Chapter 29 | Vertebrates

Introduction

Vertebrates are among the most recognizable organisms of the animal kingdom. More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, which reached sizes not seen before or after in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out in a mass extinction near the end of the Cretaceous period. Although it is not known with certainty what caused their extinction, a great deal is known about the anatomy of the dinosaurs, given the preservation of skeletal elements in the fossil record.

Currently, a number of vertebrate species face extinction primarily due to habitat loss and pollution. According to the International Union for the Conservation of Nature, more than 6,000 vertebrate species are classified as threatened. Amphibians and mammals are the classes with the greatest percentage of threatened species, with 29 percent of all amphibians and 21 percent of all mammals classified as threatened. Attempts are being made around the world to prevent the extinction of threatened species. For example, the Biodiversity Action Plan is an international program, ratified by 188 countries, which is designed to protect species and habitats.

29.1 | Chordates

By the end of this section, you will be able to:

- Describe the distinguishing characteristics of chordates
- Identify the derived character of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates
Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure 29.2). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as “second mouth,” consist of two phyla: Chordata and Echinodermata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.

Figure 29.2 All chordates are deuterostomes possessing a notochord.

Characteristics of Chordata

Animals in the phylum Chordata share four key features that appear at some stage during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail (Figure 29.3). In some groups, some of these are present only during embryonic development.

The chordates are named for the notochord, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal’s lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).
In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Which of the following statements about common features of chordates is true?

a. The dorsal hollow nerve cord is part of the chordate central nervous system.

b. In vertebrate fishes, the pharyngeal slits become the gills.

c. Humans are not chordates because humans do not have a tail.

d. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

The dorsal hollow nerve cord derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsal to the notochord. In contrast, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods, the slits are modified into components of the ear and tonsils. Tetrapod literally means “four-footed,” which refers to the phylogenetic history of various groups that evolved accordingly, even though some now possess fewer than two pairs of walking appendages. Tetrapods include amphibians, reptiles, birds, and mammals.

The post-anal tail is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans, the post-anal tail is vestigial, that is, reduced in size and nonfunctional.

Chordates and the Evolution of Vertebrates

Chordata also contains two clades of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development.
**Urochordata**

Members of **Urochordata** are also known as **tunicates** (Figure 29.4). The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body of tunicates. Although adult tunicates are classified as chordates, they do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form, however, possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate’s body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.

![Figure 29.4](a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear. (credit: modification of work by Dann Blackwood, USGS)

Most tunicates live a sessile existence on the ocean floor and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate’s body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net (pharyngeal slits) and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

**Cephalochordata**

Members of **Cephalochordata** possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage (Figure 29.5). The notochord extends into the head, which gives the subphylum its name. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. *Pikaia* fossils were recovered from the Burgess shales of Canada and dated to the middle of the Cambrian age, making them more than 500 million years old.

Extant members of Cephalochordata are the **lancelets**, named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.
The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atrio pore.

**Craniata and Vertebrata**

A **cranium** is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure 29.6). Most bilaterally symmetrical animals have a head; of these, those that have a cranium compose the clade **Craniata**. Craniata includes the hagfishes (Myxini), which have a cranium but lack a backbone, and all of the organisms called “vertebrates.”

Vertebrates are members of the clade **Vertebrata**. Vertebrates display the four characteristic features of the chordates; however, members of this group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrata is named for the **vertebral column**, composed of vertebrae, a series of separate bones joined together as a backbone (Figure 29.7). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.
Based on molecular analysis, vertebrates appear to be more closely related to lancelets (cephalochordates) than to tunicates (urochordates) among the invertebrate chordates. This evidence suggests that the cephalochordates diverged from Urochordata and the vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates. This evidence suggests that vertebrates arose during the Cambrian explosion. Recall that the “Cambrian explosion” is the name given to a relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the traditional groups Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata. Many modern authors classify birds within Reptilia, which correctly reflects their evolutionary heritage. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the agnathans, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as gnathostomes, which means “jawed mouth.” Gnathostomes include fishes and tetrapods—amphibians, reptiles, birds, and mammals. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living, and this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally shed egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.

**29.2 | Fishes**

By the end of this section, you will be able to:
- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.

**Jawless Fishes**

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as 1. Chen, J. Y., Huang, D. Y., and Li, C. W., “An early Cambrian craniate-like chordate,” *Nature* 402 (1999): 518–522, doi:10.1038/990080.
separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the ostracoderms (which translates to “shell-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

**Myxini: Hagfishes**

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals (Figure 29.8). Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. A unique feature of these animals is the slime glands beneath the skin that release mucus through surface pores. This mucus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies in a knot to feed and sometimes eat carcasses from the inside out.

**Figure 29.8** Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish’s body. Hagfishes do not replace the notochord with a vertebral column during development, as do true vertebrates.

**Petromyzontidae: Lampreys**

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys. Lampreys are similar to hagfishes in size and shape; however, lampreys possess some vertebral elements. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes (Figure 29.9).

**Figure 29.9** These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and fresh waters, and have a worldwide distribution, except for in the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Eggs are fertilized externally, and the larvae
distinctly differ from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days.

Lampreys possess a notochord as adults; however, this notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily early form of the vertebral column.

**Gnathostomes: Jawed Fishes**

**Gnathostomes** or “jaw-mouths” are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes to become mobile predators. The ability of gnathostomes to exploit new nutrient sources likely is one reason that they replaced most jawless fishes during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms (Figure 29.10), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.

![Figure 29.10 Dunkleosteous](credit:Nobu Tamura) Dunkleosteous was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. (credit: Nobu Tamura)

**Chondrichthyes: Cartilaginous Fishes**

The clade Chondrichthyes is diverse, consisting of sharks (Figure 29.11), rays, and skates, together with sawfishes and a few dozen species of fishes called chimaeras, or “ghost” sharks.” Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had skeletons made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin, called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.
Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, with the latter perhaps the most sensitive of any animal. Organs called **ampullae of Lorenzini** allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the **lateral line**, which is used to detect movement and vibration in the surrounding water, and is often considered homologous to “hearing” in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish’s body.

Sharks reproduce sexually, and eggs are fertilized internally. Most species are ovoviviparous: The fertilized egg is retained in the oviduct of the mother’s body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother’s body. embryos are protected by a shark egg case or “mermaid’s purse” (**Figure 29.12**) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous: The young develop within the mother’s body and she gives live birth.

**Figure 29.11** Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

**Figure 29.12** Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

Rays and skates comprise more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (**Figure 29.13**). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.
Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reversed in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a swim bladder, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two extant clades: Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes).

Actinopterygii, the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon (Figure 29.14a), among others. Ray-finned fishes are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone (Figure 29.14b). Living members of this clade include the less-familiar lungfishes and coelacanths.

29.3 | Amphibians

By the end of this section, you will be able to:
- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians
Amphibians are vertebrate tetrapods. **Amphibia** includes frogs, salamanders, and caecilians. The term amphibian loosely translates from the Greek as “dual life,” which is a reference to the metamorphosis that many frogs and salamanders undergo and their mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods.

