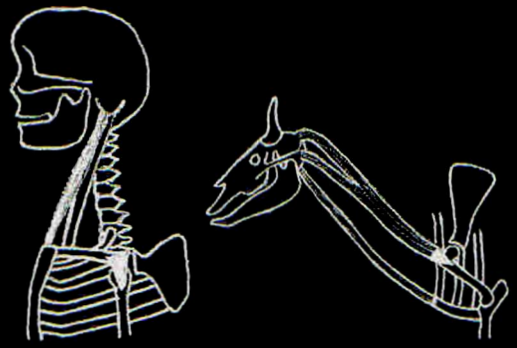




Muscular System of Vertebrates

Seth M. Kisia
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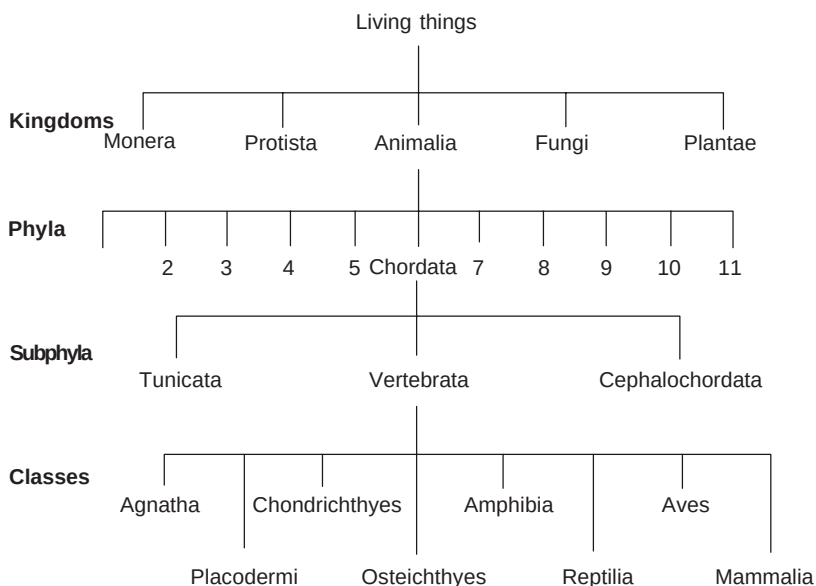
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This text is by no means a complete reference material on vertebrate musculature. The text has captured salient topics relevant to the understanding of vertebrate musculature including evolution and development of various muscles, the various types present and their morphological organization and physiology. This book should serve as a useful reference material for students of zoology, agriculture, ecology and other related fields. The book can also serve as a reference to veterinary and medical students as well as scientists who wish to know the different muscles of vertebrates and their origin.

1

General Introduction to Vertebrate Muscular System

Vertebrates are quite diverse and, together with arthropods, are the most conspicuous animals on land, water and air. The subphylum Vertebrata belongs to the phylum Chordata and its classification in relation to other forms of life is shown below:



The two other subphyla of chordates (collectively known as protochordates) are Tunicata, comprising about 2,000 species (mainly sessile sea squirts) and Cephalochordata (Gr. *kephale*

head, *chorde* cord) with 45 species, most of which are amphioxus (Gr. *amphi* both, *oxys* sharp). Chordates possess a notochord at least at some point in their life cycle, a neural tube and pharyngeal pouches that often open to the outside as slits. The notochord is a hydroskeleton composed of turgid fluid-filled cells surrounded by a tough connective tissue sheath. This structure still persists in adult hagfishes and lampreys and in most early stages of vertebrates. As development proceeds in vertebrates, vertebral bodies replace this structure so that it is greatly reduced or disappears in adult life. In the absence of other forms of skeleton, the notochord prevents the shortening and compression of the body when muscles contract while allowing side to side bending of the body.

Vertebrates include the extinct class Placodermi and the extant classes Agnatha, Chondrichthyes, Osteichthyes (all fishes), Amphibia (amphibians), Reptilia (reptiles), Aves (birds), and Mammalia (mammals). The subphylum Vertebrata comprises over 40,000 species, of which about half are fish. This number is likely to increase as more species of vertebrates (especially fish) continue to be discovered. Many species of vertebrates have become extinct over the 500 million years of vertebrate evolution. Their fossil records are, however, useful in drawing the evolutionary tree, their possible structure, and relationships among various vertebrates.

Vertebrates live in different environments on the earth (only lacking in the interior of Antarctica, Greenland, and the North Polar ice pack) and have evolved different modes of locomotion and feeding habits. They range in size from minute fishes (about 1.5 g) to elephants (4-5 tons) and baleen whales (up to 150 tons). As they display different forms of movement, their skeletal and muscular systems are bound to show some differences.

The outstanding features of vertebrates are the presence of a vertebral column (lacking in hagfishes), a head which has a differentiated tubular brain and three pairs of sense organs (nasal, optic, and otic) and a closed circulatory system with red blood cells that contain the oxygen carrying pigment hemoglobin. The vertebral column was not present in the first vertebrates on earth, which probably had only a notochord. In extant vertebrates, the notochord is present only during the

embryonic stages as its role is taken over by the vertebrae (vertebral bodies specifically) during most of the life of the vertebrate.

THE MUSCULAR SYSTEM

Muscles, the primary (main) effector organs of vertebrates, form a third to a half of the body weight of the group. The passive part of the locomotor apparatus (skeletal system) and the active part (muscular system) have a close functional interrelationship. Muscles perform their functions together with their accessory structures which include fasciae, tendon sheaths and bursae. These accessory structures support the function of muscles and their tendons.

Muscles have a nerve supply that contains motor, sensory and autonomic fibers. Nerves are vital for muscle development, integrity, and function. Motor nerves carry stimuli for contraction of muscle and make contact with muscle fibers at the motor end plates. Sensory fibers originate on tendon sheets and the intrafusal fibers of muscle spindles and propagate impulses to the central nervous system. Autonomic fibers originate from the central nervous system and innervate blood vessels thus regulating blood supply to muscle. Mammals have evolved encapsulated nerve endings in their tendons known as Golgi tendon organs. These mechanoreceptors are very sensitive to muscle contraction which could result from passive stretch of the tendon or isometric contraction of the muscle.

The various functions performed by muscles depend on their origin, insertion and of course their fibers in relation to the fulcrum of skeletal parts being moved. The function of nonmuscular elements of the musculoskeletal system such as the elastic element enhance performance (increase the work output) in muscle-powered accelerations, as was observed in jumping frogs (Roberts and Marsh, 2003). Elastic elements uncouple muscle fiber, shortening velocity, to allow the fibers to operate at slower shortening velocities and higher force out-

puts. The number of muscles present depends on the vertebrates and the complexity of movement; for example, the human body has over 600 skeletal muscles, most of which are paired with just a few unpaired. Evolution of the muscular system has enabled vertebrates to adapt to a more active form of life compared to some lower forms that have relied mainly on the beating of cilia and flagella for locomotion. The muscular system is also responsible for the production of body heat and maintenance of posture. To achieve the active life they live, vertebrates have evolved three kinds of muscles—smooth, skeletal, and cardiac—along with modified muscle structures, such as the conducting tissue of the heart and the electric organs found in some fish. Skeletal muscle and normal weight-bearing activity are necessary for normal skeletal integrity (Alzghoul et al., 2004).

Smooth muscles are the simplest and were the earliest of the three types to evolve. This muscle type is under the control of the autonomic (involuntary) nervous system. Smooth muscles tend not to fatigue and their contractions are slow and sustained. The unitary (visceral) smooth muscle contracts slowly and spontaneously and is usually initiated by the stretching of the muscle fibers. These contractions are myogenic but their rate and force are modulated by nerves. Such fibers are found in the wall of the gastrointestinal tract, the uterus and the urinary ducts. The multiunit smooth muscles contract only when stimulated by a nerve (neurogenic) or a hormone, resulting in contraction of many fibers slowly and simultaneously. Multiunit fibers are found in the iris of the eye, walls of many blood vessels and wall of the sperm ducts. The proteins actin, myosin, and tropomyosin are present as myofibrils but are not in regular patterns as is the case in striated muscles (cardiac and skeletal) in which myofilaments overlap and are arranged to form the striated appearance of the fibers.

The bulk of vertebrate muscle is skeletal and almost exclusively attached to the skeleton and involved in movement of the skeleton and the individual in general. These movements are voluntary and under the control of the somatic nervous system, although several muscle contractions needed for each activity are controlled by the nervous system subconsciously.

Each skeletal muscle fiber is a syncytium (Gr. *syn* together, *kytos* hollow cell or vessel) containing hundreds of nuclei that are the result of end-to-end fusion of many myoblasts during embryonic development. The vertebrate skeletal muscle system can attain efficiencies (conversion of chemical bond energy held in carbohydrates, fats, and proteins into mechanical work) of about 25% (Hill, 1950).

Cardiac muscle is found in the heart of vertebrates and combines the characteristics of both smooth and skeletal muscles. Cardiac muscle contractions are myogenic and involuntary. These contractions have greater force and speed than smooth muscles due to the arrangement of myofilaments in cardiac muscle fibers that maximizes their overlap. Contraction of any part of the cardiac muscle is almost simultaneous and proceeds from one end to the other, pumping blood out of each chamber. This synchrony is due to the presence of cardiac muscle fibers that communicate with each other through gap junctions. Cardiac muscle does not fatigue.

Modified muscle tissue includes the conducting tissue (system) of the heart, the muscle spindle, and the electric organs of some fish. The conduction tissue of the heart is modified cardiac muscle tissue and consists of the sinoatrial node (pacemaker), atrioventricular node, atrioventricular bundle, and Purkinje fibers. It is highly specialized structurally and functionally. It does not contract but is capable of generation or rapid conduction of an action potential through the heart. The action potential originates at the sinoatrial node. The autonomic nerve fibers supply the node and thus control the myogenic rhythm of the cardiac muscle. Muscle spindles are sensory organs found within the belly of vertebrate muscles with the exception of fish and are able to detect changes in tension generated by the myofibers that surround the organs. Electric organs are found in about 500 species of fish. The energy produced by these organs is utilized to produce, store, and discharge electricity. The rays of the genus *Torpedo* and several tropical freshwater teleosts such as the electric eel (*Electrophorus*) and the electric catfish (*Melapterurus*) can produce a heavy electric shock (about 500 volts).

Muscle Contraction

Skeletal muscles, which extend across one or several joints, mostly act in groups rather than singly. The normal movements seen in vertebrates are brought about by the coordinated action of several muscles (synergistic action). When some muscles in the group contract, others relax and vice versa (in an antagonistic manner), thus bringing about flexion and extension as is seen in **isotonic** (Gr. *isos* equal, *tonos* strain) contraction. The net effect of the contraction depends on the number of muscle fibers activated at any given time, which is controlled by the nervous system. If many motor units are activated, the contraction will be strong and rapid compared to weaker contractions that result when fewer units are stimulated. **Isometric** (Gr. *metron* measure) contractions normally result in little or no movement as the muscle does not shorten (remains fixed at points of origin and insertion by other forces) though tension builds in it. Muscles that contract isometrically are important in supporting an animal in its normal posture or in holding something in a fixed position.

Tonic and Phasic Muscles

Due to variation in their structural, biochemical, and physiological properties, different skeletal muscle fiber types are capable of performing tonic and phasic contractions. **Tonic** muscle fibers contract very slowly and show graded response, dependent on the frequency of nerve stimulation. These fibers are not normally involved in locomotor movements but in maintenance of posture as they are capable of sustaining isometric tension economically and do not fatigue easily. Each muscle fiber in tonic muscles is supplied by several motor end plates.

Most vertebrate muscle fibers are phasic and include the **slow oxidative**, **fast glycolytic**, and **fast oxidative**. Each phasic muscle fiber in a **motor unit**, which consists of a motor neuron and muscle fibers to which it attaches, has a single motor end plate. Contraction of a motor unit or individual phasic fibers is not graded. Once a certain threshold is reached, contraction occurs. The force generated by muscle contraction in phasic fibers

depends on the number of motor units stimulated. Slow oxidative (red) fibers, which contract about five times slower than the fast (white) fibers (but not as slowly as the tonic muscle fibers) are important in maintaining posture (isometric tension) and carrying out slow repetitive movements. They derive their energy from oxidative metabolism and thus cannot contract faster than the rate at which oxygen is supplied to them. The fast glycolytic (white) muscle fibers contract rapidly but for a short time and are adapted for high power output. They have a low thermodynamic efficiency for producing work as their energy is derived from anaerobic glycolysis, which does not require oxygen and leads to accumulation of lactic acid. Since they fatigue rapidly, most of the replenishment of their energy supplies takes place after exercise has ceased. Such fibers are recruited during bursts of activity. The intermediate or fast oxidative (pink) fibers have properties intermediate between those of the fast and slow muscle fibers. Some of these fibers have a lower intrinsic rate of contraction and a higher volume density of mitochondria than the fast glycolytic fibers. Intermediate fibers are adapted to fairly rapid movements of a repetitive nature. Normally, the slow fibers are recruited first, followed by the fast fibers as activity increases. The proportion of these fibers in different muscles and body regions depends on the activities of the different vertebrates and the roles different body regions play in movement.

Muscle contraction is brought about by an action potential initiated on the membrane of a muscle fiber by a nerve impulse. This sets in motion a number of biochemical changes that are described by the sliding filament theory of muscular contraction proposed independently by Huxley and Hanson (1954) and Huxley and Niedergerke (1954). The sliding motion is brought about by cross bridges that project from the thick (myosin) filaments which either pull or push the thin (actin) filaments, which results in the sliding of the thick and thin filaments over each other. The basic mechanism of contraction has adapted to different types of movement in the animal kingdom, thus bringing about the desired type of movement.

Development and Evolution of the Muscular System

Although muscle tissue originates from mesodermal mesenchyme, the muscles of the iris develop from the same ectoderm that gives rise to the iris and the retina. Most striated somatic (Gr. *somatikos* bodily) muscles form muscles of the “outer tube” of the body and develop directly or indirectly from the embryonic somites. They are innervated by somatic motor neurons and are associated with the adjustment of the animal to its external environment. Visceral muscles, more deeply located than somatic muscles, are associated with the “visceral system” and develop from the splanchnic layer of the lateral plate and contribute to the smooth muscle present in the walls of the visceral organs such as the digestive and urinary systems, and in blood vessels and the cardiac muscle of the heart wall. Visceral muscles are innervated by visceral motor fibers. The visceral structures of the more caudal segments have retained smooth muscle but in the pharyngeal region, important in early vertebrates for food gathering and breathing, striated musculature was retained in some instances. In teleosts, for example, striated musculature continues far back along the gut to the esophagus or even to the anterior of the stomach.

Evolution of the muscular system was accompanied by increased power, speed, and diversity in vertebrate movements. The mode of movement brought about by cilia, flagella and smooth muscle in lower forms of life became more complex with the evolution of skeletal muscles. These changes were accompanied by changes in the skeletal system, which became more rigid and complex to meet the demands of different modes of life seen in vertebrates.

In constructing the evolution of the muscular system in vertebrates, the authors have relied heavily on the skeletal system whose fossil record, though not complete, is important in reconstituting possible skeletal and related muscular changes and movement. Some fossil bones have muscle remnants useful in reconstructing muscle migration, fusion, splitting, function or loss. Position and relationships are important in understanding muscles of similar origin and this is demonstrated in muscles within vertebrate classes, orders, and families as discussed in Chapter 5.

Fish Muscular System

The muscular system forms a large percentage of fish body weight. The proportion is higher than that of other vertebrates, reaching more than 50% of body weight in some species. Fish, which form about half the number of vertebrate species, show extreme diversity in body weight ranging from about 1.5 g to several tons. Axial musculature shows a high degree of segmentation due to nonfusion of myomeres and constitutes most fish musculature. It provides the propulsive forces needed for movement as the appendicular skeleton is not as developed as in other vertebrates. Fish swim by lateral flexion of the spine with fins serving to stabilize and steer the body.

CLASSES OF VERTEBRATES

Although they represent only a small percentage of all animals on earth, vertebrates dominate their environment relative to other animals due to their size and versatility, which has been considerably shaped by their musculoskeletal system. Several vertebrates have become extinct in the course of their evolution and this has changed diversity of life on earth as the extinction of certain dominant groups has been followed by emergence or dominance of life on earth by previously less diverse species. The fossil record of vertebrates is extensive as bone is resistant to decay. Such a record has assisted considerably in the reconstruction of the muscular system and movement of vertebrates through evolution as mentioned above, the earliest vertebrates (now extinct) lacked jaws, as is the case with living hagfish and lampreys, and date back to 500 million years ago. Jawed vertebrates appeared about 100 million years later. Emergence of vertebrates on earth, commencing with jawless fishes, was followed by these groups in order of time: jawed fishes (placoderms, chondrichthyans, and osteichthyans), amphibians, reptiles, birds, and mammals.

Jawless Fishes (Class Agnatha)

The first vertebrates were agnathans (Gr. *a* without, *gnathos* jaw) and included two groups of jawless fishes—the extinct bony **ostracoderms** and the living boneless **cyclostomes** (Fig. 1.1). Ostracoderms are the oldest known vertebrates and lived during the Ordovician period, as shown in the geological time scale in Table 1.1. Most of them possessed armored bodies that were dorsoventrally compressed and lacked appendages and flourished up to the Devonian period before they became extinct, represented at present only by cyclostomes (lampreys and hagfishes). Cyclostomes are superficially slimy and have slender bodies (eel-like), large gill pouches with small round external openings, and lack paired fins. They lack jaws and have round mouths used for sucking blood and other tissues from other living fish or eating flesh from dead fish. They have lost the capacity to form bone in skin or elsewhere in the body, which is characteristic of the early agnathans. Although cyclostomes have no recognizable vertebral column, some have rudimentary vertebrae and retain a prominent notochord throughout life. The muscular system of cyclostomes is simpler than that of other vertebrates. It lacks a horizontal (lateral) septum that divides the axial musculature into epaxial and hypaxial divisions. Since their visceral skeleton is constructed into one unit, cyclostomes lack appendicular muscles. The group seems to have separated from the main line of vertebrate evolution about 400 million years ago.

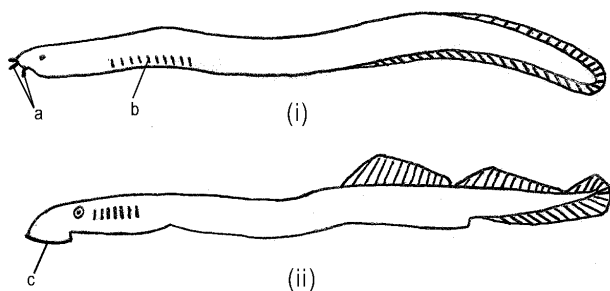


Fig. 1.1 Diagram of living cyclostomes: (i) hagfish and (ii) lamprey. (a) tentacles, (b) gill slits, and (c) circular mouth. These jawless fishes, which lack paired fins and the girdles that support them, were more abundant in the past than are today.

Jawed Fishes (Gnathostomes)

The jaws evolved from the first (mandibular) arch. The presence of jaws led to diversified feeding habits, which was supported by a more complex and efficient swimming system. In jawed fishes, the musculature is more advanced but less complex than in tetrapods. The horizontal septum divides axial muscles into epaxial and hypaxial portions. The paired fins might have evolved from flaps of flesh associated with lateral spines. Appendicular muscles evolved with the fins into extensors or levators (abductors) dorsally which move fins upward or forward and flexors or depressors (adductors) ventrally which move fins downward and backward. Such changes were accompanied by great adaptive radiation of fishes which occurred during the Devonian period.

Table 1.1 Geological time scale showing the order of events in vertebrate evolution

Eon	Era	Period	Time in years (10^6)	Events in Vertebrate Evolution
Hadean			4,500	
Archean			3,800	
Proterozoic			2,500	
Phanerozoic			600	
	Paleozoic	Cambrian	600	
		Ordovician	500	Jawless fishes. Mass extinction late in the period.
		Silurian	440	Diversification of jawless fishes, first bony fishes.
		Devonian	400	Origin and diversification of bony and cartilaginous fishes, origin of amphibians. Mass extinction late in the period.
		Carboniferous	345	Amphibians diversify, first reptiles.
		Permian	290	Reptiles (including mamal-like forms) radiate, amphibians decline. Major mass extinction, especially marine forms, at the end of period.

(Contd.)

(Contd.)

Mesozoic	Triassic	245	Early dinosaurs. Mass extinction near end of the period.
	Jurassic	195	Diverse dinosaurs, first birds and mammals.
	Cretaceous	138	Continued radiation of dinosaurs. Mammals begin diversification. Mass extinction at the end of the period, including dinosaurs.
Cenozoic	Tertiary	66	Radiation of mammals and birds
	Quaternary	2	Extinction of large mammals, evolution of <i>Homo</i> .

Placoderms

Placoderms (Gr. *placodes* plate, *derma* skin), as shown in Fig. 1.2, were the first jawed fishes and are the only group of gnathostomes (along with Acanthodii) to become completely extinct. They dominated the seas during the Devonian period since the ostracoderms were disappearing and became extinct by the end of the Devonian period. Placoderms were probably off the main line of vertebrate evolution. They were the most diverse group of the early jawed fishes and were swift predators. Their internal skeleton was cartilaginous, notochord present in the adult, and vertebral bodies (centra) absent but vertebral arches covered the spinal cord. They had paired fins and extensive body armor in the head and anterior (cranial) body trunk regions with body scales covering the rest of the body. The

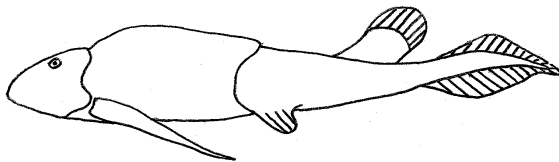


Fig. 1.2 A placoderm. Placoderms represent an extinct group of jawed fish that were flattened dorsoventrally. These fish had extensive body armor in the anterior part of the body. Most species had a heterocercal tail.

dermal bones (plates) formed head and thoracic shields that either articulated by joints or fused into units. Arthrodires, constituting two-thirds of the group, had a joint between the head and thoracic plates, which allowed the skull to be raised during such functions as feeding, as seen in the coelacanth. Pectoral fins and a heterocercal tail were present and in some species pelvic and dorsal fins were likewise present. Earlier forms lived in fresh water but secondarily became marine. Well-preserved specimens in Cleveland, Ohio (USA) deposits show the presence of myomeres. Acanthodians were a few centimeters long, had shark-like bodies and as many as five pairs of fins with webs of skin that supported hollow spines.

