

most striking ones in which the number of elements differs or the structure of homologous elements is particularly diverse. Special emphasis is given to the structures that are most obviously related to function. The chapter then reviews the functional diversity of the mammalian limb from the perspective of gross ecomorphological categories, groups that are primarily locomotory in nature. The chapter then reviews aspects of variation, genetics, and development of the mammalian limb. Finally, the early evolution of the mammalian limb is reviewed.

This chapter concentrates on terrestrial mammals. Bats and gliding mammals are covered in chapter 16, and whales and aquatic mammals in chapter 18.

General Considerations

Mammalian Taxonomy

On all points except the most major, the taxonomy in this chapter follows McKenna and Bell's (1997) *Classification of Mammals above the Species Level*. The name "Mammalia" is used here to designate the earliest common ancestor of living mammals to have an exclusively dentary-squamosal jaw joint and all descendants of that ancestor (cf. Simpson 1945; Z. Luo 1994). This traditional usage differs from that of some authors who have restricted the name "Mammalia" to the crown group—the last common ancestor of living monotremes, marsupials, and placentals and the descendants of that ancestor—and used the name *Mammaliaformes* for the more inclusive group of animals with a dentary-squamosal jaw joint (Rowe 1988, 1993; McKenna and Bell 1997). "Metatheria" and "Eutheria" are used in this paper for marsupial and placental mammals, respectively, rather than McKenna and Bell's use of "Marsupialia" and "Placentalia."

Several higher taxonomic categories of mammal are frequently referred to in this paper. Therians are the group that includes metatherians and eutherians, their last common ancestor, and the descendants of that ancestor (fig. 15.1). These mammals share the tribosphenic molar pattern and many specializations in the skeleton. Monotremes are nontherian mammals that live today in Australia and New Zealand. Multituberculates were nontherian mammals that are now extinct, but were diverse and geographically widespread during the Mesozoic and early Cenozoic. Archonta is the group of eutherian mammals that includes primates, bats, dermopterans (flying lemurs), and scandentians (tree shrews). Ungulata is the group of eutherian mammals that includes perissodactyls (horses, rhinos, and tapirs) and artiodactyls (pigs, camels, deer, cattle, antelope, etc.).

Anatomical Terminology

Anatomical structure names follow standard palaeontological and zoological usage, which is essentially that of Romer and Parsons (1977). This usage differs in details from standard usage in anthropological, medical, and veterinary disciplines. The greatest discrepancies are in the names of carpal and tarsal bones.

Many anatomies have been published that include the limbs of one or more species of mammal. Two of the most detailed are *Gray's Anatomy* of the human (Williams and Warwick 1980) and *Miller's Anatomy of the Dog* (H. E. Evans 1993). The general anatomical structure of

the limbs presented here owes a great debt to these works.

Structure and Function of Mammalian Limbs

General

The mammalian appendicular skeleton differs from that of other vertebrates in several respects (fig. 15.2A). Mammals have fewer bony elements than most other vertebrates, though the evolutionary reduction of the number of bones is compensated for by an increase in the number of muscles. With the exception of monotremes, the mammalian pectoral girdle has been reduced to a single major bone, the scapula (which incorporates a remnant of the coracoid). The number of carpals has been reduced to nine or fewer elements and the tarsals to seven or fewer. Mammals typically have an upright posture, with the humerus and femur oriented almost vertically. Compared to other tetrapods, limb movement during terrestrial locomotion is roughly in a parasagittal plane (see Jenkins and Camazine 1977 for a nuanced discussion; and see Inuzuka 1984 for an argument that desmostylians, an extinct group of manatee-like eutherian mammals, had a sprawling posture). The rotation of the limbs into an upright stance was correlated with changes in the configuration of distal limb elements, notably the repositioning of the tarsals so that the astragalus sits partially atop the calcaneum (O. J. Lewis 1989; Szalay 1994). Bony processes for the insertion of extensor muscles are also especially well developed in mammals, particularly the olecranon process of the ulna, the greater trochanter of the femur, and the tubercle of the calcaneum. The pelvis of mammals is also reorganized, with a long ilium that positions the pelvis caudoventrally to its sacral attachment. Mammals and many of their synapsid relatives also have a ventral contact between the pubis and ischium, which encloses the obturator foramen. Most of these skeletal changes are associated with changes in the posture of mammals and correlated muscular reorganizations that give mammals very fast and efficient modes of locomotion.

A large part of the diversity of mammalian limb morphology can be summarized by their stance. Habitual standing limb postures have been categorized as plantigrade, digitigrade, and unguligrade (fig. 15.2B; Howell 1944). Plantigrade mammals stand with the carpals and tarsals in contact with the substrate. Digitigrade mammals stand on the ends of their metapodials, with the carpus and tarsus raised above the substrate. Unguligrade mammals carry the digitigrade stance further and stand on the tips of their digits. These categories form a continuum, especially between plantigrade and digitigrade, and some mammals have multiple stances depending on the situation. Each stance position has its consequences for locomotion. Plantigrade mammals are able to use the feet for forward propulsion to a greater extent than digitigrade or unguligrade mammals (Clevedon Brown and Yalden 1973). Digitigrade mammals gain an extra limb segment and a proportionally longer distal limb, which increases the length of stride and, thus, the speed of movement, but they are more reliant on the proximal limb for forward momentum. Unguligrade mammals gain yet more segments and distal length, enabling them to move quickly and efficiently.

Pectoral Girdle

The pectoral girdle of mammals is light and mobile. In therians, the girdle is composed of a large scapula, a small coracoid (fused to the scapular head), and, often, a clavicle. The girdle is embedded in a muscular sling that provides scapular mobility and bodily support. When present, the clavicle connects the scapula and the sternum, but otherwise the pectoral girdle has no bony connection to the rest of the skeleton. Body weight in mammals is transmitted to the forelimb via the *serratus* muscle complex, which suspends the thorax from the dorsal margin of the scapula. Weight is transmitted through the scapula to the limb via the glenoid fossa of the scapula, which forms the proximal part of the shoulder joint. The pectoral girdle also serves as a point of origin for muscles of the arm. The pectoral girdle thus provides support, offers propulsive power, and helps absorb the impact of the forelimb during locomotion.

In monotremes and many extinct mammalian groups the pectoral girdle is more bulky and retains bones that were lost in therians, including the anterior clavicle (or proclavicle) and interclavicle. These animals retain a sprawling posture, and the humerus transmits a medial as well as vertical force vector onto the pectoral girdle. Consequently, the left and right girdles are braced at the midline via the clavicle, anterior coracoid, and interclavicles. The buttressing prevents collapse of the shoulders (Howell 1937a).

Scapula

Structure

The scapula of therian mammals is a large, flat, triangular bone that tapers distally into a neck supporting the articular region (fig. 15.3). The lateral surface is bisected by a raised spine that divides the supraspinous and infraspinous fossae. The spine terminates distally of the acromion process, which overhangs the proximal humerus. The distal scapula has a round depression called the glenoid cavity, which receives the humeral head to form the shoulder joint. The coracoid process, composed of the vestigial coracoid bone, projects around the cranial side of the glenoid. The cranial border of the scapula is usually gently curved, while the dorsal and caudal borders come together in an angle known as the teres process. The costal surface of the scapula is shallowly concave and almost completely occupied by the subscapular fossa. In some mammals, notably perissodactyls and artiodactyls, the dorsal portion of the scapula is unossified and is composed in the adult of cartilage.

Comparative Function

The shape and size of the scapula and its muscular attachments reflect the locomotory habit of the animal (fig. 15.3). The primary functional components of the scapula are (1) the relative breadth of the proximal scapula blade from the teres process to the cranial border, which determines the moment arms of flexors and extensors of the shoulder; (2) the orientation of the scapular axis, which relates to whether the scapula contributes substantially to limb flexion and extension; and (3) the size and shape of the acromion and coracoid processes, which are related to the size and moment arms of shoulder muscles. Cursorial (running) mammals, for example, usually have a long, narrow, vertically oriented scapular blade that helps increase stride length. Ambulatory (unspecialized terrestrial) mammals may also have a narrow scapula, but it is

usually more horizontally oriented. Fossorial (digging) and natatorial (swimming) mammals usually have a triangular blade with a large, robust teres process that provides the teres major muscle with more efficient leverage for powerful adduction of the forelimb. In some fossorial and natatorial animals a second low spine divides the infraspinous and teres fossae.

Clavicle

Structure

The clavicle is a long bone that connects the scapula and sternum, but which is rudimentary or absent in many mammalian groups. When present the bone usually has a bowed shaft that attaches at its medial end to the manubrium of the sternum via a saddle-shaped synovial joint, and at its distal end to the acromion of the scapula via a flat joint. The clavicle is a dermal or intermembranous bone and is the only such bone to be retained in the therian pectoral girdle. Despite this developmental categorization, the clavicle develops in part from cartilaginous precursors, and it has multiple primary and secondary ossification centers (Williams and Warwick 1980). In humans, two primary intermembranous ossification centers form and quickly fuse as ossification proceeds. True cartilage is formed at the medial and lateral ends, which are engulfed by expanding ossification. Further endochondral growth proceeds from the ends, and there are also two endochondral epiphyses that form. A secondary ossification center later appears at the sternal end. The two primary ossification centers correspond to the attachment points of the sternocleidomastoid and trapezius muscles (Howell 1937b). The clavicle is the first postcranial element to ossify in therians (Sánchez-Villagra 2002), but its ossification may not be complete until after sexual maturity.

Several muscles may attach to the clavicle, leaving their imprint on the bone. When the clavicle is fully developed, as in humans, the clavicular head of the deltoid muscle is often attached to the ventral border of the lateral end, and the trapezius to the dorsal. The sternocleidomastoid (or its equivalent) inserts on the cranial border of the medial end, and the subclavius muscle originates from the ventral border. The pectoralis major originates from the ventral border of the medial end. In groups with a reduced clavicle, such as dogs, the sternocleidomastoid and the clavicular head of the deltoid form a more or less continuous muscle with the splinterlike clavicle embedded in a tendinous sheath at the level of the shoulder.

Absence of the clavicle can occur individually in normally clavicate species. In humans, for example, the clinical condition of cleidocranial dysplasia may present symptoms of reduced or absent clavicles. Cleidocranial dysplasia can be caused by a mutation in one or both copies of the *cbfal* gene, which has its most profound effects on the ossification of membraneous bone (Mundlos 1999). In domestic dogs (*Canis familiaris*), which have small clavicles unattached to other bones, the clavicle is variable both in size and degree of ossification (H. E. Evans 1993). Among living mammals, monotremes have an exceptional clavicle, which is solidly attached to the rest of the pectoral girdle and has a much different function than in other groups. The emballonurid Ghost Bats, *Diclidurus*, also have an unusual clavicle, which is flattened and triangular with pronounced process mid-shaft (G. S. Miller 1907; Howell 1937b; N. B. Simmons, American Museum of Natural History, New York, pers. comm.).

Comparative Function

The clavicle has two major functions: it participates in shoulder movement and it maintains a fixed distance between the shoulder joint and the sternum. The clavicle's exact role depends on the presence of the bone itself and the configuration of the muscles attached to it. In humans, for example, the clavicle plays an important role in lifting the shoulder, where it acts as a lever with the fulcrum at the manubrium (Williams and Warwick 1980). The trapezius, which inserts at the distal end, pulls the clavicle cranially and thus raises the shoulder. This movement is facilitated by caudal translation of the proximal end of the scapula across its cartilaginous disc, powered by the pectoralis major. In humans, the bony clavicle adds stability to movements when the forelimb is used for manipulation and contributes to an arcuate movement of the shoulder (Jenkins 1974). In the domestic dog, where the clavicle is reduced to a splint of bone, the bone serves as an interface between the cleidocervicalis and cleidobrachialis muscles (H. E. Evans 1993). The bone's ligamentous attachments to the sternum and the scapular head prevent the scapula from moving too far caudally and allow it to be pulled cranially by the clavicular muscles.

Evolutionary loss of the clavicle allows the shoulder to move parallel to the thorax, an adaptation for cursoriality (Chubb 1932; Jenkins 1974), but its absence in species that are normally clavicate results in shoulder collapse. Those mammals that retain the clavicle—such as most marsupials, primates, and bats—often use the manus to climb, fly, or manipulate objects (Howell 1937b).

Humerus

Structure

The humerus is the only bone of the brachium. It supports the weight of the anterior body in quadrupeds, serves as the insertion point for muscles moving the brachium, and is the point of origination for muscles moving the forelimb and manus. In most groups the humerus has a long, cylindrical shaft with a rounded proximal head and a flared distal condylar region (fig. 15.4).

At its proximal end, the head of the humerus articulates with the glenoid fossa of the scapula. The proximal humerus usually has four tubercles (or tuberosities, depending on their size and shape) for muscle attachments: two immediately adjacent to the head and two further down the shaft. The greater tubercle is located at the craniolateral margin of the head and is the insertion point of the supraspinatus and infraspinatus muscles. The lesser tubercle lies on the medial margin of the head and is the insertion point of the subscapularis muscle. The muscles of the greater and lesser tubercle serve primarily to stabilize the shoulder joint and secondarily to move the brachium. Further distally, on the lateral side of the shaft, the deltoid tuberosity marks the insertion of the deltoideus muscle, a major extensor of the brachium. The teres major tuberosity is usually visible on the medial side of the shaft and is the insertion point of the teres major, a major flexor of the brachium.

At the distal end of the humerus, a condyle articulates with the radius and ulna to form the elbow joint. The condyle is divided into a medial trochlea, which is a grooved structure that articulates with the ulna, and a lateral capitulum, which is convexly rounded and articulates with the fovea of the radial head. Immediately above the condyle are the medial and lateral

epicondyles, which are the points of origin for muscles of the antebrachium. The medial epicondyle is the point of origin for the pronator teres muscle, which pronates the forearm, and the common flexors of the carpus and digits. The lateral epicondyle is the origin of the common extensors of the carpus and digits. Just proximal to the lateral epicondyle is the lateral supracondylar ridge, or supinator crest, from which the supinator muscle arises. In many mammals, an entepicondylar foramen runs through the medial epicondyle. The entepicondylar foramen serves as a retinaculum for the median nerve and sometimes the brachial artery (Landry 1958). Presence of the canal is the ancestral condition for mammals, but it has been lost independently in many groups that have reduced the epicondyle in association with restricting the ability to abduct the humerus and supinate the forearm.

