13

Speciation and Evolutionary Change

CHAPTER 13

Chapter Outline

Key Concepts	Applications
Understand what is meant by the term speciation.	• Recognize the steps necessary for speciation to occur. • Understand the importance of reproductive isolation to the process of speciation and several ways in which isolation can occur. • Recognize why different species do not interbreed with one another. • Appreciate that subspecies are genetically distinct populations of a species.
Understand the concept of genetic isolation.	• Recognize that many plant species originated as a result of polyploidy. • Describe how a study of chromosomes could determine if a species is a polyploid.
Understand the theory of evolution.	• Understand that evolution is a well-supported theory at the center of all biological thinking. • Understand that our perception of evolution has changed with new information and that our understanding will continue to change. • Realize that new discoveries refine our understanding of evolution rather than refute this theory. • Divergence is a basic pattern of evolution, but there are other patterns of evolution. • Recognize that the rate of evolution is variable. • Appreciate that evidence indicates that humans have an evolutionary history.

13.1 Species: A Working Definition

Before we consider how new species are produced, let's recall from chapter 11 how one species is distinguished from another. A **species** is commonly defined as a population of organisms whose members have the potential to interbreed naturally to produce fertile offspring but *do not* interbreed with other groups. This is a working definition; it applies in most cases but must be interpreted to encompass some exceptions. There are two key ideas within this definition. First, a species is a population of organisms. An individual—you, for example—is not a species. You can only be a member of a group that is recognized as a species. The human species, *Homo sapiens,* consists of over 6 billion individuals, whereas the endangered California condor species, *Gymnogyps californianus,* consists of about 160 individuals.

Second, the definition involves the ability of individuals within the group to produce fertile offspring. Obviously, we cannot check every individual to see if it is capable of mating with any other individual that is similar to it, so we must make some judgment calls. Do most individuals within the group potentially have the capability of interbreeding to produce fertile offspring? In the case of humans we know that some individuals are sterile and cannot reproduce, but we don't exclude them from the human species because of this. If they were not sterile, they would have the potential to interbreed. We recognize that, although humans normally choose mating partners from their subpopulations, humans from all parts of the world are potentially capable of interbreeding. We know this to be true because of the large number of instances of reproduction involving people of different ethnic and racial backgrounds. The same is true for many other species that have local subpopulations but have a wide geographic distribution.

Another way to look at this question is to think about gene flow. **Gene flow** is the movement of genes from one generation to the next or from one region to another. Two or more populations that demonstrate gene flow between them constitute a single species. Conversely, two or more populations that do not demonstrate gene flow between them are generally considered to be different species. Some examples will clarify this working definition.

The mating of a male donkey and a female horse produces young that grow to be adult mules, incapable of reproduction (figure 13.1). Because mules are nearly always sterile, there can be no gene flow between horses and donkeys and they are considered to be separate species. Similarly, lions and tigers can be mated in zoos to produce offspring. However, this does not happen in nature and so gene flow does not occur naturally; thus they are considered to be two separate species.

Still another way to try to determine if two organisms belong to different species is to determine their genetic similarity. The recent advances in molecular genetics allows scientists to examine the sequence of bases in genes present in individuals from a variety of different populations. Those that have a great deal of similarity are assumed to have resulted from populations that have exchanged genes through sexual reproduction in the recent past. If there are significant differences in the genes present in individuals from two populations, they have not exchanged genes recently and are more likely to be members of separate species. Interpretation of the results obtained by examining genetic differences still requires the judgment of experts. It

(a) (b) (c)

Figure 13.1

Hybrid Sterility
Even though they do not do so in nature, (*a*) horses and (*b*) donkeys can be mated. The offspring is called a (*c*) mule and is sterile. Because the mule is sterile, the horse and the donkey are considered to be of different species.

will not unequivocally settle every dispute related to the identification of species, but it is another tool that helps clarify troublesome situations.

13.2 How New Species Originate

The fossil record contains examples of the origin of huge numbers of new species. The fossil record also indicates that most species have gone extinct. There are several mechanisms thought to be involved in generating new species. We will look at two mechanisms that are probably responsible for the vast majority of speciation events: geographic isolation and polyploidy.

Geographic Isolation

The geographic area over which a species can be found is known as its **range.** The range of the human species is the entire world, whereas that of a bird known as a snail kite is a small region of southern Florida. As a species expands its range or environmental conditions change in some parts of the range, portions of the population can become separated from the rest. Thus, many species consist of partially isolated populations that display characteristics significantly different from other local populations. Many of the differences observed may be directly related to adaptations to local environmental conditions. This means that new colonies or isolated populations may have infrequent gene exchange with their geographically distant relatives. As you will recall from chapter 11, these genetically distinct populations are known as subspecies.

A portion of a species can become totally isolated from the rest of the gene pool by some geographic change, such as the formation of a mountain range, river valley, desert, or ocean. When this happens the portion of the species is said to be in **geographic isolation** from the rest of the species. If two populations of a species are geographically isolated they are also reproductively isolated, and gene exchange is not occurring between them. The geographic features that keep the different portions of the species from exchanging genes are called **geographic barriers.** The uplifting of mountains, the rerouting of rivers, and the formation of deserts all may separate one portion of a gene pool from another. For example, two kinds of squirrels are found on opposite sides of the Grand Canyon. Some people consider them to be separate species; others consider them to be different isolated subpopulations of the same species (figure 13.2). Even small changes may cause geographic isolation in species that have little ability to move. A fallen tree, a plowed field, or even a new freeway may effectively isolate populations within such species. Snails in two valleys separated by a high ridge have been found to be closely related but different species. The snails cannot get from one valley to the next because of the height and climatic differences presented by the ridge (figure 13.3).

The separation of a species into two or more isolated subpopulations is not enough to generate new species. Even after many generations of geographic isolation, these separate groups may still be able to exchange genes (mate and produce fertile offspring) if they overcome the geographic barrier, because they have not accumulated enough genetic differences to prevent reproductive success. Differences in environments and natural selection play very important roles

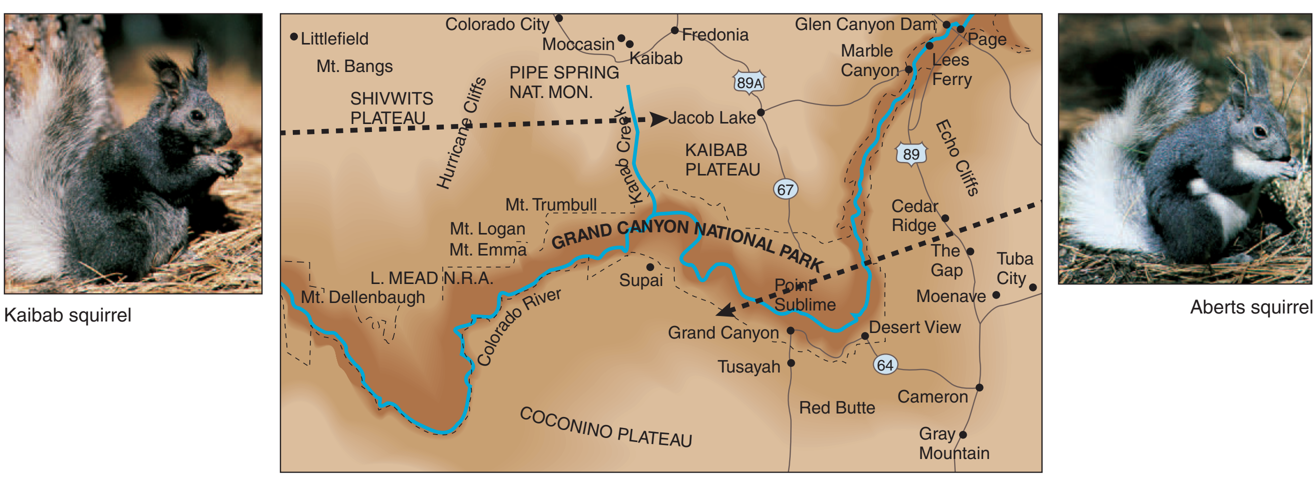


Figure 13.2

Isolation by Geographic Barriers
These two squirrels are found on opposite sides of the Grand Canyon. Some people consider them to be different species; others consider them to be distinct populations of the same species.

