black and white and red colobus monkeys. The olive colobus monkey is not as arboreal as its close relatives and is said to come close to the ground, living in the lower most canopy, predominantly in riverine forests. Unlike any other higher primates, mothers of *P. verus* have been reported to carry their very young infants in their mouths. As in all colobines, the stomach of this monkey is sacculated as is the rectum in connection with their rather specialized leaf diet (Chivers, 1994).

Males of this species measure 48 cm in body length, and females are somewhat smaller, measuring 46 cm. Tails are about 61 cm long. These are the smallest colobine monkeys, and their range is restricted to the coastal forests of Guinea (West Africa).

[22]The five species of genus *Procolobus* (subgenus *Piliocolobus*) listed here are regarded as subspecies of *Procolobus badius* by some, rather than valid species (Oates et al., 1994). Oates et al. additionally distinguish nine other subspecies of *P. badius*. Many other authors believe that the red colobus monkeys should be regarded as subspecies of *Colobus badius*. Rowe (1996) only attributed three of the listed species as belonging to genus *Procolobus* and subgenus *Piliocolobus*, namely, *Procolobus [Piliocolobus] badius*, *C.[P]. pennanti*, and *C.[P]. rufomitratus*, as well as an additional fourth species *C.[P]. preussi*. Overall, the taxonomy of the red colobus monkeys is rather confused as well as confusing. A subspecies of *Procolobus badius*, *C. badius waldroni*, is on the list of endangered primates (Konstant et al., 2002).

[23]This species is variously listed as *Colobus*, *Piliocolobus*, or *Procolobus rufomitratus* and is listed in the most endangered primates list (Konstant et al., 2002).

Figure 4.38 *Procolobus kirkii*, also thought to be one of nine subspecies of the red colobus. Courtesy of Thomas T. Struhsaker. From Ankel-Simons, 2000.

Presbytis (Eschscholtz, 1821)
Langurs, Leaf or
Leaf-eating Monkeys

Presbytis femoralis
Presbytis thomasi
Presbytis melalophos
Presbytis comata
Presbytis hosei
Presbytis potenziani
Presbytis rubicunda
Presbytis frontata
Presbytis federicae
Presbytis siamensis
Presbytis natunae[24]

[24]This species is on the endangered primates list (Konstant et al., 2002).

We recognize here 8 species of genus *Presbytis* (Figure 4.39), but as many as 14 species and more than 80 subspecies have been proposed at one time or another. Langurs are well adapted to many habitats; they occur high in the mountains, rain forests, mangrove thickets, and dry areas, and they range into villages, towns, and temple areas. The langurs or leaf monkeys are the most widespread of colobines and live across a wide range of East Asia (India, Pakistan, Sri Lanka, Thailand, Malaysia, southwestern China, Indochina, Sumatra, Java, Borneo, as well as many of the smaller islands). The heads of langurs are globular in outline; unlike guerezas, the snout is short, and the nasal openings are positioned close to each other but separated widely from the upper lip—in other words, the nose is very short and the upper lip area high. The faces are sparsely haired or naked. Hair tufts on crown, cheeks, and above the eyes vary the appearance among species. The body fur is long and has various color patterns among the different species. Newborn langurs typically differ markedly in color from adults. White circles around the eyes and white lips characterize the two species, *P. femoralis* and *P. melalophos*. These medium-sized monkeys all have

Figure 4.39 *Presbytis obscurus* (now regarded to be genus *Trachypithecus* by some), the dusky or spectacled leaf monkey. Photo courtesy of Michael D. Stuart. From Ankel-Simons, 1983.

sacculated stomachs. Body length ranges from 40 to 80 cm, and tail length is between 50 and 110 cm for this genus. In all the langurs, the ischial callosities are relatively small and separated from each other. The limbs of langurs are slender, with intermembral indices below 80, but their bodies are bulky. Langurs are well adapted to an arboreal way of life. Many species spend a considerable amount of their active time on the ground, however. The group size of langurs ranges commonly from only a few individuals to more than 100, and the sex ratio within these groups also varies.

Langurs inhabit well-defined territories, the size of which varies considerably in accordance with differences of the environment. Groups are led by dominant adult males. In some species, dominance behavior can be pronounced in males, among which hierarchies are established by fighting. Infanticide of previously born young has been reported to be important when all-male bands take over a group of females and kill or drive out those that were previously in control. The strategy of infanticide has been called "ursurper strategy" (Blaffer-Hrdy, 1977). The adult female status in a group changes in accordance with the change of the sexual cycle. Care for young is generally intensive, and all adult females have a role in it. Allomothering occurs frequently. Within the wide geographic range inhabited by langurs, the presence or absence of a distinct breeding season also seems to vary widely with environmental differences. Diet among species of this genus is variable, but in general these monkeys seem to eat fewer leaves than do species of genera *Colobus* and *Procolobus*. Besides leaves, langurs also feed on fruit, flowers, and even bark but seem not to add any kind of animal protein to their diets.

Semnopithecus (Desmarest, 1822) Hanuman Langurs	*Semnopithecus entellus* *Semnopithecus johnii* *Semnopithecus vetulus*

Although there was formerly only one species of *Semnopithecus* (Figure 4.40), three are now recognized. This genus was formerly included in genus *Presbytis* and has been separated on the generic level from the latter in 1993 by Groves. The Hanuman langurs are the most widespread Asian colobines. Their range reaches from the Himalayas and Nepal, areas with an altitude of 4000 m, across the Indian subcontinent, and across the ocean to Sri Lanka. Many of the hanuman populations are terrestrial in their behavior, and they have adapted well to human environments. The color of their coats varies but is predominantly brown, golden, or gray with a silver hue. Their naked faces are black and have pronounced brow ridges. The hair around the cheeks and chin is comparatively long, giving the impression of beards. The ears are dark and visible. Young infants are usually dark. Their size varies considerably, with the largest specimens in the north and the smallest on the island of Sri Lanka. Body length ranges from 40 cm to almost 100 cm in females and from 50 to 78 cm in males. Tail length exceeds the body length and varies between 70 cm and 1 m in females and 75 to about 100 cm in

Figure 4.40 *Semnopithecus entellus*, subadult Hanuman langur. Photo courtesy of Michael D. Stuart. From Ankel-Simons, 1983.

males. The intermembral index ranges up to about 80. Their diet is mainly vegetarian with the bulk being leaves, but they have been seen, although rarely, to eat animal prey, mostly insects. They live in groups of varying numbers, between almost 100 individuals to as few as 5, depending on food resources and environmental constraints.

Trachypithecus (Reichenbach, 1862) Brow-ridged Langurs	*Trachypithecus barbei* *Trachypithecus delacouri* *Trachypithecus geei* *Trachypithecus pileatus* *Trachypithecus phayrei* *Trachypithecus francoisi* *Trachypithecus cristatus* *Trachypithecus auratus* *Trachypithecus johnii*

Trachypithecus laotum
Trachypithecus obscurus
Trachypithecus poliocephalus[25]
Trachypithecus villosus

Whereas there were formerly 7 species in genus *Trachypithecus*, now there are 13. These have previously been subsumed in genus *Presbytis* (Napier and Napier, 1967). In 1989, Groves transferred the species listed here to their own genus based on morphological and behavioral variation. Compared with species

Figure 4.41 *Trachypithecus francoisi*, Francois's langur. Photo by Jason Langer, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

[25]Two *Trachypithecus* species, *T. poliocephalus* and *T. delacouri*, and one subspecies, *T. poliocephalus leucocephalus*, are on the endangered primate species list (Konstant et al., 2002).

of *Presbytis*, they have relatively shorter hind limbs with an intermembral index of about 90 and a predominantly quadrupedal running and climbing locomotion. Their newborn offspring are much lighter in color compared with the adult animals. The infants of three of the *Trachypithecus* species (*T. auratus*, *cristatus*, and *phayrei*) are bright orange to yellow with light gray or tan faces in contrast to their almost black-colored parents. Infants of *T. pileatus* are almost white and have pink faces, and those of *T. francoisi* (Figure 4.41), *geei*, and *johnii* also are differently and lighter colored than the adults of their species. Adult body length varies from 42 to 66 cm in females and 42 to 71 cm in males; tail length ranges between 62 and 102 cm. The adults of *T. auratus*, *cristatus*, *francoisi*, *johnii*, *obscurus*, and *phayrei* are predominantly black. Two of these species (*T. obscurus* and *phayrei*) have light-colored rings around their eyes and almost white snouts. *T. geei* are golden orange all over, called the "golden langur" because of this striking hue, and they have black faces and black soles on their hands and feet. A variety of *T. francoisi* with a range that is restricted to China have white heads, with the white hair extending onto the upper back; some have slight white adornments around their faces and on their tails. They are all diurnal, arboreal, and strictly vegetarian. *T. cristatus* is the most widespread species of the genus and occurs across Burma, Indochina, and on Borneo. *T. auratus* is restricted to Java, Bali, and Lombok. *T. francoisi* occurs in Vietnam, Laos, China, Thailand, and on the Malay Peninsula. *T. phayrei* roams Laos, Vietnam, Burma, Thailand, and southern China. *T. geei* occurs only in a small, mountainous area of the northeastern corner of India and Buthan, whereas *T. johnii* inhabits southwestern areas of the Indian subcontinent, and *T. pileatus* occurs in the most eastern reaches of northern India, Burma, and southwestern China.

Pygathrix (E. Geoffroy Saint-Hilaire, 1812) Douc Langurs	*Pygathrix nemaeus*[26] *Pygathrix nigripes*

Only two very rare species are known of genus *Pygathrix: P. nemaeus* and *P. nigripes.* They are the douc langurs that occur in remote areas of Laos and Vietnam, and on the island of Hainan. Douc langurs live in tropical rain forests. Individuals of *P. nemaeus* have yellowish white faces and throats and somewhat obliquely placed dark eyes. Chest and shoulders show a red crescent outlined in black. In this genus, the ears are less conspicuous than in members of genus *Presbytis*, and the snout is somewhat more protruding than in the latter. The body size varies between 55 and 82 cm, and tail length is between 59 and 77 cm. No marked dimorphism of size between the sexes is seen. Little is known about the douc langurs in the wild (but see Jablonski, 1998).

[26]A subspecies of *P. nemaeus*, *P. n. cinerea* is on the endangered species list (Konstant et al., 2002).

Rhinopithecus (Milne-Edwards, 1872)[27] Snub-nosed Langurs	*Rhinopithecus roxellana*
	Rhinopithecus avunculus
	Rhinopithecus bieti
	Rhinopithecus brelichi

Genus *Rhinopithecus* had only one species, *R. roxellana*, until three subspecies were elevated to species status by Groves (1993). Groves also conveyed *R. roxellana* and the three former subspecies of *Rhinopithecus* (*R. roxellana avunculus*, *R. r. bieti*, and *R. r. breichi*) into genus *Pygathrix*, making *Rhinopithecus* into a subgenus. To maintain a degree of taxonomic stability, I am not following this latter transformation but consider the three former subspecies of *Rhinopithecus* as species, thus making it four species for the genus. Others have done the same, and Groves (2001) reversed his earlier decision to refer to the species of *Rhinopithecus* as *Pygathrix* and acknowledged the scheme for *Rhinopithecus* species listed here. So much for the creation of taxonomic confusion.

These diurnally active monkeys are restricted to high altitudes in western China and northern Vietnam. The back and tail of *Rhinopithecus roxellana*, with the common name of golden snub-nosed monkey, are covered with dark brown hair. Very light-colored long hairs cover the shoulders and the tip of the tail. The underside of the entire body is also light-colored, fading from orange to buff-colored tints. The eyes stand out, surrounded by an area of pale blue skin, and the muzzle is white. The characteristic snub nose is very short and opens forward. These rare animals are found in bamboo and conifer thickets in elevations of above 3000 m, and they are well adapted to very cold temperatures. Adult animals are between 60 and 67 cm long and have tails of about 70 to 100 cm length. Females weigh between 6.5 and 10 kg, and males average between 15 and 40 kg. Their comparatively short legs are about the same length as their arms, with an intermembral index of 95. Their locomotion is predominantly quadrupedal while climbing and walking. They occasionally engage in suspensory behavior. The tail is carried above the back during quadrupedal locomotion. They live in groups of up to 200 individuals and sometimes congregate in numbers of up to 6000. They live in trees and travel on the ground. Their diet consists predominantly of leaves, flower buds, lichen. and occasionally fruit.

Rhinopithecus avunculus, commonly known as the Tonkin snub-nosed monkey, is almost black on the upper side of its body. Their underparts are yellowish orange to white, and there is a light-colored fur area over the elbow. On their faces, the skin covering the nose and over the upper lip is bluish gray, and their rather thick lips are pink in color. The top of the head and ears are covered with beige-colored fur. The nose opens forward, is snub-nosed, and short. The dark brown tail has a white tip. In males, the scrotum is white, and

[27] *Rhinopithecus avunculus*, *R. bieti*, and *R. brelichi* are on the 2002 most endangered primate list (Konstant et al., 2002).

the penis is dark, almost black. The newborn monkeys are light gray and become darker with age. Body length varies between 55 to 65 cm, and the tail is somewhat longer than the body, varying in length between 65 to 85 cm. Females weigh about 8.5 kg, and adult males weigh about 14 kg. Locomotion is quadrupedally walking and climbing. Group size is about 25 individuals. The diet of these diurnal monkeys consists predominantly of fruit, leaves, and seeds. They occur only in two restricted areas of northern Vietnam and reportedly have been diminished to only about 150 animals in the wild.

Rhinopithecus biety is also highly endangered and occurs only in a restricted area of western China. Overall, these monkeys are predominantly dark gray to black, with the thighs and lower back somewhat lighter in color. The underside of the body and the ears are almost white. Their bare face under a banglike hairdo is white, the nose is very short, and the nostrils open forward. The large, fleshy lips are pink in color. Their chin is surrounded by a light-gray beard. On the tip of the tail, the hair extends into a tuft. These large monkeys measure from 75 to 80 cm for females and about 83 cm for males. Females weigh an average of 9 kg and males up to 15 kg. These diurnal monkeys live in a mountainous region at an elevation of about 4500 m, are well adapted to cold temperatures and eat grasses, leaves, fruits, and lichens. They locomote predominantly quadrupedally in the trees and on the ground. Group size varies widely, from 20 to 200 animals.

The fourth species of *Rhinopithecus*, *R. brelichi*, is similar to the other species but differs in the golden orange fur on the top of their heads, shoulders, and arms. They live in a restricted area of southwestern China at elevations between 1000 and 2300 m. Group size varies and can reach as many as 430 individuals. They spend their active time during the day in trees, and they travel on the ground in a quadrupedal manner between tree patches. Only about 1000 individuals of these highly endangered animals are believed to exist today in the wild.

Simias (Miller, 1903) *Simias concolor*
Pigtailed Langur

The single genus and species of *Simias concolor* are the only colobines that have a very short tail, hence the common name. The tail is said to be bare except for a small tuft of hair at the very tip. The limbs of these robustly built primates are of approximately equal length. Ischial callosities are comparatively large and joined medially in adult males. Their body length varies between 50 to 52 cm, and the tails are only 14 to 15 cm. There is no sexual dimorphism. These arboreal monkeys are diurnal and are only found in swampy areas and dense rain forests on the Mentawai Islands off the west coast of the island of Sumatra, where they are difficult to locate. They have been described as being "cryptic" (Tilson, 1977). Being overall dark gray and blackish brown, they are hidden in the dense foliage. Groups are small, one male, multi female, and variable in size. Atypical among Asian colobines, females have obvious sexual swellings (Tenaza 1989), and their

diet consists predominantly of leaves with some fruit (Wantabe, 1981). The black faces of adult pig-tailed langurs sport very small snub noses. This colobine primate was classified as *Nasalis concolor* by Groves (1970), but I do not follow this suggestion here because the two genera are not only geographically distinct but also not at all similar in their appearance (see also Oates et al., 1994).

Nasalis (E. Geoffroy Saint-Hilaire, 1812) Proboscis Monkey	*Nasalis larvatus*

Genus ***Nasalis*** only has one species (Figures 4.42 and 4.43). These large monkeys occur exclusively on the island of Borneo, where they live in forests and coastal mangrove swamps. The comparatively flat top of the head, as well as the back of the trunk and limbs, are bright orange. Their faces are naked and adorned by the large, fleshy nose that gives the genus its name. The faces are orange-pink in adult proboscis monkeys, and the noses of infants are dark blue. The scrotum is black, and the penis, which is erect when the animals are excited, is bright red and highly visible. The underside of the trunk and limbs as well as the tail are light grayish to light orange in color. The unique enormous, fleshy, pendulous nose of male proboscis monkeys droops down beyond the mouth when flaccid and inflates when the animal becomes excited. There is considerable size dimorphism between the sexes; males weigh almost twice as much as females, which is also reflected in the smaller nose of the female, although for a primate it is still unusually large. The female nose is slightly tilted upward.

The diet of these diurnal and predominantly arboreal colobines is combined of large portions of seeds, some mostly unripe fruit, flowers, and an occasional prey animal. The fur is comparatively long, and the ischial callosities are large. Body size ranges from 73 to 76 cm in length in males and 61 to 64 cm in females. Tail length varies between 57 to 67 cm. Proboscis monkeys are able and avid swimmers. Their second and third toes are webbed. They seek refuge by diving into the water when threatened and have been observed to swim for distances of about 20 m submerged underwater (Bennet and Sebastian, 1988).

Table 4.2 lists the infraorders Platyrrhini and Catarrhini.

Superfamily Hominoidea (Simpson, 1931)
Family Hylobatidae (Gray, 1877)[28]

Bunopithecus (Hoolok)	*Hoolok hoolok*
Nomascus[29] (Miller, 1933)	*Nomascus concolor*
	Nomascus gabriellae
	(Nomascus leucogenys?)[30]

[28]At this time, the taxonomy of the lesser apes is thoroughly confused and confusing (Groves 2001; Mootnick and Groves, 2005; Geissmann, 2003). See also footnotes 29–31.

[29]*Nomascus concolor nasutus* is on the endangered primate list (Konstant et al., 2002).

[30]Also listed as *Hylobates leucogenys* (Geissmann, 2003).

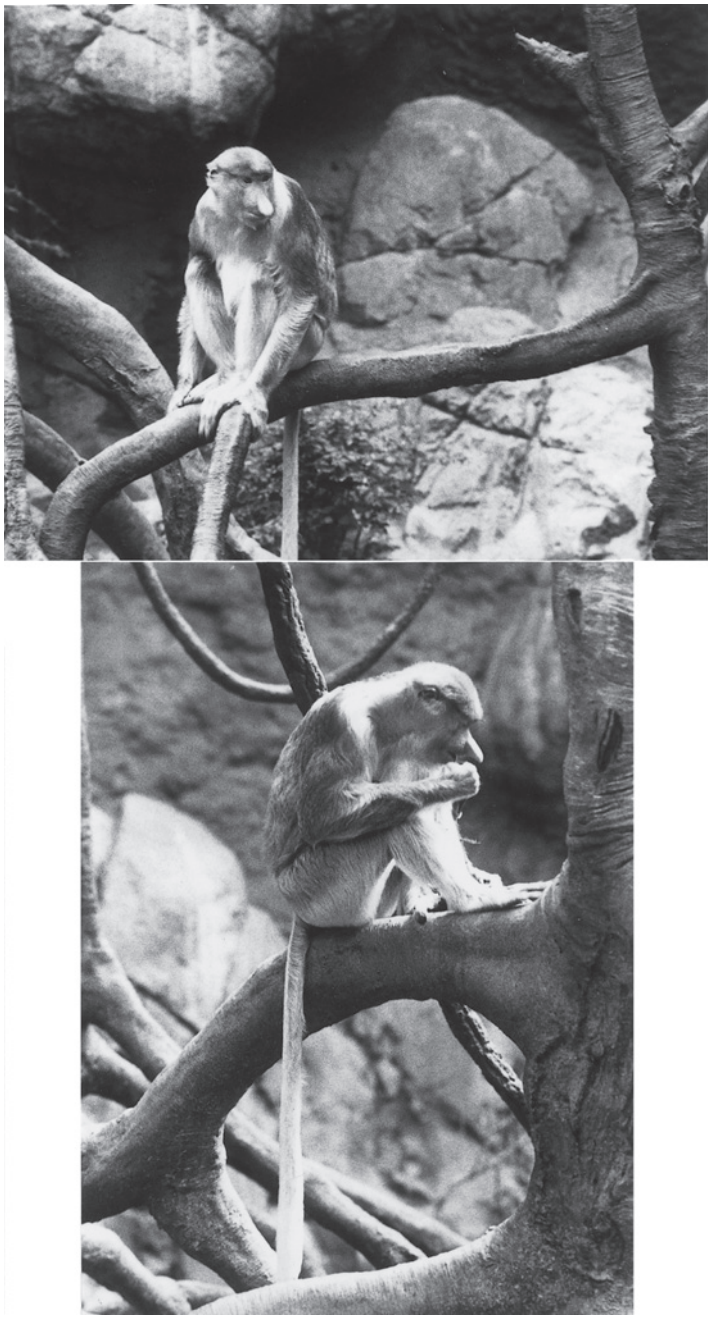


Figure 4.42 *Nasalis larvatus*, female of the proboscis monkey. From Ankel-Simons, 2000.

Figure 4.43 *Nasalis larvatus*, male of the proboscis monkey. From Ankel-Simons, 2000.

Hylobates (Illiger, 1811)	*Hylobates lar*
Gibbons, Lesser Apes	*Hylobates agilis*
	Hylobates moloch
	Hylobates klossii
	Hylobates pileatus
	Hylobates muelleri
	(Hylobates leucogenys?)[31]

The lesser apes are subdivided into two genera, one of which, genus ***Hylobates*** has been subdivided into up to ten different species (Figures 4.44 and 4.45). We recognize here seven species for this genus. The other lesser ape genus, *Symphalangus*, has only one species.

Gibbons have limb proportions that are unlike any of the prosimian or monkey species. In accordance with their rather specialized locomotion of arm swinging, also known as "brachiation," moving under branches swinging hand over hand

[31]Probably a subspecies of what was *Hylobates concolor* (see also Rowe, 1996). Groves (2001) listed *Hylobates hoolok* as subgenus *H. (Bunopithecus) hoolok*. Things became more complex when *Bunopithecus* was changed to a new genus of Hylobatidae—namely, *Hoolok* with two species, *H. hoolok* and *H. leuconedys* (Mootnick and Groves, 2005).

Table 4.2

Suborder Anthropoidea

Suborder anthropoidea	Infraorder Platyrrhini		Infraorder Catarrhini
Superfamily	Ceboidea		Cercopithecoidea
Family	Callitrichidae	Cebidae	Cercopithecidae
Cebus	*Callithrix*	*Cebus*	*Macaca*
Cervical vertebrae	7	7	7
Thoracic vertebrae: with ribs	13	14	12
Thoracic vertebrae: articulation	12	11	10
Lumbar vertebrae	6–7	7	8
Functional lumbar vertebrae	8	8	8
Sacral vertebrae	3	3	3
Caudal vertebrae	27	28–31	17
Proportions	Limbs about equal in length.	Arms longer.	Arms slightly longer.
Length of arms in % of body length	98	Cebus 125; Ateles 180	113 (Long olecranon).
Length of legs in % of body length	96	Cebus 118; Ateles 132	100
Hand length in % of body length	28	Cebus 34; Ateles 47	29
Foot length in % of body length	44	Cebus 52; Ateles 58	44
Thorax depth in % of thorax depth	87	90	88
Locomotor activity	Claw climbing, quadrupedal running. Hallux reduced with rail. Heel with dermoglyphics.	Arboreal quadrupedal running, climbing. Prehensile tailed climbing (Alouatitnae and Atelinae). Pollex not opposable, lacking in Ateles and Brachyteles.	Arboreal and terrestrial quadrupedalism, digitigrade walking. Pollex opposable.
Activity pattern	Diurnal	Diurnal with one exception; *Aotus,* the Owl monkey	Diurnal
Geographical distribution	South America	South and Middle America	Africa and southern most tip of Europe (Gibraltar)

Figure 4.44 *Hylobates leucogenys*, female with young (formerly thought to be a subspecies of *H. concolor*). From Ankel-Simons, 2000.

with their enormously elongated arms, their intermembral indices vary between 120 and 130.

Body length varies between the species from 42 to 64 cm. Tails, as in all hominoids, are completely reduced, and thus gibbons have no external tail. They do have comparatively small ischial callosities. Gibbons are rather widely spread in eastern Asia—from the northeast of India, throughout Burma, Cambodia, Thailand, Laos, Vietnam, and western China, on the Malay Peninsula, the large Indonesian islands Sumatra and Borneo, and the Mentawai Islands.

The two sexes of *Hylobates lar*, the white-handed gibbons, have a white ring of fur around their black, hairless faces and both white hands and white feet. Generally, the head is globular in gibbons, and the ears are not very big and often hidden in the long fur. In contrast to the white-handed gibbons, black-handed gibbons, *H. agilis*, often have brownish fur and black hands and feet, and they have white "eyebrows" above their eyes and also white rings of fur around their hairless faces. Fur color patterns are highly variable among the various species, races, and even individuals within gibbon species. These color patterns change with age. The fur of gibbons is generally rough in texture, and in some species,

Figure 4.45 *Hylobates leucogenys*, young male. From Ankel-Simons, 2000.

hair tufts form characteristic patterns around the bare and typically black faces.

All gibbons are diurnal and predominantly arboreal but occasionally go to the ground where they may walk bipedally, using their long arms as balancing rods. They also walk bipedally on horizontal branches that have sufficiently large diameters. Gibbons are monogamous and define their territories with characteristic, far-reaching, melodic hooting songs. Actual territorial fighting between adjacent groups seems to be rare, and there is no considerable sexual dimorphism in body or canine tooth size; both sexes have rather large, dagger-shaped canines. Differences in dominance do not appear to be clearly defined among gibbons. Newborn babies have been seen throughout the year, and there is no discrete breeding season. Gibbons live in small family units—a parental pair with several offspring; up to four offspring in a family group have been observed.

Male black gibbons—*Hylobates (Nomascus) concolor*—are either entirely black or black with white to yellowish white cheek tufts. Females are often brown or slightly yellow, but their naked faces are charcoal black. Infants are fawn colored at birth but change to black when they reach six months. Mutual grooming

Figure 4.46 *Symphalangus syndactylus*. Photo by Steve Underwood, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

occurs frequently within family groups and seems to play an important role within the array of social interactions (Curtin and Chivers, 1978). Gibbons are usually active during the daytime hours and live on a combined diet of fruit, leaves, flowers, buds, insects, bird's eggs, and small birds (see also Preuschoft et al., 1984).

Symphalangus[32] (Gloger, 1841) *Symphalangus syndactylus*
Siamang

The siamang—***Symphalangus*** *syndactylus* (Figure 4.46)—is considerably larger and more robust than members of the closely related genus *Hylobates* and is sometimes called the greater gibbon. The body length of siamangs varies between 74 and 89 cm. Siamangs occur only on the Malay Peninsula and on the island of Sumatra. There they range into mountainous areas, as do the lesser gibbons. Siamang are ebony black all over except for the snout, which is light brown. The hair of the coat is long, and its shaggy appearance is almost like that of a chimpanzee. Adult male siamangs have a tuft of hair in the genital area that covers it from the posterior aspect. Their ischial callosities are well defined and

[32]Genus *Symphalangus* is regarded to be *Hylobates* by some.

joined medially. Both sexes have a large, naked air sac at the throat; it functions as a resonance body for their penetratingly loud and euphonic hooting chorus.

Their locomotion is like that of *Hylobates*, and their intermembral index is the highest of all extant primates, ranging around 148 and up to 160, thus about 20 points higher than that of gibbons. The generic and species name (*syn/sym* = Greek for "together," "joined"; phalanx = Greek for "finger"; dactylos = Greek "finger," "toe") of the siamang refers to the fact that the second and third toes are joined together by skin. These webs can reach all the way to the distal interphalangeal joint. Siamangs, like gibbons, live as mated pairs or nuclear family groups, and their loud vocalizations play an important role in their territoriality. Their diet consists mainly of leaves, with added fruit, flowers, some animal prey, and seeds according to availability. Their activity pattern is diurnal.

Family Pongidae,[33] (Elliot, 1913) **Great Apes**

Pongo (Lacépède, 1799)	*Pongo pygmaeus*
Orangutans	*Pongo abelii*[34]

The two island populations of the Asian great apes, the orangutans, have been assigned to just one species (Figure 4.47). Only recently has cytological and molecular investigation supported that the two orangutan populations on Borneo and Sumatra, respectively, should be assigned to two different subspecies, *Pongo pygmaeus abelii*, the Sumatra orangutan, and *P. pymaeus pygmaeus*, the Bornean orangutan. Some scientists would prefer to elevate *P. p. abelii* to a separate species, *P. abelii*, although the morphological and behavioral differences are not that apparent. The geographic separation of the two populations is evident, however. A comparative study of the mitochondrial DNA of the two separate orangutan groups also led authors to suggest that the animals' mitochondrial DNA is completely different, more so than that of the two chimpanzee species (*Pan troglodytes* and *Pan paniscus*) and that they therefore should be put into two species (Xu and Arnason, 1996). Members of the two populations are able to interbreed and to produce fertile offspring, however. Here I take the conservative road, recognizing the two orangutan populations as subspecies within genus *Pongo*, because it seems that differences on the molecular level are much more obscure than are those of morphological and behavioral characteristics.

The Sumatran orangutan distribution is restricted to the western tip of the island, whereas the Bornean population occurs predominantly in the center of

[33]An alternative taxonomy puts Pongidae into superfamily Pongoidea and our own family, Hominidae, into superfamily Hominoidea.

[34]Some scientists disagree with the change of *Pongo pygmaeus abelii* to *Pongo abelii*, which thus has been ranked as a species (Groves, 2001). We are not following this recommendation here. This subspecies is also on the endangered species list (Konstant, 2002).

Figure 4.47 *Pongo pygmaeus*, male orangutan. Photo by Steve Underwood, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

Borneo. These large apes have pronounced snouts and deep concave facial profiles. The eyes are comparatively small and positioned near each other, and supraorbital ridges are much less well developed than they are in African apes. The upper lip is remarkably high so that the nasal openings typically are closer to the eyes than to the upper lip of the mouth. In adult males, large flanges extend out from the sides of the face in the cheek region. These greatly broaden the face and thus enhance the appearance of great size, which is effective during threatening behavior. Orangutan faces are usually less hairy than those of African apes, but the Sumatran orangutan sometimes has frosted white facial hairs. The skin of orangutans often has a blue-gray almost metallic tint, whereas the long hair all over the body is coarse; its color ranges from carrot red to reddish brown. Many orangutans have beautiful red beards. Also, adult males have large air sacs

on the throat that function to amplify their far-reaching cries. The ears of orangutans are comparatively small and positioned inconspicuously. These apes are highly size dimorphic, and the body length averages 77 cm for females and 95 cm for males. The arms are very long, considerably longer than the hind limbs; the length from shoulder to wrist averages 112% of the leg length from hip to ankle. When walking on the ground quadrupedally, orangutans put the outside of their inward-bent hands on the ground ("fist walking"), or they place the hands in a plantigrade position but with fingers turned out laterally. These apes are mainly tree dwellers that climb about in a careful and deliberate manner, often hanging by any and all four hands and feet. Sometimes they travel on the ground for some distance, a behavior especially common in older males.

Orangutans build sleeping nests. These can be more intricately constructed than those of African great apes because they not only contain a resting platform of branches but may have overhead branches pulled together above as a shelter from rain. Orangutans have only tree nests. They almost never defecate in them or build nests on the ground as gorillas commonly do. Nests are built anew every evening. Orangutans live rather unsociable lives. Adult males frequently live alone; adult females only in the company of their offspring. It appears that one old male patrols through and defends an extended territory, wherein he breeds with several females that have their own subterritories. The daily movements of orangutan are strongly influenced by the availability of food in their home ranges. These apes often encounter each other in fruit trees and then seem to share access placidly, although territorial conflicts between males occasionally occur. Female orangutans do not exhibit any seasonal swellings or changes of coloration in the circumgenital region. The "old man of the forest" is reported to live mainly on fruits, and many other vegetarian food items. They also add an occasional bird egg to their diet.

Pan (Oken, 1816) Chimpanzees and Bonobos	*Pan troglodytes* *Pan paniscus*

The chimpanzee is perhaps the best known of all great apes and the primate most closely related to humans. Two species, *Pan troglodytes*—the common chimpanzee—and *Pan paniscus*—the pygmy chimpanzee or bonobo—are usually distinguished. *P. troglodytes* occurs in at least three varieties or subspecies that are not different enough to be assigned to separate species. These subspecies of *P. troglodytes* occur in a series of different environments in central Africa, including woodland, rain forest, savannah, and mountainous regions up to about 3000 m. Much more restricted in extent is the rain forest area inhabited by the pygmy chimpanzees; these appear only in one region south of the Congo (formerly the Zaire) River, where it arches farthest north. Because pygmy chimpanzees cannot swim, the Congo strictly limits their range on the west and north, and the Lualaba River, a tributary of the Congo, limits its distribution to the east.

Chimpanzees have very large ears that vary greatly in size, outline, and positioning. The combination of facial features is also variable; consequently, there is a high range of individuality to chimpanzees' faces. It is clear that each of these apes learns to recognize many individuals. The center of the face around the eyes, the somewhat protruding snout, and the lips are essentially hairless. The nasal openings are positioned relatively high above the upper lip, are separated by a narrow internasal septum, and vary in outline and relative size. There is a marked superorbital torus above the eyes, which are positioned relatively far apart. The amount, length, and direction of head hair also differs individually. For example, both sexes of the common chimpanzee tend to become bald on the top of the head relatively early in life, and pygmy chimpanzees often have longer head hair with a natural part in the middle. The skin of bonobos is usually black all over, and it is more often flesh colored in *P. troglodytes*. *P. troglodytes* varies, however, in the coloration of the skin. The fur is usually black or dark brown except for a supra-anal white hair tuft in very young animals and the grizzled-gray and white of aged chimpanzees.

P. troglodytes varies in body length between 74 and 96 cm, with females being slightly smaller than males. Pygmy chimpanzees are usually slightly smaller than the common chimpanzee, measuring between 70 and 83 cm in body length. The forelimbs of common chimpanzees are longer than the hind limbs, and the intermembral index is about 114 for this species. Fore- and hind limbs of bonobos are of almost equal length, so that the legs are relatively longer than in the common chimpanzee and the intermembral index is close to 100 at 102. Common chimpanzees spend a considerable fraction of their daily active time on the ground. They walk on the knuckles (second phalanges) of the second to fifth fingers when moving quadrupedally (Tuttle, 1969, 1975). *Pan paniscus* (Figure 4.48) is generally more lightly built than the common chimpanzee. This species tends to walk upright more often than the other, vocalizes differently, and, unlike other primates, copulates frontally.

The behavior of both chimpanzee species in their natural habitats has been documented in great detail. The common chimpanzee's behavior varies considerably across different environmental settings. They live in large groups with up to 50 individuals. There are groups made up exclusively of mothers with their offspring of all ages and both sexes, of males only, and of mixed groups of adults and young animals of both sexes. Relationships between individuals of the same group tend to be placid, but while feeding females and young typically defer to males. Common chimpanzees spend a considerable fraction of their daily active time on the ground.

In situations when common chimpanzees would engage in aggression, bonobos engage in sexual activity. This behavior makes their social behavior exceptionally peaceful. The bonobo social system is matriarchal (De Waal and Lanting, 1997). Female chimpanzees have large swellings in the anogenital region that turn bright

Figure 4.48 *Pan paniscus*, female bonobo. Photo by Steve Underwood, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

red at the time of estrus. Females in estrus usually accept copulation with several males. This allows considerable power of female choice. In Tanzania, sexual activity is heightened between August and October; however, there is no evidence for an accurately defined breeding season because newborns are seen throughout the year. Group size and movement appear to be influenced by the availability of food in the area. All chimpanzees have an elaborate communication system using facial expressions, gestures, body movements, and vocalizations. Grooming is an important chimpanzee social activity. Chimpanzees sleep in tree nests that are seldom constructed more than 4 to 5 meters above ground and are newly built every evening. The chimpanzees' diet consists mainly of fruit and plant material. They do, however, eat small mammals, including young chimpanzees, monkeys, birds, insects, and fish when able to obtain these prey items.

Gorilla (I. Geoffroy Saint-Hilaire, 1852) Gorillas[35]	*Gorilla gorilla*

[35]The two subspecies of *Gorilla*, *G. beringei beringei* and *G. gorilla gorilla*, are on the endangered primate species list (Konstant, 2002).

The largest of extant primates is the gorilla (Figure 4.49), the present populations of which are barely hanging on in the highland and lowland rain forests of central and west Africa, extending east as far as the north end of Lake Tanganyika, and south into southwestern Uganda. The only species, *Gorilla gorilla*, is commonly subdivided into two subspecies or races: *G. g. gorilla*—the so-called lowland or western gorilla—and *G. g. beringei*—the highland, mountain, or eastern gorilla. A third subspecies was proposed as the eastern lowland gorilla, *G. g. manyema* (Groves, 1967).

Gorilla's skin color is black; the body hair is usually black or dark brown, but hair on top of the head is sometimes reddish. With increasing age, the hair on the back of old male gorillas turns more silver, and they are therefore often referred to as "old silverback." In the face, only the area around the eyes, nose,

Figure 4.49 *Gorilla gorilla*, western lowland gorilla. Photo by Steve Underwood, courtesy of the San Francisco Zoological Society. From Ankel-Simons, 2000.

and lips is bare; the cheeks are usually covered with fuzzy hair. The eyes are deeply set under pronounced supraorbital tori, and the nasal openings are nearer to the upper edge of the mouth than in chimpanzees or orangutans. Gorillas have small ears that lie back apressed to the sides of the head rather than standing out, as in chimpanzees. The nasal openings vary considerably in outline and size. These openings have raised bulging rims around them in some individuals and thus can give particular gorilla faces highly individual distinction. Adult male gorillas grow to around 170 cm in body length, females around 150 cm; there is considerable sexual dimorphism in body size, and males can weigh twice as much as females, so that dimorphism reaches extremes with this extant primate species. The forelimbs of gorillas are somewhat longer than the hind limbs, and their intermembral index is about 115.

Adult gorillas are mainly terrestrial, and only the young frequently climb into trees. Like chimpanzees, gorillas progress quadrupedally with their hands held in a knuckle-walking manner. They also sleep in nests that are built anew each evening. Gorillas usually make their nests on the ground or low in trees. They are frequently found to be soiled with excrement. As with chimpanzees, the group size of gorillas is variable. Groups ranging from 5 up to about a maximum of 30 members have been counted. The old "silver-backed" males normally assume group leadership. Such old males, according to Schaller (1963), lead the foraging group and set the pattern of feeding and sleeping times. They usually tolerate one or a few other adult males, but some males wander alone. For young males, group ranks seem to be defined by age; for females, ranking is defined by the presence of infants. Mother normally groom their offspring. Young gorillas of both sexes play together in a placid and quiet manner (Schaller, 1963). Groups habitually do not move any farther than about 1.5 km (1 mile) per day. Meetings between different groups and between adult males usually lack any open hostilities. Interactions among adult gorillas consist mainly of chest-beating gestures, different postures, facial expressions, and vocalizations that practically never lead to physical conflict. There is no restricted breeding season in the natural habitat. Young gorillas stay with their mothers for up to three years. Female gorillas have only a slight degree of sexual swelling during estrus. The gorilla diet consists mainly of leaves, shoots, roots, bark, vines, and a small amount of fruit. They appear to be entirely vegetarian, and herbivores of this size must consume a considerable amount of plant food daily to thrive (Fossey and Harcourt, 1977). Most of their daily activities consequently involve foraging.

Homo (Linnaeus, 1758) *Homo sapiens*
Modern Humans

There can be no doubt that *Homo sapiens sapiens* (Figure 4.50) is the most successful of all extant primate species. Unlike any other primate, modern humans have been able to adapt to all kinds of environments and thus inhabit all

Figure 4.50 *Homo sapiens sapiens.* From Ankel-Simons, 2000.

continents of our planet. As we are all human, a detailed description of our anatomy appears to be unnecessary in this context. Let us just review a few striking characteristics that apply strictly to modern humans. Human body size has never been measured with the same methodology that is commonly applied to record the body size of other mammals. Both human females and males vary vastly in body size and totally overlap each other in this measure.

It appears that, anatomically, humans are habitually omnivorous, eat a great variety of foodstuffs, live in all kinds of variable compositions, and have invaded every habitat imaginable. Humans vary in skin color on a scale of shades from deep ebony through pale orange, yellowish to white, and even pinkish. The skin is more or less bare all over the body except for some hair tufts covering the pubic area and hair of variable texture, length, color, and density that adorns the back of the head, starting at the forehead. Also, the trunk, arms, and legs may

be covered by sparsely distributed short hairs, a condition that occurs more markedly in males of the species than in females. All fingers and toes have nails, the generalized hands are tools that enable precision grasping and manipulation while the feet are uniquely derived to function as terrestrial walking gear. Legs are longer than arms, and the intermembral index approximates 70. Human newborns are totally dependent on parental care. Birth is usually given to one offspring and while twinning and triplets can occur, it is rare. Human social behavior is extraordinarily complex and dominated by the ability to communicate with language. Humans are remarkably territorial, a characteristic that often causes conflict. Humans are the one primate species that is not at all in danger of extinction. To the contrary, humans are, together with rats, among the most prolific of extant mammals and are in the process of endangering the existence of most other primate species, as well as many other living things.

We humans have conquered this world and adapted it to our own needs with little regard for the world around us. Humans are united by the same biological genus, species, and subspecies and the unrestricted ability to interbreed. At the same time, they are deeply divided by religion, skin color, prejudice, and greed. The species name of the great ape of wisdom, *sapiens*, does not befit humans well. It seems that wisdom is an elusive quality. Indeed, our species is the most destructive of all the great apes.

Table 4.3 lists the infraorders Superfamily Hominoidea.

Table 4.3

Superfamily Hominoidea

Suborder		Infraorder catarrhini			
Anthropoidea					
Superfamily		Hominoidea			
Family		Pongidae			
Genera	Hylobatidae *Hylobates*	*Pongo*	*Pan*	*Gorilla*	Hominidae *Homo*
Cervical vertebrae	7	7	7	7	7
Thoracicvertebrae: with ribs	13	12	13	12	12
Thoracic vertebrae: articulation	12	12	13	13	12
Lumbar vertebrae	6	4	4	4	5
Functional lumbar vertebrae	7	4	4	4	5
Sacral vertebrae	5	5	6	6	5
Caudal vertebrae	3	3	3	3	4
Proportions	Arms much longer.	Arms much longer.	Arms longer.	Arms longer.	Legs much longer.
Length of arms in % of body length	243 (Short olecranon).	200	172	170	148
Length of legs in % of body length	146	116	128	124	169
Hand length in % of body length	59	53 Pollex musculature reduced.	43 Pollex musculature reduced.	40 Pollex musculature reduced.	37
Foot length in % of body length	52	62	50	47	48
Thorax depth in % of thorax depth	117	126	127	138	128
Locomotor activity	Pollex short, but present, not opposable.	Deliberate arboreal climbing. Fist walking. Pollex not truly opposable.	Knuckle walking, Pollex not truly opposable.	Knuckle walking. Pollex not truly opposable.	Bipedalisn. Long tarsus, short toes. Toes 2–5 reduced in length, first toe strongest. Pollex truly opposable.
Activity pattern	Diurnal	Diurnal	Diurnal	Diurnal	Diurnal (sometimes "cathemeral" by choice)
Geographical distribution	Asia	Asia	Africa	Africa	World wide

Chapter 5

Skull

Skull Development and the Two Types of Bone
Orbital Region
Nasal Region
Skull Base, Braincase, and Foramen Magnum Position
Ear Region
The Sinuses
Comparative Primate Skull Morphology
Prosimiae
Anthropoidea

A number of the characteristics unique to the order Primates are manifest in the structure and composition of the skull. These characteristics become apparent when we compare primates with other, less derived groups of mammals. Among primates, several major trends exist, such as the enlargement and increasing complication of the brain; this trend is expressed in the enlargement of the braincase. Another crucial adaptation is the increased refinement of eyesight and the acquisition of stereoscopic vision. These trends are apparent in the position, size, and the manner of enclosure of the eye sockets, or orbits. Relative reduction of the sense of olfaction is expressed in a concurrent reduction of the proportion of the skeletal elements that make up the nasal region. Some functions of the dentition and snout of primitive mammals have been partially taken over by the grasping and sensitive abilities of the pentadactyl hands in primates. Number and size of teeth, and thus the size and overall morphology of the mouth cavity, the mandibular angulation, the height of the mandibular ascending ramus and its articulation with the skull, and the bone strength reflected in its thickness are all part of the functional unit skull. Variations of skull shape are therefore likely to reflect directly or indirectly the size and spatial arrangement of different sensible and mechanical adaptations and requirements within the morphological unit that is the skull. The position of the foramen magnum on the base of the skull—the

point of articulation between the skull and the spinal column—has a tendency to shift forward under the base of the skull toward its center in successively more advanced groups of primates instead of remaining at the back of the skull as in other mammals. This trend of moving the position of the foramen magnum forward also indicates a change in the way the head is carried during locomotion, particularly in bipedal, upright humans.

Various reasons for skull shape adaptations have been investigated that often lead to inconclusive results. A recent comparative functional analysis of skull morphology of tree-gauging primates demonstrates this. The study showed that no skull modifications clearly reflect the vigorous gnawing activity of these animals (Vinyard et al., 2003; Daegling, 2004).

A new technology (generalized procrustes analysis, or GPA) has been applied to evaluate the taxonomy of the baboons (Papionina, Cercopithecidae) with the help of 45 three-dimensional landmarks of the skull that were digitized and evaluated with multivariate statistics (Frost et al., 2003). This skull-based approach resulted in an interesting taxonomic and geographic separation of the genera, species, and subspecies (for detailed discussion of the results see Jolly, 2003).

SKULL DEVELOPMENT AND THE TWO TYPES OF BONE

There is yet another point of view that must be considered when looking at the skull: different parts of the skull are of phylogenetically and ontogenetically differing origins. In vertebrates, there are two fundamentally distinct kinds of bone formation. Within one morphological unity, the skull in extant mammals, both kinds of bone—cartilage replacement bone and dermal bone—participate. Cartilage replacement bone is preformed in cartilage. This cartilage is replaced by bone during ontogenetic development. All the bony elements of the postcranial skeleton—except the clavicle or breastbone—develop in this way. Within the skull, the main parts of the skull base or basicranium, the bony elements of the inner nose, the ear ossicles, and the cranial portion of the hyoid apparatus in the throat are ontogenetically premolded by cartilage. The other type of bone development, which results in the formation of the dermal or intermembrane bones, begins ontogenetically with the connective tissue giving rise directly to bone within the skin. During ontogeny, the connective tissue is also replaced by bone. Most of the flat bones of the skull develop from dermal origins, including the bony elements that build the facial portion and the braincase and, as noted earlier, apart from the skull, the clavicle.

To understand why this difference in bone formation exists in recent mammals, we must look at the evolutionary history of different bones. We have to reflect

back to an initial stage of vertebrate history. It all began when early, very simple ancestral vertebrates first acquired several pairs of external sense organs in the cephalic (*kephale, -os* is Greek for "head") region. Three of these sense organs (there were actually others that are irrelevant for the case being made here), the nasal sacs, the eyes, and the inner ears, have persisted across time. These parts are preformed by cartilage and are called the primordial portion of the skull (or chondrocranium), a region that even today remains in this cartilaginous state in selachians—sharks, dogfish, skates, and rays—an entire vertebrate order that exists without a trace of ossification and has a completely cartilaginous skeleton. Selachii have been existing on Earth from Devonian times until the present day (Romer, 1971). It is hypothesized that this chondrocranium of such early and primitive stages persisted and still occurs in all mammals during early ontogenetic development. The elements of the cartilaginous preformed skull in mammal embryos are actually identical to the equivalent segments in the selachian (subclass Chondrichthyes) skull. The true cranium of all higher vertebrates is now completed by the addition of true bone, which originates from two sources, cartilage and dermal bones. In all recent mammals, the true cranium originates with the chondrocranium with the addition of true bone. Ontogenetically, the cartilaginous bones appear first, followed by the dermal bones.

Cartilage bones emerge at ossification centers within the cartilage of the primordial skull. They occur primarily in those places where added strain and stress or movable joints will develop. The origin of bone formation seems to have evolved for physiological reasons. Ross and Metzger (2004, p. 387) pointed out that "Different strain magnitudes in different areas of the same animal are hypothesized to reflect optimization to different criteria." This essentially means that morphological design results in compromises between various functional demands. For example, cartilage capsules in early vertebrates occur around the optical nerve. Such capsules function to protect sensitive skull parts. In extant vertebrates, bone formation begins within the cartilage near the temporo–mandibular joint in the *quadrate* of the skull and the *articulare* of the mandible to establish this joint between the two mobile elements of the skull. An identical event occurs in the formation of the *exoccipitals* of early vertebrates, which later become the occipitals surrounding the foramen magnum at the base of the skull of modern vertebrates. The foramen magnum accommodates the articulation between the cranium and the first vertebra of the spinal region, the atlas. These physiological necessities led to cartilage bones. In turn, the cartilage bones of historically early forms have retained their ancient topographical relationships and shapes within the ontogenetic development of today's vertebrates and thus allow the tracing of homologous parts within the skull throughout all vertebrates with certainty. Table 5.1 lists the ontogenetic origin of cranial elements.

Knowledge about the history of bone development in mammals makes it possible to understand its effect on the normal formation of the primate skeleton.

Table 5.1
The Ontogenetic Origin of Cranial Elements

Dermal Bones	Replacement Bones
Nasal	*Occipital*
Vomer	*Sphenoid*
Palate	*Petrosal part of temporal*
Frontal	Ear ossicles
Lacrimal	*Temporal bone: mastoid/petrous*
Premaxilla	Ethmoid
Maxilla	Styloid
Zygoma (jugal)	Hyoid
Squama of the temporal	
Tympanic of the temporal	
Squama of the sphenoid—pterygoid	
Uppermost portion of occipital (interparietal)	
Parietal	
Mandible (dentary)	

Italics indicate that bones are part of mixed dermal and replacement bones.

It appears that at least part—the sternal portion—of the clavicle is a dermal bone. The evolutionary and ontogenetic origin of the dermal clavicula is less clear and less well documented than that of the cartilage replacement bones of the skull. It has been shown that the clavicle is derived from a phylogenetically old element of the outer skeleton of primitive tetrapods. However, the best proof for the fact that the clavicle is at least partially originating from a dermal (or intermembral) bone is a well-documented human developmental defect: in some rare cases, the ontogenetic development of intermembral bones in humans malfunctions, resulting in deficient ossification of these bones. Humans who are stricken with this malformation have incomplete skulls. This affliction is called cleidocranial dystostosis (*kleis, kleidos*, Greek for "clavicle") and is the cause of serious malformations of the head because the flat bones encasing the braincase do not develop normally (Wilson and Bruce, 1955). In addition, the shoulder girdles of these individuals are not properly braced apart in front, because their clavicles also are not normally developed. Consequently, their shoulder joint is not fixed to the sternum in front, and they can move their shoulder joints to the side and even in front of the upper trunk.

The evolutionary history of cartilage replacement bone or endoskeleton is closely related to the development of a strong axial skeleton and powerful limb girdles as a framework for the support of muscles. In contrast, the development of the dermal or intermembrane bone begins with the connective tissue directly giving rise to bone within the skin. During ontogeny, the connective tissue is gradually replaced by bone.

Having completed this discussion of the evolutionary history of the bones that combine to make up the mammal skull, we can return to consider the morphological trends that characterize the skull of primates. Within the order Primates, there are distinctive differences between prosimians and anthropoids in the details of skull configuration.

ORBITAL REGION

In all prosimians except for the enigmatic East Asian primates, the tarsiers, the eyes are surrounded from the back and the side by a bony ring. This ring is formed from the jugal (or zygomatic) and the frontal bones. This structure is shaped according to the mechanical stresses that are exerted on the orbital rim area by muscles and by biting force (Witzel et al., 2004). In the Anthropoidea, the eyes are almost completely enclosed by eye sockets. In the latter group, orbital walls in back and at the side are composed of plates, extending out from the jugal and frontal and in back from the sphenoid. The enormous eyes of *Tarsius* are, similar to Anthropoidea, partially enclosed by a bony socket. This bony region leaves open an area to the sides and below the eyeball, even though it is closed by ligaments in life. The jugal in *Tarsius* is expanded outward as part of a circular flange extending out from the skull and encircling the eye, but it does not, as in anthropoids, contribute to the bony enclosure of the eye socket. The eye socket of *Tarsius* is comparatively much larger than in any other extant primate, including those of other nocturnal prosimians. Hence, in *Tarsius*, only the frontal, and a part of the sphenoid (the alisphenoid portion) participate in forming the partial postorbital closure. The roots of the upper molars enter into the orbital floor in tarsiers (Haines, 1950; Ankel-Simons, personal observation). In sum, postorbital closure is not as complete as it is in Anthropoidea, and considerable opening remains between the maxilla and the jugal in the back floor of the orbit of *Tarsius* (Figure 5.1).

Among Anthropoidea, postorbital closure is usually more complete than in *Tarsius* (Figures 5.2 and 5.3), with one exception: the South American night monkey *Aotus* (the only nocturnal higher primate with comparatively large eyes) resembles *Tarsius* because it also retains a fairly large opening that is, however, walled off by a jugal expansion. Most extant anthropoideans show a much more reduced inferior orbital fissure. In *Aotus*, the main part of the lateral closure of the eye socket is primarily formed by the jugal bone. As noted earlier, in *Tarsius* the jugal contributes primarily to the circumorbital flange.

The external margin of the orbits is formed by the frontal (above), jugal (laterally), and maxillary (below) bones. As we have seen, among prosimians, the orbits are not closed up posterolaterally. The jugal and frontal contribute to a postorbital bar, and the lateral postorbital wall of higher primates and in *Tarsius* is also formed by these bony elements and the alisphenoid.

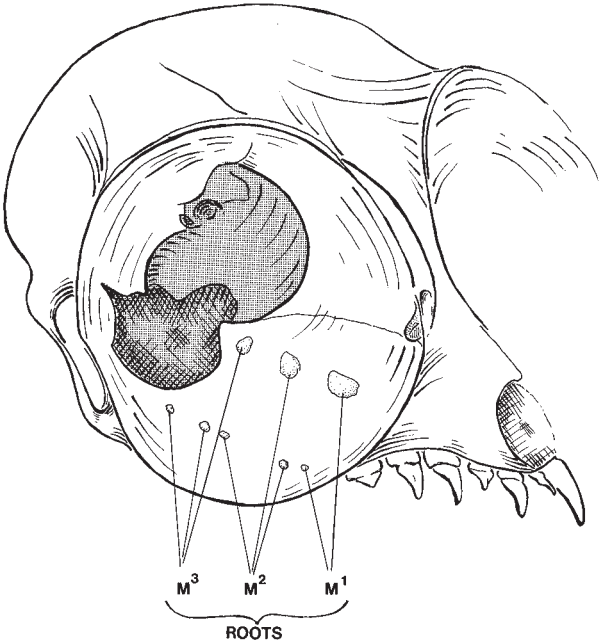


Figure 5.1 View into the right orbit of a tarsier *(Tarsius syrichta)* showing the tips of the molar roots and the large opening at the back of the orbit (shaded).

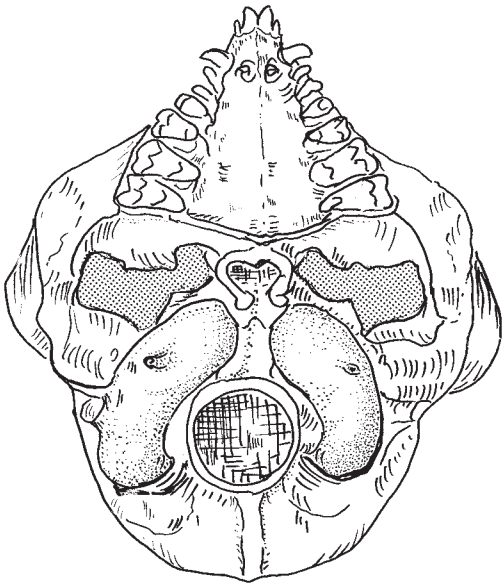


Figure 5.2 Basicranium of the skull of a tarsier *(Tarsius syrichta)* showing the openings (shaded) in the orbits and the auditory bullae that dominate the basicranium laterally and anteriorly to the foramen magnum.

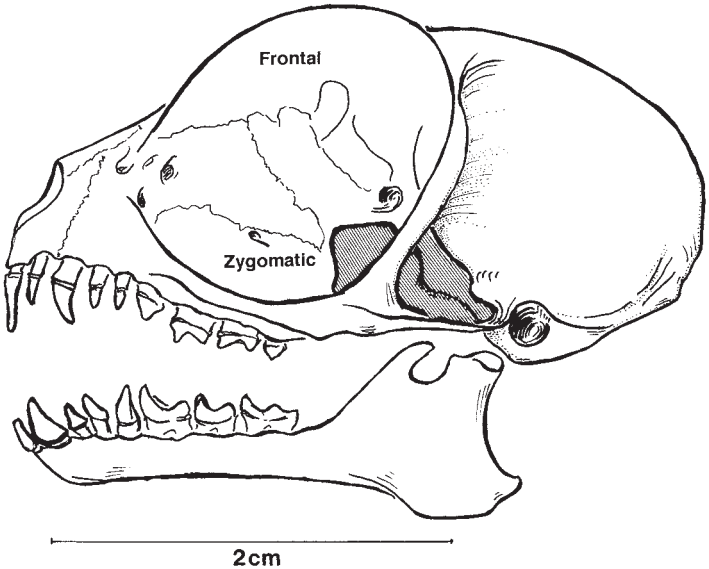


Figure 5.3 Lateral view of the globular tarsier skull *(Tarsius syrichta)* showing the fenestra in the orbital region.

The function of the mammalian postorbital bar has been the object of much discussion. The question of "what it is for" is the subject of disagreement (Ravosa et al., 2000; Martin and Ross, 2005). As is usual, there is likely a combination of "reasons," not a single, apparently mechanical advantage, because postorbital bars stiffen the lateral orbital wall (Heesy, 2004, 2005). In this context, it has been claimed that the orbit of anthropoids and the postorbital bar of prosimian primates exist to prevent the chewing musculature (temporal muscle) from interfering with vision and, consequently, the ability to move safely without predator discovery while eating. This idea sounds plausible if we do not consider the fact that primates do not move about while eating and chewing; they habitually sit down while doing so. The argument that they are unable to see and discover potential predators while chewing is also problematic because the primate sentries that watch for predators do not eat while doing so and thus are perfectly capable of giving warning while others chew and eat. Thus, it does not matter whether the chewing musculature affects the eyeball, which it does ever so slightly under artificial conditions (Ravosa et al., 2000). There must be other causes for the development of bony orbits and orbital rims around primate eyes. The possible hypotheses that have been formulated are based strictly on research in the laboratory, without consideration of animal behavior in the wild, and this leads to erroneous interpretations.

The medial lower part of the orbit is formed by a small, flat, paired membrane bone, the lacrimale. Within the lacrimale is the outer opening of the lacrimal canal (tear duct). This canal, or foramen lacrimale, is normally positioned outside the orbits in Lemuridae. With the latter primates, the lacrimale bone also extends beyond the orbital margin into the cheek area. In higher primates, the lacrimal bone usually does not extend beyond the orbital margin or does so only slightly. Also, in Anthropoidea, the opening of this canal is positioned within the orbita. There are exceptions to this rule in some individuals of the genera *Cebus, Macaca*, and *Papio* in which the opening of the lacrimal bone can frequently be positioned within the margin or slightly outside the orbital rim.

NASAL REGION

Forward and downward from the orbital area lies the nasal region. The nasal cavity is covered above by the nasal bones forming the bridge of the nose. In the center of the nasal cavity is the medially positioned nasal septum that is combined of the ethmoid bone on top and the vomer below; together, these separate the two nasopharyngeal fossae. The vomer rests on top of the palate and the maxillae, and it is contacted by the ethmoid and sphenoid from above and behind, respectively. In living primates, both the median nasal septum and the anterior margins of the nasals and maxillary bones are extended forward by cartilage. These cartilaginous nasal wings are usually broad in South American monkeys and narrow in Old World monkeys, lesser and great apes, and humans.

This morphological difference of the nasal openings led to the taxonomic distinction of these two monkey groups into the infraorders Platyrrhini and Catarrhini. This distinction has been criticized because the breadth of the cartilaginous nasal wings is highly variable in primates and thus of minor taxonomic value. Still, South American monkeys with their widely separated nostrils do look different from Old World higher primates.

A series of convoluted, thin, bony plates and scrolls, the turbinals and the nasal conchae, extend shelflike into the nasal cavities and function as support for the mucous membrane that lines the nasal cavity, a portion of which contains the olfactory receptors. Thus, enlargement of the surface area in the nasal cavities is provided by these bony structures (conchae or turbinals). There are four pairs of ethmoturbinals (the paper-thin lamellae that are part of the ethmoid and are covered with mucous membrane tissue) in Tupaidae and Lemuridae, whereas *Daubentonia* is the only primate to have five or even six pairs (Le Gros Clark, 1959; Martin, 1990). The ability to identify unequivocally the number of turbinals of *Daubentonia* is confounded by the lack of sagitally sectioned skulls; even unsectioned skulls are rare. There is a picture by Owen (1863) that shows a sagittal sectioned aye-aye skull (Figure 5.4) where it can be clearly seen that the

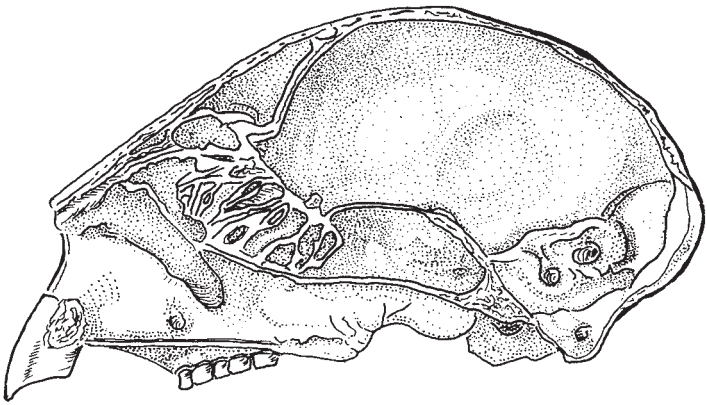


Figure 5.4 Sagittal cut through the skull of *Daubentonia madagascariensis*, the aye-aye, showing huge frontal and sphenoid sinuses and the convoluted nasa turbinalia. Redrawn from Owen (1863).

turbinals are convoluted and complex; this, in turn, makes identifying and counting them difficult.

The possibility that these turbinals may vary in number among individuals cannot be excluded. Neither Owen (1863) nor Peters (1866) discussed this issue in their monographs describing the aye-aye anatomy. The ethmoturbinalia lie shelflike, one above the other, with each successive lower pair positioned further back. They are formed of cartilaginous replacement bone, as is the ethmoid but not the vomer. Whereas the turbinalia are paired, the vomer is a single, paper-thin bone that separates the two nasal cavities medially from each other; it is part of the nasal septum. As in all higher primates including *Homo*, the number of ethmoturbinals is reduced to two pairs. Here these fragile bones are positioned one above the other rather than one posterior to the other. Above the ethmoturbinals lie the nasoturbinals. Both nasoturbinals and ethmoturbinals are components of the ethmoid bone. Beneath these turbinals and extending from the lateral wall of the nasal cavities is another pair of turbinals. Although this pair (unlike the other turbinals that are cartilage replacement bone) is a developmentally separate membrane or dermal bone emanating from the maxillary, it is called the maxilloturbinal bone. The maxilloturbinal of the nonhuman primates is homologous with the interior nasal conchae of human anatomy. The superior and middle nasal conchae are called ethmoturbinals in human anatomy (Weber, 1904). A detailed description of the development of the cercopithecoid nasal capsule, accompanied by instructive drawings, has focused on the ethmoidal region (Maier, 2000). This study has led the author to the conclusion that cercopithecoids are similar to hylobatids and playtyrhines and more derived than hominoids.

As discussed earlier, the ethmoid is also present to differing degrees on the inner wall of the orbit in various primates. Figure 5.5 depicts the orbital region of an Old World monkey and of a lemur.

Recall that the surface of all the bony structures within the nasal cavity are covered with a ciliated mucous membrane. A portion of this membrane functions as the olfactory organ and is located in the upper part of the nasal cavity. It is equipped with olfactory receptors. The lower portion of the nasal region functions mainly as a warming humidifier and also cleans the inhaled air stream as it enters the respiratory system during breathing. It is devoid of olfactory receptors.

In long-snouted prosimian primates, the nasal cavity and the inner surface within the nasopharyngeal tract are comparatively larger than in higher primates. This difference is also expressed in the reduction of turbinals in the nasal cavity of anthropoid primates. However, the relative size of nasal cavities cannot necessarily be directly correlated with presumed, corresponding differences in

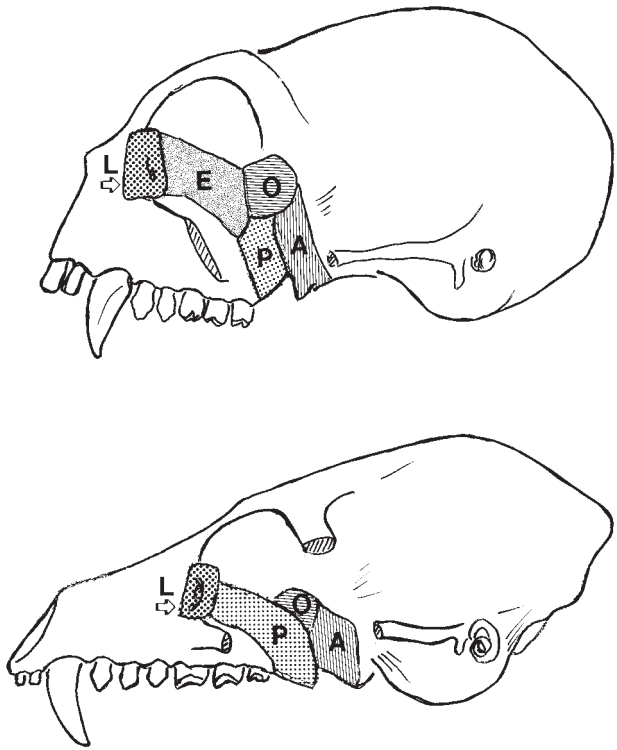


Figure 5.5 Composition of the bony elements in the orbital region of an Old World monkey (above) and a lemur (below). A = alisphenoid; E = ethmoid; L = lacrimal; O = orbitosphenoid; P = palatine.

smelling ability. It is not the size of nasal membrane surface that determines the acuity of this sense but the number and capacity of neural olfactory receptors per unit area of membrane. Because knowledge of the relative olfactory abilities of primates is still restricted, the idea that large-snouted primates have better olfactory abilities than short-snouted primates has not yet been proven and there are other reasons for having long snouts. In baboons, for example, the snout is considerably elongated, in apparent correlation with enlargement of the chewing apparatus and elongation of the tooth row, but it does not enhance olfaction or respiration.

In the front of the snout and under the nasal aperture are two small bony elements that in adult primates are fused to the maxillary bones located behind them. These small bones carry the alveolae of the incisor roots and are known as ossa inciciva, ossa intermaxilare, or premaxillae. They are connected to the front of the palate. The existence of these small bony elements in humans has been disputed because the sutures between the maxillary bone and the premaxilla fuses early (Barteczko and Jacob, 2004). This suture is, however, visible in many nonhuman primates, and this small bone is an important element for the integrity of the front of the snout. It is reduced to a narrow bony band in some prosimian primates that do not have any incisors (*Lepilemur leucopus;* see Figure 7.7).

The ethmoid is a fragile bone, located in front and center of the skull, that is paired in early ontogeny, but it fuses later into a single bony element. It forms not only part of the nasal cavity but also part of the inner wall of the orbits with its very thin lateral plates that are known as the laminae papyracea (or papyrus, "paper"—paper-thin sheaths). The sphenoid shapes the front part of the nasal septum. On top, this fragile bone in the center of the nasal cavity and between the orbits is covered by another thin plate, called the cribriform plate, lamina cribriformis, which is perforated by many small foramina that are penetrated by branches of the olfactory nerve. This sievelike arrangement gives the bone its name—both "ethmoid" from the Greek *ethmos* and "cribriformis" from the Latin *cribrum* mean "sieve."

The ethmoid also helps to form the inner wall of the orbits in various primates. In Lorisidae, Tarsiidae, and higher primates, as well as among a few Madagascar lemurs *(Microcebus, Allocebus)*, the paper-thin lamella of the ethmoid—which is also known as lamina papyracea—is positioned between the frontal and the maxillary bone. This place is occupied by an extension of the palatine in Tupaiidae and most Lemuridae and Indriidae, where the ethmoidal lamina is occasionally identified (Cartmill, 1978). The lamina papyracea never occurs in the inside orbital wall of *Daubentonia* and *Propithecus*. In the Lorisidae and Tarsiidae and in all higher primates, the palatine participates with a small plate on the medial wall of the orbit behind the ethmoid.

The palatine also forms a small area of the hind part of the orbital wall in insectivores, where the frontal bone usually directly contacts the maxilla. These

sutural combinations within the primate orbits are, however, variable intraspecifically.

In back, the ethmoid is joined by the much larger, complex sphenoid. The word *sphenos* means "wedge" in Greek. The sphenoid is a single bone in adult primates but consists of eight parts in early ontogeny. There are two ossification centers in the basiphenoid, two in the orbitosphenoids, two in the alisphenoids, and two in the pterygoid. Ontogenetically the sphenoid is made up of both kinds of bone. Although the largest portion is made up of cartilage replacement bone, the alisphenoid and the pterygoid plates ossify in membrane and thus are dermal bones. The sphenoid bone forms part of the hind wall of the orbits (upper aspect of the greater sphenoid wings) as well as the outside wall of the cranium behind the orbit (lateral aspect of the greater wings). Right in the center of the sphenoid body, there is a groove at approximately the center of the cranial cavity. This groove is part of the inner floor of the cranium and holds the hypophysis, or pituitary. This groove is delimited in front and back by a bony thickening, and the groove is also called the *sella turcica* (*sella* is Latin for "chair," "saddle") or Turk's saddle. The sphenoid is posteriorly joined by the occipital bone.

SKULL BASE, BRAINCASE, AND FORAMEN MAGNUM POSITION

The occipital bone surrounds the foramen magnum and makes up the medial and hind parts of the base of the skull (Figure 5.6). The body of the sphenoid has a narrow, bridgelike extension at the posterior end that joins the front end of the occipital (basioccipitale) anterior to the foramen magnum. Here in juvenile skulls these two bones form a distinctive suture. Some researchers use fusion of this suture in primate skulls as a feature for relative age determination, in particular, to determine if the specimen is a juvenile or an adult.

Early in ontogeny, the occipital bone begins to form from five separate ossification centers: one in the central part, the basioccipital in front of the foramen magnum; two lateral parts at the sides of the foramen magnum, the exoccipitals, that include the occipital condyles; and two in the flat back part, the squama (Latin for "scale," "flat bone"), which forms the back of the cranium. The occipital bone, like the sphenoid, is ontogenetically mixed. The anterior part, that is, the basi- and exoccipitals, are cartilage replacement bone, whereas the upper posterior portion, the squama, develops as membrane bone.

In contrast, the flat bones that combine to shape the major portion of the cranial vault proper are membrane bones. Above the occipital and covering most of the upper part and the sides of the cranial vault are the parietals. In those primates with well-developed skull musculature and small braincases, bony skull

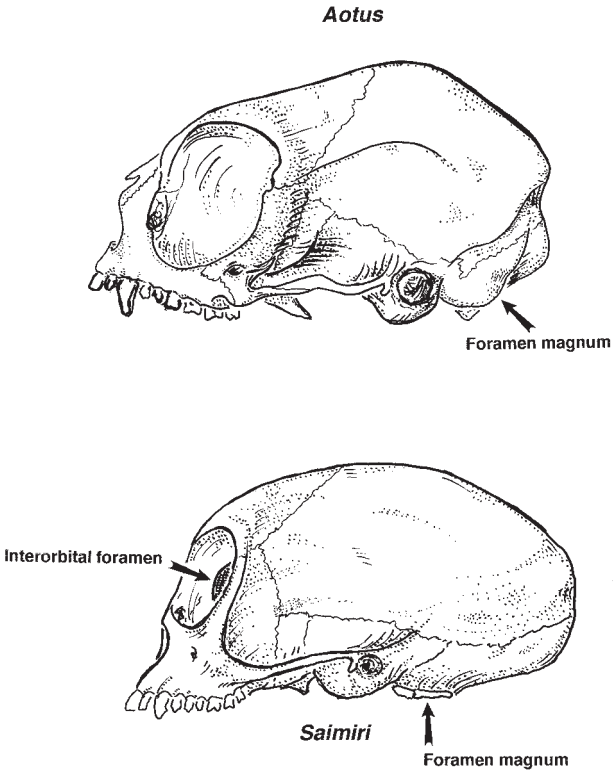


Figure 5.6 Comparison of the skulls of two New World monkeys. Above the side view of the Owl monkey *(Aotus)* skull, showing the large orbits of the only nocturnal higher primate. Below the skull of the Squirrel monkey *(Saimiri)*. Arrows indicate position of foramen magnum and the unique interorbital foramen in the Squirrel monkey. Both primates have about the same overall size.

crests develop medially. These crests enlarge the area of attachment for the chewing musculature. Bony crests are most developed in adult males, but the size and shape of these structures vary individually. The side of the skull is encased by the flat squama of the temporal bone, and the frontal bone adjoins the parietals anteriorly.

In prosimians, the backwardly directed position of the foramen magnum, the opening on the base of the skull that meets the vertebral column, results from the straight skull base. Again, *Tarsius* is an exception among the prosimians. In *Tarsius*, the foramen magnum is positioned centrally under the braincase. The extraordinary overall shape and appearance of the skull of *Tarsius* is primarily caused by the animal's enormous eyes.

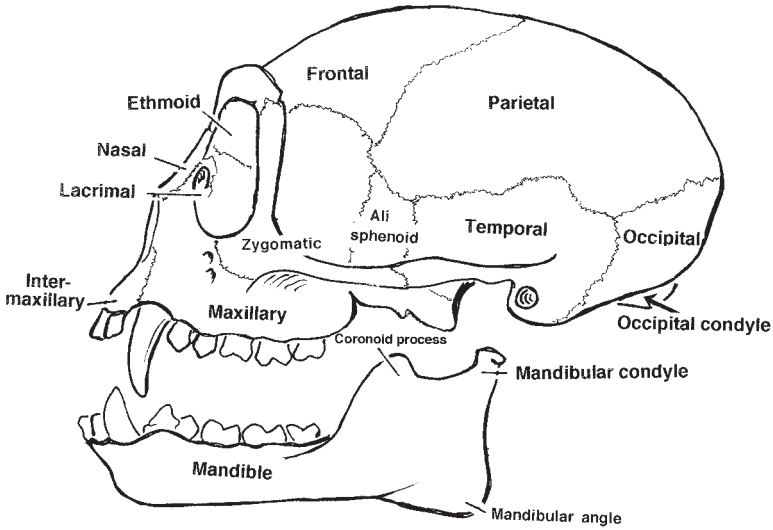
In the quadrupedal South American monkey *Saimiri*, the foramen magnum has the most central position in the center of the skull base of all primates, including humans. This indicates that the position of the foramen magnum must result from a complex number of causes.

The brain of prosimians itself is ovoid and flat compared with that of monkeys. The inner part of the skull base—from front to back—formed by the sphenoid, pterygoid, and basioccipital is typically flattened in prosimians other than *Tarsius*. In most higher primates, except *Alouatta*, the inner part of the skull base is bent. In back, the part of the inner skull base, the postsellar skull base, that is formed by the basioccipital and the sphenoid posterior to the dorsum sellae (= sella turcica) or hypophyseal fossa is bent downward to varying degrees. The postsellar skull base thus forms an angle with the front part of the inner skull base. The presellar skull base is combined of the portion of the sphenoid that lies anterior to the sella turcica and the dorsal surface of the ethmoid (the crista galli, which ascends upward medially and in front of the ethmoid is not part of the inner skull base). The inner skull base angle is highest in lemurs measuring 170 degrees—almost a straight line—and lowest in modern humans at only 60 degrees (Biegert, 1963).

The inner skull base has been discussed as being the key to understanding the hypotheses surrounding the complicated issue of primate evolution (Shea, 1985; MacCarthy and Lieberman, 2001). Among many attempts to address this issue, it has been hypothesized that the size of the brain is a crucial factor in shaping the angle of the inner cranial base and its angulation and that it plays an important role in early primate and ultimately hominid evolution (Lieberman et al., 2000). However, a comparative study of primate prenatal basicranial development led to the conclusion that body size appears to be more influential in causing changes in the nonhominoid cranial base shape than is the relative increase of brain size (Jeffery, 2003). Figure 5.7 depicts the various bony elements of the skull in the gibbon (genus *Hylobates*).

EAR REGION

As mentioned, the paired temporal bones participate in the framework of the braincase contributing their flat parts—the squamae—which make up the side of the skull. Extending forward from the squama is the back part of the jugal arch, which is part of the temporal bone. It arises in front of and above the external auditory meatus. At the base the temporal bone surrounds the ear region. The temporal bone is yet another bone in the primate skull that is made up ontogenetically of the two kinds of bone. As part of the skull base, the temporal bones are wedged between the sphenoid in front and the occipital in back. The flat part, the squama, is membrane bone. Three ontogenetically



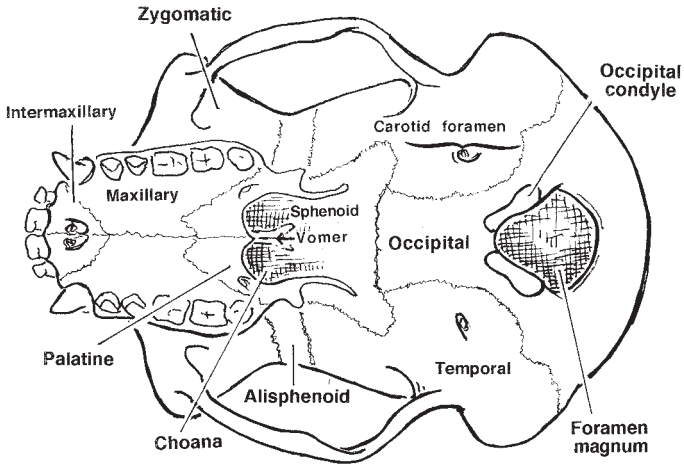


Figure 5.7 Skull and mandible of a gibbon (genus *Hylobates*) showing the various bony elements.

different replacement bone components are combined to form the basal portion of the temporal bones: the tympanic enclosing the middle ear, the mastoid portion on the outside, the petrosal part adjoining further forward and extending anteromedially, where it ends at the basioccipital. In humans, the mastoid is developed as a prominent and rounded process. Sometimes it is also prominent in mature specimens of genera *Papio, Macaca, Gorilla, Pan*, and *Pongo*, but less so than in humans (Sherwood, 1999). The term "petrosal" is derived from the Latin word *petrus*, meaning "rock." This name describes the fact that in humans and many of the higher primates, the petrosal's ventral surface has a rough, rocklike texture. Among prosimians and many of the South American monkeys, however, the homologous part of the temporal is often blown up like a balloon and is called an auditory bulla. Nothing much is known about the origin of these structural differences. We do not know whether there might be functional differences between these structurally distinct morphologies. This also holds true for morphological variances of the three ear ossicles. Thus, attempts to evaluate these structures in an effort to use them as taxonomic characteristics must be regarded as being of dubious value. The petrosal contains the inner ear, with the opening of the internal acoustic meatus opening medially. The middle ear bones (ear ossicles *malleus, incus*, and *stapes*, all cartilage replacement bone) are also situated in this area.

When sorting primates into groups, some anatomists emphasize differences in the position of one basicranial foramen. This is the carotid foramen for the arteria carotis interna, a large and important supply artery to the head. The foramen's position varies in apparent correlation to changes in the petrosal (or bulla) in primates. Hence, the various positions of this foramen are regarded as having taxonomic value in recent and fossil forms. Sometimes too much significance can be ascribed to positional differences of skull features. Many "characteristic" morphological details of the primate skull, such as the position of this foramen caroticum and the shape of the bones of the ear region (bulla, petrosal, and tympanic), are mainly dependent on the integral shape of head and neck together and cannot be evaluated in isolation from the overall head morphology and function. The carotid artery runs up the side of the neck and enters the skull near the ear region. However, the artery does not supply the ear region but the brain. Generally speaking, with the change from prosimian to higher primate, this foramen moves from the back and behind the ear region toward the center of the skull and in front of the ear region. In addition, the diameter of the foramen increases with the increase of relative brain size among primates. These factors also are cause for changes of the carotid foramen position. Except in Lorisidae the artery runs through a bony tube that penetrates the inner ear area or petrosal adjacent to the inner ear.

In Tupaiidae, Indriidae, and Lemuridae—with the exception of Cheirogaleinae—the foramen caroticum penetrates into the skull behind the bulla. Thus, the

foramen is called foramen caroticum posterius (*posterius* in Latin means "behind") in tree shrews, indris, and lemurs (Figure 5.8). The bony tube that houses this artery splits after penetrating the region of the eardrum. One of these two branches, the arteria stapedia, runs through the stirrup bone or stapes and then continues into the brain region (this passes through the ear region, although it functionally has no relation to the region and gives the arterial branch its name, stapedial artery). The second branch after the split is called arteria promontorii (also entocarotis or carotis interna). It fuses with the arterial formation called the circle of Willis, the major arterial supply system for the brain, on the base of the brain.

In genus *Tarsius* as in all higher primates, the stapedial artery is present early in fetal life but disappears later in ontogeny. A stapedial artery is typical of primitive mammals, where it has branches in the orbital region (replaced by a branch of the internal carotid in higher primates) and in the upper and lower jaws (supplied by branches of the external carotid artery in higher primates); see Figures 5.9 and 5.10. For Lorisidae and cheirogaleines, there are two interpretations concerning the internal and stapedial arteries.

The first interpretation is that the internal carotid splits into a stapedial and promontory artery before it enters the skull base, the arteria promontorii being of larger diameter than the stapedial branch (just the reverse of the relative proportions in Lemuridae). After the split, the promontory artery, according to this interpretation, enters the skull though the foramen lacerum—a foramen that is absent in Lemuridae—that lies in front of the bulla, and the small stapedial artery enters through a tiny foramen behind the bulla (C.F. Werner, 1960).

Contrary to the first interpretation, Saban (1963) maintained that the situation of the internal carotid of Cheirogaleinae and Lorisidae does not differ from the arrangement of these arteries in Lemuridae. His description is that the internal carotid artery also enters the skull behind the bulla in Lorisidae and Cheirogaleinae. In Saban's view, the artery entering the skull in front of the bulla is an additional branch off the stem artery: arteria communis. This branch is the anterior carotid artery that, according to Cartmill (1975), is actually the ascending pharyngeal artery. This artery enters the skull through the foramen lacerum medium. The artery is of comparatively large diameter. Figure 5.11 depicts the carotis in anthropoids.

In Tarsiidae, the internal carotid enters at the center of the large bulla. This is presumably because of the habitual vertical posture of tarsiers, which has caused a marked forward shift of the foramen magnum. The carotid passes into the skull relatively posterior to the petrosal in South American monkeys, whereas it enters the skull of Cercopithecoidea approximately at the middle of the petrosal and enters the skull of Hominoidea in front of the petrosal area. (For detailed discussions of these complex issues, see also Martin, 1990; Fleagle and Kay, 1994).

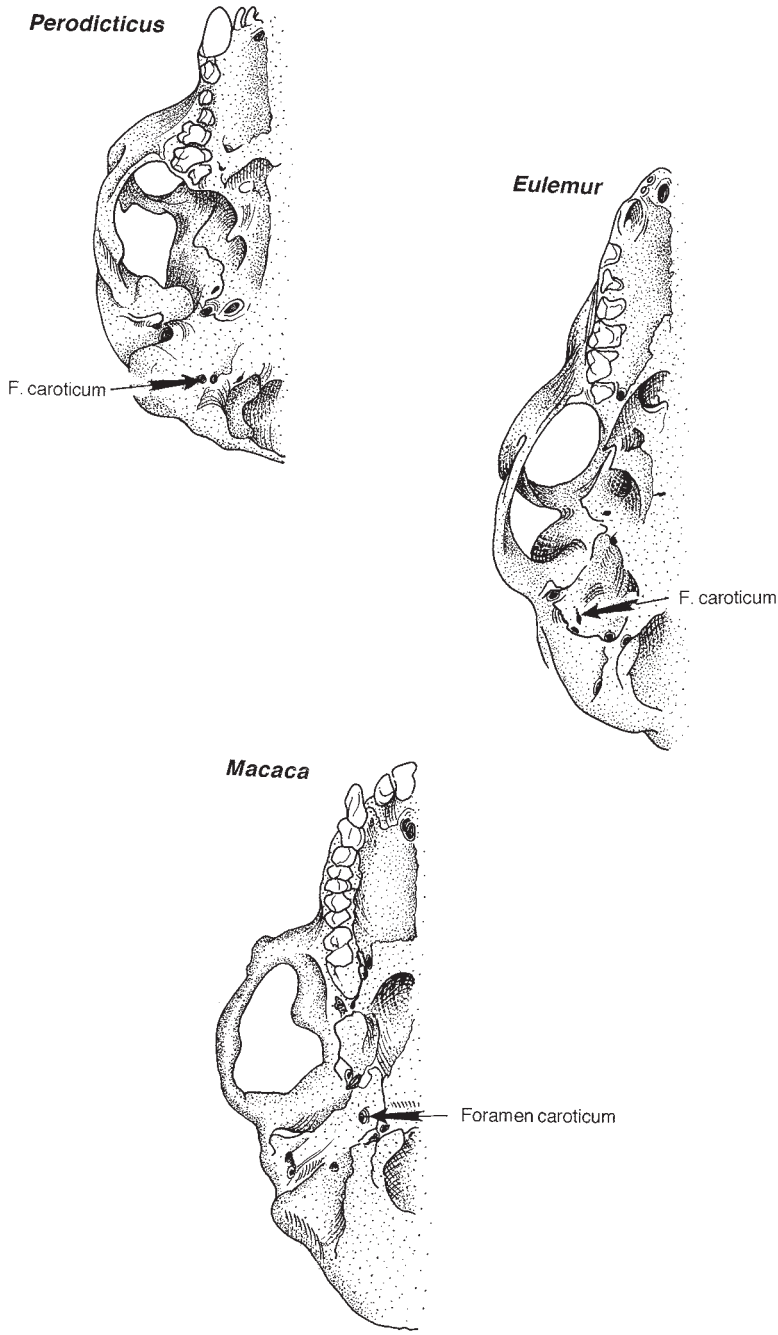


Figure 5.8 Various positions of the foramen caroticum in a lorisid (Potto, genus *Perodicticus*), a lemurid (genus *Eulemur*), and a macaque (genus *Macaca*).

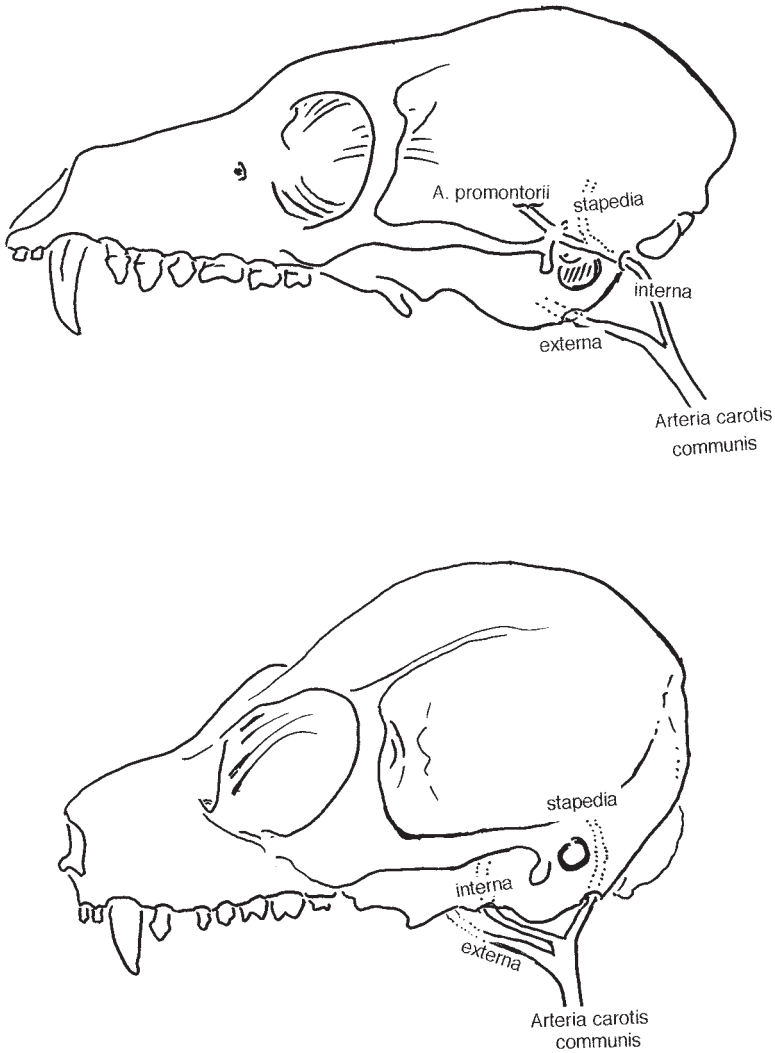


Figure 5.9 Arteria carotis pathway in a lemur (genus *Eulemur,* top) and a loris (genus *Perodicticus*, bottom).

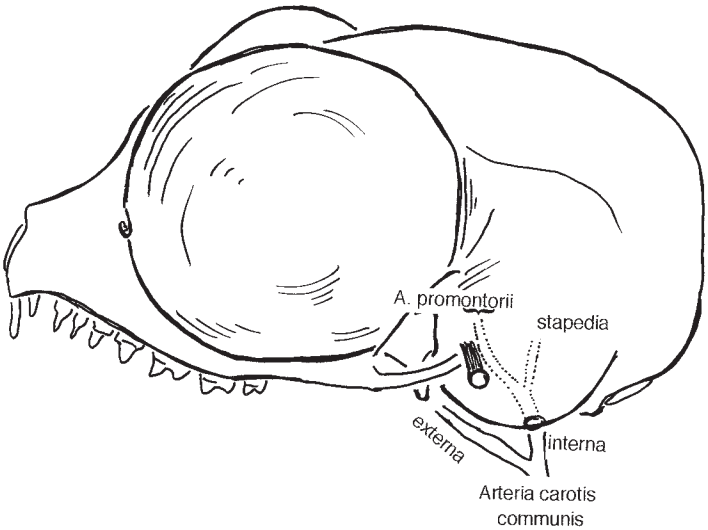


Figure 5.10 The arteria carotis pathway in a tarsier (genus *Tarsius*).

THE SINUSES

Bone structures are often made lighter and at the same time mechanically strengthened by internal cavities and trabecular (*trabs, trabis* is Latin for "beam," "strut") subdivisions within them. These structures are called sinuses (*sinus*, Latin for "bay," "curvature") within the cranium (Figure 5.12). The recent development of new technologies (e.g., high-definition magnetic resonance imaging; computed tomography) that make it possible to peer inside skulls without opening or breaking them has allowed enhanced research and scholarly discussion.

Primates have sinuses within the frontal area, centrally within the skull in the body of the sphenoid, and in the maxillary region. The maxillary sinuses appear to be most common. Why and where these sinuses occur is the object of various inquiries. Sinuses vary in size and shape, both intra- and intergenerically, and have also been thought to reflect taxonomic relationships (Koppe et al., 1999; Rae et al., 2002; Rossie, 2006).

Among prosimians, the aye-aye *(D. madagascariensis)* has large frontal sinuses and a huge sphenoidal sinus (Owen, 1863; see Figure 5.4). There is no mention of these sinuses in later publications, and in Owen's figure of a sagitally cut aye-aye skull, it appears as if the size of the sphenoidal sinus could be related to the expanded nasal area.

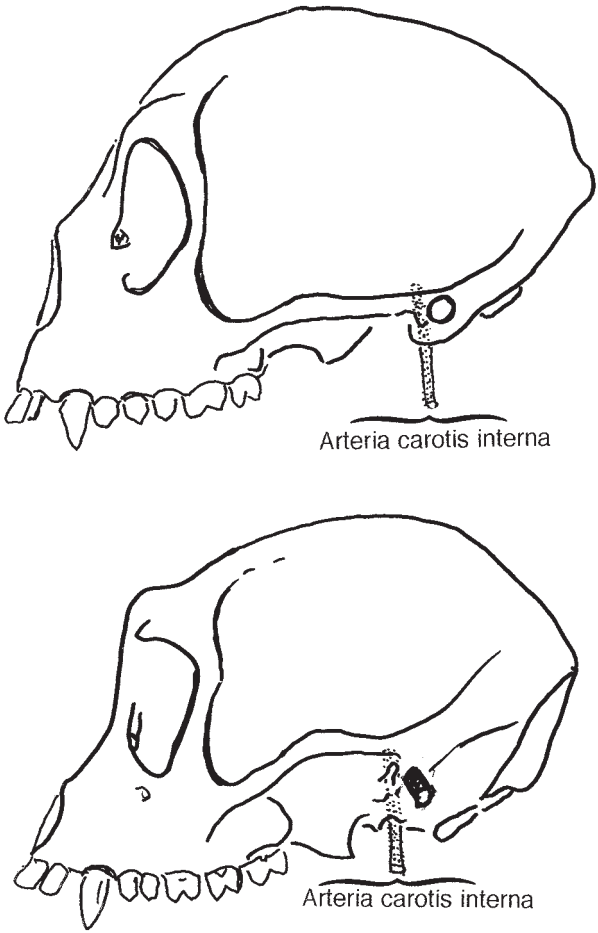


Figure 5.11 The arteria carotis pathway in a platyrrhine monkey (top), and a catarrhine monkey (bottom).

The maxillary sinuses in particular have been studied extensively because they occur in humans, the great apes, macaques among the Old World monkeys, and apparently in various New World monkeys (Nishimura et al., 2005; Smith, et al. 2005). Cercopithecinae, with the exception of genus *Macaca*, lack this paranasal structure. Modern humans have all of the possible sinuses that have openings to the airways and are thus subjected to inflammatory events.

Any putative correlation between sinuses, taxonomy, and phylogeny has not been irrefutably established. The function of these variable structures is also

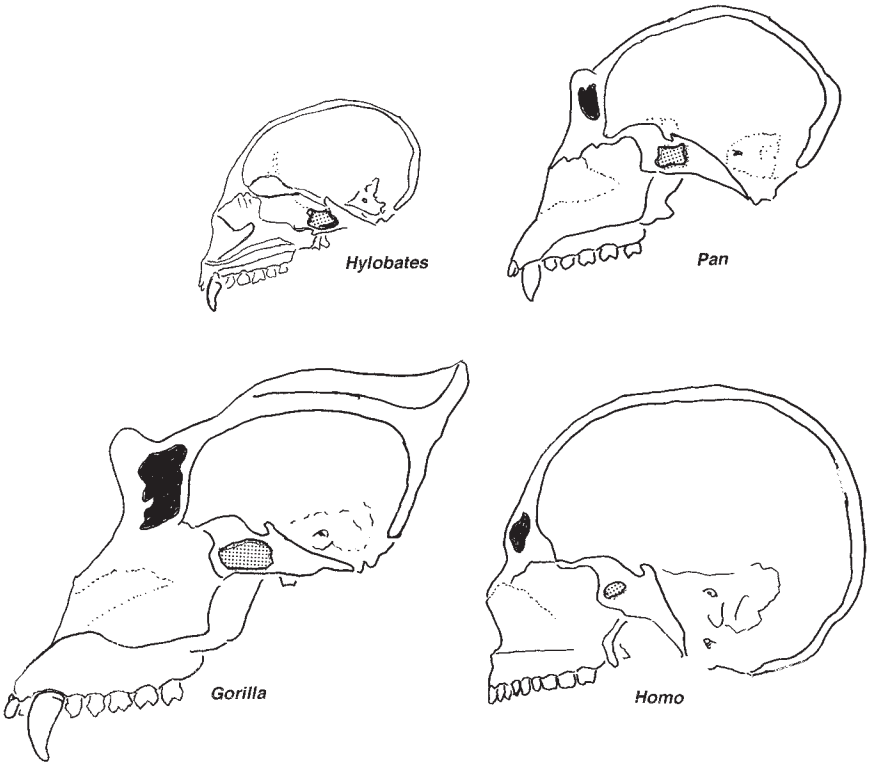


Figure 5.12 Cross-sections of hominoid primates showing sinuses. Frontal sinuses are pictured in black, and sphenoidal sinuses are shaded (adapted from 1991 British Museum of Natural History's *Guide to Man's Place in Evolution*).

under much discussion. Sinuses lighten and, at the same time, strengthen areas of thick bone within the skull.

COMPARATIVE PRIMATE SKULL MORPHOLOGY

PROSIMIAE

Lemuridae

In extant Lemuridae the skull is generally fairly elongated with a long tapering snout, shallow mandibular ramus, and complete postorbital bar. Relative to monkeys, apes, and humans, the braincase is comparatively small and positioned entirely behind the facial region. Also among these animals, the orbits are

situated back from the facial skeleton and may be directed somewhat laterally. Thus, many lemurs have skulls that are narrow and elongated. The foramen magnum at the back of the skull opens backward. The internal morphology of the lemur skull is also elongated, correlating with the overall shape; the inner cranial floor remains almost straight. This means that the anterior part of the skull base that is formed mainly by the ethmoid and the posterior portion, consisting of the sphenoid and basioccipital bone, do not form an angle. Figure 5.13 shows various morphologies of the bulla. Figure 5.14 depicts the skull base of genus *Eulemur.*

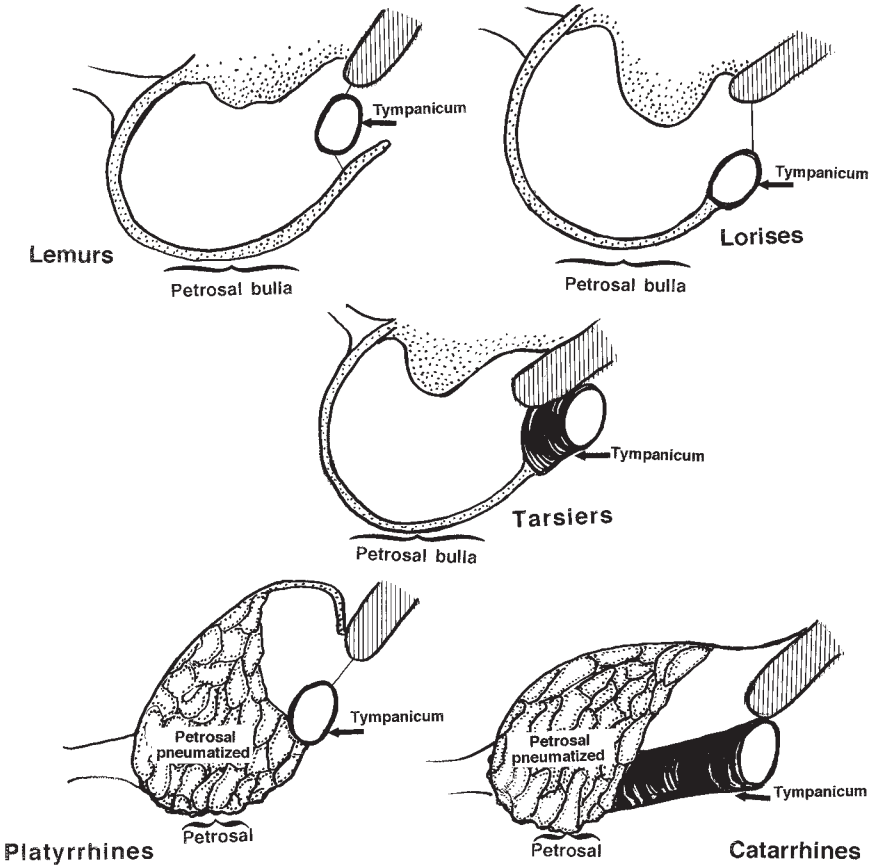


Figure 5.13 The various morphologies of the petrosal bulla and petrosal in prosimians, tarsiers, and anthropoids. Tympanic rings (black) in lemurs and lorises, external acoustic meatus in tarsiers and catarrhines, and tympanic ring in platyrrhines.

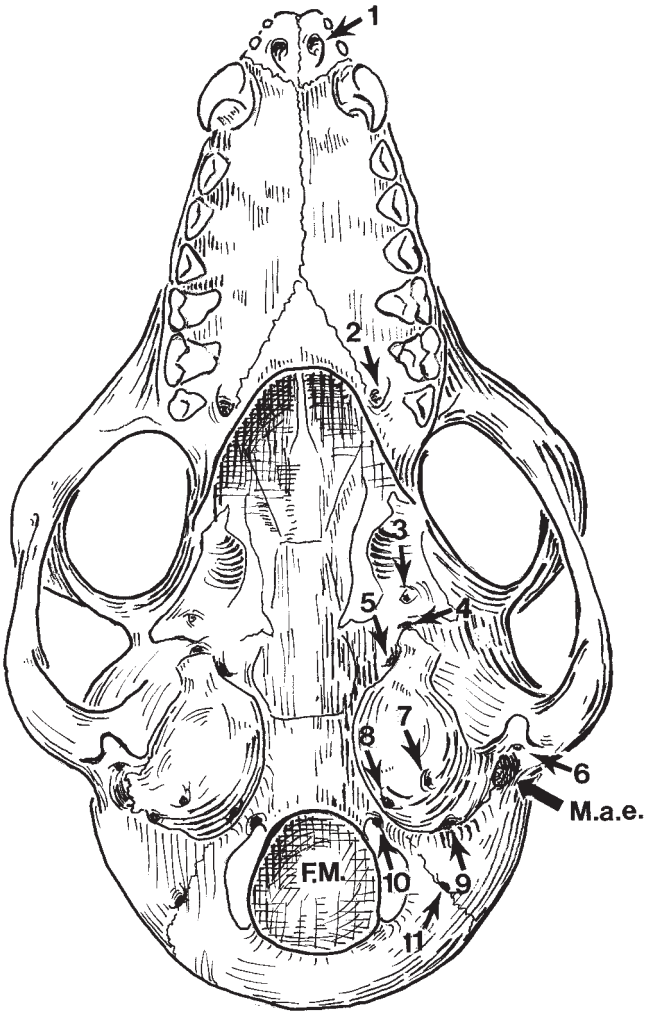


Figure 5.14 Skull base of a lemur, genus *Eulemur*, showing basicranial foramina. 1) Foramen (f.) incisivum; 2) f. palatinum majus and minus combined; 3) f. pterygoideum; 4) f. ovale; 5) tuba auditiva; 6) f. postglenoideum; 7) f. caroticum; 8) f. jugulare; 9) f. stylomastodeum; 10) f. condyloideum; 11) f. mastoideum; M.a.e. = meatus acousticus externus; F.M. = foramen magnum.

Overall skull shape among Indriidae is strikingly different from that of Lemuridae. In indriids, the skull is broader and higher compared with both height and width of the lemur skull, but the facial skeleton is still positioned in front of the braincase. The indriid snout is considerably shorter than that of lemurs, especially among species of genus *Propithecus*, but less pronounced in genus

Indri. The mandible is much deeper and more robust in Indriidae than in Lemuridae, and it is rounded in the back, extending downward, not elongated into an upward directed point. It is surprising that the shape of the *Propithecus* mandible, if seen from the side, is almost identical to that of the South American night monkey *Aotus*. Viewed from above, however, there are obvious differences between the mandibles of the sifaka *(Propithecus)* and the night monkey. The former is still V-shaped, and the symphyseal area is long and slanted anteroposteriorly. In contrast, the symphysis of *Aotus* is comparatively steep up and down and not nearly as long. The front end of the night monkeys mandible is rounded, so that the overall shape when seen from above is U-shaped. The V-shaped condition of the mandible and the mandibular tooth row is different from the maxillary arrangement of the teeth, which overlap the lower teeth outward, and the upper jaw has a more U-shaped outline when seen from below.

There is no real occlusion of the anterior dentition in most prosimians because the upper incisors are more or less reduced and the lower incisors in most cases highly specialized.

Daubentoniidae

The cranial morphology of the aye-aye, family Daubentoniidae, is highly specialized because of the relatively large brain and the reduction in number and complexity of the teeth in *Daubentonia* (Figure 5.15). Although the cheek teeth are reduced, in both number and morphological complication, the anterior teeth of the aye-aye are unique among extant prosimians: they resemble front teeth of the rodent dentition. Because the front teeth are large, curved, and prominently projecting forward in both maxilla and mandible, the snout of the aye-aye is high and narrow, giving the skull a morphology that is unlike any other lemur. Compared with other lemurs, however, the snout is short. Furthermore, the rather large orbits of this nocturnal animal cause the skull to widen abruptly behind the facial region. There are large frontal sinuses in adult specimens. The braincase is globular, and the orbits are directed somewhat sideways and upward. The foramen magnum points backward as in other lemurs. The lower angle of the oddly shaped mandible is not enlarged, having only a slight protrusion downward, and looks unlike any other primate's mandibular angle. Also, the coronoid process is comparatively low, and the articular process does not extend upward, but is directed backward and positioned lower than the mandibular molars.

Lorisidae

The skulls of Lorisidae, compared with those of other prosimians, give the impression of being dorsoventrally flat, especially in species of genera *Perodicticus* and *Nycticebus*. The interorbital distance is generally smaller in Lorisidae than

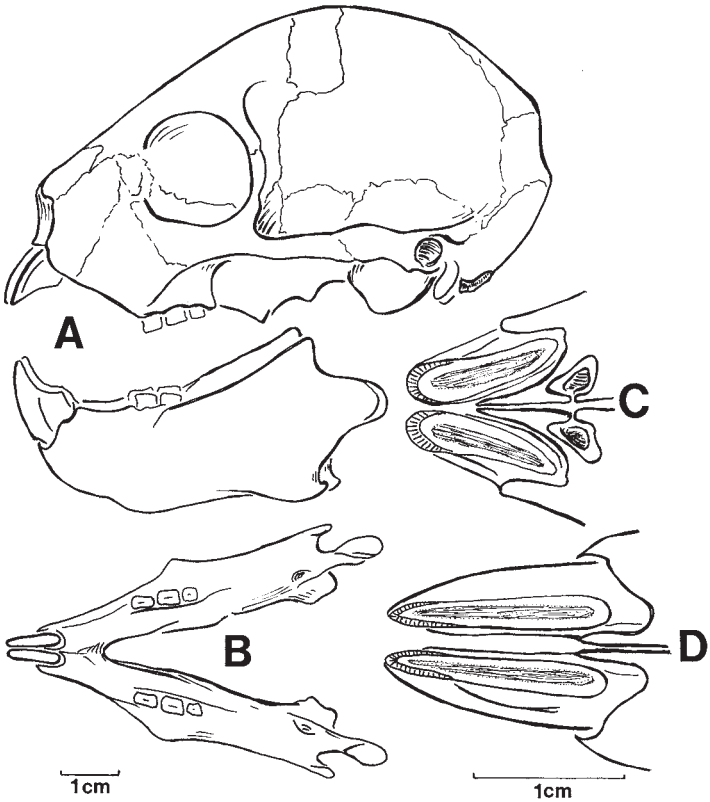


Figure 5.15 Skull and jaw of the most unusual primate, the aye-aye *(Daubentonia madagascariensis)*: A) skull and mandible seen from left side and B) occlusal view of mandible. C) Upper and D) lower incisors are pictured from below and above, respectively, showing the thick anterior enamel layer (striped).

in Malagasy Lemuridae or Indriidae. This narrowness is also seen in lorisids in the lessened postorbital breadth of the skull, or "postorbital constriction." Moreover, among lorisids the snout does not taper toward the front as much as in Lemuridae and thus gives the impression of being less long and pointed comparatively. Among lorisines, the nasal bones are flatter than in Lemuridae. A characteristic elongation of the snout beyond the front end of the tooth row is found in species of the two lorisid genera *Arctocebus* and *Loris*. This phenomenon is brought about as a result of their comparatively large premaxillae, the upper margins of which project forward. The nasal bones also enter this projection, thus forming a pipelike nasal opening. In addition, the snout is narrow in *Arctocebus* and *Loris*. In *Nycticebus*, the occipital is flattened and faces backward.

The foramen magnum opens most directly backward in *Nycticebus* of all Lorisidae. Skulls of galagids resemble those of lorisids, but slight differences can be detected. For example, with galagids the cranial vault is slightly more rounded than in Lorisidae, and the interorbital distance is somewhat wider. The postorbital constriction, however, is much more marked in Galagidae than in Lemuridae. The small lacrimal bone at the lower inside corner of the orbit extends considerably forward onto the outside of the orbital wall, and the lacrimal canal (tear duct) is positioned externally. Figure 5.16 shows the skull base of a loris genus *Perodicticus*.

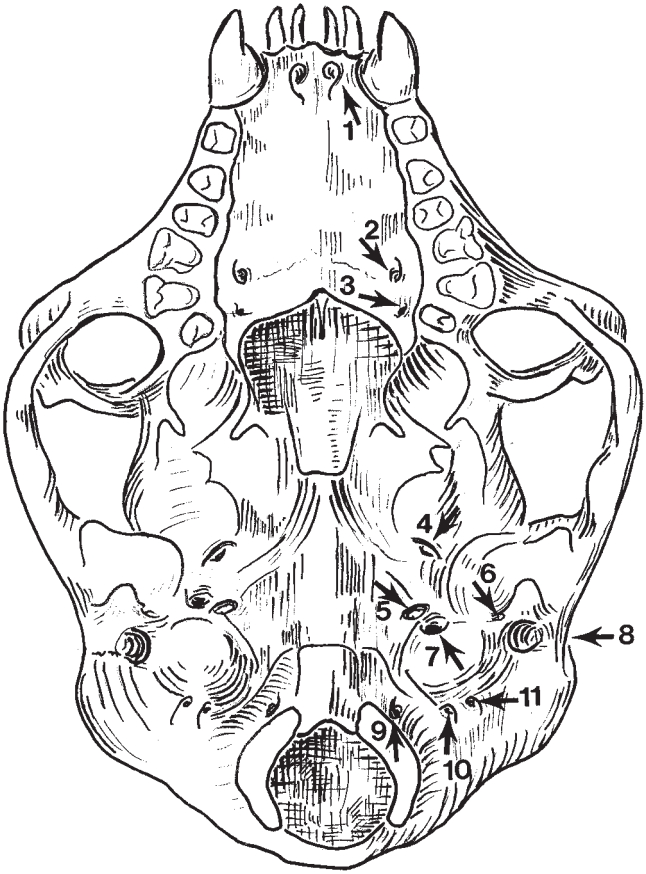


Figure 5.16 Skull base of a loris genus *Perodicticus* showing basicranial foramina. 1) Foramen incisivum; 2) f. palatinum major; 3) f. palatinum minus; 4) foramen ovale; 5) foramen lacerum; 6) f. postglenoideum; 7) Tuba auditiva; 8) Meatus acousticus externus; 9) f. condyloideum; 10) f. jugulare; 11) f. caroticum.

Tarsiidae

In *Tarsius*, the shape of the skull is dominated by the huge eyes, which dominate the morphology of the skull, just as the peculiar dentition of *Daubentonia* dominates the shape of its skull. In fact, the volume of one eyeball of *Tarsius bancanus* is nearly as big as the volume of the entire brain of these animals (Sprankel, 1965). Sprankel's measurements are as follows (comparison of brain volume versus eyeball volume of *Tarsius bancanus*):

Brain without dura	2.14 cm^3
Eyeball I	2.03 cm^3
Eyeball II	1.81 cm^3

It appears that the tarsier skull is the most globular skull of all prosimians. The braincase is almost spherical, and a short, blunt, and narrow snout adds to the overall globular appearance of the skull as a whole. As already mentioned, the huge and flaring eye sockets are only partially closed in *Tarsius*. This condition is the one exception to the rule that all prosimians have postorbital rings. Perhaps in correlation with its upright clinging and leaping habits, the foramen magnum of *Tarsius* is centrally located on the skull base. The bullae are fairly large and located near each other and close to the foramen magnum, almost in the center of the skull base.

Anthropoidea

Old and New World Monkeys

If one compares skulls of New World monkeys with those of Old World monkeys, one can see that the former usually have comparatively smaller facial skeletons than do Old World monkeys (see Figure 5.17 for a depiction of the *Macaca* skull base). There is one exception to this rule in genus *Alouatta*, the howler monkey in which the skull morphology is influenced by a substantial enlargement of the hyoid bone of the throat (Figure 5.18). The lower jaw is unusually deep, and the mandibular symphysis is steeply oblique. In the area of the braincase, the skull is flattened, and the tooth rows are tilted upward at the front, a condition that has been termed "airorrhynchie" (from the Greek: *aer*, for "air," and *rhynchos* for "snout," "trunk"), which, roughly translated, means having the snout up in the air. This condition also occurs in the skulls of old male orangutans (Hofer, 1965). In addition, the foramen magnum of howlers opens far more backward compared with any other South American primates. Unlike other platyrrhine monkeys, the posterior portion of the skull (the occipital) behind the mandibular ascending ramus is shorter in howlers than in other monkeys. The enlargement of the hyoid is much greater in male than in female howlers.

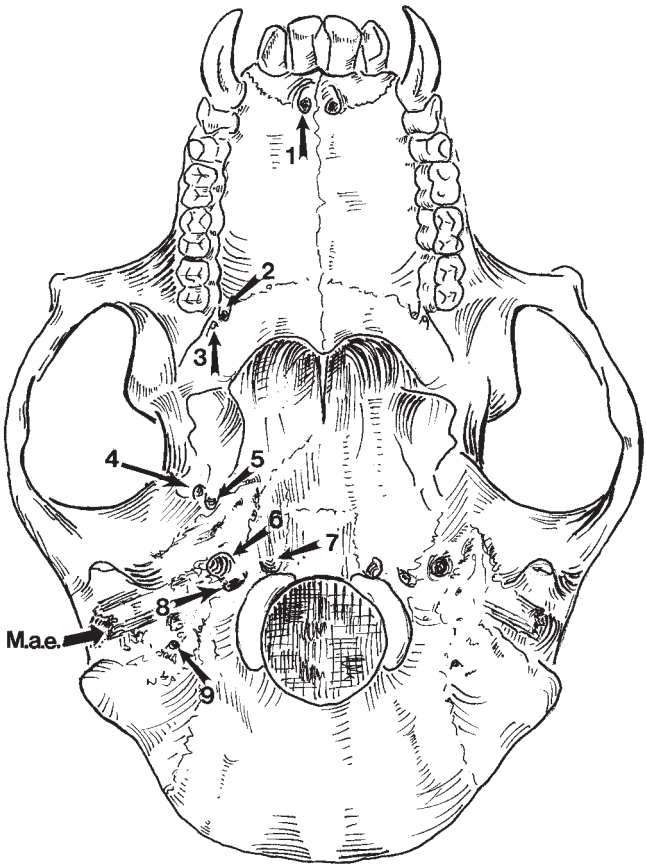


Figure 5.17 Skull base of an anthropoid genus *Macaca* showing basicranial foramina. 1) Foramen (f.) incisivum; 2) f. palatinum magnus; 3) f. palatinum minus; 4) f. pterygoideum; 5) f. ovale; 6) f. caroticum; 7) f. condyloideum; 8) f. jugulare; 9) f. stylomastoideum; M.a.e. = meatus acousticus externus.

Petrosal bones of some of the small-bodied South American monkeys have comparatively inflated, large bullae. In the temporal fossa of New World monkeys, there is usually a suture between the jugal and parietal bones, as is also frequently the case in the colobines of the Old World (Vogel, 1968).

The genus *Saimiri*, the squirrel monkey, has a rather peculiar skull. *Saimiri* is the smallest cebid monkey, and whereas the facial skeleton is comparatively small, its relatively large brain dominates conformation of the skull. The foramen magnum is shifted far forward toward the center of the skull. The occipital portion of the skull projects much further backward than in other monkeys as

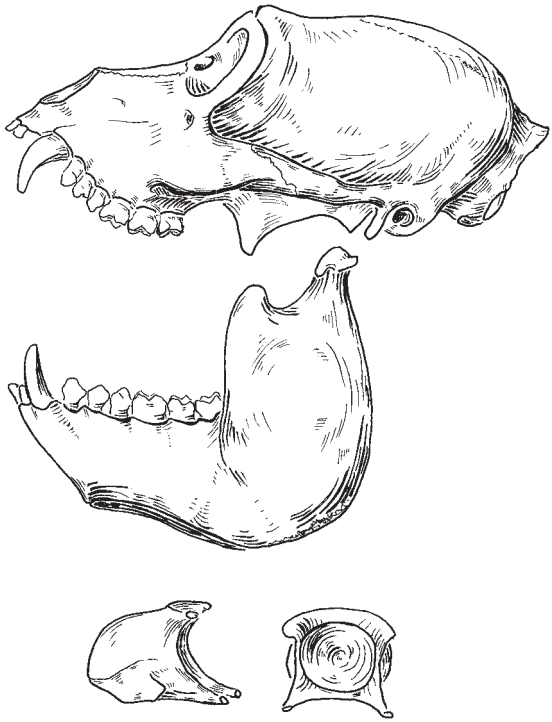


Figure 5.18 Skull, mandible, and inflated hyoid of a male howler monkey, genus *Alouatta*. Hyoid seen from left side and from posterior.

well, and consequently the foramen projects straight downward. The result of this combination of features is that the foramen magnum is situated relatively farther forward toward the front of the skull compared even with humans. In humans, the central position of the foramen magnum can be explained in part by their unique bipedal, upright locomotion. This is not so in the *Samiri*, a quadrupedal runner (Biegert, 1963).

Here we have a perfect example of two similar morphological traits that have arisen for very different reasons in these two types of primates. Additionally, the likeness of the position of the foramen magnum in *Tarsius*, *Saimiri*, and *Homo sapiens* shows that the central position need not, as was once thought, be an indicator of upright walking or even of vertical clinging and leaping.

In *Saimiri*, the comparatively large size of the brain is partly related to the fact that *Saimiri* is the smallest cebid monkey and that its brain is relatively complex. The squirrel monkey's brain, like that of all the Cebidae, is more derived than that of marmosets or tamarins, the other South American monkeys,

which are of similar body size to *Saimiri*. Although squirrel monkeys have large brains, the size of the masticatory and olfactory apparatus of these small monkeys is unusually small, even in direct proportionality to the larger cebids. Thus, the unique skull morphology of squirrel monkeys appears to be a compromise between a small facial skeleton and a relatively large braincase.

There is another unique feature of the *Saimiri* skull: all squirrel monkeys have a comparatively large hole in the bony intraorbital (ethmoid) wall (Maier, 1980). This hole usually measures more than 1.5 cm in diameter and cannot be found in any other primate. As yet, there is no clear understanding of this structure, but its presence in a late Oligocene fossil ceboid, *Dolichopithecus*, makes it of ancient origin. The hole certainly cannot be a response to eye size, because squirrel monkeys are diurnal primates and do not have enlarged eyeballs. In contrast, in the night monkey *Aotus*, with its enlarged eyes, the hole does not occur. Correlated with this feature of *Saimiri*, the interorbital breadth is much reduced.

Compared with braincase size, the facial part of the skull, is larger in catarrhines than in platyrrhines. Among the catarrhines, the snout is frequently long and prominent, a feature that is especially marked in those forms—such as the baboons and great apes—that are comparatively large. In the case of these primates, the prominent anterior part of the skull, also called the snout or rostrum, is not enlarged in correlation with the expanded olfactory region and sense of smell as it is, for example, in the dog family. Rather, its size seems to be related to the large masticatory apparatus typical of the Pongidae. In the case of the Cercopithecidae, large snouts have been correlated with both the enormously enlarged canines and the lengthened tooth row and associated chewing musculature in baboons (genera *Papio, Madrillus*, and *Theropithecus;* see Figure 5.19).

Napier and Napier (1967) called the long snout in Malagasy lemur genera and the tree shrews such as *Tupaia* an "olfactory snout"; in contrast, they called the long snout in baboons and pongids a "dental snout." Among the great apes, the "dental snout" is relatively large compared with their brain size. This phenomenon is partly the result of their allometric increase in body size relative to their ancestors. With increasing overall body bulk, the masticatory apparatus also increases, but the proportionate size of the brain does not increase at the same rate (Biegert, 1963; Martin, 1990).

Among Old World higher primates, the petrosal is not expanded into a balloon-like protrusion as it is among Prosimii and New World primates. Laterally, the petrosal of Old World monkeys is fused with the tympanic, or ectotympanic (*ecto* is Greek for "outside") bone, as a tube extending sideways in all Old World higher primates from the middle ear region toward the external ear opening at the lateral outside of the skull. It forms the external auditory meatus, a bony structure in catarrhine primates that, in contrast, consists of unossified cartilaginous material in platyrrhine monkeys (Figure 5.20; see Figure 5.13).

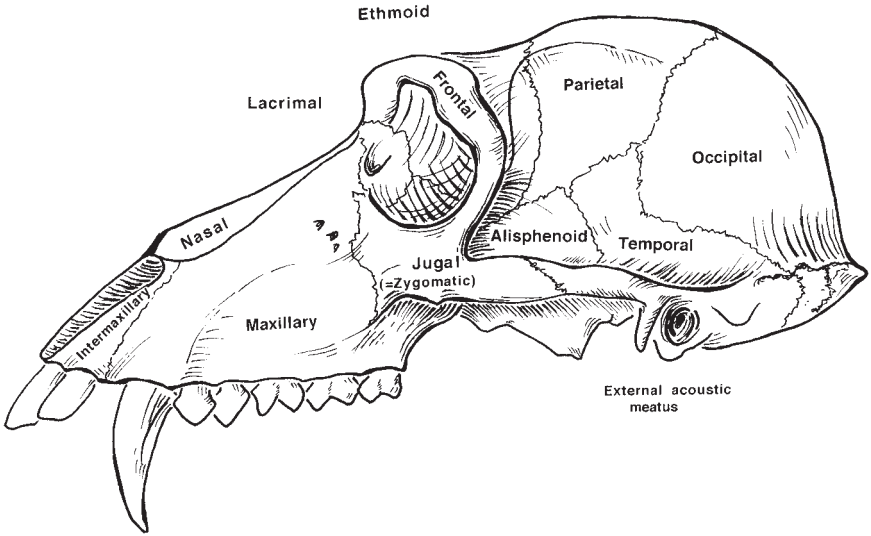


Figure 5.19 Side view of the skull of a baboon genus *Papio* showing the various bones.

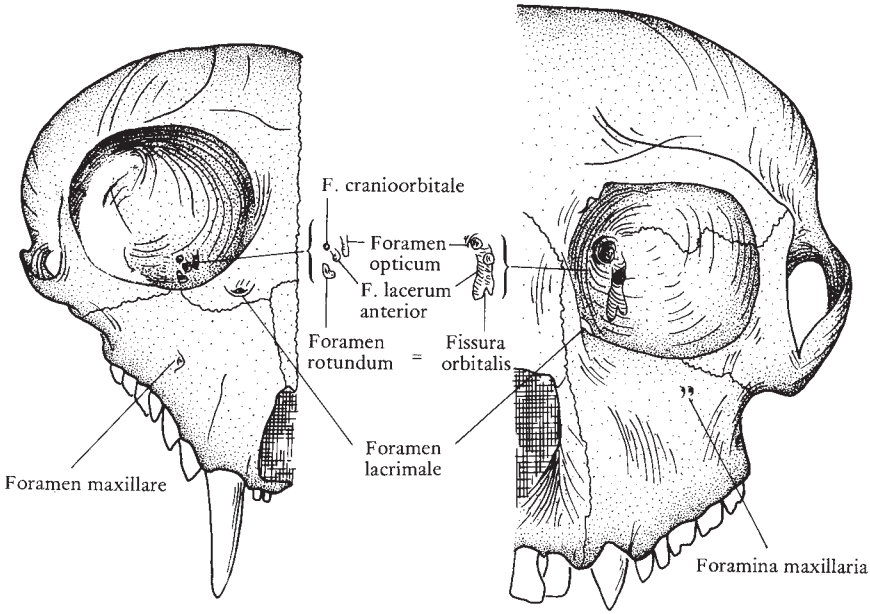


Figure 5.20 Frontal view of the skull of a lemur genus *Eulemur* (left) and an anthropoid monkey genus *Macaca* (right) showing foramina of the orbit and face.

The position of the lacrimal bone varies among Anthropoidea. In the cercopithecine monkeys, the lacrimal bone encloses entirely the opening of the tear duct (also called fossa lacrimalis). This opening is the drainage canal for the tear gland, which is located above and lateral to the outside of the eyeball. A different arrangement of bones around the tear ducts occurs in platyrrhines and among catarrhines in both Colobinae and Hominoidea, in which the maxillary and the lacrimal bones enclose the fossa lacrimalis equally on its two sides. In species of *Cebus, Macaca*, and *Papio*, the lacrimal bone usually extends outside beyond the bony orbital margin, but in the other higher primates, it remains inside the orbital wall. As mentioned earlier, almost all prosimian primates contrast with Anthropoidea in that the lacrimal fossa is situated outside the orbital wall, and the lacrimal bone containing it extends out over the orbital rim onto the face.

Lateral to and behind the orbital region lies the temporal fossa, where the relationships of contact between adjacent bones varies among Old World monkeys. Here in Cercopithecinae, one usually finds that the frontal bone meets the temporal bone in a suture common to both (Figure 5.21). In contrast, among Colobinae, the

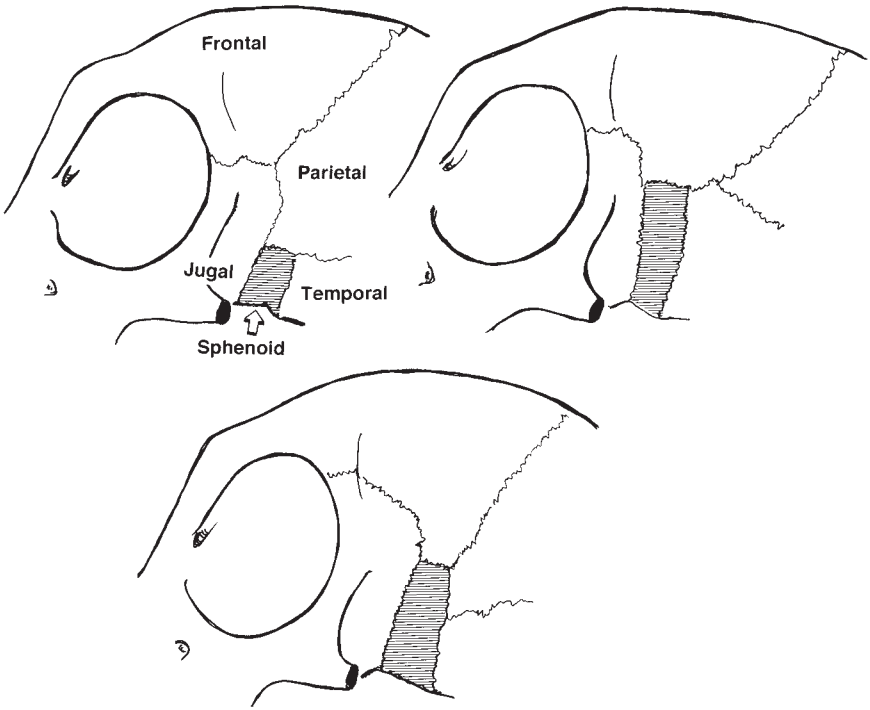


Figure 5.21 The possible arrangements and variations of bone sutures in the temporal groove among Cercopithecinae (alisphenoid is striped).

most common arrangement of the bones in the temporal fossa is that in which the frontal bone is separated from the temporal because the zygomatic or jugal and the parietal that have sutural contact, keeping apart the frontal and temporal bones. Such contacts of the bones that form the braincase in the temporal fossa thus typify the two Old World monkey families, but sometimes these relationships vary for particular groups and even between individuals.

Lesser and Great Apes

At first glance, one can see that the facial part of the skull of the lesser apes is comparatively small, and the overall shape of the skull is dominated by the large braincase. In addition, the orbital openings of both the lesser and great apes are comparatively large and typically larger than in Old World monkeys. In the skull of the lesser apes, there are strongly developed vertical ridges under the eye openings at both sides of the nasal aperture called the canine pillars. These prominent ridges are formed around the roots of the large canines that are of equal size in both sexes of lesser apes. Behind these ridges, the maxillary bone is deeply depressed inward to form the fossa canina (canine fossa or groove). The mandible is comparatively slender and shallow in lesser apes, and the ascending branches or rami of those mandibles do not rise very high. In species of both *Hylobates* and *Symphalangus*, the supraorbital tori, also known as brow ridges, that are so characteristic of great apes are not expressed.

In species of the two African genera of great apes, *Pan* and *Gorilla*, the orbits are also comparatively large and overhung by massive supraorbital tori. Posterior to this bony torus, the skull is usually constricted from side to side. Orbital size is comparatively somewhat smaller in genus *Gorilla* than in the other two great ape genera. In the Asian genus *Pongo*, the orangutan, the brow ridges are either missing or only weakly developed. In contrast to chimpanzees, in which the sexes are almost equally large, sexual size disparity is striking in the skulls of gorillas and orangutans. These differences in cranial dimensions are related to the differences in body size between males and females. In adult males of the latter two genera, the skulls have distinctive sagittal and occipital bone crests. The height of the sagittal skull crest is correlated with the bulk of the temporal chewing muscle, and the extension of the occipital crest enlarges the insertion area for the neck musculature of these large animals. The size of both these bony crests has an allometrically positive correlation with their body size. Such crests, for example, are not found among primates of small body size that have relatively large brains such as the talapoin monkey (*Miopithecus talapoin*, the smallest cercopithecoid monkey) or the squirrel monkey (*Saimiri*, the smallest of ceboid monkeys). The same is true for lesser apes. In all these animals, the braincase is large and the area of the flat bones that make up the cranial vault have sufficient surface area to accommodate insertion of the masticatory muscles without building up an additional attachment area at the midline.

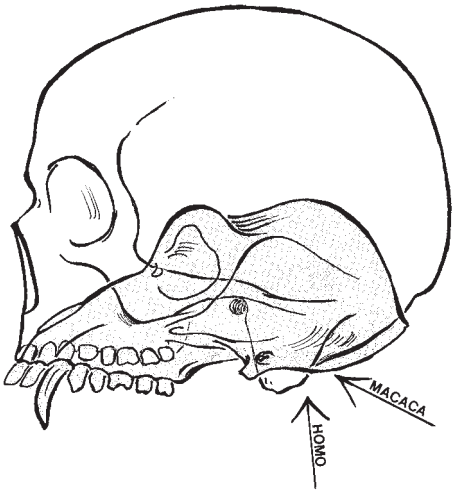
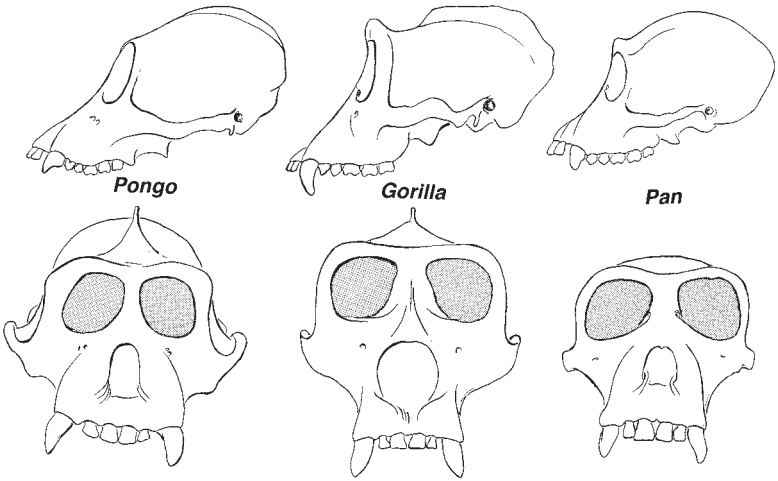


Figure 5.22 Human and macaque (shaded) skulls are superimposed to show the morphological differences between the two.

A series of studies have shown that skull crests in primates are caused by topographical and functional requirements (Vogel, 1962; Hofer, 1965). Sometimes, but very rarely, cranial crests are found in exceptionally robust female gorillas and orangutans. Crests have also occasionally been found in large and aged chimpanzees as well as some monkeys, especially in the genera *Cebus* or *Colobus*.

For means of comparison among primates, Figures 5.22 and 5.23A, B, and C are included here.



A

Figure 5.23 A) Comparison of the skulls of the three great apes brought to approximately the same size. Lateral view (above) and frontal view (below).

(Continues)

B

Figure 5.23 *Continued* B) Right side view and C) top view of adult male *Pan* (top), *Gorilla* (center), and *Pongo* (bottom) to show the different overall shape (not to scale).

C

Figure 5.23 *Continued*

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Chapter 6

Brain

Brain Morphology
Tupaiidae
Lemuridae and Lorisidae
Tarsiidae
Anthropoidea
Gene Expression
New Insights into Brain Function

What is it that really makes us human? Among primates it is the human brain that appears to be the most highly developed; however, dolphins also have very elaborate and capable brains and have not dominated the world like humans have. Dolphins, however, are restricted to their environment: the sea. They don't have hands, two factors that have constrained their evolutionary path. It is apparent that the human brain is comparatively the largest primate brain. (Table 6.1 shows primate brain progression indices.) Primates generally have larger and more refined brains than other mammals do, but humans have surpassed them all. (See also Table 6.2 documenting cranial capacities of representative primates.)

By and large, all primates remained generalized in their postcranial organization. This becomes most obviously apparent if the trends that govern this order are compared with those of other groups of mammals such as ungulates. Thus, it seems that primates display the unique combination of an unspecialized postcranial morphology together with an increasingly refined central nervous system. There can be no doubt that one representative of the order Primates, *Homo sapiens*, our own species, is distinct from other mammalian groups because of its unique progressive development of the brain in combination with such features as hands freed from locomotion and a vocal ability that allows speech, as in language, writing, reading, composing and so much more. Figure 6.1 provides a comparison of various primate brains.