**Characteristics of Amphibians**

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (cutaneous respiration). Additional characteristics of amphibians include pedicellate teeth—teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue—and a papilla amphibiorum and papilla basilaris, structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively. Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

**Evolution of Amphibians**

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from fishes represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period. One of the earliest known tetrapods is from the genus **Acanthostega**. *Acanthostega* was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that *Acanthostega* lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded *Acanthostega*?

In 2006, researchers published news of their discovery of a fossil of a “tetrapod-like fish,” *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs (*Figure 29.15*). *Tiktaalik* likely lived in a shallow water environment about 375 million years ago.

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The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the “age of the amphibians.”

**Modern Amphibians**

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: **Urodela** (“tailed-ones”), the salamanders; **Anura** (“tail-less ones”), the frogs; and **Apoda** (“legless ones”), the caecilians.

**Urodela: Salamanders**

*Salamanders* are amphibians that belong to the order Urodela. Living salamanders (Figure 29.16) include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while “walking” their arms and legs fore and aft. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among different species. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings thus resemble tiny adults.

**Figure 29.16** Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)
Anura: Frogs

*Frogs* are amphibians that belong to the order Anura (Figure 29.17). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans have a body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals from glands in the skin that are poisonous to predators.

**Figure 29.17** The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. A moist environment is required as eggs lack a shell and thus dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle of frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the **tadpole**, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form (Figure 29.18). During this stage, the gills, tail, and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.
Figure 29.18 A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

**Apoda: Caecilians**

An estimated 185 species comprise *caecilians*, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle, and they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs, evidence that they evolved from a legged ancestor.
The Paleozoic Era and the Evolution of Vertebrates

The climate and geography of Earth was vastly different during the Paleozoic Era, when vertebrates arose, as compared to today. The Paleozoic spanned from approximately 542 to 251 million years ago. The landmasses on Earth were very different from those of today. Laurentia and Gondwana were continents located near the equator that subsumed much of the current day landmasses in a different configuration (Figure 29.19). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia. This contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea’s climate, affecting the distribution of vertebrate life.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today. As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to mammals, and, on the other hand, to reptiles and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.
29.4 | Reptiles

By the end of this section, you will be able to:

- Describe the main characteristics of amniotes
- Explain the difference between anapsids, synapsids, and diapsids, and give an example of each
- Identify the characteristics of reptiles
- Discuss the evolution of reptiles

The amniotes—reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted egg, which is protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes were provided with their own aquatic environment, which led to less dependence on water for development and thus allowed the amniotes to branch out into drier environments. This was a significant development that distinguished them from amphibians, which were restricted to moist environments due to their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The shells of bird eggs are composed of calcium carbonate and are hard, but fragile. The shells of reptile eggs are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes). Instead, the embryo grows within the mother’s body; however, even with this internal gestation, amniotic membranes are still present.

Characteristics of Amniotes

The amniotic egg is the key characteristic of amniotes. In amniotes that lay eggs, the shell of the egg provides protection for the developing embryo while being permeable enough to allow for the exchange of carbon dioxide and oxygen. The albumin, or egg white, provides the embryo with water and protein, whereas the fattier egg yolk is the energy supply for the embryo, as is the case with the eggs of many other animals, such as amphibians. However, the eggs of amniotes contain three additional extra-embryonic membranes: the chorion, amnion, and allantois (Figure 29.20). Extra-embryonic membranes are membranes present in amniotic eggs that are not a part of the body of the developing embryo. While the inner amniotic membrane surrounds the embryo itself, the chorion surrounds the embryo and yolk sac. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg’s external environment. The amnion protects the embryo from mechanical shock and supports hydration. The allantois stores nitrogenous wastes produced by the embryo and also facilitates respiration. In mammals, membranes that are homologous to the extra-embryonic membranes in eggs are present in the placenta.
Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

**Evolution of Amniotes**

The first amniotes evolved from amphibian ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids and sauropsids. Synapsids include all mammals, including extinct mammalian species. Synapsids also include therapsids, which were mammal-like reptiles from which mammals evolved. Sauropsids include reptiles and birds, and can be further divided into anapsids and diapsids. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of temporal fenestrae behind each eye (Figure 29.21). Temporal fenestrae are post-orbital openings in the skull that allow muscles to expand and lengthen. Anapsids have no temporal fenestrae, synapsids have one, and diapsids have two. Anapsids include extinct organisms and may, based on anatomy, include turtles. However, this is still controversial, and turtles are sometimes classified as diapsids based on molecular evidence. The diapsids include birds and all other living and extinct reptiles.

Figure 29.21 Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids diverged into two groups, the Archosauromorpha (“ancient lizard form”) and the Lepidosauromorpha (“scaly lizard form”) during the Mesozoic period (Figure 29.22). The lepidosaurs include modern lizards, snakes, and tuataras. The archosaurs include modern crocodiles and alligators, and the extinct pterosaurs (“winged lizard”) and dinosaurs (“terrible lizard”). Clade Dinosauria includes birds, which evolved from a branch of dinosaurs.
This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. We will consider birds as a group distinct from reptiles for the purpose of this discussion with the understanding that this does not completely reflect phylogenetic history and relationships.

**Characteristics of Reptiles**

Reptiles are tetrapods. Limbless reptiles—snakes and other squamates—have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay eggs enclosed in shells on land. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display ovoviviparity, with the eggs remaining in the mother’s body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin, containing the protein keratin and waxy lipids, which reduced water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all breathe with lungs.

Reptiles are ectotherms, animals whose main source of body heat comes from the environment. This is in contrast to endotherms, which use heat produced by metabolism to regulate body temperature. In addition to being ectothermic, reptiles are categorized as poikilotherms, or animals whose body temperatures vary rather than remain stable. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up and finding shady spots or going underground to cool down. The advantage of ectothermy is that metabolic energy from food is not required to heat the body; therefore, reptiles can survive on about 10 percent of the calories required by a similarly sized endotherm. In cold weather, some reptiles such as the garter snake brumate. **Brumation** is similar to hibernation in that the animal becomes less active and can go for long periods without eating, but differs from hibernation in that brumating reptiles are not asleep or living off fat reserves. Rather, their metabolism is slowed in response to cold temperatures, and the animal is very sluggish.
Evolution of Reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is Casineria, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptiles was Hylonomus. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period. The Permian period also saw a second major divergence of diapsid reptiles into archosaurs (predecessors of crocodilians and dinosaurs) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period, when the archosaurs became the dominant terrestrial group due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the dinosaurs and the pterosaurs.

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs (Figure 29.23). Pterosaurs had a number of adaptations that allowed for flight, including hollow bones (birds also exhibit hollow bones, a case of convergent evolution). Their wings were formed by membranes of skin that attached to the long, fourth finger of each arm and extended along the body to the legs.

Figure 29.23 Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

The dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species identified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds (Figure 29.24); others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs, and a number of nests containing fossilized eggs have been found. It is not known whether dinosaurs were endotherms or ectotherms. However, given that modern birds are endothermic, the dinosaurs that served as ancestors to birds likely were endothermic as well. Some fossil evidence exists for dinosaurian parental care, and comparative biology supports this hypothesis since the archosaur birds and crocodilians display parental care.

