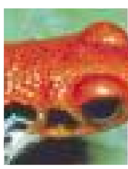
34 Deuterostomate Animals



Complex social systems, in which individuals associate with one another to breed and care for their offspring, characterize many species of fish, birds, and mammals—the most conspicuous and familiar deuterostomate animals. We tend to think of these social systems as having evolved relatively recently, but some amphibians, members of an ancient deuterostomate group, also have elaborate courtship and parental care behavior. For example, the male of the European midwife toad gathers eggs around his hind legs as the female lays them. He then carries the eggs until they are ready to hatch.

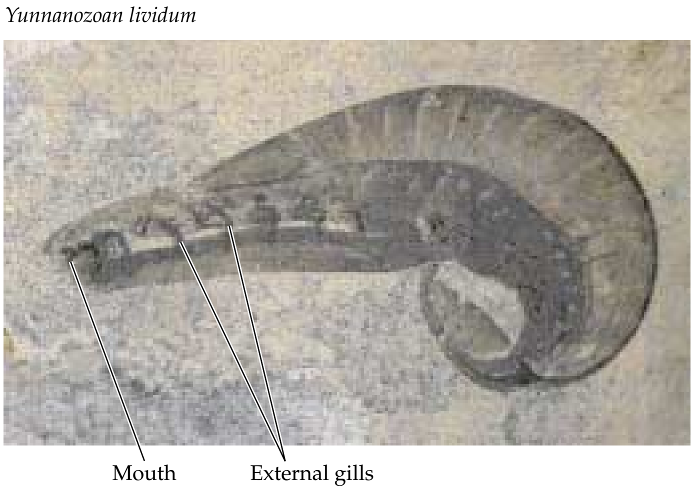
In the Surinam toad, mating and parental care are exquisitely coordinated, as an elaborate mating "dance" results in the female depositing eggs on the male's belly. The male fertilizes the eggs and, as the ritual ends, he presses them against the female's back, where they are carried until they hatch. The female poison dart frog lays clutches of eggs on a leaf or on the ground, which both parents then work to keep moist and protected. When the tadpoles hatch, they wiggle onto the back of one of their parents, who then carries the tadpoles to water.

There are fewer major lineages and many fewer species of deuterostomes than of protostomes (Table 34.1 on page 658), but we have a special interest in the deuterostomes because we are members of that lineage. In this chapter, we will describe and discuss the deuterostomate phyla: Echinodermata, Hemichordata, and Chordata. We close with a brief overview of some major themes in the evolution of animals.

Some Amphibian Parents Nurture Their Young Poison dart frogs (*Dendrobates reticulatus*) of the Amazon basin lay their eggs on land. Both parents protect and nurture the eggs until they hatch, at which time a parent carries the tadpoles to water on its back.

Deuterostome Ancestors

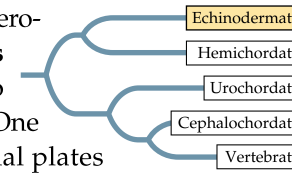
A group of extinct animals known as the yunnanozoans are the likely ancestors of all deuterostomes. Many fossils of these animals have been discovered in China's Yunnan province. These well-preserved fossils show that the animals had a large mouth, six pairs of external gills, and a lightly cuticularized, segmented posterior body section (Figure 34.1). Later in deuterostome evolution, gills became internal and were connected to the exterior via slits in the body wall. These gill slits subsequently were lost in the lineage leading to the modern echinoderms.



34.1 The Ancestral Deuterostomes Had External Gills The extinct Yunnanozoan lineage is probably ancestral to all deuterostomes. This fossil, which dates from the Cambrian, shows the six pairs of external gills and segmented posterior body that characterized these animals.

Modern deuterostomes fall into two major clades (Figure 34.2). One clade, composed of echinoderms and hemichordates, is characterized by a three-part coelom and a bilaterally symmetrical, ciliated larva. The ancestors of the other clade, containing the chordates, had a distinctly different, nonfeeding, tadpole-like larva and a unique dorsal supporting structure.

Echinoderms: Pentaradial Symmetry

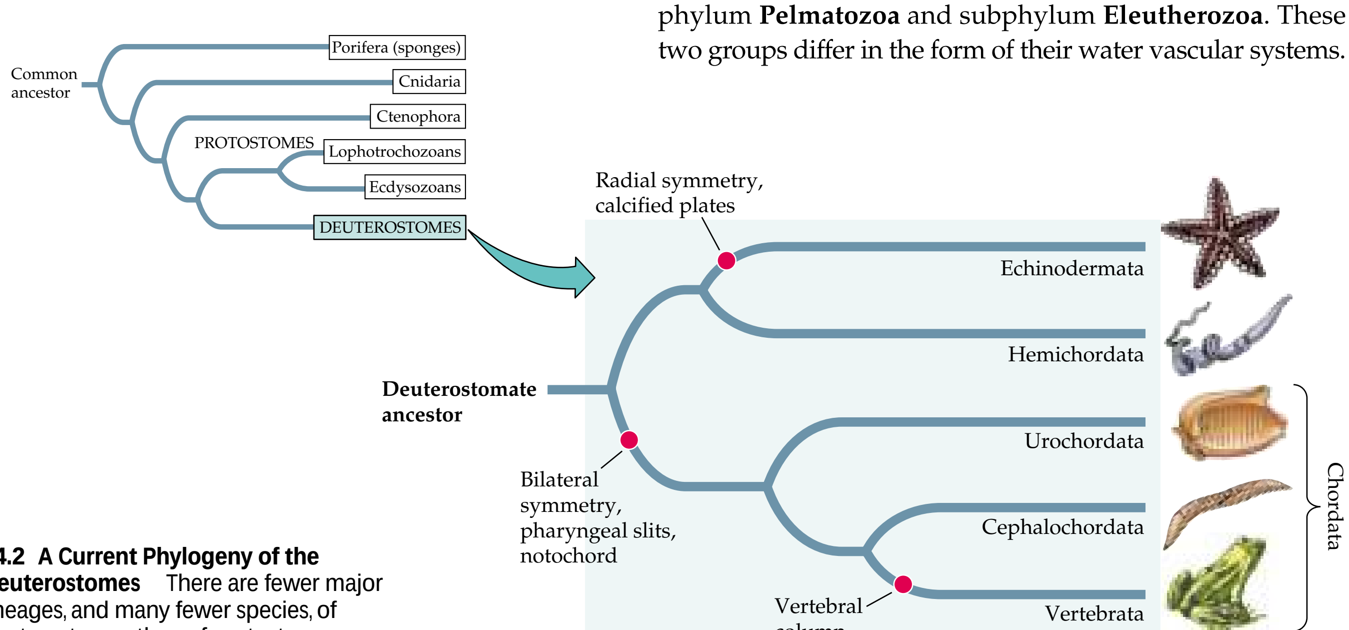


During the evolution of one deuterostomate lineage, the **echinoderms** (phylum **Echinodermata**), two major structural features arose. One was a system of calcified internal plates covered by thin layers of skin and some muscles. The calcified plates of early echinoderms later became enlarged and thickened until they fused inside the entire body, giving rise to an internal skeleton.

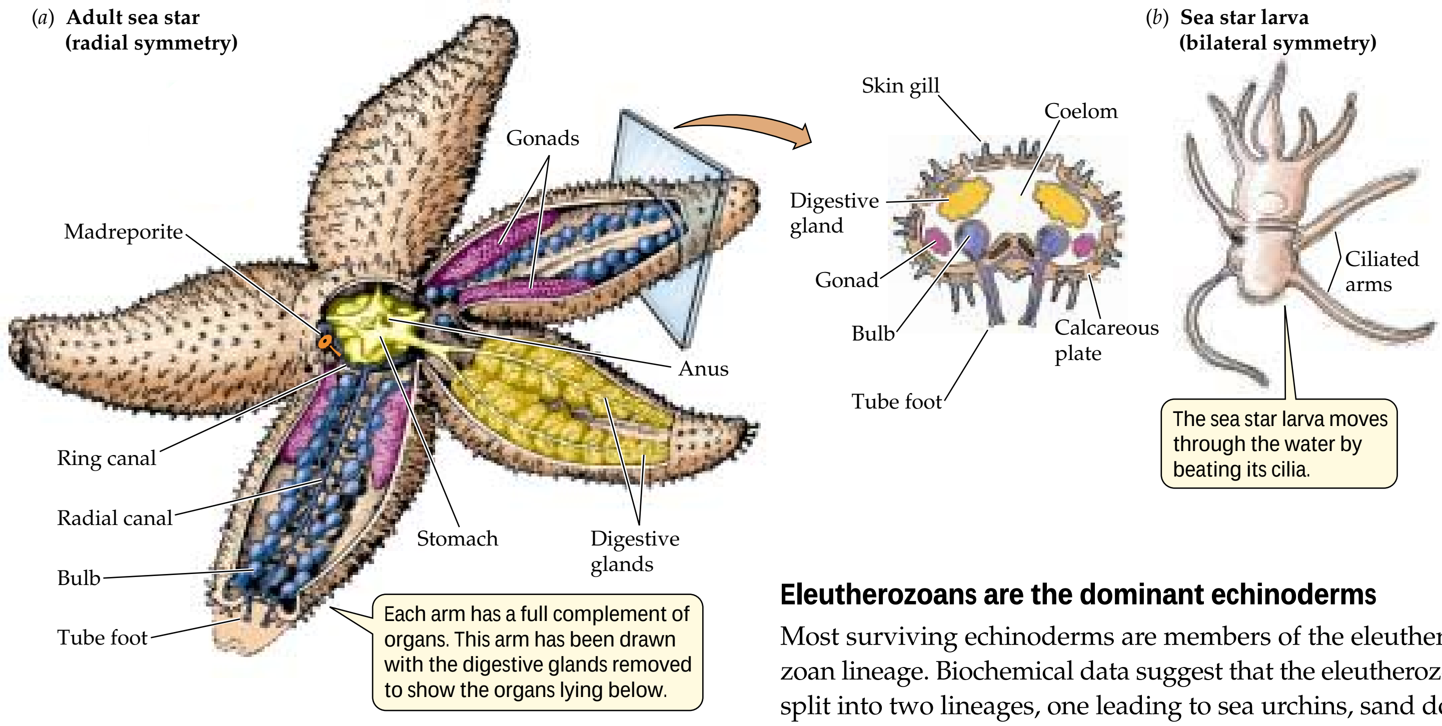
The other feature was a *water vascular system*, a network of water-filled canals leading to extensions called *tube feet*. This system functions in gas exchange, locomotion, and feeding (Figure 34.3*a*). Seawater enters the system through a perforated *madreporite*. A calcified canal leads from the madreporite to another canal that rings the *esophagus* (the tube leading from the mouth to the stomach). Other canals radiate from this *ring canal*, extending through the arms (in species that have arms) and connecting with the tube feet.

The development of these two structural innovations resulted in a striking evolutionary radiation. About 23 classes of echinoderms, of which only 6 survive today, have been described from fossils. The 13,000 species described from their fossil remains are probably only a small fraction of those that actually lived. Nearly all 7,000 species that survive today live only in marine environments. Some have bilaterally symmetrical, ciliated larvae (Figure 34.3*b*) that feed for some time as planktonic organisms before settling and transforming into adults with *pentaradial symmetry* (symmetry in five or multiples of five).

Living echinoderms are members of two lineages: subphylum **Pelmatozoa** and subphylum **Eleutherozoa**. These two groups differ in the form of their water vascular systems.



34.2 A Current Phylogeny of the Deuterostomes There are fewer major lineages, and many fewer species, of deuterostomes than of protostomes.



34.3 Echinoderms Display Two Evolutionary Innovations
(*a*) A dorsal view of a sea star displays the canals and tube feet of the echinoderm water vascular system, as well as a calcified internal skeleton. (*b*) The ciliated sea star larva has bilateral symmetry.

Pelmatozoans have jointed arms

Sea lilies and feather stars (class **Crinoidea**) are the only surviving pelmatozoans. Sea lilies were abundant 300–500 million years ago, but only about 80 species survive today. Most sea lilies attach to a substratum by means of a flexible stalk consisting of a stack of calcareous discs. The main body of the animal is a cup-shaped structure that contains a tubular digestive system. Five to several hundred arms, usually in multiples of five, extend outward from the cup. The jointed calcareous plates of the arms enable them to bend.

A sea lily feeds by orienting its arms in passing water currents. Food particles strike and stick to the tube feet, which are covered with mucus-secreting glands. The tube feet transfer these particles to grooves in the arms, where ciliary action carries the food to the mouth. The tube feet of sea lilies are also used for gas exchange and elimination of nitrogenous wastes.

Feather stars are similar to sea lilies, but they have flexible appendages with which they grasp the substratum (Figure 34.4*a*). Feather stars feed in much the same manner as sea lilies. They can walk on the tips of their arms or swim by rhythmically beating their arms. About 600 living species of feather stars have been described.

Eleutherozoans are the dominant echinoderms

Most surviving echinoderms are members of the eleutherozoan lineage. Biochemical data suggest that the eleutherozoa split into two lineages, one leading to sea urchins, sand dollars, and sea cucumbers, and the second leading to sea stars and brittle stars.

Sea urchins and sand dollars (class **Echinoidea**) lack arms, but they share a five-part body plan with all other echinoderms. Sea urchins are hemispherical animals that are covered with spines attached to the underlying skeleton via ball-and-socket joints (Figure 34.4*b*). The spines of sea urchins come in varied sizes and shapes; a few produce toxic substances. Many sea urchins consume algae, which they scrape from rocks with a complex rasping structure. Others feed on small organic debris that they collect with their tube feet or spines. Sand dollars, which are flattened and disc-shaped, feed on algae and fragments of organic matter found on the seafloor or suspended organic material.

