Concepts of Biology

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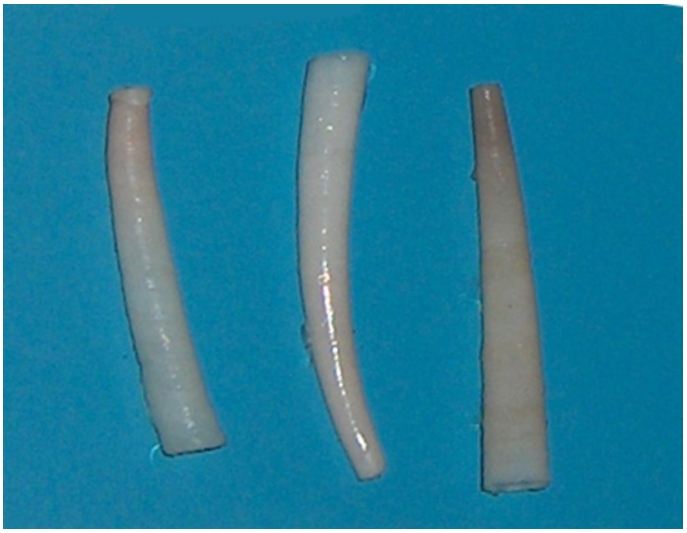


Figure 15.28 *Antalis vulgaris* shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell." (credit: Georges Jansoone)

Annelida

Phylum **Annelida** are segmented worms found in marine, terrestrial, and freshwater habitats, but the presence of water or humidity is a critical factor for their survival in terrestrial habitats. The name of the phylum is derived from the Latin word *annellus*, which means a small ring. Approximately 16,500 species have been described. The phylum includes earthworms, polychaete worms, and leeches. Like mollusks, annelids exhibit protostomic development.

Annelids are bilaterally symmetrical and have a worm-like appearance. Their particular segmented body plan results in repetition of internal and external features in each body segment. This type of body plan is called **metamerism**. The evolutionary benefit of such a body plan is thought to be the capacity it allows for the evolution of independent modifications in different segments that perform different functions. The overall body can then be divided into head, body, and tail.

Physiological Processes of Annelida

The skin of annelids is protected by a cuticle that is thinner than the cuticle of the ecdysozoans and does not need to be molted for growth. Chitinous hairlike extensions, anchored in the skin and projecting from the cuticle, called **chaetae**, are present in every segment in most groups. The chaetae are a defining character of annelids. Polychaete worms have paired, unjointed limbs called parapodia on each segment used for locomotion and breathing. Beneath the cuticle there are two layers of muscle, one running around its circumference (circular) and one running the length of the worm (longitudinal). Annelids have a true coelom in which organs are distributed and bathed in coelomic fluid. Annelids possess a well-developed complete digestive system with specialized organs: mouth, muscular pharynx, esophagus, and crop. A cross-sectional view of a body segment of an earthworm is shown in **Figure 15.29**; each segment is limited by a membrane that divides the body cavity into compartments.

Annelids have a closed circulatory system with muscular pumping "hearts" in the anterior segments, dorsal and ventral blood vessels that run the length of the body with connections in each segment, and capillaries that service individual tissues. Gas exchange occurs across the moist body surface. Excretion is carried out by pairs of primitive "kidneys" called metanephridia that consist of a convoluted tubule and an open, ciliated funnel present in every segment. Annelids have a well-developed nervous system with two ventral nerve cords and a nerve ring of fused ganglia present around the pharynx.

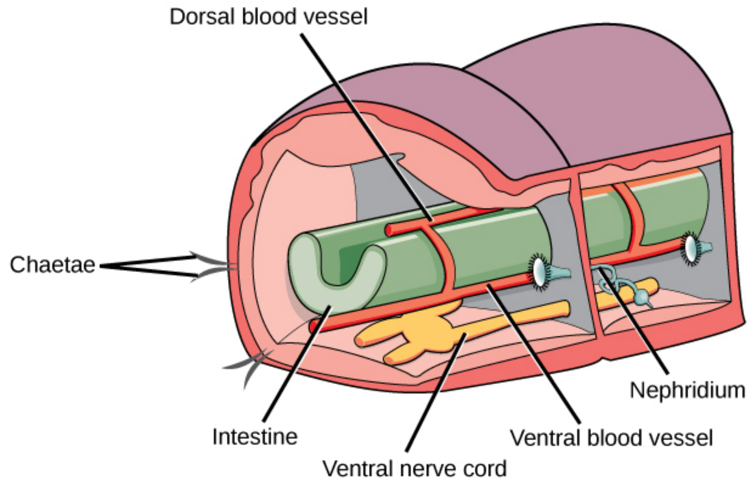


Figure 15.29 In this schematic showing the basic anatomy of annelids, the digestive system is indicated in green, the nervous system is indicated in yellow, and the circulatory system is indicated in red.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads (as in polychaetes).

