

# 19

## Descent with Modification

▼ **Figure 19.1** How is this caterpillar protecting itself from predators?



### KEY CONCEPTS

- 19.1** The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species
- 19.2** Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life
- 19.3** Evolution is supported by an overwhelming amount of scientific evidence

### OVERVIEW

## Endless Forms Most Beautiful

A hungry bird would have to look very closely to spot this caterpillar of the moth *Synchlora aerata*, which blends in well with the flowers on which it feeds (**Figure 19.1**). The disguise is enhanced by the caterpillar's flair for "decorating"—it glues pieces of flower petals to its body, transforming itself into its own background.

This striking caterpillar is a member of a diverse group, the more than 120,000 species of lepidopteran insects (moths and butterflies). All lepidopteran species go through a juvenile stage characterized by a well-developed head with chewing mouthparts: the ravenous, efficient feeding machines we call caterpillars. As adults, all lepidopterans share other features, such as three pairs of legs and two pairs of wings covered with small scales. But the many lepidopteran species also differ from one another, in both their caterpillar and adult forms. How did there come to be so many different moths and butterflies, and what causes their similarities and differences?

The self-decorating caterpillar and its many close relatives illustrate three key observations about life:

- the striking ways in which organisms are suited for life in their environments\*
- the many shared characteristics (unity) of life
- the rich diversity of life

A century and a half ago, Charles Darwin was inspired to develop a scientific explanation for these three broad observations. When he published his hypothesis in *The Origin of Species*, Darwin ushered in a scientific revolution—the era of evolutionary biology.

For now, we will define **evolution** as *descent with modification*, a phrase Darwin used in proposing that Earth's many species are descendants of ancestral species that were different from the present-day species. Evolution can also be defined more narrowly as a change in the genetic composition of a population from generation to generation (as discussed further in Chapter 21).

Whether it is defined broadly or narrowly, we can view evolution in two related but different ways: as a pattern and as a process. The *pattern* of evolutionary change is revealed by data from a range of scientific disciplines, including biology, geology, physics, and chemistry. These data are

\*Here and throughout this book, the term *environment* refers to other organisms as well as to the physical aspects of an organism's surroundings.

facts—they are observations about the natural world. The *process* of evolution consists of the mechanisms that produce the observed pattern of change. These mechanisms represent natural causes of the natural phenomena we observe. Indeed, the power of evolution as a unifying theory is its ability to explain and connect a vast array of observations about the living world.

As with all general theories in science, we continue to test our understanding of evolution by examining whether it can account for new observations and experimental results. In this and the following chapters, we'll examine how ongoing discoveries shape what we know about the pattern and process of evolution. To set the stage, we'll first retrace Darwin's quest to explain the adaptations, unity, and diversity of what he called life's "endless forms most beautiful."

## CONCEPT 19.1

### The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species

What impelled Darwin to challenge the prevailing views about Earth and its life? Darwin's revolutionary proposal developed over time, influenced by the work of others and by his travels (**Figure 19.2**). As we'll see, his ideas had deep historical roots.

#### *Scala Naturae* and Classification of Species

Long before Darwin was born, several Greek philosophers suggested that life might have changed gradually over time. But one philosopher who greatly influenced early Western science, Aristotle (384–322 BCE), viewed species as fixed (unchanging). Through his observations of nature, Aristotle recognized certain "affinities" among organisms. He concluded that life-forms could be arranged on a ladder, or scale, of increasing



▲ **Figure 19.2** Unusual species inspired novel ideas. Darwin observed this species of marine iguana and many other unique animals when he visited the Galápagos Islands in 1835.

complexity, later called the *scala naturae* ("scale of nature"). Each form of life, perfect and permanent, had its allotted rung on this ladder.

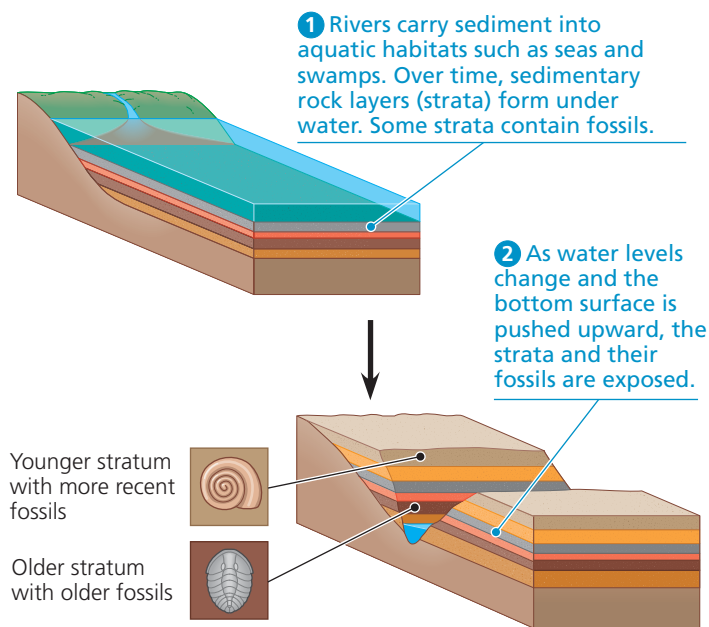
These ideas were generally consistent with the Old Testament account of creation, which holds that species were individually designed by God and therefore perfect. In the 1700s, many scientists interpreted the often remarkable match of organisms to their environment as evidence that the Creator had designed each species for a particular purpose.

One such scientist was Carolus Linnaeus (1707–1778), a Swedish physician and botanist who sought to classify life's diversity, in his words, "for the greater glory of God." Linnaeus developed the two-part, or *binomial*, format for naming species (such as *Homo sapiens* for humans) that is still used today. In contrast to the linear hierarchy of the *scala naturae*, Linnaeus adopted a nested classification system, grouping similar species into increasingly general categories. For example, similar species are grouped in the same genus, similar genera (plural of genus) are grouped in the same family, and so on.

Linnaeus did not ascribe the resemblances among species to evolutionary kinship, but rather to the pattern of their creation. A century later, however, Darwin argued that classification should be based on evolutionary relationships. He also noted that scientists using the Linnaean system often grouped organisms in ways that reflected those relationships.

#### Ideas About Change over Time

Among other sources of information, Darwin drew from the work of scientists studying **fossils**, the remains or traces of organisms from the past. As depicted in **Figure 19.3**, many fossils are found in sedimentary rocks formed from the



▲ **Figure 19.3** Formation of sedimentary strata with fossils.



sand and mud that settle to the bottom of seas, lakes, and swamps. New layers of sediment cover older ones and compress them into layers of rock called **strata** (singular, *stratum*). The fossils in a particular stratum provide a glimpse of some of the organisms that populated Earth at the time that layer formed. Later, erosion may carve through upper (younger) strata, revealing deeper (older) strata that had been buried.

**Paleontology**, the study of fossils, was developed in large part by French scientist Georges Cuvier (1769–1832). In examining strata near Paris, Cuvier noted that the older the stratum, the more dissimilar its fossils were to current life-forms. He also observed that from one layer to the next, some new species appeared while others disappeared. He inferred that extinctions must have been a common occurrence, but he staunchly opposed the idea of evolution. Cuvier speculated that each boundary between strata represented a sudden catastrophic event, such as a flood, that had destroyed many of the species living in that area. Such regions, he reasoned, were later repopulated by different species immigrating from other areas.

In contrast, other scientists suggested that profound change could take place through the cumulative effect of slow but continuous processes. In 1795, Scottish geologist James Hutton (1726–1797) proposed that Earth's geologic features could be explained by gradual mechanisms, such as valleys being formed by rivers wearing through rocks. The leading geologist of Darwin's time, Charles Lyell (1797–1875), incorporated Hutton's thinking into his proposal that the same geologic processes are operating today as in the past, and at the same rate.

Hutton and Lyell's ideas strongly influenced Darwin's thinking. Darwin agreed that if geologic change results from slow, continuous actions rather than from sudden events, then Earth must be much older than the widely accepted age of a few thousand years. It would, for example, take a very long time for a river to carve a canyon by erosion. He later reasoned that perhaps similarly slow and subtle processes could produce substantial biological change. Darwin was not the first to apply the idea of gradual change to biological evolution, however.

## Lamarck's Hypothesis of Evolution

Although some 18th-century naturalists suggested that life evolves as environments change, only one of Charles Darwin's predecessors proposed a mechanism for *how* life changes over time: French biologist Jean-Baptiste de Lamarck (1744–1829). Alas, Lamarck is primarily remembered today *not* for his visionary recognition that evolutionary change explains patterns in fossils and the match of organisms to their environments, but for the incorrect mechanism he proposed.

Lamarck published his hypothesis in 1809, the year Darwin was born. By comparing living species with fossil forms, Lamarck had found what appeared to be several lines



◀ **Figure 19.4**  
**Acquired traits cannot be inherited.**

This bonsai tree was “trained” to grow as a dwarf by pruning and shaping. However, seeds from this tree would produce offspring of normal size.

of descent, each a chronological series of older to younger fossils leading to a living species. He explained his findings using two principles that were widely accepted at the time. The first was *use and disuse*, the idea that parts of the body that are used extensively become larger and stronger, while those that are not used deteriorate. Among many examples, he cited a giraffe stretching its neck to reach leaves on high branches. The second principle, *inheritance of acquired characteristics*, stated that an organism could pass these modifications to its offspring. Lamarck reasoned that the long, muscular neck of the living giraffe had evolved over many generations as giraffes stretched their necks ever higher.

Lamarck also thought that evolution happens because organisms have an innate drive to become more complex. Darwin rejected this idea, but he, too, thought that variation was introduced into the evolutionary process in part through inheritance of acquired characteristics. Today, however, our understanding of genetics refutes this mechanism: Experiments show that traits acquired by use during an individual's life are not inherited in the way proposed by Lamarck (**Figure 19.4**).

Lamarck was vilified in his own time, especially by Cuvier, who denied that species ever evolve. In retrospect, however, Lamarck did recognize that the match of organisms to their environments can be explained by gradual evolutionary change, and he did propose a testable explanation for how this change occurs.

### CONCEPT CHECK 19.1

1. How did Hutton's and Lyell's ideas influence Darwin's thinking about evolution?
2. **MAKE CONNECTIONS** Scientific hypotheses must be testable and falsifiable (see Concept 1.3). Applying these criteria, are Cuvier's explanation of the fossil record and Lamarck's hypothesis of evolution scientific? Explain your answer in each case.

For suggested answers, see Appendix A.

## CONCEPT 19.2

# Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life

As the 19th century dawned, it was generally thought that species had remained unchanged since their creation. A few clouds of doubt about the permanence of species were beginning to gather, but no one could have forecast the thundering storm just beyond the horizon. How did Charles Darwin become the lightning rod for a revolutionary view of life?

## Darwin's Research

Charles Darwin (1809–1882) was born in Shrewsbury, England. He had a consuming interest in nature—reading nature books, fishing, hunting, and collecting insects. Darwin's father, a physician, could see no future for his son as a naturalist and sent him to medical school in Edinburgh. But Charles found medicine boring and surgery before the days of anesthesia horrifying. He enrolled at Cambridge University, intending to become a clergyman. (At that time many scholars of science belonged to the clergy.)

At Cambridge, Darwin became the protégé of John Henslow, a botany professor. Henslow recommended him to Captain Robert FitzRoy, who was preparing the survey ship HMS *Beagle* for a voyage around the world. FitzRoy, who was himself an accomplished scientist, accepted Darwin because he was a skilled naturalist and because they were of similar age and social class.

## The Voyage of the Beagle

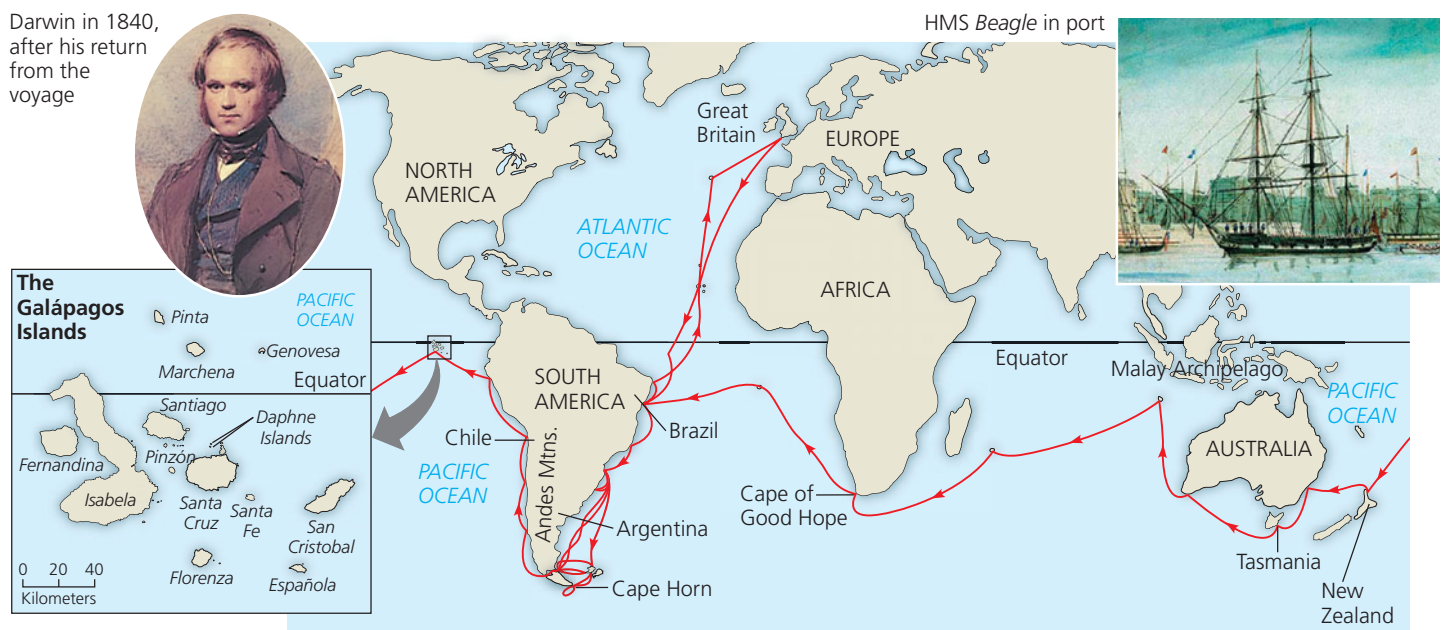
Darwin embarked on the *Beagle* in December 1831. The primary mission of the voyage was to chart poorly known stretches of the South American coastline. Darwin spent most of his time on shore, observing and collecting thousands of plants and animals. He noted the characteristics that made organisms well suited to such diverse environments as Brazil's humid jungles, Argentina's broad grasslands, and the Andes' towering peaks.

Darwin observed that the plants and animals in temperate regions of South America more closely resembled species living in the South American tropics than species living in temperate regions of Europe. Furthermore, the fossils he found, though clearly different from living species, distinctly resembled the living organisms of South America.

Darwin also read Lyell's *Principles of Geology* during the voyage. He experienced geologic change firsthand when a violent earthquake shook the coast of Chile, and he observed afterward that rocks along the coast had been thrust upward by several feet. Finding fossils of ocean organisms high in the Andes, Darwin inferred that the rocks containing the fossils must have been raised there by many similar earthquakes. These observations reinforced what he had learned from Lyell: Physical evidence did not support the traditional view that Earth was only a few thousand years old.

Darwin's interest in the geographic distribution of species was further stimulated by the *Beagle's* stop at the Galápagos, a group of volcanic islands located near the equator about 900 km west of South America (Figure 19.5). Darwin was fascinated by the unusual organisms there. The birds he collected included several kinds of mockingbirds. These mockingbirds, though similar to each other, seemed to be different species.

Darwin in 1840, after his return from the voyage



▲ Figure 19.5 The voyage of HMS *Beagle*.



Some were unique to individual islands, while others lived on two or more adjacent islands. Furthermore, although the animals on the Galápagos resembled species living on the South American mainland, most of the Galápagos species were not known from anywhere else in the world. Darwin hypothesized that the Galápagos had been colonized by organisms that had strayed from South America and then diversified, giving rise to new species on the various islands.

### Darwin's Focus on Adaptation

During the voyage of the *Beagle*, Darwin observed many examples of **adaptations**, inherited characteristics of organisms that enhance their survival and reproduction in specific environments. Later, as he reassessed his observations, he began to perceive adaptation to the environment and the origin of new species as closely related processes. Could a new species arise from an ancestral form by the gradual accumulation of adaptations to a different environment? From studies made years after Darwin's voyage, biologists have concluded that this is indeed what happened to the diverse group of Galápagos finches (see Figure 1.16). The finches' various beaks and behaviors are adapted to the specific foods available on their home islands (**Figure 19.6**). Darwin realized that explaining such adaptations was essential to understanding evolution. As we'll explore further, his explanation of how adaptations arise centered on **natural selection**, a process in which individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.

By the early 1840s, Darwin had worked out the major features of his hypothesis. He set these ideas on paper in 1844, when he wrote a long essay on descent with modification and its underlying mechanism, natural selection. Yet he was still reluctant to publish his ideas, apparently because he anticipated the uproar they would cause. During this time, Darwin continued to compile evidence in support of his hypothesis. By the mid-1850s, he had described his ideas to Lyell and a few others. Lyell, who was not yet convinced of evolution, nevertheless urged Darwin to publish on the subject before someone else came to the same conclusions and published first.

In June 1858, Lyell's prediction came true. Darwin received a manuscript from Alfred Russel Wallace (1823–1913), a British naturalist working in the South Pacific islands of the Malay Archipelago (**Figure 19.7**). Wallace had developed a hypothesis of natural selection nearly identical to Darwin's. He asked Darwin to evaluate his paper and forward it to Lyell if it merited publication. Darwin complied, writing to Lyell: "Your words have come



(a) **Cactus-eater.** The long, sharp beak of the cactus ground finch (*Geospiza scandens*) helps it tear and eat cactus flowers and pulp.



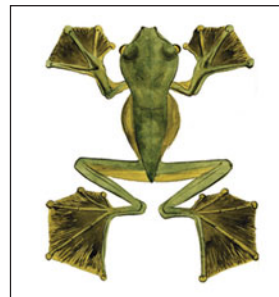
(c) **Insect-eater.** The green warbler finch (*Certhidea olivacea*) uses its narrow, pointed beak to grasp insects.



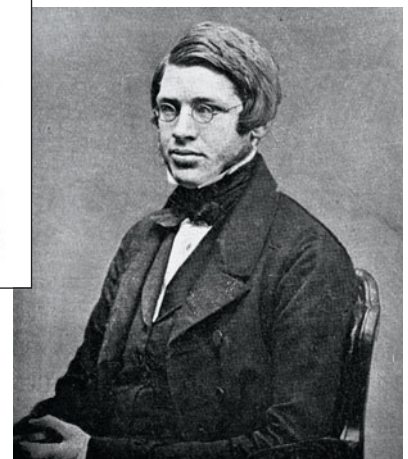
(b) **Seed-eater.** The large ground finch (*Geospiza magnirostris*) has a large beak adapted for cracking seeds on the ground.

**▲ Figure 19.6 Three examples of beak variation in Galápagos finches.** The Galápagos Islands are home to more than a dozen species of closely related finches, some found only on a single island. A striking difference among them is their beaks, which are adapted to specific diets.

**MAKE CONNECTIONS** Review Figure 1.16. To which of the other two species shown above is the cactus-eater more closely related (that is, with which does it share a more recent common ancestor)?



**► Figure 19.7 Alfred Russel Wallace.** The inset is a painting Wallace made of a flying tree frog from the Malay Archipelago.



true with a vengeance. . . . I never saw a more striking coincidence . . . so all my originality, whatever it may amount to, will be smashed." On July 1, 1858, Lyell and a colleague presented Wallace's paper, along with extracts from Darwin's unpublished 1844 essay, to the Linnean Society of London. Darwin quickly finished his book, titled *On the Origin of Species by Means of Natural Selection* (commonly referred to as *The Origin of Species*), and published it the next year. Although Wallace had submitted his ideas for publication first, he admired Darwin and thought that Darwin had developed the idea of natural selection so extensively that he should be known as its main architect.

Within a decade, Darwin's book and its proponents had convinced most scientists that life's diversity is the product of

evolution. Darwin succeeded where previous evolutionists had failed, mainly by presenting a plausible scientific mechanism with immaculate logic and an avalanche of evidence.

Ideas from *The Origin of Species*

In his book, Darwin amassed evidence that descent with modification by natural selection explains the three broad observations about nature listed in the Overview: the unity of life, the diversity of life, and the match between organisms and their environments.

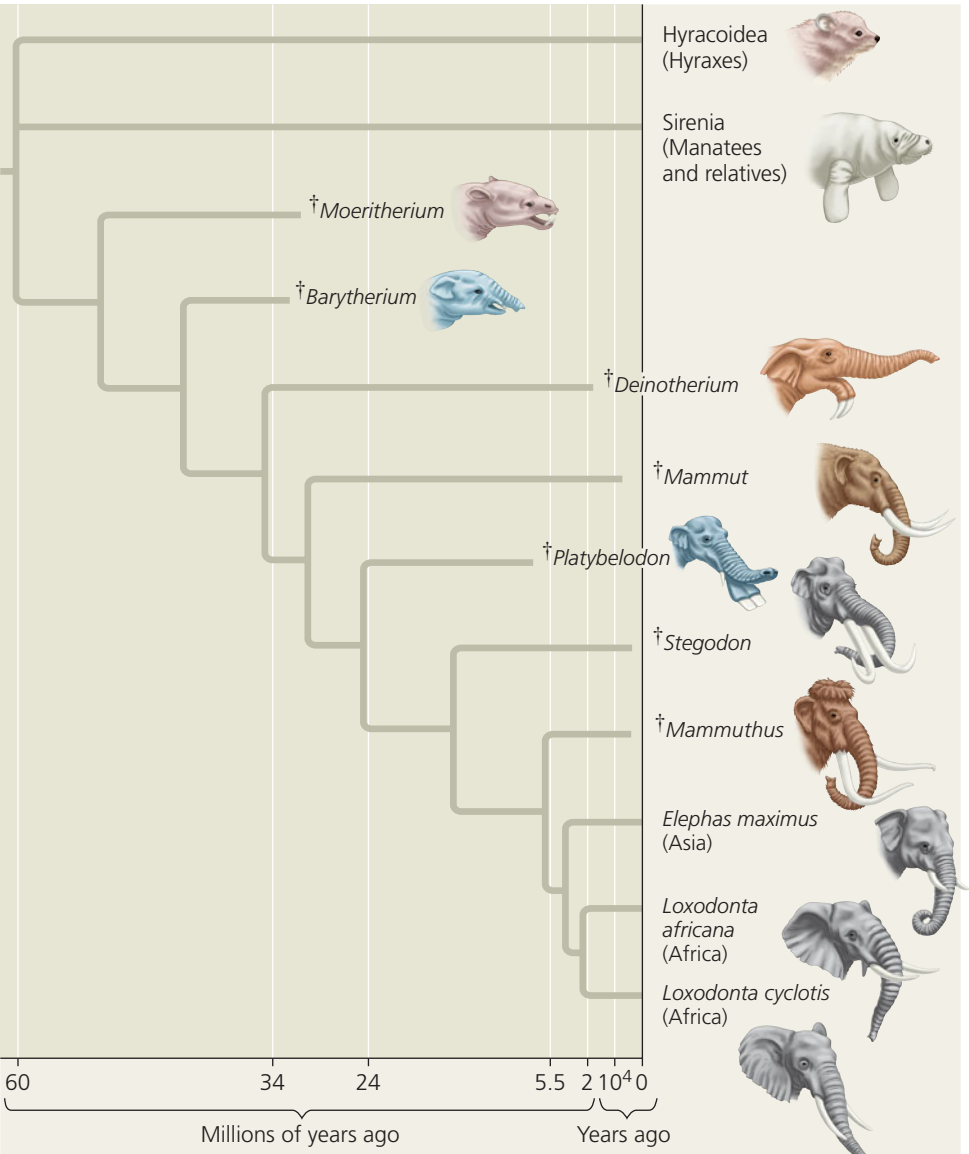
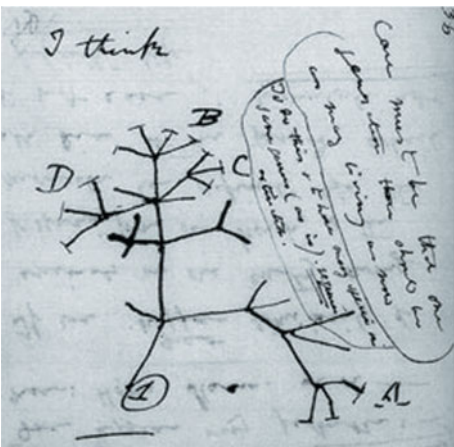
Descent with Modification

In the first edition of *The Origin of Species*, Darwin never used the word *evolution* (although the final word of the book is “evolved”). Rather, he discussed *descent with modification*, a phrase that summarized his view of life. Organisms share many characteristics, leading Darwin to perceive unity in life. He attributed the unity of life to the descent of all organisms from an ancestor that lived in the remote past. He also thought that as the descendants of that ancestral organism lived in various habitats over millions of years, they accumulated diverse modifications, or adaptations, that fit them to specific ways of life. Darwin reasoned that over a long time, descent with modification eventually led to the rich diversity of life today.

Darwin viewed the history of life as a tree, with multiple branchings from a common trunk out to the tips of the youngest twigs (Figure 19.8). In his diagram, the tips of the twigs that are labeled A, B, C, and D represent several groups of organisms living in the present day, while the unlabeled branches represent groups that are extinct. Each fork of the tree represents the most recent common ancestor of all the lines of evolution that subsequently branch from that point. Darwin reasoned that such a branching process, along with past extinction events, could explain the large morphological gaps (differences in form) that sometimes exist in between related groups of organisms.

As an example, consider the three living species of elephants: the Asian elephant (*Elephas maximus*) and two species of African elephants (*Loxodonta africana* and *L. cyclotis*). As shown in the tree diagram in Figure 19.9, these closely related species are very similar because they shared the same line of

► **Figure 19.8** “I think . . .” In this 1837 sketch, Darwin envisioned the branching pattern of evolution. Branches that end in twigs labeled A–D represent particular groups of living organisms; all other branches represent extinct groups.



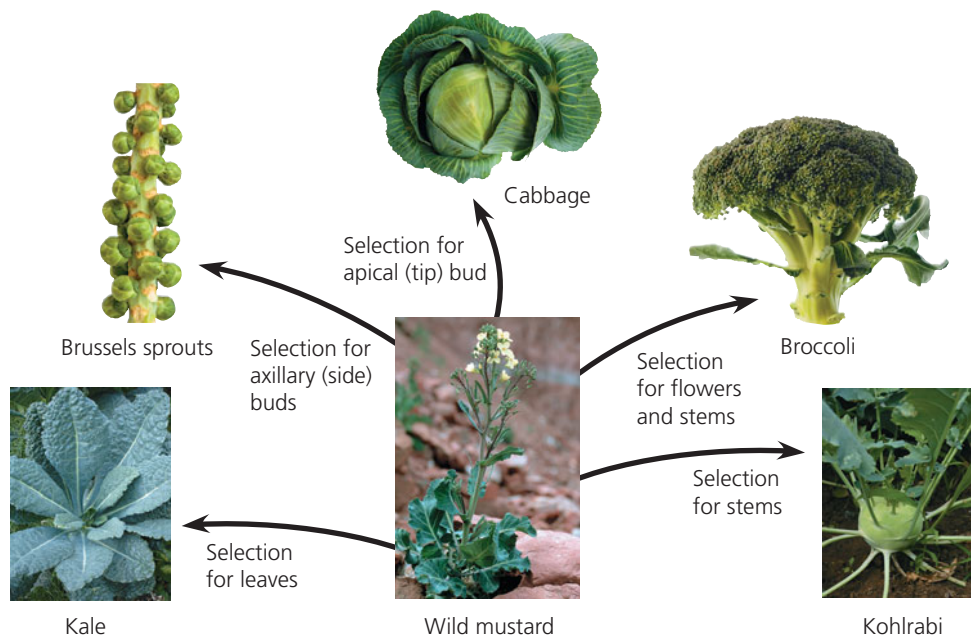
▲ **Figure 19.9 Descent with modification.** This evolutionary tree of elephants and their relatives is based mainly on fossils—their anatomy, order of appearance in strata, and geographic distribution. Note that most branches of descent ended in extinction (denoted by the dagger symbol †). (Time line not to scale.)

? Based on the tree shown here, approximately when did the most recent ancestor shared by Mammuthus (woolly mammoths), Asian elephants, and African elephants live?



descent until a relatively recent split from their common ancestor.

Note that seven lineages related to elephants have become extinct over the past 32 million years. As a result, there are no living species that fill the morphological gap between elephants and their nearest relatives today, the hyraxes and the manatees and their relatives. Such extinctions are not uncommon. In fact, many evolutionary branches, even some major ones, are dead ends: Scientists estimate that over 99% of all species that have ever lived are now extinct. As in Figure 19.9, fossils of extinct species can document the divergence of present-day groups by “filling in” gaps between them.



### Artificial Selection, Natural Selection, and Adaptation

Darwin proposed the mechanism of natural selection to explain the observable patterns of evolution. He crafted his argument carefully, hoping to persuade even the most skeptical readers. First he discussed familiar examples of selective breeding of domesticated plants and animals. Humans have modified other species over many generations by selecting and breeding individuals that possess desired traits, a process called **artificial selection** (Figure 19.10). As a result of artificial selection, crops, livestock animals, and pets often bear little resemblance to their wild ancestors.

Darwin then argued that a similar process occurs in nature. He based his argument on two observations, from which he drew two inferences.

▲ **Figure 19.10 Artificial selection.** These different vegetables have all been selected from one species of wild mustard. By selecting variations in different parts of the plant, breeders have obtained these divergent results.

**Observation #1:** Members of a population often vary in their inherited traits (Figure 19.11).

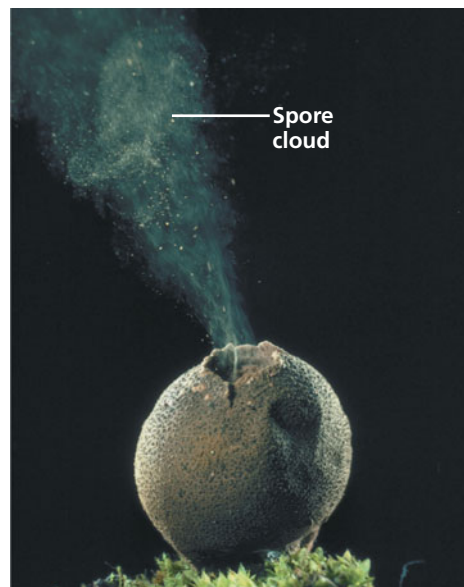
**Observation #2:** All species can produce more offspring than their environment can support (Figure 19.12), and many of these offspring fail to survive and reproduce.

**Inference #1:** Individuals whose inherited traits give them a higher probability of surviving and reproducing in a given environment tend to leave more offspring than other individuals.

**Inference #2:** This unequal ability of individuals to survive and reproduce will lead to the accumulation of favorable traits in the population over generations.



▲ **Figure 19.11 Variation in a population.** Individuals in this population of Asian ladybird beetles vary in color and spot pattern. Natural selection may act on these variations only if (1) they are heritable and (2) they affect the beetles’ ability to survive and reproduce.



◀ **Figure 19.12 Overproduction of offspring.** A single puffball fungus can produce billions of offspring. If all of these offspring and their descendants survived to maturity, they would carpet the surrounding land surface.



As inferences #1 and #2 suggest, Darwin saw an important connection between natural selection and the capacity of organisms to “overreproduce.” He began to make this connection after reading an essay by economist Thomas Malthus, who contended that much of human suffering—disease, famine, and war—resulted from the human population’s potential to increase faster than food supplies and other resources. Similarly, Darwin realized that the capacity to overreproduce was characteristic of all species. Of the many eggs laid, young born, and seeds spread, only a tiny fraction complete their development and leave offspring of their own. The rest are eaten, starved, diseased, unmated, or unable to tolerate physical conditions of the environment such as salinity or temperature.

An organism’s heritable traits can influence not only its own performance, but also how well its offspring cope with environmental challenges. For example, an organism might have a trait that gives its offspring an advantage in escaping predators, obtaining food, or tolerating physical conditions. When such advantages increase the number of offspring that survive and reproduce, the traits that are favored will likely appear at a greater frequency in the next generation. Thus, over time, natural selection resulting from factors such as predators, lack of food, or adverse physical conditions can lead to an increase in the proportion of favorable traits in a population.

How rapidly do such changes occur? Darwin reasoned that if artificial selection can bring about dramatic change in a relatively short period of time, then natural selection should be capable of substantial modification of species over many hundreds of generations. Even if the advantages of some heritable traits over others are slight, the advantageous variations will gradually accumulate in the population, and less favorable ones will diminish. Over time, this process will increase the frequency of individuals with favorable adaptations and refine the match between organisms and their environment.

### Natural Selection: A Summary

Let’s now recap the main ideas of natural selection:

- Natural selection is a process in which individuals that have certain heritable traits survive and reproduce at a higher rate than other individuals because of those traits.
- Over time, natural selection can increase the match between organisms and their environment (**Figure 19.13**).
- If an environment changes, or if individuals move to a new habitat, natural selection may result in adaptation to these new conditions, sometimes giving rise to new species.

One subtle but important point is that although natural selection occurs through interactions between individual organisms and their environment, *individuals do not evolve*. Rather, it is the population that evolves over time.

A second key point is that natural selection can amplify or diminish only those heritable traits that differ among the individuals in a population. Thus, even if a trait is heritable, if all

(a) A flower mantid in Malaysia



(b) A leaf mantid in Borneo



**▲ Figure 19.13 Camouflage as an example of evolutionary adaptation.** Related species of the insects called mantids have diverse shapes and colors that evolved in different environments.

**?** Explain how these mantids demonstrate the three key observations about life introduced in the Overview: the match between organisms and their environments, unity, and diversity.

the individuals in a population are genetically identical for that trait, evolution by natural selection cannot occur.

Third, remember that environmental factors vary from place to place and over time. A trait that is favorable in one place or time may be useless—or even detrimental—in other places or times. Natural selection is always operating, but which traits are favored depends on the context in which a species lives and mates.

Next, we’ll survey the wide range of observations that support a Darwinian view of evolution by natural selection.

### CONCEPT CHECK 19.2

1. How does the concept of descent with modification explain both the unity and diversity of life?
2. **WHAT IF?** Predict whether a fossil of an extinct mammal that lived high in the Andes would more closely resemble present-day mammals that live in South American jungles or present-day mammals that live high in African mountains? Explain.
3. **MAKE CONNECTIONS** Review the relationship between genotype and phenotype (see Figure 11.6). Suppose that in a particular pea population, flowers with the white phenotype are favored by natural selection. Predict what would happen over time to the frequency of the *p* allele in the population, and explain your reasoning.

For suggested answers, see Appendix A.

## Evolution is supported by an overwhelming amount of scientific evidence

In *The Origin of Species*, Darwin marshaled a broad range of evidence to support the concept of descent with modification. Still—as he readily acknowledged—there were instances in which key evidence was lacking. For example, Darwin referred to the origin of flowering plants as an “abominable mystery,” and he lamented the lack of fossils showing how earlier groups of organisms gave rise to new groups.

In the last 150 years, new discoveries have filled many of the gaps that Darwin identified. The origin of flowering plants, for example, is much better understood (see Chapter 26), and many fossils have been discovered that signify the origin of new groups of organisms (see Chapter 23). In this section, we’ll consider four types of data that document the pattern of evolution and illuminate the processes by which it occurs.

### Direct Observations of Evolutionary Change

Biologists have documented evolutionary change in thousands of scientific studies. We’ll examine many such studies throughout this unit, but let’s look at two examples here.

#### Natural Selection in Response to Introduced Plant Species

Animals that eat plants, called herbivores, often have adaptations that help them feed efficiently on their primary food sources. What happens when herbivores begin to feed on a plant species with different characteristics than their usual food source?

An opportunity to study this question in nature is provided by soapberry bugs, which use their “beak,” a hollow, needlelike mouthpart, to feed on seeds located within the fruits of various plants. In southern Florida, the soapberry bug (*Jadera haematoloma*) feeds on the seeds of a native plant, the balloon vine (*Cardiospermum corindum*). In central Florida, however, balloon vines have become rare. Instead, soapberry bugs in that region now feed on seeds of the goldenrain tree (*Koelreuteria elegans*), a species recently introduced from Asia.

Soapberry bugs feed most effectively when their beak length closely matches the depth at which the seeds are found within the fruit. Goldenrain tree fruit consists of three flat lobes, and its seeds are much closer to the fruit surface than are the seeds of the plump, round native balloon vine fruit. Researchers at the University of Utah predicted that in populations that feed on goldenrain tree, natural selection would result in beaks that are *shorter* than those in populations that feed on balloon vine (**Figure 19.14**). Indeed, beak lengths are shorter in the populations that feed on goldenrain tree.

#### ▼ Figure 19.14 Inquiry

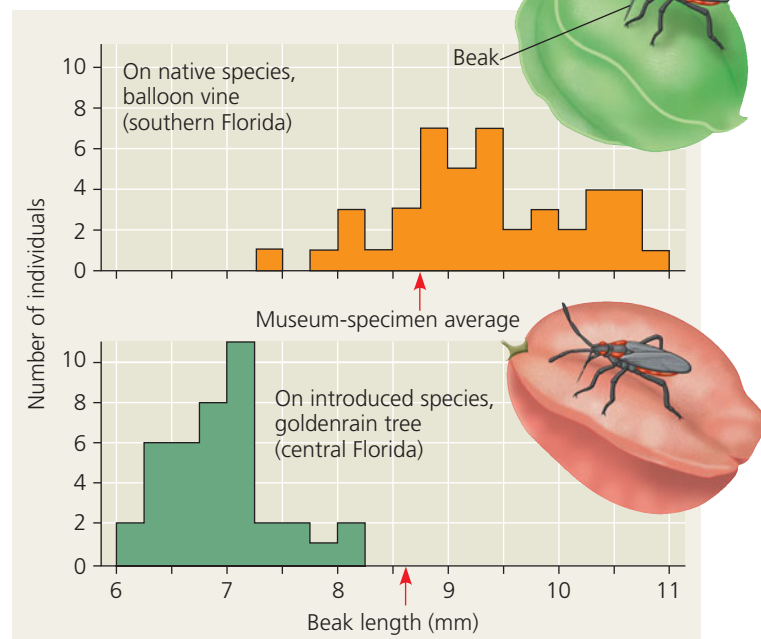
### Can a change in a population’s food source result in evolution by natural selection?

**Field Study** Soapberry bugs feed most effectively when the length of their “beak” closely matches the depth of the seeds within the fruit. Scott Carroll and his colleagues measured beak lengths in soapberry bug populations feeding on the native balloon vine. They also measured beak lengths in populations feeding on the introduced goldenrain tree. The researchers then compared the measurements with those of museum specimens collected in the two areas before the goldenrain tree was introduced.



Soapberry bug with beak inserted in balloon vine fruit

**Results** Beak lengths were shorter in populations feeding on the introduced species than in populations feeding on the native species, in which the seeds are buried more deeply. The average beak length in museum specimens from each population (indicated by red arrows) was similar to beak lengths in populations feeding on native species.



**Conclusion** Museum specimens and contemporary data suggest that a change in the size of the soapberry bug’s food source can result in evolution by natural selection for matching beak size.

**Source** S. P. Carroll and C. Boyd, Host race radiation in the soapberry bug: natural history with the history, *Evolution* 46:1052–1069 (1992).

**WHAT IF?** Additional results showed that when soapberry bug eggs from a population fed on balloon vine fruits were reared on goldenrain tree fruits (or vice versa), the beak lengths of the adult insects matched those in the population from which the eggs were obtained. Interpret these results.

Researchers have also studied beak length evolution in soapberry bug populations that feed on plants introduced to Louisiana, Oklahoma, and Australia. In each of these locations, the fruit of the introduced plants is larger than the fruit of the native plant. Thus, in populations feeding on introduced species in these regions, the researchers predicted that natural selection would result in the evolution of *longer* beaks. Again, data from field studies upheld this prediction.

The adaptation observed in these soapberry bug populations had important consequences: In Australia, for example, the increase in beak length nearly doubled the success with which soapberry bugs could eat the seeds of the introduced species. Furthermore, since historical data show that the goldenrain tree reached central Florida just 35 years before the scientific studies were initiated, the results demonstrate that natural selection can cause rapid evolution in a wild population.

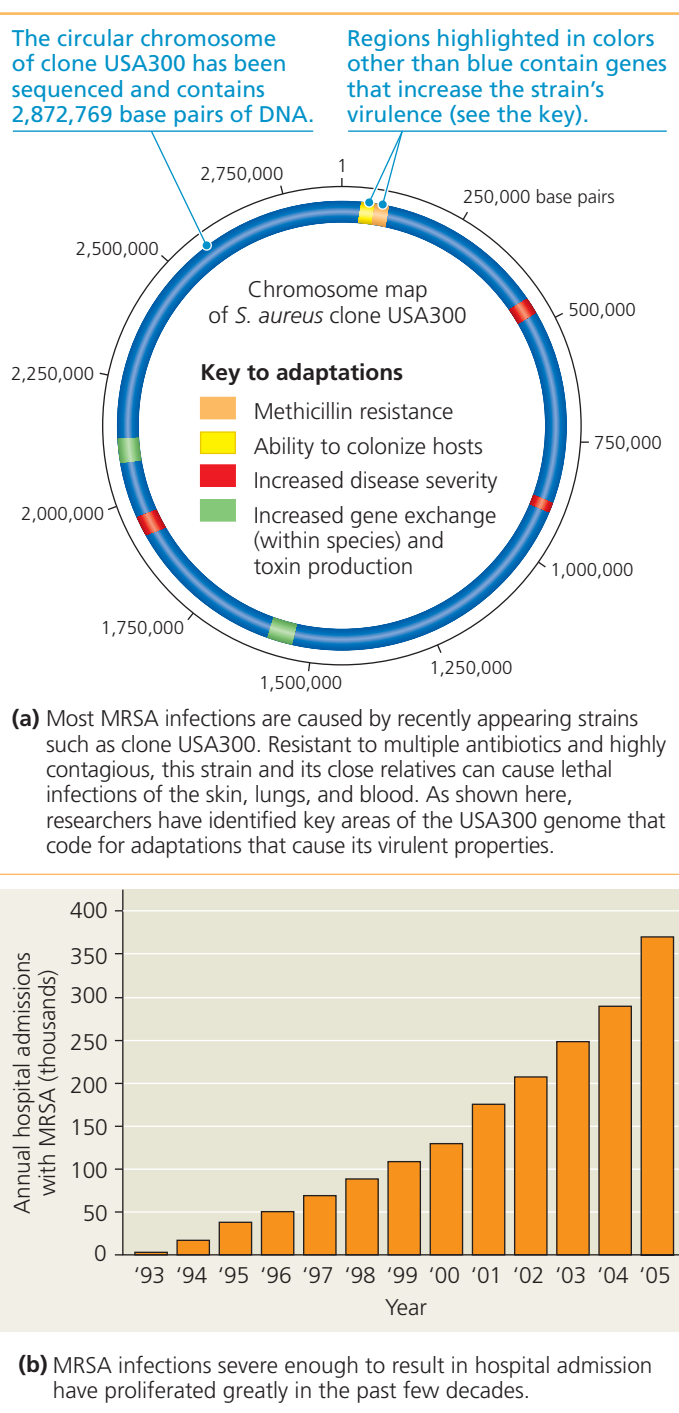
### The Evolution of Drug-Resistant Bacteria

An example of ongoing natural selection that dramatically affects humans is the evolution of drug-resistant pathogens (disease-causing organisms and viruses). This is a particular problem with bacteria and viruses because resistant strains of these pathogens can proliferate very quickly.

Consider the evolution of drug resistance in the bacterium *Staphylococcus aureus*. About one in three people harbor this species on their skin or in their nasal passages with no negative effects. However, certain genetic varieties (strains) of this species, known as methicillin-resistant *S. aureus* (MRSA), are formidable pathogens. The past decade has seen an alarming increase in virulent forms of MRSA such as clone USA300, a strain that can cause “flesh-eating disease” and potentially fatal infections (**Figure 19.15**). How did clone USA300 and other strains of MRSA become so dangerous?

The story begins in 1943, when penicillin became the first widely used antibiotic. Although penicillin and other antibiotics have since saved millions of lives, by 1945, over 20% of the *S. aureus* strains seen in hospitals were resistant to penicillin. These bacteria had an enzyme, penicillinase, that could destroy penicillin. Researchers developed antibiotics that were not destroyed by penicillinase, but some *S. aureus* populations developed resistance to each new drug within a few years.

Then, in 1959, doctors began using the powerful antibiotic methicillin. But within two years, methicillin-resistant strains of *S. aureus* appeared. How did these resistant strains emerge? Methicillin works by deactivating a protein that bacteria use to synthesize their cell walls. However, *S. aureus* populations exhibited variations in how strongly their members were affected by the drug. In particular, some individuals were able to synthesize their cell walls using a different protein that was not affected by methicillin. These individuals survived the methicillin treatments and reproduced at higher rates than did other individuals. Over time, these resistant individuals became increasingly common, leading to the spread of MRSA.



**▲ Figure 19.15 The rise of methicillin-resistant *Staphylococcus aureus* (MRSA).**

Initially, MRSA could be controlled by antibiotics that work differently from the way methicillin works. But this has become increasingly difficult because some MRSA strains are resistant to multiple antibiotics—probably because bacteria can exchange genes with members of their own and other species (see Figure 24.17). Thus, the present-day multidrug-resistant strains may have emerged over time as MRSA strains that were resistant to different antibiotics exchanged genes.

The *S. aureus* and soapberry bug examples highlight two key points about natural selection. First, natural selection is



a process of editing, not a creative mechanism. A drug does not *create* resistant pathogens; it *selects for* resistant individuals that are already present in the population. Second, natural selection depends on time and place. It favors those characteristics in a genetically variable population that provide advantage in the current, local environment. What is beneficial in one situation may be useless or even harmful in another. Beak lengths arise that match the size of the typical fruit eaten by a particular soapberry bug population. However, a beak length suitable for fruit of one size can be disadvantageous when the bug is feeding on fruit of another size.

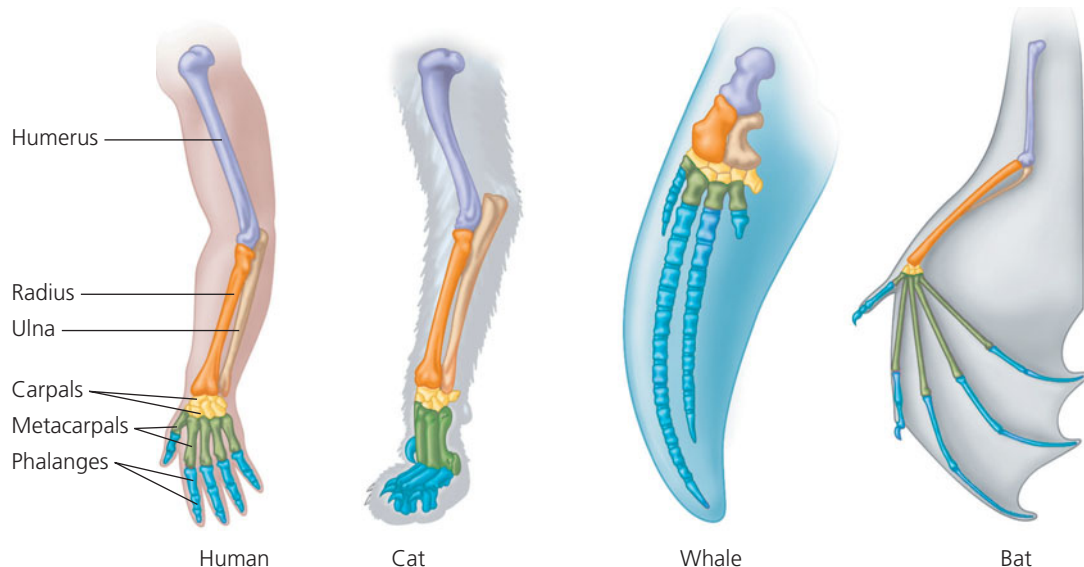
## Homology

A second type of evidence for evolution comes from analyzing similarities among different organisms. As we've discussed, evolution is a process of descent with modification: Characteristics present in an ancestral organism are altered (by natural selection) in its descendants over time as they face different environmental conditions. As a result, related species can have characteristics that have an underlying similarity yet function differently. Similarity resulting from common ancestry is known as **homology**. As we'll describe in this section, an understanding of homology can be used to make testable predictions and explain observations that are otherwise puzzling.

