Unit 4

EVOLUTION

CHAPTERS

"The past, the finite greatness of the past! For what is the present, after all, but a growth out of the past."

Walt Whitman

Charles Darwin studied the giant tortoises, above, on the Galápagos Islands. Observations Darwin made during his voyage on the H.M.S. Beagle, right, led him to look for a mechanism by which evolution occurs.

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Archaeologists scrutinize fossilized remains of human ancestors for clues to human evolution. Darwin observed a number of finches, right, on the Galápagos Islands and found that each species was adapted to a different food source.

CHAPTER 14

ORIGIN OF LIFE

Molten rock breaks through Earth's crust in the form of a volcano. Conditions in a volcano are similar to those thought to have been present on early Earth.

FOCUS CONCEPT: *Matter, Energy, and Organization*

As you read, look for examples of the many scientific processes that help answer questions about how life began.

BIOGENESIS

SECTION 14-1

OBJECTIVES

▲ Define *spontaneous generation,* and list some of the observations that led people to think that life could arise from nonliving things.

● Summarize the results of experiments by Redi and by Spallanzani that tested the hypothesis of spontaneous generation.

■ Describe how Pasteur's experiment disproved the hypothesis of spontaneous generation.

The principle of ***biogenesis*** *(BIE-oh-JEN-uh-sis), which states that all living things come from other living things, seems very reasonable to us today. Before the seventeenth century, however, it was widely thought that living things could also arise from nonliving things in a process called* ***spontaneous generation.*** *This seemed to explain why maggots appeared on rotting meat and why fish appeared in ponds that had been dry the previous season—people thought mud might have given rise to the fish. In attempting to learn more about the process of spontaneous generation, scientists performed controlled experiments. As you read about these experiments, refer to the figures that show the experimental design.*

REDI'S EXPERIMENT

Flies have often been viewed as pesky creatures. Most people are too busy trying to get rid of them to even think about studying them. In the middle of the seventeenth century, however, the Italian scientist Francesco Redi (1626–1697) noticed and described the different developmental forms of flies. Redi observed that tiny wormlike maggots turned into sturdy oval cases, from which flies eventually emerge. He also observed that maggots seemed to appear where adult flies had previously landed. These observations led him to question the commonly held belief that flies were generated spontaneously from rotting meat.

Figure 14-1 shows an experiment that Redi conducted in 1668 to test his hypothesis that meat kept away from adult flies would

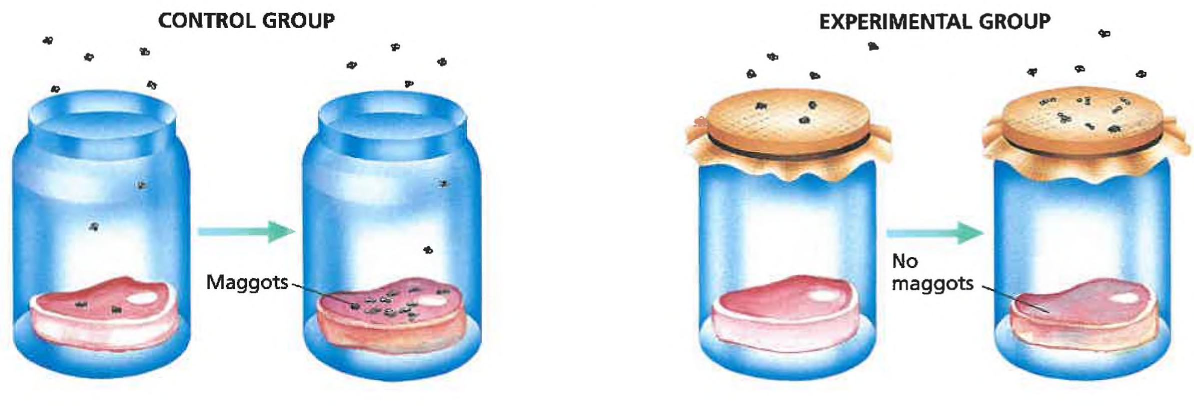


FIGURE 14-1
In Redi's experiment, maggots were found only in the control jars because that was the only place where adult flies could reach the meat to lay eggs.

remain free of maggots. The experimental group consisted of netting-covered jars that contained meat. The control group consisted of uncovered jars that also contained meat. The netting allowed air to enter and prevented flies from landing on the meat. After a few days, maggots swarmed over the meat in the open jars, while the net-covered jars remained free of maggots. Redi's experiment showed convincingly that flies come only from eggs laid by other flies. Redi's hypothesis was confirmed, and a major blow was struck against the hypothesis of spontaneous generation.

SPALLANZANI'S EXPERIMENT

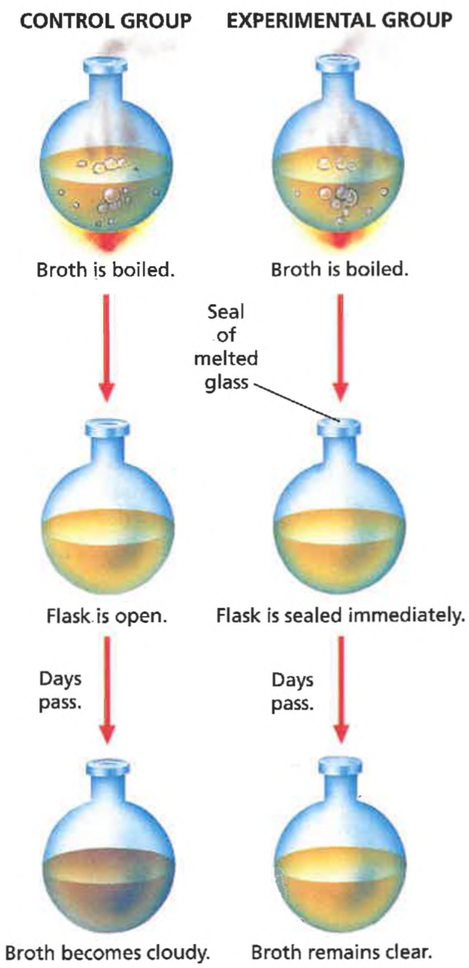
At about the same time that Redi carried out his experiment, other scientists began using a new tool—the microscope. Their observations with the microscope revealed that the world is teeming with tiny creatures. They discovered that microorganisms are simple in structure and amazingly numerous and widespread. Many investigators at the time thus concluded that microorganisms arise spontaneously from a "vital force" in the air.

In the 1700s, another Italian scientist, Lazzaro Spallanzani (1729–1799), designed an experiment to test the hypothesis of spontaneous generation of microorganisms, as shown in Figure 14-2. Spallanzani hypothesized that microorganisms formed not from air but from other microorganisms. He knew that microorganisms grew easily in food. Therefore, he decided to test their growth in meat broth. Spallanzani reasoned that boiling broth in a flask would kill all the microorganisms in the broth, on the inside of the glass, and in the air in the flask. For his experimental group, Spallanzani boiled clear, fresh broth until the flasks filled with steam. He then sealed the flasks by melting their glass necks closed while the broth was hot. The control-group flasks of broth were left open. The broth in the sealed flasks remained clear and free of microorganisms, while that in the open flasks became cloudy due to contamination with microorganisms.

Spallanzani concluded that the boiled broth became contaminated only when microorganisms from the air entered the flask. Spallanzani's opponents, however, objected to his method and disagreed with his conclusions. They claimed that Spallanzani had heated the experimental flasks too long, destroying the "vital force" in the air inside them. Air lacking this "vital force," they claimed, could not generate life. Thus, those who believed in spontaneous generation of microorganisms kept the idea alive for another century.

FIGURE 14-2

In Spallanzani's experiment, he boiled meat broth in open flasks. Then he sealed the flasks of the experimental group by melting the glass necks of the flasks closed. The broth inside remained uncontaminated by microorganisms.



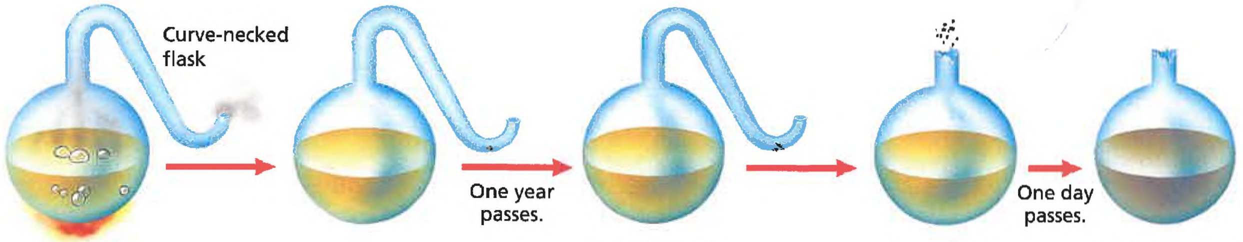


FIGURE 14-3

In Pasteur's experiment, a flask with a curved but open neck prevented microorganisms from entering. Broth boiled in the flasks became contaminated by microorganisms only when the curved necks were removed from the flasks.

PASTEUR'S EXPERIMENT

By the mid-1800s the controversy over spontaneous generation had grown fierce. The Paris Academy of Science offered a prize to anyone who could clear up the issue once and for all. The winner of the prize was the French scientist Louis Pasteur (1822–1895).

Figure 14-3 shows how Pasteur set up his prize-winning experiment. To answer objections to Spallanzani's experiment, Pasteur made a curve-necked flask that allowed the air inside the flask to mix with air outside the flask. The curve in the neck of the flask prevented solid particles, such as microorganisms, from entering the body of the flask. Broth boiled inside the experimental curve-necked flasks remained clear for up to a year. But when Pasteur broke off the curved necks, the broth became cloudy and contaminated with microorganisms within a day. Pasteur reasoned that the contamination was due to microorganisms in the air.

Those who had believed in the spontaneous generation of microorganisms gave up their fight. With Pasteur's experiment, the principle of biogenesis became a cornerstone of biology.

Word Roots and Origins

biogenesis

from the Greek *bioun,* meaning "to live," and *gignesthai,* meaning "to be born"

SECTION 14-1 REVIEW

1. What does the term *spontaneous generation* mean?
2. Explain how Redi's experiment disproved the hypothesis of spontaneous generation in flies.
3. What caused people to think there was a "vital force" in the air that produced living organisms?
4. Did Spallanzani's experiment disprove the hypothesis that microorganisms could arise spontaneously from a "vital force" contained in the air? Explain why Spallanzani's procedure did or did not disprove such a possibility.
5. In conducting his experiment, Spallanzani demonstrated a technique that would become universally used in the preservation of food. What was this technique?
6. **CRITICAL THINKING** What would have happened if Pasteur had tipped one of his flasks so that the broth in the flask came into contact with the curve of the neck? Explain how this result would or would not have supported his conclusion.

SECTION

14-2

OBJECTIVES

▲ Outline the modern scientific understanding of the formation of Earth.

● Summarize the concept of *half-life.*

■ Describe the production of organic compounds in the Miller-Urey apparatus.

◆ Summarize the possible importance of cell-like structures produced in the laboratory.

EARTH'S HISTORY

The phylogenetic tree of all living things is a history of cell-based life. Cells may evolve and change, but new cells always arise from existing cells. How, then, did the first cells originate? Using models thought to approximate the conditions found on early Earth, scientists attempt to reconstruct the processes that gave rise to the first cellular life.

THE FORMATION OF EARTH

Evidence from computer models of the sun suggests that about 5 billion years ago, our solar system was a swirling mass of gas and dust, as shown in Figure 14-4. Over time, most of this material collapsed inward, forming the sun. The remaining gas, dust, and debris circled the young sun. The planets are thought to have been formed from repeated violent collisions of this space debris. During its 400-million-year-long period of formation, Earth grew increasingly large as it was bombarded by debris. These collisions not only added to Earth's mass but also released a great deal of thermal energy. Each collision between the young and growing Earth and a large piece of space debris, for example, would have released enough energy to melt the entire surface of Earth.

Earth's Age

The estimated age of Earth, more than 4 billion years, is about 700,000 times as long as the period of recorded history. It is about 50 million times as long as an average human life span. How can we determine what happened so long ago? Scientists have drilled deep into Earth and examined its many layers to establish a fairly complete picture of its geologic history. Early estimates of Earth's age were made from studying layers of sediment in Earth's crust. The age of Earth could not be estimated accurately, however, until the middle of the twentieth century, when modern methods of establishing the age of materials were developed.

Radioactive Dating

Methods of establishing the age of materials include the techniques known as **radioactive dating.** Recall from Chapter 2 that the atomic number of an element is the number of protons in the nucleus. All atoms of an element have the same atomic number, but their number of neutrons can vary. Atoms of the same element that differ in the number of neutrons they contain are called **isotopes**

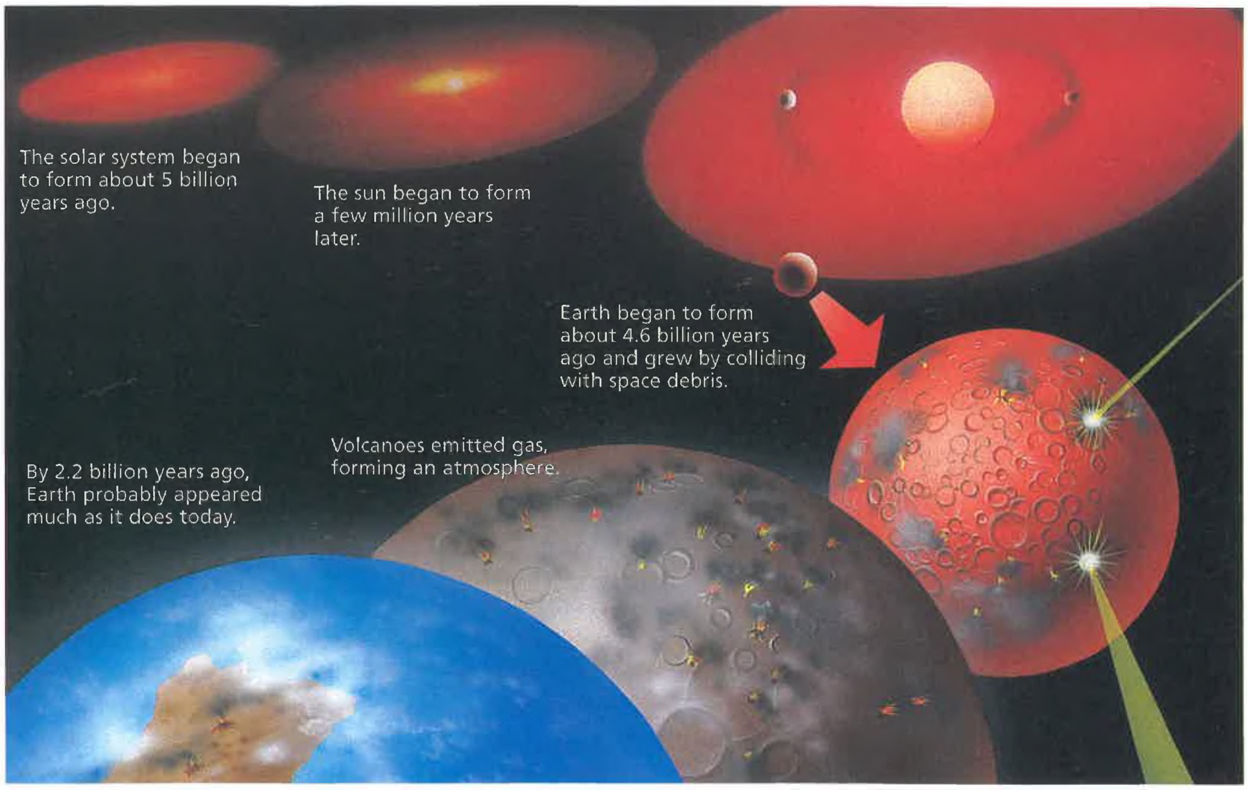


FIGURE 14-4
It took about one-half of a billion years for modern Earth to form from a swirling mass of gases.

(IE-suh-TOHPS). Most elements have several isotopes. The **mass number** of an isotope is the total number of protons and neutrons in the nucleus. The mass number of the most common carbon isotope is 12. If you recall that the atomic number of carbon is 6, you can calculate that this carbon isotope has six protons and six neutrons. Isotopes are designated by their chemical name followed by their mass number; for example, carbon exists as both *carbon-12* and *carbon-14*.

Some isotopes have unstable nuclei, which tend to undergo **radioactive decay;** that is, their nuclei tend to release particles or radiant energy, or both. Such isotopes are called **radioactive isotopes.** Rates of decay of radioactive isotopes have been determined for many isotopes. The length of time it takes for one-half of any size sample of an isotope to decay is called its **half-life.** Depending on the isotope, half-lives vary from a fraction of a second to billions of years.

The age of a material can be determined by measuring the amount of a particular radioactive isotope it contains. This quantity is compared with the amount of some other substance in the fossil that remains constant over time. For example, relatively young fossils can be dated by measuring the ratio of the amount of carbon-14, a radioactive isotope, to the amount of a stable isotope, carbon-12. Living things take carbon into their bodies constantly. Most of the carbon is in the form of carbon-12. A very small proportion of it, however, is in the form of carbon-14, which undergoes decay. This ratio of carbon-14 to carbon-12 is a known quantity for

Word Roots and Origins

isotope

from the Greek *iso,* meaning "equal," and *topos,* meaning "place" internet**connect**

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TABLE 14-1 Some Isotopes Used in Radioactive Dating

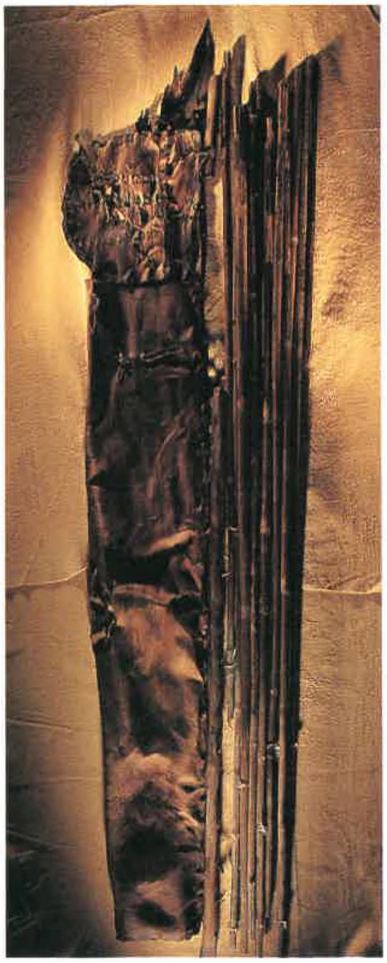
Isotope	Half-life
Carbon-14	5,730 y
Thorium-230	75,000 y
Potassium-40	1,300,000,000 y
Uranium-238	4,500,000,000 y

living organisms. When an organism dies, its uptake of carbon stops, and decay of the existing carbon-14 continues. Thus, over time, the amount of carbon-14 declines with respect to the amount of the stable carbon-12. After 5,730 years, half of the carbon-14 in a sample will have decayed. After another 5,730 years, half of the remaining carbon-14 in the sample likewise will have decayed. Use of carbon-14 dating is limited to organic remains less than about 60,000 years old, like the leather quiver and wooden bow and arrows shown in Figure 14-5. Isotopes with longer half-lives are used to date older fossils and rocks. Some of the isotopes commonly used in radioactive dating procedures appear in Table 14-1.

Scientists have estimated Earth's age by using a dating method that is based on the decay of uranium and thorium isotopes in rock crystals. Collisions between Earth and large pieces of space debris probably caused the surface of Earth to melt many times as the planet was formed. Therefore, the age of the oldest unmelted surface rock should tell us when these collisions stopped and the cooling of Earth's surface began. Scientists have found zircon crystals that are 4.2 billion years old. We can infer that organic molecules could have survived and begun to accumulate sometime after this.

FIGURE 14-5

This deerskin quiver, with a wooden bow and arrows, is about 3,000 years old. Carbon-14 dating methods can be used for organic materials less than 60,000 years old.



THE FIRST ORGANIC COMPOUNDS

All of the elements found in organic compounds are thought to have existed on Earth and in the rest of the solar system when the Earth formed. But how and where were these elements assembled into the organic compounds found in life? One of the most popular hypotheses proposed to solve this puzzle was developed by the Soviet scientist Alexander I. Oparin in 1923. Oparin (1894–1980) suggested that the atmosphere of the primitive Earth was very different from that of today. Oparin thought the early atmosphere contained ammonia, NH_3; hydrogen gas, H_2; water vapor, H_2O; and compounds made of hydrogen and carbon, such as methane, CH_4. At temperatures well above the boiling point of water, these gases might have formed simple organic compounds, such as amino acids. According to Oparin, when Earth cooled and water vapor condensed to form lakes and seas, these simple organic compounds would have collected in the water. Over time these compounds could have entered complex chemical reactions, fueled by energy from lightning and ultraviolet radiation. These reactions, Oparin reasoned, ultimately would have resulted in the macromolecules essential to life, such as proteins.

The Experimental Synthesis of Organic Compounds

Oparin carefully developed his hypotheses, but he did not perform experiments to test them. So in 1953, an American graduate student, Stanley L. Miller (1930–), and his professor, Harold C. Urey (1893–1981), set up an experiment using Oparin's hypotheses as a starting point. Their apparatus, illustrated in Figure 14-6, included a chamber containing the gases Oparin assumed were present in the young Earth's atmosphere. As the gases circulated in the chamber, electric sparks, substituting for lightning, supplied energy to drive chemical reactions. The Miller-Urey experiment, and other variations that have followed, produced a variety of organic compounds, including amino acids.

Since the 1950s, scientists have continued to explore the origin of simple organic compounds. Their experiments have produced a variety of compounds, including various amino acids, ATP, and the nucleotides in DNA. Such results suggest many ways that vital organic compounds might have formed on the young Earth.

In recent years, new hypotheses regarding early Earth's atmosphere have been proposed by investigators who study planet formation. In contrast to Oparin's hypotheses, it has been suggested that the atmosphere of early Earth was composed largely of carbon dioxide, CO_2; nitrogen, N_2; and water vapor, H_2O. Laboratory simulations of these atmospheric conditions have shown that both carbon dioxide and oxygen gas interfere with the production of organic compounds. Therefore, it is thought that conditions in areas protected from the atmosphere, such as those that exist in undersea hot springs, might have favored the production of organic compounds.

Organic Compounds from Beyond Earth

Recently, a broad mixture of organic compounds was found in a newly fallen meteorite that was recovered before it was contaminated with organic compounds from Earth. These compounds, which had not been destroyed by heat as the meteoroid entered Earth's atmosphere, must have formed in space. Some scientists hypothesize that after the period of Earth's formation, some organic compounds may have accumulated on the surface of Earth in this way, carried by space debris rather than originating here.

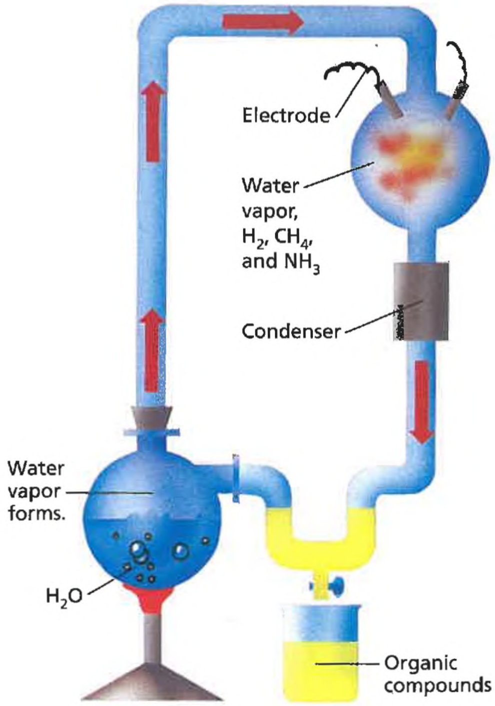


FIGURE 14-6
Miller and Urey's apparatus was a model for the atmospheric and temperature conditions of early Earth.

Quick Lab

Inferring Probability

Materials 3 × 5 in. cards (12) labeled with organic compounds

Procedure

1. Deal three cards, and try to make one of the following combinations: $NH_2–CH_2–COOH$, $CH_3–COOH$, or $CH_3–CH_2–COOH$. Each of these combinations represents an organic molecule.
2. Record your results. Replace the dealt cards in the set and shuffle the cards. Repeat the procedure 19 times.
3. Count the number of molecules you were able to form. Then calculate the probability of forming a molecule with each deal.

Analysis How can you compare a simple game of chance to the synthesis of organic compounds?

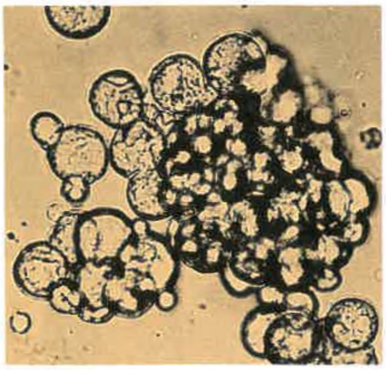


FIGURE 14-7

Membrane-bound structures, such as these, have been formed in the laboratory under conditions that may have existed on early Earth. Structures such as these may have enclosed replicating molecules of RNA and may have been the forerunners of the first cells.

FROM MOLECULES TO CELL-LIKE STRUCTURES

Sidney Fox (1912–) and others have done extensive research on the physical structures that may have given rise to the first cells. These cell-like structures, like the ones shown in Figure 14-7, form spontaneously in the laboratory from solutions of simple organic chemicals. The structures include **microspheres,** which are spherical in shape and are composed of many protein molecules that are organized as a membrane, and **coacervates** (coh-AS-uhr-vayts), which are collections of droplets that are composed of molecules of different types, including linked amino acids and sugars.

For many years, it had been assumed that all cell structures and the chemical reactions of life required enzymes that were specified by the genetic information of the cell. Both coacervates and microspheres, however, can form spontaneously under certain conditions. For example, the polymers that form microspheres can arise when solutions of simple organic chemicals are dripped onto the surface of hot clay. The heat vaporizes the water, encouraging polymerization. Coacervates and microspheres have a number of lifelike properties, including the ability to take up certain substances from their surroundings. Coacervates can grow, and microspheres can bud to form smaller microspheres. These properties of coacervates and microspheres show that some important aspects of cellular life can arise without direction from genes. Thus, these studies suggest that the gap between the nonliving chemical compounds and cellular life may not be quite as wide as previously thought.

When considering the evolution of cells from simpler structures, it is important to remember that microspheres and coacervates could not have responded to natural selection. Recall from Chapter 1 that natural selection is an important driving force of evolution—which is descent with modification, or change over generations. The laboratory-produced cell-like structures do not have hereditary characteristics. Thus, although these cell-like structures have some of the properties of life, they are not alive because they do not have heredity.

SECTION 14-2 REVIEW

1. The oldest rocks on Earth date from about 4.2 billion years ago. What does this suggest about the interval between 4.6 billion years ago, when the Earth started to form, and 4.2 billion years ago?
2. If a radioactive isotope had a half-life of 1 billion years, how much of it would be left after each of the following intervals of time: 1 billion years, 2 billion years, 3 billion years, and 4 billion years.
3. What are two possible sources of simple organic compounds on the early Earth?
4. What was Oparin's hypothesis, and how was it tested?
5. What properties do microspheres and coacervates share with cells?
6. CRITICAL THINKING Some radioactive isotopes that are used in medicine as tracers in the bloodstream have very short half-lives, often only a few years or less, rather than thousands of years. Would these isotopes also be useful in dating fossils? Why or why not?

THE FIRST LIFE-FORMS

SECTION

14-3

OBJECTIVES

▲ Explain the importance of the chemistry of RNA in relation to the origin of life.

● List three inferred characteristics that describe the first forms of cellular life on Earth.

■ Name two types of autotrophy and explain the difference between them.

◆ Explain how photosynthesis and aerobic respiration are thought to be related.

▲ Define *endosymbiosis,* and explain why it is important in the history of eukaryotes.

A remote and desolate corner of Australia was nicknamed the North Pole by disappointed gold prospectors in the 1800s. But this region has been a "gold mine" after all for twentieth-century scientists. It was there that the oldest known cellular fossils—3.5-billion-year-old traces of early unicellular organisms—were found.

THE ORIGIN OF HEREDITY

Chapter 10 provides a detailed explanation of how hereditary information affects the phenotype of cells. Recall that the hereditary information contained in a DNA molecule is first transcribed into an RNA message, and then the RNA message is translated into a protein, as shown in Figure 14-8. Thus, DNA serves as the template for RNA, which in turn serves as the template for specific proteins.

In recent years, scientists have taken a closer look at the DNA-RNA-protein sequence. Why is RNA necessary for this process? Why doesn't DNA, which is a template itself, carry out protein synthesis directly? The clues to a more complete understanding of RNA function may be found in its shape. Unlike DNA, RNA molecules can take on a great variety of shapes, for example, the t shape of transfer RNA, shown in Figure 14-8. These shapes are dictated by hydrogen bonds between particular nucleotides in an RNA molecule, much as the shapes of proteins depend on hydrogen bonds between particular amino acids. These questions and observations led to the speculation that some RNA molecules might actually behave like proteins and catalyze chemical reactions.

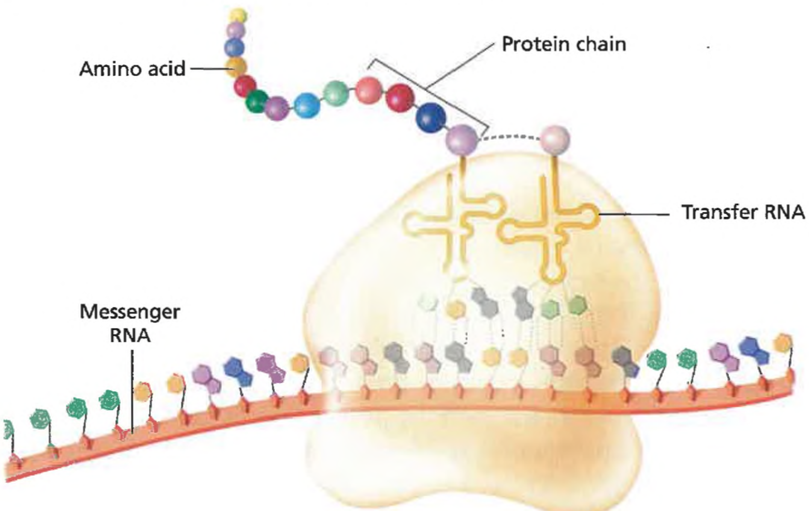


FIGURE 14-8

Messenger RNA is transcribed from a DNA template. Transfer RNA translates the three-base codons in the mRNA, assembling a protein from the specified amino acids.

Eco Connection

Archaebacteria

Some species of archaebacteria, such as *Methanosarcina barkeri* pictured in Figure 14-9, are referred to as methanogens. Within these bacteria, hydrogen gas reacts with carbon dioxide to produce methane, a simple carbon compound. Methanogens are poisoned by oxygen, but they can live in watery environments where other bacteria have consumed all free oxygen, such as in swamps and even the intestines of animals.

Methanogens may prove useful to humans in two significant ways: they are currently used in the cleanup of organic waste, such as sewage, and they may eventually be harnessed for large-scale production of methane for use as a fuel source.

Other species of archaebacteria are being used in the cleanup of petroleum spills into soil, such as occur when underground gasoline tanks develop leaks. This technique, called bioremediation, often relies on bacteria already present in the soil. These bacteria are activated by application of nutrient-rich solutions formulated to their taste. As the bacteria multiply, they metabolize petroleum, releasing harmless byproducts.

THE ROLES OF RNA

In the early 1980s, researcher Thomas Cech (1947–) found that a type of RNA found in some unicellular eukaryotes is able to act as an enzyme. Cech used the term **ribozyme** (RIE-boh-ziem) for an RNA molecule that can act as an enzyme and promote a specific chemical reaction. Hypothetically, a ribozyme could act as an enzyme *and* have the ability to replicate itself.

Recent studies based on Cech's discovery have indicated that life may have started with self-replicating molecules of RNA. RNA molecules would have heredity and would be able to respond to natural selection and thus evolve. How could a single molecule respond to natural selection? Replication—or reproduction of the RNA molecule—might involve competing with other similar, but not identical, RNA molecules for a fixed number of available nucleotides. An RNA molecule that is more successful in getting nucleotides from its environment has an advantage over other RNA molecules. This advantage would then be passed on to the "offspring" of the RNA molecules, the new RNA molecules created by replication.

Since Cech's discovery, other ribozymal activities have been discovered, and it is clear that RNA plays a vital role in DNA replication, protein synthesis, RNA processing, and other basic biochemistry. Perhaps most or all of the chemistry and genetics of early cells were based on RNA.

As exciting as these discoveries have been, there are several questions left unanswered. For one thing, investigators still have not made or found a ribozyme capable of producing other ribozymes. Moreover, it is unclear how such RNA molecules could have evolved into cellular life. Perhaps self-replicating molecules of RNA started to evolve inside cell-like structures similar to microspheres or coacervates. If these RNA molecules were able to alter the phenotype of the cell-like structure that carried them, cellular life could have begun. The self-replicating RNA would have provided the hereditary information that the cell-like structures lack.

THE FIRST PROKARYOTES

What clues do we have about the nature of the first cellular life? When the first organisms arose, there was little or no oxygen gas in existence. Thus, the first cells must have been anaerobic. The small size of the oldest of the microfossils indicates that these early cells were prokaryotes. These cells probably were heterotrophs taking in organic molecules from their environment.

