7. Archosaurs II: Birds

Major concepts

- There are more than 10,000 living species of birds.
- Birds are ubiquitous members of Earth ecosystems, present on all continents and seas and in all biomes.
- Many aspects of bird anatomy relate to adaptations for flight.

Goals for this lab

- Learn the synapomorphies of birds.
- Study structure and function of birds using dissections and skeletal material.
- Overview diversity of major bird groups.
- Study ecomorphological adaptations of bird feet, beaks, wings, and skeletons.

Station 1. Phylogenetic context

Birds are **endothermic theropod dinosaurs** (Figure 6-7). In this lab, we focus on diversity, structure, and function of living birds, **Aves** (Figure 7-1).

Many characters of Aves evolved in stem groups. For example, the Cretaceous toothed bird †*Ichthyornis* had a keeled sternum that is retained in crown-group Aves (Figure 7-1). In this lab, we will study the keeled sternum along with other plesiomorphic features of Aves (e.g., asymmetrical flight feathers, pygostyle, and synsacrum).

There are two easily seen and understood anatomical synapomorphies for Aves.

Synapomorphies of Aves

- ***Tibiotarsus*** *– bone of the lower leg formed by the fusion of some tarsal bones (= ankle bones) with the tibia.*
- ***Beak*** *– all living birds have beaks made of keratin. Beak sizes and shapes vary with diet.*

Aves contains two major groups: **Paleognathae** and **Neognathae** (Figure 7-1) Paleognathae means **old jaw**, and the palate of **paleognathous birds** resembles that of earlier

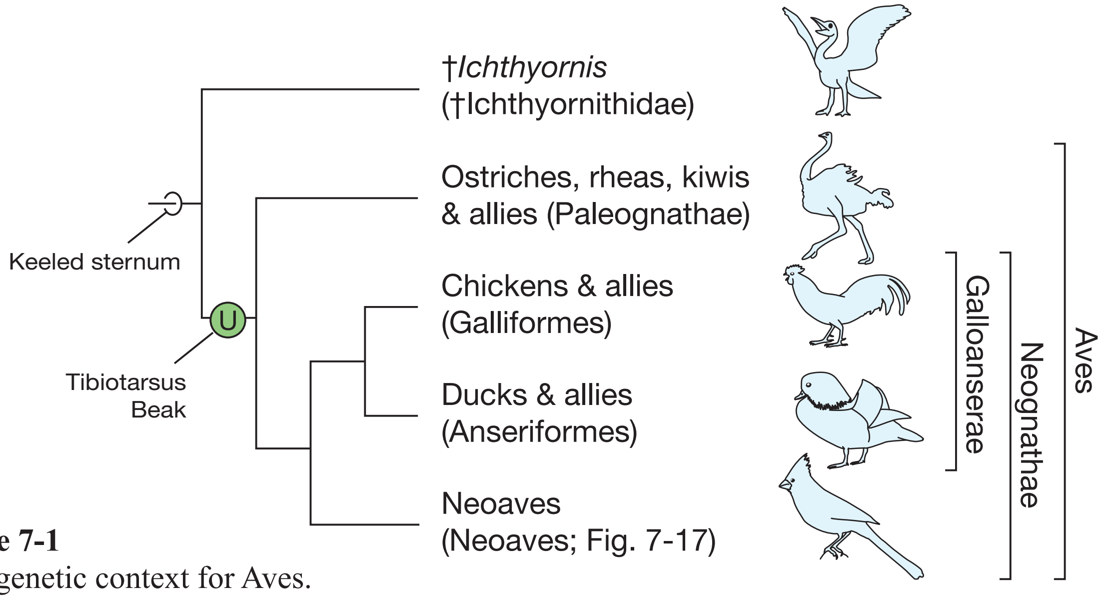
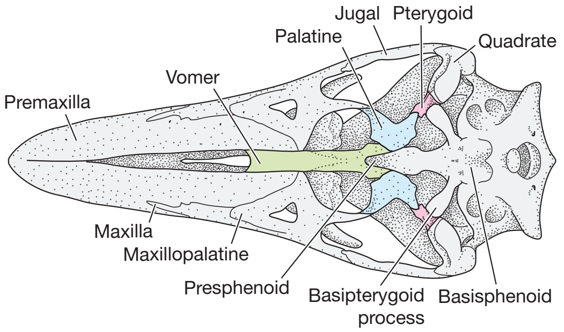
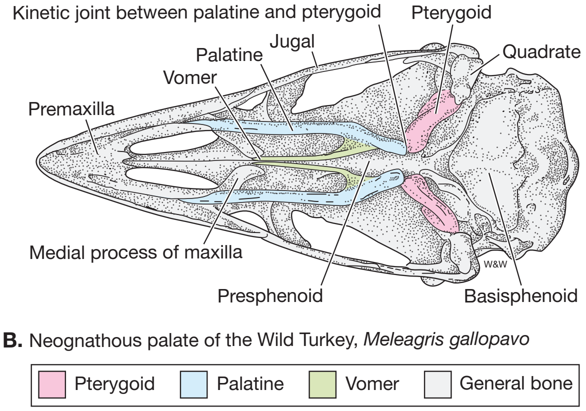


Figure 7-1
Phylogenetic context for Aves.



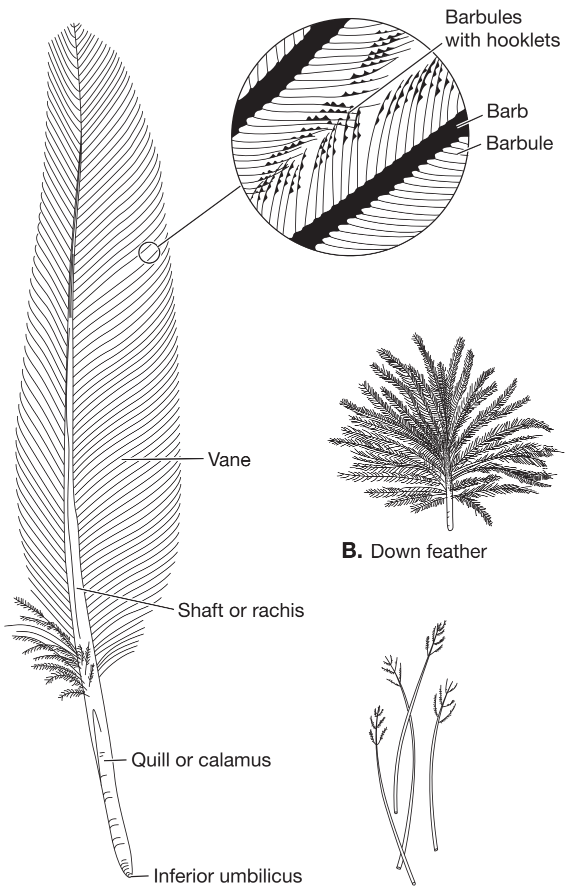
A. Paleognathous palate of a Rhea, *Rhea*



B. Neognathous palate of the Wild Turkey, *Meleagris gallopavo*

Figure 7-2
Palates of Aves.

theropods. In contrast, **neognathous** birds have a more lightly built palate with elongated **palatine bones** (Figure 7-2). A kinetic joint between the **pterygoid** and palatine bones allows the palate a role in **cranial kinesis** of neognathous birds. Reduction of the **vomer** further increases skull kinesis.



B. Down feather

A. Anatomy of a contour feather

C. Filoplumes

Figure 7-3
Feather anatomy.

Station 2. External anatomy

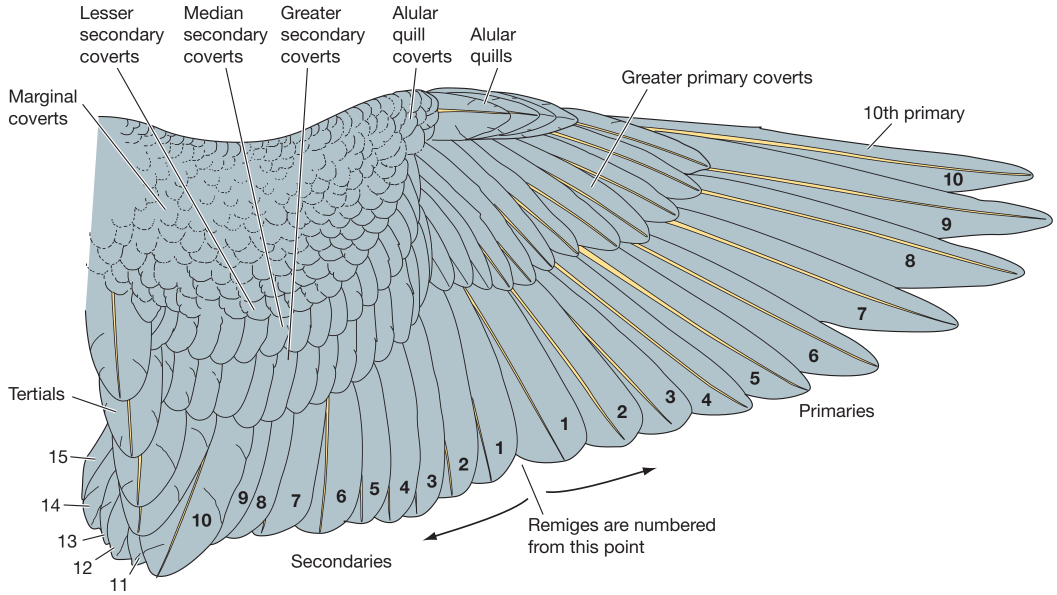
Use specimens at this station to study the external anatomy of birds

Feathers

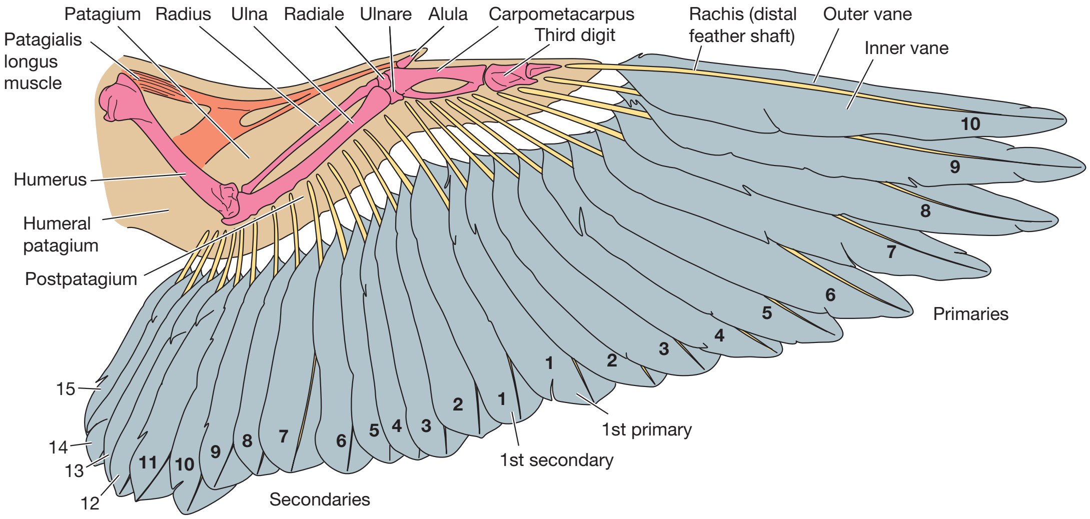
Among extant animals, **feathers** are unique to birds, making them immediately recognizable despite diverse body forms, colors, and life histories. Feathers function in flight in most extant species of birds, and they also play roles in swimming, camouflage, hearing, sound production, tactile sensation, repelling and transporting water, and providing support for the body. Feathers can also function in communication, for example as threat signals or sexually dimorphic signals used in courtship.

Feathers are built around a central shaft, which is divided into the **rachis** and the **calamus** (Figure 7-3A). The calamus, also known as the **quill**, is rooted in the bird's skin. Extending from the rachis are many **barbs**, which together make up the **vane**. In some kinds of feathers, **barbules** extend off the barbs, and **hooklets** extend off the barbules. These interlocking elements make the vane into a cohesive, semi-rigid structure.

There are five major types of feathers. **Contour feathers** are the most visible feathers on a bird and include both body and flight feathers. Insulation comes from **semiplumes**, which have a rachis, and **down feathers**, which do not (Figure 7-3B). **Bristles** consist of a stiff ra-



A. Dorsal view of wing surface showing coverts, alular quills and remiges



B. Ventral view of wing showing nine primaries and 15 secondaries after removal of covert feathers

Figure 7-4
Types of feathers on a wing.

chis without barbs; they are found near the eyes and mouth, where they act like the eyelashes or whiskers of mammals. **Filoplumes** (Figure 7-3C) are like bristles but have a cluster of short barbs at the tip. These barbs adhere to the surfaces of contour feathers, and nerve endings at the base of the filoplume send information to the brain on the position and movement of the feathers.

Groups of contour feathers are named based on function and position. For example, there are two groups of flight feathers—the **remiges** (on the wing) and the **rectrices** (on the tail). The remiges include the **primaries**, which are rooted in the "hand" or **manus**, and the **secondaries**, which are rooted in the ulna (Figure 7-4). The **alular quills** attach to a digit in the manus and can be raised to form a "slot" to keep the wing from stalling when it flies slowly. **Covert** and **tertial feathers** are contour feathers that form

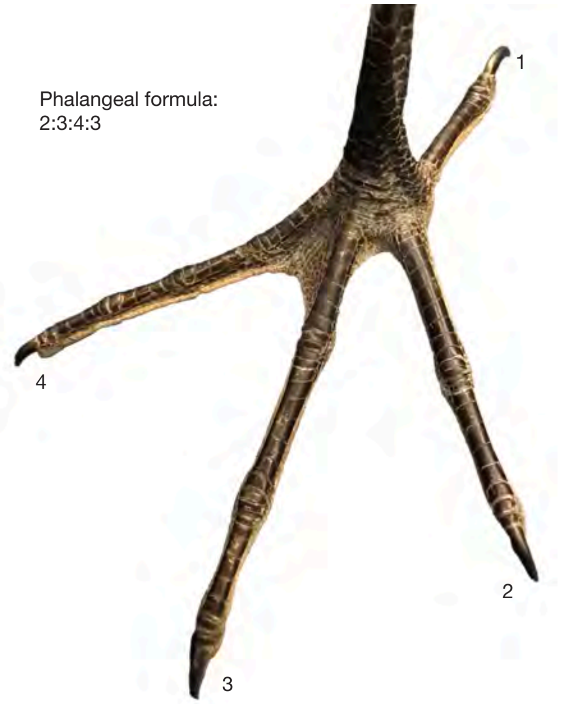


Figure 7-5
Right foot of Great Blue Heron, *Ardea herodias*.

smooth surfaces on the dorsal and ventral sides of the wings. **Tertial feathers** are rooted on the humerus.

Bird legs and feet are covered with scales, and each toe bears a claw. Most species have four toes in an **anisodactyl** arrangement, with the big toe (digit 1) pointing posteriorly, as in herons (Figure 7-5). We will study other arrangements of the toes at Station 3.

Birds are very visual animals and have relatively large eyes and correspondingly large midbrains. Some other senses, however, are greatly reduced. For example, olfaction is well developed in only a few birds such as the Turkey Vulture, *Cathartes aura*. (Figure 7-6). Its olfactory bulb is proportionately much larger than in other birds.

†*Ichthyornis* and other outgroup theropods, including †*Archaeopteryx* (Figure 7-7), had teeth but **all extant birds lack teeth**. Teeth are heavy, and are presumed to have been lost as an adaptation for flight. The **beak** made of keratin is a synapomorphy of Aves (Station 1). Although beaks perform many of the functions of teeth, such as cutting or tearing food into pieces, they are not well suited for grinding and crushing food. This function can be accomplished in the **gizzard** (Station 9).

The **uropygial gland** is a small, heart-shaped gland located on the back near the base of the tail. In most birds, it produces an oil that the bird applies to the feathers during **preening** to maintain and weatherproof them. Some birds have reduced or lost the uropygial gland.

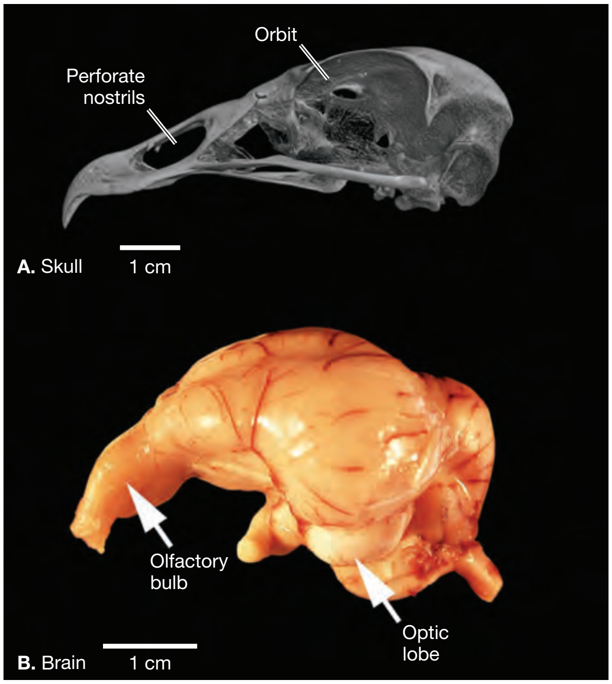


Figure 7-6
Turkey Vulture, *Cathartes aura*. (Part B from Grigg et al. 2017 doi.org/10.1038/s41598-017-17794-0; CCA 4.0 International License.)

Figure 7-7
Replica skull of †*Archaeopteryx lithographica*.

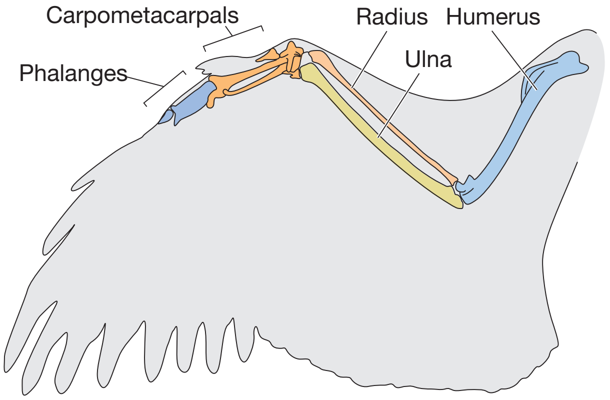


Figure 7-8
Wing bones and flying surface of a bird.

Station 3. Ecomorphology

Shapes, sizes, and anatomy of the wings, feet, and beaks of birds can give you important clues about their biology and ecology

Wings – Variations in wing size and shape impact maneuverability and the ways that wings are used for **flapping flight** and for **soaring**. To understand how wings vary, start by studying the general morphology of the wing bones (Figure 7-8). The wing is supported by the **humerus**, **radius**, and **ulna**. Distally, the **carpometacarpals** represent fusions of the wrist, or carpal bones, with the metacarpal bones. Distal to the metacarpals are the **phalanges** or finger bones. These are fused, too, reducing weight and simplifying the structure of the hand. The feathers extend far beyond the skeleton of the wing to form the **flying surface**.

Relative proportions of wing bones are one of the most important ways that wing morphology varies. Flapping birds, such as **hummingbirds** that fly using quick, powerful wing strokes, have a relatively elongated manus (Figure 7-9A). The carpometacarpals and phalanges that make up the manus serve as the attachment sites for the 10 primary feathers that generate thrust (Figure 7-4B). Feathers attached to the ulna serve to generate lift, and hummingbirds have only six secondary feathers. As a result, hummingbirds cannot soar. In contrast, **frigatebirds** fly using a mixture of powered and dynamic soaring flight, and the arm, forearm, and "hand" are roughly equivalent in length (Figure 7-9B). Frigatebirds have 11 primaries and 23 secondaries, indicating the importance of lift generation for soaring. **Albatrosses** have even more elongated forearm bones for attachment of secondary feathers, creating a large flying surface for soaring (Figure 7-9C).

Birds such as the Red-footed Booby (*Sula sula*, Figure 7-10A) have **long, narrow, high-aspect ratio wings** (aspect ratio = wing

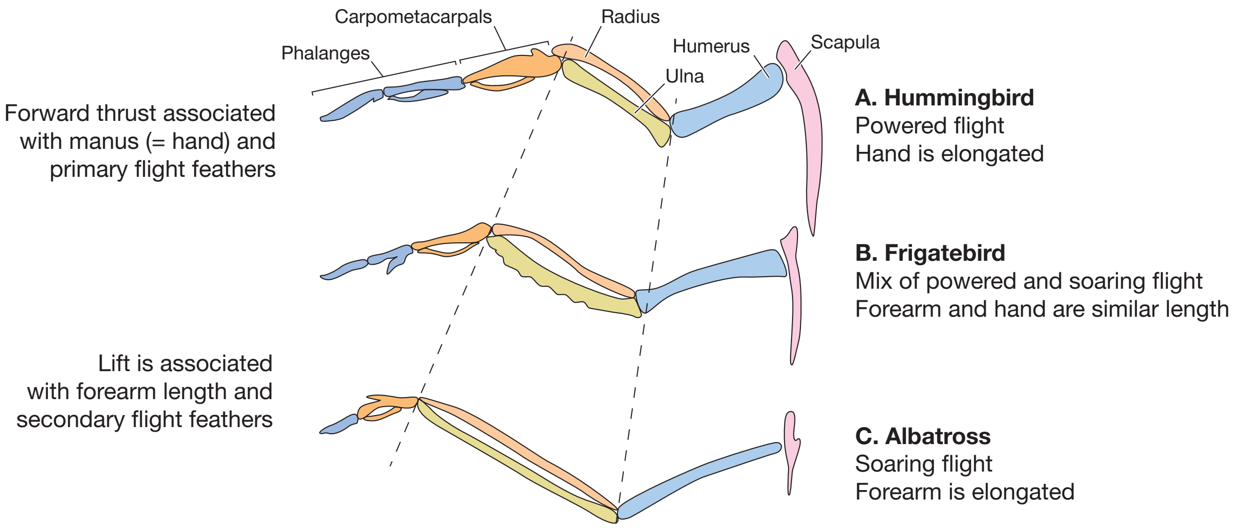


Figure 7-9
Relative proportions of the skeleton in three types of wings.

A. Red-footed Booby *Sula sula*

B. Great White Pelican *Pelecanus onocrotalus*

C. Cabot's Tragopan *Tragopan caboti*

D. Roadrunner *Geococyx californianus*

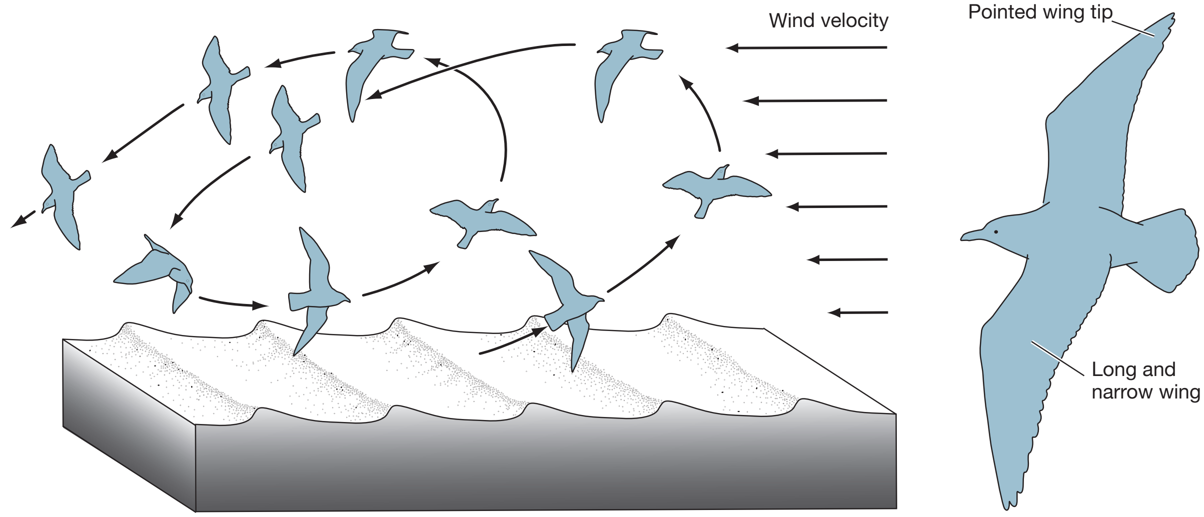
Figure 7-10
Types of wings.

length/wing width). This type of wing is excellent for **dynamic soaring** in winds blowing over the open ocean (Figure 7-11A and B). To do this, a bird must get aloft using powered flight before spreading its wings and heading directly into the wind. The wind passing around the wing generates lift, so the bird's body rises in the air. Wind velocity has a gradient over the ocean surface, with faster winds higher above the water surface. Thus, the bird can continue to rise in the air column. At an appropriate height, it turns away from the wind and soars down before turning to head back into the wind, rising and repeating the soaring motion.

In addition to the elongated forearm bones, soaring birds such as pelicans (Figure 7-10B) have **intermediate aspect-ratio wings** and spaces between the primaries that serve as adjustable **slots**, allowing these birds to make tight turns within a rising mass of air during static soaring (Figure 7-11C-D). This type of wing is described as **slotted-high lift**. Swallows and other fast fliers have high aspect ratio wings but without the long forearm associated with soaring. Birds with **low aspect ratio** or **elliptical wings** live in structured environments such as forests, where maneuverability is important (e.g., pheasants; Figure 7-10C). Road runners are a special case (Figure 7-10D). The short and almost **rectangular wing** is suited only for short flights.

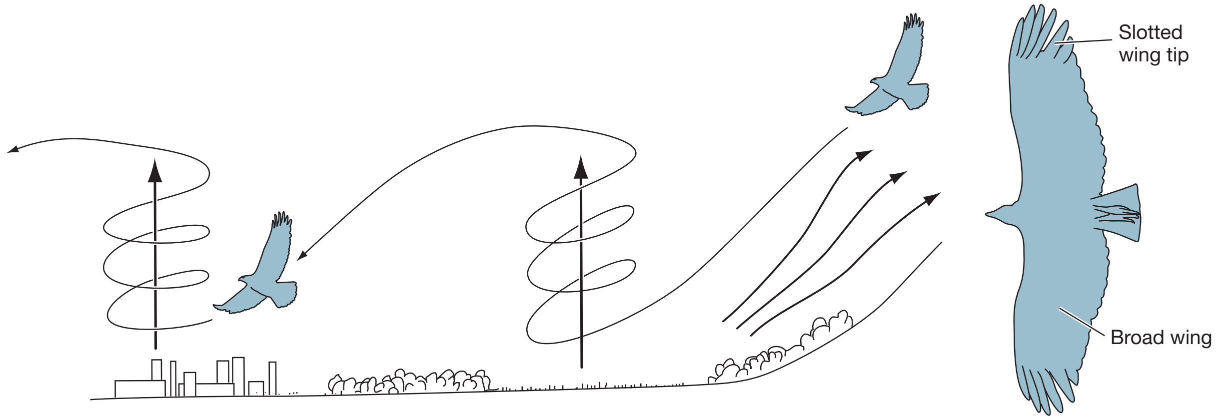
Toes and Feet – Foot morphology and the arrangement of toes offer additional guides to a bird's ecology. The most common arrangement of toes is **anisodactyly**, in which the first toe points posteriorly and the other three toes point anteriorly (Figures 7-5, 7-12A). In the **zygodactylous** condition, which evolved independently in woodpeckers, parrots and seven other lineages, the first and fourth toes point posteriorly and the second and third toes point anteriorly (Figure 7-12B), an arrangement that helps when climbing vertical surfaces or clinging to branches. The first and fourth toes of swifts (Apodidae) can be rotated from anterior to posterior, an arrangement known as **pamprodactyly** (Figure 7-12C). Swifts have tiny feet, and they use these rotatable toes to cling to vertical surfaces (such as chimneys) when roosting. Flightless running birds have heavy legs and feet and reduced numbers of toes. For example ostriches have only two toes, a **didactylous** arrangement (Figure 7-12D).

Many aquatic birds use webbed feet to move in the water (Figure 7-13). Birds with **palmate**



A. Dynamic soaring

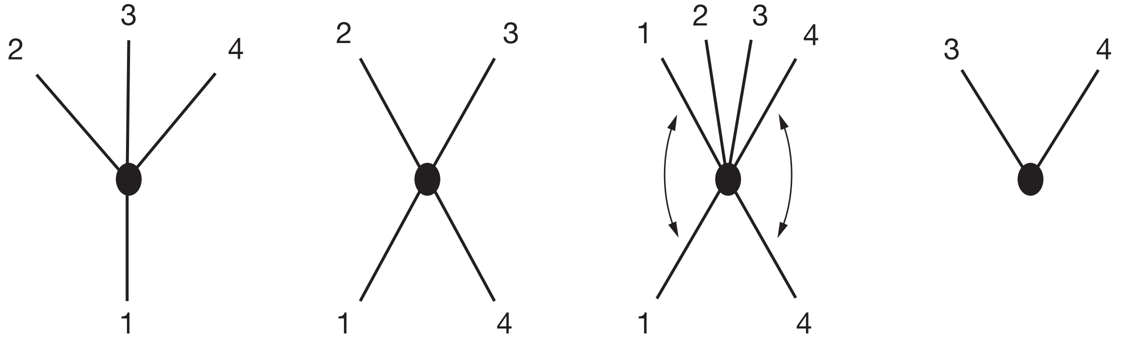
B. Wings of a dynamic soarer



C. Static soaring

D. Wings of a static soarer

Figure 7-11
Dynamic versus static soaring.



A. Anisodactylous (most common)

B. Zygodactylous (e.g., woodpeckers)

C. Pamprodactylous (e.g. swifts)

D. Didactylous (ostriches)

Figure 7-12
Examples of different arrangements of toes in birds.

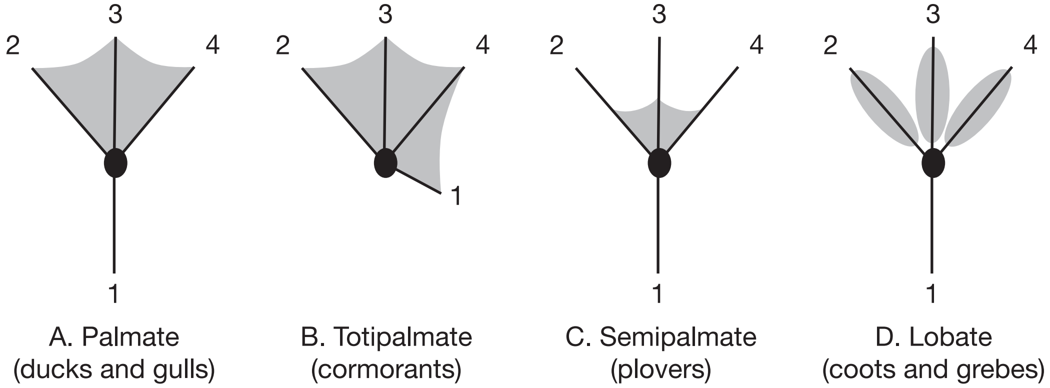


Figure 7-13
Different types of webbing in the feet of water birds.

webbing such as ducks and gulls have webs that extend between the three forward-facing toes (Figure 7-13A). In cormorants, which use their feet to swim underwater, the skin extends between all toes in an arrangement called **totipalmate webbing** (Figure 7-13B). Wading birds such as plovers have incomplete webbing in an arrangement termed **semipalmate webbing** (Figure 7-13C). Coots and grebes independently evolved **lobate webbing** (Figure 7-13D) used to swim underwater. Toes 2-4 have large flaps of skin around them like paddles, but the paddles are not connected from toe to toe. The bird's paddles are spread wide during the power stroke of swimming but folded back against the toes for the recovery stroke. By analogy with a rower's oar we can say that the paddles are feathered on the return stroke.

Beaks – The terms **beak** and **bill** are synonymous, but we think of beaks as narrow and sharp whereas bills are broad and rounded, as in ducks. Beak sizes and shapes vary greatly among birds in relation to feeding. Walk past the bird cases and examine the range of beak shapes. Birds with short, sharp beaks often eat insects or fruit such the Northern Mockingbird,

Figure 7-14
Northern Mockingbird, *Mimus polyglottos*. Photograph by K. E. Bemis.

Figure 7-15
Tree Swallow, *Tachycineta bicolor*. Photograph by W. E. Bemis.

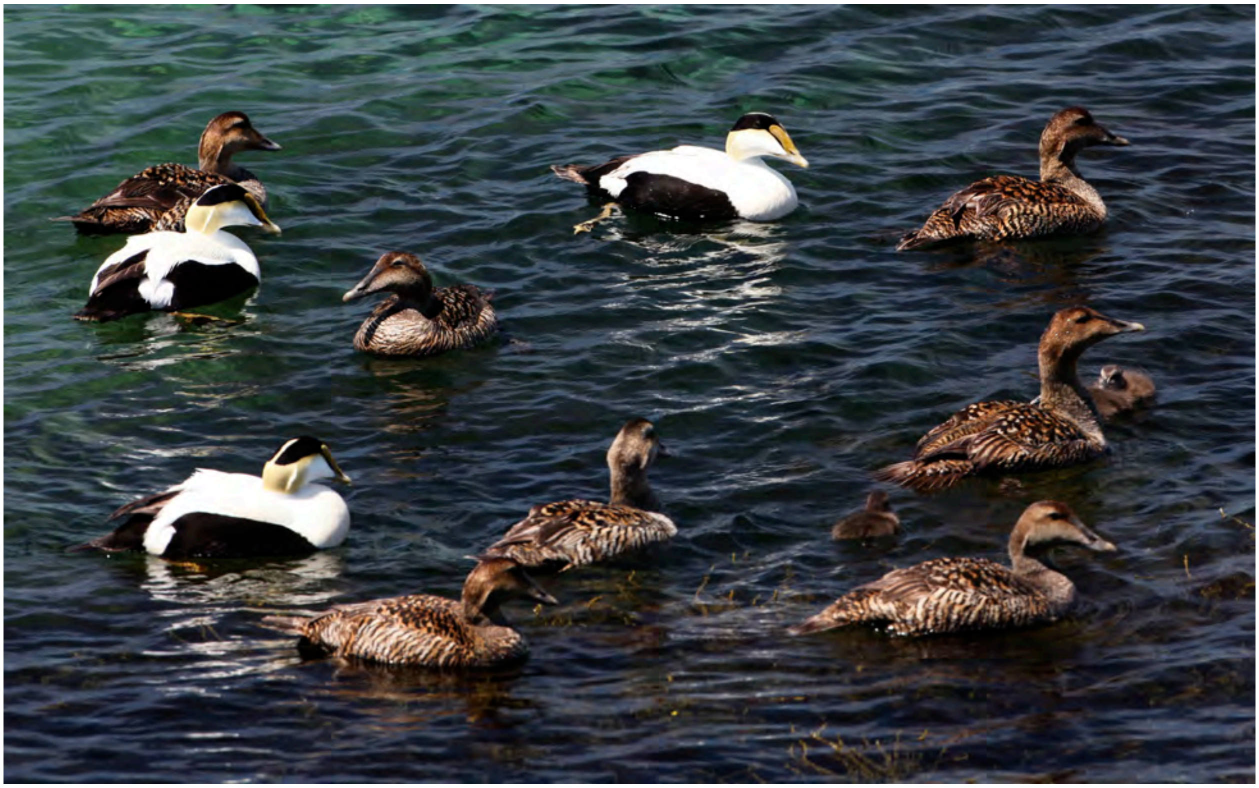


Figure 7-16
A group of male (white and black) and female (brown) Common Eiders (*Somateria mollissima*) at Appledore Island, Maine, in the late spring. Photograph by W. E. Bemis.