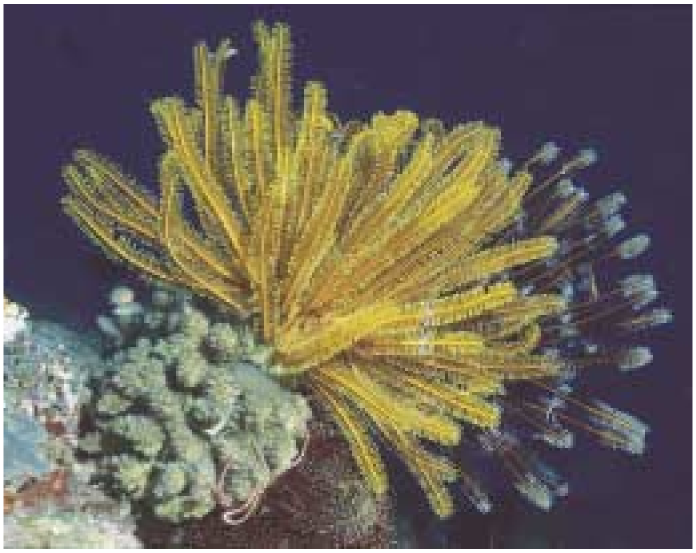
The sea cucumbers (class **Holothuroidea**) lack arms, and their bodies are oriented in an atypical manner for an echinoderm. The mouth is anterior and the anus is posterior, not oral and aboral as in other echinoderms. Sea cucumbers use their tube feet primarily for attaching to the substratum rather than for moving. The anterior tube feet are modified into large, feathery, sticky tentacles that can be protruded from the mouth (Figure 34.4*c*). Periodically, the sea cucumber withdraws the tentacles, wipes off the material that has adhered to them, and digests it.

Sea stars (class **Asteroidea**; Figure 34.4*d*) are the most familiar echinoderms. Their digestive organs and gonads are located in the arms. Their tube feet serve as organs of locomotion, gas exchange, and attachment. Each tube foot of a sea star is also an adhesive organ consisting of an internal ampulla connected by a muscular tube to an external suction

34.1 *Summary of Living Members of the Kingdom Animalia*

PHYLUM	NUMBER OF LIVING SPECIES DESCRIBED	MAJOR GROUPS
Porifera: Sponges	10,000	
Cnidaria: Cnidarians	10,000	Hydrozoa: Hydras and hydroids Scyphozoa: Jellyfishes Anthozoa: Corals, sea anemones
Ctenophora: Comb jellies	100	
PROTOSTOMES		
Lophotrochozoans		
Platyhelminthes: Flatworms	20,000	Turbellaria: Free-living flatworms Trematoda: Flukes (all parasitic) Cestoda: Tapeworms (all parasitic) Monogenea (ectoparasites of fishes)
Rotifera: Rotifers	1,800	
Ectoprocta: Bryozoans	4,500	
Brachiopoda: Lamp shells	340	More than 26,000 fossil species described
Phoronida: Phoronids	20	
Nemertea: Ribbon worms	900	
Annelida: Segmented worms	15,000	Polychaeta: Polychaetes (all marine) Oligochaeta: Earthworms, freshwater worms Hirudinea: Leeches
Mollusca: Mollusks	50,000	Monoplacophora: Monoplacophorans Polyplacophora: Chitons Bivalvia: Clams, oysters, mussels Gastropoda: Snails, slugs, limpets Cephalopoda: Squids, octopuses, nautiloids
Ecdysozoans		
Kinorhyncha: Kinorhynchs	150	
Chaetognatha: Arrow worms*	100	
Nematoda: Roundworms	20,000	
Nematomorpha: Horsehair worms	230	
Onychophora: Onychophorans	80	
Tardigrada: Water bears	600	
Chelicerata: Chelicerates	70,000	Merostomata: Horseshoe crabs Arachnida: Scorpions, harvestmen, spiders, mites, ticks
Crustacea	50,000	Crabs, shrimps, lobsters, barnacles, copepods
Hexapoda	1,500,000	Insects
Myriapoda	13,000	Millipedes, centipedes
DEUTEROSTOMES		
Echinodermata: Echinoderms	7,000	Crinoidea: Sea lilies, feather stars Ophiuroidea: Brittle stars Asteroidea: Sea stars Concentricycloidea: Sea daisies Echinoidea: Sea urchins Holothuroidea: Sea cucumbers
Hemichordata: Hemichordates	95	Acorn worms and pterobranchs
Chordata: Chordates	50,000	Urochordata: Sea squirts Cephalochordata: Lancelets Agnatha: Lampreys, hagfishes Chondrichthyes: Cartilaginous fishes Osteichthyes: Bony fishes Amphibia: Amphibians Reptilia: Reptiles Aves: Birds Mammalia: Mammals

* The position of this phylum is uncertain. Many researchers place them in the deuterostomes.

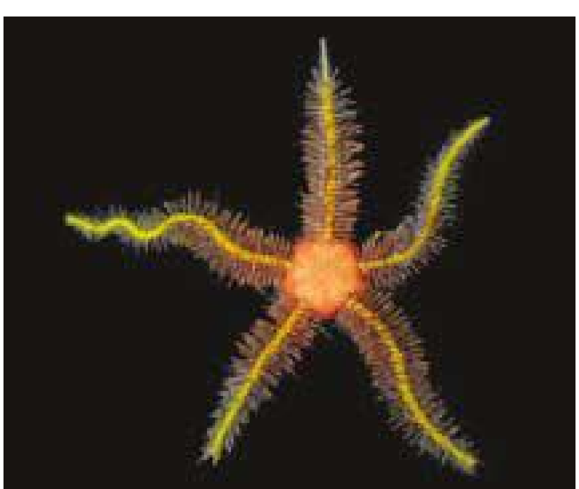


(*a*) *Oxycomanthus bennetti*

(*b*) *Strongylocentrotus purpuratus*

(*c*) *Bohadschia argus*

(*d*) *Henricia leviuscula*



(*e*) *Ophiothrix spiculata*

34.4 Diversity among the Echinoderms (*a*) The flexible arms of this golden feather star are clearly visible. (*b*) Purple sea urchins are important grazers on algae in the intertidal zone of the Pacific Coast of North America. (*c*) This sea cucumber lives on rocky substrata in the seas around Papua New Guinea. (*d*) The blood sea star is typical of many sea stars; some species, however, have more than five arms. (*e*) The arms of the brittle star are composed of hard but flexible plates.

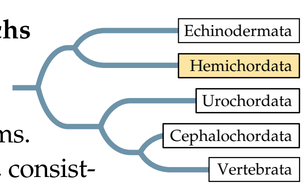
cup. The tube foot is moved by expansion and contraction of the circular and longitudinal muscles of the tube.

Many sea stars prey on polychaetes, gastropods, bivalves, and fish. They are important predators in many marine environments, such as coral reefs and rocky intertidal zones. With hundreds of tube feet acting simultaneously, a sea star can exert an enormous and continuous force. It can grasp a clam in its arms, anchor the arms with its tube feet, and, by steady contraction of the muscles in the arms, gradually exhaust the muscles the clam uses to keep its shell closed. Sea stars that feed on bivalves are able to push the stomach out through the mouth and then through the narrow space between the two halves of the bivalve's shell. The stomach secretes enzymes that digest the prey.

Brittle stars (class **Ophiuroidea**) are similar in structure to sea stars, but their flexible arms are composed of jointed hard plates (Figure 34.4*e*). Brittle stars generally have five arms, but each arm may branch a number of times. Most of the 2,000 species of brittle stars ingest particles from the upper regions of sediments and assimilate the organic material from them, but some species remove suspended food particles from the water; others capture small animals. Brittle stars eject the indigestible particles through their mouths because, unlike most other echinoderms, they have only one opening to the digestive tract.

An additional group, the sea daisies (class **Concentricycloidea**) were discovered only in 1986, and little is known about them. They have tiny disc-shaped bodies with a ring of marginal spines, and two ring canals, but no arms. Sea daisies are found on rotting wood in ocean waters. They apparently eat prokaryotes, which they digest outside their bodies and absorb either through a membrane that covers the oral surface or via a shallow, saclike stomach. Recent molecular data suggest that they are greatly modified sea stars.

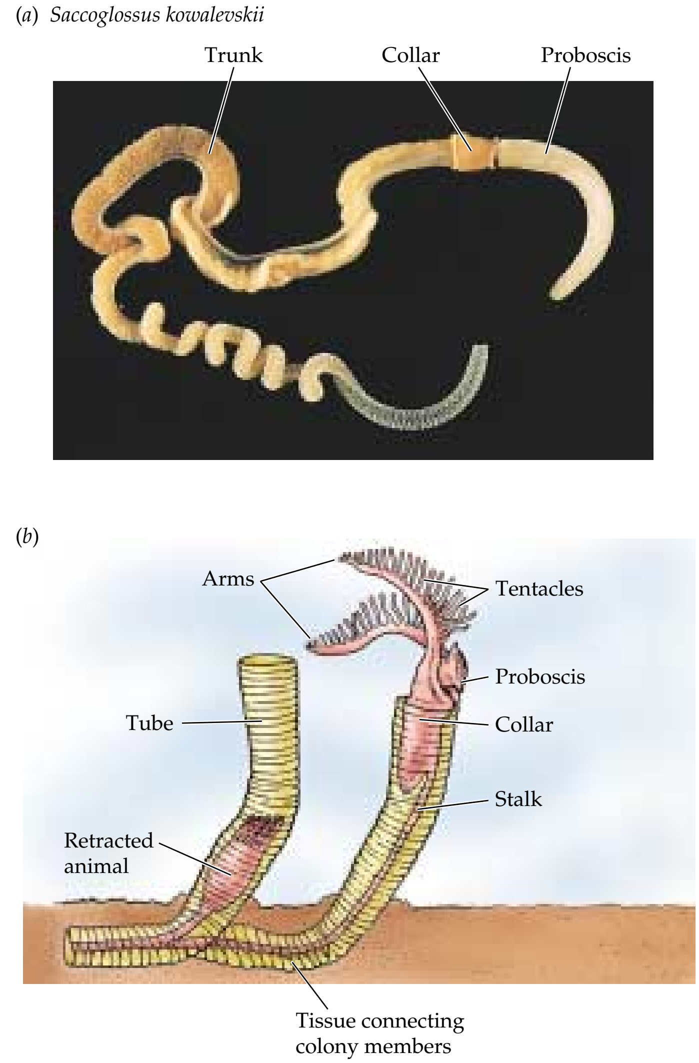
Hemichordates: Conservative Evolution



Acorn worms and **pterobranchs** (phylum **Hemichordata**) are probably similar in form to the ancestor they share with the echinoderms. They have a three-part body plan, consisting of a proboscis, a collar, and a trunk.

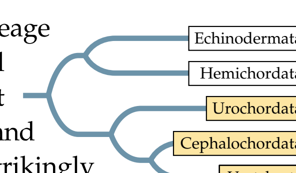
The 70 species of acorn worms range up to 2 meters in length. They live in burrows in muddy and sandy marine sediments. The large proboscis of an acorn worm is a digging organ (Figure 34.5*a*). It is coated with a sticky mucus that traps small organisms in the sediment. The mucus and its attached prey are conveyed by cilia to the mouth. In the esophagus, the food-laden mucus is compacted into a ropelike mass that is moved through the digestive tract by ciliary action. Behind the mouth is a muscular *pharynx*, a tube that connects the mouth to the intestine. The pharynx opens to the outside through a number of *pharyngeal slits* through which water can exit. Highly vascularized tissue surrounding the pharyngeal slits serves as a gas exchange apparatus. An acorn worm breathes by pumping water into its mouth and out through its pharyngeal slits.

The 10 living species of pterobranchs are sedentary animals up to 12 mm in length that live in a tube secreted by the proboscis. Some species are solitary; others form colonies of individuals joined together. Behind the proboscis is a collar with 1–9 pairs of arms, bearing long tentacles that capture prey and function in gas exchange (Figure 34.5*b*).



34.5 Hemichordates (*a*) The proboscis of this acorn worm is modified for digging. This individual has been extracted from its burrow. (*b*) Pterobranchs may be colonial or solitary.

Chordates: New Ways of Feeding



Members of the second major lineage of deuterostomes evolved several modifications of the coelom that provided new ways of capturing and handling food. They evolved a strikingly different body plan, characterized by an internal dorsal supporting structure. The pharyngeal slits, which originally functioned as sites for the uptake of O_2 and elimination of CO_2, and for eliminating water, were further enlarged. The result was a phylum (Chordata) of bilaterally (*a*) *Rhopalaea crassa*

(*b*) *Pegea socia*

34.6 Urochordates (*a*) The tunic is clearly visible in this transparent sea squirt. (*b*) A chainlike colony of salps floats in tropical waters.

symmetrical animals with body plans characterized by the following shared features at some stage in their development:

- *Pharyngeal slits*
- A dorsal, hollow *nerve cord*
- A ventral *heart*
- A *tail* that extends beyond the anus
- A dorsal supporting rod, the *notochord*

The **notochord** is the distinctive derived trait of the lineage. It is composed of a core of large cells with turgid fluid-filled vacuoles that make it rigid but flexible. In some urochordates, the notochord is lost during metamorphosis to the adult stage. In vertebrates, it is replaced by other skeletal structures that provide support for the body.

The **tunicates** (subphylum **Urochordata**) may be similar to the ancestors of the chordates. All 2,500 species of tunicates are marine animals, most of which are sessile as adults. Their swimming, tadpole-like larvae reveal the close evolutionary relationship between tunicates and chordates (as Darwin realized; see Figure 25.4).

In addition to its pharyngeal slits, a tunicate larva has a dorsal, hollow nerve cord and a notochord that is restricted to the tail region. Bands of muscle surround the notochord, providing support for the body. After a short time swimming in the water, the larvae of most species settle to the seafloor and transform into sessile adults. The tunicate pharynx is enlarged into a *pharyngeal basket*, with which the animal feeds by extracting plankton from the water. Some urochordates are solitary, but others produce colonies by asexual budding from a single founder.

