48

Vertebrates

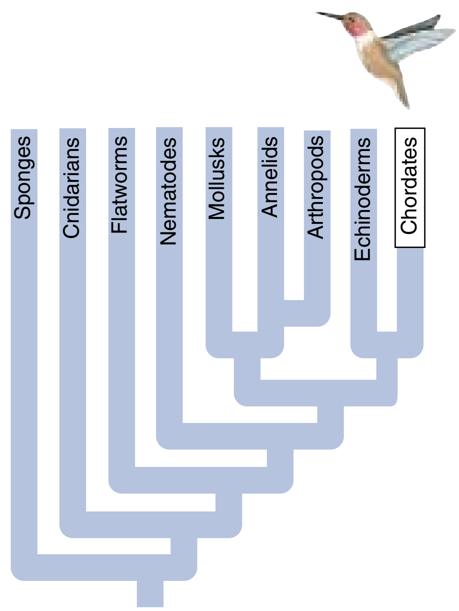
Concept Outline

FIGURE 48.1
A typical vertebrate. Today mammals, like this snow leopard, *Panthera uncia*, dominate vertebrate life on land, but for over 200 million years in the past they were a minor group in a world dominated by reptiles.

Members of the phylum Chordata (figure 48.1) exhibit great improvements in the endoskeleton over what is seen in echinoderms. As we saw in the previous chapter, the endoskeleton of echinoderms is functionally similar to the exoskeleton of arthropods; it is a hard shell that encases the body, with muscles attached to its inner surface. Chordates employ a very different kind of endoskeleton, one that is truly internal. Members of the phylum Chordata are characterized by a flexible rod that develops along the back of the embryo. Muscles attached to this rod allowed early chordates to swing their backs from side to side, swimming through the water. This key evolutionary advance, attaching muscles to an internal element, started chordates along an evolutionary path that led to the vertebrates—and, for the first time, to truly large animals.

48.1 Attaching muscles to an internal framework greatly improves movement.

The Chordates



Chordates (phylum Chordata) are deuterostome coelomates whose nearest relations in the animal kingdom are the echinoderms, the only other deuterostomes. However, unlike echinoderms, chordates are characterized by a *notochord*, *jointed appendages*, and *segmentation*. There are some 43,000 species of chordates, a phylum that includes birds, reptiles, amphibians, fishes, and mammals.

Four features characterize the chordates and have played an important role in the evolution of the phylum (figure 48.2):

1. A single, hollow **nerve cord** runs just beneath the dorsal surface of the animal. In vertebrates, the dorsal nerve cord differentiates into the brain and spinal cord.
2. A flexible rod, the **notochord,** forms on the dorsal side of the primitive gut in the early embryo and is present at some developmental stage in all chordates. The notochord is located just below the nerve cord. The notochord may persist throughout the life cycle of some chordates or be displaced during embryological development as in most vertebrates by the vertebral column that forms around the nerve cord.
3. **Pharyngeal slits** connect the **pharynx,** a muscular tube that links the mouth cavity and the esophagus, with the outside. In terrestrial vertebrates, the slits do not actually connect to the outside and are better termed pharyngeal pouches. Pharyngeal pouches are present in the embryos of all vertebrates. They become slits, open to the outside in animals with gills, but disappear in those lacking gills. The presence of these structures in all vertebrate embryos provides evidence to their aquatic ancestry.
4. Chordates have a **postanal tail** that extends beyond the anus, at least during their embryonic development. Nearly all other animals have a terminal anus.

All chordates have all four of these characteristics at some time in their lives. For example, humans have pharyngeal slits, a dorsal nerve cord, and a notochord as embryos. As adults, the nerve cord remains while the notochord is replaced by the vertebral column and all but one pair of pharyngeal slits are lost. This remaining pair forms the Eustachian tubes that connect the throat to the middle ear.

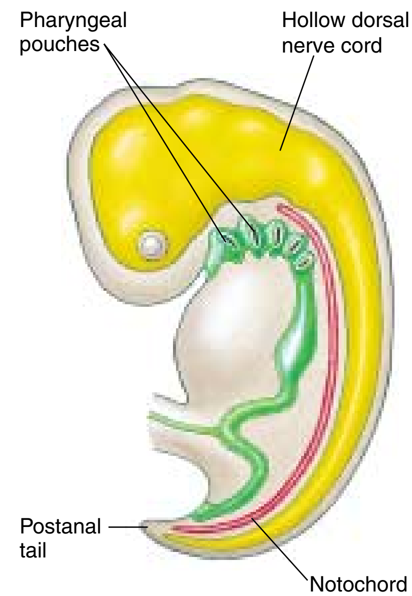


FIGURE 48.2
Some of the principal features of the chordates, as shown in a generalized embryo.

FIGURE 48.3
A mouse embryo. At 11.5 days of development, the mesoderm is already divided into segments called somites (stained dark in this photo), reflecting the fundamentally segmented nature of all chordates.

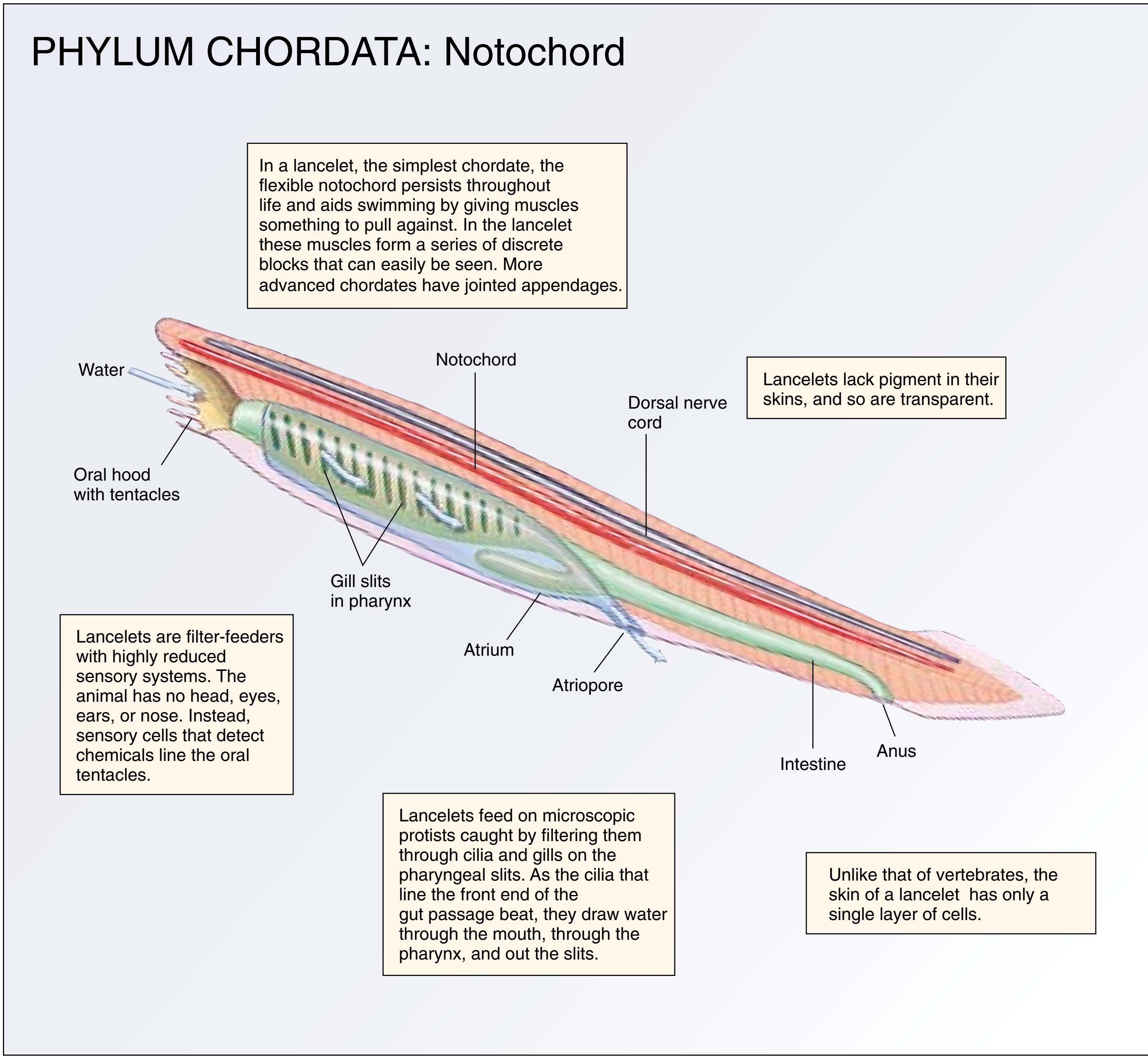


FIGURE 48.4
Evolution of a notochord. Vertebrates, tunicates, and lancelets are chordates (phylum Chordata), coelomate animals with a flexible rod, the notochord, that provides resistance to muscle contraction and permits rapid lateral body movements. Chordates also possess pharyngeal slits (reflecting their aquatic ancestry and present habitat in some) and a hollow dorsal nerve cord. In vertebrates, the notochord is replaced during embryonic development by the vertebral column.

A number of other characteristics also distinguish the chordates fundamentally from other animals. Chordates' muscles are arranged in segmented blocks that affect the basic organization of the chordate body and can often be clearly seen in embryos of this phylum (figure 48.3). Most chordates have an internal skeleton against which the muscles work. Either this internal skeleton or the notochord (figure 48.4) makes possible the extraordinary powers of locomotion that characterize the members of this group.

Chordates are characterized by a hollow dorsal nerve cord, a notochord, pharyngeal gill slits, and a postanal tail at some point in their development. The flexible notochord anchors internal muscles and allows rapid, versatile movement.

48.2 Nonvertebrate chordates have a notochord but no backbone.

The Nonvertebrate Chordates

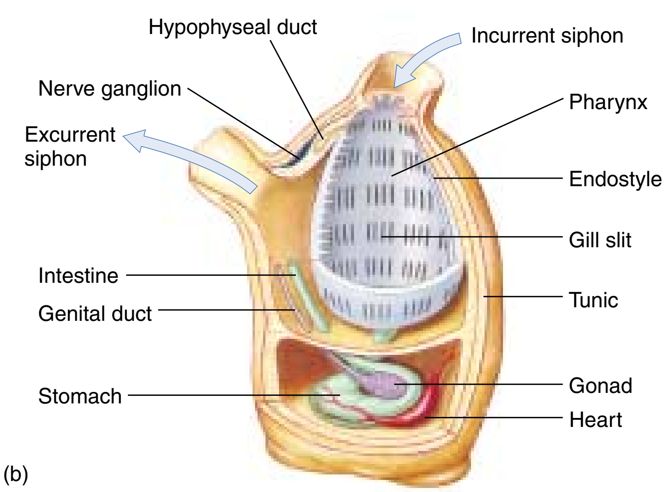
Tunicates

The tunicates (subphylum Urochordata) are a group of about 1250 species of marine animals. Most of them are sessile as adults (figure 48.5*a*,*b*), with only the larvae having a notochord and nerve cord. As adults, they exhibit neither a major body cavity nor visible signs of segmentation. Most species occur in shallow waters, but some are found at great depths. In some tunicates, adults are colonial, living in masses on the ocean floor. The pharynx is lined with numerous cilia, and the animals obtain their food by ciliary action. The cilia beat, drawing a stream of water into the pharynx, where microscopic food particles are trapped in a mucous sheet secreted from a structure called an *endostyle*.

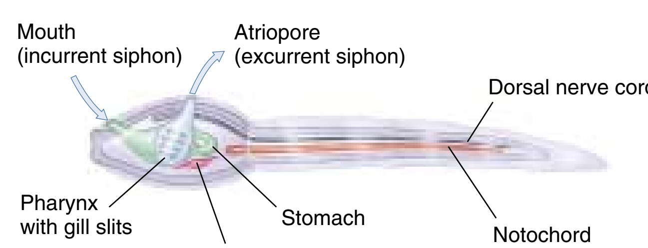
The tadpolelike larvae of tunicates plainly exhibit all of the basic characteristics of chordates and mark the tunicates as having the most primitive combination of features found in any chordate (figure 48.5*c*). The larvae do not feed and have a poorly developed gut. They remain free-swimming for only a few days before settling to the bottom and attaching themselves to a suitable substrate by means of a sucker.

Tunicates change so much as they mature and adjust developmentally to a sessile, filter-feeding existence that it would be difficult to discern their evolutionary relationships by examining an adult. Many adult tunicates secrete a **tunic,** a tough sac composed mainly of cellulose. The tunic surrounds the animal and gives the subphylum its name. Cellulose is a substance frequently found in the cell walls of plants and algae but is rarely found in ani-

(a)



(b)



(c)

FIGURE 48.5
Tunicates (phylum Chordata, subphylum Urochordata). (*a*) The sea peach, *Halocynthia auranthium*. (*b*) Diagram of the structure of an adult tunicate. (*c*) Diagram of the structure of a larval tunicate, showing the characteristic tadpolelike form. Larval tunicates resemble the postulated common ancestor of the chordates.

mals. In colonial tunicates, there may be a common sac and a common opening to the outside. There is a group of Urochordates, the Larvacea, which retains the tail and notochord into adulthood. One theory of vertebrate origins involves a larval form, perhaps that of a tunicate, which acquires the ability to reproduce.

FIGURE 48.6
Lancelets. Two lancelets, *Branchiostoma lanceolatum* (phylum Chordata, subphylum Cephalochordata), partly buried in shell gravel, with their anterior ends protruding. The muscle segments are clearly visible; the square objects along the side of the body are gonads, indicating that these are male lancelets.

Lancelets

Lancelets are scaleless, fishlike marine chordates a few centimeters long that occur widely in shallow water throughout the oceans of the world. Lancelets (subphylum Cephalochordata) were given their English name because they resemble a lancet—a small, two-edged surgical knife. There are about 23 species of this subphylum. Most of them belong to the genus *Branchiostoma*, formerly called *Amphioxus*, a name still used widely. In lancelets, the notochord runs the entire length of the dorsal nerve cord and persists throughout the animal's life.

Lancelets spend most of their time partly buried in sandy or muddy substrates, with only their anterior ends protruding (figure 48.6). They can swim, although they rarely do so. Their muscles can easily be seen as a series of discrete blocks. Lancelets have many more pharyngeal gill slits than fishes, which they resemble in overall shape. They lack pigment in their skin, which has only a single layer of cells, unlike the multilayered skin of vertebrates. The lancelet body is pointed at both ends. There is no distinguishable head or sensory structures other than pigmented light receptors.

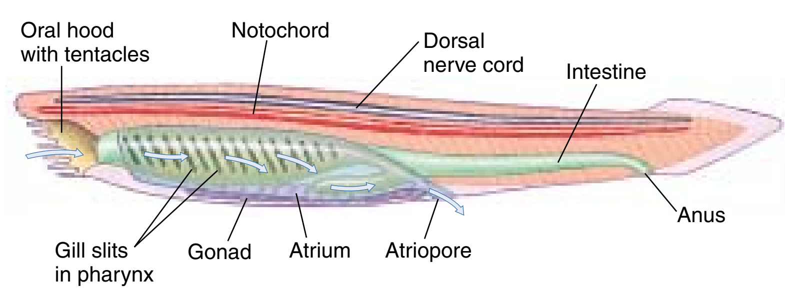


FIGURE 48.7
The structure of a lancelet. This diagram shows the path through which the lancelet's cilia pull water.

Lancelets feed on microscopic plankton, using a current created by beating cilia that lines the oral hood, pharynx, and gill slits (figure 48.7). The gill slits provide an exit for the water and are an adaptation for filter feeding. The oral hood projects beyond the mouth and bears sensory tentacles, which also ring the mouth. Males and females are separate, but no obvious external differences exist between them.

Biologists are not sure whether lancelets are primitive or are actually degenerate fishes whose structural features have been reduced and simplified during the course of evolution. The fact that lancelets feed by means of cilia and have a single-layered skin, coupled with distinctive features of their excretory systems, suggest that this is an ancient group of chordates. The recent discovery of fossil forms similar to living lancelets in rocks 550 million years old—well before the appearance of any fishes—also argues for the antiquity of this group. Recent studies by molecular systematists further support the hypothesis that lancelets are vertebrates' closest ancestors.

Nonvertebrate chordates, including tunicates and lancelets, have notochords but not vertebrae. They are the closest relatives of vertebrates.

48.3 The vertebrates have an interior framework of bone.

Characteristics of Vertebrates

Vertebrates (subphylum Vertebrata) are chordates with a spinal column. The name *vertebrate* comes from the individual bony segments called vertebrae that make up the spine. Vertebrates differ from the tunicates and lancelets in two important respects:

1. **Vertebral column.** In vertebrates, the notochord is replaced during the course of embryonic development by a bony vertebral column. The column is a series of bones that encloses and protects the dorsal nerve cord like a sleeve (figure 48.8).
2. **Head.** In all vertebrates but the earliest fishes, there is a distinct and well-differentiated head, with a skull and brain. For this reason, the vertebrates are sometimes called the **craniate chordates** (Greek *kranion*, "skull").

In addition to these two key characteristics, vertebrates differ from other chordates in other important respects:

1. **Neural crest.** A unique group of embryonic cells called the neural crest contributes to the development of many vertebrate structures. These cells develop on the crest of the neural tube as it forms by an invagination and pinching together of the neural plate (see chapter 60 for a detailed account). Neural crest cells then migrate to various locations in the developing embryo, where they participate in the development of a variety of structures.
2. **Internal organs.** Among the internal organs of vertebrates, livers, kidneys, and endocrine glands are characteristic of the group. The ductless endocrine glands secrete hormones that help regulate many of the body's functions. All vertebrates have a heart and a closed circulatory system. In both their circulatory and their excretory functions, vertebrates differ markedly from other animals.
3. **Endoskeleton.** The endoskeleton of most vertebrates is made of cartilage or bone. Cartilage and bone are specialized tissue containing fibers of the protein collagen compacted together. Bone also contains crystals of a calcium phosphate salt. Bone forms in two stages. First, collagen is laid down in a matrix of fibers along stress lines to provide flexibility, and then calcium minerals infiltrate the fibers, providing rigidity. The great advantage of bone over chitin as a structural material is that bone is strong without being brittle. The vertebrate endoskeleton makes possible the great size and extraordinary powers of movement that characterize this group.

