

# Evolution and Extinction

## Chapter Themes

How did early theories of evolution differ from Darwin's?  
What sorts of evidence led Darwin to his theory of evolution?  
How is genetic information stored and transmitted from parents to offspring?  
What produces genetic variation?  
What is the evidence for natural selection?  
How do new species and other groups originate?  
What is the evidence for evolution?  
How does extinction affect evolution?

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## 4.1 Introduction

Charles Darwin (1809–1882) is rightfully credited with founding the modern theory of evolution because the basic foundation of the theory laid down by him has remained largely intact to the present. Darwin's theory supported, and was supported by, the notion of deep time implicated by Hutton and Lyell (see Chapter 1). Recall from Chapter 1, however, that the view of Earth espoused by Lyell was one of strict equilibrium: no net change. But with Darwin's theory came the growing realization that not only has life evolved but so too have Earth's physical systems. Natural systems can exhibit directionality or secular change, because they are open systems, that is, they can *evolve*. Darwin's theory is therefore not only fundamental to the study of the history and evolution of life but also strengthened the inkling that physical systems—and thus Earth—can evolve as well.

Like so many theories, however, Darwin's was preceded by others. To fully comprehend the significance of the modern theory of evolution, we must examine these earlier theories. In doing so we get another glimpse as to how scientists think and how theories are

developed and modified, leading to new questions. As we will see, several of these questions stem from a better understanding of the fossil record: How do new species arise? How do new anatomic structures like wings or eyes and wholly new groups of organisms—like reptiles or mammals—arise? How do mass extinctions of the biosphere—well documented in the fossil record—create new evolutionary opportunities?

## 4.2 Early Theories of Evolution

Two of Darwin's predecessors, both French, stand out for their views on evolution: Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck, or just Lamarck (1744–1829), and Baron Georges Cuvier (1762–1839) (FIGURE 4.1). Lamarck originally believed that certain groups of organisms—now called species—were fixed and did not evolve, but began to change his views as his studies progressed (BOX 4.1). Lamarck based his theory of evolution on spontaneous generation which stated that living matter arises from nonliving matter. Lamarck based his acceptance of spontaneous generation on his observation that the simplest organisms had no obvious organs, so Lamarck reasoned they must have evolved directly from nonliving substances.



(a)



(b)

**FIGURE 4.1** (a) Jean Baptiste Pierre Antoine de Monet, Chevalier de Lamarck (1744–1829). (b) Baron Georges Cuvier (1762–1839).

## BOX 4.1 Evolution of Biologic Classification and the Species Concept

A **species** is a group of organisms that interbreed with one another *and* produce fertile offspring. The point of reproduction is to propagate the species. Species are usually recognized by physical features thought to reflect the identity of the species, such as anatomic traits, distinctive coloration, or behavior. Many species have “common” names used by lay people. However, these terms can be confusing, especially if they are used to refer to different species. To avoid confusion among scientists, each species is given a scientific name consisting of two names: the genus and the species. For example, the scientific name of human beings is *Homo sapiens*. *Homo* is the genus and *sapiens* is the species. The scientific name for humans means “prescient man,” referring to the mental ability of humans to foresee into the future and anticipate the consequences of their actions and those of nature. By international convention the scientific name is always underlined or set off from the surrounding text in some other manner, and the genus name is always capitalized, whereas the species name is not (species is used for both the singular and plural; there is no such word as “specie”). Each genus is represented by one or more species. Thus, when referring to a particular species one cites both names—genus and species—not just the species name by itself, because there could well be another completely different genus represented by a species with the same species name.

The first naturalist to systemically catalog and describe animals and plants was the Swedish botanist, Carolus Linnaeus (1707–1778), who held that species were fixed. He eventually described about 4200 species of animals and 7700 species of plants. There are now about 1.4 million described species, which may represent only about one-tenth of all modern species. Many species have common names, but the same common name may be used in different areas for different species. To avoid confusion Linnaeus gave each species a Latinized description. However, use of the description was quite clumsy, and he decided to give each species a “nickname.” This led to the establishment of **binomial nomenclature** in which each species is recognized by two names, as described above. Linnaeus’ system is still used today. In fact, his monumental work, *Systema Naturae*, first published in 1758, is taken as the starting point of binomial no-

menclature, and any species described before this time are considered invalid. However, species originally described after 1758 may still be redescribed or placed in new groupings based on new data.

As evolutionary theory began to take hold, Linnaeus’ system of biologic classification began to take on a new meaning: evolutionary relationships. A classification recognizes similarities or dissimilarities between objects, in this case species. The purpose of a biologic classification is to show evolutionary relationships, or **phylogeny**, between different groups of organisms, or taxa (taxon, singular). Biologic classification and phylogenetic relationships are hierarchies. These hierarchies consist of different levels, or categories—kingdom, phylum, class, order, family, genus, and species—each of which may be further subdivided or lumped together. The actual groups, or taxa (such as particular species), are placed into higher taxa corresponding to the different categories; thus, each taxon shares characteristics with the other members of the same taxon. The science of biologic classification is called **taxonomy**. A biologic classification is therefore like a series of boxes nested within progressively larger boxes. In biologic classification these boxes are called categories with the categories becoming more and more inclusive. Taxa and categories may also be subdivided (for example, subclasses) or lumped together (for example, superfamilies). For example, *Homo sapiens* is classified as follows:

CATEGORY: TAXON

Kingdom: Animalia

Phylum: Chordata (animals with some form of backbone)

Class: Mammalia (mammals, which are warm-blooded, possess hair, and produce milk for their young)

Order: Primates (monkeys, apes, humans)

Superfamily: Hominoidea

Family: Hominidae

Genus: *Homo*

Species: *sapiens*

Besides the Kingdom Animalia, several other kingdoms are recognized: Plantae, Fungi (mushrooms, etc., including microscopic fungi), Protista (single-celled plants and animals), and two kingdoms of bacteria, the Archaea and the Eubacteria.

## BOX 4.1 Evolution of Biologic Classification and the Species Concept (Continued)

The modern view of biologic classification and the concept of species have themselves evolved. Biologists recognize that within a species there is typically a broad range of variation in physical features. Sometimes this range can be quite broad, such as that found among different breeds of dogs. Despite their tremendous differences in size and coloration, different breeds of dogs are thought to be descended from an ancestral wolf lineage. This lineage alone contained the DNA from which all different purebred lines of dogs have been bred. Obviously, this range of variation in physical traits can sometimes make it difficult to decide if one is studying separate species or variation within the same species. This was the basic problem confronted by early evolutionary biologists who began to describe different types of organisms. Lamarck saw the possibility for almost endless variation and the continued production of new forms from nonliving matter; nature was just too “fluid” in his view to have such distinct biologic boundaries that

separated species. On the other hand, Cuvier had a very narrow notion of a species, in which a particular specimen was supposed to represent all members of that species; this kind of thinking originated with the Greek philosopher Plato, who viewed all living things as having an “ideal type.”

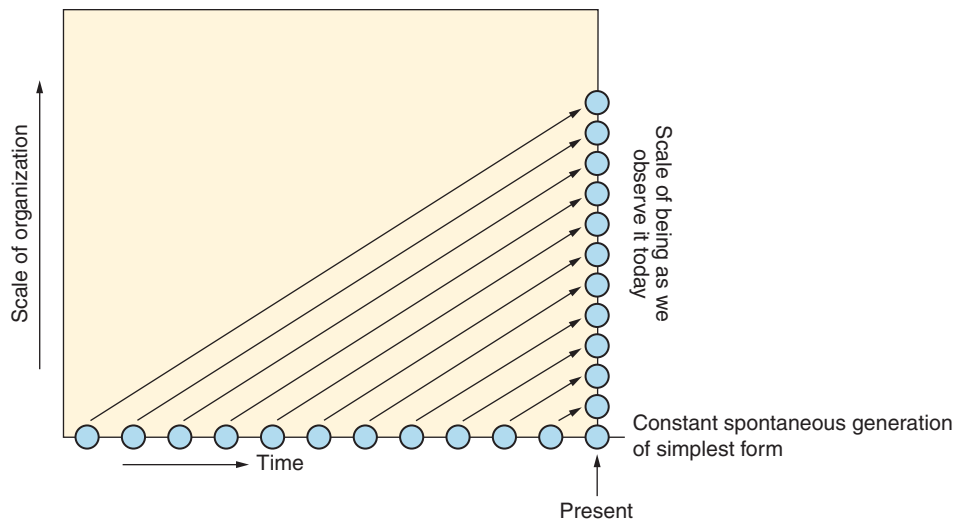
Darwin also wrestled with this problem and eventually recognized that each species can vary within broad limits. In other words most specimens resemble the “average” appearance of the species, but many specimens deviated from the species’ average, sometimes quite strongly. Nevertheless, the existence of species was actually used as an argument *against* Darwinian and earlier theories of evolution. The reasoning was that because species are not observed to change into new species, species do not evolve. Even though Darwin used the results of animal breeding experiments to support the process of natural selection, new species were never produced. Some of Darwin’s critics used this evidence against his theory, as well.

Lamarck also believed in the concept of a “Chain of Being” which stated that all organisms could be arranged in a continuous hierarchy stretching from the simplest organisms all the way to humans at the top (FIGURE 4.2). The origins of the Chain of Being concept can be traced all the way back to Aristotle. According to this view, because only the simplest animals could evolve from nonliving matter, more complex species must be descended from simpler ones in a progressive manner. Thus, in Lamarck’s view new, simple creatures evolved through separate acts of spontaneous generation and then moved up the Chain of Being along a kind of evolutionary “escalator.” The dead residues fell back to the base of the escalator to be used again, in a cyclic manner, in the evolutionary process. A particular group’s complexity was therefore a measure of its age: the more primitive a group, the more recently it had evolved. Because the Chain of Being emphasized that evolution was progressive, it also emphasized that evolution progressed toward more perfect forms, namely humans.

Finally, Lamarck believed that organisms were capable of evolving the organs they needed and could change their characteristics through an internal

“striving” in response to new environmental conditions; organisms evolved new structures according to their “need” through use and disuse. This **theory of the inheritance of acquired characteristics** asserted, for example, that the short-necked ancestors of modern giraffes had lengthened their necks as members of each generation strove to reach the foliage higher in trees; the slightly longer neck of each generation was passed to the next during reproduction. In other words evolution was *teleological*, meaning it was goal-oriented or purposeful, a view held by many other naturalists before and after Lamarck. But the theory of the inheritance of acquired characteristics begged the question as to how the characteristics are passed on to offspring. Consequently, Lamarck’s theory was never widely accepted, and some scientists dismissed him as a crank.

One such scientist was Georges Cuvier. Cuvier developed a classification scheme based on his studies of comparative anatomy for which he was renowned (Box 4.1). By observing a single bone or tooth Cuvier could predict the rest of the animal’s skeleton through his knowledge of anatomic relationships (what Cuvier



**FIGURE 4.2** The Chain of Being, as envisioned by Lamarck. Note how new groups of organisms (arrows) originating earlier reach a more advanced stage than those groups originating later. [Modified from: Bowler, P. 1989. *Evolution: The History of an Idea*. Revised ed. Berkeley: University of California Press. Figure 10 (p. 85).]

called the “correlation of parts”). Based on anatomic relationships Cuvier concluded that species and other taxa were so complex they could only be fixed and unchangeable (Box 4.1). Instead of an escalator-like progression from simple to more complex creatures, different groups of organisms were viewed as being separate branches in a tree-like arrangement. One branch was no more advanced than another; branches were merely different because each was adapted to a different mode of life.

Through his studies of fossil forms, Cuvier also gradually realized a series of extinctions had occurred. Because the changes between fossil assemblages were abrupt, he concluded a series of extinctions had occurred caused by movements of the land and sea. Cuvier was therefore lumped into the catastrophist camp by Lyell (see Chapter 1). However, contrary to what Lyell said, Cuvier did not explain the repopulation of Earth after an extinction as the work of a Creator, and he refused to equate the last extinction with the biblical Deluge. Cuvier did not accept the evolution of species (or transmutation, as it was then called) after extinction but instead suggested that populations repopulated Earth from refuges after extinction.

Despite Cuvier’s long-standing influence, however, other workers saw tantalizing patterns in the classification—or groupings—of different plants and animals groups, and the concept of transmutation started to make headway once again in the 1830s (Box 4.1). This was basically the state of evolutionary biology when Charles Darwin came onto the scene.

### Concept and Reasoning Checks

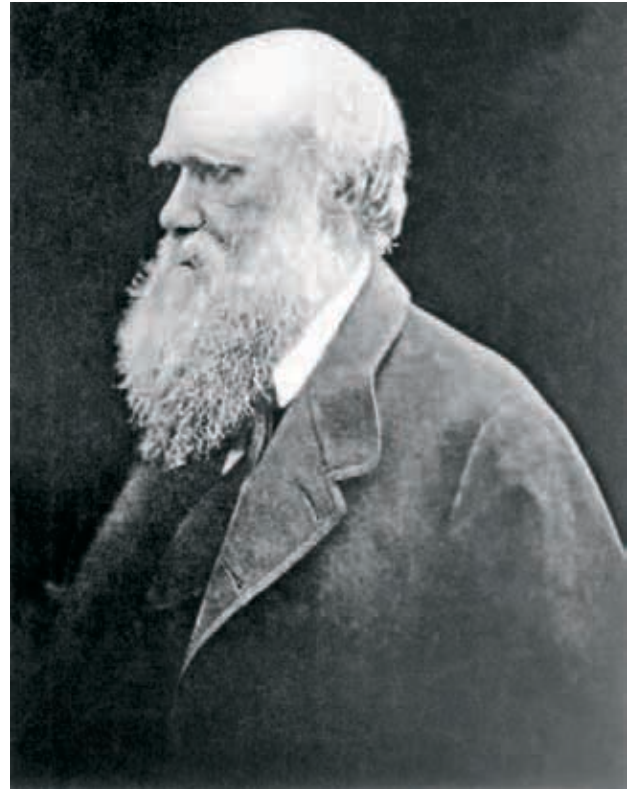
1. Was Darwin the first person to recognize a theory of evolution?
2. Why were species originally thought to indicate a lack of evolution?

## 4.3 Charles Darwin and the Beginnings of the Modern Theory of Evolution

To fully appreciate the perspective and power of the evolutionary viewpoint, we need to briefly examine how Darwin arrived at his theory. Charles Darwin (FIGURE 4.3) was the naturalist on the voyage of the *H.M.S Beagle* from 1831 to 1836. During the expedition Darwin visited the Canary Islands in the Atlantic Ocean, made multiple short expeditions into the interior of South America from both the east and west coasts, and explored the Galápagos Islands about 600 miles west of South America and coral reefs of the South Pacific. Being the keen naturalist that he was, Darwin filled his notebooks with many observations during the trip and sent crate after crate of specimens back to England. At least two fundamental themes run through his observations and *still serve as foundations for the modern theory of evolution*: the seemingly infinite variety and variation of plants and animals in nature (Box 4.1) and their biogeographic distribution (see Chapter 2). Why, Darwin asked himself, would a Creator produce so many different kinds



(a)



(b)

**FIGURE 4.3** Charles Darwin (a) in 1849 at the age of 40, ten years before publication of *On the Origin of Species*. (b) Darwin in 1881, the year before his death.

