

25

The History of Life on Earth

KEY CONCEPTS

- 25.1 Conditions on early Earth made the origin of life possible
- 25.2 The fossil record documents the history of life
- 25.3 Key events in life's history include the origins of unicellular and multicellular organisms and the colonization of land
- 25.4 The rise and fall of groups of organisms reflect differences in speciation and extinction rates
- 25.5 Major changes in body form can result from changes in the sequences and regulation of developmental genes
- 25.6 Evolution is not goal oriented



◀ *Cryolophosaurus* skull

▲ **Figure 25.1** On what continent did these dinosaurs roam?

Lost Worlds

Early Antarctic explorers encountered one of Earth's harshest, most barren environments, a land of extreme cold and almost no liquid water. Antarctic life is sparse and small—the largest fully terrestrial animal is a fly 5 mm long. But even as they struggled to survive, some of these explorers made an astonishing discovery: fossil evidence that life once thrived where it now barely exists. Fossils reveal that 500 million years ago, the ocean around Antarctica was warm and teeming with tropical invertebrates. Later, the continent was covered in forests for hundreds of millions of years. At various times, diverse animals stalked through these forests, including 3-m-tall predatory “terror birds” and giant dinosaurs such as the voracious *Cryolophosaurus* (Figure 25.1), a 7-m-long relative of *Tyrannosaurus rex*.

Fossils discovered in other parts of the world tell a similar story: Past organisms were very different from those presently living. The sweeping changes in life on Earth as revealed by fossils illustrate **macroevolution**, the broad pattern of evolution above the species level. Examples of macroevolutionary change include the emergence of terrestrial vertebrates through a series of speciation events, the impact of mass extinctions on biodiversity, and the origin of key adaptations such as flight.

Taken together, such changes provide a grand view of the evolutionary history of life. We'll begin by examining hypotheses regarding the origin of life. This is the most speculative topic of the entire unit, for no fossil evidence of that seminal

episode exists. We will then turn to evidence from the fossil record about major events in the history of life and the factors that have shaped the rise and fall of different groups of organisms over time.

CONCEPT 25.1

Conditions on early Earth made the origin of life possible

Direct evidence of life on early Earth comes from fossils of microorganisms that lived 3.5 billion years ago. But how did the first living cells appear? Observations and experiments in chemistry, geology, and physics have led scientists to propose one scenario that we'll examine here. They hypothesize that chemical and physical processes could have produced simple cells through a sequence of four main stages:

1. The abiotic (nonliving) synthesis of small organic molecules, such as amino acids and nitrogenous bases
2. The joining of these small molecules into macromolecules, such as proteins and nucleic acids
3. The packaging of these molecules into **protocells**, droplets with membranes that maintained an internal chemistry different from that of their surroundings
4. The origin of self-replicating molecules that eventually made inheritance possible

Though speculative, this scenario leads to predictions that can be tested in the laboratory. In this section, we'll examine some of the evidence for each stage.

Synthesis of Organic Compounds on Early Earth

Our planet formed 4.6 billion years ago, condensing from a vast cloud of dust and rocks that surrounded the young sun. For its first few hundred million years, Earth was bombarded by huge chunks of rock and ice left over from the formation of the solar system. The collisions generated so much heat that all of the available water was vaporized, preventing the formation of seas and lakes.

This massive bombardment ended about 4 billion years ago, setting the stage for the origin of life on our young planet. The first atmosphere had little oxygen and was probably thick with water vapor, along with various compounds released by volcanic eruptions, including nitrogen and its oxides, carbon dioxide, methane, ammonia, and hydrogen. As Earth cooled, the water vapor condensed into oceans, and much of the hydrogen escaped into space.

During the 1920s, Russian chemist A. I. Oparin and British scientist J. B. S. Haldane independently hypothesized that Earth's early atmosphere was a reducing (electron-adding) environment, in which organic compounds could have formed from simpler molecules. The energy for this synthesis could have come from lightning and UV radiation.



▲ Figure 25.2 Amino acid synthesis in a simulated volcanic eruption. In addition to his classic 1953 study, Miller also conducted an experiment simulating a volcanic eruption. In a 2008 reanalysis of those results, researchers found that far more amino acids were produced under simulated volcanic conditions than were produced in the conditions of the original 1953 experiment.

MAKE CONNECTIONS How could more than 20 amino acids have been produced in the 2008 experiment? (See Concept 5.4.)

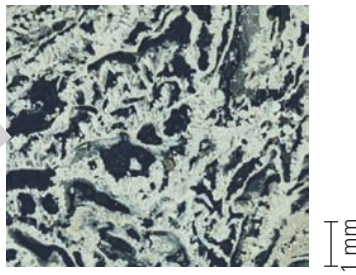
Haldane suggested that the early oceans were a solution of organic molecules, a “primitive soup” from which life arose.

In 1953, Stanley Miller, working with Harold Urey at the University of Chicago, tested the Oparin-Haldane hypothesis by creating laboratory conditions comparable to those that scientists at the time thought existed on early Earth (see Figure 4.2). His apparatus yielded a variety of amino acids found in organisms today, along with other organic compounds. Many laboratories have since repeated Miller’s classic experiment using different recipes for the atmosphere, some of which also produced organic compounds.

However, some evidence suggests that the early atmosphere was made up primarily of nitrogen and carbon dioxide and was neither reducing nor oxidizing (electron removing). Recent Miller-Urey-type experiments using such “neutral” atmospheres have also produced organic molecules. In addition, small pockets of the early atmosphere, such as those near the openings of volcanoes, may have been reducing. Perhaps the first organic compounds formed near volcanoes. In a 2008 test of this hypothesis, researchers used modern equipment to reanalyze molecules that Miller had saved from one of his experiments. The 2008 study found that numerous amino acids had formed under conditions that simulated a volcanic eruption (**Figure 25.2**).

Another hypothesis is that organic compounds were first produced in deep-sea **hydrothermal vents**, areas on the seafloor where heated water and minerals gush from Earth’s interior into the ocean. Some of these vents, known as “black smokers,” release water so hot (300–400°C) that organic compounds formed there may have been unstable. But other deep-sea vents, called **alkaline vents**, release water that has a high pH (9–11) and is warm (40–90°C) rather than hot, an environment that may have been more suitable for the origin of life (**Figure 25.3**).

Studies related to the volcanic-atmosphere and alkaline-vent hypotheses show that the abiotic synthesis of organic molecules is possible under various conditions. Another



◀ **Figure 25.3 Did life originate in deep-sea alkaline vents?** The first organic compounds—and indeed, the first cells—may have arisen in warm alkaline vents similar to this one from the 40,000-year-old “Lost City” vent field in the mid-Atlantic Ocean. These vents contain hydrocarbons and are full of tiny pores (inset) lined with iron and other catalytic minerals. Early oceans were acidic, and so a pH gradient would have formed between the interior of the vents and the surrounding ocean water. Energy for the synthesis of organic compounds could have been harnessed from this pH gradient.

source of organic molecules may have been meteorites. For example, fragments of the Murchison meteorite, a 4.5-billion-year-old rock that landed in Australia in 1969, contain more than 80 amino acids, some in large amounts. These amino acids cannot be contaminants from Earth because they consist of an equal mix of D and L isomers (see Chapter 4). Organisms make and use only L isomers, with a few rare exceptions. Recent studies have shown that the Murchison meteorite also contained other key organic molecules, including lipids, simple sugars, and nitrogenous bases such as uracil.

Abiotic Synthesis of Macromolecules

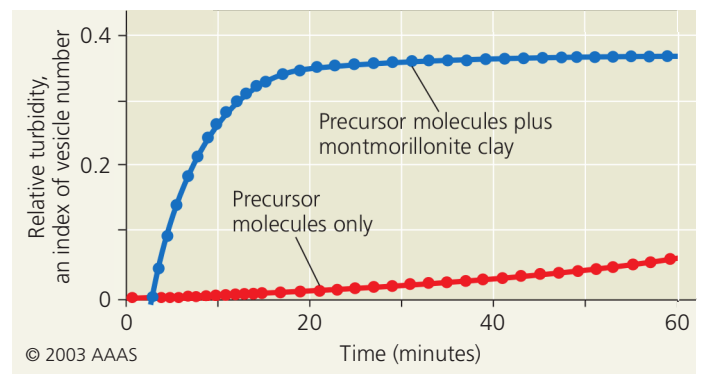
The presence of small organic molecules, such as amino acids and nitrogenous bases, is not sufficient for the emergence of life as we know it. Every cell has many types of macromolecules, including enzymes and other proteins and the nucleic acids needed for self-replication. Could such macromolecules have formed on early Earth? A 2009 study demonstrated that one key step, the abiotic synthesis of RNA monomers, can occur spontaneously from simple precursor molecules. In addition, by dripping solutions of amino acids or RNA nucleotides onto hot sand, clay, or rock, researchers have produced polymers of these molecules. The polymers formed spontaneously, without the help of enzymes or ribosomes. Unlike proteins, the amino acid polymers are a complex mix of linked and cross-linked amino acids. Still, it is possible that such polymers acted as weak catalysts for a variety of chemical reactions on early Earth.

Protocells

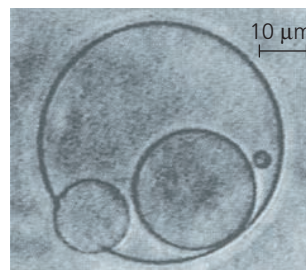
All organisms must be able to carry out both reproduction and energy processing (metabolism). DNA molecules carry

genetic information, including the instructions needed to replicate themselves accurately during reproduction. But DNA replication requires elaborate enzymatic machinery, along with an abundant supply of nucleotide building blocks provided by the cell’s metabolism. This suggests that self-replicating molecules and a metabolism-like source of building blocks may have appeared together in early protocells. The necessary conditions may have been met in *vesicles*, fluid-filled compartments enclosed by a membrane-like structure. Recent experiments show that abiotically produced vesicles can exhibit certain properties of life, including simple reproduction and metabolism, as well as the maintenance of an internal chemical environment different from that of their surroundings (**Figure 25.4**).

For example, vesicles can form spontaneously when lipids or other organic molecules are added to water. When this occurs, the hydrophobic molecules in the mixture organize into a bilayer similar to the lipid bilayer of a plasma membrane. Adding substances such as *montmorillonite*, a soft mineral clay produced by the weathering of volcanic ash, greatly increases the rate of vesicle self-assembly (see Figure 25.4a). This clay, which is thought to have been common on early Earth, provides surfaces on which organic molecules become concentrated, increasing the likelihood that the molecules will react with each other and form vesicles. Abiotically produced vesicles can “reproduce” on their own (see Figure 25.4b), and



(a) **Self-assembly.** The presence of montmorillonite clay greatly increases the rate of vesicle self-assembly.



(b) **Reproduction.** Vesicles can divide on their own, as in this vesicle “giving birth” to smaller vesicles (LM).



(c) **Absorption of RNA.** This vesicle has incorporated montmorillonite clay particles coated with RNA (orange).

▲ **Figure 25.4 Features of abiotically produced vesicles.**

they can increase in size (“grow”) without dilution of their contents. Vesicles also can absorb montmorillonite particles, including those on which RNA and other organic molecules have become attached (see Figure 25.4c). Finally, experiments have shown that some vesicles have a selectively permeable bilayer and can perform metabolic reactions using an external source of reagents—another important prerequisite for life.

Self-Replicating RNA

The first genetic material was most likely RNA, not DNA. RNA plays a central role in protein synthesis, but it can also function as an enzyme-like catalyst (see Chapter 17). Such RNA catalysts are called **ribozymes**. Some ribozymes can make complementary copies of short pieces of RNA, provided that they are supplied with nucleotide building blocks.

Natural selection on the molecular level has produced ribozymes capable of self-replication in the laboratory. How does this occur? Unlike double-stranded DNA, which takes the form of a uniform helix, single-stranded RNA molecules assume a variety of specific three-dimensional shapes mandated by their nucleotide sequences. In a particular environment, RNA molecules with certain nucleotide sequences may have shapes that enable them to replicate faster and with fewer errors than other sequences. The RNA molecule with the greatest ability to replicate itself will leave the most descendant molecules. Occasionally, a copying error will result in a molecule with a shape that is even more adept at self-replication than the ancestral sequence. Similar selection events may have occurred on early Earth. Thus, life as we know it may have been preceded by an “RNA world,” in which small RNA molecules were able to replicate and to store genetic information about the vesicles that carried them.

A vesicle with self-replicating, catalytic RNA would differ from its many neighbors that lacked such molecules. If that vesicle could grow, split, and pass its RNA molecules to its daughters, the daughters would be protocells. Although the first such protocells likely carried only limited amounts of genetic information, specifying only a few properties, their inherited characteristics could have been acted on by natural selection. The most successful of the early protocells would have increased in number because they could exploit their resources effectively and pass their abilities on to subsequent generations.

Once RNA sequences that carried genetic information appeared in protocells, many additional changes would have been possible. For example, RNA could have provided the template on which DNA nucleotides were assembled. Double-stranded DNA is a more chemically stable repository for genetic information than is the more fragile RNA. DNA also can be replicated more accurately. Accurate replication was advantageous as genomes grew larger through gene duplication and other processes and as more properties of the

protocells became coded in genetic information. Once DNA appeared, the stage was set for a blossoming of new forms of life—a change we see documented in the fossil record.

CONCEPT CHECK 25.1

1. What hypothesis did Miller test in his classic experiment?
2. How would the appearance of protocells have represented a key step in the origin of life?
3. **MAKE CONNECTIONS** In changing from an “RNA world” to today’s “DNA world,” genetic information must have flowed from RNA to DNA. After reviewing Figures 17.3 and 19.8, suggest how this could have occurred. Is such a flow a common occurrence today?

For suggested answers, see Appendix A.

CONCEPT 25.2

The fossil record documents the history of life

Starting with the earliest traces of life, the fossil record opens a window into the world of long ago and provides glimpses of the evolution of life over billions of years. In this section, we’ll examine fossils as a form of scientific evidence: how fossils form, how scientists date and interpret them, and what they can and cannot tell us about changes in the history of life.

The Fossil Record

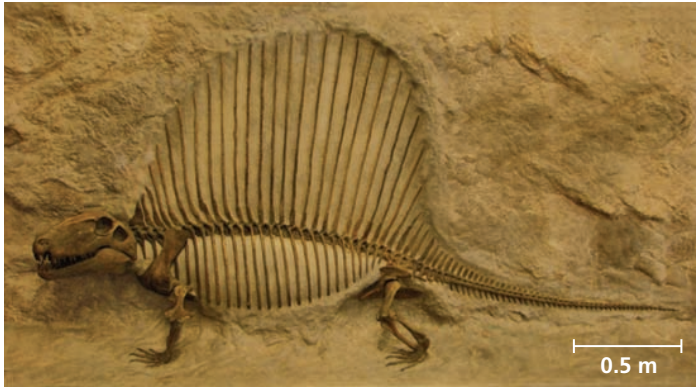
Sedimentary rocks are the richest source of fossils. As a result, the fossil record is based primarily on the sequence in which fossils have accumulated in sedimentary rock layers, called *strata* (see Figure 22.3). Useful information is also provided by other types of fossils, such as insects preserved in amber (fossilized tree sap) and mammals frozen in ice.

The fossil record shows that there have been great changes in the kinds of organisms on Earth at different points in time (**Figure 25.5**). Many past organisms were unlike organisms living today, and many organisms that once were common are now extinct. As we’ll see later in this section, fossils also document how new groups of organisms arose from previously existing ones.

As substantial and significant as the fossil record is, keep in mind that it is an incomplete chronicle of evolutionary change. Many of Earth’s organisms did not die in the right place at the right time to be preserved as fossils. Of those fossils that were formed, many were destroyed by later geologic processes, and only a fraction of the others have been discovered. As a result, the known fossil record is biased in favor of species that existed for a long time, were abundant and widespread in certain kinds of environments, and had hard shells, skeletons, or other parts that facilitated their

▼ **Figure 25.5 Documenting the history of life.** These fossils illustrate representative organisms from different points in time. Although prokaryotes and unicellular eukaryotes are shown only at the base of the diagram, these organisms continue to thrive today. In fact, most organisms on Earth are unicellular.

▼ *Dimetrodon*, the largest known carnivore of its day, was more closely related to mammals than to reptiles. The spectacular “sail” on its back may have functioned in temperature regulation.



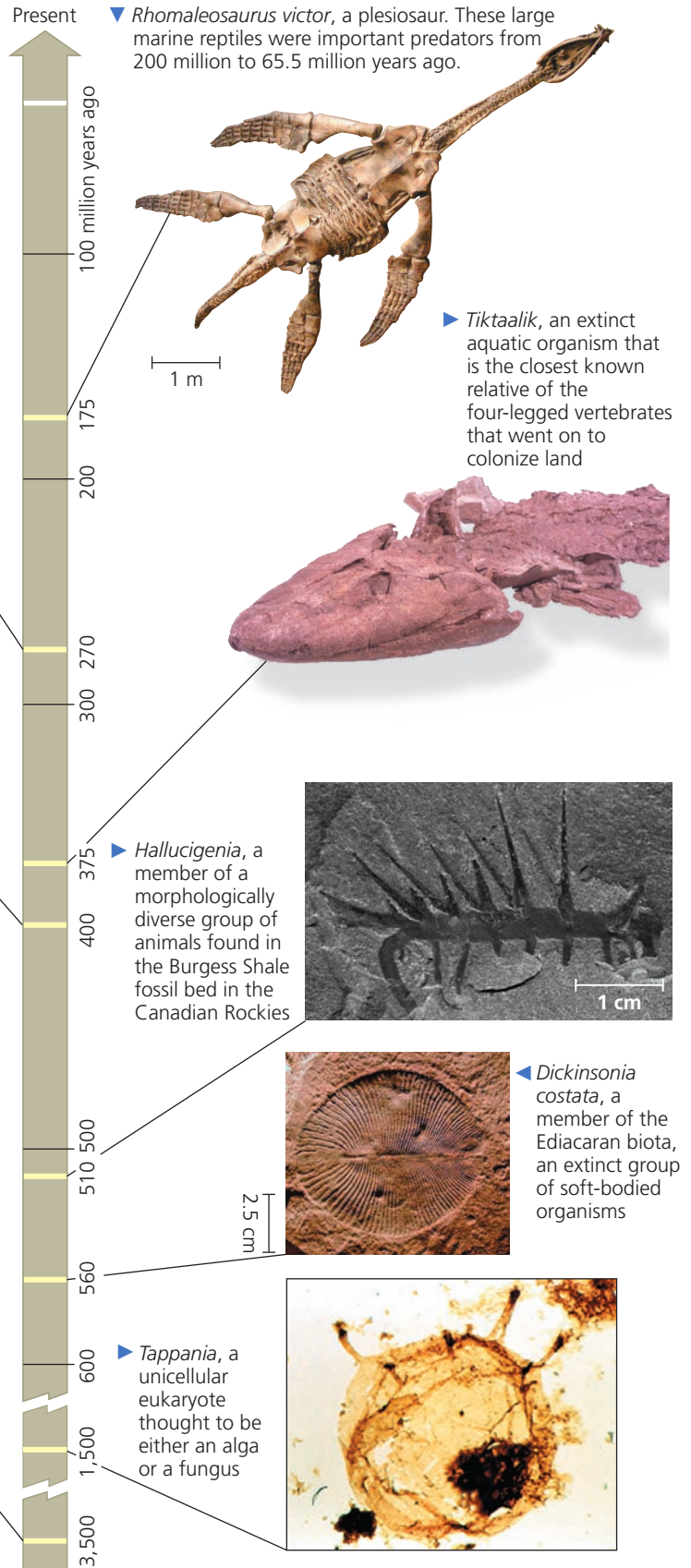
▲ *Coccosteus cuspidatus*, a placoderm (fishlike vertebrate) that had a bony shield covering its head and front end



▲ Some prokaryotes bind thin films of sediments together, producing layered rocks called stromatolites, such as these in Shark Bay, Australia.



▲ A section through a fossilized stromatolite



fossilization. Even with its limitations, however, the fossil record is a remarkably detailed account of biological change over the vast scale of geologic time. Furthermore, as shown by the recently unearthed fossils of whale ancestors with hind limbs (see Figures 22.19 and 22.20), gaps in the fossil record continue to be filled by new discoveries.

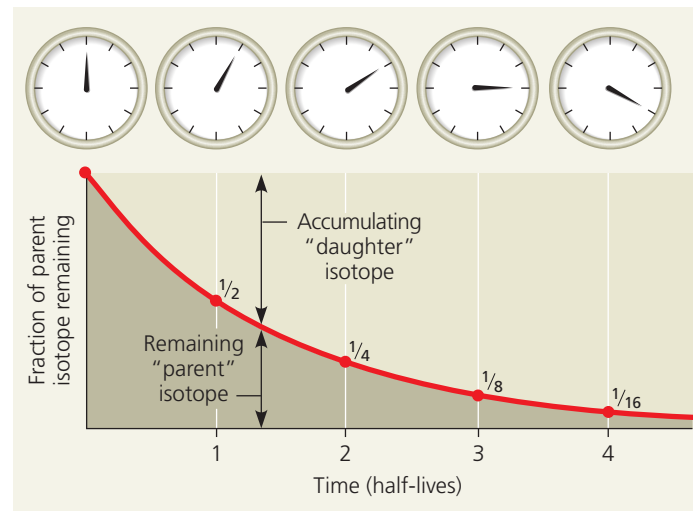
How Rocks and Fossils Are Dated

Fossils are valuable data for reconstructing the history of life, but only if we can determine where they fit in that unfolding story. While the order of fossils in rock strata tells us the sequence in which the fossils were laid down—their relative ages—it does not tell us their actual (absolute) ages. Examining the relative positions of fossils is like peeling off layers of wallpaper in an old house. You can infer the sequence in which the layers were applied, but not the year each layer was added.

How can we determine the absolute age of a fossil? (Note that “absolute” does not mean errorless, but that an age is given in years rather than relative terms such as *before* and *after*.) One of the most common techniques is **radiometric dating**, which is based on the decay of radioactive isotopes (see Chapter 2). In this process, a radioactive “parent” isotope decays to a “daughter” isotope at a characteristic rate. The rate of decay is expressed by the **half-life**, the time required for 50% of the parent isotope to decay (**Figure 25.6**). Each type of radioactive isotope has a characteristic half-life, which is not affected by temperature, pressure, or other environmental variables. For example, carbon-14 decays relatively quickly; its half-life is 5,730 years. Uranium-238 decays slowly; its half-life is 4.5 billion years.

Fossils contain isotopes of elements that accumulated in the organisms when they were alive. For example, a living organism contains the most common carbon isotope, carbon-12, as well as a radioactive isotope, carbon-14. When the organism dies, it stops accumulating carbon, and the amount of carbon-12 in its tissues does not change over time. However, the carbon-14 that it contains at the time of death slowly decays into another element, nitrogen-14. Thus, by measuring the ratio of carbon-14 to carbon-12 in a fossil, we can determine the fossil’s age. This method works for fossils up to about 75,000 years old; fossils older than that contain too little carbon-14 to be detected with current techniques. Radioactive isotopes with longer half-lives are used to date older fossils.

Determining the age of these older fossils in sedimentary rocks is challenging. Organisms do not use radioisotopes with long half-lives, such as uranium-238, to build their bones or shells. In addition, the sedimentary rocks themselves tend to consist of sediments of differing ages. So while we may not be able to date these older fossils directly, an indirect method can be used to infer the age of fossils that are sandwiched between two layers of volcanic rock. As lava



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▲ Figure 25.6 Radiometric dating. In this diagram, each division of the clock face represents a half-life.

DRAW IT Relabel the x-axis of this graph in years to illustrate the radioactive decay of uranium-238 (half-life = 4.5 billion years).

cools into volcanic rock, radioisotopes from the surrounding environment become trapped in the newly formed rock. Some of the trapped radioisotopes have long half-lives, allowing geologists to estimate the ages of ancient volcanic rocks. If two volcanic layers surrounding fossils are determined to be 525 million and 535 million years old, for example, then the fossils are roughly 530 million years old.

The Origin of New Groups of Organisms

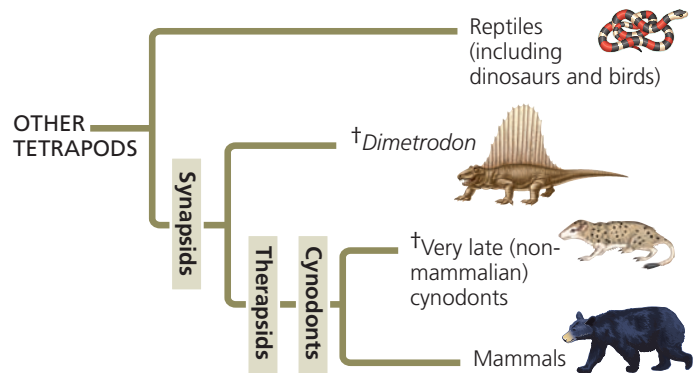
Some fossils provide a detailed look at the origin of new groups of organisms. Such fossils are central to our understanding of evolution; they illustrate how new features arise and how long it takes for such changes to occur. We’ll examine one such case here: the origin of mammals.

Along with amphibians and reptiles, mammals belong to the group of animals called *tetrapods* (from the Greek *tetra*, four, and *pod*, foot), named for having four limbs. Mammals have a number of unique anatomical features that fossilize readily, allowing scientists to trace their origin. For example, the lower jaw is composed of one bone (the dentary) in mammals but several bones in other tetrapods. In addition, the lower and upper jaws in mammals hinge between a different set of bones than in other tetrapods. Mammals also have a unique set of three bones that transmit sound in the middle ear, the hammer, anvil, and stirrup, whereas other tetrapods have only one such bone, the stirrup (see Chapter 34). Finally, the teeth of mammals are differentiated into incisors (for tearing), canines (for piercing), and the multi-pointed premolars and molars (for crushing and grinding). In contrast, the teeth of other tetrapods usually consist of a row of undifferentiated, single-pointed teeth.

As detailed in **Figure 25.7**, the fossil record shows that the unique features of mammalian jaws and teeth evolved

Exploring The Origin of Mammals

Over the course of 120 million years, mammals originated gradually from a group of tetrapods called synapsids. Shown here are a few of the many fossil organisms whose morphological features represent intermediate steps between living mammals and their synapsid ancestors. The evolutionary context of the origin of mammals is shown in the tree diagram at right (the dagger symbol † indicates extinct lineages).

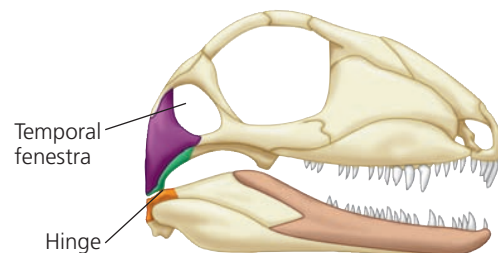


Key to skull bones

- Articular
- Dentary
- Quadrate
- Squamosal

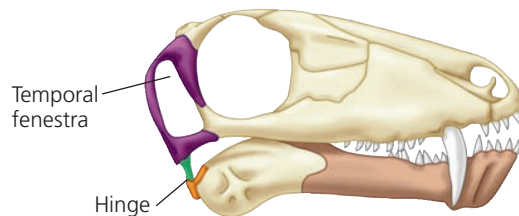
Synapsid (300 mya)

Synapsids had multiple bones in the lower jaw and single-pointed teeth. The jaw hinge was formed by the articular and quadrate bones. Synapsids also had an opening called the temporal fenestra behind the eye socket. Powerful cheek muscles for closing the jaws probably passed through the temporal fenestra. Over time, this opening enlarged and moved in front of the hinge between the lower and upper jaws, thereby increasing the power and precision with which the jaws could be closed (much as moving a doorknob away from the hinge makes a door easier to close).



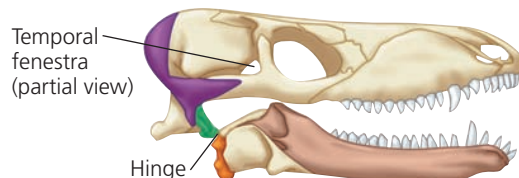
Therapsid (280 mya)

Later, a group of synapsids called therapsids appeared. Therapsids had large dentary bones, long faces, and the first examples of specialized teeth, large canines. These trends continued in a group of therapsids called cynodonts.



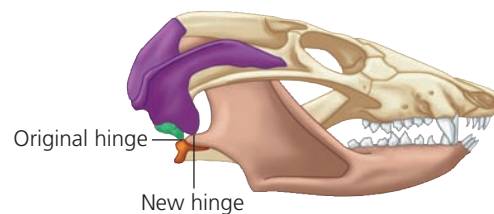
Early cynodont (260 mya)

In early cynodont therapsids, the dentary was the largest bone in the lower jaw, the temporal fenestra was large and positioned forward of the jaw hinge, and teeth with several cusps first appeared (not visible in the diagram). As in earlier synapsids, the jaw had an articular-quadrate hinge.



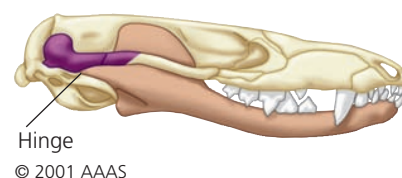
Later cynodont (220 mya)

Later cynodonts had teeth with complex cusp patterns and their lower and upper jaws hinged in two locations: They retained the original articular-quadrate hinge and formed a new, second hinge between the dentary and squamosal bones. (The temporal fenestra is not visible in this or the below cynodont skull at the angles shown.)



