25

The History of Life on Earth

▲ **Figure 25.1** **What does fossil evidence say about where these dinosaurs lived?**

EVOLUTION

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 single-celled and multicelled 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

OVERVIEW

Lost Worlds

▲ ***Cryolophosaurus* skull**

Visitors to Antarctica today encounter one of Earth's harshest, most barren environments. In this land of extreme cold where there is almost no liquid water, life is sparse and small—the largest fully terrestrial animal is a fly that is 5 mm long. But even as early Antarctic explorers struggled to survive, some of them made an astonishing discovery: fossil evidence that life once thrived where it now barely exists. Fossils reveal that 500 million years ago, the ocean waters surrounding Antarctica were warm and teeming with tropical invertebrates. Later, the continent was covered in forests for hundreds of millions of years. At various times, a wide range of 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, if not quite as surprising, 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 the diversity of life, and the origin of key adaptations such as flight in birds.

Taken together, such changes provide a grand view of the evolutionary history of life on Earth. We'll examine that history in this chapter, beginning with hypotheses regarding the origin of life. The origin of life 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 and what it tells us about major events in the history of life, paying particular attention to factors that have helped to shape 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 are about 3.5 billion years old. But when and 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 on early Earth, aided by the emerging force of natural selection, could have produced very 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 will examine some of the evidence for each stage.

Synthesis of Organic Compounds on Early Earth

There is scientific evidence that Earth and the other planets of the solar system formed about 4.6 billion years ago, condensing from a vast cloud of dust and rocks that surrounded the young sun. For the first few hundred million years, life probably could not have originated or survived on Earth because the planet was still being bombarded by huge chunks of rock and ice left over from the formation of the solar system. The collisions generated enough heat to vaporize the available water and prevent seas from forming. This early phase likely ended about 4.2–3.9 billion years ago.

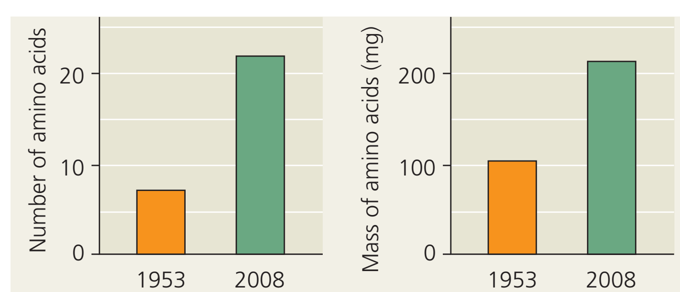
As the bombardment of early Earth slowed, conditions on the planet were extremely different from those of today. The first atmosphere was probably thick with water vapor, along with various compounds released by volcanic eruptions, including nitrogen and its oxides, carbon dioxide, methane, ammonia, hydrogen, and hydrogen sulfide. As Earth cooled, the water vapor condensed into oceans, and much of the hydrogen escaped into space.

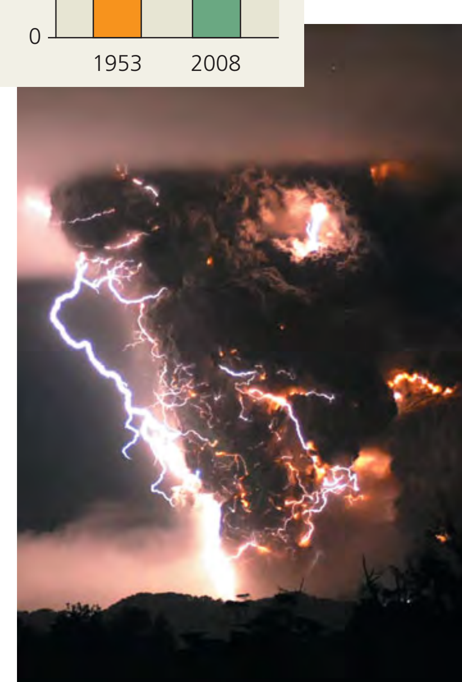
During the 1920s, Russian chemist A. I. Oparin and British scientist J. B. S. Haldane independently hypothesized that Earth's early atmosphere was a reducing (electron-adding) environment, in which organic compounds could have formed from simpler molecules. The energy for this organic synthesis could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

During 1953, Stanley Miller, working under the guidance of 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, it is unclear whether the atmosphere of early Earth contained enough methane and ammonia to be reducing. 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, it is likely that small pockets of the early atmosphere—perhaps near the openings of volcanoes—were reducing. Perhaps the first organic compounds formed near volcanoes or deep-sea vents, where hot water and minerals gush into the ocean from Earth's interior. In a 2008 test of this volcanic-atmosphere hypothesis, researchers used modern equipment to reanalyze molecules that Miller had saved from one of his experiments. The study found that numerous amino acids had formed under conditions that simulated a volcanic eruption **(Figure 25.2)**.

Miller-Urey-type experiments demonstrate that the abiotic synthesis of organic molecules is possible under various assumptions about the composition of the early atmosphere. A second source of organic molecules may have been meteorites. Among the meteorites that land on Earth are carbonaceous chondrites, rocks that are 1–2% carbon compounds by mass. Fragments of the Murchison meteorite, a 4.5-billion-year-old chondrite that fell to 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.





▲ **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 *After reviewing Concept 5.4 (pp. 78–80), explain how more than 20 amino acids could have been produced in the 2008 experiment.*

Abiotic Synthesis of Macromolecules

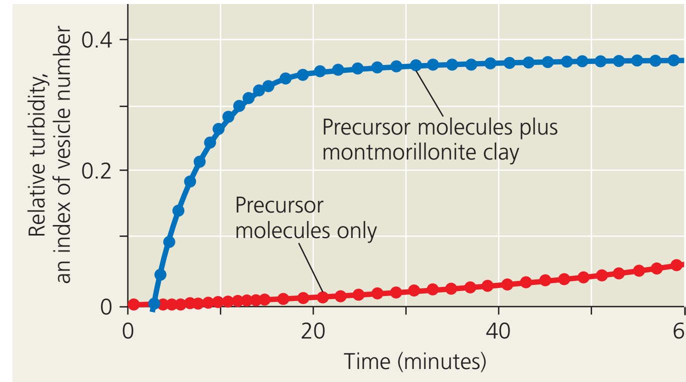
The presence of small organic molecules, such as amino acids and nitrogenous bases, is not sufficient for the emergence of life as we know it. Every cell has a vast assortment of macromolecules, including enzymes and other proteins and the nucleic acids that are essential for self-replication. Could 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. Nevertheless, it is possible that such polymers may have acted as weak catalysts for a variety of chemical reactions on early Earth.

Protocells

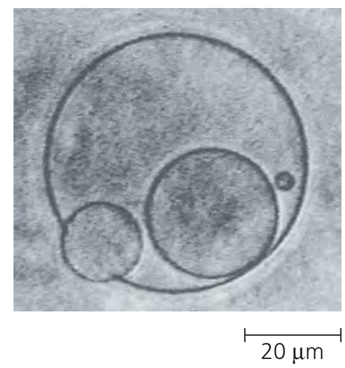
All organisms must be able to carry out reproduction and energy processing (metabolism). Life cannot persist without both of these functions. DNA molecules carry genetic information, including the instructions needed to replicate themselves accurately during reproduction. But the replication of DNA requires elaborate enzymatic machinery, along with a copious supply of nucleotide building blocks that are provided by the cell's metabolism (see Chapter 16). This suggests that self-replicating molecules and a metabolism-like source of the building blocks may have appeared together in early protocells. How did that happen?

The necessary conditions may have been met in *vesicles*, fluid-filled compartments bounded 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.

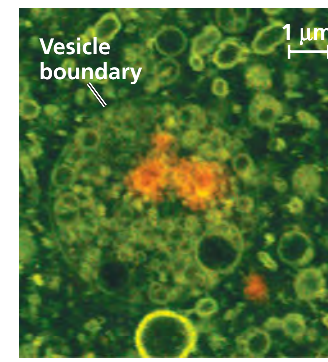
For example, vesicles can form spontaneously when lipids or other organic molecules are added to water. When this occurs, the hydrophobic molecules in the mixture organize into a bilayer similar to the lipid bilayer of a plasma membrane. Adding substances such as *montmorillonite*, a soft mineral clay produced by the weathering of volcanic ash, greatly increases the rate of vesicle self-assembly **(Figure 25.3a)**. 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 **(Figure 25.3b)**, and 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



(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 25.3 Features of abiotically produced vesicles.**

(Figure 25.3c). 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 and the Dawn of Natural Selection

The first genetic material was most likely RNA, not DNA. Thomas Cech, of the University of Colorado, and Sidney Altman, of Yale University, found that RNA, which plays a central role in protein synthesis, can also carry out a number of enzyme-like catalytic functions. Cech called these RNA catalysts **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 base sequences are more stable and replicate faster and with fewer errors than other sequences. The RNA molecule whose sequence is best suited to the surrounding environment and has the greatest ability to replicate itself will leave the most descendant molecules. Occasionally, a copying error will result in a molecule that folds into a shape that is even more stable or more adept at self-replication than the ancestral sequence. Similar selection events may have occurred on early Earth. Thus, the molecular biology of today may have been preceded by an "RNA world," in which small RNA molecules that carried genetic information were able to replicate and to store information about the vesicles that carried them.

A vesicle with self-replicating, catalytic RNA would differ from its many neighbors that did not carry RNA or that carried RNA without such capabilities. If that vesicle could grow, split, and pass its RNA molecules to its daughters, the daughters would be protocells that had some of the properties of their parent. Although the first such protocells must have 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 further 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 stable repository for genetic information than the more fragile single-stranded 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. After DNA appeared, perhaps RNA molecules began to take on their present-day roles as regulators and intermediates in the translation of genes. The stage was now set for a blossoming of diverse life-forms—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 (p. 329) and 19.8 (p. 389), 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 explore what the fossil record reveals about the major changes in the history of life—what those changes have been and how they may have occurred.

