POSTCRANIAL SKELETON AND LOCOMOTOR ADAPTATIONS

After completing this lab you should be able to recognize the individual major bones of an articulated mammalian skeleton, know and apply underlined terms, name the stance, and identify mode of locomotion of a mammal from examination of articulated limb bones.

The skeleton is divided into the axial skeleton, which is the skull and vertebral column, and the appendicular skeleton, the skeleton of the limbs, pelvic girdle, and pectoral girdle. The mammal-like therapsids of the later Permian and Triassic had changes in skull, teeth, and skeleton compared to modern mammals and compared to reptiles. Therapsids (Fig. 33) stood more erect than typical reptiles (Fig. 32), with the elbows pointed backward and the knees forward. Contrast the mounted alligator (or articulated lizard skeleton) in the lab today with the articulated skeletons of the cat (*Felis catus*) or the bobcat (*Lynx rufus*) (Fig. 34).

Figure 32. Lateral view of a primitive reptile from > 250 MYA (millions years ago) (Romer and Parsons 1977).

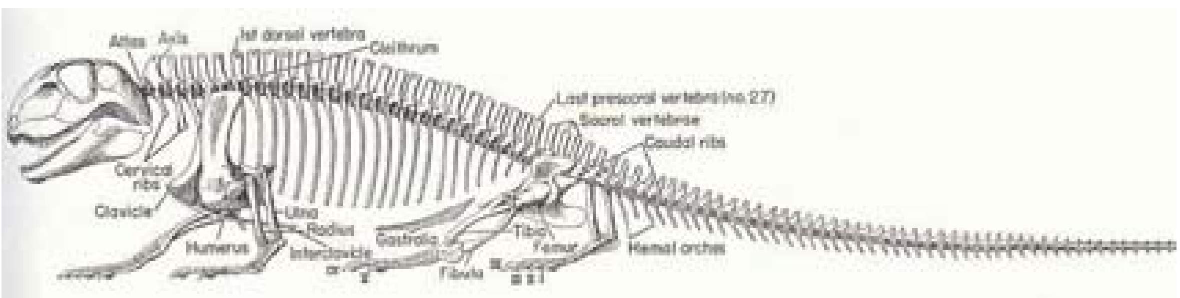


Figure 33. Lateral view of a Cynodont skeleton (*Thrinaxodon*) from ca. 200 MYA (Vaughn 2003).

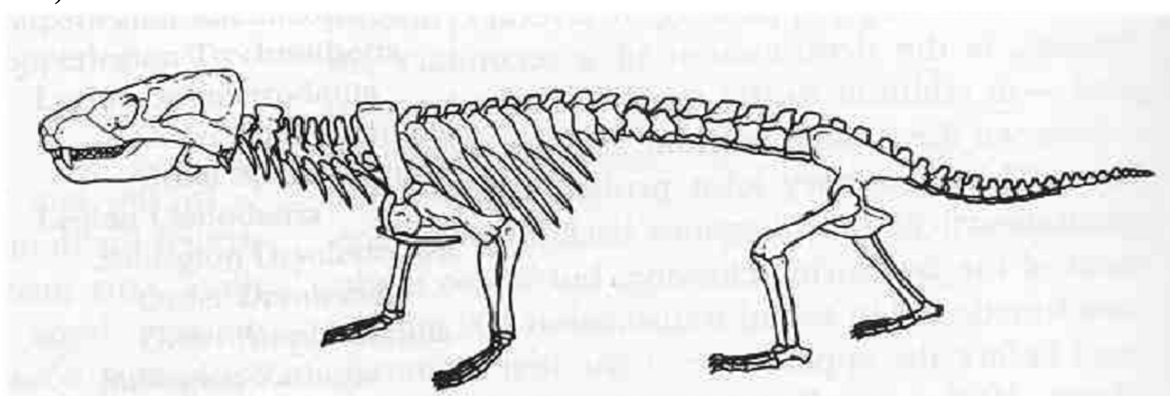


Figure 34. Lateral view of cat (*Felis catus*) skeleton (Hickman et al. 1997) and of a bobcat (*Lynx rufus*) skeleton (photograph of UMD collection specimen).