We can reason that a growing population of heterotrophs that depended on spontaneously formed organic molecules for food

Word Roots and Origins

archaebacteria

from the Greek *arche,* meaning "the beginning," and *bactron,* meaning "a staff" eventually would have removed most of these molecules from the environment. At this point, there would have been strong environmental pressure for autotrophs to evolve. These first autotrophs, however, probably did not depend on photosynthesis the way that most autotrophs do today.

Chemosynthesis

If we look for living organisms that may be similar to these early organisms, we find the **archaebacteria** (AR-kuh-bak-TIR-ee-uh). The archaebacteria constitute a kingdom of unicellular organisms, many of which thrive under extremely harsh environmental conditions. *Methanosarcina barkeri,* the archaebacterium shown in Figure 14-9, lives in anaerobic marine sediments. Many species of archaebacteria are autotrophs that obtain energy by chemosynthesis (KEE-moh-SIN-thuh-sis) instead of photosynthesis. In the process of **chemosynthesis,** CO_2 serves as a carbon source for the assembly of organic molecules. Energy is obtained from the oxidation of various inorganic substances, such as sulfur.

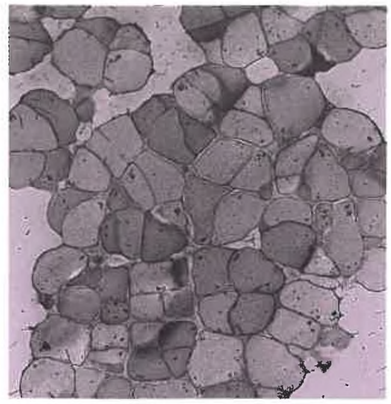


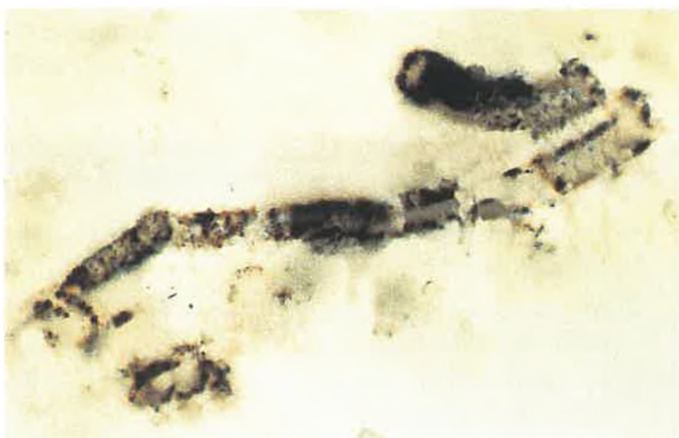
FIGURE 14-9
This archaebacterium species, *Methanosarcina barkeri,* produces methane during metabolism. Archaebacteria are thought to be similar to the types of cellular life that first populated Earth about 4 billion years ago.

Photosynthesis and Aerobic Respiration

Oxygen, a byproduct of photosynthesis, was damaging to many early unicellular organisms. Oxygen could destroy some coenzymes essential to cell function. Within some organisms, however, oxygen bonded to other compounds, thereby preventing the oxygen from doing damage. This bonding was one of the first steps in aerobic respiration. Thus, an early function of aerobic respiration may have been to prevent the destruction of essential organic compounds by oxygen.

Some forms of life had become photosynthetic by 3 billion years ago. In the mid-1990s, scientists discovered traces of carbon in geological formations off the coast of Greenland. These traces were likely left by some type of photosynthetic organism more than 3.8 billion years ago. The 3.5-billion-year-old microfossils found in Australia, shown in figure 14-10, are probably of photosynthetic unicellular organisms that are related to modern **cyanobacteria** (SIE-uh-no-bak-TIR-ee-uh), a group of photosynthetic unicellular prokaryotes.

FIGURE 14-10
These filament-shaped microfossils from the Fig Tree Chert formation in northern Australia represent the oldest-known cellular life. These organisms lived 3.5 billion years ago.



It took a billion years or more for oxygen gas levels to reach today's levels. The oxygen, O_2, eventually reached the upper part of the atmosphere, where it was bombarded with sunlight. Some wavelengths of sunlight can split O_2 to form highly reactive single oxygen atoms, O. These react with O_2 and form **ozone,** O_3. Ozone is poisonous to both plant and animal life, but in the upper atmosphere, a layer of ozone absorbs intense ultraviolet radiation from the sun. Ultraviolet radiation damages DNA, and without the protection of the ozone layer, life could not have come to exist on land.

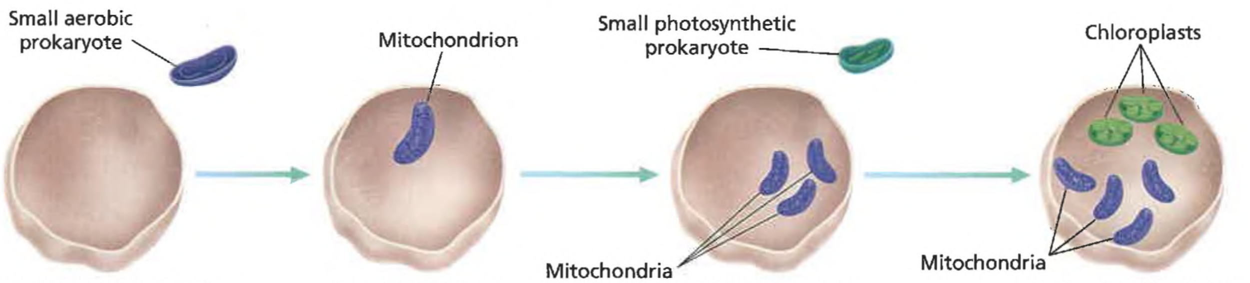


FIGURE 14-11

According to the hypothesis of endosymbiosis, large prokaryotic, unicellular organisms were invaded by smaller prokaryotic, unicellular organisms. These smaller organisms eventually gave rise to modern mitochondria and chloroplasts, which carry their own DNA and replicate independently from the rest of the cell that contains them.

THE FIRST EUKARYOTES

Recall from Chapter 4 that eukaryotic cells differ from prokaryotic cells in several ways. Eukaryotic cells are larger, their DNA is organized into chromosomes in a cell nucleus, and they contain membrane-bound organelles. How did such a complex type of cell evolve from the simple prokaryotes? A large body of evidence now suggests that between about 2.0 and 1.5 billion years ago, a type of small aerobic prokaryote entered and began to live and reproduce *inside* larger, anaerobic prokaryotes. Researcher Lynn Margulis (1938–) has proposed that what may have started as an invasion became a successful, mutually beneficial relationship—called **endosymbiosis** (EN-doh-sim-bee-OH-sis), shown in Figure 14-11. It is thought that the aerobic prokaryote eventually gave rise to modern mitochondria, which are the site of aerobic respiration in eukaryotic cells.

Sometime later, there was a second successful invasion of pre-eukaryotic cells. This time, the invader was a relative of modern photosynthetic cyanobacteria. These invaders eventually gave rise to chloroplasts, the sites of photosynthesis. There is compelling evidence to support this hypothesis of eukaryotic evolution. Both chloroplasts and mitochondria replicate independently from the replication cycle of the cell that contains them. Moreover, chloroplasts and mitochondria contain some of their own genes, which are different from those of the rest of the cell. These genes are found in the organelles themselves, in a circular piece of DNA, an arrangement characteristic of prokaryotic, though not eukaryotic, DNA.

SECTION 14-3 REVIEW

1. **Why do different molecules of RNA assume many different shapes?**
2. **Why do scientists think the first forms of life on Earth were anaerobic?**
3. **How might aerobic respiration have protected early cells from damage?**
4. **What evidence supports the hypothesis that mitochondria were once free-living prokaryotic cells?**
5. **Explain how the first eukaryotes may have evolved.**
6. **CRITICAL THINKING Some forms of air pollution damage Earth's ozone layer. How might such damage affect life?**

CHAPTER 14 REVIEW

SUMMARY/VOCABULARY

14-1

- Before the 1600s, it was generally thought that organisms could arise from nonliving material by spontaneous generation.
- Redi showed in 1668 that rotting meat kept away from flies would not produce new flies. Maggots appeared only on meat that had been exposed to flies.
- Spallanzani showed in the 1700s that microorganisms would not grow in broth when its container was heated and then sealed. This seemed to indicate that microorganisms that cause food spoilage do not arise from spontaneous generation but, rather, are carried in the air.
- Pasteur used a variation of Spallanzani's design to prove that microorganisms are carried in the air and do not arise by spontaneous generation.

Vocabulary

biogenesis (261)
spontaneous generation (261)

14-2

- Earth is thought to have been formed by repeated collisions of debris moving through space.
- The mass number of an element is the total number of protons and neutrons in the nucleus. The number of neutrons in atoms of an element can vary. Atoms with varying numbers of neutrons are called isotopes.
- An isotope's half-life is the time it takes for one-half of a sample of the isotope to decay.
- The ages of objects like fossils and rocks can be determined by measuring the amount of radioactive decay that has occurred in radioactive isotopes found in the sample.
- The first simple organic compounds may have been formed at high temperatures on early Earth in an atmosphere of ammonia, hydrogen gas, and water vapor.
- Macromolecules important to life may have been assembled from simple organic compounds. Lightning may have supplied the energy for these chemical reactions.
- Some organic compounds may have been deposited on Earth by meteorites.
- Cell-like structures, including microspheres and coacervates, form spontaneously in certain kinds of solutions. These structures do not show heredity.

Vocabulary

coacervate (268)
half-life (265)
isotope (264)
mass number (265)
microsphere (268)
radioactive dating (264)
radioactive decay (265)
radioactive isotope (265)

14-3

- In addition to its role as a template for protein assembly, some RNA molecules can act as enzymes.
- The first molecule that held hereditary information may have been RNA rather than DNA.
- RNA can assume different shapes, much as proteins do. These shapes depend on areas of attraction between the RNA nucleotides.
- The first cells that formed on Earth were probably heterotrophic prokaryotes.
- The first autotrophic cells probably used chemosynthesis to make food.
- An important initial function of aerobic respiration may have been to bind oxygen and prevent it from doing damage to early organisms.
- Eukaryotic cells may have evolved from large prokaryotic cells that were invaded by smaller prokaryotic cells. These small prokaryotic invaders may have been the ancestors of organelles, including mitochondria and chloroplasts.

Vocabulary

archaebacteria (271)
chemosynthesis (271)
cyanobacteria (271)
endosymbiosis (272)
ozone (271)
ribozyme (270)

REVIEW

Vocabulary

1. Explain the difference between biogenesis and spontaneous generation.
2. What is the relationship between radioactive decay and the half-life of an isotope?
3. Name two nonliving, cell-like structures that can form in certain solutions.
4. How is a ribozyme like an enzyme?
5. What is photosynthesis. What is chemosynthesis?

Multiple Choice

6. In the seventeenth and eighteenth centuries, the hypothesis of spontaneous generation was used to explain (a) how new life started (b) how simple organic compounds formed (c) how coacervates and microspheres formed (d) how eukaryotes evolved.
7. Redi's experiment was important because it showed that (a) maggots give rise to microorganisms (b) flies swarm on rotting meat (c) flies do not form from rotting meat (d) air contains a "vital force."
8. People objected to Spallanzani's experiment because he (a) used an open jar of meat as a control (b) boiled his flasks of broth for a long time (c) drew the necks of his flasks into a curved shape (d) did not have a control group.
9. The neck of Pasteur's flasks (a) allowed both air and particles to enter the flask (b) allowed air to enter the flask but kept particles out (c) allowed particles to enter but kept air out (d) kept both air and particles out.
10. During the first half-billion years of its existence, Earth and the other planets of the solar system grew by a process involving (a) the synthesis of organic molecules (b) collisions with space debris (c) flames from the sun (d) tidal forces generated on the moon.
11. The oldest fossil of cellular life found on Earth is (a) about 4.6 billion years old (b) about 4.2 billion years old (c) about 3.5 billion years old (d) less than 2 billion years old.
12. Coacervates and microspheres cannot evolve because they have no (a) genetic information (b) cell membrane (c) complex organic molecules (d) fluid in their interior.
13. Miller and Urey's experiment (a) proved Oparin's hypothesis about the origin of life (b) disproved Oparin's hypothesis about the origin of organic molecules (c) provided support for Oparin's hypothesis about the origin of organic molecules (d) is irrelevant to any hypothesis regarding the origin of life.
14. Coacervates and microspheres are (a) collections of organic molecules enclosed within a boundary (b) identical to the first forms of life (c) the oldest microfossils (d) new forms of bacteria.
15. The generation of organisms from nonliving material does not occur today mostly because (a) the presence of oxygen in the atmosphere prevents organic compounds from forming spontaneously (b) coacervates and microspheres take up all the extra nutrients on Earth (c) coacervates and microspheres cannot form today (d) there is not enough energy to drive the chemical reactions needed to form the complex organic compounds necessary for life.

Short Answer

16. Explain the role of the gases CH_4, H_2, and NH_3 and the role of the electric spark in the apparatus shown.

17. Why did the theory of biogenesis pose a dilemma regarding the origin of life?
18. What modern organisms are thought to be most like the first life-forms on Earth?
19. What environmental factors probably favored the evolution of autotrophs?
20. Organic compounds will not form in the Miller-Urey apparatus if O_2 is present. Why is this not a serious problem for scientists who study the origin of life?
21. How might the bonding of oxygen gas have served evolving organisms?
22. How did the formation of the ozone layer permit organisms to colonize land?
23. What energy sources do some nonphotosynthetic autotrophs use?
24. Why have many scientists who investigate the origin of life focused on RNA chemistry?
25. What problems remain with the hypothesis that ribozymes or similar molecules may have been the first self-replicating structures?

CRITICAL THINKING

1. People once believed fish could form from the mud in a pond that sometimes dried up. How could you demonstrate that this conclusion is false?
2. According to a recent hypothesis, lightning may not have existed on early Earth. How could you modify the Miller-Urey experiment to reflect this new idea? What sources of energy could you use to replace lightning?
3. RNA is copied the same way that DNA is copied—by base pairing. RNA, unlike double-stranded DNA, exists as a single strand. If a ribozyme is copied, would the copy be another identical ribozyme or something else? If the copy is not identical to the original, how could the original be replicated?
4. The term *chemical evolution* is sometimes applied to the series of events that might have resulted in the spontaneous origin of life. How do the events that are thought to have produced living organic matter from nonliving inorganic matter represent a process of evolution?
5. The graph below represents radioactive decay of an isotope. If the half-life of carbon-14 is 5,730 years, how many years would it take for $7/8$ of the original amount of carbon-14 in a sample to decay?

Amount Remaining of Radioactive Sample

EXTENSION

1. Read "To Hell and Back" in *Discover,* July 1999, on page 76, and answer the following questions: What were some of the extreme conditions in the environment where the microbes lived? What substances besides oxygen do some deep-Earth-dwelling bacteria use for respiration? What precautions were taken to protect the organisms in the rock samples from being poisoned by the surface atmosphere?
2. Investigators studying the atmosphere have observed a large, thin area in the ozone layer above the continent of Antarctica. Use current science magazines to find out about this phenomenon. Present a report to your class summarizing different hypotheses about the causes of this thinning of the ozone layer.

CHAPTER 14 INVESTIGATION

Making Microspheres

OBJECTIVES

- Make microspheres from amino acids by simulating the conditions found on early Earth.
- Compare the structure of microspheres with the structure of living cells.

PROCESS SKILLS

- observing
- comparing and contrasting
- modeling
- relating

MATERIALS

- safety goggles
- lab apron
- heat-protective gloves
- 500 mL beaker
- hot plate
- 125 mL Erlenmeyer flasks, 2
- ring stand with clamp
- balance
- amino acid mixture (of at least six different amino acids)
- glass stirring rod
- tongs
- clock or timer
- 1% sodium chloride (NaCl) solution
- 50 mL graduated cylinder
- dropper
- microscope slide
- coverslip
- compound light microscope
- 1% sodium hydroxide (NaOH) solution

Background

1. Microspheres are very small, spherical vessels that are bounded by a membranelike layer of amino acids. Microspheres can be created in the laboratory under controlled conditions.
2. How do microspheres differ from living cells?
3. How do microspheres resemble living cells?
4. What role might have been played by microspheres or similar structures before life began on Earth?

Procedure

1. Put on safety goggles, a lab apron, and heat-protective gloves before beginning this investigation.
2. CAUTION **Do not plug in or unplug the hot plate with wet hands. Use care to avoid burns when working with the hot plate. Do not touch the hot plate. Use tongs to move heated objects. Turn off the hot plate when not in use.** Fill a 500 mL beaker half full with water, and heat it on a hot plate. You will use the beaker as a hot-water bath. Leave space on the hot plate for a 125 mL Erlenmeyer flask, to be added later.
3. While waiting for the water to boil, clamp a 125 mL Erlenmeyer flask to a ring stand. Add 6 g of the amino acid mixture to the flask.
4. When the water in the beaker begins to boil, move the ring stand carefully so that the flask of amino acids sits in the hot-water bath.
5. When the amino acids have heated for 20 minutes, measure 10 mL of NaCl solution in a graduated cylinder and pour the solution into a second Erlenmeyer flask. Place the second flask on the hot plate beside the hot-water bath.

6. When the NaCl solution begins to boil, use tongs to remove the flask containing the NaCl solution from the hot plate. Then, while holding the flask with tongs, slowly add the NaCl solution to the hot amino acids while stirring.
7. Let this NaCl–amino acid solution boil for 30 seconds.
8. Remove the solution from the water bath, and allow it to cool for 10 minutes.
9. CAUTION **Slides break easily. Use caution when handling them.** Use a dropper to place a drop of the solution on a microscope slide, and cover the drop with a coverslip.
10. Place the slide on the microscope stage. Examine the slide under low power for tiny spherical structures. Then examine the structures under high power. These tiny sphere-shaped objects are microspheres.
11. CAUTION **If you get the sodium hydroxide (NaOH) solution on your skin or clothing, wash it off at the sink while calling to your teacher. If you get the sodium hydroxide solution in your eyes, immediately flush your eyes at the eyewash station while calling to your teacher.** Place a drop of 1% NaOH solution at the edge of the coverslip to raise the pH as you observe the microspheres. What happens?
12. In your lab report, make a table similar to the one shown below. Based on your observations of microspheres and cells, complete your table. Consider the appearance of microspheres and cells, their method of reproduction, their interaction with their environment, and any other characteristics that you observe.
13. Clean up your lab materials and wash your hands before leaving the lab.

Analysis and Conclusions

1. Suggest how the microspheres formed.
2. What did you observe when the pH was raised in step 11?
3. What does this suggest about the relationship of pH to microsphere formation?
4. Compare and contrast microspheres with living cells.
5. What characteristics would microspheres have to exhibit in order to be considered living?
6. How might the conditions you created in the lab be similar to those that are thought to have existed when life first evolved on Earth?
7. Predict what would happen to microspheres if they were placed in hypotonic and hypertonic solutions.

Further Inquiry

1. What do you think would happen if you added too much or too little heat? What happens to proteins at high temperatures? How can you test for the right amount of heat to use?
2. Do you think your microsphere experiment would have worked if you had substituted other amino acids? How can you test your hypothesis?

TABLE A *COMPARING MICROSPHERES WITH CELLS*

Cell-like characteristics	Characteristics that are not cell-like

CHAPTER 15

EVOLUTION: EVIDENCE AND THEORY

Giant tortoises, Geochelone elephantopus, *crowd a puddle on the Galápagos Islands.*

FOCUS CONCEPT: *Evolution*

As you read, note the many lines of evidence that support evolutionary theory.

The Fossil Record

SECTION

15-1

OBJECTIVES

▲ Define *fossil,* and tell how the examination of fossils led to the development of evolutionary theories.

● Explain the law of superposition and its significance to evolutionary theory.

■ Describe how early scientists inferred a succession of life-forms from the fossil record.

◆ Tell how biogeographic observations suggest descent with modification.

Fossil evidence shows a long history of life on Earth. The fossil record shows that forms of organisms appeared, lasted for long periods of time, and then disappeared, only to be followed by newer forms of life that also eventually disappeared. The history of life is one of constant change and a tremendous diversity of life-forms.

NATURE OF FOSSILS

A **fossil** is a trace of a long-dead organism. Fossils are often found in layers of sedimentary rock, which is formed when **sediment,** such as dust, sand, or mud, is deposited by wind or water. Sedimentary fossils usually develop from the hard body parts of an organism, such as the shell, bones, teeth, or, in the case of plants, the woody stem. Over long periods of time, hard minerals replace the tissue of the organism, leaving rocklike structures.

A type of fossil called a **mold** is essentially an imprint in rock in the shape of an organism. Limestone owes its spongelike texture to the many molds scattered throughout its structure. Some molds eventually are filled with hard minerals, forming a **cast,** a rocklike model of the organism.

As you can see in Figure 15-1, many different kinds of fossils have been found. Some fossils are in the form of lacy carbon tracings of a fern, captured for all time on a flat plate of slate. Others, such as the tracks of animals or the fossilized marks on the bones of some human ancestors, are evidence of behavior.

How did people in the past regard these natural curiosities? Perhaps the most widely held view was that fossils were simply a naturally occurring part of rocks. Beginning in the late seventeenth century, however, a flurry of scientific investigation occurred. In

(a) (b)

FIGURE 15-1
There are several different types of fossils. (a) Amber, the fossilized sap of trees, holds well-preserved insects. (b) This fossilized shell is that of a trilobite, *Modocia typicalus,* a dominant life-form in early seas.

1668, Robert Hooke (1635–1703) published his conclusion that fossils are the remains of plants and animals. Hooke was one of the first scientists to study fossils, principally petrified wood, with the aid of a microscope. Hooke thought the detail he saw with the microscope was too fine and precise to have been formed by the rock itself. He hypothesized that living organisms had somehow been turned to rock.

DISTRIBUTION OF FOSSILS

Hooke's view was shared by another scientist of his time, Nicolaus Steno (1638–1686). Steno made an important contribution toward a modern understanding of Earth's geological and biological history. In 1669, he proposed the **law of superposition** (SOO-puhr-puh- ZISH-uhn), which states that successive layers of rock or soil were deposited on top of one another by wind or water. The lowest **stratum,** or layer, in a cross section of Earth is the oldest, while the top stratum

TABLE 15-1 ***Geological History of Earth***

Millions of years ago	Era	Period	Epoch	Organisms
	Cenozoic	Quaternary	Recent	modern humans arise
0.01				
			Pleistocene	humans arise
1.8				
		Tertiary	Pliocene	large carnivores arise
5.3				
			Miocene	mammals diversify
23.8				
			Oligocene	diverse grazing animals arise
33.7				
			Eocene	early horses arise
54.8				
			Paleocene	more modern mammals arise
65				
	Mesozoic	Cretaceous		dinosaurs go extinct; mass extinction
144				
		Jurassic		dinosaurs diversify; birds arise
208				
		Triassic		primitive mammals arise; mass extinction; dinosaurs arise
245				
	Paleozoic	Permian		seed plants arise; reptiles diversify; mass extinction
290				
		Carboniferous		reptiles arise
354				
		Devonian		amphibians arise; mass extinction
417				
		Silurian		land plants arise
443				
		Ordovician		fishes arise; mass extinction
490				
		Cambrian		marine invertebrates arise
540				
	Precambrian			prokaryotes, then eukaryotes arise
4,600				
	Formation of the Earth			

is the most recent. Thus, fossils within a single stratum are of the same approximate age. Using Steno's law, observers could establish the **relative age** of a fossil; that is, they could say that a given fossil was younger or older than another fossil. The fossil's **absolute age** (its age in years) could be estimated from radiological evidence.

Eventually the application of these geologic principles, coupled with modern technological methods, told a compelling story. The history of Earth, as shown in Table 15-1, is more than 100,000 times longer than recorded human history.

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Succession of Forms

Fossil-bearing strata show that species of organisms appeared, existed for a while, and then disappeared, or became **extinct.** In turn, newer species continued to arise. In Table 15-1, notice the order in which different types of organisms arose, beginning with prokaryotes in the Precambrian era. The fossil record indicates that there were several **mass extinctions,** brief periods during which large numbers of species disappeared. Some of these life-forms were unlike any organisms alive today. Look back at Figure 15-1 to see the fossil of a trilobite, which lived during the Paleozoic era. Most trilobite species disappeared during the Permian extinction, 245 million years ago. Mass extinctions probably resulted from drastic changes in the environment, perhaps following periods of volcanic activity or collisions with asteroids. Ash and dust in the atmosphere may have blocked sunlight for long periods of time and caused a decrease in temperatures around the world.

Biogeography

The study of the geographical distribution of fossils and of living organisms is called **biogeography** (BIE-oh-jee-AH-gruh-fee). A comparison of recently formed fossil types with types of living organisms in the same geographic area shows that new organisms arise in areas where similar forms already lived. Thus, armadillos appeared in North and South America, where glyptodonts, shown in Figure 15-2, lived in the past. Modern kangaroos appeared only in Australia, where the now-extinct giant kangaroo had lived.

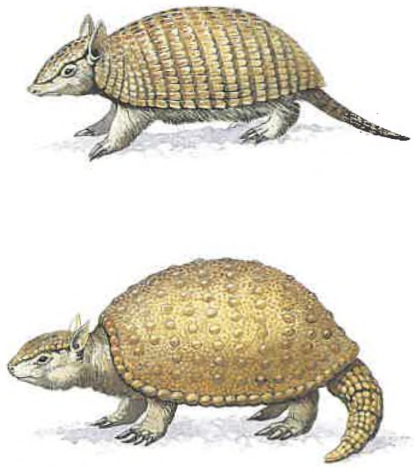


FIGURE 15-2
The modern armadillo (top) resembles the extinct glyptodont (bottom), although the glyptodont was much larger. Life-forms arise in the same areas where similar, older forms once existed.

SECTION 15-1 REVIEW

1. Define the term *fossil,* and name three different kinds of fossils.
2. What was Robert Hooke's contribution to the understanding of fossils?
3. How does the law of superposition allow paleontologists to assign relative ages to fossils?
4. In what geological era did the first organisms arise?
5. How do biogeographic observations suggest that a modification process caused new species to arise?
6. CRITICAL THINKING What can you conclude if you find identical examples of a fossilized organism in two adjacent geologic strata?

Research Notes

Solving the Burgess Puzzle

Were the animals that lived in the seas 550 million years ago, during the Cambrian period, more diverse than those that inhabit modern seas? A small limestone quarry tucked away 800 m above sea level in the Canadian Rocky Mountains is slowly yielding answers to this and other evolutionary puzzles. These rocks, which contain the fossil remains of organisms from a Cambrian sea buried by an ancient mudslide, are known collectively as the Burgess Shale (named for the Burgess Pass, where the quarry was found).

Discovered in 1909 by Charles Doolittle Walcott, head of the Smithsonian Institution at the time, the Burgess fossils remained in museum drawers until 1971, when Cambridge University professor Harry Whittington and two graduate students reexamined them.

Attaching a device known as a *camera lucida* to a microscope, the scientists used mirrors to project enlarged images of the fossils onto a flat surface. Then they carefully made illustrations of the ancient animal forms. In the process, they discovered that they could learn more from the large-scale drawings than they could from the actual tiny specimens.

The very fine-grained silt that surrounded the organisms helped preserve soft tissues in addition to bony structures. Thus, the remains of organisms that might have otherwise remained unknown were preserved. The variety of organisms found in the Burgess Shale is evidence of the explosion of life-forms that took place during the Cambrian period.

The Burgess organisms lived much as organisms do today. They lived in an ecosystem that included a wide range of animals, each with specialized organs for movement and feeding. Many of the organisms were ancestors of common sea creatures such as mollusks, segmented worms, and crustaceans. Whittington's team also discovered fossils of animals that were completely different from any inhabiting modern oceans.

What does this mean? The shale fossils reveal that the earliest multicellular animals included a much broader range of body plans than expected—some so different that they cannot be classified into any group of modern animals.

These conclusions about Cambrian life-forms are supported by recent discoveries in China, Australia, and Greenland. Scientists have unearthed similarly diverse and complex fossils dating back to the beginning of the Cambrian period, 550 million years ago. Thus, it appears that a high level of diversity and complexity developed in animals in a relatively short span of geologic time.

One of the most exciting Burgess finds was the discovery of the 5 cm (2 in.) long Pikaia gracilens. *It is a very early representative of phylum Chordata. Organizationally, it resembles the simple living chordate* Amphioxus.

THEORIES OF EVOLUTION

The word evolution *refers to an orderly succession of changes. Biological evolution is the change of populations of organisms over generations. Early scientists noticed that new life-forms appeared to be modifications of fossil forms found in the same geographical area. This strongly implied that a natural modification process was at work.*

SECTION

15-2

OBJECTIVES

▲ Define *evolution.*

● Explain Lamarck's theory of evolution, and describe how it was flawed.

■ List some of the evidence that led Darwin to his idea of how species might change over time.

◆ Explain Darwin's two major theories.

LAMARCK'S EXPLANATION

The French scientist Jean Baptiste de Lamarck (1744–1829) was one of the first to propose a unifying hypothesis of species modification. Lamarck proposed that similar species descended from a common (the same) ancestor—thus, living species were descended from similar extinct species evident in the fossil record. Lamarck cataloged an extensive collection of invertebrates (animals without a backbone), and he related fossil forms to living animals based on their similar appearance.

To explain how species change, he hypothesized that acquired traits were passed on to offspring. An **acquired trait** is one that is not determined by genes. Instead, it arises during an organism's lifetime as a result of the organism's experience or behavior.

Lamarck made a study of the habits and physiology of shore birds, and he believed that the webbed foot of water birds resulted from repeated stretching of the membrane between the toes. Over time, Lamarck said, this produced a broad webbed foot, a trait that would be preserved by reproduction. In other words, offspring of parents who had acquired webbed feet would have webbed feet as well. In the same way, an organism that did not use some part of its anatomy, such as a tail, would produce offspring with a smaller version of that body part.

Lamarck's hypotheses were fiercely attacked, primarily by scientists who rejected the idea of evolution itself. Although Lamarck's hypothesis of the passage of acquired traits was easily disproved, his work was an important forerunner of modern evolutionary theory. Lamarck was the first to clearly state that types of organisms change over time and that new types of organisms are modified descendants of older types. This idea was presented more convincingly more than 50 years later by Charles Darwin.

FIGURE 15-3

Charles Darwin began the work that would lead to his theory of evolution when he was a young man.

Quick Lab

Analyzing Relationships

Materials set of hardware items, paper, pencil

Procedure

1. Find one object that has characteristics common to all the objects, and place it at the middle of the paper near the bottom. This is the "common ancestor" of all the hardware.
2. Separate the remaining objects into two groups that have a single, basic difference.
3. Form two branches from the common ancestor by arranging the members of each group on the paper. Each of the two branches may then form smaller branches.
4. Draw lines connecting each object to the one above and below it, forming a tree.

Analysis What characteristic did the common ancestor have that made it similar to both groups? What criteria did you use to separate the two groups? What was the trend in the evolution of each group?

THE BEGINNING OF MODERN EVOLUTIONARY THOUGHT

In the mid-1800s, both Charles Darwin (1809–1882) and Alfred Wallace (1823–1913) independently proposed the hypothesis that species were modified by natural selection. In the process of **natural selection,** organisms best suited to their environment reproduce more successfully than other organisms. Thus, over generations, the proportion of organisms with favorable traits increases in a **population,** or interbreeding single-species group. While Darwin and Wallace announced their hypotheses at the same time, Darwin's name became more associated with evolutionary theory after his book *The Origin of Species* was published in 1859.

Charles Darwin

Darwin, shown as a young man in Figure 15-3, was born in 1809, the son of wealthy British physician. Darwin attended medical school at the University of Edinburgh and then enrolled at Cambridge University to study for the clergy. He had little enthusiasm for either course of study. At Cambridge University, a friendship with a professor of botany, John Henslow, awakened Darwin's interest in natural history. In 1831, Darwin sailed on the ship H.M.S. *Beagle.* The *Beagle* was chartered for a five-year mapping and collecting expedition to South America and the South Pacific. Darwin assumed the post of ship naturalist, which required that he collect specimens and keep careful records of his observations.

Voyage of the Beagle

Soon after leaving England, Darwin read a geology book that had been given to him by Henslow. This book, *Principles of Geology,* by Charles Lyell, emphasized the great age of Earth and the principles of **uniformitarianism** (YOON-uh-FORM-uh-TER-ee-uhn-IZ-uhm). The principles of uniformitarianism hold that the geological structure of Earth resulted from cycles of observable processes and that these same processes operate continuously through time. For example, silt is deposited by modern rivers in the same way it was deposited by ancient rivers. Modern volcanoes spew forth lava and ash in the same way those on early Earth did. Lyell's book spurred Darwin's interest in the study of geology, and it allowed him to consider the possibility that the modification of environments might be a very slow process requiring long periods of time. In Chile, Darwin observed the results of an earthquake. The land around a harbor had been lifted more than a meter (3.3 ft). In the nearby Andes Mountains, Darwin observed fossil shells of marine organisms in rock beds about 4,300 m (14,100 ft) above sea level. These observations convinced Darwin that Lyell was correct in saying that geologic changes, such as the elevation of the Andes, required many millions of years. Darwin reasoned that the formation of mountain ranges would slowly change habitats, requiring organisms that

FIGURE 15-4

Darwin spent five years as the ship naturalist on the H.M.S. *Beagle* as the ship sailed around the world.

lived there to adapt to these changes. Furthermore, he reasoned that the pace of those adaptations would be so slow with respect to a human life span that they would be difficult to detect.