Mimus polyglottos (Figure 7-14). Birds that feed on insects in the air often have broad beaks and large gapes, such as the Tree Swallow, *Tachycineta bicolor* (Figure 7-15). Short, strong beaks are used to crack seeds (e.g., cardinals). Some carnivorous birds such as crows use sturdy bills to kill prey, but others such as hawks use sharp talons to kill and hooked beaks to rip off pieces of prey items.

Many birds feed in water. Some fish-eating divers have straight beaks with serrated edges (e.g., mergansers). In others, the beak is hooked (e.g., pelicans) or sharp to stab prey items (e.g. herons). Broad, flattened beaks are used to sift through water and sediments for food (e.g., ducks, spoonbills). But some ducks are carnivorous, such as Common Eiders (*Somateria mollissima*, Figure 7-16), which wrest mussels from rocks and crush the shells in their powerful gizzard.

Station 4. Parental care and life history

Birds exhibit extensive parental care, but the duration of care, and the self-sufficiency of chicks upon hatching, varies widely. **Precocial young** hatch feathered and capable of walking and feeding. **Altricial young** hatch naked and require extensive care because they cannot feed or thermoregulate on their own. There is a continuum from precocial to altricial, with differing degrees of self-sufficiency of the young at hatching. Observe the differences between the precocial and altricial hatchlings on display.

Most birds are **biparental**, a term that means both parents care for the young. But this is not the case in all species. For example, male Common Eiders, *Somateria mollissima*, abandon females after eggs are laid. Females care for ducklings in groups known as **crèches**.

Birds have diverse mating systems. Most species are **socially monogamous** (one male and one female, as in the Eastern Bluebird, *Sialia sialis*). Some species are **polygynous** (one male with multiple females, such as the Red Winged Blackbird, *Agelaius phoeniceus*), others are **polyandrous** (one female with multiple males, as in the African Jacana, *Actophilornis africanus*). Some terrestrial birds form **leks**, in which multiple males congregate at traditional display sites. Females choose mates based on these displays, as in the Wild Turkey, *Meleagris gallopavo*. Molecular genetic techniques show that many socially monogamous species are not genetically monogamous – that is, the social father is not the father of all nestlings in his nest.

Station 5. Avian diversity I

Paleognathae – As you learned at Station 1 (Figures 7-1, 7-2), paleognaths are the sister group of neognaths. The living paleognaths are the ostriches, rheas, cassowaries, emu, kiwis, and tinamous. Tinamous can fly, but all of the others are flightless and lack a keeled sternum. Collectively, the flightless forms are known as **ratites**, a word that refers to a raft, which is a boat without a keel (L. *ratis* = raft).

Of the two species of ostriches, the Common Ostrich *Struthio camelus* from Africa is more familiar. At 2.5 m, these are the tallest extant birds. Study the skeleton in the case at the back of the laboratory to identify the flat, raft-like sternum and didactylous feet.

The three extant species of rheas are from South America.

The Emu, *Dromaius novaehollandiae*, is native to Australia; it reaches 1.9 m in height. There are three large species of cassowaries from northern Australia and Indonesia. These omnivorous forest birds feed mainly on fruits. The largest species, the Southern Cassowary, *Casuarius casuarius*, is only slightly smaller than the ostriches and the emu. All three species of cassowaries have a large casque on their heads, which may serve to amplify sounds or aid in movement through dense forest vegetation.

Kiwis weigh 3-7 pounds. They are endemic to New Zealand, and all five species face conservation risk. Like the other species, the Tokoeka, also known as the Common Kiwi, (*Apteryx australis*), is a nocturnal forest dweller that eats worms and other invertebrate prey. Kiwis lay huge eggs relative to their body size (up to 1/3 the weight of the female!).

There are 48 species of tinamous, most of which come from South America.

Many large flightless paleognaths have gone extinct due to predation by humans. The Elephant Birds, endemic to Madagascar, were the largest known members of Aves. The largest species was up to 3 m tall, weighing more than 385 kg. Seven species in two genera were extinct by the end of the 17th century. Their extinction is thought to be the result of human hunting, introduction of diseases carried by domestic birds like chickens, or predators such as rats, cats, and dogs.

Ten species of moas exemplified by the North Island Giant Moa, †*Dinornis novaezealandiae*, were endemic to New Zealand. Some reached heights of 3.6 m and 225 kg. They are the only birds known to have lost their forelimbs (other flightless paleognaths have vestigial wings). Because there are no native mammals on New Zealand, moas were the large herbivores on the island, filling the ecological role of the grazing ungulates on other continents. Prior to the arrival of the Maori people, their only predator was the giant Haast's Eagle, †*Hieraaetus moorei*, estimated to have reached 15 kg with a wing span of 9 m. Moas are thought to have gone extinct by the beginning of the 16th century due to human predation.

Neognathae – The first extant clade within Neognathae is **Galloanserae**, which includes chickens, ducks and allies (Figure 7-1).

Galliformes – Members of Galliformes (>300 species) include quail, grouse, pheasants, turkeys, chickens, and megapodes. They are herbivores or omnivores that forage on the ground, varying in size, from small quails

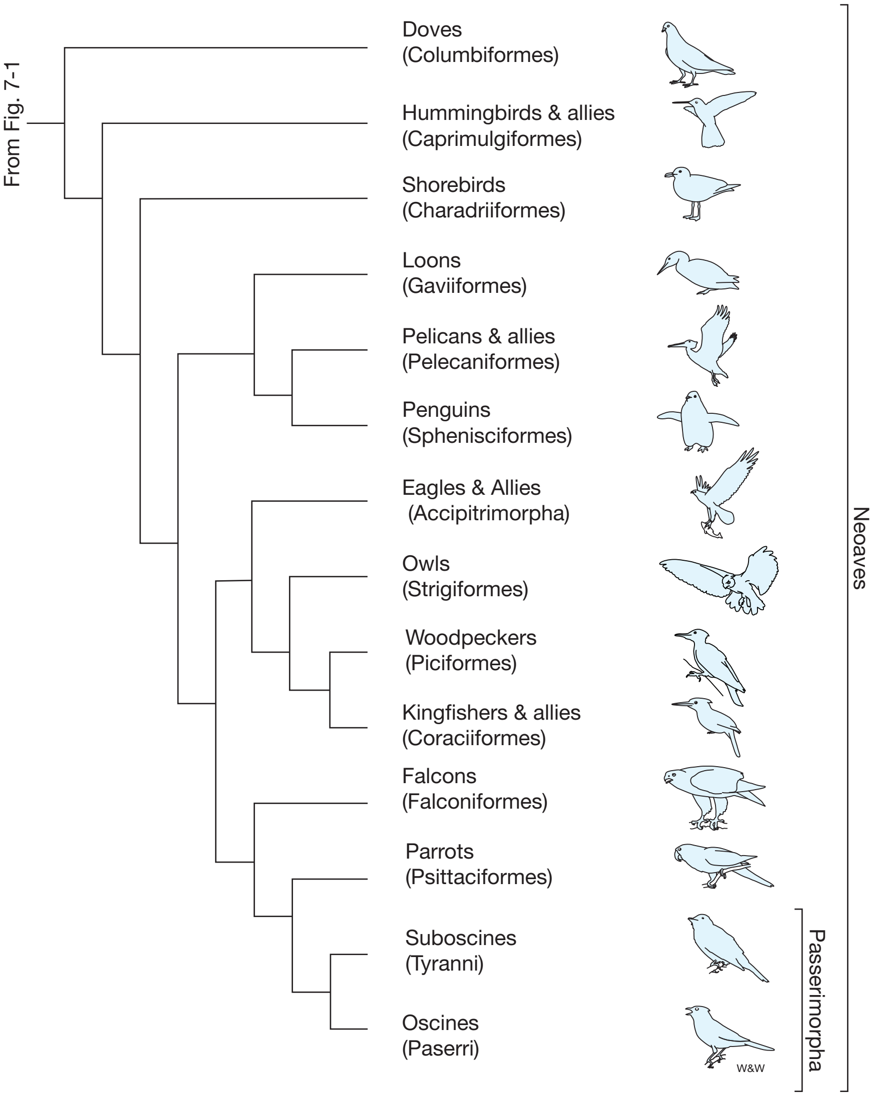


Figure 7-17
Pruned tree from Jarvis et al. (2014) showing taxa of Neoaves considered here.

to large turkeys. Local species include Wild Turkey, *Meleagris gallopavo*, Ruffed Grouse, *Bonasa umbellus*, and the introduced Common Pheasant, *Phasianus colchicus*. The Greater Prairie Chicken, *Tympanuchus cupido*, was once abundant in the central United States, but its populations declined because 19th century settlers ate them. Much of their grassland habitat then was converted to agricultural uses, and one subspecies, the Heath Hen, of Atlantic coastal regions, went extinct in the early 1900's. Greater Prairie Chickens are notable for impressive visual and auditory (booming) displays by males during lekking.

Anseriformes – There are about 170 extant species of anseriforms, commonly known as waterfowl. The group includes ducks, geese, and swans. Most species use webbed palmate feet to swim (Figure 7-13). The Mallard Duck, *Anas platyrhynchos*, and Canada Goose, *Branta canadensis*, are common local anseriforms that are widely distributed in North America.

Neoaves – Neoaves includes the remaining diversity of extant birds (Figure 7-17). Phylogenetic relationships among the 35 or more orders of Neoaves have been revised many times, and there are conflicts between trees based on anatomy and molecular phylogenetic characters.

Figure 7-18
Female Ruby Throated Hummingbird, *Archilochus colubris.* Photograph by W. E. Bemis.

Here, we base Figure 7-17 on the tree in Jarvis et al. (2014), which we simplified by pruning to include the following groups.

Columbiformes – Pigeons and doves are within the single family contained within the Columbiformes. There are ~350 species worldwide. They can be identified by their small heads and biparental care, during which parents feed the young a substance known as “pigeon’s milk” produced in the crop. The Mourning Dove, *Zenaida macroura*, is a common local columbiform with a distinctive mournful call.

Caprimulgimorpha – We focus here on **Caprimulgiformes** an order with about 600 species such as nighthawks, hummingbirds, and swifts. Nighthawks are crepuscular or nocturnal species with long wings and short legs. They feed on moths and other flying insects that they catch with their wide, short bills. More than 360 species of hummingbirds occur only in the New World. Many species are small, but some grow to 20 cm. The Ruby Throated Hummingbird, *Archilochus colubris*, migrates to central New York to breed (Figure 7-18). Swifts occur worldwide, and all of the ~ 200 species are aerial insectivores. Many hummingbirds and swifts exhibit **nighttime torpor**, during which the body temperature drops to save energy.

Charadriiformes – Commonly known as shorebirds, this group of > 300 species includes gulls, terns, skimmers, plovers, puffins, and auks. They feed on invertebrates or aquatic invertebrates and vertebrates. The Herring Gull, *Larus argentatus*, is a common local species (Figure 7-19).

Gaviiformes — The five extant species are commonly known as loons. Their first three toes are webbed, and they frequent freshwater lakes where they dive for food and feed primarily on fish. When examining the specimen, pay attention to the posterior position of the feet on the body; this morphology is an adaptation for diving. The Common Loon, *Gavia immer*, breeds in the Adirondacks and can be readily identified by its distinctive call. They overwinter along the coast and in the southern United States.

Pelecaniformes – This group includes more than 100 species of pelicans, herons, bitterns, ibises, and spoonbills. Pelicans have a large gular pouch; some species dive for fish while others hunt cooperatively at the surface. Herons, bitterns, ibises, and spoonbills have long bills and long legs suited for wading. A common local species is the Great Blue Heron, *Ardea herodias*, readily identifiable based on its large size (up to 4 feet tall), grey-blue body color, and the black stripe and plume of feathers on the otherwise white head of mature adults. Other local species include the Green Heron, *Butorides virescens*, and Great Egret, *Casmerodius albus*.

Sphenisciformes – There are 18 species of penguins, distributed mostly in the southern hemisphere (one species, the Galápagos Penguin, can occasionally be found north of the equator). Their distinctive black and white plumage functions as **countershading** while in the water. The wing bones of penguins are

Figure 7-19
Herring Gull, *Larus argentatus*, gliding over a beach. Photograph by K. E. Bemis.

highly adapted for swimming, and no penguin species is capable of flight in air. Penguin feathers are also unique among birds—they are scale-like in texture, another adaptation to their aquatic environment. The location of the feet at the very end of the penguin body aids in swimming efficiency, giving these birds their characteristically comical waddle while on land. The smallest penguin species is the Little Blue Penguin, *Eudyptula minor*, of Australia and New Zealand, which weights ~2 pounds. The Emperor Penguin, *Aptenodytes forsteri*, is the largest species, ≥ 36 kg (80 lbs).

Accipitrimorpha – This group contains **Accipitriformes**, an order that includes ~250 extant species such as ospreys, hawks, eagles, and Old World vultures. They typically have long, broad wings that can be used for soaring. Common local species include the Red-tailed Hawk, *Buteo jamaicensis*, Bald Eagle, *Haliaeetus leucocephalus*, and Osprey, *Pandion haliaetus*. Members of this order kill or scavenge prey; many have a sharply hooked beak. New World vultures including the Turkey Vulture, *Cathartes aura,* are placed within **Cathartiformes**, a separate order within Accipitrimorpha.

Strigiformes – Owls are readily identifiable by their large heads, forward-facing eyes, long, sharp, hooked claws, and soft plumage that allows silent flight. The 236 species worldwide are nocturnal predators that locate prey by sound. Local species include the Barred Owl, *Strix varia*, and Great Horned Owl, *Bubo virginianus*.

Piciformes — This order includes the toucans and woodpeckers. There are > 240 species of woodpeckers worldwide. They use strong, straight beaks to drill into tree trucks to find food and build cavity nests. They also drum

Figure 7-20
Blue and Yellow Macaw, *Ara ararauna*. Photograph by K. E. Bemis.

on trees, using the beak to advertise territory during breeding season. **Zygodactylous feet** (Figure 7-12) allow them to climb up vertical surfaces. Common local woodpeckers include the Downy Woodpecker, *Picoides pubescens*, and Pileated Woodpecker, *Dryocopus pileatus*.

Coraciiformes – This order includes the kingfishers, rollers, and bee-eaters. Many species of kingfishers feed on fishes, invertebrates, or other vertebrates in or near aquatic habitats. They have large, straight, pointed bills and block-shaped heads and feathers in shades of blue, white, orange, or brown. Our local species is the Belted Kingfisher, *Megaceryle alcyon*.

Falconiformes — There are about 65 species of falcons; most are swift birds of prey with long tails and pointed wings. They have a **tomial tooth** formed by keratin along each side of the upper beak to quickly kill prey. Local species include the Peregrine Falcon, *Falco peregrinus*, and American Kestrel, *Falco sparverius*.

Psittaciformes — This order includes the parrots, colorful tropical birds with well-known vocal capabilities. A familiar example is the Blue and Yellow Macaw, *Ara ararauna* (Figure 7-20). Other members include cockatoos, cockatiels, and lories. Cockatiels and cockatoos have a crest of feathers on their heads. Members of Psittaciformes have a hinge between their upper bill and the skull that gives them the ability for some cranial kinesis. They independently evolved zygodactylous feet.

Station 6. Avian diversity II: Passeriformes

With > 5,600 species, Passeriformes includes more than half of all extant bird species. Commonly known as "perching birds" the group includes two suborders: Tyranni, and Passeri. You will only need to be able to identify examples to suborder and you do not need to learn the families, which are listed here only as matter of organizational convenience.

Tyranni — This clade, also known as **suboscines**, includes ~ 1200 species with innate songs. The syrinx is simple in comparison to Passeri. Here, we consider only the group with members in our region.

Tyrannidae — Tyrant flycatchers occur in North, Central, and South America. Many of the ~400 species are aerial insectivores. Local species include the Eastern Phoebe, *Sayornis phoebe*.

Passeri — This clade, also known as **oscines**, includes ~ 4600 species that have a complex syrinx and can learn songs. Here, we consider only those groups with members in our region.

Laniidae – Shrikes are predatory birds with strong hooked bills. The ~30 species in this family are distributed in Africa, Europe, Asia and North America. When foraging, they sit and wait on perches for prey and then attack. Common prey items are birds, rodents, reptiles, and large insects. They also have the delightful habit of impaling prey items on sharp things, where

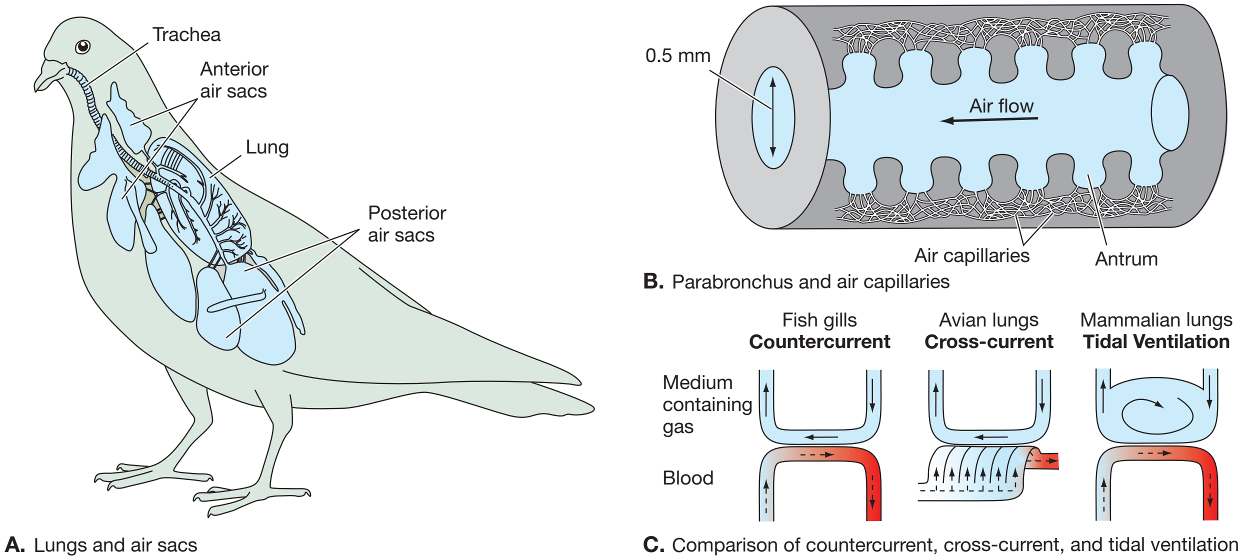


Figure 7-21
Anatomy of avian respiratory system with comparisons to others.

they leave them hanging to mark their territory.

Corvidae — This family contains about 120 species of jays, crows, ravens, magpies, and relatives, including the largest passerine, the Common Raven, *Corvus corax*. Corvids are gregarious and omnivorous. Common local species include the American Crow, *Corvus brachyrhynchos*, and Blue Jay, *Cyanocitta cristata*. Corvids are intelligent, and can learn to identify individual people and solve puzzles. They also have among the largest brain to body weight ratios within Aves, comparable to Great Apes.

Paridae – The Black-capped Chickadee, *Poecile atricapillus*, and Tufted Titmouse, *Baeolophus bicolor*, are common local representatives of this family of about 60 species. The common name “chickadee” derives from their call.

Mimidae – Mimids have large song repertoires, and their name derives from their ability to mimic sounds. Local species include the Northern Mockingbird, *Mimus polyglottos*, Gray Catbird, *Dumetalla carolinensis* and Brown Thrasher, *Toxostoma rufum*.

Passerellidae – This family of ~135 species contains the New World sparrows, towhees, and juncos. Most species eat seeds and supplement their diet with insects. Local species include the Song Sparrow, *Melospiza melodia*, and Dark-eyed Junco, *Junco hyemalis*.

Cardinalidae – Most of the 50 species in this family have strong beaks used to eat hard seeds. The Northern Cardinal, *Cardinalis cardinalis*, and Rose-breasted Grosbeak, *Pheucticus ludovicianus*, occur locally.

Station 7. Respiration and circulation

Respiration – You use the familiar in-out, or **tidal**, pattern of air movement to ventilate your lungs. Birds are different: air passes **one way through the lungs** to maximize the amount of gas exchange and to limit mixing of fresh and stale air.

The **trachea** branches into two **primary bronchi**, one leading to each lung (right and left). Each bronchus branches into **secondary bronchi**, which branch into **parabronchi**. Each parabronchus opens to many tiny cavities, called **air capillaries**, where gas exchange occurs.

Birds have up to nine **air sacs** (Figure 7-21). Some extend into cavities in pneumatic bones. Air is stored in the air sacs during the breathing cycle, but no gas exchange occurs in them.

Here, we focus on the **two-breath model**

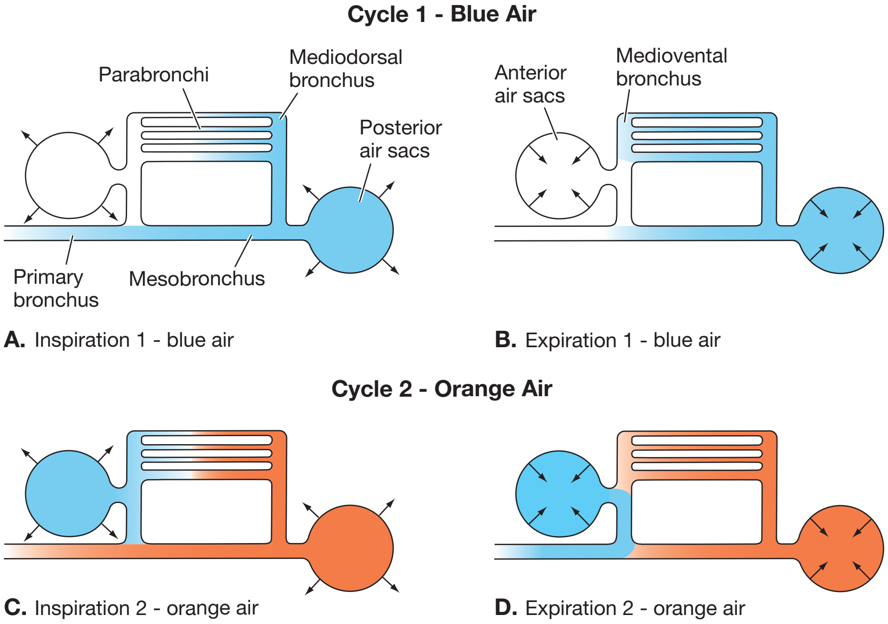


Figure 7-22
The two-breath model of air flow during avian respiration.

for air flow from posterior air sacs through the parabronchi and into the anterior air sacs (Figure 7-22).

1. During inspiration 1, air moves to the posterior air sacs (Figure 7-22A).
2. During expiration 1, air moves through the parabronchi of the lungs (Figure 7-22B).
3. During inspiration 2, air that has passed through the parabronchi moves to the anterior air sacs (Figure 7-22C).
4. During expiration 2, air is expelled from the respiratory system (Figure 7-22D).

One-directional movement of air through avian lungs leads to extremely efficient exchange of oxygen because air is always moving in one direction through the lung, and blood is moving in a roughly opposite direction, in a pattern termed **crosscurrent flow** that maximizes gas exchange. This is similar to countercurrent exchange in fish gills (Laboratory 3).

Syrinx — Birds use the syrinx to vocalize. It is located at the base of the trachea at the point where it branches into the primary bronchi (Figure 7-23A). Sound is produced via vibration of membranes in the syrinx, and changes in pitch are possible through modulation of the tension of these membranes. The Whooping Crane, *Grus americana*, famous for its vocalizations, has an elongate trachea that acts like the coils of a bugle to make loud, resonant calls.

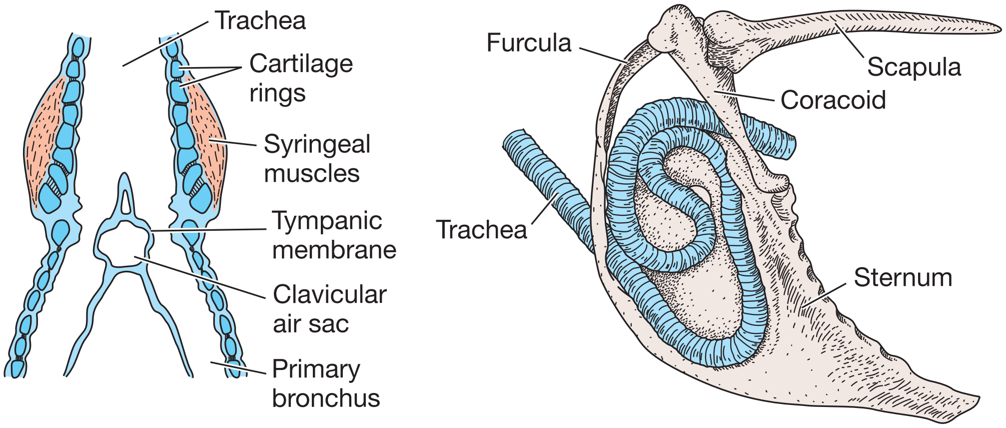
Circulation — Birds have a **four-chambered heart** and, unlike crocodilians (Figure 6-12) cannot shunt blood between the pulmonary and systemic circuits.

Birds are **endothermic** — they generate heat through their own metabolism instead of relying on heat in the environment as ectotherms do. This allows birds to live in extreme environments from the arctic to the desert and everywhere in between. The disadvantage of endothermy is that it requires energy, and therefore birds must continually eat.

Station 8. Skeletal anatomy

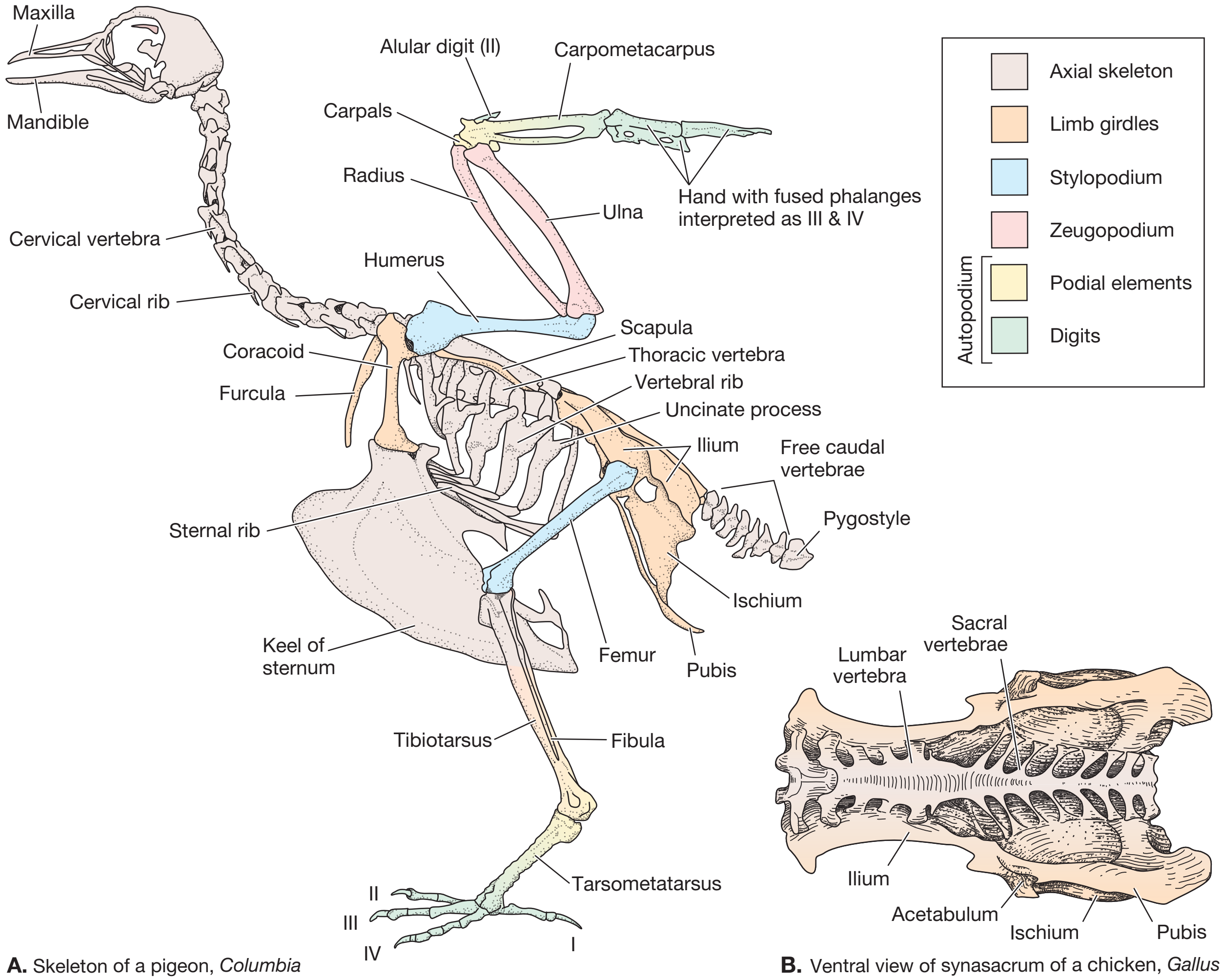
Many aspects of the avian skeleton have been modified for flight (Figure 7-24). Modifications include:

1. A bird's body mass is roughly equivalent to that of a mammal of similar size, but the distribution of weight differs. For example, the hind limbs of a bird are heavier relative to their body size than are those of mammals.



A. Syrinx of a blackbird **B.** Sternum and trachea of a whooping crane

Figure 7-23
Syrinx and elongated trachea used in vocalization.



A. Skeleton of a pigeon, *Columbia* **B.** Ventral view of synasacrum of a chicken, *Gallus*

Figure 7-24
Skeletal features of pigeon and chicken.

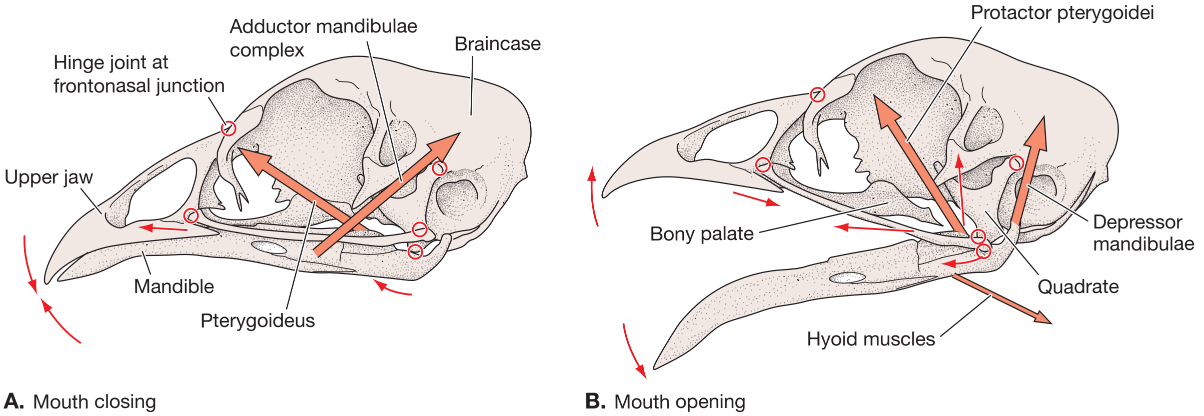


Figure 7-25
Cranial kinesis in a chicken. The four kinetic joints are indicated with red circles.

2. Bones of the skull are very light, and fenestrae help reduce the weight of the head. Replacement of teeth with the **keratinized beak** also makes the skull lighter.
3. The skull is highly **kinetic**. Functionally, the avian skull consists of four units: (1) **braincase**, (2) **bony palate and quadrate**, (3) **upper jaw**, and (4) **mandible** (Figure 7-25A). The quadrate allows anteroposterior movements. The bony palate also slides back and forth. A hinge joint is present at the **frontonasal junction**.
4. Many bones are **pneumatic**, or air-filled, decreasing their weight, The cavities in these bones are extensions of the air sacs of the respiratory system.
5. The clavicles fuse into the springy **furcula**, or wishbone. The furcula, along with the **blade-like scapula**, braces the shoulders when the wings flap, while the thick **coracoid** acts as a strut to keep the chest from collapsing due to the compression force of the downstroke of flight (Figure 7-26). The region where these three bones join forms a hole called the **triosseal foramen**. The sternum has a large protrusion, or **keel**, that serves as the origin for the flight muscles. The ribs have projections, known as **uncinate processes**, that keep the body cavity from collapsing during flight.
6. The highly modified forelimbs function as wings. The **humerus** is similar in shape to that of other vertebrates but it is pneumatic. The **ulna** is larger than the **radius** to allow attachment of the secondary flight feathers. The bones of the hand (metacarpals and phalanges) are highly reduced and fused, with only three digits remaining.
7. The **femur** is often pneumatic. The tibia fuses with some of the tarsal bones to form the **tibiotarsus**. The **fibula** is a slender bone on the side of the tibiotarsus. The remaining tarsal bones fuse with the metatarsals to form the **tarsometatarsus**. Birds usually have four digits on the foot (ostriches have two and relatives such as the emu have three). The phalanges in the feet of birds resemble those of other vertebrates.
8. **Cervical vertebrae** are often specialized to allow extensive movements of the neck. **Thoracic vertebrae** are compact and less mobile, and the **lumbar and sacral vertebrae** fuse with some of the **caudal vertebrae** and the **pubis**, **ilium** and **ischium** to form the **synsacrum**. Other caudal vertebrae do not fuse together, allowing movement of the tail, while the last few are fused to form the **pygostyle**, which supports the tail feathers.