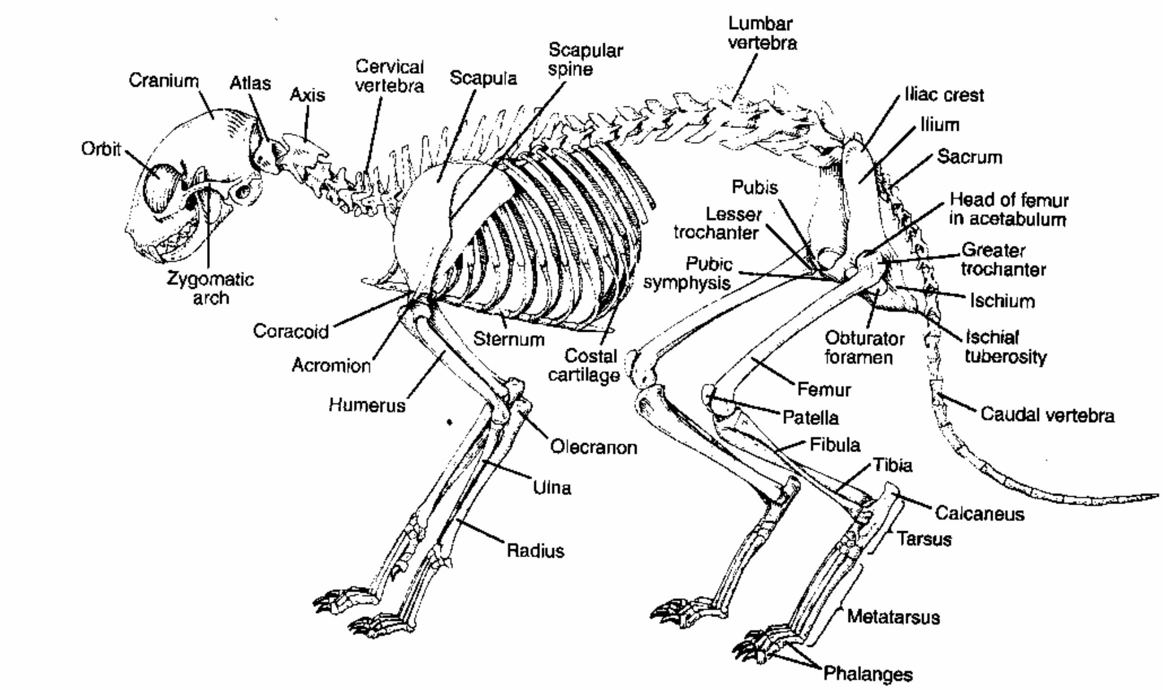
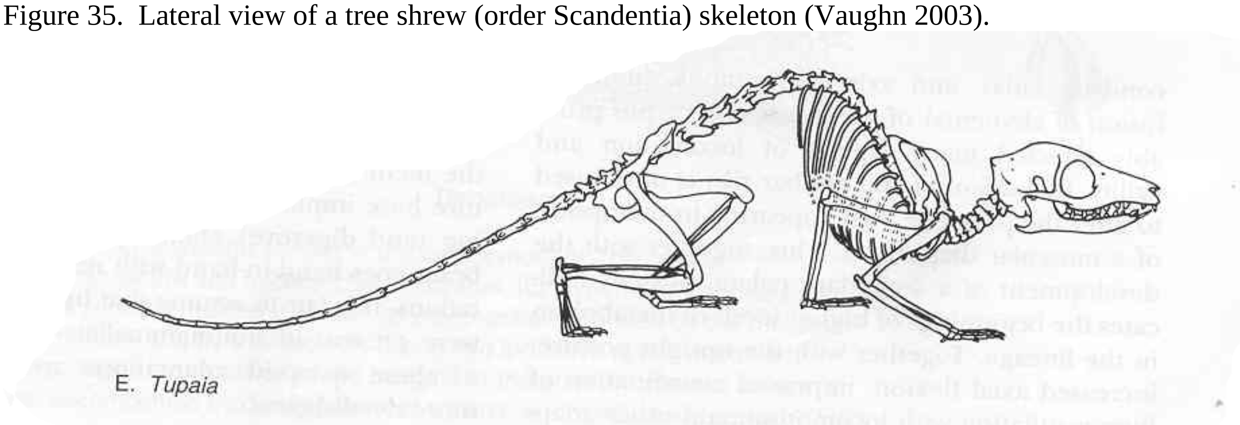


Figure 35. Lateral view of a tree shrew (order Scandentia) skeleton (Vaughn 2003).



The broad adaptive radiation of mammals means that many mammal skeletons do not look like the tree shrew (Fig. 35). Early mammals were four-footed (quadrupedal) and each foot had five toes (pentadactyl). Humans retain portions of the ancestral arrangement, with modifications for the bipedal gait.