During the *Beagle*'s five-year trip, as shown in Figure 15-4, Darwin often left the ship at one port and was picked up months later at another port. During his time on land, Darwin trekked hundreds of kilometers through unmapped regions. He collected many different types of fossils and observed thousands of species of organisms.

Analysis of Darwin's Data

When Darwin returned to England, in October 1836, his collections from the voyage were praised by experts from the scientific community. A bird specialist who studied Darwin's collection of finches from the Galápagos Islands reported that Darwin had collected 13 similar but separate species of finches. Each finch species has a distinctive bill that is specialized for a particular food source. Despite the bill differences, the overwhelming similarities of the Galápagos finches implied that the finches shared a recent common ancestor, meaning they descended from a single species. Over a period of years after returning to England, Darwin analyzed his data. Darwin considered the possibility that all of the islands' finches had descended from a few birds or even a single female that had been blown off course from South America, 1,000 km (620 mi) to the east. Because the Galápagos are geologically young islands (they are about 5 million years old), Darwin assumed that the offspring of the original finches had been adapting to different environments and food sources for a relatively short time. Darwin reasoned, therefore, that over many millions of years, many large differences could accumulate between species.

Publication of *The Origin of Species*

Darwin was forced to abandon his leisurely approach to the review and testing of his hypothesis on natural selection in 1858, when he was approached by a young naturalist, Alfred Wallace. Wallace had been collecting specimens in South America and the Malay Archipelago. Wallace asked Darwin to review his paper outlining the process of evolution by natural selection. This prompted Darwin to finally publish his own work on evolution by natural selection, which he had spent 21 years refining. Darwin's and Wallace's hypotheses were presented side by side to the Linnaean Society of London in 1858. The following year, Darwin published his now-famous book on the subject, *On the Origin of Species by Means of Natural Selection*, commonly known as *The Origin of Species*.

DARWIN'S THEORIES

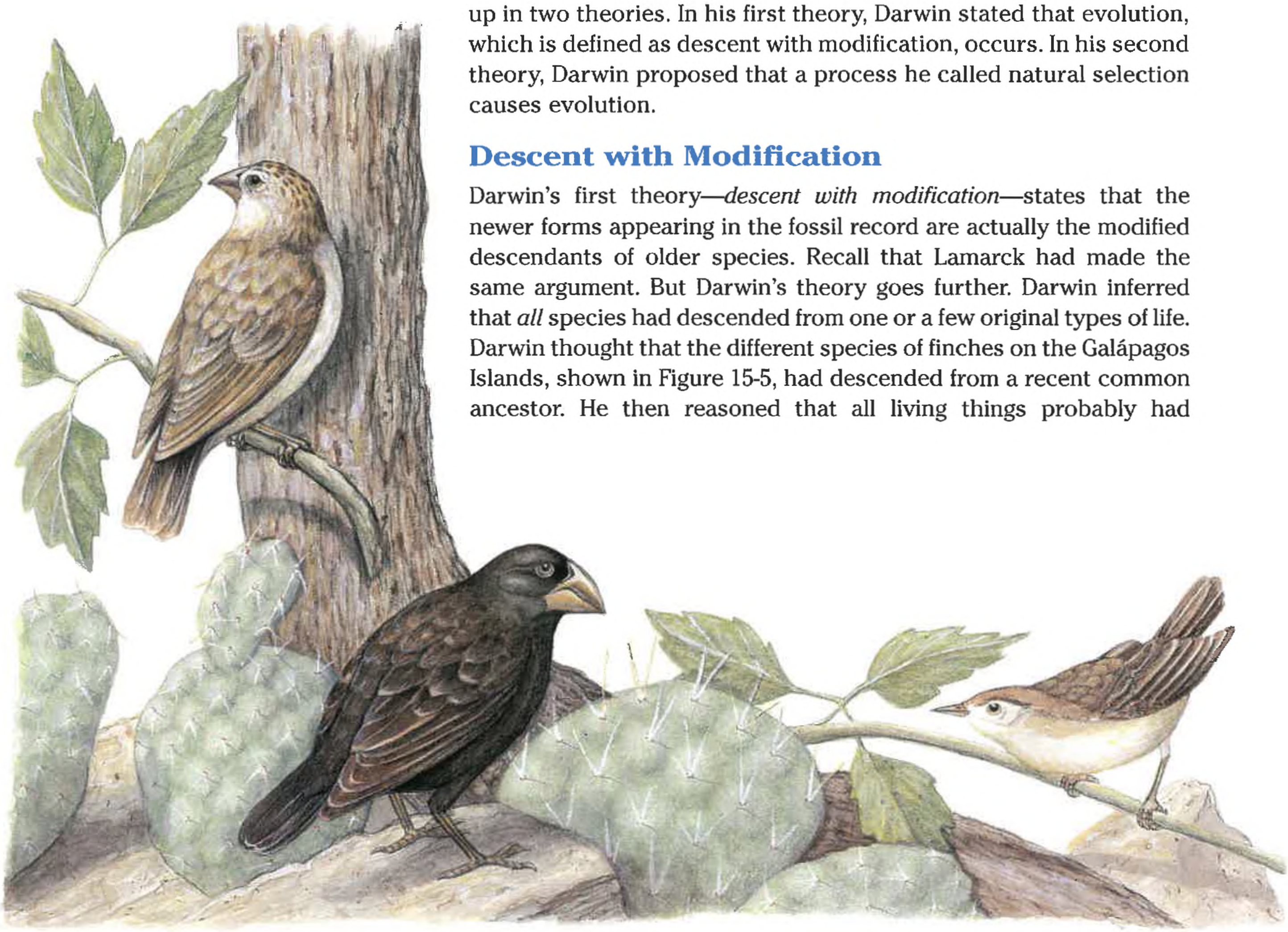
Darwin's ideas about evolution and natural selection are summed up in two theories. In his first theory, Darwin stated that evolution, which is defined as descent with modification, occurs. In his second theory, Darwin proposed that a process he called natural selection causes evolution.

Descent with Modification

Darwin's first theory—*descent with modification*—states that the newer forms appearing in the fossil record are actually the modified descendants of older species. Recall that Lamarck had made the same argument. But Darwin's theory goes further. Darwin inferred that *all* species had descended from one or a few original types of life. Darwin thought that the different species of finches on the Galápagos Islands, shown in Figure 15-5, had descended from a recent common ancestor. He then reasoned that all living things probably had

FIGURE 15-5

The beaks of the Galápagos finches are adapted to different food sources. The beak of the large ground finch, *Geospiza magnirostris*, center, is suited to cracking the seeds that compose the bird's diet. The narrower beaks of the woodpecker finch, *Camarynchus pallidus*, top left, and the warbler finch, *Certhidea olivacea*, bottom right, are specialized for capturing insects.



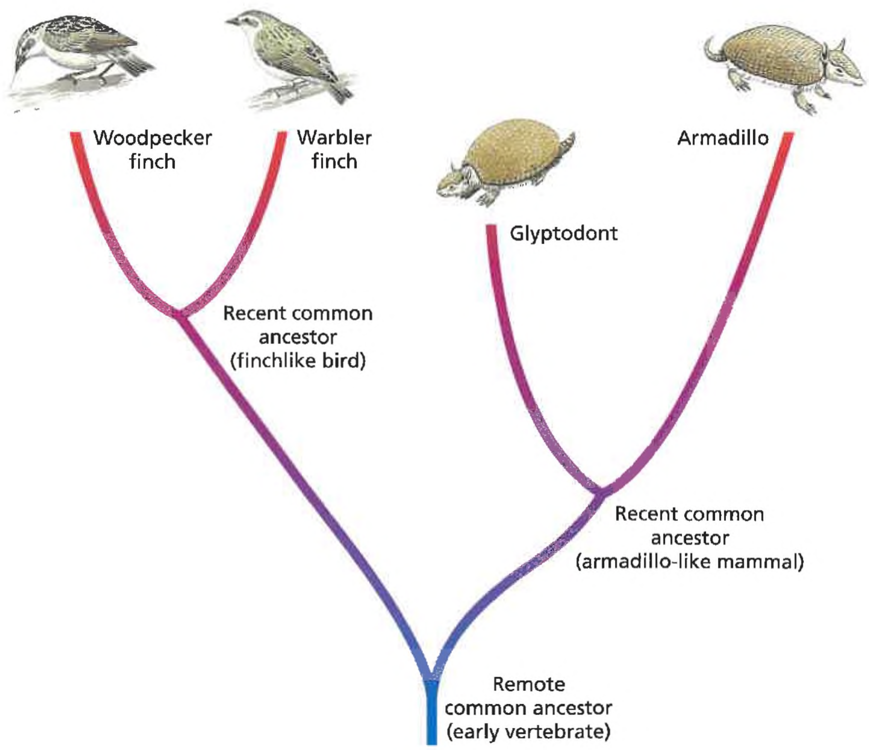


FIGURE 15-6

Darwin reasoned that if the Galápagos finches were similar to each other because of recent common ancestry, then organisms that are more dissimilar, such as finches and armadillos, share a more remote ancestor.

likewise descended from one, or perhaps a few, remote common ancestors that lived a very long time ago. For example, all vertebrates, such as the birds and mammals shown in Figure 15-6, probably descended from a vertebrate that lived in the distant past. Bear in mind that the terms *recent ancestor* and *remote ancestor* are used in the context of geologic history—the span of time represented in Table 15-1—rather than in the context of a single human lifetime.

Darwin's first theory accounted for the fact that similar organisms arise in the same geographic location. Darwin's theory of evolution explained the observation that organisms give rise to others similar to themselves. Thus, it would be natural for modern kangaroos to evolve from a now-extinct ancestor very much like them.

Modification by Natural Selection

Darwin's second theory—*modification by natural selection*—states how evolution occurs. Darwin was heavily influenced by the English clergyman Thomas Malthus (1766–1834), who had published a thesis pointing out that populations (Malthus was referring to humans) have the potential of doubling and redoubling their numbers. Malthus proposed that the growth of human populations was limited by adverse conditions, such as war, disease, or a limited supply of resources.

Agreeing with Malthus's views, Darwin noted that although populations of all organisms have the potential to grow unchecked, most do not. He reasoned that the environment limits the growth of populations by increasing the rate of death or decreasing the rate of reproduction, or both.

Eco Connection

Galápagos Islands

The exotic and fragile ecosystem of the Galápagos that fascinated Charles Darwin in the mid-1830s has been in danger since the discovery of the Galápagos in 1535. For 400 years, the islands were a favorite stopping place for pirates and whalers. Herman Melville, the author of *Moby Dick*, saw and wrote of the giants of the islands, the Galápagos tortoises, while on a whaling expedition in 1841. The tortoises, pictured in the opening photograph of this chapter, were a frequent target of sailors. The animals were valued as a meat source because they could live for long periods aboard ship with little or no food or water. Over the years, the tortoise population has been reduced from about 250,000 animals to about 15,000 animals.

Over the past 40 years, the government of Ecuador has taken steps to preserve and restore the Galápagos and their wildlife. The Charles Darwin Research Station conducts breeding programs for endangered animals and has bred and released several thousand tortoises, representing most of the 14 tortoise species found on the islands.

internetconnect

SCiLINKS NSTA
TOPIC: Natural selection
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KEYWORD: HM288

Darwin proposed that the environment may affect individual organisms in a population in different ways because individuals of a species are not identical. Some organisms have traits that make them better able to cope with their environment. Organisms that have a greater number of these favorable traits tend to leave more offspring than organisms with fewer beneficial traits. Darwin called the different degrees of successful reproduction among organisms in a population natural selection.

If a trait both increases the reproductive success of an organism *and* is inherited, then that trait will tend to be passed on to many offspring. A population of organisms **adapt** to their environment as their proportion of genes for favorable traits increases. The resulting change in the genetic makeup of a population is evolution. In an evolving population, a single organism's genetic contribution to the next generation is termed **fitness.** Thus, an individual with high fitness is well adapted to its environment and reproduces more successfully than an individual with low fitness.

Bear in mind that natural selection is not an active process. Organisms do not purposefully acquire traits that they need, although it may seem that this is true. The environment "selects" the traits that will increase in a population. The kinds of traits that are favorable depend on the demands of the environment. An organism may be able to run fast, or it may be strong or have coloring that acts as camouflage from predators. Traits that are favorable for some organisms in some environments are not necessarily favorable for all organisms or all environments. For example, the large body size of large mammals such as the elephant would not be beneficial to a species of flying birds if size prevented flight. A favorable trait is said to give the organism that has it an **adaptive advantage.**

Selection conditions change as the demands of the environment change. For example, a significant change in climate or available food can cause rapid evolutionary change as populations adapt to the change. If the environmental change is too extreme, however, populations cannot adapt quickly enough and they become extinct.

SECTION 15-2 REVIEW

1. What is an acquired characteristic? Do acquired characteristics change the genotype of an organism?
2. How did Lyell's book *Principles of Geology* help Darwin see that natural selection over many generations could explain species modification?
3. How many years have passed since the publication of *The Origin of Species*? Why is its publication still considered so important?
4. Do Darwin's theories of evolution by natural selection contradict the principles of biogeography? Why or why not?
5. What did Darwin think limits the growth of populations?
6. **CRITICAL THINKING** If a favorable trait increases the life span of an organism without affecting reproductive success, does it contribute to evolution?

SECTION

15-3

OBJECTIVES

▲ Describe the difference between homologous, analogous, and vestigial structures.

● Tell how similarities in macromolecules and embryos of different species suggest a relationship between them.

■ Explain the difference between coevolution, and divergent and convergent evolution.

EVOLUTION IN PROCESS

Evolution is a continuous process. By examining genotypic and phenotypic evidence in modern organisms, we can see evidence that evolution has occurred. By considering species in relation to one another, we can also detect definite patterns of evolution.

EVIDENCE OF EVOLUTION

If organisms change through a process of gradual modifications, we should be able to see evidence of this process. Living things, in fact, display many different clues to their evolutionary history.

Homologous and Analogous Structures

It seems obvious that the beaks of the finches shown in Figure 15-5 derive from the same embryonic structure of each different species. Moreover, they are modifications of a feature found in an ancestor common to all birds. Similar features that originated in a shared ancestor are described as **homologous** (hoh-MAHL-uh-guhs) features.

Some examples of homologous features are not as obvious as the beaks of birds. Compare the forelimbs shown in Figure 15-7. Although the limbs look strikingly different and vary greatly in function, they are very similar in skeletal structure, and they derive from the same structures in the embryo. Homologous features can result from modifications that change an original feature

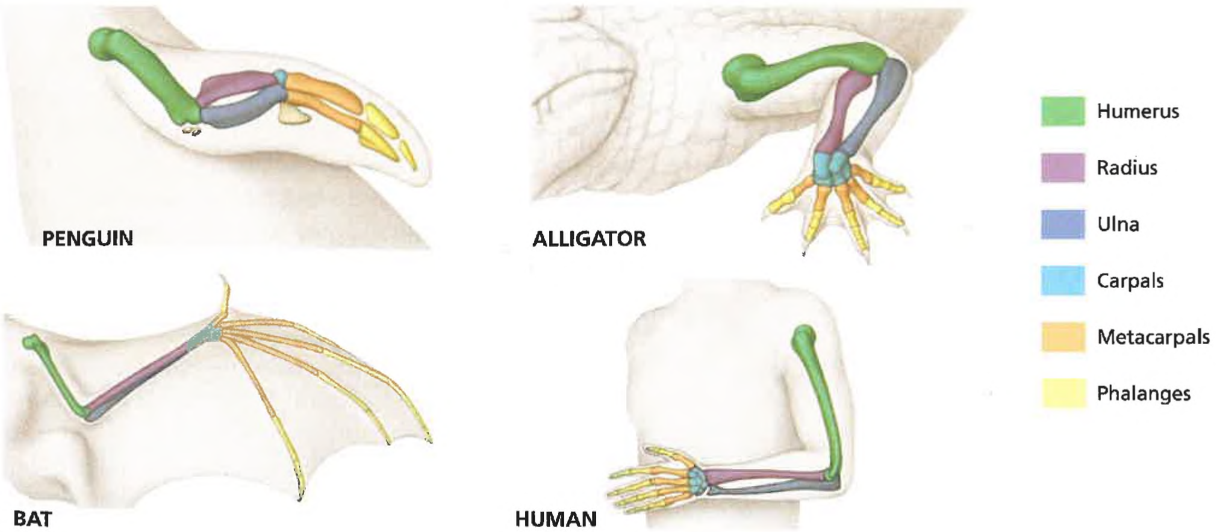


FIGURE 15-7
The forelimbs of the penguin, alligator, bat, and human all derive from the same embryological structures.

FIGURE 15-8

The wings of the hummingbird, *Selasphorus rufus*, top, and the humming moth, *Hemaris thysbe*, bottom, serve similar functions, but they differ in structure and derive from different embryological structures.

to two extremely different types, such as a wing and an arm. The presence of homologous features in different species indicates that the species shared a fairly recent common ancestor.

Analogous (uh-NAL-uh-guhs) features serve identical functions, and they look somewhat alike. They have very different embryological development, however, and may be very different in internal anatomy. Figure 15-8 shows a hummingbird and a humming moth. Both organisms can hover to feed on the sugar-rich nectar from flowers. There is no anatomical or embryological similarity, however, between their wings. Birds and insects differ greatly in anatomy and in embryological development. Although birds and insects do share a very remote ancestor, we can infer that their wings evolved independently and differently in more-recent ancestors of each animal.

Vestigial Structures

Many organisms have features that seem to serve no useful function. For example, humans have a tailbone at the end of the spine that is of no apparent use. The human appendix, a small, fingerlike projection from the intestine, also has no known function. Some snakes have tiny pelvic bones and limb bones. Whales also have pelvic bones, along with a four-chambered stomach like that of a cow.

These apparently useless features are said to be vestigial. **Vestigial** (ves-TIJ-ee-uhl) features were useful to an ancestor, but they are not useful to the modern organism that has them. The vestigial tailbone in humans is homologous to the functional tails of other vertebrate species. A vestigial feature in a modern organism is evidence that the structure *was* functional in some ancestor of the modern organism. Moreover, an organism with a vestigial feature probably shares common ancestry with an organism that has a functional version of the same feature.

So what sort of evolutionary clues can vestigial features provide? Consider that normal sperm whales, like all whales, have small pelvic bones but no hind legs. A very small percentage of sperm whales, however, have vestigial leg bones, and some sperm whales even have bone-supported bumps protruding from their body.

Whales probably are descended from an ancestor that lived on land. In the whales' genome, many of the genes needed to make hind legs have been **conserved,** or have remained unchanged. In normal whales, the genes for hind legs are turned off. In rare cases, however, the genes are partially turned on, and vestigial hind legs form. Thus, whales and other living things may display their evolutionary history in the usually unexpressed genes they carry.

Similarities in Embryology

The early stages of different vertebrate embryos are strikingly similar to each other, as you can see in Figure 15-9. The German zoologist Ernst Haeckel (1834–1919), who was also struck by these similarities, declared that "ontogeny recapitulates phylogeny." This statement can be translated to "embryological development repeats evolutionary history." We now know that this is a bit of an exaggeration. For example, during no stage of development does a gorilla look like an adult fish. In the early stages of development, all vertebrate embryos are similar, but those similarities fade as development proceeds. Nevertheless, the similarities in early embryonic stages of vertebrates can be taken as yet another indication that vertebrates share a common ancestry.

Similarities in Macromolecules

Darwin hypothesized that more-similar forms of organisms have a more recent common ancestor than do less-similar forms. He arrived at this hypothesis by observing anatomical features only. He could not have known how true this rule would prove at the molecular level—for homologous proteins, as well as RNA and DNA molecules. For example, many species have the red-blood-cell protein, hemoglobin. The amino acid sequences in the hemoglobin molecules of different species are similar, but not identical. The amino acid sequences in human hemoglobin and gorilla hemoglobin differ by one amino acid, while the hemoglobin molecules of humans and frogs differ by 67 amino acids. The number of amino acid differences in homologous proteins of two species is proportional to the length of time that has passed since the two species shared a common ancestor. Thus, the more-similar the homologous proteins are in different species, the more closely related the species are thought to be. Information provided by molecular biology can confirm the evolutionary histories suggested by fossils and anatomy.

FIGURE 15-9

This is a modernized version of Haeckel's drawings of embryological stages in different species. Although modern embryologists have discovered that Haeckel exaggerated some features in his drawings, it is true that early embryos of many different vertebrate species look remarkably similar.

PATTERNS OF EVOLUTION

There are several ways that species can change to adapt to their habitats. The pattern and speed of evolutionary change result from the changing requirements of the environment.

Coevolution

The change of two or more species in close association with each other is called **coevolution.** Predators and their prey sometimes coevolve, parasites and their hosts often coevolve, and plant-eating animals and the plants they feed on also coevolve. One example of coevolution is plants and the animals that pollinate them.

In tropical regions, some species of bats feed on the nectar of flowers, as shown in Figure 15-10. These bats have a slender muzzle and a long tongue with a brushlike tip, which aid them in feeding. The fur on the bat's face and neck picks up pollen, which the bat takes to the next flower. Flowers that have coevolved with these bats are light in color, enabling the bats, which are active at night, to easily locate them. The flowers also have a fruity odor that is attractive to bats.

FIGURE 15-10

Some species of bats, such as this long-nosed fruit bat, have coevolved with the flowers they feed on.

FIGURE 15-11

The rate of divergent evolution among dogs has been increased by artificial selection by humans.

Convergent Evolution

Sometimes organisms that appear to be very similar, such as a shark and a porpoise, are not closely related at all. This kind of similarity is the result of **convergent evolution.** Convergent evolution occurs when the environment selects similar phenotypes, even though the ancestral types were quite different from each other. Sharks and porpoises have very different origins. Sharks are fishes, and porpoises are mammals. Many features of these animals are similar, however, and have been selected by the environment they share. Their large, streamlined bodies and even their fins resemble each other. Analogous structures, such as similar fins in very different animals, are associated with convergent evolution.

Divergent Evolution

In **divergent evolution,** two or more related populations or species become more and more dissimilar. Divergence is nearly always a response to differing habitats, and it can ultimately result in new species.

One important type of divergent evolution is adaptive radiation. In **adaptive radiation,** many related species evolve from a single ancestral species. The Galápagos finches are an example of adaptive radiation. They diverged in response to the availability of different types of food in their different habitats.

Sometimes the process of divergence can be sped up artificially, through **artificial selection.** All domestic dogs are the same species, *Canis familiaris.* Dogs have been bred by humans for certain phenotypic characteristics, resulting in different breeds with different traits, as you can see in Figure 15-11. Thus, the process of divergent evolution in this species has sped up many times beyond what could have occurred in nature. Divergent evolution operating over very long periods of time has produced the seemingly endless variety of species alive today.

SECTION 15-3 REVIEW

1. The mouthparts of an adult horsefly are modified for biting. The mouthparts of a mosquito are modified for piercing skin and sucking blood. Are the mouthparts of the two species homologous or analogous? Explain your answer.
2. Birds and bees have wings. Are their wings homologous features or analogous features? Explain your answer.
3. The hemoglobin of humans is nearly identical to that of a gorilla. What does this suggest about the length of time that has passed since the last common ancestor of humans and gorillas lived?
4. Fruit fly embryos and frog embryos differ from each other more than frog embryos and human embryos do. What does this tell us about how the three species are related?
5. Are vestigial structures acted on by natural selection?
6. CRITICAL THINKING Some monarch butterflies contain chemicals that are toxic to birds. Another species of butterfly, the viceroy, has some protection from predation because it closely resembles the monarch. What pattern of evolution is illustrated by this example?

CHAPTER 15 REVIEW

SUMMARY/VOCABULARY

15-1

- A fossil is a trace of a long-dead organism.
- The law of superposition states that new geologic strata are deposited on top of older strata.
- The history of Earth and its life-forms can be inferred by examining the fossil record.
- The fossil record shows that new life-forms have arisen continually during the history of life on Earth.
- The study of biogeography shows that organisms arise in areas where similar, now-extinct organisms once lived.

Vocabulary

absolute age (281)
biogeography (281)
cast (279)
extinct (281)
fossil (279)
law of superposition (280)
mass extinction (281)
mold (279)
relative age (281)
sediment (279)
stratum (280)

15-2

- Lamarck proposed that species evolve over time. He incorrectly hypothesized that species modification is the result of acquired characteristics and that these characteristics can be passed on to offspring.
- Charles Darwin began his work on evolution when he was employed as a naturalist for a voyage of the H.M.S. *Beagle*.
- Darwin was influenced by Charles Lyell, who proposed the principles of uniformitarianism, which hold that the structure of Earth results from cycles of observable processes.
- Darwin found evidence of species modification in both modern and extinct species.
- Darwin hypothesized that related species, such as the Galápagos finches, descended from a common ancestor.
- Darwin wrote *The Origin of Species,* in which he proposed that natural selection is the principal driving force behind evolution.
- A population of organisms adapt to their environment as their proportion of genes for favorable traits increases.
- Evolution is the change in the genetic makeup of a population over generations.

Vocabulary

acquired trait (283)
adapt (288)
adaptive advantage (288)
fitness (288)
natural selection (284)
population (284)
uniformitarianism (284)

15-3

- Evidence supporting evolution is found in the body structures of living organisms. Homologous structures have a common evolutionary origin. Analogous structures are similar in function but have different evolutionary origins.
- A species with a vestigial structure probably shares evolutionary origins with a species that has a functional form of the structure.
- Similar embryological development among species indicates a common evolutionary history.
- Similarity in macromolecules such as RNA, DNA, and proteins indicates a common evolutionary history.
- In coevolution, two or more closely associated species, such as a predator and its prey, change in response to each other.
- In convergent evolution, organisms that are not closely related resemble each other because they have responded to similar environments.
- In divergent evolution, related populations become less similar as they respond to different environments. Adaptive radiation is a type of divergent evolution.

Vocabulary

adaptive radiation (292)
analogous (290)
artificial selection (292)
coevolution (291)
conserve (290)
convergent evolution (292)
divergent evolution (292)
homologous (289)
vestigial (290)

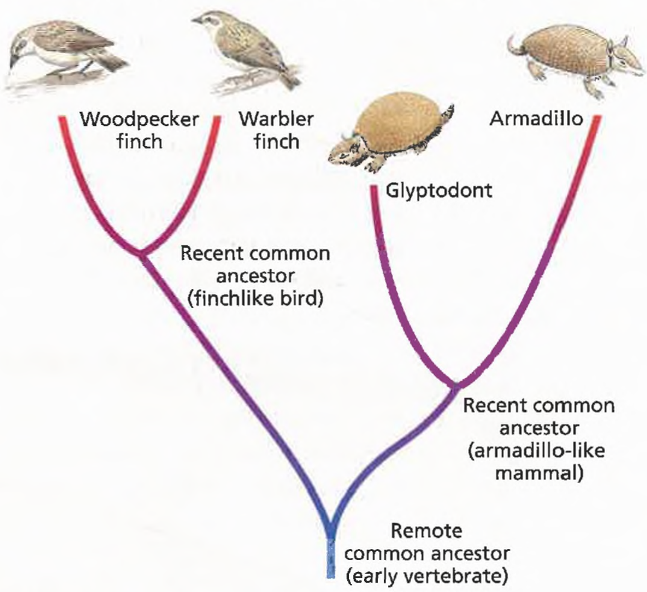
REVIEW

Vocabulary

1. What is the difference between a mold and a cast?
2. Explain the relationship between geologic strata and relative age.
3. What is the difference between an acquired trait and a genetic trait?
4. Distinguish between homologous structures and analogous structures.
5. How are divergent evolution and adaptive radiation related?

Multiple Choice

6. Lamarck's explanation for the modification of species depended on (a) inheritance of acquired characteristics (b) convergent evolution (c) the law of superposition (d) natural selection.
7. The idea that processes occurring now on Earth are much the same as those that occurred long ago is called (a) uniformitarianism (b) relativism (c) evolutionism (d) convergent evolution.
8. The observation that organisms arise in locations where similar, extinct organisms lived is referred to as (a) superposition (b) biogeography (c) uniformitarianism (d) evolution.
9. The similarities in the Galápagos finches implied (a) coevolution (b) convergent evolution (c) adaptive radiation (d) descent from different remote ancestors.
10. Difference in reproductive success is (a) an acquired trait (b) adaptive radiation (c) natural selection (d) coevolution.
11. Great similarity between species implies (a) recent common ancestry (b) remote common ancestry (c) successful reproduction (d) extinction.
12. Features that were useful in ancestors but are no longer useful are called (a) analogous features (b) vestigial features (c) homologous features (d) favorable traits.
13. Similar features in different species that originated in a shared ancestor are called (a) vestigial features (b) analogous features (c) homologous features (d) unexpressed genes.
14. A hummingbird and a humming moth have a number of superficial features in common with each other. This is an example of (a) divergent evolution (b) coevolution (c) convergent evolution (d) superposition.
15. The phylogenetic tree below implies that modern finches and armadillos (a) are unrelated (b) share a remote common ancestor (c) share a recent common ancestor (d) did not evolve from older forms of life.



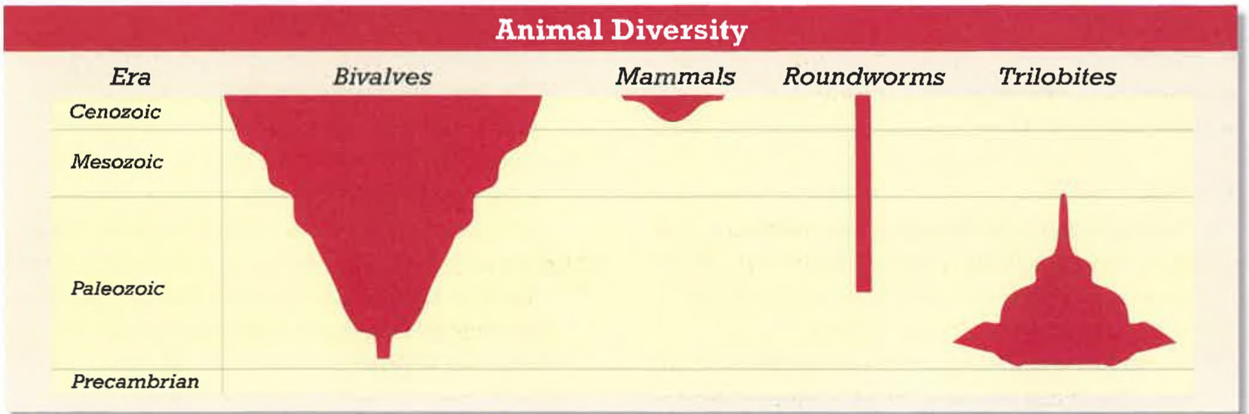
Short Answer

16. What led Hooke to argue that fossils had once been living organisms?
17. What did Malthus observe about the potential for growth in populations?
18. How was Darwin's theory of evolution different from Lamarck's theory?
19. What does the existence of very similar embryological forms among species imply?
20. Why are some traits favorable for some species and not for others?
21. What pattern of evolution is demonstrated by the Galápagos finches?
22. What is an example of a vestigial structure in humans?
23. How does the structure of macromolecules, such as proteins, act as an index of relatedness between species?
24. What kind of evolution is demonstrated by nectar-feeding bats and the flowers they feed on?

25. Could a characteristic that is not controlled by genetics be selected by the environment? Would this characteristic contribute to the evolution of the organism that has it?

CRITICAL THINKING

1. In recent years, paleontologists have claimed that in some cases the evolution of a new species occurs quite suddenly—in less than a thousand years. Darwin stated that evolution was a gradual process. What effect does generation time have on evolution rate?
2. The process of natural selection throughout the history of life on Earth has resulted in the success of some species and the extinction of other species. Why has natural selection not resulted in the existence of a single best-adapted species?
3. Many vestigial traits, such as the human tailbone, seem to be largely neutral, that is, neither beneficial nor harmful. The appendix is an example of a vestigial structure in humans. How might having an appendix be harmful to humans?
4. The graph below shows the diversity of different groups of animals over time. The width of the colored-in areas is proportional to the number of different types of bivalves, mammals, roundworms, and trilobites that were alive during different eras. Use the graph to answer the following questions:
   a. Which group was the last to evolve?
   b. Which group is or was the most diverse? The least diverse?
   c. Which group diversified rapidly soon after evolving?
   d. Which group(s) became extinct?
   e. Which groups did not live at the same time?



EXTENSION

1. Read "A Dinosaur Named Sue" in *National Geographic,* June 1999, on page 47, and answer the following questions: What technique was used to examine the inside of the skull of the 67-million-year-old *Tyrannosaurus rex* fossil? How many *T. rex* fossils have ever been discovered, and what makes Sue unique? When and where was Sue discovered, and what was the principal reason Sue's ownership was in question?
2. Though he never became as famous as Charles Darwin, Alfred Wallace made many important contributions to the field of biology in the late nineteenth and early twentieth centuries. Use biographies, autobiographies, and an encyclopedia to find information on the life of Alfred Wallace. Write a short report highlighting Wallace's contributions to biology.

CHAPTER 15 INVESTIGATION

Modeling Selection

OBJECTIVES

- Simulate the generation of variation.
- Model the selection of favorable traits in new generations.

