34

The Origin and Evolution of Vertebrates

▲ **Figure 34.1** **What is the relationship of this ancient organism to humans?**

Half a Billion Years of Backbones

Early in the Cambrian period, some 530 million years ago, an immense variety of invertebrate animals inhabited Earth's oceans. Predators used sharp claws and mandibles to skewer their prey. Many animals had protective spikes or armor as well as modified mouthparts that enabled their bearers to filter food from the water. Worms slithered in the bottom muck, feeding on organic matter. Amidst this bustle, it would have been easy to overlook certain slender, 3-cm-long creatures gliding through the water: *Myllokunmingia fengjiaoa* **(Figure 34.1)**. Although lacking armor and appendages, this ancient species was closely related to one of the most successful groups of animals ever to swim, walk, slither, or fly: the **vertebrates**, which derive their name from vertebrae, the series of bones that make up the vertebral column, or backbone.

For more than 150 million years, vertebrates were restricted to the oceans, but about 365 million years ago, the evolution of limbs in one lineage of vertebrates set the stage for these vertebrates to colonize land. There they diversified into amphibians, reptiles (including birds), and mammals.

There are approximately 52,000 species of vertebrates, a relatively small number compared to, say, the 1 million insect species on Earth. But what vertebrates lack in species diversity they make up for in *disparity*, varying enormously in characteristics such as body mass. Vertebrates include the heaviest animals ever to walk on land, plant-eating dinosaurs as massive as 40,000 kg (more than 13 pickup trucks). They also include the biggest animal ever to exist on Earth, the blue whale, which can exceed a mass of 100,000 kg. On the other end of the spectrum, a fish discovered in 2004 is just 8.4 mm long and has a mass roughly 100 billion times smaller than that of a blue whale.

In this chapter, you will learn about current hypotheses regarding the origins of vertebrates from invertebrate ancestors. We will track the evolution of the vertebrate body plan, from a notochord to a head to a mineralized skeleton. We'll also explore the major groups of vertebrates (both living and extinct), as well as the evolutionary history of our own species.

CONCEPT 34.1

Chordates have a notochord and a dorsal, hollow nerve cord

Vertebrates are members of the phylum Chordata, the chordates. **Chordates** are bilaterian (bilaterally symmetrical) animals, and within Bilateria, they belong to the clade of animals known as Deuterostomia (see Chapter 32). The best-known deuterostomes, aside from vertebrates, are the echinoderms, the group that includes sea stars and sea urchins.
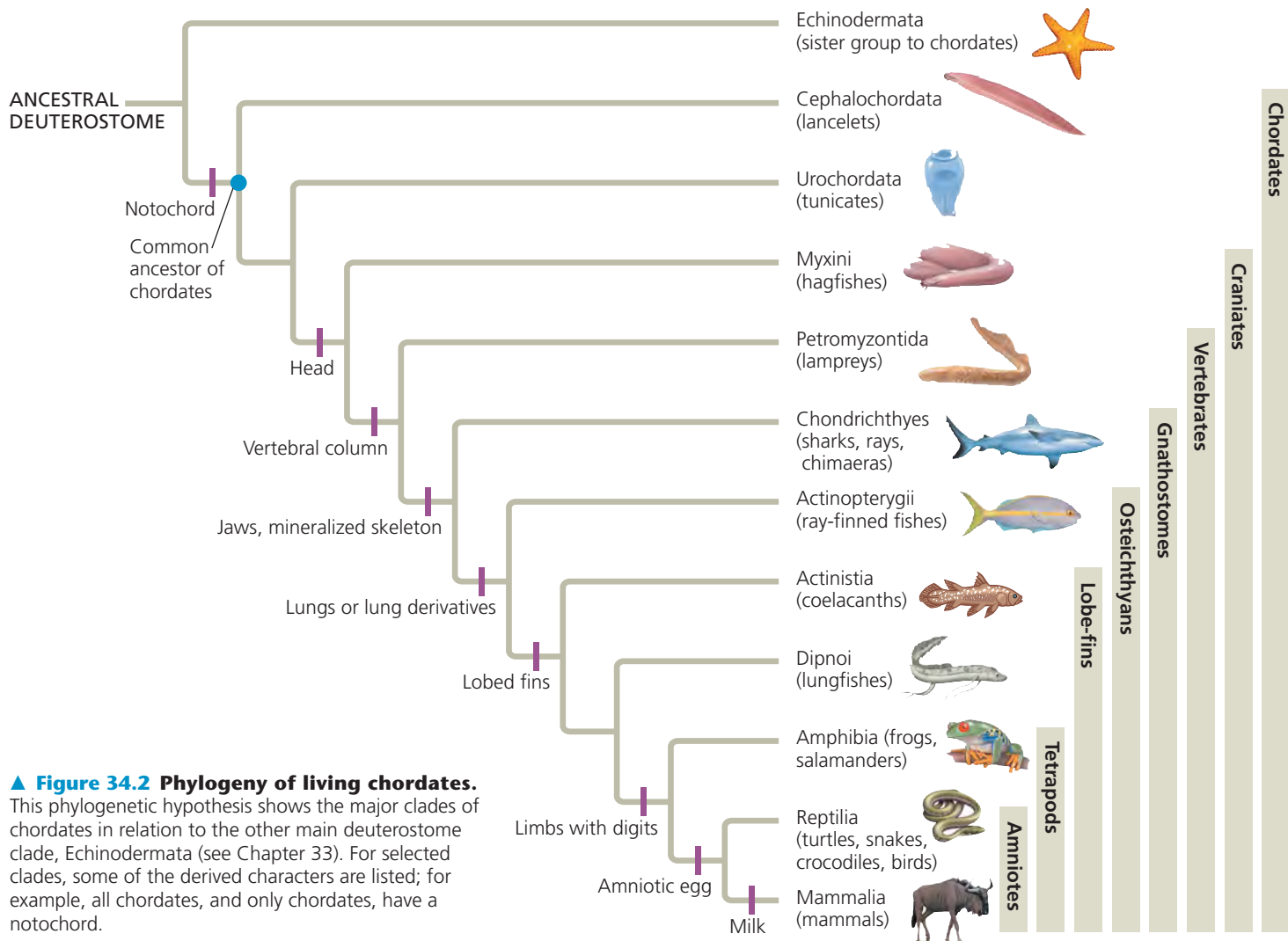
▲ **Figure 34.2 Phylogeny of living chordates.**
This phylogenetic hypothesis shows the major clades of chordates in relation to the other main deuterostome clade, Echinodermata (see Chapter 33). For selected clades, some of the derived characters are listed; for example, all chordates, and only chordates, have a notochord.

However, as shown in **Figure 34.2**, the cephalochordates and the urochordates are two groups of invertebrate deuterostomes that are more closely related to vertebrates than to other invertebrates. Along with the hagfishes and the vertebrates, they make up the chordates.

Derived Characters of Chordates

All chordates share a set of derived characters, though many species possess some of these traits only during embryonic development. **Figure 34.3** illustrates four key characters of chordates: a notochord; a dorsal, hollow nerve cord; pharyngeal slits or clefts; and a muscular, post-anal tail.

Notochord

Chordates are named for a skeletal structure, the notochord, present in all chordate embryos as well as in some adult chordates. The **notochord** is a longitudinal, flexible rod located between the digestive tube and the nerve cord. It is composed of large, fluid-filled cells encased in fairly stiff, fibrous tissue. The notochord provides skeletal support throughout most of
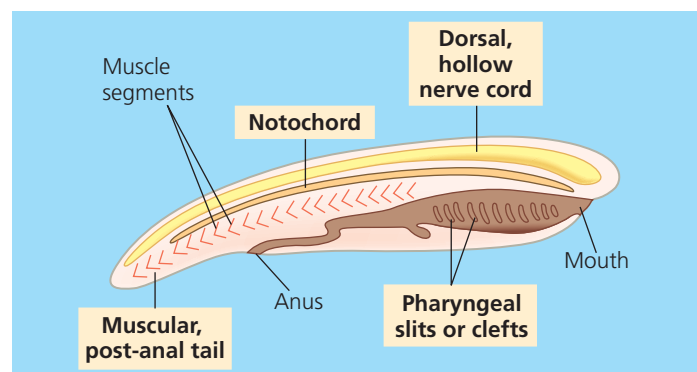
▲ **Figure 34.3 Chordate characteristics.** All chordates possess the four highlighted structural trademarks at some point during their development.

the length of a chordate, and in larvae or adults that retain it, it also provides a firm but flexible structure against which muscles can work during swimming. In most vertebrates, a more complex, jointed skeleton develops around the ancestral notochord, and the adult retains only remnants of the embryonic

notochord. In humans, the notochord is reduced and forms part of the gelatinous disks sandwiched between the vertebrae.

Dorsal, Hollow Nerve Cord

The nerve cord of a chordate embryo develops from a plate of ectoderm that rolls into a tube located dorsal to the notochord. The resulting dorsal, hollow nerve cord is unique to chordates. Other animal phyla have solid nerve cords, and in most cases they are ventrally located. The nerve cord of a chordate embryo develops into the central nervous system: the brain and spinal cord.
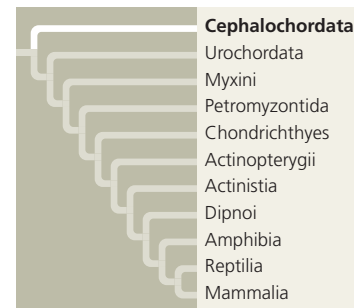
Pharyngeal Slits or Clefts

The digestive tube of chordates extends from the mouth to the anus. The region just posterior to the mouth is the pharynx. In all chordate embryos, a series of pouches separated by grooves forms along the sides of the pharynx. In most chordates, these grooves (known as **pharyngeal clefts**) develop into slits that open to the outside of the body. These **pharyngeal slits** allow water entering the mouth to exit the body without passing through the entire digestive tract. Pharyngeal slits function as suspension-feeding devices in many invertebrate chordates. In vertebrates (with the exception of vertebrates with limbs, the tetrapods), these slits and the structures that support them have been modified for gas exchange and are known as gill slits. In tetrapods, the pharyngeal clefts do not develop into slits. Instead, they play an important role in the development of parts of the ear and other structures in the head and neck.

Muscular, Post-Anal Tail

Chordates have a tail that extends posterior to the anus, although in many species it is greatly reduced during embryonic development. In contrast, most nonchordates have a digestive tract that extends nearly the whole length of the body. The chordate tail contains skeletal elements and muscles, and it helps propel many aquatic species in the water.

Lancelets

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
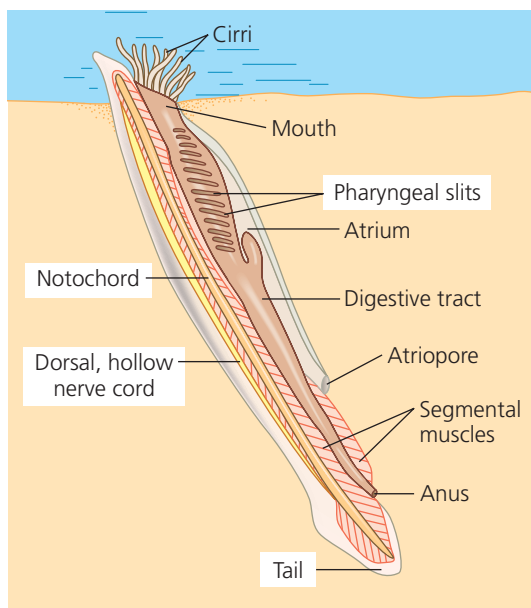Dipnoi
Amphibia
Reptilia
Mammalia

The most basal (earliest-diverging) group of living chordates are animals called **lancelets** (Cephalochordata), which get their name from their bladelike shape **(Figure 34.4)**. As larvae, lancelets develop a notochord, a dorsal, hollow nerve cord, numerous pharyngeal slits, and a post-anal tail. The larvae feed on plankton in the water column, alternating between upward swimming and passive sinking. As the larvae sink, they trap plankton and other suspended particles in their pharynx.

Adult lancelets can reach 6 cm in length. They retain key chordate traits, closely resembling the idealized chordate shown in Figure 34.3. Following metamorphosis, an adult lancelet swims down to the seafloor and wriggles backward into the sand, leaving only its anterior end exposed. Cilia draw seawater into the lancelet's mouth. A net of mucus secreted across the pharyngeal slits removes tiny food particles as the water passes through the slits, and the trapped food enters the intestine. The pharynx and pharyngeal slits play a minor role in gas exchange, which occurs mainly across the external body surface.

A lancelet frequently leaves its burrow to swim to a new location. Though feeble swimmers, these invertebrate chordates display, in a simple form, the swimming mechanism of fishes.

Cirri
Mouth
Pharyngeal slits
Atrium
Notochord
Digestive tract
Dorsal, hollow nerve cord
Atriopore
Segmental muscles
Anus
Tail

1 cm

◀ **Figure 34.4 The lancelet *Branchiostoma*, a cephalochordate.** This small invertebrate displays all four main chordate characters. Water enters the mouth and passes through the pharyngeal slits into the atrium, a chamber that vents to the outside via the atriopore; large particles are blocked from entering the mouth by tentacle-like cirri. The serially arranged segmental muscles produce the lancelet's wavelike swimming movements.

Coordinated contraction of muscles arranged like rows of chevrons (<<<<) along the sides of the notochord flexes the notochord, producing side-to-side undulations that thrust the body forward. This serial arrangement of muscles is evidence of the lancelet's segmentation. The muscle segments develop from blocks of mesoderm called *somites*, which are found along each side of the notochord in all chordate embryos.

Globally, lancelets are rare, but in a few regions (including Tampa Bay, along the Florida coast), they occasionally reach densities in excess of 5,000 individuals per square meter.

Tunicates

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia
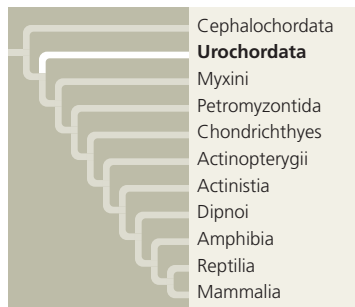
Contrary to what was formerly thought, recent molecular studies suggest that the **tunicates** (Urochordata) are more closely related to other chordates than are lancelets. The chordate characters of tunicates are most apparent during their larval stage, which may be as brief as a few minutes **(Figure 34.5a)**. In many species, the larva uses its tail muscles and notochord to swim through water in search of a suitable substrate on which it can settle, guided by cues it receives from light- and gravity-sensitive cells.

Once a tunicate has settled on a substrate, it undergoes a radical metamorphosis in which many of its chordate characters disappear. Its tail and notochord are resorbed; its nervous system degenerates; and its remaining organs rotate 90°. As an adult, a tunicate draws in water through an incurrent siphon; the water then passes through the pharyngeal slits into a chamber called the atrium and exits through an excurrent siphon **(Figure 34.5b** and **c)**. Food particles are filtered from the water by a mucous net and transported by cilia to the esophagus. The anus empties into the excurrent siphon. Some tunicate species shoot a jet of water through their excurrent siphon when attacked, earning them the informal name of "sea squirts."

The loss of chordate characters in the adult stage of tunicates appears to have occurred after the tunicate lineage branched off from other chordates. Even the tunicate larva appears to be highly derived. For example, tunicates have 9 *Hox* genes, whereas all other chordates studied to date—including the early-diverging lancelets—share a set of 13 *Hox* genes. The apparent loss of 4 *Hox* genes indicates that the chordate body plan of a tunicate larva is built using a different set of genetic controls than other chordates.

Early Chordate Evolution

Although lancelets and tunicates are relatively obscure animals, they occupy key positions in the history of life and can provide clues about the evolutionary origin of vertebrates. As you have read, for example, lancelets display key chordate characters as adults, and their lineage branches from the base of the chordate phylogenetic tree. These findings suggest that the ancestral chordate may have looked something like a lancelet—that is, it had an anterior end with a mouth; a notochord; a dorsal, hollow nerved cord; pharyngeal slits; and a post-anal tail.

Research on lancelets has also revealed important clues about the evolution of the chordate brain. Rather than a full-fledged brain, lancelets have only a slightly swollen tip on the anterior end of their dorsal nerve cord. But the same *Hox* genes that organize major regions of the forebrain, midbrain,
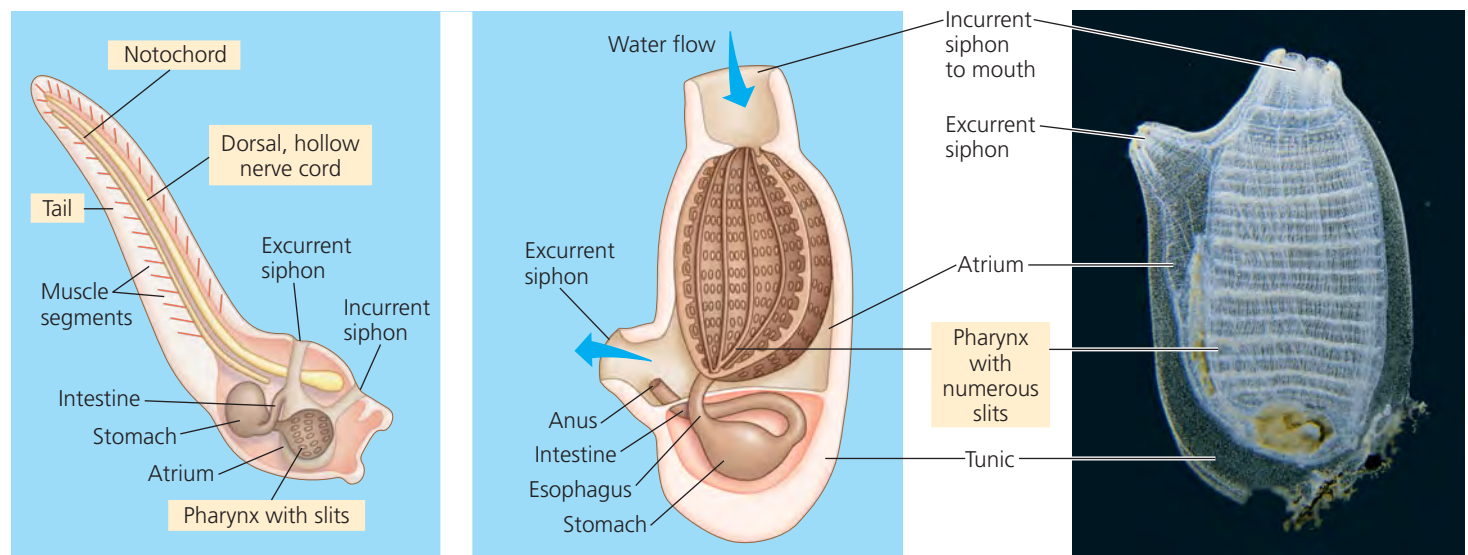
**(a)** A tunicate larva is a free-swimming but nonfeeding "tadpole" in which all four main characters of chordates are evident.

(b) In the adult, prominent pharyngeal slits function in suspension feeding, but other chordate characters are not obvious.

(c) An adult tunicate, or sea squirt, is a sessile animal (photo is approximately life-sized).

▲ **Figure 34.5 A tunicate, a urochordate.**
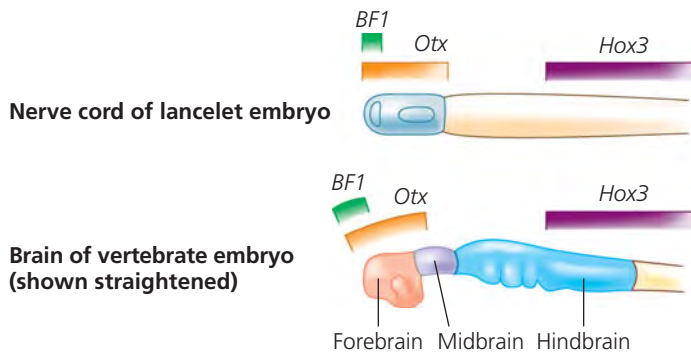
▲ Figure 34.6 Expression of developmental genes in lancelets and vertebrates. *Hox* genes (including *BF1*, *Otx*, and *Hox3*) control the development of major regions of the vertebrate brain. These genes are expressed in the same anterior-to-posterior order in lancelets and vertebrates. Each colored bar is positioned above the portion of the brain whose development that gene controls.

MAKE CONNECTIONS *What do these results and those in Figure 21.18 indicate about* Hox *genes and their evolution?*

and hindbrain of vertebrates express themselves in a corresponding pattern in this small cluster of cells in the lancelet's nerve cord **(Figure 34.6)**. This suggests that the vertebrate brain is an elaboration of an ancestral structure similar to the lancelet's simple nerve cord tip.

As for tunicates, their genome has been completely sequenced and can be used to identify genes likely to have been present in early chordates. Researchers taking this approach have suggested that ancestral chordates had genes associated with vertebrate organs such as the heart and thyroid gland. These genes are found in tunicates and vertebrates but are absent from nonchordate invertebrates. In contrast, tunicates lack many genes that in vertebrates are associated with the long-range transmission of nerve impulses. This result suggests that such genes arose in an early vertebrate and are unique to the vertebrate evolutionary lineage.