Stance describes the way an animal stands. Locomotion describes how an animal moves. Humans stand on the soles of the feet in a plantigrade stance. While walking and jogging, the stance is still plantigrade. When humans sprint, the stance can become digitigrade (on toes or digits). Look at the different articulated skeletons that are available and Figs. 32-35, as well as the figures and pictures below and determine if they have a digitigrade or plantigrade stance.

Forelimb. Identify the bones of the forelimb on skeletons of several species. A detailed view of the forelimb of some of the species in the laboratory is given in Fig. 36. The pectoral girdle of most mammals is composed of two elements. The scapula is a large, typically flat bone dorsal to the ribs. It is embedded in back muscles and does not articulate directly to the axial skeleton. A clavicle, or collar bone, is usually present. This rod-like bone extends from the scapula to the sternum, providing a firm support for the front limbs. The clavicle is often reduced or absent in mammals that run on hard ground, absorbing the shock of the feet hitting the ground with soft tissues around the scapula.

Figure 36. Forelimbs of some of the specimens available in the lab today. Included are the Norway rat (*Rattus norvegicus*), echidna or spiny anteater (*Tachyglossa* sp.), and the rabbit (*Oryctolagus cuniculus*).

See Color Handout

The pectoral limb consists of three major parts. The proximal humerus has a large head which is articulated to the scapula by a ball-and-socket joint. Distally (away from the base or point of attachment) the humerus meets the ulna and the radius. The ulna has a proximal extension, the olecranon process, which serves as the short arm of the lever for the muscles extending the forearm. The ulna and radius are usually able to rotate around each other, enhancing mobility of the forefoot. The forefoot or hand (manus) includes three different sets of bones. The first, proximal group forms the carpus, or wrist. The individual elements are called the carpals. They are followed by the metacarpals, one for every digit. The most distal series of bones is called the phalanges (singular, phalanx). In the primitive pattern, the first digit of the forelimb, or pollex, has two phalanges. The rest of the digits contain three. The ancestral mammalian phalangeal formula is 2-3-3-3-3, a reduction from the general reptilian formula of 2-3-4-5-3.

Hindlimb. Identify the bones of the hindlimb on skeletons of several species. A detailed view of the hindlimb of some of the species in the laboratory is given in Fig. 37. The hip or pelvic girdle is composed of two symmetrical halves, the innominate bones, each of which was formed by the fusion of three bones. The ilia (singular, ilium) extend anterodorsally and articulate with the lower vertebral column. The ischia (singular, ischium) extend posteriorly and form the bony part of the rump. The pubic bones project anteroventrally and are joined at their distal ends. These three pairs of bones, together with their articulated vertebrae, form a ring through which the reproductive, urinary, and digestive tracts leave the body.

The pelvic limb is similar to the front limb. The proximal bone (corresponding to the humerus) is the femur. The middle segment of the hindlimb includes the larger tibia and narrower fibula. These two bones are often partly fused. Many mammals have a patella or knee-cap. This bone is formed independently from the other leg bones; it protects the knee joint. The hindfoot, or pes, consists of three series of bony elements. The most proximal are the tarsals. The largest of the tarsals, the calcaneum or heel bone, has a posterior process which serves as an attachment site for the tendon of the extensor muscle of the hind foot. The tarsals are followed by the metatarsals and, as in the manus, the distal phalanges. The number of the phalanges is the same as in the corresponding digits of the forefoot. The first digit (the "big toe") is the hallux. Carpals and tarsals are referred to collectively as podials, metacarpals and metatarsals together are called metapodials.

Figure 37. Hindlimb of some of the specimens available in the lab today. Included are the Norway rat (*Rattus norvegicus*), echidna or spiny anteater (*Tachyglossa* sp.), and the rabbit (*Oryctolagus cuniculus*).

See Color Handout

Adaptations to Distinctive Habitats

Terrestrial adaptations.--Early mammals were small, terrestrial, pentadactyl quadrupeds. They had the ancestral limb structure discussed above with a stance in which the sole of the foot contacts the ground as the animal walks. This plantigrade stance persists or has developed secondarily in many mammals. When running many plantigrade mammals increase the effective length of the leg by lifting the heel off the ground for cursorial (running) locomotion. Some carnivores that rely on running speed and endurance to catch their prey are always in a digitigrade stance. Compare the lengths and relative positions of the various limb bones for digitigrade and plantigrade mammals.