CONCEPT in ACTION

This **video and animation (http://openstaxcollege.org/l/annelid2)** provides a close-up look at annelid anatomy.

Annelid Diversity

Phylum Annelida includes the classes Polychaeta and Clitellata (**Figure 15.30**); the latter contains subclasses Oligochaeta, Hirudinoidea, and Branchiobdellida.

Earthworms are the most abundant members of the subclass Oligochaeta, distinguished by the presence of the **clitellum**, a ring structure in the skin that secretes mucus to bind mating individuals and forms a protective cocoon for the eggs. They also have a few, reduced chaetae (oligo- = "few"; -chaetae = "hairs"). The number and size of chaetae is greatly diminished in oligochaetes as compared to the polychaetes (poly- = "many"; -chaetae = "hairs"). The chaetae of polychaetes are also arranged within fleshy, flat, paired appendages on each segment called parapodia.

The subclass Hirudinoidea includes leeches. Significant differences between leeches and other annelids include the development of suckers at the anterior and posterior ends, and the absence of chaetae. Additionally, the segmentation of the body wall may not correspond to internal segmentation of the coelomic cavity. This adaptation may allow leeches to swell when ingesting blood from host vertebrates. The subclass Branchiobdellida includes about 150 species that show similarity to leeches as well as oligochaetes. All species are obligate symbionts, meaning that they can only survive associated with their host, mainly with freshwater crayfish. They feed on the algae that grows on the carapace of the crayfish.

(a) (b)

Figure 15.30 The (a) earthworm and (b) leech are both annelids. (credit a: modification of work by "schizoform"/Flickr; credit b: modification of work by "Sarah G..."/Flickr)

15.5 | Echinoderms and Chordates

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

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

Deuterostomes include the phyla Echinodermata and Chordata (which includes the vertebrates) and two smaller phyla. Deuterostomes share similar patterns of early development.

Echinoderms

Echinodermata are named for their spiny skin (from the Greek "echinos" meaning "spiny" and "dermos" meaning "skin"). The phylum includes about 7,000[5] described living species, such as sea stars, sea cucumbers, sea urchins, sand dollars, and brittle stars. **Echinodermata** are exclusively marine.

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles (**Figure 15.31**), although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells, which may also possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. These animals have a true coelom, a portion of which is modified into a unique circulatory system called a **water vascular system**. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

Physiological Processes of Echinoderms

Echinoderms have a unique system for gas exchange, nutrient circulation, and locomotion called the water vascular system. The system consists of a central ring canal and radial canals extending along each arm. Water circulates through these structures allowing for gas, nutrient, and waste exchange. A structure on top of the body, called the **madreporite**, regulates the amount of water in the water vascular system. "Tube feet," which protrude through openings in the endoskeleton, may be expanded or contracted using the hydrostatic pressure in the system. The system allows for slow movement, but a great deal of power, as witnessed when the tube feet latch on to opposite halves of a bivalve mollusk, like a clam, and slowly, but surely pull the shells apart, exposing the flesh within.

5. "Number of Living Species in Australia and the World," A.D. Chapman, Australia Biodiversity Information Services, last modified August 26, 2010, http://www.environment.gov.au/biodiversity/abrs/publications/other/species-numbers/2009/03-exec-summary.html.

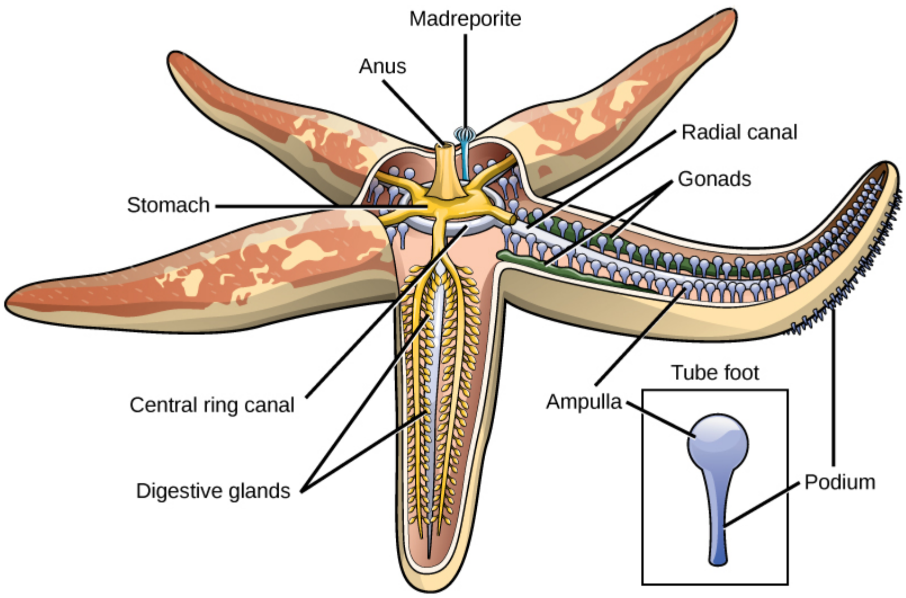


Figure 15.31 This diagram shows the anatomy of a sea star.