To test your understanding of avian skeletal anatomy, study the skeleton of a penguin (Figure 7-27). Penguins are highly specialized for

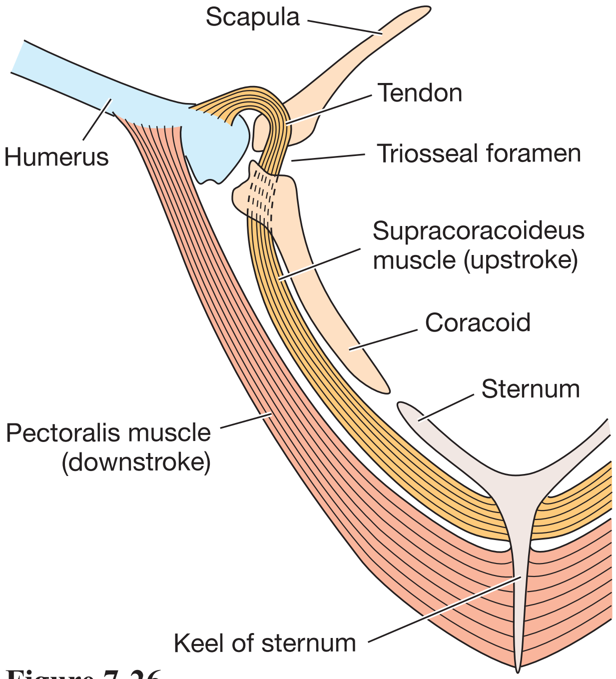


Figure 7-26
Origins of the pectoralis and supracoracoideus muscles on the keel of the sternum and their insertions on the humerus.

subaqueous flight using short, flattened wings that look like flippers. Among many other skeletal differences, penguin wing bones are broader, more flattened, and denser than those of flying birds. Penguins lack primary and secondary feathers, and the wings and body are covered with short, bristle-like feathers. Unlike birds that fly in air, penguins derive forward thrust during both the wing upstroke and downstroke, which causes the body to move up and down with each stroke. As you might predict, their pectoralis and supracoracoideus are more similar in size than they are in birds that fly in air.

Station 9. Internal Anatomy

In most birds, the **keel of the sternum** serves as the attachment for the large flight muscles (Figure 7-26). Use a scalpel to cut along the length of the keel of a pigeon and peel back the skin to reveal the muscles. The largest and most obvious flight muscle is the **pectoralis major**, which originates on the keel and inserts on the ventral surface of the humerus. Its contraction powers the **downstroke**. Contraction of the **supracoracoideus**, a smaller muscle, provides the upstroke during flight. You can find this by using a scalpel to separate the pectoralis from the keel — the supracoracoideus originates from the sternum and lies beneath the pectoralis. The cranial end of the supracoracoideus terminates in a tendon that runs through the **triosseal foramen** to insert on the dorsal surface of the humerus. If the general shapes of the pectoralis and supracoracoideus muscles look familiar it my be because you have seen them as "chicken breasts" and "chicken tenders."

Cut through the jaw if necessary to open the specimen's mouth. Identify the **tongue** and **glottis**, which is the opening leading to the **respiratory tract**. Trace the throat posteriorly until you reach the **esophagus**.

Remove the sternum by making a slit into the body cavity at the caudal end of the sternum, and using scissors to cut through the ribs and

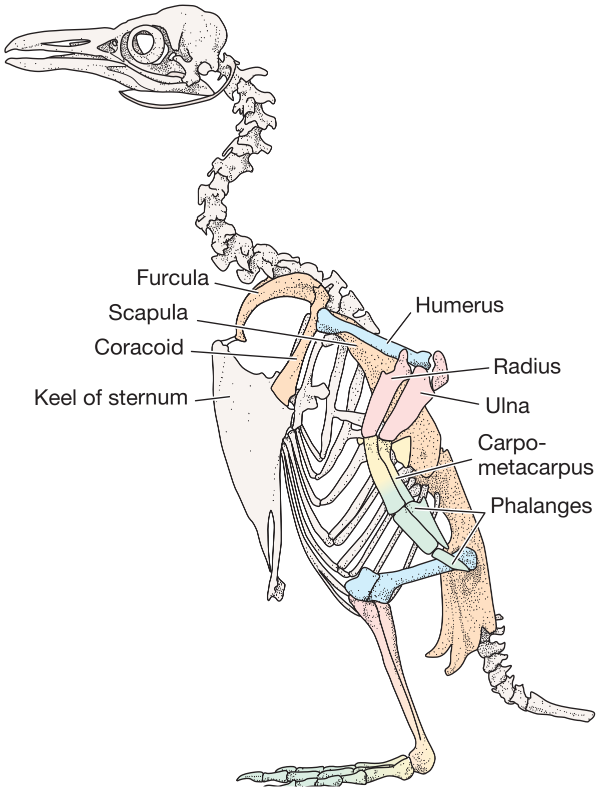


Figure 7-27
Skeleton of a penguin.

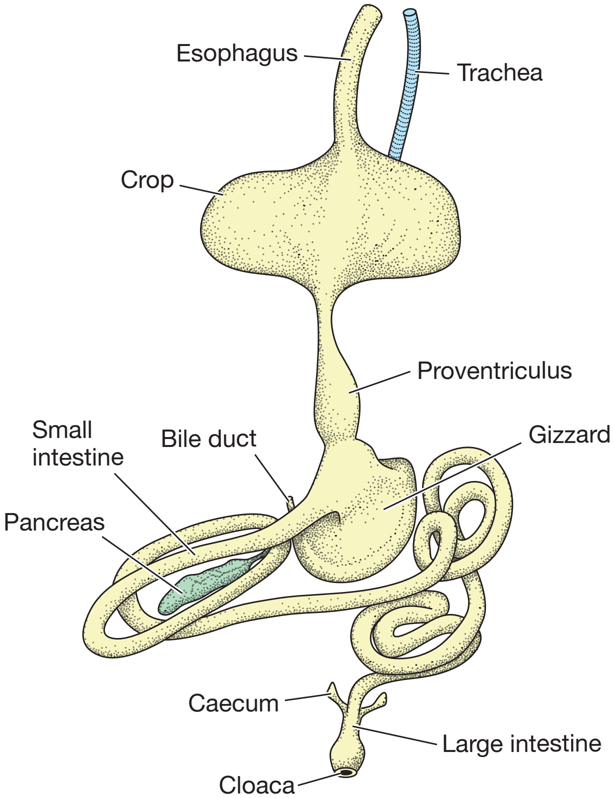


Figure 7-28
Ventral view of digestive tract of a pigeon.

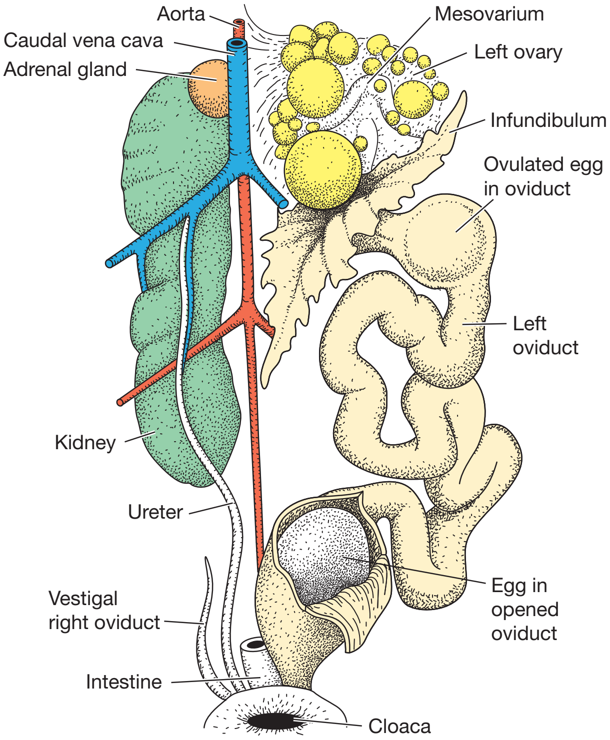


Figure 7-29
Kidneys and reproductive tract of female chicken

coracoid bones. Cut open the skin of the neck, but avoid cutting into the crop, which is closely associated with the skin at the base of the neck.

In the neck, find the **trachea** with its **cartilaginous rings**. The **syrinx** is at the base of the trachea, just before it splits into the two **primary bronchi** (Figure 7-23A) Near the cranial end of the sternum, the esophagus swells into a structure called the **crop**, which holds food before passing it along to the stomach.

The **pericardial sac** containing the **heart** is cranial to the liver. Cut it open and remove the heart to study its four chambers. Find the **proventriculus**, which is the glandular and enzymatic portion of the stomach, and the **gizzard**, or muscular stomach used to mechanically breakdown food. The **intestines** terminate at the **cloaca**, Latin for “sewer.” The **pancreas** lies between the sides of the first loop of the intestines.

Along the dorsal body wall, identify the **lungs** and **kidneys**, which lie in pockets in the synsacrum. Remove a lung to see deep indentations from the ribs. The **gonads** lie near the anterior end of the kidneys (Figure 7-29). Identify the **single left ovary and oviduct** in females (the right ovary and oviduct are vestigial in most birds) or the paired, **bean-shaped testes** and **ductus deferens** of males. In both females and males the reproductive ducts, as well as the **ureters** from the kidney terminate at the cloaca.

8. Mammalia I: Structure and Function

Major concepts

- Mammals are highly active endotherms, and correspondingly need efficient feeding, respiratory, and circulatory systems.

- Mammalian diets are reflected in the anatomy of their teeth and digestive systems.

- Except for joints for the jaw and between middle ear bones, mammalian skulls are akinetic.

- Mammalian limbs are generally beneath the body rather than splayed laterally.

Goals for this lab

- Understand mammalian synapomorphies.

- Learn about mammalian organ systems and study skin derivatives including mammary glands, hair, teeth, horns, and antlers.

Station 1. Phylogenetic context

Mammals belong to Synapsida (Figure 8-1) and have a single temporal fenestra (Figure 5-4).

Synapomorphies of Mammalia

- ***Cusps of molar teeth*** *— form a triangle.*

- ***Jaw joint*** *– is between dentary and squamosal.*

- ***Incus*** *and* ***malleus*** *— together with stapes, these form three middle ear ossicles.*

- ***Secondary palate*** *— allows breathing while chewing.*

- ***Hair*** *— many functions.*

- ***Mammary glands*** *— secrete milk.*

- ***Red blood cells lack nuclei*** *— the nucleus is extruded from the cell as it matures.*

- ***Four-chambered heart*** *— convergently similar to four-chambered heart of birds.*

- ***Muscular diaphragm*** *— used in ventilating lungs.*

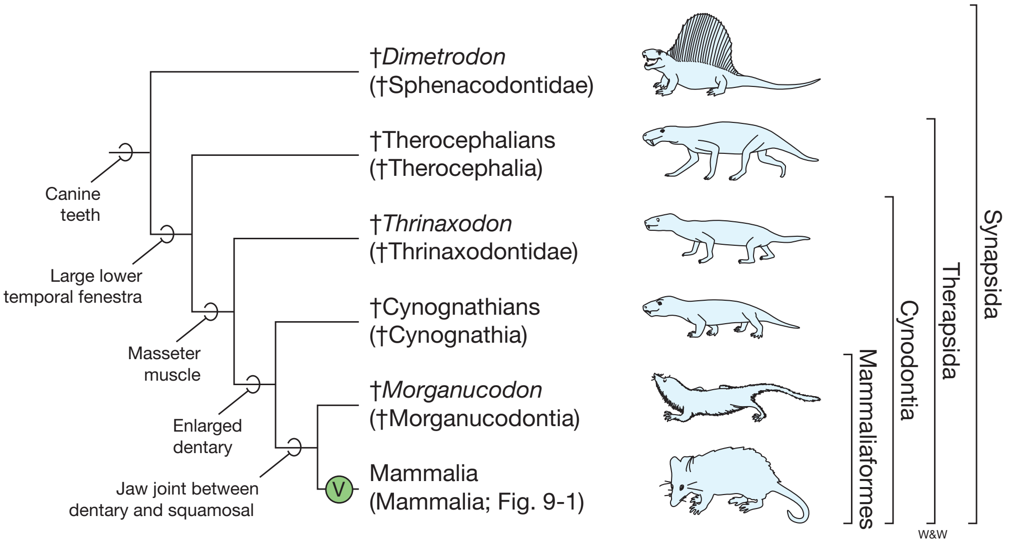
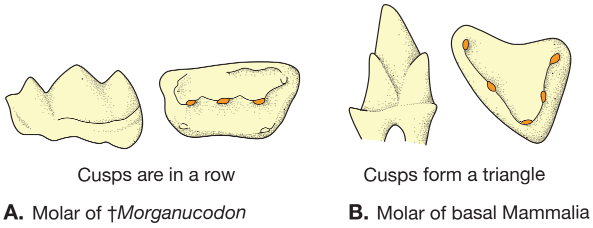


Figure 8-1
Phylogenetic context for Mammalia. Green node V corresponds to Figure 2-1.

Figure 8-2
Teeth of a crocodile are similar shaped and have only one cusp.



Cusps are in a row

A. Molar of †*Morganucodon*

Cusps form a triangle

B. Molar of basal Mammalia

Figure 8-3
Mammaliaform and mammalian molars.

Mammalian teeth, jaws, and jaw muscles

Many of the most important evolutionary specializations of mammals relate to changes in the teeth, skull, lower jaw, and jaw muscles. For example, the tree in Figure 8-1 indicates the acquisition of several key anatomical features during the evolution of Synapsida. These include the evolution of **canine teeth**, **enlargement of the lower temporal fenestra**, differentiation of the **masseter muscle**, **enlargement of the dentary**, and the evolution of the **dentary–squamosal jaw joint**. These changes have allowed mammals to eat and chew a great variety of foods, and many of the great radiations within Mammalia relate to them. Changes in the jaw joint allowed the evolution of a new pathway for sound vibrations to travel from the tympanum to the inner ear.

Teeth – To understand these changes, start with the teeth and study a reptile such as a crocodile (Figure 8-2). Note that it has similarly shaped teeth. We describe such dentitions as **homodont** even though the teeth can be of different sizes. A crocodile's teeth are **unicuspid**, meaning that there is a single point or **cusp** at the tip of each tooth. Mammalian teeth, in contrast, vary both in tooth shape and the number of cusps.

Molar teeth of fossil Mammaliaformes such as †*Morganucodon* (Figure 8-1) have three cusps in a row (Figure 8-3A). In contrast, molar cusps of Mammalia are arranged as a triangle (Figure 8-3B). The triangles of the upper and lower molars point in opposite directions, so that when they occlude they can shear food between them. In upper molars, the apex of the triangle points lingually (= toward the tongue); in lower molars, it points labially (= toward the lips). Because of this, we refer to mammals as having a **reversed triangular pattern of occlusion**.

Mammalian teeth are also **heterodont** in reference to differently shaped teeth along the length of the jaw. In a typical mammal, the dentition includes **incisor**, **canine**, **premolar**, and **molar teeth** (Figure 8-4). Incisor teeth are rooted in the premaxilla. Upper canine, premolar, and molar teeth are rooted in the maxilla. All teeth in the lower jaw are rooted in the den-

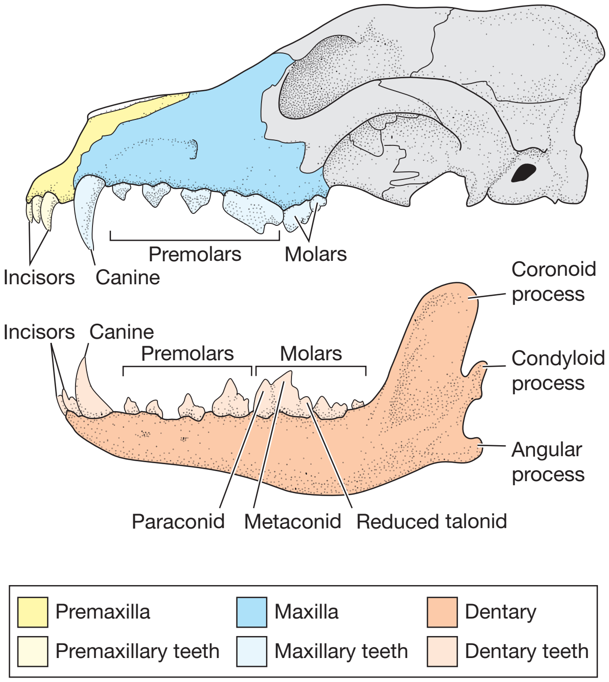
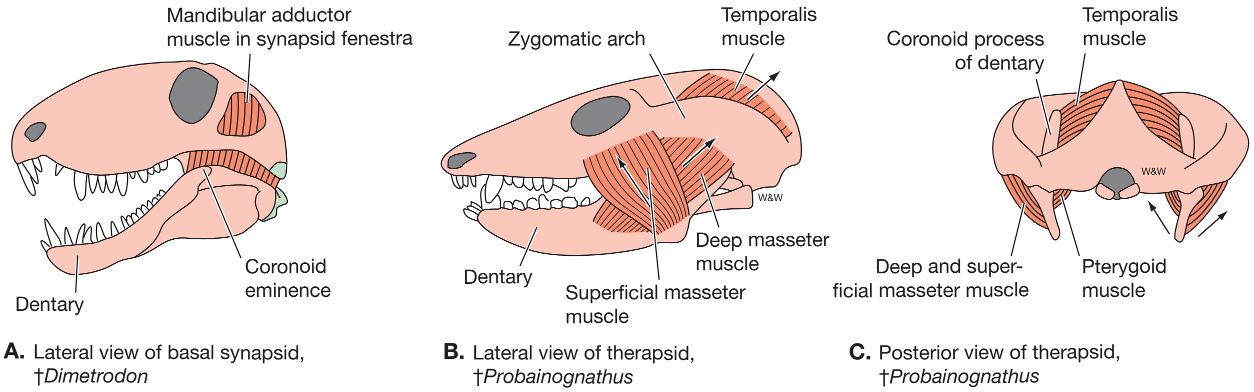


Figure 8-4
Dentition of a dog, *Canis*.



A. Lateral view of basal synapsid, †*Dimetrodon*

B. Lateral view of therapsid, †*Probainognathus*

C. Posterior view of therapsid, †*Probainognathus*

Figure 8-5
Evolution of jaw-closing muscles.

tary, which is the only bone in the lower jaw of mammals. Incisors have one root and function in clipping relatively soft food. Canines have 1 root, and function in puncturing and holding prey. Premolars can have 1, 2, or 3 roots, and typically function in grinding. Upper molars have three roots but lower molars have two roots; they function together in grinding.

Identify the different types of teeth in the skulls at this station. Some taxa, such as rodents, lack canines, leaving a wide gap, or **diastema**, between the incisors and the premolars. The premolars and molars can be difficult to distinguish in adults, and are sometimes referred to collectively as **cheek teeth**.

Diversity in the shapes of mammalian teeth, a topic taken up in more detail later in this laboratory, relates to their roles in mechanically breaking down food into smaller pieces by chewing or **mastication**. Unlike most non-mammalian tetrapods, which swallow food whole or in large chunks, mammals rely on **shearing**, **grinding**, and **crushing** to break food into smaller pieces that can be more easily digested. To place food between the teeth so that it can be chewed, mammals evolved a **highly mobile, muscular tongue**.

Jaw closing muscles – The jaw closing muscles of mammals are more differentiated than those of reptiles and basal synapsids, such as †*Dimetrodon* (Figures 8-1, 8-5A). The large **mandibular adductor muscle** of †*Dimetrodon* originates on the skull and inserts on the **coronoid eminence** of the lower jaw. Its fibers run in one direction, and act to pull the lower jaw up and slightly back.

The jaw closing muscles are more differentiated in derived synapsids such as †T*hrinaxodon* (Figure 8-1) or *†Probainognathus*. (Figure 8-5B,C). The mandibular adductor now has several discrete parts. These are the **temporalis muscle**, which inserts on the c**oronoid process of the dentary** and performs the same function as the old mandibular adductor muscle of pulling the lower jaw up and back (Figure 8-5B, C). The **superficial masseter muscle** originates on the **zygomatic arch** ventral to the eye and inserts on the lower jaw at the **angular process** (Figures 8-4, 8-5B). It functions to pull the lower jaw up and forward creating a forward grinding stroke for the upper and lower molar teeth. The **deep masseter muscle** originates more posteriorly on the zygomatic arch, and its fibers insert anteriorly on the lower jaw (Figure 8-5B). It acts to pull the lower jaw posteriorly to create a backward grinding stroke for the molar teeth. The final set of jaw closing muscles, the **pterygoid muscles**, originate on the pterygoid bones and attach to the inner surface of the jaw; they act to pull the jaw inwards, and are counteracted by the outward pull of the deep and superficial masseter muscles (Figure 8-5C).

These changes in jaw closing muscles are important for two reasons. First, they facilitate

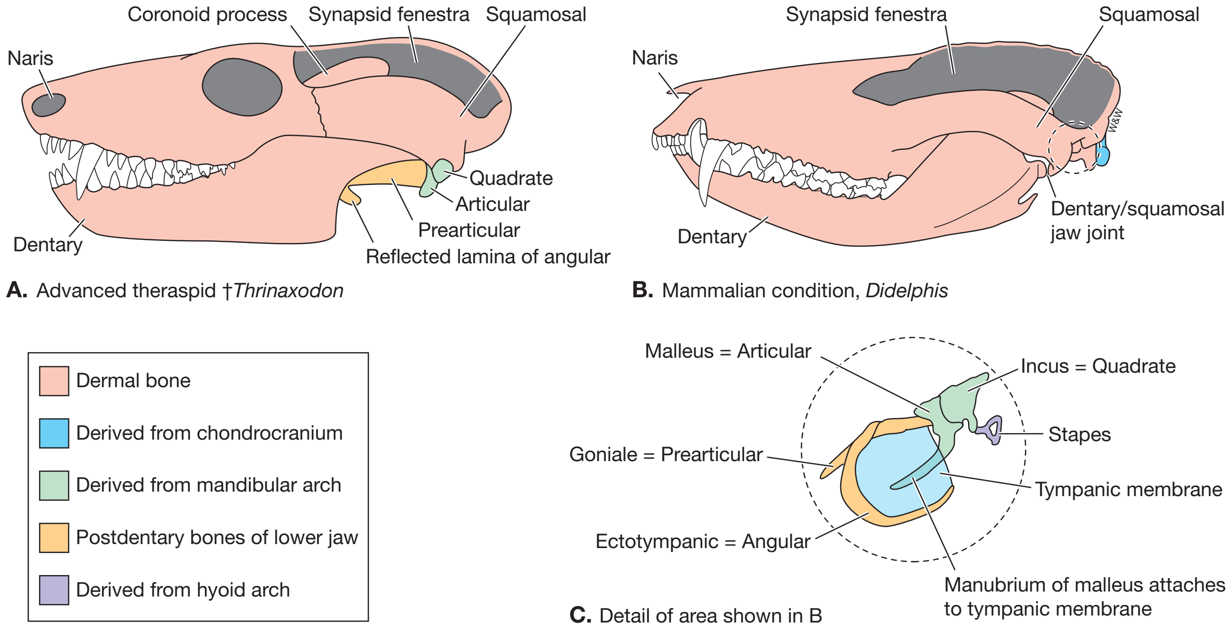


Figure 8-6
Evolution of mammalian jaw joint and middle ear bones.

food processing by molar teeth, which in turn allowed further evolutionary changes in the structure of molar teeth. Second, the new arrangement of jaw muscles provided a muscular "sling" for the lower jaw, which reduced forces on the jaw joint. This change resulted in enlargement of the dentary bone and its coronoid process and reductions in the sizes of the postdentary bones in the lower jaw (Figure 8-1). The changes ultimately resulted in the evolutionary replacement of the old articular–quadrate jaw joint with the dentary–squamosal jaw joint that characterizes mammals.

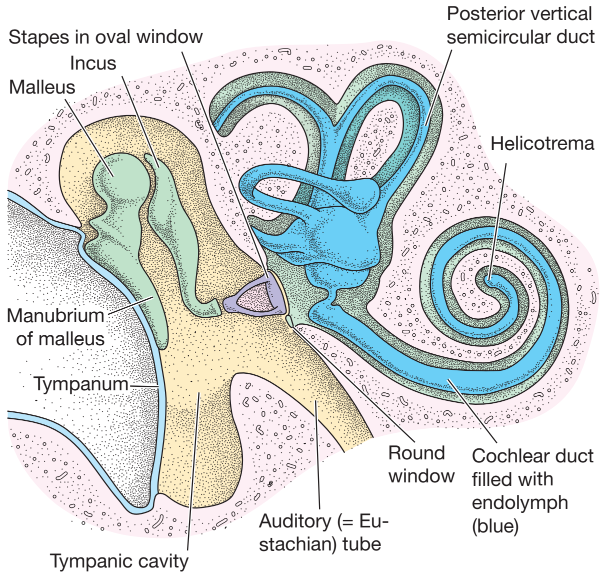
Middle ear ossicles and hearing

The evolution of the mammalian middle ear ossicles is documented by a series of fossil therapsids (see synapomorphies in Figures 8-1).

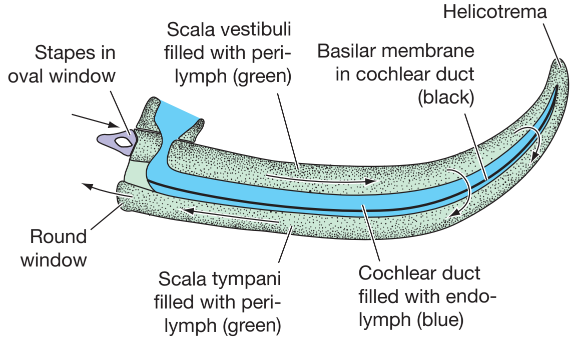
If you examine the skulls of a non-mammalian amniote such as *Sphenodon* (Figure 5-8A), then you will see that there several bones in the lower jaw including the **articular bone**. The articular bone meets with the **quadrate bone** to

Table 8-1. Homologies of mammalian middle ear ossicles, Malleus, Incus and Stapes.

Visceral Arch	**Elasmobranchii** (Figure 2-3, 2-11)	**Actinopterygii** (Figure 3-14)	**Lissamphibia** (Figure 4-6)	**Reptilia** (Figure 5-9)	**Mammalia** (Figure 8-6)
Mandibular arch: lower jaw	Mandibular cartilage	Articular	Articular	Articular	Malleus
Mandibular arch: upper jaw	Palatoquadrate cartilage	Quadrate	Quadrate	Quadrate	Incus
Hyoid arch	Hyomandibula	Hyomandibula	Columella	Columella	Stapes



A. Human ear in schematic section



B. Schematic diagram of fluid flow in the cochlea

Figure 8-7
Anatomy of human ear.

form the jaw joint.

Forms such as †*Thrinaxodon* (Figure 8-1, 8-6A) retain this ancestral jaw joint between the quadrate and articular bones. They also retain several **postdentary bones** including the **prearticular** and **angular** (Figure 8-6A).

In mammals, such as an opossum (Figure 8-6B), however, the lower jaw consists entirely of the **dentary** and it articulates with the **squamosal bone**. But what happened to the bones of the old jaw joint as well as the postdentary bones?

Here, development offers some clues because, during early development of *Didelphis*, you can observe the quadrate and articular transition from contact with the lower jaw joint to their adult location as **middle ear ossicles** posterior and dorsal to the dentary–squamosal jaw joint (Figure 8-6B,C). The articular and quadrate elements of other gnathostomes are homologous with the mammalian **malleus** and **incus**, respectively (Table 8-1). As in other tetrapods, the **stapes** is derived from the hyomandibula (Figure 2-3, Table 8-1), and together these three bones transmit vibrations from the tympanum to the inner ear (Figure 8-7).

Now consider how the three middle ear ossicles function to transmit sound from the tympanum to the inner ear (Figure 8-7). The ossicles are contained within the **tympanic cavity**, which is continuous with the **auditory** or **eustachian tube** extending to the posterior corner of the oral cavity. By means of this connection, air pressure within the tympanic cavity is equalized with air pressure surrounding the animal's head, which is essential for detecting the tiny displacements of the tympanic membrane needed for hearing.

The malleus (L., = hammer) has a long process called the **manubrium** that attaches to the inner surface of the tympanic membrane (Figures 8-6C, 8-7A). Vibrations of the malleus are transferred to the incus (L., = anvil) via a joint that is homologous to the jaw joint in forms such as †*Thrinaxodon* (Figures 8-6A, C; 8-7A). The incus in turn transfers vibrations to the stirrup-shaped stapes (L., = stirrup; Figures 8-6C, 8-7A). As in non-mammalian tetrapods, the footplate of the stapes lies in the **oval window** (Figure 8-7), where it transfers mechanical motion of the middle ear ossicles to the **perilymph** in the inner ear (Figure 8-7A; perilymph is indicated by light green).

The **cochlear duct** (L., cochlea = snail shell) and **semicircular ducts** of the inner ear are filled with fluid **endolymph** (Figure 8-7A; endolymph indicated in blue).Vibrations in the perilymph travel down the length of the **scala vestibuli** toward the tip of cochlea, or **helicotrema** (Figure 8-7) and are transferred to the endolymph in the **cochlear duct**, where they are

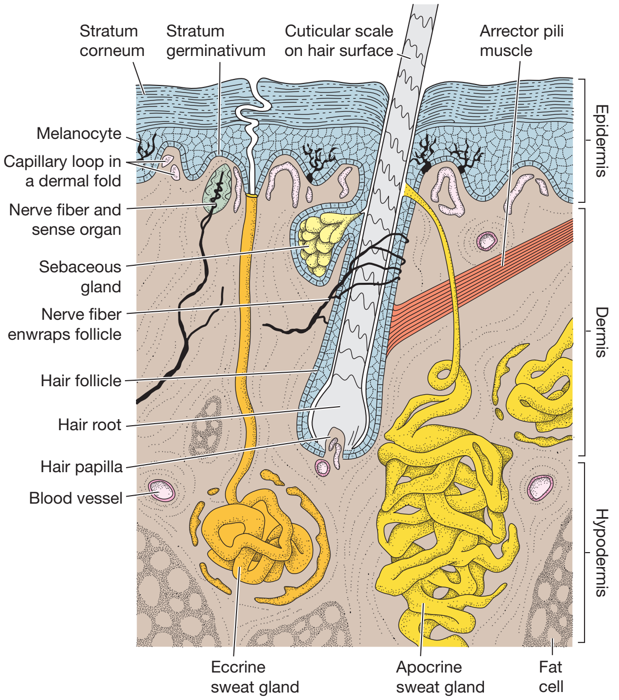


Figure 8-8
Idealized section through human skin.

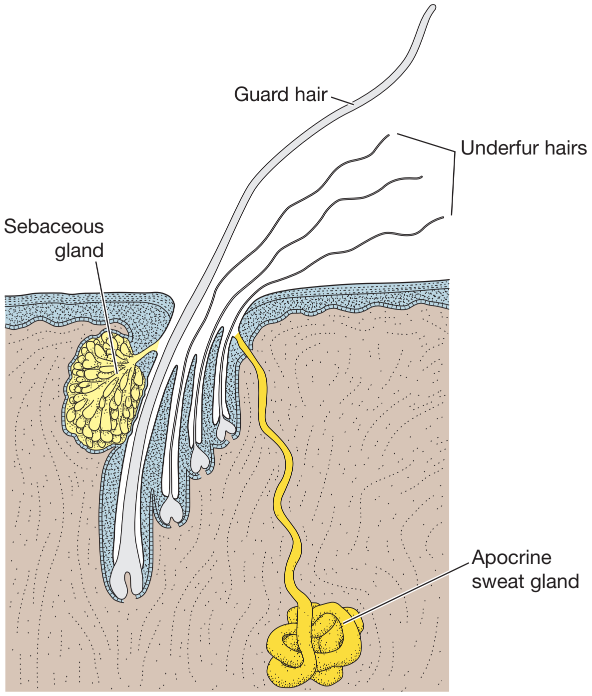


Figure 8-9
Pilosebaceous unit of a fur seal.

detected by hair cells on the **basilar membrane** (Figure 8-7B). Waves of pressure in the perilymph travel via the **scala tympani** to end in a membrane spanning the **round window**. The membrane bulges into the tympanic cavity as needed to dissipate pressure in the perilymph.

External ears, or **pinnae**, function to collect and carry sound waves to the middle ear. Mammals such as horses, rabbits, or wolves can rotate their pinnae to determine directionality of sounds. Study the model of a human ear to identify the pinna and three middle ear bones.

Mammalian skin and mammary glands

As a tissue, mammalian skin can have an array of glands, specialized sense organs and free nerve endings, pigments cells, muscles and hairs (Figure 8-8). The **epidermis** consists of two layers. Its deeper layer, or **stratum germinativum**, contains living cells that divide to generate new epidermal cells. The superficial layer, or **stratum corneum**, consists of cells that progressively fill with α-keratin, eventually die, and are sloughed off at the surface of the skin.

Unlike reptiles, mammals have an array of skin glands. **Eccrine sweat glands** are located in the dermis and open at the skin's surface (Figure 8-8). They function in thermoregulation by secreting a dilute fluid that evaporates and cools the skin. Two types of glands are associated with hair follicles. **Apocrine sweat glands** are larger than eccrine glands and secrete an odorless, waxy secretion into hair follicles. Bacterial breakdown of the secretion results in odoriferous molecules. All hair follicles have **sebaceous glands** that secrete a waxy material known as **sebum** to lubricate hairs.

The distribution of skin glands varies over the body surface, and different groups of mammals have characteristic distributions of the glands. For example, eccrine glands are widely distributed in human skin, but dogs only have eccrine glands in areas of the body not covered with fur, such as the nose and paws.