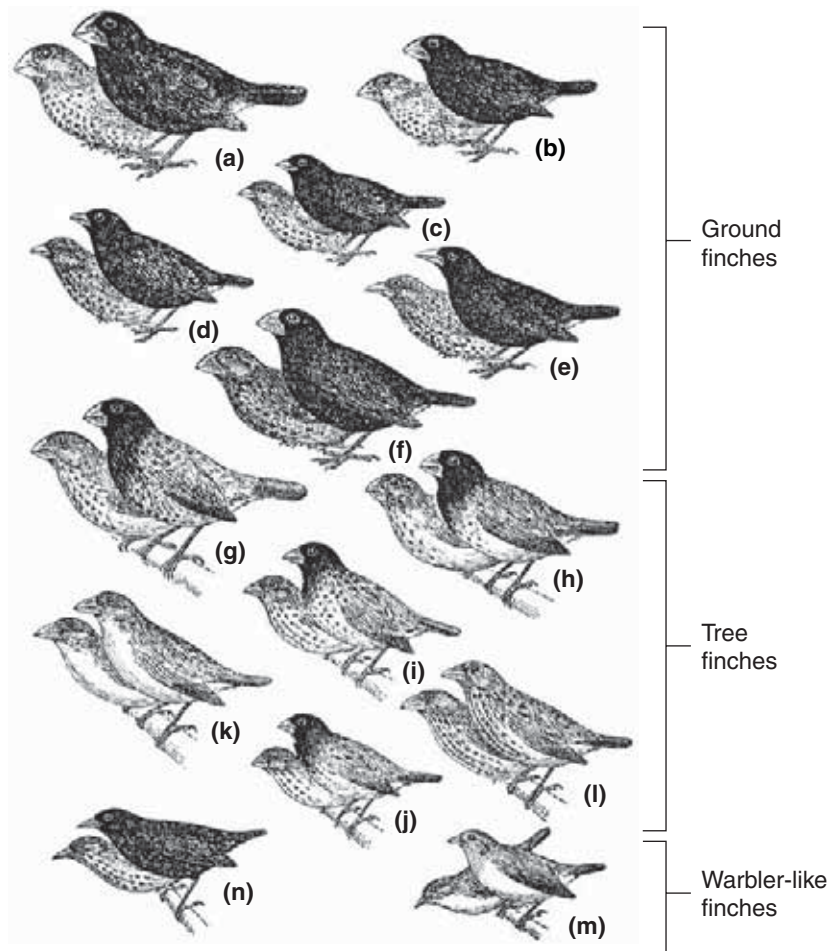
of organisms, and why would the Creator distribute them in different places over the planet?

One of the most often-cited examples of Darwin's observations is "Darwin's finches" (FIGURE 4.4). Different islands of the Galápagos, sometimes within sight of one another, are inhabited by different species of finches. The beaks of the finch populations were so different from one another that Darwin did not realize how closely related the species were. After study by a noted ornithologist in England upon Darwin's return, it became clear that the beaks reflected the adaptation and evolution of finch populations on different islands into different species in response to different food sources. For example, finches with robust beaks ate large seeds, whereas others with longer beaks pried insects from underneath bark. Why should this be? Similarly, while visiting the Galápagos Darwin was informed by one of the inhabitants that one could tell which island he or she was on simply by looking at the tortoises (refer to this chapter's frontispiece). Like the finches and tortoises, plants and other organisms also varied from one island to the next. Darwin absorbed this information, as well.

Upon his return to England, Darwin devoted the rest of his life to synthesizing the observations recorded in his notebooks from the voyage into a series

of books (BOX 4.2). From his observations Darwin began to develop general hypotheses about nature. As it turned out one of the most influential works Darwin ever read was Charles Lyell's *Principles of Geology* (see Chapter 1). He received the first volume before leaving on the expedition of the *Beagle* and received the later two volumes during the trip, and Darwin and Lyell became close colleagues after Darwin's return.

Although Darwin had long intended to gather his observations into a theory and a book, he procrastinated, despite the warnings of Lyell and other colleagues that someone else might "scoop" him. In science, as in the rest of society, priority means a great deal in terms of recognition and prestige. In fact, Alfred Russel Wallace (FIGURE 4.5), another British naturalist who had also developed a keen interest in beetles as a young man, contacted Darwin in 1858 about his own theory of evolution. Wallace had spent many years in the tropical rain forests of the Amazon and southeast Asia and had developed a theory remarkably similar to that of Darwin's. Wallace reported that he first realized his theory while suffering from one of numerous feverish bouts with malaria while working in Indonesia; the idea occurred to him that individuals less resistant to disease, predation, and environmental change would be culled from natural populations.



**FIGURE 4.4** Darwin's finches. [Reproduced from: Lack, D. 1947. *Darwin's Finches: An Essay on the General Biology Theory of Evolution*, 1st ed. Cambridge, UK: Cambridge University Press. Illustration by Lt. Col. William Percival Cosnahan Tenison.]

## BOX 4.2 Charles Darwin, the Person

Charles Darwin was the son of Robert Darwin, a prominent physician, who encouraged Charles to follow in his footsteps by attending medical school at Edinburgh. Charles attended the school but was bored by the lectures and horrified by anatomy classes, and he eventually fled. Unfortunately for Robert Darwin, Charles seemed to have had no other interests than beetle-collecting and hunting. Consequently, his father decided that Charles should become a minister, which in those days would have served as a respectable occupation to allow Charles to continue with his naturalistic pursuits.

So Charles next attended Cambridge University, which was then, along with Oxford University, a bastion

of the Anglican Church. There, Darwin met some of the scientific luminaries of the day. These included the famous geologist Adam Sedgwick, who would eventually introduce him to the field of geology in Wales, and John Henslow, who taught mineralogy and botany and who would recommend Darwin for the position of naturalist on the voyage of the *H.M.S. Beagle*. Charles's father at first objected to the trip but eventually relented when his uncle and future father-in-law, Josiah Wedgwood, intervened.

After his return to England, Darwin eventually married his first cousin, Emma Wedgwood, and they settled briefly in London before moving to Downe, located west of London, in 1842. Darwin probably

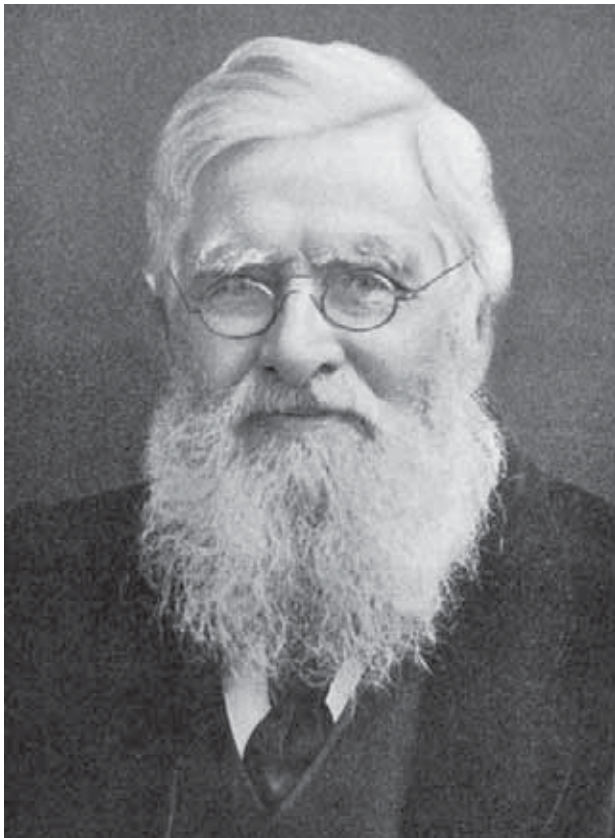
## BOX 4.2 Charles Darwin, the Person (Continued)

wanted to spend more time thinking and writing and less time on professional activities and the hubbub of London, all of which seemed a distraction to him. Emma and Charles settled into a comfortable existence at Downe, during which Charles spent much of his time writing in his study, conducting experiments or dissecting specimens, and taking long walks in his garden. Darwin developed a deep respect for the organisms he studied and eventually abandoned hunting altogether.

Emma and Charles dearly loved one another and had 10 children, 2 of whom died of disease and another, who was apparently mentally retarded, died at a young age. However, it was the loss of his beloved daughter, Anne Elizabeth (“Annie”), at the age of 10 that may have finally shaken Darwin’s belief in God once and for all; Darwin did not attend Annie’s funeral and could never bring himself to visit her grave.

Although he had been in good health as a young man and during most of the *Beagle’s* voyage, Darwin’s health suffered through the years, and he frequently visited spas for so-called water cures. It is thought that Darwin may have contracted a parasitic disease while in South America. Also, given his religious background the implications of his theory of evolution must have also caused Darwin a great deal of mental anguish (compare Figures 4.3, A and B). Emma was quite religious, and she and Charles learned not to speak directly of Charles’s work, instead communicating about it by notes when necessary.

Charles Darwin died suddenly at Downe House. He had wished to be buried next to his children, but after a state funeral he was entombed in Westminster Abbey, only a few feet away from Sir Isaac Newton, who was at that time regarded as the preeminent scientist of all time.



**FIGURE 4.5** Alfred Russel Wallace (1823–1913). Wallace’s middle name resulted from a misspelling on his birth certificate.

When Wallace communicated with Darwin about his theory of evolution, Darwin began to panic. At the suggestion of Lyell and other colleagues, Darwin and Wallace copublished a brief abstract, and then Darwin set to work on his *On the Origin of Species*, the first edition of which was published in 1859. Twelve hundred fifty copies of the first edition were printed and sold out overnight. Darwin was keenly aware of the implications of his theory for human evolution, but he refrained from tackling this problem in the *Origin* and only published his arguments later in *The Descent of Man*. Nevertheless, many lay people and scientists immediately understood the implications of Darwinian evolution for humans, and it is therefore not surprising the *Origin* received many negative reviews when it was first published.

## 4.4 Basic Premises of Darwinian Evolution

Like Lyell had done in his *Principles of Geology* (see Chapter 1), Darwin marshaled a mountain of evidence to support his theory in the *Origin*. Based on this evidence he developed an inductive argument (see Chapter 1) for his theory based on a number of premises. As noted previously two basic observations led to Darwin’s theory of evolution: the great diversity of plants and animals and their biogeographic distribution. The fundamental questions, then, were how



did diversity arise and how did the organisms come to live in different areas? Darwin had to develop a satisfactory mechanism for evolution to occur. It was not enough just to say that evolution occurred; Darwin had to say *how* evolution occurred. Scientists are extreme skeptics until a particular mechanism (cause) can be identified that accounts for a particular effect. Unfortunately for Darwin, he never found the exact mechanism (for reasons we discuss shortly), but Darwin reasoned that tiny differences occurred in the natural variation of organisms and that these variations could be passed from one generation to the next. Another of Darwin's basic premises was that plant and animal populations do not grow unchecked. Darwin therefore reasoned there must be a "struggle for existence" that eliminates "unfit"

individuals, those with less suitable variations, whereas fitter individuals survive. Darwin called the struggle for existence **natural selection**; he coined the term based on artificial breeding or selection, which is still used today to produce more productive lines of plants and animals for food. If there is natural selection, with unfit individuals weeded out, then, Darwin reasoned, there must be **differential reproduction**: Survivors live long enough to reproduce and pass their more favorable traits to their offspring so there is **descent with modification**. In this way natural selection for more "fit" individuals occurs over long intervals of time. Thus, depending on how one wants to view it, natural selection acts as negative feedback (see Chapter 1) on unfit individuals or as positive feedback on more fit ones (**BOX 4.3**).

### BOX 4.3 Misuse of Darwin's Theory

Darwin based his thinking in part on Thomas Malthus' *Essay on the Principle of Population*, first published in 1797 (Wallace had also read Malthus' book some time before his bouts with malaria). Malthus' views, along with those of others of the time, have echoed down to the present and have often been misused. Thomas Malthus believed "the passion between the sexes" was too great to overcome; thus, human populations would increase "geometrically" (or exponentially), meaning that after a slow increase, human population would suddenly skyrocket upward. In contrast, according to Malthus, agricultural food production would increase at a much slower arithmetic rate, behaving like a straight line. Thus, according to Malthus, starvation would always be part of the human condition. Malthus also concluded that poverty was natural and could never be eradicated, and there should be no attempts at state support of the poor. Malthus, not Darwin, first coined the phrase "struggle for existence" in his description of primitive tribes and believed that in his own society competition was best for all.

However, Malthus was perhaps not as ruthless as social reformers of the time portrayed him. Malthus believed the wealthy had not become rich because they possessed superior abilities, and he viewed wealth as a responsibility that required its use to help society in terms of employment and progress. He also advocated educating the poor in an attempt to eliminate poverty.

Today, Malthus is viewed by some as an alarmist. As the human population has increased, technologic breakthroughs have generally increased the ability of

food supplies to sustain human populations over much of Earth. The massive starvation predicted by Malthus has not occurred in *developed* countries, but famine has indeed occurred frequently in underdeveloped countries with large populations. Today, many believe biotechnology holds the greatest promise for sustaining human populations, even as expanding populations continue to impact the environment (see Chapter 17).

By all accounts Darwin's sociopolitical views were "Whiggish," meaning he was inclined toward what we now consider a moderate-to-liberal social and political viewpoint. Unfortunately, Darwin's adaptation of Malthus' views continued to be used to espouse what is called **social Darwinism**, in which society is supposed to improve by the action of natural selection on human efforts: some persons naturally succeed, whereas others fail. One of the most notable persons identified with social Darwinism was Herbert Spencer (1820–1903), who emphasized *laissez-faire* economic views. Spencer certainly believed in societal progress, but he also believed it should occur in a Lamarckian-style "upward striving" of individuals, not through natural selection. Still others claim that the strongly pro-Darwin stance of the famous German zoologist, Ernst Haeckel, planted the seeds of the National Socialist (Nazi) movement in Germany and Austria. These and other movements, not just in Germany but also in Great Britain and America, promoted the movement of racial stereotyping and selective breeding of humans called **eugenics**.

Darwin also argued that natural selection of the small differences between organisms could account for trends seen in the fossil record. Thus, Darwin became keenly aware of the tremendous amount of time required for natural selection to produce evolutionary change. This is not unlike Lyell's view of slow, gradual change through time, except that Darwin's theory resulted in *directional* change, something Lyell initially rejected (see Chapter 1).

### Concept and Reasoning Checks

1. What were some of the basic observations Darwin made during the voyage of the *Beagle*?
2. What are the basic tenets of the theory Darwin developed after his return to England?

## 4.5 Inheritance and Variation

To make his theory of evolution credible, Darwin had to provide evolution with a mechanism of inheritance. He already knew, based on the experiments of animal breeders, that agricultural stocks had been improved to feed the expanding human population, so there was obviously some sort of mechanism for parental traits to be passed to the offspring. This same mechanism, he reasoned, would result in the gradual modification of traits over many generations in natural populations. Up to and after Darwin's time, Lamarck's theory of acquired characteristics was one of only two theories of inheritance that had been suggested. The other widely accepted theory of inheritance in Darwin's time was that of **blending inheritance**, which stated the traits of individuals were simple blends of those of its parents, like mixing a bucket of red and white paint to produce pink. Based on Lamarckian theory and blending inheritance, Darwin developed his own theory of inheritance: "pangenesis." Darwin suggested that each organ of an individual's body developed special particles called "gemmules," which were transported by the bloodstream to the gonads (testes or ovaries). Because the gemmules originated in the body's cells, they could take on characteristics in the manner Lamarck had described. Each offspring would be a blend of gemmules from both parents, although in some cases the offspring might receive more gemmules from one parent than the other.