Very late cynodont (195 mya)

In some very late (non-mammalian) cynodonts and early mammals, the original articular-quadrate hinge was lost, leaving the dentary-squamosal hinge as the only hinge between the lower and upper jaws, as in living mammals. The articular and quadrate bones migrated into the ear region (not shown), where they functioned in transmitting sound. In the mammal lineage, these two bones later evolved into the familiar hammer (malleus) and anvil (incus) bones of the ear.



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gradually over time, in a series of steps. As you study, bear in mind that it includes just a few examples of the fossil skulls that document the origin of mammals. If all the known fossils in the sequence were arranged by shape and placed side by side, their features would blend smoothly from one group to the next. Some of these fossils would reflect how the features of a group that dominates life today, the mammals, gradually arose in a previously existing group, the cynodonts. Others would reveal side branches on the tree of life—groups of organisms that thrived for millions of years but ultimately left no descendants that survive today.

CONCEPT CHECK 25.2

1. Your measurements indicate that a fossilized skull you unearthed has a carbon-14/carbon-12 ratio about $\frac{1}{16}$ that of the skulls of present-day animals. What is the approximate age of the fossilized skull?
2. Describe an example from the fossil record that shows how life has changed over time.
3. **WHAT IF?** Suppose researchers discover a fossil of an organism that lived 300 million years ago but had mammalian teeth and a mammalian jaw hinge. What inferences might you draw from this fossil about the origin of mammals and the evolution of novel skeletal structures? Explain.

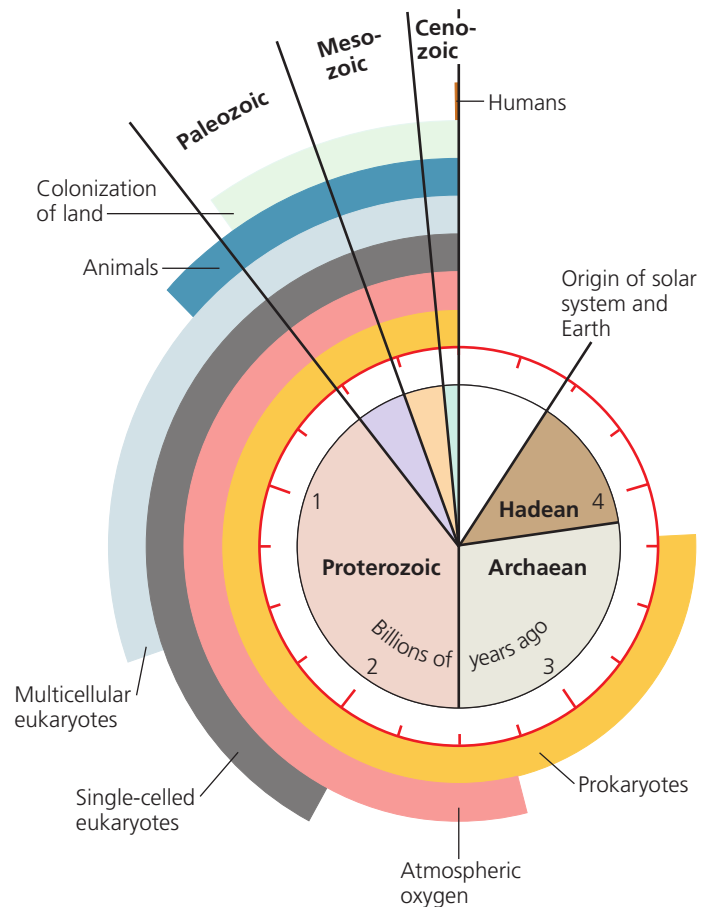
For suggested answers, see Appendix A.

CONCEPT 25.3

Key events in life’s history include the origins of unicellular and multicellular organisms and the colonization of land

The study of fossils has helped geologists establish a **geologic record**: a standard time scale that divides Earth’s history into four eons and further subdivisions (Table 25.1). The first three eons—the Hadean, Archaean, and Proterozoic—together lasted about 4 billion years. The Phanerozoic eon, roughly the last half billion years, encompasses most of the time that animals have existed on Earth. It is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic. Each era represents a distinct age in the history of Earth and its life. For example, the Mesozoic era is sometimes called the “age of reptiles” because of its abundance of reptilian fossils, including those of dinosaurs. The boundaries between the eras correspond to major extinction events seen in the fossil record, when many forms of life disappeared and were replaced by forms that evolved from the survivors.

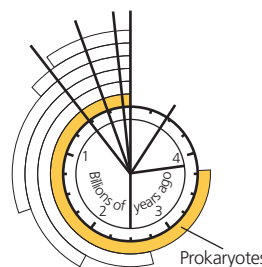
As we’ve seen, the fossil record provides a sweeping overview of the history of life over geologic time. Here we will focus on a few major events in that history, returning to study the details in Unit Five.



▲ Figure 25.8 Clock analogy for some key events in Earth’s history. The clock ticks down from the origin of Earth 4.6 billion years ago to the present.

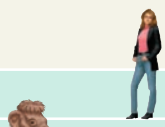









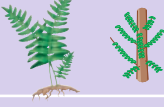






Figure 25.8 uses the analogy of a clock to place these events in the context of the geologic record. This clock will reappear at various points in this section as a quick visual reminder of when the events we are discussing took place.

The First Single-Celled Organisms

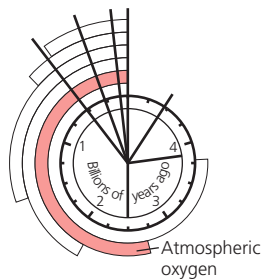


The earliest direct evidence of life, dating from 3.5 billion years ago, comes from fossilized stromatolites (see Figure 25.5). **Stromatolites** are layered rocks that form when certain prokaryotes bind thin films of sediment together. Present-day stromatolites are found in a few shallow marine bays. Stromatolites and other early prokaryotes were Earth’s sole inhabitants for more than 1.5 billion years. As we will see, these prokaryotes transformed life on our planet.

Table 25.1 The Geologic Record

Relative Duration of Eons	Era	Period	Epoch	Age (Millions of Years Ago)	Some Important Events in the History of Life	
Phanerozoic	Cenozoic	Quaternary	Holocene	0.01	Historical time	
			Pleistocene	2.6	Ice ages; origin of genus <i>Homo</i>	
		Neogene	Pliocene	5.3	Appearance of bipedal human ancestors	
			Miocene	23	Continued radiation of mammals and angiosperms; earliest direct human ancestors	
		Paleogene	Oligocene	33.9	Origins of many primate groups	
			Eocene	55.8	Angiosperm dominance increases; continued radiation of most present-day mammalian orders	
			Paleocene	65.5	Major radiation of mammals, birds, and pollinating insects	
			Mesozoic	Cretaceous	145.5	Flowering plants (angiosperms) appear and diversify; many groups of organisms, including most dinosaurs, become extinct at end of period
		Jurassic		199.6	Gymnosperms continue as dominant plants; dinosaurs abundant and diverse	
		Triassic		251	Cone-bearing plants (gymnosperms) dominate landscape; dinosaurs evolve and radiate; origin of mammals	
Proterozoic	Paleozoic	Permian	299	Radiation of reptiles; origin of most present-day groups of insects; extinction of many marine and terrestrial organisms at end of period		
		Carboniferous	359	Extensive forests of vascular plants form; first seed plants appear; origin of reptiles; amphibians dominant		
		Devonian	416	Diversification of bony fishes; first tetrapods and insects appear		
	Archaean	Silurian	444	Diversification of early vascular plants		
		Ordovician	488	Marine algae abundant; colonization of land by diverse fungi, plants, and animals		
		Cambrian	542	Sudden increase in diversity of many animal phyla (Cambrian explosion)		
		Ediacaran	635	Diverse algae and soft-bodied invertebrate animals appear		
Hadean				1,800	Oldest fossils of eukaryotic cells appear	
				2,500	Concentration of atmospheric oxygen begins to increase	
				2,700	Oldest fossils of cells (prokaryotes) appear	
				3,500	Oldest known rocks on Earth's surface	
				3,850	Origin of Earth	
				Approx. 4,600		

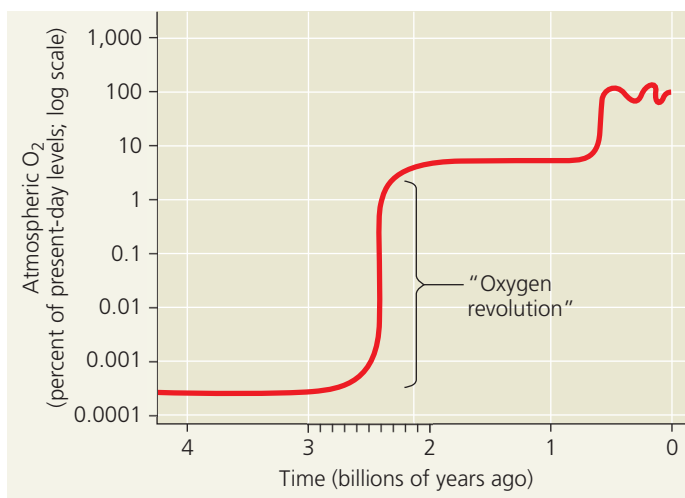
Photosynthesis and the Oxygen Revolution



Most atmospheric oxygen gas (O_2) is of biological origin, produced during the water-splitting step of photosynthesis. When oxygenic photosynthesis first evolved, the free O_2 it produced probably dissolved in the surrounding water until it reached a high enough concentration to react with elements dissolved in water, including iron. This would have caused the iron to precipitate as iron oxide, which accumulated as sediments. These sediments were compressed into banded iron formations, red layers of rock containing iron oxide that are a source of iron ore today. Once all of the dissolved iron had precipitated, additional O_2 dissolved in the water until the seas and lakes became saturated with O_2 .

After this occurred, the O_2 finally began to “gas out” of the water and enter the atmosphere. This change left its mark in the rusting of iron-rich terrestrial rocks, a process that began about 2.7 billion years ago. This chronology implies that bacteria similar to today’s cyanobacteria (oxygen-releasing, photosynthetic bacteria) originated before 2.7 billion years ago.

The amount of atmospheric O_2 increased gradually from about 2.7 to 2.4 billion years ago, but then shot up relatively rapidly to between 1% and 10% of its present level (Figure 25.9). This “oxygen revolution” had an enormous impact on life. In certain of its chemical forms, oxygen attacks chemical bonds and can inhibit enzymes and damage cells. As a result, the rising concentration of atmospheric O_2 probably doomed many prokaryotic groups. Some species survived in habitats that remained anaerobic, where we find their descendants living today (see Chapter 27). Among

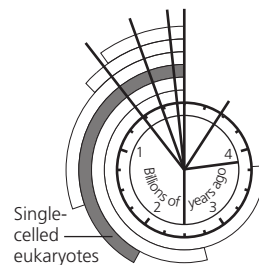


▲ **Figure 25.9** The rise of atmospheric oxygen. Chemical analyses of ancient rocks have enabled this reconstruction of atmospheric oxygen levels during Earth’s history.

other survivors, diverse adaptations to the changing atmosphere evolved, including cellular respiration, which uses O_2 in the process of harvesting the energy stored in organic molecules.

The rise in atmospheric O_2 levels left a huge imprint on the history of life. A few hundred million years later, another fundamental change occurred: the origin of the eukaryotic cell.

The First Eukaryotes



The oldest widely accepted fossils of eukaryotic organisms are 1.8 billion years old. Recall that eukaryotic cells have more complex organization than prokaryotic cells: Eukaryotic cells have a nuclear envelope, mitochondria, endoplasmic reticulum, and other internal structures that prokaryotes lack. Also, unlike prokaryotic cells, eukaryotic cells have a well-developed cytoskeleton, a feature that enables eukaryotic cells to change their shape and thereby surround and engulf other cells.

How did such eukaryotic features evolve from prokaryotic cells? Much evidence supports the **endosymbiont theory**, which posits that mitochondria and plastids (a general term for chloroplasts and related organelles) were formerly small prokaryotes that began living within larger cells. The term *endosymbiont* refers to a cell that lives within another cell, called the *host cell*. The prokaryotic ancestors of mitochondria and plastids probably entered the host cell as undigested prey or internal parasites. Though such a process may seem unlikely, scientists have directly observed cases in which endosymbionts that began as prey or parasites developed a mutually beneficial relationship with the host in as little as five years.

By whatever means the relationship began, we can hypothesize how the symbiosis could have become beneficial. For example, in a world that was becoming increasingly aerobic, a host that was itself an anaerobe would have benefited from endosymbionts that could make use of the oxygen. Over time, the host and endosymbionts would have become a single organism, its parts inseparable. Although all eukaryotes have mitochondria or remnants of these organelles, they do not all have plastids. Thus, the hypothesis of **serial endosymbiosis** supposes that mitochondria evolved before plastids through a sequence of endosymbiotic events (Figure 25.10).

A great deal of evidence supports the endosymbiotic origin of mitochondria and plastids:

• The inner membranes of both organelles have enzymes and transport systems that are homologous to those found in the plasma membranes of living prokaryotes.

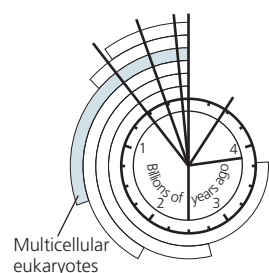
- Mitochondria and plastids replicate by a splitting process that is similar to that of certain prokaryotes. In addition, each of these organelles contains circular DNA molecules that, like the chromosomes of bacteria, are not associated with histones or large amounts of other proteins.
- As might be expected of organelles descended from free-living organisms, mitochondria and plastids also have the cellular machinery (including ribosomes) needed to transcribe and translate their DNA into proteins.
- Finally, in terms of size, RNA sequences, and sensitivity to certain antibiotics, the ribosomes of mitochondria and plastids are more similar to prokaryotic ribosomes than they are to the cytoplasmic ribosomes of eukaryotic cells.

In Chapter 28, we'll return to origin of eukaryotes, focusing on what genomic data have revealed about the prokaryotic lineages that gave rise to the host and endosymbiont cells.

The Origin of Multicellularity

An orchestra can play a greater variety of musical compositions than a violin soloist can; the increased complexity of the orchestra makes more variations possible. Likewise, the appearance of structurally complex eukaryotic cells sparked the evolution of greater morphological diversity than was possible for the simpler prokaryotic cells. After the first eukaryotes appeared, a great range of unicellular forms evolved, giving rise to the diversity of single-celled eukaryotes that continue to flourish today. Another wave of diversification also occurred: Some single-celled eukaryotes gave rise to multicellular forms, whose descendants include a variety of algae, plants, fungi, and animals.

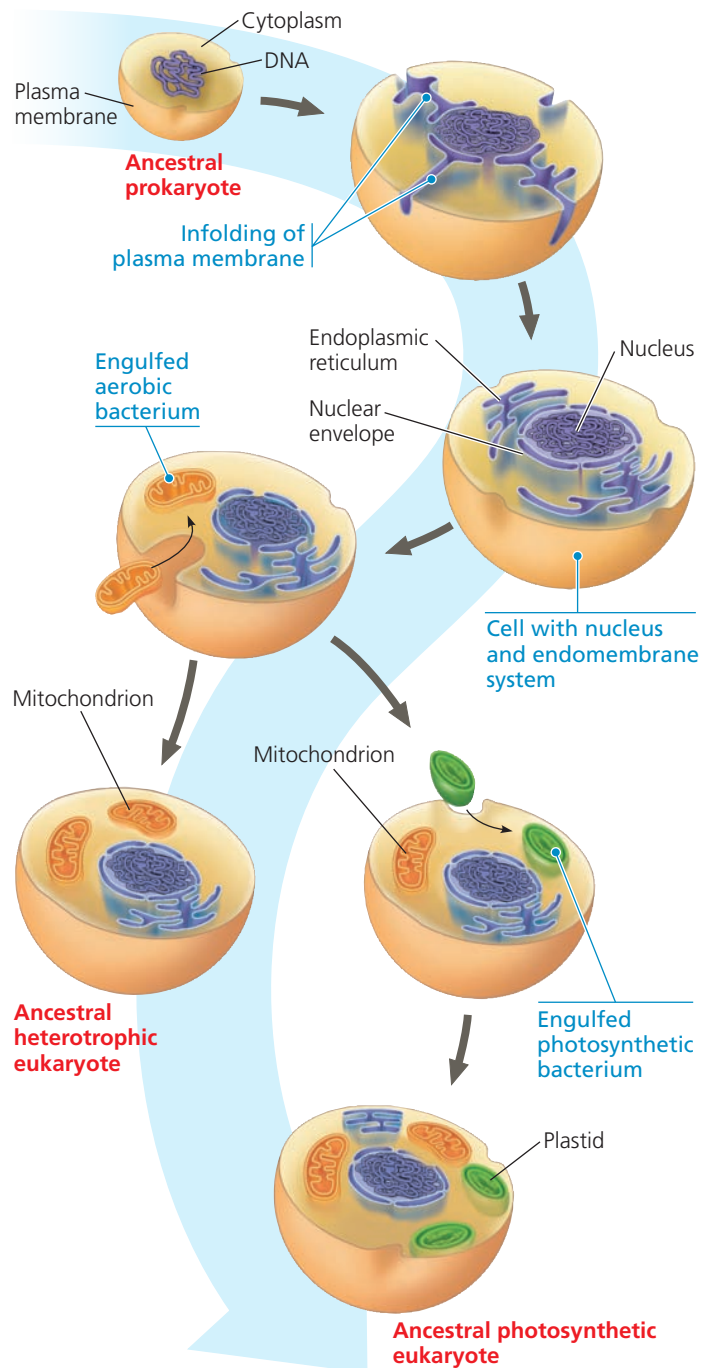
Early Multicellular Eukaryotes



The oldest known fossils of multicellular eukaryotes that can be resolved taxonomically are of relatively small red algae that lived 1.2 billion years ago; even older fossils, dating to 1.8 billion years ago, may also be of small, multicellular eukaryotes. Larger and more diverse multicellular

eukaryotes do not appear in the fossil record until about 600 million years ago (see Figure 25.5). These fossils, referred to as the Ediacaran biota, were of soft-bodied organisms—some over 1 m long—that lived from 600 to 535 million years ago. The Ediacaran biota included both algae and animals, along with various organisms of unknown taxonomic affinity.

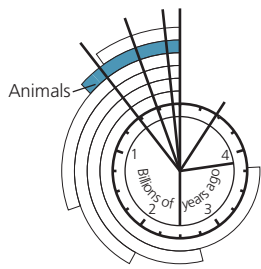
The rise of large eukaryotes in the Ediacaran period represents an enormous change in the history of life. Before that time, Earth was a microbial world: Its only inhabitants



▲ **Figure 25.10** A hypothesis for the origin of eukaryotes through serial endosymbiosis. The proposed ancestors of mitochondria were aerobic, heterotrophic prokaryotes (meaning that they used oxygen to metabolize organic molecules obtained from other organisms). The proposed ancestors of plastids were photosynthetic prokaryotes. In this figure, the arrows represent change over evolutionary time.

were single-celled prokaryotes and eukaryotes, along with an assortment of microscopic, multicellular eukaryotes. As the diversification of the Ediacaran biota came to a close about 535 million years ago, the stage was set for another, even more spectacular burst of evolutionary change.

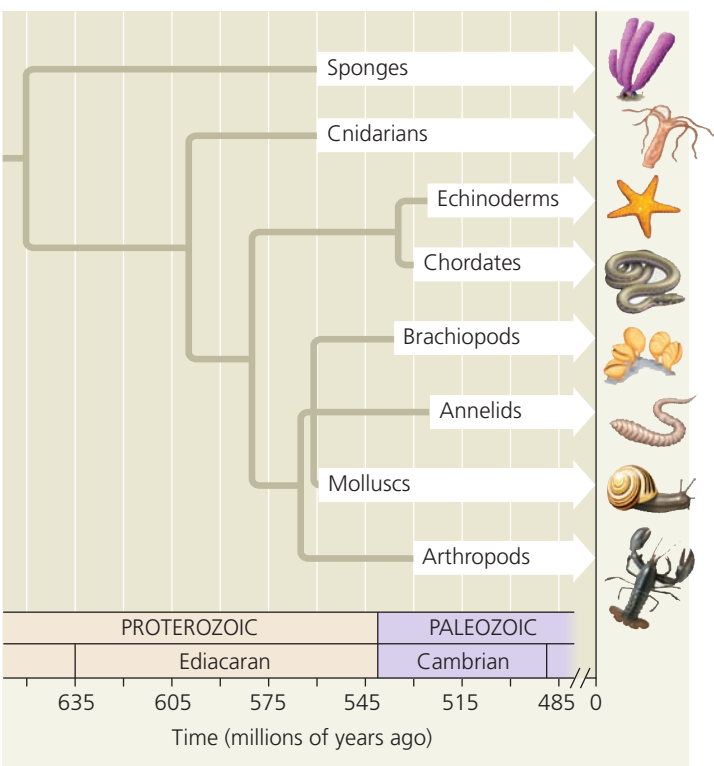
The Cambrian Explosion



Many present-day animal phyla appear suddenly in fossils formed 535–525 million years ago, early in the Cambrian period. This phenomenon is referred to as the **Cambrian explosion**. Fossils of several animal groups—sponges, cnidarians (sea anemones and their relatives), and molluscs

(snails, clams, and their relatives)—appear in even older rocks dating from the late Proterozoic (**Figure 25.11**).

Prior to the Cambrian explosion, all large animals were soft-bodied. The fossils of large pre-Cambrian animals reveal little evidence of predation. Instead, these animals appear to have been grazers (feeding on algae), filter feeders, or scavengers, not hunters. The Cambrian explosion changed all of that. In a relatively short period of time (10 million years), predators over 1 m in length emerged that had claws and other features for capturing prey; simultaneously, new defensive adaptations, such as sharp spines and heavy body armor, appeared in their prey (see Figure 25.5).

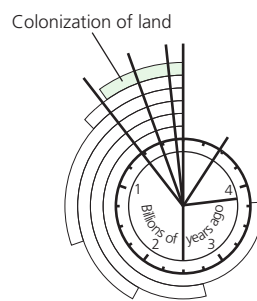


▲ **Figure 25.11** Appearance of selected animal groups. The white bars indicate earliest appearances of these animal groups in the fossil record.

DRAW IT Circle the branch point that represents the most recent common ancestor of chordates and annelids. What is a minimum estimate of that ancestor's age?

Although the Cambrian explosion had an enormous impact on life on Earth, it appears that many animal phyla originated long before that time. Recent DNA analyses suggest that sponges, an early-diverging animal group, had evolved by 700 million years ago; such analyses also indicate that the common ancestor of arthropods, chordates, and other animal phyla that radiated during the Cambrian explosion lived 670 million years ago. Researchers have unearthed 710-million-year-old fossils containing steroids indicative of a particular group of sponges—a finding that supports the molecular data. In contrast, the oldest fossil assigned to an extant animal phylum is that of the mollusc *Kimberella*, which lived 560 million years ago. Overall, molecular and fossil data indicate that the Cambrian explosion had a “long fuse”—at least 25 million years long based on the age of *Kimberella* fossils, and over 100 million years long based on some DNA analyses. We’ll explore factors that may have triggered the Cambrian explosion in Chapter 32.

The Colonization of Land

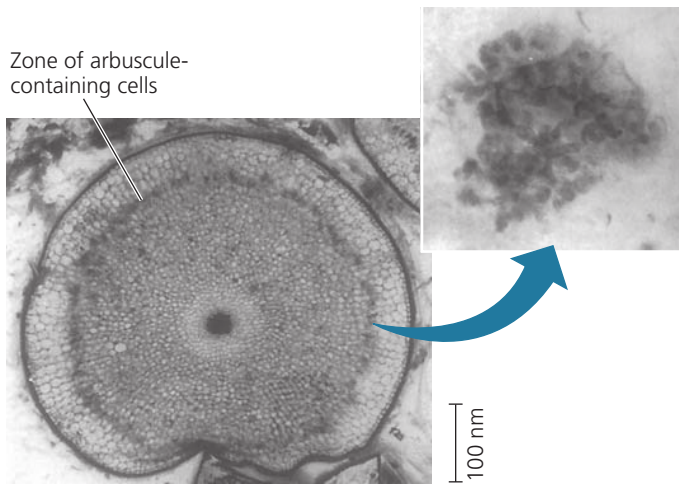


The colonization of land was another milestone in the history of life. There is fossil evidence that cyanobacteria and other photosynthetic prokaryotes coated damp terrestrial surfaces well over a billion years ago. However, larger forms of life, such as fungi, plants, and animals, did not begin to colonize land until about 500

million years ago. This gradual evolutionary venture out of aquatic environments was associated with adaptations that made it possible to reproduce on land and that helped prevent dehydration. For example, many land plants today have a vascular system for transporting materials internally and a waterproof coating of wax on their leaves that slows the loss of water to the air. Early signs of these adaptations were present 420 million years ago, at which time small plants (about 10 cm high) existed that had a vascular system but lacked true roots or leaves. By 40 million years later, plants had diversified greatly and included reeds and treelike plants with true roots and leaves.

Plants colonized land in the company of fungi. Even today, the roots of most plants are associated with fungi that aid in the absorption of water and minerals from the soil (see Chapter 31). These root fungi (or *mycorrhizae*), in turn, obtain their organic nutrients from the plants. Such mutually beneficial associations of plants and fungi are evident in some of the oldest fossilized plants, dating this relationship back to the early spread of life onto land (**Figure 25.12**).

Although many animal groups are now represented in terrestrial environments, the most widespread and diverse land



▲ **Figure 25.12 An ancient symbiosis.** This 405-million-year-old fossil stem (cross section) documents mycorrhizae in the early land plant *Aglaophyton major*. The inset shows an enlarged view of a cell containing a branched fungal structure called an arbuscule; the fossil arbuscule resembles those seen in plant cells today.

animals are arthropods (particularly insects and spiders) and tetrapods. Arthropods were among the first animals to colonize land, roughly 450 million years ago. The earliest tetrapods found in the fossil record lived about 365 million years ago and appear to have evolved from a group of lobe-finned fishes (see Chapter 34). Tetrapods include humans, although we are late arrivals on the scene. The human lineage diverged from other primates around 6–7 million years ago, and our species originated only about 195,000 years ago. If the clock of Earth’s history were rescaled to represent an hour, humans appeared less than 0.2 second ago.

CONCEPT CHECK 25.3

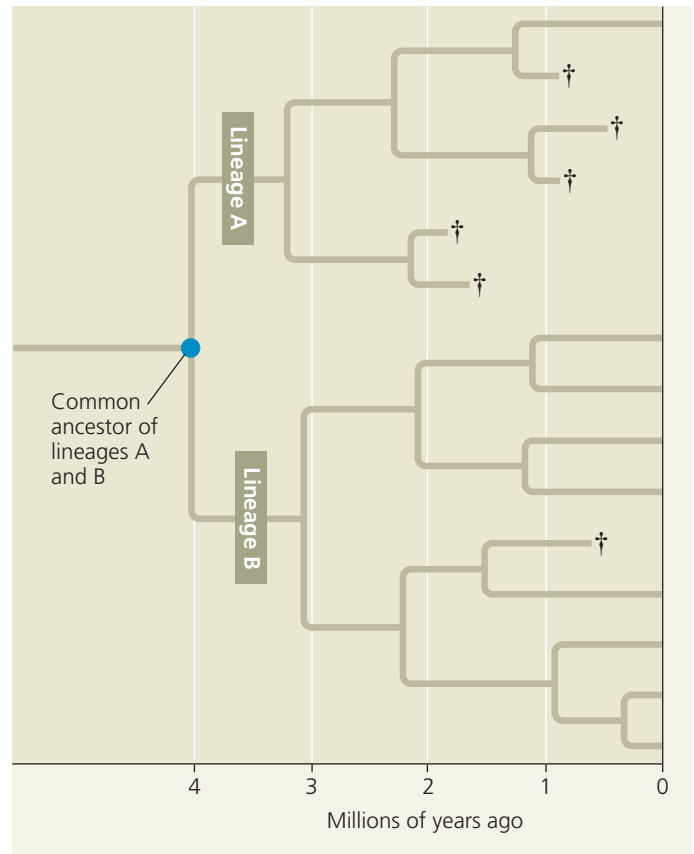
1. The first appearance of free oxygen in the atmosphere likely triggered a massive wave of extinctions among the prokaryotes of the time. Why?
2. What evidence supports the hypothesis that mitochondria preceded plastids in the evolution of eukaryotic cells?
3. **WHAT IF?** What would a fossil record of life today look like?

For suggested answers, see Appendix A.

CONCEPT 25.4

The rise and fall of groups of organisms reflect differences in speciation and extinction rates

From its beginnings, life on Earth has been marked by the rise and fall of groups of organisms. Anaerobic prokaryotes originated, flourished, and then declined as the oxygen content of the atmosphere rose. Billions of years later, the first tetrapods emerged from the sea, giving rise to several major



▲ **Figure 25.13 How speciation and extinction affect diversity.** The species diversity of an evolutionary lineage will increase when more new member species originate than are lost to extinction. In this hypothetical example, by 2 million years ago both lineage A and lineage B have given rise to four species, and no species have become extinct (denoted by a dagger symbol). By time 0, however, lineage A contains only one species while lineage B contains eight species.