Beneath the dermis is the **hypodermis**, which in mammals includes many fat cells (Figure 8-8). The thickness of hypodermis varies in different groups of mammals. For example,

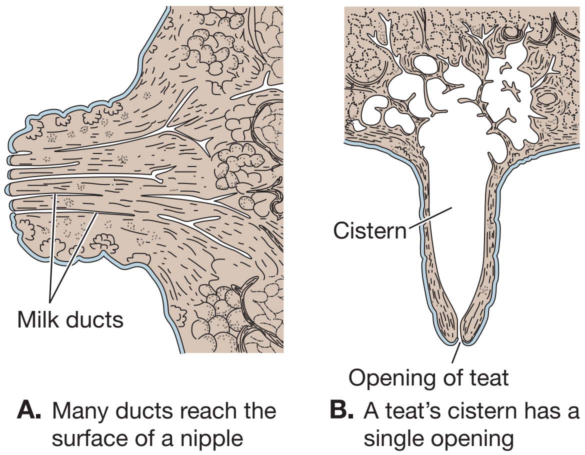


Figure 8-10
Comparison of nipples and teats.

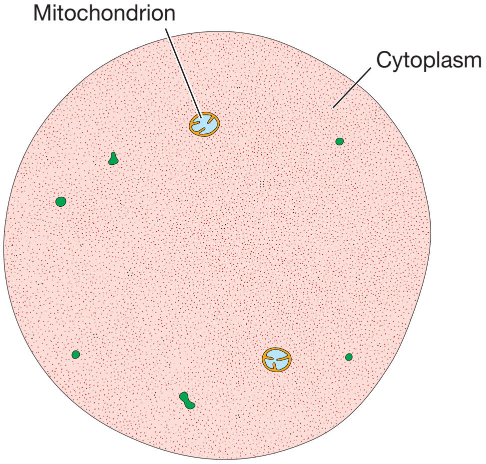


Figure 8-11
Human erythrocyte.

whales have a particularly thick hypodermis known as **blubber** that functions to reduce heat loss from the body.

Hair follicles are invaginations of the epidermis deep into the dermis (Figure 8-8). At the base of the follicle are the **hair root** and **hair papilla**, where new cells for the hair are generated. Specialized small bundles of smooth muscle form **arrector pilli muscles**, which originate higher in the dermis and insert on the hair follicle (Figure 8-8). Contractions of these involuntary, or **autonomic**, muscles cause the hair follicle and the skin around it to rise, producing goosebumps.

In many mammals, hair follicles and their hairs form large **pilosebaceous units** composed of thick **guard hairs** and thinner **underfur** (Figure 8-9). Because of their thickness, guard hairs are stiffer than underfur. Abundant sebum, from large sebaceous glands near their root, renders the hair resistant to water penetration. Color patterns in a mammal's skin are made by different coloration of guard hairs. Underfur forms a dense, soft layer that functions in thermoregulation.

In addition to its primary role in thermoregulation, mammalian **hair** functions in crypsis, disruptive patterns, and warning coloration. It serves sensory functions because the bases of individual hairs are well-innervated, particularly in specialized **whiskers**. Hair has been modified for defense in groups such as echidnas and porcupines. Examine slides to study hair from different species of mammals.

Mammalian mammary glands secrete milk during the process of **lactation** to nourish offspring. The glands consist of secretory alveoli and canals interpreted as highly modified apocrine glands. Mammals evolved different solutions to deliver milk to offspring. For example, in monotremes such as the platypus, *Ornithorhynchus anatinus*, milk is secreted directly onto the skin surface, where young can lap it up. Many groups of mammals have **nipples**, in which multiple milk ducts open onto the surface of the nipple (Figure 8-10). Artiodactyls, such

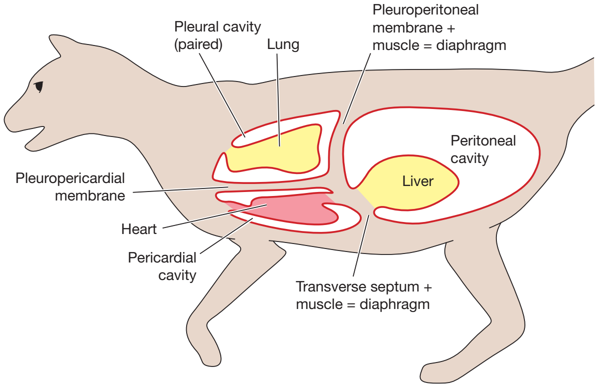


Figure 8-12
Schematic view of the three subdivisions of the coelom in a mammal such as a cat.

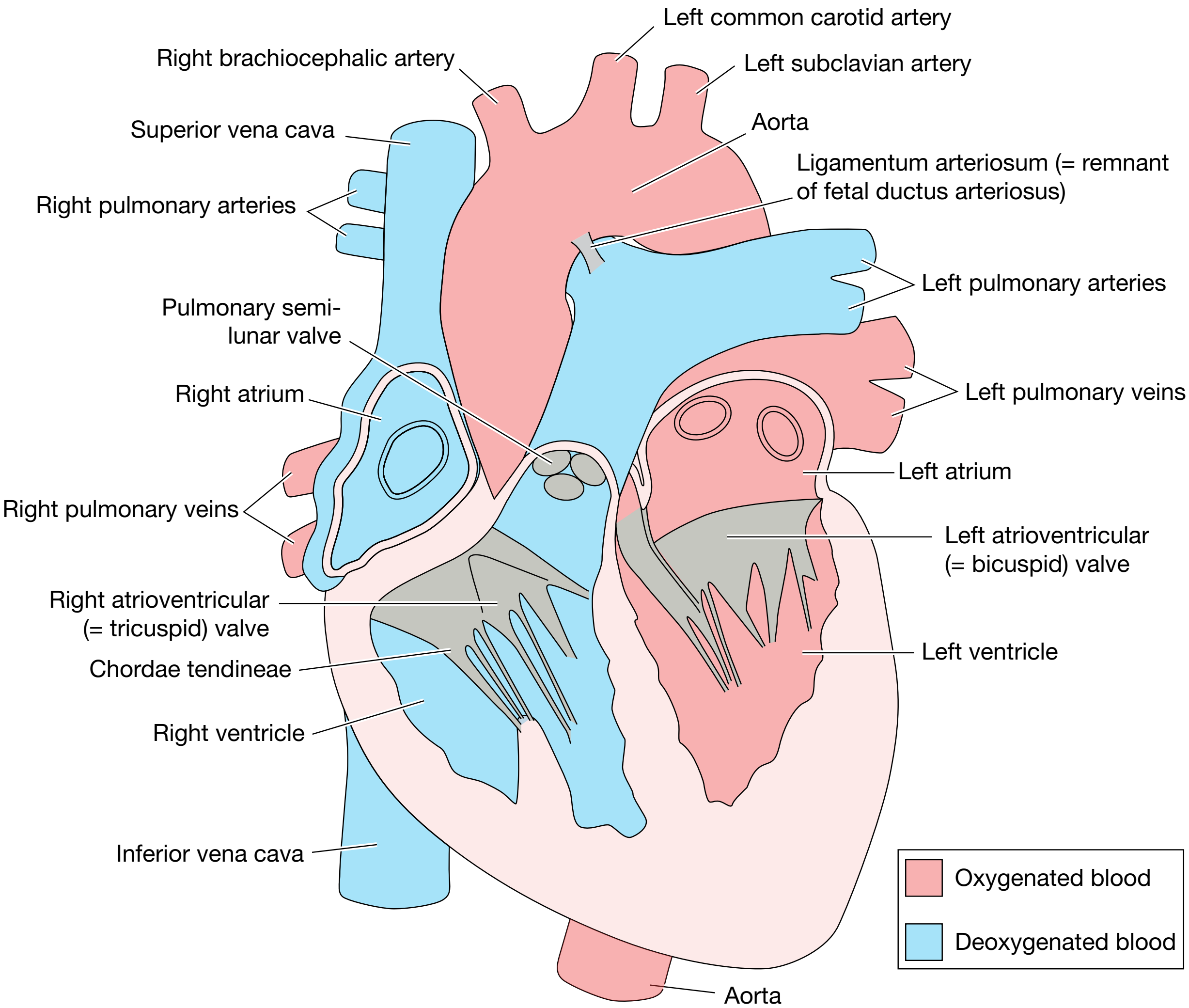


Figure 8-13
Schematic view of a human heart.

as cattle in the genus *Bos*, have **teats** in which secreted milk is stored in each teat's cistern. Examine slides of inactive and lactating mammary tissue, noting differences in the relative sizes of alveoli.

An enucleated red blood cell or **erythrocyte** of a mammal is a small, biconcave disc with a large surface area to exchange oxygen (Figure 8-11). A developing erythrocyte has a nucleus and other organelles, and can make proteins needed for hemoglobin and typical cell metabolism. The nucleus is eliminated as the cell develops, so that by the time the cell is mature, it is packed with hemoglobin. In contrast to mammals, other vertebrates have large, oval, nucleated red blood cells.

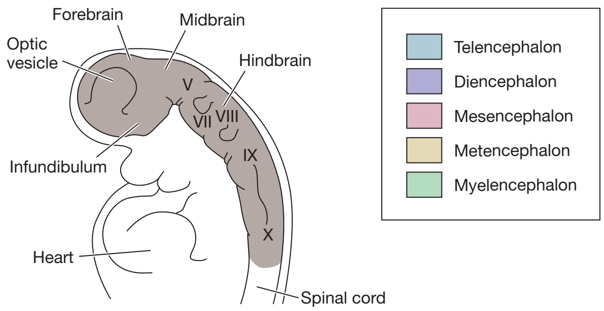
The **coelom** or body cavity of a mammal has three subdivisions (Figure 8-12). The **peritoneal cavity** contains the liver, digestive tract, spleen and other organs of the viscera. The **pericardial cavity** contains the heart, and is separated from the **peritoneal cavity** by the transverse septum. Mammalian lungs are contained within paired **pleural cavities** that are divided from the peritoneal cavity by the **pleuroperitoneal membrane**. The **diaphragm** is a muscular sheet that includes parts of the transverse septum and pleuroperitoneal membrane.

When muscles of the diaphragm contract, the pleural cavity expands, drawing air into the lungs through the trachea. Exhalation happens when the diaphragm relaxes, and the thoracic cavity decreases in size. Additional muscles of the body wall and ribs also contribute to lung ventilation, as they do in non-mammalian vertebrates that lack a diaphragm,

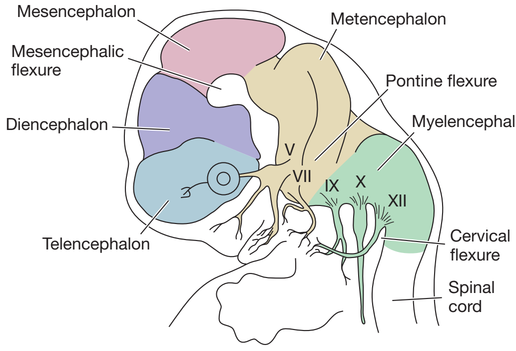
Station 2. Mammalian hearts

Examine demonstration dissections of the sheep heart (Figure 8-13). Be sure to identify the **left** and **right atria**, **left** and **right ventricles**, the **pulmonary artery**, **pulmonary veins**, the **superior vena cava**, the **inferior vena cava**, the **aorta**, and **ligamentum arteriosum**, which is a remnant of the fetal **ductus arteriosus**. ***Most vessels are better seen in freeze-dried hearts than in fluid-preserved hearts.*** For internal anatomy, study the large model of the human heart. Be sure that you can identify all of the external anatomical structures listed above as well as the following internal structures: the **tricuspid valve** (= right atrioventricular valve), **bicuspid valve** (= left atrioventricular valve), **pulmonary semilunar valve**, **aortic semilunar valve**, and **chordae tendineae**.

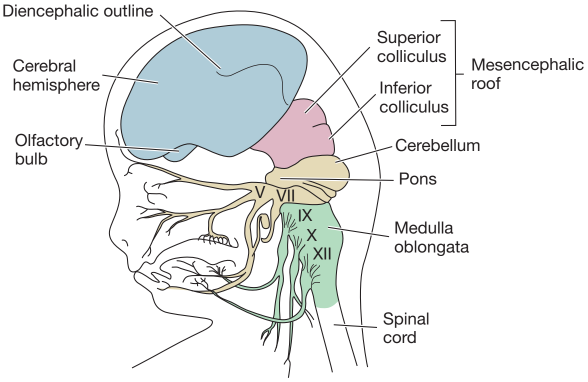
Use models to review and compare heart anatomy and function in elasmobranchs, ray-fined fishes, amphibians, reptiles, birds, and mammals. Make a table listing the number of atria and ventricles in each taxon, and be able to describe the patterns of blood flow through the major vessels and heart chambers.



A. Human brain at 3 mm long



B. Human brain and crainial nerves at 7 weeks

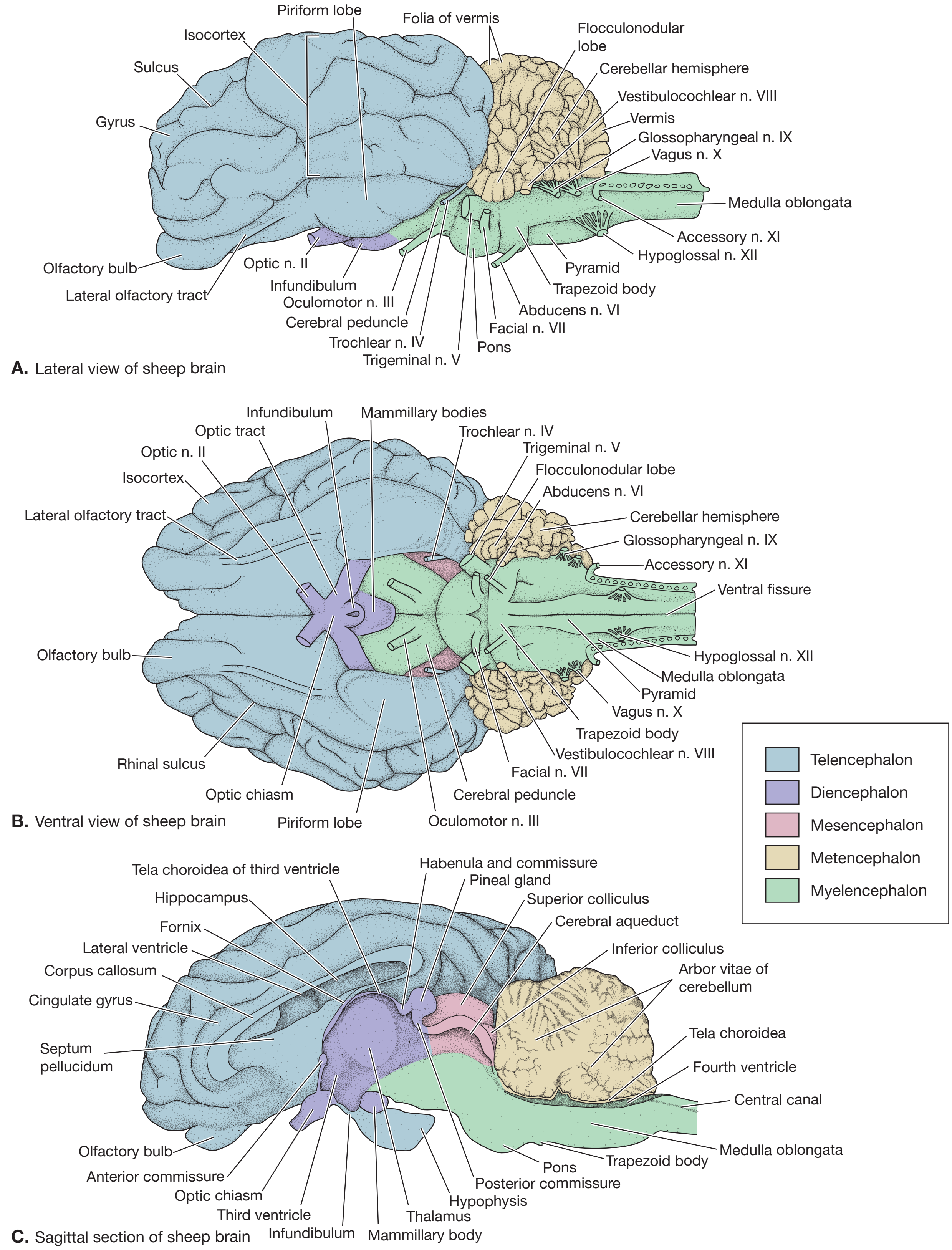


C. Human brain and cranial nerves at 3 months

Figure 8-14
Early development of the human brain, spinal cord, and cranial nerves V, VII, IX, X and XII.

Station 3. Mammalian brains

Early mammalian embryos have three primary brain regions: the **forebrain**, **midbrain**, and **hindbrain**. Notice in Figure 8-14A that these regions are arranged linearly along the neural tube. As development proceeds, the forebrain gives rise to two of the adult brain regions, which are the **telencephalon** and **diencephalon** (Figure 8-14B). The embryonic midbrain forms the **mesencephalon**, and the neural tube bends to form the **mesencephalic flexure**. The embryonic hindbrain gives rise to the **metencephalon**, and **myelencephalon** (Figure 8-14B). Still later in development, the **cerebral hemispheres** of the telencephalon enlarge to cover the diencephalon and portions of the mesencephalon (Figure 8-14C). With further development, the cerebral hemispheres will eventually cover most of the mesencephalon. For example, the cerebral hemispheres of an adult sheep brain completely



A. Lateral view of sheep brain

B. Ventral view of sheep brain

C. Sagittal section of sheep brain

Figure 8-15
Anatomy of a sheep brain.

cover the mesencephalon, obscuring it in lateral view (Figure 8-15A).

Use Figure 8-15 and demonstration dissections of the sheep brain to identify these 13 neuroanatomical structures and their general functions:

1. **Cerebrum** – large, paired hemispheres with many functions, including learning, motor control, and interpretation of sensory information.
2. **Corpus callosum** – connects right and left cerebral hemispheres to integrate information from each.
3. **Optic chiasm** – crossing of the optic nerves that directs visual information to both sides of brain from each eye, enabling stereoscopic vision.
4. **Pineal organ** – secretes melatonin, helping to regulate biological clock.
5. **Olfactory bulbs** – receive and process input from olfactory nerves.
6. **Superior colliculi** – homologue of optic lobe of outgroups that functions in spatial interpretation of visual information.
7. **Inferior colliculi** – processing of auditory information.
8. **Cerebellum** – controls motor coordination and equilibrium.
9. **Medulla oblongata** – controls autonomic functions such as respiration and heart rate.
10. **Gyri** – convex ridges in cerebrum and cerebellum.
11. **Sulci** – concave grooves in cerebrum and cerebellum.
12. **Spinal cord** – confluent with medulla oblongata; has a central canal through which cerebrospinal fluid flows.
13. **Dura mater** – tough, outermost meninge that covers the brain and spinal cord.

Use Figure 8-16 and models of vertebrate brains to compare the relative sizes and structures of the major parts of the brain in different vertebrates. One general pattern that we see is an increase in brain size relative to body size; more specifically, the brains of birds and mammals are about 15 times larger than those of other vertebrates of similar body size. The table sheet at the station shows variation in brain structure *within* mammals.

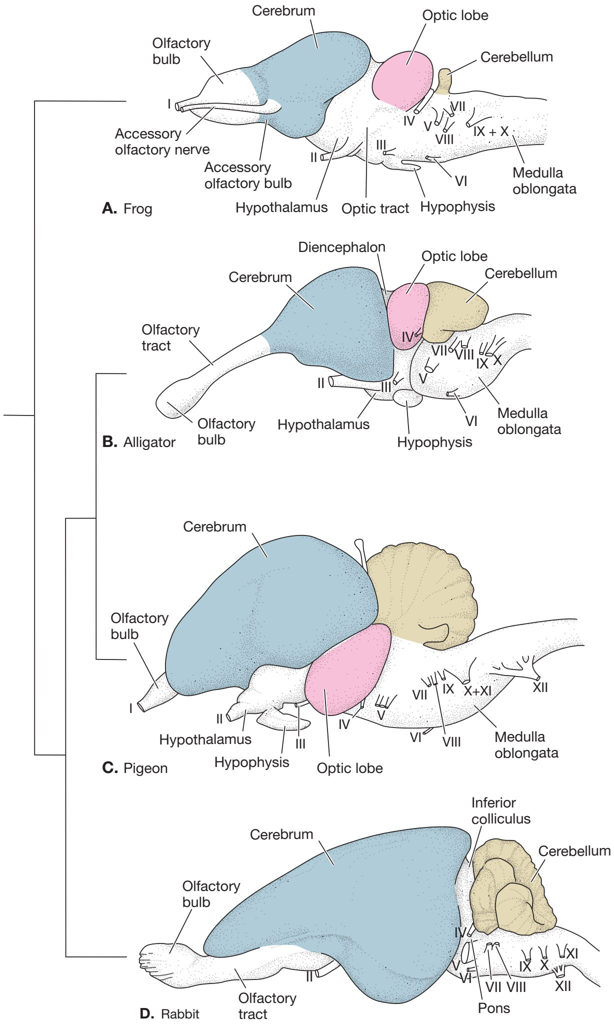


Figure 8-16
Brain evolution of tetrapods, emphasizing changes in the cerebrum, optic lobes, and cerebellum. Roots of cranial nerve are also indicated.

Station 4: Digestive system

A generalized mammalian gastrointestinal tract includes the esophagus, stomach, small intestine, caecum, and large intestine. We briefly examine these structures and their functions before turning to variation in mammalian gastrointestinal tracts.

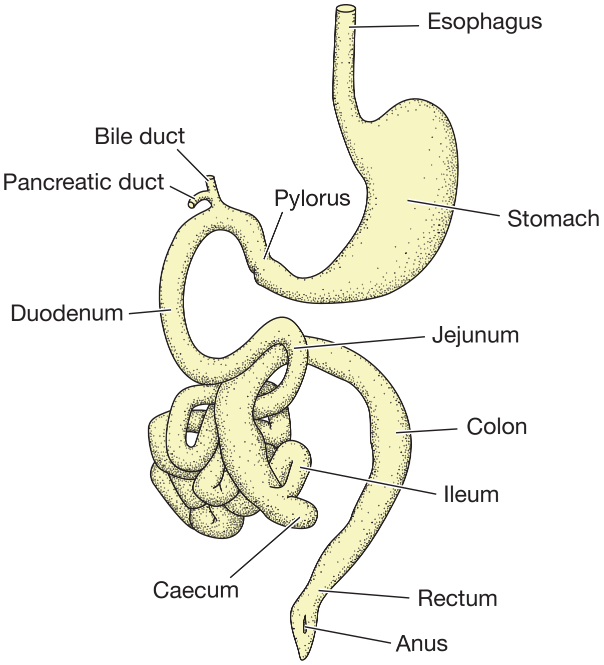


Figure 8-17
Gastrointestinal tract of a cat.

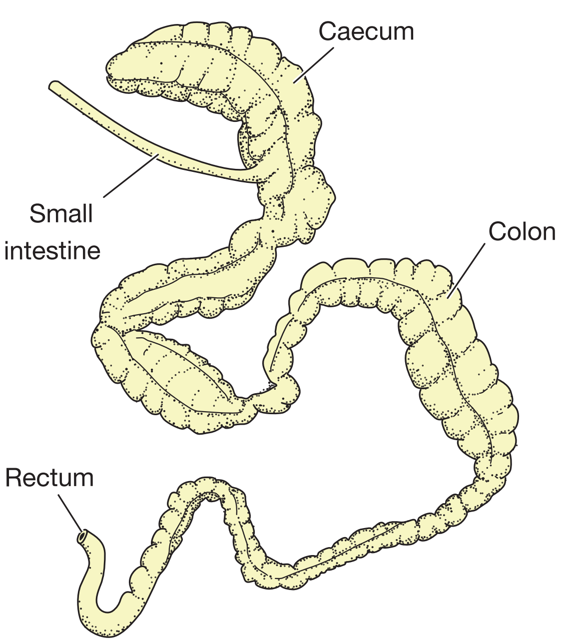


Figure 8-18
Caecum and colon of a zebra.

Once food has been mechanically broken down in the mouth by mastication (= chewing), it passes down the muscular **esophagus** to enter the **stomach** (Figure 8-17). The stomach is the primary food storage organ of mammals, and it typically has elastic, muscular walls. Protein breakdown in the stomach occurs in an acidic environment, which is necessary for the function of the stomach enzyme **pepsin**. The **pylorus** has a valve that allows food to pass into the **small intestine**.

More enzymatic digestion occurs in the relatively basic environment of the **small intestine**. Its first portion, the **duodenum**, receives the **pancreatic duct**, which delivers the enzyme **trypsin** made by the pancreas, and the **bile duct**, which delivers **bile** from the liver (Figure 8-17). Bile emulsifies fats. The small intestine continues as the **jejunum** and **ileum**. The small intestine is typically the longest region of the gastrointestinal tract, and most nutrient absorption takes place there. It may have a blind sac or **caecum** at its junction with the large intestines, which functions in water and electrolyte absorption. The **large intestine** or **colon** also functions in absorption of water and electrolytes; feces are formed before the tract ends at the **rectum**. In some mammals, such as rabbits and other hindgut fermenters, the caecum and large intestine are packed with microorganisms that ferment cellulose; nutrients are absorbed in both locations.

Not all structures mentioned above occur in all mammals, and their shapes and relative sizes can vary markedly. A first distinction is between carnivores and herbivores. Mammals that eat meat, such as a cat (Figure 8-17) or mink have relatively simple gastrointestinal tracts. The stomach is little more than a muscular sac, which empties into a relatively short intestine. The caecum is either very small or missing. This simplicity is possible because of the high nutritional value and relative digestibility of the food. Long and complex intestines are unnecessary to extract adequate nutrition from each meal.

Examine the gastrointestinal tract of the mink. Note its small stomach and short intestines. Can you find the caecum or distinguish between small and large intestines?

In contrast to carnivores, herbivores have

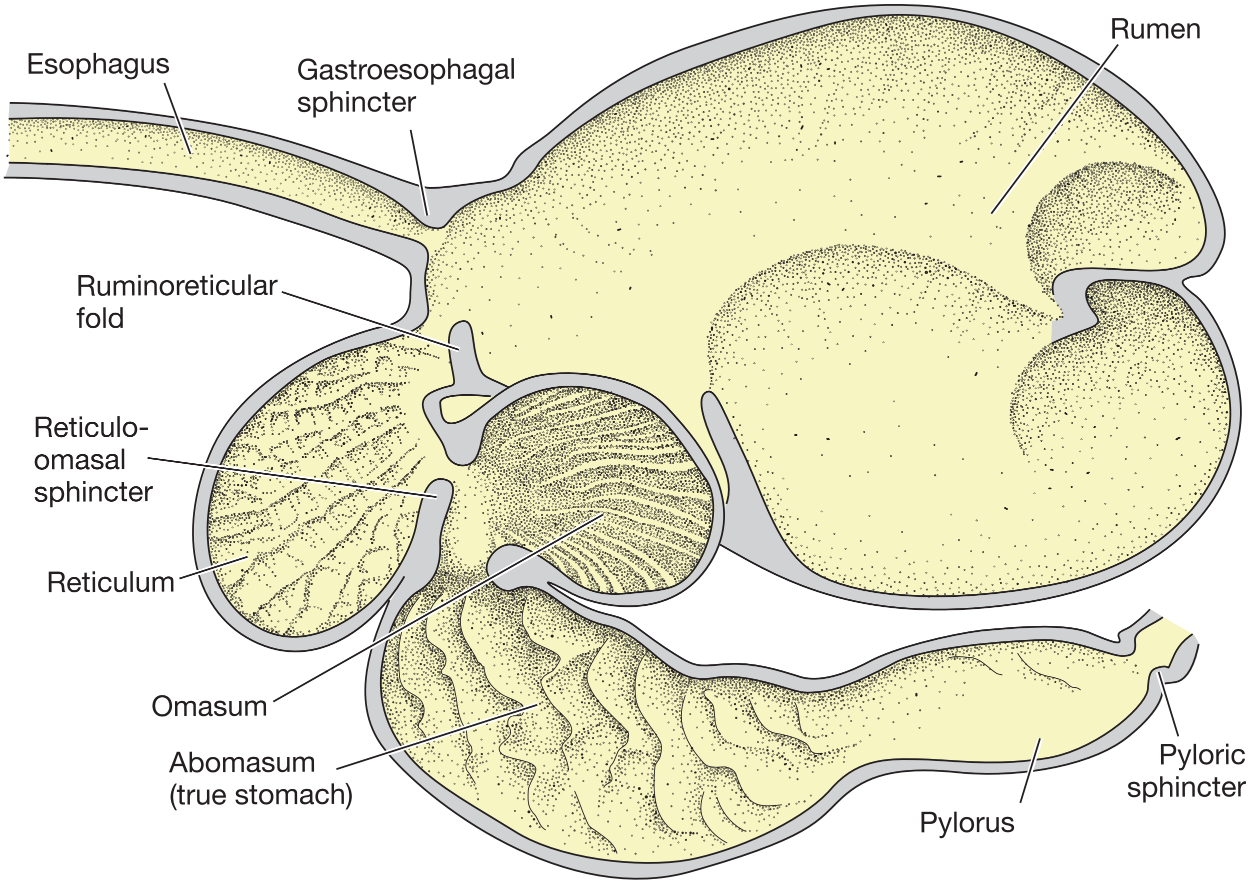


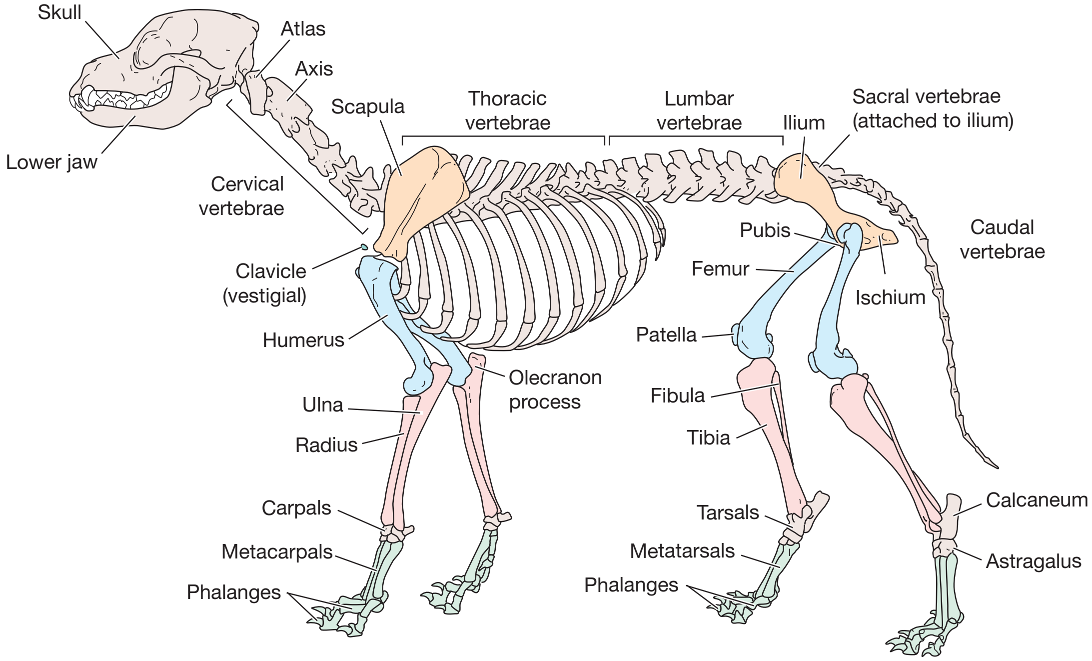
Figure 8-19
Four chambers of a cow stomach, a ruminant.

long, convoluted guts because their food is relatively nutrient poor and difficult to break down. We distinguish hindgut and foregut fermenters. **Hindgut fermenters** such as zebras (Figure 8-18) pass vegetation through the stomach and small intestine into the enormous, sacculated caecum and colon, where bacterial fermentation and nutrient absorption occur. Similar hindgut specializations are found in elephants, rabbits, and some rodents.

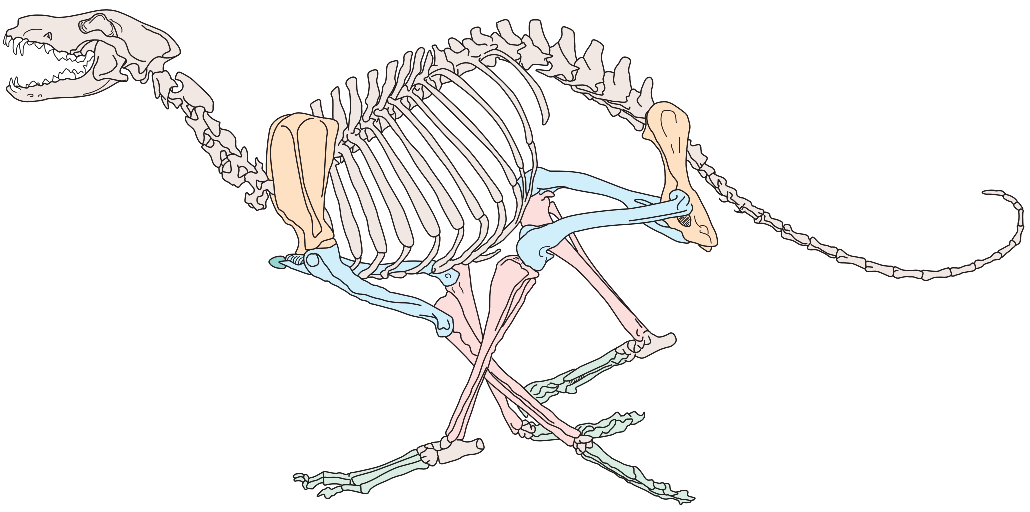
Foregut fermenters such as cows have a more efficient digestive system because plant material is broken down in the stomach before reaching absorptive surfaces of the small intestine. This is accomplished in multi-chambered stomachs (Figure 8-19), the various chambers serving different functions. We refer to such animals as **ruminants**, meaning that they regurgitate and chew partially digested material, termed **cud**, as part of the digestive process.

In a cow, the esophagus enters the large **four-chambered stomach** between two of the chambers, the larger **rumen** and smaller **reticulum** (Figure 8-19). Coarsely chewed vegetation is first shunted into the rumen, where bacterial fermentation begins. Fermented material then passes to the reticulum, where it is packed into cud and sent back up the esophagus for rumination. After adequate fermentation and rumination, smaller particles of food continue into the third chamber, the **omasum**, which is lined with long folds. Water is reabsorbed here before the food finally enters the **abomasum**, where regular acid and pepsin digestion takes place (as in a human stomach).