Figure 29.24 Edmontonia was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)
Dinosaurs dominated the Mesozoic Era, which was known as the “age of reptiles.” The dominance of dinosaurs lasted until the end of the Cretaceous, the last period of the Mesozoic Era. The Cretaceous-Tertiary extinction resulted in the loss of most of the large-bodied animals of the Mesozoic Era. Birds are the only living descendants of one of the major clades of dinosaurs.

Visit this site to see a video (http://openstaxcollege.org/l/K-T_extinction) discussing the hypothesis that an asteroid caused the Cretaceous-Triassic (KT) extinction.

Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species.

**Crocodilia**

Crocodilia ("small lizard") arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians (Figure 29.25) live throughout the tropics and subtropics of Africa, South America, Southern Florida, Asia, and Australia. They are found in freshwater, saltwater, and brackish habitats, such as rivers and lakes, and spend most of their time in water. Some species are able to move on land due to their semi-erect posture.

![Figure 29.25](image)

**Sphenodontia**

Sphenodontia ("wedge tooth") arose in the Mesozoic era and includes only one living genus, *Tuatara*, comprising two species that are found in New Zealand (Figure 29.26). Tuataras measure up to 80 centimeters and weigh about 1 kilogram. Although quite lizard-like in gross appearance, several unique features of the skull and jaws clearly define them and distinguish the group from the squamates.
This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

**Squamata**

*Squamata* ("scaly") arose in the late Permian, and extant species include lizards and snakes. Both are found on all continents except Antarctica. Lizards and snakes are most closely related to tuataras, both groups having evolved from a lepidosaurian ancestor. *Squamata* is the largest extant clade of reptiles (Figure 29.27). Most lizards differ from snakes by having four limbs, although these have been variously lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are present in lizards. Lizard species range in size from chameleons and geckos, which are a few centimeters in length, to the Komodo dragon, which is about 3 meters in length. Most lizards are carnivorous, but some large species, such as iguanas, are herbivores.

![Figure 29.26](image1.png)

*Figure 29.26* This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago (Figure 29.28). Snakes comprise about 3,000 species and are found on every continent except Antarctica. They range in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects. The snake body form is so specialized that, in its general morphology, a “snake is a snake.” Their specializations all point to snakes having evolved to feed on relatively large prey (even though some current species have reversed this trend). Although variations exist, most snakes have a skull that is very flexible, involving eight rotational joints. They also differ from other squamates by having mandibles (lower jaws) without either bony or ligamentous attachment anteriorly. Having this connection via skin and muscle allows for great expansion of the gape and independent motion of the two sides—both advantages in swallowing big items.

![Figure 29.27](image2.png)

*Figure 29.27* This Jackson’s chameleon (*Trioceros jacksonii*) blends in with its surroundings.
Figure 29.28 The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)

**Testudines**

Turtles are members of the clade *Testudines* ("having a shell") (Figure 29.29). Turtles are characterized by a bony or cartilaginous shell. The shell consists of the ventral surface called the plastron and the dorsal surface called the carapace, which develops from the ribs. The plastron is made of scutes or plates; the scutes can be used to differentiate species of turtles. The two clades of turtles are most easily recognized by how they retract their necks. The dominant group, which includes all North American species, retracts its neck in a vertical S-curve. Turtles in the less speciose clade retract the neck with a horizontal curve.

Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Similar to other reptiles, turtles are ectotherms. They lay eggs on land, although many species live in or near water. None exhibit parental care. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term "turtle" is sometimes used to describe only those species of Testudines that live in the sea, with the terms "tortoise" and "terrapin" used to refer to species that live on land and in fresh water, respectively.

Figure 29.29 The African spurred tortoise (*Geochelone sulcata*) lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit: Jim Bowen)
The most obvious characteristic that sets birds apart from other modern vertebrates is the presence of feathers, which are modified scales. While vertebrates like bats fly without feathers, birds rely on feathers and wings, along with other modifications of body structure and physiology, for flight.

**Characteristics of Birds**

Birds are endothermic, and because they fly, they require large amounts of energy, necessitating a high metabolic rate. Like mammals, which are also endothermic, birds have an insulating covering that keeps heat in the body: feathers. Specialized feathers called **down feathers** are especially insulating, trapping air in spaces between each feather to decrease the rate of heat loss. Certain parts of a bird’s body are covered in down feathers, and the base of other feathers have a downy portion, whereas newly hatched birds are covered in down.

Feathers not only act as insulation but also allow for flight, enabling the lift and thrust necessary to become airborne. The feathers on a wing are flexible, so the collective feathers move and separate as air moves through them, reducing the drag on the wing. **Flight feathers** are asymmetrical, which affects airflow over them and provides some of the lifting and thrusting force required for flight (**Figure 29.30**). Two types of flight feathers are found on the wings, primary feathers and secondary feathers. **Primary feathers** are located at the tip of the wing and provide thrust. **Secondary feathers** are located closer to the body, attach to the forearm portion of the wing and provide lift. **Contour feathers** are the feathers found on the body, and they help reduce drag produced by wind resistance during flight. They create a smooth, aerodynamic surface so that air moves smoothly over the bird’s body, allowing for efficient flight.

**Figure 29.30** Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

Flapping of the entire wing occurs primarily through the actions of the chest muscles, the pectoralis and the supracoracoideus. These muscles are highly developed in birds and account for a higher percentage of body mass than in most mammals. These attach to a blade-shaped keel, like that of a boat, located on the sternum. The sternum of birds is
larger than that of other vertebrates, which accommodates the large muscles required to generate enough upward force to generate lift with the flapping of the wings. Another skeletal modification found in most birds is the fusion of the two clavicles (collarbones), forming the **furcula** or wishbone. The furcula is flexible enough to bend and provide support to the shoulder girdle during flapping.

An important requirement of flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich, and while it is much smaller than the largest mammals, it is flightless. For birds that do fly, reduction in body weight makes flight easier. Several modifications are found in birds to reduce body weight, including pneumatization of bones. **Pneumatic bones** are bones that are hollow, rather than filled with tissue (Figure 29.31). They contain air spaces that are sometimes connected to air sacs, and they have struts of bone to provide structural reinforcement. Pneumatic bones are not found in all birds, and they are more extensive in large birds than in small birds. Not all bones of the skeleton are pneumatic, although the skulls of almost all birds are.

![Figure 29.31](image)

Many birds have hollow, pneumatic bones, which make flight easier.

Other modifications that reduce weight include the lack of a urinary bladder. Birds possess a cloaca, a structure that allows water to be reabsorbed from waste back into the bloodstream. Uric acid is not expelled as a liquid but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in the urinary bladder, which would increase body weight. Most bird species only possess one ovary rather than two, further reducing body mass.

The air sacs that extend into bones to form pneumatic bones also join with the lungs and function in respiration. Unlike mammalian lungs in which air flows in two directions, as it is breathed in and out, airflow through bird lungs travels in one direction (Figure 29.32). Air sacs allow for this unidirectional airflow, which also creates a cross-current exchange system with the blood. In a cross-current or counter-current system, the air flows in one direction and the blood flows in the opposite direction, creating a very efficient means of gas exchange.