### Anatomical and Molecular Homologies

The view of evolution as a remodeling process leads to the prediction that closely related species should share similar features—and they do. Of course, closely related species share the features used to determine their relationship, but they also share many other features. Some of these shared features make little sense except in the context of evolution. For example, the forelimbs of all mammals, including humans, cats, whales, and bats, show the same arrangement of bones from the shoulder to the tips of the digits, even though these appendages have very different functions: lifting, walking, swimming, and flying

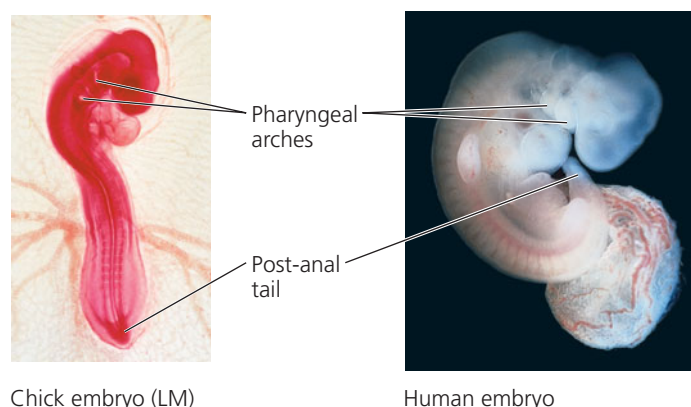
► **Figure 19.16 Mammalian forelimbs: homologous structures.** Even though they have become adapted for different functions, the forelimbs of all mammals are constructed from the same basic skeletal elements: one large bone (purple), attached to two smaller bones (orange and tan), attached to several small bones (gold), attached to several metacarpals (green), attached to approximately five digits, each of which is composed of phalanges (blue).



(**Figure 19.16**). Such striking anatomical resemblances would be highly unlikely if these structures had arisen anew in each species. Rather, the underlying skeletons of the arms, forelegs, flippers, and wings of different mammals are **homologous structures** that represent variations on a structural theme that was present in their common ancestor.

Comparing early stages of development in different animal species reveals additional anatomical homologies not visible in adult organisms. For example, at some point in their development, all vertebrate embryos have a tail located posterior to (behind) the anus, as well as structures called pharyngeal (throat) arches (**Figure 19.17**). These homologous throat arches ultimately develop into structures with very different functions, such as gills in fishes and parts of the ears and throat in humans and other mammals.

Some of the most intriguing homologies concern “leftover” structures of marginal, if any, importance to the organism. These **vestigial structures** are remnants of features that served a function in the organism’s ancestors. For instance, the



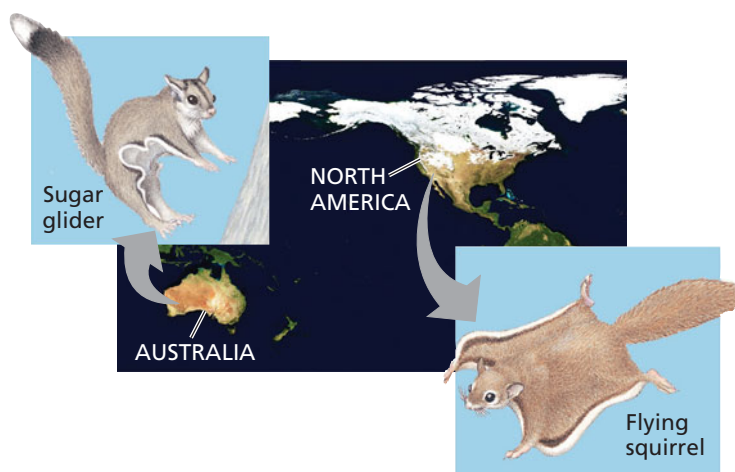
▲ **Figure 19.17 Anatomical similarities in vertebrate embryos.** At some stage in their embryonic development, all vertebrates have a tail located posterior to the anus (referred to as a post-anal tail), as well as pharyngeal (throat) arches. Descent from a common ancestor can explain such similarities.

skeletons of some snakes retain vestiges of the pelvis and leg bones of walking ancestors. Another example is provided by eye remnants that are buried under scales in blind species of cave fishes. We would not expect to see these vestigial structures if snakes and blind cave fishes had origins separate from other vertebrate animals.

Biologists also observe similarities among organisms at the molecular level. All forms of life use the same genetic language of DNA and RNA, and the genetic code is essentially universal. Thus, it is likely that all species descended from common ancestors that used this code. But molecular homologies go beyond a shared code. For example, organisms as dissimilar as humans and bacteria share genes inherited from a very distant common ancestor. Some of these homologous genes have acquired new functions, while others, such as those coding for the ribosomal subunits used in protein synthesis (see Figure 14.17), have retained their original functions. It is also common for organisms to have genes that have lost their function, even though the homologous genes in related species may be fully functional. Like vestigial structures, it appears that such inactive “pseudogenes” may be present simply because a common ancestor had them.

### A Different Cause of Resemblance: Convergent Evolution

Although organisms that are closely related share characteristics because of common descent, distantly related organisms can resemble one another for a different reason: **convergent evolution**, the independent evolution of similar features in different lineages. Consider marsupial mammals, many of which live in Australia. Marsupials are distinct from another group of mammals—the eutherians—few of which live in Australia. (Eutherians complete their embryonic development in the uterus, whereas marsupials are born as embryos and complete their development in an external pouch.) Some Australian marsupials have eutherian look-alikes with superficially similar adaptations. For instance, a forest-dwelling Australian marsupial called the sugar glider looks very similar to flying squirrels, gliding eutherians that live in North American forests (Figure 19.18). But the sugar glider has many other characteristics that make it a marsupial, much more closely related to kangaroos and other Australian marsupials than to flying squirrels or other eutherians. Again, our understanding of evolution can explain these observations: Although they evolved independently from different ancestors, these two mammals have adapted to similar environments in similar ways. In such examples in which species share features because of convergent evolution, the resemblance is said to be **analogous**, not homologous. Analogous features share similar function,



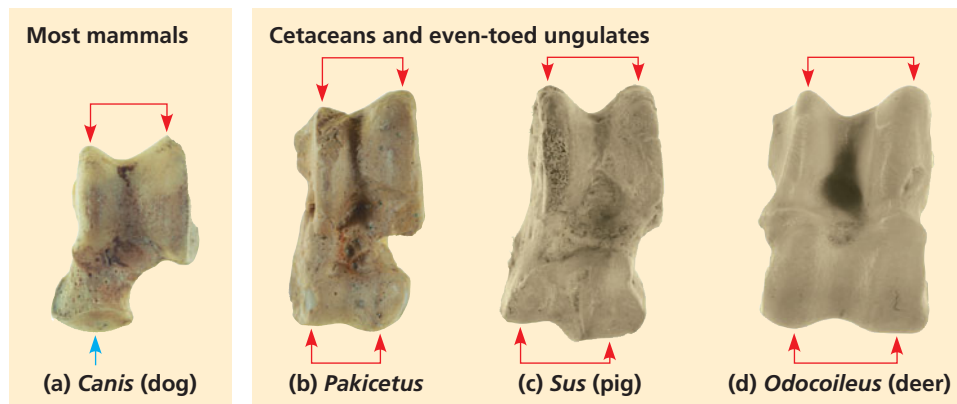
▲ **Figure 19.18 Convergent evolution.** The ability to glide through the air evolved independently in these two distantly related mammals.

but not common ancestry, while homologous features share common ancestry, but not necessarily similar function.

### The Fossil Record

A third type of evidence for evolution comes from fossils. The fossil record documents the pattern of evolution, showing that past organisms differed from present-day organisms and that many species have become extinct. Fossils also show the evolutionary changes that have occurred in various groups of organisms. To give one of hundreds of examples, researchers found that the pelvic bone in fossil stickleback fish became greatly reduced in size over time in a number of different lakes. The consistent nature of this change suggests that the reduction in the size of the pelvic bone may have been driven by natural selection.

Fossils can also shed light on the origins of new groups of organisms. An example is the fossil record of cetaceans, the mammalian order that includes whales, dolphins, and porpoises. As shown in Figure 19.19, some of these fossils

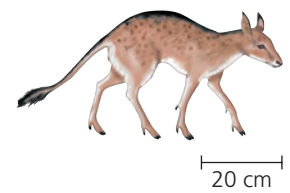


▲ **Figure 19.19 Ankle bones: one piece of the puzzle.** Comparing fossils and present-day examples of the astragalus (a type of ankle bone) provides one line of evidence that cetaceans are closely related to even-toed ungulates. (a) In most mammals, the astragalus is shaped like that of a dog, with a double hump on one end (indicated by the red arrows) but not at the opposite end (blue arrow). (b) Fossils show that the early cetacean *Pakicetus* had an astragalus with double humps at both ends, a shape otherwise found only in even-toed ungulates, such as (c) pigs and (d) deer.

provided an unexpected line of support for a hypothesis based on DNA sequence data: that cetaceans are closely related to even-toed ungulates, a group that includes deer, pigs, camels, and cows. What else can fossils tell us about cetacean origins? The earliest cetaceans lived 50–60 million years ago. The fossil record indicates that prior to that time, most mammals were terrestrial. Although scientists had long realized that whales and other cetaceans originated from land mammals, few fossils had been found that revealed how cetacean limb structure had changed over time, leading eventually to the loss of hind limbs and the development of flippers and tail flukes. In the past few decades, however, a series of remarkable fossils have been discovered in Pakistan, Egypt, and North America. These fossils document steps in the transition from life on land to life in the sea, filling in some of the gaps between ancestral and living cetaceans (**Figure 19.20**).

Collectively, the recent fossil discoveries document the formation of new species and the origin of a major new group of mammals, the cetaceans. These discoveries also show that cetaceans and their close living relatives (hippopotamuses, pigs, deer, and other even-toed ungulates) are much more different

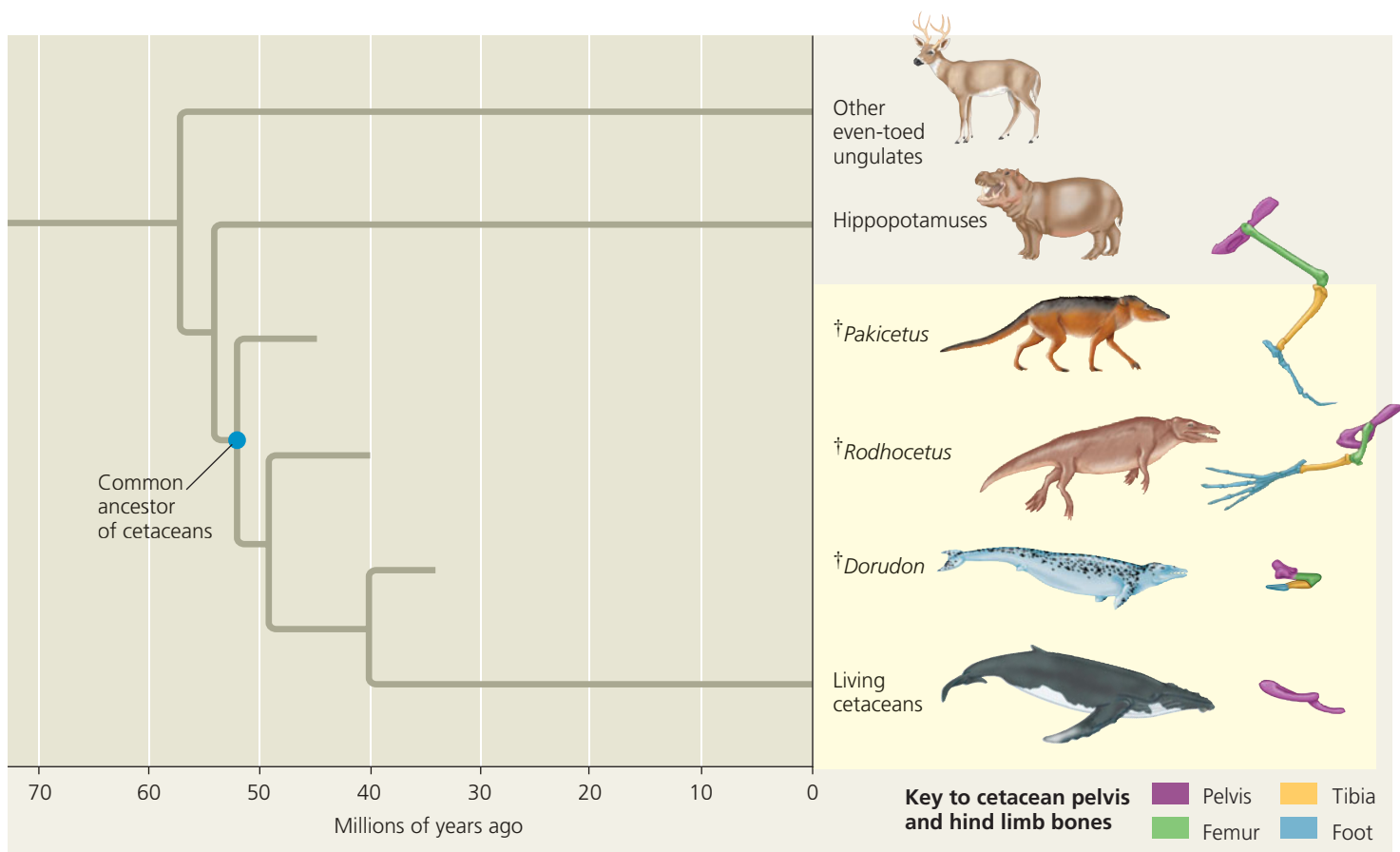
from each other than were *Pakicetus* and early even-toed ungulates, such as *Diacodexis*. Similar patterns are seen in fossils documenting the origins of other major new groups of organisms, including mammals (see Chapter 23), flowering plants (see Chapter 26), and tetrapods (see Chapter 27). In each of these cases, the fossil record shows that over time, descent with modification produced increasingly large differences among related groups of organisms, ultimately resulting in the diversity of life we see today.



▲ *Diacodexis*, an early even-toed ungulate

## Biogeography

A fourth type of evidence for evolution has to do with **biogeography**, the scientific study of the geographic distributions of species. The geographic distributions of organisms are influenced by many factors, including *continental drift*, the slow movement of Earth's continents over time. About 250 million years ago, these movements united all of Earth's landmasses into a single large continent called **Pangaea** (see Figure 23.8).



▲ **Figure 19.20 The transition to life in the sea.** Multiple lines of evidence support the hypothesis that cetaceans evolved from terrestrial mammals. Fossils document the reduction over time in the pelvis and hind limb bones of extinct cetacean ancestors, including *Pakicetus*, *Rodhocetus*, and *Dorudon*. DNA sequence data support the hypothesis that cetaceans are most closely related to hippopotamuses.

? Which happened first during the evolution of cetaceans: changes in hind limb structure or the origin of tail flukes?



Roughly 200 million years ago, Pangaea began to break apart; by 20 million years ago, the continents we know today were within a few hundred kilometers of their present locations.

We can use our understanding of evolution and continental drift to predict where fossils of different groups of organisms might be found. For example, scientists have constructed evolutionary trees for horses based on anatomical data. These trees and the ages of fossils of horse ancestors suggest that present-day horse species originated 5 million years ago in North America. At that time, North and South America were close to their present locations, but they were not yet connected, making it difficult for horses to travel between them. Thus, we would predict that the oldest horse fossils should be found only on the continent on which horses originated—North America. This prediction and others like it for differ-

ent groups of organisms have been upheld, providing more evidence for evolution.

We can also use our understanding of evolution to explain biogeographic data. For example, islands generally have many plant and animal species that are **endemic**—they are nowhere else in the world. Yet, as Darwin described in *The Origin of Species*, most island species are closely related to species from the nearest mainland or a neighboring island. He explained this observation by suggesting that islands are colonized by species from the nearest mainland. These colonists eventually give rise to new species as they adapt to their new environments. Such a process also explains why two islands with similar environments in distant parts of the world tend to be populated not by species that are closely related to each other, but rather by species related to those of the nearest mainland, where the environment is often quite different.

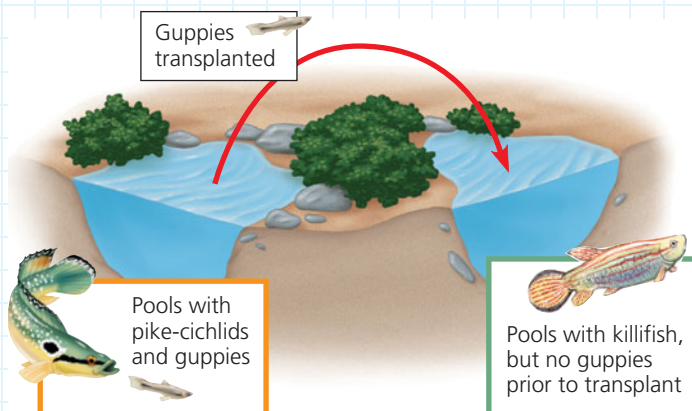
## Scientific Skills Exercise

### Making and Testing Predictions

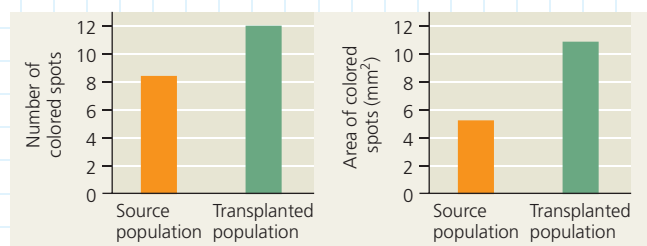
**Can Predation Result in Natural Selection for Color Patterns in Guppies?** What we know about evolution changes constantly as new observations lead to new hypotheses—and hence to new ways to test our understanding of evolutionary theory. Consider the wild guppies (*Poecilia reticulata*) that live in pools connected by streams on the Caribbean island of Trinidad. Male guppies have highly varied color patterns, which are controlled by genes that are only expressed in adult males. Female guppies choose males with bright color patterns as mates more often than they choose males with drab coloring. But the bright colors that attract females also make the males more conspicuous to predators. Researchers observed that in pools with few predator species, the benefits of bright colors appear to “win out,” and males are more brightly colored than in pools where predation is intense.

One guppy predator, the killifish, preys on juvenile guppies that have not yet displayed their adult coloration. Researchers predicted that if guppies with drab colors were transferred to a pool with only killifish, eventually the descendants of these guppies would be more brightly colored (because of the female preference for brightly colored males).

**How the Experiment Was Done** Researchers transplanted 200 guppies from pools containing pike-cichlid fish, intense guppy predators, to pools containing killifish, less active predators that prey mainly on juvenile guppies. They tracked the number of bright-colored spots and the total area of those spots on male guppies in each generation.



**Data from the Experiment** After 22 months (15 generations), researchers compared the color pattern data for the source and transplanted populations.



#### Interpret the Data

1. Identify the following elements of hypothesis-based science in this example: (a) question, (b) hypothesis, (c) prediction, (d) control group, and (e) experimental group. (For additional information about hypothesis-based science, see Chapter 1 and the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.)
2. Explain how the types of data the researchers chose to collect enabled them to test their prediction.
3. (a) What conclusion would you draw from the data presented above? (b) What additional questions might you ask to determine the strength of this conclusion?
4. Predict what would happen if, after 22 months, guppies from the transplanted population were returned to the source pool. Describe an experiment to test your prediction.

**Data from** J.A. Endler, Natural selection on color patterns in *Poecilia reticulata*, *Evolution* 34:76–91 (1980).

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

## What Is Theoretical About Darwin's View of Life?

Some people dismiss Darwin's ideas as “just a theory.” However, as we have seen, the *pattern* of evolution—the observation that life has evolved over time—has been documented directly and is supported by a great deal of evidence. In addition, Darwin's explanation of the *process* of evolution—that natural selection is the primary cause of the observed pattern of evolutionary change—makes sense of massive amounts of data. The effects of natural selection also can be observed and tested in nature.

What, then, is theoretical about evolution? Keep in mind that the scientific meaning of the term *theory* is very different from its meaning in everyday use. The colloquial use of the word *theory* comes close to what scientists mean by a hypothesis. In science, a theory is more comprehensive than a hypothesis. A theory, such as the theory of evolution by natural selection, accounts for many observations and explains and integrates a great variety of phenomena. Such a unifying theory does not become widely accepted unless its predictions stand up to thorough and continual testing by experiment and additional observation (see Chapter 1). As the rest of this unit demonstrates, this has certainly been the case with the theory of evolution by natural selection.

The skepticism of scientists as they continue to test theories prevents these ideas from becoming dogma. For example, although Darwin thought that evolution was a very slow process, we now know that this isn't always true. New species can

form in relatively short periods of time—a few thousand years or less (see Chapter 22). Furthermore, evolutionary biologists now recognize that natural selection is not the only mechanism responsible for evolution. Indeed, the study of evolution today is livelier than ever as scientists use a wide range of experimental approaches and genetic analyses to test predictions based on natural selection and other evolutionary mechanisms. In the **Scientific Skills Exercise**, you'll work with data from an experiment on natural selection in wild guppies.

Although Darwin's theory attributes the diversity of life to natural processes, the diverse products of evolution nevertheless remain elegant and inspiring. As Darwin wrote in the final sentence of *The Origin of Species*, “There is grandeur in this view of life . . . [in which] endless forms most beautiful and most wonderful have been, and are being, evolved.”

### CONCEPT CHECK 19.3

1. Explain how the following statement is inaccurate: “Antibiotics have created drug resistance in MRSA.”
2. How does evolution account for (a) the similar mammalian forelimbs with different functions shown in Figure 19.16 and (b) the similar forms of the two distantly related mammals shown in Figure 19.18?
3. **WHAT IF?** Fossils show that dinosaurs originated 250–200 million years ago. Would you expect the geographic distribution of early dinosaur fossils to be broad (on many continents) or narrow (on one or a few continents only)? Explain.

For suggested answers, see Appendix A.

## 19 Chapter Review

### SUMMARY OF KEY CONCEPTS

#### CONCEPT 19.1

**The Darwinian revolution challenged traditional views of a young Earth inhabited by unchanging species (pp. 366–367)**

- Darwin proposed that life's diversity arose from ancestral species through natural selection, a departure from prevailing views.
- Cuvier studied fossils but denied that evolution occurs; he proposed that sudden catastrophic events in the past caused species to disappear from an area. Hutton and Lyell thought that geologic change could result from gradual, continuous mechanisms. Lamarck hypothesized that species evolve, but the underlying mechanisms he proposed are not supported by evidence.

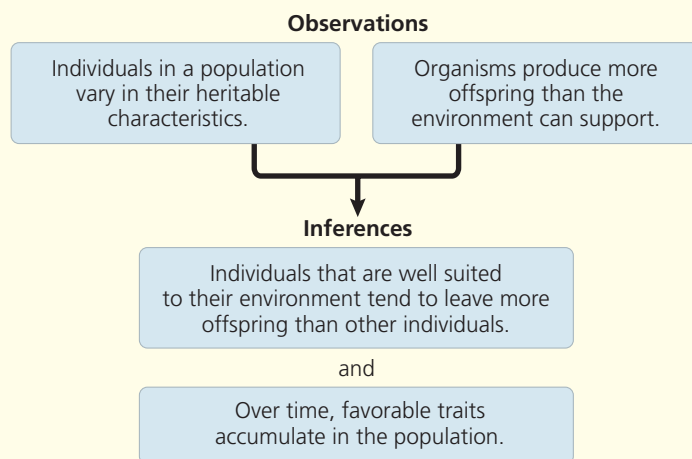
**?** Why was the age of Earth important for Darwin's ideas about evolution?

#### CONCEPT 19.2

**Descent with modification by natural selection explains the adaptations of organisms and the unity and diversity of life (pp. 368–372)**

- Darwin's voyage on the *Beagle* gave rise to his idea that species originate from ancestral forms through the accumulation of

**adaptations.** He refined his theory for many years and finally published it in 1859 after learning that Wallace had come to the same idea. In *The Origin of Species*, Darwin proposed that evolution occurs by **natural selection**.



**?** Describe how overreproduction and heritable variation relate to evolution by natural selection.

## CONCEPT 19.3

### Evolution is supported by an overwhelming amount of scientific evidence (pp. 373–379)

- Researchers have directly observed natural selection leading to adaptive evolution in many studies, including research on soapberry bug populations and on MRSA.
- Organisms share characteristics because of common descent (**homology**) or because natural selection affects independently evolving species in similar environments in similar ways (**convergent evolution**).
- Fossils show that past organisms differed from living organisms, that many species have become extinct, and that species have evolved over long periods of time; fossils also document the origin of major new groups of organisms.
- Evolutionary theory can explain biogeographic patterns.

**?** Summarize the different lines of evidence supporting the hypothesis that cetaceans descended from land mammals and are closely related to even-toed ungulates.

## TEST YOUR UNDERSTANDING

### Level 1: Knowledge/Comprehension

1. Which of the following is *not* an observation or inference on which natural selection is based?
  - a. There is heritable variation among individuals.
  - b. Poorly adapted individuals never produce offspring.
  - c. Species produce more offspring than the environment can support.
  - d. Individuals whose characteristics are best suited to the environment generally leave more offspring than those whose characteristics are less well suited.
  - e. Only a fraction of an individual's offspring may survive.
2. Which of the following observations helped Darwin shape his concept of descent with modification?
  - a. Species diversity declines farther from the equator.
  - b. Fewer species live on islands than on the nearest continents.
  - c. Birds live on islands located farther from the mainland than the birds' maximum nonstop flight distance.
  - d. South American temperate plants are more similar to the tropical plants of South America than to the temperate plants of Europe.
  - e. Earthquakes reshape life by causing mass extinctions.

### Level 2: Application/Analysis

3. Within six months of effectively using methicillin to treat *S. aureus* infections in a community, all new infections were caused by MRSA. How can this result best be explained?
  - a. *S. aureus* can resist vaccines.
  - b. A patient must have become infected with MRSA from another community.
  - c. In response to the drug, *S. aureus* began making drug-resistant versions of the protein targeted by the drug.
  - d. Some drug-resistant bacteria were present at the start of treatment, and natural selection increased their frequency.
  - e. The drug caused the *S. aureus* DNA to change.

4. The upper forelimbs of humans and bats have fairly similar skeletal structures, whereas the corresponding bones in whales have very different shapes and proportions. However, genetic data suggest that all three kinds of organisms diverged from a common ancestor at about the same time. Which of the following is the most likely explanation for these data?
  - a. Humans and bats evolved by natural selection, and whales evolved by Lamarckian mechanisms.
  - b. Forelimb evolution was adaptive in people and bats, but not in whales.
  - c. Natural selection in an aquatic environment resulted in significant changes to whale forelimb anatomy.
  - d. Genes mutate faster in whales than in humans or bats.
  - e. Whales are not properly classified as mammals.
5. DNA sequences in many human genes are very similar to the sequences of corresponding genes in chimpanzees. The most likely explanation for this result is that
  - a. humans and chimpanzees share a relatively recent common ancestor.
  - b. humans evolved from chimpanzees.
  - c. chimpanzees evolved from humans.
  - d. convergent evolution led to the DNA similarities.
  - e. humans and chimpanzees are not closely related.

### Level 3: Synthesis/Evaluation

#### 6. SCIENTIFIC INQUIRY

**DRAW IT** Mosquitoes resistant to the pesticide DDT first appeared in India in 1959, but now are found throughout the world. (a) Graph the data in the table below. (b) Examining the graph, hypothesize why the percentage of mosquitoes resistant to DDT rose rapidly. (c) Suggest an explanation for the global spread of DDT resistance.

Month	0	8	12
Mosquitoes Resistant* to DDT	4%	45%	77%

**Source** C. F. Curtis et al., Selection for and against insecticide resistance and possible methods of inhibiting the evolution of resistance in mosquitoes, *Ecological Entomology* 3:273–287 (1978).

\*Mosquitoes were considered resistant if they were not killed within 1 hour of receiving a dose of 4% DDT.

#### 7. FOCUS ON EVOLUTION

Explain why anatomical and molecular features often fit a similar nested pattern. In addition, describe a process that can cause this not to be the case.

#### 8. FOCUS ON INTERACTIONS

Write a short essay (about 100–150 words) evaluating whether changes to an organism's physical environment are likely to result in evolutionary change. Use an example to support your reasoning.

For selected answers, see Appendix A.

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# 20

## Phylogeny

▼ **Figure 20.1** What kind of organism is this?



### KEY CONCEPTS

- 20.1** Phylogenies show evolutionary relationships
- 20.2** Phylogenies are inferred from morphological and molecular data
- 20.3** Shared characters are used to construct phylogenetic trees
- 20.4** Molecular clocks help track evolutionary time
- 20.5** New information continues to revise our understanding of evolutionary history

### OVERVIEW

## Investigating the Evolutionary History of Life

**L**ook closely at the organism in **Figure 20.1**. Although it resembles a snake, this animal is actually a legless lizard known as the eastern glass lizard (*Ophisaurus ventralis*). Why isn't this glass lizard considered a snake? More generally, how do biologists distinguish and categorize the millions of species on Earth?

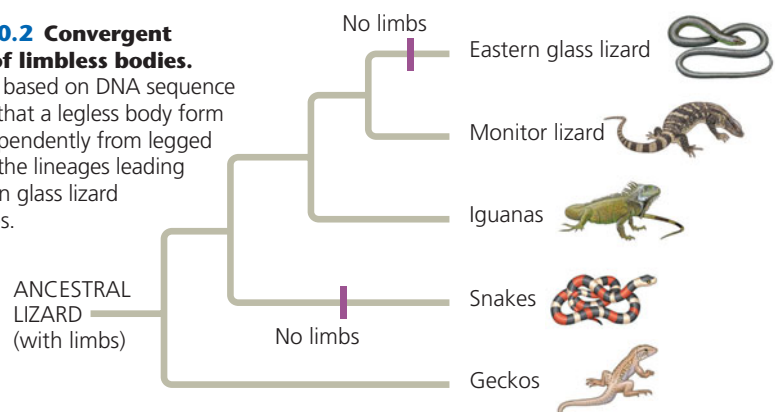
An understanding of evolutionary relationships suggests one way to address these questions: We can decide in which category to place a species by comparing its traits with those of potential close relatives. For example, the eastern glass lizard does not have a highly mobile jaw, a large number of vertebrae,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

Snakes and lizards are part of the continuum of life extending from the earliest organisms to the great variety of species alive today. To help make sense of that diversity, biologists trace **phylogeny**, the evolutionary history of a species or group of species. A phylogeny of lizards and snakes, for example, indicates that both the eastern glass lizard and snakes evolved from lizards with legs—but they evolved from different lineages of legged lizards (**Figure 20.2**). Thus, it appears that their limbless body forms evolved independently.

In fact, a broader survey of the lizards reveals that a snakelike body form has evolved in many different groups of lizards. Most lizards with such a body form are burrowers or live in grasslands. The repeated

### ► **Figure 20.2** Convergent evolution of limbless bodies.

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



evolution of a snakelike body form in a consistent set of environments suggests that this change has been driven by natural selection: The legs of these organisms became reduced in size, or even disappeared, over generations as the species adapted to their environments.

In this chapter, we'll examine how biologists reconstruct and interpret phylogenies using **systematics**, a discipline focused on classifying organisms and determining their evolutionary relationships.

## CONCEPT 20.1

### Phylogenies show evolutionary relationships

Organisms share many characteristics because of common ancestry (see Chapter 19). As a result, we can learn a great deal about a species if we know its evolutionary history. For example, an organism is likely to share many of its genes, metabolic pathways, and structural proteins with its close relatives. We'll consider practical applications of such information later in this section, but first we'll examine how organisms are named and classified, the scientific discipline of **taxonomy**. We'll also look at how we can interpret and use diagrams that represent evolutionary history.

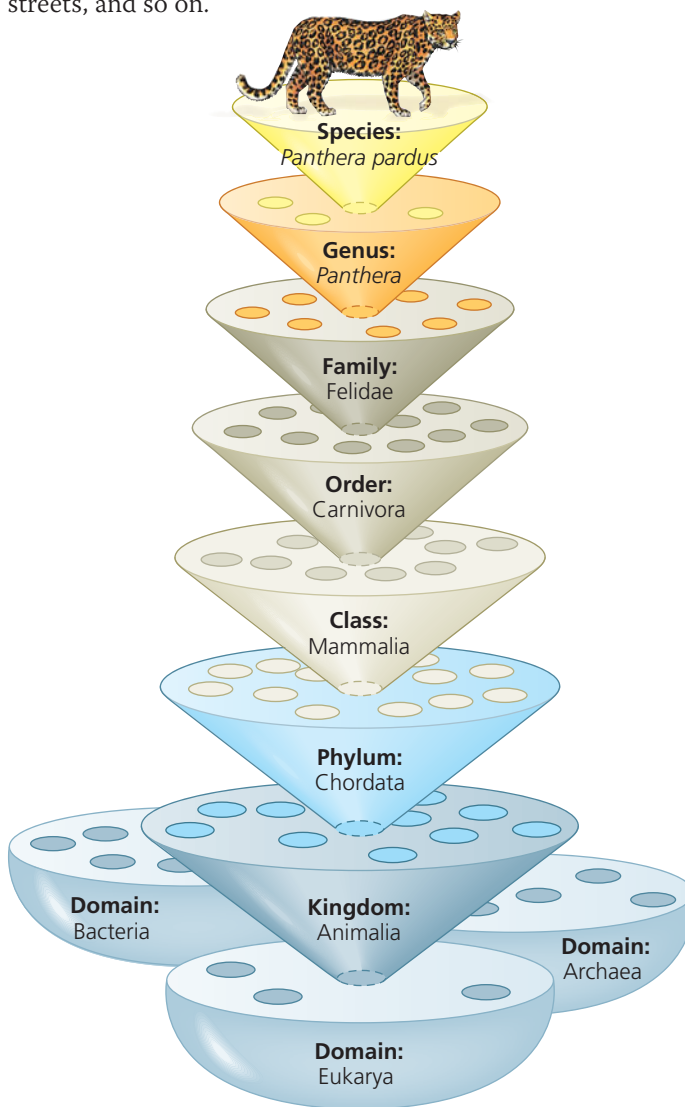
#### Binomial Nomenclature

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

To avoid ambiguity when communicating about their research, biologists refer to organisms by Latin scientific names. The two-part format of the scientific name, commonly called a **binomial**, was instituted in the 18th century by Carolus Linnaeus (see Chapter 19). The first part of a binomial is the name of the **genus** (plural, *genera*) to which the species belongs. The second part, called the specific epithet, is unique for each species within the genus. An example of a binomial is *Panthera pardus*, the scientific name for the large cat commonly called the leopard. Notice that the first letter of the genus is capitalized and the entire binomial is italicized. (Newly created scientific names are also “latinized”: You can name an insect you discover after a friend, but you must add a Latin ending.) Many of the more than 11,000 binomials assigned by Linnaeus are still used today, including the optimistic name he gave our own species—*Homo sapiens*, meaning “wise man.”

### Hierarchical Classification

In addition to naming species, Linnaeus also grouped them into a hierarchy of increasingly inclusive categories. The first grouping is built into the binomial: Species that appear to be closely related are grouped into the same genus. For example, the leopard (*Panthera pardus*) belongs to a genus that also includes the African lion (*Panthera leo*), the tiger (*Panthera tigris*), and the jaguar (*Panthera onca*). Beyond genera, taxonomists employ progressively more comprehensive categories of classification. The taxonomic system named after Linnaeus, the Linnaean system, places related genera into the same **family**, families into **orders**, orders into **classes**, classes into **phyla** (singular, *phylum*), phyla into **kingdoms**, and, more recently, kingdoms into **domains** (**Figure 20.3**). The resulting biological classification of a particular organism is somewhat like a postal address identifying a person in a particular apartment, in a building with many apartments, on a street with many apartment buildings, in a city with many streets, and so on.



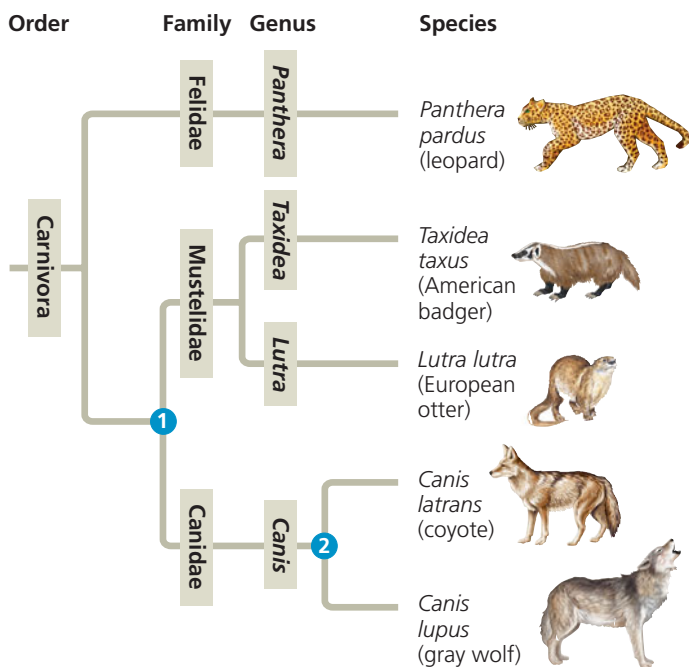
▲ **Figure 20.3 Linnaean classification.** At each level, or “rank,” species are placed in groups within more inclusive groups.

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

Classifying species is a way to structure our human view of the world. We lump together various species of trees to which we give the common name of pines and distinguish them from other trees that we call firs. Taxonomists have decided that pines and firs are different enough to be placed in separate genera, yet similar enough to be grouped into the same family, Pinaceae. As with pines and firs, higher levels of classification are usually defined by particular characters chosen by taxonomists. However, characters that are useful for classifying one group of organisms may not be appropriate for other organisms. For this reason, the larger categories often are not comparable between lineages; that is, an order of snails does not exhibit the same degree of morphological or genetic diversity as an order of mammals. Furthermore, as we'll see, the placement of species into orders, classes, and so on, does not necessarily reflect evolutionary history.

## Linking Classification and Phylogeny

The evolutionary history of a group of organisms can be represented in a branching diagram called a **phylogenetic tree**. As in **Figure 20.4**, the branching pattern often matches how

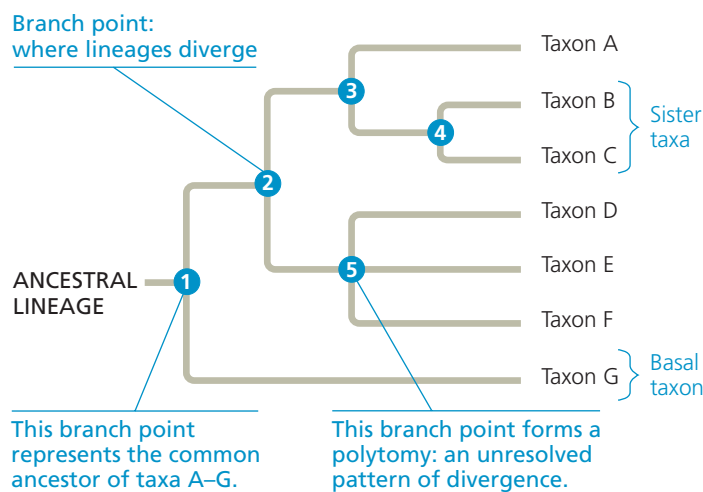


▲ **Figure 20.4 The connection between classification and phylogeny.** Hierarchical classification can reflect the branching patterns of phylogenetic trees. This tree traces possible evolutionary relationships between some of the taxa within order Carnivora, itself a branch of class Mammalia. The branch point 1 represents the most recent common ancestor of all members of the weasel (Mustelidae) and dog (Canidae) families. The branch point 2 represents the most recent common ancestor of coyotes and gray wolves.

taxonomists have classified groups of organisms nested within more inclusive groups. Sometimes, however, taxonomists have placed a species within a genus (or other group) to which it is *not* most closely related. One reason for such a mistake might be that over the course of evolution, a species has lost a key feature shared by its close relatives. If DNA or other new evidence indicates that an organism has been misclassified, the organism may be reclassified to accurately reflect its evolutionary history. Another issue is that while the Linnaean system may distinguish groups, such as amphibians, mammals, reptiles, and other classes of vertebrates, it tells us nothing about these groups' evolutionary relationships to one another. Such difficulties in aligning Linnaean classification with phylogeny have led many systematists to propose that classification be based entirely on evolutionary relationships.

Regardless of how groups are named, a phylogenetic tree represents a hypothesis about evolutionary relationships. These relationships often are depicted as a series of dichotomies, or two-way **branch points**. Each branch point represents the divergence of two evolutionary lineages from a common ancestor. In **Figure 20.5**, for example, branch point 3 represents the common ancestor of taxa A, B, and C. The position of branch point 4 to the right of 3 indicates that taxa B and C diverged after their shared lineage split from that of taxon A. (Note also that tree branches can be rotated around a branch point without changing their evolutionary relationships.)

In Figure 20.5, taxa B and C are **sister taxa**, groups of organisms that share an immediate common ancestor (branch point 4) and hence are each other's closest relatives. In addition, this tree, like most of the phylogenetic trees in this book, is **rooted**, which means that a branch point within the tree (often drawn farthest to the left) represents the most recent common ancestor of all taxa in the tree. The term **basal taxon**



▲ **Figure 20.5 How to read a phylogenetic tree.**

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



refers to a lineage that diverges early in the history of a group and hence, like taxon G in Figure 20.5, lies on a branch that originates near the common ancestor of the group. Finally, the lineage leading to taxa D–F includes a **polytomy**, a branch point from which more than two descendant groups emerge. A polytomy signifies that evolutionary relationships among the taxa are not yet clear.

## What We Can and Cannot Learn from Phylogenetic Trees

Let's summarize three key points about phylogenetic trees. First, they are intended to show patterns of descent, not phenotypic similarity. Although closely related organisms often resemble one another due to their common ancestry, they may not if their lineages have evolved at different rates or faced very different environmental conditions. For example, even though crocodiles are more closely related to birds than to lizards (see Figure 20.15), they look more like lizards because morphology has changed dramatically in the bird lineage.

Second, the sequence of branching in a tree does not necessarily indicate the actual (absolute) ages of the particular species. For example, the tree in Figure 20.4 does not indicate that the wolf evolved more recently than the European otter; rather, the tree shows only that the most recent common ancestor of the wolf and otter (branch point ①) lived before the most recent common ancestor of the wolf and coyote (②). To indicate when wolves and otters evolved, the tree would need to include additional divergences in each evolutionary lineage, as well as the dates when those splits occurred. Generally, unless given specific information about what the branch lengths in a phylogenetic tree mean—for example, that they are proportional to time—we should interpret the diagram solely in terms of patterns of descent. No assumptions should be made about when particular species evolved or how much change occurred in each lineage.

Third, we should not assume that a taxon on a phylogenetic tree evolved from the taxon next to it. Figure 20.4 does not indicate that wolves evolved from coyotes or vice versa. We can infer only that the lineage leading to wolves and the lineage leading to coyotes both evolved from the common ancestor ②. That ancestor, which is now extinct, was neither a wolf nor a coyote. However, its descendants include the two *extant* (living) species shown here, wolves and coyotes.

## Applying Phylogenies

Understanding phylogeny can have practical applications. Consider maize (corn), which originated in the Americas and is now an important food crop worldwide. From a phylogeny of maize based on DNA data, researchers have been able to identify two species of wild grasses that may be maize's closest living relatives. These two close relatives may be useful

as “reservoirs” of beneficial alleles that can be transferred to cultivated maize by cross-breeding or genetic engineering (see Concept 13.4).

A different use of phylogenetic trees is to infer species identities by analyzing the relatedness of DNA sequences from different organisms. Researchers have used this approach to investigate whether “whale meat” has been harvested illegally from whale species protected under international law rather than from species that can be harvested legally, such as Minke whales caught in the Southern Hemisphere (**Figure 20.6**).

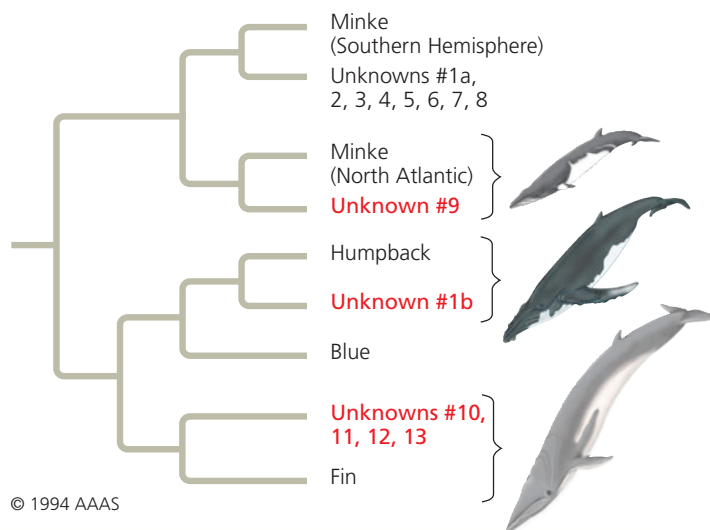
How do researchers construct trees like those we've considered here? In the next section, we'll begin to answer that question by examining the data used to determine phylogenies.

### ▼ Figure 20.6 Inquiry

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

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

**Results** The analysis yielded the following gene tree:



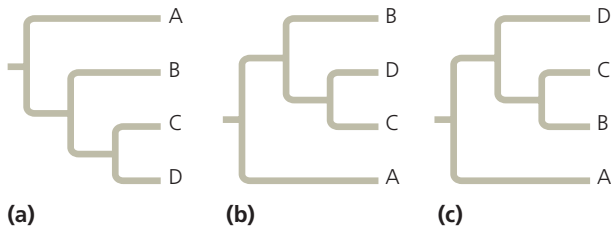
**Conclusion** This analysis indicated that mtDNA sequences of six of the unknown samples (in red) were most closely related to DNA sequences of whales that are not legal to harvest.

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

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

### CONCEPT CHECK 20.1

1. Which levels of the classification in Figure 20.3 do humans share with leopards?
2. What does the phylogenetic tree in Figure 20.4 indicate about the evolutionary relationships between the leopard, badger, and wolf?
3. Which of the trees shown here depicts an evolutionary history different from the other two? Explain.



4. **WHAT IF?** Suppose new evidence indicates that taxon E in Figure 20.5 is the sister taxon of a group consisting of taxa D and F. Redraw the tree to accommodate this new finding.

For suggested answers, see Appendix A.

current Hawaiian islands formed. We'll discuss how scientists use molecular data to estimate such divergence times later in this chapter.

## Sorting Homology from Analogy

A potential source of confusion in constructing a phylogeny is similarity due to convergent evolution—called **analogy**—rather than to shared ancestry (homology). Convergent evolution occurs when similar environmental pressures and natural selection produce similar (analogous) adaptations in organisms from different evolutionary lineages. For example, the two mole-like animals illustrated in **Figure 20.7** are similar in their external appearance. However, their internal anatomy, physiology, and reproductive systems are very dissimilar. Australian “moles” are marsupials; their young complete their embryonic development in a pouch on the outside of the mother’s body. North American moles, in contrast, are eutherians; their young complete their embryonic development in the uterus within the mother’s body. Indeed, genetic comparisons and the fossil record provide evidence that the common ancestor of these animals lived 140 million years ago, about the time the marsupial and eutherian mammals diverged. This common ancestor and most of its descendants were not mole-like, but analogous characteristics evolved independently in these two lineages as they became adapted to similar lifestyles.

Distinguishing between homology and analogy is critical in reconstructing phylogenies. To see why, consider bats and birds, both of which have adaptations that enable flight. This superficial resemblance might imply that bats are more closely related to birds than they are to cats, which cannot fly. But a closer examination reveals that a bat’s wing is far more similar to the forelimbs of cats and other mammals than to



**▲ Figure 20.7 Convergent evolution of analogous burrowing characteristics.** An elongated body, enlarged front paws, small eyes, and a pad of thickened skin that protects a tapered nose all evolved independently in the marsupial Australian “mole” (top) and a eutherian North American mole (bottom).

## CONCEPT 20.2

### Phylogenies are inferred from morphological and molecular data

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

#### Morphological and Molecular Homologies

Recall that phenotypic and genetic similarities due to shared ancestry are called *homologies*. For example, the similarity in the number and arrangement of bones in the forelimbs of mammals is due to their descent from a common ancestor with the same bone structure; this is an example of a morphological homology (see Figure 19.16). In the same way, genes or other DNA sequences are homologous if they are descended from sequences carried by a common ancestor.