CONCEPT CHECK 34.1

1. Identify four derived characters that all chordates have at some point during their life.
2. You are a chordate, yet you lack most of the main derived characters of chordates. Explain.
3. **WHAT IF?** Suppose lancelets lacked a gene found in tunicates and vertebrates. Would this imply that the chordates' most recent common ancestor also lacked this gene? Explain.

For suggested answers, see Appendix A.

CONCEPT 34.2

Craniates are chordates that have a head

After the evolution of the basic chordate body plan, that seen in lancelets and tunicate larvae, the next major transition in chordate evolution was the appearance of a head. Chordates with a head are known as **craniates** (from the word *cranium*, skull). The origin of a head—consisting of a brain at the anterior end of the dorsal nerve cord, eyes and other sensory organs, and a skull—enabled chordates to coordinate more complex movement and feeding behaviors. (Note that heads evolved independently in other animal lineages as well; see Chapter 33.)

Derived Characters of Craniates

Living craniates share a set of derived characters that distinguish them from other chordates. As a result of gene duplication, craniates possess two or more sets of *Hox* genes (lancelets and tunicates have only one). Other important families of genes that produce signaling molecules and transcription factors are also duplicated in craniates. Divergence of sequences in the duplicate genes led to additional genetic complexity. This may have made it possible for craniates to develop more complex morphologies than those of lancelets and tunicates.

One feature unique to craniates is the **neural crest**, a collection of cells that appears near the dorsal margins of the closing neural tube in an embryo **(Figure 34.7)**. Neural crest cells disperse throughout the body, where they give rise to a variety of structures, including teeth, some of the bones and cartilage of the skull, the inner layer of skin (dermis) of the facial region, several types of neurons, and the sensory capsules in which eyes and other sense organs develop.

In aquatic craniates, the pharyngeal clefts evolved into gill slits. Unlike the pharyngeal slits of lancelets, which are used primarily for suspension feeding, gill slits are associated with muscles and nerves that allow water to be pumped through
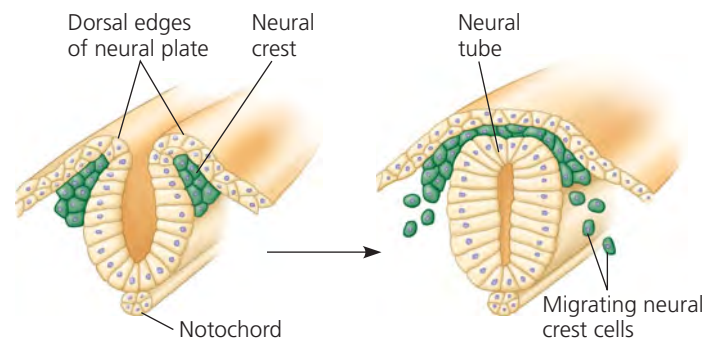
(a) The neural crest consists of bilateral bands of cells near the margins of the embryonic folds that form the neural tube.

(b) Neural crest cells migrate to distant sites in the embryo.

(c) The migrating neural crest cells give rise to some of the anatomical structures unique to vertebrates, including some of the bones and cartilage of the skull. (A fetal human skull is depicted here.)

▲ Figure 34.7 The neural crest, embryonic source of many unique craniate characters.

the slits. This pumping can assist in sucking in food, and it facilitates gas exchange. (In terrestrial craniates, the pharyngeal clefts develop into other structures, as we'll explain later.)

Craniates, which are more active than lancelets and tunicates, also have a higher metabolic rate and a much more extensive muscular system. Muscles lining their digestive tract aid digestion by moving food through the tract. Craniates also have a heart with at least two chambers, red blood cells with hemoglobin, and kidneys that remove waste products from the blood.

The Origin of Craniates

In the late 1990s, paleontologists working in China discovered a vast supply of fossils of early chordates that appear to straddle the transition to craniates. The fossils were formed during the Cambrian explosion 530 million years ago, when many groups of animals were diversifying (see Chapter 32).

The most primitive of the fossils are the 3-cm-long *Haikouella* **(Figure 34.8)**. In many ways, *Haikouella* resembled a lancelet. Its mouth structure indicates that, like lancelets, it probably was a suspension feeder. However, *Haikouella* also had some of the characters of craniates. For example, it had a well-formed brain, small eyes, and muscle segments along the body, as do the vertebrate fishes. It also had respiratory gills in its pharynx, which all the more basal chordates lack. However, *Haikouella* did not have a skull or ear organs, suggesting that these characters emerged with further innovations to the

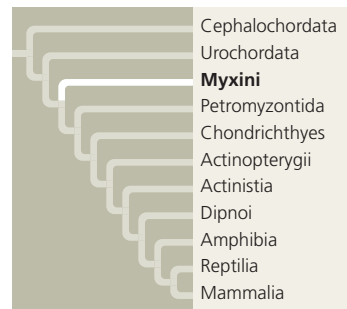

5 mm

Segmented muscles

Pharyngeal slits
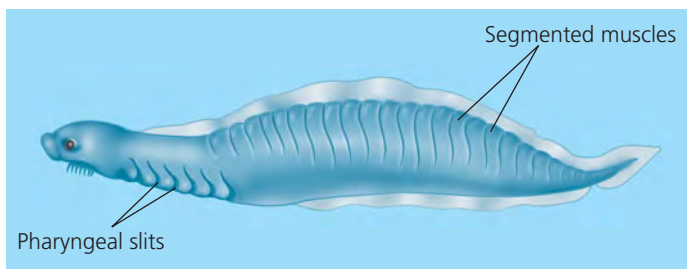
▲ **Figure 34.8 Fossil of an early chordate.** Discovered in 1999 in southern China, *Haikouella* had eyes and a brain but lacked a skull, a derived trait of craniates. The colors in the illustration are fanciful.

chordate nervous system. (The earliest "ears" were organs for maintaining balance, a function still performed by the ears of humans and other living vertebrates.)

In other Cambrian rocks, paleontologists have found fossils of more advanced chordates, such as *Myllokunmingia* (see Figure 34.1). About the same size as *Haikouella, Myllokunmingia* had ear capsules and eye capsules, parts of the skull that surround these organs. Based on these and other characters, paleontologists have identified *Myllokunmingia* as a true craniate.

Hagfishes

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

The most basal group of craniates is Myxini, the hagfishes **(Figure 34.9)**. Hagfishes have a skull made of cartilage, but they lack jaws and vertebrae. They swim in a snakelike fashion by using their segmental muscles to exert force against their notochord, which they retain in adulthood as a strong, flexible rod of cartilage. Hagfishes have a small brain, eyes, ears, and a nasal opening that connects with the pharynx. Their mouths contain toothlike formations made of the protein keratin.

All of the 30 living species of hagfishes are marine. Measuring up to 60 cm in length, most are bottom-dwelling scavengers that feed on worms and sick or dead fish. Rows of slime glands on a hagfish's flanks secrete a substance that absorbs water, forming a slime that may repulse other scavengers when a hagfish is feeding (see Figure 34.9). When attacked by a predator, a hagfish can produce several liters of slime in less than a minute. The slime coats the gills of the attacking fish, sending it into retreat or even suffocating it. Several teams of biologists and engineers are investigating the properties of hagfish slime in hopes of producing an artificial slime that could act as a space-filling gel. Such a gel might be used, for instance, to curtail bleeding during surgery.

Slime glands

▲ **Figure 34.9 A hagfish.**

1. What characteristics do hagfishes have that lancelets and tunicates lack?
2. Which extinct chordate is more closely related to humans, *Myllokunmingia* or *Haikouella*? Explain.
3. **WHAT IF?** In several different animal lineages, organisms with a head first appeared roughly 530 million years ago. Does this finding constitute proof that having a head is favored by natural selection? Explain.

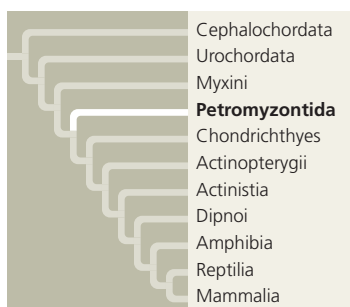For suggested answers, see Appendix A.

CONCEPT 34.3

Vertebrates are craniates that have a backbone

During the Cambrian period, a lineage of craniates gave rise to vertebrates. With a more complex nervous system and a more elaborate skeleton than those of their ancestors, vertebrates became more efficient at two essential tasks: capturing food and avoiding being eaten.

Derived Characters of Vertebrates

After vertebrates branched off from other craniates, they underwent another gene duplication, this one involving a group of transcription factor genes called the *Dlx* family. The resulting additional genetic complexity may be associated with innovations in the vertebrate nervous system and skeleton, including a more extensive skull and a backbone composed of vertebrae. In some vertebrates, the vertebrae are little more than small prongs of cartilage arrayed dorsally along the notochord. In the majority of vertebrates, however, the vertebrae enclose the spinal cord and have taken over the mechanical roles of the notochord. Aquatic vertebrates also acquired dorsal, ventral, and anal fins stiffened by bony structures called fin rays, which provide thrust and steering control when swimming after prey or away from predators. Faster swimming was supported by other adaptations, including a more efficient gas exchange system in the gills.

Lampreys

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

Lampreys (Petromyzontida) are the most basal lineage of living vertebrates. Like hagfishes, lampreys may offer clues to early chordate evolution, but they have also acquired unique characters.

There are about 35 species of lampreys inhabiting

▲ **Figure 34.10 A sea lamprey.** Most lampreys use their mouth (inset) and tongue to bore a hole in the side of a fish. The lamprey then ingests the blood and other tissues of its host.

various marine and freshwater environments **(Figure 34.10)**. Most are parasites that feed by clamping their round, jawless mouth onto the flank of a live fish. They then use their rasping tongue to penetrate the skin of the fish and ingest the fish's blood.

As larvae, lampreys live in freshwater streams. The larva is a suspension feeder that resembles a lancelet and spends much of its time partially buried in sediment. Some species of lampreys feed only as larvae; following several years in streams, they mature sexually, reproduce, and die within a few days. Most lampreys, however, migrate to the sea or lakes as they mature into adults. Sea lampreys (*Petromyzon marinus*) have invaded the Great Lakes over the past 170 years and have devastated a number of fisheries there.

The skeleton of lampreys is made of cartilage. Unlike the cartilage found in most vertebrates, lamprey cartilage contains no collagen. Instead, it is a stiff matrix of other proteins. The notochord of lampreys persists as the main axial skeleton in the adult, as it does in hagfishes. However, lampreys also have a flexible sheath around their rodlike notochord. Along the length of this sheath, pairs of cartilaginous projections related to vertebrae extend dorsally, partially enclosing the nerve cord.

Fossils of Early Vertebrates

After the ancestors of lampreys branched off from other vertebrates during the Cambrian period, many other lineages of vertebrates emerged. Like lampreys, the early members of these lineages lacked jaws, but the resemblance stopped there.

Conodonts were slender, soft-bodied vertebrates with prominent eyes controlled by numerous muscles. Most conodonts were 3–10 cm in length, although some may have been as long as 30 cm. They probably hunted with the help of their large eyes, impaling prey on a set of barbed hooks at the anterior end of their mouth. These hooks were made of dental tissues that were *mineralized*—composed of minerals such as calcium that provide rigidity **(Figure 34.11)**. The food was then passed back to the pharynx, where a different set of dental elements sliced and crushed the food.
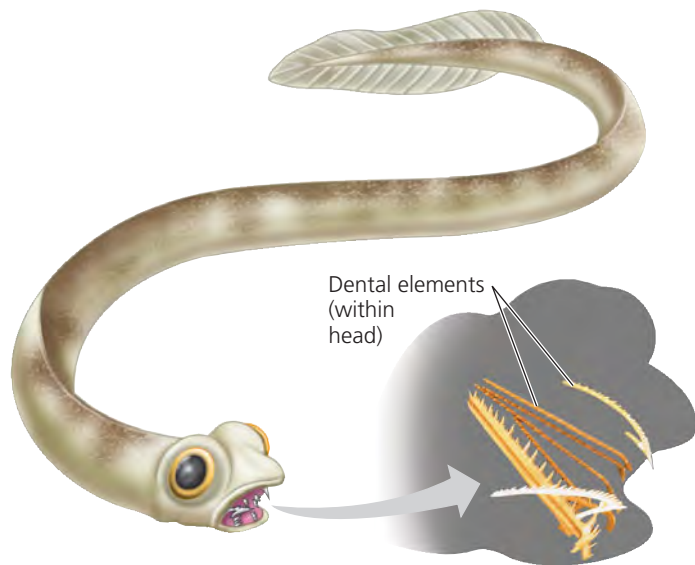
▲ **Figure 34.11 A conodont.** Conodonts were early vertebrates that lived from the late Cambrian until the late Triassic. Unlike lampreys, conodonts had mineralized mouthparts, which they used for either predation or scavenging.

Conodonts were extremely abundant for over 300 million years. Their fossilized dental elements are so plentiful that they have been used for decades by petroleum geologists as guides to the age of rock layers in which they search for oil. (These elements also gave conodonts their name, which means "cone teeth.")

Vertebrates with additional innovations emerged during the Ordovician, Silurian, and Devonian periods. These vertebrates had paired fins and, as in lampreys, an inner ear with two semi-circular canals that provided a sense of balance. Although they, too, lacked jaws, they had a muscular pharynx, which they may have used to suck in bottom-dwelling organisms or detritus. They were also armored with mineralized bone, which covered varying amounts of their body **(Figure 34.12)**. The armor, which in some species included spines, may have offered protection from predators. There were many species of these
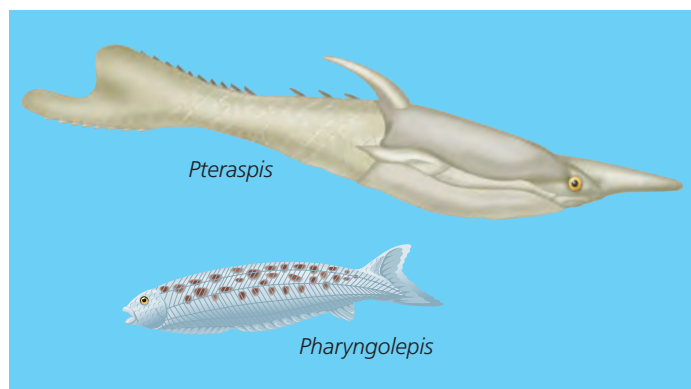
▲ **Figure 34.12 Jawless armored vertebrates.** *Pteraspis* and *Pharyngolepis* were two of many genera of jawless vertebrates that emerged during the Ordovician, Silurian, and Devonian periods.

jawless, armored swimming vertebrates, but they all became extinct by the end of the Devonian period.

Origins of Bone and Teeth

The human skeleton is heavily mineralized bone, whereas cartilage plays a fairly minor role. But a bony skeleton was a relatively late development in the history of vertebrates. As we've seen, the vertebrate skeleton evolved initially as a structure made of unmineralized cartilage.

What initiated the process of mineralization in vertebrates? One hypothesis is that mineralization was associated with a transition in feeding mechanisms. Early chordates probably were suspension feeders, like lancelets, but over time they became larger and were able to ingest larger particles, including some small animals. The earliest known mineralized structures in vertebrates—conodont dental elements—were an adaptation that may have allowed these animals to become scavengers and predators. In addition, when the bony armor of later jawless vertebrates was examined under the microscope, scientists found that it was composed of small tooth-like structures. These findings suggest that mineralization of the vertebrate body may have begun in the mouth and later was incorporated into protective armor. Only in more derived vertebrates did the endoskeleton begin to mineralize, starting with the skull. As you'll read in the next section, more recent lineages of vertebrates underwent even further mineralization.

CONCEPT CHECK 34.3

1. How are differences in the anatomy of lampreys and conodonts reflected in each animal's feeding method?
2. **WHAT IF?** Suggest key roles that mineralized bone might have played in early vertebrates.

For suggested answers, see Appendix A.

CONCEPT 34.4

Gnathostomes are vertebrates that have jaws

Hagfishes and lampreys are survivors from the early Paleozoic era, when jawless craniates were common. Since then, jawless vertebrates have been far outnumbered by jawed vertebrates, known as **gnathostomes**. Living gnathostomes are a diverse group that includes sharks and their relatives, ray-finned fishes, lobe-finned fishes, amphibians, reptiles (including birds), and mammals.

Derived Characters of Gnathostomes

Gnathostomes ("jaw mouth") are named for their jaws, hinged structures that, especially with the help of teeth, enable gnathostomes to grip food items firmly and slice them.

► **Figure 34.13 Hypothesis for the evolution of vertebrate jaws.** The skeleton of the jaws and their supports may have evolved from two pairs of skeletal rods (red and green) located between gill slits near the mouth. According to this hypothesis, pairs of rods anterior to those that formed the jaws were either lost or incorporated into the cranium or jaws.

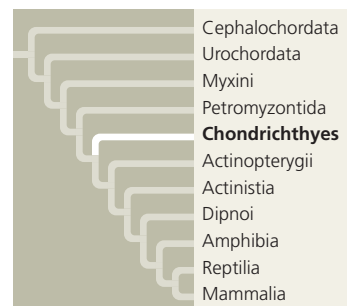Gill slits — Cranium — Mouth — Skeletal rods

▲ **Figure 34.14 Fossil of an early gnathostome.** The placoderm *Dunkleosteus* grew up to 10 m in length. A 2006 analysis of its jaw structure concluded that *Dunkleosteus* could exert a force of 560 kg/cm^2 (8,000 pounds per square inch) at the tip of its jaws.

0.5 m
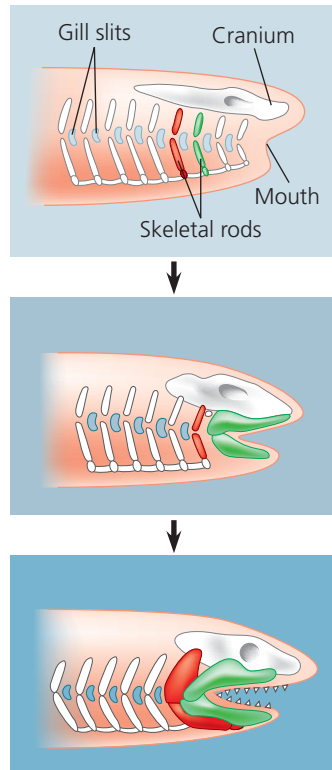
According to one hypothesis, gnathostome jaws evolved by modification of the skeletal rods that had previously supported the anterior pharyngeal (gill) slits **(Figure 34.13)**. The remaining gill slits, no longer required for suspension feeding, remained as the major sites of respiratory gas exchange with the external environment.

Gnathostomes share other derived characters besides jaws. The common ancestors of all gnathostomes underwent an additional duplication of *Hox* genes, such that the single set present in early chordates became four. In fact, the entire genome appears to have duplicated, and together these genetic changes likely enabled the origin of jaws and other novel features in gnathostomes. The gnathostome forebrain is enlarged compared to that of other craniates, mainly in association with enhanced senses of smell and vision. Another characteristic of aquatic gnathostomes is the **lateral line system**, organs that form a row along each side of the body and are sensitive to vibrations in the surrounding water. Precursors of these organs were present in the head shields of some jawless vertebrates.

Fossil Gnathostomes

Gnathostomes appeared in the fossil record in the late Ordovician period, about 450 million years ago, and steadily became more diverse. Their success probably resulted from a combination of anatomical features: Their paired fins and tail (which were also found in jawless vertebrates) allowed them to swim efficiently after prey, and their jaws enabled them to grab prey or simply bite off chunks of flesh.

The earliest gnathostomes in the fossil record include extinct lineages of armored vertebrates known as **placoderms**,

which means "plate-skinned." Most placoderms were less than a meter long, though some giants measured more than 10 m **(Figure 34.14)**. Other groups of jawed vertebrates, collectively called **acanthodians**, emerged at roughly the same time and radiated during the Silurian and Devonian periods (444–359 million years ago). Placoderms had disappeared by 359 million years ago, and acanthodians became extinct about 70 million years later.

In the past several years, new fossil discoveries have revealed that 450–420 million years ago was a period of tumultuous evolutionary change. Gnathostomes that lived during this period had highly variable forms, and by 420 million years ago, they had diverged into the three lineages of jawed vertebrates that survive today: chondrichthyans, ray-finned fishes, and lobe-fins.

Chondrichthyans (Sharks, Rays, and Their Relatives)

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

Sharks, rays, and their relatives include some of the biggest and most successful vertebrate predators in the oceans. They belong to the clade Chondrichthyes, which means "cartilage fish." As their name indicates, the **chondrichthyans** have a skeleton composed predominantly of cartilage, though often impregnated with calcium.