Chondrichthyes

Chondrichthyans (about 700 species) are a group of cartilaginous fish represented by sharks, skates, rays and chimaeras (Fig. 1.3). Their internal skeleton consists of cartilage, which may be strengthened in some areas by calcification. The ancestors of chondrichthyans had a bony skeleton. Some of these ancient forms were heavily armored. The skin of cartilaginous fish is flexible and leathery and sometimes bears bristly projections known as **placoid scales**, remnants of their ancestral heavy body armor. Most cartilaginous fishes are heavy-bodied swift swimmers in contrast to the fish that preceded them. They have a pair of pectoral fins behind the gill slits and a pair of pelvic fins

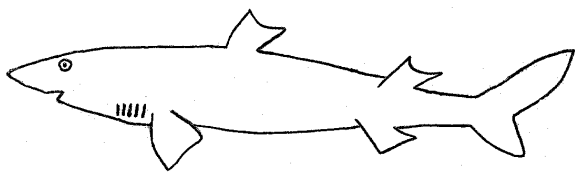


Fig. 1.3 A shark. These mainly heavy-bodied fish are found in sea water and over time reduced their body armor to placoid scales compared to their heavily armored ancestors. Note the vertical gill slits anterior to the pectoral fin which is a characteristic of elasmobranchs. Holocephalans such as chimaexas normally have a fleshy operculum covering the gills on each side. Sharks and rays seem to be the last major group of fish to leave a fossil record.

in front of the anal region. These appendages are important in providing balance and mobility. Cartilaginous fishes first appeared in Devonian marine deposits. They originated in the sea and only a few have been able to adapt to fresh water secondarily. Cartilaginous fishes are comparable with placoderms in that both groups of fish have an internal skeleton consisting of cartilage and lack lungs and swim bladders. Cartilaginous fish are thought to have diverged from marine placoderms.

Osteichthyes

The most abundant and diverse of the fish classes are osteichthyes (approximately 20,000 species). Originally fresh-water fish, this class comprises fish that live in both fresh and sea water. Their internal skeleton consists of bone though a few species retain considerable cartilage, some of which is later replaced by bone. The lungs in most of these fishes have evolved into swim bladders that mainly serve as organs of buoyancy. This enables the bony fishes to regulate their depth in water by controlling the amount of air in the swim bladder with little muscular effort contrary to cartilaginous fishes. Lungs and swim bladder were secondarily lost in some bottom-dwelling species. The gill slits open into a single opercular chamber on each side of the head and are usually covered by a bony operculum that grows from the second visceral (hyoid) arch.

Acanthodii (spiny sharks) were mainly freshwater fishes but some became marine later. This group died out at the beginning of the Permian. Acanthodians were small fish with a heterocercal tail and spines that preceded their fins. Their internal skeleton was partly ossified and a bony operculum covered the gills.

Actinopterygians are the largest group of osteichthyans and have bony rays in their fins (Fig. 1.4). The skeletal axis does not extend into their fins. Movement of the rays (which attach deeper into the body wall) is mainly brought about by body trunk muscles. A group of actinopterygians, **Chondrosteans**, were the dominant group of fishes during the Paleozoic era but today are represented by sturgeon, bichir, reed fish, and paddle fish. Their pectoral fins are fleshy but pelvic, dorsal anal, and

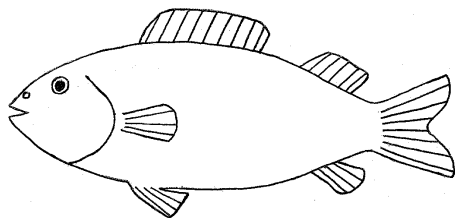


Fig. 1.4 Diagram of a bony ray-finned fish. These fish, comprising more than 20,000 marine and freshwater species, are the most abundant in the world. They have bony rays in their fins.

tail fins ray finned. The sturgeon retains several rows of bony plates in its skin. Another group of actinopterygians, **Neopterygians**, comprises the majority of freshwater fishes. Neopterygians (except gars) are able to bend faster and more powerfully due to the presence of thin flexible cycloid and ctenoid scales. Their jaws, more mobile compared to those of chondrosteans, permit powerful sucking action. Apart from the gar, *Lepisosteus*, and the bowfin *Amia*, all other neopterygians are teleosts. The neural arches of teleosts are modified in the caudal vertebrae, which ensures stiffness of the dorsal and ventral half of the caudal fin.

Sarcopterygians (fleshy finned fish), which include lungfishes, coelacanths, and the extinct rhipidistians (Fig. 1.5) are thought to be the ancestors of terrestrial vertebrates. The features these fish possess suggest that they had a common ancestor which differed from that of other bony fishes. They possess fins with a

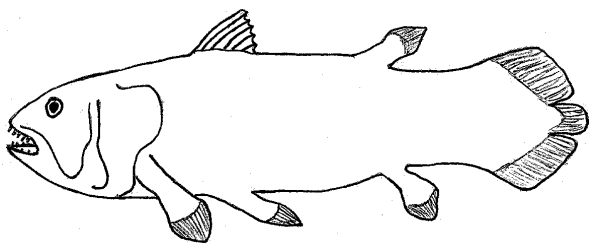


Fig. 1.5 The only surviving coelacanth, *Latimeria chalumnae*, a relative of the extinct rhipidistians. A few specimens have been caught off the coast of the Comoro islands near Madagascar, Southeast Asia, and East Africa (Kenya). The anterior dorsal fin of the fish is ray finned as in actinopterygians while the others are fleshy finned.

distinct skeletal axis corresponding closely to the proximal skeletal elements of the early tetrapod limbs and surrounded by muscles that extend into fins, unlike the ray fins of actinopterygians. The muscular fins could have evolved as an adaptation to living at the bottom of the water and the fins could have been used as paddles for movement. Early crossopterygians (lobe-finned fishes) resembled early amphibians and were bony fishes possessing lungs and gills and are represented by the living coelacanth. Descendants of crossopterygians are thought to have invaded land during the Devonian period to the Mesozoic era when the group flourished. A study of fossil and living fish has contributed to our understanding of how fins evolved into legs. The fins of crossopterygians (as seen in the coelacanth) were attached to the body by short bony limbs that could have enlarged into limbs enabling the early amphibian to crawl on land. The only extant coelacanth is *Latimeria chalumnae*, first caught at the mouth of the Chalumna River off the Comoro islands near Madagascar in 1938.

Lungfishes are now represented by three forms: *Neoceratodus* (Australia), *Lepidosiren* (South America), and *Protopterus* (Africa). They possess well-developed lungs and their internal skeleton is ossified to a limited extent. *Lepidosiren* and *Protopterus* have longer and thin paired appendages compared to *Neoceratodus* that has thick and shorter paired fins. These fishes possess soft anatomical features comparable with those seen in the ancestors of terrestrial vertebrates. Lungfishes have also lost their premaxillae and maxillae which make up the upper jaw. Fossil records show that the extinct rhipidistians could have shared a common ancestor with amphibians (Schultze, 1991). There are many skeletal similarities between rhipidistians and early amphibians, suggesting that their skeletal muscles could have been similar. Early rhipidistians had a better ossified and stronger internal skeleton than lungfishes. A suture that represents the remains of a transverse joint in the cranium of rhipidistians is found in early amphibians. The pattern of bones in limbs and roof of the skull of rhipidistians resembles that of early amphibians.

TETRAPOD MUSCULAR SYSTEM

The proportion of axial in relation to appendicular muscles diminishes in tetrapods as the limbs take over the propulsive role and their muscles enlarge. As the axial skeleton becomes firmer in tetrapods due to the supportive role it is to play, muscles develop longer fibers that span several myotomes and the axial musculature performs the role of flexion and extension of the spine, which is rare in fishes.

Amphibians

Amphibians (Gr. *Amphi* both, double, *bios* life) are the lowest tetrapods and the first vertebrates to occupy the terrestrial environment successfully. The oldest known amphibians were **labyrinthodonts** and resembled crossopterygians. They were discovered in rocks from the end of the Devonian or beginning of the Carboniferous period in Greenland. They had four limb-like fins for movement on land and a caudal fin they used for swimming when they returned to water. Labyrinthodonts resembled tailed amphibians but retained many fishlike features that are not present in modern amphibians, such as a tail for swimming that contains fin rays. The axial musculature of amphibians is transitional between that of fishes and reptiles. Most amphibians spend part or all their adult lives on land but lay their eggs in water. Evolution of amphibians from crossopterygian-like ancestors involved a change of the fleshly fins into walking legs, an adaptation necessary for movement on land. This transformation changed movement from use of fins to crawl in water, as seen in catfish and *Latimeria*, to use of limbs, as seen in terrestrial vertebrates, a design only slightly modified throughout the evolution of terrestrial vertebrates. Such a transition in the skeletal system of the limbs was accompanied by changes in muscle structure and further evolution of other muscles has enabled terrestrial vertebrates to cope with their changed mode of movement. Due to differences in physical and chemical properties of water and air, the transition occurred over millions of years. Air, unlike water, does not offer buoyancy but does offer less resistance to movement.

The demands of a terrestrial environment occasioned development of sturdy muscular fins and a strong skeleton. The early amphibian legs were used for crawling between ponds and streams but as they developed further, became suitable for movement on land. Most anurans (frogs and toads) and urodeles (newts and salamanders) have a sturdy skeletal system and their organs are adapted to life on land although they prefer humid and damp environments. In urodeles the axial musculature, most important for propulsion, is the largest and segmented. Their limbs are weak and carried forward passively with undulations of the body. Anuran epaxial musculature is considerably reduced.

Devonian deposits show that the earliest amphibians were the extinct ichthyostegalian (Fig. 1.6), an order in the subclass Labyrinthodontia. They had four limb-like fins for use on land and a caudal fin used for swimming. Their pectoral girdle did not articulate with the head and the spine. Muscles evolved that held the girdle to the trunk. The pelvic girdle then formed an articulation with the spine and did not need muscular support.

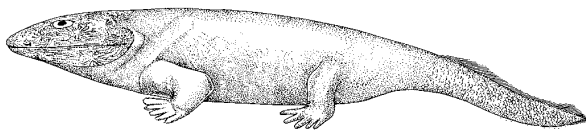


Fig. 1.6 Ichthyostegalian, the earliest known amphibian. These animals spent their lives both in water and on land. They were abundant during the Carboniferous and Permian periods but became extinct at the beginning of the Triassic (after Jarvik, 1980).

The skull of amphibians was lightened through reduction in number of bones and extent of ossification. Cranial muscles are used for moving the jaw, and in respiration and swallowing. Each limb has two main muscle masses used for moving the limb forward and medially and backward and laterally.

Reptiles

Reptiles (*L. reptare*, to crawl) have evolved characteristics that make them more adaptable to terrestrial environment than

amphibians. The reptilian skeletal system is stronger than that of amphibians. The pelvic girdle is attached to the axial skeleton by at least two sacral vertebrae in those with limbs. Such a joint is stronger and is necessary for transmission of forces originating from the pelvic limb to propel the body forwards. The center of gravity is low in reptiles. The epaxial muscles of reptiles are semisegmented.

Early reptiles (order **Captorhinida**) originated from labyrinthodonts and resembled the lizards. They were heavily built with powerful limbs particularly common during the Carboniferous period. They underwent various changes in locomotion and feeding patterns with concomitant changes in the relevant skeletal and muscular structure. Members of this order appear to have evolved into several groups of reptiles, including the order **Chelonia** (turtle group), **Synapsida** which later developed mammal-like characteristics over time, and **Saurapsida** that gave rise to reptiles and birds.

Some saurapsids (subclass Lepidosauria) are represented by more primitive tuatara (*Sphenodon*) found off the coast of New Zealand, lizards, the worm-like amphisbaenians and snakes (squamates). This diverse group of reptiles (about 6,000 species) have undergone changes in their skull from the original diapsid skull. Their jaws are quite flexible due to the loss of a single bone (lizards and amphisbaenians) or two bones (snakes) that border the two temporal fenestrae. Snakes can thus swallow prey that is larger than their heads due to the presence of the streptostylic jaw suspension. Squamates have reduced the size of their limbs or lack them altogether as seen in snakes, most amphisbaenians and some lizards, and have developed elongate bodies. Such an arrangement tends to greatly reduce the need for limb muscles seen in other reptiles. Snakes have a dermal muscle (costocutaneous muscle) that attaches to the scales and can erect them, thereby providing friction for locomotion and preventing a backward slip of the body in undulatory motion.

The other group of saurapsids, the **archosaurs** (large reptiles) comprising dinosaurs (orders Ornithischia and Saurischia), flying reptiles (order Pterosauria), and crocodiles were the dominant reptiles during the Mesozoic era. Ornithischians ("bird pelvis")

and their relatives were the dominant herbivores, quadruped, and with heavy muscles. Saurischians (“lizard pelvis”) on the other hand, were the largest carnivores and had well-developed hind limbs (therefore bipedal) and long strong tails that were well muscled. Pterosaurs had membranous wings used for flying so they must have had well-developed pectoral and patagial muscles. Most of the archosaurs had become extinct by the end of the Mesozoic era. The only survivors that evolved from the early archosaurs are the crocodiles and birds.

Two groups of reptiles evolved from the early saurapsids and adjusted to a marine environment—**ichthyosaurs** (order Ichthyosauria) and marine **plesiosaurs** (order Sauropterygia). Ichthyosaurs were the most important marine predators and resembled fish with large caudal fins. Plesiosaurs had paddle-like appendages for swimming. The body trunk musculature of ichthyosaurs and plesiosaurs probably resembled that of modern-day fish.

Tetrapod evolution from the synapsids occurred around the end of the Carboniferous period. Evolution into mammals by synapsids involved skeletal changes and corresponding muscular changes to a much more active and diversified life.

BIRDS

Birds and mammals, being endothermic, have much higher metabolic rates than other vertebrates that are ectothermic (fish, amphibians and reptiles). Birds and mammals are thus more active than ectothermic vertebrates and their body systems such as digestive, respiratory, and circulatory have adjusted to the demands of high levels of metabolism. Radiation of birds occurred during the Cenozoic era. Birds could have evolved from saurischian dinosaurs as seen in the skeleton of the *Archaeopteryx* (Fig. 1.7) recovered from Jurassic deposits. It had a long tail, was bipedal, lacked an ossified sternum, had feathers and teeth. *Archaeopteryx* also had three fingers on each wing that were not united and had claws and the tarsal (ankle) and metatarsal bones

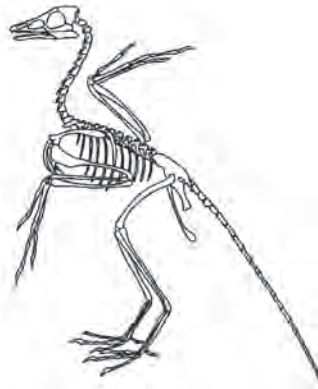


Fig. 1.7 Reconstruction of the skeleton of *Archaeopteryx*, the oldest bird that flourished during the Jurassic period. The bird was a poor flier compared to modern flying birds (after Heilmann, 1927).

were not united, as seen in modern birds. Evolution of an ossified sternum as seen in the modern bird reflects a transformation of the musculoskeletal system from a weak flier, e.g. the *Archaeopteryx*, to a strong flying modern bird. The oldest beaked bird, *Confuciusornis* (“Confucius bird”) appeared after *Archaeopteryx* about 139 million years ago. A well-preserved skeleton of the bird with feathers longer than its body, a horny beak and an arch dividing the upper and lower temporal fenestrae as seen in diapsid skulls has been found (Hou et al., 1999). *Confuciusornis* had three fingers with the index finger supporting flight feathers. It had some grasping ability as the thumb and middle fingers converged on one another. Structurally, birds tend to be related to each other due to their adaptation to flight. The skeleton and muscles of birds have been modified through evolution to serve this purpose. Many bones of birds are pneumatic (contain air spaces) that communicate with the air sacs of the lungs. Pockets (diverticula) of these air sacs enter the medullary cavities of long bones and medullary spaces of spongy bones through foramina pneumatica during early stages of development. This adaptation makes the bones of birds lighter. Birds lack a diaphragm (the most important muscle of inspiration in mammals) and have evolved air sacs that fill and empty in an alternate manner, thereby effecting inspiratory and expiratory ventilation of the lungs. The muscles of the thorax and

abdomen also play a role in these movements. The hind legs can also be used for swimming in some birds. The head and cervical vertebrae in birds are very mobile, enabling birds to use their eyes effectively in orientation in space and also their beaks in performing complex functions. As birds lack lips, cheeks, nose and external ears, there is much reduction in their facial musculature, which is innervated by the facial nerve and determines facial expression. Muscle arrangement in the region of the coccygeal vertebrae can be complex and powerful as it has to perform the function of supporting and steering the tail feathers, as is seen in the peacock.

The trunk of birds is short and relatively rigid as an adaptation to flight. The vertebral column of the trunk, has undergone fusion to a large extent, resulting in great reduction in the dorsal muscles as their function has been reduced (compared to other vertebrates). The sternum has been modified into a wide bone with a vertical keel which increases the surface area for attachment of enlarged pectoral muscles. Flightless birds (superorder **Paleognathae**), with wing vestiges, such as the ostrich of Africa, rhea of South America, emu of Australia, cassowary of New Guinea, and kiwi of New Zealand, lacking a keel have a broad sternum which suggests they might have had a flying ancestor. These birds could have evolved in areas where terrestrial predation was low. The rest of the birds, comprising about 8,700 species, belong to the superorder **Neognathae**.

Muscles that move the wings are the heaviest part of the body and account for as much as one-half of the total body weight. The two main muscles attaching to the wing are the *pectoralis* and *supracoracoideus*. The surficial pectoral muscle is the largest locomotor muscle and depresses the wing in flight while the embedded pectoral muscle and supracoracoideus are smaller and antagonistic to the surficial pectoral muscle so they raise the wing. Both muscles are attached to the keel. The main muscle mass in birds is close to the body placing it near the bird's center of gravity. The main leg muscle surrounds the femur in the thigh while a smaller mass occurs around the tibiotarsus. Thin, strong tendons surround the distal part of the legs to the toes. The feet have hardly any muscles and are composed mainly of bones, tendons and tough scaly skin. The

toe-locking mechanism is found in perching birds and prevents birds from falling from the perch while they are asleep and is also useful for gripping prey.

Since birds lack vocal cords, the syrinx (voice box) produces sound when vibrations are sent across the organ. The more the number of muscles attached to the syrinx, the more sounds it makes.

Intrinsic integumentary muscles of birds (found in the dermis) include *arrectores plumorum* (mostly smooth muscle) that attaches to the feather follicles and causes ruffling of feathers for insulation or in response to danger.

MAMMALS

Mammals originated from the extinct reptilian order **Therapsida** in the Mesozoic era and became more prominent during the Cenozoic era after most of the other groups of reptiles had become extinct. Being agile and active with a well-developed brain and complex behavior, mammals became the dominant terrestrial animals and occupied different niches on earth with corresponding changes in their locomotor apparatus. Transformation of the pectoral and pelvic girdles resulted in positioning of the limbs underneath the body from the reptilian arrangement wherein limbs protrude from the side of the body. Such an arrangement in mammalian limbs led to increased agility. Mammals have retained the general pattern of the reptilian epaxial musculature but have greatly reduced the segmentation present in reptiles. Changes in mammalian locomotion have resulted in altered proportions and specific functions of related reptilian muscles. Modification of some bones, especially the distal ones, has occurred in some mammals. Although the mammalian forelimb is adapted for performing different types of movements, it is composed of similar types of bones regardless of the use to which it is put—manipulating objects as seen in the primate forelimb or the flippers of sea mammals such as whales, seals

and dugongs. Compared to reptiles, mammals have undergone major changes in their limb structure, and pelvic and pectoral girdles, resulting in reduction in size of the ventral adductor muscles in the pectoral region, which are necessary in supporting and raising the body from the ground as seen in reptiles. There is also reduction in size of the tail musculature. Further, the shoulder joint is supported by enlarged dorsal muscles which have benefited also from migration of some ventral muscles.

Several muscles have evolved in mammals which are lacking in other vertebrates. The diaphragm is a dome-shaped muscle wall that completely separates the thorax from the abdomen and is the most important muscle of inspiration in mammals. The cutaneous muscles (*panniculus carnosus*) are a sheath of muscles found in the fasciae of many mammals but not much developed in amphibians and reptiles except for the occasional presence of a few fibers in the pectoral musculature. These muscles are poorly developed or absent in primates and permit local movements of skin independent of deeper muscles. They also play a role in heat generation in response to cold stress through shivering. They enable animals such as armadillos to roll into a ball when endangered. In marsupials, a sphincter portion of this muscle surrounds the entrance to the marsupium. The arrector pili muscle is associated with hair and causes erection of individual hairs when it is cold, thereby improving insulation of the body by trapping air. Jaw muscles, e.g. the muscles of mastication, are well developed in mammals and allow sideways movement of the jaws in many mammalian species. Related to these muscles during evolution is the tensor tympani from the adductor mandibularis. The cutaneous musculature of the face (mimetic muscles), derived mainly from superficial sheets of hyoid musculature and spread on the face, is particularly well developed in carnivores and primates, especially man. These muscles enable primates, especially man, to express emotions without talking.

The surviving mammals belong to two subclasses: **Prototheria** (monotremes) which includes the platypus and echidnas of Australia and New Guinea and **Theria** (marsupials and placentals). The monotremes (Gr. *monos* single, *trema* hole) lack teeth, do not have well-developed muscles of mastication as seen in other

mammals, and have many skeletal and muscular features similar to those of reptiles. Marsupials (infraclass Metatheria) differ from placentals (infraclass Eutheria) in many skeletal and dental features. Eutherian mammals have undergone adaptive radiation to occupy different environments. For example, in sirenians (dugongs and manatees) that live in water, the pelvis is vestigial and the hindlimbs lacking while the forelimbs are modified into flippers, as is the case with many marine mammals. The equivalent muscles in these modified body regions have become vestigial or modified. The presence of wings in bats necessitated development of patagial muscles that are slips of pectoral muscles which insert on the skin of the wing membrane.

Muscle Types

INTRODUCTION

To appreciate the various types of muscles encountered in vertebrates, insight into muscle classification is essential. Vertebrate musculature may be classified using three main approaches; **structural**, **functional** or a **combination** of these two approaches. In general, the structural approach takes into account the morphological characteristics of a muscle tissue, in particular the arrangement of myofilaments (contractile protein filaments) within a muscle fiber. Under this scheme two types of muscles have been identified: **striated** with typical cross-banding pattern or striations (examples include skeletal and cardiac muscles) and **smooth** in which the myofilaments do not form a definite cross-banding pattern and hence there are no striations. The functional approach relies mainly, however, on the type of innervation and accompanying response of the muscle tissue on neural stimulation. In this regard, **voluntary** muscles, essentially innervated by somatic nerves, are under conscious control by the individual and hence respond at will. All skeletal muscles fall in this category. On the other hand, **involuntary** muscles, innervated by the autonomic nervous system, respond to nervous stimulation independent of an animal's consciousness. All smooth and cardiac muscles belong to this latter group. In combination, these two approaches leads to recognition of three basic types of muscles:

- (1) Striated muscles whose actions are under the direct influence of the individual's consciousness. These are referred to as **striated voluntary** muscles, e.g skeletal muscles.