INTERPRET THE DATA Consider the period from 2 million years ago to time 0. For each lineage, determine how many speciation and extinction events occurred during that time.

new groups of organisms. One of these, the amphibians, went on to dominate life on land for 100 million years, until other tetrapods (including dinosaurs and, later, mammals) replaced them as the dominant terrestrial vertebrates.

The rise and fall of these and other major groups of organisms have shaped the history of life. Narrowing our focus, we can also see that the rise or fall of any particular group is related to the speciation and extinction rates of its member species (Figure 25.13). Just as a population increases in size when there are more births than deaths, the rise of a group of organisms occurs when more new species are produced than are lost to extinction. The reverse occurs when a group is in decline. In the **Scientific Skills Exercise**, you will interpret data from the fossil record about changes in a group of snail species in the early Paleogene period. Such changes in the fates of groups of organisms have been influenced by large-scale processes such as plate tectonics, mass extinctions, and adaptive radiations.

SCIENTIFIC SKILLS EXERCISE

Estimating Quantitative Data from a Graph and Developing Hypotheses

Do Ecological Factors Affect Evolutionary Rates?

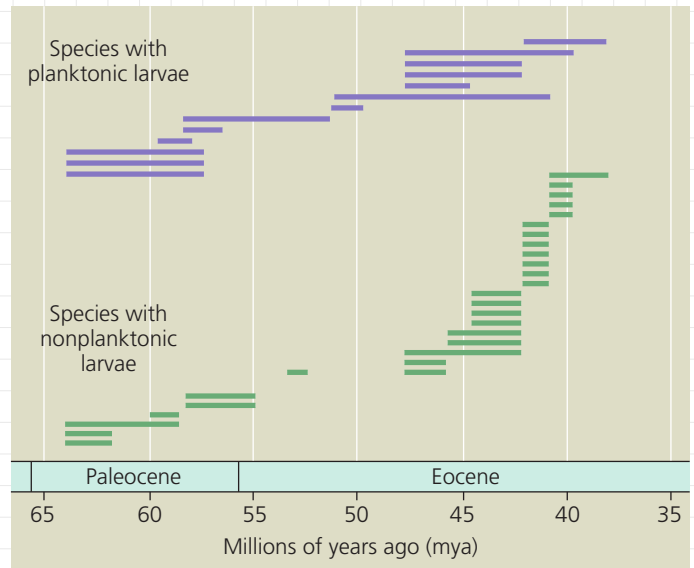
Researchers studied the fossil record to investigate whether differing modes of larval dispersal might explain species longevity within one taxon of marine snails, the family Volutidae. Some of the snail species had nonplanktonic larvae: They developed directly into adults without a swimming stage. Other species had planktonic larvae: They had a swimming stage and could disperse very long distances. The adults of these planktonic species tended to have broad geographic distributions, whereas nonplanktonic species tended to be more isolated.



How the Research Was Done The researchers studied the stratigraphic distribution of volutes in outcrops of sedimentary rocks located along North America's Gulf coast. These rocks, which formed from 65 to 37 million years ago, early in the Paleogene period, are an excellent source of well-preserved snail fossils. The researchers were able to classify each fossil species of volute snail as having planktonic or nonplanktonic larvae based on features of the earliest formed whorls of the snail's shell. Each bar in the graph shows how long one species of snail persisted in the fossil record.

Interpret the Data

1. You can estimate quantitative data (fairly precisely) from a graph. The first step is to obtain a conversion factor by measuring along an axis that has a scale. In this case, 25 million years (my; from 65 to 40 million years ago (mya) on the x-axis) is represented by a distance of 7.0 cm. This yields a conversion factor (a ratio) of $25 \text{ my}/7.0 \text{ cm} = 3.6 \text{ my/cm}$. To estimate the time period represented by a horizontal bar on this graph, measure the length of that bar in centimeters and multiply that measurement by the conversion factor, 3.6 my/cm . For example, a bar that measures 1.1 cm on the graph represents a persistence time of $1.1 \text{ cm} \times 3.6 \text{ my/cm} = 4 \text{ million years}$.
2. Calculate the mean (average) persistence times for species with planktonic larvae and species with nonplanktonic larvae.



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3. Count the number of new species that form in each group beginning at 60 mya (the first three species in each group were present around 64 mya, the first time period sampled, so we don't know when those species first appear in the fossil record).
4. Propose a hypothesis to explain the differences in longevity of snail species with planktonic and nonplanktonic larvae.

 A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

Data from: T. A. Hansen, Larval dispersal and species longevity in Lower Tertiary gastropods, *Science* 199:885–887 (1978). Reprinted with permission from AAAS.

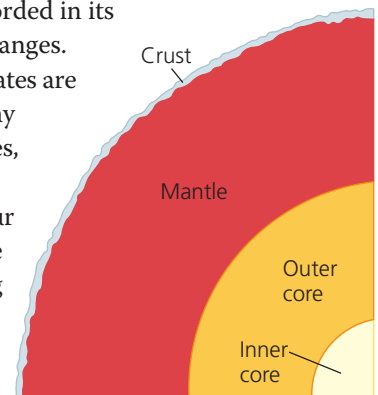
Plate Tectonics

If photographs of Earth were taken from space every 10,000 years and spliced together to make a movie, it would show something many of us find hard to imagine: The seemingly “rock solid” continents we live on move over time. Over the past 1.5 billion years, there have been three occasions (1.1 billion, 600 million, and 250 million years ago) when most of the landmasses of Earth came together to form a supercontinent, then later broke apart. Each time, this breakup yielded a different configuration of continents. Looking into the future, some geologists have estimated that the continents will come together again and form a new supercontinent roughly 250 million years from now.

According to the theory of **plate tectonics**, the continents are part of great plates of Earth's crust that essentially float on the hot, underlying portion of the mantle (**Figure 25.14**). Movements in the mantle cause the plates to move over time in a process called *continental drift*. Geologists can measure the rate at which the plates are moving now, usually only a

few centimeters per year. They can also infer the past locations of the continents using the magnetic signal recorded in rocks at the time of their formation. This method works because as a continent shifts its position over time, the direction of magnetic north recorded in its newly formed rocks also changes.

Earth's major tectonic plates are shown in **Figure 25.15**. Many important geologic processes, including the formation of mountains and islands, occur at plate boundaries. In some cases, two plates are moving away from each other, as are the North American and Eurasian plates, which are currently drifting apart at a rate of about 2 cm per year.



▲ Figure 25.14 Cutaway view of Earth. The thickness of the crust is exaggerated here.

In other cases, two plates are sliding past each other, forming regions where earthquakes are common. California's infamous San Andreas Fault is part of a border where two plates slide past each other. In still other cases, two plates collide, producing violent upheavals and forming new mountains along the plate boundaries. One spectacular example of this occurred 45 million years ago, when the Indian plate crashed into the Eurasian plate, starting the formation of the Himalayan mountains.

Consequences of Continental Drift

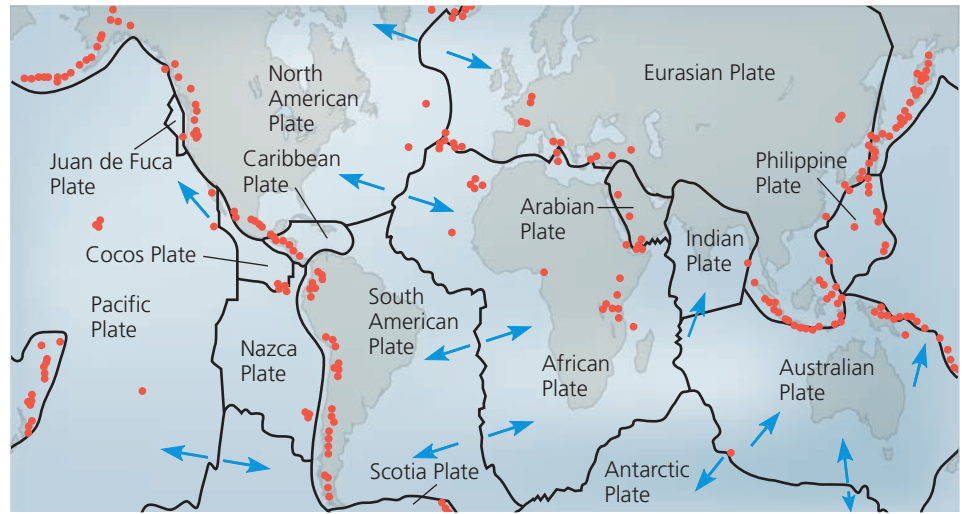
Plate movements rearrange geography slowly, but their cumulative effects are dramatic. In addition to reshaping the physical features of our planet, continental drift also has a major impact on life on Earth.

One reason for this is that continental drift alters the habitats in which organisms live. Consider the changes shown in **Figure 25.16**. About 250 million years ago, plate movements brought previously separated landmasses together into a supercontinent named **Pangaea**. Ocean basins became deeper, which lowered sea levels and drained shallow coastal seas. At that time, as now, most marine species inhabited shallow waters, and the formation of Pangaea destroyed much of that habitat. Pangaea's interior was cold and dry, probably an even more severe environment than that of central Asia today. Overall, the formation of Pangaea greatly altered the physical environment and climate, which drove some species to extinction and provided new opportunities for groups of organisms that survived the crisis.

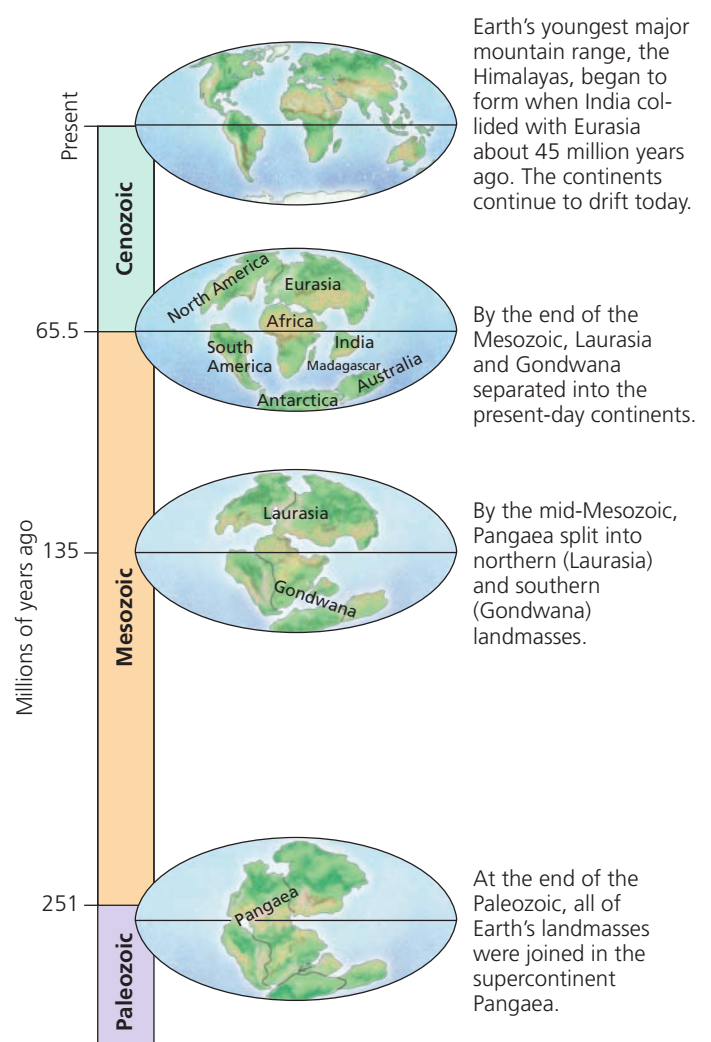
Organisms are also affected by the climate change that results when a continent shifts its location. The southern tip of Labrador, Canada, for example, once was located in the tropics but has moved 40° to the north over the last 200 million years. When faced with the changes in climate that such shifts in position entail, organisms adapt, move to a new location, or become extinct (this last outcome occurred for many organisms stranded on Antarctica).

Continental drift also promotes allopatric speciation on a grand scale. When supercontinents break apart, regions that once were connected become isolated. As the continents drifted apart over the last 200 million years, each became a separate evolutionary arena, with lineages of plants and animals that diverged from those on other continents.

Finally, continental drift can help explain puzzles about the geographic distribution of extinct organisms, such as why fossils of the same species of Permian freshwater reptiles have been discovered in both Brazil and the West African nation of Ghana. These two parts of the world, now separated by 3,000 km of ocean, were joined together when



▲ **Figure 25.15** Earth's major tectonic plates. The arrows indicate direction of movement. The reddish orange dots represent zones of violent tectonic activity.



▲ **Figure 25.16** The history of continental drift during the Phanerozoic eon.

? Is the Australian plate's current direction of movement (see *Figure 25.15*) similar to the direction it traveled over the past 65 million years?

these reptiles were living. Continental drift also explains much about the current distributions of organisms, such as why Australian fauna and flora contrast so sharply with those of the rest of the world. Marsupial mammals fill ecological roles in Australia analogous to those filled by eutherians (placental mammals) on other continents (see Figure 22.18). Fossil evidence suggests that marsupials originated in what is now Asia and reached Australia via South America and Antarctica while the continents were still joined. The subsequent breakup of the southern continents set Australia “afloat,” like a giant raft of marsupials. In Australia, marsupials diversified, and the few eutherians that lived there became extinct; on other continents, most marsupials became extinct, and the eutherians diversified.

Mass Extinctions

The fossil record shows that the overwhelming majority of species that ever lived are now extinct. A species may become extinct for many reasons. Its habitat may have been destroyed, or its environment may have changed in a manner unfavorable to the species. For example, if ocean temperatures fall by even a few degrees, species that are otherwise well adapted may perish. Even if physical factors in the environment remain stable, biological factors may change—the origin of one species can spell doom for another.

Although extinction occurs regularly, at certain times disruptive changes to the global environment have caused the rate of extinction to increase dramatically. The result is a **mass extinction**, in which large numbers of species become extinct worldwide.

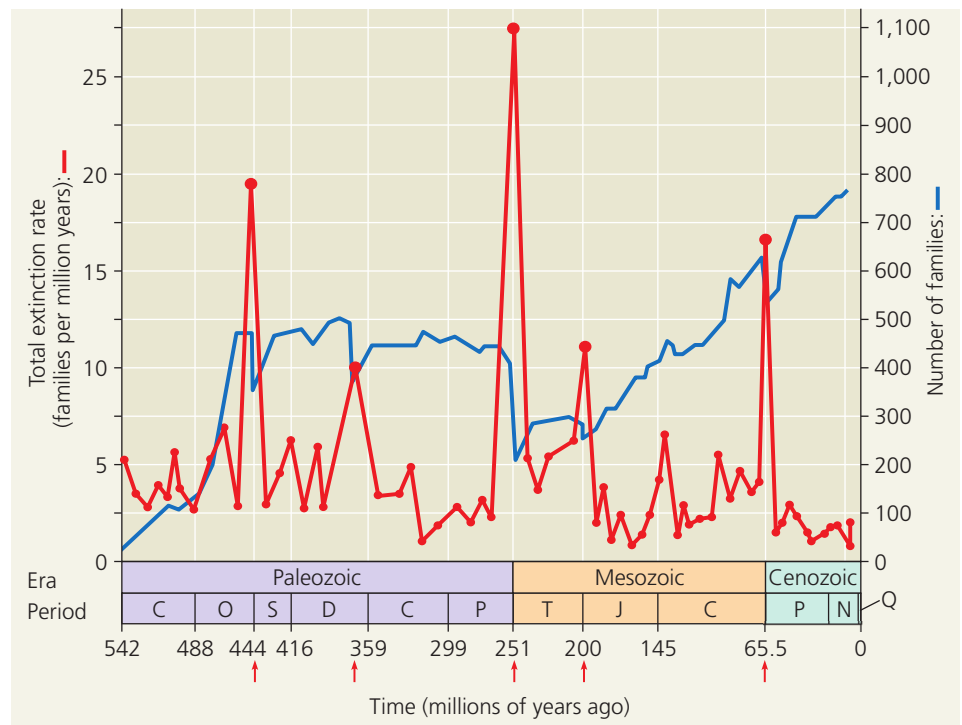
The “Big Five” Mass Extinction Events

Five mass extinctions are documented in the fossil record over the past 500 million years (Figure 25.17). These events are particularly well documented for the decimation of hard-bodied animals that lived in shallow seas, the organisms for which the fossil record is most complete. In each mass extinction, 50% or more of marine species became extinct.

Two mass extinctions—the Permian and the Cretaceous—have received the most attention. The Permian mass extinction, which defines the boundary between the Paleozoic and Mesozoic eras (251 million years ago), claimed about 96% of marine animal species and

drastically altered life in the ocean. Terrestrial life was also affected. For example, 8 out of 27 known orders of insects were wiped out. This mass extinction occurred in less than 500,000 years, possibly in just a few thousand years—an instant in the context of geologic time.

The Permian mass extinction occurred during the most extreme episode of volcanism in the past 500 million years. Geologic data indicate that 1.6 million km² (roughly half the size of western Europe) in Siberia was covered with lava hundreds of meters thick. The eruptions are thought to have produced enough carbon dioxide to warm the global climate by an estimated 6°C, harming many temperature-sensitive species. The rise in atmospheric CO₂ levels would also have led to ocean acidification, thereby reducing the availability of calcium carbonate, which is required by reef-building corals and many shell-building species (see Figure 3.11). The explosions would also have added nutrients such as phosphorous to ecosystems, stimulating the growth of microorganisms. Upon their deaths, these microorganisms would have provided food for bacterial decomposers. Bacteria use oxygen as they decompose the bodies of dead organisms, thus causing oxygen concentrations to drop. This would have harmed oxygen-breathers and promoted the growth of anaerobic bacteria that emit a poisonous metabolic by-product,



▲ **Figure 25.17 Mass extinction and the diversity of life.** The five generally recognized mass extinction events, indicated by red arrows, represent peaks in the extinction rate of marine animal families (red line and left vertical axis). These mass extinctions interrupted the overall increase in the number of marine animal families over time (blue line and right vertical axis).

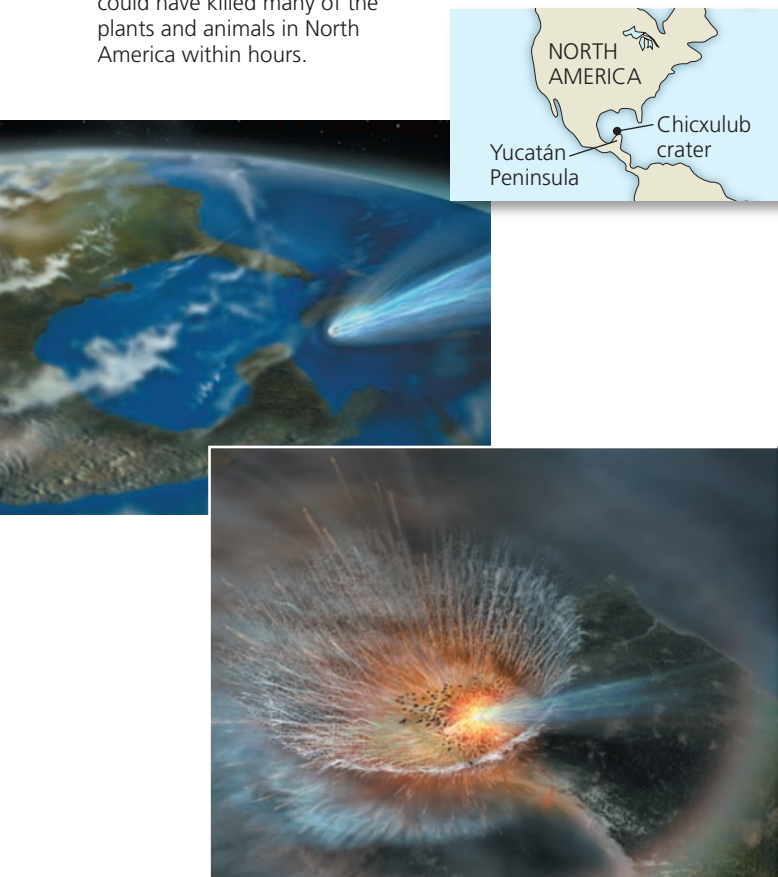
INTERPRET THE DATA 96% of marine animal species became extinct in the Permian mass extinction. Explain why the blue curve shows only a 50% drop at that time.

hydrogen sulfide (H₂S) gas. Overall, the volcanic eruptions appear to have triggered a series of catastrophic events that together resulted in the Permian mass extinction.

The Cretaceous mass extinction occurred 65.5 million years ago. This event extinguished more than half of all marine species and eliminated many families of terrestrial plants and animals, including all dinosaurs (except birds, which are members of the same group; see Chapter 34). One clue to a possible cause of the Cretaceous mass extinction is a thin layer of clay enriched in iridium that dates to the time of the mass extinction (about 65 million years ago). Iridium is an element that is very rare on Earth but common in many of the meteorites and other extraterrestrial objects that occasionally fall to Earth. As a result, researchers proposed that this clay is fallout from a huge cloud of debris that billowed into the atmosphere when an asteroid or large comet collided with Earth. This cloud would have blocked sunlight and severely disturbed the global climate for several months.

Is there evidence of such an asteroid or comet? Research has focused on the Chicxulub crater, a 65-million-year-old scar beneath sediments off the coast of Mexico (**Figure 25.18**).

▼ **Figure 25.18 A trauma for Cretaceous life.** Beneath the Caribbean Sea, the 65-million-year-old Chicxulub crater measures 180 km across. The horseshoe shape of the crater and the pattern of debris in sedimentary rocks indicate that an asteroid or comet struck at a low angle from the southeast. This drawing represents the impact and its immediate effect: a cloud of hot vapor and debris that could have killed many of the plants and animals in North America within hours.

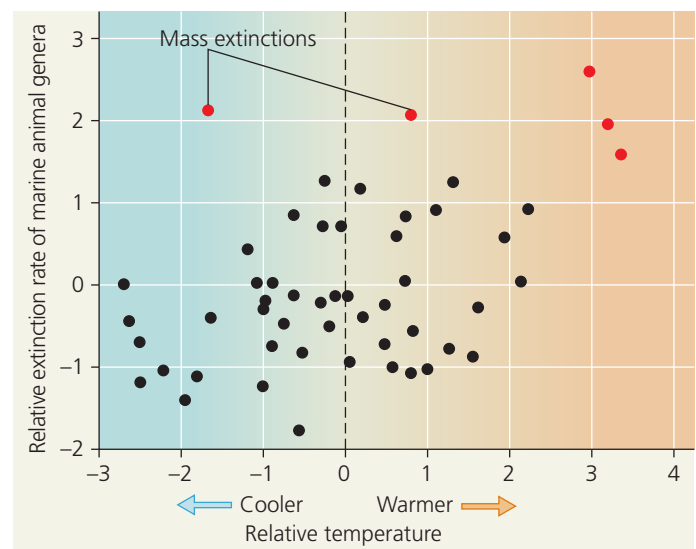


The crater is the right size to have been caused by an object with a diameter of 10 km. Critical evaluation of this and other hypotheses for mass extinctions continues.

Is a Sixth Mass Extinction Under Way?

As you will read further in Chapter 56, human actions, such as habitat destruction, are modifying the global environment to such an extent that many species are threatened with extinction. More than a thousand species have become extinct in the last 400 years. Scientists estimate that this rate is 100 to 1,000 times the typical background rate seen in the fossil record. Is a sixth mass extinction now in progress?

This question is difficult to answer, in part because it is hard to document the total number of extinctions occurring today. Tropical rain forests, for example, harbor many undiscovered species. As a result, destroying tropical forest may drive species to extinction before we even learn of their existence. Such uncertainties make it hard to assess the full extent of the current extinction crisis. Even so, it is clear that losses to date have not reached those of the “big five” mass extinctions, in which large percentages of Earth’s species became extinct. This does not in any way discount the seriousness of today’s situation. Monitoring programs show that many species are declining at an alarming rate due to habitat loss, introduced species, overharvesting, and other factors. Recent studies on a variety of organisms, including lizards, pine trees, and polar bears, suggest that climate change may hasten some of these declines. The fossil record also highlights the potential importance of climate change: Over the last 500 million years, extinction rates have tended to increase when global temperatures were high (**Figure 25.19**).



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▲ **Figure 25.19 Fossil extinctions and temperature.** Extinction rates increased when global temperatures were high. Temperatures were estimated using ratios of oxygen isotopes and converted to an index in which 0 is the overall average temperature.

Overall, the evidence suggests that unless dramatic actions are taken, a sixth, human-caused mass extinction is likely to occur within the next few centuries or millennia.

Consequences of Mass Extinctions

Mass extinctions have significant and long-term effects. By eliminating large numbers of species, a mass extinction can reduce a thriving and complex ecological community to a pale shadow of its former self. And once an evolutionary lineage disappears, it cannot reappear. The course of evolution is changed forever. Consider what would have happened if the early primates living 66 million years ago had died out in the Cretaceous mass extinction. Humans would not exist, and life on Earth would differ greatly from what it is today.

The fossil record shows that it typically takes 5–10 million years for the diversity of life to recover to previous levels after a mass extinction. In some cases, it has taken much longer than that: It took about 100 million years for the number of marine families to recover after the Permian mass extinction (see Figure 25.17). These data have sobering implications. If current trends continue and a sixth mass extinction occurs, it will take millions of years for life on Earth to recover.

Mass extinctions can also alter ecological communities by changing the types of organisms residing there. For example, after the Permian and Cretaceous mass extinctions, the percentage of marine organisms that were predators increased substantially (Figure 25.20). A rise in the number of predators can increase both the risks faced by prey and the competition among predators for food. In addition, mass extinctions can curtail lineages with novel and advantageous features. For example, in the late Triassic a group of gastropods (snails and their relatives) arose that could drill through the shells of bivalves (such as clams) and feed on the animals inside. Although shell drilling provided access

to a new and abundant source of food, this newly formed group was wiped out during the mass extinction at the end of the Triassic (about 200 million years ago). Another 120 million years passed before another group of gastropods (the oyster drills) exhibited the ability to drill through shells. As their predecessors might have done if they had not originated at an unfortunate time, oyster drills have since diversified into many new species. Finally, by eliminating so many species, mass extinctions can pave the way for adaptive radiations, in which new groups of organisms proliferate.

Adaptive Radiations

The fossil record shows that the diversity of life has increased over the past 250 million years (see blue line in Figure 25.17). This increase has been fueled by **adaptive radiations**, periods of evolutionary change in which groups of organisms form many new species whose adaptations allow them to fill different ecological roles, or niches, in their communities. Large-scale adaptive radiations occurred after each of the big five mass extinctions, when survivors became adapted to the many vacant ecological niches.

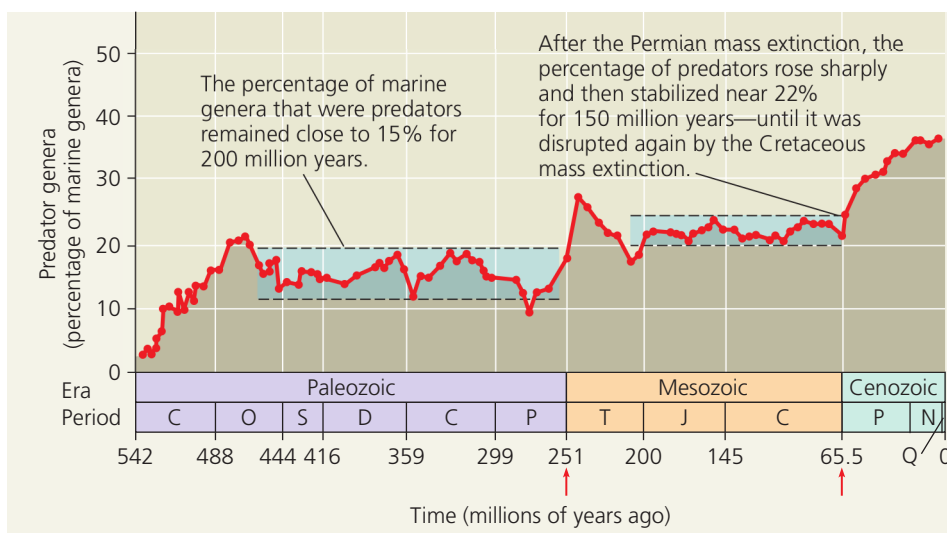
Adaptive radiations have also occurred in groups of organisms that possessed major evolutionary innovations, such as seeds or armored body coverings, or that colonized regions in which they faced little competition from other species.