PROCESS SKILLS

- observing
- testing
- measuring

MATERIALS

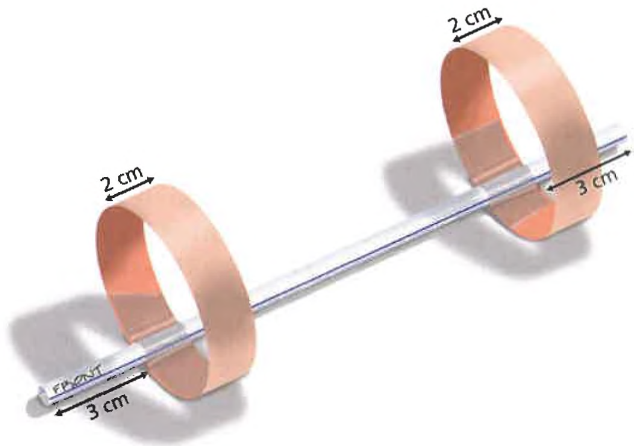
- construction paper
- cellophane tape
- soda straws
- penny, or other coin
- six-sided die
- scissors
- meterstick or tape measure
- metric ruler

Background

1. The Egyptian Origami Bird *(Avis papyrus)* lives in arid regions of North Africa. Only the birds that can fly the long distances between oases live long enough to breed successfully.
2. Successful evolution requires the generation of variety by mutation and then selection by the environment of the most-fit individuals.

PART A Parental Generation

1. First cut two strips of paper, 2 cm × 20 cm each. Make a loop with one strip of paper, overlapping the paper 1 cm, and tape the loop closed. Repeat for the other strip. Tape one loop 3 cm from each end of the straw, as shown in the figure at the top of the next column. Mark the front end of the bird with a felt-tip marker. This bird will represent the parental generation.
2. In your lab report, prepare a data table like the one shown on the facing page.
3. Test how far your bird can fly by releasing it with a gentle overhand pitch. Test the bird twice. Then record the bird's average flight distance in your data table.



PART B F_1 Generation

4. Breed offspring. Each Origami Bird lays a clutch of three eggs. Assume that the first egg has no mutations. It is a clone of the parent.
5. Assume that the other two chicks have mutations. Follow the steps below to determine the effects of each mutation. Record the mutations and the dimensions of each offspring in your data table. The circumference of the wings can be calculated by measuring the length of the strips of paper used to form the wings and subtracting 1 cm for the overlap.

Step A A coin flip determines which part of the bird is affected by the mutation.
Heads = anterior (front)
Tails = posterior (back)

Step B A die throw determines how the mutation affects the wing.

 (1) = The wing position changes 1 cm toward the end of the straw.

 (2) = The wing position changes 1 cm toward the middle of the straw.

 (3) = The circumference of the wing increases 2 cm.

 (4) = The circumference of the wing decreases 2 cm.

 (5) = The width of the wing increases 1 cm.

 (6) = The width of the wing decreases 1 cm.

Step C A mutation that results in a wing falling off or a wing with a circumference smaller than that of the straw is lethal. If you get a lethal mutation, disregard it and breed another chick.

6. Test the birds. Release each bird with a gentle overhand pitch. It is important to release the birds as uniformly as possible. Test each bird at least twice.

7. The most successful bird is the one that flies the farthest. Record the flight distance of each offspring bird in your data table.

PART C F_2 Generation

8. Assume that the most successful bird in the F_1 generation is the sole parent of the next (F_2) generation. Continue to breed, test, and record data for 10 generations.

9.  Clean up your materials before leaving the lab.

Analysis and Conclusions

1. Did your selection process result in birds that fly better?

2. Describe two aspects of this investigation that model evolution of biological organisms.

3. Your most successful bird has a different lineage from the most successful bird of your neighboring groups. Compare your winning bird with those of your neighbors. How does it differ?

4. What might happen to your last bird if the environmental conditions change?

5. How might this lab help explain the observations Darwin made about finches on the Galápagos Islands?

Further Inquiry

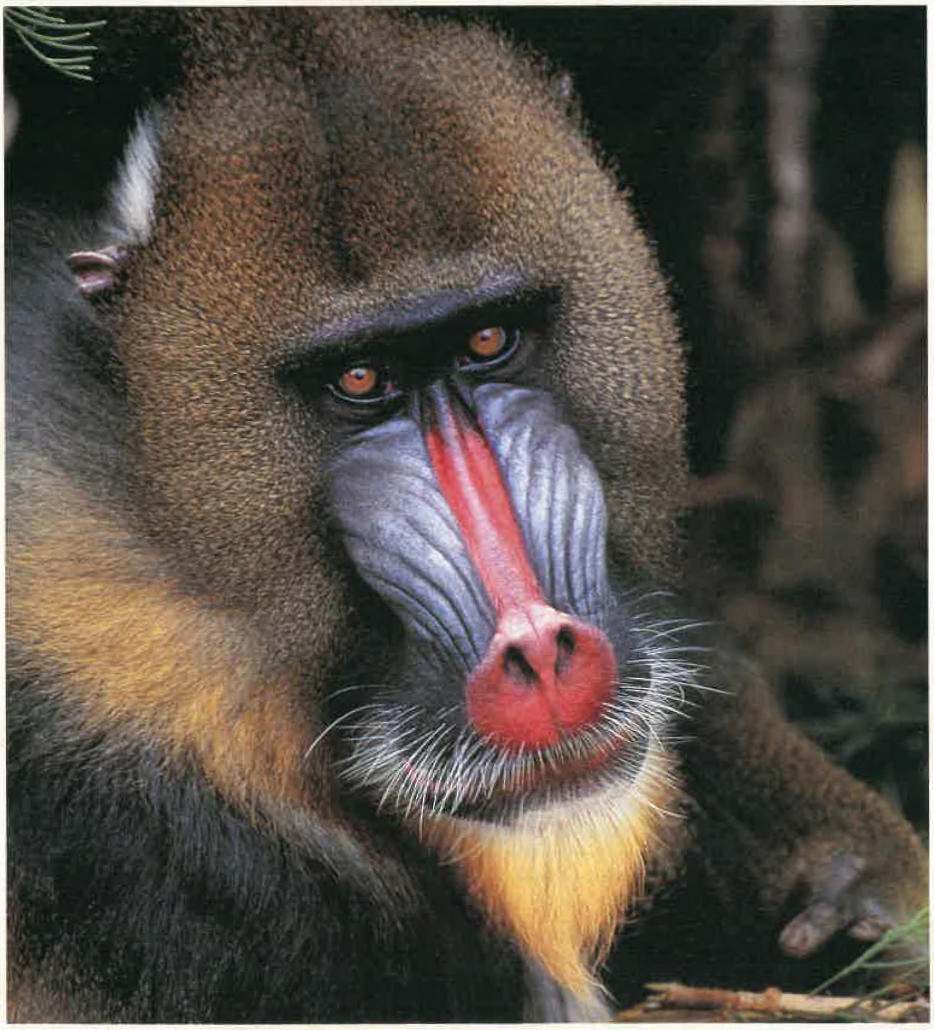
A flock of Origami Birds is blown off the mainland and onto a very small island. These birds face little danger on the ground, but they experience significant risk when flying because they can be blown off the island. Birds that cannot fly at all are most likely to survive and reproduce. Continue the experiment for several generations, selecting birds that can't fly.

TABLE A *MUTATIONS AMONG OFFSPRING*

Generation	Coin flip (heads or tails)	Die throw (1–6)	Measurements of most successful offspring		Distance flown
Parental	not applicable	not applicable	anterior wing	width 2 cm	______ m
				circumference 19 cm	
			posterior wing	width 2 cm	
				circumference 19 cm	
			anterior wing position	from front 3 cm	
			posterior wing position	from back 3 cm	
F_1			anterior wing	width ______ cm	______ m
				circumference ______ cm	
			posterior wing	width ______ cm	
				circumference ______ cm	
			anterior wing position	from front ______ cm	
			posterior wing position	from back ______ cm	
F_2			anterior wing	width ______ cm	______ m
				circumference ______ cm	
			posterior wing	width ______ cm	
				circumference ______ cm	
			anterior wing position	from front ______ cm	
			posterior wing position	from back ______ cm	

CHAPTER 16

THE EVOLUTION OF POPULATIONS AND SPECIATION



Sexual selection, which is one variation of natural selection, influences the development of extreme phenotypic traits, particularly in males. The vibrant red stripe on the blue muzzle of this male mandrill baboon, Mandrillus sphinx, *does not appear in females.*

FOCUS CONCEPT: *Reproduction and Inheritance*

As you read, pay attention to the steps that lead to the formation of new species.

SECTION

16-1

GENETIC EQUILIBRIUM

By the time of Darwin's death, in 1882, the idea of evolution by natural selection had gained wide acceptance among scientists. But with the birth of the field of genetics in the early 1900s, spurred by the rediscovery of Mendel's work on the mechanics of inheritance, many questions about evolution and natural selection resurfaced.

OBJECTIVES

▲ Explain the importance of the bell curve to population genetics.

● Describe two causes of genotypic variation in a population.

■ Explain how to compute allele frequency and phenotype frequency.

◆ Explain Hardy-Weinberg genetic equilibrium.

VARIATION OF TRAITS IN A POPULATION

Population genetics is the study of evolution from a genetic point of view. Evolution is a gradual change in the genetic material of a population. Recall from Chapter 15 that a population consists of a collection of individuals of the same species that routinely interbreed. Populations are important to the study of evolution because a population is the smallest unit in which evolution occurs.

Within a population, individuals may vary in observable traits. For example, fish of a single species in a pond may vary in size. Biologists often study variation in a trait by measuring that trait in a large sample. Figure 16-1 shows a common result of such measurements. It is a graph of the frequency of lengths in a population of mature fish. Because the shape of the curve looks like a bell, it is called a **bell curve.** The bell curve shows that while a few fish in this population are extremely short and a few are extremely long, most are of average length. In nature, many quantitative traits in a population—such as height and weight—tend to show variation that follows a bell curve pattern.

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Length in a Population of Fish

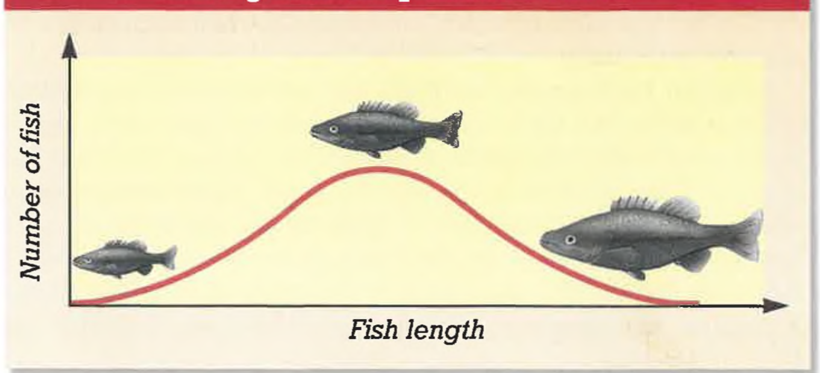


FIGURE 16-1

A bell curve illustrates that most members of a population have similar values for a given, measurable trait. Only a few individuals display extreme variations of the trait.

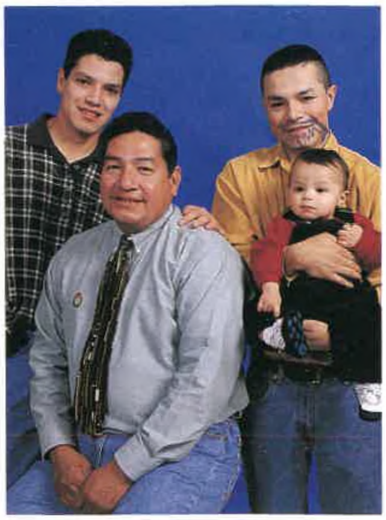


FIGURE 16-2

Many varied but similar phenotypes occur within families because members of a family share some alleles but not others.

Causes of Variation

What causes variation in traits? Some variations are influenced by environmental factors, such as the amount or quality of food available to an organism. Variation is often influenced by heredity. Usually, both factors play a role.

To consider variability, think about phenotypes within a single human family. Two parents, each with a distinct genotype, may produce several children. In the picture of the family in Figure 16-2, the two young-adult brothers are not identical to each other, even though their genotypes are combinations of the genotypes of the same two parents. Both young men resemble their father, though in different traits. The baby resembles his young father, his grandfather, and his uncle. Thus, these males representing three generations look similar but not identical. What causes the genes to vary? The answer lies in the way gametes are produced and in the way gametes fuse with each other.

Variations in genotype arise in three main ways. (1) *Mutation* results from flawed copies of individual genes. (2) *Recombination* is the reassociation of genes in a diploid individual. Recombination occurs during meiosis by the independent assortment of genes on nonhomologous, or different, chromosomes and by crossing-over between genes located on homologous chromosomes. (3) The *random fusion of gametes* is essentially a game of chance played by individual gametes. Often there are hundreds of millions of sperm involved in a mating. The one that actually fertilizes an egg is largely a matter of chance. These processes ensure that offspring are not carbon copies of their parents.

ALLELE FREQUENCIES AND THE GENE POOL

Population geneticists use the term **gene pool** to describe the total genetic information available in a population. It is easy to imagine genes for the next generation as existing in an imaginary pool. If you could inventory this pool and know the alleles that are present, then you could apply a simple set of rules based on probability theory to predict expected genotypes and their frequencies for the next generation.

Suppose, for example, that there are two forms of a hypothetical allele, *A* and *a*, in a set of 10 gametes. If half the gametes in the set (5 gametes) carry the allele *A*, we would say that the allele frequency of the *A* allele is 0.5, or 50 percent. **Allele frequency** is determined by dividing the number of a certain allele (five instances of the *A* allele) by the total number of alleles of all types in the population (10 gametes, each with either an *A* or an *a* allele). Remember that gametes are haploid and therefore carry only one form of the allele.

Predicting Phenotype

The population of four o'clock flowers, shown in Figure 16-3, illustrates how phenotype can change from generation to generation. Homozygous *RR* flowers are red. Homozygous *rr* flowers are white. Heterozygous *Rr* flowers are pink rather than red, as you might expect. These flowers show incomplete dominance for color, meaning heterozygotes show a trait that falls between the dominant trait and the recessive trait. Thus, homozygotes and heterozygotes can be easily identified by observing the phenotype.

Compare the parent generation with the offspring generation of the four o'clock flowers shown in Figure 16-3. There are equal numbers of plants with the *RR* genotype and the *Rr* genotype in the first generation. You can compute the phenotype frequencies from the figure. A **phenotype frequency** is equal to the number of individuals with a particular phenotype divided by the total number of individuals in the population. Phenotype frequencies in the first generation are 0.5 pink (4 pink plants out of a total of 8 plants), 0.5 red (4 red plants out of a total of 8 plants), and 0.0 white. Recall that allele frequencies are computed using the same principle: the allele frequencies in the first generation plants are 0.75 *R* (12 *R* alleles out of a total of 16 alleles) and 0.25 *r* (4 *r* alleles out of a total of 16 alleles).

We now can predict the genotypes and phenotypes of the second generation. If a male gamete encounters a female gamete, they will produce a new four o'clock plant whose genotype is the combination of both parental gametes. Thus, an *R* male gamete combined with an *R* female gamete will produce a plant with the *RR* genotype, which has red flowers. According to the laws of probability, the chance of an *R* gamete (a single allele) meeting with another *R* gamete is the arithmetic product of their allele frequencies in the gene pool:

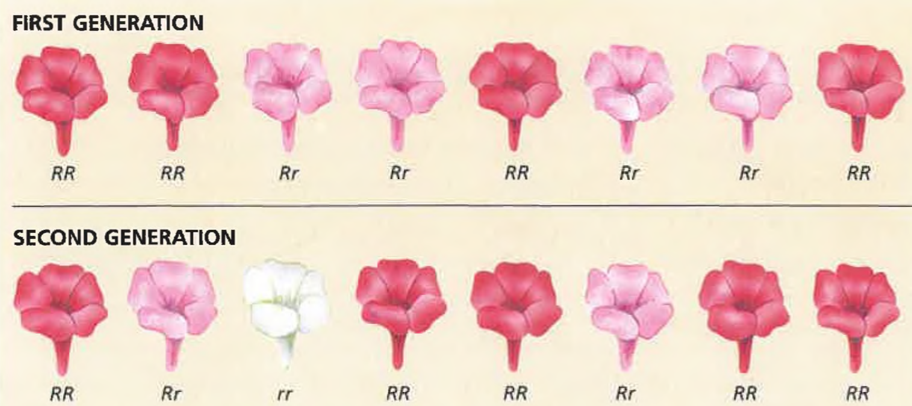
$$\text{frequency of } R \times \text{frequency of } R = \text{frequency of } RR \text{ pair}$$
$$0.75 \times 0.75 = 0.5625$$

The expected frequency of the *rr* genotype is then

$$\text{frequency of } r \times \text{frequency of } r = \text{frequency of } rr \text{ pair}$$
$$0.25 \times 0.25 = 0.0625$$

FIGURE 16-3

Although the four o'clock flowers differ phenotypically from generation to generation, the allele frequencies remain the same.



	PHENOTYPE FREQUENCY		ALLELE FREQUENCY
First generation	White	0	*R* = 0.75
	Pink	0.5	*r* = 0.25
	Red	0.5	
Second generation	White	0.125	*R* = 0.75
	Pink	0.25	*r* = 0.25
	Red	0.625	

FIGURE 16-4

This flock of mallards, *Anas platyrhynchos,* likely violates some or all of the conditions necessary for Hardy-Weinberg genetic equilibrium.

The frequencies of all types expected in the second generation must add up to 1.0, just as fractions of a whole must add up to 1. Having established the probabilities of getting an *RR* and an *rr* plant, we can compute the expected frequency of the *Rr* plants. All those plants that are neither *RR* nor *rr* will be *Rr,* so

$$1.0 - \text{frequency of } RR - \text{frequency of } rr = \text{frequency of } Rr$$
$$1.0 - 0.5625 - 0.0625 = 0.375$$

HARDY-WEINBERG GENETIC EQUILIBRIUM

It is clear from the example of the four o'clock flowers that phenotype frequencies can change dramatically from generation to generation. But what happens to allele frequencies over generations? A German physician, Wilhelm Weinberg (1862–1937), and a British mathematician, Godfrey Hardy (1877–1947), independently showed that allele frequencies in a population tend to remain the same from generation to generation unless acted on by outside influences. This is referred to as **Hardy-Weinberg genetic equilibrium,** and it is based on a set of assumptions about an ideal hypothetical population that is not evolving:

1. No net mutations occur; that is, allele frequencies do not change overall because of mutation.
2. Individuals neither enter nor leave the population.
3. The population is large (ideally, infinitely large).
4. Individuals mate randomly.
5. Selection does not occur.

Bear in mind that true genetic equilibrium is a theoretical state. Real populations, such as the flock of mallards in Figure 16-4, may violate conditions necessary for genetic equilibrium. By providing a model of how genetic equilibrium is maintained, Hardy-Weinberg genetic equilibrium allows us to consider what forces disrupt equilibrium.

Word Roots and Origins

equilibrium

from the Latin *aequilibris,* meaning "evenly balanced"

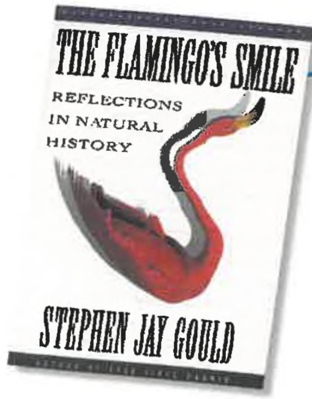
SECTION 16-1 REVIEW

1. **How does the distribution of traits in a population look when displayed as a graph?**
2. **What is meant by the term *human gene pool*?**
3. **Fifty percent of an experimental population of four o'clock flowers are red-flowered plants, and 50 percent are white-flowered plants. What is the frequency of the *r* allele?**
4. **How is phenotype frequency computed?**
5. **What is genetic equilibrium?**
6. **CRITICAL THINKING Is it easier to analyze genotype by observing phenotype in organisms with complete dominance or in organisms with incomplete dominance?**

Literature & Life

Opus 100

This excerpt is from the 100th in a regular series of columns by Stephen Jay Gould published in *Natural History* magazine. It was reprinted in a collection of Gould's columns called *The Flamingo's Smile.*

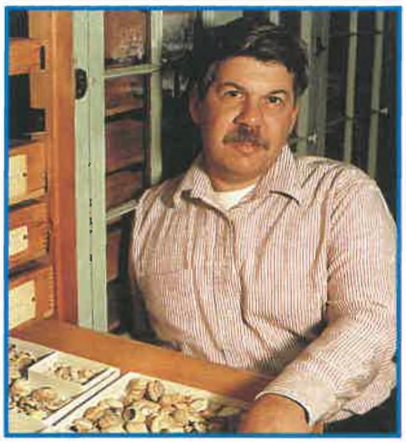


This passage describes some of the discoveries of Gould and fellow biologist David Woodruff as they began to study various species of Cerion, *a land snail of the West Indian islands.*

About fifteen names had been proposed for the *Cerions* of Grand Bahama and neighboring Abaco Island. After a week, Woodruff and I recognized that only two distinct populations inhabited these islands, each restricted to a definite and different environment. . . .

As Woodruff and I moved from island to island on Great Bahama Bank, we found the same pattern of two different populations, always in the same distinctive environments. On Little Bahama Bank, a dozen invalid names had fallen into this pattern. On Great Bahama Bank, they collapsed, literally by the hundred. About one-third of all *Cerion* "species" (close to 200 in all) turned out to be invalid names based on minor variants within this single pattern. We had reduced a chaos of improper names to a single, ecologically based order. . . .

Bahamian islands have two different kinds of coastlines. Major islands lie at the edge of their banks. The banks themselves are very shallow across their tops but plunge precipitously into deep ocean at their edges. Thus, bank-edge coasts abut the open ocean and tend to be raw and windy. Dunes build along windy coasts and solidify eventually into rock (often mistakenly called "coral" by tourists). Bank-edge coasts are, therefore, usually rocky as well. By contrast, coastlines that border the interior parts of banks—I will call



them bank-interior coasts—are surrounded by calm, shallow waters that extend for miles and do not promote the building of dunes. Bank-interior coasts, therefore, tend to be vegetated, low, and calm.

Woodruff and I found that bank-edge coasts in the northern Bahamas are invariably inhabited by thick-shelled, strongly ribbed, uniformly colored (white to darkish brown), relatively wide, and parallel-sided *Cerions*. To avoid writing most of the rest of this column in Latin, I will skip the formal names and refer to these forms as the "ribby populations." Bank-interior coasts are the home of thin-shelled, ribless or weakly ribbed, variegated (usually with alternating blotches of white and brown), narrow, and barrel-shaped *Cerions*—the "mottled populations." (Mottled *Cerions* also live away from coasts in the centers of islands, while ribby *Cerions* are confined exclusively to bank-edge coasts.)

This pattern is so consistent and invariable that we can "map" hybrid zones even before we visit an island, simply by looking at a chart of bathymetry. Hybrid zones occur where bank-edge coasts meet bank-interior coasts. . . .

The distinction of mottled and ribby resolved nearly all the two hundred names previously given to *Cerions* from the northern Bahamas. . . .

Reading for Meaning

Make a chart comparing snails of the two snail populations Gould and Woodruff identified.

Read Further

Think about what you have learned about adaptations. What factors might have caused the differences between the two species of *Cerion* that Gould wrote about in this passage?

SECTION

16-2

OBJECTIVES

▲ List five conditions that can cause evolution to take place.

● Give an example of how migration can affect evolution.

■ Define *genetic drift,* and tell how it affects endangered species.

◆ Contrast the effects of stabilizing, directional, and disruptive selection on variations in a trait over time.

▲ Give an example of sexual selection.

DISRUPTION OF GENETIC EQUILIBRIUM

Evolution is the change in a population's genetic material over generations, that is, a change of the population's allele frequencies or genotype frequencies. Any violation of the five conditions necessary for Hardy-Weinberg equilibrium can result in evolution.

MUTATION

The first requirement of genetic equilibrium is that allele frequencies not change overall because of mutations. Spontaneous mutations occur constantly, at a very low rate and under normal conditions. But if an organism is exposed to mutagens—mutation-causing agents such as radiation and certain chemicals—mutation rates can increase significantly. Mutations can affect genetic equilibrium by producing totally new alleles for a trait. Many, if not most, mutations are harmful. Because natural selection operates only on genes that are expressed, it is very slow to eliminate harmful recessive mutations. In the long run, however, beneficial mutations are a vital part of evolution.

MIGRATION

The second requirement of genetic equilibrium is that the population remain constant. **Immigration,** the movement of individuals into a population, and **emigration,** the movement of individuals out of a population, can change gene frequencies.

The behavioral ecology of some animal species encourages immigration and emigration. Common baboons live on the savannas of central Africa in social and breeding groups called troops. A troop is dominated by a few adult males, and it may have from 10 to 200 members. Females tend to remain with the troop they are born into, however, younger or less dominant males leave their birth troop, eventually joining another troop. This constant movement of male animals ensures gene flow. **Gene flow** is the process of genes moving from one population to another.

Word Roots and Origins

immigration

from the Latin *immigrare,* meaning "to go into"

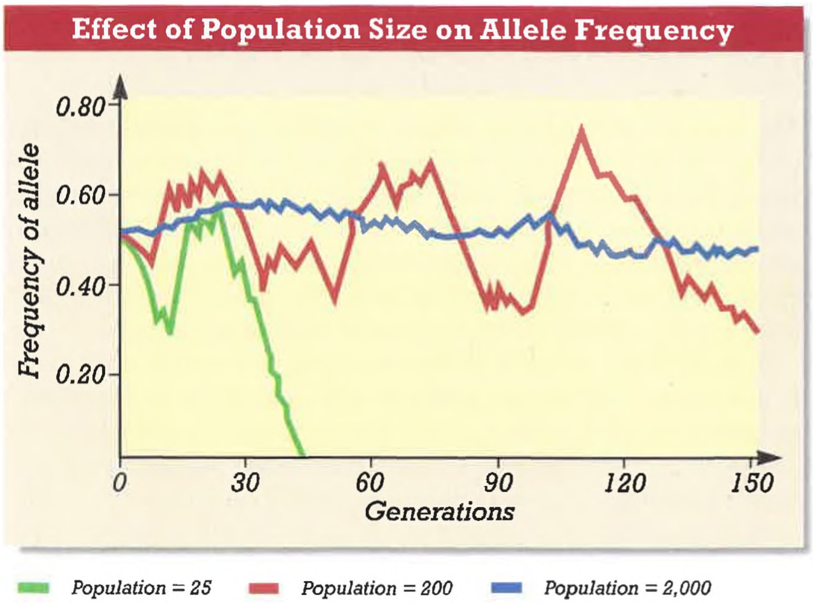


FIGURE 16-5

Genetic drift is significant only in small and medium-sized populations. In a small population, a particular allele may disappear completely over a few generations. In a larger population, a particular allele may vary widely in frequency due to chance but still be present in enough individuals to be maintained in the population. In a much larger population, the frequency of a particular allele may vary slightly due to chance but remain relatively stable over generations.

GENETIC DRIFT

The third requirement of genetic equilibrium is the presence of a large population. The Hardy-Weinberg principle is based on the laws of probability, which do not necessarily hold for small and medium-sized populations. **Genetic drift** is the phenomenon by which allele frequencies in a population change as a result of random events, or chance. In small populations, the failure of even a single organism to reproduce can significantly disrupt the allele frequency of the population, as can greater-than-normal reproduction by an individual, resulting in genetic drift.

Figure 16-5 shows a graph of genetic drift in populations of three differing sizes. Small populations can undergo abrupt changes in allele frequencies, exhibiting a large degree of genetic drift, while large populations retain fairly stable allele frequencies, maintaining a small degree of genetic drift. In the smallest population shown in Figure 16-5, the frequency of the example allele reaches zero at about the 45th generation. If we assume that we started with two alleles for a trait, then only one allele is left and every individual is homozygous for the remaining allele. Once this happens, the population is in danger of becoming extinct because there is no variation for natural selection to act on. For example, a new disease could wipe out the entire population. This is why endangered species, like the northern elephant seal, *Mirounga angustirostris*, shown in Figure 16-6, remain in peril of extinction even if their numbers increase significantly from near-extinction.

FIGURE 16-6

Individuals of the once nearly extinct northern elephant seal, *Mirounga angustirostris*, have lost genetic variability—they are homozygous for all of their genes that have been tested. This result of genetic drift could cause extinction because it limits the species' ability to further evolve.

Quick Lab

Evaluating Selection

Materials unlined paper, colored pencils, 25 colored candies

Procedure

1. Fold a sheet of unlined paper in half, top over bottom. Using colored pencils, decorate half the paper with different colored patterns. Make each colored pattern about the size of a quarter.
2. Scatter your "population" of candies over the undecorated half of the sheet of paper. Count and record how many candies match the background color.
3. Now scatter the candies over the decorated half of the sheet of paper. Count and record how many candies match the background color.
4. Candies that match the background color are camouflaged. Calculate the ratio of camouflaged candies to uncamouflaged candies in steps 2 and 3.
5. Repeat steps 2–4 two times, and average your results.
6. Exchange paper with another group, and repeat steps 2–5.

Analysis Was your population more successfully camouflaged on the white background or on the colored background? How did color diversity affect your population's success on the colored background? Based on your results, predict which type of selection might increase your population's fitness for a multicolored environment.

NONRANDOM MATING

The fourth requirement of genetic equilibrium is random matings, without regard to genetic makeup. Many species do not mate randomly. Mate selection is often influenced by geographic proximity, and this can result in mates with some degree of kinship. Matings of related individuals can amplify certain traits and can result in offspring with disorders caused by recessive genes, which, although rare, may be present in the genomes of related individuals.

In another example of nonrandom mating, individuals often select a mate that has similar physical characteristics and therefore probably has some similar genes. The selection of a mate based on similarity of characteristics is called **assortative mating.** While nonrandom mating can profoundly affect genotypes, that is, the *combinations* of alleles of a population, it does not affect overall allele frequencies.

NATURAL SELECTION

The fifth requirement of genetic equilibrium is the absence of natural selection. Natural selection is an ongoing process in nature, and it is the single most significant factor that disrupts genetic equilibrium. As you learned in Chapter 15, as a result of natural selection, some members of a population are more likely to contribute their genes to the next generation than are other members. Any of several broad types of natural selection—including stabilizing, directional, disruptive, and sexual—can cause evolution.

Stabilizing Selection

In **stabilizing selection,** individuals with the average form of a trait have the highest fitness. The average represents the optimum for most traits; extreme forms of most traits confer lower fitness on the individuals that have them. Consider a hypothetical species of lizard in which larger-than-average individuals might be more easily spotted, captured, and eaten by predators. On the other hand, lizards that are smaller than average might not be able to run fast enough to escape.

Figure 16-7a shows the effect of stabilizing selection on body size in these lizards. The red curve shows the initial variation in lizard size as a standard bell curve. The blue curve represents the variation in body size several generations after a new predator was introduced. This predator easily captured the large, visible lizards and the small, slower lizards. Thus, selection against these extreme body types reduced the size range of the lizards. Stabilizing selection is the most common kind of selection. It operates on most traits and results in very similar morphology between most members of a species.

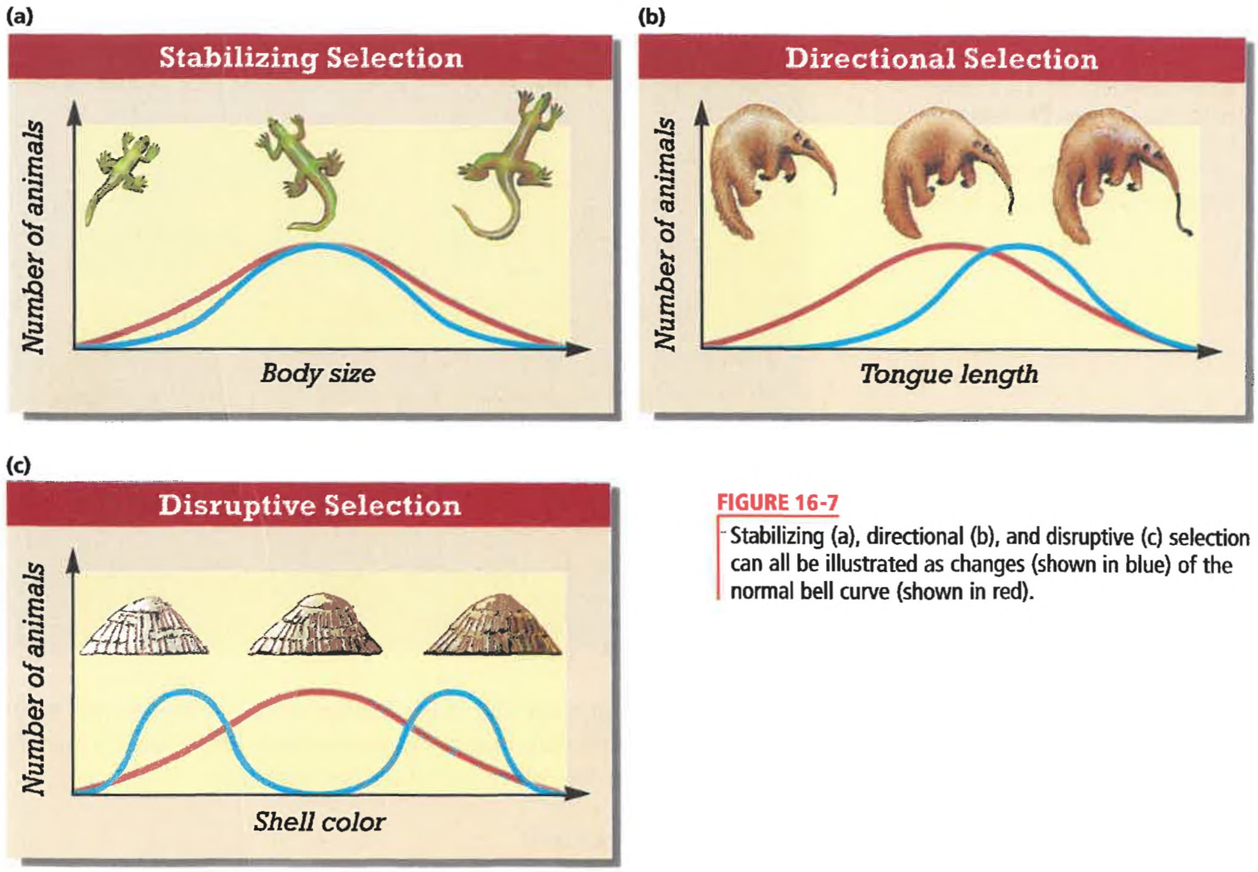


FIGURE 16-7

Stabilizing (a), directional (b), and disruptive (c) selection can all be illustrated as changes (shown in blue) of the normal bell curve (shown in red).