- (2) Striated muscles whose actions are independent of consciousness. These are **striated involuntary** muscles, e.g cardiac muscles.
- (3) Nonstriated muscles whose actions are independent of the individual's consciousness. These are **nonstriated involuntary** muscles, e.g smooth muscles.

Smooth Muscles

Smooth muscles generally occur in the **skin** and **walls of tubular organs** with their associated **glands**. Smooth muscle cells are long and fusiform (spindle shaped) with centrally located nuclei (Figs. 2.1 and 2.2). Often these cells assume an arrangement in a muscle tissue wherein the thin end of one cell is closely applied to the thick middle portion of the adjacent cells. This gives the tissue a characteristic “dovetail” appearance in longitudinal sections (Fig. 2.2) and a cross-sectional appearance of irregular polygonal profiles. Under ordinary circumstances,

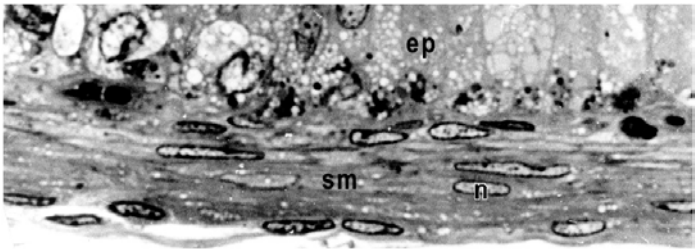


Fig. 2.1 Light micrograph of a section of a mammalian cauda epididymis. The epithelium of the duct (ep) is surrounded by a thick muscular wall formed by smooth muscle cells (sm). The cells have elongated centrally located nuclei (n) (X 1250).

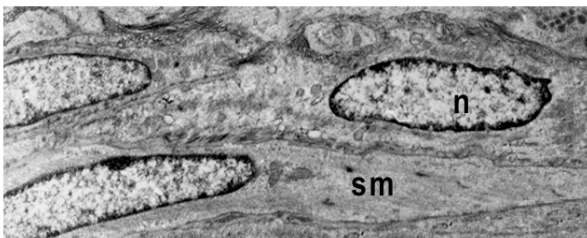


Fig. 2.2 Electron micrograph showing a “dovetail” arrangement of smooth muscle cells. (sm) smooth muscle cell, (n) cell nucleus (X 3,000).

smooth muscle cells do not show striations but after application of special stains, striations are demonstrable representing typical myofilaments found in the skeletal and cardiac muscles. Unlike skeletal muscles, these protein myofilaments are highly unstable being assembled and disassembled as the need arises.

Based on the structure and functions, smooth muscles may be classified as: (a) **multiunit muscles** occurring mainly in the pilomotor muscles of the mammalian skin, nictitating membranes of the eyelids of frogs, ciliary body of the eye and blood vessels. In this type of smooth muscle, the cells have no direct electrical contact with each other and the contraction of each fiber is initiated by an independent nerve branch terminating on each of the fibers. Multiunit fiber contractions occur almost all at the same time. These contractions are stimulated by a neurotransmitter substance, usually acetylcholine, or pharmacological agents which mimic this neurotransmitter substance. (b) **Unitary smooth muscles**; these are abundant in the **visceral organs**, especially the digestive system. The muscle cells here have a direct contact with each other and the contraction is elicited through propagation of electrical stimuli from one cell to the next through gap junctions or **nexi**. The cells in this type of muscle are organized into definite bundles, each supplied by a nerve branch. As a result, contractions of muscle cells in this case are spontaneous, gradual and independent of neuronal control, as typically exemplified in peristalsis.

Cardiac Muscles

Cardiac muscles or **myocardia** arise from the splanchnic mesoderm associated with the developing heart tube. From early embryonic times, the muscle fibers contract rhythmically without fatigue and independent of any direct nervous stimulation; hence they are referred to as **myogenic fibers**. The myocardial fibers (Figs. 2.3 and 2.4) have one or two centrally located nuclei and sarcoplasmic **striations** similar to, but not as distinctly organized as, those of skeletal muscles. Often, the fibers appear **branched** interlocking at their ends with each other to form a **syncytium**. This syncytial arrangement enables the cardiac muscles to contract as a unit. As in skeletal muscles, striations in cardiac muscles are due to the presence of alternating bands of actin and myosin filaments (Figs. 2.5 and 2.6).

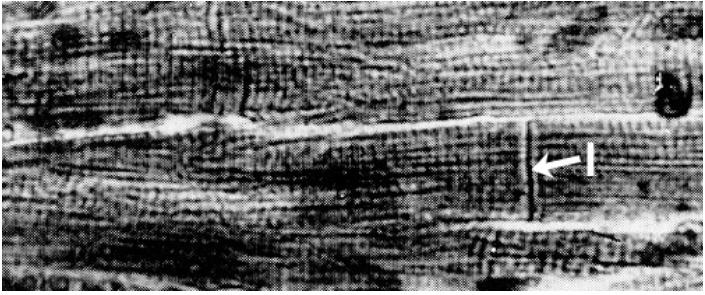


Fig. 2.3 Longitudinal section through cardiac muscle showing specialized junctions or intercalated disks (I) between adjacent cardiac muscle cells. Note the presence of sarcoplasmic striations within the cells (X 200).

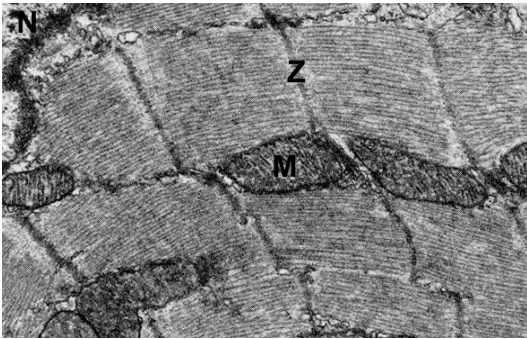


Fig. 2.4 Electron micrograph of a cardiac cell showing elongated mitochondria (M) and numerous sarcoplasmic striations. Z-lines mark the boundary between adjacent sarcomeres. The cell nucleus (N) is at the extreme left (X 12,000).

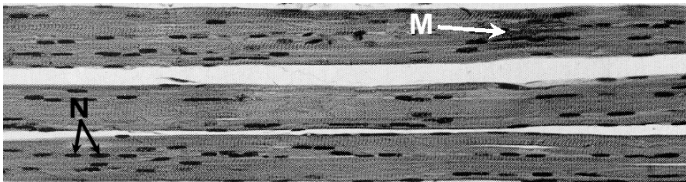


Fig. 2.5 Longitudinal section through skeletal muscle fibers showing the characteristic sarcoplasmic striations and numerous peripherally located nuclei (N). Occasional termination of nerve endings on the fibers forming the motor end plate (M) are encountered (X 100).

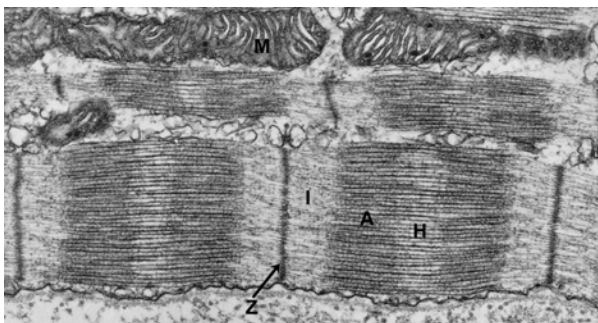


Fig. 2.6 High power electron micrograph of part of a skeletal muscle cell. Notice the orderly arrangement of myofilaments into bands, giving the cell its typical striations. Some of the bands recognized in this micrograph are: 1) A-band consisting of both actin and myosin filaments, 2) H-band made up of myosin filaments only, and 3) I-band comprising actin filaments only. Actin filaments of the two I-bands from adjacent sarcomeres meet at the Z-line (Z). (X 25,000). For further details see Chapter 4.

Intercalated disks

At the interlocking ends where adjacent fibers meet, junctional specializations similar to the Z-line of skeletal muscle fibers with stairwell arrangements occur. These junctional specializations are called **intercalated disks** (Figs. 2.3 and 2.4). These disks allow the spread of electrical activity from one cell to another, facilitating syncytial contraction of cardiac muscles. Since these disks receive the filaments of the I-band from both ends of adjacent fibers, they transmit mechanical energy of contraction from one cardiac muscle fiber to the next.

Impulse generation and conduction in cardiac muscles: Rhythmic contraction of cardiac muscles is a result of stimulation by electrical impulses generated at the **sinoatrial node (SAN)** or **pace-maker** situated at the junction of venae cavae and the right atrium. From the SAN, impulses spread to the **atrioventricular node (AVN)** located at the interventricular septum through three fiber tracts: **ventral**, **middle**, and **dorsal** internodal pathways (Berne and Levy, 1993). Simultaneously, diametrical spread of impulses occurs from the SAN to fibers of the left atrium via a special pathway, the **ventral interatrial myocardial band** or **Bachmann's bundle**, ensuring that the two atria contract

almost at the same time. Fibers of SAN and AVN generally resemble those of the myocardium. From the AVN, impulses are carried by special fibers which, by and large, resemble myocardial fibers. These fibers are called the **bundle of His**. Fibers of this bundle occur along the atrioventricular septum and divide into two main groups as His approaches the ventricles; the **right bundle** courses into the right ventricle and the left bundle into the left ventricle. The left bundle further divides giving rise to the left major and minor bundles. These fibers are continuous with the **Purkinje fibers** found on the ventricular walls on either side of the heart. Electrical impulses from the bundle of His spread to the entire ventricular wall through the Purkinje fibers. These Purkinje fibers are generally larger than cardiac muscle fibers with centrally located nuclei and scattered peripherally situated myofibrils, sometimes shrinking toward the center. They have numerous mitochondria and intercalated disks. These impulse-conducting muscle fibers are referred to as **modified cardiac muscles**.

Skeletal Muscles

Skeletal muscles are generally responsible for voluntary movements in vertebrates. They are mainly found applied to the external surface of the skeleton and their contraction results in movements of joints or associated structures. Skeletal muscle cells or fibers have numerous peripherally located nuclei with conspicuously organized striations in the sarcoplasm (Figs. 2.5 and 2.6). The striations occur as a result of alternating bands of thin (**actin**) and thick (**myosin**) filaments (see Chapter 4 for details on contraction). Contrary to cardiac muscles, cells of skeletal muscles do not show branching and anastomosis and contain abundant glycogen granules.

FIBER TYPES

Muscle fiber types may be classified according to functional and structural characteristics. The following types are therefore

recognized: **tonic**, **slow phasic (red)**, **fast phasic glycolytic (white)**, and intermediate **fast phasic oxidative (pink)**. Whereas these fiber types have distinct locations in fish, they occur in different proportions in muscles of other vertebrates depending on the type of contraction performed.

Tonic Muscle Fibers

These are very slow contracting muscle fibers that exhibit a continual partial contraction in a muscle. They do not produce a significant response when stimulated with a single stimulus and show no recognizable contraction and movement, but do cause tautness as a result of contraction of a small number of the total muscle fibers in a muscle. Tonic muscle fibers are innervated by multiple nerves and show graded response to stimulation of different frequencies, leading to contraction in relays by groups of muscle fibers in a muscle. The fibers are important for maintaining posture as they can maintain isometric contractions economically since they have a very long cross-bridge cycle. Muscles with less tone than normal are referred to as **flaccid** and those with more tone than normal are described as **spastic**. Muscle tone (tonic contraction) is maintained by negative feedback mechanisms centered in the spinal cord.

Slow Phasic (Red) Fibers

These fibers contain a high content of myoglobin, an oxygen-carrying pigment in muscle. Slow fibers have thick myofilaments made of a type of myosin that reacts at a slow rate. Due to their slow contraction, the fibers are able to produce adenosine triphosphate (ATP) quickly enough to meet the energy demands of myosin and avoid fatigue. This is enhanced by the high density of mitochondria and capillaries, and also the high content of myoglobin. There is a complete breakdown of glucose to carbon dioxide, water, and energy in slow fibers. The energy conversion efficiency here is 38% - 44%, which is much better than the 20%-25% typical of most machines. Slow fibers are suited for contractions seen in postural muscles.

Fast Phasic (White) Fibers

Fast muscle fibers contain little myoglobin, have a faster type of myosin, and their sarcoplasmic reticulum and T-tubule system are more efficient in delivering calcium ions to the sarcoplasm. Due to their rapid rate of contraction, ATP is depleted rapidly. Fast fibers rely on anaerobic respiration to regenerate ATP due to their low content of mitochondria, though the fibers are rich in glycogen. During anaerobic respiration, a glucose molecule is broken down into two pyruvic acid molecules. This process releases about 5% of the energy stored in the chemical bonds of glucose molecules and generates small amounts of ATP in the process. In the presence of oxygen, pyruvic acid is converted to acetyl-CoA which enters the citric acid cycle in the mitochondria and transfers chemical energy to the maximum number of ATP molecules via oxidative phosphorylation. In most human cells, one glucose molecule produces enough usable chemical energy to synthesize 36 ATP molecules. If oxygen is not available, pyruvic acid is converted to lactic acid, incurring an oxygen debt. The oxygen debt is later repaid when ATP produced via oxidative phosphorylation is used to convert lactic acid back to pyruvic acid or even all the way back to glucose. As a result, fast fibers cannot sustain a contraction for long. Glycolysis takes place in the sarcoplasm of muscle fibers whereas the citric acid cycle occurs in their mitochondria. They are thus found in muscles that generate great force quickly but not for long, such as muscles that move fingers in primates and the bulk of fish musculature (accounting for 70-80% of fish musculature).

Intermediate Phasic (Pink) Fibers

Intermediate fibers have characteristics between those of fast and slow fibers. They are essentially the same as the fast phasic fibers except for the high densities of mitochondria. Therefore, they are more fatigue resistant than the fast fibers and can contract with greater force more rapidly than the slow fibers. They are found in muscles that perform postural support and can also generate rapid and powerful contractions, for example the soleus of mammals which supports the hind limb and can also be used in walking, running and jumping.

Motor Unit

A motor unit consists of all muscle fibers that are innervated by the same motor neuron. Such fibers have similar characteristics and contract simultaneously when their motor neuron conducts an action potential. Since most vertebrate muscles are activated in an “all-or-none” manner, either fully switched on or switched off with no part activation, variation in contractile force occurs as a result of the recruitment of different members of motor units. The number of fibers supplied by a motor neuron depends on the type of movements performed by each muscle. The fewer the number of fibers supplied by a motor neuron, as in the extraocular muscles of the eye of vertebrates and hand muscles in primates, the more precise the movements such muscles produce. In muscles adapted for large powerful movements, for example the large limb and abdominal muscles that do not produce precise movements and mainly perform course control, a motor neuron may supply more than a hundred muscle fibers.

ACCESSORY STRUCTURES ASSOCIATED WITH MUSCLE

Accessory structures here include fasciae, synovial bursae, and tendon sheaths. These structures are mainly associated with skeletal muscles of higher vertebrates and complement the function of muscles and their tendons.

Fasciae

These are tough and thin connective tissue membranes (sheets) consisting mainly of collagenous and elastic fibrils. Their color depends on composition, though mainly white to yellowish. Fasciae (dense regular connective tissue) run oblique to the direction of muscle fibers. Fasciae may surround a muscle or group

of muscles, divide into several layers giving rise to intermuscular septae or lamellae, or form chordlike structures. The body surface of vertebrates is enclosed by fasciae consisting of two layers in mammals. Large body cavities are also lined by fasciae. Fasciae may serve as a point of origin or insertion for some muscles.

Synovial Bursae

These are pillow-like structures found in loose connective tissue and contain synovial-like fluid. They act as gliding surfaces or fluid-filled cushions between tightly stretched muscles, tendons, ligaments, fasciae or skin passing over skeletal prominences. Such an arrangement minimizes injury to such soft structures and facilitates movement when contact is made with a hard surface. A synovial bursa has a tough outer fibrous membrane layer and a delicate inner synovial layer that often has villi. Many bursae are not constant structures in the body.

Tendon Sheaths

A tendon sheath is a tube-like structure that completely surrounds a tendon. Such sheaths are found in areas where tendons are under high tension, for example over bone. They are filled with a synovial-like fluid and their walls are similar to those of synovial bursae. Tendon sheaths aid in smooth gliding movements of tendons and also minimize injury to the tendons.

Muscle pennation

In higher vertebrates, skeletal muscles often arise from a rather static position called the **origin** and terminate at a comparatively more mobile position known as the **insertion**. Naming of muscles, in a number of cases, takes into account the origin and insertion. For example, the name **sternomandibularis** implies that this muscle originates from the sternum and inserts at the mandible. At their points of origin and insertion, skeletal muscles are anchored by strong bands of collagenous fibers called **tendons**. The arrangement of parallel muscle fibers between

their tendons of origin and insertion gives a characteristic pattern referred to as **pennation** (Fig. 2.7). When fibers originate from one tendon and converge on a single tendon, they are said to be **unipennate** (Fig. 2.7a). Some muscle fibers may arise from or insert on more than one tendon. Such fibers are described as **multipennate**. A number of multi pennate fibers sometimes arise from a single tendon but on insertion converge on two distinct tendons forming a **bipennate** pattern (Fig. 2.7b). Others may originate from more than one tendon and insert on two or more tendons. These arrangements may be referred to as **tripennate**, **quadripennate**, etc.

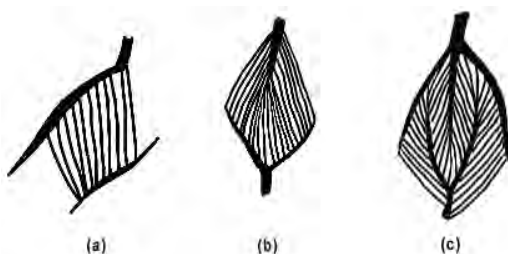


Fig. 2.7 Diagrams showing different kinds of pennation in skeletal muscles. (a) unipennate, (b) bipennate, and (c) multipennate

Skeletal muscle movements and functions

Movements associated with skeletal muscles include; (a) **flexion** (reduction in the angle circumscribed by a joint), (b) **extension** (increase in the angle circumscribed by a joint), (c) **rotation**, (d) **nodding**, (e) **abduction** (movement away from the median plane) (f) **adduction** (movement toward the median plane), and (g) **circumduction**.

Skeletal muscles occur in various regions of the body where they perform varied functions:

- Under the **skin (cutaneous muscles)** where they may cause **wrinkling** movements of the skin.
- In the **head region** where they reflect alter the **mood** of the animal (**muscles of facial expression**), participate in **chewing (muscles of mastication)**, **swallowing (hyoid muscles)** or intrinsic movements of **laryngeal cartilages (laryngeal muscles)**.

- In the **neck region** where they may effect **flexion, extension, and lateral deviation** of the neck. Some may control **nodding** and **rotatory** movements of the head over the neck.
- On the **limbs**, facilitating **locomotion**.
- On the body trunk, enabling various body movements including **respiration** and **abdominal press**.

Muscle groups in vertebrates

Detailed descriptions of individual muscles of the vertebrate body can be obtained from standard anatomical textbooks. The list provided here is by no means exhaustive and, moreover, not all the muscles listed are found in all vertebrates. Many of these muscles will be found only in higher vertebrates such as mammals. Some may be missing in an animal altogether while others may have been modified to perform various functions. Some of the important muscle groups are shown in Fig. 2.8 and include:

(i) Cutaneous muscles

These are found underneath the skin and are often dissected out together with the skin.

- (a) Head: *Dorsal cutaneous faciei (frontalis or epicranius)*
Ventral cutaneous faciei
- (b) Neck: *Sphincter colli superficialis*
Platysma
Sphincter colli profundus
Cutaneous colli profundus
- (c) Trunk: *Cutaneous trunci*
Cutaneous omobrachialis
Preputiales (male)
Supramammarii (female)

(ii) Muscles of facial expression

These are small superficial muscles found in the head region and are well developed in carnivores and primates, especially man. Their function is to reflect the mood of the animal at any given time. Some of these muscles are:

- *Levator nasolabialis*
- *Levator labii maxillaris*

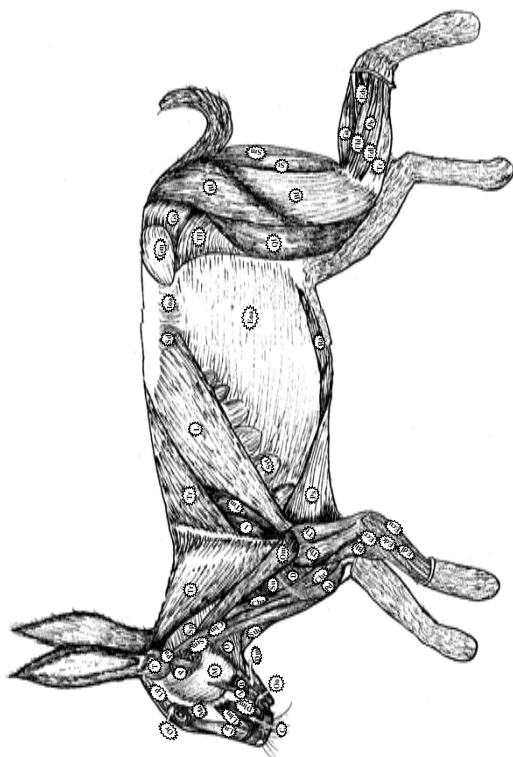


Fig. 2.8 Schematic diagram of a rabbit showing some of its exposed muscles. **B** buccinator, **Bb** biceps brachii, **Bf** biceps femoris, **C** caninus, **Cba** cleidobasalis, **Cbr** cleidobrachialis, **Cbm** cleidomastoideus, **D** deltoideus, **Dlm** depressor labii maxillaris, **Dm** depressor labii mandibularis, **Ecr** extensor carpi radialis, **Ecu** extensor carpi ulnaris, **Ede** extensor digitoris communis, **Eel** extensor digitoris lateralis, **Ede** extensor digitoris superficialis, **Eoa** enternal oblique abdominis, **Fhl** flexor hallucis longus, **Ga** gastrocnemius, **Gm** gluteus medius, **Gs** gluteus superficialis, **I** infraspinatus, **Ioa** internal oblique abdominis, **L** latissimus dorsi, **Llm** levator labii maxillaris, **Ln** levator nasolabialis, **Lp** levator palpebrae superioris, **M** masseter, **Ma** caudal malaris (depressor palpebrae inferioris), **O** omohyoideus, **Om** Omotransversarius, **Oo** orbicularis oris, **Or** orbicularis oculi, **P** parotid gland, **Pa** parotidauricularis, **Pd** Pectoralis descendens, **Pe** Pectoralis longus, **Ps** Pectoralis ascendens, **Qf** quadriceps femoris, **Ra** rectus abdominis, **Sd** serratus dorsalis, **Sm** semimembranosus, **Sp** splenius, **St** semitendinosus, **Sth** sternothyrohyoideus, **Stm** sternomastoideus, **Su** supraspinatus, **Svt** serratus ventralis thoracis, **T** Temporalis, **Tb** triceps brachii, **Tc** tibialis cranialis, **Tfl** tensor fascia latae, **Tm** Teres major, **Tr** trapezius and **Z** zygomaticus.