When the name Chondrichthyes was first coined in the 1800s, scientists thought that chondrichthyans represented an early stage in the evolution of the vertebrate skeleton and that mineralization had evolved only in more derived lineages (such

as "bony fishes"). However, as conodonts and armored jawless vertebrates demonstrate, the mineralization of the vertebrate skeleton had already begun before the chondrichthyan lineage branched off from other vertebrates. Moreover, bone-like tissues have been found in early chondrichthyans, such as the fin skeleton of a shark that lived in the Carboniferous period. Traces of bone can also be found in living chondrichthyans—in their scales, at the base of their teeth, and, in some sharks, in a thin layer on the surface of their vertebrae. Such findings strongly suggest that the restricted distribution of bone in the chondrichthyan body is a derived condition, emerging after chondrichthyans diverged from other gnathostomes.

There are about 1,000 species of living chondrichthyans. The largest and most diverse group consists of the sharks, rays, and skates **(Figure 34.15a** and **b)**. A second group is composed of a few dozen species of ratfishes, or chimaeras **(Figure 34.15c)**.

Most sharks have a streamlined body and are swift swimmers, but they do not maneuver very well. Powerful movements of the trunk and the tail fin propel them forward. The dorsal fins function mainly as stabilizers, and the paired pectoral (fore) and pelvic (hind) fins are important for maneuvering. Although a shark gains buoyancy by storing a large amount of oil in its huge liver, the animal is still more dense than water, and if it stops swimming it sinks. Continual swimming also ensures that water flows into the shark's mouth and out through the gills, where gas exchange occurs. However, some sharks and many skates and rays spend a good deal of time resting on the seafloor. When resting, they use muscles of their jaws and pharynx to pump water over the gills.

The largest sharks and rays are suspension feeders that consume plankton. Most sharks, however, are carnivores that swallow their prey whole or use their powerful jaws and sharp teeth to tear flesh from animals too large to swallow in one piece. Sharks have several rows of teeth that gradually move to the front of the mouth as old teeth are lost. The digestive tract of many sharks is proportionately shorter than that of many other vertebrates. Within the shark intestine is a *spiral valve*, a corkscrew-shaped ridge that increases surface area and prolongs the passage of food through the digestive tract.

Acute senses are adaptations that go along with the active, carnivorous lifestyle of sharks. Sharks have sharp vision but cannot distinguish colors. The nostrils of sharks, like those of most aquatic vertebrates, open into dead-end cups. They function only for olfaction (smelling), not for breathing. Like some other vertebrates, sharks have a pair of regions in the skin of their head that can detect electric fields generated by the muscle contractions of nearby animals. Like all (non-mammalian) aquatic vertebrates, sharks have no eardrums, structures that terrestrial vertebrates use to transmit sound waves in air to the auditory organs. Sound reaches a shark through water, and the animal's entire body transmits the sound to the hearing organs of the inner ear.
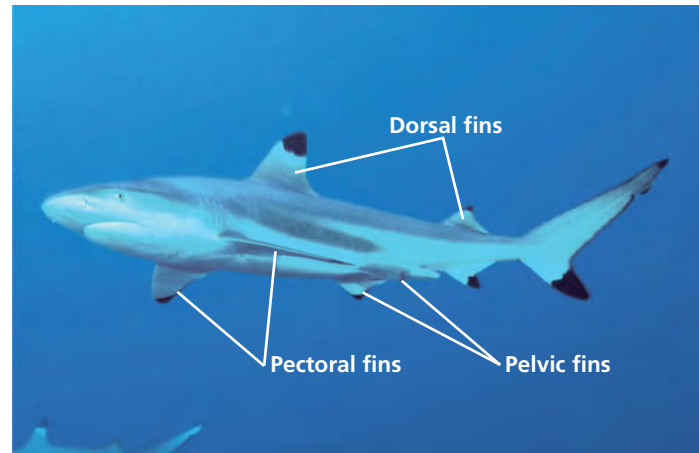
(a) Blacktip reef shark (*Carcharhinus melanopterus*). Sharks are fast swimmers with acute senses. Like all gnathosomes, they have paired pectoral and pelvic fins.

(b) Southern stingray (*Dasyatis americana*). Most rays are bottom-dwellers that feed on molluscs and crustaceans. Some rays cruise in open water and scoop food into their gaping mouth.

(c) Spotted ratfish (*Hydrolagus colliei*). Ratfishes, or chimaeras, typically live at depths greater than 80 m and feed on shrimp, molluscs, and sea urchins. Some species have a venomous spine at the front of their first dorsal fin.

▲ **Figure 34.15 Chondrichthyans.**

Shark eggs are fertilized internally. The male has a pair of claspers on its pelvic fins that transfer sperm into the reproductive tract of the female. Some species of sharks are **oviparous**; they lay eggs that hatch outside the mother's body. These sharks release their eggs after encasing them in protective coats. Other species are **ovoviviparous**; they retain the fertilized eggs in the oviduct. Nourished by the egg yolk, the embryos develop into young that are born after hatching within the uterus. A few species are **viviparous**; the young develop within the uterus and obtain nourishment prior to birth by receiving nutrients from the mother's blood through a yolk sac placenta, by absorbing a nutritious fluid produced by the uterus, or by eating other eggs. The reproductive tract of the shark empties along with the excretory system and digestive tract into the **cloaca**, a common chamber that has a single opening to the outside.

Although rays are closely related to sharks, they have adopted a very different lifestyle. Most rays are bottom-dwellers that feed by using their jaws to crush molluscs and crustaceans. They have a flattened shape and use their greatly enlarged pectoral fins like water wings to propel themselves through the water. The tail of many rays is whiplike and, in some species, bears venomous barbs that function in defense.

Chondrichthyans have thrived for over 400 million years. Today, however, they are severely threatened with overfishing. A recent report indicated that shark stocks in the northwest Atlantic had declined 75% over a 15-year period.

Ray-Finned Fishes and Lobe-Fins

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

The vast majority of vertebrates belong to the clade of gnathostomes called Osteichthyes. Unlike chondrichthyans, nearly all living **osteichthyans** have an ossified (bony) endoskeleton with a hard matrix of calcium phosphate. Like many other taxonomic names, the name Osteichthyes ("bony fish") was coined long before the advent of phylogenetic systematics. When it was originally defined, the group excluded tetrapods, but we now know that such a taxon would be paraphyletic (see Figure 34.2). Therefore, systematists today include tetrapods along with bony fishes in the clade Osteichthyes. Clearly, the name of the group does not accurately describe all of its members.

In this section, we'll discuss the aquatic osteichthyans known informally as fishes. Most fishes breathe by drawing water over four or five pairs of gills located in chambers covered by a protective bony flap called the **operculum (Figure 34.16)**. Water is drawn into the mouth, through the pharynx, and out between the gills by movement of the operculum and contraction of muscles surrounding the gill chambers.

Most fishes can control their buoyancy with an air sac known as a **swim bladder**. Movement of gases from the blood to the swim bladder increases buoyancy, making the animal rise; transfer of gas back to the blood causes the animal to sink. Charles Darwin proposed that the lungs of tetrapods evolved from swim bladders, but strange as it may sound, the opposite seems to be true. Osteichthyans in many early-branching lineages have lungs, which they use to breathe air as a supplement to gas exchange in their gills. The weight of evidence indicates that lungs arose in early osteichthyans; later, swim bladders evolved from lungs in some lineages.

In nearly all fishes, the skin is covered by flattened, bony scales that differ in structure from the tooth-like scales of sharks. Glands in the skin secrete a slimy mucus over the skin, an adaptation that reduces drag during swimming. Like the ancient aquatic gnathostomes mentioned earlier, fishes have a lateral line system, which is evident as a row of tiny pits in the skin on either side of the body.

The details of fish reproduction vary extensively. Most species are oviparous, reproducing by external fertilization after the female sheds large numbers of small eggs. However, internal fertilization and birthing characterize other species.
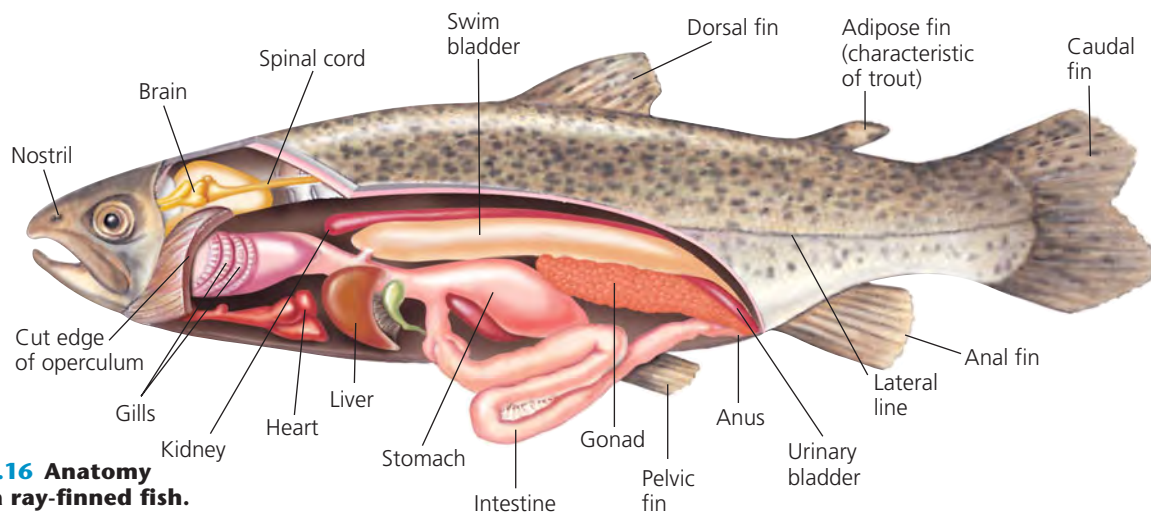
▲ **Figure 34.16 Anatomy of a trout, a ray-finned fish.**

Ray-Finned Fishes

Nearly all the aquatic osteichthyans familiar to us are among the over 27,000 species of **ray-finned fishes** (Actinopterygii) **(Figure 34.17)**. Named for the bony rays that support their fins, the ray-finned fishes originated during the Silurian period (444–416 million years ago). The group has diversified greatly since that time, as suggested by modifications in body form and fin structure that affect maneuvering, defense, and other functions (see Figure 34.17).
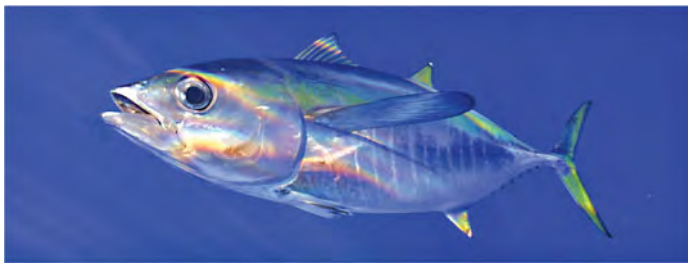
▲ Yellowfin tuna (*Thunnus albacares*) is a fast-swimming, schooling fish that is commercially important worldwide.

▶ Native to coral reefs of the Pacific Ocean, the brightly colored red lionfish (*Pterois volitans*) can inject venom through its spines, causing a severe and painful reaction in humans.

▲ The sea horse has a highly modified body form, as exemplified by *Hippocampus ramulosus,* shown above. Sea horses are unusual among animals in that the male carries the young during their embryonic development.

▲ The fine-spotted moray eel (*Gymnothorax dovii*) is a predator that ambushes prey from crevices in its coral reef habitat.

▲ **Figure 34.17 Ray-finned fishes (Actinopterygii).**

Ray-finned fishes serve as a major source of protein for humans, who have harvested them for thousands of years. However, industrial-scale fishing operations appear to have driven some of the world's biggest fisheries to collapse. For example, after decades of abundant harvests, in the 1990s the catch of cod (*Gadus morhua*) in the northwest Atlantic plummeted to just 5% of its historic maximum, bringing codfishing there to a near halt. Despite ongoing restrictions on the fishery, cod populations have yet to recover to sustainable levels. Ray-finned fishes also face other pressures from humans, such as the diversion of rivers by dams. Changing water flow patterns can hamper the fishes' ability to obtain food and interferes with migratory pathways and spawning grounds.

Lobe-Fins

Like the ray-finned fishes, the other major lineage of osteichthyans, the **lobe-fins** (Sarcopterygii), also originated during the Silurian period **(Figure 34.18)**. The key derived character of lobe-fins is the presence of rod-shaped bones surrounded by a thick layer of muscle in their pectoral and pelvic fins. During the Devonian (416–359 million years ago), many lobe-fins lived in brackish waters, such as in coastal wetlands. There they may have used their lobed fins to swim and "walk" underwater across the substrate (as do some living lobe-fins). Some Devonian lobe-fins were gigantic predators. It is not uncommon to find spike-shaped fossils of Devonian lobe-fin teeth as big as your thumb.

By the end of the Devonian period, lobe-fin diversity was dwindling, and today only three lineages survive. One lineage,

5 cm

Lower jaw   Scaly covering   Dorsal spine
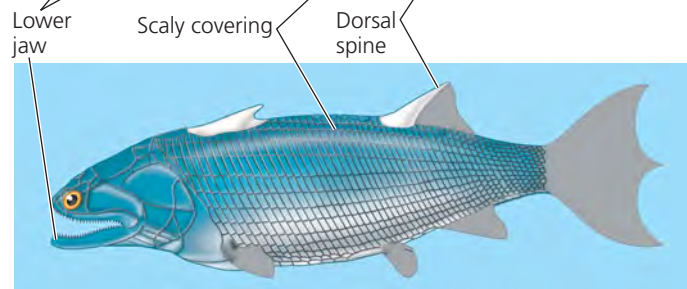
▲ **Figure 34.18 A reconstruction of an ancient lobe-fin.** Discovered in 2009, *Guiyu oneiros* is the earliest known lobe-fin, dating to 420 million years ago. The fossil of this species was nearly complete, allowing for an accurate reconstruction.

▲ **Figure 34.19 A coelacanth (*Latimeria*).** These lobe-fins were found living off the coasts of southern Africa and Indonesia.

the coelacanths (Actinistia), was thought to have become extinct 75 million years ago. However, in 1938, fishermen caught a living coelacanth off the east coast of South Africa **(Figure 34.19)**. Until the 1990s, all subsequent discoveries were near the Comoros Islands in the western Indian Ocean. Since 1999, coelacanths have also been found at various places along the eastern coast of Africa and in the eastern Indian Ocean, near Indonesia. The Indonesian population may represent a second species.

The second lineage of living lobe-fins, the lungfishes (Dipnoi), is represented today by six species in three genera, all of which are found in the Southern Hemisphere. Lungfishes arose in the ocean but today are found only in fresh water, generally in stagnant ponds and swamps. They surface to gulp air into lungs connected to their pharynx. Lungfishes also have gills, which are the main organs for gas exchange in Australian lungfishes. When ponds shrink during the dry season, some lungfishes can burrow into the mud and estivate (wait in a state of torpor; see Chapter 40).

The third lineage of lobe-fins that survives today is far more diverse than the coelacanths or the lungfishes. During the mid-Devonian, these organisms adapted to life on land and gave rise to vertebrates with limbs and feet, called tetrapods—a lineage that includes humans. The tetrapod clade is the topic of the next section.

CONCEPT CHECK 34.4

1. What derived characters do sharks and tuna share? What are some characteristics that distinguish tuna from sharks?
2. Describe key adaptations of aquatic gnathostomes.
3. **WHAT IF?** Imagine that we could replay the history of life. Is it possible that a group of vertebrates that colonized land could have arisen from aquatic gnathostomes other than the lobe-fins? Explain.

For suggested answers, see Appendix A.

Tetrapods are gnathostomes that have limbs

One of the most significant events in vertebrate history took place about 365 million years ago, when the fins of some lobe-fins evolved into the limbs and feet of tetrapods. Until then, all vertebrates had shared the same basic fishlike anatomy. After tetrapods moved onto land, they took on many new forms, from leaping frogs to flying eagles to bipedal humans.

Derived Characters of Tetrapods

The most significant character of **tetrapods** gives the group its name, which means "four feet" in Greek. In place of pectoral and pelvic fins, tetrapods have limbs with digits. Limbs support a tetrapod's weight on land, while feet with digits efficiently transmit muscle-generated forces to the ground when it walks.

Life on land brought numerous other changes to the tetrapod body plan. In tetrapods, the head is separated from the body by a neck that originally had one vertebra on which the skull could move up and down. Later, with the origin of a second vertebra in the neck, the head could also swing from side to side. The bones of the pelvic girdle, to which the hind legs are attached, are fused to the backbone, permitting forces generated by the hind legs against the ground to be transferred to the rest of the body. Except for some fully aquatic species (such as the axolotl discussed below), the adults of living tetrapods do not have gills; during embryonic development, the pharyngeal clefts instead give rise to parts of the ears, certain glands, and other structures.

As you will see, some of these characters were dramatically altered or lost in various lineages of tetrapods. In birds, for example, the pectoral limbs became wings, and in whales, the entire body converged toward a fishlike shape.
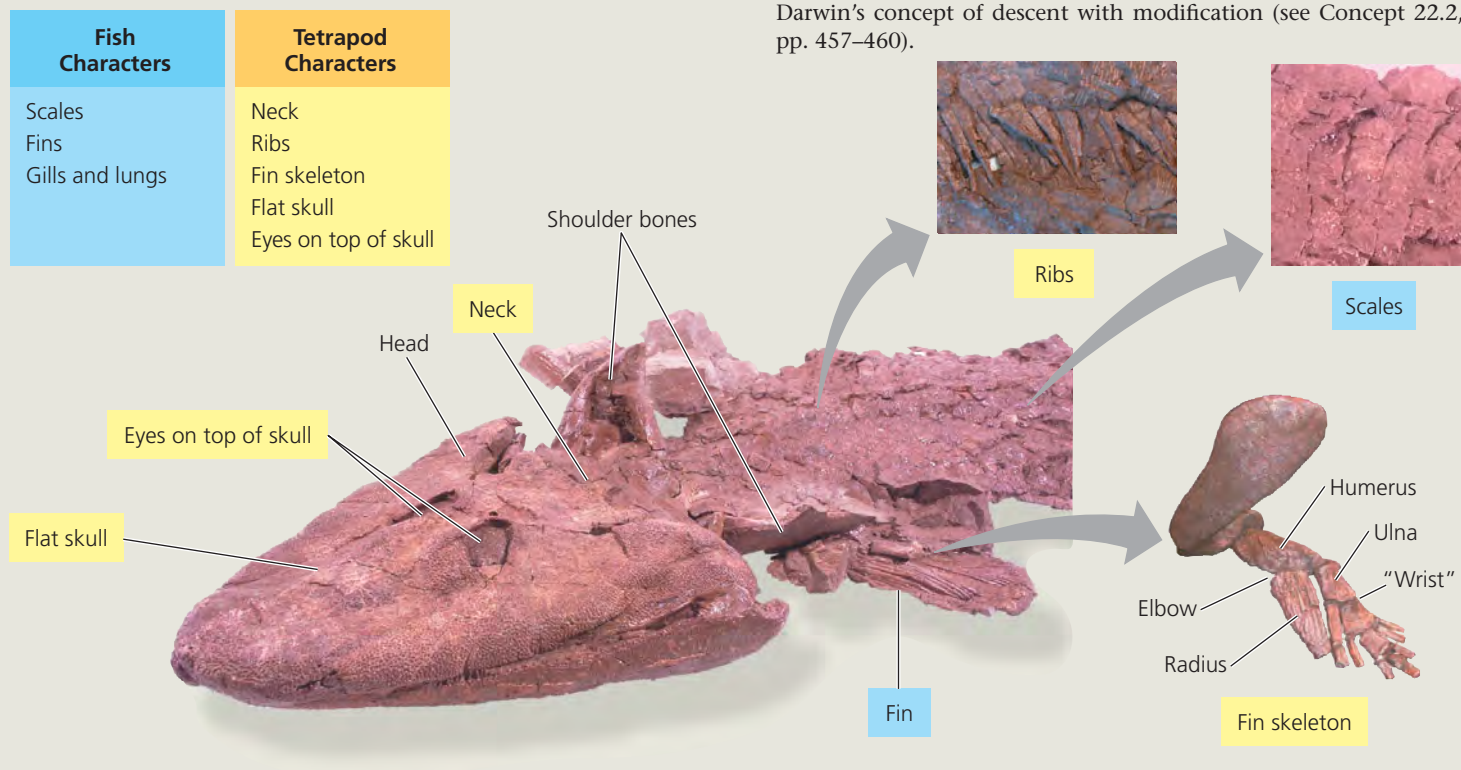
The Origin of Tetrapods

As you have read, the Devonian coastal wetlands were home to a wide range of lobe-fins. Those that entered particularly shallow, oxygen-poor water could use their lungs to breathe air. Some species probably used their stout fins to help them move across logs or the muddy bottom. Thus, the tetrapod body plan did not evolve "out of nowhere" but was simply a modification of a preexisting body plan.