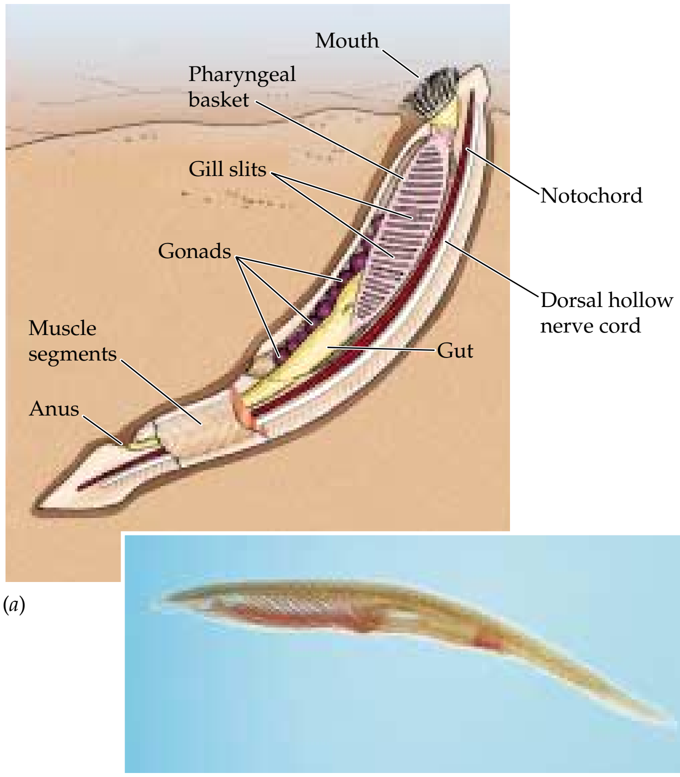
There are three major urochordate groups: ascidians, thaliaceans, and larvaceans. More than 90 percent of the known species of tunicates are *ascidians* (sea squirts). Individual sea squirts range in size from less than 1 mm to 60 cm in length, but colonies may measure several meters across. The baglike body of an adult ascidian is enclosed in a tough tunic that is secreted by epidermal cells. The tunic is composed of proteins and a complex polysaccharide. Much of the body is occupied by a large pharyngeal basket lined with cilia, whose beating moves water through the animal (Figure 34.6*a*).

Thaliaceans (salps and others) float in tropical and subtropical oceans at all depths down to 1,500 meters (Figure 34.6*b*). They live singly or in chainlike colonies up to several meters long. *Larvaceans* are solitary planktonic animals usually less than 5 mm long. They retain their notochords and nerve cords throughout their lives.

The 25 species of **lancelets** (subphylum **Cephalochordata**) are small, fishlike animals that rarely exceed 5 cm in length. Their notochord extends the entire length of the body throughout their lives. Lancelets live partly buried in soft marine sediments. They extract small prey from the water with their pharyngeal baskets (Figure 34.7).

A jointed vertebral column replaced the notochord in vertebrates

In another chordate lineage, the enlarged pharyngeal basket came to be used to extract prey from mud. This lineage gave rise to the **vertebrates** (subphylum **Vertebrata**) (Figure 34.8). Vertebrates take their name from the jointed, dorsal **vertebral column** that replaced the notochord as their primary sup-



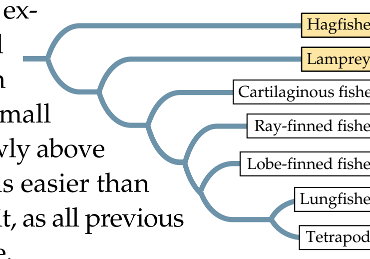
34.7 Lancelets (*a*) The internal structure of a lancelet. Note the large pharyngeal basket with gill slits. (*b*) This lancelet, which is about 6 cm long, has been excavated from the sediment to show its entire body.

port. The vertebrate body plan (Figure 34.9) can be characterized as follows:

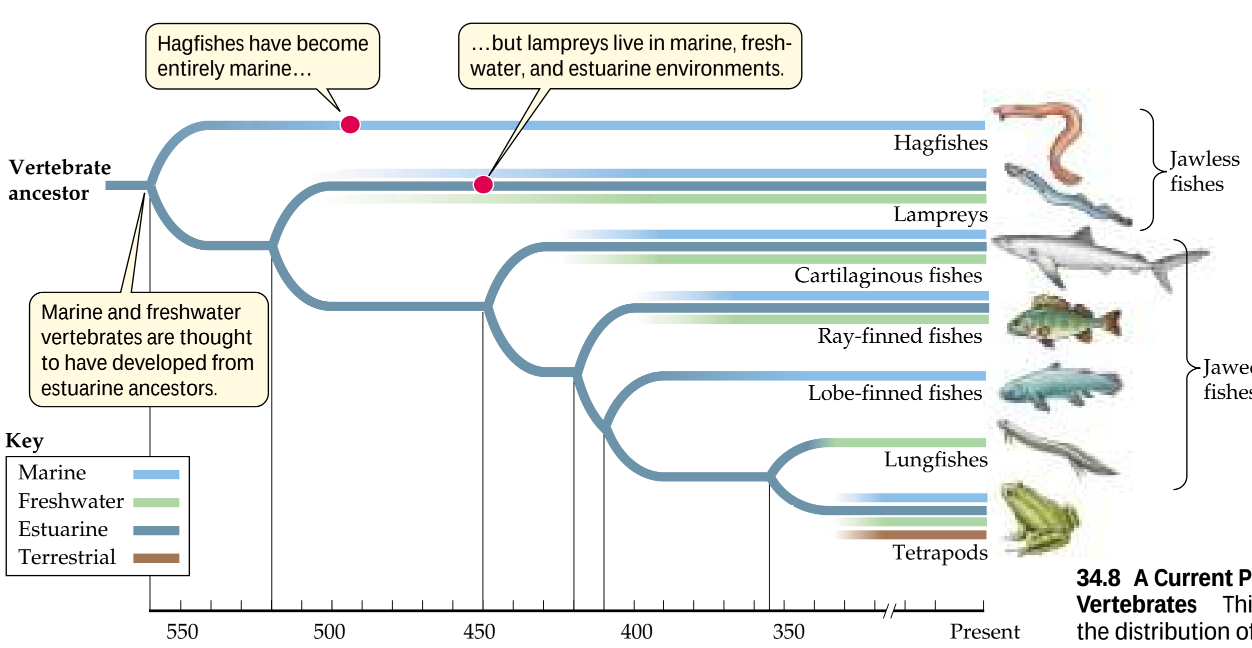
- A rigid *internal skeleton*, with the vertebral column as its anchor, that provides support and mobility
- Two pairs of *appendages* attached to the vertebral column
- An anterior *skull* with a large *brain*
- Internal organs suspended in a large *coelom*
- A well-developed *circulatory system*, driven by contractions of a ventral *heart*

The ancestral vertebrates lacked jaws. They probably swam over the bottom, sucking up mud and straining it through the pharyngeal basket to extract microscopic food particles. The vascularized tissues of the basket also served a gas-exchange function. These animals gave rise to the jawless fishes.

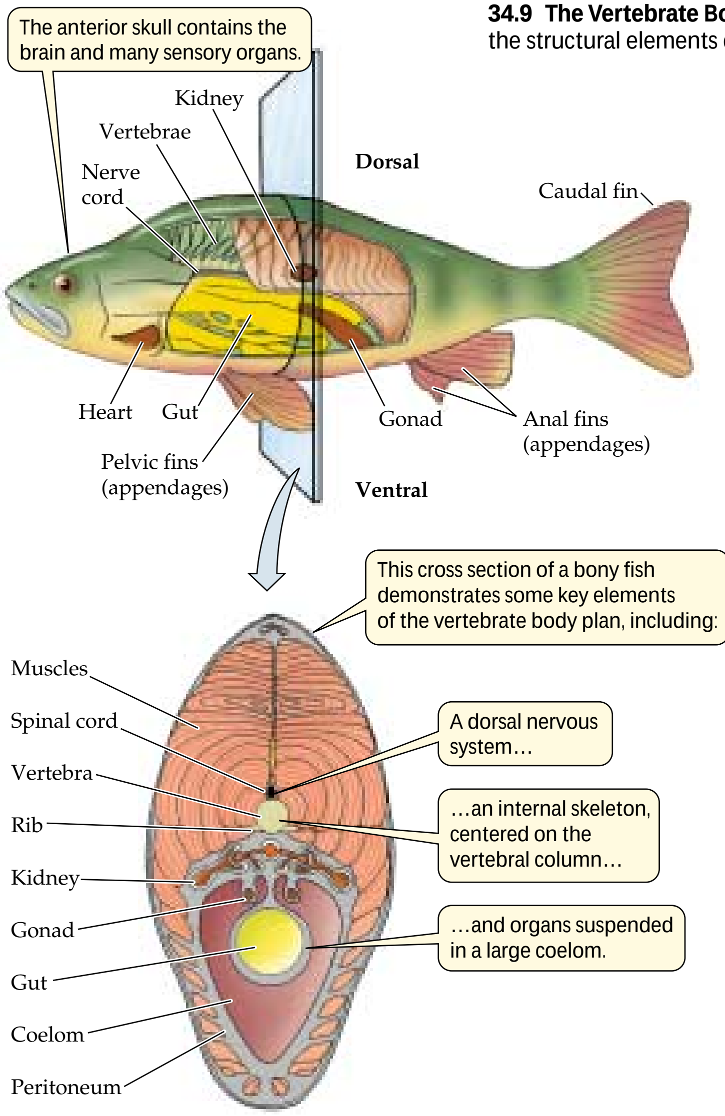
One group of jawless fishes, called **ostracoderms** ("shell-skinned"), evolved a bony external armor that protected them from predators. With their heavy armor, these small fish could safely swim slowly above the substratum, which was easier than having to burrow through it, as all previous sediment feeders had done.



Jawless fishes could attach to dead organisms and use suction created by the pharynx to pull fluids and partly decomposed tissues into the mouth. Hagfishes and lampreys, the only jawless fishes to survive beyond the Devonian, feed on both dead and living organisms in this way (Figure 34.10). These fishes, often placed in the class **Agnatha**, have tough skins instead of external armor. They lack paired appendages



34.8 A Current Phylogeny of the Vertebrates This phylogeny shows the distribution of lineages over the major types of environments.



34.9 The Vertebrate Body Plan A ray-finned fish is used here to illustrate the structural elements common to all vertebrates.

(fins). The round mouth is a sucking organ with which the animals attach to their prey and rasp at the flesh. The lineages leading to modern hagfishes probably diverged from other groups first (see Figure 34.8). The 60 species of hagfishes are entirely marine, but the 50 species of lampreys live in both fresh and salt water.

Jaws improved feeding efficiency

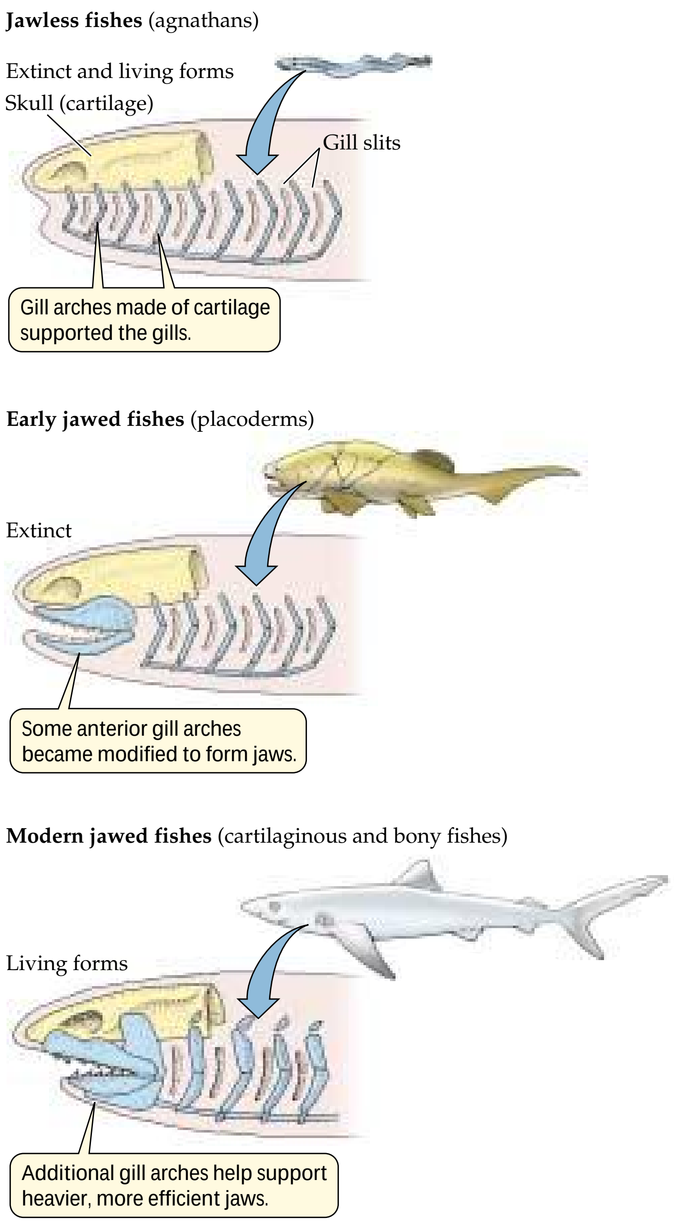
During the Devonian period, many new kinds of fishes evolved in the seas, estuaries, and fresh waters. Although most of these fishes were jawless, in one lineage, some of the skeletal arches that supported the gills evolved into jaws (Figure 34.11). A fish with jaws can grasp and subdue large prey. Further development of jaws and teeth enabled some fishes to chew both soft and hard body parts of prey. Chewing aided chemical digestion and improved the fishes' ability to extract nutrients from their prey.

The dominant early jawed fishes were the heavily armored **placoderms** (class **Placodermi**). Some of these fishes evolved elaborate fins and relatively sleek body forms that improved their ability to maneuver in open water. A few became huge (10 m long) and, together with squids (cephalopod mollusks), were probably the major predators in the Devonian oceans. Despite their early abundance, however, most placoderms had disappeared by the end of the Devonian period; none survived to the end of the Paleozoic era.

34.10 Modern Jawless Fishes (*a*) The Pacific hagfish. (*b*) Two sea lampreys using their large, jawless mouths to suck blood and flesh from a trout. The sea lamprey can live in either fresh or saltwater.

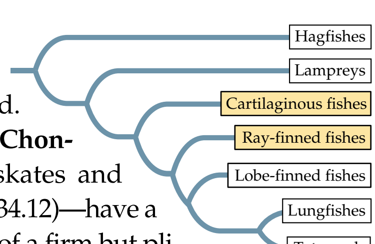
(*a*) *Eptatretus stouti*

(*b*) *Petromyzon marinus*



34.11 Jaws from Gill Arches This series of diagrams illustrates one probable scenario for the evolution of jaws from the anterior gill arches of fishes.

Fins improved mobility



Several other groups of fishes became abundant during the Devonian period. **Cartilaginous fishes** (class **Chondrichthyes**)—the sharks, skates and rays, and chimaeras (Figure 34.12)—have a skeleton composed entirely of a firm but pliable material called *cartilage*. Their skin is flexible and leathery, sometimes bearing scales that give it the consistency of sandpaper.