In general, organisms that share very similar morphologies or similar DNA sequences are likely to be more closely related than organisms with vastly different structures or sequences. In some cases, however, the morphological divergence between related species can be great and their genetic divergence small (or vice versa). Consider Hawaiian silversword plants: Some of these species are tall, twiggy trees, while others are dense, ground-hugging shrubs. But despite these striking phenotypic differences, the silverswords’ genes are very similar. Based on these small molecular divergences, scientists estimate that the silversword group began to diverge 5 million years ago, which is also about the time when the oldest of the

a bird's wing. Bats and birds descended from a common tetrapod ancestor that lived about 320 million years ago. This common ancestor could not fly. Thus, although the underlying skeletal systems of bats and birds are homologous, their *wings* are not. Flight is enabled in different ways—stretched membranes in the bat wing versus feathers in the bird wing. Fossil evidence also documents that bat wings and bird wings arose independently from the forelimbs of different tetrapod ancestors. Thus, with respect to flight, a bat's wing is *analogous*, not homologous, to a bird's wing. Analogous structures that arose independently are also called **homoplasies** (from the Greek, meaning “to mold in the same way”).

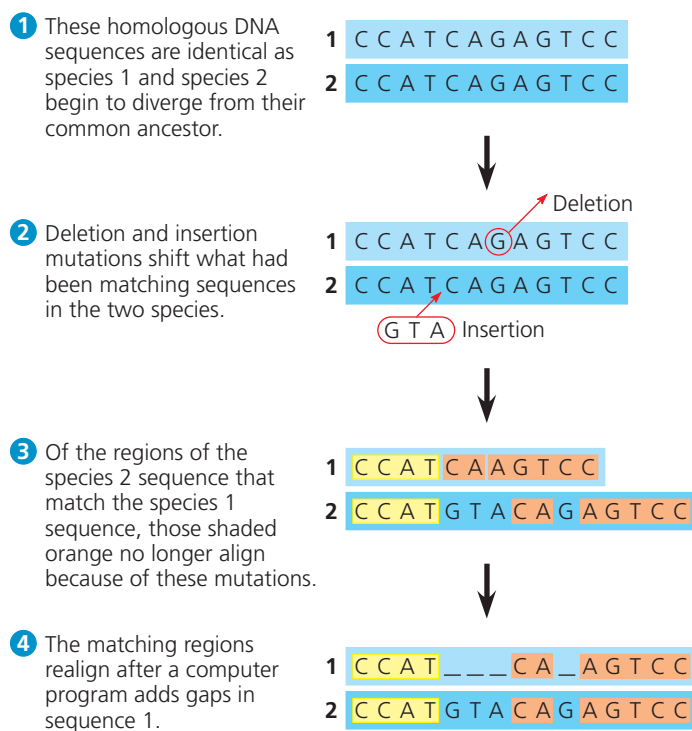
Besides corroborative similarities and fossil evidence, another clue to distinguishing between homology and analogy is the complexity of the characters being compared. The more elements that are similar in two complex structures, the more likely it is that they evolved from a common ancestor. For instance,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

## Evaluating Molecular Homologies

Comparing DNA molecules often poses technical challenges for researchers. The first step after sequencing the molecules is to align comparable sequences from the species being studied. If the species are very closely related, the sequences probably differ at only one or a few sites. In contrast, comparable nucleic acid sequences in distantly related species usually have different bases at many sites and may have different lengths. This is because insertions and deletions accumulate over long periods of time.

Suppose, for example, that certain noncoding DNA sequences near a particular gene are very similar in two species, except that the first base of the sequence has been deleted in one of the species. The effect is that the remaining sequence shifts back one notch. A comparison of the two sequences that does not take this deletion into account would overlook what in fact is a very good match. To address such problems, researchers have developed computer programs that estimate the best way to align comparable DNA segments of differing lengths (**Figure 20.8**).

Such molecular comparisons reveal that many base substitutions and other differences have accumulated in the comparable genes of an Australian mole and a North American mole. The many differences indicate that their lineages have diverged



**▲ Figure 20.8 Aligning segments of DNA.** Systematists search for similar sequences along DNA segments from two species (only one DNA strand is shown for each species). In this example, 11 of the original 12 bases have not changed since the species diverged. Hence, those portions of the sequences still align once the length is adjusted.

greatly since their common ancestor; thus, we say that the living species are not closely related. In contrast, the high degree of gene sequence similarity among the silversword plants indicates that they are all very closely related, in spite of their considerable morphological differences.

Just as with morphological characters, it is necessary to distinguish homology from analogy in evaluating molecular similarities for evolutionary studies. Two sequences that resemble each other at many points along their length most likely are homologous (see Figure 20.8). But in organisms that do not appear to be closely related, the bases that their otherwise very different sequences happen to share may simply be coincidental matches, called molecular homoplasies (**Figure 20.9**).



**▲ Figure 20.9 A molecular homoplasy.** These two DNA sequences from organisms that are not closely related coincidentally share 23% of their bases. Statistical tools have been developed to determine whether DNA sequences that share more than 25% of their bases do so because they are homologous.

**?** Why might you expect organisms that are not closely related to nevertheless share roughly 25% of their bases?



Scientists have developed statistical tools that can help distinguish “distant” homologies from such coincidental matches in extremely divergent sequences.

### CONCEPT CHECK 20.2

1. Decide whether each of the following pairs of structures more likely represents analogy or homology, and explain your reasoning: (a) a porcupine’s quills and a cactus’s spines; (b) a cat’s paw and a human’s hand; (c) an owl’s wing and a hornet’s wing.
2. **WHAT IF?** Suppose that species 1 and species 2 have similar appearances but very divergent gene sequences and that species 2 and species 3 have very different appearances but similar gene sequences. Which pair of species is more likely to be closely related: 1 and 2, or 2 and 3? Explain.

For suggested answers, see Appendix A.

## CONCEPT 20.3

### Shared characters are used to construct phylogenetic trees

In reconstructing phylogenies, the first step is to distinguish homologous features from analogous ones (since only homology reflects evolutionary history). Next we must choose a method of inferring phylogeny from these homologous characters. A widely used set of methods is known as cladistics.

#### Cladistics

In the approach to systematics called **cladistics**, common ancestry is the primary criterion used to classify organisms. Using this methodology, biologists attempt to place species into groups

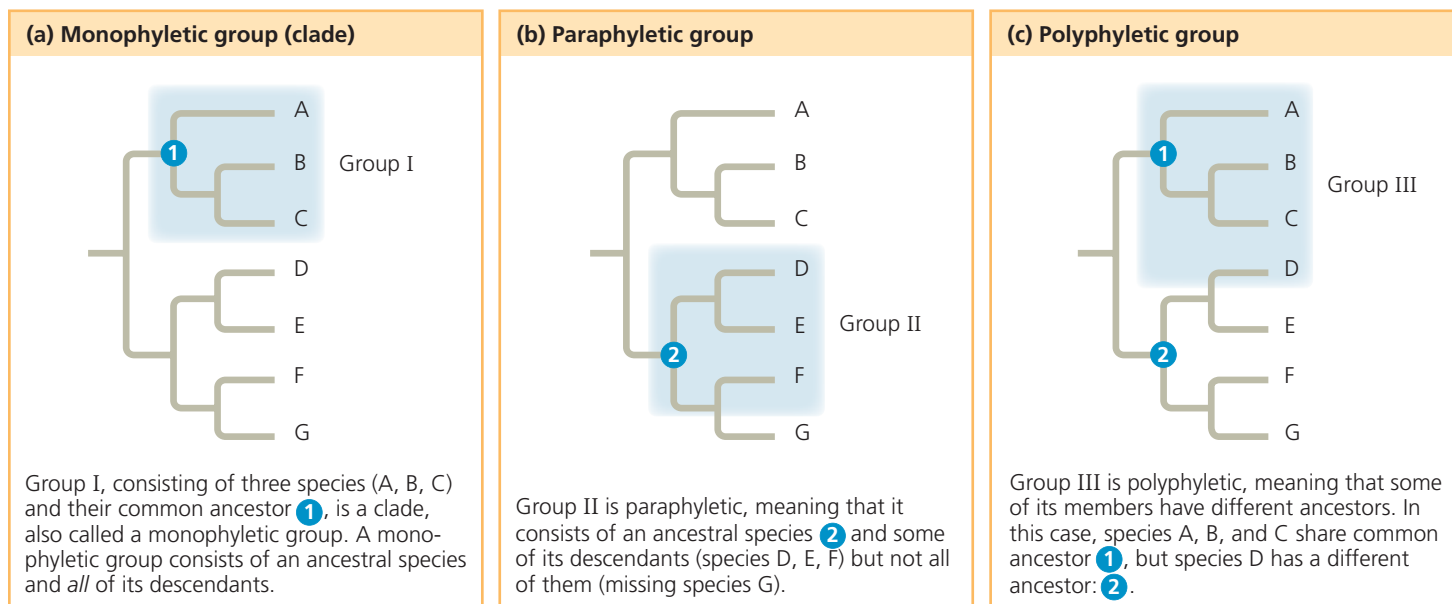
called **clades**, each of which includes an ancestral species and all of its descendants (**Figure 20.10a**). Clades, like taxonomic ranks, are nested within larger clades. In Figure 20.4, for example, the cat group (Felidae) represents a clade within a larger clade (Carnivora) that also includes the dog group (Canidae).

However, a taxon is equivalent to a clade only if it is **monophyletic** (from the Greek, meaning “single tribe”), signifying that it consists of an ancestral species and all of its descendants (see Figure 20.10a). Contrast this with a **paraphyletic** (“beside the tribe”) group, which consists of an ancestral species and some, but not all, of its descendants (**Figure 20.10b**), or a **polyphyletic** (“many tribes”) group, which includes taxa with different ancestors (**Figure 20.10c**). Note also that in a paraphyletic group, the most recent common ancestor of all members of the group *is* part of the group, whereas in a polyphyletic group, the most recent common ancestor of all members of the group *is not* part of the group. Next we’ll discuss how clades are identified using shared derived characters.

#### Shared Ancestral and Shared Derived Characters

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

▼ **Figure 20.10** Monophyletic, paraphyletic, and polyphyletic groups.



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

Inferring Phylogenies Using Derived Characters

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

To see how this analysis is done, consider the set of characters shown in Figure 20.11a for each of five vertebrates—a leopard, turtle, frog, bass, and lamprey (a jawless aquatic vertebrate). As a basis of comparison, we need to select an outgroup. An outgroup is a species or group of species from an evolutionary lineage that is known to have diverged before the lineage that includes the species we are studying (the ingroup). A suitable outgroup can be determined based on evidence from morphology, paleontology, embryonic development, and gene sequences. An appropriate outgroup for our example is the lancelet, a small animal that lives in mudflats and (like vertebrates) is a member of the more inclusive group called the chordates. Unlike the vertebrates, however, the lancelet does not have a backbone.

By comparing members of the ingroup with each other and with the outgroup, we can determine which characters were derived at the various branch points of vertebrate evolution. For example, all of the vertebrates in the ingroup have backbones: This character was present in the ancestral vertebrate,

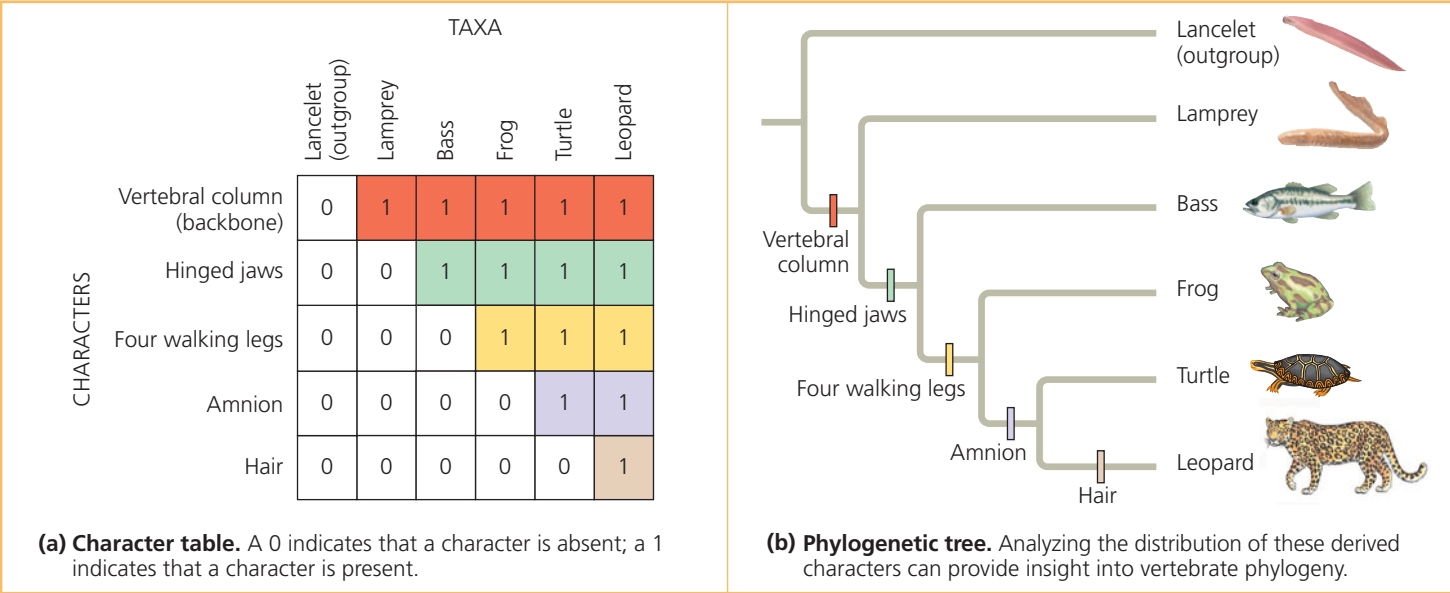
but not in the outgroup. Now note that hinged jaws are a character absent in lampreys but present in other members of the ingroup; this character helps us to identify an early branch point in the vertebrate clade. Proceeding in this way, we can translate the data in our table of characters into a phylogenetic tree that groups all the ingroup taxa into a hierarchy based on their shared derived characters (Figure 20.11b).

Phylogenetic Trees with Proportional Branch Lengths

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

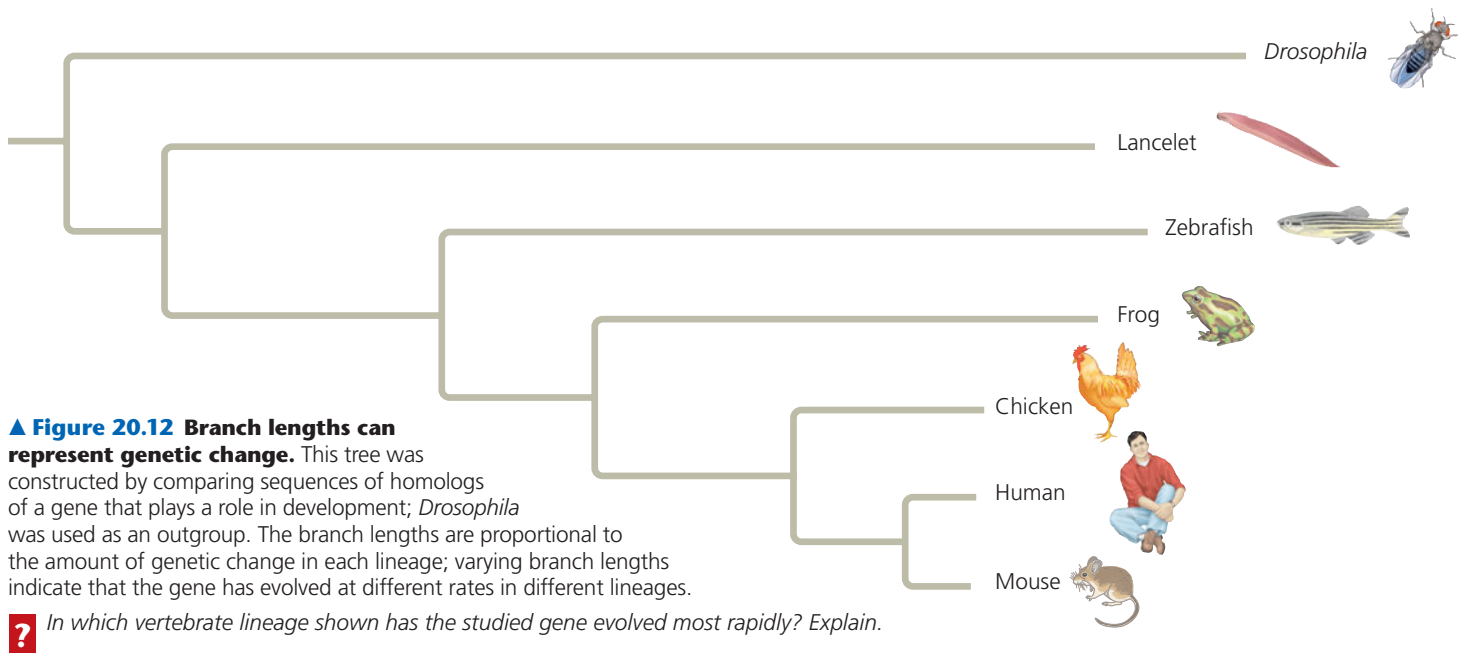
In Figure 20.12, for example, the branch length of the phylogenetic tree reflects the number of changes that have taken place in a particular DNA sequence in that lineage. Note that the total length of the horizontal lines from the base of the tree to the mouse is less than that of the line leading to the outgroup species, the fruit fly *Drosophila*. This implies that in the time since the mouse and fly diverged from a common ancestor, more genetic changes have occurred in the *Drosophila* lineage than in the mouse lineage.

Even though the branches of a phylogenetic tree may have different lengths, among organisms alive today, all the different lineages that descend from a common ancestor have survived



▲ **Figure 20.11 Constructing a phylogenetic tree.** The characters used here include the amnion, a membrane that encloses the embryo inside a fluid-filled sac (see Figure 27.25).

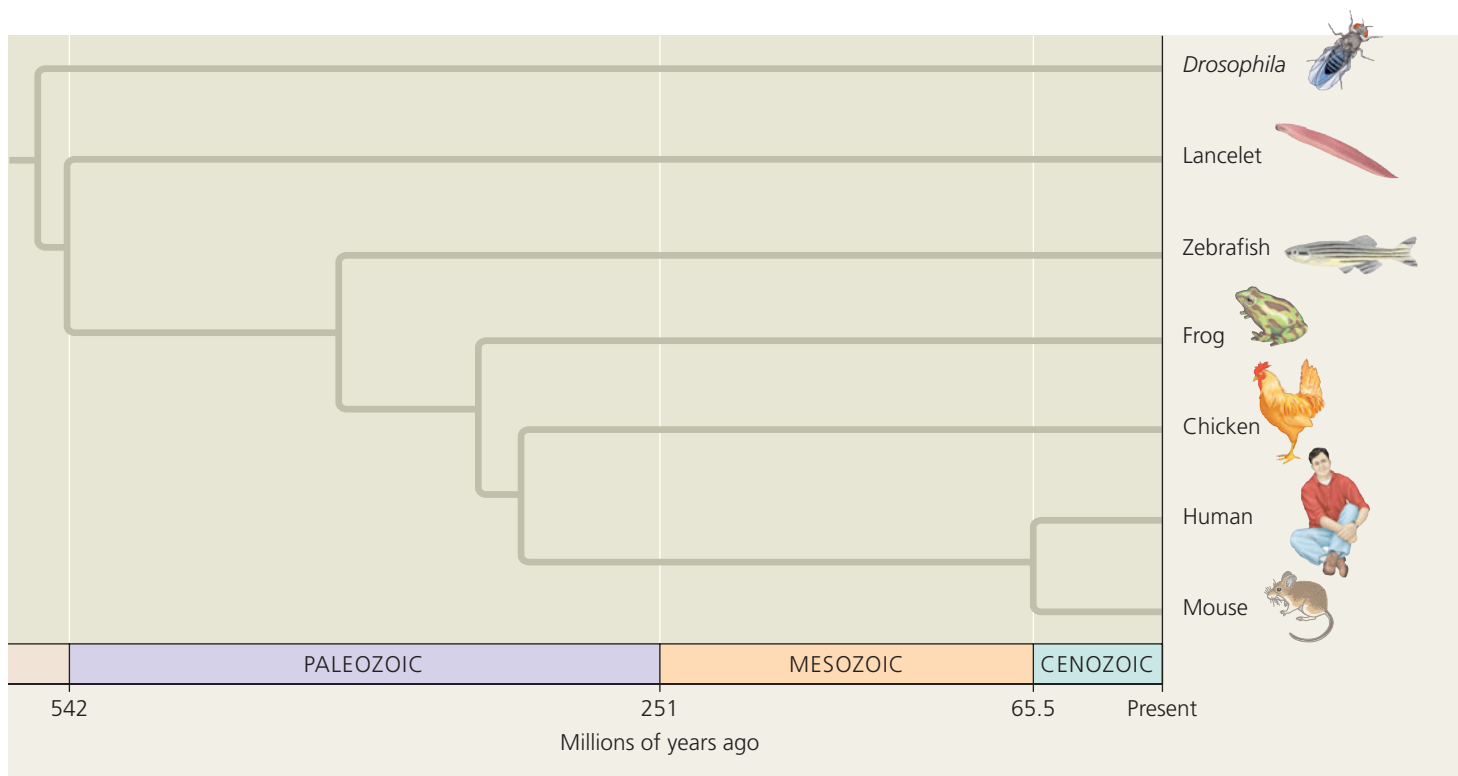
**DRAW IT** In (b), circle the most inclusive clade for which a hinged jaw is a shared ancestral character.



for the same number of years. To take an extreme example, humans and bacteria had a common ancestor that lived over 3 billion years ago. Fossils and genetic evidence indicate that this ancestor was a single-celled prokaryote. Even though bacteria have apparently changed little in their morphology since that common ancestor, there have nonetheless been 3 billion

years of evolution in the bacterial lineage, just as there have been 3 billion years of evolution in the lineage that ultimately gave rise to humans.

These equal spans of chronological time can be represented in a phylogenetic tree whose branch lengths are proportional to time (**Figure 20.13**). Such a tree draws on fossil data to place





## Applying Parsimony to a Problem in Molecular Systematics

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

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



Species I

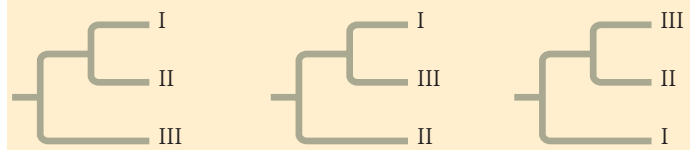


Species II



Species III

Three phylogenetic hypotheses:

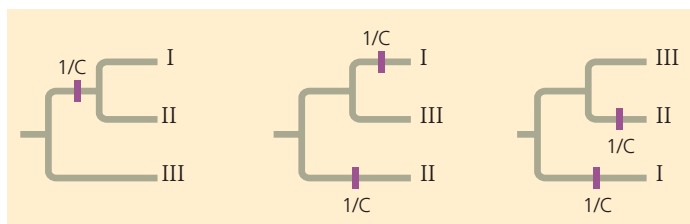


- 1 First, draw the three possible phylogenies for the species. (Although only 3 trees are possible when ordering 3 species, the number of possible trees increases rapidly with the number of species: There are 15 trees for 4 species and 34,459,425 trees for 10 species.)

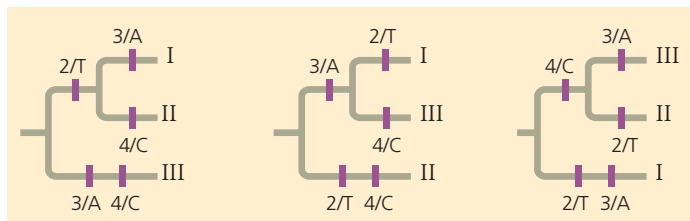
- 2 Tabulate the molecular data for the species. In this simplified example, the data represent a DNA sequence consisting of just four nucleotide bases. Data from several outgroup species (not shown) were used to infer the ancestral DNA sequence.

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

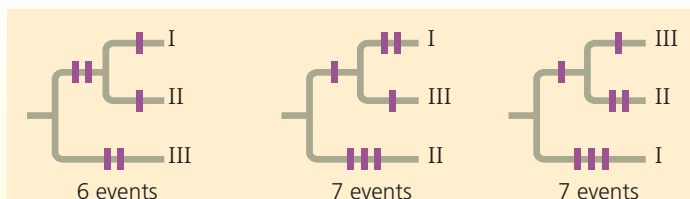
- 3 Now focus on site 1 in the DNA sequence. In the tree on the left, a single base-change event, represented by the purple hatchmark on the branch leading to species I and II (and labeled 1/C, indicating a change at site 1 to nucleotide C), is sufficient to account for the site 1 data. In the other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



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



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



branch points in the context of geologic time. Additionally, it is possible to combine these two types of trees by labeling branch points with information about rates of genetic change or dates of divergence.

## Maximum Parsimony

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

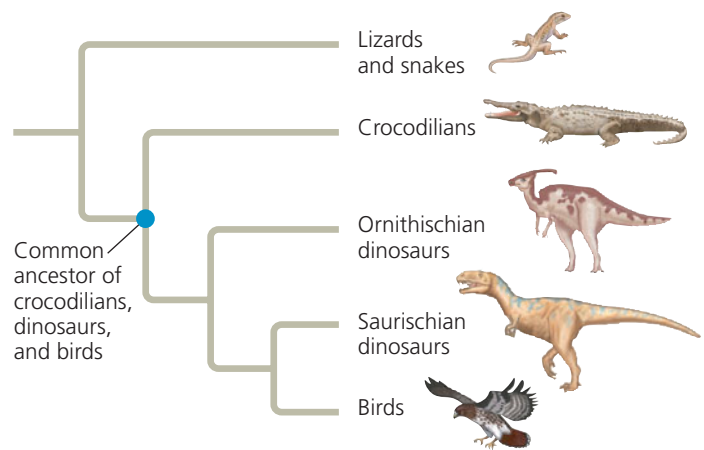
According to the principle of **maximum parsimony**, we should first investigate the simplest explanation that is consistent with the facts. (The parsimony principle is also called “Occam’s razor” after William of Occam, a 14th-century English philosopher who advocated this minimalist problem-solving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

Scientists have developed many computer programs to search for trees that are parsimonious. When a large amount of accurate data is available, the methods used in these programs usually yield similar trees. As an example of one method, **Figure 20.14** walks you through the process of identifying the most parsimonious molecular tree for a three-species problem. Computer programs use the principle of parsimony to estimate phylogenies in a similar way: They examine large numbers of possible trees and select the tree or trees that require the fewest evolutionary changes.

## Phylogenetic Trees as Hypotheses

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

Thinking of phylogenies as hypotheses also allows us to use them in a powerful way: We can make and test predictions based on the assumption that a phylogeny—our hypothesis—is correct. For example, in an approach known as *phylogenetic bracketing*, we can predict (by parsimony) that features shared by two groups of closely related organisms are present in their



▲ **Figure 20.15** A phylogenetic tree of birds and their close relatives.

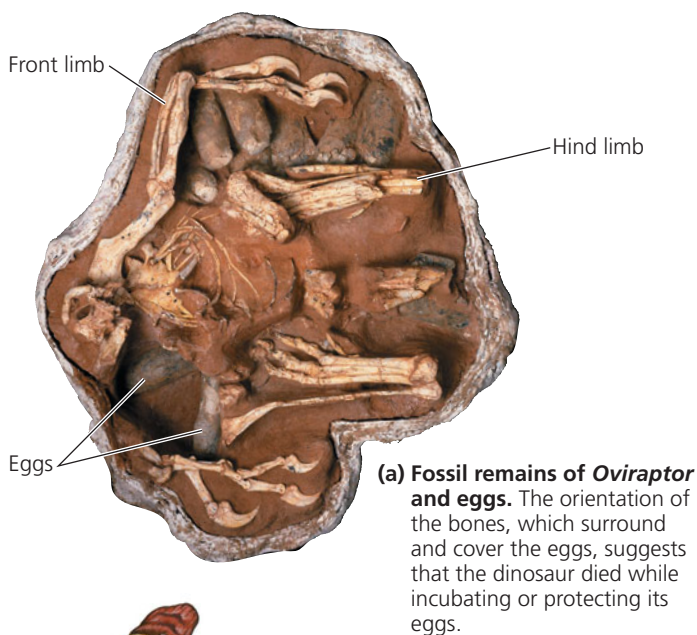
? What is the most basal taxon represented in this tree?

common ancestor and all of its descendants unless independent data indicate otherwise. (Note that “prediction” can refer to unknown past events as well as to evolutionary changes yet to occur.)

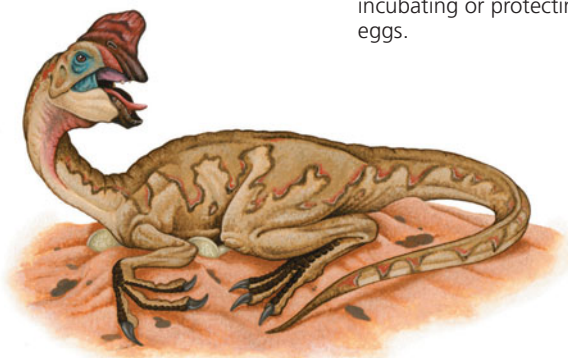
This approach has been used to make novel predictions about dinosaurs. For example, there is evidence that birds descended from the theropods, a group of bipedal saurischian dinosaurs. As seen in **Figure 20.15**, the closest living relatives of birds are crocodiles. Birds and crocodiles share numerous features: They have four-chambered hearts, they “sing” to defend territories and attract mates (although a crocodile’s “song” is more like a bellow), and they build nests (**Figure 20.16**). Both birds and crocodiles also care for their eggs by *brooding*, a behavior in which a parent warms the eggs with its body. Birds brood by sitting on their eggs, whereas crocodiles cover their eggs with their neck. Reasoning that any feature shared by birds and crocodiles is likely to have been present in their common ancestor (denoted by the blue dot in Figure 20.15) and *all* of its descendants, biologists predicted that dinosaurs had four-chambered hearts, sang, built nests, and exhibited brooding.



▲ **Figure 20.16** A crocodile guards its nest. After building its nest mound, this female African dwarf crocodile will care for the eggs until they hatch.



(a) **Fossil remains of *Oviraptor* and eggs.** The orientation of the bones, which surround and cover the eggs, suggests that the dinosaur died while incubating or protecting its eggs.



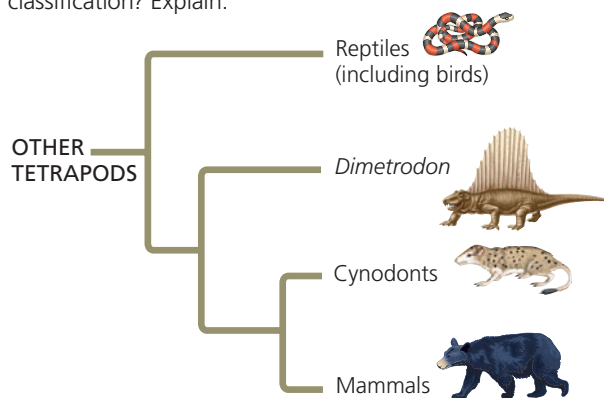
(b) **Artist's reconstruction of the dinosaur's posture based on the fossil findings.**

▲ **Figure 20.17 Fossil support for a phylogenetic prediction: Dinosaurs built nests and brooded their eggs.**

Internal organs, such as the heart, rarely fossilize, and it is, of course, difficult to test whether dinosaurs sang to defend territories and attract mates. However, fossilized dinosaur eggs and nests have provided evidence supporting the prediction of brooding in dinosaurs. First, a fossil embryo of an *Oviraptor* dinosaur was found, still inside its egg. This egg was identical to those found in another fossil, one that showed an adult *Oviraptor* crouching over a group of eggs in a posture similar to that seen in brooding birds today (Figure 20.17). Researchers suggested that the *Oviraptor* dinosaur preserved in this second fossil died while incubating or protecting its eggs. The broader conclusion that emerged from this work—that dinosaurs built nests and exhibited brooding—has since been strengthened by additional fossil discoveries that show that other species of dinosaurs built nests and sat on their eggs. Finally, by supporting predictions based on the phylogenetic hypothesis shown in Figure 20.15, fossil discoveries of nests and brooding in dinosaurs provide independent data that suggest that the hypothesis is correct.

### CONCEPT CHECK 20.3

1. To distinguish a particular clade of mammals within the larger clade that corresponds to class Mammalia, would hair be a useful character? Why or why not?
2. The most parsimonious tree of evolutionary relationships can be inaccurate. How can this occur?
3. **WHAT IF?** Draw a phylogenetic tree that includes the relationships from Figure 20.15 and those shown here. Traditionally, all the taxa shown besides birds and mammals were classified as reptiles. Would a cladistic approach support that classification? Explain.



For suggested answers, see Appendix A.

## CONCEPT 20.4

### Molecular clocks help track evolutionary time

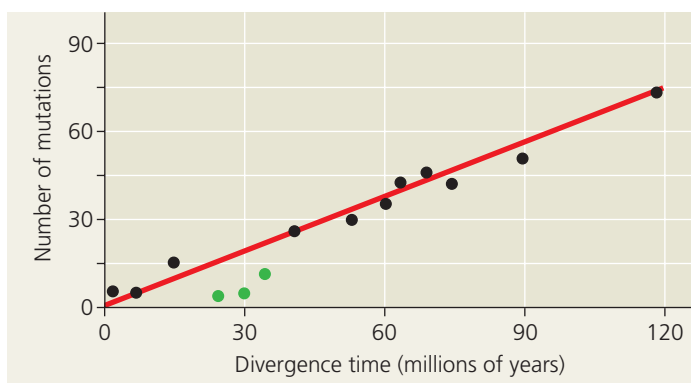
One goal of evolutionary biology is to understand the relationships among all organisms, including those for which there is no fossil record. However, if we attempt to determine the timing of phylogenies that extend beyond the fossil record, we must rely on an important assumption about how change occurs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

#### Molecular Clocks

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

We can calibrate the molecular clock of a gene that has a reliable average rate of evolution by graphing the number of genetic differences—for example, nucleotide, codon, or amino acid differences—against the dates of evolutionary branch





▲ **Figure 20.18 A molecular clock for mammals.** The number of accumulated mutations in seven proteins has increased over time in a consistent manner for most mammal species. The three green data points represent primate species, whose proteins appear to have evolved more slowly than those of other mammals. The divergence time for each data point was based on fossil evidence.

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

points that are known from the fossil record (**Figure 20.18**). The average rates of genetic change inferred from such graphs can then be used to estimate the dates of events that cannot be discerned from the fossil record, such as the origin of the silverswords discussed earlier.

Of course, no gene marks time with complete precision. In fact, some portions of the genome appear to have evolved in irregular bursts that are not at all clocklike. And even those genes that seem to act as reliable molecular clocks are accurate only in the statistical sense of showing a fairly smooth *average* rate of change. Over time, there may still be deviations from that average rate. Furthermore, the same gene may evolve at different rates in different groups of organisms. Finally, when comparing genes that are clocklike, the rate of the clock may vary greatly from one gene to another; some genes evolve a million times faster than others.

### Differences in Clock Speed

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

### Potential Problems with Molecular Clocks

In fact, molecular clocks do not run as smoothly as expected if the underlying mutations were selectively neutral. Many irregularities are likely to be the result of natural selection in which certain DNA changes are favored over others. Indeed, evidence suggests that almost half the amino acid differences in proteins of two *Drosophila* species, *D. simulans* and *D. yakuba*, are not neutral but have resulted from natural selection. But because the direction of natural selection may change repeatedly over long periods of time (and hence may average out), some genes experiencing selection can nevertheless serve as approximate markers of elapsed time.

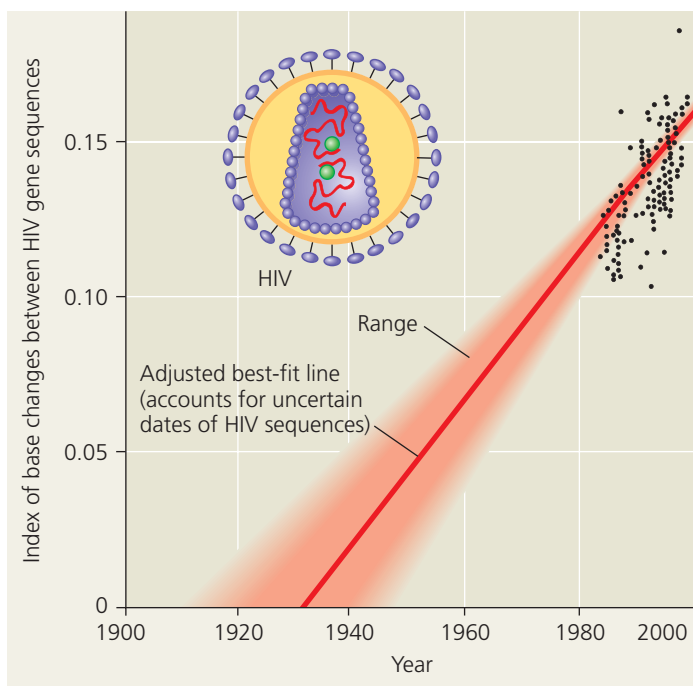
Another question arises when researchers attempt to extend molecular clocks beyond the time span documented by the fossil record. Although some fossils are more than 3 billion years old, these are very rare. An abundant fossil record extends back only about 550 million years, but molecular clocks have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

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

### Applying a Molecular Clock: Dating the Origin of HIV

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

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



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**▲ Figure 20.19 Dating the origin of HIV-1 M.** The black data points are based on DNA sequences of an HIV gene in patients' blood samples. (The dates when these individual HIV gene sequences arose are not certain because a person can harbor the virus for years before symptoms occur.) Projecting the gene's rate of change in the 1980s and 1990s backward in time suggests that the virus originated in the 1930s.

sequences showed that the virus has evolved in a clocklike fashion (**Figure 20.19**). Extrapolating backward in time using the molecular clock indicates that the HIV-1 M strain first spread to humans during the 1930s.

Despite their limitations, molecular clocks can be a useful tool for biologists trying to reconstruct phylogenies. As with data from any other source, researchers must re-evaluate their hypotheses when molecular clocks provide new information—and this process sometimes leads to significant changes.

#### CONCEPT CHECK 20.4

1. What is a molecular clock? What assumption underlies the use of a molecular clock?
2. **MAKE CONNECTIONS** Review Concept 14.5. Explain how numerous base changes could occur in an organism's DNA yet have no effect on its fitness.
3. **WHAT IF?** Suppose a molecular clock dates the divergence of two taxa at 80 million years ago, but new fossil evidence shows that the taxa diverged at least 120 million years ago. Explain how this could happen.

For suggested answers, see Appendix A.

## Scientific Skills Exercise

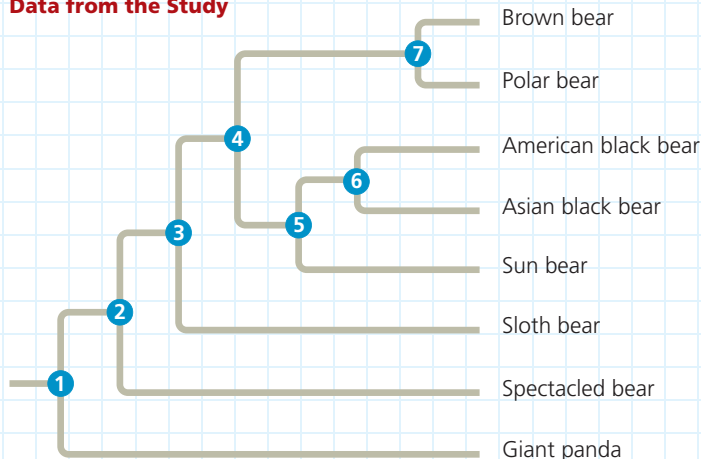
### Interpreting Data in a Phylogenetic Tree

#### What Are the Evolutionary Relationships among Bears?

Researchers have long debated different hypotheses for the phylogeny and classification of species in the bear family, Ursidae. In this exercise, you will interpret the results of one study using DNA sequence data to infer relationships among living bear species.

**How the Study Was Done** In 2008, researchers obtained complete mitochondrial DNA (mtDNA) genome sequences for the eight living species of bears. The mtDNA sequences were aligned and compared using maximum parsimony and other methods. The researchers then constructed the phylogenetic tree shown below.

#### Data from the Study



#### Interpret the Data

1. First, practice reading phylogenetic relationships from the tree. Which number represents the most recent common ancestor of (a) all bears, (b) sloth bears and spectacled bears, and (c) the Asian black bear and the brown bear?
2. Is this phylogenetic tree rooted? Explain.
3. According to the data represented in this tree, is the sun bear more closely related to the sloth bear or the polar bear? Explain.
4. Which species is a basal taxon among the bears? What does this mean about its evolution compared with that of the others?

In a study published in 2000, researchers sequenced part of the mitochondrial cytochrome *b* gene from 61 brown bears; 31 of these bears were from coastal mainland Alaska, while the rest were from the ABC islands in southeastern Alaska. Mainland and ABC brown bears differ by 11 fixed nucleotide substitutions in the cytochrome *b* gene. The researchers compared the sequences of the brown bears with those of 55 polar bears. They found that polar bears and ABC brown bears differ at only three nucleotides in this gene, whereas polar bears and mainland brown bears had more differences.

5. (a) Do the results from the 2000 study indicate that brown bears are monophyletic, paraphyletic, or polyphyletic? Explain. (b) Redraw the tree to reflect the hypothesis supported by the 2000 study, and circle the sister taxon of polar bears.
6. Describe in words how the two trees differ.

**Data from** J. Krause et al., Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary, *BMC Evolutionary Biology* 8: 220 (2008).

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

## CONCEPT 20.5

### New information continues to revise our understanding of evolutionary history

The discovery that the glass lizard in Figure 20.1 evolved from a different lineage of legless lizards than did snakes is one example of how our understanding of life's diversity is affected by systematics. The **Scientific Skills Exercise** describes another example and gives you an opportunity to interpret phylogenetic data from bear species. Indeed, in recent decades, systematists have gained insight into even the very deepest branches of the tree of life by analyzing DNA sequence data.

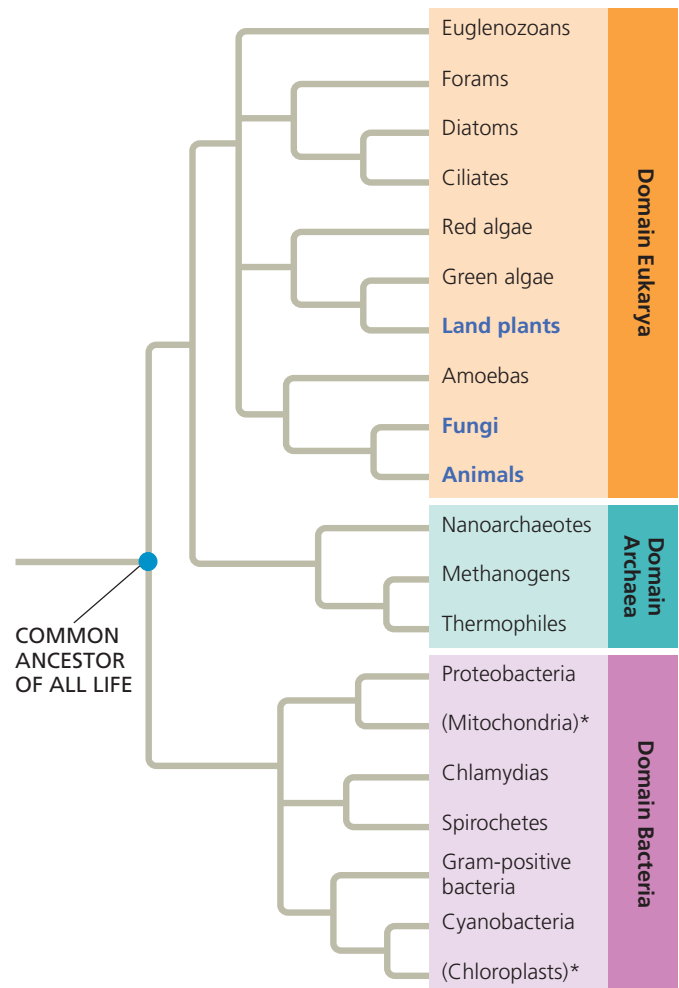
#### From Two Kingdoms to Three Domains

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

However, phylogenies based on genetic data soon began to reveal a problem with this system: Some prokaryotes differ as much from each other as they do from eukaryotes. Such difficulties have led biologists to adopt a three-domain system (Figure 20.20). The three domains—Bacteria, Archaea, and Eukarya—are a taxonomic level higher than the kingdom level. The validity of these domains is supported by many studies, including a recent study that analyzed nearly 100 completely sequenced genomes.

The domain Bacteria contains most of the currently known prokaryotes, while the domain Archaea consists of a diverse group of prokaryotic organisms that inhabit a wide variety of environments. The domain Eukarya consists of all the organisms that have cells containing true nuclei. This domain includes many groups of single-celled organisms as well as multicellular plants, fungi, and animals. Figure 20.20 represents one possible phylogenetic tree for the three domains and the many lineages they encompass.

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



**▲ Figure 20.20 The three domains of life.** This phylogenetic tree is based on sequence data for rRNA and other genes. For simplicity, only some of the major branches in each domain are shown. The lineages within Eukarya that are dominated by multicellular organisms (plants, fungi, and animals) are indicated by blue type. The two lineages denoted by an asterisk are based on DNA from cellular organelles. All other lineages consist solely or mainly of single-celled organisms.

**MAKE CONNECTIONS** After reviewing endosymbiont theory (see Figure 4.16), explain the specific positions of the mitochondrion and chloroplast lineages on this tree.

have members in two different domains. The kingdom Protista has also crumbled because it includes members that are more closely related to plants, fungi, or animals than to other protists (see Chapter 25).

#### The Important Role of Horizontal Gene Transfer

In the phylogeny shown in Figure 20.20, the first major split in the history of life occurred when bacteria diverged from other organisms. If this tree is correct, eukaryotes and archaea are more closely related to each other than either is to bacteria.

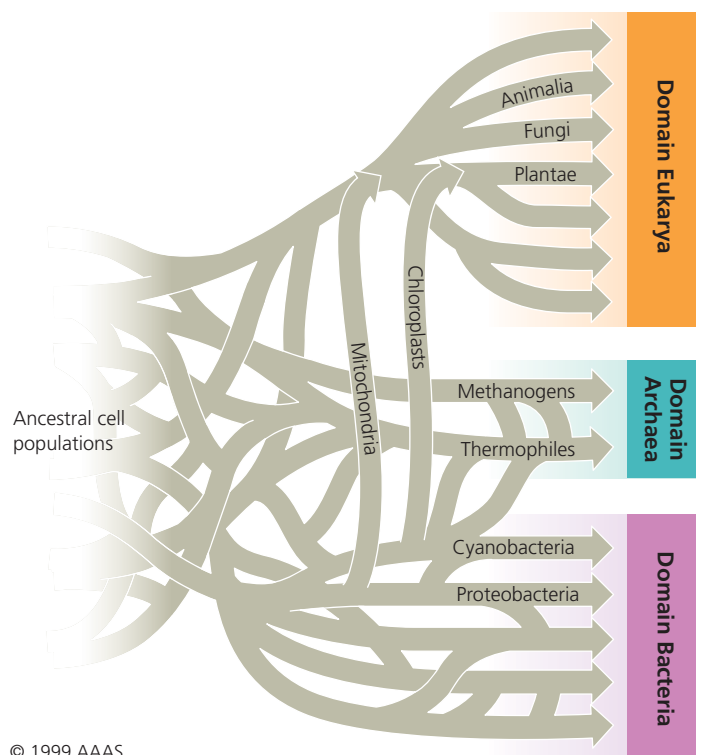
This reconstruction of the tree of life is based largely on sequence comparisons of rRNA genes, which code for the



RNA components of ribosomes. Because ribosomes are fundamental to the workings of the cell, rRNA genes have evolved so slowly that homologies between distantly related organisms can still be detected, making these genes very useful for determining evolutionary relationships between deep branches in the history of life. However, other genes reveal a different set of relationships. For example, researchers have found that many of the genes that influence metabolism in yeast (a unicellular eukaryote) are more similar to genes in the domain Bacteria than they are to genes in the domain Archaea—a finding that suggests that the eukaryotes may share a more recent common ancestor with bacteria than with archaea. As we'll discuss in Chapter 25, these conflicting results may reflect how eukaryotes originated: as a “fusion” between two prokaryotes, one of which was a bacterium and the other an archaean.

Comparisons of complete genomes from the three domains show that there have been substantial movements of genes between organisms in the different domains. These took place through **horizontal gene transfer**, a process in which genes are transferred from one genome to another through mechanisms such as exchange of transposable elements and plasmids, viral infection (see Chapter 17), and perhaps fusions of organisms. Recent research reinforces the view that horizontal gene transfer is important. For example, a 2008 analysis indicated that, on average, 80% of the genes in 181 prokaryotic genomes had moved between species at some point during the course of evolution. Because phylogenetic trees are based on the assumption that genes are passed vertically from one generation to the next, the occurrence of such horizontal transfer events helps to explain why trees built using different genes can give inconsistent results.