The Fossil Record

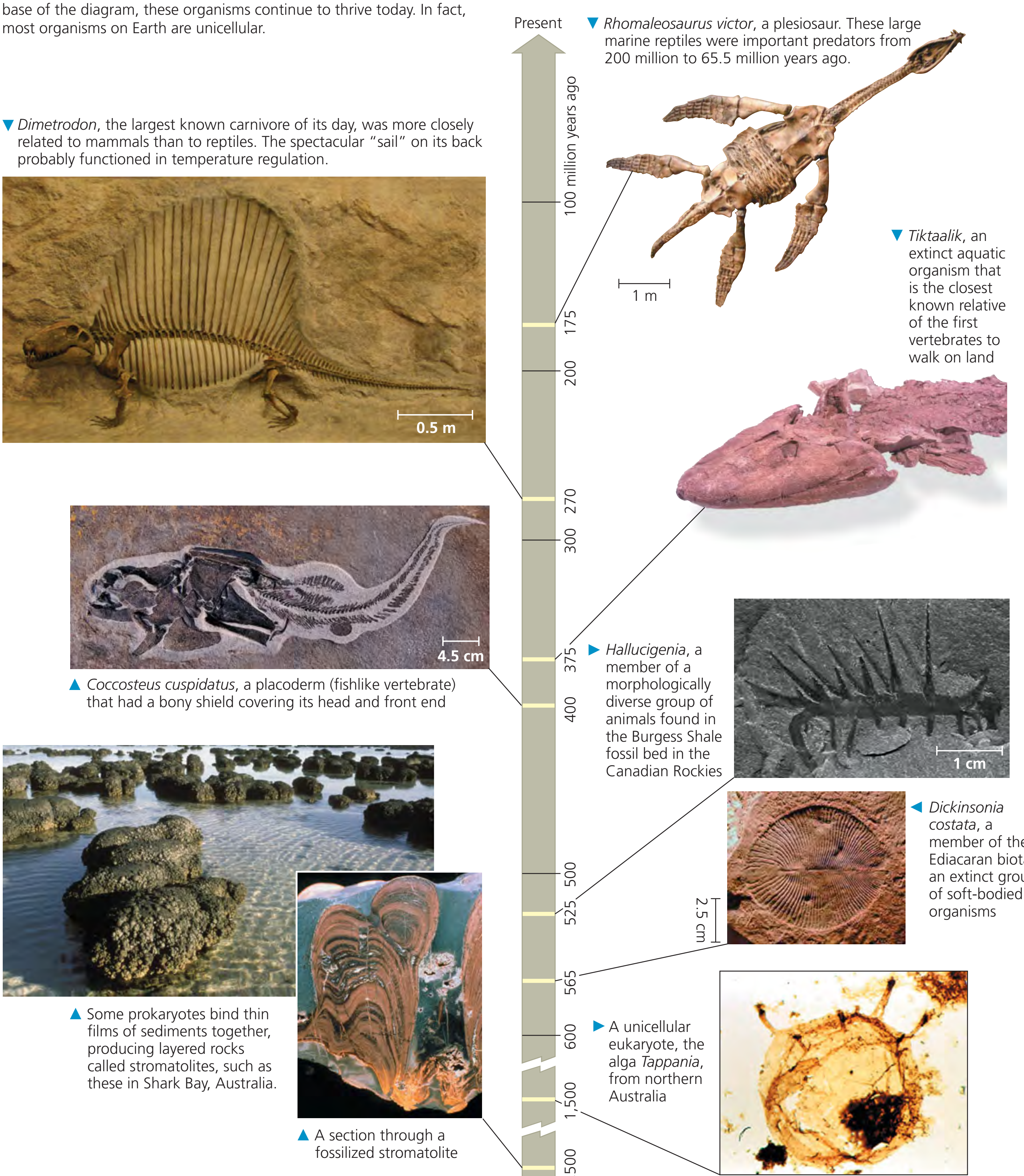
Recall from Chapter 22 that sedimentary rocks are the richest source of fossils. As a result, the fossil record is based primarily on the sequence in which fossils have accumulated in sedimentary rock layers, called *strata* (see Figure 22.3). Useful information is also provided by other types of fossils, 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 25.4)**. Many past organisms were unlike today's organisms, and many organisms that once were common are now extinct. As we'll see later, 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 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.

Although some of these new discoveries are fortuitous, others illustrate the predictive nature of paleontology. For instance, researchers seeking to discover a close ancestor of early terrestrial vertebrates predicted that such a fossil would most likely be located in a river bed (which would have sedimentary rocks) containing rocks that were 375 million years old (an age based on previously known fossils). After digging for several years in one of the few such places on Earth, their predictions bore fruit with the discovery of *Tiktaalik*, an aquatic organism closely related to the first vertebrates to walk on land (see Figures 25.4 and 34.20).

▼ **Figure 25.4 Documenting the history of life.** These fossils illustrate representative organisms from different points in time. Although prokaryotes and unicellular eukaryotes are only shown at the base of the diagram, these organisms continue to thrive today. In fact, most organisms on Earth are unicellular.



▼ *Rhomaleosaurus victor*, a plesiosaur. These large marine reptiles were important predators from 200 million to 65.5 million years ago.

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

▼ *Tiktaalik*, an extinct aquatic organism that is the closest known relative of the first vertebrates to walk on land

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

▶ *Hallucigenia*, a member of a morphologically diverse group of animals found in the Burgess Shale fossil bed in the Canadian Rockies

◀ *Dickinsonia costata*, a member of the Ediacaran biota, an extinct group of soft-bodied organisms

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

▶ A unicellular eukaryote, the alga *Tappania*, from northern Australia

▲ A section through a fossilized stromatolite

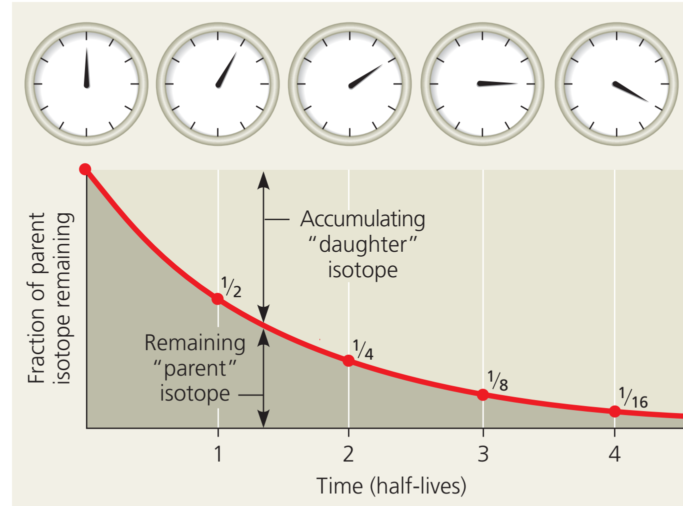
How Rocks and Fossils Are Dated

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 in strata is like peeling off layers of wallpaper in an old house. You can determine 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" dating does not mean errorless dating, but only 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 fixed rate. The rate of decay is expressed by the **half-life**, the time required for 50% of the parent isotope to decay (**Figure 25.5**). 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; it has a half-life of 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. Moreover, the sedimentary rocks themselves tend to consist of sediments of differing ages. Though we usually cannot date these old fossils directly, an indirect method can be used to infer the age of fossils that are sandwiched between two layers of volcanic rocks. As lava 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.



▲ **Figure 25.5 Radiometric dating.** In this diagram, each division of the clock face represents a half-life.

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

Now that we've seen how fossils can be dated, let's turn to an example of what we can learn from them.

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.

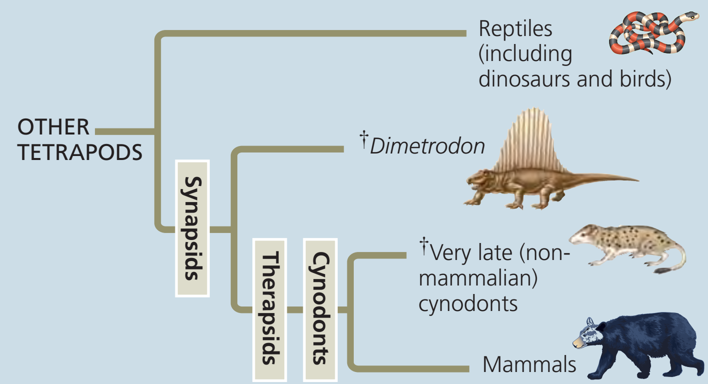
Along with amphibians and reptiles, mammals belong to the group of animals called *tetrapods* (from the Greek *tetra*, four, and *pod*, foot), named for having four limbs. Mammals have a number of unique anatomical features that fossilize readily, allowing scientists to trace their origin. For example, 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 hinge between a different set of bones in mammals than in other tetrapods. As we'll explore in Chapter 34, 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). 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 25.6**, the fossil record shows that the unique features of mammalian jaws and teeth evolved gradually over time, in a series of steps. As you study Figure 25.6, bear in mind that it includes just a few examples of the fossil skulls that document the origin of mammals. If all the

▼ **Figure 25.6**

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).

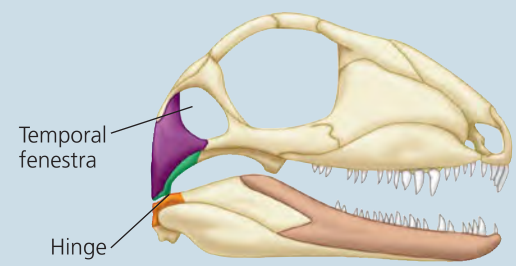


Key to skull bones

- Articular
- Quadrate
- Dentary
- Squamosal

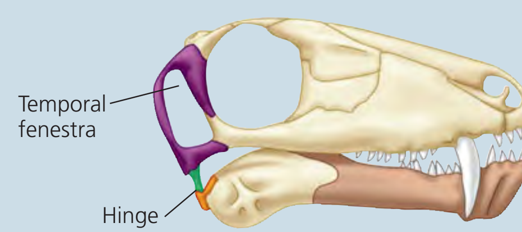
Synapsid (300 mya)

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).



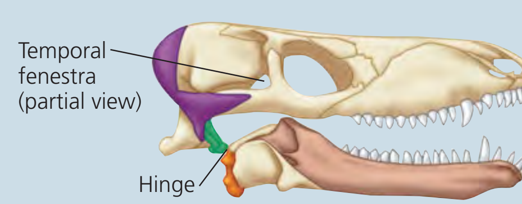
Therapsid (280 mya)

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.



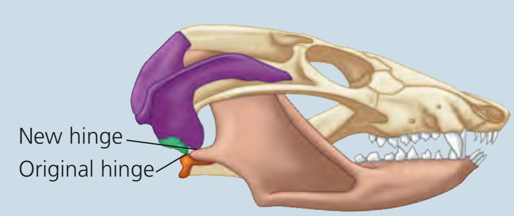
Early cynodont (260 mya)

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) shown in Figure 34.31.

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 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.