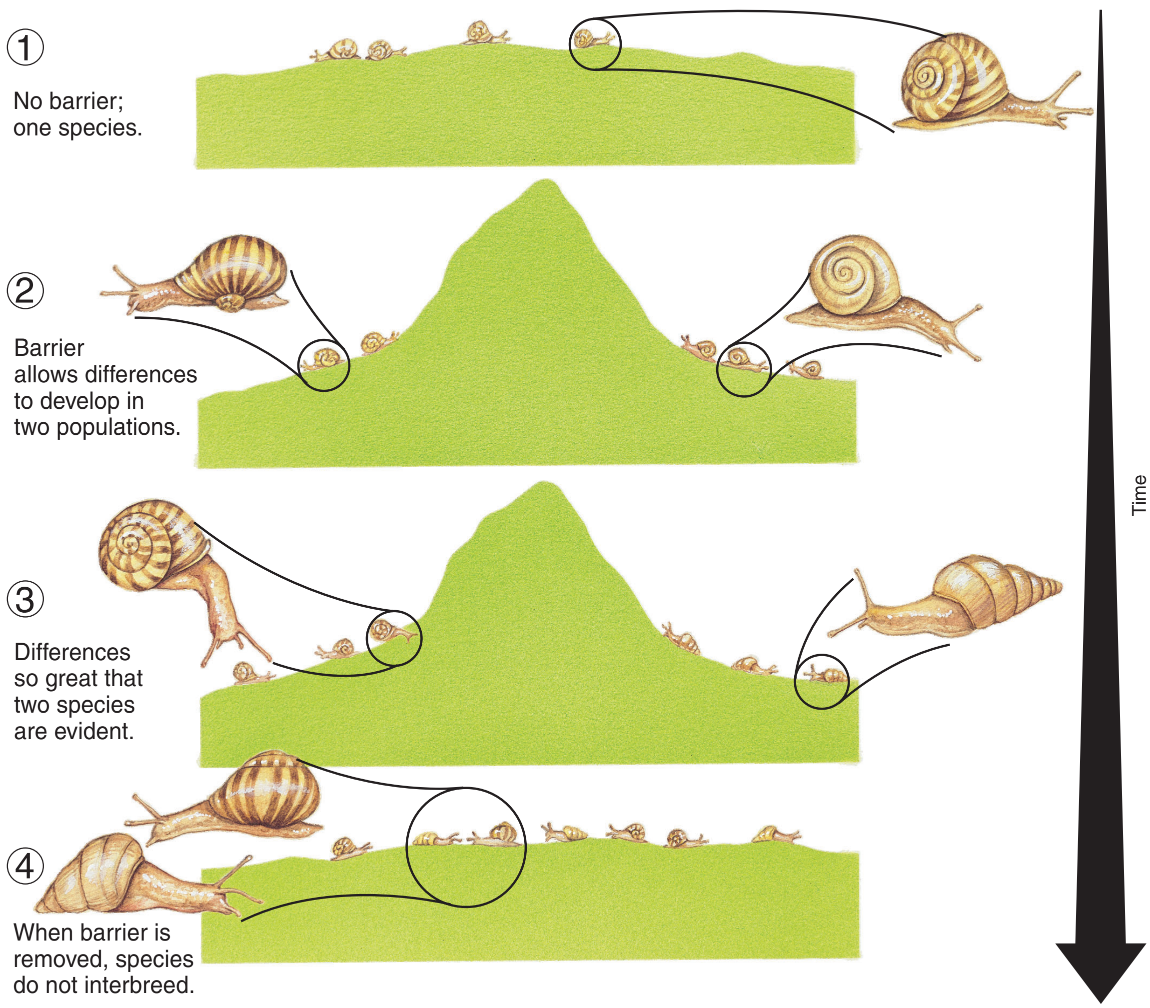


Figure 13.3

The Effect of Geographic Isolation
If a single species of snail was to be divided into two different populations by the development of a ridge between them, the two populations could be subjected to different environmental conditions. This could result in a slow accumulation of changes that could ultimately result in two populations that would not be able to interbreed even if the ridge between them were to erode. They would be different species.

in the process of forming new species. Following separation from the main portion of the gene pool by geographic isolation, the organisms within the small, local population are likely to experience different environmental conditions. If, for example, a mountain range has separated a species into two populations, one population may receive more rain or more sunlight than the other (figure 13.4). These environmental differences act as natural selecting agents on the two gene pools and, acting over a long period of time, account for different genetic combinations in the two places. Furthermore, different mutations may occur in the two isolated populations, and each may generate different random combinations of genes as a result of sexual reproduction. This would be particularly true if one of the populations was very small. As a result, the two populations may show differences in color, height, enzyme production, time of seed germination, or many other characteristics.

Over a long period of time, the genetic differences that accumulate may result in regional populations called **subspecies** that are significantly modified structurally, physiologically, or behaviorally. The differences among some subspecies may be so great that they reduce reproductive success when the subspecies mate. **Speciation** is the process of generating new species. This process has occurred only if gene flow between isolated populations does not occur even after barriers are removed. In other words, the process of

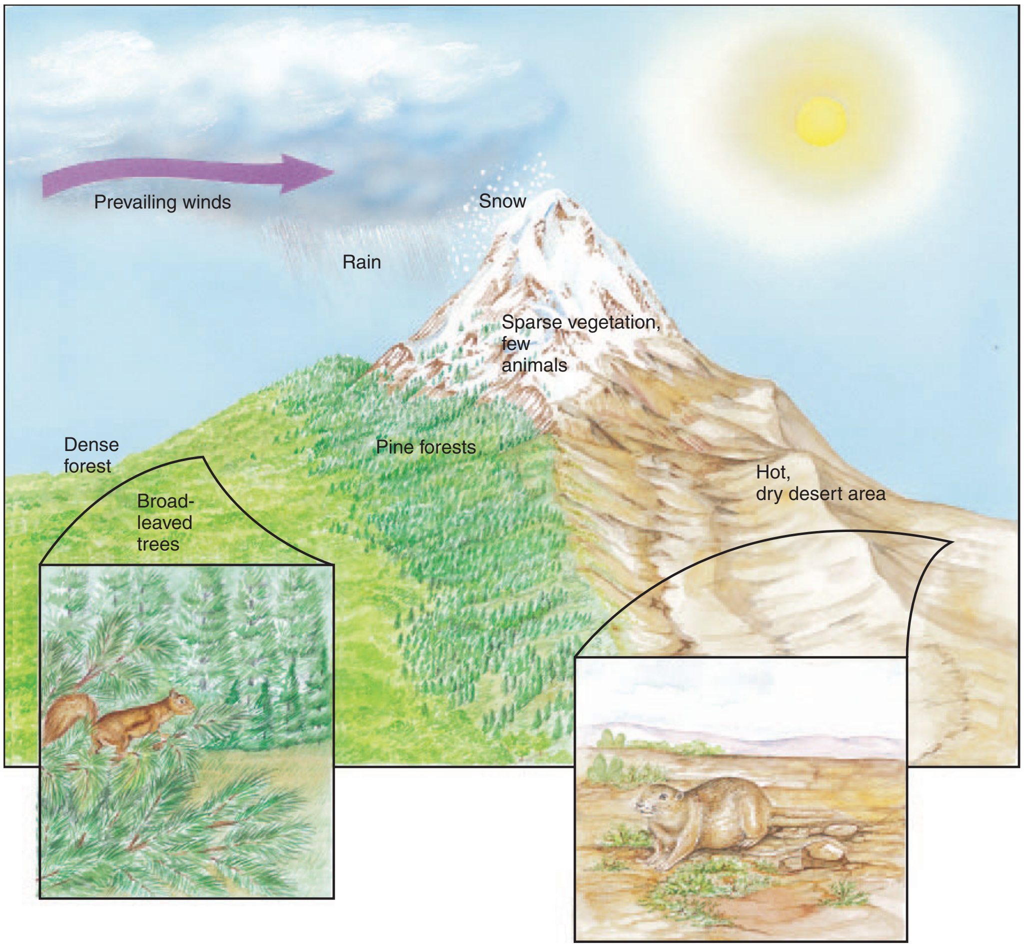


Figure 13.4

Environmental Differences Caused by Mountain Ranges
Most mountain ranges affect the local environment. Because of the prevailing winds, most rain falls on the windward side of the mountain. This supports abundant vegetation. The other side of the mountain receives much less rain and is drier. Often a desert may exist. Both plants and animals must be adapted to the kind of climate typical for their regions. Cactus and ground squirrels would be typical of the desert and pine trees and tree squirrels would be typical of the windward side of the mountain.

speciation can begin with the geographic isolation of a portion of the species, but new species are generated only if isolated populations become separate from one another *genetically*. Speciation by this method is really a three-step process. It begins with geographic isolation, is followed by the action of selective agents that choose specific genetic combinations as being valuable, and ends with the genetic differences becoming so great that reproduction between the two groups is impossible.

Speciation Without Geographic Isolation

It is also possible to envision ways in which speciation could occur without geographic isolation being necessary. Any process that could result in the reproductive isolation of a portion of a species could lead to the possibility of speciation. For example, within populations, some individuals may breed or flower at a somewhat different time of the year. If the difference in reproductive time is genetically based, different breeding populations could be established, which could eventually lead to speciation. Among animals, variations in the genetically determined behaviors related to courtship and mating could effectively separate one species into two or more separate breeding populations. In plants, genetically determined incompatibility of the pollen of one population of flowering plants with the flowers of other populations of the same species could lead to separate species.

(a) (b)

Figure 13.5

Polyploidy
Many species of plants have been created by increasing the chromosome number. Many large-flowered varieties have been produced artificially by means of this technique.
(*a*) A normal diploid *Hibiscus moscheutos*.
(*b*) A polyploid variety of this hibiscus. Note the differences in flower size and petal shape.

Polyploidy: Instant Speciation

Another important mechanism known to generate new species is polyploidy. **Polyploidy** is a condition of having multiple sets of chromosomes rather than the normal haploid or diploid number. The increase in the number of chromosomes can result from abnormal mitosis or meiosis in which the chromosomes do not separate properly. For example, if a cell had the normal diploid chromosome number of six ($2n = 6$), and the cell went through mitosis but did not divide into two cells, it would then contain 12 chromosomes. It is also possible that a new polyploid species could result from crosses between two species followed by a doubling of the chromosome number. Because the number of chromosomes of the polyploid is different from that of the parent, successful reproduction with the parent species would be difficult. This is because meiosis would result in gametes that had different chromosome numbers from the original, parent organism. In one step, the polyploid could be isolated reproductively from its original species. A single polyploid plant does not constitute a new species. However, because most plants can reproduce asexually, they can create an entire population of organisms that have the same polyploid chromosome number. The members of this population would all have the same chromosome number and would probably be able to undergo normal meiosis and would be capable of sexual reproduction among themselves. In effect, a new species can be created within a couple of generations. Some groups of plants, such as the grasses, may have 50% of their species produced as a result of polyploidy. Many economically important species are polyploids. Cotton, potatoes, sugarcane, wheat, and many garden flowers are examples (figure 13.5). Although it is rare in animals, polyploidy is found in a few groups that typically use asexual reproduction in addition to sexual reproduction. Certain lizards have only female individuals and lay eggs that develop into additional females. Different species of these lizards appear to have developed by polyploidy.

