21

The Evidence for Evolution

Concept Outline

21.1 Fossil evidence indicates that evolution has occurred.

The Fossil Record. When fossils are arranged in the order of their age, a continual series of change is seen, new changes being added at each stage.

The Evolution of Horses. The record of horse evolution is particularly well-documented and instructive.

21.2 Natural selection can produce evolutionary change.

The Beaks of Darwin's Finches. Natural selection favors stouter bills in dry years, when large tough-to-crush seeds are the only food available to finches.

Peppered Moths and Industrial Melanism. Natural selection favors dark-colored moths in areas of heavy pollution, while light-colored moths survive better in unpolluted areas.

Artificial Selection. Artificial selection practiced in laboratory studies, agriculture, and domestication demonstrate that selection can produce substantial evolutionary change.

21.3 Evidence for evolution can be found in other fields of biology.

The Anatomical Record. When anatomical features of living animals are examined, evidence of shared ancestry is often apparent.

The Molecular Record. When gene or protein sequences from organisms are arranged, species thought to be closely related based on fossil evidence are seen to be more similar than species thought to be distantly related.

Convergent and Divergent Evolution. Evolution favors similar forms under similar circumstances.

21.4 The theory of evolution has proven controversial.

Darwin's Critics. Critics have raised seven objections to Darwin's theory of evolution by natural selection.

FIGURE 21.1
A window into the past. The fossil remains of the now-extinct reptile *Mesosaurus* found in Permian sediments in Africa and South America provided one of the earliest clues to a former connection between the two continents. *Mesosaurus* was a freshwater species and so clearly incapable of a transatlantic swim. Therefore, it must have lived in the lakes and rivers of a formerly contiguous landmass that later became divided as Africa and South America drifted apart in the Cretaceous.

Of all the major ideas of biology, the theory that today's organisms evolved from now-extinct ancestors (figure 21.1) is perhaps the best known to the general public. This is not because the average person truly understands the basic facts of evolution, but rather because many people mistakenly believe that it represents a challenge to their religious beliefs. Similar highly publicized criticisms of evolution have occurred ever since Darwin's time. For this reason, it is important that, during the course of your study of biology, you address the issue squarely: Just what is the evidence for evolution?

21.1 Fossil evidence indicates that evolution has occurred.

At its core, the case for evolution is built upon two pillars: first, evidence that natural selection can produce evolutionary change and, second, evidence from the fossil record that evolution has occurred. In addition, information from many different areas of biology—including fields as different as embryology, anatomy, molecular biology, and biogeography (the study of the geographic distribution of species)—can only be interpreted sensibly as the outcome of evolution.

The Fossil Record

The most direct evidence that evolution has occurred is found in the fossil record. Today we have a far more complete understanding of this record than was available in Darwin's time. Fossils are the preserved remains of once-living organisms. Fossils are created when three events occur. First, the organism must become buried in sediment; then, the calcium in bone or other hard tissue must mineralize; and, finally, the surrounding sediment must eventually harden to form rock. The process of fossilization probably occurs rarely. Usually, animal or plant remains will decay or be scavenged before the process can begin. In addition, many fossils occur in rocks that are inaccessible to scientists. When they do become available, they are often destroyed by erosion and other natural processes before they can be collected. As a result, only a fraction of the species that have ever existed (estimated by some to be as many as 500 million) are known from fossils. Nonetheless, the fossils that have been discovered are sufficient to provide detailed information on the course of evolution through time.

Dating Fossils

By dating the rocks in which fossils occur, we can get an accurate idea of how old the fossils are. In Darwin's day, rocks were dated by their position with respect to one another (*relative dating*); rocks in deeper strata are generally older. Knowing the relative positions of sedimentary rocks and the rates of erosion of different kinds of sedimentary rocks in different environments, geologists of the nineteenth century derived a fairly accurate idea of the relative ages of rocks.

Today, rocks are dated by measuring the degree of decay of certain radioisotopes contained in the rock (*absolute dating*); the older the rock, the more its isotopes have decayed. Because radioactive isotopes decay at a constant rate unaltered by temperature or pressure, the isotopes in a rock act as an internal clock, measuring the time since the rock was formed. This is a more accurate way of dating rocks and provides dates stated in millions of years, rather than relative dates.

A History of Evolutionary Change

When fossils are arrayed according to their age, from oldest to youngest, they often provide evidence of successive evolutionary change. At the largest scale, the fossil record documents the progression of life through time, from the origin of eukaryotic organisms, through the evolution of fishes, the rise of land-living organisms, the reign of the dinosaurs, and on to the origin of humans (figure 21.2).

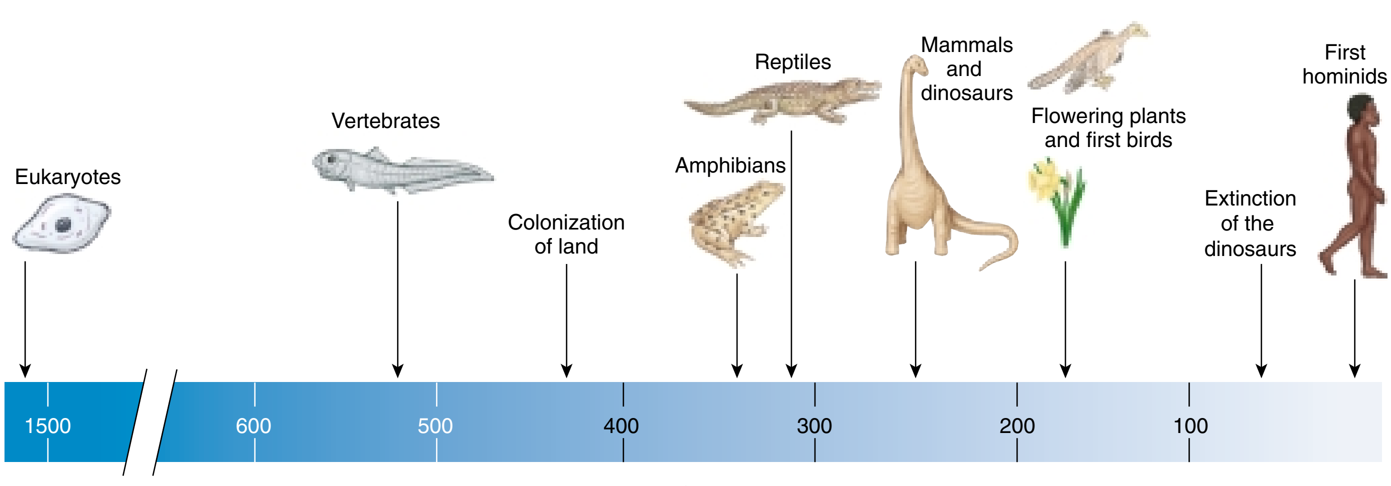

FIGURE 21.2
Timeline of the history of life as revealed by the fossil record.

Gaps in the Fossil Record

This is not to say that the fossil record is complete. Given the low likelihood of fossil preservation and recovery, it is not surprising that there are gaps in the fossil record. Nonetheless, paleontologists (the scientists who study fossils) continue to fill in the gaps in the fossil record. While many gaps interrupted the fossil record in Darwin's era, even then, scientists knew of the *Archaeopteryx* fossil transitional between dinosaurs and birds. Today, the fossil record is far more complete, particularly among the vertebrates; fossils have been found linking all the major groups. Recent years have seen spectacular discoveries closing some of the major remaining gaps in our understanding of vertebrate evolution. For example, recently a four-legged aquatic mammal was discovered that provides important insights concerning the evolution of whales and dolphins from land-living, hoofed ancestors (figure 21.3). Similarly, a fossil snake with legs has shed light on the evolution of snakes, which are descended from lizards that gradually became more and more elongated with simultaneous reduction and eventual disappearance of the limbs.

On a finer scale, evolutionary change within some types of animals is known in exceptional detail. For example, about 200 million years ago, oysters underwent a change from small curved shells to larger, flatter ones, with progressively flatter fossils being seen in the fossil record over a period of 12 million years (figure 21.4). A host of other examples all illustrate a record of successive change. The demonstration of this successive change is one of the strongest lines of evidence that evolution has occurred.

The fossil record provides a clear record of the major evolutionary transitions that have occurred through time.

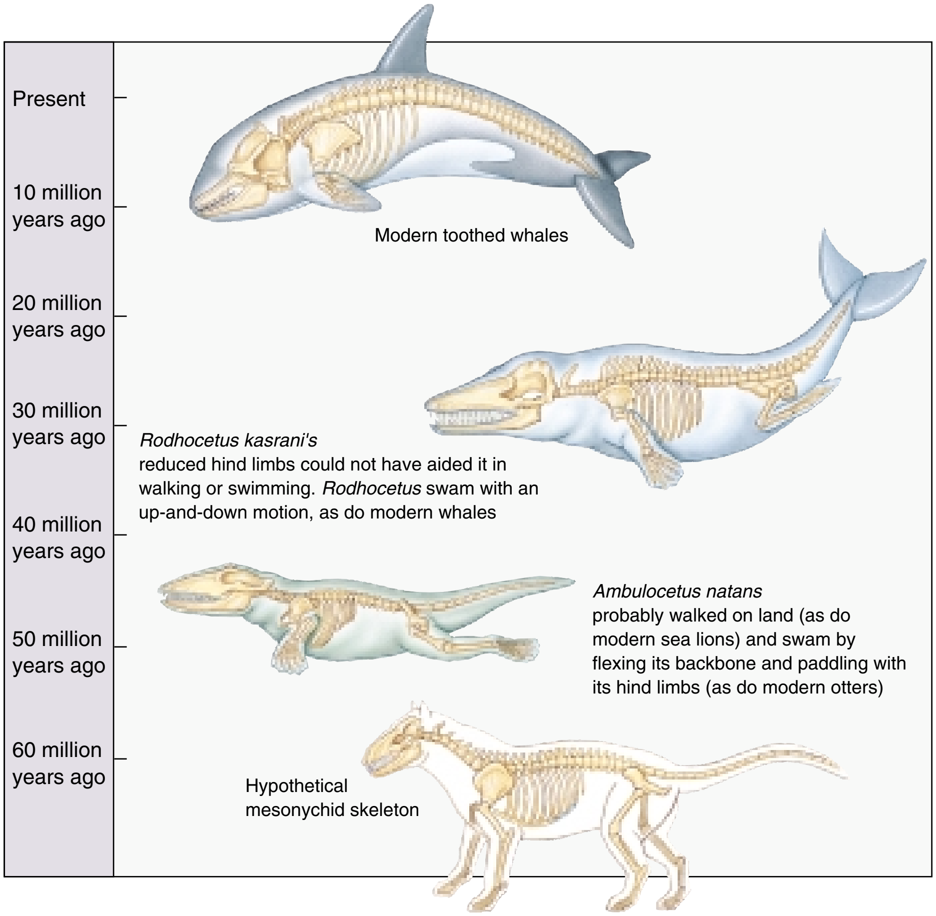

FIGURE 21.3
Whale "missing links." The recent discoveries of *Ambulocetus* and *Rodhocetus* have filled in the gaps between the mesonychids, the hypothetical ancestral link between the whales and the hoofed mammals, and present-day whales.