The discovery of the basic mechanism of inheritance is rightfully attributed to an Augustinian monk



FIGURE 4.6 Gregor Mendel (1822–1884).

named Gregor Mendel (FIGURE 4.6). About the mid-1860s Mendel conducted experiments involving the crossing of pure-breeding lines of peas in the gardens of a monastery in Brunn (Brno), in what is now the Czech Republic. Based on the results of many different kinds of experimental crosses, Mendel concluded that genetic traits occurred in pairs (one each from the male and female) called alleles. Alleles behaved like particles, and Mendel's theory came to be called the **particulate theory of inheritance**. Alleles were either *dominant* or *recessive*. Mendel reasoned that a recessive trait was only expressed when both alleles were recessive (now called homozygous recessive); otherwise, the dominant trait was expressed if both alleles were dominant (homozygous dominant) or if the dominant allele was present in just one "dose" (heterozygous). Thus, even if organisms appear outwardly identical, they may be different genetically. However, even if organisms are genetically identical, they may still appear slightly different. Genetically identical twins, for example, typically have slightly different appearances because of slight differences in environment (different diets, etc.). We must therefore differentiate between "genotype" and "phenotype." The term genotype refers to the actual genetic makeup of the organism (homozygous dominant, heterozygous, or homozygous recessive);

phenotype refers to a particular genotype plus the effects of the environment on the genotype. Mendel's particulate theory of inheritance was highly significant, because it contradicted the blending theory of inheritance. Unfortunately, Mendel published the results of his work in a rather obscure journal, so the significance of his results lay dormant until around the turn of the century. Later, workers discovered that Mendel had sent a copy of his paper to Darwin, but Darwin apparently never read it.

Still, two basic questions remained: what were the particles and how did they behave when observed under the microscope? If the particles could be identified, then perhaps their exact behavior could be understood. During the last half of the 19th century chromosomes ("colored body") were found to duplicate and separate from one another during cell division and were therefore thought to be involved in heredity. Then, Mendel's results were rediscovered about 1900, and their full significance for heredity and the production of variation was realized. Each species has a characteristic number of chromosomes. The number varies substantially between species and does not indicate the species' level of evolutionary complexity. When gametes (sperm and egg) are produced by the process of gametogenesis the chromosomes are shuffled much like a deck of cards. During gametogenesis one half of *each* duplicated pair of chromosomes has an equal chance of going into one of the two cells resulting from each cell division. This is much like flipping a coin, during which one has a 50:50 chance of obtaining heads or tails. Thus, the potential number of chromosome combinations (and therefore potential genotypes of gametes) is equal to 2 raised to the power of the number of pairs of chromosomes. In humans the chromosome number is 46, so there are 23 pairs of chromosomes. So, the total number of different genotypes of gametes in humans (excluding mutation, discussed in Section 4.6 below) is  $2^{23}$ , or about 8.4 million! No wonder there was so much variation within the same species: gametogenesis and sexual reproduction resulted in **genetic recombination** that produced vast numbers of genotypes on which natural selection could act.

## 4.6 Genetic Code and Mutation

Still, this was not the complete picture of heredity and variation. Breeding experiments established that changes in the appearance of certain portions of chromosomes corresponded to certain alterations in body parts and coloration. Thus, variation

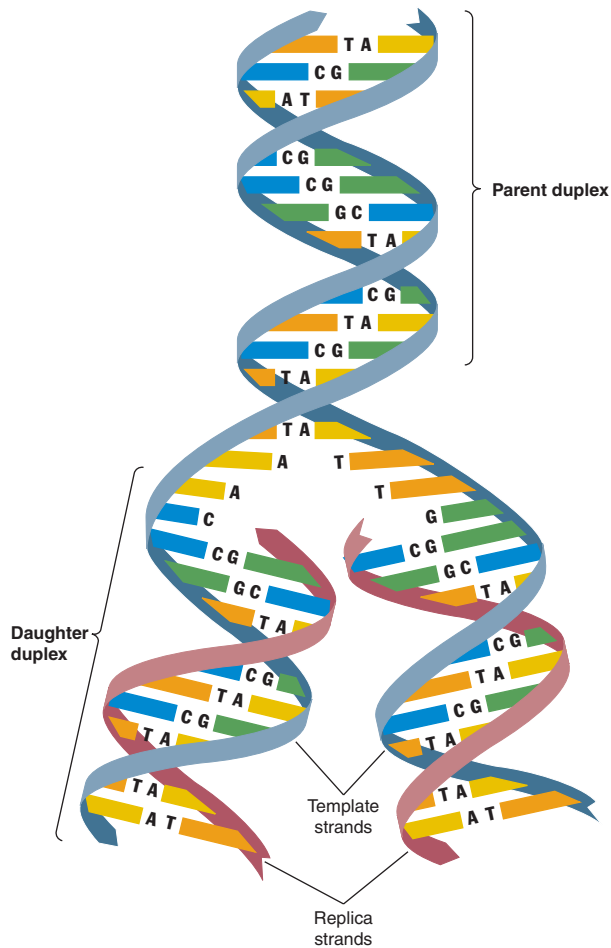
also originated from changes, or *mutations*, to certain portions of the genetic material called genes; at the time it was thought that a particular gene coded for a particular trait. Mutations resulted in even greater amounts of genetic recombination than gametogenesis alone. In fact, mutations are now recognized as providing the "raw material" upon which natural selection acts. But what was the exact genetic material in the chromosomes, its structure, and chemical composition? Answers to these questions would show *how* the genetic information was encoded and passed on to offspring.

The fact that deoxyribonucleic acid, or DNA, serves as the hereditary code was not established until the 1940s. The actual structure of DNA was determined shortly thereafter in the 1950s, with the bulk of the credit normally given to James Watson (a geneticist) and Francis Crick (a biochemist). The fundamental building blocks of DNA are called nucleotides (adenine, guanine, thymine, and cytosine); nucleotides are attached to a double-stranded "spiral staircase" composed of sugars and phosphates (**FIGURE 4.7**).

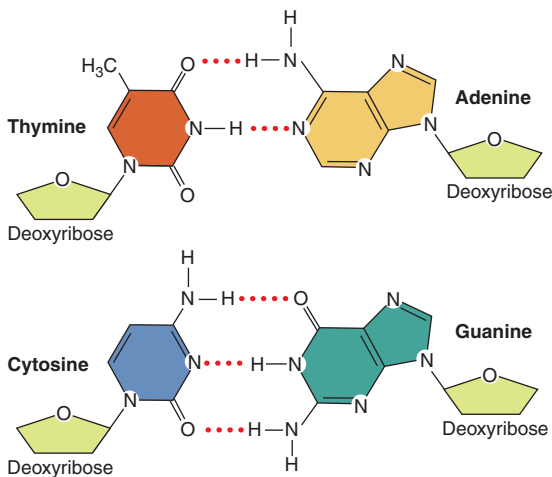
The sequence of nucleotides along the sugar-phosphate backbone comprises the genetic code. The code is "decoded" to produce other molecules and structures according to the Central Dogma of cell biology. The **Central Dogma** of cell biology states the genetic code stored in DNA is read by the process of **transcription** to produce messenger RNA (mRNA), and the message turned into other molecules and structures. The mRNA is single stranded, and once it has been synthesized from DNA it is released from the DNA and travels out of the cell nucleus to the cell's cytoplasm. The mRNA is read or **translated** into proteins in the cytoplasm. In diagrammatic form,

DNA → mRNA → protein

There are three main types of molecules in all creatures: carbohydrates (sugars), lipids (fats), and **proteins**. Although carbohydrates and lipids are both involved in metabolism and growth, neither is particularly different from one species to another. It is the proteins that give each species its characteristics. Proteins occur as structural proteins that give a cell shape and aid in cellular movement and as organic catalysts called **enzymes**. Each enzyme molecule consists of one or more proteins, which in turn consist of strands of amino acids (**FIGURE 4.8**). After each strand is initially produced, it "balls up" into a characteristic shape based on the distribution of positive and negative



(a)



(b)

**FIGURE 4.7** The basic structure of DNA. **(a)** The double helix unwinds in order to duplicate itself or to be transcribed to produce messenger RNA. The nucleotides along the unwound strands of DNA serve as templates which are read to produce the complementary strands. **(b)** Complementary nucleotides along the helices bond through weak hydrogen bonds (red dots). The hydrogen bonds are easily broken and re-made during DNA duplication and transcription.

charges and the strength of chemical bonds (Figure 4.8). One or more of the protein balls then forms the actual enzyme molecule.

Enzymes are highly specific for certain biochemical reactions. In these reactions an enzyme molecule binds with a substrate molecule for much, much less than a split second; the enzyme catalyzes the chemical change in the substrate (perhaps a chemical bond is broken or made, or a particular chemical grouping changed slightly), and then the altered substrate molecule is released for use in another reaction. The enzyme molecule and its substrate molecule react at the enzyme's **active site**. The active site is highly specific for the substrate molecule because of the distribution of positive and negative charges at the active site and because of the active site's shape. Thus, the substrate behaves like a key inserted into the lock represented by the enzyme (Figure 4.8). If any changes to the active site's structure or the distribution of positive or negative charges occur because of a mutation, it is very likely that the enzyme will be dysfunctional. An important step in a metabolic pathway might not be catalyzed properly, and the organism would likely die.

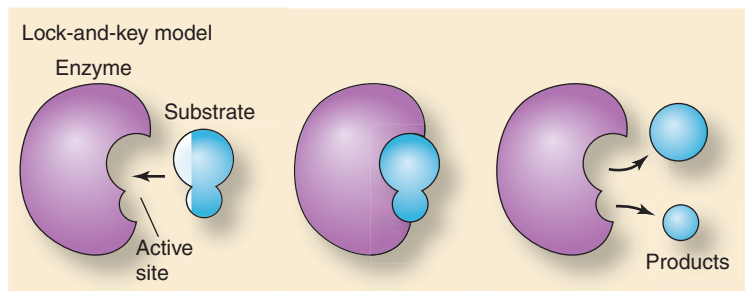
Thus, mutations are typically lethal. Nevertheless, some mutations are beneficial, or at least "neutral," and so may persist in natural populations rather than being weeded out by natural selection. Mutations, coupled with the process of genetic recombination, are acted on by natural selection to produce evolutionary change that results in new species.

### Concept and Reasoning Checks

1. What processes produce genetic variation?
2. What is the importance of enzymes and how do mutations potentially affect enzyme function?

## 4.7 Evidence for Natural Selection

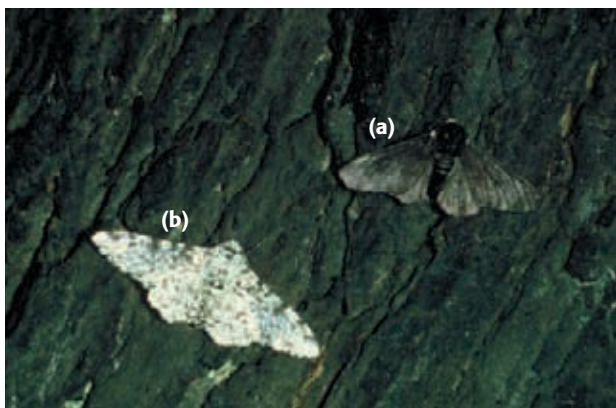
Despite the voluminous evidence that Darwin marshaled in support of his theory of evolution and despite the theory's wide explanatory power, Darwin regarded natural selection as a hypothesis. Darwin based the hypothesis of natural selection on artificial breeding experiments and the fact that natural populations do not exhibit wild fluctuations in abundance. Darwin further supported his hypothesis through his studies of **sexual selection**. Sexual selection acts on mating success, either through competition of the members



**FIGURE 4.8** The enzyme lock-and-key mechanism. [Adapted from: Mathews, C. K., van Holde, K. E., and Ahern, K. G., 1999. *Biochemistry*, 3rd ed. Upper Saddle River, NJ: Prentice Hall.]

of one sex of a species for mates, through choices by members of the opposite sex, or some combination. Sexual selection results in what are seemingly bizarre mating rituals and exaggerated phenotypes such as beautiful coloration in birds or large antlers in elk and other mammals.

Since Darwin's time a number of cases of natural selection have been well documented that further substantiate his hypothesis. The most famous example is **industrial melanism** in England ("melanic" refers to dark colored). During the industrial revolution in England pollution controls were unheard of and the countryside, especially around the heavily-industrialized city of Manchester, was often blackened with the soot from the burning of coal. Consequently, the background on which the peppered moth, *Biston betularia*, lived began to darken (**FIGURE 4.9**). A similar phenomenon occurred among other species of insects. The peppered look of the moth had originally served to camouflage it from predators, especially birds. As tree trunks and other substrates were darkened by soot, black moths, which were always present in very small numbers



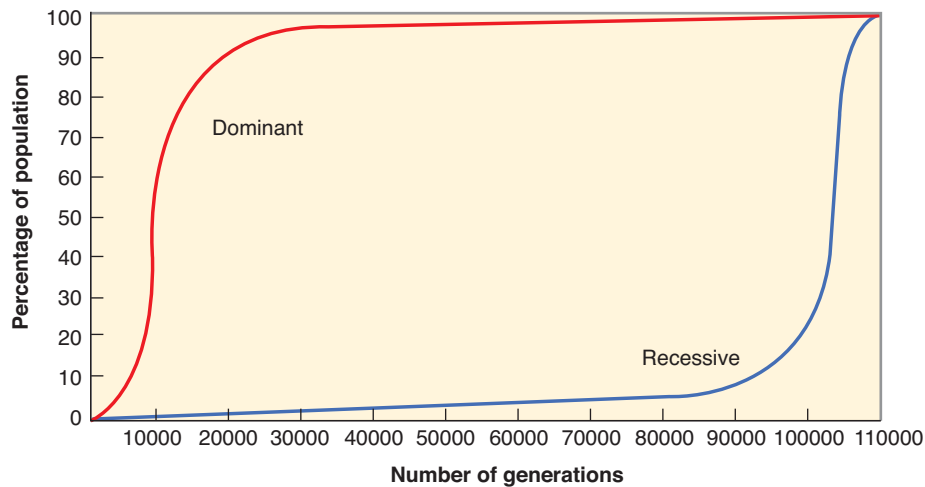
**FIGURE 4.9** Industrial melanism in the peppered moth, *Biston betularia* on a (a) dark (melanic) and (b) pale, "peppered" form.

in natural populations, became the dominant form because birds served as a selective agent and were more likely to prey on lighter-colored moths. With the decline of coal use in later years, the original peppered coloration spread once again through most of the population.

It is now known that the black allele is a dominant allele and the white is recessive. Thus, the natural populations before the onset of pollution were represented by animals that were homozygous recessive for the white allele. This sort of natural selection is referred to as **directional selection**, because the genotypes in the population are dominated by one genotype. Although dominant mutations normally spread quickly, even after many generations, they still do not comprise 100% of genotypes of the population (**FIGURE 4.10**). On the other hand, even though recessive mutations normally take many generations to spread, they can still spread quite rapidly because of directional selection.

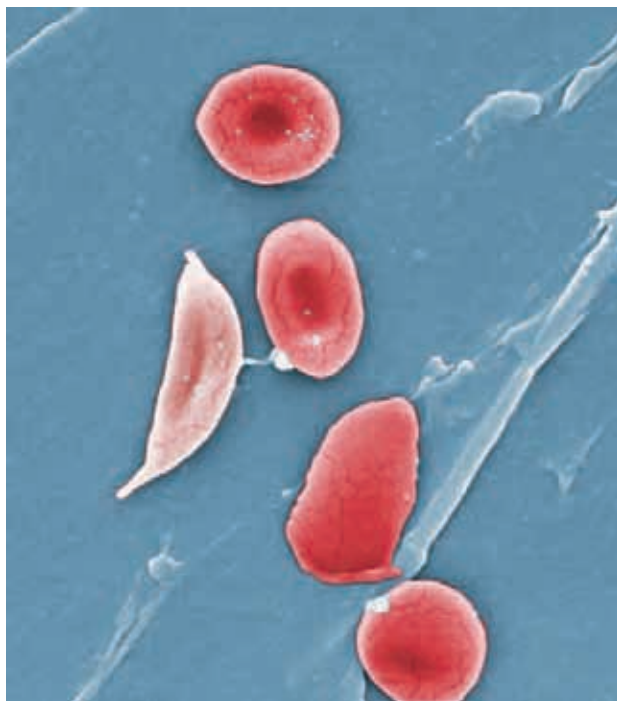
Other examples of natural selection are related to the role of medicine and agriculture in society. For example, natural selection also acts in the case of sickle-cell anemia. Sickle-cell anemia is found mainly in African-Americans and causes the collapse of red blood cells so they have a crescent (sickle)-shaped appearance rather than a disc-like appearance (**FIGURE 4.11**). Sickled red blood cells carry less oxygen to the body's tissues and organs, resulting in fatigue or death. Sickle-cell anemia results from a single slight mutation in the DNA code. This mutation affects the ability of the protein, hemoglobin, in red blood cells to bind oxygen.