![Figure 29.32](image)

Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

**Evolution of Birds**

The evolutionary history of birds is still somewhat unclear. Due to the fragility of bird bones, they do not fossilize as well as other vertebrates. Birds are diapsids, meaning they have two fenestrations or openings in their skulls. Birds belong to a group of diapsids called the archosaurs, which also includes crocodiles and dinosaurs. It is commonly accepted that birds evolved from dinosaurs.

Dinosaurs (including birds) are further subdivided into two groups, the Saurischia (“lizard like”) and the Ornithischia (“bird like”). Despite the names of these groups, it was not the bird-like dinosaurs that gave rise to modern birds. Rather, Saurischia diverged into two groups: One included the long-necked herbivorous dinosaurs, such as Apatosaurus. The second group, bipedal predators called **theropods**, includes birds. This course of evolution is suggested by similarities between theropod
fossils and birds, specifically in the structure of the hip and wrist bones, as well as the presence of the wishbone, formed by the fusing of the clavicles.

One important fossil of an animal intermediate to dinosaurs and birds is *Archaeopteryx*, which is from the Jurassic period (Figure 29.33). *Archaeopteryx* is important in establishing the relationship between birds and dinosaurs, because it is an intermediate fossil, meaning it has characteristics of both dinosaurs and birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. The fossilized skeleton of *Archaeopteryx* looks like that of a dinosaur, and it had teeth whereas birds do not, but it also had feathers modified for flight, a trait associated only with birds among modern animals. Fossils of older feathered dinosaurs exist, but the feathers do not have the characteristics of flight feathers.

![Figure 29.33 (a) Archaeopteryx lived in the late Jurassic Period around 150 million years ago. It had teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil.](image)

It is still unclear exactly how flight evolved in birds. Two main theories exist, the arboreal (“tree”) hypothesis and the terrestrial (“land”) hypothesis. The arboreal hypothesis posits that tree-dwelling precursors to modern birds jumped from branch to branch using their feathers for gliding before becoming fully capable of flapping flight. In contrast to this, the terrestrial hypothesis holds that running was the stimulus for flight, as wings could be used to improve running and then became used for flapping flight. Like the question of how flight evolved, the question of how endothermy evolved in birds still is unanswered. Feathers provide insulation, but this is only beneficial if body heat is being produced internally. Similarly, internal heat production is only viable if insulation is present to retain that heat. It has been suggested that one or the other—feathers or endothermy—evolved in response to some other selective pressure.

During the Cretaceous period, a group known as the *Enantiornithes* was the dominant bird type (Figure 29.34). *Enantiornithes* means “opposite birds,” which refers to the fact that certain bones of the feet are joined differently than the way the bones are joined in modern birds. These birds formed an evolutionary line separate from modern birds, and they did not survive past the Cretaceous. Along with the *Enantiornithes*, Ornithurae birds (the evolutionary line that includes modern birds) were also present in the Cretaceous. After the extinction of *Enantiornithes*, modern birds became the dominant bird, with a large radiation occurring during the Cenozoic Era. Referred to as *Neornithes* (“new birds”), modern birds are now classified into two groups, the *Paleognathae* (“old jaw”) or ratites, a group of flightless birds including ostriches, emus, rheas, and kiwis, and the *Neognathae* (“new jaw”), which includes all other birds.
**Veterinarian**

Veterinarians treat diseases, disorders, and injuries in animals, primarily vertebrates. They treat pets, livestock, and animals in zoos and laboratories. Veterinarians usually treat dogs and cats, but also treat birds, reptiles, rabbits, and other animals that are kept as pets. Veterinarians that work with farms and ranches treat pigs, goats, cows, sheep, and horses.

Veterinarians are required to complete a degree in veterinary medicine, which includes taking courses in animal physiology, anatomy, microbiology, and pathology, among many other courses. The physiology and biochemistry of different vertebrate species differ greatly.

Veterinarians are also trained to perform surgery on many different vertebrate species, which requires an understanding of the vastly different anatomies of various species. For example, the stomach of ruminants like cows has four compartments versus one compartment for non-ruminants. Birds also have unique anatomical adaptations that allow for flight.

Some veterinarians conduct research in academic settings, broadening our knowledge of animals and medical science. One area of research involves understanding the transmission of animal diseases to humans, called zoonotic diseases. For example, one area of great concern is the transmission of the avian flu virus to humans. One type of avian flu virus, H5N1, is a highly pathogenic strain that has been spreading in birds in Asia, Europe, Africa, and the Middle East. Although the virus does not cross over easily to humans, there have been cases of bird-to-human transmission. More research is needed to understand how this virus can cross the species barrier and how its spread can be prevented.

**Mammals**

By the end of this section, you will be able to:

- Name and describe the distinguishing features of the three main groups of mammals
- Describe the proposed line of descent that produced mammals
- List some derived features that may have arisen in response to mammals’ need for constant, high-level metabolism

**Mammals** are vertebrates that possess hair and mammary glands. Several other characteristics are distinctive to mammals, including certain features of the jaw, skeleton, integument, and internal anatomy. Modern mammals belong to three clades: monotremes, marsupials, and eutherians (or placental mammals).
The presence of hair is one of the most obvious signs of a mammal. Although it is not very extensive on certain species, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation to retain heat generated by metabolic work. Hair traps a layer of air close to the body, retaining heat. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit information about sensation, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration or be part of social signaling, such as when an animal’s hair stands “on end.”

Mammalian integument, or skin, includes secretory glands with various functions. Sebaceous glands produce a lipid mixture called sebum that is secreted onto the hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. Eccrine glands produce sweat, or perspiration, which is mainly composed of water. In most mammals, eccrine glands are limited to certain areas of the body, and some mammals do not possess them at all. However, in primates, especially humans, sweat figures prominently in thermoregulation, regulating the body through evaporative cooling. Sweat glands are located over most of the body surface in primates. Apocrine glands, or scent glands, secrete substances that are used for chemical communication, such as in skunks. Mammary glands produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not. Mammary glands likely are modified sebaceous or eccrine glands, but their evolutionary origin is not entirely clear.

The skeletal system of mammals possesses many unique features. The lower jaw of mammals consists of only one bone, the dentary. The jaws of other vertebrates are composed of more than one bone. In mammals, the dentary bone joins the skull at the squamosal bone, while in other vertebrates, the quadrate bone of the jaw joins with the articular bone of the skull. These bones are present in mammals, but they have been modified to function in hearing and form bones in the middle ear (Figure 29.35). Other vertebrates possess only one middle ear bone, the stapes. Mammals have three: the malleus, incus, and stapes. The malleus originated from the articular bone, whereas the incus originated from the quadrate bone. This arrangement of jaw and ear bones aids in distinguishing fossil mammals from fossils of other synapsids.

The adductor muscle that closes the jaw is composed of two muscles in mammals: the temporalis and the masseter. These allow side-to-side movement of the jaw, making chewing possible, which is unique to mammals. Most mammals have heterodont teeth, meaning that they have different types and shapes of teeth rather than just one type and shape of tooth. Most mammals are diphyodonts, meaning that they have two sets of teeth in their lifetime: deciduous or “baby” teeth, and permanent teeth. Other vertebrates are polyphyodonts, that is, their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart. Mammals also have a specialized group of cardiac fibers located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. Mammalian erythrocytes (red blood cells) do not have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

The kidneys of mammals have a portion of the nephron called the loop of Henle or nephritic loop, which allows mammals to produce urine with a high concentration of solutes, higher than that of the blood. Mammals lack a renal portal system, which is a system of veins that moves blood from the hind or lower limbs and region of the tail to the kidneys. Renal portal systems are present in all other vertebrates except jawless fishes. A urinary bladder is present in all mammals.