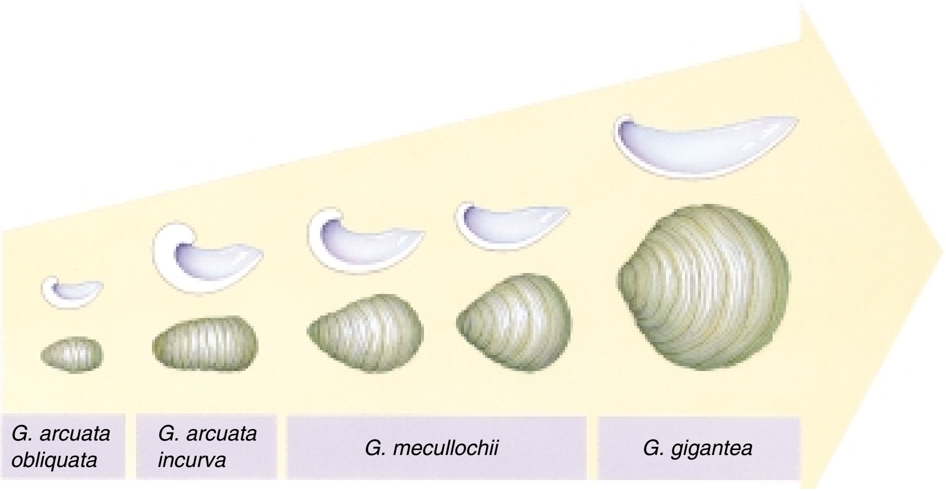

FIGURE 21.4
Evolution of shell shape in oysters. Over 12 million years of the Early Jurassic Period, the shells of this group of coiled oysters became larger, thinner, and flatter. These animals rested on the ocean floor in a special position called the "life position," and it may be that the larger, flatter shells were more stable in disruptive water movements.

The Evolution of Horses

One of the best-studied cases in the fossil record concerns the evolution of horses. Modern-day members of the Equidae include horses, zebras, donkeys and asses, all of which are large, long-legged, fast-running animals adapted to living on open grasslands. These species, all classified in the genus *Equus*, are the last living descendants of a long lineage that has produced 34 genera since its origin in the Eocene Period, approximately 55 million years ago. Examination of these fossils has provided a particularly well-documented case of how evolution has proceeded by adaptation to changing environments.

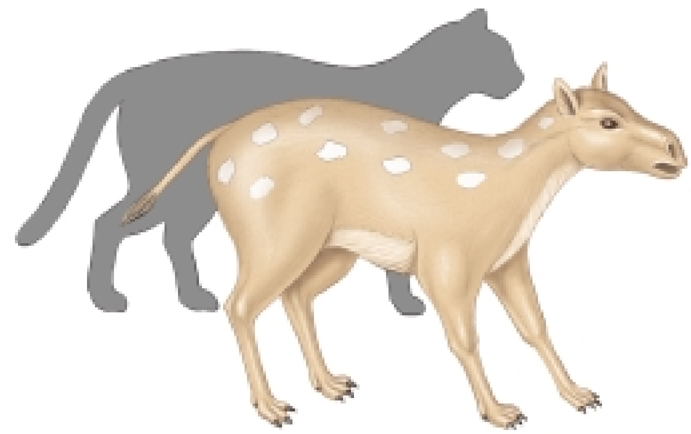

FIGURE 21.5
***Hyracotherium sandrae*, one of the earliest horses, was the size of a housecat.**

The First Horse

The earliest known members of the horse family, species in the genus *Hyracotherium*, didn't look much like horses at all. Small, with short legs and broad feet (figure 21.5), these species occurred in wooded habitats, where they probably browsed on leaves and herbs and escaped predators by dodging through openings in the forest vegetation. The evolutionary path from these diminutive creatures to the workhorses of today has involved changes in a variety of traits, including:

Size. The first horses were no bigger than dogs, with some considerably smaller. By contrast, modern equids can weigh more than a half ton. Examination of the fossil record reveals that horses changed little in size for their first 30 million years, but since then, a number of different lineages exhibited rapid and substantial increases. However, trends toward decreased size were also exhibited among some branches of the equid evolutionary tree (figure 21.6).

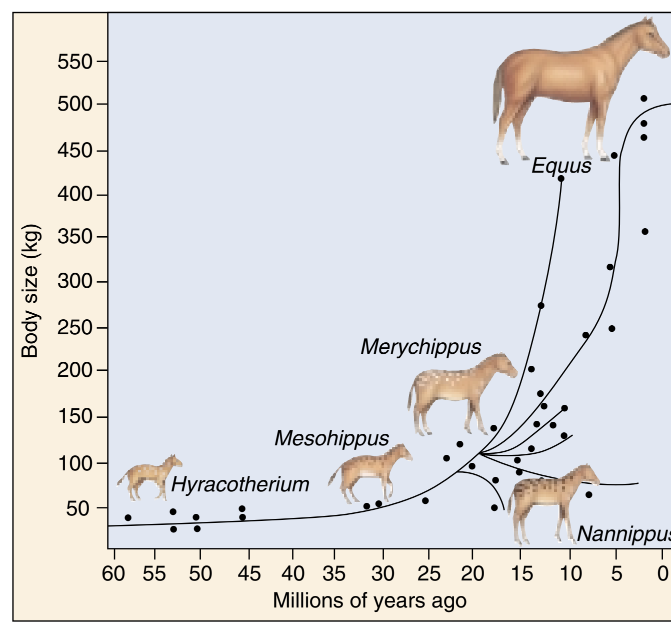

FIGURE 21.6
Evolutionary change in body size of horses. Lines show the broad outline of evolutionary relationships. Although most change involved increases in size, some decreases also occurred.

Toe reduction. The feet of modern horses have a single toe, enclosed in a tough, bony hoof. By contrast, *Hyracotherium* had four toes on its front feet and three on its hindfeet. Rather than hooves, these toes were encased in fleshy pads. Examination of the fossils clearly shows the transition through time: increase in length of the central toe, development of the bony hoof, and reduction and loss of the other toes (figure 21.7). As with body size, these trends occurred concurrently on several different branches of the horse evolutionary tree. At the same time as these developments, horses were evolving changes in the length and skeletal structure of the limbs, leading to animals capable of running long distances at high speeds.

Tooth size and shape. The teeth of *Hyracotherium* were small and relatively simple in shape. Through time, horse teeth have increased greatly in length and have developed a complex pattern of ridges on their molars and premolars (figure 21.7). The effect of these changes is to produce teeth better capable of chewing tough and gritty vegetation, such as grass, which tends to wear teeth down. Accompanying these changes have been alterations in the shape of the skull that strengthened the skull to withstand the stresses imposed by continual chewing. As with body size, evolutionary change has not been constant through time. Rather, much of the change in tooth shape has occurred within the past 20 million years.

All of these changes may be understood as adaptations to changing global climates. In particular, during the late

Miocene and early Oligocene (approximately 20 to 25 million years ago), grasslands became widespread in North America, where much of horse evolution occurred. As horses adapted to these habitats, long-distance and high-speed locomotion probably became more important to escape predators and travel great distances. By contrast, the greater flexibility provided by multiple toes and shorter limbs, which was advantageous for ducking through complex forest vegetation, was no longer beneficial. At the same time, horses were eating grasses and other vegetation that contained more grit and other hard substances, thus favoring teeth and skulls better suited for withstanding such materials.

Evolutionary Trends

For many years, horse evolution was held up as an example of constant evolutionary change through time. Some even saw in the record of horse evolution evidence for a progressive, guiding force, consistently pushing evolution to move in a single direction. We now know that such views are misguided; evolutionary change over millions of years is rarely so simple.

Rather, the fossils demonstrate that, although there have been overall trends evident in a variety of characteristics, evolutionary change has been far from constant and uniform through time. Instead, rates of evolution have varied widely, with long periods of little change and some periods of great change. Moreover, when changes happen, they often occur simultaneously in different lineages of the horse evolutionary tree. Finally, even when a trend exists, exceptions, such as the evolutionary decrease in body size exhibited by some lineages, are not uncommon. These patterns, evident in our knowledge of horse evolution, are usually discovered for any group of plants and animals for which we have an extensive fossil record, as we shall see when we discuss human evolution in chapter 23.

Horse Diversity

One reason that horse evolution was originally conceived of as linear through time may be that modern horse diversity is relatively limited. Thus, it is easy to mentally picture a straight line from *Hyracotherium* to modern-day *Equus*. However, today's limited horse diversity—only one surviving genus—is unusual. Indeed, at the peak of horse diversity in the Miocene, as many as 13 genera of horses could be found in North America alone. These species differed in body size and in a wide variety of other characteristics. Presumably, they lived in different habitats and exhibited different dietary preferences. Had this diversity existed to modern times, early workers presumably would have had a different outlook on horse evolution, a situation that is again paralleled by the evolution of humans.