13.3 Maintaining Genetic Isolation

In order for a new species to continue to exist, it must reproduce but continue to remain genetically distinct from other similar species. The speciation process typically involves the development of **reproductive isolating mechanisms** or **genetic isolating mechanisms.** These mechanisms prevent matings between species and therefore help maintain distinct species. A great many types of genetic isolating mechanisms are recognized.

In central Mexico, two species of robin-sized birds called *towhees* live in different environmental settings. The collared towhee lives on the mountainsides in the pine forests; the spotted towhee is found at lower elevations in oak forests. Geography presents no barriers to these birds. They are perfectly capable of flying to each other's habitats, but they do not. Because of their **habitat preference** or **ecological isolation,** mating between these two similar species does not occur. Similarly, areas with wet soil have different species of plants than nearby areas with drier soils.

Some plants flower only in the spring of the year, whereas other species that are closely related flower in midsummer or fall; therefore, the two species are not very likely to pollinate one another. Among insects there is a similar spacing of the reproductive periods of closely related species so that they do not overlap. Thus, **seasonal isolation** (differences in the time of the year at which reproduction takes place) is an effective genetic isolating mechanism.

Inborn behavior patterns that prevent breeding between species result in **behavioral isolation.** The mating calls of frogs and crickets are highly specific. The sound pattern produced by the males is species-specific and invites only females of the same species to engage in mating. The females have a built-in response to the particular species-specific call and only mate with those that produce the correct call.

The courtship behavior of birds involves both sound and visual signals that are species-specific. For example, groups of male prairie chickens gather on meadows shortly before dawn in the early summer and begin their dances. The air sacs on either side of the neck are inflated so that the bright-colored skin is exposed. Their feet move up and down very rapidly and their wings are spread out and quiver slightly (figure 13.6). This combination of sight and sound attracts females. When they arrive, the males compete for the opportunity to mate with them. Other related species of birds conduct their own similar, but distinct, courtship displays. The differences among the dances are great enough so that a female can recognize the dance of a male of her own species.

Behavioral isolating mechanisms such as these occur among other types of animals as well. The strutting of a peacock, the fin display of Siamese fighting fish, and the flashing light patterns of "lightning bugs" of different species are all examples of behaviors that help individuals identify members of their own species and prevent different species from interbreeding (figure 13.7).

The specific shapes of the structures involved in reproduction may prevent different species from interbreeding. Among insects, the structure of the penis and the reciprocal structures of the female fit like a lock and key and therefore breeding between different species is very difficult. This can be called **mechanical** or **morphological isolation.** Similarly the shapes of flowers may permit only certain animals to carry pollen from one flower to the next.

There are a vast number of biochemical activities that take place around the union of egg and sperm. Molecules on the outside of the egg or sperm may trigger events that prevent their union if they are not from the same species. This can be called **biochemical isolation.**

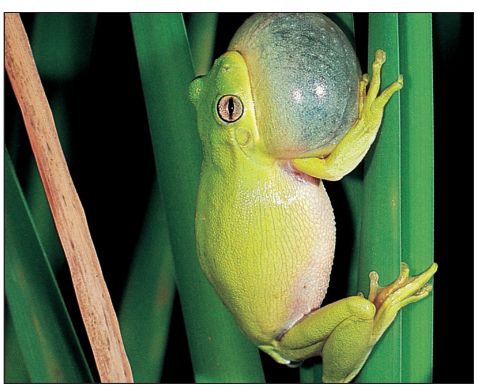
Figure 13.6

Courtship Behavior (Behavioral Isolation)
The dancing of a male prairie chicken attracts female prairie chickens, but not females of other species. This behavior tends to keep prairie chickens reproductively isolated from other species.

13.4 The Development of Evolutionary Thought

Today, most scientists consider speciation an important first step in the process of evolution. However, this was not always the case. For centuries people believed that the various species of plants and animals were fixed and unchanging—that is, they were thought to have remained unchanged from the time of their creation. This was a reasonable assumption because people knew nothing about DNA, meiosis, or population genetics. Furthermore, the process of evolution is so slow that the results of evolution were usually not evident during a human lifetime. It is even difficult for modern scientists to recognize this slow change in many kinds of organisms. In the mid-1700s, Georges-Louis Buffon, a French naturalist, expressed some curiosity about the possibilities of change (evolution) in animals, but he did not suggest any mechanism that would result in evolution.

In 1809, Jean-Baptiste de Lamarck, a student of Buffon's, suggested a process by which evolution could occur. He proposed that acquired characteristics could be transmitted to offspring. For example, he postulated that giraffes originally had short necks. Because giraffes constantly stretched their necks to obtain food, their necks got slightly longer. This slightly longer neck acquired through stretching could be passed to the offspring, who were themselves stretching their necks, and over time, the necks of giraffes would get longer and longer. Although we now know Lamarck's theory was wrong (because acquired characteristics are not inherited), it stimulated further thought as to how evolution could occur. All during this period, from the mid-1700s to the mid-1800s, lively arguments continued about the possibility of



(a)

(b)

Figure 13.7

Animal Communication by Displays
Most animals have specific behaviors that they use to communicate with others of the same species. (*a*) The croaking of a male frog is specific to its species and is different from that of males of other species. (*b*) The visual displays of Siamese fighting fish are also used to communicate with others of the same species.

evolutionary change. Some, like Lamarck and others, thought that change did take place; many others said that it was not possible. It was the thinking of two English scientists that finally provided a mechanism to explain how evolution could occur.

In 1858, Charles Darwin and Alfred Wallace suggested the theory of natural selection as a mechanism for evolution. They based their theory on the following assumptions about the nature of living things:

1. All organisms produce more offspring than can survive.
2. No two organisms are exactly alike.
3. Among organisms, there is a constant struggle for survival.
4. Individuals that possess favorable characteristics for their environment have a higher rate of survival and produce more offspring.
5. Favorable characteristics become more common in the species, and unfavorable characteristics are lost.

Using these assumptions, the Darwin-Wallace theory of evolution by natural selection offers a different explanation for the development of long necks in giraffes (figure 13.8):

1. In each generation, more giraffes would be born than the food supply could support.
2. In each generation, some giraffes would inherit longer necks, and some would inherit shorter necks.
3. All giraffes would compete for the same food sources.
4. Giraffes with longer necks would obtain more food, have a higher survival rate, and produce more offspring.
5. As a result, succeeding generations would show an increase in the neck length of the giraffe species.

This logic seems simple and obvious today, but remember that at the time Darwin and Wallace proposed their theory, the processes of meiosis and fertilization were poorly understood, and the concept of the gene was only beginning to be discussed. Nearly 50 years after Darwin and Wallace suggested their theory, the rediscovery of the work of Gregor Mendel (chapter 10) provided an explanation for how characteristics could be transmitted from one generation to the next. Not only did Mendel's idea of the gene provide a means of passing traits from one generation to the next, it also provided the first step in understanding mutations, gene flow, and the significance of reproductive isolation. All of these ideas are interwoven into the modern concept of evolution. If we look at the same five ideas from the thinking of Darwin and Wallace and update them with modern information, they might look something like this:

1. An organism's capacity to over-reproduce results in surplus organisms.
2. Because of mutation, new genes enter the gene pool. Because of sexual reproduction, involving meiosis and fertilization, new combinations of genes are present in every generation. These processes are so powerful that each individual in a sexually reproducing population is genetically unique. The genes present are expressed as the phenotype of the organism.
3. Resources such as food, soil nutrients, water, mates, and nest materials are in short supply, so some individuals will do without. Other environmental factors, such as disease organisms, predators, or helpful partnerships with other species also affect survival. All these factors that affect survival are called selecting agents.
4. Selecting agents favor individuals with the best combination of genes. They will be more likely to survive and reproduce, passing more of their genes on to the next generation. An organism is selected against if it has fewer offspring than other individuals that have a more favorable combination of genes. It does not need to die to be selected against.
5. Therefore, genes or gene combinations that produce characteristics favorable to survival will become more common, and the species will become better adapted to its environment.

13.5 Evolutionary Patterns Above the Species Level

The development of a new species is the smallest irreversible unit of evolution. Because the exact conditions present when a species came into being will never exist again it is unlikely that they will evolve back into an earlier stage in their development. Furthermore, because species are reproductively isolated from one another, they usually do not combine with other species to make something new; they can only diverge (separate) further. Higher levels of evolutionary change, those that occur above the species level, are the result of differences accumulated from a long series of speciation events leading to greater and greater diversity. The basic evolutionary pattern is one of **divergent evolution** in which individual speciation events cause successive branches in the evolution of a group of organisms. This basic pattern is well illustrated by the evolution of the horse shown in figure 13.9. Each of the many branches of the evolutionary history of the horse began with a speciation event that separated one species into two or more species as each separately adapted to local conditions. Changes in the environment from moist forests to drier grasslands would have set the stage for change. The modern horse, with its large size, single toe on each foot, and teeth designed for grinding grasses, is thought to be the result of accumulated changes beginning from a small, dog-sized animal with four toes on its front feet, three toes on its hind feet, and teeth designed for chewing leaves and small twigs. Even though we know much about the evolution of the horse, there are still many gaps that need to be filled before we have a complete evolutionary history.