The echinoderm nervous system has a nerve ring at the center and five radial nerves extending outward along the arms. There is no centralized nervous control. Echinoderms have separate sexes and release their gametes into the water where fertilization takes place. Echinoderms may also reproduce asexually through regeneration from body parts.

Echinoderm Diversity

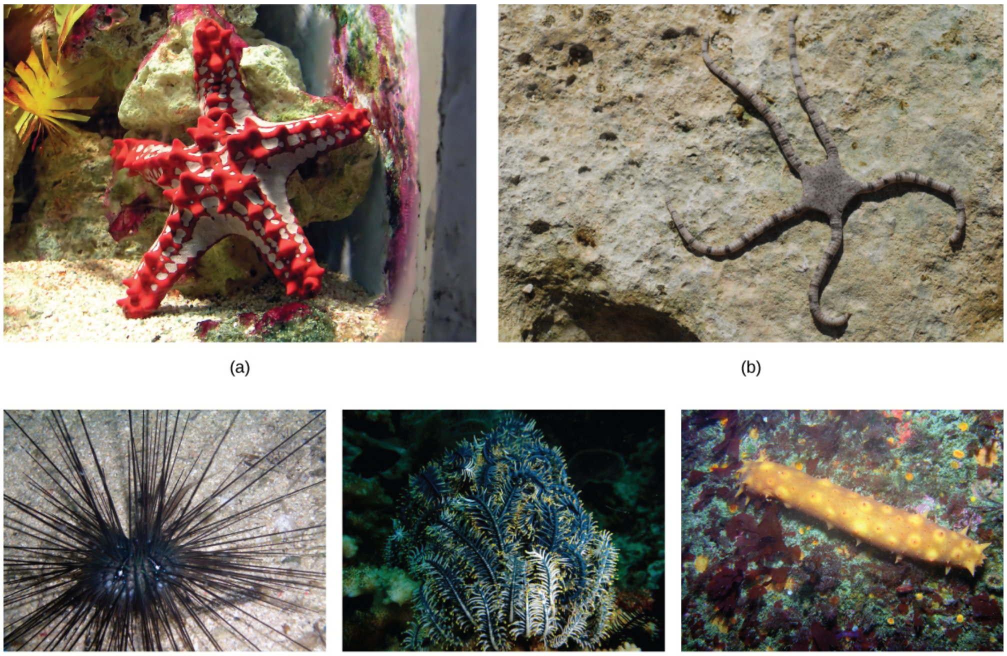
This phylum is divided into five classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) (**Figure 15.32**).

Perhaps the best-known echinoderms are members of the class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known. The characteristics of sea stars that set them apart from other echinoderm classes include thick arms that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which they can evert through their mouths to secrete digestive juices into or onto prey before ingestion. This process can essentially liquefy the prey and make digestion easier.

CONCEPT in ACTION

View this **video (http://openstaxcollege.org/l/echinoderm2)** to explore a sea star's body plan up close, watch one move across the sea floor, and see it devour a mussel.

Brittle stars have long, thin arms that do not contain any organs. Sea urchins and sand dollars do not have arms but are hemispherical or flattened with five rows of tube feet, which help them in slow movement. Sea lilies and feather stars are stalked suspension feeders. Sea cucumbers are soft-bodied and elongate with five rows of tube feet and a series of tube feet around the mouth that are modified into tentacles used in feeding.



(a) (b) (c) (d) (e)

Figure 15.32 Different members of Echinodermata include the (a) sea star in class Asteroidea, (b) the brittle star in class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (d) sea cucumbers representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)

Chordates

The majority of species in the phylum Chordata are found in the subphylum Vertebrata, which include many species with which we are familiar. The vertebrates contain more than 60,000 described species, divided into major groupings of the lampreys, fishes, amphibians, reptiles, birds, and mammals.

Animals in the phylum **Chordata** share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail (**Figure 15.33**). In certain groups, some of these traits 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** (the spine).

The **dorsal hollow nerve cord** is derived from ectoderm that sinks below the surface of the skin and rolls into a hollow tube during development. In chordates, it is located dorsally to the notochord. In contrast, other animal phyla possess 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 from the water that enters the mouth. In fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, jaw supports. In tetrapods, the slits are further modified into components of the ear and tonsils, since there is no longer any need for gill supports in these air-breathing animals. ***Tetrapod*** means "four-footed," and this group includes amphibians, reptiles, birds, and mammals. (Birds are considered tetrapods because they evolved from tetrapod ancestors.)

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 may also function in balance, locomotion, courting, and signaling when danger is near. In many species, the tail is absent or reduced; for example, in apes, including humans, it is present in the embryo, but reduced in size and nonfunctional in adults.