Table 6.1
Progression Indices of Primate Brains

Basal insectivore	1
Lemuridae	17.5–23.2
Hapalemur	10.0–12.0
Lepilemur	10.0–12.0
*Tarsius**	21.5
Callitrichidae	26.3–29.5
Alouatta	20.8
*Aotus**	34
Cebus	60
Colobidae	40
Cercopithecus	55
Macaca	75
Pan	84
Homo	214

Data from Stephan (1969).
*Large because of the highly developed geniculate body, optical tectum, and visual cortex.

Many new ways to explore the powers of the primate brain have been discovered, and new insights have been gained. New dimensions of studying the primate brain's capacities have been added by exploring the human brain. Capabilities such as perceptual and cognitive processes have aimed the focus on the function and origin of brain laterality: the fact that important functions are predominantly executed in only one of the brain's hemispheres. Anatomical and functional lateralization, first documented in humans, has now also been shown for birds, rodents, and nonhuman primates (Vallortigara et al., 1999; Vauclair et al., 1999, 2006). This issue has been the focal point of an enormous body of evidence in scientific publications and books (Rogers and Andrew, 2002). It is now known that brain lateralization is also well established in genus *Macaca* but appears to be most elaborate in humans. The fact that lateralization is established in nonhuman primates seems to indicate that this neurological arrangement was present early in primate evolution. In humans, the understanding of time, language skills, and even some well-described psychiatric disorders are located in the left hemisphere, whereas visual, spatial, musical, and mathematical abilities; holistic thought processes; emotions; and certain benign psychiatric qualities have been assigned to the right hemisphere (Falk, 1987).

Very different levels of brain conformation are found among the range of primates, varying from the simplest prosimian type of organization through that of monkeys and apes to a culmination in the great complexity seen in the brain of modern humans. This is the case despite the fact that the solution of

Table 6.2
Cranial Capacities

	Body weight	Cranial capacity	Relative cranial capacity
Tree Shrews			
Tupaia glis	150	3.4	3.5
Lemurs			
Microcebus murinus	60	1.8	3.4
Mirza coquereli	385	5.8	3.1
Cheirogaleus medius	178	2.6	2.4
Cheirogaleus major	403	5.6	2.9
Phaner furcifer	440	6.7	3.3
Lepilemur mustelinus	630	8.1	3.1
Eulemur mongoz	1669	23.0	4.5
Varecia variegata	3388	31.8	3.9
Avahi laniger	1071	9.8	2.6
Propithecus verreauxi	3384	30.6	3.7
Indri indri	6250	33.4	2.7
Hapalemur griseus	830	14.6	4.6
Daubentonia madagascariensis	2800	45.2	6.3
Lorises			
Galago demidovii	63	2.6	4.8
Galago senegalensis	229	3.7	2.8
Galago alleni	246	3.7	2.7
Galago crassicaudatus	1340	10.2	2.3
Euoticus elegantulus	287	5.1	3.3
Arctocebus calabarensis	203	7.6	6.3
Perodicticus potto	1053	13.1	3.5
Nycticebus coucang	1110	11.9	3.1
Loris tardigradus	271	6.4	4.4
Tarsiers			
Tarsius	112	3.0	3.7
New world monkeys			
Aotus trivirgatus	985	16.9	4.8
Callicebus moloch	1078	18.3	4.9
Saimiri sciureus	914	23.6	7.0
Cebus apella	2437	76.2	11.7
Ateles species	8200	108.8	7.3
Lagothix lagotricha	6248	97.2	7.8
Alouatta seniculus	6556	60.3	4.7
Callimico goeldii	471	11.1	5.2
Cebuella pygmaea	72	6.1	10.2
Callithrix jacchus	203	7.2	6.0
Saguinus species	534	9.9	4.3

(Continues)

Table 6.2 *(Continued)*

	Body weight	Cranial capacity	Relative cranial capacity
Old world monkeys			
Miopithecus talapoin	1250	39.0	9.4
Cercopithecus ascanias	3605	63.4	7.4
Cercocebus albigena	7758	96.9	6.7
Macaca mulatta	4600	83.0	8.2
Papio anubis	16,650	177.0	7.3
Theropithecus gelada	21,500	133.0	4.6
Colobus badius	8617	61.6	4.0
Lesser and great apes and humans			
Hylobates lar	5442	99.9	8.8
Symphalangus syndactylus	10,725	123.7	6.9
Pongo pygmaeus	55,000	418.0	7.7
Pan troglodytes	45,290	393.0	8.2
Gorilla gorilla	1,114,450	465.0	5.2
Homo sapiens	65,000	1409.0	23.0

Adapted from Martin (1990).

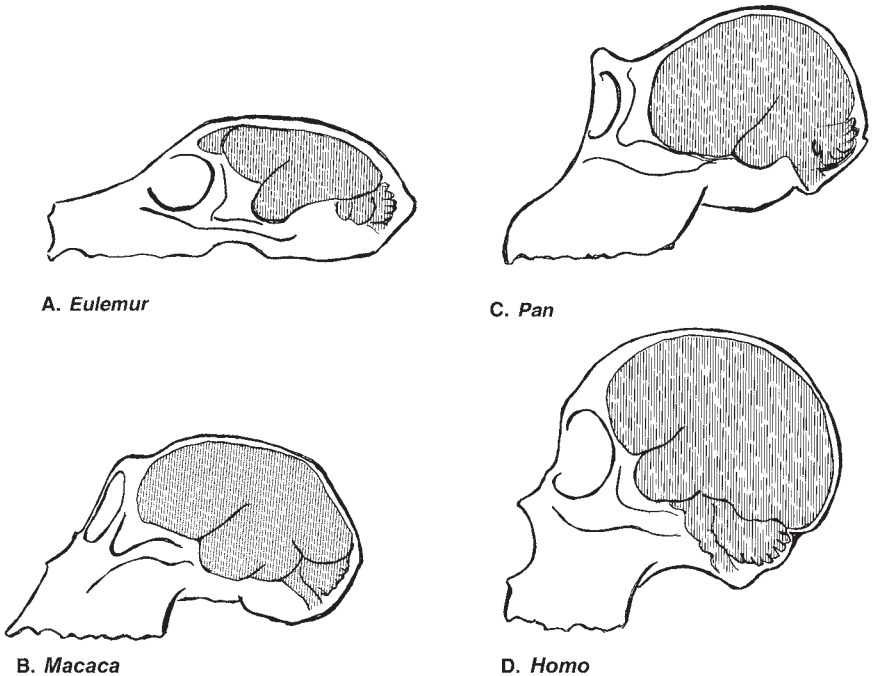

Figure 6.1 Sagittal cut through the skulls of A) a prosimian; B) an anthropoid; C) a pongid; and D) a human (all brought to approximately the same length) showing brain size (shaded).

the question why the human neocortex is comparatively much larger than are those of nonhuman primates has been elusive. For example, the maternal metabolic capacity hypothesis has been proposed by Martin (1996). Here it is assumed that brain size is directly related to maternal investment and the duration and placental intimacy of gestation. Various other hypotheses have been brought forward and discussed in the attempt to understand the question of why and how the primate brain has evolved to be relatively larger than those of any other terrestrial mammals (Falk and Gibson, 2001; Finlay et al., 2001). This enlargement, however, applies mainly to the neocortical areas. Even though there are still no definite answers to the open questions when we attempt to relate human mental capacity such as cognitive abilities (e.g., quantitative thinking) to single neural mechanisms (Preuss, 2001). The human brain is much more complex than a simply supersized monkey or ape brain would be (Changeux, 2005).

Generations of scientists have tried to propose valid hypotheses and theories to explain why and how the human brain has such an extraordinarily large neocortex. Primate neocortex size has been compared with the size of other parts of the brain, for example, the medulla, the cerebellum, or the diameter of the foramen magnum, to overall body size or size exemplified by the dimensions of molar teeth, gestation length, maternal investment, the correlation of fetal head to maternal pelvis dimensions, the developmental timing, neoteny, retardation of postnatal body growth, expensive tissue hypothesis, gut size, the "radiator theory," mating systems, group size, foraging methods and diet, social behavior, and ecological factors. In most cases the authors of such ideas have to refine their discoveries with various exemptions from the proposed rule (Jerison, 1973; Falk, 1986; Shea, 1989; Aiello and Wheeler, 1997; Rice, 1997, 2002; Dunbar, 1993, 1998, 2002; Rilling and Insel, 1998; Vrba, 1998; Kudo and Dunbar, 2003; Fish and Lockwood, 2003; Vinicius, 2005). Some of these hypotheses, such as the expensive tissue hypothesis or the radiator theory need to be valiantly defended (Aiello et al., 2001; Falk, 1990a, 1990b). The great cost involved in having a human-sized brain has been correlated with improved nutrition during the course of human evolution. The reduction of functional muscle tissue versus the increase of body fat has been assumed to be vital for brain development in human infants (Leonard et al., 2003) and brain maintenance among adults. The beginning of a change in body composition in tandem with crucial improvements in the quality of the human diet are historically equated with the emergence of large human brains.

Most of the time, these scenarios are only explored within the primate order, and phenomena such as the equally large neocortex of dolphins are not comparatively considered. Some of these size-related hypotheses might report some truth, but none is likely to stand alone as a quid pro quo situation in which a simple cause-and-effect scenario is presented. These hypotheses often are

convincing at first glance; however, after closer contemplation, it is not the size of the brain but its intricate cellular and electric circuit system and the way brain functions are genetically encoded in each organism that are most important. Although size does matter to some extent, it is not the singular cause giving rise to the developmental and evolutionary increase of neocortex size in tandem with increasingly complex brain function among primates (see Table 6.1). It is function that is crucial (Holloway, 1966; Gould, 2001; Preuss, 2001).

The following trends generally characterize the primate brain: 1) increase in the size of the neoencephalon (*neos* is Greek for "new," and *enkephalon* means "brain") or neocortex (*cortex*, *cortices* is Latin for "bark," "rind"), 2) the phylogenetically new and young parts of the brain cortex, 3) increasing dominance of the optical system, which was initiated early on, presumably as a prosimian adaptation to living in an arboreal environment—the visual system has become highly developed, attaining the ability to evaluate accurately the scope of three-dimensional space (stereoscopic vision, from *stereos*, Greek for three-dimensional)—4) and increasing sensitivity of the tactile pads on hands and feet, and in some South American monkeys, the motor and sensory augmentation of the fifth limb—the useful prehensile tail. Another trend is the alleged relative decrease of olfaction and taste, two senses that are intimately connected to each other.

This postulated decline in the senses of taste and smell has often been accepted as almost a platitude for the primates. The simple conjecture being that the general trend of size reduction of the nasal region and snout length, as well as the increase of the importance of eyesight in primates, the senses of taste and smell had to have been greatly reduced or lost. It is difficult to test the ability of smell in animals. Recent studies of the tasting abilities among living primates have shown that these senses vary widely among primates (Glaser et al., 1995). Thus, it is now possible to compare the sense of taste of many primates and to contrast it with that of nonprimates. From his new evidence it seems that statements about the increasing reduction of olfaction and taste within the more advanced primates have been uncritically accepted and are not totally substantiated. The fact that the relative size of the olfactory bulb is reduced in higher primates has been well documented, however (Stephan, 1972; Martin, 1990).

Within the order Primates we can recognize trends toward an increase of the relative and the absolute volume of the brain (Falk and Gibson, 2001). But when considering brain volume, we must keep in mind that brain size is correlated to body size. Also, sexual dimorphism of brain size has been documented for many mammals. The functional meaning of these differences is, however, rather obscure (Holloway, 1996; Cahill, 2006). Furthermore, brain volume is only a crude measure of the evolutionary level of intelligence and achievement of an animal or species. To regard brain volume as an indicator of cerebralization or, to express this differently, as a measure of the degree of evolutionary development

of the brains—even within quite specific groups of animals—is an erroneous or, at best, a superficial measure (Gould, 1975; Holloway, 1996; Starck, 1965, 1995). Students of brain evolution have pointed out repeatedly the usefulness and the limitations of cranial capacity estimates (see, e.g., Edinger, 1961; Holloway, 1972, Starck, 1965; Hofer, 1972; Radinsky, 1972; Martin, 1990; Finlay et al., 2001, to mention only a few). Even if brains of different but related genera are equal-sized and look similar macroscopically, they can differ considerably in the architecture of their functional internal configuration (Cahill, 2006). Brains are highly complex organs, composed of parts that are histologically different and that develop at varying growth rates. Only the cytoarchitecture (histology or cell and tissue structure: *histos* is Greek for "tissue"), electrophysiological mapping of brains, and, more recently, the noninvasive techniques of functional magnetic resonance imaging (fMRI) or positron emission topography (PET) can tell us about function of particular brain regions and consequently about degree of functional ability and development (Starck, 1965; Holloway, 1996; Dehaene et al., 2005). Macroscopic comparison of brains can only give valid information about relative degrees of neurological development within taxonomic closely related groups (see Table 6.2).

Body-to-brain size ratios are surprisingly similar in closely related groups of mammals. Stephan (1972) and Stephan et al. (1981) contrasted functionally various parts of primate brains to the equivalent areas among those of basal insectivores. He took for his basal group only such insectivores that, in terms of their brains, are comparatively underived according to him (Stephan, 1972). Thus, he only used animals such as the shrew *(Sorex)* and the European hedgehog *(Erinaceus europaeus)*, animals with brains that can be regarded as useful basic models for comparison with primate brains. The basal lipotyphlan terrestrial insectivores have served him as models for the definition of specializations in primate brains. These insectivores are accepted as the most primitive extant placental mammals (Martin, 1990). Contrasting the primates—with the exception of humans—to other groups of mammals made it possible to show that a high degree of encephalization—that is, absolute brain size—is not an exclusive characteristic of nonhuman primates because it is exceeded by that of some of the immature Odontoceti (toothed whales), dolphins, and elephants (Marino, 1996; Kaskan and Finlay, 2001). Marino showed that the closest ape relative of humans, the chimpanzee, is not nearly as "brainy" (measured in encephalization quotients, or EQ) as several dolphin species. But what good does it do to have a highly evolved brain when living submerged in the sea without any capable hands? It turns out the neocortical neuron organization differs markedly between humans and dolphins, yet high EQs of both are said to be correlated with complex social group behaviors.

The trend toward high elaboration and development of the central nervous system, especially of the cerebral cortex and its end organs, is a

striking characteristic common to all primate groups (Armstrong, 1985; Jerison, 1973).

We have seen that comparison of brain volume has to be restricted to taxonomically closely related groups that are adaptively similar. If closely related genera show divergent adaptations, the results may be distorted. For example, comparison of relative neocortex size in two prosimians with similar body weight, *Tarsius* and *Microcebus* would generate misleading results. Although their brains are equal in size, *Tarsius* would rank considerably higher in such a comparative measure than would *Microcebus*. This result arises not from an overall higher development of the neocortex of *Tarsius*. It is the outcome of the fact that the optical system (occipital lobe) of *Tarsius* is notably enlarged in accordance with its unique nocturnal and insectivorous feeding habits (Starck, 1995). It also has to be kept in mind that the brain cannot really be regarded as a single evolutionary or functionally homogenous entity similar to other organs such as the liver or spleen. The brain is differentiated into parts that have the functional value of partially separate organs of varied structure and function. These different parts of the macroscopic entity known as the brain can evolve at quite different rates and independently from each other (Armstrong, 1990; Armstrong and Falk, 1982; Holloway, 1996). Nevertheless, we know that these functionally different structures of the brain are often intrinsically interwoven. The nervous system's ability to process information depends on the efficiency with which stimuli can be transferred to the main information center, the brain. The transmission of nerve impulses is complicated and involves four kinds of receptors that are identical for both smell and taste (chemical receptors). Transfer of information between neurons occurs with the help of electrochemical impulses (Kleinsmith and Kish, 1995). Increasingly better understanding of these complicated processes shows that taste and olfactory abilities of animals depend on the intricate efficiency of the neural system, not its size.

BRAIN MORPHOLOGY

The brain is enveloped by the skull's braincase. Five major parts can be distinguished in the brain's gross morphology. These subdivisions develop from three vesicles in the very early embryo (Greek *embryon* meaning "offspring"):

1. the prosencephalon or forebrain (*pros* is Greek for "front end"; *kephale* for "head"),
2. the mesencephalon or midbrain (*mesos* Greek for "middle"), and
3. the rhombencephalon or hindbrain.

These three vesicles soon give rise to two additional buds: 1) the prosencephalon subdivides into the telencephalon (cerebrum, endbrain) and diencephalon

(between brain), 2) the mesencephalon remains unchanged, and 3) the rhombencephalon proliferates into the metencephalon and myelencephalon (medulla oblongata; *myelos* is Greek for "marrow" or "brain").

These five vesicles of very early ontogeny correspond to the five major subdivisions of the adult mammal brain (Figure 6.2). The cavities of these vesicles of the early brain buds develop into the ventricles (fluid-filled spaces) within the adult brain (Figure 6.3).

The most caudal (posterior) portion of the hindbrain, the myelencephalon, is also called the medulla oblongata (*medulla* is Latin for "marrow," or "innermost," *oblongata* means "elongated") (Figure 6.4). The medulla is the brain region that connects to the spinal cord. The cranial portion of the hindbrain, the metencephalon, in turn is subdivided into two distinguishable parts, the cerebellum and the pons (*cerebellum* is Latin for "little brain," "pons" for "bridge"). Cranial nerves VII through XII originate from the medulla oblongata. Many sensory and motor tracts pass through this region connecting the higher centers of the brain. Cranial nerves V and VI originate from the pons. Many of these nervous pathways function as projecting tracts crossing over from one side of the medulla to the other. Also many centers of the autonomic nervous system are located here, for example, cranial nerve X—Nervus vagus (*vagus* is Latin for "prowl," "wander")—which meanders through the body to serve many of the major organs, reaching down as far as the colon.

The pons is positioned on the floor of the brain in front of the medulla and is attached to the overlying cerebellum by means of three nerve trunks on each side. The nuclei pontis (*nucleus* is Latin for "kernel") are major relay stations that transfer impulses from the cerebral cortex to the cerebellum.

The mesencephalon or midbrain is situated between the diencephalon and the pons, and the only parts of it that are visible from the base of the brain in higher primates are the cerebral peduncles (diminutive to *pes, pedis* Latin for "stalk"). In the center of the midbrain, the cerebral aqueduct passes through the mesencephalon and connects with the third and fourth ventricles (compare Figure 6.3). Lateral to the peduncles is cranial nerve IV, and between them is cranial nerve III. The peduncles consist mainly of motor fibers descending from the cerebrum. Ascending sensory fibers passing to the thalamus (*thalamos* is Greek for layer) lie deep to the peduncles. On the dorsal surface of the midbrain, the tectum (*tectum* is Latin for "roof") is composed of four rounded bumps, the corpora quadrigemina (*corpus* is Latin for "body;" *quadra* for "four;" and *geminus* is "twin," "double," "twofold") are located. This part of the brain contains the stratum opticum. The medial and lateral geniculate bodies that are part of the diencephalon (thalamus) are situated on the sides of the mesencephalon. In the diencephalon, the substructure shows a sequence of different layers in various extant primates (see also Martin, 1990). Anthropoid primates and tarsiers usually have four layers, two large-celled layers situated close to the optical tract

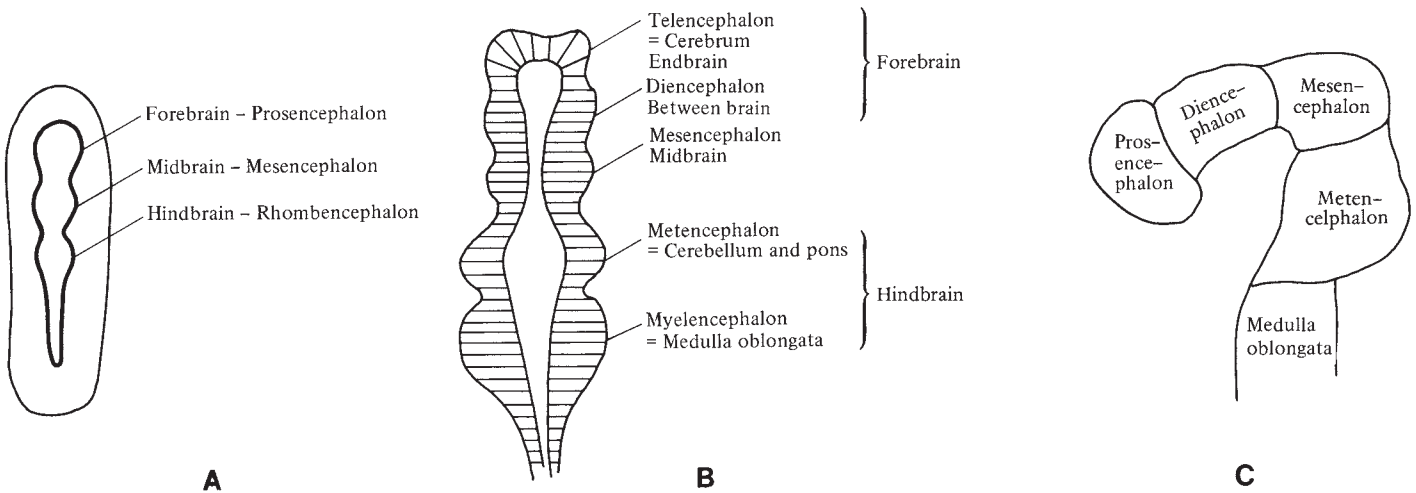

Figure 6.2 Diagram of the early ontogenetic development of the brain. A) Three-vesicle stage; B) five-vesicle stage; and C) five-vesicle stage, sideview.

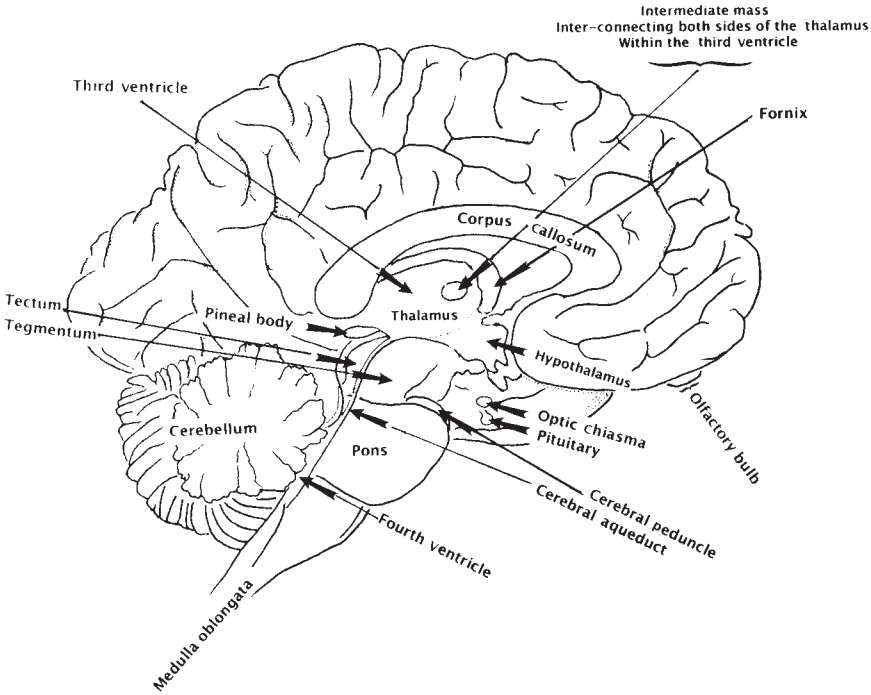

Figure 6.3 Sagittal cut through the human brain showing the position of the vesicles.

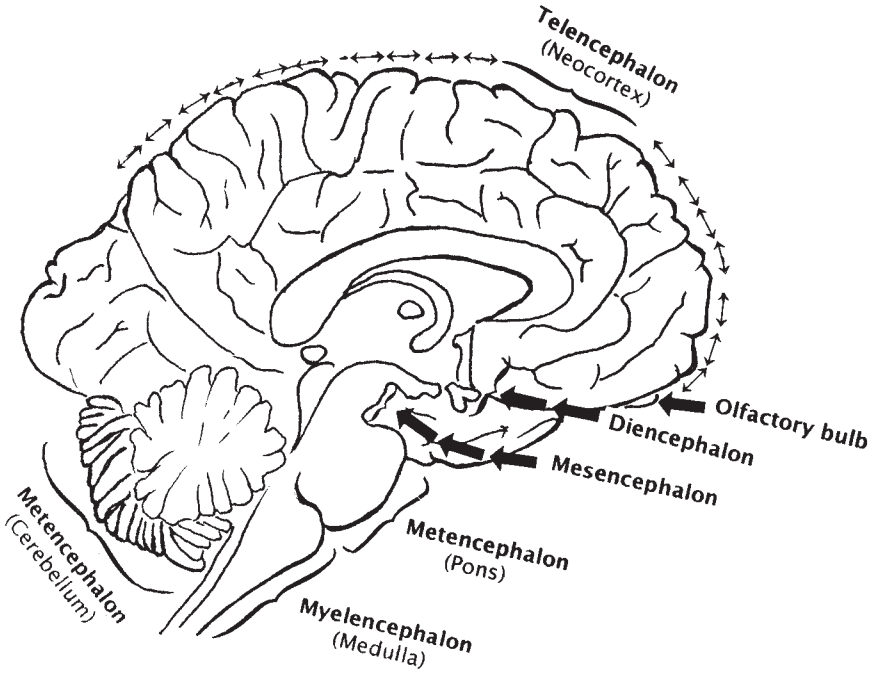

Figure 6.4 Sagittal cut through the human brain to show major components.

and two layers with small cells positioned away from the optical tract. It appears that lemurs and lorises have two additional tiny cell layers (Kaas et al., 1972). This can be understood in connection with the increasing development and elaboration of the visual sense. The lateral geniculate nuclei on each side of the brain are the first relay stations for the optic nerves and for optic radiation to the cerebral cortex. Functionally, the midbrain is a major relay station for auditory, visual, and tactile impulses.

The cerebellum is highly differentiated structurally: its surface is folded up into numerous tightly packed, deep fissures. Also, its lobes are considerably smaller than those of the cerebrum and are, therefore, called folia (Latin for "leaves"). The connections of the cerebellum with the cerebrum are numerous and close, as are the connections with the spinal cord. Major functions of the cerebellum are those of maintenance of muscle tone (maintenance of equilibrium and positioning of the body in space as well as coordination of the body movements). This is achieved by signals emitted by the neurons that are located within the muscle spindles and the neural organs of the tendons. Changes of muscle and tendon tension are registered by these neurons and the information is rapidly relayed to the cerebellum. This sensitive information system is known as proprioceptive feedback, resulting in the reception of stimuli that originate within the organism. The cerebellum harbors proprioreceptors that receive such information and are sensitive to stimuli from the body, as, for example, signals from stretch receptors in muscles that convey messages about body position and movement. Also, the cerebellar cortex is involved in coordination of visual, acoustical, and tactile sensations. The middle lobe of the cerebellum plays an important role in the coordination of the voluntary musculature and is connected by fiber tracts to the cortex of the cerebrum. The lateral hemispheres of the cerebellum are responsible for the autonomic regulation of the equilibrium. These hemispheres are consequently joined up by tracts to the statoacoustic organ of the ear.

Ontogenetically, the diencephalon, as we have seen, constitutes a part of the forebrain. The diencephalon is unpaired and consists of the thalamus, the epithalamus, the pineal body, the hypothalamus, and the infundibulum. The diencephalon also contains the third ventricle whose lateral walls are called thalami. The thin roof of the third ventricle is the epithalamus, the floor of the third ventricle the hypothalamus. In fact, the entire thalamus is one of the most important sensory centers and relay stations of the entire body. The thalamus integrates tactile sensations, spatial perceptions, and feelings of pain and temperature as well as olfactory and visual functions. The thalamus also serves as a relay station for the motor control of facial and limbic gestures. A vascular structure—the chorioid plexus—produces the cerebrospinal fluid within the epithalamus. A small cone—the pineal body—projects upward from the posterior

part of the epithalamus. The pineal body has endocrine functions and secretes vasotocin, a peptide hormone that stimulates muscle contractions of smooth muscles thus, among other functions, causing blood vessel constriction, and melantonin, which causes restriction of melanin granules in melanocytes resulting in lightening of skin color and which may be involved in sleep patterns in mammals. The pineal body may also be involved in the regulation of biological rhythms.

Among other functional attributes, the hypothalamus contains autonomic centers of thermoregulation, circulatory functions, regulation of hunger feelings, digestion, and centers controlling sleep and wakefulness. The hypothalamus also carries out complicated functions governing hormonal secretion of various peptide hormones, including releasing factors for pituitary hormones from the pituitary stalk (the infundibulum). The area of the hypothalamus contains higher centers of the autonomous nervous system, such as aspects of heat regulation (e.g., sweating and shivering) and control of eating, drinking, or mating behaviors. Control of the water, fat, and carbohydrate metabolism is carried out in cooperation with the posterior lobe of the pituitary (also called the adenohypophysis) and is ontogenetically not a part of the hypothalamus of the brain. This anterior part of the hypophysis produces a number of hormones such as adrenocorticotropin (ACTH, a growth stimulator), prolactin (LTH, which stimulates milk production in female mammals, among other reproduction-related functions that are associated with the corpus luteum), the gonadotropins, thyroid-stimulating hormone, oxytocin (induces contraction of smooth muscles), and vasopressin (also stimulates contraction of smooth muscles, causes constriction of capillaries, raises blood pressure, and has an antidiuretic effect by causing water resorption in kidney tubules). Also, in the area of the diencephalon is the optic chiasma.

Most obvious are the evolutionary and ontogenetic changes in the cerebrum. The cortex (pallium) or mantle of this main part of the brain is smooth only among the smallest prosimians and the smallest monkeys (Figure 6.5). The construction of the pallium is as a superficial layer, and it is never thicker than about 5 mm. Its essential characteristics are those of a surface integration tissue that coordinates the input of neural signals. With an increase in the number of surface cells, the number of afferent and efferent fibers also increases. If the number and density of such fibers gets too high to be accommodated within a certain area, the spacing between neural cells must also increase. In this case, the pallium grows two-dimensionally, and if the space available within the braincase is insufficient for such two-dimensional expansion of surface tissue, the pallium begins to fold up. Through these means, a large increase of brain volume is avoided, and the surface character of the tissue is maintained.

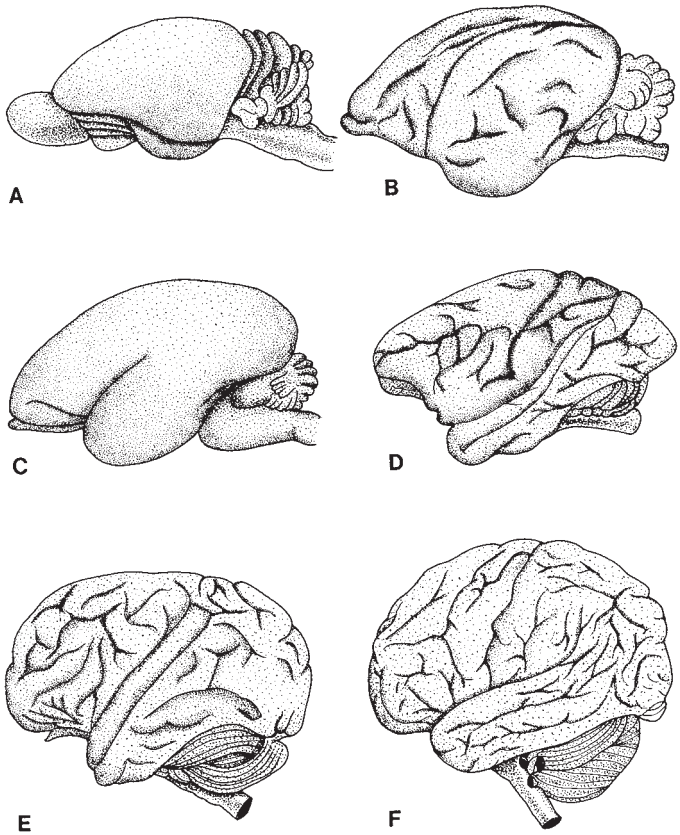

Figure 6.5 Diagram comparing primate brains (reduced to approximately the same length): A) treeshrew (genus *Tupaia*), B) lemur (genus *Eulemur*), C) marmoset (genus *Callithrix*), D) Old World monkey (genus *Macaca*), E) great ape (genus *Gorilla*), and F) modern human (genus *Homo*).

There are two reasons for increase of the number of neurons in the pallium of the brain:

1. If body mass increases, the volume of peripheral organs that have to be innervated grows concomitantly.
2. An increase in neuron number can result from a higher elaboration of brain functions, namely, the integrative functions.

Because enlargement of the cerebral cortex can be brought about by both of these factors, the cause of brain volume increase and folding of the cerebral cortex must be determined carefully (Kaas, 2004).

The cerebrum itself consists of two hemispheres that are divided by a deep longitudinal fissure. The cerebrum is also separated from the cerebellum by a

transverse fissure. At the bottom of the longitudinal fissure, the two hemispheres are connected with each other by several commissures and by a large fiber bundle of white cerebral tissue, the corpus callosum. Neurological cell tissue of the brain and spinal cord that appears white consists predominantly of myelinated plasma axons (nerve fibers), whereas cell tissue of the spinal cord and brain that appears gray (or gray matter) is made up mainly of the cell bodies of neurons. The rounded, convex convolutions of the folded brain surface are called gyri (*gyros* is Greek for "round" or "rounded"), and the deep valleys that are between them are sulci (*sulcus* is the Latin word for "furrow"). The gyri and sulci in different regions of the cortex have also been named, and it is necessary to know a few of these names to delimit macroscopically important cortical areas and their functions. The relative development of these areas helps us to understand evolutionary trends within primate brains.

When we look at the brain from the lateral aspect, a prominent fissure begins just above the temporal region and extends obliquely backward and upward. This fissure is called the sylvian fissure or sulcus lateralis. Inside its most posterior region a hidden area called the insula is found. The lateral or sylvian fissure separates the temporal lobe from the major portion of the cerebral hemispheres in front and above it. This sylvian fissure or sulcus is present in all primates. Another major fissure that is, however, not found in most prosimians is the central sulcus or fissure of Rolando. This sulcus begins at the highest point of the hemispheres running down and slightly backward in anthropoid primates and slightly forward in great apes and humans. It ends above the sylvian fissure close to its midpoint. This fissure separates the frontal from the parietal lobes of the brain. The gyrus, located anterior to it, is called the precentral gyrus and contains the motor region of the cerebral cortex. The gyrus posterior to the central sulcus, or postcentral gyrus, contains the area for tactile sensation.

In structurally underived mammals such as the insectivore *Sorex* we find the neopallium (= neocortex) to be smooth and without fissuration. This situation is also called lissencephalic (*lissos* is Greek for "smooth"). The opposite to lissencephalic is gyrencephalic (*gyrus* is Greek for "spiral," "convoluted") for brains with fissured neopallium surfaces such as those in higher primates in general and humans in particular, as well as in elephants. Fissuring and concomitant proliferation of lobes increases with the enlargement of the neopallium. The progressive cortex of the forebrain is called neopallium because it is an evolutionarily young (that is, new or "neo") acquisition of the mammal brain. The living brain is positioned inside an enveloping cerebral fluid. In many Hominoidea, the pattern of sulci and gyri is not imprinted into the endocranium as it is in lower primates. This has been thought to be the reason that fossil and extant endocranial casts of hominoid primates provide us with less information on surface structure than do those of lower primates (Radinsky, 1972; Starck,

1974). Nevertheless, this lack of detail in hominoid brain endocasts cannot entirely be explained and is not really understood.

All comparisons in the following discussion of some of the major differences that can be observed in the morphology of the brain among living primates are based on, and related to, a comparison with the brain of underived (unspecialized) members of orders such as Insectivora or Scandentia (the tree shrews such as *Tupaia*). No contemporary animal, however, such as *Tupaia*, can be used as an exact model representing an ancestral form. All extant animals have ascended through the same dimension of time to evolve into what they are today. Consequently, today's mammals can only tentatively be proposed as models for evolutionarily early forms.

In this chapter, Tupaiidae will be used as the morphological basis for the description of specific changes or trends in primate brain morphology. Stephan (1967, 1969) established a progression index for neopallium size in primates that is based on generalized insectivores as "1."

Tupaiidae

Tupaia (Tree Shrew)

Relative to the other genera in this taxonomic group (Scandentia), there is a slight reduction of the olfactory region. The olfactory bulbs are situated frontal to the brain and are comparatively small. In tupaias, the optical area is large, in proportion to the well-developed visual sense in these diurnal animals (Tigges, 1963). Tupaias also show some enlargement of the neopallium in the temporal and occipital regions. However, the surface of the pallium is still lissencephalic, mainly because of the small body size of *Tupaia*. The cytological structure of the cortical–neural layer of the neopallium is more complex than in underived mammals. The frontal and parietal portions of the cortex remain small compared with those of higher primates. The temporal lobes are comparatively large and downward directed, forming a temporal pole or projection. There is a sylvian fissure, beginning in a dent forming a sylvan fossa. In the mesencephalon the colliculus superior (containing the stratum opticum) of the tectum and the corpus geniculatum laterale are well developed. In fact, the organization of these rather highly advanced areas of the visual part of the brain is more progressive in *Tupaia* than in many prosimians. The brain is also relatively large in genus *Tupaia*, well within the range of many lemurs. The mesencephalon and cerebellum remain comparatively simple.

Lemuridae and Lorisidae

Among extant prosimians the smallest representative, *Microcebus,* has what seems to be the simplest brain, probably mainly because of its small body size.

The mouse lemur's brain is lissencephalic. A deeply engraved sylvan fissure is present. The olfactory bulb is partly covered above by the frontal lobes of the brain.

In genus *Eulemur* the olfactory region is more reduced than in *Microcebus*. The neopallium is convoluted and exhibits sulci that are mainly longitudinally directed. Many present-day prosimians retain well-developed olfactory regions (e.g., *Daubentonia, Nycticebus,* and *Galago*). Also, the long snoutlike nasal region of *Eulemur* as well as the shorter snout of *Propithecus* are still structured like that of animals with a highly developed olfactory sense (Starck, 1962). As we have seen, long snouts are not necessarily correlated with olfactory acuity.

Morphological differences would be expected in the visual area of the brain of the predominantly diurnal lemurs and the nocturnal lorisoids; this is not the case. It seems that the requirements of nocturnal visual acuity are not too different from diurnal vision because the intrinsic morphologies of the lorisoid and lemuroid brains, as far as we know, are very similar with one exception: the lateral geniculate bodies that are part of the diencephalon (thalamus) and are situated on the sides of the mesencephalon are the location where most of the optic tract fibers are ending. This large and complex visual center is increasingly complex, setting out with the rather simply organized lateral geniculate of *Tupaia*, getting more intricate across all the other primates with increasingly elaborate areas, and culminating in the most complex lateral geniculate bodies among primates—those of humans. The arrangement of the position of the lateral geniculate bodies in relation to the thalamus is different in the various primate genera. These different positions change the arrangement of the insertion area of the optical fibers. The lateral geniculate bodies are located laterally to the thalamus in *Tupaia,* in various ventrolateral positions in genus *Eulemur,* and ventrolaterally in *Tarsius;* they move ventrally and rotate in higher primates. There are microscopically distinctive layers or lamina of different neurons: layers made up of large, macrocells, and layers made up of parvo (small) cells. The cell layer arrangement is more uniform in higher primates than in prosimians. The macrocell layers are inverted (convex from outside) in prosimians including *Tarsius* but positioned differently, laterally in lemurs and tarsiers and ventrally in *Perodicticus,* a representative of the lorisoids. Unlike any other primate, the innervation of the dorsolateral geniculate bodies is reversed in tarsiers (Rosa et al., 1996). No other positional differences of the specific cell layers between the lemurid and lorisoid prosimians have been noted (Noback and Moskowitz, 1963).

Overall the brain morphology of *Daubentonia madagascariensis* (aye-aye) is unusual among primates in general and lemurs in particular. The relatively large olfactory bulbs are overlapped by the frontal part of the brain and deflected downward. The brain shows more convolutions than any other prosimian primate (Stephan and Bauchot, 1965). This unusual size and structure of the brain of the aye-aye appears to be closely correlated to the bizarre morphology of the skull

and unique hands and the highly intelligent foraging behavior of this prosimian (C. J. Erikson, 1995).

Among the non-Malagasy prosimians, the Asian genera *Nycticebus* and *Loris* have more cerebral convolutions than do the brains of bushbabies. Information about the degree of gyrification of the two African lorisoids *Arctocebus* and *Perodicticus* are wanting.

It appears that attempts to find functional homologies of brain regions among various primates are often confounded by the fact that such homologies do not exist (Sereno and Tootell, 2005). This fact has been shown by these authors for visual regions. It also is made clear that effects of body size are difficult to correlate in any reliable way to the factor encephalization.

Tarsiidae

Figure 6.6 depicts a side view of a tarsier (genus *Tarsius*) brain. In many respects, tarsiers are extraordinarily derived. Such specialization clearly appears in the configuration of their brain. Both skull and brain reflect that *Tarsius* is a highly visually oriented animal. Starck (1953) and later Sprankel (1965) pointed out that the volume of each eyeball exceeds that of the brain.

Compared with other prosimians, the olfactory region of the tarsier brain is much reduced. The pronounced separation of the temporal lobe from the cerebral hemispheres is not brought about by a high degree of organizational development in this area, but mainly by an indentation made by the huge orbits in this region. There are no fissures on the surface of tarsier brains except the calcarian fissure that is located posteriorly on the medial (inside) aspect of the hemispheres. Almost half of the neopallium in tarsiers is occupied by the visual cortical areas. The structure of the cortex is no more differentiated than that in the mouse lemur,

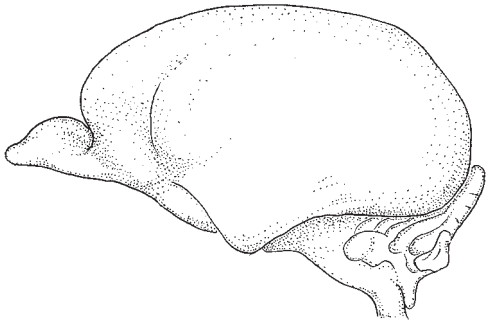

Figure 6.6 Side view of a tarsier (genus *Tarsius*) brain: note the entirely smooth neocortex. (Adapted from Woollard, 1925.)

Microcebus. The secondary areas in the temporal and parietal regions of the pallium are also small and not elaborate.

The foregoing shows that the extreme development of one of the special senses, in this case, vision, can result in considerable modification of the corresponding areas in the central nervous system. The remaining principal characteristics of the tarsier brain are not more advanced than those of other prosimians (see also Collins et al., 2005).

Anthropoidea

As pointed out by Starck (1965), the development of the brain in both the New World ceboids and all the Old World monkeys appears to have reached a rather similar stage. They represent similar evolutionary grades with respect to relative brain-to-body size and in the elaboration of the visual system exhibiting a high occurrence of parallelism. Even though these two primate groups are similar throughout in their organizational level, the New World monkeys show a more varied differentiation into adaptive types than do the relatively uniform Old World monkeys. Among Platyrrhines of the family Cebidae, it is the subfamily Atelinae that exhibits the highest development of neural organization (Hofer, 1958), clearly greater than can be found among cebines, alouattines, or pithecines. Both groups show a higher degree of fissuring and consequently gyral formation in the neopallium than do most prosimian groups. Separation into clear-cut successive grades of organization is not possible for some prosimians, such as certain lemurids; the indriids and the lemurid genus *Daubentonia* have more convoluted neocortices than do the callithrichids. In contrast, the cerebrum has attained a higher degree of neural elaboration in callithrichids than in prosimians; this condition is also true for parts of the cerebellum and the region of the thalamus.

In all higher primates, the lateral geniculate body shows high differentiation, apparently with the attainment of stereoscopic vision in these primates. The olfactory organ and the olfactory centers have decreased in size. In the higher primates, the tactile sense has become more elaborate than it is among prosimians.

Whereas the main brain fissures in prosimians of large body size show predominant arrangement in longitudinal (anterioposterior) direction, their arrangement in monkeys tends to be more radial (superioinferior). It is most difficult to try to homologize the gyri and sulci of the brain in different mammals, except in those species in which detailed cortical mapping has been done. Such mapping is spread in a random way across mammalian orders, and therefore our knowledge is rather spotty. The general agreement seems to be that fissures occur predominantly between areas of the brain cortex that undergo expansion.

South American marmosets—Callitrichidae—emerge to have the most underived brains of any higher primates. However, they do have an elaborate, expanded neopallium. "Reverse" allometry (or secondary dwarfism) may be the cause of a primitive appearance of the callithrichid brain, especially in its lack of folding.

Even though the South American Callitrichidae have the most primitive brain among higher primates, it is larger than that of prosimians of similar body size. Marmosets and tamarins have about the same body weight as do some of the African bushbabies, but the brain volume of marmosets is about three times as large as typifies African bushbabies (Starck, 1965). The callithrichid neopallium is more expanded than that of prosimians. Their cerebellum and neoencephalon are covered by the occipital lobe of the cerebrum, and the temporal lobe is large. With callithrichids, the olfactory bulbs and the paleocortex (the phylogenetically old part of the cortex) are much more reduced than, for instance, in *Tarsius*. Individuals of *Cebuella,* the smallest genus of Callitrichidae, do not have any fissure pattern of the neo-pallium surface. Also, the cortex of *Cebuella* shows a higher differentiation in cell structure when compared to that of prosimian primates. Species of Callitrichidae of larger body size than the pygmy marmoset, *(Cebuella pygmaea)* do have a well-defined sylvan fissure, the fissure that is characteristic for primates (as is the calcarian fissure on the median aspect of the hemispheres).

After much speculation that the callithrichids are small and relatively underived and therefore good models for the ancestry of Cebidae (Hershkovitz, 1977), it has now been convincingly shown that the Callitrichidae are secondarily small and not to be regarded as useful hypothetical ancestors of Cebidae (Ford, 1980). The overall impression of the callithrichid brain is the fact that it is lacking the derived folding pattern of all other primates. The olfactory region is less prominent than in prosimian primates. Areas where integrational neural processes take place in the frontal, temporal, and parietal regions are enlarged, especially in the temporal lobe. The cytological substructure of the cortical areas appear to be more complicated than those of prosimians. All members of Callitrichidae show a deep sylvan fissure and in addition a few other shallow fissures and the brain surface. In *Cebuella,* the smallest marmosets only the calcarine fissure (on the medial inside of the hemispheres) can be recognized. The area of the calcarine fissure is the cortical center for vision and receives fibers that come from the lateral geniculate body. This important region is involved in the identification of such visual qualities as color, size, form, motion, illumination, and transparency.

In the only nightly active higher primate, the South American night monkey genus *Aotus,* a reflection of the nocturnal habits is expressed in a distinct expansion and elaboration of the optical brain areas. The visual cortex of owl monkeys has been studied in great detail and been shown to be comparatively large and complex (Allman et al., 1994).

Among the cebid New World monkeys the Alouattinae and Atelinae are assisted in their locomotion by a fifth extremity: their prehensile tail. It can be shown that in both these subfamilies, not only the skeleton and the musculature but also the vascular and nervous systems of the tail are all derived for these prehensile faculties (see, e.g., Wrobel, 1966; Ankel, 1972; Leutenegger, 1973). As early as 1907, C. Vogt and O. Vogt demonstrated that in *Ateles* the cortical motor representation area for the tail is larger than the motor area for arm and leg together. *Ateles* is also the most skillful of the New World monkeys in tail manipulation (or "caudipulation"). Structural evidence for this is provided, as well by the presence of a short sulcus additional to all the others in the motor cortex of species belonging to this genus, separating an expanded tail control area from that of the rest of the body.

In both Old and New World monkeys, large integration relay areas occur within the frontal, parietal, temporal, and occipital lobes. The conformity of many details in the brains of the two groups of monkeys is high. Their olfactory region appears to be reduced, and their optical areas are highly developed in accordance with the elaboration of three-dimensional vision (the geniculate body shows a more refined structure than in prosimians and in callithrichids). In addition to all the other similarities, the fissural pattern of the neopallium is comparable in both of these large groups of monkeys; among them, the larger cebids resemble Old World monkeys in their sulcal pattern.

Speculations about the meaning of such major trends as the elaboration and enlargement of the frontal lobe—the area of autonomic effects on blood circulation, respiration, reaction of the pupils of the eye, and other visceral reactions within higher primates—are controversial (Holloway, 1996). Concordant with this is the question of whether the development of a more pronounced forehead that culminates in the greatly enlarged, high foreheads of modern humans *(Homo s. sapiens)* can be explained by functional elaboration. In Hominoidea and some Colobinae, according to Starck (1974), the enlargement and differentiation of the parietal lobes is pronounced, more so than in other Old World primates. Whether this has functional implications and what these may be is also unknown. It appears that the sulci of the neopallium actually delineate areas of different function; for example, the central sulcus demarcates the boundary between the functional–motor area and the somatic–sensory area.

The progressive compilation and elaboration of the external brain structure in Pongidae, possibly partially related to body size increase, is further developed in Hominidae. In humans the prefrontal, temporal, and parietal lobes together have increased substructural organization. Although the human frontal lobes show the greatest expansion among primates, it still has not been possible to define in a clear-cut manner the functions of the frontal lobe. There is no agreement among researchers of primate brains as to where in the human brain are located those qualities that make us human. There is not even agreement as to whether these

human characteristics are caused by a combination of factors. These qualities include perhaps exclusively human characteristics such as foresight and insight, initiative, and advanced learning abilities.

As we have seen among some anthropoid apes, for example, the orangutan, genus *Pongo* (and also spider monkeys, genus *Ateles*), a slightly developed forehead occurs. This hint of a forehead might be related to circumstances other than large frontal lobes, however, such as short snouts, relatively large total brain size, or even insertions of the muscles operating the masticatory mechanism. Furthermore, in the more primitive extinct species of *Homo, H. erectus,* and *H. habilis,* forehead expansion was not really similar to that of *H. sapiens*. It is also not possible to equate large forehead size with large frontal lobe size in extinct hominids.

Up to the present, there has been no certainty of finding correlations between morphological structures of the hominid brain and psychological performance such as memory or the ability to form abstract concepts, although literature documenting quantitative correlations between intelligence tests and perceptual abilities and brain size is growing. In Hominidae, the morphologically underived and rather primitive or generalized five-rayed hands have become the executing instruments that have participated in the creation of culture and civilization at the direction of a highly advanced, highly refined brain.

All living primates—prosimians, monkeys, apes, and modern humans—have gone through the same time span of evolutionary development and have brains that are well adapted to their needs. Even though some of the smaller whales, such as porpoises, have almost equally well-developed brains as humans; the fact that they are marine swimmers without having the executing five-fingered hands has prevented these mammals from becoming anything like human. The rapid increase of relative hominid brain size appears to be a phylogenetically recent event. Whereas Odontoceti reached their high level of encephalization about 15 million years ago, this event took place as recently as only the last 2 million years among hominids (Jerison, 1978). Somehow different or accelerated rates of change have led our own species to the forefront of brain development in the animal kingdom.

GENE EXPRESSION

It has been recognized that mammals do not differ according to assumed evolutionary levels as far as brain complexity is concerned. Therefore, evolutionary hypotheses based on generalized brain morphology and behavioral traits are likely to be misleading (Kaas, 2002).

A new way to look at brains is the possibility of deciphering gene expression in various organs including the brain (Ernard et al., 2002). It appears that gene

expression in the human cortex is vastly increased compared with chimpanzees, although the two are very similar in the gene expression of organs such as the heart and liver. Thus it could be that the way genes function is the reason humans and chimpanzees are different in many aspects of their being even though the number of genes appears to be similar (Càceres et al., 2003).

NEW INSIGHTS INTO BRAIN FUNCTION

In 1982, a student of neurology put forward an intriguing new concept about the way we should look at and understand the human brain (MacLean, 1982). MacLean suggested that the brain we see is actually composed of three evolutionary and functionally different portions that he called the triune brain (the Latin prefix *tri* meaning "three" and *une* from Latin *unus* or "one"). These are as follows:

1. **Archiopallium:** The brainstem (medulla) and cerebellum together being the oldest, primitive part, the archiopallium. The functions that are processed here are self-preservation and aggression. Muscle control, balance, and autonomic functions such as the heartbeat are controlled here.
2. **Paleopallium:** The intermediate or middle part of the brain, termed the limbic system by MacLean, includes the thalamus, hypothalamus, amygdala, and hippocampus; like the archiopallium, it is evolutionarily ancient. It processes irrational emotions (joy, misery, pleasure, fear, rage, pain), instincts, food-related input, antagonism, escape and sexual activities, creativity, irrationality. It has vast neural interconnections with the neocortex.
3. **Neopallium:** The neopallium or neocortex is the last addition during brain evolution; it adds the new functional dimension of intellectual achievement. The neocortex is divided into two hemispheres. Each has four lobes: the *frontal lobe,* which is associated with reasoning, planning, parts of speech, movement, emotions, and problem solving; the *parietal lobe,* associated with movement, orientation, recognition, perception of stimuli; the *occipital lobe,* which is involved in visual processing; and the *temporal lobe* that functions with perception and recognition of auditory stimuli, memory, and speech.

The three parts of the brain are intrinsically interconnected with each other. The cortex is separated medially by a gap into two halves, the right and left hemispheres; it unilaterally controls the two sides of the body—the left hemisphere controls the right side of the body, and the right hemisphere controls the left. Whereas the right brain is concerned with spatial, abstract mathematical, musical,

and artistic activities, the left hemisphere expresses rationality, time, verbal, language, and symbolic skills. Thus, the two halves have different functions. This was recognized long ago when Broca (1861a, 1861b) and subsequently Wernicke (1874) determined which areas of the left neocortex control language.

All this has to do with "neurological wiring." There are simplified and popularized views about brain lateralization, and sorting the theory from reality can be difficult. Nonetheless, noninvasive technologies have recently opened new ways that allow better understanding of the way the living brain works (Semendeferi, 2001).

Here enters a fact that, although known for a long time, has been neglected but recently rediscovered (Vallortigara et al., 1999; Vallortigara and Bisazza, 2002): the issue is the functional and structural lateralization of the brain simply known as lateralization. Obviously, the way the brain is "wired" is important to understanding how the brain works, especially where the human primate is concerned. The focus within the realm of human neurology and cognition as it involves language acquisition, handedness, vision, and other important human qualities has spawned a vast amount of publications, controversy, and confusion (Corballis, 2003; Walker, 2003 [commentary on Corballis]). In tandem, the question whether the phenomenon of brain lateralization is also evident in nonhuman primates has created a plethora of studies, and it is evident that lateralization occurs not only in invertebrates but also in fish, frogs, lizards, birds, nonprimate mammals, and nonhuman primates. Lateralization is genetically programmed and manifests itself developmentally (McManus and Bryden, 1992; Levin, 2005).

Chapter 7

Teeth

Tooth Morphology and Diet—Can They Be Reliably Correlated?
Tooth Structure
Tooth Replacement and Orientation
Dental Formulae
Dental Typology
Functional Surface
Functional and Morphological Variation
Evolutionary Trends of Tooth Morphology
Chewing Mechanics
Dental Formulae and Morphology
Genus *Tupaia*
Prosimii
Anthropoidea
What Is New in Primate Tooth Research?

Even today the most detailed study of the morphology and ontogeny of the dentitions of extant primates is the monograph by Remane (1960), which was to a great extent based on Remane's own research. Unfortunately, this monograph has not been translated from the rather complex German and is no longer available. Comprehensive studies in English are the books by W. K. Gregory (1922) and James (1960). Martin (1990) has written the most detailed and useful discussion of primate dentitions, both extinct and extant, and the evolutionary history of primate tooth patterns. Swindler's (1976) compilation of information on the morphology, size, and eruption sequence of the teeth of extant primates is a valuable source for data on this topic, as are, for example, Dahlberg's (1971) book on dental morphology and evolution and Hillson's (1996) dental studies in archaeology, even though primates are only briefly mentioned in the latter two. Godfrey et al. (2003) discussed dental developmental sequences in small-bodied folivorous lemurs. They came to the conclusion that they differ markedly and do not follow Schultz's rule assuming a close relationship of tooth-eruption sequences

and times with general growth patterns of small folivorous lemurs. In contrast to this rule, Godfrey et al. documented that molar crowns of permanent teeth actually erupt very early in jaws that seem to be too small to support them.

Another study of tooth development has addressed the problem of interdependency between jaw space and tooth development (Boughner and Dean, 2004). The authors found no significant differences between baboons and either chimpanzee species in molar crown development and concluded that availability of space in the mandible does not govern the timing of permanent molar crown initiation.

A new, much more detailed, and useful edition of the Swindler et al. book on the teeth of nonhuman primates (2002) is now available. It considers tooth development, deciduous dentitions, and dental eruption sequences and provides a comprehensive odontometric data base. Yet another new volume (Lucas, 2004) generally deals with tooth function, although it does not mention interesting details such as the prosimian toothcomb.

TOOTH MORPHOLOGY AND DIET—CAN THEY BE RELIABLY CORRELATED?

Attempts to correlate tooth morphology with diet have been numerous. However, in-depth information about primate diets is sparse and often only records brief, short-term observations. It would be necessary to acquire several years' worth of year-round data with records of seasonal changes over longer time periods for many primate populations to equate tooth morphology and particular diets with accuracy. For example, the genus *Hapalemur* has a highly specialized diet; the species of this group feed almost exclusively on bamboo, yet share nearly identical tooth morphology with genus *Eulemur,* lemurs that never feed on bamboo. A thorough, long-term, comparative study of three sympatric *Hapalemur* species groups (*H. griseus, H. aureus,* and *H. simus*) documents that all three species rely on the giant bamboo *Cathariostachys madagasgariensis* as food source, which contains toxic cyanide. A limited amount of grass (family Poaceae) is added to their diet. All three *Hapalemur* species feed on different parts of the bamboo, changing their preferences according to season, which results in niche partitioning between them (Tan, 1999). In contrast, *Eulemur* species have highly varied diets; they do not eat nor can they digest the toxic bamboo.

Terms such as "insectivore," "folivore," or "frugivore" are vague: insects, leaves, and fruit are not of uniform textures and consistencies, and therefore, these much-used categories are not at all precise. We all know that the textures of fruits such as bananas, strawberries, pears, apples, and pineapples—to mention only a few fruits that are commonly eaten by humans—do not share a single

texture. Neither do leaves or insects have consistency of composition. So, too, fungi, butterflies, moths, grubs, roaches, and beetles have different morphologies and densities as foodstuff (see also Lucas and Teaford, 1994; Lucas, 2005). To some extent it may be possible to hypothesize with great caution that certain occlusal tooth morphologies did evolve in response to specialized dietary habits. Correlations such as the scoop-shaped, chisel-edged incisors[1] with the consumption of soft food item, crested molars with the slicing of tough food items, or flat and low-cusped molars with the crunching of food items are difficult to document in extant primates. For example, we now know that the prosimian procumbent toothcomb is not used exclusively for social grooming activities but is also involved in scooping up sap and gum for food (see also Martin, 1990).

Body size and diet are correlated with each other to a certain degree. Animals, including primates with a specialized plant based diet are often larger than related animals that include animal protein in their menu. Different foods provide different amounts of energy, and it is not only an animal's teeth but its entire digestive tract (e.g., salivary glands, gut area, and digestive bacteria) that have important differences related to food intake and digestion. Smaller animals usually require more energy-efficient foodstuffs that are high in protein (such as insects) than do larger animals.

What follows is a review that provides an example of how science advances and how newly acquired knowledge changes scientific insight. Kay (1975) documented a correlation among primate diets, body weight, and molar morphology. He stated in an article on functional adaptations of primate molars that the "total amount of food preparation as inferred from measures of shearing, crushing, and grinding design on molars is consistently greater among primates which specialize in diets of leaves or insects than it is among primate frugivores of the same body size. It has been shown that living primates that specialize in leaf eating do not overlap in absolute body size with those that specialize in insect eating" (p. 122). Kay concluded, "Thus, it is possible from the combined data of body weight and dental dimensions to completely segregate specialized frugivores, insectivores and leaf eaters."

At the time, these findings were exiting, and it was Gingerich (1980) who detected a "rule" for primates in Kay's discovery. Gingerich (p. 128) stated that "Kay (1975) has shown that insectivorous and folivorous primates differ in body size, with the former usually being smaller than 500 g and the latter being greater than 500 g in body mass. This size threshold at about 500 g may appropriately be called 'Kay's threshold.' " Gingerich continued to apply this "rule" to fossil primate taxa, and so did others.

[1]Incisors that generally have a cutting edge on the occlusal surface have a functional name in German: *Schneidezähne* which means "cutting teeth."

Kay's threshold was redefined by Fleagle (1988, p. 236) as the body weight (approximately 500 g) that is roughly the upper size limit of predominantly insectivorous primates and the lower size limit of predominantly foliverous primates.

Thus, Fleagle put Kay's threshold into the realm of textbook knowledge, which is now taught to students everywhere.

In 1990, Conroy cautiously discussed Kay's threshold, saying that in general, heavier primate species could be expected to eat lower-quality, more widely available, and more difficult to digest food stuffs than smaller species, which would eat higher-quality, harder to obtain, and more easy to digest food items. By this time, much more was known about the complexity of primate diets than 15 years earlier. Conroy (p. 34) redefined primate diet categories as follows:

1. Various parts of animals, both vertebrates and invertebrates
2. Reproductive parts of plants (flowers, buds, fruits, nectar, and other resins)
3. Structural parts of plants (leaves, stems, bark, and other plant materials containing a high proportion of structural carbohydrates such as cellulose)

Conroy went on to say, "Richard Kay and his colleagues at Duke University have concluded that primates weighing more than about 350 g are usually not primarily insectivorous (that is, insects would provide no more than a fraction of their energy needs), and that folivory would be difficult to sustain for a primate weighing less than 500 g, a point of demarcation that has come to be known as Kay's threshold."

We now know that it is quite difficult to pinpoint the diet of primates sufficiently to construct conclusive definitions such as "frugivore," "folivore," or "insectivore" (see also Chapter 9, which includes a section on the digestive tract and diet). Most living primates have mixed diets that change not only between populations of the same species but also during the seasons. To define what kind of fruit intake constitutes a truly frugivorous diet is difficult; different fruits have different fiber content, various degrees of ripeness, and, thus, different toughness. The same is true for leaves, which can be soft when they are newly developed or tough and full of fiber; it is equally so for insects, whose larvae are often soft and chewy while their imago can be very tough. Insectivorous, frugivorous, and folivorous are therefore basket terms for mutable food categories. We also know that tarsiers are likely to be the only small-bodied primate that has an obligatory animal protein diet. Yet even tarsiers do not subsist on insects alone; they also feed on small lizards, frogs, birds, bats, and snakes—hardly a combination of food items that should be termed "insectivore."

Thus, the rule of Kay's threshold concerning primates that weigh less than 500 g, if strictly applied, seems only pertinent to the unusual genus *Tarsius,* the

only true insectivore or, better, faunivore (Chivers and Hladik, 1980) among the order Primates. Unfortunately, there are many more exceptions to the dietary threshold rule than can be mentioned here. Two examples are mouse lemurs genus *Microcebus* (the smallest of lemurs, weighing less than 150 g) and pygmy marmosets (the smallest of South American monkeys, weighing less than 175 g), which both have only a fraction of insects or other animal protein in their diet. Otherwise they mainly consume fruits, flower buds, leaf buds, seeds, and plant exudates. It has recently been documented that *Microcebus rufus* eats predominantly fruit (Atsalis, 1999), This finding obviously contradicts the hypothesis that tiny primates must eat animal protein to survive.

In contrast, the smallest primate that appears to be predominantly folivorous is *Lepilemur leucopus* (the white-footed sportive lemur), with an average weight of 560 g and a diet that consists predominantly of leaves and flowers. On the other end of extremes of Kay's threshold, we know that colobus monkeys, formerly categorized as obligate folivores, have a much more varied diet than previously believed (Oates, 1994). Species belonging to genus *Colobus* have an average weight of roughly 8 kg. When members of the genus *Cercopithecus* are evaluated using new dietary field data, the actual food that they consume differs strikingly from Kay's assessment of their diet (Martin and MacLarnon, 1988). The highly dietarily specialized *Hapalemur* discussed earlier has an average weight between 900 and 2400 g. On the other hand, howler monkeys (genus *Alouatta*), New World monkeys that have a specialized vegetarian diet that consists predominantly of leaves, flowers, buds, and fruit, have an approximate average weight of about 10 kg. Thus, a threshold of 500 g separating insectivorous primates from folivores is an inconclusive measure. In a review of primate digestion and dietary habits, Lambert (1998) stated: "Body size arguments neither encompass nor explain the range of dietary and digestive adaptations observed in primates." This confirms what was stated earlier in this chapter. The issues of fiber digestibility and body size thresholds are discussed in detail by Cork (2005).

It is tempting for students of primates to categorize and define every aspect of their behavior. However, as in all examples of primate adaptation, correlations between morphology and function are problematic. Primates are endlessly adaptable because of their very nature. Animals with large brains, four unspecialized and very dexterous limbs, and comparatively unspecialized dentitions and digestive systems are not likely to be adapted to such precise degrees that the correlation between morphology and function becomes incontestable. Valid correlations can only be cited in extreme cases of adaptation such as, for example, the dentition of *Daubentonia madagascariensis,* the aye-aye, which among extant primates has the most derived tooth morphology.

TOOTH STRUCTURE

Figure 7.1 provides a general overview of tooth basics. Primates, like all mammals have two sets of teeth: those of the maxillary and premaxillary (or upper teeth) and the mandibular or (lower teeth). Each tooth has two major functional parts, the crown above the gums, and the root or, several roots, below the gumline. The roots are implanted 1) into the bones of the skull (the premaxillary and maxillary) and 2) the jaw (the mandibular or dentary). The sockets for the tooth roots are called alveoli. The alveoli are usually perfect molds of the tooth roots they hold. Thus, it is possible to get some information about the size of teeth even from specimens (e.g., fossils) that have lost their teeth but have the alveoli preserved. The crown of the mammalian tooth is covered with enamel. Under the enamel is dentine, which surrounds a pulp cavity. The roots of a mammalian tooth are covered with *cementum*. Under the cement lies the dentine, which, as in the crown, surrounds a pulp cavity containing soft tissue as well as the nerve and blood supply for the tooth. The material of which teeth are made is a composite of mineral and organic components that have characteristic proportions in the various tooth structures. Teeth are mostly made up of calcium carbonate and calcium phosphates, and the organic ingredient is mostly collagen, a fibrous protein. The enamel, which covers the tooth crown is the hardest part of the teeth, contains very little organic material (less than 1%), and is basically

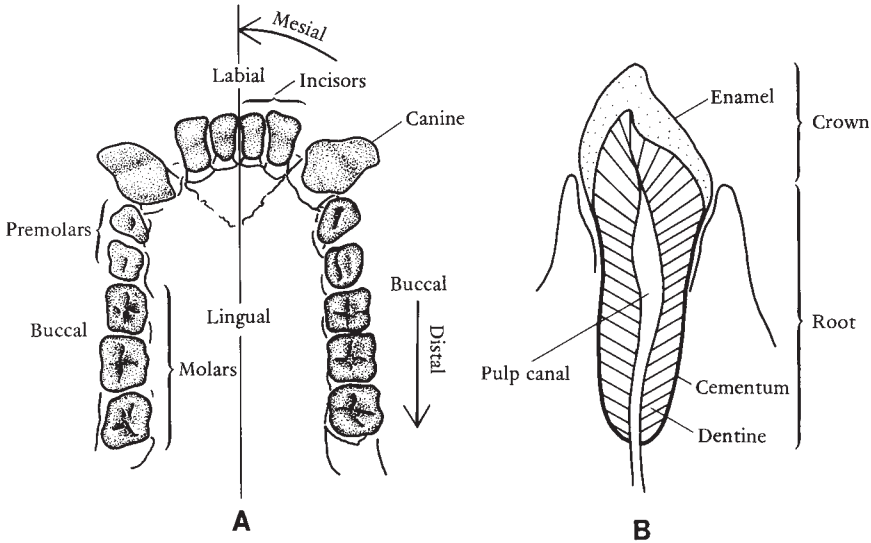

Figure 7.1 A) Terms of orientation as it applies to teeth. Note incisors in the premaxilla (also known as intermaxillary). B) Basic tooth histology (incisor).

made up of crystallites. Hence, enamel is made of bundles of these crystallites called prisms, and they vary within and between species in typical, complex patterns. Enamel thickness and patterns have been used for taxonomic and evolutionary interpretations especially of hominoids (Maas and Dumont, 1999). The dentine, in contrast, contains considerably more organic material; it is about 17.5% to 18.5% collagen and is consequently softer and weaker than the enamel. Coating the dentine in the root portion of teeth is a thin, layered covering of material called cementum, which contains about 25% of collagen, being structurally very similar to bone.

Unlike many of the ungulates, such as elephants, tooth whales, and rodents, whose tooth crowns are also covered by cement, cement is not found on the crowns of primate teeth. Dentists call the area where the lower border of the enamel meets the cement layer of the root the "neck" of the tooth. The dentition of primates is, without exception, heterodont (*hetero* is Greek for "different"; *dont* is Greek for "toothed"). As in all toothed animals, the dentition of each side of the jaw is a mirror image of the other side, across the midsagittal plane. Thus, it is sufficient to describe only one half of a dentition of either the lower and upper jaws—the number of teeth is not necessarily the same in the maxillary and mandibular set of teeth—to know the entire structure. The dentition of an ancestral, generalized primate (or mammal) commonly is a combination of four types of teeth. In front we find the incisors, numbering two times three in most generalized mammals, numbering two times two in most primates. The incisors are followed by a single canine on each side. The canines are in turn followed by four or five premolars in generalized mammals, a number that is reduced to two or three on each side in primates. Behind the premolars are two or three molars in primitive mammals and also in primates that typically have the most complex occlusal morphology of all four types of teeth.

Tooth Replacement and Orientation

Figure 7.2 shows generalized mammal dentition. To render intelligible discussion of primate dentition, it is essential to know some basic comparative terms of anatomical position. The tooth surfaces facing the cheeks are called buccal (or outside) surfaces, and the tooth surfaces facing the tongue are called labial (or inside) surfaces. The tooth side facing the median line in the dental arcade is the mesial (or anterior) surface, and the tooth surface oriented away from the median line in the dental arch is the distal (or posterior) surface. Mesial and distal also describe the positional relationship of one tooth to another. For example, incisors are positioned mesial to canines, and molars are distal to premolars. (See Figure 7.1.)

During individual ontogeny, some of the teeth are replaced by a second tooth generation, the so-called permanent dentition. Those teeth that appear first in the

Figure 7.2 Generalized mammal dentition with (from left to right): three incisors (white), one canine (black), four premolars (shaded), and three molars (white).

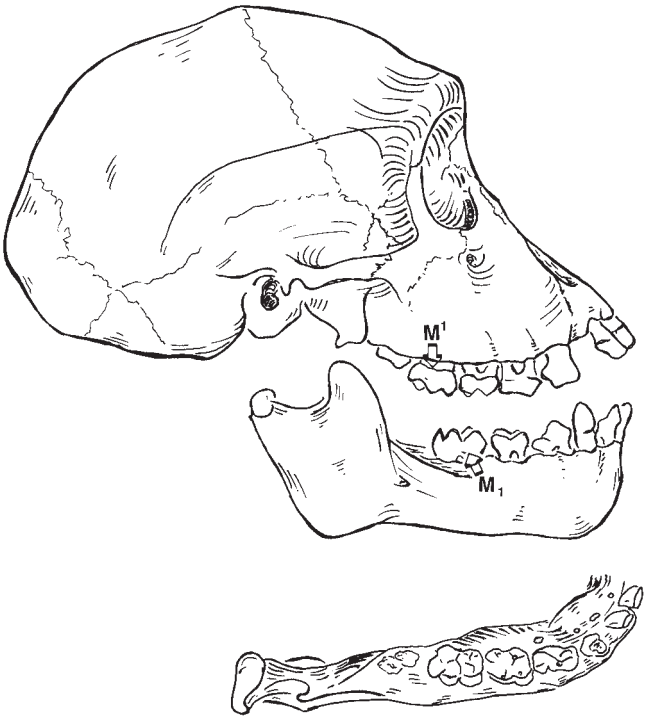

Figure 7.3 An approximately three-year-old infant *Pan troglodytes* with deciduous dentition and the first molars in place.

mouth of placental mammals and are replaced at a later stage in life are called deciduous teeth or milk dentition. Teeth that are replaced in this way are the incisors, canines, and premolars. The molars appear only in the permanent set of teeth. This means that the deciduous dentition only has incisors, canines, and premolars. These first-generation premolars are usually called milk or deciduous molars and are replaced by permanent premolars later in life. (see Figure 7.3.)

There has been some discussion about whether milk incisors, canines, and (pre)molars make up the first tooth generation (Bolk, 1915) and the permanent incisors, canines, premolars, and molars the second generation. Or, alternatively, whether the milk incisors, milk canines, milk (pre)molars together with the molars are form one single (first) generation of teeth, and only the replaced incisors, canines, and premolars should be regarded to represent the second tooth generation (Bennejeant, 1935). Once a tooth has been formed and has erupted above the gumline, its morphology does nor change thereafter except by wear or decay. Milk teeth are generally somewhat simpler than permanent teeth. With time, the roots of the deciduous teeth are resorbed by the permanent tooth buds as they push up under the milk teeth.

DENTAL FORMULAE

The number in which each tooth type occurs in an individual dentition is constant for mammalian species and often also for higher taxonomic groups. Because of this consistency, the number of each type of tooth for an animal species can be written down as a so-called dental formula. Dental formulae, in turn, can be useful to differentiate animal species and groups.

The dental formula is written for one side of the dentition starting at the midline:

$$\frac{\text{I-C-P-M}}{\text{I-C-P-M}} = \frac{\text{Incisors-Canine-Premolars-Molars}}{\text{Incisors-Canine-Premolars-Molars}}.$$

The teeth represented above the line are the maxillary or premaxillary teeth, and those below are the mandibular teeth. Capital letters are often used for permanent teeth, whereas milk teeth are usually indicated by lowercase letters, for example:

$$\frac{\text{i-c-m}}{\text{i-c-m}}$$

The basic number of teeth in most early tertiary placental mammals is usually three incisors, one canine, four premolars, and three molars. Written in the short manner of the dental formula this is

$$\frac{\text{3I-1C-4P-3M}}{\text{3I-1C-4P-3M}} = 44$$

and, in a juvenile,

$$\frac{\text{3i-1c-4m}}{\text{3i-1c-4m}} \quad \text{or} \quad \frac{\text{3i-1c-4p}}{\text{3i-1c-4p}}.$$

There is never more than one canine (even though unconvincing attempts have been made to show that there would be two canines, namely, the true canine and the anterior, caniniform first premolar [Osborn, 1978] in each half of a dentition). Even shorter and simpler is the numerical tooth formula that can be written as follows:

$$\frac{\text{3-1-4-3}}{\text{3-1-4-3}} = 44$$

The corresponding numerical tooth formula for the milk dentition is written

$$\frac{\text{3-1-4}}{\text{3-1-4}} = 32$$

For example, the adult dental formula for *Homo s. sapiens* is

$$\frac{\text{2-1-2-3}}{\text{2-1-2-3}}$$

and that of the human milk or deciduous dentition consequently is

$$\frac{\text{2-1-2}}{\text{2-1-2}}$$

However, milk or deciduous teeth are not always replaced by a permanent tooth. This is indeed the case in the extraordinary modern lemuroid prosimian *Daubentonia madagascariensis,* the aye-aye, in which neither the deciduous canine nor one of the upper premolars (of two deciduous premolars that are found in both jaws) is replaced in the permanent dentition (Ankel-Simons, 1996). The dental formula of the adult aye-aye is

$$\frac{\text{1-0-1-3}}{\text{1-0-0-3}}$$

whereas the deciduous formula is

$$\frac{\text{1-1-2}}{\text{1-1-2}}$$

There also have been discussions about the nature of the teeth that are incorporated in the toothcomb of indriid lemurs (J. H. Schwartz, 1974). Some authors believe that the small lower canine in their deciduous dentition does not have a replacement in the permanent dentition (Leche, 1896; Spreng, 1938; Remane, 1960). According to their opinion the deciduous dentition of Indriidae is as follows:

$$\frac{2\text{-}1\text{-}2}{2\text{-}1\text{-}2} \quad \text{or} \quad \frac{2\text{-}1\text{-}3}{2\text{-}1\text{-}3}$$

according to Swindler (1976), and the permanent formula is

$$\frac{2\text{-}1\text{-}2\text{-}3}{2\text{-}0\text{-}2\text{-}3}$$

with the lower canine not being replaced. James (1960) believed that the indrid toothcomb consists of one incisor and the canine, with a tooth formula like this:

$$\frac{2\text{-}1\text{-}2\text{-}3}{1\text{-}1\text{-}2\text{-}3}$$

Schwartz (1978) came up with a totally different and rather unusual interpretation of the lower teeth in indriids:

$$\frac{2\text{-}1\text{-}2}{1\text{-}1\text{-}4}$$

which would mean that one milk incisor and two milk premolars are not replaced in the permanent dentition, but this assumption has not generally been accepted.

Whether the Indriidae do, in fact, have a lower canine and only one lower incisor or have two incisors and no canine in the permanent dentition or whether they have four deciduous premolars can only be proven through study of a series of early developmental stages of indriid dentitions, specimens with milk dentitions, and fossils (Remane, 1956).

Each tooth is also given a number. An animal with the dental formula

$$\frac{3\text{-}1\text{-}4\text{-}3}{3\text{-}1\text{-}4\text{-}3}$$

has the following teeth:

$$\frac{I^1I^2I^3C\ P^1P^2P^3P^4M^1M^2M^3}{I_1I_2I_3C\ P_1P_2P_3P_4M_1M_2M_3}$$

The South American marmoset with a dental formula of

$$\frac{2\text{-}1\text{-}3\text{-}2}{2\text{-}1\text{-}3\text{-}2}$$

has the following teeth:

$$\frac{I^1 I^2 C\ P^2 P^3 P^4 M^1 M^2}{I_1 I_2 C\ P_2 P_3 P_4 M_1 M_2}$$

This example demonstrates some important trends in dental reduction. When reduction of the original (primitive) number of teeth occurs in the incisors, it is usually the lateral incisors that are lost first. Therefore, it will be I^{1+2} and I_{1+2} that are retained and I^3 and I_3 that are lost. Premolar reduction, as in *Callithrix,* from the original four to three premolars occurs through the loss of the mesial (anterior) premolars. It is therefore P^1 and P_1 that no longer develop and P^{2-4} and P_{2-4} that are still present. With molars, the loss is of the distal (posterior) molars—namely, M^3 and M_3—rather than the mesial ones.

The morphology of tooth shape and of the occlusal (functional) surfaces also show differences of high diagnostic value, as, for example, between Cercopithecoidea (Old World monkeys) and Hominoidea (apes and humans) as we will see, but is of lesser use in drawing distinctions between the two families of New World monkeys. The number of teeth, however, enables one to distinguish with a quick glance between dentitions of Old World and New World monkeys. Tooth number also makes for easy recognition and separation of the members of the two New World monkey families, Cebidae and Callitrichidae.

An "alveolar diastema" or "apparent diastema" is frequently found in primates. This means that the sockets of two adjoining teeth are separated by a stretch of intervening bone, but that the crowns of the same teeth touch each other (e.g., orangutan incisors). The diastema is an expression of the fact that either the crowns of the teeth are much broader than the roots or that the teeth are implanted in such a way that the long axes of the two adjacent teeth are tilted toward each other. According to Remane (1960), a "real diastema" occurs when both the crowns and the edges of the roots are spaced apart and do not contact each other. This distinction is important, for one kind of diastema can be mistaken for the other in fossils in which tooth crowns have been broken away.

The crowns of teeth function in different ways and according to their morphology. The incisors of extant primates are usually quite simple and conical or wedge-shaped. They usually have biting, tearing, slicing, or scraping functions. Canines are habitually dagger-like, sharp, and pointed teeth that pierce, puncture, or grasp. Incisors and canines together are often referred to as the front dentition (or front teeth), and the premolars and molars are called cheek teeth. Premolars and molars usually show enlarged functional (or occlusal) surfaces that have differently structured and differently functioning surface reliefs—cusps, ridges, and raised outside rims or *cingula* (= singular is *cingulum*). In very old individuals, the tooth crowns can be worn down so that no surface relief remains and the dentine is exposed over the entire crown. The occlusal surfaces—the various cusps and grooves—of the upper and lower premolars and molars fit perfectly

together with each other to function properly in shearing, slicing, or crushing actions when the cheek teeth are processing food matter.

DENTAL TYPOLOGY

As mentioned earlier, the incisors of extant primates are usually quite simple and conical or wedge-shaped. Incisors are always single rooted. Many extant mammals have three incisors (four sets of three); however, no primate has more than two incisors.

All upper incisors are implanted in the premaxillary bones, although some authors have argued that this is not always the case; but it is true in all extant primates. The premaxilla is also known as the os incisivum, Latin for the "incisor bone." The suture between premaxillary (also known as the intermaxillare, which means the bone between the maxillary bones) and maxillary bones is still visible in young primates. This suture makes it easy to decide how many incisors are present in the upper dentition. The number of incisors in the lower dentition is often obscured, as the canines can be incisiform, which means that the canines adopt the same shape as the incisors. Because there is no other bone involved in shaping the mandible than one bony element, the decision of whether there is or is no canine can sometimes be difficult.

Members of the Prosimii, with the exception of *Tarsius,* have extremely specialized incisors. The lower incisors are tilted forward (called procumbent) and flattened laterally, forming a toothcomb. These incisors are tilted forward more or less in the direction of the long axis of the mandibular ramus. Additionally the crown of these incisors is angled in a manner that enhances the procumbency. The lower canine is frequently included in this toothcomb, and its morphology is assimilated to the shape of the procumbent incisors. If this is so, the first premolar usually resembles the canine (caniniform premolar) and takes over the canine's function. This can easily be observed because when the jaws are closed, the upper, true canine rides down anterior to the canine-shaped lower tooth that is in fact a premolar and not behind it. Typically in primates with caniniform true lower canines, the true upper canine rides down behind the lower canine, not in front of it. In those prosimians that have a toothcomb in the front of the lower jaw, the contact between the lower and upper incisors is frequently lost. Consequently, there is often a reduction, even complete loss, of the upper incisors (Remane, 1960). As the size of the upper incisors decreases, the size of the premaxilla also undergoes reduction. In all cases in which upper incisors are lost, however, small premaxillae do remain but are reduced relative to those of typical prosimians with rather big incisors (e.g., *Propithecus,* the indriid Sifaka).

Total reduction of the upper incisors is found in *Lepilemur,* the sportive lemur. In this genus, the premaxilla struts across the front of the upper jaw and also

embraces the nasal opening from both sides. In front of the palatine (the bone that shapes the roof of the mouth) the premaxilla forms the surroundings of the large incisive foramen. Thus, the premaxilla of *Lepilemur* is the smallest among all living primates, only a clasplike, narrow bony structure. Among higher primates, some of the callithrichids also have somewhat procumbent lower incisors, as do the cebid monkeys *Cacajao, Pithecia,* and *Chiropotes,* where also the upper incisors are somewhat procumbent. This procumbency, however, is less pronounced than that of prosimians, the canines are not incorporated, and these incisors do not function as true toothcombs that are used for grooming purposes but rather as scoops or for slicing of soft food items. Fruit-eating primates often have scooplike, large incisors. Those primates that gauge holes into bark and trees have robustly developed incisors. Leaf eaters, on the other hand, have small incisors, only involved in grasping or nipping.

Canines follow distally behind the incisors. These teeth are called canines because of their dagger-like shape—"canine" meaning the dog tooth (*canis* is Latin for "dog"). Generally in primates, the canines are larger than the incisors or premolars; canines are pointed and frequently curve distally. Among the South American Callitrichidae, those that belong to the genera *Callithrix* and *Cebuella* have comparatively long lower incisors in combination with canines that are of approximately the same length as the incisors. They therefore are often called short-tusked marmosets (or titis). In contrast, genera *Saguinus* and *Leontopithecus* are called long-tusked marmosets (or tamarins) because the length of their canines exceeds considerably that of the incisors (Napier and Napier, 1967). The short-tusked condition seems to be correlated in these small primates with the activity of gnawing holes into trees to elicit the flow of edible sappy exudates (Martin, 1990).

In some primate genera, the canines are dimorphic between the two sexes—larger in males and smaller in females of the same species (e.g., *Papio,* the baboons; *Gorilla*, the gorillas); in others, the canines are subequal in size in males and females (e.g., *Hylobates,* the gibbons; many of the prosimians; and the South American owl monkey, *Aotus*). Distal to the canines are the premolars. Premolars in their simplest form have only one cusp. Around the base of this cusp, a thickening of enamel or *cingulum* is often formed. A *cingulum* is found on many premolars and molars and sometimes also on incisors and canines (e.g., the upper incisors and canines of *Tarsius*). Premolars often have two cusps, one situated buccally, one lingually. On upper premolars, these cusps are named paracone, located on the buccal (out-)side, and the protocone, on the lingual (in-)side. A single-cusped premolar has only the paracone. Names of the lower premolar (and molar) cusps end with the suffix -id, thus designating the cusps and the tooth clearly as being of the lower dentition. Lower molars of early (primitive) primates have a distal basin consisting of an unstructured enamel thickening that may bear one or two cusps. The anterior part of the lower

premolar of primitive primates also has two cusps, the protoconid on the outside (buccally) and the metaconid on the inside (lingually). The protoconid is usually the highest and largest cusp. In higher primates, lower premolars typically have only the two anterior cusps, the protoconid and the metaconid, and lack the distal basin.

In some cases, the distal premolars resemble the molars, and the premolar series grades morphologically into the molar shape. For example, in extant galagos, the fourth premolar is morphologically very much like the first molar.

The molars are the most distally positioned type of teeth. They are also the most complicated teeth. Cusps, groves, fissures, ridges, and in some cases wrinkles (e.g., in the hominoid *Pongo,* or orangutan) give structure to the occlusal enamel. In primates, the simplest upper molars have three main cusps. Cusps are also called cones. Smaller cusps that complicate the structure of the occlusal surface are commonly called conules, and they habitually form within the range of ridges that connect the main cusps with each other. On the upper molar, two of the three main cusps are located on the buccal (outside) edge, namely, the paracone in the front (mesially) of the tooth and the metacone in the back (distally) of the molar. The third main cusp lies lingually and is called the protocone. A fourth cusp, the hypocone, is present on the upper molars of most primates. This latter cusp occurs on the distal–lingual (the back and inside of the tooth) occlusal surface (Hunter and Jernvall, 1995).

One root is located under each of these main cusps. Thus, all the upper molars have three roots. Each root is set into the maxillary bone, and the bony alveoli—the tooth sockets—are perfect negative images of the roots. The root dentine covered only by a thin layer of cementum, is connected in turn to the alveolar bone by the periodontal membrane, also called the alveolar ligament.

Functional Surface

The triangular arrangement of the cusps and roots in upper molars is called the "trigon" or "trigonum" (or triangle). This type of tooth is also called a tritubercular or tribosphenic molar (Simpson, 1936). The latter term is a functional term meaning grinding wedge (*tribo* means to grind, rub, or rasp in Greek, and *sphen* is Greek for "wedge") and was taken as the basic tooth type for upper molars from which all teeth of extant mammals can be derived following Cope and Osborne's tritubercular theory (*tri* meaning "three" in Greek, and *tuberculum* is Latin for a small, rounded knob) (Osborn, 1888). Upper molars have three roots.

The lower molars consist of two parts that are positioned in front and back of individual teeth. Both parts have three main cusps, and thus lower molars of early primates have six main cusps. The three cusps of the two components of the cheek teeth also form triangles to form the basic lower molar occlusal pattern.

The triangle in front has two cusps at the lingual side (paraconid mesially, metaconid distally within the toothrow), and on cusp at the buccal (out) side named the protoconid—just the inverse of the upper triangle. This mesial (anterior) triangle is called the trigonid and is believed to be phylogenetically older than the back part, the talonid (or heel). The talonid consists of one buccal cusp, the hypoconid; one lingual cusp, the entoconid; and one distal cusp, the hypoconulid. The two triangular parts are fused together to combine and form an elongated molar tooth, and in early forms the trigonid occlusal level in the front of the tooth lies considerably higher than that of the talonid. Among extant primates, this condition is still expressed to some extent in genus *Tarsius.*

Lower molars have two roots anchoring the tooth into the mandible, one mesial root (anteriorly) under the trigonid and one distal root (posteriorly) under the talonid. In most extant primates the two components of lower molars, the trigonid and the talonid, have their occlusal surfaces at almost the same level.

FUNCTIONAL AND MORPHOLOGICAL VARIATION

There is functional and morphological dependency between the maxillary and mandibular tooth rows. The structures (cusps, crests, and grooves) of the occlusal surfaces of all the corresponding upper and lower teeth fit into each other (Kay and Hiiemae, 1974; Hiiemae, 1978). The morphology of the teeth varies in relationship to their active role in mastication. The following discussion considers a number of primate dental morphologies and their functions.

The primary function of incisors for primates is the preparation of food items for mastication. Hylander (1975) has documented a relationship between incisor size and the diets of higher primates. Higher primates that feed primarily on large objects (e.g., fruit) often have larger incisors than primates that eat small and harder objects (e.g., seeds, leaves, grasses) because it is necessary for them to reduce the size of their food so that they can chew it between their molars. *Callithrix* and *Cebuella,* two small New World monkeys, have relatively long lower incisors that they use to gouge holes into bark to induce gum and sap to flow (Coimbra-Filho and Mittermeier, 1977). As described previously, members of Prosimii, with the exception of *Tarsius,* have specialized lower incisors that predominantly function as a grooming comb. Evidently, however, the toothcomb is also used in spooning up soft food items such as fruit pulp (see also Martin, 1990, pp. 255–256).

The relationship between canine morphology, variation, and function is less well understood in primates than is this relationship for incisors, premolars, and molars. Many primates use their canines for ripping or slicing of food items. Nevertheless, canines are also used in aggressive encounters by many primates, both as a weapon and as a threat display. *Callithrix, Cebuella,* and *Phaner*

furcifer use their canines in combination with the incisors to gouge holes into and through bark.

Morphological variations of premolars, like those of canines, are not clearly understood in relation to function. The anterior lower premolar of many primates with large canines acts as a hone to sharpen the distal crest of the upper canines. The most highly developed examples of this functional condition are seen in such Old World monkeys as baboons and macaques in which the P_3 is elongated mesiodistally with a long slanted surface on its front that hones the upper canine (see Figures 7.15 and 7.16). *Euoticus elegantulus* (a species that was formerly included in genus *Galago*) has a P_2 that is caniniform and comparatively large. In this species, the specialized premolar is used to gouge holes in bark (Charles-Dominique, 1977) to cause gum, which makes up a great portion of their diet, to ooze from these holes.

As mentioned before, the molars are the most complex teeth morphologically. Reflecting the close ties between occlusal surface morphology and chewing, the molars are also the most complex teeth functionally. The primary action of the molars is mastication and preparation of food for proper digestion. Mastication for primates is fairly stereotypic (Hiiemae, 1978; Mills, 1978). Chewing time is an important factor that is closely correlated to the ability to digest food items (Alexander, 2005). Not only biting down but shearing and crushing forces are exerted on the food particles during mastication. There have been multiple attempts to correlate chewing activity and tooth wear, as well as the food properties and chewing muscle arrangements. Because there are a plethora of factors involved, the issue remains largely unresolved. Resulting ideas that have been derived from a wide variety of studies that attempt to quantify and explain chewing activities in primates have not yet led to a clear-cut understanding of mastication in extant primates. Certain structures of the molars are elaborate in different primates, presumably to increase the efficiency of mastication. Here, however, as in other correlations between morphology and function, such as locomotion of primates, the functional potential of primate molars exceeds by far the possibility of exact determination of the relationships between tooth morphology and particular food items that are ingested. Only certain trends can be distinguished. For example, for primates that eat primarily leaves or insects, it appears to be more important to reduce these comparatively tough food into small particles during mastication to facilitate digestion than for those primates that eat predominantly soft food, such as fruit (Lucas, 2005). One of the reasons for this is that the digestibility of cellulose of leaves and chitin from many insects is increased when the food is reduced to small particles. Because fruit, on the other hand, is soft, it is thus crushed and digested much more easily. Often leaf- and insect-eating primates have longer shearing crests on the occlusal surface than do fruit-eating primates. Such crests are much better suited to cut up or macerate hard food items such as leaves than are teeth that lack shearing crests.

Evolutionary Trends of Tooth Morphology

Within the order Primates are several trends modifying the number of cusps that combine to form the occlusal surfaces of molar teeth. Almost certainly *Tarsius* is the extant primate genus that most nearly exhibits an occlusal tooth morphology resembling the original primitive eutherian molar pattern described earlier, in which there are three major cusps in upper and six cusps in lower molars.

The most common trend affecting structure of teeth in primates is the addition of the hypoconid to upper molars and the reduction or total loss except in *Tarsius* of the anterior cusp (the paraconid), situated at the mesial trigonid end of the lower molars. The hypocone is usually derived from the *cingulum*. Hypocone, however, is only a positional name for the cusp that is known to have arisen independently several times. In cases when the hypocone originates from the cingulum, it is called a true hypocone. If a cusp in the same position develops by splitting of the protocone into two cusps, the new cusp is called a pseudohypocone, a term first used by Stehlin (1916). The subject of occurrence of hypocones among primates has also been discussed in detail by Gregory and Hellman (1927). In the North American early Eocene primate lineage running from *Pelycodus* to its descendant *Notharctus,* it can be seen that a pseudhypocone has arisen by splitting of the protocone. Among extant prosimians, one can find a number of transitional stages between the three-cusped and the four-cusped types of upper molars. In all cases, however, the hypocone, be it small or large, is derived from the cingulum. Hunter and Jernvall (1995) and Kangas et al. (2004) documented that adaptations are rooted in preadaptation, a fact that is beautifully supported by the evolutionary development of the hypocone.

In lower molars, the general trend is toward reduction of the anterior or mesiolingual cusp, the paraconid. Also the most posterior or "third" cusp of the talonid, the hypoconulid, is reduced on the M_1 and M_2 of many extant primates.

CHEWING MECHANICS

Biting and chewing functions are generally complex. They not only vary with the shape and size of the teeth involved but also with the effects of the objects that are bitten or chewed. The morphology of the temporomandibular articulation, as well as the insertion and strength of the biting and chewing musculature, and consequently the shape of the mandible as well as the shape of the entire skull, particularly the maxillary and temporal regions, all are affected by the biting and chewing process. One of the major roles is played by the occlusal morphology of the teeth and their age-related changes. In many primates, the enamel structure

varies, and with continued use the enamel is abraded and the softer dentine exposed between enamel areas. Wear also causes the enamel to be resculpted into more or less sharp cutting edges that are differently angled toward the occlusal surface, which is the functional part of the tooth.

The position and shape of the temporomandibular joint (Figure 7.4) is different among primates, often directing or restricting the possible movement of the mandible in a defined manner. This articulation differs in the indriids from that of the other lemurs, and both in turn differ from this region in lorisid prosimians in which it is positioned deep within the side of the large bulla comprising the dorsomedial wall. On the lateral aspect of the joint, the zygomatic provides the bony wall extending downward that causes the temporal counterpart of the articulation (glenoid fossa) to have the shape of a comparatively deep bowl. The mandibular articular surface is almost ball-shaped, extending downward onto the posterior aspect of the mandibular ramus in the shape of an elongated triangle. The long axis of this triangle covers the hind aspect of the mandibular ramus downward for about one-fourth of its height and ends in a tip. In lemurs the temporal part of the temporomandibular articulation is rather flat, with neither the bullar side nor the posterior wall (postglenoid process) delineating the glenoid fossa, being either high or steep. There is no bony barrier at the outside as the temporal articular surface, which smoothly extends onto the lower aspect of the zypomatic arch and then fades out. On the mandibular ramus the articulation consists of a half rod on top of the articular process, its long axis being perpendicular to the long axis of the mandibular ascending ramus. This cylinder is covered by the articular surface on its upper side. In lorisid primates, the temporal part of this articulation is equally flat as in lemurs, but it differs from them in having a rather sturdy postglenoid process. Functionally seen, among prosimians the mobility of the mandible is most obviously restricted in the

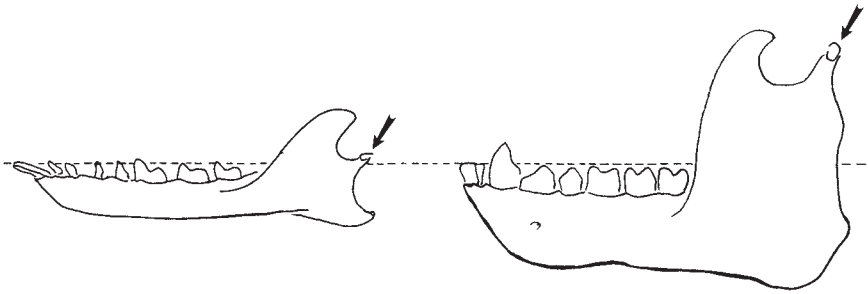

Figure 7.4 Lemur mandible on left and anthropoid mandible on right (seen from left side) contrasting the various levels of occlusal (functional surface) tooth plane (stippled line) and lever arm height of the ascending ramus (arrows indicate the position of the mandibular articulation with the skull).

indriids and most freely mobile in lemurs. In *Tarsius,* this articulation is rather similar to that of indriids. The glenoid fossa of *Daubentonia* is totally flat, anterioposteriorly long like a slide, and unrestricted to the front and back. The articular process at the back of the jaw is positioned rather low on the ascending mandibular ramus, and the articulation is ball-shaped and not very wide; the articular surface slopes backward onto the mandibular ramus. This arrangement of the mandibular articulation is unrestricted and allows the rotary swivel-like movement of the lower jaw during the process of gnawing of holes.

Typically in anthropoids the temporomandibular joint is rather flat and wide in both the anterior and lateral directions, but backward movement is limited by the glenoid process.

A detailed analysis (Hiiemae and Crompton, 1985) of mastication, food transport, and swallowing in mammals showed that the basic sequence of food intake and processing is rather stereotyped in mammals, including primates. Food items of a size appropriate to fit into the eaters' mouths have to be taken in, processed, swallowed, and digested. Finally, indigestible waste has to be discarded.

There is a cycle of actions involved:

1. The mouth is opened to put the food item into it, either by picking it up directly with the snout or by putting it into the mouth by hand.
2. The food is bitten off from an item that is too large to fit into the mouth or otherwise manipulated between the jaws.
3. The jaws close with the food inside the mouth, and the food is brought between the upper and lower teeth to be processed.
4. Processing requires several jaw movements either alternating tooth-row sides or chewing it on the side of the mouth. There is closed-mouth movement of the upper and lower teeth against each other while the food is positioned between the teeth. This part of the chewing activity has been labeled the "powerstroke." Mastication requires that the food is moved back and forth and from side to side, or rearranged on one side of the mouth with the help of tongue, teeth, and cheek musculature. With mouth closed, the teeth must separate and reclose numerous times while chewing. The number of powerstrokes needed to process one bite depends on the texture of the food as well as the occlusal morphology of the teeth. Powerstrokes result in puncturing, breaking, shearing, or crushing the food, and saturation of it with saliva continues until the food can be safely swallowed. There are also bilateral jaw movements that do not require much straight up and down biting force and result in food trituration.
5. After the food has been swallowed, the mouth can be reopened again for a new bite to enter the process. All these chewing activities leave wear marks (wear facets) on the teeth, that can, but may not, be characteristic for certain

foods and certain animals. Interstitial wear between adjacent teeth also occurs because adjoining teeth move against each other during chewing.

Attempts to quantify chewing function in primates are many, but they are not necessarily coherent and often more confusing than informative.

DENTAL FORMULAE AND MORPHOLOGY

In the following morphological descriptions, the first (mesial) incisors (= I^1 and I_1) are referred to as central or inner incisors, the second pair (= I^2 and I_2) as distal, second, or lateral incisors. With the premolars, the assumption is that during the evolutionary reduction of the number of premolars, the teeth in the front of series are lost. Therefore, in primates with three premolars these are technically premolars 2, 3, and 4, which are retained in extant primates (that is, P^2, P^3, and P^4 in the maxillary dentition and P_2, P_3, and P_4 in the mandibulary dentition). The reverse is the case with the molars that are phylogenetically lost where the reduction occurs at the end of the tooth row. Thus, primates with three molars retain M^1 M^2 M^3 in the maxilla and M_1 M_2 M_3 in the mandible. In the following descriptions, premolars are referred to by the number according to their position within the jaw, namely, to P^2 and P_2 as first premolars, P^3 and P_3 as second premolars, and P^4 and P_4 as third premolars. There is no difference between the positional number assignment and the phylogenetic assignment for molars because M^1 M^2 M^3 as well as M_1 M_2 M_3 are, in fact, first, second, and third molars both phylogenetically and in their position within the tooth row.

Phylogenetic tooth assignment in extant primates are as follows:

$$\frac{I^1 I^2 C\ P^2 P^3 P^4 M^1 M^2 M^3}{I_1 I_2 C\ P_2 P_3 P_4 M_1 M_2 M_3}$$

Positional tooth assignment in extant primates are as follows:

$$\frac{\text{Central I} \cdot \text{Lateral I} \cdot \text{C} \cdot \text{First P} \cdot \text{Second P} \cdot \text{Third P} \cdot \text{First M} \cdot \text{Second M} \cdot \text{Third M}}{\text{Central I} \cdot \text{Lateral I} \cdot \text{C} \cdot \text{First P} \cdot \text{Second P} \cdot \text{Third P} \cdot \text{First M} \cdot \text{Second M} \cdot \text{Third M}}$$

Figure 7.5 Dentition of the tree shrew *Tupaia glis*. From left to right: three incisors (white) in the mandibular dentition, canines (black), premolars (shaded), molars (white).

GENUS *TUPAIA*

Tree shrews (Figure 7.5) are often compared to primates because they are both similar to them but also much less derived because they have a dental formula of:

$$\frac{2\text{-}1\text{-}3\text{-}3}{3\text{-}1\text{-}3\text{-}3},$$

retaining three lower incisors, unlike any of the extant primates (see Figure 7.5).

Upper Incisors

The upper incisors are of simple, cylindrical shape. The central pair is longer than the lateral pair and also larger in diameter. There are large diastemata between the two central incisors and between the central and lateral incisors.

Lower Incisors

The two inner lower incisors are comparatively long and slightly spatulate. The lateral pair of incisors is smaller in length and diameter than the two other pairs and cylindrical in shape. Upper and lower incisors do not have any bite contact when the mouth is closed but function more or less like a pair of clasps. The lower incisors are tilted forward and are implanted almost in line with the long axis of the mandibular ramus; in other words, they are procumbent.

Upper Canine

A wide diastema separates the upper canine from the lateral incisors. The canine morphology is only slightly different from that of the lateral incisors when

unworn and is essentially like it when the tip is worn off. The canine is slightly more pointed than the lateral incisor when unworn and curves somewhat backward.

Lower Canine

The lower canine is separated about as much from the lateral incisor as is the latter from the middle incisor. The lower canine is larger in diameter compared with the first two incisors but of similar length and shape. It is caniniform with a backward directed apex. The lower canine is larger than the upper canine and implanted procumbently into the mandible.

Upper Premolars

In the following discussion, I refer to the positionally first premolar of Tupaiiformes as first premolar and the distally following two as second and third, although historically in mammals with only three premolars, such as tupaiids and primates, the positionally first premolar is actually the second premolar equivalent to the premolars of ancient mammals. It is the first and most mesially positioned premolar of the original four that is commonly lost in mammals during the process of evolutionary change.

A small gap separates the topographically first, simply shaped upper premolar from the canine. It is a low, single-cusped tooth, also separated from the second premolar by a small gap. Second and third premolars are increasingly larger in occlusal surface diameter and are triangular when viewed from the outside. These teeth have a single buccal cusp, the paracone. These cusps are much higher and more dagger-like in P^2 and P^3 than are the two buccal cusps on each of the three molars.

Lower Premolars

The three lower premolars are different from each other in shape and projection height. The positionally first lower premolar is much smaller than the canine (less than half the canine size) and is separated from the canine by a small gap. It is also somewhat procumbent and is pointed with one cusp. The first and second premolars are separated from each other by a small, real diastema. When unworn, the second premolar projects nearly twice as high as the first. P_2 commonly has only one cusp. In some individuals, P_2 has a small *cingulum* on the inner side that extends all the way to the end of the tooth, forming a small, talonid-like extension. Following behind the second premolar is the two-rooted and two-cusped third premolar. The protoconid is the dominating cusp in front of the tooth and the metaconid, adjoining distally, is much smaller. There can be a small talonid extension on the third premolar situated much lower than the metaconid.

No distinctive cusps can be recognized on the small talonid of P_3 that juts back under the slightly forward projecting paraconid of the following M_1. The shape of P_3 is transitional into the shape of the first molar.

Upper Molars

M^1 is the largest of the three molars. The first and second molar have a large inner cingulum that is especially marked on M^1, where it bulges out on the inside of the tooth, giving the occlusal surface a quadrangular shape. There is often a hypocone, derived from the cingulum, on M^1. All three upper molars have three cusps and three roots positioned under the cusps. M^2 is smaller than M^1 and M^3 is very small, having only about a third of the occlusal surface of M^2.

Lower Molars

M_1 is only slightly larger than M_2. The occlusal surface of the trigonid is distinctly higher than the occlusal surface of the talonid. The protoconid is the highest cusp in unworn molars. An enamel protrusion on the front of M_2 extends under the backward, projecting small hypoconulid of M_1 like a strut. The same type of interlock occurs between M_2 and M_3. In both M_1 and M_2, the hypoconulid is crowded inside toward the entoconid and is separated from the hypoconid.

Prosimii

The morphology of teeth is variable to a degree within genera and even within species. There can be details that randomly vary between individuals and even bilaterally on the same individual.

Lemuriformes and Lorisiformes

The dental formula of living Lemuridae and Lorisiformes is identical with one exception: in *Lepilemur* (as well as the subfossil genus *Megaladapis*), the upper incisors are not replaced in the permanent dentition. In both family Lemuridae (including *Lepilemur*) and the infraorder Lorisiformes, the lower incisors are procumbent, forming a toothcomb together with the canines (Figure 7.6). The dental formula of Lemuridae except *Lepilemur* and Lorisidae is:

$$\frac{2\text{-}1\text{-}3\text{-}3}{2\text{-}1\text{-}3\text{-}3}$$

and the dental formula of *Lepilemur* is:

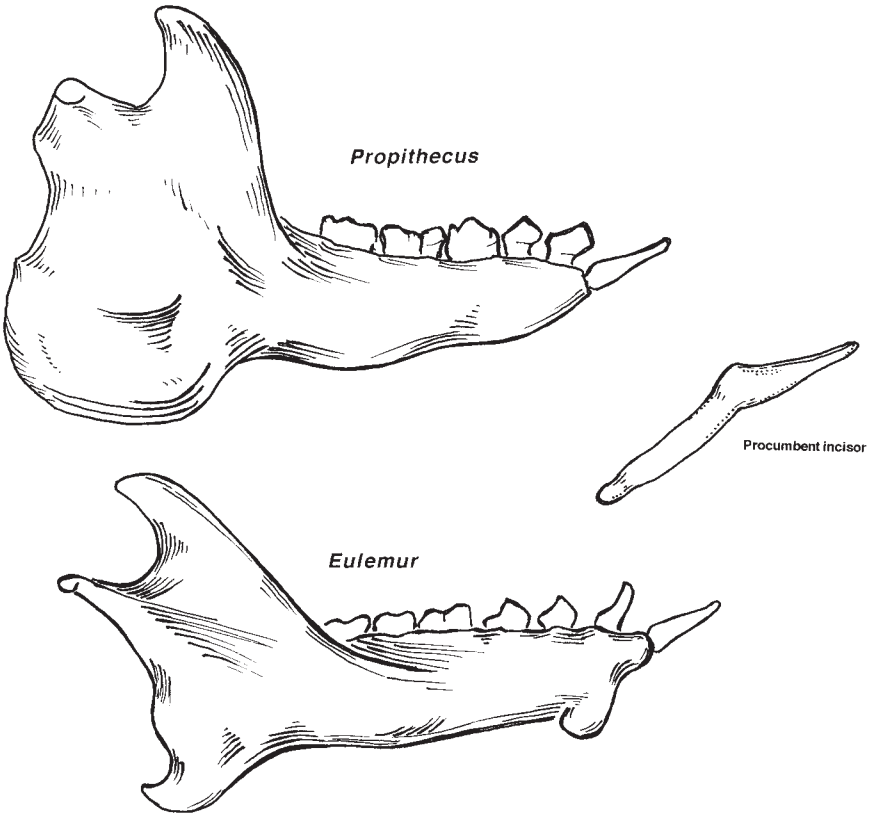

Figure 7.6 Mandibles of two prosimian primates seen from the right: a sifaka *(Propithecus)* and a lemur *(Eulemur)*, showing difference of build, procumbency of mandibular canines and incisors (toothcomb), and a procumbent incisor.

$$\frac{0\text{-}1\text{-}3\text{-}3}{2\text{-}1\text{-}3\text{-}3}$$

In the milk dentition of *Lepilemur,* small upper incisors are present, so that the deciduous dental formula of *Lepilemur* is:

$$\frac{2\text{i-}1\text{c-}3\text{m}}{2\text{i-}1\text{c-}3\text{m}}$$

Lemuridae and Lorisidae, sometimes grouped as strepsirrhines, are comparatively uniform in their dental morphology. Lorisid genera *Arctocebus* and *Loris* have very small upper incisors. Also remarkable is the already noted difference characterizing the lemurid genus *Lepilemur,* namely, the lack of upper

incisors of and the striking morphological difference in genus *Phaner,* which is described in detail later.

Genera *Lemur, Eulemur,* and *Lepilemur*

Upper Incisors

As an exception to the rule, genus *Lepilemur* does not have any upper incisors and accordingly the premaxillare is reduced to a mere strip of bone (Figure 7.7).

The upper incisors are reduced in size to small and short cylindrical teeth. The central pair is somewhat smaller than the lateral pair. These two pairs of incisors are implanted rather laterally in the premaxilla and are separated by a wide gap. A result of this is that during occlusion with upper and lower jaws aligned, the entire toothcomb (I_1-I_2-C) is positioned between the central upper incisors (Figure 7.8).

Lower Incisors

These teeth are procumbent and slightly angled so that the tooth crown is nearly parallel to the long axis of the mandible. The procumbency is most expressed in genus *Eulemur* and less pronounced in the Lorisidae. There is no contact at all between lower and upper incisors. The lower incisors have long crowns, are very narrow and flat, and are implanted close to each other.

Upper Canine

In both sexes, the upper canines are dagger-like, long, pointed, and bent backward. These canines are positioned closely to the lateral incisors but separated from the first premolar by a large diastema.

Lower Canine

In the mandible the canines are also procumbent and are included in the toothcomb. Their crowns are nearly as long as those of the incisors but slightly more bladelike, or, in other words, the canines are somewhat broader than the latter. Also, the canine tooth crown tilts slightly inward toward the jaw's midline and is not aligned with its root.

Upper Premolars

A comparatively wide diastema separates the first upper premolar from the canine. This tooth consists of one prominent cusp, the paracone, with a steep

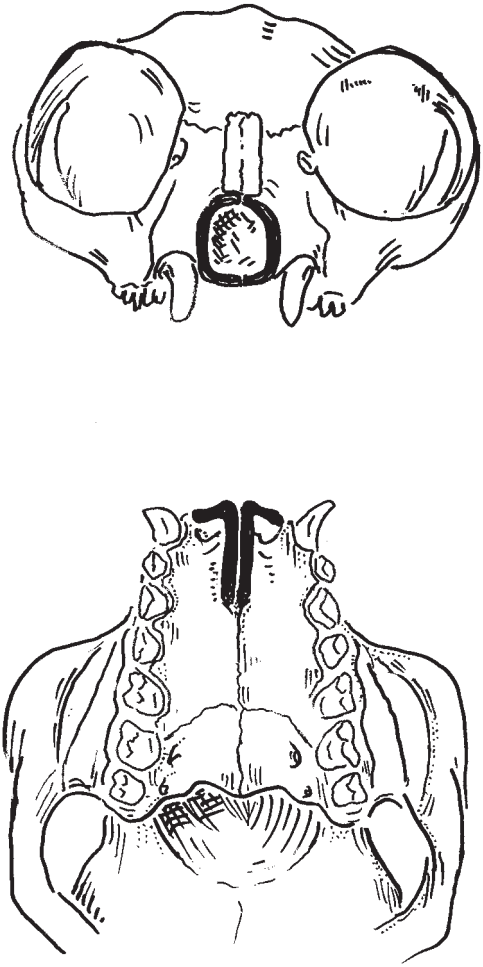

Figure 7.7 Front of the skull of *Lepilemur leucopus* (the sportive lemur), front view (above) and occlusal view (below) showing the premaxilla (black) that is reduced to a narrow band around the nostrils and does not support any incisors.

cutting edge on its anterior and posterior slopes, resulting in a pointed tooth. Seen from a lateral view, the second and third premolars are separated by a small diastema in some individuals. An additional cusp on the lingual side of the tooth, the protocone, enlarges the occlusal surface of the second premolar considerably compared with the first premolar. In the third premolar, the protocone is larger and more distinctive than the second premolar. The upper premolars gradually integrate morphologically into the molar morphology.

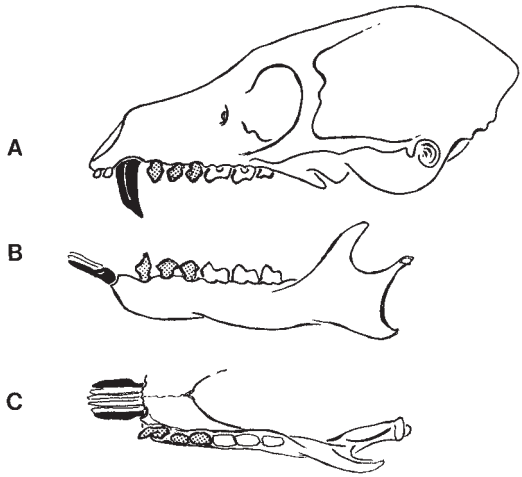

Figure 7.8 Lemur dentition (from left to right): incisor (white), canines (black), premolars (shaded), molars (white). A) Skull (seen from left side) with upper dentition, B) mandible and lower dentition with procumbent toothcomb (incisors and canines), and C) mandible seen from above, showing toothcomb configuration.

Lower Premolars

The first lower premolar has one cusp and at the back a short heel. This tooth is shaped like a canine, compressed from side to side, with one high-pointed cusp. The entire height of the tooth may not exceed its greatest length at its base. A small gap separates the first premolar from the canine, and a gap of approximately the same size separates the former from the second premolar. The second premolar is considerably smaller than the first premolar and is positioned closely appressed to the third premolar. The shape of the second premolar resembles that of the first premolar; it has, however, only about half the length of the latter. The tooth also has a heel that is somewhat broader than the heel of the first premolar. Three cusps can readily be identified in the trigonid region of the third premolar. The paraconid is not as high as the protoconid and the metaconid, the protoconid being somewhat higher than the metaconid. No distinctive cusp can be recognized on the talonid basin, which consists of a central groove surrounded by a continuous ridge. The talonid of the third premolar juts under the front end of the first lower molar with its hind end.

Upper Molars

The protocone is large in the first two molars and somewhat forward positioned. A distinctive cingulum at the inside holds two cups in the first molar: in the front

the pericone and at the back the somewhat smaller hypocone. This additional anterior cone within the inner cingulum, the pericone (Stehlin, 1916), is much bigger than the hypocone in *Eulemur mongoz* and *E. macaco* (Remane, 1960). Swindler (1976) calls this cusp the protostyle. Also in the second molar, the pericone is well developed, whereas the hypocone is usually absent. The first and second molars are subequal in size, the latter somewhat smaller in occlusal surface size and slightly lower in its projection above the alveolar margin. The third molar is considerably smaller than the second and simply shaped with three cusps. *Lepilemur* and *Hapalemur* are distinguished from *Lemur* and *Eulemur* in lacking the pericone and hypocone: all three molars are strictly tricuspid with only the paracone, metacone, and protocone present.

Lower Molars

The first lower molar does not have a paraconid. In the trigonid area, the protoconid is the most prominent cusp. A crest connects it with the somewhat lower metaconid. There is a low ridge at the front of the tooth, and together with the ridge that connects the two cusps this ridge surrounds the slightly inwardly shifted trigonid groove. The occlusal surface of the talonid is not much lower than that of the trigonid. In the talonid area the hypoconid is the highest and most distinctive cusp. The hypoconid is incorporated into a ridge that encircles the entire talonid area. Other cusps are not easily discerned in the talonid. The distinctive talonid groove is surrounded by this crest and mesially by the trigonid elevation. The first molar is slightly larger than or equal in occlusal area to the second molar. Seen from the side the first molar projects somewhat higher than the second molar, which is exceeded in height by the third molar. The occlusal surface of the third molar is much smaller than that of the two preceding teeth. The third molar's crown pattern is simplified to an oblique crest that connects the protoconid with the metaconid, and the talonid is surrounded by crests. The lower molars of *Hapalemur* are very similar to those of genera *Lemur* and *Eulemur.* In *Lepilemur,* the lower molars are characterized by comparatively small trigonid sections and well-developed hypoconids in large talonids. Only the third molar has a small hypoconulid.

Genus *Phaner*

This lemurid genus differs from the above described genera in several remarkable dental features (Figure 7.9).

Upper Incisors

The central incisor is considerably larger than the lateral incisor. Even though the roots of the internal incisors are separated from each other by a large gap,

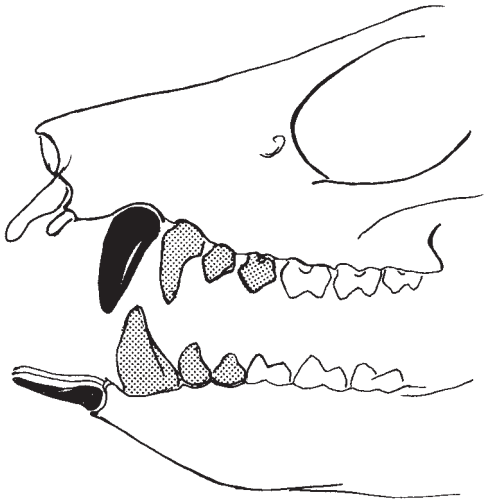

Figure 7.9 The unusual dentition of *Phaner furcifer* (the fork-marked lemur). From left to right: incisors (white), canines (black), premolars (shaded), and molars (white). Note the caniniform first lower premolar.

the crowns slope inward toward each other. Even though, the tips of these incisors do not touch each other. The lateral incisors are tiny and peglike and are closely positioned to the lateral incisors. A wide diastema separates them from the canines.

Lower Incisors

The internal and external incisors are about identical in size, closely appressed to each other, and procumbent. Their crowns are comparatively longer than those of other lemurs.

Upper Canine

The upper canine is robust, comparatively thick buccolingually and projects high above the occlusal surface of the incisors as well as the cheek teeth.

Lower Canine

The lower canine is closely appressed to the lateral incisor and only slightly wider than the latter. It is incorporated into the procumbent toothcomb and of the same crown length as the incisors.

Upper Premolars

The shape of the first premolar is almost identical to that of the canine. It is separated from the canine by a diastema and only slightly smaller overall; in combination the canine–premolar region is unusually large—larger than in any other extant prosimian. To accommodate these wide teeth, the maxillary bone bulges out where it contains the canine and first premolar roots. The two following premolars are tiny, the second premolar being single cusped, the third premolar having two cusps, with the large paracone on the outside (bucal) and lower leveled and smaller protocone (lingually) on the inside.

Lower Premolars

The first lower premolar is large and caniniform, projecting high above the two following premolars. It functions as a powerful crunching tool in combination with the large upper canine in front of it and the first premolar engaging behind it when the two jaws are in full occlusion. Second and third premolars have only one cusp, are less than half as big as the first premolar, and are slightly elongated backward by a small cingular shelf.

Upper Molars

The upper molars are tricuspid and almost subequal in size, with the third molar being only slightly smaller than the two preceding teeth. In some individuals the second molar has a slight hint of a hypocone. All three molars are so small that they do not exceed in mesiodistal length the combined mesiodistal length of the canine and first premolar.

Lower Molars

The three lower molars are subequal in size and have four cusps.

Indriidae

The three prosimian genera *Indri, Propithecus,* and *Avahi* belong in family Indriidae and have a dental formula that differs from that of family Lemuridae (Figure 7.10). Indriids have only two premolars in their deciduous dentition and the milk tooth formula reads:

$$\frac{2\text{i-}1\text{c-}2\text{m}}{2\text{i-}1\text{c-}2\text{m}}$$

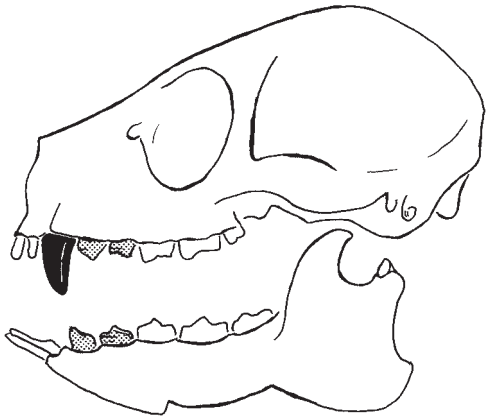

Figure 7.10 Indriid *(Propithecus)* dentition. From left to right: incisors (white), canines (black), premolars (shaded), and molars (white).

The small lower canine that occurs in the deciduous dentition is not replaced in the permanent tooth row, and consequently the tooth formula for the permanent dentition of indriidae is:

$$\frac{2\text{-}1\text{-}2\text{-}3}{2\text{-}0\text{-}2\text{-}3}$$

This interpretation of the permanent number of teeth in the indriid dentition is based on studies by Bennejeant (1935), Friant (1935), and Remane (1960). An alternative interpretation of the teeth in the front of the indriid lower jaw would be that one of the deciduous incisors is not replaced and the lower deciduous canine is replaced by an inciviform, procumbent canine that is incorporated into the narrow toothcomb (James, 1960; J. H. Schwartz, 1974; Swindler, 1976). In this case the tooth formula would be:

$$\frac{2\text{-}1\text{-}2\text{-}3}{1\text{-}1\text{-}2\text{-}3}$$

In the three indriid genera, the toothcomb is less procumbent than in genus *Eulemur* or the Lorisidae, with the latter having an intermediate degree of toothcomb procumbency. The mandible of indriids is considerably higher and more robust than the gracile mandibles of the lemurid and lorisid genera. In the mandible, the ascending ramus is considerably longer mesiodistally and higher than in the other extant prosimians. The mandibular angle is rounded in the indriid genera and does not extend backward into an upward directed apex. In *Propithecus* and *Avahi,* the symphysis slopes backward all the way to the level of M_2. Because the snout is considerably longer in *Indri* than in *Propithecus* and *Avahi,* the mandible of the *Indri* is comparatively long and narrow and the lower

end of the mandibular symphysis ends under the front end of the first molar, not at the level of the second molar.

Upper Incisors

The upper central incisors are separated from each other by a gap. The roots are further removed from each other than are the tooth crowns. The tooth crowns are also wider than the roots and concave from the inside. In *Propithecus* and *Indri,* the lateral incisors are much smaller than the internal pair, have the same overall shape, and are much shorter than the latter. In genus *Avahi,* both upper incisors are subequal in size and shape; they are more or less peg-shaped, and the internal pair are also separated by a large gap.

Lower Incisors

The central incisors are bladelike, compressed from side to side, and slightly curved upward. The crowns of the lateral incisors are approximately twice as wide as the internal pair's in *Propithecus* and *Indri* and only slightly wider in *Avahi*. The outside of the crowns slopes inward toward the tip, and the crowns are, just as those of the internal incisors, slanted upward to form a scoop.

Upper Canine

In genus *Indri,* the upper canines are separated from the external incisors by a wide gap. There is only a small gap between these teeth in *Propithecus* and no gap or only a very small gap in genus *Avahi*. In all three genera, the upper canines are not projecting much higher than the occlusal level of the crowns of the distally adjacent premolars. Their shape is almost triangular as seen from the outside. There is a mesially directed slight elongation on the bottom of the crown of the canine that juts under and outside the front end of the following premolar, causing these teeth to form a continuous blade in this area.

Lower Canine

The lower canine is missing in the adult dentition. Even though the lateral tooth that is incorporated into the procumbent toothcomb has been regarded as the canine by some authors, it is considered here as the lateral incisor.

Upper Premolars

The first two premolars are of simple design, each with only one cusp. Sharp cutting edges slope down from the tip, and the crowns are mediodistally longer than high. The base of the crown of the first premolar has a slight cingulum that

is closely appressed at the base to the distal base of the canine and similarly in back to the base of the second premolar. The second premolar is equally appressed at the base to both, the first premolar in front and the first molar in back. On the lingual aspect both premolars have a cingulum-like extension sloping distally to the base of the crown of the caniniform first premolar and the second mandibular premolar, respectively. When the jaw is closed the caniniform first lower premolar is positioned behind the upper canine, not in front of the upper canine where the lower canine would be positioned.

Lower Premolars

In the mandible the first premolar has one prominent cusp and has evolved the shape of a canine, thus replacing the canine functionally. Its true nature can be identified as a premolar because it occludes behind the upper, true canine, whereas a lower canine (if functioning) would be positioned in front of the upper canine when the jaws are in occlusion. There is a gap between the lateral incisor and the caniniform first premolar. Seen from the inside, the first premolar is concave and spoon-shaped. The second premolar has only one cusp, and the crown is not as high as that of the first premolar. Like in the upper premolars, these teeth are closely appressed to each other at the base of their crowns, both in the front and back, thus creating a sharp ridge.

Upper Molars

The first two molars are essentially four cusped and not much longer than wide. The buccal cusps are larger than the lingual ones. On the buccal side, there are small knobs mesiobucally within the cingulum on both the paracone and the metacone, called the parastyle and mesostyle respectively. The hypocone is well developed on both molars. Seen from the buccal and lingual aspect, the teeth have a deep groove in the middle separating the bulbous pillars under the cusps from each other. The third molar lacks the hypocone, is smaller than the two other molars, and has a triangular occlusal shape. In worn teeth, the comparatively thin enamel is elevated above the more deeply worn area of the exposed dentine and thus creates sharp cutting edges.

Lower Molars

All three molars are longer than they are wide and have four well-developed cusps. There is no paraconid, but a diminutive parastyle is seen on the first molar. There is no cingulum, and only the third molar has a small hypoconulid in the back. The cusps are sharp and pointed when unworn, and in the first molar the buccal protoconid is positioned further forward than the lingual metaconid, and

the more distal cusps hypoconid and entoconid are positioned lingually–buccally adjacent to each other. As seen from above, all three molars have a restriction in the middle, separating the frontal tooth portion with metaconid and protoconid from that in the back with hypoconid and endoconid; in occlusal view, this gives these teeth an hourglass shape. The molars are closely appressed to each other.

Daubentoniidae

The family Daubentoniidae with only one extant genus and species, *Daubentonia madagascariensis,* is characterized by the most highly derived dentition among all extant primates (Figure 7.11). The front teeth of *Daubentonia,* the aye-aye, are reminiscent of the dentition of rodents, a fact that misled early naturalists to describe and classify the aye-aye as belonging in the mammalian order Rodentia.

This peculiar tooth morphology of *Daubentonia* also affects the outline and overall shape of the entire skull, contributing to its rodent-like appearance. The anterior dentition of *Daubentonia* resembles that of rodents not only in the number and shape of the teeth, but also in the distribution of the histological material that makes up the tooth. Enamel, if present at all, is very thin except on the anterior aspect of the front teeth where it is very thick. It appears that the wear on these front teeth is governed by the hardness of the anterior layer of enamel. Moreover, it is quite unlikely that the lower gnawing teeth of the aye-aye are canines, as some have erroneously suggested (e.g., Winge, 1895; Gregory, 1922). There can be no doubt about the fact that the rodent-like upper front teeth

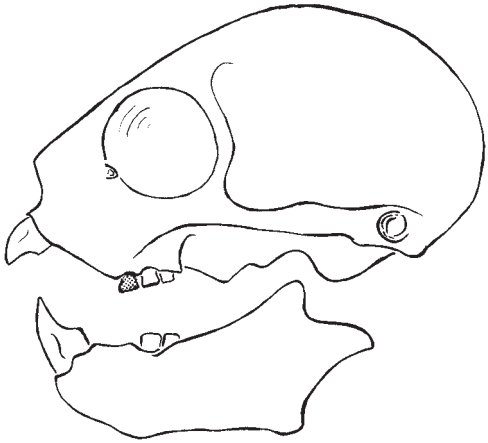

Figure 7.11 Dentition of the aberrant lemur *Daubentonia madagascariensis* (the aye-aye). From left to right: large incisors (white), no canines, premolar (shaded), and two molars (white).

develop in and are implanted within the premaxillae and are consequently incisors, as can be seen in newborn and subadult specimens (Peters, 1866; Ankel-Simons, 1996). It can therefore be safely assumed that the lower front teeth are also incisors. It has been shown (Ankel-Simons, 1996) that *Daubentonia* has in both the mandible and maxilla one deciduous incisor, one deciduous canine, and two deciduous premolars. Consequently, the milk-tooth formula is:

$$\frac{1i\text{-}1c\text{-}2p}{1i\text{-}1c\text{-}2p}$$

The permanent tooth formula reads:

$$\frac{1\text{-}0\text{-}1\text{-}3}{1\text{-}0\text{-}0\text{-}3}$$

and thus it appears that the deciduous incisors are replaced in the permanent dentition, but the deciduous canines are not replaced, nor are one of the two upper milk premolars; both lower deciduous premolars are not replaced either by permanent teeth. Three peglike molars are added in the adult dentition. Thus, five deciduous teeth are not replaced by permanent teeth. For an alternative and less widely accepted interpretation of *Daubentonia*'s dental formulae, see Tattersall and Schwartz (1974).

Upper and Lower Incisors

Both the upper and lower incisors are similar in shape and reach far back into the maxilla and mandible, respectively. In fact, the roots of these ever-growing incisors extend all the way to the area beneath the second molar in the maxilla and, in the mandible, beyond the third molar into the root of the ascending mandibular ramus. These teeth are compressed laterally and curved just like rodent front teeth. As stated already, the chisel shape of the aye-aye's most anterior teeth as seen from the side is, in part, a product of the anterior comparatively thick enamel layer on these teeth that prevents the front aspect from being worn down at the same rate as the occlusal surface that is made up only of dentine. The lower deciduous incisor is implanted in a procumbent manner, parallel to the long axis of the mandible, reminiscent of orientation in a toothcomb.

Canines

Both deciduous canines are not replaced in the permanent dentition. The lower milk canine is implanted in a procumbent manner, with its long axis parallel to the long axis of the mandible.

Premolars

A tiny, peglike tooth with one root is positioned distally to a considerable gap that separates it from the incisor and represents the upper permanent premolar. This tooth has one low cusp in an unworn state, and its occlusal surface becomes totally flat after wear has eroded the cusp away. The lower deciduous premolars are not replaced in the permanent dentition. Their occlusal surface is more or less rounded as seen from above.

Upper Molars

The upper molars are much larger than the diminutive premolar. The first and second molar have four low, rounded cusps and are almost equally wide as long, only slightly oblong mesiodistally. The third and smallest molar in an unworn state has three low cusps.

Lower Molars

These molars are separated from the incisor by a large gap. Each has four low cusps and the occlusal surfaces of these lower molars are considerably larger than those of the upper molars: the second lower molar has a surface area that is 1.5 times that of the upper second molar. In both upper and lower molars, the low cusps are abraded off rather quickly, leaving a more or less flat occlusal surface. The occlusal surface of these lower molars regularly has a slight mesiodistal groove running along the middle. The first lower molar is slightly smaller than the second. The first and second molar have an oblong occlusal surface, and that of the third molar is square. The third molar is slightly smaller than the others.

Tarsiidae

This extant family has but one genus, *Tarsius,* with seven species, including *Tarsius pumilus,* a former subspecies declared to be a valid species based on museum specimens (Musser and Dagosto, 1985) (Figure 7.12). Reduction of the number of teeth is regarded as an evolutionary progressive feature in primates. *Tarsius* and *Daubentonia* are the only extant primates that have only one lower incisor. The tooth morphology of tarsiers, however, most closely resembles the primitive occlusal pattern of early mammals. Among primates the *Tarsius* tooth morphology is most like that of fossil anaptomorphines, a group of small early to middle Eocene primates that have been documented predominantly in North America. Only one genus, *Teilhardina,* is also known from Europe. Their tooth morphology is primitive.

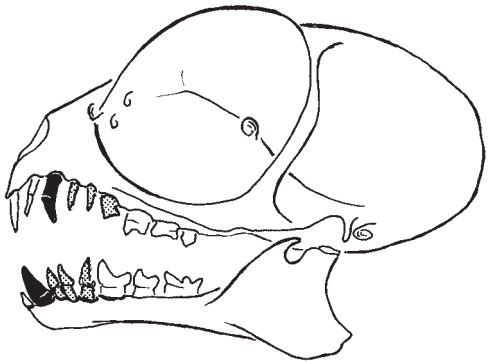

Figure 7.12 Dentition of tarsiers *(Tarsius syrichta)* showing insectivorous occlusal morphology. From left to right: incisors (white; note that *Tarsius* has only one lower incisor, which is unique for an extant primate), canines (black), premolars (shaded), and molars (white).

The tooth formula of genus *Tarsius* is as follows:

$$\frac{2\text{-}1\text{-}3\text{-}3}{1\text{-}1\text{-}3\text{-}3}$$

Upper Incisors

The inner pair of cone-shaped incisors is much larger than the lateral pair. Both pairs have the same simple and basic conical morphology.

Lower Incisors

Only one small, cone-shaped incisor is present. This pair is not implanted in a procumbent manner as in toothcomb prosimians but are directed upward.

Upper Canine

The upper canine is caniniform, only very slightly curved distally. It does not, however, project much higher than the lateral incisors and does not stand as high as the central incisors do. At its base, the canine is wider than the central incisor, however, which in turn is wider than the lateral incisor. There is only a very small gap between the lateral incisor and the canine.

Lower Canine

The lower canines are larger than the incisor pair and are shaped like typical canines, slightly curved distally and with a cutting edge on the labial aspect. There is practically no gap between the canine and the incisor.