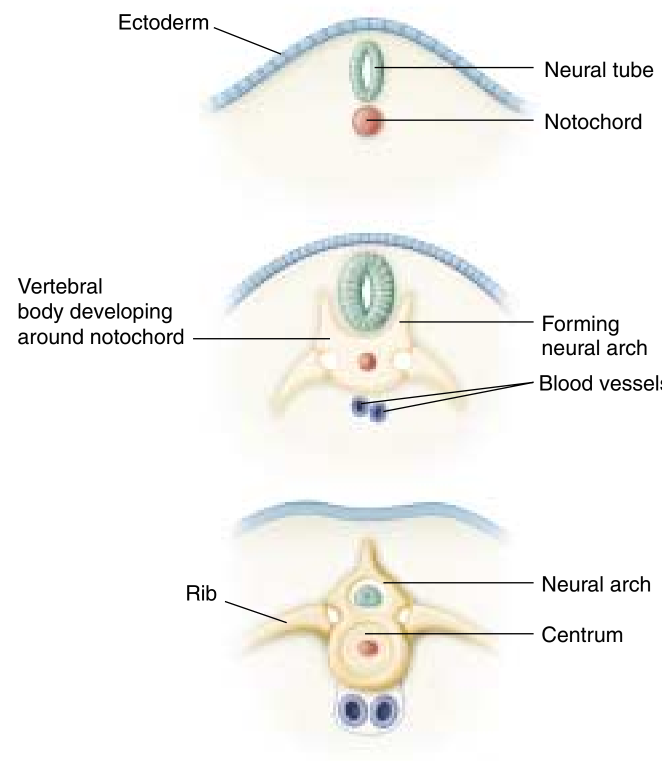


FIGURE 48.8
Embryonic development of a vertebra. During the course of evolution of animal development, the flexible notochord is surrounded and eventually replaced by a cartilaginous or bony covering, the centrum. The neural tube is protected by an arch above the centrum, and the vertebra may also have a hemal arch, which protects major blood vessels below the centrum. The vertebral column functions as a strong, flexible rod that the muscles pull against when the animal swims or moves.

Overview of the Evolution of Vertebrates

The first vertebrates evolved in the oceans about 470 million years ago. They were jawless fishes with a single caudal fin. Many of them looked like a flat hot dog, with a hole at one end and a fin at the other. The appearance of a hinged jaw was a major advancement, opening up new food options, and jawed fishes became the dominant creatures in the sea. Their descendants, the amphibians, invaded the land. Salamander-like amphibians and other, much larger now-extinct amphibians were the first vertebrates to live successfully on land. Amphibians, in turn, gave rise to the first reptiles about 300 million years ago. Within 50 million years, reptiles, better suited than amphibians to living out of water, replaced them as the dominant land vertebrates.

With the success of reptiles, vertebrates truly came to dominate the surface of the earth. Many kinds of reptiles evolved, ranging in size from smaller than a chicken to big-

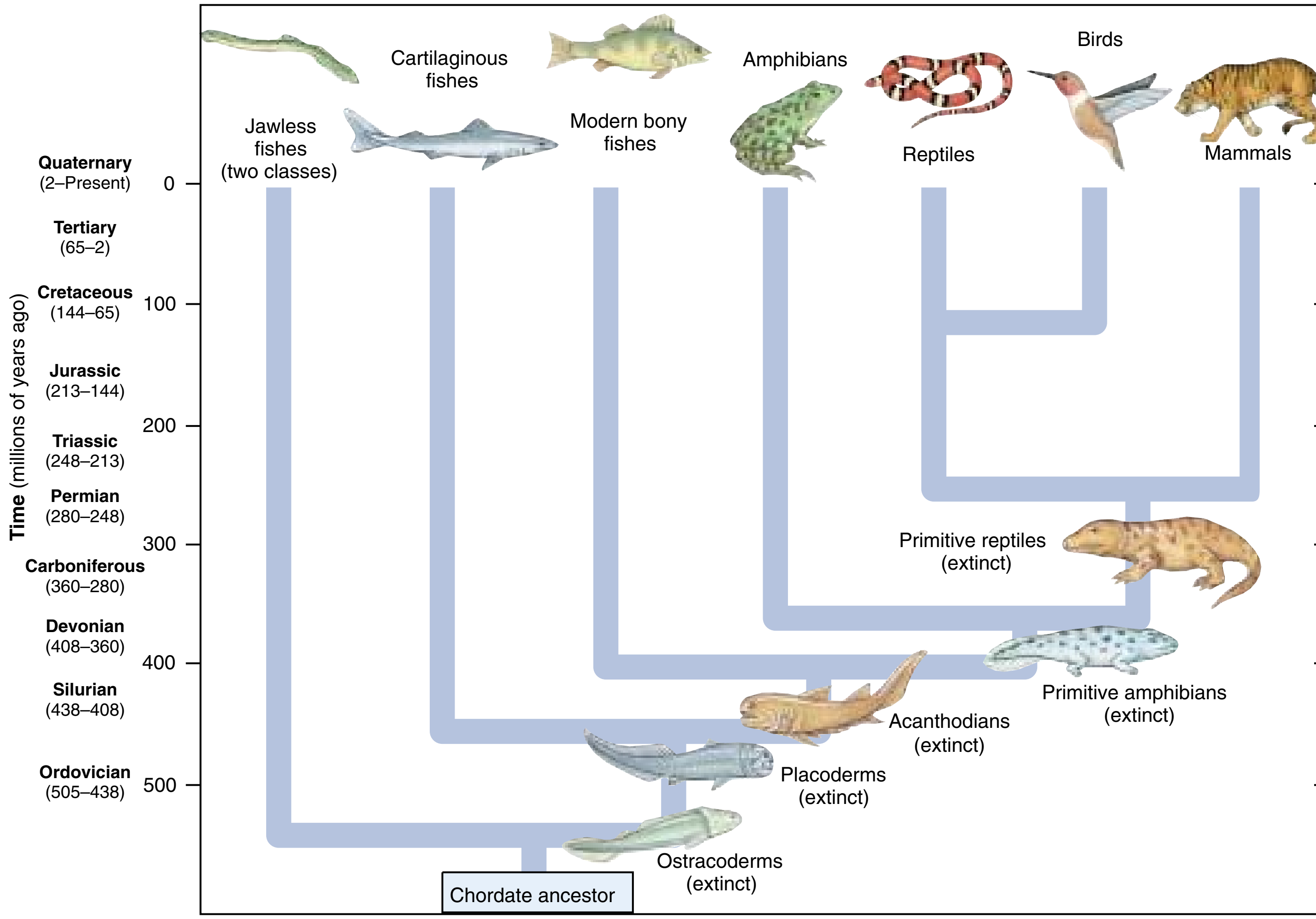


FIGURE 48.9
Vertebrate family tree. Two classes of vertebrates comprise the Agnatha, or jawless fishes. Primitive amphibians arose from fish. Primitive reptiles arose from amphibians and gave rise to mammals and to dinosaurs, which survive today as birds.

ger than a truck. Some flew, and others swam. Among them evolved reptiles that gave rise to the two remaining great lines of terrestrial vertebrates, birds (descendants of the dinosaurs) and mammals. Dinosaurs and mammals appear at about the same time in the fossil record, 220 million years ago. For over 150 million years, dinosaurs dominated the face of the earth. Over all these centuries (think of it—over *a million centuries!*) the largest mammal was no bigger than a cat. Then, about 65 million years ago, the dinosaurs abruptly disappeared, for reasons that are still hotly debated. In their absence, mammals and birds quickly took their place, becoming in turn abundant and diverse.

The history of vertebrates has been a series of evolutionary advances that have allowed vertebrates to first invade the sea and then the land. In this chapter, we will examine the key evolutionary advances that permitted vertebrates to invade the land successfully. As you will see, this invasion was a staggering evolutionary achievement, involving fundamental changes in many body systems.

Vertebrates are a diverse group, containing members adapted to life in aquatic habitats, on land, and in the air. There are eight principal classes of living vertebrates (figure 48.9). Four of the classes are fishes that live in the water, and four are land-dwelling **tetrapods,** animals with four limbs. (The name *tetrapod* comes from two Greek words meaning "four-footed.") The extant classes of fishes are the superclass Agnatha (the jawless fishes), which includes the class Myxini, the hagfish, and the class Cephalaspidomorphi, the lampreys; Chondrichthyes, the cartilaginous fishes, sharks, skates, and rays; and Osteichthyes, the bony fishes that are dominant today. The four classes of tetrapods are Amphibia, the amphibians; Reptilia, the reptiles; Aves, the birds; and Mammalia, the mammals.

Vertebrates, the principal chordate group, are characterized by a vertebral column and a distinct head.

48.4 The evolution of vertebrates involves invasions of sea, land, and air.

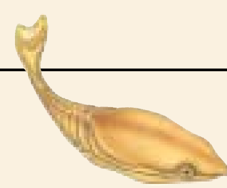
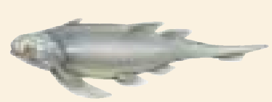
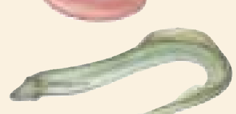
Fishes

Over half of all vertebrates are fishes. The most diverse and successful vertebrate group (figure 48.10), they provided the evolutionary base for invasion of land by amphibians. In many ways, amphibians, the first terrestrial vertebrates, can be viewed as transitional—fish out of water. In fact, fishes and amphibians share many similar features, among the host of obvious differences. First, let us look at the fishes (table 48.1).

The story of vertebrate evolution started in the ancient seas of the Cambrian Period (570 to 505 million years ago), when the first backboned animals appeared (figure 48.11). Wriggling through the water, jawless and toothless, these first fishes sucked up small food particles from the ocean floor like miniature vacuum cleaners. Most were less than a foot long, respired with gills, and had no paired fins—just a primitive tail to push them through the water. For 50 million years, during the Ordovician Period (505 to 438 million years ago), these simple fishes were the only vertebrates. By the end of this period, fish had developed primitive fins to help them swim and massive shields of bone for protection. Jawed fishes first appeared during the Silurian Period (438 to 408 million years ago) and along with them came a new mode of feeding. Later, both the cartilaginous and bony fishes appeared.

FIGURE 48.10
Fish are diverse and include more species than all other kinds of vertebrates combined.

Table 48.1 Major Classes of Fishes

Class	Typical Examples		Key Characteristics	Approximate Number of Living Species
Placodermi	Armored fishes		Jawed fishes with heavily armored heads; often quite large	Extinct
Acanthodii	Spiny fishes		Fishes with jaws; all now extinct; paired fins supported by sharp spines	Extinct
Osteichthyes	Ray-finned fishes		Most diverse group of vertebrates; swim bladders and bony skeletons; paired fins supported by bony rays	20,000
	Lobe-finned fishes		Largely extinct group of bony fishes; ancestral to amphibians; paired lobed fins	7
Chondrichthyes	Sharks, skates, rays		Streamlined hunters; cartilaginous skeletons; no swim bladders; internal fertilization	850
Myxini	Hagfishes		Jawless fishes with no paired appendages; scavengers; mostly blind, but a well-developed sense of smell	43
Cephalaspidomorphi	Lampreys		Largely extinct group of jawless fishes with no paired appendages; parasitic and nonparasitic types; all breed in fresh water	17

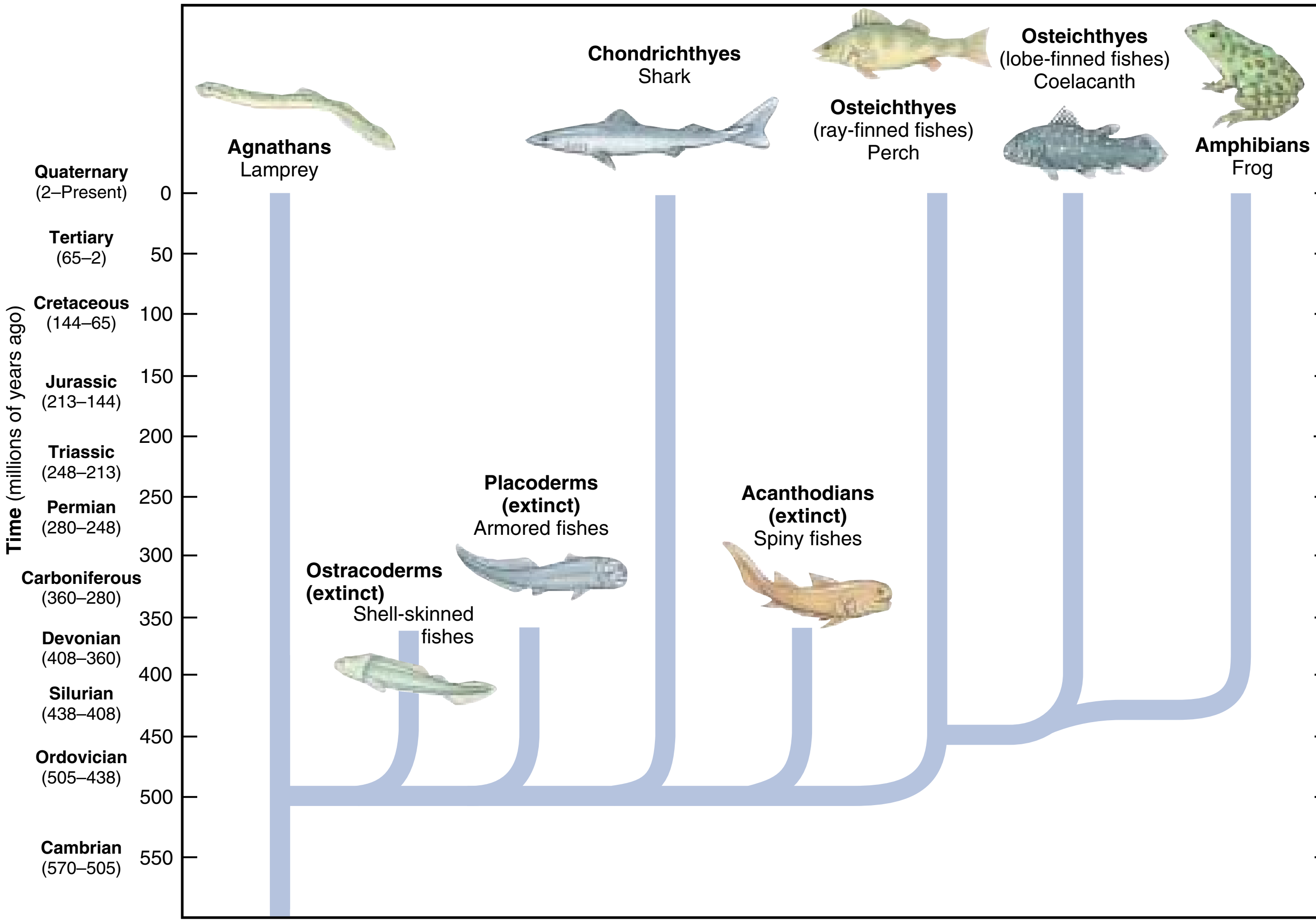


FIGURE 48.11
Evolution of the fishes. The evolutionary relationships among the different groups of fishes as well as between fishes and amphibians is shown. The spiny and armored fishes that dominated the early seas are now extinct.

Characteristics of Fishes

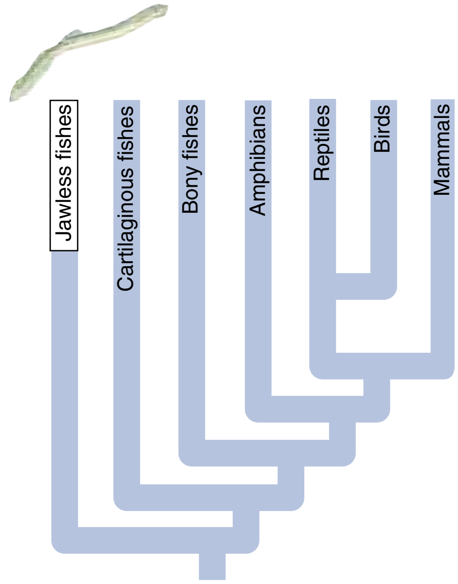
From whale sharks that are 18 meters long to tiny cichlids no larger than your fingernail, fishes vary considerably in size, shape, color, and appearance. Some live in freezing Arctic seas, others in warm freshwater lakes, and still others spend a lot of time out of water entirely. However varied, all fishes have important characteristics in common:

1. **Gills.** Fishes are water-dwelling creatures and must extract oxygen dissolved in the water around them. They do this by directing a flow of water through their mouths and across their gills. The gills are composed of fine filaments of tissue that are rich in blood vessels. They are located at the back of the pharynx and are supported by arches of cartilage. Blood moves through the gills in the opposite direction to the flow of water in order to maximize the efficiency of oxygen absorption.
2. **Vertebral column.** All fishes have an internal skeleton with a spine surrounding the dorsal nerve cord, although it may not necessarily be made of bone. The brain is fully encased within a protective box, the skull or cranium, made of bone or cartilage.
3. **Single-loop blood circulation.** Blood is pumped from the heart to the gills. From the gills, the oxygenated blood passes to the rest of the body, then returns to the heart. The heart is a muscular tube-pump made of four chambers that contract in sequence.
4. **Nutritional deficiencies.** Fishes are unable to synthesize the aromatic amino acids and must consume them in their diet. This inability has been inherited by all their vertebrate descendants.

Fishes were the first vertebrates to make their appearance, and today they are still the largest vertebrate class. They are the vertebrate group from which all other vertebrates evolved.

History of the Fishes

The First Fishes



The first fishes were members of the five Ostracoderm orders (the word means "shell-skinned"). Only their head-shields were made of bone; their elaborate internal skeletons were constructed of cartilage. Many ostracoderms were bottom dwellers, with a jawless mouth underneath a flat head, and eyes on the upper surface. Ostracoderms thrived in the Ordovician Period and in the period which followed, the Silurian Period (438 to 408 million years ago), only to become almost completely extinct at the close of the following Devonian Period (408 to 360 million years ago). One group, the jawless Agnatha, survive today as hagfish and parasitic lampreys (figure 48.12).