Cartilaginous fishes control their movement with pairs of unjointed appendages called *fins:* a pair of pectoral fins just behind the gill slits and a pair of pelvic fins just in front of the anal region (see Figure 34.9). A dorsal median fin stabilizes the fish as it moves. Sharks move forward by means of lateral undulations of their bodies and tail fins. Skates and rays propel themselves by means of vertical undulating movements of their greatly enlarged pectoral fins.

Most sharks are predators, but some feed by straining plankton from the water. The world's largest fish, the whale shark (*Rhincodon typhus*), is a filter feeder. It may grow to more than 12 meters in length and weigh more than 12,000 kilograms. Most skates and rays live on the ocean floor, where they feed on mollusks and other invertebrates buried in the sediments. Nearly all cartilaginous fishes live in the oceans, but a few are estuarine or migrate into lakes and rivers. One group of stingrays is found only in river systems of South America. The chimaeras are found in deep ocean waters and are seen less often than the sharks and rays.

Swim bladders allowed control of buoyancy

Ray-finned fishes (class **Actinopterygii**) have internal skeletons of calcified, rigid bone rather than flexible cartilage. The outer surface of most species of ray-finned fishes is covered with flat, thin, lightweight scales that provide some protection or enhance their movement through the water.

The gills of ray-finned fishes open into a single chamber covered by a hard flap. Movement of the flap improves the flow of water over the gills, where gas exchange takes place. Early ray-finned fishes also evolved gas-filled sacs that supplemented the action of the gills in respiration. These features enabled early ray-finned fishes to live where oxygen was periodically in short supply, as it often is in freshwater environments. The lunglike sacs evolved into *swim bladders*, which function as organs of buoyancy in most ray-finned fishes today. By adjusting the amount of gas in its swim bladder, a fish can control the depth at which it is suspended in the water without expending energy.

Ray-finned fishes radiated during the Tertiary into about 24,000 species, encompassing a remarkable variety of sizes, shapes, and lifestyles (Figure 34.13). The smallest are less than 1 cm long as adults; the largest weigh up to 900 kilograms. Ray-finned fishes exploit nearly all types of aquatic food sources. In the oceans they filter plankton from the water, rasp algae from rocks, eat corals and other colonial invertebrates, dig invertebrates from soft sediments, and prey upon virtually all other fishes. In fresh water they eat plankton, devour insects of all aquatic orders, eat fruits that fall into the water in flooded forests, and prey on other aquatic vertebrates and, occasionally, terrestrial vertebrates.

(*a*) *Triaenodon obesus*

(*b*) *Trygon pastinaca*

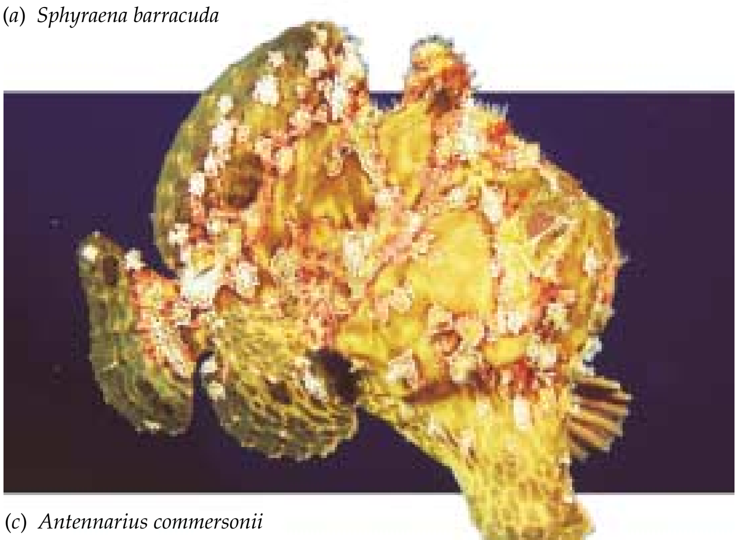
(*c*) *Chimaera* sp.

34.12 Cartilaginous Fishes (*a*) Most sharks, such as this whitetip reef shark, are active marine predators. (*b*) Skates and rays, represented here by a stingray, feed on the ocean bottom. Their modified pectoral fins are used for propulsion. (*c*) A chimaera, or ratfish. These deep-ocean fish often possess poisonous dorsal fins.

34.13 Diversity among Ray-Finned Fishes (*a*) The barracuda has the large teeth and powerful jaws of a predator. (*b*) The coral grouper lives on tropical coral reefs. (*c*) Commerson's frogfish can change its color over a range from pale yellow to orange-brown to deep red, thus enhancing its camouflage abilities. (*d*) This weedy sea dragon is difficult to see when it hides in vegetation. It is a larger relative of the more familiar seahorse.

(*a*) *Sphyraena barracuda*

(*b*) *Plectorhinchus chaetodonoides*



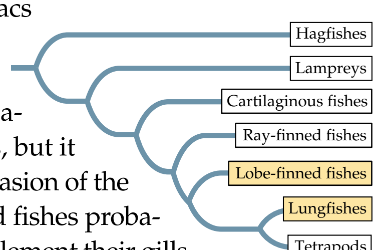
(*c*) *Antennarius commersonii*

(*d*) *Phyllopteryx taeniolatus*

Some fishes live buried in soft sediments, capturing passing prey or emerging at night to feed. Many fishes are solitary, but in open water others form large aggregations called *schools*. Many fishes perform complicated behaviors by means of which they maintain schools, build nests, court and choose mates, and care for their young.

Although ray-finned fishes can readily control their positions in open water, their eggs tend to sink. A few species produce small eggs that are buoyant enough to complete their development in the open water. However, most marine fishes move to food-rich shallow waters to lay their eggs, which is why coastal waters and estuaries are so important in the life cycles of many species. Some, such as salmon, actually abandon salt water when they breed, ascending rivers to spawn in freshwater streams and lakes.

Colonizing the Land: Obtaining Oxygen from the Air



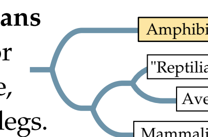
The evolution of lunglike sacs in fishes appears to have been a response to the inadequacy of gills for respiration in oxygen-poor waters, but it also set the stage for the invasion of the land. Some early ray-finned fishes probably used their lungs to supplement their gills when oxygen levels in the water were low, as lungfishes do today. This ability would also have allowed them to leave the water temporarily and breathe air when pursued by predators unable to do so. But with their unjointed fins, these fishes could only flop around on land, as most fish out of water do today. Changes in the structure of the fins allowed these fishes to move on land.

The **lobe-finned fishes** (class **Actinistia**) were the first lineage to evolve jointed fins. Lobe-fins flourished from the Devonian period until about 65 million years ago, when they were thought to have become extinct. However, in 1938, a living lobe-fin was caught by commercial fishermen off South Africa. Since that time, several dozen specimens of this extraordinary fish, *Latimeria chalumnae*, have been collected. *Latimeria*, a predator on other fish, reaches a length of about 1.8 meters and weighs up to 82 kilograms (Figure 34.14*a*). Its skeleton is mostly composed of cartilage, not bone. A second species, *L. menadoensis*, was discovered in 1998 off the Indonesian island of Sulawesi.

Lungfishes (class **Dipnoi**) were important predators in shallow-water habitats in the Devonian, but most lineages died out. The three surviving species live in stagnant swamps and muddy waters in the Southern Hemisphere, one each in South America, Africa, and Australia (Figure 34.14*b*). Lungfishes have both gills and lungs. When ponds dry up, they can burrow deep into the mud and survive for many months in an inactive state.

It is believed that descendants of some lungfishes began to use terrestrial food sources, became more fully adapted to life on land, and eventually evolved to become the **tetrapods**—the four-legged amphibians, reptiles, birds, and mammals.

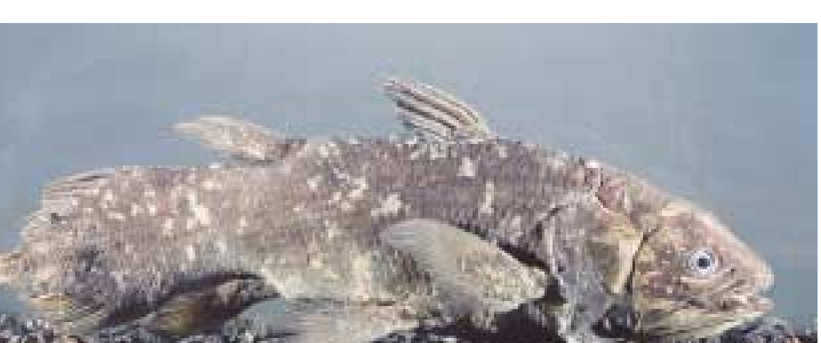
Amphibians invaded the land



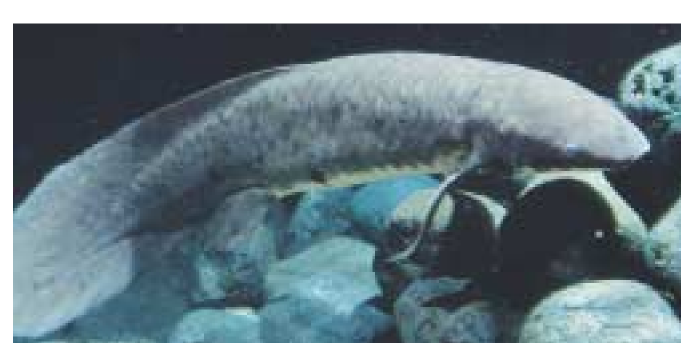
During the Devonian period, **amphibians** (class **Amphibia**) arose from an ancestor they shared with lungfishes. In this lineage, stubby, jointed fins evolved into walking legs. The basic design of these legs has remained largely unchanged throughout the evolution of terrestrial vertebrates.

The Devonian predecessors of amphibians were probably able to crawl from one pond or stream to another by slowly pulling themselves along on their finlike legs, as do some modern species of catfishes. They gradually evolved the ability to live in swamps and, eventually, on dry land. Modern

34.14 Fishes with Jointed Fins (*a*) This lobe-fin fish, found in deep waters of the Indian Ocean, represents one of two surviving species of a lineage that was once thought to be extinct. (*b*) All surviving lungfish lineages live in the Southern Hemisphere.



(*a*) *Latimeria chalumnae*



(*b*) *Neoceratodus forsteri*

(*a*) *Dermophis mexicanus*

(*b*) *Gyrinophilus porphyriticus*

(*c*) *Scaphiophryne gottlebei*

34.15 Diversity among the Amphibians (*a*) Burrowing caecilians superficially look more like worms than amphibians. (*b*) A Kentucky spring salamander. (*c*) This rare frog species was discovered in a national park on the island of Madagascar.

amphibians have small lungs, and most species exchange gases through their skins as well. Most terrestrial species are confined to moist environments because they lose water rapidly through their skins when exposed to dry air, and because they require water for reproduction.

About 4,500 species of amphibians live on Earth today, many fewer than the number known only from fossils. Living amphibians belong to three orders (Figure 34.15): the wormlike, limbless, tropical, burrowing caecilians (order Gymnophiona), the frogs and toads (order Anura, which means "tailless"), and the salamanders (order Urodela, which means "tailed"). Most species of frogs and toads live in tropical and warm temperate regions, although a few are found at very high latitudes and altitudes. Some toads have tough skins that enable them to live for long periods of time in dry places. Salamanders are most diverse in temperate regions, but many species are found in cool, moist environments in Central American mountains. Many salamanders that live in rotting logs or moist soil lack lungs. They exchange gases entirely through the skin and mouth lining. Amphibians are the focus of much attention today because populations of many species are declining rapidly (see Chapter 1).

Most species of amphibians live in water at some time in their lives. In the typical amphibian life cycle, part or all of the adult stage is spent on land, but adults return to fresh water to lay their eggs (Figure 34.16). Amphibian eggs can survive only in moist environments because they are enclosed within delicate envelopes that cannot prevent water loss in dry conditions. The fertilized eggs of most species give rise to larvae that live in water until they undergo metamorphosis to become terrestrial adults. Some amphibians, however, are entirely aquatic, never leaving the water at any stage of their lives. Others are entirely terrestrial, laying their eggs in moist places on land and skipping the aquatic larval stage.

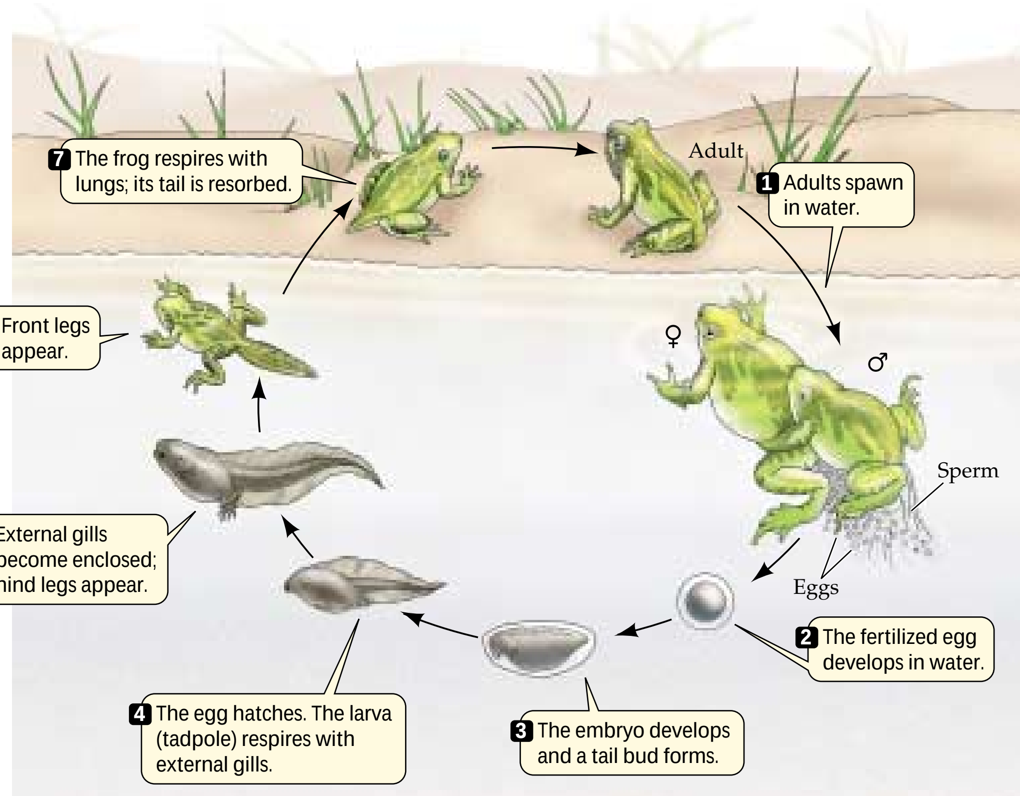
Amniotes colonized dry environments

Two morphological changes contributed to the ability of one lineage of tetrapods to control water loss and, therefore, to exploit a wide range of terrestrial habitats:

- Evolution of an egg with a shell that is relatively impermeable to water
- A combination of traits that included a tough skin impermeable to water and kidneys that could excrete concentrated urine

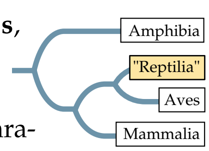
The vertebrates that evolved both of these traits are called **amniotes**. They were the first vertebrates to become widely distributed over the terrestrial surface of Earth.