Worldwide Adaptive Radiations

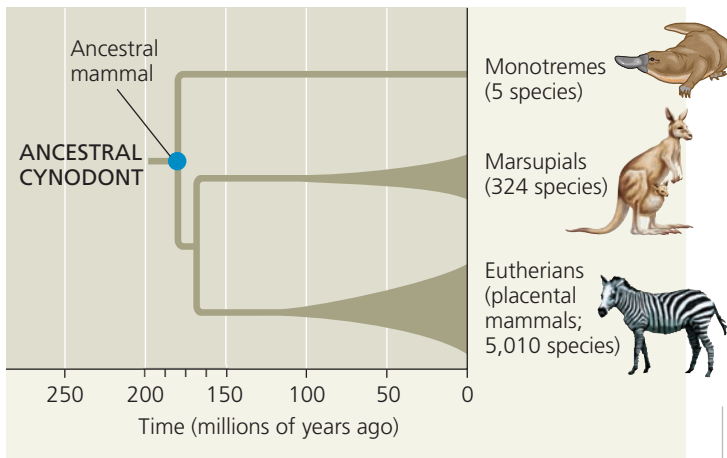
Fossil evidence indicates that mammals underwent a dramatic adaptive radiation after the extinction of terrestrial dinosaurs 65.5 million years ago (Figure 25.21). Although mammals originated about 180 million years ago, the mammal fossils older than 65.5 million years are mostly small and not morphologically diverse. Many species appear to have

been nocturnal based on their large eye sockets, similar to those in living nocturnal mammals. A few early mammals were intermediate in size, such as *Repenomamus giganticus*, a 1-m-long predator that lived 130 million years ago—but none approached the size of many dinosaurs. Early mammals may have been restricted in size and diversity because they were eaten or outcompeted by the larger and more diverse dinosaurs. With the disappearance of the dinosaurs (except for birds), mammals expanded greatly in both diversity and size, filling the ecological roles once occupied by terrestrial dinosaurs.

The history of life has also been greatly altered by radiations in which groups of organisms increased in diversity as they came to play entirely new



▲ Figure 25.20 Mass extinctions and ecology. The Permian and Cretaceous mass extinctions (indicated by red arrows) altered the ecology of the oceans by increasing the percentage of marine genera that were predators.



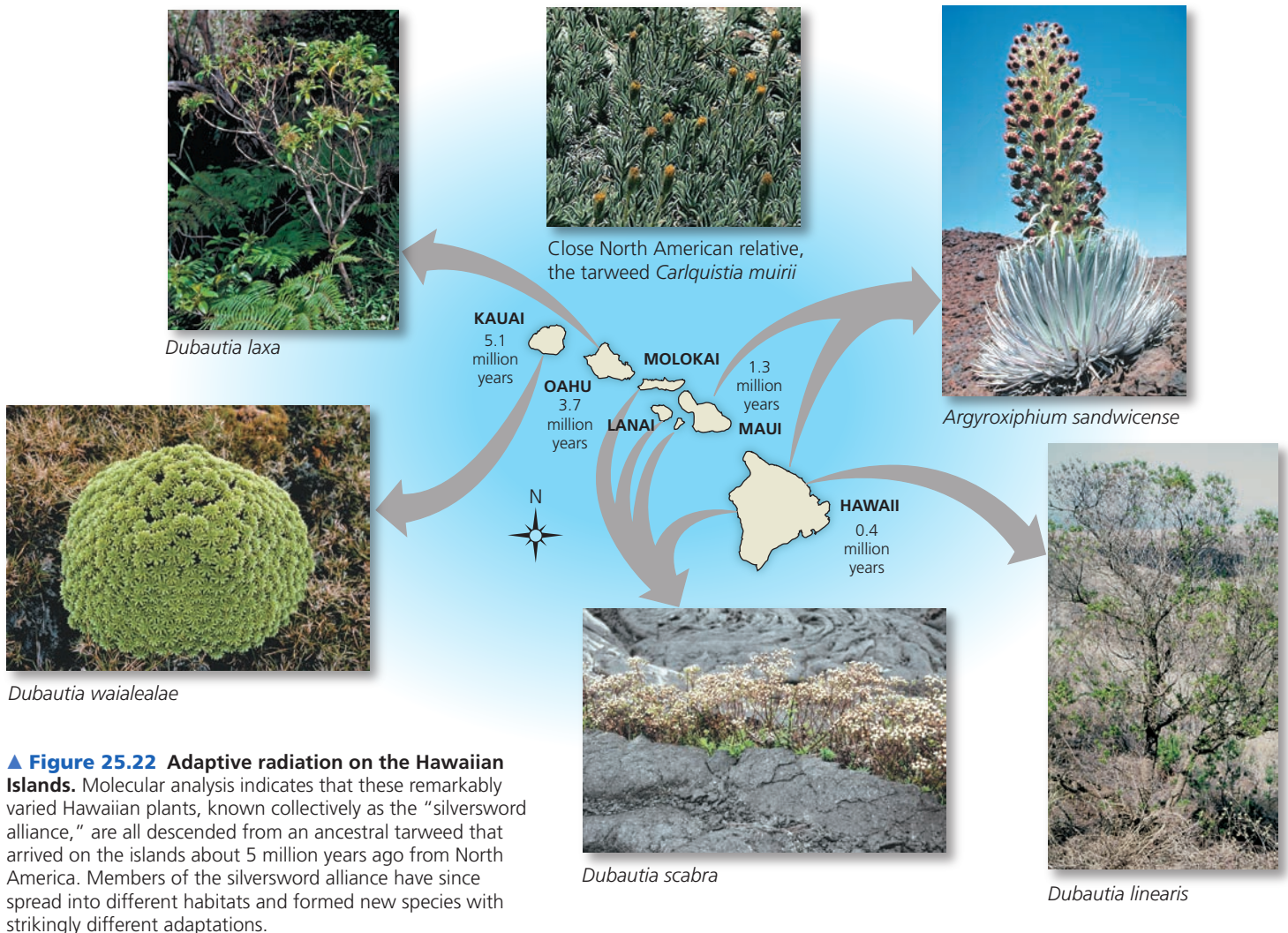
▲ **Figure 25.21** Adaptive radiation of mammals.

ecological roles in their communities. Examples include the rise of photosynthetic prokaryotes, the evolution of large predators in the Cambrian explosion, and the radiations following the colonization of land by plants, insects, and

tetrapods. Each of these last three radiations was associated with major evolutionary innovations that facilitated life on land. The radiation of land plants, for example, was associated with key adaptations, such as stems that support plants against gravity and a waxy coat that protects leaves from water loss. Finally, organisms that arise in an adaptive radiation can serve as a new source of food for still other organisms. In fact, the diversification of land plants stimulated a series of adaptive radiations in insects that ate or pollinated plants, one reason that insects are the most diverse group of animals on Earth today.

Regional Adaptive Radiations

Striking adaptive radiations have also occurred over more limited geographic areas. Such radiations can be initiated when a few organisms make their way to a new, often distant location in which they face relatively little competition from other organisms. The Hawaiian archipelago is one of the world's great showcases of this type of adaptive radiation (**Figure 25.22**). Located about 3,500 km from the



▲ **Figure 25.22** Adaptive radiation on the Hawaiian Islands. Molecular analysis indicates that these remarkably varied Hawaiian plants, known collectively as the “silversword alliance,” are all descended from an ancestral tarweed that arrived on the islands about 5 million years ago from North America. Members of the silversword alliance have since spread into different habitats and formed new species with strikingly different adaptations.

nearest continent, the volcanic islands are progressively older as one follows the chain toward the northwest; the youngest island, Hawaii, is less than a million years old and still has active volcanoes. Each island was born “naked” and was gradually populated by stray organisms that rode the ocean currents and winds either from far-distant land areas or from older islands of the archipelago itself. The physical diversity of each island, including immense variation in elevation and rainfall, provides many opportunities for evolutionary divergence by natural selection. Multiple invasions followed by speciation events have ignited an explosion of adaptive radiation in Hawaii. As a result, most of the thousands of species that inhabit the islands are found nowhere else on Earth.

CONCEPT CHECK 25.4

1. Explain the consequences of plate tectonics for life on Earth.
2. What factors promote adaptive radiations?
3. **WHAT IF?** Suppose that an invertebrate species was lost in a mass extinction caused by a sudden catastrophic event. Would the last appearance of this species in the fossil record necessarily be close to when the extinction actually occurred? Would the answer to this question differ depending on whether the species was common (abundant and widespread) or rare? Explain.

For suggested answers, see Appendix A.

CONCEPT 25.5

Major changes in body form can result from changes in the sequences and regulation of developmental genes

The fossil record tells us what the great changes in the history of life have been and when they occurred. Moreover, an understanding of plate tectonics, mass extinction, and adaptive radiation provides a picture of how those changes came about. But we can also seek to understand the intrinsic biological mechanisms that underlie changes seen in the fossil record. For this, we turn to genetic mechanisms of change, paying particular attention to genes that influence development.

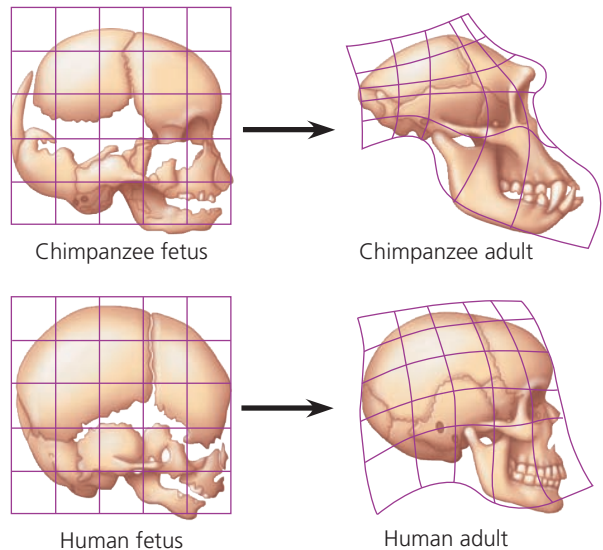
Effects of Developmental Genes

As you read in Chapter 21, “evo-devo”—research at the interface between evolutionary biology and developmental biology—is illuminating how slight genetic differences can produce major morphological differences between species. In particular, large morphological differences can result from genes that alter the rate, timing, and spatial pattern of change in an organism’s form as it develops from a zygote into an adult.



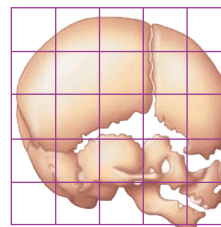
Chimpanzee infant

Chimpanzee adult

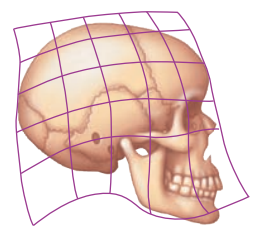


Chimpanzee fetus

Chimpanzee adult



Human fetus



Human adult

▲ **Figure 25.23** Relative skull growth rates. In the human evolutionary lineage, mutations slowed the growth of the jaw relative to other parts of the skull. As a result, in humans the skull of an adult is more similar to the skull of an infant than is the case for chimpanzees.

Changes in Rate and Timing

Many striking evolutionary transformations are the result of **heterochrony** (from the Greek *hetero*, different, and *chronos*, time), an evolutionary change in the rate or timing of developmental events. For example, an organism’s shape depends in part on the relative growth rates of different body parts during development. Changes to these rates can alter the adult form substantially, as seen in the contrasting shapes of human and chimpanzee skulls (**Figure 25.23**). Other examples of the dramatic evolutionary effects of heterochrony include how increased growth rates of finger bones yielded the skeletal structure of wings in bats (see **Figure 22.15**) and how slowed growth of leg and pelvic bones led to the reduction and eventual loss of hind limbs in whales (see **Figure 22.20**).

Heterochrony can also alter the timing of reproductive development relative to the development of nonreproductive organs. If reproductive organ development accelerates compared to other organs, the sexually mature stage of a species may retain body features that were juvenile structures in an ancestral species, a condition called **paedomorphosis** (from the Greek *paedos*, of a child, and *morphosis*, formation). For example, most salamander species have



▲ **Figure 25.24 Paedomorphosis.** The adults of some species retain features that were juvenile in ancestors. This salamander is an axolotl, an aquatic species that becomes a sexually mature adult while retaining certain larval (tadpole) characteristics, including gills.

aquatic larvae that undergo metamorphosis in becoming adults. But some species grow to adult size and become sexually mature while retaining gills and other larval features (**Figure 25.24**). Such an evolutionary alteration of developmental timing can produce animals that appear very different from their ancestors, even though the overall genetic change may be small. Indeed, recent evidence indicates that a change at a single locus was probably sufficient to bring about paedomorphosis in the axolotl salamander, although other genes may have contributed as well.

Changes in Spatial Pattern

Substantial evolutionary changes can also result from alterations in genes that control the spatial organization of body parts. For example, master regulatory genes called **homeotic genes** (described in Chapters 18 and 21) determine such basic features as where a pair of wings and legs will develop on a bird or how a plant's flower parts are arranged.

The products of one class of homeotic genes, the *Hox* genes, provide positional information in an animal embryo. This information prompts cells to develop into structures appropriate for a particular location. Changes in *Hox* genes or in how they are expressed can have a profound impact on morphology. For example, among crustaceans, a change in the location where two *Hox* genes (*Ubx* and *Scr*) are expressed correlates with the conversion of a swimming appendage to a feeding appendage. Similarly, when comparing plant species, changes to the expression of homeotic genes known as *MADS-box* genes can produce flowers that differ dramatically in form (see Chapter 35).

The Evolution of Development

The 560-million-year-old fossils of Ediacaran animals in Figure 25.5 suggest that a set of genes sufficient to produce complex animals existed at least 25 million years *before* the Cambrian explosion. If such genes have existed for so long, how can we explain the astonishing increases in diversity seen during and since the Cambrian explosion?

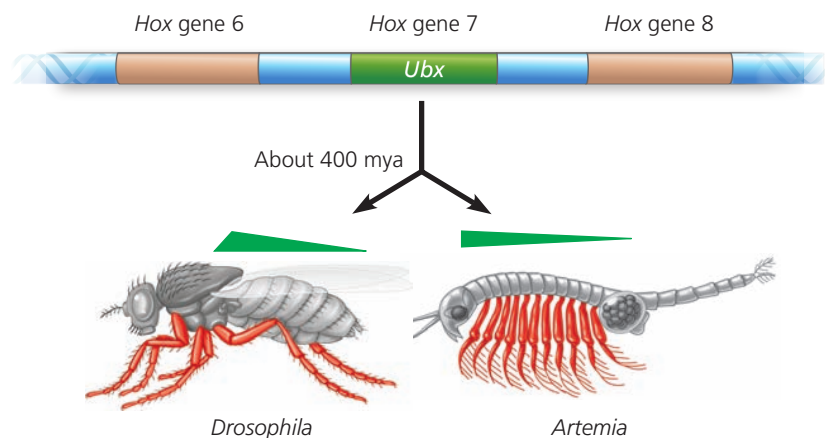
Adaptive evolution by natural selection provides one answer to this question. As we've seen throughout this unit, by sorting among differences in the sequences of protein-encoding genes, selection can improve adaptations rapidly. In addition, new genes (created by gene duplication events) can take on new metabolic and structural functions, as can existing genes that are regulated in new ways.

Examples in the previous section suggest that developmental genes may have been particularly important. Thus, we'll turn next to how new morphological forms can arise from changes in the nucleotide sequences or regulation of developmental genes.

Changes in Genes

New developmental genes arising after gene duplication events very likely facilitated the origin of novel morphological forms. But since other genetic changes also may have occurred at such times, it can be difficult to establish causal links between genetic and morphological changes that occurred in the past.

This difficulty was sidestepped in a study of developmental changes associated with the divergence of six-legged insects from crustacean-like ancestors that had more than six legs. In insects, such as *Drosophila*, the *Ubx* gene is expressed in the abdomen, while in crustaceans, such as *Artemia*, it is expressed in the main trunk of the body (**Figure 25.25**). When expressed, the *Ubx* gene suppresses leg formation in insects but not in crustaceans. To examine the workings of this gene, researchers cloned the *Ubx* gene from *Drosophila* and *Artemia*. Next, they genetically engineered fruit fly embryos to express either the *Drosophila Ubx* gene or the *Artemia Ubx* gene throughout their bodies. The *Drosophila* gene suppressed 100% of the limbs in the embryos, as expected, whereas the *Artemia* gene suppressed only 15%.



▲ **Figure 25.25 Origin of the insect body plan.** Expression of the *Hox* gene *Ubx* suppresses the formation of legs in fruit flies (*Drosophila*) but not in brine shrimp (*Artemia*), thus helping to build the insect body plan. Fruit fly and brine shrimp *Hox* genes have evolved independently for 400 million years. The green triangles indicate the relative amounts of *Ubx* expression in different body regions.

The researchers then sought to uncover key steps involved in the evolutionary transition from a crustacean *Ubx* gene to an insect *Ubx* gene. Their approach was to identify mutations that would cause the *Artemia Ubx* gene to suppress leg formation, thus making the crustacean gene act more like an insect *Ubx* gene. To do this, they constructed a series of “hybrid” *Ubx* genes, each of which contained known segments of the *Drosophila Ubx* gene and known segments of the *Artemia Ubx* gene. By inserting these hybrid genes into fruit fly embryos (one hybrid gene per embryo) and observing their effects on leg development, the researchers were able to pinpoint the exact amino acid changes responsible for the suppression of additional limbs in insects. In so doing, this study provided evidence linking a particular change in the nucleotide sequence of a developmental gene to a major evolutionary change: the origin of the six-legged insect body plan.

Changes in Gene Regulation

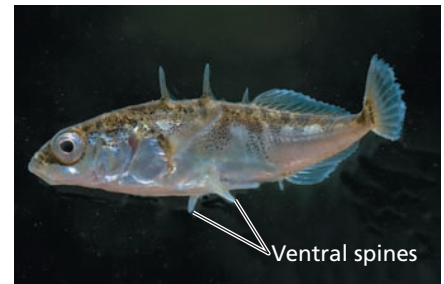
A change in the nucleotide sequence of a gene may affect its function wherever the gene is expressed, while changes in the regulation of gene expression can be limited to one cell type (see Chapter 18). Thus, a change in the regulation of a developmental gene may have fewer harmful side effects than a change to the sequence of the gene. This reasoning has prompted researchers to suggest that changes in the form of organisms may often be caused by mutations that affect the regulation of developmental genes—not their sequences.

This idea is supported by studies of a variety of species, including threespine stickleback fish. These fish live in the open ocean and in shallow, coastal waters. In western Canada, they also live in lakes formed when the coastline receded during the past 12,000 years. Marine stickleback fish have a pair of spines on their ventral (lower) surface, which deter some predators. These spines

▼ Figure 25.26 Inquiry

What causes the loss of spines in lake stickleback fish?

Experiment Marine populations of the threespine stickleback fish (*Gasterosteus aculeatus*) have a set of protective spines on their lower (ventral) surface; however, these spines have been lost or reduced in some lake populations of this fish. Working at Stanford University, Michael Shapiro, David Kingsley, and colleagues performed genetic crosses and found that most of the reduction in spine size resulted from the effects of a single developmental gene, *Pitx1*. The researchers then tested two hypotheses about how *Pitx1* causes this morphological change.



▲ Threespine stickleback (*Gasterosteus aculeatus*)

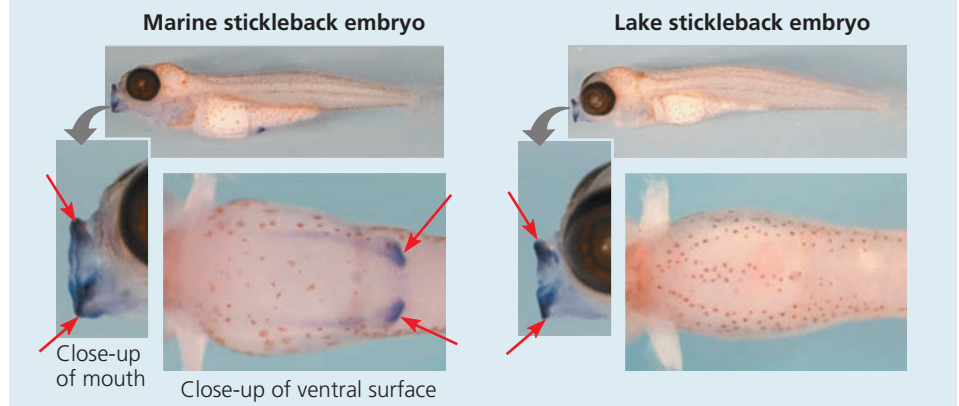
Hypothesis A: A change in the DNA sequence of *Pitx1* had caused spine reduction in lake populations. To test this idea, the team used DNA sequencing to compare the coding sequence of the *Pitx1* gene between marine and lake stickleback populations.

Hypothesis B: A change in the regulation of the expression of *Pitx1* had caused spine reduction. To test this idea, the researchers monitored where in the developing embryo the *Pitx1* gene was expressed. They conducted whole-body *in situ* hybridization experiments (see Chapter 20) using *Pitx1* DNA as a probe to detect *Pitx1* mRNA in the fish.

Results

Test of Hypothesis A:	Are there differences in the coding sequence of the <i>Pitx1</i> gene in marine and lake stickleback fish?	Result: No →	The 283 amino acids of the <i>Pitx1</i> protein are identical in marine and lake stickleback populations.
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Test of Hypothesis B:	Are there any differences in the regulation of expression of <i>Pitx1</i> ?	Result: Yes →	Red arrows (→) indicate regions of <i>Pitx1</i> gene expression in the photographs below. <i>Pitx1</i> is expressed in the ventral spine and mouth regions of developing marine stickleback fish but only in the mouth region of developing lake stickleback fish.
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Conclusion The loss or reduction of ventral spines in lake populations of threespine stickleback fish appears to have resulted primarily from a change in the regulation of *Pitx1* gene expression, not from a change in the gene's sequence.

Source: M. D. Shapiro et al., Genetic and developmental basis of evolutionary pelvic reduction in three-spine sticklebacks, *Nature* 428:717–723 (2004).

WHAT IF? Describe the set of results that would have led researchers to the conclusion that a change in the coding sequence of the *Pitx1* gene was more important than a change in regulation of gene expression.

are often reduced or absent in stickleback fish living in lakes that lack predatory fishes and that are also low in calcium. Spines may have been lost in such lakes because they are not advantageous in the absence of predators, and the limited calcium is needed for purposes other than constructing spines.

At the genetic level, the developmental gene *Pitx1* was known to influence whether stickleback fish have ventral spines. Was the reduction of spines in some lake populations due to changes in the *Pitx1* gene or to changes in how the gene is expressed (Figure 25.26)? The researchers' results indicate that the regulation of gene expression has changed, not the DNA sequence. Moreover, lake stickleback fish do express the *Pitx1* gene in tissues not related to the production of spines (for example, the mouth), illustrating how morphological change can be caused by altering the expression of a developmental gene in some parts of the body but not others. In a 2010 follow-up study, researchers showed that changes to the *Pel* enhancer, a noncoding DNA region that affects expression of the *Pitx1* gene, resulted in the reduction of ventral spines in lake sticklebacks.

CONCEPT CHECK 25.5

1. How can heterochrony cause the evolution of different body forms?
2. Why is it likely that *Hox* genes have played a major role in the evolution of novel morphological forms?
3. **MAKE CONNECTIONS** Given that changes in morphology are often caused by changes in the regulation of gene expression, predict whether noncoding DNA is likely to be affected by natural selection. See Concept 18.3 to review noncoding DNA and regulation of gene expression.

For suggested answers, see Appendix A.

CONCEPT 25.6

Evolution is not goal oriented

What does our study of macroevolution tell us about how evolution works? One lesson is that throughout the history of life, the origin of new species has been affected by both the small-scale factors described in Chapter 23 (such as natural selection operating in populations) and the large-scale factors described in this chapter (such as continental drift promoting bursts of speciation throughout the globe). Moreover, to paraphrase the Nobel Prize–winning geneticist François Jacob, evolution is like tinkering—a process in which new forms arise by the modification of existing structures or existing developmental genes. Over time, such tinkering has led to three key features of the natural world described in Chapter 22: the striking ways in which organisms are suited for life in their environments; the many shared characteristics of life; and the rich diversity of life.

Evolutionary Novelties

François Jacob's view of evolution harkens back to Darwin's concept of descent with modification. As new species form, novel and complex structures can arise as gradual modifications of ancestral structures. In many cases, complex structures have evolved in increments from simpler versions that performed the same basic function. For example, consider the human eye, an intricate organ constructed from numerous parts that work together in forming an image and transmitting it to the brain. How could the human eye have evolved in gradual increments? Some argue that if the eye needs all of its components to function, a partial eye could not have been of use to our ancestors.

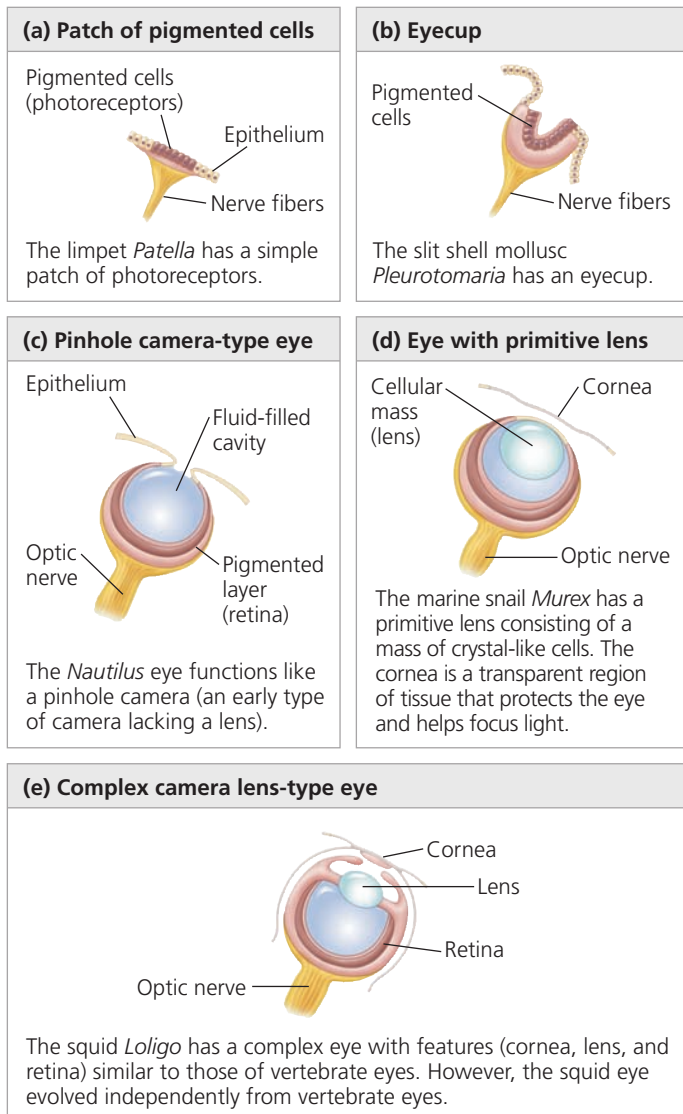
The flaw in this argument, as Darwin himself noted, lies in the assumption that only complicated eyes are useful. In fact, many animals depend on eyes that are far less complex than our own. The simplest eyes that we know of are patches of light-sensitive photoreceptor cells. These simple eyes appear to have had a single evolutionary origin and are now found in a variety of animals, including small molluscs called limpets. Such eyes have no equipment for focusing images, but they do enable the animal to distinguish light from dark. Limpets cling more tightly to their rock when a shadow falls on them, a behavioral adaptation that reduces the risk of being eaten (Figure 25.27). Limpets have had a long evolutionary history, demonstrating that their “simple” eyes are quite adequate to support their survival and reproduction.

In the animal kingdom, complex eyes have evolved independently from such basic structures many times (Figure 25.28, on the next page). Some molluscs, such as squids and octopuses, have eyes as complex as those of humans and other vertebrates. Although complex mollusc eyes evolved independently of vertebrate eyes, both evolved from a simple cluster of photoreceptor cells present in a common ancestor. In each case, the complex eye evolved through a



▲ **Figure 25.27** Limpets (*Patella vulgata*), molluscs that can sense light and dark with a simple patch of photoreceptor cells.

▼ **Figure 25.28** A range of eye complexity among molluscs.



series of steps that benefited the eyes' owners at every stage. Evidence of their independent evolution can be found in their structure: Vertebrate eyes detect light at the back layer of the retina and conduct nerve impulses toward the front, while complex mollusc eyes do the reverse.