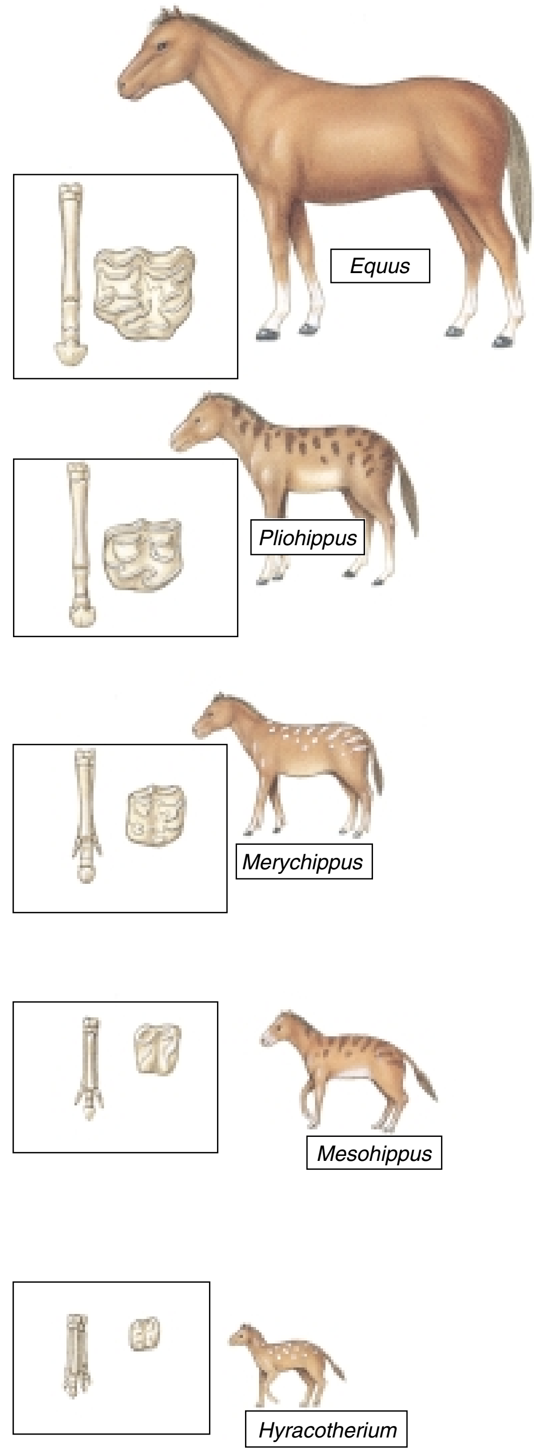

FIGURE 21.7
Evolutionary changes in horses through time.

The extensive fossil record for horses provides a detailed view of the evolutionary diversification of this group from small forest dwellers to the large and fast modern grassland species.

21.2 Natural selection can produce evolutionary change.

As we saw in chapter 20, a variety of different processes can result in evolutionary change. Nonetheless, in agreement with Darwin, most evolutionary biologists would agree that natural selection is the process responsible for most of the major evolutionary changes that have occurred through time. Although we cannot travel back through time, a variety of modern-day evidence confirms the power of natural selection as an agent of evolutionary change. These data come from both the field and the laboratory and from natural and human-altered situations.

The Beaks of Darwin's Finches

Darwin's finches are a classic example of evolution by natural selection. Darwin collected 31 specimens of finch from three islands when he visited the Galápagos Islands off the coast of Ecuador in 1835. Darwin, not an expert on birds, had trouble identifying the specimens, believing by examining their bills that his collection contained wrens, "grossbeaks," and blackbirds. You can see Darwin's sketches of four of these birds in figure 21.8.

The Importance of the Beak

Upon Darwin's return to England, ornithologist John Gould examined the finches. Gould recognized that Darwin's collection was in fact a closely related group of distinct species, all similar to one another except for their bills. In all, there were 13 species. The two ground finches with the larger bills in figure 21.8 feed on seeds that they crush in their beaks, whereas the two with narrower bills eat insects. One species is a fruit eater, another a cactus eater, yet another a "vampire" that creeps up on seabirds and uses its sharp beak to drink their blood. Perhaps most remarkable are the tool users, woodpecker finches that pick up a twig, cactus thorn, or leaf stalk, trim it into shape with their bills, and then poke it into dead branches to pry out grubs.

The correspondence between the beaks of the 13 finch species and their food source immediately suggested to Darwin that evolution had shaped them:

> "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends."

Was Darwin Wrong?

If Darwin's suggestion that the beak of an ancestral finch had been "modified for different ends" is correct, then it ought to be possible to see the different species of finches acting out their evolutionary roles, each using their bills to acquire their particular food specialty. The four species that crush seeds within their bills, for example, should feed on different seeds, those with stouter beaks specializing on harder-to-crush seeds.

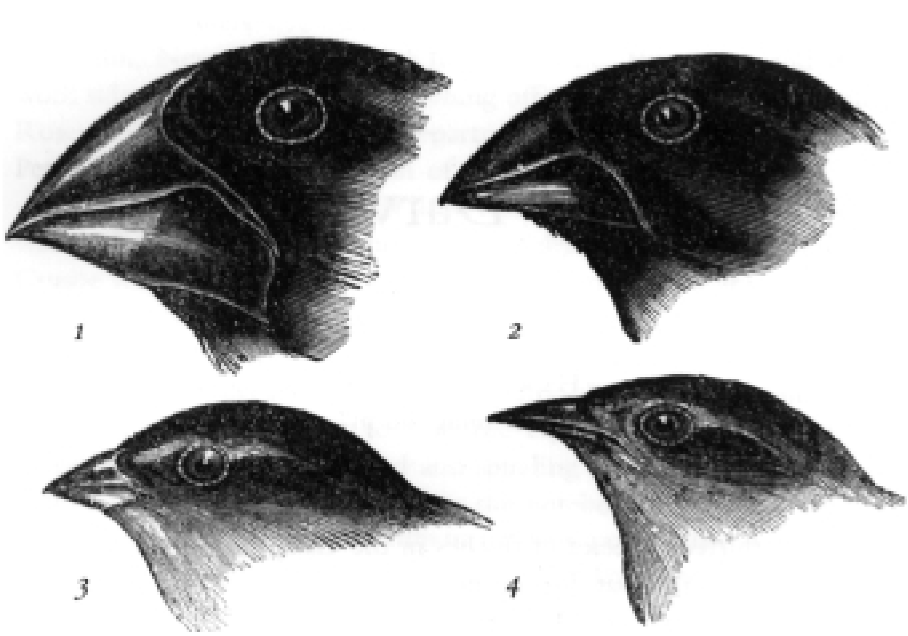

FIGURE 21.8
Darwin's own sketches of Galápagos finches. From Darwin's *Journal of Researches:* (*1*) large ground finch *Geospiza magnirostris;* (*2*) medium ground finch *Geospiza fortis;* (*3*) small tree finch *Camarhynchus parvulus;* (*4*) warbler finch *Certhidea olivacea.*

Many biologists visited the Galápagos after Darwin, but it was 100 years before any tried this key test of his hypothesis. When the great naturalist David Lack finally set out to do this in 1938, observing the birds closely for a full five months, his observations seemed to contradict Darwin's proposal! Lack often observed many different species of finch feeding together on the same seeds. His data indicated that the stout-beaked species and the slender-beaked species were feeding on the very same array of seeds.

We now know that it was Lack's misfortune to study the birds during a wet year, when food was plentiful. The finch's beak is of little importance in such flush times; small seeds are so abundant that birds of all species are able to get enough to eat. Later work has revealed a very different picture during leaner, dry years, when few seeds are available and the difference between survival and starvation depends on being able to efficiently gather enough to eat. In such times, having beaks designed to be maximally effective for a particular type of food becomes critical and the species diverge in their diet, each focusing on the type of food to which it is specialized.

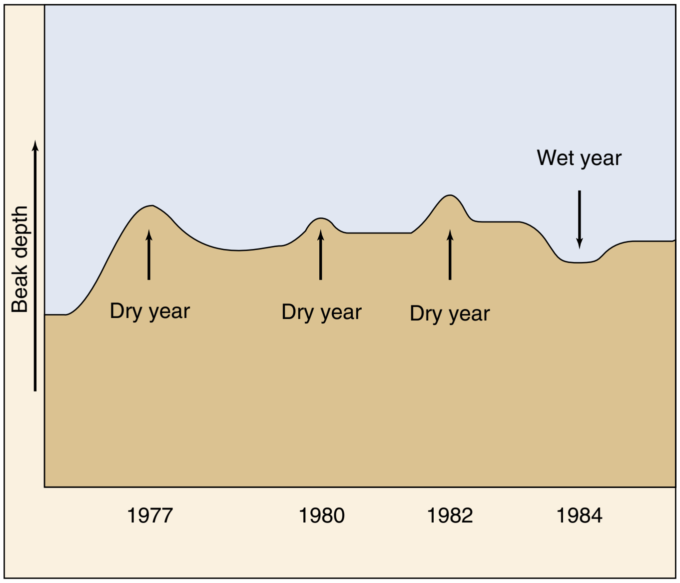

FIGURE 21.9
Evidence that natural selection alters beak size in *Geospiza fortis*. In dry years, when only large, tough seeds are available, the mean beak size increases. In wet years, when many small seeds are available, smaller beaks become more common.

A Closer Look

The key to successfully testing Darwin's proposal that the beaks of Galápagos finches are adaptations to different food sources proved to be patience. Starting in 1973, Peter and Rosemary Grant of Princeton University and generations of their students have studied the medium ground finch *Geospiza fortis* on a tiny island in the center of the Galápagos called Daphne Major. These finches feed preferentially on small tender seeds, produced in abundance by plants in wet years. The birds resort to larger, drier seeds, which are harder to crush, only when small seeds become depleted during long periods of dry weather, when plants produce few seeds.