Another basic pattern in the evolution of organisms is extinction. Notice in figure 13.9 that most of the species that

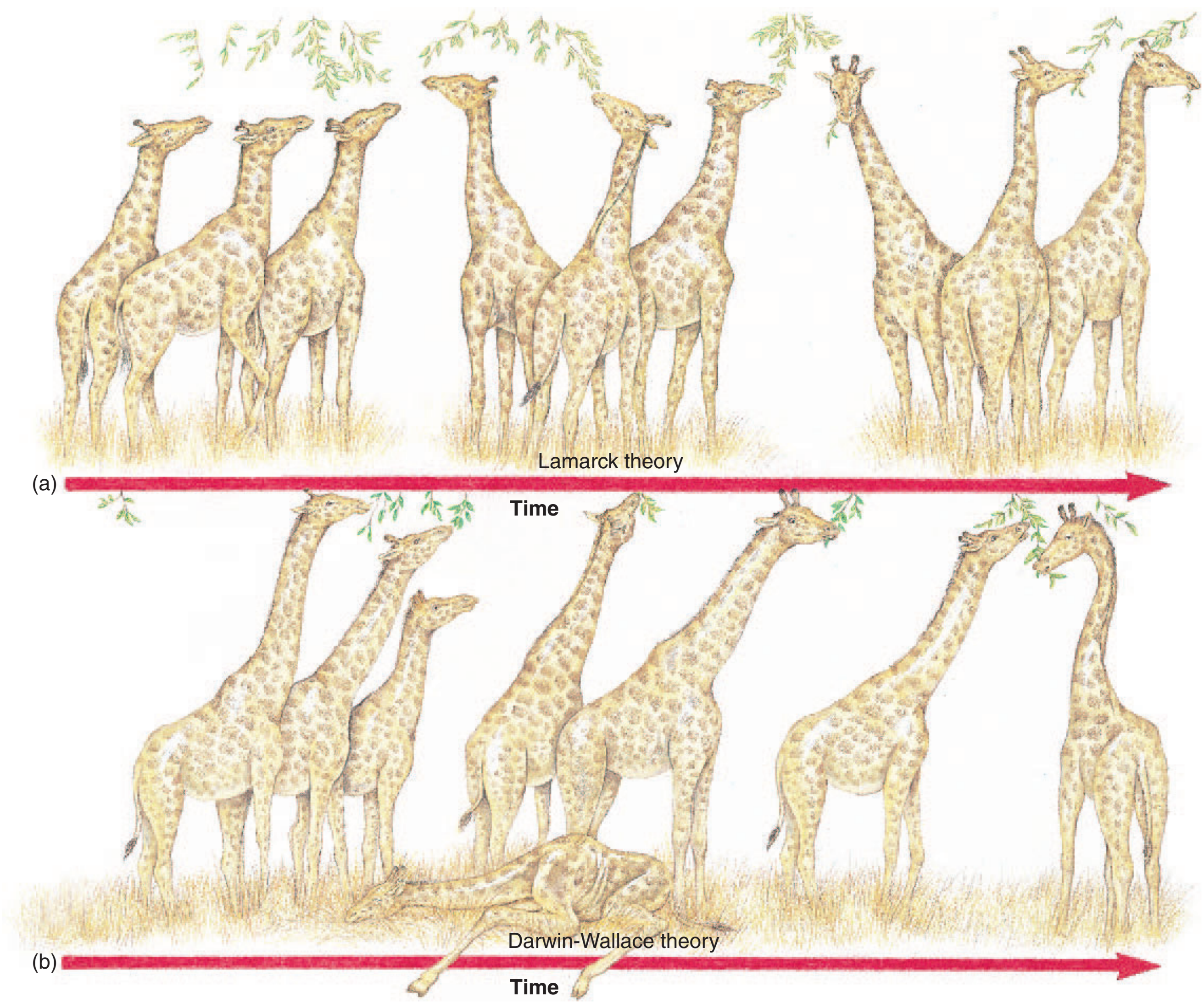


Figure 13.8

Two Theories of How Evolution Occurs

(*a*) Lamarck thought that acquired characteristics could be passed on to the next generation. Therefore, he postulated that as giraffes stretched their necks to get food, their necks got slightly longer. This characteristic was passed on to the next generation, which would have longer necks. (*b*) The Darwin-Wallace theory states that there is variation within the population and that those with longer necks would be more likely to survive and reproduce and pass their genes for long necks on to the next generation.

developed during the evolution of the horse are extinct. This is typical. Most of the species of organisms that have ever existed are extinct. Estimates of extinction are around 99%; that is, 99% or more of all the species of organisms that ever existed are extinct. Given this high rate of extinction, we can picture current species of organisms as the product of much evolutionary experimentation, most of which resulted in failure. This is not the complete picture though. From chapter 12 we recognize that organisms are continually being subjected to selection pressures that lead to a high degree of adaptation to a particular set of environmental conditions. Organisms become more and more specialized. However, the environment does not remain constant and often changes in such a way that the species that were originally present are unable to adapt to the new set of conditions. The early ancestors of the modern horse were well adapted to a moist tropical environment, but when the climate became drier, most were no longer able to survive. Only some kinds had the genes necessary to lead to the development of modern horses.

Furthermore, it is important to recognize that many extinct species were very successful organisms for millions of years. They were not failures for their time but simply did not survive to the present. It is also important to realize that many currently existing organisms will eventually become extinct.

Tracing the evolutionary history of an organism back to its origins is a very difficult task because most of its ancestors no longer exist. We may be able to look at fossils of extinct organisms but must keep in mind that the fossil record is incomplete and provides only limited information about the biology of the organism represented in that record. We may know a lot about the structure of the bones and teeth or the stems and leaves of an extinct ancestor but know almost nothing about its behavior, physiology, and natural history. Biologists must use a great deal of indirect evidence to piece together the series of evolutionary steps that led to a current species. Figure 13.10 is typical of evolutionary diagrams that help us understand how time and structural changes are related in the evolution of birds, mammals, and reptiles.

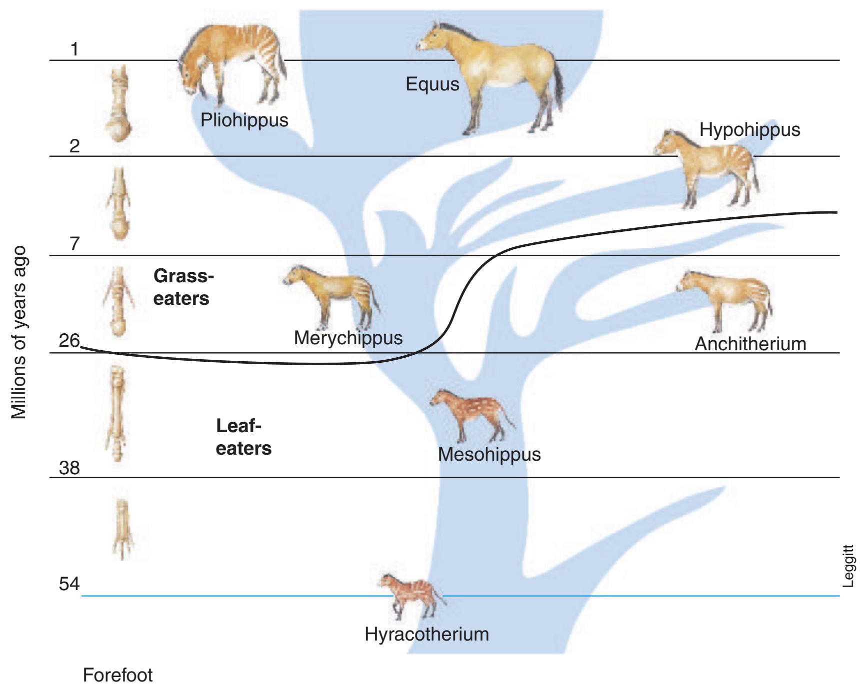


Figure 13.9

Divergent Evolution

In the evolution of the horse, many speciation events followed one after another. What began as a small, leaf-eating, four-toed animal of the forest evolved into a large, grass-eating, single-toed animal of the plains. There are many related animals alive today, but early ancestral types are extinct.

Although divergence is the basic pattern in evolution, it is possible to superimpose several other patterns on it. One special evolutionary pattern, characterized by a rapid increase in the number of kinds of closely related species, is known as **adaptive radiation.** Adaptive radiation results in an evolutionary explosion of new species from a common ancestor. There are basically two situations that are thought to favor adaptive radiation. One is a condition in which an organism invades a previously unexploited environment. For example, at one time there were no animals on the landmasses of the earth. The amphibians were the first vertebrate animals able to spend part of their lives on land. Fossil evidence shows that a variety of different kinds of amphibians evolved rapidly and exploited several different kinds of lifestyles.

Another good example of adaptive radiation is found among the finches of the Galápagos Islands, located 1,000 kilometers west of Ecuador in the Pacific Ocean. These birds were first studied by Charles Darwin. Because these islands are volcanic and arose from the floor of the ocean, it is assumed that they have always been isolated from South America and originally lacked finches and other land-based birds. It is thought that one kind of finch arrived from South America to colonize the islands and that adaptive radiation from the common ancestor resulted in the many different kinds of finches found on the islands today (figure 13.11). Although the islands are close to one another, they are quite diverse. Some are dry and treeless, some have moist forests, and others have intermediate conditions. Conditions were ideal for several speciation events. Because the islands were separated from one another, the element of geographic isolation was present. Because environmental conditions on the islands were quite different, particular characteristics in the resident birds would have been favored. Furthermore the absence of other kinds of birds meant that there were many lifestyles that had not been exploited.

In the absence of competition, some of these finches took roles normally filled by other kinds of birds elsewhere in the world. Although finches are normally seed-eating birds, some of the Galápagos finches became warblerlike, insect-eaters, others became leaf-eaters, and one uses a cactus spine as a tool to probe for insects.