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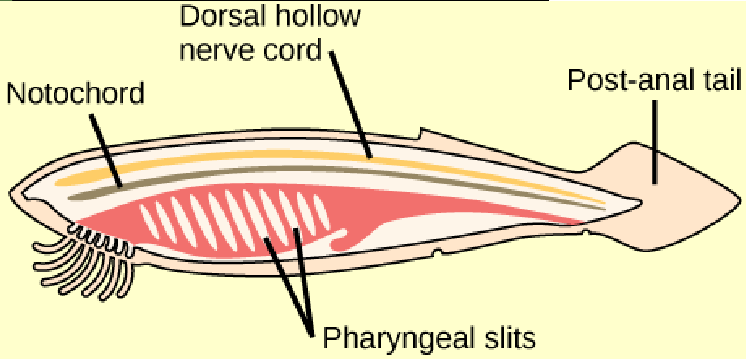


Figure 15.33 In chordates, four common features appear at some point in development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. The anatomy of a cephalochordate shown here illustrates all of these features.

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.

Invertebrate Chordates

In addition to the vertebrates, the phylum Chordata contains two clades of invertebrates: **Urochordata** (tunicates) and **Cephalochordata** (lancelets). Members of these groups possess the four distinctive features of chordates at some point during their development.

The **tunicates** (**Figure 15.34**) are also called sea squirts. The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body. Although tunicates are classified as chordates, the adult forms are much modified in body plan and do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form 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 by the head to the substrate and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.

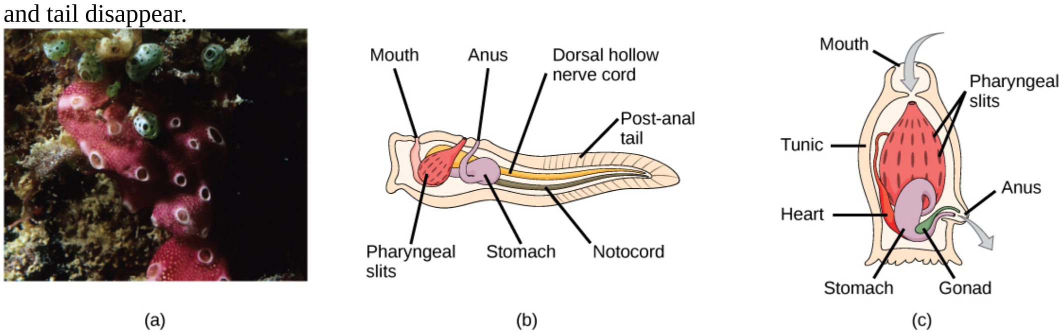


Figure 15.34 (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. In the (b) larval stage, the tunicate can swim freely until it attaches to a substrate to become (c) an adult. (credit a: modification of work by Dr. Dwayne Meadows, NOAA/NMFS/OPR)

Most tunicates live a sessile existence in shallow ocean waters 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 mucus net (pharyngeal slits) and is passed into the intestine through the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water.

Lancelets possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage (**Figure 15.35**). The notochord extends into the head, which gives the subphylum its name (Cephalochordata). Extinct fossils of this subphylum date to the middle of the Cambrian period (540–488 mya).The living forms, the lancelets, are 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.

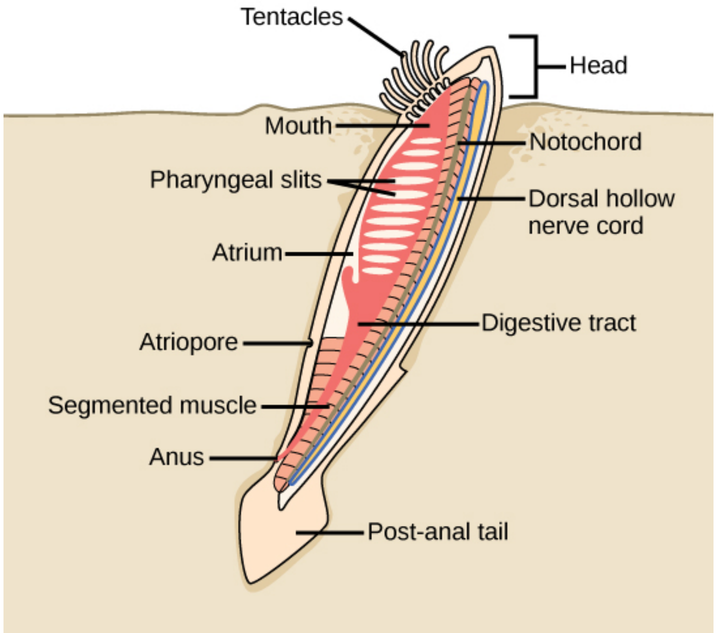


Figure 15.35 Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

15.6 | Vertebrates

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

- Describe the difference between jawless and jawed fishes
- Explain the main characteristics of amphibians, reptiles, and birds
- Describe the derived characteristics in birds that facilitate flight
- Name and describe the distinguishing features of the three main groups of mammals
- Describe the derived features that distinguish primates from other animals

Vertebrates are among the most recognizable organisms of the animal kingdom (**Figure 15.36**). 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, reaching sizes not seen before or since in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out near the end of the Cretaceous period in a mass extinction. A great deal is known about the anatomy of the dinosaurs, given the preservation of their skeletal elements in the fossil record.