Comparative Function

Many of the morphological differences among mammalian humeri have direct functional correlations. The size, shape, and orientation of the tubercles, the orientation of the head, the width of the epicondyles, and the shape of the condyle are often indicative of the range of movements in the forearm and the locomotory style of the animal (fig. 15.4). For example, in the pronghorn antelope (*Antilocapra americana*), a cursor, the deltoid and teres major tubercles are proportionally located about a quarter of the way down the shaft. The moment arm for the deltoid and teres major muscles is consequently short, allowing rapid but relatively weak flexion and extension of the forelimb. The same tubercles in the natatorial otter (*Lontra canadensis*) are located nearly halfway down the shaft, providing for proportionally more powerful flexion and extension. The proportions of the epicondylar region in the same species are also quite different. The pronghorn, whose stabilized forearm is incapable of supination, has narrow epicondyles and consequently short moment arms for the pronator and supinator muscles. The otter has wide epicondyles and a pronounced supinator crest, providing long moment arms for powerful pronation and supination abilities that are used by the animal in swimming and food manipulation. The same phenomenon is seen in the condyles. In the pronghorn, both trochlea and capitulum are hingelike, but in the otter the capitulum is broadly rounded for rotation of the radial head in supinating movements. In carnivores, cursors without the ability to supinate the forelimb apparently have a restricted maximum body mass, whereas generalists that retain supination can reach very large body sizes (K. Andersson and Werdelin 2003).

Radius and Ulna

Structure

The radius and ulna make up the forearm, or antebrachium (fig. 15.5). The radius provides the primary support for anterior body mass, and the ulna stabilizes the elbow joint and provides a point of insertion for elbow extensors. In some mammals, particularly cursorial ones, these bones are fused and the ulna reduced.

The radius has a head at its proximal end, a long shaft, and an enlarged distal extremity with articulation surfaces for the ulna and carpal. The radial head is usually oval in outline with a concave proximal end, the articular fovea. The fovea contacts the capitulum of the humerus. The surface around the margin of the head makes rotational contact with the radial notch of the

ulna. On the medial side of the proximal shaft is the radial tuberosity, the insertion point of the radial head of the biceps brachii muscle. The radius usually broadens at its distal end where it articulates with the carpals. On the cranial side, grooves are often visible for the tendons of the abductor pollicis longus, the extensor carpi radialis, and the extensor digitalis. On the lateral surface of the extremity there is usually a concave ulnar notch that provides the distal point of rotation of the radius against the ulna. The distal end has a concave articular surface for the scaphoid and lunate bones of the carpus. A radial styloid process projects from the medial side of the distal end.

The ulna has a large proximal end, a tapering body, and usually a distal end with an articular surface for the carpals. The proximal end has a crescent-shaped semilunar notch that receives the trochlea of the humerus. The large olecranon process projects from the proximal end of the ulna and receives the insertions of the extensor muscles, most notably the triceps brachii. The distal border of the trochlear notch terminates in the coronoid process of the ulna. Distal to the coronoid process of the trochlear notch is a concave surface, the radial notch, which receives the articular circumference of the radial head. The distal extremity thickens into the pointed styloid process and has a facet called the ulnar articular circumference that contacts the distal head of the radius. The styloid processes of ulna and radius provide lateral support for the carpals, and are homologous to the radiale and ulnare carpal bones of ancestral tetrapods (Cihak 1972).

Comparative Function

The function of the forelimb bones has been extensively studied (Howell 1944; Jenkins 1973). Important factors for comparative forelimb function include (1) the degree of fusion of the radius and ulna; (2) the shape of the radial head and corresponding ulnar articular surface; (3) the proportional length of the olecranon process; and (4) the proportional position of the radial and ulnar tuberosities. The degree of fusion and the shape of the radial head help determine the range of pronation-supination movement possible at the manus. Cursorial mammals often have restricted pronation-supination, whereas scansorial mammals can usually completely supinate the manus. Pronation-supination movements are accomplished by flipping the distal radius over the distal ulna, rotating the radius about its long axis. As the radius rotates, the radial head rolls within the radial notch of the ulna. Round radial heads roll easily, whereas flattened heads do not. Morphometric ordination of the outline of the radial head alone does a good job of discriminating scansorial, fossorial, ambulatory, and cursorial species (MacLeod and Rose 1993). The length of the olecranon determines the moment of effort for forelimb extension. The olecranon is relatively longer in fossorial and natatorial animals, and shorter in cursorial ones. The position of the tuberosities affects the moment arm of effort for forearm flexion.

These differences are illustrated by a comparison of the forelimb of a dog with that of a pig (fig. 15.5). Dogs are relatively agile, medium-weight digitigrade cursors, while pigs are less agile, heavier unguligrade cursors. The olecranon process, which is the in-lever of the system used to extend the forelimb, is proportionally longer in the pig than in the dog. This gives the pig a more efficient moment arm for extension, which is related partly to the larger mass of the pig but also to differences in distal limb morphology (pigs have a longer carpus and manus, which compensate for the relatively short radius and ulna in providing overall length to the limb). Consequently, the pig has a slower, more powerful extension than the weaker but rapid extension

of the dog. Pigs have a close fit between radius and ulna, which provides stability and completely restricts pronation-supination of the manus. Dogs have a looser fit between the two elements, although supination is restricted compared to some other mammals. Though it is not visible in the figure, the radial head of the dog is ovate, whereas that of the pig has an irregular shape that locks it into the ulnar notch, preventing supination.

Manus

Structure

The manus consists of the wrist, or carpus, the metacarpus, and the digits (fig. 15.6). The carpus is composed of a dual series of carpal and sesamoid bones. The proximal series articulates with the radius and ulna, whereas the distal one articulates with the metacarpals. The number and shape of the carpal bones vary among mammalian groups, with both evolutionary fusions and losses of bones having occurred. In the ancestral therian there were three proximal carpals, which from medial to lateral are the scaphoid, lunate, and triquetral. The first two articulate with the radius and are fused in many groups (notably in Carnivora), and the last articulates with the ulna. The pisiform, a sesamoid bone with an important function in flexion of the carpus, lies lateral and caudal to the triquetrum. The distal carpals are, from medial to lateral, the trapezium, trapezoid, capitate, and hamate. The first three articulate individually with the first three metacarpals, while the fourth carpal articulates with both the fourth and fifth metacarpals. The triquetral often contacts the fifth metacarpal as well.

One to five metacarpal bones (depending on the group) extend distally from the distal carpals. They each have a blocky base with an articular face for the carpals, a long body, and a rounded head with a joint surface for articulation with the digits. Usually, the number of metacarpals corresponds directly to the number of digits. Some mammalian groups, such as equids, have reduced the number of metacarpals to only one, while others retain the ancestral number of five. Interestingly, the first metacarpal has a growth plate at the proximal and distal ends (as does the first metatarsal), whereas the other four have growth plates only at their distal ends (Shively 1978).

Distal to the metacarpals are the digits (one per metacarpal bone), most of which are each composed of three phalanges (proximal, middle, and distal). The first digit, the pollex, has only two phalanges. The distal phalanx is usually specialized for supporting a nail, claw, or hoof.

Comparative Function

The manus of mammals differs in extreme and remarkable ways (fig. 15.1). The number of digits ranges from one (in Equidae, the horses) to five (the ancestral condition, which is retained in many living groups). Cursorial mammals often have a reduced number of digits, though the number and amount of reduction varies considerably. Canids, for example, have reduced the first digit so that they retain four fully functional ones; tapirs have reduced the first and fifth, leaving three large ones; and cervids have reduced digits one, two, and four, functioning with only two primary digits. Arboreal animals often have the full complement of five, usually with an opposable pollex and long metacarpals and phalanges. Bats have extremely elongated digits that support their wing membranes. Seals and sea lions have a broad manus with paddlelike

proportions.

Most marsupials retain all five digits of their manus, regardless of the locomotory specializations of the hindlimb. The ubiquity of generalized, grasping hands in marsupials may be due to constraints imposed by metatherian reproduction. Metatherian young are born at a very early embryonic stage and continue development attached to the nipple after climbing there with precociously developed forelimbs (Lillegraven 1975; L. S. Hall and Hughes 1987; Szalay 1994). Neonatal marsupials are effectively "scansorial" in that they have to climb hand over hand from vulva to nipple, requiring them to have well-developed forelimbs and the ability to grasp and pull. Eutherians, with their intrauterine development, are not so constrained and have a much wider diversity of forelimb specialization.

Pelvis

Structure

The pelvis (fig. 15.7) anchors the hindlimb to the axial skeleton, transmits weight from the body onto the hindlimb, and supports and protects the internal organs in the posterior part of the body cavity. The left and right halves of the pelvis are known as innominate bones, or *os coxae*. Each innominate is made up of the fusion of the ilium, ischium, pubis, and acetabular bone. The pelvis is attached to the sacrum at the iliac crest, and the two halves are attached to one another at the pubic symphysis. On the lateral faces of the pelvis is the round depression known as the acetabulum that receives the ball of the femur. The obturator foramen lies on the ventral aspect of the pelvis between the pubis and ischium.

Many mammals, especially living metatherians, have epipubic bones. These slender bones extend cranially into the abdominal wall from the pubis. Whereas textbooks often associate epipubic bones with support of a pouch, or marsupium, they are present in both pouched and pouchless metatherians, and they are found in monotremes and early eutherian groups.

Comparative Function

The shape of the pelvis is closely associated with the body mass and locomotory repertoire of the animal. Differences are most notable in the orientation of the iliac crests and in the shape and depth of the acetabulum. The orientation of the iliac crest is related to the habitual posture of the animal. Bipedal mammals, such as humans, have an upright ilium that parallels the vertical orientation of the sacroiliac joint, whereas quadrupedal mammals usually have a horizontally oriented ilium that parallels their horizontal vertebral column (Schultz 1936). Orientation is also related to body mass, most notably among quadrupedal species. Heavy mammals tend to have a more upright pelvis than do light ones (compare the shrew, *Crocidura suaveolens*, the dog, *Canis familiaris*, the horse, *Equus caballus*, and the elephant, *Elephas maximus*, in fig. 15.1). The vertical orientation is capable of supporting greater weight without dislocating the sacroiliac joint or putting undue torsion on the vertebral column. The shape of the acetabulum is also related to locomotory style (Jenkins and Camazine 1977). Ambulatory mammals have a wide range of hip movements, including significant abduction of the femur. The acetabulum in these animals is more shallow and open than that of cursorial mammals. The lengths and angles of the

ilium and ischium relative to the acetabulum also have important functional consequences because the surfaces of these bones are the origination points for most of the extensors and flexors of the hips. The primary extensors of the hip arise from the lateral face of the ilium (the gluteus muscles) and from the ischiatic tuberosity (the semimembranosus and other muscles). The lengths and angles of these areas of the pelvis thus determine the moment arms for hip extension, which provides forward momentum during locomotion.

Most likely, the epipubic bones have multiple functions, including support of the ventral body wall, influencing movements of the pelvis during locomotion, and support of young (Szalay 1994). Interestingly, T. D. White (1989) found in pouchless marsupials a direct relationship between litter mass on the one hand and size of the epipubic bones and their degree of sexual dimorphism on the other; however, among pouched species the relationship was not so strong, suggesting that the litter-supporting function of the bones is greater in species without a pouch and that other functions predominate in pouched species.

Femur

Structure

The femur is a long bone with a distinctive ball-like head at the proximal end and a large, triangular distal end with a groove on the cranial side for the patella and patellar tendon (fig. 15.8). The head is usually located on a restricted neck and is surrounded by three large processes, or trochanters, whose positions help determine the lever advantage for the flexors and extensors of the hip. The greater trochanter arises lateral to the femoral neck and projects proximally. Three extensors of the hip—the gluteus medius, gluteus profundus, and piriformis muscles—insert on it. The lesser trochanter lies distal to the head on the caudomedial margin of the femur. The iliopsoas muscle, a flexor of the hip, inserts on the lesser trochanter. The third trochanter lies more distally down the body of the femur and is more variable in size from group to group. Another extensor of the hip, the gluteus superficialis muscle, inserts on the third trochanter. The body of the femur is usually long with a rounded cross section. At the distal end, two condyles curve caudally, with the patellar groove lying between them on the cranial face and the intercondyloid fossa between them on the caudal face. The length and depth of the patellar groove are often correlated with locomotory type. On the caudal side, just above the condyles, are the lateral and medial supracondylar tuberosities, which are the origin of the gastrocnemius muscle.

Comparative Function

Some functionally important characters of the femur are (1) the length and orientation of the greater trochanter; (2) the size of the third trochanter; (3) the shape of the head and position of the fovea; and (4) the depth of the patellar groove. The greater trochanter functions as a primary lever for extension of the hip. Consequently, it is often long and robust in cursorial mammals. The muscles that insert on the greater trochanter run caudally from the anterior pelvis, pulling the trochanter forward, which helps extend the limb by pivoting it around the head. The longer the trochanter, the more efficient the moment arm for extension. The third trochanter is well developed in cursorial mammals because it is also the insertion point of hip extensors. These

muscles run in the opposite direction from the posterior part of the pelvis, from where they pull the distal femur caudally by tugging on the third trochanter. The head of the femur is broader and more proximally directed in species that significantly abduct the femur during locomotion, such as ambulatory mammals (Jenkins and Camazine 1977). The patellar groove is longer and deeper in cursorial and saltatory mammals than it is in ambulatory or scansorial ones. The patella, or kneecap, itself is a sesamoid bone embedded in the tendon of the quadriceps femoris muscle. The patella rides in the patellar groove along with the tendon. The extra depth of the groove provides stabilization for the knee via the patellar tendon.