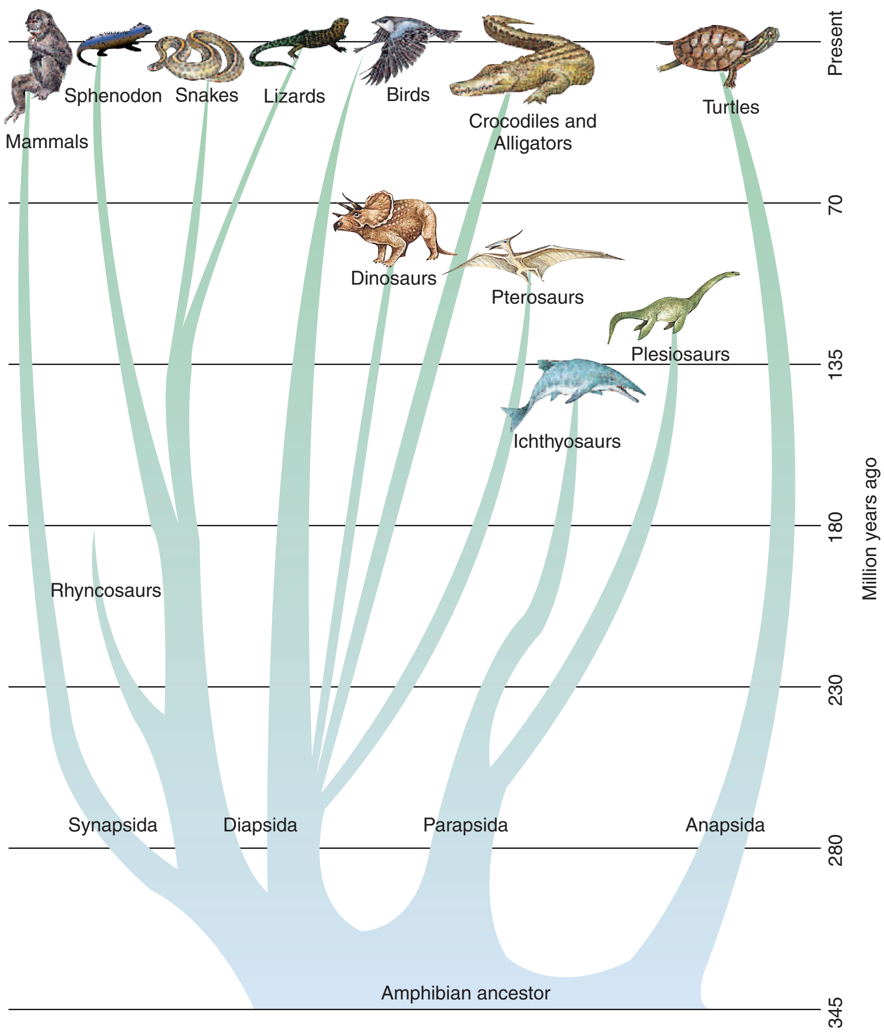


Figure 13.10

An Evolutionary Diagram
This diagram shows how present-day reptiles, birds, and mammals are thought to have evolved from primitive reptilian ancestors. Notice that an extremely long period of time is involved (over 300 million years) and that many of the species illustrated are extinct.

A second set of conditions that can favor adaptive radiation is one in which a type of organism evolves a new set of characteristics that enable it to displace organisms that previously filled roles in the environment. For example, although amphibians were the first vertebrates to occupy land, they lived only near freshwater where they would not dry out and could lay eggs, which developed in the water. They were replaced by reptiles with such characteristics as dry skin, which prevented the loss of water, and an egg that could develop on land. The adaptive radiation of reptiles was extensive. They invaded most terrestrial settings and even evolved forms that flew and lived in the sea. Subsequently, the reptiles were replaced by the birds and mammals, which went through a similar radiation. Perhaps the development of homeothermism (the ability to maintain a constant body temperature) had something to do with the success of birds and mammals. Figure 13.12 shows the sequence of radiations that occurred within the vertebrate group. The number of species of amphibians and reptiles has declined, whereas the number of species of birds and mammals has increased.

Another evolutionary pattern, **convergent evolution,** occurs when organisms of widely different backgrounds develop similar characteristics. This particular pattern often leads people to misinterpret the evolutionary history of organisms. For example, many kinds of plants that live in desert situations have thorns and lack leaves during much of the year. Superficially they may resemble one another to a remarkable degree, but may have a completely different evolutionary history. The presence of thorns and the absence of leaves are adaptations to a desert type of environment: the thorns discourage herbivores and the absence of leaves reduces water loss. Another example involves animals that survive by catching insects while flying. Bats, swallows, and dragonflies all obtain food in this manner. They all have wings, good eyesight or hearing to locate flying insects, and great agility and speed in flight, but they are evolved from quite different ancestors (figure 13.13). At first glance, they may appear very similar and perhaps closely related, but detailed study of their wings and other structures shows that they are quite different kinds of animals. They have simply converged in structure, type of food eaten, and method of obtaining food. Likewise, whales, sharks, and tuna appear to be similar. They have a streamlined shape that aids in rapid movement through the water, a dorsal fin that helps prevent rolling, fins or flippers for steering, and a large tail that provides the power for swimming. They are quite different kinds of animals that happen to live in the open ocean where they pursue other animals as prey. The structural similarities they have are adaptations to being fast-swimming predators.

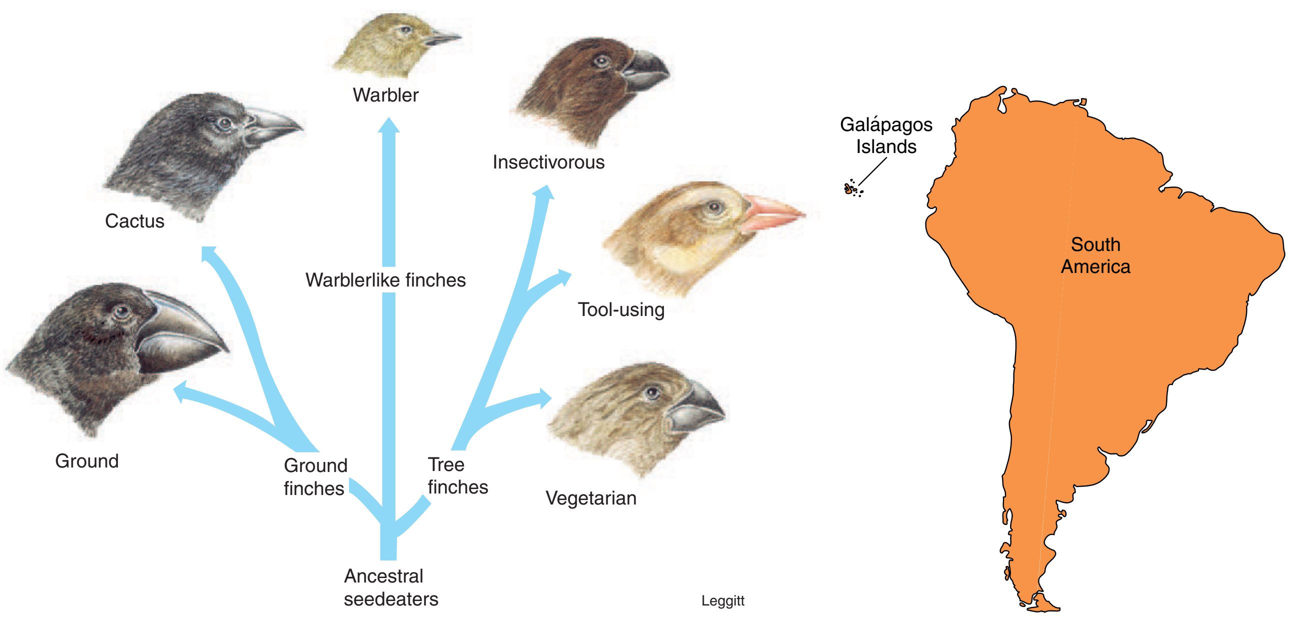


Figure 13.11

Adaptive Radiation

When Darwin discovered the finches of the Galápagos Islands, he thought they might all have derived from one ancestor that arrived on these relatively isolated islands. If they were the only birds to inhabit the islands, they could have evolved very rapidly into the many different types shown here. The drawings show the specializations of beaks for different kinds of food.

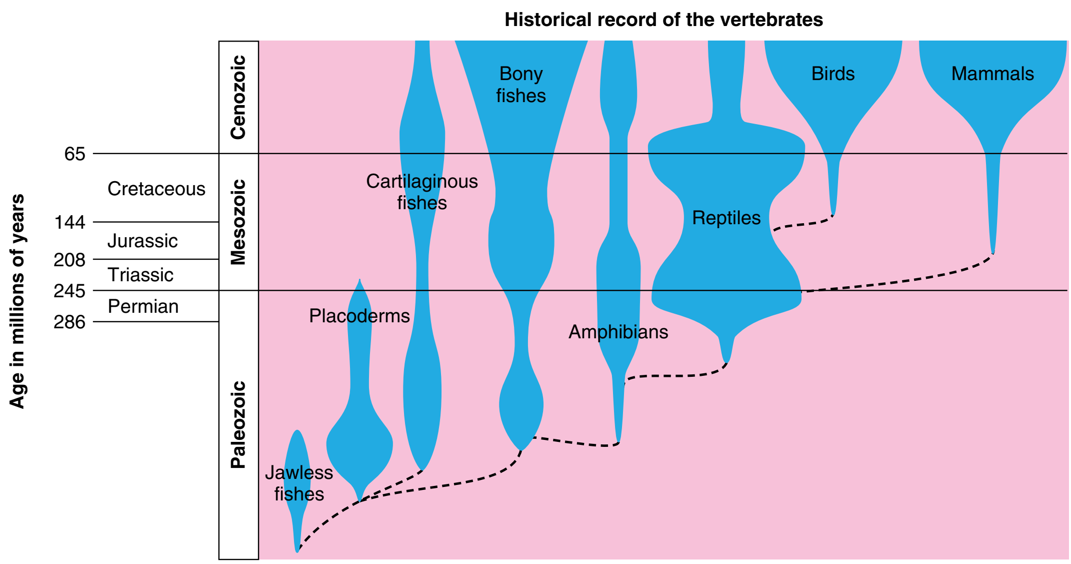


Figure 13.12

Adaptive Radiation in Terrestrial Vertebrates

The amphibians were the first vertebrates to live on land. They were replaced by the reptiles, which were better adapted to land. The reptiles, in turn, were replaced by the adaptive radiation of birds and mammals. (Note: The width of the colored bars indicates the number of species present.)