Directional Selection

In **directional selection,** individuals that display a more extreme form of a trait have greater fitness than individuals with an average form of the trait. Figure 16-7b shows the effects of directional selection on tongue length in anteaters. Anteaters feed by breaking open termite nests, extending their sticky tongue into the nest, and lapping up termites. Suppose that an area was invaded by a new species of termite that built very deep nests. Anteaters with long tongues could more effectively prey on these termites than could anteaters with short or average tongues. Thus, directional selection would act to direct the trait of tongue length away from the average and toward one extreme.

Disruptive Selection

In **disruptive selection,** individuals with either extreme variation of a trait have greater fitness than individuals with the average form of the trait. Figure 16-7c shows the effect of disruptive selection on shell color in marine animals called limpets. The shell color of limpets varies from pure white to dark tan. White-shelled limpets that are on rocks covered with goose barnacles, which are also white, are at an advantage. Birds that prey on limpets have a hard time distinguishing the white-shelled limpets from the goose barnacles. On bare, dark-colored rocks, dark-shelled limpets are at an advantage. Again, the limpet-eating birds have a hard time locating

FIGURE 16-8
Males sometimes display extreme traits, like the large tail of this peacock, *Pavo cristatus.* This trait is favorable if it attracts females and increases the reproductive fitness of the male.

the dark shells against the dark background. However, the birds easily spot limpets with shells of intermediate color, which are visible against both the white and dark backgrounds.

Sexual Selection

In many species of birds, the males are brightly colored and often heavily plumed, like the peacock shown in Figure 16-8. These elaborately decorated males are easy for predators to see. Why would natural selection work in favor of an organism being conspicuous to a predator? Females tend to choose the males they mate with based on certain traits. This is referred to as **sexual selection.** In order to leave offspring, a male must be selected by the female, and the peacock's gaudy plumage increases his chances of being selected. Extreme traits, such as heavy, brightly colored plumage, may give the female an indication of the quality of the male's genes. While survival to reproductive maturity is necessary, survival alone is not enough to further evolution. The genes of successful *reproducers,* rather than those of merely successful *survivors,* are amplified through natural selection.

SECTION 16-2 REVIEW

1. What is genetic drift?
2. Explain how mutation and immigration disrupt genetic equilibrium.
3. Compare and contrast stabilizing, directional, and disruptive selection.
4. What is sexual selection?
5. Name the five violations of the conditions necessary for Hardy-Weinberg genetic equilibrium that can cause evolution to occur.
6. CRITICAL THINKING Human newborns with either a very high or a very low birth weight are more likely to die in infancy. What type of selection does this seem to be?

FORMATION OF SPECIES

SECTION

16-3

OBJECTIVES

▲ Explain the difference between the morphological concept of species and the biological species concept.

● Define *geographic isolation,* and explain how it can lead to speciation.

■ Name three kinds of reproductive isolation.

◆ Summarize the punctuated equilibrium hypothesis, and contrast it with the hypothesis of gradual change.

How many species of organisms exist on Earth today? Undiscovered species are so numerous that we have no accurate answer. For example, even small areas of tropical rain forests can contain thousands of species of plants, animals, and microorganisms. New species are discovered and others become extinct at an incredible rate. In this section, you will learn how one species can become two through a process called speciation.

THE CONCEPT OF SPECIES

You have learned that existing species are essentially changed versions of older species. The process of species formation, **speciation** (SPEE-shee-AY-shun), results in many related populations of organisms. Some are very similar to their shared ancestral species, while other populations become quite different.

Morphological Concept of Species

For many years, scientists used the internal and external structure and appearance of an organism—its **morphology** (mor-FAHL-uh-jee)—as the chief criterion for classifying it as a species. Using the morphological concept of species, a species is defined primarily according to its structure and appearance. Because morphological characteristics are easy to observe, making species designations based on morphology proved convenient.

The morphological concept of species has limitations, however. There can be phenotypic differences among individuals in a single population. Notice, for example, the variation between the two red-tailed monkeys shown in Figure 16-9. To further complicate the matter, some organisms that appear different enough to belong to different species interbreed in the wild and produce fertile offspring. In response to the capacity of dissimilar organisms to reproduce, the biological species concept arose.

FIGURE 16-9
Individual red-tailed monkeys, *Cercopithecus ascanius,* can have different facial features.

(a)

(b)

FIGURE 16-10

Two types of pupfish that have limited ranges in the western United States are (a) *Cyprinodon macularius* and (b) *Cyprinodon nevadensis.*

The Biological Species Concept

According to the **biological species concept,** as proposed by German-born, American biologist Ernst Mayr (1904–), a species is a population of organisms that can successfully interbreed but cannot breed with other groups. While this definition is useful for living animals, the biological species concept does not provide a satisfactory definition for species of extinct organisms, whose reproductive compatibility cannot be tested. Nor is it useful for organisms that do not reproduce sexually. Thus, our modern definition of species includes components of both the morphological and biological species concepts. A species is a single type of organism. Members of a species are morphologically similar and can interbreed to produce fully fertile offspring. The many species alive today diverged from a smaller number of earlier species.

ISOLATING MECHANISMS

How do species give rise to other, different species? Speciation begins with isolation. In isolation, two parts of a formerly interbreeding population stop interbreeding. Two important types of isolation frequently drive speciation.

Geographic Isolation

Geographic isolation is the physical separation of members of a population. Populations may be physically separated when their original habitat becomes divided. A deep canyon could develop, a river could change course, or a drying climate in a valley could force surviving fragments of an original population into separate mountain ranges. Once the subpopulations become isolated, gene flow between them stops. Natural selection and genetic drift cause the two subpopulations to diverge, eventually making them incompatible for mating.

In pupfish, small freshwater fish shown in Figure 16-10, speciation following geographic isolation apparently took place in parts of the western United States, including the desert of Death Valley. Death Valley has a number of isolated ponds formed by springs. Each pond contains a species of fish that lives only in that one pond, but the fish species of various ponds in the area are quite similar.

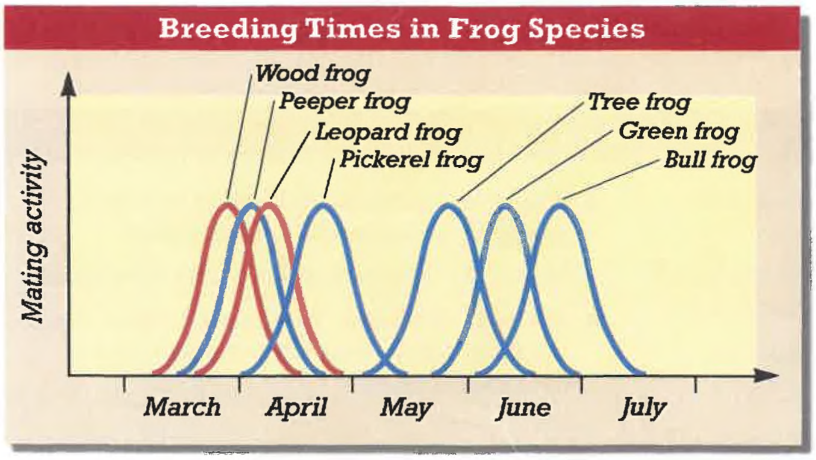
How did these different populations of fish become isolated in Death Valley? Geologic evidence indicates that most of Death Valley was covered by a lake during the last ice age. When the ice age ended, the region became dry, and only small, spring-fed ponds remained. Members of a fish species that previously formed a single population in the lake may have become isolated in different ponds. The environments of the isolated ponds differ enough that the separate populations of fish diverged. Eventually, the fishes in the different ponds diverged enough to be considered separate species.

Reproductive Isolation

Sometimes groups of organisms within a population become genetically isolated without being geographically isolated. **Reproductive isolation** results from barriers to successful breeding between population groups in the same area. Reproductive isolation and the species formation that follows it may sometimes arise through disruptive selection. Remember that in disruptive selection, the two extremes of a trait in a given population are selected for and the organisms begin to diverge. Once successful mating is prevented between members of the two subpopulations, the effect is the same as what would have occurred if the two subpopulations had been geographically isolated. There are two broad types of reproductive isolation: **prezygotic** (pree-zie-GAHT-ik) **isolation,** which occurs *before* fertilization, and **postzygotic isolation,** which occurs *after* fertilization.

If two potentially interbreeding species mate and fertilization occurs, success is measured by the production of healthy, fully fertile offspring. But this may be prevented by one of several types of postzygotic isolation. The offspring of interbreeding species may not develop completely and may die early, or, if healthy, they may not be fertile. From an evolutionary standpoint, if death or sterility of offspring occurs, the parent organisms have wasted their gametes producing offspring that cannot, in turn, reproduce.

This situation favors prezygotic mechanisms, such as incompatible behavior, that reduce the chance of hybrid formation. For example, a mating call that is not recognized as such by a potential mate can contribute to isolation. Differences in mating times are another type of prezygotic isolation. Both mechanisms are in effect for the frogs shown in Figure 16-11. Their mating calls and peak mating times, as shown in the graph, differ, reducing the chance of interbreeding. As a result, the wood frog and the leopard frog are reproductively isolated. Though these two frogs interbreed in captivity, they do not interbreed where their ranges overlap in the wild. As you can see in Figure 16-11, the wood frog usually breeds in late March and the leopard frog usually breeds in mid-April.



Word Roots and Origins

prezygotic

from the Latin *prae,* meaning "before," and the Greek *zygotos,* meaning "yoked"

FIGURE 16-11

As the graph shows, peak mating activity in frog species can vary widely. Such variance, coupled with different calls, has led to reproductive isolation in the wood frog, *Rana sylvatica,* top, and the leopard frog, *Rana pipiens,* bottom.

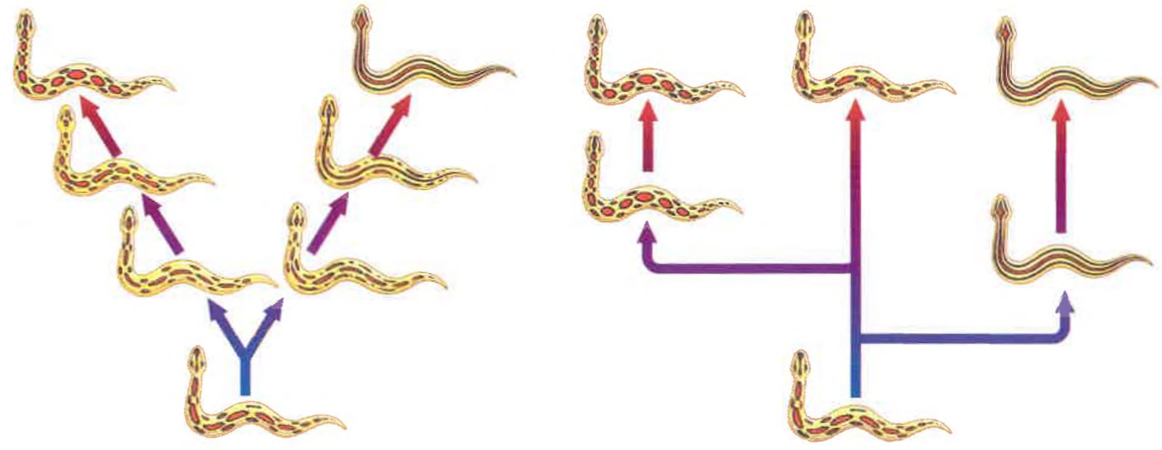


FIGURE 16-12

In the model of speciation presented on the left, species evolve gradually, at a stable rate. In the punctuated equilibrium model of speciation, illustrated on the right, species arise abruptly and are quite different from the root species. These species then change little over time.

RATES OF SPECIATION

Speciation sometimes requires millions of years. But apparently some species can form more rapidly. For example, Polynesians introduced banana trees to the Hawaiian Islands about a thousand years ago. Today, there are several species of moths that are unique to the Hawaiian Islands and that feed only on bananas. Because these species are closely related to other plant-eating moths in Hawaii, it seems likely that they have descended from ancestral moths during the past thousand years, since bananas were introduced to Hawaii.

Divergence of organisms and thus speciation may not occur smoothly and gradually. Indeed, the fossil record suggests that rapid speciation may be the norm rather than the exception. The fossil record seems to indicate that many species existed without change for long periods of time. The periods of stability were separated by an "instant" change in terms of geologic time. That is, a change occurred in a few thousand, rather than a few million, years. Scientists call this pattern of species formation **punctuated equilibrium.** The *punctuated* part of this term refers to the sudden shift in form that is often seen in the fossil record. Figure 16-12 shows two contrasting models, punctuated and gradual, of the evolution of two hypothetical species of snakes.

SECTION 16-3 REVIEW

1. What are two shortcomings of the biological species concept?
2. How can geographic isolation lead to speciation? What is the principal cause of such speciation?
3. Give two examples of postzygotic isolation mechanisms.
4. What is less metabolically costly to an animal, prezygotic or postzygotic isolation? Why?
5. What is the hypothesis of punctuated equilibrium?
6. CRITICAL THINKING What effect would a very short generation time, such as that of bacteria, have on speciation?

CHAPTER 16 REVIEW

SUMMARY/VOCABULARY

16-1

- Biologists study many different traits in populations, such as size and color.
- Traits vary and can be mapped along a bell curve, which shows that most individuals have average traits, while a few individuals have extreme traits.
- Variations in genotype arise by mutation, recombination, and the random fusion of gametes.
- The total genetic formation available in a population is called the gene pool.
- Allele frequencies in the gene pool do not change unless acted upon by certain forces.
- The Hardy-Weinberg genetic equilibrium, a theoretical model of a population in which no evolution occurs, tends to maintain the population as it is.

Vocabulary

allele frequency (300)
bell curve (299)
gene pool (300)
Hardy-Weinberg genetic equilibrium (302)
phenotype frequency (301)
population genetics (299)

16-2

- Evolution can take place if the genetic equilibrium of a population is disrupted.
- Immigration can bring new genes into a population, causing evolution.
- Nonrandom mating can alter the genotypes of a population, but it does not affect allele frequencies.
- Genetic drift operates in small populations; the contribution or lack of contribution of the genes of one or a few organisms can change the population's gene pool significantly.
- Stabilizing selection encourages the formation of average traits.
- Directional selection encourages the formation of more-extreme traits, such as a very long tongue in anteaters.
- Disruptive selection selects for extreme traits rather than average traits.
- In sexual selection, the development of traits that may seem harmful can actually enhance reproductive fitness if they encourage mating.

Vocabulary

assortative mating (306)
directional selection (307)
disruptive selection (307)
emigration (304)
gene flow (304)
genetic drift (305)
immigration (304)
sexual selection (308)
stabilizing selection (306)

16-3

- According to the biological species concept, a species is a population of organisms that can successfully interbreed and cannot breed with other groups.
- *Speciation* means species formation, and it always begins with a population that has become isolated.
- Geographic isolation results from the division of an original population.
- Reproductive isolation results from barriers to successful breeding. Prezygotic isolation occurs before fertilization. Postzygotic isolation occurs after fertilization and results in wasted gametes.
- Some scientists think that enormous phenotypic changes in species occur in sharp (punctuated) steps, rather than along a gradual curve, as Darwin proposed.

Vocabulary

biological species concept (310)
geographic isolation (310)
morphology (309)
postzygotic isolation (311)
prezygotic isolation (311)
punctuated equilibrium (312)
reproductive isolation (311)
speciation (309)

REVIEW

Vocabulary

1. Explain why the term *bell curve* is appropriate for a graph of a normal distribution of traits.
2. Explain the relationship between allele frequency and phenotype frequency.
3. Distinguish between the terms *directional selection* and *disruptive selection.*
4. Name the two broad types of reproductive isolation.
5. Explain the difference between punctuated equilibrium and gradual evolution.

Multiple Choice

6. Phenotypic traits often vary between two extremes, with most individuals having an average version of the trait. This can be graphed as a (a) Punnet square (b) bell curve (c) straight line (d) genotype frequency table.
7. Variations in genotype arise by random fusion of gametes, mutation, and (a) recombination (b) translation (c) transcription (d) sorting by phenotype.
8. The total genetic information in a population is called the (a) allele frequency (b) phenotype frequency (c) gene pool (d) distribution of traits.
9. Saint Bernards and Chihuahuas (two breeds of domestic dogs) cannot mate normally owing to great differences in size. Thus, they are reproductively isolated to some extent. What type of isolating mechanism is operating here? (a) developmental (b) prezygotic (c) postzygotic (d) geographic.
10. If a population is in genetic equilibrium,
    (a) evolution is occurring
    (b) speciation is occurring
    (c) allele frequencies change from one generation to the next
    (d) allele frequencies remain the same from one generation to the next.
11. Mutations affect genetic equilibrium by (a) maintaining it (b) introducing new alleles (c) causing immigration (d) causing emigration.
12. Directional selection, disruptive selection, and stabilizing selection are all examples of (a) genetic equilibrium (b) natural selection (c) mutation (d) speciation.
13. The most common way for new species to form is through (a) mutation (b) stabilizing selection (c) geographic and reproductive isolation (d) genetic equilibrium.
14. The tendency for males to develop extreme versions of traits that appeal to females is a result of (a) random mating (b) speciation (c) reproductive isolation (d) sexual selection.
15. In the population of four o'clock flowers shown below, what is the allele frequency of the *R* allele? (a) 33% (b) 25% (c) 50% (d) 67%

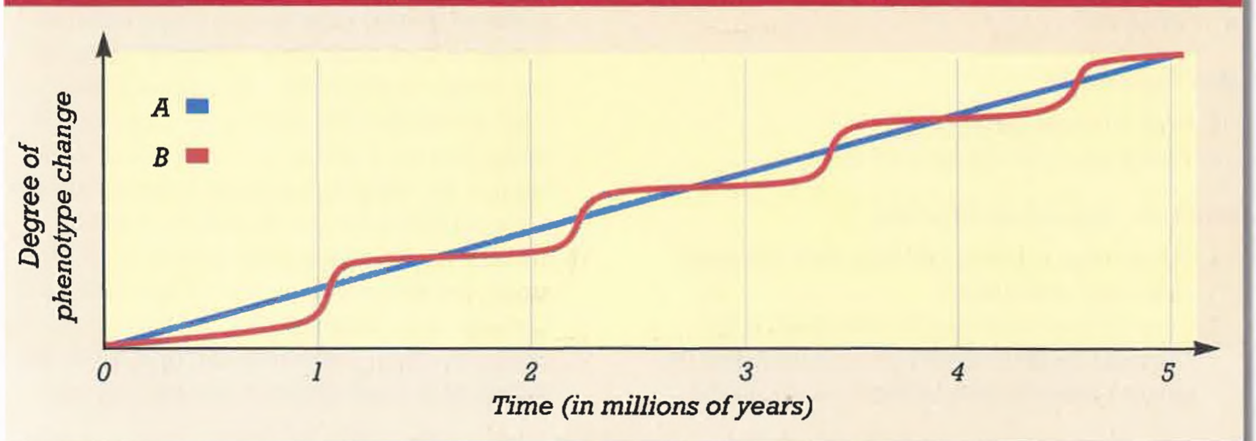
Short Answer

16. What causes variations in the traits of organisms?
17. What conditions are necessary for Hardy-Weinberg equilibrium?
18. What is gene flow?
19. How can immigration alter allele frequencies in a population?
20. What results can be expected from nonrandom mating?
21. What type of selection is shown when the bell curve narrows over time?
22. What kind of selection can result in speciation?
23. What is the relationship between natural selection and sexual selection?
24. Why do prezygotic isolating mechanisms have an advantage over postzygotic isolating mechanisms?
25. What is the relationship between evolution and natural selection?

Critical Thinking

1. Where populations of two related species of frogs overlap geographically, their mating calls are different. Where the species don't overlap, their calls are identical. What type of isolating mechanism is in operation?
2. Freeways may provide an effective geographic isolating mechanism for some slow-moving animals. Why are such artificial barriers not likely to result in complete speciation?
3. The most common definition of *species* states that a species is a group of organisms that can interbreed and produce fertile offspring in nature. A mule is a sterile offspring of a horse and a donkey. By the definition above, do a horse and a donkey belong to the same species? Explain your answer.
4. In the late nineteenth century, hunting reduced the population of the northern elephant seal to about 20 individuals. How might such a reduction in population have disrupted genetic equilibrium?
5. The graph below shows change in phenotype of two hypothetical species, A and B, over time. Use the graph to answer the following:
   a. What kind of evolution, punctuated or gradual, does the curve for species A represent?
   b. What kind of evolution does the curve for species B represent?
   c. Are the overall rates of change different for species A and B?
   d. What might have caused the vertical parts of the curve for species B?
   e. What do the horizontal parts of the curve for species B represent?

Phenotypic Change over Time in Two Species



Extension

1. Read "Evolving Backward" in *Discover*, September 1998, on page 64. Describe the two hypotheses that Dr. Diamond has developed to explain why humans have lost evolutionary traits, such as tails and body hair. Describe the eyes of a blind mole rat, and explain how the mole rat uses them.
2. Visit an area where plants or animals are bred. Possible places include farms, zoos, arboretums, seed companies, and nurseries. Find out how the breeders manipulate the genetic makeup of the plants or animals, and prepare an oral report on how this manipulation speeds up or slows down evolution. If you cannot visit one of the suggested locations, look in the *Readers' Guide to Periodical Literature* or use a CD-ROM-based index of periodic literature for articles on plant and animal breeding.

CHAPTER 16 INVESTIGATION

Predicting Allele Frequency

OBJECTIVES

- Demonstrate the effect of natural selection on genotype frequencies.

PROCESS SKILLS

- modeling
- predicting
- calculating
- analyzing

MATERIALS

- 200 black beads
- 200 white beads
- 3 containers
- labeling tape
- marking pen

Background

1. What is natural selection?
2. What is the result of natural selection?

PART A Random Mating

1. Obtain three containers, and label them "Parental," "Offspring," and "Dead."
2. Place 200 black beads and 200 white beads in the "Parental" container. Assume that each black bead represents a dominant allele for black coat *(B)* and that each white bead represents a recessive allele for white coat *(b)* in a hypothetical animal. Assume that the container holds gametes from a population of 200 of these hypothetical animals: 50 *BB*, 100 *Bb*, and 50 *bb*.
3. Without looking, remove two beads from the "Parental" container. What does this simulate?
4. In your lab report, make a data table like Table A below. Record the genotype and phenotype of the resulting offspring in your data table. Then put the alleles into the "Offspring" container.
5. Repeat steps 3 and 4 forty-nine times. Record the genotype and phenotype of each offspring in your data table.
6. Calculate the frequencies of alleles in the offspring. First make a table in your lab report like Table B shown on the next page. Then count and record the number of black beads in the "Offspring" container. This number divided by the total number of beads (100) and multiplied by 100% is the frequency of *B* alleles. Then count and record the number of white beads in the "Offspring" container. Determine the frequency of *b* alleles as you did with the *B* alleles.
7. Calculate the frequencies of phenotypes in the offspring. First make a table in your lab report like Table C, shown on the next page. Then count and record the number of offspring with black coat color. Divide this number by the total number of offspring (50) and

TABLE A MATING

Trial	Random mating		Nonrandom mating	
	Offspring genotype	**Offspring phenotype**	**Offspring genotype**	**Offspring phenotype**
1				
2				
3				
4				
5				

TABLE B ALLELE FREQUENCIES

Generation	Number of *B* alleles	*B* alleles/ total alleles	*B* allele frequency	Number of *b* alleles	*b* alleles/ total alleles	*b* allele frequency
Parental	200	200/400	50%	200	200/400	50%
Offspring						

TABLE C PHENOTYPE FREQUENCIES

Generation	Number of black animals	Black animals/ total animals	Frequency of black animals	Number of white animals	White animals/ total animals	Frequency of white animals
Parental	100	150/200	75%	50	50/200	25%
Offspring						

multiply by 100% to determine the frequency of black phenotype. Repeat this calculation to determine the frequency of white coat color among the offspring.

PART B Nonrandom Mating

8. Return the beads in the "Offspring" container to the container labeled "Parental."
9. Assume that animals with white-coat phenotype are incapable of reproducing. What is the genotype of animals with a white coat? To simulate this situation, remove 100 white beads from the container labeled "Parental," and set them aside.
10. Start by removing two beads from the container labeled "Parental," and record the results in your Table A. If the offspring has a white-coat phenotype, put its alleles in the container labeled "Dead." If the offspring has a black-coat phenotype, put its alleles in the container labeled "Offspring."
11. If animals with a white-coat phenotype cannot reproduce, predict what would happen to allele frequency if step 10 were repeated until the parental gene pool was empty. Write your prediction in your lab report.
12. Repeat step 10 until the parental gene pool is empty. Record the results of each pairing in your lab report in Table A. Compare your results with your prediction.
13. Transfer the beads from the "Offspring" container to the "Parental" container. Leave the beads that you have placed in the "Dead" container in that container. Do not return those beads to the parental container.
14. Repeat step 10 again until the parental pool is empty. Record your results in your data table.
15. Repeat steps 13 and 14 two more times.
16. Calculate the frequencies of the final genotypes produced, as you did in Part A. Compare the results with your prediction from step 11.
17. Clean up your materials before leaving the lab.

Analysis and Conclusions

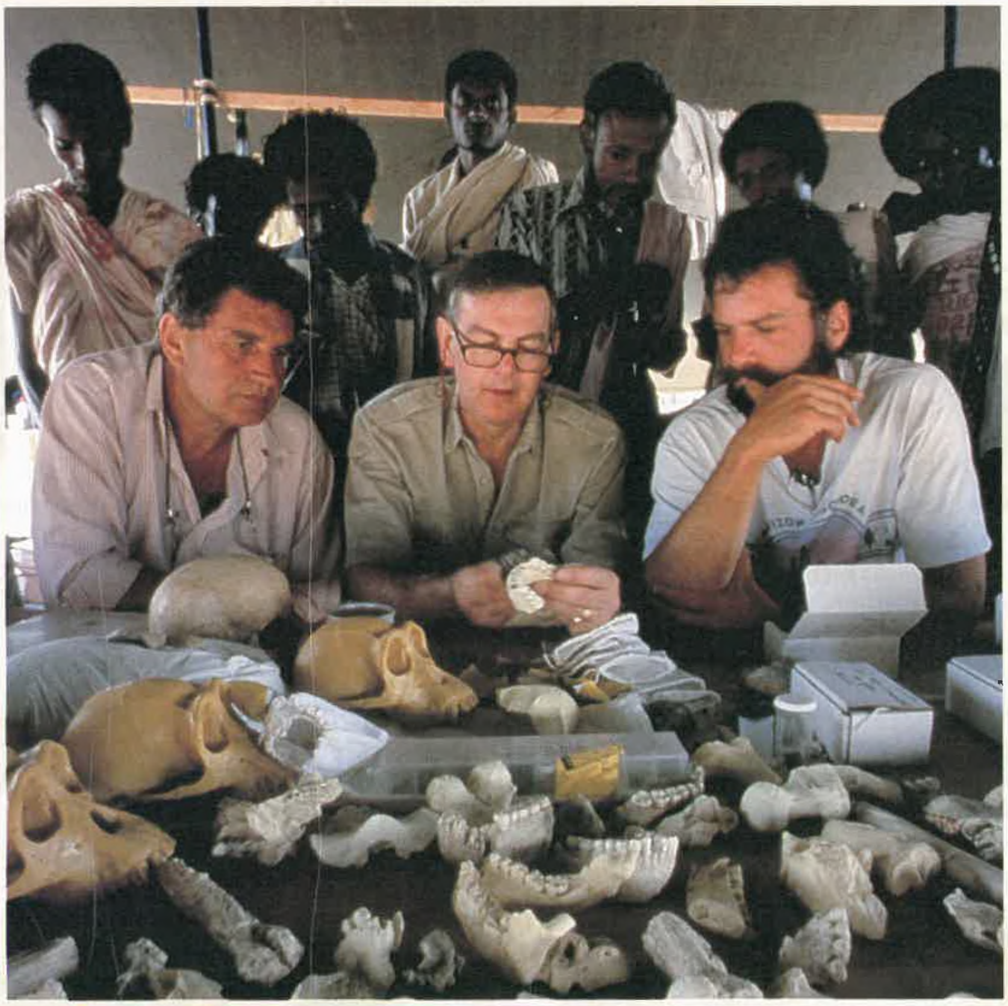
1. Compare the frequency of recessive alleles produced in Part A with that produced in Part B. Did you correctly predict the frequencies?
2. Did the frequency of the *b* allele change uniformly through all generations? If not, what happened?
3. Why did you remove 100 white beads from the "Parental" container in Step 9?
4. How did this change the phenotype frequency of white animals in the parental generation from the original ratio of 50/200?

Further Inquiry

If you continued Part B, would you eventually eliminate the *b* allele? Form a hypothesis and test it.

CHAPTER 17

HUMAN EVOLUTION



Scientists Yoel Rak (seated at left), Donald Johanson (center), and William Kimbel (right), together with a group of Afar tribesmen, examine an early hominid jawbone at a field laboratory at Hadar, Ethiopia.

FOCUS CONCEPT: *Evolution*

As you read, pay attention to how scientific methods are used to formulate conclusions about human origins.

THE STUDY OF HUMAN ORIGINS

To understand the story of human evolution, we must understand both our ancestry and our relationship to our closest living kin. Humans are members of the ancient mammalian order Primates. Primates have grasping hands, acute vision, and large brains. Primate parents provide extended periods of intense care for their young, and many primate species live in complex social groups. As you will see, many of our behaviors and characteristics are similar to those of other primates, and some are uniquely human.

SECTION

17-1

OBJECTIVES

▲ Describe how paleoanthropologists gather evidence of human ancestry.

● List some traits shared by all primates.

■ Name two distinguishing characteristics of anthropoids.

◆ Give examples of traits unique to humans.

THE HOMINID FOSSIL RECORD

Scientists who study fossil evidence of human evolution are called **paleoanthropologists** (PAY-lee-oh-AN-thro-PAHL-uh-jists) or biological anthropologists. Just as detectives try to solve mysteries, paleoanthropologists piece together an assortment of clues to construct models of how and when different stages of human evolution occurred. Much of the information available about human evolution comes from the fossilized bones of early **hominids** (HAHM-uh-nidz), a group that comprises humans and their immediate ancestors. Fossilized hominid remains are seldom complete skeletons—often only fragments of fossilized bone are found. Scientists pay close attention to subtle clues in these fossils. For example, the curvature of the spine, the position at which the spine attaches to the skull, and the shape of the **pelvis,** or hipbones, can indicate whether an organism walked upright. Similarly, a skull fragment can be used to estimate brain size, and wear on a fossil tooth can give some indication of an organism's diet.

Often the immediate surroundings of a fossil give important clues to how the species lived. Sometimes stone tools and the bones of prey are found with the fossil, and the geologic stratum in which the fossil is found can give the approximate age of the fossil. Other information, such as climate, forestation, and food sources prevalent at the time the fossil species lived, can sometimes be determined from traces of plant remains and pollen grains.

Word Roots and Origins

hominid

from the Latin *homo,* meaning "human being," and the Greek *-ides,* meaning "a thing belonging to"

FIGURE 17-1

The grasping fingers and toes and front-facing eyes of the tarsier, *Tarsius* sp., are primate characteristics that serve well for a life in the trees. The tarsier, like many prosimian primates, is nocturnal.

PRIMATE CHARACTERISTICS

Hominids belong to the order of mammals known as **primates.** Two large divisions of modern primates are recognized. The **anthropoid** (AN-thruh-POID) **primates** include marmosets, monkeys, apes, and humans. **Prosimian** (proh-SIM-ee-uhn) **primates,** many of which resemble very early primate forms, include lemurs, lorises, and tarsiers, like the one shown in Figure 17-1. Fossils of extinct primates reveal that the majority of them lived in trees, as do most modern species. Many of the characteristics that primates share apparently evolved as adaptations to life in trees.

Primates have movable fingers and toes, and most have flattened nails rather than claws. The hands and, in some species, the feet are **prehensile** (pree-HEN-sil), or grasping. Unlike most mammals, primates have color vision. This may have arisen when primates became more active during the day than at night, a change that occurred about 60 million years ago. The front-facing eyes found in primates result in broadly overlapping fields of vision. This allows primates to perceive depth—a useful trait for an animal that moves by swinging or jumping from branch to branch in trees.