The recent discovery of a fossil called *Tiktaalik* has provided new details on how this process occurred. Like a fish, this species had fins, gills, and lungs, and its body was covered in scales. But unlike a fish, *Tiktaalik* had a full set of ribs

▼ Figure 34.20

IMPACT

Discovery of a "Fishapod": *Tiktaalik*

Paleontologists were on the hunt for fossils that could shed light on the evolutionary origin of tetrapods. Based on the ages of previously discovered fossils, researchers were looking for a dig site with rocks about 365–385 million years old. Ellesmere Island, in the Canadian Arctic, was one of the few such sites likely to contain fossils, because it was once a river. The search at this site was rewarded by the discovery of fossils of a 375-million-year-old lobe-fin, named *Tiktaalik*. As shown in the chart and photographs below, *Tiktaalik* exhibits both fish and tetrapod characters. (Figure 34.21, on the facing page, includes an artist's conception of what *Tiktaalik* might have looked like.)

WHY IT MATTERS As the most tetrapod-like fish known, *Tiktaalik* documents key steps in the vertebrate transition from water to land. Since *Tiktaalik* predates the oldest known tetrapod by 10 million years, its features suggest that key "tetrapod" traits, such as a wrist, ribs, and a neck, were in fact ancestral to the tetrapod lineage. The discovery also shows the predictive capacity of paleontology in identifying likely locations of fossils of interest.

FURTHER READING E. B. Daeschler, N. H. Shubin, and F. A. Jenkins, A Devonian tetrapod-like fish and the evolution of the tetrapod body plan, *Nature* 440:757–763 (2006).

MAKE CONNECTIONS Describe how *Tiktaalik*'s features illustrate Darwin's concept of descent with modification (see Concept 22.2, pp. 457–460).

Fish Characters	Tetrapod Characters
Scales	Neck
Fins	Ribs
Gills and lungs	Fin skeleton
	Flat skull
	Eyes on top of skull

that would have helped it breathe air and support its body **(Figure 34.20)**. Also unlike a fish, *Tiktaalik* had a neck and shoulders, allowing it to move its head about. Finally, the bones of *Tiktaalik*'s front fin have the same basic pattern found in all limbed animals: one bone (the humerus), followed by two bones (the radius and ulna), followed by a group of small bones that comprise the wrist. Although it is unlikely that *Tiktaalik* could walk on land, its front fin skeleton suggests that it could prop itself up in water on its fins.

Tiktaalik and other extraordinary fossil discoveries have allowed paleontologists to reconstruct how fins became progressively more limb-like over time, culminating in the appearance of the first tetrapods 365 million years ago **(Figure 34.21)**. Over the next 60 million years, a great diversity of tetrapods arose. Judging from the morphology and locations of their fossils, most of these early tetrapods probably remained tied to water, a characteristic they share with some members of a group of living tetrapods called amphibians.

Amphibians
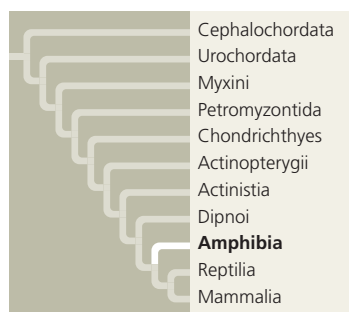
The **amphibians** (class Amphibia) are represented today by about 6,150 species of salamanders (order Urodela, "tailed ones"), frogs (order Anura, "tail-less ones"), and caecilians (order Apoda, "legless ones").

About 550 species of urodeles are known. Some are entirely aquatic, but others live on land as adults or
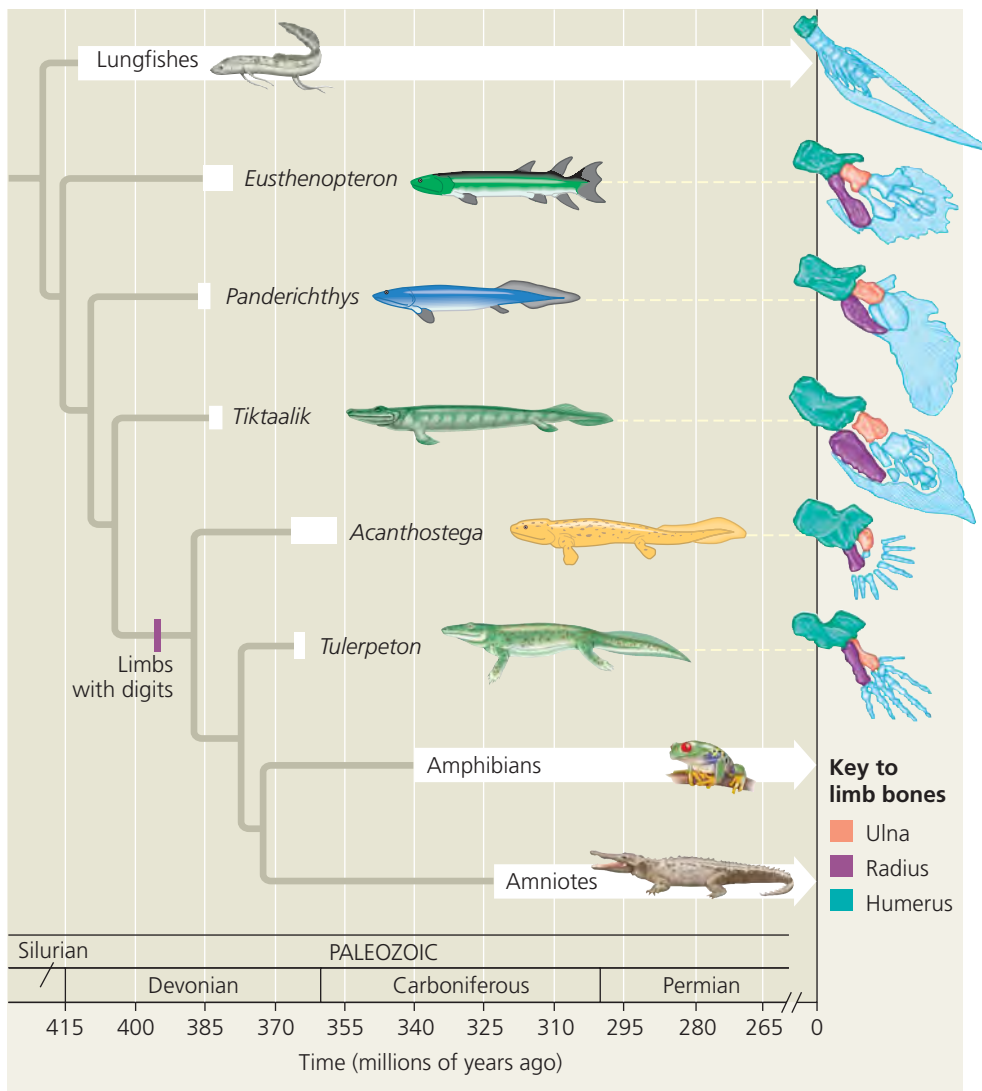
◀ **Figure 34.21 Steps in the origin of limbs with digits.** The white bars on the branches of this diagram place known fossils in time; arrowheads indicate lineages that extend to today. The drawings of extinct organisms are based on fossilized skeletons, but the colors are fanciful.

WHAT IF? *If the most recent common ancestor of* Tulerpeton *and living tetrapods originated 380 million years ago, what range of dates would include the origin of amphibians?*

throughout life. Most salamanders that live on land walk with a side-to-side bending of the body, a trait also found in early terrestrial tetrapods **(Figure 34.22a)**. Paedomorphosis is common among aquatic salamanders; the axolotl, for instance, retains larval features even when it is sexually mature (see Figure 25.22).

Anurans, numbering about 5,420 species, are more specialized than urodeles for moving on land **(Figure 34.22b)**. Adult frogs use their powerful hind legs to hop along the terrain. Although often distinctive in appearance, the animals known as "toads" are simply frogs that have leathery skin or other adaptations for life on land. A frog nabs insects and other prey by flicking out its long, sticky tongue, which is attached to the front of the mouth. Frogs display a great variety of adaptations that help them avoid being eaten by larger predators. Their skin glands secrete distasteful or even poisonous mucus. Many poisonous species have bright coloration, which predators apparently associate with danger (see Figure 54.5b). Other frogs have color patterns that camouflage them (see Figure 54.5a).

▶ **Figure 34.22 Amphibians.**

(a) Order Urodela. Urodeles (salamanders) retain their tail as adults.

(b) Order Anura. Anurans, such as this poison dart frog, lack a tail as adults.

(c) Order Apoda. Apodans, or caecilians, are legless, mainly burrowing amphibians.

Apodans, the caecilians (about 170 species), are legless and nearly blind, and superficially they resemble earthworms **(Figure 34.22c)**. Their absence of legs is a secondary adaptation, as they evolved from a legged ancestor. Caecilians inhabit tropical areas, where most species burrow in moist forest soil. A few South American species live in freshwater ponds and streams.

Amphibian (derived from *amphibious*, meaning "both ways of life") refers to the life stages of many frog species that live first in water and then on land **(Figure 34.23)**. The larval stage of a frog, called a tadpole, is usually an aquatic herbivore with gills, a lateral line system resembling that of aquatic vertebrates, and a long, finned tail. The tadpole initially lacks legs; it swims by undulating its tail. During the metamorphosis that leads to the "second life," the tadpole develops legs, lungs, a pair of external eardrums, and a digestive system adapted to a carnivorous diet. At the same time, the gills disappear; the lateral line system also disappears in most species. The young frog crawls onto shore and becomes a terrestrial hunter. In spite of their name, however, many amphibians do not live a dual—aquatic and terrestrial—life. There are some strictly aquatic or strictly terrestrial frogs, salamanders, and caecilians. Moreover, salamander and caecilian larvae look much like the adults, and typically both the larvae and the adults are carnivorous.

Most amphibians are found in damp habitats such as swamps and rain forests. Even those adapted to drier habitats spend much of their time in burrows or under moist leaves, where humidity is high. Amphibians generally rely heavily on their moist skin for gas exchange with the environment. Some terrestrial species lack lungs and breathe exclusively through their skin and oral cavity.

Fertilization is external in most amphibians; the male grasps the female and spills his sperm over the eggs as the female sheds them (see Figure 34.23c). Amphibians typically lay their eggs in water or in moist environments on land; the eggs lack a shell and dehydrate quickly in dry air. Some amphibian species lay vast numbers of eggs in temporary pools, and egg mortality is high. In contrast, other species lay relatively few eggs and display various types of parental care. Depending on the species, either males or females may house eggs on their back **(Figure 34.24)**, in their mouth, or even in their stomach. Certain tropical tree frogs stir their egg masses into moist, foamy nests that resist drying. There are also some ovoviviparous and viviparous species that retain the eggs in the female reproductive tract, where embryos can develop without drying out.

Many amphibians exhibit complex and diverse social behaviors, especially during their breeding seasons. Frogs are usually quiet, but the males of many species vocalize to defend their breeding territory or to attract females. In some species, migrations to specific breeding sites may involve vocal communication, celestial navigation, or chemical signaling.

Over the past 30 years, zoologists have documented a rapid and alarming decline in amphibian populations in locations throughout the world. There appear to be several causes, including the spread of a disease-causing chytrid fungus (see Figure 31.26), habitat loss, climate change, and pollution. These and other factors have not only reduced populations, but led to extinctions. A recent study indicates that at least 9 amphibian species have become extinct since 1980; more than 100 other species have not been seen since that time and are considered possibly extinct.

(a) The tadpole is an aquatic herbivore with a fishlike tail and internal gills.

(b) During metamorphosis, the gills and tail are resorbed, and walking legs develop. The adult frog will live on land.
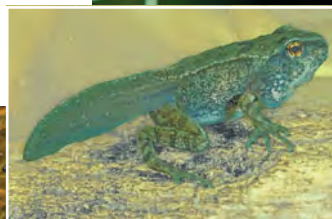
(c) The adults return to water to mate. The male grasps the female, stimulating her to release eggs. The eggs are laid and fertilized in water. They have a jelly coat but lack a shell and would desiccate in air.

▲ **Figure 34.23** **The "dual life" of a frog (*Rana temporaria*).**

▲ **Figure 34.24** **A mobile nursery.** A female pygmy marsupial frog, *Flectonotus pygmaeus,* incubates her eggs in a pouch of skin on her back, helping to protect the eggs from predators. When the eggs hatch, the female deposits the tadpoles in water where they begin life on their own.

1. Describe the origin of tetrapods and identify some of their key derived traits.
2. Some amphibians never leave the water, whereas others can survive in relatively dry terrestrial environments. Contrast the adaptations that facilitate these two lifestyles.
3. **WHAT IF?** Scientists think that amphibian populations may provide an early warning system of environmental problems. What features of amphibians might make them particularly sensitive to environmental problems?

For suggested answers, see Appendix A.

Amniotes are tetrapods that have a terrestrially adapted egg

The **amniotes** are a group of tetrapods whose extant members are the reptiles (including birds) and mammals **(Figure 34.25)**. During their evolution, amniotes acquired a number of new adaptations to life on land.

Derived Characters of Amniotes

Amniotes are named for the major derived character of the clade, the **amniotic egg**, which contains four specialized membranes: the amnion, the chorion, the yolk sac, and the
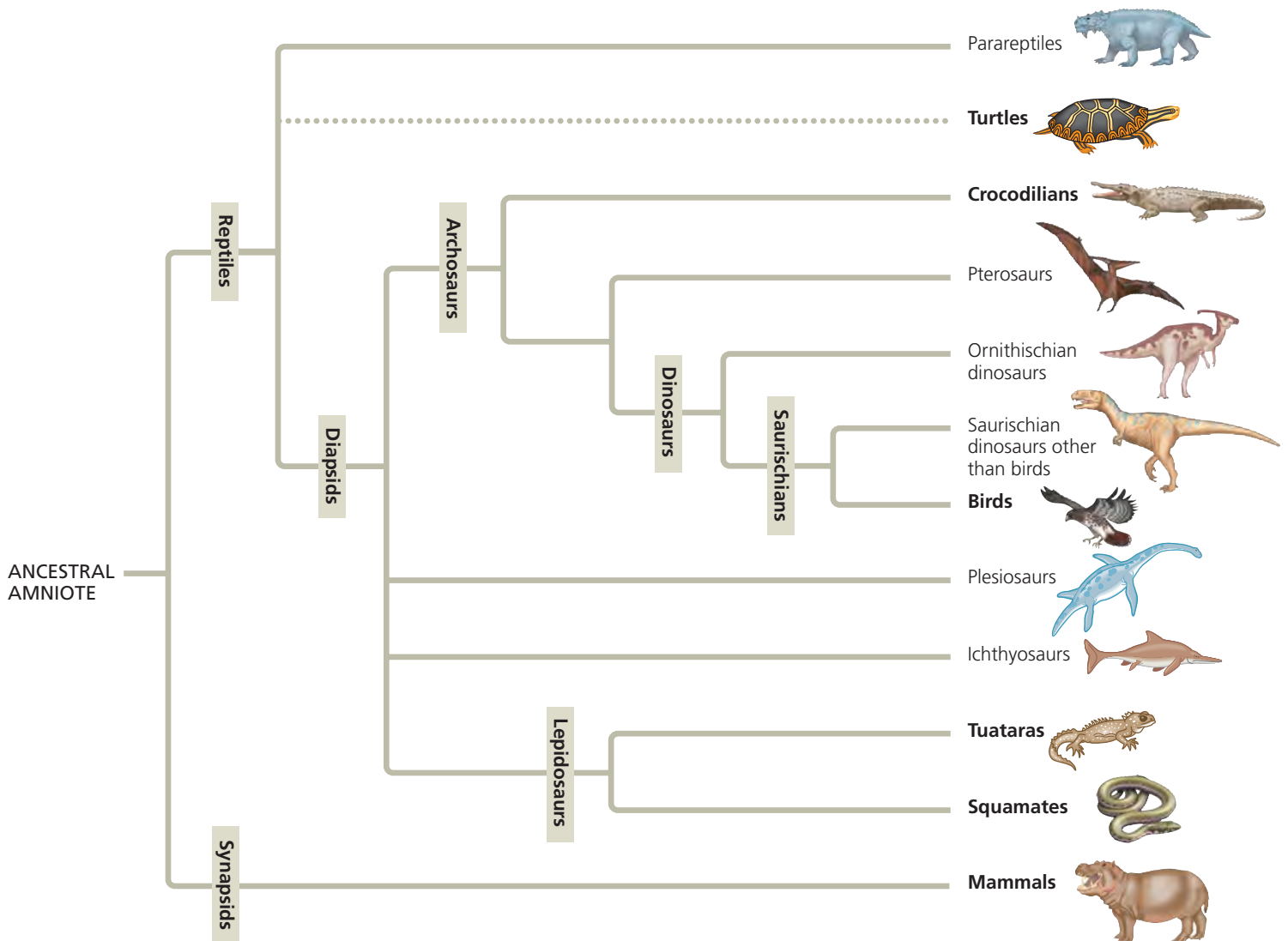
▲ **Figure 34.25 A phylogeny of amniotes.** Extant groups are named at the tips of the branches in boldface type. The dotted line of the turtle branch indicates the uncertain relationship of turtles to other reptiles. Turtles may be a sister group to parareptiles (as indicated by some morphological data), or they may be diapsids more closely related to lepidosaurs (as indicated by other morphological analyses) or to archosaurs (as indicated by many molecular studies).

? *Based on this phylogeny, DNA sequences in birds are likely most similar to DNA sequences in which other extant group of amniotes? Explain.*

► **Figure 34.26 The amniotic egg.** The embryos of reptiles and mammals form four extraembryonic membranes: the amnion, chorion, yolk sac, and allantois. This diagram shows these membranes in the shelled egg of a reptile.

Extraembryonic membranes

Allantois. The allantois is a disposal sac for certain metabolic wastes produced by the embryo. The membrane of the allantois also functions with the chorion as a respiratory organ.

Chorion. The chorion and the membrane of the allantois exchange gases between the embryo and the air. Oxygen and carbon dioxide diffuse freely across the shell.

Amnion. The amnion protects the embryo in a fluid-filled cavity that cushions against mechanical shock.

Yolk sac. The yolk sac contains the yolk, a stockpile of nutrients. Blood vessels in the yolk sac membrane transport nutrients from the yolk into the embryo. Other nutrients are stored in the albumen ("egg white").

Embryo

Amniotic cavity with amniotic fluid

Yolk (nutrients)

Shell

Albumen

allantois **(Figure 34.26)**. Called *extraembryonic membranes* because they are not part of the body of the embryo itself, these membranes develop from tissue layers that grow out from the embryo. The amniotic egg is named for the amnion, which encloses a compartment of fluid that bathes the embryo and acts as a hydraulic shock absorber. The other membranes in the egg function in gas exchange, the transfer of stored nutrients to the embryo, and waste storage. The amniotic egg was a key evolutionary innovation for terrestrial life: It allowed the embryo to develop on land in its own private "pond," hence reducing the dependence of tetrapods on an aqueous environment for reproduction.

In contrast to the shell-less eggs of amphibians, the amniotic eggs of most reptiles and some mammals have a shell. The shells of bird eggs are calcareous (made of calcium carbonate) and inflexible, while the eggshells of many other reptiles are leathery and flexible. Either kind of shell significantly slows dehydration of the egg in air, an adaptation that helped amniotes to occupy a wider range of terrestrial habitats than amphibians, their closest living relatives. (Seeds played a similar role in the evolution of land plants, as we discussed in Chapter 30.) Most mammals have dispensed with the eggshell over the course of their evolution, and the embryo avoids desiccation by developing within the amnion inside the mother's body.

Amniotes have acquired other key adaptations to life on land. For example, amniotes use their rib cage to ventilate their lungs. This method is more efficient than throat-based ventilation, which amphibians use as a supplement to breathing through their skin. The increased efficiency of rib cage ventilation may have allowed amniotes to abandon breathing through their skin and develop less permeable skin, thereby conserving water.
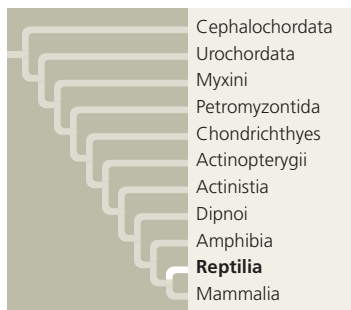
Early Amniotes

The most recent common ancestor of living amphibians and amniotes likely lived about 350 million years ago. No fossils of amniotic eggs have been found from that time, which is not surprising given how delicate they are. Thus, it is not yet possible to say when the amniotic egg evolved, although it must have existed in the last common ancestor of living amniotes, which all have amniotic eggs.

Based on where their fossils have been found, the earliest amniotes lived in warm, moist environments, as did the first tetrapods. Over time, however, early amniotes expanded into a wide range of new environments, including dry and high-latitude regions. The earliest amniotes were small and had sharp teeth, a sign that they were predators **(Figure 34.27)**. Later groups also included herbivores, as evidenced by their grinding teeth and other features.

▲ **Figure 34.27 Artist's reconstruction of *Hylonomus*, an early amniote.** About 25 cm long, this species lived 310 million years ago and probably ate insects and other small invertebrates.

Reptiles

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

The **reptile** clade includes tuataras, lizards, snakes, turtles, crocodilians, and birds, along with a number of extinct groups, such as plesiosaurs and ichthyosaurs (see Figure 34.25).