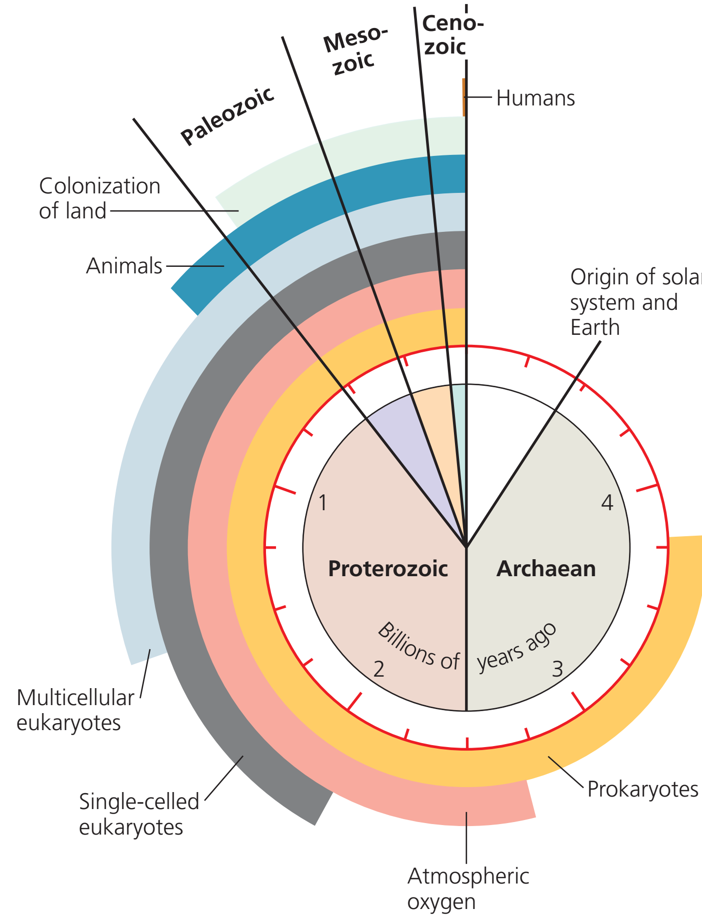
For suggested answers, see Appendix A.

CONCEPT 25.3

Key events in life's history include the origins of single-celled and multicelled organisms and the colonization of land

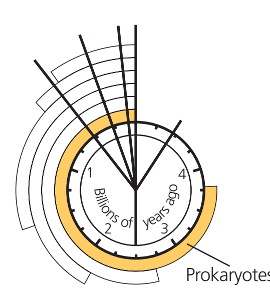
The study of fossils has helped geologists establish a **geologic record** of Earth's history, which is divided into three eons (**Table 25.1**, on the facing page). The first two eons—the Archaean and the Proterozoic—together lasted approximately 4 billion years. The Phanerozoic eon, roughly the last 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 25.7** 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.



▲ **Figure 25.7 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.

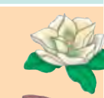
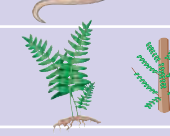
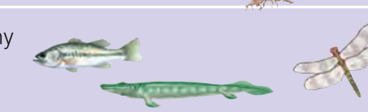
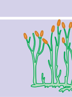
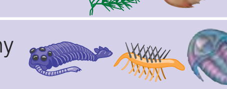
The First Single-Celled Organisms



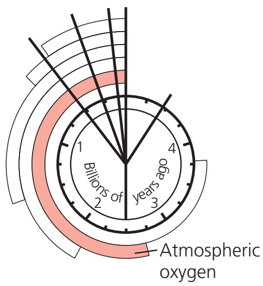
The earliest direct evidence of life, dating from 3.5 billion years ago, comes from fossilized stromatolites (see Figure 25.4). **Stromatolites** are layered rocks that form when certain prokaryotes bind thin films of sediment together. Present-day stromatolites are found in a few warm, shallow, salty bays. If microbial communities complex enough to form stromatolites existed 3.5 billion years ago, it is a reasonable hypothesis that single-celled organisms originated much earlier, perhaps as early as 3.9 billion years ago.

Early prokaryotes were Earth's sole inhabitants from at least 3.5 billion years ago to about 2.1 billion years ago. As we will see, these prokaryotes transformed life on our planet.

Table 25.1 The Geologic Record

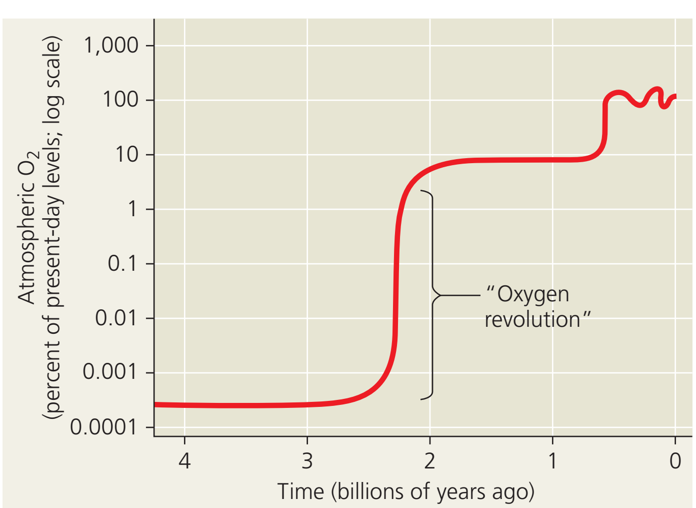
Relative Duration of Eons	Era	Period	Epoch	Age (Millions of Years Ago)	Some Important Events in the History of Life	
Phanerozoic	Cenozoic	Quaternary	Holocene	0.01	Historical time	
			Pleistocene	2.6	Ice ages; origin of genus *Homo*	
		Neogene	Pliocene	5.3	Appearance of bipedal human ancestors	
			Miocene	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	
	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	
		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)	
Proterozoic		Ediacaran		635	Diverse algae and soft-bodied invertebrate animals appear	
				2,100	Oldest fossils of eukaryotic cells appear	
				2,500		
Archaean				2,700	Concentration of atmospheric oxygen begins to increase	
				3,500	Oldest fossils of cells (prokaryotes) appear	
				3,800	Oldest known rocks on Earth's surface	
				Approx. 4,600	Origin of Earth	

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 dissolved 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 well before 2.7 billion years ago.

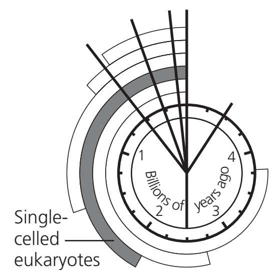
The amount of atmospheric O_2 increased gradually from about 2.7 to 2.3 billion years ago, but then shot up relatively rapidly to between 1% and 10% of its present level **(Figure 25.8)**. This "oxygen revolution" had an enormous impact on life. In certain of its chemical forms, oxygen attacks chemical 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 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.



▲ **Figure 25.8 The rise of atmospheric oxygen.** Chemical analyses of ancient rocks have enabled this reconstruction of atmospheric oxygen levels during Earth's history.

As mentioned previously, the early, gradual rise in atmospheric O_2 levels was probably brought about by ancient cyanobacteria. A few hundred million years later, the rise in O_2 accelerated. What caused this acceleration? One hypothesis is that this rise followed the evolution of eukaryotic cells containing chloroplasts, as we will discuss next.

The First Eukaryotes

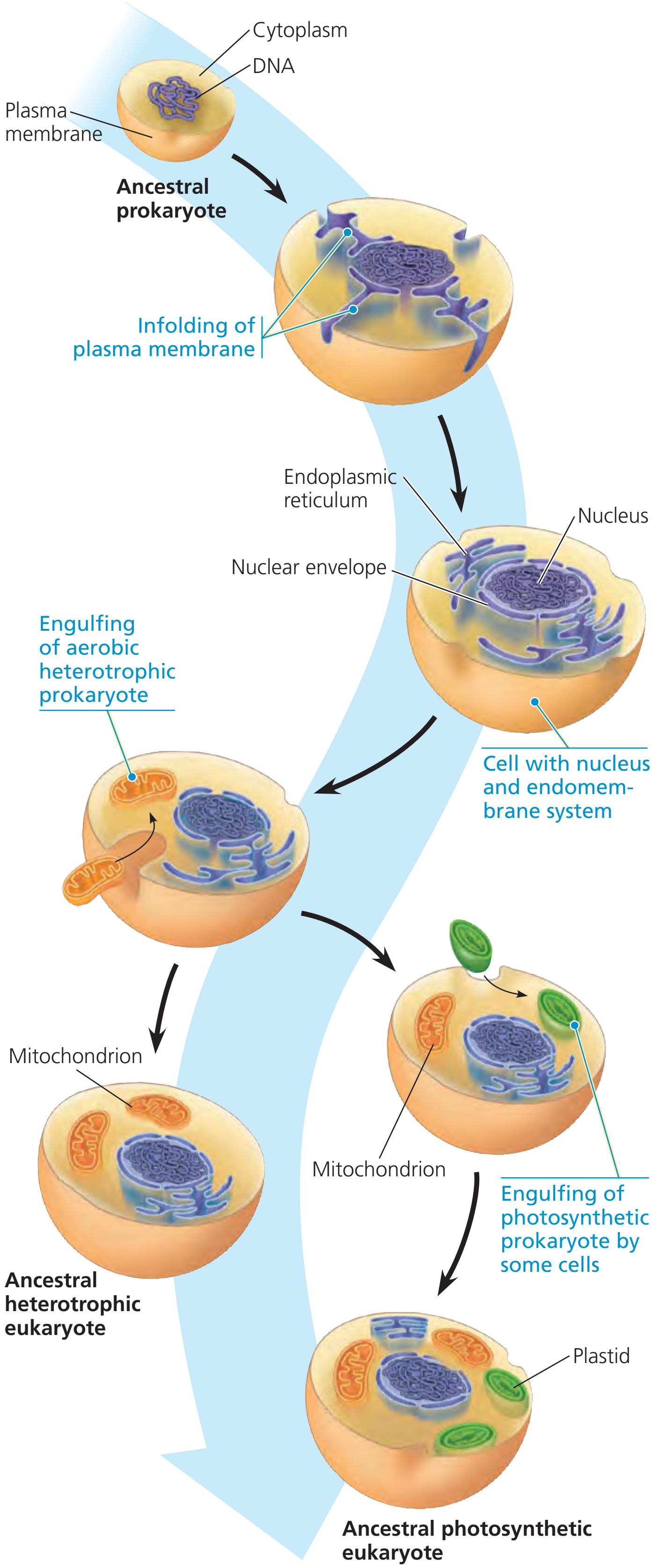


The oldest widely accepted fossils of eukaryotic organisms are about 2.1 billion years old. Recall that eukaryotic cells have more complex organization than prokaryotic cells: Eukaryotic cells have a nuclear envelope, mitochondria, endoplasmic reticulum, and other internal structures that prokaryotes lack. Also, unlike prokaryotic cells, eukaryotic cells have a cytoskeleton, a feature that enables eukaryotic cells to change their shape and thereby surround and engulf other cells.