Sickle-cell anemia was originally widespread in tropical Africa. Malaria is also widespread there because of heavy rainfall and standing water, which mosquitoes (the vectors or carriers of the disease) use for breeding (**FIGURE 4.12**). Malaria is actually caused by a protist that infects red blood cells and causes them to burst (hence, the fever associated with malaria). However, the protist cannot infect sickled cells. Thus, humans either homozygous dominant for the allele



**FIGURE 4.10** Spread of dominant and recessive alleles in a hypothetical population of organisms. Notice that the dominant mutation spreads quickly, but even after many generations has still not spread completely through the population. On the other hand, the recessive mutation takes many generations to spread, but eventually spreads quite rapidly. [Adapted from: Patterson, C. 1978. *Evolution*, 1st ed. Ithaca, NY: British Museum of Natural History/Cornell University Press. Figure 23 (p. 73).]

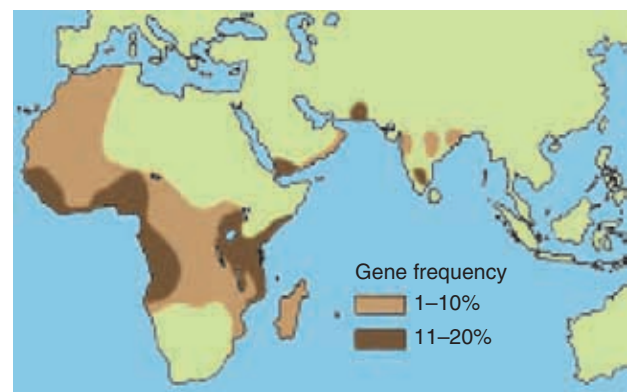
for normal hemoglobin or homozygous recessive for the allele for sickle-cell anemia are more likely to die of anemia or malaria, respectively, than individuals that are heterozygous (Figure 4.12). Individuals with one allele of each are more likely to get enough oxygen while avoiding infection of blood cells by malaria. This example is one of **balancing selection**, in which a relatively stable proportion of genotypes is maintained in a population by a selective force (in this case, malaria).



**FIGURE 4.11** Normal and sickled red blood cells.

Balancing selection is exhibited in other ways. In **hybrid vigor** crosses of inbred strains sometimes produce offspring that exhibit greater crop yields than the parent strains. Each parent strain is homozygous dominant or homozygous recessive for a particular allele that produces only one type of protein, whereas the offspring are heterozygous for the allele. The offspring therefore produce two types of proteins and may be at a selective advantage. In humans inbred strains are frequently homozygous recessive for genes that produce defects that are lethal; this is why laws prohibit the marriage of first cousins, who are too closely related genetically (see Box 4.2).

Another example of natural selection is antibiotic resistance. Bacteria grown in culture and treated with antibiotics such as penicillin quickly become resistant to the antibiotics. Bacteria reproduce quite



**FIGURE 4.12** The occurrence of sickle-cell anemia in tropical Africa. The highest occurrence is in tropical west Africa, from where most slaves originated. [Adapted from: Strickberger, M. W. 1985. *Genetics*, 3rd ed. New York: MacMillan.]

quickly, often in a matter of hours, and if mutants resistant to antibiotics appear they spread through the culture populations quite rapidly. In recent years antibiotic use has become very widespread and so has antibiotic resistance. Thus, new antibiotics may have to be developed in the future to counteract resistant bacteria.

Natural selection is also put to use in genetic engineering. **Genetic engineering** is the science that manipulates the DNA of viruses, bacteria, and other organisms, including humans, and is used to increase the yield and disease resistance of crops. It is also being used to combat disease and birth defects in humans.

## 4.8 Speciation

So we now know how genetic traits are passed from parents to offspring. But how do new species arise? This is really the question that Darwin and others were trying to answer.

Mutations are spread through populations by interbreeding. Thus, speciation could occur by geographic isolation of populations so they are prevented from interbreeding. This type of speciation is known as **allopatric speciation**. Biologic populations are not uniformly distributed over their geographic ranges and typically consist of a main population with smaller isolated populations on their periphery. According to allopatric speciation new species originate by geographic isolation of local populations, called **demes** or **peripheral isolates**, by rivers and streams, mountain chains, or changes in local climate from one side of a valley to another, such as sunlight and moisture. Although the populations are **reproductively isolated**, they begin to diverge genetically from one another. If the populations remain isolated for a long enough time for sufficient genetic divergence to occur, the populations become reproductively isolated from another and are therefore new species.

Genetic transformation of the demes to new species may occur in several ways. Obviously, the addition of mutations adds more variety to the genotypes of demes, and mutations spread much more quickly through small populations than large ones. Speciation may be accelerated in small populations by two other processes. In the **founder effect** a new deme is not genetically representative of the original parent population from which it came. Imagine a box full of solid black and solid white balls mixed together, from which 10 balls are randomly chosen. The likelihood that the proportion of black to white balls chosen (the deme) is exactly the same as the proportion in the much larger collection in the box (parent population)

is not very high. The founder effect accounts for the establishment of the finch populations in the Galápagos (Figure 4.4). Genetically different populations of finches settled on different islands, so that the founding populations on each island were already different at the outset. Another mechanism involved in speciation involves genetic drift. In **genetic drift** some genetic traits are simply lost by chance from demes, whereas others are passed on. In this way demes may also change genetically through time.

Given enough time, then, geographic isolation leads to reproductive isolation and allopatric speciation. Reproductive isolation may develop because of different seasonal times of reproduction, behavioral differences associated with mating rituals, and so on. However, if the barriers to isolation are removed before reproductive isolation has been completed, the populations can still interbreed. Populations that have partly diverged from one another but not developed into full-fledged species are called **subspecies**. In humans these differences are less pronounced and are recognized as **races**. Racial differences between humans are therefore a matter of natural biologic evolution. For example, dark skin is the result of the production of the dark pigment, melanin, that protects the skin from excessive sunlight in the tropics.

### Concept and Reasoning Checks

1. What is the difference between balancing and directional selection?
2. How might directional selection be involved in speciation?
3. What is the difference between the founder effect and genetic drift and why are both processes important to speciation?

## 4.9 Evolution and the Fossil Record

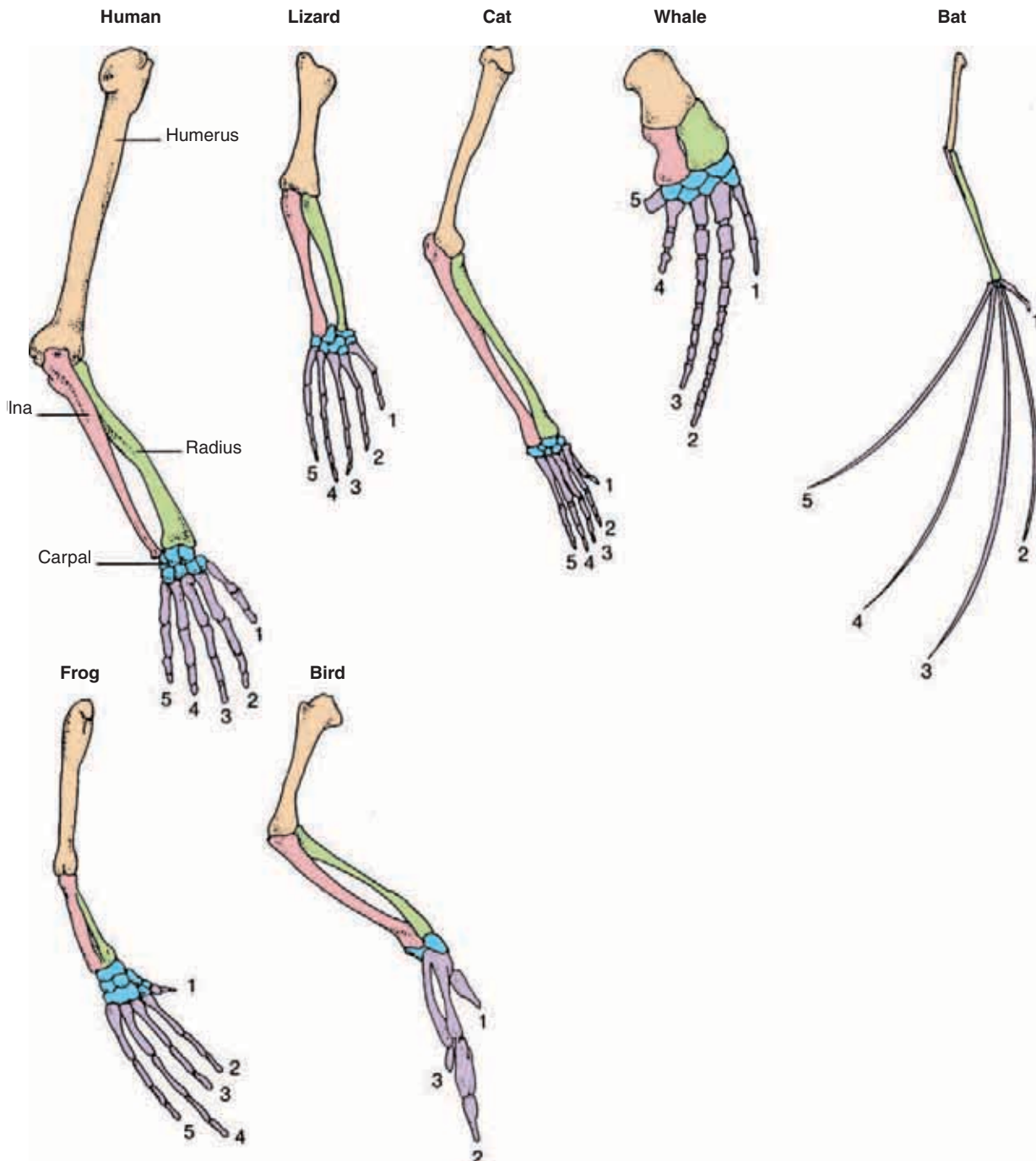
Much of the evidence so far marshaled in support of evolution in this chapter has come from biology. However, as Darwin and his contemporaries recognized, much of the basic evidence for evolution comes from the fossil record.

### 4.9.1 Comparative anatomy

Some of the evidence for evolution in the fossil record was already well known before Darwin. For example, studies of comparative anatomy recognized two basic kinds of structures. **Homologous structures** have a

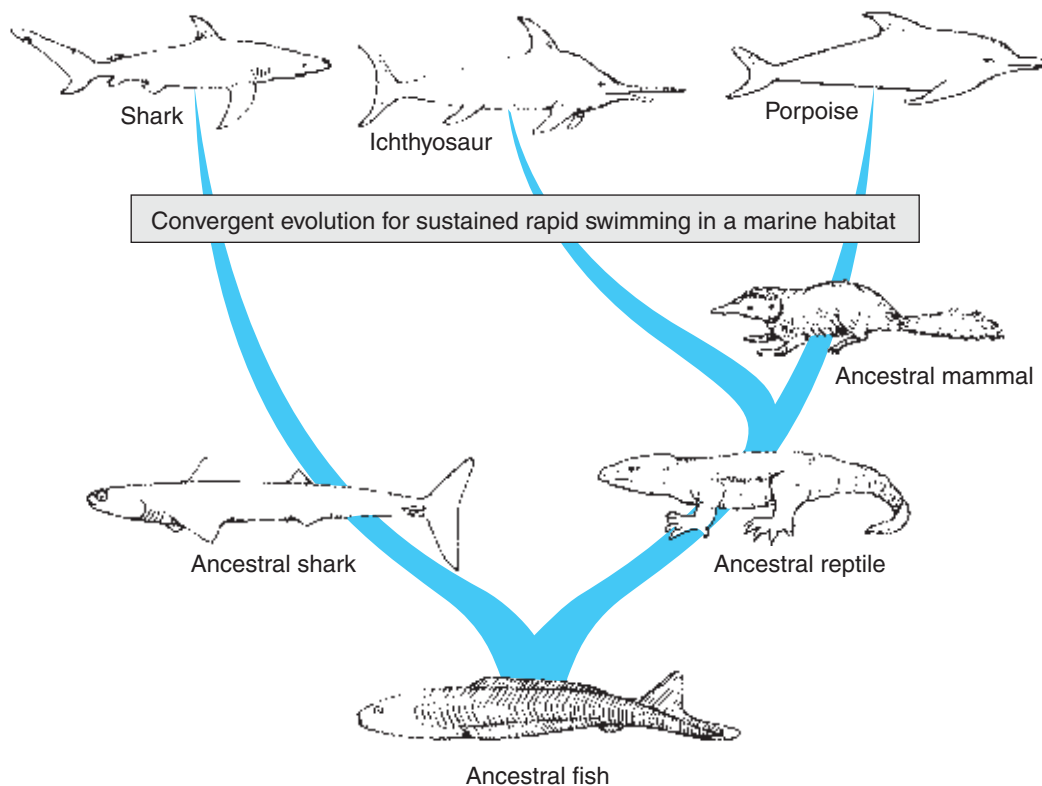
common evolutionary ancestry but are dissimilar in function, such as the limbs of mammals (FIGURE 4.13). These structures are similar because they share a common ancestry, but they have evolved or diverged for different functions through *divergent evolution*. Conversely, *analogous structures* are similar in function but dissimilar in structure. Examples include the wings of birds, bats (mammals), and butterflies and the streamlined bodies of fish, ichthyosaurs (extinct marine rep-

tiles), and dolphins (mammals) (FIGURE 4.14). These groups are not closely related by evolution. Analogous structures arise through *convergent evolution*, in which natural selection acts on very different taxa to evolve or converge on, for example, wings for flight or streamlined bodies for moving through water quickly. Although analogous structures are not used to determine evolutionary relationships, they serve as yet another example of the action of natural selection, namely



**FIGURE 4.13** Homologous structures of the limbs of different mammals. Numbers and colors refer to bones with a common evolutionary ancestry.





**FIGURE 4.14** Analogous structures arise through convergent evolution. The streamlined bodies of fish, ichthyosaurs (extinct marine reptiles) and dolphins (mammals) arose through convergent evolution. If these three taxa were classified into the same taxon based on body shape alone, the taxon would be a grade, not a clade. However, many other features indicate that these taxa are not closely related.

that depending on their habitat and niche, very different groups of organisms may evolve similar structures because they are subject to the same selective pressures.

Because biologic classification is supposed to represent true phylogenetic, or evolutionary, relationships, all the members of a particular category must be descended from a common ancestor (see Box 4.1). Such taxa are called **clades**, and for this reason branching or divergent evolution is sometimes referred to as *cladogenesis*. Clades are considered to be “monophyletic,” meaning each represents a distinct taxon that reflects its true evolutionary relationships. Taxa that do not share a common ancestry but are mistakenly misclassified together are referred to as **grades** because convergent evolution has resulted in very different taxa attaining the same “grade” or superficial appearance. Such grades are said to be “polyphyletic” because they include taxa not closely related evolutionarily.