Throughout their evolutionary history, eyes retained their basic function of vision. But evolutionary novelties can also arise when structures that originally played one role gradually acquire a different one. For example, as cynodonts gave rise to early mammals, bones that formerly comprised the jaw hinge (the articular and quadrate; see Figure 25.7) were incorporated into the ear region of mammals, where they eventually took on a new function: the transmission of sound (see Chapter 34). Structures that evolve in one context but become co-opted for another function are sometimes called *exaptations* to distinguish them from the adaptive origin of the original structure. Note that the concept of exaptation does not imply that a structure

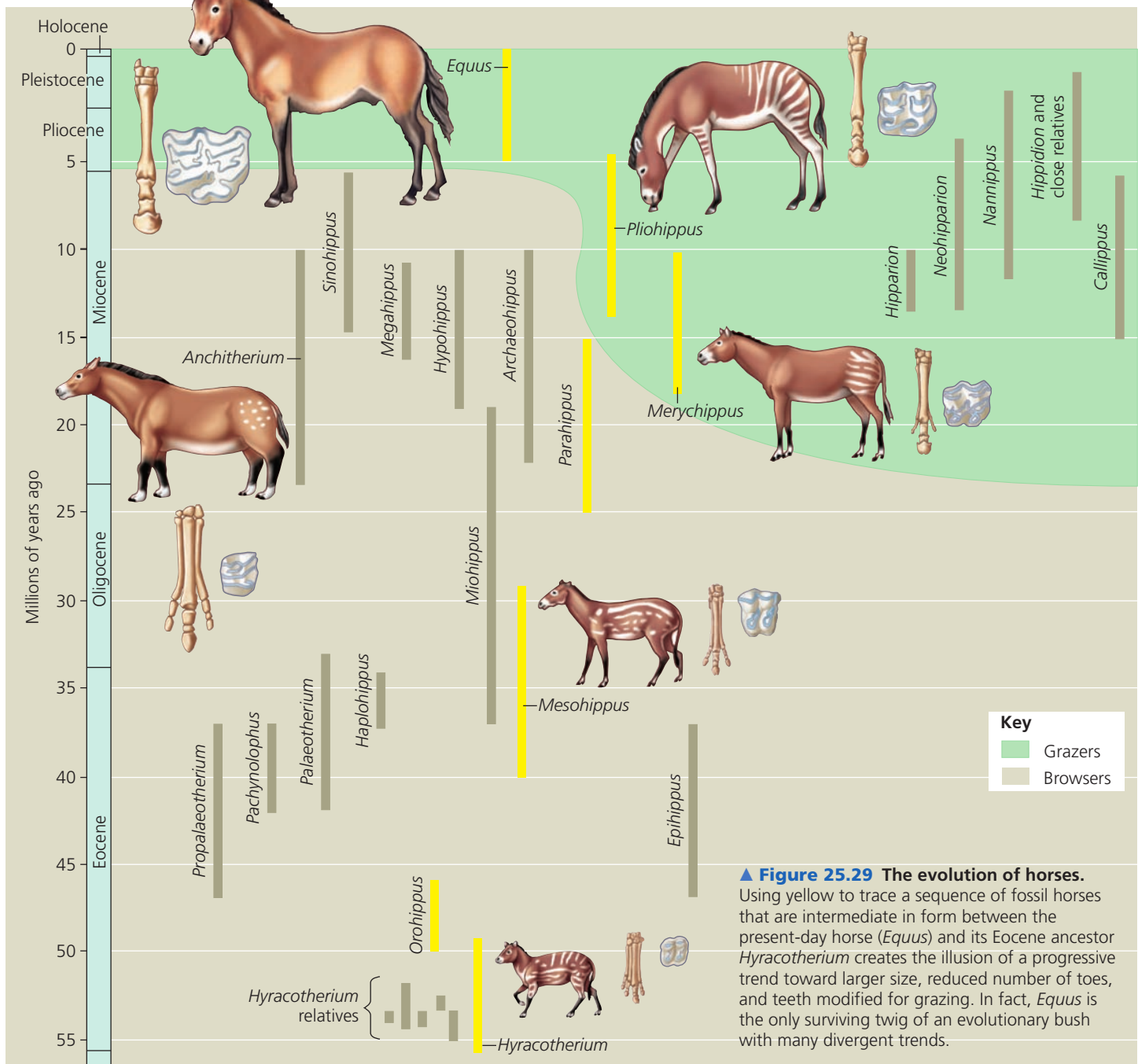
somehow evolves in anticipation of future use. Natural selection cannot predict the future; it can only improve a structure in the context of its *current* utility. Novel features, such as the new jaw hinge and ear bones of early mammals, can arise gradually via a series of intermediate stages, each of which has some function in the organism's current context.

Evolutionary Trends

What else can we learn from patterns of macroevolution? Consider evolutionary "trends" observed in the fossil record. For instance, some evolutionary lineages exhibit a trend toward larger or smaller body size. An example is the evolution of the present-day horse (genus *Equus*), a descendant of the 55-million-year-old *Hyracotherium* (Figure 25.29). About the size of a large dog, *Hyracotherium* had four toes on its front feet, three toes on its hind feet, and teeth adapted for browsing on bushes and trees. In comparison, present-day horses are larger, have only one toe on each foot, and possess teeth modified for grazing on grasses.

Extracting a single evolutionary progression from the fossil record can be misleading, however; it is like describing a bush as growing toward a single point by tracing only the branches that lead to that twig. For example, by selecting certain species from the available fossils, it is possible to arrange a succession of animals intermediate between *Hyracotherium* and living horses that shows a trend toward large, single-toed species (follow the yellow highlighting in Figure 25.29). However, if we consider *all* fossil horses known today, this apparent trend vanishes. The genus *Equus* did not evolve in a straight line; it is the only surviving twig of an evolutionary tree that is so branched that it is more like a bush. *Equus* actually descended through a series of speciation episodes that included several adaptive radiations, not all of which led to large, one-toed, grazing horses. In fact, phylogenetic analyses suggest that all lineages that include grazers are closely related to *Parahippus*; the many other horse lineages, all of which are now extinct, remained multi-toed browsers for 35 million years.

Branching evolution *can* result in a real evolutionary trend even if some species counter the trend. One model of long-term trends views species as analogous to individuals: Speciation is their birth, extinction is their death, and new species that diverge from them are their offspring. In this model, just as populations of individual organisms undergo natural selection, species undergo *species selection*. The species that endure the longest and generate the most new offspring species determine the direction of major evolutionary trends. The species selection model suggests that "differential speciation success" plays a role in macroevolution similar to the role of differential reproductive success in microevolution. Evolutionary trends can also result directly from natural selection. For example, when horse ancestors invaded the grasslands that spread during the mid-Cenozoic,



▲ Figure 25.29 The evolution of horses. Using yellow to trace a sequence of fossil horses that are intermediate in form between the present-day horse (*Equus*) and its Eocene ancestor *Hyracotherium* creates the illusion of a progressive trend toward larger size, reduced number of toes, and teeth modified for grazing. In fact, *Equus* is the only surviving twig of an evolutionary bush with many divergent trends.

there was strong selection for grazers that could escape predators by running faster. This trend would not have occurred without open grasslands.

Whatever its cause, an evolutionary trend does not imply that there is some intrinsic drive toward a particular phenotype. Evolution is the result of the interactions between organisms and their current environments; if environmental conditions change, an evolutionary trend may cease or even reverse itself. The cumulative effect of these ongoing interactions between organisms and their environments is enormous: It is through them that the staggering diversity of life—Darwin’s “endless forms most beautiful”—has arisen.

CONCEPT CHECK 25.6

1. How can the Darwinian concept of descent with modification explain the evolution of such complex structures as the vertebrate eye?
2. **WHAT IF?** The myxoma virus kills up to 99.8% of infected European rabbits in populations with no previous exposure to the virus. The virus is transmitted between living rabbits by mosquitoes. Describe an evolutionary trend (in either the rabbit or virus) that might occur after a rabbit population first encounters the virus.

For suggested answers, see Appendix A.

25 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 25.1

Conditions on early Earth made the origin of life possible (pp. 520–522)

- Experiments simulating possible early atmospheres have produced organic molecules from inorganic precursors. Amino acids, lipids, sugars, and nitrogenous bases have also been found in meteorites.
- Amino acids and RNA nucleotides polymerize when dripped onto hot sand, clay, or rock. Organic compounds can spontaneously assemble into **protocells**, membrane-bounded droplets that have some properties of cells.
- The first genetic material may have self-replicating, catalytic RNA. Early protocells containing such RNA would have increased through natural selection.

? Describe the roles that montmorillonite clay and vesicles may have played in the origin of life.

CONCEPT 25.2

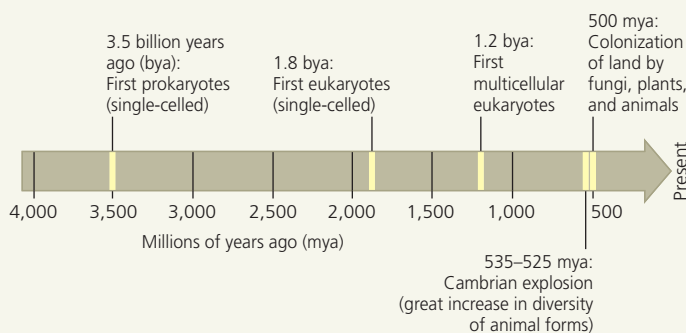
The fossil record documents the history of life (pp. 522–526)

- The **fossil record**, based largely on fossils found in sedimentary rocks, documents the rise and fall of different groups of organisms over time.
- Sedimentary strata reveal the relative ages of **fossils**. The absolute ages of fossils can be estimated by radiometric dating and other methods.
- The fossil record shows how new groups of organisms can arise via the gradual modification of preexisting organisms.

? What are the challenges of estimating the absolute ages of old fossils? Explain how these challenges may be overcome in some circumstances.

CONCEPT 25.3

Key events in life's history include the origins of unicellular and multicellular organisms and the colonization of land (pp. 526–531)



? What is the “Cambrian explosion,” and why is it significant?

CONCEPT 25.4

The rise and fall of groups of organisms reflect differences in speciation and extinction rates (pp. 531–538)

- In **plate tectonics**, continental plates move gradually over time, altering the physical geography and climate of Earth. These changes lead to extinctions in some groups of organisms and bursts of speciation in others.
- Evolutionary history has been punctuated by five **mass extinctions** that radically altered the history of life. Some of these extinctions may have been caused by changes in continent positions, volcanic activity, or impacts from meteorites or comets.
- Large increases in the diversity of life have resulted from **adaptive radiations** that followed mass extinctions. Adaptive radiations have also occurred in groups of organisms that possessed major evolutionary innovations or that colonized new regions in which there was little competition from other organisms.

? Explain how the broad evolutionary changes seen in the fossil record are the cumulative result of speciation and extinction events.

CONCEPT 25.5

Major changes in body form can result from changes in the sequences and regulation of developmental genes (pp. 538–541)

- Developmental genes affect morphological differences between species by influencing the rate, timing, and spatial patterns of change in an organism's form as it develops into an adult.
- The evolution of new forms can be caused by changes in the nucleotide sequences or regulation of developmental genes.

? How could changes in a single gene or DNA region ultimately lead to the origin of a new group of organisms?

CONCEPT 25.6

Evolution is not goal oriented (pp. 541–543)

- Novel and complex biological structures can evolve through a series of incremental modifications, each of which benefits the organism that possesses it.
- Evolutionary trends can be caused by factors such as natural selection in a changing environment or species selection. Like all aspects of evolution, evolutionary trends result from interactions between organisms and their current environments.

? Explain the reasoning behind the statement “Evolution is not goal oriented.”

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

1. Fossilized stromatolites
 - a. formed around deep-sea vents.
 - b. resemble structures formed by bacterial communities that are found today in some shallow marine bays.
 - c. provide evidence that plants moved onto land in the company of fungi around 500 million years ago.
 - d. contain the first undisputed fossils of eukaryotes and date from 1.8 billion years ago.

2. The oxygen revolution changed Earth's environment dramatically. Which of the following took advantage of the presence of free oxygen in the oceans and atmosphere?
 - a. the evolution of cellular respiration, which used oxygen to help harvest energy from organic molecules
 - b. the persistence of some animal groups in anaerobic habitats
 - c. the evolution of photosynthetic pigments that protected early algae from the corrosive effects of oxygen
 - d. the evolution of chloroplasts after early protists incorporated photosynthetic cyanobacteria
3. Which factor most likely caused animals and plants in India to differ greatly from species in nearby southeast Asia?
 - a. The species became separated by convergent evolution.
 - b. The climates of the two regions are similar.
 - c. India is in the process of separating from the rest of Asia.
 - d. India was a separate continent until 45 million years ago.
4. Adaptive radiations can be a direct consequence of three of the following four factors. Select the exception.
 - a. vacant ecological niches
 - b. genetic drift
 - c. colonization of an isolated region that contains suitable habitat and few competitor species
 - d. evolutionary innovation
5. Which of the following steps has *not* yet been accomplished by scientists studying the origin of life?
 - a. synthesis of small RNA polymers by ribozymes
 - b. formation of molecular aggregates with selectively permeable membranes
 - c. formation of protocells that use DNA to direct the polymerization of amino acids
 - d. abiotic synthesis of organic molecules

LEVEL 2: APPLICATION/ANALYSIS

6. A genetic change that caused a certain *Hox* gene to be expressed along the tip of a vertebrate limb bud instead of farther back helped make possible the evolution of the tetrapod limb. This type of change is illustrative of
 - a. the influence of environment on development.
 - b. paedomorphosis.
 - c. a change in a developmental gene or in its regulation that altered the spatial organization of body parts.
 - d. heterochrony.
7. A swim bladder is a gas-filled sac that helps fish maintain buoyancy. The evolution of the swim bladder from the air-breathing organ (a simple lung) of an ancestral fish is an example of
 - a. exaptation.
 - b. changes in *Hox* gene expression.
 - c. paedomorphosis.
 - d. adaptive radiation.

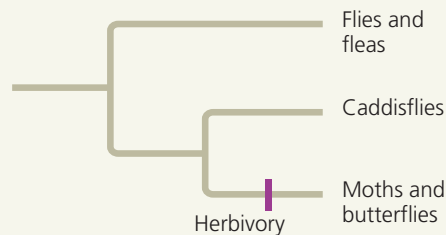
LEVEL 3: SYNTHESIS/EVALUATION

8. EVOLUTION CONNECTION

Describe how gene flow, genetic drift, and natural selection all can influence macroevolution.

9. SCIENTIFIC INQUIRY

Herbivory (plant eating) has evolved repeatedly in insects, typically from meat-eating or detritus-feeding ancestors (detritus is dead organic matter). Moths and butterflies, for example, eat plants, whereas their "sister group" (the insect group to which they are most closely related), the caddisflies, feed on animals, fungi, or detritus. As illustrated in the following phylogenetic tree, the combined moth/butterfly and caddisfly group shares a common ancestor with flies and fleas. Like caddisflies, flies and fleas are thought to have evolved from ancestors that did not eat plants.



There are 140,000 species of moths and butterflies and 7,000 species of caddisflies. State a hypothesis about the impact of herbivory on adaptive radiations in insects. How could this hypothesis be tested?

10. WRITE ABOUT A THEME: ORGANIZATION

You have seen many examples of how form fits function at all levels of the biological hierarchy. However, we can imagine forms that would function better than some forms actually found in nature. For example, if the wings of a bird were not formed from its forelimbs, such a hypothetical bird could fly yet also hold objects with its forelimbs. In a short essay (100–150 words), use the concept of "evolution as tinkering" to explain why there are limits to the functionality of forms in nature.

11. SYNTHESIZE YOUR KNOWLEDGE



In 2010, the Soufriere Hills volcano on the Caribbean island of Montserrat erupted violently, spewing huge clouds of ash and gases into the sky. Explain how the volcanic eruptions at the end of the Permian period and the formation of Pangaea, both of which occurred about 251 million years ago, set in motion events that altered evolutionary history.

For suggested answers, see Appendix A.

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5

THE EVOLUTIONARY HISTORY
OF BIOLOGICAL DIVERSITY

AN INTERVIEW WITH

Nicole King

Winner of a MacArthur Fellowship “genius” award, Nicole King is an Associate Professor of Genetics, Genomics, and Development at the University of California, Berkeley. Dr. King earned a B.S. in biology from Indiana University and a Ph.D. in biochemistry from Harvard University. Dr. King and her students are using an exciting mix of molecular genetic, developmental, and genomic approaches to reconstruct steps in a key event in the evolutionary history of life—how animals, which are multicellular, arose from their unicellular ancestors.

**How did you first become interested in the history of life?**

Growing up in Florida, my brother and I spent many hours exploring a creek near our home that was littered with fossilized sharks’ teeth. We found tons of teeth, along with fossils of manta rays and other marine organisms. We could see that the land where we lived had once been covered by the ocean. Those fossils, combined with my love of being outdoors in nature, set the stage for my interest in the history of life. Also, my father is a historian. He took me on trips when he was working with Native American communities on reconstructing their oral histories. Just as you can learn about a human society today by studying its history, I became interested in what we can learn about animal biology by studying how animals first evolved.

“Just as you can learn about a human society today by studying its history, I became interested in what we can learn about animal biology by studying how animals first evolved.”

Just as you can learn about a human society today by studying its history, I became interested in what we can learn about animal biology by studying how animals first evolved.

You’re studying choanoflagellates in your lab. What are these organisms?

Choanoflagellates are single-celled organisms, although some also form simple colonies. Each cell has a flagellum that is surrounded at its base by projections that form a “collar.” To me, the collar looks like a sieve or filter. The collar traps bacteria, which the cell then eats. Sponges, which are very simple animals, have cells that are almost indistinguishable from choanoflagellate cells. Thus, based on shape alone, the early indication was that choanoflagellates were related to animals. And now, with the benefit of genomics and other methods, the jury is in—choanoflagellates and animals are each other’s closest relatives.


And now, with the benefit of genomics and other methods, the jury is in—choanoflagellates and animals are each other’s closest relatives.

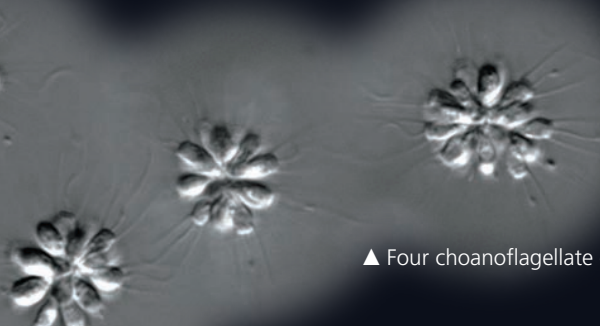
What can you learn about the origin of animals by studying choanoflagellates?

A key step in the origin of animals was the evolution of true multicellularity. This occurs when an organism’s cells can’t survive on their own—they have to be associated with other cells. My students and I discovered that choanoflagellates possess some of the genes necessary for multicellularity in animals. Previously, these genes were thought to be unique to animals. We’ve also been studying a particular species of choanoflagellate that can form simple colonies. By studying this organism in detail, we are learning how it transitions from a single cell to a colony—a change that can help us to answer the evolutionary question, “How does multicellularity evolve from organisms that are unicellular?”

What is a typical work day like for you, and what advice do you have for students?

Each day is different, but I always try to talk with people in my lab about their research. Sometimes they share an exciting new result, or they describe an experiment that is failing and we brainstorm about what might be going wrong. A few times, it turned out that an experiment was done correctly, but the results were very different from what we expected. It can be hard to determine what causes such unexpected results, but doing so can reveal features of an organism’s biology that you had no idea existed! I’m really lucky, because I love what I do, and I have a diverse and talented group of scientists in my lab. They all are learning from each other, and I’m learning from them. Overall, I think the key to a happy and successful career is to do what you love.

 For an extended interview and video clip, go to the Study Area in **MasteringBiology**.



26

Phylogeny and the Tree of Life



▲ **Figure 26.1** What kind of organism is this?

KEY CONCEPTS

- 26.1 Phylogenies show evolutionary relationships
- 26.2 Phylogenies are inferred from morphological and molecular data
- 26.3 Shared characters are used to construct phylogenetic trees
- 26.4 An organism's evolutionary history is documented in its genome
- 26.5 Molecular clocks help track evolutionary time
- 26.6 Our understanding of the tree of life continues to change based on new data

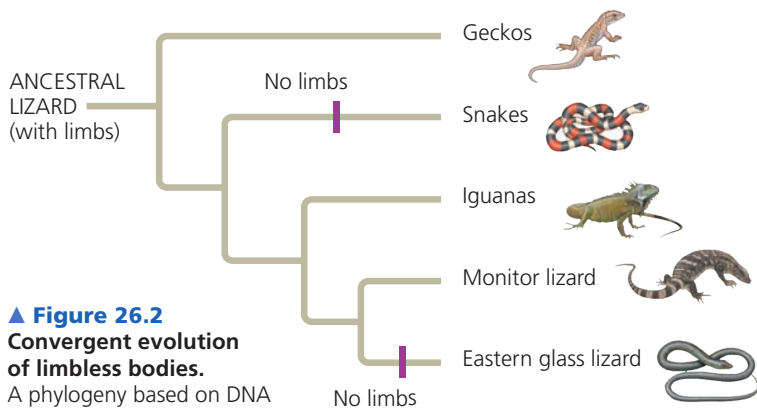
Investigating the Tree of Life

Look closely at the organism in **Figure 26.1**. Although it resembles a snake, this animal is actually a legless lizard known as the eastern glass lizard (*Ophisaurus ventralis*). Why isn't this glass lizard considered a snake? More generally, how do biologists distinguish and categorize the millions of species on Earth?

An understanding of evolutionary relationships suggests one way to address these questions: We can decide in which category to place a species by comparing its traits with those of potential close relatives. For example, the eastern glass lizard does not have a highly mobile jaw, a large number of vertebrae, or a short tail located behind the anus, three traits shared by all snakes. These and other characteristics suggest that despite a superficial resemblance, the glass lizard is not a snake.

Snakes and lizards are part of the continuum of life extending from the earliest organisms to the great variety of species alive today. In this unit, we will survey this diversity and describe hypotheses regarding how it evolved. As we do so, our emphasis will shift from the *process* of evolution (the evolutionary mechanisms described in Unit Four) to its *pattern* (observations of evolution's products over time).

To set the stage for surveying life's diversity, in this chapter we consider how biologists trace **phylogeny**, the evolutionary history of a species or group of species. A phylogeny of lizards and snakes, for example, indicates that both the eastern glass lizard and snakes evolved from lizards with legs—but they evolved from



▲ Figure 26.2
Convergent evolution of limbless bodies.

A phylogeny based on DNA sequence data reveals that a legless body form evolved independently from legged ancestors in the lineages leading to the eastern glass lizard and to snakes.

different lineages of legged lizards (Figure 26.2). Thus, it appears that their legless conditions evolved independently. As we'll see, biologists reconstruct and interpret phylogenies like that in Figure 26.2 using **systematics**, a discipline focused on classifying organisms and determining their evolutionary relationships.

CONCEPT 26.1

Phylogenies show evolutionary relationships

Organisms share many characteristics because of common ancestry (see Chapter 22). As a result, we can learn a great deal about a species if we know its evolutionary history. For example, an organism is likely to share many of its genes, metabolic pathways, and structural proteins with its close relatives. We'll consider practical applications of such information later in this section, but first we'll examine how organisms are named and classified, the scientific discipline of **taxonomy**. We'll also look at how we can interpret and use diagrams that represent evolutionary history.

Binomial Nomenclature

Common names for organisms—such as monkey, finch, and lilac—convey meaning in casual usage, but they can also cause confusion. Each of these names, for example, refers to more than one species. Moreover, some common names do not accurately reflect the kind of organism they signify. Consider these three “fishes”: jellyfish (a cnidarian), crayfish (a small lobsterlike crustacean), and silverfish (an insect). And of course, a given organism has different names in different languages.

To avoid ambiguity when communicating about their research, biologists refer to organisms by Latin scientific names. The two-part format of the scientific name,

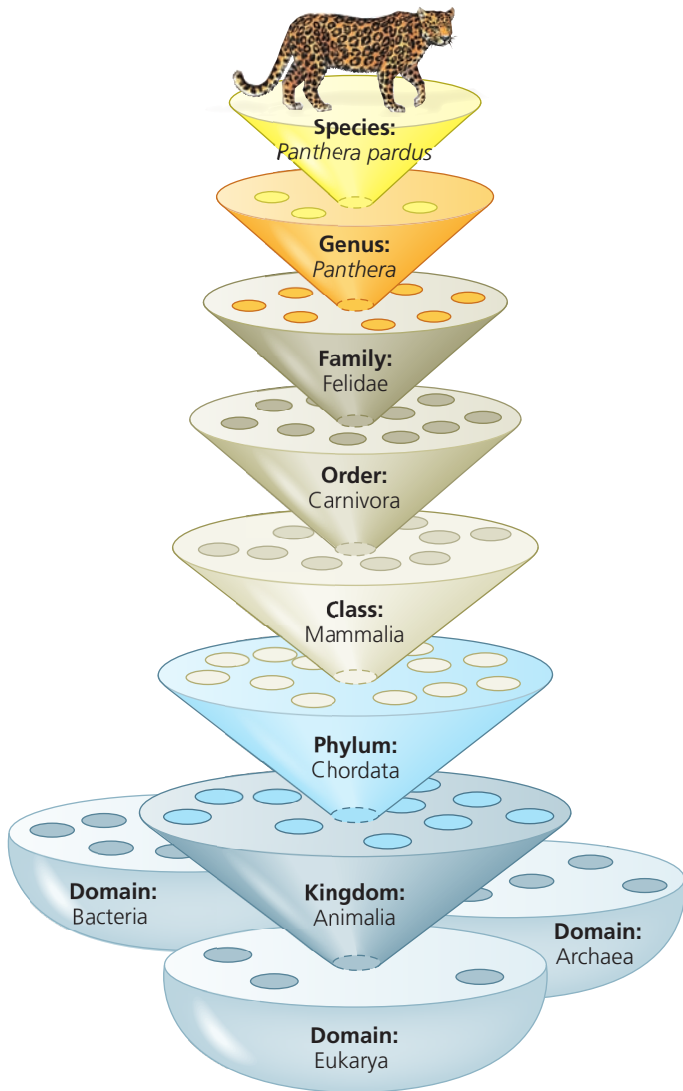
commonly called a **binomial**, was instituted in the 18th century by Carolus Linnaeus (see Chapter 22). The first part of a binomial is the name of the **genus** (plural, *genera*) to which the species belongs. The second part, called the specific epithet, is unique for each species within the genus. An example of a binomial is *Panthera pardus*, the scientific name for the large cat commonly called the leopard. Notice that the first letter of the genus is capitalized and the entire binomial is italicized. (Newly created scientific names are also “latinized”: You can name an insect you discover after a friend, but you must add a Latin ending.) Many of the more than 11,000 binomials assigned by Linnaeus are still used today, including the optimistic name he gave our own species—*Homo sapiens*, meaning “wise man.”

Hierarchical Classification

In addition to naming species, Linnaeus also grouped them into a hierarchy of increasingly inclusive categories. The first grouping is built into the binomial: Species that appear to be closely related are grouped into the same genus. For example, the leopard (*Panthera pardus*) belongs to a genus that also includes the African lion (*Panthera leo*), the tiger (*Panthera tigris*), and the jaguar (*Panthera onca*). Beyond genera, taxonomists employ progressively more comprehensive categories of classification. The taxonomic system named after Linnaeus, the Linnaean system, places related genera in the same **family**, families into **orders**, orders into **classes**, classes into **phyla** (singular, *phylum*), phyla into **kingdoms**, and, more recently, kingdoms into **domains** (Figure 26.3). The resulting biological classification of a particular organism is somewhat like a postal address identifying a person in a particular apartment, in a building with many apartments, on a street with many apartment buildings, in a city with many streets, and so on.

The named taxonomic unit at any level of the hierarchy is called a **taxon** (plural, *taxa*). In the leopard example, *Panthera* is a taxon at the genus level, and Mammalia is a taxon at the class level that includes all the many orders of mammals. Note that in the Linnaean system, taxa broader than the genus are not italicized, though they are capitalized.

Classifying species is a way to structure our human view of the world. We lump together various species of trees to which we give the common name of pines and distinguish them from other trees that we call firs. Taxonomists have decided that pines and firs are different enough to be placed in separate genera, yet similar enough to be grouped into the same family, Pinaceae. As with pines and firs, higher levels of classification are usually defined by particular characters chosen by taxonomists. However, characters that are useful for classifying one group of organisms may not be appropriate for other organisms. For this reason, the larger categories often are not comparable between lineages; that is, an

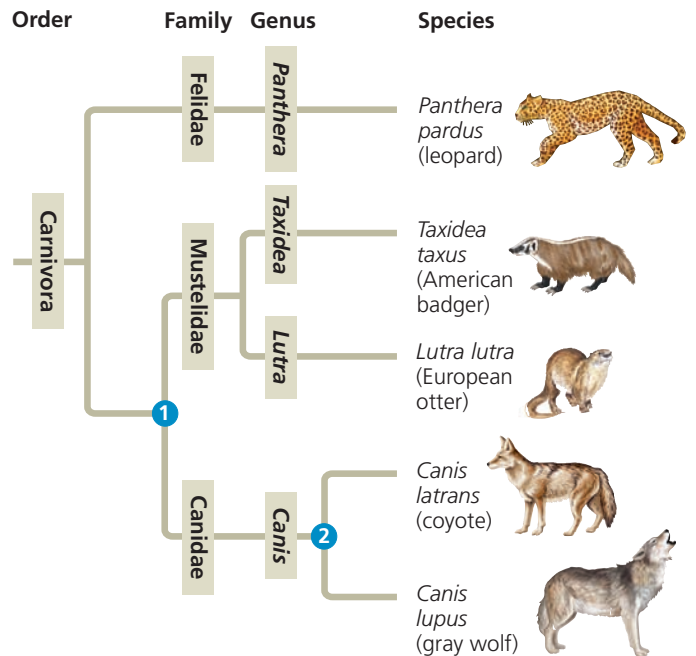


▲ **Figure 26.3** Linnaean classification. At each level, or “rank,” species are placed in groups within more inclusive groups.

order of snails does not exhibit the same degree of morphological or genetic diversity as an order of mammals. Furthermore, as we’ll see, the placement of species into orders, classes, and so on, does not necessarily reflect evolutionary history.