Upper Premolars

Of the upper premolars, the first is considerably smaller than the canine, and it is unicuspid. P^3 (the second premolar) also has one cusp, and P^4 (the third premolar) has two, with the inside cusp (protocone) smaller than the outside cusp (paracone). The third premolar is the largest of the three, the first the smallest. The relatively conical premolar crowns, taken together with the conical canines and incisors, make the front teeth of *Tarsius* relatively uniform or homomorphic.

Lower Premolars

All three premolars are conical and have only one cusp. They gradually increase in size from the first to the third. There is a small heel-like extension distolingually at the base. No gaps occur between the canines, premolars, and molars.

Upper Molars

The three upper molars are tricuspid. They are approximately equal in occlusal area but decrease in crown height from the first to the third. Almost as in Insectivora or Chiroptera (bats), the three main cusps—paracone, protocone, and metacone—are very pointed and prominent. The paracone and metacone on the buccal side of these teeth are higher than the protocone on the lingual aspect. A well-developed cingulum on the linguodistal side of the molars shows a thickening that represents the hypocone. Both the cingulum and the incipient hypocone are usually very small and occasionally absent in M^3.

Lower Molars

In tarsiers, the trigonid of the lower molars retains three very steep and pointed cusps. They are the only extant primates that retain the most anterior cusp of the trigonid, the paraconid. The occlusal surface of the talonid area is lower than that of the trigonid. The talonid cusps—hypoconid bucally and the entoconid lingually—are well developed, whereas the hypoconulid is comparatively small. The crown of the third molar is somewhat lower than those of the two preceding teeth, but its occlusal surface is just as large.

ANTHROPOIDEA

Tooth number as well as tooth morphology are more uniform among living higher primates than they are in extant prosimians. Common to higher primates—except the South American family Callitrichidae—is the presence of four cusps in all first (M^1) and second maxillary molars (M^2). Another uniform feature is

the loss of the paraconid on lower molars in all higher primates as well as all modern prosimians except *Tarsius*. Swindler (1976) mentioned one exception to this general loss of the paraconid: he claimed that a paraconid occasionally occurs on M_1 of the rare South American cebid genus *Brachyteles*. Although among early mammals the trigonid in the front of the lower molar is highly elevated and the talonid crowns on the back of M_1 much lower, these two areas are of subequal height in the lower molars of extant anthropoids. The number of premolars is distinctively different in the two major groups of higher primates: all higher primates of the Old World have only two premolars in the upper and lower jaws, whereas all higher primates of the New World have three premolars. Their dental formulae look like this:

New World Cebidae, three premolars:

$$\frac{2\text{-}1\text{-}3\text{-}3}{2\text{-}1\text{-}3\text{-}3}$$

New World Callitrichidae, three premolars:

$$\frac{2\text{-}1\text{-}3\text{-}2}{2\text{-}1\text{-}3\text{-}2}$$

Old World Anthropoidea, two premolars:

$$\frac{2\text{-}1\text{-}2\text{-}3}{2\text{-}1\text{-}2\text{-}3}$$

New World Cebidae

Upper Incisors

In general, ceboids have upper incisors that are spatulate, with the central pair much broader and also longer than the lateral (Figure 7.13). There usually is a diastema between the incisors and the large, tusklike canine. The crowns of the lateral incisors are tilted toward the midline. The three genera *Cacajao, Chiropotes,* and *Pithecia,* have a specialized front dentition; both upper and lower incisors tilt strongly forward, rather than downward. The forward tilt of the incisors in these three genera is more pronounced in the upper dentition than it is in the mandibular incisors. The aberrant species *Callimico goeldii* also has incisors that tilt forward but to a lesser degree.

Lower Incisors

The lower incisors are subequal in size, slender, and long, with a small diastema, lacking in all other genera, that can be detected between the incisors

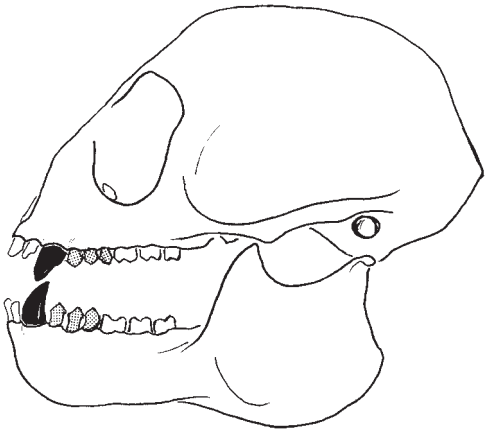

Figure 7.13 Cebid dentition. From left to right: incisors (white), canines (black), premolars (shaded), and molars (white).

and canines in the genera *Chiropotes, Pithecia,* and *Cacajao.* As with the upper incisors, the lateral incisors of the mandibular dentition tend to be tilted mesially. Usually only the central upper pair of incisors have bite contact with the lower incisors during occlusion. The incisors of *Cacajao, Chiropotes,* and *Pithecia* are procumbent, but unlike the toothcomb in prosimians where the procumbency results from a combination of root implantation in line with the mandibular long axis plus angulation of the incisor crown farther beyond the long axis of the root, the procumbency in cebids is solely the result of tilted implantation of straight teeth into a forwardly angled mandible. When occluded in *Cacajao, Chiropotes,* and *Pithecia,* the upper and lower incisors meet at an angle of about 90 degrees. Thus, the front teeth in these three genera function like a pair of tweezers, not like scissors with cutting edges.

Upper Canine

The upper canines are large, robust, caniniform teeth that project at least twice as high above the occlusal level of the premolars. There usually is a cingulum on the labial base and a groove on the mesial aspect. These canines are slightly outward directed in *Chiropotes, Cacajao,* and *Pithecia.*

Lower Canine

The lower canines do not exceed the height of either the incisors or the premolars very much and they have a shelflike extension on the lingual base

of the crown. There is often a small diastema between the canine and first premolar. The crown base is larger than that of the incisors and the premolars.

Upper Premolars

These teeth are bicuspid (paracone and protocone), with the labial cusp being higher than the buccal cusp. These premolars increase slightly in size from the first to the third premolar. In Howler monkeys *(Alouatta)*, the first premolar sometimes has only one cusp (the paracone).

Lower Premolars

The first of the three premolars is larger than the two following teeth, a rather unusual characteristic. All three teeth are usually bicuspid (protoconid and metaconid) with a cingulum surrounding the inner cusp. The enlarged first premolar functions against the back of the upper canine as a honing mechanism. Sometimes the third premolar is tricuspid in *Ateles,* and if this is the case, the third cusp is assumed to be the hypoconid.

Upper Molars

Molar morphology is fairly variable in cebids. M^1 and M^2 are usually square with four cusps (paracone, protocone, metacone, and hypocone). There is often a distinct crest between protocone and metacone on the first and second molar that is called a postprotocrista (it is also known as crista obliqua). The third molar is often considerably smaller than the two preceding molars, usually having three or even two cusps only. Third molars with four cusps occur only rarely. Incipient, tiny cuspules are common on the lingual cingula.

Lower Molars

The lower molars usually have four cusps (protoconid, metaconid, hypoconid, and entoconid). A hypoconulid is often found on all three molars in genus *Ateles* and occasionally on M_3 in genera *Brachyteles* and *Alouatta*. In the front, a crest (the protocristid) often connects the two cusps, protoconid and metaconid. Some cebids (e.g., *Cebus* and *Brachyteles*) have the cusps arranged in a manner somewhat similar to the bilophodont molar condition in Old World monkeys. This similarity has suggested to some that bilophodont teeth have been derived more than once from the archaic primate molar pattern.

New World Callitrichidae

In the subfamily Callitrichinae, one can distinguish two groups that are easily recognized by the crown height of their canines: the crowns of the lower canines of genera *Callithrix* and *Cebuella* are barely longer than the adjacent incisors and premolars. In contrast, species of genera *Saguinus* and *Leontopithecus* have mandibular canines that rise considerably higher than their incisor and premolar crowns. The former callithrichid genera are therefore called short-tusked marmosets, and the latter two genera are called long-tusked tamarins. The enigmatic genus *Callimico* is retained here in its own subfamily Callimiconinae within family Callitrichidae together with the marmosets and tamarins, although its dental formula is the same as that of family Cebidae.

Callimico

Upper Incisors Like in the other South American monkeys, the central upper incisors are larger than the lateral incisors. The crowns widen slightly toward the cutting edge reaching rather straight across. There are no cingula, and the teeth are implanted with a slightly procumbent forward tilt. Distal from the lateral incisor is a large diastema to accommodate the robust lower canine.

Lower Incisors The lower incisors are subequal in size, with the crown of the lateral pair tilting toward the central incisors.

Upper Canine The upper canine is robust with a sharp tip. It projects well above the occlusal surface of the adjacent teeth and has a small cingulum on its labial aspect. Its basal diameter is larger than that of the lower canine.

Lower Canine The lower canine is more pointed than the upper and has a large cingulum on its lingual base. There is a sharp edge on the inside, beginning at the tip and running all the way down to the crown base. This tooth reaches far above the occlusal surface of the neighboring teeth, being long tusked.

Upper Premolars The upper premolars one to three are subequal in size, only slightly increasing from the first to the third. Their occlusal outline is triangular, with the tip of the triangle on the labial side of the tooth. They are bicuspid with the higher cusp (paracone) positioned bucally and a deep groove between it and the lingual cusp (protocone). These premolars are in fact very similar to those of genus *Callithrix*.

Lower Premolars The mandibular premolars are morphologically very similar to the upper premolars. However, they are rather quadrangular in occlusal

view and have a ridge between the higher buccal cusp and the lingual cusp that is narrow, sharp, and more distinct. There is a small groove both in front (mesially) and behind (distally) this ridge. All three teeth are about the same size.

Upper Molars The first molar is the largest of the three, the third molar being diminutive in size. M^2 and M^3 have three cusps and have a well developed lingual cingulum. They have a triangular occlusal outline. A hypocone is not developed. The third molar only has two cusps and is usually considerably smaller—less than half as big in occlusal outline than the second molar. This third upper molar is clearly a rudimentary tooth.

Lower Premolars M_1 and M_2 are quadrangular teeth that have four cusps. The front (trigonid part) of the tooth is somewhat higher than the back (talonid part). The two mesial cusps, the protoconid on the buccal side and the metaconid lingually, are connected by a blunt ridge, the protocristid. The third molar is but a small, often rounded peg, reduced like the upper one.

Callitrichidae

The four callithrichid genera, *Callithrix, Cebuella, Saguinus,* and *Leontopithecus,* do not differ much as to the occlusal morphology of their teeth. Any marked differences are discussed in the following description (Figure 7.14).

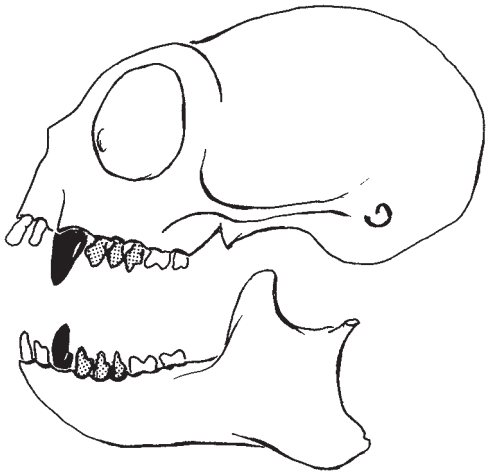

Figure 7.14 Callithrichid dentition. From left to right: incisors (white), canines (black), premolars (shaded), and molars (white).

Upper Incisors The upper incisors are spatulate, the central pair being considerably higher and wider than the lateral pair. The lateral pair has a comparatively pointed tip rather than a cutting edge. All four have a lingual cingulum. The crowns of the lateral incisors are slightly bent mesially. They are implanted in a forward direction, and there is no contact between the upper and lower incisors when the jaws are occluded.

Lower Incisors *Callithrix* and *Cebuella* have peglike, bluntly tipped lower incisors with high crowns. They are of the same crown size and are slightly bent in a forward direction; and both internal and external incisors are of the same crown height. They do not have cingula, and the lateral pair of incisors is positioned slightly behind the central pair on the front of the jaw, together forming a rounded scoop like structure. In contrast, the other two genera have spatulate incisors with crowns that widen slightly from the base toward the cutting edge. Central and lateral incisors are of equal size, and the lateral incisor has an enamel extension on the labial aspect of the crown base.

Upper Canine The canines are robust, sharply pointed, slightly bent distally, with a cingulum on the lingual side of the base. Crown height exceeds that of the adjacent teeth considerably. There is a variably sized groove on the mesial side of the tooth. Wettstein (1963) pointed out that the canines (atypically) are higher in females than in males.

Lower Canine Canines in genera *Callithrix* and *Cebuella* have a crown height that does not exceed that of the incisors, and these primates are therefore called short-tusked marmosets. These cone-shaped, pointed teeth are part of the incisor scoop in the two genera. In contrast, *Saguinus* and *Leontopithecus* have lower canines with crown height considerably exceeding that of the incisors; they are therefore called long-tusked tamarins. In all four genera, there is a well-developed cingulum on the lingual base of the robust canine, also known as a distostylid. The canines are larger than the lateral incisors.

Upper Premolars The first upper premolar is bicuspid except in *Leontopithecus,* where it has only one cusp and is slightly canine shaped. All other upper premolars have two cusps with the buccal cusp (paracone) being higher and more pointed than the lingual (protocone) cusp. There is a slight size increase from the first to the third premolar. A small buccal and a lingual cingulum are present.

Lower Premolars The buccal cusp dominates the first two premolars. In *Saguinus* and *Leontopithecus,* the first premolar is often unicuspid and somewhat caniniform. The protocone size increases from the first to the third premolar. The third premolar can have a small distal heel.

Upper Molars Callithrichids are unusual among extant anthropoids in having only two molars, the third molar having been lost. This condition has been interpreted as a secondary reduction, not as plesiomorphic (primitive) character state. They are also the only higher primates that show only three cusps on their upper molars (paracone and metacone bucally and protocone lingually). There is a cingulum on the lingual distal aspect of the first molar. The second molar is considerably smaller than the first. Small hypocones can be found occurring in low frequencies among species of *Saguinus* and *Callithrix* (Swindler, 1976; Swindler et al., 2000).

Lower Molars The lower molars are almost square in shape. They have four cusps and a central groove. The first molar is much larger than the second molar. The two cusps in the front, the protoconid and metaconid, are connected by a strong ridge, the protocristid. There is no crest between the two distal cusps (hypoconid and entoconid). The hypoconulid is not present.

Old World Cercopithecoidea

All genera and species of Cercopithecoidea (e.g., Figure 7.15, Catarrhine dentition) have an identical dental formula:

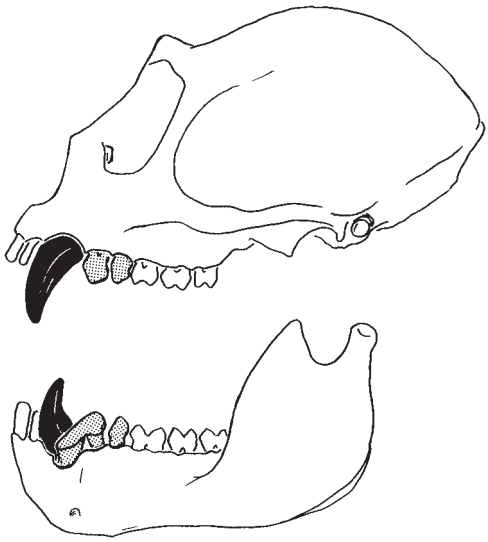

Figure 7.15 Catarrhine dentition (shown here is that typical of cercopithecoids). From left to right: incisors (white), canines (black), premolars (shaded), and molars (white). Note the sectorial first lower premolar.

$$\frac{2\text{-}1\text{-}2\text{-}3}{2\text{-}1\text{-}2\text{-}3}$$

Within this superfamily, the tooth morphology in general and molar morphology in particular is consistent. The main cusps of the molars are positioned in two pairs inside and outside, and they are directly opposite to each other, situated as at the corners of a square. They are usually connected by variably prominent cross-ridges that run at right angles to the long axis of the tooth row. Individual cusps are usually prominent in crown height. In front of the mesial ridge there is often a small grove, and distal to the hind ridge is a larger groove. This symmetrical position of the molar cusps and their connection across the tooth form a characteristic molar cusp pattern called bilophodont. This pattern is found not only in cercopithecoid primates but also in pigs, tapirs, rhinoceroses, and, in somewhat modified form, in a few marsupials. This tooth pattern seems to be related to folivory. As noted earlier, folivory is vaguely defined, as are the descriptions of the diets of these animals; the correlations between dental function and morphology are equally unspecific. The bilophodont tooth pattern is found in cercopithecoid monkeys in the three upper molars as well as the first and second lower molars. In the mandibular molar, an elongated heel at the back of the tooth carrying a fifth cusp, the hypoconulid is added on to the typical bilophodont tooth. This mandibular hypoconulid is usually missing in species of genus *Cercopithecus* and in *Erythrocebus patas,* which consequently have third lower molars exhibiting the typical bilophodont tooth pattern. The bilophodont molar cusps of colobines are steeper and more pointed than those of cercopithecines. Recent research has attempted to show that the percentage of leaves ingested by extant cercopithecoid primates is proportionally connected to the steepness of the bilophodont molar cusps: more leaves in the diet, steeper cusps; fewer leaves in the diet, more rounded cusps (Lucas and Teaford, 1994).

Upper Incisors

The upper incisors are spatulate, and the cutting edge of the central pair is always wider than those of the lateral pair; the central incisors are broader overall. Typically the upper incisors are not implanted as orthally (straight up and down) as the lower ones but slope forward. Frequently the lateral pair is tilted mesially. This condition is pronounced in baboons. In individual cases, it can result in crowding of the incisors—a slight overlapping of the mesial edge and tip of the lateral incisor over the lateral tip of the central incisor. The relative size difference of the upper incisor pairs (large central, smaller lateral incisors) is much more pronounced in Cercopithecinae than in Colobinae. There is a central sulcus down the middle of the lingual aspect of the central incisors. The enamel

is somewhat thickened on the inside margins of these teeth. These ridges are more pronounced on the central incisor than on the lateral tooth.

Lower Incisors

The lower incisors of Old World monkeys are usually spatulate and subequal in size. The central pair in cercopithecines tends to be somewhat broader than the lateral pair, in colobines the lower lateral incisors tend to be slightly broader than the central ones. The incisors are implanted in a straight, upward-directed way, thus being orthally oriented rather than procumbent. The cutting edge of the central incisor is straight, and that of the lateral incisors slightly slopes down distally. The lingual aspect of the incisors is slightly concave and triangular in outline, and the labial aspect of the crown is convex.

Upper Canine

The upper canines are strong and dagger-like. They are considerably longer than the lower canines and curve backward. Their cross-section is triangular with rounded-off angles; the short side of the triangle faces medially and has a central groove along the length of the tooth. The labial aspect is somewhat convex and directed distally and inward, whereas the lingual inside also has a medial groove. The medially facing side of this triangular tooth is sharpened against the distal aspect of the lower canine. The lingual inside of the upper canine is honed by the slanted, elongated front edge of the first two-rooted lower sectorial premolar. The rounded outside aspect of the canine remains untouched. It does have a groove running down the crown that is also extended down the entire length of the root in baboons. Thus, together with the lower canine and the highly specialized first lower premolar, the upper canines not only function as efficient shearing devices, the upper canines, lower canines, and first lower premolars also sharpen each other constantly while moving up and down against each other (see also Every, 1970). This honing mechanism sharpens the shearing edges of both upper and lower canines into bladelike, acute cutting edges, a phenomenon that is most pronounced in male baboons.

Lower Canine

There is a marked sexual dimorphism of the canines in many of the living representatives of the Cercopithecoidea, most marked in genus *Papio*.

The canines are pointed, powerful teeth that curve backward and splay slightly laterally. They have a heel-like extension on their distal base. The lower canines of baboons have also a marked groove running up and down the anterior aspect of the tooth crown. This condition is more marked in males than females.

In addition, a similar groove is also found on the mesial face of the upper canine of cercopithecoids. The cross-section of the lower canine is a compressed ovoid rather than triangular. The distal aspect of the tooth is covered by a marked honing facet, and the labial aspect is rounded. The mesial aspect of the tooth does not have a distinctive wear facet.

Upper Premolars

The cercopithecoid upper premolars have comparatively simple structures. Both have two principal cusps (paracone on the outside and protocone on the inside) that are connected with each other by a cross ridge. The paracone is usually higher than the protocone. The second premolar has a larger occlusal surface than the first. However, the two teeth are of equal crown height. Both the mesial and distal ends of the unworn occlusal surface are outlined by cross-ridges that are less prominent but narrower than the central cross ridge. In the second premolar part of the distal ridge forms a small heel of variable expression in the different genera. The upper premolars usually have three roots, two positioned under the outside of the crown and one under the inside.

Lower Premolars

The first lower premolar (P_3) is highly specialized in all the genera of superfamily Cercopithecoidea; it commonly has two roots, the anterior of which is considerably shorter mesiodistally than the distal one. The enamel forms a sharp cutting edge that extends downward from the apex of this tooth. This edge slants downward and forward onto the mesial (front) root from the crown's apex that is positioned straight above the distal root. The mesial root is implanted into the mandible further buccally than is the hind root. The enamel extends down onto the mesial and lateral aspect of the mesial root. The second premolar has a larger occlusal surface than the first. On the occlusal surface of the first, honing premolar, the single cusp is situated in the middle, and there is a large heel on the distal aspect. The crown height of the two morphologically different premolars is the same. This highly derived first lower premolar of Cercopithecoidea is called a sectorial premolar (Figure 7.16). There is also a heel on the second premolar that resembles in overall appearance the upper premolars in occlusal morphology. Unlike the upper premolars, it has only two roots, a larger one mesially under the cusp and a thinner, somewhat shorter root distally under the heel.

Upper Molars

All three upper molars (M^1–M^3) show the typical bilophodont cusp pattern. They have four cusps, paracone and metacone on the buccal side of the teeth and

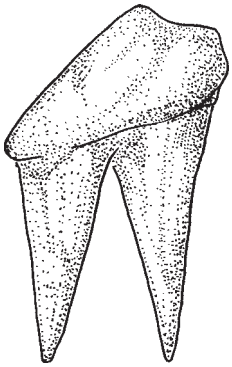

Figure 7.16 Sectorial lower left premolar (P_3) of cercopithecines (mesial at left; distal at right).

protocone and hypocone on the lingual side. The cusps are arranged opposite each other inside and outside and are connected to each other by cross-ridges. The outside (buccal) cusps usually project higher than the inside cusps in both unworn and worn teeth. The molars are longer than they are wide. In some of the genera of small body size, including the smallest of cercopithecoid monkeys, *Miopithecus talapoin,* for example, the first molar has the least size of the three teeth, with only three cusps, lacking the hypocone. In the upper molars, the size difference between the three molars is usually less pronounced than in the lower molars. Upper molars have three roots, two buccally and one lingually. The molar cusps of colobines are often more pointed than those of cercopithecines, which are comparatively blunt in shape.

Lower Molars

The lower molars are similar in occlusal morphology to the upper molars. They have the bilophodont four-cusped pattern, and in the trigonid area the paraconid is lost (just as in all other extant primates except *Tarsius*) but is usually replaced by a ridge. The level of this ridge or crest is positioned low near the base of the cusps. The lingual cusps usually project higher than the buccal cusps. The first molar is commonly the smallest of the three teeth, and the third is the largest. In genera *Cercopithecus* and *Erythrocebus* and some of the Colobinae, however, the size difference between the lower molars is less pronounced than in the genera *Papio, Mandrillus,* or *Macaca,* for example. Lower molars have two main roots, one proximal and one distal, but each may occasionally divide into two tips toward the root's apex.

Hominoidea

Gregory (1916) described the cusps and fissure pattern of the lower molars belonging to the fossil hominoid genus *Dryopithecus*. He considered this pattern of the occlusal surface to be typical of all hominoid primates, whether fossil or extant. This *Dryopithecus* molar pattern of the occlusal molar surface in contrast to the bilophodont pattern of cercopithecines is of crucial diagnostic value as a feature separating the two superfamilies of Old World Primates, the Hominoidea and the Cercopithecoidea. (See Figures 7.17 and 7.18 for depictions of their dental evolution.)

The typical *Dryopithecus* pattern, also known as the Y-5 pattern, was originally described for lower molars. The molar with typical *Dryopithecus* pattern has three buccal cusps and two lingual cusps. The paraconid is lost. These five cusps are separated from each other by Y-shaped fissures; the two upper arms of the letter Y open bucally and are next to the hypoconid, separating it from the protoconid antreriorly and the hypoconulid distally. The long lower arm of this Y separates the two inside cusps, the entoconid distally from the metaconid mesially. However, the *Dryopithecus* pattern is rarely found in this typical and more or less symmetrical configuration. The pattern undergoes numerous variations and simplifications and is often transposed even between the three lower molars of individual tooth rows. Among recent primates, the pattern is most typically and uniformly expressed in lower molars of gorillas (Remane, 1960).

In the upper molars of hominoid primates, we find the characteristic crista obliqua, or oblique crest, a ridge that connects the metacone and protocone and which also delineates the hind edge of the original evolutionary early tricuspid (tritubercular) upper molar, behind which the hypocone has been added through time. Typically, the small, additional cusp that can sometimes be found between metacone and protocone in the original tricuspid upper molar, the metaconule (*conule* is the diminuitive of Latin *conus*, "cusp") is incorporated into the crista obliqua. This crest is a typical feature of hominoid upper molars and not of cercopithecoids. Also the four cusps (when present) in hominoid upper molars are usually arranged in alternative positions (as if at the corners of a diamond) and not opposite to each other as in bilophodont upper molars of the Cercopithecoidea.

Hylobatidae

There is little sexual dimorphism between male and female gibbons in canine size. Both have long, projecting, dagger-like and distally recurved upper and lower canines. The first lower premolar of gibbons is slightly enlarged in a mesiolingual direction and functions together with the hind edge of the upper

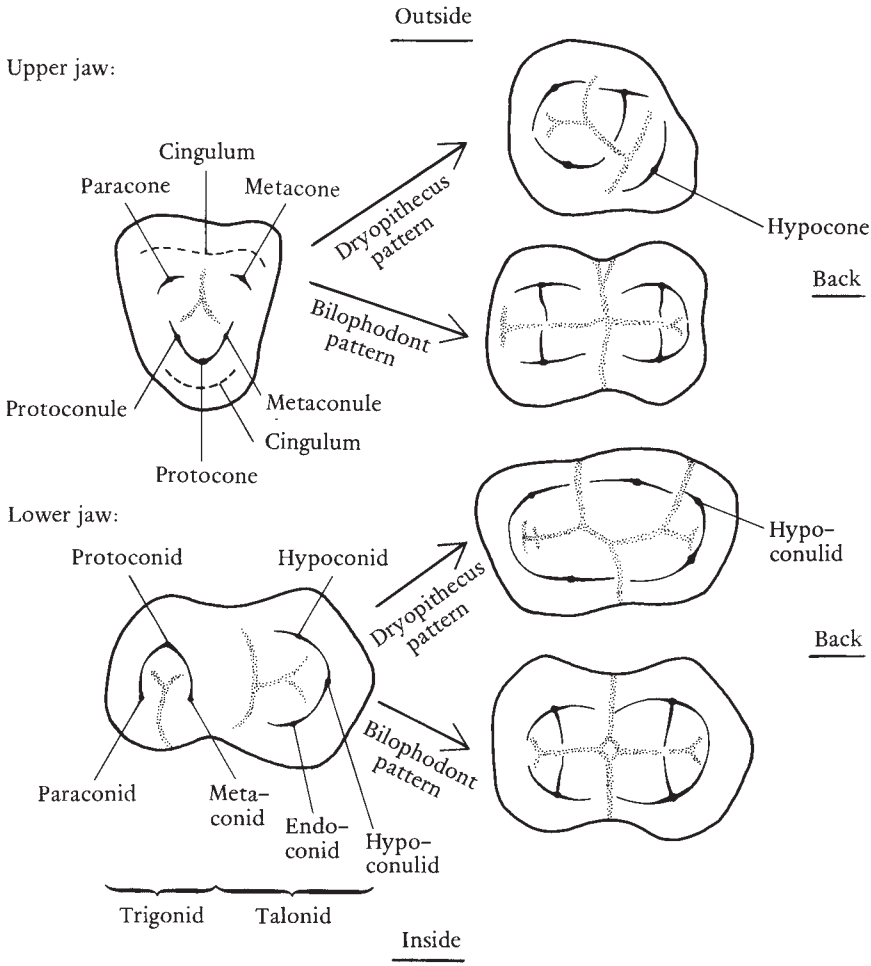

Figure 7.17 Diagram showing the evolutionary development originating from the tritubercular pattern (left) of the two occlusal molar patterns that are characteristic for Catarrhine primates (right): the bilophodont pattern (Cercopithecoidea) and the *Dryopithecus* pattern (Hominoidea). Crests are black, and valleys are stippled.

canine as a shearing device similar to the honing apparatus of the Cercopithecoidea, which consists of a combination of three teeth: the upper canine, the lower canine, and the first lower premolar (P_2).

Upper Incisors The central pair is slightly broader than the lateral incisors. The teeth are spatulate and the crowns are triangular, as seen from the labial

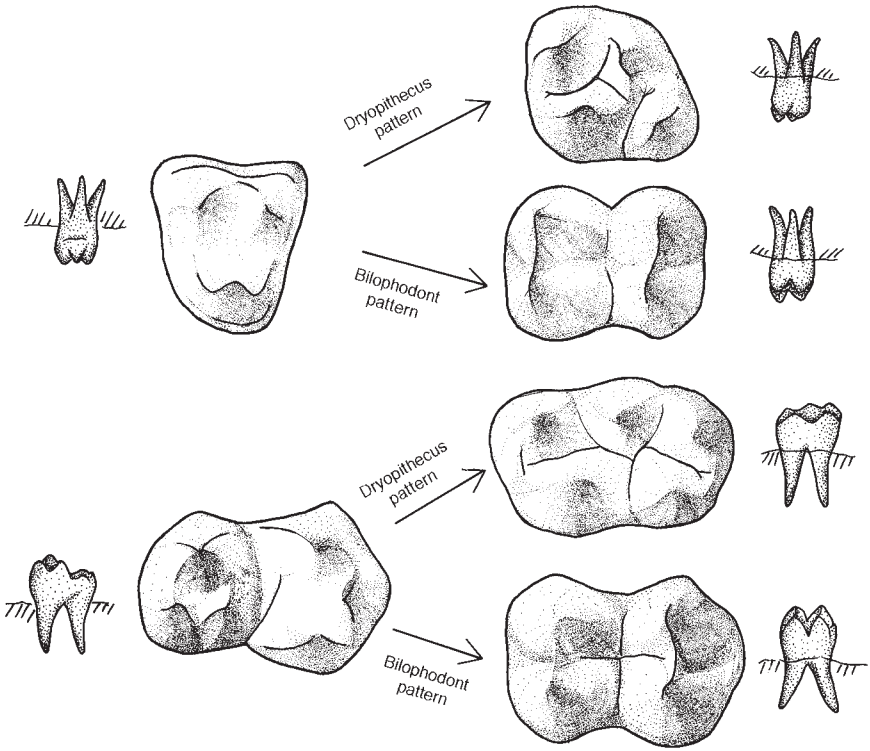

Figure 7.18 Diagram of the evolutionary development from tritubercular teeth to bilophodont and *Dryopithecus* molars, respectively. Note that maxillary molars have three roots, and mandibular molars have two roots.

aspect and somewhat concave. There is a well-developed cingulum on the base of the tooth. The lateral incisors are more compressed from side to side and have a lateral crest on the crowns lingual aspect as well as a slight cingulum on the inner base. There is a diastema between the lateral incisor and the canine. These teeth are implanted in a slightly procumbent manner.

Lower Incisors Central and lateral incisors are subequal in size, with the cutting edges being the same width and with equal crown height. Their implantation is comparatively vertical in the shallow mandible.

Upper Canine The crowns of the upper canines are high and much broader across their base than the crowns of the lower canines. There are grooves on both the mesial and the distal face of the crown. They are slightly recurved, pointed, sharp, and dagger-like. The long blade of the crown is honed against the first

lower premolar on its inner aspect. There is no sexual dimorphism in the size of the canines.

Lower Canine The crown of the lower canine is less high than that of the upper canine. It is curved distally and slightly slanted outward. There is a large heel-like extension on the lingual base of the tooth. Its buccal surface is sharpened against the upper canine.

Upper Premolars The upper premolars are bicuspid, with the paracone being the larger of the two cusps. These teeth are comparatively small. A slight crest connects across the occlusal surface between the two cusps, the paracone on the outside and the protocone on the inside. There are small cingula, either on the buccal base or on the lingual base of these premolars in a variable distribution; they can also be absent.

Lower Premolars The first lower premolar has a crown that is mesiodistally elongated and slanted mesially. It functions as a hone against the inside of the upper canine. This first premolar has only one cusp, the protoconid, and is elongated distally at its base by a cingulum. The second premolar is bicuspid, having both protoconid and metaconid, with the occlusal surface as long as it is wide and considerably shorter than the first premolar. On the back of the tooth is a heel-like extension formed by the cingulum.

Upper Molars The upper molars usually have four cusps, although the hypoconid is of variable size and sometimes small. The cusps are low and comparatively flat. Usually the second molar has the largest occlusal surface with the first molar's being slightly smaller. The third molar is the smallest of the three. There is usually a well-developed crista obliqua.

Lower Molars The first lower molar is the smallest of the three, and M_2 and M_3 are nearly equal in size. Usually all five cusps are present in all three of the molars. The hypoconulid however, can be missing in the third molar. Generally the cusps are low and flat. The characteristic Y-5 pattern is usually found in M_1 and often also expressed in the two following molars as well but somewhat altered.

Pongidae

Upper Incisors The incisors are broad and spatulate. Implantation can be quite procumbent in a manner that makes the incisors project out at the front end of the snout. The central incisors have a broad cutting edge with the lateral incisors being narrower, especially in genus *Pongo,* in which the cutting edge can be

almost pointed. The crowns of both incisors are curved lingually, which is most obvious in the central pair as the crowns of these teeth are so much wider. There are lateral enamel ridges on the inside of the tooth crowns that continue into a cingulum at the lingual crown base. Occasionally vertical grooves can be seen on the labial aspect of the central incisors, especially in genus *Gorilla*. Also there can be up and down ridges on the inside face of the central incisor as well as enamel crenulations that make the lingual surface of the crown slightly rugose.

Lower Incisors The lower incisors are typically subequal in size, although the central incisor can sometimes be smaller than the lateral incisor. There is a tendency toward a slightly procumbent implantation, but the lower incisors are usually projected vertically in relation to the long axis of the mandible. They are both spatulate and considerably narrower than the central upper incisors. A cingulum at the lingual base of the crown creates a heel-like extension.

Upper Canine Marked sexual dimorphism of these large, tusk-shaped teeth is characteristic in pongids in accordance with their sexual dimorphism in body size. It is thus most apparent between females and males of the larger genera *Pongo* and *Gorilla* and not as marked in the two species of genus *Pan,* the chimpanzees. Canine height of female and male chimpanzees overlaps considerably. Consequently, in genus *Pan* this measure cannot be used to distinguish the sexes (see Remane, 1960). There is usually a large diastema between the lateral incisor and the canine, accommodating the crown of the lower canine when the teeth are occluded. Diastemata, however, are variable among pongids (Remane, 1921; Schultz, 1948). On the lingual base, the crown has a cingulum. The mesial side of the recurved tooth is equipped with a sharp cutting edge, whereas the labial side is rounded. There can be a fine groove vertically across the mesial aspect of the crown.

Lower Canine As with the upper canines, there is marked sexual dimorphism. In females, the tip of the canine crown often just barely reaches higher than the occlusal surface of the adjacent teeth. There is a cingulum at the lingual base forming a small shelflike extension. The distolingual aspect of the tooth is sharpened by the labial side of the upper canine, which, in tandem, is sharpened by the lower canine. These powerful teeth are slightly recurved.

Upper Premolars The upper premolars are bicuspid with the outer cusp being slightly higher than the inside cusp. There is a deep groove in the center of the tooth separating the two cusps. This groove is sometimes delineated by a low crest in the front of the tooth, which is more pronounced in the first than second premolar. The occlusal surface of these teeth is crenulated by a fine net of irregular, spiraling fissures with multiple branchings. This infrastructure of

the occlusal surface is especially noticeable in genus *Pongo*. The two premolars are of equal size and have either two or three roots.

Lower Premolars The first lower premolar is larger than the second, and its enamel surface is somewhat extended downward in front onto the mesial aspect of the root. This extension is involved in the honing mechanism of the distolingual aspect of the upper canine but is much less well developed than in genus *Papio*. The two roots of this tooth are often fused together to form only one, large root. This tooth often has two cusps with the outside paracone much higher and more strongly developed than the inside protocone. There is a ridge between the inner and outer cusps. There is a small linguodistal talonlike extension on the base of this premolar. The cross-section of the second premolar is rather round and not elongated like the first premolar, where the long axis of the cross section is from the outside front to the inside back of the tooth. The second premolar has two roots, one located mesially and the other distally under the crown.

Upper Molars All three upper molars usually have four cusps that are not directly opposite each other; the outside cusps, the paracone and protocone, are positioned somewhat further forward than the two inside cusps, the protocone and hypocone. They usually increase slightly in occlusal surface area from front to back, M^1 being the smallest and M^3 the largest of the three. However, M^3 occasionally is the same size as is M^2 or even smaller than M^2. This means that the last molar is very variable in size. The cusps are rather low and more or less blunt in both *Pongo* and *Pan* and always pointed and comparatively higher in genus *Gorilla*. The crista obliqua, connecting the metacone with the protocone, is usually present. The occlusal surface shows a variable surface pattern of wrinkles as described for the premolars, and this additional wrinkling of the occlusal surface texture is most strongly developed on the molars of orangutans (Figure 7.19).

Lower Molars The three lower molars have five cusps. The protoconid bucally and the metaconid lingually are positioned directly opposite from each other. The metaconid and entoconid are separated from each other by a conspicuous groove, the stem of the letter upsilon in the Y-5 pattern. The two grooves that represent the arms of the upper half of the letter Y embrace the hypoconid between each other in the typical *Dryopithecus* pattern of the hominoid lower molars. As stated earlier, there are numerous modifications of this pattern, depending on variations in size and position of the cusps relative to each other that are correlated with consequent changes in the arrangement of grooves. A reduction of the Y pattern to a simple cross-pattern, usually in connection with the loss of one cusp, is frequently found in chimpanzees and humans. This can

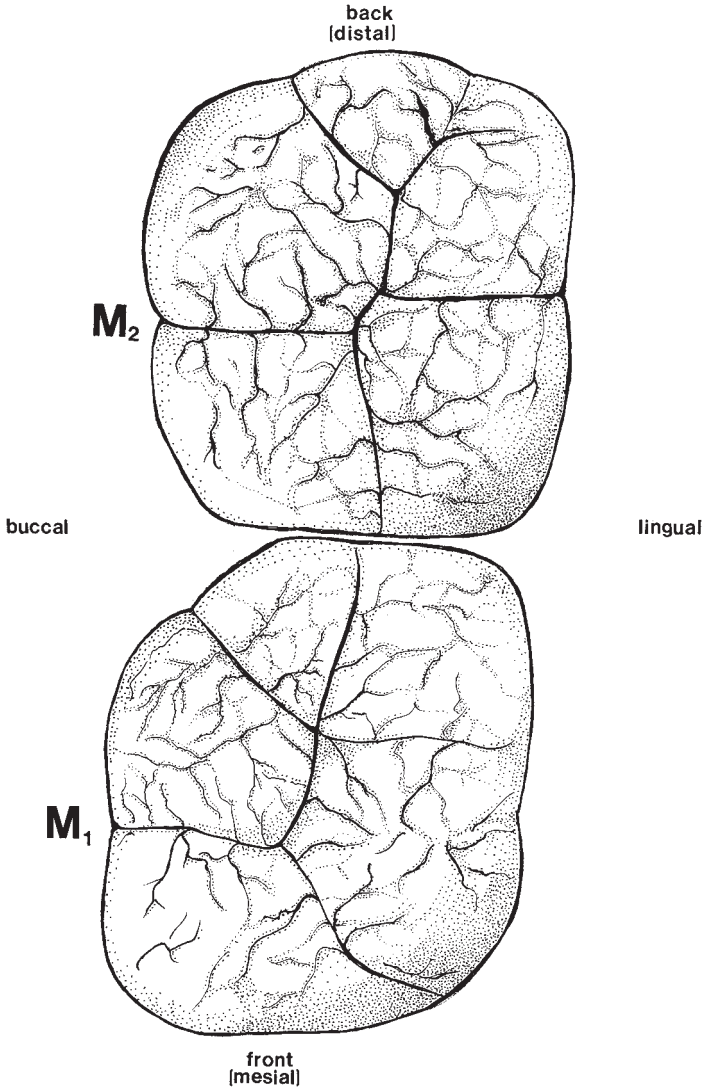

Figure 7.19 Orangutan *(Pongo Pygmaeus)* occlusal molar wrinkling.

either come about through an enlargement of the hypoconid area, causing all grooves to meet or cross in the center of the occlusal surface of the tooth so that the grooves form a five-armed star, or, alternatively, the reduction and loss of the hypoconulid can result in a four-cusped, lower molar with a simple right angle cross of the grooves and a quadratic occlusal surface outline. Size variation of

the lower molars follows the same general pattern as the upper molars. As for the additional wrinkling of the occlusal surface, genus *Pongo* again has the most elaborate and distinctive pattern.

Hominidae

In most respects, the dentition of hominids is similar to that of Pongidae. The following is a brief discussion of some important differences that distinguish these dentitions. One of the most characteristic features of the hominid dentition is the reduced size of both upper and lower canines, which are essentially incisiform. Their tips rarely project any higher than the cutting edges of the incisors and the occlusal surfaces of the premolars. The dental arcade of modern hominid is different from those of all other primates. It is shaped more or less like a half circle in accordance with the rearrangement of the overall morphology of the human face. Typically the incisors and canines of modern hominids are implanted straight up and down in both the maxillary and the mandibular dentitions. Both the upper and lower premolars are bicuspid, with the buccal cusps larger than the lingual cusps and the two teeth being of equal size. Adjacent teeth are positioned close to each other and are touching; diastemata occur only rarely. The third molar is often diminuitive and habitually erupts later in life or not at all in modern humans. It is commonly called the "wisdom tooth" presumably because its eruption occurs considerably later than that of all other teeth, at a time when people come of age and may be presumed to be wiser.

In hominids the lower molars tend to have lost the hypoconulid and to have the remaining four cusps arranged in a cross or a star pattern. The latter occurs in those lower molars that still retain all five cusps. Both length and breadth of the occlusal surface of lower hominid molars are usually subequal, resulting in rather square outlines.

Third molars show a strong tendency toward reduction of details of occlusal morphology.

WHAT IS NEW IN PRIMATE TOOTH RESEARCH?

A study of howler monkeys (DeGusta et al., 2003) has documented that the functional occlusal surface size of molar teeth is a crucial survival factor for howlers in the natural habitat. This work documented that molar size is under natural selection, and not heritability. Another investigation of Asian Colobines in the wild has also clearly shown that different environments and dissimilar food supplies crucially modify tooth shape and not phylogenetic relationship (Pan and Oxnard, 2003). Both studies unmistakably illustrate the fundamental interaction between natural selection and adaptation and thus the process of evolution.

As with all research, new findings are expected by the use of new technologies. One of these is the use of geographic information systems to decipher occlusal tooth topography and delineate it with the food that is chewed (Zuccotti et al., 1998; Teaford et al., 2006). Primate molars are evaluated in three-dimensional comparisons using Geographic Resources Analysis Support Systems (GRASS) computer software. This computer technology makes it possible to quantify and compare the details of tooth morphology and point out that this approach has great potential if applied to study joints, skulls, and other biological surface reliefs. Such precise three-dimensional measurements may provide detailed information about the impact that different foods with various degrees of toughness have on dental wear (Ungar and M'Kirera, 2003). Because dental morphology is related to tooth function, this technology makes it possible to formulate detailed inferences about the structure and, possibly, the function of fossil teeth (Ungar and Williamson, 2000).

This technology has now been used to show how various mammals, including primates, are able to develop new functional cutting edges during the process of wearing down the original occlusal chewing surface (Teaford, 2003). Application of geographic information system technology is also widely used in attempts to decipher dietary variability in fossil primates (Ungar et al., 2003; Scott et al., 2005).

A long-term, important study (King et al., 2005) of tooth wear in a long-lived prosimian primate with the help of geographical information system technology has resulted in in-depth understanding of reproductive success. In a 20-year study of *Propithecus edwardsi* in southern Madagascar, it has been possible to document that aging females (maximum reported life span greater than 27 years) with heavily worn teeth still produce viable offspring. These primates produce compensatory shearing blades while wearing down their molar crowns until about age 18 years. These teeth thus remain functional until they are totally worn flat. It is important to note that sifakas never drink water actively but get their water supply from the leaves they eat. Female sifakas with no remaining functional shearing function continue to give birth to offspring. During the period of lactation, there is a strong correlation among mothers with worn-down teeth, high infant mortality, and the amount of seasonal rainfall. It appears that the lack of rain and consequent lack of moist leaves results in increased infant mortality among the offspring of aged mothers (King et al., 2005).

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Chapter 8

Postcranial Skeleton

Spine and Thorax
Cervical Region
Thoracic Region and Thorax
Lumbar Region
Sacral Region
Caudal Region
Comparative Morphology
Shoulder Girdle
Forelimbs
Pelvic Girdle
Hind Limbs
Hands and Feet
Fifth Extremity
Muscles
Locomotion
Prosimian Primate Locomotion
New World Monkey Locomotion
Old World Monkey Locomotion
Arm Swinging and Knuckle Walking
Obligatory Bipedal Walking
Efficiency of Primate Locomotion
New Technologies Applied to Study Primate Locomotion

There is considerable intraspecific variation among primates, a fact that is most obvious if we look at humans. Not only do size and proportions vary, but many of the detailed articular surfaces within the postcranial skeleton can differ considerably. This means that elaborate evaluations of morphological details that are assigned to specific locomotor capabilities should always be checked for multiple specimens to avoid overinterpretation. In another way, comparing humans, there is no question that the sexes vary in their morphology and behavior along scales of gradation between two extremes: on one end of this scale are very

"male" males (e.g., Arnold Schwarzenegger), standard males are in the middle, and on the other end of the scale are "female" males (e.g., Truman Capote). The same is true for females: there are ultra-female females (e.g., Marilyn Monroe), the regular female in the middle, and, again, on the other end of the range the "male" female (Gertrude Stein). This applies to behavior, robusticity, and size. The same is likely to be true for nonhuman primates. However, this fact has unfortunately been ignored by both morphologists and students of behavior.

Whereas the skull of vertebrates represents an obvious functional entity, the postcranial skeleton can be considered to be composed of four different structurally and functionally cohesive subunits: (1) the vertebral column and thorax, (2) the shoulder girdle with the forelimbs, (3) the pelvic girdle with the hind limbs, and (4) the postcranial skeletal musculature.

The axial skeleton consists of the vertebral column and its correlates, the ribs and sternum. Ribs and sternum join with the vertebrae, making up the thorax or ribcage. Most central to the body, the vertebral column interlocks with the two limb girdles or appendicular skeleton. The proximal shoulder girdle consists of the shoulder blades, clavicles, and forelimbs. The distal pelvic girdle is made up of the pelvis, that sacrum which is also part of the vertebral column and the hind limbs. The appendicular skeleton provides the solid framework for active powers that move the primate (and generally vertebrate) body, whereas the axial skeleton is the unifying component. The fourth unit of the postcranial skeleton, the muscular system, directly moves the passive skeleton.

In the first section of this chapter, these four subunits are discussed separately. The subsequent discussion of locomotion describes the integration of the functional roles of the four skeletal subunits and shows how the postcranial skeleton is an integral part of a whole and viable organism.

Figure 8.1 depicts the differences in orientation of bipedal and quadrupedal species and introduces some of the essential terminology that is used in discussions of skeletal anatomy.

SPINE AND THORAX

The vertebral column is the axial or longitudinal internal skeleton of the body of every vertebrate. It is, in fact, the structure that gives the subphylum Vertebrata belonging to phylum Chordata its name. This column connects the head on the front, the forelimbs and hind limbs more or less in the middle, and the tail, if present, at the end. The column is an aggregation of several morphologically different groupings of vertebrae (*vertebrae* is plural, whereas *vertebra* is singular). The vertebrae articulate with each other within the region of the neural arch and are connected to each other by elastic discs within the region of the

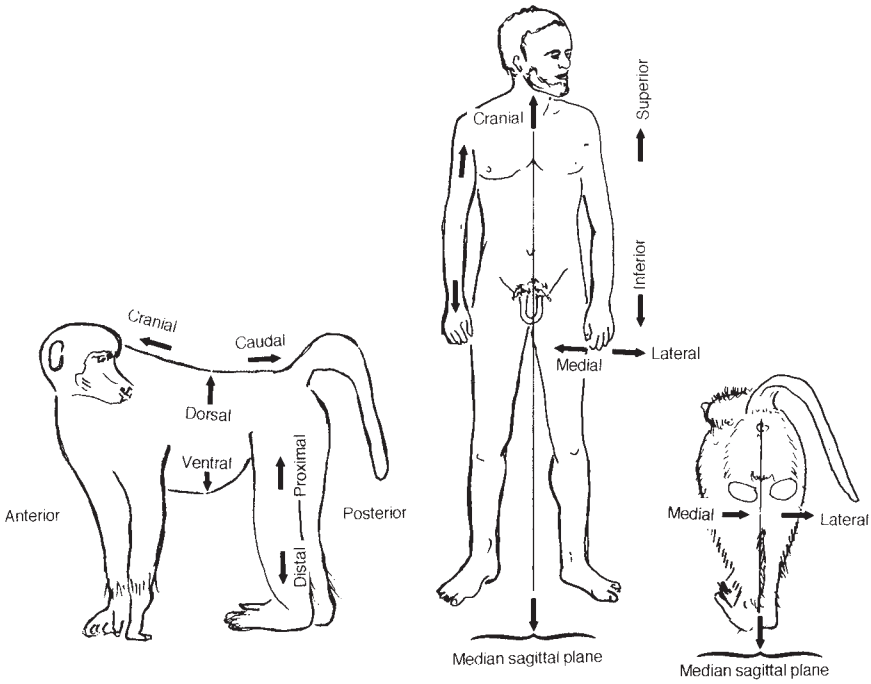

Figure 8.1 Orientations as they differ between bipedal humans *(Homo)* and quadrupedal primates *(Macaca)*.

vertebral bodies. The vertebral column is both stable and flexible at the same time.

Illustrations of vertebrae in human anatomy books often are in an upside-down position where the vertebral bodies are up and the neural arch is down. This is the anatomical position of the human corps in gross anatomy or in the morgue, resting on its back. This is not the position in which any other vertebrates usually are depicted: they are shown with the vertebral body beneath the neural arch, ventral side down, as in the quadrupedal locomotor position. The anatomical upside-down illustration of human vertebrae has occasionally also been used for quadrupedal primates, even though it is not only confusing but inappropriate in the context of comparative anatomy and, therefore, will not be adopted in this text.

Each vertebra is made up of different parts. The vertebral body, or centrum, is the largest component in most vertebrae, and it serves mainly weight-bearing and shock-absorbing purposes. The vertebral bodies are connected to each other by means of elastic cushion-like pads of fibro-cartilage, the so-called intervertebral discs. These discs allow two vertebral bodies positioned adjacent to each other

to move slightly against each other: minor circular and slight to-and-fro movements are possible between adjoining vertebral bodies because of the intervertebral disc. Every movement between two adjoining vertebrae has its pivotal center at each end of the vertebral body. These movements are directed and restricted in characteristic ways and regulated by bony processes, some of which articulate with each other. It has to be kept in mind that any movement of the vertebral column or its distinctive regions is created only by the summation of multiple but singularly insignificant individual movements between adjacent vertebrae. The bony processes on the vertebrae also function as lever arms for the tendons and muscles that are inserted on them. These lever arms restrict the movements in characteristic ways.

There are five discrete regions making up the vertebral column that function differently according to distinct morphological characteristics. The regions are:

1. **Cervical** or region of the neck: in all mammals as a rule made up of seven vertebrae
2. **Thoracic** or chest region
3. **Lumbar** or lower back region
4. **Sacral** region, the region where the pelvis articulates with the vertebral column
5. **Caudal** region or the tail, which is the most likely region to be variable in length

At the top of each vertebral body, pointing backward in bipedal man and upward in quadrupedal primates, a bony arch, also called a neural arch, rises up. The uprising lateral parts of the arch are also called pedicles in human anatomy, and the dorsal portion, or roof of the neural canal that fuses at the midline is called lamina in human anatomy. Dorsally in the midline rises the *processus spinosus,* a bony process for the attachment of the spinalis muscle and the supraspinal ligament. The spinous process is always single and can terminate in either a point, a knob, or even in double tubercles. It also varies considerably in its length, strength, and direction. The neural arch covers and protects the major postcranial central nervous system, the spinal cord, which is positioned on top of the upper aspect of the vertebral bodies. On each side of the neural arches, left and right, we find two bony articular processes pointing in anterior direction and, at the back, two pointing posteriorly. These two pairs of articular processes have smooth articular surfaces and meet between vertebrae: the joints on the front are inwardly and upwardly directed and the backward-pointing articular surfaces on the caudal rim of the neural arch are directed down and somewhat laterally. The direction of these articulations is typically different in different regions of the vertebral column. The posterior processes are embraced by the anterior articular processes of the caudally following vertebra. These articular processes positioned within the neural arch are also called zygapophyses (from

Greek *zygos* meaning girder, beam; *apo* means away; *physis, physeos* means grown). The position of these articular processes or zygapophyses is characteristically different in the five regions of the vertebral column. The zygapophyses in front are pre-zygapophyses and the ones in back are post-zygapophyses. In human anatomy, the zygapophyses are also known as mammillary processes. They are guides for the limited amount of movement that is possible between adjacent vertebrae (Figure 8.2).

Zygapophyses are the directional guides for restricted movement between vertebrae. Thus, as a rule, each individual vertebra has three points of articulation with the adjoining vertebra: the vertebral body and the two zygapophyses on each end. With this three point linkage, turning movements in lateral direction between two adjoining vertebrae are nonexistent in all three regions that are shown in

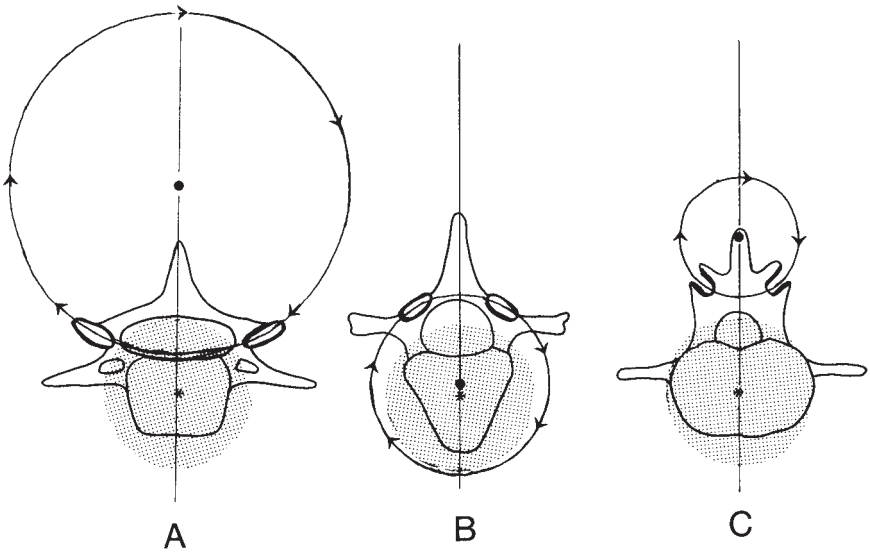

Figure 8.2 Vertebrae seen from the front. Diagram showing the characteristically different orientations of the articular facets (outlined in black) in different vertebral column regions. A) Vertebra characteristic for the cervical; B) thoracic; C) lumbar region of the vertebral column. The black circles with arrows (centers •) show the theoretical turning circle of two vertebrae against each other within the different region as controlled by the articular facets. The shaded circles (center *) are correlated with the minute circular movement that is possible between two vertebral bodies (connected to each other by intervertebral discs). As both circles are involved, turning would only be possible where the centers of the two circles coincide. Obviously no turning movements are possible between either two vertebrae in all three regions (cervical, thoracic, and lumbar) because the centers of the two circles are separated from each other. The circle centers are positioned most closely to each other in the thoracic region, but usually do not coincide here either, resulting in no turning movement between adjacent vertebrae.

Figure 8.2. Only in the thoracic region are the centers of the two hypothetical circles close to each other or coinciding; even so, turning of one thoracic vertebra against the other is not possible. However, this rule of the three point vertebral articulation has several exceptions as we shall see below (Ankel-Simons and Simons, 2003).

Cervical Region

The number of vertebrae of a vertebral column is counted from cranial to caudal. The first vertebra is called the **atlas** and it makes the first exception from the above rule of inter-vertebral articulation. The atlas is ring-shaped, lacking the vertebral body. Cranially, there are two comparatively large, concave articular facets on the anterior half of the ring, facing forward (or upward in bipedal humans) and cradling the occipital condyles on the anterior aspect of the foramen magnum on the underside of the skull. This joint is oval in shape and allows fore and aft movements between the head and atlas. This is the articulation where human nodding in agreement does occur. These cranially directed atlas to skull articulations are positioned opposite to articular facets on the other side of the atlas ring: two caudally directed articulations that meet two articular facets of the second cervical vertebra which are located on both sides of the upper (cranial) aspect of its vertebral body. These articular facets are set further medially on the anterior aspect of the bony ring of the atlas, causing the lumen of this vertebra to be shaped like a mushroom. The second cervical vertebra also has its very own name, the **axis** (also known as epistropheus). Thus, we can see that the atlas articulates directly with the sides of the vertebral body of the axis: there is no intervertebral disc involved in this joint. The joint is positioned in a way that it will allow rotation of the atlas together with the head around the dens of the axis: the shaking of the head from left to right and back occurs in this particular articulation. In humans it habitually expresses the "no" gesture. The second neck vertebra, the axis, got its name from the fact that its body is elongated cranially by a bony, conical projection, also called the dens (*dens* is Latin for tooth). There is an articular facet on the ventral aspect of the dens that articulates with a corresponding articular facet on the inside of the ventral part of the atlas. There is no articulation by means of zygapophyses between atlas and axis. The dens is cradled in a depression in the middle of the ventral arch (anterior arch) of the atlas. During life, a strong transverse ligament keeps the dens safely in place and separates it from the lumen of the neural canal of the first vertebra. This dens has different angles in primates that have contrasting postures: it is bent dorsally in quadrupedal primates, only slightly bent dorsally in the knuckle walking African great apes, and totally straight in the direction of the long axis of the vertebral body in upright humans (Figure 8.3; Ankel, 1970, 1972). This is a good example for a morphological difference that is correlated to postural differences

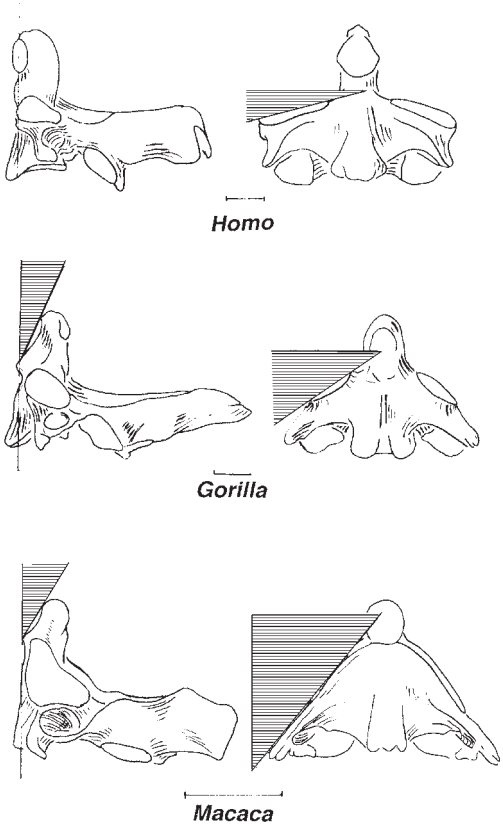

Figure 8.3 Characteristic angles of the dens epistrophei (on the left seen from lateral) and the anterio-lateral articular facets on the right seen from below).

among primates. The retroflexion of the dens in quadrupedal primates positions the head plus atlas somewhat further backward on the vertebral column than it would be if the dens was straight which causes the head plus atlas vertebra to be positioned in line with the long axis of the vertebral column (Figure 8.4).

At its caudal end, the second vertebra or axis articulates with the subsequent third cervical vertebra in the manner already described as typical, with a fibrocartilaginous intervertebral disc and two articular processes on the neural arch.

There are two other exceptions to the three point rule of vertebral articulation. The sacral vertebrae—following the lumbar region distally—are commonly fused to each other: The sacrum is the place of articulation between the vertebral column and the pelvis with the hind extremities. Thus, several vertebrae lose

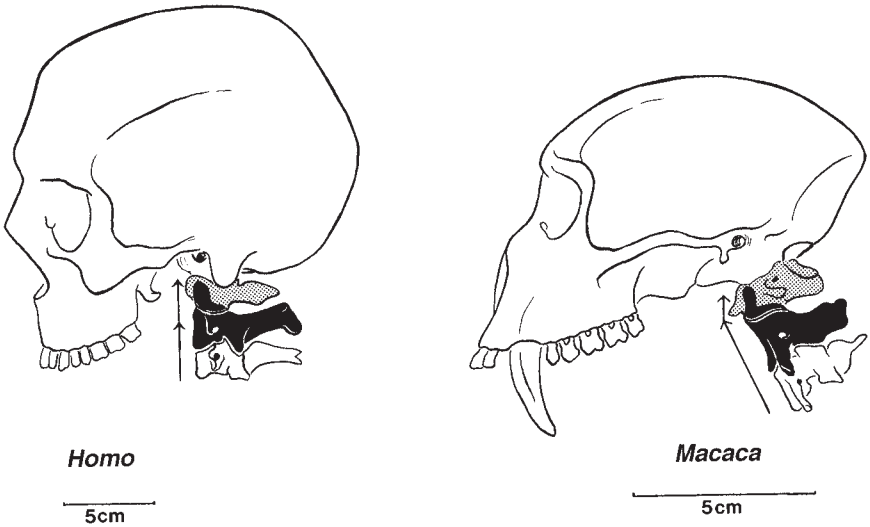

Figure 8.4 Differences in the orientation of the skull on the first two cervical vertebrae. Comparison between a bipedal (left) and a quadrupedal primate (right). Atlas shaded, axis black, third cervical vertebra white.

their articulations and are continuous or locked into each other, forming a solid and elongated element within the vertebral column, the sacrum (Figure 8.5).

The third instance of an exception in the manner of articulation between vertebrae is found within the tail. The peripheral tail (caudal) vertebrae lose all the bony extensions; these vertebrae are represented only by elongated vertebral bodies, connected to each other by intervertebral discs. This condition allows unrestricted mobility of the tail vertebrae in all directions: tail mobility is only restricted by the thickness and elasticity of the intervertebral discs and the length, size, and shape of the vertebral bodies (Ankel-Simons and Simons, 2003).

The cervical region is a combination of seven vertebrae in almost all mammals. Regular exceptions to this rule are the Xenarthra *Choelopus hoffmanni* (two-toed tree sloth), with only six cervical vertebrae, genus *Bradypus* (three-toed tree sloth), usually having nine cervical vertebrae, but sometimes eight or even ten, and *Tamandua* (lesser anteaters, or Tamanduas), with eight. Yet, this otherwise comparatively stable number of seven sometimes varies in humans and with other individual primates. The vertebral bodies in this region are more or less square in cross-section and their cranial and caudal ends are saddle shaped: In front, they overlap the joining vertebral bodies from the sides, and in back, the lower edge of the vertebral body protrudes over the adjoining vertebra in a shingle-like manner. This arrangement allows backward movements between cervical vertebral bodies, only little or no forward bending, and practically no turning.

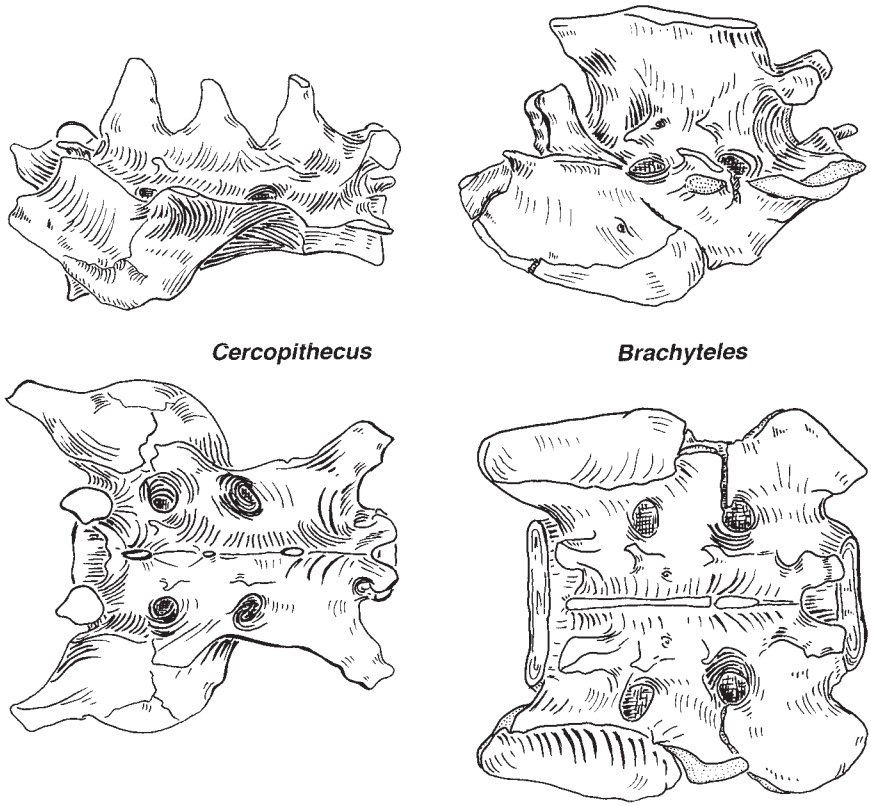

Figure 8.5 Sacral region of an Old World monkey *(Cercopithecus)* on the left and a New World monkey *(Brachyteles)* on the right. Seen from the left side (top) and from dorsally (bottom).

The transverse processes usually extend further lateral than the lateral edge of the vertebral body and are perforated by anterio-posterior foramina (foramina costo-transversalia) through which the arteria vertebralis is passing to the head. These foramina are of comparatively large diameter and are characteristic for cervical vertebrae one through six, but regularly lacking in the seventh cervical vertebra. The articular surfaces of the zygapophyses are thus, spread rather far apart and not positioned directly above the vertebral body but rather further lateral. In all the other regions of the vertebral column, these articulations are positioned above the vertebral body. The diameter of the neural arch is the largest in the cervical region within the vertebral column. All articular facets, beginning at the caudal end of the axis and to the cranial end of the seventh cervical vertebra, are positioned almost parallel to the dorsal surface of the vertebral body but are turned slightly upward and sideways.

Thoracic Region and Thorax

The region of the vertebral column distally adjoining the cervical region is the thoracic region. In front, the first thoracic vertebra has zygapophyses that are still in the characteristic position for the cervical region, the position of the distal zygapophyses of this intermediate vertebra is typical for the adjoining thoracic region. The thoracic region is characterized as the rib bearing area. The thoracic vertebrae are characterized by the presence of articular facets for the ribs on the vertebral bodies and the transverse processes.

In this region, the vertebral bodies are typically heart-shaped if seen from the proximal or distal end. The transverse processes of the thoracic region have on their ends ventrally facing articular facets (fovea costalis transversus) for one of the two articulations at the vertebral end of each rib: it is called tuberculum costae and it is the articulation that is on the caudal aspect of the rib and as far removed from the end of the rib as the transverse process is long. This area between the two articulations is also called the rib's neck. The second articulation between ribs and vertebral column is positioned at the head of the rib which articulates with the side of the vertebral body dorsally on both ends of adjacent vertebrae (capitulum costae, see Figure 8.6).

Throughout the cranial third of the thoracic region, this articular facet is divided and runs across two adjoining vertebral bodies straddling the intervertebral disc. Further caudally the facet is undivided and moves onto the cranial aspect of the side on the vertebral body. Running down the series, the vertebral bodies gradually elongate cranio-caudally, and their diameters increase as well. The rate of size increases in the vertebral bodies varies between primate species. The neural arch decreases its diameter in some primates in a cranio-caudal direction, as is the obvious case in humans.

Within the thoracic region, the paired zygapophyses on the neural arch are positioned above (dorsal to) the vertebral centra. Seen from the cranial or caudal aspect, these articular facets lie more or less flat above the dorsal plane of the vertebral body, with their inner side slightly above the outer side. As we have already mentioned, the first vertebra in the thoracic region has anterior articular processes in the same position as do the cervical vertebrae; at its posterior end, the first thoracic vertebra has articular processes in the position characteristic of the thoracic region. Toward the end of the rib-bearing region, the articular processes at the front end of the transitional vertebra are positioned in the manner that is characteristic of this region. The articular processes at the hind end of the last thoracic vertebra are angled steeply to the midsagittal plane, as is typical for all the vertebrae of the lumbar region. It is particularly important for functional stability that the direction of the articular facets of zygapohyses does not change gradually from vertebra to vertebra. It changes abruptly within one vertebra which is also called the transitional vertebra. Because the position of these

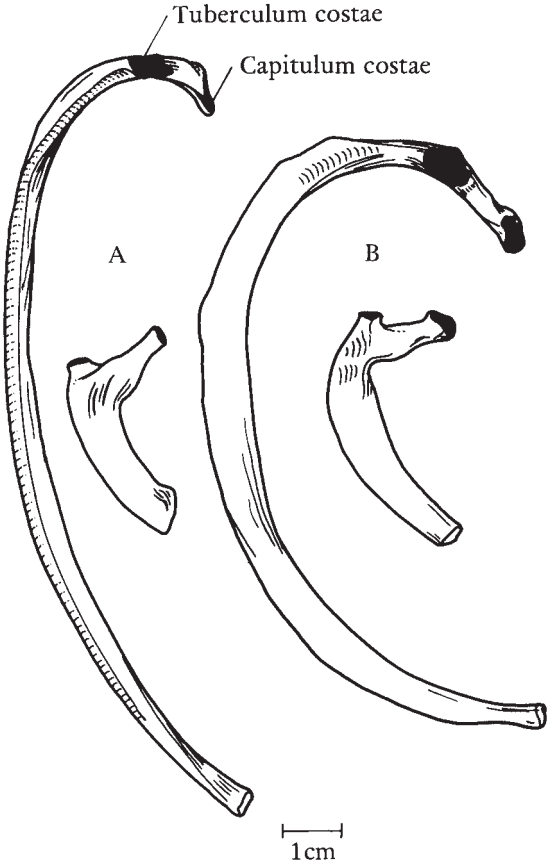

Figure 8.6 A) Seventh (on the left) and first (on the right) ribs characteristic for Old World monkeys *(Theropithecus gelada)* and B) seventh (on the left) and first (on the right) ribs of a gibbon *(Symphalangus syndactylus)* characteristic for Hominoidea. (Articular surfaces are black.) Both primates are of approximately the same body size.

vertebral articulations does not change by degrees from one vertebra to the other like all the other characteristics do, the functional integrity and stability of an entire region of the vertebral column is secured. The essential functional stability of the vertebral column would not be possible without this abrupt change in orientation of the articular processes.

The functionally transitional vertebra between the thoracic and lumbar regions does usually not coincide with the last rib-bearing vertebrae. Therefore, the number of functional thoracic vertebrae (i.e., vertebrae with zygapophyses in the characteristic position of the thoracic region) does usually not coincide with

the number of rib-bearing vertebrae that are commonly counted as thoracic vertebral elements. Thus, the functional thoracic region can be considerably shorter than the rib-bearing thoracic region (Table 8.1).

The relationships between the ribs and the thoracic vertebrae are complicated and collectively responsible for the shape of the ribcage or thorax. The overall shape of the thorax is not only dependent on the way the ribs are bent, on the length of the rib's neck, the position of the articulations between rib and thoracic vertebra (the tuberculum and the capitulum costae), the length of the processus transversus, its direction and degree of angulation as well as the position of its articulation with the tuberculum costae (see Figure 8.6). The shape of the thorax also depends on the length of the thoracic vertebrae themselves. The thoracic region is comparatively inflexible.

Table 8.1

Average Number of Vertebrae

		Prosimii			
	Insectivora		Lorisiformes		
Region	Tupaiiformes	Lemuriformes	Lorisidae	Galagidae	Tarsiiformes
Cervical	7	7	7	7	7
Thoracic (# of ribs)	(13)*	(13) 11	(16)	(13)	(13) 12
Lumbar	6	7/8	7	6	6/7
Sacral	3	3	7	3	3
Caudal	25	25	9	25	29
Caudal		*Indri* 10			

	Anthropoidea		
Region	Callitrichidae	Cebidae	Cercopithecidae
Cervical	7	7	7
Thoracic (# of ribs)	(13) 11	(14) 11	(12) 10
Lumbar	7/9	5/8	7/9
Sacral	3	3	3
Caudal	27	30	17
Regions	Hylobatidae	Pongidae	Homo
Cervical	7	7	7
Thoracic (# of ribs)	(13) 13	(13) 13	(12) 12
Lumbar	5	6	5
Sacral	5	6	5
Caudal	3	3	4

Data adapted from Schultz, 1969; Shapiro, 1993.

*Numbers in parentheses are the number of thoracis vertebrae counted according to the number of ribs. Thoracic numbers not in parentheses are the number of vertebrae counted according to the position of the intervertebral articulations. Higher numbers of lumbar vertebrae counted according to articulation.

The way ribs are curved shows distinctive differences between prosimians and monkeys on one hand and apes and humans on the other. The ribs are much less bent on their vertebral end in the former than they are among hominoids. The high degree of bending of the ribs (along their long axis) in apes and humans results in a barrel-shaped thorax that is broad from side to side in these primates, in contrast to the transversely narrow thorax of prosimians and monkeys. Also, the apes have comparatively barrel-shaped rib cages, which appear to be rather funnel-shaped in chimpanzees. Additionally, this difference in rib bending brings about a different position of the vertebral column within the framework of the thorax. In prosimians and monkeys, the ribs usually hang down from the vertebral column. In apes and humans, the vertebral column is positioned more or less within the thorax as the ribs extend backwards near the vertebral column and before they extend ventrally (Figure 8.7).

Incipient broadening of the rib cage can also be found, apart from hominoids, in a couple of prosimians (genus *Propithecus*), genus *Tarsius,* and a few monkeys (genera *Ateles* and *Colobus*). Exclusively in apes and humans, however, the barrel-shaped thorax is also expanded in its ventral bony elements that make up the sternum or breastbone. Because of this broadening, hominoids have also been called "the Latisternalia" (meaning the animals with wide sternum, and "sternon" is the Greek word for chest) (Figure 8.8).

The spinous processes vary both in projective length and angulation. Within the thoracic region they are commonly directed caudally.

Lumbar Region

All longbones in the mammal body have so-called epiphyses (singular = epiphyses from Greek: the prefix "epi" means upon, and "physis" is Greek for growing) on their ends. Epiphyses have a separate ossification center and allow articulations between longbones to be in place and functional before the growth

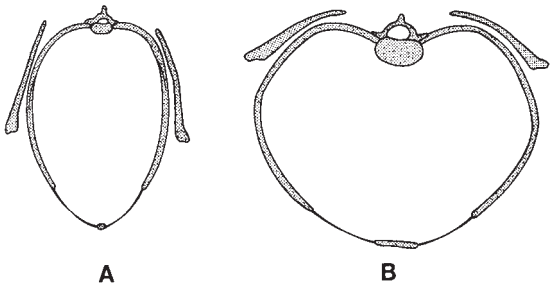

Figure 8.7 Contrast between A) narrow (characteristic for prosimians and monkeys) and B) barrel shaped (characteristic for hominoids) rib cages.

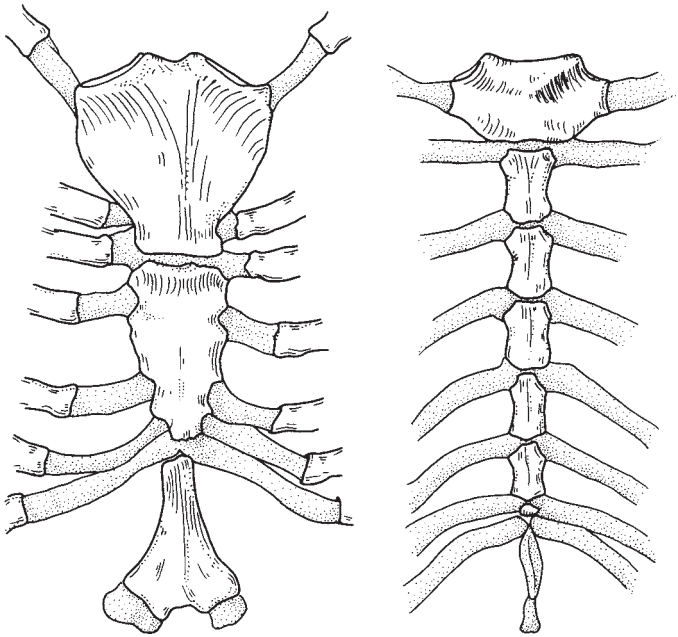

Figure 8.8 Broad sternum, typical for hominoid primates (left) and narrow sternum (right), typical for all other primates.

process is completed as growth goes on in the area between the longbone diaphysis and the epiphysis. With adulthood, the epiphyses fuse with the bone, becoming its terminal portion. Epiphyses are also found on both ends of vertebral bodies. In 1968, Rose et al. interpreted ring-shaped epiphyses that were found on fossil lumbar vertebrae as taxonomically distinct from plate-shaped epiphyses. However, the author discovered that ring-shaped and plate-shaped epiphyses occur on vertebral bodies within the same individual vertebral column of primates and thus document the cranio-caudal growth factor. The epiphyses within the cervical region achieve plate shapes before the epiphyses in the caudally adjacent regions that remain ringshaped for a longer time. Further back in the vertebral column, the vertebral bodies have increasingly narrow ring-shaped epiphyses (Figure 8.9) that also become plate shaped later in life.

In lumbar vertebrae, the position of the anterior and posterior articular processes is steep, enclosing narrow angles with the median sagittal plane. Thus, in this region, there is strictly back and forth movement between adjoining vertebrae. The main characteristics between lumbar vertebrae are the laterally projecting transverse processes. In some primates there are additional small bony projections that are positioned underneath the posterior zygapophyses, projecting

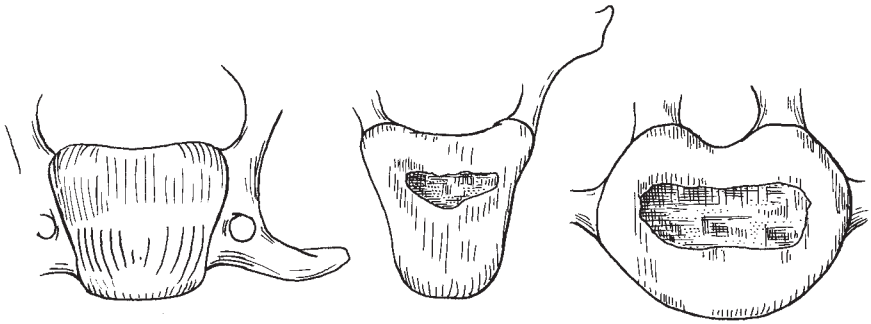

Figure 8.9 Plate-shaped epiphysis on a cervical vertebral body, wide ring-shaped epiphysis of a thoracic vertebra and narrow ring-shaped epiphysis of a lumbar vertebra within the same individual vertebral column of a subadult monkey.

caudally and locking the anterior zygapophyses of the caudally joining vertebrae into place (Figure 8.10). These processes are called accessory processes. In the lumbar region also, the dorsal spines are usually very robust and high and bent cranially.

Sacral Region

The fourth region of the vertebral column in all mammals—and thus primates—is the so-called sacrum (*sacer, sacra, sacrum* actually means holy in Latin, but it also has the transmuted meaning of being large, which applies in this context, as the sacrum is often the largest element of the vertebral column). Here we have fusion of several vertebral segments into one elongated element. The sacrum is not only the longest element of the vertebral column, but it also connects the axial skeleton with the pelvic girdle and hind limbs. In fact, this is the only solid connection of the vertebral column with the remainder of the postcranial skeleton. The shoulder girdle together with the forelimbs is not directly connected with the axial skeleton.

The transverse parts of the sacrum are enlarged into wing-like bony shelves that provide a close connection with the iliac blades of the pelvis. All articulations between neural arches within the sacrum are fused. Between adjacent pairs of sacral vertebrae, intervertebral foramina are located within the lateral transverse wing of each side. These foramina communicate with the neural canal and are open dorsally and ventrally. Their diameter is indicative for the caliber of the nerve and blood vessel branches that are passing through them. There is a clear relationship between nerve and vascularization supply passing through the sacral region depending on the length and function of the caudal region (Tigges, 1964; Ankel, 1965). The intervertebral discs are omitted between fused sacral vertebral

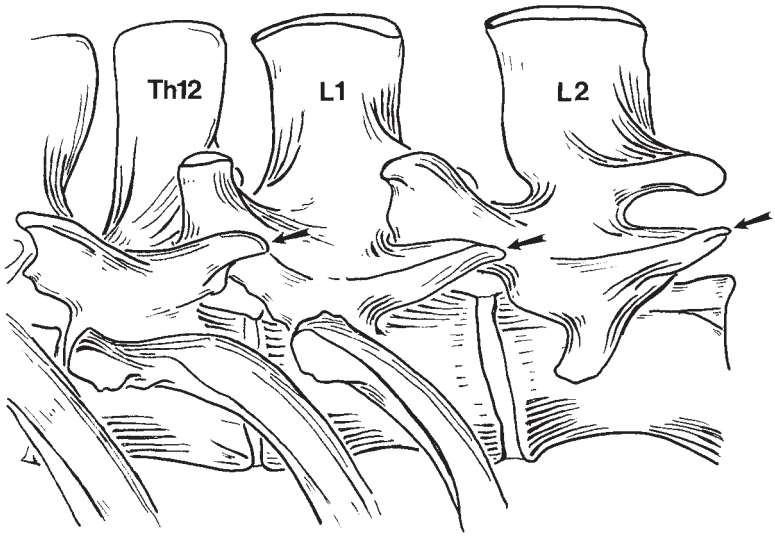

Figure 8.10 Transition from thoracic to lumbar region of a New World monkey showing accessory processes (indicated by arrows). Th12 = twelfth thoracic vertebra, L1 = first lumbar vertebra, L2 = second lumbar vertebra.

bodies. All articulations between neural arches within the sacrum are fused. The neural spines are fused also to form a sagittal crest (medial sacral crest). In cases where the spinous processes are not totally fused together, they are at least connected at their bases. The neural arch articulations within the sacral region have basically the same position as the articulations of the lumbar region, but they are generally reduced to insignificant bony projections. The zygapophyses at the front and hind end of the sacrum, however, continue generally to have the lumbar position. This also means that these three regions—lumbar, sacral, and proximal caudal—are functionally identical to each other, even though mobility is usually lost in the sacral region (see Figure 8.5).

Caudal Region

The tail, or caudal, vertebrae are typically smaller than all other vertebrae. Among primates this region is the most variable in terms of the number of segments that combine to form the tail. Only a few of the first, most proximal vertebrae have a fully developed neural arch with all the typical processes; the arch decreases rapidly from one vertebra to the other farther down the tail. There is evidence of a direct correlation between the total length and function (prehensile

tail among South American monkeys species) of the primate tail and the number of first tail vertebrae that are roofed over by neural arches.

These same tail vertebrae have transverse processes and dorsal spines. Tail vertebrae are characterized by so-called ventral arches, also known as haemapophyses (*haima, haimatos* is the Greek word for blood, body fluid) or chevron bones. These bony structures are short, V-shaped bone clasps that embrace the caudal artery. However, farther backwards towards the tip of the tail these structures become two small separate bony nubs. Chevron bones occur exclusively in the caudal region. They are situated under the front end of the vertebral bodies, attached by ligaments, and are often lost during the process of preparation of a skeleton, especially the more distal and therefore smaller chevron bones. Chevron bones can, however, be easily identified in X-ray photographs (Figure 8.11).

The bodies of the first caudal vertebrae are comparatively short. Backward, the vertebral bodies increase in length, whereas the bony superstructures (the neural arch and its bony protrusions), the transverse processes, and the ventral arches are reduced in size. The increase in length of the vertebral bodies continues to reach a vertebra of maximal length. Then, beginning with the longest vertebra, the body length and diameter decreases toward the tail end. The longest tail vertebra has different positions in different primate genera, and these positions are determined by the length as well as functional abilities of the tail. In those primates that do not have prehensile tails, the last tail vertebrae are thin and short (Figure 8.12).

Comparative Morphology

Generally, the vertebral columns of primates are fairly uniform in their morphology, which also indicates functional uniformity. There are, however, some specializations.

Within the prosimiae we find morphological uniqueness in the Lorisinae. All the other prosimians (Lemuridae, Indriidae, Daubentoniidae, and Galaginae) have more or less uniform and undifferentiated vertebral columns. This uniformity

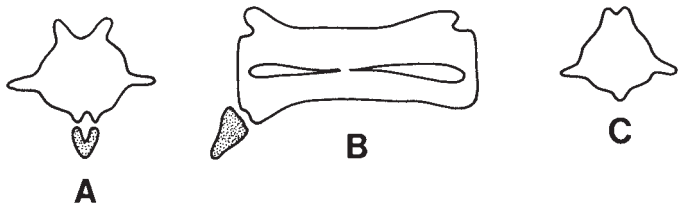

Figure 8.11 Position of haemaphophyses (shaded) under the bodies of tail vertebrae A) frontal view, B) lateral view and C) caudal view.

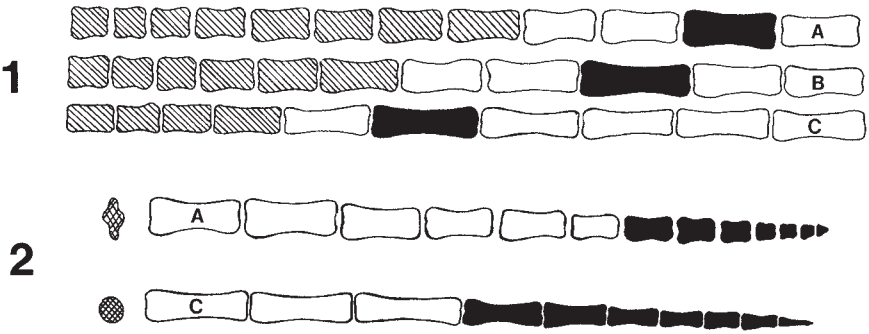

Figure 8.12 Proximal tail vertebrae (cranial is left). 1) Proximal neural arch bearing tail vertebrae (shaded) and longest vertebra (black) A) of a prehensile tailed monkey, B) of a prehensile tailed monkey lacking a friction pad at tail end *(Cebus)* and C) of a primate that does not use the tail as a grasping limb. 2) Shape of distal tail vertebrae of A) a prehensile tailed monkey and C) a monkey with a nonprehensile tail (cross section shaded, last seven vertebrae black).

of the vertebrae, ribs, and breastbones makes it virtually impossible to easily identify the family, genus, or species of vertebral columns—or even less—of single vertebral elements.

In genus *Tarsius* the vertebral column is derived, but principally in the cervical region. There, the articular processes between the hind end of the third cervical vertebra through the front end of the first thoracic vertebra (eighth vertebra in the row) are positioned differently than are those of any other primate. These articular facets are positioned in the same plane with the plane of the ends of the vertebral bodies, that is, in a plane that forms a right angle with the median sagittal plane through the vertebral body. This position of these articulations is presumably partially involved in the ability of *Tarsius* to turn its head about 180 degrees from the normal forward position to look straight backward over the shoulders without moving the body (Figure 8.13). This ability is superficially similar to the same movement in owls. The morphology of the vertebral column of *Tarsius* and owls, however, is totally different and thus is not structurally comparable.

It has been observed in other primate genera—*Cebuella, Propithecus,* and *Avahi*—that they are able to turn their heads backward almost as well as *Tarsius,* but none of them show the unique position of the articular processes of the cervicals. The thorax of *Tarsius* appears to be broader than is usually the case in nonhominoid primates. This shape is not the result of heavily bent ribs, but is the product of the unique length between tuberculum and capitulum costae in the upper thoracic region as well as the relative length of the lower ribs that are comparatively longer than in other primates of equivalent body size. All presacral vertebrae are rather short cranio-caudally and lack a distinct keel sagittally in

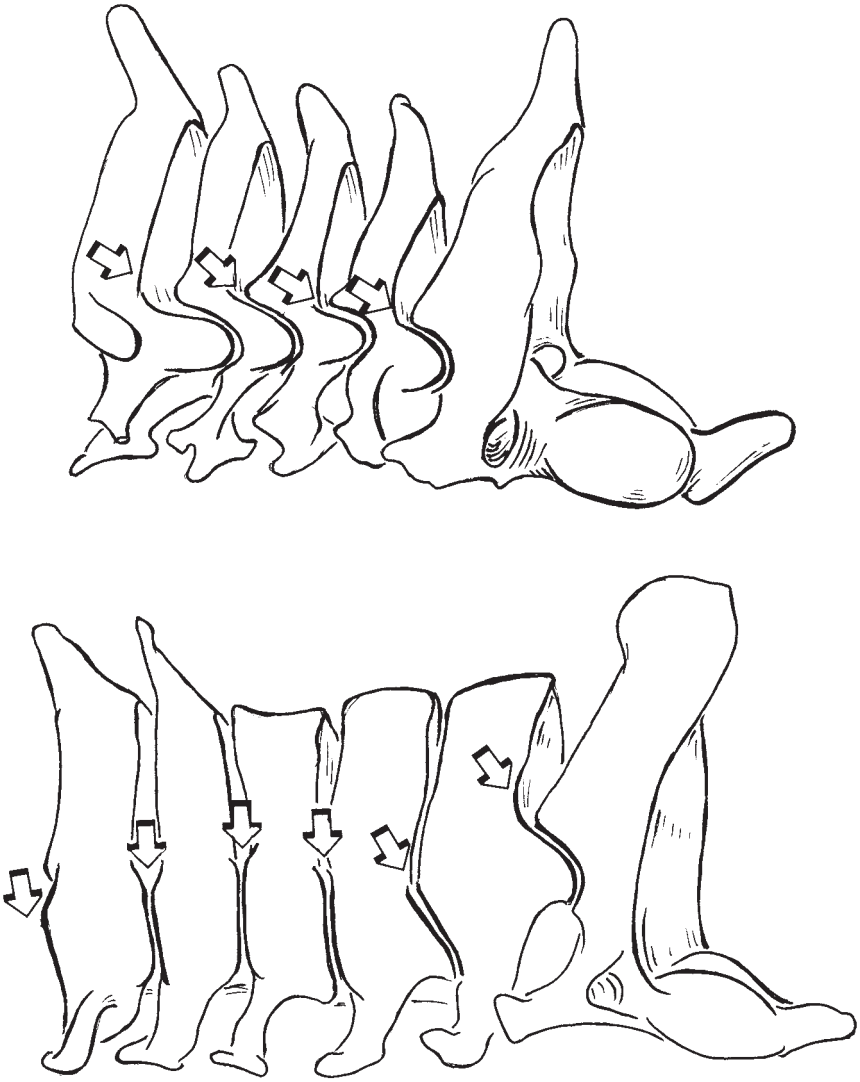

Figure 8.13 Position of the articular processes in the cervical region indicated by arrows. Top *Loris tardigradus,* cervical vertebrae 2–6. Bottom: *Tarsius bancanus,* cervical vertebrae 2–6.

the middle of the ventral aspect of the vertebral bodies of the lumbar region that is characteristic for prosimian primates, and also present, but often less well developed, in many monkeys.

In spite of the fact that *Tarsius* uses its tail as support when clinging to an upright branch in a vertical position, there seems to be no difference in the morphology of the tail vertebrae when compared to other long-tailed primates. In cebids that use their tails as fifth extremities, the vertebral column shows changes adapted to this function, as we shall see (compare Figure 8.12).

In their vertebral columns, the lorises appear to be among the most derived group of primates. All bony protrusions in the vertebrae of the Lorisinae show a greater degree of smoothness than any other primates.

Most of the projections are rounded off and not pointed at the tips. An exception to this rounding off phenomenon is found in some of the dorsal spines of the African species *Perodicticus potto.*

Starting at the third cervical vertebra and increasing in height on the following vertebrae, the dorsal spines become most prominent and pointed. The two last cervical vertebrae (vertebrae six and seven) and the first two thoracics are involved. In fact, here the spines are considerably higher dorsally than in any other of the nonhominoid primates. For instance, in pottos the highest dorsal spine in the second thoracic vertebra (vertebra nine) is twice as high as the vertebral body plus neural canal are together. The dorsal spine of the third thoracic is much reduced in length (Figure 8.14). These long and pointed dorsal

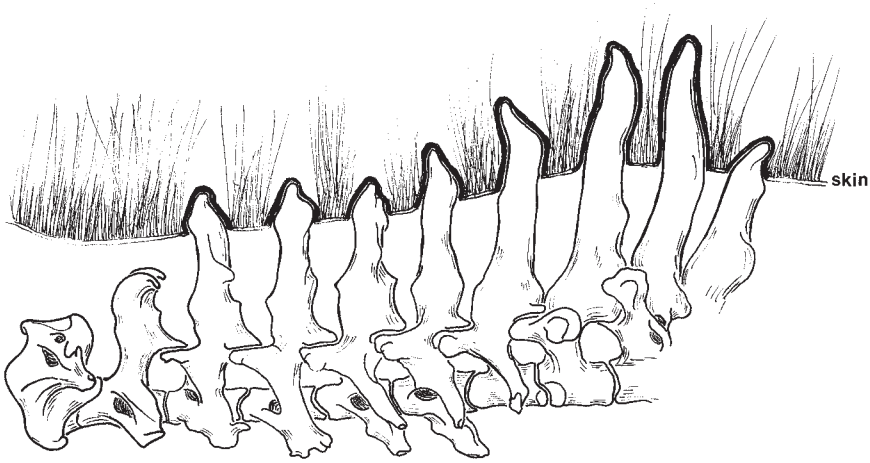

Figure 8.14 Cervical region and thoracic vertebrae 1–3 of *Perodcticus potto* showing elongated dorsal spines (C3-Th3) that are protruding through the skin and covered with cornified epithelium.

spines protrude through the skin in adult pottos and are covered with a cornified, rather tough epithelium (*epi* is a Greek word as well as a syllable with many meanings. In combinations like epi-thelium it usually means upon, on, or over. Thelium in this context means cell layer). This peculiar structure has historically been interpreted in different ways. At one time it was believed to be used as a defensive structure involved in head jarring with the head bent down toward the chest and the area on top of the back involved in attacks with these pointed spines.

Later, Walker (1970) discovered that the neck bending behavior is not at all correlated with aggression but plays a role in nonantagonistic social encounters. Walker observed pottos rubbing their necks in greeting ceremonies and other, peaceful social contacts. Led by these observations, Walker looked at the histology of the covering epithelium in the potto's neck. He found that this epithelium is highly sensitive and equipped with tactile nerve endings. Now it appears to be quite obvious that these dorsal spines cannot possibly be defensive organs. Looking at them with Walker's explanation in mind, one can see that the spines are indeed totally surrounded and submerged into the dense fur of the animals and thus could not be of much harm to a possible enemy.

Lorises (*Loris, Nycticebus,* and *Perodicticus*) also have more presacral vertebrae and thus longer trunks than other prosimians. In pottos the trunk is comparatively barrel-shaped. All four genera of the Lorisinae have characteristic dorso-ventral foramina that are located in the bases of the transverse processes of the thoracic vertebrae (Figure 8.15). This feature distinguishes the subfamily from all other primates. The other African genus of this family, *Arctocebus,* has most peculiar ribs. These ribs are broad and shingle-like in their vertebral third, and they overlap each other, just like shingles on the roofs of houses. Jenkins (1970) compared these ribs with those of the sloths, which show the same shingle-like rib morphology. However, here again, a lack of behavioral data about these rare and elusive prosimians makes it impossible to give a valid functional interpretation for these unusual ribs, although Schultz (1961) believed that the overlapping ribs might give protection to these animals by making the ribcage solid like an internal armor. Positioned inside the body and only overlapping in a small area of the back, the ribs could hardly prevent a fatal bite from behind, as can the hard, interlocking surface in armadillos.

The two Asian lorisine genera—*Nycticebus* and *Loris*—do not exhibit any such unique traits in the vertebral column. They are very much like African *Arctocebus* in not having pointed cervical spinous processes, but they also have the foramina in the transverse processes in the thoracic region. All four lorisine genera have reduced tails, which in Asian *Nycticebus* and African *Perodicticus* is correlated with comparatively high numbers of sacral vertebrae. Most other prosimians have long tails. Within the Prosimii tail reduction is also the case for

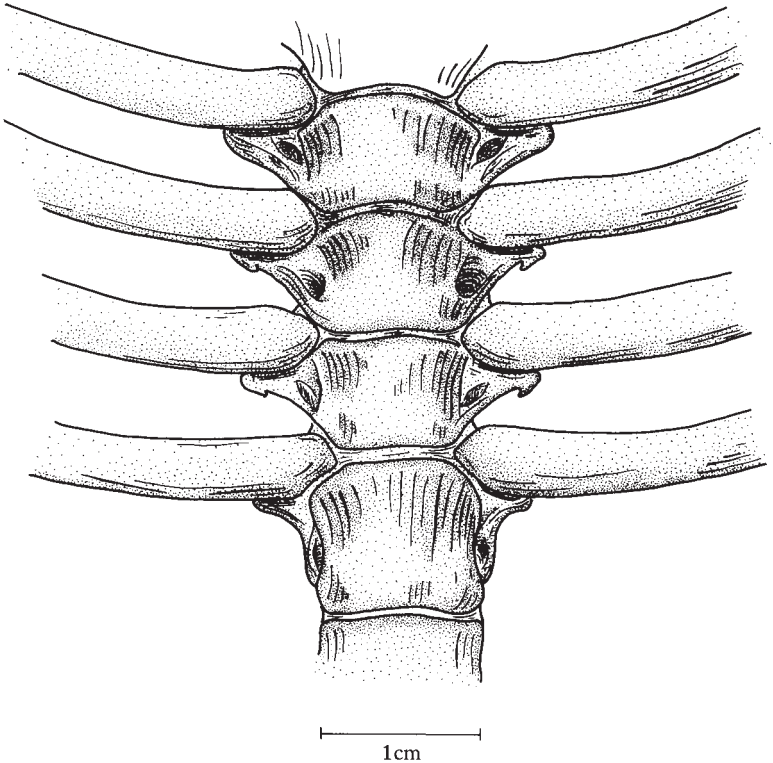

Figure 8.15 Ventral view of the thoracic vertebrae (13–15) and the first lumbar vertebra (cranial is up) of *Perodicticus potto* showing the foramina that are typical for lorisiform prosimians.

the Malagasy genus *Indri* which, however, does not have an elongated sacrum. The sacrum of the *Indri* is combined of three vertebrae.

The vertebral column of Anthropoidea does not exhibit many distinctive or unusual morphological features. Thus the appearance of the vertebral column is rather uniform in all the Cercopithecoidea. Partly at least, they show one obvious feature distinguishing their lumbar vertebrae from those of South American Cebidae and the Hominoidea. In cercopithecoid monkeys the processus transversus arises directly from the sides of the vertebral body, usually at the site where its diameter is widest. In the larger cebids genera *Alouatta, Lagothrix, Ateles,* and *Brachyteles,* as well as in all Hominoidea, however, the processes arise from the bases of the neural arch above the vertebral body (Figure 8.16). In some of the smaller South American monkeys as well as the callithrichids, the transverse processes of the lumbar region arise from downward extensions of the neural arches that extend over the side of the vertebral body and directly give rise to

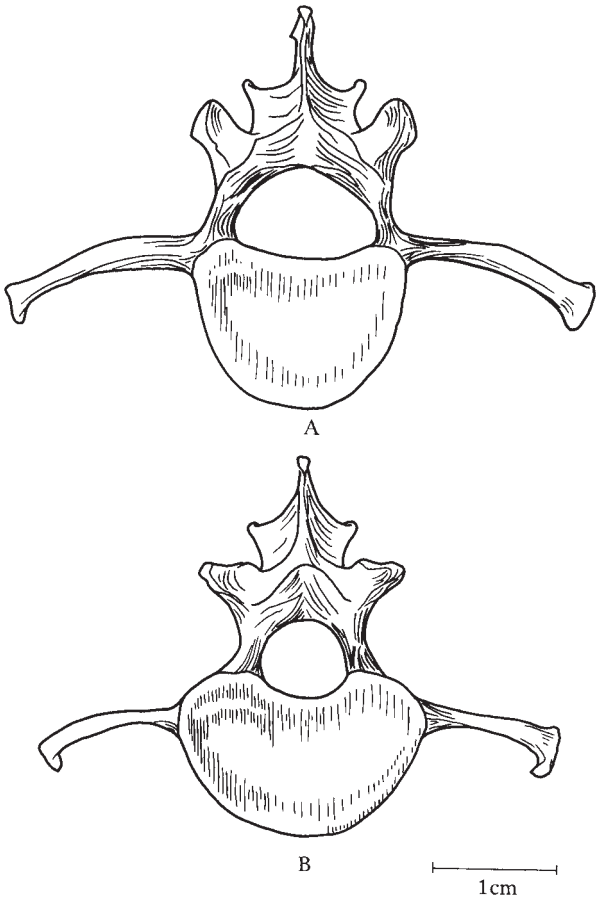

Figure 8.16 A) Fourth lumbar vertebra of *Ateles,* typical for New World monkeys, and B) fourth lumbar vertebra of *Macaca,* typical for Old World monkeys.

the downward and forward directed transverse processes. In these South American primates, their origin thus is also at the sides of the area where the diameter of the vertebral bodies is widest and not above them. No crucial functional consequences are resulting from these positional differences.

There is variety in the vertebral columns of South American monkeys where there is uniformity among the Old World monkeys.

In 1963, Erikson suggested that vertebrae of the thoracic and lumbar regions should be counted "functionally" and advocated not to follow the traditional subdivision into rib-bearing and non-rib-bearing thoracic and lumbar vertebrae. Erikson proposed that the change in position of the articular processes

(zygapophyses) is much more informative and important than the presence or absence of ribs. The dorso-ventral back and forth movement between vertebrae with the typical lumbar position of the articular processes can involve up to three vertebrae that have usually been attributed to the thoracic region as they bear ribs. Consequently, the position of articulations, not the presence or absence of ribs, are tallied in Erikson's method of counting.

In all vertebrates, the lumbar region is a rather rigid structure. The position of the articular processes prevents adjoining vertebrae from any degree of turning against each other. This situation is additionally reinforced by the accessory bone projections (processus accessorii) locking these articulations from below and from the sides (see Figure 8.10).

In some cebids the dorsal spines of the lumbar region are cranio-caudally so long that little interspace remains between individual dorsal spines. Additionally, these spines are elongated cranially into a point and are split into a V-shaped groove at their hind end. Thus, only the slightest amount of dorsal bending of this region is possible because the cranial points of the spinal processes become locked into the V-shaped end of the spine in front of it, preventing any backward bending. This condition could be related to the use of the tail as a fifth limb as it provides stability to the trunk.

The sacrum of the South American prehensile tailed monkeys reflects the high functional abilities of the adjoining caudal region in different ways. In prehensile-tailed monkeys, the contact surface of the sacrum with the sacral articulation of the iliac blades is known to have a rougher relief than other long-tailed monkeys, thus enlarging the area of interlocking contact between sacrum and pelvis (Leutenegger, 1974). The morphological differences between prehensile-tailed monkeys and long-tailed monkeys that do not use their tails as a prehensile limb are less obvious than the remarkable functional differences. This can be easily understood: When hanging on the tip of the tail only, an action often exercised by prehensile-tailed monkeys, the body weight is not supported through the pelvis but passes primarily through the axial skeleton. The axial skeleton in prehensile tailed monkeys is more robust and stronger than in primates with long tails that are not actively involved in locomotor or feeding behavior. But the basic morphological "Bauplan" of the axial skeleton remains the same. This morphology provides the architectural potential for a high variety of functional adaptations.

The sacrum is also an indicator of tail length and function. In long-tailed primates, the sacrum is usually composed of three sacral vertebrae. In many cases, when tail length decreases, there is an increase in the number of sacral vertebrae, even though this is not always the case in prosimians or monkeys with reduced tails. Hominoidea, which do not have an outer tail, all have sacra that are combinations of more than three vertebrae, with three being the usual number of sacral vertebrae in primates. In addition, one can observe that the neural arch

tapers posteriorly to a very small diameter in the sacra of apes and humans. Looking at the sacral region of many primates, one can see that there is quite a degree of difference between primate genera in the size of the neural canal of sacra. Comparing the cranial opening with the caudal opening of the sacral neural arch, we can observe the following: generally the diameter of the neural canal is triangular in the sacrum. In long-tailed lemurs, Callitrichidae, and Cercopithecinae, the cross sectional area of the opening at the front is broader at the base than it is high, and the opening at the hind end remains nearly as high, but the breadth has decreased considerably. In Hominoidea the opening at the front-end of the canal is shaped like an equal-sided triangle, the caudal opening however is usually very small and not much broader than high, if there is an opening at all. Both height and breadth are also reduced in some macaques and in baboons, in combination with some reduction of tail length region. In South American *Cacajao*—the only New World monkey that exhibits reduction of the caudal region—the opening at the end of the sacral neural canal is low and broad, with the breadth reduced to about one third of the front opening (Ankel, 1972).

In those South American monkeys that have a prehensile tail, the opening of the sacral canal at the caudal end is as large as or sometimes even higher (but not broader) then the opening at the front. This condition is also reflected in the height of the neural arches (and the diameter of the neural canal) of the first tail vertebrae. These arches are considerably higher in South American prehensile-tailed monkeys than in any of the primates with long tails that do not have a grasping function. In primates with no tail or short tails, there is also no neural arch above the few vestigial vertebral bodies that are remaining. While common long-tailed primates usually have no more than three or four tail vertebrae with neural arches, in the prehensile-tailed woolly spider monkeys, spider monkeys, woolly monkeys, and howler monkeys, about seven to eight of the proximal tail vertebrae are equipped with neural arches that are elevated high above the vertebral bodies. In the Hominoidea the neural cord proper ends in one of the most proximal lumbar vertebrae while the neural canal ends within the sacral region. The diameter of the neural canal is generally correlated to the diameter of the spinal cord, the accompanying blood vessels, and the three membranes called meninges: the dura mater (*durus* is Latin for hard, mater means mother), the arachnoid mater (*arachnoid* is Greek for spider web like), and the pia mater (*pius* is Latin for tender), as well as enveloping fluid.

The spinal cord is known to have a comparatively large diameter in the sacra of prehensile tailed monkeys, and the canal contains the double system (arteries and veins) of blood vessels as well. Both the nervous system and the vascular system have to supply the highly sensitive area at the ventral third of the tail end that is equipped with a well developed tactile friction skin in the South American

genera *Brachyteles, Ateles, Lagothrix,* and *Alouatta* (Figure 8.17). These primates also have very deep ventral arches in their tails.

Yet another morphological expression of the great functional potential of the caudal region is found in the position of the longest tail vertebra of prehensile tails. It is farther away from the root of the tail than in long-tailed monkeys that do not actively use their tail. The vertebrae at the tip of prehensile tails are dorso-ventrally flat and cranio-caudally much shorter than those of nonprehensile tails. This means that both at the root of the tail as well as towards the tail end there are more joints between adjacent vertebrae as the vertebral bodies are shorter, and these regions are consequently more flexible than they are in monkeys with fewer vertebrae and intervertebral discs per unit of tail length (see Figure 8.12).

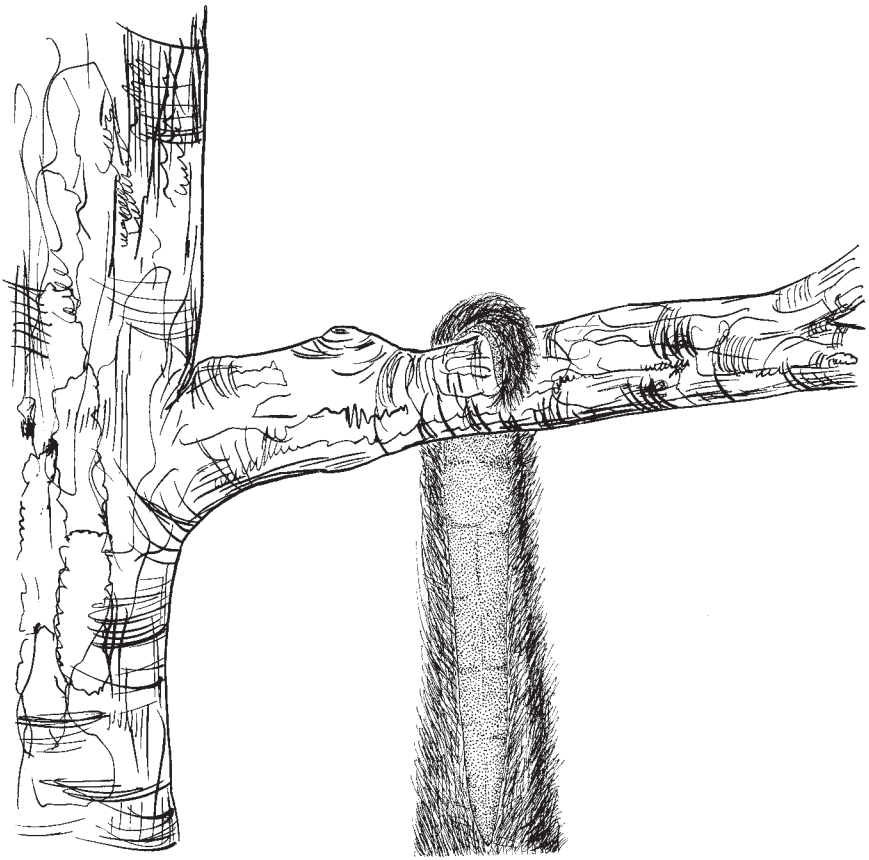

Figure 8.17 Prehensile tail of New World ateline monkey using only the very tip of the tail to hang on a branch.

The Cercopithecoidea are amazingly uniform in the morphology of their vertebral columns. The tail is reduced to some degree in baboons and several macaques.

Hominoidea have several characteristics in common in the vertebral region that distinguish them from all other primates. In the cervical region, Pongidae have enormous dorsal processes, associated with the accordingly well-developed musculature (predominantly musculus splenius capitis, m. longissimus capitis, m. semispinalis capitis) that are especially massive in male orangutans and gorillas. These processes are comparatively not as long as the prominent spinal processes of *Perodicticus potto.* They are only present in the cervical region where the dorsal spine of the seventh vertebra is usually the most prominent one. The processes are not pointed but end in a protuberance. Enlargement of the dorsal spines in the cervical region is obviously correlated with the enormous bulk of the neck musculature at the back of the heavy head in the largest primates. In humans also, the seventh cervical vertebra has the longest dorsal spine. It is the one that can be felt below the skin at the base of the neck, and was therefore named the *vertebra prominens,* the prominent vertebra.

Farther back in the vertebral column of Hominoidea, the increase in diameter in the vertebral bodies is more apparent than the increase in length. The same is true for the bony processes of the lumbar region of humans: the neural arches, the zygapophyses, and the transverse processes increase their width more than their length. The opposite is the case in all prosimian and monkey vertebrae, as their length increases much more than the breadth throughout the presacral vertebral column and especially in the lumbar region. Thus, in the lumbar region of Hominoidea and especially Hominidae, the vertebrae are short and rather broad. They do not have the ventral keel that is found in the lumbar vertebral bodies of all the other primates with the only exception of genus *Tarsius*. In living Hominoidea, the sacrum is long and tapers at its caudal end, whereas the tail has been reduced to only a few tiny elements and it is not visible externally in living Hominoidea. The articular surfaces with the pelvis and the sacrum in humans are larger than in pongids of the same approximate body weight. It is thought that this enlargement has developed as a result of upright posture and locomotion, for we know that this is the area where the entire weight of the presacral body of humans is transmitted through the vertebral column to the pelvis and hence to the legs.

The ribs of all Hominoidea are more heavily bent near their articulation with the thoracic vertebrae than in other primates. The transverse processes of the thoracic region are at the same time angulated more backward. This angulation of the struts which support the tuberculum of the ribs and their bending result in a barrel-shaped rather than narrow rib cage in all Hominoidea. The thoracic vertebrae thus come into a position within the rib cage, with the ribs extending further dorsally than the thoracic vertebrae. In all nonhominoid primates the less

bent ribs are "hanging down" from the vertebrae and the thoracic vertebrae are positioned dorsally of, not within, the rib cage. As already mentioned, concomitantly with the broadening of the rib cage the breastbones are also wide, whereas they are narrow in prosimians and anthropoids.

Ontogenetically, the ossification of the elements that shape the breast bone appear in seriated ossification centers within its ontogenetical predecessor, the cartilage, and results in separate, seriated bony elements, the so-called sternebrae that are interconnected by cartilaginous tissue. These bones remain separate from each other throughout life in all prosimians and monkeys. Thus, their breast bones remain segmented, which in contrast become fused to one long breastbone in Hominoidea. Sternal fusion in the Hominoidea begins at the caudal end of the sternum, at the so-called "sword process" (xiphoid process—*xiphoid* is the Greek term for sword, or *processus ensiformis*—as *ensis* is the Latin word for sword). Also the largest, most cranial element of the sternum—the manubrium, called the "handle" of the breastbone because of its peculiar, handle-like shape—that articulates with the claviculae fuses with the rest of the sternum in humans, rarely in the apes and not at all in all other primates. Craniolaterally, the manubrium has two articular facets for the clavicles (the *incisurae clavicularis*) that are separated in the middle by a notch, the so-called *incisura jugularis*. Further caudally on the manubrium we find the insertion of the cartilaginous ends *(cartilagines costales)* extending caudally from the first pair of ribs. In Hominoidea the distal end of the sternum, the xiphoid process, ossifies late in individual development, whereas it ossifies early in the Prosimii and Anthropoidea. On the sides of the sternum and between the sternalia the cartilaginous distal ends of ribs are inserted (see Figure 8.8).

The ribs are subdivided according to the place and manner of their connection with the breastbone. Most of the ribs, beginning with the first pair, insert with their cartilaginous ventral end in the area between adjoining sternal segments. These are called true ribs or sternal ribs (in the Latin expression *costae verae* or *costae sternales*). Some of the more caudally situated ribs combine their cartilaginous ends to jointly insert at the distal end of the last sternal segment, so that the xiphoid process is positioned between them. The joined cartilaginous ends of these ribs make up the so-called coastal arch. These ribs are therefore called arch ribs (or *costae arcuatae*). Two or three pairs of the most caudal ribs do not have any connection with the breastbone at all but are embedded in the musculature. These are the so-called free ribs (or *costae fluctuantes*).

Ribs in their basic structure are long, narrow, and flat bones; they are bent at their vertebral end in two directions. There is a slight rotation along their long axis as well as a distinct arch of the rib's body near the vertebra (see Figure 8.6). Also, true ribs have two articular facets: one articulating with the dorsal aspect of the thoracic vertebral body at the rib's vertebral end, the *capitulum costae* or rib's head, and another, further lateral on the rib and dorsally, contacting the end

of the ventrally adjoining vertebral transverse process, the *tuberculum costae,* that is positioned caudal to the first articulation. The distance between the two rib articulations changes according to the change of length and position of the transverse processes of the vertebrae. The heads of the true ribs usually articulate at the cranio-dorsal end of the thoracic vertebrae; thus, they are also partially situated over the intervertebral disc. Farther back in the thoracic region, with the transverse processes of the vertebrae becoming gradually and increasingly shorter and the vertebral bodies increasing in cranio-caudal length, the *tuberculum costae* and its contact with the transverse process is progressively reduced. Thus, the more distal ribs are only connected to the thoracic vertebral bodies with their heads and are lacking the *tuberculum*. Concomitantly, the articulation of the ribs' heads moves onto the side of the more distally situated thoracic vertebra. The first ribs are much shorter than the following pairs, and they are not twisted around their longitudinal axis. From front to back, the ribs quickly increase in length, remain more or less of the same overall length in the middle of the region, and decrease in length again distally. The most distal free ribs are usually short; typically they are not twisted around their longitudinal axis and are but slightly bent overall. The last ribs may occasionally actually fuse into one or both sides of the vertebrae, thus producing an elongated transverse process-like structure that is positioned just as these processes are in the lumbar region (Ankel, 1967). In genus *Tarsius,* both the tuberculum and the capitulum costae are fused into one long articulation that corresponds to an equally elongated area of attachment on the underside of the thoracic transverse processes. This morphological specialization is unique for tarsiers which also have rather highly bent ribs resulting in a slightly barrel-shaped thorax (Figure 8.18).

In concluding this account of the vertebral column, it should be pointed out that many studies have shown how the numbers of vertebrae vary within the different regions intraspecifically in all primates (see also Tables I, II, III, and IV in Schultz, 1961). This variability almost never affects the cervical region, with the stable count of seven in all primates and most mammals. Variability is greatest within the caudal region, which also represents the free end of the vertebral column that is caudally not joined by another region of the vertebral column. This fact might partially be the reason that variability of the number of caudal vertebrae is not only largest intraspecifically but also interspecifically among primates.

SHOULDER GIRDLE

We have seen that the vertebral column and thorax of many nonhominoid primates are unspecialized and thus, not very different from each other or the vertebral columns of other mammals—for example, the house cat. We also have

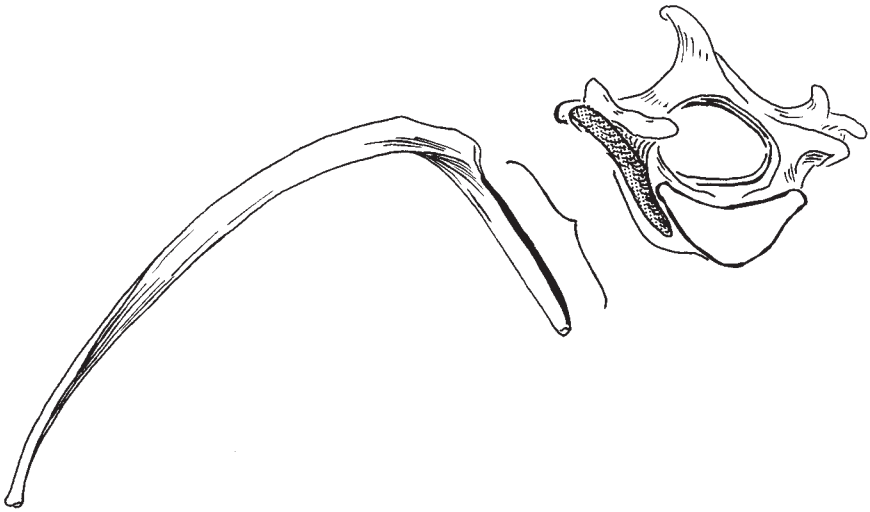

Figure 8.18 The highly bent fourth rib of *Tarsius syrichta* with the elongated articular surface (black); tuberculum and capitulum costae fused together. Fourth thoracic vertebra with attachment area for rib (shaded).

reviewed how the extant members of the Hominoidea differ significantly from other primates in the morphology of the axial skeleton and in the shape of their ribcage. Among these apes and humans, as has been stated, the thorax is broad and shallow, and the vertebral column is positioned within the outline of the ribcage, rather than at the utmost dorsal edge of the thorax. The real reason for the appearance of barrel-shaped trunks in hominoids is not well understood (Shapiro, 1993). Nor do we know when this broadening of the trunk first arose in the evolutionary history of the hominoid primates (Figure 8.19). There are different factors that could have influenced the original development of barrel-shaped rib cages. One such factor could be the large, absolute size and concomitant increase in relative mass of the respiratory system and viscera. This factor, however, could not apply to those few smaller primates, such as *Tarsius, Propithecus,* or *Ateles,* which also show chest broadening. Another cause for the change in chest shape could be sought in diet. We know that mammals which live predominately on leaves or grass tend to have broader trunks than those that subsist on high protein diets, for example, carnivores. There are, however, primates that are specialized for an almost exclusive leaf diet—for example, the South and Central American howler monkeys, which have narrow and deep trunks, not unlike any other monkey. A third factor could be locomotion. Primates with barrel-shaped trunks not only have broad and shallow rib cages, but this broadness also affects the pelvis in hominoid primates (broad ilia), even though

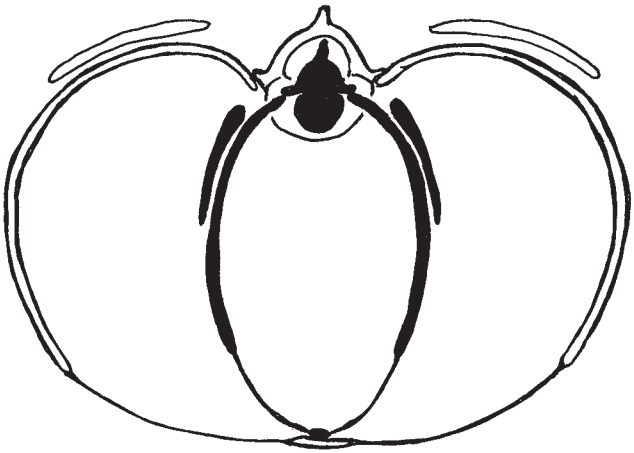

Figure 8.19 Rib cages of human and macacque (black) superimposed to show the morphological difference between the two.

the shape of the ribcage does not affect the width of the ilia in *Tarsius, Perodicticus,* or *Ateles.* This condition can in turn be influential for the position and function of the hind limbs. However, discussing the primate shoulder girdle, we want to evaluate the influence of the broad thorax on locomotion and forelimb movement, as it perhaps relates to improved climbing abilities. Only primates with barrel-shaped trunks have a more or less flat back and chest. In those primates, the shoulder blades are positioned on the back and not on the side of the rib cage as in mammals with narrow trunks. In the latter the shoulder blades are positioned laterally. Thus, the shape of the trunk critically influences the morphology and function of the entire forelimb girdle.

All primates retain clavicles that are lost in many other mammals—for example, cats, dogs, and horses. As we have seen, clavicles are the only remnant of the exoskeletal elements derived from early vertebrates, and the clavicle is the only dermal bone in the primate postcranial skeleton.

The clavicle attaches medioventrally at the manubrium stem and laterally with the acromion of the shoulder blade (scapula). Thus, the clavicle acts as a strut holding the shoulder blades apart. We have also noted that the clavicular articulation with the breastbone is the only attachment of the upper limb girdle to the postcranial skeleton. In those mammals that have lost clavicles, the upper limb girdle is embedded and attached to the trunk solely by musculature. In animals with clavicles, the upper limb girdle is also attached mainly by the muscles that both move it and hold it in place. This condition in turn gives a high degree of mobility to that region. It is the function of the clavicles to keep the scapulae, and consequently the upper arm articulation, in a lateral position, or,

as in hominoids with a broad trunk, in a dorsal position. This position gives a higher degree of mobility to the articulation of scapula and humerus, and thus the entire upper extremity—a feature that is of great importance to animals that live in a three dimensional environment (Jenkins et al., 1978; Larson, 1993; Larson and Stern, 2006).

Primates in particular, with their broad trunks, dorsal scapulae and the presence of clavicles, have a three-dimensional range of forearm function, as compared to, for instance, horses, in which the forearm movement is restricted to an antero-posterior parasagittal plane that is essentially two dimensional. In sum, the presence of the clavicles in the primate shoulder girdle is of critical importance for many forelimb activities that are, in part, responsible for the high adaptability of primates. In barrel-trunked primates, the clavicles are comparatively longer than in primates with narrow trunks and are also directed cranio-laterally rather than strictly laterally as in lower primates.

While the hind leg is connected to the axial skeleton by means of the amphiarthrosis between sacrum and pelvis, the forearm articulates with the mobile shoulder blade that is exclusively held onto the trunk with the help of muscle loops. The shoulder blade (or scapula) therefore is able to slide two-dimensionally (to a certain degree) on the thorax. The shoulder blade itself is a more or less triangular, flat bone. It has a cranial, medial, and a lateral edge. The lateral upper angle enlarges or spreads out around the concave glenoid fossa—the articular facet for the globular head of the humerus. From this angle to the vertebral edge of the scapular triangle runs the *spina scapulae,* or scapular spine, an elevated bony ridge that flattens out toward the vertebral edge of the bone. This spine becomes robust and broad near the glenoid fossa where it protrudes into a wide and strong bony process, the so-called acromion of the scapula. The acromion is somewhat tilted in a ventral direction, forward and medially; it thus overlaps the humeral head where it meets the lateral end of the clavicle. The *spina scapulae* divides the shoulder blade into two planes of variable dimensions, called *fossa supra-* and *infraspinata*. The two fossae are very variable in shape, both intra- and intergenerically. In addition, the outline of the entire bone is variable to some extent within and between different primate genera. On the (ventral) inside of the lateral part of the cranial margin, directly medial to the glenoid area, a bony extension protrudes into a strong, beak-like bony process. This process, the so-called coracoid (*korax* is Greek for "crow"), is shaped like a strong hook that extends above and beyond the articular facet of the glenoid articular surface. This strong process is connected to the acromion by the coraco-acromial ligament, which, together with ligaments to the clavicula, is part of the articular capsule for the humeral head. The coracoid also serves as point of attachment for a ligament with the clavicula. Three arm muscles are also inserting here (*musculus pectoralis minor, m. coraco-brachialis,* and the short head of the *biceps brachii*).

As an entity, the shoulder blade has a framelike construction. The blade is thick at the edges and in the area of the spine. The spine of the shoulder blade not only serves as a bony ridge for the attachment of muscles but also stiffens the entire bone (according to the T-beam principle). The planes of the shoulder blade are very (paper) thin at their centers, often even fenestrated, especially the large infraspinal plane of the largest primate shoulder blades—for example, those of *Gorilla* or humans.

The parts of the scapula that are subject to forces are the edges and bony processes: the scapular spine, the glenoid for articulation with the humeral head, and the acromial and coracoid processes.

Numerous muscles attach at the edges, the spina, the acromion, and the coracoid process of the scapula. These muscles move the shoulder blade upon the ribcage and hold it in place. Thus the shoulder blade "hangs" in an envelope of muscle (Roberts, 1974).

The arm shifts its position in unison with the scapula and, consequently, the length and proportions of the scapula act as lever arms and are important for the degree of mobility of the upper limb. The shape and proportion of primate shoulder blades are correlated with different types of forelimb use (Figures 8.20 and 8.21). Shoulder blades of gibbons, for example, are elongated and narrow. The scapulo-humeral articulation, the glenoid fossa, is small and shallow and thus adds to the fact that this articulation is free and mobile. This entire articulation

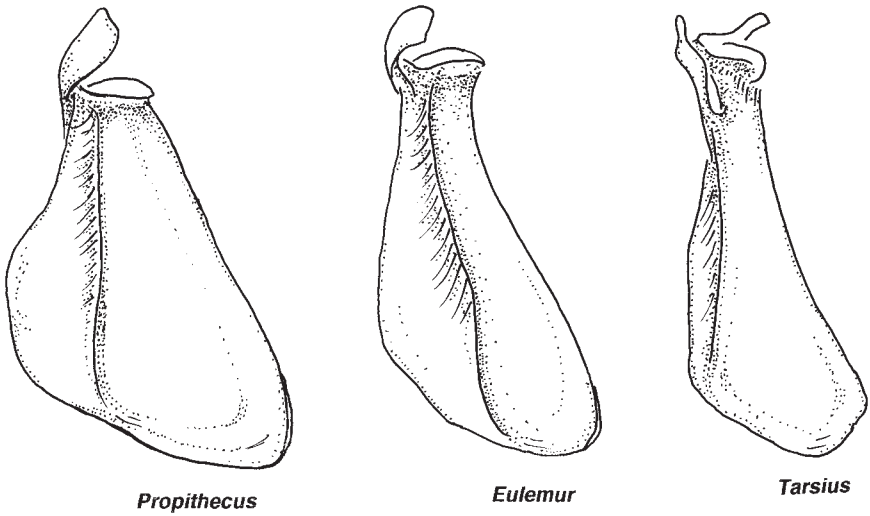

Figure 8.20 Right shoulder blades of three prosimians: *Propithecus,* a vertical clinger and leaper, *Eulemur,* a quadrupedal climber, and *Tarsius,* the aberrant and highly specialized vertical clinging and leaping primate that, overall, has a prosimian grade organization.

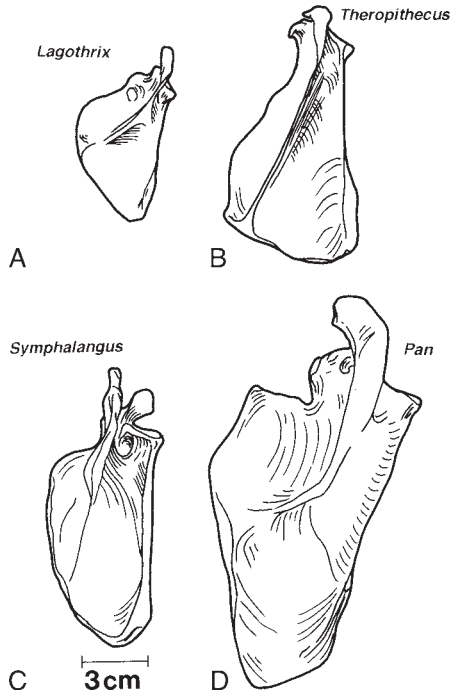

Figure 8.21 Right shoulder blades of A) a New World prehensile tailed monkey *(Lagothrix)*, B) a predominantly terrestrial Old World quadruped *(Theropithecus)*, C) a true brachiator *(Symphalangus)* and D) a knuckle walker *(Pan)*.

is secured mainly by tendons and musculature. This articulation of gibbons is highly mobile but not very stable (Larson, 1993).

In all the barrel-chested primates the position of the shoulder blades is different from that of the primates with narrow chests. The high position of the shoulder blades dorsally on the broad trunks of hominoid primates results in an exposed articulation of the upper arm, while in narrow-chested primates this articulation is tucked to the latero-ventral aspect of the trunk. In hominoid primates the range of the scapulo-humeral articulation and of the upper extremity is therefore much higher than in nonhominoid primates.

The fore-extremity can be envisioned as moving along the radius of a circle, the center of which is the scapulo-humeral articulation. The circle's radius is the entire length of the forelimb including the length of the hand. The mobility of the forelimb is greatly depending on body size. Increased body size is accompanied by an enlargement of all inner organs. It also requires an increase in bulk of musculature and the muscles, in turn, need more insertion surface. More forelimb use can also result in enlargement of the muscle bulk. Even diet can influence

the dimensions of the alimentary tract and thus may result in a different shape of the trunk. Locomotion, posture, and pelvic breadth can also be important to trunk dimensions. Trunk dimensions and rib shape, rib length, and position are intrinsically linked to the mobility of the iliac blade.

FORELIMBS

Very unusual among all primates is the comparatively very stout and robust humerus of the aye-aye (Soligo, 2005; Figure 8.22).

As already mentioned above, the broadening of the trunk is also accompanied by a change of the relative position of the upper and lower articulations of the humerus. This condition is called humeral torsion. This torsion actually occurs along the diaphysis shaft of the humerus rather than by shifts or by twisting of either the humeral head or the lesser tubercle. The question of where humeral torsion

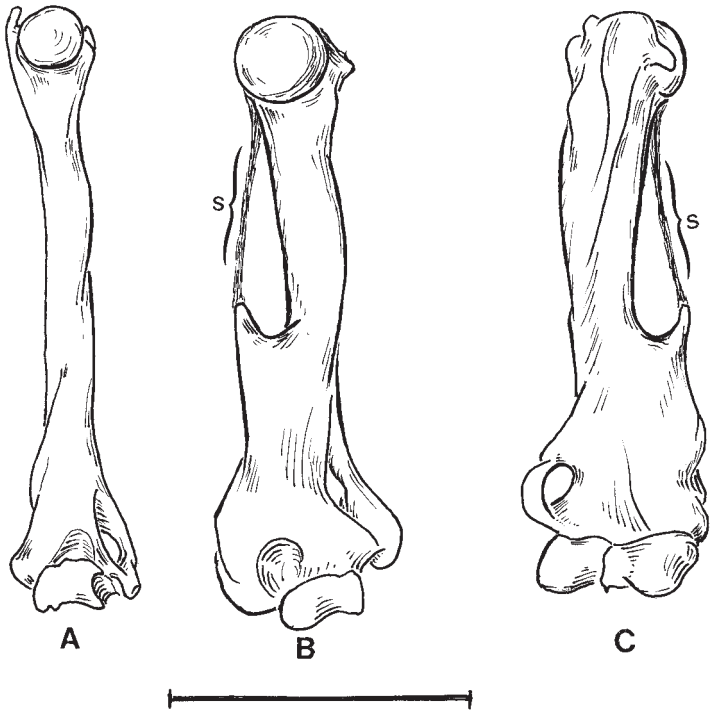

Figure 8.22 The very robust humerus of *Daubentonia madagascariensis,* the aye-aye compared to the femur of *Eulemur fulvus* A) *E. fulvus* left humerus of an adult male, dorsal view. B) *D. madagascariensis* left humerus of and adult male, dorsal view, C) the latter, ventral view. Scale 5 cm.

occurs has been addressed differently by different authors (see also Larson, 1993, page 61), as some assume it is just the humeral head having changed direction in various primate types. Alternatively, humeral torsion is said to be effected by a move of the lesser tubercle of the humerus, while the greater tubercle is not affected by any positional change. However, much earlier findings that are based on developmental studies have been able to document that humeral torsion occurs with rotation within the diaphysis in the distal part of the humerus (Oliver, 1962). Torsion is directed medially and amounts to about 80° in humans, about 30° in Hylobatids (the least degree of humeral torsion among hominoids), and about 10° in terrestrial *Macaca* (Larson, 1988). The angle of humeral torsion in African apes approaches that of humans, and it is greater in the gorilla (75°) than in the chimpanzee (63°). Without such torsion within the humeral shaft, the hands of hominoids, and especially those of humans, would always be turned outward (extreme supination) when the arms are in a relaxed position. To say it differently, if the lower articulation of the humerus is positioned perpendicular to the long axis of the body, the head of the humerus faces backward in hominoid primates (Figure 8.23).