The Grants quantified beak shape among the medium ground finches of Daphne Major by carefully measuring beak depth (width of beak, from top to bottom, at its base) on individual birds. Measuring many birds every year, they were able to assemble for the first time a detailed portrait of evolution in action. The Grants found that beak depth changed from one year to the next in a predictable fashion. During droughts, plants produced few seeds and all available small seeds quickly were eaten, leaving large seeds as the major remaining source of food. As a result, birds with large beaks survived better, because they were better able to break open these large seeds. Consequently, the average beak depth of birds in the population increased the next year, only to decrease again when wet seasons returned (figure 21.9).

Could these changes in beak dimension reflect the action of natural selection? An alternative possibility might be that the changes in beak depth do not reflect changes in gene frequencies, but rather are simply a response to diet—perhaps during lean times the birds become malnourished and then grow stouter beaks, for example. To rule out this possibility, the Grants measured the relation of parent bill size to offspring bill size, examining many broods over several years. The depth of the bill was passed down faithfully from one generation to the next, regardless of environmental conditions, suggesting that the differences in bill size indeed reflected genetic differences.

Darwin Was Right After All

If the year-to-year changes in beak depth indeed reflect genetic changes, as now seems likely, and these changes can be predicted by the pattern of dry years, then Darwin was right after all—natural selection does seem to be operating to adjust the beak to its food supply. Birds with stout beaks have an advantage during dry periods, for they can break the large, dry seeds that are the only food available. When small seeds become plentiful once again with the return of wet weather, a smaller beak proves a more efficient tool for harvesting the more abundant smaller seeds.

Among Darwin's finches, natural selection adjusts the shape of the beak in response to the nature of the available food supply, adjustments that can be seen to be occurring even today.

Peppered Moths and Industrial Melanism

When the environment changes, natural selection often may favor new traits in a species. The example of the Darwin's finches clearly indicates how natural variation can lead to evolutionary change. Humans are greatly altering the environment in many ways; we should not be surprised to see organisms attempting to adapt to these new conditions. One classic example concerns the peppered moth, *Biston betularia*. Until the mid-nineteenth century, almost every individual of this species captured in Great Britain had light-colored wings with black specklings (hence the name "peppered" moth). From that time on, individuals with dark-colored wings increased in frequency in the moth populations near industrialized centers until they made up almost 100% of these populations. Black individuals had a dominant allele that was present but very rare in populations before 1850. Biologists soon noticed that in industrialized regions where the dark moths were common, the tree trunks were darkened almost black by the soot of pollution. Dark moths were much less conspicuous resting on them than were light moths. In addition, the air pollution that was spreading in the industrialized regions had killed many of the light-colored lichens on tree trunks, making the trunks darker.

Selection for Melanism

Can Darwin's theory explain the increase in the frequency of the dark allele? Why did dark moths gain a survival advantage around 1850? An amateur moth collector named J. W. Tutt proposed what became the most commonly accepted hypothesis explaining the decline of the light-colored moths. He suggested that peppered forms were more visible to predators on sooty trees that have lost their lichens. Consequently, birds ate the peppered moths resting on the trunks of trees during the day. The black forms, in contrast, were at an advantage because they were camouflaged (figure 21.10). Although Tutt initially had no evidence, British ecologist Bernard Kettlewell tested the hypothesis in the 1950s by rearing populations of peppered moths with equal numbers of dark and light individuals. Kettlewell then released these populations into two sets of woods: one, near heavily polluted Birmingham, the other, in unpolluted Dorset. Kettlewell set up rings of traps around the woods to see how many of both kinds of moths survived. To evaluate his results, he had marked the released moths with a dot of paint on the underside of their wings, where birds could not see it.

In the polluted area near Birmingham, Kettlewell trapped 19% of the light moths, but 40% of the dark ones. This indicated that dark moths had a far better chance of surviving in these polluted woods, where the tree trunks were dark. In the relatively unpolluted Dorset woods, Kettlewell recovered 12.5% of the light moths but only 6% of the dark ones. This indicated that where the tree trunks were still light-colored, light moths had a much better chance of survival. Kettlewell later solidified his argument by placing hidden blinds in the woods and actually filming birds eating the moths. Sometimes the birds Kettlewell observed actually passed right over a moth that was the same color as its background.

FIGURE 21.10
Tutt's hypothesis explaining industrial melanism. These photographs show color variants of the peppered moth, *Biston betularia.* Tutt proposed that the dark moth is more visible to predators on unpolluted trees (*top*), while the light moth is more visible to predators on bark blackened by industrial pollution (*bottom*).

Industrial Melanism

Industrial melanism is a term used to describe the evolutionary process in which darker individuals come to predominate over lighter individuals since the industrial revolution as a result of natural selection. The process is widely believed to have taken place because the dark organisms are better concealed from their predators in habitats that have been darkened by soot and other forms of industrial pollution, as suggested by Kettlewell's research.

Dozens of other species of moths have changed in the same way as the peppered moth in industrialized areas throughout Eurasia and North America, with dark forms becoming more common from the mid-nineteenth century onward as industrialization spread.

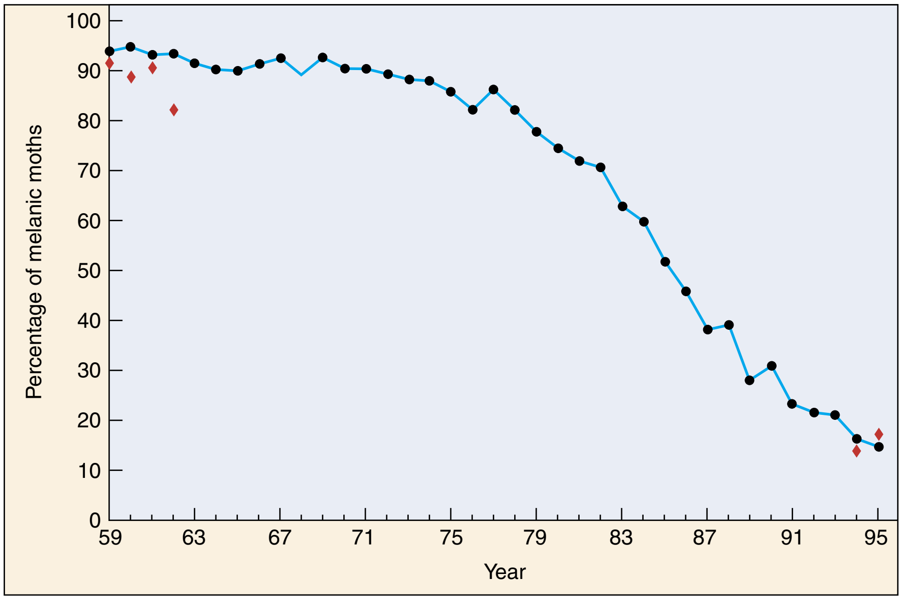

FIGURE 21.11
Selection against melanism. The circles indicate the frequency of melanic *Biston* moths at Caldy Common in England, sampled continuously from 1959 to 1995. Diamonds indicate frequencies in Michigan from 1959 to 1962 and from 1994 to 1995.
Source: Data from Grant, et al., "Parallel Rise and Fall of Melanic Peppered Moths" in *Journal of Heredity*, vol. 87, 1996, Oxford University Press.

Selection against Melanism

In the second half of the twentieth century, with the widespread implementation of pollution controls, these trends are reversing, not only for the peppered moth in many areas in England, but also for many other species of moths throughout the northern continents. These examples provide some of the best documented instances of changes in allelic frequencies of natural populations as a result of natural selection due to specific factors in the environment.

In England, the pollution promoting industrial melanism began to reverse following enactment of Clean Air legislation in 1956. Beginning in 1959, the *Biston* population at Caldy Common outside Liverpool has been sampled each year. The frequency of the melanic (dark) form has dropped from a high of 94% in 1960 to its current (1994) low of 19% (figure 21.11). Similar reversals have been documented at numerous other locations throughout England. The drop correlates well with a drop in air pollution, particularly with tree-darkening sulfur dioxide and suspended particulates.

Interestingly, the same reversal of industrial melanism appears to have occurred in America during the same time that it was happening in England. Industrial melanism in the American subspecies of the peppered moth was not as widespread as in England, but it has been well-documented at a rural field station near Detroit. Of 576 peppered moths collected there from 1959 to 1961, 515 were melanic, a frequency of 89%. The American Clean Air Act, passed in 1963, led to significant reductions in air pollution. Resampled in 1994, the Detroit field station peppered moth population had only 15% melanic moths (see figure 21.11)! The moths in Liverpool and Detroit, both part of the same natural experiment, exhibit strong evidence of natural selection.

Reconsidering the Target of Natural Selection

Tutt's hypothesis, widely accepted in the light of Kettlewell's studies, is currently being reevaluated. The problem is that the recent selection against melanism does not appear to correlate with changes in tree lichens. At Caldy Common, the light form of the peppered moth began its increase in frequency long before lichens began to reappear on the trees. At the Detroit field station, the lichens never changed significantly as the dark moths first became dominant and then declined over the last 30 years. In fact, investigators have not been able to find peppered moths on Detroit trees at all, whether covered with lichens or not. Wherever the moths rest during the day, it does not appear to be on tree bark. Some evidence suggests they rest on leaves on the treetops, but no one is sure.

The action of selection may depend less on the presence of lichens and more on other differences in the environment resulting from industrial pollution. Pollution tends to cover all objects in the environment with a fine layer of particulate dust, which tends to decrease how much light surfaces reflect. In addition, pollution has a particularly severe effect on birch trees, which are light in color. Both effects would tend to make the environment darker and thus would favor darker color in moths.