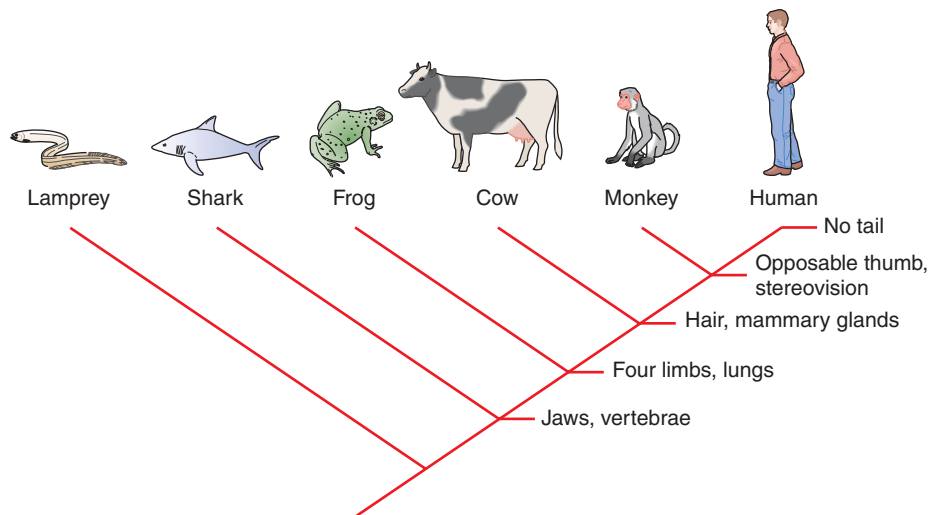
### 4.9.2 Cladistics

For many years evolutionary relationships were established based on simple comparisons of anatomy of modern and fossil species like those described above. However, the new science of **cladistics** classifies taxa according to whether or not different taxa share the

same traits. All sorts of traits have been used in cladistics, ranging from anatomic (for example, the number and arrangement of bones in a skeleton) to the sequences of nucleotides in DNA and RNA and amino acids in proteins.

But the basic procedure in cladistics is always the same. The basic assumption of cladistics is that two taxa share the same trait because they have a common ancestry. These relationships are represented in a **cladogram** like that shown for the major groups of vertebrates in **FIGURE 4.15**. All the vertebrate groups shown possess jaws. Such a trait, which is shared by all the taxa, must have appeared first and is therefore considered **primitive**. **Derived traits**—lungs, claws, scales, fur, and mammary glands—appear later in succession in each of the remaining vertebrate taxa: amphibians, reptiles, and mammals. Birds, which are characterized by feathers, are probably an offshoot of small bipedal dinosaurs (dinosaurs that walked or ran on their hind legs) that appear to have used feathers for insulation. Mammals were probably also derived from another group of reptiles that share certain anatomic features with mammals.

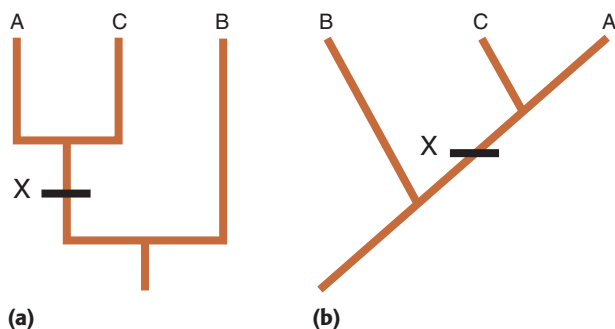
Although this particular cladogram was constructed for higher taxonomic categories (some major



**FIGURE 4.15** A cladogram of some vertebrates showing the successive appearance of major features through time at each branching point. Jaws are considered a primitive trait because all of the taxa, except lampreys, possess them, whereas the other features are said to be derived. [Adapted from: Prothero, D. R. 1998. *Bringing Fossils to Life: An Introduction to Paleobiology*, 1st ed. New York: WCB/McGraw-Hill. Figure 4.2 (p. 48).]

taxa of vertebrates), the same basic procedure is used to examine the relationships at much lower levels, such as the species belonging to a particular genus or the genera belonging to a particular family. As before, more primitive traits are thought to be shared by different groups, whereas derived traits are shared by fewer groups. A hypothetical, evolutionary tree is shown in **FIGURE 4.16**. Figure 4.16A implies time on the vertical scale, whereas the relative distances between taxa A, B, and C in the diagram roughly correspond to their anatomic differences, which presumably reflect their evolutionary relationships.

These relationships are shown differently in a cladogram. Figure 4.16B represents the cladogram of the common and derived characters of taxa A, B,



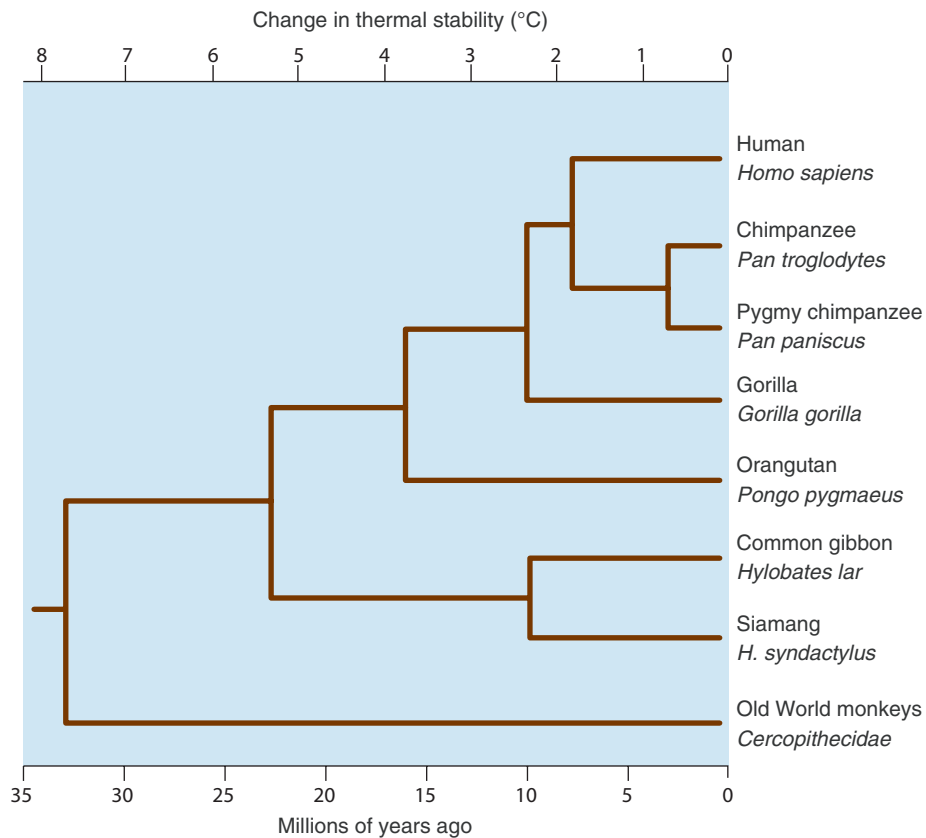
**FIGURE 4.16** (a) Traditional evolutionary tree, in which phylogenetic relationships are depicted between three taxa (A, B, and C). Two taxa (A and C) share a newly derived character (X) and taxon B is ancestral to taxa A and C. Time is vertical (upward). (b) Cladogram of relationships between A, B, and C. Note that in the cladogram, no indication of ancestry is shown. However, both diagrams indicate that A and C are more closely related to one another (because they both share “X”) than to B.

and C. According to the cladogram A and C are more closely related to each other than they are to B.

Traditional evolutionary “trees” and cladograms do not always yield the same classifications, however. For example, **FIGURE 4.17** shows a cladogram of the relationships between humans and related groups. The traditional classification places all humans in the same family, Hominidae, and other forms such as gorillas and chimpanzees in the family Pongidae. In this view the families Hominidae and Pongidae are considered to be monophyletic. However, this view is undoubtedly highly anthropocentric, or “human centered.” Many workers view the family Pongidae as being a “grab bag” or “wastebasket” of all taxa that are not considered “human”; such a taxon is said to be “paraphyletic” because it does not include all of its descendants. In fact, the cladogram in Figure 4.17 suggests that humans basically lie on a continuum of traits they share with the other taxa. Thus, according to the alternative cladogram in Figure 4.17, orangutans, gorillas, chimpanzees, and humans should all be placed in the same taxon, which is in turn considered monophyletic.

### 4.9.3 Microevolution

Another way in which evolutionary relationships can be inferred from the fossil record is to trace the succession of different species through time in the sedimentary record. For many decades, the succession of species in the fossil record was viewed as occurring by slow, gradual *processes* collectively termed **microevolution**. Microevolution was thought to result from the kinds of short-term genetic processes like those



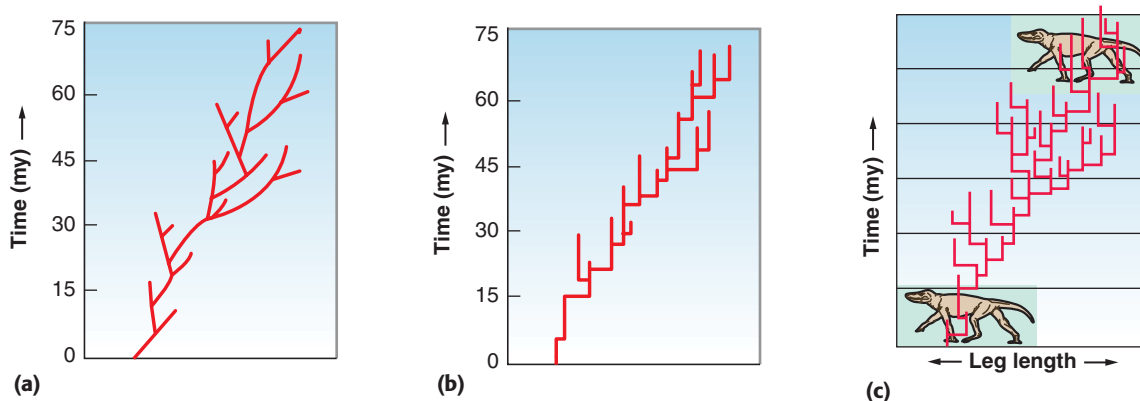
**FIGURE 4.17** The evolutionary relationships of humans portrayed by a standard evolutionary tree. This particular tree is based on the thermal stability of DNA, which has been used as a measure of evolutionary relationships between different taxa. [Adapted from: Sibley, C. G. and Ahlquist, J. E. 1984. The phylogeny of the hominoid primates, as indicated by DNA–DNA hybridization. *Journal of Molecular Evolution* 20, 2–15.]

documented in genetic experiments and biogeographic studies of the distribution of species.

The *pattern* of speciation in the fossil record that was thought to result from microevolution was referred to as **phyletic gradualism** (FIGURE 4.18). The gradual transition of one species into another is called *anagenesis* (as opposed to cladogenesis) and results

in the **pseudoextinction** of the first species. Although anagenesis was often inferred from the fossil record, it was rarely observed. The lack of observed transitions was therefore dismissed as an artifact of the geologic record due to nonpreservation or erosion.

However, an alternative mode of speciation was developed in the 1970s by the paleontologists



**FIGURE 4.18** Modes of evolution suggested by the fossil record. **(a)** Phyletic gradualism, which represents slow, gradual evolution. **(b)** Punctuated equilibrium, which is basically the record of allopatric speciation in the fossil record. Occasionally, following punctuated speciation, lineages persist to the present essentially unchanged as living fossils. **(c)** A hypothetical example of species sorting, in which species lineages are “pruned” sometime after they appear, and which may cause lineages to evolve in new directions. [Adapted from: Stanley, S. M. 1989. *Earth and Life Through Time*, 2nd ed. New York: W.H. Freeman & Company.]

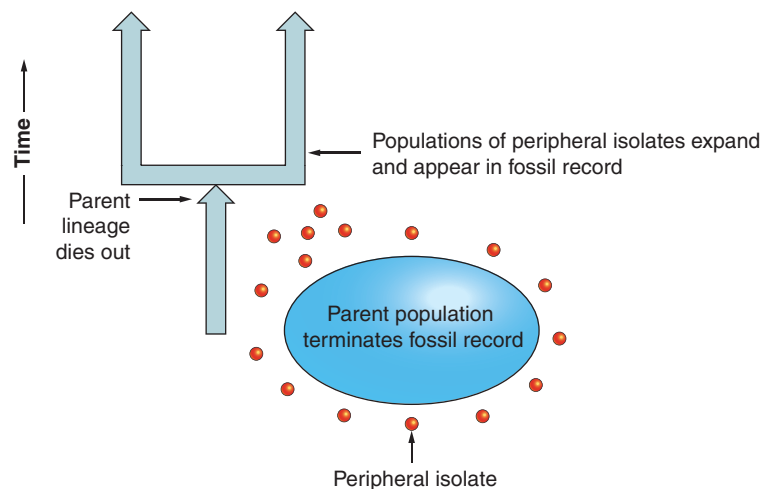
Niles Eldredge and Stephen Jay Gould called **punctuated equilibrium**. These workers argued that the fossil record was not nearly as incomplete as most workers had said and that apparent phyletic gradualism really represented long intervals of slow, nondirectional change (what they called “stasis”) punctuated by abrupt appearances of new species (Figure 4.18). Punctuated equilibrium is basically a record of allopatric speciation preserved in the fossil record (FIGURE 4.19). According to this theory the main parental population dominates in the fossil record because it is widespread and therefore more likely to be preserved and eventually found. However, occasionally the main population goes extinct and disappears from the fossil record. At this time the peripheral isolates that have been present all along (but not preserved in the fossil record because of their patchy distribution and small population sizes) expand and radiate into the environment left vacant by the extinction of the main population (Figure 4.19). The peripheral isolates therefore appear suddenly in the fossil record as new species. Recent studies of over 100 animal, plant, and fungal lineages suggest that new species may evolve in these peripheral isolates relatively rapidly, as would be expected given their small population size and the potential for the spread of mutations that might result in reproductive isolation. Once established, these species settle down to stasis once again. Usually, the taxa established by the peripheral isolates eventually go extinct or are replaced, but on rare occasions lineages may persist to the present essentially unchanged as **living fossils**. One of the most

famous living fossils is the coelacanth, which belongs to the same taxon (lobe-finned fishes) that gave rise to amphibians (see below).

Punctuated equilibrium explains a common misconception of creationists regarding what are called **missing links**. The term “missing link” builds on the concept of the Chain of Being. Missing links are taxa that are intermediate in their traits between one taxon and another. A prime example is *Archaeopteryx*, which is commonly considered to be the first bird. *Archaeopteryx* possesses the traits of both reptiles (teeth, long tail, claws) and birds (hollow bones, feathers). However, missing links like *Archaeopteryx* are rare. Creationists argue that if evolution occurs, there should be many more examples of missing links in the fossil record. However, evolution in relatively small populations such as peripheral isolates means that it is unlikely missing links are preserved in the fossil record.

### Concept and Reasoning Checks

1. How does the use of homologous and analogous structures to infer evolutionary relationships differ from the use of cladograms?
2. Indicate where the processes of allopatric speciation are taking place next to a diagram of punctuated equilibrium.
3. Why is population size important to speciation?