In some primates a foramen is found at the inner side of the outer end of the humerus. This foramen is a feature that has survived from archaic mammals, and has the complicated name "entepicondylar foramen." Where it is present, the median nerve and the brachial artery pass through this foramen. It has been retained in most living prosimians except the two African genera of lorises *Perodicticus* and *Arctocebus,* where it is only variably present. It is especially large in the unusually robust humerus of the aye-aye, *Daubentonia madagascariensis*. Species of many South American monkey genera also have this foramen—for instance, in *Saimiri, Saguinus [Oedipomidas], Pithecia, Cacajao,* and sometimes *Cebus* and *Aotus* (Figure 8.24). This foramen is not normally found in *Cebuella, Callithrix, Ateles, Alouatta,* and *Callicebus,* nor is it present among any living catarrhine primates. It is said that the entepicondylar foramen occurs in rare or exceptional cases among most primates where it is not a regular feature, sometimes even in *Homo.*

The forearm contains two bones, radius and ulna, from which both mobility and stability of the forearm originate. They are positioned parallel to each other when the volar (inner) surface of the hand is directed upward, and the thumb points laterally. This position of forearm and hands is called supination. In this position the radius is the lateral element, and the ulna is positioned medially. If the volar surface of the hands faces downward, the thumb lies medially and this position is known as pronation. During pronation the radius crosses over the ulna: the upper head of the radius rolls slightly inward on its articular facet with the ulna when the hand is pronated, and it rolls in the opposite direction when the hand is supinated (Figure 8.25). This great rotary range of the forearm is of importance for primates that live in trees and equally important for human manipulation of the capable hands. A primate's hands have to be able to grasp

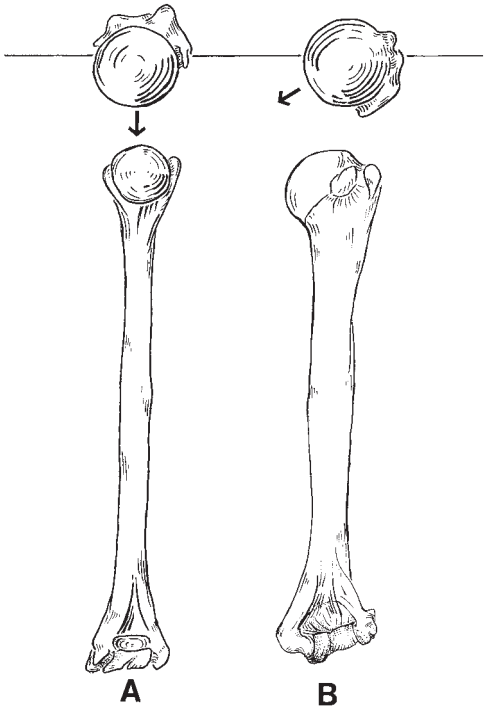

Figure 8.23 Head (cranial view) and right humerus (posterior view) of A) an unspecialized quadruped *(Macaca)* and B) a bipedal human. Humeral head facing backward (caudally) in the quadruped and dorsomedially in the bipedal human. Note that the line indicates the position of the axis through the elbow joints. Arrows indicate the center of articulation of the humeral head with the shoulder blade.

branches and to hold on in many different positions. Thus, the rotary mobility of the forearm adds to the faculties of the upper extremity. In humans and apes the distal end of the ulna is reduced to a narrow styloid process and does not articulate intricately with the carpals (triquetrum and pisiform) as it does in monkeys. This feature was believed to be typical for hominoid primates. Cartmill and Milton (1977), however, have shown that these features of the wrist are also found in lorisiform prosimians, and thus, they cannot be interpreted as being correlated with arm swinging locomotion, as had been done.

We will see the fundamental differences in form and function of the two limb girdles. The shoulder girdle does not have a solid bony connection with the trunk and consequently is highly mobile. It is predominantly fit into place by muscles and tendons. Contrary to this, the hind-limb girdle appears to be rather rigid and designed for stability, the transfer of propulsive forces, as well as for weight-

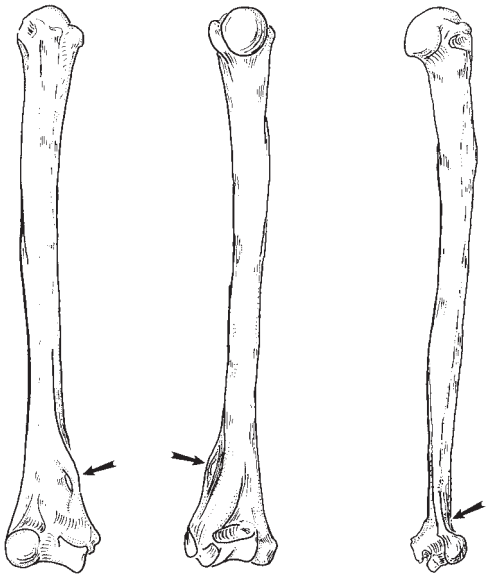

Figure 8.24 Right humerus of *Pithecia* with entepicondylar foramen (arrow indicating foramen). Anterior view (left), posterior view (middle), and medial view (right).

bearing purposes. The entire hind limb is much more restricted in its three dimensional range than is the forelimb, which individually almost covers the three-dimensional shape of a sphere.

Adaptation to terrestrial living usually reduces the range and flexibility of limb movements. Thus, for example, in horses who mainly move with anteroposterior excursions of the limbs, the clavicles are eliminated, and ulna and radius as well as tibia and fibula, respectively, are fused together into single elements, as are many of the hand and foot bones.

In contrast, the broad-chested primates like apes have broad breastbones and a long, s-curved clavicle. Also in narrow chested monkeys, the clavicle is well developed in order to strut the articulation of the upper arm sideways. This latter arrangement allows for greater reach of the highly moveable forelimb than is possible in mammals without clavicles.

PELVIC GIRDLE

The hind-limb girdle differs fundamentally from the shoulder girdle, for it has an extensive bony connection with the axial skeleton. The sacral region, which is the longest element within the vertebral column (being a combination

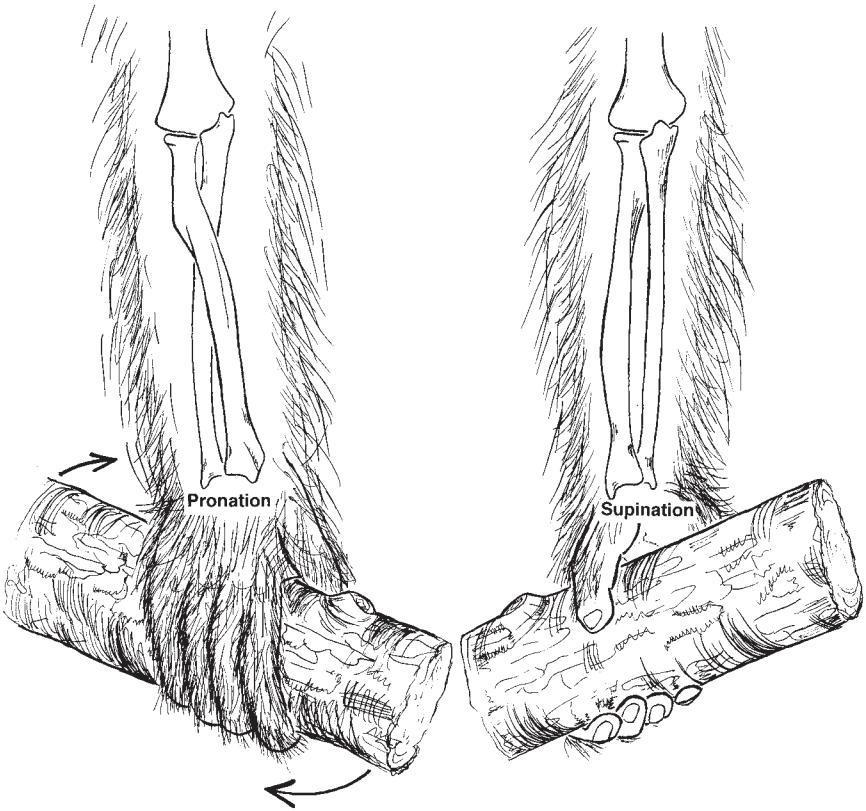

Figure 8.25 Position of radius and ulna in the forearm in pronation (left) and supination (right).

of three or more vertebral segments that are fused together), acts as a keystone between the two iliac blades of the pelvis (Figure 8.26). The transverse parts of the sacrum are enlarged laterally and have a rough dorsolateral surface that fits onto the corresponding ventral surface of the iliac blades. Both these connecting surfaces are bound together with strong, tight ligaments, forming an immobile capsule, a so-called "amphiartrosis." This type of connection or "articulation" is not constructed for mobility but rather for stability and absorption of shock. Among some primates this amphiartrosis can even ossify in old age.

The pelvis is formed by a pair of hipbones. They meet dorso-caudally at the sacral articulation and ventro-caudally in a symphysis (*sym* is Greek for "together" and *physis* for "growing"), which is an area where two bones join each other and are bound together by fibrocartilage and are slightly mobile. If they fuse together in later development, the symphysis becomes solid and immobile (another

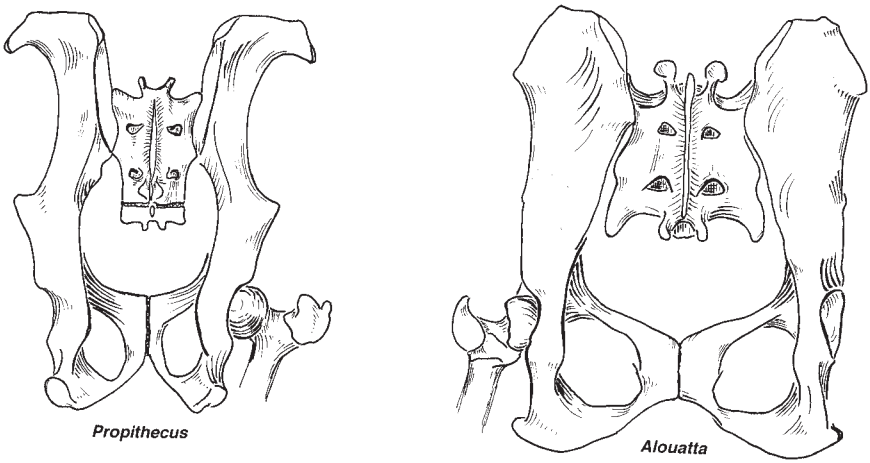

Figure 8.26 Comparison of the pelvis of a prosimian primate *(Propithecus)*, a capable vertical clinger and leaper, and a New World monkey *(Alouatta)*, a cautious quadrupedal climber with a prehensile tail. Note that the head of the femur is more deeply enclosed in the pelvic socket of *Alouatta* indicating greater mobility of the hip joint in *Propithecus*.

example is the mandibular symphysis). This normally tight pelvic symphysis can temporarily loosen somewhat during the birth process in humans, when the large headed young to be born has to pass through the bony birth canal of the pelvis that is made up of the sacrum and hipbones. The pelvic symphysis ossifies only late in the life of primates. The symphysis is said to remain permanently open (that is, unfused) in the prosimian species *Loris tardigradus*.

Each hipbone, or os coxae, is a combination of three elements that ossify independently and fuse when primates reach adulthood, after which time the three parts of the bone can no longer be recognized (Figure 8.27). The three elements making up the hipbone are the ilium, the ischium, and the pubis. The iliac blades form the proximal part of the pelvis, which at its base, includes about a third or so of the articular fossa or acetabulum, which holds the femoral head. Inside the acetabulum on the lateral rim the band-shaped articular surface, or lunate articular surface, is located; it does not extend all the way around, but leaves an opening ventrally which is called the acetabular notch (see Figure 8.27). The width of the lunate articular surface band is correlated to the depth of the acetabulum and, consequently, to the diameter of the femoral head. The wider the articular band is, the deeper the acetabulum. The center of the acetabulum inside of the lunar area is not covered with a smooth articular surface, and this portion is called the acetabular fossa. In the center of this fossa the ligament (ligamentum teres) to the center of the femoral head attaches. The ventral bony

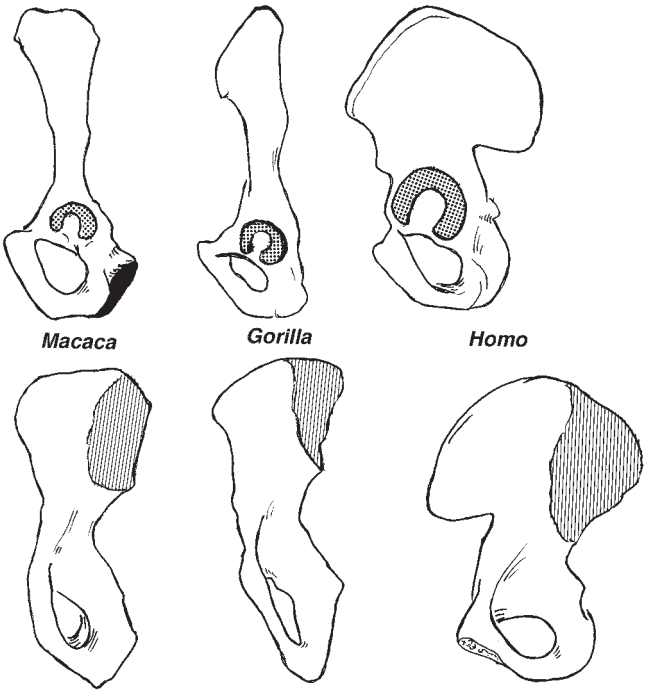

Figure 8.27 Hip bones of three higher primates (brought to the same length) showing differences in the size of the lunate surface of the acetabulum (stippled) and the sacral articulation (also called the auricular surface) (striped).

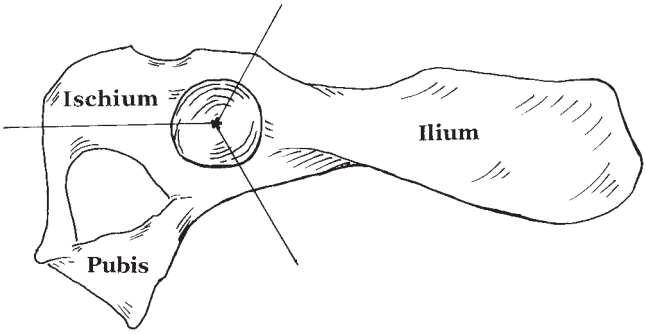

Figure 8.28 Right hip bone seen from lateral view showing the three elements. The three elements meet in the center of the acetabulum.

part of the os coxae—including the symphysis—is called the pubis, and dorsal to the pubis lies the third of the three elements, the ischium. Both pubis and ischium meet in the ischio-pubic ramus and together form the lower part of the acetabulum. Pubis and ischium also enclose a large opening behind the acetabulum on each side, the so-called obturator foramen: the ischium forms the dorsal and the pubis the ventral rim around this large foramen. The obturator foramen is positioned more or less ventro-caudally to the acetabulum. This foramen is covered by ligamentous tissue in living animals which forms the obturator membrane that provides surface for m. obturator internus and externus respectively. The point where the three bony elements that form the os coxae (ilium, ischium, and pubis) meet roughly positioned in the center of the acetabulum (Figure 8.28).

As is well known, the pelvis surrounds the birth canal of females. The pelvis is also subjected to forces that originate from the locomotor activities of the hind legs, and it is partly affected by stresses that result from resting postures (sitting). These distinct roles combine together to create specific functional demands on the pelvic morphology. This condition is especially demanding in those primates where the inner diameter of the female pelvis and the circumference of the full-term newborn offspring are critically close to each other—for example, in some macaques, in some New World monkeys, namely *Saimiri* and *Cebus* (Leutenegger, 1970), and in *Homo sapiens*. In such primates the infant may be unable to pass through during labor and both mother and infant may die because of this. Only humans are capable to remedy this critical situation by means of surgical interference (cesarean section). This crucial "bottleneck" situation also exists in other nonhuman primates that combine single births, highly developed brains, and newborns that are relatively large in correlation to the body size of the mother. Schultz (1962) earlier reported such birth difficulties in colonies of hamadryas baboons *(Papio hamadryas)*.

In many prosimians the ilium is narrow, round in cross-section, and rod-shaped. It has three surfaces: the dorso-laterally directed gluteal surface, the ventro-medially facing iliac surface, and the medially directed sacral surface, or sacro-iliac articulation. The cranial edge is called the iliac crest. In monkeys the ilium is commonly an elongated blade that is bent along its long axis in such a way that it is dorso-laterally concave (Figure 8.30I). The pelvis is broad and straight in pongids and, to a lesser degree, in Hylobatids, the ilia forming flat blades in all apes (Figure 8.29E). The ilium is short, broad and curved ventrally (concave from the ventral aspect) in hominids (Figure 8.29C). In humans the articulation between pelvis and sacrum is also larger, both relatively and absolutely, than in any other primate. In humans these uniquely characteristic changes narrow the distance between the sacro-iliac articulation and the hip joint, and form a distinctive indentation (seen from laterally) caudally adjacent to the

sacro-iliac articulation area (Figure 8.29B). This angle or notch is typical for hominids and is called *incisura ischiadica* (or greater sciatic notch), as it is enclosed by both, the ilium and ischium (see Figure 8.29B, arrow). All these changes in the human pelvis are correlated with the comparatively large bulk of the extensor musculature in the hip articulation (the bulk and shift in position of the gluteal musculature). Especially the musculus gluteus maximus has shifted in relative position to the hip joint in bipedal, upright humans; it inserts cranially to the center of the hip articulation in quadrupedal primates and extends caudally, laterally, and ventrally over this articulation in humans. Consequently, the m. gluteus maximus is also changing its function between the two extremes (bipedality and quadrupedality), being mainly a flexor and abductor in the hip joint of quadrupedal primates and a very powerful extensor in bipedal *Homo.*

In all Old World monkeys, the ischium is greatly enlarged dorso-caudally. These extensions widen to form a flat surface of variable characteristic shape dorso-caudally. These enlargements are covered by ligamentous and cornified tissue and are not covered by fur. Catarrhine monkeys sit on these padded "ischial callosities" that are often large. The shape of the ischial callosities varies significantly between different genera (Figure 8.31). Humans, not having ischial callosities, sit on a cushion that is composed of the gluteus maximus muscle plus subcutaneous fat, which together form a padded cushion for the bony ischium while sitting down. Small ischial callosities are found in rare cases in both, lesser and great apes.

Fleagle and Anapol (1992) maintain that the ischium is extended dorsally in a characteristic manner in those primates that locomote in a vertical jumping and clinging manner such as *Tarsius,* the galagoes, and the indriids among the lemurs of Madagascar.

The ventral, cranial, and caudal edges of the articular fossa for the femoral head are strengthened by a semicircular thickening of the bone. This is especially well developed in bipedal humans. Variation in the ventral length of the pubis and the outline of the obturator foramen show sexual dimorphism in species with narrow birth canals and large-headed newborns (Gingerich, 1972). As already stated, examples of this evolutionary bottleneck include humans, macaques, baboons, and the South American squirrel monkey *Saimiri.*

In those South American monkeys who have prehensile tails that function as true fifth extremities, the articulation between the sacrum and the ilium of the pelvis is larger, angled ventrally, and has a more rugged articular surface than these articular surfaces do in nonprehensile-tailed monkeys (Leutenegger, 1974). This enlargement of the articular relief between these sacra and the pelvis is the morphological response to a functional requirement. The fact that the prehensile

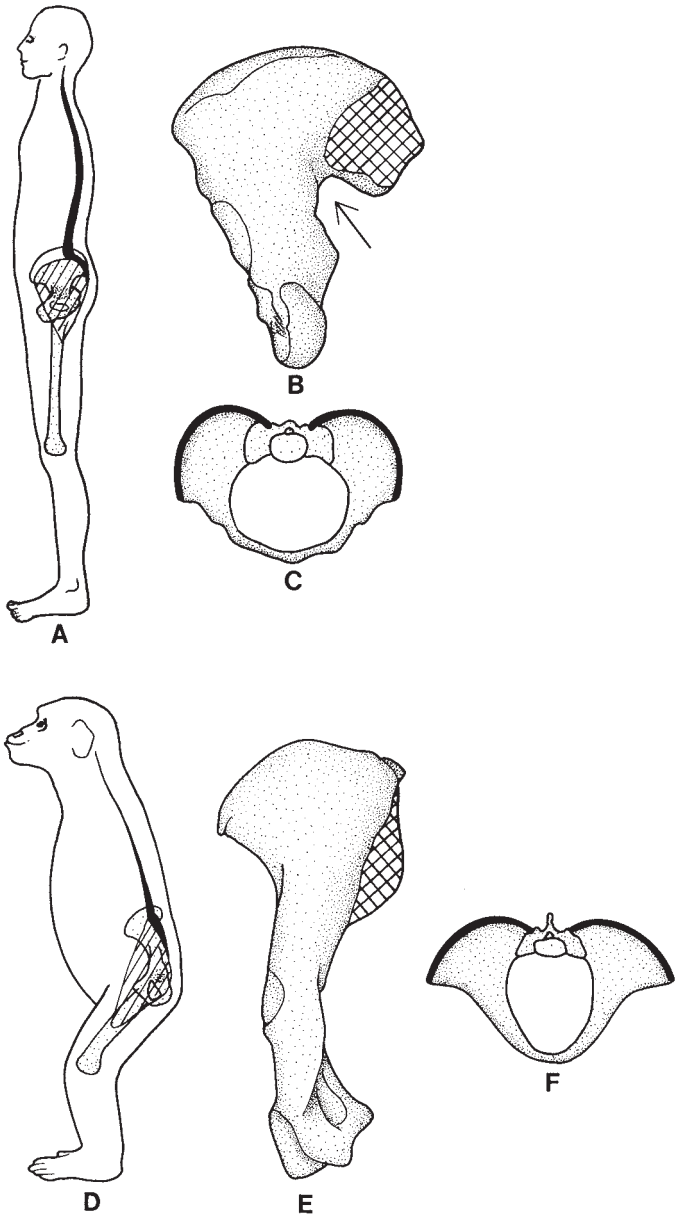

Figure 8.29 The stance of a human and chimpanzee A) and gluteus maximus position (wide stripes), B) medial view of the ilium with iliosacral articulation area (crosshatched), and C) cranial view of pelvis showing iliac crests (black). The same is shown for a chimpanzee (D–F).

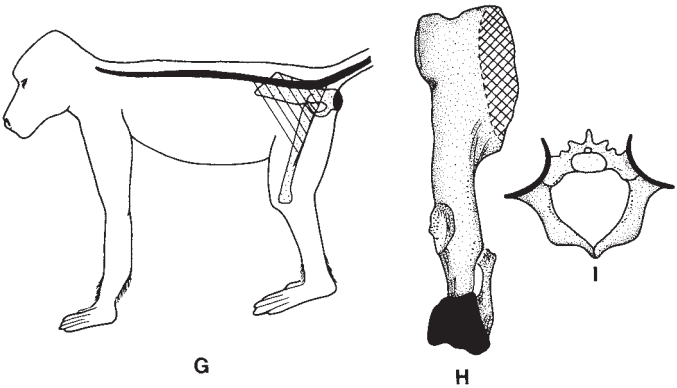

Figure 8.30 The stance of a macaque G) axis is black, gluteus maximus muscle striped, H) ilium with iliosacral articulation area (crosshatched), ischial callosity is black, I) cranial view of pelvis showing iliac crest curvature (black).

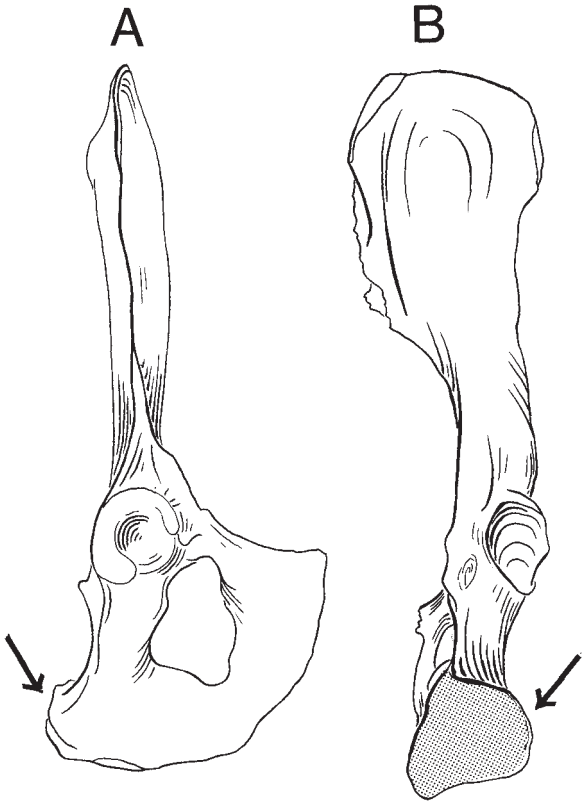

Figure 8.31 Right hip bone of an Old World monkey *(Theropithecus gelada)*. A) Lateral view and B) dorsal view showing position of ischial callosity (arrows and shaded area).

tail is regularly used in bearing the weight of the entire body among these primates is reflected by the enlargement and articular surface enhancement of this articulation. We find these derived articular sacral/pelvic articulations in monkeys with friction pads on the distal ventral aspect of the tail (*Ateles, Brachyteles, Lagothrix,* and *Alouatta*) and to a lesser extent in species of genus *Cebus,* which have nascent prehensile tails that are not equipped with tactile pads but are actively used.

Hind Limbs

Femur, tibia, and fibula are the three long bones of the hind limbs. The proximal segment contains one rigid bone, the femur. The femur is the largest of the three long elements of the primate hind leg. It has three, sometimes four, bony protuberances on the proximal end. These are: (1) the inwardly directed femoral neck and head which are projecting upward and inward; (2) at the lateral side of the proximal end a second protrusion, the *trochanter major,* or greater trochanter is found; (3) below the femoral head and somewhat further backward on the femoral shaft there is the third protrusion, the *trochanter minor,* or lesser trochanter; and (4) occasionally yet another bony protuberance is found, which is called the *trochanter tertius,* or third trochanter. This is a small elevation laterally on the shaft and below the *trochanter major.* This third trochanter may also be called *tuberositas glutea*. On the frontal aspect of the femur both the greater and lesser trochanter are connected by a bone crest that is called the intertrochanteric line. On the backside of the femoral shaft is another bony crest, the *linea aspera*. This is the line of insertion of several important muscles (m. gluteus maximus, m. adductor magnus, m. adductor brevis, m. biceps femoris caput breve). At the knee the femur ends in two more or less rounded articular protuberances, the inner (medial) and outer (lateral) condyles. Femoral neck length and angle vary with differences in overall pelvic morphology and correlated differences in locomotion. In most primates the femoral head has a globular shape. The femoral head of bipedal humans is relatively large, especially compared to the proximal articulation of the humerus. The opposite size proportion between these articular heads is found in gibbons, which move predominantly with their arms. In quadrupedal primates the diameters of the humeral and femoral heads are subequal in diameter. In the highly derived jumping prosimians belonging to the prosimian families Galagidae and Tarsiidae, as well as in the Indriidae, the femoral heads tend to be cylindrical rather than rounded, with the long axis of the cylinder more or less perpendicular to the long axis of the femur. The femoral shaft is comparatively straight in upright jumping prosimians (Figure 8.32). In *Tarsius* the femur is considerably longer than the humerus (Figure 8.33).

In many of the more terrestrial primates, the femoral shaft is usually somewhat curved cranio-caudally. On the femur's distal end the two articular condyles are

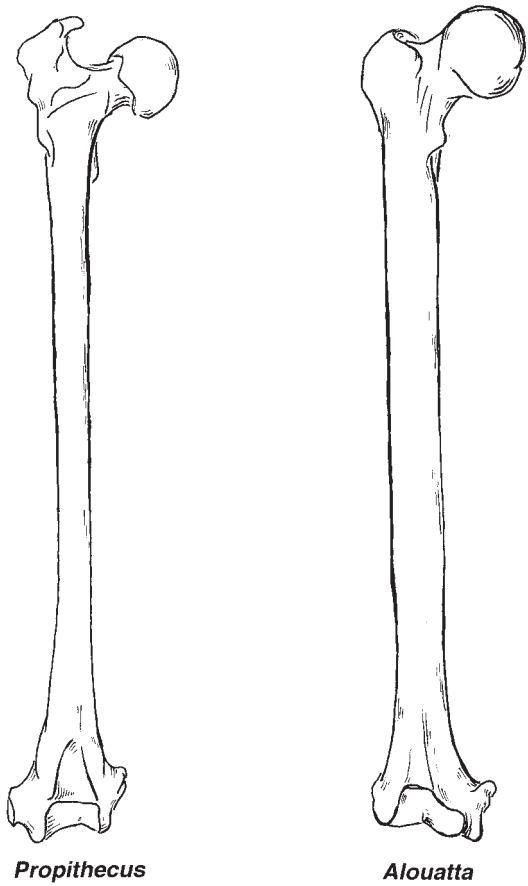

Figure 8.32 Comparison of the right femur of a vertical clinging and leaping prosimian *(Propithecus)* and a cautious quadrupedal climber *(Alouatta)* of about the same body size.

about equal in size in quadrupeds. In humans, with their very broad pelvis and the considerable distance between the two pelvic articulations with the femoral heads, the thighs tend to converge downward, while exactly the opposite is true in pongids. Consequently, the medial or inner distal condyle of the femur is larger than the lateral condyle in humans. The lateral condyle is the larger of the two in pongids. The axis through the center of these distal femoral articulations lies approximately at a right angle with the long axis of the femur. This angle varies somewhat in a characteristic fashion in different primates (Figures 8.32 and 8.34). The femoral shaft is narrow, slender, and straight in lesser apes and it is very robust and somewhat bent forward in pongids. On the front face of the femur,

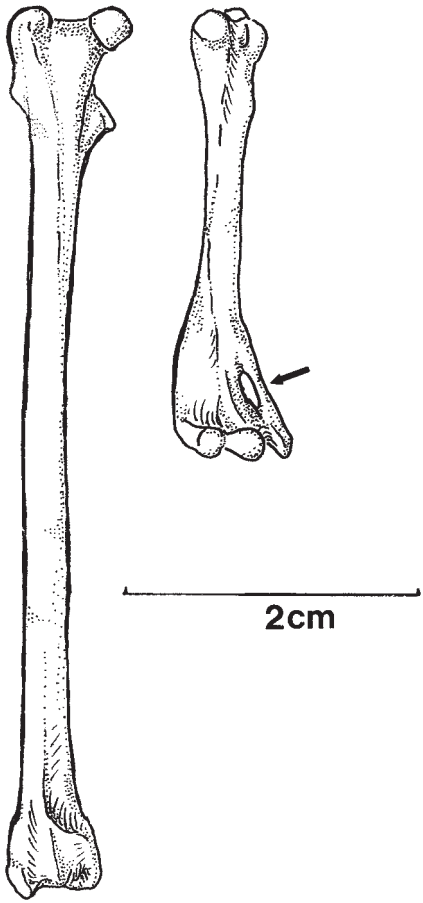

Figure 8.33 Left femur and humerus of *Tarsius,* an extreme vertical clinger and leaper. Note that the arrow indicates the foramen entepicondyloideum.

the distal condyles enclose between them the *facies patellaris.* In all hominoids the frontal aspect of the lower articulation has a deep central groove for the patella within the patellar tendon, which inserts on the upper end of the adjoining and major weight-bearing long bone, the tibia.

On the upper articular facet of the tibia, the two articular areas with the femoral condyles are separated by a bony prominence, the so-called *eminentia intercondylaris*. The condylar area on the top is the widest part, which forms a bony rim around the bone of the tibia and it narrows down under this rim. The tibial shaft is considerably less wide and robust medio-laterally in quadrupedal primates than in hominids or pongids where it is rather robust. Medially on the

front of the tibia, a more or less roughly sculpted ridge—the tibial tuberosity—is rounded on the top but narrows downward into an anterior ridge which brings about a triangular cross-section of this bone which farther distally fades out into a more circular shaped cross-section. This ridge marks the anterior margin of the tibial shaft. Laterally on the backside of the upper end is the articular surface for the fibula, or tibio-fibular articulation. At the lower end, the tibia extends on the inside into a prong-like bony extension: the medial malleolus that extends over the talus of the foot. Looking at the underside of the tibial lateral condyle protrusion, one finds a small articular facet that accommodates the head of the third long bone of the lower leg, the fibula, which is positioned laterally (or on the outside) of the tibia. It is also known as the fibular notch. On the backside of the tibia, an oblique ridge crosses the shaft, beginning outside on the upper end under the lateral condyle, extending downward over about one quarter of the shaft length, and ending on the inner face of the shaft. This oblique ridge is accurately termed the *linea obliqua* or soleal line and is of variable length and prominence in different primates. It is the linear line of the tibial origin of *musculus soleus* in humans. Central on the upper part of the tibial backside we find another small ridge, the so-called vertical line.

The smaller of the two long bones of the lower leg, the fibula, is much more thin and slender than the tibia. It is not significantly involved in weight-bearing among many of the primates (except in humans and to a lesser degree in pongids). This bone is connected to the tibia by means of two only slightly mobile articulations (synoval articulations) on both the upper and lower ends. Both ends of the fibula are enlarged, especially in *Homo* and the great apes where a certain amount of weight is also carried on this bone. The upper enlargement of the fibula is called the fibular head *(caput fibulae)*. This head is usually positioned slightly behind and below the upper end of the tibia and does not have any connection with the knee joint. Its attachment to the tibia is secured by ligaments in front and back. On the inner aspect of the fibular head, we find an articular facet that contacts with the tibia. The lower end of the fibula is usually larger than the head and protrudes down and outward as the lateral malleolus on the outside of the ankle. On the inner aspect a large, rounded articular facet contacts the corresponding facet on the talus of the foot. The shaft of the fibula has a triangular cross-section in most primates. In species of genus *Tarsius* the tibia is a comparatively large bone and the fibula is reduced in size to nothing more than a pin-like clasp with a free proximal pin head and the distal end fused to the tibia.

In 1972 an extensive evaluation of the long bones of the anthropoid hind leg was published (Halaczek, 1972). We will review some of the results of this study.

It appears that among New World monkeys the major factor that influences the morphology of the long bones of the hind leg is absolute body size and not the mode of locomotion. This could be the case because among New World

monkeys locomotion is rather uniform among the small-bodied genera, namely, quadrupedal climbing. The larger Cebidae locomote with the help of the prehensile tail and tend to use their arms more than the former. Two different hind-leg morphologies can be distinguished. They are called the *Aotus* group by Halaczek, containing Callitrichidae and cebids of small body size as well as *Pithecia* (the genera *Chiropotes* and *Cacajao* were not available for this study) and the *Ateles* group—covering *Ateles, Brachyteles, Lagothrix,* and *Alouatta,* the large South American monkeys. Interestingly, members of genus *Cebus* which is intermediate in terms of size and does not have a tactile friction pad on its prehensile tail, does not fit well into either of the two groups but exhibits an intermediate morphology. In the small-bodied group, the skeleton of the hind limb is shorter than their skeletal trunk length, and in the larger-sized group (excepting *Alouatta*), the skeleton of the hind limb is longer than the skeletal trunk. In the small-bodied group, the femur is generally shorter than the tibia, and in the large-sized group, the femur is always longer than the tibia. Among the small-sized New World monkeys, there is a third trochanter which always is missing in the large-sized genera of Platyrrhines. The *Aotus*-group shows a tendency to have a convex medial curvature (as seen from the front) of the femoral shaft. Contrary to this, the femoral shaft in the *Ateles*-group appears to be convex laterally when seen from the front. The *facies patellaris* is always higher than broad in the *Aotus*-group while it is almost, but not quite, as high as it is broad in the *Ateles*-group. The angle between tangents on the distal condyles of the femur is open laterally in the small monkeys and open medially in the large group. Moreover, there is an inward torsion in the femur of the small New World monkeys and an outward torsion in the larger kinds of monkeys. The upper portion of the fibular diaphysis is positioned laterally and behind the tibia in the smaller-sized group, and in the larger-body-size group it is positioned laterally to the tibia.

Halaczek also concluded that in basic construction the three long bones of the hind leg in New World monkeys cannot easily be distinguished morphologically from those of Old World monkeys.

Among Old World higher primates the morphology of the three hind-leg bones exhibits a characteristic combination of features in each of the four families (Cercopithecidae, Hylobatidae, Pongidae, and Hominidae).

In Cercopithecidae the length of femur plus tibia is shorter than the length of the skeletal trunk length, with one exception, namely the proboscis monkey, *Nasalis*. In Hylobatidae, the femur plus tibia are about 25% longer than the skeletal trunk length. Among Pongidae we find that in the orangutan, hind-leg length and trunk length are about equal, whereas leg length slightly exceeds trunk length in the chimpanzee and gorilla.

In *Homo sapiens* the leg length always exceeds the length of the trunk. Cercopithecidae typically have a femur and tibia of about equal length, but the

tibia can sometimes be slightly shorter than the femur. The hind-leg bones of gibbons are characterized by the fact that the tibia is, as a rule, shorter than the femur. This condition is also the case in pongids and hominids. Commonly in orangutans, chimpanzees, and ourselves, the head of the femur extends above the level of the greater trochanter. In the gorilla the trochanter major and the upper level of the femoral head are about equal. With the exception of some colobines, the trochanter major extends up higher than does the femoral head in Cercopithecines. Contrary to this the head of the femur is elevated above that of the trochanter major in Hylobatidae.

Concerning the robusticity of femur and tibia, we find that both these long bones are about equal among Cercopithecidae. In the gibbon family the femur and tibia are rather slender and the tibia is thicker than the femur. Contrary to this condition in the lesser apes, these leg bones are rather robust among Pongidae, and in the latter family the thickness of the femur exceeds that of the tibia. In *Homo* the robusticity of femur and tibia is less pronounced than in pongids, but the human tibia exceeds the femur in robusticity. Also characteristic for the human lower leg is the strong development of the m. gastrocnemius and soleus and their strong, exceptionally long and and wide tendon, which is fused together in humans and inserts into the calcaneal tuberosity, the tendo calcaneus, or the so-called Achilles tendon.

Frequently, Cercopithecidae have the smooth articular surface covering the femoral head extended onto the hinder aspect of the neck, and the articular surface does not exceed beyond the caput femoris in both the lesser and the greater apes. In contrast, this same articular surface extends onto the anterior aspect of the femoral neck in *Homo sapiens*. These differences appear to be correlated with the different modes of locomotion of these groups.

The angle between the long axis of the femoral shaft and that through the femoral neck and head measures about 120 degrees in cercopithecids, and it usually measures about 130 degrees in the lesser apes and chimpanzee, whereas it averages 127 degrees in gorillas, 140 degrees in orangutans, and 131 degrees in humans. New World monkeys show modification of these proportions in the Atelinae, where both forelimbs and hind limbs are elongated and the skeletal trunk length is relatively shortened.

Among both lesser and greater apes the forelimb is greatly elongated, most markedly in *Hylobates* and *Pongo*. In contrast, a pronounced elongation of the hind limbs typifies modern humans. Extreme elongation of limbs within order Primates is only found in species with the most derived locomotor behavior—that is, in the leaping, the arm swinging, and the bipedal species.

In correlation with the increased weight-bearing demands on the hind limbs of humans, all the articular surfaces of the hind-limb long bones, as well as those of the talus and calcaneus of the foot, have increased in surface area. Likewise, size enlargement of the articular surfaces on arm bones can be seen in those

primates exhibiting forelimb elongation and forelimb preference during locomotion. This includes both knuckle-walkers, i.e., the African great apes, and the true brachiators, i.e., the lesser apes. Although in cercopithecids and lesser apes the shaft of the humerus shows no torsion, it does exhibit a considerable outward torsion among large apes. In humans a high degree of inward torsion is the rule.

In both cercopithecids and humans, two tangents drawn along the anterior and posterior aspects of the distal femoral condyles will usually diverge laterally (Figures 8.35 and 8.36). Both these condyles are equal in size in lesser apes and thus, the tangents do not enclose an angle but run parallel to each other. Contrary to this, the great apes exhibit a large medial condyle, and the angle between the two tangents already described opens medially as a rule (see Figure 8.36).

The aberrant genus *Tarsius* has a fused tibio-fibula (Figure 8.37). Tarsiers are highly specialize vertical clingers and leapers and the combined tibio-fibula is one of several morphological manifestations of this fact. Tarsiers are the only living primates with this hind-limb specialization.

In all of the Old World monkeys and apes the lateral part of the lower articular surface of the tibia tilts in a proximal direction. This articular surface is flat in its entirety in humans and is always positioned at a right angle to the long axis of the bone. With Old World monkeys and apes we find that the tibia shows a

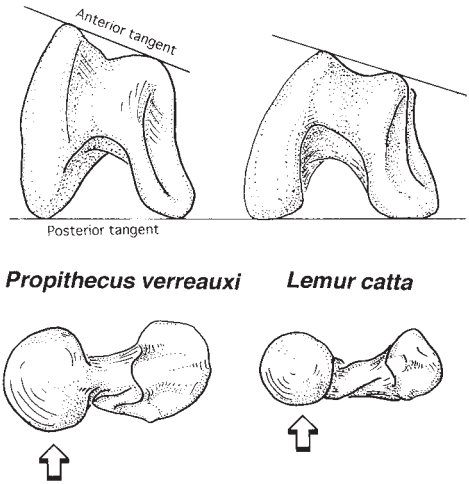

Figure 8.34 Distal and proximal ends of the right femora of a semiterrestrial quadrupedal prosimian *(Lemur catta)* and a vertical clinging and leaping prosimian *(Propithecus verreauxi)*. Arrows point at the differences in posterior femoral head morphology characteristic for each genus due to differences in habitual locomotor behavior.

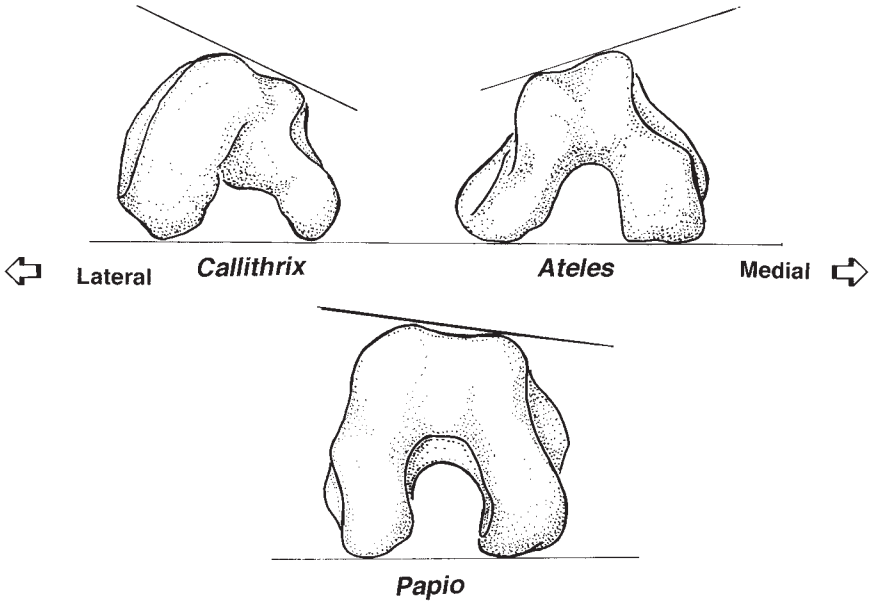

Figure 8.35 Distal end of right femora of a callithricid, an ateline and a cercopithecoid monkey (not to scale). Tangents drawn on anterior and posterior aspects of condyles open laterally in callithricids and cercopithecoids and open medially in atelines.

distinctive inward (medial) torsion. This torsion is especially developed among Hylobatidae, *Gorilla,* and *Pongo.* In *Homo* there is a characteristic tibial torsion that is always directed laterally. The fibula is characteristically shorter than the tibia in Cercopithecoidea, Hylobatidae, and Pongidae. Only in Hominidae is the fibula sometimes found to be longer than the tibia.

With unspecialized primates the hind extremities are usually longer than the fore extremities and shorter than the skeletal trunk length. Femur and tibia are of equal length. These general proportions are found in both unspecialized New World monkeys and among Cercopithecoidea of small body size. They also occur in both the predominantly terrestrial *Erythrocebus* (the Patas monkey) and arboreal Callitrichidae (Marmosets).

HANDS AND FEET

Both the hands and feet of primates pass through an early ontogenetic stage that is reminiscent of a plesiomorphic (that is primitive or unspecialized) tetrapod. From this early developmental pattern, which has fifteen hyaline central elements,

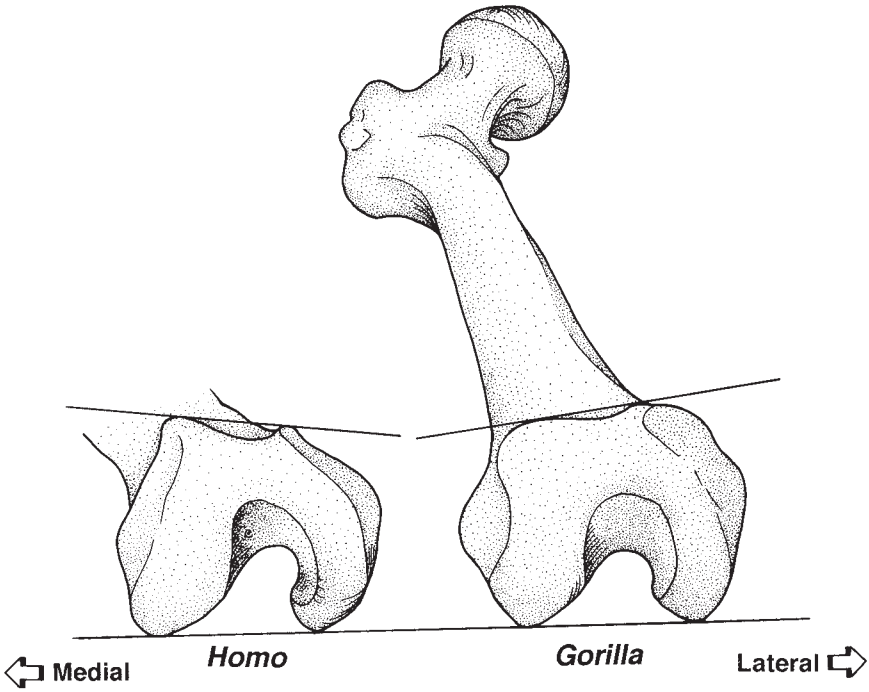

Figure 8.36 Distal end of right femora (brought to approximately the same size) of a human *(Homo)* and a pongid *(Gorilla)*. Tangents drawn on anterior and posterior aspect of condyles typically open medially in humans and laterally in pongids.

hands and feet have evolved differently (Figure 8.38, Table 8.2). Adult primates retain either eight or nine carpal elements, whereas the tarsus of adults usually consists of seven different bony elements.

With the carpal centrals we find that the distal ulnar centrale fuses early with the navicular or, alternatively, is re-absorbed and disappears among three prosimian genera, *Indri, Lepilemur, and Avahi,* and also in the hominoid genera *Pan, Gorilla,* and *Homo.* It is present in the orangutan and the hylobatids and all other anthropoid primates. Because of this fusion, or re-absorption, species of these six genera named above have only eight carpal elements while all other primates have nine (Figure 8.39). Also, only in prosimian primates does the os centrale contact the hamatum (also called unciform). The proximal ulnar centrale is either not developed or disappears very early during the ontogenetic development of the hand skeleton of primates (Steiner, 1965).

Steiner also points out that the ontogenetically early configuration of the five-fingered hands and five-toed feet of primates are indicative of their evolutionary

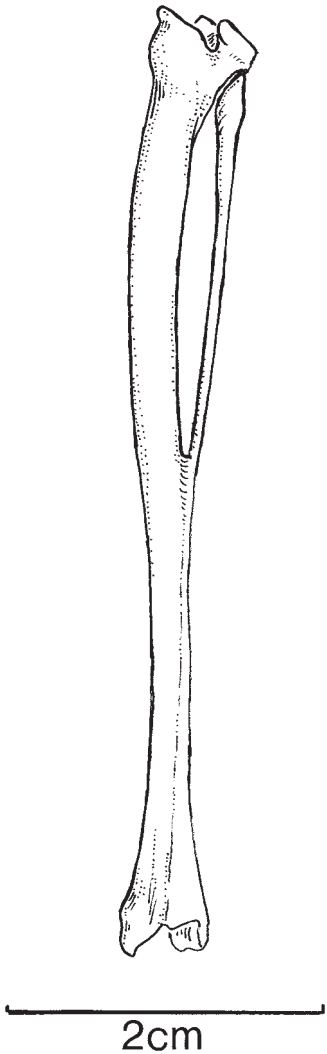

Figure 8.37 Left tibiofibula of *Tarsius syrichta*.

origin as able grasping tools in an arboreal environment. In Table 8.2, the different sequences of the ontogenetic development of embryonic hands and feet into adult hands and feet of primates are outlined (adapted from Steiner, 1951).

Relative differences in lengths of fingers and toes are usually expressed in the so-called digital formulae. The formulae simply give the number of the longest

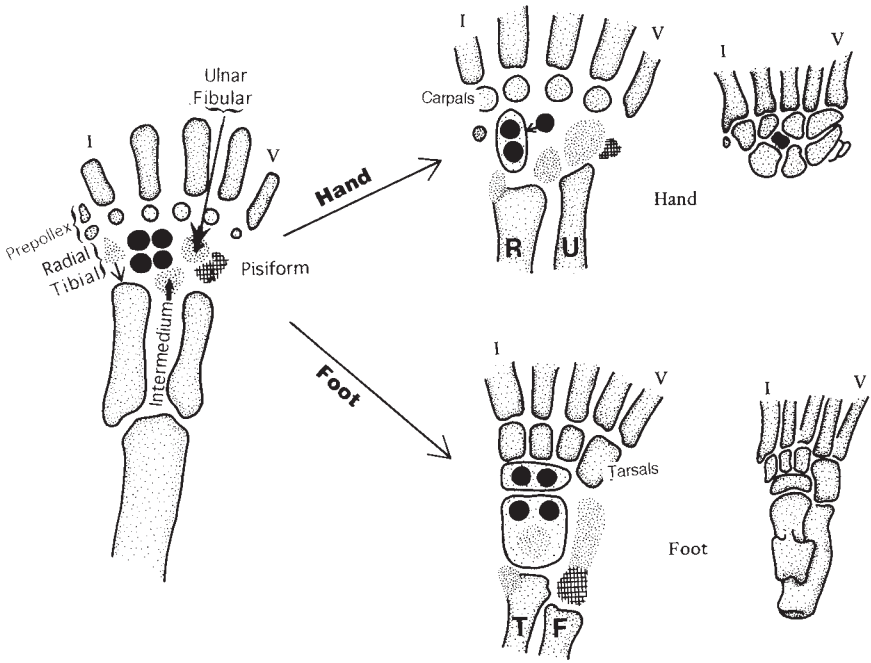

Figure 8.38 Phylogeny of primate hand and foot. Left: unspecialized extremity which is the initial stage for both hand and foot. Above (middle) diagram of primate carpals and below (middle) diagram of primate tarsus. Carpals and tarsals are shaded; prepollex—big dots; proximal elements—fine dots; pisiform—crosshatched; centrals—black. (See Table 8.2.)

digit first, that of the shortest last, and order the remaining three according to their decreasing length. Thus, the digital formula of the human hand is usually 3 > 4 > 2 > 5 > 1 or 3 > 2 > 4 > 5 > 1. The formula for the human foot is 1 > 2 > 3 > 4 > 5, or less commonly 2 > 1 > 3 > 4 > 5.

The second finger of hands is also called the index finger, as it is used to point.

Young primates also have epiphyses on the longbones of their hands and feet (Figure 8.40).

A few primates have webbed hands or feet, that is, some of their fingers and toes are connected by variably developed skin folds. Thus, in the prosimian genera *Propithecus* and in the species *Indri indri,* certain fingers and toes are webbed together.

In species of *Propithecus*—the sifaka—digits three and four are webbed together by a small skin fold on the base of these fingers. The webbing between toes two, three, and four is rather more extensive than that of the fingers and the skin fold almost reaches as far as the proximal articulation of the metatarsals. In

Table 8.2
Phylogenetic Derivation of Carpus and Tarsus in Primates

Unspecialized Carpus/Tarsus	Primate Carpus	Primate Tarsus
Carpals/tarsals		
1	Trapezium	Cuneiform 1
2	Trapezoid	Cuneiform 2
3	Capitate	Cuneiform 3
4	Hamate	Cuboid
5	Lost	Lost
2 Proximal centrals	—	Form Talus together with Intermedium
	—	
2 Distal centrals		Navicular
2 Medial (radial) centrals	Scaphoid	—
2 Lateral (ulnar) centrals	Proximal ulnar central reduced	—
	Distal ulnar central either remains separate or incorporated into Scaphoid which occurs in *Indri, Avahi, Lepilemur Pan, Gorilla, Homo*	
Intermedium	Lunate	Intermedium together with 2 proximal Centrals form Talus
Ulnar	Ulnar forms Triquetrum	
Fibular	—	—
Pisiform	Pisiforme	Fibular together with Tarsal pisiform combine into Calcaneus
Radial	Radial fuses with Radius	
Tibial	—	—
		Tibial fuses with Tibia

Data from Steiner (1951).

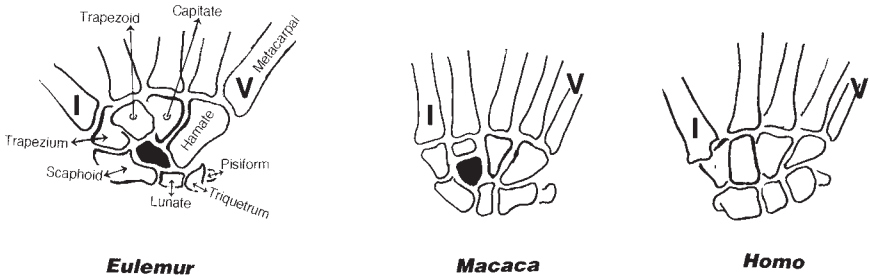

Figure 8.39 Carpus with nine carpal elements in *Eulemur* and *Macaca* and with eight carpal elements in *Homo*. (Brought to approximately the same size.)

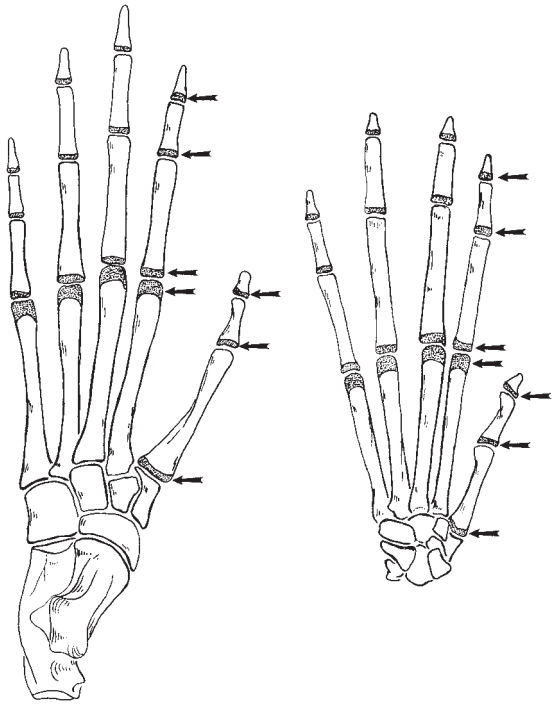

Figure 8.40 Epiphyses indicated by arrows on feet and hands of young primates.

the *Indri*—babacoot or giant lemur—the webbing on the hands extends between fingers two and three and three and four and reaches as far as slightly beyond the proximal metacarpal joints. Equally, the second, third, and fourth toes of the feet are connected by skin folds that reach as far as or beyond the most proximal metatarsal joints of the toes. As this webbing is more extensive than in *Propithecus,* it certainly prevents fingers and toes 2 through 4 from moving independently: Moreover, the membrane extends out further than the first joint between these fingers and toes, making for a close attachment of the *Indri*'s fingers and toes (Figure 8.41).

Also, the lorisid *Perodicticus potto* exhibits slight webbing in both hands and feet: The third and fourth digit are connected to each other by a slight skin fold. The toes 3, 4, and 5 are also joined at the base by a skin web that does not exceed further than the proximal third of the toes. Among some species of *Macaca,* skin folds do occur that join the second toes through fifth toes together, and these three webs almost reach the first metatarsal joint. Among some *Cercopithecus* species fingers 2 to 5 can be slightly connected by proximo-distally short webbings

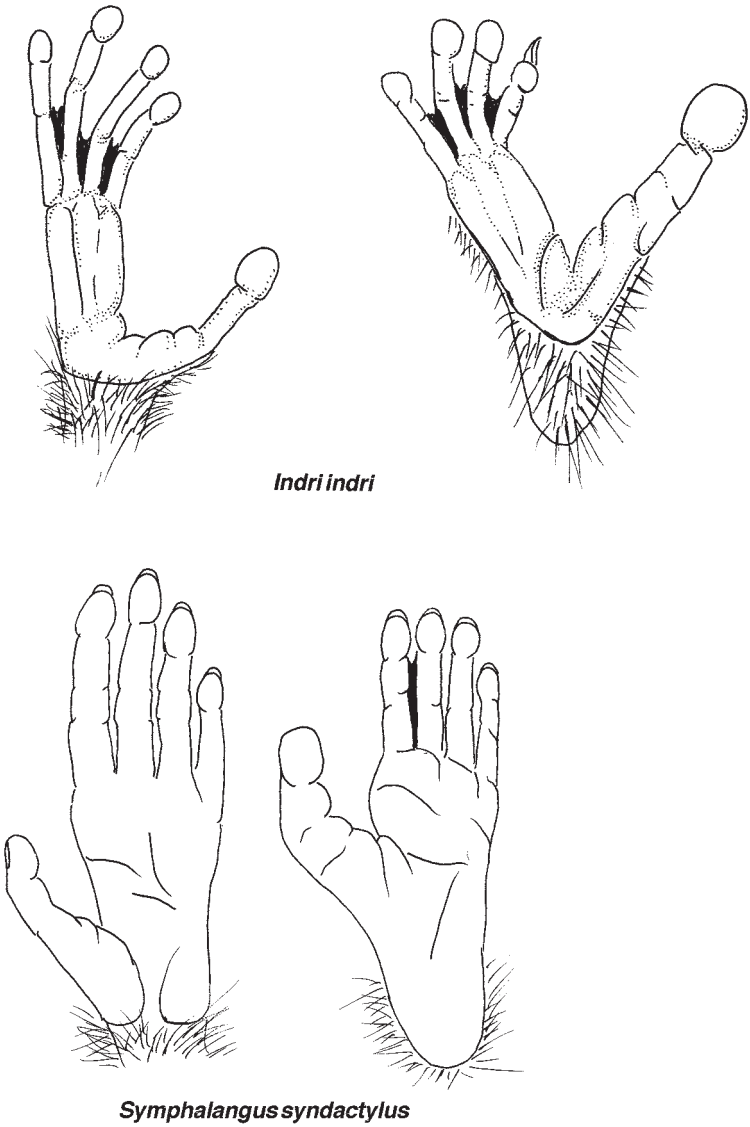

Figure 8.41 Webbing between fingers and toes in a prosimian *(Indri)* and of toes in an anthropoid primate *(Symphalangus)*. Webbing shown in black.

while toes 2 and 3 as well as 3 and 4 are connected by obvious skin folds that reach close to the first metatarsal joint.

A somewhat different case of webbing by means of an extensive skin fold between the second and third toes of the feet of the larger genus belonging to the Hylobatidae *Symphalangus syndactylus* (*sym-phalangus* meaning joined fingers in Greek and *syn-dactylus* also Greek meaning fingers that are together) gives this species both its generic and species names. This web tightly joins toes 2 and 3 into one. The web reaches to the second metatarsal joint just below the end-phalanges and thus makes it impossible for these two toes to move independently: They have become a functional unit (Biegert, 1961). Such webbing is also occasionally found in members of the related genus *Hylobates*. Among the great apes, Gorillas often have fingers 2 through 5 joined by skin folds as well as toes 2 to 5.

The two most important horn structures of the skin among mammals in addition to hair are claws, hoofs, or nails, the horny envelopes on the dorsal aspect of the terminal phalanges of hands and feet. Claws have, for example, evolved into the hoofs of running mammals (horses) and flat nails among primates. Claws are characteristically curved ventrally and compressed sideways along their long axis. Claws are widely distributed in the animal kingdom and have undergone a wide variety of adaptive changes in different groups of animals. Claws and nails reinforce the dorsal ends of fingers and toes and are derived from the claws of reptiles. They serve a multitude of functions, such as tools for digging and obtaining and processing food items, and are effective as weapons and useful in scratching. Claws are also involved in different locomotor activities such as climbing. They are pointed at their ends and their horny material is harder on the upper outside than on the underside. Claws have two different horny layers, namely a thick, deep layer (deep stratum, *stratum* is Latin for layer) and a covering layer that is considerably thinner, hardened, and that functions as a protective envelope (superficial stratum). Underneath both claws or nails, the terminal finger or toe bones have the same shape as the claw or the nail and thus are virtual molds of the overlying horny structure. In contrast to claws, nails are flat and not as curved and they do not extend beyond the tips of fingers or toes. The ends of nails are not pointed and usually consist only of the upper so-called superficial, hard stratum (Figure 8.42).

Primates, with only a few exceptions, typically retain plesiomorphic (unspecialized) hands with five digits. The dorsal aspect of the tips of fingers and toes are equipped with either claws or nails, and moreover, typical nails are only found among primates. Many primates have both claws and nails on different fingers or toes. For example, all prosimians have nails on their fingers and toes except on the second toe of the feet: This claw is called the "toilet claw," or grooming claw, as it plays an active role in grooming activities such as scratching.

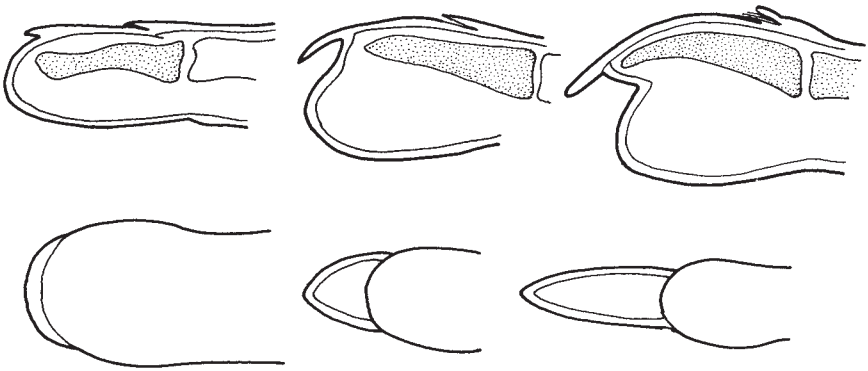

Figure 8.42 Fingernails and claws; human nail (left); nail of a monkey (middle); and mammalian claw (right).

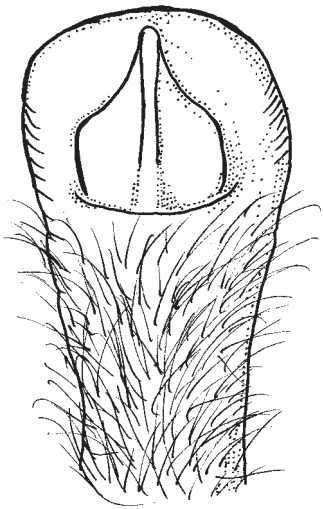

Figure 8.43 Keeled nail of the needle-clawed galago *(Euoticus)*.

The needle-clawed bushbaby *Euoticus* has uniquely keeled nails on all digits except the thumb of the hands and the big toe and second phalanx of the foot which have claws: The other seven endphalanges bear a nail that has a prominent central ridge which ends in a needle-like point at the tips of these nails (Figure 8.43).

All species of the Tupaiiformes or treeshrews have both hands and feet that are equipped with claws. The five digits of their hands are positioned close to each other, which is not usually the case for primates. Nevertheless, the tree

shrew thumb (pollex) can be somewhat spread away from digits 2 to 5. Even though the pollex can be spread away from the other fingers to some extent, it always remains in the same plane with them and cannot be put in opposition to fingers 2 to 5.

The carpo-metacarpal joint of the pollex of primates will be considered in detail because many authors believe that the thumb and its relative independence of movement from the rest of the digits in the hand of humans must have played a major role for the emergence of *Homo* as a manipulative, civilized, and cultured creature with the ability to create complicated machines and art (see Biegert, 1963). Hands and thumbs are of crucial importance for many activities of primates. They are not only involved in locomotor activities such as climbing, but in feeding, holding, the manipulation of young, and grooming to name a few.

In the nonprimate tree shrews or the small-sized South American monkeys, the marmosets, grasping with the hands habitually involves all five-clawed digits drawn together and acting in unison (Figure 8.44). Among more advanced primates, the ability to spread and flex the fingers independently and to separate the thumb from fingers 2 to 5 and to bring it into opposition to them (namely palmar aspect of thumb facing the palmar aspect of fingers 2 to 5) becomes increasingly important and structurally more elaborate. However, the degree of manipulative ability is not solely reflected by the kind of articulation the thumb has with the hand. Thumb length, finger length, and tactile abilities provided by elaborate nervous supply are equally influential for the different kinds of manipulative abilities we find among primates.

To provide a comparative base for the evaluation of primate hands we have to look at the functionally and evolutionary simple hands of tree shrews. In the tree shrew *Tupaia* both the first and the fifth digits of the hands can be spread away from the adjoining fingers to some degree. Altner (1968) conducted a very thorough study of the early ontogenetic development of the hand skeleton, focusing mainly on *Tupaia* as having a "spreading hand." Interestingly, it turns out that in *Tupaia glis* the articulation between the basal carpal and metacarpal of the pollex has the morphological structure of a hinge joint (movement possible only in one direction around the long axis through the hinge). Altner also found a hinge joint in *Tarsius* but not between basal carpal and metacarpal (which is immobile in tarsiers), rather one segment further distally between the distal end of the metacarpal and the proximal end of the basal phalanx. It turns out that in the mouse lemur species *Microcebus murinus* there is in ontogenetically early stages a saddle articulation (movements possible along two axes that are positioned at right angles toward each other), which indicates greater mobility of the pollex than in tree shrews or tarsiers. However, this saddle-shaped joint in the mouse lemur is rather shallow, and remains so in the adult animal. Therefore, it is regarded to be an incipient saddle articulation. It appears that, in addition to

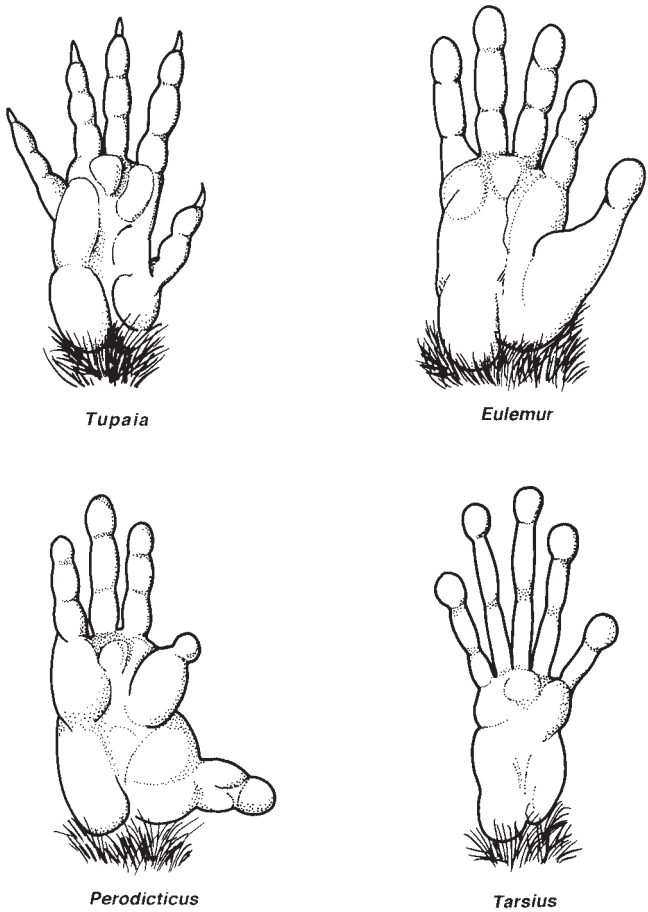

Figure 8.44 Hand of a tree shrew *(Tupaia)*, a lemur *(Eulemur)*, a lorisid *(Perodicticus)*, and a tarsier *(Tarsius)*.

Microcebus, different grades of elaboration of this saddle joint can be found in *Lemur mongoz.* In the galagoes *Galago senegalensis* and *Otolemur crassicaudatus* this articulation is even more truly saddle-shaped. The articulation is deeper in both its convexity and concavity than in the hands of lemurs.

Some of the New World monkeys (*Callithrix jacchus, Leontocebus rosalia,* and *Cebus apella*) have hinge-shaped carpo-metacarpal articulations of their thumbs. The ceboids, however, show a slight morphological adaptation toward a two-axial saddle articulation in the pollex joint. In contrast, *Saimiri,* the South American squirrel monkey, has a true saddle-shaped articulation of this joint.

Overall, this crucial articulation of the thumb is less accomplished in New World primates than in the Old World monkeys, great apes, and humans. As we shall see below, the lesser apes are exceptional with regard to the carpo-metacarpal joint of their pollex.

It was Napier who defined the different manipulative properties of primate hands. According to Napier (1961; Napier and Napier, 1967), primates show three distinctive kinds of grasping with their hands. These are mainly determined by the degree of independence of the thumb movements, and can be listed as follows:

Group 1. Nonopposable thumbs: Tarsiers and Marmosets
Group 2. Pseudo-opposable thumbs: all prosimians and Cebidae
Group 3. Opposable thumbs: Old World monkeys, great apes, and humans
Group 4. Opposable, comparatively long thumbs: Hylobatidae

Napier also included the lesser apes in his group 3. Nevertheless, since it has been shown that the thumb of the lesser apes is not only unique in its mode of articular morphology (ball joint) and proportions (Schultz, 1944), but also in its function (Lorenz, 1971), Hylobatidae are here assigned to a distinct group, separate from all other primates. During brachiation, the thumb of lesser apes functions together and stays in the same plane with fingers 2 to 5. However, Hylobatidae are unique in using their thumbs as a tactile probe when investigating and exploring novelties. Lorenz (1971) states: "To function as probe-finger—as well as to perform a powerful and precise opposable grip—the thumb has to have length, strength, a ball-shaped carpometacarpal joint, and the necessary complex of muscles."

It turns out that all the above-mentioned features are unique characteristics of the hylobatid thumb that has no equivalent among primates. The comparatively long pollex of gibbons is separated from the index finger by a deep cleft that extends down into the metacarpal region (Figure 8.45). Interestingly, human infants can also be observed using their thumbs as probing fingers in a gibbon-like fashion (observations by the author) to explore textures and shapes in a manner that is very similar to the use of the thumb by lesser apes.

According to Altner (1968), only the nonprimate *Tupaia* (a tree shrew) and the unique genus *Tarsius* have truly hinge-shaped carpo-metacarpal articulations of their pollex. However, in *Tarsius* the main place of mobility of the thumb is not the carpo-metacarpal joint—which actually is immobile in tarsiers—but between metacarpal and basal phalanx (Napier, 1961). In this respect, tarsiers differ in the manner of pollex movement from all other primates. Even though other primates do have some mobility in the metacarpo-phalangeal joint, the main location of pollex mobility is usually in the carpo-metacarpal joint. All the primates that are grouped together (Group 2) as having pseudo-opposable thumbs do show variable degrees of incipient hinge or even shallow saddle articulations

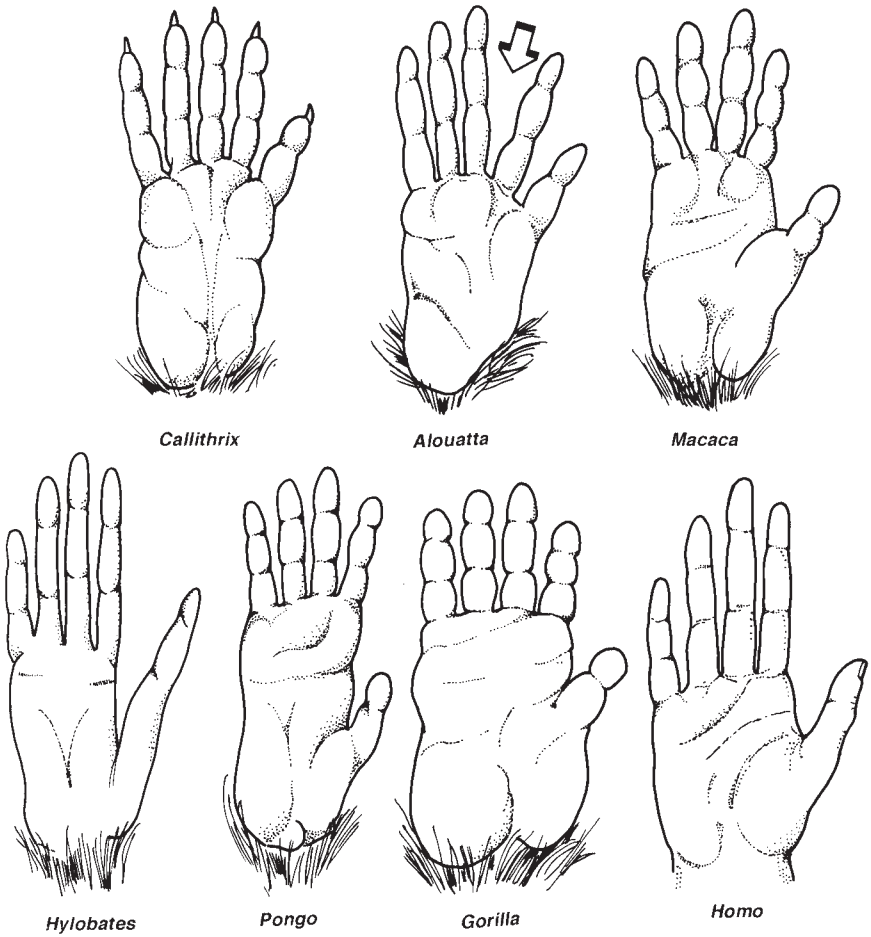

Figure 8.45 Hands of anthropoid monkeys (above) and hominoids (below).

in the carpo-metacarpal region and thus are not a morphologically homogenous group.

Functionally the hands of tree shrews and marmosets are very similar: both usually grasp with an adducted thumb and thus, all five-clawed digits move in unison. This is not a very precise way of grasping. It appears that this is so, in spite of the fact that some of the marmosets (e.g., *Callithrix jaccchus*) do have a carpo-metatarsal pollex articulation that is similar to a saddle joint.

Most prosimians have thumbs that can be spread away from digits 2 trough 5 to a considerable degree. This capacity to spread the thumb away from the 2nd finger is especially pronounced among Lorisidae (see Figure 8.44).

Most cebids show a tendency to grasp small branches and objects between the second and third fingers (see Figure 4.25). This type of grasping is reasonably typical for all the large South American monkeys and can frequently be observed in human infants, as well. Species of the genera *Ateles* and *Brachyteles,* whose pollex is totally reduced, have to grasp between digits two and three.

Only Old World monkeys, great apes, and humans are truly capable of thumb opposability: rotating the pollex inward into opposition to the other digits in a way that puts the volar surface of the thumb onto the volar surface of the other digits. In correlation with the intricate tactile nervous supply of the volar skin, opposability makes skillful manipulation of even tiny objects possible. However, even some of the Old World monkeys do have greatly reduced thumbs (Colobinae), as we shall soon see. In consequence, these monkeys have little ability to adequately oppose their fingers 2 to 5 for grasping purposes.

Among Lorisidae we find that the second finger is very much shortened (see Figure 8.44). The thumb diverges at an angle of about 180 degrees away from finger 3. This gap between the thumb and fingers 3 to 5, and the short stump of finger 2 make these hands into a perfect pair of powerfully gripping pliers. Thus, Lorisidae are capable on an incredibly strong grasp. Together with this unusual hand morphology Lorisidae have a specialized vascular supply within their hands and feet: the so-called miracle nets *(retia mirabilia)* of capillaries. This sustained blood supply enables lorisids to grasp a branch and hang on to it completely immobilized for hours, without their hands and feet turning numb. Humans, for example, cannot sustain a strong grasp around a dowel or handle for extended periods of time, basically because the blood circulation of these hands is not augmented by such a net of capillaries and therefore our hands do get numb when we attempt to hold on to something for an extended period.

In tarsiers the volar pads of the fingertips are enlarged and shaped like discs that can function as suction cups (see Figure 4.21). Among tarsiers we also find that fingers are comparatively long, and metacarpals short. The friction skin on the palm of tarsiers is highly derived and unlike those of any other primate (Biegert, 1961). *Tarsius* is the only primate that has two toilet claws: one on the second toe and another on the third toe of their feet.

Not only is the thumb reduced to a hardly visible stump in *Ateles* and *Brachyteles,* but the same has happened among members of the Old World monkey family Colobinae. Very short thumbs are the rule in species of genus *Presbytis.* Among the great apes it is the orangutan that has the shortest thumb (see Figure 8.45).

Macaques and baboons, when walking, put the volar aspects of fingers 2 through 5 on the ground, whereas, in contrast, the African apes place the dorsal side of the middle and terminal phalanges of fingers 2 through 5 on the ground (Figure 8.46). This latter mode of locomotion, commonly referred to as "knuckle-

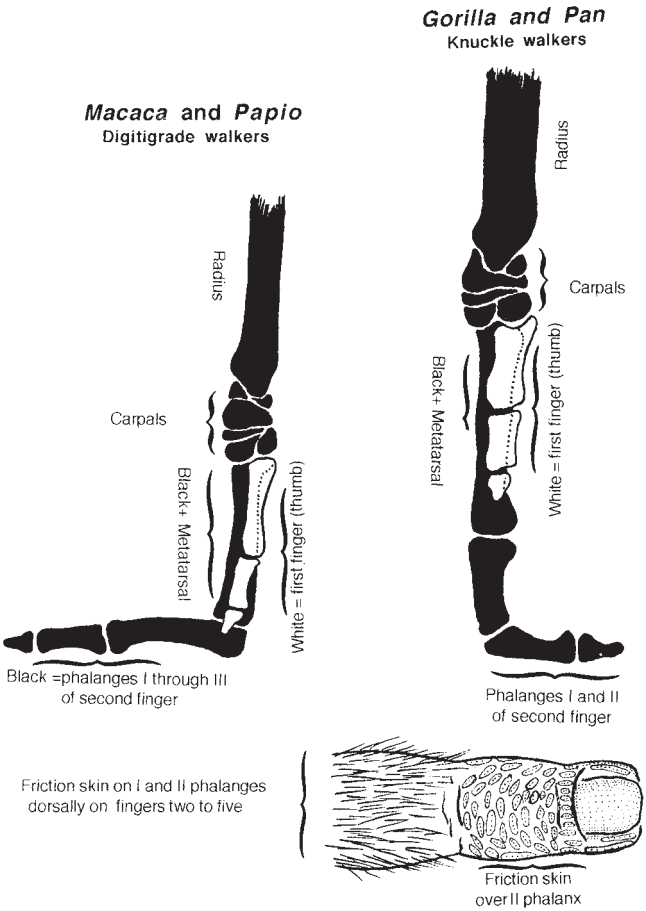

Figure 8.46 Diagram of different positions of fingers during digitigrade locomotion in macaques and baboons (left) and knuckle-walking apes (right). The dorsal aspect of a gorilla finger showing the unique dorsal fingerprints. (Gorilla finger adapted from Biegert, 1961.)

walking," has been described and analyzed by Tuttle (1969). Orangutans, when on the ground, do engage either in fist-walking or in palmigrade hand positions while walking quadrupedally. During fist-walking the fingers are curled up into a fist and the hand is aligned with the forearm with the outside of the hand on the ground while in the palmigrade hand position the entire flat inside (palma) of the hand is placed on the ground. In the knuckle-walking gorilla (Figure 8.47) and chimpanzees, we even find a friction skin on those dorsal aspects of the fingers that contact the ground (digits 2 to 5) during this highly derived mode of locomotion.

Figure 8.47 Gorilla in knuckle-walking position.

The digitigrade positioning of the hands of macaques and baboons, as well as the knuckle-walking hands of African great apes, equally results in a slight elongation of the entire forearm; this is the case because with all these monkeys the length of the metacarpus and carpus (and in the African great apes also the length of the basal phalanges) is added to the arm length when walking on their fingers, rather than flat on their hands. This type of walk also elevates the upper body and head somewhat higher than it would be elevated if these primates were quadrupedally walking by putting down the entire palm of their hands.

Another astounding adaptation of hands is found in the aye-aye, where all digits are clawed. The hand of the aye-aye is remarkable: among their very long digits 2 through 5 (digit 4 is the longest), digit 3 is surprisingly thin and wire-like (Figure 8.48). At the terminal phalanx, digit 3 is adorned with a large, curved,

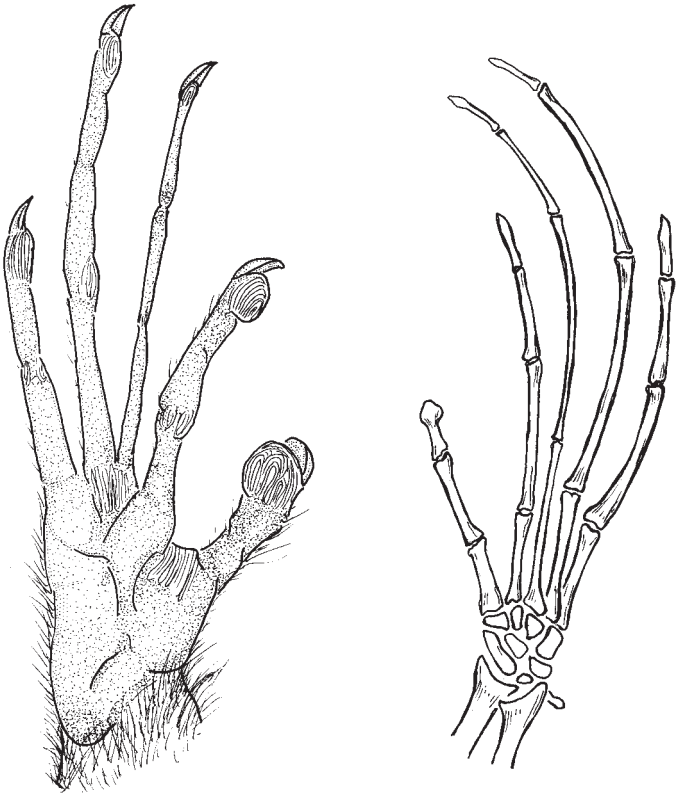

Figure 8.48 Specialized wire-like third finger of the aye-aye *(Daubentonia madagascariensis)*. Palmar aspect of the right hand is on the left and the skeleton is on the right.

and pointed claw. This third finger is used to pull insect larvae, especially grubs, out from under the bark of and cracks of trees and other hiding places. Aye-ayes also use this skinny finger to pump up liquid, for example, from a coconut: After gnawing a hole into the hard, outer shell they put the third finger of one hand into it, their mouth right onto the opening, and start pumping the finger up and down in a rapid succession, by this means forcing the coconut milk into their open mouth to drink (FAS, personal observations).

Claws are also found on all terminal digits of the hands of South American Callitrichidae. These latter "claws" are regarded by some as secondarily re-shaped nails. However, the layer of the deep stratum—characteristic of claws—is present under the claws of Callitrichidae, even though it is rather thin. This documents that the claws of marmosets cannot be secondarily claw-shaped nails, as nails always lack the deep stratum. The German common name for Callitrichidae, "Krallen Äffchen," which means "little clawed monkeys," refers

to the fact that these monkeys do have claws on all their fingers and toes except for the nail on the great toe.

All other primates have nails on their hands and feet. Among South American monkeys, the nails are often less broad and flattened than in the majority of Old World monkeys; they are somewhat compressed laterally in many of the Cebidae.

On the inside of hands and feet (palmar and plantar surfaces), primates have cushioned pads that are covered by a very sensitive skin. The papillae of this so-called "friction skin" that covers palms and soles are arranged in parallel curved lines that form elevated ridges. Also, the ducts of abundant sweat glands of the skin open on top of these ridges. This friction skin is supplied with numerous nerve endings (Meissner's corpuscles), and thus is a close-up sense organ. The ridges of the friction skin occur in complicated patterns that are individually different in all primates and can be used for various identification processes (e.g., the use of finger prints in human forensic investigations). One of the important mechanical or functional aspects of this friction skin is to allow a secure grip.

In most primates the hallux (big toe) is often large, but it is not opposed to digits 2 through 5 in the same way as is the case in primate hands. Except for Hominidae we can speak of a pseudo-opposition of the hallux in primates: Most primates have feet capable of grasping. Only in one of the great apes, the orangutan, is the big toe reduced in length. The longest big (or great) toes are found among Lemuridae, Indriidae, and Lorisidae (Figure 8.49). Additionally, orangutans, callithrichids, and terrestrial cercopithecids have short "big toes." Relative to foot length, the big toe in humans is not especially large. This toe appears to be big because the other four toes are relatively short and small (Figure 8.50).

With some prosimians we find an elongation of the tarsal elements calcaneus and navicular. This is true for Cheirogaleinae, but is even more pronounced in Galagidae and especially in Tarsiidae (Figure 8.51). Galagidae and Tarsiidae are very adept leapers, and the elongation of these tarsal elements can be understood in this context. As already mentioned, Tarsiidae show yet another specialization of the hind leg that can be interpreted as being related to the highly specialized locomotion of these animals: namely, tibia and fibula in the lower leg are fused together and elongated (compare Figure 8.37).

Among Lorisidae we find that the big toe diverges from toes 2 to 5 in an angle that is close to 180 degrees (see Figure 8.52). The foot of the African lorisid *Arctocebus calabarensis* is highly unique in that the great toe is directed opposite to the second toe, forming a straight line along the two.

Unlike the second finger the second toe is not reduced among Lorisidae and it is adorned—as in all other prosimians—with an elongated claw which is often referred to as "the toilet claw." This claw, indeed, is used in toilet activities such as grooming and scratching. These are actually not typical claws but rather laterally compressed, elongated nails. As already pointed out, only among Tarsiidae do we find two toilet claws on both the second and third toe as well

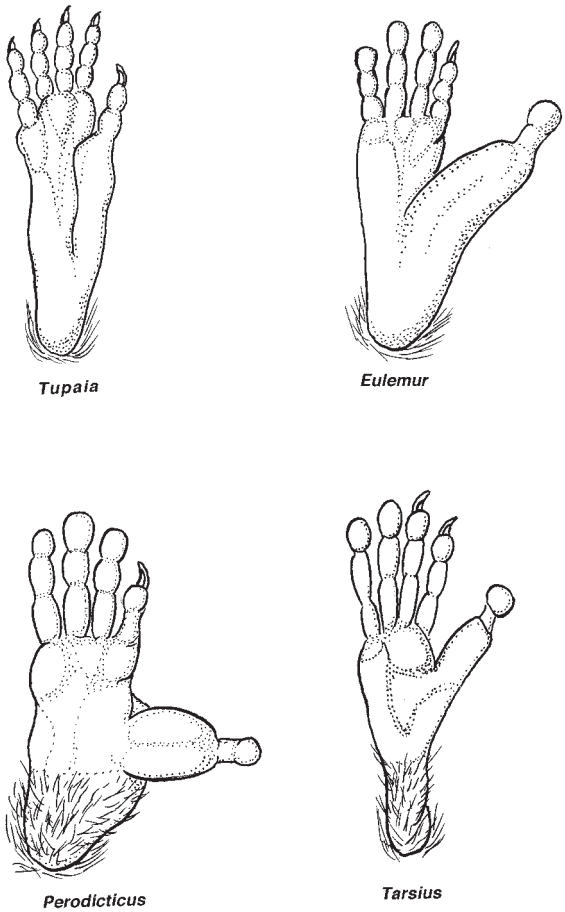

Figure 8.49 Prosimian feet (brought to approximately the same length).

(compare Figure 4.21). More primitive than primates, Tupaiidae have claws on all five toes, whereas all prosimians have a flat, broad nail on their big toes and nail on toes 3 through 5 as well. The other exception to this rule is the aye-aye with a flat nail on the hallux and claws on toes 2 through 5.

Yet another specialization of the fingernails and toenails is found in two species of the bushbabies: *Phaner furcifer* and *Galago (Euoticus) elegantulus,* with the common name "needle-clawed bushbaby" that refers to the shape of their claws. As mentioned before, they have nails that are keeled in the middle and end in a sharp point (see Figure 8.43).

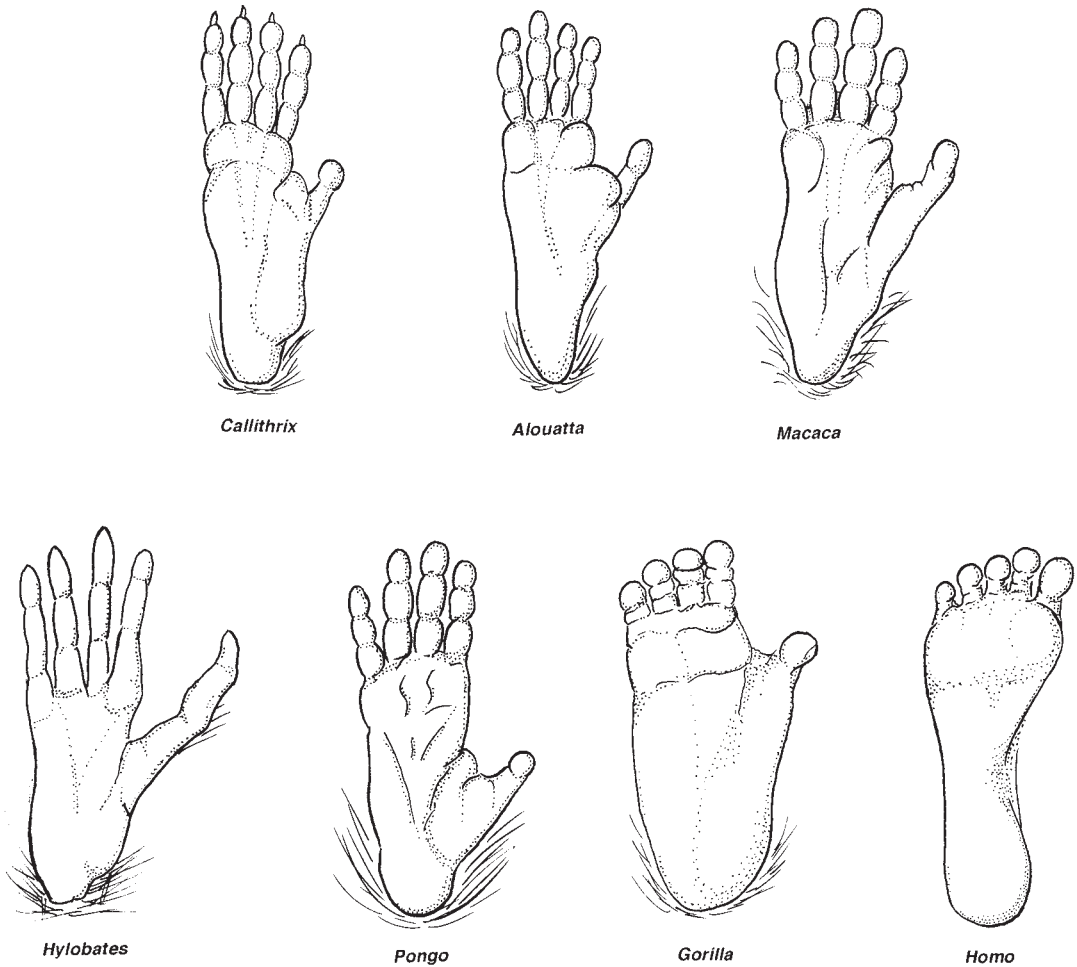

Figure 8.50 Upper row shows the feet of monkeys, lower row shows those of hominoids (brought to approximately the same length).

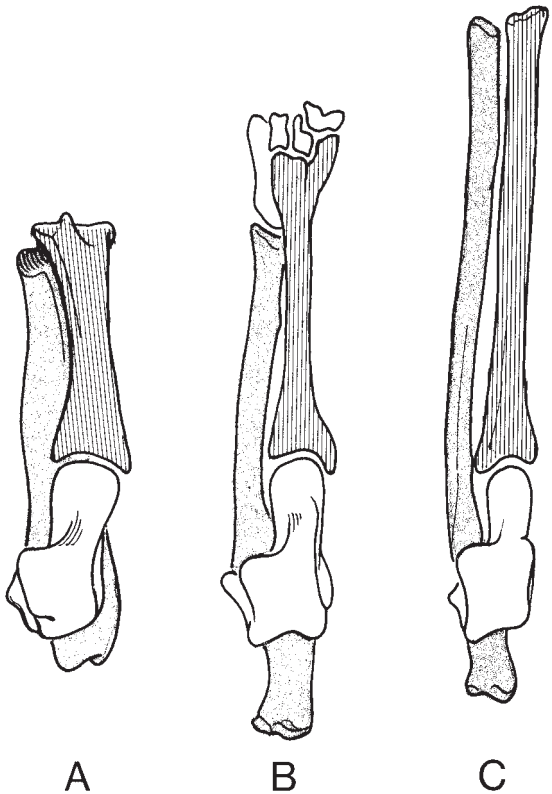

Figure 8.51 Comparison of elongated tarsal elements of three prosimian genera; talus—white, calcaneus—gray, navicular—striped. A) *Microcebus murinus,* an arboreal, quadrupedal runner, B) *Galago crassicaudatus,* a large "vertical clinging and leaping" primate, and C) the small and highly specialized vertical clinger and leaper, *Tarsius bancanus*. (Brought to the same talus length.)

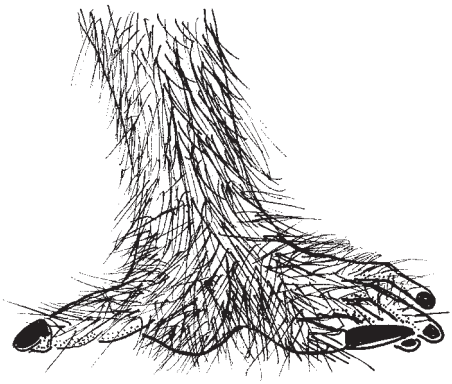

Figure 8.52 Highly specialized left foot of *Arctocebus calabarensis,* a unique lorisid.

Also, South American callitrichids have claws on all toes with the exception of the hallux, which is adorned with a flat nail. The remaining New and Old World monkeys, the lesser and greater apes, and humans have nails on all toes.

Seven bony elements establish the tarsus of the foot. The talus—also called *astralagus*—is the large tarsal element that articulates with the two long bones of the lower leg, tibia and fibula. It has articular facets on all the surfaces that articulate with the adjacent bones (Figure 8.53). The lower ends of the tibia and fibula embrace the talus from above and both sides, medially with the tibial malleolus and laterally with the malleolus of the fibula (Figure 8.54). This articulation is maintained by strong ligaments. Movements at this joint are mainly flexion and extension, even though there can be slight movements between the distal ends of tibia and fibula. The range of these movements varies between different species of primates. The talus shows differences of the posterior aspect that appear to be typical for prosimian primates where the groove for the flexor of the musculus hallucis longus slopes outward and is offset from the medial part of the trochlea, while the lateral talo-fibular facet slopes outward. In anthropoidea, including tarsiers, the m. flexor hallucis longus groove is positioned medially on the trochlea and the talo-fibular articular facet is positioned straight up and down (see also Gebo, 1993).

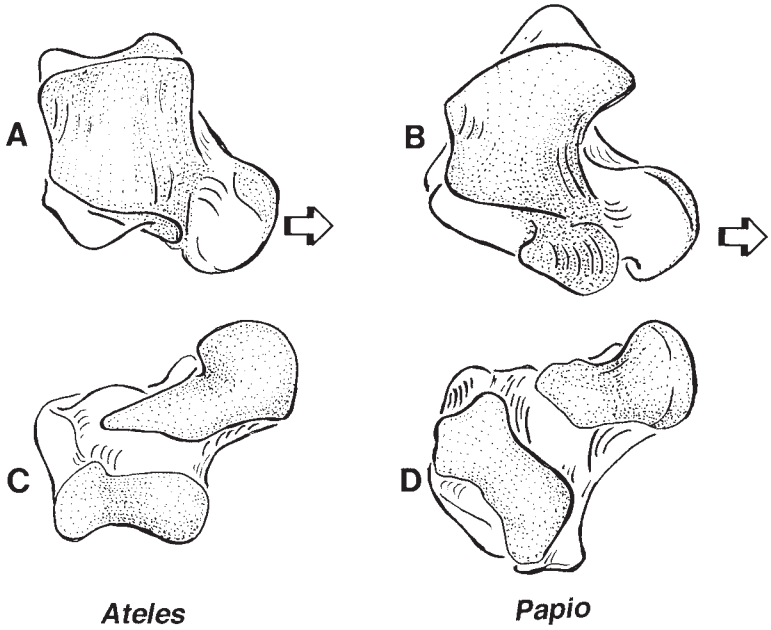

Figure 8.53 Left tali of an arboreal ateline monkey *(Ateles);* A) from above, C) plantar aspect, and a terrestrial cercopithecine monkey *(Papio);* B) from above, D) plantar aspect. (Arrows indicate distal direction.)

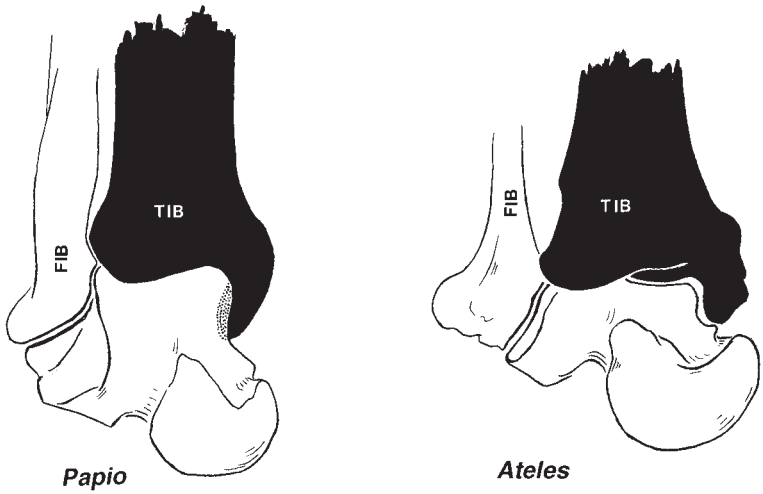

Figure 8.54 Fibula and tibia embracing talus (see from distal) in a terrestrial cercopithecine *(Papio)* and an arboreal ateline *(Ateles)*.

All living primates have the above-described tibiofibular articulation with the talus with the marked exception of tarsiers (see Figure 8.54). This is the case because the fibula of tarsiers is reduced and fuses into the distal half of the strongly built tibia. The fused fibula establishes a strong talar process on the inside of the tibio-fibula, while on the outside the tibia embraces the talus: this entirely ossified tibio-fibular joint with the talus totally constricts the talus to forward and backward movements only.

Medio-distally on the talus, a robust process, the talar neck, projects forward and slightly downward and terminates in a rounded articulation: the talar head. This talar head is covered by an articular facet and articulates distally with the navicular. The underside of the neck articulates with the sustentaculum tali of the calcaneus, a shelf-like extension on the medial aspect of the calcaneus (Figures 8.55 and 8.56). The latter is usually the largest bony element of the foot, which in turn articulates distally with the cuboid.

In most anthropoids the talo-navicular and calcaneo-cuboid, or mid-tarsal, joints are positioned parallel and adjacent to each other. They are, however, widely separated antrio-posteriorly in such forms that make exceptions of this rule and have an elongated calcaneus. The navicular elongates concomitantly with the elongation of the calcaneus. This is especially pronounced in tarsiers and bushbabies, primates with a highly specialized leaping locomotion (Figure 8.57).

It is very important to always keep in mind that morphological features can vary widely interspecifically among primates. Figure 8.58 illustrates this fact, showing variation in the conformation of the articular facets on baboon calcanei and chimpanzee tali.

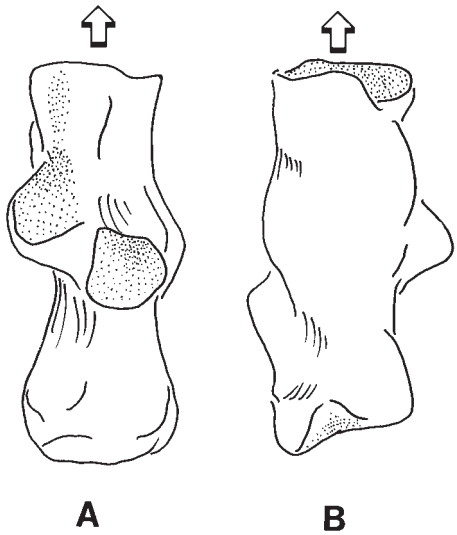

Figure 8.55 Primate calcaneus; A) viewed from above, B) plantar view. Arrows indicate distal direction. Articular facets are shaded.

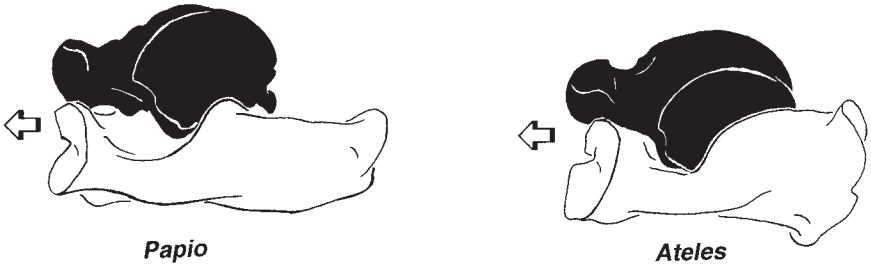

Figure 8.56 Left talus (black) and calcaneus (white) of a terrestrial cercopithecine *(Papio)* and an arboreal ateline *(Ateles)* seen from lateral. Arrows indicate distal direction.

The other family of prosimian primates that moves predominantly by powerful upright leaps interchanged by clinging in an upright position on vertical supports is the family Indriidae. These large-bodied prosimians are spectacular leapers, similar to bushbabies and tarsiers, and lack the elongation of the tarsal elements calcaneus and navicular.

The navicular—as its name implies—is a boat-shaped element in most primates. The navicular has a concave joint proximally that embraces the talar head and a convex joint distally for the complementary concave surfaces of the

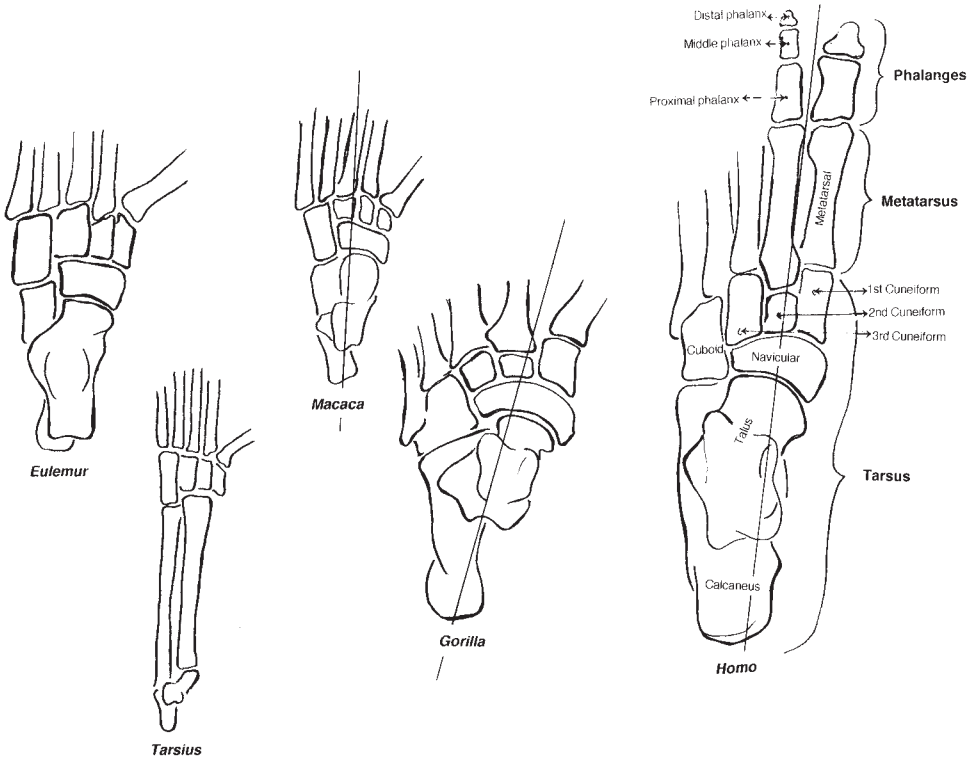

Figure 8.57 Differences in tarsal element arrangement in various primates.

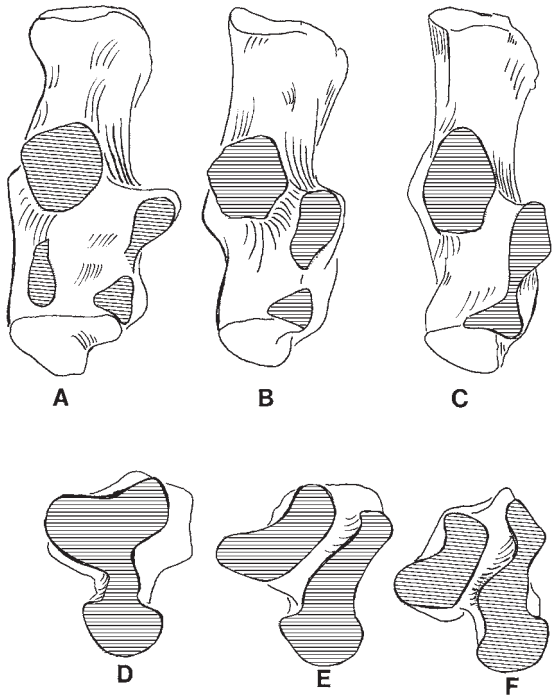

Figure 8.58 This figure shows intrageneric variation of articular facets in baboon *(Papio)* calcanei (A, B, & C), and in chimpanzee *(Pan)* tali (D, E, & F). Distal ends are down.

distally adjoining three cuneiform elements. If the navicular is elongated, it becomes more or less quadrangular *(Microcebus, Mirza, Cheirogaleus)* or, in extreme cases, long and cylindrical as in *Galago* and *Tarsius,* which show the most elongated navicular (and calcaneal) foot elements. The three cuneiform bones and the cuboid are joined by the metatarsals distally. The metatarsals articulate with the phalanges, which usually have two elements in the first ray of hallux and three elements for toes 2 through 5. All these tarsal elements vary in relative length and shape between the different primate species. In Lemuridae and Indriidae the foot is habitually not flat if put onto an even surface. It is usually in an inverted position with the 5th (lateral) toe on the surface and toes 4, 3, and 2 respectively positioned above each other (Lewis, 1980).

An elongation of the metatarsals is found among many primates such as baboons *(Papio),* as well as in other mammals, as the treeshrew *(Tupaia),* kangaroos, and many rodents. However, in all primates the general combination of the tarsal elements is fundamentally the same.

Great apes—when on the ground—usually walk with the weight on the outside of their feet. The hallux diverges away from toes 2 through 5 in all primates

except *Homo,* where the big toe is aligned with the other toes. Accordingly, the feet of all nonhuman primates are efficient grasping tools. This condition is somewhat modified in the feet of the orangutans, which have the relatively longest toes 2 to 5 of all higher primates, and yet, the shortest hallux.

The human foot is clearly specialized: it is stiff all over, the hallux is in alignment with the other four toes, and it is no longer very well adapted for grasping. Talus and calcaneus are also aligned with the long axis of the foot and positioned on top of each other. The neck with the head of the human talus does not diverge medially from the long axis of the foot as much as in other primates. This appears to be in context with the weight-bearing properties of human feet and a morphological expression of the fact that the human hallux has lost its grasping function. Also, the hallux is adducted to toes 2 to 5 and thus incorporated into the characteristic arch of the human foot. This arch functions as a spring during walking, running, and standing.

The arch of the human foot is established by the position of the metatarsals. The proximal metatarsals 1 through 4 are habitually elevated off the ground and elevated into the arch that is established by the metatarsus. The distal ends of all metatarsals 1 to 4 are touching the surface and metatarsal 5 habitually touches the ground along its entire length of the outside of the human foot. This arch can be understood by looking at the footprint produced by a normal human adult. The arch of the human foot develops gradually during ontogeny. In babies the feet are usually flat. The arch is not yet developed in children until about three years of age, when it slowly begins to rise up and is nearly complete by about six years of age. In Figure 8.59, the middle footprint of a five-year-old shows the arch comparatively early, for most of the central arched region does not any longer touch the ground at the age of five.

Considering the enormous lever arm of the upright human body in comparison to the length of the foot, the human foot in its entirety is comparatively small. Our sturdy foot structure has to support the upright body during standing, walking, running, dancing, and numerous other activities. Human upright stance requires the feet to constantly maintain the body's equilibrium, a functional task that can only be secured by the strongly powered spring-like human foot with its axis through the big toe. Humans who have accidentally lost their big toes have great difficulties standing upright for any length of time without the support of a cane.

In prosimian primates the plantar surface of the proximal tarsus, the heel, is not covered with padded friction skin but it is covered with hair. As usual, there is an exception to the rule: in one genus and species of the Lemuridae, namely the most terrestrial quadrupedal prosimian *Lemur catta,* the heel is naked. It is, however, not covered with a friction skin and lacks the development of ridges. In contrast to prosimians the entire plantar surface of anthropoid primates, including humans, is covered with friction skin with characteristic "fingerprint" or, better, footprint patterns.

Figure 8.59 Human footprints of an adult (left), a five-year-old (middle) and a two-year-old (right). The arch is not yet developed at right, in the state of rising up in the middle, and fully formed at left.

To sum up what we have learned: Primates generally have grasping hands and feet. Only humans uniquely have hands that are freed from locomotion for more sophisticated endeavors and feet that are made for walking (Figures 8.60 and 8.61).

FIFTH EXTREMITY

Some South American monkeys have a versatile fifth extremity: their long and muscular tail. On the ventral aspect of the distal third of the tail they exhibit a friction skin just like that on their hands and feet. The tail is supplied with nerve-receptors and thus, highly sensitive to touch. "Finger-print" patterns on the tail vary between genera, species, and individuals. Species of genera *Ateles, Brachyteles*, *Lagothrix*, and *Alouatta* belonging to the family Cebidae all have this very useful "fifth extremity." All these species are able to hang upside down only supported by the very tips of their tails. These species are even able

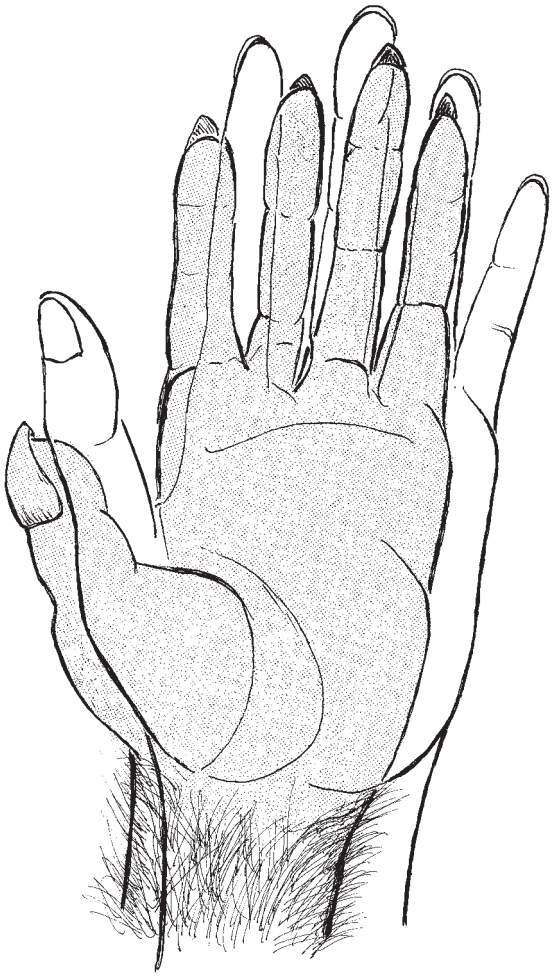

Figure 8.60 Human and macaque (shaded) hands superimposed to show the morphological difference between the two.

to hold their own plus the weight of another monkey in this position, so that both are only suspended by the one tail. Scientists call this kind of tail a prehensile tail.

A functionally and morphologically incipient fifth extremity is found in the New World genus *Cebus*. However, this tail is haired all over and thus not quite as useful as the true prehensile tail with a friction pad of the genera mentioned above (Ankel, 1972). That ancestors of apes and humans long ago lost the useful distal appendage, the tail; the loss of an extra fifth "hand" seems almost regrettable

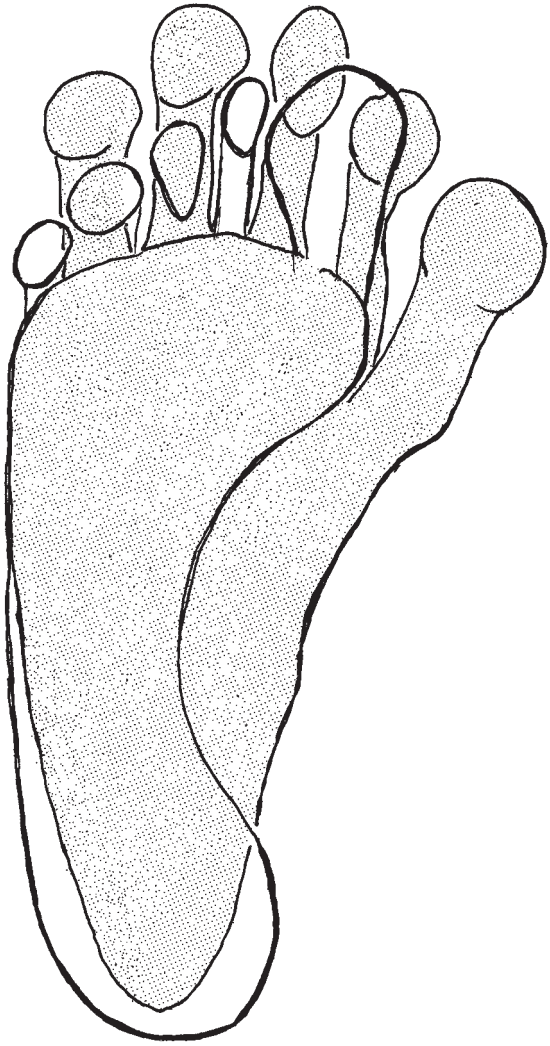

Figure 8.61 Human and macaque (shaded) feet superimposed to show the morphological difference between the two.

at times. Think of all the practical uses a tail could have had for us, and the great opportunities it would have offered the imagination of fashion designers!

Another primate with a friction pad on the underside of the tail is *Tarsius bancanus*. This friction pad, however, is located at the base of the ventral aspect of the tail that is used in a tripod fashion, propping up the body during vertical clinging and resting activities (Sprankel, 1965).

In those New World monkeys with a true prehensile tail with a friction skin on the ventral third of the tail, not only the vertebrae but also the caudal muscles, the vascularization, and the nervous system are clearly adapted to the exceptional agility and strength of this "fifth extremity." In the proximal part of the tail the dorsal muscles (musculus extensor caudae medialis and lateralis and m. abductor caudae dorsalis, as well as the m. interspinales and intercostarii caudae) are considerably bigger with larger transverse diameters than the ventral muscles (m. flexor caudae lateralis and mediales, m. infracaudalis). Near the middle of the tail, both muscle systems are of equal diameters, and toward the end of the tail, the ventral portion of the tail musculature is larger than the ventral portion. This correlation is about equal throughout the tail length in nonprehensile primate tails. The distribution of the musculature in prehensile-tailed South American Cebidae clearly reflects their functional abilities: the major upward and lateral movement of prehensile tails occurs near the tail root while ventral flexions and gripping are predominantly occurring near the tail end that is also equipped with the highly sensitive friction pad (compare Figure 8.17).

MUSCLES

The muscles of the vertebrate body are the contractile tissue that actively move body parts and also form portions of several internal organs such as the heart. There are three main types of muscles: 1) striated, or striped, muscles, which make up the skeletal musculature; 2) smooth muscles, which are part of internal organs and make up the muscle layer of the arteries; and 3) the cardiac muscles of the heart. Muscle cells are made up of contractile protein microfibrils which tighten up concurrently. In the following chapter we will be focusing on the skeletal muscles of primates.

The relationship between skeletal musculature and bones in the vertebrate body is both ontogenetically and mechanically a close one. Muscles are the active partners, while bones make up the passive support structure of the primate body on which the muscles and their tendons exert forces (usually pulling and stretching forces). Bones provide surface area for the attachment of the muscles. For example, on the surface of some primate skulls, bony crests are building up during growth. These crests serve to enlarge the surface area for insertion of the temporalis (chewing) muscles. Bone is a living tissue that responds to use.

The shapes of the different elements of the skull and of the postcranial skeleton are thus sculpted in response to the many functions that these body parts carry out. Bones also form to support the organs of the body, in correspondence to their size and their requirements.

Differences in bone architecture accommodate different organs and in turn this configuration reflects different functions. For example, as already mentioned,

primates with a nocturnal activity pattern, such as bushbabies and tarsiers, have large eyes that are surrounded by large bony supports. In contrast, diurnally active primates have small eyes and, accordingly, their eye-sockets are small.

In the postcranial skeleton of primates the basic morphology is adapted to a great variety of locomotor, postural, and feeding activities. Postcranially, primates are not very specialized and this is apparent if they are compared to horses, giraffes, other ungulates, or even more strikingly to such uniquely specialized mammals as whales. Basically, the anatomy of all primates follows the same general morphological pattern. This is consequently also true for the system of muscles, as well as their vascular and nervous supply, which activate the skeletal elements. The functional systems that make up the unity of the body differ, however, in those areas that have undergone adaptive specialization.

Major muscle groups are altogether more or less identical among primates with only moderate differences in bulk, attachment, and positioning that are adjusted to various skeletal differences. Thus, in the muscle system of primates we only find major differences in those species that exhibit true and manifest uniqueness in their activity patterns and locomotor or feeding behavior. The latter (specialization for feeding purposes) is expressed most obviously in the re-arrangement of skeletal elements and musculature of the hand in the aye-aye *(Daubentonia madagascariensis)* where the third and fourth fingers are considerably elongated and wire thin. Aye-ayes use these specialized fingers to extract insect grubs from wood cavities or to pump up liquids from large nuts such as the coconut.

Obvious examples of major changes in locomotor morphology and behavior among primates are the vertically leaping and clinging bushbabies, tarsiers, and indriids. These primates have adaptive changes in hind-leg and foot anatomy corresponding to their specialized locomotor behavior. Other primates that deviate from the generalized postcranial anatomy found in most primates are the prehensile-tailed South American monkeys, with their strongly developed tail musculature and different morphology of tail vertebrae, and the lesser apes, with their long arms and their powerful chest and arm musculature. On the other side of the spectrum are the bipedal humans, with major morphological changes in the vertebral column, pelvis, hind leg, and foot areas and their powerful leg and thigh muscles.

To express this differently, only those primates that have acquired obvious and real specializations in their feeding or locomotor behavior have specialized skeletons and musculature, which are strikingly different from those primates that remain unchanged from the basic morphological primate pattern such as rhesus macaques or the talapoin monkey. Thus, among the majority of primates, the patterns of skeletal and musculature postcranial morphology are comparatively similar to each other or only slightly changed in proportions and general anatomical arrangements. For this reason they are only briefly discussed and illustrated.

Anatomical reference books that discuss human anatomy, as well as the excellent volume comparing the anatomy of baboons, chimpanzees, and humans by Swindler and Wood (1973), the volume on rhesus macaques by Strauss (1971), and the superb "Introduction to Human Evolutionary Anatomy" by Aiello and Dean (1990) will provide detailed answers to questions about primate anatomy.

We here include pictures of the layers of back muscles of a New World monkey, the Capuchin, genus *Cebus,* to document the similarity with the back musculature of other primates, including *Homo* (Figures 8.62–8.65).

LOCOMOTION

One of the fundamental activities of vertebrates is their locomotion, their manner of getting about. Because part of this activity is postural, the topic also includes resting behavior. How animals move about is influenced by many different factors, both internal and external. Locomotor activities are induced by such internal factors as the feeling of hunger, thirst, extreme temperature, or escape from danger. External factors are originating from the surrounding world, like, for example, predator activity, social interactions involving conspecific partners, or sudden changes of the native habitat which can be caused by natural events or human interference. Also, physical characteristics such as body size, limb length, type of the environment they inhabit, and climate all play important roles in relation to locomotion. Evolution has produced a high degree of correlation between environmental substrate, morphology, and locomotor adaptation. This is clearly illustrated by the common fish-like shape of habitually water-living mammals such as whales or porpoises, or, alternatively, by the birdlike bodies and wings of mammals capable of flight like bats or flying foxes. But these latter mammals live in extreme environments, and therefore they display extreme morphological adaptations. Many other groups of mammals, which, unlike primates, live in a predominantly terrestrial environment, have rather uniform locomotor behaviors as well as postcranial morphologies. This becomes obvious when we regard orders such as Artiodactyla (as for example camels, hippos, or antilopes) and Perissodactyla (such as horses, rhinos, or tapirs). Within these groups both locomotion and the locomotor skeleton are rather indistinguishable. These latter two groups do not have the versatile five digits on both hands and feet that characterize primates, as their hands and feet are reduced to just two digits (the third and fourth digits) and one digit (the third), respectively, that are carrying the main load of the body.

In this respect, primates remain relatively underived in terms of the morphology of both their bodies and limbs. They have retained many of the features characterizing the locomotor apparatus of early mammals that have been lost in other mammal groups, for example, the pentadactyle (five-fingered) hands and

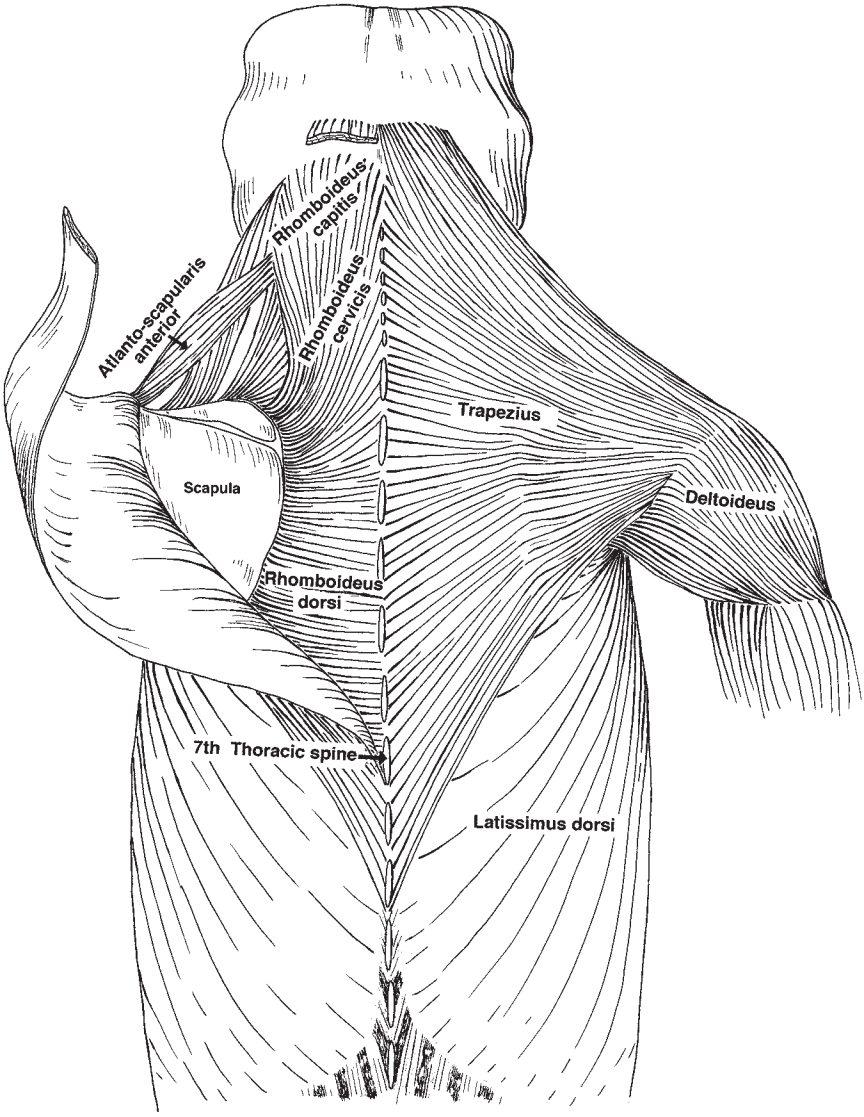

Figure 8.62 *Cebus capuchinus* showing the superficial layer of back musculature.

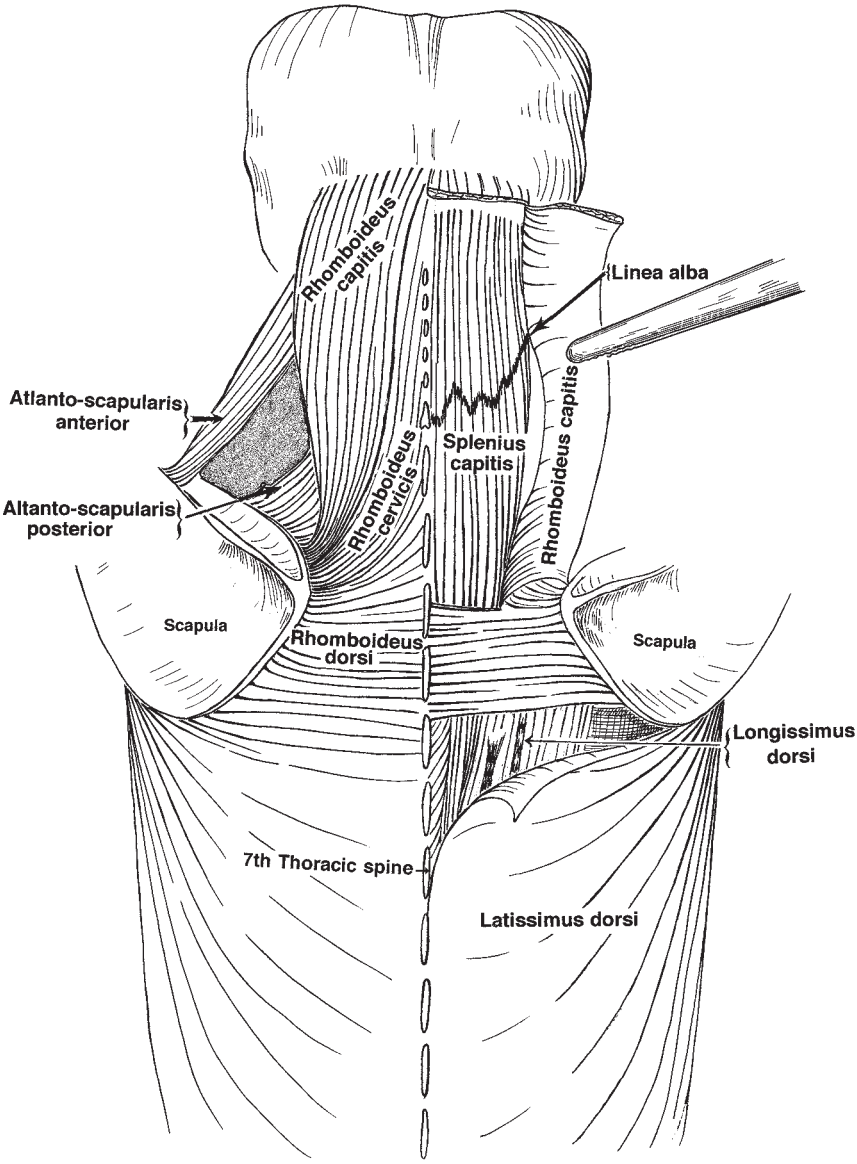

Figure 8.63 *Cebus capuchinus* showing second layer of back musculature.

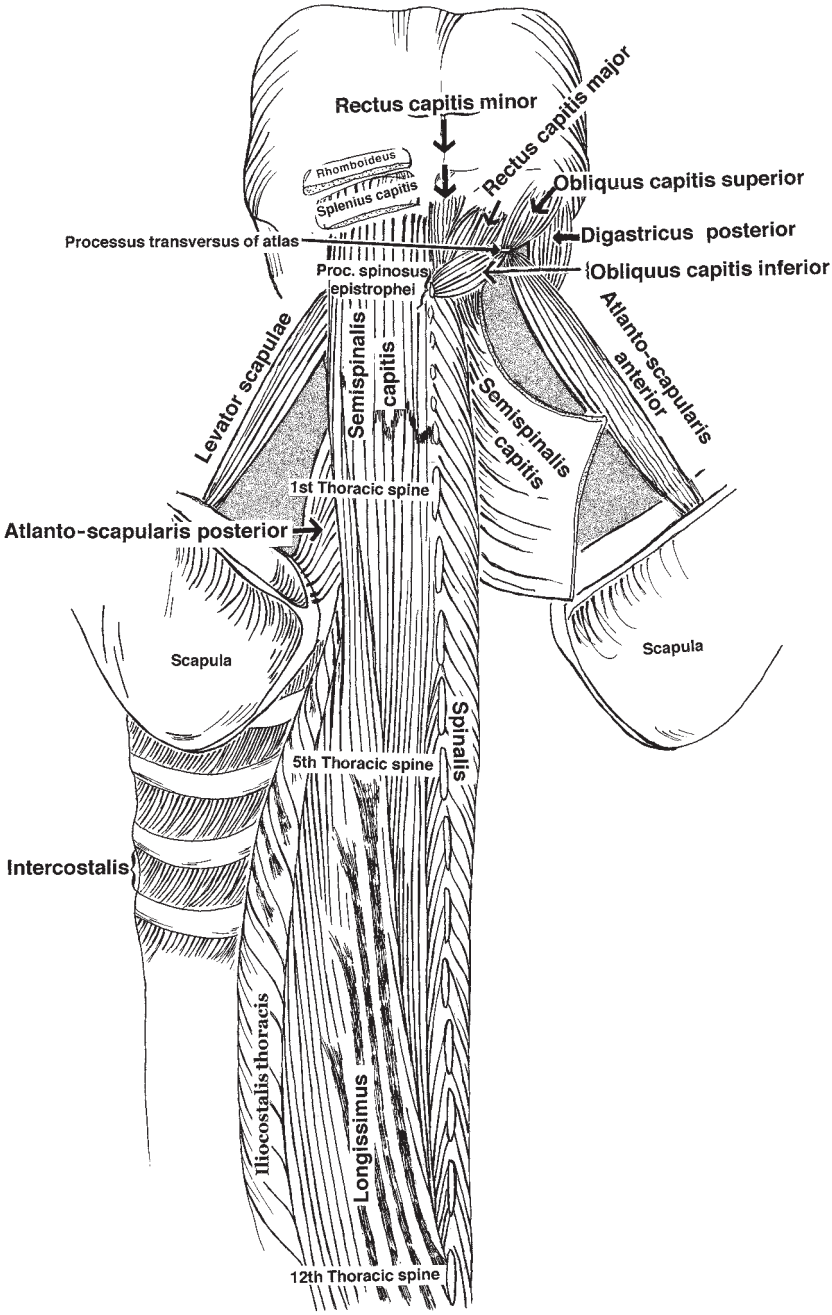

Figure 8.64 *Cebus capuchinus* showing third layer of back musculature.

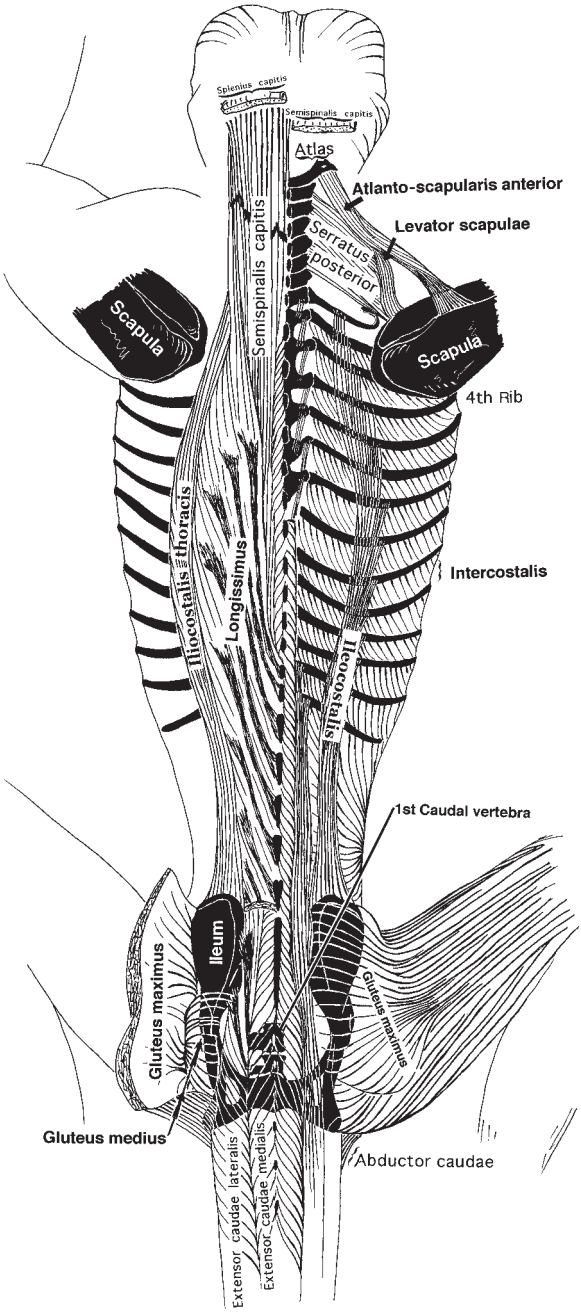

Figure 8.65 *Cebus capuchinus* showing the deepest layer of back muscles.

feet as well as clavicles. Because of their adaptable morphology, primates in general are capable of engaging in a wide variety of disparate locomotor activities. One of the most successful mammals, *Homo sapiens,* is unique in terms of habitual locomotor type compared to all other mammals. One could even ask whether human success as an organism is in any possible way correlated to our unique way of moving about? Answering this question could contribute a basic element to our self-understanding. It does indeed appear that the freeing of the hands from locomotor activities in combination with their increased tactile sensitivity and a highly refined brain, as well as the elevated height of the visual organs, the eyes, indeed have played an important role in the human success story.