Some prey species stand only on the longest, medial digits. The side toes were reduced, and the remaining digits strengthened and elongated. The claws increased in size to support the toes and eventually surrounded the tips, creating hooves which are the only parts of the feet to touch the ground. Members of two living orders show this unguligrade stance--most artiodactyls and the horse. Most artiodactyls have two digits of equal size on each foot. Pairs of metacarpals and metatarsals are often fused to form a single cannon bone to reinforce stability and strength. Horses (Equidae) have only the medial digit in each foot. Many artiodactyls and Equids have also reduced and fused the ulna to the radius and the fibula to the tibia. This results in only a single bone in the middle segment of the limbs. The trend towards long limbs specialized for high speed is generally accompanied by reduced lateral mobility.

Figure 38. Front and lateral views of a horse (*Equus caballus*) limb and front view of a cow (*Bos taurus*) limb in the laboratory. Also included are 2 front views of an Irish elk (*Megaloceros giganteus*) forelimb at the Smithsonian Museum of Natural History.

See Color Handout

A foot with an even number of toes is called paraxonic; the toes are situated beside (*para*) the axis of symmetry of the foot. A foot with an odd number of toes is mesaxonic; the axis of symmetry passes through the middle (*meso*) of the foot. Examine mounted limbs of unguligrade mammals (Fig. 38). Compare lengths and arrangement of elements with those of digitigrade mammals. What joint(s) restrict lateral movement in the unguligrade limb?

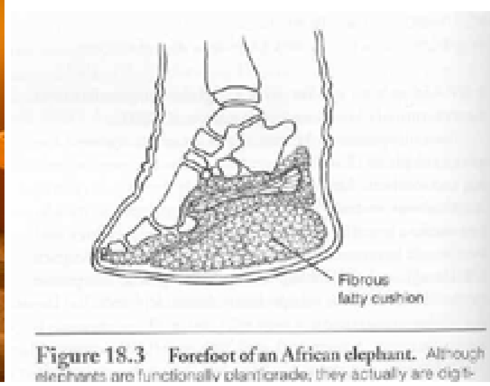
When a running squirrel or rabbit jumps forward, the stronger and longer hind legs leave the ground last, and the front legs touch it first when the animal lands. The hind limbs provide the major part of the thrust. Several mammals, including lagomorphs (other than pikas) and many rodents, use this saltatorial locomotion. In contrast, kangaroo rats and kangaroos are completely bipedal. Their front feet are not used for locomotion. The hind feet are elongated and the usually strong, long tails provide support and counterbalance. Locomotion of animals like the kangaroo is termed ricochetal.

Figure 39. Hindlimb of saltatory and ricochetal mammals, rabbit (*Oryctolagus cuniculus*) and the kangaroo (Macropodidae). Tail vertebrae are missing from the kangaroo. Note the relative lengths of elements in the fore- and hind limbs.

See Color Handout

Some large terrestrial mammals like the elephant have <u>graviportal</u> limbs. The leg bones are in a straight, vertical line, and the feet are large and broad, distributing the weight of the animal over a larger area. Elephants are partially digitigrade animals. The digits are arrayed in a semi-circular pattern, around an enormous heel pad. This thick cushion of dense connective tissue carries the bulk of the animal's weight.

Figure 40. Mastodon (*Mammut*) skeleton in Smithsonian Museum of Natural History. Note the thick limbs and the position of the animals "toes". Next to this figure is a close-up drawing of the foot of an elephant (mastodon and mammoth feet would be similar).



Fossorial adaptations. Many mammals dig occasionally, e.g., coyotes (*Canis latrans*) digging up a cache or enlarging a burrow to shelter the young. Other mammals dig burrows and use them as a permanent home. Badgers (*Taxidea taxus*), armadillos (Edentata:Dasypodidae), prairie dogs (Rodentia:Sciuridae:*Cynomys*), or marmots (Rodentia:Sciuridae:*Marmota* spp.) spend large amounts of time excavating and maintaining burrows. Adaptations for this semifossorial way of life are increasingly small ears and stronger limbs and claws. These prey species also keep senses of sight and hearing and rapid mobility above ground. Compare the general body shape of a badger with that of a raccoon. What modifications for semifossorial life appear in the badger?

Figure 41. Scanned images of raccoon (*Procyon lotor*) and badger (*Taxidea taxus*).