- *Caninus (dilator naris lateralis)*
- *Transversus nasi (dilator naris apicalis)*
- *Depressor labii maxillaris*
- *Depressor labii mandibularis*
- *Buccinator*
- *Orbicularis oris*
- *Zygomaticus*
- *Orbicularis oculi*
- *Retractor anguli oculimedialis and oculilateralis*
- *Levator palpebrae superioris*
- *Depressor palpebrae inferioris*
- *Malaris*
- *Mentalis*
- *Incisivus maxillaris and mandibularis*
- *Auriculares rostrales, dorsales, caudales and ventrales*

(iii) Muscles of mastication

These muscles are useful during the chewing process. Members of this group include:

- *Masseter*
- *Pterygoideus medialis and lateralis*
- *Temporalis*
- *Digastricus*

(iv) Hyoid muscles

These muscles play an important role in the swallowing process, causing movements of the tongue, pharynx and larynx. They are:

- *Mylohyoideus*
- *Stylohyoideus*
- *Occipitohyoideus (Jugulohyoideus)*
- *Geniohyoideus*
- *Ceratohyoideus*
- *Hyoideus transversus*
- *Sternothyrohyoideus (sternohyoideus and sternothyroideus)*
- *Omohyoideus*

All of them are paired except *hyoideus transversus*.

(v) Extrinsic muscles of the tongue

This group of muscles influences movements of the tongue in higher vertebrates, resulting in depression, protrusion or

retraction of the tongue. In lower vertebrates, however, the tongue is either lacking or poorly developed.

- *Styloglossus*
- *Genioglossus*
- *Hyoglossus*

(vi) Intrinsic muscles of the larynx

These muscles cause movements of laryngeal cartilages, resulting in alteration of the shape of the vocal folds and consequently changing the quality of sound produced.

- *Cricothyroideus*
- *Cricoarytenoideus dorsalis*
- *Cricoarytenoideus lateralis*
- *Arytenoideus transversus*
- *Thyroarytenoideus*

All are paired except *arytenoideus transversus*.

(vii) Muscles of the neck

These muscles enable extension, flexion, and lateral deviation of the neck. Members include:

- (a) Ventrolateral group:
- Brachiocephalicus*
 - Sternocephalicus*
 - Omotransversarius*
 - Sternothyrohyoideus*
 - Omohyoideus*
 - Scalenus*
 - Iliocostalis cervicis*
 - Longus colli*
 - Longus capitis (Rectus capitis ventralis major)*
 - Rectus capitis ventralis minor*
 - Rectus capitis lateralis*
 - Intertransversarii*

The evolution of *brachiocephalicus* in various vertebrate groups is discussed in Chapter 5. In Fig. 2.8 this muscle is represented by *cleidobrachialis*, *cleidobasalis* and *cleidomastoideus*. In some mammalian groups, *sternomastoideus* provides a small branch to the mandible called *sternomandibularis*. In such animals, these two muscles (*sternomandibularis* and *sternomastoideus*) are collectively known as *sternocephalicus*. *Sternothyrohyoideus* is a muscle consisting of two components: *sternothyroideus* and *sternohyoideus*,

both originating from the sternum as one unit and ending either at the thyroid cartilage of the larynx or the hyoid bone.

- (b) Dorsolateral group:
- Trapezius cervicis*
 - Serratus ventralis cervicis*
 - Splenius*
 - Longissimus cervicis, capitis, and atlantis*
 - Semispinalis capitis*
 - Spinalis and semispinalis cervicis*
 - Multifidi cervicis*
 - Rectus capitis dorsalis major*
 - Rectus capitis dorsalis minor*
 - Obliquus capitis cranialis*
 - Obliquus capitis caudalis*

(viii) Muscles of the thoracic girdle

These muscles secure the thoracic limb on the body trunk and may also effect cranial or caudal pull on this limb. Members of this group include:

- *Trapezius (cervicis and thoracis)*
- *Rhomboideus (cervicis and thoracis)*
- *Serratus ventralis (cervicis and thoracis)*
- *Latissimus dorsi*
- *Pectoralis descendens*
- *Pectoralis transversus*
- *Pectoralis ascendens*
- *Subclavius*

Pectoralis muscles are fairly well developed in birds in order to support flight.

(ix) Muscles of the thorax

These muscles increase or decrease the volume of the thoracic rib cage either by exerting cranial or caudal pull on the ribs, or by their own intrinsic contraction or relaxation as in the *diaphragm*. These movements have the net effect of facilitating inspiration or expiration. This group includes:

- *Levator costarum*
- *Intercostales externi and interni*
- *Rectus thoracis*

- *Retractor costae*
- *Transversus thoracis*
- *Serratus dorsalis (cranialis and caudalis)*
- *Diaphragm*

(x) Muscles of the abdominal wall

These muscles form the ventral support for the abdominal viscera and are therefore recruited during **abdominal press**. Abdominal press refers to conscious application of pressure on the visceral organs thereby aiding such important physiological processes as micturition (urination), defecation, parturition and forced expiration. The muscles of this group include:

- *External oblique abdominis*
- *Internal oblique abdominis*
- *Transversus abdominis*
- *Rectus abdominis*

The last muscle (*rectus abdominis*) is also important in arching the dorsum of the body. The *internal oblique abdominis* gives off a detachment at its point of insertion forming the *cremaster* muscle.

(xi) Epaxial muscles of the back

These muscles are found dorsal to the transverse processes of the vertebral column mainly occupying the space between the transverse and spinous processes. They extend the vertebral column and may cause lateral flexion as well. From lateral to medial, members of this group include:

- *Iliocostalis (lumborum and thoracis)*
- *Longissimus (lumborum and thoracis)*
- *Spinalis and semispinalis thoracis*
- *Multifidi (lumborum and thoracis)*
- *Intertransversarii*
- *Interspinales*

(xii) Muscles of the tail

These muscles cause elevation, depression, or lateral deviation of the tail. The elevators occur dorsally, depressors ventrally, and the flexors lie between the elevators and depressors. Members of this group are:

- *Sacrocaudalis (sacrococcygeus) dorsalis medialis and lateralis*

- *Sacrocaudalis (sacrococcygeus) ventralis medialis and lateralis*
- *Intertransversarii caudae*
- *Coccygeus*
- *Levator ani*

(xiii) Sublumbar muscles

This group of muscles occupies the ventral surfaces of the bodies of lumbar vertebrae coursing through the pelvic cavity to terminate partly on the pelvic bone and partly on the femur. Their contraction causes flexion of the vertebral column, especially at the lumbar region, and the hip joint. Included here are:

- *Psoas minor*
- *Psoas major*
- *Iliacus*
- *Quadratus lumborum*

To a large extent, *iliacus* and *psoas major* pursue a similar course toward their insertion, forming one muscle called *iliopsoas*.

(xiv) Muscles of the shoulder

These muscles mainly originate from the shoulder girdle and insert on the humerus. They enable extension and flexion of the shoulder joint. Members are divided into two main divisions:

- | | |
|--------------------|-------------------------|
| (a) Lateral group: | <i>Supraspinatus</i> |
| | <i>Infraspinatus</i> |
| | <i>Deltoideus</i> |
| | <i>Teres minor</i> |
| (b) Medial group: | <i>Teres major</i> |
| | <i>Subscapularis</i> |
| | <i>Coracobrachialis</i> |

(xv) Muscles of the elbow joint

The muscles in this group control extension and flexion of the elbow joint. They are situated mainly around the humerus. Members include:

- *Brachialis*
- *Biceps brachii*
- *Triceps brachii*
- *Anconeus*
- *Tensor fasciae antebrachii*

The last three muscles in this group are extensors of the elbow joint.

(xvi) Rotators of the forearm

This group of muscles rotates the radius and ulna resulting into **supination** and **pronation**. In species where movements between radius and ulna are limited, these muscles are rudimentary. Included in this group are;

- (a) Supinators: *Brachioradialis*
Supinator
- (b) Pronators: *Pronator quadratus*
Pronator teres

(xvii) Muscles of the carpal joint

These are long slender muscles causing extension and flexion of the carpal joint. Members include:

- *Extensor carpi radialis*
- *Extensor carpi ulnaris*
- *Flexor carpi radialis*
- *Flexor carpi ulnaris*

(xviii) Muscles of the digits

These muscles facilitate movements of the digits resulting in extension, flexion and even abduction and adduction (as in the first digit or *pollux* where it occurs). Included here are:

- (a) Long muscles: *Extensor digitis communis*
Extensor digitalis lateralis
Extensor pollicis and indicis longus
Abductor pollicis longus
Flexor digitalis superficialis
Flexor digitalis profundus
Interflexorii
- (b) Short muscles: *Interossei*
Lumbricales
Flexor digitalis brevis
Flexor pollicis brevis
Abductor pollicis brevis
Adductor pollicis
Adductor digiti indicis
Adductor digiti minimi
Abductor digiti minimi
Flexor digiti minimi

(xix) Outer hip and croup muscles

These include some of the most powerful muscles useful in transmitting propulsive force to the trunk. This group includes:

- *Gluteus superficialis*
- *Gluteus medius*
- *Piriformis*
- *Gluteus profundus*
- *Tensor fasciae latae*

(xx) Caudolateral muscles of the thigh (muscles of the buttocks)

These muscles cover the caudolateral aspect of the thigh. They extend the hip joint, flex the stifle (knee) and may, through the Achille's tendon, extend the hock (ankle) joint. These muscles are collectively referred to as the *hamstring muscles*.

- *Biceps femoris*
- *Semitendinosus*
- *Semimembranosus*

(xxi) Medial muscles of the thigh

These are found on the medial surface of the thigh. They flex and adduct the hip joint. The group includes:

- *Sartorius*
- *Gracilis*
- *Pectineus*
- *Adductores*

(xxii) Deep muscles of the hip joint

These muscles lie close to the hip joint covered by the medial group of muscles. They rotate the thigh and extend the hip joint. Muscles in this group include:

- *Obturator externus* and *internus*
- *Gemelli*
- *Quadratus femoris*
- *Articularis coxae* (acts as a stretch receptor)

(xxiii) Special muscles of the stifle joint

These are muscles that specifically act on the stifle joint. They may extend or flex the joint.

- *Quadriceps femoris* (*vastus medialis, lateralis, intermedius* and *rectus femoris*)
- *Popliteus* (flexes the joint)

(xxiv) Muscles of the hock joint

This group includes extensors and flexors of the hock (tarsal) joint.. Members of this group are:

- *Tibialis cranialis*
- *Peroneus brevis, tertius, and longus*
- *Gastrocnemius*
- *Soleus*

The last two muscles are extensors forming *Triceps surae* while the rest are flexors.

(xxv) Muscles of the digits

As in the thoracic limb, these muscles also facilitate movements of the digits of the pelvic limb. Members fall into two groups;

- (a) Long muscles: *Extensor digitalis longus*
 Extensor digitalis lateralis
 Extensor hallucis longus (*hallux*: first digit)
 Flexor digitalis superficialis
 Flexor digitalis profundus (*flexor hallucis longus, tibialis caudalis, and flexor digitalis longus*)
- (b) Short muscles: *Extensor digitalis brevis*
 Interossei
 Lumbricales
 Flexor digitalis brevis
 Flexor hallucis brevis
 Interflexorii
 Quadratus plantae
 Adductor digiti indicis and minimi
 Abductor digiti indicis and minimi

Muscle Development

ORIGIN OF MUSCLE CELLS

Barring a few exceptions, the origin of muscle cells or histogenesis can be traced to the mesodermal layer of the primitive embryo. Exceptions include the smooth muscles of the iris, sweat glands, and mammary glands whose cells originate from the ectodermal layer. All muscle cells of mesodermal origin, regardless of muscle type, differentiate from the primitive **myoblasts**, themselves residents of this mesodermal layer.

Primitive mesenchymal cells destined to become myoblasts begin by **elongating**, forming at their ends cellular interconnections or **syncytia**. Soon thin myofilaments appear in the sarcoplasm of these myoblasts as a result of the union and realignment of the sarcoplasmic granules. Further condensation of the myofilaments leads to formation of myofibrils which then multiply within the sarcoplasm by splitting.

ORIGIN OF VERTEBRATE MUSCULATURE

Vertebrate muscles originate from three main sources;

- (1) **splanchnic mesoderm** from where visceral musculature are derived. These muscles are primarily of the smooth type and are generally associated with hollow organs;

- (2) **branchial arches** from where most muscles of the head and some muscles of the neck are derived; and
- (3) **somitic myotomes**, which give rise mainly to the skeletal muscles of the neck, trunk, and limbs.

Smooth Muscles

Smooth muscles are derived from the splanchnic mesoderm from where they migrate to colonize hollow organs of the body. In the definitive site of smooth muscle development, for example visceral organs, primitive mesenchymal cells aggregate, enlarge, and elongate. Subsequently, homogeneous threads of myofibrils begin to appear in their sarcoplasm. Contrary to cardiac and skeletal muscles, myofibrils of smooth muscle cells remain as homogeneous threads throughout life. The nuclei of smooth muscle cells retain their central position but also elongate to conform to the spindle shape of smooth muscles.

Cardiac Muscles

Like smooth muscles, cardiac muscles develop from the splanchnic mesoderm surrounding the primitive cardiac tube; they are the only striated muscles derived from the splanchnic mesoderm. The splanchnic mesoderm around the developing cardiac tube thickens and envelopes the tube, forming a wall that later becomes the myocardium.

Prenatally, the cells of the primitive myocardium contain a single centrally located nucleus but soon after birth, two or more nuclei retaining their central location may be encountered. The myofibrils begin to appear initially at the cell periphery but in a short while extend through the entire length of the cell. Cardiac muscles are easily recognized by the presence of junctional specializations on adjacent cell boundaries called intercalated disks. This becomes observable in later fetal life since they become more frequent with advancing age of the fetus.

Skeletal Muscles

Vertebrate skeletal muscles are, largely, of myotomic origin; exceptions are those of the head and some muscles of the neck. This latter group of muscles is derived from the branchial arches.

Development and subsequent positioning of skeletal muscles is influenced by certain theoretical concepts, of which the most important are:

- (i) **Longitudinal and tangential splitting** of myotomes or branchial arch muscles to give rise to two or more separate but related muscles.
- (ii) **Fusion** of adjacent myotomes to form one composite muscle. Several muscles of the vertebrate body are formed in this manner.
- (iii) **Change in orientation** of muscle fibers. Often, muscle fibers change orientation or direction from the original one.
- (iv) **Degeneration** of full or part of the myotome, resulting in formation of ligaments or aponeurotic tissue.

Generally, muscles tend to retain their original innervation throughout life. Therefore, a group of muscles supplied by the same nerve is likely to be of common origin. For example, parts of the *sternomastoideus* and *trapezius* muscles receive their innervation from a spinal accessory nerve embryologically considered part of the vagus, suggesting that these two muscles are of branchial arch origin. In some instances, especially during bone marrow malfunction such as seen during injury, the marrow cells may convert to form marrow-derived muscle cell colonies, eventually giving rise to skeletal muscle cells (Abedi et al., 2004). A subset of stem-like cells from the bone marrow, referred to as marrow stromal cells (MSCs), has been shown to be capable of differentiating into osteoblasts, chondrocytes, adipocytes, myocytes, astrocytes, and perhaps neurons (Prockop et al., 2000).

Muscles of the head

Muscles of the head largely originate from the mesenchyme of branchial arches.

There are *five* branchial arches, each giving rise to specific muscles or muscle groups innervated accordingly by the corresponding cranial nerve. The muscular derivatives of the arches and their innervations are as follows;

- (1) The **first branchial arch** gives rise to muscles of **mastication** which are innervated by branches of the **fifth cranial (trigeminal) nerve**.
- (2) The **second branchial arch** contributes to formation of muscles of **facial expression**. These muscles are innervated by the **seventh cranial (facial) nerve**.
- (3) The **third branchial arch** participates in formation of some of the **pharyngeal musculature**. These are innervated by branches of the **ninth cranial (glossopharyngeal) nerve**.
- (4) The **fourth and fifth branchial arches** form the **laryngeal, most pharyngeal, and palatine musculature**—all innervated by branches of the **tenth cranial (vagus) nerve**.

Exceptions to the branchial arch origin of the head muscles are the **lingual** and **extraocular** muscles. Both extrinsic (styloglossus, genioglossus, and hyoglossus) and intrinsic (transversus, verticalis, and longitudinalis) linguae muscles which, by and large, control elongation and protrusion of the tongue (McClung and Goldberg, 2000), are innervated by the **twelfth cranial (hypoglossal) nerve**, itself a derivative of the occipital somite. Consequently, this group of muscles is thought to be of somitic origin, arising from myotomes of the occipital region.

In lower fishes and reptiles, the extraocular muscles arise from three specialized myotomic mesenchymal masses close and rostral to the otocysts. The pattern of development of the extraocular muscles in higher vertebrates also follows that of lower fishes and reptiles. As a testimony to the myotomic origin of the extraocular muscles in higher vertebrates, their innervations come from three cranial nerves (oculomotor, trochlear, and abducens), themselves comparable to the ventral branches of somatic nerves.

Muscles of the neck and trunk

Skeletal muscles of the neck and trunk are mainly derived from **somites** and in particular, **myotomes**. Somites are segmental condensations of mesenchyme on either side of the neural tube. Further differentiation of somites leads to formation of specialized mesenchymal tissue called the **sclerotome** adjacent to the neural tube and notochord, **myotome** in the middle, and

dermatome as the outer wall (Fig. 3.1). While sclerotome and dermatome develop to form the skeleton and dermis of the skin respectively, the myotome becomes specialized to form skeletal muscles of the body (Browder et al., 1991). Myotomes in various classes of vertebrates are modeled to suit the functions performed by the definitive muscles in such vertebrates. The simplest modification of myotomes is to be found in free-swimming vertebrates in which they form **V- or W-shaped** masses suited for the wavy contraction essential for propulsion in water. In these lower vertebrates, this wavy mass has no distinct division into dorsal and ventral muscle primordia. In higher vertebrates, however, this myotomic mass is separated by a horizontal septum into **epaxial** and **hypaxial** divisions. In the chick, medial and lateral borders of dermomyotome give rise exclusively to epaxial and hypaxial muscles (Gross et al., 2004). Epaxial division eventually gives rise to all the muscles of the neck and trunk dorsal to the body axis (the body axis being roughly defined by a longitudinal plane through the transverse processes of the vertebrae). They are generally innervated by **dorsal branches** of corresponding spinal nerves associated with myotomes of each specific body region. These epaxial muscles include the **long muscles of the back (erectors of the spine or extensors of the vertebral column)** such as longissimus dorsi, iliocostalis, spinalis and semispinalis and **deeper muscles of the back**, among which are multifidi, interspinales and intertransversarii. These deep muscles appear to have retained

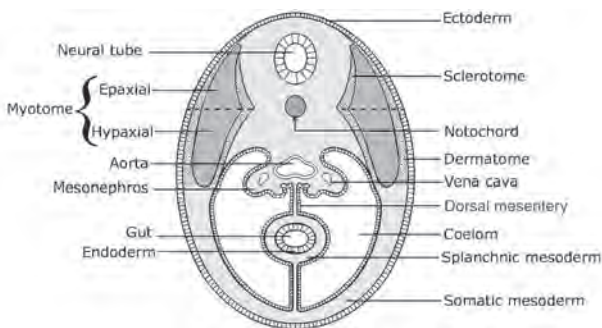


Fig. 3.1 Diagram of a cross-section of an embryo showing various structures. Early somitic differentiation is marked by formation of dermatome, myotome, and sclerotome. Myotomes are divided by a horizontal septum into epaxial and hypaxial divisions.

their segmental locations since they run short distances between contiguous vertebrae. The hypaxial division extends laterally downward to form the muscles ventral to the body axis. They are innervated by the **ventral branches** of corresponding nerves supplying myotomes of each respective region of the body. These hypaxial muscles occur ventral to the vertebrae extending to the lateral and ventral body wall, covering the thoracic and abdominal walls. Those found ventral to the vertebrae form the **prevertebral** muscles which include the psoas muscles, while the lateral and ventral body walls are formed by muscles such as the scalenus, obliquus and rectus abdominis, and parts of the trapezius and sternomastoideus. These hypaxial muscles form **flexors of the vertebral column**.

Muscles of the limb

The origin of limb musculature varies somewhat with the class of vertebrates such that in fishes, the fin muscles appear as ventral extensions of the hypaxial divisions of myotomes. On the contrary, in higher vertebrates such as birds and mammals the limb muscles develop from a preexisting local mesenchyme found within the developing limb bud. This local mesenchyme soon differentiates into extensors and flexors with the former appearing earlier than the latter. The forelimb muscles seem to precede those of the hind limb in development, resulting in early establishment of the forelimb muscles. It has been suggested that limb muscles in higher vertebrates may also arise from the hypaxial division of myotomes, but these suggestions are rather inconclusive. In lower vertebrates, postembryonic development of muscle is by hyperplastic and hypertrophic development of muscle fibers while in higher ones (e.g. mammals), it occurs by hypertrophy alone, leading to increase in the density of myofilaments.

Muscle Contraction

Muscle contraction is a highly ordered event involving complex but systematic interactions among inorganic molecules, mainly calcium, contractile proteins and enzymes. What is finally manifested as muscle shortening can be traced to the sliding movement of one contractile protein filament over the other in a series of sarcomeres. In skeletal muscles, a **sarcomere** is the unit of contraction in striated muscles.