Within the order Primates we recognize a wide variety of locomotor habits. Most nonhuman primates spend at least some time during the day in trees. Indeed, the majority rarely descend to the ground at all. Primates are usually living in an arboreal environment where the ability to grasp and hold on with their pentadactyl hands and feet is essential. Moreover, grasping abilities allow a wide range of locomotor (as well as other) activities.

The works of many of the early primate researchers show that locomotion has long been considered important in the study of primate evolution (Keith, 1903; Wood-Jones, 1929; Gregory, 1934). Nevertheless, such discussions were for the most part theoretical because until more recently very little was known about the locomotion of extant primates in their natural habitats. Information about primate locomotion initially came from observations on captive animals in unnatural surroundings or from sketchy reports on accidental observations in the field that often turned out to be anecdotal. These tales were often exaggerated and certainly not always accurate. It is understandable then, that the overall anatomical similarities of the Hominoidea in the morphology of the trunk and forelimb led to the long-lasting and widespread belief that the lesser and great apes all practiced the same type of locomotion—"brachiation"—and that humans have originated from arm-swinging ancestors. "Brachiation" is a type of arboreal locomotion where progress is made by propelling the body forward with the arms, which are extended above the head. When arm-swinging locomotion is rapid and efficient, both hands are free between alternating grips. We now know that only the lesser apes habitually brachiate to any great extent. As will soon be discussed, the great apes have their own distinctive modes of locomotion. This demonstrates that an overall similar morphology does not necessarily mean similar locomotion.

In 1964 Ashton and Oxnard were the first who made an attempt to classify the living primates into a behavioral classification scheme according to their mode of locomotion. Three years later Napier and Walker (1967) proposed a new primate locomotor category for some prosimians ("a newly recognized category

of locomotor behavior of primates") that they called Vertical Clinging and Leaping (or short VCL) (Figure 8.66), which they declared to be the only known locomotor behavior of Eocene fossil primates. Later it became obvious that this locomotor behavior actually includes very different adaptations to more or less vertical leaping and clinging.

Napier and Napier (1967) elaborated and perfected this classification in their "Handbook of Living Primates," introducing so-called locomotor groups (Table 8.3).

These locomotor categories have by now become classics and it is important to know about their origin because they are still being widely modified and used. Most of the categories have been redefined as more detailed observations of locomotor behavior for many primate genera have been reported. More recently,

Figure 8.66 A true prosimian vertical clinger and leaper *(Propithecus verreauxi)* clinging to an upright support. Photograph courtesy of Verne Simons. From Ankel-Simons, 2000.

Table 8.3

Locomotor Classification Proposed by Napier and Napier, 1967

Category	Sub-type	Activity	Primate Genera
1. Vertical clinging and Leaping		Leaping in trees and hopping on the ground	*Galago* *Avahi* *Hapalemur* *Lepilemur* *Propithecus* *Indri* *Tarsius*
2. Quadrupedalism	(i) Slow climbing type	Cautious climbing—no leaping or branch running	*Arctocebus* *Perodicticus* *Loris* *Nycticebus*
	(ii) Branch running and walking type	Climbing, springing, branch running, and jumping	*Lemur* *Phaner* *Cheirogaleus* *Callithrix* *Cebuella* *Saguinus* *Leontopithecus* *Callimico* *Callicebus* *Saimiri* *Aotus* *Cacajao* *Chiropotes* *Pithecia* *Cebus* *Cercopithecus*
	(iii) Ground running and walking type	Climbing, ground running	*Macaca* *Mandrillus* *Papio* *Theropithecus* *Erythrocebus*
	(iv) New World semi-brachiation type	Arm-swinging with use of prehensile tail, little leaping	*Alouatta* *Ateles* *Brachyteles* *Lagothrix*
	(v) Old World semi-brachiation type	Arm-swinging and leaping	*Colobus* *Nasalis* *Rhinopithecus* *Simias* *Presbytis* *Pygathrix*
3. Brachiation	(i) True brachiation	Gibbon type of brachiation	*Hylobates* *Symphalangus*
	(ii) Modified brachiation	Chimpanzee and orangutan type of brachiation	*Gorilla* *Pan* *Pongo*
4. Bipedalism		Striding	*Homo*

Fleagle (1992) published a list of primate locomotor categories which looks like this:

Arboreal quadrupedalism: walking and running on all fours along branches.
Terrestrial quadrupedalism: moving on all fours on the ground. A variation of this is knuckle walking, in which the animals uses its knuckles for support.
Leaping: moving between tree trunks and branches by rapid extension of the hind limbs.
Suspension: hanging below arboreal supports.
Bipedalism: walking and running on two limbs.

This list, like any other potential lists of so-called locomotor categories, is equally partially misleading. For example, primates engage in many other ways of leaping and jumping than by "rapid extension of the hind limb." For example, any of the arboreal quadrupeds are able to incorporate considerable leaps into their running activities. Other primates leap out of terminal branches by taking off and landing with all four extremities clasping branches.

Locomotor classifications into groups do have some utility as they attempt to make order of the great variety of locomotor adaptations among primates. Whereas these classifications do offer a description of the range of locomotor adaptations for primate groups, they also cause misconceptions. First, it is not clear if these categories are behavioral or anatomical classifications. Second, similar morphology has been interpreted to mean similar locomotion; this relationship however, does not always hold true. Third, similar locomotion has been perceived to mean similar anatomical adaptation; this correlation also is not always correct. These problems become more evident in the following examples.

The classifications of Ashton and Oxnard (1964) and Napier and Napier (1967) recognize "semi-brachiation" categories. Both include *Alouatta, Ateles, Brachyteles,* and *Lagothrix* as New World and *Presbytis, Rhinopithecus, Nasalis,* and *Colobus* as Old World "semibrachiation," and in addition, Napier and Napier (1967) include *Pygathrix* and *Simias* in the latter group. A "semibrachiator," as considered by these researchers, is an animal that arm-swings fairly regularly, supplementing its locomotion with leaping and/or quadrupedal progression. This category may, however, be more cohesive morphologically than behaviorally. In their musculature and skeleton, all these animals have been found to be intermediate in form between "brachiators" and "quadrupeds." Apparently, from this similarity in anatomical structure, the animals were assumed to share similar locomotor patterns. Field studies have shown that animals initially grouped in this category actually have widely varied locomotor adaptations. Mittermeier (1978) and Fleagle and Mittermeier (1976) found, in species of *Ateles,* that the usage of armswinging varies at an average between 26 to 39 percent, while *Alouatta* does not use arm-swinging at all (Mendel, 1976). Morbeck (1975) documented that *Colobus guereza* never uses arm swinging locomotion and

hanging by the arms, or so-called suspensory activity, was only observed very rarely (no more than 3 percent of all locomotor activities). Additionally, Fleagle (1977a) reports that the locomotion of *Presbytis obscura* and *P. melalophos* includes less than 5 percent of arm swinging. This clearly showed that the locomotor category "semi-brachiation" did not apply for the primates that were assigned to it and the term was soon abolished and replaced with the descriptive term "suspensory behavior" for such primates that move about by occasionally hanging under branches (Rollison and Martin, 1981). The term brachiation should only be used in the context of describing the locomotor behavior of the true brachiators, the lesser apes, genera *Hylobates* (Figure 8.67) and *Symphalangus*. Also, the assignment of the great apes to the brachiation subgroup "modified brachiation" has been shown to be incorrect as we shall see.

Another behavioral locomotor category of sorts was added to the list describing the use of small, terminal branches to move about and feed (Grand, 1972). This

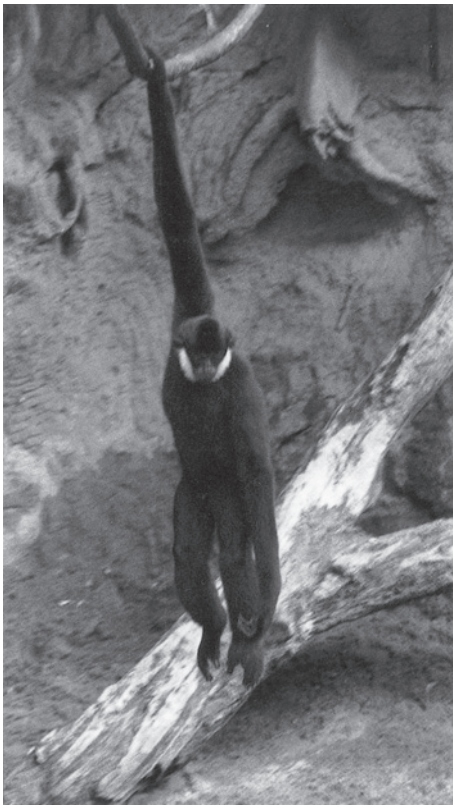

Figure 8.67 *Hylobates leucogenys* (young male), a true brachiator, hanging by one arm. (Note the enormous length of the arms.)

locomotor category, "terminal branch feeding," is practiced by many arboreal primates, especially some of the New World monkeys.

We do use the morphology of the primate skeleton widely to interpret and correlate the behavior of extant primates and—where possible—its manifestation in morphology to be able to infer the locomotor behavior of fossil primates who exhibit analogous morphologies. It is mandatory that great care must be taken to carry out such indirect conclusions. Competent groups of researchers have engaged in animated discussions and disagreements based on the locomotor evaluation of the same fossil postcranial elements (e.g., postcranial fossil remains of *Australopithecus*).

The vast majority of field research on primates has been done since 1960. Initially, primatologists focused mainly on observations of social behavior and tended to neglect the study of locomotor and postural behavior in the natural habitat. Even now, recent books dealing with different primate taxa do not have the word "locomotion" listed in their index, indicating that there is still a distinct separation between primatologists who are interested in social primate behavior and those who focus on locomotor behavior (e.g., Davies et al., 1994 on Colobines; Kinzey, 1997 on New World Primates). Now, a better basis for our understanding of the locomotor behavior of different primates is slowly unfolding. Even though there are a number of careful documentations of the locomotor activities that primates exhibit in the wild, our records are still far from being comprehensive. It also becomes increasingly evident that often even primates of the same species living in different environments can engage in entirely different locomotor behaviors. The mode of locomotion of primates is highly dependent on the structure of the environment that they inhabit. For example, while early observers of the New World monkey *Callimico* in the wild reported that these frequently engage in a vertical clinging and leaping mode of locomotion (Kinsey et al., 1975), a recent report based on long-term observations of *Callimico* in the natural habitat does not corroborate this attribution (Christen, 1998). The recent studies were unable to confirm the earlier observations. There could be different reasons for this. The earlier observed groups might have moved in a different environment, such as bamboo thickets with predominantly vertical supports and had to cling vertically. Or, alternatively, the earlier reports might have been based on less careful locomotor evaluation. There might be a different interpretation of what the category "vertical leaping and clinging" constitutes. Whatever the reason for such discrepancies, they are most likely caused by the fact that overall primates are not very specialized as far as their postcranial skeleton is concerned. Another reason is that they are quite capable of engaging in many varied locomotor activities which cannot easily be precisely defined. And a third reason for some stormy disagreements between scholars who evaluate the morphology of fossil primates such as australopithecines is the fact that skeletal details are often functionally overinterpreted; limited functions can be assigned to structural

details of the postcranial skeleton that are often not necessarily exclusive to the functions they are presumed to govern.

There are now many studies which attempt to correlate the relationships between morphology, locomotion, and habitat utilization (for example compiled in Morbeck et al., 1979; or more recently Gebo, 1993), as well as many papers that are found in scholarly journals (such as Fleagle and Mittermeier, 1978; Fleagle and Meldrum, 1988). All these studies provide information essential to understanding the relationships between morphology, locomotion, and habitat use.

Prosimian Primate Locomotion

All of the prosimian primates are predominantly arboreal, with the exception of *Lemur catta,* which spends up to one third of its time on the ground. *L. catta* is the most terrestrial prosimian primate. Galagos and tarsiers share a similar foot morphology, which is correlated within their ability (and categorization) as vertical clingers and leapers; they all have more or less elongated tarsal elements, the calcaneum and navicular. This elongation appears to be an adaptation for efficient leaping, the primary mode of locomotion for these small (with the exception of the largest bushbaby, *Galago crassicaudatus* which, even though it has the elongated tarsals, does not leap as much as the smaller galagos) nocturnal primates (Charles-Dominique, 1977) that are highly specialized. Tarsiers additionally have a fused tibio-fibula, making this hind-limb element more stable towards the forces of leaping. Also, the tiniest lemurs, genus *Microcebus,* have elongated tarsal elements, but they do not locomote in an upright leaping and clinging manner.

Genera of the Indriidae (*Propithecus* and *Indri*) are also predominantly leapers; even though they are equally capable as bushbabies or tarsiers to jump across considerable gaps between trees and branches, these large diurnal prosimians do not share the foot adaptation characteristic for galagos and tarsiers. Also, the lemuriform genera *Avahi, Hapalemur,* and *Lepilemur* are vertical leapers and clingers rather than arboreal quadrupeds. Leaping may be in fact an important part of the locomotion of all species belonging to these genera. This behavioral locomotor group, however, is artificial as it includes two different morphological locomotor adaptations (Cartmill, 1972). These members of the VCL locomotor category do not have elongated tarsal elements. In contrast, they have elongated thighs and metatarsals as their morphological adaptation for upright leaping. The weakness of the VCL concept of locomotion is that it covers structurally very different adaptations. Further, not all of these so-called VCL prosimians move habitually between vertical supports. According to McArdle (1981), the largest bushbaby, *Galago crassicaudatus,* as well as the smallest member of the genus *G. demidovii* are primarily quadrupedal runners and

climbers even though they have the elongated tarsal elements of all the galagos. Thus, the locomotor category VCL lumps together animals that are leaping and clinging in a vertical position (e.g., *Galago alleni,* tarsiers and Indriidae) with animals whose habitual mode of locomotion and postcranial morphologies cannot correctly be categorized as "vertical clinging and leaping" (e.g. many of the *Galago* species, *Hapalemur, Avahi, Lepilemur*), even though they sometimes do leap and cling in an upright position. We have to keep in mind that "vertical clinging" is only possible in areas where suitable vertical supports are available. Primates such as species of *Hapalemur,* who dwell exclusively in bamboo thickets and have a diet that is predominantly made up of bamboo, have only vertical supports available to cling on, and consequently cannot help but be vertical clingers and leapers. *Hapalemur* morphology, however, is not adapted to this way of moving about.

Members of the Lorisidae can also be categorized by distinctive locomotion. They are slow and cautious climbers, and the African pottos *(Perodicticus)* and Asian slow loris *(Nycticebus)* prefer to locomote on larger substrates than the angwantibo (African genus *Arctocebus*) and slender loris (the Asian genus *Loris*) do (McArdle, 1981). The so-called "slow" Lorisids can be unbelievably quick when catching prey. All the other prosimians are usually lumped together as arboreal quadrupeds.

New World Monkey Locomotion

All the monkeys of the New World are also highly arboreal animals. The smaller monkeys of the New World, the Callitrichidae, are habitually moving fast, and quadrupedal leaping within the sequence of running motion appears to be the primary mode of rapid progress. Marmosets are known to consume a considerable amount of tree exudates such as sap. To be able to get to this food source they are known often to cling to more or less upright large tree trunks with the help of their claws where they gouge holes into the bark to get the juices flowing. This postural behavior is the reason that Kinsey (1975) also attributed the locomotor category VCL to several of the small New World monkeys. He reports that particularly the smallest monkey, *Cebuella pygmaea,* as well as the marmoset *Callithrix jacchus,* move about by using vertical clinging and leaping activities. This leaping activity, however, is quite unlike the vertical leaps of prosimians. The "vertical clinging" adaptation of marmosets, facilitated by their hands and feet that are equipped with claws, is habitually practiced during harvesting of tree exudates which are usually available on the larger branches and vertical tree trunks rather than on thin, more horizontally diverging branches (Soini, 1988). The "vertical clinging" of South American monkeys is totally unlike the VCL locomotion of prosimian primates. Also, two superficially similar (by clinging to a vertical support in an upright posture) behaviors have totally

different underlying morphologies. South American monkeys are not able to jump like indriids, bushbabies, or tarsiers through seemingly boundless distances in a partially upright position, virtually flying through the air. Their locomotor morphology is that of quadrupedal runners and jumpers and totally different from the vertical clinging and leaping described specializations for vertical clinging and leaping prosimians. It is unfortunate that here the same terminology has been applied to lump together totally incompatible locomotor behaviors with completely incompatible locomotor morphologies.

The callithrichid genera *Saguinus* and *Leontopithecus* are said to primarily walk and run quadrupedally and to leap between terminal branches. They also descend on larger trunks both in an upright position, tail first, as well as up-side-down, head first.

The small cebid monkeys *Aotus, Callicebus,* and *Saimiri* are said to be quadrupedal walkers, leapers, and runners, and to prefer terminal branch feeding. Genus *Cebus* is basically a quadrupedal walker, climber, and runner. Capuchin monkeys leap comparatively less than the smaller cebid monkeys. Capuchin monkeys also use their prehensile tail (which does not have a tactile friction skin area) actively as additional support during locomotion and feeding activities.

Howler monkeys are basically deliberate quadrupedal climbers that always use their prehensile tail (with dorsoventral friction skin) to secure their movements. They also hang on the tip of their tails during feeding in terminal branches. They do not leap, and are said to use their tails in bridging maneuvers between branches to allow their young to cross. *Alouatta seniculus* and *A. palliata* are also avid and capable swimmers (Kinsey, 1997). Genera *Ateles* and *Brachyteles* are arboreal quadrupeds and habitually use the arms for suspensory activities. They also leap and use their prehensile tails, which do have highly sensitive friction pads, not only during locomotion, but also during terminal branch feeding activities (Grand, 1972).

The third genus of the Atelinae, *Lagothrix,* the woolly monkeys, are predominantly quadrupedal walkers and always employ their fifth extremity (the prehensile tail with a well developed friction pad) to secure their movements. Woolly monkeys are very able to pick up food items with the tip of their tail and can hang by the tip of the tail only when feeding. They do not leap habitually but are able to drop into adjacent terminal branches below. On the ground, woolly monkeys are quite apt in standing and walking bipedally on their hind legs, while holding the tail erect, parallel to their back.

The Pithecinae have generally been classified as arboreal quadrupeds. It appears that the uakari (genus *Cacajao*) is the most athletic of the three genera and uses leaping, hind-limb suspension, and dropping from higher supports, bridging and hopping more frequently than *Chiropotes* and *Pithecia* (Walker, 1993). Bearded sakis (genus *Chiropotes*) employ leaping much less frequently than *Pithecia*. The former tends to take off from pronograde position, habitually

landing in bushy, terminal branches, while sakis (genus *Pithecia*) hurdle themselves from an upright position holding onto a vertical support at take off. Their progression through the canopy of trees is very rapid and the medium-sized monkeys appear literally to be flying through the tree canopy (Kinsey, 1995).

Old World Monkey Locomotion

There is also a wide variety of locomotor adaptations among Old World monkeys. A number of species spend most of the time on the ground and are called terrestrial quadrupeds. These include the baboons (genus *Papio*) as well as the gelada baboon (genus *Theropithecus*), and several of the macaques (genus *Macaca*) as well as the patas monkey (genus *Erythrocebus*). When these monkeys are on the ground, they do not walk on the palms of their hands, rather they walk on dorsiflexed digits of fingers two to five. This kind of locomotion is called digitigrade walking (see Figure 8.46). Also, some of the vervets (e.g., *Cercopithecus [Chlorocebus] aethiops*) spend a considerable amount of every day on the ground and do walk on the palms of their hands and therefore can be called palmigrade concerning the use of their hands during locomotion (see also Whitehead, 1993). All these predominantly terrestrial cercopithecines, however, move back into the trees or onto steep rocks and cliffs for the night. Their locomotion differs enough from those monkeys that live principally in trees that they are classified as terrestrial quadrupeds. Most of the other Old World monkeys spend the majority of their time in trees and can be considered acrobatic arboreal quadrupeds. Some of the Colobinae appear to incorporate more leaping into their locomotor repertoire than any of the other Old World primates. Genera that use a distinctive amount of leaping in their locomotion are *Colobus guereza* (Morbeck, 1975) and *Presbytis melalophos* (Fleagle, 1977).

Arm Swinging and Knuckle Walking

The locomotor behavior of the apes was not very well studied, and the concept arose that all the apes were arm swinging forms. From this misconception, early paleoanthropologists deduced that human ancestors must have been brachiators (e.g., Avis, 1962). There now can be no doubt that only the lesser apes—gibbons (genus *Hylobates*) and siamangs (genus *Symphalangus*)—can be regarded as true brachiators (Stern and Oxnard 1973; Fleagle, 1974). In 1965, Tuttle documented that the African great apes exhibit a unique type of locomotion very different from brachiation; he described their way of walking as quadrupedal knuckle walking. Knuckle walkers support the front of their body, when walking quadrupedally, on the dorsal aspect of the second and third phalanges of digits 2 to 5 of their hands. In gorillas the dorsal aspect of their fingers that touch the surface during knuckle walking are covered with friction skin and incipient

fingerprints. The way of knuckle walking practiced by African apes is morphologically rather similar to the way of walking that is practiced by New World anteaters (order Xenarthra, family Myrmecophaga) (Orr, 2005). This similarity is interesting, even though how pertinent this case of parallel evolution in two kinds of very different animals can be for the understanding of great ape locomotion remains an open question. Even though they knuckle-walk when adults, youngsters of African apes also do arm swinging to move about. Yet, this type of arm swinging is different from the arm swinging true brachiation of lesser apes. The largest African apes, the gorillas, are simply too large and heavy to be able to get around by means of arm swinging, and they never do. Especially in male gorillas, the body weight is too great as to allow most climbing activities. Horn (1976) has observed the locomotor behavior of the pygmy chimpanzee in the natural habitat. He saw the animal locomoting in a quadrupedal manner, both in trees and on the ground. They knuckle-walk on the ground but position their hands in a plantigrade manner when walking in trees. Apparently, the pygmy chimpanzee uses arm swinging and leaping in trees considerably more than the common chimpanzee. This difference might very well be caused by the difference in weight between adult chimpanzees (up to 60 kg in *P. troglodytes* and no more than 40 kg in *P. paniscus*). It is pointed out that bonobos *(Pan paniscus)* habitually locomote quadrupedally, both on the ground and in trees while also engaging in bouts of bipedality. However, the difference between quadrupedal and bipedal walking is said to be rather subtle in these small chimpanzees and a great overlap between the two locomotor modes that they use is obvious, functionally and morphologically (D'Août et al., 2004).

Obligatory Bipedal Walking

It has been recognized that human bipedal walking is relatively economical if compared to quadrupedal locomotion of mammals with the same body mass as humans. Locomotor efficiency is closely related to body size. However, human running is an expensive way of using metabolic energy while moving about (Alexander, 2004). Actually, it is bipedal standing for any amount of time that exerts considerable balancing action on legs, feet, and the entire body. Bipedal standing is more problematical than walking or running as the entire upright body has to constantly be kept upright and in balance.

Both species of chimpanzees use bipedal walking and stance at intervals and seemingly more often than was previously believed (Stanford, 2006). Adult gorillas travel predominantly on the ground. It has been suggested that their huge body size is not easily supported by arboreal environments. They use their hands in the typical knuckle-walking position during quadrupedal locomotion. Like chimpanzees they are quite able to use bipedal postures and engage in some sort of walking for short distance locomotion. Field studies of the Asian great ape,

the orangutan, have documented that these large apes walk and climb most carefully and deliberately. They are the most arboreal of the great apes but do come occasionally to the ground to travel between forest areas. They habitually put the outside (fifth digit) of their hands onto the ground with slightly flexed digits. This mode of locomotion is also known as fist walking and characteristic only for orangutans. Like the common chimpanzee and the gorilla, adult orangutans do not use arm swinging as a mode of locomotion.

The distinctive locomotor activities of apes (brachiation of the lesser apes, knuckle walking of the African apes, and quadrupedal fist walking and deliberate climbing of orangutans) are specialized locomotor types in their own right. Even though all apes great and small are using upright posture and walk at times as part of their locomotor pattern and notwithstanding the fact that there are overall similarities between them, there is no reason to believe that any one of these locomotor repertoires must have evolved from one of the other. We do now understand that our knowledge of extant primate locomotion must be profound in order to provide a source for interpretation of the locomotor apparatus of extinct species.

Efficiency of Primate Locomotion

The formulation of locomotor categories is helpful when researchers are discussing the postcranial morphology of primates. There is no other order of extant mammals where body sizes vary between only about 30 grams (dwarf mouse lemurs) up to 170,000 grams (gorillas) and whose general postcranial morphology is so unspecialized that they are capable of practicing an infinite variety of locomotor activities. All efficient locomotor activities are closely correlated not only to the habitat that the animals concerned are inhabiting, but also by their overall size and proportions. It is obvious that a small marmoset cannot be an efficient brachiator. But a gibbon or siamang is perfectly adapted to the brachiating mode of locomotion. In contrast, gibbons lack the appropriate size and proportions to be efficient bipedal striders like humans. Even though humans can move more or less efficiently by arm swinging and gibbons can walk upright, neither one of these activities can be perpetually beneficial for them.

It is unfortunate that the terminology of most locomotor categories is unsatisfactory. It has traditionally been difficult to define such categories. For example, the term "semibrachiation" should be abolished as it is not possible to define it properly. The locomotor category "vertical clinging and leaping" is only appropriate for tarsiers, some of the galago species, and the indriids, and should not be applied to superficially similar locomotor activities of other primates such as South American monkeys. This is the case because true vertical clinging and leaping is morphologically distinct in the three groups of prosimian primates that unmistakably use this mode of locomotion. And this morphological manifestation

actually varies even within the VCL category as the three groups of primates that are locomoting in this mode have characteristically different adaptations in their hind-leg anatomy. Also, Fleagle (1992) states that leapers "have relatively long hind limbs and long, flexible backs, particularly in the lower (lumbar) region." This is, for example, actually not true for tarsiers, whose lumbar region is rather stout and not near as flexible as those of monkeys such as callithrichids.

Limb proportions have been used widely as indicators of the locomotor type used by various primates. Among the apes a common morphological feature is the length of the forelimbs. All apes have elongated arms, a feature that is most evident in the lesser apes. These elongated forelimbs erroneously were regarded as indicating that all apes were arm swingers. In 1970, C.J. Jolly demonstrated that forelimb elongation need not necessarily correlate with arm swinging or brachiation. Jolly studied very large, extinct open-country baboons and concluded that they were too large to be able to live in trees. They lived in arid environments and yet had long forelimbs. Some of these huge baboons were as large as female gorillas and at least one species had much longer forelimbs than hind limbs. They were at first ranked in their own genus *Simopithecus,* but Jolly realized their similarity to the present-day gelada baboon *Theropithecus* and placed them in this genus. The gelada baboon is a highly terrestrial primate that lives today in the treeless high country of Ethiopia and is totally unable to use arm swinging locomotion.

It has been documented that the robusticity of the forelimb bones is greater in terrestrial monkeys than in arboreal monkeys while the hind limbs are relatively long and strong compared to the predominantly terrestrial primates (Kimura, 2003). These results have been confirmed by laboratory testing that relates peak hind limb to forelimb force during terrestrial versus arboreal locomotion (Schmitt and Hanna, 2004). These authors were able to document that the peak load difference varies notably more in forelimbs as compared to hindlimbs: the forelimb load force is reduced during arboreal locomotion.

The important factor of above branch balance during arboreal quadrupedal locomotion has been studied in five Old World monkey species (Larson and Stern, 2006). It is stressed that successful maintenance of balance during walks and runs on small branches depends to a great extent on the involvement of long tails. It is discussed that the morphology of the elbow joint provides forearm stability in hominoids during pronation and supination. It is suggested that the morphology of the elbow joint of early hominoid primates (lateral trochlear ridge on the distal end of the humerus; Rose, 1993) is suitably adapted to assist with balance, suspensory activities, and stability in a wide range of locomotor activities.

A recent study compares body proportions and locomotion of two closely related cercopithecines (Anapol et al., 2005). It is concluded that differences in

body proportions between the two species can be attributed to the (slight) differences in locomotor activities. Even though it appears that other factors such as sexual dimorphism can alter the true relationship between body proportion and locomotor activity.

One possible and useful approach to classify locomotor behavior of primates requires measuring the percentage of time that is spent using specific locomotor patterns during periods of activity. Let us look at the locomotor activities of modern humans to illustrate this approach. For example, how much time does the average adult human being spend moving about in the typical upright walking locomotion? Between 10 to 50% of the active time during a 10-hour average day is said to cover the extremes. Equally important for our understanding of human locomotion and postcranial morphology is the time adult humans engage in different locomotor activities such as climbing, swimming, running, bike riding, ice skating, skiing, dancing, raking, digging, or driving automobiles: all activities humans are capable of doing, all activities that can be categorized as locomotion. These secondary locomotor activities, however, are less significant adaptively than human upright, bipedal walking. This illustrates that a normal adult human locomotes predominantly by walking bipedally, and we can justify their locomotor classification as bipedal walkers. On the other hand, it has been averaged for today's true brachiators, the lesser apes, that they brachiate about 80% of the time when actively moving. Therefore, they are correctly assigned to the locomotor category "brachiation."

It does not prevent a primates with long arms such as gibbons or great apes from walking bipedally on their hind legs, equally as the elongated tarsals of prosimians do not exclude them from moving about in a quadrupedal manner. We all know that morphologically and behaviorally bipedal humans are capable of engaging in all manner of locomotor behaviors that are not easily deducible from their specialized hind-limb and pelvic anatomy. Basically, all primates can be made to move about in manners that are not their habitual locomotor pattern. It is this unlimited ability to locomote in various ways that makes primates highly adaptable and difficult to assign to precise locomotor categories.

In a recent study Lemelin and Schmitt (1998) investigate the relationships between primate hand anatomy and lococomotor behavior with the help of kinematic documentation. They follow Jouffroy et al. (1991) in their definition of three types of primate hands that are based on morphological data:

1. Ectaxonic hands, as in *Nycticebus* where the fourth ray is the longest, which are characteristic for "strepsirhine" primates.
2. Mesaxonic hands, which have a longer third ray and are said to be found in most "haplorhines."
3. Paraxonic hands, where rays III and IV are nearly equal in length as in some cebid monkeys.

Lemelin and Schmitt state "Clearly, primates with mesaxonic or paraxonic (i.e., *Ateles*) hands are capable of using a wide range of hand positions that appear to vary according to substrate differences," and finally conclude: "This evidence suggests that hand kinematics is adjusted (sic) according to the substrate rather than being constrained by the anatomy. Also differences in how ulnar deviation was achieved (either at the midcarpal joint or at the metacarpophalangeal joints) reflected an intriguing phylogenetic signal that separated Lorisids and cercopithecids." This conclusion confirms that often functional potential supersedes functional anatomical adaptation in primates.

The relationship of environment, body size, and locomotion of primates can be analyzed during field studies. The relationship between postcranial anatomy and locomotion can best be understood through analysis in the laboratory. An increasing number of such studies have been carried out over the years. Brief reviews of some of these most instructive research projects will illustrate what can be learned from this kind of analysis.

Fleagle's (1977 a, b) research on two sympatric species of Malaysian leaf monkeys, *Presbytis obscura (Trachypithecus obscurus)* and *P. melalophos,* provides valuable insight of possible correlations between locomotor behavior, substrate use, and anatomical structure.[1] He found *P. obscura* to be primarily a quadrupedal monkey that prefers to move on large supports. In contrast, *P. melalophos* leaps much more frequently and prefers to locomote on smaller supports. Further, *P. obscura* spends the majority of its time in the horizontally continuous main tree canopy, whereas *P. melalophos* frequents the discontinuous lower level of the forest. Finally, Fleagle has documented a number of statistically significant anatomical differences between these two species. In each case these differences make structural sense when considered with the locomotor behaviors of these primates in mind.

Mittermeier and Fleagle (1976) carefully compare and evaluate similarities and differences in the locomotor behavior of *Ateles geoffroyi* and *Colobus guereza* and spell out the uselessness of locomotor categories such as "semibrachiation." Both these monkeys have repeatedly been classified as "semibrachiators," but it turns out that their locomotor behaviors are as different as can be. Also, the authors caution that it is almost certainly misleading to generalize locomotor behavior from one particular population to other populations of the same species. Troops that live in different environments often exhibit clear-cut locomotor differences within the same species, differences that are thus not likely to be reflected in the morphology.

Another interesting field study is that of Fleagle and Mittermeier (1980), in which they document the locomotion of seven species of New World monkeys in relation to these monkeys' body size and ecology. For the seven species

[1]*Presbytis obscura* is *Trachypithecus obscurus* according to Groves (2001).

studied—*Saguinus midas, Saimiri sciureus, Pithecia pithecia, Chiropotes satanas, Cebus apella, Alouatta seniculus,* and *Ateles pansicus*—the authors noted the following trends: smaller forms tend to leap more than larger forms, whereas larger forms habitually climb more than smaller forms. Also, larger monkeys tend to prefer larger supports. However, these trends have two exceptions. *Saguinus* preferred relatively larger, and *Ateles* preferred relatively smaller substrates than would be predicted from body size alone. Finally, these authors found no relationship between locomotor behavior and diet.

NEW TECHNOLOGIES APPLIED TO STUDY PRIMATE LOCOMOTION

Experimental research on primate locomotion is very important because it provides a rigorous test for hypothesized morphology, and locomotor behavior relationships. Radiography and electromyography (EMG), video photography, and computerized support sensoring are powerful techniques for testing function. In 1981, Jenkins identified by radiography a morphological adaptation for brachiation in the wrist of *Ateles* and *Hylobates*. He found that the proximal row of carpals form a socket that rotates around a ball formed by the capitate and hamate. Jenkins did not find this morphological complex in the quadrupedal primates he examined. Thus, this research has identified a morphology, which if discovered in a fossil primate would be highly suggestive of a brachiation adaptation.

Also, forearm rotators have been examined with the help of EMG during "over-ground and above branch quadrupedal walking" (Larson and Stern, 2006). Investigation of five species of Old World monkey has shown that a shift in body weight is used by all these monkeys as an important move that assisted them to keep their balance. Also, the swinging action of long tails has been used by these monkeys to counteract and recover from imbalance.

Stern and Sussman (1981) examined by telemetered EMG the function of the gluteus medius muscle of *Hylobates lar, Pongo pygmaeus,* and *Pan troglodytes*. Most researchers had considered this muscle to be primarily an extensor of the thigh on the basis of its origin and insertion. Stern and Sussman, however, found the gluteus medius muscle of these apes to function primarily as a medial rotator of the thigh, as it does in humans. These authors conclude that during bipedal walking the gluteus medius muscle provides side-to-side balance of the trunk at the hip in both humans and apes. This research is an example of how a hypothesized morphological-behavioral relationship can be rigorously tested by an experimental technique. The EMG showed that this muscle is active in these apes when they rotate their thighs medially, not during thigh extension. The assumption by Stern and Sussman, however, that ". . . Gluteus superficialis need

not have changed its action in the step from pongid to hominid" is misleading. There is no fossil pongid pelvis to show that the pelvic morphology of extant apes was already manifest in a fossil pongid that could qualify as a forerunner for hominid evolution. Extant apes have very specialized pelves. In fact, their pelves are so specialized that they can hardly be considered as a possible stage during the evolution of the human pelvis/femur complex.

For the first time, Demes et al. (1995) have recently used artificial take-off and landing beams (so-called suppliant force poles) in experiments set up to measure the locomotor forces that are applied during locomotion by various prosimians with different locomotor behaviors. These support beams with force sensors are directly connected to a computer and register the amount of force that is applied onto the support by the limbs during locomotor activity (vertical leaping and landing). At the same time the animals were videotaped. It was determined that leaping is strongly governed by the takeoff and landing substrates. The takeoff substrate responds with swaying away from the takeoff direction. Therefore force measurements involving rigid, nonreactive takeoff supports do not allow accurate measurement of the forces involved in leaping from a flexible vertical support. In another study it was shown that indriid leaping is governed by adduction and medial rotation during takeoff acceleration. This is said to be morphologically expressed in the spherical head and acetabulum of these primates. The foot is rarely involved in propulsion activities (Demes et al., 1996).

Recent field research has shown that most primates habitually spend less than 10% of the day locomoting. The vast majority of these animals' time is devoted to postural activities, such as sitting, lying, hanging, or leaning. All these postures exert stress and strains on the body of the animals. Therefore, these postures are undoubtedly factors that also shape the anatomy of an animal. Posture is therefore an important factor that researchers need to consider when they are analyzing the anatomy of any primate to ascertain specific functional or adaptive morphological characteristics and complexes.

Primate gaits have become the focus of study as new technology such as computer analyzed video equipment is available for use in the wild and in the laboratory and makes it possible to evaluate locomotor behavior (Polk et al., 2005). Thus, it has recently been shown that retaining grasping hands and feet geometrically elongates arms and legs and redistributes limb mass of quadrupedal primates which in turn reflects on locomotor efficiency (Raichlin, 2004). Comparison between primates and a tree living opossum *(Caluromys philander)* of similar body size and habitat appear to document identical locomotor mechanics (Schmitt and Lemelin, 2002). Equally small, quadrupedally-moving and leaping species of galagos are also very similar in their locomotor behavior as they are living in the same midcanopy environment (Off and Gebo, 2005). In contrast, large South American atelines have been found to have gait and climbing

characteristics that are most similar to African apes (Isler, 2003). It has also been possible to record and evaluate gait parameters of aboreal locomotion in the natural habitat of the large colobine *Rhinopithecus bieti* (Isler and Grüter, 2005). Here it has been found that the locomotion of *Rhinopithecus* is very similar to that of the atelines and gorillas. Isler (2004) discusses how locomotor performance among primates is strongly dependent on size, especially weight, body and limb proportions, and habitat use. Elsewhere it is suggested that arboreal vertical climbing of spider monkeys generally is better pre-adapted to bipedal locomotion than is the more specialized quadrupedal locomotion of macaques (Hirasaki et al., 2000). In sum, these studies show that generally speaking, primate locomotion is similar in animals with similar body size that inhabit similar environments, and that the overall generalized postcranial primate morphology is very flexible and thus, adaptable.

Trying to create an overall picture of primate locomotor activities and their morphological adaptations seems to be a rather daunting task. Most primates are quite capable to engage in many locomotor activities that are atypical for their usual locomotor behavior. With a group of animals whose morphology is comparatively unspecialized, we can expect that the scope of behavioral possibilities by far outnumbers the habitually employed activities. The overall impression of the postcranial morphology among primates with their grasping hands and feet, long limbs, and comparatively flexible trunks is that of typically unspecialized mammals. Only in those few primate groups that are truly specialized in their locomotor activities such as the leaping and clinging tarsiers, bushbabies, and indris, as well as the brachiating lesser apes, the knuckle- and fist-walking apes, and bipedal humans do we find unequivocal manifestations of these functions in uniquely specialized adaptations of the locomotor apparatus morphology. Examples for this are the elongated tarsal elements of tarsiers and bushbabies, the adaptations of the hand of knuckle walkers, the length of the forelimb and the highly mobile positioning of the shoulder girdle in the brachiating lesser apes, and last but not least, the morphological reconstruction of the hip/leg/foot complex in bipedal humans. None of these, however, keep these primates that have a comparatively derived locomotor morphology from engaging in all kinds and varieties of different locomotor activities.

Many teams of scientists are studying different aspects of primate locomotion. There is special interest in the unique human bipedal walk, its efficiency, and origin. Various sophisticated methods have been developed to investigate this and these now have also been applied to nonhuman primate locomotor behavior with particular attention to the apes. Some data collecting processes that strive to accurately establish the physical and mechanical properties of primate motion are often arduous and unfortunately destructive to the cadavers that are studied, while the final results can be seriously compromised by the innate, considerable intraspecific variability (Isler et al., 2006).

The attempt to liken the movement of legs during bipedal and quadrupedal walking to the physical paradigm of the "inverted pendulum" (Cavagna et al., 1977; Full and Koditschek, 1999) are inherently faulty: the entire leg has a joint (the knee), the inverted pendulum does not. The knee joint is never "locked" during normal bipedal and quadrupedal locomotion. The "inverted pendulum" paradigm therefore can only be applied to the movement of the lower leg proper around the pivot point of the ankle joint if the "inverted pendulum" is brought into the equation.

To sum up all that was said before, it is body size in all its representations (overall weight; forelimb and hind-limb length, weight and proportions, hand and foot morphology and mass, the mobility and length of the trunk) which is the crucial factor that ultimately determines the mode of energy efficient locomotion (Ankel, 1967; Ankel-Simons, 2000). To successfully unravel these multifaceted factors and to create comprehensive and comprehensible mechanical models of the various patterns of primate locomotor activities remains a challenge and, because of the nature of the subject, can only be an educated guess (pers. communication, V.F. Simons). This is the case because even though, within boundaries, biological kinetics follow the laws of inanimate mechanics, these laws can be compromised by the very different nature of mechanical versus biological structures. Endeavors to properly describe and understand biological phenomena with the help of strictly mathematical operations and the application of the rules of physics and mechanics can only be approximate and are not likely to ever be an exact science. Bones, muscles, tendons, ligaments, nerves, and blood vessels are very much alive and constantly compliant and will never strictly function like metal beams or plates, ball bearing joints, nuts and bolts, wheels, chains, ropes, rubber bands, or inverted pendula (Kuo et al., 2005).

There can be no doubt that the functional potential among primates is higher than their placement in different locomotor categories would suggest. In most primates the functional locomotor potential is much higher than adaptational pressures. Primates are well adapted to deal with a great variety of environmental challenges as they not only have grasping hands and feet, but also large brains and excellently capable senses such as vision and hearing which are part of being able to move about successfully.

Chapter 9

Sense Organs and Viscera

Nose and Olfaction
- Outer Nose and Rhinarium
- Nose-Based Taxonomy
- Olfaction
- The Olfactory Epithelium
- The Genetic Connection of Olfaction
- The Vomeronasal Organ
- The Genetic Connection of Pheromone Perception
- The Septal Organ of Masera
- Olfactory Messages

Oral Cavity, Tongue, and Taste
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The Large Intestine
Liver and Spleen
The Genetic Connection of Digestion
Touch
The Sensitive Skin
The Genetic Connection of Touch

In mammals (as in all other animals), bodily functions are orchestrated by the central nervous system: the brain and spinal cord. All organs are intrinsically interconnected functionally and with the brain by the peripheral nervous system. The peripheral nervous system has two functionally distinctive components: the somatic nervous system and the autonomic nervous system. The somatic, or voluntary, nervous system combines the peripheral nerve fibers with their ganglia that are connected with the skeletal muscular system. It transmits to the brain sensations and impulses that are received from external sources. The nerves of the autonomic, or involuntary, nervous system control internal, involuntary muscle activities (such as the beating of the heart), the viscera, and the glands. In the following, the sense organs and viscera are discussed in contexts that are specifically important to primates.

NOSE AND OLFACTION

Outer Nose and Rhinarium

In most mammals one finds a moist and shiny glandular area around the nostrils; this area is the so-called rhinarium. Commonly the rhinarium is not connected with the sense of olfaction or smell (*olfaction* means "sense of smell, process of smelling") and does not contain any olfactory receptor cells. The glabrous skin of the rhinarium does contain touch receptors (Merkel cells). The vomeronasal organ (VNO) that is situated in the front and on the bottom of the nasal cavity on both sides of the nasal septum, however, has a connection to the front of the mouth (see the following). If the rhinarium is in any way involved in smell perception it can only be through a connection with the vomeronasal

organ and pheromone perception. Such an association has been documented in great detail for the Opossum (Poran, 1998), for genera of the family Talpidae (moles), and for both Erinaceidae (hedgehogs) and Soricidae (shrews) (Catania, 2000, 2005). This sort of link has not been clearly established for strepsirrhines that have functional vomeronasal organs. It has been suggested that the nasopharyngeal ducts, which connect the front and base of the nasal cavity with the top and front of the mouth (through the nasopalatine duct that transits through the foramina incisiva), may provide pheromonal sensory information. A relationship of this sort has actually been verified for the strepsirrhine species *Microcebus murinus,* which has a well-developed, functional VNO and papillary nose prints on the nasal surface (Schilling, 1970). Such is likely to be the case for other primates with functional VNOs and nasopalatine ducts.

Only if the nose is brought close up to a blossom or anything else fragrant, in the attempt to precisely perceive its odor, can olfaction be called a close-up sense, and the nose a close-up sense organ. The sensitive olfactory epithelium, however, is actually located in the back and on the top of the nasal cavity, while the rhinarium around the outside of some noses does not contain any olfactory neurons.

At the middle the rhinarium in most mammals runs down to the upper lip (Figure 9.1). The rhinarium contains receptors of touch and thus functions as a

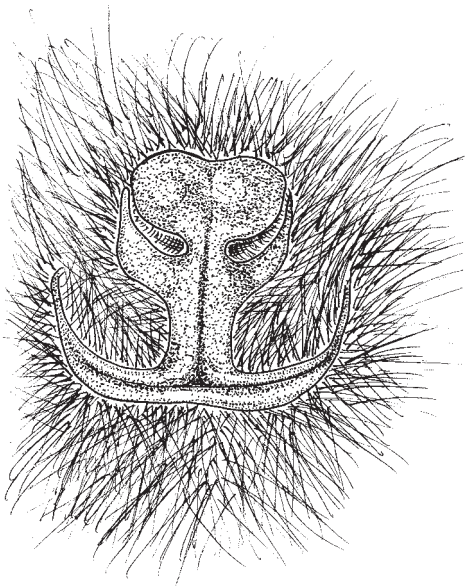

Figure 9.1 Mammalian rhinarium.

mechanoreceptor organ for close-up perception. Although the rhinarium is not involved in smell perception, while receiving close-up pheromone messages it is also sensitive to touch during sniffing (Schmidt and Wöhrmann-Repenning, 2004).

Inside and medially the upper lip is attached to the gums of the upper jaw beneath the nose, and overlaying the premaxilla, by a fold of mucous membrane, termed the philtrum. Where a philtrum is present there is usually a gap between the two inner (or first) incisors as well as the bones of the premaxillae. Such a philtrum is found among members of families Lemuridae, Indriidae, and Lorisidae (Figure 9.2). Those primates with philtrum and wet rhinarium have therefore been classified together as Strepsirrhini (Geoffroy, 1812) because of the structural similarity of these two characters in the nasal area. (*Strepho* means "turned inward" in Greek and *rhinos* is Greek for "nose.") In those primates whose snout is reduced in length and whose incisors are positioned close to each other, the

Figure 9.2 *Perodicticus potto* mother (above) and offspring (below) nuzzling. Note primate rhinarium.

rhinarium disappears. This is the case for tarsiers and anthropoids among primates, and therefore they were labeled together as Haplorhini (*haplo* means "simple, single" in Greek).

In some of the bushbabies and lorises, the rhinarium does not extend all the way to the rim of the upper lip, but its labial part is also folded inward into a deep medial groove, and outside this area is entirely covered with hair. The naked area of the rhinarium in *Galago senegalensis* and *Microcebus murinus* even has a well-developed pattern of epidermal crests—which are analogous to the ridges on the palms of hands and feet—situated below and between the nostrils (Figure 9.3). Little wartlike structures are found on the rhinarium of *Lemur, Eulemur, Nycticebus,* and *Perodicticus,* and incipient tactile ridges are found among species of *Phaner.* Biegert (1961) has interpreted these tactile ridges on the noses of *M. murinus* and *G. senegalensis* as a highly developed close-up sense organ. As neither simple rhinaria nor these nose prints contain any olfactory receptors, this interpretation is incorrect. The outer nose could only be a close-up sense organ if its perception is touch, not olfaction. However, Meissner's corpuscules that are touch receptors have not yet been documented in the nose prints of mouse lemurs (Timothy Smith, personal communication).

In the Tarsiidae and all anthropoid primates, a rhinarium is lacking or is restricted around the nostrils and remains dry. The upper lip is covered with hair, and the medial attachment to the gums in the premaxillar region has been totally

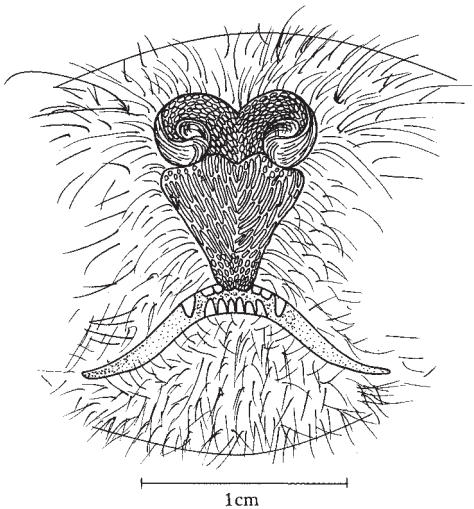

Figure 9.3 Front of the snout of *Microcebus murinus.* Rhinarium with "fingerprint" pattern (in this case it actually should be nose print pattern) that is sensitive to touch.

reduced (Maier, 1980). Thus, the upper lip is freely mobile—which is not the case in primates with a philtrum—and is supplied with musculature that participates in changes of facial expressions that Strepsirrhini are supposedly incapable of (see also Burrows and Smith, 2003). This increased mobility of the upper lip plays an important role in social interactions among higher primates (but not at all among tarsiers) and makes it possible for humans to be able to whistle.

All the Anthropoidea including the atypical genus *Tarsius*—if you wish a haplorhine as it lacks a rhinarium—(*haplo* is Greek for "simple" and *rhinos* is Greek for nose) have dry noses, a coincidence that has led some scholars to classify genus *Tarsius* and Anthropoidea together, and to contrast them to Strepsirrhini as a separate suborder Haplorhini (Pocock, 1918). This nose-based classification, however, is not necessarily very useful because there are many valid reasons to classify the aberrant prosimian *Tarsius* separately from Anthropoidea, but not necessarily with Strepsirrhini either. The outer nasal area of *Tarsius* is actually different from other living primates, as there is a crescent-shaped horny shield embracing the outside of the nasal openings. This horny crescent is also seen in the newborn aye-aye (*Daubentonia madagascariensis,* Ankel-Simons, personal observation; Figure 9.4) and should therefore be considered a primitive feature. Taking into account the many unusual characteristics of genus *Tarsius,* it perhaps rather qualifies for placement in its own infraorder Tasiiformes.

Hofer (1980) showed that the strepsirrhine condition is typically developed in marsupials and primitive eutherians. Among primates it is found in Lemuridae and Lorisidae. Hofer also documents that most individuals of *Tarsius bancanus borneanus* that he was able to examine have the strepsirrhine condition, and only one specimen approached the haplorhine configuration and was therefore transitional between the two nostril shape conditions. Hofer concluded that "Strepsirrhinism and haplorrhinism[1] are taxonomically irrelevant concepts, since it has been demonstrated that the strepsirrhine condition may occur in species regarded taxonomically as haplorrhine primates. This is true for *Tarsius* which was the classical case for haplorrhinism."

The moist glandular skin of the rhinarium that has been lost among the tarsiers and the higher primates has been thought to have been diminished because of an assumed weakened olfactory ability among these primates. The nasal passages have other functions aside from being air ducts: They perform as warming and cleaning organs for breathing and at the same time provide olfactory information at the same time.

[1]Haplorhine is spelled incorrectly haplo-rrhine, with two *r*s, in Hofer's paper. According to Greek grammar the *r* before "-rhine" following prefixes is not duplicated after a long *o* like in "haplo." It is duplicated after *a, i,* and *y* (Pape, 1888).

Figure 9.4 Face of a newborn aye-aye *(Daubentonia madagascariensis)* showing the cornified areas beside and above the nostrils (black).

The two senses of taste and smell are functionally and regionally intrinsically associated with each other, and it is difficult to consider them separately (Glaser, 2002). Considering noses, we can state that prominent facial protrusions like those of humans are not very common in other primates. Three species of colobines that live in remote areas of Asia, however, do exhibit generically characteristic, prominent noses. Two generic names for these colobines have been descriptively based on the animals' possession of impressively large noses: These genera are *Nasalis* and *Rhinopithecus*. *Nasus* (in Latin) and *rhinos* (in Greek) are both words for "nose."

Genus *Nasalis*—also commonly known as the proboscis monkey—has the largest nose found in any primate, for the male proboscis monkey even outdoes humans in this respect. In the adult male *Nasalis* the rather bulbous nose hangs down past the mouth and even beyond the chin. In females the nose is considerably smaller and slightly turned up. Whenever the male proboscis monkey becomes agitated, his nose may swell and turn reddish.

In Southern China and Western and Northern Vietnam, a species of genus *Rhinopithecus* survives in relatively remote areas. Both sexes have snub noses that are not very big. The third "nosed" genus is *Simias,* a medium-sized monkey that only inhabits some small islands off the coast of Sumatra. *Simias* monkeys

are snub-nosed like *Rhinopithecus,* but their noses, also prominent, are still somewhat smaller than those of the latter. All these enlarged primate noses have been interpreted as secondary sex characteristics. In addition, in male *Nasalis,* the nose seems to function as an organ of resonance in vocalization, rather like a trumpet. An occasional individual with a small nose can also be found among members of species belonging to genus *Colobus*. From this we can conclude that prominent noses among primates are restricted to the Old World colobines and to humans.

The nasal region of the face among gorillas is also especially interesting (Hofer, 1972). Not only is the comparatively flat nasal area large in relation to the overall size of the face, but it can also be quite conspicuous. The morphology of the nose in gorillas varies widely intraspecifically and thus can easily be used to identify individual animals. In field studies this characteristic difference of gorilla nasal areas has been proven very useful for individual identification (Schaller, 1963). The shape of the nose is also potentially characteristic for humans, within families and individually. This can be misleading, however, as modern plastic surgery provides excellent "nose jobs" that can totally rearrange the characteristics of a human profile.

Another feature of the nostrils in primates is of interest: In prosimians the nostrils are shaped by cartilage where the nose extends beyond the bony nasal skeleton. In eulemurs cartilaginous tubes extend into the tip of the nose and are positioned more or less parallel and close to each other. These tubes diverge from each other in tarsiers, and consequently, the nostrils open sideways in these animals. Another important observation is the fact that Old and New World monkeys can easily be distinguished by the position of the openings of their nostrils. The nasal openings in Old World higher primates are located close to each other and directed forward or downward, whereas in New World monkeys the nostrils are far apart, directed sideways, and separated from each other by a wide nasal septum. Actually, these differences are caused by two factors, namely the positioning of the cartilaginous wings that support the nostrils as well as the persistence of a portion belonging to the cartilaginous chondrocranium in early individual development among New World monkeys. In all higher primates the nostrils are only tubelike during early ontogeny. Later in development the space between the two nostrils is filled up on the inside with connective tissue, which is covered on the outside by a wide area of naked skin in Platyrrhini that gives this infraorder—*platyrrhine* meaning "wide, flat, or broad nosed"—its name.

Nose-Based Taxonomy

Among Old World monkeys, including humans, the nostrils are usually closely appressed medially, and the fact that they typically open downward (or forward)

is expressed in this infraorder's name: Catarrhini (*catarrhine* means "down-nosed"). The cartilaginous wings that support the sides of the nostrils are separated into two among Old World higher primates. In New World monkeys only a lateral split appears in the nasal cartilage, but it does not lead to separation into two independent cartilages. These clefted cartilaginous wings open sideways in New World monkeys and thus bring about the relative greater distance between the outer nasal openings in these primates (Wen, 1930; Maier, 1980). These differences can be easily perceived in the faces of all monkeys (Figure 9.5) and apes and is one of the reasons for the taxonomic separation of New World monkeys and Old World monkeys into Platyrrhini and Catarrhini, respectively (Hemprich, 1820). The validity of this "nose classification," however, has been widely discussed and argued against, just as the nose-related terms Strepsirrhini and Haplorhini have been criticized. Unlike the latter pair of terms, however, the categories Platyrrhini and Catarrhini have remained current ever since they were coined and are useful and obvious distinctions between the higher primates of the New World and Old World. Even if one dislikes this distinction for taxonomic reasons, these terms persist. It seems that no harm is done by this terminology either, unlike the use of the terms Strepsirrhini and Haplorhini that neither have colloquial nor taxonomic precision. Tarsiers, in their stage of evolution, do not belong with Anthropoidea—even though these two very disparate groups are often placed together under the term Haplorhini. This taxonomic assignment was established principally on account of nasal characteristics that are superficially

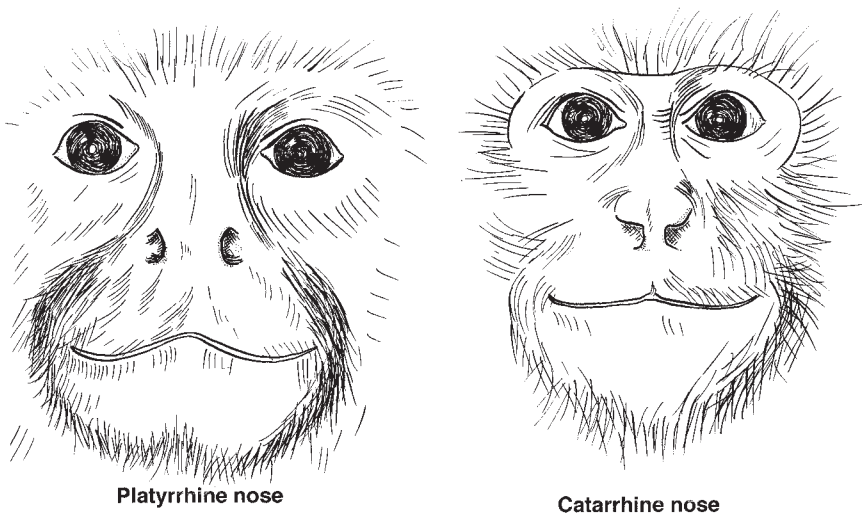

Figure 9.5 Platyrrhine nostrils separated widely by nasal septum (left) and catarrhine nostrils close to each other, separated by a narrow septum (right).

similar in both. The two groups seem to share a few other morphological characteristics that, even though they appear to be similar, presumably do not mean anything if one considers the fact that tarsiers are the most divergent group of living primates, both morphologically and behaviorally. They are certainly not nearly as derived as any anthropoid and are very unlike them. In contrast, Platyrrhini and Catarrhini are two large and varied groups of primates that are geographically separate and taxonomically compatible within themselves, because each is quite homogenous in evolutionary development and structure.

Olfaction

There is no doubt that release and reception of multifaceted odorants are crucial vectors for chemical communication between living things (Buck, 2000; Wyatt, 2003). Two distinct chemical sensory or olfactory areas are commonly attributed to terrestrial mammals: 1) the main olfactory receptors (main olfactory epithelium [MOE]) that is located within the nasal cavity and predominantly perceives airborne, volatile odorants known as olfactants and 2) the secondary sensible receiver that is regarded as accessory and only variably present or absent in several mammalian orders (vomeronasal organ, commonly abbreviated as VNO, see below, and also known as "Jacobson's Organ"). Initially the function of these two olfactory systems were thought to be distinctively separate from each other (Berghard et al., 1996). The MOE was said to receive messages from volatile, airborne odorants, while the VNO was thought to be the receiver of nonvolatile odorants called pheromones. Pheromones (from Greek *phero,* meaning "carry" and *hormao,* meaning "to put in motion") were defined as "substances secreted to the outside of an individual and received by a second individual of the same species in which they release a specific reaction, for example, a definite behaviour or developmental process" (Karlson and Lüscher, 1959).

This first definition of the term "pheromone" has been repeatedly modified and amended, because the original definition failed to adequately incorporate the various subsequently discovered functional effects related to the VNO (Wyatt, 2003; Brennan and Keverne, 2004), which continues to add to the general perplexity surrounding the issue of mammal olfactory perception. However, we now understand much better that the alleged strictly functional separation of these two olfactory systems can no longer be accepted as correct (Baxi et al., 2006).

Initially it had been emphasized that the VNO of mammals perceives nonvolatile, water-soluble odorants that variously arise from glands and solid or liquid sources, such as, for example, glandular excretions, dung, sweat, or urine

(Berghard et al., 1996; Stowers and Marton, 2005), thus emphasizing the close-up nature of VNO function. However, the far reaching pheromones of moths, where males are attracted at distances as far as 6 miles by female pheromones, suggests that such pheromones must be "volatile" to some extent. This is the case because obviously such airborne pheromones do travel far, and their volatility depends on their molecular weight. Chemical signals greatly depend on environmental circumstances (among other factors) such as humidity and temperature that affect the molecular weight of scent marks (Wyatt, 2003).

The messages that the VNO receives are directly transmitted to an accessory olfactory bulb (AOB), which is much smaller than the main olfactory bulb (MOB). The AOB joins the paired main olfactory bulbs on their posterior dorsal surface, provided that a functional VNO is present (Keverne, 1999). The size of the AOB varies widely in primates: it is large in prosimians, variable in size but present in New World monkeys, and usually not fully if at all developed in adults of the Old World monkeys, in apes, and in humans (Meisami et al., 1998; Meisami and Bhatnagar, 1998). The AOB is actually comparatively very large in the aye-aye (Allman and Hakeem, personal communication; Stephan et al., 1982).

The MOB and the AOB not only process information from olfactory messages but also are intrinsically involved in visual perception and circadian behaviors (Mick et al., 1993; Cooper et al., 1994). It is now clear that the two olfactory systems are not strictly separate from each other in their ability to receive olfactory or pheromone messages, but that they actually overlap functionally (Martini et al., 2001; Wyatt, 2003 loc. cit. page 180). In primates the primary olfactory receptor areas (MOE) are distinctive, bilateral patches within the mucous epithelium that lines the nasal cavity including the conchae, turbinals, and sinuses (see also Chapter 5, describing the skull). Thus, the main olfactory epithelium is limited to a restricted area on top and in back of the nasal cavity within the larger epithelium that lines the entire nasal surface. The number of turbinals (or conchae) varies widely among mammals and to some extent among primates. These bony structures are part of the air conditioning system of the nasal cavity and, to a lesser degree, also may increase olfactory capabilities. It should be kept in mind that the area of olfactory epithelium (OE) on the surface of the turbinalia varies unpredictably among primates (Smith et al., 2004). An increase or decrease of these epithelial-surface-area–expanding features have been correlated with a concomitant increase or decrease of olfactory capacity.

The tupaias, Lorisidae, and Lemuridae have five *turbinalia* or *conchae nasales* (excluding *Daubentonia madagascariensis,* which has six). Five turbinals are also found in insectivores, rodents, and carnivores. Whether the higher number in the aye-aye has any functional olfactory implications is unknown. Aye-ayes

have been reported to forage for grubs within large tree branches and trunks by employing their fingers in percussion and listening, not obviously using their olfactory abilities (Erickson et al., 1998). All anthropoids, including humans and tarsiers, have only three conchae.

The paired VNO is situated on the floor and in front of the nasal cavity on each side of the nasal septum, distinctly separated from the MOE, and is encased in a ductlike structure that is cartilaginous in primates but can ossify in other mammals. There may also be a cartilaginous end plate across the cranial end of the VNO tube known as the *lamina lateralis posterior.* It separates the nasopharyngeal duct and thus creates a chamberlike recess *(recessus cupularis posterior)* that in species of genus *Eulemur* is said to be partially covered with OE. The lamina is present in most strepsirrhine primates, Galagidae, and Lorisidae (J. Rossie, personal communication) that have been examined but is not found in either anthropoids or *Tarsius.* Rossie reported that he found both the lamina transversalis posterior and the cupular recess that is created by the lamina in computed tomography (CT) scans of *Loris tardigradus.*

The olfactory receptors and taste receptors proper are the only neurons in the entire body that are able to regenerate if they are injured and that are also continuously replaced on a regular basis.

A third, additional olfactory subsystem has now been described as being involved in olfaction of mice and rats (see the following). This olfactory system, the septal organ of Masera, has not been discovered in primates; the reason for this may be that no one has actually looked for it.

It once was commonly believed that the sense of smell has little importance for primates. Even the foreshortening of the snout in higher primates—in comparison with the long snouts of strepsirrhines—has frequently been directly correlated with an assumed reduction of the sense of smell among the larger and more advanced anthropoids (Gilad et al., 2003). Theories about the reduction of olfactory abilities among humans—and to some extent the apes—being related to the length of limbs and therefore removal of the nasal area far away from the ground have been formulized (Shepherd, 2004; Aiello and Dean, 1990). The possibility that the attainment of trichromatic color vision in primates directly caused the reduction of the use of pheromone communication also has been proposed (Zhang and Webb, 2003).

It has long been stated that the VNO is reduced or absent in Old World primates while it is still functional to some extent among prosimian and New World primates. This is actually incorrect inasmuch as strepsirrhines and New World primates that have been investigated have well-developed, functional VNOs (for the case among galagos see Smith et al., 2005). Although generally reduction of the sense of smell is true for this order, if we cursorily compare primates with such animals as the dog that rely to a great extent on a much more refined sense of olfaction, higher primates do retain a sense of smell, and it

does play an important role in their life. Why else would New World marmosets and tamarins (Callitrichidae) have scent glands and engage in urine washing if they were unable to take up such smell messages and would not be capable of processing the information that is carried between individuals by olfactory dissemination?

It seems less surprising that urine marking of a territory occurs among prosimians *(Perodicticus, Microcebus, Cheirogaleus)*. Species of *Lemur, Eulemur, Hapalemur,* and *Varecia* also scent mark with scent glands, located either on their wrists, inside the elbow, on genital areas, or on the throat. The glands on the inside of the elbow joint in slow loris *(Nycticebus coucang)* produce a foul smelling exudate that is licked and spread all over young offspring, seemingly as a protectant. The little slow loris offspring are parked by their mothers after having been covered with the odoriferous exudates (Krane et al., 2003). It has been suggested that this glandular exudate is toxic, and this is indicated in the fact that bites by *Nycticebus* inflict serious reactions in humans potentially culminating in anaphylactic shock. The toxin enters the mouth during grooming activities, mixes with the saliva, and is thus introduced into bite wounds. It has also been suggested that such toxicity equally applies to the saliva of the African equivalent of Asian *Nycticebus,* the potto *(Perodicticus potto)* (Alterman, 1995). However, I have been bitten severely by an adult female potto in the company of her small offspring with no ill effects at all. I therefore doubt that potto bites are likely to be as dangerous as are the bites inflicted by slow loris.

Male *Propithecus* have scent glands on the throat and scent mark for many reasons and in various behavioral contexts (Pochron et al., 2005a, b). *Hapalemur simus* males also scent mark, and their scent glands are situated in a rather atypical place on the inside of the upper arm, right next to the armpit. Males of *Lemur catta* actually engage in "stink fights" after scent marking their tails by massaging them between the scent glands on the inside of their wrists. Subsequently, during direct confrontation, they carry their scent-marked tails erect, high above their body, to then flick them at opponent males (Jolly, 1966; Schilling, 1979). Also, areas of body skin that are covered with scent glands have been described in detail for many South American monkeys (Epple and Lorenz, 1967, summarized by Wyatt, 2003). All these strepsirrhines have comparatively lengthened snouts and nasal areas. However, the only measure of the extent of an animal's capacity in smelling is the size of the epithelium containing olfactory receptors. Within the olfactory epithelium it is the combination of the density and number of olfactory receptor cells proper, their representation in the brain, and their genetic manifestation that are crucial for the ability to function. Equally the perception of pheromones is only possible if there are the proper receptor cells with suitable connectivity in the recipient's accessory olfactory bulb (Bhatnagar and Meisami, 1998). There can be no question that even in humans

the sense of smell has retained importance. For example, we can smell when food is spoiled, which reminds us that we would be better off not eating it. Where would the vast industry promoting perfume and antiperspirant be if we could not smell with precision? A new development is the "pheromones" that can now be bought through the Internet and reputedly are powerful enhancers of pleasure in humans during sexual interaction. However, there is little or no scientific substantiation that so-called "pheromones" even exist that have any effect on human behavior. This simple conclusion is supported by the following statement: "However, no bioassay-guided study has led to the isolation of true human pheromones, despite claims appearing in popular media (e.g., Web sites) and even suggested in some peer reviewed media" (Wysocki and Preti, 2004, loc. cit. page 1204).

No matter how well such issues as the human ability to perceive pheromones have been explored, there are always new opinions that contradict others, as a well-developed VNO has purportedly been documented in adult humans (Monti-Bloch et al., 1994). However, it appears that this documentation is only based on the application of "vomeropherins" to the surface of the VNO area via multifunctional electrodes, indicating a "potentially functional VNO" receptor in humans (Chiarelli, 2001). This however does not constitute an indubitable documentation of the existence of a fully functional VNO in humans. One might be equally justified to suggest that instead the septal organ of Masera could be involved in this "pheromone perception" phenomenon (see the following).

We definitely know that adult humans and cercopithecines do not have functional VNOs with the necessary neural connectivity, and it has now been conclusively documented that there is no VNO-transmitted human pheromone perception. It is believed that any presumed "pheromone perception" that supposedly occurs in humans is mediated through the MOE and that pheromones are somehow perceived by cercopithecines that have not even a vestige of the VNO (T. Smith, personal communication; Shepherd, 2006; Spehr et al., 2006). These facts invalidate the old dogma that there is a strict separation between olfaction being mediated by the MOE and pheromones exclusively being perceived by the VNO.

It has been stressed that the practice of cooking plays an important part in our olfactory repertoire (Wrangham and Conklin-Brittain, 2003). Indeed, because the nasopharyngeal duct connects the mouth with the nasal area, the odors of food also enter the nose and reach the olfactory epithelium (Shepherd, 2004).

However, for reasons that are easy to understand, there have not been many studies undertaken that attempt to quantify the absolute degree of olfactory ability throughout the whole range of primates. It seems rather complicated to measure the information that is introduced into the olfactory region through the air or directly by sniffing. An animal would have to be asked to calibrate and qualify the degrees of their perception, a task that even for humans is difficult.

Such data that are known about the surface area of the olfactory mucous membrane within the nasal cavity are limited and only of superficial use. Comparisons of the dimensions of the olfactory epithelium area and attempts to correlate such findings with the putative capacity and ability of the olfactory epithelium to receive olfactory messages have been rather superficial. Even so, the comparative numbers that have been published for the olfactory epithelium surface area among selected mammals (Starck, 1995; Issel-Tarver and Rine, 1997; and many others) can provide an overall, approximate, but rather cursory idea of the surface dimensions that the olfactory epithelium holds in various mammals. Among domestic dogs the Dachshund breed reputedly has a 750 mm^2 area of olfactory tissue, while the considerably larger German shepherds have 1500 mm^2. The European deer's olfactory epithelium measures 900 mm^2; that of the aberrant prosimian *Tarsius bancanus* measures 39 mm^2, and the average measure for humans is 25–50 mm^2. Obviously such measures vary not only interspecifically but also intraspecifically. Starck also records the assumed numbers of olfactory receptor cells: rabbit, 10^8; deer, 3×10^8; domestic dog, 2.5×10^8; and humans, 3×10^7.

Issues pertaining to the problem of differential smelling abilities in primates have been researched and discussed in detail by Smith et al. (2004). These authors also concluded that the surface areas of olfactory tissue in various primates are not at all developmentally definite or species specific. The crucial issue is correct estimation of the number of active, properly connected olfactory neural receptors and their appropriate genetic underpinning. Apparently, among primates, during development not even the ratio between the respiratory versus the olfactory epithelium remain constant. Thus we must conclude that the overall size of the nose really has nothing to do with the ability to smell or to perceive pheromones.

It is important to understand that the epithelium within the nasal cavity is separated into morphologically distinct regions that have different substructures and therefore different functions: they are discerned as *pars respiratoria,* which functions as air conditioner and air purifier, and the much more restricted sensitive *pars olfactoria,* which is lined with the olfactory epithelium and contains neural chemoreceptors. However, there also is no relevant information that directly relates the size. Critical knowledge about the very important number of smell receptors per unit of olfactory mucous membrane in the nasal area is still very limited as to accurate assessment. It is said that the density of olfactory receptor cells in dogs is 100 times the number of such cells per square centimeter of the olfactory epithelium of humans. Again, it must be kept in mind that such number counts would tend to vary individually. Actually, the distinctiveness of the more highly developed and refined ability of dogs to smell, as compared with primates and particularly humans, has presumably been known ever since dogs have been human companions. This can easily be confirmed because of obvious behavioral

evidence that has now also been documented genetically (Issel-Tarver and Rine, 1997; Olender et al., 2004). The nature of the neural connection of the sensible olfactory epithelium with the olfactory bulb and the brain cortex is of crucial importance.

THE OLFACTORY EPITHELIUM

The main olfactory epithelium of primates is restricted to a small area of the roof in the nasal cavity (compare Figure 9.6). Only about 5% of the mucous nasal epithelium is specialized for olfactory capabilities, while the other 95% or so is "respiratory," in which small hairlike bristles clean the incoming air while the mucous membrane both moistens and warms it before it enters the trachea and lungs. The olfactory epithelium proper is located bilaterally in back of the roof of the nasal cavity (see Figure 9.6). It contains three different cell types:

1. olfactory receptor cells, which are actually neurons,
2. supporting cells, and
3. basal cells.

The olfactory receptor neurons are bipolar cells with nuclei that lie in the center of the epithelial stratum. Their axons form small nerves and merge dorsally through the cribriform plate of the ethmoid bone. These thin nerve branches combine into the olfactory nerve and merge more or less directly on either side

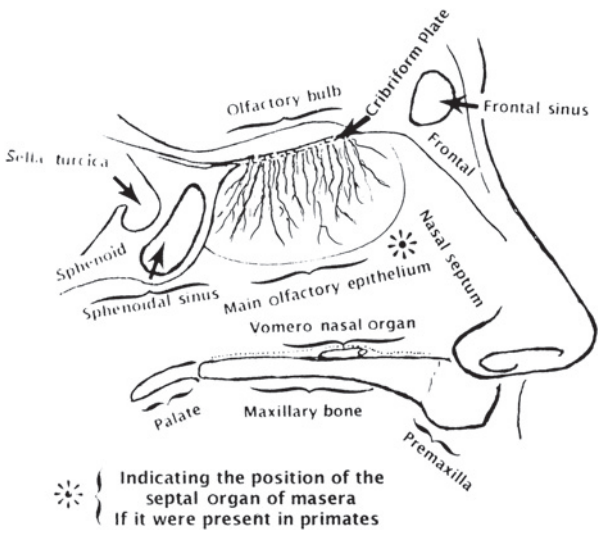

Figure 9.6 Diagram of the position of the main olfactory epithelium (MOE), the frontal sinus, the putative vomeronasal organ (VNO) that is reduced and nonfunctional in humans, and the septal organ of Masera that has not yet been discovered in, but might be present in, primates.

with the paired olfactory bulbs that are positioned on the cribriform plate. The olfactory bulbs transfer received messages through olfactory tracts directly to the cerebral cortex and to the thalamus and neocortex from where the messages are relayed (Bear et al., 2001). From the nuclei the branches of the olfactory receptors extend into the nasal cavity as immobile, neural cilia that receive olfactory messages. These cilia are embedded in mucosa. The receptor cells are interspersed by sustentacular (supporting) cells and the ducts of the large serous glands of Bowman that lie, together with basal cells and venous plexuses, within the *lamina propria* situated directly under the cribriform plate. The glands of Bowman provides the continuous stream of mucus that surrounds the cilia, and it functions by dissolving incoming odorants. The mucus is water based and is constantly exuded.

Olfactory receptor cells are primary receptor cells, in contrast to the taste receptor cells, which are secondary receptor cells. Olfactory receptor cells and taste receptor cells are the only neurons in the entire nervous system that are regularly replaced. Their life span is said to last between 10 days and about 4 to 8 weeks in mammals (Bear et al., 2001). In nonhuman animals receptor cells appear to have a life span of up to 1 year (Hinds et al., 1984). In humans these neuroreceptors are said to be replaced on a regular basis after about 40 days of becoming active, a process that slows down with increasing age. Information concerning the life expectancy of such receptor cells varies widely. It has been surmised that their life span is directly proportional with the intensity of their usage, with heavy use shortening their viability (Glaser, personal communication).

An interesting issue is the fact that the bilateral patches of olfactory epithelium are distinctly colored yellow. It appears that albino animals do not have any pigmentation in this area and have been found also to lack any sense of smell. This implies that the coloration of the olfactory epithelium is somehow related to its function. The neurotransmitter Acetylcholine is likely to be involved in this yellow coloration of both the olfactory epithelium and the macula lutea of the eye (see also page 455).

The Genetic Connection of Olfaction

In 1991 Buck and Axel discovered genes that read proteins that are only found within the olfactory epithelium. Their most astonishing discovery was that there are a surprising number of up to 1000 separate olfactory receptor proteins (ORs) on the olfactory neurons, which are equivalent to related genes. These findings appear to apply to the majority of mammals, including primates and humans. However, a variable fraction of these genes are pseudogenes in the different taxa and are therefore nonfunctional. Thus mammals are able to perceive and distinguish a vast but highly variable number of odorants (Buck, 2000). The OR gene family consists of approximately 1000 genes (or 1% of the human genome)

that is capable of perceiving uncountable odors. It appears that olfactory genes are expressed on olfactory neurons strictly in a one to one relationship (Buck, 2000). Malnic et al. (2004) identified 339 intact OR genes and 297 pseudogenes—a total of 636—in the human genome database. This means that the human OR gene family has many more nonfunctional pseudogenes than the OR gene family of mice or dogs, indicating different selection pressures on olfaction in humans. However, functionally it still appears that humans are able to recognize as many as 10,000 different odors (Shepherd, 2004).

All these human OR genes are found in 51 different locations on 21 of the 23 chromosomes; only chromosome 20 and the Y chromosome appear to lack any OR genes. A total of 172 human OR subfamilies were identified, illustrating the wide range of the capacity of human olfactory perception. It is now believed that in humans about 56% of OR genes are nonfunctional, while dogs and mice have only about 20% nonfunctional OR genes. Thus the latter animals have three times as many functional OR genes than humans. It has also been shown that the great apes *(Pan, Gorilla,* and *Pongo)* as well as rhesus macaques *(Macaca mulatta)* have considerably fewer nonfunctional OR genes than humans (Gilad et al., 2003, 2005). If these are compared to the full complement of OR genes in mice it appears that humans and apes have the highest number of nonfunctional OR pseudogenes among primates at an average of 50% (between 39% and 70%). Old World monkeys that have been tested (macaques and baboons) have an average of 27% OR pseudogenes (between 20% and 35%), while only one pseudogene was found in New World marmosets and squirrel monkeys, and lemurs have as many as 37% (Rouquier et al., 2000). Looking at these numbers among members of various primate groups, the percentage of pseudogenes and the expected degree of olfactory abilities among primates does not seem to follow any putative "evolutionary" line. Therefore it is difficult to understand why these authors make the following concluding statement: "Finally we hypothesize that the study of the evolution of the OR gene repertoire through the determination of pseudogene fraction could mirror the evolution of the olfactory sensory function in microsmatic and macrosmatic mammals" (loc. cit. page 2874).

As a new beginning in the exploration of nonhuman primate olfaction, Glaser et al. (1995) published for the first time olfactory perception thresholds among pygmy marmosets *(Cebuella pygmaea)* for vanillin with the use of a computerized olfactometer. These "vanillin" results in the pygmy marmosets have been compared to the vanillin sensitivity in humans. Identical equipment and experimental procedures were used. Also, identical methods of data analysis were applied in the comparisons between marmosets and humans. In consequence it is acceptable to compare the threshold values of both. The data obtained in humans and *Cebuella* support the proposal by Adrian (1956), Moulton et al. (1960), and Laing (1975) "that there is no significant difference in the ability of different vertebrates to detect novel odorants" (Glaser, 2002 loc. cit. page 137).

However, the similar sensitivity in these two disparate primates applies only to the odorant vanillin and species difference between them could still be very large for other odorants.

The olfactory sensitivities of four adult female spider monkeys, *Ateles geoffroyi,* and three male and one female adult pigtail macaques, *Macaca nemestrina,* have been tested for sensitivity to several carboxylic acids (Laska et al., 2004, 2006). The results were unexpected since both the Old and New World monkey species turned out to be almost equally capable of recognizing odorants presented, and both were about the same or even better than the rat or dog. Hence these results show that neither comparison of the numbers of functional OR genes nor contrast of the neuroanatomical features between species are useful to foretell olfactory capability (Laska et al., 2004). Molecules known as "enantiomeres have previously been used in various biological testing situations, with taste perception being one of them. Enantiomers are mirror symmetric odor molecules: with the help of these molecules it has been possible to document that odor perception depends on molecular shape of the odorants" (Buck and Axel, 1991; Rubin and Katz, 2001 loc. cit. page 355). These volatile optical isomers have previously been shown to be of different odor quality and intensity for humans who are tested with them. Therefore, enantiomere odorants have been applied to comparatively test one species of Old World monkey *(Macaca nemestrina)* and one species of New World monkey *(Saimiri sciureus)*, and both were compared with data from human subjects. Again these results were inconclusive (Laska et al., 2005). Because of morphological and genetic olfactory differences between the test groups, one would have predicted that the two nonhuman primates and the humans should be very different in their ability to perceive the enantiomers, but they were not. The conclusions from these experiments as offered by the authors are that neither the olfactory brain structures nor the number of olfactory receptor genes appeared to be reliable predictors of olfactory discrimination ability among these various primates (Laska et al., 2005). However, could it not be possible that the complex biochemical theory, on which the methodology of the tests was based, was ill conceived? It seems that these various unexpected test results should be received with caution.

The Vomeronasal Organ

Unfortunately the nomenclature applied to pheromone receptor genes is inconsistent among groups of researchers (TRP Nomenclature Committee White et al., 1997; Montell et al., 2002). This obviously muddles the possibility of having a clear understanding of pheromone-related genetics.

The vomeronasal organ does somehow function as a chemical sense organ in vertebrates and is thought to be involved in the perception of hormonal changes in the urine of female mammals during the sexual cycle (Estes, 1972). However,

according to Starck (1995, vol. I, page 120) it has never been possible to unequivocally document that the vomeronasal organ does indeed have this capacity. One reason for the ambiguity regarding whether the VNO has this function is predominantly based on the following findings. When the VNO was excised in very young mice, the lack of it did not make any difference in the animals' mating behavior when mature in comparison with mice whose VNOs were intact (Pankevich et al., 2004). Currently the role of the vomeronasal organ among primates has only been studied in random species and therefore its purpose remains rather obscure. The question whether this hard to identify organ of olfaction is even present and functional in humans (Johnson et al., 1985; Witt and Wozniak, 2006) is still under dispute. Presently the scale seems to be tipping toward a negative answer to this puzzle.

Nevertheless, in the context of reviewing the sense of smell, the bilateral vomeronasal or Jacobson's organ is widely discussed in textbooks. For primates the name "Jacobson's organ" is actually somewhat inappropriate, as the "vomeronasal organ" was originally described by Jacobson for nonhuman mammals in general, not for humans or primates. For a detailed report on the history of the discovery of the VNO see Bertmar, 1981; Bhatnagar and Smith (2003); Trotier et al. (2000); and Witt and Wozniak (2006). For our purposes we will refer to the organ as the vomeronasal organ or VNO.

Where fully developed the VNO is a paired, tubular structure that is hidden in front on the floor of the nasal cavity. The two tubes lie next to the nasal septum and thus next to the vomer. The tubes end blind to the back and throughout have an epithelial lining. They are hidden under the nasal membrane, encased in a cartilaginous or osseous compartment. If the VNO is enclosed by nothing but cartilage it is not likely to be fossilized and could not be of use for investigative exploration of possible past olfactory abilities. The lumen is lined with a crescent-shaped olfactory membrane that contains neural receptors. It is filled with fluid that is produced by vomeronasal glands and has a small rostral opening into the nasal cavity. Blood vessels and nerve endings surround the cavity, and these function in a pumping action to flush matter through the small opening into the lumen (Keverne, 1999). Also in front are small connections that lead to the mouth. It is said that these paired nasopalatine ducts (known as *foramina incisiva*), seen in the front of the palate in skulls and which open medially at the front of the roof of the mouth in mammals, are significantly involved in smell perception. Here the VNO canals penetrate through these foramina in cases where a functional VNO is present, for example in rodents, thereby transmitting olfactory messages from the oral cavity to the nasal cavity (Shimp et al., 2003). The VNO is clearly separated from the air stream that passes through the nasal cavity. The epithelial lining of the organ not only contains neural receptor cells but also supporting and basal cells. The receptor neurons lack the cilia that are characteristic for the neuroreceptors in the MOE but have microvilli extending into the lumen of the VNO. The microvilli extend neural axons that merge into vomeronasal nerves. These thin nerves run

between the MOBs and merge into the AOBs that are positioned on the rostral and dorsal aspect of the MOB. Because of the VNO's importance among mammals this olfactory bulb should, however, more appropriately be called a vomeronasal bulb (Døving and Trotier, 1998). From this point the messages are relayed to the amygdala, the part of the temporal lobe that is, among other responses, involved in perception of emotions. From here the messages received from the VNO are transferred to the hypothalamus, where metabolic and various autonomic functions are processed. The neural messages from the VNO thus take a distinctly different pathway to the neural processing area than the messages from the main olfactory epithelium (Bhatnagar and Meisami, 1998; Keverne, 1999).

Among primates a VNO is found in all prosimians, including *Tarsius* (Starck, 1975; Smith et al., 2003b) (Figure 9.7) as well as in New World monkeys, but may not be developed in Old World monkeys. The VNO is likely to be atypical and not functioning in the perception of pheromones in chimpanzees and humans

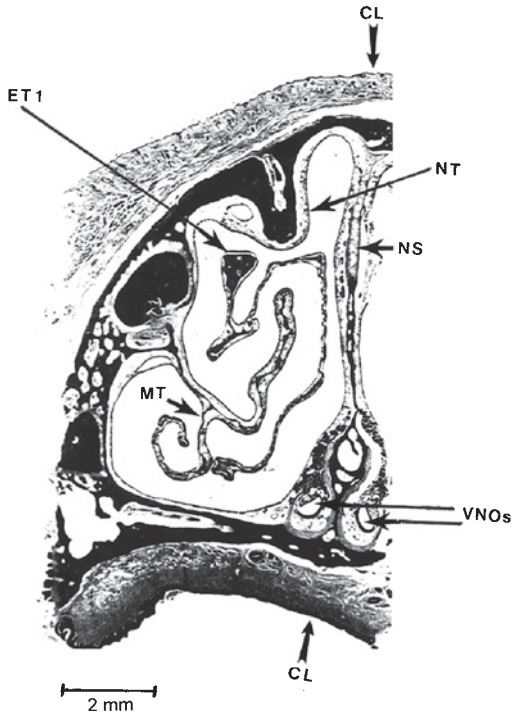

Figure 9.7 Coronal section through the snout of *Galago (Otolemur) garnetti,* showing both well-developed vomeronasal organs (VNOs) and the sensory VNO epithelium (the black lines in the VNOs). CL = Center line of snout, slightly bent; ET 1 = ethmoturbinal 1; NS = cartilaginous nasal septum; NT = nasoturbinal; MT = maxilloturbinal. Original photo courtesy of Timothy Smith, adapted for publication here.

(Smith et al., 2001a, b). The fact that human and chimpanzee embryos develop a VNO appears to have been undisputedly documented (Smith and Bhatnagar, 2000; Meredith, 2001; Smith et al., 2002; Witt and Wozniak, 2006). Furthermore, even though a vestigial vomeronasal pit can be ascertained in adults of both genera, there are no neural receptors connected, and these vestiges are thought to be nonfunctional after birth. These structures are present in these hominoids, but whether the embryonic VNO is functional before birth and if the "pits" should function in adult life is not known. Whether the remnant "pit" has any other function, such as a secretion, is also uncertain. An intriguing question arises as to why some prenatal humans have well-developed VNOs that only become vestigial after birth. Could these organs, for some unknown reason, be crucial during early development before they disappear after birth and obviously when usefulness is lost? Or are they somewhat similar to the appendix and our wisdom teeth, little more than evolutionary relics? This issue has not yet been clarified (Moran et al., 1995; Meredith, 2001; Dennis et al., 2004). However, it seems very likely that the prenatal VNOs of humans and chimpanzees do not have any function and are nothing but vestiges (Martínez-Marcos, 2001). The vomeronasal organ could only be truly functional in pheromone perception if it had the appropriate nervous connections, which appear to be absent in adult humans.

The VNO of most adult lemurids and lorisids is well developed and links up between the nasal cavity and the front of the mouth by way of the nasopalatine duct through the *foramina incisiva* (located in the premaxilla). The nasopalatine ducts are well developed in the prosimian *Arctocebus calabarensis* and two reported South American monkey species, *Aotus trivirgatus* and *Saguinus fuscicollis,* while they are not found in species of *Atele*s (Hunter et al., 1984). *Tarsius* has both a VNO and nasopalatine ducts (Smith et al., 2003b).

Most New World monkeys appear to have fully developed VNOs. Again, the howler monkey *(Alouatta)* is of interest as it not only has functional trichromatic color vision, unlike any other platyrrhine, but still has a VNO and consequently the ability to perceive pheromones, thus documenting that the two senses are not necessarily mutually exclusive in an evolutionary setting and that full trichromacy does not necessarily account for loss of pheromone detection.

The Genetic Connection of Pheromone Perception

Pheromones are thought to be mainly received by sensory neurons in the VNO. The messages received there are mainly of sensory nature and are relayed through the accessory olfactory bulb and from there on to the medial amygdala and hypothalamus of the brain.

In contrast to the high number of OR genes, the vomeronasal organ has only two different receptor families: V1Rs and V2Rs (Buck, 2000). Buck speculated (loc. cit. page 612) "that the different receptor families are uniquely suited to the

distinct functions they presumably subserve: the perceptual discrimination of a multitude of volatile chemicals versus the generation of programmed endocrine and behavioral responses to pheromones." It appears that "pheromones" and their function are still shrouded in mystery (Stowers and Marton, 2005). These authors state "that the family of pheromone molecules and their mechanism of action is far more diverse than previously thought. Consequently the working definition of pheromones is now in flux" (loc. cit. page 702).

The amount of research that has been devoted in exploring the question of whether humans actively perceive pheromones is vast. When in the seventies and eighties it was claimed that the onset of the menstrual period among human females is synchronized by hormonal, hence "pheromonal" responses, this elicited much controversy, but the theory is by now effectively invalidated (Strassman, 1999; Wysocki and Preti, 2004). Wysoki and Preti conclude their recent work with the observation that any plausible neuroreceptor for pheromones is most likely to reside in the MOE, and as the VNO in adult humans is vestigial at best, one can conclude that it is not likely to be functional.

Even as there may or may not be some vague evidence that chemical communication among humans does exist, there is no demonstrable evidence for the existence of any actual human pheromones (Meredith, 2001). Furthermore, all V1R-like sequences such as are involved in pheromone recognition among rodents are nonfunctional pseudogenes in humans (Giorgi et al., 2000).

It is now clear that the genes that permit pheromone recognition are the clues to understanding the ability of mammals to receive pheromone messages. A putative pheromone receptor gene has been reported in humans that is thought to be expressed in the main olfactory mucosa (Rodriguez et al., 2000; Rodriguez and Mombaerts, 2002). However, in 2001 Kouros-Mehr et al. had confirmed that in humans 95% of all VR1 genes are nonfunctional and that it is thus very credible that the human VNO is vestigal. The finding by Rodriguez and Mombaerts has also been questioned by other scientists who only found pseudogenes in marmosets, a New World monkey group that, in adulthood, does have a functional VNO. The authors suggest that the methodology of searching for functional pheromone genes by comparing such genes that are functional in rodents with primate DNA might be inconclusive and that marmosets *(Callithrix jacchus)* could have their own, as yet unrecognized, set of functional pheromone receptor genes (Giorgi and Rouquier, 2002).

Another study addressing this issue with the help of transient receptor potential (TRP) channels is used to decipher pheromone reception. TRP is a multifunctional protein that functions as a cation channel as well as a protein vector (Voets and Nilius, 2003; Ramsey et al., 2005). Cation channels are supposed to perceive sensory stimuli (Montell, 2005).

Liman and Innan (2003 loc. cit. page 3332) observe, "It is interesting to note that, although NW monkeys show prominent scent marking behavior, it has not

been demonstrated that this form of chemical communication acts through the VNO or that it serves a unique function." This statement is based on the observation that the fundamental locus for pheromone detection, TRPC2, that has been demonstrated to have this function in mice, is thought to be a pseudogene in humans. These authors state that MOE and VNO sensory neurons are strikingly different in the way they transfer olfactory information. However, these authors admonish us that understanding of the mechanism involved is not complete. TRPC2 is reported to be a crucial messaging compound that transmits sensory signals that are received by VNO pheromone-sensitive microvilli (Liman et al., 1999).

Later Liman and Innan (2003, page 3332) observe: "Our data suggest that, in NW monkeys, signaling through the VNO may, if present, be redundant, leading to relaxation of selection on all signaling components within the VNO." One has to wonder why, then, the New World monkeys have rather well-developed VNOs. According to Liman and Innan (2003) it appears that two species of lemurs, *Varecia variegata,* the black and white ruffed lemur, and *Lemur catta,* the ring-tailed lemur, do have the active TRPC2 locus, an observation that they extend to imply that this gene has been retained in all prosimians (loc. cit. page 3331). This subject becomes somewhat confusing as far as the New World monkeys are concerned. It is suggested that among platyrrhines the TRPC2 gene function and with it the usefulness of the VNO pheromone detection is on the evolutionary way out. We find the following statement (loc. cit. page 3332): "It is interesting to note that, although NW monkeys show prominent scent marking behavior, it has not been demonstrated that this form of chemical communication acts through the VNO or that it serves a unique function." This conclusion appears to be based on the finding that the marmoset *Callithrix jacchus,* though it has a functional VNO and demonstrates pheromone-induced behavior, has been shown to have only pseudogenes among the known pheromone-sensing receptor genes (Giorgi and Rouquier, 2002). In contrast to the conclusion by Limman and Innan (2003), Giorgi and Rouquier (2002) suggest that mammals that have functional VNOs and rely on pheromone-mediated sensing have their own set of vomeronasal genes.

We must conclude that our knowledge about the genetic foundation for olfactory activity is still rather imperfect, and thus speculation is unbridled among scientists (Montell, 2005). This point is also shown by the fact that a gene that encodes the VNO pheromone sensitivity (TRP2) is functional in howlers, while it is not in Old World monkeys, in which it is a pseudogene (Webb et al., 2004). These authors also introduce behavioral and anatomical data for *Alouatta* in support of their genetic findings and in support of the fact that the VNO is functional.

In contrast to the reports of Webb et al. (2004), another group of researchers came to the exact opposite conclusion (Gilad et al., 2004) studying the regular

OR genes. These authors base their conclusion on the finding (loc. cit. page 120) "that a decrease in size of the intact olfactory repertoire occurred independently in two evolutionary lineages: in the ancestor of OWMs and apes, and in the New World howler monkey." It is speculated that a high proportion of OR pseudogenes, which they found in Old World monkeys and the New World monkey *Alouatta,* indicates a decline of reliance on the sense of smell that must be correlated with the acquisition of trichromatic vision. Even though the latter authors agree that the TRP2 gene, which is an important factor in pheromone recognition (loc. cit. page 123), "was found to be intact in several New World monkey species but is a pseudogene in Old World monkeys and apes." They report further that this indicates that an intact TRP2 gene also found in howlers is inconsistent with the hypothesis that trichromacy replaced pheromone perception in primates. In spite of all this, they still conclude (loc. cit. page 123) "that although at this point we are unable to demonstrate that the decline in the sense of smell is a direct result of the evolution of color vision, our results strongly suggest an exchange in the importance of these two senses in primate evolution."

A study of some primate pheromone receptor genes in selected Old World monkeys, gibbons, the great apes, and humans has been carried out (Mundy and Cook, 2003). While humans, the gorilla *(Gorilla gorilla)*, three species of howler monkey *(Alouatta palliata, A. sara, and A. seniculus),* and the pygmy marmoset *(Cebuella pygmaea)* have been found to have functional V1RL1 genes,[2] in the remaining eight species that have been sequenced for this gene it is said to be a pseudogene (these species are *Pongo pygmaeus, Pan troglodytes, Cebus albifrons, Aotus* spe., *Callimico goeldii, Leontopithecus chrysomelas, Saguinus fuscicollis,* and *Callithrix jacchus*). The authors' conclusion is that "reconstruction of V1RL1 pseudogene formation over the independently established primate phylogeny suggests that it occurred independently several times during anthropoid evolution, in terminal lineages" (Mundy and Cook, 2003, loc. cit. page 1807).

We can only conclude that pseudogene evolution and the development of the VNO occurs in a rather random fashion among living primates, and investigation of the function of the VNO among primates is still in its infancy. Unfortunately, knowledge about pheromone perception and its genetic programming in primates is still very speculative.

The Septal Organ of Masera

The function of the septal organ of Masera, an additional region of possible olfaction, was recently explored in rats (Ma et al., 2003; Weiler and Farbman, 2003; Breer et al., 2005; Witt and Wozniak, 2006). This "organ" may or may

[2]Despite the 2002 (Montell et al.) revision of the vomeronasal receptor-like genes nomenclature, the assigning of V1R or V1RL1 for such genes is yet another, different identifier.

not be present in primates and could, if it indeed can be demonstrated to be present, potentially play an as yet unrecognized role in the overall ability of mammals, including primates, to perceive odorants and pheromones. The septal organ of Masera was originally observed in neonate mice by German scientist Broman (1920), who named it "Riech Epithel Insel" (island of olfactory epithelium), but this was only described in detail by Rodolfo-Masera in 1943. This organ may explain the potential ability to perceive volatile and nonvolatile olfactory cues that have not been reliably related to the function of the MOE and VNO, either separately or together. However, the septal organ's function and neurogenetic involvement in odor recognition have not yet been widely explored, and, as mentioned, it is not yet known to be present in primates (see Figure 9.6).

Olfactory Messages

Glandular areas are used in scent marking, an activity that requires a high degree of olfactory perception by the animal species. As already stated, if we compare primates with relatively large-bodied mammals like dogs or wolves, the sense of smell seems less important than it is among these Canids. However, it is known that among higher primates at least the New World monkeys use scent marking to a considerable degree within the framework of sexual, aggressive, and territorial behaviors. One group of scientists working in South America reported that recognizing and getting close to groups of *Alouatta seniculus* (red howler monkeys) was obvious because of their specific strong odor, which could be detected before the animals were actually seen (Collias and Southwick, 1952). We now know that howler monkeys not only have perfect trichromatic vision but also an ability to perceive pheromones and olfactants. To pitch the sense of olfaction against trichromatic vision into a causative relationship, namely that one improves while the other diminishes, has no clear basis. These two events are not proportionally correlated, nor do they incontrovertibly contribute to each other. It seems that, even though the senses of vision and olfaction of primates work together, they develop independently.

It is a widespread mantra among primate biologists that there is a decrease in the importance of olfaction within the order Primates beginning from a Cretaceous "smell-oriented" ancestor, and this decline has often been assumed to have been correlated with increasingly more advanced levels of organization, especially relating to the senses of vision and touch.

This generalization about a progressive decline in the sense of smell has typically been coupled with a similarly theoretical assumption about a general reduction of the sense of taste among primates. These traditional generalizations about reduction through time have also been based on the superficial observation that the number of nasal turbinal bones and associated conchae is now reduced

in primates as compared with other mammals. The reduction of the number of turbinals has been equated to an assumed concomitant reduction in the level of smelling and tasting abilities. However, such a trend can only be properly understood if it is assessed as a part of the overall changes that occur through time in the evolution of the primate skull. As already stated, only the absolute number of receptors of the olfactory nerve *(bulbus olfactorius)* per surface area of the nasal olfactory epithelium are relevant for the assessment of the olfactory capabilities of any particular animal species. The *nervus olfactorius*—or olfactory nerve—is usually regarded as a part of the brain itself and not as a peripheral nervous ganglion. This is so because of the more or less direct connection between the olfactory epithelium and the MOB. As we have seen, the size of the surface area of the nasal mucous membrane does not necessarily give information about the olfactory ability of an animal. However, Napier and Napier (1967) distinguished between primates with an "olfactory" muzzle, which they consider a characteristic for "certain Lemuridae and Lorisidae," and a "dental" muzzle, which in their view describes certain ground living Cercopithecidae such as baboons, as well as the great apes because of their enlarged masticatory apparatus. As we have seen, this kind of assignment can no longer be upheld. Napier and Napier did not really distinguish between the functional qualities of an "olfactory" muzzle in contrast to a "dental" muzzle. These two factors, olfaction and mastication, do not affect the size of a primate muzzle independently. They are correlated to other developmental, evolutionary, morphological, or functional forces.

As far as the role of the sense of smell among primates is concerned we may conclude with a slight modification of Hamlet's exclamation: "There are more things in nose and snout, Horatio, than are dreamt of in your philosophy."

ORAL CAVITY, TONGUE, AND TASTE

THE PALATE

The palate is mechanically involved in the action of food intake and food processing. The bony palate separates the nasal cavity from the mouth. The top of the oral cavity in primates is characterized by differently structured palatal cross-ridges *(rugae palatinae)* between the tooth rows. These palatine ridges—structures of the hard palate and the mucous membrane—are found in all mammals except the whales (Odontoceti, toothed whales). Such ridges are of mechanical help in holding and transporting food items within the oral cavity between the tongue, teeth, and palate and even aid to some extent in the mechanics of processing and reducing food particles. Palatine ridges appear early in ontogeny and do not change their overall shape later on (Schultz, 1958). Rugae are well

developed in all prosimian primates, usually occurring in numbers as high as seven to eight in lemurs and as low as five to six in Lorisidae. In *Tarsius,* even though this animal has a very short snout, there may be as many as ten to eleven rugae. Anthropoidea have about four to nine, Callitrichidae have four to six, and humans zero to four rugae. Number and arrangement of these ridges are individually quite variable. It is typical of prosimians that these ridges cover the hard palate backward to the end of the last molars. In higher primates the ridges usually do not extend as far back and are often of irregular patterns (unlike those in prosimians). Within Hominoidea these ridges are perhaps the most reduced and irregular. In humans, usually only four comparatively shallow ridges, if any, cover the palate in the area between premolars and canines, meaning that they are only developed in the very front of the mouth.

The Tongue

Both the hard palate and the tongue are also intricately involved in the process of noise production and the human ability to speak. Primate tongues are not very different from the tongues of other mammals. The tongue (Latin *lingua;* Greek *glossa*) has a variety of differing functions. In addition to helping with intake and positioning of food items within the mouth and between the upper and lower teeth, this structure participates in vocalization; the ability to speak in humans (the Latin name for the tongue, *lingua,* means also "language"); and its main function, testing and tasting of food and drink. The tongue is also involved in cleaning the mouth and teeth and in some primates in visual signaling: some callitrichidae flicker their tongues at conspecifics.

A map of the tongue indicating delineation and distinctive distribution of the individual areas of taste reception applying to the four taste qualities sweet, salty, bitter, and sour is still found in textbooks and publications (Figure 9.8A). This "taste map" was originally published by Hänig (1901), who describes a taste belt around the edge of the tongue and observes that the center lacks any taste receptors. Actually, taste receptors are found all over the tongue's surface. Hänig did, however, correctly suspect that these specific taste areas, which he assigned to the four taste qualities (e.g., sweet receptors on the tip of the tongue) that were recognized at the time, functionally overlap each other. However, it increasingly becomes clear that this characteristic taste receptor map is incorrect.

Humans have about 2000 taste buds in the mouth at any one time (although this number varies individually), and each taste bud contains about 50 cells. Some of these cells are involved in taste perception, and single receptor cells have a life span or functional activity period of about 4–5 hours in humans. Thus, in reality, the number of taste receptors varies continuously throughout the human lifetime and appears to be successively reduced as humans age. It has also been reported that taste receptor cells differ in topographical origin, in their shape and

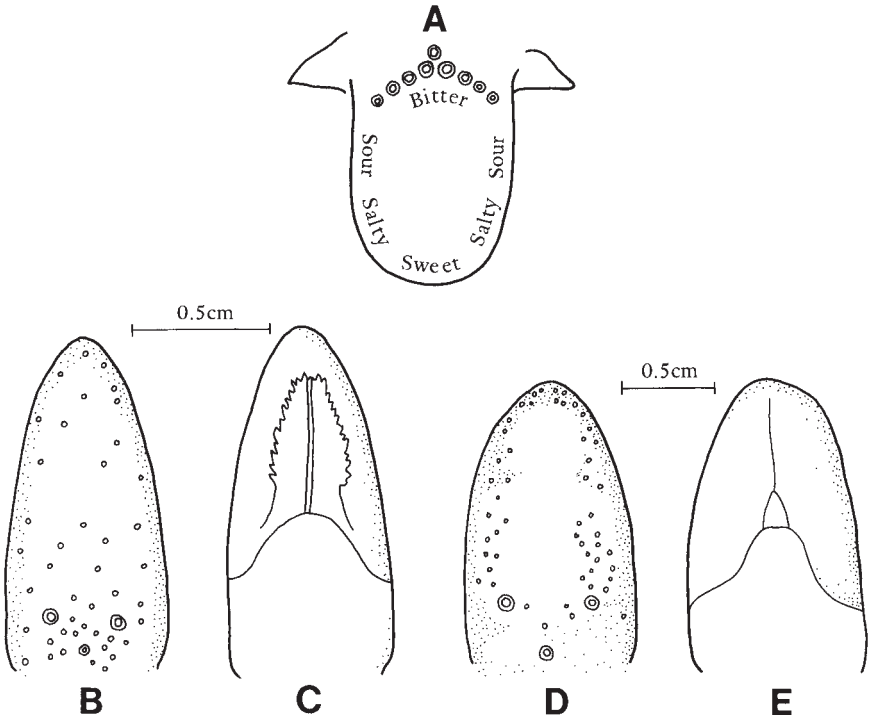

Figure 9.8 A) Surface of tongue indicating areas of sensitivity to the four basic taste qualities: bitter, sweet, salty, and sour. B) Upper aspect of prosimian tongue showing taste buds (ring-shaped *vallate papillae*). C) Underside of prosimian tongue showing serrated independent sublingua. D) Upper side of callithrichid tongue. E) Underside of callithrichid tongue showing small, reduced sublingual structure.

age and presumably also in their function throughout their individual lifetime (Stone, et al., 2002; Finger, 2005; Harada and Kanemaru, 2005). However, even though the various cells appear to represent several distinctive types, it is possible that these types in fact may represent various developmental stages of a single cell category.

Age-related changes in the combination of the different kinds and numbers of taste buds and their relationship to the gustatory ability have been investigated in the New World common marmoset *Callithrix jacchus.* Similar to humans, the number of taste buds increased from birth until 2 months of age, when a decrease of active taste buds sets in. It has been suggested that these numbers might vary individually, and it has been implied that the change of the number of taste buds is accompanied by an alteration in taste sensitivity (Yamaguchi et al., 2001). Because taste stimuli differ greatly in chemical substance, molecular size,

lipophilicity (attraction to fat), and pH, there are a variety of neural mechanisms in place to read and evaluate taste stimuli. Taste receptor proteins are received by two unrelated protein receptor families: T1R and T2R. T1R initially was believed to be broadly tuned to sweet and umami flavor recognition, while T2R receptors were believed to receive bitter-tasting compounds (Kinnamon, 2000). Umami, however, is not a specific flavor comparable to sweet, sour, salty, and bitter but is very changeable according to the flavor to which it is added. Also it now has been proposed that specific taste reception is not restricted to particular taste buds, but that these receptors cooperate with each other. The fact that the taste qualities salty and sour are recognized along signaling pathways that clearly differ from the recognition of sweet, bitter, and umami stimuli indicates that multiple receptors are co-expressed in the same subset of receptor cells (Adler et al., 2000; Zhang et al., 2003). "Umami" has now actually been recognized as the taste of protein that uses synergism, thus enhancing the effect of various distinct taste qualities (de Araujo et al., 2003).

The principal taste receptors of primates are located on the tongue, but some are also found on the soft palate and the epiglottis. On the surface the tongue is covered with numerous papillae that give it a rough surface. This surface structure is important for the transport and sensory exploration of the texture and size of food items. Normally, the papillae can be divided into four types that are shaped differently and also have been thought to perform different functions.

Filiform papillae: The majority of papillae are small and usually end in a few points or filamentous processes that give them their name: filiform papillae. Such filiform (*filum* being the Latin name for "thread") papillae have a brush-like texture, cover most of the mucous surface of the tongue, and function as mechanical structures. They are well equipped for transportation and holding of food particles and do not contain taste buds.

Fungiform papillae: Less numerous and larger are the fungiform papillae (*fungus* being the Latin name for "mushroom"). These are so named because they are shaped like mushrooms, having a stalk expanding toward their tops. Each fungiform papilla contains a capillary loop. The fungiform papillae are concentrated at the tip of the tongue and on its sides; they contain taste buds.

Foliate papillae: These structures are situated around the edge of the tongue. There are about five such papillae on each side of the tongue.

Circumallate Papillae: The majority of taste buds are located on the largest type of papilla, the vallate papillae. The term "vallate papillae" describes papillae that are shaped like a truncated cone. The largest diameter of the cone points up and away from the tongue, and the smallest diameter is at the attachment of such cones. The buds are surrounded by a circular tissue wall. Papilla and wall are separated by a furrow or duplication of the epithelium.

Especially on the wall but also within the furrow exists a high concentration of taste buds. The vallate papillae are located on top of the tongue base; their number varies between eight and twelve in modern humans. Taste buds are also scattered over the sides and the back of the tongue and adjacent parts of the mouth and palate.

Primates of small body size usually have only three of the vallate papillae on the base of the tongue, and they are arranged in a triangle. It is reported that the number of vallate papillae varies according to absolute size of the tongue. There are also small glands that are distributed over the tongue's surface, and these are often clustered around the tongue's margins and underside among primates. Large salivary glands are usually positioned above the mylohyoideus muscle, and the sublingual gland is, as the name indicates, positioned underneath the tongue (Leppi, 1967). Most oral secretions come from the submandibular and parotid glands. Some saliva is exuded by sublingual and minor salivary glands that are scattered around the oral cavity and on the inside of the lips. There are two types of glands, mucus-secreting glands and serous-secreting glands, and some glands produce a mixture of mucus and serous. The function of saliva is to keep the mucous membranes moist, moisten food particles and make them palatable, neutralize toxins, start digestion, and kill microbes. In both humans (Leppi and Spicer, 1966), and *Nycticebus* (Tandler et al., 1996) the sublingual and submandibular glands are known to contain granular secretions that are assumed to be correlated with saliva secretion.

One astonishing phenomenon has been reported about the saliva of the Asian slow loris, *Nycticebus*. This shy and very cuddly–looking, predominantly nocturnal primate has a bad reputation because its bite is certainly harmful and can be almost deadly to humans. (See also discussion in the section on olfaction.)

Tongues of genera belonging to infraorders Lemuriformes and Lorisiformes are different from those of other primates because these tongues have a dense field of cornified papillae (these being somewhat larger, tougher, and longer papillae than the filiform type) beyond the vallate papillae down toward the throat. These tongues clearly have developed strong mechanical functions to facilitate swallowing.

The Sublingua

A duplication of the muscular primary tongue is found below the tongue itself and therefore is called a sublingua or under-tongue. This structure appears in some primitive mammals (Scandentia and Marsupials, but it is attached to the tongue in the latter) as well as in prosimian primates, including tarsiers, in which it is most obviously developed. Other structures that can be found on the under

surface of the tongue in callithrichid monkeys are not equivalent to the prosimian sublingua (Hofer, 1969; Rommel, 1981). The sublingua is not present in Cercopithecoidea, and the so-called *plica fimbriata* (*plica* is Latin for "skin fold"; *fimbria* is Latin for "fringe, filament") that is located under the tongue of the great apes has been interpreted as being a residue of the prosimian sublingua.

The sublingua of prosimian primates appears to be unique. The prosimian sublingua is well developed and keratinized; its medial axis is a thick structure that attaches the sublingua to the under surface of the tongue. Only the tip and lateral margins of the sublingua are free and mobile. The sublingua extends below the tip of the tongue in lemurs, lorises, and galagoes; the tip is hardened and splits into several serrated points. The under-tongue's function has been described by Bluntschli (1938) as a "toothbrush" for the front dentition in those forms that have a specialized procumbent tooth comb. In fact, the median thickening of the sublingua is equipped with a hook-shaped structure in *Daubentonia,* the Madagascar aye-aye. This hook is a specialization that correlates with the very unusual front dentition of *Daubentonia* (Figure 9.9). The hook-shaped, sturdy sublingual tip fits perfectly into the interspace between the two lower incisors and thus keeps this area clean.

In *Tarsius* the sublingua is shaped more simply and lacks the serration of the sublingua of lemurs. This difference is correlated with the fact that tarsiers

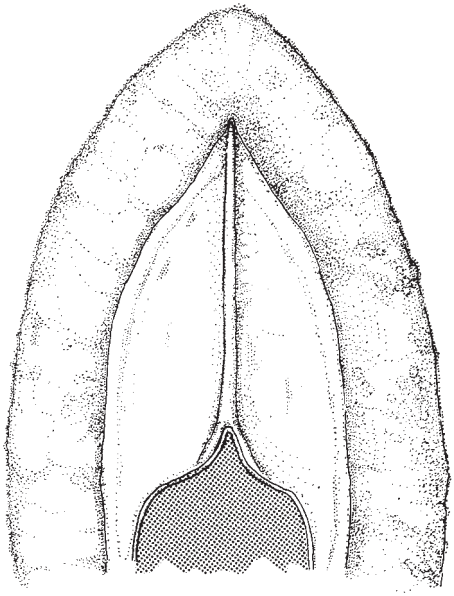

Figure 9.9 *Daubentonia madagascariensis* under-tongue (Lyssa), which is used to keep the space between the lower incisors clean.

do not have the specialized lower toothcomb of the other prosimians that is associated with the serrated under-tongue. The surface of the tongue of *Tarsius* differs from those of all other prosimians in that the tips of the filiform papillae split up into numerous filaments. Furthermore, the cornified papillae on the upper surface of the root of the tongue found in lemurs and lorises are missing in *Tarsius*.

Marmosets have a small sublingua that more or less resembles that of *Tarsius*. This sublingua is only weakly serrated and does not extend as far forward as the tip of the tongue. A fold of mucous membrane skin found along the edges of the lower surface of the tongue in humans, the great apes, and Cebidae is called the *plica fimbriata*. As mentioned already, this fold is often thought to be a remnant of the sublingua of marmosets and prosimians. The same structure is even more reduced or totally missing in the various cercopithecid monkeys.

Hofer (1969) studied and discussed some sublingual structures in the South American monkey *Callicebus* and later in the prosimian *Perodicticus* (Hofer, 1971). He states that the structure that has been described as sublingua or frenal lamella in *Callicebus* is not a true sublingua. He found that this structure—unlike anything described for other primates—contains the excretory ducts of salivary glands, around which are located the taste buds. The body of the sublingual organ lacks any musculature and therefore moves passively together with the tongue; this is also true among prosimians with a true sublingua. Ever since Bluntschli first introduced the functional interpretation of the sublingua in prosimians as a "toothbrush," there has been little or no clear confirmation of this function. Even now we lack careful anatomical and functional studies of the sublingual organs of most primates or among tree shrews and marsupials, studies that would allow for more precise definition of the origin and function of this structure among primates.

Taste

The sense of taste is topographically close to and functionally and physiologically intertwined with the sense of smell but differs considerably from it genetically. While olfaction is encoded by a large multigene family of OR genes numbering to about 1000, taste is less complicated and only two gene families are involved: TR1 and TR2. Very similar to the problems that make it difficult to test the sense of smell in primates is the issue of how to test their sense of taste. These technical problems were the reason for the fact that nothing much was known about either one of these important senses until the late 1960s when the first exact data were published that quantified the ability to taste certain compounds. The first data concerning taste were obtained for humans. Initially, the generally agreed-upon four basic taste qualities were sweet, sour, salty, and bitter. A very interesting and profound overview recounting the history of the

human interest in the perception of taste, beginning as early as the fifth to fourth centuries BC has been compiled by Glaser (1999).

Understandably, taste qualities are intrinsically correlated with the ability of an animal to identify edible food-stuffs or reject inedible and potentially poisonous substances. This capacity is crucial for success in life for any mammal. It is clear that taste and smell are intricately combined in the process of eating and drinking.

People have historically discerned between the four discrete qualities of taste, sweet, sour, salty, and bitter, although during the nineteenth century gastronomists had suggested about 12 qualities of taste, namely sweet, bitter, sour, salty, astringent, rough, ruinous, spirituos, aromatic, acrid, putrid, and insipid. A fifth taste quality, "alkaline" or *umami* ("delicious"), has now entered the taste scene. It was discovered in the early years of the twentieth century by a Japanese physicist, Kikunae Ikeda (Ikeda, 1909; translated by Ogiwara and Ninomiya, 2002; Zhang et al., 2003). Ikeda found that there had to be yet another distinct sense of taste that was different from the four basic widely accepted and well-known qualities of taste. Ikeda thought that this different taste quality could not be the result of a combination of any of the other four, recognized taste traits. He realized that this different taste sensation was somehow correlated to eating meat, fish, cheese, tomatoes, asparagus, and especially a broth made with the seaweed, *Laminaria japonica,* that is widely used as a food ingredient in Japan. He called this new taste quality "umami" and proposed that umami is a basic taste quality. Umami may be a "meaty" taste and is represented by monosodium glutamate (MSG), a salt of glutamic acid; the distinctive taste is only found in the L-form of MSG. (Only the unprocessed, unadulterated, and unfermented glutamic acid is composed of one form of a single amino acid, L-glutamic acid, and nothing else.) MSG reportedly enhances other tastes in the presence of NaCl, especially in the foods Ikeda described. However, it still has not been unquestionably established that MSG indeed represents a separate taste quality. Experts believe that MSG is only a taste enhancer (Glaser, personal communication) that increases the taste quality of the four basic taste qualities and added flavors such as vanilla.

There can be no doubt that the sense of taste does not function by itself; both smell and visual stimuli are intrinsically intertwined with the human sense of taste and enjoyment of food. Although the data on the sense of smell or olfaction among primates have greatly increased recently, it is still difficult to test smell receptivity in nonhuman primates for reasons that are easy to understand. Also, smell is coded genetically with as many as one thousand gene families in mammals, while taste is genetically much simpler, with only two such genetic coding families. It is extraordinarily difficult to quantify odors in the air that ultimately delivers odorants to their receptors in the MOE or VNO. This is not the case with the sense of taste. In the late sixties and seventies, Glaser (1968;

1970a, b; 1972a) began to publish the first data about the tasting abilities among nonhuman primates. Taste experiments are easier to conduct and to verify by exactly measuring taste compounds and electro-physiological responses than are assessments of smell. At the time of Glaser's studies nothing much was known about the tasting abilities of most primates for all the qualities of taste other than in a few select higher primates including humans. Because in mammals, including all primates, taste receptors are located within the mouth and predominantly on the surface of the tongue, the quality, and more importantly the quantity, of taste-inducing substances can be measured with a high degree of accuracy. It has been shown that in most of the components of taste human sensitivities are equal to or even better than those of the other primates tested (Glaser, 1993, 1994; Glaser et al., 1995). It also appears that primates in general have about the same level of ability in taste perception as other mammals that have been tested, such as rodents, lagomorphs, artiodactyls, carnivores, edentates, and marsupials. It seems that in the four taste qualities, there is no difference in ability to recognize tastes between prosimians and anthropoids (Glaser, 1972a). It also appears that humans have the ability to detect bitterness (chininhydrochloride) and sourness (acetic acid) in a much lower concentration than do the other primates that have been tested. In general, it appears that only rarely are the tasting abilities of humans inferior to those of other mammals that have been studied. Hellekant et al. (1976) have sought for the possible mechanisms of gustatory effects, correlating behavioral reactions with electrophysiological responses of the chorda tympany nerve proper that conveys sourness, saltiness, and sweetness from the anterior part of the tongue. The taste quality "bitter" is perceived at the base of the tongue and mediated by the glossopharyngeal nerve. A few taste buds are thought to be located in the epiglottis and on the palate, and these are supplied by the vagus nerve.

Interestingly, Glaser (1972b) has also measured variations in tasting abilities of humans with the chemical compound phenyltiocarbamid, commonly known as PTC, which had been used by anthropologists to distinguish between different races or populations. Glaser showed that PTC cannot be used to distinguish races and populations of humans according to their ability to taste or not to taste PTC as many researchers had believed.

In 1994 Glaser and collaborators demonstrated that, among primates, strikingly diverse tasting preferences and tasting abilities can be correlated with geographic distribution and high-level taxonomic groups: the protein Thaumatin (extracted from African berries, genus *Thaumatococcus*), which tastes intensely sweet to humans, can equally be tasted by all members of the Old World primates (Catarrhini) but is not at all recognized by any Prosimii, *Tarsius,* or New World monkeys. Interestingly, these findings show that tarsiers are more closely aligned to all prosimians and not to Old World higher primates. The authors stated that from a gustatory point of view, the Catarrhini might as well be called

"Thaumatina." Haefeli et al. (1998) found that several species of callithrichids that were tested as to their ability to taste sweetness appear to have the lowest developed sweetness receptors in the primate order.

The way the taste quality "salt" is perceived is still under investigation. In a recent study of the fungiform salt taste receptor cells in rats and mice the authors came to the conclusion that salt perception is activated by a cation channel (Lyall et al., 2005). In humans, for example, only 20% of salt perception can be accounted for by the known sodium channel that mediates salty taste (Feldman et al., 2003). It actually has been suggested that salt perception is a recent culturally acquired taste characteristic to humans (Hladik et al., 2002).

The taste quality "sour" appears to be the least investigated taste quality as far as primates are concerned (Lyall et al., 2001). Sour, though involved in the palatability of many fruits and leaves, has not yet been explored in relation to primates. As previously mentioned, the taste qualities "salty" and "sour" are mediated differently (by ion channeling) from the other taste qualities and only recently a hypothesis has been proposed that addresses the hitherto unsolved problem of predicting the intensity of sour perception in acid solutions or acidified foods (Johanningsmeier et al., 2005).

As soon as humans were able to manipulate fire they entered a new world of taste and smell that is strikingly different from that of other primates. When they began to modify the natural texture, consistency, and aroma of their fare by cooking, distilling, fermenting, roasting, macerating, and otherwise altering it (Wrangham and Conklin-Brittain, 2003) they moved their nutrition out of the realm of natural supplies and ultimately into the world of gastronomy.

The Neural Connection

Humans are able to convey obvious individual differences in their tastes to each other. We also know that tastes are able to convey memories of particular foods and the situation in which we smelled and ate them. There also appears to be some degree of learning involved in human tasting preferences. As far as the neural connection of taste receptor pathways to the brain are concerned our knowledge is still rather sketchy. It has been reported that primates differ remarkably in this matter from rodents (Pritchard et al., 1989, 2005). Food tasting not only involves the four (or five) taste qualities (sweet, salty, bitter, sour, and possibly umami) but also sight, as far as the visual impression is involved, and qualities of texture and temperature. Verhagen et al. (2004) investigated these issues by studying the primate primary cortical taste area of the brain and report that: "Some neurons respond to taste, texture, and temperature unimodally, but others combine these inputs. None of these orally responsive neurons responded to odor or to the sight of food. These results provide fundamental evidence about the information channels traveled to represent taste, texture such as viscosity and

grittiness, and temperature of food in the first cortical area involved in taste in the primate brain" (loc. cit. page 1685). The authors also discovered that primates do not have a direct neural taste pathway from the brainstem to the hypothalamus and amygdala as rodents do. In primates the neural pathway reaches the primary taste cortex first and then the amygdala and orbitofrontal cortex. This purportedly shows that the fundamental functional pathways of taste differ remarkable between these two mammal groups, provided that it is correct to generalize about primates from results obtained by investigating only one nonhuman primate species, *Macaca mulatta*.

A very crucial entity in taste perception is timing. Thus, temporal coding in the gustatory cortex has only recently been addressed (Katz, 2005), and not much is known about behavioral responses to taste sensation and their reaction time (e.g., the time between bitter recognition and spitting out the bitter morsel).

The Genetic Connection of Taste

Unlike olfaction, which is genetically programmed by as many as 1000 genes in mammals, the ability to perceive taste depends on a much smaller array of genetic coding. Two gene families have now been identified: T1R (simply "T" or "Tas" for taste) and T2R.[3] Sweet receptors in primates have been recognized for some time (Glaser et al., 1995, 2000; Nofre et al., 1996; Montmayeur et al., 2001). Taste receptor genes for the taste quality "bitter" have now also been identified that are located on human chromosomes 7 and 12 (Adler et al., 2000; Conte et al., 2002).

The taste qualities sour and salty are actually perceived by mechanisms that are different from the perception of sweet, bitter, and umami. Salty and sour are transduced by ion and proton channels, while sweet, bitter, and umami are recognized by G-protein signaling pathways (Dulac, 2000; Montmayeur et al., 2001). Our understanding of the genetic base for sweet and bitter taste recognition has recently been enormously refined. For example, in 2000 it was discovered that there must be several sweet receptor genes (Glaser, 2002; Montmayeur et al., 2001; Li, 2002).

There appear to be only three T1R sweet detector genes in the mammalian genome (Bachmanov et al., 2002; Li et al., 2002), while there are more than thirty T2R bitter receptor genes (Adler et al., 2000; Shi et al., 2003). The ability to detect bitter compounds has been variously correlated with the ability to perceive poisonous and otherwise adverse compounds in the mouth before ingesting them. However, among humans there appear to be more nonfunctional pseudogenes for bitter taste detection than in mice. These genes are located on

[3]Unfortunately another gene with a very similar assignation: "T3R" is encoding the function of thyroid hormones and has nothing at all to do with taste perception (Fraichard et al., 1997).

chromosomes 6 and 15 in mice and chromosomes 5, 7, and 12 in humans and the 11 nonhuman primate genera that were studied. It was documented that hominoids and Old World monkeys have more pseudogenes among bitter taste receptor genes than New World monkeys and prosimians (Conte et al., 2003; Go et al., 2005). Thus it appears that especially among modern humans the ability to detect bitter-tasting foods is less acute than that among the other primates. Fischer et al. (2005) sequenced the TR2 gene repertoire of humans and great apes *(Pan troglodytes and P. paniscus, Gorilla gorilla and Pongo pygmaeus)* and, for comparison, a macaque *(Macaca mulatta)* and a baboon *(Papio cynocephalus)*. They confirmed that in humans all bitter taste receptor genes, except T2R1, which resides on chromosome 5, are clustered on chromosomes 7 and 12. They found that the fraction of T2R pseudogenes in humans is 29% while it ranges from 15 to 28% in the apes and the two Old World monkeys that have been studied. Thus, the proportion of nonfunctional pseudogenes and the total number of bitter taste receptor genes appears not to differ between humans and the non-human primates that have been studied (loco cit. page 434) "suggesting that T2R genes as a group did not evolve under marked species-specific pressures." Whether this might be related to the fact that humans are modifying their food since they began to use fire, and that they are able to learn from each other about adverse reactions to eating poisonous things, remains elusive speculation. There is no doubt that among humans the process of identifying food; preparing it; discussing it; changing its temperature; and seeing, smelling, serving, and finally eating it is adding new dimensions and is deeply anchored in human cognitive, social, and even emotional qualities.

AUDITORY REGION, HEARING, AND VOCALIZATION

While vision is a reflective sense in that it receives and processes input from external sources, audition (hearing) and sound generation are intrinsically interrelated with each other and are tuned to initiate, receive, and comprehend species-specific and therefore identifiable noise messages as well as to the reception and filtering out of unrelated environmental sounds (Brown, 2003; Ghazanfar and Santos, 2003). Receiving sound messages is very important in predator avoidance behavior, species-specific social interactions, and group cohesiveness.

Outer Ear

There is evidence that both the size and shape of the outer ear and the width of the head are important for sound reception. The latter translates into the

distance between sound reception of both ears, and thus the ability to have three-dimensional, spatial hearing. This capability assists in the skill of localizing the source of incoming sounds, which is crucial for appropriate behavioral response. Also, the shape of the outer ear is related to sound catching. Many predominantly nocturnal primates have large, mobile ears that can be directed to better catch incoming sounds, an ability that is mostly lost among anthropoids, who have to turn their head to achieve this.

The scientific term for the outer ear is auricle (Latin *auris,* meaning "the ear, hearing") or *pinna* (Latin for "feather, appendage, fin"); it is formed by an elastic cartilage *(cartilago auriculae)* that is covered with skin and connected to the skull by ligaments, muscles, and fibrous tissue. The central part of the external ear is called *concha,* a word derived from Greek (for "mollusk, sea shell") and transferred into Latin. The concha is attached to the head around the external opening of the ear and forms an irregular "funnel" of various sizes around it. The part of this funnel extending above the ear opening is called the *scapha* (Greek for "boat"). The scapha, together with an upward and backward extension, forms the helix. If the scapha extends below the ear opening, it forms the lobule or ear lobe. The outer opening of the external auditory meatus is partly covered by two cartilaginous extensions, the *tragus* (Greek for "buck," meaning "horn, outgrowth" in this context) in front and the smaller *anitragus* in the back (Figure 9.10). A more or less pronounced transverse fold, the so-called *plica principalis* (*plica* is Latin for "fold") delimits the concha in its upper part and is sometimes enlarged into a flap. This, for example, is the case in bushbabies (genus *Galago*) and tarsiers (genus *Tarsius*). Thus we find that among species of these two genera the upper part of the auricle is very large and is equipped with additional crossfolds (Figures 9.11 and 9.12). These large, membranaceous outer ears are not rolled in at the margin and can be folded down toward the ear opening with help of the intrinsic musculature *(musculus corrigator pinnae)* that is incorporated into the auricle. This muscle—where it is functional—changes the shape and direction of the outer ear and folds it down. Bushbabies and tarsiers can move both ears independently from one another in order to locate the origin of sound. The *musculus corrigator pinnae* is absent in all Anthropoidea, including humans.

The entire outer ear can be moved by several intrinsic small muscles (*m. depressor auris, m. retrahens auris, m. rotator auris, m. attrahens auris,* and *m. attolens auris*) that respectively pull the ear down, pull it back, rotate it, pull it forward and upward, and only pull it upward. This allows primates with large ear funnels to home in on the direction from which sound originates by moving one or both auricles toward the direction from where the sound appears to originate.

Among anthropoids the outer ear consists mainly of a single piece of cartilage, covered with skin, that gives the auricle its shape. This cartilage does not extend

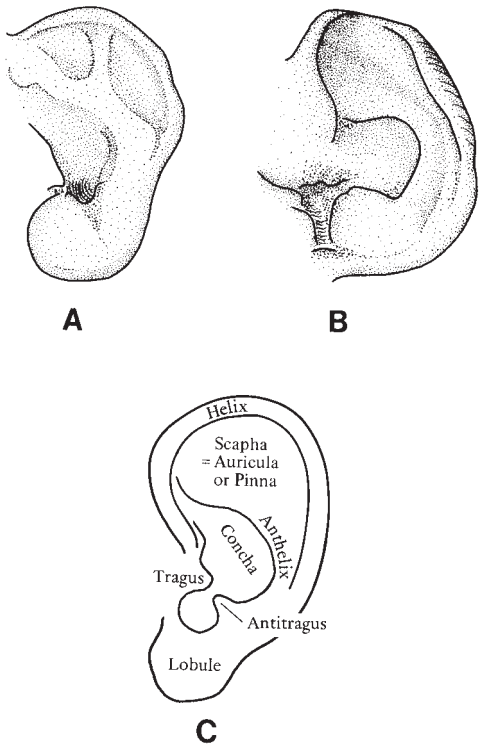

Figure 9.10 A) Ear of a treeshrew *(Tupaia)*, B) ear of a New World monkey *(Cebus)*, and C) primate ear and its constituent parts.

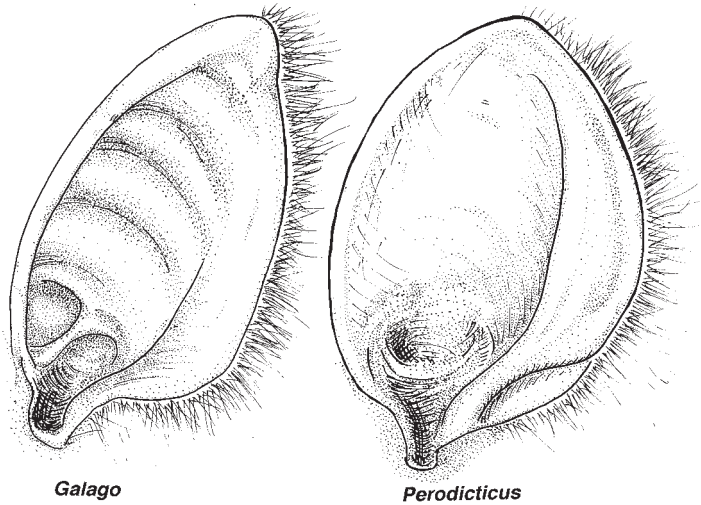

Figure 9.11 Outer ears of a bushbaby *(Galago)* with crossridges and of a lorisid *(Perodicticus)* without crossridges. Magnified to approximately the same size.

Figure 9.12 Nocturnal prosimian primate *Perodicticus potto*. Note large ears, large eyes, rhinarium, reduced second finger, and toilet claw on second toe.

into the lobule of the ear. The lobule is composed of areolar (a type of connective tissue consisting of fibroblasts and mast cells that are embedded into a matrix of glycoprotein and proteoglycans which contain collagen and elastin fibers) and adipose (a type of connective tissue that is made up of cells that contain fat droplets) tissue and is rather soft and pliable, unlike the stiffened part of the ear held up by cartilage.

Where the outer ear is concerned, great variability between and within primate genera, even within species (such as in chimpanzees and modern humans), can be observed. Thus, for example, Lasinsky (1960) was able to show that not only the shape, but also the relative size of ears is most variable throughout order Primates. With prosimian primates differences in size and shape of the outer ear are extreme.