The length of the intestine, size and shape of the stomach, and size and shape of the caecum vary markedly across mammalian species.



A. Skeleton of a dog, *Canis*, in standing posture



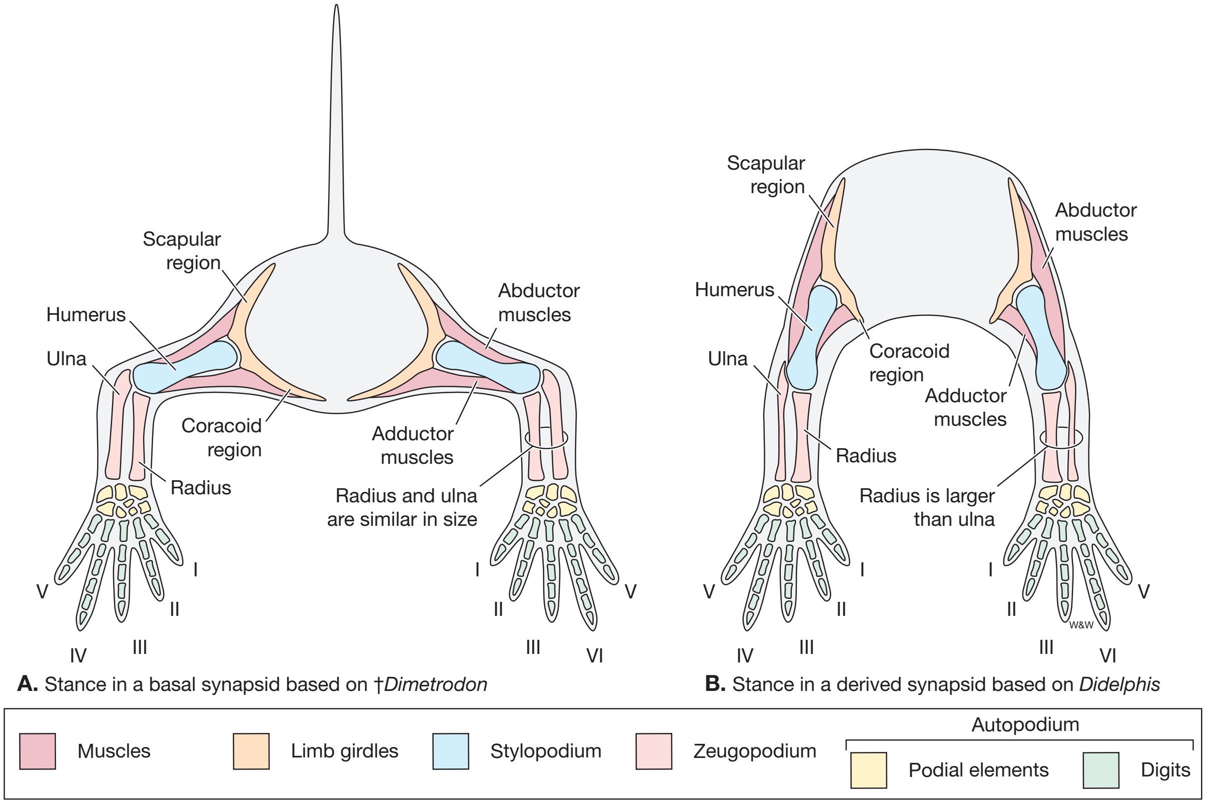
B. Skeleton of a dog, *Canis*, in flight stage of a full gallop

☐ Axial skeleton ☐ Limb girdles ☐ Stylopodium ☐ Zeugopodium
Autopodium: ☐ Podial elements ☐ Digits

Figure 8-20
Skeleton of a dog.

One generality is that species feeding at lower trophic levels (e.g., herbivores) have longer intestines and larger caecae than those that feed at higher trophic levels (e.g., carnivores). Study the table sheet showing variation in mammalian digestive tracts in relation to diet.

Compare the gastrointestinal tracts of the mink, a carnivore, and a rabbit, a herbivore. Identify the stomach, small intestine, and large intestine of each. Note that a caecum is present



A. Stance in a basal synapsid based on †*Dimetrodon*

B. Stance in a derived synapsid based on *Didelphis*

Figure 8-21
Comparison of stance in basal synapsids and therian mammals.

in the rabbit but not in the mink. Rabbits are hindgut fermenters; although their stomachs are large, they are not multi-chambered. Study the model of the cow stomach, a foregut fermenter, and note how the four chambers differ.

Station 5: Skeletal anatomy

Examine the articulated cat or dog skeleton at this station. Use the figure of a dog skeleton in Figure 8-20 to identify these post-cranial bones.

Axial skeleton – vertebrae

1. Atlas vertebra
2. Axis vertebra
3. Cervical vertebrae
4. Thoracic vertebrae
5. Lumbar vertebrae
6. Sacral vertebrae
7. Caudal vertebrae

Appendicular skeleton – pectoral limb

8. Scapula
9. Clavicle
10. Humerus
11. Radius
12. Ulna
13. Carpals
14. Metacarpals
15. Phalanges

Appendicular skeleton – pelvic limb

16. Ilium
17. Ischium
18. Pubis
19. Femur
20. Tibia
21. Fibula
22. Tarsals
    - Calcaneum
    - Astragalus
23. Metatarsals
24. Phalanges

The limbs of early synapsids **splayed out** laterally (Figure 8-21A). In therian mammals, the limbs are **rotated beneath the body**, per-

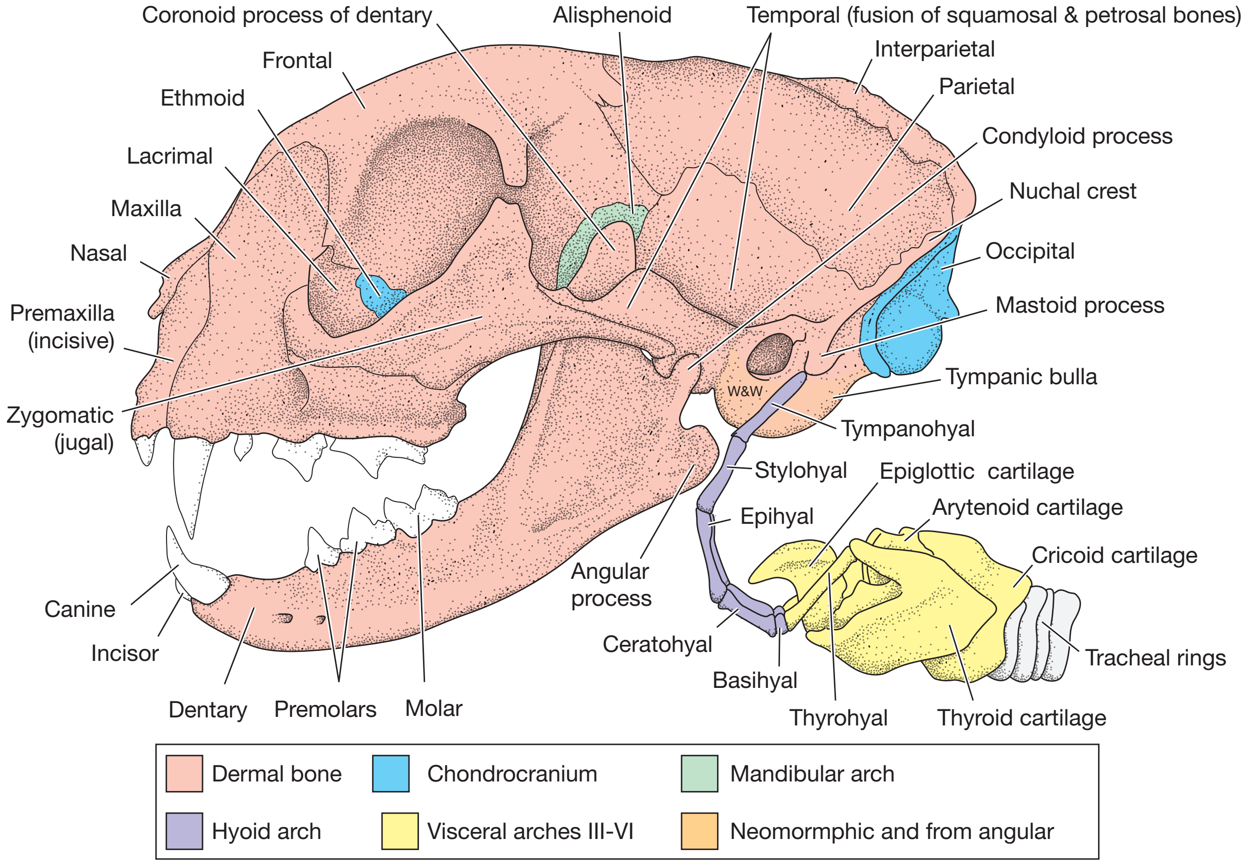


Figure 8-22
Lateral view of skull, lower jaw, hyoid apparatus and larynx of cat, *Felis catus*.

mitting more efficient locomotion (Figure 8-21B). Examine other skeletons at this station to compare limb position in an alligator, platypus, and cat.

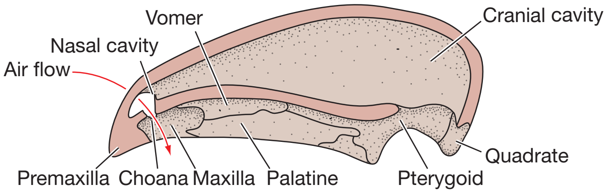
Examine the skull and lower jaw of a cat. Using the labeled diagram in Figure 8-22, identify these bones and processes:

1. Dentary
2. Condyloid process
3. Coronoid process
4. Angular process
5. Maxilla
6. Premaxilla
7. Nasals
8. Frontals
9. Parietals
10. Occipitals
11. Squamosal
12. Zygomatic (= jugal)

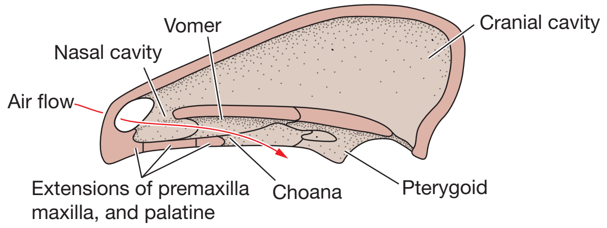
Note that a cat skull is **akinetic**, having no intrinsic joints other than the jaw joint and those between the bones of the middle ear. Also examine a human skull. How does cranial kinesis of mammals compare with that of snakes and birds?

Mammals have a **secondary palate**. Excellent fossils allow us to trace palatal evolution from basal synapsids such as †*Dimetrodon* to therapsids and mammals (Figure 8-23). The secondary palate allows young mammals to suckle and breathe at the same time. It also allows adult mammals to chew and breathe at the same time.

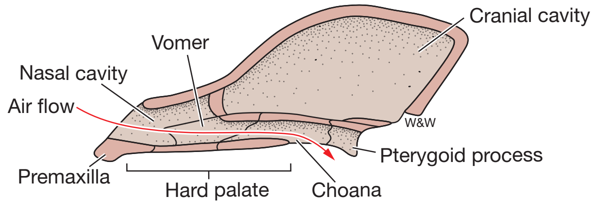
Recall that mammals are synapsids; they have one opening in the temporal region (Figure 5-4C). This opening is best seen in the cast of the skull of †*Dimetrodon*, a basal synapsid; you



A. Sagittal view of synapsid skull, based on †*Dimetrodon*



B. Sagittal view of therapsid skull, based on †*Probainognathus*



C. Sagittal view of mammal skull, based on *Canis*

Figure 8-23
Evolution of secondary palate of synapsids.

should also confirm this by studying the skull of a Virginia Opossum, *Didelphis virginiana*.

Examine occipital condyles on a cat skull, and compare them to an alligator skull. Note that mammals have two occipital condyles whereas alligators have only one. This important innovation gives mammals an increased range of head motion, which has implications for predator avoidance, prey acquisition, and many other aspects of mammalian biology.

Station 6: More on mammalian teeth

Teeth are composed of two mineralized tissues: **enamel** and **dentine**. (Figure 8-24). There is also the soft tissue of the **pulp cavity**. The part of the tooth extending above the gum line is the **crown**, and the part below the gum line is the **root**. Examine the slide of a section through a mammalian tooth.

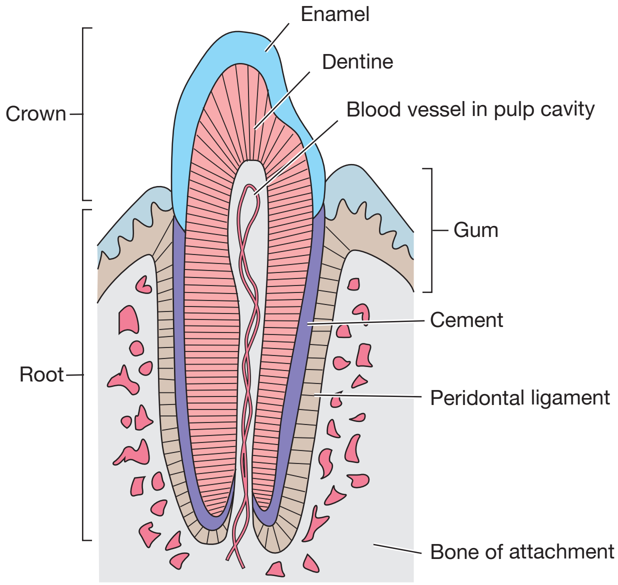
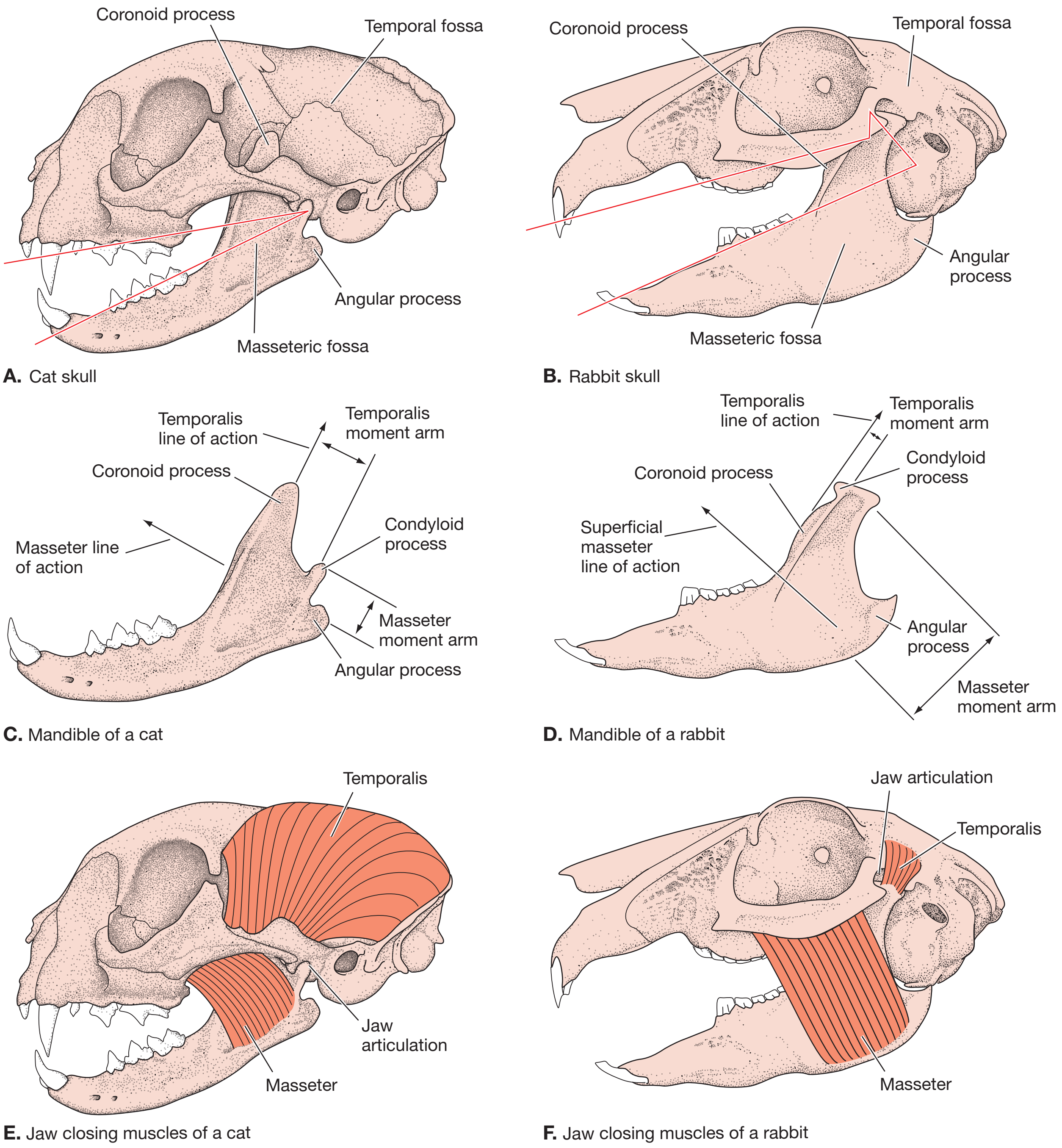


Figure 8-24
General anatomy of a mammalian tooth.

Mammalogists use **dental formulae** to characterize the number of each tooth type. Dental formulae may be written in different ways, but we will write them for one half of the jaw and use the letters I, C, P, and M to indicate tooth type. For example, the dental formula for a dog would be written: I 3/3; C 1/1; P 4/4; M 2/3. In each fraction, the numerator indicates the number of teeth that are in one half of the *upper* jaw and the denominator indicates the number of teeth in one half of the *lower* jaw. In cases where it is impossible to tell which teeth are premolars and which are molars, the dental formula can be written to combine the cheek teeth. For example, in a dog this would be written: I 3/3; C 1/1; P+M 6/7.

Examine skulls at this station and write a dental formula for each. You should be able to identify a tooth's type and its position in all of these specimens.

In general, the molars of herbivores wear down as they grind up coarse plant material. Natural selection has therefore led them to have continuously growing teeth with extremely high crowns. These high-crowned molars are described as **hypsodont**. In many herbivores, the teeth have a relatively flat occlusal surface because the ancestral cusps have become connected by a series of laterally running ridges termed



A. Cat skull

B. Rabbit skull

C. Mandible of a cat

D. Mandible of a rabbit

E. Jaw closing muscles of a cat

F. Jaw closing muscles of a rabbit

Figure 8-25
Jaw mechanics and muscles of a cat and a rabbit.

lophs; such teeth are described as **lophodont**.

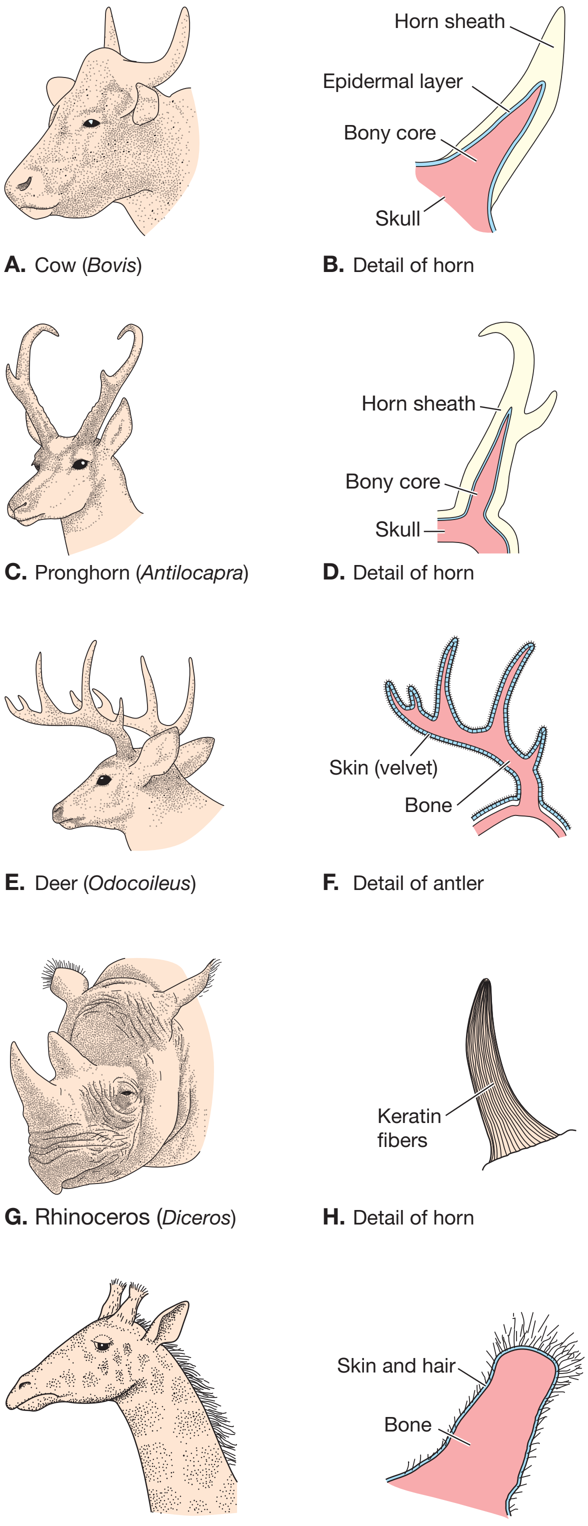
Aside from prominent canines, which are used to hold and kill prey, the primary dental modification for a carnivorous lifestyle was the development of **secodont** cheek teeth. These teeth are used for slicing flesh. Specifically, carnivores have a **carnassial apparatus**, formed by the **fourth premolar** of the upper jaw and the **first molar** of the lower jaw.

Omnivores, like carnivores, generally have low-crowned or **brachyodont** teeth. Because such teeth must process a broad range of food, they are intermediate in form between the teeth of herbivores and carnivores. This compromise resulted in the evolution of **bunodont teeth** which are low with rounded cusps. Humans and pigs are classic examples of omnivores with bunodont teeth.

Examine skulls at this station and note the dentition. As you examine these specimens, consider what you have learned so far about the types of teeth and how they have become modified for certain dietary needs. Based on what you know, could you make predictions about how these animals live or what they might eat? After examining some of the most common dental patterns seen in mammals, look at the examples of particularly bizarre or impressive dental specializations.

A final topic related to dentition and chewing is the arrangement, origins, and insertions of muscles used in jaw closing (Figure 8-25). In Figure 8-25A and B, red lines through the teeth indicate how the upper and lower teeth occlude as the jaws closes. In a cat, the teeth form a pair of scissors, but in a rabbit, they form a nutcracker in which the upper and lower cheek teeth can crush food. The longer moment arm of the **temporalis muscle** in the cat (Figure 8-25C) enhances its function to pull up and backwards on the lower jaw. In contrast, the moment arm of the **masseter muscle** of the rabbit (Figure 8-25D) means that the jaw can be forcefully pulled up and forward during jaw closing. These mechanical features are correlated with the relative sizes, origins, and insertions of the temporalis and masseter muscles (Figure 8-25E and F). For example, the temporalis muscles is large in the cat but smaller in the rabbit, facilitating the cutting stroke of the cat's "scissors." In contrast the large masseter muscle of the rabbit is positioned to powerfully crush food in its "nutcracker."

You can interpret jaw mechanics of a dry or even a fossil jaw without any muscles by exam-



A. Cow (*Bovis*) **B.** Detail of horn

C. Pronghorn (*Antilocapra*) **D.** Detail of horn

E. Deer (*Odocoileus*) **F.** Detail of antler

G. Rhinoceros (*Diceros*) **H.** Detail of horn

I. Giraffe (*Giraffa*) **J.** Detail of horn

Figure 8-26
Horns and antlers in surface views and sagittal sections.

ining the position of the jaw joint and the relative sizes of the **coronoid** and **angular processes**. In a carnivore, the coronoid process is long but the angular process is short. In an herbivore, the coronoid process is short and the angular process is large. Test your understanding of this by comparing the lower jaws of a ruminant such as a cow, sheep, or antelope with the those of an extreme carnivore such as a mink.

Station 7: Horns and antlers

True horns and antlers are found in the artiodactyl families Bovidae and Cervidae, respectively (Figure 8-26A-F). **True horns** have a bone core, covered by a sheath of keratin. Horns are unbranched and never shed. They are found only in Bovidae (cattle, sheep, gazelles and allies). Horns grow from their bases throughout the animal's life. They are found on males; females of some larger species may also have horns but they are usually smaller than those of males. Some domestic breeds of bovids lack horns entirely. In most, a single pair of horns is present, but one species of antelope has two pairs. Not surprisingly, this species is known as *Tetracerus quadricornis* (= four-horned four-horn).

Antlers are made of bone, have a branching morphology, and are grown and shed on a regular schedule (often annually). They occur in members of Cervidae (deer, elk, moose and allies). Males of almost all cervid species have antlers. Females do not carry antlers, except for caribou (*Rangifer tarandus*), though in this case the antlers of the females are still smaller than those of the males. Antlers grow from an extension of the frontal bone called the pedicel. As an antler grows from the pedicel, it is covered with highly vascularized skin that is covered in hair (velvet). The velvet and blood vessels in the bone nourish the growing antler until it is fully ossified, at which point the blood supply is cut and the velvet dies and falls off.

Other horn-like features in mammals (like those in rhinoceroses, giraffes, and pronghorn antelope) are neither true horns nor antlers. The horns (1 or 2) of rhinoceroses are not attached to bone and are made of a solid mass of fibers formed from keratinized epidermal cells. Giraffe horns do not grow out from bones of the skull, but instead ossify from central cores that eventually fuse to the skull. Finally, pronghorns break the "horn rules" by having **branched horns whose sheaths are shed annually**.

Study examples of true horns. Identify the bony core and keratinized sheath. Note that the core is not necessarily as long as the horn itself, so much of the horn is hollow.

Examine the antlers of the white-tailed deer and moose. How do they differ?

Compare the antlers to the various horns at the station. Note the major differences (e.g., bone vs. keratin, solid vs. hollow). Also study the horns of a rhinoceros and pronghorn antelope on display. What is unusual about these structures?

9. Mammalia II: Diversity and Locomotion

Major concepts

- The three extant lineages of mammals differ in reproductive biology including modes of reproduction (oviparity or viviparity), length of gestation (short or long in viviparous forms), and reproductive anatomy.
- Mammals exhibit diverse skeletal adaptations associated with modes of locomotion.
- There are 29 extant orders: Prototheria (1 order); Metatheria (7 orders) and Eutheria (21 orders). Mammalian diversity is closely linked to biogeography.

Goals for this lab

- Learn about reproductive biology of Prototheria, Metatheria, and Eutheria.
- Explore adaptations for locomotion.
- Study extant orders of mammals.

Station 1. Phylogenetic context

Within Mammalia, the first extant branch is **Prototheria** (Figure 9-1). It includes four species of **Echidnas**, or Spiny Anteaters in the family Tachyglossidae and the **Duckbilled Platypus**, *Ornithorhynchus anatinus* (Figure 9-2). As in reptiles, prototherians retain a **cloaca**. The

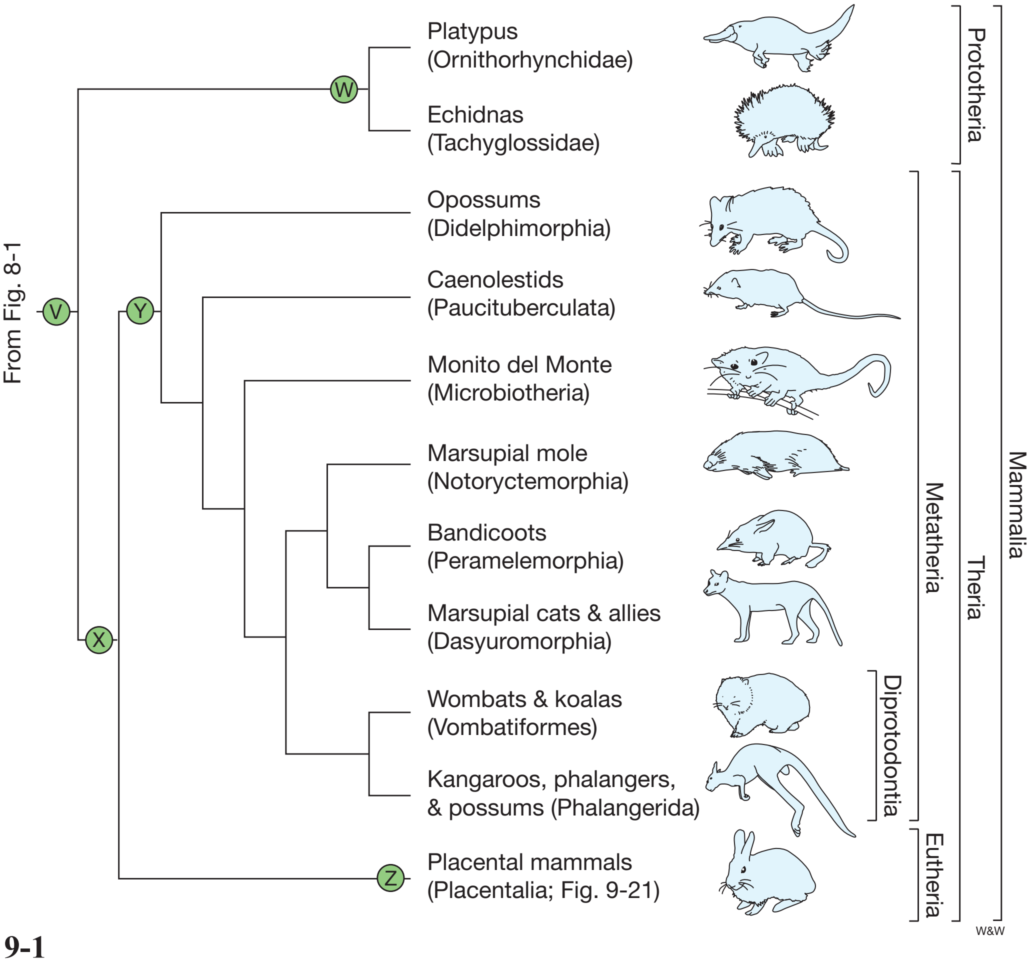
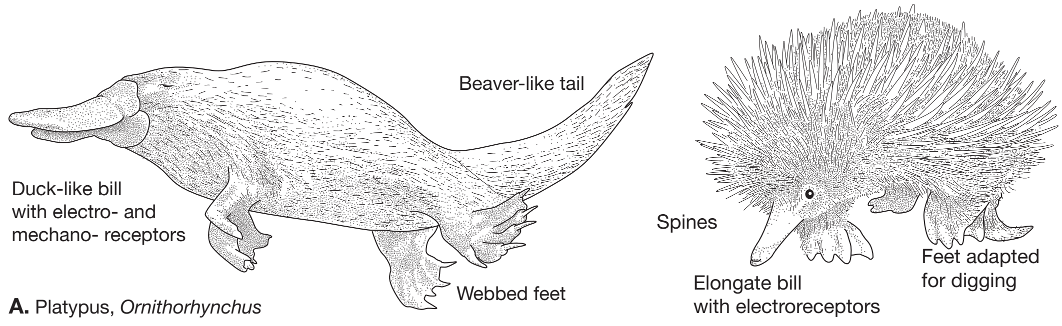


Figure 9-1
Phylogeny of Mammalia. Green nodes V, W, X, Y, and Z correspond to Figure 2-1.



A. Platypus, *Ornithorhynchus*

B. Echidna, *Tachyglossus*

Figure 9-2
Diversity of living Prototheria.

urethra and **reproductive ducts** meet at the **urogenital sinus** (Figure 9-3), which joins with the **rectum** to form the cloaca. Prototherians are oviparous (Table 9-1). Monotremes and marsupials have **epipubic bones**.

> **Synapomorphies of Prototheria**
>
> - ***Adults lack teeth*** *– all adult monotremes are edentate. Young echidnas lack teeth, but young platypuses have vestigial teeth.*
> - ***Adult males have spurs on hind limbs*** *– spurs function in defense and intraspecific fighting. Platypus spurs connect to venom glands in the thigh. The glands of echidnas may produce a secretion used in scent-marking.*
> - ***Electroreceptors on bill or beak*** *– Recall that electroreception was lost in amniotes, but it has re-evolved in prototheria.*

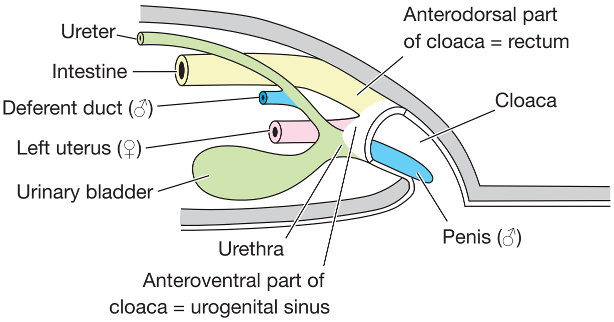


Figure 9-3
Schematic diagram of prototherian cloaca.

The semiaquatic platypus (Figure 9-2A) uses **electrosensory** and **mechanosensory** systems in the skin of its bill to find prey underwater. Echidnas are also electrosensory, although they have fewer electroreceptors on the beak than the platypus has on its bill. Echidnas evolved from a semiaquatic ancestry and only secondarily invaded terrestrial habitats, where they gather insect larvae, termites, and ants with the long beak and specialized tongue.

For many years it was difficult to associate monotremes with other groups of mammals because adult platypus lack teeth, and teeth are absent in echidnas. Eventually, paleontologists discovered a fossil platypus †*Obdurodon* that retains molar teeth with the reversed triangular occlusal pattern diagnostic for Mammalia (Figure 8-3).

Echidna females typically produce a single egg that is retained in the reproductive tract for three weeks. After it is laid, the female carries the egg in the pouch for ten days before it hatches. The hatchling, known as a **puggle**, suckles in the pouch for seven weeks.

Table 9-1. Modes of reproduction and types of placentation of Mammalia.

	Mode	**Placenta**
Prototheria	Oviparity	None
Metatheria	Viviparity (short gestation time)	Yolk-sac placenta
Eutheria	Viviparity (long gestation time)	Chorioallantoic placenta

Theria includes **Metatheria** (marsupials) and **Eutheria** (placental mammals; Figure 9-1, Table 9-1). Therians share several important synapomorphies related to reproduction, most importantly, **viviparity**, in which females give birth to young after a period of **gestation**.