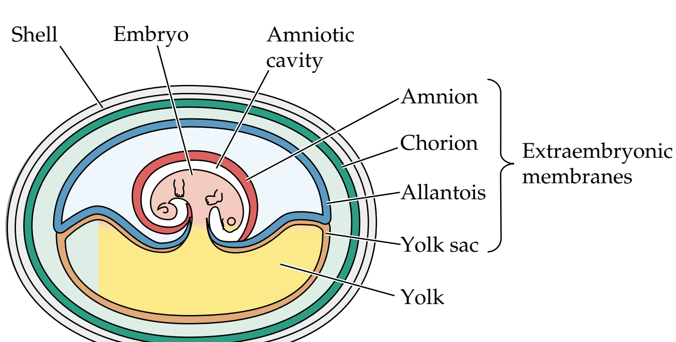
The amniote egg has a leathery or a brittle, calcium-impregnated shell that retards evaporation of the fluids inside but permits O_2 and CO_2 to pass through. Such an egg does not require a moist environment and can be laid anywhere. Within the shell and surrounding the embryo are membranes that protect the embryo from desiccation and assist its respiration and excretion of waste nitrogen. The egg also stores large quantities of food as *yolk*, permitting the embryo to attain a relatively advanced state of development before it hatches and must feed itself (Figure 34.17).



34.16 In and Out of the Water Most stages in the life cycle of temperate-zone frogs take place in water. The aquatic tadpole is transformed into a terrestrial adult through metamorphosis.

An early amniote lineage, the **reptiles**, arose from a tetrapod ancestor in the Carboniferous period (Figure 34.18). The class "Reptilia," as we use the term here, is a paraphyletic group because some reptiles (crocodilians) are in fact more closely related to the birds than they are to lizards, snakes, and turtles (see Figure 25.8). However, because all members of "Reptilia" are structurally similar, it serves as a convenient group for discussing the characteristics of amniotes. Therefore, we use the traditional classification of "Reptilia" as a basis for our discussion while recognizing that, technically, the birds should be included within it.





34.17 An Egg for Dry Places The evolution of the amniote egg, with its shell, four extraembryonic membranes, and embryo-nourishing yolk, was a major step in the colonization of the terrestrial environment.

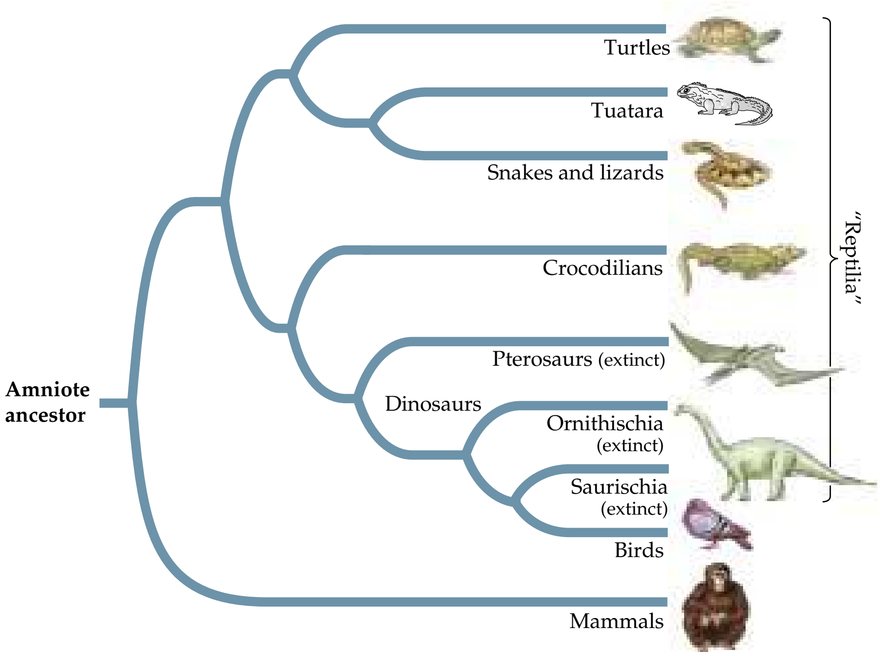
About 6,000 species of reptiles live today. Most reptiles do not care for their eggs after laying them. In some species, the eggs do not develop shells, but are retained inside the female's body until they hatch. Some of these species evolved a structure called the *placenta* that nourishes the developing embryos.

The skin of a reptile is covered with horny scales that greatly reduce loss of water from the body surface. These scales, however, make the skin unavailable as an organ of gas exchange. In reptiles, gases are exchanged almost entirely by the lungs, which are proportionally much larger in surface area than those of amphibians. A reptile forces air into and out of its lungs by bellows-like movements of its ribs. The reptilian heart is divided into three and one-half or four chambers that partially separate oxygenated from unoxygenated blood. With this type of heart, reptiles can generate higher blood pressures than amphibians, which have three-chambered hearts, and can sustain higher levels of muscular activity.

Reptilian lineages diverged

The lineages leading to modern reptiles began to diverge about 250 mya. One lineage that has changed very little over the intervening millenia is the turtles (subclass **Testudines**). Turtles have a combination of ancestral traits and highly specialized characteristics that they do not share with any other vertebrate group. For this reason, their phylogenetic relationships are uncertain.

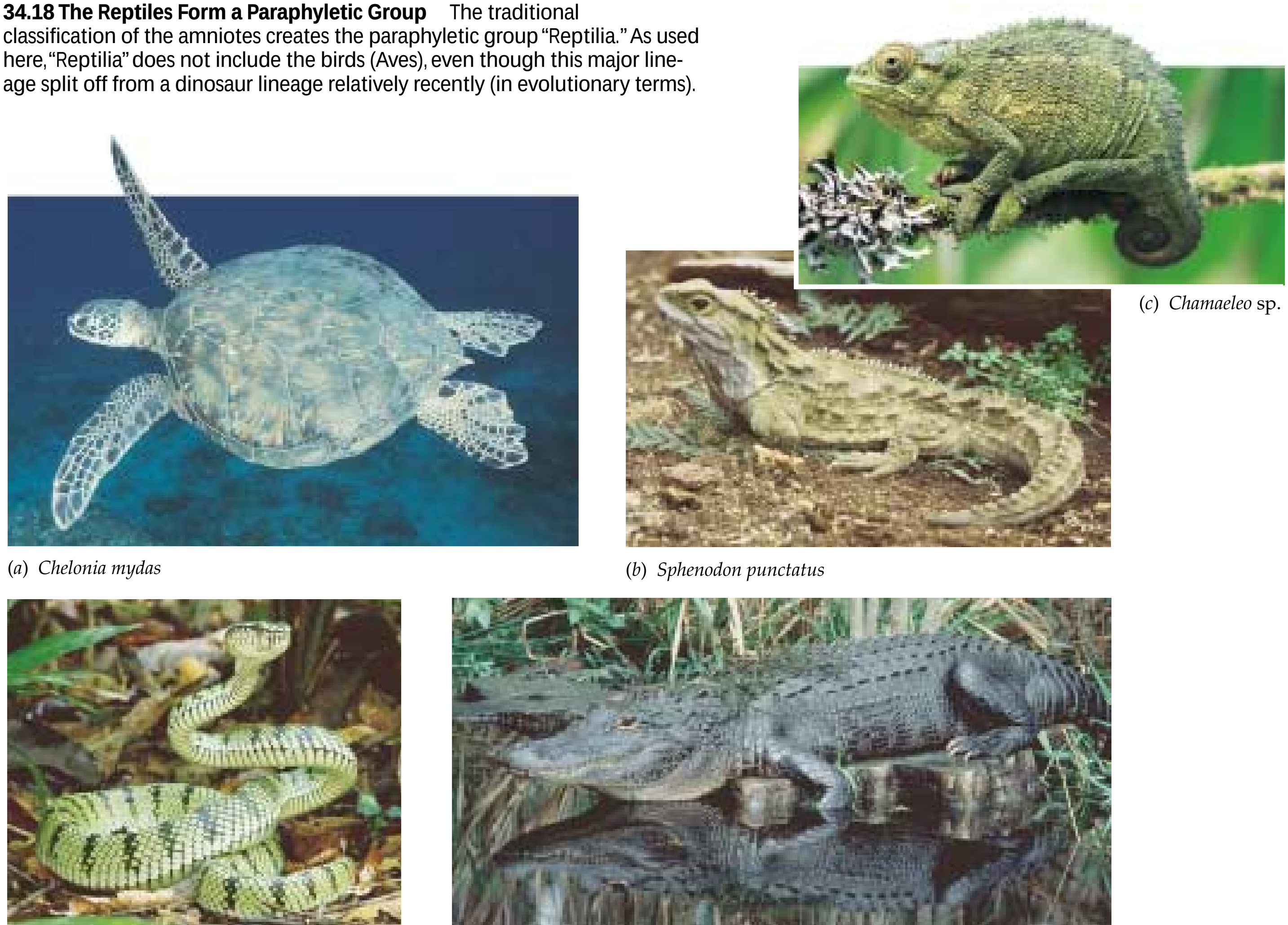
The dorsal and ventral bony plates of modern turtles and tortoises form a shell into which the head and limbs can be



34.18 The Reptiles Form a Paraphyletic Group The traditional classification of the amniotes creates the paraphyletic group "Reptilia." As used here, "Reptilia" does not include the birds (Aves), even though this major lineage split off from a dinosaur lineage relatively recently (in evolutionary terms).

withdrawn (Figure 34.19*a*). Most turtles live in lakes and ponds, but tortoises are terrestrial; some live in deserts. Sea turtles spend their entire lives at sea except when they come ashore to lay eggs. All seven species of sea turtles are endangered. A few species of turtles and tortoises are carnivores, but most species are omnivores that eat a variety of aquatic and terrestrial plants and animals.

The subclass **Squamata** includes lizards and snakes as well as the amphisbaenians (a group of legless, wormlike, burrowing animals with greatly reduced eyes). The tuataras (subclass **Sphenodontida**) are a sister group to the lizards and snakes. Sphenodontids were diverse dur-



(*a*) *Chelonia mydas*

(*b*) *Sphenodon punctatus*

(*c*) *Chamaeleo* sp.

(*d*) *Trimeresurus sumatranus*

(*e*) *Alligator mississippiensis*

34.19 Reptilian Diversity (*a*) The green sea turtle is widely distributed in tropical oceans. (*b*) This tuatara represents one of only two surviving species in a lineage that separated from lizards long ago. (*c*) The African chameleon, a lizard, has large eyes that move independently in their sockets. (*d*) This venomous Sumatran pit viper is coiled to strike. (*e*) Alligators live in warm temperate environments in China and, like this one, in the southeastern United States.

ing the Mesozoic era, but today they are represented only by two species restricted to a few islands off the coast of New Zealand (Figure 34.19*b*). Tuataras superficially resemble lizards, but differ from them in tooth attachment and several internal anatomical features.

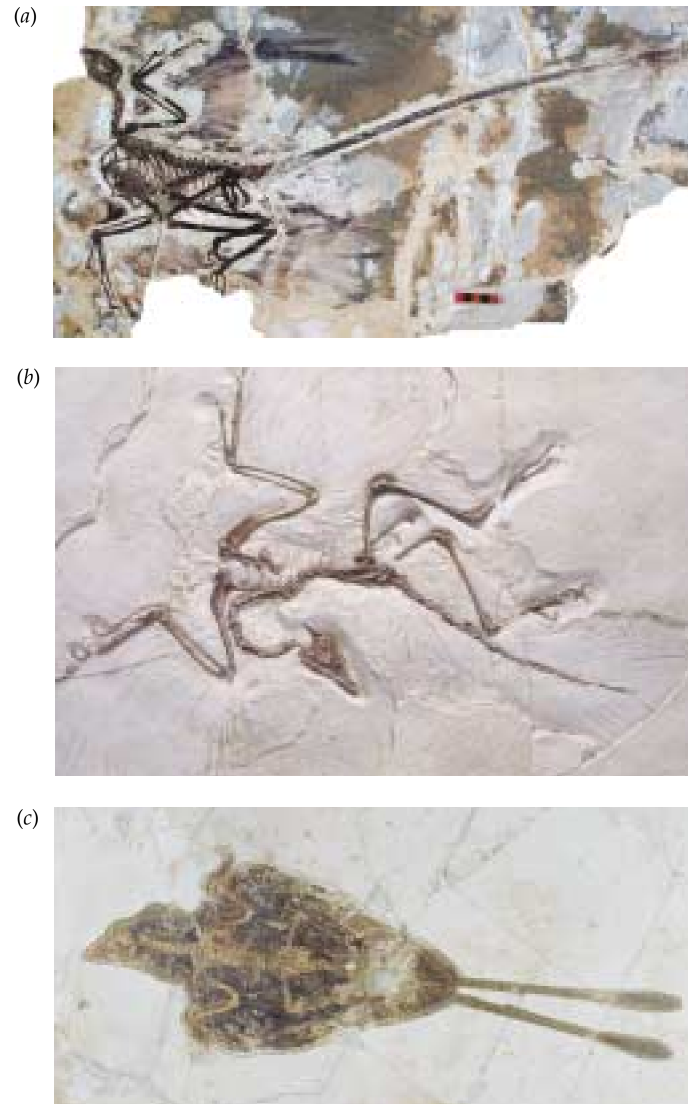
Most lizards are insectivores, but some are herbivores; a few prey on other vertebrates. The largest lizards, growing as long as 3 meters, are certain monitor lizards (such as the Komodo dragon) that live in the East Indies. Most lizards walk on four limbs (Figure 34.19*c*), but some are limbless, as are all snakes, which are descendants of burrowing lizards.