Horizontal gene transfer has played a key role throughout the evolutionary history of life, and it continues to occur today. Some biologists have argued that horizontal gene transfer is so common that the early history of life should be represented not as a dichotomously branching tree like that in Figure 20.20, but rather as a tangled network of connected branches (**Figure 20.21**). Although scientists continue to debate whether early steps in the history of life are best represented as a tree or a tangled web, in recent decades there have been many exciting discoveries about evolutionary events that



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▲ **Figure 20.21 A tangled web of life.** Horizontal gene transfer may have been so common in the early history of life that the base of a “tree of life” might be more accurately portrayed as a tangled web.

occurred later in time. We’ll explore the mechanisms that underlie such events in the rest of this unit’s chapters, beginning with factors that cause genetic change in populations.

#### CONCEPT CHECK 20.5

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

For suggested answers, see Appendix A.

## 20 Chapter Review

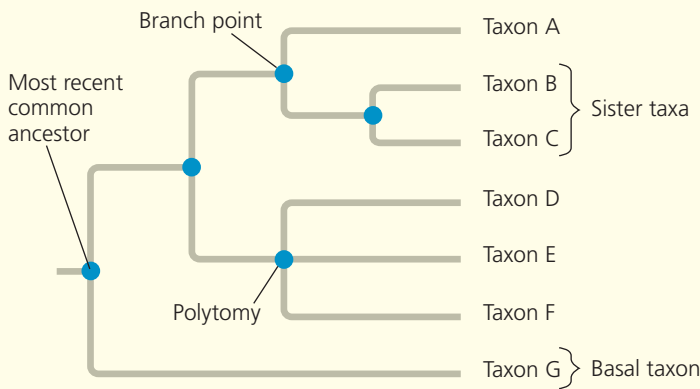
### SUMMARY OF KEY CONCEPTS

#### CONCEPT 20.1

**Phylogenies show evolutionary relationships**  
(pp. 382–385)

- Linnaeus’s **binomial** classification system gives organisms two-part names: a **genus** plus a specific epithet.

- In the Linnaean system, species are grouped into increasingly broad taxa: Related genera are placed into the same family, families into orders, orders into classes, classes into phyla, phyla into kingdoms, and (more recently) kingdoms into domains.
- Systematists depict evolutionary relationships as branching **phylogenetic trees**. Many systematists propose that classification be based entirely on evolutionary relationships.



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

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

## CONCEPT 20.2

### Phylogenies are inferred from morphological and molecular data (pp. 385–387)

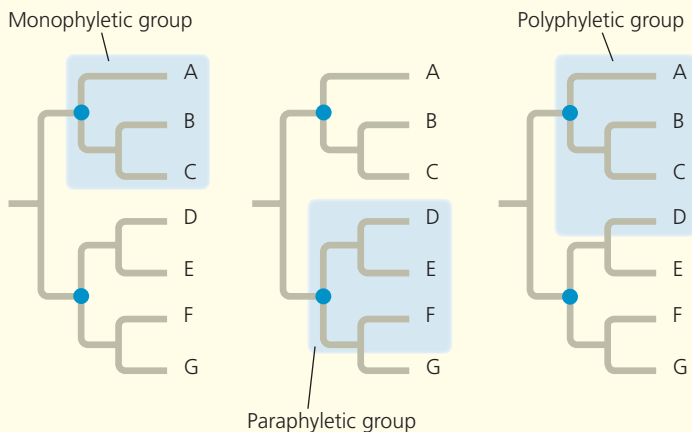
- Organisms with similar morphologies or DNA sequences are likely to be more closely related than organisms with very different structures and genetic sequences.
- To infer phylogeny, **homology** (similarity due to shared ancestry) must be distinguished from **analogy** (similarity due to convergent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

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

## CONCEPT 20.3

### Shared characters are used to construct phylogenetic trees (pp. 387–392)

- A **clade** is a monophyletic grouping that includes an ancestral species and all of its descendants.
- Clades can be distinguished by their **shared derived characters**.



- Branch lengths can be proportional to amount of evolutionary change or time.

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

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

## CONCEPT 20.4

### Molecular clocks help track evolutionary time (pp. 392–394)

- Some regions of DNA change at a rate consistent enough to serve as a **molecular clock**, in which the amount of genetic change is used to estimate the date of past evolutionary events. Other DNA regions change in a less predictable way.
- A molecular clock analysis suggests that the most common strain of HIV jumped from primates to humans in the 1930s.

? *Describe some assumptions and limitations of molecular clocks.*

## CONCEPT 20.5

### New information continues to revise our understanding of evolutionary history (pp. 394–396)

- Past classification systems have given way to the current view of the tree of life, which consists of three great **domains**: Bacteria, Archaea, and Eukarya.
- Phylogenies based on rRNA genes suggest that eukaryotes are most closely related to archaea, while data from some other genes suggest a closer relationship to bacteria.
- Genetic analyses indicate that extensive horizontal gene transfer has occurred throughout the evolutionary history of life.

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

## TEST YOUR UNDERSTANDING

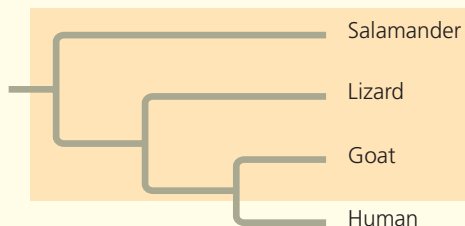
### Level 1: Knowledge/Comprehension

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

### Level 2: Application/Analysis

- In Figure 20.4, which similarly inclusive taxon descended from the same common ancestor as Canidae?
  - Felidae
  - Mustelidae
  - Carnivora
  - Canis
  - Lutra

4. Three living species X, Y, and Z share a common ancestor T, as do extinct species U and V. A grouping that consists of species T, X, Y, and Z (but not U or V) makes up
- a monophyletic taxon.
  - a clade.
  - an ingroup, with species U as the outgroup.
  - a paraphyletic group.
  - a polyphyletic group.
5. Based on the tree below, which statement is *not* correct?



- The salamander lineage is a basal taxon.
  - Salamanders are a sister group to the group containing lizards, goats, and humans.
  - Salamanders are as closely related to goats as to humans.
  - Lizards are more closely related to salamanders than to humans.
  - The group highlighted by shading is paraphyletic.
6. If you were using cladistics to build a phylogenetic tree of cats, which of the following would be the best outgroup?
- lion
  - domestic cat
  - wolf
  - leopard
  - tiger
7. The relative lengths of the frog and mouse branches in the phylogenetic tree in Figure 20.12 indicate that
- frogs evolved before mice.
  - mice evolved before frogs.
  - the genes of frogs and mice have only coincidental homoplasies.
  - the homolog has evolved more slowly in mice.
  - the homolog has evolved more rapidly in mice.

### Level 3: Synthesis/Evaluation

#### 8. SCIENTIFIC INQUIRY

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

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

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

#### 9. FOCUS ON EVOLUTION

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

#### 10. FOCUS ON INFORMATION

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

For selected answers, see Appendix A.

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# 21

## The Evolution of Populations

### KEY CONCEPTS

- 21.1** Genetic variation makes evolution possible
- 21.2** The Hardy-Weinberg equation can be used to test whether a population is evolving
- 21.3** Natural selection, genetic drift, and gene flow can alter allele frequencies in a population
- 21.4** Natural selection is the only mechanism that consistently causes adaptive evolution

### OVERVIEW

## The Smallest Unit of Evolution

One common misconception about evolution is that individual organisms evolve. It is true that natural selection acts on individuals: Each organism's traits affect its survival and reproductive success compared with that of other individuals. But the evolutionary impact of natural selection is only apparent in the changes in a *population* of organisms over time.

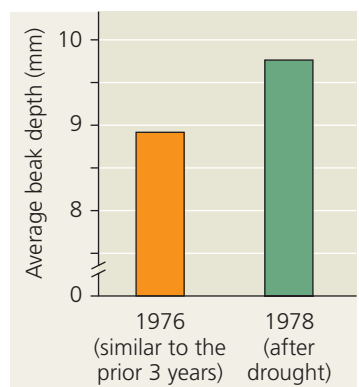
Consider the medium ground finch (*Geospiza fortis*), a seed-eating bird that inhabits the Galápagos Islands (**Figure 21.1**). In 1977, the *G. fortis* population on the island of Daphne Major was decimated by a long period of drought: Of some 1,200 birds, only 180 survived. Researchers Peter and Rosemary Grant observed that during the drought, small, soft seeds were in short supply. The finches mostly fed on large, hard seeds that were more plentiful. Birds with larger, deeper beaks were better able to crack and eat these larger seeds, and they survived at a higher rate than finches with smaller beaks. Since beak depth is an inherited trait in these birds, the average beak depth in the next generation of *G. fortis* was greater than it had been in the pre-drought population (**Figure 21.2**). The finch population had evolved by natural selection. However, the *individual* finches did not evolve. Each bird had a beak of a particular size, which did not grow larger during the drought. Rather, the proportion of large beaks in the population increased from generation to generation: The population evolved, not its individual members.

▼ **Figure 21.1** Is this finch evolving?



► **Figure 21.2 Evidence of selection by food source.** The data represent adult beak depth measurements of medium ground finches hatched in the generations before and after the 1977 drought. In a single generation, evolution by natural selection resulted in a larger average beak size in the population.

 A related Experimental Inquiry Tutorial can be assigned in MasteringBiology.



Focusing on evolutionary change in populations, we can define evolution on its smallest scale, called **microevolution**, as a change in allele frequencies in a population over generations. As you will see in this chapter, natural selection is not the only cause of microevolution. In fact, there are three main mechanisms that can cause allele frequency change: natural selection, genetic drift (chance events that alter allele frequencies), and gene flow (the transfer of alleles between populations). Each of these mechanisms has distinctive effects on the genetic composition of populations. However, only natural selection consistently improves the match between organisms and their environment (adaptation). Before we examine natural selection and adaptation more closely, let's revisit a prerequisite for these processes in a population: genetic variation.

## CONCEPT 21.1

### Genetic variation makes evolution possible

In *The Origin of Species*, Darwin provided abundant evidence that life on Earth has evolved over time, and he proposed natural selection as the primary mechanism for that change. He observed that individuals differ in their inherited traits and that selection acts on such differences, leading to evolutionary change. Although Darwin realized that variation in heritable traits is a prerequisite for evolution, he did not know precisely how organisms pass heritable traits to their offspring.

Just a few years after Darwin published *The Origin of Species*, Gregor Mendel wrote a groundbreaking paper on inheritance in pea plants (see Chapter 11). In that paper, Mendel proposed a model of inheritance in which organisms transmit discrete heritable units (now called genes) to their offspring. Although Darwin did not know about genes, Mendel's paper set the stage for understanding the genetic differences on which evolution is based. Here we'll examine such genetic differences and how they are produced.

### Genetic Variation

Individuals within a species vary in their specific characteristics. Among humans, you can easily observe phenotypic variation in facial features, height, and voice. And though you cannot identify a person's blood group (A, B, AB, or O) from his or her appearance, this and many other molecular traits also vary extensively among individuals.

Such phenotypic variations often reflect **genetic variation**, differences among individuals in the composition of their genes or other DNA sequences. Some heritable phenotypic differences occur on an "either-or" basis, such as the flower colors of Mendel's pea plants: Each plant had flowers that were either purple or white (see Figure 11.3). Characters that vary in this



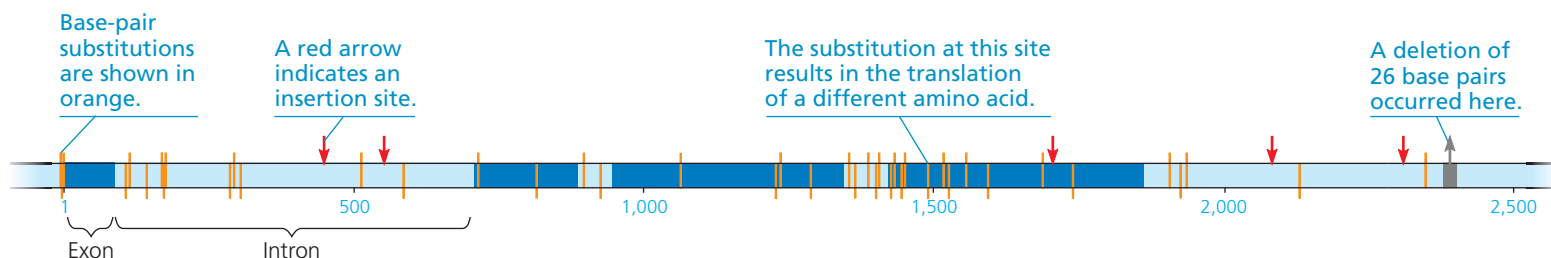
▲ **Figure 21.3 Phenotypic variation in horses.** In horses, coat color varies along a continuum and is influenced by multiple genes.

way are typically determined by a single gene locus, with different alleles producing distinct phenotypes. In contrast, other phenotypic differences vary in gradations along a continuum. Such variation usually results from the influence of two or more genes on a single phenotypic character. In fact, many phenotypic characters are influenced by multiple genes, including coat color in horses (**Figure 21.3**), seed number in maize (corn), and height in humans.

How much do genes and other DNA sequences vary from one individual to another? Genetic variation at the whole-gene level (*gene variability*) can be quantified as the average percentage of loci that are heterozygous. (Recall that a heterozygous individual has two different alleles for a given locus, whereas a homozygous individual has two identical alleles for that locus.) As an example, on average the fruit fly *Drosophila melanogaster* is heterozygous for about 1,920 of its 13,700 loci (14%) and homozygous for all the rest.

Considerable genetic variation can also be measured at the molecular level of DNA (*nucleotide variability*). But little of this variation results in phenotypic variation because many of the differences occur within *introns*, noncoding segments of DNA lying between *exons*, the regions retained in mRNA after RNA processing (see Figure 14.12). And of the variations that occur within exons, most do not cause a change in the amino acid sequence of the protein encoded by the gene. In the sequence comparison summarized in **Figure 21.4**, there are 43 nucleotide sites with variable base pairs (where substitutions have occurred), as well as several sites where insertions or deletions have occurred. Although 18 variable sites occur within the four exons of the *Adh* gene, only one of these variations—at site 1,490—results in an amino acid change. Note, however, that this single variable site is enough to cause genetic variation at the level of the gene, and two different forms of the *Adh* enzyme are produced.





▲ **Figure 21.4 Extensive genetic variation at the molecular level.** This diagram summarizes data from a study comparing the DNA sequence of the alcohol dehydrogenase (*Adh*) gene in several fruit flies (*Drosophila melanogaster*). The *Adh* gene has four exons (dark blue) separated by introns (light blue); the exons include the coding regions that are ultimately translated into the amino acids of the *Adh* enzyme. Only one substitution has a phenotypic effect, producing a different form of the *Adh* enzyme.

**MAKE CONNECTIONS** Review Figures 14.6 and 14.12. Explain how a base-pair substitution that alters a coding region of the *Adh* locus could have no effect on amino acid sequence. Then explain how an insertion in an exon could have no effect on the protein produced.

It is important to bear in mind that some phenotypic variation is not heritable (Figure 21.5 shows a striking example in a caterpillar of the southwestern United States). Phenotype is the product of an inherited genotype and many environmental influences (see Concept 11.3). In a human example, bodybuilders alter their phenotypes dramatically but do not pass their huge muscles on to the next generation. In general, only the genetically determined part of phenotypic variation can have evolutionary consequences. As such, genetic variation provides the raw material for evolutionary change: Without genetic variation, evolution cannot occur.

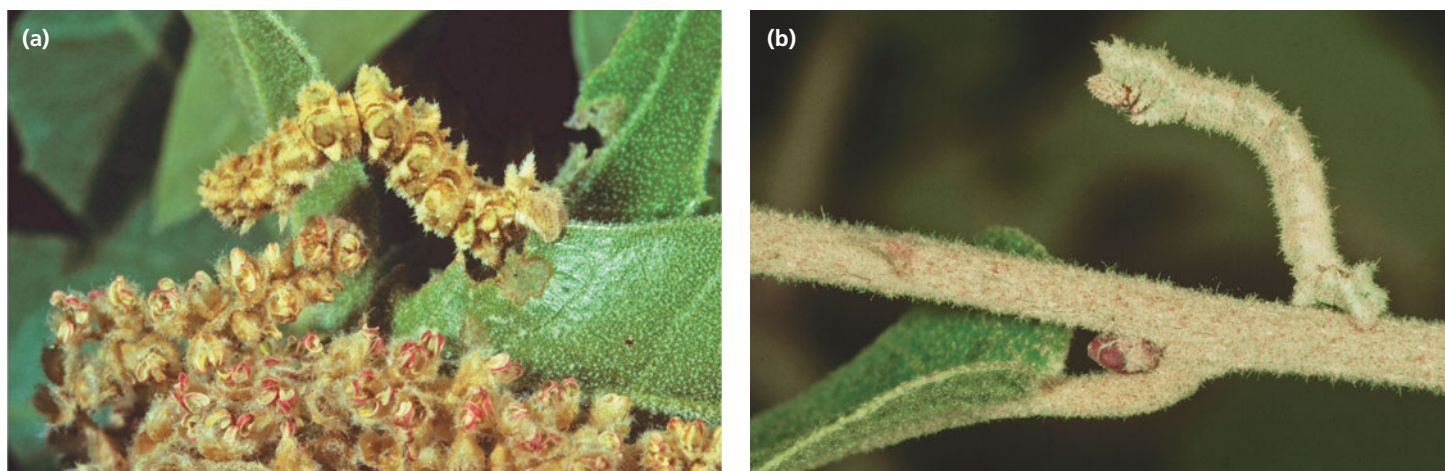
## Sources of Genetic Variation

The genetic variation on which evolution depends originates when mutation, gene duplication, or other processes produce new alleles and new genes. Genetic variants can be produced in short periods of time in organisms that reproduce rapidly. Sexual reproduction can also result in genetic variation as existing genes are arranged in new ways.

## Formation of New Alleles

New alleles can arise by *mutation*, a change in the nucleotide sequence of an organism's DNA. A mutation is like a shot in the dark—we cannot predict accurately which segments of DNA will be altered or in what way. In multicellular organisms, only mutations in cell lines that produce gametes can be passed to offspring. In plants and fungi, this is not as limiting as it may sound, since many different cell lines can produce gametes. But in most animals, the majority of mutations occur in somatic cells and are lost when the individual dies.

A change of as little as one base in a gene, called a “point mutation,” can have a significant impact on phenotype, as in sickle-cell disease (see Figure 14.25). Organisms reflect many generations of past selection, and hence their phenotypes tend to be well matched to their environments. As a result, it's unlikely that a new mutation that alters a phenotype will improve it. In fact, most such mutations are at least slightly harmful. But since much of the DNA in eukaryotic genomes does not code for protein products, point mutations in these noncoding



▲ **Figure 21.5 Nonheritable variation.** These caterpillars of the moth *Nemoria arizonaria* owe their different appearances to chemicals in their diets, not to differences in their genotypes. (a) Caterpillars raised on a diet of oak flowers resemble the flowers, whereas (b) their siblings raised on oak leaves resemble oak twigs.



regions are generally harmless. Also, because of the redundancy in the genetic code, even a point mutation in a gene that encodes a protein will have no effect on the protein's function if the amino acid composition is not changed. And even where there is a change in the amino acid, it may not affect the protein's shape and function. However, as you will see later in this chapter, a mutant allele may on rare occasions actually make its bearer better suited to the environment, enhancing reproductive success.

### **Altering Gene Number or Position**

Chromosomal changes that delete, disrupt, or rearrange many loci at once are usually harmful. However, when such large-scale changes leave genes intact, they may not affect the organisms' phenotypes. In rare cases, chromosomal rearrangements may even be beneficial. For example, the translocation of part of one chromosome to a different chromosome could link DNA segments in a way that produces a positive effect.

A key potential source of variation is the duplication of genes due to errors in meiosis (such as unequal crossing over), slippage during DNA replication, or the activities of transposable elements (see Concept 18.4). Duplications of large chromosome segments, like other chromosomal aberrations, are often harmful, but the duplication of smaller pieces of DNA may not be. Gene duplications that do not have severe effects can persist over generations, allowing mutations to accumulate. The result is an expanded genome with new genes that may take on new functions.

Such increases in gene number appear to have played a major role in evolution. For example, the remote ancestors of mammals had a single gene for detecting odors that has since been duplicated many times: Humans today have about 350 functional olfactory receptor genes, and mice have 1,000. This proliferation of olfactory genes probably helped mammals over the course of evolution, enabling them to detect faint odors and to distinguish among many different smells.

### **Rapid Reproduction**

Mutation rates tend to be low in plants and animals, averaging about one mutation in every 100,000 genes per generation, and they are often even lower in prokaryotes. But prokaryotes have many more generations per unit of time, so mutations can quickly generate genetic variation in populations of these organisms. The same is true of viruses. For instance, HIV has a generation span of about two days. It also has an RNA genome, which has a much higher mutation rate than a typical DNA genome because of the lack of RNA repair mechanisms in host cells (see Chapter 17). For this reason, it is unlikely that a single-drug treatment would ever be effective against HIV; mutant forms of the virus that are resistant to a particular drug would no doubt proliferate in relatively short order. The most effective AIDS treatments to date have been drug "cocktails" that combine several medications. It is less likely that a set of

mutations that together confer resistance to *all* the drugs will occur in a short time period.

### **Sexual Reproduction**

In organisms that reproduce sexually, most of the genetic variation in a population results from the unique combination of alleles that each individual receives from its parents. Of course, at the nucleotide level, all the differences among these alleles have originated from past mutations. Sexual reproduction then shuffles existing alleles and deals them at random to produce individual genotypes.

Three mechanisms contribute to this shuffling: crossing over, independent assortment of chromosomes, and fertilization (see Chapter 10). During meiosis, homologous chromosomes, one inherited from each parent, trade some of their alleles by crossing over. These homologous chromosomes and the alleles they carry are then distributed at random into gametes. Then, because myriad possible mating combinations exist in a population, fertilization brings together gametes that are likely to have different genetic backgrounds. The combined effects of these three mechanisms ensure that sexual reproduction rearranges existing alleles into fresh combinations each generation, providing much of the genetic variation that makes evolution possible.

#### **CONCEPT CHECK 21.1**

1. Explain why genetic variation within a population is a prerequisite for evolution.
2. Of all the mutations that occur in a population, why do only a small fraction become widespread?
3. **MAKE CONNECTIONS** If a population stopped reproducing sexually (but still reproduced asexually), how would its genetic variation be affected over time? Explain. (See Concept 10.4.)

For suggested answers, see Appendix A.

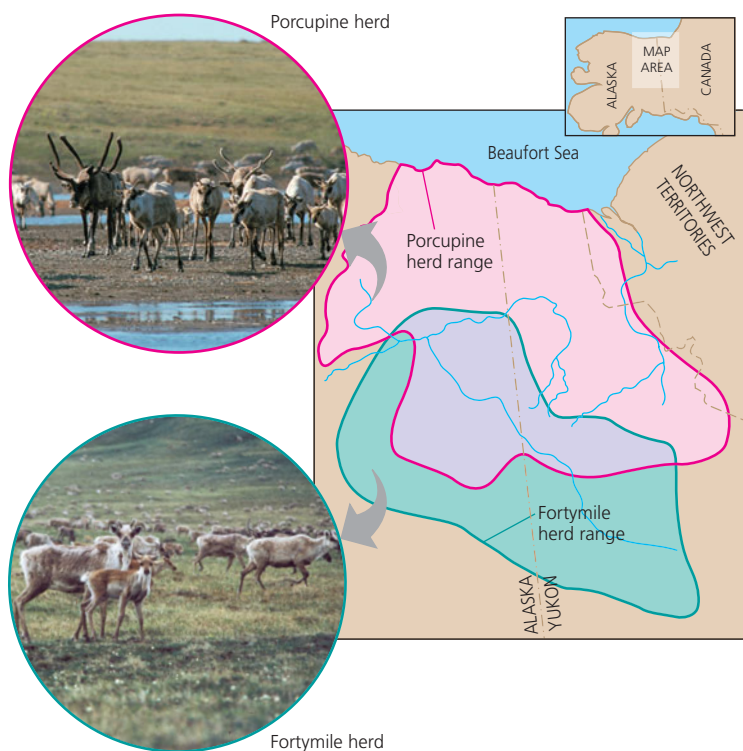
## **CONCEPT** 21.2

### **The Hardy-Weinberg equation can be used to test whether a population is evolving**

Although the individuals in a population must differ genetically for evolution to occur, the presence of genetic variation does not guarantee that a population will evolve. For that to happen, one of the factors that cause evolution must be at work. In this section, we'll explore one way to test whether evolution is occurring in a population. First, let's clarify what we mean by a population.

### **Gene Pools and Allele Frequencies**

A **population** is a group of individuals of the same species that live in the same area and interbreed, producing fertile offspring. Different populations of a single species may

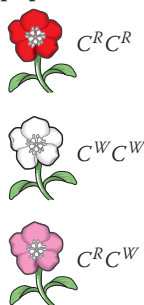


▲ **Figure 21.6 One species, two populations.** These two caribou populations in the Yukon are not totally isolated; they sometimes share the same area. Still, members of either population are most likely to breed within their own population.

be isolated geographically from one another, exchanging genetic material only rarely. Such isolation is common for species that live on widely separated islands or in different lakes. But not all populations are isolated, nor must populations have sharp boundaries (Figure 21.6). Still, members of a population typically breed with one another and thus on average are more closely related to each other than to members of other populations.

We can characterize a population's genetic makeup by describing its **gene pool**, which consists of all copies of every type of allele at every locus in all members of the population. If only one allele exists for a particular locus in a population, that allele is said to be *fixed* in the gene pool, and all individuals are homozygous for that allele. But if there are two or more alleles for a particular locus in a population, individuals may be either homozygous or heterozygous.

Each allele has a frequency (proportion) in the population. For example, imagine a population of 500 wild-flower plants with two alleles,  $C^R$  and  $C^W$ , for a locus that codes for flower pigment. These alleles show incomplete dominance (see Figure 11.10); thus, each genotype has a distinct phenotype. Plants homozygous for the  $C^R$  allele ( $C^R C^R$ ) produce red pigment and have red flowers; plants homozygous for the  $C^W$  allele ( $C^W C^W$ ) produce no red pigment and have



white flowers; and heterozygotes ( $C^R C^W$ ) produce some red pigment and have pink flowers.

In our population, suppose there are 320 plants with red flowers, 160 with pink flowers, and 20 with white flowers. Because these are diploid organisms, these 500 individuals have a total of 1,000 copies of the gene for flower color. The  $C^R$  allele accounts for 800 of these copies ( $320 \times 2 = 640$  for  $C^R C^R$  plants, plus  $160 \times 1 = 160$  for  $C^R C^W$  plants). Thus, the frequency of the  $C^R$  allele is  $800/1,000 = 0.8$  (80%).

When studying a locus with two alleles, the convention is to use  $p$  to represent the frequency of one allele and  $q$  to represent the frequency of the other allele. Thus,  $p$ , the frequency of the  $C^R$  allele in the gene pool of this population, is  $p = 0.8$  (80%). And because there are only two alleles for this gene, the frequency of the  $C^W$  allele, represented by  $q$ , must be  $q = 1 - p = 0.2$  (20%). For loci that have more than two alleles, the sum of all allele frequencies must still equal 1 (100%).

Next we'll see how allele and genotype frequencies can be used to test whether evolution is occurring in a population.

## The Hardy-Weinberg Principle

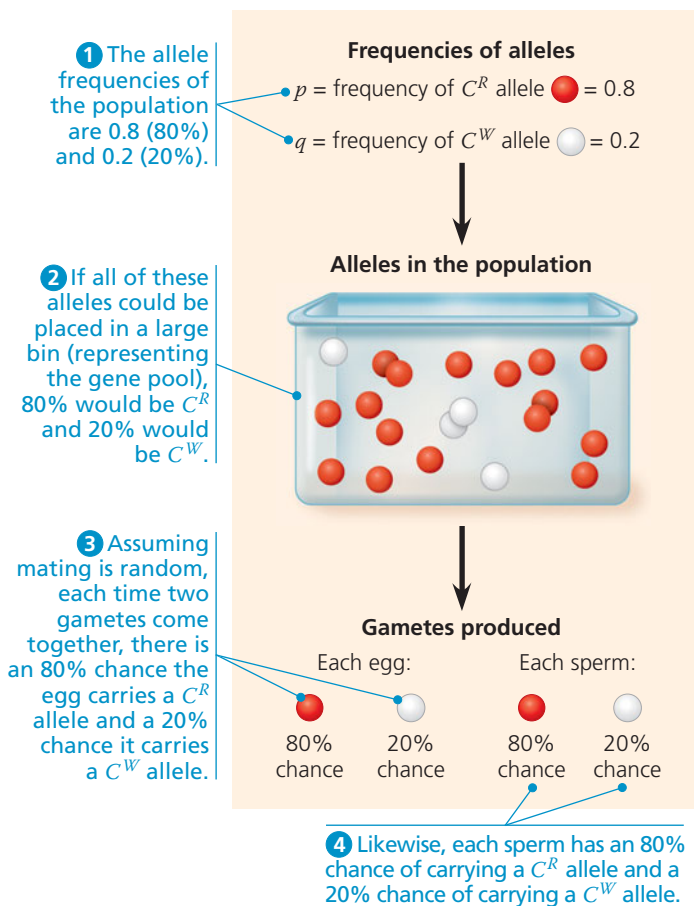
One way to assess whether natural selection or other factors are causing evolution at a particular locus is to determine what the genetic makeup of a population would be if it were *not* evolving at that locus. We can then compare that scenario with the data that we actually observe for the population. If there are no differences, we can conclude that the population is not evolving. If there are differences, this suggests that the population may be evolving—and then we can try to figure out why.

### Hardy-Weinberg Equilibrium

The gene pool of a population that is not evolving can be described by the **Hardy-Weinberg principle**, named for the British mathematician and German physician, respectively, who independently derived it in 1908. This principle states that the frequencies of alleles and genotypes in a population will remain constant from generation to generation, provided that only Mendelian segregation and recombination of alleles are at work. Such a gene pool is in *Hardy-Weinberg equilibrium*.

To use the Hardy-Weinberg principle, it is helpful to think about genetic crosses in a new way. Previously, we used Punnett squares to determine the genotypes of offspring in a genetic cross (see Figure 11.5). Here, instead of considering the possible allele combinations from one cross, we'll consider the combination of alleles in *all* of the crosses in a population.

Imagine that all the alleles for a given locus from all the individuals in a population are placed in a large bin. We can think of this bin as holding the population's gene pool for that locus. "Reproduction" occurs by selecting alleles at random from the bin; somewhat similar events occur in nature when fish release sperm and eggs into the water or when pollen (containing plant sperm) is blown about by the wind. By viewing reproduction as a process of randomly selecting and combining alleles from

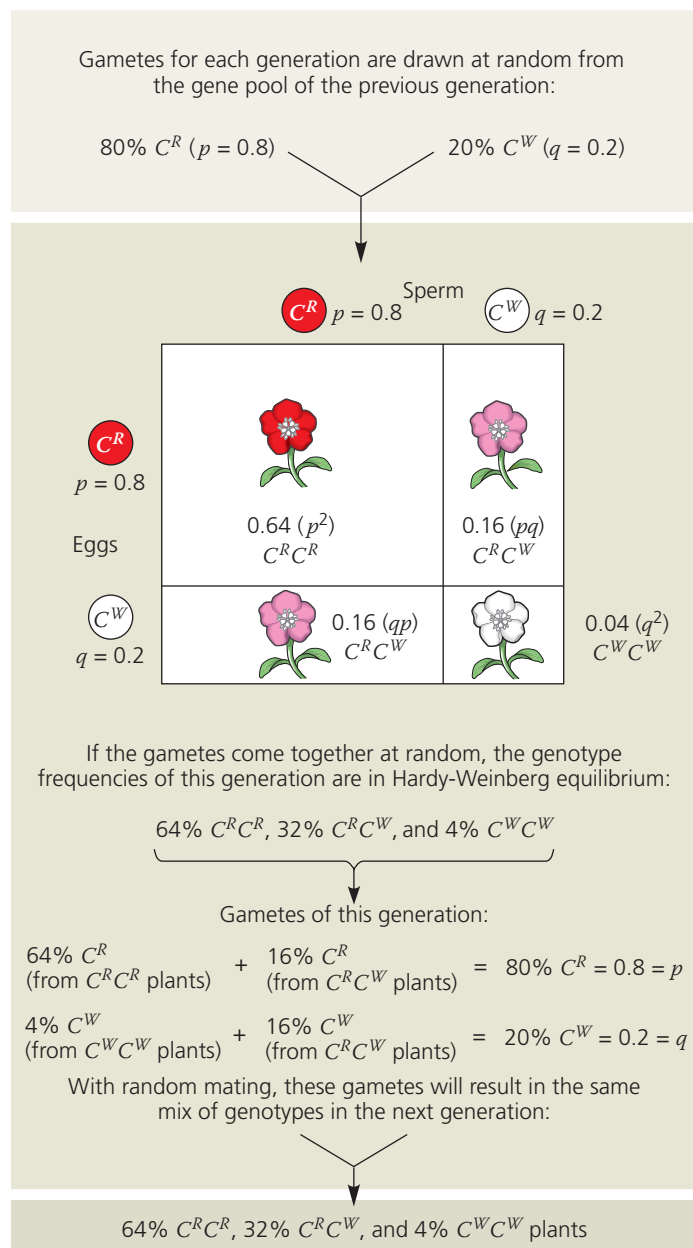


▲ **Figure 21.7** Selecting alleles at random from a gene pool.

the bin (the gene pool), we are in effect assuming that mating occurs at random—that is, that all male-female matings are equally likely.

Let's apply the bin analogy to the hypothetical wildflower population discussed earlier (**Figure 21.7**). In that population of 500 flowers, the frequency of the allele for red flowers ( $C^R$ ) is  $p = 0.8$ , and the frequency of the allele for white flowers ( $C^W$ ) is  $q = 0.2$ . In other words, a bin holding all 1,000 copies of the flower-color gene in the population would contain 800  $C^R$  alleles and 200  $C^W$  alleles. Assuming that gametes are formed by selecting alleles at random from the bin, the probability that an egg or sperm contains a  $C^R$  or  $C^W$  allele is equal to the frequency of these alleles in the bin. Thus, as shown in **Figure 21.7**, each egg has an 80% chance of containing a  $C^R$  allele and a 20% chance of containing a  $C^W$  allele; the same is true for each sperm.

Using the rule of multiplication (see **Figure 11.9**), we can now calculate the frequencies of the three possible genotypes, assuming random unions of sperm and eggs. The probability that two  $C^R$  alleles will come together is  $p \times p = p^2 = 0.8 \times 0.8 = 0.64$ . Thus, about 64% of the plants in the next generation will have the genotype  $C^R C^R$ . The frequency of  $C^W C^W$  individuals is expected to be about  $q \times q = q^2 = 0.2 \times 0.2 = 0.04$ , or 4%.  $C^R C^W$  heterozygotes can arise in two different



▲ **Figure 21.8** The Hardy-Weinberg principle. In our wildflower population, the gene pool remains constant from one generation to the next. Mendelian processes alone do not alter frequencies of alleles or genotypes.

**?** If the frequency of the  $C^R$  allele is 0.6, predict the frequencies of the  $C^R C^R$ ,  $C^R C^W$ , and  $C^W C^W$  genotypes.

ways. If the sperm provides the  $C^R$  allele and the egg provides the  $C^W$  allele, the resulting heterozygotes will be  $p \times q = 0.8 \times 0.2 = 0.16$ , or 16% of the total. If the sperm provides the  $C^W$  allele and the egg the  $C^R$  allele, the heterozygous offspring will make up  $q \times p = 0.2 \times 0.8 = 0.16$ , or 16%. The frequency of heterozygotes is thus the sum of these possibilities:  $pq + qp = 2pq = 0.16 + 0.16 = 0.32$ , or 32%.

As shown in **Figure 21.8**, the genotype frequencies in the next generation must add up to 1 (100%). Thus, the equation for Hardy-Weinberg equilibrium states that at a locus



with two alleles, the three genotypes will appear in the following proportions:

$$\begin{array}{ccccccc}
 p^2 & + & 2pq & + & q^2 & = & 1 \\
 \text{Expected} & & \text{Expected} & & \text{Expected} & & \\
 \text{frequency} & & \text{frequency} & & \text{frequency} & & \\
 \text{of genotype} & & \text{of genotype} & & \text{of genotype} & & \\
 C^R C^R & & C^R C^W & & C^W C^W & & 
 \end{array}$$

Note that for a locus with two alleles, only three genotypes are possible (in this case,  $C^R C^R$ ,  $C^R C^W$ , and  $C^W C^W$ ). As a result, the sum of the frequencies of the three genotypes must equal 1 (100%) in *any* population—regardless of whether the population is in Hardy-Weinberg equilibrium. A population is in Hardy-Weinberg equilibrium only if the genotype frequencies are such that the actual frequency of one homozygote is  $p^2$ , the actual frequency of the other homozygote is  $q^2$ , and the actual frequency of heterozygotes is  $2pq$ . Finally, as suggested by Figure 21.8, if a population such as our wildflowers is in Hardy-Weinberg equilibrium and its members continue to mate randomly generation after generation, allele and genotype frequencies will remain constant. The system operates somewhat like a deck of cards: No matter how many times the deck is reshuffled to deal out new hands, the deck itself remains the same. Aces do not grow more numerous than jacks. And the repeated shuffling of a population's gene pool over the generations cannot, in itself, change the frequency of one allele relative to another.

### Conditions for Hardy-Weinberg Equilibrium

The Hardy-Weinberg principle describes a hypothetical population that is not evolving. But in real populations, the allele and genotype frequencies often *do* change over time. Such changes can occur when at least one of the following five conditions of Hardy-Weinberg equilibrium is not met:

- 1. No mutations.** The gene pool is modified if mutations alter alleles or if entire genes are deleted or duplicated.
- 2. Random mating.** If individuals tend to mate within a subset of the population, such as their near neighbors or close relatives (inbreeding), random mixing of gametes does not occur, and genotype frequencies change.
- 3. No natural selection.** Differences in the survival and reproductive success of individuals carrying different genotypes can alter allele frequencies.
- 4. Extremely large population size.** The smaller the population, the more likely it is that allele frequencies will fluctuate by chance from one generation to the next (a process called genetic drift).
- 5. No gene flow.** By moving alleles into or out of populations, gene flow can alter allele frequencies.

Departure from these conditions usually results in evolutionary change, which, as we've already described, is common in natural populations. But it is also common for natural populations to be in Hardy-Weinberg equilibrium for specific genes. This apparent contradiction occurs because a population can be evolving at some loci, yet simultaneously be in Hardy-Weinberg equilibrium at other loci. In addition, some populations evolve so slowly that the changes in their allele and genotype frequencies are difficult to distinguish from those predicted for a nonevolving population.

### Applying the Hardy-Weinberg Principle

The Hardy-Weinberg equation is often used as an initial test of whether evolution is occurring in a population (you'll encounter an example in Concept Check 21.2, question 3). The equation also has medical applications, such as estimating the percentage of a population carrying the allele for an inherited disease. For example, consider phenylketonuria (PKU), a metabolic disorder that results from homozygosity for a recessive allele and occurs in about one out of every 10,000 babies born in the United States. Left untreated, PKU results in mental disability and other problems. (Newborns are now tested for PKU, and symptoms can be largely avoided with a diet very low in phenylalanine. For this reason, products that contain phenylalanine, such as diet colas, carry warning labels.)

To apply the Hardy-Weinberg equation, we must assume that no new PKU mutations are being introduced into the population (condition 1), and that people neither choose their mates on the basis of whether or not they carry this gene nor generally mate with close relatives (condition 2). We must also ignore any effects of differential survival and reproductive success among PKU genotypes (condition 3) and assume that there are no effects of genetic drift (condition 4) or of gene flow from other populations into the United States (condition 5). These assumptions are reasonable: The mutation rate for the PKU gene is low, inbreeding and other forms of nonrandom mating are not common in the United States, selection occurs only against the rare homozygotes (and then only if dietary restrictions are not followed), the U.S. population is very large, and populations outside the country have PKU allele frequencies similar to those seen in the United States. If all these assumptions hold, then the frequency of individuals in the population born with PKU will correspond to  $q^2$  in the Hardy-Weinberg equation ( $q^2$  = frequency of homozygotes). Because the allele is recessive, we must estimate the number of heterozygotes rather than counting them directly as we did with the pink flowers. Since we know there is one PKU occurrence per 10,000 births ( $q^2$  = 0.0001), the frequency ( $q$ ) of the recessive allele for PKU is

$$q = \sqrt{0.0001} = 0.01$$

and the frequency of the dominant allele is

$$p = 1 - q = 1 - 0.01 = 0.99$$

## Using the Hardy-Weinberg Equation to Interpret Data and Make Predictions

**Is Evolution Occurring in a Soybean Population?** One way to test whether evolution is occurring in a population is to compare the observed genotype frequencies at a locus with those expected for a nonevolving population based on the Hardy-Weinberg equation. In this exercise, you'll test whether a soybean population is evolving at a locus with two alleles,  $C^G$  and  $C^Y$ , that affect chlorophyll production and hence leaf color.

**How the Experiment Was Done** Students planted soybean seeds and then counted the number of seedlings of each genotype at day 7 and again at day 21. Seedlings of each genotype could be distinguished visually because the  $C^G$  and  $C^Y$  alleles show incomplete dominance:  $C^G C^G$  seedlings have green leaves,  $C^G C^Y$  seedlings have green-yellow leaves, and  $C^Y C^Y$  seedlings have yellow leaves.


### Data from the Experiment

Number of Seedlings				
Time (days)	Green ( $C^G C^G$ )	Green-yellow ( $C^G C^Y$ )	Yellow ( $C^Y C^Y$ )	Total
7	49	111	56	216
21	47	106	20	173

### Interpret the Data

1. Use the observed genotype frequencies from the day 7 data to calculate the frequencies of the  $C^G$  allele ( $p$ ) and the  $C^Y$  allele ( $q$ ). (Remember that the frequency of an allele in a gene pool is the number of copies of that allele divided by the total number of copies of all alleles at that locus.)

2. Next, use the Hardy-Weinberg equation ( $p^2 + 2pq + q^2 = 1$ ) to calculate the expected frequencies of genotypes  $C^G C^G$ ,  $C^G C^Y$ , and  $C^Y C^Y$  for a population in Hardy-Weinberg equilibrium.
3. Calculate the observed frequencies of genotypes  $C^G C^G$ ,  $C^G C^Y$ , and  $C^Y C^Y$  at day 7. (The observed frequency of a genotype in a gene pool is the number of individuals with that genotype divided by the total number of individuals.) Compare these frequencies to the expected frequencies calculated in step 2. Is the seedling population in Hardy-Weinberg equilibrium at day 7, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.
4. Calculate the observed frequencies of genotypes  $C^G C^G$ ,  $C^G C^Y$ , and  $C^Y C^Y$  at day 21. Compare these frequencies to the expected frequencies calculated in step 2 and the observed frequencies at day 7. Is the seedling population in Hardy-Weinberg equilibrium at day 21, or is evolution occurring? Explain your reasoning and identify which genotypes, if any, appear to be selected for or against.
5. Homozygous  $C^Y C^Y$  individuals cannot produce chlorophyll. The ability to photosynthesize becomes more critical as seedlings age and begin to exhaust the supply of food that was stored in the seed from which they emerged. Develop a hypothesis that explains the data for days 7 and 21. Based on this hypothesis, predict how the frequencies of the  $C^G$  and  $C^Y$  alleles will change beyond day 21.

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

The frequency of carriers, heterozygous people who do not have PKU but may pass the PKU allele to offspring, is

$$2pq = 2 \times 0.99 \times 0.01 = 0.0198$$

(approximately 2% of the U.S. population)

Remember, the assumption of Hardy-Weinberg equilibrium yields an approximation; the real number of carriers may differ. Still, our calculations suggest that harmful recessive alleles at this and other loci can be concealed in a population because they are carried by healthy heterozygotes. The **Scientific Skills Exercise** provides another opportunity for you to apply the Hardy-Weinberg principle to allele data for a population.

### CONCEPT CHECK 21.2

1. A population has 700 individuals, 85 of genotype AA, 320 of genotype Aa, and 295 of genotype aa. What are the frequencies of alleles A and a?
2. The frequency of allele a is 0.45 for a population in Hardy-Weinberg equilibrium. What are the expected frequencies of genotypes AA, Aa, and aa?
3. **WHAT IF?** A locus that affects susceptibility to a degenerative brain disease has two alleles, V and v. In a population, 16 people have genotype VV, 92 have genotype Vv, and 12 have genotype vv. Is this population evolving? Explain.

For suggested answers, see Appendix A.

## CONCEPT 21.3

### Natural selection, genetic drift, and gene flow can alter allele frequencies in a population

Note again the five conditions required for a population to be in Hardy-Weinberg equilibrium. A deviation from any of these conditions is a potential cause of evolution. New mutations (violation of condition 1) can alter allele frequencies, but because mutations are rare, the change from one generation to the next is likely to be very small. Nonrandom mating (violation of condition 2) can affect the frequencies of homozygous and heterozygous genotypes but by itself has no effect on allele frequencies in the gene pool. (Allele frequencies can change if individuals with certain inherited traits are more likely than other individuals to obtain mates. However, such a situation not only causes a deviation from random mating; it also violates condition 3, no natural selection.) For the rest of this section, we will focus on the three mechanisms that alter allele frequencies directly and cause most evolutionary change: natural selection, genetic drift, and gene flow (violations of conditions 3–5).

## Natural Selection

The concept of natural selection is based on differential success in survival and reproduction: Individuals in a population exhibit variations in their heritable traits, and those with traits that are better suited to their environment tend to produce more offspring than those with traits that are not as well suited (see Chapter 19).

In genetic terms, we now know that selection results in alleles being passed to the next generation in proportions that differ from those in the present generation. For example, the fruit fly *D. melanogaster* has an allele that confers resistance to several insecticides, including DDT. This allele has a frequency of 0% in laboratory strains of *D. melanogaster* established from flies collected in the wild in the early 1930s, prior to DDT use. However, in strains established from flies collected after 1960 (following 20 or more years of DDT use), the allele frequency is 37%. We can infer that this allele either arose by mutation between 1930 and 1960 or was present in 1930, but very rare. In any case, the rise in frequency of this allele most likely occurred because DDT is a powerful poison that is a strong selective force in exposed fly populations.

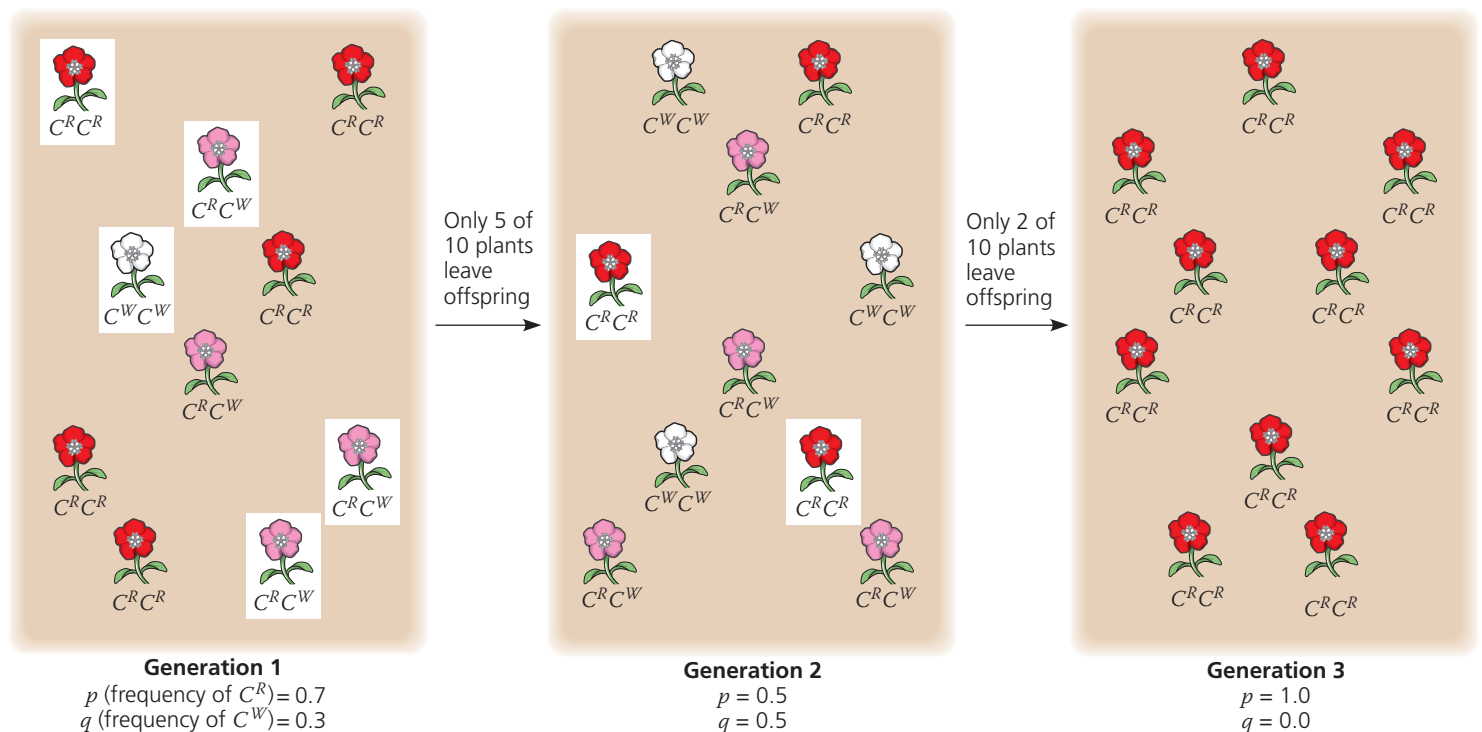
As the *D. melanogaster* example shows, an allele that confers resistance to an insecticide will increase in frequency in a population exposed to that insecticide. Such changes are not coincidental. By consistently favoring some alleles over others, natural selection can cause *adaptive evolution* (evolution that

results in a better match between organisms and their environment). We'll explore this process in more detail a little later in this chapter.