Synapomorphies of Theria

- ***Viviparity*** *– therians give birth to live young (Table 9-1). Metatherians have relatively shorter gestation periods than do Eutherians, and young marsupials are less well developed at birth (Figure 9-4).*
- ***Loss of cloaca*** *– digestive and urogenital passages of adult therians open separately (Figure 9-5).*
- ***Scrotum*** *– external sac holds the testes; anterior to penis in marsupials; posterior to penis in placentals; Figure 9-5D).*
- ***Nipples or teats*** *– females deliver milk to young via nipples or teats (Figures 8-10, 9-4).*
- ***Tribosphenic molars*** *– cusps of upper molars occlude with basins in lower molars to crush food (Figure 9-6).*

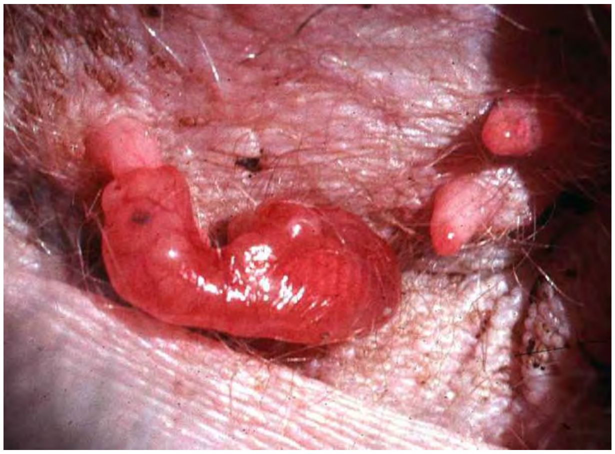
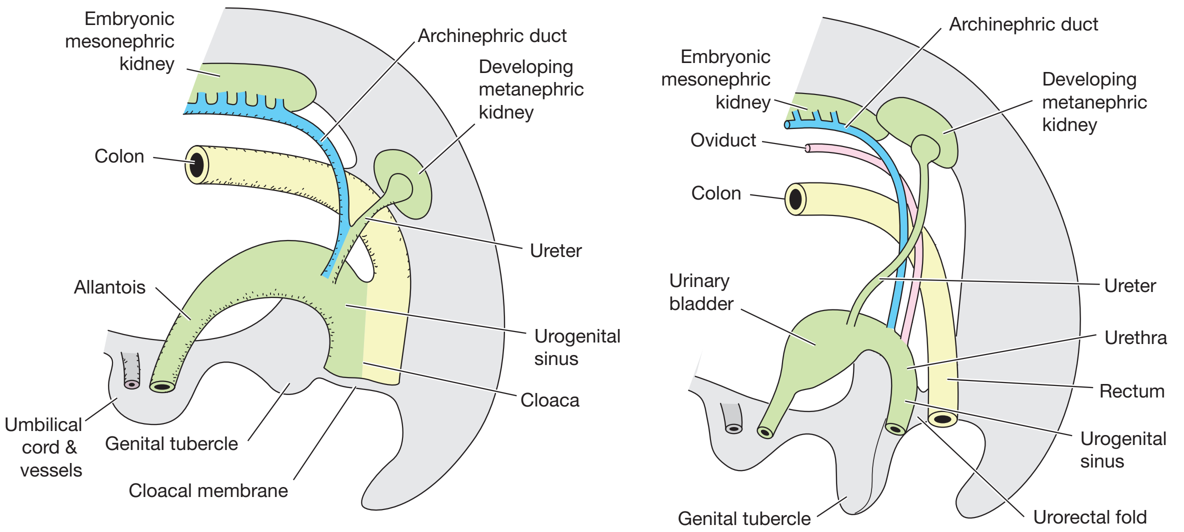


Figure 9-4
Newborn kangaroo. Geoff Shaw CC-BY-SA 3.0

Trace cloacal development to understand its loss in Theria (Figure 9-5). Early in development, therian embryos pass through a **sexually indifferent stage** in which the colon, urinary ducts, and reproductive ducts connect together at the **cloaca** (Figure 9-5A). At this stage, the cloaca is separated from the outside surface by the **cloacal membrane**, and the **allantois** serves as the receptacle for urine. Subsequently, the **urorectal fold** divides the **rectum** from the **urogenital sinus** (Figure 9-5B). This marks the loss of the cloaca in a developing therian. Subsequent development results in additional differences between adult females and males (Figure 9-5C,D).

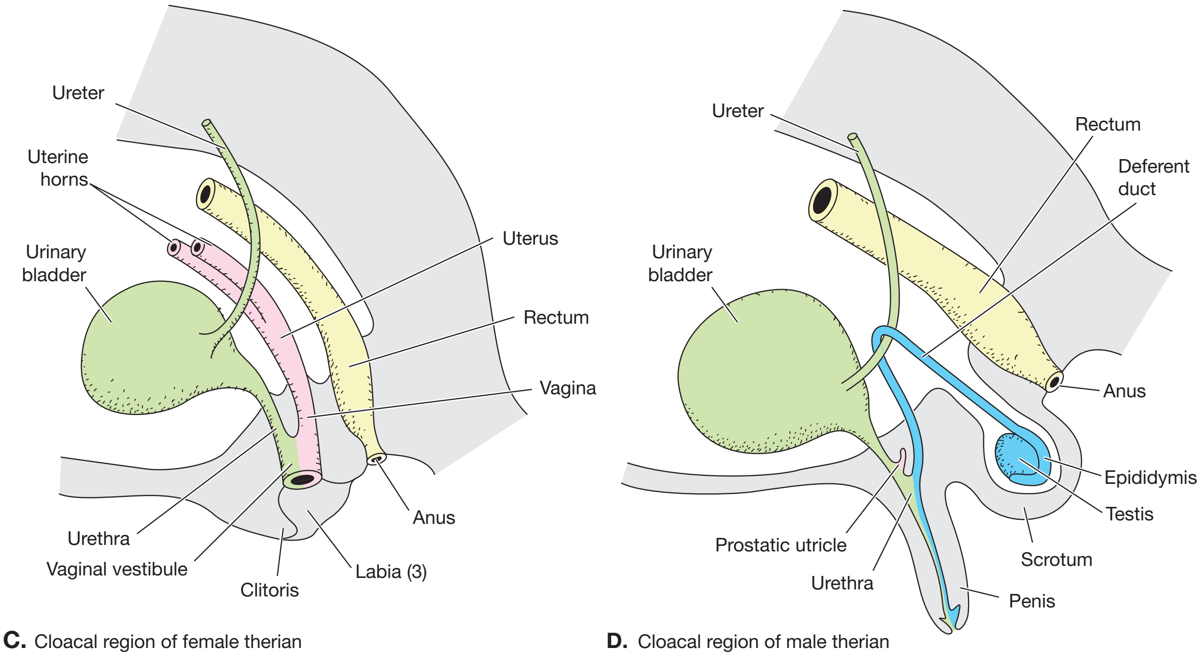
Tribosphenic molars of Theria represent a further refinement on the reversed triangular pattern of occlusion characteristic of Mammalia (Figure 8-1B). These are best studied in a dry skull and lower jaw of the Virginia Opossum, *Didelphis virginiana*, a basal metatherian (Figure 9-1). Figure 9-6 shows the arrangement and structure of its dentition. Study a specimen and confirm that its dental formula is I5/I4:C1/C1:P3/P3:M4/M4. Focus on the molar teeth and the structures indicated with colored dots in Figure 9-6. Start with the upper molars and find the three primary cusps indicated with yellow dots (●). These are the **Protocone**, **Metacone**, and **Paracone** (Figure 9-6A, upper left; by convention, cusp names start with capital letters in the upper jaw). Note that the Protocone is on the side of the tooth that faces the tongue (lingual side), as is typical for the reversed triangular pattern of occlusion synapomorphic for Mammalia.

Now examine the structure of a lower molar (Figure 9-6A, inset lower right). The triangular cusp pattern indicated with red dots (●)is reversed from that in upper molars, with the **protoconid** at the apex of the triangle on the outer side towards the lips (= labial). The **metaconid** and **paraconid** are on the lingual margin of the tooth. Together, these are the **trigonid cusps** because they form the lower triangle of the re-



A. Early sexually indifferent stage of embryonic therian

B. Later sexually indifferent stage of embryonic therian



C. Cloacal region of female therian

D. Cloacal region of male therian

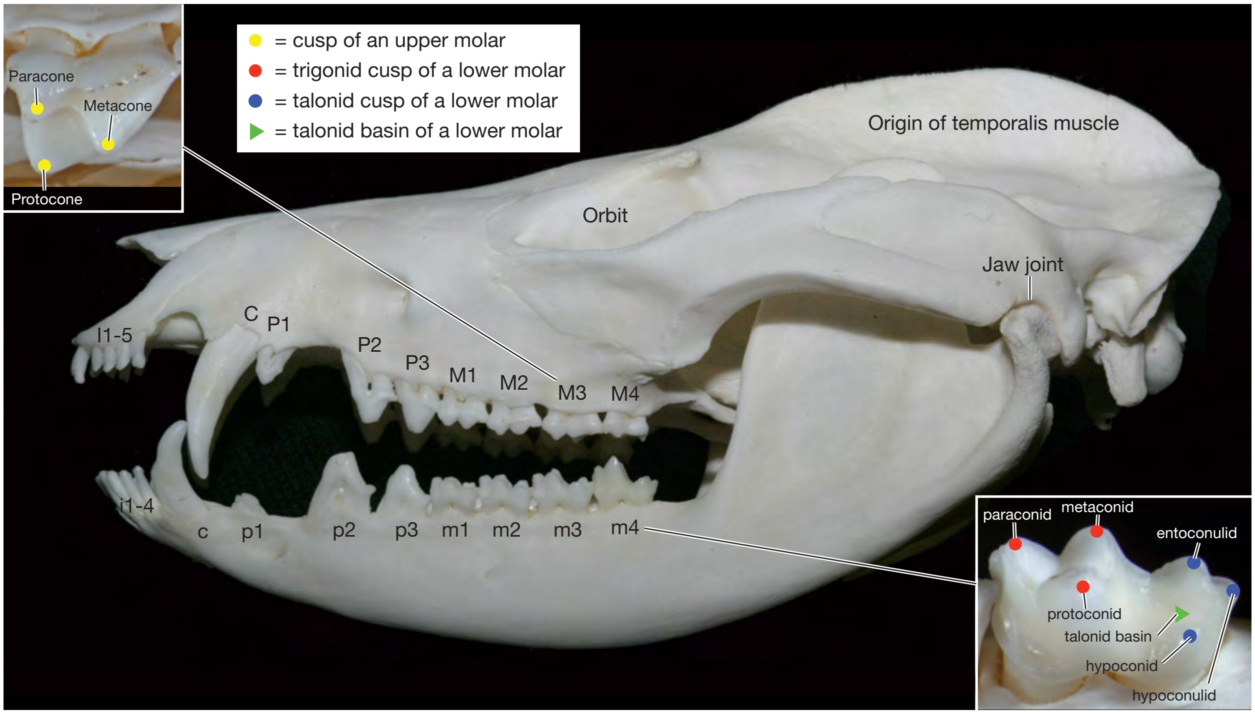
Figure 9-5
Schematic diagram of development of the cloacal region in therians based on a eutherian.

---

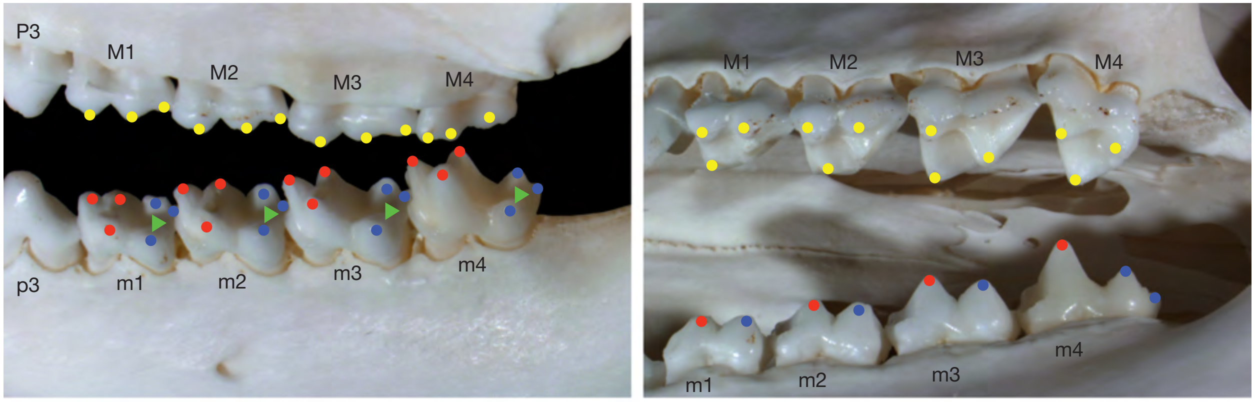
versed triangular pattern of occlusion.

Talonid basins in the lower molars, indicated with green triangles (▶) in Figure 9-6, are key to understanding the structure and function of tribosphenic molars. The basins are posterior additions to lower molars. Three cusps, indicated with blue dots (●), surround the talonid basin. These are called the **entoconid** on the lingual side, **hypoconulid** on the posterior side, and **hypoconid** on the labial side (Figure 9-6A inset lower right).

Now that you understand the arrangement of the cusps and basins, study the oblique views of the molars in Figure 9-6 B and C and how the upper and lower molars occlude with each other. Test you understanding, and demonstrate to yourself that each Protocone fits neatly into the corresponding talonid basin in a lower molar.

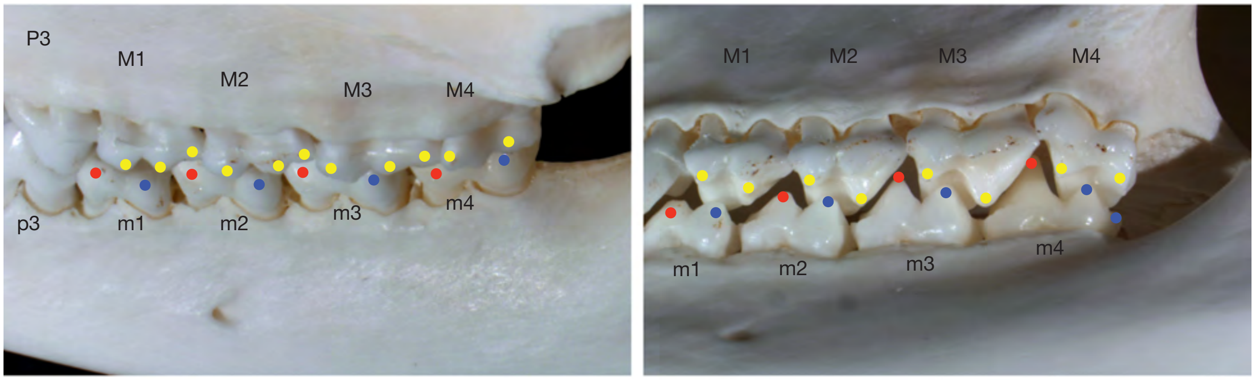


A. Dentition of the Virginia opossum, *Didelphis virginiana*. Insets identify molar cusps for M3 and m4 and talonid basin for m4.



B. Oblique view of lower molars showing cusps and talonid basins.

C. Oblique view of upper molars showing cusps.



D. Oblique view of upper and lower molars in occlusion.

E. Cusps in occlusion create shearing and pounding surfaces.

Figure 9-6
Anatomy and occlusion of eutherian tribosphenic molar teeth in the Virginia Opossum, *Didelphis virginiana.*

This creates a pounding surface that can crush prey in addition to shearing it between the other cusps. Tribosphenic molars occur not only in metatherians but also basal eutherians, such as shrews. Most extant groups of therians, however, evolved further specializations of molars to process different types of foods.

Metatheria – We recognize seven extant clades of marsupials in Metatheria (Figure 9-1). They exhibit fascinating biogeographical distributions and share several anatomical characters.

Synapomorphies of Metatheria

- ***Only the third premolars are lost and replaced*** *– unique pattern of tooth development and eruption that differs from eutherians, which typically replace all teeth except molars.*
- ***Palatal vacuities*** *– The palate of marsupials has characteristic fenestrae.*
- ***Females have paired vaginae*** *– Females have paired lateral vaginae through which sperm are transported and a central canal through which they give birth.*

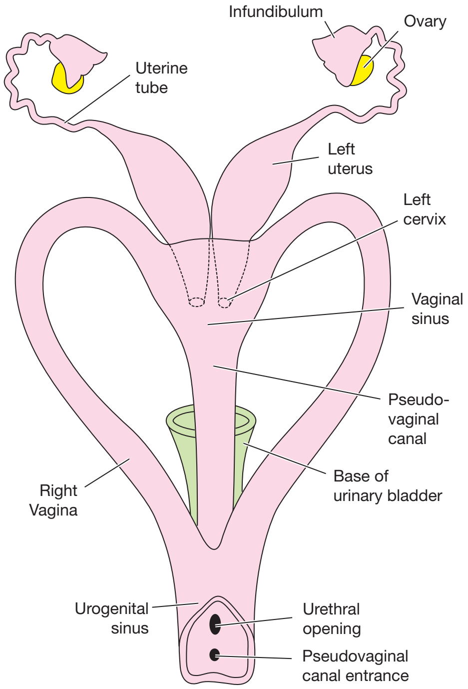
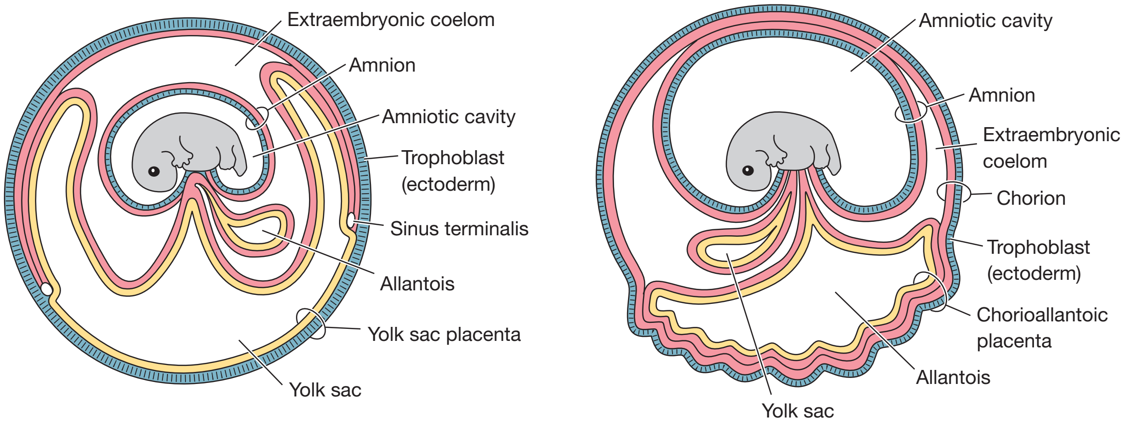


Figure 9-7
Reproductive tract of female kangaroo.

Female metatherians have paired vaginae (Figure 9-7). The anterior ends of the vaginae unite to form the **vaginal sinus**, into which the **paired uteri** enter. Each uterus has its own **cervix**. From each **infundibulum** a narrow **uterine tube** connects to the uterus. Many male marsupials have a **bifid penis**, and sperm travel up both vaginae. The **pseudovaginal canal**, present in marsupials such as kangaroos (Figure



A. Yolk sac placenta typical of most marsupials **B.** Chorioallantoic placenta of a typical eutherian

Figure 9-8
Comparison of yolk-sac and chorioallantoic placentae of Theria.

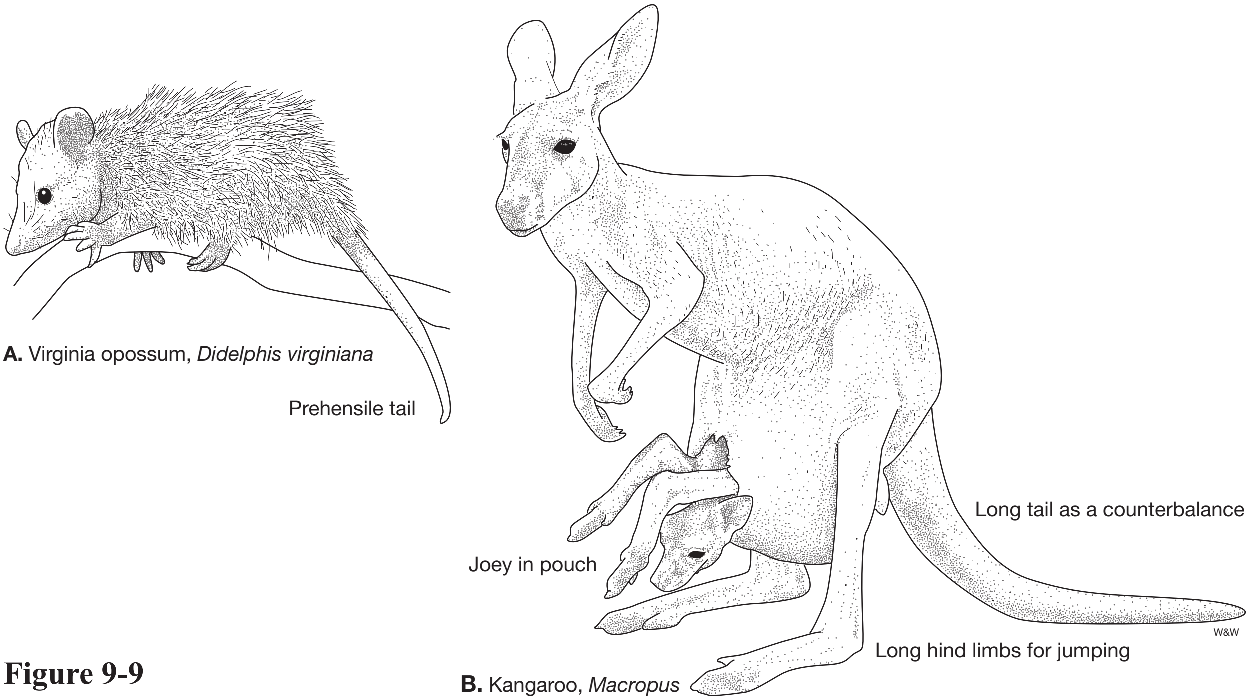


Figure 9-9
Examples of living Metatheria.

9-7), connects the vaginal sinus to the outside and serves as the birth canal.

Notice in Table 9-1 that Metatheria have a **short gestation time**; most species have a **choriovitelline placenta**, commonly known as a **yolk-sac placenta**(Figure 9-8A). This type of placenta is an exchange surface for respiratory gases and nutrients, but it is only loosely attached to the uterine wall.

Didelphimorphia (Figure 9-1) includes the omnivorous Virginia opossum, *Didelphis virginiana* (Figure 9-9A) in North America, where its range has expanded in the last century. Related forms occur in Central and South America. *Didelphis* provides important clues about the locomotor and feeding systems of early mammals. Some didelphids have prehensile tails that allow them to hang from branches. The small mouse opossum, *Monodelphis domestica*, is a model species for genetic and developmental studies.

Paucituberculata (Figure 9-1) comprises seven species of shrew opossums, small, secretive, terrestrial insectivores from western South America.

Notoryctemorphia (Figure 9-1) contains two species of Marsupial Moles (*Notoryctes*) from central and western Australia. They are the only completely fossorial marsupials, and are convergently similar to Golden Moles (Chrysochloridae) and True Moles (Talpidae), which are placental mammals. Like talpids, they use enlarged front feet as shovels to push soil aside to burrow.

About 20 species of bandicoots (**Peramelemorphia**, Figure 9-1) live in Australia and New Guinea. These hopping, rat-sized omnivores forage in ground litter and dig among roots for food.

Dasyuromorphia (Figure 9-1) includes carnivorous marsupials of Australia and New Guinea such as the cat-like quolls (*Dasyurus*) , the Tasmanian devil (*Sarcophilus*), and the Tasmanian tiger (†*Thylacinus cynocephalus*; also known as the Tasmanian wolf). Most are small scavengers or predators that feed on invertebrates and small rodents, but the sturdy skull of the Tasmanian Devil, *Sarcophilus harrisii*, is remarkably convergent on the skull of placental carnivores, such as bears. The Tasmanian tiger resembled placental dogs so closely that their skulls can be difficult to distinguish. The story of its extinction in the 20th century offers sad lessons in the impacts of bounty hunting, habitat loss, and introduced species. Today, Tasmanian devils are endangered, their populations decimated by a transmissible cancer that causes devil facial tumor disease.

Most living species of Australian marsupials are herbivores in **Diprotodontia** (Figure 9-1). This name is based on the presence of two large incisors on the lower jaw (Gr., di = two + proto = front + odont = teeth).

Vombatiformes (Figure 9-1) is the order for wombats and koalas. Wombats resemble North American woodchucks. The Koala, *Phascolarctos cinereus* (Figure 9-10) feeds on leaves of only a few species of eucalyptus trees. They shelter during the day in burrows and emerge in the evening to feed.

Phalangerida includes animals commonly called possums, gliders, wallabies, and kangaroos. The Common Brushtail Possum, *Trichosurus vulpecula*, is a nocturnal, arboreal omnivore that thrives in cities as well the bush. It was deliberately introduced to New Zealand, where it is now regarded as pest because it destroys native plants and competes with native birds and mammals. The diminutive Honey Possum, *Tarsipes* uses its long, tubular mouth to feed on nectar and pollen. Gliders, such as the Feather-tailed Glider, *Acrobates* have loose skin folds between their front and hind legs and glide gracefully from tree to tree as they forage.

The dominant herbivores of Australia today are saltatory wallabies and large kangaroos in the genus *Macropodus* (L., macro = big + poda = foot; Figure 9-9B). Macropodids are ecologically similar to placental mammals such as deer and antelope, although they have different locomotor styles. Tree-kangaroos, *Dendrolagus*, live in trees and have prehensile tails; they evolved from an ancestor that lived in open country.

Be sure to watch the excellent video, *Birth of the Red Kangaroo* (link is on the course web site, to learn more about the biology and reproduction of these fascinating animals.

Figure 9-10
Koala, *Phascolarctos cinereus*, in a eucalyptus tree. Photograph by David Brown.

Eutherians differ from metatherians in the type of placentation and length of gestation as well as other features. A few metatherians (e.g., koalas and wombats) have a rudimentary chorioallantoic placenta while retaining a yolk sac placenta. This partially explains the inadequacy of the commonly used terms ‘marsupial’ and ‘placental’. Not all metatherians have a **marsupium** (pouch), and both metatherians and eutherians have placentae.

Synapomorphies of Eutheria

- ***Chorioallantoic placenta*** *– As its name indicates, this type of placenta involves the chorion and allantois of the embryo (Figure 9-8B). In many species, finger-like projections of the chorion invade the uterine lining.*
- ***Females have a single vagina*** *— serves for passage of sperm and birth of young.*
- ***Corpus callosum*** *– The corpus callosum is a band of nervous tissue that connects the two cerebral hemispheres (Figure 8-15C).*

Extant eutherians lack epipubic bones.

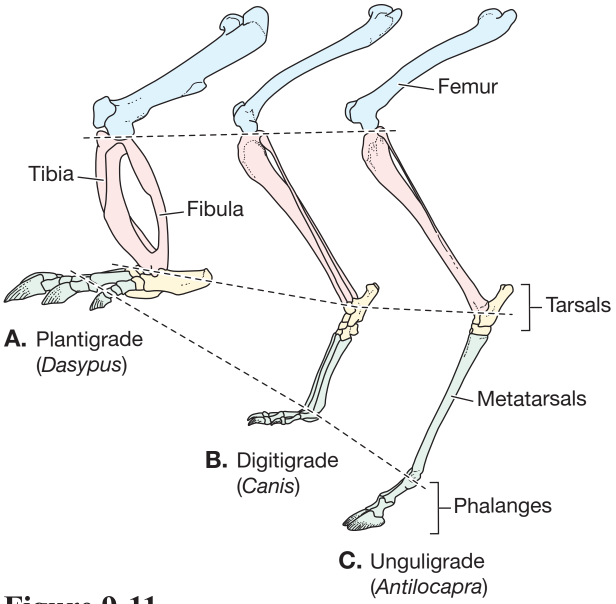


Figure 9-11
Foot postures of mammals. Femur of each species scaled to same size to emphasize changes in proportions of distal parts of limbs.

Station 2. Foot postures

Few aspects of an animal's natural history have a greater influence on form and function than how they get around. The method of locomotion that a species employs is usually tightly linked to its trophic ecology, skeletal morphology, posture, and strategies for avoiding predation. The ancestral condition for mammalian locomotion is a wide stance with limbs projecting laterally. A platypus offers an excellent example of this primitive, reptile-like posture. The waddling walk of these ancient mammals is not particularly efficient because muscles are required to move each limb forward and backward with every step. The evolution of limbs that descend straight down from the body (found in metatherians and eutherians) was a big step forward in locomotor efficiency. Such limbs are **pendular**, using gravity and the body's momentum to help move the limb with each stride.

Platypus also demonstrate the ancestral condition of mammalian foot posture. In this state, all the bones of the fore and hind feet, from the tarsals or carpals to the phalanges, are pressed against the ground as the animal walks. This foot posture is termed **plantigrade**, and is typically seen in ambulatory (walking) species with five digits on each foot. Plantigrade feet occur throughout Mammalia, from monotremes to marsupials, rodents to humans.

Plantigrade feet provide good stability, but are not ideal for animals in a hurry. **Cursorial**

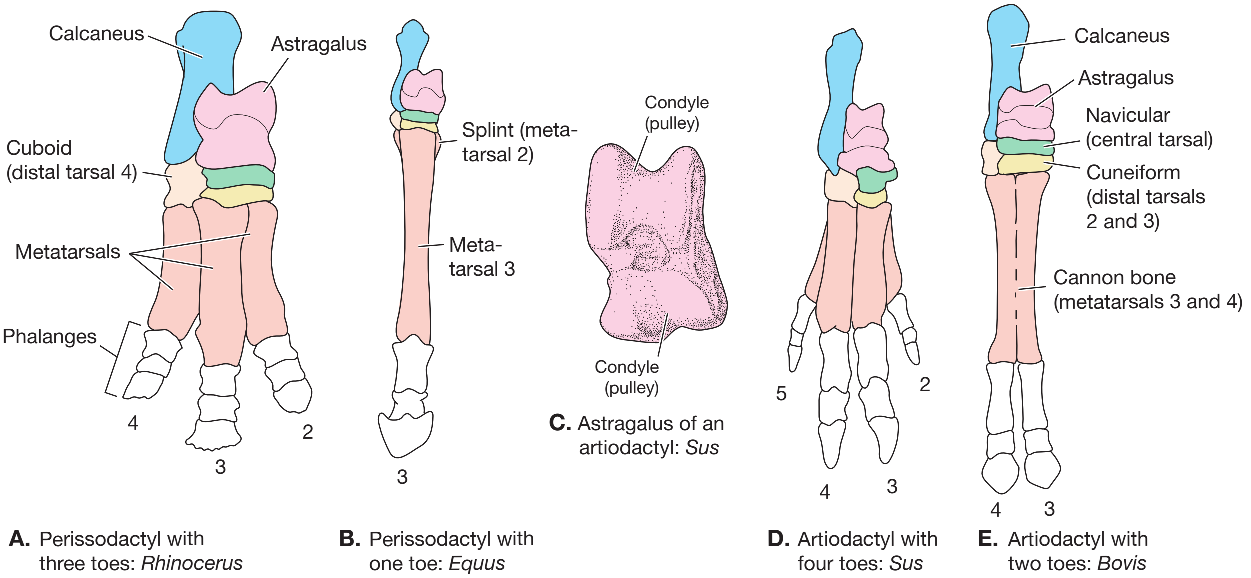


Figure 9-12
Ankles and hind feet of perissodactyls versus artiodactyls.

species have evolved the ability to run swiftly by either increasing the length of their strides or by increasing the stride rate. There are several ways to lengthen a stride. As any sprinter knows, one simple way is to stand up on the balls of your feet. Such a foot posture in which the weight rests only on the digits (phalanges) is termed **digitigrade**. Many mammals are permanently digitigrade, including canids (dogs) and felids (cats).

Study the dog skeleton in Figure 8-20 and the hindlimb in Figure 9-11. How many digits are present? Do all the digits touch the ground? Identify the bones of the feet, and note which bones are elongated, greatly increasing the length of each limb and the overall stride length.

Unguligrade mammals take this strategy of lengthening stride to the extreme. Animals such as horses and deer literally walk on the tips of their toes (Figures 9-11C, 9-12). Typically, the radius fuses with the ulna and tibia fuses with the fibula. The number of digits may be greatly reduced. For example, horses retain one digit on each foot (Figure 9-12B) and cows retain two digits on each foot (Figure 9-12E).

Examine the goat at this station and note the unguligrade foot posture.

Station 3. Cursorial mammals

Aside from lengthening the limb elements and standing on the tips of their digits, cursorial (= running) mammals can also increase the length of their stride by freeing the scapula to move with the limb. Rather than lying horizontally against the dorsal surface of a broad rib cage (as in humans), the scapula is positioned vertically, lateral to a deep, narrow rib cage and in the same plane as the forelimbs. During locomotion, the scapula swings forward and back with each step. This motion is clearly visible in dogs, cats (unfortunately our articulated skeletons are immobile), and ungulates. To free up the scapula's range of motion, the clavicle is often reduced in size in cursorial mammals. Note the small size of the dog or cat clavicle. Ungulates have lost the clavicle entirely (check the goat skeleton at Station 2).

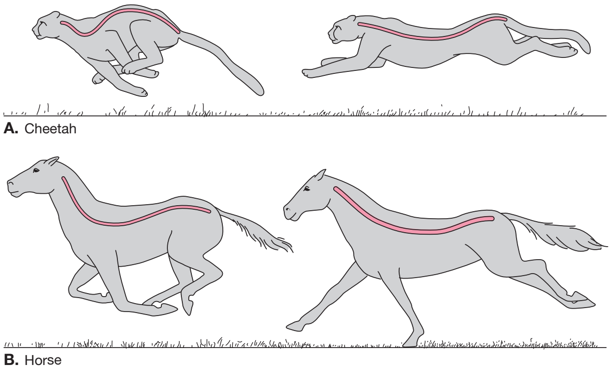


Figure 9-13
Vertebral column extension during running.