SARCOMERE STRUCTURE

Muscles are made up of several bundles of fibers, each containing myofibrils whose cross-banding pattern is typical in skeletal as well as cardiac muscles. This cross-banding pattern arises from interdigitation of protein myofilaments within myofibrils. A single myofibril contains a series of sarcomeres each defined by the presence of **Z-lines** at both ends. The distance between these two Z-lines is the **sarcomere length** (Figs. 2.6 and 4.1). Running across each of the Z-lines are thin actin filaments which interdigitate with the centrally located thick myosin filaments. Associated with the thin actin filaments at their points of contact with Z-lines are the α -actinin proteins. Myosin filaments have a central thickening which together, form the **M-line**. Each myosin filament is thickened at its central part and the thickened areas of several filaments are in register and form the transverse striations known as the **M-line** which hydrolyzes

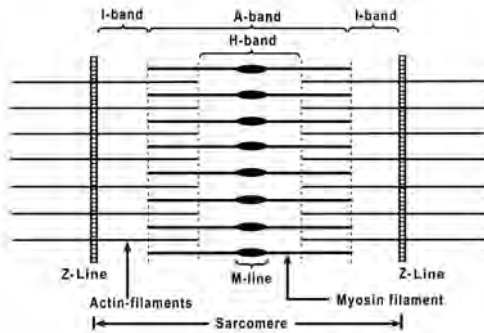


Fig. 4.1 A single sarcomere of a myofibril showing actin (thin) and myosin (thick) protein filaments and the various lines/bands associated with each of these filaments. The I-band consists of actin filaments alone while the A-band is defined by the entire length of myosin filaments. It also consists of an H-band made up solely of myosin filaments and local midline thickenings of myosin filaments forming the M-line. At their ends, myosin filaments interdigitate with actin filaments. Z-lines demarcate the sarcomere boundaries.

ATP during muscle contraction to release the energy needed for muscle contraction. That part of the sarcomere comprising only the actin filament is called the **I-band (isotropic band)** while the part traversed by the entire length of the myosin filament is the **A-band (anisotropic band)** (Huxley and Hanson, 1954; Huxley and Niedergerke, 1954).

The A-band therefore consists of two zones—one that consists solely of myosin filaments, the **H-band** (Fig. 4.2a), and a second that contains the interdigitating ends of actin and myosin filaments at either end of the A-band. This latter zone forms a cross-sectional pattern displaying a hexagonal lattice arrangement in which each inner thick filament is surrounded by six thin filaments (Fig. 4.2b).

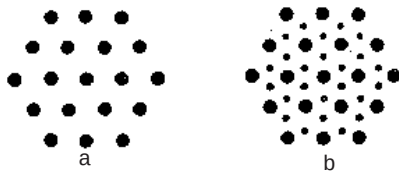


Fig. 4.2 Cross-sectional profiles of (a) myosin filaments at the H-band and (b) interdigitating ends of the actin and myosin filaments showing a hexagonal lattice in which each inner thick filament is surrounded by six thin filaments (after Fawcett, 1994).

CONTRACTILE PROTEINS

There are two main contractile protein myofilaments in a muscle—thick **myosin** and thin **actin** filaments. Myosin and actin filaments are ubiquitous within eukaryotic cells where they may be involved in locomotion or changes in cell shape (Bagshaw, 1993). Between the two filaments, actin is fairly well conserved among species but myosin shows various forms differing in amino acid composition and ATPase activity. Although these protein filaments are stable with respect to skeletal muscles, they are highly unstable in nonspecialized cells where they are assembled and disassembled when required.

Actin

The actin filament comprises a double-stranded core unit interwoven in a helical pattern. This double-stranded structure is referred to as F-actin. It is formed by **molecular realignment** or **polymerization** of G-actin molecules in the presence of magnesium ions. A complete F-actin filament contains both tropomyosin and the three subunits of troponin protein components (Fig. 4.3). This double-stranded F-actin filament contains sites for formation of cross bridges with globular heads of myosin.

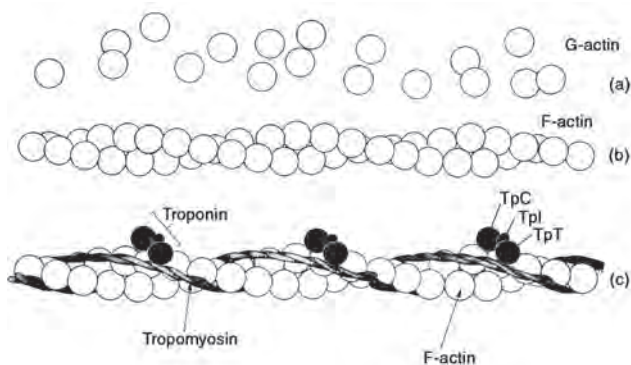


Fig. 4.3 Formation of double-stranded F-actin filament from the G-actin molecules. (a) G-actin molecules polymerize to form (b) F-actin onto which (c) tropomyosin and troponin components are added. T_pC = Troponin C; T_pI = Troponin I and T_pT = Troponin T.

Myosin

Each myosin filament consists of a long **fibrous part** connected to two **globular heads** (Fig. 4.4a). The core of the fibrous part is made up of a double helical structure, each with a single globular head at the end. Partial digestion of the myofilament using trypsin further revealed the existence of two biochemically distinct parts: (1) **light meromyosin fragment** in which ATPase activity is diminished, and hence poor F-actin binding, and (2) **heavy meromyosin fragment** comprising a short fibrous part or hinge in which ATPase activity is not exhibited and therefore does not bind to F-actin, and two globular heads in which abundant ATPase activity occurs as well as F-actin binding property. Several myosin molecules join together to form a single strand from which globular heads project to make contact with the F-actin filament during contraction (Fig. 4.4b). All vertebrates express a family of light and heavy fragments (isoforms) that together are primary determinants of force, velocity, and power in muscle fibers. Studies using single intact muscle fibers from frogs show that myosin fragments have a relationship with mechanical performance of intact single muscle fibers (Lutz and Lieber, 2002).

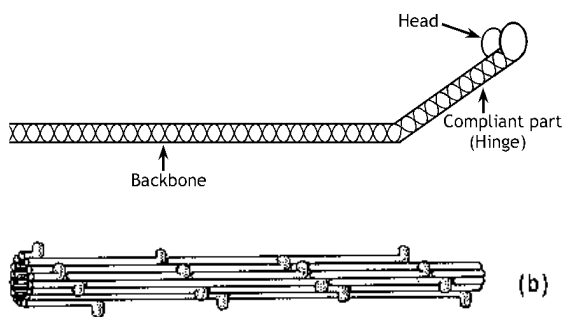


Fig. 4.4 Diagrams of (a) a single myosin molecule showing the light meromyosin (backbone) and the heavy meromyosin consisting of the hinge (or compliant part) and the globular heads and (b) several myosin molecules joining together to form a single myosin strand. Note the projecting heads of myosin molecules.

Tropomyosin

Tropomyosin is a fibrous molecule made up of α - and β -chains. It is present in all muscles and muscle-like tissues. It lies in a groove between the two F-actin polymers. In a relaxed state tropomyosin molecules cover and conceal the myosin binding sites present in the F-actin groove. During contraction, however, tropomyosin molecules are displaced by troponin components and thereby expose these binding sites.

Troponin

Troponin is found exclusively in striated muscles and consists of three separate subunits, namely troponin-T, troponin-I and troponin-C. Troponin-T binds to tropomyosin as well as the other two troponin protein molecules (troponin-I and -C). Troponin-I on the other hand, not only inhibits F-actin-myosin interaction but also binds to troponin-T and -C. Troponin-C is a calcium binding protein analogous to the commonly occurring calmodulin, a calcium-dependent regulator. These troponin molecules are responsible for displacement of the tropomyosin molecule from the attachment site of the globular head of the myosin filament. In addition, they provide binding sites for the calcium ions essential during enzymatic hydrolysis of ATP.

Actinin

This is an actin binding protein that occurs in two forms: α - and β -actinin. The α -actinin binds adjacent actin monomers of F-actin and strengthens the fibers. It also assists in attaching actin filaments to the Z-line of the sarcomere. β -actinin, on the other hand, binds to F-actin and plays a major role in limiting the length of the actin filament.

MECHANISM OF MUSCLE CONTRACTION

Skeletal Muscles

The arrangements of these protein myofilaments confer striations on myofibrils, each consisting of repeating units or sarcomeres along its length (Figs. 2.6 and 4.1). Muscle contraction essentially consists of cyclical attachment and detachment of the globular head of myosin to the F-actin filament resulting in a sliding movement of actin past myosin (Huxley and Hanson, 1954; Huxley and Niedergerke, 1954; Goldspink, 1980). This sliding movement requires energy provided by hydrolysis of ATP. Hydrolysis of ATP occurs in the globular head of myosin but F-actin is necessary for acceleration of the rate of this process and release of the byproducts (ADP and P_i). In the absence of F-actin, the myosin head hydrolyzes ATP but the byproducts cannot be released. Once the byproducts are released, a new ATP attaches to the myosin-actin complex, changing the conformation of the myosin molecule and therefore the angle of the myosin-actin attachment site. Consequent to this conformational change a sliding movement of actin over myosin filament takes place and subsequent release of myosin head or relaxation for the next attachment. In this movement, the myosin filament is usually stationary while the actin filament is mobile. Expressed in terms of the sarcomere bands, a fully contracted muscle fiber has its I- and H-band completely obliterated while the A-band persists.

Smooth Muscle

Smooth muscle fibers lack T-tubules and have poorly developed sarcoplasmic reticula; hence calcium required for contraction is stored outside the cell. Striations are missing since the protein filaments are formed only when needed and dissociate soon after. In smooth muscles, calcium normally binds to the protein calmodulin and not troponin, as is the case in skeletal muscles, in order to trigger off a contraction. The myofilaments in smooth muscles attach to the cell's plasma membrane. Since these filaments are not organized into sarcomeres as in skeletal

or cardiac muscle fibers (Fig. 4.5), they exhibit a greater degree of movement and can contract to shorter lengths than either of the former two muscle fiber types.

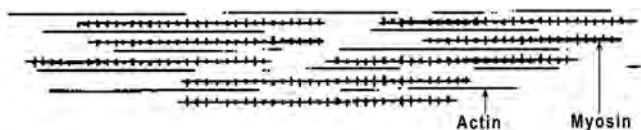


Fig. 4.5 Diagram showing arrangement of protein myofilaments in smooth muscles. The myofilaments are very unstable and dissociate soon after use. This makes smooth muscles appear nonstriated.

The two types of smooth muscles (visceral or single-unit and multiunit muscles) show different types of contraction and innervation. Visceral smooth muscle fibers show spontaneous and rhythmic contractions that are usually initiated by the stretching of muscle fibers. Individual visceral smooth muscle fibers are joined by gap junctions into large continuous sheets. The autorhythms (initiated by a fiber whose plasma membrane is depolarized) spread across the entire smooth muscle until the spreading waves of contraction become strong enough to push contents of a hollow organ progressively along its lumen in a phenomenon known as **peristalsis**. Although these contractions are myogenic, their rate and force may be regulated by neurons that terminate on some of the muscle fibers. Such smooth muscle fibers are found in the digestive tract, urinary bladder, and the uterus.

Multiunit smooth muscle fibers comprise many single independent units. Nerve fibers terminate on most of these smooth muscle fibers and their contractions are neurogenic (initiated by nerve impulses). Such fibers are found in walls of blood vessels, iris of the eye, vas deferens of the male reproductive system, and arrector pili muscle of the mammalian skin.

REGULATION OF MUSCLE CONTRACTION

Muscle contraction in vertebrates is regulated by two mechanisms: actin-based and myosin-based mechanisms. Calcium ions

play a significant role in the regulation of muscle contraction. All muscles contain myosin, actin, and tropomyosin proteins but only striated muscles include the troponin system. Therefore, the actin-based regulatory mechanism occurs in all vertebrate striated muscles while the myosin-based mechanism predominantly exists in smooth muscles.

Skeletal Muscles

Principally, the actin-based mechanism relies on exposure or concealment of the myosin head binding sites on the F-actin. At rest, striated muscles are inhibited by the troponin system. Thus, troponin-I inhibits binding of the myosin head to F-actin either by changing the conformation of F-actin through tropomyosin or direct positioning of tropomyosin onto the F-actin groove to block the myosin head attachment sites. When excited through release of acetylcholine from the nerve terminals, striated muscles rapidly release calcium ions from the sarcoplasmic reticulum through the T-system into the sarcoplasm in striated muscles, the sarcoplasmic reticulum is the major organelle responsible for regulation of free calcium ions (Devlin, 1997; Tupling, 2004). Subsequently, calcium ions come to occupy their binding sites on troponin-C. The calcium ion laden troponin-C then interacts with troponin-I and -T in a way that alters their relationship with tropomyosin. As a result, tropomyosin either moves out of the groove or changes the conformation of F-actin leading to exposure of the myosin head binding sites on the F-actin. The myosin head then binds to the F-actin groove leading to the onset of sliding movement. Sequestration of calcium ions by the sarcoplasmic reticulum through the pumping action of the calcium ion pump marks the onset of relaxation.

Cardiac Muscle

Cardiac muscle (striated involuntary) fibers form electrically coupled junctions known as **intercalated disks** and also bridges or branches with other fibers. These features allow cardiac muscle to form a continuous, electrically coupled mass known as a

syncytium or unit of combined cells. The entire cardiac muscle thus forms a unit that spreads a single impulse across the entire sarcolemma of the heart, causing rhythmic and continuous contractions that pump blood in a coordinated manner to the rest of the vertebrate body.

Cardiac muscle fibers have sparse sarcoplasmic reticulum compared to skeletal muscle fibers. During cardiac muscle contractions, much of the calcium ions enter the sarcoplasm from outside the cell. Since the sarcolemma of the cardiac muscle is capable of sustaining a longer impulse than that of the skeletal muscle at any time, Ca^{2+} will remain in the sarcoplasm of the cardiac muscle cells for a longer time. Cardiac muscle fibers contracting at the same time show prolonged contraction and do not exhibit rapid twitch as a result. This process prevents impulses from traveling rapidly enough to produce tetanus. Cardiac muscle therefore does not show signs of fatigue as a result of running out of ATP since it cannot sustain long tetanic contractions. Cardiac muscle contractions are myogenic and exhibit a continuous rhythm of excitation regulated by the autonomic nervous system and hormones.

Smooth Muscles

Since smooth muscle lacks the troponin system, its regulation of contraction is therefore myosin-based. The driving principle in this case is phosphorylation of the myosin light chain. Smooth muscle myosin contains a light chain called the p-light chain, which inhibits binding of the myosin molecule to F-actin under resting conditions. On stimulation, calcium ions are released into the sarcoplasm where they bind to calmodulin carrier protein. The calcium ion carrying calmodulin then activates the cAMP-independent myosin light chain kinase. This activated light chain kinase therefore phosphorylates the myosin p-light chain. Following phosphorylation of the light chain, the p-light chain inhibition is removed, resulting in binding of myosin to F-actin. As a consequence F-actin activates the ATPase, thereby commencing the contraction process in smooth muscles.

MUSCLE RELAXATION

During muscle relaxation in striated muscles, calcium ions in the sarcoplasm are pumped back into the sarcoplasmic reticulum, a process that lasts a few milliseconds. The active transport carriers of the sarcoplasmic reticulum have a greater affinity for the Ca^{2+} than troponin. Lack of Ca^{2+} leads to blockage of active sites on actin by tropomyosin. This blocks myosin bridging sites, preventing formation of cross bridges in the process, which arrests muscle contraction.

In smooth muscles, relaxation occurs when there is a reduction of calcium ion concentration in the sarcoplasm. When this happens, the calmodulin-bound calcium ions dissociate causing inactivation of the myosin light chain kinase. Once this enzyme is inactivated, phosphorylation of p-light chain ceases, occasioning inhibition of myosin-F-actin interaction, hence, relaxation.

TEMPERATURE AND SLIDING FILAMENT MECHANISM

The sliding filament mechanism is able to operate at a wide temperature range as seen in ectothermic vertebrates. The contractile apparatus have been shown to differ in fish living at different temperatures. The Antarctic fish, which lives at temperatures of -1° to 4°C , has been shown to have a high specific ATPase activity at the low temperature range (Johnston et al., 1975b). The myofibrils of such fish are very susceptible to heat denaturation as the myosin has a more rigid type of molecular structure compared to the heat-stable contractile system present in fish that live at higher temperatures. It has been shown (Johnston, 1979) that temperature acclimation in fish is accompanied by changes in the rate at which cross bridges work (myosin ATPase activity). Such changes may involve the rate at which active sites on actin filaments become available; an activity that involves the troponin complex.

TYPES OF MUSCLE CONTRACTION

Energy consumption during muscle contraction varies depending on muscle types and kinds of contraction they perform. Such contractions include; **isometric**, **isotonic**, and **negative**.

Isometric Contractions

During isometric contractions, the muscle length remains the same though tension increases. Isometric contractions are usually less costly than isotonic contractions (Abbott, 1951). More energy is usually spent during the first phase of an isometric contraction than the latter part in which the contraction is maintained (Aubert, 1956). Isometric contractions save a lot of energy, as seen in slow contracting muscles with slow and tonic fibers. This is because the cross bridge cycle is longer in slow fibers compared to fast ones, leading to less utilization of ATP, which is usually broken down when cross bridges detach. During *in situ* isometric contractions both heads of the myosin molecule cooperate in a pairwise manner to form cross bridges. Similarly, in the case of unloaded shortening myosin cross bridges may also be capable of cooperation that is sensitive to longer range interactions transmitted from other cross bridges (Barnett, 2001).

Isotonic Contractions

Isotonic contractions cause development of force and shortening of muscles. Such contractions result in vertebrate movements or their parts. Contractile efficiency varies depending on species and type of muscle involved. For example, tortoise muscle appears to be more efficient than frog muscle, suggesting that speed has been sacrificed for efficiency during the course of evolution (Goldspink, 1980). Slow muscles have a higher maximum efficiency than fast ones because they tend to perform more work per molecule of ATP broken down. Energy utilization (ATP broken down) decreases when the optimum velocity of contraction is exceeded because the thin filaments

are moving too rapidly for enough cross bridges to make contact and complete their cycle.

Negative Work Contractions

This type of contraction occurs when a muscle is stretched while developing force or tension concomitantly. A good example of this kind of contraction is seen when animals walk downhill. Negative work contractions develop more tension than would be the case by the same muscles during an isometric contraction. The extra tension developed does not cost the muscles extra energy as might be expected from the extra tension developed by pulling out the cross bridges.

MUSCLE FATIGUE

Physiological muscle fatigue is caused by relative lack of ATP, which renders myosin cross bridges incapable of producing the force required for muscle contraction. Low levels of ATP result from low levels of O₂ and glucose or inability of muscle fibers to regenerate ATP at a rate that meets muscular demands. High levels of lactic acid and metabolites also contribute to physiological fatigue.

RIGOR MORTIS

Rigor mortis (Latin, stiffness of death) is stiffness of skeletal muscles some time after death. At the time of death, some postural muscles are still in contraction because myosin and actin cross bridges are still intact. Depletion of ATP leads to failure of the calcium ion pump in the sarcoplasmic reticulum. When this happens, the calcium ion concentration in the

sarcoplasm remains high, thereby saturating the binding sites on troponin-C. Consequently, the myosin head-binding sites on F-actin remain exposed, leading to sustained engagement of these myosin heads to F-actin. As a result, the striated muscle exhibits sustained contraction leading to a condition known as **rigor mortis**. ATP is necessary in order to pump calcium ions out of the myofibers. This action is followed by muscle relaxation. As the ATP reserves are quickly exhausted from muscle contraction and other cellular processes, actin and myosin fibers will remain linked until the muscles themselves start to decompose due to tissue decay and leaking of lysosomal intracellular digestive enzymes.

SHORTENING AND POWER OUTPUT OF MUSCLES

Striated vertebrate muscle, with approximately parallel fibers, is capable of shortening (contraction distance) by nearly 60% of its stretched length or as much as 30% of its resting length; the longer the muscle, the greater the contraction distance. Further shortening is prevented when the thick filaments are able to make contact with the Z-line. Smooth muscle can undergo a considerable degree of shortening as actin filaments can interact with several myosin filaments in succession (see Fig. 4.5).

An increase in the force developed by muscle and its rate of shortening results in an increase in power output and vice versa. The maximum sustainable power is seen in some bird flight muscles such as the humming bird. Limiting factors to maximum power output seem to be oxygen supply and accumulation of metabolites rather than limitations in the sliding filament mechanism.

Body Support in Vertebrates

Locomotion is brought about by skeletal muscle in vertebrates. The design of the musculoskeletal system together with the nature of joints and ligaments determines the type of movements possible in different body parts of vertebrates. Cartilaginous or bony parts of the skeleton can be united by interstitial tissue (mainly connective tissue) whose composition determines the degree of movement possible. Some joints lack joint cavities (gaps) and are greatly limited in the movements they perform while others are freely movable as a result of loss of interstitial tissue and development of synovial cavities. Synovial joints are found in most joints of the vertebrate body. Since vertebrates live in different environments and perform different types of movements, the support offered to the body and the locomotion performed by each group are considered separately here.

SWIMMING

Although most vertebrates can perform some degree of swimming, this mode of locomotion remains the main type of movement in fishes, marine mammals, some reptiles, and larval amphibians. Primary swimmers such as fish and a few secondary swimmers such as salamanders and crocodiles move by lateral undulations of the body trunk. Most secondary swimmers and a few fishes propel themselves by oscillations or paddle-like

movements of their appendages while others, such as whales, perform dorsoventral undulations of their caudal flukes. This section discusses fish swimming as an example of vertebrate movement in water.

Fish Swimming

Many fish have evolved a streamlined torpedo-shaped body as an adaptation to swimming in water, which offers more resistance to movement than air albeit offering bouyancy to fish. Fish show (most often) various degrees of ovoid shape in cross section. The bodies of fish are also covered by mucus which smoothens surface irregularities and reduces viscosity, thereby reducing the drag effect. Fish show departures from the general fusiform shape as an adaption to a specialized mode of life. Some fish show compressed, depressed and elongate forms. Fish have to generate enough momentum to overcome the downward pull not compensated for by bouyancy if they are to avoid sinking, especially those that lack a swim (gas) bladder. This puts some extra energy demands on fish which do not have to expend extra energy for thermoregulation, as do birds and mammals.

In fishes, muscular contractions frequently result in movements of the entire body rather than appendages only. Lateral undulatory contractions in the body trunk and tail regions are brought about by the segmented myomeres that are chevron-, w-, or v-shaped (Fig. 5.1). Serial contractions of myomeres form a smooth wave along the body as a result of the overlapping of myomeres. Since each myomere is a separate muscle that runs transversly on each side of the body, and myomeres have not undergone differentiation into several short and long muscles that are innervated separately, contraction of myomeres on one side of the fish results in bending of the head and tail to the same side. The presence of a vertebral column prevents the body from shortening during such contractions. The generated propulsive forces pass along the trunk in a caudal direction from the head to the tail region. The caudal trunk and tail region show greater lateral undulatory movements than the rest of the body. Together with a broad and flat tail, the amount of

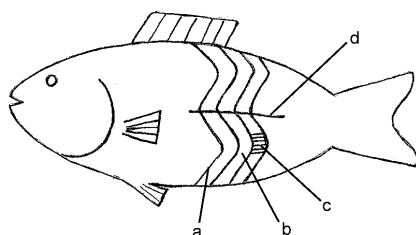


Fig. 5.1 Schematic presentation of a fish. (a) myoseptum, (b) myomere, (c) direction of muscle fibers, and (d) horizontal septum.

water moved by the caudal part of the fish is greater than other parts of the body. Fish are also capable of swimming backward when the body wave starts from the tail to the head region. This type of movement is seen in elongated fishes that have anguilliform locomotion (see types of fish swimming) such as eels. Lampreys are an exception to this type of swimming as they cannot produce reverse waves and compensate this lack with very flexible bodies capable of performing the tightest hair-pin turn with ease.