(a) (b) (c)

Figure 15.36 Examples of critically endangered vertebrate species include (a) the Siberian tiger *(Panthera tigris altaica*), (b) the Panamanian golden frog (*Atelopus zeteki*), and (c) the Philippine eagle (*Pithecophaga jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Brian Gratwicke; credit c: modification of work by "cuatrok77"/Flickr)

Fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, and jawless fishes were the earliest of these. Jawless fishes—the present day hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates. The jawed fishes evolved later and are extraordinarily diverse today. Fishes are active feeders, rather than sessile, suspension feeders.

Jawless Fishes

Jawless fishes are **craniates** (which includes all the chordate groups except the tunicates and lancelets) that represent an ancient vertebrate lineage that arose over one half-billion years ago. Some of the earliest jawless fishes were the **ostracoderms** (which translates as "shell-skin"). Ostracoderms, now extinct, were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

The clade **Myxini** includes 67 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 15.37a**). 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 are able to release an extraordinary amount of mucus through surface pores. This mucus may allow the hagfish to escape from the grip of predators. Hagfish are known to enter the bodies of dead or dying organisms to devour them from the inside.

(a) (b)

Figure 15.37 (a) Pacific hagfishes are scavengers that live on the ocean floor. (b) 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 a: modification of work by Linda Snook, NOAA/CBNMS; credit b: modification of work by USGS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord, which runs the length of the body, and a skull. This notochord provides support to the fish's body. Although they are craniates, hagfishes are not vertebrates, since they do not replace the notochord with a vertebral column during development, as do the vertebrates.

The clade **Petromyzontidae** includes approximately 40 species of lampreys. **Lampreys** are similar to hagfishes in size and shape; however, lampreys have a brain case and incomplete vertebrae. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Some species are parasitic as adults, attaching to and feeding on the body fluids of fish (**Figure 15.37b**). Most species are free-living.

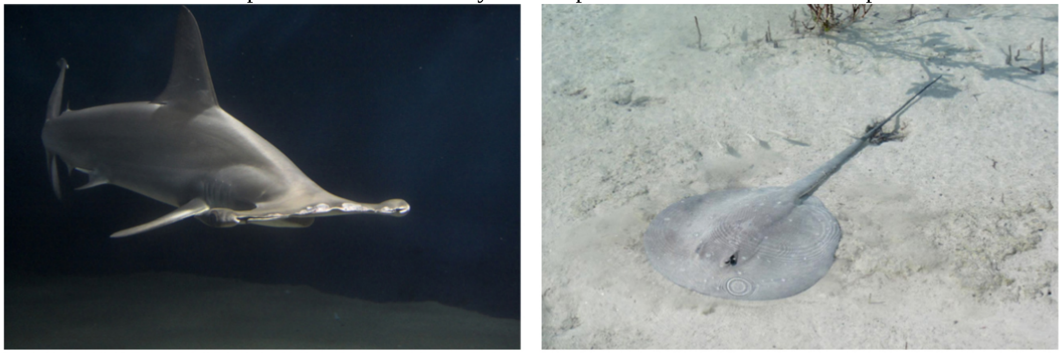
Lampreys live primarily in coastal and fresh waters and have a worldwide temperate region distribution. All species spawn in fresh waters. Eggs are fertilized externally, and the larvae are distinctly different from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days. Lampreys have a notochord as adults.

Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that have jaws and include both cartilaginous and bony fishes. One of the most significant developments in early vertebrate evolution was the origin 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.

The clade **Chondrichthyes**, the cartilaginous fishes, is diverse, consisting of sharks (**Figure 15.38a**), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or ghost sharks. Chondrichthyes have paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the middle Devonian. They are thought to have descended from an extinct group that had a skeleton made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of the 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 some 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. Some species of sharks and rays are suspension feeders that feed on plankton.



(a) (b)

Figure 15.38 (a) This hammerhead shark is an example of a predatory cartilaginous fish. (b) This stingray blends into the sandy bottom of the ocean floor when it is feeding or awaiting prey. (credit a: modification of work by Masashi Sugawara; credit b: modification of work by "Sailn1"/Flickr)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, the latter being 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, also have a sense organ called the **lateral line**, which is used to detect movement and vibration in the surrounding water, and a sense that is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of the fish's body.

Sharks reproduce sexually and eggs are fertilized internally. Most species are ovoviviparous, that is, 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" 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, that is, the young develop within the mother's body, and she gives live birth.

Rays and skates include 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 15.38b**). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.