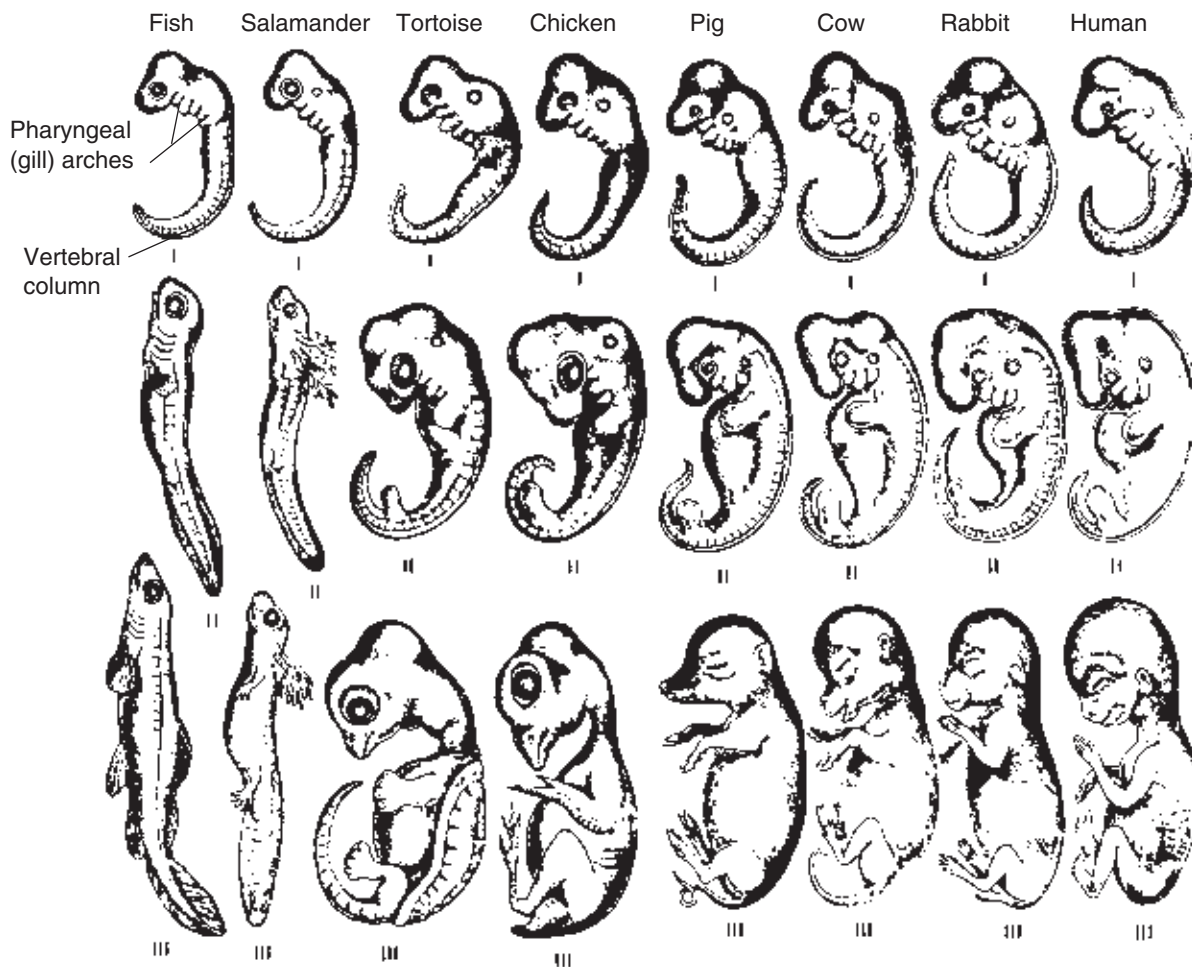
**FIGURE 4.19** The relation of allopatric speciation to punctuated equilibrium. Allopatric speciation is the process by which new species arise while punctuated equilibrium is the pattern of allopatric speciation preserved in the fossil record. The parent population persists relatively unchanged and is more likely to be found in the fossil record than peripheral isolates because of the parent population’s larger numbers and geographic extent. However, if the parent population dies out, one or more of the peripheral isolates will move into the vacated habitat and expand in numbers and geographic area so that new species will be found suddenly appearing in the fossil record. The new species will then remain relatively unchanged because of their large population size. However, they too may eventually go extinct, so that the pattern is repeated in the fossil record.

### 4.9.4 Macroevolution

The fossil record reveals other evolutionary patterns and therefore perhaps other evolutionary processes. Indeed, the fossil record indicates that new species or taxa belonging to categories higher than species may evolve because of rapid genetic change, or **macroevolution**, in small populations.

The coupling of Darwinian evolution with modern genetics is often referred to as the modern synthesis or **neo-Darwinism**. The modern synthesis appeared after World War II and has strongly influenced evolutionary thought to the present day. The modern synthesis dismissed macroevolution because of the results of genetic experiments on human time scales. These experiments indicated that large-scale mutations that presumably had to occur to cause rapid or drastic evolutionary change normally do not occur and that when they do they are lethal. Instead, evolutionary biologists opted for slow, microevolutionary changes in the occurrences of genotypes within populations.

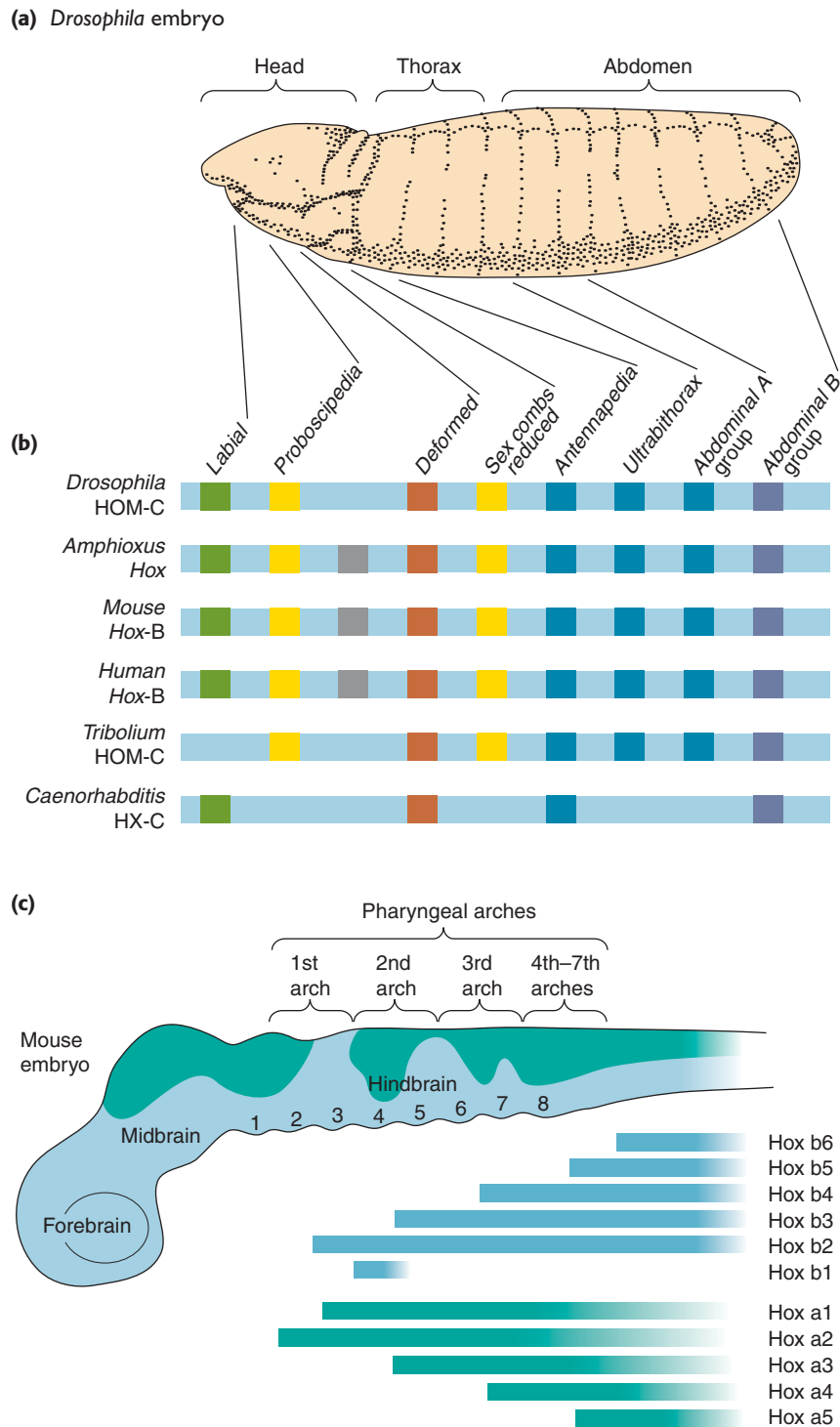
One of the earliest pieces of evidence cited in support of macroevolution was the biogenetic law proposed by the German zoologist, Ernst Haeckel, in the later 1800s (Box 4.3). The **biogenetic law** is usually stated as “ontogeny tends to recapitulate phylogeny.” This means the development of the individual organism (**ontogeny**) reflects (recapitulates) its evolutionary relationships or phylogeny (evolutionary history). The prime example is the appearance and later disappearance of gill slits (which are used for breathing by fish) during the early development of the human embryo (**FIGURE 4.20**). The appearance of gill slits during human embryonic development presumably reflected the fact that humans were ultimately descended from fish and was frequently cited in older textbooks as proof of evolution. However, the biogenetic law was later downplayed because it was realized that embryologic development is far, far more complex than such a sequence of figures like that in Figure 4.20 suggests.



**FIGURE 4.20** Early embryonic development of different vertebrates according to Ernst Haeckel. Note the appearance and loss of gill slits, which was used in support of the biogenetic law. [Reproduced from: G. J. Romanes. 1910. *Darwin, and After Darwin, First edition*. Chicago, I.L.: The Open Court Publishing Company.]

In retrospect, however, Haeckel had discovered something of tremendous importance. Recently, scientists have discovered regulatory genes called *Homeobox*, or *Hox*, genes. These genes control the early development of certain body regions into particular segments or structures (FIGURE 4.21). *Hox* genes

occur along the length of chromosomes, almost like beads on a string, with each bead corresponding to a particular body region or segment (Figure 4.21). Each *Hox* gene or cluster of genes has been given a name. For example, the protein Sonic Hedgehog (named after one worker's favorite video game character) stimulates



**FIGURE 4.21** (a) The distribution of Hox genes in the fruit fly *Drosophila*. (b, c) Note the similarity of the Hox genes in *Drosophila* to those of other widely differing taxa, including arthropods (*Tribolium*), worms (*Caenorhabditis*), and the mouse. Forms similar to *Amphioxus* are thought to have given rise to vertebrates.

the formation and secretion of a growth-stimulating protein during early embryonic development of vertebrate limbs. Increasingly, however, *Hox* genes are referred to as “*Hox 1*,” “*Hox 2*,” and so on for the sake of clarity. Some *Hox* genes establish the anterior (front) to posterior (tail) axis of the animal or the dorsal (top) to ventral (bottom) orientation of the body. Other *Hox* genes code for the initial subdivision of the body into segments and still others for limb generation, the fate of muscles, and light receptors such as eyes.

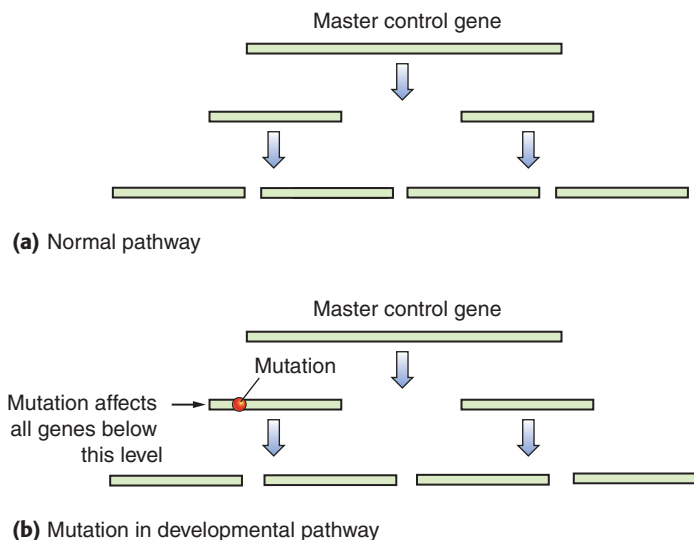
*Hox* genes themselves have been duplicated and modified in different groups through time. As its name implies, the gene *Antennapedia* codes for antennae and legs in the anterior region of the fruit fly. In mice and humans this gene has been duplicated four times, but it is still involved in the differentiation of the head region. Another example of gene duplication is the long row of vertebrae in extinct marine reptiles such as plesiosaurs and land-dwelling sauropods (see Chapter 13). Because identical or nearly identical *Hox* genes have been found in a variety of creatures ranging from worms to insects to vertebrates (based on sequences of DNA nucleotides), these genes must have been present early in evolution and passed on in subsequent lineages through time. In fact, approximately 99% of the genes in chimpanzees and humans are identical; the two species differ primarily because of the regulatory genes expressed during development.

Experiments have been conducted in which the *Antennapedia* gene of the fruit fly (an insect widely used in laboratory genetic experiments) was transplanted into worms with a mutant form of the *Antennapedia* gene. After transplantation the worm’s offspring developed normally. These sorts of experiments indicate that during

embryonic development different *Hox* genes are “turned on” and “turned off” by positive and negative feedback. Proteins coded by certain regions of DNA affect the formation of different types of tissues and organs at specific locations during development. The differentiation of cells into tissues and organs may in turn trigger the activation of other DNA sites for transcription and so on in a kind of developmental cascade (FIGURE 4.22).

Indeed, certain DNA sequences are referred to as **master control genes**. Master control genes are like the master switch on the electric service panel in a house that controls all the circuit breakers. The circuit breakers are analogous to genes that code for enzymes in different metabolic pathways. If a circuit breaker is flipped from the “on” to the “off” position, electricity will not flow through the circuits it controls, and the lights will not come on in certain parts of the house or the washing machine won’t wash, for example. However, all other circuits to the rest of the house remain unaffected. But if the master switch is thrown, all circuit breakers and circuits are inactivated because the flow of electricity into the entire house has been completely shut off. The same is true of master control genes, which control the DNA transcription of a number of genes and metabolic pathways “downstream”.