A fundamentally important evolutionary advance occurred in the late Silurian Period, 410 million years ago—the development of jaws. Jaws evolved from the most anterior of a series of arch-supports made of cartilage that were used to reinforce the tissue between gill slits, holding the slits open (figure 48.13). This transformation was not as radical as it might at first appear. Each gill arch was formed by a series of several cartilages (later to become bones) arranged somewhat in the shape of a V turned on its side, with the point directed outward. Imagine the fusion of the front pair of arches at top and bottom, with hinges at the points, and you have the primitive vertebrate jaw. The top half of the jaw is not attached to the skull directly except at the rear. Teeth developed on the jaws from modified scales on the skin that lined the mouth.

Armored fishes called placoderms and spiny fishes called acanthodians both had jaws. Spiny fishes were very common during the early Devonian, largely replacing ostracoderms, but became extinct themselves at the close of the Permian. Like ostracoderms, they had internal skeletons made of cartilage, but their scales contained small plates of bone, foreshadowing the much larger role bone would play in the future of vertebrates. Spiny fishes were predators and far better swimmers than ostracoderms, with as many as seven fins to aid them swimming. All of these fins were reinforced with strong spines, giving these fishes their name. No spiny fishes survive today.

FIGURE 48.12
Specialized mouth of a lamprey. Lampreys use their suckerlike mouths to attach themselves to the fishes on which they prey. When they have done so, they bore a hole in the fish with their teeth and feed on its blood.

By the mid-Devonian, the heavily armored placoderms became common. A very diverse and successful group, seven orders of placoderms dominated the seas of the late Devonian, only to become extinct at the end of that period. The front of the placoderm body was more heavily armored than the rear. The placoderm jaw was much improved from the primitive jaw of spiny fishes, with the upper jaw fused to the skull and the skull hinged on the shoulder. Many of the placoderms grew to enormous sizes, some over 30 feet long, with two-foot skulls that had an enormous bite.

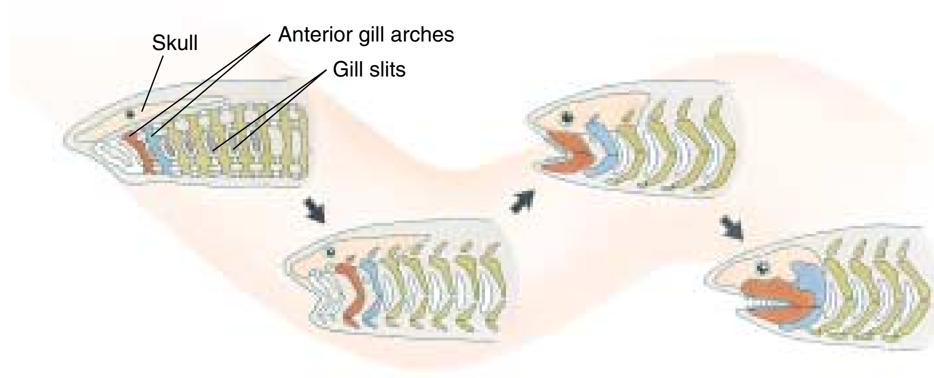


FIGURE 48.13
Evolution of the jaw. Jaws evolved from the anterior gill arches of ancient, jawless fishes.

The Rise of Active Swimmers

At the end of the Devonian, essentially all of these pioneer vertebrates disappeared, replaced by sharks and bony fishes. Sharks and bony fishes first evolved in the early Devonian, 400 million years ago. In these fishes, the jaw was improved even further, with the first gill arch behind the jaws being transformed into a supporting strut or prop, joining the rear of the lower jaw to the rear of the skull. This allowed the mouth to open very wide, into almost a full circle. In a great white shark, this wide-open mouth can be a very efficient weapon.

The major factor responsible for the replacement of primitive fishes by sharks and bony fishes was that they had a superior design for swimming. The typical shark and bony fish is streamlined. The head of the fish acts as a wedge to cleave through the water, and the body tapers back to the tail, allowing the fish to slip through the water with a minimum amount of turbulence.

In addition, sharks and bony fishes have an array of mobile fins that greatly aid swimming. First, there is a propulsion fin: a large and efficient tail (caudal) fin that helps drive the fish through the water when it is swept side-to-side, pushing against the water and thrusting the fish forward. Second, there are stabilizing fins: one (or sometimes two) dorsal fins on the back that act as a stabilizer to prevent rolling as the fish swims through the water, while another ventral fin acts as a keel to prevent side-slip. Third, there are the paired fins at shoulder and hip ("A fin at each corner"), consisting of a front (pectoral) pair and a rear (pelvic) pair. These fins act like the elevator flaps of an airplane to assist the fish in going up or down through the water, as rudders to help it turn sharply left or right, and as brakes to help it stop quickly.

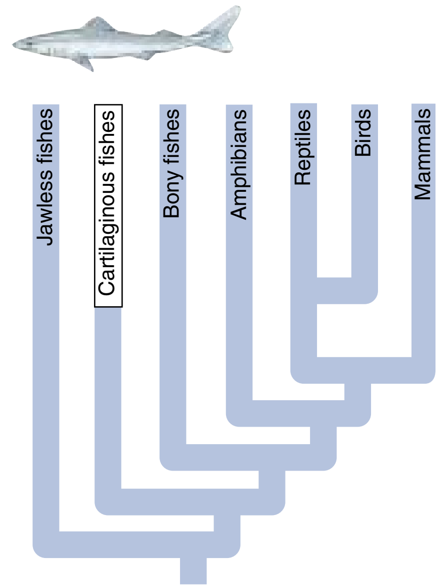


FIGURE 48.14
Chondrichthyes. Members of the class Chondrichthyes, such as this bull shark, are mainly predators or scavengers and spend most of their time in graceful motion. As they move, they create a flow of water past their gills, extracting oxygen from the water.

Sharks Become Top Predators

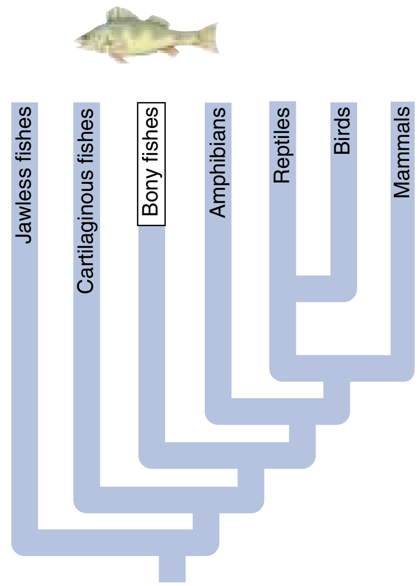
In the period following the Devonian, the Carboniferous Period (360 to 280 million years ago), sharks became the dominant predator in the sea. Sharks (class Chondrichythes) have a skeleton made of cartilage, like primitive fishes, but it is "calcified," strengthened by granules of calcium carbonate deposited in the outer layers of cartilage. The result is a very light and strong skeleton. Streamlined, with paired fins and a light, flexible skeleton, sharks are superior swimmers (figure 48.14). Their pectoral fins are particularly large, jutting out stiffly like airplane wings—and that is how they function, adding lift to compensate for the downward thrust of the tail fin. Very aggressive predators, some sharks reached enormous size.

Sharks were among the first vertebrates to develop teeth. These teeth evolved from rough scales on the skin and are not set into the jaw, as yours are, but rather sit atop it. The teeth are not firmly anchored and are easily lost. In a shark's mouth, the teeth are arrayed in up to 20 rows, the teeth in front doing the biting and cutting, while behind them other teeth grow and await their turn. When a tooth breaks or is worn down, a replacement from the next row moves forward. One shark may eventually use more than 20,000 teeth. This programmed loss of teeth offers a great advantage: the teeth in use are always new and sharp. The skin is covered with tiny teeth-like scales, giving it a rough "sandpaper" texture. Like the teeth, these scales are constantly replaced throughout the shark's life.

Reproduction among the Chondrichythes is the most advanced of any fishes. Shark eggs are fertilized internally. During mating, the male grasps the female with modified fins called claspers. Sperm run from the male into the female through grooves in the claspers. Although a few species lay fertilized eggs, the eggs of most species develop within the female's body, and the pups are born alive.

Many of the early evolutionary lines of sharks died out during the great extinction at the end of the Permian Period (280 to 248 million years ago). The survivors thrived and underwent a burst of diversification during the Mesozoic era, when most of the modern groups of sharks appeared. Skates and rays (flattened sharks that are bottom-dwellers) evolved at this time, some 200 million years after the sharks first appeared. Sharks competed successfully with the marine reptiles of that time and are still the dominant predators of the sea. Today there are 275 species of sharks, more kinds than existed in the Carboniferous.

Bony Fishes Dominate the Water



Bony fishes (members of the class Osteichthyes, figure 48.15) evolved at the same time as sharks, some 400 million years ago, but took quite a different evolutionary road. Instead of gaining speed through lightness, as sharks did, bony fishes adopted a heavy internal skeleton made completely of bone. Such an internal skeleton is very strong, providing a base against which very strong muscles could pull. The process of *ossification* (the evolutionary replacement of cartilage by bone) happened suddenly in evolutionary terms, completing a process started by sharks, who lay down a thin film of bone over their cartilage. Not only is the internal skeleton ossified, but also the external skeleton, the outer covering of plates and scales. Many scientists believe bony fishes evolved from spiny sharks, which also had bony plates set in their skin. Bony fishes are the most successful of all fishes, indeed of all vertebrates. There are several dozen orders containing more than 20,000 living species.

Unlike sharks, bony fishes evolved in fresh water. The most ancient fossils of bony fishes are found in freshwater lake beds from the middle Devonian. These first bony fishes were small and possessed paired air sacs connected to the back of the throat. These sacs could be inflated with air to buoy the fish up or deflated to sink it down in the water.

Most bony fishes have highly mobile fins, very thin scales, and completely symmetrical tails (which keep the fish on a straight course as it swims through the water). This is a very successful design for a fish. Two great groups arose from these pioneers: the lobe-finned fishes, ancestors of the first tetrapods, and the ray-finned fishes, which include the vast majority of today's fishes.

The characteristic feature of all ray-finned fishes is an internal skeleton of parallel bony rays that support and stiffen each fin. There are no muscles within the fins; they are moved by muscles within the body. In ray-finned fishes, the primitive air sacs are transformed into an air pouch, which provides a remarkable degree of control over buoyancy.

Important Adaptations of Bony Fishes

The remarkable success of the bony fishes has resulted from a series of significant adaptations that have enabled them to dominate life in the water. These include the swim bladder, lateral line system, and gill cover.

Swim Bladder. Although bones are heavier than cartilaginous skeletons, bony fishes are still buoyant because they possess a swim bladder, a gas-filled sac that allows them to regulate their buoyant density and so remain suspended at any depth in the water effortlessly (figure 48.16). Sharks, by contrast, must move through the water or sink, as their bodies are denser than water. In primitive bony fishes, the swim bladder is a ventral outpocketing of the pharynx behind the throat, and these species fill the swim bladder by simply gulping air at the surface of the water. In most of today's bony fishes, the swim bladder is an independent organ that is filled and drained of gases, mostly nitrogen and oxygen, internally. How do bony fishes manage this remarkable trick? It turns out that the gases are released from their blood. Gas exchange occurs across the wall of the swim bladder and the blood vessels located near the swim bladder. A variety of physiological factors controls the exchange of gases between the blood stream and the swim bladder.

Lateral Line System. Although precursors are found in sharks, bony fishes possess a fully developed lateral line system. The lateral line system consists of a series of sensory organs that project into a canal beneath the surface of the skin. The canal runs the length of the fish's body and is open to the exterior through a series of sunken pits. Move-

FIGURE 48.15
Bony fishes. The bony fishes (class Osteichthyes) are extremely diverse. This Korean angelfish in Fiji is one of the many striking fishes that live around coral reefs in tropical seas.

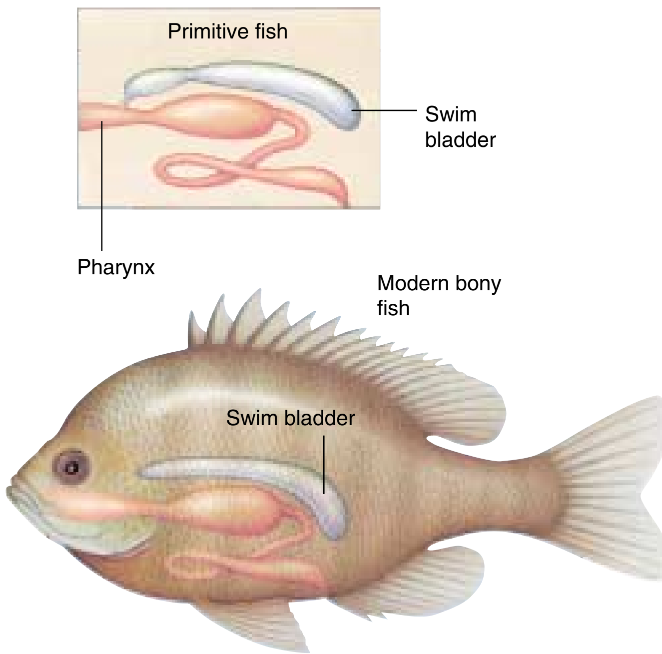


FIGURE 48.16
Diagram of a swim bladder. The bony fishes use this structure, which evolved as a ventral outpocketing of the pharynx, to control their buoyancy in water.

FIGURE 48.17
The living coelacanth, *Latimeria chalumnae*. Discovered in the western Indian Ocean in 1938, this coelacanth represents a group of fishes that had been thought to be extinct for about 70 million years. Scientists who studied living individuals in their natural habitat at depths of 100 to 200 meters observed them drifting in the current and hunting other fishes at night. Some individuals are nearly 3 meters long; they have a slender, fat-filled swim bladder. *Latimeria* is a strange animal, and its discovery was a complete surprise.

ment of water past the fish forces water through the canal. The sensory organs consist of clusters of cells with hairlike projections called cilia, embedded in a gelatinous cap. The hairs are deflected by the slightest movement of water over them. The pits are oriented so that some are stimulated no matter what direction the water moves (see chapter 55). Nerve impulses from these sensory organs permit the fish to assess its rate of movement through water, sensing the movement as pressure waves against its lateral line. This is how a trout orients itself with its head upstream.

The lateral line system also enables a fish to detect motionless objects at a distance by the movement of water reflected off the object. In a very real sense, this is the fish equivalent of hearing. The basic mechanism of cilia deflection by pressure waves is very similar to what happens in human ears (see chapter 55).

Gill Cover. Most bony fishes have a hard plate called the operculum that covers the gills on each side of the head. Flexing the operculum permits bony fishes to pump water over their gills. The gills are suspended in the pharyngeal slits that form a passageway between the pharynx and the outside of the fish's body. When the operculum is closed, it seals off the exit. When the mouth is open, closing the operculum increases the volume of the mouth cavity, so that water is drawn into the mouth. When the mouth is closed, opening the operculum decreases the volume of the mouth cavity, forcing water past the gills to the outside. Using this very efficient bellows, bony fishes can pass water over the gills while stationary in the water. That is what a goldfish is doing when it seems to be gulping in a fish tank.

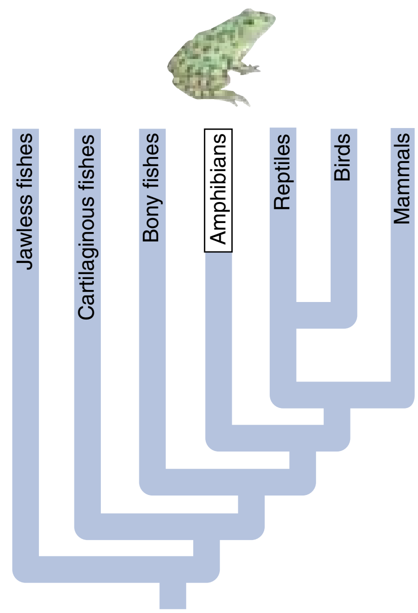
The Path to Land

Lobe-finned fishes (figure 48.17) evolved 390 million years ago, shortly after the first bony fishes appeared. Only seven species survive today, a single species of coelacanth and six species of lungfish. Lobe-finned fishes have paired fins that consist of a long fleshy muscular lobe (hence their name), supported by a central core of bones that form fully articulated joints with one another. There are bony rays only at the tips of each lobed fin. Muscles within each lobe can move the fin rays independently of one another, a feat no ray-finned fish could match. Although rare today, lobe-finned fishes played an important part in the evolutionary story of vertebrates. Amphibians almost certainly evolved from the lobe-finned fishes.

Fishes are characterized by gills and a simple, single-loop circulatory system. Cartilaginous fishes, such as sharks, are fast swimmers, while the very successful bony fishes have unique characteristics such as swim bladders and lateral line systems.

Amphibians

Frogs, salamanders, and caecilians, the damp-skinned vertebrates, are direct descendants of fishes. They are the sole survivors of a very successful group, the amphibians, the first vertebrates to walk on land. Most present-day amphibians are small and live largely unnoticed by humans. Amphibians are among the most numerous of terrestrial animals; there are more species of amphibians than of mammals. Throughout the world amphibians play key roles in terrestrial food chains.



Characteristics of Living Amphibians

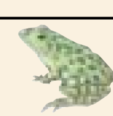
Biologists have classified living species of amphibians into three orders (table 48.2): 3680 species of frogs and toads in 22 families make up the order Anura (“without a tail”); 369 species of salamanders and newts in 9 families make up the order Urodela or Caudata (“visible tail”); and 168 species (6 families) of wormlike, nearly blind organisms called caecilians that live in the tropics make up the order Apoda or Gymnophiona (“without legs”). They have key characteristics in common:

1. **Legs.** Frogs and salamanders have four legs and can move about on land quite well. Legs were one of the key adaptations to life on land. Caecilians have lost their legs during the course of adapting to a burrowing existence.
2. **Cutaneous respiration.** Frogs, salamanders, and caecilians all supplement the use of lungs by respiring directly across their skin, which is kept moist and provides an extensive surface area. This mode of respiration is only efficient for a high surface-to-volume ratio in an animal.
3. **Lungs.** Most amphibians possess a pair of lungs, although the internal surfaces are poorly developed, with much less surface area than reptilian or mammalian lungs. Amphibians still breathe by lowering the floor of the mouth to suck air in, then raising it back to force the air down into the lungs.
4. **Pulmonary veins.** After blood is pumped through the lungs, two large veins called pulmonary veins return the aerated blood to the heart for repumping. This allows the aerated blood to be pumped to the tissues at a much higher pressure than when it leaves the lungs.
5. **Partially divided heart.** The initial chamber of the fish heart is absent in amphibians, and the second and last chambers are separated by a dividing wall that helps prevent aerated blood from the lungs from mixing with nonaerated blood being returned to the heart from the rest of the body. This separates the blood circulation into two separate paths, pulmonary and systemic. The separation is imperfect; the third chamber has no dividing wall.