Mammalian brains have certain characteristics that differ from other vertebrates. In some, but not all mammals, the cerebral cortex, the outermost part of the cerebrum, is highly folded, allowing for a greater surface area than is possible with a smooth cortex. The optic lobes, located in the midbrain, are divided into two parts in mammals, whereas other vertebrates
possess a single, undivided lobe. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

**Evolution of Mammals**

Mammals are synapsids, meaning they have a single opening in the skull. They are the only living synapsids, as earlier forms became extinct by the Jurassic period. The early non-mammalian synapsids can be divided into two groups, the pelycosaurs and the therapsids. Within the therapsids, a group called the cynodonts are thought to be the ancestors of mammals (Figure 29.36).

![Figure 29.36 Cynodonts, which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals. (credit: Nobu Tamura)](image)

A key characteristic of synapsids is endothermy, rather than the ectothermy seen in most other vertebrates. The increased metabolic rate required to internally modify body temperature went hand in hand with changes to certain skeletal structures. The later synapsids, which had more evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth, which are specialized for chewing, mechanically breaking down food to speed digestion and releasing the energy needed to produce heat. Chewing also requires the ability to chew and breathe at the same time, which is facilitated by the presence of a secondary palate. A secondary palate separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted during chewing. A secondary palate is not found in pelycosaurs but is present in cynodonts and mammals. The jawbone also shows changes from early synapsids to later ones. The zygomatic arch, or cheekbone, is present in mammals and advanced therapsids such as cynodonts, but is not present in pelycosaurs. The presence of the zygomatic arch suggests the presence of the masseter muscle, which closes the jaw and functions in chewing.

In the appendicular skeleton, the shoulder girdle of therian mammals is modified from that of other vertebrates in that it does not possess a procoracoid bone or an interclavicle, and the scapula is the dominant bone.

Mammals evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period, some 205 million years ago. Early mammals were small, about the size of a small rodent. Mammals first began to diversify in the Mesozoic Era, from the Jurassic to the Cretaceous periods, although most of these mammals were extinct by the end of the Mesozoic. During the Cretaceous period, another radiation of mammals began and continued through the Cenozoic Era, about 65 million years ago.

**Living Mammals**

The eutherians, or placental mammals, and the marsupials together comprise the clade of therian mammals. Monotremes, or metatherians, form their sister clade.

There are three living species of monotremes: the platypus and two species of echidnas, or spiny anteaters. The leathery-beaked platypus belongs to the family Ornithorhynchidae (“bird beak”), whereas echidnas belong to the family Tachyglossidae (“sticky tongue”) (Figure 29.37). The platypus and one species of echidna are found in Australia, and the other species of echidna is found in New Guinea. Monotremes are unique among mammals as they lay eggs, rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but are a leathery shell, similar to the shells of reptile eggs. Monotremes have no teeth.
Marsupials are found primarily in Australia, though the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure 29.38), and several other species. Most species of marsupials possess a pouch in which the very premature young reside after birth, receiving milk and continuing to develop. Marsupials differ from eutherians in that there is a less complex placental connection: The young are born at an extremely early age and latch onto the nipple within the pouch.

Eutherians are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. Eutherian mammals are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.

29.7 | The Evolution of Primates

By the end of this section, you will be able to:

- Describe the derived features that distinguish primates from other animals
- Explain why scientists are having difficulty determining the true lines of descent in hominids

Order Primates of class Mammalia includes lemurs, tarsiers, monkeys, apes, and humans. Non-human primates live primarily in the tropical or subtropical regions of South America, Africa, and Asia. They range in size from the mouse lemur at 30 grams (1 ounce) to the mountain gorilla at 200 kilograms (441 pounds). The characteristics and evolution of primates is of particular interest to us as it allows us to understand the evolution of our own species.
Characteristics of Primates

All primate species possess adaptations for climbing trees, as they all descended from tree-dwellers. This arboreal heritage of primates has resulted in hands and feet that are adapted for brachiation, or climbing and swinging through trees. These adaptations include, but are not limited to: 1) a rotating shoulder joint, 2) a big toe that is widely separated from the other toes and thumbs, which are widely separated from fingers (except humans), which allow for gripping branches, 3) stereoscopic vision, two overlapping fields of vision from the eyes, which allows for the perception of depth and gauging distance. Other characteristics of primates are brains that are larger than those of most other mammals, claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

Order Primates is divided into two groups: prosimians and anthropoids. Prosimians include the bush babies of Africa, the lemurs of Madagascar, and the lorises, pottos, and tarsiers of Southeast Asia. Anthropoids include monkeys, apes, and humans. In general, prosimians tend to be nocturnal (in contrast to diurnal anthropoids) and exhibit a smaller size and smaller brain than anthropoids.

Evolution of Primates

The first primate-like mammals are referred to as proto-primates. They were roughly similar to squirrels and tree shrews in size and appearance. The existing fossil evidence (mostly from North Africa) is very fragmented. These proto-primates remain largely mysterious creatures until more fossil evidence becomes available. The oldest known primate-like mammals with a relatively robust fossil record is Plesiadapis (although some researchers do not agree that Plesiadapis was a proto-primate). Fossils of this primate have been dated to approximately 55 million years ago. Plesiadapiforms were proto-primates that had some features of the teeth and skeleton in common with true primates. They were found in North America and Europe in the Cenozoic and went extinct by the end of the Eocene.

The first true primates were found in North America, Europe, Asia, and Africa in the Eocene Epoch. These early primates resembled present-day prosimians such as lemurs. Evolutionary changes continued in these early primates, with larger brains and eyes, and smaller muzzles being the trend. By the end of the Eocene Epoch, many of the early prosimian species went extinct due either to cooler temperatures or competition from the first monkeys.

Anthropoid monkeys evolved from prosimians during the Oligocene Epoch. By 40 million years ago, evidence indicates that monkeys were present in the New World (South America) and the Old World (Africa and Asia). New World monkeys are also called Platyrrhini—a reference to their broad noses (Figure 29.39). Old World monkeys are called Catarrhini—a reference to their narrow noses. There is still quite a bit of uncertainty about the origins of the New World monkeys. At the time the platyrhines arose, the continents of South American and Africa had drifted apart. Therefore, it is thought that monkeys arose in the Old World and reached the New World either by drifting on log rafts or by crossing land bridges. Due to this reproductive isolation, New World monkeys and Old World monkeys underwent separate adaptive radiations over millions of years. The New World monkeys are all arboreal, whereas Old World monkeys include arboreal and ground-dwelling species.