How did these eukaryotic features evolve from prokaryotic cells? A range of 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 gained entry to 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 came to have a mutually beneficial relationship with the host in as little as five years.

By whatever means the relationships began, we can hypothesize how the symbiosis could have become mutually beneficial. A host that is a heterotroph (an organism that eats other organisms or substances derived from them) could use nutrients released from photosynthetic endosymbionts. And in a world that was becoming increasingly aerobic, a host that was itself an anaerobe would have benefited from endosymbionts that turned the oxygen to advantage. 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 25.9)**.

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



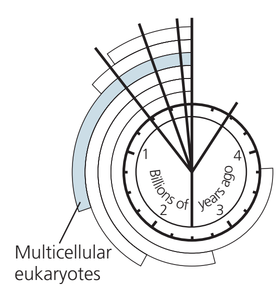
▲ **Figure 25.9 A hypothesis for the origin of eukaryotes through serial endosymbiosis.** The proposed ancestors of mitochondria were aerobic, heterotrophic prokaryotes (meaning they used oxygen to metabolize organic molecules obtained from other organisms). The proposed ancestors of plastids were photosynthetic prokaryotes. In this figure, the arrows represent change over evolutionary time.

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 a single, circular DNA molecule that, like the chromosomes of bacteria, is 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.

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.

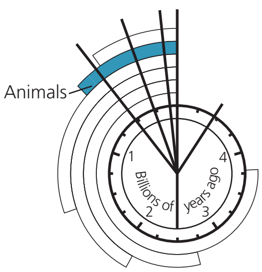
The Earliest Multicellular Eukaryotes



Based on comparisons of DNA sequences, researchers have suggested that the common ancestor of multicellular eukaryotes lived 1.5 billion years ago. This result is in rough agreement with the fossil record; the oldest known fossils of multicellular eukaryotes are of relatively small algae that lived about 1.2 billion years ago. Larger and more diverse multicellular eukaryotes do not appear in the fossil record until about 575 million years ago (see Figure 25.4). These fossils, referred to as the Ediacaran biota, were of soft-bodied organisms—some over 1 m long—that lived from 575 to 535 million years ago.

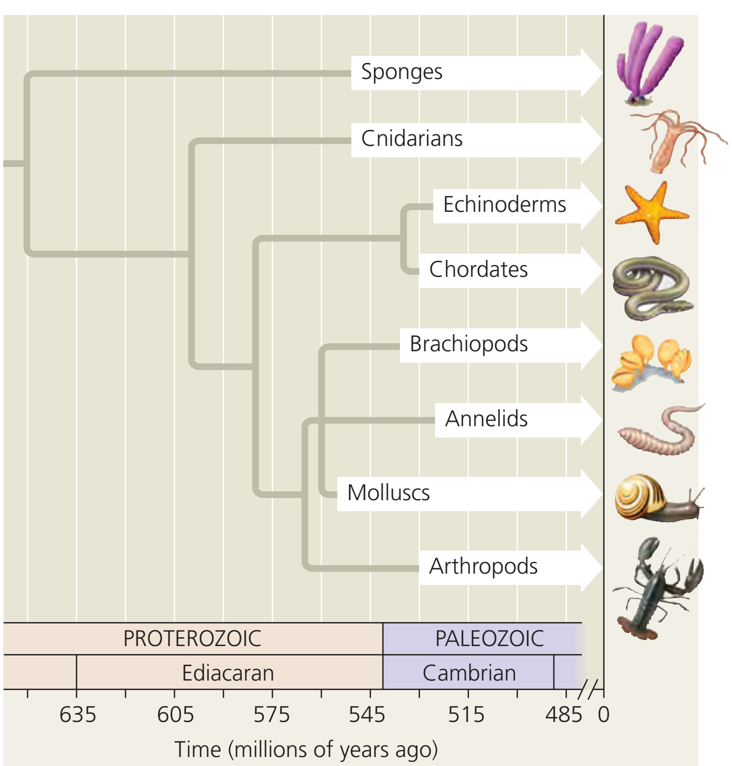
Why were multicellular eukaryotes limited in size and diversity until the late Proterozoic? One hypothesis stems from geologic evidence indicating that a series of severe ice ages occurred from 750 to 580 million years ago. At various times during this period, glaciers covered all of the planet's landmasses, and the seas were largely iced over. The "snowball Earth" hypothesis suggests that most life would have been confined to areas near deep-sea vents and hot springs or to equatorial regions of the ocean that lacked ice cover. The fossil record of the first major diversification of multicellular eukaryotes (beginning about 575 million years ago) corresponds roughly to the time when snowball Earth thawed. As that diversification came to a close about 40 million years later, the stage was set for another, even more spectacular burst of evolutionary change.

The Cambrian Explosion



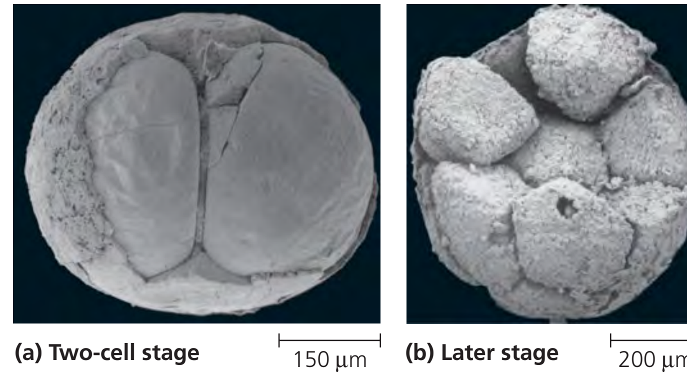
Many present-day animal phyla appear suddenly in fossils formed early in the Cambrian period (535–525 million years ago), a phenomenon referred to as the **Cambrian explosion**. Fossils of several animal groups—sponges, cnidarians (sea anemones and their relatives), and molluscs—appear in even older rocks dating from the late Proterozoic **(Figure 25.10)**.

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), suspension 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 25.4).



▲ **Figure 25.10 Appearance of selected animal groups.** The white bars indicate earliest appearances of these animal groups in the fossil record.

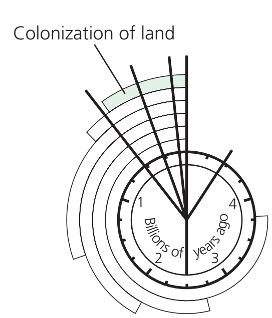
DRAW IT *Circle the branch point that represents the most recent common ancestor of chordates and annelids. What is a minimum estimate of that ancestor's age?*



▲ **Figure 25.11 Proterozoic fossils that may be animal embryos (SEM).**

Although the Cambrian explosion had an enormous impact on life on Earth, it is possible that many animal phyla originated long before that time. Some DNA analyses suggest that most animal phyla originated and began to diverge from one another as early as 700 million to 1 billion years ago. Even if these estimates are not correct, recent fossil discoveries in China suggest that animals similar to members of living animal phyla were present tens of millions of years before the Cambrian explosion. The discoveries include 575-million-year-old fossils of beautifully preserved specimens interpreted by most scientists either as animal embryos or as members of extinct groups closely related to animals **(Figure 25.11)**. Overall, it appears that the Cambrian explosion had a "long fuse"—at least 40 million years long, based on the Chinese fossils. The fuse may have been hundreds of millions of years long if some animal phyla originated as far back as some DNA-based estimates suggest.

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 about 50 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, 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 roots, dating this relationship back to the early spread of life onto land.

Although many animal groups are now represented in terrestrial environments, the most widespread and diverse land animals are arthropods (particularly insects and spiders) and tetrapods. Arthropods were the first animals to colonize land, roughly 420 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 seen 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 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.

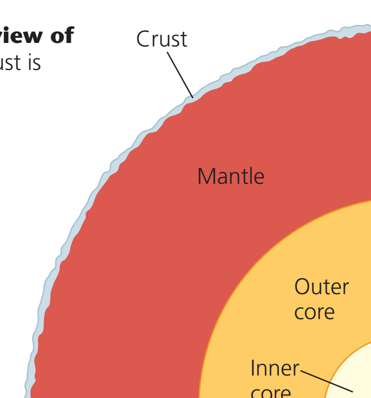
The rise and fall of these and other major groups of organisms have shaped the history of life. Narrowing our focus, we can also see that the rise or fall of any particular group is related to the speciation and extinction rates of its member species. Just as a population increases in size when there are more births than deaths, the rise of a group of organisms occurs when it produces more new species than are lost to extinction. The reverse occurs when a group is in decline. As we'll see, 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.

Plate Tectonics

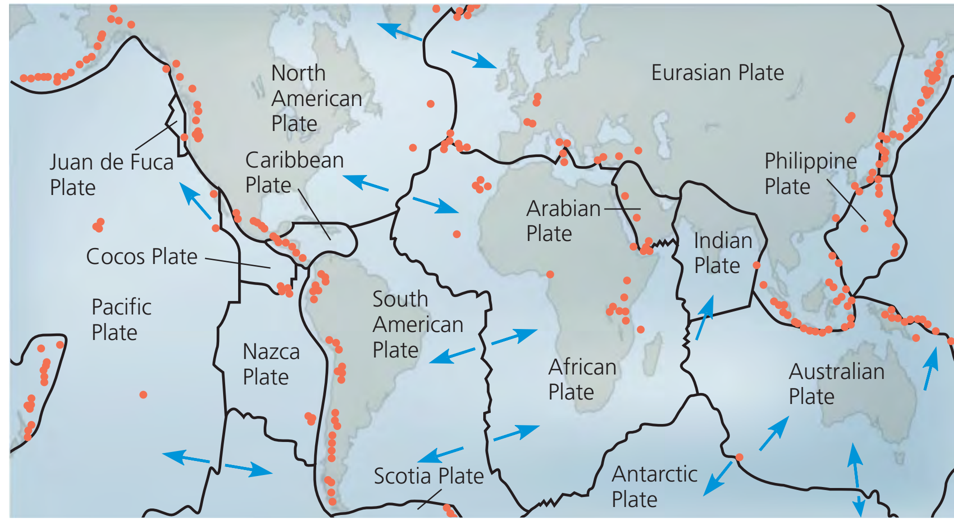
If photographs of Earth were taken from space every 10,000 years and spliced together to make a movie, it would show something many of us find hard to imagine: The seemingly "rock solid" continents we live on move over time. Since the origin of multicellular eukaryotes roughly 1.5 billion years ago, 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 they 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 25.12**). 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.