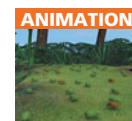
## Genetic Drift

If you flip a coin 1,000 times, a result of 700 heads and 300 tails might make you suspicious about that coin. But if you flip a coin only 10 times, an outcome of 7 heads and 3 tails would not be surprising. The smaller the number of coin flips, the more likely it is that chance alone will cause a deviation from the predicted result. (In this case, the prediction is an equal number of heads and tails.) Chance events can also cause allele frequencies to fluctuate unpredictably from one generation to the next, especially in small populations—a process called **genetic drift**.

**Figure 21.9** models how genetic drift might affect a small population of our wildflowers. In this example, drift leads to the loss of an allele from the gene pool, but it is a matter of chance that the  $C^W$  allele is lost and not the  $C^R$  allele. Such unpredictable changes in allele frequencies can be caused by chance events associated with survival and reproduction. Perhaps a large animal such as a moose stepped on the three  $C^W C^W$  individuals in generation 2, killing them and increasing the chance that only the  $C^R$  allele would be passed to the next generation. Allele frequencies can also be affected by chance events that occur during fertilization. For example, suppose two individuals



▲ **Figure 21.9 Genetic drift.** This small wildflower population has a stable size of ten plants. Suppose that by chance only five plants of generation 1 (those in white boxes) produce fertile offspring. (This could occur, for example, if only those plants happened to grow in a location that provided enough nutrients to support the production of offspring.) Again by chance, only two plants of generation 2 leave fertile offspring. As a result, by chance the frequency of the  $C^W$  allele first increases in generation 2, then falls to zero in generation 3.



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of genotype  $C^R C^W$  had a small number of offspring. By chance alone, every egg and sperm pair that generated offspring could happen to have carried the  $C^R$  allele and not the  $C^W$  allele.

Certain circumstances can result in genetic drift having a significant impact on a population. Two examples are the founder effect and the bottleneck effect.

### The Founder Effect

When a few individuals become isolated from a larger population, this smaller group may establish a new population whose gene pool differs from the source population; this is called the **founder effect**. The founder effect might occur, for example, when a few members of a population are blown by a storm to a new island. Genetic drift, in which chance events alter allele frequencies, will occur in such a case if the storm indiscriminately transports some individuals (and their alleles), but not others, from the source population.

The founder effect probably accounts for the relatively high frequency of certain inherited disorders among isolated human populations. For example, in 1814, 15 British colonists founded a settlement on Tristan da Cunha, a group of small islands in the Atlantic Ocean midway between Africa and South America. Apparently, one of the colonists carried a recessive allele for retinitis pigmentosa, a progressive form of blindness that afflicts homozygous individuals. Of the founding colonists' 240 descendants on the island in the late 1960s, 4 had retinitis pigmentosa. The frequency of the allele that causes this disease is ten times higher on Tristan da Cunha than in the populations from which the founders came.

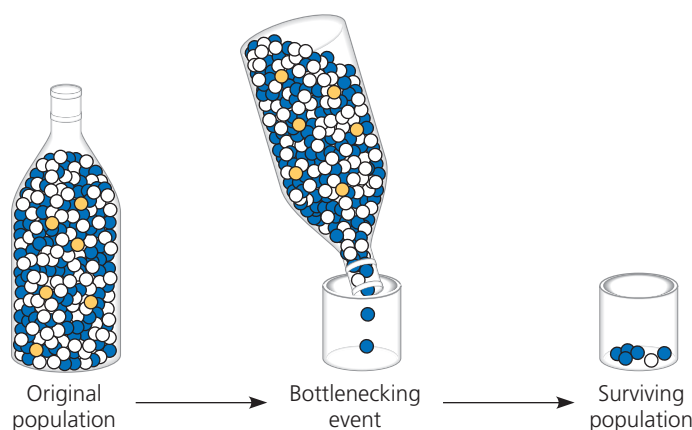
### The Bottleneck Effect

A sudden change in the environment, such as a fire or flood, may drastically reduce the size of a population. A severe drop in population size can cause the **bottleneck effect**, so named because the population has passed through a “bottleneck” that reduces its size (**Figure 21.10**). By chance alone, certain alleles may be overrepresented among the survivors, others may be underrepresented, and some may be absent altogether. Ongoing genetic drift is likely to have substantial effects on the gene pool until the population becomes large enough that chance events have less impact. But even if a population that has passed through a bottleneck ultimately recovers in size, it may have low levels of genetic variation for a long period of time—a legacy of the genetic drift that occurred when the population was small.

One reason it is important to understand the bottleneck effect is that human actions sometimes create severe bottlenecks for other species, as the following example shows.

### Case Study: Impact of Genetic Drift on the Greater Prairie Chicken

Millions of greater prairie chickens (*Tympanuchus cupido*) once lived on the prairies of Illinois. As these prairies were converted to farmland and other uses during the 19th and



(a) Shaking just a few marbles through the narrow neck of a bottle is analogous to a drastic reduction in the size of a population. By chance, blue marbles are overrepresented in the surviving population, and gold marbles are absent.



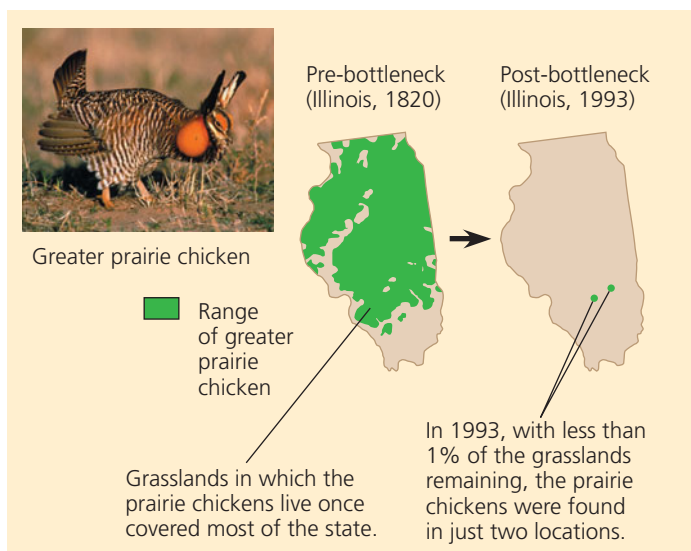
(b) Similarly, bottlenecking a wild population tends to reduce genetic variation, as in the Florida panther (*Puma concolor coryi*), a subspecies in danger of extinction.

▲ **Figure 21.10 The bottleneck effect.**

20th centuries, the number of greater prairie chickens plummeted (**Figure 21.11a**). By 1993, only two Illinois populations remained, which together harbored fewer than 50 birds. The few surviving birds had low levels of genetic variation, and less than 50% of their eggs hatched, compared with much higher hatching rates of the larger populations in Kansas and Nebraska (**Figure 21.11b**).

These data suggest that genetic drift during the bottleneck may have led to a loss of genetic variation and an increase in the frequency of harmful alleles. To investigate this hypothesis, researchers extracted DNA from 15 museum specimens of Illinois greater prairie chickens. Of the 15 birds, 10 had been collected in the 1930s, when there were 25,000 greater prairie chickens in Illinois, and 5 had been collected in the 1960s, when there were 1,000 greater prairie chickens in Illinois. By studying the DNA of these specimens, the researchers were able to obtain a minimum, baseline estimate of how much genetic variation was present in the Illinois population *before* the population shrank to extremely low numbers. This baseline estimate is a key piece of information that is not usually available in cases of population bottlenecks.

The researchers surveyed six loci and found that the 1993 Illinois greater prairie chicken population had lost nine alleles



(a) The Illinois population of greater prairie chickens dropped from millions of birds in the 1800s to fewer than 50 birds in 1993.

Location	Population size	Number of alleles per locus	Percentage of eggs hatched
Illinois			
1930–1960s	1,000–25,000	5.2	93
1993	<50	3.7	<50
Kansas, 1998 (no bottleneck)	750,000	5.8	99
Nebraska, 1998 (no bottleneck)	75,000–200,000	5.8	96

(b) As a consequence of the drastic reduction in the size of the Illinois population, genetic drift resulted in a drop in the number of alleles per locus (averaged across six loci studied) and a decrease in the percentage of eggs that hatched.

▲ **Figure 21.11 Genetic drift and loss of genetic variation.**

that were present in the museum specimens. The 1993 population also had fewer alleles per locus than the pre-bottleneck Illinois or the current Kansas and Nebraska populations (see Figure 21.11b). Thus, as predicted, drift had reduced the genetic variation of the small 1993 population. Drift may also have increased the frequency of harmful alleles, leading to the low egg-hatching rate. To counteract these negative effects, 271 birds from neighboring states were added to the Illinois population over four years. This strategy succeeded: New alleles entered the population, and the egg-hatching rate improved to over 90%. Overall, studies on the Illinois greater prairie chicken illustrate the powerful effects of genetic drift in small populations and provide hope that in at least some populations, these effects can be reversed.

## Effects of Genetic Drift: A Summary

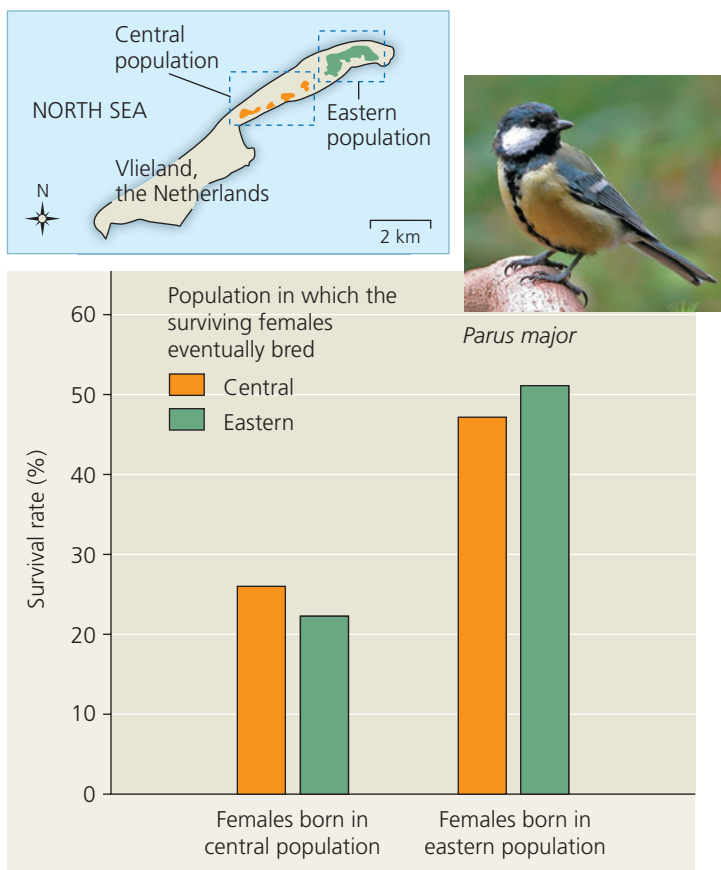
The examples we've described highlight four key points:

- Genetic drift is significant in small populations.** Chance events can cause an allele to be disproportionately over- or underrepresented in the next generation. Although chance events occur in populations of all sizes, they tend to alter allele frequencies substantially only in small populations.
- Genetic drift can cause allele frequencies to change at random.** Because of genetic drift, an allele may increase in frequency one year, then decrease the next; the change from year to year is not predictable. Thus, unlike natural selection, which in a given environment consistently favors some alleles over others, genetic drift causes allele frequencies to change at random over time.
- Genetic drift can lead to a loss of genetic variation within populations.** By causing allele frequencies to fluctuate randomly over time, genetic drift can eliminate alleles from a population. Because evolution depends on genetic variation, such losses can influence how effectively a population can adapt to a change in the environment.
- Genetic drift can cause harmful alleles to become fixed.** Alleles that are neither harmful nor beneficial can be lost or become fixed entirely by chance through genetic drift. In very small populations, genetic drift can also cause alleles that are slightly harmful to become fixed. When this occurs, the population's survival can be threatened (as in the case of the greater prairie chicken).

## Gene Flow

Natural selection and genetic drift are not the only phenomena affecting allele frequencies. Allele frequencies can also change by **gene flow**, the transfer of alleles into or out of a population due to the movement of fertile individuals or their gametes. For example, suppose that near our original hypothetical wildflower population there is another population consisting primarily of white-flowered individuals ( $C^w C^w$ ). Insects carrying pollen from these plants may fly to and pollinate plants in our original population. The introduced  $C^w$  alleles would modify our original population's allele frequencies in the next generation. Because alleles are transferred between populations, gene flow tends to reduce the genetic differences between populations. In fact, if it is extensive enough, gene flow can result in two populations combining into a single population with a common gene pool.

Alleles transferred by gene flow can also affect how well populations are adapted to local environmental conditions. Researchers studying the songbird *Parus major* (great tit) on the small Dutch island of Vlieland noted survival differences between two populations on the island. Females born in the eastern population survive twice as well as females born in the central population, regardless of where the females eventually



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**▲ Figure 21.12 Gene flow and local adaptation.** In *Parus major* populations on Vlieland, the yearly survival rate of females born in the eastern population is higher than that of females born in the central population. Gene flow from the mainland to the central population is 3.3 times higher than gene flow to the eastern population, and birds from the mainland are selected against in both populations. These data suggest that gene flow from the mainland has prevented the central population from adapting fully to its local conditions.

settle and raise offspring (Figure 21.12). This finding suggests that females born in the eastern population are better adapted to life on the island than females born in the central population. But extensive field studies also showed that the two populations are connected by high levels of gene flow (mating), which should reduce genetic differences between them.

So how can the eastern population be better adapted to life on Vlieland than the central population? The answer lies in the unequal amounts of gene flow from the mainland. In any given year, 43% of the first-time breeders in the central population are immigrants from the mainland, compared with only 13% in the eastern population. Birds with mainland genotypes survive and reproduce poorly on Vlieland, and in the eastern population, selection reduces the frequency of these genotypes. In the central population, however, gene flow from the mainland is so high that it overwhelms the effects of selection. As a result, females born in the central population have many immigrant genes, reducing the degree to which members of that population are adapted to life on the island. Researchers are currently investigating why gene flow is so much higher in the central

population and why birds with mainland genotypes survive and reproduce poorly on Vlieland.

Gene flow can also transfer alleles that improve the ability of populations to adapt to local conditions. For example, gene flow has resulted in the worldwide spread of some insecticide-resistance alleles in the mosquito *Culex pipiens*, a vector of West Nile virus and other diseases. Each of these alleles has a unique genetic signature that allowed researchers to document that it arose by mutation in only one or a few geographic locations. In their population of origin, these alleles increased because they provided insecticide resistance. These beneficial alleles were then transferred to new populations, where again, their frequencies increased as a result of natural selection. Finally, gene flow has become an increasingly important agent of evolutionary change in human populations. People today move much more freely about the world than in the past. As a result, mating is more common between members of populations that previously had very little contact, leading to an exchange of alleles and fewer genetic differences between those populations.

### CONCEPT CHECK 21.3

1. In what sense is natural selection more “predictable” than genetic drift?
2. Distinguish genetic drift from gene flow in terms of (a) how they occur and (b) their implications for future genetic variation in a population.
3. **WHAT IF?** Suppose two plant populations exchange pollen and seeds. In one population, individuals of genotype AA are most common (9,000 AA, 900 Aa, 100 aa), while the opposite is true in the other population (100 AA, 900 Aa, 9,000 aa). If neither allele has a selective advantage, what will happen over time to the allele and genotype frequencies of these populations?

For suggested answers, see Appendix A.

## CONCEPT 21.4

### Natural selection is the only mechanism that consistently causes adaptive evolution

Evolution by natural selection is a blend of chance and “sorting”: chance in the creation of new genetic variations (as in mutation) and sorting as natural selection favors some alleles over others. Because of this favoring process, the outcome of natural selection is *not* random. Instead, natural selection consistently increases the frequencies of alleles that provide reproductive advantage and thus leads to **adaptive evolution**.

#### Natural Selection: A Closer Look

In examining how natural selection brings about adaptive evolution, we’ll begin with the concept of relative fitness and



the different ways that an organism's phenotype is subject to natural selection.

### Relative Fitness

The phrases “struggle for existence” and “survival of the fittest” are commonly used to describe natural selection, but these expressions are misleading if taken to mean direct competitive contests among individuals. There *are* animal species in which individuals, usually males, lock horns or otherwise spar to determine mating privilege. But reproductive success is generally more subtle and depends on many factors besides outright battle. For example, a barnacle that is more efficient at collecting food than its neighbors may have greater stores of energy and hence be able to produce more eggs. A moth may have more offspring than other moths in the same population because its body colors more effectively conceal it from predators, improving its chance of surviving long enough to produce more offspring. These examples illustrate how in a given environment, certain traits can lead to greater **relative fitness**: the contribution an individual makes to the gene pool of the next generation *relative to* the contributions of other individuals.

Although we often refer to the relative fitness of a genotype, remember that the entity that is subjected to natural selection is the whole organism, not the underlying genotype. Thus, selection acts more directly on the phenotype than on the genotype; it acts on the genotype indirectly, via how the genotype affects the phenotype.

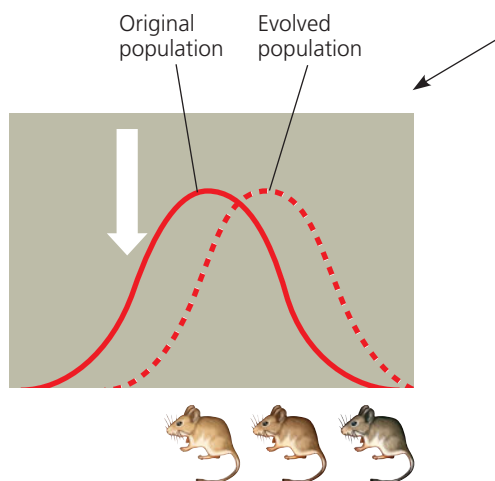
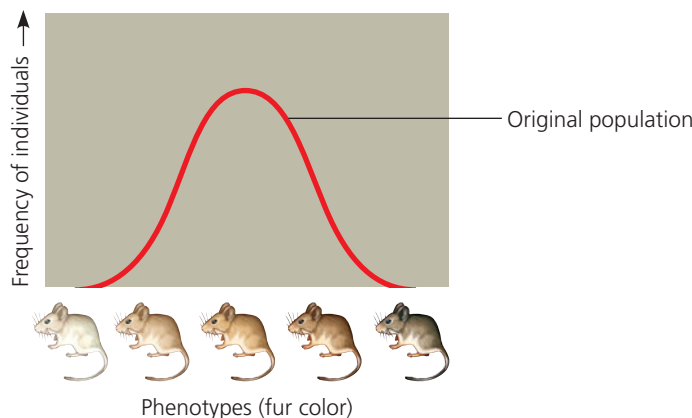
### Directional, Disruptive, and Stabilizing Selection

Natural selection can occur in three ways, depending on which phenotypes in a population are favored. These three modes of selection are called directional selection, disruptive selection, and stabilizing selection.

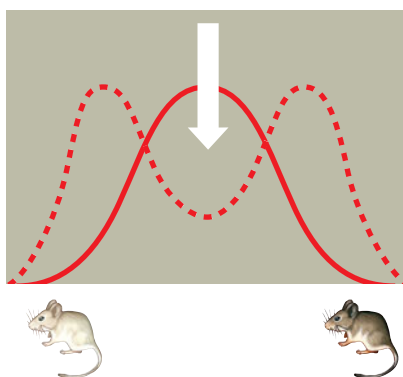
**Directional selection** occurs when conditions favor individuals at one extreme of a phenotypic range, thereby shifting a population's frequency curve for the phenotypic character in one direction or the other (**Figure 21.13a**). Directional selection is common when a population's environment changes or when members of a population migrate to a different habitat. For instance, an increase in the relative abundance of large seeds over small seeds led to increased beak depth in a population of Galápagos finches (see Figure 21.2).

▼ **Figure 21.13 Modes of selection.** These cases describe three ways in which a hypothetical deer mouse population with heritable variation in fur coloration from light to dark might evolve. The graphs show how the frequencies of individuals with different fur colors change over time. The large white arrows symbolize selective pressures against certain phenotypes.

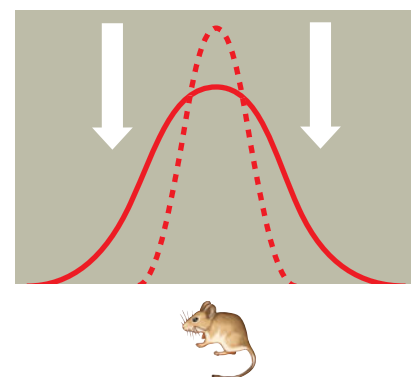
**MAKE CONNECTIONS** Review Figure 19.14. Which mode of selection has occurred in soapberry bug populations that feed on the introduced goldenrain tree? Explain.



**(a) Directional selection** shifts the overall makeup of the population by favoring variants that are at one extreme of the distribution. In this case, lighter mice are selected against because they live among dark rocks, making it harder for them to hide from predators.



**(b) Disruptive selection** favors variants at both ends of the distribution. These mice have colonized a patchy habitat made up of light and dark rocks, with the result that mice of an intermediate color are selected against.



**(c) Stabilizing selection** removes extreme variants from the population and preserves intermediate types. If the environment consists of rocks of an intermediate color, both light and dark mice will be selected against.

**Disruptive selection** (Figure 21.13b) occurs when conditions favor individuals at both extremes of a phenotypic range over individuals with intermediate phenotypes. One example is a population of black-bellied seedcracker finches in Cameroon whose members display two distinctly different beak sizes. Small-billed birds feed mainly on soft seeds, whereas large-billed birds specialize in cracking hard seeds. It appears that birds with intermediate-sized bills are relatively inefficient at cracking both types of seeds and thus have lower relative fitness.

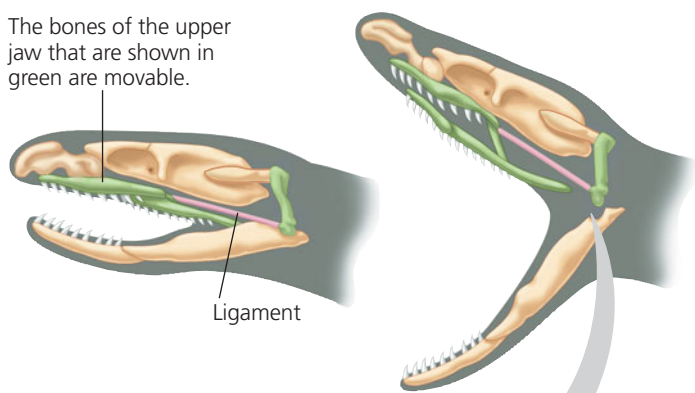
**Stabilizing selection** (Figure 21.13c) acts against both extreme phenotypes and favors intermediate variants. This mode of selection reduces variation and tends to maintain the status quo for a particular phenotypic character. For example, the birth weights of most human babies lie in the range of 3–4 kg (6.6–8.8 pounds); babies who are either much smaller or much larger suffer higher rates of mortality.

Regardless of the mode of selection, however, the basic mechanism remains the same. Selection favors individuals whose heritable phenotypic traits provide higher reproductive success than do the traits of other individuals.

## The Key Role of Natural Selection in Adaptive Evolution

The adaptations of organisms include many striking examples. Certain octopuses, for instance, can change color rapidly, enabling them to blend into different backgrounds. Another example is the remarkable jaws of snakes (Figure 21.14), which

The bones of the upper jaw that are shown in green are movable.



The skull bones of most terrestrial vertebrates are relatively rigidly attached to one another, limiting jaw movement. In contrast, most snakes have movable bones in their upper jaw, allowing them to swallow food much larger than their head.



▲ **Figure 21.14** Movable jaw bones in snakes.

allow them to swallow prey much larger than their own head (a feat analogous to a person swallowing a whole watermelon). Other adaptations, such as a version of an enzyme that shows improved function in cold environments, may be less visually dramatic but just as important for survival and reproduction.

Such adaptations can arise gradually over time as natural selection increases the frequencies of alleles that enhance survival and reproduction. As the proportion of individuals that have favorable traits increases, the match between a species and its environment improves; that is, adaptive evolution occurs. Note, however, that the physical and biological components of an organism's environment may change over time. As a result, what constitutes a “good match” between an organism and its environment can be a moving target, making adaptive evolution a continuous, dynamic process.

And what about genetic drift and gene flow? Both can, in fact, increase the frequencies of alleles that improve the match between organisms and their environment, but neither does so consistently. Genetic drift can cause the frequency of a slightly beneficial allele to increase, but it also can cause the frequency of such an allele to decrease. Similarly, gene flow may introduce alleles that are advantageous or ones that are disadvantageous. Natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.

## Sexual Selection

Charles Darwin was the first to explore the implications of **sexual selection**, a form of natural selection in which individuals with certain inherited characteristics are more likely than other individuals to obtain mates. Sexual selection can result in **sexual dimorphism**, a difference in secondary sexual characteristics between males and females of the same species (Figure 21.15). These distinctions include differences in size, color, ornamentation, and behavior.



▲ **Figure 21.15** Sexual dimorphism and sexual selection.

Peacocks (above left) and peahens (above right) show extreme sexual dimorphism. There is intrasexual selection between competing males, followed by intersexual selection when the females choose among the showiest males.

How does sexual selection operate? There are several ways. In *intrasexual selection*, meaning selection within the same sex, individuals of one sex compete directly for mates of the opposite sex. In many species, intrasexual selection occurs among males. For example, a single male may patrol a group of females and prevent other males from mating with them. The patrolling male may defend his status by defeating smaller, weaker, or less fierce males in combat. More often, this male is the psychological victor in ritualized displays that discourage would-be competitors but do not risk injury that would reduce his own fitness. Intrasexual selection has also been observed among females in a variety of species, including ring-tailed lemurs and broad-nosed pipefish.

In *intersexual selection*, also called *mate choice*, individuals of one sex (usually the females) are choosy in selecting their mates from the other sex. In many cases, the female's choice depends on the showiness of the male's appearance or behavior (see Figure 21.15). What intrigued Darwin about mate choice is that male showiness may not seem adaptive in any other way and may in fact pose some risk. For example, bright plumage may make male birds more visible to predators. But if such characteristics help a male gain a mate, and if this benefit outweighs the risk from predation, then both the bright plumage and the female preference for it will be reinforced because they enhance overall reproductive success.

How do female preferences for certain male characteristics evolve in the first place? One hypothesis is that females prefer male traits that are correlated with “good genes.” If the trait preferred by females is indicative of a male's overall genetic quality, both the male trait and female preference for it should increase in frequency. **Figure 21.16** describes one experiment testing this hypothesis in gray tree frogs (*Hyla versicolor*).

Other researchers have shown that in several bird species, the traits preferred by females are related to overall male health. Here, too, female preference appears to be based on traits that reflect “good genes,” in this case alleles indicative of a robust immune system.

## The Preservation of Genetic Variation

Some of the genetic variation in populations represents **neutral variation**, differences in DNA sequence that do not confer a selective advantage or disadvantage. But variation is also found at loci affected by selection. What prevents natural selection from reducing genetic variation at those loci by culling all unfavorable alleles? The tendency for directional and stabilizing selection to reduce variation is countered by mechanisms that preserve or restore it, such as diploidy and balancing selection.

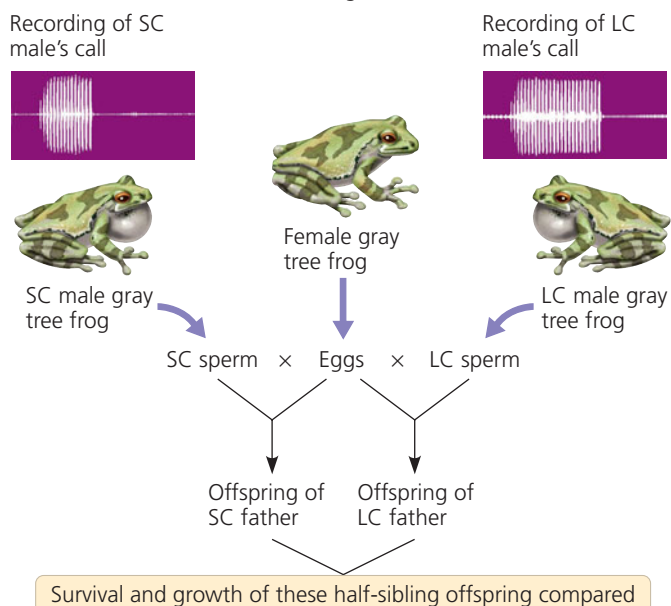
### Diploidy

In diploid organisms, a considerable amount of genetic variation is hidden from selection in the form of recessive alleles. Recessive alleles that are less favorable than their dominant

## ▼ Figure 21.16 Inquiry

### Do females select mates based on traits indicative of “good genes”?

**Experiment** Female gray tree frogs (*Hyla versicolor*) prefer to mate with males that give long mating calls. Allison Welch and colleagues, at the University of Missouri, tested whether the genetic makeup of long-calling (LC) males is superior to that of short-calling (SC) males. The researchers fertilized half the eggs of each female with sperm from an LC male and fertilized the remaining eggs with sperm from an SC male. In two separate experiments (one in 1995, the other in 1996), the resulting half-sibling offspring were raised in a common environment and their survival and growth were monitored.



### Results

Offspring Performance	1995	1996
Larval survival	LC better	NSD
Larval growth	NSD	LC better
Time to metamorphosis	LC better (shorter)	LC better (shorter)
NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.		

**Conclusion** Because offspring fathered by an LC male outperformed their half-siblings fathered by an SC male, the team concluded that the duration of a male's mating call is indicative of the male's overall genetic quality. This result supports the hypothesis that female mate choice can be based on a trait that indicates whether the male has “good genes.”

**Source** A. M. Welch et al., Call duration as an indicator of genetic quality in male gray tree frogs, *Science* 280:1928–1930 (1998).

**Inquiry in Action** Read and analyze the original paper in *Inquiry in Action: Interpreting Scientific Papers*.

**WHAT IF?** Why did the researchers split each female frog's eggs into two batches for fertilization by different males? Why didn't they mate each female with a single male frog?

counterparts or even harmful in the current environment can persist by propagation in heterozygous individuals. This latent



variation is exposed to natural selection only when both parents carry the same recessive allele and two copies end up in the same zygote. This happens only rarely if the frequency of the recessive allele is very low. Heterozygote protection maintains a huge pool of alleles that might not be favored under present conditions, but which could bring new benefits if the environment changes.

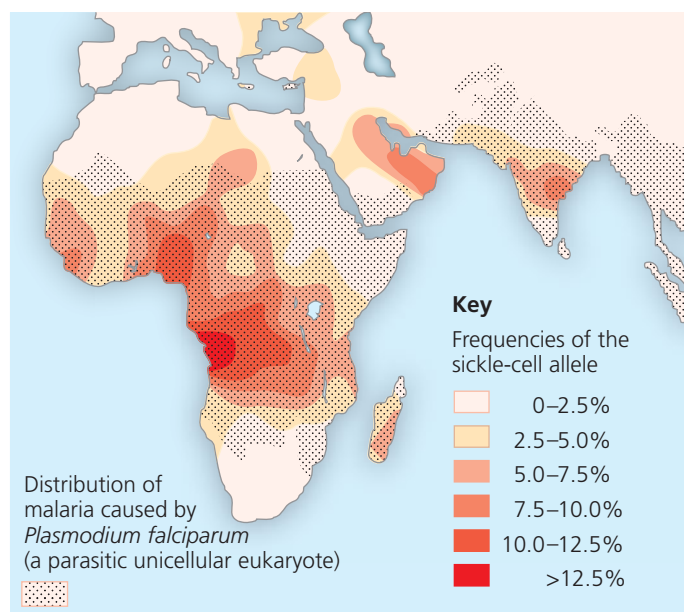
### Balancing Selection

Selection itself may preserve variation at some loci. **Balancing selection** occurs when natural selection maintains two or more forms in a population. This type of selection includes heterozygote advantage and frequency-dependent selection.

**Heterozygote Advantage** If individuals who are heterozygous at a particular locus have greater fitness than do both kinds of homozygotes, they exhibit **heterozygote advantage**. In such a case, natural selection tends to maintain two or more alleles at that locus. Note that heterozygote advantage is defined in terms of *genotype*, not phenotype. Thus, whether heterozygote advantage represents stabilizing or directional selection depends on the relationship between the genotype and the phenotype. For example, if the phenotype of a heterozygote is intermediate to the phenotypes of both homozygotes, heterozygote advantage is a form of stabilizing selection.

An example of heterozygote advantage occurs at the locus in humans that codes for the  $\beta$  polypeptide subunit of hemoglobin, the oxygen-carrying protein of red blood cells. In homozygous individuals, a certain recessive allele at that locus causes sickle-cell disease. The red blood cells of people with sickle-cell disease become distorted in shape, or *sickled*, under low-oxygen conditions (see Figure 3.22), as occurs in the capillaries. These sickled cells can clump together and block the flow of blood in the capillaries, resulting in serious damage to organs such as the kidney, heart, and brain. Although some red blood cells become sickled in heterozygotes, not enough become sickled to cause sickle-cell disease.

Heterozygotes for the sickle-cell allele are protected against the most severe effects of malaria, a disease caused by a parasite that infects red blood cells (see Figure 25.26). One reason for this partial protection is that the body destroys sickled red blood cells rapidly, killing the parasites they harbor (but not affecting parasites inside normal red blood cells). Protection against malaria is important in tropical regions where the disease is a major killer. In such regions, selection favors heterozygotes over homozygous dominant individuals, who are more vulnerable to the effects of malaria, and also over homozygous recessive individuals, who develop sickle-cell disease. The frequency of the sickle-cell allele in Africa is generally highest in areas where the malaria parasite is most common (**Figure 21.17**). In some populations, it accounts for 20% of the hemoglobin alleles in the gene pool, a very high frequency for such a harmful allele.



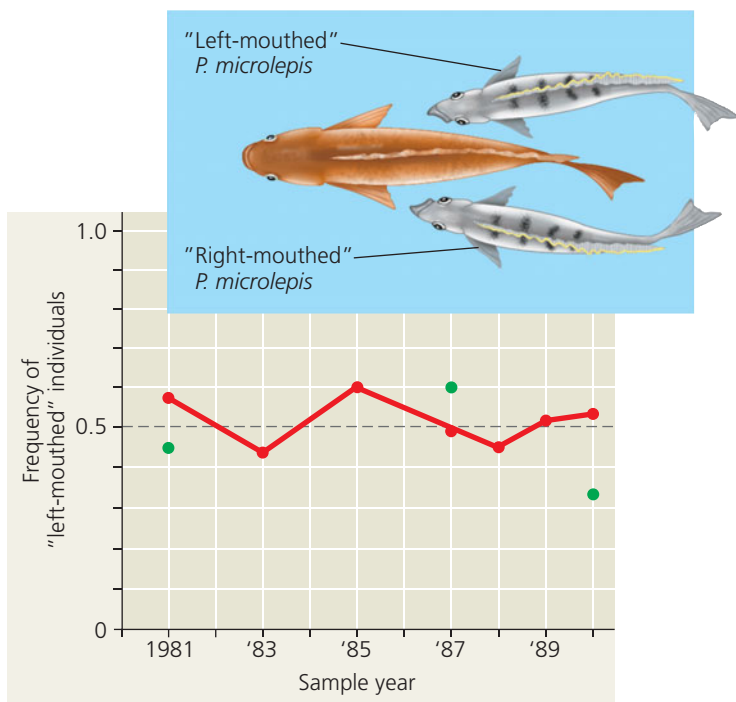
**▲ Figure 21.17 Mapping malaria and the sickle-cell allele.** The sickle-cell allele is most common in Africa, but it is not the only case of heterozygote advantage providing protection against malaria. Alleles at other loci (not shown on this map) are also favored by heterozygote advantage in populations near the Mediterranean Sea and in Southeast Asia where malaria is widespread.

**Frequency-Dependent Selection** In **frequency-dependent selection**, the fitness of a phenotype depends on how common it is in the population. Consider the scale-eating fish (*Perissodus microlepis*) of Lake Tanganyika, in Africa. These fish attack other fish from behind, darting in to remove a few scales from the flank of their prey. Of interest here is a peculiar feature of the scale-eating fish: Some are “left-mouthed” and some are “right-mouthed.” Simple Mendelian inheritance determines these phenotypes, with the right-mouthed allele being dominant to the left-mouthed allele. Because their mouth twists to the left, left-mouthed fish always attack their prey’s right flank (**Figure 21.18**). (To see why, twist your lower jaw and lips to the left and imagine trying to take a bite from the left side of a fish, approaching it from behind.) Similarly, right-mouthed fish always attack from the left. Prey species guard against attack from whatever phenotype of scale-eating fish is most common in the lake. Thus, from year to year, selection favors whichever mouth phenotype is least common. As a result, the frequency of left- and right-mouthed fish oscillates over time, and balancing selection (due to frequency dependence) keeps the frequency of each phenotype close to 50%.

### Why Natural Selection Cannot Fashion Perfect Organisms

Though natural selection leads to adaptation, nature abounds with examples of organisms that are less than ideally suited for their lifestyles. There are several reasons why.

1. **Selection can act only on existing variations.** Natural selection favors only the fittest phenotypes among those



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**▲ Figure 21.18 Frequency-dependent selection.** In a population of the scale-eating fish *Perissodus microlepis*, the frequency of left-mouthed individuals rises and falls in a regular manner (shown in red). At each of three time periods when the phenotypes of breeding adults were assessed, a majority of the adults that reproduced (represented by green dots) had the opposite phenotype of that which was most common in the population. Thus, it appears that right-mouthed individuals were favored by selection when left-mouthed individuals were more common, and vice versa.

**?** What did the researchers measure to determine which phenotype was favored by selection? Are any assumptions implied by this choice? Explain.

currently in the population, which may not be the ideal traits. New advantageous alleles do not arise on demand.

- 2. Evolution is limited by historical constraints.** Each species has a legacy of descent with modification from ancestral forms. Evolution does not scrap the ancestral anatomy and build each new complex structure from scratch; rather, evolution co-opts existing structures and adapts them to new situations. We could imagine that if a terrestrial animal were to adapt to an environment in which flight would be advantageous, it might be best just to grow an extra pair of limbs that would serve as wings. However, evolution does not work this way; instead, it operates on the traits an organism already has. Thus, in birds and bats, an existing pair of limbs took on new functions for flight as these organisms evolved from nonflying ancestors.
- 3. Adaptations are often compromises.** Each organism must do many different things. A seal spends part of its time on rocks; it could probably walk better if it had legs instead of flippers, but then it would not swim nearly as well. We humans owe much of our versatility and athleticism to our prehensile hands and flexible limbs, but these



**▲ Figure 21.19 Evolutionary compromise.** The loud call that enables a Túngara frog to attract mates also attracts more dangerous characters in the neighborhood—in this case, a bat about to seize a meal.

also make us prone to sprains, torn ligaments, and dislocations: Structural reinforcement has been compromised for agility. **Figure 21.19** depicts another example of evolutionary compromise.

- 4. Chance, natural selection, and the environment interact.** Chance events can affect the subsequent evolutionary history of populations. For instance, when a storm blows insects or birds hundreds of kilometers over an ocean to an island, the wind does not necessarily transport those individuals that are best suited to the new environment. Thus, not all alleles present in the founding population's gene pool are better suited to the new environment than the alleles that are "left behind." In addition, the environment at a particular location may change unpredictably from year to year, again limiting the extent to which adaptive evolution results in a close match between the organism and current environmental conditions.

With these four constraints, evolution does not tend to craft perfect organisms. Natural selection operates on a "better than" basis. We can, in fact, see evidence for evolution in the many imperfections of the organisms it produces.

#### CONCEPT CHECK 21.4

1. What is the relative fitness of a sterile mule? Explain.
2. Explain why natural selection is the only evolutionary mechanism that consistently leads to adaptive evolution.
3. **WHAT IF?** Consider a population in which heterozygotes at a certain locus have an extreme phenotype (such as being larger than homozygotes) that confers a selective advantage. Does such a situation represent directional, disruptive, or stabilizing selection? Explain your answer.
4. **WHAT IF?** Would individuals who are heterozygous for the sickle-cell allele be selected for or against in a region free from malaria? Explain.

For suggested answers, see Appendix A.

# 21 Chapter Review

## SUMMARY OF KEY CONCEPTS

### CONCEPT 21.1

#### Genetic variation makes evolution possible (pp. 400–402)

- **Genetic variation** refers to genetic differences among individuals within a population.
- The nucleotide differences that provide the basis of genetic variation originate when mutation and gene duplication produce new alleles and new genes.
- New genetic variants are produced rapidly in organisms with short generation times. In sexually reproducing organisms, most of the genetic differences among individuals result from crossing over, the independent assortment of chromosomes, and fertilization.

? Typically, most of the nucleotide variability that occurs within a genetic locus does not affect the phenotype. Explain why.

### CONCEPT 21.2

#### The Hardy-Weinberg equation can be used to test whether a population is evolving (pp. 402–406)

- A **population**, a localized group of organisms belonging to one species, is united by its **gene pool**, the aggregate of all the alleles in the population.
- The **Hardy-Weinberg principle** states that the allele and genotype frequencies of a population will remain constant if the population is large, mating is random, mutation is negligible, there is no gene flow, and there is no natural selection. For such a population, if  $p$  and  $q$  represent the frequencies of the only two possible alleles at a particular locus, then  $p^2$  is the frequency of one kind of homozygote,  $q^2$  is the frequency of the other kind of homozygote, and  $2pq$  is the frequency of the heterozygous genotype.

? Is it circular reasoning to calculate  $p$  and  $q$  from observed genotype frequencies and then use those values of  $p$  and  $q$  to test if the population is in Hardy-Weinberg equilibrium? Explain your answer. (Hint: Consider a specific case, such as a population with 195 individuals of genotype AA, 10 of genotype Aa, and 195 of genotype aa.)

### CONCEPT 21.3

#### Natural selection, genetic drift, and gene flow can alter allele frequencies in a population (pp. 406–410)

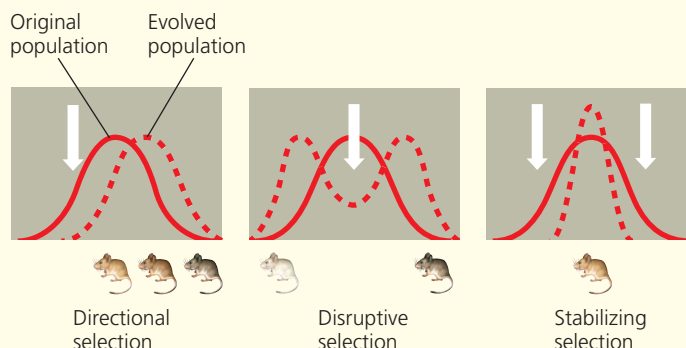
- In natural selection, individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.
- In **genetic drift**, chance fluctuations in allele frequencies over generations tend to reduce genetic variation.
- **Gene flow**, the transfer of alleles between populations, tends to reduce genetic differences between populations over time.

? Would two small, geographically isolated populations in very different environments be likely to evolve in similar ways? Explain.

### CONCEPT 21.4

#### Natural selection is the only mechanism that consistently causes adaptive evolution (pp. 410–415)

- One organism has greater **relative fitness** than a second organism if it leaves more fertile descendants than the second organism. The modes of natural selection differ in how selection acts on phenotype (the white arrows in the summary diagram below represent selective pressure on a population).



- Unlike genetic drift and gene flow, natural selection consistently increases the frequencies of alleles that enhance survival and reproduction, thus improving the match between organisms and their environment.
- **Sexual selection** influences evolutionary change in secondary sex characteristics that can give individuals advantages in mating.
- Despite the winnowing effects of selection, populations have considerable genetic variation. Some of this variation represents **neutral variation**; additional variation can be maintained by diploidy and **balancing selection**.
- There are constraints to evolution: Natural selection can act only on available variation; structures result from modified ancestral anatomy; adaptations are often compromises; and chance, natural selection, and the environment interact.

? How might secondary sex characteristics differ between males and females in a species in which females compete for mates?

## TEST YOUR UNDERSTANDING

### Level 1: Knowledge/Comprehension

1. Natural selection changes allele frequencies because some \_\_\_\_\_ survive and reproduce more successfully than others.  
a. alleles  
b. loci  
c. gene pools  
d. species  
e. individuals
2. No two people are genetically identical, except for identical twins. The main source of genetic variation among human individuals is  
a. new mutations that occurred in the preceding generation.  
b. genetic drift due to the small size of the population.  
c. the reshuffling of alleles in sexual reproduction.  
d. natural selection.  
e. environmental effects.
3. Sparrows with average-sized wings survive severe storms better than those with longer or shorter wings, illustrating  
a. the bottleneck effect.  
b. disruptive selection.  
c. frequency-dependent selection.  
d. neutral variation.  
e. stabilizing selection.



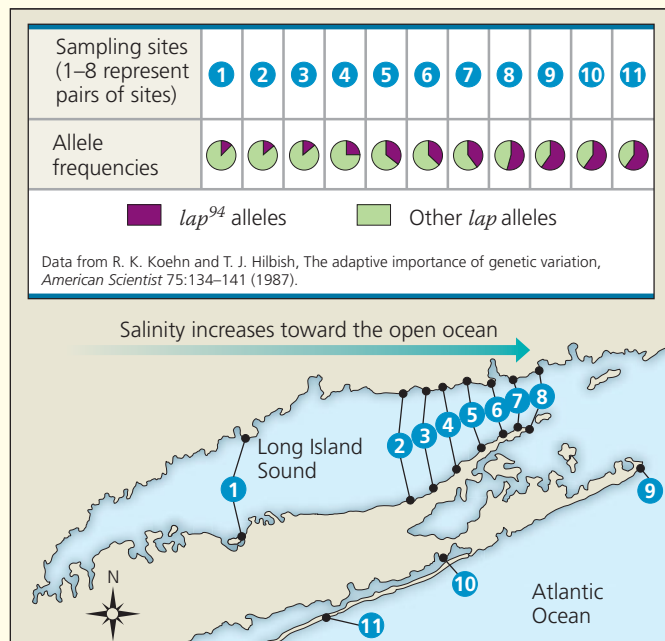
## Level 2: Application/Analysis

4. If the nucleotide variability of a locus equals 0%, what is the gene variability and number of alleles at that locus?
  - a. gene variability = 0%; number of alleles = 0
  - b. gene variability = 0%; number of alleles = 1
  - c. gene variability = 0%; number of alleles = 2
  - d. gene variability > 0%; number of alleles = 2
  - e. Without more information, gene variability and number of alleles cannot be determined.
5. There are 25 individuals in population 1, all with genotype *AA*, and there are 40 individuals in population 2, all with genotype *aa*. Assume that these populations are located far from each other and that their environmental conditions are very similar. Based on the information given here, the observed genetic variation most likely resulted from
  - a. genetic drift.
  - b. gene flow.
  - c. disruptive selection.
  - d. nonrandom mating.
  - e. directional selection.
6. A fruit fly population has a gene with two alleles, *A1* and *A2*. Tests show that 70% of the gametes produced in the population contain the *A1* allele. If the population is in Hardy-Weinberg equilibrium, what proportion of the flies carry both *A1* and *A2*?
  - a. 0.7
  - b. 0.49
  - c. 0.21
  - d. 0.42
  - e. 0.09

## Level 3: Synthesis/Evaluation

### 7. SCIENTIFIC INQUIRY

**DRAW IT** Researchers studied genetic variation in the marine mussel *Mytilus edulis* around Long Island, New York. They measured the frequency of a particular allele (*lap<sup>94</sup>*) for an enzyme involved in regulating the mussel's internal saltwater balance. The researchers presented their data as a series of pie charts linked to sampling sites within Long Island Sound, where the salinity is highly variable, and along the coast of the open ocean, where salinity is constant:



Create a data table for the 11 sampling sites by estimating the frequency of *lap<sup>94</sup>* from the pie charts. (*Hint*: Think of each pie chart as a clock face to help you estimate the proportion of the shaded area.) Then graph the frequencies for sites 1–8 to show how the frequency of this allele changes with increasing salinity in Long Island Sound (from southwest to northeast). How do the data from sites 9–11 compare with the data from the sites within the Sound?