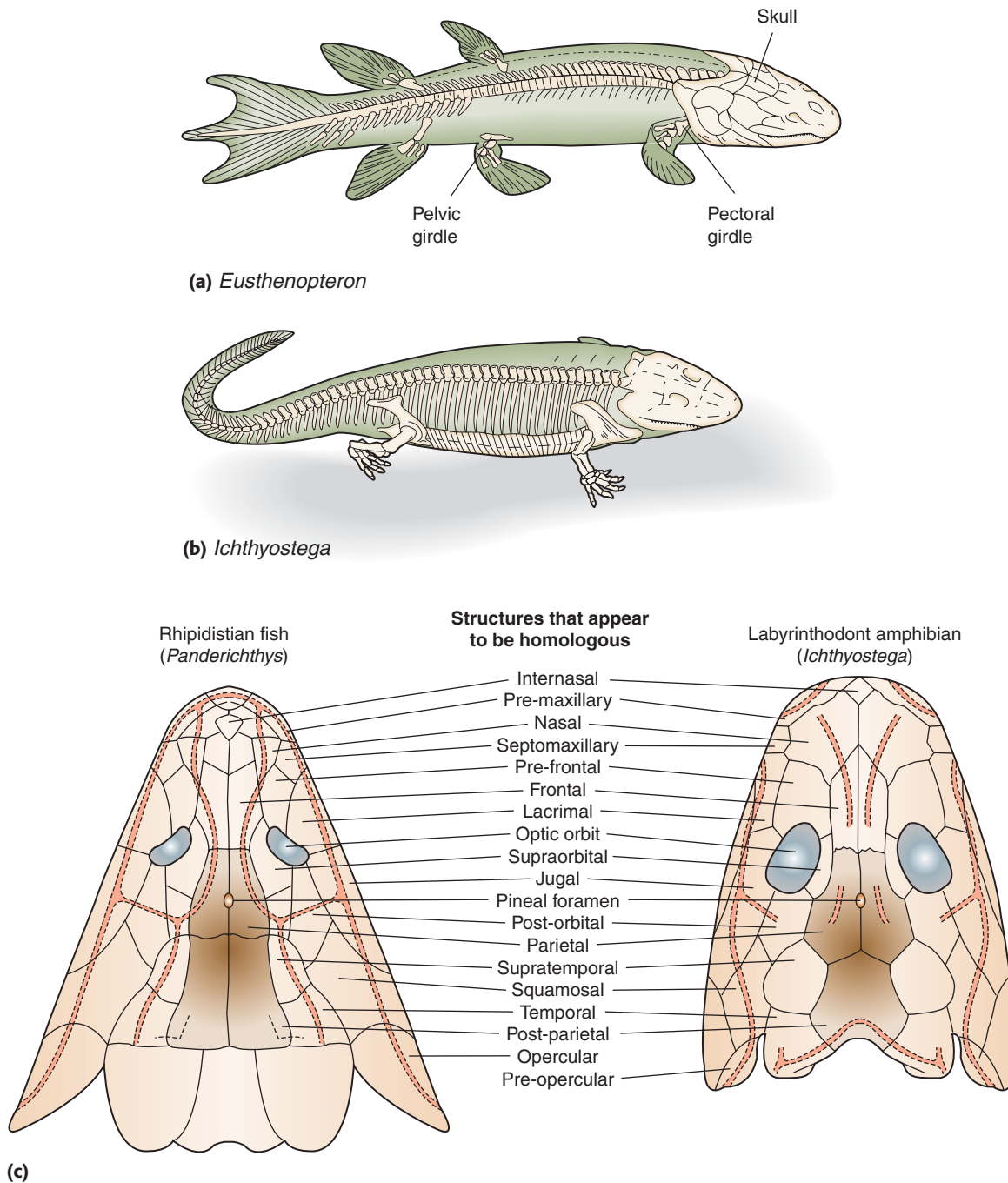
If a mutation occurs in a *Hox* gene or another gene that is involved in early development, it may cause a cascade of genetic and developmental changes that affect all the other genetic pathways downstream. Normally, mutations that occur early during the embryonic development of an organism are lethal because embryonic development is a tightly controlled process. Early development tends to “lock in” later developmental pathways, such as the differentiation of new tissues



**FIGURE 4.22** Effects of mutations in genetic cascades. **(a)** Normal developmental pathway. **(b)** A mutation in a developmental pathway affects later developmental pathways controlled by the DNA in which the mutation occurs.

and organs and their positions in the embryo. But if important genetic changes occur that affect early development and the changes are nonlethal, they can affect subsequent gene expression and biochemical pathways further along in development (Figure 4.22). These sorts of changes explain anatomic similarities such as homologous structures (Figure 4.13).

A mechanism of rapid evolutionary change also related to changes in developmental pathways is **preadaptation** or “latent potential.” Preadaptation refers to the existence of a structure adapted for a particular function or environmental condition that turns out by chance to be adapted for rapid evolution into a different niche (**FIGURE 4.23**). How, for example, can



**FIGURE 4.23** Preadaptation in ancient lobe-finned fish and primitive amphibians. **(a)** *Eusthenopteron*, a primitive lobe-finned fish. [Adapted from: Romer, A. S. and Parsons, T. S. 1977. *The Vertebrate Body*, 5th ed. Philadelphia: W. B. Saunders]. **(b)** *Ichthyostega*, a primitive labyrinthodont or temnospondyl. **(c)** Comparison of skull structure of a primitive lobe-finned fish and temnospondyl. [Adapted from: Duellman, W. E. and Trueb, L. 1986. *Biology of Amphibians*, 1st ed. New York: McGraw-Hill; Part 2 adapted from: Coates, M. I. and Clack, J. A. 1990. Polydactyly and the earliest known tetrapod limbs. *Nature* 347, 66–69.]



an eye or a wing evolve through intermediate stages to its final form? Wouldn't intermediate stages of a structure put creatures at such a selective disadvantage they would be culled by natural selection almost instantly? This question had long plagued evolutionary biologists, including Darwin.

Since Darwin's time a number of examples of preadaptation have been documented. Primitive light-sensing and temperature-regulating organs were preadapted to give rise to eyes and wings, respectively, in arthropods. In experimental studies of insects, small wings are used to regulate body temperature; as the wings increase in size, the advantages for flight become dominant just as the benefits of wings for body temperature regulation begin to level off. As demonstrated by the fossil record, the stubby limbs of primitive **lobe-finned fish** (related to the coelacanth) may have helped them scoot along shallow bottoms, but the limbs were preadapted for a rapid transition to land by primitive amphibians called **labyrinthodonts** (now called "temnospondyls"; Figure 4.23). Based on the striking similarity of bone structure in these two groups, relatively small changes in developmental pathways could easily have transformed the lobe-finned limb into that of a primitive amphibian; as described above, the genetic changes could have spread rapidly through relatively small, isolated populations along the shore. In fact, the limb bone structure of both groups has long been considered homologous.

Darwin was also aware of the existence of vestigial structures in a wide range of animals (FIGURE 4.24). As the term indicates, **vestigial structures** are vestiges of organs or structures that previously performed a particular function but that later degenerated and now have little or no use; the appendix of humans and dewclaws of dogs are examples (Figure 4.24). On the surface vestigial structures also posed the problem of intermediate stages in evolution. However, rather than being preadapted for *future* use (as a teleologic view of evolution would demand), vestigial structures were just the opposite: they were a waste of energy to produce and were being selected against, according to Darwin's theory. Thus, vestigial structures argue for natural selection and evolution, not against it.

Another example of macroevolution *may* be long-term patterns of species' appearances and extinctions in the fossil record called **species sorting**. In theory, species sorting resembles punctuated equilibria, but instead of individuals being selected against, natural selection acts to weed out whole species. Unfortunately, species sorting was originally referred to as

"species selection." This upset some evolutionists, who objected to the implication that the mechanism of natural selection, as applied to populations, could be applied to species or higher taxa. In fact, species sorting has nothing to do *directly* with natural selection; rather, it is envisioned to act more like pruning a bush. Some species are more likely to leave more "offspring" (new species) than others so there are differential "births" and "deaths" of species.

### Concept and Reasoning Checks

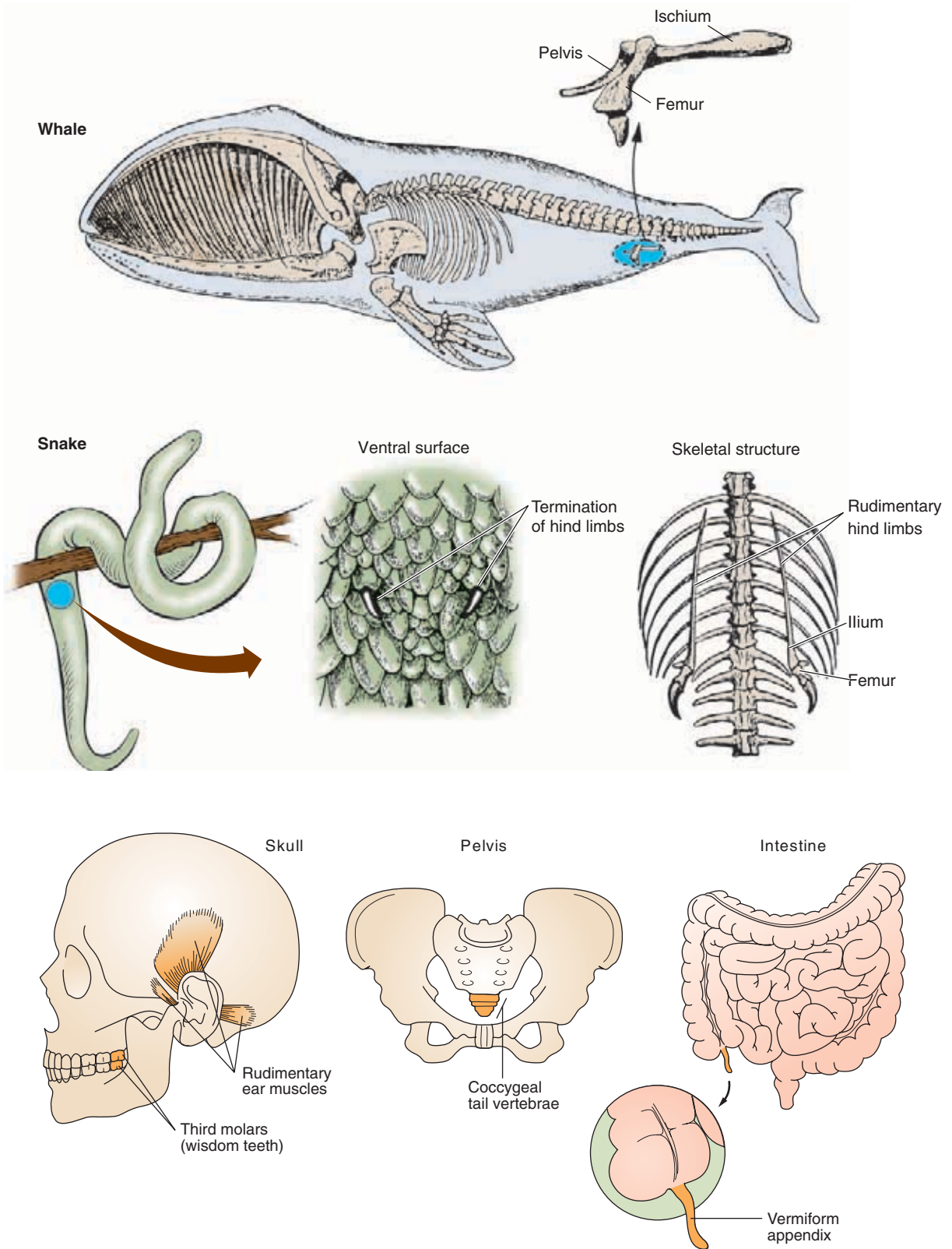
1. Both microevolution and macroevolution involve mutation. How, then, do the processes of macroevolution differ from those of microevolution?
2. What is the importance of preadaptation to macroevolution?

## 4.10 Mass Extinction

Extinction is normal and has occurred through geologic time as a kind of **background extinction**. Despite all their adaptations produced in response to natural selection, most taxa have become extinct. In fact, the fossil record indicates that more than 99.9% of all species that have ever existed have become extinct. Many taxa died out when the biosphere was decimated during **mass extinctions**. As we will see in later chapters, mass extinctions have resulted from different causes, among them global cooling, massive volcanism, decreased oxygen in the oceans, and meteor impacts.

Despite the negative consequences for the biosphere, mass extinction is exceedingly important to biologic evolution. Mass extinction may have been necessary to increase Earth's biodiversity, for without extinction far fewer evolutionary opportunities would have occurred because all the habitats and niches would otherwise have been filled long ago. Extinction, then, is a mechanism of macroevolutionary change that might not otherwise occur. Thus, *mass extinction produces history by altering the course of life*.

The phenomenon by which new species fill the niches of previously existing species after mass extinction is called **ecologic replacement**. The process of ecologic replacement can be envisaged as a theater in which the "stage" (planet Earth) has existed through time but on which the "actors" (taxa) have changed



**FIGURE 4.24** Examples of vestigial structures. [Part 1 modified from: Romanes, G. J. 1910. *Darwin, and After Darwin*, 1st ed. Chicago: The Open Court Publishing Company.]

through time because of changes to the stage or physical environment of Earth. A prime example is the extinction of dinosaurs at the end of the Cretaceous Period, which allowed the evolutionary diversification of mammals, leading eventually to humans. When massive ecological replacement (such as that of the dinosaurs by the mammals) or diversification (for whatever reason) occurs among a particular taxon, it is referred to as an **adaptive radiation**.

All mass extinctions seem to have some common features. First, the survival of species depends on their tolerance to environmental change. Eurytopic species are more likely to survive than stenotopic ones because eurytopic taxa are tolerant of environmental change and are more likely to be widespread, increasing their chances of survival in refuges (Chapter 2). Eurytopic taxa are also much more variable genetically than stenotopic taxa; if this were not the case eurytopic taxa would not be as tolerant of environmental change and would not be as widely distributed. Thus, once extinction has ceased, eurytopic taxa rapidly evolve new adaptations as they radiate into the habitats and niches left vacant by the extinction of previously existing taxa.

Second, after extinction (called the **recovery phase**), any and all mechanisms of microevolution and macroevolution may give rise to new taxa through adaptive radiation. However, extinction does not mean that “anything goes” as the biosphere recovers and new taxa evolve. In fact, the founding taxa are subject to similar natural selection pressures and limitations of genetic constraints as their ancestors. This is evidenced by the phenomenon of convergent evolution *between* taxa belonging to widely different evolutionary lineages to produce analogous structures or features (Figure 4.14). A similar phenomenon known as **iterative evolution** occurs *within* the same taxa that are more closely related by evolution. For example, at different times during Earth’s history both a mass extinction and a smaller **minor extinction** decimated planktonic organisms called foraminifera. After each of these extinctions, new species of foraminifera evolved that closely resembled the taxa that lived before each extinction (**FIGURE 4.25**).

Thus, the fossil record indicates that the evolution of new taxa after extinction is constrained by the “genetic baggage” of the surviving taxa. Surviving taxa serve as the ancestors of the taxa that diversify during the recovery phase. Thus, certain genetic programming is already “hard-wired” into the founding taxa and constrains the evolution of new traits. In other words the evolution of new taxa during the recovery phase

is constrained by a kind of founder effect but on a much more massive scale. Many new classes, orders, families, genera, and species may certainly evolve after an extinction—especially a mass extinction—but no new phyla appear because the basic body plans (**groundplans**) of phyla remained the same. These genetically based groundplans served as the foundation on which the new taxa are reconstructed. In other words evolution occurred *within* phyla, but wholly new phyla or groundplans did not appear.

### Concept and Reasoning Check

1. How does the genetic composition of a species influence its evolutionary potential?

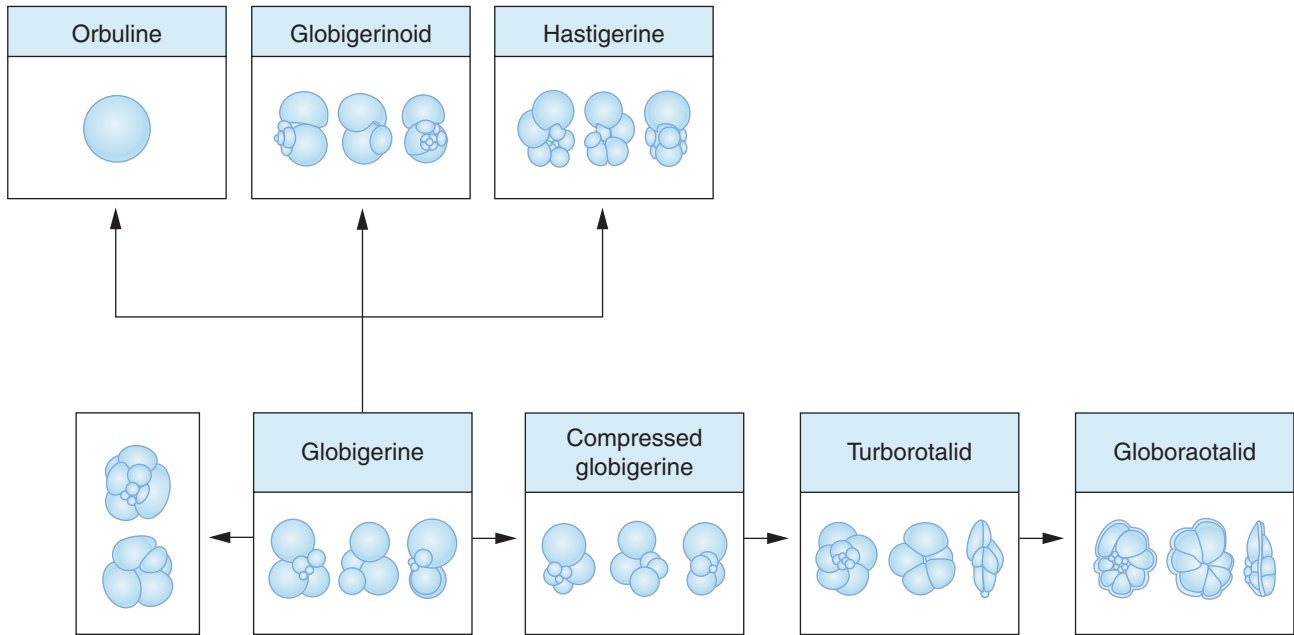
## 4.11 Biodiversity Through the Phanerozoic

So far we have examined evolution at the micro and macro levels with regard to the appearance of new species and new higher taxa and their extinction. But how have some of these changes played out during the broad evolution of the biosphere through the Phanerozoic Eon?