▶ Figure 25.12 Cutaway view of Earth. The thickness of the crust is exaggerated here.



Earth's major tectonic plates are shown in **Figure 25.13**. 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. 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 are colliding. Typically, oceanic plates (those found on the bottom of the ocean) are more dense than terrestrial plates. As a result, when an oceanic plate collides with a terrestrial plate, the oceanic plate usually sinks below the terrestrial plate. When two oceanic plates or two terrestrial plates collide with each other, violent upheavals occur and mountains form 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.



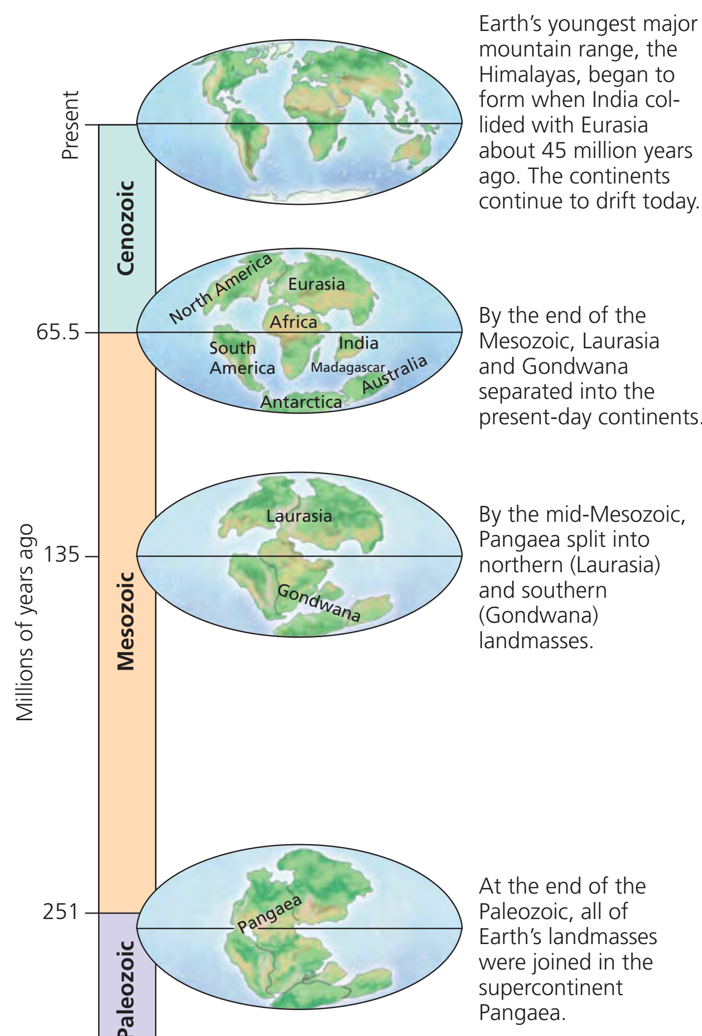
▲ **Figure 25.13 Earth's major tectonic plates.** The arrows indicate direction of movement. The reddish orange dots represent zones of violent tectonic activity.

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 its great impact on life is that continental drift alters the habitats in which organisms live. Consider the changes shown in **Figure 25.14**. About 250 million years ago, plate movements brought all the previously separated landmasses together into a supercontinent named **Pangaea**. Ocean basins became deeper, which lowered sea level and drained shallow coastal seas. At that time, as now, most marine species inhabited shallow waters, and the formation of Pangaea destroyed a considerable amount of that habitat. The interior of the vast continent was cold and dry, probably an even more severe environment than that of central Asia today. Overall, the formation of Pangaea had a tremendous impact on the physical environment and climate, which drove some species to extinction and provided new opportunities for groups of organisms that survived the crisis.

Another aspect of continental drift that affects organisms is 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,



▲ **Figure 25.14 The history of continental drift during the Phanerozoic eon.**

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 geographically 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 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

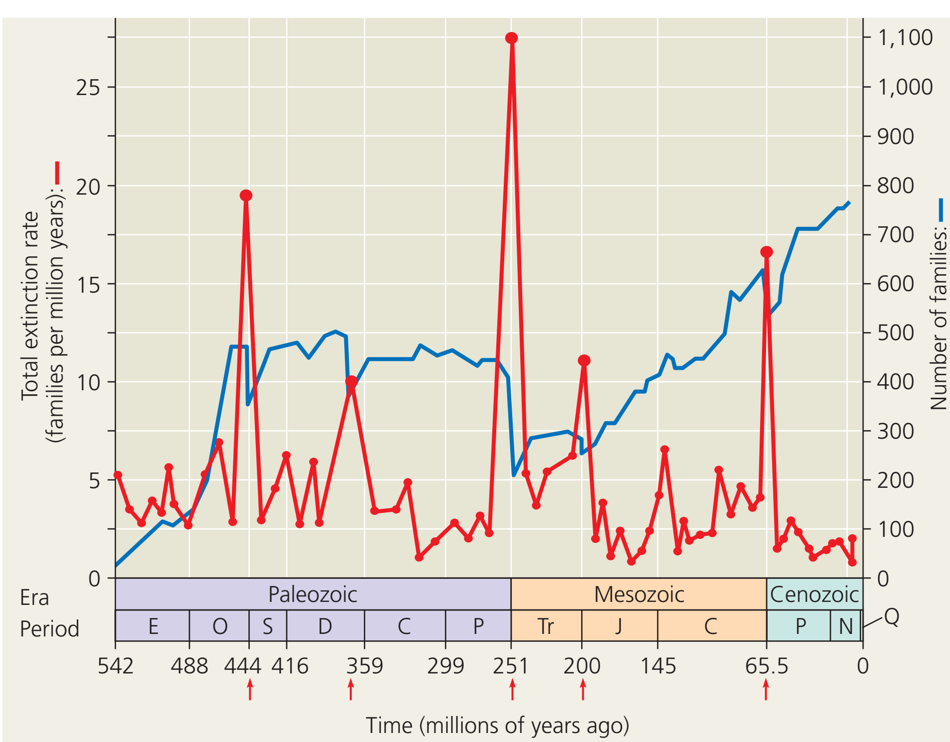
The fossil record shows that the overwhelming majority of species that ever lived are now extinct. A species may become extinct for many reasons. Its habitat may have been destroyed, or its environment may have changed in a manner unfavorable to the species. For example, if ocean temperatures fall by 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 on a regular basis, at certain times disruptive global environmental changes have caused the rate of extinction to increase dramatically. When this occurs, a **mass extinction** results, in which large numbers of species become extinct throughout Earth.

The "Big Five" Mass Extinction Events

Five mass extinctions are documented in the fossil record over the past 500 million years **(Figure 25.15)**. 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 Earth's 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.



◀ **Figure 25.15 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).

? *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.*

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 at the time of enormous volcanic eruptions in what is now Siberia. This period was the most extreme episode of volcanism to have occurred during the past half billion years. Geologic data indicate that an area of 1.6 million km^2 (roughly half the size of western Europe) was covered with a layer of lava hundreds to thousands of meters thick. Besides spewing enormous amounts of lava and ash, the eruptions may have produced enough carbon dioxide to warm the global climate by an estimated 6°C. Reduced temperature differences between the equator and the poles could have slowed the mixing of ocean water, which in turn could have led to a widespread drop in oxygen concentrations. The resulting low-oxygen condition, called *ocean anoxia*, would have suffocated oxygen-breathers and promoted the growth of anaerobic bacteria that emit a poisonous metabolic by-product, hydrogen sulfide (H_2S) gas. As this gas bubbled into the atmosphere, it could have caused further extinctions by directly killing land plants and animals and by initiating chemical reactions that destroy the ozone layer, a "shield" that ordinarily protects organisms from life-threatening levels of UV radiation.

The Cretaceous mass extinction occurred about 65.5 million years ago and marks the boundary between the Mesozoic and Cenozoic eras. 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 separates sediments from the Mesozoic and Cenozoic eras. 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. Walter Alvarez and the late Luis Alvarez, of the University of California, Berkeley, and their colleagues 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.

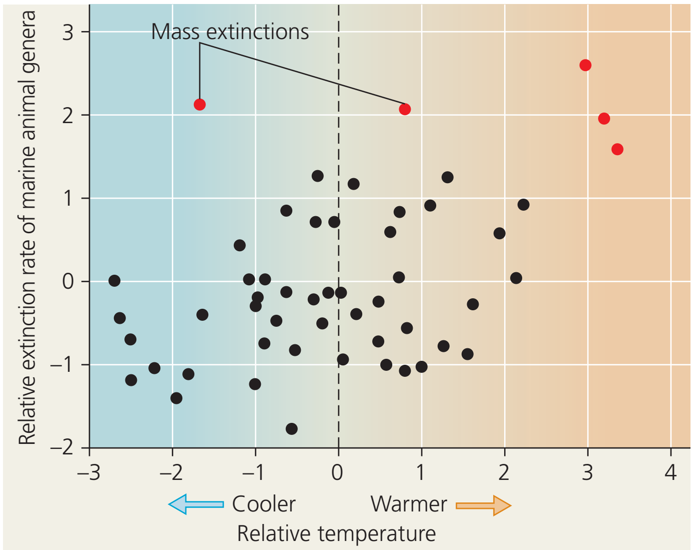
Is there evidence of such an asteroid or comet? Research has focused on the Chicxulub crater, a 65-million-year-old scar beneath sediments off the Yucatán coast of Mexico (**Figure 25.16**). The crater is the right size to have been caused by an object with a diameter of 10 km. Critical evaluation of this and other hypotheses for mass extinctions continues.

Is a Sixth Mass Extinction Under Way?

As we will explore 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

▲ **Figure 25.16 Trauma for Earth and its Cretaceous life.** Beneath the Caribbean Sea, the 65-million-year-old Chicxulub impact 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 artist's interpretation 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.



▲ **Figure 25.17 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.