Construct a hypothesis that explains the patterns you observe in the data and that accounts for the following observations: (1) The *lap<sup>94</sup>* allele helps mussels maintain osmotic balance in water with a high salt concentration but is costly to use in less salty water; and (2) mussels produce larvae that can disperse long distances before they settle on rocks and grow into adults.

### 8. FOCUS ON EVOLUTION

Using at least two examples, explain how the process of evolution is revealed by the imperfections of living organisms.

### 9. FOCUS ON ORGANIZATION

Heterozygotes at the sickle-cell locus produce both normal and abnormal (sickle-cell) hemoglobin (see Concept 11.4). When hemoglobin molecules are packed into a heterozygote's red blood cells, some cells receive relatively large quantities of abnormal hemoglobin, making these cells prone to sickling. In a short essay (approximately 100–150 words), explain how these molecular and cellular events lead to emergent properties at the individual and population levels of biological organization.

For selected answers, see Appendix A.

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# 22

## The Origin of Species

▼ **Figure 22.1** How did this flightless bird come to live on the isolated Galápagos Islands?



### KEY CONCEPTS

- 22.1** The biological species concept emphasizes reproductive isolation
- 22.2** Speciation can take place with or without geographic separation
- 22.3** Hybrid zones reveal factors that cause reproductive isolation
- 22.4** Speciation can occur rapidly or slowly and can result from changes in few or many genes

### OVERVIEW

## That “Mystery of Mysteries”

When Darwin came to the Galápagos, he noted that these volcanic islands, despite their geologic youth, were teeming with plants and animals found nowhere else in the world (**Figure 22.1**). Later he realized that these species had formed relatively recently. He wrote in his diary: “Both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this Earth.”

The “mystery of mysteries” that captivated Darwin is **speciation**, the process by which one species splits into two or more species. Speciation fascinated Darwin (and many biologists since) because it leads to the tremendous diversity of life, repeatedly yielding new species that differ from existing ones. Speciation also explains the many features that organisms share (the unity of life). When a species splits, the species that result share many characteristics because they are descended from this common ancestor. At the DNA sequence level, such similarities indicate that the flightless cormorant (*Phalacrocorax harrisi*) in **Figure 22.1** is closely related to flying cormorants found in the Americas. This suggests that the flightless cormorant may have originated from an ancestral cormorant that flew from the mainland to the Galápagos.

Speciation also forms a conceptual bridge between **microevolution**, changes over time in allele frequencies in a population, and **macroevolution**, the broad pattern of evolution above the species level. An example of macroevolutionary change is the origin of new groups of organisms, such as mammals or flowering plants, through a series of speciation events. We examined microevolutionary mechanisms in Chapter 21, and we’ll turn to macroevolution in Chapter 23.

In this chapter, we’ll explore the “bridge”—the mechanisms by which new species originate from existing ones. First, however, we need to establish what we actually mean by a “species.”

### CONCEPT

## 22.1

## The biological species concept emphasizes reproductive isolation

The word *species* is Latin for “kind” or “appearance.” In daily life, we commonly distinguish between various “kinds” of organisms—dogs and cats, for instance—from differences in their appearance. But are organisms truly

divided into the discrete units we call species, or is this classification an arbitrary attempt to impose order on the natural world? To answer this question, biologists compare not only the morphology (body form) of different groups of organisms but also less obvious differences in physiology, biochemistry, and DNA sequences. The results generally confirm that morphologically distinct species are indeed discrete groups, differing in many ways besides their body forms.

## The Biological Species Concept

The primary definition of species used in this textbook is the **biological species concept**. According to this concept, a **species** is a group of populations whose members have the potential to interbreed in nature and produce viable, fertile offspring—but do not produce viable, fertile offspring with members of other such groups (**Figure 22.2**). Thus, the members of a biological species are united by being reproductively compatible, at least potentially. All human beings, for example, belong to the same species. A businesswoman in Manhattan may be unlikely to meet a dairy farmer in Mongolia, but if the two should happen to meet and mate, they could have viable babies that develop into fertile adults. In contrast, humans and chimpanzees remain distinct biological species even where they live in the same region, because many factors keep them from interbreeding and producing fertile offspring.

What holds the gene pool of a species together, causing its members to resemble each other more than they resemble members of other species? To answer this question, we need to return to the evolutionary mechanism called *gene flow*, the transfer of alleles into or out of a population (see Concept 21.3). Typically, gene flow occurs between the different populations of a species. This ongoing transfer of alleles tends to hold the populations together genetically. As we'll explore in the following sections, the absence of gene flow plays a key role in the formation of new species, as well as in keeping them apart once their potential to interbreed has been reduced.

### Reproductive Isolation

Because biological species are defined in terms of reproductive compatibility, the formation of a new species hinges on **reproductive isolation**—the existence of biological barriers that impede members of two species from interbreeding and producing viable, fertile offspring. Such barriers block gene flow between the species and limit the formation of **hybrids**, offspring that result from an interspecific mating. Although a single barrier may not prevent all gene flow, a combination of several barriers can effectively isolate a species' gene pool.

Clearly, a fly cannot mate with a frog or a fern, but the reproductive barriers between more closely related species are not so obvious. These barriers can be classified according to whether they contribute to reproductive isolation before or after fertilization. **Prezygotic barriers** ("before the zygote") block fertilization from occurring. Such barriers typically act in one of three ways: by impeding members of different species



(a) **Similarity between different species.** The eastern meadowlark (*Sturnella magna*, left) and the western meadowlark (*Sturnella neglecta*, right) have similar body shapes and colorations. Nevertheless, they are distinct biological species because their songs and other behaviors are different enough to prevent interbreeding should they meet in the wild.



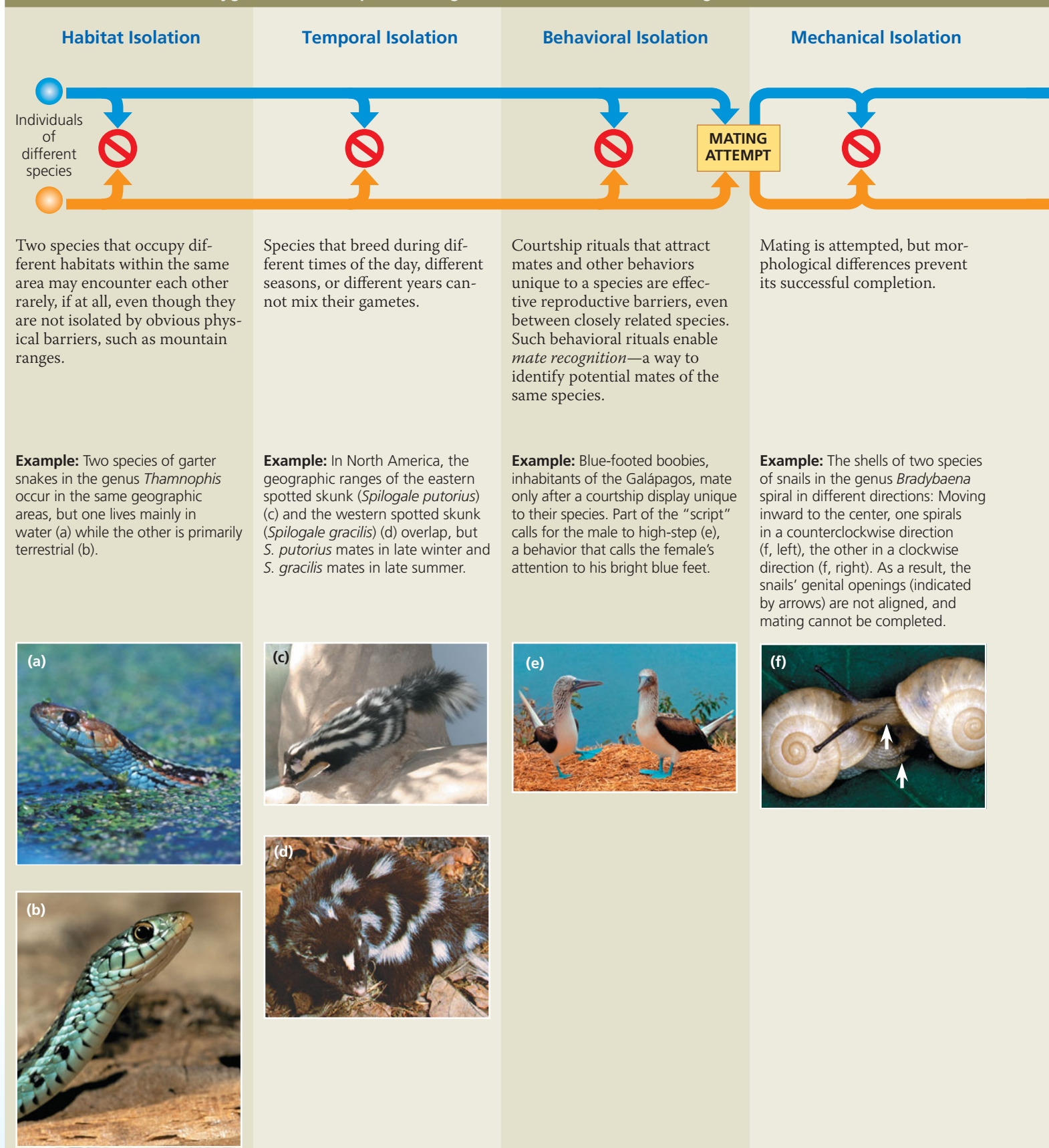
(b) **Diversity within a species.** As diverse as we may be in appearance, all humans belong to a single biological species (*Homo sapiens*), defined by our capacity to interbreed successfully.

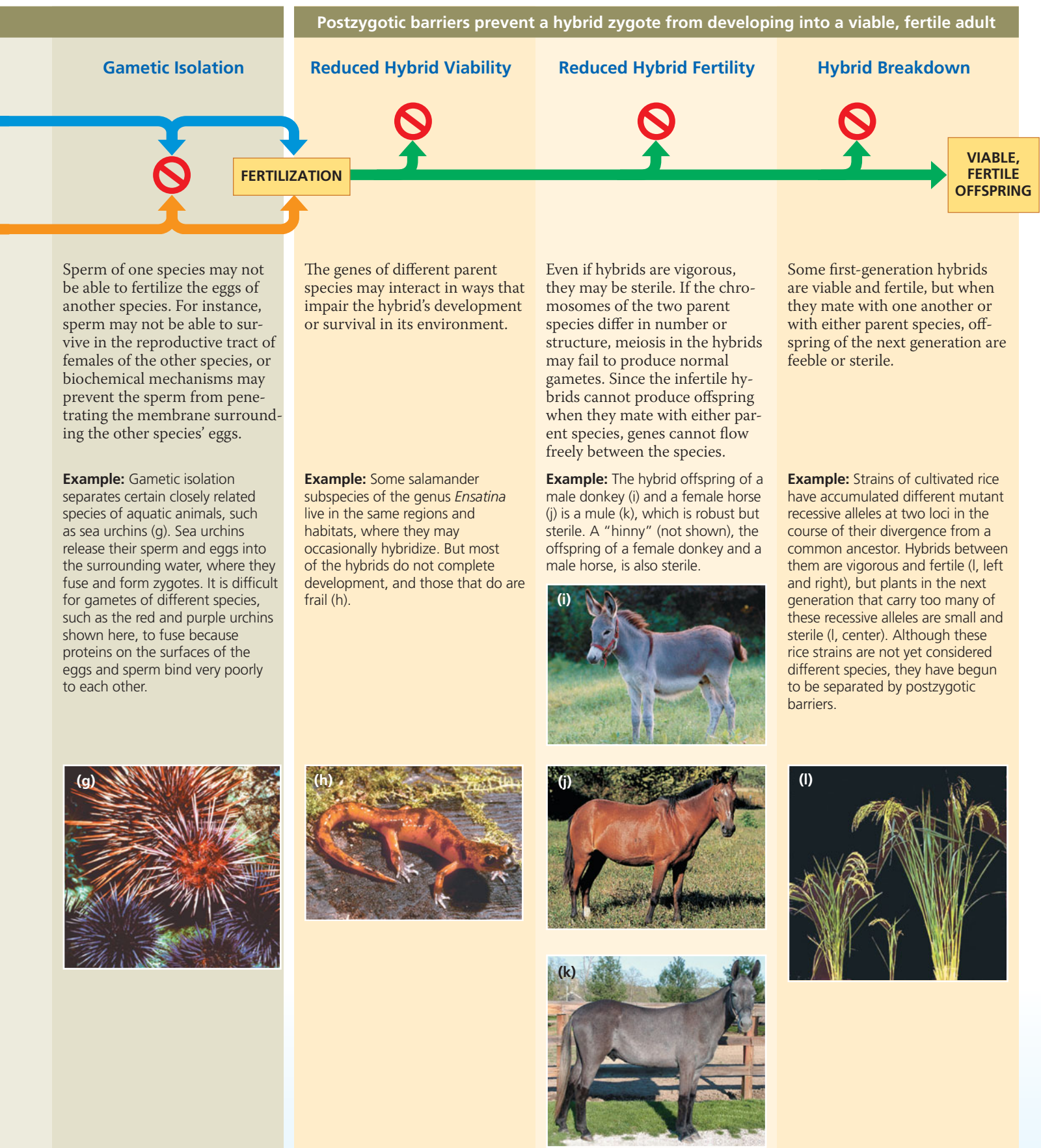
▲ **Figure 22.2** The biological species concept is based on the potential to interbreed rather than on physical similarity.

from attempting to mate, by preventing an attempted mating from being completed successfully, or by hindering fertilization if mating is completed successfully. If a sperm cell from one species overcomes prezygotic barriers and fertilizes an ovum from another species, a variety of **postzygotic barriers** ("after the zygote") may contribute to reproductive isolation after the hybrid zygote is formed. For example, developmental errors may reduce survival among hybrid embryos. Or problems after birth may cause hybrids to be infertile or may decrease their chance of surviving long enough to reproduce. **Figure 22.3** describes prezygotic and postzygotic barriers in more detail.



Prezygotic barriers impede mating or hinder fertilization if mating does occur







## Limitations of the Biological Species Concept

One strength of the biological species concept is that it directs our attention to a way by which speciation can occur: by the evolution of reproductive isolation. However, the number of species to which this concept can be usefully applied is limited. There is, for example, no way to evaluate the reproductive isolation of fossils. The biological species concept also does not apply to organisms that reproduce asexually all or most of the time, such as prokaryotes. (Many prokaryotes do transfer genes among themselves, as we will discuss in Chapter 24, but this is not part of their reproductive process.) Furthermore, in the biological species concept, species are designated by the *absence* of gene flow. But there are many pairs of species that are morphologically and ecologically distinct, and yet gene flow occurs between them. An example is the grizzly bear (*Ursus arctos*) and polar bear (*Ursus maritimus*), whose hybrid offspring have been dubbed “grolar bears” (Figure 22.4). As we’ll discuss, natural selection can cause such species to remain distinct even though some gene flow occurs between them. This observation has led some researchers to argue that the biological species concept overemphasizes gene flow and downplays the role of natural selection. Because of the limitations to the biological species concept, alternative species concepts are useful in certain situations.



◀ Grizzly bear (*U. arctos*)

▼ Polar bear (*U. maritimus*)

▲ Hybrid “grolar bear”

▲ **Figure 22.4** Hybridization between two species of bears in the genus *Ursus*.

## Other Definitions of Species

While the biological species concept emphasizes the *separateness* of species from one another due to reproductive barriers, several other definitions emphasize the *unity within* a species. For example, the **morphological species concept** characterizes a species by body shape and other structural features. The morphological species concept can be applied to asexual and sexual organisms, and it can be useful even without information on the extent of gene flow. In practice, scientists often distinguish species using morphological criteria. A disadvantage of this approach, however, is that it relies on subjective criteria; researchers may disagree on which structural features distinguish a species.

The **ecological species concept** views a species in terms of its ecological niche, the sum of how members of the species interact with the nonliving and living parts of their environment (see Chapter 41). For example, two species of oak trees might differ in their size or in their ability to tolerate dry conditions, yet still occasionally interbreed. Because they occupy different ecological niches, these oaks would be considered two separate species even though some gene flow occurs between them. Unlike the biological species concept, the ecological species concept can accommodate asexual as well as sexual species. It also emphasizes the role of disruptive natural selection as organisms adapt to different environmental conditions.

The **phylogenetic species concept** defines a species as the smallest group of individuals that share a common ancestor, forming one branch on the tree of life. Biologists trace the phylogenetic history of a species by comparing its characteristics, such as morphology or molecular sequences, with those of other organisms. Such analyses can distinguish groups of individuals that are sufficiently different to be considered separate species. Of course, the difficulty with this species concept is determining the degree of difference required to indicate separate species.

In addition to those discussed here, more than 20 other species definitions have been proposed. The usefulness of each definition depends on the situation and the research questions being asked. For our purposes of studying how species originate, the biological species concept, with its focus on reproductive barriers, is particularly helpful.

### CONCEPT CHECK 22.1

1. (a) Which species concept(s) could you apply to both asexual and sexual species? (b) Which would be most useful for identifying species in the field? Explain.
2. **WHAT IF?** Suppose you are studying two bird species that live in a forest and are not known to interbreed. One species feeds and mates in the treetops and the other on the ground. But in captivity, the birds can interbreed and produce viable, fertile offspring. What type of reproductive barrier most likely keeps these species separate in nature? Explain.

For suggested answers, see Appendix A.



## CONCEPT 22.2

### Speciation can take place with or without geographic separation

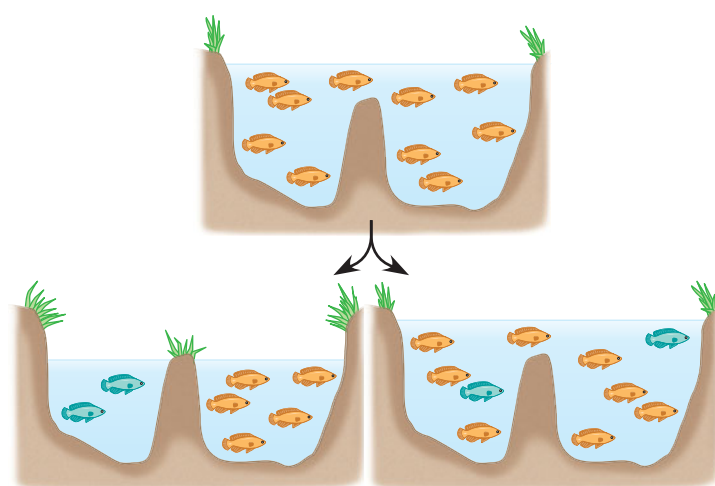
Now that we have a clearer sense of what constitutes a unique species, let's return to our discussion of the process by which such species arise from existing species. Speciation can occur in two main ways, depending on how gene flow is interrupted between populations of the existing species (**Figure 22.5**).

#### Allopatric ("Other Country") Speciation

In **allopatric speciation** (from the Greek *allos*, other, and *patra*, homeland), gene flow is interrupted when a population is divided into geographically isolated subpopulations. For example, the water level in a lake may subside, resulting in two or more smaller lakes that are now home to separated populations (see **Figure 22.5a**). Or a river may change course and divide a population of animals that cannot cross it. Allopatric speciation can also occur without geologic remodeling, such as when individuals colonize a remote area and their descendants become isolated from the parent population. The flightless cormorant in **Figure 22.1** likely originated in this way from an ancestral flying species that reached the Galápagos Islands.

#### The Process of Allopatric Speciation

How formidable must a geographic barrier be to promote allopatric speciation? The answer depends on the ability of the organisms to move about. Birds, mountain lions, and coyotes can cross rivers and canyons—as can the windblown pollen of pine trees and the seeds of many flowering plants. In contrast, small rodents may find a wide river or deep canyon a formidable barrier.

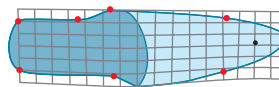


**(a) Allopatric speciation.** A population forms a new species while geographically isolated from its parent population.

**(b) Sympatric speciation.** A subset of a population forms a new species without geographic separation.

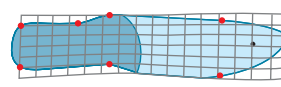
▲ **Figure 22.5** Two main modes of speciation.

**(a) Under high predation**



In ponds with predatory fishes, the head region of the mosquito-fish is streamlined and the tail region is powerful, enabling rapid bursts of speed.

**(b) Under low predation**



In ponds without predatory fishes, mosquitofish have a different body shape that favors long, steady swimming.

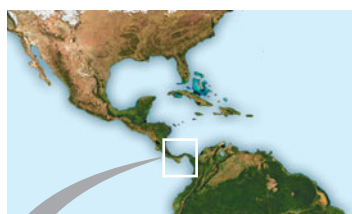
▲ **Figure 22.6** Reproductive isolation as a by-product of selection. Bringing together mosquitofish from different ponds indicates that selection for traits that enable mosquitofish in high-predation ponds to avoid predators has isolated them reproductively from mosquitofish in low-predation ponds.

Once geographic separation has occurred, the separated gene pools may diverge. Different mutations arise, and natural selection and genetic drift may alter allele frequencies in different ways in the separated populations. Reproductive isolation may then arise as a by-product of the genetic divergence that results from selection or drift.

Let's consider an example. On Andros Island, in the Bahamas, populations of the mosquitofish *Gambusia hubbsi* colonized a series of ponds that later became isolated from one another. Genetic analyses indicate that little or no gene flow currently occurs between the ponds. The environments of these ponds are very similar except that some contain many predatory fishes, while others do not. In the "high-predation" ponds, selection has favored the evolution of a mosquitofish body shape that enables rapid bursts of speed (**Figure 22.6**). In low-predation ponds, selection has favored a different body shape, one that improves the ability to swim for long periods of time. How have these different selective pressures affected the evolution of reproductive barriers? Researchers studied this question by bringing together mosquitofish from the two types of ponds. They found that female mosquitofish prefer to mate with males whose body shape is similar to their own. This preference establishes a behavioral barrier to reproduction between mosquitofish from high-predation and low-predation ponds. Thus, as a by-product of selection for avoiding predators, reproductive barriers have started to form in these allopatric populations.

#### Evidence of Allopatric Speciation

Many studies provide evidence that speciation can occur in allopatric populations. Consider the 30 species of snapping shrimp in the genus *Alpheus* that live off the Isthmus of Panama, the land bridge that connects South and North America. Fifteen of these species live on the Atlantic side of the isthmus, while the other 15 live on the Pacific side. Before the isthmus formed, gene flow could occur between the Atlantic and Pacific populations of snapping shrimp. Did the species



▼ **Figure 22.7 Allopatric speciation in snapping shrimp (*Alpheus*).** The shrimps pictured are just 2 of the 15 pairs of sister species that arose as populations were divided by the formation of the Isthmus of Panama. The color-coded type indicates the sister species.



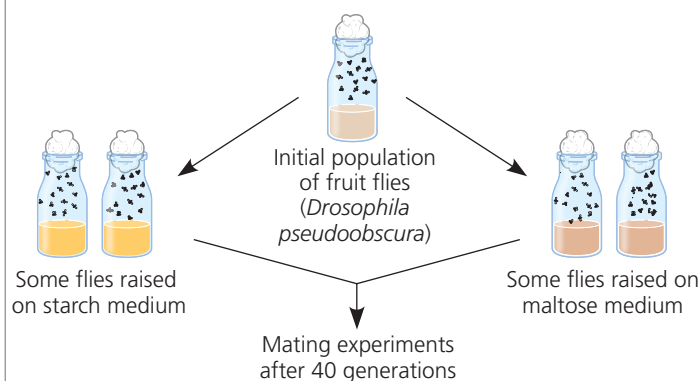
on different sides of the isthmus originate by allopatric speciation? Morphological and genetic data group these shrimp into 15 pairs of *sister species*, pairs whose member species are each other's closest relative (see Figure 20.5). In each of these 15 pairs, one of the sister species lives on the Atlantic side of the isthmus, while the other lives on the Pacific side (**Figure 22.7**), strongly suggesting that the two species arose as a consequence of geographic separation. Furthermore, genetic analyses indicate that the *Alpheus* species originated from 9 million to 3 million years ago, with the sister species that live in the deepest water diverging first. These divergence times are consistent with geologic evidence that the isthmus formed gradually, starting 10 million years ago and closing completely about 3 million years ago.

The importance of allopatric speciation is also suggested by the fact that regions that are isolated or highly subdivided by barriers typically have more species than do otherwise similar regions that lack such features. For example, many unique plants and animals are found on the geographically isolated Hawaiian Islands (we'll return to the origin of Hawaiian species in Chapter 23). Similarly, unusually high numbers of butterfly species are found in regions of South America that are subdivided by many rivers.

## ▼ Figure 22.8 Inquiry

### Can divergence of allopatric populations lead to reproductive isolation?

**Experiment** A researcher divided a laboratory population of the fruit fly *Drosophila pseudoobscura*, raising some flies on a starch medium and others on a maltose medium. After one year (about 40 generations), natural selection resulted in divergent evolution: Populations raised on starch digested starch more efficiently, while those raised on maltose digested maltose more efficiently. The researcher then put flies from the same or different populations in mating cages and measured mating frequencies. All flies used in the mating preference tests were reared for one generation on a standard cornmeal medium.



**Results** Mating patterns among populations of flies raised on different media are shown below. When flies from "starch populations" were mixed with flies from "maltose populations," the flies tended to mate with like partners. But in the control group (shown on the right), flies from different populations adapted to starch were about as likely to mate with each other as with flies from their own population; similar results were obtained for control groups adapted to maltose.

		Female	
		Starch	Maltose
Male	Starch	22	9
	Maltose	8	20

Number of matings  
in experimental group

		Female	
		Starch population 1	Starch population 2
Male	Starch population 1	18	15
	Starch population 2	12	15

Number of matings  
in control group

**Conclusion** In the experimental group, the strong preference of "starch flies" and "maltose flies" to mate with like-adapted flies indicates that a reproductive barrier was forming between these fly populations. Although this reproductive barrier was not absolute (some mating between starch flies and maltose flies did occur), after 40 generations it appeared to be under way. This barrier may have been caused by differences in courtship behavior that arose as an incidental by-product of differing selective pressures as these allopatric populations adapted to different sources of food.

**Source** D. M. B. Dodd, Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*, *Evolution* 43:1308–1311 (1989).

**WHAT IF?** Why were all flies used in the mating preference tests reared on a standard medium (rather than on a starch or maltose medium)?

Field observations show that reproductive isolation between two populations generally increases as the geographic distance between them increases. Researchers have also tested whether intrinsic reproductive barriers develop when populations are isolated experimentally and subjected to different environmental conditions. In such cases, too, the results provide strong support for allopatric speciation (Figure 22.8, on the preceding page).

We need to emphasize here that although geographic isolation prevents interbreeding between allopatric populations, physical separation is not a biological barrier to reproduction. Biological reproductive barriers such as those described in Figure 22.3 are intrinsic to the organisms themselves. Hence, it is biological barriers that can prevent interbreeding when members of different populations come into contact with one another.

## Sympatric ("Same Country") Speciation

In **sympatric speciation** (from the Greek *syn*, together), speciation occurs in populations that live in the same geographic area. How can reproductive barriers form between sympatric populations while their members remain in contact with each other? Although such contact (and the ongoing gene flow that results) makes sympatric speciation less common than allopatric speciation, sympatric speciation can occur if gene flow is reduced by such factors as polyploidy, habitat differentiation, and sexual selection. (Note that these factors can also promote allopatric speciation.)

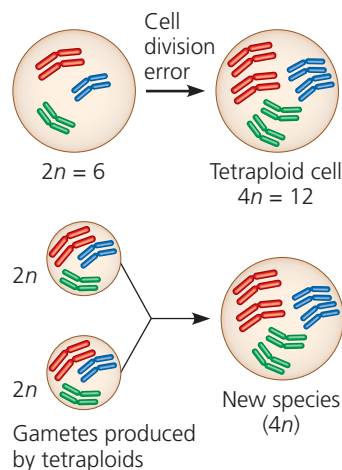
## Polyploidy

A species may originate from an accident during cell division that results in extra sets of chromosomes, a condition called **polyploidy**. Polyploid speciation occasionally occurs in animals; for example, the gray tree frog *Hyla versicolor* (see Figure 21.16) is thought to have originated in this way. However, polyploidy is far more common in plants. Botanists estimate that more than 80% of the plant species alive today are descended from ancestors that formed by polyploid speciation.

Two distinct forms of polyploidy have been observed in plant (and a few animal)

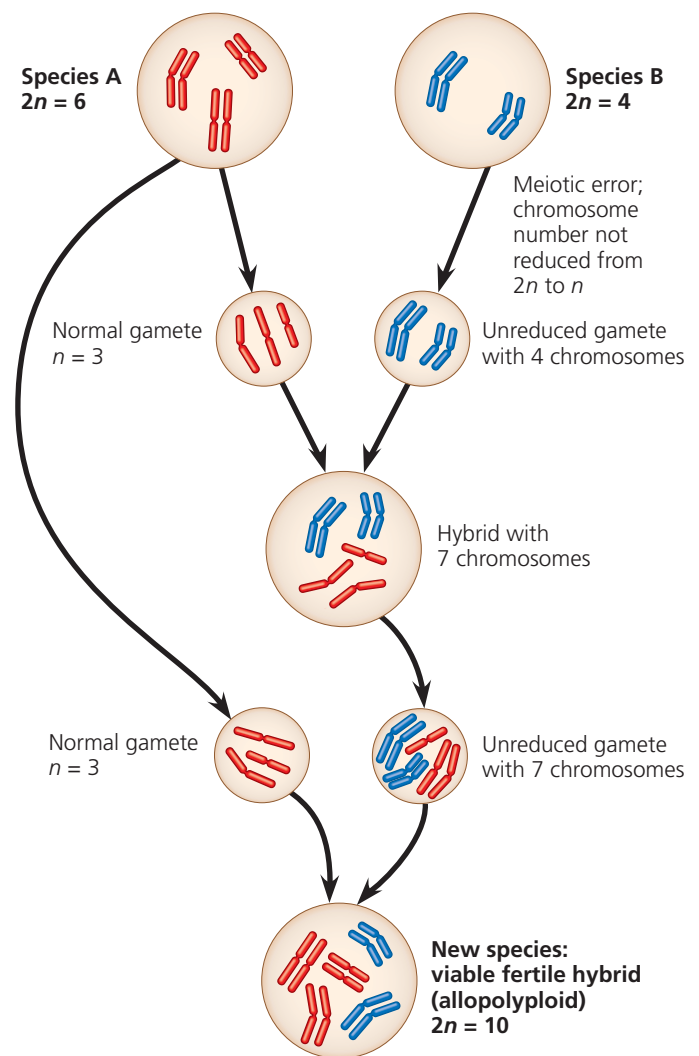
populations. An **autopolyploid** (from the Greek *autos*, self) is an individual that has more than two chromosome sets that are all derived from a single species. In plants, for example, a failure of cell division could double a cell's chromosome number from the diploid number ( $2n$ ) to a tetraploid number ( $4n$ ).

A tetraploid can produce fertile tetraploid offspring by



self-pollinating or by mating with other tetraploids. In addition, the tetraploids are reproductively isolated from diploid plants of the original population, because the triploid ( $3n$ ) offspring of such unions have reduced fertility. Thus, in just one generation, autopolyploidy can generate reproductive isolation without any geographic separation.

A second form of polyploidy can occur when two different species interbreed and produce hybrid offspring. Most such hybrids are sterile because the set of chromosomes from one species cannot pair during meiosis with the set of chromosomes from the other species. However, an infertile hybrid may be able to propagate itself asexually (as many plants can do). In subsequent generations, various mechanisms can change a sterile hybrid into a fertile polyploid called an **allopolyploid** (Figure 22.9). The allopolyploids are fertile when mating with



▲ **Figure 22.9 One mechanism for allopolyploid speciation in plants.** Most hybrids are sterile because their chromosomes are not homologous and cannot pair during meiosis. However, such a hybrid may be able to reproduce asexually. This diagram traces one mechanism that can produce fertile hybrids (allopolyploids) as new species. The new species has a diploid chromosome number equal to the sum of the diploid chromosome numbers of the two parent species.



each other but cannot interbreed with either parent species; thus, they represent a new biological species.

Although polyploid speciation is relatively rare, even in plants, scientists have documented that at least five new plant species have originated in this way since 1850. One of these examples involves the origin of a new species of goatsbeard plant (genus *Tragopogon*) in the Pacific Northwest. *Tragopogon* first arrived in the region when humans introduced three European species in the early 1900s. These three species are now common weeds in abandoned parking lots and other urban sites. In 1950, a new *Tragopogon* species was discovered near the Idaho-Washington border, a region where all three European species also were found. Genetic analyses revealed that this new species, *Tragopogon miscellus*, is a tetraploid hybrid of two of the European species. Although the *T. miscellus* population grows mainly by reproduction of its own members, additional episodes of hybridization between the parent species continue to add new members to the *T. miscellus* population—just one of many examples in which scientists have observed speciation in progress.

Many important agricultural crops—such as oats, cotton, potatoes, tobacco, and wheat—are polyploids. The wheat used for bread, *Triticum aestivum*, is an allohexaploid (six sets of chromosomes, two sets from each of three different species). The first of the polyploidy events that eventually led to modern wheat probably occurred about 8,000 years ago in the Middle East as a spontaneous hybrid of an early cultivated wheat species and a wild grass. Today, plant geneticists generate new polyploids in the laboratory by using chemicals that induce meiotic and mitotic errors. By harnessing the evolutionary process, researchers can produce new hybrid species with desired qualities, such as a hybrid that combines the high yield of wheat with the hardiness of rye.

### Habitat Differentiation

Sympatric speciation can also occur when genetic factors enable a subpopulation to exploit a habitat or resource not used by the parent population. Such is the case with the North American apple maggot fly (*Rhagoletis pomonella*), a pest of apples. The fly's original habitat was the native hawthorn tree, but about 200 years ago, some populations colonized apple trees that had been introduced by European settlers. As apples mature more quickly than hawthorn fruit, natural selection has favored apple-feeding flies with rapid development. These apple-feeding populations now show temporal isolation from the hawthorn-feeding *R. pomonella*, providing a prezygotic restriction to gene flow between the two populations. Researchers also have identified alleles that benefit the flies that use one host plant but harm the flies that use the other host plant. As a result, natural selection operating on these alleles provides a postzygotic barrier to reproduction, further limiting gene flow. Altogether, although the two populations are still classified as subspecies rather than separate species, sympatric speciation appears to be well under way.

### Sexual Selection

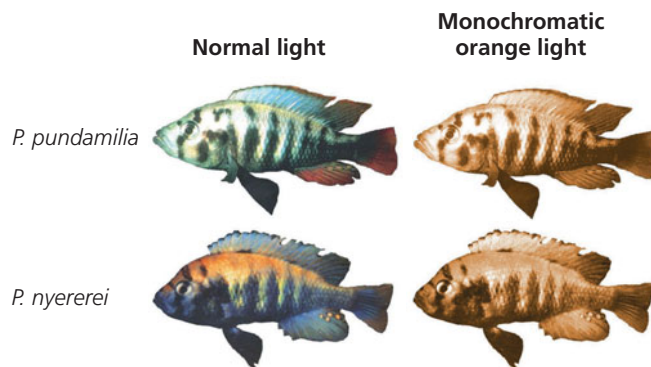
There is evidence that sympatric speciation can also be driven by sexual selection. Clues to how this can occur have been found in cichlid fishes from one of Earth's hot spots of animal speciation, East Africa's Lake Victoria. This lake was once home to as many as 600 species of cichlids. Genetic data indicate that these species originated within the last 100,000 years from a small number of colonizing species that arrived from rivers and lakes located elsewhere. How did so many species—more than double the number of freshwater fish species known in all of Europe—originate within a single lake?

One hypothesis is that subgroups of the original cichlid populations adapted to different food sources and that the resulting genetic divergence contributed to speciation in Lake Victoria.

#### ▼ Figure 22.10 Inquiry

#### Does sexual selection in cichlids result in reproductive isolation?

**Experiment** Researchers placed males and females of *Pundamilia pundamilia* and *P. nyererei* together in two aquarium tanks, one with natural light and one with a monochromatic orange lamp. Under normal light, the two species are noticeably different in male breeding coloration; under monochromatic orange light, the two species are very similar in color. The researchers then observed the mate choices of the females in each tank.



**Results** Under normal light, females of each species strongly preferred males of their own species. But under orange light, females of each species responded indiscriminately to males of both species. The resulting hybrids were viable and fertile.

**Conclusion** The researchers concluded that mate choice by females based on male breeding coloration is the main reproductive barrier that normally keeps the gene pools of these two species separate. Since the species can still interbreed when this prezygotic behavioral barrier is breached in the laboratory, the genetic divergence between the species is likely to be small. This suggests that speciation in nature has occurred relatively recently.

**Source** O. Seehausen and J. J. M. van Alphen, The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex), *Behavioral Ecology and Sociobiology* 42:1–8 (1998).

**WHAT IF?** Suppose that female cichlids living in the murky waters of a polluted lake could not distinguish colors well. How might the gene pools of these species change over time?

But sexual selection, in which (typically) females select males based on their appearance (see Chapter 21), may also have been a factor. Researchers have studied two closely related sympatric species of cichlids that differ mainly in the coloration of breeding males: Breeding *Pundamilia pundamilia* males have a blue-tinged back, whereas breeding *Pundamilia nyererei* males have a red-tinged back (Figure 22.10, on the preceding page). Their results suggest that mate choice based on male breeding coloration is the main reproductive barrier that normally keeps the gene pools of these two species separate.

### Allopatric and Sympatric Speciation: A Review

Now let's recap the two main modes by which new species form. In allopatric speciation, a new species forms in geographic isolation from its parent population. Geographic isolation severely restricts gene flow. As a result, other reproductive

barriers from the ancestral species may arise as a by-product of genetic changes that occur within the isolated population. Many different processes can produce such genetic changes, including natural selection under different environmental conditions, genetic drift, and sexual selection. Once formed, intrinsic reproductive barriers that arise in allopatric populations can prevent interbreeding with the parent population even if the populations come back into contact. In the **Scientific Skills Exercise**, you will interpret data from a study of reproductive isolation in geographically separated salamander populations.

Sympatric speciation, in contrast, requires the emergence of a reproductive barrier that isolates a subset of a population from the remainder of the population in the same area. Though rarer than allopatric speciation, sympatric speciation can occur when gene flow to and from the isolated subpopulation is blocked. This can occur as a result of polyploidy, a condition in which an organism has extra sets of chromosomes.

## Scientific Skills Exercise

### Identifying Independent and Dependent Variables, Making a Scatter Plot, and Interpreting Data

**Does Distance Between Salamander Populations Increase Their Reproductive Isolation?** The process of allopatric speciation begins when populations become geographically isolated, preventing mating between individuals in different populations and thus stopping gene flow. It seems logical that as distance between populations increases, so will their degree of reproductive isolation. To test this hypothesis, researchers studied populations of the dusky salamander (*Desmognathus ochrophaeus*) living on different mountain ranges in the southern Appalachian Mountains.


**How the Experiment Was Done** The researchers tested the reproductive isolation of pairs of salamander populations by leaving one male and one female together and later checking the females for the presence of sperm. Four mating combinations were tested for each pair of populations (A and B)—two *within* the same population (female A with male A and female B with male B) and two *between* populations (female A with male B and female B with male A).

**Data from the Experiment** The researchers used an index of reproductive isolation that ranged from a value of 0 (no isolation) to a value of 2 (full isolation). The proportion of successful matings for each mating combination was measured, with 100% success = 1 and no success = 0. The reproductive isolation value for two populations is the sum of the proportion of successful matings of each type within populations (AA + BB) minus the sum of the proportion of successful matings of each type between populations (AB + BA). The following table provides data for 27 pairs of dusky salamander populations:

#### Interpret the Data

1. State the researchers' hypothesis, and identify the independent and dependent variables in this study. Explain why the researchers used four mating combinations for each pair of populations.
2. Calculate the value of the reproductive isolation index if (a) *all* of the matings within a population were successful, but *none* of the matings between populations were successful; (b) salamanders are equally successful in mating with members of their own population and members of another population.
3. Make a scatter plot of one variable against the other to help you visualize whether or not there is a relationship between the variables. (For additional information about graphs, see the Scientific Skills Review in Appendix F and in the Study Area in MasteringBiology.) Plot the dependent variable on the y-axis and the independent variable on the x-axis.
4. Interpret your graph by (a) explaining in words the relationship between the variables that can be visualized by graphing the data and (b) hypothesizing the possible cause of this relationship.

**Data from** S. G. Tilley, P. A. Verrell, and S. J. Arnold, Correspondence between sexual isolation and allozyme differentiation: A test in the salamander *Desmognathus ochrophaeus*, *Proceedings of the National Academy of Sciences USA*. 87:2715–2719 (1990).

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

Geographic Distance (km)	15	32	40	47	42	62	63	81	86	107	107	115	137	147
Reproductive Isolation Value	0.32	0.54	0.50	0.50	0.82	0.37	0.67	0.53	1.15	0.73	0.82	0.81	0.87	0.87
Distance (continued)	137	150	165	189	219	239	247	53	55	62	105	179	169	
Isolation (continued)	0.50	0.57	0.91	0.93	1.50	1.22	0.82	0.99	0.21	0.56	0.41	0.72	1.15	

Sympatric speciation also can occur when a subset of a population becomes reproductively isolated because of natural selection that results from a switch to a habitat or food source not used by the parent population. Finally, sympatric speciation can result from sexual selection.

Having reviewed the geographic context in which species originate, we'll next explore in more detail what can happen when new or partially formed species come into contact.

#### CONCEPT CHECK 22.2

1. Summarize key differences between allopatric and sympatric speciation. Which type of speciation is more common, and why?
2. Describe two mechanisms that can decrease gene flow in sympatric populations, thereby making sympatric speciation more likely to occur.
3. **WHAT IF?** Is allopatric speciation more likely to occur on an island close to a mainland or on a more isolated island of the same size? Explain your prediction.
4. **MAKE CONNECTIONS** Review meiosis in Figure 10.8. Describe how an error during meiosis could lead to polyploidy.

For suggested answers, see Appendix A.

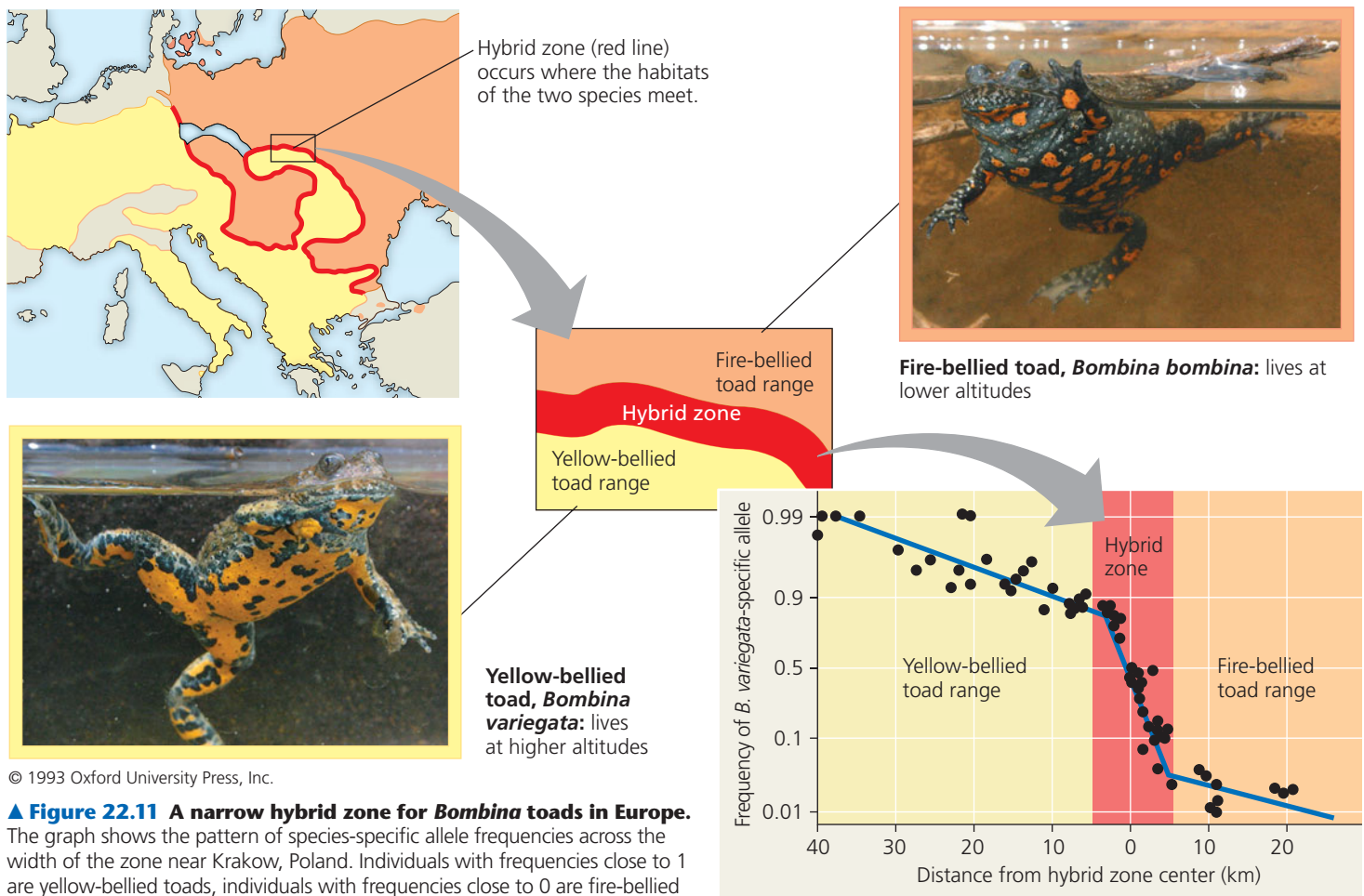
## CONCEPT 22.3

### Hybrid zones reveal factors that cause reproductive isolation

What happens if species with incomplete reproductive barriers come into contact with one another? One possible outcome is the formation of a **hybrid zone**, a region in which members of different species meet and mate, producing at least some offspring of mixed ancestry. In this section, we'll explore hybrid zones and what they reveal about factors that cause the evolution of reproductive isolation.

#### Patterns Within Hybrid Zones

Some hybrid zones form as narrow bands, such as the one depicted in **Figure 22.11** for two species of toads in the genus *Bombina*, the yellow-bellied toad (*B. variegata*) and the fire-bellied toad (*B. bombina*). This hybrid zone, represented by the red line on the map, extends for 4,000 km but is less than 10 km wide in most places. The hybrid zone occurs where the higher-altitude habitat of the yellow-bellied toad meets the



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**▲ Figure 22.11 A narrow hybrid zone for *Bombina* toads in Europe.**

The graph shows the pattern of species-specific allele frequencies across the width of the zone near Krakow, Poland. Individuals with frequencies close to 1 are yellow-bellied toads, individuals with frequencies close to 0 are fire-bellied toads, and individuals with intermediate frequencies are considered hybrids.

**?** Does the graph indicate that gene flow is spreading fire-bellied toad alleles into the range of the yellow-bellied toad? Explain.



lowland habitat of the fire-bellied toad. Across a given “slice” of the zone, the frequency of alleles specific to yellow-bellied toads typically decreases from about 90% at the edge where only yellow-bellied toads are found, to 50% in the central portion of the zone, to less than 10% at the edge where only fire-bellied toads are found.

What causes such a pattern of allele frequencies across a hybrid zone? We can infer that there is an obstacle to gene flow—otherwise, alleles from one parent species would also be common in the gene pool of the other parent species. Are geographic barriers reducing gene flow? Not in this case, since the toads can move throughout the hybrid zone. A more important factor is that hybrid toads have increased rates of embryonic mortality and a variety of morphological abnormalities, including ribs that are fused to the spine and malformed tadpole mouthparts. Because the hybrids have poor survival and reproduction, they produce few viable offspring with members of the parent species. As a result, hybrid individuals rarely serve as a stepping-stone from which alleles are passed from one species to the other. Outside the hybrid zone, additional obstacles to gene flow may be provided by natural selection in the different environments in which the parent species live.