Linking Classification and Phylogeny

The evolutionary history of a group of organisms can be represented in a branching diagram called a **phylogenetic tree**. As in **Figure 26.4**, the branching pattern often matches how taxonomists have classified groups of organisms nested within more inclusive groups. Sometimes, however, taxonomists have placed a species within a genus (or other group) to which it is *not* most closely related. One reason for such a mistake might be that over the course of evolution, a species has lost a key feature shared by its close relatives. If



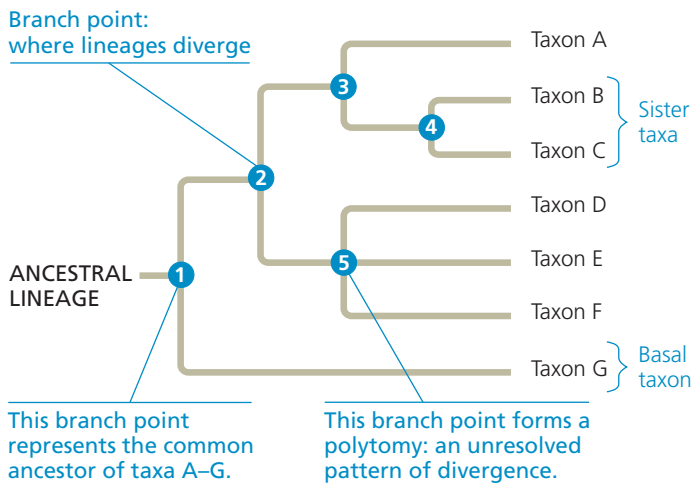
▲ **Figure 26.4** The connection between classification and phylogeny. Hierarchical classification can reflect the branching patterns of phylogenetic trees. This tree traces possible evolutionary relationships between some of the taxa within order Carnivora, itself a branch of class Mammalia. The branch point **1** represents the most recent common ancestor of all members of the weasel (Mustelidae) and dog (Canidae) families. The branch point **2** represents the most recent common ancestor of coyotes and gray wolves.

? What does this phylogenetic tree indicate about the evolutionary relationships between the leopard, badger, and wolf?

DNA or other new evidence indicates that an organism has been misclassified, the organism may be reclassified to accurately reflect its evolutionary history. Another issue is that while the Linnaean system may distinguish groups, such as amphibians, mammals, reptiles, and other classes of vertebrates, it tells us nothing about these groups’ evolutionary relationships to one another.

Such difficulties in aligning Linnaean classification with phylogeny have led some systematists to propose that classification be based entirely on evolutionary relationships. In such systems, names are only assigned to groups that include a common ancestor and all of its descendants. As a consequence of this approach, some commonly recognized groups would become part of other groups previously at the same level of the Linnaean system. For example, because birds evolved from a group of reptiles, Aves (the Linnaean class to which birds are assigned) would be considered a subgroup of Reptilia (also a class in the Linnaean system).

Regardless of how groups are named, a phylogenetic tree represents a hypothesis about evolutionary relationships. These relationships often are depicted as a series of dichotomies, or two-way **branch points**. Each branch point



▲ **Figure 26.5** How to read a phylogenetic tree.

DRAW IT Redraw this tree, rotating the branches around branch points 2 and 4. Does your new version tell a different story about the evolutionary relationships between the taxa? Explain.

represents the divergence of two evolutionary lineages from a common ancestor. In **Figure 26.5**, for example, branch point 3 represents the common ancestor of taxa A, B, and C. The position of branch point 4 to the right of 3 indicates that taxa B and C diverged after their shared lineage split from the lineage leading to taxon A. Note also that tree branches can be rotated around a branch point without changing their evolutionary relationships.

In **Figure 26.5**, taxa B and C are **sister taxa**, groups of organisms that share an immediate common ancestor (branch point 4) and hence are each other’s closest relatives. In addition, this tree, like most of the phylogenetic trees in this book, is **rooted**, which means that a branch point within the tree (often drawn farthest to the left) represents the most recent common ancestor of all taxa in the tree. The term **basal taxon** refers to a lineage that diverges early in the history of a group and hence, like taxon G in **Figure 26.5**, lies on a branch that originates near the common ancestor of the group. Finally, the lineage leading to taxa D–F includes a **polytomy**, a branch point from which more than two descendant groups emerge. A polytomy signifies that evolutionary relationships among the taxa are not yet clear.

What We Can and Cannot Learn from Phylogenetic Trees

Let’s summarize three key points about phylogenetic trees. First, they are intended to show patterns of descent, not phenotypic similarity. Although closely related organisms often resemble one another due to their common ancestry, they may not if their lineages have evolved at different rates or faced very different environmental conditions. For

example, even though crocodiles are more closely related to birds than to lizards (see **Figure 22.17**), they look more like lizards because morphology has changed dramatically in the bird lineage.

Second, the sequence of branching in a tree does not necessarily indicate the actual (absolute) ages of the particular species. For example, the tree in **Figure 26.4** does not indicate that the wolf evolved more recently than the European otter; rather, the tree shows only that the most recent common ancestor of the wolf and otter (branch point 1) lived before the most recent common ancestor of the wolf and coyote (2). To indicate when wolves and otters evolved, the tree would need to include additional divergences in each evolutionary lineage, as well as the dates when those splits occurred. Generally, unless given specific information about what the branch lengths in a phylogenetic tree mean—for example, that they are proportional to time—we should interpret the diagram solely in terms of patterns of descent. No assumptions should be made about when particular species evolved or how much change occurred in each lineage.

Third, we should not assume that a taxon on a phylogenetic tree evolved from the taxon next to it. **Figure 26.4** does not indicate that wolves evolved from coyotes or vice versa. We can infer only that the lineage leading to wolves and the lineage leading to coyotes both evolved from the common ancestor 2. That ancestor, which is now extinct, was neither a wolf nor a coyote. However, its descendants include the two *extant* (living) species shown here, wolves and coyotes.

Applying Phylogenies

Understanding phylogeny can have practical applications. Consider maize (corn), which originated in the Americas and is now an important food crop worldwide. From a phylogeny of maize based on DNA data, researchers have been able to identify two species of wild grasses that may be maize’s closest living relatives. These two close relatives may be useful as “reservoirs” of beneficial alleles that can be transferred to cultivated maize by cross-breeding or genetic engineering (see **Chapter 20**).

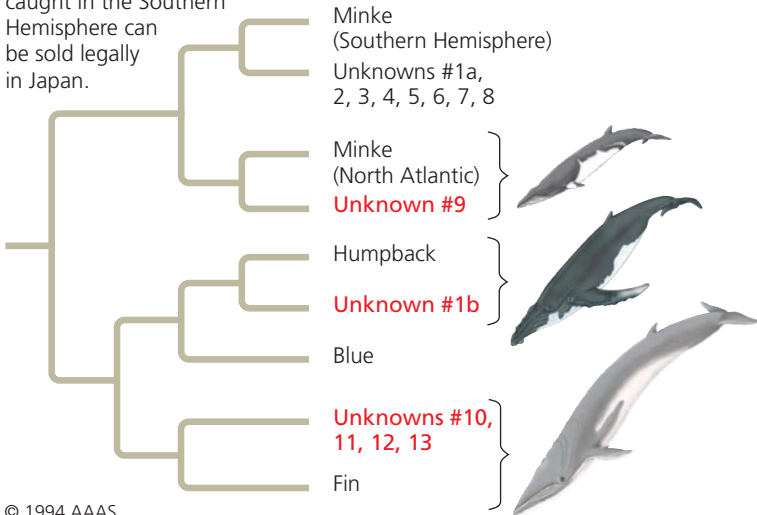
A different use of phylogenetic trees is to infer species identities by analyzing the relatedness of DNA sequences from different organisms. Researchers have used this approach to investigate whether “whale meat” had been harvested illegally from whale species protected under international law rather than from species that can be harvested legally (**Figure 26.6**).

How do researchers construct trees like those we’ve considered here? In the next section, we’ll begin to answer that question by examining the data used to determine phylogenies.

What is the species identity of food being sold as whale meat?

Experiment C. S. Baker and S. R. Palumbi purchased 13 samples of “whale meat” from Japanese fish markets. They sequenced part of the mitochondrial DNA (mtDNA) from each sample and compared their results with the comparable mtDNA sequence from known whale species. To infer the species identity of each sample, the team constructed a *gene tree*, a phylogenetic tree that shows patterns of relatedness among DNA sequences rather than among taxa.

Results Of the species in the resulting gene tree, only Minke whales caught in the Southern Hemisphere can be sold legally in Japan.



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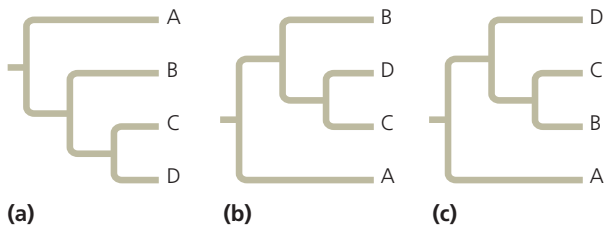
Conclusion This analysis indicated that mtDNA sequences of six of the unknown samples (in red) were most closely related to mtDNA sequences of whales that are not legal to harvest.

Source: C. S. Baker and S. R. Palumbi, Which whales are hunted? A molecular genetic approach to monitoring whaling, *Science* 265:1538–1539 (1994). Reprinted with permission from AAAS.

WHAT IF? What different results would have indicated that the whale meat had not been harvested illegally?

CONCEPT CHECK 26.1

- Which levels of the classification in Figure 26.3 do humans share with leopards?
- Which of the trees shown here depicts an evolutionary history different from the other two? Explain.



- WHAT IF?** Suppose new evidence indicates that taxon E in Figure 26.5 is the sister taxon of a group consisting of taxa D and F. Redraw the tree accordingly.

For suggested answers, see Appendix A.

CONCEPT 26.2

Phylogenies are inferred from morphological and molecular data

To infer phylogeny, systematists must gather as much information as possible about the morphology, genes, and biochemistry of the relevant organisms. It is important to focus on features that result from common ancestry, because only such features reflect evolutionary relationships.

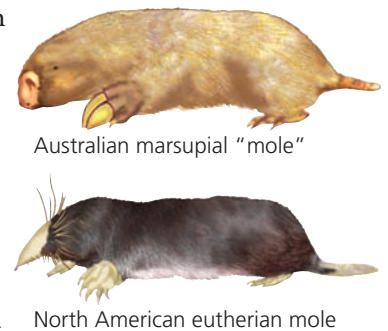
Morphological and Molecular Homologies

Recall that phenotypic and genetic similarities due to shared ancestry are called *homologies*. For example, the similarity in the number and arrangement of bones in the forelimbs of mammals is due to their descent from a common ancestor with the same bone structure; this is an example of a morphological homology (see Figure 22.15). In the same way, genes or other DNA sequences are homologous if they are descended from sequences carried by a common ancestor.

In general, organisms that share very similar morphologies or similar DNA sequences are likely to be more closely related than organisms with vastly different structures or sequences. In some cases, however, the morphological divergence between related species can be great and their genetic divergence small (or vice versa). Consider the Hawaiian silversword plants: some of these species are tall, twiggy trees, while others are dense, ground-hugging shrubs (see Figure 25.22). But despite these striking phenotypic differences, the silverswords’ genes are very similar. Based on these small molecular divergences, scientists estimate that the silversword group began to diverge 5 million years ago. We’ll discuss how scientists use molecular data to estimate such divergence times later in this chapter.

Sorting Homology from Analogy

A potential source of confusion in constructing a phylogeny is similarity between organisms that is due to convergent evolution—called **analogy**—rather than to shared ancestry (homology). Convergent evolution occurs when similar environmental pressures and natural selection produce similar (analogous) adaptations in organisms from different evolutionary lineages. For example, the two mole-like animals shown in Figure 26.7



▲ Figure 26.7 Convergent evolution in burrowers. A long body, large front paws, small eyes, and a pad of thick skin that protects the nose all evolved independently in these species.

look very similar. However, their internal anatomy, physiology, and reproductive systems are very dissimilar. Indeed, genetic and fossil evidence indicate that the common ancestor of these moles lived 140 million years ago. This common ancestor and most of its descendents were not mole-like, but analogous characteristics evolved independently in these two mole lineages as they became adapted to similar lifestyles.

Distinguishing between homology and analogy is critical in reconstructing phylogenies. To see why, consider bats and birds, both of which have adaptations that enable flight. This superficial resemblance might imply that bats are more closely related to birds than they are to cats, which cannot fly. But a closer examination reveals that a bat's wing is more similar to the forelimbs of cats and other mammals than to a bird's wing. Bats and birds descended from a common tetrapod ancestor that lived about 320 million years ago. This common ancestor could not fly. Thus, although the underlying skeletal systems of bats and birds are homologous, their *wings* are not. Flight is enabled in different ways—stretched membranes in the bat wing versus feathers in the bird wing. Fossil evidence also documents that bat wings and bird wings arose independently from the forelimbs of different tetrapod ancestors. Thus, with respect to flight, a bat's wing is *analogous*, not homologous, to a bird's wing. Analogous structures that arose independently are also called **homoplasies** (from the Greek, meaning “to mold in the same way”).

Besides corroborative similarities and fossil evidence, another clue to distinguishing between homology and analogy is the complexity of the characters being compared. The more elements that are similar in two complex structures, the more likely it is that they evolved from a common ancestor. For instance, the skulls of an adult human and an adult chimpanzee both consist of many bones fused together. The compositions of the skulls match almost perfectly, bone for bone. It is highly improbable that such complex structures, matching in so many details, have separate origins. More likely, the genes involved in the development of both skulls were inherited from a common ancestor. The same argument applies to comparisons at the gene level. Genes are sequences of thousands of nucleotides, each of which represents an inherited character in the form of one of the four DNA bases: A (adenine), G (guanine), C (cytosine), or T (thymine). If genes in two organisms share many portions of their nucleotide sequences, it is likely that the genes are homologous.

Evaluating Molecular Homologies

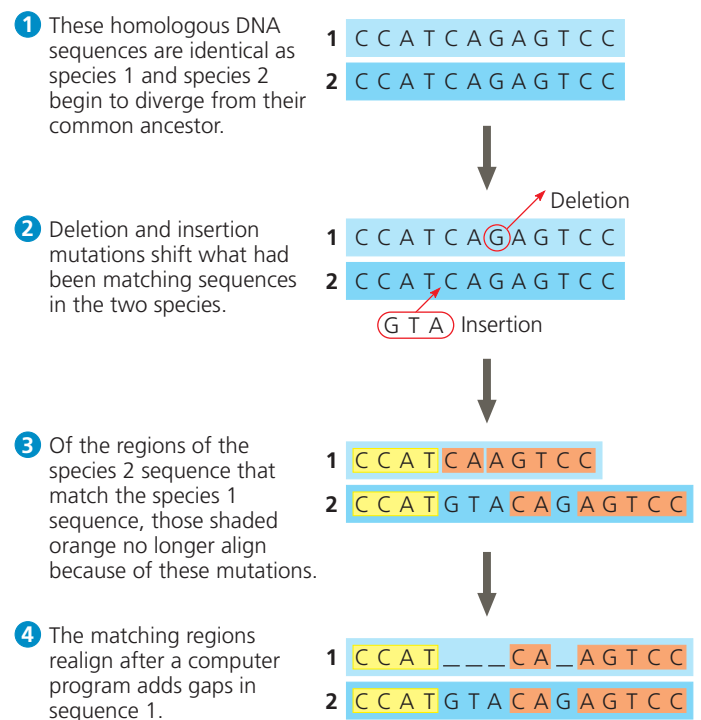
Comparing DNA molecules often poses technical challenges for researchers. The first step after sequencing the molecules is to align comparable sequences from the species being studied. If the species are very closely related, the sequences probably differ at only one or a few sites. In contrast, comparable nucleic acid sequences in distantly related

species usually have different bases at many sites and may have different lengths. This is because insertions and deletions accumulate over long periods of time.

Suppose, for example, that certain noncoding DNA sequences near a particular gene are very similar in two species, except that the first base of the sequence has been deleted in one of the species. The effect is that the remaining sequence shifts back one notch. A comparison of the two sequences that does not take this deletion into account would overlook what in fact is a very good match. To address such problems, researchers have developed computer programs that estimate the best way to align comparable DNA segments of differing lengths (**Figure 26.8**).

Such molecular comparisons reveal that many base substitutions and other differences have accumulated in the comparable genes of an Australian mole and a North American mole. The many differences indicate that their lineages have diverged greatly since their common ancestor; thus, we say that the living species are not closely related. In contrast, the high degree of gene sequence similarity among the silver-sword plants indicates that they are all very closely related, in spite of their considerable morphological differences.

Just as with morphological characters, it is necessary to distinguish homology from analogy in evaluating molecular similarities for evolutionary studies. Two sequences that



▲ Figure 26.8 Aligning segments of DNA. Systematists search for similar sequences along DNA segments from two species (only one DNA strand is shown for each species). In this example, 11 of the original 12 bases have not changed since the species diverged. Hence, those portions of the sequences still align once the length is adjusted.

ACGGATAGTCCACTAGGCACTA
 TCACCGACAGGTCTTTGACTAG

▲ **Figure 26.9** A molecular homoplasy.

resemble each other at many points along their length most likely are homologous (see Figure 26.8). But in organisms that do not appear to be closely related, the bases that their otherwise very different sequences happen to share may simply be coincidental matches, called molecular homoplasies. For example, if the two DNA sequences in **Figure 26.9** were from distantly related organisms, the fact that they share 23% of their bases would be coincidental. Statistical tools have been developed to determine whether DNA sequences that share more than 25% of their bases do so because they are homologous.

CONCEPT CHECK 26.2

1. Decide whether each of the following pairs of structures more likely represents analogy or homology, and explain your reasoning: (a) a porcupine's quills and a cactus's spines; (b) a cat's paw and a human's hand; (c) an owl's wing and a hornet's wing.
2. **WHAT IF?** Suppose that two species, A and B, have similar appearances but very divergent gene sequences, while species B and C have very different appearances but similar gene sequences. Which pair of species is more likely to be closely related: A and B or B and C? Explain.

For suggested answers, see Appendix A.

CONCEPT **26.3**

Shared characters are used to construct phylogenetic trees

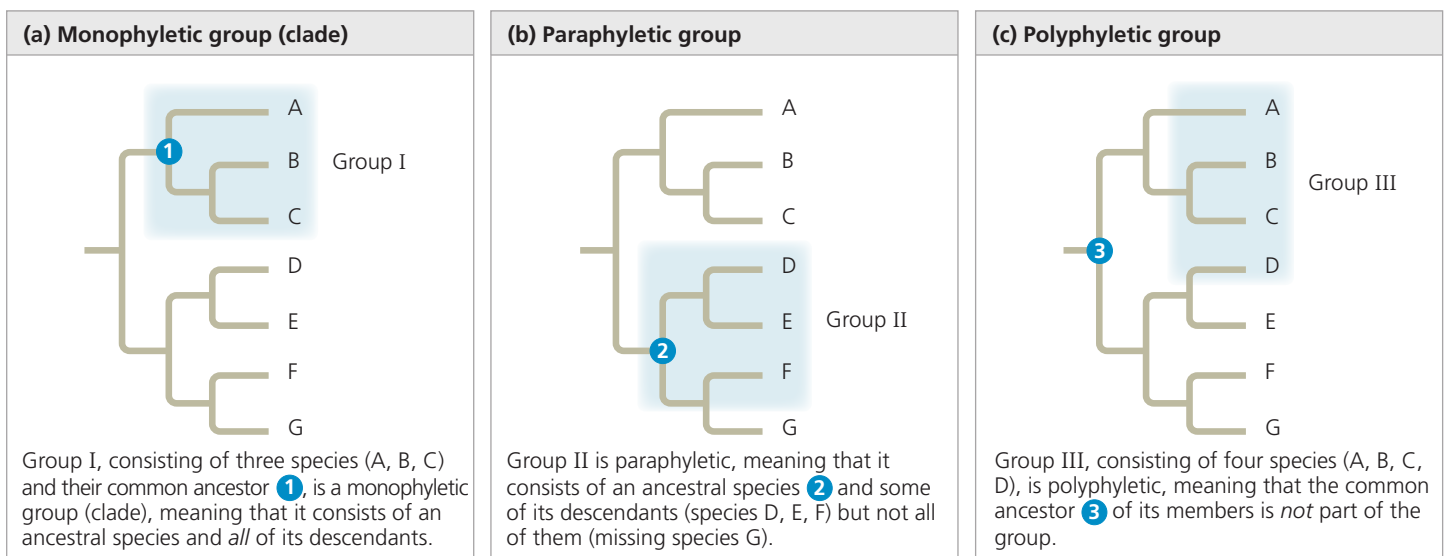
As we've discussed, a key step in reconstructing phylogenies is to distinguish homologous features from analogous ones (since only homology reflects evolutionary history). We must also choose a method of inferring phylogeny from these homologous characters. A widely used set of methods is known as cladistics.

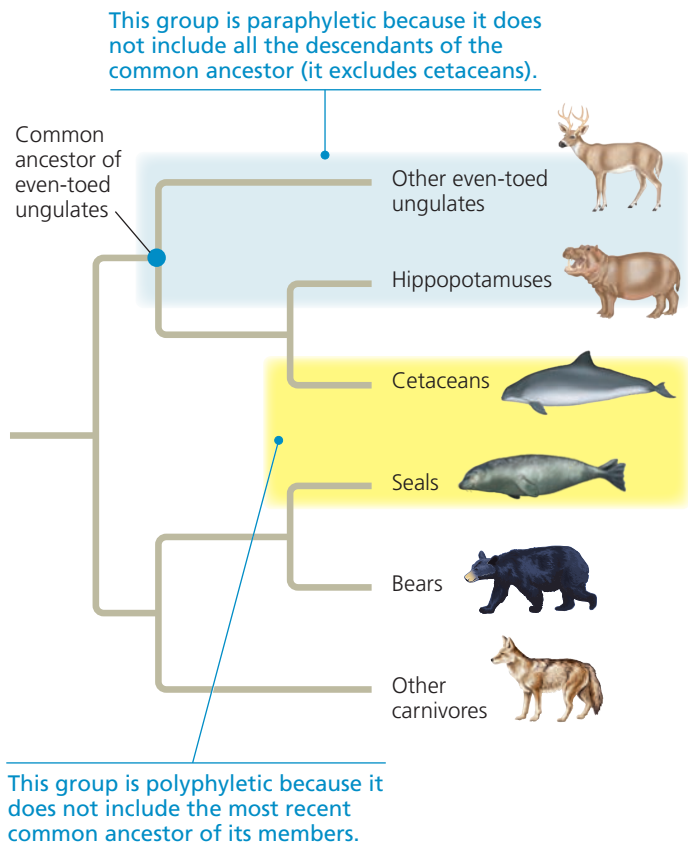
Cladistics

In the approach to systematics called **cladistics**, common ancestry is the primary criterion used to classify organisms. Using this methodology, biologists attempt to place species into groups called **clades**, each of which includes an ancestral species and all of its descendants (**Figure 26.10a**). Clades, like taxonomic categories of the Linnaean system, are nested within larger clades. In Figure 26.4, for example, the cat group (Felidae) represents a clade within a larger clade (Carnivora) that also includes the dog group (Canidae).

However, a taxon is equivalent to a clade only if it is **monophyletic** (from the Greek, meaning "single tribe"), signifying that it consists of an ancestral species and all of its descendants (see Figure 26.10a). Contrast this with a **paraphyletic** ("beside the tribe") group, which consists of an ancestral species and some, but not all, of its descendants (**Figure 26.10b**), or a **polyphyletic** ("many tribes") group, which includes distantly related species but does not include their most recent common ancestor (**Figure 26.10c**).

▼ **Figure 26.10** Monophyletic, paraphyletic, and polyphyletic groups.





▲ **Figure 26.11** Examples of a paraphyletic and a polyphyletic group.

? Circle the branch point that represents the most recent common ancestor of cetaceans and seals. Explain why that ancestor would not be part of a cetacean–seal group defined by their similar body forms.

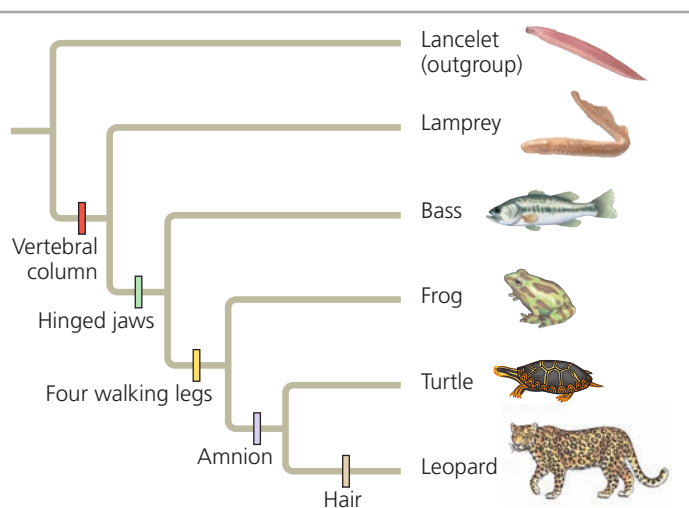
Note that in a paraphyletic group, the most recent common ancestor of all members of the group *is* part of the group, whereas in a polyphyletic group the most recent common ancestor *is not* part of the group. For example, a group consisting of even-toed ungulates (hippopotamuses, deer, and their relatives) and their common ancestor is paraphyletic because it includes the common ancestor but excludes cetaceans (whales, dolphins, and porpoises), which descended from that ancestor (**Figure 26.11**). In contrast, a group consisting of seals and cetaceans (based on their similar body forms) would be polyphyletic because it does not include the common ancestor of seals and cetaceans. Biologists avoid defining such polyphyletic groups; if new evidence indicates that an existing group is polyphyletic, organisms in that group are reclassified.

Shared Ancestral and Shared Derived Characters

As a result of descent with modification, organisms have characteristics they share with their ancestors, and they also have characteristics that differ from those of their ancestors. For example, all mammals have backbones, but a backbone does not distinguish mammals from other vertebrates because *all* vertebrates have backbones. The backbone predates the branching of mammals from other vertebrates. Thus for mammals, the backbone is a **shared ancestral character**, a character that originated in an ancestor of the taxon. In contrast, hair is a character shared by all mammals but *not* found in their ancestors. Thus, in mammals, hair is considered a **shared derived character**, an evolutionary novelty unique to a clade.

CHARACTERS	TAXA					
	Lancelet (outgroup)	Lamprey	Bass	Frog	Turtle	Leopard
Vertebral column (backbone)	0	1	1	1	1	1
Hinged jaws	0	0	1	1	1	1
Four walking legs	0	0	0	1	1	1
Amnion	0	0	0	0	1	1
Hair	0	0	0	0	0	1

(a) **Character table.** A 0 indicates that a character is absent; a 1 indicates that a character is present.



(b) **Phylogenetic tree.** Analyzing the distribution of these derived characters can provide insight into vertebrate phylogeny.

▲ **Figure 26.12** Constructing a phylogenetic tree. The characters used here include the amnion, a membrane that encloses the embryo inside a fluid-filled sac (see Figure 34.25).

DRAW IT In (b), circle the most inclusive clade for which a hinged jaw is a shared ancestral character.

Note that it is a relative matter whether a character is considered ancestral or derived. A backbone can also qualify as a shared derived character, but only at a deeper branch point that distinguishes all vertebrates from other animals.

Inferring Phylogenies Using Derived Characters

Shared derived characters are unique to particular clades. Because all features of organisms arose at some point in the history of life, it should be possible to determine the clade in which each shared derived character first appeared and to use that information to infer evolutionary relationships.

To see how this analysis is done, consider the set of characters shown in **Figure 26.12a** for each of five vertebrates—a leopard, turtle, frog, bass, and lamprey (a jawless aquatic vertebrate). As a basis of comparison, we need to select an outgroup. An **outgroup** is a species or group of species from an evolutionary lineage that is known to have diverged before the lineage that includes the species we are studying (the **ingroup**). A suitable outgroup can be determined based on evidence from morphology, paleontology, embryonic development, and gene sequences. An appropriate outgroup for our example is the lancelet, a small animal that lives in mudflats and (like vertebrates) is a member of the more inclusive group called the chordates. Unlike the vertebrates, however, the lancelet does not have a backbone.