Crus

Structure

The lower hindlimb between knee and ankle is the crus, and is made up of the tibia and fibula, plus several sesamoid bones (fig. 15.9). In most mammals, the tibia is the larger bone. It lies medial to the fibula and supports most of the body weight. The proximal end flares at the knee joint, and tapers distally into a long body. The proximal articular surface is divided into a lateral and medial condyle, with an intercondyloid eminence between them. Just distal to the articular surface on the cranial border is the tibial tuberosity, which is the insertion point of the quadriceps femoris and the sartorius muscles. A small articulation surface for the fibular head is located on the lateral side of the proximal end. The position of the contact between tibia and fibula varies considerably among mammal groups. In placentals the articulation is just distal to the margin of the lateral condyle, whereas in monotremes and many marsupials the contact is at the margin itself, often with the head of the fibula extending proximally to the level of the distal femur (Szalay 1994). At the distal end the tibia flares again, with an articular surface for the ankle joint. The articular surface is often grooved, sometimes quite deeply, to receive the ridges of the astragalus. A distal projection on the medial side forms the medial malleolus, which wraps around the medial face of the astragalar trochlea. In some taxa the articular surface and malleolus tightly envelop the astragalus, restricting movement to parasagittal plane, whereas in others, especially marsupials, the articulation is more open, allowing more freedom of movement for the foot (Szalay 1994). The lateral side of the distal tibia has an articular surface for contact with the fibula. The fibula is usually thin (especially in eutherians) and serves mostly for muscle attachment and to stabilize the lateral ankle joint. In some taxa the fibula is fused to the tibia, and in some it is extremely reduced. The proximal head is usually enlarged and has a small articulation surface for contact with the tibia. The distal end is enlarged into the lateral malleolus, which usually participates in forming the ankle joint.

Comparative Function

Functional variety in the tibia and fibula is not as visually obvious as it is in other limb structures. The most conspicuous functional differences are seen in the distal articular surface of the tibia. This joint surface can be deeply grooved in cursorial mammals, spiraled in species with significant limb abduction (some ambulatory mammals) or those capable of hindfoot reversal (scansorial mammals), or comparatively flat (some ambulatory and scansorial species). The shape of the surface contributes to the degree of ankle stabilization and parasagittal movement. The degree of fusion of the fibula also varies among mammals, but mostly in relation to body

mass. The tibia and fibula are often fused at the distal end in the smallest mammals, and occasionally in saltatory or cursorial mammals. Freedom of the fibula enhances abduction/adduction of the ankle, which can be important for scansorial mammals, especially marsupials, which normally have a proportionally large fibula.

Pes

Structure

The ankle, or tarsus, consists of several blocky bones (fig. 15.10). The ancestral therian had seven tarsal bones, a number that has been reduced in some cases by loss or fusion of elements. The largest tarsals are the calcaneum and astragalus (also known as the talus in medical terminology). These bones, especially the astragalus, articulate with the crus at the tibiotarsal, or upper ankle joint. The astragalus is divided into a body, neck, and distal head. The proximal (or dorsal) surface of the body forms the tibial articular surface, or trochlea. The shape of the trochlear surface mirrors the shape of the distal articular surface of the tibia. In most groups, the trochlea has articular surfaces on its medial and lateral faces, which articulate with the inner surfaces of the malleoli of the tibia and fibula, respectively. Facets for articulation with the calcaneum are found on the plantar surface of the body. The neck and head lie distal to the body. The head articulates with the navicular bone, and the neck (and sometimes head) contacts the calcaneum (and sometimes the cuboid bone). The calcaneum is elongate, with the long axis paralleling the long axis of the foot. A large calcaneal process, or tuber, projects caudally and is the point of insertion for the large tendons of the calf muscles. The calcaneum has a large facet for articulation with the astragalus on its dorsal side and for the cuboid on its distal end. In many mammals, especially eutherians, a large process called the sustentaculum astragali projects from the medial side of the calcaneum to support the neck of the astragalus. The joint between astragalus and calcaneum is the astragalocalcaneal, or lower ankle joint. The navicular bone lies distal to the astragalar head and the cuboid distal to the calcaneum. The joint between the proximal and distal tarsals is the transverse tarsal joint, which is composed of the astragalonavicular joint and the calcaneocuboid joint. Distal to the navicular and medial to the cuboid are the lateral, intermediate, and medial cuneiforms. These and the cuboid collectively articulate with the metatarsals.

Comparative Function

Like the manus, the functional morphology of the pes is complex and varied, so only a few aspects will be considered here. Comparative movements of the pes can be most easily understood by considering several major joints and axes of rotation (Szalay 1984, 1994). The upper ankle joint is the primary joint for dorsiflexion and plantarflexion, and it is the point where force is transmitted between crus and pes. The shape of the upper ankle joint surface has both taxonomic and functional variety. The upper ankle joint of metatherians has a relatively smooth, simple structure where some abduction and adduction occurs along with dorsi- and plantarflexion. In didelphids, the astragalus is mediolaterally expanded so that it has three facets, two for the tibia and one for the fibula, which is a weight-bearing bone (Jenkins and McClearn 1984; Szalay 1994). The upper ankle joint of eutherians usually has a sculpted surface, often with two ridges along the edges of the astragalar trochlea with corresponding grooves in the

distal tibial articulation. These ridges and grooves have the greatest relief in cursorial and saltatorial mammals, where they restrict plantarflexion to a parasagittal plane and provide stabilization for the ankle. The upper ankle joint of multituberculates is markedly different from the same structure in therians in that the distal tibia bears two condyles rather than a single concavity and the astragalus has dual grooves rather than ridges (Jenkins and Krause 1983). The shape of these surfaces is spiraled to facilitate hindfoot reversal. The lower ankle joint is also functionally diverse, and movement there may occur in many circumstances. In some taxa the lower ankle joint is especially important in hindfoot inversion (useful to scansorial mammals) because specialized facets allow the calcaneum to slide around the astragalus and so twist the distal foot into an inverted position (Jenkins and McClearn 1984). The lower ankle joint is tightly locked in cursorial mammals to prevent inversion or other distal foot rotation. The transverse tarsal joint varies similarly, with considerable rotation in mammals capable of hindfoot inversion, but tight interlocking in cursorial mammals.

The observation is worth making that pronation and supination of the manus are accomplished by movement in the forelimb, but that inversion and eversion of the pes are accomplished at tarsal joints.

Ecomorphologic Diversity of Mammalian Limbs

Mammalian limbs are often categorized into locomotory or ecomorphologic types (fig. 15.11). Locomotory classifications have been based on gaits (Heglund et al. 1974; Alexander and Jayes 1983), on combinations of musculoskeletal features (Dublin 1903; Gregory 1912; Maynard Smith and Savage 1956; M. E. Taylor 1974; Van Valkenburgh 1985), on limb ratios (Gambaryan 1974; Gonyea 1976; Hildebrand 1980; Christiansen 2002), and on combinations of these criteria. Systems have also been proposed for specific taxonomic groups. Many authors have lamented that locomotory classification schemes are not specific enough to be useful (e.g., Clevedon Brown and Yalden 1973), but in most cases increased specificity inhibits broad applicability. In this chapter only a few general ecomorphologic categories will be discussed, primarily because only very loose groupings can be applied across the whole of Mammalia.

Overviews of limb mechanics and functional diversity are found in Flower (1870), Muybridge (1893), Howell (1944), Tricker and Tricker (1967), Gambaryan (1974), Oxnard (1984), Hildebrand (1988), and Alexander (1983a, 2003).

Generalized or Ambulatory Mammals

Some mammals do not have obvious specializations for any particular locomotor style, substrate, or activity, and are often categorized as "generalized" or "ambulatory." The raccoon, *Procyon lotor*, and the opossum, *Didelphis virginiana*, are examples of these generalized or ambulatory mammals (Jenkins and Camazine 1977). Walking, running, climbing, and manipulating objects are all possible for ambulatory mammals because they do not have skeletal specializations that limit any particular activity. Ambulatory mammals have relatively mobile joints, the ability to pronate-supinate the manus, five digits (often with opposable hallux and pollex), and a plantigrade to semi-digitigrade posture. The proportions of the three major limb segments are

roughly equal (see *Marmota*, *Spermophilus*, and *Rattus* data in plate 15.1). Ambulatory mammals range in body mass from small (e.g., *Mus musculus*) through medium (e.g., *Didelphis virginiana*) to large (e.g., *Ursus arctos*).

Several skeletal traits are associated with an ambulatory mode of locomotion. The scapula is often triangular, providing a powerful moment arm for the flexors of the forearm. The deltoid crest of the humerus is often prominent and positioned well down the length of the shaft, almost to the midpoint in some cases. Ambulatory mammals often have a clavicle (Jenkins 1974). The supinator crest is large, the capitulum is rounded, the radial head is ovate to circular in outline (MacLeod and Rose 1993), and the radius and ulna are not fused, allowing supination of the manus. Ambulatory species have a wide range of hip movements, including significant abduction, and their acetabulae are accordingly open, the balls of their femora are broadly rounded, and the angle of the neck is obtuse relative to the axis of the femoral shaft (Jenkins and Camazine 1977). The tarsal joints permit a variety of movements, including some abduction and adduction at the upper ankle joint in marsupials (Jenkins and McClearn 1984).

Cursorial Specializations

Many ungulates and carnivores have specializations that allow greater running speeds, specializations that are called "cursorial" (fig. 15.11B). Horses, *Equus caballus*, goitered gazelles, *Gazella subgutturosa*, and cheetahs, *Acinonyx jubatus*, are examples of mammals with well-developed cursorial traits. Cursorial animals typically have relatively long limbs with distal segments proportionally longer than proximal ones (e.g., see *Gazella*, *Dama*, *Equus*, *Acinonyx*, and *Lepus* species in plate 15.1). The posture of cursors is usually digitigrade or unguligrade. Limb joints, especially in the hindlimb, are often structured to permit only parasagittal motion, which stabilizes them against mediolateral collapse during running. The scapula of cursors tends to be long, with a short teres process. The reduction or loss of the clavicle further enhances scapular mobility and parasagittal flexion and extension of the forelimb (Jenkins 1974). The deltoid and teres tuberosities of the humerus are proximally located. Restriction of the ability to supinate the manus and invert the pes contributes to joint stabilization. The pelvis and thigh of cursors are organized to maximize parasagittal movement, which is most obvious in the cylindrical nature of the acetabulum and the horizontal orientation of the femoral neck (Jenkins and Camazine 1977). The carpals and tarsals are often closely packed and structured to inhibit movements among them. The tibiotarsal joint has a hinge/groove structure that stabilizes it and restricts flexion and extension of the foot to a parasagittal plane (Van Valkenburgh 1985; Van Valkenburgh 1987). The metapodials and proximal phalanges are often greatly elongated, which increases the length of stride. The peripheral digits of cursors are often reduced or lost, the most extreme example being in the horses, where the number is reduced to one.

The shapes of bones and the positions of muscle origins and insertions give cursors a high "gear ratio" (Hildebrand 1988). The combination of short in-levers and long out-levers produces rapid translation of the manus and pes, but comparatively little power. Consequently, cursors also have specializations that lighten the distal limb. The number of digits is often reduced, with the single digit found in the horse being an extreme example. Muscles in the distal segment are also reduced. Centrifugal force, elongated tendons, and spring ligaments often combine to assist with segment extension (Camp and Smith 1942; C. R. Taylor et al. 1980; Alexander and Jayes 1983). The limbs of cursors may not be optimized for maximum speed, as

suggested by Howell (1944), but for minimization of locomotory energy costs (Gambaryan 1974; Garland and Janis 1993; Christiansen 2002).

Saltatory Specializations

Some desert and grassland mammals have specializations for jumping, or saltation. Many saltatory specializations are simply exaggerations of cursorial ones, such as long distal limb segments, high gear ratios, digit reduction, and hinged joints (Hall-Craggs 1965; Clevedon Brown and Yalden 1973). However, bipedal saltators, such as the red kangaroo, *Macropus rufus*, or the jerboa, *Jaculus jaculus*, differ markedly from their quadrupedal counterparts in that their fore- and hindlimbs have dissimilar specializations because saltation is performed bipedally. The forelimbs of saltatory animals often resemble those of ambulatory or scansorial species, particularly the mobile elements and grasping hands. Consequently, saltators can be recognized by their limb ratios because of their proportionally shorter manus than pes (e.g., *Allactaga*, *Eremodipus*, *Jaculus*, *Pygeretmus*, *Gerbillus*, and *Macropus* species in plate 15.1). Because saltators move bipedally, they must balance their weight over the hindlimb. In many species, a long, heavy tail counterbalances the weight of the forelimbs and head.

Saltators use their hindlimbs for propulsion, weight support, and maneuverability, which requires a stable hindfoot. Many saltators have a tridactyl foot, which provides stability and allows adjustment to direction of movement.

Despite claims that bipedal saltation might be more energy efficient for covering the distances necessary to forage in the desert, some studies have found that bipedal and quadrupedal locomotion are similar in energy costs at typical foraging speeds (S. D. Thompson 1985).

Scansorial Specializations

Scansorial, or climbing mammals, characteristically have mobile limbs and the ability to grasp with their hands and often their feet (fig. 15.11C). The terms “scansorial” and “arboreal” have an overlapping usage. Here “scansorial” is used for the general climbing locomotory category, whereas “arboreal” is used only in reference to species that live in trees. Scansorial locomotion is found in many mammal groups, and examples include such divergent species as the red squirrel, *Sciurus vulgaris*, the howler monkey, *Alouatta alouatta*, the three-toed sloth, *Bradypus tridactylus*, the kinkajou, *Potos flavus*, and the tree kangaroo, *Dendrolagus bennettianus*. Most primates, all scandentians (tree shrews), and many rodents, didelphids, and carnivores are scansorial to a greater or lesser degree. However, there is considerable diversity in the amount of time spent climbing, the method and speed of climbing, and the morphological structures that can clearly be associated with a scansorial lifestyle (Dublin 1903). Some climbers suspend themselves from tree limbs, such as sloths or gibbons, and have elongated limbs; others, such as tree squirrels, scamper on limbs and climb by clinging to projections and irregularities. And yet others, such as tarsiers, spring from place to place in the trees. Some scansors spend their entire lives in trees, while some climb only occasionally. Universal scansorial features are thus difficult to identify.

Caveats aside, some features are stereotypical of scansors (Dublin 1903). Most are

plantigrade and have grasping feet and hands. In some cases the manus and pes have become elongated, either at the tarsus for jumping scansors, or at the metatarsus and digits in suspensory and brachiating mammals. Suspensory species, such as sloths, have highly modified distal phalanges with long, curved claws for grasping. Many scansorial species have long, dorsoventrally thickened claws (Cartmill 1974). In almost all cases, the forelimb is capable of extensive pronation and supination, and the radius is mobile with a rounded head. The clavicle is often present, which stabilizes the shoulder, and the scapula is often triangular. The limbs as a whole are often elongated, the forelimb more than the hindlimb in brachiating species (Erikson 1963). Many scansorial mammals have prehensile tails.