Several other specialized characteristics are shared by all present-day amphibians. In all three orders, there is a zone of weakness between the base and the crown of the teeth. They also have a peculiar type of sensory rod cell in the retina of the eye called a “green rod.” The exact function of this rod is unknown.

Amphibians, with legs and more efficient blood circulation than fishes, were the first vertebrates to walk on land.

Table 48.2 Orders of Amphibians

Order	Typical Examples		Key Characteristics	Approximate Number of Living Species
Anura	Frogs, toads		Compact tailless body; large head fused to the trunk; rear limbs specialized for jumping	3680
Caudata	Salamanders, newts		Slender body; long tail and limbs set out at right angles to the body	369
Apoda (Gymnophiona)	Caecilians		Tropical group with a snakelike body; no limbs; little or no tail	168

History of the Amphibians

The word *amphibia* (a Greek word meaning "both lives") nicely describes the essential quality of modern day amphibians, referring to their ability to live in two worlds: the aquatic world of their fish ancestors and in the terrestrial world that they first invaded. In this section, we will review the checkered history of this group, almost all of whose members have been extinct for the last 200 million years. Then, in the following section, we will examine in more detail what the few kinds of surviving amphibians are like.

Origin of Amphibians

Paleontologists (scientists who study fossils) agree that amphibians must have evolved from the lobe-finned fishes, although for some years there has been considerable disagreement about whether the direct ancestors were coelacanths, lungfish, or the extinct rhipidistian fishes. Good arguments can be made for each. Many details of amphibian internal anatomy resemble those of the coelacanth. Lungfish and rhipidistians have openings in the tops of their mouths similar to the internal nostrils of amphibians. In addition, lungfish have paired lungs, like those of amphibians. Recent DNA analysis indicates lungfish are in fact far more closely related to amphibians than are coelacanths. Most paleontologists consider that amphibians evolved from rhipidistian fishes, rather than lungfish, because the pattern of bones in the early amphibian skull and limbs bears a remarkable resemblance to the rhipidistians. They also share a particular tooth structure.

They successful invasion of land by vertebrates involved a number of major adaptations:

1. Legs were necessary to support the body's weight as well as to allow movement from place to place (figure 48.18).
2. Lungs were necessary to extract oxygen from air. Even though there is far more oxygen available to gills in air than in water, the delicate structure of fish gills requires the buoyancy of water to support them and they will not function in air.
3. The heart had to be redesigned to make full use of new respiratory systems and to deliver the greater amounts of oxygen required by walking muscles.
4. Reproduction had to be carried out in water until methods evolved to prevent eggs from drying out.
5. Most importantly, a system had to be developed to prevent the body itself from drying out.

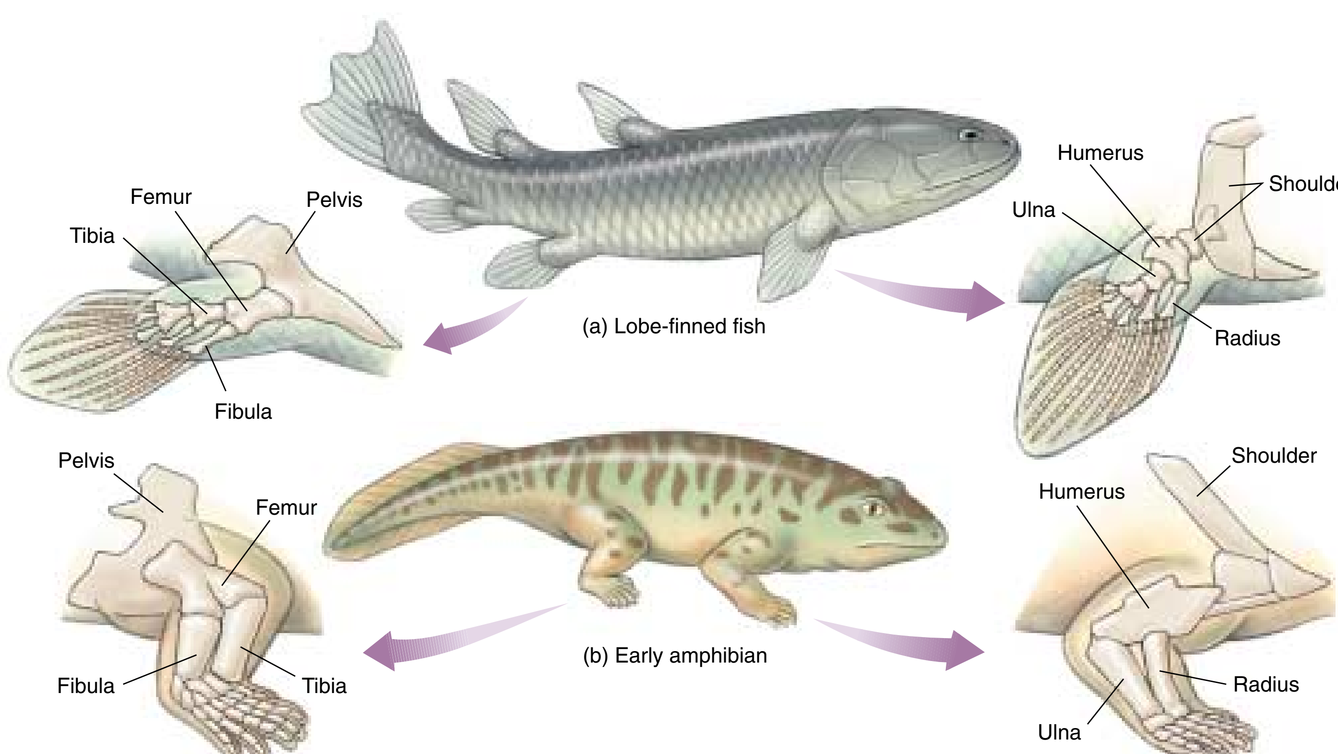


FIGURE 48.18
A comparison between the limbs of a lobe-finned fish and those of a primitive amphibian. (*a*) A lobe-finned fish. Some of these animals could probably move onto land. (*b*) A primitive amphibian. As illustrated by their skeletal structure, the legs of such an animal could clearly function on land much better than the fins of the lobe-finned fish.

The First Amphibian

Amphibians solved these problems only partially, but their solutions worked well enough that amphibians have survived for 350 million years. Evolution does not insist on perfect solutions, only workable ones.

Ichthyostega, the earliest amphibian fossil (figure 48.19) was found in a 370-million-year-old rock in Greenland. At that time, Greenland was part of the North American continent and lay near the equator. For the next 100 million years, all amphibian fossils are found in North America. Only when Asia and the southern continents all merged with North America to form the supercontinent Pangaea did amphibians spread throughout the world.

Ichthyostega was a strongly built animal, with four sturdy legs well supported by hip and shoulder bones. The shoulder bones no longer attached to the skull as in fish. The hipbones were braced against the backbone unlike in fish, so the limbs could support the animal's weight. To strengthen the backbone further, long, broad ribs that overlap each other formed a solid cage for the lungs and heart. The rib cage was so solid that it probably couldn't expand and contract for breathing. Instead, *Ichthyostega* obtained oxygen somewhat as a fish does, by lowering the floor of the mouth to draw air in, then raising it to push air down the windpipe into the lungs.

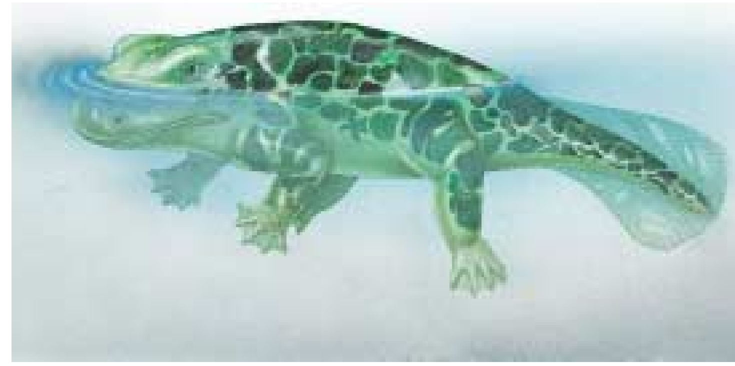


FIGURE 48.19
Amphibians were the first vertebrates to walk on land. Reconstruction of *Ichthyostega*, one of the first amphibians with efficient limbs for crawling on land, an improved olfactory sense associated with a lengthened snout, and a relatively advanced ear structure for picking up airborne sounds. Despite these features, *Ichthyostega*, which lived about 350 million years ago, was still quite fishlike in overall appearance and represents a very early amphibian.

The Rise and Fall of Amphibians

Amphibians first became common during the Carboniferous Period (360 to 280 million years ago). Fourteen families of amphibians are known from the early Carboniferous, nearly all aquatic or semiaquatic, like *Ichthyostega*. By the late Carboniferous, much of North America was covered by low-lying tropical swamplands, and 34 families of amphibians thrived in this wet terrestrial environment, sharing it with pelycosaurs and other early reptiles. In the early Permian Period that followed (280 to 248 million years ago), a remarkable change occurred among amphibians—they began to leave the marshes for dry uplands. Many of these terrestrial amphibians had bony plates and armor covering their bodies and grew to be very large, some as big as a pony (figure 48.20). Both their large size and the complete covering of their bodies indicate that these amphibians did not use the skin respiratory system of present-day amphibians, but rather had an impermeable leathery skin to prevent water loss. By the mid-Permian, there were 40 families of amphibians. Only 25% of them were still semiaquatic like Ichthyostega; 60% of the amphibians were fully terrestrial, 15% were semiterrestrial.

This was the peak of amphibian success. By the end of the Permian, a reptile called a therapsid had become common, ousting the amphibians from their newly acquired niche on land. Following the mass extinction event at the end of the Permian, therapsids were the dominant land vertebrate and most amphibians were aquatic. This trend continued in the following Triassic Period (248 to 213 million years ago), which saw the virtual extinction of amphibians from land. By the end of the Triassic, there were only 15 families of amphibians (including the first frog), and almost without exception they were aquatic. Some of these grew to great size; one was 3 meters long. Only two groups of amphibians are known from the following Jurassic Period (213 to 144 million years ago), the anurans (frogs and toads) and the urodeles (salamanders and newts). The Age of Amphibians was over.

FIGURE 48.20
A terrestrial amphibian of the Permian. *Cacops*, a large, extinct amphibian, had extensive body armor.

Amphibians Today

All of today's amphibians descended from the two families of amphibians that survived the Age of the Dinosaurs. During the Tertiary Period (65 to 2 million years ago), these moist-skinned amphibians underwent a highly successful invasion of wet habitats all over the world, and today there are over 4200 species of amphibians in 37 different families.

Anura. Frogs and toads, amphibians without tails, live in a variety of environments from deserts and mountains to ponds and puddles (figure 48.21*a*). Frogs have smooth, moist skin, a broad body, and long hind legs that make them excellent jumpers. Most frogs live in or near water, although some tropical species live in trees. Unlike frogs, toads have a dry, bumpy skin, short legs, and are well adapted to dry environments. All adult anurans are carnivores, eating a wide variety of invertebrates.

Most frogs and toads return to water to reproduce, laying their eggs directly in water. Their eggs lack water-tight external membranes and would dry out quickly out of the water. Eggs are fertilized externally and hatch into swimming larval forms called tadpoles. Tadpoles live in the water, where they generally feed on minute algae. After considerable growth, the body of the tadpole gradually changes into that of an adult frog. This process of abrupt change in body form is called **metamorphosis.**

Urodela (Caudata). Salamanders have elongated bodies, long tails, and smooth moist skin (figure 48.21*b*). They typically range in length from a few inches to a foot, although giant Asiatic salamanders of the genus *Andrias* are as much as 1.5 meters long and weigh up to 33 kilograms. Most salamanders live in moist places, such as under stones or logs, or among the leaves of tropical plants. Some salamanders live entirely in water.

Salamanders lay their eggs in water or in moist places. Fertilization is usually external, although a few species practice a type of internal fertilization in which the female picks up sperm packets deposited by the male. Unlike anurans, the young that hatch from salamander eggs do not undergo profound metamorphosis, but are born looking like small adults and are carnivorous.

Apoda (Gymnophiona). Caecilians, members of the order Apoda (Gymnophiona), are a highly specialized group of tropical burrowing amphibians (figure 48.21*c*). These legless, wormlike creatures average about 30 centimeters long, but can be up to 1.3 meters long. They have very small eyes and are often blind. They resemble worms but have jaws with teeth. They eat worms and other soil invertebrates. The caecilian male deposits sperm directly into the female, and the female usually bears live young. Mud eels, small amphibians with tiny forelimbs and no hind limbs that live in the eastern United States, are not apodans, but highly specialized urodelians.

(a)

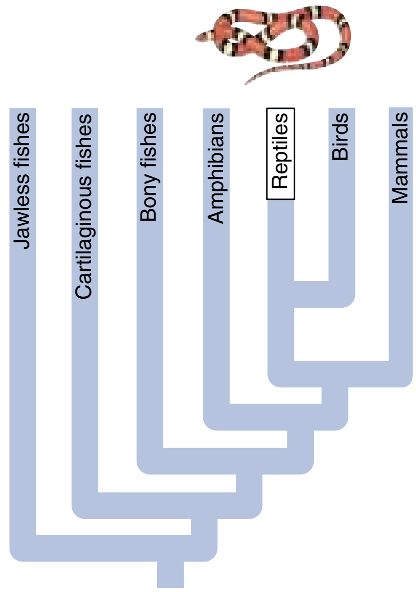
(b)

(c)

FIGURE 48.21
Class Amphibia. (*a*) Red-eyed tree frog, *Agalychnis callidryas* (order Anura). (*b*) An adult barred tiger salamander, *Ambystoma tigrinum* (order Caudata). (*c*) A XXXXXXX caecilian, *XXXXXXXX xxxxxxxxx* (order Gymnophiona).

Amphibians ventured onto land some 370 million years ago. They are characterized by moist skin, legs (secondarily lost in some species), lungs (usually), and a more complex and divided circulatory system. They are still tied to water for reproduction.

Reptiles



If one thinks of amphibians as a first draft of a manuscript about survival on land, then reptiles are the finished book. For each of the five key challenges of living on land, reptiles improved on the innovations first seen in amphibians. Legs were arranged to support the body's weight more effectively, allowing reptile bodies to be bigger and to *run*. Lungs and heart were altered to make them more efficient. The skin was covered with dry plates or scales to minimize water loss, and eggs were encased in watertight covers (figure 48.22). Reptiles were the first truly *terrestrial* vertebrates.

Over 7000 species of reptiles (class Reptilia) now live on earth (table 48.3). They are a highly successful group in today's world, more common than mammals. There are three reptile species for every two mammal species. While it is traditional to think of reptiles as more primitive than mammals, the great majority of reptiles that live today evolved from lines that appeared after therapsids did (the line that leads directly to mammals).

Key Characteristics of Reptiles

All living reptiles share certain fundamental characteristics, features they retain from the time when they replaced amphibians as the dominant terrestrial vertebrates. Among the most important are:

1. **Amniotic egg**. Amphibians never succeeded in becoming fully terrestrial because amphibian eggs must be laid in water to avoid drying out. Most reptiles lay watertight eggs that contain a food source (the yolk) and a series of four membranes—the yolk sac, the amnion, the allantois, and the chorion (figure 48.22). Each membrane plays a role in making the egg an independent life-support system. The outermost membrane of the egg is the **chorion,** which lies just beneath the porous shell. It allows respiratory gases to pass through, but retains water within the egg. Within, the **amnion** encases the developing embryo within a fluid-filled cavity. The **yolk sac** provides food from the yolk for the embryo via blood vessels connecting to the embryo's gut. The **allantois** surrounds a cavity into which waste products from the embryo are excreted. All modern reptiles (as well as birds and mammals) show exactly this same pattern of membranes within the egg. These three classes are called amniotes.
2. **Dry skin.** Living amphibians have a moist skin and must remain in moist places to avoid drying out. Reptiles have dry, watertight skin. A layer of scales or armor covers their bodies, preventing water loss. These scales develop as surface cells fill with keratin, the same protein that forms claws, fingernails, hair, and bird feathers.
3. **Thoracic breathing.** Amphibians breathe by squeezing their throat to pump air into their lungs; this limits their breathing capacity to the volume of their mouth. Reptiles developed pulmonary breathing, expanding and contracting the rib cage to suck air into the lungs and then force it out. The capacity of this system is limited only by the volume of the lungs.

Reptiles were the first vertebrates to completely master the challenge of living on dry land.