All snakes are carnivores; many can swallow objects much larger than themselves. This is the mode of feeding of the largest snakes, the pythons, which can grow to more than 10 meters long. Several snake lineages evolved a combination of venom glands and the ability to inject venom rapidly into their prey (Figure 34.19*d*).

A separate diverging lineage led to the crocodilians (subclass **Crocodylia**) and to the dinosaurs. The crocodilians—crocodiles, caimans, gharials, and alligators—are confined to tropical and warm temperate environments (Figure 34.19*e*). Crocodilians spend much of their time in water, but they build nests on land or on floating piles of vegetation. The eggs are warmed by heat generated by decaying organic matter that the parents place in the nest. Typically the female guards the eggs until they hatch. All crocodilians are carnivorous; they eat vertebrates of all classes, including large mammals.

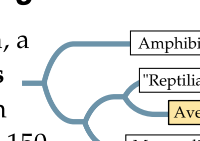
The **dinosaurs** rose to prominence about 215 mya and dominated terrestrial environments for about 150 million years. During that time, virtually all terrestrial animals more than a meter in length were dinosaurs. Some of the largest dinosaurs weighed up to 100 tons. Many were agile and could run rapidly. The ability to breathe and run simultaneously, which we take for granted, was a major innovation in the evolution of terrestrial vertebrates. Not until the evolution of the lineages leading to the mammals, dinosaurs, and birds did the legs assume vertical positions directly under the body, which reduced the lateral forces on the body during locomotion. Special muscles that enabled the lungs to be filled and emptied while the limbs moved also evolved. We can infer the existence of such muscles in dinosaurs from the structure of the vertebral column in fossils and the capacity of many dinosaurs for bounding, bipedal (two-legged) locomotion.

Several fossil dinosaurs discovered recently in early Cretaceous deposits in Liaoning Province, in northeastern China, clearly show that in some small predatory dinosaurs, the scales had been highly modified to form feathers. One of these dinosaurs, *Microraptor gui*, had feathers on all four limbs, and those feathers were structurally similar to those of modern birds (Figure 34.20*a*).



34.20 Mesozoic Birds and Their Ancestors Fossil remains demonstrate the probable evolution of birds from reptilian ancestors. (*a*) *Microraptor gui*, a feathered dinosaur from the early Cretaceous (about 140 mya). (*b*) *Archaeopteryx*, the oldest known bird. (*c*) The elongated tail feathers of a male *Confuciusornis sanctus* ("sacred bird of Confucius") fossil suggest that the males used them in courtship displays.

Birds: More Feathers and Better Flight



During the Mesozoic era, about 175 mya, a dinosaur lineage gave rise to the **birds** (subclass **Aves**). The oldest known avian fossil, *Archaeopteryx*, which lived about 150 mya, had teeth, unlike modern birds, but was covered with feathers that are virtually identical to those of modern birds. It also had well-developed wings, a long tail (Figure 34.20*b*), and a furcula, or "wishbone," to which some of the flight muscles were probably attached. *Archaeopteryx* had clawed fingers on its forelimbs, but it also had typical perching bird claws, suggesting that it lived in trees and shrubs and used the fingers to assist it in clambering over branches. Because the avian lineage separated from other reptiles long before *Archaeopteryx* lived, existing data are insufficient to identify the ancestors of birds with certainty. Most paleontologists believe that birds evolved from feathered terrestrial bipedal dinosaurs that used their forelimbs for capturing prey.

Many remains of other early birds have been discovered in 120–125-million-year-old fossil beds in northeastern China. One of these birds, *Confuciusornis sanctus*, is known from hundreds of complete specimens. The males had greatly elongated tail feathers (Figure 34.20*c*), which they probably used in communal courtship displays. Large numbers of individuals have been found together, as would be expected if many males assembled on communal display grounds, as some birds do today.

Birds range in size from the 2-gram bee hummingbird of the West Indies to the 150-kilogram ostrich (Figure 34.21). Some flightless birds of Madagascar and New Zealand known from fossils were even larger. These birds were exterminated by humans soon after they colonized those islands. There are about 9,600 species of living birds, more than in any other major vertebrate group except ray-finned fishes.

As a group, birds eat almost all types of animal and plant material. A few aquatic species have bills modified for filtering small food particles from water. Insects are the most important dietary items for terrestrial species. Birds are major predators of flying insects during the day, and some species exploit that food source at night. In addition, birds eat fruits and seeds, nectar and pollen, leaves and buds, carrion, and other vertebrates. By eating the fruits and seeds of plants, birds serve as major agents of seed dispersal.

The feathers developed by some dinosaurs may originally have had thermoregulatory or display functions. Birds also use them for flying. Large quills that arise from the skin of the fore-

34.21 Diversity among the Birds (*a*) Penguins such as these gentoos are widespread in the cold waters of the Southern Hemisphere. They are expert swimmers, although they have lost the ability to fly. (*b*) Perching birds, represented here by a male northern cardinal, are the most species-rich of all the bird lineages. (*c*) Parrots are a diverse group of birds, especially in the Tropics of Asia, South America, and Australia. This king parrot is one member of Australia's rich parrot fauna. (*d*) The flightless ostrich is the largest bird species in existence today.

(*a*) *Pygoscelis papua*

(*b*) *Cardinalis cardinalis*

(*c*) *Alisterus scapularis*

(*d*) *Struthio camelus*

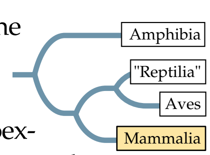
limbs create the flying surfaces of wings. Other strong feathers sprout like a fan from the shortened tail and serve as stabilizers during flight. The feathers that cover the body, along with an underlying layer of down feathers, provide insulation.

The bones of birds are modified for flight. They are hollow and have internal struts for strength. The *sternum* (breastbone) forms a large, vertical keel to which the flight muscles are attached. These muscles pull the wings downward during the main propulsive movement in flight. Flight is metabolically expensive. A flying bird consumes energy at a rate about 15–20 times faster than a running lizard of the same weight! Because birds have such high metabolic rates, they generate large amounts of heat. They control the rate of heat loss using their feathers, which may be held close to the body or elevated to alter the amount of insulation they provide.

The brain of a bird is larger in proportion to its body than a lizard or crocodile brain, primarily because the cerebellum, the center of sight and muscular coordination, is enlarged.

Most birds lay their eggs in a nest, where they are warmed by heat from an adult that sits on them. Because birds have such high body temperatures, the eggs of most species hatch within a few weeks. The offspring of many species are *altricial* (hatch at a relatively helpless stage) and are fed for some time by their parents. The young of other bird species, such as chickens, sandpipers, and ducks, are *precocial* (can feed themselves shortly after hatching). Adults of nearly all species attend their offspring for some time, warning them of and protecting them from predators, protecting them from bad weather, leading them to good foraging places, and feeding them.

The Origin and Diversity of Mammals



Mammals (class **Mammalia**) appeared in the early part of the Mesozoic era, about 225 million years ago, branching from a lineage of mammal-like reptiles. Small mammals coexisted with reptiles and dinosaurs for at least 150 million years. After the large reptiles and dinosaurs disappeared during the mass extinction at the close of the Mesozoic era, mammals increased dramatically in numbers, diversity, and size. Today, mammals range in size from tiny shrews and bats weighing only about 2 grams to the endangered blue whale, which measures up to 33 meters long and weighs up to 160,000 kilograms—the largest animal ever to live on Earth.

Skeletal simplification accompanied the evolution of early mammals from their larger reptilian ancestors. During mammalian evolution, some bones from the lower jaw were incorporated into the middle ear, leaving a single bone in the lower jaw. The number of bones in the skull also decreased. The bulk of both the limbs and the bony girdles from which they are suspended was reduced. Mammals have far fewer, but more highly differentiated, teeth than reptiles do. Differences in the number, type, and arrangement of teeth in mammals reflect their varied diets.

Skeletal features are readily preserved as fossils, but the soft parts of animals are seldom fossilized. Therefore, we do not know when mammalian features such as mammary glands, sweat glands, hair, and a four-chambered heart evolved. Mammals are unique among animals in supplying their young with a nutritive fluid (milk) secreted by mammary glands. Mammalian eggs are fertilized within the female's body, and the embryos undergo a period of development, called *gestation*, within a specialized organ, the *uterus*, prior to being born. In many species, the embryos are connected to the uterus and nourished by a placenta. In addition, mammals have a protective and insulating covering of hair, which is luxuriant in some species but has been almost entirely lost in whales, dolphins, and humans. In whales and dolphins, thick layers of insulating fat (blubber) replace hair as a heat-retention mechanism. Clothing assumes the same role for humans. The approximately 4,000 species of living mammals are divided into two major subclasses: Prototheria and Theria. The subclass **Prototheria** contains a single order, the Monotremata, with a total of three species, which are found only in Australia and New Guinea. These mammals, the duck-billed platypus and the spiny anteaters, or echidnas, differ from other mammals in lacking a placenta, laying eggs, and having legs that poke out to the side (Figure 34.22). Monotremes supply milk for their young, but they have no nipples on their mammary glands; rather, the milk simply oozes out and is lapped off the fur by the offspring.

Members of the other subclass, **Theria**, are further divided into two groups. In most species of the first group, the **Marsupialia**, females have a ventral pouch in which they carry and feed their offspring (Figure 34.23*a*). Gestation in marsupials is short; the young are born tiny but with well-developed forelimbs, with which they climb to the pouch. They attach to a nipple, but cannot suck. The mother ejects milk into the tiny offspring until they grow large enough to suckle. Once her offspring have left the uterus, a female marsupial may become sexually receptive again. She can then carry fertilized eggs capable of initiating development and replacing the offspring in her pouch should something happen to them.

There are about 240 living species of marsupials. At one time marsupials were found on all continents, but today the majority of species are restricted to the Australian region, with a modest representation in South America (Figure 34.23*b*). One species, the Virginia opossum, is widely distributed in the United States. Marsupials radiated to become terrestrial herbivores, insectivores, and carnivores, but no marsupial species live in the oceans or can fly, although some are gliders. The largest living marsupial is the red kangaroo of Australia (Figure 34.23*a*), which weighs up to 90 kilo-

(*a*) *Tachyglossus aculeata*

(*b*) *Ornithorhynchus anatinus*

34.22 Monotremes (*a*) The short-beaked echidna is one of the two surviving species of echidnas. (*b*) The duck-billed platypus is the other surviving monotreme species.

grams. Much larger marsupials existed in Australia until they were exterminated by humans soon after they reached the continent (about 50,000 years ago).

Most living mammals belong to the second therian group, the **eutherians**. (Eutherians are sometimes called *placental mammals*, but this name is not accurate because some marsupials also have placentas.) Eutherians are more developed at birth than are marsupials, and no external pouch houses them after birth. The nearly 4,000 species of eutherians are placed into 16 major groups (Figure 34.24), the largest of which is the rodents (order Rodentia) with about 1,700 species. The next largest group, the bats (order Chiroptera), has about 1,000 species, followed by the moles and shrews (order Insectivora) with slightly more than 400 species.

Eutherians are extremely varied in their form and ecology. Several lineages of terrestrial eutherians subsequently colonized marine environments to become whales, dolphins, seals, and sea lions. Eutherian mammals are—or were, until they were greatly reduced in numbers by humans—the most important grazers and browsers in most terrestrial ecosystems. Grazing and browsing have been an evolutionary force intense enough to select for the spines, tough leaves, and difficult-to-eat growth forms found in many plants—a striking example of coevolution.

Primates and the Origin of Humans

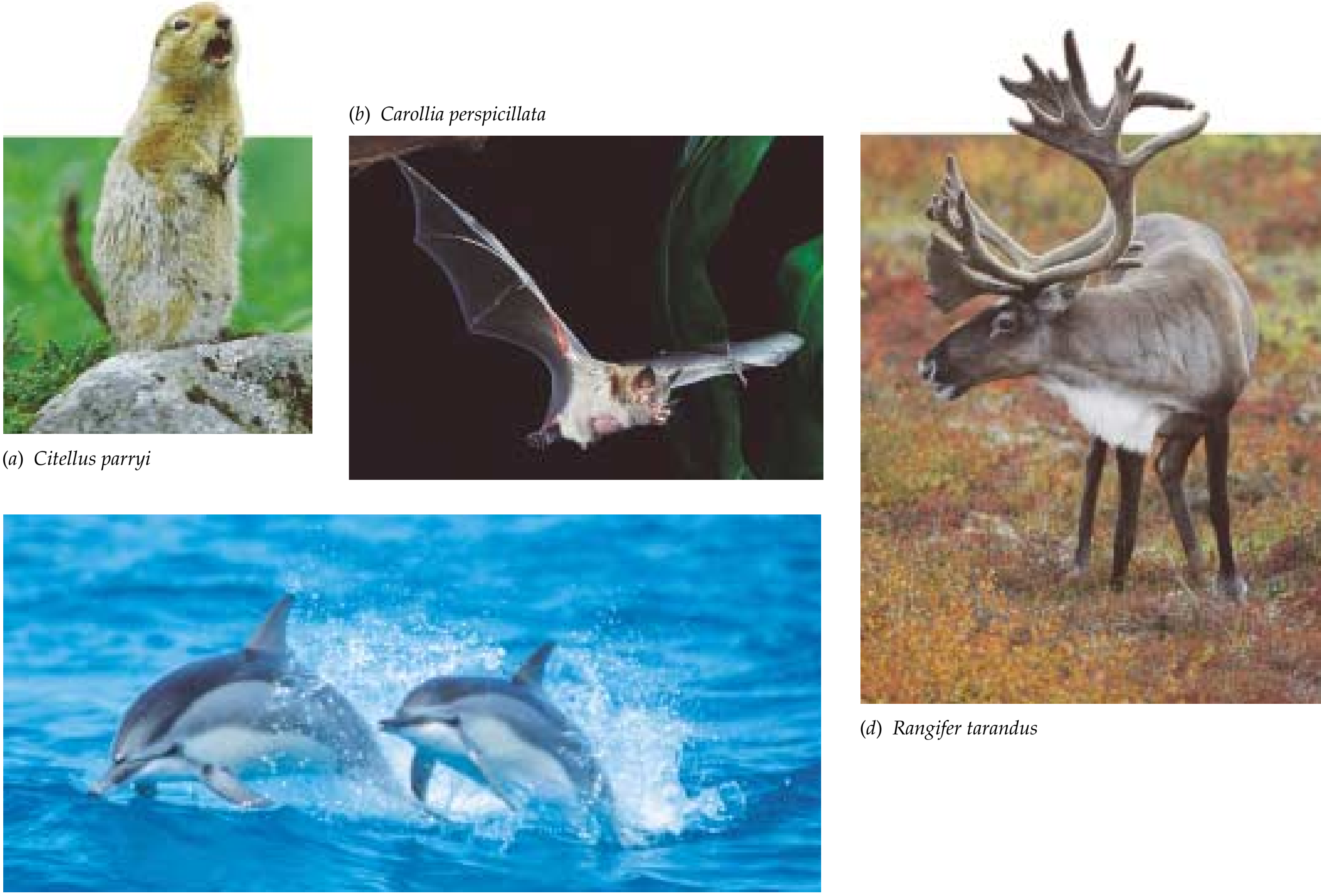
A eutherian lineage that has had dramatic effects on ecosystems worldwide is the **primate** lineage, which has undergone extensive recent evolutionary radiation. Primates probably

(*a*) *Macropus rufus*

(*b*) *Caluromys philander*

(*c*) *Sarcophilus harrisii*

34.23 Marsupials (*a*) Australia's red kangaroos are the largest living marsupials. The marsupial radiation also produced (*b*) arboreal species, such as this South American opossum, and (*c*) carnivores, such as the Tasmanian devil.