Some cursorial mammals, such as cheetahs, have extremely flexible spines, which they alternately bend and extend as they run (Figure 9-13A). This is another way to increase stride length. Compare this to a running horse (Figure 9-13B). There are many interesting functional anatomical interpretations based on this comparison, such as the anatomy of a cat's vertebral column as an archer's bow (Figure 9-14A) in which the spine between the fore and hindlimbs is flexible and bends. This contrasts to a horse's vertebral column, which is much more rigid and analogous to the bow of a violin, which does not bend (Figure 9-14B).

Station 4. Fossorial mammals

Fossorial (= digging) mammals spend most of their time underground and display many adaptations associated with a digging lifestyle. Most have large claws on their forefeet, a fusiform-shaped body, reduced/absent pinnae, thick fur, vestigial eyes, and a leathery nose shield.

Examine the mole skeleton. Note the narrow, dorso-ventrally flattened skull, which presumably minimizes resistance as the mole digs through soil. The pectoral girdle and forelimbs have undergone the major modifications. Note the robust bones of the pectoral girdle, which has been shifted forward relative to the rib cage, leaving very little in the way of a neck. The

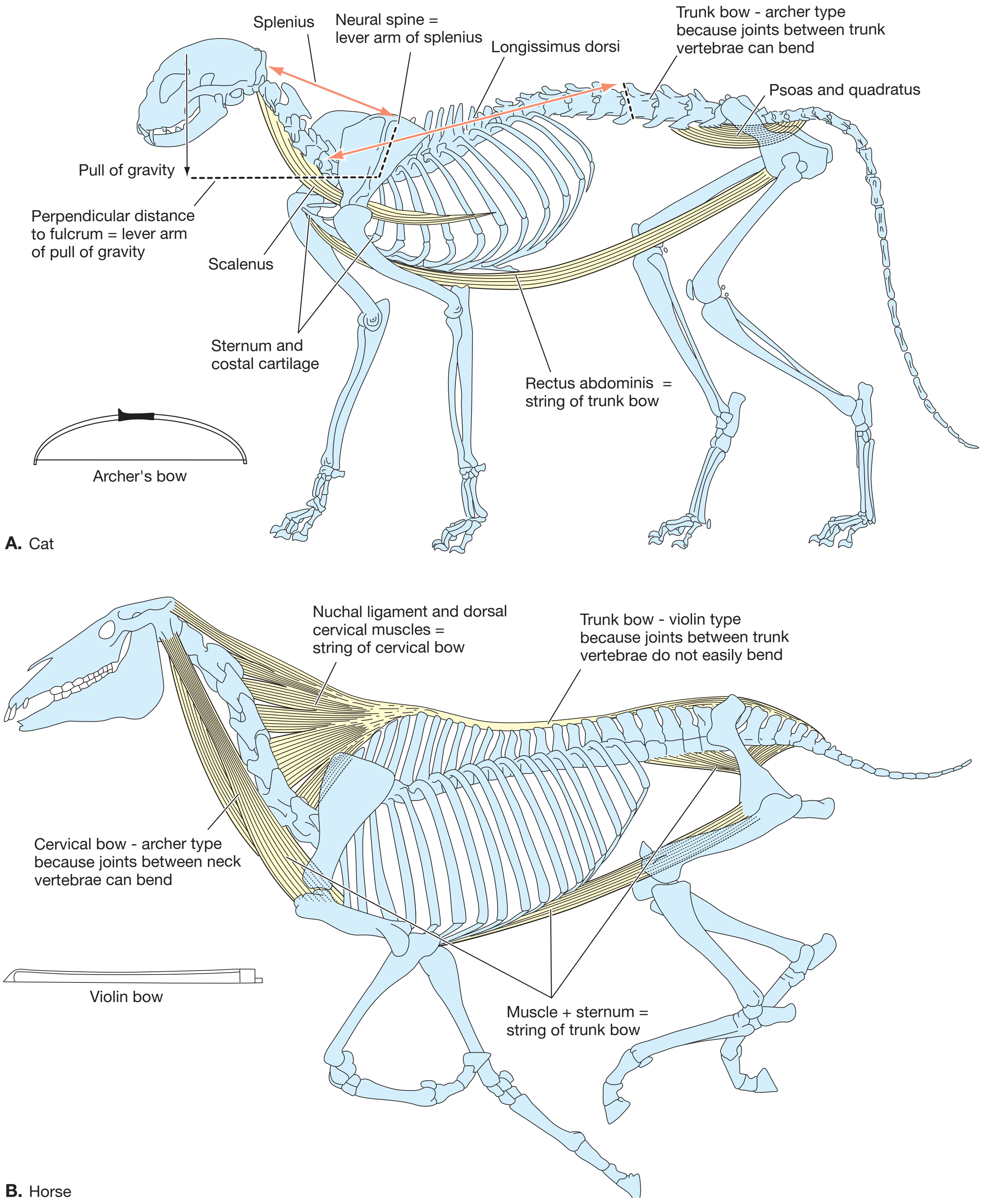


Figure 9-14
Functional morphology of mammalian trunk skeletons.

Figure 9-15
Massive hands of the Eastern Mole, *Scalopus aquaticus* used to excavate tunnels. Medial to the thumb is the skin covering the falciform bone. Photograph by Kenneth Catania, Vanderbilt University. CC-BY

clavicle is particularly large and blocky and the sternum is keeled (compare to the fragile clavicle of the much larger cat). Note the spade-like forelimbs and extra bone, called the **falciform bone**, on the hand (Figure 9-15). Possibly the most striking bone in the skeleton is the massive humerus, with many attachment points for the powerful muscles that work the digging apparatus.

Pocket gophers dig with incisors rather than forelimbs. Note how the skeleton differs from that of a mole.

Station 5. Scansorial and brachiating mammals

Not all mammals live on the ground, of course. Many have evolved climbing adaptations to occupy the three- dimensional worlds of forests and rocky cliffs. Animals that climb are referred to as being scansorial. Many scansorial animals are arboreal, meaning that they spend much of their time in trees. Scansorial mammals gain several advantages by climbing, including access to food resources, protection from ground predators, improved field of view, sheltered nest sites, and faster routes of travel.

When we consider the diverse strategies that enable mammals to climb, it is easy to overlook a simple and critically important issue: friction. Friction is a climbing animal's best friend, enabling it to hold a position on or push off from a vertical tree trunk or rock wall. As such, most animals that are adept climbers have adaptations to maximize friction at points of contact with the substrate. Scansorial mammals typically are plantigrade, which increases the surface area of the feet. They usually have soft and supple pads on their hands and feet, which improve friction by molding to the shape of the substrate and increasing the number of points of contact.

Many arboreal mammals have prehensile tails. Prehensile tails may be used simply to aid in climbing, or they may be strong enough to support the full weight of the animal. They are generally long and sensitive and curled at the tip. Non-prehensile tails may still be useful for climbing by aiding in balance. Watch a squirrel run through the trees and you will quickly see that it is moving its tail very deliberately to counterbalance its weight. Sloths use hook-like claws to suspend themselves from a branch.

Primates excel at grasping and climbing in an arboreal environment, and they have several adaptations that reflect this lifestyle. First, their long limbs give them excellent length of reach. The bones of the feet and hands are also modified to increase their gripping ability. These bones tend to be loosely attached to one another, giving hands and feet extraordinary flexibility and dexterity. Most animals that grasp with their hands and feet have opposable digits. Finally, the limbs of scansorial species must be able to go through the maximum possible range of motion at every joint, so joints are loosely articulated.

As primates diversified into arboreal niches, they developed an entirely new form of locomotion: brachiation (arm swinging). Rather than running along branches, a brachiating monkey travels beneath them, swinging along hand-over-hand exactly as you would swing beneath a jungle gym. The undisputed champions of brachiating are the gibbons, who can race through the treetops with their long arms, covering distance at a rate of 3 m per swing. They use gravity and their own momentum to increase their velocity, much in the same way that a person on a swing pumps to swing higher and higher. There are several skeletal adaptations for brachiation, including exceptionally long arms and a wrist joint that acts as a swivel.

Station 6. Saltatorial mammals

Animals that move about by **saltation** (jumping) with their hind feet providing most of the force behind the leap, are called saltatorial. Saltatorial mammals that use their forefeet for balance during locomotion (i.e., they are quadrupedal) are considered to spring (e.g., hares, rabbits), while the leap of purely bipedal mammals is called a ricochet (e.g., kangaroos, kangaroo rats, jumping mice).

Saltation evolved independently many times in various mammalian lineages, but these lineages share certain characteristics that are associated with this mode of transportation. The most obvious skeletal modification in saltatorial mammals is that the hind limbs are much larger than the forelimbs. Many of these mammals have fused or lost digits in their hind limbs (e.g., kangaroos, bandicoots, and jerboas).

Look at the kangaroo's hind foot. Note the length of the bones and look for the attachment points of the large muscles that power them.

Compare the fore and hindlimbs of the jerboa and kangaroo rat. Note which bones are fused. Both animals are great jumpers, but based on the relative lengths of fore and hindlimbs and the degree of fusion in the bones of the hind limb and foot, which of these seems to be most modified for a saltatorial lifestyle? Also, note the posture of each, which is very like that of the kangaroo.

How does the skeleton of the rabbit (a quadrupedal saltatorial mammal) compare with the others? Which limb bones are fused? How does it compare with the cursorial mammals at Station 3?

As the disparity between the size of fore and hindlimbs increases, the use of forelimbs in locomotion decreases. In the fully bipedal ricochetal species, forelimbs are exclusively reserved for activities such as gathering food, grooming, and burrowing. If the forelimbs are not involved in locomotion, maintaining balance becomes a major issue. To address this problem, ricochetal animals have long tails that are held aloft and serve as a counterweight for the trunk during saltation. The tail also serves as a tool for helping the animal steer. When saltatorial mammals are at rest, the tail often sits on the ground and is used to prop up the body. Kangaroo tails offer an excellent example of the dual functions of the ricochetal mammal's tail.

Saltation applies extreme forces to the trunk and neck. To cope with this, it is adaptive to have increased rigidity in the axial skeleton. Jumping mammals may have fused cervical vertebrae, robust lumbar vertebrae, and strong fusion between the pelvic girdle and the sacral vertebrae.

Examine skeletons of a rabbit, jerboa, and kangaroo rat. Which of these have fused cervical vertebrae? How does the apparent rigidity of the spine compare with that of the cursorial mammals that you examined at Station 3?

Station 7. Gliding and flying mammals

Many different adaptations have evolved in various lineages of mammals to allow them to take to the air. **Gliding** (the ability to travel through the air without power, but with some maneuverability) has evolved multiple times in mammals as diverse as marsupials and rodents. Only the bats, however, have evolved the ability to sustain themselves in the air through true powered flight.

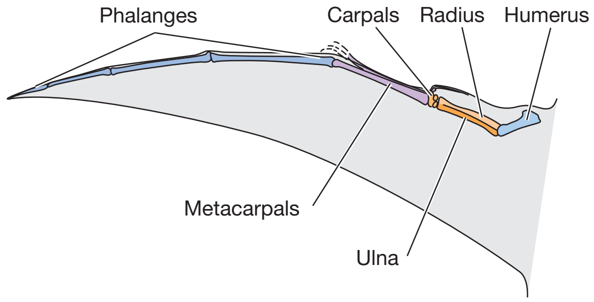
The primary mammalian adaptation for gliding is a broad flap of skin (**patagium**) that connects at least the arms and legs, and sometimes extends to the neck and/or tail. In some species, the feet are webbed and the tail is used as a rudder for controlling the direction of the glide. The broad, flat tails of our local flying squirrels are excellent examples of this. Various skeletal modifications have arisen to help hold the patagium in place during gliding. For example, long cartilaginous struts extend from the wrists of flying squirrels to provide added rigidity.

When a gliding mammal begins a glide, it leaps from a position of height and immediately begins a steep descent. As it falls it picks up speed, which is critical to providing lift. Once it attains adequate airspeed, the pressure of the air moving against the bottom of its open patagium is sufficient to allow it to level out its angle of descent.

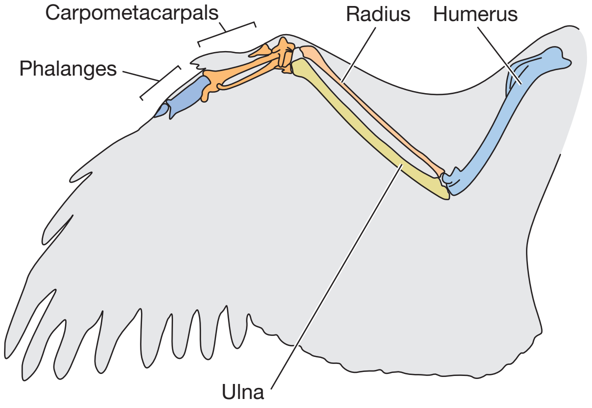
As an example of a local gliding mammal, study the flying squirrel skeleton at this station. Note the cartilaginous strut that attaches to the wrist and helps extend the patagium.

Bats are exceptional among mammals in that they are capable of powered flight. They evolved this ability independently of the other extant vertebrate fliers (birds), so the wings and musculoskeletal system that enable them to fly is unique (Figure 9-16). Unlike birds, whose feathers provide most of the surface area of the wing, bats have largely naked flight membranes (some hairs may be present). To achieve adequate surface area for flight, the flight membrane (patagium) extends to the terminal phalanges of digits 2-4, which are long and slender. The thumb is typically clawed, relatively short, and not involved in extending the patagium.

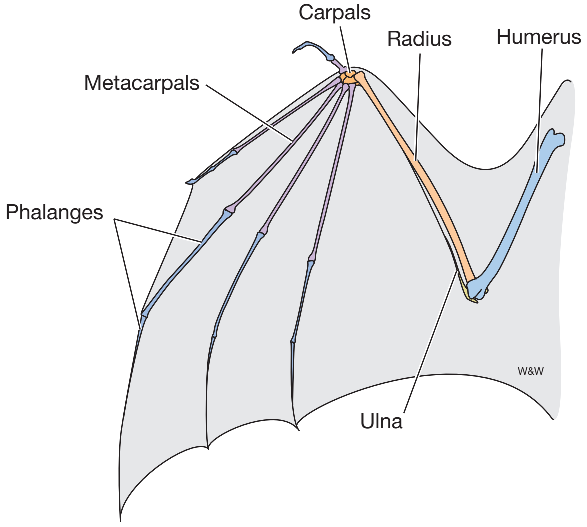
Not surprisingly, many of the most distinctive skeletal features of bats are related to flight. The greatly elongated phalanges and metacarpals in the forelimbs differ markedly from most other mammals, as does the great length of the forelimbs relative to the hind limbs. Bat hind limbs are typically rotated outward at the hip by 90º to 180º relative to other mammals, making it easier to hang upside down and grasp perches with the feet when making a landing. They also have a **calcar bone** off the heel to support the



A. †Pterosaur: airfoil made of skin supported by one long digit



B. Bird: airfoil made of feathers



C. Bat: airfoil made of skin supported by four long digits

Figure 9-16
Comparative anatomy of the wings of flying vertebrates to illustrate differences in the skeleton and tissues of the airfoil.

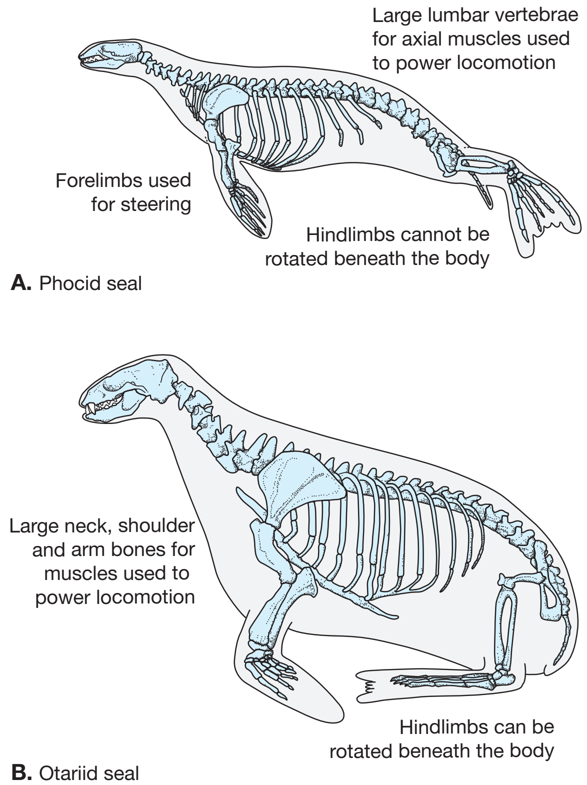


Figure 9-17
Skeletons of phocid seal and sea lion.

flight membrane between the hind legs.

Like all mammals, the muscles that move the forelimbs up (dorsally) originate on the back, while the muscles that move the wing down (ventrally) originate from the chest. This differs from the situation in birds, in which both sets of muscles for raising and lowering the wing are positioned on the ventral surface. In bats, as in birds, the chest muscles provide most of the power for flight, so they tend to be relatively large. Also, similar to birds, the sternum is often deeply keeled, providing a large attachment surface for muscles. What other mammal have you seen with a deeply keeled sternum? (hint: it's about as far from flight as it can get)

Examine the bat skin and articulated skeleton. Identify the different bones of the forelimbs, as well as the scapula and clavicle.

Compare the skeletons of the bat and bird. How are they similar? Identify the bones of the bird that are homologous to the ones you just identified on the bat. Note that the bird also has a keeled sternum and sturdy clavicle.

On the bat skeleton, note the orientation of the hind limbs relative to the body.

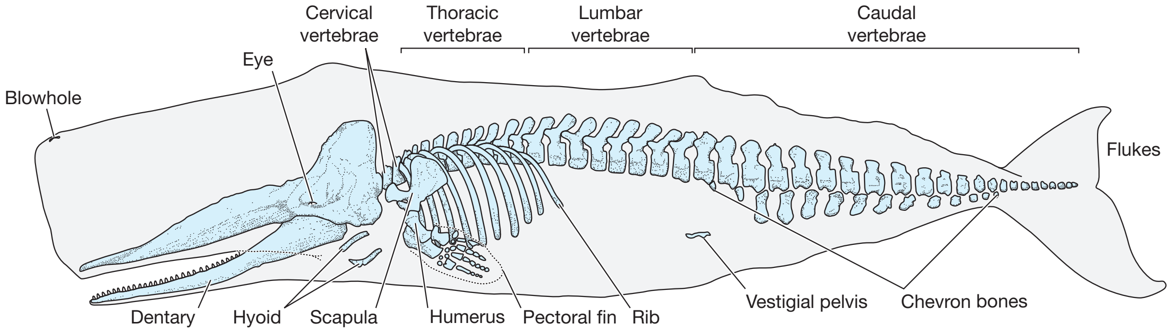
Station 8. Aquatic mammals

Although mammals originally evolved on land, many different mammalian lineages have independently become adapted to fill niches that involve spending a lot of time in the water. Semi-aquatic mammals (e.g., otters, beavers, water shrews, polar bears, platypus) are primarily terrestrial, but they exhibit adaptations for an aquatic lifestyle (e.g., webbed feet, fusiform body, flattened tail with a thick base, valves on ears and nostrils, reduced pinnae, nictitating membrane that protects the eye).

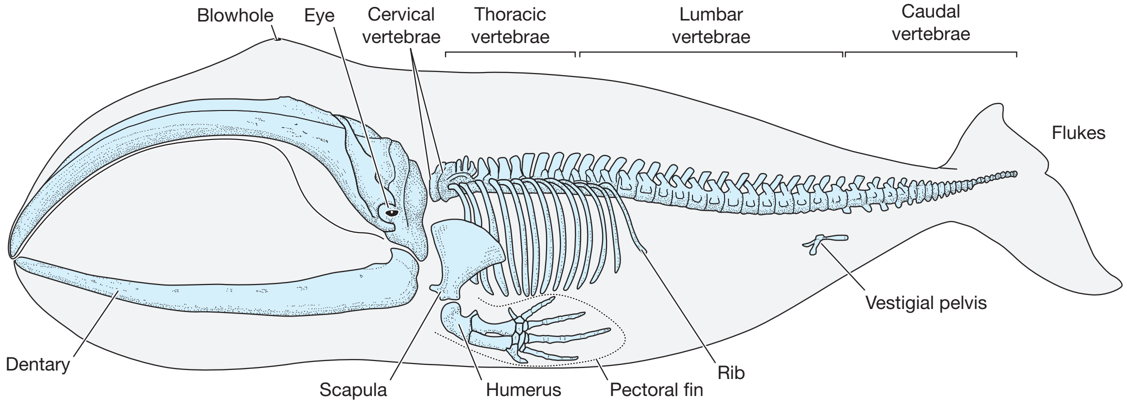
Examine the mounted beaver. What aquatic adaptations can you identify?

Amphibious mammals spend most of their time in the water, but occasionally haul out to bask, mate, or give birth (e.g., seals, sea lions, walruses). These animals are highly adapted for life in the water (e.g., fusiform bodies, limbs modified into flippers, simplified dentition adapted for a diet of fish), but they retain some features that facilitate terrestrial locomotion. Sea lions and walruses, for example, have limbs that are modified into flippers, but they can rotate them forward and down to use them to move around on land.

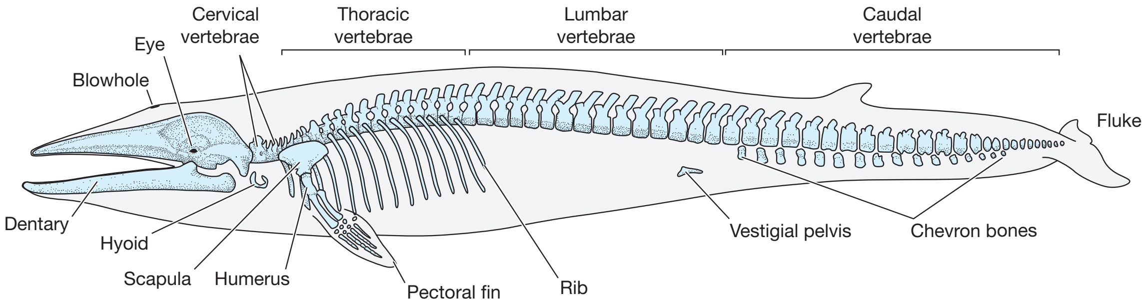
Pinnipeds use the forelimbs and hindlimbs for swimming, but there are striking anatomical and functional differences within the group (Figure 9-17). Phocid seals such as gray seals (*Halichoerus grypus*; Figure 9-17A) use vertical undulations of the vertebral column to apply thrust to the hindlimbs, and, accordingly the lumbar vertebrae are large to support this musculature (Figure 9-17A). In contrast, otariid seals such as sea lions (*Zalophus californianus*; Figure 9-17B) use the forelimbs to power swimming, and, accordingly, bones of the cervical region, shoulder and arm are large and sturdy. Phocid seals are more specialized for aquatic life in that



A. Skeleton of sperm whale, *Physeter macrocephalus*



B. Skeleton of bowhead whale, *Balaena mysticetus*



C. Skeleton of fin whale, *Balaenoptera physalus*

Figure 9-18
Cetacean skeletons.

they cannot rotate the hindlimbs under the body (Figure 9-17A), so they are less agile on land than are otariid seals.

Fully aquatic mammals are those that spend all their lives in the water. These are cetacean species (dolphins and whales) within Cetartiodactyla and Sirenia (dugongs and manatees), and are highly modified for aquatic life. Modifications include fusiform bodies, front limbs that are paddles, vestigial or absent hind limbs, dor-

Figure 9-19
Skull of a Common Minke Whale, *Balaenoptera acutorostrata*.

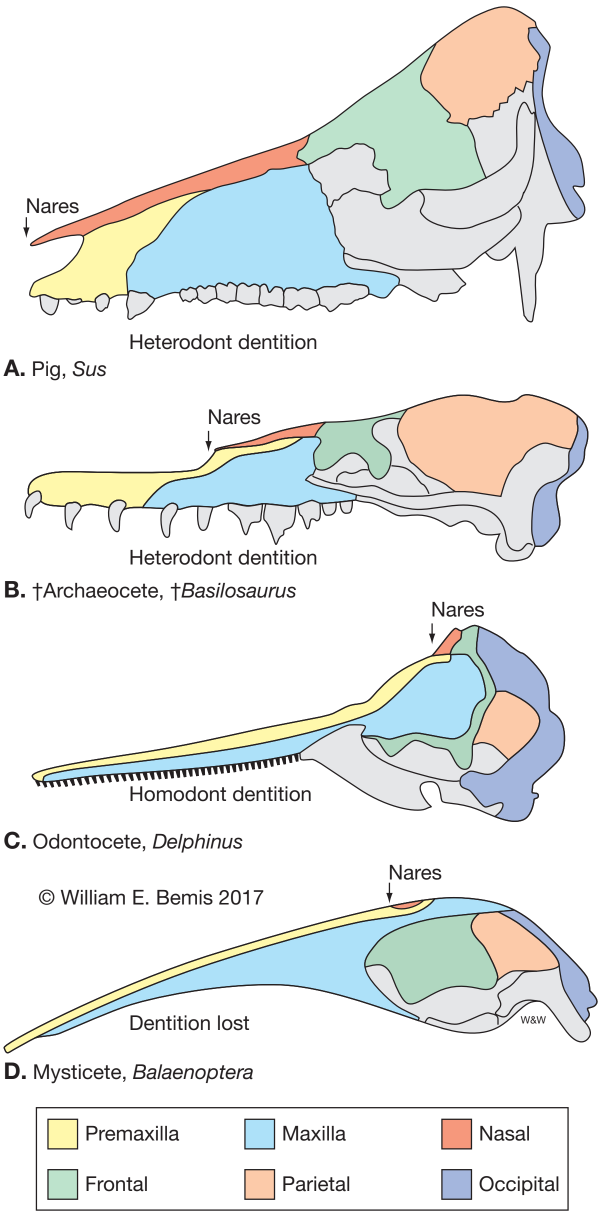


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Figure 9-20
Evolution of cranial bones in Cetartiodactyla.

soventrally flattened tail, vestigial or absent pinnae, largely hairless bodies, nostrils positioned dorsally (in cetaceans they form the blowhole on top of the head), and reduced and sometimes fused cervical vertebrae.

Cetaceans have short stiff necks. Examine the cetacean vertebrae at this station. Note the compression and partial fusion of the vertebrae. Not surprisingly, much of cetacean morphology has converged on characteristics that are found in fishes. Obvious similarities aside from general body shape include pectoral flippers (analogous to pectoral fins), a large dorsal fin, and a large flattened tail with flukes (analogous to the caudal fin, though in fish the caudal fin is vertical and in cetaceans the flukes are horizontal). There are skeletal similarities as well. The different regions of the post-cervical axial skeleton (thoracic, lumbar, sacral, and caudal vertebrae) are indistinct. The vertebrae themselves are simplified, with few articulation points. **Compare the overall skeletal morphology of fishes and cetaceans.** What features do they have in common that probably relate to their aquatic habitat? What features differ, perhaps due to phylogenetic history?

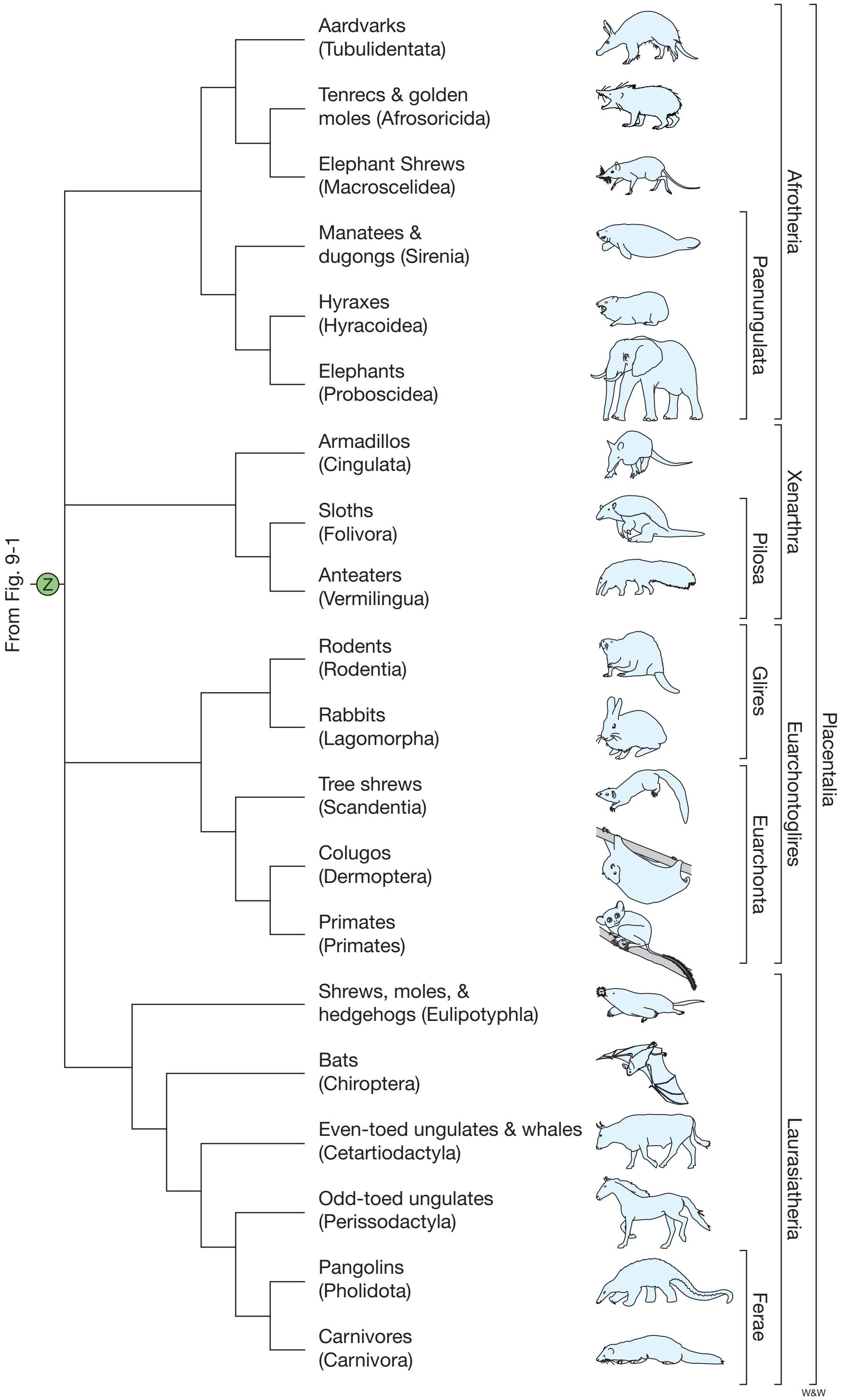
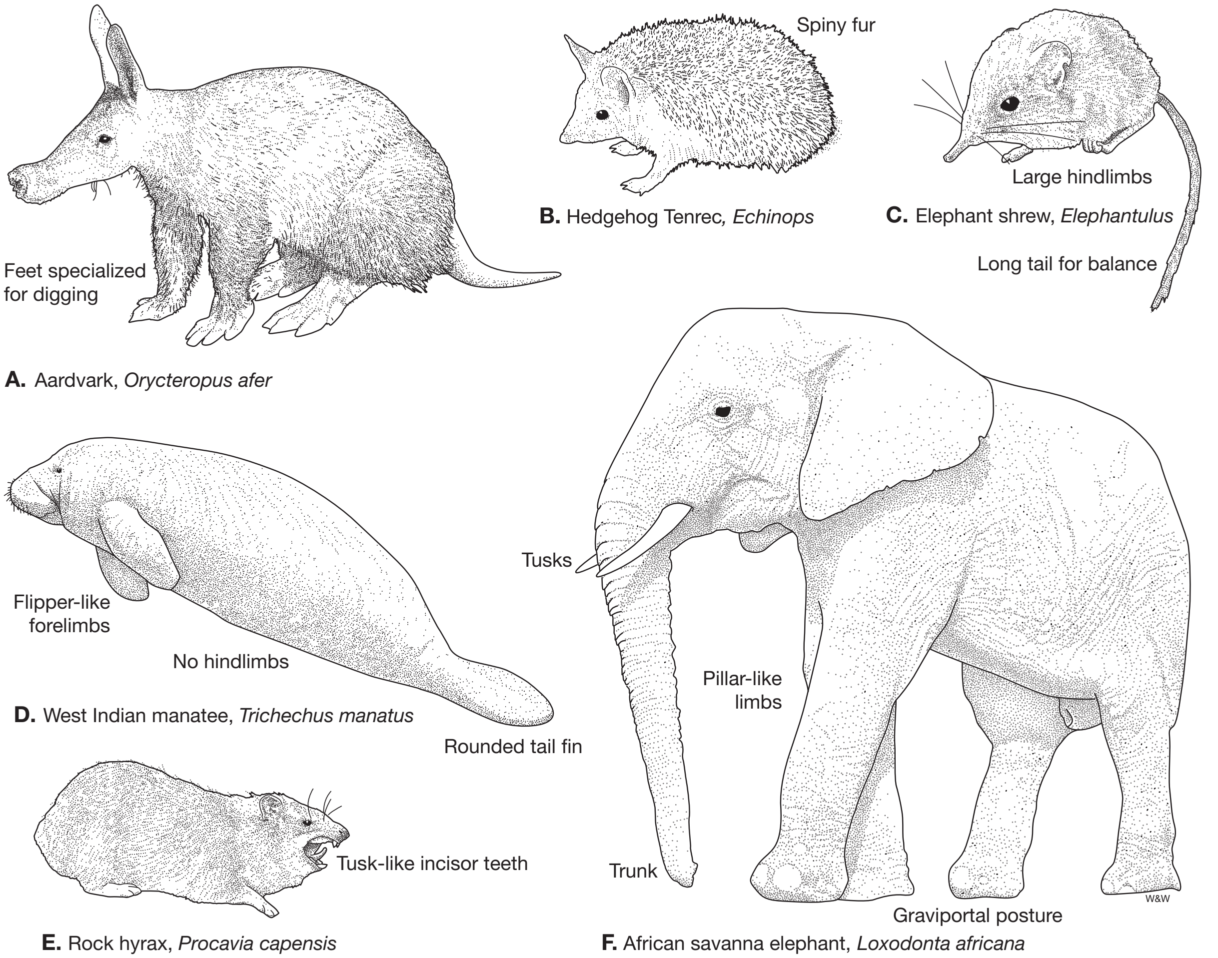


Figure 9-21
Phylogeny of Placentalia.