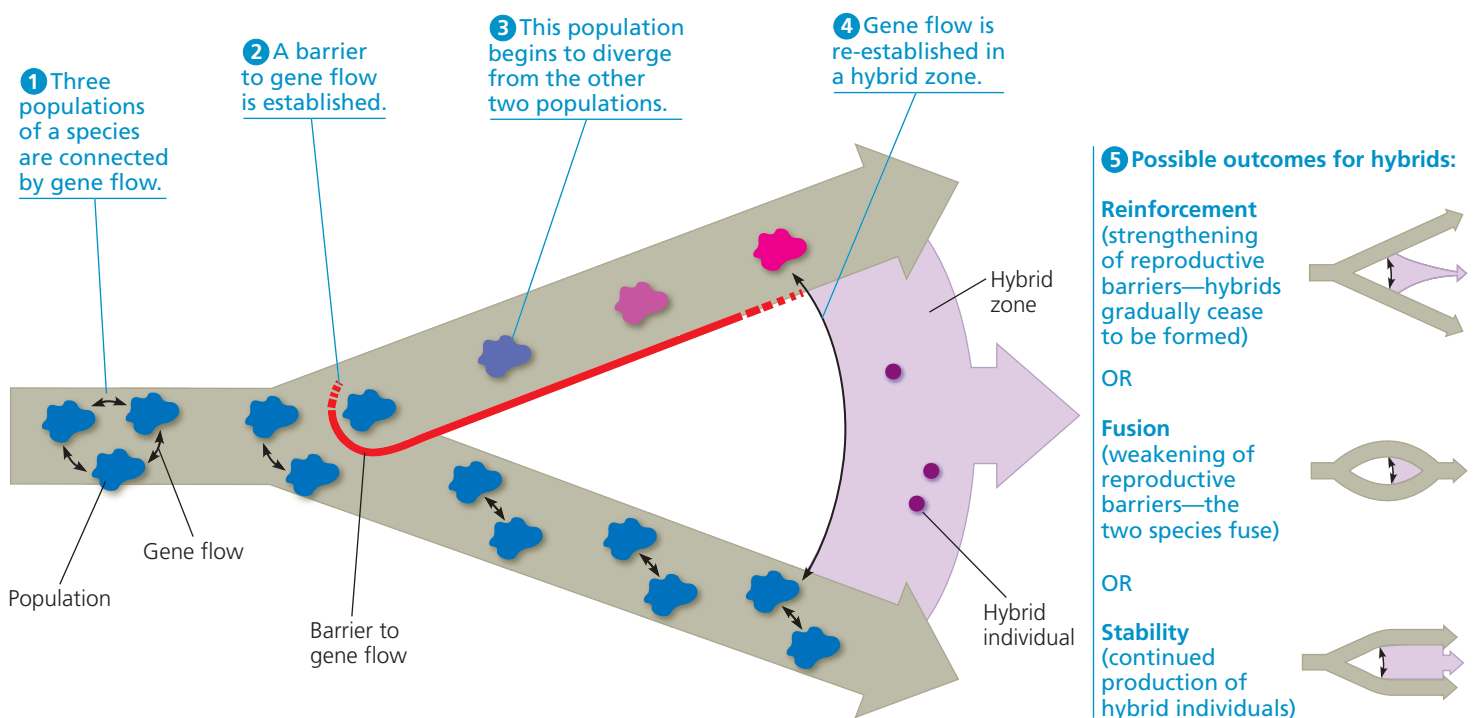
Hybrid zones typically are located wherever the habitats of the interbreeding species meet. Those regions often resemble a group of isolated patches scattered across the landscape—more like the complex pattern of spots on a Dalmatian than

the continuous band shown in Figure 22.11. But regardless of whether they have complex or simple spatial patterns, hybrid zones form when two species lacking complete barriers to reproduction come into contact. Once formed, how does a hybrid zone change over time?

## Hybrid Zones over Time

Studying a hybrid zone is like observing a naturally occurring experiment on speciation. Will the hybrids become reproductively isolated from their parents and form a new species, as occurred by polyploidy in the goatsbeard plant of the Pacific Northwest? If not, there are three possible outcomes for the hybrid zone over time: reinforcement of barriers, fusion of species, or stability (**Figure 22.12**). We'll discuss each of these outcomes in turn.

- **Reinforcement:** When hybrids are less fit than members of their parent species, natural selection tends to strengthen prezygotic barriers to reproduction, thus reducing the formation of unfit hybrids. Because this process involves *reinforcing* reproductive barriers, it is called reinforcement. If reinforcement is occurring, a logical prediction is that barriers to reproduction between species should be stronger for sympatric populations than for allopatric populations. Evidence in support of this prediction has been observed in birds, fishes, insects, plants, and other organisms.



▲ **Figure 22.12** Formation of a hybrid zone and possible outcomes for hybrids over time. The thick colored arrows represent the passage of time.

**WHAT IF?** Predict what might happen if gene flow were re-established at step 3 in this process.

- **Fusion:** Barriers to reproduction may be weak when two species meet in a hybrid zone. Indeed, so much gene flow may occur that reproductive barriers weaken further and the gene pools of the two species become increasingly alike. In effect, the speciation process reverses, eventually causing the two hybridizing species to fuse into a single species. Such a situation may be occurring among Lake Victoria cichlids. Many pairs of ecologically similar cichlid species are reproductively isolated because the females of one species prefer to mate with males of one color, while females of the other species prefer to mate with males of a different color (see Figure 22.10). Murky waters caused by pollution may have reduced the ability of females to use color to distinguish males of their own species from males of closely related species. In some polluted waters, many hybrids have been produced, leading to fusion of the parent species' gene pools and a loss of species (**Figure 22.13**).
- **Stability:** Many hybrid zones are stable in the sense that hybrids continue to be produced. In some cases, this occurs because the hybrids survive or reproduce better than members of either parent species, at least in certain habitats or years. But stable hybrid zones have also been observed in cases where the hybrids are selected *against*—an unexpected result. For example, hybrids continue to be formed in the *Bombina* hybrid zone even though they are strongly selected against. What could explain this finding? One possibility relates to the narrowness of the *Bombina* hybrid

zone (see Figure 22.11). Evidence suggests that members of both parent species migrate into the zone from the parent populations located outside the zone, thus leading to the continued production of hybrids. If the hybrid zone were wider, this would be less likely to occur, since the center of the zone would receive little gene flow from distant parent populations located outside the hybrid zone.

As we've seen, events in hybrid zones can shed light on how barriers to reproduction between closely related species change over time. In the next section, we'll examine how interactions between hybridizing species can also provide a glimpse into the speed and genetic control of speciation.

### CONCEPT CHECK 22.3

1. What are hybrid zones, and why can they be viewed as "natural laboratories" in which to study speciation?
2. **WHAT IF?** Consider two species that diverged while geographically separated but resumed contact before reproductive isolation was complete. Predict what would happen over time if the two species mated indiscriminately and (a) hybrid offspring survived and reproduced more poorly than offspring from intraspecific matings or (b) hybrid offspring survived and reproduced as well as offspring from intraspecific matings.

For suggested answers, see Appendix A.

## CONCEPT 22.4

### Speciation can occur rapidly or slowly and can result from changes in few or many genes

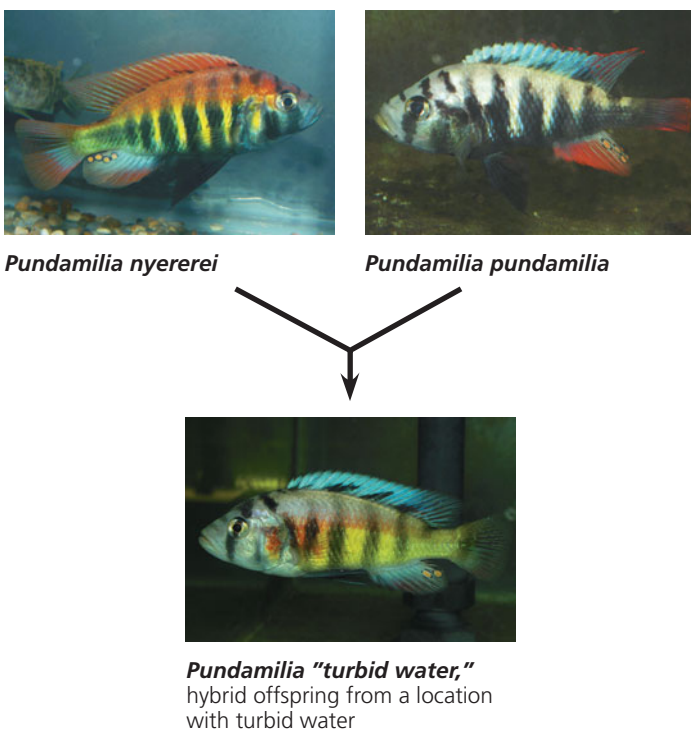
Darwin faced many questions when he began to ponder that "mystery of mysteries"—speciation. He found answers to some of those questions when he realized that evolution by natural selection helps explain both the diversity of life and the adaptations of organisms (see Chapter 19). But biologists since Darwin have continued to ask fundamental questions about speciation. For example, how long does it take for new species to form? And how many genes change when one species splits into two? Answers to these questions are also beginning to emerge.

### The Time Course of Speciation

We can gather information about how long it takes new species to form from broad patterns in the fossil record and from studies that use morphological data (including fossils) or molecular data to assess the time interval between speciation events in particular groups of organisms.

### Patterns in the Fossil Record

The fossil record includes many episodes in which new species appear suddenly in a geologic stratum, persist essentially unchanged through several strata, and then disappear. For example, there are dozens of species of marine invertebrates that make

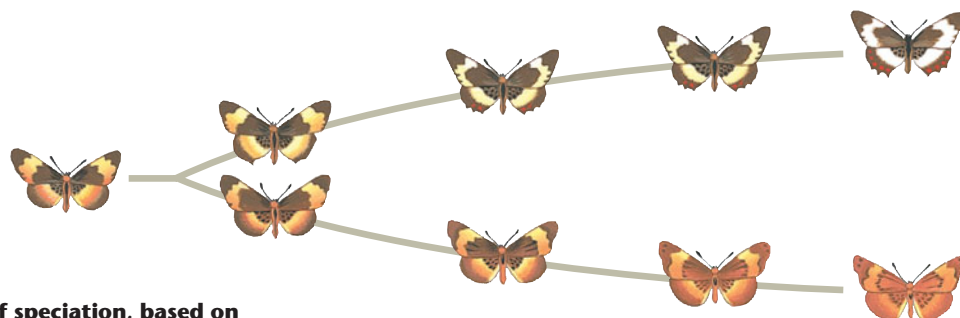


**▲ Figure 22.13 Fusion: The breakdown of reproductive barriers.** Increasingly cloudy water in Lake Victoria over the past 30 years may have weakened reproductive barriers between *P. nyererei* and *P. pundamilia*. In areas of cloudy water, the two species have hybridized extensively, causing their gene pools to fuse.

(a) In a punctuated model, new species change most as they branch from a parent species and then change little for the rest of their existence.



(b) In a gradual model, species diverge from one another more slowly and steadily over time.



▲ **Figure 22.14** Two models for the tempo of speciation, based on patterns observed in the fossil record.

their debut in the fossil record with novel morphologies, but then change little for millions of years before becoming extinct. Paleontologists Niles Eldredge and Stephen Jay Gould coined the term **punctuated equilibria** to describe these patterns in the fossil record: periods of apparent stasis punctuated by sudden change (**Figure 22.14a**). Other species do not show a punctuated pattern; instead, they appear to have changed more gradually over long periods of time (**Figure 22.14b**). For example, the fossil record shows that many species of trilobites (early arthropods) changed gradually over the course of 10–20 million years.

What might punctuated and gradual patterns tell us about how long it takes new species to form? Suppose that a species survived for 5 million years, but most of the morphological changes that caused it to be designated a new species occurred during the first 50,000 years of its existence—just 1% of its total lifetime. Time periods this short (in geologic terms) often cannot be distinguished in fossil strata, in part because the rate of sediment accumulation may be too slow to separate layers formed so close together in time. Thus, based on its fossils, the species would seem to have appeared suddenly and then lingered with little or no change before becoming extinct. Even though such a species may have originated more slowly than its fossils suggest (in this case taking up to 50,000 years), a punctuated pattern indicates that speciation occurred relatively rapidly. For species whose fossils changed much more gradually, we also cannot tell exactly when a new biological species formed, since information about reproductive isolation does not fossilize. However, it is likely that speciation in such groups occurred relatively slowly, perhaps taking millions of years.

### Speciation Rates

The existence of fossils that display a punctuated pattern suggests that once the process of speciation begins, it can be completed relatively rapidly—a suggestion supported by recent

studies. For example, rapid speciation appears to have produced the wild sunflower *Helianthus anomalus*. Genetic evidence indicates that this species originated by the hybridization of two other sunflower species, *H. annuus* and *H. petiolaris*. The hybrid species *H. anomalus* is ecologically distinct and reproductively isolated from both parent species (**Figure 22.15**). Unlike the outcome of allopolyploid speciation, in which there is a change in chromosome number after hybridization, in these sunflowers the two parent species and the hybrid all have the same number of chromosomes ( $2n = 34$ ). How, then, did speciation occur? To study this question, researchers performed an experiment designed to mimic events in nature: They crossed the



▲ **Figure 22.15** A hybrid sunflower species and its dry sand dune habitat. The wild sunflower *Helianthus anomalus* originated via the hybridization of two other sunflowers, *H. annuus* and *H. petiolaris*, which live in nearby but moister environments.



two parent species and followed the fate of the hybrid offspring over several generations (**Figure 22.16**). Their results indicated that natural selection could produce extensive genetic changes in hybrid populations over short periods of time. These changes appear to have caused the hybrids to diverge reproductively from their parents and form a new species, *H. anomalus*.

The sunflower example, along with the apple maggot fly, Lake Victoria cichlid, and fruit fly examples discussed earlier, suggests that new species can arise rapidly *once divergence begins*. But what is the total length of time between speciation events? This interval consists of the time that elapses before populations of a newly formed species start to diverge from one another plus the time it takes for speciation to be complete once divergence begins. It turns out that the total time between speciation events varies considerably. For example, in a survey of data from 84 groups of plants and animals, the interval between speciation events ranged from 4,000 years (in cichlids of Lake Nabugabo, Uganda) to 40 million years (in some beetles). Overall, the time between speciation events in the groups studied averaged 6.5 million years and was rarely less than 500,000 years.

These data suggest that on average, millions of years may pass before a newly formed plant or animal species will itself give rise to another new species. As we'll see in Chapter 23, this finding has implications for how long it takes life on Earth to recover from mass extinction events. Moreover, the extreme variability in the time it takes new species to form indicates that organisms do not have a "speciation clock" ticking inside them, causing them to produce new species at regular time intervals. Instead, speciation begins only after gene flow between populations is interrupted, perhaps by changing environmental conditions or by unpredictable events, such as a storm that transports a few individuals to an isolated area. Furthermore, once gene flow is interrupted, the populations must diverge genetically to such an extent that they become reproductively isolated—all before other events cause gene flow to resume, possibly reversing the speciation process (see Figure 22.13).

## Studying the Genetics of Speciation

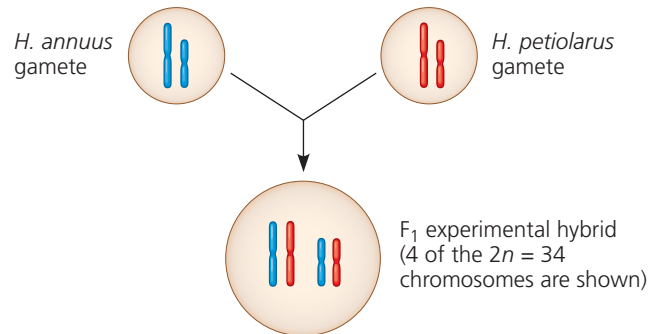
The central quest of studying the genetics of speciation is to identify genes that cause reproductive isolation. In general, genes that influence a particular trait can be identified by performing genetic crosses and analyzing gene linkages—but such studies are by definition hard to do when studying different species (since they do not interbreed). However, studies of ongoing speciation (as in hybrid zones) have uncovered specific traits that cause reproductive isolation. By identifying the genes that control those traits, scientists can explore a fundamental question of evolutionary biology: How many genes change when a new species forms?

In a few cases, the evolution of reproductive isolation is due to a change in a single gene. For example, in Japanese snails of the genus *Euhadra*, a change in a single gene results in a

## ▼ Figure 22.16 Inquiry

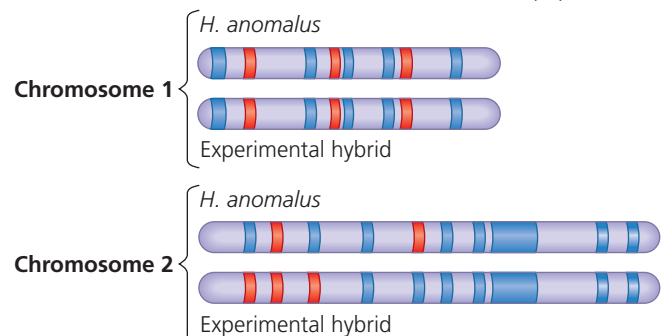
### How does hybridization lead to speciation in sunflowers?

**Experiment** Researchers crossed the two parent sunflower species, *H. annuus* and *H. petiolaris*, to produce experimental hybrids in the laboratory (for each gamete, only two of the  $n = 17$  chromosomes are shown).



Note that in the first ( $F_1$ ) generation, each chromosome of the experimental hybrids consisted entirely of DNA from one or the other parent species. The researchers then tested whether the  $F_1$  and subsequent generations of experimental hybrids were fertile. They also used species-specific genetic markers to compare the chromosomes in the experimental hybrids with the chromosomes in the naturally occurring hybrid *H. anomalus*.

**Results** Although only 5% of the  $F_1$  experimental hybrids were fertile, after just four more generations the hybrid fertility rose to more than 90%. The chromosomes of individuals from this fifth hybrid generation differed from those in the  $F_1$  generation (see above) but were similar to those in *H. anomalus* individuals from natural populations:



■ Comparison region containing *H. annuus*-specific marker  
 ■ Comparison region containing *H. petiolaris*-specific marker  
 © 1996 AAAS

**Conclusion** Over time, the chromosomes in the population of experimental hybrids became similar to the chromosomes of *H. anomalus* individuals from natural populations. This suggests that the observed rise in the fertility of the experimental hybrids may have occurred as selection eliminated regions of DNA from the parent species that were not compatible with one another. Overall, it appeared that the initial steps of the speciation process occurred rapidly and could be mimicked in a laboratory experiment.

**Source** L. H. Rieseberg et al., Role of gene interactions in hybrid speciation: Evidence from ancient and experimental hybrids, *Science* 272:741–745 (1996).

**WHAT IF?** The increased fertility of the experimental hybrids could have resulted from natural selection for thriving under laboratory conditions. Evaluate this alternative explanation for the result.

mechanical barrier to reproduction. This gene controls the direction in which the shells spiral. When their shells spiral in different directions, the snails' genitalia are oriented in a manner that prevents mating (Figure 22.3f shows a similar example in a different genus of snail).

A major barrier to reproduction between two closely related species of monkey flower, *Mimulus cardinalis* and *M. lewisii*, also appears to be influenced by a relatively small number of genes. These two species are isolated by several prezygotic and postzygotic barriers. Of these, one prezygotic barrier, pollinator choice, accounts for most of the isolation: In a hybrid zone between *M. cardinalis* and *M. lewisii*, nearly 98% of pollinator visits were restricted to one species or the other.

The two monkey flower species are visited by different pollinators: Hummingbirds prefer the red-flowered *M. cardinalis*, and bumblebees prefer the pink-flowered *M. lewisii*. Pollinator choice is affected by at least two loci in the monkey flowers, one of which, the “yellow upper,” or *yup*, locus, influences flower color (Figure 22.17). By crossing the two parent species to produce F<sub>1</sub> hybrids and then performing repeated backcrosses of these F<sub>1</sub> hybrids to each parent species, researchers succeeded in transferring the *M. cardinalis* allele at this locus into *M. lewisii*, and vice versa. In a field experiment, *M. lewisii* plants with the *M. cardinalis* *yup* allele received 68-fold more visits from hummingbirds than did wild-type *M. lewisii*. Similarly, *M. cardinalis* plants with the *M. lewisii* *yup* allele received 74-fold more visits from bumblebees than did wild-type *M. cardinalis*. Thus, a mutation at a single locus can influence pollinator preference and hence contribute to reproductive isolation in monkey flowers.

In other organisms, the speciation process is influenced by larger numbers of genes and gene interactions. For example, hybrid sterility between two subspecies of the fruit fly *Drosophila pseudoobscura* results from gene interactions among at least four loci, and postzygotic isolation in the sunflower hybrid zone discussed earlier is influenced by at least 26 chromosome segments (and an unknown number of genes). Overall, studies suggest that few or many genes can influence the evolution of reproductive isolation and hence the emergence of a new species.

## From Speciation to Macroevolution

As you've seen, speciation may begin with differences as seemingly small as the color on a cichlid's back. However, as speciation occurs again and again, such differences can accumulate and become more pronounced, eventually leading to the formation of new groups of organisms that differ greatly from their ancestors (as in the origin of whales from land-dwelling mammals; see Figure 19.20). Furthermore, as one group of organisms increases in size by producing many new species, another group of organisms may shrink, losing species to extinction. The cumulative effects of many such speciation and extinction events have helped shape the sweeping evolutionary



(a) Typical *Mimulus lewisii*



(b) *M. lewisii* with an *M. cardinalis* flower-color allele



(c) Typical *Mimulus cardinalis*



(d) *M. cardinalis* with an *M. lewisii* flower-color allele

### ▲ Figure 22.17 A locus that influences pollinator choice.

Pollinator preferences provide a strong barrier to reproduction between *Mimulus lewisii* and *M. cardinalis*. After transferring the *M. lewisii* allele for a flower-color locus into *M. cardinalis* and vice versa, researchers observed a shift in some pollinators' preferences.

**WHAT IF?** If *M. cardinalis* individuals that had the *M. lewisii* *yup* allele were planted in an area that housed both monkey flower species, how might the production of hybrid offspring be affected?

changes that are documented in the fossil record. In the next chapter, we turn to such large-scale evolutionary changes as we begin our study of macroevolution.

### CONCEPT CHECK 22.4

1. Speciation can occur rapidly between diverging populations, yet the length of time between speciation events is often more than a million years. Explain this apparent contradiction.
2. Summarize evidence that the *yup* locus acts as a prezygotic barrier to reproduction in two species of monkey flowers. Do these results demonstrate that the *yup* locus alone controls barriers to reproduction between these species? Explain.
3. **MAKE CONNECTIONS** Compare Figure 10.11 with Figure 22.16. What cellular process could cause the hybrid chromosomes in Figure 22.16 to contain DNA from both parent species? Explain.

For suggested answers, see Appendix A.

# 22 Chapter Review

## SUMMARY OF KEY CONCEPTS

### CONCEPT 22.1

#### The biological species concept emphasizes reproductive isolation (pp. 418–422)

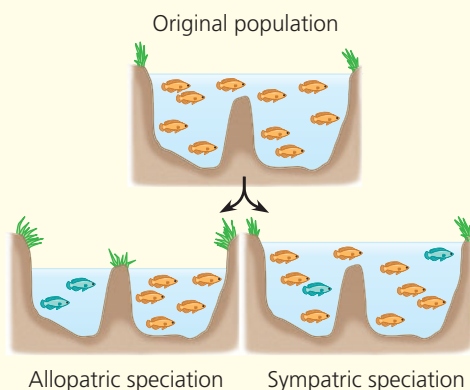
- A biological **species** is a group of populations whose individuals have the potential to interbreed and produce viable, fertile offspring with each other but not with members of other species. The **biological species concept** emphasizes reproductive isolation through prezygotic and postzygotic barriers that separate gene pools.
- Although helpful in thinking about how speciation occurs, the biological species concept has limitations. For instance, it cannot be applied to organisms known only as fossils or to organisms that reproduce only asexually. Thus, scientists use other species concepts, such as the **morphological species concept**, in certain circumstances.

? Explain the importance of gene flow to the biological species concept.

### CONCEPT 22.2

#### Speciation can take place with or without geographic separation (pp. 423–428)

- In **allopatric speciation**, gene flow is reduced when two populations of one species become geographically separated from each other. One or both populations may undergo evolutionary change during the period of separation, resulting in the establishment of prezygotic or postzygotic barriers to reproduction.
- In **sympatric speciation**, a new species originates while remaining in the same geographic area as the parent species. Plant species (and, more rarely, animal species) have evolved sympatrically through polyploidy. Sympatric speciation can also result from habitat shifts and sexual selection.



? Can factors that cause sympatric speciation also cause allopatric speciation? Explain.

### CONCEPT 22.3

#### Hybrid zones reveal factors that cause reproductive isolation (pp. 428–430)

- Many groups of organisms form **hybrid zones** in which members of different species meet and mate, producing at least some offspring of mixed ancestry.

- Many hybrid zones exhibit **stability** in that hybrid offspring continue to be produced over time. In others, **reinforcement** strengthens prezygotic barriers to reproduction, thus decreasing the formation of unfit hybrids. In still other hybrid zones, barriers to reproduction may weaken over time, resulting in the **fusion** of the species' gene pools (reversing the speciation process).

? What factors can support the long-term stability of a hybrid zone if the parent species live in different environments?

### CONCEPT 22.4

#### Speciation can occur rapidly or slowly and can result from changes in few or many genes (pp. 430–433)

- New species can form rapidly once divergence begins—but it can take millions of years for that to happen. The time interval between speciation events varies considerably, from a few thousand years to tens of millions of years.
- New developments in genetics have enabled researchers to identify specific genes involved in some cases of speciation. Results show that speciation can be driven by few or many genes.

? Is speciation something that happened only in the distant past, or are new species continuing to arise today? Explain.

## TEST YOUR UNDERSTANDING

### Level 1: Knowledge/Comprehension

1. The *largest* unit within which gene flow can readily occur is a
  - a. population.
  - b. species.
  - c. genus.
  - d. hybrid.
  - e. phylum.
2. Males of different species of the fruit fly *Drosophila* that live in the same parts of the Hawaiian Islands have different elaborate courtship rituals. These rituals involve fighting other males and making stylized movements that attract females. What type of reproductive isolation does this represent?
  - a. habitat isolation
  - b. temporal isolation
  - c. behavioral isolation
  - d. gametic isolation
  - e. postzygotic barriers
3. According to the punctuated equilibria model,
  - a. natural selection is unimportant as a mechanism of evolution.
  - b. given enough time, most existing species will branch gradually into new species.
  - c. most new species accumulate their unique features relatively rapidly as they come into existence, then change little for the rest of their duration as a species.
  - d. most evolution occurs in sympatric populations.
  - e. speciation is usually due to a single mutation.

### Level 2: Application/Analysis

4. Bird guides once listed the myrtle warbler and Audubon's warbler as distinct species. Recently, these birds have been reclassified as eastern and western forms of a single species, the



yellow-rumped warbler. Which of the following pieces of evidence, if true, would be cause for this reclassification?

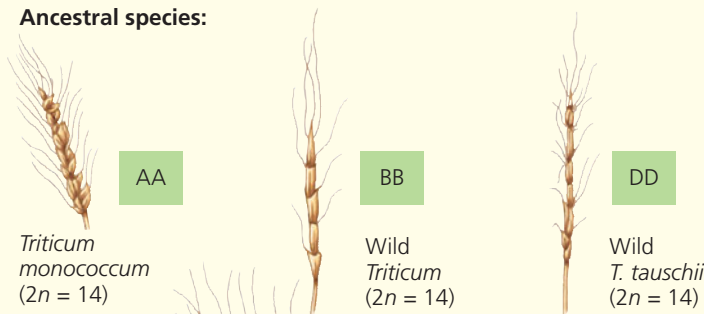
- The two forms interbreed often in nature, and their offspring survive and reproduce well.
  - The two forms live in similar habitats.
  - The two forms have many genes in common.
  - The two forms have similar food requirements.
  - The two forms are very similar in coloration.
5. Which of the following factors would *not* contribute to allopatric speciation?
- A population becomes geographically isolated from the parent population.
  - The separated population is small, and genetic drift occurs.
  - The isolated population is exposed to different selection pressures than the ancestral population.
  - Different mutations begin to distinguish the gene pools of the separated populations.
  - Gene flow between the two populations is extensive.
6. Plant species A has a diploid number of 12. Plant species B has a diploid number of 16. A new species, C, arises as an allopolyploid from A and B. The diploid number for species C would probably be
- 12.
  - 14.
  - 16.
  - 28.
  - 56.

### Level 3: Synthesis/Evaluation

#### 7. SCIENTIFIC INQUIRY

**DRAW IT** In this chapter, you read that bread wheat (*Triticum aestivum*) is an allohexaploid, containing two sets of chromosomes from each of three different parent species. Genetic analysis suggests that the three species pictured following this question each contributed chromosome sets to *T. aestivum*. (The capital letters here represent sets of chromosomes rather than individual genes.) Evidence also indicates that the first polyploidy event was a spontaneous hybridization of the early cultivated wheat species *T. monococcum* and a wild *Triticum* grass species. Based on this information, draw a diagram of one possible chain of events that could have produced the allohexaploid *T. aestivum*.

#### Ancestral species:



#### Product:



#### 8. SCIENCE, TECHNOLOGY, AND SOCIETY

In the United States, the rare red wolf (*Canis lupus*) has been known to hybridize with coyotes (*Canis latrans*), which are much more numerous. Although red wolves and coyotes differ in terms of morphology, DNA, and behavior, genetic evidence suggests that living red wolf individuals are actually hybrids. Red wolves are designated as an endangered species and hence receive legal protection under the Endangered Species Act. Some people think that their endangered status should be withdrawn because the remaining red wolves are hybrids, not members of a “pure” species. Do you agree? Why or why not?

#### 9. FOCUS ON EVOLUTION

What is the biological basis for assigning all human populations to a single species? Can you think of a scenario by which a second human species could originate in the future?

#### 10. FOCUS ON INFORMATION

In sexually reproducing species, each individual begins life with DNA inherited from both parent organisms. In a short essay (100–150 words), apply this idea to what occurs when organisms of two species that have homologous chromosomes mate and produce ( $F_1$ ) hybrid offspring. What percentage of the DNA in the  $F_1$  hybrids’ chromosomes comes from each parent species? As the hybrids mate and produce  $F_2$  and later-generation hybrid offspring, describe how recombination and natural selection may affect whether the DNA in hybrid chromosomes is derived from one parent species or the other.

For selected answers, see Appendix A.

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# Broad Patterns of Evolution

▼ **Figure 23.1** On what continent did these dinosaurs roam?



## KEY CONCEPTS

**23.1** The fossil record documents life's history

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

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

**23.4** Evolution is not goal oriented

## OVERVIEW

### Lost Worlds

**E**arly Antarctic explorers encountered one of Earth's harshest, most barren environments, a land of extreme cold and almost no liquid water.

Antarctic life is sparse and small—the largest fully terrestrial animal is a fly 5 mm long. But even as they struggled to survive, some of these explorers made an astonishing discovery: fossil evidence that life once



▲ *Cryolophosaurus* skull

thrived where it now barely exists. Fossils reveal that 500 million years ago, the ocean around Antarctica was warm and teeming with tropical invertebrates. Later, the continent was covered in forests for hundreds of millions of years. At various times, diverse animals stalked through these forests, including 3-m-tall predatory “terror birds” and giant dinosaurs, such as the voracious *Cryolophosaurus* (**Figure 23.1**), a 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. In this chapter, we'll examine how fossils form and the evidence they provide about the pattern of life's evolution, focusing on factors that have helped shape the rise and fall of different groups of organisms over time. The next unit (Chapters 24–27) will explore major steps in the history of life.

## CONCEPT

### 23.1

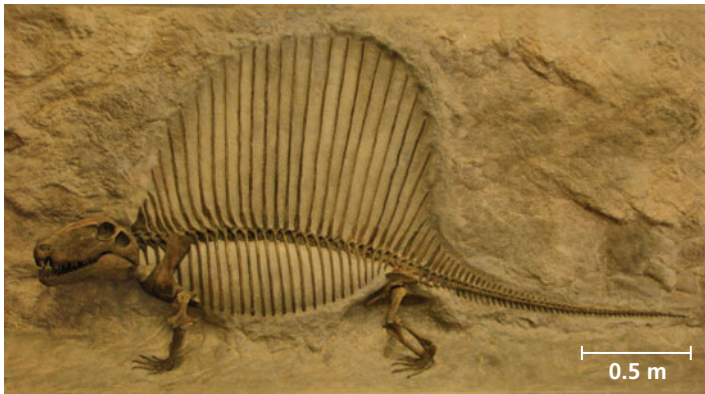
### The fossil record documents life's history

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 (**Figure 23.2**). In this section, we'll examine fossils as a form of scientific evidence: how fossils form, how scientists date and interpret them, and what they can and cannot tell us about changes in the history of life.



▼ **Figure 23.2 Documenting the history of life.** These fossils illustrate representative organisms from different points in time. Although prokaryotes and unicellular eukaryotes are shown only at the base of the diagram, these organisms continue to thrive today. In fact, most organisms on Earth are unicellular.

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



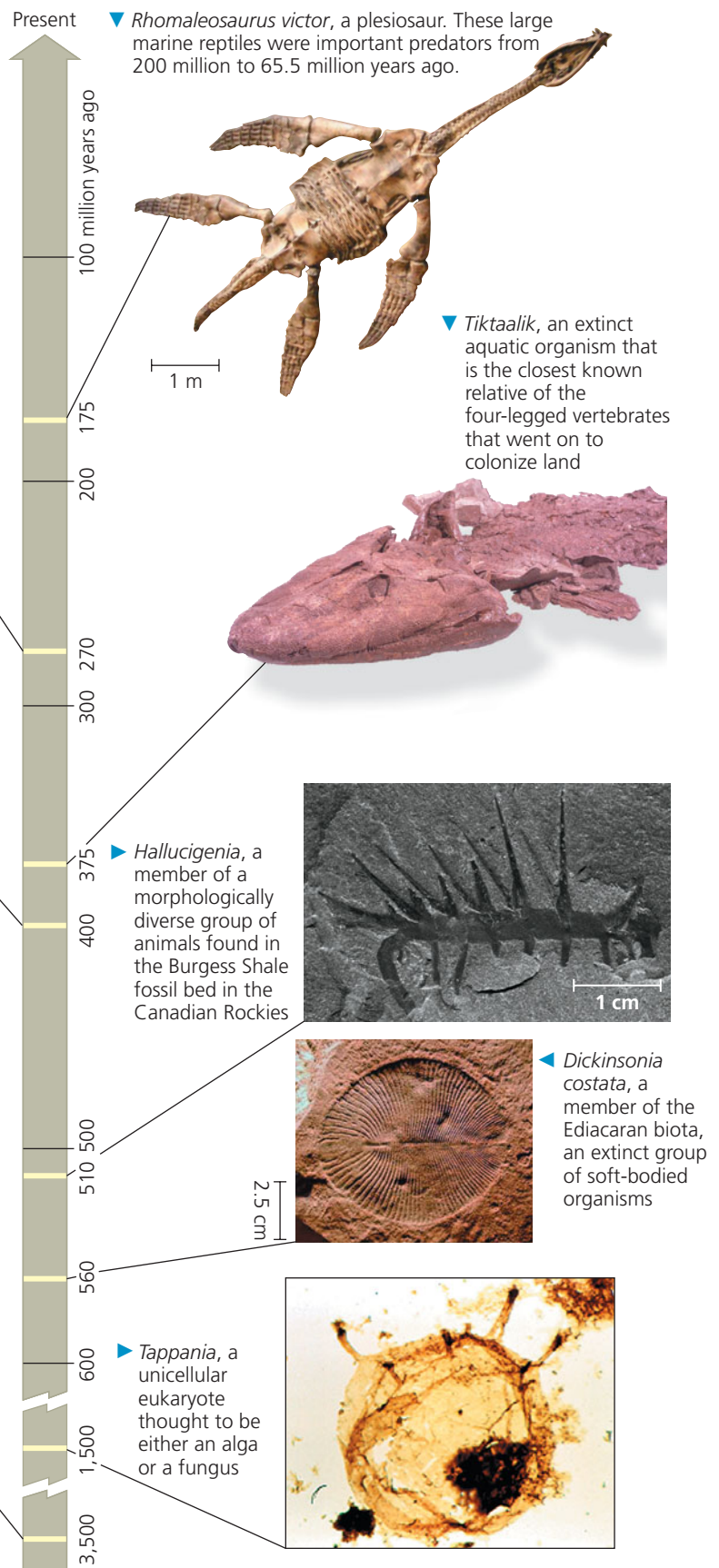
▲ *Coccosteus cuspidatus*, a placoderm (fishlike vertebrate) that had a bony shield covering its head and front end



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



▲ A section through a fossilized stromatolite





## The Fossil Record

Sedimentary rocks are the richest source of fossils. As a result, the fossil record is based primarily on the sequence in which fossils have accumulated in sedimentary rock layers, called *strata* (see Figure 19.3). Useful information is also provided by other types of fossils, such as insects preserved in amber (fossilized tree sap) and mammals frozen in ice.

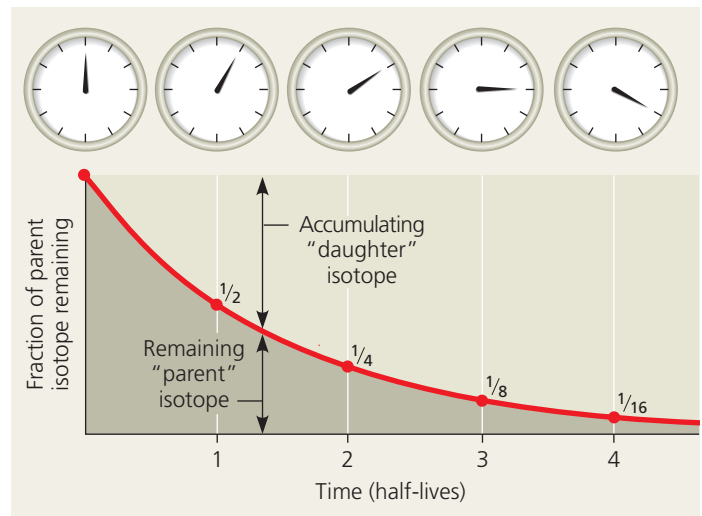
The fossil record shows that there have been great changes in the kinds of organisms on Earth at different points in time (Figure 23.2). Many past organisms were unlike organisms living today, and many organisms that once were common are now extinct. As we'll see later in this section, fossils also document how new groups of organisms arose from previously existing ones.

As substantial and significant as the fossil record is, keep in mind that it is an incomplete chronicle of evolutionary change. Many of Earth's organisms did not die in the right place at the right time to be preserved as fossils. Of those fossils that were formed, many were destroyed by later geologic processes, and only a fraction of the others have been discovered. As a result, the known fossil record is biased in favor of species that existed for a long time, were abundant and widespread in certain kinds of environments, and had hard shells, skeletons, or other parts that facilitated their 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 19.18 and 19.19), gaps in the fossil record continue to be filled by new discoveries. Although some of these discoveries are fortuitous, others illustrate the predictive nature of paleontology (see Figure 27.22).

## How Rocks and Fossils Are Dated

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

How can we determine the absolute age of a fossil? (Note that “absolute” 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 characteristic rate. The rate of decay is expressed by the **half-life**, the time required for 50% of the parent isotope to decay (Figure 23.3). 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



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▲ **Figure 23.3 Radiometric dating.** In this diagram, each division of the clock face represents a half-life.

quickly; it has a half-life of 5,730 years. Uranium-238 decays slowly; its half-life is 4.5 billion years.












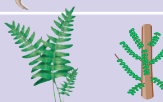



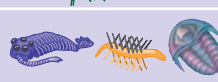


Fossils contain isotopes of elements that accumulated in the organisms when they were alive. For example, a living organism contains the most common carbon isotope, carbon-12, as well as a radioactive isotope, carbon-14. When the organism dies, it stops accumulating carbon, and the amount of carbon-12 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. In addition, the sedimentary rocks themselves tend to consist of sediments of differing ages. So while we may not be able to date these older fossils directly, an indirect method can be used to infer the age of fossils that are sandwiched between two layers of volcanic rock. As lava cools into volcanic rock, radioisotopes from the surrounding environment become trapped in the newly formed rock. Some of the trapped radioisotopes have long half-lives, allowing geologists to estimate the ages of ancient volcanic rocks. If two volcanic layers surrounding fossils are determined to be 525 million and 535 million years old, for example, then the fossils are roughly 530 million years old.

## The Geologic Record

The study of fossils has helped geologists establish a **geologic record**, a standard time scale that divides Earth's history into four eons and further subdivisions (Table 23.1). The first three

**Table 23.1 The Geologic Record**

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

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

The earliest direct evidence of life comes from the Archaean eon, based on 3.5 billion-year-old fossils of stromatolites (see Figure 23.2). **Stromatolites** are layered rocks that form when certain prokaryotes bind thin films of sediment together. These and other early prokaryotes were Earth’s sole inhabitants for more than 1.5 billion years. Early prokaryotes transformed life on our planet by releasing oxygen to the atmosphere during the water-splitting step of photosynthesis (see Chapter 24).

The ensuing increase in atmospheric oxygen—a process that began about 2.4 billion years ago—led to the extinction of some organisms and the proliferation of others. One group that flourished was the eukaryotes, which originated about 1.8 billion years ago (see Chapter 25). The rise of the eukaryotes was associated with a series of other key events in the history of life, including the origin of multicellular organisms and the colonization of land. Fossil evidence and molecular clock estimates based on DNA sequence data suggest that simple multicellular organisms emerged about 1.5 billion years ago. Later, more complex multicellular organisms arose independently in several groups of eukaryotes, including those that eventually moved onto land: plants, fungi, and animals (see Chapters 26 and 27).

## 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. 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 23.4**, 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 23.4, bear in mind that it includes just a few examples of the fossil skulls that document the origin of mammals. If all the known fossils in the sequence were arranged by shape and placed side by side, their features would blend smoothly from one group to the next. Some of these fossils would reflect how the features of a group that dominates life today, the mammals, gradually arose in a previously existing group, the cynodonts. Others would reveal side branches on the tree of life—groups of organisms that thrived for millions of years but ultimately left no descendants that survive today.

### CONCEPT CHECK 23.1

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. **DRAW IT** Relabel the x-axis of the graph in Figure 23.3 with time measurements in years to illustrate the radioactive decay of uranium-238 (half-life = 4.5 billion years).
4. **WHAT IF?** What would a fossil record of life today look like?
5. **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 23.2

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

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

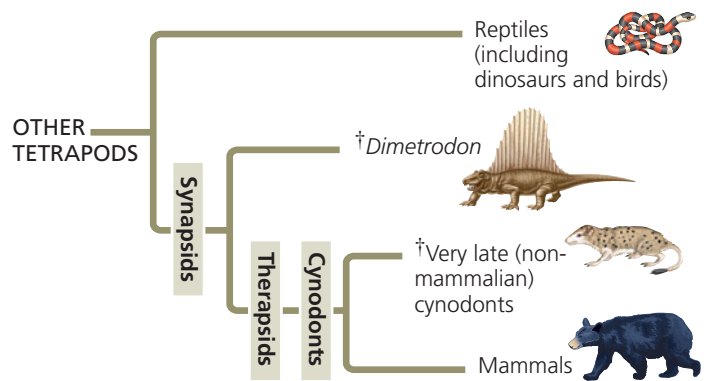
The rise and fall of these and other major groups of organisms have shaped the history of life. Narrowing our focus, we can also see that the rise or fall of any particular group of organisms is related to the speciation and extinction rates of



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 early synapsid ancestors. The evolutionary context of the origin of mammals is shown in the tree diagram at right (the dagger symbol † indicates extinct lineages).

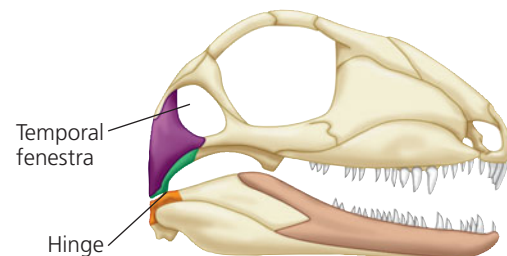
#### Key to skull bones

- |   |   |
|---|---|
| <span style="display:inline-block; width:15px; height:15px; background-color:orange; border:1px solid black;"></span> Articular | <span style="display:inline-block; width:15px; height:15px; background-color:lightbrown; border:1px solid black;"></span> Dentary |
| <span style="display:inline-block; width:15px; height:15px; background-color:green; border:1px solid black;"></span> Quadrate   | <span style="display:inline-block; width:15px; height:15px; background-color:purple; border:1px solid black;"></span> Squamosal   |



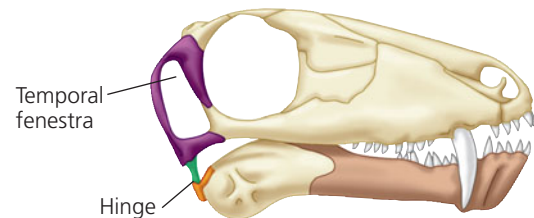
### Synapsid (300 mya)

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



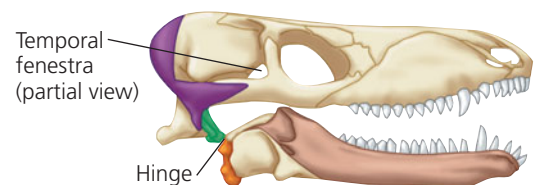
### Therapsid (280 mya)

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



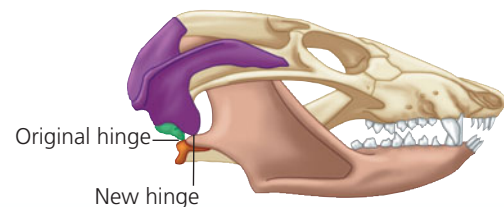
### Early cynodont (260 mya)

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



### Later cynodont (220 mya)

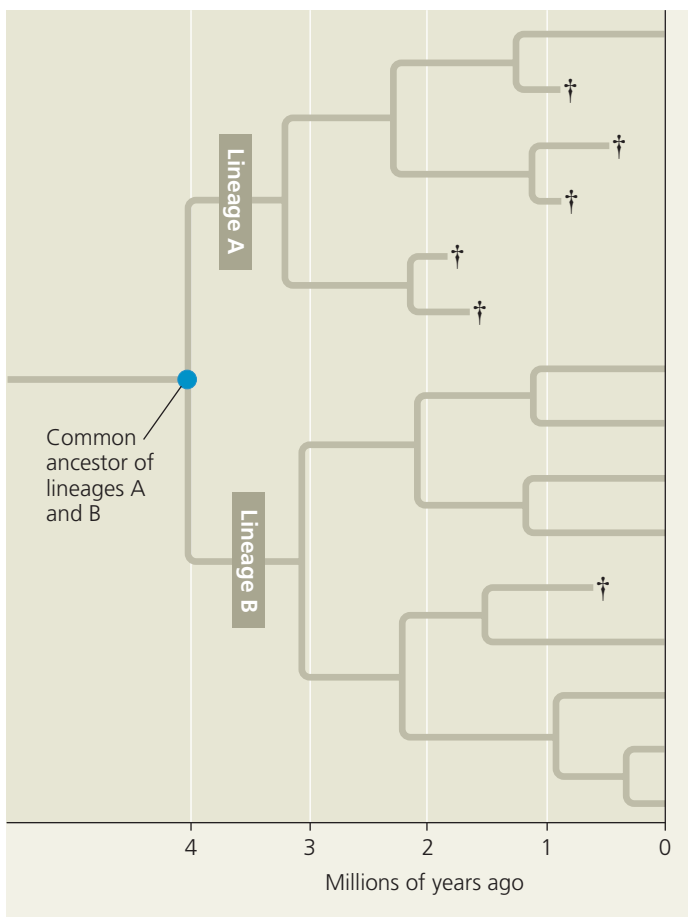
Later cynodonts had teeth with complex cusp patterns and their lower and upper jaws hinged in two locations: They retained the original articular-quadrate hinge and formed a new, second hinge between the dentary and squamosal bones. (The temporal fenestra is not visible in this or the below cynodont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



### Very late cynodont (195 mya)

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





▲ **Figure 23.5** How speciation and extinction affect diversity.

The species diversity of a particular evolutionary lineage will increase when more new member species originate than are lost to extinction. In the hypothetical example shown here, by 2 million years ago both lineage A and lineage B have given rise to four species, and no species have become extinct (denoted by a dagger symbol †). Over the next 2 million years, however, lineage A experiences higher extinction rates than lineage B. As a result, after 4 million years (that is, by time 0), lineage A contains only one species while lineage B contains eight species.