Bony Fishes

Members of the clade **Osteichthyes**, or 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 reverted in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered in 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. Unlike sharks, some bony fish depend on their eyesight to locate prey. Bony fish are also unusual in possessing taste cells in the head and trunk region of the body that allow them to detect extremely small concentrations of molecules in the water.

All bony fishes, like the cartilaginous 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. Unlike sharks, bony fishes have a **swim bladder**, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two clades with living members: **Actinopterygii** (ray-finned fishes) and **Sarcopterygii** (lobe-finned fishes).

The ray-finned fishes include many familiar fishes—tuna, bass, trout, and salmon (**Figure 15.39a**), among others. Ray-finned fishes are named for the form of their fins—webs of skin supported by bony spines called rays. In contrast, the fins of lobe-finned fishes are fleshy and supported by bone (**Figure 15.39b**). Living members of lobe-finned fishes include the less familiar lungfishes and coelacanth.

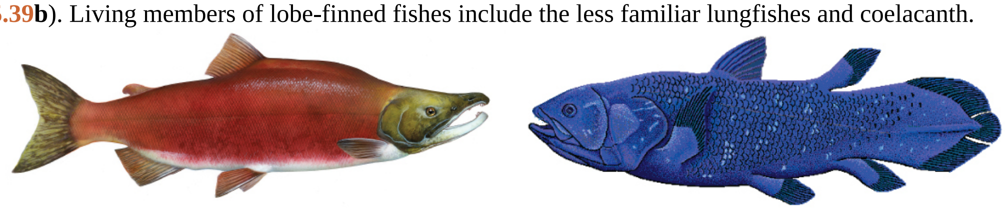


Figure 15.39 The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period 100 million years ago until one was discovered in 1938 between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)

Amphibians

Amphibians are vertebrate tetrapods. **Amphibia** includes frogs, salamanders, and caecilians. The term amphibian means "dual life," which is a reference to the metamorphosis that many frogs undergo from a tadpole to an adult and the mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved in the Devonian period and were the earliest terrestrial tetrapods.

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians possess only vestigial limbs. An important characteristic of extant amphibians is a moist, permeable skin, achieved by mucus glands. The moist skin allows oxygen and carbon dioxide exchange with the environment, a process called **cutaneous respiration**. All living adult amphibian species are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Amphibian Diversity

Amphibia comprise an estimated 6,500 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: **Urodela** ("tailed-ones"), the salamanders and newts; **Anura** ("tail-less ones"), the frogs and toads; and **Apoda** ("legless ones"), the caecilians.

Living **salamanders** (**Figure 15.40a**) include approximately 500 species, some of which are aquatic, others 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. Some salamanders are lungless, and respiration occurs through the skin or external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

(a) (b)

Figure 15.40 (a) Most salamanders have legs and a tail, but respiration varies among species. (b) The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source. (credit a: modification of work by Valentina Storti; credit b: modification of work by Evan Pickett)

CONCEPT in ACTION

Watch this **video (http://openstaxcollege.org/l/river_monster2)** about an unusually large salamander species.

Frogs (**Figure 15.40b**) are the most diverse group of amphibians, with approximately 5,000 species that live on all continents except Antarctica. Frogs have a body plan that is more specialized than the salamander body plan for movement on land. Adult frogs use their hind limbs to jump many times their body length on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage and defensive chemicals that are poisonous to predators secreted from glands in the skin.

Frog eggs are fertilized externally, as they are laid in moist environments. Frogs demonstrate a range of parental behaviors, with some species exhibiting little care, to species that carry eggs and tadpoles on their hind legs or backs. The life cycle consists of two 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, but no limbs. At the end of the tadpole stage, frogs undergo a gradual metamorphosis into the adult form. During this stage, the gills 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 15.41**).

(a) (b) (c)

Figure 15.41 A frog begins as a (a) tadpole and undergoes metamorphosis to become (b) a juvenile and finally (c) an adult. (credit: modification of work by Brian Gratwicke)

Caecilians comprise an estimated 185 species. They lack external limbs and resemble giant earthworms. They inhabit soil and are found primarily in the tropics of South America, Africa, and southern Asia where they are adapted for a soil-burrowing lifestyle and are nearly blind. Unlike most of the other amphibians that breed in or near water, reproduction in a drier soil habitat means that caecilians must utilize internal fertilization, and most species give birth to live young (**Figure 15.42**).

Figure 15.42 Caecilians lack external limbs and are well adapted for a soil-burrowing lifestyle. (credit: modification of work by "cliff1066"/Flickr)

Reptiles and Birds

The **amniotes**—reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted (shelled) egg and an embryo protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes could develop within an aquatic environment inside the egg. This led to less dependence on a water environment for development and allowed the amniotes to invade drier areas. This was a significant evolutionary change 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 membranes of the amniotic egg also allowed gas exchange and sequestering of wastes within the enclosure of an eggshell. The shells of bird eggs are composed of calcium carbonate and are hard and brittle, but possess pores for gas and water exchange. The shells of reptile eggs are more leathery and pliable. Most mammals do not lay eggs; however, even with internal gestation, amniotic membranes are still present.