Station 9. Diversity of Placentalia

Eutheria includes many extinct taxa, and its crown group for the living species is **Placentalia**. Study the tree in Figure 9-21, which summarizes relationships for the four large clades of Placentalia based on molecular phylogenetic information. The discovery of these relation-



A. Aardvark, *Orycteropus afer*

B. Hedgehog Tenrec, *Echinops*

C. Elephant shrew, *Elephantulus*

D. West Indian manatee, *Trichechus manatus*

E. Rock hyrax, *Procavia capensis*

F. African savanna elephant, *Loxodonta africana*

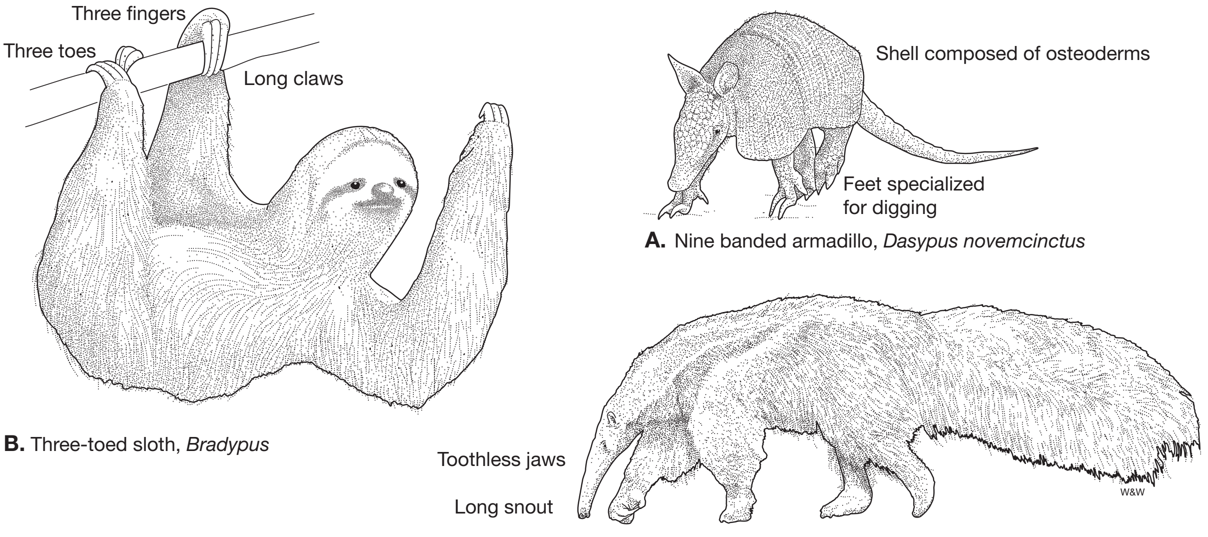
Figure 9-22
Example Afrotheria

ships in the 1990's revolutionized thinking about mammalian phylogeny and biogeography. Specifically, two of these clades originated in the Southern hemisphere: Afrotheria (Africa) and Xenarthra (South America). The other two clades, Euarchontoglires and Laurasiatheria originated and diversified in the Northern hemisphere.

Afrotheria

Tubulidentata contains a single living species, the aardvark (*Orycteropus afer*; Figure 9-22A), which ranges widely across sub-Saharan Africa. Aardvarks specialize in eating ants and termites using a long, sticky tongue. This specialization evolved convergently in other mammals, such as the anteaters of South America and pangolins of Asia. Aardvark teeth lack enamel, so the surface wears away. A unique, ever-growing type of dentine, known as tubulidentine, forms the occlusal surface of their teeth. We name the group based on this synapomorphy.

The tree in Figure 9-21 groups tenrecs and golden moles as **Afrosoricida**. Tenrecs such as the hedgehog tenrec, *Echinops* (Figure 9-22B) are omnivorous shrew- to rat- sized mammals. Most tenrecs are from Madagascar; otter shrews, however, are from west-central Africa. Tenrecs maintain a lower body temperature than most placental mammals and have a cloaca rather than separate openings for urine, genital materials, and feces as typical for most placentals. About 20 living species of golden moles



A. Nine banded armadillo, *Dasypus novemcinctus*

B. Three-toed sloth, *Bradypus*

C. Giant anteater, *Myrmecophaga*

Figure 9-23
Example Xenarthra.

(Chrysochloridae) are burrowing mammals native to South Africa.

Elephant shrews belong to **Macroscelidea**, the sister taxon of Afrosoricida (Figure 9-21). The common name refers to the long snout, as seen in *Elephantulus* (Figure 9-22C). Elephant shrews use the snout to probe for invertebrate prey in leaf litter or soil and elongated hindlimbs for saltation, a feature convergently evolved in many other groups of small mammals.

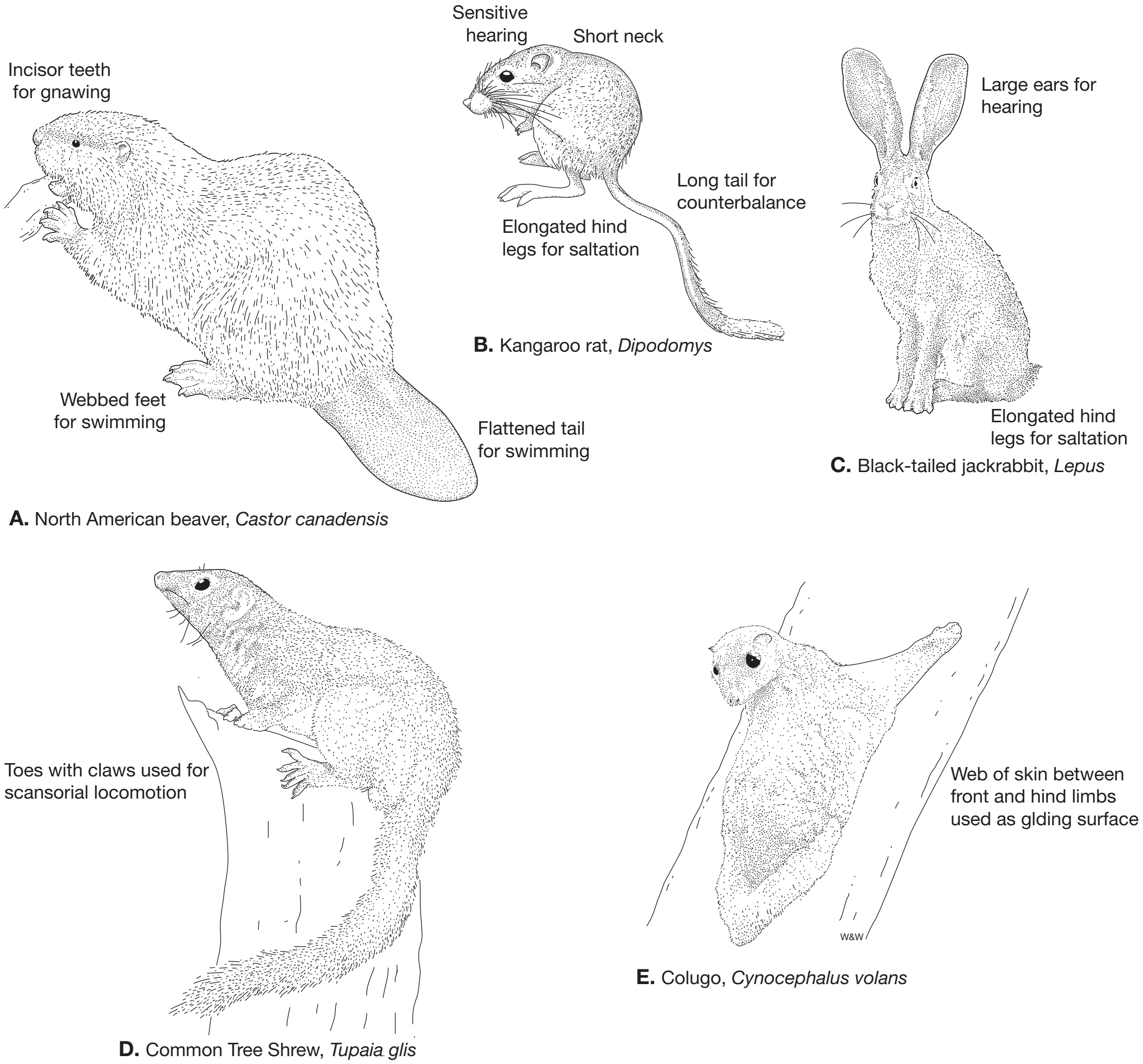
Dugongs and manatees (**Sirenia**), Hyraxes (**Hyracoidea**), and elephants (**Proboscidea**) form **Paenungulata** (Figure 9-21). Sirenians are large, aquatic herbivores that live in near-shore marine environments, estuaries or rivers. They lack externally visible hindlimbs and have a single, broad, horizontal, caudal fluke. Because of the West Indian manatee (*Trichechus manatus*; Figure 9-22D), we often think of sirenians as subtropical to tropical forms. However, until exterminated by humans in the 18th or early 19th century, the †Steller sea cow (†*Hydrodamalis*) inhabited very cold waters of the Bering Sea. Extant sirenians have dense bones for ballast, a condition known as pachyostosis.

Procavia (Figure 9-22E) and two other genera of hyraxes are herbivorous mammals known today only from Africa and the Middle East. Like elephants, hyraxes have ever-growing, tusk-like incisors composed primarily of dentine. All species have specialized pads on the soles of their feet, and are good climbers.

There are two extant genera of proboscideans: Indian elephants (*Elephas*) and African elephants (*Loxodonta*; Figure 9-22F). Elephants have unique cheek teeth, pillar-like limbs, tusk-like incisors, and a trunk. Their massive skull is filled with air pockets to make it lighter.

Xenarthra

Xenarthra (Gr., xenos = different + arthros = articulation, referring to unique articulations between vertebrae which add rigidity to the axial skeleton; Figure 8-26A) includes armadillos, sloths, and anteaters, (Figures 9-21, 9-23). This clade radiated in South America. Living members of the group have reduced numbers of digits with modified claws. About 20 living species of armadillos, exemplified by the nine-banded armadillo *Dasypus novemcinctus* (Figure 9-23A) have bony plates in the skin that form a carapace over the back; they curl up to present this armor to potential predators. Armadillos and sloths retain teeth, although they are highly modified from those of early eutherians. Living sloths eat leaves while suspended from tree branches by



A. North American beaver, *Castor canadensis*

B. Kangaroo rat, *Dipodomys*

C. Black-tailed jackrabbit, *Lepus*

D. Common Tree Shrew, *Tupaia glis*

E. Colugo, *Cynocephalus volans*

Figure 9-24
Example Euarchontoglires.

their long arms and claws, particularly apparent in the three-toed sloth, *Bradypus variegatus* (Figure 9-23A); giant ground sloths occurred in the Pleistocene. The four living species of anteaters lack teeth as adults and are highly specialized for a diet of ants and termites, which they capture using an elongate tongue. The giant anteater, *Myrmecophaga tridactyla* (Figure 9-23B) reaches 2.1m in total length. Instead of secreting hydrochloric acid in the stomach for digestion, formic acid produced by their prey provides a sufficiently acidic environment for the enzyme pepsin to work.

Euarchontoglires

Euarchontoglires is defined on the basis of DNA sequence data. It contains two clades supported by both molecular and morphological character data, which are **Glires** and **Euarchonta** (Figure 9-21).

Glires

As shown in Figure 9-21, Glires (L., gliris = a dormouse) includes rodents (**Rodentia**) and rabbits (**Lagomorpha**). Rodents and lagomorphs lack canine teeth and have a diastema (a gap in the tooth row between the incisor teeth and the cheek teeth). Rodents have a single pair of incisors in both the upper and

A. *Lemur*

B. *Gorilla*

Figure 9-25
Example Primates.

lower jaws. Rodent incisors are rootless and ever-growing, and enamel is present only on the anterior surfaces, which makes the incisors self-sharpening and contributes to their function in gnawing. Rodentia is astonishingly diverse, with more than 2,200 species organized into 30 extant families, such as beavers (Castoridae; 9-24A), squirrels (Sciuridae), Norway rats and domestic mice (Muridae), hamsters and voles (Cricetidae), New-World porcupines (Erethizontidae), gophers (Geomyidae), and kangaroo rats (Dipodidae; Figure 9-24B). Some species of rodents exhibit striking functional anatomical specializations, such as legs, vertebrae, and tails modified for jumping; forelimbs modified for burrowing; and kidneys modified for water conservation.

Rabbits and their close relatives have a unique arrangement of the upper incisor teeth, in which a pair of peg-like incisors is located immediately behind a pair of elongate, chisel-like incisors. This allows a rabbit to use its lower incisors to shear against the chisel-like upper incisors and pound against the peg-like upper incisors. Most rabbits have long ears and short, tufted tails. Jackrabbits (*Lepus*; Fig 9-24C) are excellent saltators.

Euarchonta

Euarchonta (Figure 9-21) includes tree shrews, colugos, and primates. Five extant genera of tree shrews (Scandentia) are native to forests of Southeast Asia. Figure 9-24D shows the common tree shrew, *Tupaia glis*. Some authors historically placed tree shrews within Primates, although this is not the view we depict. Tree shrews have a hole in the zygomatic arch and the middle four lower incisors form a tooth comb used in grooming.

Two genera and two species of colugos (**Dermoptera**) are herbivorous forest dwellers from Southeast Asia. Sometimes called "flying lemurs," colugos are not lemurs nor do they fly. Instead, they glide from tree to tree using their gliding membrane, which extends from the neck to the tips of the fingers, toes, and tail. Colugos have double-rooted canines and comb-like lower incisors, probably used to scrape food. An example is the Philippine flying lemur, *Cynocephalus volans* (Figure 9-24E).

Primates includes lemurs, "monkeys," and hominoids (Figure 9-21, 9-25). Primates is an unusual case of a name that is spelled the same way in both formal and common use, the only difference being the capitalization of the formal name. The presence of fingernails, instead of claws, is synapomorphic for primates. Early primates resembled insectivores, differing primarily in features related to foraging for insects, fruits, and soft plant food in trees. Most living primates are arboreal, but some, including humans, adapted to a terrestrial mode of life. The major groups of primates are the Strepsirrhini (seven families) and the Haplorrhini (eight families).

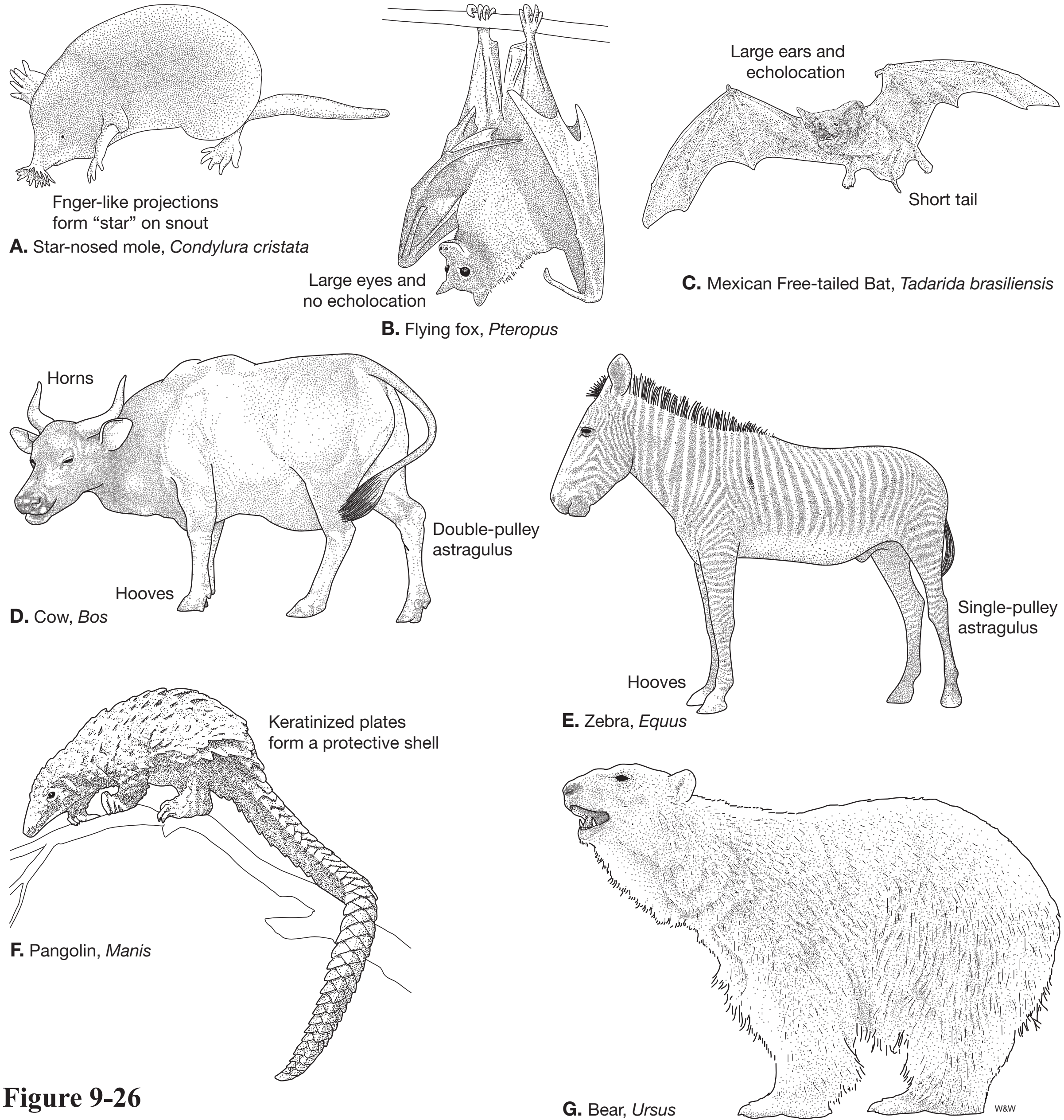
Strepsirrhini refers to the inward turning, comma-shaped nostrils characteristic of this group (Gr., strep = turning + rhinos = nose) It includes the galagos (Galagidae), which are nocturnal, tree-dwellers of Africa, and lemurs (Lemuridae), native to Madagascar, where they occupy many ecological niches. The ring-tailed lemur, *Lemur catta*, is one of the most familiar (Figs. 9-25A). Strepsirrhines have a laterally flaring talus (ankle bone), a postorbital bar, a tooth comb formed by procumbent lower incisors and canines, and a "toilet claw" on the second digit of the foot. Strepsirrhines also have a well-developed sense of smell.

All remaining primates belong to Haplorrhini. Haplorrhini includes the tarsiers (Tarsiiformes) and the New World monkeys, Old World monkeys, and hominoids (Simiiformes). All members of Haplorrhini have a postorbital plate as compared to the postorbital bar of Strepsirrhini. The three species of tarsiers are specialized for a nocturnal life in the trees. They have very large eyes, and their elongated ankles help them leap through the forest canopy. Members of Simiiformes have large brains. The olfactory lobe of the brain is reduced, but the surface of the brain is more convoluted than in outgroup forms. Most are social, diurnal animals. Many brachiate, that is, they use their long arms to swing suspended from the branches of trees. They use their opposable hallux (= big toe) for grasping.

The primates we commonly term "monkeys" do not form a monophyletic group. The pollex (= thumb) of New World monkeys (Platyrrhini) is only weakly capable of being opposed against other digits or the palm. Platyrrhini includes howler monkeys (*Alouatta*), which have unique specializations of the larynx used to produce loud vocalizations; spider monkeys (*Ateles*), which use their long, prehensile tails while moving through the canopy; and colorful, small marmosets and tamarins, which scramble along tree branches like squirrels. Platyrrhines have three pairs of upper and lower premolars and broad, outward facing nostrils (Gr., platy = broad).

The thumb can oppose the other digits of the palm in the remaining simiiforms, which is synapomorphic for Catarrhini. This feature is important in some types of locomotion and manipulation of objects. Catarrhines also have two pairs of upper and lower premolars, and nostrils that are close together and downward directed (Gr., cata = down + rhinos = nose). Old-World monkeys (Cercopithecidae) occur today from southern Europe (Gibraltar) across Africa to Arabia, Southeast Asia, and Japan. The rhesus monkey, *Macaca mulatta* is a familiar, diurnal, omnivorous cercopithecid that is strongly terrestrial. Arboreal cercopithecids can brachiate, but unlike the New World monkeys their short tails are never prehensile.

Loss of the tail is synapomorphic for Hominoidea. Gibbons (Hylobatidae) have exceptionally long arms and are excellent brachiators.



A. Star-nosed mole, *Condylura cristata*

B. Flying fox, *Pteropus*

C. Mexican Free-tailed Bat, *Tadarida brasiliensis*

D. Cow, *Bos*

E. Zebra, *Equus*

F. Pangolin, *Manis*

G. Bear, *Ursus*

Figure 9-26
Example Laurasiatheria.

They do not grasp a limb but rather use their fingers as a U-shaped hook. Their thumb is relatively short. Living members of Hominidae are the three species of tree-dwelling orangutans (*Pongo*) from Southeast Asia, the two species of terrestrial gorillas (*Gorilla*; Figure 9-25B) from the forests and mountains of Africa, the two species of chimpanzees from Africa (*Pan*), and humans (*Homo sapiens*). The fossil record of humans includes genera such as †*Australopithecus*, known from several species found in the Pliocene and Pleistocene of Africa, as well as several extinct species in the genus *Homo*.

Laurasiatheria

Laurasiatheria (Figure 9-21) includes many familiar mammals, such as bats, horses, cows, pigs, whales, cats, dogs and seals. It is a geographic clade of mammals identified by molecular phylogenetic data that evolved in the northern supercontinent of Laurasia, which was the precursor to modern North America, Europe, and Asia.

Eulipotyphla

The first clade within Laurasiatheria is **Eulipotyphla** (Figure 9-21). Eulipotyphlans retain plesiomorphic features of placental mammals. Most species are small, nocturnal, insect-eating animals with well-developed senses of smell and hearing but small eyes. Their full complement of teeth is well adapted for piercing, killing, cutting, and crushing food. Five clawed toes are present, and the first toe can oppose the others to some extent. Some eulipotyphlans, such as moles (Talpidae) burrow through soil using forefeet modified into spade-like structures. The star nose mole, *Condylura cristata* (Figure 9-26A) is named for series of finger-like projections at the tip of the snout. The shrew family (Soricidae) includes the smallest living eutherians, with some species maturing at a mass of just 2 g. Hedgehogs (Erinaceidae) superficially resemble the tenrecs of Madagascar (Tenrecidae) in that both families include forms with spine-like fur that can be erected for defense. These spines are a convergently evolved specialization. Moles and hedgehogs have complete zygomatic arches whereas shrews lack them. Some types of phylogenetic data group moles and shrews (Soricomorpha) to the exclusion of hedgehogs (Erinaceomorpha), but other data support different sister group relationships of these three groups of eulipotyphlans.

Chiroptera

The next clade within Laurasiatheria is **Chiroptera**, the order that contains the bats (Figure 9-21). Bats are the only mammals that engage in powered flight. Their wings are composed of the fingers of the hand, which support a web of elastic skin between them. Mammalogists traditionally recognize two groups of bats: **Megachiroptera** (Gr., mega = big + cheiro = hand + ptera = wing) and **Microchiroptera** (Gr., micro = small + cheiro = hand + ptera = wing). We have a surprisingly good fossil record for bats, including an Eocene stem bat from the Green River Formation in Wyoming, †*Onychonycteris finneyi*. †*Onychonycteris* could fly, but not echolocate, which suggests that the evolution of flight in bats preceded the evolution of echolocation. Flying foxes (*Pteropus*) and most other megachiropterans are frugivorous (= fruit-eating) bats from the Old World tropics. They roost in large social groups, called camps, and fly out at night to forage. Vision is very important to megachiropterans, and they have large eyes.

Microchiropterans form one of the most diverse clades of mammals and have many fascinating anatomical and physiological specializations. Most microchiropterans are nocturnal insectivores, but others eat fruits, nectar, fishes, blood, or other foods. As their name suggests, most species of Microchiroptera are small. Unlike megachiropterans, the second digit of the hand of a microchiropteran lacks a claw and is enclosed fully in the wing membrane. Microchiropterans roost in social groups, sometimes reaching millions of individuals, as at Carlsbad Caverns in New Mexico, which is famous for its colony of the Mexican free-tailed bat *Tadarida brasiliensis* (Figure 9-26C). The external ears of microchiropterans often are large and complex, and the nose and face may have a peculiar appearance. These features relate to ultrasonic echolocation, a sensory system used by microchiropterans to locate food and other objects. To do this, a bat uses its larynx to produce ultrasonic vocalizations, which are emitted through either the nose or the mouth. By definition, human auditory systems cannot detect ultrasonic frequencies (a young person can detect up to about 20,000 Hz). Echolocating bats typically use frequencies between 20,000 Hz and 100,000 Hz. Objects reflect the sound, which the bat then detects and processes in its brain. All of this takes place so rapidly that the bat can adjust its flight to avoid collisions or to capture prey. Insectivorous bats catch prey on the wing directly in the mouth or in the wing or tail membranes. Among the more famous microchiropterans are the New

World vampire bats (*Desmodus*, *Diphylla*, and *Diaemus*), which feed on vertebrate blood. Seasonal hibernation is very important for many bats that live in the temperate zone, such as the little brown bat (*Myotis lucifugus*) from eastern North America. Sadly, a fungal disease known as white nose syndrome has decimated this species, killing perhaps as many as 6 million bats in the last decade. Because this is a long-lived species, slow to reproduce, the impacts of this disease are likely to last for decades.

Cetartiodactyla

Cetartiodactyla includes several familiar groups of large terrestrial and aquatic mammals commonly known as even-toed ungulates and whales (Figures 9-21, 9-26). Basal artiodactyls have jaws and teeth specialized for browsing or grazing on plant foods, and most have elongate limbs used to outrun predators. Artiodactyls have an even number of toes or digits (Gr., artios = even + daktylos = finger or toe). In addition to an even number of toes, cetartiodactyls share a unique double-pulley modification of a bone in the ankle, the astragalus (Figure 9-12). The double-pulley shape of the astragalus allows great mobility between the shank and the foot. Each toe bears a hoof. Artiodactyls such as pigs walk or stand on their digits in a digitigrade posture. In contrast, swift running antelopes and allies walk on just the toe tips and hooves, the unguligrade posture (Figure 9-11). The presence of four toes is the plesiomorphic condition for artiodactyls, and hippopotamuses (Hippopotamidae), pigs and peccaries (Suina) retain this four-toed condition (Figure 9-12D). Extant camels, llamas, and vicuñas (Camelidae) and deer (Cervidae), giraffes (Giraffidae), and antelopes (Bovidae) are **didactylous**, meaning that they have two toes on each foot (Figure 9-12E). Hippopotamus and pigs have hindgut fermentation, and microorganisms break down cellulose in the cecum and large intestine (see lab 8). In contrast, camelids and ruminants (the group containing deer, giraffes, and antelopes) are foregut fermenters. Camelids have three chambers in the stomach; ruminants have four. Bovids have horns, and this diverse family includes more than 100 species, including goats (*Capra*), sheep (*Ovis*), bison (*Bison*), cattle (*Bos*; Figure 9-26D), and many species of African antelopes.

Living cetaceans are highly specialized aquatic cetartiodactyls with streamlined bodies, no hindlimbs, a horizontal tail with two flukes, and dorsally located nostrils known as blowholes. Most species live in marine environments; a few live in fresh water. A series of remarkable fossil intermediates reveals the terrestrial ancestry of cetaceans (including presence of the double-pulley astragalus), and molecular phylogenetic characters provide additional strong support. Cetaceans have reduced hair because blubber (i.e., fat deposits in the hypodermis) provides thermal insulation. Cetacean skulls are highly modified, with the nares shifted far posteriorly. Skulls of toothed whales have striking left–right asymmetries, a condition that is linked to their sophisticated echolocation systems for detecting objects underwater. Although most species of cetaceans retain teeth, their dentition is highly modified relative to other mammals in that it consists of rows of similarly shaped (homodont) teeth. Examples of toothed cetaceans include dolphins (e.g., *Lagenorhynchus*), porpoises (*Phocoena*), pilot whales (*Globicephala*), killer whales (*Orcinus*), and sperm whales (e.g., *Physeter catodon*). The most specialized cetaceans are the baleen whales, which lack teeth but have plates of baleen hanging from the roof of the mouth (baleen is commonly called whalebone, although it is actually a keratinized skin derivative similar to hair). All baleen whales are filter-feeders. This group includes the right and bowhead whales (*Eubalaena*), the humpback whale (*Megaptera novaeangliae*), and the largest known vertebrate, the blue whale (*Balaenoptera musculus*), which reaches a length of 31 m and a weight of 160,000 kg.

Perissodactyla

Extant odd-toed ungulates, Perissodactyla (Gr., perissos = odd + daktylos = finger or toe; Figure 9-21) are the tapirs (Tapiridae), rhinoceroses (Rhinocerotidae), and horses and zebras (Equidae; Figure 9-26E). These animals have an odd number of toes, either three (plesiomorphic state) or one (derived state). Hooves protect their toes, and they walk or run using an unguligrade posture. Perissodactyls have an extensive early Cenozoic fossil record, but their species diversity declined over the past 30 million years as grasslands expanded and cetartiodactyls diversified. Perissodactyls have an astragalus with a pulley-shaped upper surface only, and they display hindgut fermentation.

Ferae

Pholidota (pangolins) + Carnivora is known as Ferae (Figure 9-21). Pangolins were traditionally grouped with anteaters (both groups lack teeth and have long tongues) and armadillos, but the new placement of pangolins as the sister group of carnivores is strongly supported by molecular phylogenetic analyses. An anatomical character shared by pangolins and carnivores is an ossified tentorium (= bone that forms in a connective tissue fold) that separates the cerebral and cerebellar portions of the braincase.

Pholidota

Pholidota (Gr., pholidotos = armed with scales) includes eight living species of pangolins, which today occur only in the Old World tropics (Manis; Figure 9-26F). This group independently evolved specializations for ant and termite eating, including long tongues, toothless jaws, and claws for breaking into anthills and termite mounds. Like armadillos, the dorsal surface of a pangolin's body is armored, but pangolins accomplished this in an entirely different way by using keratinized plates derived from modified hair. These plates, often called scales, can make up to ½ of a pangolin's body mass.

Carnivora

Carnivora (L., carnis = flesh) includes 15 extant families. Carnivores use specialized carnassial teeth, consisting of the fourth upper premolar and the first lower molar, for cutting through meat or scraping meat from bones. Cats, dogs and weasels are predaceous, flesh-eating carnivores, but bears, raccoons, and a few other species of carnivorans secondarily evolved specializations for omnivory, and, in a few cases, herbivory. Members of Carnivora have a keen sense of smell and large olfactory lobes in the brain. Carnivora has two familiar clades: cats and allies, or Feliformia, and dogs and allies, or Caniformia. Feliformia includes the African palm civet (Nandiniidae), cats (Felidae), civets and genets (Viverridae), hyenas (Hyaenidae), meerkat and mongooses (Herpestidae) and Madagascar carnivores (Eupleridae). Most living species of feliforms are terrestrial, although some are arboreal and a few species construct burrows. African lions (*Panthera leo*) live in social groups, but other felids, such as the tiger (*Panthera tigris*), are solitary hunters. Felids are often described as hypercarnivores because their diet consists almost entirely of flesh. They have a short rostrum with increased bite force at the front of the mouth. Teeth used for seizing and cutting are key. Most species of feliforms have sharp, retractable claws used for catching prey. The familiar species of hyena from the African savannas is the spotted or laughing hyena *Crocuta crocuta*. As a group, hyenas are anatomically convergent on dogs and wolves, for example, in having non-retractable claws and relying on teeth to catch prey.

Wolves and dogs (Canidae) are at the base of the Caniformia clade. *Canis* is the genus of wolves and dogs. Canids have a long rostrum, with force focused toward the back of the mouth (carnassial apparatus). They have a more generalized diet than felids and this is reflected in their teeth. Remaining members of Caniformia belong to the clade Arctoidea. Many but not all arctoid groups are associated with aquatic habitats. Ursidae includes largely carnivorous bears such as the polar bear, *Ursus maritimus* (Figure

9-26G) as well as the bamboo-eating giant panda, *Ailuropoda melanoleuc*a, which has lost the carnassial apparatus entirely. Clade Musteloidea includes the red panda (Ailuridae), skunks (Mephitidae), racoons and coatis (Procyonidae) and otters, weasels, and allies (Mustelidae). Several species of mustelids forage and live in aquatic habits, including the American mink (*Neovison vison*), the North American river otter (*Lontra canadensis*), and sea otter (*Enhydra lutris*).

Earless seals, sea lions, and walruses are marine carnivores in the clade Pinnipedia. Phocidae includes 13 extant genera of true or earless seals, such as the gray seal *Halichoerus grypus*. The term "earless" refers only to their lack of an external ear or pinna: earless seals can hear perfectly well, and the evolutionary loss of the pinna is an adaptation for reducing drag when swimming. Although all pinnipeds are capable of diving, phocids make the longest and deepest dives. They are awkward on land because they cannot raise themselves on their front flippers or rotate their hind flippers underneath the body, so they simply hunch along on their bellies (Figure 9-17). The single species of walrus, *Odobenus rosmarus*, is a subarctic and arctic carnivore that eats clams and other molluscs, which it detects underwater using remarkably specialized whiskers, or vibrissae. Walruses are incredibly gregarious, hauling out in herds of hundreds or thousands of individuals. The upper canines of both males and females are modified into tusks, which function in intraspecific display and agonistic interactions, interspecific defense (for example, against polar bears), and as hooks to help individuals haul out on ice or land. Fur seals and sea lions are commonly known as eared seals, which is the source of the family name Otariidae. The pinnae are small but visible in species such as the California sea lion, *Zalophus californianus*. Otarids are more agile on land than are phocids because they can pull their hind flippers under the body and walk on front and hind flippers (Figure 9-17).

Station 10. Mammalian sounds

Listen to sounds of mammals of the Northeast. You will not be tested on these – it is just for fun!