Fossorial Specializations

Some mammals have fossorial or digging adaptations (fig. 15.11A). Fossorial mammals include those that dig occasionally in pursuit of food or in the construction of burrows, such as badgers, *Meles meles*, and wombats, *Vombatus ursinus*, and those that live most of their lives below the surface, such as mole rats (e.g., *Cryptomys damarensis*) and moles (e.g., *Talpa europea*). Many insectivorous mammals, especially those that eat ants, also have fossorial specializations, including armadillos, pangolins, and anteaters.

Fossorial specializations are most pronounced in the forelimbs, which are the primary tools of excavation (Shimer 1903; Reed 1951). In all fossorial mammals, the limbs have a "low gear ratio" (Hildebrand 1988), which emphasizes strength of extension rather than speed. In semifossorial burrowers, such as the wombat, the low gear ratio is manifested in the long teres process of the scapula, which increases the moment arm of the teres major muscle, the strong deltoid and teres tubercles, and the long olecranon process of the ulna. In subterranean mammals such as moles the differences are more extreme. The manubrium of the sternum is long, which moves the pectoral girdle forward so that it is at the very front of the animal; the clavicles are short, which pull the shoulders close to the body; the scapula is extremely long and narrow; the humeri are bizarrely shaped with large tubercles for muscles of flexion, extension, abduction, and adduction (fig. 15.4A); the radius and ulna are tightly interlocked, the olecranon process is long and robust, and the distal articular surfaces of both bones are flared to provide a massive contact with the carpus; and the manus is broad and inflexible, with interlocking carpals, extremely short metacarpals and phalanges, and long, thick claws (Reed 1951; Yalden 1966). Adaptations to digging are covered in more detail elsewhere (chap. 17).

Natatorial Specializations

Some mammals are adapted to life in water, and those that use the limbs as their primary means of propulsion are called "natatorial." The most extreme examples are cetaceans, or whales, and pinnipeds, or seals, sealions, and walruses; however, many other animals swim regularly, such as beavers, otters, nutrias, water voles, and water shrews (Osburn 1903). Depending on the degree of specialization, mammals may be classified as natatorial (swimming) or aquatic.

Natatorial features of the forelimb are similar to those of semifossorial mammals, but in swimmers the hindlimbs are also specialized (fig. 15.11D). Swimmers require powerful forelimb extension for pushing through the dense medium of the water. Accordingly, natatorial mammals

have large teres processes, short humeri with large deltoid and teres tubercles, and long ulnar olecranon process. Unlike diggers, swimmers have an elongated manus with especially long digits. The proximal hindlimb is sometimes reduced in length, but the crus is often long, and the pes paddlelike. In many cases, the toes are webbed (like in the beaver) or have become flippers (as in seals and sea lions). The sternum of natatorial mammals is often reduced, and the clavicles are usually absent (Osburn 1903). Aquatic and natatorial adaptations are covered in detail elsewhere (chap. 18).

Graviportal Specializations

Mammals with extremely large body masses require special features simply to support their weight during locomotion (fig. 15.11E). Animals that show such skeletal specializations are said to be graviportal. The most obvious graviportal features are the diameter of the limb bones, which are disproportionately large to support a body mass that has increased as the cube of body length (Schmidt-Nielsen 1984). The orientation of the pelvis is also a notable graviportal feature. The orientation of the ilium is highly correlated with body mass, and it becomes more vertical as body mass increases (fig. 15.1). The vertical orientation reduces the torque placed on the pelvis and sacrum under large loads. It is often said that decreased length of the distal limb segments, especially the metapodials and digits, is a graviportal specialization (Hildebrand 1988), but close inspection of plate 15.1 shows that this is not the case. In the plate, the standardized lengths of the proximal, middle, and distal limb segments of both the forelimb and hindlimb are shown. They have been ordered by the relative length of the pes, with the longest at the top of the graph and the shortest at the bottom. Elephants, which are the very largest of living land mammals, are indeed found at the bottom of the graph because of the reduced length of their manus and pes. However, the next heaviest mammal, the giraffe, *Giraffa camelopardalis*, is at the top because of its proportionally long manus and pes. Other large mammals, such as the bison, are found scattered through, suggesting that the short manus and pes of the elephants is a feature specific to the Proboscidea and not an adaptation to large body mass.

Bipedality

An unusual locomotory specialization of mammals is non-saltatory bipedalism (fig. 15.11F). Humans are the only habitual nonjumping bipeds, although some other species, mostly primates and bears, are facultative bipeds. Bipeds are typically plantigrade, have short tails, and vertically oriented pelvises. The human hindlimb has unique specializations for bipedalism, which include a short, flared ilium, an extremely long femur, a down-turned tuber of the calcaneum, and a large, elongated pollex (O. J. Lewis 1989).

Variability, Genetics, and Development in Mammalian Limbs

The interplay between structure, function, and development makes mammalian limbs a particularly interesting system, one that remains fertile despite its long history of study (Mariani and Martin 2003). The mammal limb skeleton has a particularly high genetic component. The size, shape, and structure of limb bones are sufficiently distinctive as to reliably indicate the

species from which it came (B. M. Gilbert 1973), and the phylogenetic continuity of limb structure is remarkable (Szalay 1994), even though superficial homoplastic resemblances develop as rapid evolution scampers across the same substrates again and again. In another sense, though, limbs are improbably plastic. Bones remodel rapidly in response to the stress and strain they encounter. Habitual exertion can leave a marked impact on the structure of limbs, from bowlegged cowboys, to asymmetrically armed Anglo-Saxon bowmen, to the eerily humanlike pelvis of Slijper's bipedal goat (Slijper 1946). Excision and tendon-severing experiments suggest that the structure of limb bones is due more to the forces impinging on them than to anything fundamentally heritable. The ecophenotypic plasticity of the limb skeleton suggests a lack of heritable variance. Some have suggested that the latter has wrongly encouraged systematists to reject limb characters from phylogenetic analyses (Szalay 1977). Almost in contradiction, patterns of expression of intrinsic skeletal genes are known to influence morphology and have been used to explain evolutionary transformations (Lovejoy et al. 2000). The evolutionary transformations of the limb are clearly a fuzzy combination of the genetic and epigenetic, the selective and the ecophenotypic (nongenetic, life historical), the developmental and the functional. Mammal limbs provide a potentially fruitful venue for exploring the interaction among these factors because they have a greater structural complexity in terms of muscles and bony features than those of other vertebrates, allowing a greater diversity of approach to functional interpretation; mammals have evolved a greater functional diversity than other vertebrate groups; and the mammalian fossil record is particularly rich in its posterania.

Selected literature on variability, genetics, and development in mammalian limbs is reviewed here. In considering variability, it is important to distinguish between ontogenetic variation, population variation, and interspecific or evolutionary variation. Ontogenetic and population variation are discussed in this section and related to intraspecific variation, which was discussed above. It is also important to distinguish among variation in different kinds of traits: variation can be in the dimensions of bones (either uniformly as "size" or nonuniformly as "shape"), variation can be in the structure of limb elements (such as the surface shape of a joint articulation, for example), and variation can be polymorphic (such as polydactyly). These different types of trait probably have radically different genetic and epigenetic underpinnings. Consequently, quantitative or experimental data on one type of trait may have little explanatory power over another. Trait types may be functionally integrated, however, as the previous discussion of limb segment ratios and skeletal structure demonstrates.

Quantitative Variability

Variation in the dimensions of limb bones has been studied since Galileo noted that the diameter of long bones is disproportionately large compared to their lengths in mammals with large body mass (Galilei 1914, as described by Schmidt-Nielsen 1984). The functional correlates of quantitative variation in mammal limbs have been the subject of many recent interesting studies (Schmidt-Nielsen 1984; Van Valkenburgh 1985, 1987; Ruff and Runestad 1992; Heinrich and Biknevicius 1998; Polk et al. 2000; Ruff 2000), and the relationship is becoming reasonably well understood. But what is the genetic and developmental context of the evolution of quantitative aspects of limb morphology?

One fundamental issue is the extent to which limb size traits are heritable. It is well known that environmental factors such as nutrition and body mass can affect limb dimensions, so

it is interesting to know how much of the variance in limb elements is genetic. There have been few studies of heritability in limb elements (see reviews by Cock 1966; Thorpe 1981) except for a series of papers on the quantitative genetics of skeletal traits in mice by Leamy and coworkers (Leamy 1974, 1975, 1977, 1981; Leamy and Bradley 1982; Leamy and Sustarsic 1978). These studies considered osteological traits of the skull and limbs, along with measures of body size. Several limb traits were included: innominate length, ilium length, obturator foramen (all pelvis traits), femur length, tibia length, scapula length, humerus length, and radio-ulna length. These traits collectively represent all of the segments of both limbs, excluding the feet themselves.

Heritability of limb element lengths in mice was high, on average slightly higher than skull or body traits (Leamy 1974). This result dispels the notion that limb traits exhibit greater nongenetic, ecophenotypic variation than do other skeletal traits. Heritability of forelimb elements was generally higher than for those of the hindlimb, but the two were comparable. A multivariate component analysis grouped osteological traits into related factors, including a skull factor, a limb factor, a pelvic factor, and a width factor (Leamy 1975). The pelvis thus appears to be partly dissociated from other limb traits, including the scapula.

Even though the heritability of limb traits is high, they do not appear to evolve as quickly on microevolutionary time scales as do molar or skull traits. Leamy and Sustarsic (1978) looked at variation between different inbred lines of mice, finding that limb traits did not differ as much as did tooth traits. Despite their possibly slower rate, limb traits do evolve on very small evolutionary timescales. Schnell and Selander (1981) found that pelvic length showed greater differentiation among populations of *Mus musculus musculus* and *M. musculus domesticus* than did ulna length or hindfoot length. Means of ulna length, condylar width of the humerus, pelvic length, and hindfoot length were significantly different in the two subspecies.

A high heritability does not in itself explain the mechanism by which the heritable variance is transmitted. Limb traits have long been known to be pleiotropic, or influenced by many genes (Lande 1978), and now a bewildering array of genes have been identified that are active during various stages of limb development (Karsenty 2003; Mariani and Martin 2003). These genes interact in complex, dynamic ways to produce skeletal structures, and their contribution to gross heritability of limb measurements is not straightforward. For example, Hox genes are involved in patterning the segments of limbs (A. P. Davis et al. 1995), but so does pleiotrophin, an extracellular growth-differentiation factor, which is expressed long after limb patterning has taken place (Tare et al. 2002). Both genes act directly on skeletal development, but there are other sources of heritable variance that act indirectly through nonskeletal tissues. The muscular and vascular systems are the most obvious sources of such epigenetic interactions, but less obvious sources, such as the nervous system, also have an effect on skeletal development (Wermel 1934). Heritable variance may also be transmitted through interactions among elements of the limb skeleton themselves, as early excision experiments indicate. For example, the removal of part of either the radius or ulna results in an increase in thickness and decrease in length of the other bone (Wermel 1934; Murray 1936). Habitual behaviors can also contribute to heritable variation, or at least to species-specific limb morphology. Modified behaviors have a demonstrable effect on the limb skeleton, as observation of habitually bipedal rats and goats has shown (H. S. Colton 1929; Slijper 1946). Whereas bipedal goats and rats are so extreme as to be unlikely in the "natural" world, learned behaviors such as gait or resting posture may have a substantial effect on limb bones and may contribute to the shared morphology of a population or species. Some journals discourage morphometric studies of the

limb skeleton of zoo animals because of the systematic effects that captive life can exert on limb morphology.

Polymorphic Variability

Limb elements may exhibit polymorphic variability, or multiple discontinuous manifestations of a trait within the same population (Yablokov 1974). Examples of polymorphic variation include polydactyly, supernumerary bones or muscles, or achondroplastic dwarfism.

The most common polymorphisms involve missing bones (or parts of bones) associated with otherwise normal tissues. Most of these types of polymorphism are caused by events that happen after the basic limb pattern is specified. Recently, Packard et al. (1993) argued that such malformations are caused primarily by teratogenic effects on the arterial system rather than the skeletal system per se. Development of the arterial system is closely associated with the development of the skeletal system (Karsenty 2003), and its malformation impedes the normal development of the bone. The nonheritable condition of mice in which fibulae and feet are both missing but the rest of the skeleton is normal (Grüneberg 1952) is probably an example.

Not all losses of limb elements are teratogenic, however. The mouse polydactylous condition known as "luxate" produces a reduced or absent tibia, which is replaced by a ligament. The fibula is also malformed, usually bent, and medial digits are polydactylous. The luxate condition has a semidominant inheritance pattern (Grüneberg 1952) and is caused by a mutation that reduces the size of the domain of Fgf-8 expression in the preaxial (radial) side of the limb at the initial stage of limb development (Yada et al. 2002; see also T. C. Carter 1954 for a similar argument that an anterior shift in the apical ectodermal ridge was responsible for the luxate condition). The reduction in the Fgf domain allows Shh to be expressed more anteriorly, which expands the expression domains of other genes normally confined to the posterior bud. The result is polydactyly of the anterior (radial) digits. The gene involved in the mouse luxate mutation is now known to be a member of a large family of luxoid genes. Interestingly, Grüneberg (1952) reported that there are several types of inherited preaxial polydactylism in mammals, but postaxial polydactylism is much rarer.

The example of the luxate condition illustrates the possibility that some common genetic limb polymorphisms may have few evolutionary consequences. Luxate limbs, though heritable, are so universally detrimental that they are almost certain to be removed from a population by selection, even though mutations leading to the condition are common enough for luxoid conditions to be taxonomically widespread (Grüneberg 1952; Pucek 1965; Herreid 1958).

Other limb polymorphisms exist that may be of evolutionary significance, however. For example, Yablokov (1974) reported that the pisiform and some distal carpals were variably absent in *Delphinapterus leucas*, the Beluga whale, and that extra elements were commonly present between the proximal and distal carpals. Whales as a group are characterized by hyperphalangy, or the possession of extra phalanges in the digits, and the variation described by Yablokov is probably not detrimental for whales as it would be for horses. The condition of having extra elements was apparently heritable in the belugas because similar carpal patterns were found in mothers and calves (Belkovich and Yablokov 1965). Another limb polymorphism with interesting patterns of variation was also found in belugas, whose fourth digit is often forked (a comparatively rare postaxial polydactyl condition). In a few populations, however, the

fifth digit rather than the fourth is bifid (Yablokov 1974).