The step from a semifossorial animal to one living and foraging permanently underground requires greater anatomical change. Fossorial mammals generally have sturdy, compact bodies, the length of neck and tail is reduced, tactile and olfactory senses are improved, the pinnae are small or absent, and the eyes are small and sometimes non-functional. Specialized digging limbs have evolved. Fossorial insectivores (the moles) and marsupials (the marsupial mole, *Notoryctes*) have front limbs with large hands, strong claws, and powerful muscles. The palms of the hands point backwards. Fossorial rodents (like pocket gophers (e.g., *Geomys bursarius*) and mole rats) tend to use powerful, procumbent incisors for digging. The limbs are robust, but generally are used only to move the loosened soil backwards.

Figure 42. Skeleton of a mole (*Condylura cristata*). Compare the structures of the hind limbs and the forelimbs, and the structure of limbs in this skeleton compared to others.

See Color Handout

Examine the skin of a mole. Brush the hair in different directions. What is the advantage of this type of pelage to a fossorial mammal?

Arboreal adaptations. Even mammals without obvious adaptations climb trees, either to reach food or to find places to rest or escape. Many smaller rodents and insectivores with unspecialized hands are excellent climbers and forage in trees and shrubs. Cats, martens, raccoons, bears, and even goats and some foxes spend time in trees.

Tree squirrels have an essentially terrestrial structure. Their arboreal specializations are limited to very sharp claws and long bushy tails that aid in balance. They tend to live in the trees, where they have their nests, but they also forage on the ground. Tree squirrels are considered scansorial ("scampering") animals. A similar body shape is found in the tree shrews (Order Scandentia) (Fig. 35). Do you see differences in the skull and dentition of a tree shrew compared to the squirrel skull next to the case? What are they?

Mammals specialized for life in trees are called arboreal. They often have opposable digits or prehensile tails, or both. Monkeys and most apes are essentially arboreal animals. Animals like the orangutan that have a "hand" on every limb are termed quadrumanal. Gibbons employ one form of locomotion above all others: they hang by their hands and move forward by swinging from branch to branch. This brachiation is often compared to an up-side-down bipedal walk. Brachiating mammals have especially long fingers and short thumbs. Tree sloths hang from hook-like claws on manus and pes. Their arboreal locomotion resembles a slow up-side-down quadrupedal walk. Sloths are bradypodal ("slow-footed") animals. On the ground they walk on the sides of their feet.

Figure 43. Skeleton of a two-toed sloth (Edentata: Megalonychidae). Note the claws gripping around the branch.

See Color Handout

Some arboreal mammals like the colugos ("flying lemurs" which are not lemurs and do not fly) and "flying" squirrels (which do not fly but are squirrels!) have increased surface areas with flaps of skin that extend between their hind and front legs. This patagium is spread out when the animal leaps from one tree to another, allowing the animal to glide. Such glissant animals can travel great distances in one leap and control the direction of glide and rate of descent. No glissant mammal really flies. Nonetheless gliding is a successful strategy and has developed independently in several orders.

Figure 46. Flying squirrel (*Glaucomys sabrinus*) study skin with extended patagium.

See Color Handout

Examine the skulls of arboreal mammals. Do they have the orbits directed anteriorly to provide binocular vision from the overlapping visual ranges? What is the selective advantage of depth perception, which binocular vision makes possible, in these forms?

Specimen list

Order	Family	Species	Common name
Insectivora	Talpidae	*Condylura cristata*	Star-nosed mole
Carnivora	Felidae	*Lynx rufus*	Bobcat
Carnivora	Felidae	*Felis catus*	Cat
Scandentia	Tupaiidae		Tree shrew
Rodentia	Muridae	*Rattus norvegicus*	Rat
Monotremata	Tachyglossidae	*Tachyglossa* sp.	Spiny anteater
Lagomorpha	Leporidae	*Oryctolagus cuniculus*	Domestic rabbit
Edentata	Dasypodidae	*Dasypus novemcinctus*	armadillo
Carnivora	Otariidae		Seal
Perissodactyla	Equidae	*Equus caballus*	Horse
Artiodactyla	Bovidae	*Bos taurus*	Cow
Diprotodontia	Macropodidae		Kangaroo
Rodentia	Sciuridae	*Sciurus carolinensis*	Gray squirrel
Rodentia	Sciuridae	*Glaucomys sabrinus*	Flying squirrel
Edentata	Megalonychidae		Two-toed sloth
Chiroptera	Pteropodidae		Fruit bat
Primates	Galagonidae		Bushbaby

Class Reptilia

Order Crocodylia	Alligatoridae	*Alligator mississippiensis*	American alligator