Fossil evidence indicates that the earliest reptiles lived about 310 million years ago and resembled lizards. Reptiles have diverged greatly since that time, but as a group they share several derived characters that distinguish them from other tetrapods. For example, unlike amphibians, reptiles have scales that contain the protein keratin (as does a human nail). Scales help protect the animal's skin from desiccation and abrasion. In addition, most reptiles lay their shelled eggs on land **(Figure 34.28)**. Fertilization must occur internally, before the eggshell is secreted. Many species of snakes and lizards are viviparous; in such species, the extraembryonic membranes form a kind of placenta that enables the embryo to obtain nutrients from its mother.

Reptiles such as lizards and snakes are sometimes described as "cold-blooded" because they do not use their metabolism extensively to control their body temperature. However, they do regulate their body temperature by using behavioral adaptations. For example, many lizards bask in the sun when the air is cool and seek shade when the air is too warm. A more accurate description of these reptiles is to say that they are **ectothermic**, which means that they absorb external heat as their main source of body heat. (This topic is discussed in more detail in Chapter 40.) By warming themselves directly with solar energy rather than through

▲ **Figure 34.28 Hatching reptiles.** These bushmaster snakes (*Lachesis muta*) are breaking out of their parchment-like shells, a common type of shell among living reptiles other than birds.

the metabolic breakdown of food, an ectothermic reptile can survive on less than 10% of the food energy required by a mammal of the same size. But the reptile clade is not entirely ectothermic; birds are **endothermic**, capable of maintaining body temperature through metabolic activity.

The Origin and Evolutionary Radiation of Reptiles

The oldest reptilian fossils, found in rocks from Nova Scotia, date from the late Carboniferous period. As reptiles diverged from their lizard-like ancestors, one of the first major groups to emerge were the **parareptiles**, which were mostly large, stocky, quadrupedal herbivores. Some parareptiles had plates on their skin that may have provided them with defense against predators. Parareptiles died out by about 200 million years ago, at the end of the Triassic period.

As parareptiles were dwindling, another ancient clade of reptiles, the **diapsids**, was diversifying. One of the most obvious derived characters of diapsids is a pair of holes on each side of the skull, behind the eye socket; muscles pass through these holes and attach to the jaw, controlling jaw movement. The diapsids are composed of two main lineages. One lineage gave rise to the **lepidosaurs**, which include tuataras, lizards, and snakes. This lineage also produced a number of marine reptiles, including the giant mososaurs. Some of these marine species rivaled today's whales in length; all of them are extinct. (We'll say more about living lepidosaurs shortly.)

The other diapsid lineage, the **archosaurs**, produced the crocodilians (which we'll discuss later), pterosaurs, and dinosaurs. **Pterosaurs**, which originated in the late Triassic, were the first tetrapods to exhibit flapping flight. The pterosaur wing was completely different from the wings of birds and bats. It consisted of a collagen-strengthened membrane that stretched between the trunk or hind leg and a very long digit on the foreleg. Well-preserved fossils show evidence of muscles, blood vessels, and nerves in the wing membranes, suggesting that pterosaurs could dynamically adjust their membranes to assist their flight.

The smallest pterosaurs were no bigger than a sparrow, and the largest had a wingspan of nearly 11 m. They appear to have converged on many of the ecological roles later played by birds; some were insect-eaters, others grabbed fish out of the ocean, and still others filtered small animals through thousands of fine needlelike teeth. But by the end of the Cretaceous period 65 million years ago, pterosaurs had become extinct.

On land, the **dinosaurs** diversified into a vast range of shapes and sizes, from bipeds the size of a pigeon to 45-m-long quadrupeds with necks long enough to let them browse the tops of trees. One lineage of dinosaurs, the ornithischians, were herbivores; they included many species with elaborate defenses against predators, such as tail clubs and horned crests. The other main lineage of dinosaurs, the saurischians, included the

long-necked giants and a group called the **theropods**, which were bipedal carnivores. Theropods included the famous *Tyrannosaurus rex* as well as the ancestors of birds.

There is continuing debate about the metabolism of dinosaurs. Some researchers have pointed out that the Mesozoic climate over much of the dinosaurs' range was relatively warm and unvarying, and they have suggested that the low surface-to-volume ratios of large dinosaurs combined with behavioral adaptations such as basking may have been sufficient for an ectotherm to maintain a suitable body temperature. However, some anatomical evidence supports the hypothesis that at least some dinosaurs were endotherms. Furthermore, paleontologists have found fossils of dinosaurs in both Antarctica and the Arctic; although the climate in these areas was milder when dinosaurs existed than it is today, it was cool enough that small dinosaurs may have had difficulty maintaining a high body temperature through ectothermy. The dinosaur that gave rise to birds was *certainly* endothermic, as are all birds.

Traditionally, dinosaurs were considered slow, sluggish creatures. Since the early 1970s, however, fossil discoveries and research have led to the conclusion that many dinosaurs were agile and fast moving. Dinosaurs had a limb structure that enabled them to walk and run more efficiently than could earlier tetrapods, which had a sprawling gait. Fossilized footprints and other evidence suggest that some species were social—they lived and traveled in groups, much as many mammals do today. Paleontologists have also discovered evidence that some dinosaurs built nests and brooded their eggs, as birds do today (see Figure 26.17).

All dinosaurs except birds became extinct by the end of the Cretaceous period. Their extinction may have been caused at least in part by the asteroid or comet impact you read about in Chapter 25. Some analyses of the fossil record are consistent with this idea in that they show a sudden decline in dinosaur diversity at the end of the Cretaceous. However, other analyses indicate that the number of dinosaur species had begun to decline several million years before the Cretaceous ended. Further fossil discoveries and new analyses will be needed to resolve this debate.

Lepidosaurs

One surviving lineage of lepidosaurs is represented by two species of lizard-like reptiles called tuataras **(Figure 34.29a)**. Fossil evidence indicates that tuatara ancestors lived at least 220 million years ago. These organisms thrived on many

▼ **Figure 34.29 Extant reptiles (other than birds).**

(a) Tuatara (*Sphenodon punctatus*)

(b) Australian thorny devil lizard (*Moloch horridus*)

(c) Wagler's pit viper (*Tropidolaemus wagleri*)

(d) Eastern box turtle (*Terrapene carolina carolina*)

(e) American alligator (*Alligator mississippiensis*)

continents well into the Cretaceous period, reaching up to a meter in length. Today, however, tuataras are found only on 30 islands off the coast of New Zealand. When humans arrived in New Zealand 750 years ago, the rats that accompanied them devoured tuatara eggs, eventually eliminating the reptiles on the main islands. The tuataras that remain on the outlying islands are about 50 cm long and feed on insects, small lizards, and bird eggs and chicks. They can live to be over 100 years old. Their future survival depends on whether their remaining habitats are kept rat-free.

The other major living lineage of lepidosaurs consists of the lizards and snakes, or squamates, which number about 7,900 species. Lizards are the most numerous and diverse reptiles (apart from birds) alive today **(Figure 34.29b)**. Many lizards are small; the Jaragua lizard, discovered in the Dominican Republic in 2001, is only 16 mm long—small enough to fit comfortably on a dime. In contrast, the Komodo dragon of Indonesia is a lizard that can reach a length of 3 m. It hunts deer and other large prey, delivering venom with its bite.

Snakes are legless lepidosaurs **(Figure 34.29c)**. As described in Chapter 26, snakes descended from lizards with legs. Today, some species of snakes retain vestigial pelvic and limb bones, providing evidence of their ancestry. Despite their lack of legs, snakes are quite proficient at moving on land, most often by producing waves of lateral bending that pass from head to tail. Force exerted by the bends against solid objects pushes the snake forward. Snakes can also move by gripping the ground with their belly scales at several points along the body while the scales at intervening points are lifted slightly off the ground and pulled forward.

Snakes are carnivorous, and a number of adaptations aid them in hunting and eating prey. They have acute chemical sensors, and though they lack eardrums, they are sensitive to ground vibrations, which helps them detect the movements of prey. Heat-detecting organs between the eyes and nostrils of pit vipers, including rattlesnakes, are sensitive to minute temperature changes, enabling these night hunters to locate warm animals. Venomous snakes inject their toxin through a pair of sharp teeth that may be hollow or grooved. The flicking tongue is not venomous but helps fan odors toward olfactory (smell) organs on the roof of the mouth. Loosely articulated jawbones and elastic skin enable most snakes to swallow prey larger than the diameter of the snake's head (see Figure 23.14).

Turtles

Turtles are one of the most distinctive group of reptiles alive today. All turtles have a boxlike shell made of upper and lower shields that are fused to the vertebrae, clavicles (collarbones), and ribs **(Figure 34.29d)**. Most of the 307 known species of turtles have a hard shell, providing excellent defense against predators. A 2008 study reported the discovery of the oldest known fossil of the turtle lineage, dating to 220 million years ago. This fossil has a complete lower shell but an incomplete upper shell, suggesting that turtles may have acquired full shells in stages. The marine sediments in which this fossil was found also suggest that turtles may have originated in shallow coastal waters. However, as other scientists have argued, it is also possible that turtles originated on land and that the incomplete upper shell of this fossil may have been a specialized adaptation for an aquatic lifestyle. Scientists continue to hunt for fossils that could shed light on the origin of the turtle shell.

The earliest turtles could not retract their head into their shell, but mechanisms for doing so evolved independently in two separate branches of turtles. The side-necked turtles fold their neck horizontally, while the vertical-necked turtles fold their neck vertically.

Some turtles have adapted to deserts, and others live almost entirely in ponds and rivers. Still others have returned to the sea. Sea turtles have a reduced shell and enlarged forelimbs that function as flippers. They include the largest living turtles, the deep-diving leatherbacks, which can exceed a mass of 1,500 kg and feed on jellies. Leatherbacks and other sea turtles are endangered by being caught in fishing nets, as well as by development of the beaches where the turtles lay their eggs.
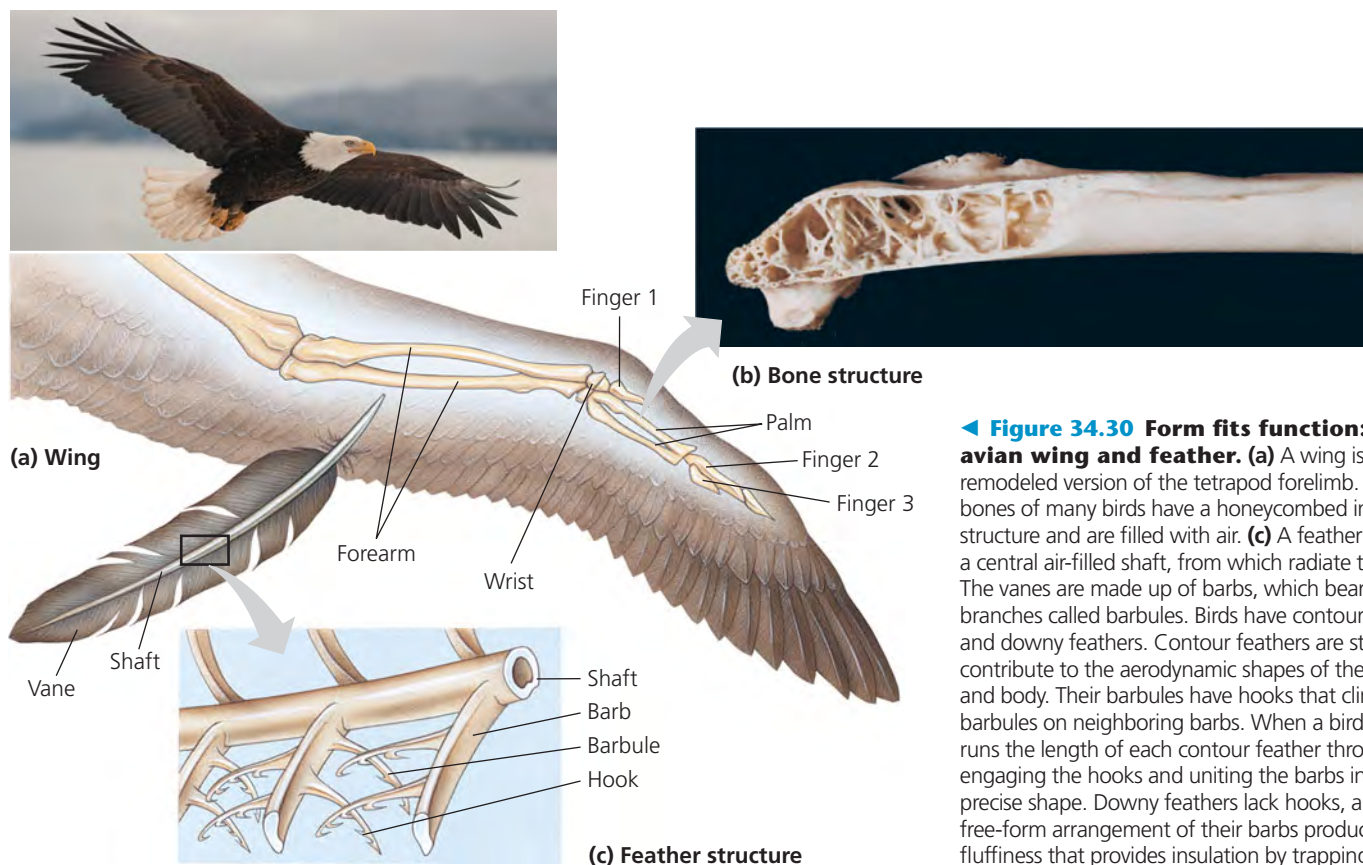
Alligators and Crocodiles

Alligators and crocodiles (collectively called crocodilians) belong to a lineage that reaches back to the late Triassic **(Figure 34.29e)**. The earliest members of this lineage were small terrestrial quadrupeds with long, slender legs. Later species became larger and adapted to aquatic habitats, breathing air through their upturned nostrils. Some Mesozoic crocodilians grew as long as 12 m and may have attacked dinosaurs and other prey at the water's edge.

The 23 known species of living crocodilians are confined to warm regions of the globe. Alligators in the southeastern United States have made a comeback after spending years on the endangered species list.

Birds

There are about 10,000 species of birds in the world. Like crocodilians, birds are archosaurs, but almost every feature of their anatomy has been modified in their adaptation to flight.

Derived Characters of Birds Many of the characters of birds are adaptations that facilitate flight, including weight-saving modifications that make flying more efficient. For example, birds lack a urinary bladder, and the females of most species have only one ovary. The gonads of both females and males are usually small, except during the breeding season, when they increase in size. Living birds are also toothless, an adaptation that trims the weight of the head.

(a) Wing

(b) Bone structure

Finger 1
Palm
Finger 2
Finger 3
Forearm
Wrist
Shaft
Vane
Shaft
Barb
Barbule
Hook

(c) Feather structure

◄ **Figure 34.30 Form fits function: the avian wing and feather. (a)** A wing is a remodeled version of the tetrapod forelimb. **(b)** The bones of many birds have a honeycombed internal structure and are filled with air. **(c)** A feather consists of a central air-filled shaft, from which radiate the vanes. The vanes are made up of barbs, which bear small branches called barbules. Birds have contour feathers and downy feathers. Contour feathers are stiff and contribute to the aerodynamic shapes of the wings and body. Their barbules have hooks that cling to barbules on neighboring barbs. When a bird preens, it runs the length of each contour feather through its bill, engaging the hooks and uniting the barbs into a precise shape. Downy feathers lack hooks, and the free-form arrangement of their barbs produces a fluffiness that provides insulation by trapping air.

A bird's most obvious adaptations for flight are its wings and feathers **(Figure 34.30)**. Feathers are made of the protein β-keratin, which is also found in the scales of other reptiles. The shape and arrangement of the feathers form the wings into airfoils, and they illustrate some of the same principles of aerodynamics as the wings of an airplane. Power for flapping the wings comes from contractions of large pectoral (breast) muscles anchored to a keel on the sternum (breastbone). Some birds, such as eagles and hawks, have wings adapted for soaring on air currents and flap their wings only occasionally; other birds, including hummingbirds, must flap continuously to stay aloft (see Figure 34.34). Among the fastest birds are the appropriately named swifts, which can fly up to 170 km/hr.

Flight provides numerous benefits. It enhances hunting and scavenging; many birds consume flying insects, an abundant, highly nutritious food resource. Flight also provides ready escape from earthbound predators and enables some birds to migrate great distances to exploit different food resources and seasonal breeding areas.

Flying requires a great expenditure of energy from an active metabolism. Birds are endothermic; they use their own metabolic heat to maintain a high, constant body temperature. Feathers and in some species a layer of fat provide insulation that enables birds to retain body heat. The lungs have

tiny tubes leading to and from elastic air sacs that improve airflow and oxygen uptake. This efficient respiratory system and a circulatory system with a four-chambered heart keep tissues well supplied with oxygen and nutrients, supporting a high rate of metabolism.

Flight also requires both acute vision and fine muscle control. Birds have color vision and excellent eyesight. The visual and motor areas of the brain are well developed, and the brain is proportionately larger than those of amphibians and nonbird reptiles.

Birds generally display very complex behaviors, particularly during breeding season, when they engage in elaborate courtship rituals. Because eggs have shells by the time they are laid, fertilization must be internal. Copulation usually involves contact between the mates' vents, the openings to their cloacas. After eggs are laid, the avian embryo must be kept warm through brooding by the mother, the father, or both, depending on the species.

The Origin of Birds Cladistic analyses of birds and reptilian fossils indicate that birds belong to the group of bipedal saurischian dinosaurs called theropods. Since the late 1990s, Chinese paleontologists have unearthed a spectacular trove of feathered theropod fossils that are shedding light on the origin of birds. Several species of dinosaurs closely related to

birds had feathers with vanes, and a wider range of species had filamentous feathers. Such findings imply that feathers evolved long before powered flight. Among the possible functions of these early feathers were insulation, camouflage, and courtship display.

How did flight evolve in the theropods? In one scenario, feathers may have enabled small, running dinosaurs chasing prey or escaping predators to gain extra lift as they jumped into the air. Or small dinosaurs could have gained traction as they ran up hills by flapping their feathered forelimbs—a behavior seen in some birds today. In a third scenario, some dinosaurs could have climbed trees and glided, aided by feathers. Whether birds took to the air from the ground up or the trees down, an essential question being studied by scientists ranging from paleontologists to engineers is how their efficient flight stroke evolved.

By 150 million years ago, feathered theropods had evolved into birds. *Archaeopteryx*, which was discovered in a German limestone quarry in 1861, remains the earliest known bird **(Figure 34.31)**. It had feathered wings but retained ancestral characters such as teeth, clawed digits in its wings, and a long tail. *Archaeopteryx* flew well at high speeds, but unlike a present-day bird, it could not take off from a standing position. Fossils of later birds from the Cretaceous show a gradual loss of certain ancestral dinosaur features, such as teeth and clawed forelimbs, as well as the acquisition of innovations found in extant birds, including a short tail covered by a fan of feathers.
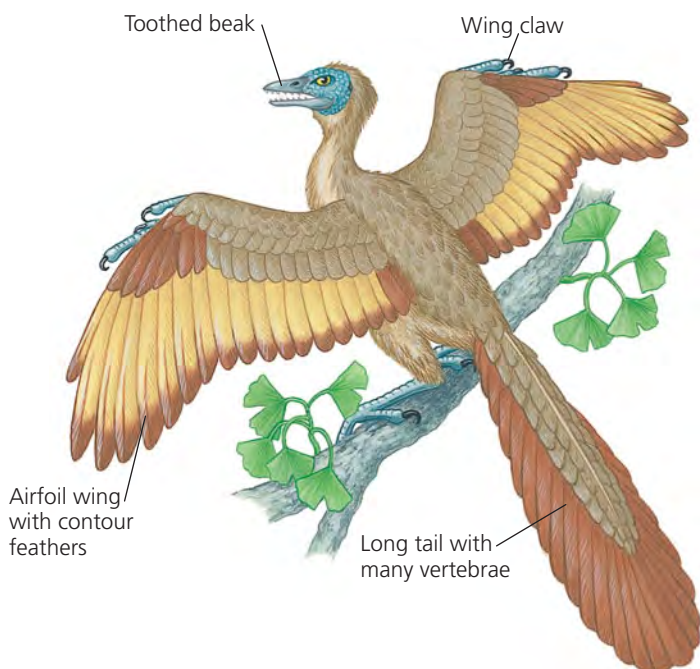
▲ **Figure 34.31 Artist's reconstruction of *Archaeopteryx*, the earliest known bird.** Fossil evidence indicates that *Archaeopteryx* was capable of powered flight but retained many characters of nonbird dinosaurs.

Toothed beak
Wing claw
Airfoil wing with contour feathers
Long tail with many vertebrae

▲ **Figure 34.32 An emu (*Dromaius novaehollandiae*), a flightless bird native to Australia.**

Living Birds Clear evidence of Neornithes, the clade that includes the 28 orders of living birds, can be found before the Cretaceous-Paleogene boundary 65.5 million years ago. Several groups of living and extinct birds include one or more flightless species. The **ratites** (order Struthioniformes), which consist of the ostrich, rhea, kiwi, cassowary, and emu, are all flightless **(Figure 34.32)**. In ratites, the sternal keel is absent, and the pectoral muscles are small relative to those of birds that can fly.