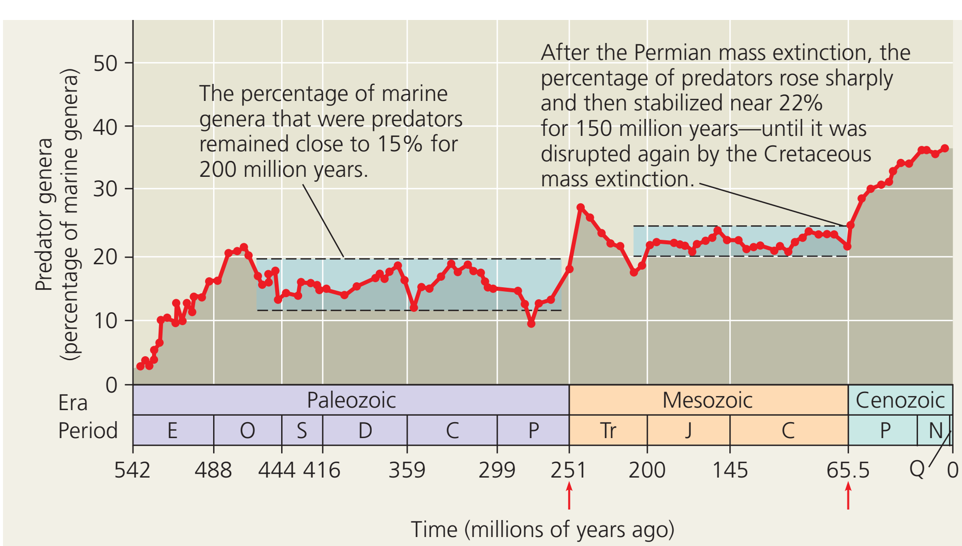
species. As a result, destroying tropical forest may drive species to extinction before we even learn of their existence. Such uncertainties make it hard to assess the full extent of the current extinction crisis. Even so, it is clear that losses to date have not reached those of the "big five" mass 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, and studies on polar bears, pine trees, and other species suggest that climate change may hasten some of these declines. Indeed, the fossil record indicates that over the last 500 million years, extinction rates have tended to increase when global temperatures were high **(Figure 25.17)**. Overall, present-day and fossil evidence both suggest 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.

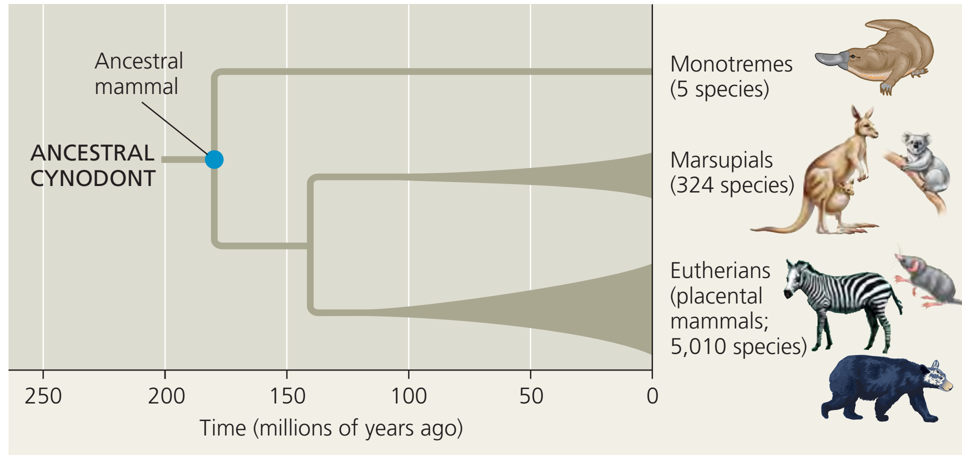
The fossil record shows that it typically takes 5–10 million years for the diversity of life to recover to previous levels after a mass extinction. In some cases, it has taken much longer than that: It took about 100 million years for the number of marine families to recover after the Permian mass extinction (see Figure 25.15). 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 found in them. For example, after the Permian and Cretaceous mass extinctions, the percentage of marine organisms that were predators increased substantially **(Figure 25.18)**. A rise in the number of predator species can increase both the pressures faced by prey and the competition among predators for food. In addition, mass extinctions can curtail lineages with highly 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



◀ **Figure 25.18 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.

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.



▲ **Figure 25.19 Adaptive radiation of mammals.**

Adaptive Radiations

The fossil record indicates that the diversity of life has increased over the past 250 million years (see blue line in Figure 25.15). 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 25.19)**. 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 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.

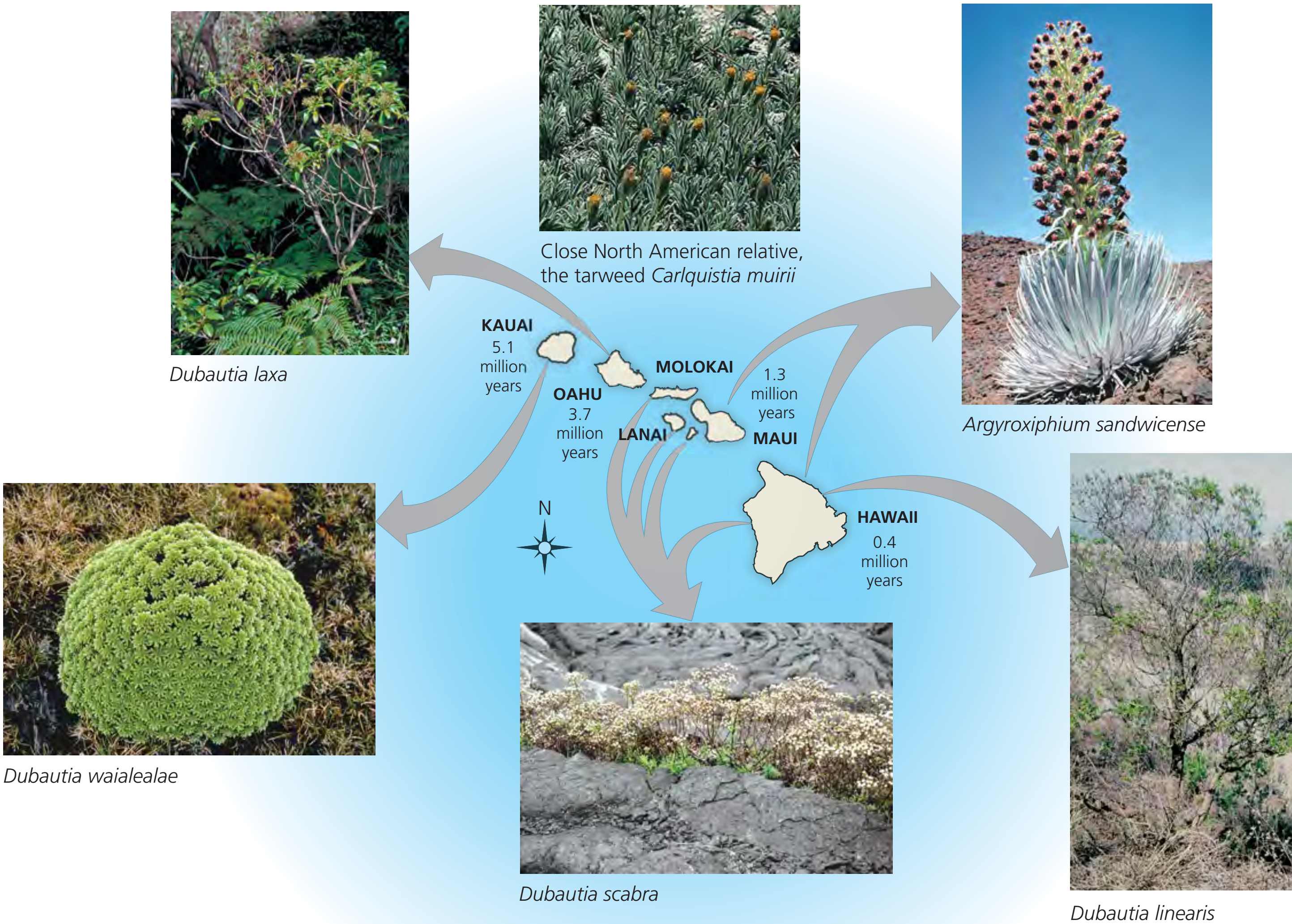
Regional Adaptive Radiations

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 25.20)**. Located about 3,500 km from the 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. 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 continental drift for life on Earth.
2. What factors promote adaptive radiations?
3. **WHAT IF?** If a mass extinction were caused by a sudden catastrophic event, would dates of the last observation in the fossil record of species lost in the extinction differ for rare versus common species? Explain.

For suggested answers, see Appendix A.



▲ **Figure 25.20 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.

CONCEPT 25.5

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

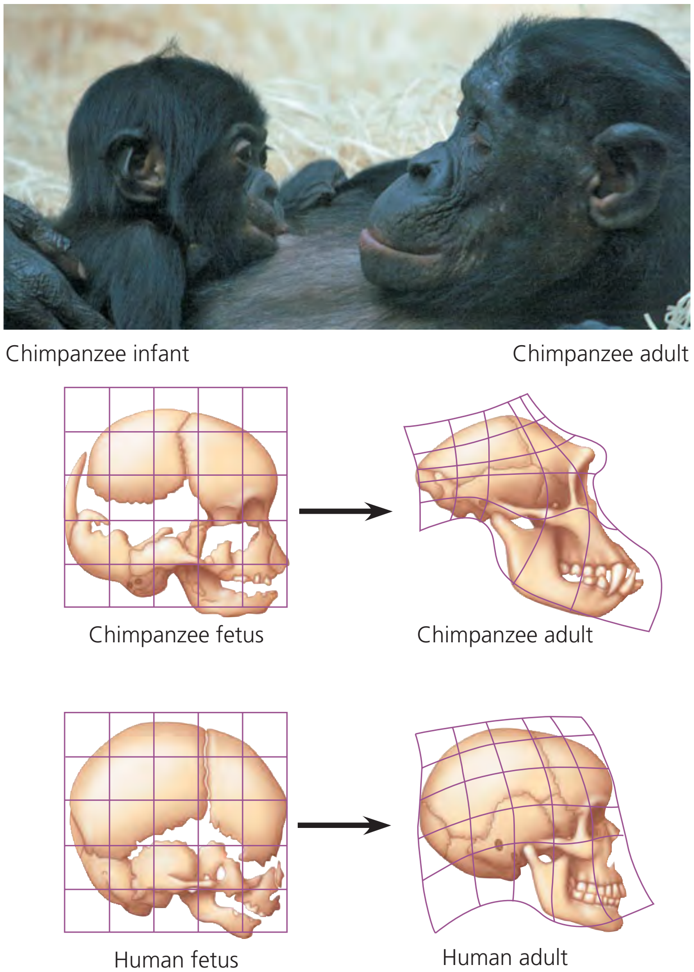
The fossil record tells us what the great changes in the history of life have been and when they occurred. Moreover, an understanding of plate tectonics, mass extinction, and adaptive radiation provides a picture of how those changes came about. But we can also seek to understand the intrinsic biological 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 divergences can produce major morphological differences between species. Genes that control development influence the rate, timing, and spatial pattern of change in an organism's form as it develops from a zygote into an adult.