Fish swimming movements

Fish swimming can be divided into four categories depending on the nature of contraction of myomeres as anguilliform or eel-like, ostraciform or trunk-like, carangiform, and thunniform.

Anguilliform locomotion is serpentine and seen in a crawling snake or swimming eel. This type of movement is brought about by sequential and alternate contractions of myomeres on each side of the body. Most of the trunk and tail move back and forth during this type of movement.

Ostraciform locomotion is a wig-wag motion involving mainly the tail as the trunk is relatively rigid. The tail will move back and forth like a paddle. The movement is induced by alternate contractions of all the muscle segments on one side of the body and then the other. The body moves in a series of short cross arcs in the water as the fish progresses forward, as seen in boxfishes.

In carangiform, the most common type of locomotion, the fish swims forward by side-to-side sweeps of the tail region. It is intermediate between anguilliform and ostraciform types.

Alternate contractions occur on one side of the body and then the other, starting from the head region and traveling backwards.

In thunniform swimming, undulations are limited to a little more than the tail. Such swimming is seen in tunas and some sharks.

TERRESTRIAL VERTEBRATES

Terrestrial vertebrates have had to adapt to an environment that does not offer buoyancy to their weight since air is not a dense medium. The vertebral column has evolved to support the weight of the body trunk and transfer the same to the girdles and their appendages. The vertebral bodies (centra) are ossified in most species and have intervertebral disks between the bodies of adjacent vertebrae that act as shock absorbers and permit bending of the vertebral column (Fig. 5.2).

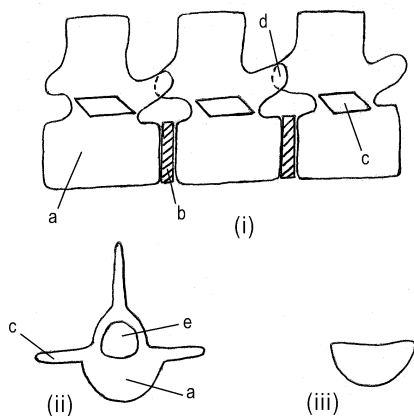


Fig. 5.2 (i) Lateral view of mammalian vertebrae. (a) vertebral centra (bodies), (b) intervertebral disk, (c) transverse process, (d) point of articulation between articular processes (zygapophyses) of neighboring vertebrae and cord passes. (ii) anteroposterior view of a vertebra, (e) vertebral canal through which the spinal cord passes. (iii) anteroposterior view of an intervertebral disk.

Birds

Flying birds are capable of flapping their wings, soaring and gliding. The two major muscles involved in the downstroke and upstroke movement of wings are *pectoralis superficialis* and *supracoracoideus* respectively (Fig. 5.3). Both are ventral muscles and their location helps maintain the low center of gravity necessary for stability while still enabling birds to move their wings up and down as a result of the way their course is designed. The upstroke is flexed to minimize aerodynamic drag and does not produce much aerodynamic force. In flight muscles, the muscle fiber composition is mixed. Such an arrangement ensures that the muscle is maintained at a reasonable weight without increasing the power requirements of flight due to extra muscle weight if the fiber types were to be distinguished, as in a two- or three-gear system. The intrinsic speed of shortening of the fibers has adjusted to the flapping frequency of the wings with smaller birds having faster muscle fibers.

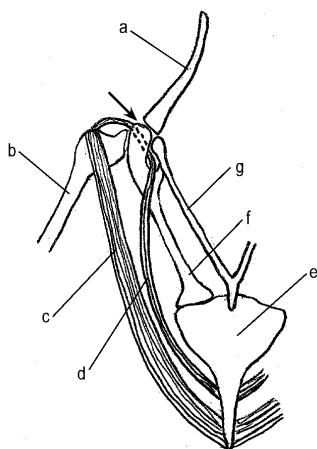


Fig. 5.3 Anterior view of a bird showing the main flight muscles. (a) scapula, (b) humerus, (c) m. *pectoralis superficialis*, (d) m. *supracoracoideus*, (e) sternum with ventrally pointing keel, (f) coracoid and (g) clavicle. Arrow indicates the location of triosseal canal.

As energy costs of gliding are low, muscle action here is mainly isometric (see Chapter 4). Slow fibers are recruited for this purpose, which is a way of saving energy, as seen in gliding large birds and certain birds during migration or in flight

for long periods. During gliding, few muscle fibers are recruited as only force for maintaining posture against air currents and the downward pull of gravity on the bird is required. More energy is required during forward flight as a bird has to overcome the drag of its body.

Tetrapods

Evolution of a stronger vertebral column, pectoral and pelvic girdles and ribs has enabled amphibians, reptiles and mammals to preclude the dorsoventral collapse of their body trunks while the animals are lying on the ground as this would put too much pressure on their viscera. Tetrapod amphibians and reptiles raise their bodies off the ground when they are moving and tend to lie down when stationary, whereas most mammals lie down when resting.

BOW AND BOWSTRING ANALOGY

The bow and bowstring analogy for support of the body was suggested by Slijper (1946). It proposed that the trunk construction of quadrupeds be likened to that of a 'bow and bowstring' or arched bridge. The theory considers this relationship to the whole, living and moving organism. The theory compares an arched bow held by a tension-fast string to a bowstring bridge and the roadway stretched between the ends of the bow.

In the tetrapod body, the "bridge" is constructed of bones, ligaments, muscles, and tendons and is capable of carrying the body weight. The arch (weight-bearing bridge) is represented by the vertebral column (thoracic and lumbar sections) together with the pelvis with its associated muscles and ligaments (Fig. 5.4). The trunk may be curved like the archer's bow, as seen in many small mammals such as guinea pigs and rabbits or may be nearly straight with the ends bent down like the violinist's bow as is the case in crocodilians, lizards, and many large mammals. The trunk takes an intermediate position in

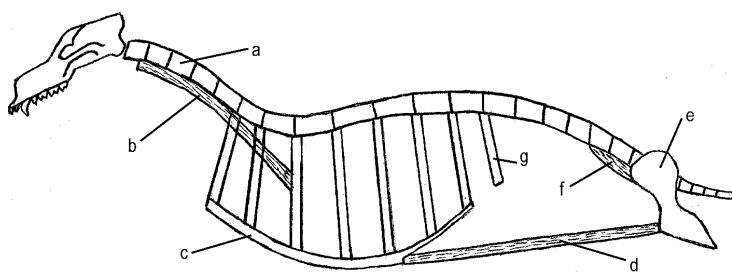


Fig. 5.4 Living “bowstring” bridge. (a) cervical vertebra, (b) *scalenus* muscle, (c) sternum, (d) *m. rectus abdominis*, (e) ilium of the pelvic girdle, (f) *mm. Psoas* and *quadratus* and (g) floating rib

carnivores. The back often forms an arch due to the presence of intervertebral disks, the ligaments and also muscles of the back. The principal string of this living bow is the abdominal musculature (principally *rectus abdominis*), the linea alba, and the sternum. The *psoas* and *quadratus* muscles under the lumbar vertebrae form a shorter secondary bowstring. The ‘string’ is connected to the bow cranially by the ribs and the *scalenus* muscle and posteriorly by the pelvic girdle. The nuchal ligament forms an inverted bow (with its strands forming multiple bowstrings) whereas the cervical vertebrae form the arch. When the neck is stretched the arch decreases.

The weight of the thoracic and abdominal organs is supported by the tension-fast “string”, which is further supported by the pressure-fast “bow” of ribs, and the transverse and oblique abdominal muscles which transfer part of the weight directly to the axis of the body. The “bowstring bridge” of the body is dynamic and can be altered by muscular action as it participates in body movements.

The human foot can be likened to a beam loaded at the center. This beam is also a bow that touches the ground at both the ball of the foot and the heel. The beam or bow is prevented from collapsing by muscles of the foot and the planter aponeurosis which is like a bowstring. Lifting the toes tightens the bowstring.

ADAPTATIONS

Tetrapods have evolved various adaptations for minimizing energy expenditure while standing and during movement. Heavy herbivores show an increased number of muscles with tendons especially those that support the limbs. Tendons are able to store energy as elastic strain energy at one stage of a locomotor cycle through a change in their length and not muscle; tendons can be stretched to 5% of their original length. The stored energy can then be released at some other stage when required. There are various elastic storage systems in animals such as the anterior interosseus tendon of sheep (Cuming et al., 1978), the ligamentum nuchae of many large mammals (Alexander, 1968), and the *gastrocnemius* tendon of kangaroos (Alexander and Vernon, 1975). As an energy store, tendons are several times more effective than muscle. Tendons can also amplify the power output of a muscle and this enables smaller animals to supplement the power output of muscles that might not be adequate for rapid acceleration.

Tendons and ligaments are composed of tightly packed bundles of collagen fibers. Ligaments unite bones at joints. Tendons and ligaments have high tensile strength and are able to resist tension and twist to a great degree but their resistance to compression is low. These two structures are thus binding and not supporting structures. The deposition of fibrocartilage or bone known as the sesamoid bone in parts of the tendon is likely to encounter considerable compressional pressure.

Muscles that provide tension to tendons do so by developing isometric tension (force) which is less costly than isotonic contractions. The muscles involved in tensioning tendons are pennate and generate great isometric forces. For example, ungulates with heavy heads have thick and strong nuchal ligaments that are rich in elastic fibers (Fig. 5.5). When these animals lower their heads, the ligaments are stretched by the weight of the head and store the energy that stretched them. When the animal raises the head it spends less energy in doing so than would be the case with muscle contraction as the energy stored

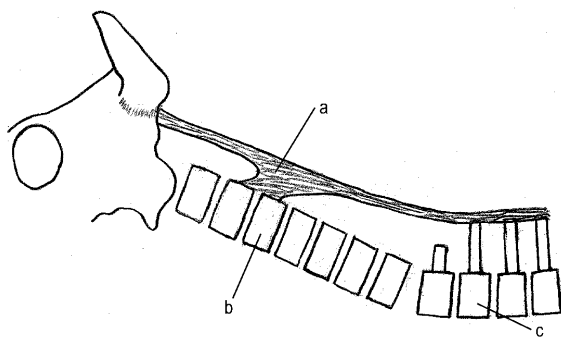


Fig. 5.5 Neck region of a large herbivore showing the nuchal ligament. (a) nuchal ligament, (b) cervical vertebra, and (c) thoracic vertebra.

in the ligaments is released and utilized in raising the head. The same principle applies to limbs during walking and running. Although isotonic contractions are involved in such movements, much energy is not required as the energy cost of running in animals with light limbs does not differ much from that of animals with heavier limbs (Taylor et al., 1974).

In a standing position, various limb joints must remain stable in order to support the animal. This action is aided by the contraction of neighboring muscles with minimal energy expenditure. Some animals have evolved methods that minimize this expenditure. The presence of strong ligaments associated with several joints and the structure of some articular surfaces restrict movement in some joints. Some neighboring bones are arranged vertically in relation to each other, thus transferring the weight of the animal directly from one bone to another and to the ground. Such a case is seen in many heavy terrestrial vertebrates, especially in the more distant joints of their appendicular skeleton such as carpometacarpal and metacarpophalan-geal articulations.

The structure of certain joints restricts movement in certain directions. The olecranon process of the ulna (at the elbow joint) and the calcaneus of the hock are levers for muscle attachment and prevent hyperextension of these joints. The cruciate and other ligaments at the back of the knee joint prevent hyperextension of this joint. Such joints do not need much muscle action to avoid hyperextension.

In the human being, the knee joint can be extended to slightly beyond vertical. When weight is put on such a limb, there is a slight rotation in a direction which prevents the joint from being extended further. Such action prevents bending of the joint in an opposite direction and provides a body in an upright position with a lock against flexion.

QUADRUPED LIMBS

Vertebrates must obey the laws of statics concerned with the construction of the body in a manner that ensures equilibrium in the total individual parts of an animal together with the body when the animal is standing still or is in motion.

The center of gravity varies in different animals and in the same animal at various times depending on posture and quantity of abdominal contents. The center will shift forwards when the head and neck are lowered and abdominal organs are empty. In quadrupeds, the center normally lies nearer the forelimbs so that they carry more weight than the hindlimbs. For example, the forelimbs carry 55% and as much as two-thirds of the body weight in the horse and dog respectively.

The arrangement and composition of limbs in terrestrial vertebrates vary considerably depending on the movements they perform. For example, the scapula, clavicle, and coracoid show a varied level of development and relationship to the trunk depending on functions performed by the forelimb. In species capable of performing several functions such as gripping, climbing, digging, flying or walking, the shoulder requires to be connected to the trunk more firmly than those whose limbs are used only for supporting body weight and walking. In flying birds, many reptiles, and monotremes, the three bones of the pectoral girdle are well developed while in many mammals in which the limbs are used mainly for support, the scapula is the most developed and the other bones are either rudimentary or missing. The pelvic girdle normally has a uniform function and thus requires less variation in structure.

There has been progressive reduction in the number of digits that make contact with the ground in tetrapods which reduces the size of the overall bearing surface and the associated friction. Reduction in the number of digits has increased stability and fleetness of foot. Such a change has resulted in increased unity of the bones of the antebrachium (radius and ulna) which has reduced their mobility. In primates, the two bones are not united and have capacity for rotation against each other in performing pronation (inward turn of the arm) and supination (outward turn of the arm).

Since many of the pectoral and pelvic limbs in most tetrapods are made up of joints with angled articulating bones and not solid vertical columns, they require special structures for stabilization, which include ligaments, muscles, and tendons.

Pectoral Limb

In the pectoral girdle region, weight is transferred from the trunk to the girdle and its appendages through a muscular sling (Fig. 5.6). The sling takes up and cushions the weight of the body as it is pushed forward by the pelvic limb. The ventral serrate muscle (*serratus ventralis*) is the most important suspensory apparatus of the trunk in mammals. In large herbivores the thoracic part of the muscle is heavily permeated by a strong

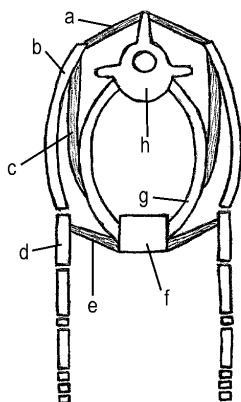


Fig. 5.6 Muscular sling of the pectoral (fore) limb. (a) *trapezius* muscle, (b) scapula, (c) *m. serratus ventralis*, (d) humerus, (e) pectoral muscles, (f) sternum, (g) rib, and (h) thoracic vertebra.

tendinous sheet. The muscle can also function as a passive supporting sling.

The forelimbs are the main weight-supporting limbs of the trunk despite having less musculature than the hind limbs. The limbs increase in their relative length from the plantigrade (walk on palms), digitigrade (walk on digits) to unguligrade (walk on tips of their digits) stance. The joints of the limbs are prevented from buckling by their ability to be “locked” (immobilized). Muscles involved in the locking mechanism are heavily permeated by tendons so as to act as contractile tension bands. The joints of the forelimb are supported by strong collateral ligaments located on either side of the joints except the shoulder joint in which the joint is reinforced by the *infraspinatus* and *subscapularis* muscles located on the lateral and medial sides of the scapula respectively. Such an arrangement ensures that in large mammals, joints distal to the shoulder joint can only flex in the transverse plane to a limited extent.

Some pectoral limb joints (in some mammalian species) have developed mechanisms that stabilize the joints and prevent them from knuckling backward and forward as is the case with the shoulder and fetlock (metacarpophalangeal) which are highly flexed and extended respectively (Fig. 5.7). In the horse, the *biceps brachii* together with its branch *lacertus fibrosus* prevent the shoulder joint from overflexing backward while the *triceps brachii* prevents it from buckling in the opposite direction. The fetlock and digital joints are stabilized by ligamentous mechanisms. The fetlock in ungulates is mainly locked by the passive stay apparatus which consists of a ligamentous sling that extends from the caudal surface of the proximal end of the metacarpal, down under the fetlock joint (where it is anchored to the sesamoid bones), and then around the proximal phalanx to insert on the cranial surfaces of the distal phalanges. The stretched ligament stores a lot of energy, which is released by returning the joint to a neutral angulation when the load is relieved.

Pelvic Limb

In the pelvic region, the pelvic girdle is fused to the sacrum and

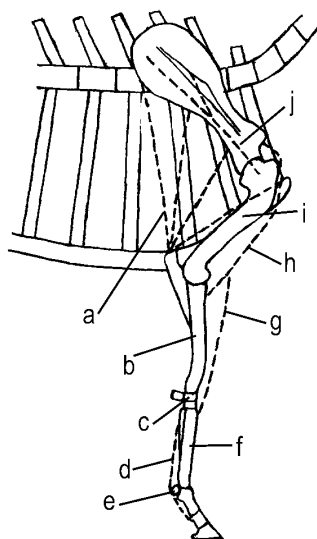


Fig. 5.7 Pectoral limb of a horse. (a) *triceps* muscle, (b) radius, (c) carpal bones and joint, (d) ligamentous sling of the fetlock, (e) proximal sesamoid bone behind the fetlock joint, (f) metacarpal (metapodial or cannon) bone, (g) *lacertus fibrosus*, (h) *biceps brachii* muscle, (i) humerus, and (j) *infraspinous* muscle. The subscapular muscle is located on the medial side of the scapula.

ribs (Fig. 5.8). The forces for forward movements transferred to the trunk depend on the number of vertebrae and ribs involved and their degree of fusion. The joints of the pelvic limb are

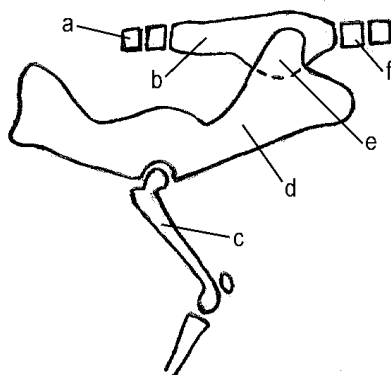


Fig. 5.8 The pelvic girdle union with the body axis. (a) caudal vertebra, (b) sacrum, (c) femur, (d) ilium of pelvic girdle, (e) sacroiliac joint, and (f) lumbar vertebra.

more acutely angled than those of the forelimb. The head of the femur is joined to the pelvis by the ligament of the femur and muscles of the hip joint in ungulates. The rest of the pelvic limb joints are fixed by tendons, ligaments and some muscles.

Large ungulates such as perissodactyls (odd-toed) and artiodactyls (even-toed) have evolved systems that minimize energy expenditure when they are in a standing position. The pelvis is held in a position passively by ligaments. As the support column of the hindlimb requires greater stability than the forelimb in the standing position, ungulates have mechanisms that stabilize the stifle (knee) and hock (ankle) joints, thereby minimizing energy expenditure. The stifle is stabilized by the *quadriceps* group and the patellar mechanism whereas the hock is kept in an extended position by the *gastrocnemius* and part of the *superficial digital flexor* (Fig. 5.9). This mechanism is subject to voluntary control. The digital joints are supported by the tendons of the long flexors and suspensory apparatus. The distal part of limb muscles are highly tendinous in herbivores. The horse can “lock” its knee and passively fix the ankle enabling the animal to stand for long hours even while asleep. When the stifle is extended, the patella (which is anchored to the tibia by

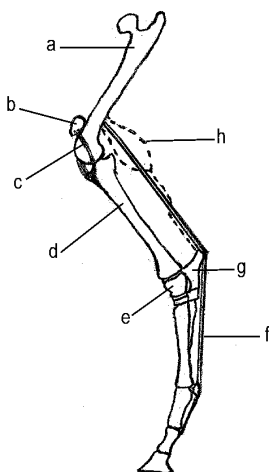


Fig. 5.9 Pelvic limb of a horse. (a) femur, (b) patella, (c) patellar ligament, (d) tibia, (e) talus of the hock (ankle) joint, (f) superficial digital flexor muscle (tendon), (g) calcaneus, and (h) gastrocnemius

three ligaments) is pulled by the *quadriceps* medially (inwards) and locks on an enlarged ridge on this side in what is known as the “patellar mechanism”. The stifle is locked and prevented from flexing in the process. The hock is simultaneously and passively fixed in the process because of the functional link between the two joints through the common calcaneal tendon that runs along the caudal surface of the tibia from the distal end of the femur to the hock in what is referred to as the “frame-saw” construction. The tibia and the common calcaneal tendon form the long arms of a parallelogram whose short arms are formed by the distal end of the femur above and the calcaneus below. The patella has to be pulled down into the patella groove by the *quadriceps femoris* and the *biceps femoris* before the limb can be flexed.

During inactivity, animals may avoid a support role by the legs, especially in species in which there is reduced permeation of muscles by tendons. In such species, muscular effort is necessary for the joint support of limbs and so they fatigue faster while standing and tend to reduce weight on their legs by resting sprawled on their ventral surface (amphibians and reptiles), crouching (rodents and rabbits), lying down (carnivores and many artiodactyls) and sitting down (primates).

Dynamics

The trunk region of heavy herbivores is more rigid compared to other mammals. This is because it has to support the weight of the herbivores and the forage consumed. The intrinsic musculature of the pectoral and pelvic limbs serve several functions which include standing, locomotion, and performing several manipulations. Although the pectoral limbs were originally used for several functions such as digging, climbing, and gripping, as seen in insectivores, many rodents and apes, the primary function of the limbs is one of support and check in forward motion. In exceptional cases such as walking uphill and climbing, the limbs play a role in pushing the trunk forward. The intrinsic musculature of the pectoral limbs has a greater static function than that of the pelvic limbs. In most mammals, the

intrinsic musculature of the pelvic limb is involved in locomotion, providing the forward propulsive forces. Pelvic limbs are adapted to perform this function as a result of the strong union between the pelvis and the sacral vertebrae, the great angulation of joints, the longer bones, and stronger muscles. The pelvic limb has one more obtuse angle (through the tarsal joint) than the forelimb. The *extensor* muscles of the pelvic limbs are well developed since they have to extend the joints in shifting the trunk forward when the limbs are pressed against the ground.