Penguins make up the flightless order Sphenisciformes, but, like flying birds, they have powerful pectoral muscles. They use these muscles to "fly" in the water: As they swim, they flap their flipper-like wings in a manner that resembles the flight stroke of a more typical bird **(Figure 34.33)**. Certain species of rails, ducks, and pigeons are also flightless.

Although the demands of flight have rendered the general body forms of many flying birds similar to one another, experienced bird-watchers can distinguish species by their profile, colors, flying style, behavior, and beak shape. The skeleton of a hummingbird wing is unique, making them the only birds

▲ **Figure 34.33 A king penguin (*Aptenodytes patagonicus*) "flying" underwater.** With their streamlined shape and powerful pectoral muscles, penguins are fast and agile swimmers.

◀ **Figure 34.34 Hummingbird feeding while hovering.** A hummingbird can rotate its wings in all directions, enabling it to hover and fly backwards.

that can hover and fly backwards **(Figure 34.34)**. Adult birds lack teeth, but during the course of avian evolution their beaks have taken on a variety of shapes suited to different diets. Some birds, such as parrots, have crushing beaks with which they can crack open hard nuts and seeds. Other birds, such as flamingoes, are filter feeders. Their beaks have remarkable 'strainers' that enable them to capture food particles from the water **(Figure 34.35)**. Foot structure, too, shows considerable variation. Various birds use their feet for perching on branches **(Figure 34.36)**, grasping food, defense, swimming or walking, and even courtship (see Figure 24.3e).

◀ **Figure 34.35 Specialized beaks.** This greater flamingo (*Phoenicopterus ruber*) dips its beak into the water and strains out the food.

▲ **Figure 34.36 Feet adapted to perching.** This great tit (*Parus major*) is a member of the Passeriformes, the perching birds. The toes of these birds can lock around a branch or wire, enabling the bird to rest for long periods.
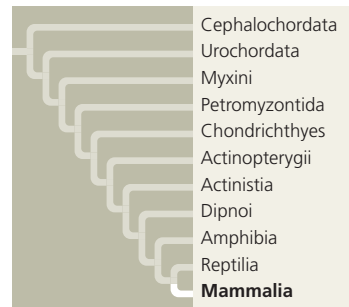
CONCEPT CHECK 34.6

1. Describe three key amniote adaptations for life on land.
2. Are snakes tetrapods? Explain.
3. Identify four avian adaptations for flight.
4. **WHAT IF?** Suppose turtles are more closely related to lepidosaurs than to other reptiles. Redraw Figure 34.25 to show this relationship, and mark the node that represents the most recent common ancestor shared by all living reptiles. Defining the reptile clade as consisting of all descendants of that ancestor, list the reptiles.

For suggested answers, see Appendix A.

CONCEPT 34.7

Mammals are amniotes that have hair and produce milk

Cephalochordata
Urochordata
Myxini
Petromyzontida
Chondrichthyes
Actinopterygii
Actinistia
Dipnoi
Amphibia
Reptilia
Mammalia

The reptiles we have been discussing represent one of the two living lineages of amniotes. The other amniote lineage is our own, the **mammals** (class Mammalia). Today, there are more than 5,300 known species of mammals on Earth.

Derived Characters of Mammals

The distinctive character from which mammals derive their name is their mammary glands, which produce milk for offspring. All mammalian mothers nourish their young with milk, a balanced diet rich in fats, sugars, proteins, minerals, and vitamins. Hair, another mammalian characteristic, and a fat layer under the skin help the body retain heat. Like birds, mammals are endothermic, and most have a high metabolic rate. Efficient respiratory and circulatory systems (including a four-chambered heart) support a mammal's metabolism. A sheet of muscle called the diaphragm helps ventilate the lungs.

Like birds, mammals generally have a larger brain than other vertebrates of equivalent size, and many species are capable learners. And as in birds, the relatively long duration of parental care extends the time for offspring to learn important survival skills by observing their parents.

Differentiated teeth are another important mammalian trait. Whereas the teeth of reptiles are generally uniform in size and shape, the jaws of mammals bear a variety of teeth with sizes and shapes adapted for chewing many kinds of foods. Humans, like most mammals, have teeth modified for shearing (incisors and canine teeth) and for crushing and grinding (premolars and molars; see Figure 41.16).

Early Evolution of Mammals

Mammals belong to a group of amniotes known as **synapsids**. Early nonmammalian synapsids lacked hair, had a sprawling gait, and laid eggs. A distinctive characteristic of synapsids is the single temporal fenestra, a hole behind the eye socket on each side of the skull. Humans retain this feature; your jaw muscles pass through the temporal fenestra and anchor on your temple. Fossil evidence shows that the jaw was remodeled as mammalian features arose gradually in successive lineages of earlier synapsids (see Figure 25.6); in all, these changes took more than 100 million years. In addition, two of the bones that formerly made up the jaw joint were incorporated into the mammalian middle ear **(Figure 34.37)**. This evolutionary change is reflected in changes that occur during development. For example, as a mammalian embryo grows, the posterior region of its jaw—which in a reptile forms the articular bone—can be observed to detach from the jaw and migrate to the ear, where it forms the malleus.

Synapsids evolved into large herbivores and carnivores during the Permian period, and for a time they were the dominant tetrapods. However, the Permian-Triassic extinctions took a heavy toll on them, and their diversity fell during the Triassic (251–200 million years ago). Increasingly mammal-like synapsids emerged by the end of the Triassic. While not true mammals, these synapsids had acquired a number of the derive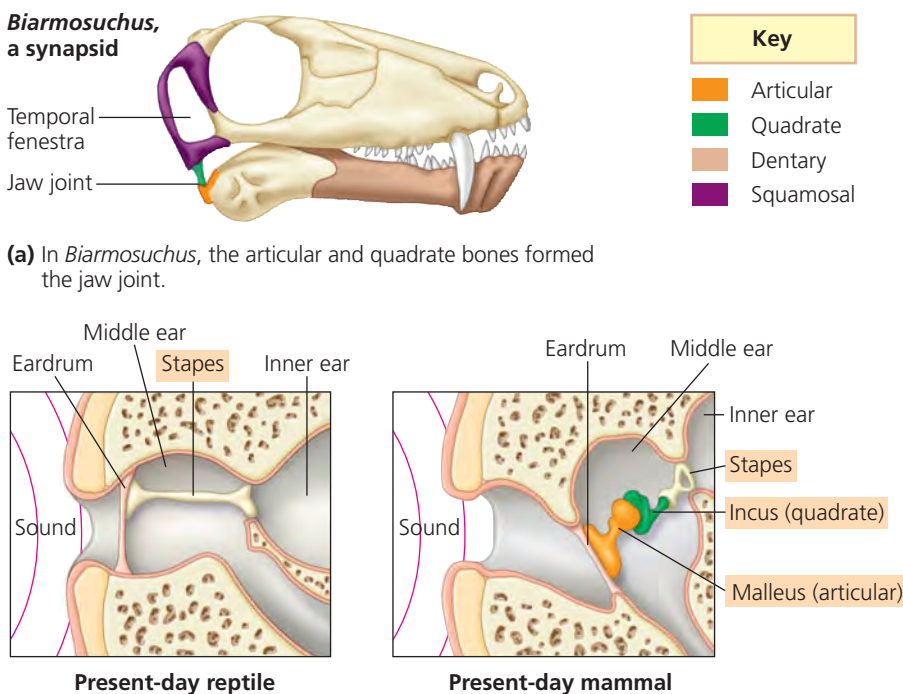d characters that distinguish mammals from other amniotes. They were small and probably hairy, and they likely fed on insects at night. Their bones show that they grew faster than other synapsids, suggesting that they probably had a relatively high metabolic rate; however, they still laid eggs.

During the Jurassic (200–145 million years ago), the first true mammals arose and diversified into many short-lived lineages. A diverse set of mammal species coexisted with dinosaurs in Jurassic and Cretaceous periods, but these species were not abundant or dominant members of their community, and most measured less than 1 m. One possible explanation for their small size is that dinosaurs already occupied ecological niches of large-bodied animals.

By the early Cretaceous, the three major lineages of mammals had emerged: those leading to monotremes (egg-laying mammals), marsupials (mammals with a pouch), and eutherians (placental mammals). After the extinction of large dinosaurs, pterosaurs, and marine reptiles during the late Cretaceous period, mammals underwent an adaptive radiation, giving rise to large predators and herbivores as well as flying and aquatic species.

Monotremes

Monotremes are found only in Australia and New Guinea and are represented by one species of platypus and four species of echidnas (spiny anteaters). Monotremes lay eggs, a character that is ancestral for amniotes and retained in most

(a) In *Biarmosuchus*, the articular and quadrate bones formed the jaw joint.

(b) During the evolutionary remodeling of the mammalian skull, a new jaw joint formed between the dentary and squamosal bones (see Figure 25.6). No longer used in the jaw, the quadrate and articular bones became incorporated into the middle ear as two of the three bones that transmit sound from the eardrum to the inner ear.

◄ **Figure 34.37 The evolution of the mammalian ear bones.** *Biarmosuchus* was a synapsid, a lineage that eventually gave rise to the mammals. Bones that transmit sound in the ear of mammals arose from the modification of bones in the jaw of nonmammalian synapsids.

MAKE CONNECTIONS *Review the definition of* exaptation *in Concept 25.6 (p. 530). Summarize the process by which exaptation occurs and explain how the incorporation of the articular and quadrate bones into the mammalian inner ear is an example.*

▲ **Figure 34.38 Short-beaked echidna (*Tachyglossus aculeatus*), an Australian monotreme.** Monotremes have hair and produce milk, but they lack nipples. Monotremes are the only mammals that lay eggs (inset).

reptiles **(Figure 34.38)**. Like all mammals, monotremes have hair and produce milk, but they lack nipples. Milk is secreted by glands on the belly of the mother. After hatching, the baby sucks the milk from the mother's fur.

Marsupials

Opossums, kangaroos, and koalas are examples of **marsupials**. Both marsupials and eutherians share derived characters not found among monotremes. They have higher metabolic rates and nipples that provide milk, and they give birth to live young. The embryo develops inside the uterus of the female's reproductive tract. The lining of the uterus and the extraembryonic membranes that arise from the embryo form a **placenta**, a structure in which nutrients diffuse into the embryo from the mother's blood.

A marsupial is born very early in its development and completes its embryonic development while nursing. In most species, the nursing young are held within a maternal pouch called a *marsupium* **(Figure 34.39a)**. A red kangaroo, for instance, is about the size of a honeybee at its birth, just 33 days after fertilization. Its back legs are merely buds, but its front legs are strong enough for it to crawl from the exit of its mother's reproductive tract to a pouch that opens to the front of her body, a journey that lasts a few minutes. In other species, the marsupium opens to the rear of the mother's body; in bandicoots, this protects the young as their mother burrows in the dirt **(Figure 34.39b)**.

Marsupials existed worldwide during the Mesozoic era, but today they are found only in the Australian region and in North and South America. The biogeography of marsupials is an example of the interplay between biological and geologic evolution (see Concept 25.4). After the breakup of the super-continent Pangaea, South America and Australia became island
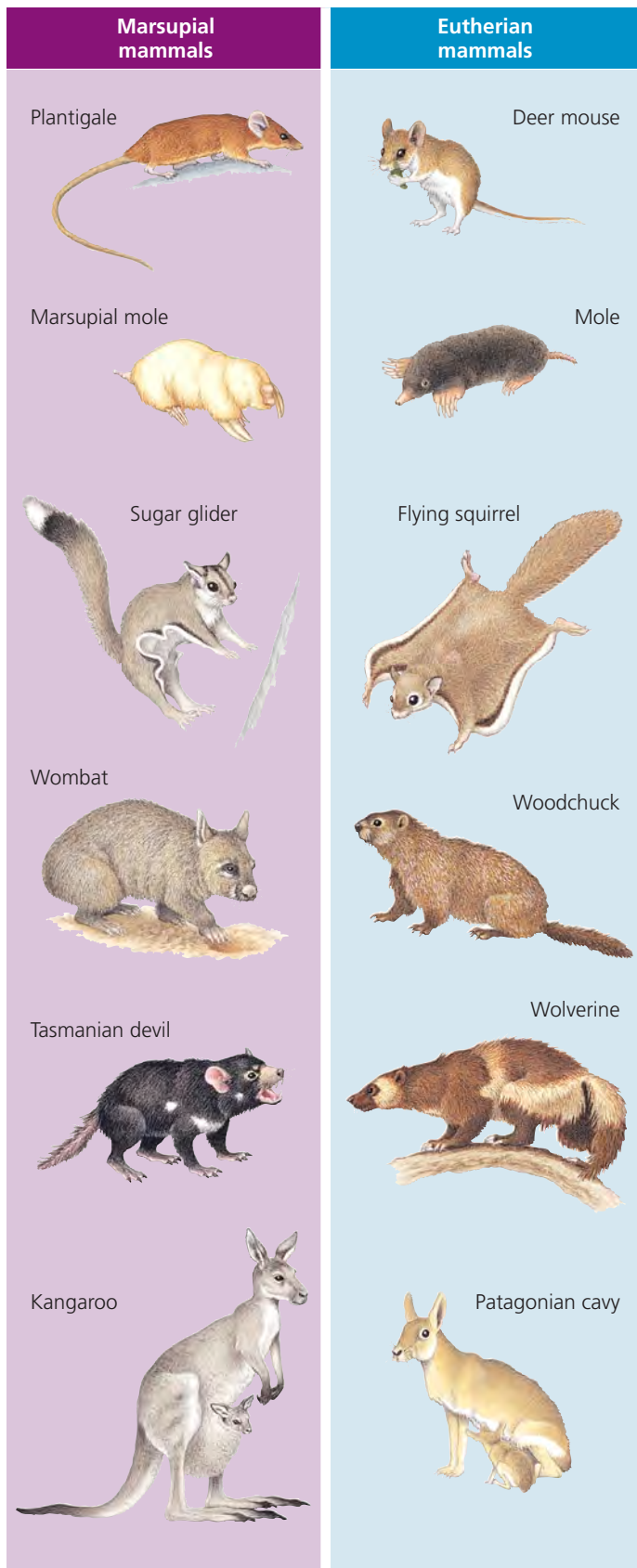

(a) A young brushtail possum. The offspring of marsupials are born very early in their development. They finish their growth while nursing from a nipple (in their mother's pouch in most species).

(b) Long-nosed bandicoot. Most bandicoots are diggers and burrowers that eat mainly insects but also some small vertebrates and plant material. Their rear-opening pouch helps protect the young from dirt as the mother digs. Other marsupials, such as kangaroos, have a pouch that opens to the front.

▲ **Figure 34.39 Australian marsupials.**

continents, and their marsupials diversified in isolation from the eutherians that began an adaptive radiation on the northern continents. Australia has not been in contact with another continent since early in the Cenozoic era, about 65 million years ago. In Australia, convergent evolution has resulted in a diversity of marsupials that resemble eutherians in similar ecological roles in other parts of the world **(Figure 34.40)**. In contrast, although South America had a diverse marsupial fauna throughout the Paleogene, it has experienced several migrations of eutherians. One of the most important migrations occurred about 3 million years ago, when North and South America joined at the Panamanian isthmus and extensive two-way traffic of animals took place over the land bridge. Today, only three families of marsupials live outside the Australian region, and the only marsupials found in the wild in North America are a few species of opossum.

Marsupial mammals	Eutherian mammals
Plantigale	Deer mouse
Marsupial mole	Mole
Sugar glider	Flying squirrel
Wombat	Woodchuck
Tasmanian devil	Wolverine
Kangaroo	Patagonian cavy

▲ **Figure 34.40 Convergent evolution of marsupials and eutherians (placental mammals).** (Drawings are not to scale.)

Eutherians (Placental Mammals)

Eutherians are commonly called placental mammals because their placentas are more complex than those of marsupials. Eutherians have a longer pregnancy than marsupials. Young eutherians complete their embryonic development within the uterus, joined to their mother by the placenta. The eutherian placenta provides an intimate and long-lasting association between the mother and her developing young.

The major groups of living eutherians are thought to have diverged from one another in a burst of evolutionary change. The timing of this burst is uncertain: It is dated to 100 million years ago by molecular data and 60 million years ago by morphological data. **Figure 34.41**, on the next two pages, explores the major eutherian orders and their possible phylogenetic relationships with each other as well as with the monotremes and marsupials.

Primates

The mammalian order Primates includes the lemurs, tarsiers, monkeys, and apes. Humans are members of the ape group.

Derived Characters of Primates Most primates have hands and feet adapted for grasping, and their digits have flat nails instead of the narrow claws of other mammals. There are other characteristic features of the hands and feet, too, such as skin ridges on the fingers (which account for human fingerprints). Relative to other mammals, primates have a large brain and short jaws, giving them a flat face. Their forward-looking eyes are close together on the front of the face. Primates also exhibit relatively well-developed parental care and complex social behavior.

The earliest known primates were tree-dwellers, and many of the characteristics of primates are adaptations to the demands of living in the trees. Grasping hands and feet allow primates to hang onto tree branches. All living primates, except humans, have a big toe that is widely separated from the other toes, enabling them to grasp branches with their feet. All primates also have a thumb that is relatively movable and separate from the fingers, but monkeys and apes have a fully **opposable thumb**; that is, they can touch the ventral surface (fingerprint side) of the tip of all four fingers with the ventral surface of the thumb of the same hand. In monkeys and apes other than humans, the opposable thumb functions in a grasping "power grip." In humans, a distinctive bone structure at the base of the thumb allows it to be used for more precise manipulation. The unique dexterity of humans represents descent with modification from our tree-dwelling ancestors. Arboreal maneuvering also requires excellent eye-hand coordination. The overlapping visual fields of the two forward-facing eyes enhance depth perception, an obvious advantage when brachiating (traveling by swinging from branch to branch in trees).
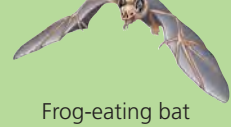
Exploring Mammalian Diversity

Phylogenetic Relationships of Mammals

Evidence from numerous fossils and molecular analyses indicates that monotremes diverged from other mammals about 180 million years ago and that marsupials diverged from eutherians (placental mammals) about 140 million years ago. Molecular systematics has helped to clarify the evolutionary relationships between the eutherian orders, though there is still no broad consensus on a phylogenetic tree. One current hypothesis, represented by the tree shown below, clusters the eutherian orders into four main clades.

Monotremes (5 species)

Marsupials (324 species)

ANCESTRAL MAMMAL

Eutherians (5,010 species)

Monotremata

Marsupialia

Proboscidea
Sirenia
Tubulidentata
Hyracoidea
Afrosoricida (golden moles and tenrecs)
Macroscelidea (elephant shrews)

This clade of eutherians evolved in Africa when the continent was isolated from other landmasses. It includes Earth's largest living land animal (the African elephant), as well as species that weigh less than 10 g.

Xenarthra

All members of this clade, which underwent an adaptive radiation in South America, belong to the order Xenarthra. One species, the nine-banded armadillo, is found in the southern United States.

Rodentia
Lagomorpha
Primates
Dermoptera (flying lemurs)
Scandentia (tree shrews)

This is the largest eutherian clade. It includes the rodents, which make up the largest mammalian order by far, with about 1,770 species. Humans belong to the order Primates.

Carnivora
Cetartiodactyla
Perissodactyla
Chiroptera
Eulipotyphla
Pholidota (pangolins)

This diverse clade includes terrestrial and marine mammals as well as bats, the only flying mammals. A growing body of evidence, including Eocene fossils of whales with feet, supports putting whales in the same order (Cetartiodactyla) as pigs, cows, and hippos (see Figures 22.19 and 22.20).

Possible phylogenetic tree of mammals.
All 20 extant orders of mammals are listed at the right of the tree. The orders in bold type are surveyed on the facing page.