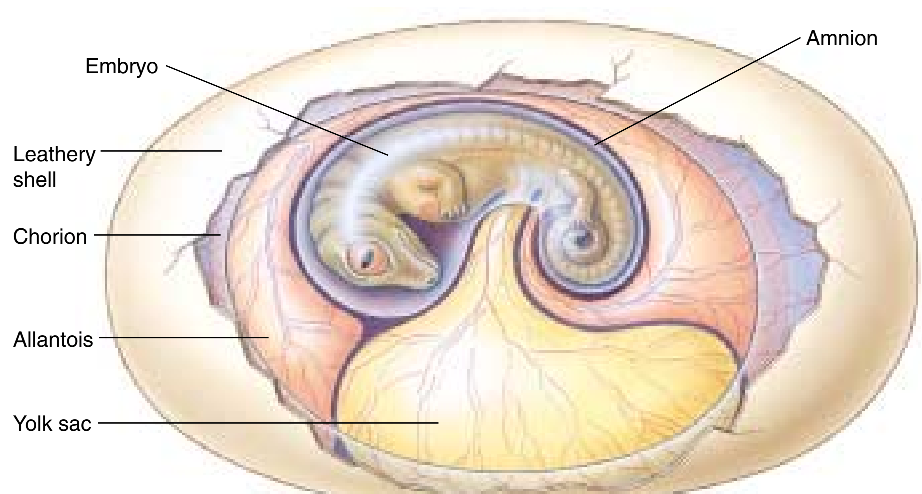
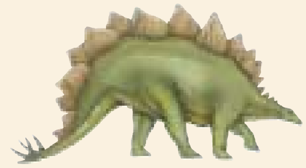
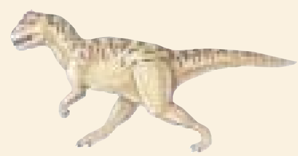
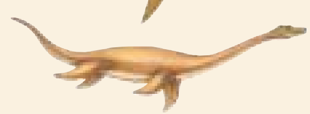
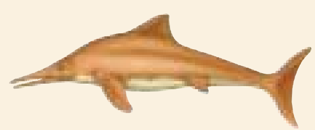
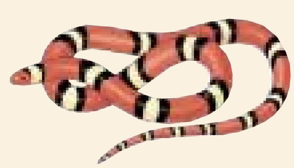
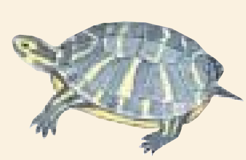
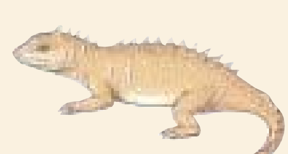


FIGURE 48.22
The watertight egg. The amniotic egg is perhaps the most important feature that allows reptiles to live in a wide variety of terrestrial habitats.

Table 48.3 Major Orders of Reptiles

Order	Typical Examples		Key Characteristics	Approximate Number of Living Species
Ornithischia	Stegosaur		Dinosaurs with two pelvic bones facing backward, like a bird's pelvis; herbivores, with turtlelike upper beak; legs under body	Extinct
Saurischia	Tyrannosaur		Dinosaurs with one pelvic bone facing forward, the other back, like a lizard's pelvis; both plant- and flesh-eaters; legs under body	Extinct
Pterosauria	Pterosaur		Flying reptiles; wings were made of skin stretched between fourth fingers and body; wingspans of early forms typically 60 centimeters, later forms nearly 8 meters	Extinct
Plesiosaura	Plesiosaur		Barrel-shaped marine reptiles with sharp teeth and large, paddle-shaped fins; some had snakelike necks twice as long as their bodies	Extinct
Ichthyosauria	Ichthyosaur		Streamlined marine reptiles with many body similarities to sharks and modern fishes	Extinct
Squamata, suborder Sauria	Lizards		Lizards; limbs set at right angles to body; anus is in transverse (sideways) slit; most are terrestrial	3800
Squamata, suborder Serpentes	Snakes		Snakes; no legs; move by slithering; scaly skin is shed periodically; most are terrestrial	3000
Chelonia	Turtles, tortoises, sea turtles		Ancient armored reptiles with shell of bony plates to which vertebrae and ribs are fused; sharp, horny beak without teeth	250
Crocodylia	Crocodiles, alligators, gavials, caimans		Advanced reptiles with four-chambered heart and socketed teeth; anus is a longitudinal (lengthwise) slit; closest living relatives to birds	25
Rhynchocephalia	Tuataras		Sole survivors of a once successful group that largely disappeared before dinosaurs; fused, wedgelike, socketless teeth; primitive third eye under skin of forehead	2

The Rise and Fall of Dominant Reptile Groups

During the 250 million years that reptiles were the dominant large terrestrial vertebrates, four major forms of reptiles took turns as the dominant type: pelycosaurs, therapsids, thecodonts, and dinosaurs.

Pelycosaurs: Becoming a Better Predator

Early reptiles like *pelycosaurs* were better adapted to life on dry land than amphibians because they evolved watertight eggs. They had powerful jaws because of an innovation in skull design and muscle arrangement. Pelycosaurs were **synapsids,** meaning that their skulls had a pair of temporal holes behind the openings for the eyes. An important feature of reptile classification is the presence and number of openings behind the eyes (see figure 48.27). Their jaw muscles were anchored to these holes, which allowed them to bite more powerfully. An individual pelycosaur weighed about 200 kilograms. With long, sharp, "steak knife" teeth, pelycosaurs were the first land vertebrates to kill beasts their own size (figure 48.23). Dominant for 50 million years, pelycosaurs once made up 70% of all land vertebrates. They died out about 250 million years ago, replaced by their direct descendants—the therapsids.

FIGURE 48.23
A pelycosaur. *Dimetrodon*, a carnivorous pelycosaur, had a dorsal sail that is thought to have been used to dissipate body heat or gain it by basking.

Therapsids: Speeding Up Metabolism

Therapsids (figure 48.24) ate ten times more frequently than their pelycosaur ancestors (figure 48.24). There is evidence that they may have been endotherms, able to regulate their own body temperature. The extra food consumption would have been necessary to produce body heat. This would have permitted therapsids to be far more active than other vertebrates of that time, when winters were cold and long. For 20 million years, therapsids (also called "mammallike reptiles") were the dominant land vertebrate, until largely replaced 230 million years ago by a cold-blooded, or ectothermic, reptile line—the thecodonts. Therapsids became extinct 170 million years ago, but not before giving rise to their descendants—the mammals.

FIGURE 48.24
A therapsid. This small weaslelike cynodont therapsid, *Megazostrodon*, may have had fur. From the late Triassic, it is so similar to modern mammals that some paleontologists consider it the first mammal.

Thecodonts: Wasting Less Energy

Thecodonts were **diapsids,** their skulls having two pairs of temporal holes, and like amphibians and early reptiles, they were ectotherms (figure 48.25). Thecodonts largely replaced therapsids when the world's climate warmed 230 million years ago. In the warm climate, the therapsid's endothermy no longer offered a competitive advantage, and ectothermic thecodonts needed only a tenth as much food. Thecodonts were the first land vertebrates to be bipedal—to stand and walk on two feet. They were dominant through the Triassic and survived for 15 million years, until replaced by their direct descendants—the dinosaurs.

FIGURE 48.25
A thecodont. *Euparkeria*, a thecodont, had rows of bony plates along the sides of the backbone, as seen in modern crocodiles and alligators.

Dinosaurs: Learning to Run Upright

Dinosaurs evolved from thecodonts about 220 million years ago. Unlike the thecodonts, their legs were positioned directly underneath their bodies, a significant improvement in body design (figure 48.26). This design placed the weight of the body directly over the legs, which allowed dinosaurs to run with great speed and agility. A dinosaur fossil can be distinguished from a thecodont fossil by the presence of a hole in the side of the hip socket. Because the dinosaur leg is positioned underneath the socket, the force is directed upward, not inward, so there was no need for bone on the side of the socket. Dinosaurs went on to become the most successful of all land vertebrates, dominating for 150 million years. All dinosaurs became extinct rather abruptly 65 million years ago, apparently as a result of an asteroid's impact.

Figures 48.27 and 48.28 summarize the evolutionary relationships among the extinct and living reptiles.

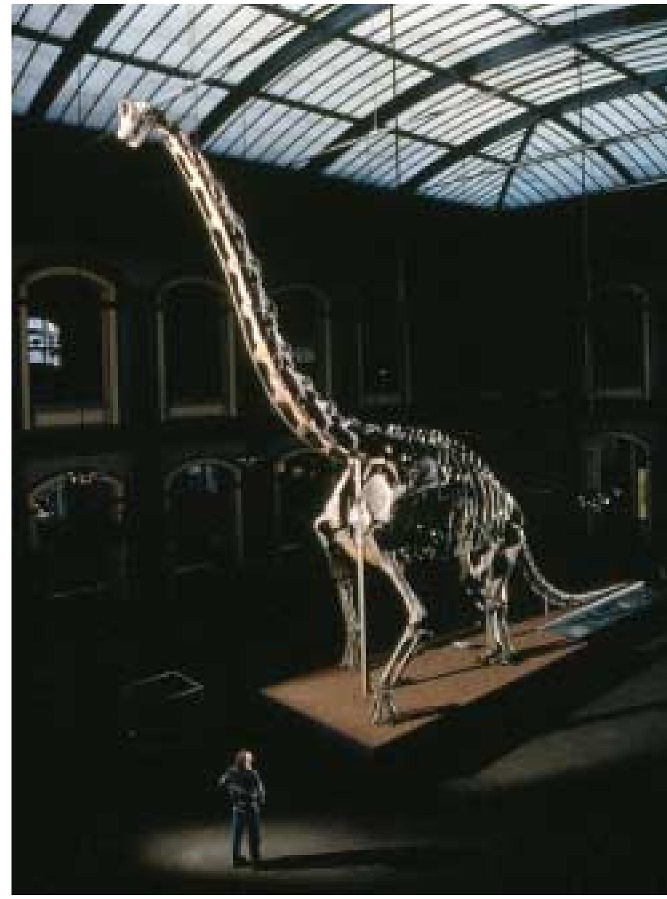


FIGURE 48.26
The largest mounted dinosaur in the world. This 145-million-year-old *Brachiosaurus*, a plant-eating sauropod over 80 feet long, lived in East Africa.

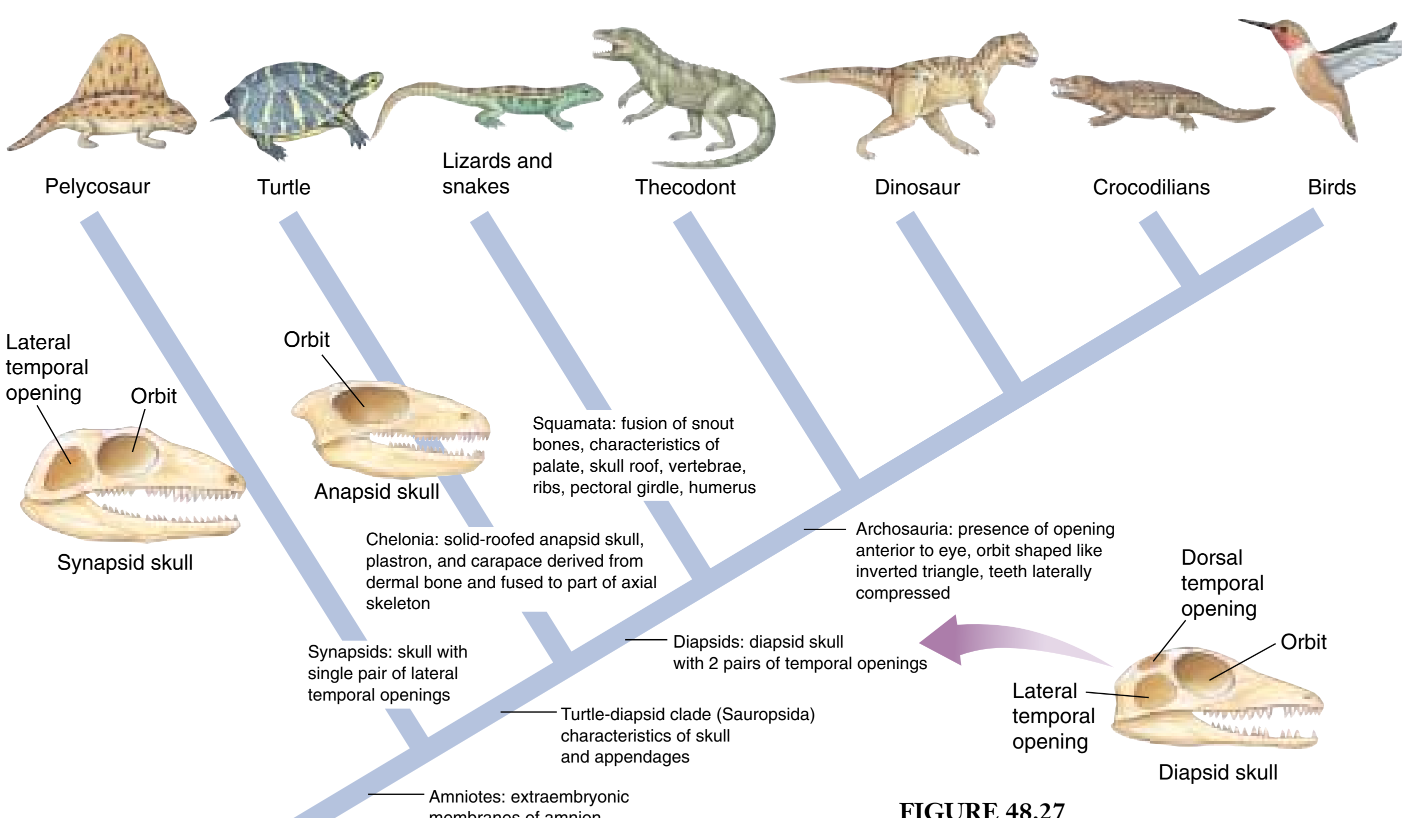


FIGURE 48.27
Cladogram of amniotes.

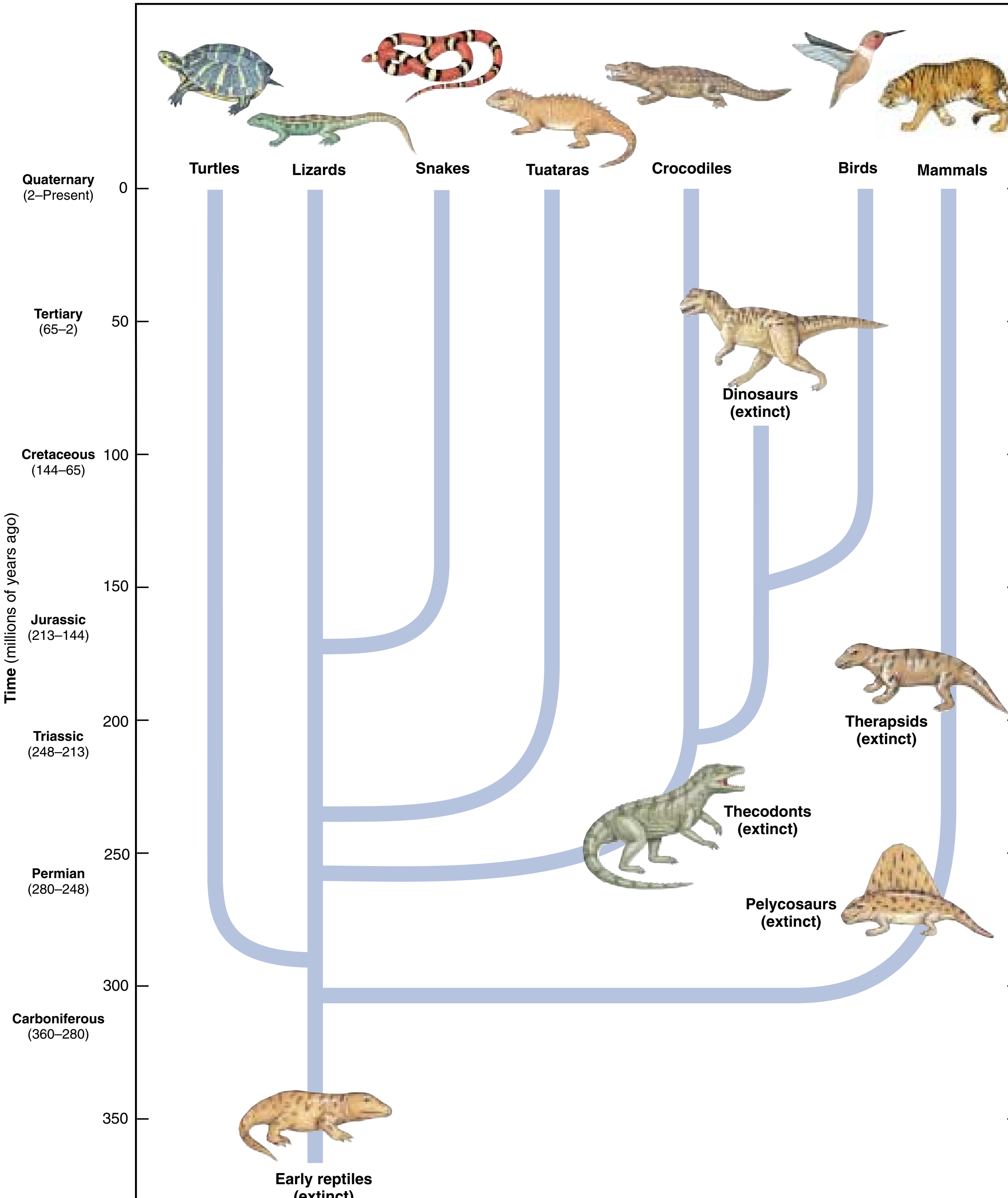
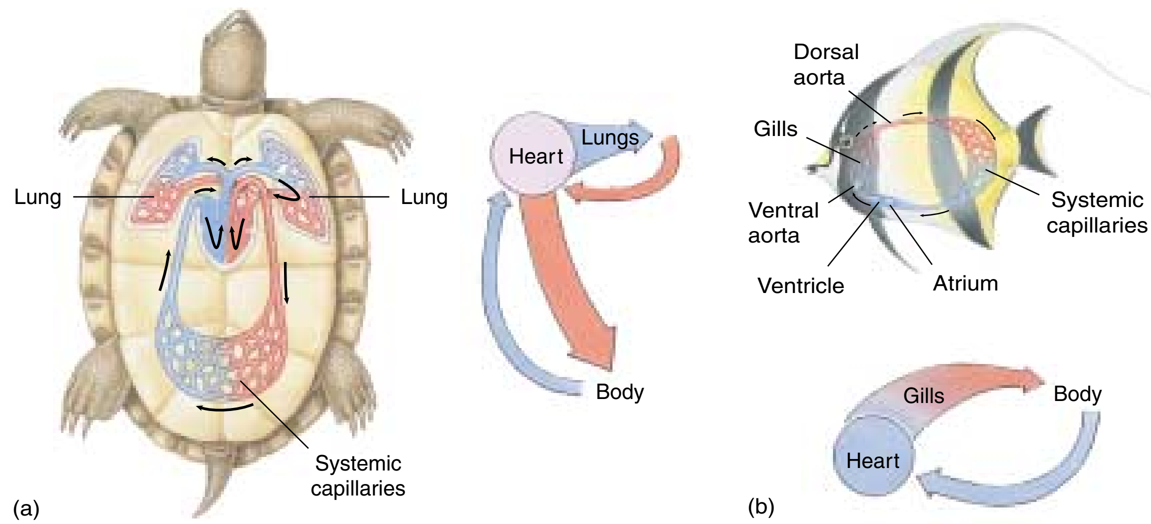


FIGURE 48.28
Evolutionary relationships among the reptiles. There are four orders of living reptiles: turtles, lizards and snakes, tuataras, and crocodiles. This phylogenetic tree shows how these four orders are related to one another and to dinosaurs, birds, and mammals.