Characteristics of Anthropoids

Anthropoid primates, such as the gibbon shown in Figure 17-2, have a well-developed collarbone, rotating shoulder joints, and partially rotating elbow joints. Anthropoids also have an **opposable thumb**—a thumb that can be positioned opposite the other fingers. This arrangement of fingers results in increased precision in the use of the hands. Additionally, nonhuman anthropoids have an opposable big toe, as seen on the chimpanzee in Figure 17-3, and this prehensile foot is an important aid to climbing.

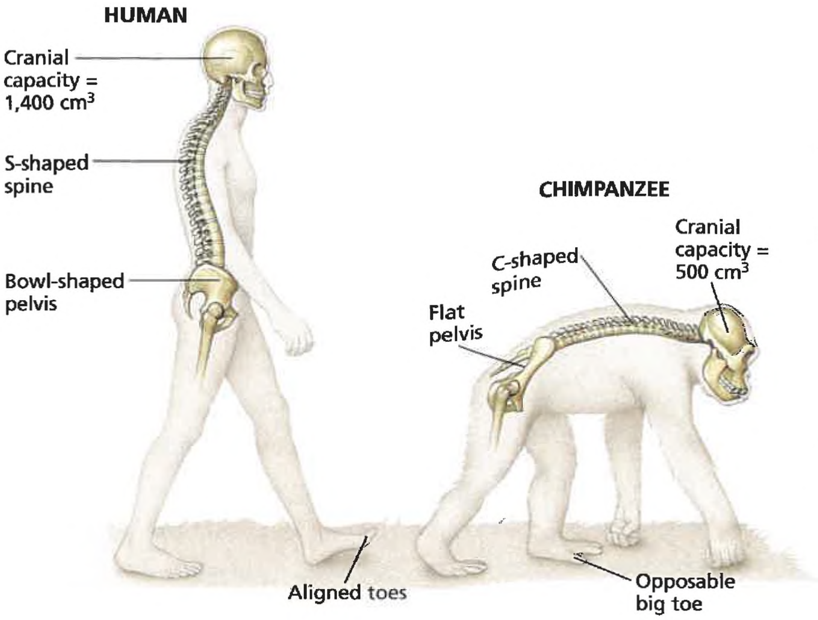
All anthropoids have a similar **dental formula,** or number and arrangement of teeth. In humans, apes, and African and Asian monkeys, each half of the upper and lower dental arches includes two incisors, one canine, two premolars, and three molars, as shown in Figure 17-3.

Compared with other primates, anthropoids have a large brain relative to their body size. The fossil record shows that as primates evolved, brain size increased. Humans and the **great apes** (gibbons, orangutans, gorillas, and chimpanzees) have a larger cranial capacity relative to body size and a more complex brain structure than other primates have.

Of the anthropoid species, the chimpanzees may be the most closely related to humans. Comparisons of chimpanzee and human DNA have shown a very high degree of similarity. This similarity suggests that humans and chimpanzees may have shared an ancestor less than 6 million years ago. It is important to understand, however, that humans are not descended from chimpanzees or from any other modern ape. Rather, modern apes and humans are probably descended from a more primitive apelike ancestor.

FIGURE 17-2

Mobile arm-and-shoulder anatomy allows anthropoids such as this gibbon, *Hylobates lar*, to swing by their arms through trees.



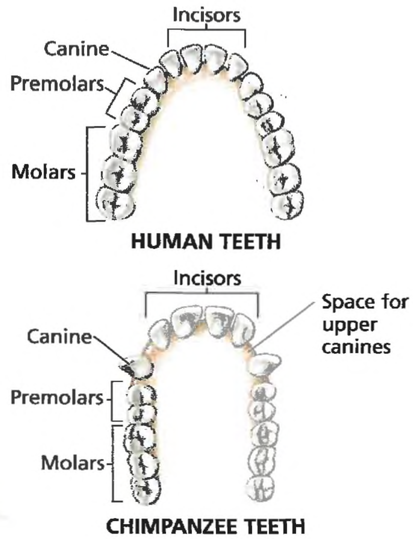


FIGURE 17-3

Some human physical characteristics differ markedly from those of the chimpanzee, a modern ape. The human jaw is rounder than the U-shaped jaw of the ape. The human pelvis is cup-shaped, compared with the flatter ape pelvis. The human spine is S-shaped, compared with the single curve of the ape spine. The human foot has short, aligned toes, compared with the longer, grasping toes—and the opposable big toe—of the ape.

Characteristics of Humans

Bipedalism (bie-PEED-uhl-iz-uhm), the ability to walk primarily on two legs, is a uniquely human trait among mammals. Figure 17-3 shows that the cup-shaped human pelvis supports the internal organs during upright walking. The human spine has two curves, resulting in an S shape that allows for upright posture.

In the human foot, the toes are much shorter than those of apes and are aligned with each other. Because humans are the only primates that have this foot structure, we can infer that the shape of the human foot is a specific adaptation for bipedalism.

The enlargement of the brain in humans has resulted in a more vertical face than that found in apes. Among other differences, the larger human brain has extensive areas devoted to the production and understanding of speech. Apes have homologous areas in their brains that are important in the production of sounds used in communication, and apes can also be taught to mimic certain forms of sign language. However, apes living in the wild have not developed any complex, flexible set of signals that can compare to those that make up the languages of humans.

SECTION 17-1 REVIEW

1. What do paleoanthropologists study, and how do they gather their information?
2. What might a paleoanthropologist infer from the surroundings of a fossilized hominid?
3. Name two characteristics of all primates, and explain how these characteristics appear to be adaptations to life in the trees.
4. What features distinguish anthropoids from the other primates?
5. What are two specifically human traits?
6. CRITICAL THINKING How might the acquisition of language account for the very fast cultural and intellectual development that has occurred in the evolution of humans?

GREAT DISCOVERIES

Africa: Cradle of Humanity

HISTORICAL PERSPECTIVE

In 1871, Charles Darwin predicted that the remains of human ancestors would be found in Africa because our closest living relatives—the great apes—are found there today. But Darwin may have been in the minority. Before 1925, many scientists believed that the first humans had evolved in Europe or Asia no more than 200,000 years ago. Kenyan-born British archaeologist Louis Leakey was firmly convinced that he would find evidence to support Darwin's prediction. Louis Leakey, working together with his wife, Mary Leakey, compiled substantial evidence that Africa, not Europe or Asia, was the birthplace of humans. Moreover, the Leakeys' many fossil discoveries suggested that the first hominids were far older than previously believed. The Leakeys were drawn to Olduvai Gorge, where they carried out much of their lifework, by the abundance of primitive stone tools that had been found in the vicinity.

A Gorgeous Site

Olduvai Gorge is a steep-sided ravine in northern Tanzania. It lies in the East African Rift Valley, an area extending from the Red Sea to Mozambique. Two million years ago, the site of the gorge was occupied by a lake, which later filled with layers of sediment and volcanic ash that were ideal conditions for fossil preservation. Layering of sediment continued for more than 2 million years, resulting in seven major layers, referred to as "beds." Cross sections of these seven beds, exposed by the erosion of the river that cut the gorge, have yielded an extraordinarily rich record of the animal and plant life that existed in the area from 2.1 million to 15,000 years ago.

Mary Leakey vividly described the landscape of Olduvai in her 1984 autobiography, *Disclosing the Past:*

Louis and Mary Leakey

> *As one comes over the shoulder of the volcanic highlands to start the steep descent...suddenly one sees the Serengeti, the plains stretching away to the horizon like the sea....Away to the right are Precambrian outcrops and an almost moon-like landscape. To the left, the great slopes of the extinct volcano Lemagrut dominate.*

Together the Leakeys excavated Olduvai Gorge and found that it yielded more information about human ancestors than any other site that had been found.

Uncovering Africa's Secrets

In July of 1959, after years of searching at Olduvai Gorge, Mary Leakey discovered a hominid skull, leg bone, jaw, and tooth. The skull was in fragments but was otherwise well preserved. After the Leakeys spent many hours patiently fitting the fragments together, the skull took shape. The teeth were large, and a massive bony ridge dominated the top of the skull, indicating that the hominid had very strong neck and jaw muscles. Most important, the hominid bones, later called *Australopithecus boisei,* were accompanied by stone artifacts and animal bones. The task that lay ahead was to determine their age.

To date the skull, the Leakeys used a relatively new technique that

Louis and Mary Leakey were first drawn to Tanzania's Olduvai Gorge by the abundance of primitive stone tools that had been found in the vicinity.

measures the ratio of potassium to argon in volcanic rocks. This method determines age by measuring the radioactive decay of isotopes of potassium with sophisticated equipment. With this technique, the skull revealed that the origin of humans dated back at least 1.75 million years.

In 1960, the Leakeys discovered fossils of a hominid species that dated as far back as 2 million years. Details of the hominid's anatomy, such as tooth characteristics and size and shape of the skull, jaw, and leg bones, were quite different from those of the earlier fossils—they were much more like those of modern humans. The species was relatively large-brained and was probably a tool user. The species was therefore named *Homo habilis,* or "handy human."

Because some of the *Homo habilis* fossils came from the same rock layers as earlier finds, it appeared that this new species may have been a contemporary of *Australopithecus.* This was an important discovery because it implies that the course of human evolution was not necessarily an orderly progression, with one species giving rise to the next. Rather, the family tree of modern humans probably has many branches. Several species may have lived at once. Most early species probably died out without leaving descendants. Modern humans probably arose from a single ancestral line that successfully adapted and evolved while its cousins perished. *Homo habilis* was accepted as an early ancestor of modern humans.

In 1978, Mary Leakey made the dramatic discovery of several sets of bipedal footprints in volcanic ash at Laetoli, a site located south of Olduvai Gorge. When the ash was analyzed, the footprints were dated at 3.6 million years old, clearly demonstrating that human ancestors became bipedal very early.

The Research Continues

The Leakeys' early work formed the basis for much of the research into human origins that continues today. In addition to paleoanthropology, Louis Leakey had a lively interest in modern primates. He directly influenced Jane Goodall's research on chimpanzee behavior, Birute Galdikas Brindamour's research on orangutan behavior, and Dian Fossey's research on mountain gorilla behavior.

Louis and Mary Leakey's son Richard Leakey and his wife, Meave Leakey, are still actively excavating sites in eastern Africa. In 1984, at Lake Turkana, near Kenya's border with Ethiopia, Richard unearthed a skull and later an entire skeleton that at the time were the earliest known specimens of *Homo erectus,* the species that directly preceded *Homo sapiens.* In 1996, Meave Leakey and her team announced the discovery of the oldest known hominid species—*Australopithecus anamensis.* These discoveries underscore the elder Leakeys' contention that Africa is the ancestral home of the human family, the place where humans first became tool users, and ultimately is the cradle of humanity.

Years of painstaking work by the Leakeys produced a great variety of hominid fossils from several different periods.

SECTION

17-2

OBJECTIVES

▲ Explain how the discovery of Lucy changed hypotheses about the evolution of bipedalism.

● Explain the significance of finding fossils of hominids that are not ancestral to modern humans.

■ List the fossil finds of 1995, and discuss their significance regarding the evolution of bipedalism in hominids.

FOSSIL EVIDENCE OF HOMINID EVOLUTION

Scientists who study the fossil remains of early hominids have inferred the evolutionary trends toward a larger brain and bipedalism. The fossils of hominids, unlike those of apes and their ancestors, show a whole spectrum of unique adaptations for upright walking.

THE FIRST HOMINIDS

Bipedalism is the principal trait that defines the hominid line. Modern nonhuman anthropoid primates are **quadrupedal** (kwah-DROO-pi-duhl); that is, they walk on four limbs. The apelike ancestors of the first hominids likely were quadrupedal as well. How long ago did the first bipedal primate, that is, the first hominid, evolve? This question has not yet been answered conclusively.

In 1974, a 3.2-million-year-old fossil of a primate was found in the Afar Valley region of eastern Africa by Donald Johanson, shown in the photograph on the first page of this chapter, and his colleagues. The fossil, shown in Figure 17-4, is unusually well preserved. The cranial capacity, which is used as an approximation of brain size, is about equal to that of a chimpanzee (475 cm^3), or about one-third that of a modern human (1,400 cm^3). The fossil primate's height ranged from 1 to 1.5 m, probably varying according to gender. The pelvis and leg bones, however, clearly indicated that the fossil organism was an upright-walking hominid.

This find changed many ideas about the evolution of humans. It was generally thought that the hallmarks of hominids—bipedalism and a large brain with areas dedicated to higher reasoning and the production of speech—had all evolved at the same time. But the new fossil showed that upright walking had apparently come before many of these other adaptations that make the hominids unique among the anthropoid primates.

Word Roots and Origins

quadrupedal

from the Latin *quattour,* meaning "four," and *pes,* meaning "foot"

internet**connect**

SCiLINKS. NSTA

TOPIC: Fossil evidence of hominid evolution
GO TO: www.scilinks.org
KEYWORD: HM324

AUSTRALOPITHECUS

The new fossil find was given the species name *Australopithecus afarensis* (abbreviated *A. afarensis*), which means "southern ape of the Afar Valley." Unofficially this female fossil is called **Lucy.** Since 1974, other specimens of the same species have been discovered. They date from about 3 million to 3.9 million years ago.

Other Australopithecines

A number of other fossils that are similar to *A. afarensis* (Lucy) have been discovered from time to time. All of these finds have now been designated **australopithecines** (aw-STRAY-loh-PITH-uh-seenz)—organisms from the genus *Australopithecus. Australopithecus africanus,* which dates from about 2.3 to 3 million years ago, probably descended from *A. afarensis. A. africanus* was taller and heavier than Lucy and had a slightly larger cranial capacity, between 430 and 550 cm^3.

Two more-recent species, *Australopithecus robustus,* shown in Figure 17-5, and *Australopithecus boisei,* date from about 1 to 2.6 million years ago. These species had heavier skulls and larger teeth than *A. afarensis.* The cranial capacity in *A. robustus* and *A. boisei* ranged from 450 to 600 cm^3. The general appearance of these other australopithecines suggests that while they may have descended from *A. afarensis* (Lucy's species), they were probably not ancestral to modern humans.

In the past two decades, fossil finds of hominids have increased dramatically due to increased research on human origins. In 1995, Meave Leakey and her colleagues at the National Museums of Kenya announced the discovery of a new fossil representing a species distinct from and older than *A. afarensis.* This species, named *Australopithecus anamensis,* is 300,000 years older than any hominid fossil previously found. While the head and neck of *A. anamensis* share several features with modern chimpanzees, a shinbone found at the site indicates that *A. anamensis* was bipedal. Fossil evidence of very early bipedal primates is not limited to fossilized bones. Fossilized footprints dating back 3.6 million years further confirm that bipedalism occurred very early, before—and not as a result of—the rapid enlargement of the hominid brain.

FIGURE 17-4

The original fossil find of *Australopithecus afarensis* consisted of a partial skeleton. The fossil was given the nickname Lucy by the team of investigators who discovered it.

FIGURE 17-5

This well-preserved *Australopithecus robustus* skull shows the heavy bone structure and large teeth characteristic of the species.

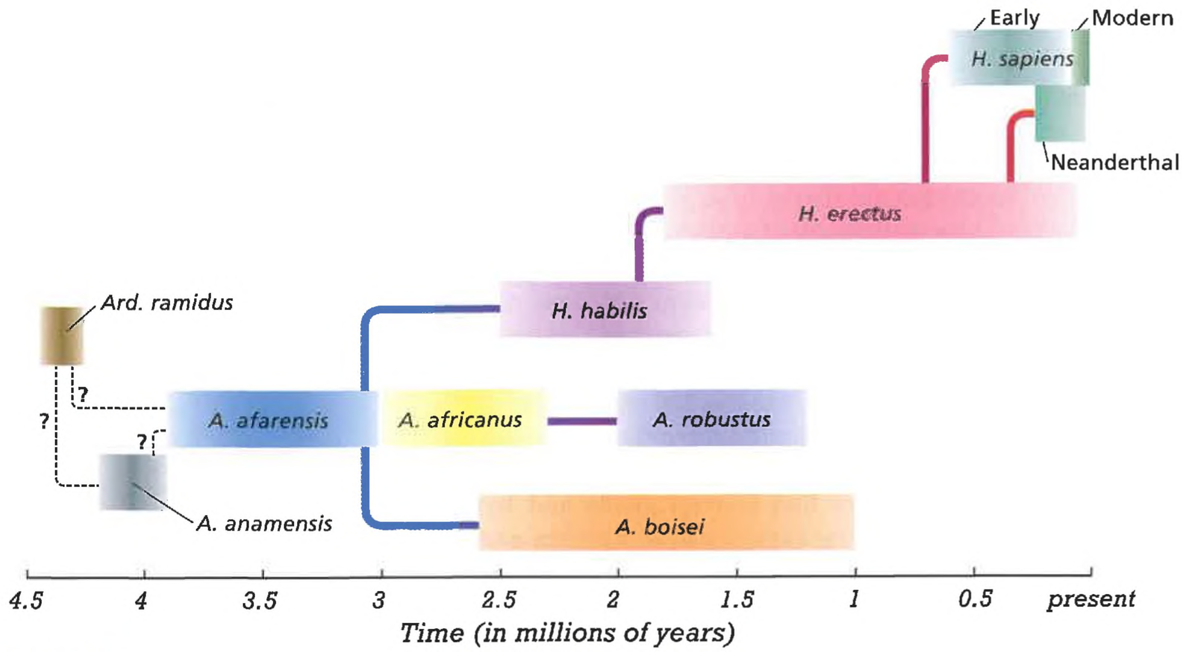


FIGURE 17-6

Physical anthropologists sometimes offer conflicting models of the progression of forms in human evolution. This phylogenetic tree represents one popular view.

An Older Hominid?

In 1995, Tim White (1950–), of the University of California–Berkeley, and his colleagues announced the discovery of fossils representing a new genus that predates the earliest known australopithecines by 200,000 years. Examination of these fossils may ultimately indicate whether the newly discovered primate, *Ardipithecus ramidus,* was bipedal and thus a hominid. It remains to be determined whether this species was ancestral to the australopithecines or whether it was one of several that died out during the course of human evolution.

It is important to understand that human evolution did not occur in a single, uninterrupted parade of increasingly humanlike forms. Rather, there is fossil evidence of several hominid forms that arose and died out, leaving no descendants. Moreover, as Figure 17-6 shows, it is clear that different species of hominids lived at the same time and, in some cases, in the same area. Thus, the human phylogenetic tree has many branches.

SECTION 17-2 REVIEW

1. Lucy was a small-brained hominid. What assumption did her discovery change?
2. What were the probable fates of *Australopithecus robustus* and *A. boisei*?
3. What does the existence of hominid species that were not ancestral to modern humans imply?
4. How do the ages of the fossil finds of 1995 compare with the ages of previous hominid finds?
5. *Ardipithecus* may be a hominid or a prehominid. What characteristic distinguishes hominids?
6. **CRITICAL THINKING** When analyzing fossils, scientists examine the foramen magnum, the opening for the spinal cord in the base of the skull. What does location of the foramen magnum on a skull tell about the posture of an animal?

SECTION

17-3

OBJECTIVES

▲ Name two behavioral advances made by *Homo* species.

● Describe where Neanderthals are placed on the hominid phylogenetic tree.

■ Contrast the multiregional hypothesis of the evolution of modern humans with the hypothesis of recent African origin.

HYPOTHESES OF HOMINID EVOLUTION

Starting in the early part of the twentieth century, scientists have worked continually to establish a robust fossil record of human evolution. This work has been rewarded by the discovery of many hominid life-forms, some of which are clearly identifiable as a known type, while others appear to be transitions between known types. As scientists fill in the puzzle of human evolution, they have been surprised by some of their discoveries: dead-end branches of the family tree, as well as evidence that two or more quite different hominid forms may have coexisted.

EARLY MEMBERS OF *HOMO*, THE HUMAN GENUS

In the early 1960s, paleoanthropologists working in East Africa found a hominid skull with a much larger brain case than that of the australopithecines. This fossil was the first evidence of an early hominid species that had a cranial capacity as large as 600 to 800 cm^3 but was only slightly taller than *A. afarensis*. The human-like morphology apparent in these fossils resulted in the grouping of this species in the human genus, *Homo*.

Homo habilis

Unlike australopithecine fossils, these newly discovered remains were found along with stone tools. This finding led to the naming of the new species as *Homo habilis*, meaning "handy human." Additional remains of *H. habilis* were later found in southern and eastern Africa, where the first fossils were found. These fossils are between 1.6 million and 2.5 million years old. Some studies of *H. habilis* skulls indicate that a region of the brain essential to speech may have existed in this species. Tool marks on animal bones found near the hominid fossils suggest that *H. habilis* ate meat.

Homo erectus

Fossils of *Homo erectus* (meaning "upright human") were found as early as 1891. They were originally found on the Pacific island of Java and have since been found in China, Europe, and Africa. Thus,

internetconnect

SCILINKS NSTA

TOPIC: *Homo erectus*
GO TO: www.scilinks.org
KEYWORD: HM327

FIGURE 17-7

This reconstruction of a *Homo erectus* skull (a) shows a prominent brow, low forehead, and large, protruding teeth. Contrast these traits with those of the skull of a modern *Homo sapiens* (b).

(a) (b)

H. erectus was apparently the first hominid to travel out of Africa. *H. erectus* fossils range from 1.8 million to less than 50,000 years old.

Compared with modern humans, *H. erectus* had a thick skull, large brow ridges, a low forehead, and large, protruding teeth, as shown in Figure 17-7. Their cranial capacity ranged from 700 to 1,250 cm^3, so the average brain size was about two-thirds that of modern humans. The fossil of an almost complete *H. erectus* skeleton, called the Turkana boy, is the remains of a 12-year-old male who stood about 1.7 m (5 ft 7 in.) tall. This means that *H. erectus* adults could easily have been as tall as modern humans.

Traces of charred bones indicate that *H. erectus* were hunters who used fires for cooking and probably for warmth. To survive in the colder climates of Europe and northern Asia, many *H. erectus* groups lived in caves.

HOMO SAPIENS

An early, now-extinct form of our species, *Homo sapiens,* probably arose from *Homo erectus* about 800,000 years ago. Over the years, evidence of hominid forms that were transitional between *H. erectus* and *H. sapiens* has been found. Some skulls have the large brow ridges of *H. erectus* and the large cranial capacity of *H. sapiens*. When *H. sapiens* arose, they did not completely replace *H. erectus* right away. Recent finds of *H. erectus* fossils indicate that this species existed until as recently as 50,000 to 35,000 years ago. Thus, *H. sapiens* and *H. erectus* may have coexisted for more than 700,000 years.

Neanderthals

FIGURE 17-8

Neanderthals had larger brains than modern humans, but they were shorter and stockier. They lived and hunted in groups. They disappeared about 35,000 years ago.

Many examples of a distinctive type of hominid fossil skeleton dating from 230,000 to 30,000 years ago have been found in Europe and Asia. They belong to a group of early *H. sapiens* called Neanderthals (nee-AND-uhr-TAHLZ). Neanderthals, shown in Figure 17-8, had heavy bones, thick brow ridges, and protruding teeth. However, the cranial capacity of Neanderthals averaged 1,450 cm^3. This is slightly larger than the cranial capacity of modern humans. Neanderthals stood about 1.5 m (5 ft) tall but were heavily built. They lived in caves and stone shelters during the last ice age. Their carefully shaped stone tools, probably used to scrape animal hides, have led scientists to speculate that they wore clothing made of skins. Many paleoanthropologists think that Neanderthals were not ancestral to modern humans. In Europe, Neanderthals disappeared at approximately the same time that modern *H. sapiens* arrived in large numbers, leading some scientists to hypothesize that the Neanderthals were killed off violently or by disease and replaced by modern humans.

Modern *Homo sapiens*

The first fossil skeletons bearing a distinct resemblance to modern humans were discovered in caves in southwestern France. The fossils are about 35,000 years old. Older fossils of the same type have been found elsewhere in Europe, as well as in Africa, Asia, and even Australia. These early modern humans are referred to as Cro-Magnons, named for the cave where they were originally discovered. Cro-Magnons had a cranial capacity equal to that of modern humans, 1400 cm^3. They are distinguished from Neanderthals by their high forehead and lack of protruding brow ridge and teeth. Taller than Neanderthals, they stood about 1.8 m (6 ft) tall.

The oldest truly modern *H. sapiens* fossils yet found are about 100,000 years old and were found in Africa. Modern *H. sapiens* probably coexisted with the Neanderthals for about 70,000 years and with *H. erectus* for more than 50,000 years. As the Neanderthals declined, modern humans became more advanced and prevalent. About 50,000 years ago, they became more efficient hunters and home builders, and their tools became distinctly more sophisticated.

SPREAD OF MODERN HUMANS

All modern humans belong to a single species, *Homo sapiens*. There are phenotypic differences, such as skin color, associated with people living in different regions. However, all *H. sapiens* are genetically similar enough to produce offspring together. How did these different phenotypes arise?

Multiregional Evolution

Some anthropologists propose that modern humans evolved in parallel all over Earth from different populations of *Homo erectus*. For this process to result in a single species of modern human, as actually exists, constant gene flow between the different populations would be necessary. Without exchanges of genes during the transition from *H. erectus* to *H. sapiens*, the different populations would tend to speciate into separate groups, in response to local environmental pressures.

If the **multiregional hypothesis,** outlined in Figure 17-9a, is correct, it would suggest that regional differences in phenotype have been developing for well over a million years. Some investigators

Quick Lab

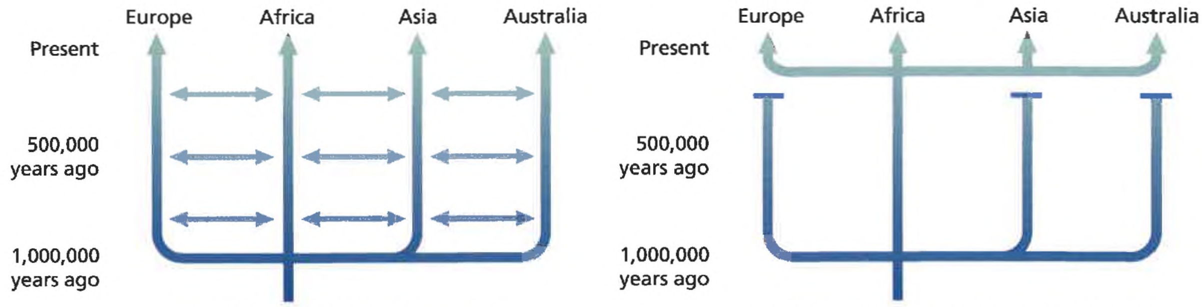
Comparing Cranial Capacities

Materials calculator, 2 L plastic soda bottles (4), graduated cylinder, water, paper, pencil, wax marking pencil

Procedure

1. Using the data provided on pp. 327–329, calculate the average cranial capacity for *Homo habilis, Homo erectus,* and both groups of *Homo sapiens* (Neanderthals and modern humans).
2. Convert your averages to milliliters. (1 cm^3 = 1 mL)
3. Label one of the plastic soda bottles *"Homo habilis."* Label another bottle *"Homo erectus."* Label the third bottle *"Homo sapiens* (Neanderthal)" and the fourth bottle "Modern *Homo sapiens."*
4. Fill a graduated cylinder with an amount of water equal to the average cranial capacity of *Homo habilis.* Pour the water in the appropriately labeled bottle.
5. Repeat step 4 for each of the remaining three species, and record your observations.
6. Calculate in cubic centimeters the change in average cranial capacity between each species over time.

Analysis Based on your calculations and observations of cranial capacities, which species had the smallest brain? How small was it? Which species had the largest brain? How large was it? Between which two species did you find the greatest change in cranial capacity? What trend can you observe in the change in cranial capacity over time? What might explain such a trend?



(a) MULTIREGIONAL HYPOTHESIS

(b) RECENT-AFRICAN-ORIGIN HYPOTHESIS

FIGURE 17-9

According to the multiregional hypothesis of human evolution (a), parallel populations of *H. sapiens* evolved from different *H. erectus* populations around the world. The hypothesis of recent African origin (b) states that modern *H. sapiens* evolved in Africa and spread throughout the world, replacing populations of *H. erectus* and early *H. sapiens.*

claim that Asian fossils of *Homo erectus* show the high cheek bones seen in modern *Homo sapiens* living in Asia.

Out of Africa

The more widely supported hypothesis, the **recent-African-origin hypothesis,** states that modern *Homo sapiens* originated in Africa only about 100,000 to 200,000 years ago and then, like *Homo erectus* before them, left Africa. They colonized the world, displacing and causing the extinction of *Homo erectus* and early *Homo sapiens,* such as the Neanderthals.

The recent-African-origin hypothesis gets much of its support from studies of the genes found in mitochondria. Because mitochondria reproduce asexually, their genes are not subject to the mixing caused by gene flow and meiosis. If humans were one large population dating back to over a million years ago, we should find human mitochondria that show a million years of accumulated mutational differences. Instead, most human mitochondria have very similar genes. The period of time needed for mitochondria to accumulate the differences actually seen is only 100,000 to 200,000 years—far short of a million years. Because all human mitochondria are so similar, supporters of this hypothesis infer that all modern humans came from one small group in Africa a fairly short time ago—100,000 or 200,000 years ago.

SECTION 17-3 REVIEW

1. **What clues do paleoanthropologists look for when they try to determine the habits and capabilities of early hominids?**
2. **What are two behavioral advances that distinguished *Homo erectus* from *H. habilis*?**
3. **How did the body types of Neanderthals and modern humans differ?**
4. **What observations of mitochondrial DNA are used to support the hypothesis of recent African origins of modern *Homo sapiens*?**
5. **Which hypothesis of human evolution attempts to explain the origin of regional phenotypic differences?**
6. **CRITICAL THINKING According to the existing fossil evidence, Neanderthals died out about 30,000 years ago. Some anthropologists hypothesize that the Neanderthals were killed off by Cro-Magnons. Others hypothesize that the two groups interbred. What evidence would you look for to evaluate these two hypotheses?**

CHAPTER 17 REVIEW

SUMMARY/VOCABULARY

17-1

- Paleoanthropologists gather data from the fossilized remains of early hominids and their ancestors. The shapes of the bones may indicate whether the organism was bipedal. Other clues may indicate diet or habits.
- Humans belong to the order of mammals known as primates. There are two divisions of primates: anthropoid primates and prosimian primates.
- Most primates have nails, instead of claws, and prehensile hands and feet. Primates have color vision and depth perception.
- Anthropoid primates include marmosets, monkeys, apes, and humans. Prosimian primates include lemurs, lorises, and tarsiers.
- Anthropoid primates have large brains relative to their body size.
- Bipedalism and language are two important traits found only in humans.

Vocabulary

anthropoid primate (320)
bipedalism (321)
dental formula (320)
great ape (320)
hominid (319)
opposable thumb (320)
paleoanthropologist (319)
pelvis (319)
prehensile (320)
primate (320)
prosimian primate (320)

17-2

- Bipedalism is the defining characteristic for the hominids—human ancestors.
- The oldest known genus of hominids is *Australopithecus*. Its members are called australopithecines.
- The earliest known hominid, *Australopithecus anamensis*, lived more than 4 million years ago.
- At least two australopithecine lines, *A. africanus* and *A. boisei*, probably were not ancestral to modern humans. They became extinct more than 1 million years ago.
- The discovery of Lucy, a nearly half-complete fossil of an early hominid, *Australopithecus afarensis*, implies that hominids became bipedal before their brains began to dramatically enlarge.
- *Ardipithecus ramidus* is a recent discovery. It is not clear whether it was bipedal. *Ard. ramidus* is 4.4 million years old.
- The existence of hominid species not ancestral to modern humans implies that the hominid phylogenetic tree is bushy in appearance, with many branches representing species that died out, leaving no descendants.

Vocabulary

australopithecine (325)
Lucy (325)
quadrupedal (324)

17-3

- Early members of the genus *Homo*, *H. habilis* and *H. erectus*, probably were ancestral to modern humans. They had larger brains than the australopithecines and may have had speech.
- Our species, *Homo sapiens*, probably evolved about 800,000 years ago.
- The brains of members of the genus *Homo* were much larger than those of the australopithecines.
- Neanderthals were early *Homo sapiens*. They may be ancestral to modern humans, or they may have died out and been replaced by modern humans.
- Some anthropologists think that *H. sapiens* evolved in parallel from populations of *H. erectus* all over the world.
- Some anthropologists propose that *H. sapiens* descended from *H. erectus* in Africa and then dispersed across Earth.

Vocabulary

multiregional hypothesis (329)
recent-African-origin hypothesis (330)

REVIEW

Vocabulary

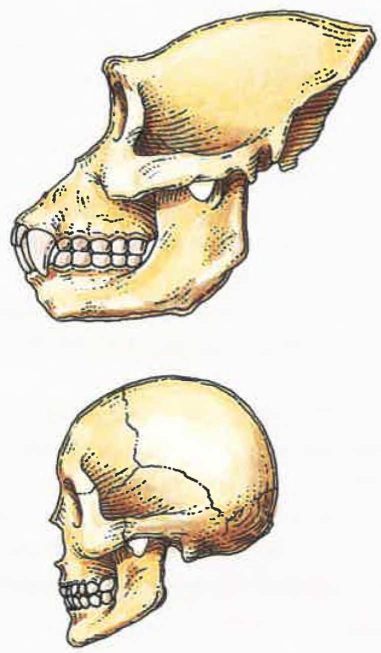
1. What is the difference between a bipedal animal and a quadrupedal animal?
2. What does the term *dental formula* mean?
3. Why is a primate thumb described as "opposable"?
4. What is the relationship between cranial capacity and brain size?
5. What does the genus name *Australopithecus* mean?