Evolution of the Vertebrate Muscular System

Cephalochordates, probably the closest living relatives of vertebrates, are a subphylum of the Phylum Chordata. They are important in understanding the morphology and evolution of chordates in general and vertebrates specifically. These fish-like marine organisms, also known as amphioxus, lancets (“little spears”) or acrania, thought to be at the transition between invertebrates and vertebrates might have had a common ancestor with vertebrates. One example of these marine creatures, acorn tongue worm, has typical chordate features such as pharyngeal slits, dorsal nerve cord, and ventral nerve cord. It lacks a true notochord but possesses a notochord-like structure projecting on the dorsal part of the pharynx, typical of members of the phylum Hemichordata. Vertebrates, protochordates (cephalochordates and tunicates), hemichordates and echinoderms have a link in the ammocoete (Gr. *ammocoetes*, something bedded in sand) larva of lampreys. Ammocoete larvae are filter feeders like protochordates and resemble amphioxus superficially with a well-developed notochord and myomeres or muscle segmentes (Fig. 6.1). The musculature of the body of cephalochordates is divided into V-shaped blocks (myomeres) and there is a postanal tail. Their fossil record is sparse since they lack hard parts. Fossil cephalochordates have been found in old rocks predating the origin of vertebrates. The earliest cephalochordate fossils known reportedly belong to *Yunnanozoon* from the Early Cambrian of southern China (Chen et al., 1995). These fossils support the view that the chordate

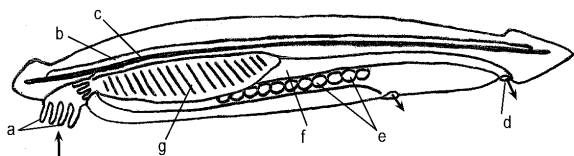


Fig. 6.1 A cephalochordate, *Amphioxus* or *Branchiostoma*, that is pointed at both ends and measures about 3-5 cm long. These chordates burrow in sand of sea water and feed by filtering food particles from the water through their gills. Note that the notochord extends all the way to the head. (a) mouth, (b) neutral tube, (c) notochord, (d) anal opening, (e) gonads, (f) digestive tract, and (g) gill slits.

lineage appeared early in the known history of the animal kingdom and point to the origin of true vertebrates from a cephalochordate-like ancestor that resembled tunicates. The larvae of tunicates resemble minute tadpoles superficially, with long tails that contain a notochord and a large part of the nerve cord. Each larva on hatching from the egg, swims about for a short time before settling down to the bottom, losing its tail and notochord, and developing into a sessile adult in most species. This form could have matured into a stage similar to the modern tunicate larva. The early ancestors of vertebrates could have separated from the tunicate evolutionary line.

Both the skeletal system (which leaves a better fossil record than soft tissues) and observation of species in which muscles have not migrated far from their embryonic origins such as fish, are important in reconstructing evolution of the vertebrate muscular system from older, lower and simpler forms of life to recent and more advanced species. Changes in the muscular structure, including loss or development of new muscles, over time have been effected by changes relating to transition from water to land, since the physical properties of the two differ and have been accompanied by changes in mode of locomotion, feeding, breathing, and general body support. Tracing the migration of muscles in relation to their embryonic origins together with their nerve supply is useful in homologizing specific muscles. Some muscles have not changed much in terms of movement from their point of origin and structure, for example the extraocular (extrinsic ocular) muscles, while others, such as the branchiomeric muscles, have undergone tremendous altera-

tions with change in life from water to land. This chapter first looks at the muscles least changed by the transition and then those most affected.

EXTRAOCULAR MUSCLES

Extraocular muscles constitute the most rostral (anterior) somatic muscles and develop from head myotomes. They attach to the surface of the eyeball and are responsible for its movement. Six extraocular muscles are present in jawed fishes and tetrapods except where the eyeball has degenerated, for example the African and South American catfishes. A seventh muscle, retractor bulbi, is present in most tetrapods but lacking in man. The muscle is responsible for retracting the eyeball deeper into the orbit. Terrestrial vertebrates have upper and lower eyelids and many have a third membrane, the nictitating membrane, that can be drawn across the surface of the eyeball rapidly. Two of the six extraocular muscles in birds, the superior and inferior recti, have partially split into *levator palpebrae superioris* and *depressor palpebrae inferioris* that raise and depress the upper and lower eyelids, respectively. These muscles are also present in mammals albeit some lack the *depressor palpebrae inferioris* whose role is taken over by the *caudal malaris*. Part of the retractor bulbi in birds forms a branch that attaches to the nictitating membrane and aids in its movement. *Retractor bulbi* could have evolved from the lateral rectus as it is innervated by the abducens (VI) nerve.

VISCERAL ARCHES

Visceral arches are cartilaginous or bony arches that develop in the wall of the pharynx between the pharyngeal slits and in-

clude the mandibular, hyoid, and five branchial arches. The jaw substitute in jawless lampreys is a rasping tongue, used for feeding on tissues of hosts. The “tongue” is stiffened by highly specialized gill structures. In extinct ostracoderms, the visceral skeleton lies lateral to the actual gills and immediately beneath the skin where it forms a continuous branchial latticework surrounding the gill region and connecting with the braincase. This arrangement is in marked contrast to the deeper position the skeleton occupies in jawed vertebrates.

In lampreys, the latticework (branchial basket) comprises visceral arches 1-9 and supports the pharynx and gill pouches (Fig. 6.2). Other cartilages support the face, buccal funnel around the mouth (annular cartilage) and the tongue. The skull in hagfishes is not as complete as that of lampreys. The “arches” that form the branchial latticework of lampreys are reduced to a single ring-cartilage which envelopes the tube connecting the esophagus to the exterior in hagfishes.

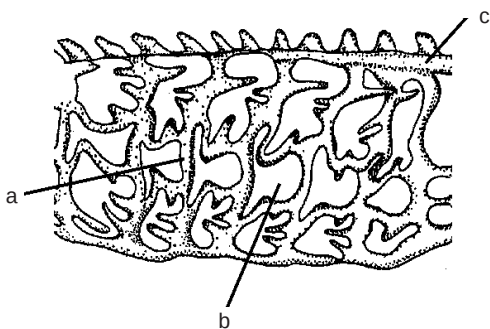


Fig. 6.2 Branchial basket (latticework) depicting the visceral skeleton of the lamprey. (a) branchial arch, (b) gill slit, and (c) notochord.

Visceral arches are found on either side of the pharynx and consist of dorsal epibranchial and ventral ceratobranchial segments (Fig. 6.3). At the upper end of each arch are pharyngobranchials turned inward over the pharynx. Frequently there are short hypobranchials below the ceratobranchials and medioventral structures known as basibranchials or copulae.

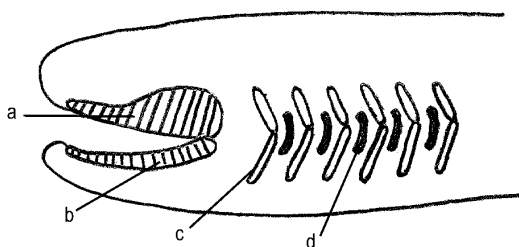


Fig. 6.3 Visceral arches of vertebrates. The first arch develops into jaws. Jawless fishes (agnathans) had more arches than the higher vertebrates. (a) Palatoquadrate, (b) mandibular cartilage (both from the mandibular arch), (c) hyoid arch, (d) gill slit. The rest of the arches are branchial (1-5) or visceral (3-7).

BRANCHIOMERIC MUSCLES

Branchiomic muscles (Gr. *branchia*, gills; *meros*, part) are striated, voluntary, located caudal to the extraocular muscles, and act on the visceral skeleton. Branchiomic muscles have undergone major changes with the transition of life from water to land in line with changes in the visceral skeleton. These muscles are important in fish as they move the visceral skeleton during feeding and breathing as they pump water over the gills. With the loss of gills in land vertebrates, many of the branchiomic muscles were also lost or transformed into those associated with the visceral arch-derived structures (jaws, auditory ossicles, larynx and hypobranchial apparatus). The primary location of the branchioskeletal muscle is rostral while that of the smooth muscle is caudal (posterior) in the wall of the digestive tract because the two parts of the system perform contrasting functions. The mouth and pharyngeal parts of the system play a major role in prehension of food and breathing and therefore need the strong voluntary contractions characteristic of skeletal muscles while the slower peristaltic contractions of the caudal parts of the digestive system have smooth muscles.

In lower vertebrates such as fish, the striated muscles may extend into the esophagus but this is of secondary importance in mammals as the role of the muscle in prehension has been taken over by other structures. In higher vertebrates, the gut wall musculature is generally the smooth type but the striated, if present, occurs in regions neighboring the gut.

MANDIBULAR MUSCLES

The mandibular arch (visceral arch 1) lies in front of the first pharyngeal pouch and develops into upper and lower jaws. The arch consists of two parts: the dorsal palatoquadrate or maxillary cartilage that constitutes the upper jaw and a ventral mandibular (Meckel's) cartilage. The left and right palatoquadrates meet at the middorsal line to form the skeleton of the upper jaw and the left and right mandibular cartilages meet midventrally to form the skeleton of the lower jaw.

In sharks, both upper and lower jaws are formed solely of paired cartilages that result from the transformed first visceral arch. The palatoquadrate cartilage is comparable to the epibranchial of the first arch and the mandibular cartilage is derived from the ceratobranchial of the same arch. Both parts of the arch articulate posteriorly. In jawed vertebrates, the part played by visceral arches in jaw formation is much reduced since the dermal bone participates in jaw formation. The dermal bone is associated with the skin and ossifies directly from the dermis. Jaw articulation remains that between the upper and lower first visceral arch in many bony fishes, amphibians, reptiles, and birds. In mammals, the entire structure of the jaws and palate is taken over by dermal elements.

Several muscles have evolved that are associated with the mandibular arch. The intermandibular muscle in fish and amphibians is a sheet at the floor of the pharyngeal cavity. In mammals, this sheet has evolved into the thicker mylohyoid and rostral part of the digastric muscle. Most of the *levator* group of mandibular muscles still found in amphibians and reptiles have been lost with the union of the upper jaw with the rest of the skull in mammals, leaving only the *tensor veli palati* of the soft palate.

Evolution of different feeding methods in tetrapods has influenced the manner in which the mandibular adductor muscle has changed (Fig. 6.4). Development of stronger jaws with more complex movements in the mammalian line of evolution led to division of the mandibular adductor muscle into four main muscles of mastication (the *masseter*, *temporalis* and medial and

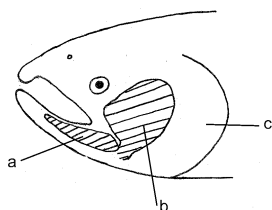


Fig. 6.4 Fish head showing (a) mandibular portion and (b) cephalic portion of *adductor mandibularis*, and (c) operculum.

lateral *pterygoids*) and the *tensor tympani* attaching to the *malleus* in the middle ear. The *malleus* is a derivative of the mandibular articular bone (Fig. 6.5). All the muscles of mastication insert on the mandible (dentary bone).

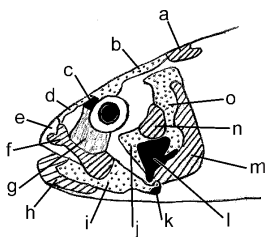


Fig. 6.5 Some of the superficial head bones of a bony fish. (a) parietal, (b) frontal, (c) prefrontal, (d) nasal, (e) premaxilla, (f) maxilla, (g) lachrymal, (h) dentary (mandible), (i) articular, (j) pterygoid, (k) angular, (l) quadrate, (m) preopercle, (n) metapterygoid, and (o) hyomandibular.

HYOID MUSCLES

The hyoid (second visceral) arch lies closer to the mandibular arch than to the third visceral (first branchial) arch. The space between each of the remaining arches is wider than that between the first two visceral arches, which has resulted in lack of a complete gill pouch between the mandibular and hyoid arches, except for the presence of spiracles in some species. The hyoid arch is specialized as an aid to jaw support. The ventral part of the arch has a small basihyal and a major ceratohyal on either side (Fig. 6.6). The hyomandibular, which is of considerable size, forms the upper part of the arch and runs from the area of jaw articulation (below) to which it is attached by ligaments to

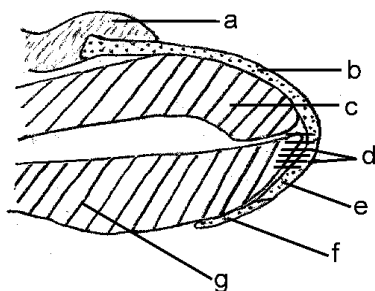


Fig. 6.6 Parts of a hyoid arch. (a) otic region of braincase, (b) hyomandibular, (c) palatoquadrate, (d) ligaments, (e) ceratohyal, (f) basihyal, and (g) mandibular cartilage.

the otic region of the braincase (above) from where it is suspended. This mechanism is an effective support for the jaws in fishes as it suspends them from the braincase. In tetrapods the hyomandibular does not support the jaws from the braincase. Additional dermal bones have enabled the upper jaws and the palatal structures to be bound to the rest of the skull. The hyomandibular has been transformed here into one of the auditory ossicles, the stapes.

In larval amphibians, gills are still functional and the arches remain prominently developed though there is some tendency toward reduction. In metamorphosed amphibians and amniotes, functional gills have disappeared. A tongue, never characteristically present in fishes, arises in the floor of the mouth in other vertebrates where the more rostral and ventral parts of the visceral arches once existed. The tongue is supported by the hyoid apparatus (Fig. 6.7). The hyoid consists of a main body

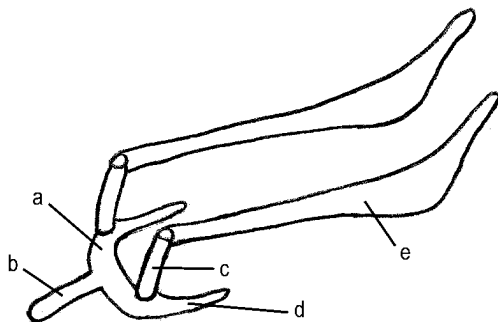


Fig. 6.7 Hyoid bone of a horse. (a) basihyoid, (b) lingual process, (c) ceratohyoid, (d) thyrohyoid and (e) stylohyoid.

(basihyoid) located at the base of the tongue and is derived from some of the medioventral arch elements (basals). Remnants of the hyoid arch and one of the three branchial arches extend outward and upward as "horns" or cornua.

With the disappearance of gills and increased importance of the lungs, skeletal structures derived from or related to the more posterior part of the visceral skeleton developed around the larynx and trachea which form the entrance to the lungs.

Muscles of the hyoid arch presumably resemble those of typical gill arches in ancestral jawless fishes. In all living jawed fish, modification of the hyoid arch has been accompanied by modified muscles innervated by the facial nerve (VII). In sharks, loss of independence of the hyoid has resulted in loss of the deeper hyoid muscles. The only remaining hyoid muscles in sharks are the superficial constrictor and levator muscles. In other fishes, a ventral part of the constrictor may form part of the intermandibular which connects jaws ventrally. The hyoid part of this muscle disappears in terrestrial vertebrates. The dorsal part of the constrictor, which develops in the gill septum of the hyoid arch, has been replaced by the bony operculum in bony fishes. The constrictor has also evolved into muscles that move the operculum, a bony covering of the gill chamber.

As the neck develops in tetrapods, the operculum disappears and the constrictor of the hyoid, the only remaining muscle in the neck region expands, circling the neck ventrally and laterally as a thin sheet known as the *sphincter colli* muscle. This expansion in mammals continues to cover the surface of the head to form muscles of the face. The muscles of the face are well developed in mammals, particularly in carnivores and primates. Nonmammalian vertebrates lack these muscles which were also missing in the ancestral mammal-like reptiles. The superficial hyoid muscles also give rise to the *platysma*. The *depressor mandibulae*, prominent in most tetrapods, is lacking in mammals. This muscle is a rostral slip of the hyoid constrictor. The depressor muscle is lost since part of the jaw that acts as a point of attachment of the muscle is either lost or taken into the ear. The hyoid musculature gives rise to another slip that replaces the depressor, known as the *digastric*. This is the caudal part of

the twin-bellied muscle that depresses the jaw thus opening the mouth. The hyoid muscles also evolved into *stylohyoideus* and *stapedius* that still maintain contact with the hyoid arch or its derivatives.

MUSCLES OF THIRD AND SUCCESSIVE PHARYNGEAL ARCHES

These subsequent visceral arches are associated with the gills (branchial arches) and are five in number (visceral arches 3 to 7 or branchial arches 1 to 5) although some sharks have more.

In cartilaginous fishes, branchiomic muscles of subsequent branchial arches are represented by dorsal and ventral constrictors (in relation to the gill chambers), levators (such as *cucullaris*), and others involved in compressing or expanding gill pouches (Fig. 6.8). In bony fishes, however, branchiomic muscles have been reduced to the hyoid arch as a result of reduction in branchial septae in presence of an operculum. The loss of gills in tetrapods has been accompanied by a reduction of branchiomic muscles caudal to the hyoid arch though gill-breathing larval amphibians still retain branchial muscles similar to those of bony fishes. Although muscles associated with the branchial arches have disappeared in terrestrial vertebrates, some still remain and have undergone modifications. Examples include those muscles that form the deep wall of the pharynx

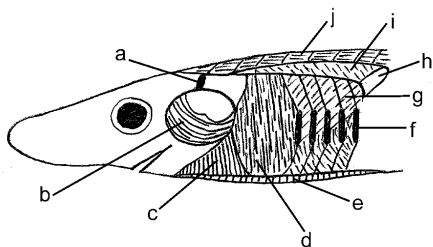


Fig. 6.8 Some of the branchiomic muscles of a shark. (a) spiracle, (b) *adductor mandibulae*, (c) *intermandibularis*, (d) ventral hyoid constrictor, (e) hypobranchial muscles, (f) gill slit, (g) superficial constrictor, (h) scapula, (i) *cucullaris* and (j) epimeres (epibranchial musculature).

(from arch III), intrinsic laryngeal muscles (from arches IV and others remaining), the *trapezius* and *sternocleidomastoideus* of man. The last muscle is twin-bellied originating from the sternum and clavicle to insert on the mastoid process of the temporal bone. In many mammals, simplification of the pectoral girdle and regression of the clavicle has resulted in modification of the *cleidomastoid* belly and the *cleidobrachialis* (deltoid) of man resulting in the union of the two muscles forming a single one, *brachiocephalicus* (L. *brachium*, arm) (Fig. 6.9). The resultant long muscle thus runs from the forearm to the head with a transverse strip of clavicular tendon at the point of fusion of the two muscles. The *trapezius*, *sternocleidomastoideus*, and *rachiocephalicus* no longer act on the visceral skeleton but the shoulder and head. These muscles are innervated by the accessory nerve (XI) which evolved from the branch of the vagus that supplied the *cucullaris* (L. *cucullus*, hood) of fish. These muscles, therefore could have originated from the *cucullaris*.

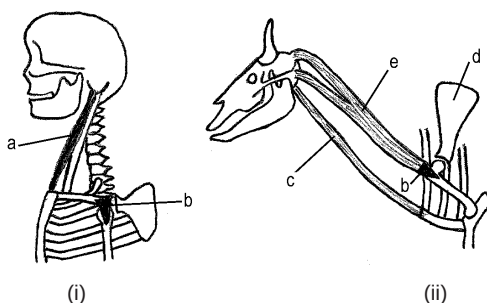


Fig. 6.9 Change of the sternocleidomastoideus as seen in man; (i) into *brachiocephalicus* as shown in a quadruped mammal (ii) (a) *m. sternocleidomastoideus*, (b) *m. cleidobrachialis*, (c) *m. sternomastoideus*, (d) scapula and (e) *brachiocephalicus*.

HYPOBRANCHIAL MUSCLES

These muscles extend from the pectoral girdle to visceral arches and are longitudinal in orientation. Sharks display simple hypobranchial muscles in comparison to teleosts and tetrapods. The complexity seen in equivalent muscles in teleosts has resulted from expansion of the buccopharyngeal cavity whereas

in terrestrial vertebrates, the complexity has resulted from evolution of sophisticated food-gathering methods as air is a less dense medium when compared to water and offers less suspensory support to food. Evolution of a muscular tongue with the support of hypobranchial muscles aids in feeding.

The prehyoid muscles found between the mandibles and hyoid bone are represented by a pair of *coracomandibularis* in sharks, which extend toward the coracoid region of the pectoral girdle in some species. With evolution of a muscular tongue in amphibians, the coracomandibular of sharks modified into the **geniohyoid** (Gr. *geneion*, chin) which not only runs from the mandibles to the hyoid, but also has some fibers that extend to the tongue. This resulted from migration of the mesenchyme from postbranchial somites cranially beneath the branchial region to give rise to hypobranchial muscles. This is clearly seen in bats where tongue muscles can extend from as far as the sternum. In tetrapods which use the tongue greatly for prehension, intake of liquids and sorting of solid food during mastication, e.g. mammals, the hypobranchial muscles become more complex. This necessitated evolution of the intrinsic *lingualis* which form the bulk of the tongue with deep fiber bundles running in longitudinal, transverse, and perpendicular manner and are able to change the shape of the tongue. It also resulted in development of extrinsic lingual muscles such as *genioglossus*, *hyoglossus*, and *styloglossus*, that are capable of moving the tongue about. The ventral hyoid muscles, which include *sternohyoideus*, *sternothyroideus*, and *omohyoideus*, are straplike and run along the ventral surface of the neck, surrounding the trachea and larynx ventrally and laterally. Their combined action pulls the hyoid apparatus and larynx, caudally dilating the pharynx in the process.

EPIBRANCHIAL MUSCLES

The epibranchial musculature in fish is interrupted cranially by the presence of gills. Change in undulatory movements of the

trunk from lateral to dorsoventral arose as a result of change in life from water to land. The trunk and epibranchial muscles played a major role here and also supported the body against gravity. There was an accompanying fusion of myomeres, resulting in longer muscles that showed a reduction in segmentation or loss of it altogether except in some amphibians such as salamanders that move by lateral undulations.

AXIAL MUSCULATURE

The axial skeleton includes the vertebral column, median fins, ribs and sternum. Its evolution depended on the environment, mode of locomotion and forces acting on the body which resulted in regional differentiation of the skeleton. The trunk skeleton of fish is very important in locomotion but does not play a major role in supporting the body against gravity since water, which is denser than air, offers buoyancy and little resistance to locomotion. A notochord is present in adult agnathans, early chondrichthyans, lungfishes, the coelacanth (*Latimeria*), and chondrosteans. These are fairly sluggish fish that do not need a strong vertebral axis to swim. In higher chondrichthyans, chondrofication replaces most of the notochord with cartilage, which is further reinforced by deposition of calcium salts in some cases. Ossification around the notochord takes place in bony fishes and this further strengthens the vertebral axis.

Ribs are well developed in bony fishes but lacking in agnathans. In bony fishes, there may be intermuscular, subperitoneal or sometimes accessory ribs. Such ribs strengthen the myosepta and transfer forces to the vertebral column. The caudal fin forms the caudal end of the vertebral column and is expanded. It differs in shape in different fish. Many fishes have one or two dorsal fins and an anal fin which provide stability by reducing the tendency to roll from side to side. The small and specialized muscles that supply the fins and perform movements independent of trunk movements arose as slips from embryonic axial myomeres.