Natural selection has favored the dark form of the peppered moth in areas subject to severe air pollution, perhaps because on darkened trees they are less easily seen by moth-eating birds. Selection has in turn favored the light form as pollution has abated.

Artificial Selection

Humans have imposed selection upon plants and animals since the dawn of civilization. Just as in natural selection, artificial selection operates by favoring individuals with certain phenotypic traits, allowing them to reproduce and pass their genes into the next generation. Assuming that phenotypic differences are genetically determined, such selection should lead to evolutionary change and, indeed, it has. Artificial selection, imposed in laboratory experiments, agriculture, and the domestication process, has produced substantial change in almost every case in which it has been applied. This success is strong proof that selection is an effective evolutionary process.

Laboratory Experiments

With the rise of genetics as a field of science in the 1920s and 1930s, researchers began conducting experiments to test the hypothesis that selection can produce evolutionary change. A favorite subject was the now-famous laboratory fruit fly, *Drosophila melanogaster*. Geneticists have imposed selection on just about every conceivable aspect of the fruit fly—including body size, eye color, growth rate, life span, and exploratory behavior—with a consistent result: selection for a trait leads to strong and predictable evolutionary response.

In one classic experiment, scientists selected for fruit flies with many bristles (stiff, hairlike structures) on their abdomen. At the start of the experiment, the average number of bristles was 9.5. Each generation, scientists picked out the 20% of the population with the greatest number of bristles and allowed them to reproduce, thus establishing the next generation. After 86 generations of such selection, the average number of bristles had quadrupled, to nearly 40. In a similar experiment, fruit flies were selected for either the most or the fewest numbers of bristles. Within 35 generations, the populations did not overlap at all in range of variation (figure 21.12).

Similar experiments have been conducted on a wide variety of other laboratory organisms. For example, by selecting for rats that were resistant to tooth decay, scientists were able to increase in less than 20 generations the average time for onset of decay from barely over 100 days to greater than 500 days.

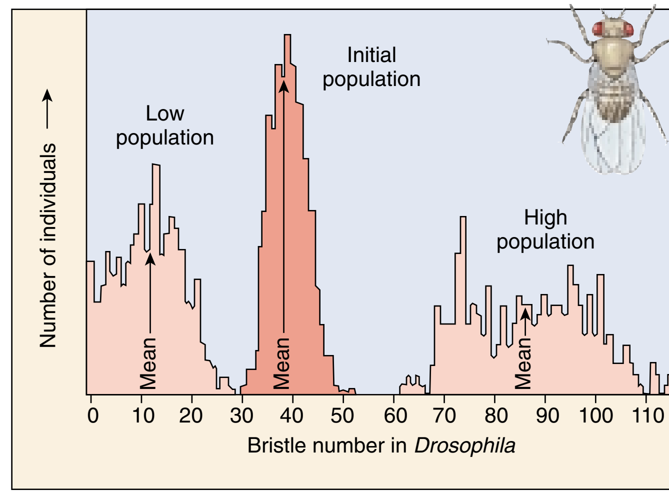

FIGURE 21.12
Artificial selection in the laboratory. In this experiment, one population of *Drosophila* was selected for low numbers of bristles and the other for high numbers. Note that not only did the means of the populations change greatly in 35 generations, but also that all individuals in both experimental populations lie outside the range of the initial population.

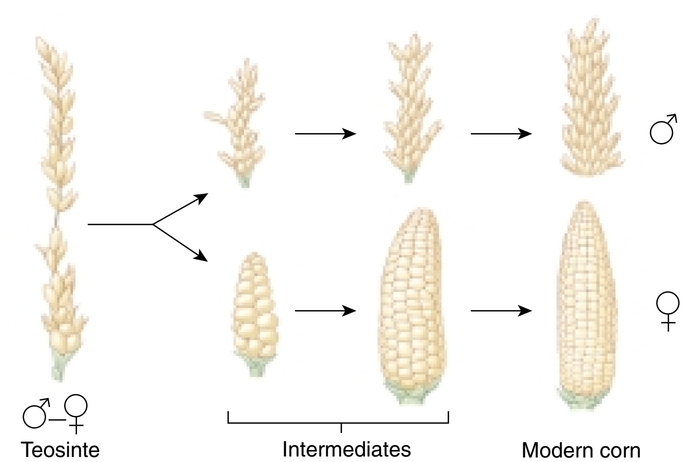

FIGURE 21.13
Corn looks very different from its ancestor. The tassels and seeds of a wild grass, such as teosinte, evolved into the male tassels and female ears of modern corn.

Agriculture

Similar methods have been practiced in agriculture for many centuries. Familiar livestock, such as cattle and pigs, and crops, like corn and strawberries, are greatly different from their wild ancestors (figure 21.13). These differences have resulted from generations of selection for desirable traits like milk production and corn stalk size.

An experimental study with corn demonstrates the ability of artificial selection to rapidly produce major change in crop plants. In 1896, agricultural scientists began selecting on oil content of corn kernels, which initially was 4.5%. As in the fruit fly experiments, the top 20% of all individuals were allowed to reproduce. In addition, a parallel experiment selected for the individuals with the lowest oil content. By 1986, at which time 90 generations had passed, average oil content had increased approximately 450% in the high-content experiment; by contrast, oil content in the low experiment had decreased to about 0.5%, a level at which it is difficult to get accurate readings.

Domestication

Artificial selection has also been responsible for the great variety of breeds of cats, dogs (figure 21.14), pigeons, cattle and other domestic animals. In some cases, breeds have been developed for particular purposes. Greyhound dogs, for example, were bred by selecting for maximal running abilities, with the end result being an animal with long legs and tail (the latter used as a rudder), an arched back (to increase the length of its stride), and great muscle mass. By contrast, the odd proportions of the ungainly basset hound resulted from selection for dogs that could enter narrow holes in pursuit of rabbits and other small game. In other cases, breeds have been developed primarily for their appearance, such as the many colorful and ornamented varieties of pigeons or the breeds of cats.

Domestication also has led to unintentional selection for some traits. In recent years, as part of an attempt to domesticate the silver fox, Russian scientists each generation have chosen the most docile animals and allowed them to reproduce. Within 40 years, the vast majority of foxes born were exceptionally docile, not only allowing themselves to be petted, but also whimpering to get attention and sniffing and licking their caretakers. In many respects, they had become no different than domestic dogs! However, it was not only behavior that changed. These foxes also began to exhibit different color patterns, floppy ears, curled tails, and shorter legs and tails. Presumably, the genes responsible for docile behavior have other effects as well (the phenomenon of pleiotropy discussed in the last chapter); as selection has favored docile animals, it has also led to the evolution of these other traits.

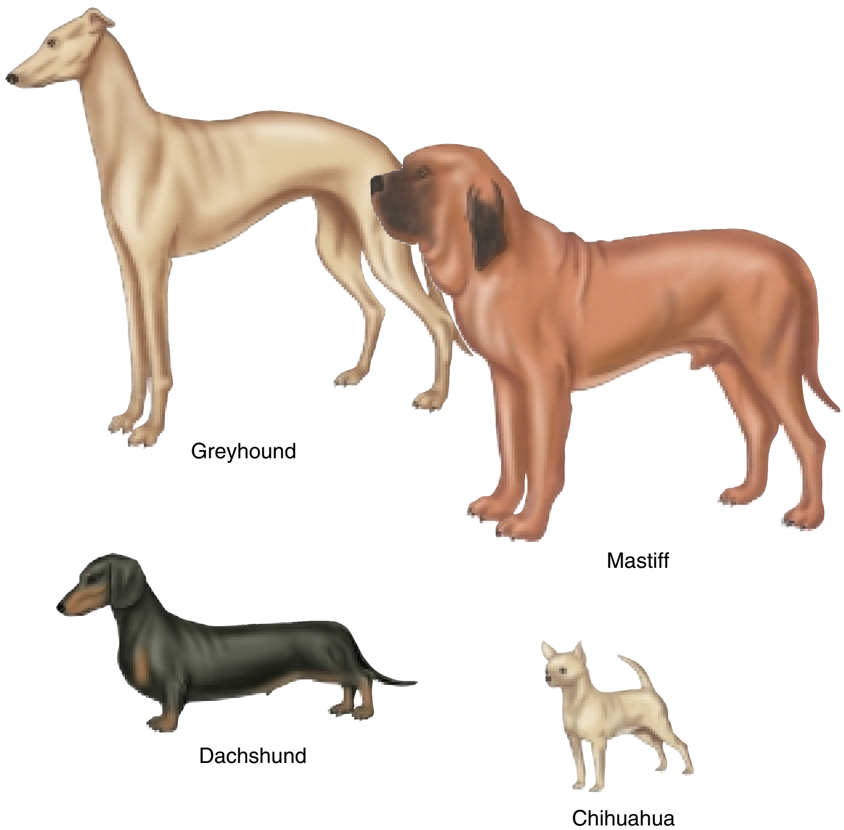

FIGURE 21.14
Breeds of dogs. The differences between these dogs are greater than the differences displayed between any wild species of canids.

Can Selection Produce Major Evolutionary Changes?

Given that we can observe the results of selection operating over relatively short periods of time, most scientists believe that natural selection is the process responsible for the evolutionary changes documented in the fossil record. Some critics of evolution accept that selection can lead to changes within a species, but contend that such changes are relatively minor in scope and not equivalent to the substantial changes documented in the fossil record. In other words, it is one thing to change the number of bristles on a fruit fly or the size of a corn stalk, and quite another to produce an entirely new species.

This argument does not fully appreciate the extent of change produced by artificial selection. Consider, for example, the breeds of dogs, all of which have been produced since wolves were first domesticated, perhaps 10,000 years ago. If the various dog breeds did not exist and a paleontologist found fossils of animals similar to dachshunds, greyhounds, mastiffs, Chihuahuas, and pomeranians, there is no question that they would be considered different species. Indeed, these breeds are so different that they would probably be classified in different genera. In fact, the diversity exhibited by dog breeds far outstrips the differences observed among wild members of the family Canidae—such as coyotes, jackals, foxes, and wolves. Consequently, the claim that artificial selection produces only minor changes is clearly incorrect. Indeed, if selection operating over a period of only 10,000 years can produce such substantial differences, then it would seem powerful enough, over the course of many millions of years, to produce the diversity of life we see around us today.