Apes evolved from the catarrhines in Africa midway through the Cenozoic, approximately 25 million years ago. Apes are generally larger than monkeys and they do not possess a tail. All apes are capable of moving through trees, although many species spend most their time on the ground. Apes are more intelligent than monkeys, and they have relatively larger
brains proportionate to body size. The apes are divided into two groups. The lesser apes comprise the family **Hylobatidae**, including gibbons and siamangs. The great apes include the genera **Pan** (chimpanzees and bonobos) (**Figure 29.40a**), **Gorilla** (gorillas), **Pongo** (orangutans), and **Homo** (humans) (**Figure 29.40b**). The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the genders are not markedly different in size); and they have relatively longer arms used for swinging through trees.

**Figure 29.40** The (a) chimpanzee is one of the great apes. It possesses a relatively large brain and has no tail. (b) All great apes have a similar skeletal structure. (credit a: modification of work by Aaron Logan; credit b: modification of work by Tim Vickers)

### Human Evolution

The family Hominidae of order Primates includes the **hominoids**: the great apes (**Figure 29.41**). Evidence from the fossil record and from a comparison of human and chimpanzee DNA suggests that humans and chimpanzees diverged from a common hominoid ancestor approximately 6 million years ago. Several species evolved from the evolutionary branch that includes humans, although our species is the only surviving member. The term **hominin** is used to refer to those species that evolved after this split of the primate line, thereby designating species that are more closely related to humans than to chimpanzees. Hominins were predominantly bipedal and include those groups that likely gave rise to our species—including **Australopithecus**, **Homo habilis**, and **Homo erectus**—and those non-ancestral groups that can be considered “cousins” of modern humans, such as Neanderthals. Determining the true lines of descent in hominins is difficult. In years past, when relatively few hominin fossils had been recovered, some scientists believed that considering them in order, from oldest to youngest, would demonstrate the course of evolution from early hominins to modern humans. In the past several years, however, many new fossils have been found, and it is clear that there was often more than one species alive at any one time and that many of the fossils found (and species named) represent hominin species that died out and are not ancestral to modern humans.
Figure 29.41 This chart shows the evolution of modern humans.

**Very Early Hominins**

Three species of very early hominids have made news in the past few years. The oldest of these, *Sahelanthropus tchadensis*, has been dated to nearly 7 million years ago. There is a single specimen of this genus, a skull that was a surface find in Chad. The fossil, informally called “Toumai,” is a mosaic of primitive and evolved characteristics, and it is unclear how this fossil fits with the picture given by molecular data, namely that the line leading to modern humans and modern chimpanzees apparently bifurcated about 6 million years ago. It is not thought at this time that this species was an ancestor of modern humans.

A second, younger species, *Orrorin tugenensis*, is also a relatively recent discovery, found in 2000. There are several specimens of *Orrorin*. It is not known whether *Orrorin* was a human ancestor, but this possibility has not been ruled out. Some features of *Orrorin* are more similar to those of modern humans than are the australopiths, although *Orrorin* is much older.

A third genus, *Ardipithecus*, was discovered in the 1990s, and the scientists who discovered the first fossil found that some other scientists did not believe the organism to be a biped (thus, it would not be considered a hominid). In the intervening years, several more specimens of *Ardipithecus*, classified as two different species, demonstrated that the organism was bipedal. Again, the status of this genus as a human ancestor is uncertain.

**Early Hominins: Genus Australopithecus**

*Australopithecus* (“southern ape”) is a genus of hominin that evolved in eastern Africa approximately 4 million years ago and went extinct about 2 million years ago. This genus is of particular interest to us as it is thought that our genus, genus *Homo*, evolved from *Australopithecus* about 2 million years ago (after likely passing through some transitional states). *Australopithecus* had a number of characteristics that were more similar to the great apes than to modern humans. For example, sexual dimorphism was more exaggerated than in modern humans. Males were up to 50 percent larger than females, a ratio that is similar to that seen in modern gorillas and orangutans. In contrast, modern human males are approximately 15 to 20 percent larger than females. The brain size of *Australopithecus* relative to its body mass was also smaller than modern humans and more similar to that seen in the great apes. A key feature that *Australopithecus* had in common with modern humans was bipedalism, although it is likely that *Australopithecus* also spent time in trees. Hominin
Footprints, similar to those of modern humans, were found in Laetoli, Tanzania and dated to 3.6 million years ago. They showed that hominins at the time of *Australopithecus* were walking upright.

There were a number of *Australopithecus* species, which are often referred to as *australopiths*. *Australopithecus anamensis* lived about 4.2 million years ago. More is known about another early species, *Australopithecus afarensis*, which lived between 3.9 and 2.9 million years ago. This species demonstrates a trend in human evolution: the reduction of the dentition and jaw in size. *A. afarensis* ([Figure 29.42](#)) had smaller canines and molars compared to apes, but these were larger than those of modern humans. Its brain size was 380–450 cubic centimeters, approximately the size of a modern chimpanzee brain. It also had **prognathic jaws**, which is a relatively longer jaw than that of modern humans. In the mid-1970s, the fossil of an adult female *A. afarensis* was found in the Afar region of Ethiopia and dated to 3.24 million years ago ([Figure 29.43](#)). The fossil, which is informally called “Lucy,” is significant because it was the most complete australopith fossil found, with 40 percent of the skeleton recovered.

![Australopithecus afarensis skull](image)

*Figure 29.42* The skull of (a) *Australopithecus afarensis*, an early hominid that lived between two and three million years ago, resembled that of (b) modern humans but was smaller with a sloped forehead and prominent jaw.
Australopithecus afarensis lived between 2 and 3 million years ago. It had a slender build and was bipedal, but had robust arm bones and, like other early hominids, may have spent significant time in trees. Its brain was larger than that of A. afarensis at 500 cubic centimeters, which is slightly less than one-third the size of modern human brains. Two other species, Australopithecus bahrelghazali and Australopithecus garhi, have been added to the roster of australopiths in recent years.

A Dead End: Genus Paranthropus

The australopiths had a relatively slender build and teeth that were suited for soft food. In the past several years, fossils of hominids of a different body type have been found and dated to approximately 2.5 million years ago. These hominids, of the genus Paranthropus, were relatively large and had large grinding teeth. Their molars showed heavy wear, suggesting that they had a coarse and fibrous vegetarian diet as opposed to the partially carnivorous diet of the australopiths. Paranthropus includes Paranthropus robustus of South Africa, and Paranthropus aethiopicus and Paranthropus boisei of East Africa. The hominids in this genus went extinct more than 1 million years ago and are not thought to be ancestral to modern humans, but rather members of an evolutionary branch on the hominin tree that left no descendants.

Early Hominins: Genus Homo

The human genus, Homo, first appeared between 2.5 and 3 million years ago. For many years, fossils of a species called H. habilis were the oldest examples in the genus Homo, but in 2010, a new species called Homo gautengensis was discovered and may be older. Compared to A. africanus, H. habilis had a number of features more similar to modern humans. H. habilis had a jaw that was less prognathic than the australopiths and a larger brain, at 600–750 cubic centimeters. However, H. habilis retained some features of older hominin species, such as long arms. The name H. habilis means “handy man,” which is a reference to the stone tools that have been found with its remains.
Visit this site (http://openstaxcollege.org/l/diet_detective) for a video about Smithsonian paleontologist Briana Pobiner explaining the link between hominin eating of meat and evolutionary trends.