Tetrapods have evolved stronger vertebrae as the vertebral column transfers the weight of the body to the pectoral and pelvic girdles and their appendages. The head and trunk no longer move as a unit, as in fish; rather each segment exercises some degree of independent movement. Regional differentiation is more marked in the vertebral axis with transition in life from water to land.

Axial muscles form most of the muscle mass and are the main propulsive muscles in fish. Transition from water to land has seen the enlargement of appendicular muscles as the axial musculature diminishes in tetrapods. Amphibians have axial musculature that is transitional between that of fishes and reptiles.

Epaxial Muscles

Epaxial muscles lie dorsal to the horizontal septum. They are normally found above the vertebrae and their transverse processes and play a major role in flexion of the spine and movement of the head. These muscles are massive and segmented in fish and are considered a single dorsolateral trunk muscle, the *dorsalis trunci*. The dorsal musculature (*dorsalis trunci*) is much reduced in relative volume in tetrapods as the limbs take over the role of propulsion from the axial muscles. In urodeles such as salamanders in which the limbs are weak and movement is the result of lateral undulations, these muscles are still highly developed. Epaxial muscles play an important role in the dorsoventral bending of the spine in tetrapods, a movement not possible in fish.

The trunk skeleton of fishes plays a minor role in support against gravity though it is vital to locomotion. It is able to resist telescoping when trunk muscles contract, resulting in lateral undulations that bring about propulsive forces. The trunk vertebrae are essentially alike. Ribs are well developed in bony fishes but lacking in hagfishes and lampreys and poorly developed in chondrichthyans. The ribs play a major role in locomotion by strengthening the myoseptae but no role in respiration since this role is played entirely by gills. The vertebral column of fish extends into the caudal fin which is important in

forward propulsive forces. The shape of the caudal fin varies depending on the mode of swimming and buoyancy. In marine mammals such as some cetaceans, the vertebrae are fused in the neck region and some of the bones lack the complex articulation of vertebrae seen in terrestrial mammals. The tail flukes which are set in a horizontal plane and supply the driving force for swimming and dorsal fins lack bony support in these mammals.

In tetrapods, the transition from water to land was accompanied by anterior vertebral changes that facilitate independent head movements. Further evolution from earlier forms resulted in stronger vertebrae which were more specialized and allowed freer movement of the head. The sacral region also became stronger as the number of sacral vertebrae increased and there were varying degrees of fusion.

Birds have a very long neck permitting great mobility of the head and which also alters the body's center of gravity during flight. The trunk has few vertebrae, partially fused, giving a short and rigid back (Fig. 6.10). In the thoracic region, vertebrae are fused to form the **notarium**. The sacrum is strong and fuses with the neighboring anterior lumbar and posterior caudal vertebrae forming the **symsacrum**, usually made up of 10-23 vertebrae. While the distal caudal vertebrae are fused into a **pygostyle** (Gr. *pyge*, rump; *stylos*, pillar), those between it and the symsacrum are not. Due to this fusion, the epaxial muscles of

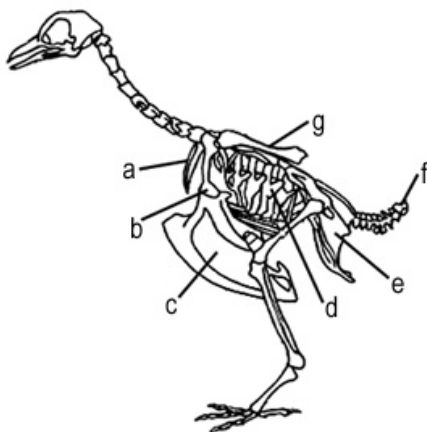


Fig. 6.10 Skeleton of a bird showing various bones. (a) clavicle, (b) coracoid, (c) sternum (keel), (d) uncinat process of vertebral rib, (e) pelvic bones, (f) caudal vertebrae, and (g) humerus. After Heilmann, 1927.

birds are greatly reduced compared to other vertebrates. The caudal vertebrae, which carry the steering tail feathers, have complex and sometimes powerful groups of muscles.

Mammals have specialized vertebrae that can be grouped into (in a craniocaudal direction): cervical, thoracic, lumbar, sacral, and caudal series. Many mammalian species have extra processes on the lateral surface of their thoracic and lumbar vertebrae that act as points for muscle and ligament attachment, thereby strengthening joints between these vertebrae. The sacral vertebrae (three or more) and their ribs are fused in mammals into a sacrum. Such a sacrum is strong and able to transmit the caudal weight of a mammal to the pelvic girdle and its limbs as well as transmitting propulsive forces from the limbs to the rest of the body. Most mammals possess tails which serve various purposes, such as locomotion as seen in the horizontal flukes of cetaceans, which are reinforced by dense connective tissue.

The complex head and trunk movements seen in mammals have necessitated evolution of several specific muscles which run from the head to the trunk and initiate atlantooccipital and atlantoaxial movements. These muscles are shorter than those that bring about coarser movement of the head and neck including feeding, maintenance of balance of the neck, and general orientation. In the third category are the long muscles of the back and loins that originate from the sacrum and pelvis and run all the way to the head. From the medial to lateral side they include the *transversospinalis*, *longissimus*, and *iliocostalis*. The *transversospinalis* is slightly segmented in mammals while in reptiles, which rely on undulations for movement, the three muscles remain partly segmented.

Hypaxial Muscles

Hypaxial musculature is normally found below the vertebrae and their transverse processes. Fossil records show that labyrinthodonts had ribs on most of their vertebrae which acted as sites for attachment of locomotor muscles as they moved by lateral undulations and also strengthened the body wall and prevented collapse of body cavity tissues by body weight when

the animals were resting on the ground. These roles have been lost in modern amphibians whose ribs are quite reduced. In reptiles, ribs extend from the first cervical vertebra (atlas) to the first few caudal vertebrae. Cranial ribs attach to the sternum. Birds have ribs that attach to their trunk vertebrae and sternum. The sternal ribs, which are cartilaginous in most terrestrial vertebrates are ossified in birds. The rib cage of birds is thus strong, a fact reinforced by the presence of uncinat processes (Fig. 6.10). Each process overlaps with a subsequent vertebral rib. Some respiratory muscles attach to these processes. The rib cage of birds is also flexible due to the presence of movable joints between vertebral and sternal ribs, which enable it to ventilate the lungs. The ribs of mammals attach to the thoracic vertebrae and sternum by costal cartilages and play a major role in respiration together with respiratory muscles. The ribs also act as points of origin or insertion of muscles that attach the forelimbs to the body trunk, thus transferring the anterior weight of a mammal to the pectoral girdle.

Hypaxial muscles are rather primitive in the amphibian tail. They are more advanced on the trunk and represented by the subvertebral group that lies below the transverse processes of vertebrae, the *rectus abdominis* between the two girdles, and the lateral group (*external oblique*, *internal oblique* and *transversus*).

Hypaxial muscles in mammals are represented by the inner lumbar musculature (subvertebral group) and abdominal muscles (*rectus*, *oblique* and *transverse abdominis*). The subvertebral group is generally reduced except in the lumbar area. The inner lumbar musculature, found on the ventral aspect of the thoracic and lumbar vertebral column and is associated with the pelvic girdle, consists of the *psaos minor*, *iliopsoas*, and *quadratus lumborum*. These muscles, on contraction, cause arching of the back and steeper angling of the pelvis. This action is more marked in mammals with longer lumbar parts of the vertebrae (compared with the thoracic part) such as carnivores and cats. The *quadratus lumborum* is particularly well developed in these animals. Arching is also important in some mammals during urination, defecation, parturition, and copulation.

The abdominal muscles support the ventral and lateral walls of the abdomen. They support the weight of the abdominal

viscera which can be quite substantial in herbivores. The original segmentation of these muscles (abdominal processes of myotomes) can still be seen clearly in muscles such as the *rectus abdominis*. Modification of the thorax in mammals has led to regression of the *transversus* in the thoracic region. The *external* and *internal oblique* became the *external* and *internal intercostal* muscles that play a role in inspiration and expiration respectively. Intercostal muscles are found throughout most of the trunk in tetrapods with extra ribs such as abdominal ribs. Other respiratory muscles such as *serratus dorsalis* separated from the superficial hypaxial muscles.

APPENDICULAR MUSCLES

The appendicular skeleton includes the skeleton of the paired fins of fishes, the girdles and limbs of tetrapods. Agnathans, caecilians, snakes, and some lizards lack an appendicular skeleton and the corresponding muscles which have been reduced in some vertebrates to various degrees. The paired fins evolved as an adaptation to a more active mode of life by jawed fish. They may have evolved from lateral bony plates.

The extinct ostracoderms lacked paired fins which later in life appeared in jawed fishes as they became more active and diversified in their swimming behavior. Evidence of the presence of an appendicular skeleton can be seen in the fossil remains of placoderms. A group of placoderms, the arthrodires, show evidence of a scapulocoracoid cartilage that had an articular surface for a pectoral fin and another group, the antiarchs, had jointed pectoral appendages. Primitive cartilaginous fishes had broad pectoral and smaller pelvic fins which became narrower in contemporary species. Their scapulocoracoid is larger than that of other fish groups.

The pectoral girdle in bony vertebrates consists of a dermal armour (membrane bones) and an underlying cartilaginous skeleton (replacement bones). The early fishes had three cartilaginous "bones" (coracoid, scapula, and suprascapula) and a series of dermal bones (clavicle, cleithrum, supracleithrum, and

posttemporal). Further evolution brought a reduction in number and size of cartilaginous bones in fishes whereas in tetrapods, the tendency was reduction in number of dermal bones. The pectoral girdle of extant bony fishes has a reduced coracoid and scapula (often united in teleosts as the coracoscapula), a large prominent cleithrum, and a supracleithrum (Fig. 6.11). A posttemporal bone connects the supracleithrum to the skull. When present, the clavicle is much reduced. In most bony fishes, cartilaginous bones are represented by coracoids, scapulae, and four radials while the dermal bones are posttemporals, supracleithra, cleithra, and postcleithra. Cartilaginous fish lack the dermal component of the pectoral girdle skeleton. Their coracoid, scapula and suprascapula remain cartilaginous throughout life.

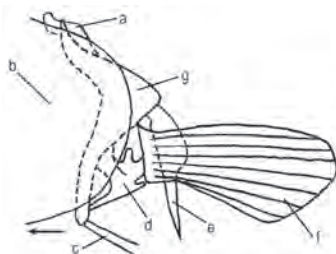


Fig. 6.11 Pectoral fin of a bony fish. (a) supracleithrum, (b) operculum, (c) part of pelvic fin, (d) coracoid, (e) postcleithrum, (f) pectoral fin, and (g) cleithrum (pectoral girdle). Arrow indicates the cranial (forward) direction.

In most fishes, the pelvic girdle has no dermal components. It consists of two cartilaginous or bony (ischiopubic) plates (basipterygium) embedded in the body wall that articulate with the pelvic fins (Fig. 6.12). The two plates usually meet medially

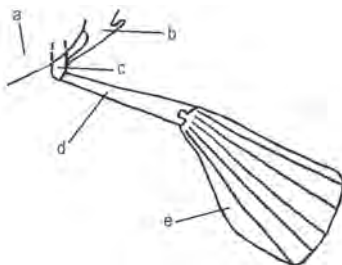


Fig. 6.12 Skeleton of the pelvic fin of a bony fish. (a) operculum, (b) coracoid, (c) cleithrum, (d) basipterygium, and (e) pelvic fin.

in a symphysis. In sharks and lungfishes, the two plates unite to form a single plate later in life. The pelvic girdle occurs in the abdominal region in primitive fish. In bony fishes, the girdle migrated forward during evolution to contact the pectoral fins.

The pectoral girdles of early tetrapods are quite similar to those of their crossopterygian ancestors (Fig. 6.13). Transition to terrestrial environment was accompanied by reduction in dermal skeleton which lost connection with the back of the skull and enlargement of the cartilaginous component of the pectoral girdle which became ossified. Evolution of the interclavicle in the midventral part of the anterior body wall as well as articulation of the coracoids with the sternum as seen in the lizard and chicken commenced. This change was necessary if the limbs were to support the anterior part of the body from the ground. The clavicle expanded to assist or even replace the coracoid in this function. The cleithrum and supracleithrum were lost in the process. The clavicle became reduced or lost altogether in crocodilians, legless lizards, and some mammals. The entire girdle is missing in snakes. The pelvic girdle enlarged, connected to the sacrum, and became ossified. With further evolution, the pelvic and pectoral appendages changed movement from the horizontal plane in ancestral tetrapods including amphibians and reptiles to the vertical plane seen in higher vertebrates.

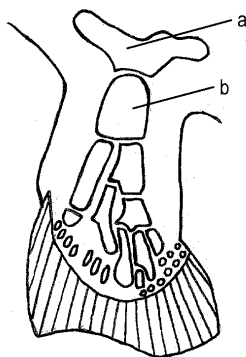


Fig. 6.13 Pectoral fin of a crossopterygian. (a) pectoral girdle and (b) evolving humerus.

Appendicular muscles are divided into a dorsal group of extensors (upward and forward) and ventral flexors (downward and backward). Tetrapods have transferred their body weight

to the girdles and the position of the appendages and the resultant movement have changed as a result. The structure and movement of the appendages in terrestrial vertebrates became more complex than those of fish fins, which resulted in appendicular muscles in tetrapods forming the bulk of the body musculature.

Transition from water to land involved change of paired fins into limbs and strengthening of the girdles. Articulations between the girdles and limbs and between various bones in limbs developed, increasing flexibility. Evolution of the labyrinthodont pectoral girdle from that of the rhipidistian involved expansion of the scapulocoracoid part of the girdle and loss of tissue that connected the girdle to the skull. Muscles evolved to hold the girdle to the trunk. The pelvic girdle of labyrinthodonts enlarged and articulated with the sacrum. In amphibians and reptiles, the scapula and coracoid underwent ossification. Some reptiles such as snakes have lost their appendicular skeletons.

The flying tetrapods, which include the extinct reptiles (pterosaurs), birds, and bats evolved wings which are modified pectoral appendages. The bones of a bird's wing are pneumatic (contain air spaces) which makes them light though still strong since they have a high mineral content. Possession of a strong coracoid that forms a movable joint with the sternum and the presence of a clavicle and scapula provide strong support for the wings. Since birds are bipeds, they have developed a strong pelvic girdle together with its two limbs, having to support the weight of the bird and also act as shock absorbers during landing. The pelvic bones have united and the ilium is solidly united with the synsacrum. The pelvis is located well forward and places the center of gravity on the hind limbs as they are the only ones that carry the weight of the body. The bones also provide a large area for insertion of the large limb muscles. Fusion of the tibia with the proximal row of tarsal bones (tibiotarsus) and the remaining tarsal bones with the metatarsus (tarsometatarsus) strengthens the ankle in the bird. The only movements possible at this joint are flexion and extension.

The mammalian girdles have undergone several changes to accommodate appendages under their bodies. The presence of

strong ventral adductor musculature in the pectoral region, which was important in raising the body from the ground and for its support, was no longer necessary, resulting in the development of a smaller coracoid region. With loss of the coracoids, the glenoid fossa of the scapula faced ventrally. The scapula also expanded to accommodate the dorsal musculature. Originally, the acromion process formed the cranial border of the scapula where the lateral end of the clavicle attached. With evolution, this end was pushed laterally to form the ridge-like scapula spine creating a supraspinous fossa (Fig. 6.14). Although the clavicle has been retained in many mammals because it stabilizes the shoulder, it has been reduced or lost in running mammalian species.

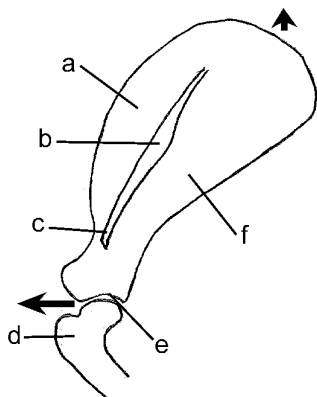


Fig. 6.14 Mammalian scapula. (a) supraspinous fossa, (b) scapula spine, (c) acromion process, (d) humerus, (e) glenoid fossa, and (f) infraspinous fossa. Longer arrow shows cranial direction; shorter one the dorsal side.

In the pelvic girdle, the three bones (ilium, pubis, and ischium) became fused in adult mammals (Fig. 6.15). The pubis lost its caudally directed process and became inclined cranially with reduction of heavy tail muscles. The pubis and ischium are smaller in mammals compared to those of early synapsids. In marine mammals such as cetaceans, the pelvic girdle is represented by two small bones embedded in the body wall and free from the backbone. The only purpose they seem to serve is attachment for muscles of the external reproductive organs. The

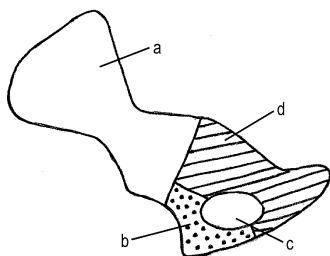


Fig. 6.15 Pelvic bones of mammals. (a) ilium, (b) ischium, (c) obturator foramen, and (d) pubis. The three bones of the pelvis fuse after birth to form the hip bone.

mammalian obturator foramen has enlarged to accommodate the enlarged pelvic muscles. Mammals with powerful limbs have well-delineated muscular processes on their humeri.

Pectoral Girdle Muscles

The *pectoralis*, which in amphibians and reptiles plays a major role in adduction and lifting of the body from the ground, has evolved into a major retractor of limbs in other tetrapods. The *supracoracoideus* is likewise present in amphibians and reptiles. These two muscles are quite enlarged in birds and are the main flight muscles. The *pectoralis* is the most prominent in size and function in birds and when the power of flight is fully developed, its weight exceeds that of all the remaining skeletal muscles. The *supracoracoideus* only appears in mammalian embryos (Chen, 1955) and grows into the *supraspinatus* and *infraspinatus* as development continues. The large *coracobrachialis* of amphibians and reptiles (with a large coracoid) is quite reduced or lost in mammals (with smaller or no coracoids) except in bats, in which it plays a role in wing adduction.

The *deltoideus* muscle, which arises from the anterior border of the scapula and the clavicle in amphibians and reptiles, partly originates from the scapular spine in mammals which shows that the spine may have been the original anterior border of the scapula. In mammals, a piece has separated from the *latissimus dorsi* to the caudal border of the scapula as the *teres major*. The *scapulohumeralis anterior* of amphibians and reptiles is represented

in mammals by the *teres minor* whereas the *subcoracoscapularis* of amphibians and reptiles expands much into the *subscapularis* muscle of mammals which originates from the entire medial surface of the scapula. The thin cutaneous muscle of the trunk (*cutaneus trunci*), which is capable of contraction independent of deep muscles, could have evolved from the appendicular muscles as it attaches to the base of the *latissimus dorsi* and the pectoral muscles.

Pelvic Girdle Muscles

Since the mammalian pelvis is firmly connected to the vertebral column by a tight joint and its ligaments, the pelvic girdle muscles are not as numerous and as active as the pectoral girdle muscles that are more actively involved in locomotion. The muscles of the pelvic girdle are also located on the ventral aspect of the thoracic and lumbar vertebral column and are also known as the inner lumbar musculature.

The role of propelling the body forward by the pelvic limb has led to evolution of intrinsic muscles that are much stronger with an arrangement and structure more complex than that of the thoracic limb. The bellies of these muscles may be very large and are concentrated in the proximal part of the limb with the distal part of the limb being mainly tendinous. Most of these muscles act on several joints.

In birds, the forward-weighted body is supported in a standing position by a pelvic girdle that extends forward for some distance and the pelvic limbs that are strongly angled at the hip and knee joints. Because the pelvic limbs perform several functions such as walking, perching and climbing, their muscles are the second largest and strongest in the bird. The muscle bellies are found in the proximal part of the leg and the distal part is mainly made up of smaller muscles and flexor and extensor tendons of the toes.

Electric Organs

These are modified muscle masses that produce, amplify, store, and discharge electricity and are found in about 250 species of

fish, including rays of the genus *Torpedo*, the electric eel of South America (*Gymnotus*) the stargazer (*Uranoscopus*), and the electric catfish of Africa (*Melapterurus*). Mermelstein et al. (2000), reviews the contribution of the cytoskeletal meshwork to the maintenance of the polarized organization of the electrocyte (cell that contains all electric properties of each electric organ). Weaker electric shocks are produced by some fishes such as rays and many tropical teleosts. Electric organs exhibit several biochemical properties and morphological features of the muscle sarcolemma. The energy produced by these organs is used for production of electricity and not for muscle contraction. The organs consist of a number of electric plates (disks) that are multinucleated (electroplaxes) and piled in either vertical or horizontal columns. The plates are innervated by nerver fibres which induce the discharge. These organs vary in position and appearance in different fishes. In *Torpedo*, an electric organ lies in each pectoral fin close to the gills. Since it is supplied by cranial nerves VII and IX it could probably be of branchiomic origin. In the electric eel and a skate (*Raia*) the electric organs are found in the tail and originated from hypaxial muscles.

The electric eel can discharge more than 500 volts and strengths of more than 200 volts have been recorded in *Torpedo*. These electric discharges might be protective devices against predators as well as weapons to stun prey. Other fish discharge electricity that is too weak to be a weapon and perhaps use it for locating prey or communicating. Many fishes emit electric signals continuously in order to detect objects while navigating in murky water and at night. The electric organ of the catfish from Africa might be from a modified skin gland rather than muscle as it encircles the whole body as a superficial sheath and its plates are not arranged in neat piles. Since the distribution of electric organs is not systematic in fish, the various types could be a result of convergent evolution.

Detection of objects by fish such as elasmobranchs (sharks, skates, and rays) requires the presence of electroreceptors located in the skin. Objects in water distort the electric fields created by these fishes, which is detected by their electroreceptors. Electroreceptors are also found in some nonelectric fishes, some amphibians, and the duckbill platypus (in its bill).

Muscle Spindles

A muscle spindle is a modified form of skeletal muscle and is found within the belly of muscles. It is spindle-shaped and encased in a connective tissue envelope that is connected to the intercellular collagen network. A muscle spindle consists of two to ten intrafusal muscle fibers that are smaller than skeletal muscle fibers, striated and rich in sarcoplasm. These fibers run parallel to the main muscle fibers. Sensory nerve terminals are wrapped around the muscle spindle fibers. The spindle is capable of sensing length and changes in length of skeletal muscle by detecting changes in tension generated by the myofibers. A stretch in skeletal muscle will stretch the spindles and their sensory nerve endings, resulting in an increase in discharge from these nerve terminals. Muscle spindles are thus proprioceptors (L. *propria*, “my own” or “self”) and monitor body position and movement of body parts. Among vertebrates, muscle spindles are lacking in fishes.

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