Alberch (1985a) argued that the distribution of supernumerary and vestigial digits among breeds of domestic dog is due to a completely unrelated phenomenon: the number of cells in the developing limb buds. Alberch argued that the number of digits was a function of the size, or number of cells in, the developing limb bud. He argued that a critical mass of cells was required before the condensation of an anlage could occur. Small breeds fell below the required threshold and often lacked a digit, whereas large breeds had more than the requisite number of cells and sometimes had an extra digit. This mechanism of polymorphic variation is an example of an interactive effect between size and number of digits. Lande (1978) provided an interesting worked example from a population genetics perspective of how such interactive polymorphisms might evolve.

An interesting limb polymorphism with widespread pathological occurrence, but which is the norm in some mammal groups, is syndactyly. A large clade of Australian marsupials, the Syndactyla, share an unusual hindfoot morphology in which digits II and III are comparatively gracile and are bound together as a single toe (fig. 15.10A). This syndactylous condition is found homologously in peramelids, notoryctids, phalangerids, vombatids, and macropodids (Szalay 1994). In these marsupials, syndactyly is the normal condition, it is heritable, and it is not associated with other major skeletal abnormalities. Syndactyly is a widespread pathology in other groups of mammals, however, where it is usually accompanied by other defects. Grüneberg (1952) reported a bilateral defect of the radius, in which carpals, metacarpals, and digits on the radial side of the hand were also missing, and digits III and IV were syndactylous. He also reviewed a defect in mice in which both hindlimbs were completely missing, the pelvis had associated defects, and digits II and III of the forelimb were syndactylous. These conditions were probably not heritable, and both were extremely detrimental to the individuals that had them. Other examples of syndactyly are heritable, but also have associated detrimental effects, such as oculo-dento-digital dysplasia in humans (Ioan et al. 2002). The disjunction between syndactyly and other skeletal (and nonskeletal) effects suggests that the molecular developmental pathway leading to marsupial syndactylism is different from in commonly studied pathologies. In the marsupials, the syndactylous condition was fixed in the ancestral population only through the conjunction of heritability, disassociation with other detrimental effects, and functional suitability.

These examples indicate that polymorphic variation can be either genetic or ecophenotypic, and that the ultimate cause of polymorphisms may be associated directly with skeletal developmental system (as in the luxate condition) or indirectly with another system, such as the arterial one.

Early Diversification of the Mammalian Limb

Most evolutionary scenarios put the ancestors of placental and marsupial mammals in the trees. The view that ancestral therian mammals were arboreal has been around since the early 20th century when Matthew (1904) argued that ancestral placental mammals may have had opposable digits on the manus and pes. Matthew was extending to placentals an earlier argument that marsupials had an arboreal ancestry (Huxley 1880; Dollo 1899), saying that the "Cretaceous

ancestors of Tertiary mammals were small arboreal animals of very uniform skeletal characters, but probably somewhat differentiated in dentition according as fruit, seeds and nuts, or insects formed the staple of their diet" (Matthew 1904: 816). Matthew's argument was based on an analysis of skeletal characters, primarily from the placental mammals in the early Cenozoic fossil record.

The arboreal origin of mammals has not gone unquestioned, however. Haines (1958) presented detailed comparative anatomical data on the feet of mammals and concluded that the earliest then known placentals were probably terrestrial and that, in fact, Cretaceous forests would have had little to offer mammals. Szalay (1984, 1994) reiterated the possibility that the earliest placental mammals were terrestrial and argued that scansorial adaptations in placentals (especially archontans) might not be homologous with scansorial features in the ancestral marsupial. A lively literature has grown up around the debate, which obviously remains open (Jenkins 1974; Cartmill 1974; O. J. Lewis 1989; Bloch and Boyer 2002, 2003; Kirk et al. 2003).

Recent finds show that early mammals were more diverse in their postcranial skeleton and locomotory habits than Matthew imagined, however (fig. 15.12). New limb morphologies have been found in eutherians in other groups of Mesozoic mammals. It is now clear that early mammals, far from being a homogeneous group of arboreal specialists, inhabited a broad range of ecological niches, partitioned by substrate, diet, body mass, and geography.

Two triconodonts, members of a paraphyletic group of mammals from the Late Jurassic and Early Cretaceous, are now known from their postcranial skeletons: the late Jurassic *Jeholodens jenkinsi* from China (Ji et al. 1999) and the Early Cretaceous *Gobiconodon ostromi* from North America (Jenkins and Schaff 1988). *Jeholodens* was most likely a terrestrial, plantigrade animal. The arrangement of tarsals is like nonmammalian cynodonts, monotremes, and multituberculates in having the axis of rotation of the upper ankle joint at an oblique angle to the main axis of the foot, a condition that suggests a posture that was sprawling. The calcaneum had a tubercle, but the astragalus was not subtended by the calcaneum as it is in therians.

One of the most surprising features of *Jeholodens* and *Gobiconodon* is that they had a scapular spine. Unlike other scapular features, the spine is a specialized structure not found in monotremes, multituberculates, or *Morganucodon* (Jenkins and Parrington 1976; Krause and Jenkins 1983). Traditionally, the spine was thought to have evolved from the cranial border of the scapula in nonmammals. It was thought that the spine had evolved by the addition of a supraspinous portion to the blade leaving a spine running along the junction of the neomorph and the "old" scapula (Romer and Parsons 1977). Paleontological and developmental information now suggests that the spine itself is the novelty, formed (developmentally and evolutionarily speaking) as part of the reorganization of the trapezius and deltoid musculature associated with the evolution of upright posture and a more mobile pectoral girdle. The spine of *Jeholodens* and *Gobiconodon* suggests that these triconodonts had a muscular anatomy that permitted extensive movement of the pectoral girdle during locomotion.

Developmental studies support the distinction between spine and the rest of the scapula. The spine develops in one of three ways: by apposition to the acromion, as an independent condensation, or as an intermuscular ossification (Sánchez-Villagra and Maier 2002; Grossman et al. 2002). In all cases, the spine has a developmental origin separate from the acromion process, which has its own condensational history and a distinctive pattern of *Hox5a* and *Pax1* coexpression (Timmons et al. 1994; Aubin et al. 2002).

Other important discoveries have come from the postcrania of multituberculates. Multituberculates were a diverse group of rodentlike animals that flourished in the Cretaceous and early Tertiary, but their postcrania have been almost completely unknown. A skeleton of *Ptilodus kummae* from the Paleocene of North America demonstrated specialized arboreal features, including a unique upper ankle joint that facilitated squirrel-like hindfoot reversal (Krause and Jenkins 1983; Jenkins and Krause 1983). Subsequent discoveries indicate that multituberculates retained an interclavicle (Serenio and McKenna 1995), that the humerus had significant torsion, that the humerus had no trochlea, that the calcaneum contacted the fifth metatarsal (compare the therian and nontherian feet in fig. 15.12), and that multituberculates had a posture that was much more sprawling than that of therians (Kielan-Jaworowska and Gambaryan 1994; Gambaryan and Kielan-Jaworowska 1997). The tarsus of *Kryptobaatar dashzevegi* and *Ptilodus kummae* is shorter and broader than therian mammals, with a wide astragalus and a calcaneum whose tuber is angled posterolateral to the main axis of the metatarsus (fig. 15.12). Most likely, the parasagittal stance (fig. 15.2) is a specifically therian condition not found more broadly among mammals. Considerable locomotory diversity existed among multituberculates, as indicated by the humeral differences among *Bulganbaatar*, *Lambdopsalis*, and *Kryptobaatar* (Kielan-Jaworowska et al. 2000).

Several new skeletons have also expanded our picture of eutherian limb diversity. One of the most striking is the 125 million-year-old *Eomaia scansoria* from Early Cretaceous of China. A contemporary of *Jeholodens*, *Eomaia* had many of the features associated with the therian and eutherian skeleton. It had a mobile scapula with well-developed spine; a well-developed ulnar olecranon and calcaneal tuber; an upright, parasagittal posture; a fibula that was significantly more gracile than the tibia; an astragalus subtended by the calcaneus; an astragalar trochlea; a calcaneum that was separated from the metatarsals by the navicular; and a long axis of the metatarsus that was roughly perpendicular to the axis of rotation in the upper ankle joint. *Eomaia* has been interpreted as being arboreal, though that interpretation is not universally accepted (Weil 2002). Other important eutherian limb skeletons that have been described recently include *Ukhaatherium nessovi*, an asioryctitherid from the Late Cretaceous of Mongolia (Horovitz 2000), and *Deccanolestes hislopi* from the Late Cretaceous of India (Prasad and Godinot 1994).

Whereas the diversity in mammal limb structure today evolved over the last 140 million years since the last common ancestor of marsupials and placentals, limb and substrate diversity was already varied in the Mesozoic. The earliest known placental, *Eomaia*, was a scansorial tree dweller; *Zhangheotherium*, a therian contemporary of *Eomaia*, was terrestrial (Hu et al. 1997), as was *Jeholodens*. Because of structural correlates to limb function, many locomotory aspects of a mammal can be reliably interpreted from its skeleton, even when it is extinct with no exact analogues among the living (Szalay 1994).

The evolutionary migration of mammals through changing environments and habitats can be traced using the bones of the same legs that carried them on daily forays during their lives. The constant requirements of support and movement mean that habitat, behavior, and growth are intertwined with bone, muscle, and tendon in phylogenetic transformations (Szalay 1981). One aspect can hardly change without the others doing likewise.

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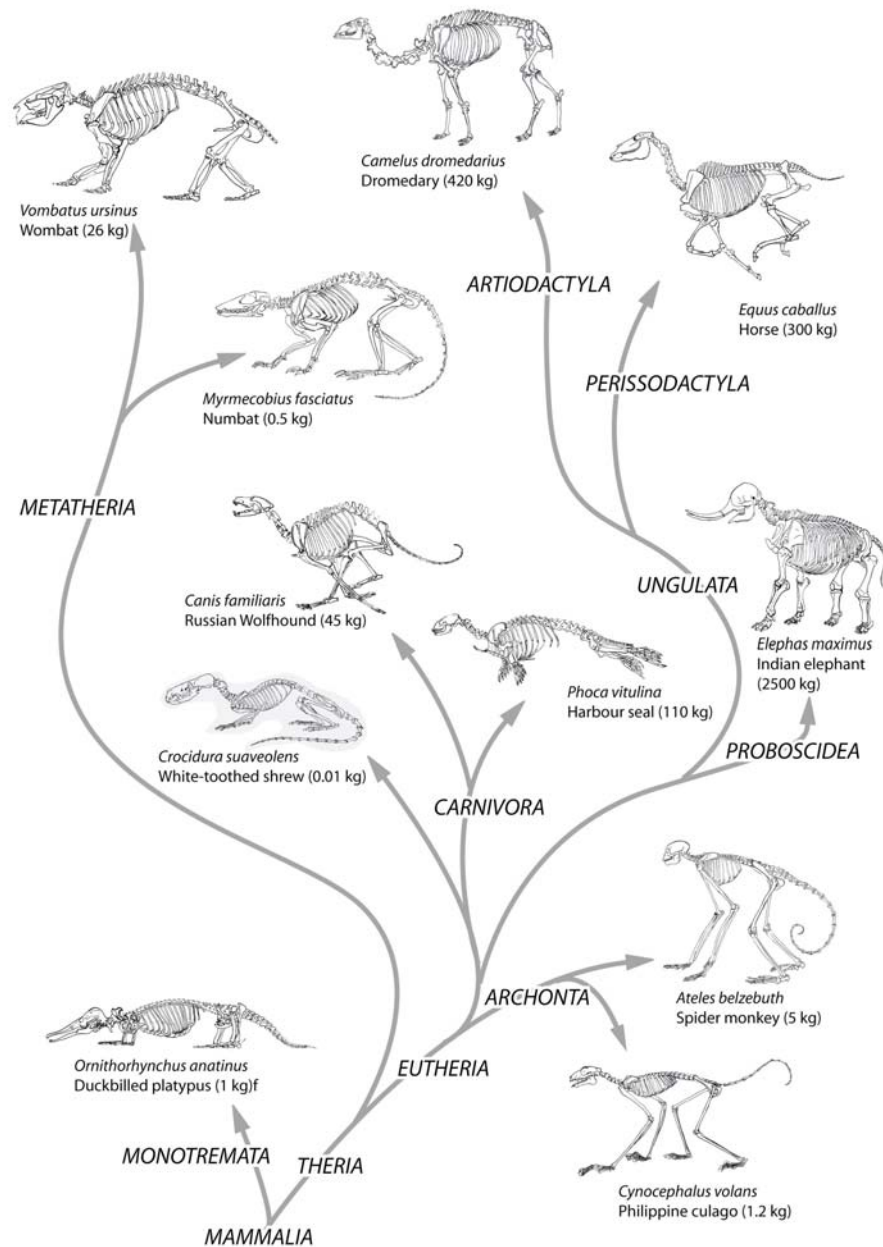


Figure 9.1

Figure 15.1.

A sample of the diversity of limb skeletons of living mammals. Monotremes have a sprawling posture, large fibulae, and multiple elements in their pectoral girdles, all of which are ancestral traits for mammals. Marsupials have epipubic bones, which are a primitive trait for mammals, and relatively large fibulae. Living placentals have lost the epipubic bones and severely reduced the size of the fibulae. Many specializations are not shown, including volant bats and aquatic whales. Note the relationship between the orientation of the pelvis and body mass. The largest mammals have vertically oriented pelvises that are perpendicular to the vertebral column, and the smallest ones have horizontally oriented pelvises that parallel the column. (*Elephas maximus* and *Camelus dromedarius* after Young 1981; all others after Gregory 1951.)