These modifications in size and shape of the outer ear are related to behavioral characteristics that call for different ear functions. Two functional factors influence the morphology of the auricle. A mobile, large auricle is moved to locate and focus on the direction from where sounds originate. Another purpose is to serve as a funnel to collect sound waves, and an added utility—if the auricle is large—is as a heat regulating surface. In primates the outer ear is more likely to function as a sound collector. One example of this kind of function can be found between two genera of tree shrews: *Ptilocercus* has large, megaphone-like outer ears, and in the closely related genus *Tupaia* the outer ears are small. The basic behavior of these two genera is also different: *Ptilocercus,* the pen-tailed tree shrews, are nocturnal animals, while tupaias are diurnal and crepuscular animals. Consequently, the large ears in *Ptilocercus* would suggest that it is more dependent on hearing than are the tree shrews, which can rely to a much greater degree on their visual sense than on their hearing. However, no studies have as yet been undertaken to prove this inferred hearing difference between the two genera. By studying behavior in both groups, it may be possible to demonstrate a distinction in hearing abilities and also to see correlated separation of structure in the central nervous system. The outer ears of the tree shrew genus *Ptilocercus* are large and membranous, as in bushbabies, and very mobile. The ears of another tree shrew genus, *Tupaia,* resemble the external ears of higher primates and even humans in a striking way (see Figure 9.10). They are neither membranous nor very mobile.

We also find distinct differences in the morphology of the outer ears of two closely related prosimian families—the Galagidae, or bushbabies, and Lorisidae, the lorises and pottos. The former have large, membranous, mobile ears that can be folded down and even into the outer ear opening. The latter have comparatively small ears that are not very mobile. Both groups are basically nocturnal in their behavioral adaptations. Yet a striking difference of the general pattern of behavior between these two groups can be observed. Galagos are very active, excitable, and agile animals, and some locomote in a vertical leaping and clinging fashion, whereas lorises and pottos habitually are slow, quadrupedally climbing, and very cautious animals and are deliberate in their movements. Here also, we do not have any published evidence for the theoretical explanation of these differences in the shape of the outer ears. No comparative behavioral or physiological studies or comparisons of the nervous system of these animals have been undertaken that might be able to show differences in their ear function and hearing abilities. We can, however, hypothesize that the bushbabies, having larger outer ears, rely on their hearing to a greater extent than lorises do.

The outer ears of most lemurs are simple in their morphology and frequently adorned with hair tufts or evenly covered with hair. Lemur ears usually stick out from the head; *tragus* and *antitragus* are simple, and the helix and anthelix are also of simple shape, with the helix not rolled inward at the margin.

Species of genera *Microcebus, Phaner,* and *Galago* have large, membranous ears. Among each of these taxa, this large ear shows a variable number of several small crossfolds (see Figure 9.11) parallel to the *plica principalis* that play a functional role when the large membranous earflap is folded down by the action of the intrinsic *musculus corrigator pinnae*. In a sound-polluted world, would it not be great to have the ability to occasionally fold our ears down to cover the ear opening and blend the noise out? Today humans have earplugs instead.

The *supratragus* (a flap covering the ear opening from above) is present but comparatively small among these small lemurs and bushbabies. Also, in *Tarsius* we find a very large, membranous, and mobile ear. Here the antitragus flap is larger than in *Galago* or *Microcebus*. It is known that the hearing ability of *Tarsius* is very acute, and that the terminal nuclei of the auditory nerves and their connections with the central nervous system are especially large.

Throughout the anthropoid primates we find that the ears are comparatively small and of the same overall pattern. Usually, the ears are rounded, and the margin of the *helix* is more or less rolled inward. The upper margin of the *helix* is not rolled in and is pointed in two genera of the Cercopithecidae, namely in *Macaca* and *Papio,* comparable to the pointed ears of many lower mammals. Anthropoid ears never go through a pointed stage during their ontogenetic development except in the two genera just mentioned.

Schultz (1965, 1969) states that the pointed ear of an "orangutan foetus" that was pictured and described by Darwin (1871) was caused by a deformation of that particular fetus, which Schultz was able to inspect (Figure 9.13). Moreover, in Schultz's judgment, the particular fetus is that of a gibbon and not of an orangutan. Also, in Darwin's "Expressions and Emotions in Man and Animal" we find two drawings of the head of a Celebes macaque that show a pointed ear (Figure 9.14). This point of the ear auricle has gone into natural history lore as "*tuberculum Darwini*" or "Darwin's point." It is still regarded by many as an atavism in humans, where the point is actually rarely found. Many human anatomy texts compare the "auricular tubercle of Darwin" with the pointed ears of "adult monkeys." Lasinsky, however, shows that the two structures have nothing in common. The auricular tubercle of Darwin has had a rather exaggerated revival in the very pointed ears of alien "Vulcans" who evolved from the fantasy of the creators of *Star Trek* and *Star Trek, the Next Generation*.

Among apes and humans the rim of the auricle is usually rolled inward at the upper and the hind margins (compare Figure 9.12). Among the large apes we find very small ears in orangutans; small ears in gorillas; and very large, flaring ears in chimpanzees. Moreover, a high degree of variability in ear shape characterizes the common chimpanzee, *Pan troglodytes*.

An ear lobule is not only typically found at the lower end of the outer ear of modern humans but can also be detected in the ears of African apes and some

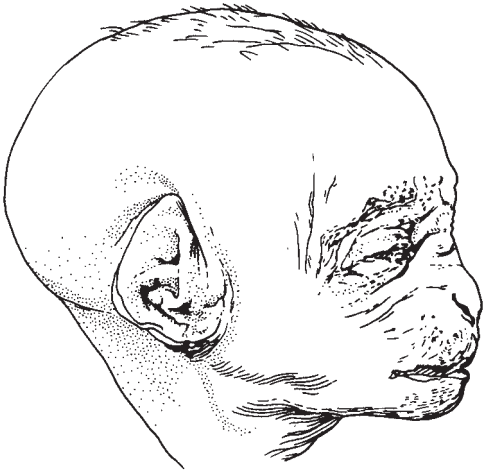

Figure 9.13 Darwin's alleged "pointed ear" of an "orangutan fetus."

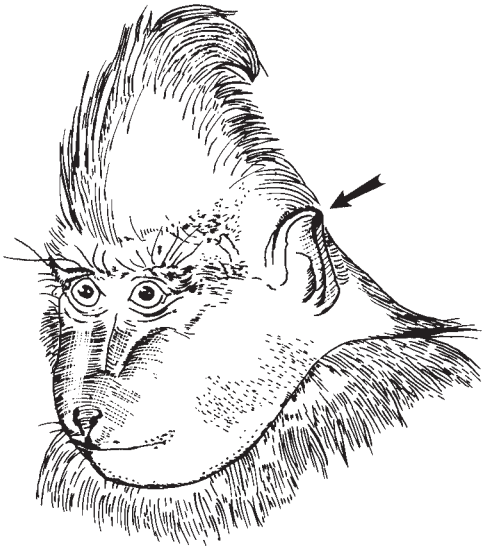

Figure 9.14 Darwin's point of the primate ear in a Celebes macaque *(Cynopithecus niger)*.

Old World monkeys, as, for example, in langurs. The lobule never occurs in any of the prosimians, New World monkeys, lesser apes, or orangutans.

Middle Ear

In all Old World monkeys, lesser and greater apes, and humans the middle ear and the eardrum communicate with the outside of the head by means of an ossified tube. The tympanic membrane thus is separated from the outer ear opening. This also means that the middle ear area is tucked underneath the skull base. In contrast, all New World monkeys have the tympanic membrane (the eardrum) positioned much closer to the lateral medial surface of the head, and the very short outer acoustic meatus is made up of cartilage. In platyrrhines the middle ear region is located closer to the lateral edge of the skull's base than in catarrhines. With the prosimians the membrane is also situated more closely to the outer ear opening than in the catarrhine primates. The tarsiers are more like catarrhines in having an ossified ear canal unlike prosimian primates; *Tarsius* has a bony outer acoustic meatus that superficially resembles the catarrhine condition. This is related to the fact that the overall shape of the tarsier skull—which is dominated by the enormous eyeballs in combination with a short snout and small brain—is rather globular, and the middle ear region together with the tympanic membrane are positioned underneath the braincase toward the middle of the skull base, not at the side of the skull, as in lemurs and lorises. Here the tympanic membrane is only suspended by a slender ring that is attached to the temporal squamosum in two places. In Lorisiformes the tympanic is fused to the skull (Werner, 1960).

The entire ear region of primates is embedded within and part of the temporal bone (see also Chapter 5 and Starck, 1955, loc. cit. page 569). The external acoustic meatus is part of the tympanic of the temporal bone, which also contains the middle ear region. On the inferior surface of the skull the middle ear region is located inside the tympanic area, which forms a roughly structured bone surface known as the petrosal in humans, apes, and Old World monkeys *(petrosal* is from Greek *petra,* meaning "rock"). This same tympanic portion of the temporal bone can be inflated into a more or less ball-like structure that is commonly known as the bulla in tarsiers, lemurs, and lorises *(bulla* is Latin for "blister"). Both the petrosal and bulla are prominent structures exposed on the basicranium of primates. In the primate literature the terms "petrosal" and "auditory bulla" are subject to much confusion even though they simply are descriptive terms for the same general anatomical area of the temporal bone (Wiedersheim, 1902, loc. cit. pages 121–122; Starck, 1995, loc. cit. pages 34–35). Both the bulla and the petrosal arise from the same developmental origins of the temporal bone, namely the entotympanic (Spatz, 1966).

The outer ear receives airborne sound waves that activate the tympanic membrane. Acoustic vibrations are picked up by the tympanic membrane and transferred to the delicate series of three ossicles that are connected to the membrane, to each other, and to the inner ear region of the skull by means of ligaments.

All these bones are housed in the middle ear cavity (tympanic cavity), which, in turn, is connected to the Eustachian tube that leads to the back of the nasal cavity. The Eustachian tube basically functions like an air valve between the middle ear region and the nose, allowing air to communicate with the middle ear. It equalizes the air pressure on both sides of the tympanic membrane, permitting the membrane to vibrate freely. Beneath the oval fenestra lies the round fenestra of the cochlea, which, like the oval fenestra, is covered by a membrane that bulges in both directions, thus alleviating pressure imbalances between both sides.

Understanding this imbalance between the sound waves in air of the outer and middle ear and the liquid in the inner ear is complicated. Because air and liquid do not transmit sound waves equally, this change of medium and wave frequency causes an effect that is known as "acoustic impedance" (Hemilä et al., 1995). Sounds that reach the outer ear are airborne, while the medium within the inner ear is liquid. The term "impedance" evaluates the differences in resistance to sound waves between the two media. Air has low impedance, while the fluid in the middle ear is a high-impedance medium. This mechanical problem is mediated by the size difference between the tympanic membrane and the much smaller oval fenestra. Furthermore, the transfer of sound waves is mediated by the intricate action of the three tiny interconnected ear ossicles. Hemilä et al. were attempting to evaluate if there is any functional impact of size (scale) changes in the middle ear region. They conclude that sound perception does not directly depend on an animal's, and thus middle ear, size (Nummela, 1995).

The first of the ear ossicles, attached to the tympanic membrane, is the *malleus* (Latin for "hammer, mallet"), which gets its name from its hammerlike shape. Adjoining the *malleus* is the *incus* (meaning "anvil" in Latin); it has a rounded body and two thin, leglike extensions. Notably, the *incus* does not really look like an anvil. The third ossicle is the *stapes* (Latin for "stirrup") and resembles a stirrup in its shape. This bone connects to the vestibule of the inner ear—or, to be more precise, to the membrane that covers the so-called oval window, or fenestra vestibuli, which is situated in the lateral wall of the vestibulum of the inner ear. There are two small muscles that insert on the malleus *(musculus tensor tympani)* and stapes *(musculus stapedius)* that stabilize the ossicles.

Some general statements can be made about ear ossicle morphology: ear ossicles of lemurs and Old World monkeys are similar to each other. Interestingly, those of the aye-aye *(Daubentonia)* show some resemblances to ear bones of certain rodents. Tarsier ossicles are similar to those of lemurs, whereas

the ear ossicles of Lorisidae resemble those of Callitrichidae. Cebidae and Cercopithecidae each have ear ossicles with some unique characteristics of their own, and the ossicles of Pongidae are quite similar to those of humans.

Inner Ear

The inner ear region is a bony cavity that is located medially to (or behind) the middle ear. It is filled with fluid and contains the membranous labyrinth consisting of three semicircular canals, which are concerned with the body's balance and position. The fluid surrounding the labyrinth is known as perilymph (*peri* is Greek for "around, surrounding"), and the fluid within the labyrinth is called endolymph (*endo* is Greek for "inside"). The endolymph functions to convert the mechanical energy of incoming sound waves into electrical, neural impulses. Where the three semicircular canals and the cochlea connect are three small chambers, the ampulla, the utricle, and the saccule, which are positioned perpendicular to each other. All three contain thousands of sensitive hair cells. Above the hair cells is a gelatinous layer that in turn is covered with a more fibrous membrane which contains crystals of calcium carbonate. It is called the otolithic membrane, is heavier than the surrounding structures, and moves on the sensitive hair cells whenever the body and head are tilted. The neuroepithelial cells are the peripheral receptors of the vestibular system; they receive and react to vibrations (Tascioglu, 2005). Ultimately, sound waves are transferred to the ear ossicles, where they are picked up by the stato-acoustic nerve.

This highly elaborate center of sound and balance perception also depends on visual cues to keep the mammalian body in balance (Minor et al., 1999; Schubert and Minor, 2004). The cochlea receives acoustic messages after the middle ear has functioned as an impedance mechanism. Impedance in acoustic events is analogous to electric impedance: acoustic impedance is expressed in a complex formula that describes how different media—external ear air at the outside of the tympanic membrane versus perilymph at the oval fenestra of the inner ear—absorb sound when converting sound pressure into sound flow velocity (Zwislocki, 1975; Hemilä et al., 1995). The inner ear containing the labyrinth and cochlea is the main organ of equilibrium as well as the organ of hearing, because it is here that the stato-acoustic (vestibulo-cochlearis) nerve receives acoustic signals and impulses that maintain the body's equilibrium. The vestibular system providing balance in space and accuracy for the visual system is highly complex (Tascioglu, 2005). Motions of the head are registered by the vestibular system. Signals of head motion are monitored by the vestibular portion of the inner ear region. This system maintains the stability of not only vision but also the body posture during movement (Minor, 1998).

The bony labyrinth within the petrosal contains the membranous labyrinth, which is surrounded by and floats within the bony labyrinth in the perilymph

and is barely attached to the bony part. The membranous labyrinth itself is filled with endolymph. There are three membranous semicircular canals that are harbored within the petrosal part of the temporal bone: the superior, the lateral, and the posterior semicircular canals which are roughly positioned at right angles to each other. The three semicircular canals are interconnected with the bony cochlea (from Latin for "snail"), the crucial structure of the inner ear that picks up and transfers auditory information to the brain as it transforms sound waves into neural impulses. The cochlea is coiled like a snail and separated into partitions by flexible laminae on the inside. Sound signals are received by hair cells in the cochlea that convert the basilar membrane motion into patterns of neural activity that flow from the cochlea up the auditory nerve and the cochlear nucleus.

New techniques using high resolution computed tomography micro scans make it now possible to "peer into ancient ears" (Stokstad, 2003). This technique has made it possible to correlate locomotor agility to the size of the semicircular canals: swift movers have larger semicircular canals in comparison with sluggish movers relative to their body size. The connection between hearing and the shape of the inner ear as viewed by CT scans is still rather tenuous (Stokstad, 2003).

Hearing

It has been established that only the chimpanzee and humans, among 19 mammals that have been tested, lack the ability to hear high-frequency sounds (Heffner et al., 1969a, b). The none primates such as the opossum *(Didelphis virginiana)* and hedgehog *(Hemiechinus auritus),* Tupaiidae *(Tupaia)*, bushbabies *(Galago)*, and common marmosets *(Callithrix)* are capable of perceiving very high–frequency sounds. *Homo* and *Pan* cannot hear sounds in high frequencies above 32 Kc/s (kilocycles per second) that can be perceived by bushbabies and tree shrews. It also appears that bushbabies are more sensitive to the discrimination of such frequencies than are hedgehogs and opossums. Humans are especially capable of perceiving low-frequency sounds. Our overall sensitivity to sound discrimination is better than that of any other mammal so far tested (Heffner et al., 1969a, b).

The successful transmission of sound cues is still not totally understood. It has been possible to document that humans are better at discriminating between certain sounds than are macaques (O'Connor and Sutter, 2003; Egnor and Hauser, 2004). Furthermore, we know that small animals are better at making and hearing high-pitched sounds than are large animals (Nummela, 1995). This is correlated to the size of the tympanic membrane and the connecting ear ossicles: large ossicles result in an increase in mechanic inertia and consequently cannot transmit high-frequency sound waves (Hemilä et al., 1995).

CT scans of the ear region to evaluate hominid fossils and their hearing acuity have been attempted. Hearing acuity is believed to be correlated with the ability to conquer the complicated communication tool known as language. In the endeavor to discover whether middle pleistocene humans were able to speak and hear, the outer and middle ear regions of five fossil hominids were compared with those of modern humans and chimpanzees. Evaluating their mainly theoretical methodology, the authors conclude that the fossil humans from Spain were able to receive (and presumably comprehend) spoken language. However, their conclusion is speculative at best (Martinez et al., 2004). This is only one example among many that illustrates the problem that has long surrounded and confounded our ability to objectively approach the issue of primate hearing and vocalization. Here, fossil humans are compared with one extant ape species in a highly theoretical study that results in a rather speculative conclusion.

One of the most crucial aspects of vocalization among primates is the cortical coding connection in the brain (Wang, 2000; Wang and Kadia, 2001). As for the genetic blueprint that enables humans to have language and nonhuman primates to communicate with each other within and without species, there is now but one genetic locus that has been connected with the human ability of speech. It is known as FOXP2 and was first discovered in songbirds (Scharff and White, 2004; Teramitsu et al., 2004). If this coding area (or gene) is in any way compromised, it causes the bearer, be it a bird or human, to have difficulties producing and, in the case of humans, comprehending proper vocalization (Lai et al., 2001).

Both humans and birds are good examples for vocal learning. This aptitude is also known to apply to dolphins, whales, bats, and three orders of birds (Haesler et al., 2004). The molecular evolution of the FOXP2 gene suggests that it has been under positive selection among all primates, which thus share an ancient relationship with song birds (Haesler et al., 2004). The authors found that FOXP2 is not only typically expressed in the song bird brain but also in the brains of birds that do not learn how to sing, in mammals, and in reptiles. It thus appears that this gene is functional in establishing brain pathways "including, but not limited to, those essential for vocal communication" (Haesler et al., 2004, loc. cit. page 3174).

Surprisingly, song birds actually are more like humans in their ability to learn their songs than are nonhuman primates (Doupe and Kuhl, 1999). One wonders whether the fact that genetically identical but geographically separated primate groups (*Microbebus murinus:* Hafen et al., 1998; *Pan troglodytes verus:* Crockford et al., 2004) have different calls or "dialects" is a reliable test for their ability to learn. This seems doubtful, as the two publications describe almost identical circumstances for groups of tiny mouse lemurs and great apes, respectively, and come to different conclusions about why these populations have different vocalization repertoires. Hafen and colleagues decided that the different

mouse lemur group vocalizations are equivalent to "dialects" of same-species bird populations that roam in different but close-by locations. In contrast, Crockford and colleagues believe that the chimpanzees are intentionally modifying their calls to make them different from those of conspecifics who live nearby. They argue that this suggests that the chimps have the ability to learn as documented by their different sounds.

A group of researchers in Japan has discovered that groups of Japanese macaques *(Macaca fuscata)* that live in different areas vocalize in different "accents," similar to human populations that speak the same language but live as much as 430 miles distant from each other (Tanaka et al., 2006). This observation has variously been attributed to the fact that the groups live in different environments that may necessitate modifying calls. One group lives on an island in a forest with tall trees. The other group lives in open but mountainous terrain with little vegetation. The forest dwellers use a higher pitch than the open-area monkeys when they vocalize—features that are said to be well adapted to the different environments. It is clear that these macaques, who are genetically identical, lived apart for more than thirty-four years and now use different vocalizations. Whether these different ways of communicating should be called "dialects" is problematic, however, because "dialect" is a human language quality and, when applied to monkeys, implies the primates are applying anthropomorphic reasoning.

Marmosets *(Callithrix kuhlii)* also have been observed to modify their "phee" calls according to differences in social context. Again this ability to adapt vocalization has been evaluated as "plasticity" in vocal communication (Rukstalis et al., 2003), but this does not imply these callithrichids have "language."

It is easy to understand that measuring sounds that occur in nature is highly complicated, because sound conductivity heavily depends on air temperature, humidity, air movement such as wind gusts and their direction or even breezes, and distance between the source and the receiving measuring device. Environmental features such as cliffs, trees, grass and brush, bodies of water, and geological relief also influence sound conveyance; consider, for example, the effect causing an echo. Therefore, measuring sound perception has to be done either in an artificial setting or by inference. Thus the study of hearing abilities is complex and complicated and much of the available information is based on laboratory experiments. The results document that emitted and perceived sound ranges are very different in mammals and what can be heard might be exclusive to certain groups of mammals (Heffner, 1998). As mentioned, the ability for researchers to document what primates can and do hear in their natural habitat is vastly complicated by geological, meteorological, floral, and geographical conditions; distance between animals; and appropriate reaction of the possible recipients of sound messages. Our knowledge about primate hearing is hampered because it is one of the more elusive aspects of primate behavior. However, there

can be no doubt that primate hearing is closely interconnected with primate visual abilities (Heffner, 2004).

Our understanding of primate auditory capabilities has somewhat increased during the beginning of the twenty-first century (Ghazanfar and Santos, 2003). For example, it has now been documented, in the natural habitat, that at least one species of anthropoid primate *(Cercopithecus diana)* responds to alarm calls that are elicited from either conspecific primates or other sympatrical animals within the inhabited area in appropriate ways (Zuberbühler, 2003).

Primate Vocalization and the Role of the Larynx

"Vocal production forms an important nexus in acoustic communication, lying at the intersection of physics, physiology, neurobiology, and evolution" (Fitch, 2003, loc. cit. page 87). Fitch emphasizes that the anatomical parts and their manifestation in the nervous system that create vocalization vary widely among primates and therefore should be understood before attempts are made to functionally evaluate primate vocalization.

Sound production starts with the airflow from the lungs and variously involves the larynx, with the vocal cords and air sacs, the hyoid, skin pouches and the shape of the mouth, the cheeks, and to some extent the teeth and tongue.

The larynx is a complex structure that is located in the front of the neck and is part of the windpipe system (Harrison, 1995). Morphologically it appears to be rather uniform among extant primates; it is believed to be merely involved in airway protection (Negus, 1929; Lieberman, 1991; Harrison, 1995; Zuberbühler, 2005).

Considering the many parts of the larynx that are potentially involved in sound production, the mechanics of vocalization in most primates are not well understood. It has been asserted that the relative distance between the larynx and the hyoid and their postnatal descent in the throat are closely related to the ability of speech in humans. This topographical descent is not unique to humans, however; it is also found in males of two species of deer, the red deer *(Cervus elaphus)* and the fallow deer *(Dama dama)* (Fitch and Reby, 2001). Variations of these features occur also in the greater and lesser apes where the hyoid and the larynx proper are separate and independently mobile. In contrast, in the Old and New World monkeys the hyoid–larynx combination functions as a unit (Nishimura, 2003). Primates have accessory laryngeal air sacs that occur in various configurations and are located in the throat. They originate from the trachea in the upper larynx. The presence or absence of these air sacs appears to be correlated to body size, as they have not been found in small-bodied primates (Hewitt et al., 2002). Neither the function nor the morphology of these inflatable accessory structures of the larynx are well understood, but they are

likely involved in the booming and far-reaching songs of gibbons, howler monkeys, indris, and variegated lemurs, for example.

The modulation of sound results from the length and tension of the vocal cords (Mergel et al., 1999). Although some information is available regarding the representation of vocalization in the brain of some nonhuman primates (Ghazanfar and Santos, 2004; Romanski et al., 2004), no comprehensive comparative anatomy of the larynx in primates seems to exist. Furthermore the eutherian mammal laryngeal complex is rather uniform in shape and thus is multifunctionally useful. There are a plethora of field studies of primate vocalization and behavioral interpretation, and a multitude of primate cognitive behavior studies and even theories about primate song evolution have been published (Geissmann, 2002; Rogers and Kaplan, 2004). The question of whether primates "learn" to understand vocal messages has been addressed in many ways. Struhsaker (1967) observed that vervet monkeys *(Cercopithecus aethiops)* have distinct alarm calls for different predators, eliciting appropriate escape responses. This appears to be universally true among primates; for example the *Varecia* groups in outdoor enclosures at the Duke University Primate Center clearly have specific warning calls that discern between aerial (Buzzards flying over) and ground predators (dogs walking by).

In the process of sound emission by nonhuman primates the receiving party can only be random. Only humans are able to intentionally and selectively give vocal messages to specific recipients. There is much debate about how to properly evaluate vocalizations of nonhuman primates (Owren and Rendall, 2001).

Primates in general are very vociferous. The most spectacular examples of primate vocalization are the far-reaching choirs of a few and select genera: the lesser apes, gibbons and siamangs, the New World howling monkeys, and among prosimians the indris and black- and white-ruffed lemurs. Their far-reaching, loud voices appear to be produced by different morphologies. Surprisingly there is no detailed information about the morphology of the throat in any of these genera. The most extreme morphological manifestation of howling is found in the enlargement of the bony hyoid in male, and to a lesser extent female, *Alouatta* (see Figure 5.18). The angle of the mandible is accordingly enlarged to accommodate the large sound-producing ossified hyoid. The entire skull of *Alouatta* is therefore different from any other New World monkey. The lesser apes, especially Siamangs *(Symphalangus syndactylus),* have a large air sac on the throat that inflates into a grapefruit-sized, resonating, globe-shaped swelling during vocalization. Analogue air sacs reputedly also occur in several other gibbon species (*Hylobates* and *Nomascus* species). Indris *(Indri indri)* characteristically purse their lips far out while calling, but no detailed morphological description of the larynx and hyoid area exists for these primates. The hyoid/laryngeal area of *Propithecus* is constructed quite unlike that of anthropoid primates (Figure 9.15). There seems to be no obvious morphological

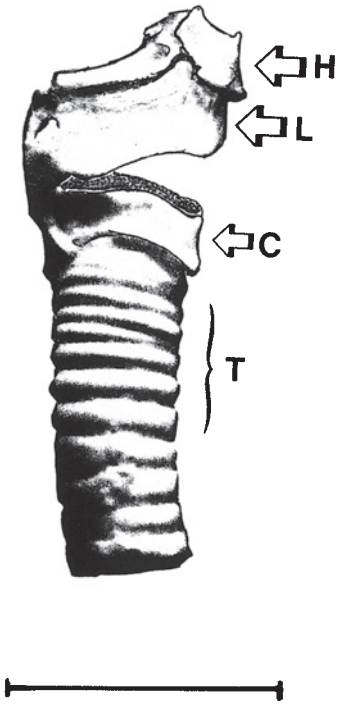

Figure 9.15 The larynx and trachea of *Propithecus verreauxi coquereli,* viewed from the right side. H = Hyoid; L = larynx; C = cricoid cartilage; T = trachea. Scale = ½ inch.

feature associated with the loud calling Varis (*Varecia variegata variegata* and *V. rubra*).

The importance of vocal communication among nonhuman primates and its connection with their social behavior has only recently been investigated (McComb and Semple, 2005). The human ability to speak and acquire language is the reason most research in primate vocalization and hearing is rooted in the study of humans (Hauser et al., 2002). A point of contention since the middle of the twentieth century has revolved around whether primates can acquire true language skills. Studying primate vocalization has been directly aimed at our endeavor to understand the beginning of human language. The focus on human language spawns anthropocentric approaches and loss of objectivity among researchers.

Researchers who study primates and their ability to learn language usually live in close quarters with their subjects in, as far as the primates are concerned, unnatural circumstances. The most remarkable fact is that strangely, these primates all appear to "speak" English just like their human mentors. Should

they not communicate in the language of their own species like Chimpanzee or Gorilla? We know that primates are smart (having more elaborate brains than many other mammals), but signing and lining up a few words cannot fittingly be called language (Vauclair, 2002). Incidentally, dolphins have an even better understanding of signaling than primates do (Herman and Uyeyama, 1999). They have better abilities to learn and their brains are more elaborate—but they lack the primates' hands and feet and live in a totally different environment.

Animals will communicate with the human masters with whom they reside. Birds, for example, are splendid at giving messages to their humans, as do dogs and even cats. But language is more than communicating with symbols that are lined up with each other. Language has grammatical rules (the dubitative if one wants to express doubt, for example) and the ability to write and read (Fitch and Hauser, 2004). Understanding language is more than signaling; it also includes the capability to learn and understand other languages or dialects (Owren and Rendall, 2001; Seyfarth and Cheney, 2002).

EYES AND EYESIGHT

Heffner (2004) has fittingly and elegantly linked two important senses, namely hearing with vision, as they clearly are functionally interdependent. For example, auditory perception frequently initiates visual activity.

How would we be able to detect the colorful hummingbird had we not first heard it buzzing? Could we discover the whereabouts of a cryptic animal with a strong odor had we not smelled it first? Would we pay special attention to a beautiful little flower had we not initially been attracted by its fragrance?

All primates, but especially the higher primates, are visual animals. Vision is the only sense that can temporarily be "turned off" (by closing the eyes). Primates have comparatively large eyes compared with other eutherian mammals, and only members of this mammal group have true color vision. Primates' eyes are predominantly positioned on the front of the head rather than at the side, as in animals such as horses, rabbits, and antelopes; this position changes the scope of the visual field. Coordinated binocular eye movement has been perfected in primates. Most anthropoids have eyes that are directed forward, with visual axes being more or less parallel with each other, not divergent. Different substructures of the visual system must first go through a process of delicate synchronized development so that they will be able to function as an integrated unit in perfect harmony with each other when mature, making vision possible. The intricate task of simultaneously perceiving light intensity, identifying color, recognizing spatial relationships, and detecting movement are crucial for this system to function properly (Clancy et al., 2000; Silveira et al., 2005). In sum, the visual system is a highly complicated and elaborate network of neural and genetic connections

that have to operate in concert to be functional (Rowe, 2002). Douglas and colleagues (1993) describe two groups of scientists conducting research on primate visual systems—namely those who focus on the occulomotor and optical apparatus versus those who attempt to analyze sensory processing throughout the retino-geniculocortical neurological circuits. These two groups of researchers often do not communicate with each other. Douglas and coworkers examine the interplay between precise ocular movements and the maintenance of visual perception in humans, namely "the integrated nature of visuomotor function [that] is illustrated by two examples: smooth pursuit eye movements and stereovision." They conclude that "both of these tasks require huge amounts of sensory processing in many visual centers, and, simultaneously, these tasks require very precise control of binocular eye position. These examples illustrate the difficulty and artificiality of assigning unique functions to any component part of the system" (loc. cit. for both quotes is page 191). It is crucial that we keep this caveat in mind as we look further into the intricacies of primate eyesight. Understanding the components involved in the phenomenon of perception is critical, and Changizi et al. (2006) discuss the dynamics of time, object size, shape, speed, and distance that underlie our ability to understand the mechanism of vision.

Among primates we distinguish two major behavioral activity patterns: nocturnal—active during the night—versus diurnal—active during daylight. As a rule, primates that are active at night have large eyes compared with primates that are active during daylight. For example, somewhat larger eyes are found in nocturnal Galagidae, in the "nocturnal" lemurid *Daubentonia,* and with the only exception to diurnality among the anthropoids, *Aotus,* the South American owl monkey. The eyes of the nocturnal tarsiers are the largest among all primates, with only one half of their eyeball actually enclosed within the bony eye socket (Figure 9.16). Moreover, the eyes of tarsiers amount to 4.5% of their total body weight. In contrast, this proportion approximates 0.3% in most nocturnal primate species, with the eyes of diurnal primates measuring about 0.15% of the entire body weight. Notably, this relation is reduced further to about 0.03% in chimpanzees and humans (Schultz, 1969). These numbers illustrate that the size of a primate's eyes does not simply reflect functional capability. Eye size does not directly correlate with body size, according to Starck (1995), and determining eyeball size is not necessarily of much value for the evaluation of eye function; a multitude of factors combine to create the functionally optimal optical system. Furthermore, relatively small eyes do not necessarily mean that the bearers are diurnal; for example, two species among the lorisids (*Perodicticus potto* and *Nycticebus coucang*) have rather small eyes weighing in at 0.2% of their body weight, even though both are functionally and behaviorally nocturnal species (Schultz, 1969; see also Howland et al., 2004). Generally eye size and body size in primates appear to vary independently of each other.

Figure 9.16 Huge eyes of the nocturnal tarsier *(Tarsius bancanus)*. Only two-thirds of the eyeball are enclosed in the orbit. Photo courtesy of Heinrich Sprankel. From Ankel-Simons, 2000.

A large database providing measurements of the axial length of eyeballs of a vast number of vertebrates confirms that eye size does vary among vertebrates generally (Howland et al., 2004) and appears not to be linked to body size in any predictable manner. Since it has been shown that eyeballs in living vertebrates are not necessarily globular (Rohen, 1962; Starck, 1995), measuring just one axis can be uninformative. However, it does appear that absolute eyeball size is to some extent correlated with diarhythmical activity (i.e., diurnal taxa have smaller eyes and sockets, whereas nocturnal taxa are likely to have larger eyes and sockets).

Among other features, some major underlying factors dictating visual ability include the difference in the eyes' functional retinal photoreceptor substructure, neurological connectivity, and ultimately in the fundamental genetic blueprint that account for the various functional visual capabilities.

The size of eyeballs is not closely linked to the size of the bony sockets that encase them. Two disparate examples for this phenomenon are the following:

1. Humans *(Homo)* have eyeballs that are considerably smaller than the bony sockets. Each eye is surrounded by extraocular muscles, a tear gland, a vascular system, and connective tissue that also normally contains some fat cells. Thus humans are able to move their eyes considerably in multidimensional directions within their sockets without moving the head.

2. At the other extreme is the tiny, taxonomically controversial primate *Tarsius,* which has eyes that are much larger than the size of the supporting orbit, into which they fit tightly. Therefore among species of this genus it is the head that is very mobile, as tarsiers can almost turn their heads and look straight

backward while their immobile, enormous eyes remain staring straight ahead of the skull's long axis (Niemitz, 1985).

Despite the tight fit of the enormous eyes in their sockets, tarsiers also have the normal complement of six extraocular eye muscles that are found in all primates, and these muscles are comparatively well developed. Evidently these muscles remain quite functional, although dwarfed somewhat by the enormous eyeballs (J. Pettigrew, personal communication). Pettigrew also suggests that the eyes of tarsiers function in a similar way to those of owls. Measurements of eye movement in owls show that they line up their visual axes (vergence) during photopic (high level) light conditions in advance of the dim light when they detect their prey and pounce on it. Pettigrew writes: "This very slow kind of eye position adjustment is to be contrasted with the saccades [rapidly dashing eye movements that occur when changing focus from one point to another] that most people think of in the context of eye movements. Owls and tarsiers do not appear to have those." Scotopic (low level) light conditions make it difficult to align the eyes accurately. Pettigrew suggests that both owls and tarsiers utilize a "sit and wait" strategy for hunting and align their eyes at the substrate before it gets too dark to do so. These predators then use the preset eye position to maximize binocular summation and hunting success. In this context it should be kept in mind that both of these predominantly nocturnal animals hunt and forage not only under dusk and dawn conditions but also during the night when moonlight brightens their environment.

Primates exhibit many variations of eye mobility between these two extremes. Heesy (2004) points out that variations in eye mobility is a reason to be cautious when measuring visual field orientation, as each field can be individually and intentionally adjusted—within limits—to react to visual demands. The visual field angle is usually measured "between the sagittal plane of the skull to the sagittal plane of the orbital rim" (Cartmill, 1972 loc. cit. page 109). However, the orbital rim itself can also be tilted dorsoventrally and can be moved three-dimensionally either laterally or medially within the overall architecture of the skull.

Most mammals have eye axes that are more or less directed laterally; in tree shrews the eye axes enclose an angle of 140 degrees. Among members of the family Lemuridae, this angle ranges between 60 degrees and 70 degrees, whereas it measures 90 degrees in *Daubentonia madagascariensis,* a lemur species whose eyes are also tilted slightly upward. Finally, the angle measures only approximately 30 degrees in monkeys. However, the axis through the center of the bony eye socket does not necessarily coincide with the optical axis of the eyeball. The optical axes of the eyeballs enclose a slightly smaller angle than the axes going through the center of the eye sockets (Schultz, 1940). Among Anthropoidea the optical axes are usually directed more or less parallel to each other and forward.

The reorientation of the orbit, and thus eyeballs, into a frontal position increases binocular overlap but at the same time diminishes the width and total size of the visual field (Simons, 2007, in press).

In species of Lorisidae the skull is dorsoventrally flattened, with the eyes directed slightly upward rather than forward or sideways. Notably, lorisids habitually move around cautiously, often with their heads pointed downward, a trait that has been correlated with the eye position. However, the tiny slender lorises *(Loris lydekkerianus)* that rush around the canopy with great agility and dexterity seem not to point their heads downward (Nancy Stevens, personal communication).

The Substructures of the Eyeball

On all but its anterior surface the globe of the eye is enveloped by three distinct cellular layers, the innermost of which (toward the center of the eyeball) is the retina. The retina is the most highly sensitive area and is where photo transduction occurs (the process by which incoming light information is translated into optical impulses that ultimately lead to visual perception). The next layer in an outward direction is known as the choroid, or uveal, layer and it constitutes a highly vascularized layer containing various interwoven capillaries that provide the blood supply to the outer portions of the retina. Toward the front of the eye this layer also forms the ring-shaped colorful iris containing muscles that control the diameter of the pupil. The third layer is the tough, opaque, outermost fibrous tunic or sclera, which forms the outer lining of the globe. It is the whitish colored sclera that merges into the clear cornea at the front of the eye. The sclera also provides a surface for insertion of the six extraocular eye muscles that rotate the eye. Outside the pupil is the ciliary body that suspends both the iris and the transparent lens with slender ligaments.

The iris is shaped like a ring and encircles the dark pupil in its center. Two counteracting muscles are located within the area of the iris. One is circular and surrounds the pupil; it is also known as the sphincter that constricts the pupil. The second muscle is radially arranged like the spokes of wheels; it enlarges the pupil. On the outside of the iris and within the ciliary body resides the ciliary muscle that controls the shape of the lens, a transparent, circular, biconvex, diaphanous structure. The lens is situated between the iris, pupil, and anterior chamber of the eye. This latter space is positioned between the lens and the cornea in the front of the eye. The clear vitreous body is located next to it on the inside and constitutes the eye globe's center.

The inside of the bony eye socket, or orbit, is lined by periosteum, which is referred to as the periorbital. In primates there are six extraocular eye muscles attached to the sclera of the eyeball. All originate from various positions within the orbit and move the eyeball. Also contained within the orbit are the tear

(lachrimal) gland and ducts in addition to various blood vessels, nerves, and connective tissue, much of which contains fat cells.

Equally important for enhancing visual acuity is the acquisition of stereoscopic, three-dimensional vision. As visual stimuli are received by the retina, they trigger a series of impulses that are ultimately transmitted to the brain by the optic nerve. An individual optic nerve carries fibers (the axons of ganglion cells) from both sides of the eyeball, the nasal (inside) portion and the temporal (outside) portion. The fibers from the temporal side of the retina remain uncrossed, whereas those of the nasal portion cross over to the other optic tract. Thus each optical nerve coming from the eye carries fibers from both sides of the eyeball: the nasal (inside) portion and the temporal (outside) portion. The nasal fibers from the right eye go to the left hemisphere of the brain, and the nasal fibers from the left eye cross over to the right hemisphere of the brain. Thus the optic fibers from the right half of the retina of both eyes are carried to the right brain hemisphere and the fibers from the left half are carried to the left hemisphere of the brain.

This crossing-over of optical fibers takes place in the chiasma opticum, or optic chiasma (*chiasma* from the Greek letter *chi,* meaning "cross"), which is situated at the base of the midbrain just in front of the hypophysis or pituitary gland (Figure 9.17). Among primitive mammals all the optic fibers are crossed (decussated) and go from either eyeball to the opposite sides of the brain. As the eyes are situated laterally on the skull in such mammals, two independent pictures are received and conveyed to the opposite sides of the brain. Thus, images from

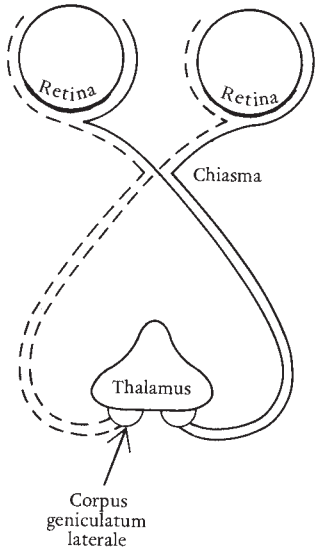

Figure 9.17 Optic chiasma.

both sides of the head are evaluated independently. Detailed depth perception is only possible in those mammals whose eyes are positioned more or less frontally and therefore are able to perceive one overlapping, binocular field of vision with both eyes and are able to project near-matching images on to the retina of each eye. Such an arrangement is termed "binocular visual field overlap" and is how a large visual space is projected on to both retinae simultaneously.

The crossing of the optic fibers makes it possible for more or less identical optical impulses from both eyes to be processed in the same area of the brain's cortex. This arrangement is what makes stereoscopic vision possible. It is known that in *Tarsius* only between 25% and 35% of the fibers remain uncrossed. In Anthropoidea and humans, approximately 40% of the optic nerve fibers remain uncrossed and continue on to the optic tract of the same side of the brain as their side of origin in the retina. Among primates that generally have well-developed visual adaptations, about 70% to 80% of the optic fibers terminate in primary optical centers, the so-called lateral geniculate bodies, that are part of the thalamus. Most of the fibers of the optic tract terminate here, and impulses are relayed from there to the visual cortex that surrounds the calcarine fissure. Distinctive differences can be found in the way these layers of neurons are arranged in their cell densities, and in the way the optic fibers terminate in them (Rosa and Tweedale, 2004; Kaas, 2005a; Werner et al., 2005).

The Retina and Its Substructures

Developmentally the retina is an extension of the central nervous system, because it converts light impulses into electric messages that are transmitted directly to the visual pathways of the brain. Thus the retina itself can be regarded as an integral extension of the optic nerve. It has two layers, which are in turn also stratified into sublayers. The outer pigment layer coheres loosely with the choroid plexus. It is made up of two different cell strata: the outer pigmented layer (away from the center of the eye), composed of pigment granules followed inward by the photoreceptors, and the innermost layer consisting of various nerve cells (Silveira et al., 2005), which in turn contact the vitreous body of the eye on the inside (near the center of the eye). Photoreceptors contain pigments that absorb light impulses and start the electrophysiological chain of events that create vision.

The photoreceptor layer of the retina is usually made up of two types of photoreceptors that connect with bipolar and horizontal nerve cells. It is their overall shape from which these receptors got their names: Cones are narrow and cylindrical in shape, and rods are longer but often have smaller diameters than cones (Figure 9.18). However, the diameter of such photoreceptors is variable and depends to some degree on the level of tightness in which they are packed together, which varies within and between retinae. If rods and cones are scattered

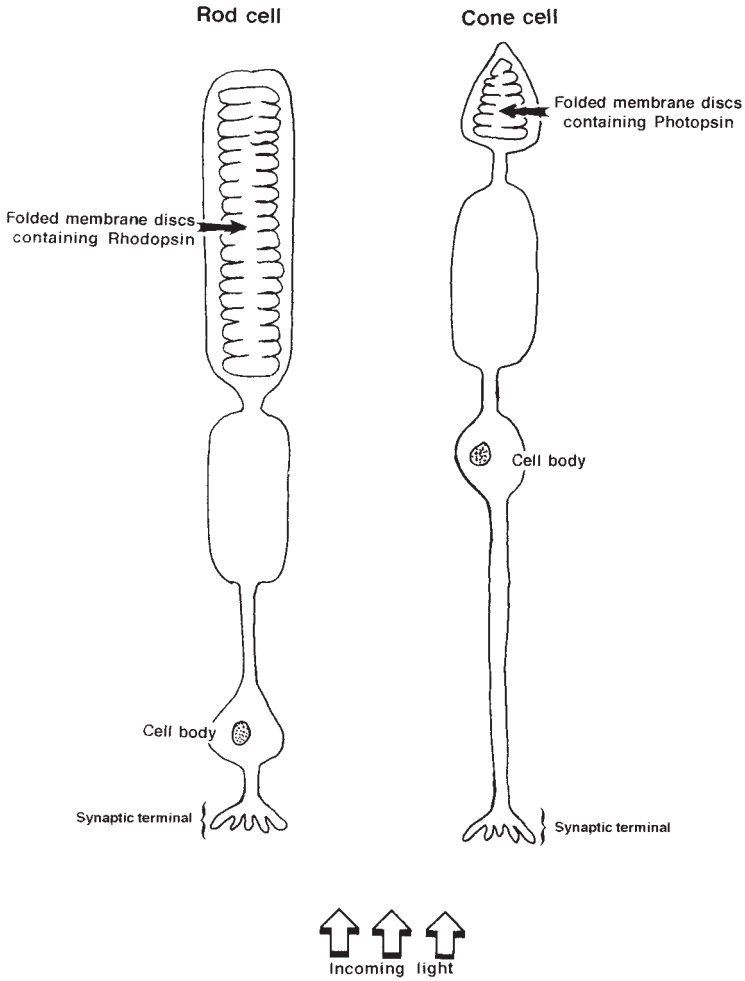

Figure 9.18 Retinal cone and rod cells.

apart, a regular mosaic pattern will not occur (Sharpe et al., 1999; Cook and Chalupa, 2000). Cones and rods are differently specialized. Cones provide high spatial resolution but are comparatively insensitive to light; they are specialized to recognize objects with acuity and with color perception. While rods are highly sensitive to light intensity and function in low light scenarios, they do not discern colors. In anthropoids cones can be linked to single bipolar cells. In contrast, multiple rods connect to single bipolar neurons. Both photoreceptor types are arranged perpendicular to the surface of the eye.

Three distinct photo pigments, which provide the basis for color perception, are found in cones. Rods have only one. The light-sensitive pigment rhodopsin is located within the outer portions of the rods. Rhodopsin (also known as visual purple) is a photoreceptor protein and a pigment of the retina that is responsible for the first events in the perception of light. It is a conjugate of the protein opsin, a phospholipid, and the vitamin A aldehyde retinal. Rhodopsin comes in ranges that are sensitive to different wavelengths and is a pigment that facilitates the absorption of low-intensity light. Thus rods are sensitive to low-level light and black and white discrimination and function predominantly at low light input (Silveira, 2004). Cones function in high-intensity light. The broad ends of the receptors are directed toward the center of the eye. The pigment in the outer portion of the cones is iodopsin, a photosensitive pigment which contains a protein similar to rhodopsin.

The process of how human cone types and their higher order neural circuits generate the sensation of color is still not entirely understood.

Generally, three different light intensity levels are recognized:

1. **Photopic** (from Greek *phos,* meaning "photos, light," and *optikos,* meaning "related to seeing") vision of high intensity light impulses is predominantly executed by the cone cells (Ali and Klyne, 1985). Photopic vision is the ability to see during normal daylight conditions for which human use at least three kinds of cones sensing three colors and their many possible combinations. The pigments of these cones have maximal absorption at wavelengths of around 445 nm (nanometer, a billionth of a meter, or 10^{-9}) (blue), 535 nm (green), and 575 nm (red). The sensibility ranges of these cones overlap each other and thus provide continuous vision throughout the entire visual spectrum of colors. Cones contain so-called opsins, complex light-absorbing proteins that allow for complex color recognition (Hunt et al., 2005).

2. **Scotopic** (from Greek *skotos,* meaning "night, darkness") vision at low light intensity, involving recognition of shades of gray and adapted to low light intensity, is performed by the rod cells. Rods contain only the light-sensitive protein rhodopsin with sensitivity at about 500 nm.[4]

3. **Mesopic** (Greek *mesos,* meaning "middle") vision is a combination between photopic and scotopic vision under low intensity light conditions. In this situation the total sensitivity of the rods that are sensitive for the blue range of color vision combine with the perception through cones. This combination results in perception of especially vivid blue hues of flowers at dusk and dawn. The term "mesopic" was initially used by Palmer (1966) and is now applied widely in optometric research (Shin et al., 2003).

[4]The definition of "scotopic vision" actually dates back to Schultze (1866), and not to Walls (1942) as Martin and Ross, 2005, page 9, proclaim.

The retinae of most primates generally express at least two different types of cones. They are sensitive to either short or middle wavelength light (S- and M/L-cones)—at least as far as is known among primates that have been studied. There are only two known exceptions among primates to this kind of arrangement: the New World owl monkey *Aotus* and the greater bushbaby among lorisoid primates have only one single M/L-cone type and no S-cones (Jacobs et al., 1996) and therefore are functionally colorblind. Mouse lemurs, *Microcebus murinus,* have been shown to have a single population of M/L-cones and few S-cones, the latter amounting to less than 2% of all cones. According to Dkhissi-Benyahya et al. (2001) "The densities of rods, cones, and ganglion cell layer neurons represent a compromise between spatial resolution and sensitivity for both photopic and scotopic vision" (loc. cit. page 490). *M. murinus* does not have true color vision.

In mammals M/L-cones usually outnumber S-cones. When the latter are present there are only typically about 1%, although there may be up to 10%, S-cones of the total cone counts (Ahnelt and Kolb, 2000; Calkins, 2001). Cones are distributed in a quasi-regular fashion but of variable density over most of the retinal surface. Moreover, the different photoreceptors and underlying neurons in the plexiform layers are usually distributed across the retina in a structured manner, forming regular patterns that are appropriately called "mosaics." It is also suggested that the neurons in the brain proper are distributed in regular mosaic patterns (Cook and Chalupa, 2000). Such patterns of rod and cone mosaics appear to be correlated with overall packing density of the photoreceptors. The more photoreceptors per retinal unit, the more coordinated the mosaic. The developmental events leading to the regular retinal cone/rod pattern are intricately correlated with the emergence of the underlying neural cells and the synthesis of rhodopsin, which identifies the rods as positional markers (Finlay et al., 2005).

As we have already noted, cones function during high-intensity light. The broad ends of the photoreceptors are directed toward the center of the eye. Rhodopsin is occasionally and erroneously also spelled rodopsin; this erroneous spelling has been explained as to supposedly be a combination of "opsin" and "rod."

Animals that have retinae which contain almost nothing but rods are usually night active (nocturnal), but as a rule even they have a few cones and are able to see during dawn and dusk (crepuscular). Those animals whose retinae are made up of a comparatively higher number of cones in relation to the number of rods are mostly active during daylight (diurnal). Interestingly, rods are much more numerous in the human retina than cones, comprising 95% of all photoreceptors (Wikler and Rakic, 1990; Sharpe et al., 1999; Finlay et al., 2005; Figure 9.19), which is also the case for other diurnal primates, indicating that visual acuity is more important than color recognition. This fact was first recognized by Osterberg in 1935.

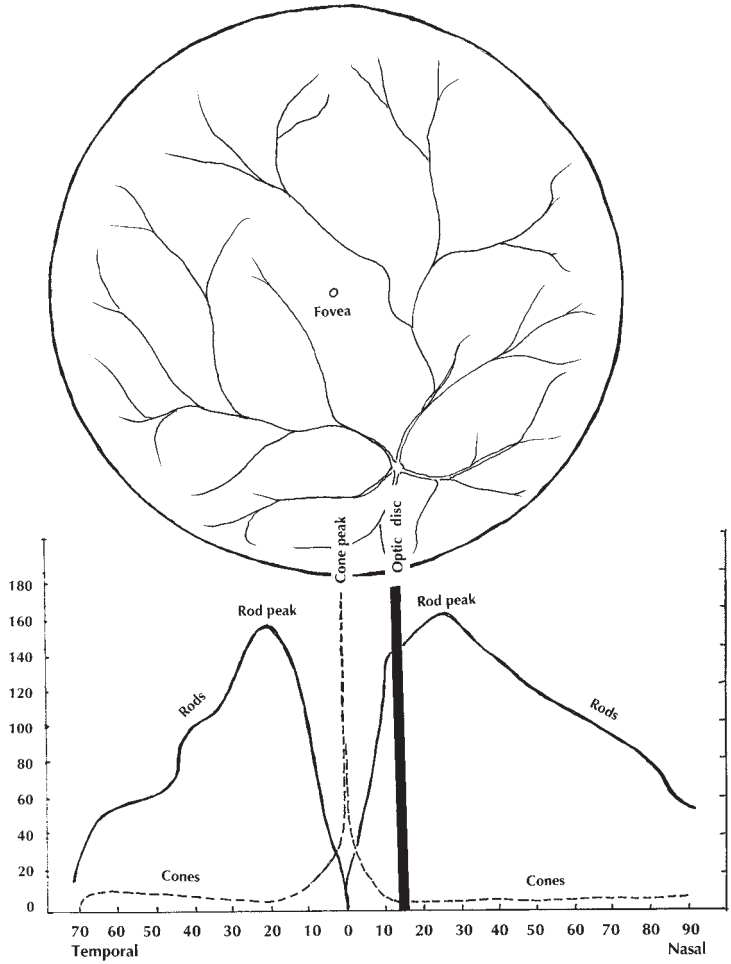

Figure 9.19 Graph showing the numbers of human cones versus rods. Vertical scale: density of receptors ($mm^{-2} \times 10^3$). Horizontal scale: eccentricity in degrees. Vertical black line = Zero photoreceptors in the blind optic disc area; dashed line = number of cones that is highest in the fovea centralis area. Thin black line = number of rods. Adapted and recomposed from Osterberg, 1935.

The number of rods versus the number of cones increases differentially during retinal neural development. In humans and marmosets *(Callithrix jacchus)* cone numbers develop by less than a factor of two, while rods increase by a factor of more than ten. This accounts for the disparate numbers of the two kinds of photoreceptors (Finlay et al., 2005).

The neural connection differs between cones and rods. The neural pathway from the cones has a one-to-one relationship between photoreceptors and nervous

conduits. Each cone is connected to only one (or very few) bipolar ganglion cell and one retinal ganglion cell. In contrast, several rods are connected to only one bipolar cell, and many bipolar cells communicate with one ganglion cell. This convergence of light input from several rods combined under scotopic conditions makes them more sensitive as multiple small signals combine to generate a large response in the bipolar cell. This convergence of several photoreceptors reduces spatial resolution but increases light sensitivity. In contrast, the neural transmission system through the cone pathway, which involves just one cone to one bipolar cell and one ganglion cell, maximizes resolving power (i.e., acuity) in addition to allowing color recognition.

In humans the cones are equidistantly distributed between the many rods at a low density across the retina in a regular mosaic pattern. Cone density in the retina increases toward the fovea while the number of rods decreases; the fovea proper is entirely made up of cones.

The Macula Lutea and Fovea Centralis

All ganglion cell axons exit the retina through a circular spot located in the nasal part of the retina. This spot is known as the "optic papilla" and is the site where the ganglion cell axons unite to form the optic nerve or tract. As there are no photoreceptors in this small area, it is appropriately referred to as the "blind spot." From this origin the optic nerve travels posteriorly through the bony orbit, through the optic canal, and to the optic chiasma at the base of the diencephalon.

Higher primates, with the exception of the New World owl monkey *(Aotus trivirgatus)*, always have a macula lutea and a fovea centralis exclusively made up of cones: This represents the area of high visual acuity. The macula with the fovea in the center is located at the midpoint where the optical axis meets the retina. A fovea is absent in all other mammals (Walls, 1942). This region of high visual acuity is possible due to the greater complexity of the synaptic relationships (minimal convergence of signal) of the nerve cells in the primate fovea. That is, in the center of the retina, more cone receptor cells are connected to more ganglion cells, and thus the transmission of photo impulses becomes more elaborate (Dacey, 1999). Notably, there are no blood vessels in the macula and fovea proper. Within the macula the cones are longer but thinner than in the outer retina and thus are more numerous and tightly packed together. It can generally be observed that in the center of the retina outside the fovea fewer receptors and connecting neurons are joined to one ganglion cell, as the absolute number of all cell units increases centrally. The differences between the retinae of various diurnal higher primates (except *Aotus*) are mainly of a quantitative rather than qualitative nature.

Among diurnal anthropoids the macula lutea is an oval yellow spot that is located in the optical axis of the retina and has a dimplelike depression in its

center, known as the fovea centralis. This small pit in the center of the retina is the area of greatest visual acuity; it is formed only by cones and is the thinnest part of the retinal "pavement" proper. Developmental centripetal migration of photoreceptors toward the central retinal area seems to be crucial for the proper formation of the foveal area (Provis et al., 1998). Here the cones are more tightly packed than anywhere else within the retina. Blood vessels are absent because of this tight packing.

Aotus has been studied extensively because it is the only anthropoid primate with the comparatively large eyes characteristic for nocturnal primates. *Aotus* does not have a true cone fovea, but the retinal area where a macula and fovea would occur does have a few cones between many rods (Finlay et al., 2005). Earlier reports state that the owl monkey is afoveate (Jones, 1965; Ferraz de Oliveira and Ripps, 1968), though Ogden (1974) reports that one in ten *Aotus* retinae have a rudimentary foveal pit. Webb and Kaas (1976) also declare that *Aotus* does not have any fovea. Ogden also found that rods are more numerous in the area centralis of *Aotus* and that unlike the foveal area of other higher primates, it is heavily vascularized. Overall owl monkey retinae have very few cones (Murray et al., 1973; Ogden, 1974). In *Aotus* as many as 200 rods are connected to a single bipolar cell (relatively high convergence), thereby facilitating increased sensitivity to low light conditions. Webb and Kass (1976) also report that *Aotus* does not have any fovea. These authors compare the central retina of owl monkeys to that of cats because in both groups the ganglion cells are tightly packed and even layered three cells deep, containing many more ganglion connections than are reported from the foveal area of diurnal primates. *Aotus* does not have the highly developed visual acuity found in diurnal anthropoids and is better equipped for scotopic perception.

Various retinal features called foveae are also present in fish, reptiles, and diurnal birds but are morphologically and functionally different from those of primates (Walls, 1942). Among mammals only the diurnal anthropoids have true foveas. Such a variety of foveas in other vertebrates are not directly comparable and cannot reliably be ordered into a unifying visual and behavioral grand scheme of foveal function and evolution among the various higher vertebrate taxa (Pettigrew, personal communication).

As already mentioned, all anthropoids exhibit both types of cone photoreceptors, the only exception being the owl monkey genus *Aotus,* in which the rods almost totally outnumber the cones (Ogden, 1975). Moreover, only one kind of M/L-cone photopigment is present in these primates. Although an S-cone photopigment has been found it seems to be nonfunctional. Based on this combination of functional photoreceptors it can be concluded that owl monkeys are colorblind.

The numerical relations between the different types of cells vary and often are characteristic for genera or even species. For example, species of the nocturnal

genus *Tarsius* have both rods and cones in combination with a fovea that is clearly packed with cones (Hendrickson et al., 2000).

Franco et al. (2000) studied cone density in the retinae of five New World primates, with special consideration of the foveal area. They observed that foveal dimensions do not vary with retinal or body size, an observation that also has been made among members of the Old World monkey genus *Macaca* and in humans. The diurnal primate fovea is functionally correlated with high visual acuity.

The Tapetum Lucidum

Tapetum lucidum is Latin and means "shining layer." It is present in almost all groups of animals. Such structures have been described in both invertebrate and vertebrate taxa, although the layer that makes eyes shine differs anatomically between the former and the latter groups. Moreover, the exact structure and distribution in primates alone still remains somewhat enigmatic (Schwab et al., 2002). Notably, there is a second phenomenon that makes eyes shine that is not related to a structural tapetum but is appropriately called eyeshine. Both features make eyes light up when they are directly illuminated by a flashlight or other powerful light sources.

The tapetum improves vision during low light conditions but may also cause what is perceived as a blur as reflected light interferes with the directly incoming incident light. Tapeta occur in many vertebrates, particularly nocturnal animals with good night vision, such as cats and dogs. This feature is responsible for the feline and canid equivalent of the "red-eye" effect, causing eyes in flash photographs to appear to "glow" in one of a wide variety of colors including blue, green, and yellow. Humans do not have a tapetum, nor do other anthropoids. In humans the well-known red-eye effect in photography occurs when the picture is taken with a photographic flash. As the speed of the flash is too fast for the iris of the eye to close the pupil, the blood-rich retina causes the red reflection of the retina at the back of the eye. The tapetum works roughly on the interference principles of thin-film optics, as seen in other reflective tissues such as butterfly wings (for example the Blue Morpho butterfly). However, different species have various types of structured tissue that lead to different mechanisms of reflective interference. Known tapetal structures include the following:

- **Retinal tapetum** is found in teleosts, crocodiles, marsupials, and fruit bats.
- **Choroidal tapetum fibrosum** is the simplest tapetum and is found principally in mammals, cetacaeans, some marsupials, and a rodent *(Cunniculus pacas)*.

- **Choroidal tapetum cellulosum** is found in cartilaginous fish, coelacanths and lungfish, seals, prosimians, and carnivores and contains a variety of reflective compounds.

There appears to be no source for reliable information or agreement about the presence or absence of tapeta among extant primates (Ollivier et al., 2004). Kay and Kirk (2000) introduce this uncertainty factor into their hypothetical discussion about tapeta in extinct stem primates. Because we know little about tapeta in extant primates, any inference about tapeta in stem primates in relation to presumed nocturnal habits remains without basis (Schwab et al., 2002). The statement that tarsiers and owl monkeys have "hypertrophied eyes because they lack a tapetum" (Cartmill, 1980; rephrased by Martin and Ross, 2005, loc. cit. page 12) invokes an unsubstantiated causality. Although this correlation may initially seem an intriguing observation, it is not supported by anatomical facts. There is no evidence for any correlation between the presence of a tapetum and the size of the eye (Schwab et al., 2002). Despite this insight the assumption that the absence of a tapetum in *Aotus* and *Tarsius* causes their eyes to be "hypertrophic" has been perpetuated (Kay et al., 2004, loc. cit. page 1157: "This hypertrophy stems from the absence in *Aotus* and *Tarsius* of a tapetum lucidum, a reflective layer behind the retina"). Notably, although the eyes of *Aotus* are comparatively large, they are by no means hypertrophic nor anywhere near as large as the eyes of tarsiers.

The tapetum is an additional cell layer located within the choroid that envelopes the retina from behind and is, like the choroid itself, extensively vascularized by a web of capillaries. A true tapetum is found in many mammals (Ollivier et al., 2004). The tapetum's light reflections are differently colored among different groups of animals, varying from green to blue in animals such as carnivores, ungulates, and rodents to yellow and red in certain marsupials and some primates. A choroidal tapetum lucidum cellulosum is found in several prosimians; some of these are nocturnally active, but many others are diurnal, including *Lemur catta* and some of the indriids (Rohen and Castenholz, 1967; Starck, 1995). A tapetum is presumed to be missing in the species of the anatomically unique nocturnal prosimian *Tarsius* and also in several diurnal or crepuscular *Eulemur* species (e.g., *Eulemur macaco, E. fulvus*). No obvious correlation exists between the diarhythm of an animal species and the presence or absence of a tapetum. The tapetum is absent among species of the tree shrew genus *Tupaia,* but is present in all the lorisids and galagids whose retinae have been studied. It is interesting to note that a *tapetum* is not only absent in some diurnal *Eulemur* species, but is present in diurnal Indriidae. Pariente (1976) studied the tapeta of several prosimians and documents the presence in them of riboflavin crystals that are arranged in different characteristic patterns.

Whether species of *Aotus,* the South American owl monkey, have a tapetum is undetermined because of conflicting statements concerning its occurrence. Thus comments about the presence or absence of a tapetum or eyeshine in *Aotus* can only be regarded as being anecdotal.[5]

Rohen and Castenholz (1967) carefully studied the eyes of *Aotus* with histological methods and state that *Aotus* does not have a cellular tapetum. Could it be that a case of eyeshine occurs in these monkeys, a phenomenon also known for humans in photographs that have been taken with the assistance of a photographic flash? Another question remains unanswered: whether tapeta can be individually present or absent within primate species. As stated previously, a tapetum seems to be lacking in the nocturnal genus *Tarsius.*

There is unfortunately still no in-depth comparative anatomical study of the distribution, structure, and function of this morphological feature of the mammalian eye, only a lot of speculation. It is therefore difficult to properly hypothesize about the occurrence of the tapetum lucidum among extant or extinct primates (see also Kirk and Kay, 2004). Interestingly, Kirk (2006) reports that the tapetum mystery might be caused by intraspecific variation—some have it, some don't—which might be the reason for the conflicting observations involving the tapetum of *Aotus.* Kirk also reports that the tapetal riboflavin in *Eulemurs* has a way of dissolving and vanishing when eyes are processed for histological investigation, which also could cause conflicting observations (Kirk, 2006).

The Genetic Connection: Opsins and Genes

A gene identified as being crucial for the development of all known eye structures across phyla, Pax-6, was originally discovered in the fruit fly *(Drosophila melanogaster).* If it is eliminated in the fruit fly, eye loss occurs (Halder et al., 1995; Hanson and Van Heyningen, 1995; Macdonald and Wilson, 1996; Callaerts et al., 1997). Pax-6 has been recognized as a homolog of the vertebrate Pax-6 gene, which causes abnormalities in vertebrates (mouse) such as aniridia (loss of iris) and reduction of eye size (Harris, 2001). However, Pax-6 is also crucial for various other normal developments of invertebrate and vertebrate organs (e.g., nasal epithelium, brain and spinal cord of the mouse). This gene appears to be generally and critically involved in eye development among several

[5]Assertions that it has a tapetum are: Walls, 1942 [who however, according to Kirk and Kay, 2004, loc. cit. footnote p. 547, retracted his earlier published assertion in a less well-known publication, Walls, 1953, p. 62]; Rohen and Castenholz, 1967; Ankel-Simons, 2000; Schwab et al., 2002; and Ollivier et al., 2004. In a footnote Osorio et al., 2005 (loc. cit. page 120) refer to a personal communication by E.J. Warrant affirming that "the owl monkey's eyeshine is 'brighter than a cat's', and this is the case for wild Panamanian owl monkeys; E.J. Warrant, personal communication."

Assertions to the contrary are: i.e., that it doesn't have one, Rohen, 1962; Hershkovitz, 1977; Kinzey, 1997; Wright, 1994; and Kirk and Kay, 2004.

disparate phyla, which has led to theories claiming that these various invertebrate and vertebrate eyes have to be the result of coincidental, similar evolution (Callaerts et al., 1997; Fernald, 2000). However, this hypothesis has now been put to rest by the following finding:

> "The molecular evidence that first challenged the concept that different eye types evolved separately in unrelated ancestors is related to a very well conserved gene called Pax-6. This so-called "eye master gene" can trigger some aspect of the eye developmental programs in many Phyla, ranging from the expression of some eye-specific proteins (see below) to the formation of an entire functional eye." (D'Alterio and Loza-Coll, 2003, loc. cit. page 27).

Considering that all living organisms are basically made of the same DNA, it is not at all surprising that there must be "master genes" that have the same or similar functions in the various animal phyla. The gene Pax-6 is an excellent example of such a gene (Pichaud et al., 2001). D'Aliero and Loza-Coll, (2003, loc. cit. page 29) sum up their observations by pointing out: "In sum, what might seem a paradox between analogy and homology at the structural and genetic levels respectively may just be a consequence of a rather limited but plastic and efficient enough spectrum of genetic programs that were used once and again during evolution to generate the most diverse structures." There is no doubt that with time we will discover many more such "master genes" as knowledge about genetic programming and developmental processes will be better understood.

Rods and cones are actually modified neurons. Both cones and rods contain so-called visual pigments called opsins. These pigment molecules, including the component retinal, are very important for vision as they transpose various light impulses (photons) into electrical impulses in the retina. Retinal is a derivative of vitamin A that is bonded to a membrane protein called an opsin. Vitamin A cannot be synthesized by mammals and therefore has to be ingested. Opsins, or apoproteins, are bound to chromophors (Sharpe et al., 1999; Stockman and Sharpe, 1999; Jacobs and Rowe, 2004) and vary in chemical structure among the different types of photoreceptors or cones. Specific opsins in combination with retinal are called photopsins and together define the light-absorbing potential of the cone photoreceptors. Cones are distinguished according to their ability to absorb different colors, namely red cones, green cones, and blue cones. These three cone types work together and overlap each other functionally, thereby making it possible to perceive many other hues than just red, green, and blue. In vertebrates the genetic sequences for a single rod opsin has been determined: RH1 is localized to rod photoreceptors (with a single gene that in humans is located on autosome 3) and is therefore known as rhodopsin. Four different cone opsin genes have been identified, including RH2 (green-sensitive cone opsins), SWS1 (ultra-violet to blue, located on autosome 7 in humans), SWS2 (blue sensitive), and M/LWS red/green sensitive opsins (located on the X sex chromosome). Most mammals generally have only three of these, namely

rhodopsin (RH1), and two photopsins, SWS1 and LWS. Hence, mammals, with the exception of primates, are basically dichromats. Several nocturnal mammals, including some nocturnal primates, appear to have also lost the SWS1 opsin; they are monochromats and thus functionally colorblind. SWS1 opsins are possibly involved in sensing ultraviolet light, which is invisible to humans and may actually harm the human retina (Hunt et al., 2005).

There are several other opsins that are located outside the cones in the retina, such as peropsin, documented in humans (Sun et al., 1997), and melanopsin that is found in retinal ganglion cells of humans, primates, and rodents and has been shown to play a major role in mammalian circadian rhythms (Dacey et al., 2005). The role of melanopsin is discussed further in the section on primate diarhythms and biochronology that follows.

As a general rule there is only one opsin gene expressed within individual cones, although occasionally individual cones express two photopigments. Whereas most extant mammals are dichromats, based on the presence of only two different cone opsin genes, encoded by SWS1 and LWS genetic areas, anthropoid primates typically have three such genes. In these cases we find that they may express subtypes of the M and L opsin variety. In fact, primate and human retinas contain cone types and we are now beginning to be able to differentiate between the short wavelength cone and the two longer wavelength cones, although they all look essentially alike morphologically. Modern specialized histochemical techniques make it possible to identify different spectral types of cones in mammalian species. In these cases we find that they may express subtypes of the M and L opsin variety. The loci for M/LWS opsins are all situated on the female sex chromosome, the X chromosome (Kremers et al., 1999; Silveira et al., 2005). For Old World primates and humans the duplicated genes generate opsins that are most sensitive to red and green wavelengths. The combination of the two M/LWS opsin genes, plus the SWS opsin gene located on chromosome 7, makes it possible for Old World primates to express three different cone photopigments, each of which is spectrally sensitive to different wavelengths of light, thereby allowing for trichromatic color vision (Table 9.1). These animals are referred to as "trichromats." Those with two cone types are dichromats, and animals with a single cone type are called monochromats. For example, among primates, humans and macaques (the latter is the most thoroughly studied genus of Old World monkeys in this respect) are normally trichromats (Jacobs et al., 1991).

Striking color signals are found among many diurnal primates. The most colorful primate species is without doubt the male gender of the Old World monkey Mandrill *(Mandrillus sphinx),* which has startling blue paranasal ridges (these are whitish-blue to white in females) along a bright red center stripe on top of the long nose. The nose and lips are bright red, and the chin is covered with white fur that blends into an orange-colored beard. The head and body

Table 9.1
Opsin Genes, Their Wavelength, Color Range, and Chromosome Location

Opsin gene	Wavelength	Color range	Chromosome location
SWS	~420–450	Blue to green	Chromosome 7
MWS/LWS	~520–580	Green to orange	X chromosome
RH1	~480–510	Bluish sensitive	Chromosome 3*
RH2	~470–540	Blue to green	Chromosome 3

*See Sparkes et al., 1986.

pelage is black, white, and reddish yellow. The anal region and base of the tail are bright red, surrounded by a vivid blue patch of skin that extends onto the rump. Males of another Old World monkey species, the Vervet *(Cercopithecus aethiops),* also sport vivid blue colors on the scrotum that surrounds a flame-red penis. Bright blue skin colors are rare among mammals and are, in addition to these few catarrhine primates, only found in a few marsupials. All primate and marsupial species that exhibit such blue colors appear to be trichromats. Recently it was reported that the blue of their skin is a structural color, not the blue caused by the physical interaction of light waves with reflective nanostructures (also known as Tyndall effect or Rayleigh scattering: the blue of cloudy media such as blue water, sky blue, butterfly wings—compare also tapetum) that are known in other animals. It now has been shown that the striking blue skin of these primates and marsupials (*Marmosa mexicana* and *Caluromys derbianus*) also are so-called structural colors that originate within superficial collagen nanostructures that superimpose a layer of melanocytes. The melanin layer absorbs the incoming light waves. However, the vivid blue of the Mandrill's face lacks the underlying melanin stratum, and here the vivid blue is created by much more extensive thickness of the collagen strands; the collagen fibers are packed twice as thick on the mandrills face than across the blue rump, where the collagen is supported by the melanin layer (Prum and Torres, 2004).

While above we described the conventional view of the trichromatic retina of Old World primates (including humans), more detailed genetic analyses of opsin loci have revealed that, at least in human females, four different photopigments may be produced (Jacobs, 1996; Sharpe et al., 1999, loc. cit. page 39; Jameson et al., 2001). Experimental tests documented that "women with four-photopigment genotypes are found to perceive significantly wider chromatic range in comparison with either male or female trichromat controls." Jameson et al. (2001) substantiate this by proposing that, from the view of molecular genetics, a number of women have more than three kinds of retinal X-linked photopigments. At present there is no documentation about the frequency of distribution of tetrachromacy among human females. Women who do have this visual capability are able to see many

more hues than trichromatic women. It is generally known that males and females differ in their ability to perceive color (Bimler et al., 2004). For example, isolated human populations exist that are totally colorblind (Sundin et al., 2000). From this we may consider that other primates have this potential to vary, with additional photopigment opsin genes yet to be discovered. Such opsin genes could provide visual potentials that are currently undocumented.

The monkeys of the New World have an intriguing combination of polymorphic color vision, caused by three allelic variants of a single locus red/green opsin gene that is located on the female X chromosome. Because males have only one X-chromosome and one Y-chromosome, they have only one allelic red/green opsin gene. Because of this X-linked pattern of inheritance, many of the South American monkeys have trichromatically capable females and males that are only dichromats. However, as we have seen before, the actual color visual acuity also depends to great extent on cone density and their distribution in the retina.

An interesting and beneficial aspect of the presence of dichromatic-male and trichromatic-female color vision within populations of the same species of South American monkeys is that it can serve as a mechanism that opens different visual food detection windows for the two sexes. Family groups with trichromatic females and dichromatic males have a greater variety of food item selection and distribution than families with only one type of color vision would have. Thus the variety of available potential food resources increases as it is spread out between the sexes. However, there is still much confusion concerning the importance of dichromace versus trichromace for primate food selection. Comparatively studying the only trichromatic New World monkeys, genus *Alouatta,* and bi/trichromatic *Ateles* in relation to ability to detect edible fruit, Stoner et al. (2005) conclude that their "findings show that the effect of polymorphism in platyrrhines on fruit detection may not be a disadvantage for frugivory" (loc. cit. page 399). Unexpectedly, the bichromats did as well as the trichromats. Another such study involving genus *Ateles* proposes that a high concentration of glucose in fruit in combination with (female) trichromace might be correlated with foraging advantages (Riba-Hernandez et al., 2005).

A fraction of theoretically visible light that has been lost to humans and likely also diurnal higher primates resides in the spectrum below 400 nm and is commonly known as ultraviolet (UV) light. Light with wavelengths below 400 nm and above 700 nm is not detectable to humans and most primates. UV light actually has the potential to harm the light receptive mechanism in the retina of anthropoids (Shi and Yokoyama, 2003; Zhang, 2003).

The opsin most sensitive to UV light is SWS1, and it has been found in some nonprimate mammals (rodents). SWS1 however has the potential to tune to violet light impulses above 400 nm that are visible and not harmful to primates. There is a possibility that some strictly nocturnal primates—if there are any that are unquestionably only active during periods of scotopic light—would benefit from

being able to perceive UV light. Any UV light that higher primates might encounter is screened out before it reaches the retina by the slightly yellowish tinted lens and vitreous body of the eyeball (Jacobs, 1992). All primates have only one single rod opsin gene that in humans is located on chromosome 3 (Hunt et al., 2005); it has sensitivity around 500 nm.

Trichromatic vision is rare in prosimians. Recent genetic studies revealed that some prosimians have opsin gene polymorphisms. Tan and Li's published data evaluate three prosimians, two of which were diurnal and one nocturnal (Tan and Li, 1999), and initially proposed that all three have trichromatic vision. However, a footnote in a subsequent publication by Heesy and Ross (2001 loc. cit. page 149) states, "It has recently been discovered that the allelic data in *Cheirogaleus major* are erroneous (Y. Tan, pers. comm.). *Cheirogaleus* does not possess a polymorphic gene for longer wavelength opsins, and therefore is not trichromatic." (See also Surridge et al., 2003 loc. cit. page 200 footnote; Table 9.2).

Tan and Li document that two of the diurnal strepsirrhines they studied, *Propithecus verreauxi coquereli* and *Varecia variegata rubra,* have not only the SWS (short wavelength sensitive) autosomal (chromosome 7) opsin gene that occurs in all primates, but also show the polymorphic M/LWS X-chromosome linked opsin genes, and thus they state that heterozygous females should be able to have three classes of opsins and consequently be trichromatic like many New World monkeys (Jacobs, 1994/95). The MWS seems to occur in the majority of individuals in these two prosimians. The presence of L pigments has been documented for two species of the mouse lemur, *Microcebus murinus* and *M. coquereli* (Dkhissi-Benyahya, et al., 2002). It appears that among different lemur species genes have been found that encode either the M or L pigments. Diurnal *Lemur catta* and *Eulemur fulvus* have S and an M/L type of cone pigments, and as no polymorphism seems to exist these two species are thought to be dichromats (Jacobs, 2002). Furthermore, both *Tarsius bancanus* and *Eulemur fulvus* species have retained the SWS opsin gene, while it has been lost in two lorisids: *Otolemur crassicaudatus* and *Nycticebus coucang* (Kawamura and Kubotera, 2004). It has been speculated that this might mean that the short-wave SWS opsin gene was lost in all lorisidae.

In contrast, anthropoid primate retinae usually contain two or three different cone photopigments that are sensitive to different light wavelengths; there is only one exception among these primates. The nocturnal South American owl monkey, genus *Aotus,* has only a single cone photopigment (Hunt et al., 2005). Owl monkeys, unlike the other South American monkeys that have been studied, appear not to be polymorphic as far as their cone opsins are concerned. Even though owl monkeys have an S-wave pigment gene that is homologous to the human S-wavelength photopigment gene, they do not appear to have a functional S-wave photopigment (Jacobs et al., 1993). In *Aotus* all males and a

Table 9.2
Summary of Primate Vision

Primate	Biorhytm	Color vision	S wavelength chromosome 7	M/L wavelength X chromosome
Old World Primates	Diurnal	Trichromats	420–450 mn	2 genes, 535, 562 nm
New World Monkeys	Diurnal	Bi/trichromats	420–450 nm	1 gene, 540, 555, 562 nm*
Exception: *Alouatta*	Diurnal	Trichromats	420–450 nm	2 genes, 535, 562 nm
Exception: *Aotus* males†	Nocturnal/ Circadian	Monochromats	S gene defective	1 gene, 540 nm Y-chromosome: 500–570 nm (?)
Exception: *Saimiri*	Diurnal			
females		Trichromats	420–450 nm (?)	1 gene, 538/551, 551/561, 538/ 561 nm*
males		Bichromats	420–450 nm (?)	1 gene, 538, 551, 561 nm
Callitrichidae	Diurnal			
females		Trichromats	420–450 nm (?)	1 gene, 543, 545, 555, 557, 559, 563, 565 nm*
males		Dichromats	420–450 nm (?)	(?)
Tarsius	Nocturnal	Monochromats	420–450 mn	(?)
Strepsirrhines/ Prosimians				
Propithecus	Diurnal	Trichromats	430 nm	545, 558 nm
Lemur catta	Diurnal	Trichromats	420–450 nm	(?)
Eulemur species	Diurnal/ Circadian	Dichromats	420–450 mn	(?)
Microcebus murinus	Nocturnal	Monochromats	(?)	(?)
Otolemur crassicaudatus	Nocturnal	Monochromats	Not retained	(?)
Nycticebus coucang	Nocturnal	Monochromats	Not retained	

Source: Ankel-Simons and Rasmussen, in preparation.
All wavelength values approximate.
(?) indicates no data but assumed to be present.
*Potential variants. Data adapted from Jacobs and Neitz (1987), Surridge et al. (2005), Osorio et al. (2005), and Kawamura and Kubotera (2004).
†Data from Kawamura et al. (2002).

few females are monochromatic and consequently colorblind. However, it has been reported that *Aotus* males do have an extra red-green opsin gene that is located on the Y chromosome (Kawamura et al., 2002). It is claimed that these opsin genes are homologous to the human red-green opsin gene that resides on the X chromosome. Whether they are expressed in the retina and thus functional has not been explored.

There is only one gene that codes for a photopigment on the X chromosome in other platyrrhine monkeys, with the exception of *Alouatta*. This gene however, has three variant alleles, which result in the expression of three dichromatic and three trichromatic phenotypes (Kremers et al., 1999). All male monkeys and female monkeys with the same gene on the X chromosome are dichromats, and females with different genes on the two X chromosomes are trichromats (Jacobs and Neitz, 1987; Hunt et al., 2005).

The New World monkeys that have been studied so far appear to have sex-linked trichromacy and dichromacy based on the presence of an SWS1 gene found on chromosome 7 and a polymorphic L/M gene which resides on the X chromosome (Silveira, 2004). Thus male New World monkeys can only combine the autosomal SWS1 gene with one allelic form of their single X chromosome and consequently are dichromats (Kremers et al., 1999).

Squirrel monkeys, genus *Saimiri,* have been studied extensively (Jacobs and Neitz, 1987), and each has been found to have one of six different variants of color vision. Three dichromatic and three trichromatic variants, which originate from individual differences in cone pigments, have been documented for *S. sciureus*. Saimiris have four different classes of color pigments, and some individuals are dichromatic while other individuals are trichromatic (Jacobs and Neitz, 1987; Jacobs, 1997). The retinas of all squirrel monkeys are thought to have cones that are sensitive to 434 nm. The other three cone classes that have been found (536 nm, 549 nm, and 564 nm), are distributed in a way so that any monkey that is functionally dichromatic also has one of the other three longer wavelength cone types. Trichromatic individuals have any combination of two other cone types in addition to the 434-nm sensitive cones. This kind of specific color vision variability is thought to be genetically based on three alleles that are restricted to a single photopigment locus which resides on the X chromosome. In contrast, humans have several additional photopigment alleles on the X chromosome, and their color vision differs from that of the squirrel monkey. Jacobs (1994/95) also documented that two species of genus *Cebus* (*C. apella* and *C. capucinus*) appear to be polymorphic as far as their color vision is concerned. Fragaszy et al. (2004) point out that the capuchin monkey's ability to see is very similar to that of humans: their visual acuity and sensitivity to brightness are more or less equivalent to macaques and humans. Male capuchins and squirrel monkeys *(Saimiri)* are dichromats, while females may have either dichromatic or trichromatic vision (Jacobs, 1998). Dichromatic and trichromatic

varieties have also been identified in the marmoset species *Callithrix jacchus* and the tamarin species *Saguinus fuscicollis* (Surridge et al., 2005) as well as the titi monkey *Callicebus moloch;* the results for species of Family Atelinae are still less well documented. Atelines also seem to individually have polymorphic color vision (Riba-Hernandez et al., 2005).

Both sexes of the New World monkey *Leontopithecus rosalia*—the Golden Lion tamarin—have vividly orange-colored pelage all over their bodies and thus are highly conspicuous to humans and trichromatic monkeys. But only trichromatic conspecific females are able to clearly see the other orange Golden Lion tamarins. They are not easily visible to the dichromatic majority of females and all dichromatic males. These dichromatic animals can only rely on shape and movement to discern their orange conspecifics (Sumner and Mollon, 2003). The authors conclude stating that the Lion tamarins' bright hues are more important as signals during interaction with trichromatic members of other species that live in the same area than for visibility within the family group.

It is now known that two species of genus *Alouatta,* the howling monkeys *A. seniculus* and *A. caraya,* have remarkably different eyesight from all the other New World monkeys. These two species have fully established trichromatic vision for both sexes not unlike all Old World anthropoids. In contrast to the other South American Monkeys, these howling monkeys have separate L and M genes on their X chromosomes, opsin genes that provide regular trichromatic vision for both females and males. Notably, this duplication event is not present in the two genera *Ateles* and *Lagothrix,* which have one polymorphic L/M gene similar to other New World monkeys (Jacobs and Deegan, 2001; Hunt et al., 2005). The rest of the New World monkeys have only one color pigment gene on the X chromosome, but multiple alleles in both males and females produce various types of dichromatic vision, and some females that are heterozygous at this locus have variations of trichromatic vision (Jacobs et al., 1996).

In sum, New World monkeys, with the exception of two genera, *Aotus* and *Alouatta,* all have color perception separating the two sexes in their visual abilities, clearly setting them apart from the genetically uniform vision among Old World primates. Among New World monkeys, trichromatic females outperform dichromatic males that are almost colorblind in their abilities to discern hues.

Research on Old World primates, including humans, indicates that all of them appear to be trichromats. This has been shown not only for species of genera *Macaca* and *Papio* but also for individuals of *Cercopithecus petaurista*, *C. cephus, C. talapoin*, and *Erythrocebus patas* (Bowmaker et al., 1991). Although the orangutan *Pongo pygmaeus* has trichromatic color vision, when testing gibbons *(Hylobates lar)* the results were variable and appear to differ from that of the orangutan (Deegan and Jacobs, 2001). Color vision in humans and its variants and pathological changes have been widely studied and are the basis for

our understanding of color vision genetics and are reflected in myriad publications on this topic (Preuss, 2004).

The Neural Connection

Most important for achievement of the proper organization and ability to function of the visual mechanisms is the complicated and fragile process of early eye development (Finlay et al., 2005). Developmentally the retina, the neural portion of the eye, actually is part of the central nervous system. In the following the terms "inner" (near the center of the eye) and "outer" (away from the center of the eye) refer to the position relative to the center of the eye.

The incoming light impulses, ultimately reaching the rods and cones and their pigmented epithelium at the back of the eye, immediately pass the receptive fields of various nerve cells that are separated in five distinct cell layers beneath the cone and rod layer. This is the inner nuclear layer. This inner layer is subdivided into two plexiform laminae, which are interspersed by the inner nuclear layer that contains five types of neurons: photoreceptors of the cones and rods in the outer segment of the retina, as well as horizontal, bipolar, amacrine, and ganglion cells, in this order, from outside inward. These cells and their neurons are separated into layers like the skins of an onion, and the cell bodies reside in the inner and outer nuclear layer and ganglion cell layer; synaptic contacts between the various neurons occur in the inner and outer plexiform layers. Thus there is a direct chain of three neural units—photoreceptor/bipolar/ganglion—that conducts the light impulse from the photoreceptor straight to the optic nerve.

At least ten types of bipolar ganglion cells are located in the outer plexiform layer, but only two kinds of horizontal ganglion cells (interweaving with each other in layers that are parallel to the retinal surfaces) are recognized. These are located in the outer and inner plexiform layers. There are two types of horizontal cells on the inner layer, and the cells in the outer layer contain 20–40 types of amacrine cells (Dacey, 1996). The neural pathways of the signals between cones, rods, and their neural connections and signals to the ganglion cells are complicated and not yet entirely understood (Lee, 1999; Werner et al., 2005).

The retina provides unusual insights into the function of the neuronal cognitive system. Many neural circuits that are able to work together to identify static or dynamic aspects of color, brightness, and contrast perception have already been recognized (Cook and Chalupa, 2000). Among them is also a signaling mechanism with ON and OFF function that is evident in the cone–to–bipolar-cell connections (Wässle, 1999).

Individual retinal ganglion cells are tuned to particular light impulses. These stimuli are transferred in an orderly fashion to the terminal ganglion of the visual nervous system; specific stimuli are reflected in receptive fields of neurons.

Primate cone bipolar cells come in two types: diffuse bipolar cells (six different variants: three with ON and three with OFF function), which connect to several

cones, and midget bipolar cells, which usually only connect to a single cone axon terminal (Dacey and Lee, 1999). The ON and OFF antagonism prevents mix-up between cone type-specific excitatory versus inhibitory inputs to retinal ganglion cells. Blue ON and yellow OFF signals originate from bipolar ganglion cells. This cone opponency mechanism functions through ON bipolar cells connecting with S-cones while the OFF bipolar cells operate L- and M-cones. A red–green opponency is suspected to be discharged by the midget bipolar cells, but this connection has not yet been reliably established. Because of the many different cell types involved in this enigmatic network the intricate details of the system still remain in the dark (Dacey, 1996; Dacey and Lee, 1999).

Many comprehensive studies focusing on the similarities and differences between human and nonhuman primates in their cognitive processing capabilities of vision have been assembled in a single volume (Dehaene et al., 2005).

Lateral Geniculate Nucleus

The visual stimuli that are received by the eye and its substructures are relayed through the optic nerve and tract to the thalamus and ultimately the visual cortex of the brain. The dorsal lateral geniculate nucleus (dLGN or LGN) is that part of the thalamus responsible for relaying optical information from the eyes to the visual cortex. In primates the LGN is structured into six crescent-shaped cellular units that are separated from each other by thin layers of neuropil (*pil* from Greek *pilos,* meaning "felt"), a dense, intricate, felt-like structure created by fine glial processes, fibrils, synaptic terminals, axons, and dendrites that shape an area between nerve cells in the gray matter of the central nervous system where most synaptic connections happen. The six laminae of the LGN, numbered one through six from bottom to top, contain two different cell types. Laminae one and two are made up of large cells and are referred to as the magnocellular (*magnus,* Latin for "big") or M-cell (MC) layer. Most of these cells transmit noncolor aspects of vision (e.g., contrast). Laminae three through six are made up of small neurons (P cells) and are termed the parvocellular (*parvus,* Latin for "small") layer. They are concerned primarily with conveying aspects of color and fine detail in the visual image. A third and distinct cellular pathway between the six laminae is made up of so-called koniocellular or K cells (KC), whose contribution to visual perception is not yet entirely understood.

There is one notable exception to this makeup: in *Tarsius* the pathway of retinal afferent signals to the more superficial layer of the dLGN differs markedly from that in all other primates (Rosa et al., 1996). The innervation of the magnocelluar dLGN layers (the way the dLGN is "wired") has been reversed in tarsiers in relation to all other primates. "The characteristic organization of this nucleus in primates, as well as its apparent phylogenetic stability, have led to the proposal that the distinct laminar arrangement of the dLGN is one of the diagnostic characters that define the order Primates" (Rosa et al., 1996, loc. cit. page 121). Thus the unusual

morphology of the retinogeniculate projections they discovered in genus *Tarsius* documents that tarsiers differ from both strepsirrhine prosimians and anthropoids and supports the conclusion that tarsiers split off the primate line very early during primate evolution (Rosa et al., 1996). Yoder (2003) came to essentially the same conclusion investigating this issue with the help of DNA sequence data.

The LGN and cortical visual pathways of primates are discussed in great detail in "The Primate Visual System," edited by Kremers (2005). (See also Bush and Allman, 2004.)

Pathways between the dLGN and the visual cortex of four genera of Old World monkeys *(Macaca, Papio, Erythrocebus,* and *Cercopithecus)* have been compared with those of two New World genera *(Saimiri and Cebus)*. It was shown that these Old World monkeys have separate visual inputs in the striate cortex, whereas eye inputs in New World monkeys overlap each other and are not separate, a significant difference between the two groups of monkeys as far as their neural visual processing is concerned (Hendrickson et al., 2004).

All structural reorganizations of the lateral geniculate body of primates are correlated to differences in visual activity and interaction that appear to be more elaborate in anthropoid primates than in prosimians or among tarsiers and are uniquely elaborate in humans (Noback and Moskowitz, 1963).

The perfected ability of human visual perception appears to be closely correlated to our highly developed ability in processing optical impressions through the integration areas of the brain's cortex, rather than through differentiation of the primary optic receptors. The ability for visual integration of the environment in which humans live is partly acquired through experience and learning and is not subconsciously instinctive.

Eyelids

All primates have upper and lower eyelids with eyelashes. These are structures that protect the eyeball from injury from small objects and allow the shutting out of any light input during sleep. Eyelids in primates are duplications of epithelium that are covered on the inside with a delicate mucous membrane, the conjunctiva. The upper eyelids are mobile—they cover the eyeball when the eyes are shut and function like windshield wipers when blinking—whereas the lower eyelids do not actively move. The eyelids maintain the corneal surface by keeping it moist with a continuous tear film. The eyelid contains two muscles: one circular muscle, musculus orbicularis orbis, which surrounds the eye opening and has the function of closing the eyelids, and the eye opening muscle, musculus levator orbis, which originates deep in the eye socket, reaches over the top of the eyeball, and merges into a tendon (the levator aponeurosis) that connects to the eyelid.

There is a third, vertical, transparent sheet of tissue arising from the conjunctiva that is located on the (nasal) inside of the eye beneath the eyelids. This membrane

moves across the eyeball and keeps the cornea moist and clean (Walls, 1942). It is found in birds, where it usually covers the entire eyeball, and also in many aquatic and terrestrial vertebrates including mammals having a range of morphologies. Only recently the fact that most primates have such a third, nictitating membrane has been brought back to my memory (Tenzaza, pers. comm.). Among primates this third lid, or plica semilunaris (*plica* is Latin for "fold" and *semilunaris* is Latin for "half-moon shaped"), has various degrees of development: It can cover the entire eyeball in the genera *Arctocebus* and *Perodicticus* but is absent in *Pan* and *Homo*. The nictitating membrane has been documented for many primate species (Arao and Perkins, 1968). The presence of this third membrane has now been confirmed and its morphology has been studied in the colobine species *Simias concolor* (Tenaza, 2007, in preparation).

The lower lid is shaped by a thin cartilaginous support structure known as the tarsal plate that connects with the orbital rim on both its medial and lateral end (canthal tendons). There is a similar, less well-defined support structure in the upper lid. Both eyelids also harbor fatty tissue. The lower eyelid's inner angle supports the opening of the tear duct, and the tear gland is positioned on the lateral upper aspect above the eye beneath the eyelid. There are small canals on the rims of both upper and lower lids that connect to the lacrimal duct. Eyelashes surround the rim of the eyelids of all primates and are rooted in close conjunction with apocrine glands (Stoeckelhuber et al., 2004). Only humans are known to have the overflow of tears caused by emotions known as crying. Tears caused by eye injury or reaction to various eye irritants can be seen in humans and other mammals (Frey and Langseth, 1985).

The eyelids not only provide protection and maintenance of the eyeball, they are also involved in signaling emotions and warnings. In some of the Old World monkeys the eyelids are colored brightly and starkly contrast the surrounding coloring of the face. Thus the eyelids in *Cercocebus aterrimus* are lightly colored, and those of *C. torquatus* are strikingly chalky white. *C. cephus* is especially notable in this respect: the eyelids are colored in a vivid violet-blue and look like elaborate eye make-up. Among macaques the eyelids are strongly distinguished, white and contrasted within the bare, light brown face of *Macaca sylvana,* which also has a white skin area above the eyes. *M. fascicularis* has an area of white skin on the inner (nasal) side of the eyelids. Contrasting, light-colored eyelids are also found in *Papio* and *Theropithecus gelada*. Eyelids with contrasting coloration from the rest of the face function as visual signals when they are "flashed" by rapid movement of the lids. These "signals" are commonly interpreted as threats. The threat yawn of baboons is very well documented, exposing to antagonists a gaping mouth with the large shiny teeth and closed, brightly colorful eyelids.

The colorful adornments of fur and skin in many of the primates, with the most conspicuous example being the Mandrill *(Mandrillus sphinx),* highlight the abi-

lity of most primates to recognize strikingly colored visual signals. Colorful primates need to have the optical ability to recognize their impressive coloration.

Recent Research and Review of Visual Adaptations

Special attention has been paid to the diameter of the optic foramen in the primate eye socket, because this feature is believed to be useful for the evaluation of the visual capabilities of extinct primates and their circadian assignment (Kay and Kirk, 2000; Bush et al., 2004; Kirk and Kay, 2004). Such measurements are useful in an approximate way only, similar to comparative measurements of brain volume.[6]

That the optic foramen index (OPI being a 100× ratio of the optic foramen area to orbit area: Kay and Kirk, 2000; Bush et al., 2004) is a proper measure for distinguishing between diurnal and nocturnal primates is typically taken for granted. Inferences are made about the diarhythms of fossils on the basis of this measure. This kind of conjecture is acceptable where diurnal and nocturnal activity is suggested. Clearly it would be extremely difficult to include the transitional additional biorhythmical behavior category "cathemeral" when inferring activity pattern in fossil primates.

Evaluating the morphology and neurological organization of the eyes of the extant genera *Tarsius* and *Aotus* under a single category "nocturnal Haplorhines" confounds such endeavors even further. Lumping these two very disparate primate genera together into the same group is similar to comparing apples to oranges: They might look alike on the surface, but structurally, behaviorally, and developmentally they are simply not comparable at all.

Ultimately it is the multifaceted substructure of the primate eye that produces their visual capability and associated behavioral patterns. The primate way of life is thus reflected in the substructures of the realm of light reception and neural signaling in the retina and visual cortex rather than in the gross anatomical features of the eye. Their ability to perceive color is a very important factor in many primates' lifestyle, be it perception of edible items (Dominy et al., 2001) or identifying environmental obstacles, traps, potential predators (Miller, 2002; Karpanty and Wright, 2005 in press), conspecific adversaries, friends, or important signals conveyed by the often brightly colored skin and hair signals presented by other primates (Schultz, 1940; Sharpe et al., 1999). Notably, not all

[6]An example of the uncertainty of such measurements is the story of the hypoglossal canal diameter that was presented as a reliable measure being directly proportional to the capability of speech in hominids (Kay et al., 1998). Before long, however, it was revealed that this presumed correlation actually is illusive (DeGusta et al., 1999). These two publications show that correlating function directly with macroscopic neural expression, such as nerve diameter and its imprint on osteological features, can be unreliable and signal a powerful caveat concerning such ideas. Presumptions of such correlations are even more speculative when fossils are considered (Martin and Ross, 2005). Most foramens transmit more than just nerves.

predators are capable of perceiving color (Sumner and Mollon, 2003). Sumner and Mollon (2003) focus on orange, reddish, and yellowish coloration of primates, explaining that the orange pelage coloration that is quite common among New World monkeys and Madagascan prosimians actually appears to be cryptic within the green foliage for bichromatic primates. However, this coloration, which is very obvious to human observers, could also adversely advertise the primates' presence to such predators, as birds of prey, for instance, and thus make them easily visible prey.

Sumner and Mollon (2003) discuss that the bright-orange colored primates in fact remain cryptic to the monochromatic and bichromatic large carnivorous potential predators in South America and the *Cryptoprocta* in Madagascar that share their environment (loc. cit. page 85). In contrast, large predatory snakes actually have either trichromatic or tetrachromatic color perception and thus are potentially capable of effortlessly discerning the brightly colored primates from the background, which thus makes primates easy prey. Most important potential primate predators, as mentioned, are large raptors. These authors elaborate that some of the aerial predators actually are able to discern color, which would turn the bright orange primates into easy targets and thus pose a selective disadvantage for them. On the other hand, color vision is possibly of little importance for the swiftly striking raptors as adaptation to color recognition reduces the all-important spatial acuity that enables raptors to hunt successfully. There appears to be no comprehensive knowledge about the color vision abilities of large monkey and lemur–eating raptors (but see Ödeen and Håstad, 2003; Håstad et al., 2005).

Sexual selection and visibility to other primates are considered as yet another alternative explanation for the striking orange and other contrasting pelage colorations among primates. Changizi et al. (2006) correlate trichromacy in primates with the need to perceive changes of whitish, reddish, and bluish hues of bare skin that are caused by oxygen saturation and characteristically occur on faces, around the rump, on legs, and in the groin areas, indicating mood and sexual receptivity changes. Thus, a new dimension has been added to the question "what is trichromatic color for?" Changizi et al. (2006) propose that changes in skin color that indicate mood and sexual receptivity might contribute to the behavioral advantage of having advanced multicolor perception in primates.

There is thus much more complexity to primate vision than just the ability to distinguish a range of colors for any single purpose, for example, for food selection. Many other aspects of visual ability, such as the perception of space and maintenance of balance, are equally crucial for successful survival in the three dimensional habitat where primates roam.

The physical properties of light, luminance and brightness, the shape of objects as either stationary or in motion, all have an enormous impact on the ability of humans to perceive and discern objects. Some believe that three dimensions are more clearly visible in color than in black and white (Walls, 1942; Livingstone and Hubel, 1988). These physical properties are equally important

for primate vision (Ilg et al., 2005; Werner et al., 2005) and life. Obviously it is much simpler to study the visual abilities of humans and what we perceive because humans are able to communicate about visual perception with each other through speech. It is much more complicated to discern what nonhuman primates are capable of visualizing and distinguishing (Preuss, 2004).

The ability of primates to discern colors has been correlated behaviorally with the importance of being able to detect edible plant foods. Many primates are indeed habitually folivorous and frugivorous, with both food preferences requiring color recognition (Dominy and Lucas, 2001; Lucas et al., 2003). However, Surridge et al. (2003) importantly point out that primate diets vary widely and that the folivory/frugivory correlation to the evolution of primate trichromacy might not be the only reason for the ability of primates to see color. Dominy et al. (2003) tested whether trichromatic females of two species of New World monkeys (*Saguinus imperator* and *S. fuscicollis imperator*) are more successful in finding edible fruit than conspecific bichromatic males. It was found that the two sexes do not differ in their ability to detect ripe fruit in mature foliage. Females and conspecific males are equally successful in the task of locating good feeding localities. This shows that trichromatic vision does not provide any food selection advantages compared with bichromacy.

We will briefly look comparatively at the tree shrews and what is known about their visual adaptations to establish a comparative base for the evaluation of visual abilities in primates. Tree shrews are an order closely related to (or a sister group of) Primates. The retina of the tree shrew *Tupaia* is predominantly made up of cones (compare Rohen and Castenholz, 1967); thus it is the retina of a diurnal animal. However, Tigges (1963) concluded from tests that attempted to check the ability of tree shrews to recognize colors that—contrary to earlier belief—tree shrews discriminate brightness rather than hue. The periphery of the retina of each eyeball is thicker in tree shrews than the inside of the retina, a fact that has been connected with the idea that species of genus *Tupaia* have already attained a certain degree of binocular vision (Wolin and Massopust, 1970) despite having the eyes situated more at the sides of the head (as opposed to primates, whose eyes are directed forward). Actually, in *Tupaia* the arteries and veins that supply the retina show an arrangement that is quite different from these structures in any primate. The arteries and veins are distributed like the radii of a circle, protruding from the papilla of the optic nerve; in primates they do not show such a clearly defined pattern of distribution but supply the retina in a rather random netlike pattern.

A great number of reports on retinal formation and eyeball morphology in Lemuridae have been published. For example, the retina of *Lemur catta* has been studied and described by several scholars (Blakeslee and Jacobs, 1985; Kirk and Kay, 2004). All these reports agree that, even though *L. catta* is predominantly diurnal, the retina of the ring-tailed lemur seems to be similar to those of

nocturnal prosimians. In ring-tailed lemurs, the photoreceptors are predominantly rods, and a tapetum cellulosum is present according to Rohen and Castenholz (1967). A behavioral study by Bierens de Haan and Frima (1930), however, shows that *L. catta* and *Eulemur mongoz* are capable of some color discrimination.

In these lemurs there is a well-defined area centralis, forming a domelike retinal thickening in the center of the retina that is situated exactly in the same place where a fovea centralis would otherwise be located. However, this area is structurally not at all like the fovea centralis that has been reported to be present only in *Hapalemur* and *Lemur catta* among prosimians. Most retinas of those lemur species that have been studied seem to be made up almost entirely of rods; furthermore, in *L. catta* a ratio of one cone to five rods has been reported. Only some species of genus *Eulemur* appear to lack a tapetum. Both *Cheirogaleus* and *Microcebus* species have retinae with only rods as photoreceptors; while species of *Microcebus* do have a tapetum it is said to be missing in *Cheirogaleus*. In addition, one species of genus *Avahi* is reported to have both a rod retina that is thickened toward the center and a tapetum. Though diurnally active, both *Propithecus verreauxi* and *Indri indri* have retinas that predominantly contain rods, with a few large cones scattered among them; they are also reported to have a distinct but comparatively small central area (Jacobs et al., 2002). The area centralis appears to be flat in *Propithecus* but is slightly dome-shaped in genus *Indri*. As already mentioned, both these latter genera have a tapetum.

Species of Tarsiidae are nocturnal animals. However, *Tarsius spectrum* has recently been shown to be most active during full moon nights (Gursky, 2003). The retina of tarsiers has been studied by several researchers, not only because its visual system appears to be strikingly different from those of other primates, but also because of widespread phylogenetic and taxonomic interest in this peculiar primate (Castenholz, 1984). It was believed that the retina of *Tarsius* is composed entirely of rods, as would be expected in a nocturnal primate and that it has a comparatively shallow fovea centralis (Rohen and Castenholz, 1967). Recently Hendrickson et al. (2000) restudied the retina of *T. spectrum*. They used a technique known as immunochemical labeling for antisera that are known to be specific for primate cone and rod opsins. The results found a number of M- and/or L-cone opsin cones and a smaller number of S- and UV-wavelength sensitive cones. It also became obvious that tarsiers have a surprisingly high number of distinguishable cones, although they are hard to differentiate from rods with morphological techniques. Rods and cones were easily differentiated after immunocytochemical labeling. The cone morphology differed little from rods. However, it appears that unlike the situation in fovea of higher primates, which is a cone fovea, the tarsier fovea is predominantly made up of rods. *Tarsius,* as already mentioned, does not have a tapetum. With tarsiids the density of the rod photoreceptors is much higher in the center of the retina than in the periphery.

The South American owl (night) monkey *Aotus trivirgatus* is one of two exceptions to the rule that higher primates have both cones and rods. This monkey has only few cones (Murray et al., 1973) among the rods that cover the retina. *Aotus* is also reported to have a vestigial fovea centralis (Rohen and Castenholz, 1967; Hershkovitz, 1977). The other astonishing exception among New World monkeys is genus *Alouatta* with its complete trichromatic color vision that is more or less identical to the color vision patterns found in Old World primates.

It is notable how human language blends terminology based on visual capabilities with our wide spectrum of verbal communication: foreseeable, scenario, having vision, opening a window, being in the dark, seeing red, being enlightened, being blinded by something, imaginary, imagine, being hazy, blurred thinking, clarity, orientation, perception, being perceptive, reflect, view, shape, saying "you see," actions or statements being opaque, diaphanous. We have a clear mind or thoughts, thinking can be hazy, reflect upon something, having a wide horizon, review, things are obscure (Huang, X., Acero, A., and Hon, H.-W., 2001).

PRIMATE DIARHYTHMS AND BIOCHRONOLOGY

Time is the most elusive dimension on our planet. It rules everything and cannot be grasped. Time is the only truly democratic entity on planet Earth; all living things are inescapably getting 24 hours older every day. Scientific interest in the field of chronobiology, as a field of scientific inquiry, began in the 1950s and has vastly increased, especially during the last 25 years of the twentieth century and into the twenty-first. In 1986 the "Journal of Biological Rhythms" was first published, and it has been going strong ever since. In 1988 the society for Research on Biological Rhythms began to meet twice annually in the United States. A second journal focusing on a somewhat more narrowly defined area of biorhythms and publishing research papers of biochronology, the "Journal of Circadian Rhythms," was created in 2003.

Rhythmical behavior patterns are manifold and complex even in unicellular organisms, but their occurrence is much more complex and elusive in multicellular organisms, including prokaryotes, plants, invertebrates, vertebrates (among these the mammals; DeCoursey 2004a; Paranjpe and Sharma, 2005). The diarhythmical term "circadian" was created in 1957 by Franz Halberg, during studies of human biorhythms (Halberg, 1969). Naturally, such biochronology also regulates the behavior of primates.

Two appropriate terms, recognized since this branch of science began, have been in use to discern between primates of two obvious behavioral subgroups: those that are active during the day, "diurnal" primates, and the nightly active "nocturnal" primates. Both terms are easily and appropriately applied to gross morphological features such as small versus large eyes and differences in visual perception. A biorhythmical subgroup "crepuscular" (active at dawn and dusk)

has also been applied to some species of primates that do not conform to the two straightforward groupings of being active during daylight or active at night. Being nocturnal is actually the most common biorhythm in mammals (DeCoursey, 2004b).

Many appropriate terms describe regularly recurring biorhythmical behavioral events (e.g., ultradian, infradian, circalunar, circannual) that go beyond the day and night activity dichotomy. Yet another biorhythmical term, "cathemeral," was coined for one subspecies of *Eulemur, E. fulrus mayottensis,* in 1987 by Tattersall, however, it is coincident with the well-established behavioral category "circadian," making the necessity for the term questionable.

"Cathemeral" has been defined as follows: "The activity of an organism may be regarded as cathemeral when it is distributed approximately evenly throughout the 24 h of the daily cycle, or when significant amounts of activity, particularly feeding and/or traveling, occur within both, the light and dark portions of that cycle" (loc. cit. page 201). The novel terminology was subsequently applied to document this kind of behavior for other primates and mammals. Unfortunately, the term "cathemeral" has destabilized a long-established nomenclature for characterizing diarhythmical behaviors—before 1987 we had diurnal, nocturnal, and the rarely used terms crepuscular and diel, the latter mostly applied to marine mammals. Circadian is defined as follows: *of or relating to biological processes occurring at 24-hour intervals; "circadian rhythms."*

Many students of lemur behavior followed Tattersall and used "cathemeral" in their discussions of diarhythmical activities. This neglected a vast body of research and a perfectly suitable, well-established terminology that was in general use since early in the twentieth century (Galbraith and Simpson, 1903; Simpson and Galbraith, 1905/06) and extensively discussed for the last 50 years (Rohles, 1996).

Some researchers who have rushed to embrace the study of "cathemeral activities" now endeavor to document its manifestation morphologically and are attributing behavioral importance to it (Kay and Kirk, 2000; Kappeler and Erkert, 2003; Erkert and Kappeler, 2004; Kirk, 2004). The two other terms that distinguish between animal groups with clearly contrasting behavioral patterns, "diurnal" and "nocturnal," are, among primates, clearly defined by obvious morphological characteristics. Cathemeral behavior is not unequivocally observable in morphological structures. Interestingly, the term "cathemeral" has not been used outside the primatology/biological anatomy fields of study despite being introduced almost twenty years ago (Dunlap et al., 2004; Foster and Kreitzman, 2004).

Attempts to classify primates according to their locomotor behavior or different diarhythmic activities or to rank them into strictly defined categories has often created confusion. For example, the locomotor morphology of most primates remains comparatively unspecialized, permitting flexibility of movement unrestricted by stringent morphological limits. Only in instances where postcranial morphology is extensively derived is primate locomotion constrained into

predictable habitual locomotor behavior, in tarsiers, gibbons, or bipedal humans (Ankel, 1967; Ankel-Simons, 2000).

Primate diarhythms are both genetically driven and maximally flexible according to the demands of constantly varying environments. Thus, categorizing diarhythmical activity is complicated by multiple factors—not only by differences in visual abilities but also by many environmental dynamics that are utterly changeable. The two diarhythmical categories diurnal and nocturnal are nevertheless clearly expressed differently in cranial morphology and visual soft and sensory tissues of the head. Attempts to infer visual activity of extinct primates result in various, sometimes conflicting, conclusions and hypotheses. For example, differing statements that all stem primates must have been nocturnal or diurnal are spread throughout the literature that hypothesize about evolutionary morphology of basal primates without much basis. Most commonly the assumption has been made that stem primates must have been nocturnal (Martin, 1990). This view has recently been rejected by Tan et al. (2005) based on genetic evaluation of short-wavelength opsin sequences in 14 prosimian lineages. Tan et al. propose that the ancestral primate lines were either diurnal or cathemeral (circadian) and that nocturnality evolved several times later in different prosimian lineages.

A new hypothesis has been proposed that addresses several issues concerning the evolution of primate visual systems. An ecological scenario is proposed considering the adaptive flexibility of primate visual systems (Ankel-Simons and D.T. Rasmussen, in preparation). This new view is supported by two important observations: "Though there are rather few mammals that could be viewed as exclusively nocturnal or diurnal, most have become specialists in some period of the day or night" (Kaskan and Finlay, 2001, loc. cit. page 20) and "Nocturnal eyes, overall have a number of features that are different from diurnal eyes. Underscored at the outset should be the fact that most eyes are duplex, with the ability to function at both night and day, but most eyes have features that optimize one or the other niche" (Finlay et al., 2005, loc. cit. page 52). Another example of this kind of adaptive flexibility is the evolution of certain tooth cusps (Hunter and Jernvall, 1995; Kangas et al., 2004), showing that this phenomenon is likely much more widespread but not yet recognized.

Overdorff and M. Rasmussen (1995) have described activities at night in species of *Eulemur* in the wild and point out that this behavior could be seasonal.

Two concurrent, long-term studies in Madagascar (Andrews and Birkinshaw, 1998; Colquhoun, 1998) that analyzed cathemeral behavior in *Eulemur macaco* separately came to the conclusion that the lemurs with diurnal visual morphology do not roam about during very dark nights (namely during the night of a new moon and three days before and after the new moon, Colquhoun, 1998). The lemurs' nighttime activities are actually correlated to moon periodicity and availability of some light. Much of their activity takes place in the early morning

hours, when the daylight begins to increase. Verification of any nighttime lemur activity is difficult in the field because it is practically impossible to follow these animals in the forest during nighttime when one can only rely on acoustic cues, not on direct visual observation.[7] And indeed, the nighttime activities of the black lemurs were actually measured by computation of vocalization and noises ("auditory group sampling," Andrews and Birkinshaw, 1998) correlated according to the degree of noise when lemurs are awake and active. Another question concerning cathemeral activities might be difficult to evaluate: Could it be that the primates are disturbed by intrusion of humans into their territory and that they are moving about at unusual times because of them?[7]

Van Schaik and Kappeler (1996) suggest that "stem" lemurs must have been nocturnal (loc. cit. page 934), having only recently exhibited opportunistic activity that led them to become cathemeral. These authors make the following observation when formulating their hypothesis in "Cathemerality and Lemur Social Systems" (Van Schaik and Kappeler, 1996, loc. cit. page 921): "The main advantage to gregariousness among diurnal taxa, predation avoidance through shared vigilance and active avoidance of predators, may not accrue to nocturnal species, which are thus forced to rely on cryptic appearance and behavior (Clutton-Brock and Harvey, 1977)."

What seems to be missed here is the fact that "cryptic appearance and behavior" of nocturnal species are purely caused by the absence of color vision during scotopic light conditions. These authors speculate that all living fauna have been greatly disturbed by the "dramatic change in human subsistence patterns and the vast increase in our numbers, [leading] to large-scale conversion or modification of natural habitats" (loc. cit. page 935). However, these evolutionary disequilibrium theories have not been supported by field observations (Wright, 1999).

We have learned from the studies by Wright (1985, 1989, 1994) that the "nocturnal" night monkeys *(Aotus trivirgatus)* were primarily active during brightly moonlit nights. These "nocturnal" monkeys however, were also active during the bright morning hours in a habitat where no aerial daytime predators were present. Thus Wright documented clearly how anthropoid primates can be visually adaptable to both scotopic and photopic light conditions. A detailed report about the circadian behavior of free-ranging *Aotus azarai* in the Argentinean and Paraguayan Chaco confirms the great adaptability of the circadian behavior of this "nocturnal" anthropoid (Fernandez-Duque, 2003).

It is surprising that behavioral studies of diurnal anthropoid primates appear to exclusively focus on daylight behavior, thus ignoring the possibility that diurnal

[7]The use of now widely available night scopes can solve this problem. Patricia C. Wright (personal communication) believes that human impact is not the cause for cathemeral behavior of *Eulemur* species.

primates stray from the behavioral assignment of "diurnal" and are, or could be, active at night. Glander (1975, loc. cit. pages 19–20, and personal communication) confirmed that this activity seems to be restricted to nights when some scotopic illumination is provided by the moon. This is also confirmed by Struhsaker (1975, loc. cit. page 86, and personal communication). Both behaviorists report that they have encountered nighttime activities carried out by "diurnal" anthropoids. Glander states that the howler monkeys *(Alouatta palliata)* he studied for many years in the wild begin feeding activities as early as 3:30 to 4:00 AM during the dry season, long before daylight. Struhsaker encountered a group of Syke's monkeys *(Cercopithecus mitis albogularis)* on Zanzibar that were climbing through trees in an apparent group progression, making contact calls, when he was out in the forest during a moonlit night looking for bushbabies. Struhsaker also reports that he observed *Cercopithecus ascanias* in the Kibale forest that were on the move at the very first light and continued moving until there was barely any light on the forest floor. He heard monkeys and chimpanzees making vocalizations suggesting that they were moving at night. Also in Kibale, baboons *(Papio anubis)* often gave alarm barks at night, but Struhsaker states that these barks could have been alarm calls in response to something heard. Also, red *Colobus* monkeys *(Procolobus rufomitratus tephrosceles)* could be heard to emit calls that are indicative of males harassing a copulating pair on rare occasions during either moonless nights (twice) or when there was some moonlight (eight nights). All these reports indicate that diurnal anthropoids are not necessarily strictly diurnal and that they can actually be active at night.

Kirk (2004) compared cornea size to eye size and writes that "eye size does not vary in a predictable fashion with activity pattern" (loc. cit. page 1096). He later asserts that any size increase of the cornea over eye diameter is proportional to the level of nocturnal behavior.

As already mentioned, to categorize the enormous-eyed and unusual genus *Tarsius* together with the New World anthropoid *Aotus* as "nocturnal haplorhines" is most confounding. To do so only blurs the issue of understanding primate eye structure, as those two "nocturnal" eye morphologies are incongruent in both form and in their evolutionary history. From field observations we know that *Aotus* can drastically change its diarhythmical behavior and become diurnal (Wright, 1989), and *Tarsius* is often active under crepuscular circumstances. According to Kirk's argument, are we to regard these two genera as both being cathemeral? It has actually been reported that tarsiers *(T. spectrum)* are active several hours before sundown and active again around dawn. They rest quietly during the middle of the night while it is really dark (Hendrickson et al., 2000, loc. cit. page 729). This pattern actually makes them crepuscular.

Gursky (2003) discovered that *Tarsius spectrum* in Sulawesi become much more active during the light of a full moon than they are under darker nightly conditions. This is also true for all the other primates that are active at night.

The ballooning of the cathemeral behavioral category is documented by Kay and Kirk (2004). Adding to the terminological confusion already outlined, the enlarged group here classified as "cathemeral" has swollen to include all the marine mammals, birds, fish, and insects whose circadian 24-hour activity pattern was previously described as "diel" (Baird et al., 2005). Diel is defined as "a twenty-four hour period, usually encompassing one day and one night." Both the terms "circadian" and "diel" were proposed by Halberg in 1955 (published 1957). Oddly, a former advocate of cathemerality, Ross (2004, loc. cit. pages 478, 714) now chooses to apply the circadian behavior term "diel" to early haplorhines.

To sum up what has been previously stated, Starck (1995) insists eye size is not correlated to body size; it relates to an animal's lifestyle. Starck warns that because the factors that ultimately determine eye size are multifaceted, exact quantitative results are not likely to be easily discovered. Let us assume that diurnal and nocturnal characteristics are strictly separate from each other both morphologically and behaviorally; only then can we expect that these strictly defined behaviors are manifest in the gross morphology and visual physiology of the eyes. It appears that mammals that are grouped as being either diurnal or nocturnal based on morphological features actually do not strictly conform to these biorhythmical assignments in their behavior, and thus the visual ability of diurnal versus nocturnal vision potentially overlaps.

For example, large eyes are found among artiodactyls and equids that live in an open savannah environment; Proboscidia have comparatively small eyes. Some crepuscular primates, such as species of *Eulemur,* species of genus *Galago,* lorisid primates, and uniquely *Aotus* among anthropoids, have large eyes. As we have seen the extreme among large-eyed mammals is the enigmatic primate *Tarsius*—the volume of just one of its eyes is larger than that of the entire brain; its eyes bulge from the eye sockets. Microchiroptera, though crepuscular, have small eyes—these creatures navigate by sonar system and are not reliant on vision. The Tachyglossidae (Australia's echidnas and spiny anteaters) have very small eyes but are said to be nocturnal (Nowak, 1991). The aye-aye, *Daubentonia madagascariensis,* is considered to be nocturnal but does not have very large eyes. Howard et al. (2004) have investigated scaling and allometry of the eyes of many vertebrates and came to the conclusion that: "It may not be possible, therefore to make generalized predictions about eye size based solely on the nocturnal or diurnal lifestyle of animal groups" (loc. cit. page 2049).

Starck also observed that the shape of the ocular globe is often approximately spherical, with the horizontal and vertical axes being of equal length, as in many Marsupialia and Carnivora (except for the Felidae and *Phoca* among the Pinnipedia) and primates. The eyeball is not globular but elongate in Cetacea, Erinaceidae, Ungulata, and *Tachyglossus* (Echidna), which has a strongly curved cornea. The horizontal axis of the eye is longer than the vertical axis among

Felidae and in many primates. Nocturnal mammals such as Marsupialia, Rodentia, *Erinaceus,* and the primates *Galago* and especially *Tarsius* have raised corneae. The optical capabilities of the cornea depends on the radius of curvature of both the front and rear surface, and on the refraction index of the corneal tissues.

Not surprisingly, current research is concentrating on recording circadian photoreceptors (Millar, 1997; Hastings, 1998; Forger and Peskin, 2005). Humans have been studied thoroughly because human diarhythmical behavior can be detrimentally destabilized by long distance travel, aging, and disease. It has long since been established that biorhythms in mammals are based on endogenous properties that are independent of external environmental factors. Light perception is channeled by the pineal gland (hypophysis) and melatonin/serotonin levels in humans and nonhuman primates (Perlow et al., 1980; Touitou, 1998).

Recently a new, significant light-sensing pathway has been described for rodents, primates, and humans (Dacey et al., 2005). A hitherto unknown opsin, melanopsin has been found within horizontal retinal ganglion cells. The horizontal ganglion cells collectively transmit visual messages from cones and rods and, with their axons, combine to form the optic nerve proper. It has now been shown that the melanopsin ganglion cell system sends signals of ambient light level changes directly to the site of the circadian regulator center, the suprachiasmatic nucleus that is located in the anterior hypothalamus and is crucially involved in regulating biorhythms (Gooley et al., 2003). This circadian regulator mechanism is located and functions inside the retina but is external to the visual image forming transduction through rods and cones and not located inside either rods or cones but between them. It has been reported that there are approximately 2000 melanopsin ganglion cells in a single human retina (Sekaran and Hankins, 2005). We now know that circadian behavior is not regulated by direct visual involvement of rods and cones, but that it is correlated through melanopsin in the eyes (Panda et al., 2002; Silva et al., 2005).

Unfortunately there are few publications about circadian clock genetics in primates, with the exception of humans, who have been extensively researched for clinical reasons. Determination of the connection between circadian primate behavior and the underlying genetic basis is still unclear. Publications about "diel" or "cathemeral" activities of prosimian primates continue to correlate these behaviors to environmental factors without attempting to establish any genetic associations (Kappeler and Erkert, 2003; Erkert and Kappeler, 2004).

Extensive knowledge about the physiology of circadian pacemaker systems or clocks has been recently accrued by researchers (DeCoursey, 2004a, b). The most important insight in this context, however, is the well-established fact that all metazoans have internal timepieces or biological clocks that clearly are genetically controlled (Takahashi, 1995; Zylka et al., 1998; Barinaga, 1999; Dunlap, 1999; Freedman et al., 1999; Travnickova-Bendova et al., 2002; Dunlap, 2004; Loros et al., 2004). Today there is no doubt that circadian rhythmicity is rooted in genetics. We also understand that such clocks can be made to malfunction by

external factors such as travel across timelines in humans, which causes the phenomenon of "jet lag" (Travis, 1998). It is thus very likely that the "cathemeral" behavioral pattern first described for *Eulemur mayottensis* (Tattersall, 1979) falls into the "circadian" diarhythm category and is a genetically encoded activity pattern (Paranjpe and Sharma, 2005).

NUTRITION AND THE INTESTINAL TRACT

Primates, like all living creatures (except for modern, civilized humans to a certain extent), are highly dependent on food sources that their environment offers. Nature's offerings change during the transition of the seasons, even in those habitats—such as tropical rainforests—where seasonality is not very pronounced. Interestingly, the overall morphology of the intestinal tract seems not to be highly influenced by minor differences in the diet of mammals, but often shows characteristics that are group specific. For example, foxes and bears, classified as carnivores, often ingest vegetarian food items if no prey is available. Food categories are mostly flexible and are rarely strictly adhered to by those who are categorized.

Thousands of scholarly publications describe, discuss, and evaluate foraging, food preference, dietary strategies, and digestibility of food in nonhuman primates (Garber, 1987; Chivers, 1998; Dominy et al., 2001). These mostly temporarily, geographically, and taxonomically spotty glimpses of primate dietary behavior and requirements are difficult to combine into one comprehensible and correct picture. It has to be stressed again in this context that all nonhuman primates, once again excepting the enigmatic tarsiers, are highly adaptable as far as their diet is concerned, and attempts to integrate certain aspects of their lifestyle into unique factual scenarios are therefore often confounded and confounding. A hungry primate will find something edible to eat and will not care whether such food items are among their preferred foods.

Attempts to categorize primates according to their food preferences are many (Visalberghi et al., 2003). The three primate food groups that have long been accepted as being predominant are frugivory, folivory, and faunivory (Chivers and Hladik, 1980). There also have been various anatomical correlations assigned to these food groupings that implicate both tooth and digestive system gross morphology (Martin, 1990; Fleagle, 1999).

The obvious exceptions from the primate dietary adaptation rule are humans. The human primate basically removed itself from any dietary categorization and dependency on foraging early on in evolutionary history. As soon as the taming of fire and the first steps toward cultivation of plants and domestication of animals entered the dietary scene, the relationship between humans and their food entered a different dimension and changed drastically. As soon as food portions were distributed to members of the clan, and as soon as food was presented on dishes,

the realm of eating entered the realm of culturally imprinted social behavior and cognition. We will have to disregard such human dietary fads as vegetarian diets, restriction to fat-free foods, carbohydrate-free fare, or vegan diets and will have to look at the human digestive system and dietary habits with different eyes from those used to evaluate the natural foraging and dietary habits of primates that live in their natural habitats. Notably, few primates are not influenced to various degrees by human interference with their environments and thus their foraging and dietary habits.

The other exception of the primate dietary rule are tarsiers, which are generally regarded as being strictly faunivorous and appear to exclusively eat living prey, rejecting any dead animal matter (Haring and Wright, 1989; Gursky, 2000).

Many attempts have been made to correlate food intake to activity periodicity, travel distance, group size, biostratigraphy of the food sources, and food availability in nonhuman primates, although such multifactor correlations are almost too complex to document (Chapman and Chapman, 2002; Chapman et al., 2003; Ganas and Robbins, 2005). There obviously is no straightforward way to delineate "what, who, and why" in relation to nonhuman primate foraging strategies.

Relationships between food plants and those who feed on them have also been explored (Burgess and Chapman, 2005). The astonishing fact that nonhuman primates are able to live on plants and foods that would be highly toxic to humans is also well documented: Several species of *Hapalemur* only feeding on toxic bamboo are able to coexist in the same habitat eating the same bamboo, as discovered by Wright and Randriamanantena (1989) and Glander et al. (1989). Details about this astonishing lemur community living situation has subsequently been studied in great detail and confirmed (Tan, 1999). Unlike many other niche phenomena among lemurs, the separation of the three species of *Hapalemur* is less geographical than food related: They do share the same geographical area but not the same parts of their food source, the toxic bamboo *(Cathariostachys madagascariensis)* that is abundantly available. Cyanide in plants can be toxic to herbivores, but it appears that there are multiple variants of the degree of toxicity of the plants and the adaptability of the animals that eat them (Gleadow and Woodrow, 2002). Furthermore, at the Duke University Primate Center lemurs that roam outdoor enclosures during the summer months have been observed to touch and eat poison ivy *(Taxicodendron radicans),* which can be highly toxic to humans, with no ill effects. There is an intimate relationship between food plants and plant-eating primates not unlike that between parasites and hosts—the relationship must be beneficial to both parties or else it is detrimental to both. However, plants have a variety of defenses against being eaten, and it has been suggested that monkeys that eat toxic plants may only be able to tolerate poisonous leaves up to a certain threshold during feeding bouts. This means that they have to control dosage by eating selectively (Lambert, 1998).

Unlike the niche separation among the three species of *Hapalemur,* niche separation between two different genera and species of lemurs, *Varecia variegata rubra* (the red ruffed lemur) and *Eulemur fulvus albifrons* (the white fronted lemur) is geographical: They are both predominantly frugivors but harvest the fruit in trees of different size and height and thus different forest strata (Vasey, 2000, 2005).

Yet another way to separate closely related primates (Indriidae) into niches has been reported. *Propithecus* and *Indri* that roam in the same forest environment have their own niches that are based on differences in food preference and gut morphology (Wright, 1997; Powzyk and Mowry, 2003; Burgess and Chapman, 2005). For primates there are many variable ways of delineating a livable niche that can be diet related, achieved by geographical distance, or related to different living height within the canopy of trees.

Niche separation has also been documented between two sympatric New World monkeys, *Lagothrix lagothricha poeppigii* and *Ateles belzebuth blezebuth,* in Amazonian Equador. Even though their dietary preferences overlap considerably, their preferences cause them to eat different kinds of fruit (Dew, 2005).

General Review of the Primate Diet

Of all primates only *Tarsius* lives exclusively on animal protein; insects, larvae, and lizards and various other small vertebrates constitute the tarsier diet. The two lorisid genera *Arctocebus* and *Loris* are, like tarsiers, said to be diet specialists that consume only animal protein (Nekaris and Rasmussen, 2003). The lemurid *Lepilemur* appears to be the smallest prosimian that is purely vegetarian and has a diet that is highly fibrous. The indriid genera *Indri* and *Propithecus* are highly specialized herbivores, and their bodies are consequently rather pear-shaped, showing the enlarged gut of a bulk eater (Campbell et al., 2000).

Among monkeys, both the South American howler monkey and the colobines of the Old World are highly specialized leaf eaters showing, however, very different degrees of specialization in this dietary adaptation, as discussed later (Milton, 1998; Cork, 2005). The highland gelada baboons—*Theropithecus gelada*—are specialized seed and root eaters (Jolly, 1970). Among the great apes, gorilla is said to be a herbivore, the orangutan predominantly a frugivore, and the chimpanzee an omnivore. The migratory habits of most primates are closely related to the availability of food. Chimpanzees, for example, go every day to areas where certain fruit are ripe and abundant, returning day by day until the supply is exhausted, and they have to find another area in which to forage. Both baboons and chimpanzees eat a variety of small mammals and antelope meat. Especially chimpanzees actively hunt in groups (Jolly, 1972) and thus assertively include meat into their diet. Predatory behavior involving two species of South

American monkeys has also been reported. Among New World monkeys the tufted capuchin *(Cebus apella)* is known to be exceptionally faunivorous, eating crabs and oysters and capturing small mammals. An adult male tufted capuchin monkey is reported to have killed and eaten an infant titi monkey *(Callicebus moloch)* (Sampaio and Ferrari, 2005; Simmen, 2005).

Members of the subfamily Cercopithecinae have food pouches in their cheeks. These enlargements of the membrane of the oral cavity outside the teeth can be enormously stretched. Such pouches are used as storage bags for food if it is abundant, or can be stuffed full in a hurry if the situation requires a hasty retreat, and then the hidden food can be retrieved and eaten in peace in a hiding place. These cheek pouches, when fully stuffed, can result in a different—even grotesque—appearance of a primate. Cheek pouches can extend far beyond the facial area, even bulging out and down into the neck. If the pouch is overstuffed, the primates often need to push the food items back out with the help of their hands because the cheek musculature is weakened by stretching.

As already mentioned, the South American howler monkeys and the Old World langurs (Colobinae) are highly specialized leaf eaters (Cork, 2005). This specialization, however, is much more elaborate in colobines than in howler monkeys (Chivers, 1994; Lambert, 1998). Langurs have been found to have a ruminant-like digestion ("ruminanting forestomach digesters," Langer, 2005, loc. cit. page 18) with sacculated stomachs that contain symbiotic bacteria (Beauchop and Martucci, 1968; Suzuki et al., 1985). This is not the case for howler monkeys, which have comparatively large stomachs and the same basic stomach anatomy as all other primates that ingest plant foods such as fruit, buds, and leaves. Also, howler monkeys ingest comparatively more fruit than do colobines, even though leaves dominate the diet of several howler monkey species (Milton et al., 1979; Prates et al., 1987; Strier, 1992).

Another food and food plant–related issue are seed eating, seed spitting, and seed defecating in primates that, potentially, can be involved in the process of food plant dispersal and thus propagation (Chapman, 1995; Lambert, 2001; Poulsen et al., 2001; Dominy and Duncan, 2005).

It is important to discern between the two mechanisms of seed-spitting and seed-defecating (oral versus digestive seed scattering): There seems to be a relationship between seeds that pass through the digestive tract unhurt and their improved germination rate as compared with seeds that are spit out (Dew and Wright, 1998). Also the size of the seeds is important; it has been observed that the spitting out of large seeds appears not to be advantageous in successful seed dispersal. Thus it is still under discussion how effective seed-spitting primates can be in the propagation of fruit trees (Dominy and Duncan, 2005). It appears that seed dispersal by primates varies considerably among groups. The mechanism of digestive seed dispersal is intimately related to the manner of defecation. It appears that the use of special defecation spots is an important factor in this

scenario. Defecating in specific areas and thus the creation of latrines has been observed in many animals but has rarely been reported for primates, with the exception of howler monkeys (Andresen, 2002). Concentrated areas of dung add to the fertility of the soil that supports growing plants (Feeley, 2005). It appears that several prosimian primates in Madagascar also show latrine behavior (Irwin et al., 2004). It can be expected that this activity has several advantageous functions: territorial marking, improving soil quality, interspecies signaling, seed dispersal, and more, depending on habitat and species-specific behavioral variation. Increasing knowledge about such circumstances will result in better understanding of these intriguing behaviors.