Orders and Examples	Main Characteristics	Orders and Examples	Main Characteristics
Monotremata Platypuses, echidnas Echidna	Lay eggs; no nipples; young suck milk from fur of mother	**Marsupialia** Kangaroos, opossums, koalas Koala	Completes embryonic development in pouch on mother's body
Proboscidea Elephants African elephant	Long, muscular trunk; thick, loose skin; upper incisors elongated as tusks	**Tubulidentata** Aardvarks Aardvark	Teeth consisting of many thin tubes cemented together; eats ants and termites
Sirenia Manatees, dugongs Manatee	Aquatic; finlike forelimbs and no hind limbs; herbivorous	**Hyracoidea** Hyraxes Rock hyrax	Short legs; stumpy tail; herbivorous; complex, multi-chambered stomach
Xenarthra Sloths, anteaters, armadillos Tamandua	Reduced teeth or no teeth; herbivorous (sloths) or carnivorous (anteaters, armadillos)	**Rodentia** Squirrels, beavers, rats, porcupines, mice Red squirrel	Chisel-like, continuously growing incisors worn down by gnawing; herbivorous
Lagomorpha Rabbits, hares, picas Jackrabbit	Chisel-like incisors; hind legs longer than forelegs and adapted for running and jumping; herbivorous	**Primates** Lemurs, monkeys, chimpanzees, gorillas, humans Golden lion tamarin	Opposable thumbs; forward-facing eyes; well-developed cerebral cortex; omnivorous
Carnivora Dogs, wolves, bears, cats, weasels, otters, seals, walruses Coyote	Sharp, pointed canine teeth and molars for shearing; carnivorous	**Perissodactyla** Horses, zebras, tapirs, rhinoceroses Indian rhinoceros	Hooves with an odd number of toes on each foot; herbivorous
Cetartiodactyla Artiodactyls Sheep, pigs, cattle, deer, giraffes Bighorn sheep	Hooves with an even number of toes on each foot; herbivorous	**Chiroptera** Bats Frog-eating bat	Adapted for flight; broad skinfold that extends from elongated fingers to body and legs; carnivorous or herbivorous
Cetaceans Whales, dolphins, porpoises Pacific white-sided porpoise	Aquatic; streamlined body; paddle-like forelimbs and no hind limbs; thick layer of insulating blubber; carnivorous	**Eulipotyphla** "Core insectivores": some moles, some shrews Star-nosed mole	Eat mainly insects and other small invertebrates

Living Primates There are three main groups of living primates: (1) the lemurs of Madagascar **(Figure 34.42)** and the lorises and bush babies of tropical Africa and southern Asia; (2) the tarsiers, which live in Sou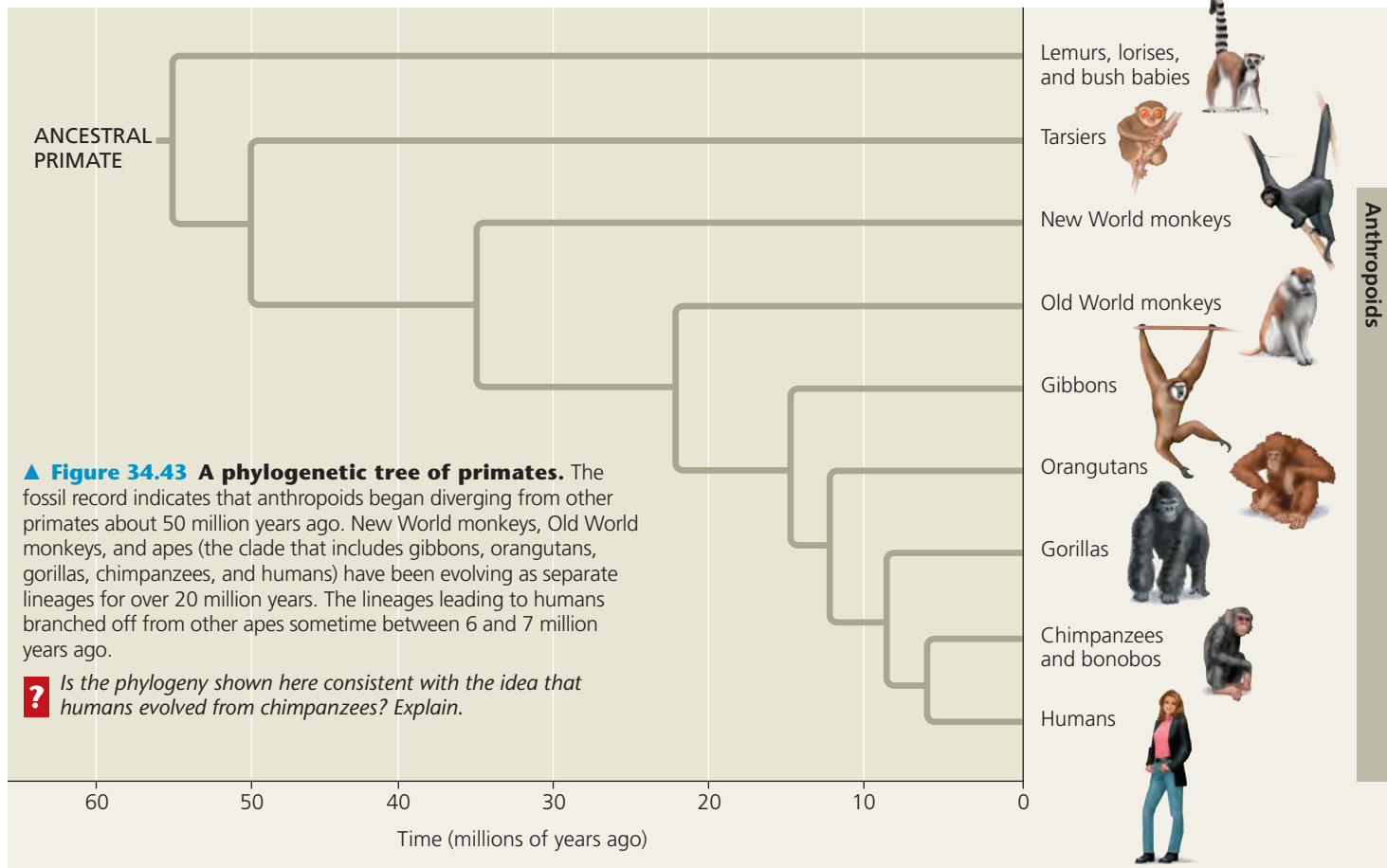theast Asia; and (3) the **anthropoids**, which include monkeys and apes and are found worldwide. The first group—lemurs, lorises, and bush babies—probably resemble early arboreal primates. The oldest known anthropoid fossils, discovered in China in mid-Eocene strata dating to 45 million years ago, indicate that tarsiers are more closely related to anthropoids than to the lemur group **(Figure 34.43)**.

You can see in Figure 34.38 that monkeys do not form a clade but rather consist of two groups, the New and Old World monkeys. Both of these groups are thought to have originated in Africa or Asia. The fossil record indicates that New World monkeys first colonized South America roughly 25 million years ago. By that time, South America and Africa had drifted apart, and monkeys may have reached South America from Africa by rafting on logs or other debris. What is certain is that New World monkeys and Old World monkeys underwent separate adaptive radiations during their many millions of years of separation **(Figure 34.44)**. All species of New World monkeys are arboreal, whereas Old World monkeys include ground-dwelling as well as arboreal species. Most monkeys in both groups are diurnal (active during the day) and usually live in bands held together by social behavior.

The other group of anthropoids consists of primates informally called apes **(Figure 34.45)**. The ape group includes the genera *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas), *Pan* (chimpanzees and bonobos), and *Homo* (humans).

► Figure 34.42
Coquerel's sifakas (*Propithecus verreauxi coquereli*), a type of lemur.

▲ **Figure 34.43 A phylogenetic tree of primates.** The fossil record indicates that anthropoids began diverging from other primates about 50 million years ago. New World monkeys, Old World monkeys, and apes (the clade that includes gibbons, orangutans, gorillas, chimpanzees, and humans) have been evolving as separate lineages for over 20 million years. The lineages leading to humans branched off from other apes sometime between 6 and 7 million years ago.

? *Is the phylogeny shown here consistent with the idea that humans evolved from chimpanzees? Explain.*

▼ **Figure 34.44 New World monkeys and Old World monkeys.**

(a) New World monkeys, such as spider monkeys (shown here), squirrel monkeys, and capuchins, have a prehensile tail and nostrils that open to the sides.

(b) Old World monkeys lack a prehensile tail, and their nostrils open downward. This group includes macaques (shown here), mandrils, baboons, and rhesus monkeys.

The apes diverged from Old World monkeys about 20–25 million years ago. Today, nonhuman apes are found exclusively in tropical regions of the Old World. With the exception of gibbons, living apes are larger than either New or Old World monkeys. All living apes have relatively long arms, short legs, and no tail. Although all nonhuman apes spend time in trees, only gibbons and orangutans are primarily arboreal. Social organization varies among the apes; gorillas and chimpanzees are highly social. Finally, compared to other primates, apes have a larger brain in proportion to their body size, and their behavior is more flexible. These two characteristics are especially prominent in the next group we'll consider, the hominins.

(a) Gibbons, such as this Muller's gibbon, are found only in southeastern Asia. Their very long arms and fingers are adaptations for brachiating (swinging by the arms from branch to branch).
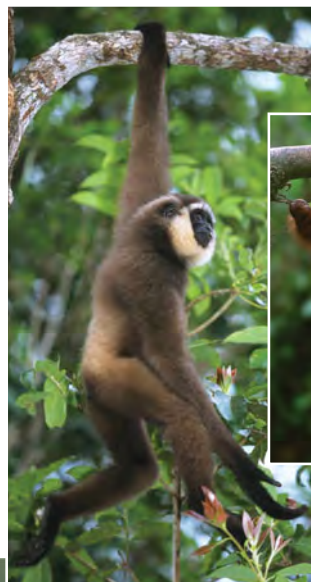
(b) Orangutans are shy apes that live in the rain forests of Sumatra and Borneo. They spend most of their time in trees; note the foot adapted for grasping and the opposable thumb.

(c) Gorillas are the largest apes; some males are almost 2 m tall and weigh about 200 kg. Found only in Africa, these herbivores usually live in groups of up to about 20 individuals.

(d) Chimpanzees live in tropical Africa. They feed and sleep in trees but also spend a great deal of time on the ground. Chimpanzees are intelligent, communicative, and social.

(e) Bonobos are in the same genus (*Pan*) as chimpanzees but are smaller. They survive today only in the African nation of Congo.

▲ **Figure 34.45 Nonhuman apes.**

CONCEPT 34.8

Humans are mammals that have a large brain and bipedal locomotion

In our tour of Earth's biodiversity, we come at last to our own species, *Homo sapiens*, which is about 200,000 years old. When you consider that life has existed on Earth for at least 3.5 billion years, we are clearly evolutionary newcomers.

Derived Characters of Humans

Many characters distinguish humans from other apes. Most obviously, humans stand upright and are bipedal (walk on two legs). Humans have a much larger brain and are capable of language, symbolic thought, artistic expression, and the manufacture and use of complex tools. Humans also have reduced jawbones and jaw muscles, along with a shorter digestive tract.

At the molecular level, the list of derived characters of humans is growing as scientists compare the genomes of humans and chimpanzees. Although the two genomes are 99% identical, a difference of 1% can translate into a large number of changes in a genome that contains 3 billion base pairs. Furthermore, changes in a small number of genes can have large effects. This point was highlighted by recent results showing that humans and chimpanzees differ in the expression of 19 regulatory genes. These genes turn other genes on and off and hence may account for many differences between humans and chimpanzees.

Bear in mind that such genomic differences—and whatever derived phenotypic traits they code for—separate humans from other *living* apes. But many of these new characters first emerged in our ancestors, long before our own species appeared. We will consider some of these ancestors to see how these characters originated.

The Earliest Hominins

The study of human origins is known as **paleoanthropology**. Paleoanthropologists have unearthed fossils of approximately 20 extinct species that are more closely related to humans than to chimpanzees. These species are known as **hominins** (**Figure 34.46**, on the facing page). (Although a majority of anthropologists now use the term *hominin*, its older synonym, *hominid*, continues to be used by some). Since 1994, fossils of four hominin species dating to more than 4 million years ago have been discovered. The oldest of these hominins, *Sahelanthropus tchadensis*, lived about 6.5 million years ago.

Sahelanthropus and other early hominins shared some of the derived characters of humans. For example, they had reduced canine teeth, and some fossils suggest that they had relatively flat faces. They also show signs of having been more upright and bipedal than other apes. One clue to their upright stance can be found in the foramen magnum, the hole at the base of the skull through which the spinal cord exits. In chimpanzees, the foramen magnum is relatively far back on the skull, while in early hominins (and in humans), it is located underneath the skull. This position allows us to hold our head directly over our body, as apparently early hominins did as well. The pelvis, leg bones, and feet of the 4.4-million-year-old *Ardipithecus ramidus* also suggest that early hominins were increasingly bipedal (**Figure 34.47**). (We will return to the subject of bipedalism later.)

Note that the characters that distinguish humans from other living apes did not all evolve in tight unison. While early hominins were showing signs of bipedalism, their brains remained small—about 300–450 cm^3 in volume, compared with an average of 1,300 cm^3 for *Homo sapiens*. The earliest hominins were also small overall. *A. ramidus*, for example, is

◄ **Figure 34.47 The skeleton of "Ardi," a 4.4-million-year-old hominin, *Ardipithecus ramidus*.**
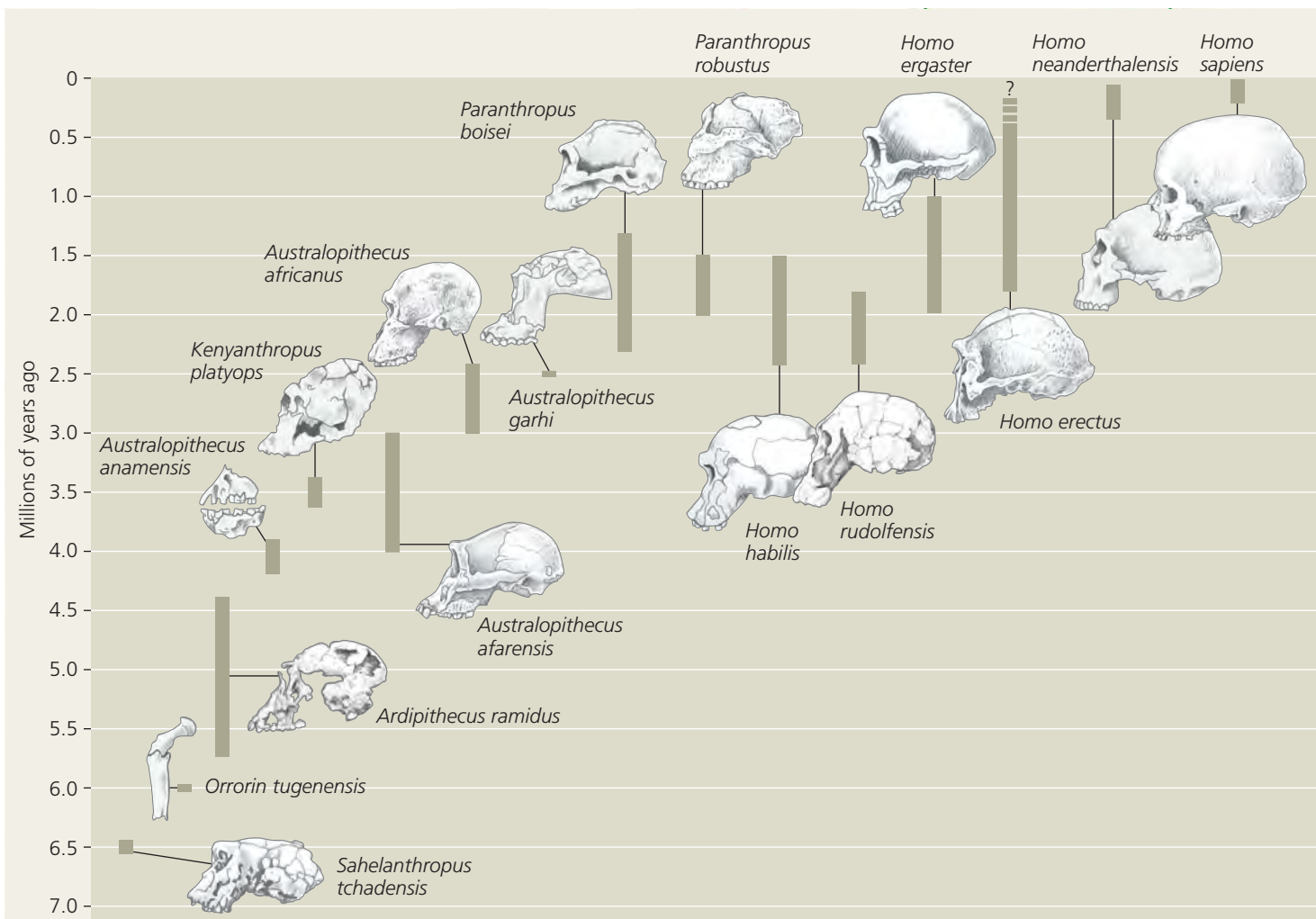
▲ **Figure 34.46 A timeline for some selected hominin species.** Most of these fossils come from sites in eastern and southern Africa. Note that at most times in hominin history, two or more hominin species were contemporaries. Some of the species are controversial, reflecting phylogenetic debates about the interpretation of skeletal details and biogeography.

estimated to have weighed only 50 kg, with relatively large teeth and a jaw that projected beyond the upper part of the face. Humans, in contrast, have a relatively flat face; compare your own face with that of the chimpanzees in Figure 34.45d.

It's important to avoid two common misconceptions when considering early hominins. One is to think of them either as chimpanzees or as having evolved from chimpanzees. Chimpanzees represent the tip of a separate branch of evolution, and they acquired derived characters of their own after they diverged from their common ancestor with humans.

Another misconception is to think of human evolution as a ladder leading directly from an ancestral ape to *Homo sapiens*. This error is often illustrated as a parade of fossil species that become progressively more like ourselves as they march across the page. If human evolution is a parade, it is a very disorderly one, with many groups breaking away to wander other evolutionary paths. At times, several hominin species coexisted. These species often differed in skull shape, body size, and diet

(as inferred from their teeth). Ultimately, all but one lineage—the one that gave rise to *Homo sapiens*—ended in extinction. But when the characteristics of all hominins that lived over the past 6 million years are considered, *H. sapiens* appears not as the end result of a straight evolutionary path, but rather as the only surviving member of a highly branched evolutionary tree.

Australopiths

The fossil record indicates that hominin diversity increased dramatically between 4 and 2 million years ago. Many of the hominins from this period are collectively called australopiths. Their phylogeny remains unresolved on many points, but as a group, they are almost certainly paraphyletic. The earliest member of the group, *Australopithecus anamensis*, lived 4.2–3.9 million years ago, close in time to older hominins such as *Ardipithecus ramidus*.

Australopiths got their name from the 1924 discovery in South Africa of *Australopithecus africanus* ("southern ape of

Africa"), which lived between 3 and 2.4 million years ago. With the discovery of more fossils, it became clear that *A. africanus* walked fully erect (was bipedal) and had human-like hands and teeth. However, its brain was only about one-third the size of the brain of a present-day human.

In 1974, in the Afar region of Ethiopia, paleoanthropologists discovered a 3.2-million-year-old *Australopithecus* skeleton that was 40% complete. "Lucy," as the fossil was named, was short—only about 1 m tall. Lucy and similar fossils have been given the species name *Australopithecus afarensis* (for the Afar region). Fossils discovered in the early 1990s show that *A. afarensis* existed as a species for at least 1 million years.

At the risk of oversimplifying, we could say that *A. afarensis* had fewer of the derived characters of humans above the neck than below. Lucy's brain was the size of a softball, a size similar to that expected for a chimpanzee of Lucy's body size. *A. afarensis* skulls also have a long lower jaw. Skeletons of *A. afarensis* suggest that these hominins were capable of arboreal locomotion, with arms that were relatively long in proportion to body size (compared to the proportions in humans). However, fragments of pelvic and skull bones indicate that *A. afarensis* walked on two legs. Fossilized footprints in Laetoli, Tanzania, corroborate the skeletal evidence that hominins living at the time of *A. afarensis* were bipedal **(Figure 34.48)**.

Another lineage of australopiths consisted of the "robust" australopiths. These hominins, which included species such as *Paranthropus boisei*, had sturdy skulls with powerful jaws and large teeth, adapted for grinding and chewing hard, tough foods. They contrast with the "gracile" (slender) australopiths, including *A. afarensis* and *A. africanus*, which had lighter feeding equipment adapted for softer foods.

Combining evidence from the earliest hominins with the much richer fossil record of later australopiths makes it possible to formulate hypotheses about significant trends in hominin evolution. Let's consider two of these trends: the emergence of bipedalism and tool use.

Bipedalism

Our anthropoid ancestors of 35–30 million years ago were still tree-dwellers. But by about 10 million years ago, the Himalayan mountain range had formed, thrust up in the aftermath of the Indian plate's collision with the Eurasian plate (see Figure 25.13). The climate became drier, and the forests of what are now Africa and Asia contracted. The result was an increased area of savanna (grassland) habitat, with fewer trees. For decades, paleoanthropologists have seen a strong connection between the rise of savannas and the rise of bipedal hominins. According to one hypothesis, tree-dwelling hominins could no longer move through the canopy, so natural selection favored adaptations that made moving over open ground more efficient. Underlying this idea is the fact that while nonhuman apes are superbly adapted for climbing trees, they are less well suited for

▶ **Figure 34.48 Evidence that hominins walked upright 3.5 million years ago.**

(a) The Laetoli footprints, more than 3.5 million years old, confirm that upright posture evolved quite early in hominin history.

(b) An artist's reconstruction of *A. afarensis*, a hominin alive at the time of the Laetoli footprints.

ground travel. For example, as a chimpanzee walks, it uses four times the amount of energy used by a human.