In the past, the most common division of amniotes has been into 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 discuss birds as a group distinct from reptiles with the understanding that this does not reflect evolutionary history.

Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes—may have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay shelled eggs on land. Even aquatic reptiles, like sea turtles, 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 prevented water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all must breathe with lungs. In addition, reptiles conserve valuable body water by excreting nitrogen in the form of uric acid paste. These characteristics, along with the shelled, amniotic egg, were the major reasons why reptiles became so successful in colonizing a variety of terrestrial habitats far from water.

Reptiles are ectotherms, that is, animals whose main source of body heat comes from the environment. Behavioral maneuvers, like basking to heat themselves, or seeking shade or burrows to cool off, help them regulate their body temperature,

Class Reptilia includes diverse species classified into four living clades. These are the Crocodilia, Sphenodontia, Squamata, and Testudines.

The **Crocodilia** ("small lizard") arose approximately 84 million years ago, and living species include alligators, crocodiles, and caimans. Crocodilians (**Figure 15.43a**) live throughout the tropics of Africa, South America, the southeastern United States, Asia, and Australia. They are found in freshwater 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.

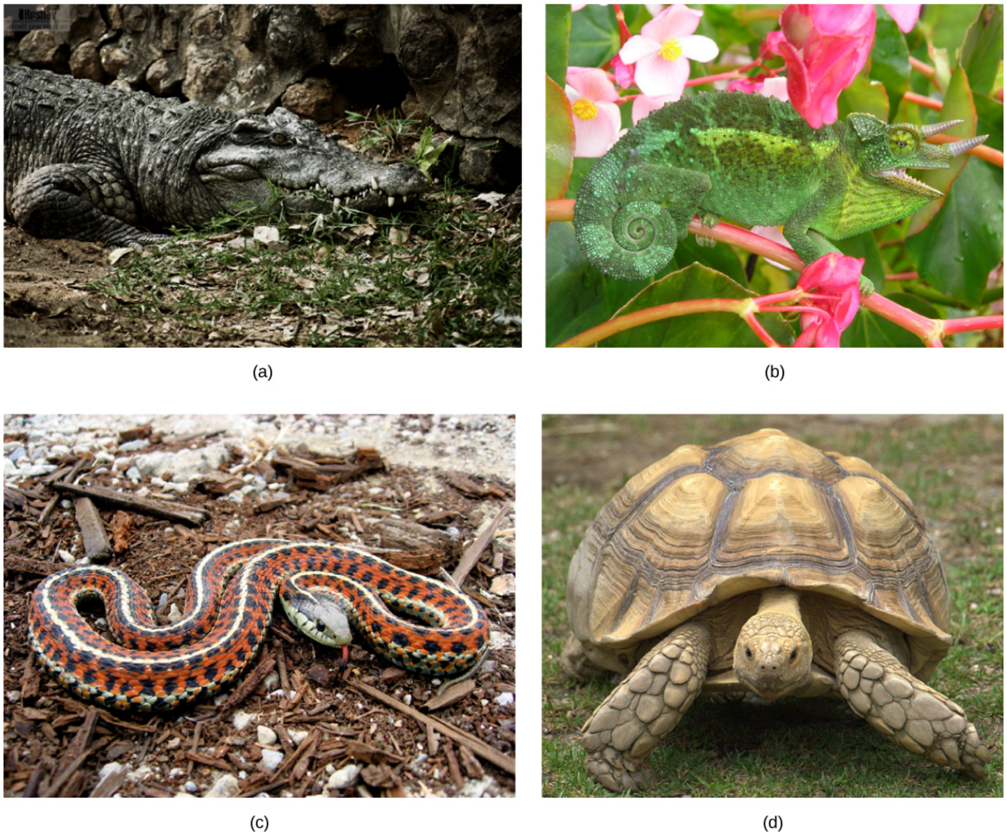


Figure 15.43 (a) Crocodilians, such as this Siamese crocodile, provide parental care for their offspring. (b) This Jackson's chameleon blends in with its surroundings. (c) The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (d) The African spurred tortoise lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit a: modification of work by Keshav Mukund Kandhadai; credit c: modification of work by Steve Jurvetson; credit d: modification of work by Jim Bowen)

The **Sphenodontia** ("wedge tooth") arose in the Mesozoic Era and includes only one living genus, *Tuatara*, with two species that are found in New Zealand. There are many fossil species extending back to the Triassic period (250–200 million years ago). Although the tuataras resemble lizards, they are anatomically distinct and share characteristics that are found in birds and turtles.

Squamata ("scaly") arose in the late Permian; living species include lizards and snakes, which are the largest extant clade of reptiles (**Figure 15.43b**). Lizards differ from snakes by having four limbs, eyelids, and external ears, which are lacking in snakes. Lizard species range in size from chameleons and geckos that are a few centimeters in length to the Komodo dragon, which is about 3 meters in length.