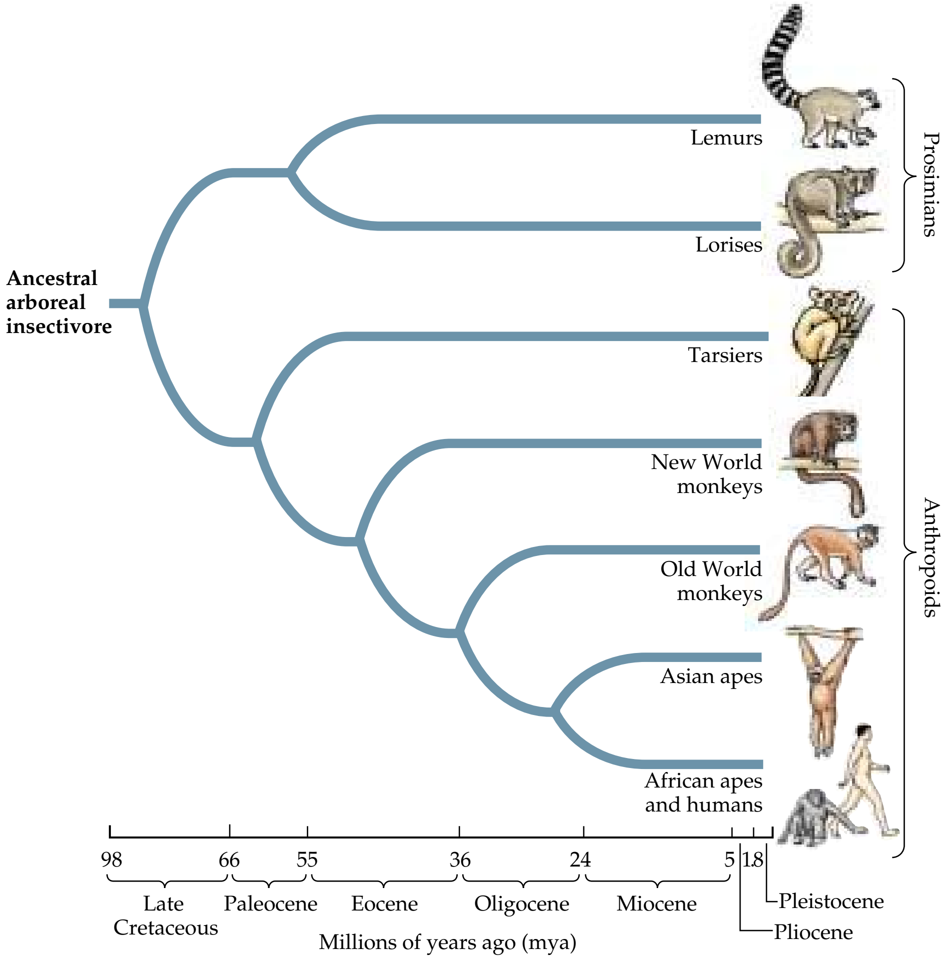
34.24 Diversity among the Eutherians (*a*) The Arctic ground squirrel is one of the many species of small, diurnal rodents found in North America. (*b*) Temperate-zone bats are all insectivores, but many tropical bats, such as this leaf-nosed bat, eat fruit. (*c*) These Hawaiian spinner dolphins represent a eutherian lineage that colonized the marine environment. (*d*) Large hoofed mammals are important herbivores in terrestrial environments. This caribou bull is grazing by himself, although caribou are often seen in huge herds.

descended from small *arboreal* (tree-living) insectivorous mammals early in the Cretaceous period. A nearly complete fossil of an early primate species, *Carpolestes*, from Wyoming, dated at 56 mya, had grasping feet with an opposable big toe that had a nail rather than a claw. Such grasping limbs are one of the major adaptations to arboreal life that distinguish primates from other mammals. However, *Carpolestes* did not have eyes positioned on the front of the face to provide good depth perception, as all modern primates do.

Early in its evolutionary history, the primate lineage split into two main branches, the prosimians and the anthropoids (Figure 34.25). **Prosimians**—lemurs, pottos, and lorises—once lived on all continents, but today they are restricted to Africa, Madagascar, and tropical Asia (Figure 34.26). All of the mainland prosimian species are arboreal and nocturnal. However, on the island of Madagascar, the site of a remarkable prosimian radiation, there are also diurnal and terrestrial species.

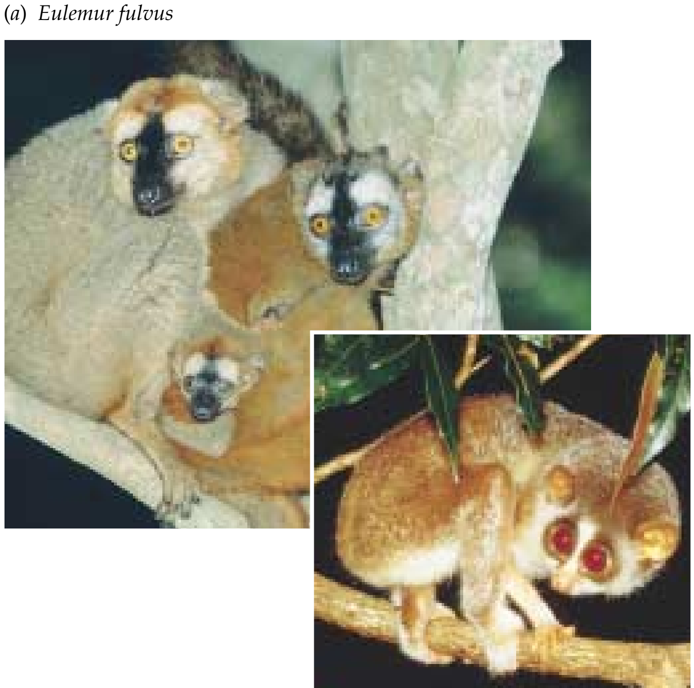
The **anthropoids**—tarsiers, monkeys, apes, and humans—evolved from an early primate lineage about 55 million years ago in Africa or Asia. New World monkeys diverged from Old World monkeys early enough that they could have reached South America from Africa when those two continents were still close to each other. All New World monkeys are arboreal (Figure 34.27*a*). Many of them have long, *prehensile* (grasping) tails with which they can hold onto branches. Many Old World primates are arboreal as well, but a number of species are terrestrial. Some of these species, such as baboons and macaques, live and travel in large groups (Figure 34.27*b*). No Old World primates have prehensile tails.

About 22 million years ago, the lineage that led to modern **apes** separated from the other Old World primates. Between 22 and 5.5 mya, as many as 100 species of apes ranged over Europe, Asia, and Africa. About 9 mya, members of one European ape lineage, *Dryopithecus*, migrated to Africa and became the ancestors of the modern African apes—gorillas and chimpanzees (Figure 34.28*a*,*b*)—and of humans. The Asian apes—gibbons and orangutans (Figure 34.28*c*,*d*)—are a different ape lineage, descendants of *Sirapithecus*.



34.25 A Current Phylogeny of the Primates Too few fossil primates have been discovered to reveal with certainty their evolutionary relationships, but this phylogenetic tree is consistent with the existing evidence.

(*a*) *Eulemur fulvus*



(*b*) *Loris tardigradus*

34.26 Prosimians (*a*) The brown lemur is one of the many lemur species found in Madagascar, where they are part of a unique assemblage of plants and animals. (*b*) The slender loris is found in India. Its large eyes tell us that it is nocturnal.

(*a*) *Leontopithecus rosalia*

(*b*) *Macaca sylvanus*

34.27 Monkeys (*a*) Golden lion tamarins are endangered New World monkeys living in coastal Brazilian rainforests. (*b*) Many Old World species, such as these Barbary macaques, live in social groups. Here two members of a group groom each other.

(*a*) *Gorilla gorilla*

(*b*) *Pan troglodytes*

(*c*) *Hylobates lar*

(*d*) *Pongo pygmaeus*

34.28 Apes (*a*) Gorillas, the largest apes, are restricted to humid African forests. This male is a lowland gorilla. (*b*) Chimpanzees, our closest relatives, are found in forested regions of Africa. (*c*) Gibbons are the smallest of the apes. The common gibbon is found in Asia, from India to Borneo. (*d*) Orangutans live in the forests of Indonesia.

Human ancestors evolved bipedal locomotion

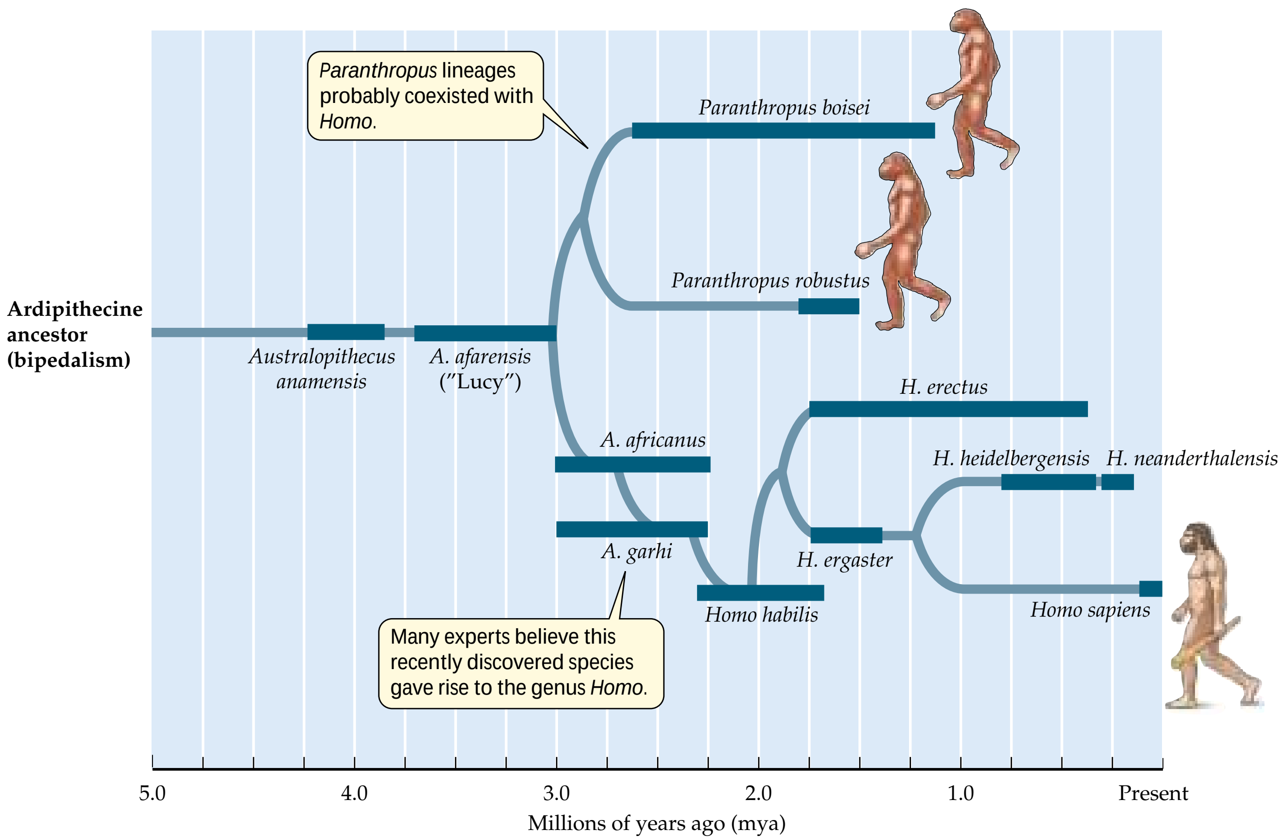
The **hominids**—the lineage that led to humans—separated from other ape lineages about 6 mya in Africa. The earliest protohominids, known as **ardipithecines**, had distinct morphological adaptations for **bipedalism**—locomotion in which the body is held erect and moved exclusively by movements of the hind legs. Bipedal locomotion frees the forelimbs to manipulate objects and to carry them while walking. It also elevates the eyes, enabling the animal to see over tall vegetation to spot predators and prey. At walking rates, bipedal movement is also energetically much more economical than quadrupedal (four-legged) locomotion. All three advantages were probably important for the ardipithecines and their descendants, the **australopithecines**.

The first australopithecine skull was found in South Africa in 1924. Since then, australopithecine fossils have been found in many sites in Africa. The most complete fossil skeleton of an australopithecine, approximately 3.5 million years old, was discovered in Ethiopia in 1974. That individual, a young female known to the world as Lucy, was assigned to the species *Australopithecus afarensis*. Fossil remains of more than 100 *A. afarensis* have now been discovered. During the past 5 years, fossils of other australopithecines that lived in Africa 4–5 million years ago have been unearthed.

Experts disagree over how many species are represented by the australopithecine fossils, but it is clear that several million years ago, at least two distinct types lived together over much of eastern Africa. The larger type (about 40 kilograms) is represented by at least two species (*Paranthropus robustus* and *P. boisei*), both of which died out suddenly about 1.5 million years ago.