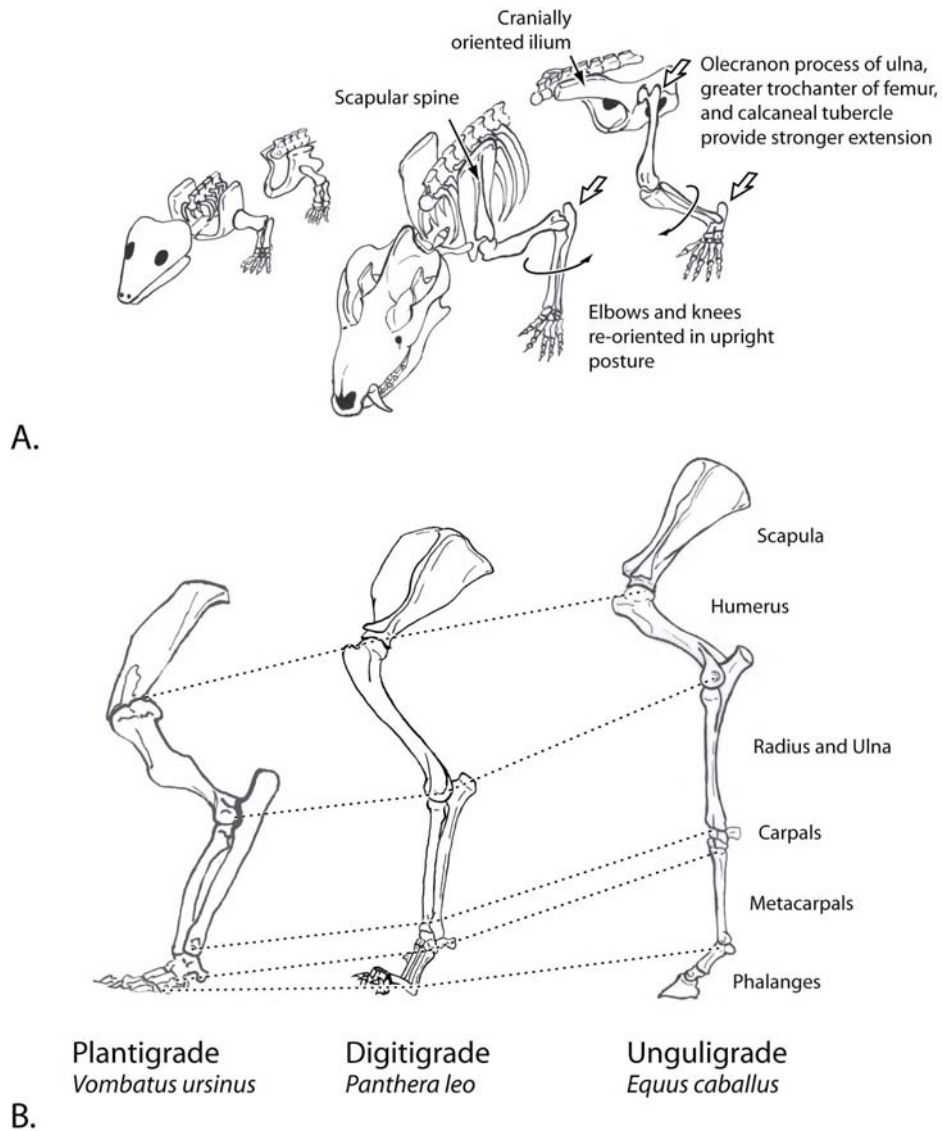


Figure 9.2

Figure 15.2.

(A) Specialized features of the mammalian limb skeleton. Mammalian limbs are positioned parasagittally under the body, with the elbow rotated posteriorly and the knee rotated anteriorly. The number of elements in the pectoral girdle is reduced, and the scapula is often highly mobile. The ilium of the pelvis is reoriented anteriorly. A number of bony processes—notably the olecranon, greater trochanter, and calcaneal tubercle—add leverage to limb extension (after Radinsky 1987). (B) Typical mammalian limb postures. Plantigrade mammals rest their entire foot on the substrate. Digitigrade mammals stand on their toes, with the wrist and ankle elevated above the substrate. Unguligrade animals carry the digitigrade posture even further, standing on the tips of the digits. Digitigrade and unguligrade postures are often associated with cursorial locomotion. (*Vombatus* after Gregory 1951; others after E. E. Thompson 1896.)

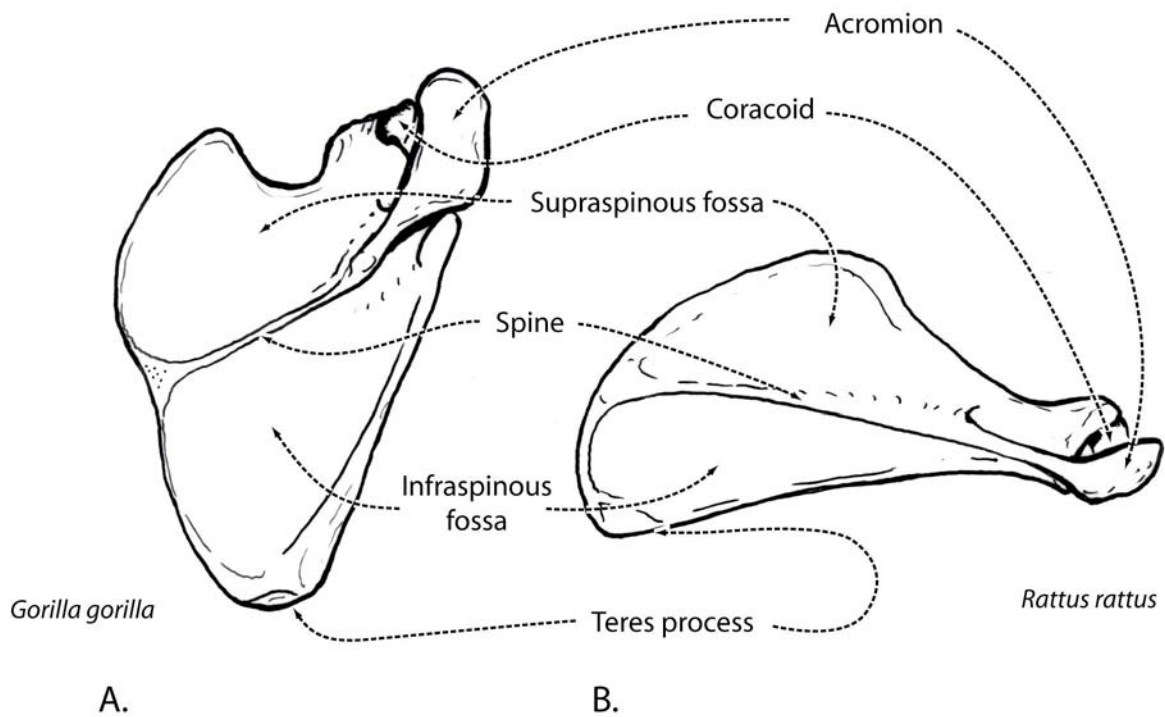
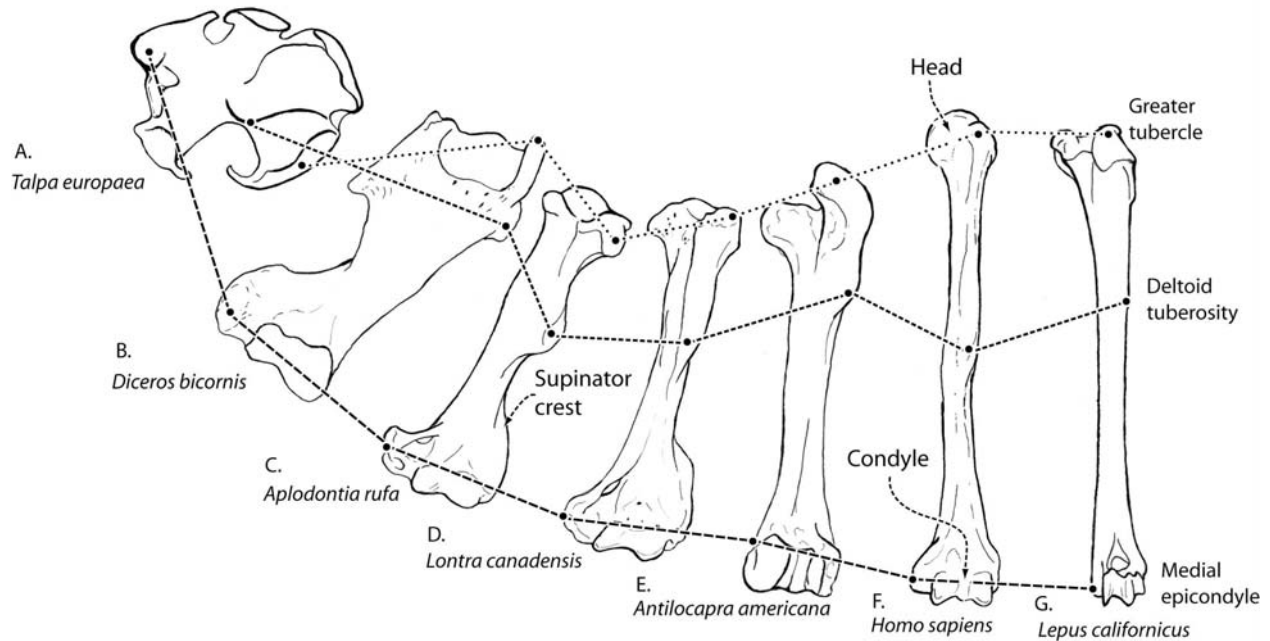


Figure 9.3

Figure 15.3.

The mammalian scapula. Both elements are in life position. (A) Right scapula of a gorilla in dorsal view. The gorilla is a very large ape, with typical body masses ranging between 90 and 200 kg. Gorillas are partially arboreal, and have a semiupright stance on the ground, where they move by knuckle-walking. The vertical orientation of the glenoid cavity and scapular spine are related to the dual function of the forelimb during brachiation and quadrupedal walking. The large acromion is associated with massive deltoideus and trapezius muscles, which provide strength of movement to the scapula and arm. The long, acute angle of the teres process provides an advantageous moment arm for the teres major, strengthening adduction of the arm (after Raven 1950). (B) Right scapula of a rat in lateral view. The rat is a medium-sized rodent, with typical body masses around 0.15 kg. Rats are terrestrial quadrupeds, with good scansorial abilities. The horizontal orientation of the glenoid cavity and scapular spine is common in mammals with small body masses (after E. C. Greene 1935).



Polly, Figure 4

Figure 15.4.

The mammalian humerus. Comparative cranial views of the left humerus of seven mammalian species (not to scale). Dotted lines show the highlight of different positions, sizes, and orientations of the functionally important greater tubercle, deltoid tubercle, and medial epicondyle. (A) Left humerus of the European mole, a small (0.1 kg) fossorial lipotyphlan insectivore. The trochanters and epicondyles are greatly enlarged to provide longer lever arms for muscles of the forelimb, particularly those involved in extension, adduction, and supination (after Gregory 1951). (B) Left humerus of the Black rhinoceros, an extremely large (800–2000 kg) perissodactyl ungulate (after R. Walker 1985). (C) Left humerus of the Mountain beaver, a medium-sized (1.3 kg) subterranean rodent. The broad epicondyles and pronounced deltoid tuberosity are typical of fossorial mammals (after B. M. Gilbert 1973). (D) Left humerus of the North American river otter, a medium-sized (5 kg) natatorial carnivoran. Note the similarities with the humerus of the fossorial Mountain beaver (after B. M. Gilbert 1973). (E) Left humerus of the Pronghorn antelope, a large (60 kg) artiodactyl cursor. Note the similarities in shape to the humerus of the Black rhinoceros, which differs mainly in the thickness required to support the much larger body mass. (F) Left humerus of a human, a large (40–100 kg) bipedal ape. Note the broad epicondyles, which provide moment arms for supination of the forearm, and the wide humeral head, which allows a wide range of movements of the arm (after Gregory 1951). (G) Left humerus of a Black-tailed jackrabbit, a medium-sized (2 kg) cursorial lagomorph. Note the narrow epicondyles and strongly hinged condyle, which stabilize the forelimb (after B. M. Gilbert 1973).

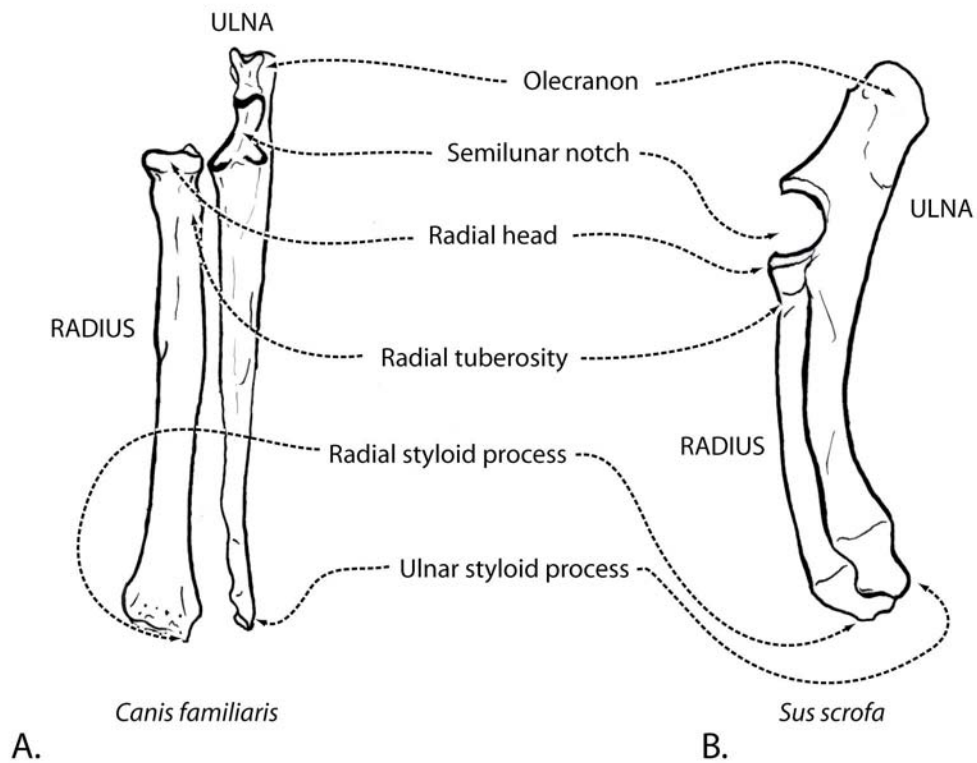


Figure 15.5.

The mammalian radius and ulna. (A) Disarticulated left radius (caudal view) and ulna (cranial view) of a dog (after H. E. Evans 1993). (B) Articulated left radius and ulna of a pig in lateral view. The radius and ulna are normally fused in adult pigs (after Sisson and Grossman 1938).