Multiple Choice

6. The earliest primates probably lived in (a) grasslands (b) forests (c) deserts (d) tundra.
7. An important difference between anthropoids and prosimians is that anthropoids have (a) larger eyes (b) a larger brain (c) a longer tail (d) no depth perception.
8. The dental formula found in humans is found (a) in all animals (b) only in hominids (c) in apes and African and Asian monkeys. (d) only in marmosets.
9. Humans are better adapted to upright walking than chimpanzees are because humans have (a) a large brain (b) a cup-shaped pelvis (c) a big toe that is opposable to the other toes (d) the ability to use language.
10. The similarity of human and chimpanzee DNA suggests that the two species (a) are identical (b) shared a relatively recent ancestor (c) are not related (d) have stopped evolving.
11. Paleoanthropologists determine the manner of walking and the physical features of human ancestors on the basis of (a) fingerprint patterns (b) comparisons of living species (c) written descriptions in ancient sources (d) shapes of fossilized bones.
12. The earliest known bipedal human ancestor was (a) *A. anamensis* (b) *A. afarensis* (c) *A. africanus* (d) *A. boisei.*
13. The species *A. afarensis* probably (a) died out (b) gave rise to the genus *Ardipithecus* (c) was ancestral to later australopithicenes (d) lived after *A. africanus.*
14. *H. habilis* was so named because evidence indicates that this species (a) was bipedal (b) used language (c) made tools (d) ate meat.
15. Cro-Magnons are regarded as (a) a type of *Homo erectus* (b) a transitional species between *Ardipithecus* and the australopithecines (c) ancestors of Neanderthals (d) modern humans.

Short Answer

16. Study the figure below of the ape skull, top, and the human skull, bottom, and name three major differences between the two skulls.

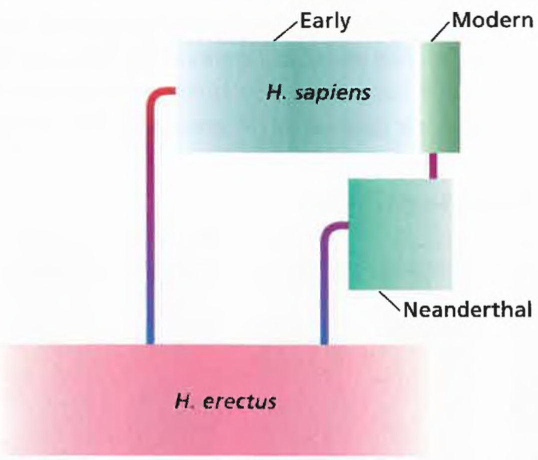


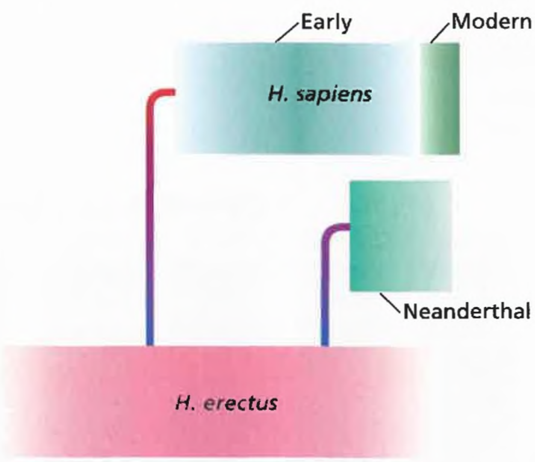
17. Why is depth perception handy for climbing in trees?
18. How is upright walking a beneficial trait for humans?
19. What are two behavioral traits unique to humans?
20. How does the jaw of humans differ from that of apes?
21. How do paleoanthropologists use fossil evidence to draw conclusions about the brain size of hominids?
22. On what continent have most fossil remains of hominids been found?
23. How did Neanderthals accommodate the cold climate of northern Europe?

24. How does the brain size of *A. afarensis* (Lucy) compare with that of chimpanzees and that of modern humans?
25. How is the human spine adapted for standing erect, compared with the spine of a chimpanzee?

CRITICAL THINKING

1. From *H. habilis* to modern *H. sapiens,* there has been a trend for brain size to increase. Is it inevitable that any future descendant species of *H. sapiens* will have larger brains than we have? Explain your answer in terms of some form of natural selection, such as directional selection.
2. Compared with humans, apes do not have a well-developed voice box or well-developed facial muscles. How might the ape's anatomy affect its ability to use spoken language?
3. According to fossil evidence, *H. habilis* made stone tools. They traveled long distances to collect specific types of rock and minerals, and then they shaped the rocks by chipping them at the edges. What does this reveal about *H. habilis*'s ability to use foresight?
4. Cro-Magnon remains have been found with reindeer bones in certain areas of southern Europe. What does this fact suggest about the diet of Cro-Magnons and the environment in which they lived?
5. The two phylogenetic trees shown below express two different views of the relationship of Neanderthals to modern humans. If Neanderthals were very genetically different from modern humans, which tree would more likely be the correct one and why?





EXTENSION

1. Read "No, After You, Afarensis" in *Discover,* January 1999, on page 81. What physical characteristics of *Australopithecus africanus* cause Berger and McHenry to disagree about the human ancestry of *A. africanus*? What reasons are given to defend the current theory that *A. afarensis* is ancestral to *A. africanus*? How long ago did each of the three species of *Australopithecus* live?
2. Visit a local zoo to observe the behavior of monkeys, apes, or other primates. Pay close attention to the facial expressions of the animals. Notice the ways in which the animals interact. Take notes on what you observe. What similarities and differences do you see between the behavior of the primates you observed and that of humans? If it is not possible to visit a zoo, study pictures or videotapes of primates. What inferences can you make about primate behavior from the pictures?

CHAPTER 17 INVESTIGATION

Relating Amino Acid Sequences to Evolutionary Relationships

OBJECTIVES

- Observe the amino acid sequence of hemoglobin and cytochrome *c* in several species.
- Compare the amino acid sequences of the same protein in different species.
- Deduce evolutionary relationships among species.

PROCESS SKILLS

- comparing and contrasting
- classifying
- analyzing
- inferring

MATERIALS

- pencil
- paper

Background

1. Hemoglobin and cytochrome *c* are two proteins commonly studied by scientists attempting to deduce evolutionary relationships from differences in amino acid sequences.
2. Researchers believe that the greater the similarity that exists between the amino acid sequences of two species, the more closely related the two species are evolutionarily.
3. The greater the differences that exist in the amino acid sequences of two species, the more distantly related the two species are.
4. The longer two species have been diverging from a common ancestor, the greater the difference that can be expected in their amino acid sequences. This principle is based on the assumption that the rate of

Cytochrome *c* Amino Acid Sequences

	Horse	Chicken	Tuna	Frog	Human	Shark	Turtle	Monkey	Rabbit
42	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln	Gln
43	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala	Ala
44	Pro	Glu	Glu	Ala	Pro	Gln	Glu	Pro	Tyr
46	Phe	Phe	Tyr	Phe	Tyr	Phe	Phe	Tyr	Pro
47	Thr	Ser	Ser	Ser	Ser	Ser	Ser	Ser	Ser
49	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr
50	Asp	Asp	Asp	Asp	Ala	Asp	Asp	Ala	Asp
53	Lys	Lys	Lys	Lys	Lys	Lys	Lys	Lys	Lys
54	Asn	Asn	Ser	Asn	Asn	Ser	Asn	Asn	Asn
55	Lys	Lys	Lys	Lys	Lys	Lys	Lys	Lys	Lys
56	Gly	Gly	Gly	Gly	Gly	Gly	Gly	Gly	Gly
57	Ile	Ile	Ile	Ile	Ile	Ile	Ile	Ile	Ile
58	Thr	Thr	Val	Thr	Ile	Thr	Thr	Ile	Thr
60	Lys	Gly	Asn	Gly	Gly	Gln	Gly	Gly	Gly
61	Glu	Glu	Asn	Glu	Glu	Gln	Glu	Glu	Glu
62	Glu	Asp	Asp	Asp	Asp	Glu	Glu	Asp	Asp
63	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr	Thr
64	Leu	Leu	Leu	Leu	Leu	Leu	Leu	Leu	Leu
65	Met	Met	Met	Met	Met	Arg	Met	Met	Met
66	Glu	Glu	Glu	Glu	Glu	Ile	Glu	Glu	Glu
100	Lys	Asp	Ser	Ser	Lys	Lys	Asp	Lys	Lys
101	Ala	Ala	Ala	Ala	Ala	Thr	Ala	Ala	Ala
102	Thr	Thr	Thr	Gly	Thr	Ala	Thr	Ala	Thr
103	Asn	Ser	Ser	Ser	Asn	Ala	Ser	Asn	Asn
104	Glu	Lys	—	Lys	Glu	Ser	Lys	Glu	Glu

change of a specific amino acid sequence is the same in all species. Think of other methods used to determine evolutionary relationships. How is this method different?

PART A Cytochrome *c*

1. Cytochrome *c*, a protein found in the mitochondria of many species, consists of a chain of 104 amino acids. The figure on page 334 shows the corresponding parts of noncontinuous parts of the cytochrome *c* amino acid sequences of nine vertebrate species. The numbers along the left side of the figure refer to the position of these sequences in the chain. The letters identify the specific amino acids in the chain.
2. Make a table to record your data in your lab report. Label the columns of your data table "Species" and "Number of Differences from Human Cytochrome *c*."

Hemoglobin Amino Acid Sequences

	Human	Chimpanzee	Gorilla	Monkey	Horse
87	Thr	Thr	Thr	Gln	Thr
88	Leu	Leu	Leu	Leu	Leu
89	Ser	Ser	Ser	Ser	Ser
90	Glu	Glu	Glu	Glu	Glu
91	Leu	Leu	Leu	Leu	Leu
92	His	His	His	His	His
93	Cys	Cys	Cys	Cys	Cys
94	Asp	Asp	Asp	Asp	Asp
95	Lys	Lys	Lys	Lys	Lys
96	Leu	Leu	Leu	Leu	Leu
97	His	His	His	His	His
98	Val	Val	Val	Val	Val
99	Asp	Asp	Asp	Asp	Asp
100	Pro	Pro	Pro	Pro	Pro
101	Glu	Glu	Glu	Glu	Glu
102	Asn	Asn	Asn	Asn	Asn
103	Phe	Phe	Phe	Phe	Phe
104	Arg	Arg	Lys	Lys	Arg
105	Leu	Leu	Leu	Leu	Leu
106	Leu	Leu	Leu	Leu	Leu
107	Gly	Gly	Gly	Gly	Gly
108	Asn	Asn	Asn	Asn	Asn
109	Val	Val	Val	Val	Val
110	Leu	Leu	Leu	Leu	Leu
111	Val	Val	Val	Val	Ala
112	Csy	Cys	Cys	Cys	Leu
113	Val	Val	Val	Val	Val
114	Leu	Leu	Leu	Leu	Val
115	Ala	Ala	Ala	Ala	Ala
116	His	His	His	His	Arg

For each vertebrate species, count the amino acids in the sequence that differ from the human sequence. List these in your data table.

3. In your lab report, list the eight vertebrate sequences in descending order according to the degree of similarity of their cytochrome *c* with that of humans. According to your analysis of the amino acid sequences, which species listed is most closely related to humans? Which species is least closely related to humans?

PART B Hemoglobin

4. Look at the hemoglobin sequences for the five species shown in the figure at left. Hemoglobin is the oxygen-carrying molecule of red blood cells. Only the portion of the chain between amino acid numbers 87 and 116 is shown in the figure.
5. In your lab report, make a table to record your data. Label the columns of your data table "Species" and "Number of Differences from Human Hemoglobin." In each species' sequence, count the number of amino acids that differ from the human sequence and list them in your data table, as you did in Part A.
6. In your lab report, list the four vertebrate sequences in descending order according to the degree of similarity of their hemoglobin with that of humans. According to your analysis of the amino acid sequences, which species listed is most closely related to humans? Which species is least closely related to humans?

Analysis and Conclusions

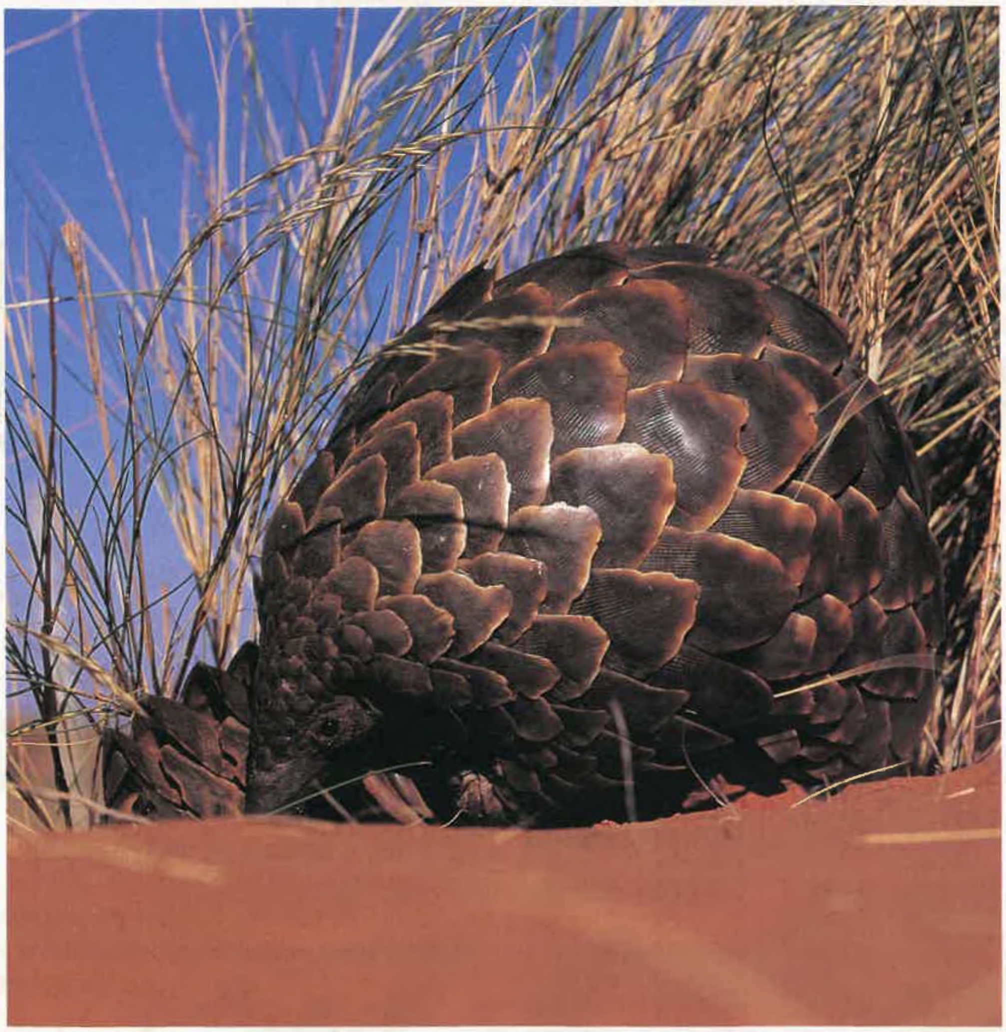
1. Why can it be said that proteins behave like molecular clocks?
2. There is a difference of only one amino acid in one portion of hemoglobin of gorillas and humans. What could have been responsible for this change?
3. If the amino acid sequences are similar in gorillas and humans, why would you expect the DNA of these two organisms to also be similar?

Further Inquiry

Would you expect to find the same number of differences in the cytochrome *c* and hemoglobin amino acid chains when comparing organisms? Or might one of these proteins have changed at a faster rate than the other? Why might the rates of change differ among proteins?

CHAPTER 18

CLASSIFICATION



The pangolin, Manis temmincki, *is a species of scaly anteater found in eastern and southern Africa. Pangolins move slowly and, when threatened, curl into a ball, as this one has done.*

FOCUS CONCEPT: *Interdependence of Organisms*

As you read, consider how the classification of a species reflects its relationships with many related species.

HISTORY OF TAXONOMY

Every year, thousands of new species are discovered. Biologists use the characteristics of each newly discovered species to classify it with organisms having similar characteristics. The ways we group organisms continue to change, and today these methods reflect the evolutionary history of organisms.

SECTION

18-1

OBJECTIVES

▲ Describe Aristotle's classification system, and explain why it was replaced.

● Explain Linnaeus's system of classification, and identify the main criterion he used to classify organisms.

■ List Linnaeus's levels of classification from the most general to the most specific.

◆ Name the primary criterion that modern taxonomists consider when they classify an organism.

EARLY SYSTEMS OF CLASSIFICATION

Taxonomy (taks-AHN-uh-mee) is the branch of biology that names and groups organisms according to their characteristics and evolutionary history. Organisms were first classified more than 2,000 years ago by the Greek philosopher Aristotle. Aristotle classified living things as either plants or animals. He grouped animals into land dwellers, water dwellers, and air dwellers. He also grouped plants into three categories, based on differences in their stems.

As modern science developed in the fifteenth and sixteenth centuries, Aristotle's system at first seemed adequate. Then, in a period of rapid scientific exploration, many new organisms were discovered. Biologists realized that Aristotle's categories were not adequate. They also found that using a common name, such as *robin* or *fir tree,* for an organism presented its own problems; common names varied from one locale to the next, just as they do today. Moreover, common names may not describe species accurately. For example, a jellyfish is not a fish at all. Some early scientists devised scientific names that consisted of long descriptions in Latin, but these names were difficult to remember and suggested nothing about how organisms were related to other organisms.

LINNAEUS'S SYSTEM

In response to the need for organization, the Swedish naturalist Carolus Linnaeus (1707–1778) devised a system of grouping organisms into hierarchical categories. For the most part, Linnaeus used an organism's morphology, that is, its form and structure, to categorize it.

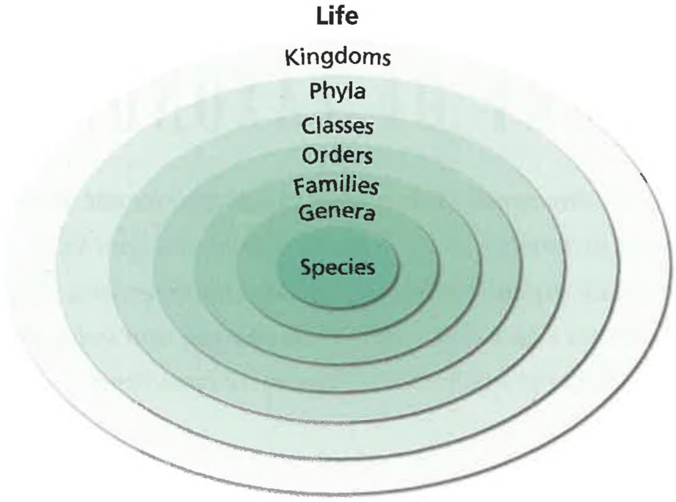
Word Roots and Origins

morphology

from the Greek *morphe,* meaning "form," and *logos,* meaning "word"

FIGURE 18-1

Linnaeus's categorization scheme used a nested hierarchy. Seven levels of organization, each more specific than the last, allowed organisms to be grouped with similar organisms.



Quick Lab

Practicing Classification

Materials paper, pencil

Procedure Using Table 18-1 as a model, classify a fruit or vegetable you would find in a grocery store. Use all seven levels of classification.

Analysis At which level did you assign the least specific name? At which level did you assign the most specific name? Would Aristotle have classified your item differently? Explain your answer.

Levels of Classification

Linnaeus devised a nested hierarchy of seven different levels of organization, as is shown in Figure 18-1. Linnaeus's largest category is called a **kingdom.** There are two kingdoms, plant and animal, which are the same as Aristotle's main categories. Each subset within a kingdom is known as a **phylum** (FIE-luhm), in the animal kingdom, or a **division,** in the plant kingdom. Within a phylum or division, each subset is called a **class,** and each subset within a class is called an **order.** Still smaller groupings are the **family** and then **genus** (JEE-nuhs). The smallest grouping of all, which contains only a single organism type, is known as the **species** (SPEE-sheez). Table 18-1 shows an example of how two similar organisms and one very different one fit into this classification system.

TABLE 18-1 *Classification Hierarchy of Organisms*

	Bobcat	Lion	Shaggy mane mushroom
Kingdom	Animalia	Animalia	Fungi
Phylum/division	Chordata	Chordata	Basidiomycota
Class	Mammalia	Mammalia	Homobasidiomycetae
Order	Carnivora	Carnivora	Agaricales
Family	Felidae	Felidae	Copricaceae
Genus	*Lynx*	*Panthera*	*Coprinus*
Species	*Lynx rufus*	*Panthera leo*	*Coprinus comatus*



Binomial Nomenclature

In Linnaeus's system, the **species name** (also called the scientific name) of an organism has two parts. The first part of the name is the genus, and the second part is the **species identifier,** usually a descriptive word. Thus, we humans are known by our genus, *Homo,* and by our species identifier, *sapiens,* which means "wise." This system of two-part names is known as **binomial nomenclature** (bi-NOH-mee-uhl NOH-muhn-KLAY-chuhr). By custom, the genus name is capitalized and both names are underlined or written in italics. Linnaeus classified thousands of organisms, and a version of Linnaeus's system of classification and binomial nomenclature is still used today. Because species names are Latinized, they are the same in every language. This enables scientists around the world to identify organisms by the same name.

A species name may describe the organism. The microscopic amoeba *Chaos chaos,* shown in Figure 18-2, might never look the same way twice. Sometimes a scientific name is chosen to honor a person, or it may suggest the geographic range of the organism. *Linnaea borealis,* a species of flower that grows in northern regions, was Linnaeus's favorite. *Borealis* means "northern."

Linnaeus's choice of seven levels of classification was arbitrary. Significant variation in some species has led taxonomists to establish additional levels of organization. Botanists sometimes split species into subsets known as **varieties.** Peaches and nectarines are fruits of two slightly different varieties of the peach tree, *Prunus persica.* Zoologists refer to variations of a species that occur in different geographic areas as **subspecies.** The variety or subspecies name follows the species identifier. *Terrapene carolina triungui* is a subspecies of the common eastern box turtle, *Terrapene carolina,* and gets its name from having three, rather than four, toes on its hind feet.

To classify organisms, modern taxonomists consider the **phylogeny** (fie-LAHJ-uh-nee), or evolutionary history, of the organism. Much of Linnaeus's work in classification is relevant today, even in this phylogenetic context. By concentrating on morphology, Linnaeus focused on features that are largely influenced by genes and that are clues of common ancestry.

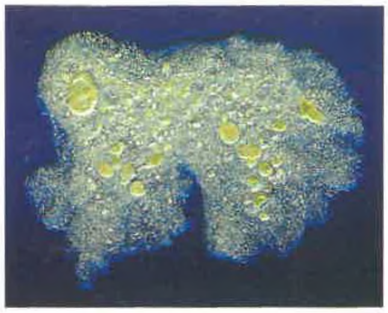


FIGURE 18-2

Names selected for some organisms reflect traits of the organism. The amoeba *Chaos chaos* (LM 56×) changes its shape constantly.

SECTION 18-1 REVIEW

1. How did Aristotle classify organisms, and why did his method prove inadequate?
2. What criterion did Linnaeus use to classify organisms?
3. What are the seven levels of organization that Linnaeus used to categorize organisms?
4. What are two reasons that species names are more precise than common names?
5. What criterion do modern taxonomists use to classify organisms?
6. **CRITICAL THINKING** Linnaeus's work was done many years before that of Darwin and Mendel. Explain why many of Linnaeus's categories are still relevant in light of genetic and evolutionary relationships among organisms.

GREAT DISCOVERIES

Creating Order Out of Chaos

HISTORICAL PERSPECTIVE

During the fifteenth and sixteenth centuries, the exploration of new lands brought large numbers of unknown animals and plants to the attention of naturalists. European explorers returned from other parts of the world with so many unidentified organisms that it became difficult to keep track of them all. Before the introduction of Carolus Linnaeus's binomial system, there was no accepted method for naming and classifying animals and plants. Linnaeus provided a system for grouping organisms in a manner that reflected the relationships between the organisms.

A Rose by Any Other Name . . .

People all over the world use familiar or common names for plants. Sometimes they use different names for the same plant or similar names for different plants. Imagine how difficult it must have been for people from different countries to share their knowledge about the natural world before there was a standard naming system for plants and other organisms.

These early naturalists needed a system for naming living things and placing them into groups of related organisms. The names needed to be short and descriptive—and they needed to be written in a language that was widely understood and accepted. Although there had been some earlier attempts at devising classification systems, Carolus Linnaeus was the first to develop a system that was widely used and accepted.

Carolus Linnaeus

Seeds of Change

Born in Sweden in 1707, Carolus Linnaeus had a great love of plants and nature, instilled in him by a father who educated him about the natural world and taught him the names of many plants. In 1732, while a lecturer at the University of Uppsala, Linnaeus undertook a trip to the then largely unexplored region of northern Scandinavia known as Lapland.

The Lapland journey helped to focus Linnaeus's attention on the need for a standard system of classification, a task that became his lifework. Using earlier research by the German botanist Rudolph Camerius, Linnaeus divided all flowering plants into 23 classes. These classes were based on the number, length, and arrangement of the stamens and pistils. His 24th class included the nonflowering plants, such as mosses.

Taking Root

The prominent Dutch botanist Jan Fredrick Gronovius was greatly impressed with Linnaeus's early botanical work. Gronovius paid for the publication of Linnaeus's *Systema Naturae* (1735), which contained the beginnings of Linnaeus's system for classifying animals and plants.

Linnaeus's greatest contribution to biology was the introduction of the binomial system, in which the

An illustration made to accompany Linnaeus's Systema Naturae *shows the division of flowering plants into 23 classes, based on the number, relative length, and arrangement of the stamens and pistil.*

species name of an organism consists of two parts based on Latin word roots. The concept of the genus name came from the French naturalist Joseph Tournefort. The concept of the second word, the species identifier, came from Linnaeus. Prior to the introduction of this two-part naming system, each type of plant was characterized by a 12-word description. Linnaeus was the first to apply the uniform use of binomials to all organisms. The advantage of this method is that it provides a standardized label for each kind of organism in place of the common name.

Linnaeus's classification system did not escape criticism by his contemporaries, however. He was denounced for imposing an artificial system on nature. Critics claimed his method of classification was based on a single, and perhaps the least important, characteristic of flowers—the arrangement of flower parts. Linnaeus acknowledged that he had sacrificed natural principles to some extent in order to devise a useful sorting principle. But his organizational system had brought together related groups.

Linnaeus first introduced his binomial system in the work *Species Planterum* (1753). This two-volume work contained every plant that Linnaeus was familiar with, and it demonstrated the utility of his system. After publication of *Species Planterum,* the binomial system became the most widely used system in botanical works. As Linnaeus commented in a letter to a friend:

> *Now the whole world is obsessed with writing in the field of botany, now they can go ahead without difficulty, thanks to my method.*

Fruits of His Labor

Since Linnaeus first devised the binomial classification, the most dramatic change has been the systematic effort to make modern taxonomic schemes reflect evolutionary relationships. As Linnaeus himself did, modern scientists have proposed revisions of the traditional classification system. In light of recent research, they have proposed creating new kingdom designations for unicellular organisms. The names of these organisms, however, are still based on the Latin binomial system devised by Linnaeus.

Mertensia virginica, *known in the United States as the bluebell, illustrates the problem with using common names. In Europe and Asia, plants of the genus* Endymion *are called bluebells. Elsewhere, certain species of the genera* Campanula, Clematis, *and* Polemonium *are also commonly known as bluebells.*

SECTION

18-2

OBJECTIVES

▲ Define *phylogenetic tree*, and explain what information a phylogenetic tree shows.

● List four types of evidence used to organize organisms in systematic taxonomy.

■ Name two differences found in the embryos of vertebrates and arthropods that suggest a very different phylogenetic history.

◆ Explain cladistic taxonomy, and identify one conclusion that is in conflict with classical, systematic taxonomy.

MODERN PHYLOGENETIC TAXONOMY

More than 200 years ago, Linnaeus based his classification system on the most evident characteristics of organisms—their morphology. Today, the young field of molecular biology can provide a wealth of information about an organism's molecular nature. When placing an organism into a taxonomic category, modern taxonomists may consider its morphology, chromosomal characteristics, nucleotide and amino acid sequences, and embryological development. These features are almost entirely inherited. Thus, consideration of all of them, together with information from the fossil record, is likely to yield reliable information about the phylogeny of an organism.

SYSTEMATICS

Most modern taxonomists agree that the classification of organisms should reflect their phylogeny. This phylogenetic approach is a cornerstone of a branch of biology called systematic taxonomy, or, more commonly, systematics. **Systematics** organizes the tremendous diversity of living things in the context of evolution. Systematic taxonomists use several lines of evidence to construct a phylogenetic tree.

A **phylogenetic tree** is a family tree that shows the evolutionary relationships thought to exist among groups of organisms. A phylogenetic tree represents a hypothesis, and it is generally based on several lines of evidence. Systematic taxonomists may evaluate an organism's morphology with respect to the morphology of similar and possibly ancestral organisms in the fossil record. Likewise, they may compare its morphology with that of living organisms. Patterns of embryological development, along with the degree of similarity of an organism's chromosomes and certain macromolecules to those of other organisms, provide further clues to phylogenetic relationships. A phylogenetic tree is subject to change, as is any hypothesis, as new information arises. A phylogenetic tree that shows possible relationships among phyla in the kingdom Animalia appears in Figure 18-3.

Word Roots and Origins

phylogenetic

from the Greek *phylon*, meaning "tribe," and *gignesthai*, meaning "to be born"

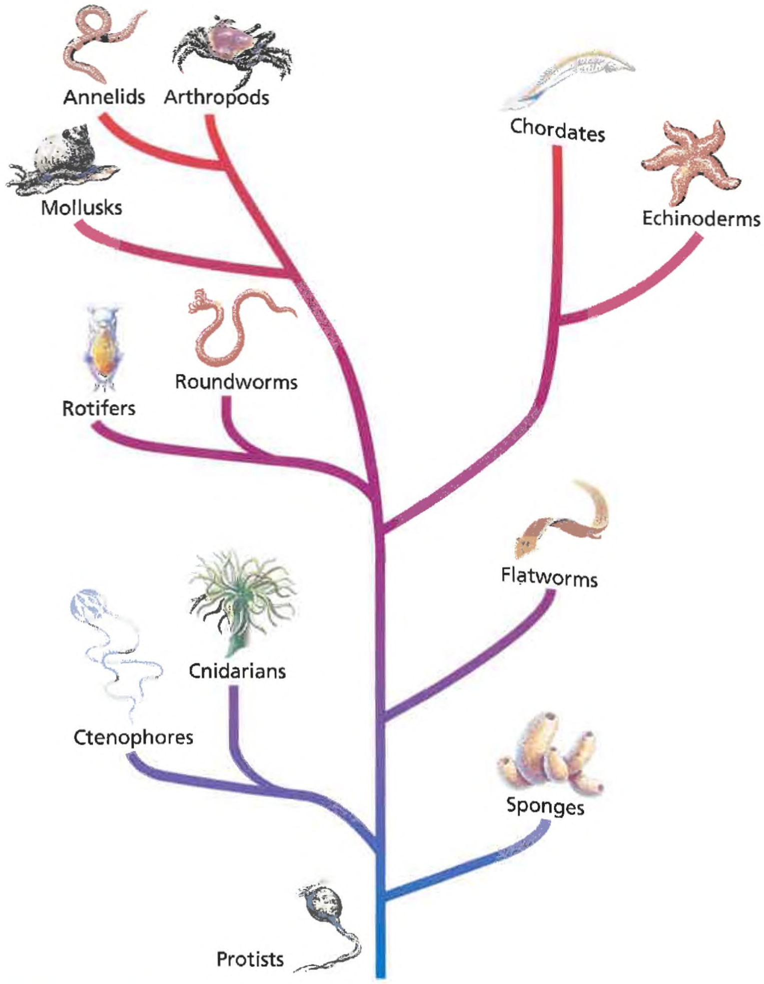


FIGURE 18-3

The branches of this phylogenetic tree show that chordates and echinoderms shared a common ancestor more recently than did echinoderms and other animals, including mollusks and arthropods. Phylogenetic trees are generally derived from several lines of evidence, including morphological, embryological, and macromolecular similarities among organisms.

The Fossil Record

The fossil record often provides clues to evolutionary relationships, but it is important to understand that the fossil record cannot be read like a history book. Some organisms, such as some ocean-living invertebrates, have fairly complete fossil records. Other organisms have incomplete fossil records; there may be series of strata in which no fossils of the organism appear. The fossil record may provide the framework of a phylogenetic tree, but a systematic taxonomist would seek to confirm the information it provided with other lines of evidence.

Morphology

Taxonomists study an organism's morphology and compare it with the morphology of other living organisms. Recall from Chapter 15 that homologous features suggest descent from a common ancestor. Naturally, it is essential to separate those features that are *truly* homologous from those that *seem* homologous but are actually analogous. For example, insects, which are arthropods, and mammals, which are vertebrates, both have legs. But it is clear from the fossil record that legs evolved independently in the two groups. The greater the number of homologous morphological features two organisms share, the more closely related they are thought to be.