FIGURE 48.29
A comparison of reptile and fish circulation. (*a*) In reptiles such as this turtle, blood is repumped after leaving the lungs, and circulation to the rest of the body remains vigorous. (*b*) The blood in fishes flows from the gills directly to the rest of the body, resulting in slower circulation.



Today's Reptiles

Most of the major reptile orders are now extinct. Of the 16 orders of reptiles that have existed, only 4 survive.

Turtles. The most ancient surviving lineage of reptiles is that of turtles. Turtles have anapsid skulls much like those of the first reptiles. Turtles have changed little in the past 200 million years.

Lizards and snakes. Most reptiles living today belong to the second lineage to evolve, the lizards and snakes. Lizards and snakes are descended from an ancient lineage of lizardlike reptiles that branched off the main line of reptile evolution in the late Permian, 250 million years ago, before the thecodonts appeared (figure 48.28). Throughout the Mesozoic era, during the dominance of the dinosaurs, these reptiles survived as minor elements of the landscape, much as mammals did. Like mammals, lizards and snakes became diverse and common only after the dinosaurs disappeared.

Tuataras. The third lineage of surviving reptiles to evolve were the Rhynchocephalonts, small diapsid reptiles that appeared shortly before the dinosaurs. They lived throughout the time of the dinosaurs and were common in the Jurassic. They began to decline in the Cretaceous, apparently unable to compete with lizards, and were already rare by the time dinosaurs disappeared. Today only two species of the order Rhynchocephalia survive, both tuataras living on small islands near New Zealand.

Crocodiles. The fourth lineage of living reptile, crocodiles, appeared on the evolutionary scene much later than other living reptiles. Crocodiles are descended from the same line of thecodonts that gave rise to the dinosaurs and resemble dinosaurs in many ways. They have changed very little in over 200 million years. Crocodiles, pterosaurs, thecodonts, and dinosaurs together make up a group called archosaurs ("ruling reptiles").

Other Important Characteristics

As you might imagine from the structure of the amniotic egg, reptiles and other amniotes do not practice external fertilization as most amphibians do. There would be no way for a sperm to penetrate the membrane barriers protecting the egg. Instead, the male places sperm inside the female, where they fertilize the egg before the membranes are formed. This is called internal fertilization.

The circulatory system of reptiles is improved over that of fish and amphibians, providing oxygen to the body more efficiently (figure 48.29). The improvement is achieved by extending the septum within the heart from the atrium partway across the ventricle. This septum creates a partial wall that tends to lessen mixing of oxygen-poor blood with oxygen-rich blood within the ventricle. In crocodiles, the septum completely divides the ventricle, creating a four-chambered heart, just as it does in birds and mammals (and probably in dinosaurs).

All living reptiles are **ectothermic,** obtaining their heat from external sources. In contrast, **endothermic** animals are able to generate their heat internally. In addition, **homeothermic** animals have a constant body temperature, and **poikilothermic** animals have a body temperature that fluctuates with ambient temperature. Thus, a deep-sea fish may be an ectothermic homeotherm because its heat comes from an external source, but its body temperature is constant. Reptiles are largely ectothermic poikilotherms; their body temperature is largely determined by their surroundings. Reptiles also regulate their temperature through behavior. They may bask in the sun to warm up or seek shade to prevent overheating. The thecodont ancestors of crocodiles were ectothermic, as crocodiles are today. The later dinosaurs from which birds evolved were endothermic. Crocodiles and birds differ in this one important respect. Ectothermy is a principal reason why crocodiles have been grouped among the reptiles.

Kinds of Living Reptiles

The four surviving orders of reptiles contain about 7000 species. Reptiles occur worldwide except in the coldest regions, where it is impossible for ectotherms to survive. Reptiles are among the most numerous and diverse of terrestrial vertebrates. The four living orders of the class Reptilia are Chelonia, Rhynchocephalia, Squamata, and Crocodilia.

Order Chelonia: Turtles and Tortoises. The order Chelonia consists of about 250 species of turtles (most of which are aquatic; figure 48.30) and tortoises (which are terrestrial). They differ from all other reptiles because their bodies are encased within a protective shell. Many of them can pull their head and legs into the shell as well, for total protection from predators. Turtles and tortoises lack teeth but have sharp beaks.

Today's turtles and tortoises have changed very little since the first turtles appeared 200 million years ago. Turtles are **anapsid**—they lack the temporal openings in the skull characteristic of other living reptiles, which are diapsid. This evolutionary stability of turtles may reflect the continuous benefit of their basic design—a body covered with a shell. In some species, the shell is made of hard plates; in other species, it is a covering of tough, leathery skin. In either case, the shell consists of two basic parts. The carapace is the dorsal covering, while the plastron is the ventral portion. In a fundamental commitment to this shell architecture, the vertebrae and ribs of most turtle and tortoise species are fused to the inside of the carapace. All of the support for muscle attachment comes from the shell.

While most tortoises have a domed-shaped shell into which they can retract their head and limbs, water-dwelling turtles have a streamlined, disc-shaped shell that permits rapid turning in water. Freshwater turtles have webbed toes, and in marine turtles, the forelimbs have evolved into flippers. Although marine turtles spend their lives at sea, they must return to land to lay their eggs. Many species migrate long distances to do this. Atlantic green turtles migrate from their feeding grounds off the coast of Brazil to Ascension Island in the middle of the South Atlantic—a distance of more than 2000 kilometers—to lay their eggs on the same beaches where they hatched.

Order Rhynchocephalia: Tuatara. The order Rhynchocephalia contains only two species today, the tuataras, large, lizardlike animals about half a meter long. The only place in the world where these endangered species are found is on a cluster of small islands off the coast of New Zealand. The native Maoris of New Zealand named the tuatara for the conspicuous spiny crest running down its back.

An unusual feature of the tuatara (and some lizards) is the inconspicuous "third eye" on the top of its head, called a parietal eye. Concealed under a thin layer of scales, the eye has a lens and retina and is connected by nerves to the

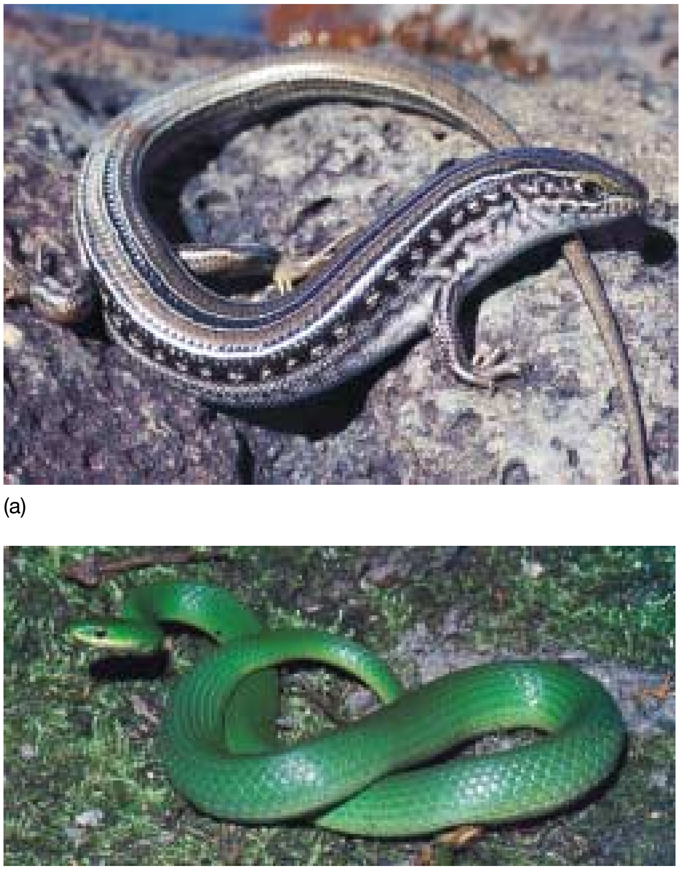
FIGURE 48.30
Red-bellied turtles, *Pseudemys rubriventris*. This turtle is common in the northeastern United States.

brain. Why have an eye, if it is covered up? The parietal eye may function to alert the tuatara when it has been exposed to too much sun, protecting it against overheating. Unlike most reptiles, tuataras are most active at low temperatures. They burrow during the day and feed at night on insects, worms, and other small animals.

Order Squamata: Lizards and Snakes. The order Squamata (figure 48.31) consists of three suborders: Sauria, some 3800 species of lizards, Amphisbaenia, about 135 species of worm lizards, and Serpentes, about 3000 species of snakes. The distinguishing characteristics of this order are the presence of paired copulatory organs in the male and a lower jaw that is not joined directly to the skull. A movable hinge with five joints (your jaw has only one) allows great flexibility in the movements of the jaw. In addition, the loss of the lower arch of bone below the lower opening in the skull of lizards makes room for large muscles to operate their jaws. Most lizards and snakes are carnivores, preying on insects and small animals, and these improvements in jaw design have made a major contribution to their evolutionary success.

The chief difference between lizards and snakes is that most lizards have limbs and snakes do not. Snakes also lack movable eyelids and external ears. Lizards are a more ancient group than modern snakes, which evolved only 20 million years ago. Common lizards include iguanas, chameleons, geckos, and anoles. Most are small, measuring less than a foot in length. The largest lizards belong to the monitor family. The largest of all monitors is the Komodo dragon of Indonesia, which reaches 3 meters in length and weighs up to 100 kilograms. Snakes also vary in size from only a few inches long to those that reach nearly 10 meters in length.

Lizards and snakes rely on agility and speed to catch prey and elude predators. Only two species of lizard are venomous, the Gila monster of the southwestern United States and the beaded lizard of western Mexico. Similarly, most species of snakes are nonvenomous. Of the 13 families of snakes, only 4 are venomous: the elapids (cobras, kraits,



(a)

(b)

FIGURE 48.31
Representatives from the order Squamata. (*a*) An Australian skink, *Sphenomorophus.* Some burrowing lizards lack legs, and the snakes evolved from one line of legless lizards. (*b*) A smooth green snake, *Liochlorophis vernalis.*

FIGURE 48.32
River crocodile, *Crocodilus acutus.* Most crocodiles resemble birds and mammals in having four-chambered hearts; all other living reptiles have three-chambered hearts. Crocodiles, like birds, are more closely related to dinosaurs than to any of the other living reptiles.

and coral snakes); the sea snakes; the vipers (adders, bushmasters, rattlesnakes, water moccasins, and copperheads); and some colubrids (African boomslang and twig snake).

Many lizards, including skinks and geckos, have the ability to lose their tails and then regenerate a new one. This apparently allows these lizards to escape from predators.

Order Crocodilia: Crocodiles and Alligators. The order Crocodilia is composed of 25 species of large, primarily aquatic, primitive-looking reptiles (figure 48.32). In addition to crocodiles and alligators, the order includes two less familiar animals: the caimans and gavials. Crocodilians have remained relatively unchanged since they first evolved.

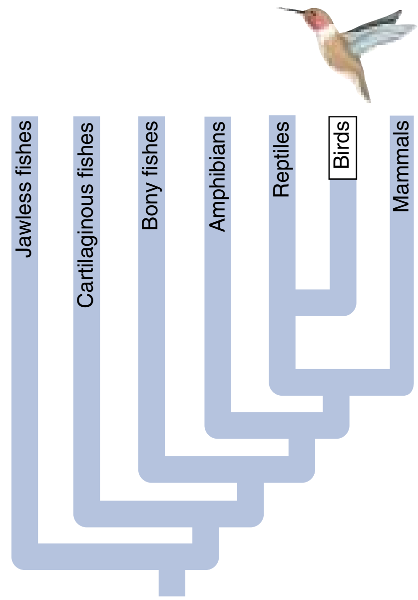
Crocodiles are largely nocturnal animals that live in or near water in tropical or subtropical regions of Africa, Asia, and South America. The American crocodile is found in southern Florida and Cuba to Columbia and Ecuador. Nile crocodiles and estuarine crocodiles can grow to enormous size and are responsible for many human fatalities each year. There are only two species of alligators: one living in the southern United States and the other a rare endangered species living in China. Caimans, which resemble alligators, are native to Central America. Gavials are a group of fish-eating crocodilians with long, slender snouts that live only in India and Burma.

All crocodilians are carnivores. They generally hunt by stealth, waiting in ambush for prey, then attacking ferociously. Their bodies are well adapted for this form of hunting: their eyes are on top of their heads and their nostrils on top of their snouts, so they can see and breathe while lying quietly submerged in water. They have enormous mouths, studded with sharp teeth, and very strong necks. A valve in the back of the mouth prevents water from entering the air passage when a crocodilian feeds underwater.

Crocodiles resemble birds far more than they do other living reptiles. Alone among living reptiles, crocodiles care for their young (a trait they share with at least some dinosaurs) and have a four-chambered heart, as birds do. There are also many other points of anatomy in which crocodiles differ from all living reptiles and resemble birds. Why are crocodiles more similar to birds than to other living reptiles? Most biologists now believe that birds are in fact the direct descendants of dinosaurs. Both crocodiles and birds are more closely related to dinosaurs, and each other, than they are related to lizards and snakes.

Many major reptile groups that dominated life on land for 250 million years are now extinct. The four living orders of reptiles include the turtles, lizards and snakes, tuataras, and crocodiles.

Birds



Only four groups of animals have evolved the ability to fly—insects, pterosaurs, birds, and bats. Pterosaurs, flying reptiles, evolved from gliding reptiles and flew for 130 million years before becoming extinct with the dinosaurs. There are startling similarities in how these very different animals meet the challenges of flight. Like water running downhill through similar gullies, evolution tends to seek out similar adaptations. There are major differences as well. The success of birds lies in the development of a structure unique in the animal world—the feather. Developed from reptilian scales, feathers are the ideal adaptation for flight—lightweight airfoils that are easily replaced if damaged (unlike the vulnerable skin wings of pterosaurs and bats). Today, birds (class Aves) are the most successful and diverse of all terrestrial vertebrates, with 28 orders containing a total of 166 families and about 8800 species (table 48.4).

Key Characteristics of Birds

Modern birds lack teeth and have only vestigial tails, but they still retain many reptilian characteristics. For instance, birds lay amniotic eggs, although the shells of bird eggs are hard rather than leathery. Also, reptilian scales are present on the feet and lower legs of birds. What makes birds unique? What distinguishes them from living reptiles?

1. **Feathers.** Feathers are modified reptilian scales that serve two functions: providing lift for flight and conserving heat. The structure of feathers combines maximum flexibility and strength with minimum weight (figure 48.33). Feathers develop from tiny pits in the skin called follicles. In a typical flight feather, a shaft emerges from the follicle, and pairs of vanes develop from its opposite sides. At maturity, each vane has many branches called barbs. The barbs, in turn, have many projections called barbules that are equipped with microscopic hooks. These hooks link the barbs to one another, giving the feather a continuous surface and a sturdy but flexible shape. Like scales, feathers can be replaced. Feathers are unique to birds among living animals. Recent fossil finds suggest that some dinosaurs may have had feathers.
2. **Flight skeleton.** The bones of birds are thin and hollow. Many of the bones are fused, making the bird skeleton more rigid than a reptilian skeleton. The fused sections of backbone and of the shoulder and hip girdles form a sturdy frame that anchors muscles during flight. The power for active flight comes from large breast muscles that can make up 30% of a bird's total body weight. They stretch down from the wing and attach to the breastbone, which is greatly enlarged and bears a prominent keel for muscle attachment. They also attach to the fused collarbones that form the so-called "wishbone." No other living vertebrates have a fused collarbone or a keeled breastbone.

Birds are the most diverse of all terrestrial vertebrates. They are closely related to reptiles, but unlike reptiles or any other animals, birds have feathers.

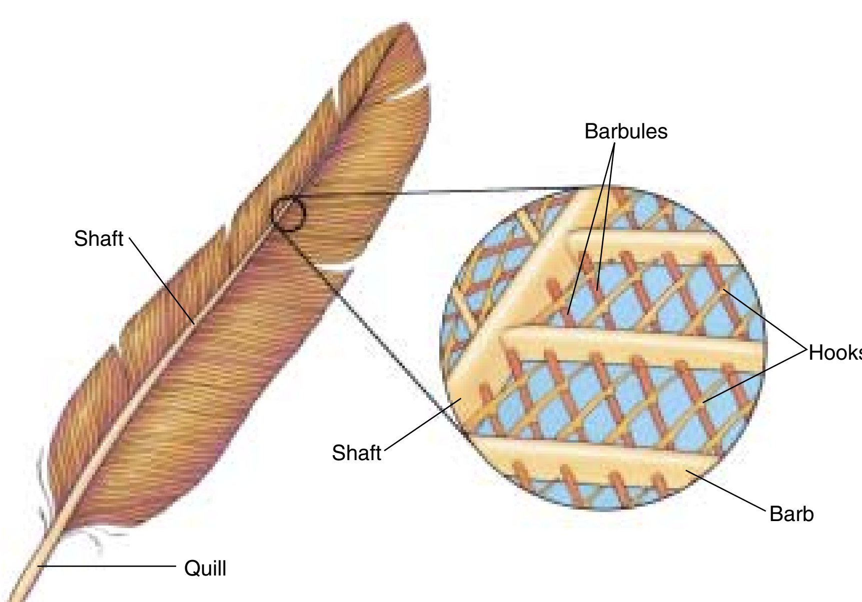
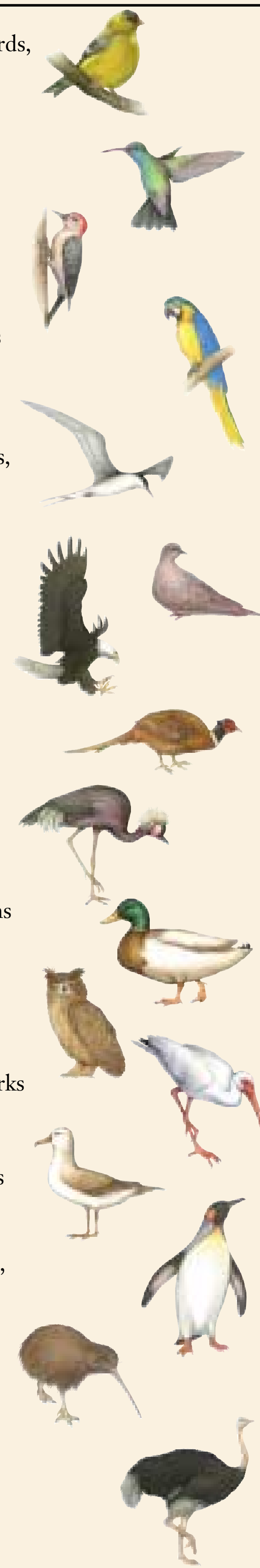


FIGURE 48.33
A feather. This enlargement shows how the vanes, secondary branches and barbs, are linked together by microscopic barbules.