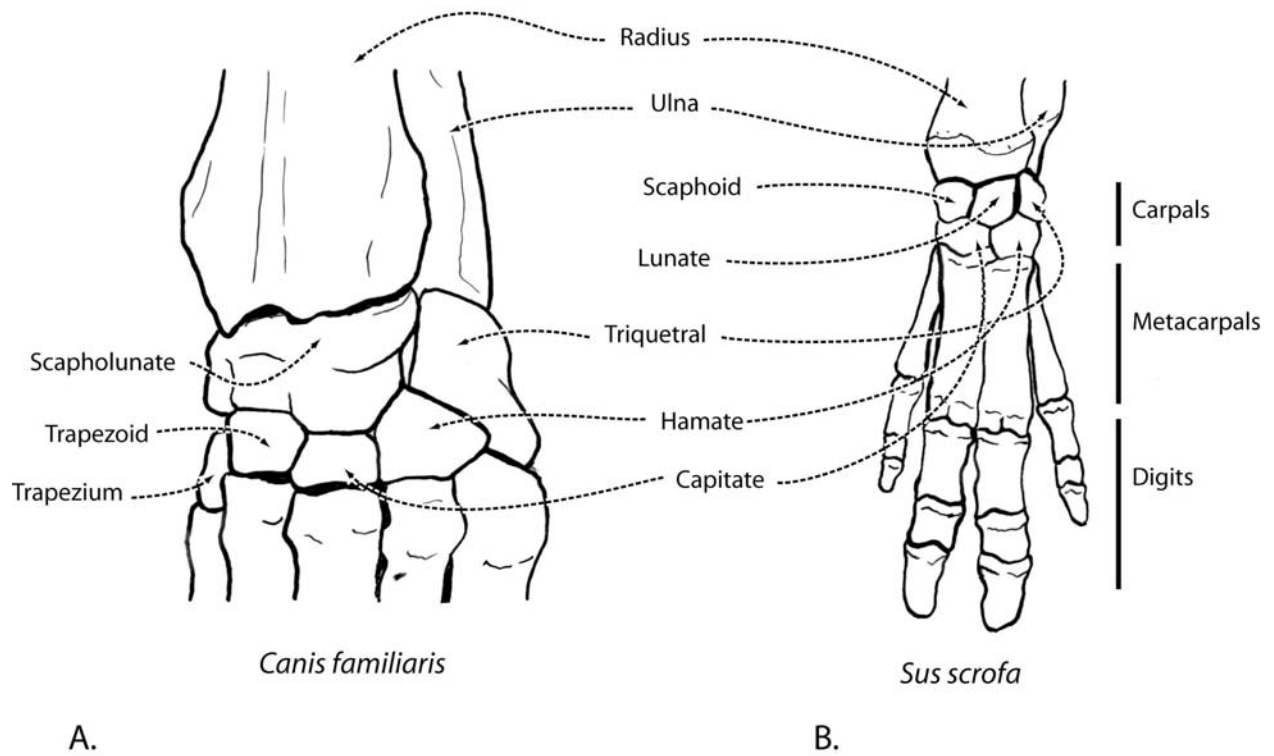


Figure 15.6.

The mammalian carpus and manus. (A) Left carpus of a dog in cranial view (after H. E. Evans 1993). (B) Left manus of a pig in cranial view. Note the reduction in digits and associated carpal bones (after Sisson and Grossman 1938).

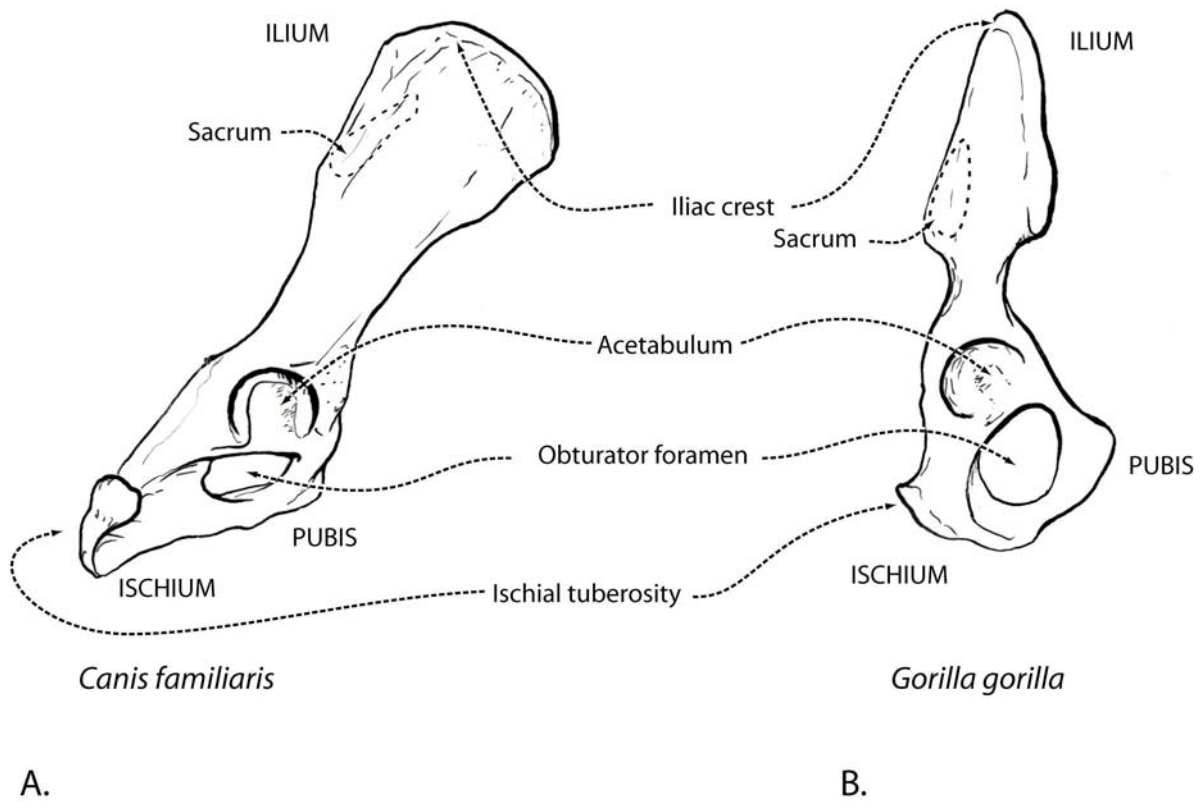


Figure 15.7.

The mammalian pelvis. (A) Right innominate of a dog. Note the anterodorsal angle of the ilium, which intersects the vertebral column at an oblique angle. This morphology is typical of terrestrial quadrupeds (after H. E. Evans 1993). (B) Right innominate of the gorilla. Note the rounded iliac crest and the upright orientation (after Raven 1950).

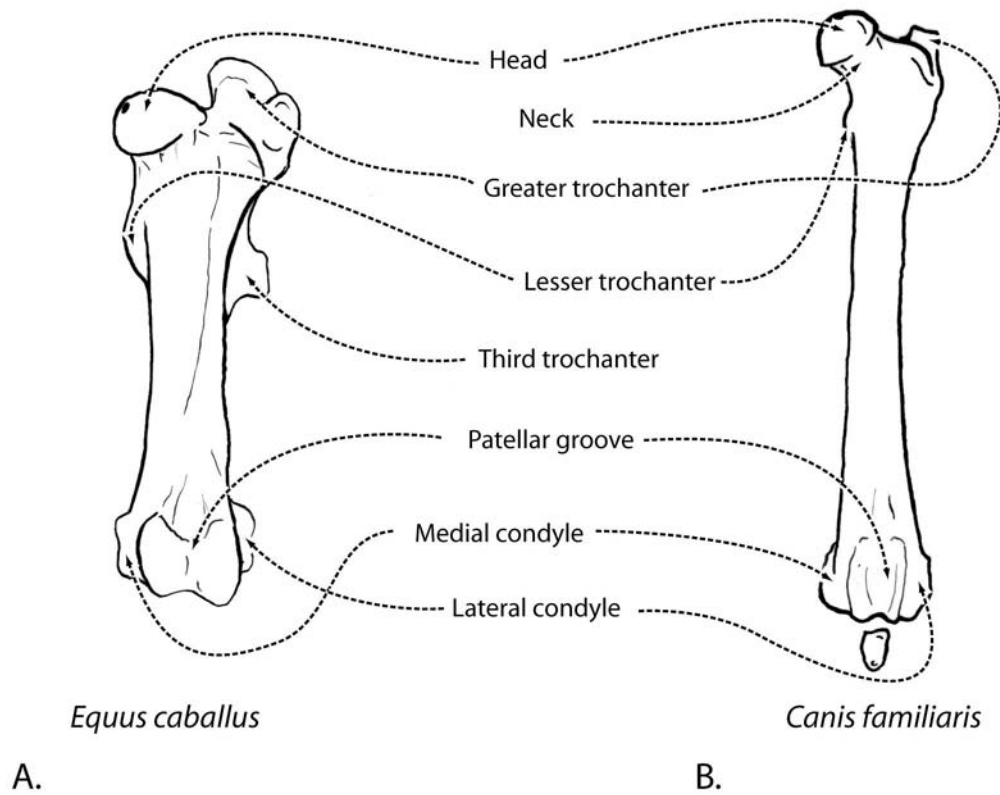


Figure 15.8.

The mammalian femur. (A) Left femur of a horse. Note the especially large third trochanter, on which insert extensors of the hip that provide important leverage for large cursors (after Sisson and Grossman 1938). (B) Left femur of a dog (after H. E. Evans 1993).

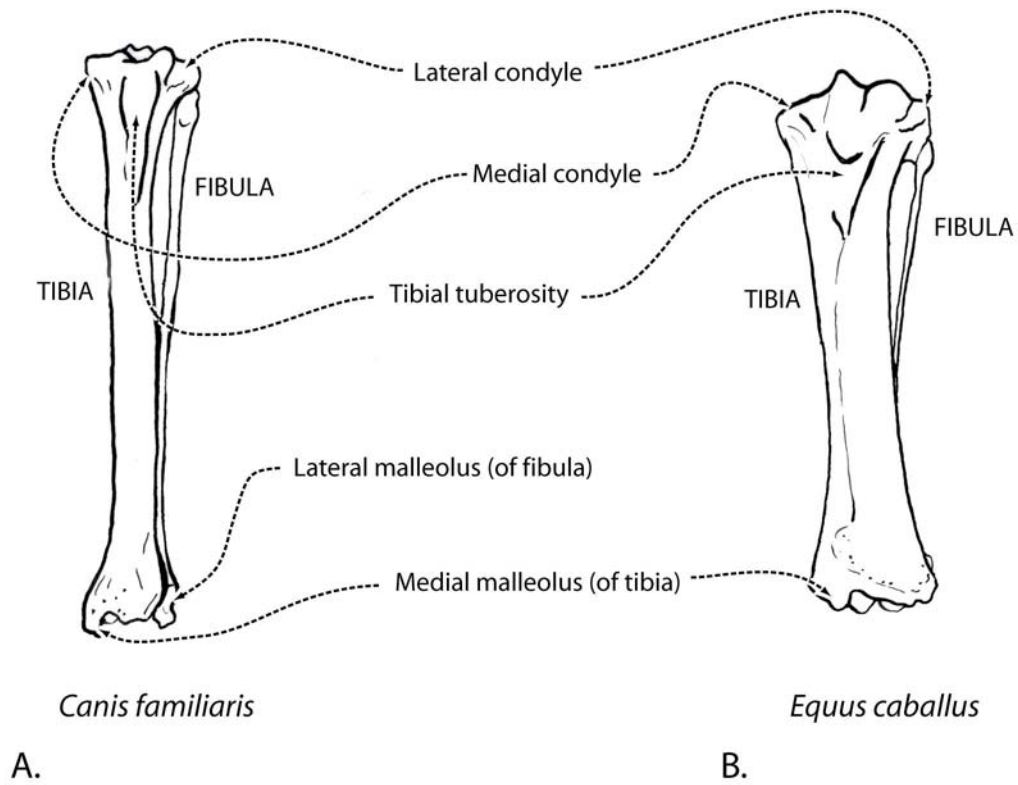


Figure 15.9.

The mammalian tibia and fibula. (A) Left tibia and fibula of a dog (after H. E. Evans 1993). (B) Left tibia and fibula of a pig. Note the reduced fibula (after Sisson and Grossman 1938).

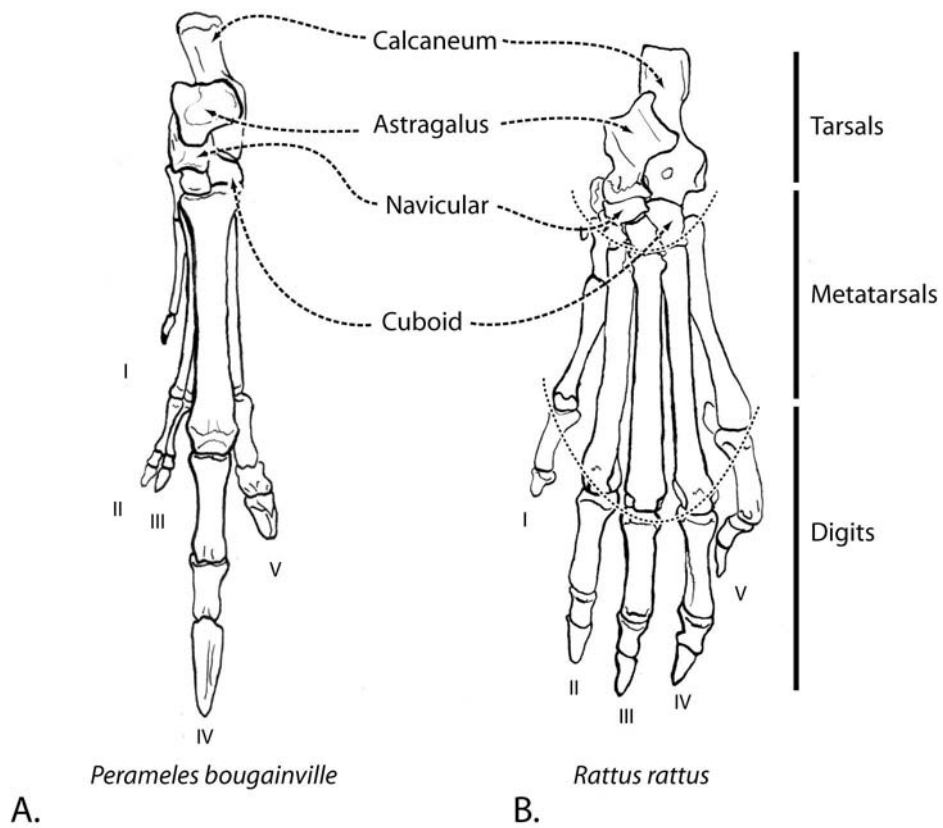


Figure 15.10.