Artificial selection often leads to rapid and substantial results over short periods of time, thus demonstrating the power of selection to produce major evolutionary change.

21.3 Evidence for evolution can be found in other fields of biology.

The Anatomical Record

Much of the power of the theory of evolution is its ability to provide a sensible framework for understanding the diversity of life. Many observations from a wide variety of fields of biology simply cannot be understood in any meaningful way except as a result of evolution.

Homology

As vertebrates evolved, the same bones were sometimes put to different uses. Yet the bones are still seen, their presence betraying their evolutionary past. For example, the forelimbs of vertebrates are all **homologous structures,** that is, structures with different appearances and functions that all derived from the same body part in a common ancestor. You can see in figure 21.15 how the bones of the forelimb have been modified in different ways for different vertebrates. Why should these very different structures be composed of the same bones? If evolution had not occurred, this would indeed be a riddle. But when we consider that all of these animals are descended from a common ancestor, it is easy to understand that natural selection has modified the same initial starting blocks to serve very different purposes.

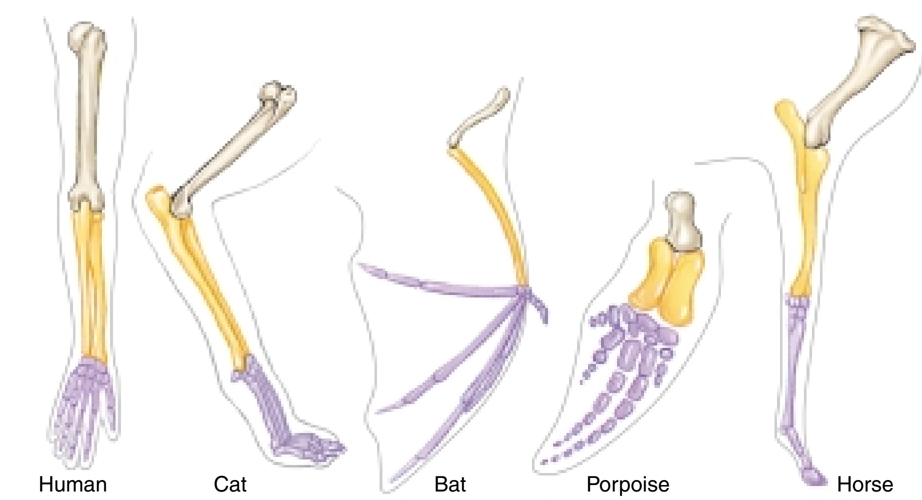

FIGURE 21.15
Homology among the bones of the forelimb. Although these structures show considerable differences in form and function, the same basic bones are present in the forelimbs of humans, cats, bats, porpoises, and horses.

Development

Some of the strongest anatomical evidence supporting evolution comes from comparisons of how organisms develop. In many cases, the evolutionary history of an organism can be seen to unfold during its development, with the embryo exhibiting characteristics of the embryos of its ancestors (figure 21.16). For example, early in their development, human embryos possess gill slits, like a fish; at a later stage, every human embryo has a long bony tail, the vestige of which we carry to adulthood as the coccyx at the end of our spine. Human fetuses even possess a fine fur (called *lanugo*) during the fifth month of development. These relict developmental forms suggest strongly that our development has evolved, with new instructions layered on top of old ones.

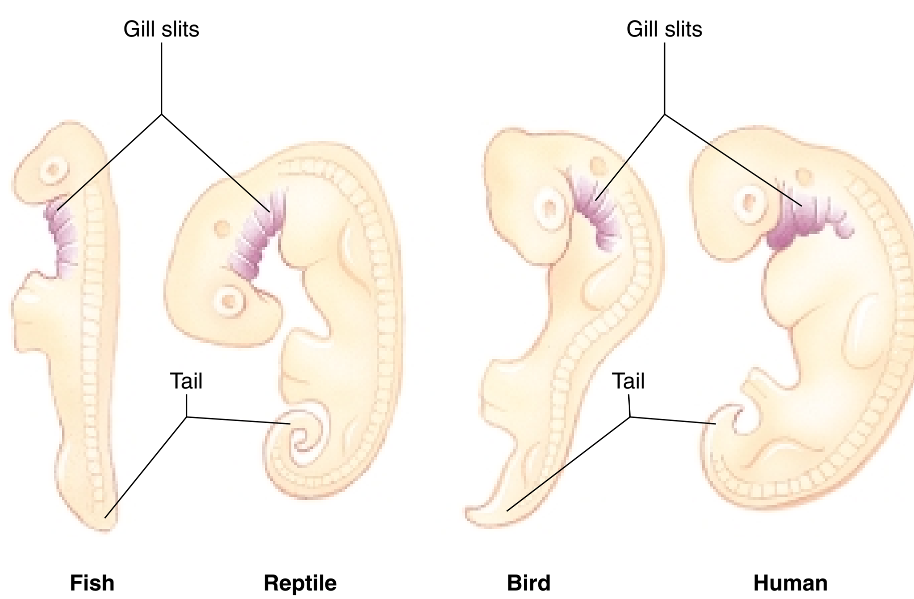

FIGURE 21.16
Our embryos show our evolutionary history. The embryos of various groups of vertebrate animals show the features they all share early in development, such as gill slits (*in purple*) and a tail.

The observation that seemingly different organisms may exhibit similar embryological forms provides indirect but convincing evidence of a past evolutionary relationship. Slugs and giant ocean squids, for example, do not bear much superficial resemblance to each other, but the similarity of their embryological forms provides convincing evidence that they are both mollusks.

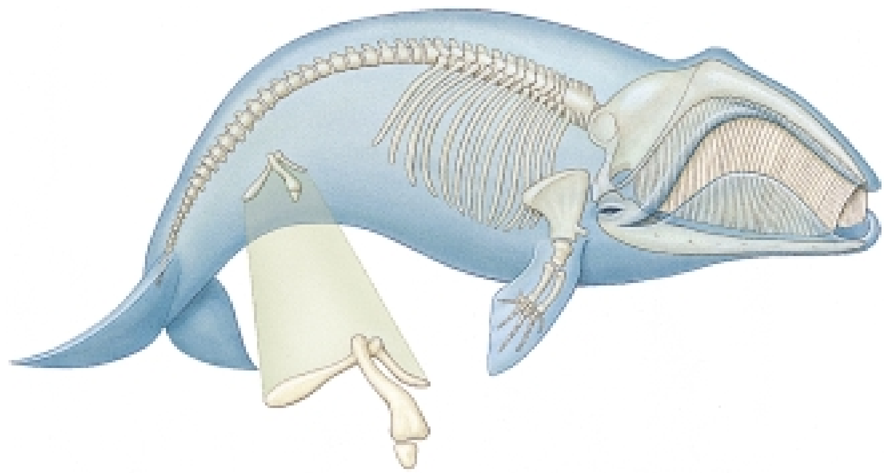

FIGURE 21.17
Vestigial features. The skeleton of a baleen whale, a representative of the group of mammals that contains the largest living species, contains pelvic bones. These bones resemble those of other mammals, but are only weakly developed in the whale and have no apparent function.

Vestigial Structures

Many organisms possess **vestigial structures** that have no apparent function, but that resemble structures their presumed ancestors had. Humans, for example, possess a complete set of muscles for wiggling their ears, just as a coyote does (table 21.1). Boa constrictors have hip bones and rudimentary hind legs. Manatees (a type of aquatic mammal often referred to as "sea cows") have fingernails on their fins (which evolved from legs). Figure 21.17 illustrates the skeleton of a baleen whale, which contains pelvic bones, as other mammal skeletons do, even though such bones serve no known function in the whale. The human vermiform appendix is apparently vestigial; it represents the degenerate terminal part of the cecum, the blind pouch or sac in which the large intestine begins. In other mammals such as mice, the cecum is the largest part of the large intestine and functions in storage—usually of bulk cellulose in herbivores. Although some suggestions have been made, it is difficult to assign any current function to the vermiform appendix. In many respects, it is a dangerous organ: quite often it becomes infected, leading to an inflammation called appendicitis; without surgical removal, the appendix may burst, allowing the contents of the gut to come in contact with the lining of the body cavity, a potentially fatal event. It is difficult to understand vestigial structures such as these as anything other than evolutionary relicts, holdovers from the evolutionary past. They argue strongly for the common ancestry of the members of the groups that share them, regardless of how different they have subsequently become.

Comparisons of the anatomy of different living animals often reveal evidence of shared ancestry. In some instances, the same organ has evolved to carry out different functions, in others, an organ loses its function altogether. Sometimes, different organs evolve in similar ways when exposed to the same selective pressures.

Table 21.1 Some Vestigial Traits in Humans

Trait	Description
Ear-wiggling muscles	Three small muscles around each ear that are large and important in some mammals, such as dogs, turning the ears toward a source of sound. Few people can wiggle their ears, and none can turn them toward sound.
Tail	Present in human and all vertebrate embryos. In humans, the tail is reduced; most adults only have three to five tiny tail bones and, occasionally, a trace of a tail-extending muscle.
Appendix	Structure which presumably had a digestive function in some of our ancestors, like the cecum of some herbivores. In humans, it varies in length from 5–15 cm, and some people are born without one.
Wisdom teeth	Molars that are often useless and sometimes even trapped in the jawbone. Some people never develop wisdom teeth.

Based on a suggestion by Dr. Leslie Dendy, Department of Science and Technology, University of New Mexico, Los Alamos.