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



▲ **Figure 25.21 Relative skull growth rates.** In the human evolutionary lineage, mutations that slowed the growth of the jaw relative to other parts of the skull produced an adult whose head resembles that of a chimpanzee infant.

during development. Changes to these rates can alter the adult form substantially, as seen in the contrasting shapes of human and chimpanzee skulls **(Figure 25.21)**. 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 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 25.22)**. 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.

▲ **Figure 25.22 Paedomorphosis.** The adults of some species retain features that were juvenile in ancestors. This salamander is an axolotl, an aquatic species that grows to full size, becomes sexually mature, and reproduces while retaining certain larval (tadpole) characteristics, including gills.

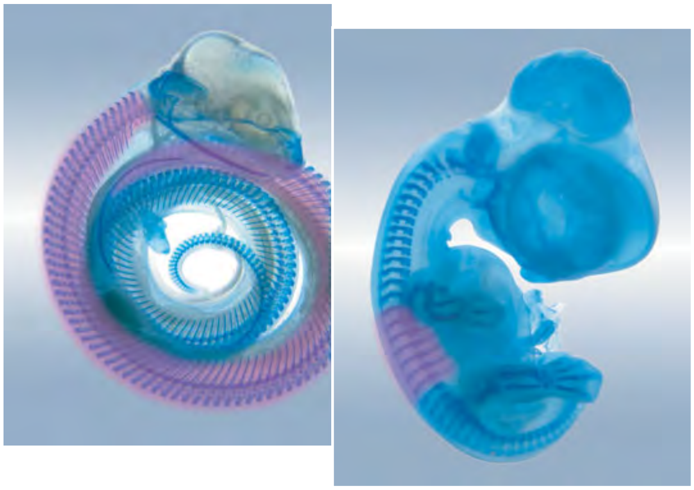
Changes in Spatial Pattern

Substantial evolutionary changes can also result from alterations in genes that control the placement and 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 a pair of legs will develop on a bird or how a plant's flower parts are arranged.

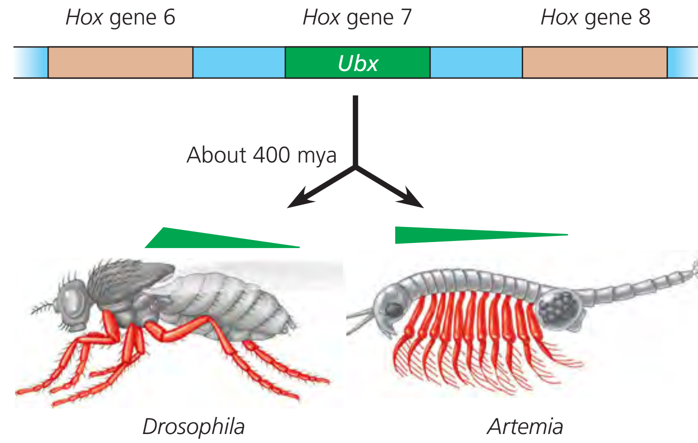
The products of one class of homeotic genes, the *Hox* genes, provide positional information in an animal embryo. This information prompts cells to develop into structures appropriate for a particular location. Changes in *Hox* genes or in how they are expressed can have a profound impact on morphology. 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. Large effects are also seen in snakes, where changes in how two *Hox* genes (*HoxC6* and *HoxC8*) are expressed suppresses limb formation **(Figure 25.23)**. 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 565-million-year-old fossils of Ediacaran animals in Figure 25.4 suggest that a set of genes sufficient to produce complex animals existed at least 30 million years *before* the Cambrian explosion. If such genes have existed for so long,



▲ **Figure 25.23** ***Hox* gene expression and limb development.** Regions of *HoxC6* gene expression (purple) correlate with limbless regions in the torsos of a snake embryo (left) and a chicken embryo (right).



▲ **Figure 25.24** **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.

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 a wide range of new metabolic and structural functions. Thus, adaptive evolution of both new and existing genes may have played a key role in shaping the great diversity of life.

Examples in the previous section suggest that developmental genes may play a critical role. Next we'll examine how new morphological forms 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 recent 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 25.24)**. 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%.

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

Changes in the nucleotide sequence or regulation of developmental genes can result in morphological changes that harm the organism (see Chapter 18). Moreover, a change in the nucleotide sequence of a gene may affect its function wherever the gene is expressed. In contrast, changes in the regulation of gene expression can be limited to a single 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 line of 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.

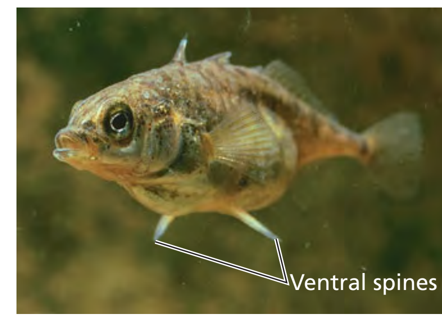
This idea is supported by studies in a variety of species, including threespine stickleback fish. These fish live in the open ocean and in shallow, coastal waters. In western Canada, they also live in lakes formed when the coastline receded during the past 12,000 years. Marine stickleback fish have a pair of spines on their ventral (lower) surface, which deter some predators. These spines 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 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 25.25**)? The researchers' results indicate that the regulation of gene expression has changed, not the DNA sequence of the gene. Furthermore, lake stickleback

▼ Figure 25.25 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*)

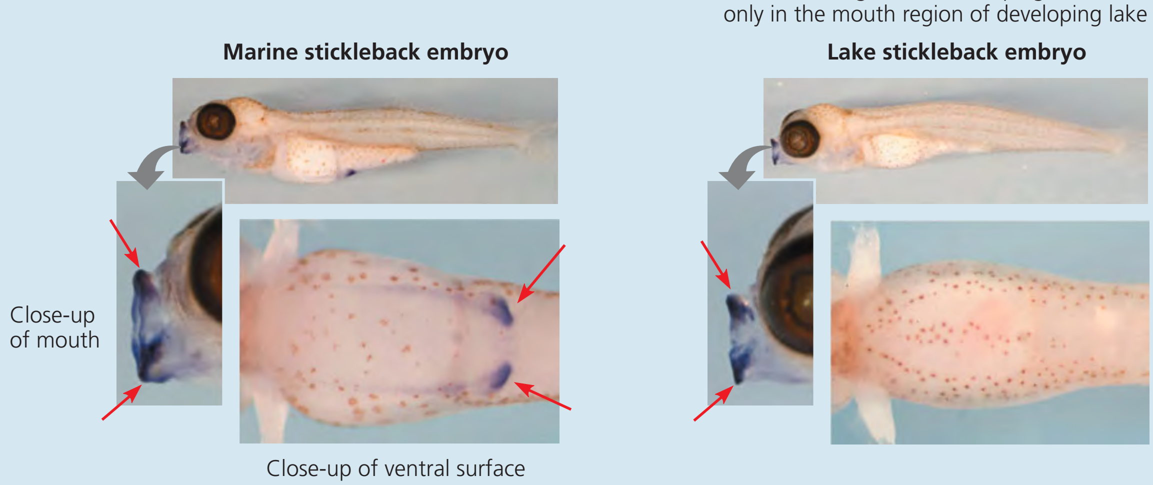
Hypothesis A: A change in the DNA sequence of *Pitx1* had caused spine reduction in lake populations. To test this idea, the team used DNA sequencing to compare the coding sequence of the *Pitx1* gene between marine and lake stickleback populations.

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 *Pitx1* gene in marine and lake stickleback fish? **Result: No** → The 283 amino acids of the *Pitx1* protein are identical in marine and lake stickleback populations.

Test of Hypothesis B: Are there any differences in the regulation of expression of *Pitx1*? **Result: Yes** → Red arrows (→) indicate regions of *Pitx1* gene expression in the photographs below. *Pitx1* 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.



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.

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.

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 (pp. 364–366) to review noncoding DNA and regulation of gene expression.

For suggested answers, see Appendix A.

CONCEPT 25.6

Evolution is not goal oriented

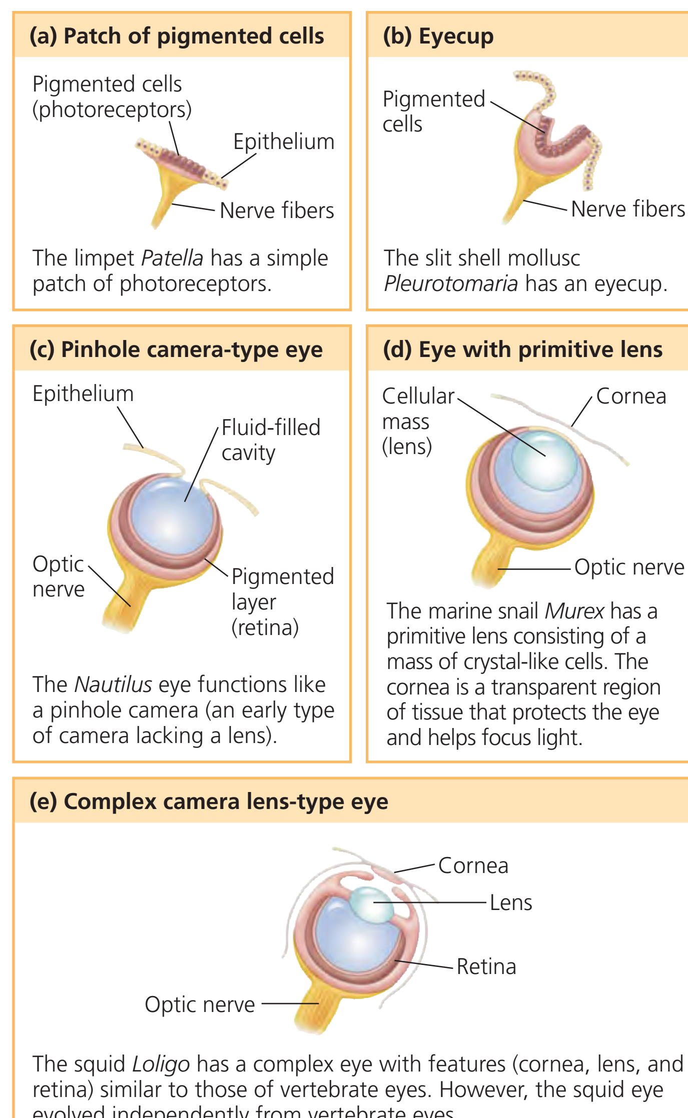
What does our study of macroevolution tell us about how evolution works? One lesson is that throughout the history of life, the origin of new species has been affected by both the bottom-up factors described in Chapter 24 (such as natural selection operating in populations) and the top-down factors described here (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 slight modification of existing forms. Even large changes, like the ones that produced the first mammals or the six-legged body plan of insects, can result from 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 **(Figure 25.26)**. 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. Because limpets have had a long evolutionary history, we can conclude that their "simple" eyes are quite adequate to support their survival and reproduction.