The mammalian pes. (A) Left pes of a Western barred bandicoot. Note the reduction in digits and associated carpals, and the syndactylous condition of digits II and III (after Szalay 1994). (B) Left pes of a rat (after E. C. Greene 1935).

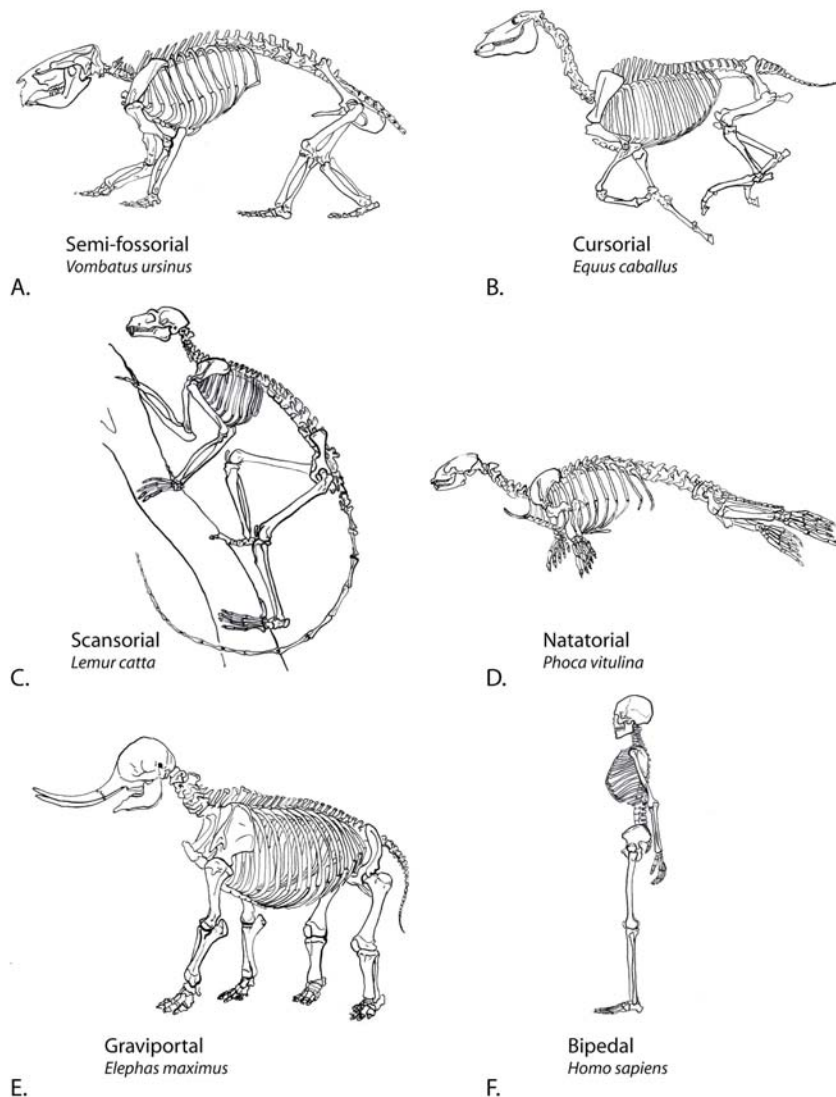


Figure 15.11.

Examples of some mammalian locomotory ecomorphs. (A) Skeleton of a semifossorial Common wombat, a medium-sized (26 kg) Australian marsupial with badgerlike burrowing habits. Note the high scapular spine, the long teres process, the pronounced deltoid tuberosity, and the long olecranon process (after Gregory 1951). (B) Skeleton of a horse, a large (300 kg) cursorial ungulate. Note the combination of cursorial (elongated distal digits and narrow, vertical scapula) and graviportal (vertical pelvis) features (after Gregory 1951). (C) Skeleton of a ring-tailed lemur, a medium-sized (3 kg) scansorial primate. Note the triangular scapula, long tarsus, and opposable pollex and hallux (after Gregory 1951). (D) Skeleton of a harbor seal, a large (100 kg) natatorial carnivoran. Note the very large teres process, the short humerus, and the long digits (after Gregory 1951). (E) Skeleton of an Indian elephant, an extremely large (2,500 kg) graviportal proboscidean. Note the long proximal and short distal limb segments, the vertical orientation of the pelvis, and the digitigrade stance (after Young 1981). (F) Skeleton of a human, a large (40–100 kg) bipedal ape. Note the unusual shape of the pelvis, the long proximal limb segments, and the pronounced plantigrade stance (after Young 1981).

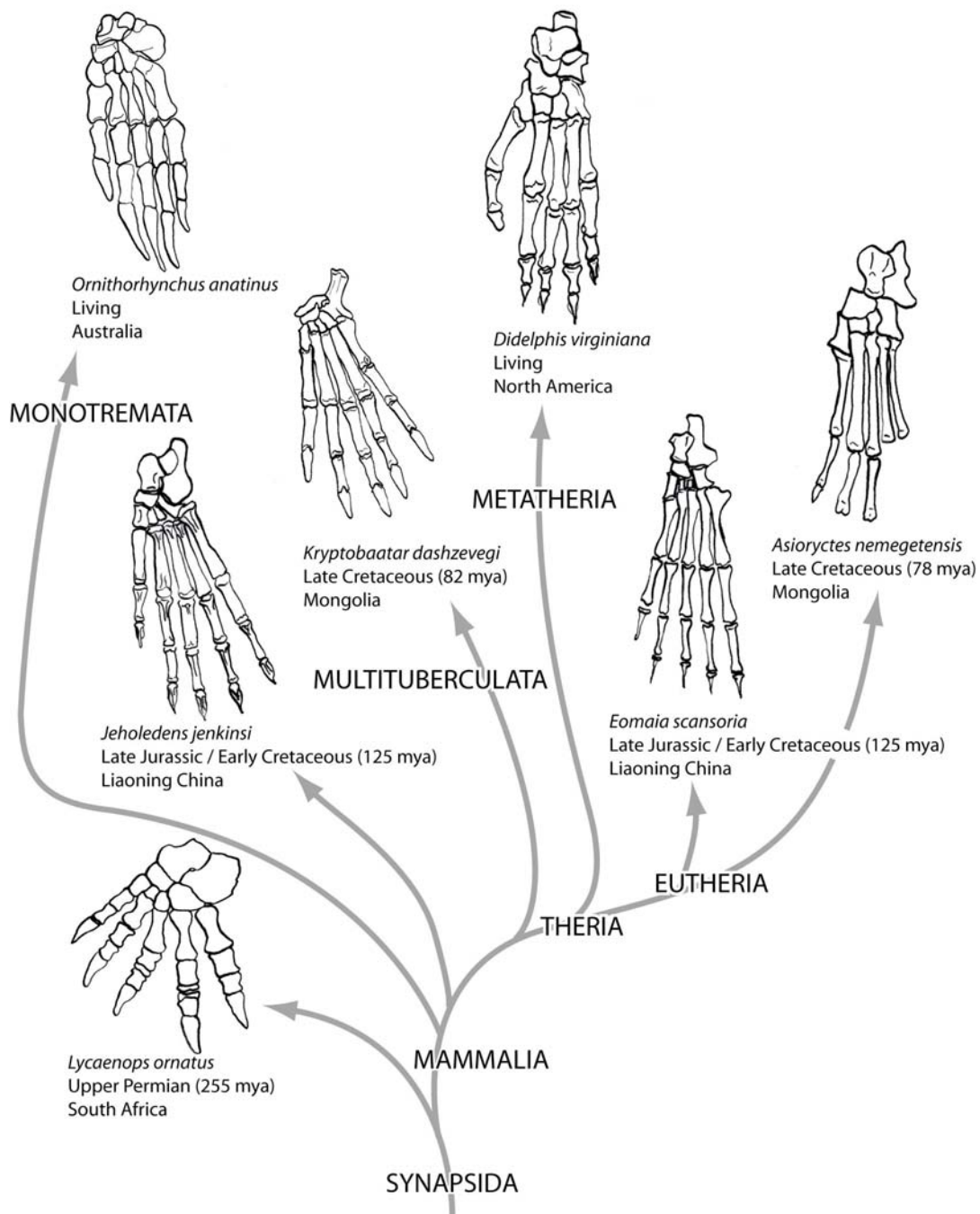


Figure 15.12.

Evolution of the mammalian tarsus. Left tarsus of selected living and extinct taxa showing the diversity and evolutionary transitions of major mammalian groups. Therian mammals share an astragalus that sits partially or fully over the calcaneum. (*Lycaenops ornatus* after Gregory 1951; *Jeholodens jenkinsi* after Ji et al. 1999; *Eomaia scansoria* after Ji et al. 2002; *Kryptobaatar dashzevegi* after Kielan-Jaworowska et al. 2000; *Ornithorhynchus anatinus* after Szalay 1994; and *Asioryctes nemegetensis* and *Didelphis virginiana* after Kielan-Jaworowska 1977.)

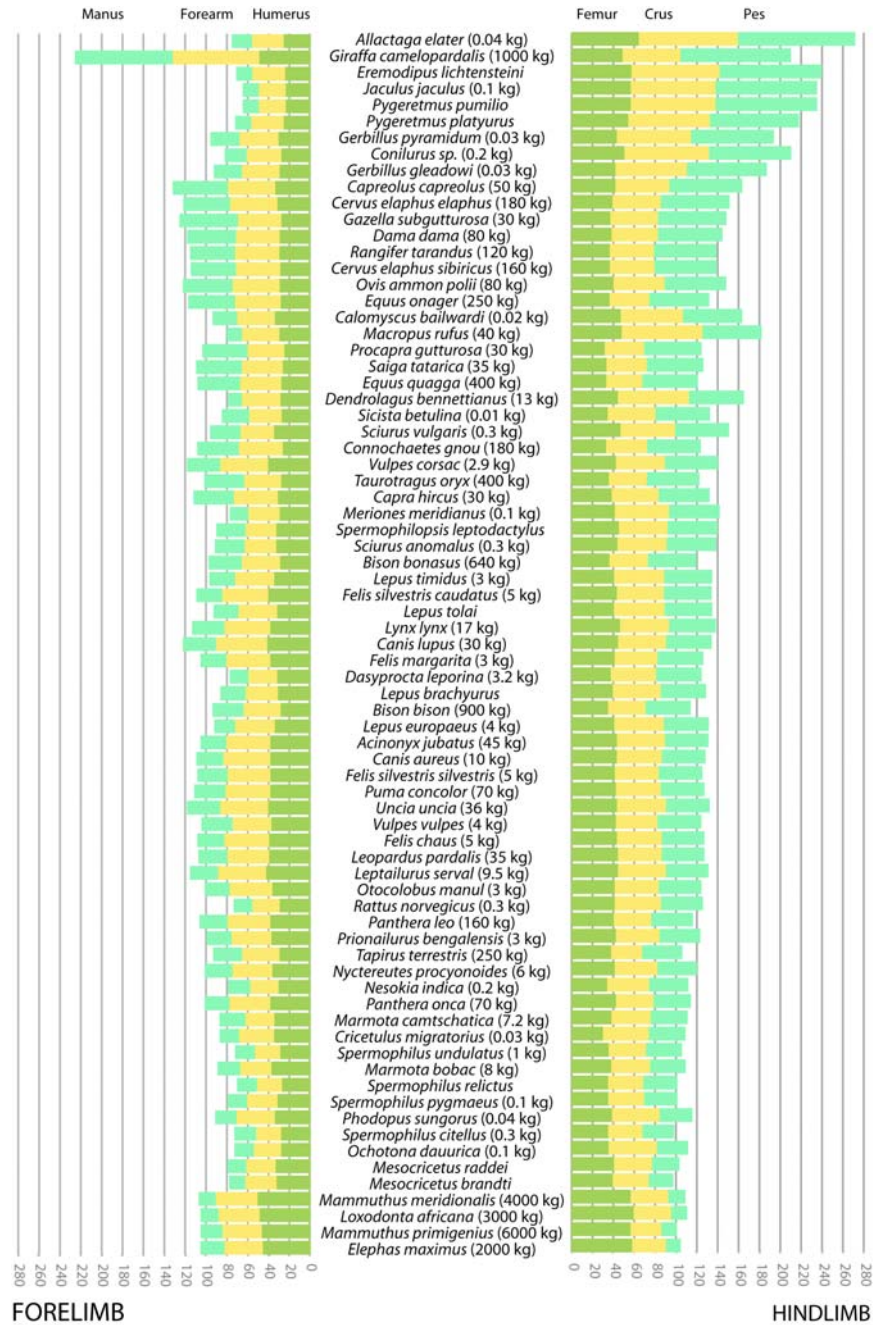


Plate 15.1.

Graph of standardized lengths of forelimb (left) and hindlimb (right) segments from 75 mammalian species. Species are sorted from those with the longest to the shortest pes. Segment lengths were standardized against the length of the thoracic and lumbar vertebrae. Most of the species represented are cursorial, saltatory, ambulatory, or graviportal and are drawn primarily from the orders Artiodactyla, Perissodactyla, Carnivora, Rodentia, and Proboscidea. Saltatory species (e.g., *Allactaga elater*, *Eremodipus lichtensteini*, *Pygeretmus pumilio*, *Jaculus jaculus*, and *Macropus rufus*) are easily picked out by their combination of long hindlimb and short forelimb segments. Note the proportionally long proximal relative to distal segments in the graviportal proboscideans (the last four species). These data demonstrate that there is only a loose correlation between the lengths of proximal and distal segments, between forelimb and hindlimb segments, and between segment proportions and body mass. (Original data from Gambaryan 1974.)