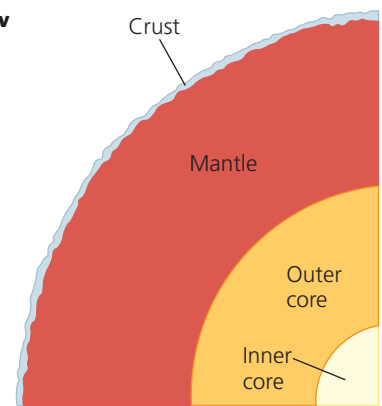
**?** Consider the period between 2 million and 1 million years ago. For each lineage, count the number of speciation and extinction events that occur during that time.

its member species (**Figure 23.5**). Just as a population grows when there are more births than deaths, a group of organisms grows (rises) when more new species appear than are lost to extinction. The reverse occurs when a group is in decline. In the **Scientific Skills Exercise**, you will interpret data from the fossil record about changes in a group of snail species in the early Paleogene period. Such changes in the fates of groups of organisms have been influenced by large-scale processes such as plate tectonics, mass extinctions, and adaptive radiations.

## 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

► **Figure 23.6** Cutaway view of Earth. The thickness of the crust is exaggerated here.



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, this breakup yielded a different configuration of continents. Looking into the future, some geologists have estimated that the continents will come together again and form a new supercontinent roughly 250 million years from now.

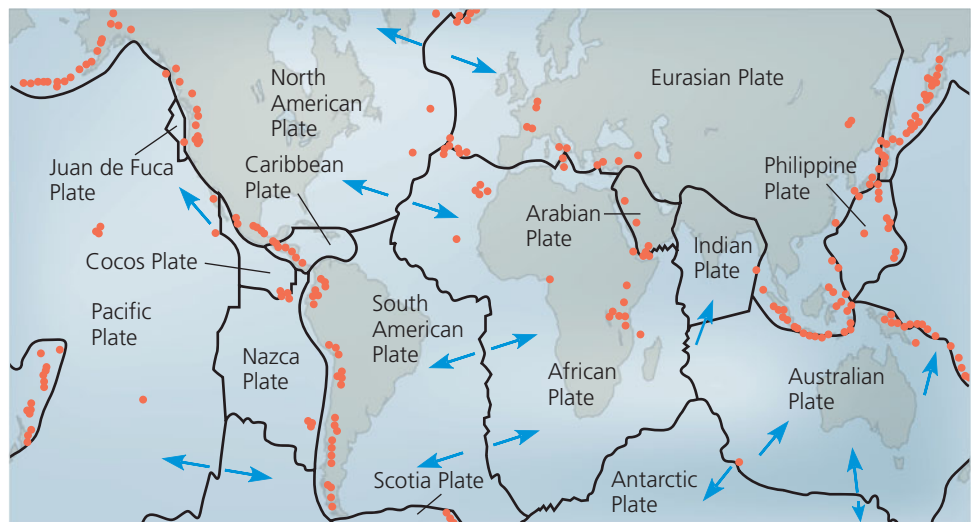
According to the theory of **plate tectonics**, the continents are part of great plates of Earth’s crust that essentially float on the hot, underlying portion of the mantle (**Figure 23.6**). Movements in the mantle cause the plates to move over time in a process called *continental drift*. Geologists can measure the rate at which the plates are moving now, usually only a few centimeters per year. They can also infer the past locations of the continents using the magnetic signal recorded in rocks at the time of their formation. This method works because as a continent shifts its position over time, the direction of magnetic north recorded in its newly formed rocks also changes.

Earth’s major tectonic plates are shown in **Figure 23.7**. 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 slide past each other, forming regions where earthquakes are common. California’s infamous San Andreas Fault is part of a border where two plates slide past each other. In still other cases, two plates collide, producing violent upheavals and forming new mountains along the plate boundaries. One spectacular example of this occurred 45 million years ago, when the Indian plate crashed into the Eurasian plate, starting the formation of the Himalayan mountains.

## Consequences of Continental Drift

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

► **Figure 23.7 Earth's major tectonic plates.** The arrows indicate direction of movement. The reddish orange dots represent zones of violent tectonic activity.



## Scientific Skills Exercise

### *Estimating Quantitative Data from a Graph and Developing Hypotheses*

**Do Ecological Factors Affect Evolutionary Rates?** Researchers studied the fossil record to investigate whether differing modes of dispersal could explain differences in the longevity of species within one taxon of marine snails, the family Volutidae. Some volute snails had planktonic larvae that could disperse over great distances on ocean currents. Other volute snails had nonplanktonic larvae, which developed directly into adults without a swimming stage. The dispersal of snails with nonplanktonic larvae was limited by the distance they can crawl as adults.

**How the Research Was Done** The researchers studied the distribution of volute snail fossils in outcrops of sedimentary rocks located along North America's Gulf Coast. These rocks, which formed during the early Paleogene period, between 65 and 37 million years ago, contain many well-preserved snail fossils. Based on features of

the snail's shell, the researchers classified each fossil species as having planktonic or nonplanktonic larvae. Each bar in the graph shows how long one snail species persisted in the fossil record.

#### Interpret the Data

1. Here's a method for estimating quantitative data (fairly precisely) from a graph:

- The first step is to measure along an axis that has a scale to obtain a conversion factor. In this case, 25 million years (my; from 40 to 65 million years ago (mya) on the x-axis) is represented by a distance of 7.0 cm.


This yields a conversion factor (a ratio) of

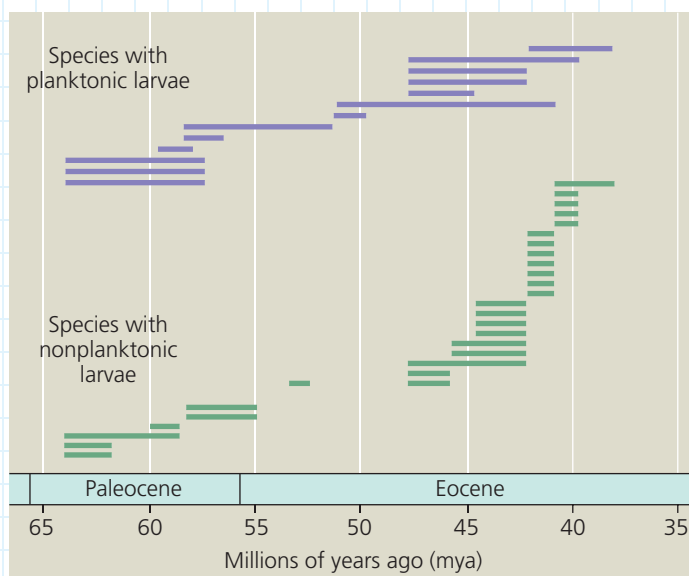
$$25 \text{ my} / 7.0 \text{ cm} = 3.6 \text{ my/cm}$$

- Each horizontal bar represents the timespan during which a given snail species appears in the fossil record—the species' persistence time. To estimate the time period represented by a horizontal bar on this graph, measure the length of that bar in cm and multiply that measurement by the conversion factor, 3.6 my/cm. For example, the top (planktonic) bar on the graph has a length of about 1.1 cm; thus, that bar represents  $1.1 \text{ cm} \times 3.6 \text{ my/cm} = 4.0$  million years persistence time.

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

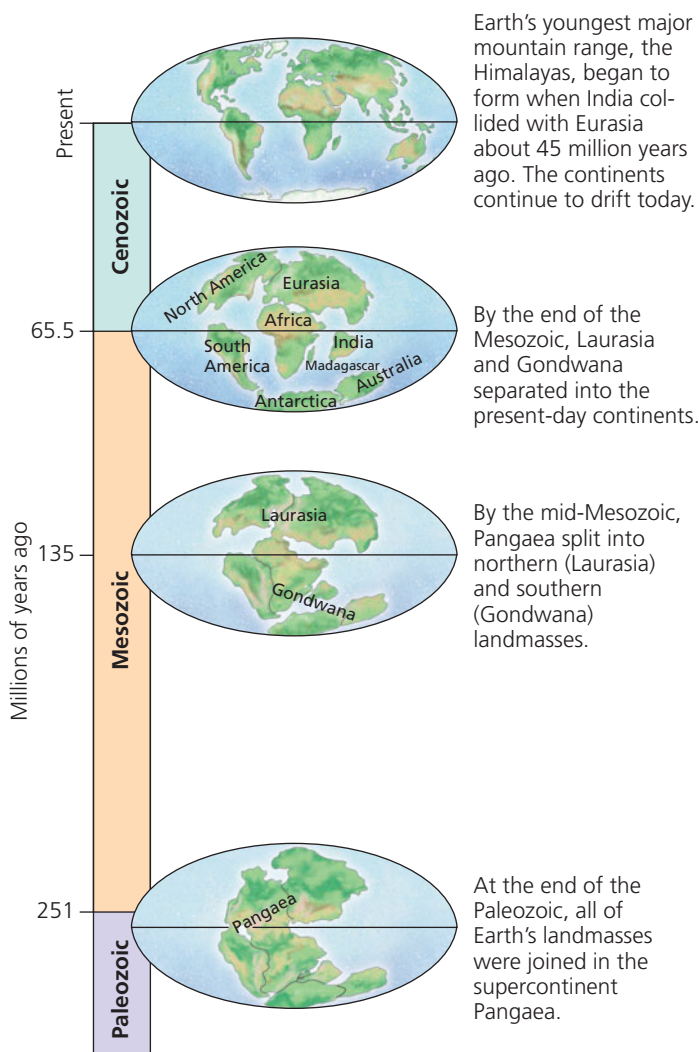
**Data from** T. Hansen, Larval dispersal and species longevity in Lower Tertiary gastropods, *Science* 199:885–887 (1978).

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



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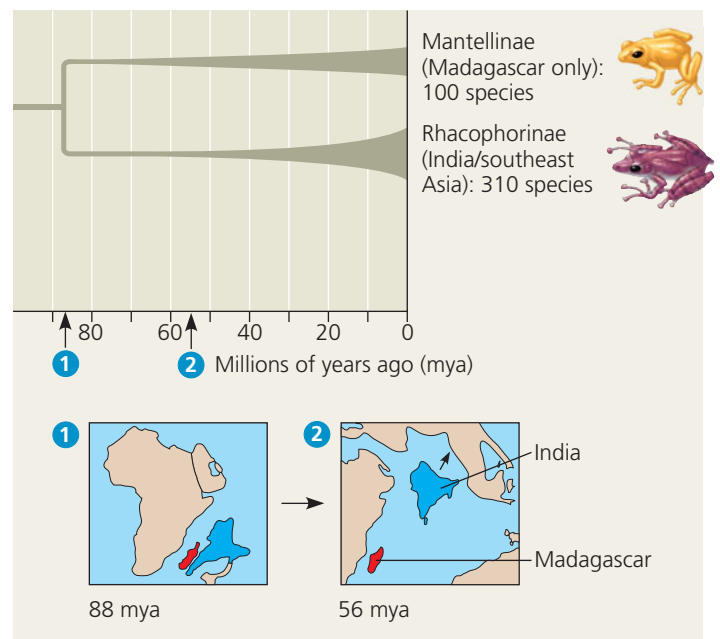


▲ **Figure 23.8** The history of continental drift during the Phanerozoic eon.

**?** Is the Australian plate's current direction of movement (see Figure 23.7) similar to the direction it traveled over the past 65 million years?

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 23.8**. 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,



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▲ **Figure 23.9** Speciation in frogs as a result of continental drift. When present-day Madagascar began to separate from India **1**, the frog subfamilies Mantellinae and Rhacophorinae started to diverge, ultimately forming hundreds of new species in each location. The maps show the movement of Madagascar (red) and India (blue) over time.

once was located in the tropics but has moved 40° to the north over the last 200 million years. When faced with the changes in climate that such shifts in position entail, organisms adapt, move to a new location, or become extinct (this last outcome occurred for many organisms stranded on Antarctica).

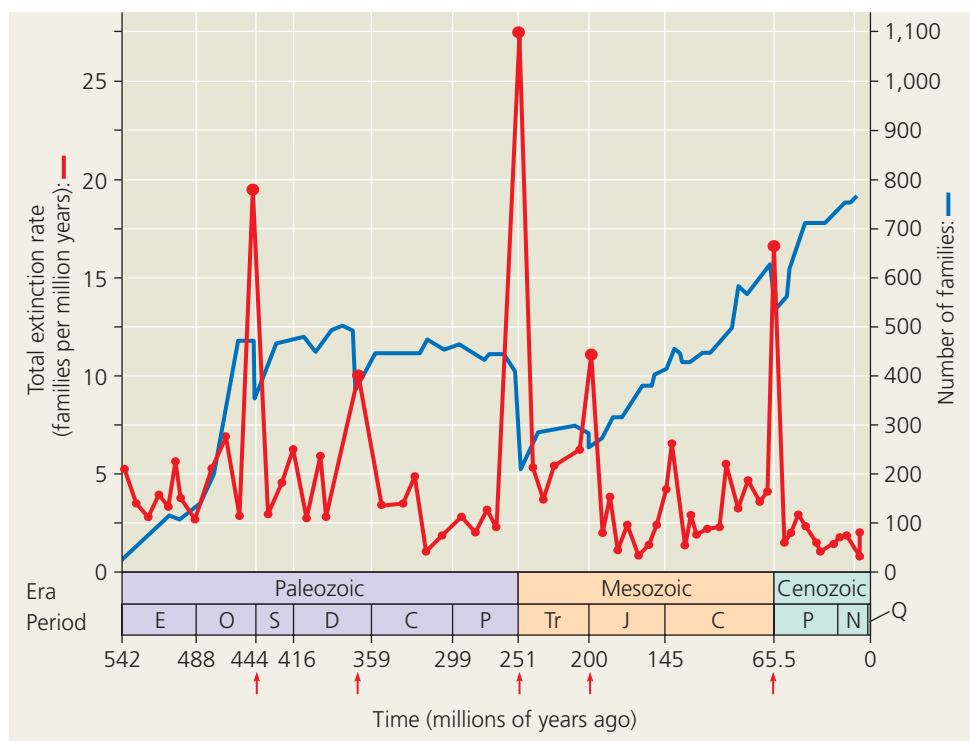
Continental drift also promotes allopatric speciation on a grand scale. When supercontinents break apart, regions that once were connected become geographically isolated. As the continents drifted apart over the last 200 million years, each became a separate evolutionary arena, with lineages of plants and animals that diverged from those on other continents. For example, genetic and geologic evidence indicates that two present-day groups of frog species, the subfamilies Mantellinae and Rhacophorinae, began to diverge when Madagascar separated from India (**Figure 23.9**). 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.

## 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

► **Figure 23.10 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.



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 changes to the global environment have caused the rate of extinction to increase dramatically. When this occurs, a **mass extinction** results, in which large numbers of species become extinct worldwide.

### The “Big Five” Mass Extinction Events

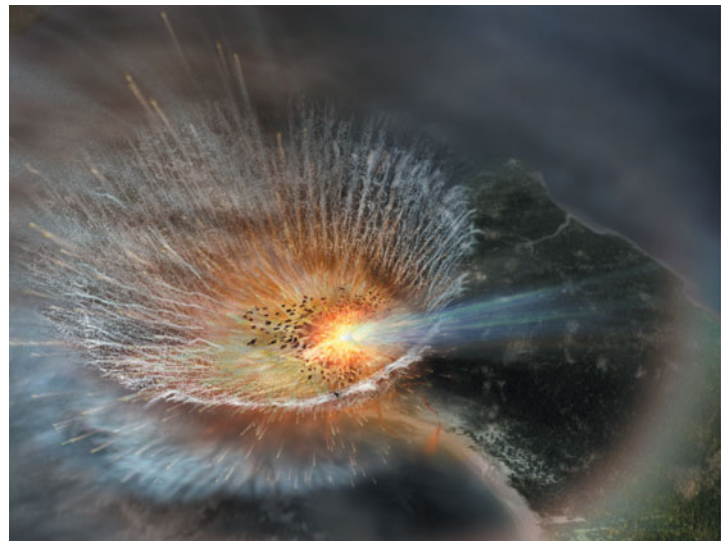
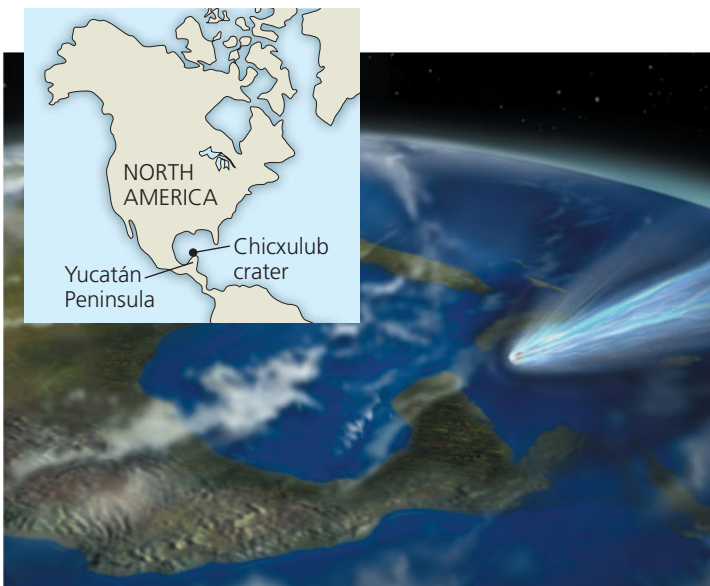
Patterns of the disappearance of species from the fossil record reveal that five mass extinctions have occurred during the past 500 million years (Figure 23.10). These events are particularly well documented for the decimation of hard-bodied animals that lived in shallow seas, the organisms for which 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. 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 a 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<sup>2</sup> (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. If this hypothesis is correct, 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<sub>2</sub>S) 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 27). 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. This suggests that the high-iridium clay may be 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.



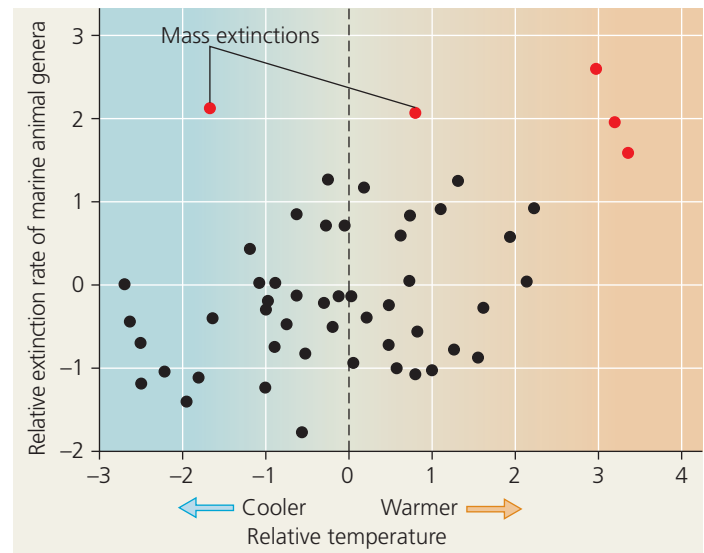
▲ **Figure 23.11 Trauma for Earth and its Cretaceous life.** Beneath the Caribbean Sea, the 65-million-year-old Chicxulub impact crater measures 180 km across. The horseshoe shape of the crater and the pattern of debris in sedimentary rocks indicate that an asteroid or comet struck at a low angle from 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.

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

### Is a Sixth Mass Extinction Under Way?

As you will read further in Chapter 43, 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 number of extinctions occurring today. Tropical rain forests, for example, harbor many undiscovered species; destroying tropical forest may drive species to extinction before we even learn of their existence. Such uncertainties make it hard to assess the extent of the current extinction crisis. Even so, it is clear that losses have not reached those of the “big five” mass extinctions, in which large percentages of Earth’s species became extinct. This does not discount the seriousness of today’s situation. Monitoring programs show that many species are declining at an alarming rate due to habitat loss, introduced species, overharvesting, and other factors. Ongoing 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 23.12**). Overall, evidence suggests that unless



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▲ **Figure 23.12 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.

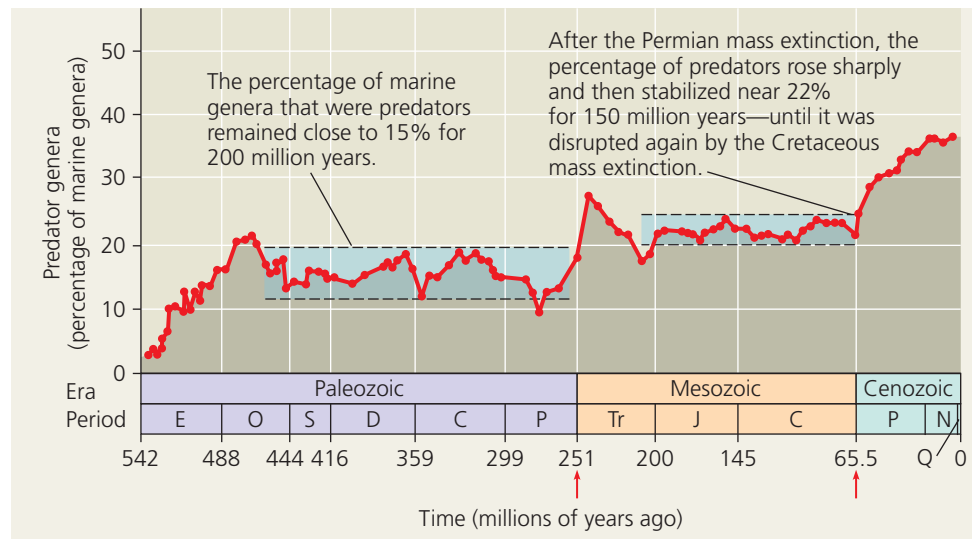
dramatic actions are taken, a sixth, human-caused mass extinction is likely to occur within the next few centuries or millennia.

### 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



► **Figure 23.13 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.



Cretaceous mass extinction. Humans would not exist, and life on Earth would differ greatly from what it is today.

The fossil record shows that 5–10 million years typically pass after a mass extinction before the diversity of life recovers to previous levels. In some cases, it has taken much longer: It took about 100 million years for the number of marine families to recover after the Permian mass extinction (see Figure 23.10). These data have sobering implications. If a sixth mass extinction occurs, it will take millions of years for life on Earth to recover its diversity.

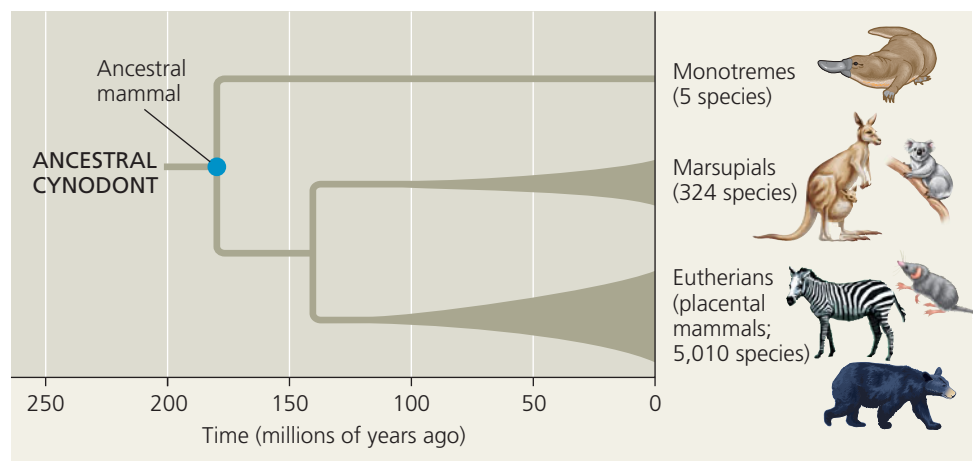
Mass extinctions can also alter ecological communities by changing the types of organisms residing there. For example, after the Permian and Cretaceous mass extinctions, the percentage of marine organisms that were predators grew substantially (Figure 23.13). An increase in predators can increase both the pressures faced by prey and the competition among predators for food. In addition, mass extinctions can curtail lineages with novel and advantageous features. For example, in the late Triassic, a group of gastropods (snails and their relatives) arose that could drill through the shells of bivalves (such as clams) and feed on the animals inside. Although shell drilling provided access to a new and abundant source of food, this newly formed group was wiped out during the Triassic mass extinction (about 200 million years ago). Another 120 million years passed before another group of gastropods (the oyster drills) exhibited this drilling ability. As their predecessors might have done if they had not originated at an unfortunate time, oyster drills have since diversified into many new species. Finally, by eliminating so many species, mass extinctions can pave the way for adaptive radiations, in which new groups of organisms proliferate.

## Adaptive Radiations

The fossil record indicates that the diversity of life has increased over the past 250 million years (see blue line in Figure 23.10). 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 23.14). Although mammals originated about 180 million years ago, the mammal fossils



▲ **Figure 23.14 Adaptive radiation of mammals.**

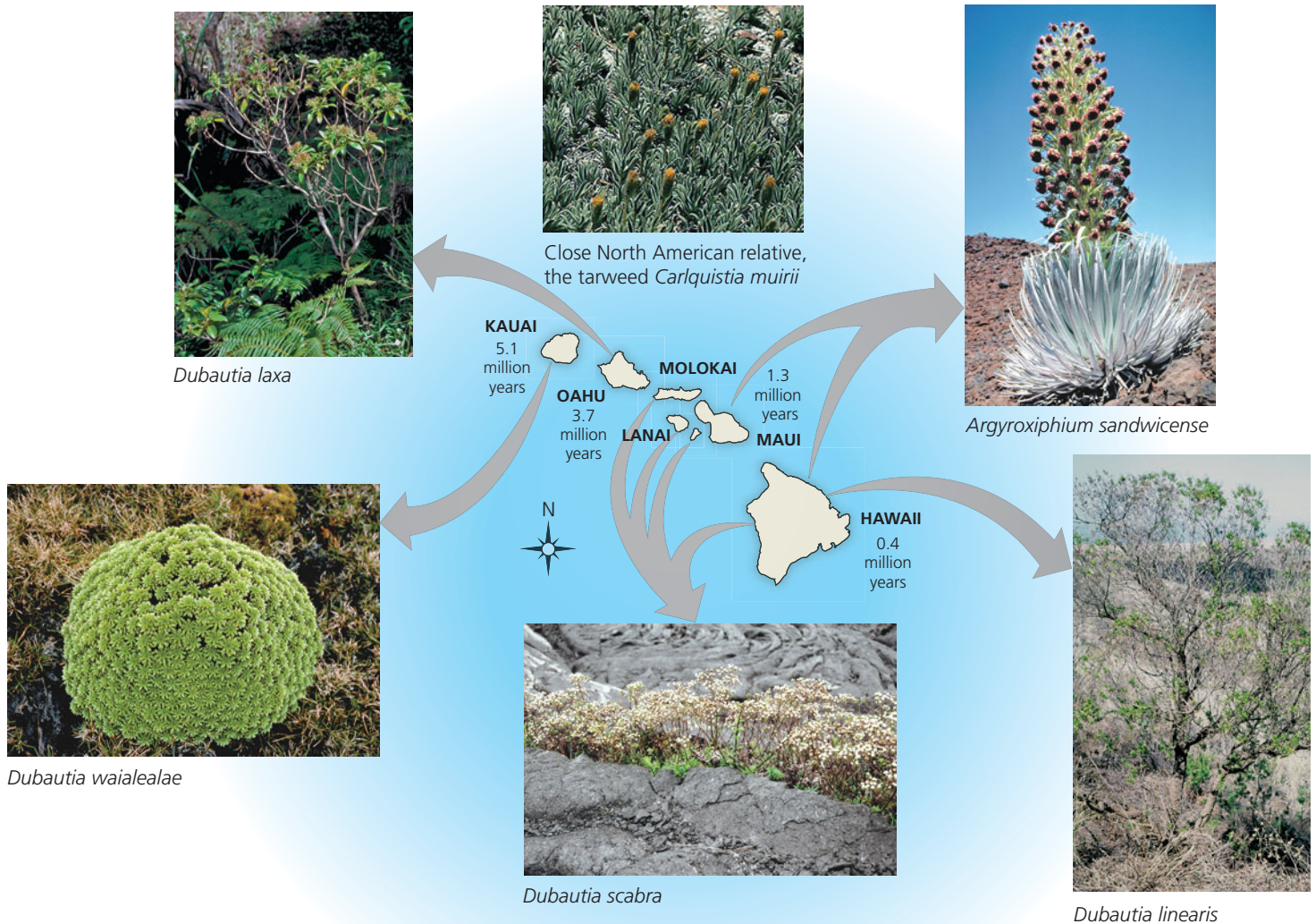
older than 65.5 million years are mostly small and not morphologically diverse. Many species appear to have been nocturnal based on their large eye sockets, similar to those in living nocturnal mammals. A few early mammals were intermediate in size, such as *Repenomamus giganticus*, a 1-m-long predator 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 early Cambrian, 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 23.15**).



**▲ Figure 23.15 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.



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. As a result, most of the thousands of species that inhabit the islands are found nowhere else on Earth. Besides the silverswords in Figure 23.15, organisms unique to Hawaii include a large group of colorful birds called Hawaiian honeycreepers and hundreds of fruit fly species.

### CONCEPT CHECK 23.2

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

For suggested answers, see Appendix A.

## CONCEPT 23.3

### 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 15, evo-devo—research at the interface between evolutionary biology and developmental biology—is

illuminating how slight genetic differences can produce major morphological differences between species. 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

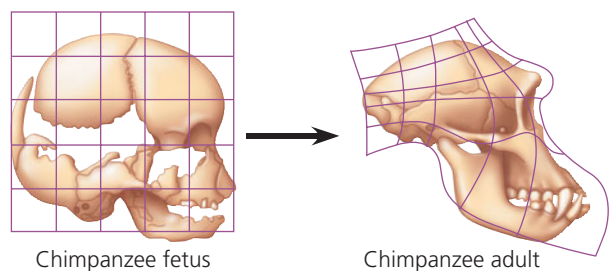
Many striking evolutionary transformations are the result of **heterochrony** (from the Greek *hetero*, different, and *chronos*, time), an evolutionary change in the rate or timing of developmental events. For example, an organism’s shape depends in part on the relative growth rates of different body parts during development. Changes to these rates can alter the adult form substantially, as seen in the contrasting shapes of human and chimpanzee skulls (**Figure 23.16**).

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



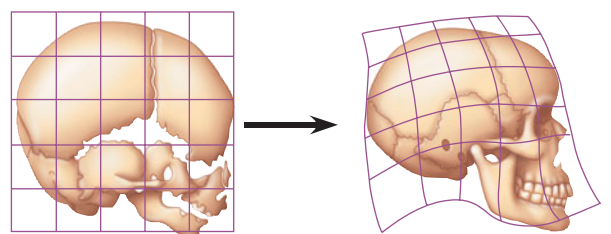
Chimpanzee infant

Chimpanzee adult



Chimpanzee fetus

Chimpanzee adult

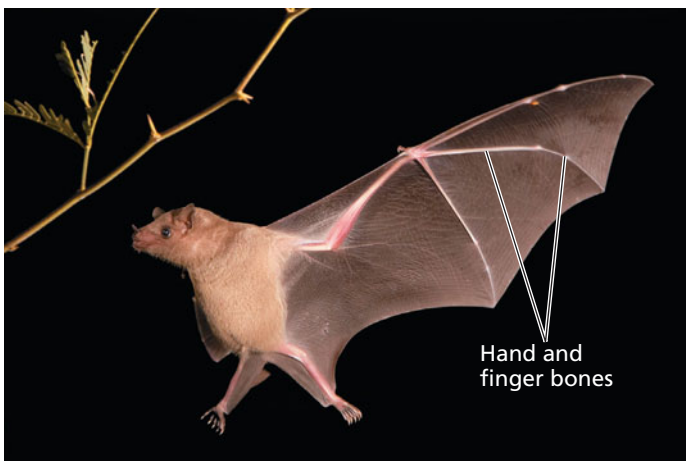


Human fetus

Human adult

▲ **Figure 23.16 Relative skull growth rates.** In the human evolutionary lineage, mutations slowed the growth of the jaw relative to other parts of the skull. As a result, in humans the skull of an adult is more similar to the skull of an infant than is the case for chimpanzees.





▲ **Figure 23.17 Elongated hand and finger bones in a bat wing.** Heterochrony is responsible for the increased total length of hand and finger bones in a bat compared to that of other mammals.

**MAKE CONNECTIONS** Locate the bat's wrist and elbow joints (see Figure 19.16). Calculate the ratio of the length of the bat's longest set of hand and finger bones to the length of its radius. Compare this ratio to the ratio of the bones in your own hand and arm.

(Figure 23.17) and how slowed growth of leg and pelvic bones led to the reduction and eventual loss of hind limbs in whales (see Figure 19.19).

Heterochrony can also alter the timing of reproductive development relative to the development of nonreproductive organs. If reproductive organ development accelerates compared with 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 23.18). Such an evolutionary alteration of developmental timing can produce animals that appear very different from their ancestors, even though the overall genetic change may be small. Indeed, recent evidence indicates that a change at a single locus was probably sufficient to bring about paedomorphosis in the axolotl salamander, although other genes may have contributed as well.

### Changes in Spatial Pattern

Substantial evolutionary changes can also result from alterations in genes that control the placement and spatial organization of body parts. For example, master regulatory genes called **homeotic genes** (described in Chapters 16 and 18) 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



▲ **Figure 23.18 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.

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 suppress limb formation. 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 28).

## The Evolution of Development

Large members of most animal phyla appear suddenly in fossils formed 535–525 million years ago. This rapid diversification of animals is referred to as the *Cambrian explosion* (see Concept 27.2). Yet the discovery of 560-million-year-old fossils of Ediacaran animals (see Figure 23.2) suggests that a set of genes sufficient to produce complex animals existed at least 25 million years before that time. If such genes have existed for so long, how can we explain the astonishing increases in diversity seen during and since the Cambrian explosion?

Adaptive evolution by natural selection provides one answer to this question. As we've seen throughout this unit, by sorting among differences in the sequences of protein-encoding genes, selection can improve adaptations rapidly. In addition, new genes (created by gene duplication events) can take on 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 be particularly important. Next we'll examine

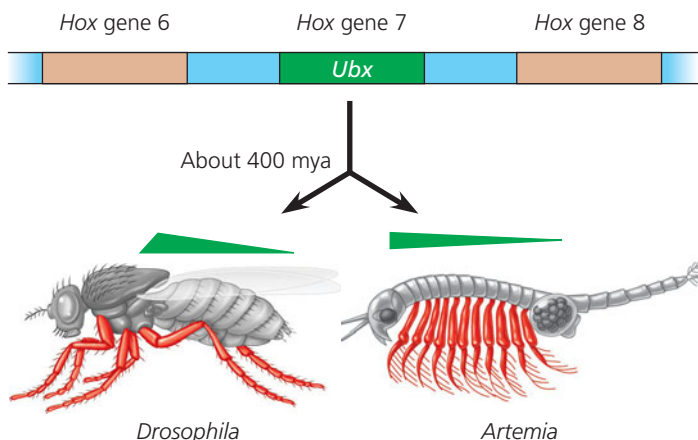
how new morphological forms arise from changes in the nucleotide sequences or regulation of developmental genes.

### Changes in Gene Sequence

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 23.19**). 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



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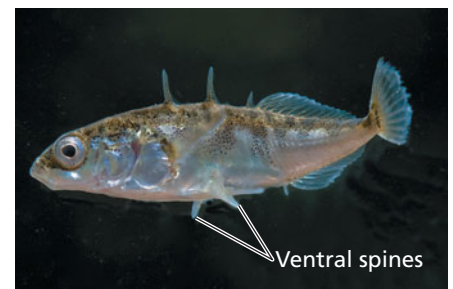
▲ **Figure 23.19** **Origin of the insect body plan.** Expression of the *Hox* gene *Ubx* suppresses the formation of legs in fruit flies (*Drosophila*) but not in brine shrimp (*Artemia*), thus helping to build the insect body plan. Fruit fly and brine shrimp *Hox* genes have evolved independently for 400 million years. The green triangles indicate the relative amounts of *Ubx* expression in different body regions.

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 16). However, a change in the nucleotide sequence of a gene may affect its function wherever the gene is expressed, while changes in the regulation of gene expression can be limited to a single cell type. 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 of a variety of species, including threespine stickleback fish. These fish live in the open ocean and in shallow, coastal waters. In western Canada, they also live in lakes formed when the coastline receded during the past 12,000 years. Marine stickleback fish have a pair of spines on their ventral (lower) surface, which deter some predators. These spines are often reduced or absent in stickleback fish living in lakes that lack predatory fishes and that are also low in calcium. Spines may have been lost in such lakes because they are not advantageous in the absence of predators, and the limited calcium is needed for purposes other than constructing spines.



▲ **Threespine stickleback**  
(*Gasterosteus aculeatus*)

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 sequence of the *Pitx1* gene or to changes in how the gene is expressed? **Figure 23.20**, on the next page, describes an experiment designed to study this question. The researchers' results indicate that the regulation of gene expression has changed, not the DNA sequence of the gene. Furthermore, lake stickleback fish do express the *Pitx1* gene in tissues not related to the production of spines (for example, the mouth), illustrating how morphological change can be caused by altering the expression of a developmental gene in some parts of the body but not others.

## ▼ Figure 23.20 Inquiry

### What caused the loss of spines in lake stickleback fish?

**Experiment** Marine populations of the threespine stickleback fish 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. Researchers 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.

**Hypothesis A:** A change in the DNA sequence of *Pitx1* 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* 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 Concept 15.4) 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

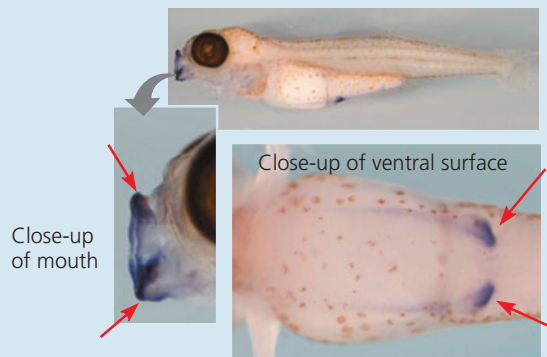
The 283 amino acids of the *Pitx1* protein are identical in marine and lake stickleback populations.

**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.

**Marine stickleback embryo**



**Lake stickleback embryo**



**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?** What results would have led researchers to conclude that a change in the coding sequence of *Pitx1* was more important than a change in regulation of gene expression?

#### CONCEPT CHECK 23.3

1. How can heterochrony cause evolution of novel 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. (Review Concept 15.3.)

For suggested answers, see Appendix A.

## CONCEPT 23.4

### 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 small-scale factors (described in Chapter 21), such as natural selection operating in populations, and the large-scale factors described



in this chapter, such as continental drift promoting bursts of speciation throughout the globe. Moreover, to paraphrase the Nobel Prize–winning geneticist François Jacob, evolution is like tinkering—a process in which new forms arise by the 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 (see Chapter 19): 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

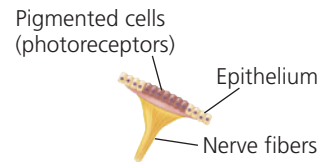
François Jacob’s view of evolution harkens back to Darwin’s concept of descent with modification. As new species form, novel and complex structures can arise as gradual modifications of ancestral structures. In many cases, complex structures have evolved in increments from simpler versions that performed 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 23.21**). 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.

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 23.21). 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.

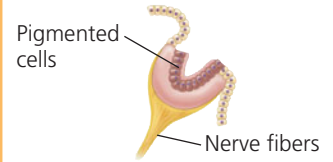
▼ **Figure 23.21** A range of eye complexity in molluscs.

### (a) Patch of pigmented cells



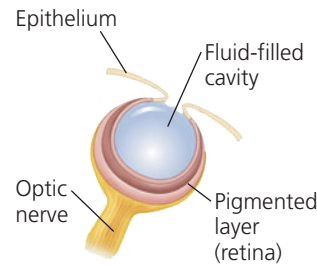
The limpet *Patella* has a simple patch of photoreceptors.

### (b) Eyecup



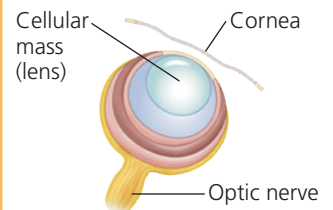
The slit shell mollusc *Pleurotomaria* has an eyecup.

### (c) Pinhole camera-type eye



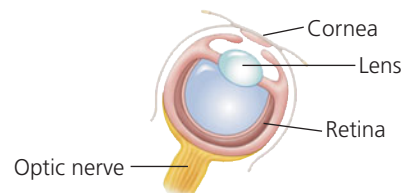
The *Nautilus* eye functions like a pinhole camera (an early type of camera lacking a lens).

### (d) Eye with primitive lens



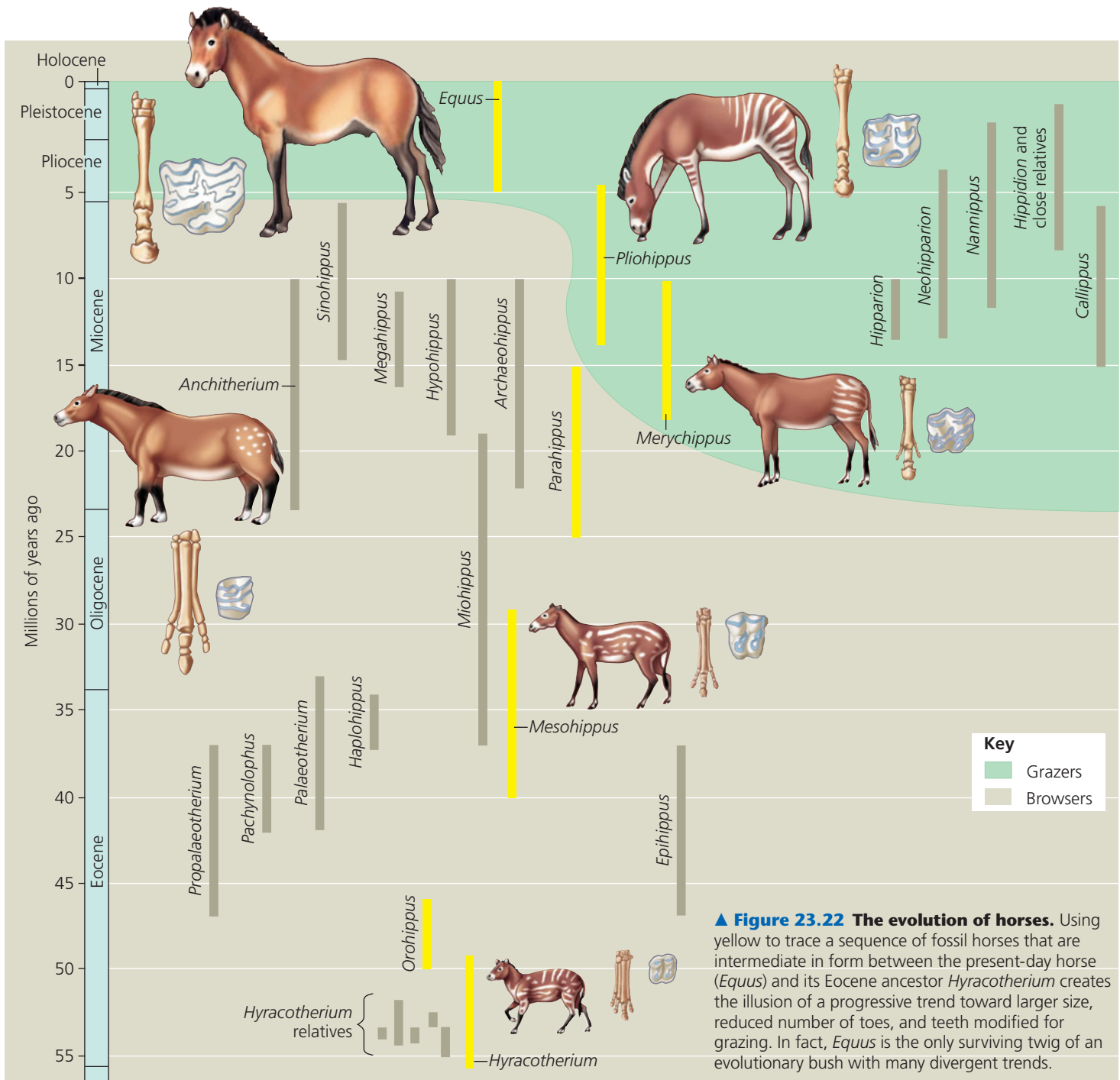
The marine snail *Murex* has a primitive lens consisting of a mass of crystal-like cells. The cornea is a transparent region of tissue that protects the eye and helps focus light.

### (e) Complex camera lens-type eye



The squid *Loligo* has a complex eye with features (cornea, lens, and retina) similar to those of vertebrate eyes. However, the squid eye evolved independently from vertebrate eyes.

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 23.4) were incorporated into the ear region of mammals, where they eventually took on a new function: the transmission of sound. 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 23.22). 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 23.22). However, if we consider *all* fossil horses known today, this apparent trend vanishes. The genus *Equus* did not evolve in a straight line; it is the only surviving twig of an evolutionary tree that is so branched that it is more like a bush. *Equus* actually descended

through a series of speciation episodes that included several adaptive radiations, not all of which led to large, one-toed, grazing horses. In fact, phylogenetic analyses suggest that all lineages that include grazers are closely related to *Parahippus*; the many other horse lineages, all of which are now extinct, remained multi-toed browsers for 35 million years.

Branching evolution *can* result in a real evolutionary trend even if some species counter the trend. One model of long-term trends views species as analogous to individuals: Speciation is their birth, extinction is their death, and new species that diverge from them are their offspring. In this model, just as populations of individual organisms undergo natural selection, species undergo *species selection*. The species that endure the longest and generate the most new offspring species determine the direction of major evolutionary trends. The species selection model suggests that “differential speciation success” plays a role in macroevolution similar to the role of differential reproductive success in microevolution. Evolutionary trends can also result directly from natural selection. For example, when horse ancestors invaded the grasslands that spread during the mid-Cenozoic, 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 23.4

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 by mosquitoes, which only bite living rabbits. 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.

## 23 Chapter Review

### SUMMARY OF KEY CONCEPTS

#### CONCEPT 23.1

##### The fossil record documents life’s history (pp. 436–440)

- 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 study of fossils has helped geologists establish a **geologic record** of Earth’s history.
- 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 23.2

##### The rise and fall of groups of organisms reflect differences in speciation and extinction rates (pp. 440–449)

- 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 23.3

##### Major changes in body form can result from changes in the sequences and regulation of developmental genes (pp. 449–452)

- 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 23.4

##### Evolution is not goal oriented (pp. 452–455)

- 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. 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.
2. 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
3. A researcher discovers a fossil of what appears to be one of the oldest-known multicellular organisms. The researcher could estimate the age of this fossil based on
  - a. the amount of carbon-14 in the fossil.
  - b. the amount of uranium-238 in the fossil.
  - c. the amount of carbon-14 in the sedimentary rocks in which the fossil was found.
  - d. the amount of uranium-238 in volcanic layers surrounding the fossil.
  - e. the amount of uranium-238 in the sedimentary rocks in which the fossil was found.

### Level 2: Application/Analysis

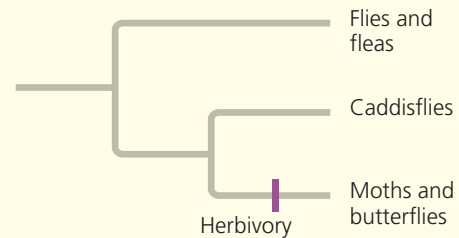
4. A genetic change that caused a certain *Hox* gene to be expressed along the tip of a vertebrate limb bud instead of farther back helped make possible the evolution of the tetrapod limb. This type of change is illustrative of
  - a. the influence of environment on development.
  - b. paedomorphosis.
  - c. a change in a developmental gene or in its regulation that altered the spatial organization of body parts.
  - d. heterochrony.
  - e. gene duplication.
5. A swim bladder is a gas-filled sac that helps fish maintain buoyancy. The evolution of the swim bladder from the air-breathing organ (a simple lung) of an ancestral fish is an example of
  - a. an evolutionary trend.
  - b. exaptation.
  - c. changes in *Hox* gene expression.
  - d. paedomorphosis.
  - e. adaptive radiation.
6. **MAKE CONNECTIONS** Review Figure 20.10. Based on the phylogeny shown in Figure 23.4, identify the most inclusive clade to which both *Dimetrodon* and mammals belong. Explain.

### Level 3: Synthesis/Evaluation

#### 7. 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?



#### 8. 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?

#### 9. FOCUS ON EVOLUTION

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

#### 10. FOCUS ON ORGANIZATION

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

For selected answers, see Appendix A.

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