Humans arose from australopithecine ancestors

Early members of the genus *Homo* lived contemporaneously with australopithecines for perhaps half a million years (Figure 34.29). The oldest fossils of the genus, an extinct species called *H. habilis*, were discovered in the Olduvai Gorge, Tanzania. These fossils are estimated to be 2 million years old. Other fossils of *H. habilis* have been found in Kenya and Ethiopia. Associated with the fossils are tools that these early hominids used to obtain food.



34.29 A Current Phylogeny of *Homo sapiens* At times in the past, more than one species of hominid lived on Earth. The heavy dark blue lines indicate the time frame over which each species lived.

Another extinct species of our genus, *Homo erectus*, evolved in Africa about 1.6 mya. Soon thereafter it had spread as far as eastern Asia. As it expanded its range and increased in abundance, *H. erectus* may have exterminated *H. habilis*. Members of *H. erectus* were as large as modern people, but their bones were considerably heavier. *Homo erectus* used fire for cooking and for hunting large animals, and made characteristic stone tools that have been found in many parts of the Old World. Although *H. erectus* survived in Eurasia until about 250,000 years ago, it was replaced in tropical regions by our species, *Homo sapiens*, about 200,000 years ago.

Human brains became larger

The earliest members of *Homo sapiens* had larger brains than members of the earlier species of *Homo*. Brain size in the lineage increased rapidly, reaching modern size by about 160,000 years ago. This striking change was probably favored by an increasingly complex social life. The ability of group members to communicate with one another would have been valuable in cooperative hunting and gathering and for improving one's status in the complex social interactions that must have characterized early human societies, just as they do ours today. But why did brains become larger only in the human lineage?

A clue to the answer is provided by brain chemistry. The human brain is a fat-rich organ. About 60 percent of its structural material is made up of lipids, most of them long-chain polyunsaturated omega-3 and omega-6 fatty acids. Humans must consume omega fatty acids in their diet because the body cannot synthesize these molecules fast enough from the other fatty acids found in vegetables, nuts, and seeds to supply their brains. Animal brains and livers contain omega fatty acids, but fish and shellfish are by far the best sources.

Therefore, because savannas and open woodlands provide few sources of omega fatty acids, the traditional view that early human evolution took place in those environments is being questioned. In contrast, the shores of Africa's many lakes would have been rich sources of fish and mollusks. Thus, access to fat-rich foods from aquatic environments may have been the key factor that supported the dramatic expansion of the human brain. The archeological record of the past 100,000 years includes hundreds of piles of mollusk shells and fish bones, as well as carved points used for fishing. Chimpanzees remained in the forest and ate fruits and nuts. They may have lacked food sources to support much larger brains.

Several *Homo* species existed during the mid-Pleistocene epoch, from about 1.5 million to about 300,000 years ago. All were skilled hunters of large mammals, but plants continued to be important components of their diets. During this period another distinctly human trait emerged: rituals and a concept of life after death. Deceased individuals were buried with tools and clothing, presumably supplies for their existence in the next world.

One species, *Homo neanderthalensis*, was widespread in Europe and Asia between about 75,000 and 30,000 years ago. Neanderthals were short, stocky, and powerfully built humans whose massive skulls housed brains somewhat larger than our own. They manufactured a variety of tools and hunted large mammals, which they probably ambushed and subdued in close combat. For a short time, their range overlapped that of the *H. sapiens* known as Cro-Magnons, but then the Neanderthals abruptly disappeared. Many scientists believe that they were exterminated by the Cro-Magnons, just as *H. habilis* may have been exterminated by *H. erectus*.

Cro-Magnon people made and used a variety of sophisticated tools. They created the remarkable paintings of large mammals, many of them showing scenes of hunting, that have been discovered in European caves (Figure 34.30). The animals depicted were characteristic of the cold steppes and grasslands that occupied much of Europe during periods of glacial expansion. Cro-Magnon people spread across Asia, reaching North America perhaps as early as 20,000 years ago, although the date of their arrival in the New World is still uncertain. Within a few thousand years, they had spread southward through North America to the southern tip of South America.

Humans evolved language and culture

As our ancestors evolved larger brains, their behavioral capabilities increased, especially the capacity for language. Most animal communication consists of a limited number of signals, which refer mostly to immediate circumstances and are associated with changed emotional states induced by those circumstances. Human language is far richer in its symbolic character than any other animal vocalizations. Our words can refer to past and future times and to distant places. We are capable of learning thousands of words, many of them referring to abstract concepts. We can rearrange words to form sentences with complex meanings.

The expanded mental abilities of humans are largely responsible for the development of **culture**, the process by which knowledge and traditions are passed along from one generation to another by teaching and observation. Culture can change rapidly because genetic changes are not necessary for a cultural trait to spread through a population. A potential disadvantage of culture is that its norms must be taught to each generation.

Cultural learning greatly facilitated the spread of domestic plants and animals and the resultant conversion of most human societies from ones in which food was obtained by hunting and gathering to ones in which *pastoralism* (herding large animals) and *agriculture* dominated.

34.30 Hunting Inspires Art Cro-Magnon cave drawings such as those found in Lascaux Cave, France, typically depict the large mammals that these people hunted.

The development of agriculture led to an increasingly sedentary life, the growth of cities, greatly expanded food supplies, rapid increases in the human population, and the appearance of occupational specializations, such as artisans, shamans, and teachers.

Deuterostomes and Protostomes: Shared Evolutionary Themes

The evolution of deuterostomes paralleled the evolution of protostomes in several important ways. Both lineages exploited the abundant food supplies buried in soft marine substrata, attached to rocks, or suspended in water. Many groups of both lineages developed elaborate structures for moving water and extracting prey from it.

In some lineages of both groups, the body cavity became divided into compartments that allowed better control of shape and movement. Some members of both groups evolved mechanisms for controlling their buoyancy in water using gas-filled internal spaces. Planktonic larval stages evolved in marine members of many protostomate and deuterostomate phyla.

Both protostomes and deuterostomes colonized the land, but the consequences were very different. The jointed external skeletons of arthropods, although they provide excellent support and protection in air, cannot support large animals, as the internal skeletons developed by deuterostomes can.

Terrestrial deuterostomes recolonized aquatic environments a number of times. Suspension feeding evolved once again in several of these lineages. The largest living animals, baleen (toothless) whales, feed upon small prey only a few centimeters long, which they extract from the water with large straining structures in their mouths.

Chapter Summary

Origins of the Deuterostomes

▶ The deuterostomate lineage separated from the protostomate lineage early in animal evolution. The ancestral deuterostome had external gills. **Review Figure 34.1**

▶ There are only two major deuterostomate lineages, and there are fewer species of deuterostomes than protostomes, but as members of the lineage, we have a special interest in its members. **Review Figure 34.2. See Web/CD Activity 34.1**

Echinoderms: Pentaradial Symmetry

▶ Echinoderms have a pentaradially symmetrical body plan, a unique water vascular system, and a calcified internal skeleton. **Review Figure 34.3*a***

▶ Nearly all living species of echinoderms have a bilaterally symmetrical, ciliated larva that feeds as a planktonic organism. **Review Figure 34.3*b***

▶ Six major groups of echinoderms survive today, but 23 other lineages existed in the past. Some groups of echinoderms have arms, but others do not.

Hemichordates: Conservative Evolution

▶ Acorn worms and pterobranchs are similar to ancestral deuterostomes. **Review Figure 34.5**

Chordates: New Ways of Feeding

▶ Members of another deuterostomate lineage evolved enlarged pharyngeal slits used as feeding devices and a dorsal supporting rod, the notochord.

▶ Most urochordates are sessile as adults and filter prey from seawater with large pharyngeal baskets. But some species retain their notochords and nerve cords as planktonic adults.

Evolution of the Chordates

▶ Cephalochordates probably resemble the ancestors of all other chordates. **Review Figure 34.7**

▶ Vertebrates evolved jointed internal skeletons that enabled them to swim rapidly. Early vertebrates used the pharyngeal basket to filter small animals from mud. **Review Figures 34.8, 34.9**

▶ Jaws, which evolved from anterior gill arches, enabled their possessors to grasp and chew their prey. Jawed fishes rapidly became dominant animals in both marine and fresh waters. **Review Figure 34.11**

▶ Fishes evolved two pairs of unjointed fins, with which they control their swimming movements and stabilize themselves in the water, and swim bladders, which help keep them suspended in open water.

▶ Ray-finned fishes come in a wide variety of sizes and shapes. Many species have complex social systems.

Colonizing the Land: Obtaining Oxygen from the Air

▶ Two lineages of fishes—lobe-finned fishes and lungfishes—evolved jointed fins.

▶ Amphibians, the first terrestrial vertebrates, arose from lungfish ancestors.

▶ The 4,500 species of amphibians living today belong to three groups: caecilians, frogs and toads, and salamanders.

▶ Most amphibians live in water at some time in their lives, and their eggs must remain moist. **Review Figure 34.16. See Web/CD Tutorial 34.1**

▶ Amniotes evolved eggs with shells impermeable to water and thus became the first vertebrates to be independent of water for reproduction. **Review Figure 34.17. See Web/CD Activity 34.2**

▶ Modern reptiles are members of four lineages: snakes and lizards, tuataras, turtles and tortoises, and crocodilians. **Review Figure 34.18**

▶ Dinosaurs rose to dominance about 215 mya and dominated terrestrial environments for about 150 million years until they became extinct about 65 mya.

▶ Some dinosaurs evolved feathers and were capable of flight.

Birds: More Feathers and Better Flight

▶ Birds arose about 175 mya from feathered dinosaur ancestors.

▶ The 9,600 species of birds are characterized by feathers, high metabolic rates, and parental care.

The Origin and Diversity of Mammals

▶ Mammals evolved during the Mesozoic era, about 225 mya.

▶ The eggs of mammals are fertilized within the body of the female, and embryos develop for some time within a uterus before being born. Mammals are unique in suckling their young with milk secreted by mammary glands.

▶ The three species of mammals in subclass Prototheria lay eggs, but all other mammals give birth to live young.

▶ Therian mammals are divided into two major groups: the marsupials, which give birth to tiny young that are, in most species, raised in a pouch on the female's belly, and the eutherians, which give birth to relatively well-developed offspring.

Primates and the Origin of Humans

▶ The primates split into two major lineages, one leading to the prosimians (lemurs and lorises) and the other leading to the tarsiers, monkeys, apes, and humans. **Review Figure 34.25**

▶ Hominids evolved in Africa from terrestrial, bipedal ancestors. **Review Figure 34.29**

▶ Early humans evolved large brains, language, and culture. They manufactured and used tools, developed rituals, and domesticated plants and animals. In combination, these traits enabled humans to increase greatly in number and to transform the face of Earth.

Deuterostomes and Protostomes: Shared Evolutionary Themes

▶ Both protostomes and deuterostomes evolved structures to filter prey from the water, mechanisms to control their buoyancy in water, and planktonic larval stages.

See Web/CD Activity 34.3 for a concept review of this chapter.

Self-Quiz

1. Which of the following deuterostomate groups have a three-part body plan?
   a. Acorn worms and tunicates
   b. Acorn worms and pterobranchs
   c. Pterobranchs and tunicates
   d. Pterobranchs and lancelets
   e. Tunicates and lancelets
2. The structure used by adult ascidians to capture food is a
   a. pharyngeal basket.
   b. proboscis.
   c. lophophore.
   d. mucus net.
   e. radula.
3. The pharyngeal gill slits of chordates originally functioned as sites for
   a. uptake of oxygen only.

b. release of carbon dioxide only.
c. both uptake of oxygen and release of carbon dioxide.
d. removal of small prey from the water.
e. forcible expulsion of water to move the animal.

4. The key to the vertebrate body plan is a
a. pharyngeal basket.
b. vertebral column to which internal organs are attached.
c. vertebral column to which two pairs of appendages are attached.
d. vertebral column to which a pharyngeal basket is attached.
e. pharyngeal basket and two pairs of appendages.

5. Which of the following fishes do *not* have a cartilaginous skeleton?
a. Chimaeras
b. Lungfishes
c. Sharks
d. Skates
e. Rays

6. In most fishes, lunglike sacs evolved into
a. pharyngeal gill slits.
b. true lungs.
c. coelomic cavities.
d. swim bladders.
e. none of the above

7. Most amphibians return to water to lay their eggs because
a. water is isotonic to egg fluids.
b. adults must be in water while they guard their eggs.
c. there are fewer predators in water than on land.
d. amphibians need water to produce their eggs.
e. amphibian eggs quickly lose water and desiccate if their surroundings are dry.

8. The horny scales that cover the skin of reptiles prevent them from
a. using their skin as an organ of gas exchange.
b. sustaining high levels of metabolic activity.
c. laying their eggs in water.
d. flying.
e. crawling into small spaces.

9. Which statement about bird feathers is *not* true?
a. They are highly modified reptilian scales.
b. They provide insulation for the body.
c. They exist in two layers.
d. They help birds fly.
e. They are important sites of gas exchange.

10. Monotremes differ from other mammals in that they
a. do not produce milk.
b. lack body hair.
c. lay eggs.
d. live in Australia.
e. have a pouch in which the young are raised.

11. Bipedalism is believed to have evolved in the human lineage because bipedal locomotion is
a. more efficient than quadrupedal locomotion.
b. more efficient than quadrupedal locomotion, and it frees the forelimbs to manipulate objects.
c. less efficient than quadrupedal locomotion, but it frees the forelimbs to manipulate objects.
d. less efficient than quadrupedal locomotion, but bipedal animals can run faster.
e. less efficient than quadrupedal locomotion, but natural selection does not act to improve efficiency.

For Discussion

1. In what animal phyla has the ability to fly evolved? How do the structures used for flying differ among these animals?
2. Extracting suspended food from the water column is a common mode of foraging among animals. Which groups contain species that extract prey from the air? Why is this mode of obtaining food so much less common than extracting prey from the water?
3. Large size both confers benefits and poses certain risks. What are these risks and benefits?
4. Amphibians have survived and prospered for many millions of years, but today many species are disappearing and populations of others are declining seriously. What features of amphibian life histories might make them especially vulnerable to the kinds of environmental changes now happening on Earth?
5. The body plan of most vertebrates is based on four appendages. Describe the varied forms that these appendages take and how they are used. How do the vertebrates that have kept their four appendages move?
6. Compare the ways that different animal lineages colonized the land. How were those ways influenced by the body plans of animals in the different lineages?