There seems to be no knowledge about possible interaction and ill effects between ingested poison in primates and the essential microbial intestinal population that could be diminished or destroyed by the ingested toxins (Mackie et al., 1999).

The dietary categories for primates are not meant to imply that the animals practicing them are strictly eating nothing else but either animal material, fruit, or leaves (Sussman, 1991b). The terminology applies to those types of food that preponderate in an animal's diet. It is generally believed that small-bodied mammals cannot absorb sufficient amounts of calories from eating only leaves and green things, even though it has been shown that brown mouse lemurs, *Microcebus rufus,* eat predominantly fruit (Atsalis, 1999), a finding that clearly contradicts the hypothesis that tiny primates must eat animal protein to survive.

Animal protein is much more easily digested than plant protein and provides an immediate source of energy. Therefore some small- to medium-sized primates are more likely to live on animal prey that is only occasionally supplemented by floral additions. Fruit diets are in turn augmented by prey, leaves, gum, and sap. Not only do many of the small New World monkeys eat gum, but this activity has also been found in wild chimpanzees. Chimpanzees ingest the gum exudates of a tree named *Albizia zygia,* a gum that is actually used as a binding agent in human medical tablet formulations. This gum contains sufficient amounts of calcium, manganese, magnesium, and potassium for the chimps to add to their nutritional requirements of these trace elements (Ushida et al., 2006). Strict folivores need bacterial fermentation of the ingested plant material in their guts for the hard-to-absorb materials such as cellulose to be digestible. Primates that are predominantly foliverous are the least likely to add many different other kinds of edibles to their diet.

There are apparent differences in the passage time of ingested food depending on its composition, and the time spent in the gut appears to be correlated to the fiber content of the ingested food (Schmidt et al., 2005). The time it takes for food to pass through the digestive tract is also intricately related to the varying morphology of the gastrointestinal tract. For example, ruffed lemurs (*Varecia v.*

variegata and *V. v. rubra*) have comparatively short and uncomplicated gastrointestinal tracts, and food passes rapidly through these (Campbell et al., 2000). Despite simple overall morphology of the intestines and the comparatively rapid passage of ingested food, the ruffed lemur gut is efficient in extracting adequate digestible energy for the animals to properly maintain their body mass and health (Edwards and Ullrey, 1999).

Furthermore, the food passage time among captive, seed-eating New World Pithecines has been investigated. It has been shown that the addition of seeds to the predominantly frugivorous diet slowed down the passage through the digestive tract, and the seeds are suggested to add to the fiber content and gut passage time of the food (Norconk et al., 2002). Leaves and grass contain a lot of cellulose, which is difficult and time consuming to digest. There is a close dependency in the relationship between animals and the micro microorganisms, that inhabit their gastro-gastrointestinal tract. The microbes that assisting with digestion are bacteria, ciliate protozoa, anaerobic fungi, and bacteriophages. Serious nutrition-related dietary problems will arise when the delicate balance of the various gastroenteral microbes somehow is disturbed.

Eating of Soils, Charcoal, and Other Unexpected Fare

Geophagy, or soil consumption, is likely to add needed minerals and salts that potentially aid digestion and absorb toxins.

It appears that many primates supplement their diets either occasionally or even habitually by ingesting soil and charcoal. Reports about such behavior are widespread and detailed observations of such behaviors have been reported. For a list of primates involved, references, and discussion, see Burton et al. (1999). It has been suggested that a group of free-ranging rhesus macaques that are heavily infested by intestinal parasites do not have the severe diarrhea that commonly occurs with such infestations. It is suggested that these monkeys do not suffer from diarrhea because they habitually ingest soils that contain high levels of kaolinitic clays, which are known to function as antidiarrhetics in humans (Knezevich, 1998). In fact, it has been suggested that primate ranging patterns are influenced by parasitism with intestinal helminthes (Nunn et al., 2005).

The possible reasons for eating soil are multifaceted and not likely to be caused by single factors. There are six possible hypotheses formulated as possible reasons underlying primate geophagy in relation to alleviating intestinal disorders (Krishnamani and Mahaney, 2000):

1. Soil adsorbs toxins such as phenolics and secondary metabolites.
2. Soil ingestion has an antacid action and adjusts the gut pH.

3. Soil acts as an antidiarrheal agent.
4. Soils counteract the effects of endoparasites. Soils add minerals or trace elements to the diet.
5. Soils supplement nutrient-poor diets.
6. Soils provide extra iron at high altitudes.

The authors also suggest the possibilities that eating soil may add to olfactory sensibilities, add bulk to a starvation diet, or, ultimately, may have no explicable reason at all. In sum, there are a variety of possible causes for such behaviors among primates that vary according to the situation at hand. Other scenarios have been suggested, namely that folivorous monkeys may add to the beneficial intestinal bacterial flora needed to efficiently digest hard-to-process plant materials. This connection has especially been correlated with eating termite mound soils by Sifakas (genus *Propithecus;* Norscia et al., 2005). Termites are thought to incorporate symbiotic bacteria in the walls of their mounds that could be beneficial cellulose-digesting flora.

A species of Asian leaf monkeys *(Trachypithecus phayrei)* actually spend more time and speed to get to a place where they eat soil that contains a high percentage of salt than to their food sources. It seems that groups of these monkeys actually run to the "salt lick" and extend their usual foraging home range considerably to do so (Pages et al., 2005).

Reports about primates eating or licking charcoal are not quite as widely spread geographically and taxonomically as are observations about general soil eating (Krishnamani and Mahaney, 2000; Dominy et al., 2004). Charcoal eating has been reported for Zanzibar red colobus monkeys (Cooney and Struhsaker, 1997; Struhsaker et al., 1997). Casual reports have told stories about tarsiers licking charcoal and even entering the huts of natives to do so. The purpose of this behavior is believed to be getting salt from the burned-out cinders, although there is no scientifically based publication supporting these tales. Many primates that are highly arboreal have a diversified array of food items accessible to them like leaves, buds, blossoms, young shoots, bark, sap, gum, nuts, and fruit. Bark appears to serve as emergency supplemental food for many primates (Nishida, 1976). Thus, bark gauging is known from many of the New World callitrichidae, chimpanzees, and orangutans and has now also been reported about the pygmy slow loris, a prosimian primate (Tan and Drake, 2001). Reportedly only marmosets are able to gnaw holes into the bark of trees with the help of their specialized teeth and stimulate exudate flow (Simmen, 2005).

Primates living in the canopy of trees can also prey on insects and their grubs, on snails, and occasionally an egg or even a young bird and small vertebrates such as frogs. Many primates have adapted to areas that are coinhabited by human populations. There primates can profit from human cultivation of food

products or even, at an extreme, from human garbage in the peripheries of cities and villages, for example the omnivorous *Macaca mulatta* (Goldstein and Richard, 1989) and *Papio cynocephalus* (Sapolsky, 2001). Another macaque, *M. fascicularis,* has become specialized in foraging partly on fruit, on insects, and on seafood. Thus this primate is also commonly known as the "crab-eating macaque." *M. fascicularis* live predominantly in coastal areas, catching crabs and other available seafood in shallow waters of the mangrove swamps lining the edge of the Malayan sea. Wild South American capuchin monkeys, genus *Cebus,* are known for using tools to open oysters (*C. apella;* Fernandes, 1991), for eating crabs (*C. apella;* Port-Carvalho et al., 2004), and even for vertebrate predation (*C. capucinus:* Fedigan, 1990). They *(C. libidinosus)* also use anvils and heavy pounding stones to open nuts (Fragaszy et al., 2004), and *Callimico goeldii* eats fungi (Figure 9.20).

South American capucine monkeys *(Cebus apella)* have learned to discern between full and empty nuts using the nuts' weight and sound differences as parameters (Visalberghi and Neel, 2003). A variety of primates have actually figured out an array of tool use to obtain food stuffs that without tool use would be out of their reach.

Figure 9.20 *Callimico* eating fungus. Photo courtesy of Tab Rasmussen.

Some primates that live predominantly on the ground have become specialists in root digging. This is especially true for baboons (particularly Gelada baboons; Jolly, 1970) and macaques. They eat green shoots of grasses and herbs, insects and their larvae, lizards, and seeds that are available from the grassland and bushes, as well as roots and bulbs that they dig up. Forest-living primates such as the New World capuchin monkeys (genus *Cebus*) also dig for roots, catch insects, and use tools, mostly twigs and sticks to probe for insects and stones to break nuts (Moura and Lee, 2004). The large vertically jumping and leaping Sifakas *(Propithecus)* have been observed to sniff the ground and dig up subterranean inflorescences of parasitic plants to eat (Irwin et al., in press).

Tool use among primates is mostly related to activities aimed at getting to food. Slender loris *(Loris lydekkerianus malabaricus)* have recently been described as tool users while feeding on red ants (Kumara et al., 2005). A female slender loris has been observed using a branch covered with red ants to lead the insects onto her hand and lick them off. It is assumed that the saliva on the loris's hand acted as an attractant for the ants (Kumara et al., 2004).

Complex use of flexible vegetarian tools for termite and general insect "fishing" by chimpanzees *(Pan troglodytes)* have been reported from Southeastern Senegal (McGrew et al., 2005).

Ability to learn how to use tools has long been observed in capuchin monkeys: They are the monkeys that are portrayed in many tales and artful depictions playing an organ and collecting money for their master in flea markets. Great apes also have been seen to apply "tools to other, not at all food related tasks, such as the gorilla that used a stick to test the depths of the water of a pool she was about to cross" (Breuer et al., 2005).

Tool use by two lemurs *(Eulemur fulvus and Lemur catta)* has been elicited in a captive setting (Santos et al., 2005), indicating that lemurs have the capacity to use tools, just like anthropoids. However, there are no reports about active tool use by strepsirrhine primates. The only lemur that has tools built into its own morphology is the aye-aye *(Daubentonia madagascariensis)* from Madagascar: The skinny, elongate finger is used for insect and grub "fishing." The rodentlike teeth are very effective grinders to open up branches and coconuts, remove galls, and obtain edible pulp, and the large ears are the sonars for detecting noises made by insects and their grub (Pollock et al., 1985; Erickson, 1998). Thus this unusual primate conveniently has its own toolbox built right in and does not have to resort to finding suitable sticks and rocks to get to preferred food items. However, it has been reported that aye-ayes have been tested about potential extraneous tool use and did not perform as well as their large brain might have implied. The report concludes that tool use in aye-ayes, if present, is nothing but a trial-and-error event (Sterling and Povinelli, 1999).

Morphology of the Digestive Tract

The digestive tract basically is a long tube divided into several functionally and morphologically distinct regions. It begins within the mouth, where the lips, teeth, tongue, and cheeks work together to fractionize, soften, moisten with saliva, and initiate the digestive process of food (Hiiemae, 2000; Alexander, 2005). From there the preprocessed food passes through the esophagus to the stomach proper. The stomach varies in size, morphology, and cellular equipment in correlation with the size of its bearer and the dietary input. Among primates the Afro-Asian Colobines, which are specialized leaf eaters, have stomachs that are similar to those of ruminating mammals such as cows, camels, and marsupials.

There are three main layers of tissue throughout the digestive tract from the mouth to the rectum, which are, from inside out:

1. the *tunica mucosa* or mucous epithelium,
2. the *tela submucosa* (*tela,* Latin for "web"), and
3. on the outside the *tunica muscularis* or muscle layer.

Where the intestine transgresses the abdominal cavity it is suspended by the peritoneum viscerale *(tunica serosa)*. The mucosa is rich in glandular cells, while the thin submucosa layer is made up of loosely constructed connective tissue, which allows the muscular layer on the outside to be mobile. Constrictions within the muscular layer cause the mucosa to buckle up, creating haustra (Latin *haustrum,* meaning "bucket, pouch"), and is responsible for differences in the inner visceral relief of the gut. In the upper third of the gullet or esophagus the muscles are of the skeletal, voluntary type, able to open and close the upper end of the esophagus. Further down the muscular layer only contains smooth and thus involuntary muscles. The muscular layer usually has circular muscles on the inside and longitudinal muscle fibers on the outside: these muscles work together to move the intestines and thus transport the ingesta downward by peristaltic movement (the wavelike movement of the alimentary tract). The esophagus connects to the stomach proper at the so-called "cardia."

The Stomach

The stomach basically is an enlarged and widened expansion of the gut that has many variants of its basic morphology among mammals, depending on variations of function. The basic functions are:

1. collection and storage of swallowed food
2. secretion of digestive mucus, acid, initial fermentation
3. moving, mixing, sorting according to size, and homogenizing of particles
4. resorption of water, ions, and other liquids
5. fermentation in colobines

The majority of primates have stomachs with a simple, baglike structure. The stomach (ventriculus) is divided into anatomically and functionally different parts: the corpus or body, the fornix or fundus, and the pyloric portion that is closed by a sphincter (circular) muscle. The pylorus is the stomach exit where it joins the small intestine or ileum. The stomach also has various muscles and has a circular sphincter muscle at the pyloric opening where it can open and close.

The stomach has epithelia that are stratified into four regions or zones from the top downward:

1. multilayered, occasionally cornified epithelium
2. zone of unspecific cardia glands
3. main glands
4. pyloric glands

The different strata vary considerably among mammalian orders according to their digestive requirements. Colobines rely on foregut digestion (foregut-fermenting), meaning that a considerable part of digestive process happens in the stomach proper, as compared with hindgut digestion (hindgut-fermenting), where the crucial digestive process takes place behind the stomach within the parts of the hindgut. These primates, whose nutrition depends to a great extent on plant material, have to employ symbiotic cellulose-digesting bacteria to extract nutrients from their food (Chivers, 1994; R.N.B. Kay and Davies, 1994). Thus the digestion of cellulose depends entirely on allo-enzymes (enzymes created by other organisms), while protein, fat, and monosaccharids can be digested by auto-enzymes (enzymes produced by the organism itself). Cellulose-digesting, or cellulolytic, bacteria are usually transferred from the mother to her offspring by licking. The morphology of the colobine stomach, even though it has four chambers, is not like that of ruminant mammals such as cows. It is categorized among mammals that are "non-ruminating forestomach fermenters" (Langer, 2005). The stomach of colobine monkeys has either three or four chambers; the number is based on presence or absence of the first stomach chamber:

1. the pre-saccus *(saccus gastricus)* in front of the main fermentation chambers with various types of mucosa (present in genera *Procolobus, Rhinopithecus, Pygathrix,* and *Nasalis,* and lacking in genera *Colobus, Semnopithecus, Trachypithecus,* and *Presbytis;* Caton, 1999; Figure 9.21),
2. the *saccus gastricus* or main part of stomach lined with mucus-secreting glands and lymph nodes,
3. the haustrated *tubus gastricus* that contains bacteria and has cardiac glands in the upper portion where it joins the "cardia" or entrance of the esophagus, below which are the glands that produce hydrochloric acid and various enzymes, and
4. the *pars pylorica,* which only has mucus-secreting pyloric glands.

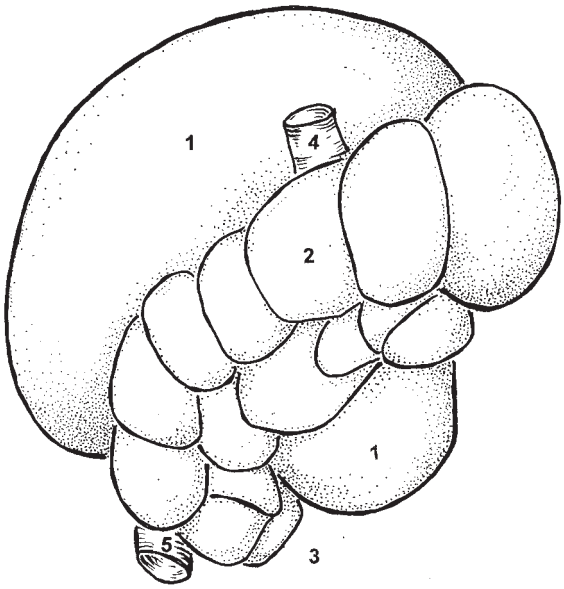

Figure 9.21 The unique Colobine sacculated foregut fermenter stomach. 1) Sacciform forestomach; 2) tubiform forestomach; 3) hindstomach; 4) cardia (junction of the esophagus with the stomach); 5) pylorus.

Notably, even though the stomachs of the leaf-eating New World howling monkeys *(Alouatta)* and the leaf-eating sifakas *(Propithecus and Indri)* of Madagascar are comparatively large, these three genera do not have the specialized chambered stomachs of the African and Asian colobines described previously (Cramer, 1968; Campbell et al., 2000). Generally, there is little or no absorption within the stomach area except for water: they are hindgut digesters. It has been shown that even though howling monkeys depend on plant food just like colobines do, their digestive system is significantly less efficient than that of the foregut digesting colobines (Edwards and Ullrey, 1999; Figure 9.22).

The stomach joins the first section of the ilium, the duodenum, at the pyloric region.

The Small Intestine

The small intestine can be subdivided into three partitions: duodenum, jejunum, and ileum. Like the stomach, the small intestine remains rather simple and uniform in all primates, varies considerably in length, and is suspended by mesenteries. Mesenteries contain blood vessels, lymphatic vessels and nodes, and nerves and mainly function as the sheath for the vascular and nervous supply to

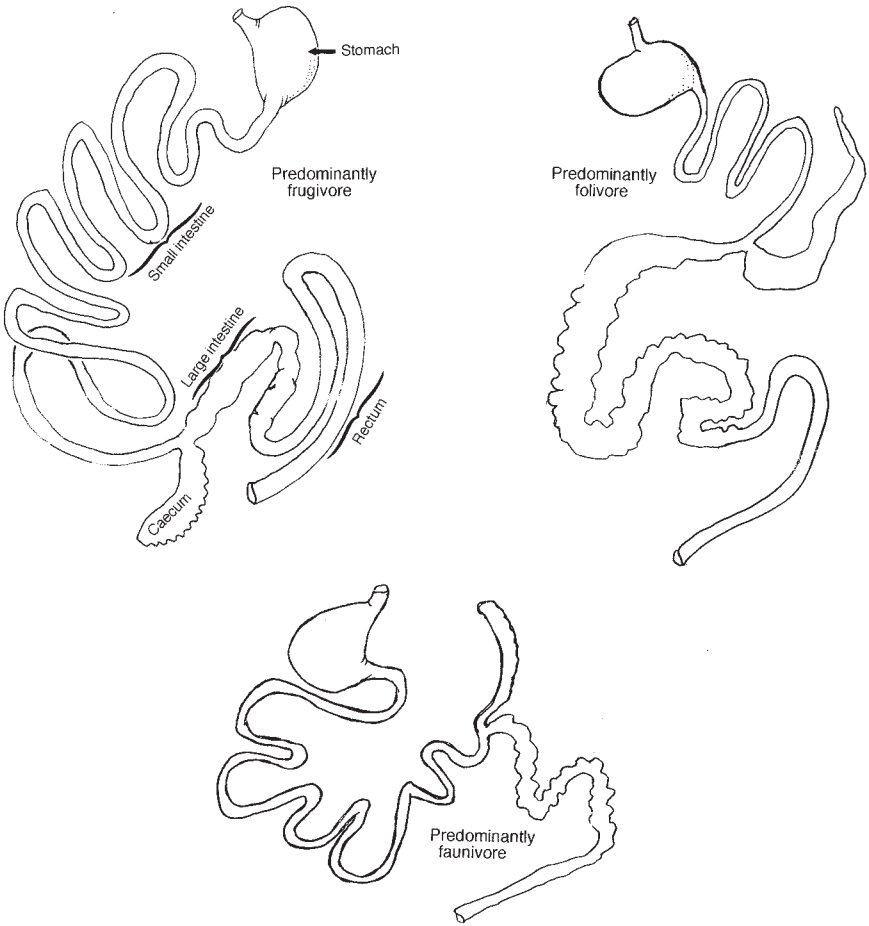

Figure 9.22 Different primate digestive tracts. The different sizes of small intestine (ileum), caecum, and large intestine (colon) are roughly correlated with the dietary differences, as indicated. (Adapted from Chivers and Hladik, 1980.)

the intestines. Inside the small intestine the mucous membrane is differentiated into multiple villi and microvilli (thin, fingerlike extensions) that considerably enlarge the absorption surface of the small intestine. The villi function in multitasking absorption of various nutrients and are assisted by the bile and the excretions of the pancreas. On the base of the villi are crypts that divide constantly to create new columnar epithelial cells. Endocrine cells secrete a variety of hormones. All these cells are continuously replaced by new cell generations through a process known as apoptosis. There are also many variably distributed

folds known as *plicae circulares,* circular folds that additionally enlarge the inner surface area of this part of the intestine.

Brunner's glands are found in the submucosa of the proximal duodenum. They start at the gastrointestinal junction and extend distally into the wall of the proximal small intestine. These secretory units primarily produce mucine, which contributes to a layer of mucus to form a slick gel that lubricates the mucosal lining of the proximal intestinal tract and has a protective function.

The duodenum receives the openings and inoculation of secretions from the bile duct that is routed through the gallbladder—the storage area for excess bile—and the accessory pancreatic duct. The pancreas is a large gland that dispenses insulin and glucagons directly into the blood, but it also secretes various digestive enzymes into the duodenum. There the pancreatic enzymes mostly break down protein, starch, and fat. The bile from the liver aids the digestive process mostly by catalysis. Thus, the duodenum is the part of the small intestine where digestive events take place.

The jejunum epithelium is a columnar absorptive epithelium interspersed with goblet cells. There are no submucosal glands (Brunner's glands) here; they are found only in the duodenum. Multiple plical folds also characterize the jejunum that are covered with many tall, slender villi. The epithelium has the same columnar absorptive surface, and more goblet cells are found in the jejunum than in the duodenum. The function of these unicellular glands is to secret mucin. The last area of the small intestine, the ilium, gives rise to the *caecum* (also spelled cecum), a saclike, blind extension of the intestine that merges at the border between the ilium and colon. The ilium also has microvilli and circular folds for absorption.

The caecum is pulled into multiple haustra by three strands of longitudinal muscles known as taeniae that are present and function in the same way on the colon. The caecum terminates in the smaller blind ending structure known as the appendix. Both the caecum and the appendix, or even a structure intermediate between the two, are found in primates. As already mentioned, the hominoid apes all have the vermiform appendix, but many nonanthropoid primates have structures that fit this definition to varying degrees. A recent reevaluation of the anatomy of the primate caecum and appendix has highlighted the difficulties in determining exactly where the caecum ends and the appendix begins (Fisher, 2000). This complication arises from the continuous, variable, and overlapping nature of caecal and appendicular tissues, both histologically and anatomically. For example, in most primates the end of the caecum is rich in lymphoid tissue and has a thickened epithelium, but it is variably narrowed into a conical appendix (Fisher, 2000).

In general, the length of the caecum, relative to that of the colon, decreases from prosimians to monkeys and apes, while the size of the appendix increases. The appendix is mostly absent in prosimians and New World monkeys, yet they

have a large caecum. In Old World monkeys the appendix is more recognizable, and it is well developed in the anthropoid apes, which lack the large cellulose-fermenting caecum. A beautiful case in fact, are the findings by Campbell et al. (2000) who show that lemur diet adaptations are clearly reflected in the morphology of their intestinal tract.

Many prosimian primates do not have a small intestine that can be subdivided into duodenum, jejunum, and ileum as in higher primates. Rather, with these prosimian primates the small intestine appears to be nearly uniform throughout in shape and histology. It is short in faunivores and long in herbivores. Among prosimian primates the entire small intestine is suspended dorsomedially by a mesentery and is not attached for the entire length between the pylorus of the stomach and the colon. This is common in tarsiers, lemurs, marmosets, and a number of cebids. The small intestine of genus *Tarsius* is simple, comparatively short, and arranged in a few basic loops. In the remaining primates the lower part of the duodenum (the part of the intestine that directly follows the pylorus of the stomach) rides firmly attached by a special ligament to the posterior abdominal wall. In primates that have this ligament the junction between small and large intestine is positioned directly ventral to the proximal portion of the small intestine. In lesser apes, great apes, and humans the duodenal portion of the small intestine is bound firmly to the posterior abdominal wall.

The small intestine functions mainly as a digestion and resorption area (see also Lambert, 1998). Differences in length that are not proportional to body size reflect differences in digestive function such as absorption of nutrient matter.

The Large Intestine

All hominoid primates have a large intestine that is relatively shorter than it is in monkeys. Moreover, there are no loops in the transverse portion. Both ascending and descending branches are closely attached dorsally to the abdominal wall. A blind ending extension of the upper colon protrudes out from the junction between the small intestine and the colon. This closed bag has the same diameter as the colon and is called a caecum; it is found in all primates. The caecum can often be hook-shaped or even be slightly spiral-shaped and is often haustrated (Langer and Takács, 2004).

The large intestine or colon has mainly excretory functions; it also shows certain interesting differences among primates. The large intestine appears less likely to be influenced by functional differences than the small intestine. However, it is uniquely variable, being smooth, haustrated, short, or long among primates according to their diet. In tarsiers the colon is very simple, and a short transverse branch is found before the colon turns straight downward. The caecum of tarsiers is about equal in length to the large intestine, and the latter lacks any flexures or coils. *Microcebus* and *Cheirogaleus* have a colon that resembles that of tarsiers.

Among Lemuridae and Lorisidae the colon is long and coiled into a number of corkscrew-like spirals or *ansa coli* (*ansa* is Latin for "loop"). The colon is especially long and arranged in a spiral in both *Propithecus* and *Indri,* possibly because in these two genera the colon is comparatively very long and thus a circular arrangement uses the available space most efficiently (Figure 9.23). Also, the circular arrangement might prevent the possibility of colon kinks, which would dangerously block the progression of the digesta (from Latin: *digestum:* "that which has been ingested") in the large tube.

In most Old and New World monkeys the connection between ileum and colon is positioned deep caudally at the right side of the abdomen. As the colon ascends from there, it extends across the abdomen higher up and descends at the left side. A high variability of colon configurations has been found among individuals of the New World monkey *Saimiri*. Old and New World monkeys often have loops in the transverse branch of the large intestine. The ascending portion of the intestine is closely attached to the dorsal abdominal wall. The large intestine has various dimensions in accordance with the general digestive specialization of various kinds of nonhuman primates. An additional blind-ending extension from the end of the caecum with a much smaller diameter is called the *appendix*

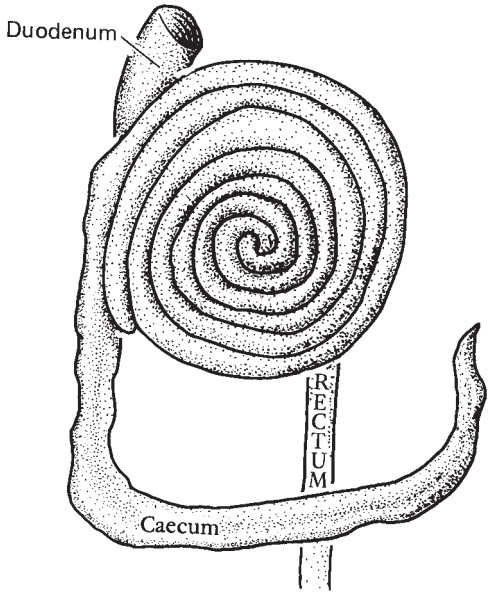

Figure 9.23 The very long large intestine (colon) of *Propithecus,* which are obligatory leaf-eaters, is arranged in two discs: the visible disc covers a second colon disc that is thus invisible.

vermiformis (Latin for "worm-shaped appendage"). This "true appendix" contains lymphatic tissue, the function of which is not quite understood. The appendix vermiformis is found in all Hominoidea. It can become inflamed in humans, requiring surgery (appendectomy) or, if not diagnosed in a timely manner, can cause death.

The intestine terminates in the short rectum that leads to the anal opening. The anal opening is regulated by a strong sphincter muscle.

Liver and Spleen

The liver and spleen also show various characteristic differences in primates. In prosimians the liver is usually differentiated into multiple lobes, much more divided than in higher primates and humans. Liver and spleen do not have a very well-defined shape of their own. Their shapes change easily, depending, among other factors, on size, form, and position of the adjoining organs such as the stomach. The spleen shows specific configurations in different primate groups. Each of the following groups shares common traits of the spleen: Prosimii, Cebidae, Callitrichidae, Cercopithecidae, Colobidae, and Pongidae (Starck, 1960).

The Genetic Connection of Digestion

The connection between primate digestion and genetic systems is not yet established (Mackie et al., 1999).

TOUCH

While all the other senses, vision, olfaction, hearing, and taste, have been well explored in primatology, there is little research and knowledge concerning the sense of touch. What we do know predominantly results from the study of humans.

The sense of touch, however, is extraordinarily important, and the entire covering of the primate body is capable of feeling touch. This largest sense organ is the skin in its various forms. Both naked (*glabrous* from the Latin adjective *glabra, glabrum,* meaning "smooth") skin and skin that is covered with hair are equally involved in sensing touch. Also integral parts of the skin are nails, claws, and hair.

The sense of touch is constantly alert, receiving information from the environment. Touch impulse transmission is unique among the senses. One of its functions, particularly on the soles of hands and feet, is to perceive the body's relationship to the support surface on which it is posited, thus comprising the

crucial sense of balance and motor control. The texture of objects that are felt and the feeling of soft touch, pressure, tension, vibrations, hot and cold sensations, itching, humidity and dryness, pain, and comfort are all sensations that are received and conveyed by the skin. Several of these sensations are associated with involuntary emotional responses. The peripheral input of these feelings is transmitted through the spinal nerves and neuroreceptors of the spinal cord and are directly and speedily processed in the sensory nervous system, causing almost immediate response. The messages received by the skin are caused by either mechanical, chemical, or thermal impulses. There are two modes of cutaneous perception of mechanical signals transmitted by the neural receptors. The first is the fast-acting or phasic response, which reacts to brief stimuli. If the stimulus is long lasting, the response to such a stimulus will decrease. The second mode of response is slowly adapting or tonic. This response will last as long as the stimulus is maintained.

The sense of touch is crucially involved in the replacement of another important sense in humans: Humans who are partially or totally blind are able to substitute their ability to see with the sensitivity of their fingertips by reading Braille. Thus the missing sense of vision is replaced by another, namely the sense of touch.

The Sensitive Skin

What we know about the touch-related substructures of primate skin is predominantly derived from the study of human skin in connection with problems of medicine, exercise, and cosmetics.

It has often been claimed that fingerprints that are typically found on palms and soles are unique for primates and not found in other mammals. These highly sensitive ridges are also known as *dermal papillae* or *dermatoglyphics* (Greek *derma, dermatos,* meaning "the skin," and the Greek verb *glypho,* meaning "cut, sculpt, engrave"). However, this is incorrect: Climbing carnivores, Scandentia, Marsupials, and Rodentia also have dermatoglyphics.

Human dermatoglyphics are individually unique and therefore crucially involved in identification techniques, both of living and deceased persons. The study of human fingerprints has a long history; in 1686 Marcellus Malphigius published a treatise about these structures. Human dermatoglyphics play an important role in forensic anthropology and in solving crimes and have been applied to ethnological studies. An enormous literature is also devoted to the documentation of illnesses and disorders in humans that are suspected to be manifest in characteristic changes of the pattern of finger, palm, and sole prints.

It has been suggested that among primates, dermatoglyphics are species-specific and therefore useful for taxonomic purposes (Biegert, 1963). Nonhuman primates not only have dermatoglyphics on their hands and feet but also on the underside of their tails and on noses. They are present on tails of tarsiers and the

prehensile tails of South American Atelinae. Various patterns of dermatoglyphics are also found on the noses of prosimians *(Perodicticus, Nycticebus, Galago, Eulemur, Phaner,* and *Microcebus),* where they are properly called nose prints (Hill, 1953). Fingerprints are thought to improve grip security in arboreal primates. The amount of friction of primate hands and feet is reduced by the plasticity and softness of the skin, but at the same time it is increased by multiple sweat gland pores that open on the dermatoglyphic ridges and provide improved bond for secure gripping (Haffner, 1998). Actually the response to touch on palms and soles is similar to that of an inflated balloon.

On the surface the skin can be separated into two major distinctive categories: skin that is covered with hair and bare or glabrous skin. Both are sensitive to touch, temperature, chemical irritation, and pressure.

Skin comprises two major layers: the superficial epidermis and a deep layer, the dermis. The two structurally identifiable entities are intrinsically interconnected: dermal papillae reach up into the epidermis. The epidermis has four cellular layers, which, from outside inward, are called *stratum corneum* (keratinized layer basically made up of dead cells that are in the process of being rubbed off and replaced), which is thick in areas of great stress, such as on the palms and soles of hands and feet where it is stratified into ridges; *stratum lucidum* (meaning shiny layer); *stratum granulosum,* and *stratum germinativum,* from where new cells are proliferated by rapid cell divisions.

Under the epidermis the considerably thicker dermis is made up of connective tissue that is interwoven with collagen and elastic fibers that have different directions in various parts of the skin. The dermis contains nerve endings, blood vessels, sebaceous and sweat glands, and *erector pili* muscles that attach to hair follicles. The follicles and sweat glands arise from underneath the dermis and traverse both layers of the skin. The dermis with its various nerve endings is the sensible command center for the sense of touch.

The elastic fibers are the structures that are responsible for elasticity. Each hair follicle is associated with elastic fibers and erector muscles. Elastic fibers are distributed in various patterns in the dermis. These fibers are arranged in a different way in humans than in all other mammals, including nonhuman primates that have been studied. They are present all over the dermis in humans, but they are concentrated around the hair follicles in other mammals. In the other mammals elastic fibers were located only in the upper part of the dermis. There usually is only one slender erector pili muscle attached to each hair follicle in mammals. The elastic fibers, as is obvious from their name, provide the skin with elasticity. According to the distribution of those fibers it is suggested that the skin of humans has a higher capacity to stretch and recoil than that in the other mammals (Starcher et al., 2005). Amusingly Starcher et al. discovered that the elastic fibers of human skin are most similar to those of *Sus domestica,* the domestic pig, among the mammals they studied.

Most important for the sense of touch are the somatosensory nervous pathways from the skin to the central nervous system (Friedman et al., 2004). All these receptors send stimuli to the dorsal root ganglia of the spinal cord, from where the messages are transmitted to the laminated dorsal horn of the spinal cord.

Potentially, there are four distinct peripheral mechanical sensory receptors distributed in various patterns in the dermis:

Pacinian corpuscules (fast adapting to pressure) are basically connective tissue capsules that are comparatively large in humans, about 1 to 3 mm long and up to 1 mm wide. They respond to pressure and vibrations. They are oval, reside deep in the skin, and are structured like onions, with many concentric layers or lamellae of connective tissue that are separated by fluid. The nerve ending is located in the center.

Meissner's corpuscules (fast adapting) are positioned directly under the epidermis and perceive low-frequency vibrations. Meissner's corpuscules are very numerous especially in the palms of hands and soles of feet. They are located in the dermal ridges of glabrous skin. These receptors have also been associated with pain reception (Paré et al., 2001).

Ruffini's endings (slow adapting) are somewhat smaller than the Pacinian corpuscules, are located directly under the epidermis, and are sensitive to stretch. They occur in both glabrous and hairy skin.

Merkel's discs (slow adapting) are mechanoreceptors found in the upper portion of the dermis attaching to the underside of the epidermal layer. They are responsive to gentle touch and shape perception. Merkel's discs are numerous around whiskers (sinus hair follicles) of many mammals (Halata et al., 2003).

There is a fifth kind of touch-related receptor:

Krause's corpuscules or end-bulbs are free cutaneous nerve bundles; however, according to Coleman et al. (2001), they are not found in primates.

Chemoreception and thermoreception is provided by free nerve endings:

Free nerve endings can overlap each other and are mainly responsive to temperature (thermoreceptors) and pain (nociceptors, from Latin *nocere* meaning "hurt") perception. While the mechanoreceptors appear to have specialized nerve endings, the thermoreceptors and nociceptors basically are free nerve endings. They do not have any capsules around the terminal endings and mostly are unmyelinated, occur in bundles beneath the epithelium, and are structurally indistinguishable. The free nerve endings reach into the epidermal skin layer. There are very many of these nerve endings distributed all over the body.

The characteristic shapes of mechanoreceptors are more easily recognized, while the nerve endings are morphologically uniform and thus much less prone to specific structural and functional evaluation.

Historically it was assumed that in humans (Johnson, 2001) and nonhuman primates all four neural mechanoreceptors are distributed and functional in variable but distinctive numbers all over both types of the skin (Bear et al., 2001), two deep in the dermis, namely the fast-adapting Pacinian corpuscules and the slow-adapting Ruffini's endings, and two superficial receptors, the slowly adapting Merkel's discs and fast-adapting Meissner's corpuscules. Recent research has changed this picture drastically. Meissner's corpuscules, which are most numerous in dermatoglyphics of the fingertips of palms and soles and in the nipples, have been the focus of attention, and the (not quite convincing) attempt has been made to correlate the number and density of Meissner's corpuscules within the dermatoglyphics with the percentage of fruit in the diet of some primates (Hoffman et al., 2004). Ruffini receptor endings are very seldom discovered in the glabrous skin of palms and soles of primates, if at all. They do seem to be tightly clustered in the area of the nail bed. Some structures that were thought to be Ruffini receptors are now reported to be innervated blood vessels (Paré et al., 2003).

Pacinian corpuscules are reportedly rare in humans and baboons and more numerous in marmosets and macaques while Meissner and Merkel corpuscules are numerous in macaques and marmosets (Paré et al., 2002). Information concerning distribution and numbers of these types of touch receptors among primates is not reliable as neither the methods of investigation nor the recognition of the various receptors are dependable. The role of Merkel's cells as sensory receptors has been confirmed (Haeberle et al., 2004).

The various aspects of touch reception appear to be better understood on the protein level than at the physical level (Papapoutian et al., 2003).

The Genetic Connection of Touch

The senses of olfaction, pheromone perception, taste, and touch all are conveyed to the central nervous system with the help of cell responses that are conveyed by proteins through cell membranes at transient receptor potential (TRP) ion channels. These signal-transducing proteins are encoded by genes. Several such voltage-gated ion channels are now known that are functionally involved in receiving environmental messages (subtle electrical charges, chemical substances, and mechanical forces) that are crucial for the well-being of the organisms involved. These cellular events involve six related mammalian protein families (Clapham, 2003). TRP channel proteins are actually present in most mammalian cells (Voetz and Nilius, 2003). Unfortunately (as already pointed out in the section on olfaction and pheromones), several of the TRPs that have

been correlated to specific functions are assigned to subgroups with similar designations (combinations of letters and numbers), and the nomenclature has been utterly confusing. An attempt has been made (Montell et al., 2002) to clarify the nomenclature, but it is still plagued by much confusion.

Discoveries about the genetic connection between sensory function of the skin and its neural foundations has focused on the ability to perceive temperature. There are two different known variants of proteins involved in thermoregulation (Peier et al., 2002; Papapoutian et al., 2003). Sensory neurons in keratinocytes in the skin of mice have been found (Moqrich et al., 2005). There are three members of TRPs that are sensitive to distinct heat temperature ranges. In mice TRPV3 has been found to be sensitive to low warmth (lower than 33 degrees C), TRPV1 is sensitive to high heat (e.g., capsaicin in peppers) up to about 42 degrees C, and TRPV2 to extreme heat (up to 52 degrees C), while TRPV4 senses warmth in the range from about 27 degrees to 42 degrees C (Xu et al., 2002; Papapoutian et al., 2003). Raw garlic elicits a burning sensation on the tongue, and two of the heat-sensing TRPs are reported to be involved in the perception of the garlic pungency in humans (Macpherson et al., 2005).

Not only the heat sensors have been explored. The peripheral nervous system of mammals also perceives cold feelings and sensations that at the extreme can be extremely painful, not unlike excessive heat. Two molecularly very different TRP channels have been suggested to be involved in the human perception of cold. TRPM8 is implicated in the ability to perceive cool temperatures (at an average of 19 degrees to 24 degrees C), and the application of menthol, a plant extract that is known for its strong cooling effect on the skin (Nealen et al., 2003). In the very cold, painful range of temperature perception a different TRP-like channel has been found to also respond to the painful reaction to capsaicin but not to menthol. It is ANKTM1 and seems to respond to temperatures as low as 12 degrees to 24 degrees C (Story et al., 2003).

It is likely that the TRP ion channels described here are indeed intrinsically involved in the detection of temperatures and the maintenance of thermoregulation in mammals. However, there is no specific research to connect these findings unequivocally in nonhuman primates.

Attempts to decipher the molecular involvement underlying the sense of touch itself have been made. In the year 2000 a protein was recognized that appears to be involved in the ability to sense the tender touch of hairy skin in mice and humans. A new family of brain ion sodium channels, or BNaCs, was discovered that seem to be involved in mammalian touch perception. When the skin hair is touched by a mechanical stimulus, nerve endings are activated. Touch causes an ion channel opening of pores in the membranes of nerve cells and allows sodium to enter the nerve cell, which responds by launching a quick electric nerve impulse. When a specific sodium ion channel protein gene, BNC1, was eliminated from the genome of "knockout" mice, their ability to perceive gentle touch was

much reduced as this ion channel was disrupted (Price et al., 2000). It is postulated that fast-responding, short-term, low-sensitivity mechanoreceptors that are located around hair follicles and perceive skin indentation in humans and nonhuman primates could be triggered by BNC1. The authors conclude: "Our identification of a molecular component for a specific cutaneous sensory modality in vertebrates is an essential first step toward a molecular description of touch" (Price et al., 2000, loc. cit. page 1010). The same gene is also suspected to be involved in pain sensation, although this connection remains elusive.

It is clear that there are many questions that have not yet been answered about sensory reception in primates (Kaas, 2005b).

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Chapter 10

Placentation and Early Primate Development

Lemuridae and Lorisidae
Tarsiidae
Ceboidea and Cercopithecoidea
Callitrichidae
Pongidae and Hominidae

It should be stressed that the use and evaluation of unitary sets of characteristics, for example placentation, with the order Primates (just as in any other group of animals) and their conversion into phylogenetic and/or systematic reconstructions are likely to be misleading and of little value by themselves. Such character complexes must be considered together with findings from all other sources of taxonomic data known for a particular group of animals. Evaluation of individual character sets are bound to be deceptive without the understanding that such characters are integrated parts of successfully functioning organisms, namely living animals, from which these characters have been selected.

Recent research about primate placentation has mainly focused on pathology as it can be applied to human development and problems in captive maintenance of nonhuman primates (Wulff et al., 2003). Another issue is the attempt to reconstruct placental evolution and the impact that the different intimate developmental connections between maternal and infantile bloodstreams might have had on the course of mammalian evolution (Carter and Enders, 2003; Crespi and Semeniuk, 2004; Wildman et al., 2006). The latter approach must remain hypothetical, even if molecular biology is invoked, as we will never know what mode of intrauterine development extinct eutherian mammals might have had.

An especially intricate variety of structures, substructures, and modes of function are those that are influential during ontogeny of any developing organism.

This fact is particularly true for the process of placentation. The overall macroscopic morphology of the placenta can to a certain extent be characteristic for taxonomic groups of mammals. However, it does not permit any insight into the intricate histological substructure, a consideration that is of importance for systematic evaluation. Considerable knowledge is needed to understand and evaluate the entire process of placentation taxonomically. Many parallel developments and functionally based adaptations can be found during the very early development of placental mammals. For example, similarities between the mature placenta of *Tarsius* and those of anthropoids have led some to the conclusion that the process of placentation must be identical between the two otherwise vastly different kinds of primates. However, the early stages of placentation in tarsiers are quite different from those in higher primates, although the end result appears similar. Insight into such intricate long-term events like placentation naturally is severely restricted by the lack of easy access to multiple consecutive developmental stages of an embryo[1] and its placenta in such primates as members of genus *Tarsius*. This is true for most primates, especially for tarsiers, which are not only exceedingly difficult to maintain in captivity but even harder to propagate under captive conditions.

Within some orders of mammals, placental relationship and similarity between members can be recognized. Thus, for example, in carnivores the mode of placentation is very uniform; this is also true for orders Cetacea, Artiodactyla, and Perissodactyla. Within the order Primates, however, we find a surprising range of differences and differentiations during early ontogeny. Thus, according to Starck (1995), differences in mode of placentation between the two suborders of prosimians (Lemuridae and Lorisidae) and anthropoids (Ceboidea, Cecopithecoidea, and Hominoidea, as well as Tarsiidae, which, however, diverge from anthropoids in the initial stages of this development) do not reflect evolutionary "grades" of development.

In all mammals (with the exception of *Cricetulus griseus,* the Chinese Hamster, which has a giant sperm tail—the largest among Eutheria—that is too big to be accommodated by the ovum) at fertilization the entire sperm—the sperm head containing the nucleus with the DNA, the midpiece containing the paternal mitochondrial DNA, and the tail (Figure 10.1)—enters the ovum. This means that the paternal mitochondria in the sperm's tail always enter into the egg. Even though the amount of paternal mtDNA is much less than that of the mother, the father's mitochondria are still visible within the zygote after the first four cell divisions, when they seem to vanish. However, they are still inside the developing embryo (Tobias, 1995; Ankel-Simons and Cummins, 1996; see also more detailed discussion in Chapter 13).

[1]An embryo is technically the very early stage of a developing animal. As soon as the main parts of the body and organs have differentiated, the embryo is called a foetus or fetus. In humans the offspring develops from the embryo into the foetus around the seventh week of gestation.

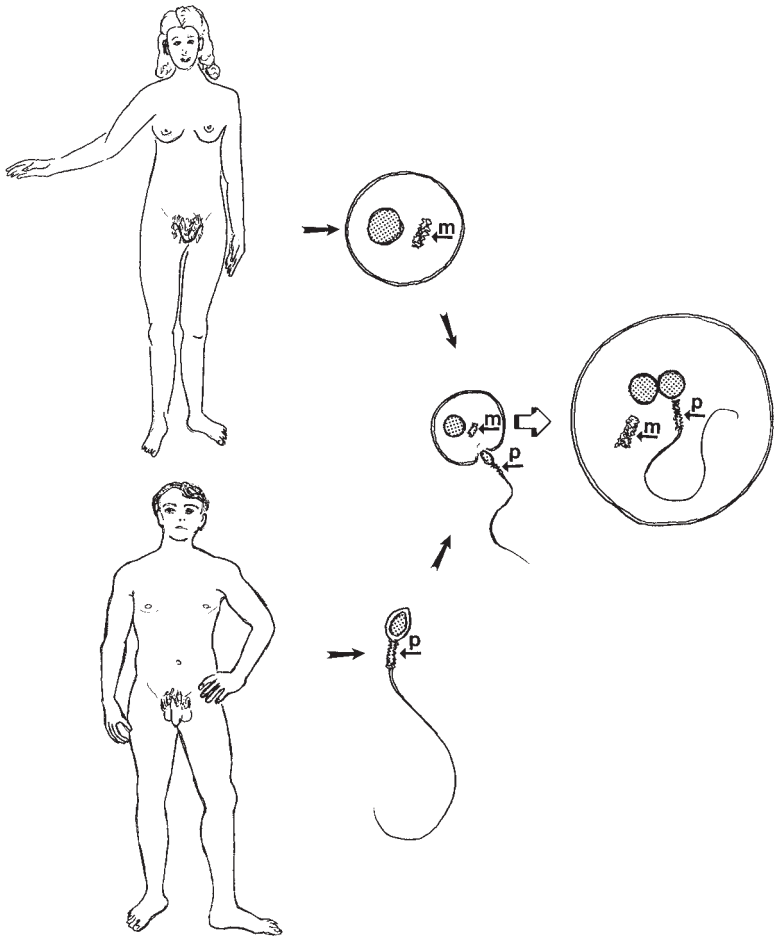

Figure 10.1 Transfer of both maternal (m) and paternal (p) mitochondrial DNA into the fertilized egg. (Adapted and rectified from Lewin, 1993; drawing by E.L. Simons.)

When a fertilized egg enters the uterus, it finds the inner uterus lining or endometrium (also called decidua) ready to receive the early blastocyst. The lining has become thick and highly vascular, its connective tissue loosened, all the capillaries plump, and the glandulae active. The outer layer of the germ or blastocyst "digests" the endometrium and implants itself into the uterine wall.

The process of successful implantation depends, however, on an intricate interplay of chemical signals that are triggered by the blastocyst and responded to by the uterine tissues. Implantation is superficial in nonhuman primates; the

fertilized egg invades the maternal uterine tissue (Wulff et al., 2003). While the germ begins to build a functional relationship with the maternal organ, the uterus also reacts to the germ's presence. If no fertilization takes place, and consequently no implantation, the inner lining of the uterus is shed after about 12–14 days following ovulation in humans. This event is called menstruation and also occurs in many nonhuman female primates. This shedding of the endometrium of the uterus involves more or less extensive vaginal bleeding. The duration of the cycle differs somewhat between species: Primate female cycles usually vary between 20 and 35 days in length (Jolly, 1972). The biological function of such obvious vaginal bleeding in humans (and other primates) has been discussed since ancient times. However, even today there is no satisfactory explanation for this biological phenomenon (Travis, 1997). If no egg is implanted, the preparatory cycle of the female reproductive system starts over again. However, if an egg is fertilized and moves into the uterus, implanting itself into the wall, the fetal membranes and the placenta begin to develop their intricate alliance. The blood circulations of the two individuals always remain separate from each other. However, in the area of contact between the two, exchange of nourishment, oxygen, and fetal waste takes place. This area is known as the trophoblast. The placental membrane can also pass certain amounts of amino acids and albumins back and forth. Other substances, for instance, certain antibodies or viruses, cannot pass through.

Primates have one of two types of uterus: Prosimian primates including tarsiers have bicornuate ("two-horned") uteri; a single uterus (uterus simplex) is found in all anthropoid primates (Figure 10.2).

The placenta is a highly complicated organ that regulates the metabolic exchange of nourishment and excretion; it regulates the embryo's fundamental biological functions and vital interrelationships between the mother and the unborn offspring (Red-Horse et al., 2004). The degree of contact between the two individuals varies among different types of placentation. These differences are the basis for the attempts to interpret taxonomic and phylogenetic interrelationships of primates and will be discussed in what follows.

The early embryo is situated within an enveloping membrane called the serosa or chorion (Greek for "skin"). At a later stage a membranous fold grows out and around the embryo. The edges of this fold, called the amnion fold (*amnion* is Greek for "sheep skin"), approach each other and finally fuse together. The result is that the embryo is surrounded by two layers of cellular material, the amnion immediately surrounding it and the serosa or chorion on the outside. The chorion establishes and maintains the connection between the maternal uterus and the offspring. Inside the chorion is a baglike structure that originates from the embryonic rectum. This protrusion of the embryonic rectum functions as a bladder that is commonly called the allantois. The allantois always remains connected with the embryo during its dependent intrauterine life. The vessels from the embryo pass through the allantois to the area of the chorion where these

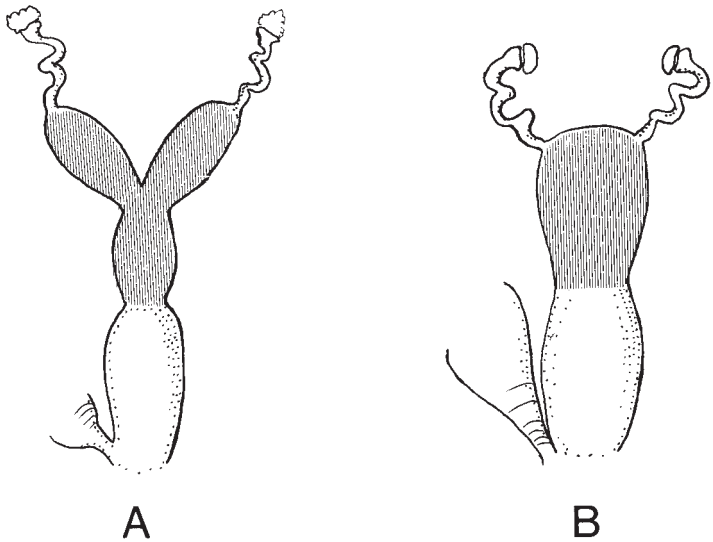

Figure 10.2 A) Bicornuate uterus of prosimian primates, and tarsiers. B) Uterus simplex, found in all anthropoid primates including Hominoidea.

vital systems of the offspring meet the maternal support system. The allantois is large in prosimian primates, small but present in *Tarsius,* and missing in anthropoid primates, including genus *Homo.* The chorion forms numerous protrusions that enlarge the contact area with the maternal uterus. The embryonic vessels intrude into those chorion protrusions that, in turn, connect more or less intimately with the maternal uterus (Figure 10.3). The placenta grows into various shapes and sizes around the embryo in different primates.

Different degrees of interdependence between embryo and maternal uterus are caused by variations of the substructures between the two. Thus in some cases the connection between the embryonic protrusions of the placenta and those of the enveloping uterine material are not closely united but only touch each other. These will separate easily from each other at the time of birth. The innermost lining of the uterus is called *membrana decidua* or, more simply, just decidua. In the case just described, when at birth the uterine lining remains unruptured, the placenta is called adeciduate. In other instances the two individual portions of the placenta are intricately connected with each other, and after expulsion of the offspring and during shedding of the placenta the decidua of the uterus does not easily separate from the placental portion and is shed together with it. In such cases the uterus suffers a rupture, referred to as a placenta decidua.

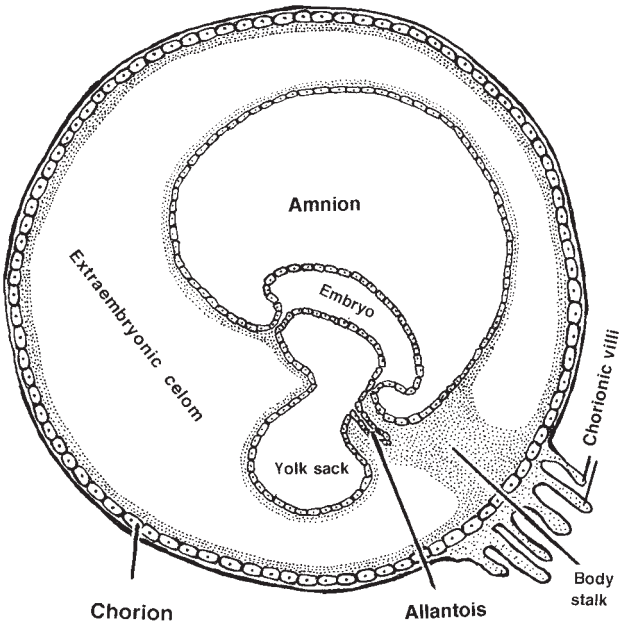

Figure 10.3 Early primate embryo.

Among primates we can distinguish morphologically between two basic chorion types and thus between two basic placental categories:

1. Chorion protrusions cover the entire placenta: placenta diffusa, usually found in epitheliochorial placentae (Prosimiae), in which the maternal membranes remain intact during pregnancy.
2. Chorion protrusions occur only in disclike areas of the placental surface: placenta discoidalis (one disc) or placenta bidiscoidalis (two discs) (see Figure 10.5), which occur in two different degrees of closeness between foetus and maternal uterus:
   a) in endotheliochorial placentae (where the chorion is directly appressed onto the endothel of the maternal blood vessels), which occurs in Chiroptera and Carnivora, but not in primates, and
   b) haemochorial placentae (where the chorion obliterates the endothel of the maternal vessels and is in direct contact with the maternal bloodstream during pregnancy), which occurs in *Tarsius* and all anthropoids including humans as well as in insectivores, lagomorphs, and rodents.

There are several other placenta types in various other mammalian orders, but they will not be discussed here because they are not found among primates.

The term "placenta" does not cover a uniform structure but is rather a term for the various structures and ways of physiological interchanges between the embryo (and, later during gestation, the fetus) and the maternal uterus.

Early during ontogeny the tissues which originally and always separate the fetal vessels from the maternal blood vessels can undergo resorption. Thus the number of tissue layers between the two individuals is reduced, and consequently the interchange between fetal and maternal bloodstream becomes more efficient and complex (Hearn, 1986). Not only is the number of layers reduced, but single layers of tissue may be reduced in thickness. Accordingly, the intensity of physiological interchange between mother and offspring differs in different types of placentation (King, 1993).

In cases where all the tissue layers of the uterus and all those of the chorion are present, we find the following six layers that separate the maternal blood flow from that of her offspring:

Epitheliochorial Placenta

Mother (Endometrium Layers):

1. Wall of maternal blood vessel (endothel)
2. Layer of connective tissue
3. Uterus epithelium (decidua)

Offspring (Chorion Layers):

4. Chorion epithelium
5. Connective tissue of chorion
6. Wall of fetal blood vessel

Where this series of layers is complete, we call the placenta epitheliochorial. This is the case in the early stages of eutherian ontogeny. The epithelium of both the maternal uterus and the embryonal chorion are present. The placenta is adeciduate.

If layers 2 and 3 are resorbed, and the epithelium of the chorion directly connects with the walls (endothel) of the maternal blood vessels, the placenta is called an endotheliochorial placenta. In this case it is the chorion epithelium that is adjoined to the endothel of the maternal blood vessels.

Endotheliochorial Placenta

Mother (Endometrium Layer):

1. Wall of maternal blood vessel (endothel)

Offspring (Chorion Layers):

4. Chorion epithelium
5. Connective tissue of chorion
6. Wall of fetal blood vessel

Among primates we also find that the maternal layers 1 through 3 undergo resorption. This means that the entire uterus endometrium is lost. In this case

the surface of the embryo's chorion is directly exposed to the maternal bloodstream. This type of placentation, called haemochorial, allows the most efficient interchange between mother and fetus. The placenta is deciduate.

Haemochorial Placenta
Mother:
Maternal blood
Offspring (Chorion Layers):
4. Chorion epithelium
5. Connective tissue of chorion
6. Wall of fetal blood vessel

These three placental types all can be said to be present in primates because all placentae inevitably start out with and go through the first stage when all six tissue layers are still intact. Primates, however, can be assigned to have either an endotheliochorial placenta (prosimians) or a haemochorial placenta (*Tarsius,* and all anthropoids including humans) (Figure 10.4). However, as mentioned,

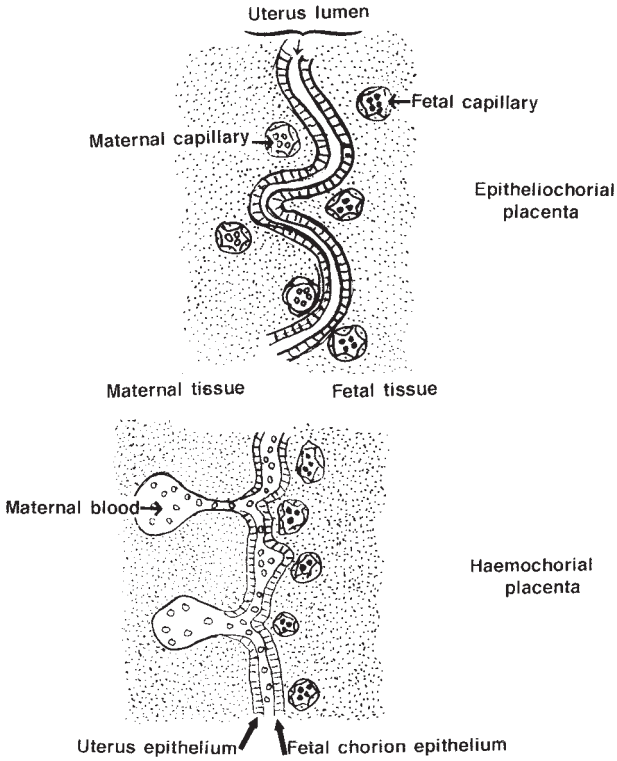

Figure 10.4 The two types of primate placentae. (Adapted from Starck, 1995.)

similarities in placentation can be caused by parallel development of structural and functional similarities and do not necessarily reflect either taxonomic or phylogenetic relationships. Also, a similarity of full-term placentae can be reached in very different ways. Differences in placentation can, for example, be caused by differences in body size and therefore various requirements for the proper development of the embryo. Furthermore, it is usually only the full-term placenta that is available for study when a birth occurs. The acquisition and study of early placental stages is only possible by invasive procedures or when the pregnant mother and the embryo die and the death is discovered almost immediately to allow careful study of the uterus, the placenta, and the unborn offspring. This naturally makes the study of placental morphology in primates (especially in rare primates and those that are difficult to rear in captivity, two conditions that usually overlap) extraordinarily complex, if not impossible.

As already pointed out, the following three higher categories of primates, 1) the Lemuridae together with the Lorisidae, 2) the Tarsiidae, and 3) the New World monkeys, together with the Old World monkeys and the Hominoidea, appear to be of rather uniform placentation within these groups.

LEMURIDAE AND LORISIDAE

The placenta of Lemuridae and Lorisidae is adeciduate, diffuse, and epitheliochorial. However, *Galago demidovii*—the dwarf galago—was studied by the French scholar Gérard (1932), who describes the placenta as having a well-defined region of the endotheliochorial type within an overall epitheliochorial placenta. Thus in the pregnant *G. demidovii* uterus all six tissue layers are present overall, except for a small and defined region where the embryo's chorion epithel is directly adjacent to the outside of the maternal blood vessels. This discovery has been widely accepted by subsequent authors but has never been reconfirmed, presumably because of a lack of material. Starck (1956), however, believes that Gérard's observations will someday be proven correct, and that therefore it is of interest to keep in mind that the dwarf galago may have an area of higher functional interchange within a placenta that is otherwise of lemuroid character.

TARSIIDAE

The mature placenta of Tarsiidae is deciduate, haemochorial, and discoidal (Figure 10.5), similar to that of Anthropoidea. The initial ontogenetic events in *Tarsius* are identical to those in prosimians (except for different patterns of implantation). Implantation of the zygote is the same as that of lemuroids and

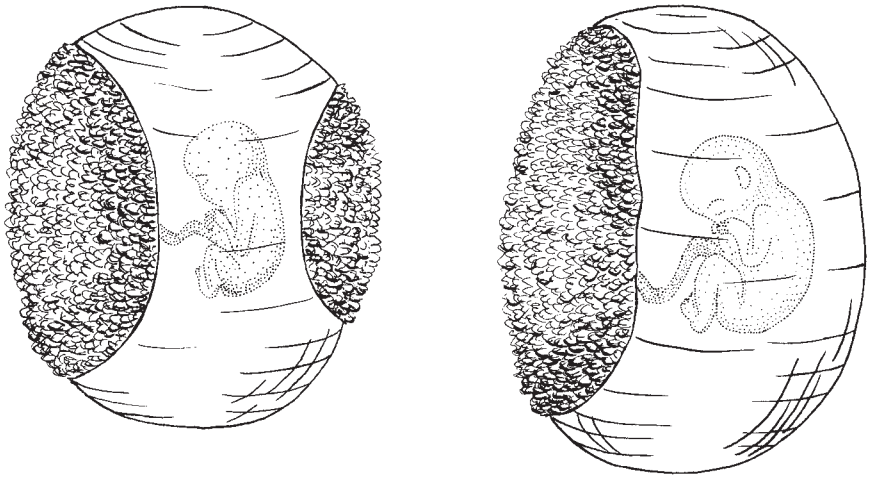

Figure 10.5 Bidiscoidal (left) and discoidal placenta (right) of higher primates. (Adapted from Starck, 1955.)

lorisoids and the other primates. During later stages of intrauterine development, unique specializations of the placental fine structure are uniquely characteristic for tarsiers. Only the full-term placenta resembles that of anthropoid primates in being haemochorial, discoidal, and deciduate (Starck, 1956, 1974).

Therefore the placentation of tarsiers and anthropoids cannot truly be called identical. The ontogeny of the tarsier placenta differs from that of higher primates. The haemochorial placenta occurs in other mammals in addition to anthropoids, such as insectivores, tenrecs, and rodents. Luckett (1993) reasserts that the tarsier mode of placentation appears to be "intermediate" between those of prosimians and anthropoids. Schwartz and Tattersall (1987) have repeatedly affirmed that the pattern of amnion development in genus *Tarsius* is unlike that of Anthropoidea and that it is, therefore, not justifiable to classify the strange and highly aberrant little tarsiers together with anthropoids in the suborder Haplorrhini, although they did not make a very convincing case as far as the mode of embryonal implantation and amniogenesis are concerned. However, the emphasis of placenta development cannot be taken as a uniquely decisive factor in determining the validity of the primate suborders Strepsirrhini and Haplorhini, because fetal membrane development varies widely.

CEBOIDEA AND CERCOPITHECOIDEA

The placenta of Ceboidea and Cercopithecoidea is deciduate, haemochorial, and bidiscoidal (see Figure 10.5). In most anthropoid monkeys the chorion

establishes two disc-shaped contact zones with the uterine wall (thus the placenta is bidiscoidal). This is the case in all those New World monkeys whose placentation is known, except genus New *Alouatta,* in which Starck (1956) found only one placenta. He reported that a comparatively high percentage of howling monkey placentae have been found to lack the secondary placentar disc, and *Alouatta* appears to be simply discoidal, not bidiscoidal as the other ceboid monkeys. Also, according to Starck (1956), there is no fundamental difference in placentation between Old and New World monkeys. Among Cercopithecidae the placentae of the genera *Macaca* and *Cercopithecus* are usually bidiscoidal; this is also the case in those Colobidae that have been studied, as well as all the specimens of genus *Papio* that have been analyzed. The two discs of this kind of placenta are of different size and are also formed at different developmental times, one after the other. The first one differentiates close to the embryonic pole (the area where the embryo is closest to the uterine wall) of the placenta and soon becomes larger than the second trophoblast that develops subsequently on the opposite side of the placenta and fuses with the opposite uterine wall. Structurally the two placental discs are alike. Anastomoses of blood vessels within the chorion connect the two placental areas. The umbilical cord of anthropoids leads to the first and larger placental disc without branching. The two discs are also known as the primary and secondary placenta.

In New World monkeys the placenta forms comparatively later during ontogeny than in Old World monkeys, and the process of implantation proceeds more slowly. The ceboid placenta never becomes as elaborate or efficient in its functional interrelationship between mother and embryo than the cercopithecoid placenta. The fully developed placentae of Cercopithecoidae and Ceboidea are very similar to each other, though their development to this point is different, especially in terms of timing and intimacy.

CALLITRICHIDAE

Many of the callithrichid monkeys regularly give birth to twins. It appears that such twins have chorionic fusion of the placenta (Bernischke and Layton, 1969). Because these twins habitually are fraternal (two separate eggs fertilized by separate sperm), it is a possibility that twin offspring of the opposite sex share the same placenta. This, in turn, causes the occurrence of freemartinism (sterile female or intersex twin born with male fraternal twin) in cattle but not in callithrichids. Freemartinism has first been described in cattle and sheep and is of importance for cattle breeding. In Callitrichidae, chorionic fusion of twin placentae is assumed to be a regular feature, as it is also documented by blood chimerism in most marmoset species. Chorionic fusion of Callitrichidae appears to occur very early in pregnancy. Placentation in Callitrichidae is unique among primates.

PONGIDAE AND HOMINIDAE

The placentae of Pongidae and Hominidae are discoidal, haemochorial, and deciduate (see Figure 10.5). Structurally the mature placentae of Pongidae and Hominidae resemble those of the Cercopithecoidea. A bidiscoidal placenta can be found in hominoids, though rarely. There are differences between the Cercopithecoidea and Hominoidea in the very early stages of their development: In hominoids implantation of the fertilized egg is more deeply within the mucosa of the uterus than in cercopithecoids and ceboids. This results in a different subsequent course of development from that in the two groups of monkeys where implantation is much more superficial. In nonprimates with a haemochorial placenta, the trophoblast is spongelike and the maternal blood circulates in the small hollow spaces of the spongy material (placenta haemochorialis labyrinthica) into which the chorion sends extensions. In anthropoids the maternal blood is contained in one large compartment into which the free tips of the chorion protrusions intrude. There they are exposed to the circulation of the maternal bloodstream (placenta villosa).

The function of these structural differences is not fully understood. At any rate, there seems to be no obvious correlation between the different types of primate placentae and the efficiency in the development of the progeny. Furthermore, it seems unlikely that different types of placentation can unequivocally be declared to be ancestral to any other type of placentation.

Attempts have been made to correlate the functional differences between the epitheliochorial and haemochorial types of placentation with such factors as body size of the mother, body size of the offspring in relation to the mother's size, or the size of the brain of the newborn primate and its requirements during pregnancy (Leutenegger, 1973). Some researchers have speculated about possible involvement of evolutionary progressiveness of different types of placentae.

According to Martin (1990), it is not possible to establish an antecedent-decedent relationship based on developmental features. He states that developmental interrelationships are influenced by the various metabolic requirements of the developing fetus. Three years later, Luckett (1993) used placental features to reconstruct the theoretical placenta of the ancestral eutherian stock and thus established the purported intermediate ontogenetic and phylogenetic position for genus *Tarsius*. In this context it is important to understand that studies of placentae of such rare primates and tarsiers have not been based on freshly prepared intrauterine ontogenetic stage specimens. Studies about *Tarsius* placentation that were done after the end of the nineteenth century had to rely on preserved specimens from the collections of eminent scholars such as European scientists A. A. W. Hubrecht and H. Bluntschli. Today rare primate embryos in utero are virtually impossible to obtain. It is (or should be) mandatory for the incontestable study of intrauterine development to have as many fresh and

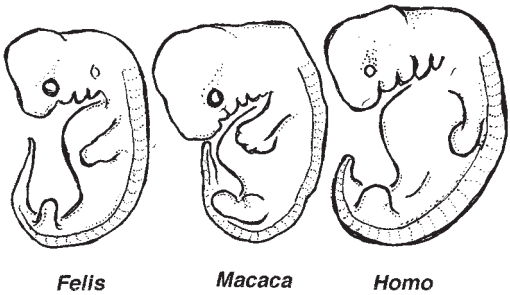

Figure 10.6 Early mammal embryos. (Adapted from Haeckel, 1902.)

consecutive stage specimens from the same species, not old specimens from unassigned or different species of the same genus. It is also necessary to study the entire uterus with the fetus and placenta undisturbed inside to procure unequivocal results. To obtain detailed and reliable information about placentation throughout pregnancy requires invasive and detrimental procedures that today are only possible where "expendable" laboratory animals such as mice are involved. Insights into placentation during pregnancy that may occasionally be possible at random due to the death of a pregnant primate can be misleading, because stages of gestation may not be exactly determined and may vary.

The early students of primate ontogeny were experts in making microscopic slides and preserving specimens. However, biological tissues deteriorate with time, no matter how well preserved they may be. The colors that serve to contrast various tissues in microscopic preparations fade, and vulnerable tissues such as placental and fetal cell structures disintegrate over long periods. Therefore, even though it is tempting to restudy the old material, it is by far preferable to rely on the original evaluation of the early ontogeny of rare and now virtually unavailable genera such as *Tarsius* (Starck, 1956). As we can see, there still are many unresolved mysteries concerning placentation in primates.

Evaluation of differences in placentation has long enticed researchers to come up with evolutionary theories based on their findings. These ideas were rooted in the idea that ontogeny recapitulates phylogeny (Haeckel, 1902; Figure 10.6). Subsequently many biologists attempted to document this kind of relationship between evolution as reflected by ontogenetic development. However, it later became obvious that ontogeny is a very intricate process that depends to various degrees on the biological requirements of the growing mammal such as body size of mother and offspring, the number of offspring for each pregnancy, and gestation length (Martin, 1990). For example, A. A. W. Hubrecht (1908) believed that the lemuriforme placenta excluded lemurs from the position of placental ancestorship to anthropoids, and he regarded the placentation of genus *Tarsius*

as being transitional between insectivores and higher primates. Hubrecht's first conclusion was quite correct, but the second idea was certainly not accurate.

A later student of mammal placentation (Mossman, 1937) even erroneously believed that the lemuroid epitheliochorial placenta documents their total phylogenetic independence from the rest of the primates.

In this context it must be stressed again that it is unwarranted to use single physiological relationships and events such as gestation to deduce evolutionary relationships. This is certainly the case with the process of ontogeny, as we now know that there are considerable functional differences in the ontogeny of various placental modes of development.

Chapter 11

Reproductive Organs, Reproduction, and Growth

Adult male primates are characterized by permanently descended testicles. All male primates have a pendulous penis. The scrotal sac that envelops the testicles is located at the sides of the penis in Callitrichidae, the gorilla, and in the lesser apes (Hylobatidae). In the latter the scrotal sac is sometimes even positioned on top of the penis. The scrotum is located underneath the penis and more or less independent of it in all other primates, including humans. The penis of many primates contains a so-called *baculum* (derived from Latin *bacillus,* "stick, rod"; diminutive, *baculum*), or penis bone, as is also found in many other mammals. It rarely is also called *os priapi*.[1] This bone is rather large in prosimian primates and may be forked at the tip. Almost all primates have a baculum except for Tarsiidae; the cebids *Lagothrix, Brachyteles,* and *Ateles;* and humans. No correlation has been found between the size of adult male primates and that of their bacula. Schultz (1969) measured the baculum of an adult *Gorilla,* weighing about 380 pounds, that was only 11 mm long, whereas that of a mandrill *(Papio sphinx)* with a weight of circa 60 pounds measured 23 mm and the baculum of a potto *(Perodicticus potto)* with an approximate weight of 2.5 pounds was 21 mm long. As a rule, the baculum of prosimian primates is relatively large. The penis bone varies according to different species in Celebesian macaques (Fooden, 1996). Testicular size has no correlation to body size in adult male primates either (Schultz, 1969). Large testes and long penises are the rule in primates whose females have large sexual swellings, such as, for example, macaques and the

[1]The *Os priapi* is named after the Greek god of fertility, Priapus, son of the goddess of love and beauty, Aphrodite, and Dionysus, the god of fertility and wine. Priapus was depicted as a grotesque little man with an enormous phallus, hence os "priapi".

chimpanzee. Adult male chimpanzees can have testicles that together weigh up to 250 grams, and in contrast those of a wild shot healthy male gorilla weighed only 36 grams. The *Gorilla* also has a very small penis. Seasonal changes in testicular size occur in the prosimian genera *Varecia, Microcebus,* and *Cheirogaleus;* this has also been found in some macaques.

Some female primates—both prosimian and New World monkeys—have a bony structure in their clitoris (the female organ that is homologous to the male penis) that is usually comparatively smaller than the male baculum. It is usually present in those genera where the males have a baculum and is similar to the males' in shape. Many prosimians, for example *Microcebus* and *Galago,* have spurlike projections on their glans penis (*glans* is Latin for "acorn" and refers to the tip of the penis). Among higher primates such penis differentiations are only known from the South American monkey genus *Ateles,* in which adult males have numerous small horny papillae. Horny papillae are also present in the vagina of female spider monkeys (Wislocki, 1936).

The testicles descend in most primates not long after their birth, and the descent is usually later in prosimians than in anthropoids. The scrotal skin contains special glands in many Malagasy lemurs, the lorisid genus *Perodicticus,* and the New World monkeys *Cebuella* and *Oedipomidas*. These glands are distinctly colored black in *Cebuella* and species of genus *Callithrix*. In some of these marmosets, e.g., *Callithrix jacchus,* the skin of the scrotum is whitish in color, thus contrasting with the dark pelage, and it is bright red in *C. argentata*. These conspicuously colored scrotal areas are involved in genital threat displays: The aggressive male callithrichid with tail erected and the testes pushed deeply into the colorful scrotum presents its rear end toward the threatened partner (Epple, 1967).

The scrotal skin is also vividly colored in *Cercopithecus* species, in *Papio sphinx,* and in *P. leucophaeus. Macaca nigra* has a vibrant cherry red colored scrotum. This skin is intensely blue to aquamarine in many of the guenons and vervets, especially in the *Cercopithecus aethiops* group, and is brilliantly red in Allen's guenon—also known as Allen's swamp monkey *(C. [Allenopithecus] nigriviridis)*. In the subgenus *Colobus (Piliocolobus)*, swellings of the skin area between the ischial callosities have an intensely iridescent pink color in juvenile males. This coloration, however, fades away with increasing age. These pink structures in young male *Colobus badius* have been interpreted as a simulation of the female peri-anal area and are said to play a social role (Kuhn, 1967). Among mandrills the circum-anal area is red. Lateral to their ischial callosities, the skin is bright blue grading into bright purplish-red at the edges. The scrotal area of mandrills exhibits a rainbow of iridescent colors: the back of the scrotum is purplish-red, the front brightly pink, the pubic region scarlet red, and the glans penis brilliantly pink. In the drill an analogous coloration of this area is even more intense in the color hues, and there is a metallic shine to the colors.

As already mentioned, the clitoris of females is homologous to the male penis. The clitoris is usually small and hidden between the *labia majora,* the large outer lips of the vulva (external female genitalia in mammals), which also has a pair of small, medial lips that are usually rather inconspicuous. Some female prosimians and cebid monkeys have an exaggerated clitoris that can be as long as or even longer than the penis and, in these cases, is pendulous like a penis. The clitoris is, just like the penis, perforated by the urethra in its center: In Lorisiformes the urethra opens at the very tip of the clitoris. In all other female primates the urethra opens near the base. The clitoris is especially similar to the male's penis in *Varecia variegata* and *Galago crassicaudatus.* The similarity of the clitoris and the penis makes a visual sex determination at a distance almost impossible. *Labia majora* are only found in prosimians, Cebidae, and humans.

The uterus develops ontogenetically from paired tubes (Müller's tubes, which develop into the oviducts later in ontogeny). These ducts fuse at the lower end to form a larger cylindrical pipe-like structure that constitutes the body of the uterus, and the extension of the fusion varies in different primates. If parts of the two ducts remain separate, they are also called "horns," and a uterus that retains separate horns of some length is called a *uterus bicornis* (Latin for "two-horned uterus," where *uterus* means "stomach cavity") or double-horned uterus. In *Tarsius* and Lorisidae the two horns are rather long. Separation of the two horns is also, though to a lesser extent, maintained in all other prosimians, but the horns are very short in most of those prosimian primates.

In all Anthropoidea the ducts are totally fused, and only one simple uterine body is present, which is called the *uterus simplex* or simple uterus. In some of the marmosets, however, a slight separation of the upper end of the uterus by a medial indentation can be seen.

In the 1930s an English researcher (Sir Solly Zuckerman) gained considerable notoriety when he stated that sex plays a crucial role in primate societies (Zuckerman, 1932). This idea made quite a stir among researchers and laypersons alike as it brought sex to the center stage of human biology. The story emphasized that male primates were always ready to mate with females, which were also always sexually responsive to the males. This statement was based on the study of captive monkeys and chimpanzees and also drawn from knowledge about human behavior. Although it is true that many anthropoid primates tend to be sexually responsive all year round when in captivity, most primates have breeding seasons in the wild. Many primates continue to breed seasonally even in captivity. Only humans are exceptional in this matter and are not at all seasonally restricted in their mating activities. The widely believed myth about totally unrestricted sexual receptivity among all primates was based on the mistaken interpretation of limited observations; it was soon revised when people began to study primates in their natural habitat. Naturally, breeding seasons are more likely to occur in

environments that are subject to obvious seasonal changes. In habitats where there is a never-changing supply of food items, such as in tropical rainforests, distinct breeding seasons are unlikely.

Mating seasons and consequently breeding and birthing seasons are restricted to only a couple of days or even hours in many prosimians. In fact, even when they are in captivity, lemur females of the same species come into estrus synchronously within hours of each other and thus such captive populations have an equally short birthing season. Seasonality in the wild makes a lot more sense than year-round mating and birthing, because the birth seasons are adapted to the availability of food and the appropriate kind of weather to ensure successful breeding in many animals. Synchronism of estrus in females of the same species has been documented even when these animals have neither visual nor olfactory contact with each other. This pattern in timing represents an inherent biorhythm. In primates that are not so strictly seasonal the birth interval is also influenced by the survival of newborn offspring. Highly synchronized mating and breeding seasons occur particularly among ring-tailed lemurs *(Lemur catta)* as well as in the New World squirrel monkey *Saimiri*. Both these species engage in heavy scent marking during the mating season, and it may be that sexual pheromones play a decisive role in the coordination of reproductive receptivity in females that come into estrus at the same time (Jolly, 1972). It appears that in many lemurs the highly restricted mating season is timed so that the infants are weaned from their mothers during the wet season in Madagascar, thus assuring the infants an abundance of suitable food at a crucial stage of development (Petter-Rousseaux, 1968). This seasonality also seems to depend on geographical location of the prosimian populations with mating seasonality. Thus *Microcebus* gives birth during September through October in Madagascar and during May through June in captivity in the northern hemisphere, where seasons are reversed. It has been documented that environmental conditions and maternal rank, age, and health are crucial factors defining infant survival in the large bodied indriid *Propithecus edwardsi* (King et al., 2005). Wild tarsiers seem to breed during the entire year in the wild: Newborn animals have been reported in all seasons with birth peaks in April, May, and November/December in *Tarsius spectrum* (Nash, 1993). Even among higher primates that appear not to have well-defined breeding seasons, births occur predominantly at a certain time of the year. Marmosets are known to have breeding seasons in the wild. Cebidae, however, evidently do not have restricted breeding seasons.

Among Old World primates *Presbytis* apparently breed throughout the year in the wild. The same is true for several cercopithecine species (e.g., *Cercopithecus ascanius, Macaca silenus, M. fascicularis*). Many other cercopithecines (e.g., *Cercopithecus campbelli, Miopithecus talapoin, Macaca sylvanus*) have been reported to show a concentration of births during the seasons with ample food supply. *Macaca mulatta* newborns are most abundant during March and April

in India, and only a few occasional ones are born as late as September. Mating occurs predominantly during January through March among Japanese macaques, and the birth season there runs from early June until the middle of August (e.g., *Macaca fuscata*). Generally, baboons seem to have seasonal peaks of mating and breeding, but no clearly defined seasonality. These peaks are much more precisely restricted in *Papio hamadryas* of Ethiopia. This condition is also true for *Cercopithecus aethiops,* which live in the same general geographic area. In Ethiopia the maximum incidence of primate births occur in April and May.

Most species of the colobines as well as the lesser great apes are believed not to have any such seasonality of breeding. The data gathered concerning mating and birth seasons in the wild are still comparatively scanty and thus inconclusive concerning many primate species. Female primates go through estrus cycles of 20 to 35 days' duration. However, ovulation of fertile eggs does not necessarily occur continuously.

Many primates have variable breeding seasons with restricted numbers of offspring during certain time spans, such as one offspring per year or one offspring every two years (Butynski, 1990).

In many prosimians the vagina opens up only during the few hours or days of estrus—the time of highest receptivity of the female. Slight and very irregular menstrual bleeding has been observed in captive tarsiers and is reported for certain New world monkeys. Periodic menstrual bleeding is of common occurrence in Old World monkeys. A feature that is restricted to the Old World primates is the marked change in coloration and degree of tumescence in the circum-anal and genital areas that occurs during ovulation. This period is also the time of highest sexual receptivity as a ripe egg is ready for impregnation. Sexual swellings of the perianal area are often accompanied by color changes of the skin in baboons and among mangabeys and are very pronounced in chimpanzees. Swellings also occur in *Cercopithecus talapoin* and several species of *Macaca;* however, these swellings are less pronounced than in the previously mentioned primates. It has been reported that *Colobus (Piliocolobus) badius* females have sexual swellings similar to those in baboons, extending into the base of the tail, and that they become permanent enlargements in adult females (Kuhn, 1967). If this is the case, however, it invalidates the sexual swellings and color changes in *C. badius* as signals of the fact that the females are in estrus (see also Dixson, 1998).

Some species of macaques show only slight changes during estrus, such as *Macaca mulatta, M. maura,* and *M. assamensis.* The genital area, root of the tail, and chest and thighs of females of these species turn red. Even the face turns red. These color changes are accompanied by slight swellings of the genital regions. *M. sylvana* exhibits circum-anal swellings that, together with the rump, turn bluish-gray rather than red, and the swellings are slate gray in *M. fascicularis.*

Many female macaques also have a strong odor during estrus that is caused by a mucous vaginal secretion. In orangutans, swelling of the sexual skin can appear during pregnancy, but not during ovulation. Chimpanzees have very large sexual swellings that are bright red during estrus and can reappear during pregnancy. The protruding sexual turgescence of female baboons sometimes ceases to subside between ovulations in old females, which makes the animal appear to be in estrus all the time. This condition can, as Schultz (1969) puts it, "attain such grotesque proportions that the poor creatures can no longer sit down." Some female chimpanzees appear to be the victims of the same predicament during peak swelling of their genital area during estrus.

Most primates have to learn how to properly mount and copulate successfully. This fact has been emphasized by the demonstrated inability to copulate by primates that have been brought up under conditions of isolation (Harlow and Harlow, 1962). Among most prosimians and monkeys the male mounts the female from the rear and embraces her around the chest. Sometimes male monkeys grasp the ankles of the females during copulation. Pottos have been observed copulating ventrally, facing each other. Rear copulations play an important part in contexts other than reproduction among social primates: They are expressions of domination. Only among Hominoidea do copulatory positions become quite variable. Especially the pygmy chimpanzee, *Pan paniscus,* has been shown to be not only very amorous but also capable of numerous variations of coital positions. Bonobos frequently use the front-to-front intercourse position that was once believed to be an exclusively human way of mating (De Waal and Lanting, 1997) and is also called the "missionary position."

The number of offspring at any given birth varies somewhat among primates. Dwarf (genus *Cheirogaleus*) and mouse (genus *Microcebus*) lemurs have up to four newborn in one litter. However, the average litter size for both of these genera is two. Among ruffed lemurs (genus *Varecia*) and the South American marmosets (genus *Callithrix*) twin births are the rule, but triplets are also relatively common. Usually, two mature eggs are released at ovulation in marmosets, and thus their twins are fraternal. The multiple births of prosimians also seem to be fraternal in the vast majority of cases. All other primates predominantly have single births, but twinning occurs in every five to six births in *Lemur catta* and some subspecies of the brown lemur *(Eulemur macaco)*. Among higher primates twins are born in about the same percentage as in humans, namely in approximately one out of a hundred births; as in human twins, 80% of these are fraternal.

Glaser (1970c) revealed that most prosimian primates and many Old World monkeys tend to have the same level of maturation in their skeletal ossification at birth as *Homo sapiens*. In fact, *Nasalis,* one genus of the Colobinae, *Hylobates,* and *Gorilla* among the apes, are somewhat ahead of the prosimians, New World monkeys, and humans in terms of bone maturation at the time of birth. Thus *Nasalis, Hylobates,* and *Gorilla* have an intermediate position in this respect,

whereas all the representatives of the subfamily Cercopithecinae that have been studied show the highest degree of ossification at birth among primates. It appears reasonable to say that all primates are dependent on their parents to a certain degree immediately after birth and to a lesser extent for an extended amount of time thereafter. Although the Cercopithecinae show a higher degree of physical maturation at birth than the other primates, their dependency on parental care lasts at an average 6 months.

The following stages of life can be recognized:

Embryo	first intrauterine phase from conception through the formation of all limbs
Fetal	second intrauterine phase from the formation of all limbs to birth
Infantile	from birth until eruption of first permanent molar
Juvenile	from eruption of first permanent molar until permanent dentition is completed
Adult	from completion of permanent dentition on
Senescence	from the termination of possible procreation to life's end

Growth not only refers to the general increase in body size but also those slowdowns of growth rates in some regions of the body that result in proportional differences in various parts of the body. Length and intensity of growth vary widely among primates. Rates are closely related to the absolute size of the adult animals and are also sex related, resulting, for example, in differences of body size and proportions of males and females of the same species. Different parts of the body grow at different rates. Thus, during prenatal life, growth occurs with a pronounced cranio-caudal gradient, resulting initially not only in larger size of the cranial parts of the body but also in a more advanced degree in their developmental refinement at birth. Fetal primates and other mammals are much more similar to each other than are adult animals. The absolute length of the different stages of life generally increases among primates from prosimians through monkeys, lesser apes, great apes, and humans. The adult stage is especially long in modern humans but, as such, can certainly be interpreted as an artifact—a result of improved general and medical care. Also, nonhuman primates in captivity appear to live longer, having profited from the same nutritional and medical improvements as humans, and especially now as the understanding of their housing and dietary requirements increase (Jones, 1968).

Among prosimian primates the intrauterine period lasts only 9 weeks in *Microcebus,* 9 or 10 weeks in *Cheirogaleus,* around 18–24 weeks among lemurs, and 20 weeks in most bushbabies. Amid anthropoids in the New World monkeys gestation length usually ranges between 20 and 25, and in the Old World monkeys macaques are born at about 24 weeks and baboons about 27 weeks of gravidity. Lesser apes are reported to need 30 weeks until the fetus is ready to be born.

The common chimpanzee has an average pregnancy length of 38 weeks, the pygmy chimpanzee pregnancy lasts 34 weeks at an average, and orangutans and gorillas need 36–38 weeks of prenatal development. Humans have a gestation period of about 38 weeks. From these data it appears that gestation length is not directly correlated with adult body size.

According to Schultz (1969), the timing of the birth is most closely defined by the size of the full-term baby and the dimensions of the female birth canal. Leutenegger (1973, 1974) also analyzed the factors governing size correlations between the diameter of the maternal birthing canal and the head size of the full-term primate offspring. His very intriguing approach must be somewhat tempered regarding evaluation of the role that locomotor requirements have in shaping the maternal birth canal, however, because he bases his observations on locomotor groups that are not valid. For example, Leutenegger lumps howler monkeys together with woolly and spider monkeys as "New World Semibrachiators." This observation is, at the least, an oversimplification, if not quite incorrect (Grand, 1968; Mittermeier and Fleagle, 1976). Some of his other locomotor classifications also weaken his interpretation. Nevertheless, the basic ideas underlying Leutenegger's reasoning are worth considering. General body size, head size of the full-term fetus, and locomotor forces shaping the birth canal of the maternal pelvis do have a part in determining the time when the fetus will be born. However, these are not the only factors that are of importance in this respect, and the events leading up to parturition are considerably more complex. The data about prenatal development and growth are still rather scanty and will most likely remain largely unsupported because of the increasing rarity of primate populations that can be studied. It was Schultz (1960) who suggested that there is a successive increase in duration of all the main life stages beginning with lemurs, through macaques, gibbons, and chimpanzees, and culminating in humans. He showed this in a diagram that subsequently has been widely republished and elaborated on by others (Figure 11.1). From this diagram one would conclude that in fact the different stages of life increase gradually throughout the array of the primates mentioned previously. This view of the stages of life in primates almost gives the impression of a "Scala naturae," or phylogenic scale advancing from primitive to highly evolved. It seems that the complexity—and in this case the length—of the life stages increases gradually from the prosimian level to an anthropoid monkey, a lesser ape, a great ape, and finally humans. This, however, is far from correct. Schultz's diagram was more or less correct at the time when it was conceived, but became irrelevant with increasing knowledge about longevity among extant primates. For example, while in 1960 lemurs were believed to live about 23–25 years, we know now that they can live in excess of 30 years without showing any obvious signs of aging and while continuing to be able to reproduce. Schultz believed that macaques had an average life span of no more than 25 years, but we know now that some macaques

can live into their upper 30s, baboons into their 40s (Rowe, 1996). Schultz attributed a life span of 34 to maximally 40 years to the common chimpanzee, but we know now that it is actually more like 50 years. Chimpanzees are still able to successfully reproduce at an age of 40 years. The same is true for the life expectancy of humans, which seems to be getting longer (70 years according to Schultz in 1960, as compared with 80–90 years at the end of the twentieth century). As Izard et al. (1988) showed, the longest gestation period among prosimians (191 days; approximately 27 weeks) so far reported, for the slow loris *Nycticebus,* is actually longer than that of the New World monkey *Cebus* (167 days, or 24 weeks) and of Old World monkeys, which are in the range of the gestation length of Hanuman Langurs *(Semnopithecus entellus)* with an average pregnancy of 184 days or 26 weeks. The duration of pregnancy in the small prosimian genus *Nycticebus* also exceeds the length of gestation among some much larger cercopithecine species such as the patas monkey *(Erythrocebus patas)* with a gestation of 167 days (or approximately 24 weeks). This indicates that there are other important factors than body size or genetic relationships that determine the duration of pregnancy. Even though Schultz's diagram seemed to make sense 40 years ago, new insights certainly suggest that behavioral and social factors as well as population dynamics may also influence gestation length, rather than a primate's position on an imaginary "ladder" based on body size, phylogenic grade, or taxonomic proximity to humans. Long gestation periods do space out offspring and tend to decrease the total number of offspring a female is able to produce during her lifetime. Hofer (in Hofer and Altner, 1972) points out that prehistoric humans and today's chimpanzees may well have had quite similar reproductive patterns in terms of the spacing of their offspring, maximum individual age, survival of adults (grandparents), and lengths of the different life stages. Schultz used absolute time for his diagram depicting the various life periods of "Lemur, Macaque, Gibbon, Chimpanzee, Man." However, if we look at total life length and at the different periods—gestation length, infancy, juvenile stage, and adulthood—as percentages of the entire life span, it turns out that these are very uniform among primates (Ankel-Simons, 2000; Figure 11.2). Only the juvenile stage is somewhat longer relative to the entire length of life in monkeys and lesser apes if compared to the length of this stage in prosimians, and the juvenile stage is markedly longer in chimpanzee and humans; we presume that learning has become a crucial factor in the adolescent development of higher primates.

Although today we have many more data, we still do not have comprehensive information about gestation length, life span, the time duration, and general developmental importance of the different life stages in many primates. Consequently, generalization must remain crude simplifications of the actual facts, and the true story of primate developmental history remains beyond our present understanding.

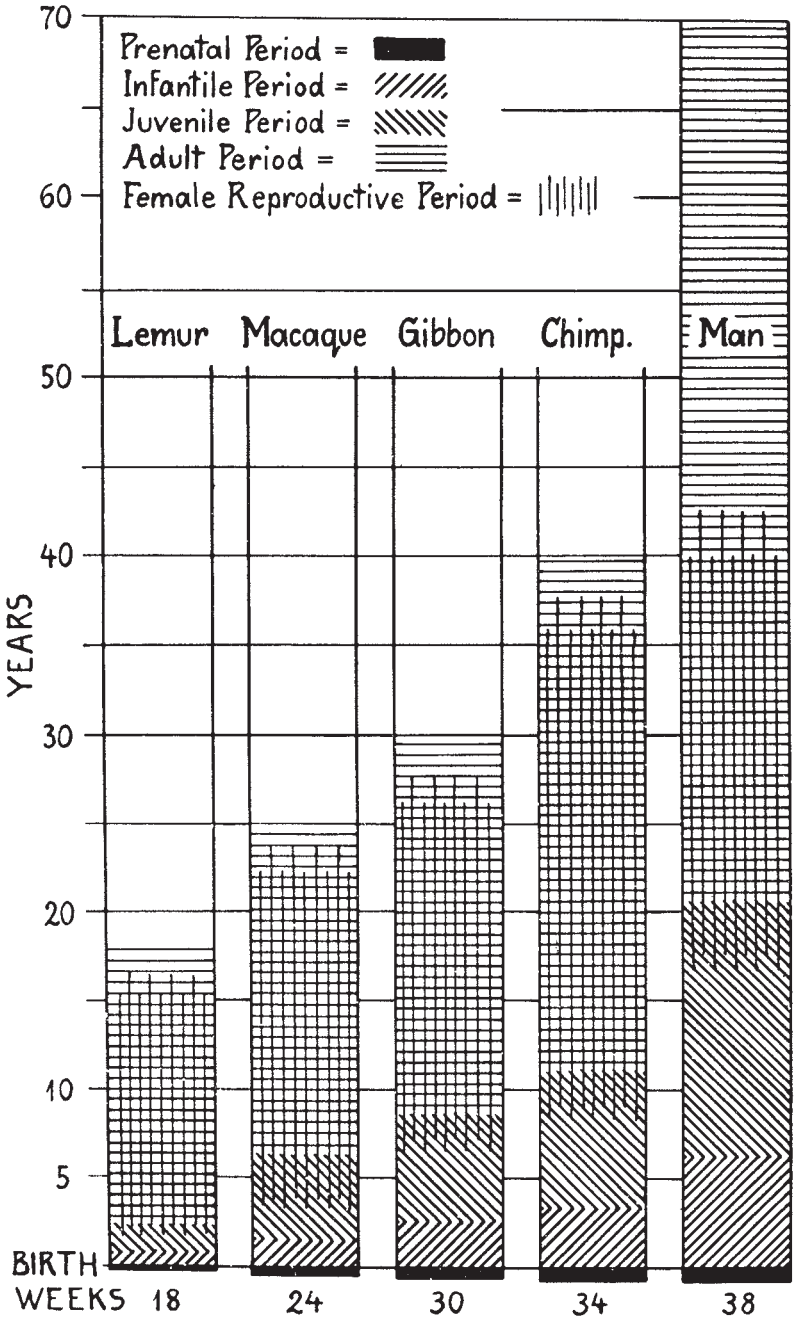

Figure 11.1 Diagram of life spans in different primates according to Schultz (1960) using absolute duration in years and showing a staggered increase of periods according to species.

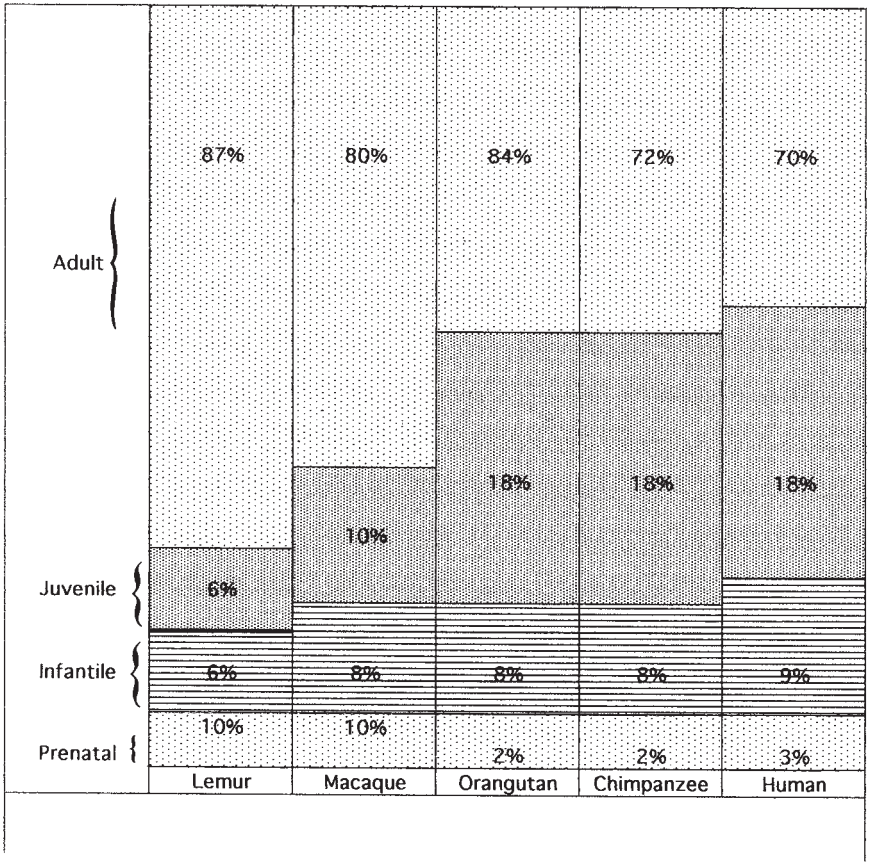

Figure 11.2 Diagram of life spans in different primates in percentages of entire life length showing uniformity of stages.

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Chapter 12

Chromosomes and Blood Groups

Chromosomes
Prosimii
Anthropoidea: Ceboidea and Callitrichidae
Cebidae
Cercopithecoidea
Hominoidea
Karyotype Evolution
Hybridization
Mitochondrial DNA
Blood Groups

CHROMOSOMES

Almost fifty years have gone by since scholars discovered that the number of chromosomes in most of the cells of human body tissue is 46 and not, as had been thought before, 48. Before the human chromosome number was definitely established the technologies of microscopy and chemical preservation of body tissues were still in their infancy, and it was very difficult to be certain how many of the tiny chromosomes there were in primate cells. The development of increasingly improved optical instruments and new staining and spreading procedures for chromosomes made possible the remarkable ability of cell biologists to now even identify single genes (Kleinsmith and Kish, 1995). Genes are the basic units of hereditary information. They are located on chromosomes and contain the information that is needed to make certain proteins that in turn produce specific ribonucleic acids (RNA). Each living cell is the carrier of a complete set of genes, which are located in a linear order on chromosomes and are species specific. Cell biology is probably the fastest advancing biological science; today's new insights can revert into old news in just a couple of weeks. Here we will be concerned with cytogenetics, the subfield of biology that studies

chromosomes, and its relation to primate evolution and phylogeny. It is interesting to remember that as recently as 1995 Marks pointed out that "The study of primate chromosomes is still in its infancy."

Conclusive proof that the human diploid set of human chromosomes was 2n = 46, and not 2n = 48, was twice confirmed in the same year by Ford and Hamerton (1956) and Tjio and Levan (1956). This was the beginning of a major breakthrough in understanding chromosome morphology, especially as our own species is concerned. It led in turn to a much better understanding of some of the trends that govern chromosome-linked heredity. Chromosome morphology is still a very important tool to address primate relationships and evolution (Stanyon et al., 2001; Ferguson-Smith et al., 2005; Wienberg, 2005). One way to distinguish individual chromosomes and their parts is by selectively staining karyotypes and their substructures with fluorescent dyes.

The word *chromosome* is derived from the Greek language and means "colored body." The name applies to those parts of each cell nucleus that are known to be the carriers of genetic information. The components for the storage and transmission of genetic information in each cell are made up of nucleic acids. Each nucleic acid molecule is made up of linear sequences of nucleotides. A nucleotide in turn is composed of a five-carbon sugar (pentose), a nitrogenous base, and a phosphate group. Two different nucleic acids are found in cells: deoxyribose and ribose. Each chromosome consists of a single, very long molecule of deoxyribonucleic acid (DNA). Every DNA molecule contains two complementary chains of deoxyribonucleic acid subunits and can be up to millions of nucleotides in length. During mitosis and meiosis these DNA strands become compacted and are therefore more visible than they are during the resting phase of the cell. Living cells go through different phases and more or less continuously divide into new cells. The visibility of the stained chromosomes is highest during the first half of mitosis, when the cells are beginning to divide at metaphase. During this phase of highest visibility, each chromosome is longitudinally paired (it consists of two identical copies); each duplicate of the chromosome is called a chromatid. In turn, the chromatid is generally divided by a constriction into two arms that are linked together at this point; the point of constriction is called the centromere. The centromere in the center of each chromosome and the telomeres making up the end of chromosomes have distinctive functions and comprise complex patterns of sequence repeats (e.g., short repeats like AATAT—see also page 563—or longer repeats like CAAAAAGCGGG). The centromere may also be called the primary constriction because the width of the chromosome is reduced to a dot at this point. In functional terms the centromere is called the kinetochore (Greek for "center of movement") because it is the place of attachment for the intercellular apparatus that pulls the pairs of chromatids apart during cell division. Centromeres are crucially involved in proper separation of all chromosomes during cell division—

mitosis and meiosis (Schueler et al., 2005). The telomere is the end of any chromosome where the nucleotide repeats protect the chromosome from enzymatic degradation (Weiss and Buchanan, 2005).

Each chromatid is made up of the highly folded and packed molecular thread containing a chain of hereditary material and genes. Genes actually are not simple and identical units of inheritance. Even though the word "gene" remains an unavoidable term for discussion of genetic concepts, Pearson (2006, loc. cit. page 399) states, "The more expert scientists become in molecular genetics, the less easy it is to be sure about what, if anything, a gene actually is." And further she goes on, "In classical genetics, a gene was an abstract concept—a unit of inheritance that ferried a characteristic from parent to child. As biochemistry came into its own, those characteristics were associated with enzymes or proteins, one for each gene." And she states further on, "This picture is still the working model for many scientists. But those at the forefront of genetic research see it as increasingly old-fashioned—a crude approximation that, at best, hides fascinat-ing new complexities and, at worst, blinds its users to useful new paths of enquiry."

It cannot be expressed any better that the term "gene" has become nothing but a manner of speech that actually addresses a multitude of totally dissimilar entities and has to be used with this understanding in mind. Single genes are not, however, directly visible on the chromosome. Genes and chromosomes are subject to constant alteration, genes by mutation and chromosomes by breaking and rejoining in a different manner. Because genes are intimately linked to the entire character of an organism, its form and its function, it follows that variations in the chromosome makeup or number should provide some information about the relation, and possibly even evolution, of animals.

There are two basic types of cells in the mammalian body: the common cells of all the tissues of the body—also known as the somatic cells—and the germ cells of the ovary and testis. Mitosis (cell division producing two identical daughter cells) occurs in the somatic cells, which have two sets of chromosomes that are similar to each other. They are not identical because one set of an individual's chromosomes was inherited from the mother's ovum and the other from the father's sperm. Within species, the number and morphology of chromosomes generally is constant. There is a pair of each chromosome in each somatic cell. In contrast, mature germ cells—the ova and sperm—have only one set of chromosomes. Therefore human germ cells contain $1n = 23$ chromosomes, whereas human somatic cells contain $2n = 46$ chromosomes. There are, however, some exceptions to this rule; the cells of some organ tissues, the liver for example, contain multiple sets of chromosomes. Also, within species that appear to be morphologically identical, the number of chromosomes can vary. This is called chromosome polymorphism. It is now known that males of the South American howling monkey genus *Alouatta* have multiple sex chromosomes (Solari and Rahn, 2005). Chromosome polymorphism means that one or several chromosomes

may occur in two or multiple alternate structural forms within the same population. Such populations may or may not be geographically separated but are not regarded separate subspecies. Karyotype polymorphisms have been known to occur in several lemurids and, for example, the South American monkey genus *Aotus*. The typical set of chromosomes of an animal species is called its karyotype. The karyotype of an animal is characterized by the complete number and form of the chromosomes. The morphology of a chromosome is determined primarily by the location of the centromere. Chromosomes of mammals are usually linear. There are also differences in the intensity of color in some chromosomes. They may have uncolored areas near the end of one pair; these uncolored areas are called achromatic (unstainable) zones and are the secondary constriction of the chromosomes (as compared with the primary constriction, the centromere). During cell division, at metaphase secondary constrictions are seen in pairs, and the primary constriction—the centromere—appears singly. Distally, the secondary constrictions are regularly adjoined by normally staining chromosomal areas that are called "satellites." The region of secondary constriction usually contains ribosomal DNA and is known as the nucleus organizer region. This ribosomal DNA is found in the "satellites" or terminal end pieces of some chromosomes, and their name is a morphological rather than a qualitative term. Chromosomes with the same arm length and identical position of the centromere that lack these achromatic zones and the satellites can be distinguished within the karyotype by banding. Note that the term "satellite" for these terminally positioned portions of ribosomal DNA can be misleading, because there is another kind of DNA, found in humans and some other primates, that is recurrent and is known as "satellite DNA"; satellite DNA has nothing to do with the ribosomal DNA satellites at the terminal ends of chromosomes (Marks, 1983).

Over time karyotypes are subject to constant changes: as already stated, chromosomes break and rejoin in many unpredictable different ways. Parts of chromosomes can be lost or transposed in the process of such events. If a large portion of a chromosome is lost within a cell, or if the reunion of chromosome pieces prevents the chromosome from being separated in half or from otherwise functioning properly and from being distributed equally at division, one or both daughter cells may disintegrate and be lost from the tissue. In the case of a germ cell, the daughter cell may be lost from the population, or, if it takes part in fertilization, an abnormal offspring may result. Such changes of chromosomes, and thus of the karyotype, are called "rearrangements." Only rearrangements in the germ cells have evolutionary effects, because these are passed on to the next generation if they are viable.

There is another type of change that works at the level of the genes. These changes are known as "gene mutations" and change the base sequence of a DNA molecule, are invisible, and are spontaneous. Gene mutations alter the molecular combination of the deoxyribonucleic acid, resulting in a change in the equilibrium

of genetic information. Geneticists today have a number of technologies available that allow the study of the substructure of DNA molecules. For example, DNA hybridization techniques are used to compare the DNA of closely related animals (for description of the technique see Sibley, 1992). Gene cutting, splicing, and sequencing with the help of bacterial restriction enzymes in combination with electrophoresis is now highly developed and also makes it possible to study so called genes (Jones, 1992). We will, however, focus here on the known karyotypes of primates; detailed discussion of all aspects of cytogenetics goes beyond the scope of this text. It would also be impossible to attempt any correlation between chromosomes and genes in this context; Marks (1992) points out that "Classical *Drosophila* genetics had suggested that chromosomes are simply a linear arrangement of genes, but we now know that most DNA is not genetic and probably has no organismal functions: the relation of gene to chromosome is like that of oasis to desert."

Let us therefore return to describing the morphology of an animal's karyotype. Both body tissue cells and immature germ cells can be used to count and describe the chromosomes. This is more complicated with cells from various somatic tissues of the body because they contain double the number of chromosomes (2n) that must be sorted out. In primordial (immature) germ cells the number of chromosomes is the same as in somatic tissue, namely 2n (diploid set of chromosomes). These cells must undergo meiotic separation of the chromosomes to produce sperm or egg cells with one set, or 1n (the haploid set), of chromosomes. However, haploid germ cells are more difficult to obtain, and the chromosomes are more difficult to see, than those of other tissues. To get reliable results it is useful and recommended to evaluate both types of cells of an organism whenever possible.

In most chromosome studies, karyotypes are constructed from mitotic metaphase chromosomes. Because of the development of techniques in the 1950s and 1960s for culturing tissues of cells in vitro (in glass), researchers are able to study cells under carefully monitored conditions. It is relatively simple to culture lymphocytes that can be obtained from blood samples. The growing cells are arrested in metaphase by the addition to the culture of the drug Colchicine, which inhibits further cell division. The chromosomes are separated by expanding them with the help of a hypotonic solution. Subsequently they are treated with a fixative to preserve their structural integrity, spread onto a microscopic slide, and stained with dyes such as Giemsa or Orcein. These stains produce a pattern of color banding (G-banding) that is typical for each chromosome and makes it possible to distinguish individual chromosomes within a karyotype. In the early 1970s it was demonstrated that fluorescent dyes such as Quinacrine (Q-banding) or Acridine Orange (Casperson et al., 1970) produced both bright and dull fluorescent bands along the length of chromosomes. The Q-banding pattern is usually the same as the G-banding pattern with a Trypsin (an enzyme) pretreatment. Reverse

bands, or R-bands, are produced with either Acridine Orange or Giemsa after heat treatment. Finer detail of banding patterns can be achieved by making the chromosome longer and using more recently developed banding techniques such as high-resolution Giemsa banding (Yunis et al., 1978). These changes can be observed with the help of staining and observing the karyotype morphology and banding with the help of microscopy.

Early on (Matthey, 1945) it was suggested that the diploid chromosome number of different mammals is less useful for the evaluation of karyological evolutionary theory than the total number of chromosome arms. This number of chromosome arms is called the fundamental number and is generally more uniform among taxonomic groups than the diploid number.

Cell synchronization is used to obtain chromosomes at early metaphase, prometaphase, and even late prophase, when the chromosomes are longer and exhibit more bands. At prometaphase and late prophase approximately 1200 bands can be identified per haploid chromosome set in humans, whereas only 300 to 500 bands are visible at metaphase. With such newly developed techniques it is now possible to follow sub-bands that are not resolved in metaphase chromosomes and to look more closely at homologies that are believed to exist between species. This made it possible to evaluate the karyotype of an animal as to the relative length of chromosomes, the position of each centromere, the presence or absence of "satellites," and characteristic banding patterns. Today the possibilities to study even smaller units of chromosomes have been highly developed in tandem with the elaboration of electron microscopy, as well as many other new biochemical techniques that work on the molecular level.

Morphological analysis of a karyotype is usually based on photographs from which individual chromosomes are cut and arranged in a particular sequence: The chromosomes are lined up according to their absolute length, beginning with the longest, and according to the position of the centromere.[1] If the centromere is positioned medially (length ratio of the arms between 1 : 1 and 1 : 1.9), the chromosome is called **metacentric.** When the arm-length ratio is between 1 : 2 to 1 : 4.9 and it has a centromere position that is submedian the chromosome is characterized as **submetacentric.** If the arm length ratio increases to above 1 : 5, and the centromere position is subterminal, the chromosome is considered **acrocentric.** It can also happen that the centromere's position is at the very end of the chromosome or terminal, and the chromosome has only one pair of very long arms; in this case the chromosome is called **telocentric** (Figure 12.1).

[1]Half a century ago a chromosome terminology according to arm length, not centromere position, has been proposed that subsequently has rarely if ever been used (Battaglia, 1955). Metacentric chromosomes with a median centromere and equal arm length were named isobrachial (even armed). Submetacentric chromosomes were called heterobrachial (uneven armed) and acrocentric chromosomes cephalobrachial (head or top armed).

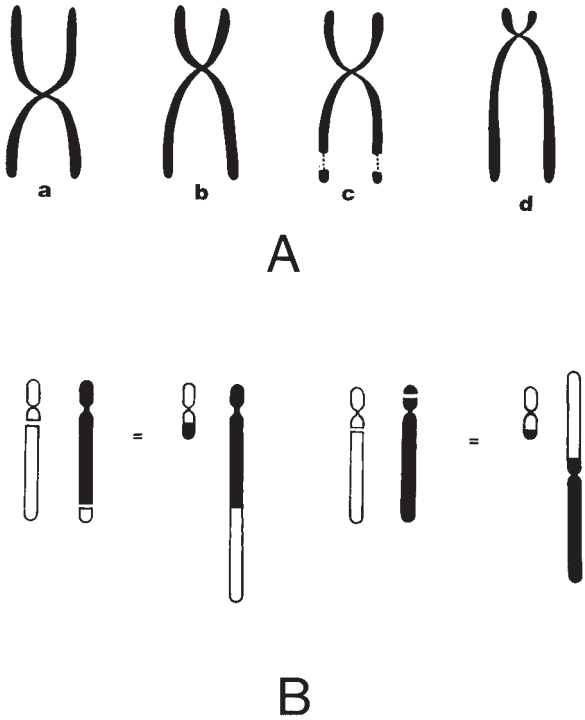

Figure 12.1 (A) Insertion types of different chromosomes. a) Metacentric chromosome (median insertion); b) submetacentric chromosome (submedian insertion; c) submetacentric chromosome with achromatic (unstainable) portions and satellites; d) acrocentric chromosome (subterminal insertion). (B) Chromosome mutations. Possible ways of recombination of two acrocentric chromosomes into two metacentric chromosomes.

Telocentric chromosomes are not found in primates and can therefore be disregarded in our discussion.

During the prophase of cell division chromosomes become highly spiralized and therefore shortened, concentrated, and thus visible. This means that the chromosomes are transformed from an active dispersed chromosome into a discrete transport chromosome. During an organism's life the following events, known as mutations, are possible and result in changes of the chromosome complement of cells:

1. Entire sets of chromosomes (one set of chromosomes is equivalent of the genome of an organism) can duplicate without subsequent division of their cell. This duplication results in an increase of the number of chromosomes (x times n), and the cell becomes polyploid. (Polyploid cells are common in a certain percentage in highly active organ tissues, for example in the liver.)

2. A change of single chromosomes can come about in various ways: One or more chromosomes may break, or pieces of chromosomes can be lost (deletion) or can be duplicated by addition or interchange of pieces (duplication). Chromosome pieces can turn over and fuse again with the same chromosome (inversion) or can be exchanged between chromosomes (translocation). All these events are rearrangements. Many rearrangements are not able to survive and are lethal for the cells involved (see Figure 12.1).

3. Another disorder occurs when chromosome pairs divide disproportionately. In humans, for example, one pair of chromosomes can have a third equivalent. Cells with this equivalent third set of one chromosome result in a condition called a "trisomy" and cause physiological and developmental deficiencies of the carrier. A cell lacking a chromosome is "monosomic." Cells that have an exact multiple of the haploid number of chromosomes are also referred to as "euploid." Cells are called "aneuploid" when they have either more or less than the exact multiple of the haploid number of chromosomes. Aneuploidy may result from a failure of chromosomes to separate or disjoin properly during cell division, a phenomenon called "nondisjunction."

Rearrangements can naturally result in loss of some chromosome material (DNA). In mammals chromosomal rearrangements also result in a change of the number and/or the type of chromosomes of given karyotypes. However, the amount of DNA in each genome remains roughly constant, namely 3.5×10^{-9} mg DNA in most mammals (Ohno, 1969). It appears that most successful changes of genetic information cannot be achieved with less genetic material. Evolution results from reorganization of genetic material: Changes in the genetic material are inherited and may lead to species differences; these in turn may lead to species separation, a step in evolutionary progression.

Some students of primate chromosomes have tried to detect differences in the amount of DNA per cell in different primates. The small differences found do not, however, exceed the range of error considering the delicate procedures of measuring DNA content of a cell. For example, the data show that the amount of DNA in a diploid cell of *Lepilemur ruficaudatus,* a prosimian, and *Callicebus lugens,* a New World monkey, with $2n = 16$ chromosomes (the lowest number of chromosomes within the order Primates; Bonvicino et al., 2003) and the amount of DNA of a *Tarsius* cell with $2n = 80$ (the highest known number of chromosomes among the order Primates) is the same and equals 7.0×10^{-9} mg. Thus even though these karyotypes differ, they contain essentially the same amount of genetic material. However, it has also been reported that there is a difference in the content of DNA between primate groups (see also Martin, 1990; Gregory, 2005a; see also Table 14.1).

Evolutionary rearrangement of the karyotype most commonly involves chromosome fusion or fission. These changes are also known as Robertsonian

translocations (Robertson, 1916). For example, during fusion two acrocentric chromosomes combine into one metacentric chromosome, while fission is the reverse process where one metacentric chromosome splits into two acrocentric chromosomes.

As already noted, chromosomes of the diploid cell appear in homologous pairs, one member of which came from the mother organism, and the other from the father. In females there is one pair of so-called sex chromosomes that are identical in shape (although one is usually inactivated functionally); they are called X-chromosomes. In males, the sex chromosomes consist of one X-chromosome and one Y-chromosome (the Y chromosome can be regarded as being haploid, as only one copy is found in the normal karyotype); they are—unlike the other chromosomes within cells—not homologous and differ from each other in banding and size. Chromosomes other than the X- and Y-sex chromosomes are called autosomes. In females the sex chromosomes often cannot easily be separated from pairs of autosomes of similar size. Y-chromosomes are usually very small and do not seem to be of much evolutionary importance as carriers of genetic information other than the determination of the male sex (see also Graves, 1995). However, improved technology known as STR (Short Tandem Repeat) amplification now routinely uses Y-chromosomes to trace the male cell line in human genealogy (Joblin and Tyler-Smith, 2003). This technology is basically the same method applied to forensic DNA profiling or DNA fingerprinting and paternity testing (Calì et al., 2002; Jobling and Gill, 2004). Very small chromosomes that cannot easily be classified according to the position of the centromere are called microchromosomes.

Despite advances in technology there are still many unanswered questions concerning primate cytogenetics. It is still not possible to reliably reconstruct relatedness of primate genera with help of their karyotypes. Attempts to correlate the degree of karyotypic diversity within mammal taxa in general and primate taxa in particular with morphological adaptations and evolutionary change have proven to be rather elusive and not always conclusive.

Prosimii

The number of chromosomes varies between 2n = 20 and 2n = 80 among the prosimii (Table 12.1). Within genus *Eulemur* the variation in diploid chromosome numbers ranges from 2n = 44 to 2n = 60. There are multiple diploid chromosome numbers found in *Eulemur fulvus* subspecies, namely 2n = 60, 52, 51, 50, and 48. A number of 2n = 58 has also been reported for several individuals. *Lepilemur ruficaudatus* has only 2n = 20 chromosomes—the lowest number of chromosomes among prosimians. In contrast, *L. mustelinus* has 2n = 34 (see also Petter et al., 1977). *Eulemur* chromosomes vary widely in length from very large macrochromosomes to very small microchromosomes. The remarkable lemurid

Table 12.1
Karyotypes of Prosimians

	Chromosomes						
	2*n*	M	S	A	X	Y	Reference
Tupaiidae							
Tupaia glis	60	8	4	46	S	A	Chu and Bender, 1961; Klinger, 1963
Lemuridae							
Lemur catta	56	4	4	46	M	A	Hamilton and Buettner-Janusch, 1977
Eulemur mongoz	60	0	4	54	A	A	Hamilton and Buettner-Janusch, 1977
Eulemur fulvus	60	0	4	54	A	A	Hamilton and Buettner-Janusch, 1977
Daubentonia madagascariensis	30		12	2	M	A	Rumpler et al., 1988
Eulemur macaco	44	12	8	22	A	A	Rumpler et al., 1988
Varecia variegata	46	16	2	26	S	A	Rumpler et al., 1988
Hapalemur g. griseus	54	4	6	42	A	A	Rumpler and Albignac, 1973
Hapalemur g. olivaceus	58	2	4	50	A	A	Rumpler and Albignac, 1973
Lepilemur ruficaudatus	20	2	16	0	M	A	Rumpler, 1975
Lepilemur mustelinus	34	0	6	26	S	A	Rumpler, 1975
Microcebus murinus	66	0	0	64	S	A	Rumpler and Dutrillaux, 1979
Cheirogaleus major	66	0	0	64	S	A	Rumpler and Dutrillaux, 1979
Cheirogaleus medius	66	0	0	64	S	A	Dresser and Hamilton, 1979
Propithecus verreauxi coquereli	48	14	16	16	S	A	Rumpler, 1975
Propithecus tattersalli	42	22	12	8	?*	?*	Simons, 1988
Indri indri	40	12	0	6	M	A	Quinn and Wilson, 2002

Lorisidae							
Nycticebus coucang	50	22	26	0	S	M	Garcia et al., 1978; Weisenseel et al., 1998
Loris tardigradus	62	18	16	26	S	?	Goonan et al., 1996
	62	18	18	24	S	?	Goonan et al., 1996
	62	16	18	26	S	A	Goonan et al., 1996
Perodicticus potto	62	16	16	28	S	A	deBoer, 1973b
Galago senegalensis	36	30	0	4	A	A	deBoer, 1973a
	37	29	1	5	A	A	deBoer, 1973a
	38	28	2	6	A	A	deBoer, 1973a
Galago crassicaudatus	62	6	6	48	S	A	deBoer, 1973a
Galago garnetti	62	6	20	34	S	A	deBoer, 1973a
Tarsiidae							
Tarsius bancanus	80	14	0	66	S	A	Egozcue, 1969; Dutrillaux et al., 1988
Tarsius syrichta	80	7		33	?	?	Dutrillaux et al., 1988

n, Haploid number; M, metacentric; S, submetacentric; A, acrocentric; X, female sex chromosome; Y, male sex chromosome.
*Based on one female.

Daubentonia madagascariensis has a diploid chromosome number of 2n = 30, with two pairs of acrocentrics and twelve pairs of metacentric and submetacentric chromosomes. Thus, the X-chromosome is metacentric, and the small Y-chromosome is acrocentric. The karyotype of the aye-aye appears to be very different from both lemurs and lorises (Rumpler et al., 1988).

A comparison of karyotypes within the prosimians reveals some regularity. If the 2n number of chromosomes is high, many chromosomes are acrocentric. If the 2n number of chromosomes is low, the majority are metacentric, and only a few acrocentrics are found. In the transitional field between these two extremes, namely around the diploid number of 2n = 50, lies the chromosome number of *Nycticebus,* and it makes an exception to this rule by having only metacentric chromosomes. Warter and Rumpler (1998) have recently confirmed that chromosomal polymorphism and intraspecific chromosomal variability are common among prosimian primates.

This correlation between high numbers of and a high proportion of acrocentric chromosomes in prosimian karyotypes lead to an evolutionary theory that will be discussed later in this chapter.

The technology of chromosome painting has been widely applied to the study of prosimian karyotypes (Warter et al., 2005). Taxonomic relationships have been reconsidered and reconfirmed (Nie et al., 2006; Stanyon et al., 2006). A close phylogenetic relationship between Scandentia (tree shrews) and primates has been suggested (Müller et al., 1999).

Anthropoidea: Ceboidea and Callitrichidae

The Callitrichidae are quite uniform in their karyotypes They are also most interesting in relation to their karyotype evolution. All the karyotypes of this family that are known have 2n = 44, 46, or 48. Most have 4 metacentric chromosomes, 24–28 submetacentrics, and 10–18 acrocentrics in their diploid set. The reduction of the diploid number from 48 to 46 and from 46 to 44 can be achieved by reducing the number of acrocentric chromosomes by two pairs and increasing the submetacentric number by one pair of chromosomes (assuming that in the case of these callithrichids evolution involved fusion and proceeded in the direction of reducing the diploid number of chromosomes—actually the opposite could be the case: namely that evolution proceeded by fission, and one metacentric chromosome split up into two acrocentrics). Fusion events could be responsible for the differences in the karyotypes of *Callimico, Saguinus, Callithrix* and *Cebuella* (Table 12.2). The mechanism in question is centric fusion: A large pair and a small pair of acrocentric chromosomes fuse to form one large pair of submetacentric chromosomes. The differences of the karyotypes between *Saguinus fuscicollis* on the one hand and *Callithrix jacchus* and *Leontideus illigeri* on the other have been explained as the results of translocations of an

Table 12.2
Karyotypes of Anthropoidea

	Chromosomes						
	2*n*	M	S	A	X	Y	Reference
Callitrichidae							
Callimico goeldii	48	4	24	18	S	A	Egozcue et al., 1968
Callithrix jacchus	46	4	28	12	S	A	Egozcue et al., 1968
Callithrix aurita	44	4	28	10	S	A	Egozcue et al., 1968
Callithrix argentata	44	4	28	10	S	M	Egozcue et al., 1968
Callithrix chrysoleucos	46	4	26	14	S	M	Egozcue et al., 1968
Cebuella pygmaea	44	4	28	10	S	A	Egozcue et al., 1968
Saguinus fuscicollis	46	4	26	14	S	M	Egozcue et al., 1968
Saguinus nigricollis	46		30	14	SM	SM	Nagamachi et al., 1997
Leontocebus rosalia	46	4	28	12	S	M	Egozcue et al., 1968
	46	32**		12	SM	ST	Nagamachi et al., 1997
Leontocebus illigeri	46	4	30	10	S	M	Chu and Bender, 1961
Leontocebus caissara	46	30**		14	SM	SM	Nagamachi et al., 1997
Cebidae							
Aotus t. trivirgatus	50	8	18	22	M	M	Yunis et al., 1976
Aotus t. griseimembra	54	10	10	32	M	A	Miller et al., 1977
	53	11	10	30	M	A	Miller et al., 1977
	52	12	10	28	M	A	Miller et al., 1977
Aotus vociferans	46	7	5	10	M	M	Torres et al., 1998
Aotus brumbacki	50	9	3	12	M	?	Torres et al., 1998
	50	5	5	14	M	M	Torres et al., 1998
Aotus nancymaae	54	9	2	15	M	M	Torres et al., 1998

(Continues)

Table 12.2 *(Continued)*

	Chromosomes						
	2*n*	M	S	A	X	Y	Reference
Aotus lemurinus	52	5	5	16	M	M	Torres et al., 1998
	54	6	5	14	M	M	Torres et al., 1998
Aotus hershkovitzi	58	32	4	20	M	?	Torres et al., 1998
Callicebus moloch	48	12	6	26	S	A	Bernischke and Bogart, 1976
Callicebus torquatus	20	2	6	10	M	?	Bernischke and Bogart, 1976
Callicebus lugens	16	4	?	3	M	?	Bonvicino et al., 2003
Pithecia pithecia	48	10	8	28	?	?	deBoer, 1975
Cacajao ribicundus	44	10	8	24	?	?	deBoer, 1975
Alouatta seniculus	44	10	6	26	A	S	Yunis et al., 1976
*Alouatta caraya**	52	4	16	30	S?	A?	Yunis et al., 1976
Saimiri sciureus	44	10	20	12	S	A	Lau and Arrighi, 1976
Ateles paniscus	32	12	16	2	S	S	Dutrillaux et al., 1981
Ateles belzebuth	34	10	20	2	S	A	Dutrillaux et al., 1981
Ateles geoffroyi	34	12	18	2	S	S	Dutrillaux et al., 1981
Ateles b. marginatus	34	?	?	?	?	?	de Oliveira et al., 2005
Brachyteles arachnoides	34	?	?	?	?	?	de Oliveira et al., 2005
Lagothrix lagotricha	62	8	22	30	S	A	Dutrillaux et al., 1980
Cebus capucinus	54	6	10	36	M	S	DeCaballero et al., 1976
Cebus apella	54	4	16	32	M	S	DeCaballero et al., 1976
Cebus albifrons	54	6	12	34	M	S	DeCaballero et al., 1976
Cercopithecidae							
Macaca mulatta	42	14	26	0	S	A	Dutrillaux et al., 1979
Macaca fascicularis	42	14	26	0	S	A	Dutrillaux et al., 1979

Cercopithecus mona	66	48**		16	S	S/A	Egozcue, 1969
Cercopithecus mitis	72	48**		22	S	S/A	Egozcue, 1969
Cercopithecus aethiops	60	14	22	22	S	A	Dutrillaux et al., 1979
Papio anubis	42	14	26	0	S	A	Dutrillaux et al., 1979
Papio papio	42	14	26	0	S	A	Dutrillaux et al., 1979
Papio hamadryas	42	14	26	0	S	A	Bernstein et al., 1980
Papio ursinus	42	14	26	0	S	A	Bernstein et al., 1980
Erythrocebus patas	54	16	28	8	M	?	Dutrillaux et al., 1978
Trachypithecus francoisi	44	?	?	?	?	?	Nai et al., 1999 (in Chinese)
Trachypithecus phayrei	44	?	?	?	?	?	Nie et al., 1998
Nasalis larvatus	48	?	?	?	?	?	Bigoni et al., 2003
Colobus polykomos	42	?	?	0	S/M	A?	Egozcue, 1969

n, Haploid number; M, metacentric; S, submetacentric; A, acrocentric; X, female sex chromosome; Y, male sex chromosome; SM, submetacentric; ST, subtelocentric.

**A. caraya* has been found to have an unusual sex-chromosome system (Mudry et al., 1998). See accompanying text.

**Some authors do not differentiate between metacentric and submetacentric chromosomes, calling both "bi-armed autosomes."

acrocentric and a submetacentric pair of chromosomes producing two metacentric chromosome pairs (Egozcue et al., 1968). Because most of the karyotypes of these species predate banding methods, chromosome banding is needed for substantiation of the hypothesis of centric fusion and rearrangement by translocation in these species. Banding studies will be able to show whether homology exists between the arms of the submetacentrics and the autosomes from which they purportedly derive.

Callimico is a genus of Ceboidea that has been much discussed with regard to its systematic placement within the superfamily. The dental formula of *Callimico* and the morphology of its skull are like those of the Cebidae. Part of the postcranial morphology and many behavioral traits resemble callithrichid monkeys rather than cebid monkeys. One of the karyotypes that has been recorded for *C. goeldii* also resembles callithrichids by having two pairs of metacentric chromosomes and a submetacentric X-chromosome. This karyotype of *Callimico* has been used by some students as additional evidence for the taxonomic placement of this genus in the family Callitrichidae. Egozcue (1969), however, found that the chromosome morphology of *C. goeldii* also puts this species between Callitrichidae and Cebidae and placed *Callimico* into a separate family, Callimiconidae.

Cebidae

The number of diploid chromosomes within the family Cebidae varies between 16 *(Callicebus lugens)* and 62 *(Lagothrix lagothricha)* and thus shows about the same range of chromosome numbers as is found among prosimians, which vary between 20 and 80. The species *Callicebus lugens* has, together with species of the prosimian *Lepilemur,* the lowest diploid chromosome number of all karyotypes in primates. *Lagothrix* has the highest number of chromosomes for cebid monkeys, 2n = 62. Four species of *Ateles* have identical diploid chromosome numbers of 2n = 34. The karyotype is a combination of 30 submetacentrics and 2 acrocentrics, while the X-chromosome is metacentric and the Y-chromosome is acrocentric or submetacentric. Three species of genus *Cebus* uniformly have 2n = 54. In contrast, two species of *Alouatta* differ in their diploid number and karyotype: One has 2n = 44 and the other 2n = 52. Two species of the comparatively rare genus *Pithecia* have the same chromosome number: 2n = 48. The owl monkey *Aotus* is highly polytypic, having a diploid number of 50 in the subspecies *A. trivirgatus trivirgatus,* and 2n = 52, 53, and 54 in *A. t. griseimembra,* another subspecies. The uneven karyotypes of these primates show that there are hybrids between subspecies of owl monkeys with different diploid chromosome numbers; namely, individuals with 2n = 53 are hybrids between individuals with karyotypes of 2n = 52 and 2n = 54. We now know that species of *Aotus* have diploid chromosome sets between 2n = 46 and 2n = 58. Ford (1994) has summarized the chromosomal

variation among the different species and subspecies of *Aotus* that have been recognized (up to nine species or even more, two of which have a subspecies each assigned to them). Several of these species are, however, cytological rather than phenotypical species. There are actually only three species (Rowe, 1996) that can visually be easily distinguished from each other. There also appear to be some cranial and dental differences between some of these putative species. The high karyotypic variability in this genus is thought to be evidence for the ability of owl monkeys to adapt to rapid change in environmental circumstances. Compared with other primate genera it appears that genus *Aotus* has been in a rather recent period of karyotypic differentiation in combination with regional speciation.

Saimiri sciureus, the squirrel monkey, also has at least three karyotypic races, each found in different geographical locations. The three races may coincide with three of the seven subspecies of *S. sciureus.* Individuals studied have a diploid set of chromosomes of 2n = 44, and may have 10, 12, or 14 acrocentric chromosomes with corresponding changes in the number of submetacentrics, which are 12, 10, and 8 respectively. Such changes between the number of acrocentric and submetacentric chromosomes, with the diploid number remaining constant, may result from pericentric inversion (inversion of chromosome segments involving the centromere).

A new Flourescens In Situ Hybridization (FISH)-based study of Ateline chromosomes verifies the diploid chromosome number for *Ateles belzebuth marginatus* and *Brachyteles arachnoides* to be 2n = 34, and proposes that the ancestral karyotype of Atelinae is 2n = 62 (de Oliveira et al., 2005).

Amazingly, *Alouatta caraya* has been said to have an unusual sex-chromosome inheritance system with two rather than only one Y-chromosome (Mudry et al., 1998; Solari and Rahn, 2005). Banding analyses have suggested that interspecies chromosome number variation could be based on the presence of multiple sex chromosomes (Ma et al., 1985). Multiplex-FISH (M-FISH) chromosome painting allows karyotype analysis (Speicher et al., 1996). This method has led to much research attempting to decipher chromosomal relationships and evolutionary changes (Stanyon et al., 2001; Yang et al., 2003; Ferguson-Smith et al., 2005; Wienberg, 2005). Special attention has been paid to the New World monkeys, once again because genus *Alouatta* stands out as being different from other primates (Mudry et al., 1998, 2001; Solari and Rahn, 2005).