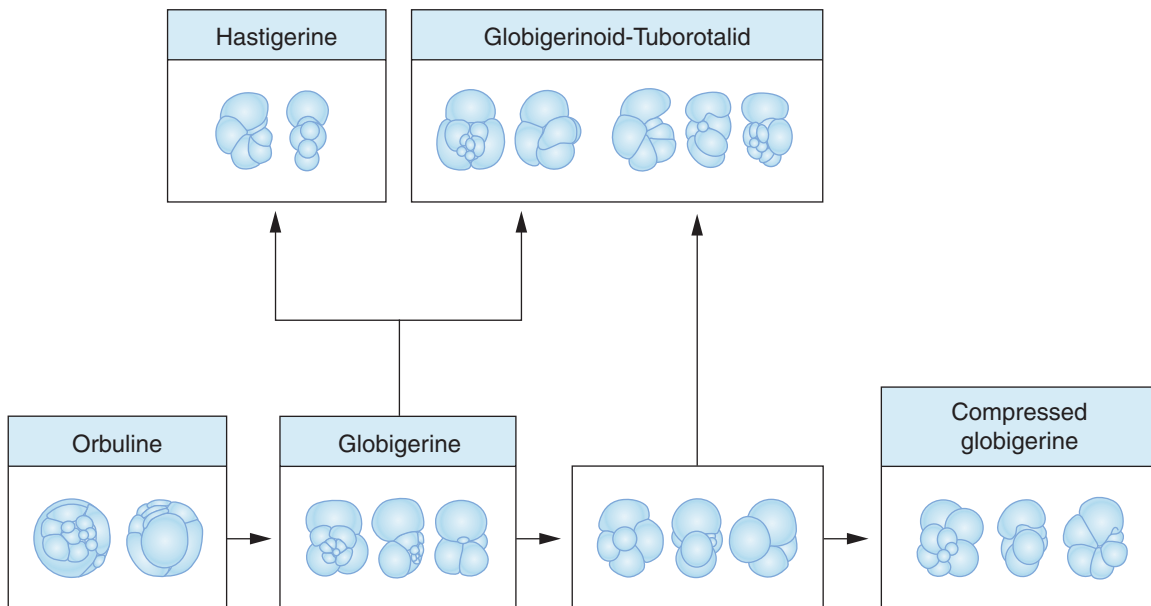
The fossil record reflects major changes in the evolution of marine and terrestrial communities through the Phanerozoic (**FIGURE 4.26**). Fossils first became abundant in the marine geologic record about 540 million years ago at the beginning of the Cambrian Period. These fossils belong to the **evolutionary fauna** called the **Cambrian Fauna**. The communities of the Cambrian Fauna appear primitive compared with those of later times and were dominated by taxa such as trilobites and jawless fish that fed very close to the sediment surface or just beneath it.

The **Paleozoic Fauna** began to diversify during the Ordovician Period, beginning about 500 million years ago, as the Cambrian Fauna began to wane (Figure 4.26). The Paleozoic Fauna was much more diverse than the Cambrian Fauna and was dominated by *suspension-feeding* taxa that fed on suspended organic matter and plankton above bottom, including corals and coral-like taxa. In fact, one of the most significant developments of the Silurian and Devonian was the appearance of widespread reefs. Jawed predators such as sharks that were capable of crushing the hard shells of prey or feeding on fish became prominent by the end of the Devonian and Early Carbon-

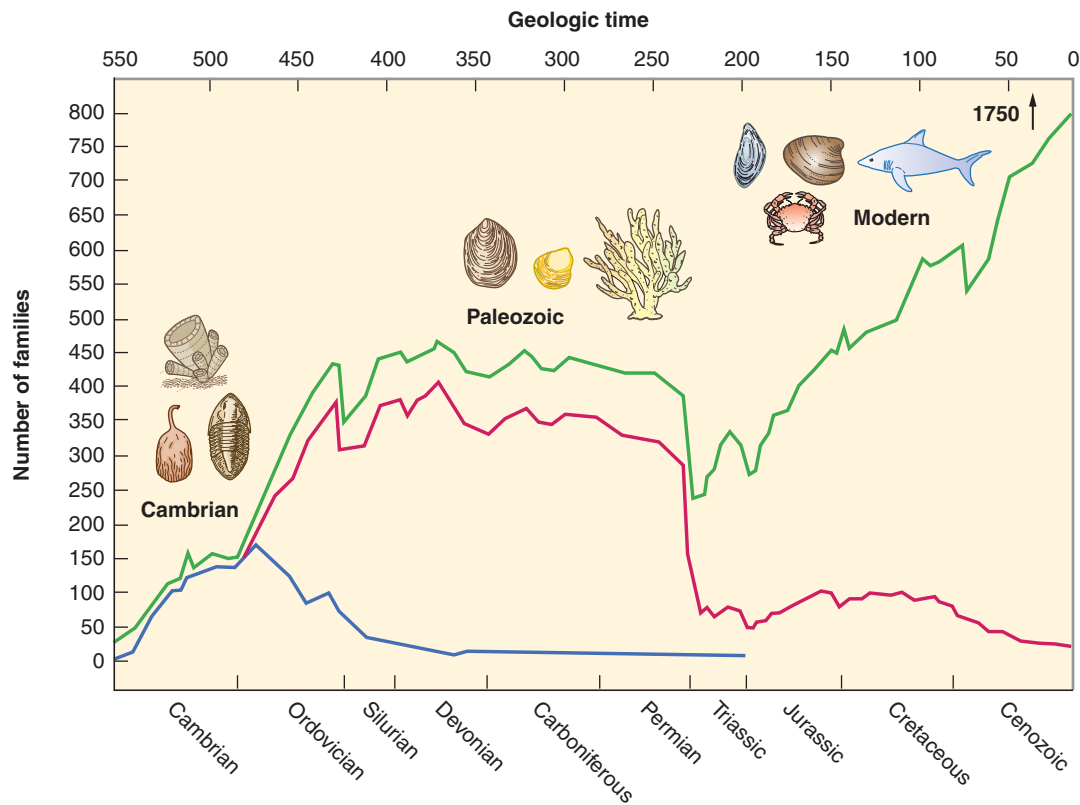
**Paleogene Adaptive Radiation**



**Miocene Adaptive Radiation**



**FIGURE 4.25** Iterative evolution is like convergent evolution (Figure 4.14) but occurs among closely related taxa, such as the species of planktonic foraminifera shown here. [Adapted from: Prothero, D.R. 1998. *Bringing Fossils to Life*. WCB/McGraw Hill. Boston, MA, Figure 11.9B (p. 197).]



**FIGURE 4.26** The major changes in marine faunas of the Phanerozoic. [Adapted from: Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7, 36–53.]

iferous periods. It therefore appears that marine food chains were lengthening and food webs becoming more complex during the Paleozoic. The lengthening of the food chains suggests increasing food (energy) availability at the base of food pyramids that could be passed upward to support the predators, which likely had elevated metabolism for locomotion and predation. Food webs also became more complex on land. The spread of forests into the interiors of continents led to the widespread coal-forming forests of the Carboniferous Period. These forests provided habitats and niches for the evolutionary diversification of insects, amphibians, and eventually reptiles. The Paleozoic Fauna suffered a number of minor extinctions and two **mass extinctions** at the end of the Ordovician and Devonian periods that contributed to evolutionary turnover through the Paleozoic. Nevertheless, the Paleozoic Fauna remained recognizable to the end of the Paleozoic Era.

The Paleozoic Fauna was replaced by the **Modern Fauna** in the Triassic Period after the greatest mass extinction in Earth's history about 250 million years ago (Figure 4.26). As its name implies, the Modern Fauna was much more like the faunas we see today. Still, the biotas of the Modern Fauna also changed through time. Marine plankton underwent a tremendous diversification, with coccolithophorids and ultimately diatoms

becoming prominent in the fossil record. One of the most significant developments in the marine realm was the great evolutionary expansion of predatory gastropods (snails), more modern fish, and large marine reptiles, again suggesting increased food availability and metabolism. On land, terrestrial forests continued to expand during the Mesozoic (Figure 4.26). Roaming these forests were the dinosaurs, whereas the seas were prowled by whale-like and dolphin-like reptiles. Flowering plants blossomed during the Cenozoic Era, whereas the dinosaurs were replaced by the mammals on both land and in the seas after yet another mass extinction at the end of the Cretaceous Period.

Thus, biodiversity *appears* to have increased through the Phanerozoic. But questions remain. Why, for example, did the Paleozoic Fauna maintain a relatively stable level of biodiversity? No one knows. And is the steep increase in diversity of the Modern Fauna real or is it an artifact of the fossil record, or both? These are among the most fundamental questions confronting Earth scientists today. As we will see in Chapter 5, younger rocks and their fossils (like those of the Mesozoic and Cenozoic eras) are more likely to be found at Earth's surface than much older ones (like those of the Paleozoic) because there has been less time for younger rocks to be eroded.

### Concept and Reasoning Checks

1. Do you suppose all the processes involved in evolution are observable or can be inferred from laboratory experiments? Why or why not?
2. What does the succession of major faunas through time indicate about directionality of Earth's history (see Chapter 1)?

## 4.12 Summary

- Charles Darwin's theory of evolution irrevocably changed the view of Earth from one of equilibrium to one of directionality and history. Darwin's theory has remained largely intact to the present.
- Darwin reasoned that new species evolve based on the following simple observations and inferences: the great diversity of plants and animals and their variation, their geographic distributions, and the fact that natural populations do not grow unchecked.
- Therefore, he reasoned, there must be a struggle for existence that eliminates unfit individuals. Based on breeders' experiments with agricultural stocks, Darwin reasoned the traits of those individuals that survive and reproduce are passed on to their offspring (differential reproduction), so there is descent with modification. Thus, there is a naturally occurring selection for fitter individuals.
- Experiments by Gregor Mendel demonstrated that genetic traits were passed from parents to offspring. Later, these traits were correlated with the appearance and behavior of chromosomes during cell division. Eventually, it was found that genetic variation is produced by mutation, coupled with the formation of gametes and sexual reproduction. Eventually, the genetic material was determined to be DNA.
- New species typically arise through allopatric speciation. In allopatric speciation natural selection acts on demes or peripheral isolates, which evolve through the accumulation of mutations, genetic drift, and the founder effect.
- In the fossil record new species may appear gradually through the process known as phyletic gradualism or through the process known as punctuated equilibrium. Once they have appeared, new species may be sorted.
- Rapid evolution of new structures and possibly whole new taxa may take place through mutations in master control or *Hox* genes that affect developmental pathways.
- Although the exact causes of extinction vary, extinction can also be considered as an agent of macroevolution because it opens up many habitats and niches simultaneously. Eurytopic species are more likely to survive extinction than stenotopic ones because eurytopic taxa are tolerant of environmental change and are more likely to be widespread, increasing their chances of survival in refuges.
- Eurytopic taxa are also much more variable genetically than stenotopic taxa, so that once extinction has ceased, eurytopic taxa rapidly evolve new adaptations as they radiate into the habitats and niches left vacant by the extinction of previously existing taxa.

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## Key Terms

- acquired characteristics, theory of inheritance of adaptive radiation
- allopatric speciation
- analogous structures, versus homologous structures
- background extinction
- binomial nomenclature
- biogenetic law
- biologic classification (taxonomy)
- Central Dogma: transcription, translation
- clade, versus grade
- cladistics: cladograms, primitive traits, derived traits
- extinction, and recovery phase
- deme (peripheral isolate)
- descent with modification
- differential reproduction
- ecologic replacement
- enzyme (active site)
- eugenics

## Key Terms (continued)

evolution, patterns of (convergent, divergent, iterative)  
evolutionary fauna: Cambrian, Paleozoic, Modern  
extinction: background, mass, minor  
founder effect  
gene, master control  
genetic drift  
genetic engineering  
genetic recombination  
groundplans  
homeobox (*Hox*) genes  
hybrid vigor  
industrial melanism  
inheritance, theories of: acquired characteristics, blending, particulate  
labyrinthodonts, and lobe-finned fish  
living fossil  
macroevolution, versus microevolution  
macroevolution, mechanisms of (*Hox* genes, preadaptation, species sorting, extinction)  
mass extinctions  
minor extinction  
missing link  
natural selection, balancing versus directional  
neo-Darwinism  
ontogeny, versus phylogeny  
phyletic gradualism, versus punctuated equilibrium  
protein  
pseudoextinction  
reproductive isolation  
sexual selection  
social Darwinism  
speciation, allopatric  
species  
subspecies, and races  
vestigial structures

## Review Questions

1. What are the basic observations that led to Darwin's theory of evolution?
2. Give any modern and ancient examples for (a) natural selection and (b) evolution.
3. What was the significance of Mendel's discoveries?
4. Diagram the replication, transcription, and translation of DNA.
5. Diagram the Central Dogma of cell biology. How does a mutation affect the kinds of proteins produced?
6. How does a mutation affect the active site of an enzyme?
7. What is involved in genetic recombination?
8. What is the difference between the terms natural selection, founder effect, and genetic drift?
9. Arrange the following in order (first to last): geographic isolation, allopatric speciation, reproductive isolation. How does one give rise to the next?
10. How can races and subspecies lead to the production of new species?
11. Construct a simple, hypothetical set of taxa with a few characteristics and then draw a cladogram for them.
12. Distinguish between monophyletic, polyphyletic, and paraphyletic. Are paraphyletic taxa polyphyletic?
13. What are the processes involved in (a) microevolution? (b) macroevolution?
14. What is a living fossil and what does it represent in terms of punctuated equilibrium?
15. Why is preadaptation important for evolution? Give examples.
16. At what taxonomic categories do microevolution and macroevolution act? Where might they overlap?
17. Using diagrams, show how allopatric speciation is related to the pattern of punctuated equilibrium seen in the fossil record.
18. What pattern(s) do microevolution and macroevolution generate in the fossil record?
19. Contrast natural selection with species sorting.
20. Why are missing links rare?
21. What is the role of extinction in evolution?
22. List as many examples of natural selection as you can that were discussed in this chapter.



## Food for Thought

1. Do you believe evolution is teleologic?
2. Compare the concept of species as defined by biologic criteria with a species as it is recognized in the fossil record. How do they differ? How are they similar? Why are they similar?
3. Exactly what is “success” in terms of natural selection?
4. What is the difference between a preadapted structure and a vestigial structure? How do both argue for evolution? Give examples.
5. Can one oppose the theory of evolution without opposing the scientific method?
6. Does science work in a cultural and political vacuum?
7. What differentiates mass, minor, and background extinction?
8. Comment on the role of causality in extinction (look ahead to chapters 11, 12, and 13).
9. What is the role of contingency (Chapter 1) in extinction?
10. Why is important to find out if the increase of fossil biodiversity is real or not?



The Grand Canyon. The Colorado River cut the canyon in only about 10 million years after uplift of the Colorado Plateau. The rocks exposed along the sides of the canyon range in age from Precambrian to Permian.