The Molecular Record

Traces of our evolutionary past are also evident at the molecular level. If you think about it, the fact that organisms have evolved successively from relatively simple ancestors implies that a record of evolutionary change is present in the cells of each of us, in our DNA. When an ancestral species gives rise to two or more descendants, those descendants will initially exhibit fairly high overall similarity in their DNA. However, as the descendants evolve independently, they will accumulate more and more differences in their DNA. Consequently, organisms that are more distantly related would be expected to accumulate a greater number of evolutionary differences, whereas two species that are more closely related should share a greater portion of their DNA.

To examine this hypothesis, we need an estimate of evolutionary relationships that has been developed from data other than DNA (it would be a circular argument to use DNA to estimate relationships and then conclude that closely related species are more similar in their DNA than are distantly related species). Such an hypothesis of evolutionary relationships is provided by the fossil record, which indicates when particular types of organisms evolved. In addition, by examining the anatomical structures of fossils and of modern species, we can infer how closely species are related to each other.

When degree of genetic similarity is compared with our ideas of evolutionary relationships based on fossils, a close match is evident. For example, when the human hemoglobin polypeptide is compared to the corresponding molecule in other species, closely related species are found to be more similar. Chimpanzees, gorillas, orangutans, and macaques, vertebrates thought to be more closely related to humans, have fewer differences from humans in the 146-amino-acid hemoglobin β chain than do more distantly related mammals, like dogs. Nonmammalian vertebrates differ even more, and nonvertebrate hemoglobins are the most different of all (figure 21.18). Similar patterns are also evident when the DNA itself is compared. For example, chimps and humans, which are thought to have descended from a common ancestor that lived approximately 6 million years ago, exhibit few differences in their DNA.

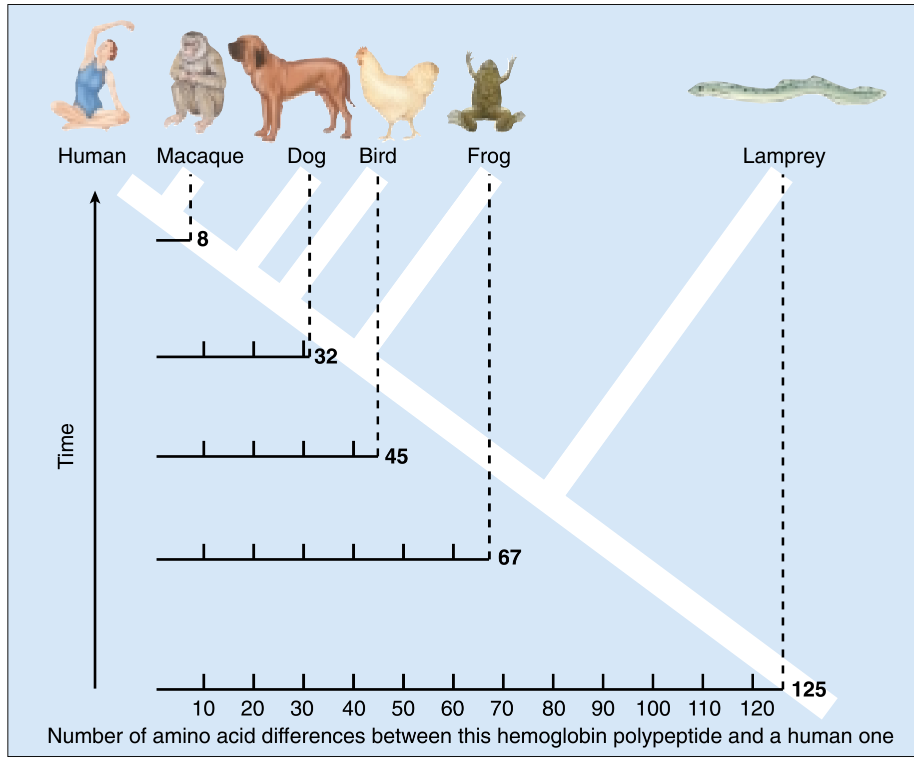

FIGURE 21.18
Molecules reflect evolutionary divergence. You can see that the greater the evolutionary distance from humans (white cladogram), the greater the number of amino acid differences in the vertebrate hemoglobin polypeptide.

Why should closely related species be similar in DNA? Because DNA is the genetic code that produces the structure of living organisms, one might expect species that are similar in overall appearance and structure, such as humans and chimpanzees, to be more similar in DNA than are more dissimilar species, such as humans and frogs. This expectation would hold true even if evolution had not occurred. However, there are some noncoding stretches of DNA (sometimes called "junk DNA") that have no function and appear to serve no purpose. If evolution had not occurred, there would be no reason to expect similar-appearing species to be similar in their junk DNA. However, comparisons of such stretches of DNA provide the same results as for other parts of the genome: more closely related species are more similar, an observation that only makes sense if evolution has occurred.

Comparison of the DNA of different species provides strong evidence for evolution. Species deduced from the fossil record to be closely related are more similar in their DNA than are species thought to be more distantly related.

Convergent and Divergent Evolution

Different geographical areas sometimes exhibit groups of plants and animals of strikingly similar appearance, even though the organisms may be only distantly related. It is difficult to explain so many similarities as the result of coincidence. Instead, natural selection appears to have favored parallel evolutionary adaptations in similar environments. Because selection in these instances has tended to favor changes that made the two groups more alike, their phenotypes have converged. This form of evolutionary change is referred to as **convergent evolution,** or sometimes, **parallel evolution.**

The Marsupial-Placental Convergence

In the best-known case of convergent evolution, two major groups of mammals, marsupials and placentals, have evolved in a very similar way, even though the two lineages have been living independently on separate continents. Australia separated from the other continents more than 50 million years ago, after marsupials had evolved but before the appearance of placental mammals. As a result, the only mammals in Australia (other than bats and a few colonizing rodents) have been marsupials, members of a group in which the young are born in a very immature condition and held in a pouch until they are ready to emerge into the outside world. Thus, even though placental mammals are the dominant mammalian group throughout most of the world, marsupials retained supremacy in Australia.

What are the Australian marsupials like? To an astonishing degree, they resemble the placental mammals living today on the other continents (figure 21.19). The similarity between some individual members of these two sets of mammals argues strongly that they are the result of convergent evolution, similar forms having evolved in different, isolated areas because of similar selective pressures in similar environments.

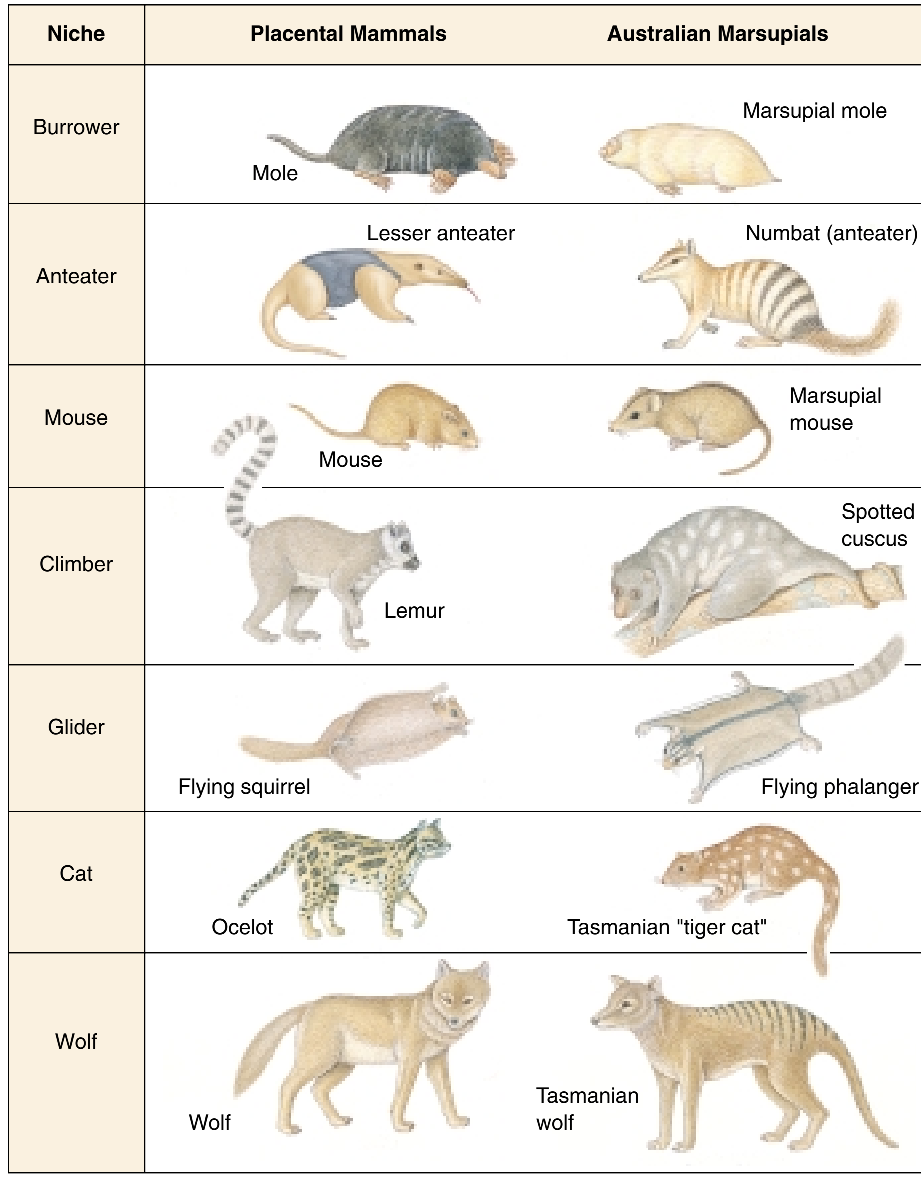

FIGURE 21.19
Convergent evolution. Marsupials in Australia resemble placental mammals in the rest of the world. They evolved in isolation after Australia separated from other continents.