Although elements of this hypothesis survive, the picture now appears somewhat more complex. Although all recently discovered fossils of early hominins show indications of bipedalism, none of these hominins lived in savannas. Instead, they lived in mixed habitats ranging from forests to open woodlands. Furthermore, whatever the selective pressure that led to bipedalism, hominins did not become more bipedal in a simple, linear fashion. *Ardipithecus* had skeletal elements indicating that it could switch to upright walking but also was well suited for climbing trees. Australopiths seem to have had various locomotor styles, and some species spent more time on the ground than others. Only about 1.9 million years ago did hominins begin to walk long distances on two legs. These hominins lived in more arid environments, where bipedal walking requires less energy than walking on all fours.

Tool Use

As you read earlier, the manufacture and use of complex tools is a derived behavioral character of humans. Determining the origin of tool use in hominin evolution is one of paleoanthro-

pology's great challenges. Other apes are capable of surprisingly sophisticated tool use. Orangutans, for example, can fashion sticks into probes for retrieving insects from their nests. Chimpanzees are even more adept, using rocks to smash open food and putting leaves on their feet to walk over thorns. It's likely that early hominins were capable of this sort of simple tool use, but finding fossils of modified sticks or leaves that were used as shoes is practically impossible.

The oldest generally accepted evidence of tool use by hominins is 2.5-million-year-old cut marks on animal bones found in Ethiopia. These marks suggest that hominins cut flesh from the bones of animals using stone tools. Interestingly, the hominins whose fossils were found near the site where the bones were discovered had a relatively small brain. If these hominins, which have been named *Australopithecus garhi*, were in fact the creators of the stone tools used on the bones, that would suggest that stone tool use originated before the evolution of large brains in hominins.

Early *Homo*

The earliest fossils that paleoanthropologists place in our genus, *Homo*, include those of the species *Homo habilis*. These fossils, ranging in age from about 2.4 to 1.6 million years, show clear signs of certain derived hominin characters above the neck. Compared to the australopiths, *H. habilis* had a shorter jaw and a larger brain volume, about 600–750 cm^3. Sharp stone tools have also been found with some fossils of *H. habilis* (the name means "handy man").

Fossils from 1.9 to 1.5 million years ago mark a new stage in hominin evolution. A number of paleoanthropologists recognize these fossils as those of a distinct species, *Homo ergaster*. *Homo ergaster* had a substantially larger brain than *H. habilis* (over 900 cm^3), as well as long, slender legs with hip joints well adapted for long-distance walking **(Figure 34.49)**. The fingers were relatively short and straight, suggesting that *H. ergaster* did not climb trees like earlier hominins. *Homo ergaster* fossils have been discovered in far more arid environments than earlier hominins and have been associated with more sophisticated stone tools. Its smaller teeth also suggest that *H. ergaster* either ate different foods than australopiths (more meat and less plant material) or prepared some of its food before chewing, perhaps by cooking or mashing the food.

Homo ergaster marks an important shift in the relative sizes of the sexes. In primates, a size difference between males and females is a major component of sexual dimorphism (see Chapter 23). On average, male gorillas and orangutans weigh about twice as much as females of their species. In chimpanzees and bonobos, males are only about 1.35 times as heavy as females, on average. In *Australopithecus afarensis*, males were 1.5 times as heavy as females. But in early *Homo*, sexual dimorphism was significantly reduced, and this trend continues through our own species: Human males average about 1.2 times the weight of females.

► **Figure 34.49 Fossil of *Homo ergaster*.** This 1.7-million-year-old fossil from Kenya belongs to a young *Homo ergaster* male. This individual was tall, slender, and fully bipedal, and he had a relatively large brain.

The reduced sexual dimorphism may offer some clues to the social systems of extinct hominins. In extant primates, extreme sexual dimorphism is associated with intense male-male competition for multiple females. In species that undergo more pair-bonding (including our own), sexual dimorphism is less dramatic. In *H. ergaster*, therefore, males and females may have engaged in more pair-bonding than earlier hominins did. This shift may have been associated with long-term care of the young by both parents. Human babies depend on their parents for food and protection much longer than do the young of other apes.

Fossils now generally recognized as *H. ergaster* were originally considered early members of another species, *Homo erectus*, and some paleoanthropologists still hold this position. *Homo erectus* originated in Africa and was the first hominin to migrate out of Africa. The oldest fossils of hominins outside Africa, dating back 1.8 million years, were discovered in 2000 in the former Soviet Republic of Georgia. *Homo erectus* eventually migrated as far as the Indonesian archipelago. Fossil evidence indicates that *H. erectus* became extinct sometime after 200,000 years ago; one group may have persisted on Java until roughly 50,000 years ago.

Neanderthals

In 1856, miners discovered some mysterious human fossils in a cave in the Neander Valley in Germany. The 40,000-year-old fossils belonged to a thick-boned hominin with a prominent brow. The hominin was named *Homo neanderthalensis* and is commonly called a Neanderthal. Neanderthals were living in Europe by 350,000 years ago and later spread to the Near East, central Asia, and southern Siberia. They had a brain as large as that of present-day humans, buried their

dead, and made hunting tools from stone and wood. But despite their adaptations and culture, Neanderthals apparently became extinct about 28,000 years ago.

At one time, many paleoanthropologists considered Neanderthals to be a stage in the evolution of *Homo erectus* into *Homo sapiens*. Now most have abandoned this view, partly due to the analysis of mitochondrial DNA **(Figure 34.50)**. These and other genetic results suggest that Neanderthals may have contributed little to the gene pool of *H. sapiens*. However, a 2010 analysis of the DNA sequence of the Neanderthal genome appears to be consistent with limited gene flow between the two species. In addition, some researchers have argued that evidence of gene flow can be found in fossils that show a mixture of *H. sapiens* and Neanderthal characteristics. Further genetic analyses and fossil discoveries will be needed to resolve the ongoing debate over the extent of genetic exchange between the two species.

Homo sapiens

Evidence from fossils, archaeology, and DNA studies has led to a compelling hypothesis about how our own species, *Homo sapiens*, emerged and spread around the world.

Fossil evidence indicates that the ancestors of humans originated in Africa. Older species (perhaps *H. ergaster* or *H. erectus*) gave rise to later species, ultimately including *H. sapiens*. Furthermore, the oldest known fossils of our own species have been found at two different sites in Ethiopia and include specimens that are 195,000 and 160,000 years old **(Figure 34.51)**. These early humans had less pronounced browridges than found in *H. erectus* and Neanderthals, and they were more slender than other recent hominins.

The Ethiopian fossils support inferences about the origin of humans from molecular evidence. As shown in Figure 34.50, DNA analyses indicate that all living humans are more closely related to one another than to Neanderthals. Other studies on human DNA show that Europeans and Asians share a relatively recent common ancestor and that many African lineages branched off more basal positions on the human family tree. These findings strongly suggest that all living humans have ancestors that originated as *H. sapiens* in Africa, which is further supported by analysis of mitochondrial DNA and Y chromosomes from members of various human populations.

The oldest fossils of *H. sapiens* outside Africa are from the Middle East and date back about 115,000 years.

▲ **Figure 34.51 A 160,000-year-old fossil of *Homo sapiens*.** This skull, discovered in Ethiopia in 2003, differs little from the skulls of living humans.

Studies of the human Y chromosome suggest that humans spread beyond Africa in one or more waves, first into Asia and then to Europe and Australia. The date of the first arrival of humans in the New World is uncertain, although the oldest generally accepted evidence puts that date at about 15,000 years ago.

New findings continually update our understanding of the evolution of *H. sapiens*. For example, in 2004, researchers reported an astonishing find: skeletal remains of adult hominins dating from just 18,000 years ago and representing a previously

unknown species, which they named *Homo floresiensis*. Discovered in a limestone cave on the Indonesian island of Flores, the individuals were much shorter and had a much smaller brain volume than *H. sapiens*—more similar, in fact, to an australopith. The researchers who discovered these fossils argue that the skeletons also display many derived traits, including skull thickness and proportions and teeth shape, suggesting that the species is descended from the larger *H. erectus*. Not convinced, some researchers have argued that the fossils represent small *H. sapiens* individuals with deformed, miniature brains, a condition called microcephaly.

However, a 2007 study found that the wrist bones of the Flores fossils are similar in shape to those of nonhuman apes and early hominins, but different from those of Neanderthals and *H. sapiens*. These researchers concluded that the Flores fossils represent a species whose lineage branched off before the origin of the clade that includes Neanderthals and humans. A later study comparing the foot bones of the Flores fossils with those of other hominins also indicated that *H. floresiensis* arose before *H. sapiens*; in fact, these researchers suggested that *H. floresiensis* may have descended from an as-yet-unidentified hominin that lived even earlier than *H. erectus*.

If further evidence continues to support the designation of *H. floresiensis* as a new hominin, one intriguing explanation for this species' apparent "shrinkage" is that isolation on the island may have resulted in selection for greatly reduced size. Such dramatic size reduction is well studied in other dwarf mammalian species that are endemic to islands, including primitive pygmy elephants found near the Flores fossils. One such study found that on islands, the brains of dwarf fossil hippos were proportionally even smaller than their bodies. One possible explanation for this finding is that smaller brains resulted from selection for reduced energy consumption (the mammalian brain uses large amounts of energy). Applying their results to the Flores fossils, the researchers concluded that the brain size of *H. floresiensis* closely matches that predicted for a dwarf hominin of its body size. Compelling questions that may yet be answered from the cache of anthropological and archaeological finds on Flores include how *H. floresiensis* originated and whether it encountered *H. sapiens*, which also was living in Indonesia 18,000 years ago.

The rapid expansion of our species may have been spurred by changes in human cognition as *H. sapiens* evolved in Africa. Evidence of sophisticated thought in *H. sapiens* includes a 2002 discovery in South Africa of 77,000-year-old art—geometric markings made on pieces of ochre **(Figure 34.52)**. And in 2004, archaeologists working in southern and eastern Africa found 75,000-year-old ostrich eggs and snail shells with holes neatly drilled through them. By 36,000 years ago, humans were producing spectacular cave paintings (see Figure 56.33a). While these developments can help us understand the spread of *H. sapiens*, it is not clear whether they played a role in the extinction of other hominins. Neanderthals, for example, also

▲ **Figure 34.52 Art, a human hallmark.** The engravings on this 77,000-year-old piece of ochre, discovered in South Africa's Blombos Cave, are among the earliest signs of symbolic thought in humans.

made complex tools and showed a capacity for symbolic thought. As a result, the earlier suggestion that Neanderthals were driven to extinction by competition with *H. sapiens* is now being questioned by some scientists.

Our discussion of humans brings this unit on biological diversity to an end. But this organization isn't meant to imply that life consists of a ladder leading from lowly microorganisms to lofty humanity. Biological diversity is the product of branching phylogeny, not ladderlike "progress," however we choose to measure it. The fact that there are more species of ray-finned fishes alive today than all other vertebrates combined is a clear indication that our finned relatives are not outmoded underachievers that failed to leave the water. The tetrapods—amphibians, reptiles, and mammals—are derived from one lineage of lobe-finned vertebrates. As tetrapods diversified on land, fishes continued their branching evolution in the greatest portion of the biosphere's volume. Similarly, the ubiquity of diverse prokaryotes throughout the biosphere today is a reminder of the enduring ability of these relatively simple organisms to keep up with the times through adaptive evolution. Biology exalts life's diversity, past and present.

CONCEPT CHECK 34.8

1. Identify some characters that distinguish hominins from other apes.
2. Provide an example in which different features of organisms in the hominin evolutionary lineage evolved at different rates.
3. **WHAT IF?** Some genetic studies suggest that the most recent common ancestor of *Homo sapiens* that lived outside of Africa spread from Africa about 50,000 years ago. Compare this date with the dates of fossils given in the text. Can both the genetic results and the dates ascribed to the fossils be correct? Explain.

For suggested answers, see Appendix A.

SUMMARY OF KEY CONCEPTS

Key Concept							Clade	Description
Concept 34.1 Chordates have a notochord and a dorsal, hollow nerve cord (pp. 697–701) ? *Describe likely features of the chordate common ancestor and explain your reasoning.*	**Chordates:** notochord; dorsal, hollow nerve cord; pharyngeal slits; post-anal tail						Cephalochordata (lancelets)	Basal chordates; marine suspension feeders that exhibit four key derived characters of chordates
							Urochordata (tunicates)	Marine suspension feeders; larvae display the derived traits of chordates
Concept 34.2 Craniates are chordates that have a head (pp. 701–703) ? *Compare the typical lifestyle of craniates with that of lancelets and tunicates.*		**Craniates:** two sets of *Hox* genes, neural crest						Myxini (hagfishes and relatives)	Jawless marine organisms; have head that includes a skull and brain, eyes, and other sensory organs
Concept 34.3 Vertebrates are craniates that have a backbone (pp. 703–704) ? *Identify the shared features of early fossil vertebrates.*			**Vertebrates:** *Dlx* genes duplication, backbone of vertebrae				Petromyzontida (lampreys)	Jawless vertebrates; typically feed by attaching to a live fish and ingesting its blood
Concept 34.4 Gnathostomes are vertebrates that have jaws (pp. 704–709) ? *How would the appearance of organisms with jaws have altered ecological interactions? Provide supporting evidence.*				**Gnathostomes:** hinged jaws, four sets of *Hox* genes			Chondrichthyes (sharks, rays, skates, ratfishes)	Aquatic gnathostomes; have cartilaginous skeleton, a derived trait formed by the reduction of an ancestral mineralized skeleton
					Osteichthyans: bony skeleton		Actinopterygii (ray-finned fishes)	Aquatic gnathostomes; have bony skeleton and maneuverable fins supported by rays
						Lobe-fins: muscular fins or limbs	Actinistia (coelacanths)	Ancient lineage of aquatic lobe-fins still surviving in Indian Ocean
							Dipnoi (lungfishes)	Freshwater lobe-fins with both lungs and gills; sister group of tetrapods
Concept 34.5 Tetrapods are gnathostomes that have limbs (pp. 709–713) ? *Which features of amphibians restrict most species to living in aquatic or moist terrestrial habitats?*							**Tetrapods:** four limbs, neck, fused pelvic girdle — Amphibia (salamanders, frogs, caecilians)	Have four limbs descended from modified fins; most have moist skin that functions in gas exchange; many live both in water (as larvae) and on land (as adults)
Concept 34.6 Amniotes are tetrapods that have a terrestrially adapted egg (pp. 713–720) ? *Explain why birds are considered reptiles.*							**Amniotes:** amniotic egg, rib cage ventilation — Reptilia (tuataras, lizards and snakes, turtles, crocodilians, birds)	One of two groups of living amniotes; have amniotic eggs and rib cage ventilation, key adaptations for life on land
Concept 34.7 Mammals are amniotes that have hair and produce milk (pp. 720–728) ? *Describe the origin and early evolution of mammals.*							Mammalia (monotremes, marsupials, eutherians)	Evolved from synapsid ancestors; include egg-laying monotremes (echidnas, platypus); pouched marsupials (such as kangaroos, opossums); and eutherians (placental mammals, such as rodents, primates)
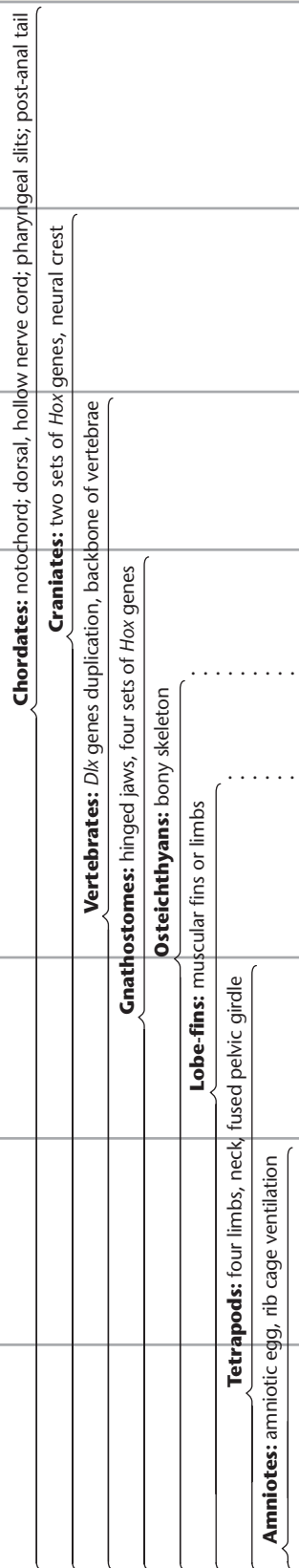
Humans are mammals that have a large brain and bipedal locomotion (pp. 728–733)

- Derived characters of humans include that we are bipedal and have a larger brain and reduced jaw compared with other apes.
- Hominins—humans and species that are more closely related to humans than to chimpanzees—originated in Africa at least 6 million years ago. Early hominins had a small brain but probably walked upright.
- The oldest evidence of tool use is 2.5 million years old.
- *Homo ergaster* was the first fully bipedal, large-brained hominin. *Homo erectus* was the first hominin to leave Africa.
- Neanderthals lived in Europe and the Near East from about 350,000 to 28,000 years ago.
- *Homo sapiens* originated in Africa about 195,000 years ago and began to spread to other continents about 115,000 years ago.

? *Explain why it is misleading to portray human evolution as a "ladder" leading to* Homo sapiens.

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Vertebrates and tunicates share
   a. jaws adapted for feeding.
   b. a high degree of cephalization.
   c. the formation of structures from the neural crest.
   d. an endoskeleton that includes a skull.
   e. a notochord and a dorsal, hollow nerve cord.

2. Some animals that lived 530 million years ago resembled lancelets but had a brain and a skull. These animals may represent
   a. the first chordates.
   b. a "missing link" between urochordates and cephalochordates.
   c. early craniates.
   d. marsupials.
   e. nontetrapod gnathostomes.

3. Which of the following could be considered the most recent common ancestor of living tetrapods?
   a. a sturdy-finned, shallow-water lobe-fin whose appendages had skeletal supports similar to those of terrestrial vertebrates
   b. an armored, jawed placoderm with two pairs of appendages
   c. an early ray-finned fish that developed bony skeletal supports in its paired fins
   d. a salamander that had legs supported by a bony skeleton but moved with the side-to-side bending typical of fishes
   e. an early terrestrial caecilian whose legless condition had evolved secondarily

4. Unlike eutherians, *both* monotremes and marsupials
   a. lack nipples.
   b. have some embryonic development outside the uterus.
   c. lay eggs.
   d. are found in Australia and Africa.
   e. include only insectivores and herbivores.

5. Which clade does *not* include humans?
   a. synapsids
   b. lobe-fins
   c. diapsids
   d. craniates
   e. osteichthyans

6. As hominins diverged from other primates, which of the following appeared first?
   a. reduced jawbones
   b. language
   c. bipedal locomotion
   d. the making of stone tools
   e. an enlarged brain

LEVEL 2: APPLICATION/ANALYSIS

7. **EVOLUTION CONNECTION**
   Living members of a vertebrate lineage can be very different from early members of the lineage, and evolutionary reversals (character losses) are common. Give examples that illustrate these observations, and explain their evolutionary causes.

LEVEL 3: SYNTHESIS/EVALUATION

8. **SCIENTIFIC INQUIRY**
   DRAW IT As a consequence of size alone, organisms that are large tend to have larger brains than organisms that are small. However, some organisms have brains that are considerably larger than expected for an animal of their size. There are high energetic costs associated with the development and maintenance of brains that are large relative to body size.
   (a) The fossil record documents trends in which brains that are large relative to body size evolved in certain lineages, including hominins. In such lineages, what can you infer about the relative magnitude of the costs and benefits of large brains?
   (b) Hypothesize how natural selection might favor the evolution of large brains despite their high maintenance costs.
   (c) Data for 14 bird species are listed below. Graph the data, placing deviation from expected brain size on the *x*-axis and mortality rate on the *y*-axis. What can you conclude about the relationship between brain size and mortality?

Deviation from Expected Brain Size*	−2.4	−2.1	2.0	−1.8	−1.0	0.0	0.3	0.7	1.2	1.3	2.0	2.3	3.0	3.2
Mortality Rate	0.9	0.7	0.5	0.9	0.4	0.7	0.8	0.4	0.8	0.3	0.6	0.6	0.3	0.6

D. Sol et al., Big-brained birds survive better in nature, *Proceedings of the Royal Society B* 274:763–769 (2007).

*Values <0 indicate brain sizes smaller than expected; values >0 indicate sizes larger than expected.

9. **WRITE ABOUT A THEME**
   Emergent Properties Early tetrapods had a sprawling gait (like that of a lizard): As the right front foot moved forward, the body twisted to the left and the left rib cage and lung were compressed; the reverse occurred with the next step. Normal breathing, in which both lungs expand equally with each breath, was hindered during walking and prevented during running. In a short essay (100–150 words), explain how the origin of organisms such as dinosaurs, whose gait allowed them to move without compressing their lungs, could have led to emergent properties in biological communities.

For selected answers, see Appendix A.

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