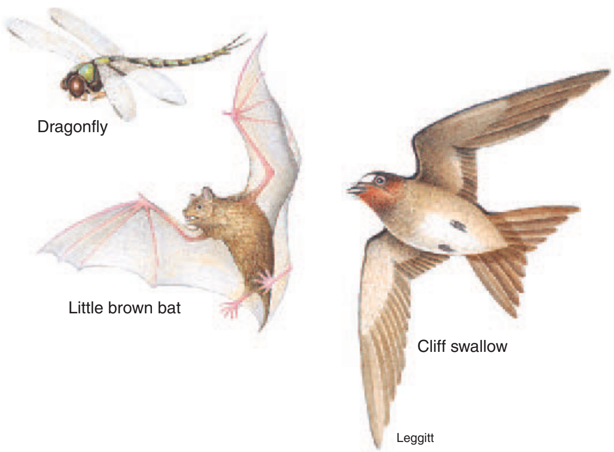


Figure 13.13

Convergent Evolution
All of these animals have evolved wings as a method of movement and capture insects for food as they fly. However, they have completely different evolutionary origins.

13.6 Rates of Evolution

Although it is commonly thought that evolutionary change takes long periods of time, you should understand that rates of evolution can vary greatly. Remember that natural selection is driven by the environment. If the environment is changing rapidly, one would expect rapid changes in the organisms that are present. Periods of rapid environmental change also result in extensive episodes of extinction. During some periods in the history of the Earth when little environmental change was taking place, the rate of evolutionary change was probably slow. Nevertheless, when we talk about evolutionary time, we are generally thinking in thousands or millions of years. Although both of these time periods are long compared to the human life span, the difference between thousands of years and millions of years in the evolutionary time scale is still significant.

When we examine the fossil record, we can often see gradual changes in physical features of organisms over time. For example, the extinct humanoid fossil *Homo erectus* shows a gradual increase in the size of the cranium, a reduction in the size of the jaw, and the development of a chin over about a million years of time. The accumulation of these changes could result in such extensive change from the original species that we would consider the current organism to be a different species from its ancestor. (Many believe that *Homo erectus* became modern humans, *Homo sapiens*.) This is such a common feature of the evolutionary record that biologists refer to this kind of evolutionary change as **gradualism** (figure 13.14*a*). Charles Darwin's view of evolution was based on gradual changes in the features of specific species he observed in his studies of geology and natural history. However, as early as the 1940s, some biologists began to challenge gradualism as the typical model for evolutionary change. They pointed out that the fossils of some species were virtually unchanged over millions of years. If gradualism were the only explanation for how species evolved, then gradual changes in the fossil record of a species would always be found. Furthermore, some organisms appear suddenly in the fossil record and show rapid change from the time they first appeared. We have many modern examples of rapid evolutionary change. The development of pesticide resistance in insects and antibiotic resistance in various bacteria occurred within our lifetime.

In 1972, two biologists, Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University, proposed the idea of **punctuated equilibrium.** This hypothesis suggests that evolution occurs in spurts of rapid change followed by long periods with little evolutionary change (figure 13.14*b*). It is important to recognize that the punctuated equilibrium concept suggests a different way of achieving evolutionary change. Rather than one species slowly accumulating changes to become a different descendant species, rapid evolution of several closely related species from isolated populations would produce a number of species that would compete with one another as the environment changed. Many of these species would become extinct and the fossil record would show change.

At the present time, the scientific community has not resolved these two alternative mechanisms for how evolutionary change occurs. However, both approaches recognize the importance of genetic diversity as the raw material for evolution and the mechanism of natural selection as the process of determining which gene combinations fit the environment. It is possible that both gradualism and punctuated equilibrium occur under different circumstances. The gradualists point to the fossil record as proof that evolution is a slow, steady process. Those who support punctuated equilibrium point to the gaps in the fossil record as evidence that rapid change occurs. As with most controversies of this nature, more information is required to resolve the question. It will take decades to collect all the information and, even then, the differences of opinion may not be reconciled.

13.7 The Tentative Nature of the Evolutionary History of Organisms

It is important to understand that thinking about the concept of evolution can take us in several different directions. First, it is clear that genetic changes do occur. Mutations introduce new genes into a species. This has been demonstrated repeatedly with chemicals and radiation. Our recognition of this danger is evident by the ways we protect ourselves against

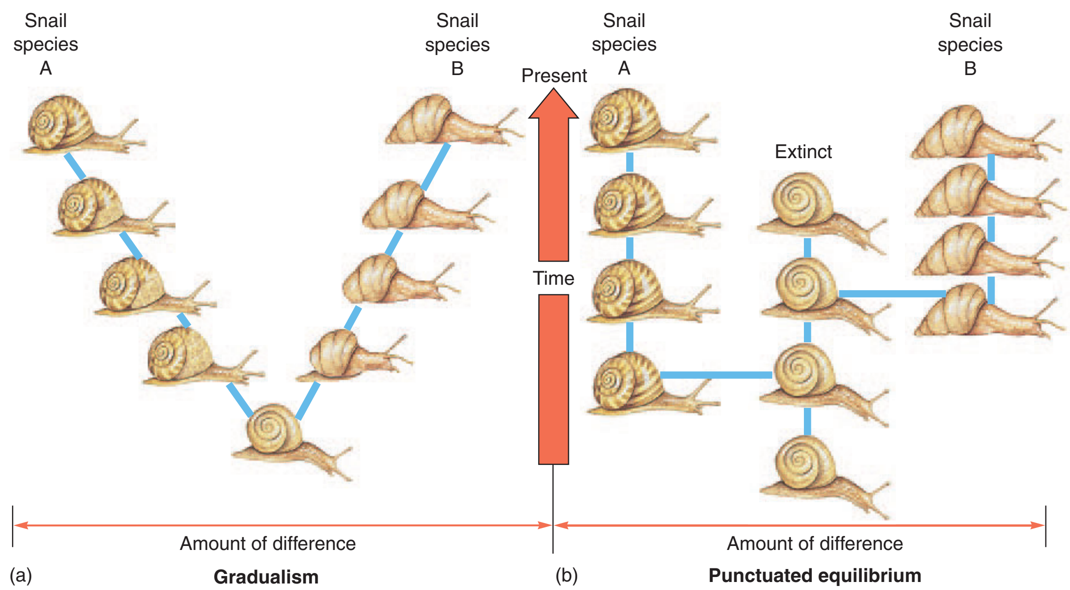


Figure 13.14

Gradualism Versus Punctuated Equilibrium
Gradualism (*a*) is the evolution of new species from the accumulation of a series of small changes over a long period of time. Punctuated equilibrium (*b*) is the evolution of new species from a large number of changes in a short period of time. Note that in both instances the ancestral snail has evolved into two species (A and B). However, it is possible that they were produced by different processes.

excessive exposure to mutagenic agents. We also recognize that species can change. We purposely manipulate the genetic constitution of our domesticated plants and animals and change their characteristics to suit our needs. We also recognize that different populations of the same species show genetic differences. Examination of fossils shows that species of organisms that once existed are no longer in existence. We even have historical examples of plants and animals that are now extinct. We can also demonstrate that new species come into existence. This is easiest to do in plants with polyploidy. It is clear from this evidence that species are not fixed, unchanging entities.

However, when we try to piece together the evolutionary history of organisms over long periods of time, we must use much indirect evidence, and it becomes difficult to state definitively the specific sequence of steps that the evolution of a species followed. Although it is clear that evolution occurs, it is not possible to state unconditionally that evolution of a particular group of organisms has followed a specific path. There will always be new information that will require changes in thinking, and equally reputable scientists will disagree on the evolutionary processes or the sequence of events that led to a specific group of organisms.

For example, the fossil record provides a great deal of information about the kinds of organisms that have existed in the past. However, the fossil record is not a complete record and new fossils are being discovered every year. There are several reasons why the fossil record is incomplete. First of all the likelihood that an organism will become a fossil is low. Most organisms die and decompose leaving no trace of their existence. (Today, road-killed opossums are not likely to become fossils because they will be eaten by scavengers, repeatedly run over, or decompose by the roadside.) In order to form a fossil the dead organism must be covered over by sediments, or dehydrated or preserved in some other way. In addition, some organisms have very resistant parts that tend to be preserved while others do not. Clams and insects are abundant in the fossil record. Worms are not. Finally, the discovery of fossils is often accidental. It is impossible to search through all the layers of sedimentary rock on the entire surface of the Earth. Therefore, there will continue to be additions of new fossils that will extend our information about ancient life into the foreseeable future. But there can be no question that evolution occurred in the past and continues to occur today (How Science Works 13.1: Accumulating Evidence of Evolution).

13.8 Human Evolution

There is intense curiosity about how our species (*Homo sapiens*) came to be and the evolution of the human species

HOW SCIENCE WORKS 13.1

Accumulating Evidence of Evolution

The theory of evolution has become the major unifying theory of the biological sciences. Medicine recognizes the dangers of mutations, the similarity in function of the same organ in related species, and the way in which the environment can interfere with the preprogramed process of embryological development. Agricultural science recognizes the importance of selecting specific genes for passage into new varieties of crop plants and animals. The concepts of mutation, selection, and evolution are so fundamental to understanding what happens in biology that we often forget to take note of the many kinds of observations that support the theory of evolution. The following list describes some of the more important pieces of evidence that support the idea that evolution has been and continues to be a major force in shaping the nature of living things.