Table 48.4 Major Orders of Birds

Order	Typical Examples	Key Characteristics	Approximate Number of Living Species
Passeriformes	Crows, mockingbirds, robins, sparrows, starlings, warblers	Songbirds Well-developed vocal organs; perching feet; dependent young	5276 (largest of all bird orders; contains over 60% of all species)
Apodiformes	Hummingbirds, swifts	*Fast fliers* Short legs; small bodies; rapid wing beat	428
Piciformes	Honeyguides, toucans, woodpeckers	*Woodpeckers or toucans* Grasping feet; chisel-like, sharp bills can break down wood	383
Psittaciformes	Cockatoos, parrots	*Parrots* Large, powerful bills for crushing seeds; well-developed vocal organs	340
Charadriiformes	Auks, gulls, plovers, sandpipers, terns	*Shorebirds* Long, stiltlike legs; slender probing bills	331
Columbiformes	Doves, pigeons	*Pigeons* Perching feet; rounded, stout bodies	303
Falconiformes	Eagles, falcons, hawks, vultures	*Birds of prey* Carnivorous; keen vision; sharp, pointed beaks for tearing flesh; active during the day	288
Galliformes	Chickens, grouse, pheasants, quail	*Gamebirds* Often limited flying ability; rounded bodies	268
Gruiformes	Bitterns, coots, cranes, rails	*Marsh birds* Long, stiltlike legs; diverse body shapes; marsh-dwellers	209
Anseriformes	Ducks, geese, swans	*Waterfowl* Webbed toes; broad bill with filtering ridges	150
Strigiformes	Barn owls, screech owls	*Owls* Nocturnal birds of prey; strong beaks; powerful feet	146
Ciconiiformes	Herons, ibises, storks	*Waders* Long-legged; large bodies	114
Procellariformes	Albatrosses, petrels	*Seabirds* Tube-shaped bills; capable of flying for long periods of time	104
Sphenisciformes	Emperor penguins, crested penguins	*Penguins* Marine; modified wings for swimming; flightless; found only in southern hemisphere; thick coats of insulating feathers	18
Dinornithiformes	Kiwis	*Kiwis* Flightless; small; primitive; confined to New Zealand	2
Struthioniformes	Ostriches	*Ostriches* Powerful running legs; flightless; only two toes; very large	1



History of the Birds

A 150-million-year-old fossil of the first known bird, *Archaeopteryx* (figure 48.34)—pronounced "archie-op-ter-ichs"—was found in 1862 in a limestone quarry in Bavaria, the impression of its feathers stamped clearly into the rocks.

Birds Are Descended from Dinosaurs

The skeleton of *Archaeopteryx* shares many features with small theropod dinosaurs. About the size of a crow, its skull has teeth, and very few of its bones are fused to one another—dinosaurian features, not avian. Its bones are solid, not hollow like a bird's. Also, it has a long reptilian tail, and no enlarged breastbone such as modern birds use to anchor flight muscles. Finally, it has the forelimbs of a dinosaur. Because of its many dinosaur features, several *Archaeopteryx* fossils were originally classified as the coelurosaur *Compsognathus*, a small theropod dinosaur of similar size—until feathers were discovered on the fossils. What makes *Archaeopteryx* distinctly avian is the presence of feathers on its wings and tail. It also has other birdlike features, notably the presence of a wishbone. Dinosaurs lack a wishbone, although thecodonts had them.

The remarkable similarity of *Archaeopteryx* to *Compsognathus* has led almost all paleontologists to conclude that *Archaeopteryx* is the direct descendant of dinosaurs—indeed, that today's birds are "feathered dinosaurs." Some even speak flippantly of "carving the dinosaur" at Thanksgiving dinner. The recent discovery of feathered dinosaurs in China lends strong support to this inference. The dinosaur *Caudipteryx*, for example, is clearly intermediate between *Archaeopteryx* and dinosaurs, having large feathers on its tail and arms but also many features of velociraptor dinosaurs (figure 48.35). Because the arms of *Caudipteryx* were too short to use as wings, feathers probably didn't evolve for flight. Instead, they probably served as insulation, much as fur does for animals. Flight is something that certain kinds of dinosaurs achieved as they evolved longer arms. We call these dinosaurs birds.

Despite their close affinity to dinosaurs, biologists continue to classify birds as Aves, a separate class, because of the key evolutionary novelties of birds: feathers, hollow bones, and physiological mechanisms such as superefficient lungs that permit sustained, powered flight. It is because of their unique adaptations and great diversity that

FIGURE 48.34
Archaeopteryx. An artist's reconstruction of *Archaeopteryx*, an early bird about the size of a crow. Closely related to its ancestors among the bipedal dinosaurs, *Archaeopteryx* lived in the forests of central Europe 150 million years ago. The true feather colors of *Archaeopteryx* are not known.

FIGURE 48.35
The evolutionary path to the birds. Almost all paleontologists now accept the theory that birds are the direct descendents of theropod dinosaurs.

birds are assigned to a separate class. This practical judgment should not conceal the basic agreement among almost all biologists that birds are the direct descendants of theropod dinosaurs, as closely related to coelurosaurs as are other theropods (see figure 48.35).

By the early Cretaceous, only a few million years after *Archaeopteryx*, a diverse array of birds had evolved, with many of the features of modern birds. Fossils in Mongolia, Spain, and China discovered within the last few years reveal a diverse collection of toothed birds with the hollow bones and breastbones necessary for sustained flight. Other fossils reveal highly specialized, flightless diving birds. The diverse birds of the Cretaceous shared the skies with pterosaurs for 70 million years.

Because the impression of feathers is rarely fossilized and modern birds have hollow, delicate bones, the fossil record of birds is incomplete. Relationships among the 166 families of modern birds are mostly inferred from studies of the degree of DNA similarity among living birds. These studies suggest that the most ancient living birds are the flightless birds, like the ostrich. Ducks, geese, and other waterfowl evolved next, in the early Cretaceous, followed by a diverse group of woodpeckers, parrots, swifts, and owls. The largest of the bird orders, Passeriformes, or songbirds (60% of all species of birds today), evolved in the mid-Cretaceous. The more specialized orders of birds, such as shorebirds, birds of prey, flamingos, and penguins, did not appear until the late Cretaceous. All but a few of the modern orders of toothless birds are thought to have arisen before the disappearance of the pterosaurs and dinosaurs at the end of the Cretaceous 65 million years ago.

FIGURE 48.36
Class Aves. This Western tanager, *Piranga ludoviciana*, is a member of the largest order of birds, the Passeriformes, with over 5000 species.

Birds Today

You can tell a great deal about the habits and food of a bird by examining its beak and feet. For instance, carnivorous birds such as owls have curved talons for seizing prey and sharp beaks for tearing apart their meal. The beaks of ducks are flat for shoveling through mud, while the beaks of finches are short, thick seed-crushers. There are 28 orders of birds, the largest consisting of over 5000 species (figure 48.36).

Many adaptations enabled birds to cope with the heavy energy demands of flight:

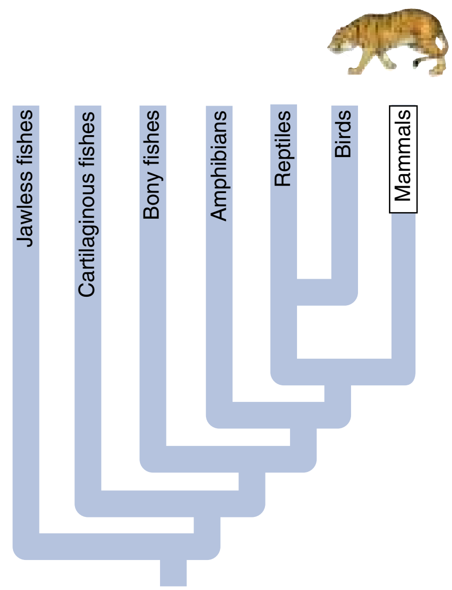
1. **Efficient respiration.** Flight muscles consume an enormous amount of oxygen during active flight. The reptilian lung has a limited internal surface area, not nearly enough to absorb all the oxygen needed. Mammalian lungs have a greater surface area, but as we will see in chapter 53, bird lungs satisfy this challenge with a radical redesign. When a bird inhales, the air goes past the lungs to a series of air sacs located near and within the hollow bones of the back; from there the air travels to the lungs and then to a set of anterior air sacs before being exhaled. Because air always passes through the lungs in the same direction, and blood flows past the lung at right angles to the airflow, gas exchange is highly efficient.
2. **Efficient circulation.** The revved-up metabolism needed to power active flight also requires very efficient blood circulation, so that the oxygen captured by the lungs can be delivered to the flight muscles quickly. In the heart of most living reptiles, oxygen-rich blood coming from the lungs mixes with oxygen-poor blood returning from the body because the wall dividing the ventricle into two chambers is not complete. In birds, the wall dividing the ventricle is complete, and the two blood circulations do not mix, so flight muscles receive fully oxygenated blood.

   In comparison with reptiles and most other vertebrates, birds have a rapid heartbeat. A hummingbird's heart beats about 600 times a minute. An active chickadee's heart beats 1000 times a minute. In contrast, the heart of the large, flightless ostrich averages 70 beats per minute—the same rate as the human heart.
3. **Endothermy.** Birds, like mammals, are endothermic. Many paleontologists believe the dinosaurs that birds evolved from were endothermic as well. Birds maintain body temperatures significantly higher than most mammals, ranging from 40° to 42°C (your body temperature is 37°C). Feathers provide excellent insulation, helping to conserve body heat. The high temperatures maintained by endothermy permit metabolism in the bird's flight muscles to proceed at a rapid pace, to provide the ATP necessary to drive rapid muscle contraction.

The class Aves probably debuted 150 million years ago with *Archaeopteryx*. Modern birds are characterized by feathers, scales, a thin, hollow skeleton, auxiliary air sacs, and a four-chambered heart. Birds lay amniotic eggs and are endothermic.

Mammals

There are about 4100 living species of mammals (class Mammalia), the smallest number of species in any of the five classes of vertebrates. Most large, land-dwelling vertebrates are mammals (figure 48.37), and they tend to dominate terrestrial communities, as did the dinosaurs that they replaced. When you look out over an African plain, you see the big mammals, the lions, zebras, gazelles, and antelope. Your eye does not as readily pick out the many birds, lizards, and frogs that live in the grassland community with them. But the typical mammal is not all that large. Of the 4100 species of mammals, 3200 are rodents, bats, shrews, or moles (table 48.5).



Key Mammalian Characteristics

Mammals are distinguished from all other classes of vertebrates by two fundamental characteristics that are unique to mammals:

1. **Hair.** All mammals have hair. Even apparently naked whales and dolphins grow sensitive bristles on their snouts. Evolution of fur and the ability to regulate body temperature enabled mammals to invade colder climates that ectothermic reptiles could not inhabit, and the insulation fur provided may have ensured the survival of mammals when the dinosaurs perished.

   Unlike feathers, which evolved from modified reptilian scales, mammalian hair is a completely different form of skin structure. An individual mammalian hair is a long, protein-rich filament that extends like a stiff thread from a bulblike foundation beneath the skin known as a hair follicle. The filament is composed mainly of dead cells filled with the fibrous protein keratin.

   One of the most important functions of hair is insulation against heat loss. Mammals are endothermic animals, and typically maintain body temperatures higher than the temperature of their surroundings. The dense undercoat of many mammals reduces the amount of body heat that escapes.

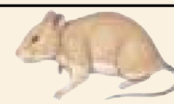
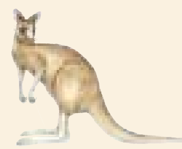
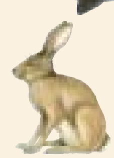
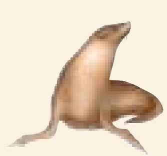
   Another function of hair is camouflage. The coloration and pattern of a mammal's coat usually matches its background. A little brown mouse is practically invisible against the brown leaf litter of a forest floor, while the orange and black stripes of a Bengal tiger disappear against the orange-brown color of the tall grass in which it hunts. Hairs also function as sensory structures. The whiskers of cats and dogs are stiff hairs that are very sensitive to touch. Mammals that are active at night or live underground often rely on their whiskers to locate prey or to avoid colliding with objects. Hair can also serve as a defense weapon. Porcupines and hedgehogs protect themselves with long, sharp, stiff hairs called quills.

2. **Mammary glands.** All female mammals possess mammary glands that secrete milk. Newborn mammals, born without teeth, suckle this milk. Even baby whales are nursed by their mother's milk. Milk is a fluid rich in fat, sugar, and protein. A liter of human milk contains 11 grams of protein, 49 grams of fat, 70 grams of carbohydrate (chiefly the sugar lactose), and 2 grams of minerals critical to early growth, such as calcium. About 95% of the volume is water, critical to avoid dehydration. Milk is a very high calorie food (human milk has 750 kcal per liter), important because of the high energy needs of a rapidly growing newborn mammal. About 50% of the energy in the milk comes from fat.

Mammals first appeared 220 million years ago, evolving to their present position of dominance in modern terrestrial ecosystems. Mammals are the only vertebrates that possess hair and milk glands.

FIGURE 48.37
Mammals. African elephants, *Loxodonta africana*, at a water hole (order Proboscidea).

Table 48.5 Major Orders of Mammals

Order	Typical Examples		Key Characteristics	Approximate Number of Living Species
Rodentia	Beavers, mice, porcupines, rats		*Small plant-eaters* Chisel-like incisor teeth	1814
Chiroptera	Bats		*Flying mammals* Primarily fruit- or insect-eaters; elongated fingers; thin wing membrane; nocturnal; navigate by sonar	986
Insectivora	Moles, shrews		*Small, burrowing mammals* Insect-eaters; most primitive placental mammals; spend most of their time underground	390
Marsupialia	Kangaroos, koalas		*Pouched mammals* Young develop in abdominal pouch	280
Carnivora	Bears, cats, raccoons, weasels, dogs		*Carnivorous predators* Teeth adapted for shearing flesh; no native families in Australia	240
Primates	Apes, humans, lemurs, monkeys		*Tree-dwellers* Large brain size; binocular vision; opposable thumb; end product of a line that branched off early from other mammals	233
Artiodactyla	Cattle, deer, giraffes, pigs		*Hoofed mammals* With two or four toes; mostly herbivores	211
Cetacea	Dolphins, porpoises, whales		*Fully marine mammals* Streamlined bodies; front limbs modified into flippers; no hind limbs; blowholes on top of head; no hair except on muzzle	79
Lagomorpha	Rabbits, hares, pikas		*Rodentlike jumpers* Four upper incisors (rather than the two seen in rodents); hind legs often longer than forelegs; an adaptation for jumping	69
Pinnipedia	Sea lions, seals, walruses		*Marine carnivores* Feed mainly on fish; limbs modified for swimming	34
Edentata	Anteaters, armadillos, sloths		*Toothless insect-eaters* Many are toothless, but some have degenerate, peglike teeth	30
Perissodactyla	Horses, rhinoceroses, zebras		*Hoofed mammals with one or three toes* Herbivorous teeth adapted for chewing	17
Proboscidea	Elephants		*Long-trunked herbivores* Two upper incisors elongated as tusks; largest living land animal	2

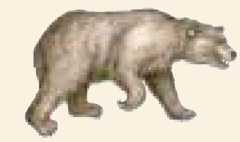
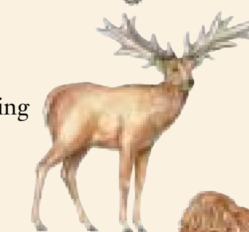
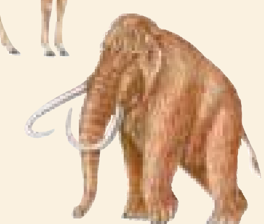
History of the Mammals

Mammals have been around since the time of the dinosaurs, although they were never common until the dinosaurs disappeared. We have learned a lot about the evolutionary history of mammals from their fossils.

Origin of Mammals

The first mammals arose from therapsids in the mid-Triassic about 220 million years ago, just as the first dinosaurs evolved from thecodonts. Tiny, shrewlike creatures that lived in trees eating insects, mammals were only a minor element in a land that quickly came to be dominated by dinosaurs. Fossils reveal that these early mammals had large eye sockets, evidence that they may have been active at night. Early mammals had a single lower jawbone. Therapsid fossils show a change from the reptile lower jaw with several bones to a jaw closer to the mammalian-type jaw. Two of the bones forming the therapsid jaw joint retreated into the middle ear of mammals, linking with a bone already there producing a three-bone structure that amplifies sound better than the reptilian ear.