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago (**Figure 15.43c**). 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 7.5 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects.

Turtles are members of the clade **Testudines** ("having a shell") (**Figure 15.43d**). Turtles are characterized by a bony or cartilaginous shell, made up of the carapace on the back and the plastron on the ventral surface, which develops from the ribs. Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Turtles lay eggs on land, although many species live in or near water. 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.

Birds

Data now suggest that birds belong within the reptile clade, but they display a number of unique adaptations that set them apart. Unlike the reptiles, birds are endothermic, meaning they generate their own body heat through metabolic processes. The most distinctive characteristic of birds is their feathers, which are modified reptilian scales. Birds have several different types of feathers that are specialized for specific functions, like contour feathers that streamline the bird's exterior and loosely structured **down feathers** that insulate (**Figure 15.44a**).

Feathers not only permitted the earliest birds to glide, and ultimately engage in flapping flight, but they insulated the bird's body, assisting the maintenance of endothermy, even in cooler temperatures. Powering a flying animal requires economizing on the amount of weight carried. As body weight increases, the muscle output and energetic cost required for flying increase. Birds have made several modifications to reduce body weight, including hollow or **pneumatic bones** (**Figure 15.44b**) with air spaces that may be connected to air sacs and cross-linked struts within their bones to provide structural reinforcement. Parts of the vertebral skeleton and braincase are fused to increase its strength while lightening its weight. Most species of bird only possess one ovary rather than two, and no living birds have teeth in their jaw, further reducing body mass.

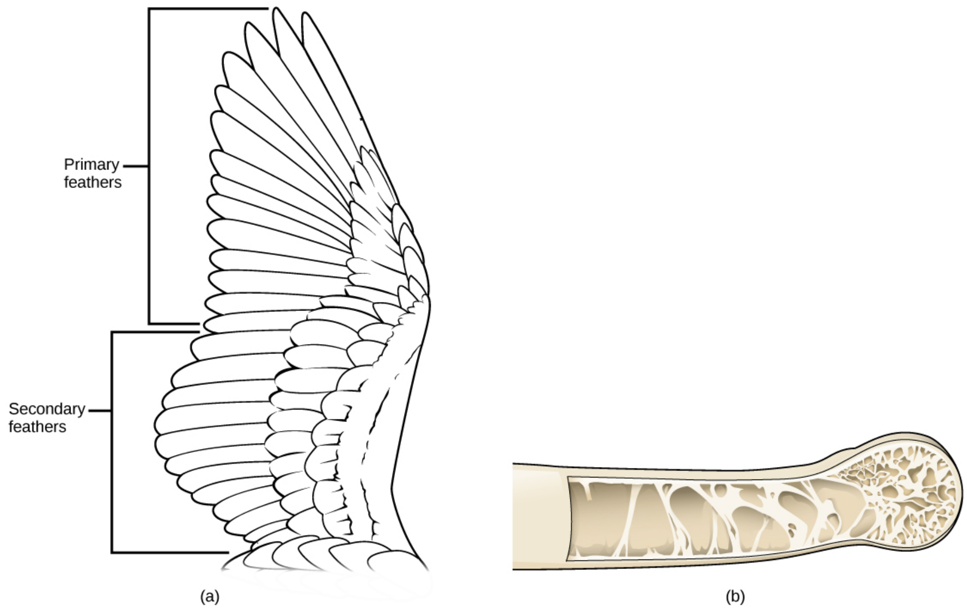


Figure 15.44 (a) Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift. (b) Many birds have hollow pneumatic bones, which make flight easier.

Birds possess a system of air sacs branching from their primary airway that divert the path of air so that it passes unidirectionally through the lung, during both inspiration and expiration. Unlike mammalian lungs in which air flows in two directions as it is breathed in and out, air flows continuously through the bird's lung to provide a more efficient system of gas exchange.

Mammals

Mammals are vertebrates that have hair and mammary glands used to provide nutrition for their young. Certain features of the jaw, skeleton, skin, and internal anatomy are also unique to mammals. The presence of hair is one of the key characteristics of a mammal. Although it is not very extensive in some groups, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation by trapping a layer of air close to the body to retain metabolic heat. Hair also serves as a sensory mechanism through specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit touch information, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration.

Mammalian 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. **Sudoriferous glands** produce sweat and scent, which function in thermoregulation and communication, respectively. **Mammary glands** produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not.

The skeletal system of mammals possesses unique features that differentiate them from other vertebrates. Most mammals have **heterodont teeth**, meaning they have different types and shapes of teeth that allow them to feed on different kinds of foods. These different types of teeth include the incisors, the canines, premolars, and molars. The first two types are for cutting and tearing, whereas the latter two types are for crushing and grinding. Different groups have different proportions of each type, depending on their diet. Most mammals are also **diphyodonts**, meaning they have two sets of teeth in their lifetime: deciduous or "baby" teeth, and permanent teeth. In other vertebrates, the teeth can be replaced throughout life.