1. Species and populations are not genetically fixed. Change occurs in individuals and populations.
   a. Mutations cause slight changes in the genetic makeup of an individual organism.
   b. Different populations of the same species show adaptations suitable for their local conditions.
   c. Changes in the characteristics displayed by species can be linked to environmental changes.
   d. Selective breeding of domesticated plants and animals indicates that the shape, color, behavior, metabolism, and many other characteristics of organisms can be selected for.
   e. Extinction of poorly adapted species is common.
2. All evidence suggests that once embarked on a particular evolutionary road, the system is not abandoned, only modified. New organisms are formed by the modification of ancestral species, not by major changes. The following list supports the concept that evolution proceeds by modification of previously existing structures and processes rather than by catastrophic change.
   a. All species use the same DNA code.
   b. All species use the same left-handed, amino acid building blocks.
   c. It is difficult to eliminate a structure when it is part of a developmental process controlled by genes. Vestigial structures are evidence of genetic material from previous stages in evolution.
   d. Embryological development of related animals is similar regardless of the peculiarities of adult anatomy. All vertebrates' embryos have an early stage that contains gill slits.
   e. Species of organisms that are known to be closely related show greater similarity in their DNA than those that are distantly related.
3. Several aspects of the fossil record support the concept of evolution.
   a. The nature of the Earth has changed significantly over time.
   b. The fossil record shows vast changes in the kinds of organisms present on Earth. New species appear and most go extinct. This is evidence that living things change in response to changes in their environment.
   c. The fossils found in old rocks do not reappear in younger rocks. Once an organism goes extinct it does not reappear, but new organisms arise that are modifications of previous organisms.
4. New techniques and discoveries invariably support the theory of evolution.
   a. The recognition that the Earth was formed billions of years ago supports the slow development of new kinds of organisms.
   b. The recognition that the continents of the Earth have separated helps explain why organisms on Australia are so different from elsewhere.
   c. The discovery of DNA and how it works helps explain mutation and allows us to demonstrate the genetic similarity of closely related species.

remains an interesting and controversial topic. We recognize that humans show genetic diversity, experience mutations, and are subject to the same evolutionary forces as other organisms. We also recognize that some individuals have genes that make them subject to early death or make them unable to reproduce. On the other hand, because all of our close evolutionary relatives are extinct, it is difficult for us to visualize our evolutionary development and we tend to think we are unique and not subject to the laws of nature.

We use several kinds of evidence to try to sort out our evolutionary history. Fossils of various kinds of human and prehuman ancestors have been found, but these are often fragmentary and hard to date. Stone tools of various kinds have also been found that are associated with human and prehuman sites. Finally, other aspects of the culture of our human ancestors have been found in burial sites, cave paintings, and the creation of ceremonial objects. Various methods have been used to age these findings. Some can be dated quite accurately, whereas others are more difficult to pinpoint.

When fossils are examined, anthropologists can identify differences in the structures of bones that are consistent with changes in species. Based on the amount of change they see and the ages of the fossils, these scientists make judgments about the species to which the fossil belongs. As new discoveries are made, opinions of experts will change and our evolutionary history may become more clear as old ideas are replaced. It is also clear from the fossil record that humans are relatively recent additions to the forms of life. Assembling all of these bits of information into a clear picture is not possible at this point, but a number of points are well accepted.

1. There is a great deal of fossil evidence that several species of hominids of the genera *Australopithecus* and *Paranthropus* were among the earliest hominid fossils. These organisms are often referred to collectively as australopiths.
2. Based on fossil evidence, it appears that the climate of Africa was becoming drier during the time that hominid evolution was occurring.
3. The earliest *Australopithecus* fossils are from about 4.2 million years ago. Earlier fossils such as *Ardipithecus* may be ancestral to *Australopithecus*. *Australopithecus* and *Paranthropus* were herbivores and walked upright. Their fossils and the fossils of earlier organisms like *Ardipithecus* are found only in Africa.
4. The australopiths were sexually dimorphic with the males much larger than the females and had relatively small brains (cranial capacity 530 cubic centimeters or less).
5. Several species of the genus *Homo* became prominent in Africa and appear to have made a change from a primarily herbivorous diet to a carnivorous or omnivorous diet.
6. All members of the genus *Homo* have relatively large brains (cranial capacity 650 cubic centimeters or more) and are associated with various degrees of stone tool construction and use. It is possible that some of the australopiths may have constructed stone tools.
7. Fossils of several later species of the genus *Homo* are found in Africa, Europe, and Asia, but not in Australia or the Americas. Only *Homo sapiens* is found in Australia and the Americas.
8. Since the fossils of *Homo* species found in Asia and Europe are generally younger than the early *Homo* species found in Africa, it is assumed that they moved to Europe and Asia from Africa.
9. Differences in size are less prominent in members of the genus *Homo* so perhaps there was less difference in activities.

When we try to put all of these bits of information together we can construct the following scenario for the evolution of our species. Monkeys, apes, and other primates are adapted to living in forested areas where their grasping hands, opposable thumbs and big toes, and wide range of movement of the shoulders allow them to move freely in the trees. As the climate became drier the forests were replaced by grasslands and, as is always the case, some organisms became extinct and others adapted to the change.

The First Hominids—The Australopiths

Various species of *Australopithecus* and *Paranthropus* were present in Africa from about 4.4 million years ago until about 1 million years ago. It is important to recognize that there are few fossils of these early humanlike organisms and that often they are fragments of the whole organism. This has led to much speculation and argument among experts about the specific position each fossil has in the evolutionary history of humans. However, from examining the fossil bones of the leg, pelvis, and foot, it is apparent that the australopiths were relatively short (males, 1.5 meters or less; females, about 1.1 meters) and stocky and walked upright like humans.

An upright posture had several advantages in a world that was becoming drier. It allowed for more rapid movement over long distances, the ability to see longer distances, and reduced the amount of heat gained from the sun. In addition, upright posture freed the arms for other uses such as carrying and manipulating objects, and using tools. The various species of *Australopithecus* and *Paranthropus* shared these characteristics and, based on the structure of their skulls, jaws, and teeth, appear to have been herbivores with relatively small brains.

Later Hominids—The Genus *Homo*

About 2.5 million years ago the first members of the genus *Homo* appeared on the scene. There is considerable disagreement about how many species there were but *Homo habilis* is one of the earliest. *Homo habilis* had a larger brain (650 cubic centimeters) and smaller teeth than australopiths and made much more use of stone tools. Some people believe that it was a direct descendant of *Australopithecus africanus*. Many experts believe that *Homo habilis* was a scavenger that made use of group activities, tools, and higher intelligence to hijack the kills made by other carnivores. The higher-quality diet would have supported the metabolic needs of the larger brain.

About 1.8 million years ago *Homo ergaster* appeared on the scene. It was much larger (up to 1.6 meters) than *H. habilis* (about 1.3 meters) and also had a much larger brain (cranial capacity of 850 cubic centimeters). A little later a similar species (*Homo erectus*) appears in the fossil record. Some people consider *H. ergaster* and *H. erectus* to be variations of the same species. The larger brain of *H. ergaster* and *H. erectus* appears to be associated with extensive use of stone tools. Hand axes were manufactured and used to cut the flesh of prey and crush the bones for marrow. These organism appears to have been predators, whereas *H. habilis* was a scavenger. The use of meat as food allows animals to move about more freely, because appropriate food is available almost everywhere. By contrast, herbivores are often confined to places that have foods appropriate to their use; fruits for fruit eaters, grass for grazers, forests for browsers, and so forth. In fact, fossils of *H. erectus* have been found in the Middle East and Asia as well as Africa. Most experts think that *H. erectus* originated in Africa and migrated through the Middle East to Asia.

About 800,000 years ago another hominid, classified as *Homo heidelbergensis,* appears in the fossil record. Since fossils of this species are found in Africa, Europe, and Asia, it appears that they constitute a second wave of migration of early *Homo* from Africa to other parts of the world. Both *H. erectus* and *H. heidelbergensis* disappear from the fossil record as two new species (*Homo neanderthalensis* and *Homo sapiens*) become common.

The Neandertals were primarily found in Europe and adjoining parts of Asia and are not found in Africa. Therefore many scientists feel they are descendants of *Homo heidelbergensis,* which was common in Europe.

The Origin of *Homo Sapiens*

Homo sapiens is found throughout the world and is now the only hominid species remaining of a long line of ancestors. There are two different theories that seek to explain the origin of *Homo sapiens*. One theory, known as the **out-of-Africa hypothesis,** states that modern humans (*Homo sapiens*) originated in Africa as had several other hominid species and migrated from Africa to Asia and Europe and displaced species such as *H. erectus* and *H. heidelbergensis* that had migrated into these areas previously. The other theory, known as the **multiregional hypothesis,** states that *H. erectus* evolved into *H. sapiens*. During a period of about 1.7 million years, fossils of *Homo erectus* showed a progressive increase in the size of the cranial capacity and reduction in the size of the jaw, so that it becomes difficult to distinguish *H. erectus* from *H. heidelbergensis* and *H. heidelbergensis* from *H. sapiens*. Proponents of this hypothesis believe that *H. heidelbergensis* is not a distinct species but an intermediate between the earlier *H. erectus* and *H. sapiens*. According to this theory, various subgroups of *H. erectus* existed throughout Africa, Asia, and Europe and that interbreeding among the various groups gave rise to the various races of humans we see today.