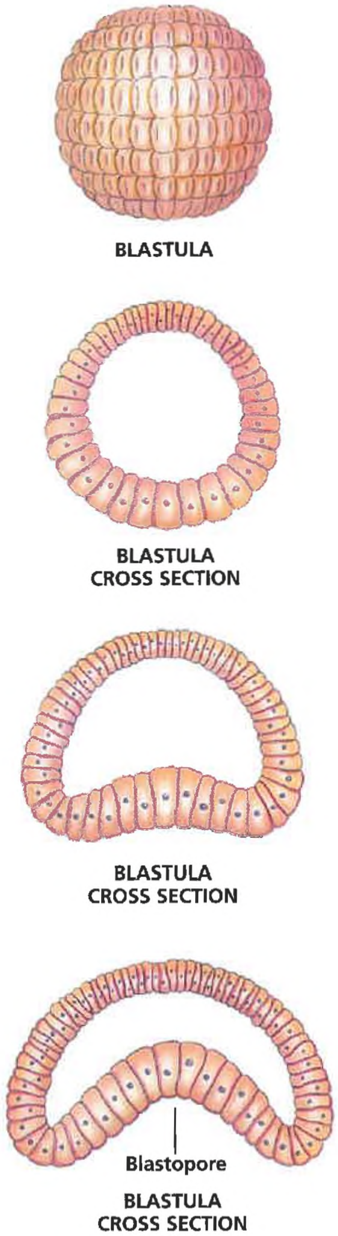


FIGURE 18-4

The blastopore, an indentation of the blastula, forms in early embryological development. The blastopore becomes the posterior end of the digestive system in chordates (which include the vertebrates) and echinoderms. In other animal phyla, the blastopore becomes the anterior end of the digestive system.

Embryological Patterns of Development

Early patterns in embryological development provide evidence of phylogenetic relationships. They also provide a means of testing hypotheses about relationships that have been developed from other lines of evidence. Refer to Figure 15-12 in Chapter 15, which shows the great similarity among embryos of three species of vertebrates.

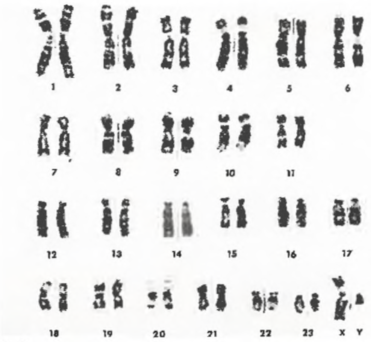
Differences among animal phyla may appear very early in embryological development. As development begins, the zygote starts to divide by mitosis. Within a matter of hours, a ball of cells called a **blastula** (BLAS-tyoo-luh), shown in Figure 18-4, forms. Soon after that, a small indentation, the **blastopore** (BLAS-toh-POR), develops on the outside of the blastula. Eventually this indentation will develop into the digestive system. In most animal phyla, the blastopore becomes the anterior end of the digestive system (the mouth). But in **echinoderms** (e-KIE-noh-DURHMZ), such as starfish and sand dollars, the blastopore becomes the posterior end of the digestive system, as it does in chordates, which include vertebrates. This pattern of development suggests that echinoderms are more closely related to vertebrates than they are to other invertebrates, such as mollusks, as shown in Figure 18-3.

Echinoderms and vertebrates share other important characteristics as well. In both phyla, each cell of the early embryo is potentially capable of forming the entire organism. For example, identical twins are formed when the early embryo splits in two. Each half becomes a complete individual, and the two individuals share the same genetic information. In contrast, when early embryos of fruit flies (phylum Arthropoda) are experimentally split, each part is already committed to becoming a certain part of the organism, such as the head. Thus, splitting an arthropod embryo will cause the two halves to die.

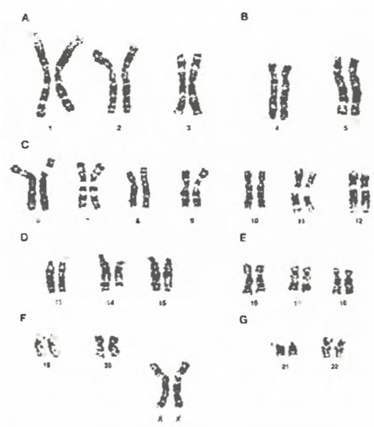
Chromosomes and Macromolecules

Taxonomists use comparisons of macromolecules such as DNA, RNA, and proteins as a kind of "molecular clock." Recall from Section 15-3 that scientists compare amino acid sequences for homologous protein molecules of different species. The number of amino acid differences is a clue to how long ago two species diverged from a shared evolutionary ancestor. This molecular-clock model is not a perfect one. It assumes that all changes in amino acid sequence are random and are not affected by natural selection. This is probably not true. Moreover, sequences of amino acids can change at different rates in different organisms. But the molecular-clock model is used, together with other kinds of data, to estimate degrees of relatedness between different species.

In a similar kind of analysis, biologists compare the karyotypes, or patterns of chromosomes, of two related species. Regions of chromosomes that have the same pattern of banding are clues to the degree of relatedness of organisms. The chromosomes of humans and chimpanzees show a surprising degree of similarity, as



(a)



(b)

FIGURE 18-5

Chimpanzees are genetically very similar to humans. (a) A karyotype of a chimpanzee's 24 chromosome pairs is remarkably similar to (b) a karyotype of a human's 23 chromosome pairs.

shown in Figure 18-5. One of the chromosomes in humans is homologous to two smaller chimpanzee chromosomes. This fused human chromosome and six inverted chromosome segments are the only observed chromosomal differences between the two species. In fruit flies, nearly that much chromosomal variation can be found within one species.

The comparison of chimpanzee and human chromosomes prompted several biologists to reevaluate the accepted estimate of how long ago chimpanzees and humans last shared an ancestor. Before chromosomal analysis, it was widely thought that the ancestors of humans and chimpanzees diverged from a common ancestor about 25 million years ago. After the comparisons of karyotypes and amino acid sequences in proteins, molecular biologists decreased the estimate from 25 million years to as little as 5 million years.

CLADISTICS

One relatively new system of phylogenetic classification is called **cladistics** (kluh-DIS-tiks). Cladistics uses certain features of organisms, called shared derived characters, to establish evolutionary relationships. A **derived character** is a feature that apparently evolved only within the group under consideration. For example, if the group being considered is birds, one example of a derived character is feathers. Most animals do not have feathers; birds are the only animals that do. Therefore, it is safe to assume that feathers evolved within the bird group and were not inherited from some distant ancestor of the birds.

Cladistic taxonomists agree that organisms that share a derived character—like feathers—probably share it because they inherited

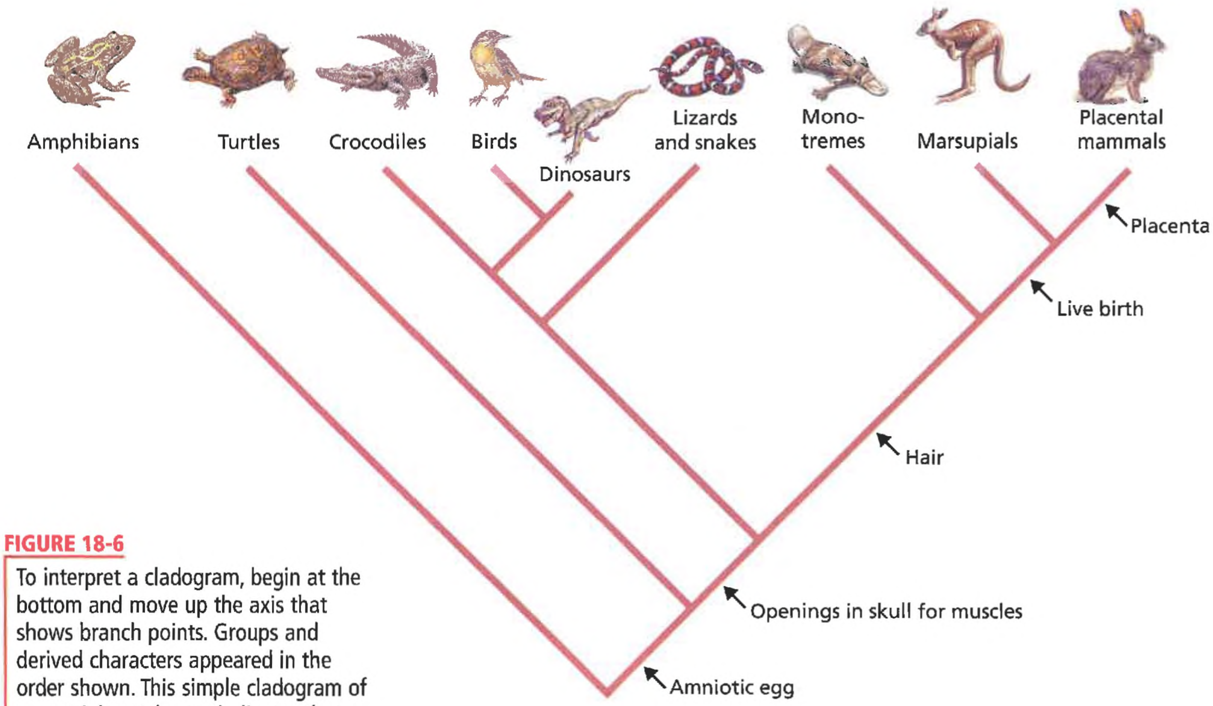


FIGURE 18-6

To interpret a cladogram, begin at the bottom and move up the axis that shows branch points. Groups and derived characters appeared in the order shown. This simple cladogram of terrestrial vertebrates indicates that amphibians arose first, turtles arose next, and placental mammals arose last. Only groups branching *above* a listing of a derived character share that character. Thus, amphibians do not have amniotic eggs, but all other groups do. Likewise, monotremes, marsupials, and placental mammals have hair, though no other groups do.

it from a common ancestor. So shared derived characters, particularly a *group* of several shared derived characters, are strong evidence of common ancestry between organisms that share them. Ancestry diagrams made by means of cladistic analysis, such as the one shown in Figure 18-6, are called **cladograms** (KLAD-uh-GRAMZ).

The application of cladistic taxonomy leads to a number of nontraditional conclusions. One of the most notable is that birds, crocodiles, and dinosaurs are more closely related to each other than any one of them is to a snake or lizard. In the more-classical systematic scheme used in this textbook, snakes, lizards, and crocodiles are classified in the reptile class, while birds are in a class by themselves. A related cladistic conclusion, which differs from that of classical taxonomy, is that the reptiles did not all spring from one common ancestor. Rather, reptiles are a composite of several branches that have occurred during the evolution of the vertebrates, as you can see in the cladogram of vertebrates shown in Figure 18-6.

SECTION 18-2 REVIEW

1. Define the term *phylogenetic tree.*
2. What is systematic taxonomy, and what kinds of data are used by a systematic taxonomist?
3. How can embryological evidence be used to show phylogenetic relationships that are not evident from either the study of morphology or the study of the fossil record?
4. What are two flaws of the molecular clock model in determining relatedness between species?
5. What is a shared derived character?
6. CRITICAL THINKING Why does the cladistic approach to classification suggest that the class Reptilia (reptiles) is not a phylogenetic classification?

TWO MODERN SYSTEMS OF CLASSIFICATION

SECTION 18-3

OBJECTIVES

▲ Describe the six-kingdom system of classification.

● List the characteristics that distinguish archaebacteria from eubacteria.

■ Explain why the protists are grouped together in the six-kingdom system in spite of having differences that are greater than those between plants and animals.

◆ Describe the evidence that prompted the creation of the three-domain system of classification.

▲ Explain the principal difference between the six-kingdom system and the three-domain system of classification.

Aristotle classified organisms as either plants or animals, but today we recognize that many forms of life are neither. In this section, you will read about two alternative classification systems that are in current use. But remember, organizational systems are imposed by humans and therefore may be flawed. As is true of everything in science, they are subject to change as new information arises.

SIX-KINGDOM SYSTEM

A classification system based on five kingdoms of organisms was preferred by taxonomists for many years. But further studies of bacteria have shown that there are two important subtypes with very different morphologies and properties. Recognition of these two broad types of bacteria has driven the acceptance of a newer, six-kingdom system, illustrated in Table 18-2, which is used in this textbook.

TABLE 18-2 *Six Kingdoms of Life*

Kingdom	Cell type	Number of cells	Nutrition
Archaebacteria	prokaryotic	unicellular	autotrophy and heterotrophy
Eubacteria	prokaryotic	unicellular	autotrophy and heterotrophy
Protista	eukaryotic	unicellular and multicellular	autotrophy and heterotrophy
Fungi	eukaryotic	unicellular and multicellular	heterotrophy
Plantae	eukaryotic	multicellular	autotrophy and (rarely) heterotrophy
Animalia	eukaryotic	multicellular	heterotrophy

FIGURE 18-7

Archaebacteria often live in very hostile environments that cannot support other forms of life, such as this hot spring, Morning Glory Pool, in Yellowstone National Park.

Kingdom Archaebacteria

The members of the **kingdom Archaebacteria** (AHR-kee-bak-TIR-ee-uh) are unicellular prokaryotes with distinctive cell membranes as well as biochemical and genetic properties that differ from all other kinds of life. Some species of archaebacteria are autotrophic, producing food by chemosynthesis. Their waste products may include flammable gases, such as methane. Many archaebacteria live in harsh environments such as sulfurous hot springs, as shown in Figure 18-7, and very salty lakes, and in anaerobic environments, such as in the intestines of mammals.

The prefix *archae-* comes from the Greek word for "ancient." Modern archaebacteria may be directly descended from and very similar to the first organisms on Earth, which flourished before the evolution of photosynthesis. These early archaebacterial ancestors evolved before the release of large amounts of oxygen gas into the environment.

FIGURE 18-8

Some protists are multicellular. This ocean-living giant kelp resembles a plant, but it lacks the organization of tissues found in true plants.

Kingdom Eubacteria

The *eu* part of **eubacteria** (YOO-bak-TEER-ee-uh) means "true." Eubacteria are unicellular prokaryotes. Most of the bacteria that affect your life—those that cause tooth decay, turn milk into yogurt, and cause food poisoning—are members of the **kingdom Eubacteria.** Most species of eubacteria use oxygen, but a few species cannot live in the presence of oxygen.

At first glance, both eubacteria and archaebacteria may seem unimportant. But remember that they include the greatest number of living things on Earth. Moreover, their ancestors, which may have been quite similar to modern bacteria, were probably the first living things on Earth.

Both archaebacteria and eubacteria reproduce by binary fission, but they do have some ways to recombine genes, allowing evolution to occur. The very short generation times of bacteria (as little as 30 minutes) allow rapid evolutionary response to environmental change. If you have ever had an antibiotic-resistant bacterial infection, you have had experience with the remarkably fast evolution of bacteria.

Kingdom Protista

The **kingdom Protista** (proh-TIS-tuh) is made up of a variety of eukaryotic, mostly single-celled organisms. Some species of **protists** (PROH-tists) exist as multicellular organisms, like the giant kelp shown in Figure 18-8. Although they look much like plants, multicellular protists lack specialized tissues. Being eukaryotes, they have a membrane-bound true nucleus with linear chromosomes, and they have membrane-bound organelles.

It is difficult to make generalizations about the protists because many protist species are more distantly related to each other than plants are to animals. The kingdom Protista contains all eukaryotes that are not plants, animals, or fungi, more than 50,000 species in all. The sexual cycles of many protists are unknown, but most are thought to have some process of genetic recombination.

Euglena and the amoebas are common types of unicellular protists. *Euglena,* shown in Figure 18-9, can feed on other organisms in the manner of an animal, but it also has chloroplasts and can perform photosynthesis if light is available. Amoebas, such as the one shown in Figure 18-2, feed on other organisms and respond to touch and light. Yet *Euglena* is not a plant, and amoebas are not animals—both are protists.

FIGURE 18-9

Euglena gracilis (LM 580×), like all species of *Euglena,* is a unicellular protist that can be autotrophic or heterotrophic, depending on its environmental conditions.

Kingdom Fungi

The **kingdom Fungi** (FUHN-jee) is made up of heterotrophic unicellular and multicellular eukaryotic organisms. Fungi absorb nutrients rather than ingesting them the way some protists, such as amoebas, do. While sexual cycles are not known for many fungi, it is likely that all species have some way of promoting gene recombination. The well-studied mold *Neurospora* has a standard sexual cycle and has been used extensively in the study of meiosis and in the genetic control of physiological functions. There are over 100,000 species of fungi, including mushrooms, puffballs, rusts, smuts, mildews, and molds.

Kingdom Plantae

As you might have expected, the **kingdom Plantae** (PLAN-tee) consists of multicellular plants. All except for a few parasitic forms are autotrophic and use photosynthesis as a source of energy. Most plants live on land, and most have a sexual cycle based on meiosis. More than 350,000 species of plants have been identified. They include mosses, ferns, conifers, and flowering plants, like the orchid shown in Figure 18-10.

FIGURE 18-10

Orchids, like this *Paphiapedilum rothschildionum,* are found in tropical climates. Flowers contain the plant's gametes, or reproductive cells.

Kingdom Animalia

The **kingdom Animalia** (AN-uh-MAH-lee-uh) is made up of eukaryotic, multicellular heterotrophic organisms. Most animals have symmetrical body organization and move about their environment. Almost all animals have a standard sexual cycle that employs meiosis for the recombination of genes.

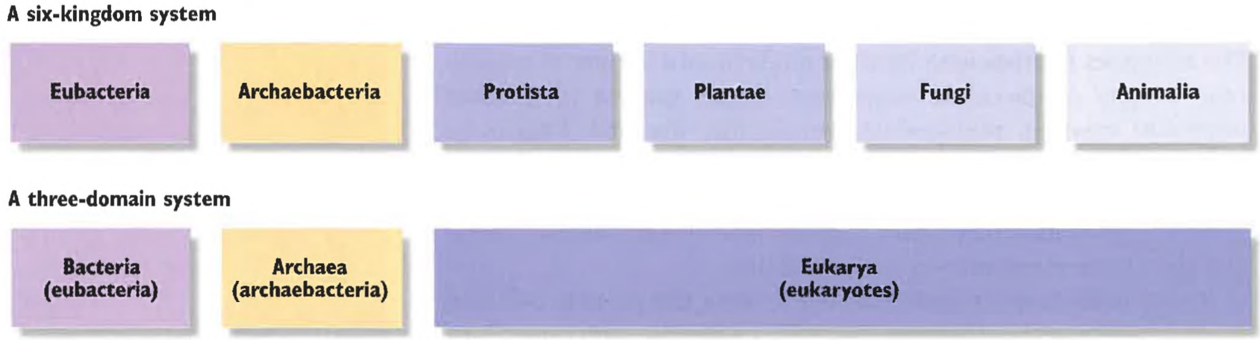


FIGURE 18-11

The three-domain system highlights the importance of archaebacteria as a life-form. This system is often used by molecular biologists. Notice that the domain Eukarya includes members of the kingdoms Protista, Plantae, Fungi, and Animalia, which are all made up of eukaryotic organisms.

THREE-DOMAIN SYSTEM

The young science of molecular biology has led to an alternative to the six-kingdom system. By comparing sequences of ribosomal RNA in different organisms, molecular biologist Carl Woese (1928–), of the University of Illinois, has estimated how long ago pairs of different organisms shared a common ancestor. Because all organisms, even prokaryotes, have ribosomes, the ribosomal RNA molecule can be used to study the degree of relationship between any two living things. The phylogenetic tree drawn from these data shows that living things seem to fall naturally into three broad groups, or **domains.** Plants, animals, and fungi are one small twig of a large branch—a domain—that includes all the eukaryotes. These domains are shown in comparison with the six kingdoms in Figure 18-11.

Word Roots and Origins

domain

from the Latin *dominium,* meaning "right of ownership"

Domain Archaea (ahr-KEE-uh) is known in the six-kingdom system as kingdom Archaebacteria. **Domain Bacteria** is known in the six-kingdom system as the kingdom Eubacteria.

Domain Eukarya (yoo-KAR-ee-uh) consists of the protists, the fungi, and the plants and animals. All eukaryotes have true nuclei with linear chromosomes and membrane-bound organelles. Most of the variation in this domain is among the protists. Surprisingly, when considered from the perspective of the complete diversity of life on Earth, the fungi, plants, and animals are quite similar to each other.

SECTION 18-3 REVIEW

1. What are the six kingdoms in the six-kingdom system of classification?
2. What are two things that make archaebacteria difficult to study?
3. What is the most heterogeneous kingdom in terms of morphology?
4. What kind of evidence indicates that organisms fall naturally into three broad domains?
5. Why do protists, fungi, plants, and animals share a domain in the six-kingdom system?
6. **CRITICAL THINKING** In the five-kingdom system, which is still used by some scientists, all species of bacteria are grouped in the kingdom Monera. Why might there have been only one bacteria kingdom recognized in the past?

CHAPTER 18 REVIEW

SUMMARY/VOCABULARY

18-1

- Taxonomy is the science of grouping organisms according to their morphology and evolutionary history.
- Carolus Linnaeus originated a seven-level hierarchy system for classifying organisms according to their morphology. Moving from the most general to the most specific, the levels are called kingdom, phylum, class, order, family, genus, and species. A version of this system is still in use.
- A species name consists of the genus name together with a species identifier. A species denotes a single organism type.

Vocabulary

binomial nomenclature (339)
class (338)
division (338)
family (338)
genus (338)
kingdom (338)
order (338)
phylogeny (339)
phylum (338)
species (338)
species identifier (339)
species name (339)
subspecies (339)
taxonomy (337)
variety (339)

18-2

- A modern approach to taxonomy is systematics, which analyzes the diversity of organisms in the context of their evolutionary history.
- Scientists consider several lines of evidence when classifying organisms according to their evolutionary history.
- An organism's relationship to organisms in the fossil record as well as to living organisms is taken into account in the formulation of a phylogenetic tree.
- Similarities in patterns of embryological development provide clues to the degree of relatedness of different organisms.
- Molecular similarities, such as those found in homologous proteins of different organisms, also indicate how closely organisms are related.
- Shared derived characters, those traits that developed within a certain group, are clues to the degree of relatedness among organisms. The system that uses shared derived characters to deduce evolutionary history is called *cladistics*.

Vocabulary

blastopore (344)
blastula (344)
cladistics (345)
cladogram (346)
derived character (345)
echinoderm (344)
phylogenetic tree (342)
systematics (342)

18-3

- Many modern taxonomists use the six-kingdom system of classification, which recognizes the unique nature of the archaebacteria.
- Archaebacteria, some of which live in extremely harsh environments, have been largely ignored until recently. Scientists now think archaebacteria closely resemble the first kinds of organisms to live on Earth.
- An alternative classification system that employs three broad domains groups all eukaryotic organisms under the domain Eukarya. Eubacteria (domain Bacteria) and archaebacteria (domain Archaea) form each of the other two domains.

Vocabulary

domain (350)
domain Archaea (350)
domain Bacteria (350)
domain Eukarya (350)
eubacteria (348)
kingdom Animalia (349)
kingdom Archaebacteria (348)
kingdom Eubacteria (348)
kingdom Fungi (349)
kingdom Plantae (349)
kingdom Protista (348)
protist (348)

REVIEW

Vocabulary

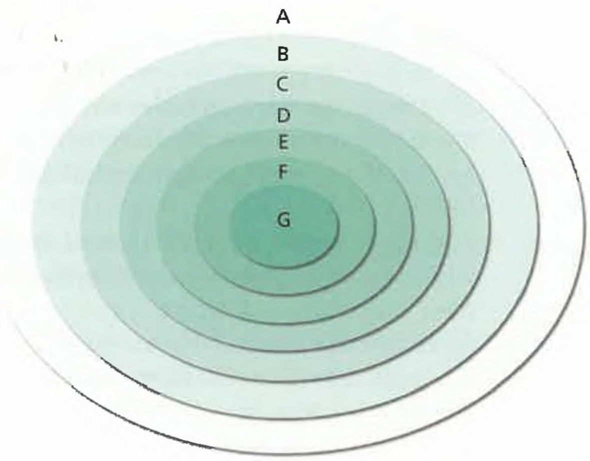
1. Distinguish between a species name and a common name.
2. What is the difference between a phylum and a division?
3. Using a dictionary, find the meaning of the word parts *phylo-* and *-geny* in *phylogeny.* Explain why this term is appropriate for discussing common ancestry of organisms.
4. What is the difference between a subspecies and a variety?
5. Look up the roots of the word *echinoderm.* How does what you found relate to the properties of a group that includes starfish, sand dollars, and sea urchins?

Multiple Choice

6. A species name includes information about (a) species and phylum (b) division and genus (c) genus and order (d) genus and species.
7. Aristotle classified plants on the basis of differences in their (a) stems (b) flowers (c) leaves (d) roots.
8. Linnaeus classified organisms based on similarities of their (a) genes (b) homologous proteins (c) morphology (d) embryology.
9. A group of related classes of organisms make up a (a) genus (b) order (c) phylum (d) kingdom.
10. The kingdom Animalia is divided into phyla. At the same level of organization, the kingdom Plantae is divided into (a) classes (b) divisions (c) species (d) genera.
11. Some animal species are divided into (a) identical species (b) varieties (c) subspecies (d) twin species.
12. Classifying organisms according to their presumed evolutionary history is called a (a) six-kingdom approach (b) morphological approach (c) phylogenetic approach (d) three-domain approach.
13. The kingdom Protista includes (a) bacteria (b) plants (c) algae (d) mushrooms.
14. Some protists are similar to plants in that they (a) carry on photosynthesis (b) have plantlike organization of tissues (c) ingest nutrients (d) are unicellular.
15. Taxonomists can use data from RNA-sequencing techniques to (a) predict future changes in species (b) estimate when two species diverged from a common ancestor (c) determine species name (d) explain the origin of life.

Short Answer

16. List the seven levels of Linnaeus's classification hierarchy from most general, *A*, to most specific, *G*.



17. How were Aristotle's and Linnaeus's classification systems for organisms similar?
18. Why are species names important in scientific work?
19. What are the differences between plants and fungi?
20. How do amino acid sequences function as a "biological clock"?
21. What do we call the system of classification that is based on an analysis of shared derived characters?
22. Name three things you might learn about an organism by investigating the meaning of its scientific name.
23. How might a taxonomist use embryological evidence in classifying an organism?
24. How do some archaebacteria produce food?
25. What do plants and fungi have in common with animals?

CRITICAL THINKING

1. Scientists agree that evolution has occurred and continues to occur, and that all of the organisms on Earth are related to each other to varying degrees. It is also obvious that the course of evolution proceeded in one way only, yet scientists often disagree about phylogenetic histories of organisms. Cladistic taxonomists regard reptiles in a different light than do more classical taxonomists. Why might scientists disagree with each other about the course of evolution?
2. The evolutionary history of reptiles can be studied using comparisons of their sequences of macromolecules. The degree of difference can be related to the time that has passed since any two species descended from a common ancestor. Would the phylogenetic tree derived from macromolecular comparisons probably more closely resemble the results of cladistic analysis or the standard classification of all reptiles as a single class of vertebrates?
3. Biologists think that there are probably millions of undescribed and unclassified species on Earth. Why might so many species still be undescribed or unclassified today?
4. Legs are an example of a shared derived character in vertebrates. Arthropods, such as lobsters and crickets, also have legs, but they are not accepted as a character shared with vertebrates. Why?
5. A number of years ago scientists found a living fish, called a coelacanth and pictured below, that was thought to have become extinct about 65 million years ago. The earliest fossils of coelacanths are about 350 million years old. Thus, the appearance of the coelacanth has remained unchanged for 350 million years. Although it is impossible to compare macromolecules such as proteins of a 350-million-year-old fossil coelacanth with that of a freshly caught coelacanth, what would you expect to find if you could?

EXTENSION

1. Read "Robust About Face" in *Science News,* April 24, 1999, on page 267. Describe the features of the head of *Australopithecus robustus*. Where do some researchers place *A. robustus* in the human lineage? According to Melanie McCollum, why is this cladistic reasoning misleading?
2. Visit the zoo, and list the scientific names of all the animals you see, or use your library to research 10 organisms. Record the scientific and common names of these organisms. For each animal, list a trait that led taxonomists to classify the organism in its particular genus or family.
3. Collect half a cup of water from a shallow pond. Using a microscope, study several samples from the water. Draw the organisms you find, and classify them as best you can into kingdom and phylum.

CHAPTER 18 INVESTIGATION

Using and Formulating Dichotomous Keys

OBJECTIVES

- Use a dichotomous key to identify leaves.
- Construct a dichotomous identification key.

PROCESS SKILLS

- identifying
- classifying
- designing
- interpreting
- organizing data
- comparing and contrasting

MATERIALS

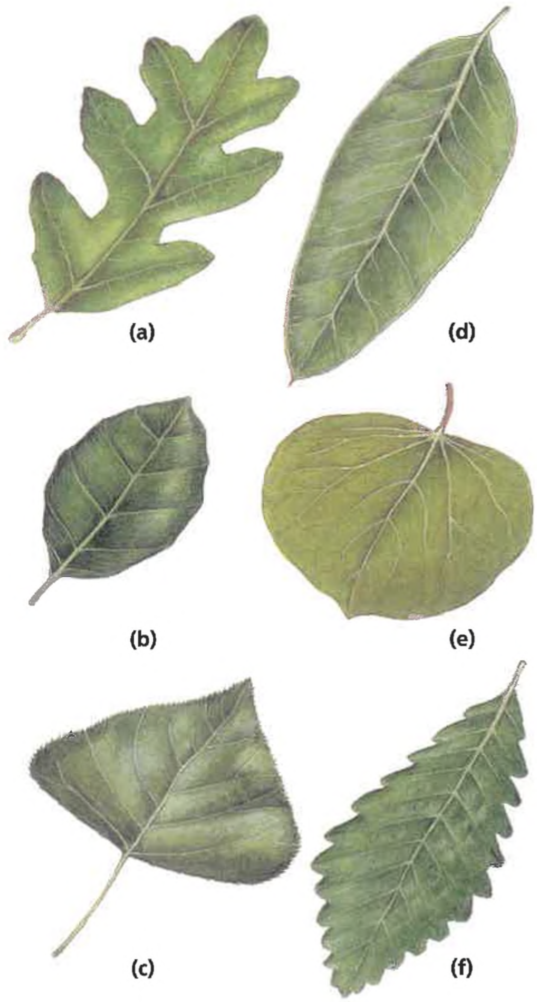
- pencil
- paper
- shoes
- masking tape
- marker

Background

1. Who developed the classification system that scientists use today to classify and group organisms according to their inherited traits?
2. Taxonomy is the science of naming and classifying organisms according to their characteristics and evolutionary history.
3. Why is classification essential to biology?
4. A dichotomous key uses pairs of contrasting, descriptive statements to lead to the identification of an organism (or other object).
5. The principle behind dichotomous keys—the forced choice—is used in many different situations to narrow the path toward an answer. If you have ever had your eyes examined for corrective lenses, you are familiar with the series of forced choices that end with the choice of the correct lenses for your eyes.

PART A Using a Dichotomous Key

1. Field guides often use dichotomous keys to identify organisms. Use the dichotomous key shown here to identify the tree leaves below. Begin with the paired descriptions 1a and 1b, and follow the directions. Proceed through the list of paired descriptions until you identify the leaf in question. In your lab report, write the names of the leaves as you identify them.



Dichotomous Key for Identifying Common Leaves

1a. If the edge of the leaf has no teeth, or lobes, go to 2 in the key.
1b. If the edge of the leaf has teeth, or lobes, go to 3 in the key.

2a. If the leaf has slightly wavy edges, it is a shingle oak.
2b. If the leaf has smooth edges, go to 4 in the key.

3a. If the leaf edge is toothed, it is a Lombardy poplar.
3b. If the leaf edge has lobes, go to 5 in the key.

4a. If the leaf is heart-shaped with veins branching from the base, it is a redbud.
4b. If the leaf is not heart-shaped, it is a live oak.

5a. If the leaf edge has a few large lobes, it is an English oak.
5b. If the leaf edge has many small lobes, it is a chestnut oak.

PART B Making a Dichotomous Key

2. Gather 10 different single shoes, and use masking tape and a marker to label the soles of the shoes with the owner's name. The labeled shoes should then be placed on a single table in the classroom.
3. Form small groups. Discuss the appearance of the shoes. In your lab report, make a table like the one below that lists some general characteristics of the shoes, such as the type and size. Also list the names of the students who own the shoes. Complete the chart by describing the characteristics of each person's shoe.
4. Use the information in your table to make a dichotomous key that can be used to identify the owner of each shoe. Remember that a dichotomous key includes pairs of opposing descriptions. At the end of each description, the key should either identify an object or give directions to go to another specific pair of descriptions. Write your dichotomous key in your lab report.
5. After all groups have completed their key, exchange keys with a member of another group. Use the key to identify the owner of each shoe, and then verify the accuracy of your identification by reading the label on the shoe. If the key has led you to an inaccurate identification, return the key so that corrections can be made.
6. Clean up your materials before leaving the lab.

Analysis and Conclusions

1. What other characteristics might be used to identify leaves with a dichotomous key?
2. Were you able to identify the shoes using another group's key? If not, describe the problems you encountered.
3. How was it helpful to list the characteristics of the shoes before making the key?
4. Does a dichotomous key begin with general descriptions and then proceed to more specific descriptions, or vice versa? Explain your answer, giving an example from the key you made.
5. Are dichotomous keys based on a phylogenetic or morphological approach to classification? Explain your answer.

Further Inquiry

List characteristics that might be used to identify birds or other animals using a dichotomous key. Compare your list of characteristics with those used in a dichotomous key in a field guide for identifying birds or other animals.

TABLE A *DISTINGUISHING FEATURES OF A SAMPLE OF SHOES*

	Left/right	Men's/women's	Laced/slip-on	Color	Size	Owner
1						
2						
3						
4						
5						