By comparing members of the ingroup with each other and with the outgroup, we can determine which characters were derived at the various branch points of vertebrate evolution. For example, *all* of the vertebrates in the ingroup have backbones: This character was present in the ancestral vertebrate, but not in the outgroup. Now note that hinged jaws are a character absent in lampreys but present in other members of the ingroup; this character helps us to identify an early branch

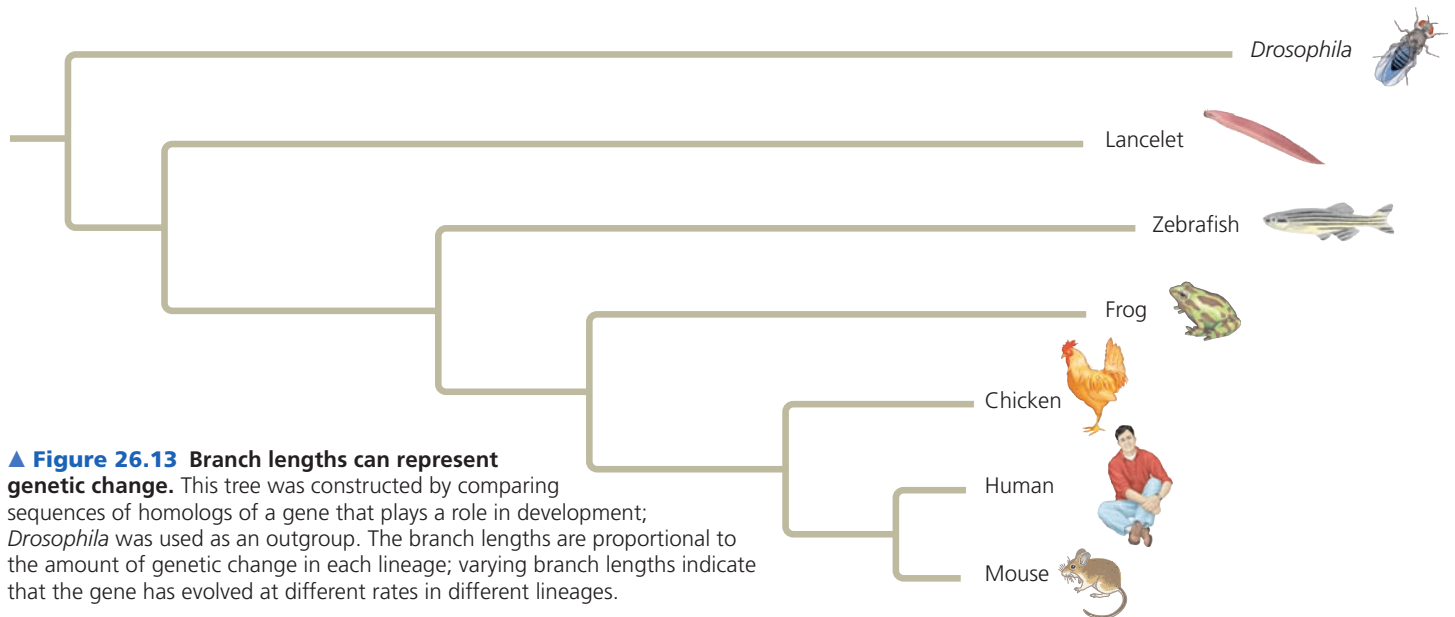
point in the vertebrate clade. Proceeding in this way, we can translate the data in our table of characters into a phylogenetic tree that groups all the ingroup taxa into a hierarchy based on their shared derived characters (**Figure 26.12b**).

Phylogenetic Trees with Proportional Branch Lengths

In the phylogenetic trees we have presented so far, the lengths of the tree's branches do not indicate the degree of evolutionary change in each lineage. Furthermore, the chronology represented by the branching pattern of the tree is relative (earlier versus later) rather than absolute (how many millions of years ago). But in some tree diagrams, branch lengths are proportional to amount of evolutionary change or to the times at which particular events occurred.

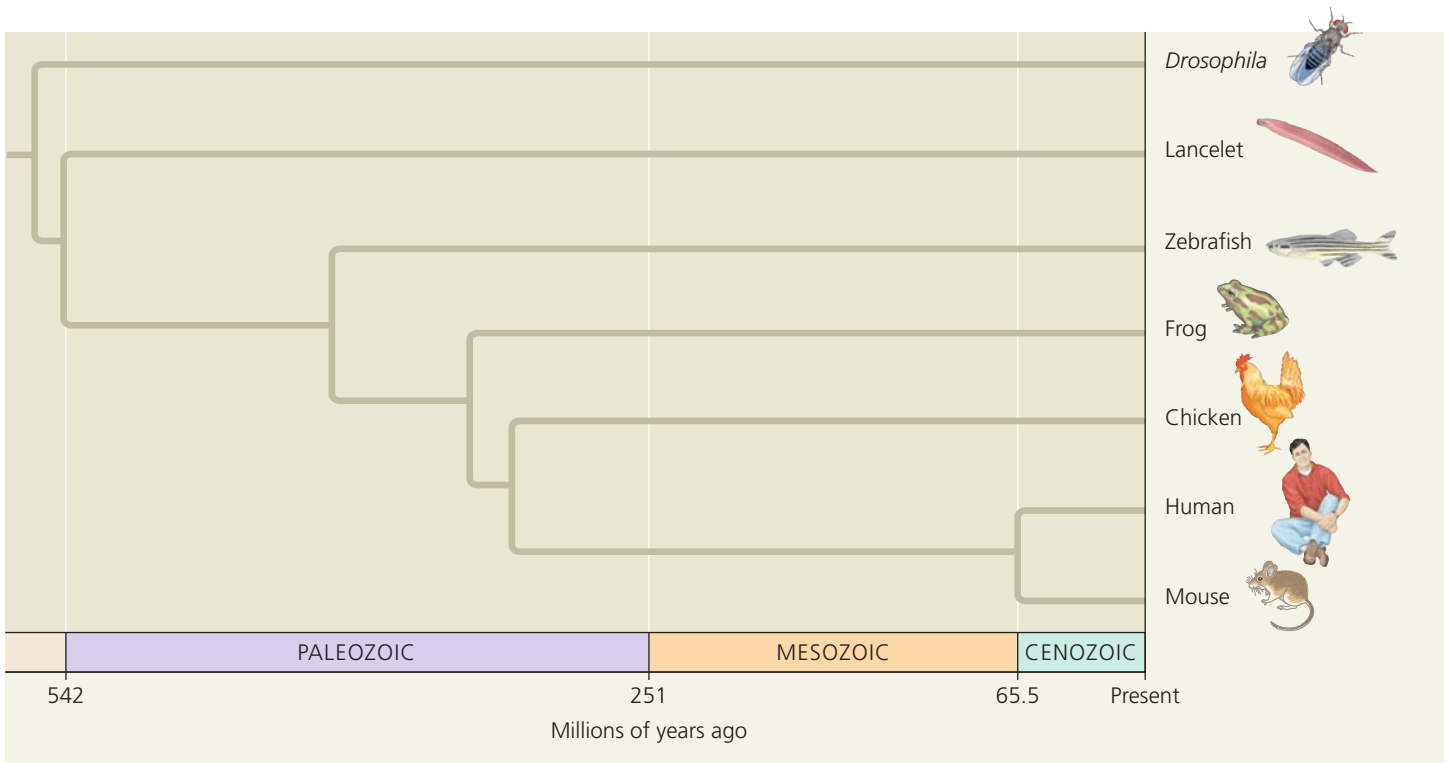
In **Figure 26.13**, for example, the branch length of the phylogenetic tree reflects the number of changes that have taken place in a particular DNA sequence in that lineage. Note that the total length of the horizontal lines from the base of the tree to the mouse is less than that of the line leading to the outgroup species, the fruit fly *Drosophila*. This implies that in the time since the mouse and fly diverged from a common ancestor, more genetic changes have occurred in the *Drosophila* lineage than in the mouse lineage.

Even though the branches of a phylogenetic tree may have different lengths, among organisms alive today, all the different lineages that descend from a common ancestor have survived for the same number of years. To take an extreme example, humans and bacteria had a common ancestor that lived over 3 billion years ago. Fossils and genetic evidence indicate that this ancestor was a single-celled prokaryote. Even though bacteria have apparently changed



▲ Figure 26.13 Branch lengths can represent genetic change. This tree was constructed by comparing sequences of homologs of a gene that plays a role in development; *Drosophila* was used as an outgroup. The branch lengths are proportional to the amount of genetic change in each lineage; varying branch lengths indicate that the gene has evolved at different rates in different lineages.

INTERPRET THE DATA In which vertebrate lineage has the studied gene evolved most rapidly? Explain.



▲ **Figure 26.14** Branch lengths can indicate time. This tree is based on the same molecular data as the tree in Figure 26.13, but here the branch points are mapped to dates based on fossil evidence. Thus, the branch lengths are proportional to time. Each lineage has the same total length from the base of the tree to the branch tip, indicating that all the lineages have diverged from the common ancestor for equal amounts of time.

little in their morphology since that common ancestor, there have nonetheless been 3 billion years of evolution in the bacterial lineage, just as there have been 3 billion years of evolution in the lineage that ultimately gave rise to humans.

These equal spans of chronological time can be represented in a phylogenetic tree whose branch lengths are proportional to time (Figure 26.14). Such a tree draws on fossil data to place branch points in the context of geologic time. Additionally, it is possible to combine these two types of trees by labeling branch points with information about rates of genetic change or dates of divergence.

Maximum Parsimony and Maximum Likelihood

As the database of DNA sequences that enables us to study more species grows, the difficulty of building the phylogenetic tree that best describes their evolutionary history also grows. What if you are analyzing data for 50 species? There are 3×10^{76} different ways to arrange 50 species into a tree! And which tree in this huge forest reflects the true phylogeny? Systematists can never be sure of finding the most accurate tree in such a large data set, but they can narrow the possibilities by applying the principles of maximum parsimony and maximum likelihood.

According to the principle of **maximum parsimony**, we should first investigate the simplest explanation that is consistent with the facts. (The parsimony principle is also called “Occam’s razor” after William of Occam, a 14th-century English philosopher who advocated this minimalist problem-solving approach of “shaving away” unnecessary complications.) In the case of trees based on morphology, the most parsimonious tree requires the fewest evolutionary events, as measured by the origin of shared derived morphological characters. For phylogenies based on DNA, the most parsimonious tree requires the fewest base changes.

A **maximum likelihood** approach identifies the tree most likely to have produced a given set of DNA data, based on certain probability rules about how DNA sequences change over time. For example, the underlying probability rules could be based on the assumption that all nucleotide substitutions are equally likely. However, if evidence suggests that this assumption is not correct, more complex rules could be devised to account for different rates of change among different nucleotides or at different positions in a gene.

Scientists have developed many computer programs to search for trees that are parsimonious and likely. When a large amount of accurate data is available, the methods used in these programs usually yield similar trees. As an example of one method, Figure 26.15 walks you through the process of identifying the most parsimonious molecular tree for a

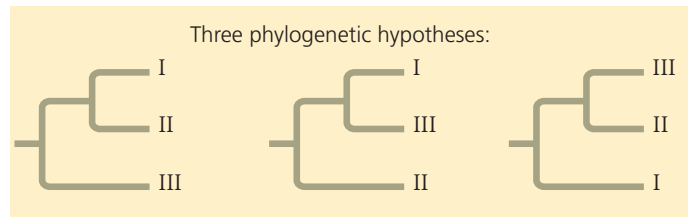
Applying Parsimony to a Problem in Molecular Systematics

Application In considering possible phylogenies for a group of species, systematists compare molecular data for the species. An efficient way to begin is by identifying the most parsimonious hypothesis—the one that requires the fewest evolutionary events (molecular changes) to have occurred.

Technique Follow the numbered steps as we apply the principle of parsimony to a hypothetical phylogenetic problem involving three closely related bird species.



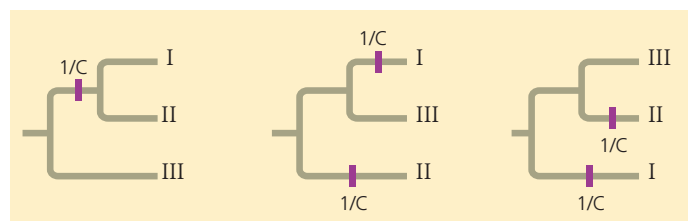
1 First, draw the three possible phylogenies for the species. (Although only 3 trees are possible when ordering 3 species, the number of possible trees increases rapidly with the number of species: There are 15 trees for 4 species and 34,459,425 trees for 10 species.)



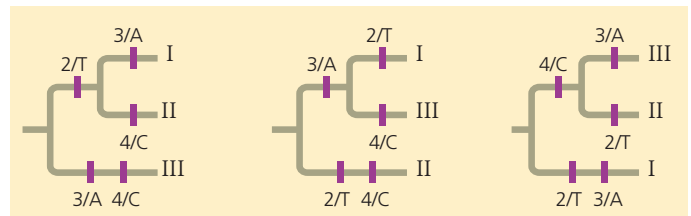
2 Tabulate the molecular data for the species. In this simplified example, the data represent a DNA sequence consisting of just four nucleotide bases. Data from several outgroup species (not shown) were used to infer the ancestral DNA sequence.

	Site			
	1	2	3	4
Species I	C	T	A	T
Species II	C	T	T	C
Species III	A	G	A	C
Ancestral sequence	A	G	T	T

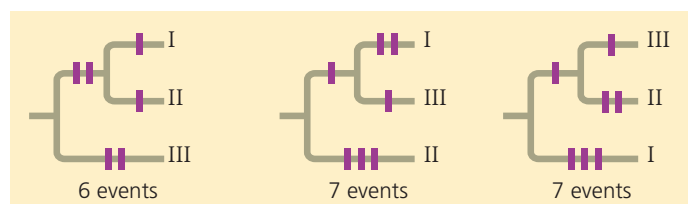
3 Now focus on site 1 in the DNA sequence. In the tree on the left, a single base-change event, represented by the purple hatchmark on the branch leading to species I and II (and labeled 1/C, indicating a change at site 1 to nucleotide C), is sufficient to account for the site 1 data. In the other two trees, two base-change events are necessary.



4 Continuing the comparison of bases at sites 2, 3, and 4 reveals that each of the three trees requires a total of five additional base-change events (purple hatchmarks).



Results To identify the most parsimonious tree, we total all of the base-change events noted in steps 3 and 4. We conclude that the first tree is the most parsimonious of the three possible phylogenies. (In a real example, many more sites would be analyzed. Hence, the trees would often differ by more than one base-change event.)



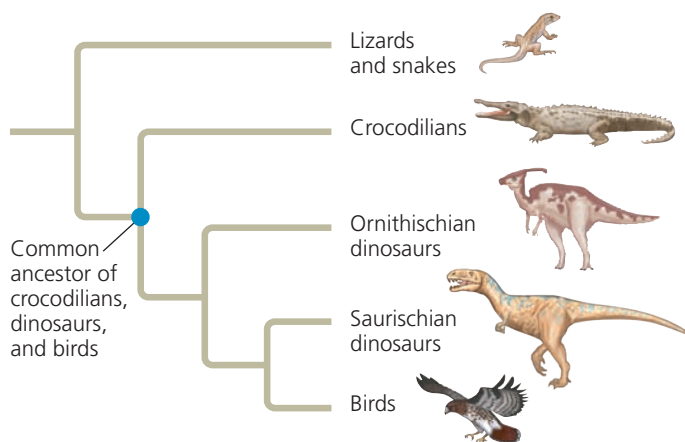
three-species problem. Computer programs use the principle of parsimony to estimate phylogenies in a similar way: They examine large numbers of possible trees and identify those that require the fewest evolutionary changes.

Phylogenetic Trees as Hypotheses

This is a good place to reiterate that any phylogenetic tree represents a hypothesis about how the organisms in the tree are related to one another. The best hypothesis is the one that best fits all the available data. A phylogenetic hypothesis may be modified when new evidence compels systematists to revise their trees. Indeed, while many older phylogenetic hypotheses have been supported by new morphological and molecular data, others have been changed or rejected.

Thinking of phylogenies as hypotheses also allows us to use them in a powerful way: We can make and test predictions based on the assumption that a particular phylogeny—our hypothesis—is correct. For example, in an approach known as *phylogenetic bracketing*, we can predict (by parsimony) that features shared by two groups of closely related organisms are present in their common ancestor and all of its descendants unless independent data indicate otherwise. (Note that “prediction” can refer to unknown past events as well as to evolutionary changes yet to occur.)

This approach has been used to make novel predictions about dinosaurs. For example, there is evidence that birds descended from the theropods, a group of bipedal saurischian dinosaurs. As seen in **Figure 26.16**, the closest living relatives of birds are crocodiles. Birds and crocodiles share numerous features: They have four-chambered hearts, they “sing” to defend territories and attract mates (although a crocodile’s “song” is more like a bellow), and they build nests. Both birds and crocodiles also care for their eggs by *brooding*, a behavior in which a parent warms the eggs with its body. Birds brood by sitting on their eggs, whereas



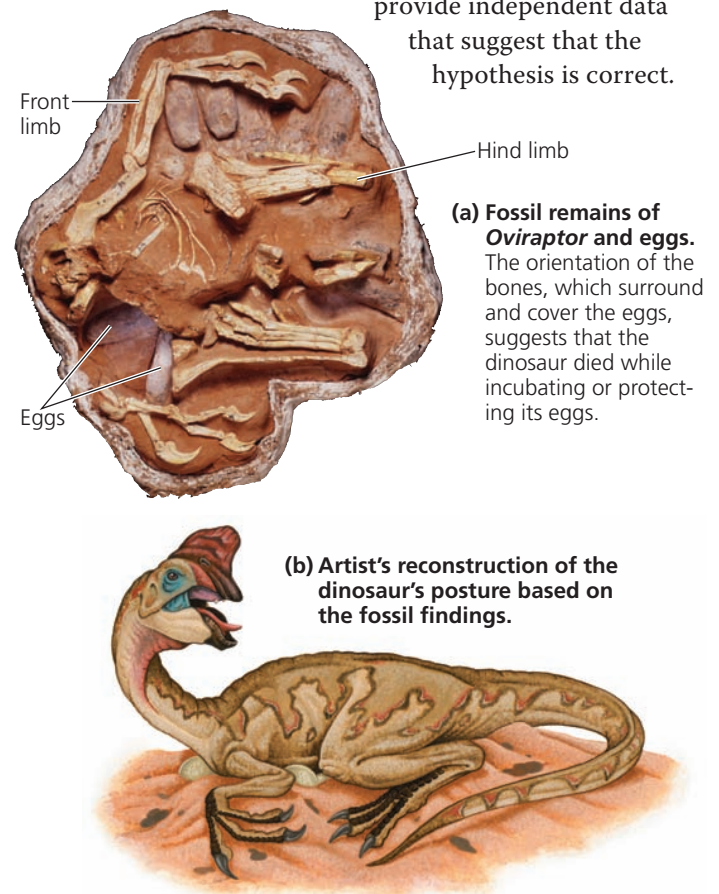
▲ Figure 26.16 A phylogenetic tree of birds and their close relatives.

? What is the most basal taxon represented in this tree?

crocodiles cover their eggs with their neck. Reasoning that any feature shared by birds and crocodiles is likely to have been present in their common ancestor (denoted by the blue dot in **Figure 26.16**) and *all* of its descendants, biologists predicted that dinosaurs had four-chambered hearts, sang, built nests, and exhibited brooding.

Internal organs, such as the heart, rarely fossilize, and it is, of course, difficult to test whether dinosaurs sang to defend territories and attract mates. However, fossilized dinosaur eggs and nests have provided evidence supporting the prediction of brooding in dinosaurs. First, a fossil embryo of an *Oviraptor* dinosaur was found, still inside its egg. This egg was identical to those found in another fossil, one that showed an *Oviraptor* crouching over a group of eggs in a posture similar to that seen in brooding birds today (**Figure 26.17**). Researchers suggested that the *Oviraptor* dinosaur preserved in this second fossil died while incubating or protecting its eggs. The broader conclusion that emerged from this work—that dinosaurs built nests and exhibited brooding—has since been strengthened by additional fossil discoveries that show that other species of dinosaurs built nests and sat on their eggs. Finally, by supporting predictions based on the phylogenetic hypothesis shown in **Figure 26.16**, fossil discoveries of nests

and brooding in dinosaurs provide independent data that suggest that the hypothesis is correct.



▲ Figure 26.17 Fossil support for a phylogenetic prediction: Dinosaurs built nests and brooded their eggs.

CONCEPT CHECK 26.3

1. To distinguish a particular clade of mammals within the larger clade that corresponds to class Mammalia, would hair be a useful character? Why or why not?
2. The most parsimonious tree of evolutionary relationships can be inaccurate. How can this occur?
3. **WHAT IF?** Draw a phylogenetic tree that includes the relationships from Figure 25.7 and Figure 26.16. Traditionally, all the taxa shown besides birds and mammals were classified as reptiles. Would a cladistic approach support that classification? Explain.

For suggested answers, see Appendix A.

CONCEPT 26.4

An organism's evolutionary history is documented in its genome

As you have seen in this chapter, molecular systematics—using comparisons of nucleic acids or other molecules to deduce relatedness—can reveal phylogenetic relationships that cannot be determined by nonmolecular methods such as comparative anatomy. For example, molecular systematics helps us uncover evolutionary relationships between groups that have little common ground for morphological comparison, such as animals and fungi. And molecular methods allow us to reconstruct phylogenies among groups of present-day organisms for which the fossil record is poor or lacking entirely.

Different genes can evolve at different rates, even in the same evolutionary lineage. As a result, molecular trees can represent short or long periods of time, depending on which

genes are used. For example, the DNA that codes for ribosomal RNA (rRNA) changes relatively slowly. Therefore, comparisons of DNA sequences in these genes are useful for investigating relationships between taxa that diverged hundreds of millions of years ago. Studies of rRNA sequences indicate, for instance, that fungi are more closely related to animals than to plants. In contrast, mitochondrial DNA (mtDNA) evolves relatively rapidly and can be used to explore recent evolutionary events. One research team has traced the relationships among Native American groups through their mtDNA sequences. The molecular findings corroborate other evidence that the Pima of Arizona, the Maya of Mexico, and the Yanomami of Venezuela are closely related, probably descending from the first of three waves of immigrants that crossed the Bering Land Bridge from Asia to the Americas about 15,000 years ago.

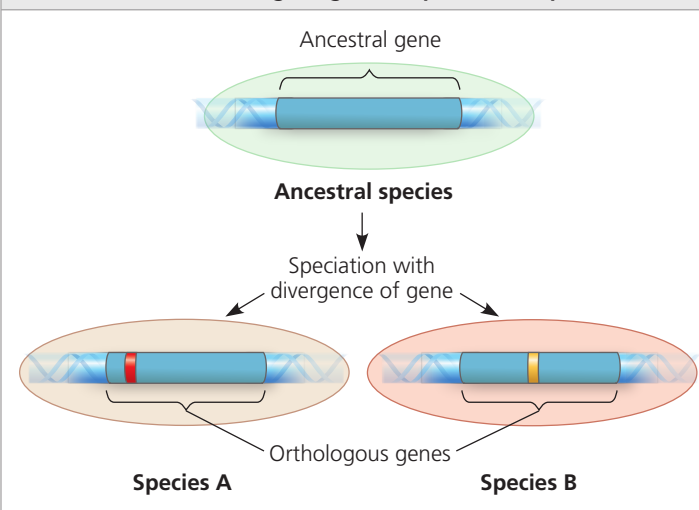
Gene Duplications and Gene Families

What do molecular data reveal about the evolutionary history of genome change? Consider gene duplication, which plays a particularly important role in evolution because it increases the number of genes in the genome, providing more opportunities for further evolutionary changes. Molecular techniques now allow us to trace the phylogenies of gene duplications. These molecular phylogenies must account for repeated duplications that have resulted in *gene families*, groups of related genes within an organism's genome (see Figure 21.11).

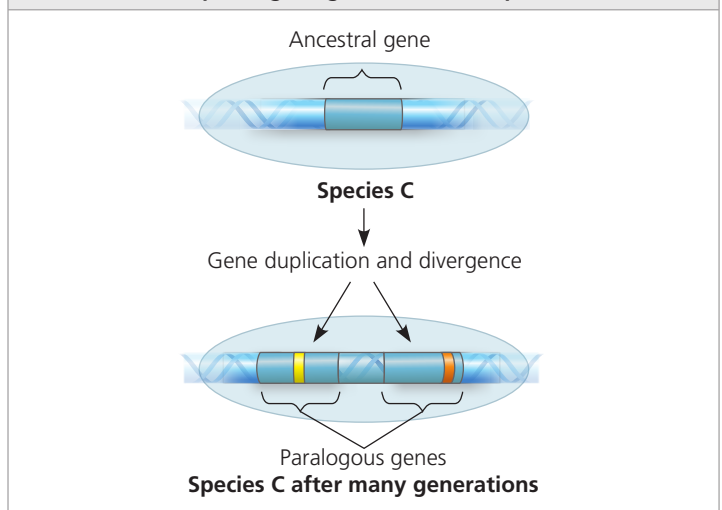
Accounting for such duplications leads us to distinguish two types of homologous genes (Figure 26.18): orthologous genes and paralogous genes. In **orthologous genes** (from the Greek *orthos*, exact), the homology is the result of a

▼ **Figure 26.18** Two types of homologous genes. Colored bands mark regions of the genes where differences in base sequences have accumulated.

(a) Formation of orthologous genes: a product of speciation



(b) Formation of paralogous genes: within a species



speciation event and hence occurs between genes found in different species (see Figure 26.18a). For example, the genes that code for cytochrome *c* (a protein that functions in electron transport chains) in humans and dogs are orthologous. In **paralogous genes** (from the Greek *para*, in parallel), the homology results from gene duplication; hence, multiple copies of these genes have diverged from one another within a species (see Figure 26.18b). In Chapter 23, you encountered the example of olfactory receptor genes, which have undergone many gene duplications in vertebrates; humans have 350 of these paralogous genes, while mice have 1,000.

Note that orthologous genes can only diverge after speciation has taken place, that is, after the genes are found in separate gene pools. For example, although the cytochrome *c* genes in humans and dogs serve the same function, the gene's sequence in humans has diverged from that in dogs in the time since these species last shared a common ancestor. Paralogous genes, on the other hand, can diverge within a species because they are present in more than one copy in the genome. The paralogous genes that make up the olfactory receptor gene family in humans have diverged from each other during our long evolutionary history. They now specify proteins that confer sensitivity to a wide variety of molecules, ranging from food odors to sex pheromones.

Genome Evolution

Now that we can compare the entire genomes of different organisms, including our own, two patterns have emerged. First, lineages that diverged long ago often share many orthologous genes. For example, though the human and mouse lineages diverged about 65 million years ago, 99% of the genes of humans and mice are orthologous. And 50% of human genes are orthologous with those of yeast, despite 1 billion years of divergent evolution. Such commonalities explain why disparate organisms nevertheless share many biochemical and developmental pathways. As a result of these shared pathways, the functioning of genes linked to diseases in humans can often be investigated by studying yeast and other organisms distantly related to humans.

Second, the number of genes a species has doesn't seem to increase through duplication at the same rate as perceived phenotypic complexity. Humans have only about four times as many genes as yeast, a single-celled eukaryote, even though—unlike yeast—we have a large, complex brain and a body with more than 200 different types of tissues. Evidence is emerging that many human genes are more versatile than those of yeast: A single human gene can encode multiple proteins that perform different tasks in various body tissues. Unraveling the mechanisms that cause this genomic versatility and phenotypic variation is an exciting challenge.

CONCEPT CHECK 26.4

1. Explain how comparing proteins of two species can yield data about the species' evolutionary relationship.
2. **WHAT IF?** Suppose gene A is orthologous in species 1 and species 2, and gene B is paralogous to gene A in species 1. Suggest a sequence of two evolutionary events that could result in the following: Gene A differs considerably between species, yet gene A and gene B show little divergence from each other.
3. **MAKE CONNECTIONS** Review Figure 18.13; then suggest how a particular gene could have different functions in different tissues within an organism.

For suggested answers, see Appendix A.

CONCEPT 26.5

Molecular clocks help track evolutionary time

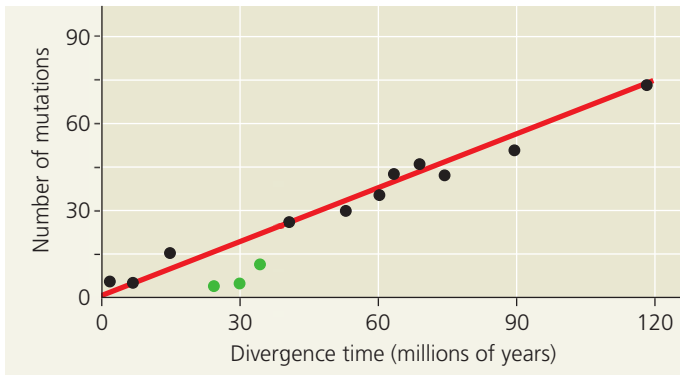
One goal of evolutionary biology is to understand the relationships among all organisms, including those for which there is no fossil record. However, if we attempt to determine the timing of phylogenies that extend beyond the fossil record, we must rely on an important assumption about how change occurs at the molecular level.

Molecular Clocks

We stated earlier that researchers have estimated that the common ancestor of Hawaiian silversword plants lived about 5 million years ago. How did they make this estimate? They relied on the concept of a **molecular clock**, an approach for measuring the absolute time of evolutionary change based on the observation that some genes and other regions of genomes appear to evolve at constant rates. An assumption underlying the molecular clock is that the number of nucleotide substitutions in orthologous genes is proportional to the time that has elapsed since the genes branched from their common ancestor (divergence time). In the case of paralogous genes, the number of substitutions is proportional to the time since the ancestral gene was duplicated.

We can calibrate the molecular clock of a gene that has a reliable average rate of evolution by graphing the number of genetic differences—for example, nucleotide, codon, or amino acid differences—against the dates of evolutionary branch points that are known from the fossil record (**Figure 26.19**). The average rates of genetic change inferred from such graphs can then be used to estimate the dates of events that cannot be discerned from the fossil record, such as the origin of the silverswords discussed earlier.