Another continuing puzzle is the relationship of humans that clearly belong to the species *Homo sapiens* with a contemporary group known as Neandertals. Some people

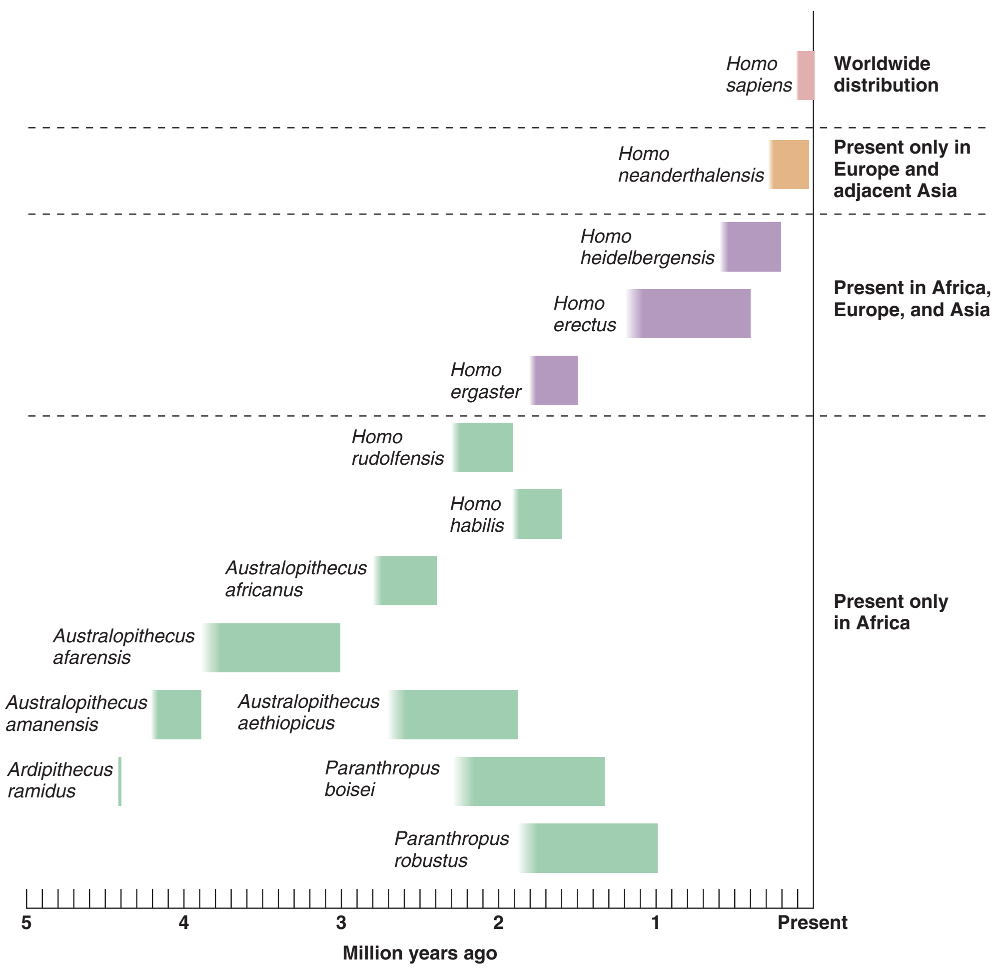


Figure 13.15

Human Evolution
This diagram shows the various organisms thought to be relatives of humans. The bars represent approximate times the species are thought to have existed. Notice that: (1) All species are extinct today except for modern humans, (2) Several different species of organisms coexisted for extensive periods, (3) All the older species are only found in Africa, (4) More recent species of *Homo* are found in Europe and Asia as well as Africa.

consider Neandertals to be a subgroup of *Homo sapiens* specially adapted to life in the harsh conditions found in postglacial Europe. Others consider them to be a separate species *Homo neanderthalensis*. The Neandertals were muscular, had a larger brain capacity than modern humans, and had many elements of culture, including burials. The cause of their disappearance from the fossil record at about 25,000 years ago remains a mystery. Perhaps climate change to a warmer climate was responsible. Perhaps contact with *Homo sapiens* resulted in their elimination either through hostile interactions or, if they were able to interbreed with *H. sapiens,* they could have been absorbed into the larger *H. sapiens* population.

Large numbers of fossils of prehistoric humans have been found in all parts of the world. Many of these show evidence of a collective group memory we call *culture*. Cave paintings, carvings in wood and bone, tools of various kinds, and burials are examples. These are also evidence of a capacity to think and invent, and "free time" to devote to things other than gathering food and other necessities of life. We may never know how we came to be, but we will always be curious and will continue to search and speculate about our beginnings. Figure 13.15 (p. 233) summarizes the current knowledge of the historical record of humans and their relatives.

SUMMARY

Populations are usually genetically diverse. Mutations, meiosis, and sexual reproduction tend to introduce genetic variety into a population. Organisms with wide geographic distribution often show different gene frequencies in different parts of their range. A species is a group of organisms that can interbreed to produce fertile offspring. The process of speciation usually involves the geographic separation of the species into two or more isolated populations. While they are separated, natural selection operates to adapt each population to its environment. If this generates enough change, the two populations may become so different that they cannot interbreed. Similar organisms that have recently evolved into separate species normally have mechanisms to prevent interbreeding. Some of these are habitat preference, seasonal isolation, and behavioral isolation. Plants have a special way of generating new species by increasing their chromosome numbers as a result of abnormal mitosis or meiosis.

At one time, people thought that all organisms had remained unchanged from the time of their creation. Lamarck suggested that change did occur and thought that acquired characteristics could be passed from generation to generation. Darwin and Wallace proposed the theory of natural selection as the mechanism that drives evolution. Evolution is basically a divergent process upon which other patterns can be superimposed. Adaptive radiation is a very rapid divergent evolution; convergent evolution involves the development of superficial similarities among widely different organisms. The rate at which evolution has occurred probably varies. The fossil record shows periods of rapid change interspersed with periods of little change. This has caused some to look for mechanisms that could cause the sudden appearance of large numbers of new species in the fossil record, which challenge the traditional idea of slow, steady change accumulating enough differences to cause a new species to be formed.

The early evolution of humans has been difficult to piece together because of the fragmentary evidence. Beginning about 4.4 million years ago the earliest forms of *Australopithecus* and *Paranthropus* showed upright posture and other humanlike characteristics. The structure of the jaw and teeth indicates that the various kinds of australopiths were herbivores. *Homo habilis* had a larger brain and appears to have been a scavenger. Several other species of the genus *Homo* arose in Africa. These forms appear to have been carnivores. Some of these migrated to Europe and Asia. The origin of *Homo sapiens* is in dispute. It may have arisen in Africa and migrated throughout the world or evolved from earlier ancestors found throughout Africa, Asia, and Europe.

THINKING CRITICALLY

Explain how all the following are related to the process of speciation: mutation, natural selection, meiosis, the Hardy-Weinberg concept, geographic isolation, changes in the Earth, gene pool, and competition.

CONCEPT MAP TERMINOLOGY

Construct a concept map to show relationships among the following concepts.

adaptive radiation
behavioral isolation
convergent evolution
divergent evolution
ecological isolation
gene flow
genetic isolating mechanisms
geographic isolation
seasonal isolation
speciation
species

KEY TERMS

adaptive radiation
behavioral isolation
biochemical isolation
convergent evolution
divergent evolution
ecological isolation
gene flow
genetic isolating mechanism
geographic barriers
geographic isolation
gradualism
habitat preference
mechanical (morphological) isolation
multiregional hypothesis
out-of-Africa hypothesis
polyploidy
punctuated equilibrium
range
reproductive isolating mechanism
seasonal isolation
speciation
species
subspecies

e—LEARNING CONNECTIONS *www.mhhe.com/enger10*

Topics	Questions	Media Resources
13.1 Species: A Working Definition	1. How does speciation differ from the formation of subspecies or races? 2. Why aren't mules considered a species? 3. Can you always tell by looking at two organisms whether or not they belong to the same species?	**Quick Overview** • Barriers to gene flow **Key Points** • Species: A working definition
13.2 How New Species Originate	4. Why is geographic isolation important in the process of speciation? 5. How does a polyploid organism differ from a haploid or diploid organism?	**Quick Overview** • Isolation **Key Points** • How new species originate **Experience This!** • Observing isolation mechanisms firsthand
13.3 Maintaining Genetic Isolation	6. Describe three kinds of genetic isolating mechanisms that prevent interbreeding between different species. 7. Give an example of seasonal isolation, ecological isolation, and behavioral isolation. 8. List the series of events necessary for speciation to occur.	**Quick Overview** • Continued isolation **Key Points** • Maintaining genetic isolation
13.4 The Development of Evolutionary Thought	9. Why has Lamarck's theory been rejected?	**Quick Overview** • Assumptions behind evolution **Key Points** • The development of evolutionary thought **Animations and Review** • Evidence for evolution
13.5 Evolutionary Patterns Above the Species Level	10. Describe two differences between covergent evolution and adaptive radiation.	**Quick Overview** • Patterns of evolution **Key Points** • Evolutionary patterns above the species level
13.6 Rates of Evolution	11. What is the difference between gradualism and punctuated equilibrium?	**Quick Overview** • Gradualism or punctuated equilibrium **Key Points** • Rates of evolution **Interactive Concept Maps** • Text concept map
13.7 The Tentative Nature of the Evolutionary History of Organisms	12. "Evolution is a fact." "Evolution is a theory." Explain how both statements can be true.	**Quick Overview** • Gaps in data and interpretation **Key Points** • The tentative nature of the evolutionary history of organisms
13.8 Human Evolution	13. What are some of the major steps thought to have been involved in the evolution of humans?	**Quick Overview** • Our evolutionary background **Key Points** • Human evolution **Animations and Review** • Hominid