Cercopithecoidea

All the karyotypes that are known for genera of genus *Macaca, Cynopithecus, Papio, Mandrillus, Theropithecus,* and *Cercocebus* have the same diploid chromosome number of 2n = 42. In addition, the karyotypes are identical in the total length of chromosome arms, as they are in combinations of metacentric and

submetacentric autosomes. The Y-chromosomes of these genera are small, acrocentric chromosomes, while the X-chromosomes are submetacentric.

Many karyotypes have been recorded for this superfamily. The chromosome number varies between 2n = 46 and 2n = 72. It was proposed that cytogenetic evolution was achieved by a progressive decrease of chromosome length in combination with an increase in chromosome numbers (Dutrillaux et al., 1988). These authors base their discussion of the evolutionary events shaping today's cercopithecine karyotypes on a "reconstructed ancestral karyotype of Cercopithecinae." This fictional karyotype has 2n = 46 chromosomes. Of 21 karyotypes that were studied, 17 different karyotypes were found, but overall, the karyotypes of cercopithecines are comparatively uniform, being a combination of metacentric, submetacentric, or acrocentric chromosomes that are morphologically very similar to each other. *Erythrocebus patas* has a diploid number of 2n = 54, *Pygathrix nemaeus* has 2n = 44, and *Nasalis larvatus* has 2n = 48 chromosomes. The diploid chromosome numbers of *Presbytis entellus*, of *P. obscurus,* and of *Colobus polykomos* all are 2n = 44. The total length and thus fundamental number of chromosome arms is the same in the previously mentioned species with diploid chromosome set between 54 and 44. *Nasalis larvatus,* with the unusual diploid chromosome number 2n = 48, had been regarded by some to be karyologically the most primitive colobine and a long-isolated genus of the group. A new study, however, applying the technique of chromosome painting has shown that the proboscis monkey has a rather derived karyotype that is solidly nested within the Asian colobines and thus separated from the African colobines (Bigoni et al., 2003).

Hominoidea

Hylobatidae

The gibbons *Hylobates lar* and *H. hoolock* have a diploid chromosome number of 2n = 44 (Table 12.3). Gibbon species have mostly metacentric and submetacentric chromosomes with few or no acrocentric chromosomes in their karyotype. The Y-chromosome of *H. lar* is very small and shaped like a dot. In *H. moloch* the Y-chromosome is somewhat larger and assumed to be metacentric. Overall, the chromosomes of *H. lar* are very different from the other *Hylobates* species and seem to be more similar to *Symphalangus,* the other genus of lesser apes. *Symphalangus* differs clearly in the karyotype from that of genus *Hylobates.* The diploid number of *Symphalangus syndactylus* chromosomes is 2n = 50, and it has one pair of acrocentric chromosomes. Like the New World owl monkeys, genus *Aotus,* the gibbons are considered to be in a phase of karyological speciation. Interestingly both owl monkeys and lesser apes are among the few mammals that are believed to be more or less monogamous, a mating system theoretically

Table 12.3
Karyotypes of Hominoidea

	2*n*	M	S	A	X	Y	References
Hylobatidae							
Symphalangus syndactylus	50	46		2	S?	S?	Egozcue, 1996
Hylobates moloch	44	28	14	0	S	A	Tantravahi et al., 1975
Hylobates lar	44	28	14	0	S	A	Tantravahi et al., 1975
Hylobates concolor	52	32	12	6	M	A	Tantravahi et al., 1975
Hylobates (Hoolok) hoolok	38						Prouty et al., 1983
Pongidae							
Pongo pygmaeus	48	6	20	20	S	A	Paris Conf., 1975
Gorilla gorilla	48	16	18	12	S	A	Paris Conf., 1975
Pan troglodytes	48	10	24	12	S	A	Paris Conf., 1975
Pan paniscus	48	10	26	10	S	A	Bogart and Bernischke, 1977
Hominidae							
Homo sapiens	46	12	22	10	S	A	Paris Conf., 1975

n, Haploid number; M, metacentric; S, submetacentric; A, acrocentric; X, female sex chromosome; Y, male sex chromosome.

advantageous for the incorporation of cytogenetic changes through genetic drift. The chromosomes of lesser apes are highly derived (Marks, 1992).

Pongidae

The three pongid genera *Pan, Gorilla,* and *Pongo* all have the same diploid chromosome number, 2n = 48. The karyotype of *Pongo pygmaeus* is composed of 26 metacentric and submetacentric chromosomes and 20 acrocentric chromosomes, 16 of which are long and 4 are short. Fourteen of the acrocentric chromosomes of *Pongo* have satellites. *Gorilla gorilla* has 34 metacentric and submetacentric chromosomes and 12 acrocentric chromosomes that also have satellites on their short arms. The karyotype of *Pan troglodytes* also contains 34 metacentric and submetacentric chromosomes and 12 acrocentrics, 10 of which have satellites on their short arms. The karyotype of *Pan paniscus* is very similar to that of *P. troglodytes*. In all four pongid species the X-chromosome is large and submetacentric, while the Y-chromosome is acrocentric and is one of the smallest chromosomes in the karyotype. Karyotypically there are more links between chimpanzees and gorillas than with either African ape or the orangutans (Marks, 1992). Humans are more closely linked to the African apes than the Asian great ape.

Hominidae

Humans have a diploid number of 2n = 46 chromosomes, 34 of which are metacentric or submetacentric and 10 acrocentric. All these acrocentric chromosomes generally have satellites on their short arms. The Y-chromosome of humans is small and acrocentric and is somewhat variable in length. The X-chromosome is submetacentric. The human karyotype is the best known of all primates, and many deviations from the normal karyotype are known. Furthermore, many of the effects of such karyological differences not only on morphology but most importantly on function in humans are well known.

Detailed comparisons have been made of human chromosomes with those of African apes, using the many new methods described at the beginning of this chapter. Chromosomes that have identical banding patterns have been found among humans and apes. DNA sequence studies have confirmed the initial conclusions about the close relationship of humans with the African apes. The presence of 46 chromosomes in humans and 48 in the African apes and the orangutan can be explained by fusion of two acrocentric chromosomes to form the human metacentric chromosome 2. Evidence for the virtual homology of the chromosome banding of human chromosomes compared with those of the great apes comes from localization of many genes to homologous chromosomes of the different primate species, as well as from the similarity of the amino acid

sequences of a large number of proteins studied in each species (King and Wilson, 1975; Marks, 1992) and from a large degree of homology between repeated DNAs that are known to be transcribed (Gasden et al., 1977). The presence of identical banding patterns and gene contents in such widely divergent species indicates a conservation of linked genes with chromosome banding over tens of millions of years.

Karyotype Evolution

Theories on how the extant primate karyotypes have evolved are numerous (Eder et al., 2003). Dutrillaux et al. (1986) constructed so-called ancestral karyotypes for lemuriformes in particular and primates in general to provide basic, hypothetical karyotypes that make comparison with extant karyotypes possible. Overall, the primary assumption is that the number of chromosomes is more likely to be reduced over time than to increase. Many prosimians (and some other primates also) have a high number of acrocentric chromosomes when they have a high diploid number and vice versa. This observation has led to the conclusion that fusion of acrocentric chromosomes to form metacentrics with a concomitant decrease of the total chromosome number in a given karyotype is an important mechanism in primate karyotype evolution. Evidence that karyotype rearrangement in genus *Eulemur,* for example, has taken place primarily by centric fusion of acrocentric chromosomes to yield metacentrics has been provided by chromosome banding studies. Banding analysis confirmed the homology of the arms of most of the metacentric chromosomes in species that have lower diploid numbers with the acrocentrics in species that have higher numbers (see Rumpler and Dutrillaux, 1976; Rumpler et al., 1988). However, if fusion of a high number of original acrocentric chromosomes led to the many metacentric chromosomes and smaller diploid chromosome numbers in higher primates, the lorisid prosimian *Nycticebus coucang* presents a problem, because all of its $2n = 50$ chromosomes are metacentric or submetacentric.

Another general assumption, that primates with high numbers of chromosomes are morphologically and functionally less advanced than primates with low diploid counts, does not always fit with the taxonomic picture derived from the study of gross morphology and behavior in primates. *Tarsius,* for example, is by no means a generalized primate but is an extraordinarily derived prosimian, and it has the highest chromosome number of all primates at $2n = 80$, with 7 pairs of metacentric or submetacentric chromosomes and 33 pairs of acrocentric chromosomes. Dutrillaux and Rumpler (1988) document that the karyotype of *T. syrichta* is not only totally unlike those of any other primate they have studied, but also is not similar to any mammals belonging to other orders that have chromosome segments or entire chromosomes in common with primates.

Within the New World monkey family Callitrichidae, explanations for the possible course of karyotype evolution are very intriguing and even convincing. The basic mechanism is believed to be fusion of acrocentric chromosomes into fewer submetacentrics or metacentrics. Additional knowledge has been derived and adds a different aspect to evolutionary speculations from the occurrence of chromosome chimerism in Callitrichidae. A chimera is an individual animal whose cells have more than one different genotype, usually caused by a single individual developing from an embryo that is created through fertilization by cells from two different individuals with different genotypes (e.g., two sperms successfully fertilize one ovum). The fact that marmosets usually give birth to twins or even triplets might be one of the reasons for the occurrence of individuals with chimerism (Ford and Evans, 1977). Among primates cell chimerism is only found in Callitrichidae with a twin of the opposite sex, and the chimerism affects the sex chromosomes (Goldschmidt et al., 2005). Consequently, a certain percentage of the cells in one individual are karyologically male and the others are female. The occurrence of chimerism in marmosets has been explained by cell exchange in very early fetal stages of heterosexual dizygotic twins through the anastomoses of blood vessels in connected chorions. A pair of autosomes can also be heterozygous in species of *Callithrix*. The existence of such heteromorphic autosomal pairs in living individuals of Callitrichidae suggests that the two different autosome types do not affect the individual's ability to produce fertile offspring. The phenomenon of twinning and karyological chimerism—callithrichid twins are genetically as different from each other as regular siblings—has been implicated in behavioral aspects of marmoset life such as paternal care and mating systems (Haig, 1999).

Ford's detailed discussion concerning possible avenues of speciation in genus *Aotus* (1994) is an excellent example for evolutionary speculation about karyological variants and their geographical distribution in an evolutionary context. Karyotypic speciation in genus *Aotus* is assumed to proceed by fusion of acrocentrics into metacentrics accompanied by a reduction of the diploid chromosome number rather than by fission events and an increase of diploid chromosomes. Ford also examines the relationships of owl monkey *(Aotus)* populations, evaluating their electrophoretic blood protein similarities. Although the chromosomes make evolutionary speculations about *Aotus* populations possible, the electrophoretic results remain inconclusive.

Chromosomal evolution among cercopithecines is said to be very complex and appears to show an increase, rather than the predicted reduction, of the number of chromosomes over time (Dutrillaux et al., 1988).

Hybridization

Hybridization between different species producing fertile offspring is of interest for the study of karyotypes. It was believed that species with similar

karyotypes would be most likely to produce fertile offspring. Contrary to this theory, species with rather different karyotypes (*Cercopithecus stuhlmanni* with *C. ascanius*) have produced fertile offspring, whereas others with very similar karyotypes failed. Embryonic development involves a fine-tuned orderly expression of many genes that were inactive in the zygote. If the two genomes in an interspecific zygote are regulated similarly and are developmentally compatible, an orderly development of the hybrid organism can be expected. However, if the patterns of the maternal and paternal gene expressions are incompatible, the probability is low that an interspecific zygote will be able to develop successfully. One such example has been described by Kumamoto and Houck (2001). In some of the cases where interspecific crosses had karyotypes that seemed to be identical, the offspring of the first generation either were abnormal, died early, or, if they lived to become adults, proved unable to produce a second generation. Other species with identical karyotypes (for example species of *Macaca* and *Papio*) are able to produce fertile hybrid offspring. Thus hybridization in primates is still not well understood.

The karyological step between the African great apes and humans seemingly involves the fusion of two acrocentric chromosomes into one metacentric chromosome and thus a diploid set that has two fewer acrocentrics and one more metacentric than that of the common chimpanzee and the gorilla. What this and other karyological differences imply remains a mystery (Murphy et al., 2003, 2005).

Basically, chromosome morphology compares groups and describes features of chromosomes whose functional contents are still widely unknown. Like most primate characteristics, we do not even know on which chromosome the genes of certain characteristics are located, much less the exact position of the gene on a particular chromosome. Chromosome morphology can only be informative if evaluated together with numerous other characteristics. This is not the case with humans, however. Concentrated research in human cytogenetics has yielded an enormous number of insights into the human genome and its functions. Gene loci are known for proteins or enzymes that are involved in malfunctions of the human body. This means that knowledge has been derived from the study of deviations from the norm. Scientists have now completed the awesome task of compiling detailed information about the entire human sequence of around 3000 million base pairs along the DNA molecule that make up the human genome (see Chapter 14).

Mitochondrial DNA

Besides the DNA that is contained in the cell nucleus, certain cellular organelles located outside the nucleus in the cytoplasm are also made up of DNA and genes. This DNA is associated with the mitochondria in the cells and is therefore called mitochondrial DNA (mtDNA). The mtDNA genome is much smaller than the

nuclear genome (about 16500 bases as compared with the approximately 3000 million bases of the nuclear DNA) and is circular. The sequence of mtDNA has been established for humans. Mitochondrial DNA is different also because it evolves at a comparatively faster rate than nuclear DNA: It lacks the repair enzymes of nuclear DNA that are able to correct mutations. Therefore genetic changes accumulate about ten times as fast as they do in nuclear DNA. mtDNA is mainly maternally inherited. This has been transposed into the mistaken assumption that in mammals the mtDNA from the paternal side is universally totally eliminated at fertilization. The paternal mitochondria are located in the midpiece of the mature sperm. A common misconception is that the entire sperm tail is lost during fertilization. Actually, among the majority of mammals the sperm, including the entire sperm tail, enter the ovum at fertilization (see Chapter 10; recall also the one exception, the Chinese hamster *Cricetulus griseus,* whose giant entire sperm tail is too large to enter the egg), and the paternal mitochondria can still be seen in mice embryos up to the 4-cell stage. Even though they are clearly present in the mouse embryo, the paternal mitochondria disappear at about the 8-cell stage when they are either destructed, inactivated, or diluted by the much greater copy number ratio of oocyte-to-sperm mtDNA, which is 10,000 : 1 (Cummins et al., 1997). The fate of the paternal mtDNA appears to be different in different mammals and is not yet known for most mammals, particularly for any primates (Ankel-Simons and Cummins, 1996; see also Chapter 13). The fact that paternal mitochondria, though very few, do enter the egg makes the assignation of mtDNA as haploid questionable, at least until the fate of the paternal mitochondria is determined in primates. Melnick and Hoelzer (1993) have summarized how studies of primate mtDNA can be useful in combination with other study results. Mitochondrial DNA has been used to establish two different species for the orangutan (Xu and Arnason, 1996) and to verify the relationship of the enigmatic South American monkey *Callimico goeldii* with callithrichids rather than cebids (Pastorini et al., 1998). New surprising insights into the possibility that mitochondrial DNA sequences (Numts) are inserted into the nuclear DNA have now surfaced (see detailed discussion in Chapter 14).

BLOOD GROUPS

As early as 1925 the first thorough studies about the blood of apes and monkeys were published by Landsteiner and Wiener. Molecular biologists have produced a great number of publications on major blood groups in primates as well as on more rare and intricate blood substances since then. However, recent information about primate blood groups is mainly concerned with zoonoses (immunology, virology, parasitology), the interchange of disease between non-human primates and humans (Wolfe et al., 2004). Interestingly, a number of

otherwise comprehensive books on primates plainly ignore the topic of primate blood groups. Nor will we go into great detail here, especially since the information available still does not cover the broad range of primate species. Rather this section will focus mainly on species that are readily available for laboratory research. Recently a few species have been sampled in the natural environment. However, blood samples of primates cannot be obtained as easily as those of humans, and even in humans it can occasionally be problematic (for details on primate blood groups, compare Erskine and Socha, 1978).

Two techniques are used to test blood groups in nonhuman primates (Wiener, 1970):

1. Primate blood can be tested for human-type blood factors. In such tests, reagents are used that were originally prepared for typing blood of humans.
2. Primate blood can be tested with reagents that are obtained either by immunization of experimental nonprimates or preferably by isoimmunization or cross-immunization with the blood of monkeys and apes.

Blood types that are recognized by either of these procedures are accordingly called human-type or simian-type blood groups, respectively. The distinction between the human-type and simian-type blood groups is, however, somewhat indistinct.

The well-known ABO blood groups have been extensively studied in humans, apes, baboons, macaques, a couple of other Old World monkeys, and several New World monkeys (Table 12.4). These blood groups are shared among many of the primates. A number of lemurs have B-like antigens on their erythrocytes. In monkeys, ABO antigens can be detected on some tissue cells and in the saliva (Socha, 1980). It has been stated that ABO systems in monkeys can only be detected by using their saliva, but this is not entirely correct, because agglutinations have also been obtained with red blood cells. *Alouatta palliata* and some marmosets were found to have human-type blood group B but to lack human-type A (Froehlich et al., 1977).

Among the monkeys the blood groups of *Macaca sylvana* have been studied (Socha et al., 1981), and several simian-type blood groups were detected for this species. Human-type blood groups were not found. Some species-specific antigens allowed the authors to point out possible taxonomic implications.

The ABO blood groups in the great apes are identical to those of humans. A, B, AB, and O have been confirmed for the chimpanzee. *Pan* also has two blood groups that are unique to this genus (Socha, 1981). Among the apes, blood group O has been verified only for chimpanzees, and *Gorilla* is most different from humans in that it has only the type B blood group.

Of the M/N blood groups that are found in humans, the M antigens are quite common in many nonhuman primates. N antigens have been found in *Pan,*

Table 12.4
ABO Blood Group Distribution among Primates

Species	O	A	B	AB	No. of Specimens
Alouatta species	0	0	52	0	52
Cebus albifrons	1	0	3	0	4
Cebus apella	0	5	0	0	5
Ateles species	1	10	4	0	15
Saimiri sciureus	1	3	0	0	4
Callithrix species	0	3	0	0	3
Papio hamadryas	0	15	107	50	172
Papio anubis	0	5	133	56	194
Papio cynocephalus	0	18	20	22	60
Papio ursinus	0	4	59	26	89
Papio papio	2	27	93	66	188
Mandrillus leucophaeus	0	4	0	0	4
Macaca mulatta	0	0	150	0	150
Macaca radiata	0	18	12	15	45
Macaca fascicularis	1	23	19	19	62
Macaca speciosa	0	0	14	0	14
Macaca nemestrina	87	18	10	3	118
Macaca maura	1	23	2	0	26
Theropithecus gelada	18	0	0	0	18
Erythrocebus patas	0	26	0	0	26
*Cercopithecus pygerythrus**					
from Ethiopia	0	126	1	1	128
from South Africa	0	39	10	10	59
Pan troglodytes	50	483	0	0	533
Pan paniscus	0	9	0	0	9
Gorilla g. gorilla	0	0	23	0	4
Gorilla g. beringei	0	0	4	0	4
Hylobates species	0	41	14	16	71
Symphalangus syndactylus	0	0	2	0	2

Modified from Erskine and Socha, 1978. **Cercopithecus pygerythrus* is regarded to be *Chlorocebus pygerythrus* by some (Groves, 2001).

Gorilla, and *Hylobates* (Landsteiner and Wiener, 1937). Blood groups of chimpanzees have been used to determine paternity in captive groups (Socha, 1981).

Transferrins are β-globulins that are found in blood serum; they are iron-ion carriers. The transferrins of primates are rather diversified (Buettner-Janusch, 1963). More variation of genetic polymorphism has been discovered among nonhuman primates than is known in humans. For example, 24 different transferrin phenotypes have been described for *Eulemur fulvus,* 4 for *Galago crassicaudatus*. Twelve to fourteen different molecular forms of transferrin

proteins have been detected in genus *Macaca,* and thirty-four phenotypes are known for this genus, but there may be many more. Other Old World monkeys have also been found to exhibit genetic polymorphism of transferrins. Scheffrahn and Glaser (1977) found three distinct transferrin phenotypes in the New World monkey *Saguinus midas tamarin*. The authors confirm that transferrins have a high degree of polymorphism in primates. The same is true for lesser and great apes.

Haptoglobin, another important blood serum protein (α_2-globulin, a serum protein that combines with hemoglobulin) has been found in only one of the species of primates that have been studied (haptoglobin allele Hp 1-1), whereas in humans three haptoglobin types are known (haptoglobin allele Hp 1-1, Hp 2-1, and Hp 2-2).

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Chapter 13

Molecular Primatology

The Genetic Material of Cells
Indirect Methods to Study Molecular Primatology
Precipitin Reaction Assay
Ouchterlony Immunodiffusion
Molecular Clocks
Immunoelectrophoresis
Protein Radioimmunoassay
Microcomplement Fixation
Major Histocompatibility Antigen Recognition
Direct Study of Genetic Material
DNA Hybridization and Polymerase Chain Reaction
Restriction Fragment Length Polymorphism Analysis
Southern Blotting
Neuraminic Acids
Mitochondrial DNA
Problems of Phylogenetic Analysis Using Molecular Data

During the past four decades the technology of determining molecular structure has advanced at a rapid pace and has become much more accessible. When the idea emerged that studying genetic material in biology is fundamental to the understanding of all animal life, it caused great excitement and enthusiasm. There can be no doubt that the subject of human molecular genetics provided deep insights into the way our body works. Scientists are now able to selectively isolate and study even single fragments of DNA thought to be genes. Within this framework was the recognition that genetic material also provides insights that make it possible to reconstruct the evolutionary history of extant organisms, and application of this ability to the study of nonhuman primates began early on (Buettner-Janusch et al., 1961; Goodman, 1962; Zuckerkandl, 1963). Probably the first application to several primate species, long before the 1960s, was the

seriological research by Nuttall in 1904. Since these beginnings molecular approaches to primatology have often been controversial. Researchers learned that it was not always possible to solve unequivocally many of the phylogenetic and taxonomic puzzles within the primate order with these new approaches; for example, the taxonomic and evolutionary position of the enigmatic tarsiers, genus *Tarsius*, and whether it is justifiable to group them together with the higher primates rather than with the prosimians (a view that is held by some on the basis of only a few morphological similarities that are shared between extant tarsiers and higher primates) is still undetermined. In 2003 Yoder observed: "There are numerous genetic data sets that support the contention that the strepsirhine-tarsier-anthropoid (*sic*) is a virtual trichotomy, with tarsiers being so derived as to be almost unresolvable as primates" (Yoder, 2003, loc. cit. page 170).

Cells are the basic units of living tissues and of the organization of life. The capability to study the molecular infrastructure of cells and their functions is comparatively recent. Most of the substructures that make up living cells are molecular combinations of sugars, fatty acids, nucleotides (nucleic acids: DNA and RNA), and amino acids. Actually, however, cells mostly consist of water. Obviously, any biochemical analysis of cells requires destruction of the cell's basic anatomy. Modern methods constituting careful disjunction techniques are able to preserve certain functions of cell components after separation. Thus the different cell organelles and substructures can be isolated from each other, purified, and subsequently analyzed. The spectrum of methods available for determining genetic relatedness is wide. Evolutionary relationships among organisms are reflected by similarities in their DNA that ultimately determine the inherited structure of a cell's proteins. There are hundreds of different proteins that serve varied functions in living tissues. Every protein is made up of a unique amino acid sequence that is genetically determined by DNA. Molecular biology evaluates information that is programmed by genes, the basic material that provides the blueprint for all living organisms.

DNA is the crucial coding substance that is replicated every time a cell divides. Similar to morphological studies, molecular studies require that recognized characters be compared with similar characters that are declared to be primitive or primary. Many molecular studies necessarily remain phenetic, which means based on similarity of phenotypic characters. It is impossible to be anything but phenetic for immunology and DNA hybridization, where there are no characters per se, only distances between pairs of taxa. Thus each evaluation is firmly based in other previously established assumptions about the grade of evolutionary advance of the species that are studied. Usually such decisions about the assumed evolutionary advance of the outgroup species employed is based on either morphological or cytogenetic characteristics. It is easy to see that it is perplexing for the molecular primatologist to hypothesize which of his study objects—either proteins or DNA sequences—are truly primitive and which traits

of the different amino acids studied are derived. Consequently, even though molecular primatology can potentially contribute interesting insights into the possible relatedness of closely associated species, it often does not offer simple or obvious solutions to taxonomic and phylogenetic questions. See, for example, Ruvolo, 1988: This research employed electrophoresis to evaluate 14 genetic loci of different proteins for 18 species belonging to genus *Cercopithecus* and analyzed the resulting data in different ways—namely with cladistic procedures and phenetic methods. Ultimately, the results are somewhat muddled because the ensuing "phylogenetic trees" do not at all agree with each other, nor do they concur with independent karyological findings.

Because the majority of studies in molecular biology have the common goal of understanding human physiology and disease, many procedures used in molecular primatology are basically those of human cell biology and molecular genetics. Today human medical cell biology is one of the fastest paced fields in modern science; today's news often becomes tomorrow's history. Here the focus is on human biology and endeavors are intended to find cures and preventive measures for genetically based human illnesses such as cancers or mental illnesses or to avoid, through genetic counseling, the occurrence of inherited birth defects. Through numerous molecular techniques many human diseases have been attributed to a defect or mutation within a single gene. Understanding the genetic basis of a disease allows for more effective medical treatments. Moreover, the future target of treatment may not be the symptoms of a disease but rather the gene itself that is causing them. Techniques of molecular biology potentially may be applied to repair or replace damaged genes.

In primatology these same molecular biology techniques are applied to decipher taxonomic and genealogical relationships and to answer questions concerning primate and human evolution. A detailed discussion of the multiple ways molecular genetics has been and can be employed in the study of primate behavior, social organization, and reproduction including research of primate population genetic structure can be found in DiFiore (2003). Before describing the techniques that are applied to research in primatology, it will be useful to briefly review basic cellular biology.

THE GENETIC MATERIAL OF CELLS

The genetic material of the cell is called deoxyribonucleic acid (DNA). DNA is the crucial coding substance that is replicated every time a cell divides. It makes up only a small part of each cell and is chemically comparatively stable. It consists of two intertwined chains (forming a double-helix) that are made up of alternating units of phosphoric acid and deoxyribose linked together by cross connections of the purine bases adenine (A) and guanine (G) and the pyrimidine

bases cytosine (C) and thymine (T). Thus the idioms of the genetic code are combined of three-letter word units, called codons, composed of the four letters A, G, C, and T. Each possible combination of three-letter word units (codons) is translated or encoded into an amino acid—the basic building blocks of proteins. For instance, a sequence of twelve DNA bases is separated into four codons, which are translated to four consecutive amino acids. Strings of these amino acids are commonly known as polypeptide chains or proteins. Variations in DNA sequence contribute to the formation of different proteins. A gene is a unit of DNA that codes for a polypeptide chain, the basic structural unit of a protein; proteins are the main constituents of living tissues. A protein can be made up of one or several polypeptide chains, which requires one or several genes or alleles.

Proteins are organic compounds that include enzymes (organic catalysts acting on molecules), hemoglobins, hormones, albumins (a group of small proteins that are soluble in water and, among other functions, have a major role in transporting fatty acids), and caseins (a group of proteins containing phosphates) and together perform most cellular functions.

The materials studied in molecular genetics are either DNA, which is the direct approach of deciphering genetic information, or the products attributable to the information provided by the DNA, namely the proteins (which provides for inferential, and thus indirect, information about the sequence of the nuclear acids that program them).

As already mentioned, the genetic code is read in blocks of three bases that determine the amino acid sequence of proteins. The vector that transcribes DNA into RNA is the enzyme polymerase. These groups of three consecutive bases in DNA and RNA are called codons. DNA, made up of 64 codons of three bases each, can be cut into fragments with the help of restriction enzymes that recognize different DNA sequences. These cutting or cleaving enzymes are very specific in their action and are produced by microorganisms such as bacteria or yeast.

The methods for direct study of the genetic material DNA have been more recently developed than the indirect approaches. Initially, the direct approach was arduous and proceeded slowly because it involved step-by-step chemical degradation of individual proteins.

INDIRECT METHODS TO STUDY MOLECULAR PRIMATOLOGY

Precipitin Reaction Assay

One of the earliest indirect methods applied to primates and many other mammals in the attempt to decipher their evolutionary relationships is called the

precipitin reaction assay. It makes use of the functions of the immune system and its reactions to foreign protein molecules. The preferred vector initially was blood serum. Basically this analysis measures the degree of in vitro clotting or precipitate formation. First, antigens from the organism being tested are injected into a different animal (usually a rabbit or chicken). The resulting antiserum that builds up is mixed with either the original donor blood or the blood of closely related species. Application of this precipitate elicits different degrees of coagulation in the tested blood. Thus, for example, human antiserum not only causes a strong reaction with the donor human blood, but also with the blood of chimpanzees, gorillas, macaques, and so on in decreasing intensity according to taxonomic distance. Nuttal (1904) calibrated the strength of this reaction into five categories based on the findings that *Homo*-antiserum resulted in medium reaction with Old World monkey blood, slow and very weak reaction with the blood of New World monkeys, and no reaction at all with lemurid blood, but strong precipitates occurred when the blood of apes was tested in this manner. These initial results, which basically substantiated the pattern of morphologically rooted relationships among humans and primates, were soon superseded by new, more precise methodologies. The first steps to obtaining more accurate results were to utilize much more precise quantities of completely purified components than Nuttall had (Mollison, 1912). Mollison also introduced titration series in his experiments to create the so-called "optimal" reaction. It therefore became possible to state that genus *Homo* had two-thirds of its species-specific albumins (which he called proteals) in common with genus *Pan*. This meant that one-third of the albumins were specific for *Homo,* while *Pan* was found to have a total of six-sevenths of its albumins in common with *Homo,* which meant that only one-seventh of the albumins were specific for *Pan*. The same procedure was applied to several other primate genera, namely *Pongo, Macaca,* and *Papio.* Genus *Gorilla* was not available to Mollison and he concluded that among his research subjects the chimpanzee, genus *Pan,* was the closest relative of humans. The orangutan, genus *Pongo,* ended up testing quite differently and was far removed from *Homo* and *Pan*. The monkeys *Macaca* and *Papio* were also removed, with genus *Papio* being further removed from *Homo* than was genus *Macaca*. Later on Mollison added filtration experiments to his techniques and was able to conclude that the molecules of albumins among primates are larger and therefore more complex in higher primates such as apes than they are in monkeys.

Ouchterlony Immunodiffusion

Another method of studying molecular relationships is to analyze antisera to blood plasma or serum, a method that was perfected by Ouchterlony in 1958 and bears his name: Ouchterlony immunodiffusion. Immunodiffusion uses two protein samples that are simultaneously diffused (spread) against an antiserum

on an agar-gel test plate. Initially in investigations involving primates, antisera were made to plasma or serum. Later this method was further developed and elaborated by making antisera to single, purified proteins (Hillis and Moritz, 1990). This technique was used to test primate albumins (which are synthesized early during fetal development) by Goodman (1962), who simply confirmed primate relationships more or less as they had originally been established based on morphological similarities and dissimilarities. For example, this immunological test corroborated that the African great apes are closer to humans than they are to the orangutan.

Great similarity was found—with the use of chicken and rabbit antisera—in antigenic structure of all Hominoidea tested, including the lesser apes, genus *Hylobates,* and the orangutan, which were found to be only slightly more divergent from the other Hominoidea. Later the same method was used to test primate gamma globulin, a protein that is only synthesized after birth. Based on gamma globulin it was found that the South American Cebidae were the most diversified primates, while neither the Old World monkeys nor the Hominoidea showed great diversity. The speculation was made that the different expression of postnatally developed gamma globulins in primates is caused by differences in placental intimacy and efficiency between mother and offspring. This explanation required the assumption that the intimacy between maternal and fetal blood interaction during pregnancy is more proficient in the Old World monkeys than in the New World monkeys. This is, in fact, correct, although the differences are minor (Starck, 1956). Among the Old World monkeys, consequently, maternal antibodies develop and eliminate incompatible fetal proteins, the ultimate result of which is that they are genetically more uniform than the New World monkeys. It was also inferred that the postnatally developed protein gamma globulin evolved at a faster rate than the ontogenetically early-developed albumin because the maternal isoimmunization increases the evolutionary stability of the early protein alleles. If these assumptions concerning the differences in the evolutionary variety of hemoproteins were correct, then the number of amino acid sequences would be greater in prosimians with an epitheliochoreal placenta that provides less maternal-to-fetal intimacy than in the Old World primates with a hemochoreal placenta and increased interchange between fetal and maternal proteins.

However, these assumptions were not supported: A higher protein variability was not found among strepsirrhini than in anthropoid primates (Sarich and Wilson, 1973), nor was a faster rate of DNA evolution found in Malagasy lemurs by Bonner et al. (1980). It therefore appears that the mode of placentation and the degree of intimacy between maternal and fetal blood circulation does not have any measurable impact on the evolutionary development of proteins in placental mammals.

Immunodiffusion technology is still used in immunological comparisons of proteins for phylogenetic evaluation. Researchers continue to use immunodiffusion

techniques to investigate the evolutionary relationships among primates (Shoshani et al., 1996). Unlike earlier studies, and because of deeper understanding about molecular structure and reactivity, the sera used in tests are now purified. The antigen–antibody reaction is proportional to the closeness of relationship between the primates tested (see also Jones, 1992).

Molecular Clocks

Sarich and Wilson (1967) first presented the idea that immunological differences between primates should be useful for the determination of the evolutionary time frame by dating phylogenetic trees. Thus they invented the immunological clock. However, as all clocks must be properly regulated into equivalent time components comparable to seconds, minutes, or hours, it soon became obvious that it is not possible to properly calibrate any biological event: Neither biology nor evolution ever follow a steady time frame. The characteristic of biology is that it is irregular and that it functions in a random pattern. Consequently it is not possible to properly calibrate biological events or to formulate strict, invariable biological laws. One of the most intriguing characteristics and challenges of biology is that it is not constant and, therefore, not easy to decipher (see also Cunningham and Collins, 1994; Graur and Martin, 2004; Hedges and Kumar, 2004).

As early as 1974 Bauer studied individual, purified proteins rather than nonpurified proteins. He prepared antisera to a series of purified human serum proteins in rabbits and compared them with serum proteins of other primates. Bauer created up to fifteen antisera to different serum proteins and tested them against serum samples from three apes *(Pan, Gorilla, and Pongo),* four Old World monkeys *(Macaca, Cercopithecus, Erythrocebus, and Cercocebus),* one New World monkey *(Cebus),* and one prosimian primate *(Galago)*. Bauer then inferred the number of antigen determinant sites for each protein tested and found that this number varied from 1 to 9, with an average of 2.4. The number of determinant sites that the different genera had in common was interpreted as an indicator of evolutionary relationship. The resulting evolutionary tree was in total agreement with the evolutionary tree created with the help of morphological characters: the galago on its own branch, as are the New World monkeys, the Old World monkeys on the third branch clustered with the three great apes (orangutan, gorilla, and chimpanzee), the gorilla and chimpanzee being closest to humans.

Immunoelectrophoresis

The next step forward in the investigation of proteins was the application of electrophoresis, which studies the differences that relate to size and electric

charge of protein molecules. Electrophoresis separates charged protein or nucleic acid molecules according to their net electrical charge and mass by drawing them through a filter material (paper or gel) using an electrical field. The molecules migrate in narrow bands along "wicks" toward the electrical pole that is charged opposite to their own electrical charge (from one pole to the other) at a differential rate. They can be stained to make them more visible and subsequently compared between species. Two-dimensional resolution of electrophoresis was applied to primate molecules with the help of starch gel electrophoresis and agar-gel precipitin testing examining the reaction of a variety of antisera to proteins (Jones, 1992).

Electrophoresis, which is no longer much used in phylogenetic research, is still widely applied to the evaluation of proteins as well as immunological studies, where it is called immunoelectrophoresis. This application can also be used to examine the reaction of antisera to whole serum.

Protein Radioimmunoassay

Today radioimmunoassay is carried out when only minute amounts of protein are available for evaluation. This technique has also been applied to fossils. Evaluation requires the material to be radioactive (Lowenstein, 1985). Albumin is often used for this procedure because it is abundant among vertebrates, relatively stable, and easily purified and requires only small amounts of tissue. Few data involving this procedure for primate fossils have yet been published.

Microcomplement Fixation

Serum albumins are predominantly used in an expeditious procedure that allows comparison of differences between homologous proteins (Maxson and Maxson, 1986). Microcomplement fixation uses reactions between soluble antigens and antibodies that are in a dilute solution. In this medium only high-affinity antibodies will react with their antigens. Basically, a serum is tested for its reaction with an antiserum as it is progressively diluted. At each step there is a point when maximal precipitation occurs. This method was applied to help determine the relationship between humans and chimpanzees by Sarich and Wilson (1966, 1967) as well as to the study of albumins and transferrins by Cronin and Sarich (1975) to decipher the taxonomic relationships among Old World monkeys. The results of studies using this method are often unexpected. For example, Hafleigh and Williams (1966) found tree shrews of the genus *Tupaia* to be similar to prosimian primates, while somewhat later Sarich (1970), using the very same technique, found that tree shrews had albumins that were

more similar to humans' than to any of the other primates'. However, Sarich himself dismissed these findings as being meaningless. By widening the scope of these investigations and by adding other mammal groups to the data that were evaluated, Sarich and his colleagues concluded 10 years later that more appropriately tree shrews are closely related to primates in general (Cronin and Sarich, 1980) and not specifically to humans.

Major Histocompatibility Antigen Recognition

Yet another procedure that measures variations among major histocompatibility antigens is used in molecular primatology studies. All body cells in mammals carry cell-surface glycogens. These glycogens are involved in antigen recognition when an immune response to some foreign substance occurs. Major histocompatibility antigens vary between individuals; two classes of these antigens are recognized: I MHC antigens and II MHC antigens.

Class I MHC molecules are triggered by antigens that originate within the cell and are therefore called endogenous antigens. Fragments inside the cell that originate from a foreign protein, such as a protein encoded by the genes of a virus, become bound to the I MHC molecules that, unlike class II MHC cells, occur in almost all cells with a nucleus. The class I MHC molecules bind with the foreign proteins and transport them to the cell surface where they can stimulate an immune response.

Class II MHC molecules are found only on the surface of cells that are involved in immune reactions. They are therefore called exogenous antigens. Class II MHC molecules are located on macrophages that process foreign antigen fragments on the outside of the cell. These exogenous antigens (such as fragments of bacterial or viral cells) are engulfed by the cell and are subsequently fractionated within the cell and then bound to II MHC molecules. The II MHC molecules then transport the foreign particles back to the cell's surface, where they are exposed to and attacked by other cells of the immune system.

Pope (1996) incorporated socioecological information collected during long-term field studies of endangered primate populations in South America (*Alouatta seniculus, Brachyteles arachnoides*, and three species of *Leontopithecus*) and Africa (*Colobus badius* and *Cercopithecus ascanius;* Struhsaker and Pope, 1991) with insights about differences of genetic diversity in these primate groups. While some of the genetic information comes from other studies, Pope (1990; 1992) used class I MHC genes as her markers for genetic variability data. Watkins et al. (1991) also used MHC I genes to examine callithrichids, which appeared to be genetically very uniform.

Many researchers have studied hemoglobins (types of proteins or amino acid sequences) as part of their endeavor to solve questions in primate phylogeny. One

result from hemoglobin research that was carried out in the 1970s was the obvious conclusion that the lorisid *Nycticebus* is not monophyletic with the lemur genera *Eulemur* and *Propithecus* but belongs to a branch between lemurs and anthropoid primates. It was also documented that the New and Old World monkeys are phyletically separate from each other, and that the callithrichid, genus *Callithrix,* is closely related to the cebid monkey, *Cebus.* It was furthermore concluded that the Old World monkey genus *Presbytis* is closely related to genera *Cercopithecus* and *Macaca,* while the lesser ape genus *Hylobates* stands far separated from *Gorilla, Pan,* and *Homo,* with the latter two genera more closely related to each other than to *Gorilla*. The most surprising result of this evaluation was the purported close relationship determined between the two New World genera *Callithrix* and *Cebus,* which are ranked in different families according to conventional classification. Somewhat later results with help of the same methodology concluded that the lorisid *Nycticebus,* together with bushbabies (genus *Galago*), are more closely aligned with anthropoid primates than they are with the lemurid genera *Eulemur* and *Propithecus*. Evaluation of genus *Tarsius* indicated that there are several characteristics that tarsiers share with anthropoid primates but that twice as many tarsier characteristics appeared to be independently acquired. It seems that determination of molecular relationships that are based on hemoglobins are often puzzling if not useless. Additional proteins such as myoglobin, fibrinopeptides, or eye lens crystallins (small, globular proteins that are the principal components of the lens in the mammal eye) have been studied and provided more sketchy information about alleged relationships among primates: This sketchiness is likely to have been caused by the randomly scattered availability of the diversified protein aggregates derived from only a few primate genera (see also Martin, 1990).

All the methods of molecular study that are described above permit only indirect conclusions about the fundamental genetic basis underlying the structure of the proteins studied. Hence they are procedures that understandably open up numerous inroads for inaccuracy.

DIRECT STUDY OF GENETIC MATERIAL

In contrast, techniques that allow the direct analysis of DNA have become more widely used during recent years, and they have been applied to problems of population genetics as well as systematics. Importantly, direct phenotype studies are now applied in the assessment of genetic diversity of endangered animal populations, which is crucial for planning species conservation in the future. Such analyses are also advantageous because small tissue samples are sufficient for analysis, and DNA can even be obtained from extinct taxa.

DNA Hybridization and Polymerase Chain Reaction

One of the techniques that allows direct comparison of different DNAs is the DNA hybridization technique.[1] This method makes it possible to estimate the degree of DNA sequence differences between genomes. Lengthy genome DNA that has been stripped and purified of proteins and RNA is first fragmented into shorter pieces (see later discussion). The double-stranded DNA fragments are heated to various temperatures (up to 100° C), which causes the hydrogen bonds that hold together the two strands of the DNA double helix to dissolve, resulting in two separate single strands of DNA. During this procedure only the hydrogen bonds between the bases are weakened; the rest of the molecule is not damaged by heat. Fractionated, single-stranded DNA is labeled radioactively to distinguish it from the DNA to be tested. Similarly treated DNA from a test subject is mixed in equal amounts with the radioactively labeled DNA. When the DNA mixture is cooled down, single strands reapproach each other in a random manner, and complementary base sequences reattach or anneal to reconstitute fragments of double-stranded DNA. Obviously there are multiple factors that affect the accuracy of such procedures. Temperature, the make-up of the solution in which the DNA is suspended, the size of the genome, and the DNA fragment size all determine the amount or extent of reassociation. When single strands of DNA that come from different species are cooled down together to 60° C, complementary regions reassociate with each other. Moreover, the fact that much of genomic DNA is repetitive, and that many DNA sequences do not encode any genetic information, complicates the hybridization procedures because the repetitive DNA has to be removed before hybridization. Nonetheless, Sibley and Ahlquist (1987), who used this method in the attempt to decipher bird evolution, have also applied DNA hybridization to hominoid samples. This method of reassociating single-strand DNA allows identification of particular DNA (or RNA) molecules. However, DNA hybridization does not allow identification of individual nucleotides or reveal which shared characters are being compared.

Basically the same methodology is used in polymerase chain reactions (PCR). PCR makes it possible to study genetic material that, for example, comes from a single primate cell, from Egyptian mummies, or from small insects that are encased in very old amber. Like in DNA hybridization, the double-stranded DNA is heated until the two strands separate, creating single strands of DNA. These single strands of DNA can be virtually copied with the help of a heat-resistant polymerase enzyme. The polymerase enzyme, also known as primer—which usually comes from bacteria *(Thermus aquaticus)* that thrive in hotsprings and

[1]Application of DNA hybridization to phylogenetic questions on a large scale was pioneered by Sibley and Ahlquist, who designed an automated apparatus called the DNA Analyzer to improve and speed up the hybridization process.

are not affected by the heating procedure—attaches itself to the original DNA, or template, and replicates it. The new strand conserves the genetic information from the parent strand and is a complementary replication of the template. This results in two identical molecules originating from the original one. Repeated heating and cooling cycles result in exponential increase of the number of copies that are created from the original DNA. This technique is used to identify mutations and certain human medical conditions (e.g., sickle cell anemia or cystic fibrosis) and is successfully applied in forensic investigations.[2] However, PCR depends on the accuracy of the pairing between original DNA template and primer. It therefore requires some prior knowledge about the original DNA sequence. The primer must be able to recognize the sequences that are targeted to be copied (Nicholl, 1998).

Interestingly, a widely used application of PCR amplification in sexing of mammals (Y chromosomal fragment amplification) failed to reliably differentiate between X and Y chromosomes in prosimians. A slightly different approach now makes reliable molecular sexing of prosimian primates possible (Fredsted and Villesen, 2004).

DNA hybridization is a potential tool to study DNA sequence evolution that supplements phenotypical evaluation of morphological characters. Therefore, since these methods of deciphering evolutionary process are independent, when the results of both are combined and evaluated together they can potentially be of great importance for the understanding of evolutionary sequences.

Restriction Fragment Length Polymorphism Analysis

Another way to study DNA directly is DNA restriction analysis and restriction fragment length polymorphism (RFLP), which identifies DNA pieces and their internal structure with the help of restriction enzymes. Genomic DNA can be fragmented, or cut into smaller pieces, by bacterial or yeast enzymes called restriction endonucleases (REs). Most REs work by recognizing a specific six–base pair palindrome sequence (reading exactly the same from left to right and right to left) and cutting the DNA at these sequences. The results are fragments of DNA of varying length that can be separated and visualized with the help of electrophoresis. There are well over 400 REs commercially available (Roberts, 1984).

[2]Forensic Short Tandem Repeat or STR technology is now routinely applied to evaluate specific regions (loci) within human nuclear DNA. Established variability in STR regions is used to distinguish one individual DNA profile from another. The Federal Bureau of Investigation (FBI) searches a standard set of 13 specific STR regions with CODIS, a software program that operates databases of DNA profiles from convicted offenders, evidence from unsolved crime scenes, or missing persons. It is implicit that the probability of two individual humans having the same 13-loci DNA profile is about one in one billion.

Changes in DNA fragment patterns are caused by mutational gains or losses of DNA sequences. Precise evaluation of mutational gains or losses can thus be accomplished by direct DNA sequencing. Because genetic diversity among individuals and species is due to mutational gains or deletions, not all genomic DNA will give rise to the same fragment pattern, because a mutation in a base pair palindrome will destroy an RE site, resulting in different length DNA. DNA sequencing is now facilitated by the development of automated and computerized DNA sequencers, which make it possible to obtain many data in a relatively short time.

Restriction fragment length polymorphisms are also applied to the study of mitochondrial DNA (mtDNA). It is possible to identify restriction site mutations by comparatively mapping the loss or addition of a single mtDNA nucleotide sequence. The study of mtDNA can be complicated, however, by the fact that mtDNA occurs in circular genomes (see also Hillis and Moritz, 1990). Researchers have focused on mtDNA with the assumption that the mode of inheritance of this extranuclear DNA is strictly maternal in all mammals, which is not entirely correct (see later discussion and discussion in Chapter 12). Many of the technologies that are used to study nuclear DNA can also be applied to the study of mtDNA.

Southern Blotting

One very useful technique that makes it possible to study single DNA genes was described by Southern in 1975 and became widely known as Southern hybridization or Southern blotting. Southern separated RE-treated DNA fragments with the help of electrophoresis on an agarose gel strip. Subsequently the single-stranded fragments were transferred to a nitrocellulose filter by "blotting." Then they were probed with a radioactively labeled nucleic acid probe sequence, which binds or hybridizes to the DNA fragments it is complementary to. Identification and separation of single DNA sequences is thus made possible as the radioactively marked probe and the gene to be studied are made visible by autoradiography.

The results of molecular studies may or may not agree with the major phylogenetic relationships among primates that were previously established and based on morphological characters. Some molecular findings however, disagree with the earlier established phylogenetic trees as well as with each other (Martin, 1990). Primatologists have predominantly been captivated by biochemical research that focuses on questions revolving around human evolution as well as the taxonomic position of humans among higher primates, particularly the African apes. Research concerning nonhuman primates is still rather sketchy and difficult to synthesize into a comprehensive synopsis. This is partly caused by the random availability of primates that can be genetically tested.

For example, the taxonomic position of the enigmatic prosimian genus *Tarsius* in relation to other primates has been reevaluated by Koop et al. (1989). Koop and his colleagues concluded from their investigation of δ- and β-globin sequences (globins are the protein constituents of hemoglobin; each hemoglobin molecule consists of four globin subunits—for example, the adult human hemoglobin is a combination of two α-globins and two β-globins) that hominoids are more closely related to Cercopithecoidea, followed by Cebidae, Tarsiidae, Lemuridae, rabbits, and goats. They then opine that it is justified to place *Tarsius* together with anthropoids in suborder Haplorhini. This placement, however, is solely based on the evaluation of findings regarding one globin gene cluster (β-globin cluster) and a single globin gene (δ-globin, a gene from the α-globin gene cluster). Although some of these molecular phylogenies support the classification of tarsiers with higher primates in suborder Haplorhini (Dene et al., 1976; Koop et al., 1989), others disagree (Sarich and Cronin, 1976). Another example of molecular inconclusiveness is the phyletic relationship of the small, elusive South American monkey *Callimico goeldii,* whose taxonomic position continues to swing back and forth between being regarded as a callithrichid and being considered a cebid monkey. Only recently Pastorini et al. (1998) have concluded from the study of *Callimico*'s mtDNA sequence data that this genus should be placed in Callitrichidae, not in Cebidae. Another enigma concerns the molecular relationship between the African apes and humans. It has not been possible to resolve either the position of *Callimico* or human/ape ties conclusively with the help of molecular studies (Horovitz et al., 1998; Pastorini et al., 1998). What molecular primatology has achieved is the accumulation of a multitude of new data, which in combination with morphological characteristics can—to a certain extent—be of help in the evaluation of primate relationships (Shoshani et al., 1996).

Only a handful of more recent reviews of molecular relationships have focused on the New World monkey genus *Aotus* (Ford, 1994); on the New World monkeys in general (in a brief abstract by von Dornum and Ruvolo, 1996); on the Old World guenons genus *Cercopithecus* (Ruvolo, 1988); on genus *Papio* (Disotell, 1994, 2000; Rogers, 2000); on the geographically widely dispersed Old World monkey genus *Macaca* (Hoelzer and Melnick, 1993); on Old World monkeys in general (Disotell, 1996); and on several prosimian genera (Pastorini et al., 2003).

Immunobiological evaluation is presently inexact and requires a combination of several different methodologies and approaches to achieve reliable information. During the 1990s molecular approaches for clarifying relatedness and ancestry among primates increasingly relied on genomic DNA or even on single genes, while many prior methodologies continued to use indirect methods studying structural components such as proteins. As mentioned previously, at present, the wide array of biochemical procedures has predominantly been applied to investigations of our own species' relationship with its closest primate relatives,

the African great apes, in order to establish which of the extant primates is our closest relative.

Molecular primatology is especially useful in long-term research of both population dynamics and population genetics among wild primate populations (Melnick and Hoelzer, 1992; Pope, 1992; Scheffrahn et al., 1993) in the attempt to decipher how evolution proceeds. DNA molecules can be helpful in solving uncertain paternity relationships (who is whose daddy?) among individual primates within groups that are the subject of long-term social behavioral studies (Martin et al., 1995). In addition, genetic fingerprinting is an indispensable tool for preserving genetic diversity of captive primate populations as part of the attempt to conserve and eventually reintroduce back to the wild endangered primates (Scheffrahn et al., 1998). Evolutionary or taxonomic evaluation of molecular data is only practicable, however, when it is rooted in conventional morphological assessments.

A good example for us to judge the usefulness of molecular data is the question revolving around the hominoid *Gorilla—Pan—Homo* triangle and the phylogenetic relatedness of these three genera to each other. Even though many molecular studies have tried to determine the ultimate relationship of these genera, an unequivocal answer has not yet been found. Apparently the genetic distance between the African apes and humans is too close to allow the final solution to this puzzle. Karyology has also failed to resolve this triple relationship. Actually, in this case it is old-fashioned morphology and behavior that are more helpful in the clarification of relatedness. It is the pygmy chimpanzee, *Pan paniscus,* that morphologically and behaviorally appears to be most closely related to humans; biochemically the two chimpanzee species and humans cannot be positively differentiated. The pygmy chimpanzee's congener species *Pan troglodytes,* or common chimpanzee, is almost as similar to humans as is the pygmy chimpanzee, while the gorillas are morphologically more distant to humans and closer to the chimpanzees. Recently, based on the study of mitochondrial DNA, genus *Pan* has been classified together with *Homo* in a clade that is separate from genus *Gorilla* (Horai et al., 1992); despite this, the trichotomy has not been abandoned by all. However, as Marks (1992) shows, many studies that addressed the "trichotomy" puzzle have come up with contradictory results, and some who claim to have solved the question have misinterpreted their findings. The genetic ape/human relationships have not (yet?) been untangled by molecular methods. There might be good reasons why they never will be solved.

Neuraminic Acids

During the development of this text there have been some new developments addressing the genetic differences between humans and chimpanzees. The so

obviously morphologically and behaviorally different species of humans *(Homo sapiens)* on one hand and the two species of chimpanzees *(Pan troglodytes and P. paniscus)* on the other have been found to be practically indistinguishable from each other as far as their genetic material goes. Two groups of scientists in the United States and in Japan have discovered a minute difference between diseases in humans and these apes (see Muchmore et al., 1998). They found that these genera differ from each other in the genetic expression of neuraminic or sialic acids. These acids are actually expressed as sugar molecules that reside on the surface of cells all over the mammalian body with the exception of brain tissue (where they are never found) and function as important cell-to-cell communicators by recruiting enzymes. They were originally identified from fetal tissues and certain human tumors and serve as binding sites for microorganisms that cause, for example, cholera, influenza, and malaria. Two kinds of sialic acids differ in their coding regions such that the resulting sugar molecule either has or does not have a single important oxygen atom. These acids are N-acetyl-neuraminic acid (Neu5Ac) and N-glycol-neuraminic acid (Neu5GC). Humans only express Neu5Ac, never Neu5GC; the reverse is true for chimpanzees, and therefore humans cannot recruit an enzyme that is found in chimpanzees. These neuraminic acids are, therefore, important for research that focuses on human diseases. Humans who are afflicted with particular inflammations or infections are known to develop antibodies against Neu5GC. The authors conclude that the lack of the oxygen atom in Neu5AC is connected to the susceptibility of humans to certain cancers and infectious diseases that chimpanzees are not susceptible to.

The hypothesis has been proposed that the lack of this one single gene in the genetic code of humans, which is present in chimpanzees, could also be the cause of the obvious phenetic differences between the two. Thus far this hypothesis is nothing but speculation, however.

Mitochondrial DNA

Mitochondrial DNA has been extensively studied in the genus *Macaca,* a geographically widely dispersed and species-rich group of Old World monkey. All these studies have been done under the assumption that mtDNA is totally lost from the paternal line and is only maternally inherited. However, the authors of one work (Melnick and Hoelzer, 1993) point out that mtDNA is likely to be misleading in studies of population genetic structure: The mtDNA genome makes up only a small fraction of the entire genetic makeup of an animal and, as Melnick and Hoelzer (1993) state, can "present a deceptive picture of the overall genetic similarities or differences within and among populations." Considering population dynamics in macaques, where females are said to habitually remain in their native group while males disperse and join different groups, and the consequent presumed matrilineal inheritance of mtDNA, the following analysis

emerged: 1) The mtDNA of several members of different macaque groups was studied with the help of restriction fragment length polymorphisms, restriction site mapping, or nucleotide sequence data (it is not specified to what extent these different techniques were applied, but Melnick and Hoelzer [1992] stated that "In some cases several types of data were combined to reconstruct the phylogeny of a group"). 2) The authors hypothesize that diversity of the nuclear genome as it is spread by male migration and transmitted by both males and females, should be more evenly dispersed between different groups. 3) The nuclear DNA should consequently be more divergent within groups and be more homogenous between different groups. 4) The alleged strictly matrilineal mtDNA that is only transmitted by mothers, who remain with their native groups, should be more diverse between groups and homogenous within groups. These predictions about the difference of genome dispersal are based on two crucial assumptions, namely 1) that it is correct that macaque males transfer out from their native groups and invest in the gene pool of different populations, and 2) that all females stay put and wait for immigrant males to arrive and mate with them, and also that these females are really passing strictly maternally inherited mtDNA to their offspring. It is actually not absolutely certain that mtDNA is strictly maternally inherited in primates (Ankel-Simons and Cummins, 1996; see also Chapter 12). Regardless, Melnick and Hoelzer (1992) were able to prove their hypothesis to be correct. At present there are only a few in-depth studies of other primate genera that are comparable to these studies of macaques. Melnick and Hoelzer (1993) point out that even though mtDNA studies are useful in analyzing population genetics—such as, for example, tracing matrilineal relationships of social groups within a population as well as investigations that document gene flow between contact populations—caution has to be employed when phylogenetic and biogeographical reconstructions that are based on mtDNA evaluation are attempted. These authors point out that there is significant intraspecific variation in mtDNA in most primate species. This variation, if not documented, in turn might be troublesome in settling on implied taxonomic relationships or phylogenetic hypotheses.

Human mtDNA has also been used to investigate migration patterns of human populations (see Hagelberg et al., 1999). For example, it has been shown that the peoples of Polynesian islands are genetically homogeneous and their mtDNA is very uniform. The Polynesian islands are therefore thought to have been only very recently colonized by a small human founder group. In contrast, the human population of the western Pacific islands show higher levels of genetic diversity; therefore, presumably, they were settled much earlier in human history than Polynesia. Two new studies, one involving mtDNA of European and African humans and apes (Awadalla et al., 1999; Eyre-Walker et al., 1999) and another evaluating the diversity of human mtDNA of western Pacific populations (Hagelberg et al., 1999) document that human paternal mtDNA does appear to recombine with maternal mtDNA. Eyre-Walker et al. conclude that, "It certainly

seems dangerous to assume that mitochondria are clonal when there is evidence against and no evidence in favour of such conjecture." These two studies have been criticized, but in the meantime other cases of paternal mtDNA recombination have been reported. Most notable is a report of a case of a paternally inherited illness that has clearly been connected to the paternal mtDNA (Schwartz and Vissing, 2002). "Leakage" of paternal mtDNA has been found in many vertebrates, including primates, and in invertebrates (Kraytsberg et al., 2004; Thalmann et al., 2004; Bandelt et al., 2005), and a lively discussion about this issue continues (Bromham et al., 2003; Rokas et al., 2003; Tsaousis et al., 2005). There can be no doubt that the paternal mitochondria enter the primate ovum at fertilization. This means that they are incorporated somehow in the developing embryo. Their ultimate fate may be unknown, but their participation in mysterious molecular events is quite possible (Woischnick and Moraes, 2002; Bromham et al., 2003; see also Chapter 14: Transposable Elements and Numts).

Although the number of published contributions to molecular primatology has increased rapidly in recent years, overall the information available about primates is still inconsistent and randomly distributed within the order Primates. A multitude of molecular studies address human biology in particular and primate biology in general. However, many of these studies use techniques that are not compatible with each other or are based on molecules of unknown function and hence are not always directly comparable or meaningful.

For example, the application of gene therapy to cure human illness has for more than 10 years been believed to be "right around the corner" according to Bolsover et al. (1997). Unfortunately this hope has not yet become reality. Genetic diseases and the genes that are responsible for them can be identified, and parents can receive genetic counseling, but treatment is still out of reach.

PROBLEMS OF PHYLOGENETIC ANALYSIS USING MOLECULAR DATA

In primatology, molecular data have no real meaning unless they are brought into a phylogenetic context. Although there have been many attempts to give phylogenetic significance to findings about proteins, immunological differences, DNA sequences, or mtDNA correlations, these have often been contradictory and disappointing. The reason for this lies in the functional background of molecular data. Even if molecular differences can be documented, they usually cannot directly be correlated with any morphological features (Müller, 1994). Such undesignated characters must then be analyzed. But how can this sensibly be done? Marks (1994) for example documents that supposed gene differences among children with attention deficit disorder appear to be randomly distributed and cannot be ascertained for many children who exhibit this kind of behavior.

An additional problem is the fact that most of the genetic coding regions (called exons) are separated by extensive areas of noncoding regions (introns). This simply means that most of the DNA in eukaryotic cells is not made up of functional genes (see Chapter 14).

More questions than answers are resulting from the multitude of new research. One serious problem remains the lack of communication between research groups using different methodologies.

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Chapter 14

Primate Genomics

The History of Genetics
Molecular Phylogenetics
The Tarsier Conundrum Still Not Solved
Genetic Expression of Human Learning
BAC, YAC, and PAC Libraries
Genes Controlling Human Behavior
View into the Future of Genomics
Transposable Elements and Numts
Outlook and Reflection

For several months the author has attempted to delve into genomics and to understand what is presently happening to biology on the molecular level. This turned out to be an arduous and convoluted journey of the mind and finally filled the author with amazement as a totally unexpected scenario was observed. It also left astonishment in realizing how many new observations in molecular primatology, presented with great confidence and assertiveness and the air of unequivocal success, are actually rather provisional if not faulty. The experts consulted seem to believe that what they have discovered during evaluation of minute units of molecular information, or a few selected proteins, is the unequivocal solution to phylogenetic puzzles and taxonomic enigmas. It has to be concluded that the science of molecular biology and consequently of molecular primatology is still in its infancy. Scientists and entrepreneurs are dabbling in the nanomolecular realm of genetics and genomics, expecting great discoveries and profits.

When studying molecules, no one seems to take into consideration what possible effect both the size and function of the selected miniscule genetic loci might have, which are used in the endeavor to reconstruct evolutionary time frames and phylogenetic relationships between living things.

The chart of all 23 human chromosomes and the loci of recognized traits on each chromosome implies that what we know about the human genome is predominantly about genetic coding that results from the identification of medical malfunction. On this chart, loci that generate normal traits are rare. The human genome is encoded by a sequence of more than three billion nucleotides (Zweiger, 2001), all tightly packed into the 3.50 picograms (pg) of DNA that make up the 46 human chromosomes. One picogram equals 0.000000000001 g, which in other words means that 1 pg is one trillionth of a gram. Try to imagine 3.5 trillionths of a gram! Expressed more visually, 1 pg is the equivalent of one drop of detergent dispersed in enough dishwater to fill a trainload of railroad tank cars 10 miles long. Or visualize a pinch of sand grains out of a huge sand dune the size of five football fields.

Among primates the total DNA amount varies between 2.59 pg in *Eulemur rubriventer* and 5.19 pg in *Allenopithecus nigroviridis.* There does not seem to be any direct correlation between chromosome number and DNA weight (Gregory, 2005a). Currently the genomes (the entire genetic complement of an organism) of only two other primates in addition to *Homo sapiens* have been completely established. Even these three primate genomes have not yet been entirely deciphered.

In 2005 an initial "shotgun sequence" of the chimp genome was documented, and a partial comparison with genome fractions between the human and chimp genomes was published (Mikkelsen et al., 2005). The chimpanzee *(Pan troglodytes)* has 2n = 48 chromosomes and 3.60–3.85 pg (average 3.73 pg) of DNA.

We understand today that the common term "the gene" is a catch-all word for indefinite numbers of DNA bits that code for various characters. These so-called "genes" are not identical to each other, not identical in the amount of DNA material, and, between species, not necessarily located on identical chromosome positions. We also really do not know with certainty how comparable various chromosomes in different primate species are. Expressed in a different way, how similar or dissimilar can 1 pg of DNA, a tiny fraction of the entire DNA, be in different organisms? Are they really equivalent? We actually don't know (Mattick, 2003, Stanley et al., 2006).

Extracting minute fractions or coding loci from genomes of various animals and using these infinitesimal amounts of DNA to decipher and speculate about evolutionary relationships and time frames is problematic at best. This is especially obvious if we consider that genetically all living organisms are based on 64 (4^3) three letter base triplets or codons or 64 "words." These words are combined by the four nitrogen bases: adenine [A], thymine [T], guanine [G], and cytosine [C], and therefore are coded similarly. These triplet words are lined up in various arrangements to write the genetic code. The genetic code is repetitive, being a series of these three letter "words" that are combined from a four letter alphabet.

The concern over identifying any specific "gene" in order to subsequently evaluate it made it apparent that there is no unified definition of the widely used vernacular "gene." It soon became evident that the definition of what a "gene" might be has become more and more elusive during the last twenty years of biomolecular research, while the number of explorations into the vast depth of interaction and function at the molecular level has immeasurably increased. What was once taught about molecular genetics and the important dogma of "one gene/one protein" or alternatively "one gene/one enzyme" is no longer correct. What we are discovering at the nanomolecular level is much more complex and malleable than would ever have previously been imagined. An excellent historical assessment of these changes is "The Century of the Gene" by Evelyn Fox Keller; this work overviews the changes and developments in the field of genetics over recent years (Keller, 2000). We stand now at a crossroads of new unexpected insights into the regulatory mechanisms of genetic information that fine tune the complex repetitive procreation of plants and animals, including humans.

THE HISTORY OF GENETICS

The study of genetics began in the year 1866, when Gregor Mendel, an Austrian Augustine monk, discovered and published his insights about the fundamental laws of inheritance, which are still valid and remain the basic principle of genetic inheritance. Mendel's work was done at the St. Thomas Monastery of the Augustinian Order in the ancient town of Brünn (at the time Brünn was located in Austria, but it is now part of Czechoslovakia).

Since Mendel's first insights, genetic research and developments have expanded at an ever-increasing speed, to the point that today they are driven by complicated and capable computer technology. High-level computer-based statistics, newfangled biochemistry, complex laboratory technology, philosophical sophistications, Hennegian cladistics, phylogeny theory and speculation, computer-based parsimony assumptions, and awe-inspiring numbers of publications have expanded into an enormous, fast-growing new realm of science. A new lingo has evolved since Mendel's initial discoveries, encompassing complicated, often incomprehensibly abbreviated terminology that is sometimes based on linguistically erroneous derivations. Unfortunately one cannot even be sure whether some scientists are referring to the same meaning when they use identical terminology. Research groups have developed their very own jargon, resulting in further confusion. The original field of genetics has multiplied into subfields: molecular biology, molecular genetics, genomics, proteonomics, and (closely related with all these new and expanding fields) bioinformatics. From all this has arisen "the Genome," which is the entire count of species-specific genetic information that activates living organisms. The task of registration of this

chemically coded information is named genomics; proteomics encompasses the biochemical attempt to decipher the secrets of enzyme production, protein interactions, protein isolation, and protein structure information.

Information that has been gleaned from genomics research is stored at international information bases sponsored by academic institutions and businesses and can be retrieved (at a price) at any time. This highly complicated, computer-generated international storage system has newly been labeled "bioinformatics."

The continuous proliferation of new insights and resulting publications are comparable only to a huge avalanche of new information being created at breathtaking speed. Much of these new insights are important, but some are farfetched. Thus this text will attempt to report those developments that are of consequence for primatology and therefore to the understanding of humans and our relatives in the mammalian order Primates.

Manipulation of genetic material, down to the tiniest information unit of what we vaguely and globally know as "the gene," has led to the creation of burgeoning new subfields like medical genomics, forensic genomics, behavioral genomics, genomics and human variability, population genetics and proteomics, bioinformatics, and—ultimately the most enigmatic branch—phylogenomics, an extensive field that attempts to decipher phylogenetic relationships of living things with the help of biochemical characters. Tissues of a multitude of living organisms are now stored and available at databases, many of them commercially owned, where they can be readily retrieved or bought and evaluated. Processing of tissues has also been streamlined by the availability of various automated laboratory machinery that processes materials and data and provides the buyer with the DNA/mtDNA or RNA sequence information they request. Computer programs can then further manipulate such data; for example, they may compute phylogenetic/evolutionary trees, taxonomic (genetic distance) assessments, or information about genetic character changes and their functional consequences.

MOLECULAR PHYLOGENETICS

Genetic information has been very useful in studying the dispersal of early mammals on our planet and realignment of major mammal groups (Stanhope et al., 1998; Seiffert, 2003). When molecular data are applied to large taxonomic groups of mammals, the realignment or regrouping of placental orders to form taxa such as Afrotheria, or the determination of close genetic relationships between Cetacaea (whales) and Artiodactyla (even-toed ungulates such as hippos and pigs) as Cetartiodactyla, molecular phylogenetics plays an important, decisive, and significant role (Kemp, 2005). The genetic picture becomes rather muddled and insoluble, however, when resolutions for phenotypically mysterious

close taxonomic relationships are sought, as for example the puzzle as to where to place *Tarsius* within the mammalian order Primates. That we are unable to solve this latter conundrum is based on the simple fact that primates are all basically made of the same genetic material. We are genetically so similar to each other that humans are only about 2% different from their next of kin, the great apes. This closeness easily explains the difficulty of drawing molecular distinction among such basically similar species.

Very assertive statements regarding the usefulness of molecular data have been made by researchers, such as "Unlike morphological data, molecular characters (i.e., DNA sequence data) and character states are obvious and not prone to subjective interpretations" (Yoder, 2003). Yet despite this confidence, such remarks later have had to be retracted, modified, or amended, because in general only certain minute fragments of the vast nuclear material that replicates species are evaluated, and in the attempt to provide "unequivocal information," researchers pick and choose small genetic sequences, resulting in frequent sampling and evaluation biases. Thus this means that (usually partial) data sets are selected and appraised, choosing any that will fulfill the goal of achieving the "expected" results and prove the hypotheses. In short, even "unbiased" molecular data are not necessarily likely to indisputably resolve problematic phylogenetic relationships among closely related extant taxa (Philippe and Laurent, 1998; Marks, 2003; Yoder, 2003).

To be able to grasp the overwhelming amount of information that is published under the heading of genomics we have to start at the beginning: chromosomes are the basic structures that underlie any investigation in molecular inquiry. Each chromosome contains tens or even hundreds of millions of base pairs. Chromosome morphology is a tool to identify considerable intraspecies variation, which is used to pinpoint the locus of genetic information that codes for illness (e.g., the cystic fibrosis "gene"). Comparative studies of genetic material always have to begin with mapping techniques comparing chromosome morphology. One of these procedures is known as fluorescence in situ hybridization (FISH) technology, which complements routine chromosome analysis by utilizing chromosome-specific DNA probes (see Chapter 12).

Even this kind of evaluation often still generates more questions than answers (Rogan and Knoll, 2005). Weiss and Buchanan (2004, loc. cit. page 76), discussing recurring sequence repeats that occur on every chromosome, observe: "The high variability in repeat numbers, within species as well as individuals, raises an important but perhaps little-appreciated point that there is no single length of the genome for a species or even in the two copies within an individual."

The astonishing variability of numbers that make up species-specific chromosome sets, and questions about the size of material that combines to shape the chromosome numbers and thus genetic material, do not follow any anticipated and regular patterns. What is possible, especially among such well-studied

chromosomes as our own, is to pinpoint differences and similarities that allow insights about relatedness, individuality, and disease. The discovery of such variations are made possible by different staining techniques, for example with the dye Giemsa, which binds preferentially with areas of the DNA that are rich in AT compounds. This technique is known as G-banding. It creates a series of either lightly or darkly stained bands across chromosomes by coloring bands of heterochromatic materials of chromosomes and thus creating the well-known banding patterns commonly seen in pictures of karyotypes. A considerable amount of heterochromatin is located at the restricted centromere (the fast evolving spot where microtubules are attached that pull the chromosomes apart during mitosis and meiosis and that contains various satellite DNA components of chromosomes)[1] and can be made visible with the help of C-banding techniques. R-banding is the reverse of C-banding and selectively stains noncentromeric regions in preference to centromeres. The same is true for the telomere end of chromosomes. Telomeres are characterized by tandem repeat minisatellite DNAs that also stain selectively.

Another way of making different areas of chromosomes visible is achieved by staining with fluorescent dye, a technique known as Q-banding. Q-banding actually is a fluorescent pattern obtained using Quinacrine for staining. The pattern of bands is very similar to that seen in G-banding. With the help of such staining techniques, morphological and banding details can be compared and evaluated within and without the karyotypes of individuals and species, and over time, more and more important comparative information is being obtained. Attempts to use chromosome painting methodology to verify phylogenetic relationships have been rather unsuccessful (for laboratory techniques of gene cloning and DNA analysis see Brown, 2003). As mentioned previously, chromosome painting with selectively staining fluorescent dyes also known as FISH is now widely employed to comparatively study karyotypes (Speicher et al., 1996; Ferguson-Smith et al., 2005; Wienberg, 2005).

The technique of polymerase chain reaction (PCR), which now makes it possible to create a multitude of copies of specific DNA sequences, has added a new dimension to the art of DNA evaluation for many applications.

While the field of genomics endeavors to study the whole of genetic information of different organisms, the much more complicated field of proteomics focuses on the structure of gene products, the various enzymes and proteins. Despite having sequenced the DNA of all human chromosomes, having completed the genome of the chimpanzee *(Pan troglodytes)* and compared it to the human genome (Varki and Altheide, 2005), and having begun the initial sequencing and analysis of the macaque *(Macaca mulatta)* transcription (Magness et al., 2005),

[1]Centromeres have recently entered the spotlight of high interest as they contain considerable amounts of rapidly evolving DNA specific to centromeric chromatin (Lamb et al., 2004; Moore, 2004). Centromeres are implicated in the reproductive isolation of new species (Henikoff et al., 2001).

it seems that more questions have been raised than answers found. Although an enormous number of illness-related DNA loci have been successfully identified in the human genome, we still lack the intricate comprehension that would make it possible to understand what makes us human and how individual traits are genetically generated.

After the announcement that itemization of the human genome was completed in 2003 and that it contained about 30,000 to 40,000 "genes," it was announced in the fall of 2004 that the "human gene number" had to be slashed to roughly 20,000 to 25,000. A declaration from the official Human Genome website states:

> Genes are chromosome pieces whose particular bases (e.g., ATTCGGA) determine how, when, and where the body makes each of the many thousands of different proteins required for life. Humans have an estimated 30,000 genes, with an average length of about 3,000 bases. Genes make up less than 2 percent of human DNA; the remaining DNA has important but still unknown functions that may include regulating genes and maintaining the chromosome structure. Researchers hunt for disease-associated genes by looking for base changes found only in the DNA of affected individuals. Numerous disorders and traits mapped to particular chromosomes are displayed in this Web site. Some disorders, such as cystic fibrosis (chromosome 7) and sickle cell anemia (chromosome 11) are caused by base sequence changes in a single gene. Many common diseases such as diabetes, hypertension, deafness, and cancers have more complex causes that may be a combination of sequence variations in several genes on different chromosomes, in addition to environmental factors.

This clearly documents how difficult the task of attempting to solve the conundrum between the interactions of genetic coding and functional expression remains. Most knowledge about the human genome appears to still operate on the incorrect "one gene/one protein" dogma that obviously has been very useful in pinpointing specific locations of genetic sequences on particular chromosomes that code for malfunctions. By looking at gene charts on the Human Genome website it is possible to examine each human chromosomes one by one, including their banding patterns and the malfunctions that are assigned to them. It is startling to realize how many possibilities there are for our genetic information to go wrong—usually accredited to single mutation effects—and how few coding sites are currently known for normal functional DNA sites. It is the understanding of the hereditary mechanisms that document how much of human disease is genetically coded that is initiating genetic research. Furthermore, although many genetic disorders seem to be caused by mutations involving only one genetic coding sequence, it becomes increasingly clear that many disorders that are obviously inherited are rooted in complicated and barely understood interactions of multiple factors, including environmental influences that remain elusive.

When it comes to understanding normal traits that make us uniquely human, we are still in the dark. Despite many totally unresolved genetic mysteries, a plethora of alleged chromosomal manifestations of such elusive human traits as the "God Gene," (Hamer, 2004) the basis of spiritual faith, spousal fidelity, fertility, longevity, addiction, loyalty, aggression, and many more, are newly stirring the old debate about the elusive relationship spurring the nurture versus nature question. More promising in the search to increase our understanding of genetic interrelationships with functional expression are comprehensive, long-term studies that address such problems as depression and are trying to identify mutational gene changes in the human genome that might be responsible for unfavorable modifications in the production of serotonin, a chemical messenger of the brain that is associated with mood swings, and thus possibly document the genetic reason for a predisposition to depression (Zhang et al., 2004). Every one of the myriad coding sequences that are assigned to genetic malfunctions is based on research and published data.

Ultimately, the concomitant rapid surge in complexity and capability of laboratory technology and computer program sophistication is occurring in tandem with the increasing ability to fractionize, pinpoint, and attempt to evaluate minute particles of genetic material.

We are still unable to answer the question "What does make us human?" The literature is vast that uses molecular data to address questions of taxonomic and phylogenetic links among living things and has a special focus on primates.

Phylogenetic studies should begin with the entire set of the genetic material of a species, the chromosomes. As already mentioned, at present a unified definition of the genetic information entity commonly known to us as the "gene" is elusive and the number of definitions mind-boggling. It would be possible to fill many pages with slight variants of definitions trying to delineate verbally what a gene actually is. Furthermore, gene definitions are different between prokaryotes and eukaryotes. Because this text deals only with eukaryotes, we will ignore the prokaryotes, in which "gene" refers to protein-coding areas, not a DNA region. In addition, in all organisms, the size of any DNA area coding for inherited traits is by no means uniform. "Gene" size varies considerably and not at all in any predictable manner. We will not settle on a single gene definition here but will use the term "gene" in a general sense.

Today the most dynamic fields of genetic research, genomics and proteomics, and the ensuing bioinformatics, promise to be the future realm of biotechnological research that will provide new insights into questions about how living organisms so successfully function. This research is also strongly powered by economic interests, facilitates raising of funds, and has spawned a plethora of biotechnology companies that commercially develop and exploit various aspects of genomics, proteomics, and bioinformatics. The financial impact of genomic research is astronomical and growing.

We will start out by restating that the genetic information of living things is stored in every living cell in the form of chromosomes. Each chromosome is made up of one comparatively long molecule of DNA—the carrier of a multitude of genetic material that is passed on from generation to generation. These long DNA molecules in turn are made up of a double-stranded substructure: two polymeric chains that are twisted into the shape of a double helix (Watson, 1986). Here the basic genetic material, two purines (adenine and guanine) and two pyrimidines (cytosine and thymine), are linked to a sugar-phosphate backbone; these combine in different ways to shape the subunits of genetic information, generally called "genes." The genes, in turn, are the carriers of genetic information that regulates the subtleties of life that can be replicated and changed by mutations (failures of DNA repair) and thus passed on through the chain of procreation from one generation to the next. It is becoming increasingly obvious that the genetic information areas on chromosomes that are generally known as "genes" are not only regulated by physiochemical activities in the nucleus of cells but that there is crucial interdependence with the extranuclear cellular environment as well.

The number of chromosomes varies considerably between organisms, as does the number of genes. However, these two entities do not necessarily appear to be linked in any clear way, and this lack of predictable linkage is known as the "C-value paradox" or C-value enigma (Bennet and Leitch, 2005, loc. cit. page 90 footnote). The mean genome size among mammals has been known to be 3.5 pg ± 0.04 (Table 14.1).

The DNA C-value is the haploid value of any species-specific set of chromosomes; the term was coined if not defined by Swift (1950). In a letter to MD Bennet (dated June 24, 1975), H. Swift stated that: "I am afraid that the letter 'C' stood for nothing more glamorous than 'constant' i.e., the amount of DNA that was characteristic of a particular genotype" (Bennet Leitch, 2005, loc. cit. page 90 footnote). Another article by the same author (cited in Gregory, 2004) discusses the possibility of DNA loss during evolutionary genome change, as opposed to DNA gain. The issue of mass change in genomic evolution addresses the C-value enigma and is discussed in detail in this fascinating article.

The relationship of cell size versus DNA content also fails to exhibit any easy-to-understand regularity (Gregory, 2001).

The combination of the highest numbers for both chromosome count and DNA mass among primates so far known is found in the enigmatic southeast Asian primate *Tarsius syrichta,* which has 80 chromosomes and a haploid genome weight of 5.26 pg.[2] The combination of the second to lowest numbers for both are recorded for the small South American cebid monkey, *Callicebus torquatus,* which has 20 chromosomes and a haploid genome size weighing but 2.26 pg.

[2]Importantly, the karyotype of *T. syrichta* is said to be totally unlike those of other primates or mammals (see also page 553).

Table 14.1

Haploid Genome Size and Diploid Chromosome Numbers of Selected Primate Species

Primates	Haploid Genome Size in pgs	Diploid No. of Chromosomes
Family Lemuridae		
Eulemur coronatus		
Crowned lemur	3.47	46
Eulemur fulvus	3.71	46
Brown lemur	3.09	48
Eulemur fulvus		
Brown lemur	3.62	48
Eulemur fulvus albocollaris		
Brown lemur	2.73	48
Eulemur fulvus mayottensis		
Brown lemur	2.86	48
Eulemur macaco		
Black lemur	2.74	48
Eulemur macaco		
Black lemur	3.13	48
Eulemur macaco		
Black lemur	3.59	48
Eulemur mongoz mongoz		
Mongoose lemur	3.09	60
Eulemur mongoz mongoz		
Mongoose lemur	3.41	60
Eulemur rubriventer		
Red-bellied lemur	2.59	50
Eulemur coronatus x Eulemur macaco		
Lemur (hybrid)	3.05	not known
Hapalemur griseus alaotrensis		
Bamboo lemur	3.18	54
Hapalemur griseus griseus		
Bamboo lemur	3.29	54
Hapalemur griseus occidentalis		
Bamboo lemur	3.25	58
Hapalemur griseus olivaceus	3.18	58
Hapalemur simus		
Broad-nosed gentle lemur	3.25	60
Lemur catta		
Ring-tailed lemur	3.11	56
Lemur catta		
Ring-tailed lemur	3.45	56
Family Lorisidae		
Galago senegalensis		
Bushbaby	4.19	36

(Continues)

Table 14.1 *(Continued)*

Primates	Haploid Genome Size in pgs	Diploid No. of Chromosomes
Galago senegalensis		
Bushbaby	3.96	36
Galagoides alleni		
Dwarf galago	3.93	40
Nycticebus coucang		
Slow loris	3.58	50
Otolemur crassicaudatus argentatus		
Greater bushbaby	3.24	62
Otolemur crassicaudatus crassicaudatus		
Greater bushbaby	3.98	62
Perodicticus potto edwardsi		
Potto	3.29	62
Perodicticus potto potto		
Potto	3.30	62
Perodicticus potto potto		
Potto	4.14	62
Family Megaladapidae		
Lepilemur mustelinus		
Weasel lemur	3.25	20
Family Cheirogaleidae		
Microcebus murinus		
Mouse lemur	3.12	66
Family Tarsiidae		
Tarsius syrichta		
Tarsier	5.26	80
Family Callitrichidae		
Callithrix jacchus		
Marmoset	3.43	44
Cebuella pygmaea		
Pygmy marmoset	3.48	44
Family Cebidae		
Alouatta caraya		
Howler monkey	3.84	52
Alouatta palliata		
Howler monkey	3.63	not known
Alouatta pigra		
Howler monkey	3.63	52
Ateles belzebuth		
Spider monkey	3.63	34
Ateles geoffroyi		
Black-handed spider monkey	3.25	34
Ateles paniscus		
Spider monkey	3.47	34

(Continues)

Table 14.1 *(Continued)*

Primates	Haploid Genome Size in pgs	Diploid No. of Chromosomes
Callicebus cupreus		
Titi monkey	2.30	46
Callicebus torquatus		
Titi monkey	2.26	20
Cebus albifrons		
Capuchin monkey	3.98	52
Cebus apella		
Capuchin monkey	3.70	54
Cebus capucinus		
Capuchin monkey	3.88	52
Cebus capucinus		
Capuchin monkey	3.80	36
Cebus olivaceus		
Capuchin monkey	3.40	52
Lagothrix lagothricha		
Woolly monkey	3.54	62
Saimiri sciureus		
Squirrel monkey	3.30	44
Family Cercopithecidae		
Allenopithecus nigroviridis		
Allen's monkey	5.19	60
Cercocebus galeritus		
Mangabey	3.51	42
Cercocebus galeritus		
Mangabey	4.73	42
Cercocebus torquatus		
Mangabey	4.90	42
Cercocebus torquatus atys		
Mangabey	3.74	42
Cercopithecus cephus		
Mustached monkey	3.54	66
Cercopithecus cephus		
Mustached monkey	5.21	66
Cercopithecus neglectus		
De Brazza's monkey	4.87	58
Cercopithecus nictitans		
White-nosed Guenon	4.40	66
Chlorocebus aethiops aethiops		
Grivet	3.9	60
Chlorocebus aethiops aethiops		
Grivet	2.95	60
Chlorocebus aethiops aethiops		
Grivet	4.48	60
Chlorocebus aethiops aethiops		
Grivet	4.19	60

(Continues)

Table 14.1 *(Continued)*

Primates	Haploid Genome Size in pgs	Diploid No. of Chromosomes
Grivet (different cytotype or species)	4.48	84
Chlorocebus aethiops griseoviridis		
Grivet	4.55	60
Chlorocebus aethiops griseoviridis		
Grivet	4.56	60
Chlorocebus pygerythrus		
Vervet	4.19	60
Chlorocebus sabaeus	4.19	60
Chlorocebus sabaeus		
Green monkey	4.02	60
Chlorocebus sabaeus		
Green monkey	3.76	60
Chlorocebus tantalus		
Savannah guenon	3.93	60
Colobus polykomos		
Black-and-white colobus monkey	3.61	44
Erythrocebus patas		
Patas monkey	3.52	54
Erythrocebus patas		
Patas monkey	3.83	54
Lophocebus albigena aterrimus		
Black mangabey	3.76	42
Macaca arctoides		
Stump-tailed macaque	3.46	42
Macaca fascicularis		
Crab-eating macaque	3.41	42
Macaca fascicularis		
Crab-eating macaque	3.45	42
Macaca fuscata		
Japanese macaque	3.56	42
Macaca maura		
Rhesus monkey	3.43	42
Macaca mulatta		
Rhesus monkey	3.59	42
Macaca mulatta		
Rhesus monkey	3.14	42
Macaca nemestrina		
Pigtail macaque	3.56	42
Macaca nigra		
Celebes ape	3.45	42
Macaca silenus		
Liontail macaque	3.63	42

(Continues)

Table 14.1 *(Continued)*

Primates	Haploid Genome Size in pgs	Diploid No. of Chromosomes
Macaca silenus		
Liontail macaque	3.18	42
Macaca sylvanus		
Barbary ape	3.50	42
Mandrillus sphinx		
Mandrill	3.50	42
Miopithecus talapoin		
Talapoin	3.67	54
Nasalis larvatus		
Proboscis monkey	4.32	48
Papio hamadryas		
Hamadryas baboon	3.53	42
Papio hamadryas		
Hamadryas baboon	3.54	42
Superfamily Hominoidea		
Family Hylobatidae		
Hylobates agilis		
Dark-handed gibbon	3.48	44
Hylobates agilis		
Dark-handed gibbon	2.77	44
Hylobates klossii		
Kloss's gibbon	3.26	44
Hylobates lar		
White-handed gibbon	3.24	44
Hylobates lar		
White-handed gibbon	2.93	44
Hylobates moloch		
Silvery gibbon	3.24	44
Hylobates muelleri muelleri		
Gray gibbon	3.32	44
Hylobates muelleri x Hylobates syndactylus		
Gibbon (hybrid)	3.50	not known?
Symphalangus syndactylus		
Siamang	3.76	50
Symphalangus syndactylus		
Siamang	2.98	50
Gorilla gorilla		
Gorilla	4.16	48
Gorilla gorilla		
Gorilla	3.57	48
Pan troglodytes		
Chimpanzee	3.76	48
Pan troglodytes		
Chimpanzee	3.63	48

(Continues)

Table 14.1 *(Continued)*

Primates	Haploid Genome Size in pgs	Diploid No. of Chromosomes
Pan troglodytes		
Chimpanzee	3.85	48
Pongo pygmaeus		
Orangutan	3.60	48
Pongo pygmaeus		
Orangutan	3.66	48
Pongo pygmaeus		
Orangutan	4.10	48
Homo sapiens		
Human: *Homo sapiens* (generally accepted standard)	3.50	46

Species names were updated according to Wilson and Reeder (2005), with taxonomy and common names following Nowak (1991). Chromosome data are primarily from the original genome size references, supplemented by data from Hsu and Benirschke (1967–1977), Matthey (1973a,b), Hayman and Martin (1974), and Egozcue (1975).

T. Ryan Gregory, 2003.

Recently, however, an even smaller chromosome number has been reported for a petite South American cebid monkey, *Callicebus lugens*, whose diploid chromosome number is said to be 16. The haploid genome size has yet to be established for this species (Bonvicino, et al., 2003).

It appears that genetic information units can be packed tightly in different density and they are interspersed by allegedly noncoding or "empty" genetic areas that are known as introns. Some of these are also called SINEs as in Short Interspersed Nuclear Elements which are less than 500 bp (bp = base pair) long, and LINEs = Long Interspersed Nuclear Elements which are variable in length but longer than 500 bps. One specific group of SINEs is known as Alu Elements or Repeats. Multiple Alu elements are predominantly found in primates including humans but have also been reported from rodents (Yang et al., 2004). They are now recognized as one of the most successful groups of mobile genetic elements in the primate genome (Batzer and Deininger, 2002). Alu sequences got their name because a fraction within the Alu repeat sequence is cleaved by the Alu restriction endonuclease Alu I that cuts at ATCG and is derived from the bacterium *Arthrobacter luteus*. Alus are now believed to actually have a function (Thomas et al., 2003) and the true role of Alu-repeat sequences in primates is slowly emerging (Hedges and Batzer, 2005; Brookfield and Johnson, 2006).

Mobile elements make up almost 50% of the human genome, where Alus add up to about 11% of all SINEs that are important in the generation of mutations and recombination events. Alu elements are about 300 pbs long and today it is thought

that Alus make possible the rearrangement of genetic information that may have guided the evolution of primates. Alus also seem to contribute to many disorders and are involved in creating genetic diversity (Lev-Maor et al., 2003). Roy-Engel et al. (2002a) point out that Alus were believed to be phylogenetically young SINEs that were inserted into the human genome after the split of humans from nonhuman primates where they, consequently, should be missing. However, multiple independent Alu insertions were found in the genome of the owl monkey *(Aotus trivirgatus)*, which suggests that Alu insertions in primate genomes are the products of independent evolutionary events and are not exclusive to humans.

As stated, the SINEs of the Alu group are the most all-pervading group of repetitive elements in the primate DNA sequence and are believed to have arisen 65 million years ago. About 500,000 Alu SINEs apparently are integrated in the human genome, composing roughly 5% of the genome mass.

Alu markers have been used to reconsider the phylogeny of New World monkeys (Singer et al., 2003). The results have aligned genus *Callimico* with Callitrichidae, which has variously been considered to belong either with the Cebidae, with Callitrichidae, or even in its very own family, Callimiconidae (Hershkovitz, 1977). Other results of their "lineage sorting" have caused these authors to state that their conclusions are nothing but a starting point that needs to be carefully reconsidered in the future.

It is important to know that repeat numbers or microsatellites can vary widely intraspecifically and individually (Weiss and Buchanan, 2004).

The terms exon and intron were coined by Gilbert (1978) in stating that "The gene is a mosaic: expressed sequences held in a matrix of silent DNA, an intronic matrix. The new dimension of epigenetic inheritance makes it possible to gain understanding of phenomena like the inexplicable correlation creating the DNA C-value enigma that formerly did not make any sense." Even though the term "epigenetic" was coined in 1942 by Waddington (Waddington, 1962) and explained in more detail 16 years later (Lederberg, 1958), it was not really understood until about 20 years later how important and even crucial knowledge about epigenetic phenomena really is. The word 'epigenetic' literally means "on genes" covering all manner of changes that can affect genes and that are caused by outside circumstances rather than changes of the DNA sequence itself. Such epigenetic events can be complex and, for example may emerge from the environment in which a very early stage organism begins to develop. There is an intricate and not yet entirely explained interaction between the epigenetic chromosomal factors (also known as genetic imprinting), which have been shown to significantly influence inheritance of characteristic traits and diseases, and the core DNA exon sequences that make proteins (Gibbs, 2003). Most genes have two copies that are active, both the maternal and the paternal copy together. Some other coding areas or genes, however, are normally either expressed maternally or paternally, while the coding sequence from the other parent remains inactive. "Genetic imprinting" refers to events where only one of the parents' genes is

active. Failure of the normal methyl tag activity can affect one or both copies of a gene. Imprinting events that incorrectly involve both paternal coding sequences where only one should be tagged have been found to cause several serious malfunctions in human newborns. Methyl tag errors are also implicated in the process of aging and human cancers.

The obvious active genetic material, located in the exons, and the elusive introns combine to form the entity of species-specific genomes. The genetic activity is more enigmatic than was originally expected: The genetic influence that does not originate with the exons (formerly called "genes") is called "epigenetic inheritance," adding another dimension to genomic heritability. Epigenetic events change gene expression during development without modifying the DNA.

A very important regulatory phenomenon is known as DNA methylation: Parts of the DNA encoding structure are controlled by complex sets of regulatory proteins that bind with the DNA of genetically active sequences and function as controls. These proteins are called "methyl tags" and are vital for the normal development and consequent function of cells. The tagging enzyme is a DNA methyltransferase: it binds methyl to cytosine nucleotides. In eukaryotes this is achieved by tagging a methyl group onto the C base that configures the DNA code. The C bases that are thus tagged are written as mC. Some bacteria have a methyl tag attached to A bases, which are then written as mA.

In mammals, including primates, methyl group tags have the important task of inhibiting gene expression. There also appears to be an important relationship between the manner in which DNA is compressed in chromosomes and how copying RNAs will access coding sequences within it. In areas where the DNA is twisted tightly, this access appears to be hampered.

Besides the well-studied methylation activities, there are other epigenetic modifiers—for example, acetyl, ethyl, and phosphoryl and even the histones can modify the structure of chromatin and thus "gene" activation. The DNA is wrapped around a histone core, making nearly two turns per nucleosome. The nucleus contains the chromosomes of the cell. Each chromosome combines a single molecule of DNA with an equal number of proteins. Collectively, the DNA of the nucleus with its associated proteins is called chromatin. Two copies of each of four kinds of histones (H2A, H2B, H3 and H4) form the protein center, also known as the nucleosome core. A DNA strand know as histone 1 (H1) winds itself around the nucleosome and links the nucleosomes to each other.

The binding of histones to DNA depends critically on the amino acid sequence of the histone. Most of the chromosomal protein consists of copies of the 5 kinds of histones. These are basic proteins, namely positively charged arginine and lysine residues, which attach tightly to the negatively charged phosphate groups of DNA.

Chromatin also contains small amounts of a wide variety of different proteins. Most of these are transcription factors (e.g., the steroid receptors), and their association with the DNA is more transient.

Many epigenetic developmental events are still poorly understood and obscure the understanding of the manner in which specific traits are genetically pre-programmed and reliably passed on from generation to generation.

As already mentioned, with time it became increasingly clear that there is much genetic material in eukaryotes that is highly repetitive and at first seemed to lack any function. The question was: so why is it there? Most of the DNA sequences that code for a protein, rRNA, or tRNA (known as exons) are interspersed by sequences that were thought not to contribute to the heritable product. These allegedly noncoding regions are called introns and are considerably longer in mammals than exons. Genetic sequences made up of both exons and introns are also called "split genes," because the intron areas are split out from their position between the exon nucleotide sequences to join the coding exons together thus forming longer DNA sequences (Gilbert, 1978). Splicing out of the intron sequences requires precise breakage of a phosphodiester bond at exon–intron junctions. In the human genome, introns outnumber the exons by a factor of about 4 to 1. Split gene exons or coding areas often are similar to other such exon sequences within species. Such analogous "gene" families occur in human α and β globins. Members of those gene families often have similar or even identical functions that, however, can change at various developmental stages and times or in different cell types. Some sequences belonging to gene families potentially lose their function. Individual sequences that belong to gene families can be made up of both exons and introns but may lack one or two of the original exons. They may have lost their introns and are thus conjoined exon areas, resulting in a loss of function. It is this noncoding genetic material that has been called "junk DNA" and supposedly is cluttered with "pseudogenes" (noncoding DNA that does not contain any introns). While most introns didn't appear to have any functionality, it has been reported by Moore (1996) that some of the "junk" actually does code for functional RNA (see also Tycowski et al., 1994, 1996). Tycowski and collaborators discuss an actively coding sequence that is contained in introns and not exons. When researchers began looking at this picture of purportedly noncoding genetic material that by far outweighs coding DNA, it seemed odd that increasingly complicated organisms have more and more of the supposedly noncoding DNA in their genome. The paper by Moore (1996) and the discovery by Tycowski et al. (1994, 1996) that introns do code for RNAs seem to have been almost forgotten. However, recently many more scientists have realized that there are completely different mechanisms of genetic coding activity which are not yet understood.

Sakharkar et al. (2004) point out that the total length of introns and noncoding genetic DNA is significantly proportional to chromosome size. They conclude

that this size dependency implicates introns in genome design. However, in 2001 Mattick (summarized in his 2003 paper) had already stated that (loc. cit. page 930): "A number of startling observations about the extent of non-protein-coding RNA (ncRNA) transcription in higher eukaryotes and the range of genetic and epigenetic phenomena that are RNA-directed suggests that the traditional view of the structure of genetic regulatory systems in animals and plants may be incorrect. NcRNA dominates the genomic output of higher organisms and has been shown to control chromosome architecture, mRNA turnover and the developmental timing of protein expression, and may also regulate transcription and alternative splicing."

According to Mattick, noncoding RNAs (ncRNA) are very important components of cellular systems. Much of hidden genetic activity is driven by RNA control at different developmental stages. Epigenetic phenomena are directed by multipurpose transacting RNAs, which signal for DNA methylation, imprinting, transvection, position effect variegation, chromatin remodeling, and activation or repression of coding activities. It is suggested that this hitherto unrecognized control system accounts for much of the elusive phenotypic variation between individuals and species. That "junk DNA" had no function was believed to be correct until it was realized that such noncoding sequences actually exert certain important controls over genomic events. To put it differently: There is a much larger realm of genetic organization beyond the well-known coding for proteins by exons. We know now that intron sequences are actively and deliberately transcribed into RNAs that perform a wide array of unexplored functions. This means that what formerly was only seen as separator "junk DNA," there solely to delineate and separate exons from each other, is in fact very much involved in shaping the discerning characteristics of different species. This discovery might lead directly to the solution of the C-value enigma.

There is yet another term that refers to changes of the genetic material that are commonly called mutations: Indels (named for a combination of the first few letters of the words "insertion" and "deletion") are small (smaller than 400 bp) changes in DNA sequences that are suspected to cause genome size variation (Gregory, 2003). Yet another unusual term is occasionally used by some authors: "nuon" or "retronuon," which represents a discrete segment of nucleic acid (Brosius and Gould, 1992). Brosius (2003a) observes that only 1.5% of the human genome consists of exons that code for proteins. He concludes that neither mouse, chimpanzee, nor human genomes appear to have many new genes, and 38% of the mouse and 42% of the human genome are composed of retronuons. Brosius suggests that most of the mammalian genome could be derived from retroposition material. Retronuons are created when any RNA is reversely transcribed; the subsequent cDNA copies become retronuons. Brosius (2003b) observes that many evolutionary changes were generated by duplication of hereditary material that is based in RNA. He says "RNA was more than a gene: it had the dual

role of harboring genotypic and phenotypic capabilities, often in the same molecule."

Even before the human genome was completely deciphered in 2003 (Collins et al., 2004), the percentage of coding material was said to be a mere 3% (ranging to less than 2% according to some; see Wong et al., 2001), while the remaining 97% (alternatively 98%) have been assumed to be the "junk" or garbage. Thus a high percentage of the genome still has no known function. Because of the vast amount of noncoding DNA, it is difficult to pinpoint functional areas (or "genes") simply by looking at DNA sequences. Coding regions are often missed even by the most advanced computational programs. It is equally complicated to identify regulatory regions within DNA—the "switches" that turn gene expression on or off—as they are nothing but poorly defined "consensus" sequences agreed upon by researchers and computer programmers (with the help of Multiple Sequence Alignment computerized programs). One such computer program is called BLAST (Basic Local Alignment Search Tool) and is described in detail by Korf et al. (2003).

Mobile discrete DNA sequences have been found in nearly all species that have been investigated. They are known as TEs, transposable elements, or transposons. Also, there are single nucleotide polymorphisms, or SNPs ("snips"), which are minute changes in sequences of DNA that occur when single nucleotides A (adenine), T (thymine), C (cytosine), and G (guanine) within the genome sequence are slightly changed. These small changes or SNPs occur in coding and noncoding regions of the genome when a single nucleotide base, such as an A (adenine), replaces one of the other three base letters, C, G, or T. Such SNPs mostly occur in noncoding sequences and have created curiosity in researchers, as they are thought to make people vulnerable to certain diseases, for example, Alzheimer's (Shedlock et al., 2000; Kraehling and Graveley, 2004).

There is now good evidence that transposons actually contribute to the organization of cells and genetic regulation of higher organisms and that they do play an important role in epigenetic inheritance, altering genetic traits. Noncoding RNA sequences are crucially involved in these events (Mattick, 2003, 2004). As for the C-value enigma, one might want to speculate that life span, generation length, body size, cell size, and various already mentioned developmental parameters have a lot to do with genetic activities about which we have no knowledge and whose complexities we do not at all understand yet.

One of the early researchers who started to dabble in the elusive nano realm of secondary genetic molecules, namely globulins and proteins, to elucidate taxonomic and phylogenetic relationships among primates was Morris Goodman (and his collaborators). The body of his research is enormous; the reliable information about problems that are addressed in such endeavors remain to be trivial. Attempts to decipher once and for all hitherto obscure problems in mammal taxonomy and phylogeny are not likely to be conclusively resolved by

selective probing of few genetic markers or secondary genetic products such as globulins.

THE TARSIER CONUNDRUM STILL NOT SOLVED

A beautiful example of such open-ended "solutions" is documented in recent research involving the enigmatic primate genus *Tarsius*. Meireles et al. (2003) assert that noncoding DNA sequence and protein evidence support a sister grouping of tarsiers with Anthropoids in the semiorder of Haplorhini that was originally established using extant morphological soft tissue characters of the nasal area. They declare that results obtained by other researchers, who group modern tarsiers with strepsirrhines based on mtDNA and coding nuclear data, are problematic and conclude their article saying (loc. cit. pages 148–149): "While the molecular evidence is at present equivocal, evidence that does exist predicts that loci examined in the future will also support the clade Haplorhini."

Using various aligning activities (of rabbit, bushbaby, and two species of *Tarsius*) of a gamma globulin locus (L1a-γ-L1ba-γ-L1b) that mainly consists of noncoding sequences adjacent to the two alleged γ genes, they assume to obtain "a well-resolved picture of cladistic relationships among primate lineages." Application of maximum parsimony and maximum likelihood algorithms to these alignments result in the authors' observation that (loc. cit. page 151): "When the non-anthropoid γ sequences were aligned against the anthropoid γ^2 sequences, the tarsiers grouped with strepsirhines (sic), but weakly so. However, when the nonanthropoid γ sequences were aligned against the anthropoid γ^1 sequences, the tarsiers grouped very strongly with anthropoids." Further manipulating the alignment tests with PAUP MP (Maximum Parsimony) and ML (Maximum Likelihood) programs, they constructed a maximum parsimony tree of all the primates in which they squarely put genus *Tarsius* into the Anthropoid clade, thus reaffirming the Haplorhini assignment, and called their methodology a "strictly genealogical taxonomy." This is concluded with the assertion that their evaluation provides an "objective phylogenetic framework for investigating evolutionary processes …"

That these authors only used 3 representatives of the strepsirrhines, 22 catarrhines, and 8 platyrrhines versus 2 species of *Tarsius* to evaluate one protein (γ globuline, a secondary genetic product) out of virtually millions of genetic characters and projected the alignments far into the past makes the assertive statements concerning extant taxonomic relationships among these primates rather dubious.

In a book about tarsiers, Yoder (2003) addresses the same issue as she reviews the history of *Tarsius* classification according to morphological and genetic data. Yoder states (loc. cit. page 165) that in case of doubt, "Unlike morphological

data, molecular characters (i.e., DNA sequence data) and character states are obvious and not prone to subjective interpretation." She further observes: "Thus, except in cases of alignment uncertainty, subjectivity and potential investigator bias are completely removed from the process of defining characters and their state." This confident statement is followed by the introduction of SINEs as ideal phylogenetic characters (Hillis, 1999). Yoder points out that 50% of the molecular data that align tarsiers with anthropoids are based on characters of the globulin family. Yoder asserts that because these data are derived from secondary products of genetic coding activities, they are not suitable for the reconstruction of phylogenetic relationships. In a study of SINE insertions to resolve the *Tarsius* puzzle, Schmitz et al. (2001) investigated four Old World monkeys, five New World monkeys, five Prosimians, and one species of *Tarsius, (Tarsius bancanus)*. Out-group comparisons came from a *Tupaia belangeri,* a rabbit, *Oryctolagsu cuniculus,* and a guinea pig, *Cavia porcellus.* These researchers ultimately discovered that only 3 out of 118 Alu (SINE) markers supported a Haplorhine relationship of Tarsiers with Anthropoids. What the other 115 markers indicated is not explained. In yet another study Hayakasa et al. (1988) based their findings on a single mtDNA data set and found that tarsiers align with lemurs and lorises. In 1990 Hasegawa et al. confirmed these earlier conclusions, but Yang and Yoder (1999) asserted that there was a taxon sampling bias that, according to them, renders these results questionable. A paper by Kuryshev et al. (2001) is also of great interest in this context. Strangely these authors investigate *Galago, Eulemur,* and *Tarsius* loci but lump all three genera in prosimians, even though they point out later that molecular comparison of two globulins among four genera—humans versus *Galago, Eulemur,* and *Tarsius*—make tarsiers a sister group of anthropoids, thus supporting Haplorhini. They then go on to state that, if one only compares nucleotide substitutions in the four sequences, humans appear to be closer to strepsirrhines than to haplorhines, findings that even further obscure the haplorhine issue. Yoder actually closes by asserting that it is impossible to resolve this conundrum on a molecular level with any degree of certainty and proposes two possible scenarios. She ultimately says that: "Thus, as we continue to investigate tarsier's placement among the primates, we are actually holding a magnifying glass to that essential period of evolutionary history wherein the defining characteristics of the primate clade were being established" (loc. cit. pages 170–171). She considers two of the three systematic scenarios she first proposes. These three possibilities are 1) Strepsirrhini versus Haplorhini, where Haplorhini lump tarsiers with Anthropoidea, contrasting them to lemurs and lorises; 2) Prosimii versus Anthropoidea, where *Tarsius* is classified together with lemurs and lorises; and 3) Tarsiiformes versus Simiolemuriformes, where *Tarsius* is regarded to be a separate sister group to all other primates, namely lemurs, lorises, monkeys, apes, and humans.

Yoder does not consider the last possibility, as it is a rather unlikely setting that never has been widely accepted. But although Yoder hypothesizes that a crucial event must have happened long, long ago in a very brief geological interval and, even though she uses "a magnifying glass" to make visible two possible scenarios for a resolution of the *Tarsius* conundrum, the question whether *Tarsius* is a haplorhine or a prosimian remains unresolved because we simply cannot see what really happened. Even if it were possible to apply a telescope looking back at the "deepest region of primate phylogeny," we still would not be able to clearly discern crucial speciation events. Here is another example of the fact that we are not able to unambiguously decide on phylogenetic events that occurred in deep time, among rather closely related groups, by evaluating a few select, minute extant molecular particles. Considering the enormity of any genome size, these attempts are similar to pulling a few hairs out of the pelt of several mammal species, then declaring some of their differences to be character states and embarking on complicated probability methods of phylogenetically resolving their (cladistic) relationships. (Concerning such problems see also Philippe and Laurent, 1998.) The phylogenetic and taxonomic questions that researchers hope to answer with molecular data combined with highly sophisticated probability operations not only proliferate research publications but also controversies (Tavaré et al., 2002). Such issues have spawned entire volumes that are dedicated to elucidating these operations (e.g., Felsenstein, 2004; Hall, 2004). Alu repeats have been widely used to build primate phylogenies (Roy-Engel et al., 2002a). Schmitz et al. (2005) explain that they believe that retroposons are important tools for investigations of pattern and process in primate evolutionary research. These authors have used the mitochondrial cytochrome b "gene" with presence-absence analysis of SINEs to figure out strepsirrhine phylogeny and relationships (Roos et al., 2004). They confirm single origin of all Malagassy primates and "common ancestry of the Asian lorisids and lorisids in general." They also confirm monophyly of lemurids and indriids, thus asserting a common origin of diurnality in combination with cathemerality. This latter conclusion is not surprising since no solid underpinning for the term cathemerality exists as a separate biorhythmical category (see Chapter 9).

The introduction of the factor "time" into fractional genome evaluations—a contradiction in itself—will always utterly depend on mathematical computer-driven likelihood approaches such as biostatistics, Bayesian probabilities, probabilistic interference methods using Markov chain, Monte Carlo, all of which are techniques that are based in statistical mathematics and attempt to objectively analyze experimental biological data with very complex statistical models that can only be used because of the increasing refinement of computer technology. There can be no question that this kind of biology is far removed from the biological reality of breathing, living organisms.

Gu and Zhang (2004) advocate dependence on whole genome comparisons in order to successfully infer phylogenetic events and state: "With rapid growth of entire genome data, whole genome approaches such as gene content become popular for genome phylogeny inference, including the tree of life." These authors compare the genome of 35 microbes that are actually available, and even though they are complicated, they are not nearly as complex as the genomes of higher eukaryotes. We are not now able to compare even 35 eukaryotes such as primates on the genomic level.

As long as we do not have the entire genome of any primate, except for *Homo sapiens* and *Pan troglodytes* no opportunity exists to attempt such enormous tasks among primates. Such work as may become possible will probably always remain fraught with speculation and mistakes because of the enormity of these genomes (see also Müller, 2005).

So what will primate genomics provide for our understanding of life on earth? On the Internet we find the following "manifesto" (www.genomics.energy.org).

Completed in 2003, the Human Genome Project (HGP) was a 13-year project coordinated by the U.S. Department of Energy and the National Institutes of Health. During the early years of the HGP, the Wellcome Trust (U.K.) became a major partner; additional contributions came from Japan, France, Germany, China, and others. See our history page for more information.

Project goals were to

- *identify* all the approximately 20,000–25,000 genes in human DNA,
- *determine* the sequences of the 3 billion chemical base pairs that make up human DNA,
- *store* this information in databases,
- *improve* tools for data analysis,
- *transfer* related technologies to the private sector, and
- *address* the ethical, legal, and social issues (ELSI) that may arise from the project.

Though the HGP is finished, analyses of the data will continue for many years. Follow this ongoing research on our Progress page. An important feature of the HGP project was the federal government's long-standing dedication to the transfer of technology to the private sector. By licensing technologies to private companies and awarding grants for innovative research, the project catalyzed the multibillion-dollar U.S. biotechnology industry and fostered the development of new medical applications.

Right now the only other high-priority primate genome that is actually in the process of being sequenced is that of *Pan troglodytes,* the chimpanzee (The International Chimpanzee Chromosome 22 Consortium, 2004). In May 2004 it

was proudly announced that sequencing of chimpanzee chromosome 22 is almost complete (Weissenbach, 2004). Chimpanzee chromosome 22 has been found to be equivalent to human chromosome 21. When the two chromosomes were compared, nucleotide for nucleotide, it appeared that there are only 1.44% of nucleotide substitutions between the two. However, this author came to the conclusion that the comparison actually was inconclusive as far as discovering any genetic coding for phenotypic differences between the genera are concerned. However, is was determined that the "gene" FOXP2, which has been found by studies of mutations to be involved with language development, differs by two amino acids between humans and chimpanzees. What this slight difference means functionally remains elusive. Weissenbach points out that the role of the language gene was actually not discovered by comparing the two species but by intraspecific mutation studies in humans with language impairment. She goes on to conclude that we will now have to compare humans and chimpanzees with the genetic information of the two other great apes to better understand what indeed makes humans phenotypically and behaviorally so different from their close primate kin.

GENETIC EXPRESSION OF HUMAN LEARNING

Recent genetic research points in the direction of crucial differences in brain structure and function between humans and other primates (Fortna et al., 2004). In a detailed study, Li et al. (2004) verified that neuropsin, a protease that is involved in human learning and memory, is found to be much more expressed in human brain tissues than in the brain of mice. They found that only humans and great apes have an open reading frame of the neuropsin II splice form; this is not present in the lesser apes or Old World monkeys. They suggest that neuropsin II is a new protease that is of comparatively recent origin in primate evolution and became functional only about 18 million years ago and "might contribute to the progressive change of cognitive abilities during primate evolution."

A recent review of comparative primate genomics (Ernard and Pääbo, 2004) sums up what is known in the field and provide a synopsis of future possibilities. This very general **overview** fails to mention the important new insights into genomic studies that show how developmental studies are our true key to understanding what makes humans different from primates. Comparative primate genomics are still mired in the initial stages of discovery because of the lack of complete primate genomes. It will take much time, effort, funding, and international cooperation to complete other primate genomes any time soon. However, preliminary steps to improve the possibilities of primate genomics have been accomplished by the establishment of bacterial artificial chromosome (BAC) libraries for several species.

BAC, YAC, AND PAC LIBRARIES

The establishment of so called BAC libraries provides for faster and cheaper means to investigate genomic materials (Choi and Wing, 1998). Bacterial artificial chromosomes are produced in *Escherichia coli* cells where entire chromosomes or DNA fragments can be introduced into a host cell with the help of vectors. Here the guest DNA is replicated in large copy numbers. BACs are employed in attempted functional analyses of coding DNA regions (genes) and also assist in the generation of genome sequences (see also Osoewaga et al., 1998). Yeast artificial chromosomes (YACs) have also been produced, but they appear to be less reliable tools.

Finally, P1-based artificial chromosomes, known as PACs, have been frequently employed as cloning tools for mapping projects. P1 is a bacteriophage of *Escherichia coli* and other enteric bacteria. It lysogenizes its hosts as a circular, low-copy-number plasmid for functional DNA exploration. BACs and PACs are useful because they have a low rate of rearrangements and can easily be used to isolate large amounts of DNA (Venter et al., 1996).

Among BACs, YACs, and PACs, the BACs appear to be the most useful and are presently coming to dominate initial genome framework construction. At present the following primate BAC libraries are completed and available online at the website of the Children's Hospital Oakland Research Institute (CHORI; http://bacpac.chori.org/home.htm); note that the list is constantly increasing:

Apes:

Pan troglodytes, male, completed
Sumatra *Pongo pygmaeus pygmaeus,* male and female
Gorilla gorilla gorilla, male
Hylobates concolor, in production
There is also a Fosmid library of *Pan troglodytes* available.

Old World Monkeys:

Papio anubis, male
Macaca mulatta, male
Cercopithecus aethiops
Macaca fuscata
Colobus guereza, in production
Rhinopithecus biety (Xu et al., 2004)

New World Monkeys:

Callicebus moloch
Saimiri species, in production
Aotus trivirgatus, in production
Callithrix jacchus, male

Prosimians:

Lemur catta
Galago (Otolemur) garnetti
Microcebus murinus, female
Eulemur macaco macaco, female, in production

Also in production are BAC libraries of *Tarsius bancanus, T. spectrum,* and *T. syrichta*

GENES CONTROLLING HUMAN BEHAVIOR

As we have already seen, the completion of the human genome has resulted in many attempts to identify genes that allegedly are related to, responsible for, or productive of human behaviors, such as the gene for female infidelity, the God gene, the gene responsible for nicotine addiction, and on and on. All such gene searches that are based on behavioral traits do not rest on a very solid scientific footing. Even when such studies are based on twin research, as for example the study of the vasopressin receptor gene (AVPR1A) and its involvement with coding for female infidelity (reported by Cherkas et al., 2004), the results are rather ambiguous. It was established that infidelity and its ramifications, being computed by the number of different sexual partners, are characteristics which are generated by some unspecified genetic influence. Naturally the two factors are statistically strongly linked. The authors admit that they were not successful when trying to pin down the behavior to a specific coding site in the human genome, although they conducted a genome-wide scan that did suggest some "nonsignificant" linkage areas on chromosomes 3, 7, and 20. The authors conclude that they failed to reliably connect the two interrelated behaviors with the genetic locus that has been implicated in sexual behavior of other female mammals. Despite this disappointing result, what was discovered provides support for evolutionary theories of human sexual behavior and that future research involving the vasopressin receptor gene is warranted.

Another twin study that investigated human malfunction and disease did produce reliable results which, in contrast to the previously mentioned twin study, documented that human behavior cannot easily be correlated with genetic expression. Kuwata et al. (2004) examined the very troubling issue of birth defects in children who are conceived through assisted reproductive technology (ART). They found that dichorionic twins who were conceived by artificial insemination have a considerably higher incident of severe birth defects than dichorionic twins who were conceived naturally. These results support the recognition that ART potentially has severe epigenetic effects during early stages of development; more than 6% of these twins had severe birth defects. One such

affliction is Prader-Willi syndrome, which is caused by a chromosomal aberration. In 60% to 70% of the individuals diagnosed with the syndrome, a deletion occurs on chromosome 15q11–13 (near the centromere) that is always inherited from the father. In 25% to 30% of these individuals the cause of the syndrome is that the child has two chromosomes 15 from the mother and none from the father. In less than 5%, there is an unbalanced translocation. In a small number of cases, less than 2%, there is an imprinting mutation (loss of function) on chromosome 15q11–q13. Infants with Prader-Willi syndrome display many symptoms of a disturbance in the hypothalamus; it is believed that some transmitter substance in the central nervous system is either absent or malfunctioning (details excerpted from the database of the Swedish National Board of Health and Welfare on rare diseases). ART has led the way for increased research focusing on genetic imprinting events.

VIEW INTO THE FUTURE OF GENOMICS

Despite the multitude of genetic research projects that now have the word "genome" in their title, it is apparent that most of them still reside within the realm of molecular genetics, not genomics. So far, true genomics has produced a truly impressive volume of insights and knowledge that come along with the sequencing of the human genome. If one looks at pictures of all human chromosomes and the identified coding sites of disease potential and the coding of physical characteristics such as hair or eye color, the impression is absolutely startling. The coding areas suspected to be related to various disorders by far outnumber those that are known to code for normal traits. (This can be found at the Human Genome website (doegenomes.org) under Gene Gateway—Exploring Genes and Genetic Disorders.)

It is the still unexplained world of epigenetics that should be the focus of our attention. The genetic machinery that is capable of creating perfect copies of living things in a never-ending succession will only be deciphered if we look into gene expression during development. In future large-scale investigations of the entire genome, the focus should be on the functional expression of the genetic code, thus generating yet another field of modern biological science known as functional and developmental genomics.

A few hints of such approaches come with the insight that the location of chromatin in the cell nucleus regulates gene expression. Coding activation has been observed in less euchromatic chromosome regions, and tightly condensed heterochromatin seems to be responsible for transcriptional repression.

Jernvall and Jung (2000) and Kangas et al. (2004) documented how dental characters in Tabby mice depend on quantitative changes of intercellular signaling. They were able to document developmentally, by changing ectodysplasin

levels in three mouse strains, that dental characters appear to develop jointly, not independently from each other as has been believed.

Galbraith (2003) reviews methodologies that are available to map global gene expression. The methodologies that are discussed will make it possible to observe and describe on the cellular level the process of normal development and gene regulation. In the future we will presumably gain the most important insights about the question "what makes humans different from all the other primates" by investigating the developmental activities of neural regulatory systems in the nervous system and brain.

Genomes, namely the entire genetic signaling mechanism of eukaryotic organisms, are vast. Attempts to use partial comparisons of DNA coding sequences remain dubious. Selectively comparing partial genomes could be likened to an attempt to compare several feature movies to each other based on a few segments of each. This is simply not possible.

Looking at developmental genetics it becomes increasingly obvious that adaptations happen in the nano realm of information exchange (Jernvall and Jung, 2000). The correlation between genetic changes on the nano level and their ultimate manifestation in morphology and behavior and vice versa are still barely understood. It appears that the genetic code is not the ultimate solution for our in-depth understanding of ontogenetic and evolutionary development (Weiss and Buchanan, 2005). It is now obvious that crucial events take place at the micro-RNA level (Roy-Engel, 2002b). Only if we can bring together all the new information about the functionality of "junk DNA" with epigenetic developmental events and the role of snRNAs (small nuclear RNA molecules) or mystery RNAs will a real understanding of genomics emerge that reveals what makes living things tick.

TRANSPOSABLE ELEMENTS AND NUMTS

Transposable DNA and mtDNA elements abound in eukaryotes. These components were discovered long ago (McClintock, 1952) but only recently entered the genomics research scene with a vengeance, mainly because of the ready availability of comparatively inexpensive methods for sequencing DNA. Transposable elements play a very important, varied, and still barely understood role in the evolution of genomes (Kidwell, 2005).

It is obvious that today's minute glimpses into the evolutionary process are both multifaceted and incredibly complex (Gregory, 2005b). Transposons are many and varied, and even though chromosomal changes have been implicated in the process of genome evolution (Bailey et al., 2004; Cheng et al., 2005) it becomes increasingly clear that much crucial evolutionary change involves extrachromosomal "epigenetic" events. There are actually various transposable

elements that also include retroviruses (Kazazian, 2004; Mayer and Meese, 2005; Medstrand et al., 2005). However, we will focus here on nuclear mitochondrial pseudogenes, as they prominently influence new insights and problems surrounding primate genomics.

Mitochondrial DNA sequence variation has been widely used to explore evolutionary relationships, and it even has been suggested that mtDNA data could be used as "barcodes" to objectively classify and label different taxa (Herbert et al., 2003). Even so, this suggestion has not been widely accepted because of several problems. One of these problems arises with the realization that mobile extranuclear mtDNA segments do translocate into nuclear DNA and can potentially be mistaken for genuine organellar mtDNA (Thalmann et al., 2004), causing incorrect evaluations. Such translocated mtDNA components within the nuclear DNA of many organisms are now very popular study objects and have been named "Numts" for nuclear mitochondrial pseudogenes (Lopez et al., 1994). Numts lose their function when they become embedded in the nuclear DNA (Bensasson et al., 2001).

Although numts are generally more abundant in plants than in metazoa, they are found in great numbers among birds and mammals. The number of numts in different genomes varies dramatically and without any comprehensible pattern (Richly and Leister, 2004). For example, there are no or very few numts found in *Anopheles* (a mosquito), *Plasmodium* (a protozoal parasite that causes malaria), *Drosophila* (the fruit fly), and *Fugu* (the blow fish), while *Arabidopsis* (mouse-ear cress), *Oryza sativa* (rice), and *Homo sapiens* have more than 500 numts embedded in their nuclear DNA. At present both the function and the great diversity among numts and noncoding nuclear DNA and the obvious lack of correlation between the two are not well understood (Richly and Leister, 2004).

Another problem with numts is the question of the mode of mtDNA inheritance, an issue that is still hotly debated and unresolved: Is mtDNA purely maternally inherited or is there paternal participation? Although it has been proposed and generally accepted by professionals that the paternal mitochondria are eliminated after they enter the oocyte during fertilization, there are reports of paternal mtDNA inheritance (Schwartz and Vissing, 2002; Hagelberg, 2003; Rokas et al., 2003; see also discussion of mtDNA in Chapter 13).

The assumption about paternal mtDNA elimination is rooted in the almost universal presence in cells of the protein ubiquitin that is involved in the degradation of certain proteins having a regulatory role: ubiquitin serves as a tag that marks proteins for elimination, a process that is executed by a proteasome (Sutovsky et al., 2000; Cummins, 2001; Eyre-Walker and Awadalla, 2001). However, more recently it has been observed that "Sperm mtDNA, which is released from degenerating mitochondria after fertilization, could be an important source of nuclear mtDNA pseudogenes." (Woischnik and Moraes, 2002, loc. cit.

page 892). This means that numts could be made up of paternal mtDNA. No matter what the solution of this enigma may be, numts have recently been discussed more and more widely (Bensasson et al., 2003).

One of the recent groups of focus in numt research are the great apes, specifically genus *Gorilla*. The question that has been addressed is the puzzle about whether the two geographically distinctly separated gorilla populations—western *G. gorilla* and eastern *G. beringei*—should have species or subspecies status. This is of crucial importance because: "Methods of investigation of genome expression now allow identification of genes whose activity and/or regulation serve as source of adaptation for survival and reproduction. This ushers in a new era of investigation in biology and provides the possibility of evaluating evolution of life history strategies in new ways" (Ryder, 2003, loc. cit. page 239). This statement appears to be a tall order, as we shall see. Noninvasive samples of mtDNA from both gorilla populations have been investigated with the help of polymerase chain reaction (PCR) technology. The results have been confusing and inconclusive (Clifford et al., 2003; Jensen-Seaman et al., 2003). First, it appears that the samples of different gorilla populations have been incongruent in available numbers, thus biasing the results and making conclusive comparisons improbable. Second, the use of PCR to evaluate "noninvasive samples" (such as feces and hairs) of a target mtDNA segment poses problems. The evaluation resulted in more than the one expected unique sequence in some individuals, presumably making the targeted study invalid.

The unexpected and confounding multiplicity of resulting sequences from individual gorillas was blamed on the presence of numts. Even further attempts to distinguish authentic mtDNA segments from numts failed, and thus it appears that the "noninvasive" samples are inadequate for such studies (Vigilant et al., 2004). A new study and revision of the mtDNA diversity among gorillas now once again claims that there are two genetically highly divergent groups that coincide with their geographical distribution (Jensen-Seaman et al., 2004). Whether this new and detailed evaluation of the old and some additional new material is really the last word concerning the genetic diversity of gorillas remains to be seen: it still stands on a rather shaky foundation. This gorilla problem shows how evaluation of selected genomic segments is likely to be misleading.

Another debate is centered around the ostensible genetic similarities and obvious morphological and behavioral dissimilarities that separate chimpanzees from humans. The literature about this issue is vast and cannot possible be exhaustively covered here. However, transposable elements (van de Lagemaat et al., 2005), numts (Richetti et al., 2004), recombination hotspots (Jeffreys and Neumann, 2005; Serre et al., 2005), Alu recombination (Sen et al., 2006), and even cultural elements (Whiten, 2005) are all discussed by numerous research groups. These groups of researchers also appear to be surprisingly unconnected.

A possible consensus about the question of what really makes humans human still seems to be far removed in the future.

While some have arrived at the conclusion that humans are 99.4% identical with chimpanzees based on a "comprehensive, genomewide genetic analysis of the place of humans in evolution" (Wildman et al., 2003, loc. cit. page 7181), others increasingly find significant differences (Ebersberger and Meyer, 2005) adding up to 5% (Britten, 2002). Wildman and colleagues even suggest that humans and chimpanzees are genetically so similar that they not only should be classified in superfamily Cercopithecoidea but taxonomically united in genus *Homo: Homo sapiens* with *H. troglodytes* and *H. paniscus,* a decision that is not likely to be widely accepted. For instance, such a ranking would imply that hybrids between the three species should be possible. There is much confusion surrounding this *Homo*/*Pan* similarity enigma, and it is obvious that much of the problem is based in the fact that most studies concentrate on fractions of the genome (Ptak et al., 2005), and that often these fractions are incongruent.

What we can conclude is that much of genome evolution actually is not only based on the transfer of cytoplasmatic, extranuclear genetic material that is either added into the nuclear DNA (Richetti et al., 2004) or sometimes removed (van de Lagemaat et al., 2005). Much of evolutionary genome change is also caused by the distinct patterns of cytoplasmatic genome heritability (Korpelainen, 2004).

OUTLOOK AND REFLECTION

One crucially important new venture in the world of genomics is the development of the field of Bioinformatics which aims to consolidate, order, and coordinate an awe-inspiring output of new information. Bioinformatics has become a huge world of business enterprises that combine biology with computer technology and offer bioinformatics products and services. These enterprising adventures are predominantly driven by pharmaceutical interests. The possibilities are truly overwhelming. To get some insight into Bioinformatics one should consult "Bioinformatics for Dummies" (Claverie and Notredam, 2003) and I am not kidding.

We have been told that we are 2% human (and we are talking about 2% of not much more than 2% of coding sequences!) and 98% chimpanzee or whatever the 98% might be (Marks, 2003). Obviously just 2% of the complicated genetic material superimposed on 98% of an ape is enough to make us radically different and truly 100% human. However, there are new studies investigating these differences that come to other conclusions (Mikkelsen et al., 2005). Which means that we have to look much deeper into the world of genomics to gain understanding of what being human really means.

Somehow our closeness with the chimps is not surprising. Even though we can speak and listen, write and read, we are slow learners. Children don't learn much from their elders. Every one of us has to make the same mistakes they did, over and over again. Historians and politicians appear to be unable to learn from history. We all have to suffer the consequences of these mistakes. Some humans are unspeakably cruel. Many of us are credulous, and well, we are really not very smart. Even though we believe that we are more intelligent than any other creature on this planet, if the truth were known: we are stuck in our primate nature and not much better than any other living beings.

The most vexing question remains whether the information that we today call "Primate Genomics" really covers the science about primate genomes? The answer is no, not yet. Even if we read it in the news that the human and chimpanzee genomes are completed, they are still not perfected, and the field of Primate Genomics will have to steadily grow with the increasing number of more or less completed genomes of all our close relatives, the primates.

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Chapter 15

Conclusions with a Glance at the Future

Primates are the most varied group of extant mammals. The extended array of primate adaptations ranges from the tiny dwarf mouse lemur (genus *Microcebus*), which weighs about 30 grams, to the enormous males of the genus *Gorilla* that weigh up to 170 kilograms. Between these two extremes are primates of all shapes and sizes: We count about 240 species in 64 genera. The Primate order also contains the most advanced of extant mammals, *Homo sapiens*. Yet almost half of the nonhuman primates are on the endangered species list.

Research on primates has increased at a rapid pace during the last decades. All primatologists, however specialized, need to have well-rounded, deep general and basic knowledge about the biology of their study subjects.

Primatology has become a cutting-edge science as humans eagerly pursue insights into human biology, behavior, genetics, and evolution by way of studying our nearest relatives.

Yet humankind is unable to stem the overpowering impact of human population growth. We lag in understanding human nature. We know little about the biology of selfishness, love, violence, sex, hatred, parenthood, teaching and learning, religion, and politics. We desperately need to learn more about our own biology if ever we are to make ours a better world. The path to reach this future goal partly proceeds through the study of primates.

Yet, our study subjects, our closest biological relatives, are disappearing at an alarmingly rapid pace, just as those who study them multiply faster and faster. Human expansion speedily devastates vast areas of primate habitat, and the primates are being destroyed with it. As they vanish so do our opportunities to learn about them. We must promote primate conservation and work toward zero human population growth as simultaneous first priorities.

Primate anatomy, best studied with the help of newly dead specimens, is already crippled by the lack of suitable material. Osteology, so important for comparative study of fossils, must rely today on museum collections established long ago. Comprehensive primate osteology collections can no longer be assembled. Yet fossils continue to be discovered and require comparison with living primates if we are to grasp their meaning.

The intricacies of primate placentation, which are believed important to unravel taxonomic and phylogenetic relationships, are poorly understood. Placentation cannot be studied adequately unless successive series of intrauterine stages are available. For such investigations pregnant mother primates together with their unborn offspring must be sacrificed. Such procedures can no longer be condoned with primates. Questions about the taxonomic and evolutionary relationship between the rare prosimian genus *Tarsius* and anthropoids, based on the mode of placentation, remain shrouded in mystery. Tarsiers are obviously an ancient group of primates. Genus *Tarsius* is not only endangered in its native habitat, but tarsiers can no longer readily be brought into captivity. When in captivity, tarsiers have always been extraordinarily difficult to maintain, and virtually impossible to propagate. Consequently, the intriguing tarsier question will probably never be answered. It will remain the focus of resourceful speculation, as certain aspects of tarsier biology can no longer be explored.

The exciting new fields of molecular primatology and primate genomics, however, seem to be an approach with a bright and unrestricted future. Molecular studies can be performed with minute tissue samples. Many different molecular configurations are under study, and the methodologies vary widely from laboratory to laboratory. At present it is almost impossible to integrate the various incompatible, sometimes contradictory, results into a comprehensive analysis. Misinterpretations abound, as do the flashy promises and often useless theories that spring from them. In the future molecular primatology should be taken over by primatologists. Biochemists or molecular biologists, however skilled at the laboratory bench, often understand little how primate biology and evolution work.

Another new trend in primate biology has emerged since computers and refined data collection technologies have appeared. Enormous databases have now been assembled from which elaborate and often incomprehensible statistical evaluations have sprung. These analyses are all too often performed by professional statisticians, not primatologists themselves; unfortunately, such studies have rarely provided useful insights into primate biology.

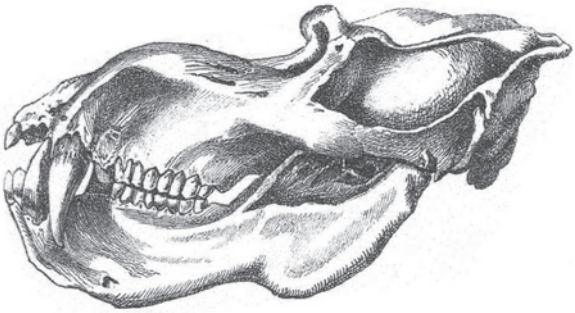
Students of primates must remember that high technological sophistication alone does not generate outstanding science. More usually good, old-fashioned common sense and deep understanding of the subject are the roots of exciting new insights.

I hope that this survey of living primates and their anatomy will prove a helpful tool for learning the basic facts of primate biology on which to build.

Humans do not have the competence to see into the future. It is therefore not possible to accurately foresee the destination of humans, primates, and primatology in years ahead.

At present the survival of most primate species seems improbable. Humans are fighting each other in warfare and hatred. We can only hope that humans may gain the wisdom to protect their intriguing relatives from extinction. But it sadly appears that humans are the most dangerous of predators and the most invincible of extant apes. This world does not need humanity, but humankind needs this world to be in equilibrium.

We must hope that members of the primate species *Homo sapiens* will be able to come to their senses in good time to save this beautiful world and all the primates in it.



Carl Vogt, Mandrillus skull, 1867.

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