*H. erectus* appeared approximately 1.8 million years ago (Figure 29.44). It is believed to have originated in East Africa and was the first hominin species to migrate out of Africa. Fossils of *H. erectus* have been found in India, China, Java, and Europe, and were known in the past as “Java Man” or “Peking Man.” *H. erectus* had a number of features that were more similar to modern humans than those of *H. habilis*. *H. erectus* was larger in size than earlier hominins, reaching heights up to 1.85 meters and weighing up to 65 kilograms, which are sizes similar to those of modern humans. Its degree of sexual dimorphism was less than earlier species, with males being 20 to 30 percent larger than females, which is close to the size difference seen in our species. *H. erectus* had a larger brain than earlier species at 775–1,100 cubic centimeters, which compares to the 1,130–1,260 cubic centimeters seen in modern human brains. *H. erectus* also had a nose with downward-facing nostrils similar to modern humans, rather than the forward facing nostrils found in other primates. Longer, downward-facing nostrils allow for the warming of cold air before it enters the lungs and may have been an adaptation to colder climates. Artifacts found with fossils of *H. erectus* suggest that it was the first hominin to use fire, hunt, and have a home base. *H. erectus* is generally thought to have lived until about 50,000 years ago.

*Figure 29.44* *Homo erectus* had a prominent brow and a nose that pointed downward rather than forward.

**Humans: Homo sapiens**

A number of species, sometimes called archaic *Homo sapiens*, apparently evolved from *H. erectus* starting about 500,000 years ago. These species include *Homo heidelbergensis*, *Homo rhodesiensis*, and *Homo neanderthalensis*. These archaic *H. sapiens* had a brain size similar to that of modern humans, averaging 1,200–1,400 cubic centimeters. They differed from modern humans by having a thick skull, a prominent brow ridge, and a receding chin. Some of these species survived until 30,000–10,000 years ago, overlapping with modern humans (Figure 29.45).
There is considerable debate about the origins of anatomically modern humans or *Homo sapiens sapiens*. As discussed earlier, *H. erectus* migrated out of Africa and into Asia and Europe in the first major wave of migration about 1.5 million years ago. It is thought that modern humans arose in Africa from *H. erectus* and migrated out of Africa about 100,000 years ago in a second major migration wave. Then, modern humans replaced *H. erectus* species that had migrated into Asia and Europe in the first wave.

This evolutionary timeline is supported by molecular evidence. One approach to studying the origins of modern humans is to examine mitochondrial DNA (mtDNA) from populations around the world. Because a fetus develops from an egg containing its mother’s mitochondria (which have their own, non-nuclear DNA), mtDNA is passed entirely through the maternal line. Mutations in mtDNA can now be used to estimate the timeline of genetic divergence. The resulting evidence suggests that all modern humans have mtDNA inherited from a common ancestor that lived in Africa about 160,000 years ago. Another approach to the molecular understanding of human evolution is to examine the Y chromosome, which is passed from father to son. This evidence suggests that all men today inherited a Y chromosome from a male that lived in Africa about 140,000 years ago.
KEY TERMS

Acanthostega  one of the earliest known tetrapods

Actinopterygii  ray-finned fishes

allantois  membrane of the egg that stores nitrogenous wastes produced by the embryo; also facilitates respiration

amnion  membrane of the egg that protects the embryo from mechanical shock and prevents dehydration

amniote  animal that produces a terrestrially adapted egg protected by amniotic membranes

Amphibia  frogs, salamanders, and caecilians

ampulla of Lorenzini  sensory organ that allows sharks to detect electromagnetic fields produced by living things

anapsid  animal having no temporal fenestrae in the cranium

anthropoid  monkeys, apes, and humans

Anura  frogs

apocrine gland  scent gland that secretes substances that are used for chemical communication

Apoda  caecilians

Archaeopteryx  transition species from dinosaur to bird from the Jurassic period

archosaur  modern crocodilian or bird, or an extinct pterosaur or dinosaur

Australopithecus  genus of hominins that evolved in eastern Africa approximately 4 million years ago

brachiation  movement through trees branches via suspension from the arms

brumation  period of much reduced metabolism and torpor that occurs in any ectotherm in cold weather

caecilian  legless amphibian that belongs to the clade Apoda

Casineria  one of the oldest known amniotes; had both amphibian and reptilian characteristics

Catarrhini  clade of Old World monkeys

Cephalochordata  chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage

Chondrichthyes  jawed fish with paired fins and a skeleton made of cartilage

Chordata  phylum of animals distinguished by their possession of a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some point during their development

chorion  membrane of the egg that surrounds the embryo and yolk sac

contour feather  feather that creates an aerodynamic surface for efficient flight

Craniata  clade composed of chordates that possess a cranium; includes Vertebrata together with hagfishes

cranium  bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones

Crocodilia  crocodiles and alligators

cutaneous respiration  gas exchange through the skin

dentary  single bone that comprises the lower jaw of mammals
diapsid  animal having two temporal fenestrae in the cranium

diphyodont  refers to the possession of two sets of teeth in a lifetime

dorsal hollow nerve cord  hollow, tubular structure derived from ectoderm, which is located dorsal to the notochord in chordates

down feather  feather specialized for insulation

eccrine gland  sweat gland

Enantiornithes  dominant bird group during the Cretaceous period

eutherian mammal  mammal that possesses a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

flight feather  feather specialized for flight

frog  tail-less amphibian that belongs to the clade Anura

furcula  wishbone formed by the fusing of the clavicles

gnathostome  jawed fish

Gorilla  genus of gorillas

hagfish  eel-like jawless fish that live on the ocean floor and are scavengers

heterodont tooth  different types of teeth that are modified for different purposes

hominin  species that are more closely related to humans than chimpanzees

hominoid  pertaining to great apes and humans

Homo  genus of humans

Homo sapiens sapiens  anatomically modern humans

Hylobatidae  family of gibbons

Hylonomus  one of the earliest reptiles

lamprey  jawless fish characterized by a toothed, funnel-like, sucking mouth

lancelet  member of Cephalochordata; named for its blade-like shape

lateral line  sense organ that runs the length of a fish’s body; used to detect vibration in the water

lepidosaur  modern lizards, snakes, and tuataras

mammal  one of the groups of endothermic vertebrates that possesses hair and mammary glands

mammary gland  in female mammals, a gland that produces milk for newborns

marsupial  one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme  egg-laying mammal

Myxini  hagfishes

Neognathae  birds other than the Paleognathae

Neornithes  modern birds
notochord flexible, rod-shaped support structure that is found in the embryonic stage of all chordates and in the adult stage of some chordates