▼ Figure 25.26 A range of eye complexity among molluscs.



In the animal kingdom, complex eyes have evolved independently from such basic structures many times. Some molluscs, such as squids and octopuses, have eyes as complex as those of humans and other vertebrates (see Figure 25.26). 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 series of incremental modifications that benefited the eyes' owners at every stage. Evidence of their independent evolution may also 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 25.6) 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 25.27)**. 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 25.27). 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.

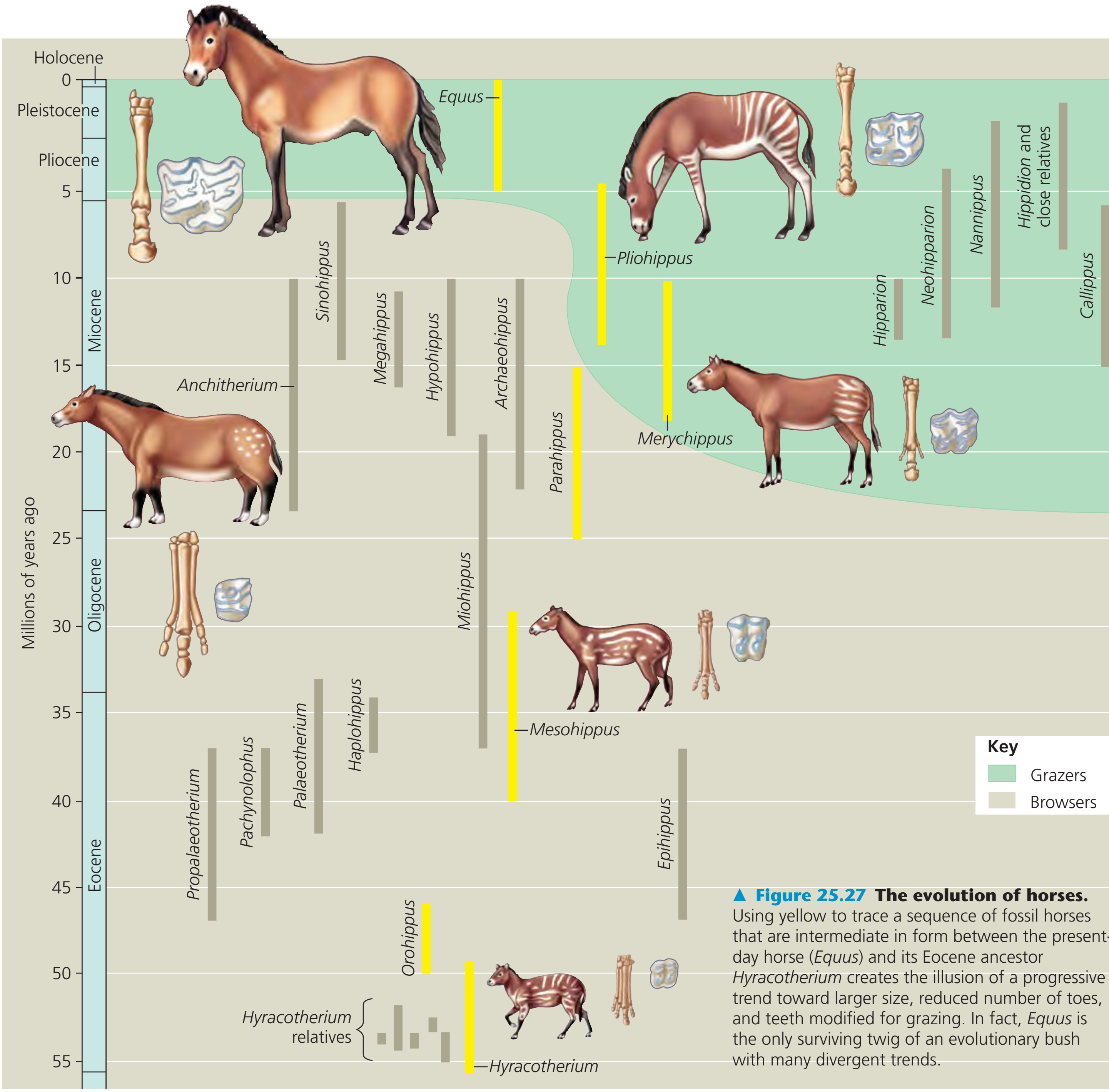
Branching evolution *can* result in a real evolutionary trend even if some species counter the trend. One model of long-term trends proposed by Steven Stanley, of Johns Hopkins University, views species as analogous to individuals: Speciation is their birth, extinction is their death, and new species that diverge from them are their offspring. In this model, Stanley suggests that 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, 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.



▲ **Figure 25.27 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.

25 CHAPTER REVIEW

SUMMARY OF KEY CONCEPTS

CONCEPT 25.1

Conditions on early Earth made the origin of life possible (pp. 507–510)

- Earth formed 4.6 billion years ago. 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 been short pieces of RNA capable of guiding polypeptide synthesis and self-replication. 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

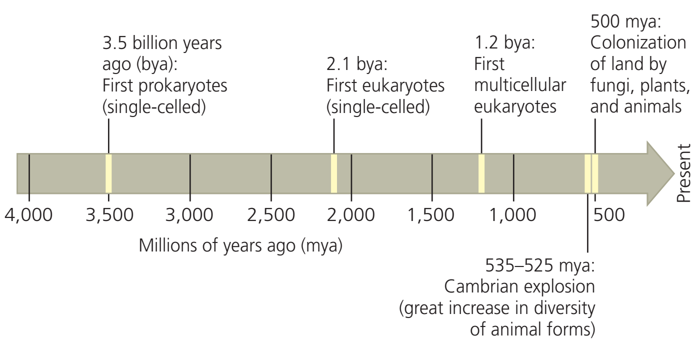
The fossil record documents the history of life (pp. 510–514)

- 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 single-celled and multicelled organisms and the colonization of land (pp. 514–519)



? *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. 519–524)

- 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. 525–529)

- 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. 529–531)

- 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. all date from 2.7 billion years ago.
 b. formed around deep-sea vents.
 c. resemble structures formed by bacterial communities that are found today in some warm, shallow, salty bays.
 d. provide evidence that plants moved onto land in the company of fungi around 500 million years ago.
 e. contain the first undisputed fossils of eukaryotes and date from 2.1 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
 e. the evolution of multicellular eukaryotic colonies from communities of prokaryotes

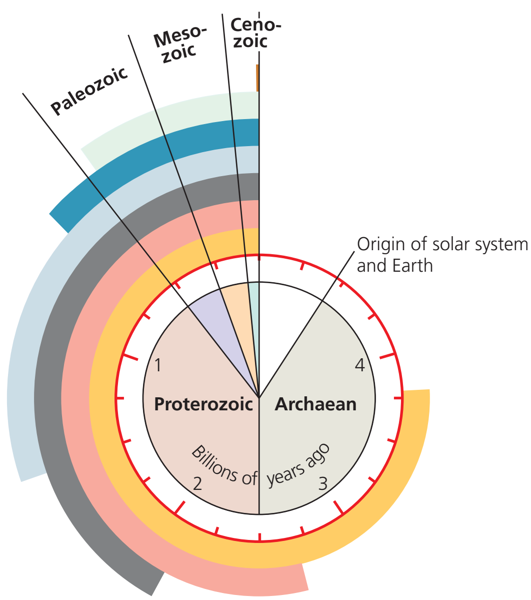
3. Which factor most likely caused animals and plants in India to differ greatly from species in nearby southeast Asia?
 a. The species became separated by convergent evolution.
 b. The climates of the two regions are similar.
 c. India is in the process of separating from the rest of Asia.
 d. Life in India was wiped out by ancient volcanic eruptions.
 e. India was a separate continent until 45 million years ago.

4. Adaptive radiations can be a direct consequence of four of the following five 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
 e. an adaptive radiation in a group of organisms (such as plants) that another group uses as food

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. abiotic synthesis of polypeptides

c. formation of molecular aggregates with selectively permeable membranes
d. formation of protocells that use DNA to direct the polymerization of amino acids
e. abiotic synthesis of organic molecules

6. **DRAW IT** Use the unlabeled clock diagram below to test your memory of the sequence of key events in the history of life described in this chapter by labeling the colored bars. As a visual aid to help you study, add labels that represent other significant events, including the Cambrian explosion, origin of mammals, and Permian and Cretaceous mass extinctions.



LEVEL 2: APPLICATION/ANALYSIS

7. 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.
e. gene duplication.

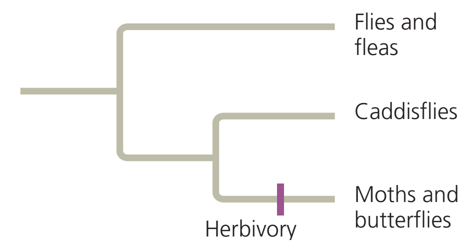
8. A swim bladder is a gas-filled sac that helps fish maintain buoyancy. The evolution of the swim bladder from lungs of an ancestral fish is an example of
a. an evolutionary trend.
b. exaptation.
c. changes in *Hox* gene expression.
d. paedomorphosis.
e. adaptive radiation.

LEVEL 3: SYNTHESIS/EVALUATION

9. **EVOLUTION CONNECTION**
Describe how gene flow, genetic drift, and natural selection all can influence macroevolution.

10. **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 phylogenetic tree below, 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?



11. **SCIENCE, TECHNOLOGY, AND SOCIETY**
Experts estimate that human activities cause the extinction of hundreds of species every year. In contrast, the natural rate of extinction is thought to average only a few species per year. If human actions continue to alter the global environment, especially by destroying tropical rain forests and changing Earth's climate, the likely result will be a wave of extinctions that could rival those at the end of the Cretaceous period. Considering that life has endured five mass extinctions, should we be concerned that we may cause a sixth mass extinction? How would such an extinction differ from previous extinctions? What might be some of the consequences?

12. **WRITE ABOUT A THEME**
Structure and Function 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.

For selected answers, see Appendix A.

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