Table 48.6 Some Groups of Extinct Mammals

Group	Description	
Cave bears	Numerous in the ice ages; this enormous vegetarian bear slept through the winter in large groups.	
Irish elk	Neither Irish nor an elk (it is a kind of deer), *Megaloceros* was the largest deer that ever lived, with horns spanning 12 feet. Seen in French cave paintings, they became extinct about 2500 years ago.	
Mammoths	Although only two species of elephants survive today, the elephant family was far more diverse during the late Tertiary. Many were cold-adapted mammoths with fur.	
Giant ground sloths	*Megatherium* was a giant 20-foot ground sloth that weighed three tons and was as large as a modern elephant.	
Sabertooth cats	The jaws of these large, lionlike cats opened an incredible 120 degrees to allow the animal to drive its huge upper pair of saber teeth into prey.	

Early Divergence in Mammals

For 155 million years, while the dinosaurs flourished, mammals were a minor group of small insectivores and herbivores. Only five orders of mammals arose in that time, and their fossils are scarce, indicating that mammals were not abundant. However, the two groups to which present-day mammals belong did appear. The most primitive mammals, direct descendents of therapsids, were members of the subclass Prototheria. Most prototherians were small and resembled modern shrews. All prototherians laid eggs, as did their therapsid ancestors. The only prototherians surviving today are the monotremes—the duckbill platypus and the echidnas, or spiny anteaters. The other major mammalian group is the subclass Theria. All of the mammals you are familiar with, including humans, are therians. Therians are viviparous (that is, their young are born alive). The two major living therian groups are marsupials, or pouched mammals, and placental mammals. Kangaroos, opossums, and koalas are marsupials. Dogs, cats, humans, horses, and most other mammals are placentals.

The Age of Mammals

At the end of the Cretaceous Period 65 million years ago, the dinosaurs and numerous other land and marine animals became extinct, but mammals survived, possibly because of the insulation their fur provided. In the Tertiary Period (lasting from 65 million years to 2 million years ago), mammals rapidly diversified, taking over many of the ecological roles once dominated by dinosaurs (table 48.6). Mammals reached their maximum diversity late in the Tertiary Period, about 15 million years ago. At that time, tropical conditions existed over much of the world. During the last 15 million years, world climates have deteriorated, and the area covered by tropical habitats has decreased, causing a decline in the total number of mammalian species. There are now 19 orders of mammals.

Characteristics of Modern Mammals

Endothermy. Mammals are endothermic, a crucial adaptation that has allowed mammals to be active at any time of the day or night and to colonize severe environments, from deserts to ice fields. Many characteristics, such as hair that provides insulation, played important roles in making endothermy possible. Also, the more efficient blood circulation provided by the four-chambered heart and the more efficient respiration provided by the *diaphragm* (a special sheet of muscles below the rib cage that aids breathing) make possible the higher metabolic rate upon which endothermy depends.

Placenta. In most mammal species, females carry their young in a uterus during development, nourishing them through a placenta, and give birth to live young. The placenta is a specialized organ within the uterus of the pregnant mother that brings the bloodstream of the fetus into close contact with the bloodstream of the mother (figure 48.38). Food, water, and oxygen can pass across from mother to child, and wastes can pass over to the mother's blood and be carried away.

Teeth. Reptiles have homodont dentition: their teeth are all the same. However, mammals have heterodont dentition, with different types of teeth that are highly specialized to match particular eating habits (figure 48.39). It is usually possible to determine a mammal's diet simply by examining its teeth. Compare the skull of a dog (a carnivore) and a deer (an herbivore). The dog's long canine teeth are well suited for biting and holding prey, and some of its premolar and molar teeth are triangular and sharp for ripping off chunks of flesh. In contrast, canine teeth are absent in deer; instead the deer clips off mouthfuls of plants with flat, chisel-like incisors on its lower jaw. The deer's molars are large and covered with ridges to effectively grind and break up tough plant tissues. Rodents, such as beavers, are gnawers and have long incisors for chewing through branches or stems. These incisors are ever-growing; that is, the ends wear down, but new incisor growth maintains the length.

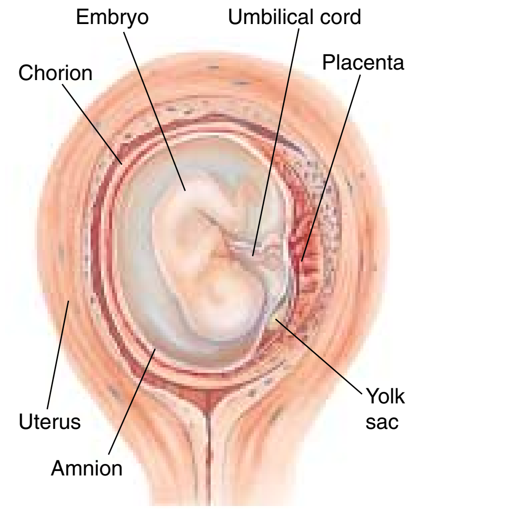


FIGURE 48.38
The placenta. The placenta is characteristic of the largest group of mammals, the placental mammals. It evolved from membranes in the amniotic egg. The umbilical cord evolved from the allantois. The chorion, or outermost part of the amniotic egg, forms most of the placenta itself. The placenta serves as the provisional lungs, intestine, and kidneys of the embryo, without ever mixing maternal and fetal blood.

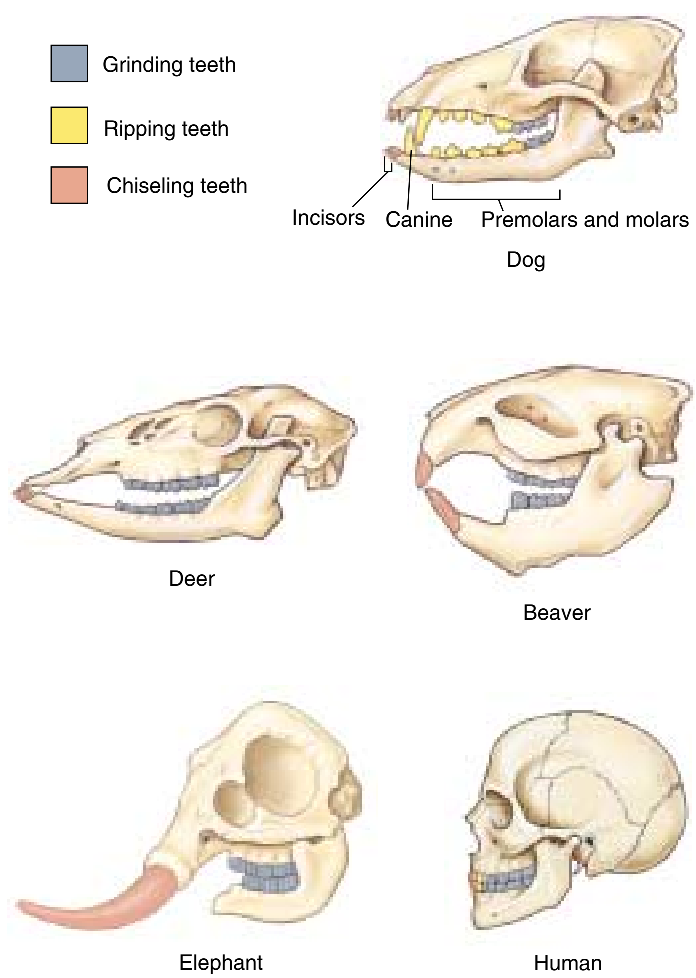


FIGURE 48.39
Mammals have different types of specialized teeth. While reptiles have all the same kind of teeth, mammals have different types of teeth specialized for different feeding habits. Carnivores such as dogs, have *canine* teeth that are able to rip food; some of the *premolars* and *molars* in dogs are also ripping teeth. Herbivores, such as deer, have *incisors* to chisel off vegetation and molars designed to grind up the plant material. In the beaver, the chiseling incisors dominate. In the elephant, the incisors have become specialized weapons, and molars grind up vegetation. Humans are omnivores; we have ripping, chiseling, and grinding teeth.

Digesting Plants. Most mammals are herbivores, eating mostly or only plants. Cellulose, the major component of plant cell walls, forms the bulk of a plant's body and is a major source of food for mammalian herbivores. The cellulose molecule has the structure of a pearl necklace, with each pearl a glucose sugar molecule. Mammals do not have enzymes that can break the links between the pearls to release the glucose elements for use as food. Herbivorous mammals rely on a mutualistic partnership with bacteria that have the necessary cellulose-splitting enzymes to digest cellulose into sugar for them.

Mammals such as cows, buffalo, antelopes, goats, deer, and giraffes have huge, four-chambered stomachs that function as storage and fermentation vats. The first chamber is the largest and holds a dense population of cellulose-digesting bacteria. Chewed plant material passes into this chamber, where the bacteria attack the cellulose. The material is then digested further in the rest of the stomach.

Rodents, horses, rabbits, and elephants are herbivores that employ mutualistic bacteria to digest cellulose in a different way. They have relatively small stomachs, and instead digest plant material in their large intestine, like a termite. The bacteria that actually carry out the digestion of the cellulose live in a pouch called the cecum that branches from the end of the small intestine.

Even with these complex adaptations for digesting cellulose, a mouthful of plant is less nutritious than a mouthful of flesh. Herbivores must consume large amounts of plant material to gain sufficient nutrition. An elephant eats 135 to 150 kg (300 to 400 pounds) each day.

Horns and Hooves. Keratin, the protein of hair, is also the structural building material in claws, fingernails, and hooves. Hooves are specialized keratin pads on the toes of horses, cows, sheep, antelopes, and other running mammals. The pads are hard and horny, protecting the toe and cushioning it from impact.

The horns of cattle and sheep are composed of a core of bone surrounded by a sheath of keratin. The bony core is attached to the skull, and the horn is not shed. The horn that you see is the outer sheath, made of hairlike fibers of keratin compacted into a very hard structure. Deer antlers are made not of keratin but of bone. Male deer grow and shed a set of antlers each year. While growing during the summer, antlers are covered by a thin layer of skin known as velvet. A third type of horn, the rhinoceros horn, is composed only of keratinized fibers with no bony core.

FIGURE 48.40
Greater horseshoe bat, *Rhinolophus ferrumequinum*. The bat is the only mammal capable of true flight.

Flying Mammals. Bats are the only mammals capable of powered flight (figure 48.40). Like the wings of birds, bat wings are modified forelimbs. The bat wing is a leathery membrane of skin and muscle stretched over the bones of four fingers. The edges of the membrane attach to the side of the body and to the hind leg. When resting, most bats prefer to hang upside down by their toe claws. Bats are the second largest order of mammals, after rodents. They have been a particularly successful group because many species have been able to utilize a food resource that most birds do not have access to—night-flying insects.

How do bats navigate in the dark? Late in the eighteenth century, the Italian biologist Lazzaro Spallanzani showed that a blinded bat could fly without crashing into things and still capture insects. Clearly another sense other than vision was being used by bats to navigate in the dark. When Spallanzani plugged the ears of a bat, it was unable to navigate and collided with objects. Spallanzani concluded that bats "hear" their way through the night world.

We now know that bats have evolved a sonar system that functions much like the sonar devices used by ships and submarines to locate underwater objects. As a bat flies, it emits a very rapid series of extremely high-pitched "clicking" sounds well above our range of human hearing. The high-frequency pulses are emitted either through the mouth or, in some cases, through the nose. The soundwaves bounce off obstacles or flying insects, and the bat hears the echo. Through sophisticated processing of this echo within its brain, a bat can determine not only the direction of an object but also the distance to the object.

The Orders of Mammals

There are 19 orders of mammals. Seventeen of them (containing 94% of the species) are placental. The other two are the primitive monotremes and the marsupials.

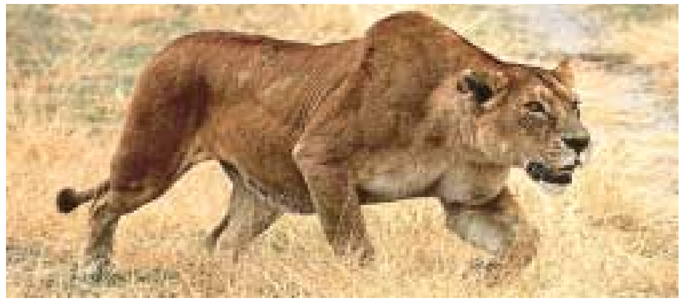
Monotremes: Egg-laying Mammals. The duck-billed platypus and two species of echidna, or spiny anteater, are the only living monotremes (figure 48.41*a*). Among living mammals, only monotremes lay shelled eggs. The structure of their shoulder and pelvis is more similar to that of the early reptiles than to any other living mammal. Also like reptiles, monotremes have a cloaca, a single opening through which feces, urine, and reproductive products leave the body. Monotremes are more closely related to early mammals than are any other living mammal.

In addition to many reptilian features, monotremes have both defining mammalian features: fur and functioning mammary glands. Young monotremes drink their mother's milk after they hatch from eggs. Females lack well-developed nipples so the babies cannot suckle. Instead, the milk oozes onto the mother's fur, and the babies lap it off with their tongues.

The platypus, found only in Australia, lives much of its life in the water and is a good swimmer. It uses its bill much as a duck does, rooting in the mud for worms and other soft-bodied animals. Echidnas of Australia and New Guinea have very strong, sharp claws, which they use for burrowing and digging. The echidna probes with its long, beaklike snout for insects, especially ants and termites.

(a)

(b)



(c)

FIGURE 48.41
Three types of mammals. (*a*) This echidna, *Tachyglossus aculeatus*, is a monotreme. (*b*) Marsupials include kangaroos, like this adult with young in its pouch. (*c*) This female African lion, *Panthera leo* (order Carnivora), is a placental mammal.

Marsupials: Pouched Mammals. The major difference between marsupials (figure 48.41*b*) and other mammals is their pattern of embryonic development. In marsupials, a fertilized egg is surrounded by chorion and amniotic membranes, but no shell forms around the egg as it does in monotremes. During most of its early development, the marsupial embryo is nourished by an abundant yolk within the egg. Shortly before birth, a short-lived placenta forms from the chorion membrane. Soon after, sometimes within eight days of fertilization, the embryonic marsupial is born. It emerges tiny and hairless, and crawls into the marsupial pouch, where it latches onto a nipple and continues its development.

Marsupials evolved shortly before placental mammals, about 100 million years ago. Today, most species of marsupials live in Australia and South America, areas that have been historically isolated. Marsupials in Australia and New Guinea have diversified to fill ecological positions occupied by placental mammals elsewhere in the world. For example, kangaroos are the Australian grazers, playing the role antelope, horses, and buffalo perform elsewhere. The placental mammals in Australia and New Guinea today arrived relatively recently and include some introduced by humans. The only marsupial found in North America is the Virginia opossum.

Placental Mammals. Mammals that produce a true placenta that nourishes the embryo throughout its entire development are called placental mammals (figure 48.41*c*). Most species of mammals living today, including humans, are in this group. Of the 19 orders of living mammals, 17 are placental mammals. They are a very diverse group, ranging in size from 1.5 g pygmy shrews to 100,000 kg whales.

Early in the course of embryonic development, the placenta forms. Both fetal and maternal blood vessels are abundant in the placenta, and substances can be exchanged efficiently between the bloodstreams of mother and offspring. The fetal placenta is formed from the membranes of the chorion and allantois. The maternal side of the placenta is part of the wall of the uterus, the organ in which the young develop. In placental mammals, unlike marsupials, the young undergo a considerable period of development before they are born.

Mammals were not a major group until the dinosaurs disappeared. Mammal specializations include the placenta, a tooth design suited to diet, and specialized sensory systems.

Chapter 48

www.mhhe.com/raven6ch/resource28.mhtml

Summary | **Questions** | **Media Resources**

48.1 Attaching muscles to an internal framework greatly improves movement.

- The chordates are characterized by a dorsal nerve cord and by the presence, at least early in development, of a notochord, pharyngeal slits, and a postanal tail. In vertebrates, a bony endoskeleton provides attachment sites for skeletal muscle.

1. What are the four primary characteristics of the chordates?

- Chordates

48.2 Nonvertebrate chordates have a notochord but no backbone.

- Tunicates and the lancelets seem to represent ancient evolutionary Chordate offshoots.

2. What are the three subphyla of the chordates? Give an example of each.

48.3 The vertebrates have an interior framework of bone.

- Vertebrates differ from other chordates in that they possess a vertebral column, a distinct and well-differentiated head, and a bony skeleton.

3. What is the relationship between the notochord and the vertebral column in vertebrates?

- Introduction to Vertebrates
- Enhancement Chapter: Dinosaurs, Sections 6 and 7

48.4 The evolution of vertebrates involves successful invasions of sea, land, and air.

- Members of the group Agnatha differ from other vertebrates because they lack jaws.
- Jawed fishes constitute more than half of the estimated 42,500 species of vertebrates and are dominant in fresh and salt water everywhere.
- The first land vertebrates were the amphibians. Amphibians are dependent on water and lay their eggs in moist places.
- Reptiles were the first vertebrates fully adapted to terrestrial habitats. Scales and amniotic eggs represented significant adaptations to the dry conditions on land.
- Birds and mammals were derived from reptiles and are now among the dominant groups of animals on land. The members of these two classes have independently become endothermic, capable of regulating their own body temperatures; all other living animals are ectothermic, their temperatures set by external conditions.
- The living mammals are divided into three major groups: (1) the monotremes, or egg-laying mammals, consisting only of the echidnas and the duck-billed platypus; (2) the marsupials, in which the young are born at a very early stage of development and complete their development in a pouch; and (3) the placental mammals, which lack pouches and suckle their young.

4. What is one advantage of possessing jaws? From what existing structures did jaws evolve?

5. What is the primary disadvantage of a bony skeleton compared to one made of cartilage?

6. What is the lateral line system in fishes? How does it function?

7. The successful invasion of land by amphibians involved five major innovations. What were they, and why was each important?

8. How does the embryo obtain nutrients and excrete wastes while contained within the egg?

9. From what reptilian structure are feathers derived?

10. How do amphibian, reptile, and mammal legs differ?

11. Exactly how would you distinguish a cat from a dog? (be specific)

- Activity: Lamprey
- Activity: Fin Fish
- Fish
- Amphibians
- Reptiles
- Birds
- Mammals
- Enhancement Chapter: Dinosaurs, Sections 5
- Book Review: *The Pope's Rhinoceros* by Norfolk
- Student Research: Phylogeny of Hylid Frogs
- Student Research: Metamorphosis in Flatfish
- Evolution of Fish