Ornithorhynchidae clade that includes the duck-billed platypus

Osteichthyes bony fish

ostacoderm one of the earliest jawless fish covered in bone

Paleognathae ratites; flightless birds, including ostriches and emus

Pan genus of chimpanzees and bonobos

Petromyzontidae clade of lampreys

pharyngeal slit opening in the pharynx

Platyrrhini clade of New World monkeys

Plesiadapis oldest known primate-like mammal

pneumatic bone air-filled bone

Pongo genus of orangutans

post-anal tail muscular, posterior elongation of the body extending beyond the anus in chordates

primary feather feather located at the tip of the wing that provides thrust

Primates order of lemurs, tarsiers, monkeys, apes, and humans

prognathic jaw long jaw

prosimian division of primates that includes bush babies of Africa, lemurs of Madagascar, and lorises, pottos, and tarsiers of Southeast Asia

salamander tailed amphibian that belongs to the clade Urodela

Sarcopterygii lobe-finned fish

sauropsid reptile or bird

sebaceous gland in mammals, a skin gland that produce a lipid mixture called sebum

secondary feather feather located at the base of the wing that provides lift

Sphenodontia clade of tuatars

Squamata clade of lizards and snakes

stereoscopic vision two overlapping fields of vision from the eyes that produces depth perception

swim bladder in fishes, a gas filled organ that helps to control the buoyancy of the fish

synapsid mammal having one temporal fenestra

Tachyglossidae clade that includes the echidna or spiny anteater

tadpole larval stage of a frog

temporal fenestra non-orbital opening in the skull that may allow muscles to expand and lengthen

Testudines order of turtles
tetrapod  phylogenetic reference to an organism with a four-footed evolutionary history; includes amphibians, reptiles, birds, and mammals

theropod  dinosaur group ancestral to birds

tunicate  sessile chordate that is a member of Urochordata

Urochordata  clade composed of tunicates

Urodela  salamanders

vertebral column  series of separate bones joined together as a backbone

Vertebrata  members of the phylum Chordata that possess a backbone

**CHAPTER SUMMARY**

29.1 Chordates

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade.

29.2 Fishes

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: Actinopterygii (ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).

29.3 Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of frogs, like the majority of amphibians, consists of two distinct stages: the larval stage and metamorphosis to an adult stage. Some species in all orders bypass a free-living larval stage.

29.4 Reptiles

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by amniotic membranes. The amniotes include reptiles, birds, and mammals. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids (mammals) and sauropsids. Sauropsids can be further divided into anapsids (turtles) and diapsids (birds and reptiles). Reptiles are tetrapods either having four limbs or descending from such. Limbless reptiles (snakes) are classified as tetrapods, as they are descended from four-limbed organisms. One of the key adaptations that permitted reptiles to live on land was the development of scaly skin containing the protein keratin, which prevented water loss from the skin. Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles).
29.5 Birds

Birds are endothermic, meaning they produce their own body heat and regulate their internal temperature independently of the external temperature. Feathers not only act as insulation but also allow for flight, providing lift with secondary feathers and thrust with primary feathers. Pneumatic bones are bones that are hollow rather than filled with tissue, containing air spaces that are sometimes connected to air sacs. Airflow through bird lungs travels in one direction, creating a cross-current exchange with the blood. Birds are diapsids and belong to a group called the archosaurs. Birds are thought to have evolved from theropod dinosaurs. The oldest known fossil of a bird is that of *Archaeopteryx*, which is from the Jurassic period. Modern birds are now classified into two groups, Paleognathae and Neognathae.

29.6 Mammals

Mammals in general are vertebrates that possess hair and mammary glands. The mammalian integument includes various secretory glands, including sebaceous glands, eccrine glands, apocrine glands, and mammary glands. Mammals are synapsids, meaning that they have a single opening in the skull. A key characteristic of synapsids is endothermy rather than the ectothermy seen in other vertebrates. Mammals probably evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period. There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to young. Eutherian mammals are sometimes called placental mammals, because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange.

29.7 The Evolution of Primates

All primate species possess adaptations for climbing trees, as they all probably descended from tree-dwellers, although not all species are arboreal. Other characteristics of primates are brains that are larger than those of other mammals, claws that have been modified into flattened nails, typically only one young per pregnancy, stereoscopic vision, and a trend toward holding the body upright. Primates are divided into two groups: prosimians and anthropoids. Monkeys evolved from prosimians during the Oligocene Epoch. Apes evolved from catarrhines in Africa during the Miocene Epoch. Apes are divided into the lesser apes and the greater apes. Hominins include those groups that gave rise to our species, such as *Australopithecus* and *H. erectus*, and those groups that can be considered “cousins” of humans, such as Neanderthals. Fossil evidence shows that hominins at the time of *Australopithecus* were walking upright, the first evidence of bipedal hominins. A number of species, sometimes called archaic *H. sapiens*, evolved from *H. erectus* approximately 500,000 years ago. There is considerable debate about the origins of anatomically modern humans or *H. sapiens sapiens*.

**ART CONNECTION QUESTIONS**

1. Figure 29.3 Which of the following statements about common features of chordates is true?
   a. The dorsal hollow nerve cord is part of the chordate central nervous system.
   b. In vertebrate fishes, the pharyngeal slits become the gills.
   c. Humans are not chordates because humans do not have a tail.
   d. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

2. Figure 29.20 Which of the following statements about the parts of an egg are false?
   a. The allantois stores nitrogenous waste and facilitates respiration.
   b. The chorion facilitates gas exchange.
   c. The yolk provides food for the growing embryo.
   d. The amniotic cavity is filled with albumen.

3. Figure 29.22 Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

**REVIEW QUESTIONS**

4. Which of the following is not contained in phylum Chordata?
   a. Cephalochordata
   b. Echinodermata
   c. Urochordata
   d. Vertebrata

5. Which group of invertebrates is most closely related to vertebrates?
   a. cephalochordates
   b. echinoderms
   c. arthropods
   d. urochordates

6. Members of Chondrichthyes differ from members of Osteichthyes by having a ________.
   a. jaw
   b. bony skeleton
c. cartilaginous skeleton
d. two sets of paired fins

7. Members of Chondrichthyes are thought to be descended from fishes that had ________.
   a. a cartilaginous skeleton  
   b. a bony skeleton 
   c. mucus glands 
   d. slime glands

8. Which of the following is not true of Acanthostega?
   a. It was aquatic. 
   b. It had gills. 
   c. It had four limbs. 
   d. It laid shelled eggs.

9. Frogs belong to which order?
   a. Anura 
   b. Urodela 
   c. Caudata 
   d. Apoda

10. During the Mesozoic period, diapsids diverged into_______.
    a. pterosaurs and dinosaurs 
    b. mammals and reptiles 
    c. lepidosaurs and archosaurs 
    d. Testudines and Sphenodontia

11. Squamata includes_______.
    a. crocodiles and alligators 
    b. turtles 
    c. tuatars 
    d. lizards and snakes

12. A bird or feathered dinosaur is ________.
    a. Neornithes

CRITICAL THINKING QUESTIONS

18. What are the characteristic features of the chordates?
19. What can be inferred about the evolution of the cranium and vertebral column from examining hagfishes and lampreys?
20. Why did gnathostomes replace most agnathans?
21. Explain why frogs are restricted to a moist environment.
22. Describe the differences between the larval and adult stages of frogs.
23. Describe the functions of the three extra-embryonic membranes present in amniotic eggs.
24. What characteristics differentiate lizards and snakes?
25. Explain why birds are thought to have evolved from theropod dinosaurs.
26. Describe three skeletal adaptations that allow for flight in birds.
27. Describe three unique features of the mammalian skeletal system.
28. Describe three characteristics of the mammalian brain that differ from other vertebrates.
29. How did archaic Homo sapiens differ from anatomically modern humans?
30. Why is it so difficult to determine the sequence of hominin ancestors that have led to modern Homo sapiens?