Of course, no gene marks time with complete precision. In fact, some portions of the genome appear to have evolved



▲ Figure 26.19 A molecular clock for mammals. The number of accumulated mutations in seven proteins has increased over time in a consistent manner for most mammal species. The three green data points represent primate species, whose proteins appear to have evolved more slowly than those of other mammals. The divergence time for each data point was based on fossil evidence.

INTERPRET THE DATA Use the graph to estimate the divergence time for a mammal with a total of 30 mutations in the seven proteins.

in irregular bursts that are not at all clocklike. And even those genes that seem to act as reliable molecular clocks are accurate only in the statistical sense of showing a fairly smooth *average* rate of change. Over time, there may still be deviations from that average rate. Furthermore, the same gene may evolve at different rates in different groups of organisms. Finally, when comparing genes that are clocklike, the rate of the clock may vary greatly from one gene to another; some genes evolve a million times faster than others.

Differences in Clock Speed

What causes such differences in the speed at which clocklike genes evolve? The answer stems from the fact that some mutations are selectively neutral—neither beneficial nor detrimental. Of course, many new mutations are harmful and are removed quickly by selection. But if most of the rest are neutral and have little or no effect on fitness, then the rate of evolution of those neutral mutations should indeed be regular, like a clock. Differences in the clock rate for different genes are a function of how important a gene is. If the exact sequence of amino acids that a gene specifies is essential to survival, most of the mutational changes will be harmful and only a few will be neutral. As a result, such genes change only slowly. But if the exact sequence of amino acids is less critical, fewer of the new mutations will be harmful and more will be neutral. Such genes change more quickly.

Potential Problems with Molecular Clocks

In fact, molecular clocks do not run as smoothly as would be expected if the underlying mutations were selectively neutral. Many irregularities are likely to be the result of natural selection in which certain DNA changes are favored over

others. Indeed, evidence suggests that almost half the amino acid differences in proteins of two *Drosophila* species, *D. simulans* and *D. yakuba*, are not neutral but have resulted from natural selection. But because the direction of natural selection may change repeatedly over long periods of time (and hence may average out), some genes experiencing selection can nevertheless serve as approximate markers of elapsed time.

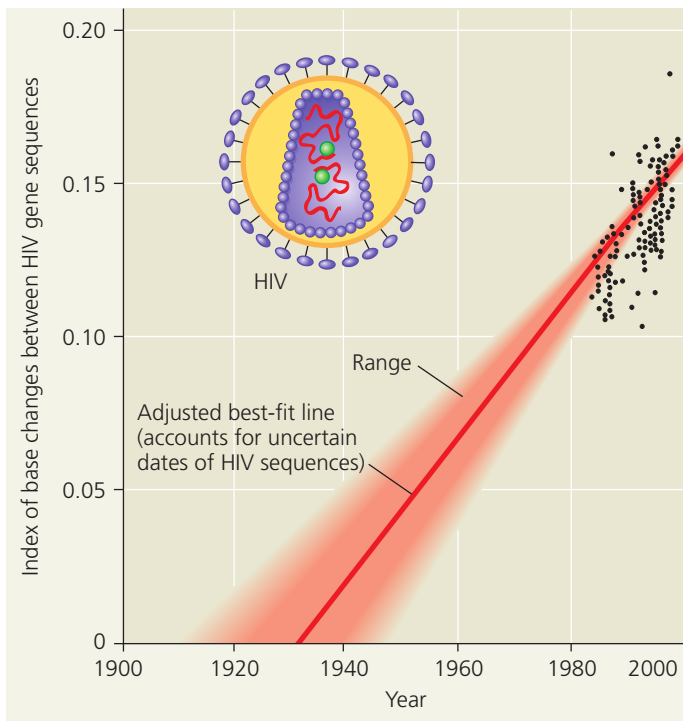
Another question arises when researchers attempt to extend molecular clocks beyond the time span documented by the fossil record. Although some fossils are more than 3 billion years old, these are very rare. An abundant fossil record extends back only about 550 million years, but molecular clocks have been used to date evolutionary divergences that occurred a billion or more years ago. These estimates assume that the clocks have been constant for all that time. Such estimates are highly uncertain.

In some cases, problems may be avoided by calibrating molecular clocks with data on the rates at which genes have evolved in different taxa. In other cases, problems may be avoided by using many genes rather than the common approach of using just one or a few genes. By using many genes, fluctuations in evolutionary rate due to natural selection or other factors that vary over time may average out. For example, one group of researchers constructed molecular clocks of vertebrate evolution from published sequence data for 658 nuclear genes. Despite the broad period of time covered (nearly 600 million years) and the fact that natural selection probably affected some of these genes, their estimates of divergence times agreed closely with fossil-based estimates. As this example suggests, if used with care, molecular clocks can aid our understanding of evolutionary relationships.

Applying a Molecular Clock: Dating the Origin of HIV

Researchers have used a molecular clock to date the origin of HIV infection in humans. Phylogenetic analysis shows that HIV, the virus that causes AIDS, is descended from viruses that infect chimpanzees and other primates. (Most of these viruses do not cause AIDS-like diseases in their native hosts.) When did HIV jump to humans? There is no simple answer, because the virus has spread to humans more than once. The multiple origins of HIV are reflected in the variety of strains (genetic types) of the virus. HIV's genetic material is made of RNA, and like other RNA viruses, it evolves quickly.

The most widespread strain in humans is HIV-1 M. To pinpoint the earliest HIV-1 M infection, researchers compared samples of the virus from various times during the epidemic, including a sample from 1959. A comparison of gene sequences showed that the virus has evolved in a clocklike



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▲ Figure 26.20 Dating the origin of HIV-1 M. The black data points are based on DNA sequences of an HIV gene in patients' blood samples. (The dates when these individual HIV gene sequences arose are not certain because a person can harbor the virus for years before symptoms occur.) Projecting the gene's rate of change backward in time suggests that the virus originated in the 1930s.

fashion (Figure 26.20). Extrapolating backward in time using the molecular clock indicates that the HIV-1 M strain first spread to humans around 1930. A later study, which dated the origin of HIV using a more advanced molecular clock approach than that covered in this book, estimated that the HIV-1 M strain first spread to humans around 1910.

CONCEPT CHECK 26.5

1. What is a molecular clock? What assumption underlies the use of a molecular clock?
2. **MAKE CONNECTIONS** Review Concept 17.5. Then explain how numerous base changes could occur in an organism's DNA yet have no effect on its fitness.
3. **WHAT IF?** Suppose a molecular clock dates the divergence of two taxa at 80 million years ago, but new fossil evidence shows that the taxa diverged at least 120 million years ago. Explain how this could happen.

For suggested answers, see Appendix A.

CONCEPT 26.6

Our understanding of the tree of life continues to change based on new data

The discovery that the glass lizard in Figure 26.1 evolved from a different lineage of legless lizards than did snakes

is one example of how our understanding of life's diversity is informed by systematics. Indeed, in recent decades, systematists have gained insight into even the very deepest branches of the tree of life by analyzing DNA sequence data.

From Two Kingdoms to Three Domains

Taxonomists once classified all known species into two kingdoms: plants and animals. Classification schemes with more than two kingdoms gained broad acceptance in the late 1960s, when many biologists recognized five kingdoms: Monera (prokaryotes), Protista (a diverse kingdom consisting mostly of unicellular organisms), Plantae, Fungi, and Animalia. This system highlighted the two fundamentally different types of cells, prokaryotic and eukaryotic, and set the prokaryotes apart from all eukaryotes by placing them in their own kingdom, Monera.

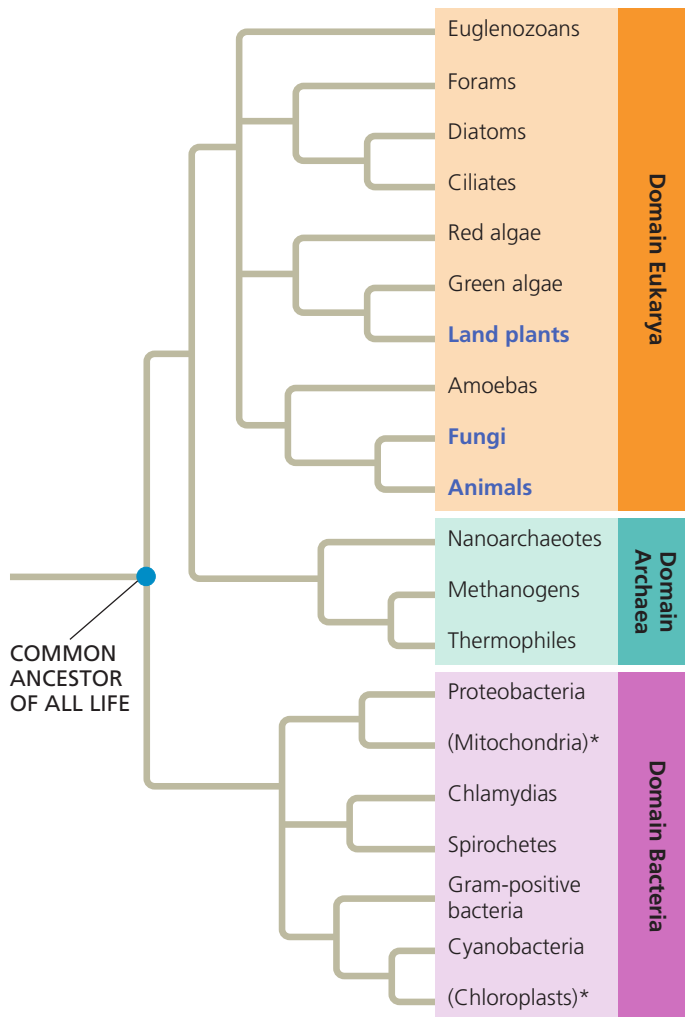
However, phylogenies based on genetic data soon began to reveal a problem with this system: Some prokaryotes differ as much from each other as they do from eukaryotes. Such difficulties have led biologists to adopt a three-domain system. The three domains—Bacteria, Archaea, and Eukarya—are a taxonomic level higher than the kingdom level. The validity of these domains is supported by many studies, including a recent study that analyzed nearly 100 completely sequenced genomes.

The domain Bacteria contains most of the currently known prokaryotes, while the domain Archaea consists of a diverse group of prokaryotic organisms that inhabit a wide variety of environments. The domain Eukarya consists of all the organisms that have cells containing true nuclei. This domain includes many groups of single-celled organisms as well as multicellular plants, fungi, and animals. Figure 26.21 represents one possible phylogenetic tree for the three domains and some of the many lineages they encompass.

The three-domain system highlights the fact that much of the history of life has been about single-celled organisms. The two prokaryotic domains consist entirely of single-celled organisms, and even in Eukarya, only the branches labeled in blue type (land plants, fungi, and animals) are dominated by multicellular organisms. Of the five kingdoms previously recognized by taxonomists, most biologists continue to recognize Plantae, Fungi, and Animalia, but not Monera and Protista. The kingdom Monera is obsolete because it would have members in two different domains. The kingdom Protista has also crumbled because it includes members that are more closely related to plants, fungi, or animals than to other protists (see Chapter 28).

The Important Role of Horizontal Gene Transfer

In the phylogeny shown in Figure 26.21, the first major split in the history of life occurred when bacteria diverged from



▲ Figure 26.21 The three domains of life. This phylogenetic tree is based on sequence data for rRNA and other genes. For simplicity, only some of the major branches in each domain are shown. Lineages within Eukarya that are dominated by multicellular organisms (land plants, fungi, and animals) are in blue type, while the two lineages denoted by an asterisk are based on DNA from cellular organelles. All other lineages consist solely or mainly of single-celled organisms.

MAKE CONNECTIONS After reviewing endosymbiont theory (see Figure 6.16), explain the specific positions of the mitochondrion and chloroplast lineages on this tree.

other organisms. If this tree is correct, eukaryotes and archaea are more closely related to each other than either is to bacteria.

This reconstruction of the tree of life is based in part on sequence comparisons of rRNA genes, which code for the RNA components of ribosomes. However, some other genes reveal a different set of relationships. For example, researchers have found that many of the genes that influence metabolism in yeast (a unicellular eukaryote) are more similar to genes in the domain Bacteria than they are to genes in the domain Archaea—a finding that suggests that the eukaryotes may share a more recent common ancestor with bacteria than with archaea.

What causes trees based on data from different genes to yield such different results? Comparisons of complete genomes from the three domains show that there have been substantial movements of genes between organisms in the different domains. These took place through **horizontal gene transfer**, a process in which genes are transferred from one genome to another through mechanisms such as exchange of transposable elements and plasmids, viral infection (see Chapter 19), and perhaps fusions of organisms (as when a host and its endosymbiont become a single organism). Recent research reinforces the view that horizontal gene transfer is important. For example, a 2008 analysis indicated that, on average, 80% of the genes in 181 prokaryotic genomes had moved between species at some point during the course of evolution. Because phylogenetic trees are based on the assumption that genes are passed vertically from one generation to the next, the occurrence of such horizontal transfer events helps to explain why trees built using different genes can give inconsistent results.

Horizontal gene transfer can also occur between eukaryotes. For example, over 200 cases of the horizontal transfer of transposons have been reported in eukaryotes, including humans and other primates, plants, birds, and the gecko shown in **Figure 26.22**. Nuclear genes have also been transferred horizontally from one eukaryote to another. The **Scientific Skills Exercise** describes one such example, giving you the opportunity to interpret data on the transfer of a pigment gene to an aphid from another species.

Overall, horizontal gene transfer has played a key role throughout the evolutionary history of life and it continues to occur today. Some biologists have argued that horizontal gene transfer was so common that the early history of life should be represented not as a dichotomously branching tree like that in Figure 26.21, but rather as a tangled network

▼ Figure 26.22 A recipient of transferred genes: the Mediterranean house gecko (*Hemidactylus turcicus*).

Recent genetic evidence indicates that this gecko is one of 17 reptile species that acquired the transposon *SPIN* as a result of horizontal gene transfer. The transposon may have been transferred from one species to another by the feeding activities of blood-sucking insects.



SCIENTIFIC SKILLS EXERCISE

Using Protein Sequence Data to Test an Evolutionary Hypothesis

Did Aphids Acquire Their Ability to Make Carotenoids Through Horizontal Gene Transfer? Carotenoids are colored molecules that have diverse functions in many organisms, such as photosynthesis in plants and light detection in animals. Plants and many microorganisms can synthesize carotenoids from scratch, but animals generally cannot (they must obtain carotenoids from their diet). One exception is the pea aphid *Acyrtosiphon pisum*, a small plant-dwelling insect whose genome includes a full set of genes for the enzymes needed to make carotenoids. Because other animals lack these genes, it is unlikely that aphids inherited them from a single-celled common ancestor shared with microorganisms and plants. So where did they come from? Evolutionary biologists hypothesize that an aphid ancestor acquired these genes by horizontal gene transfer from distantly related organisms.

How the Experiment Was Done Scientists obtained the DNA sequences for the carotenoid-biosynthesis genes from several species, including aphids, fungi, bacteria, and plants. A computer “translated” these sequences into amino acid sequences of the encoded polypeptides and aligned the amino acid sequences. This allowed the team to compare the corresponding polypeptides in the different organisms.

Data from the Experiment The sequences below show the first 60 amino acids of one polypeptide of the carotenoid-biosynthesis enzymes in the plant *Arabidopsis thaliana* (bottom) and the corresponding amino acids in five nonplant species, using the one-letter abbreviations for the amino acids (see Figure 5.14). A hyphen (-) indicates that a species lacks

a particular amino acid found in the *Arabidopsis* sequence.

Interpret the Data

1. In the rows of data for the organisms being compared with the aphid, highlight the amino acids that are identical to the corresponding amino acids in the aphid.
2. Which organism has the most amino acids in common with the aphid? Rank the partial polypeptides from the other four organisms in degree of similarity to that of the aphid.
3. Do these data support the hypothesis that aphids acquired the gene for this polypeptide by horizontal gene transfer? Why or why not? If horizontal gene transfer did occur, what type of organism is likely to have been the source?
4. What additional sequence data would support your hypothesis?
5. How would you account for the similarities between the aphid sequence and the sequences for the bacteria and plant?

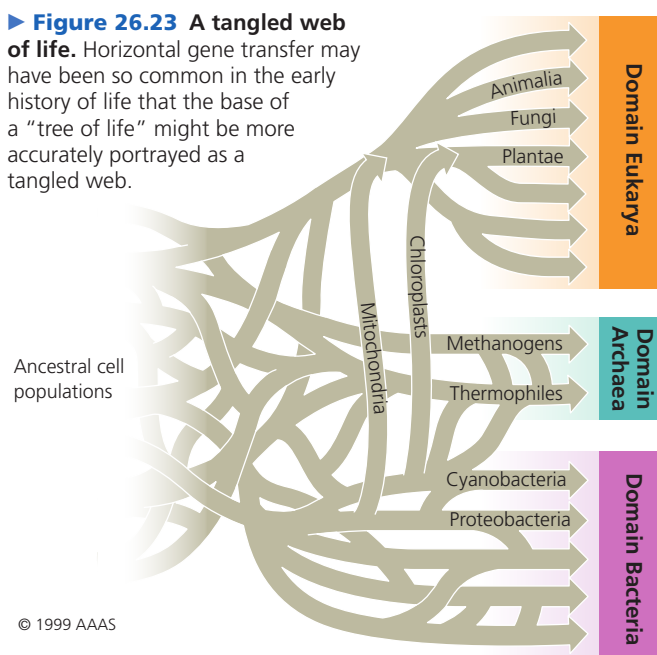
 A version of this Scientific Skills Exercise can be assigned in MasteringBiology.

Data from Nancy A. Moran, Yale University. See N. A. Moran and T. Jarvik, Lateral transfer of genes from fungi underlies carotenoid production in aphids, *Science* 328:624–627 (2010).



Organism	Alignment of Amino Acid Sequences					
<i>Acyrtosiphon</i> (aphid)	IKIIIIIGSGV	GGTAAAARLS	KKGFQVEVYE	KNSYNGGRCS	IIR-HNGHRF	DQGPSL--YL
<i>Ustilago</i> (fungus)	KKVVIIGAGA	GGTALAARLG	RRGYSVTVLE	KNSFGGGRCS	LIH-HDGHRW	DQGPSL--YL
<i>Gibberella</i> (fungus)	KSVIVIGAGV	GGVSTAARLA	KAGFKVTILE	KNDFTGGRCS	LIH-NDGHRF	DQGPSL--LL
<i>Staphylococcus</i> (bacterium)	MKIAVIGAGV	TGLAAAARIA	SQGHEVTIFE	KNNNVGGRMN	QLK-KDGFTF	DMGPTI--VM
<i>Pantoea</i> (bacterium)	KRTFVIGAGF	GGLALAIRLQ	AAGIATTVLE	QHDKPGGRAY	VWQ-DQGFTF	DAGPTV--IT
<i>Arabidopsis</i> (plant)	WDAVVIGGGH	NGLTAAAYLA	RGGLSVAVLE	RRHVIGGAAV	TEEIVPGFKF	SRCSYLQGLL

► **Figure 26.23** A tangled web of life. Horizontal gene transfer may have been so common in the early history of life that the base of a “tree of life” might be more accurately portrayed as a tangled web.



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of connected branches (**Figure 26.23**). Although scientists continue to debate whether early steps in the history of life are best represented as a tree or a tangled web, in recent decades there have been many exciting discoveries about evolutionary events that occurred over time. We’ll explore such discoveries in the rest of this unit’s chapters, beginning with Earth’s earliest inhabitants, the prokaryotes.

CONCEPT CHECK 26.6

1. Why is the kingdom Monera no longer considered a valid taxon?
2. Explain why phylogenies based on different genes can yield different branching patterns for the tree of all life.
3. **WHAT IF?** Draw the three possible dichotomously branching trees showing evolutionary relationships for the domains Bacteria, Archaea, and Eukarya. Two of these trees have been supported by genetic data. Is it likely that the third tree might also receive such support? Explain your answer.

For suggested answers, see Appendix A.

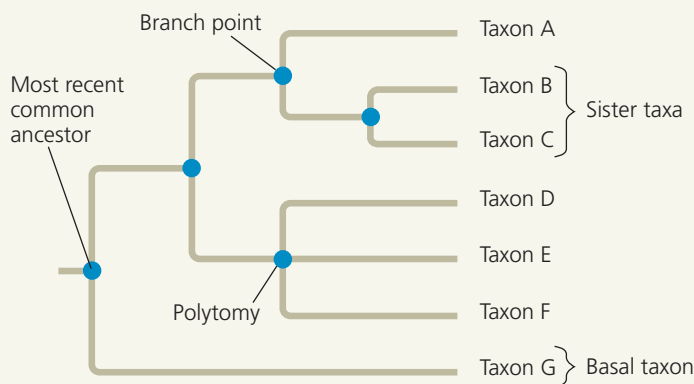
26 Chapter Review

SUMMARY OF KEY CONCEPTS

CONCEPT 26.1

Phylogenies show evolutionary relationships (pp. 548–551)

- Linnaeus's **binomial** classification system gives organisms two-part names: a **genus** plus a specific epithet.
- In the Linnaean system, species are grouped in increasingly broad taxa: Related genera are placed in the same family, families in orders, orders in classes, classes in phyla, phyla in kingdoms, and (more recently) kingdoms in domains.
- Systematists depict evolutionary relationships as branching **phylogenetic trees**. Many systematists propose that classification be based entirely on evolutionary relationships.



- Unless branch lengths are proportional to time or genetic change, a phylogenetic tree indicates only patterns of descent.
- Much information can be learned about a species from its evolutionary history; hence, phylogenies are useful in a wide range of applications.

? Humans and chimpanzees are sister species. Explain what that means.

CONCEPT 26.2

Phylogenies are inferred from morphological and molecular data (pp. 551–553)

- Organisms with similar morphologies or DNA sequences are likely to be more closely related than organisms with very different structures and genetic sequences.
- To infer phylogeny, **homology** (similarity due to shared ancestry) must be distinguished from **analogy** (similarity due to convergent evolution).
- Computer programs are used to align comparable DNA sequences and to distinguish molecular homologies from coincidental matches between taxa that diverged long ago.

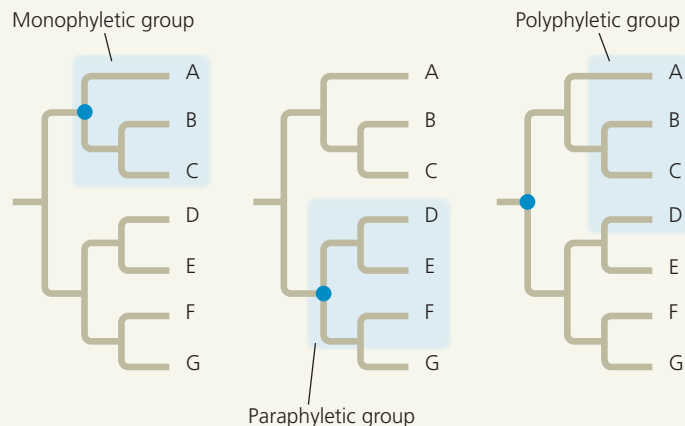
? Why is it necessary to distinguish homology from analogy to infer phylogeny?

CONCEPT 26.3

Shared characters are used to construct phylogenetic trees (pp. 553–559)

- A **clade** is a monophyletic grouping that includes an ancestral species and all of its descendants.

- Clades can be distinguished by their **shared derived characters**.



- Among phylogenies, the most parsimonious tree is the one that requires the fewest evolutionary changes. The most likely tree is the one based on the most likely pattern of changes.
- Well-supported phylogenetic hypotheses are consistent with a wide range of data.

? Explain the logic of using shared derived characters to infer phylogeny.

CONCEPT 26.4

An organism's evolutionary history is documented in its genome (pp. 559–560)

- Orthologous genes** are homologous genes found in different species as a result of speciation. **Paralogous genes** are homologous genes within a species that result from gene duplication; such genes can diverge and potentially take on new functions.
- Distantly related species often have many orthologous genes. The small variation in gene number in organisms of varying complexity suggests that genes are versatile and may have multiple functions.

? When reconstructing phylogenies, is it better to compare orthologous or paralogous genes? Explain.

CONCEPT 26.5

Molecular clocks help track evolutionary time (pp. 560–562)

- Some regions of DNA change at a rate consistent enough to serve as a **molecular clock**, in which the amount of genetic change is used to estimate the date of past evolutionary events. Other DNA regions change in a less predictable way.
- Molecular clock analyses suggest that the most common strain of HIV jumped from primates to humans in the early 1900s.

? Describe some assumptions and limitations of molecular clocks.

CONCEPT 26.6

Our understanding of the tree of life continues to change based on new data (pp. 562–564)

- Past classification systems have given way to the current view of the tree of life, which consists of three great **domains**: Bacteria, Archaea, and Eukarya.

- Phylogenies based in part on rRNA genes suggest that eukaryotes are most closely related to archaea, while data from some other genes suggest a closer relationship to bacteria.
- Genetic analyses indicate that extensive horizontal gene transfer has occurred throughout the evolutionary history of life.

? Why was the five-kingdom system abandoned for a three-domain system?

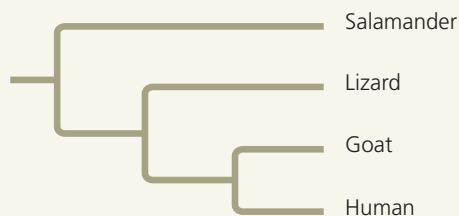
TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- In a comparison of birds and mammals, the condition of having four limbs is
 - a shared ancestral character.
 - a shared derived character.
 - a character useful for distinguishing birds from mammals.
 - an example of analogy rather than homology.
- To apply parsimony to constructing a phylogenetic tree,
 - choose the tree that assumes all evolutionary changes are equally probable.
 - choose the tree in which the branch points are based on as many shared derived characters as possible.
 - choose the tree that represents the fewest evolutionary changes, in either DNA sequences or morphology.
 - choose the tree with the fewest branch points.

LEVEL 2: APPLICATION/ANALYSIS

- In Figure 26.4, which similarly inclusive taxon descended from the same common ancestor as Canidae?
 - Felidae
 - Mustelidae
 - Carnivora
 - Lutra*
- Three living species X, Y, and Z share a common ancestor T, as do extinct species U and V. A grouping that consists of species T, X, Y, and Z (but not U or V) makes up
 - a monophyletic taxon.
 - an ingroup, with species U as the outgroup.
 - a paraphyletic group.
 - a polyphyletic group.
- Based on the tree below, which statement is *not* correct?



- The salamander lineage is a basal taxon.
 - Salamanders are a sister group to the group containing lizards, goats, and humans.
 - Salamanders are as closely related to goats as to humans.
 - Lizards are more closely related to salamanders than to humans.
- If you were using cladistics to build a phylogenetic tree of cats, which of the following would be the best outgroup?
 - wolf
 - domestic cat
 - lion
 - leopard
 - The relative lengths of the frog and mouse branches in the phylogenetic tree in Figure 26.13 indicate that
 - frogs evolved before mice.
 - mice evolved before frogs.
 - the homolog has evolved more rapidly in mice.
 - the homolog has evolved more slowly in mice.

LEVEL 3: SYNTHESIS/EVALUATION

8. EVOLUTION CONNECTION

Darwin suggested looking at a species' close relatives to learn what its ancestors may have been like. How does his suggestion anticipate recent methods, such as phylogenetic bracketing and the use of outgroups in cladistic analysis?

9. SCIENTIFIC INQUIRY

DRAW IT (a) Draw a phylogenetic tree based on characters 1–5 in the table below. Place hatch marks on the tree to indicate the origin(s) of characters 1–6. (b) Assume that tuna and dolphins are sister species and redraw the phylogenetic tree accordingly. Use hatch marks to indicate the origin(s) of characters 1–6. (c) How many evolutionary changes are required in each tree? Which tree is most parsimonious?

Character	Lancelet (outgroup)	Lamprey	Tuna	Salamander	Turtle	Leopard	Dolphin
(1) Backbone	0	1	1	1	1	1	1
(2) Hinged jaw	0	0	1	1	1	1	1
(3) Four limbs	0	0	0	1	1	1	1*
(4) Amnion	0	0	0	0	1	1	1
(5) Milk	0	0	0	0	0	1	1
(6) Dorsal fin	0	0	1	0	0	0	1

*Although adult dolphins have only two obvious limbs (their flippers), as embryos they have two hind-limb buds, for a total of four limbs.

10. WRITE ABOUT A THEME: INFORMATION

In a short essay (100–150 words), explain how genetic information—along with an understanding of the process of descent with modification—enables scientists to reconstruct phylogenies that extend hundreds of millions of years back in time.

11. SYNTHESIZE YOUR KNOWLEDGE



This West Indian manatee (*Trichechus manatus*) is an aquatic mammal. Like amphibians and reptiles, mammals are tetrapods (vertebrates with four limbs). Explain why manatees are considered tetrapods even though they lack hind limbs, and suggest traits that manatees likely share with leopards and other mammals (see Figure 26.12b). How might early members of the manatee lineage have differed from today's manatees?

For selected answers, see Appendix A.

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