Homology versus Analogy

How do we know when two similar characters are homologous and when they are analogous? As we have seen, adaptation favoring different functions can obscure homologies, while convergent evolution can create analogues that appear as similar as homologues. There is no hard-and-fast answer to this question; the determination of homologues is often a thorny issue in biological classification. As we have seen in comparing vertebrate embryos, and again in comparing slugs and squids, studies of embryonic development often reveal features not apparent when studying adult organisms. In general, the more complex two structures are, the less likely they evolved independently.

FIGURE 21.20
A Galápagos tortoise most closely resembles South American tortoises. Isolated on these remote islands, the Galápagos tortoise has evolved distinctive forms. This natural experiment is being terminated, however. Since Darwin's time, much of the natural habitat of the larger islands has been destroyed by human intrusion. Goats introduced by settlers, for example, have drastically altered the vegetation.

Darwin and Patterns of Recent Divergence

Darwin was the first to present evidence that animals and plants living on oceanic islands resemble most closely the forms on the nearest continent—a relationship that only makes sense as reflecting common ancestry. The Galápagos turtle in figure 21.20 is more similar to South American turtles than to those of any other continent. This kind of relationship strongly suggests that the island forms evolved from individuals that came from the adjacent mainland at some time in the past. Thus, the Galápagos finches of figure 21.8 have different beaks than their South American relatives. In the absence of evolution, there seems to be no logical explanation of why individual kinds of island plants and animals would be clearly related to others on the nearest mainland, but still have some divergent features. As Darwin pointed out, this relationship provides strong evidence that macroevolution has occurred.

A similar resemblance to mainland birds can be seen in an island finch Darwin never saw—a solitary finch species living on Cocos Island, a tiny, remote volcanic island located 630 kilometers to the northeast of the Galápagos. This finch does not resemble the finches of Europe, Australia, Africa, or North America. Instead, it resembles the finches of Costa Rica, 500 kilometers to the east.

Of course, because of adaptation to localized habitats, island forms are not identical to those on the nearby continents. The turtles have evolved different shell shapes, for example; those living in moist habitats have dome-shaped shells while others living in dry places have low, saddle-backed shells with the front of the shell bent up to expose the head and neck. Similarly, the Galápagos finches have evolved from a single presumptive ancestor into 13 species, each specialized in a different way. These Galápagos turtles and finches have evolved in concert with the continental forms, from the same ancestors, but the two lineages have diverged rather than converged.

It is fair to ask how Darwin knew that the Galápagos tortoises and finches do not represent the convergence of unrelated island and continental forms (analogues) rather than the divergence of recently isolated groups (homologues). While either hypothesis would argue for natural selection, Darwin chose divergence of homologues as by far the simplest explanation, because the turtles and finches differ by only a few traits, and are similar in many.

In sum total, the evidence for macroevolution is overwhelming. In the next chapter, we will consider Darwin's proposal that microevolutionary changes have led directly to macroevolutionary changes, the key argument in his theory that evolution occurs by natural selection.

Evolution favors similar forms under similar circumstances. Convergence is the evolution of similar forms in different lineages when exposed to the same selective pressures. Divergence is the evolution of different forms in the same lineage when exposed to different selective pressures.

21.4 The theory of evolution has proven controversial.

Darwin's Critics

In the century since he proposed it, Darwin's theory of evolution by natural selection has become nearly universally accepted by biologists, but has proven controversial among the general public. Darwin's critics raise seven principal objections to teaching evolution:

1. **Evolution is not solidly demonstrated.** *"Evolution is just a theory,"* Darwin's critics point out, as if theory meant lack of knowledge, some kind of guess. Scientists, however, use the word theory in a very different sense than the general public does. Theories are the solid ground of science, that of which we are most certain. Few of us doubt the theory of gravity because it is "just a theory."
2. **There are no fossil intermediates.** *"No one ever saw a fin on the way to becoming a leg,"* critics claim, pointing to the many gaps in the fossil record in Darwin's day. Since then, however, most fossil intermediates in vertebrate evolution have indeed been found. A clear line of fossils now traces the transition between whales and hoofed mammals, between reptiles and mammals, between dinosaurs and birds, between apes and humans. The fossil evidence of evolution between major forms is compelling.
3. **The intelligent design argument.** *"The organs of living creatures are too complex for a random process to have produced—the existence of a clock is evidence of the existence of a clockmaker."* Biologists do not agree. The intermediates in the evolution of the mammalian ear can be seen in fossils, and many intermediate "eyes" are known in various invertebrates. These intermediate forms arose because they have value—being able to detect light a little is better than not being able to detect it at all. Complex structures like eyes evolved as a progression of slight improvements.
4. **Evolution violates the Second Law of Thermodynamics.** *"A jumble of soda cans doesn't by itself jump neatly into a stack—things become more disorganized due to random events, not more organized."* Biologists point out that this argument ignores what the second law really says: disorder increases in a closed system, which the earth most certainly is not. Energy continually enters the biosphere from the sun, fueling life and all the processes that organize it.
5. **Proteins are too improbable.** *"Hemoglobin has 141 amino acids. The probability that the first one would be leucine is 1/20, and that all 141 would be the ones they are by chance is $(1/20)^{141}$, an impossibly rare event."* This is statistical foolishness—you cannot use probability to argue backwards. The probability that a student in a classroom has a particular birthday is 1/365; arguing this way, the probability that everyone in a class of 50 would have the birthdays they do is $(1/365)^{50}$, and yet there the class sits.
6. **Natural selection does not imply evolution.** *"No scientist has come up with an experiment where fish evolve into frogs and leap away from predators."* Is microevolution (evolution within a species) the mechanism that has produced macroevolution (evolution among species)? Most biologists that have studied the problem think so. Some kinds of animals produced by artificial selection are remarkably distinctive, such as Chihuahuas, dachshunds, and greyhounds. While all dogs are in fact the same species and can interbreed, laboratory selection experiments easily create forms that cannot interbreed and thus would in nature be considered different species. Thus, production of radically different forms has indeed been observed, repeatedly. To object that evolution still does not explain really major differences, like between fish and amphibians, simply takes us back to point 2—these changes take millions of years, and are seen clearly in the fossil record.
7. **The irreducible complexity argument.** *The intricate molecular machinery of the cell cannot be explained by evolution from simpler stages. Because each part of a complex cellular process like blood clotting is essential to the overall process, how can natural selection fashion any one part?* What's wrong with this argument is that each part of a complex molecular machine evolves as part of the system. Natural selection can act on a complex system because at every stage of its evolution, the system functions. Parts that improve function are added, and, because of later changes, become essential. The mammalian blood clotting system, for example, has evolved from much simpler systems. The core clotting system evolved at the dawn of the vertebrates 600 million years ago, and is found today in lampreys, the most primitive fish. One hundred million years later, as vertebrates evolved, proteins were added to the clotting system making it sensitive to substances released from damaged tissues. Fifty million years later, a third component was added, triggering clotting by contact with the jagged surfaces produced by injury. At each stage as the clotting system evolved to become more complex, its overall performance came to depend on the added elements. Thus, blood clotting has become "irreducibly complex"—as the result of Darwinian evolution.

Darwin's theory of evolution has proven controversial among the general public, although the commonly raised objections are without scientific merit.

Chapter 21

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Summary | **Questions** | **Media Resources**

21.1 Fossil evidence indicates that evolution has occurred.

- Fossils of many extinct species have never been discovered. Nonetheless, the fossil record is complete enough to allow a detailed understanding of the evolution of life through time. The evolution of the major vertebrate groups is quite well known.
- Although evolution of groups like horses may appear to be a straight-line progression, in fact there have been many examples of parallel evolution, and even reversals from overall trends.

1. Why do gaps exist in the fossil record? What lessons can be learned from the fossil record of horse evolution?

2. How did scientists date fossils in Darwin's day? Why are scientists today able to date rocks more accurately?

- On Science Article: featherd Dinosaurs

Book Reviews:

- *In Search of Deep Time* by Gee
- *Digging Dinosaurs* by Horner

21.2 Natural selection can produce evolutionary change.

- Natural populations provide clear evidence of evolutionary change.
- Darwin's finches have different-sized beaks, which are adaptations to eating different kinds of seeds. In particularly dry years, natural selection favors birds with stout beaks within one species, *Geospiza fortis*. As a result, the average bill size becomes larger in the next generation.
- The British populations of the peppered moth, *Biston betularia*, consisted mostly of light-colored individuals before the Industrial Revolution. Over the last two centuries, populations that occur in heavily polluted areas, where the tree trunks are darkened with soot, have come to consist mainly of dark-colored (melanic) individuals—a result of rapid natural selection.

3. Why did the average beak size of the medium ground finch increase after a particularly dry year?

4. Why did the frequency of light-colored moths decrease and that of dark-colored moths increase with the advent of industrialism? What is industrial melanism?

5. What can artificial selection tell us about evolution? Is artificial selection a good analogy for the selection that occurs in nature?

- Activity: Evolution of Fish

21.3 Evidence for evolution can be found in other fields of biology.

- Several indirect lines of evidence argue that macroevolution has occurred, including successive changes in homologous structures, developmental patterns, vestigial structures, parallel patterns of evolution, and patterns of distribution.
- When differences in genes or proteins are examined, species that are thought to be closely related based on the fossil record may be more similar than species thought to be distantly related.

6. What is homology? How does it support evolutionary theory?

7. What is convergent evolution? Give examples.

8. How did Darwin's studies of island populations provide evidence for evolution?

- Exploration: Evolution of the Heart
- Molecular Clock
- Activity: Divergence
- Student Research: Evolution of Insect Diets

On Science Articles:

- Darwinism at the Cellular Level
- Was Darwin Wrong?

21.4 The theory of evolution has proven controversial.

- The objections raised by Darwin's critics are easily answered.

9. Is "Darwinism" really science? Explain.

- On Science Article: Answering Evolution's Critics
- Bioethics Case Study: Creationism

Book Reviews:

- *Mr. Darwin's Shooter* by McDonald