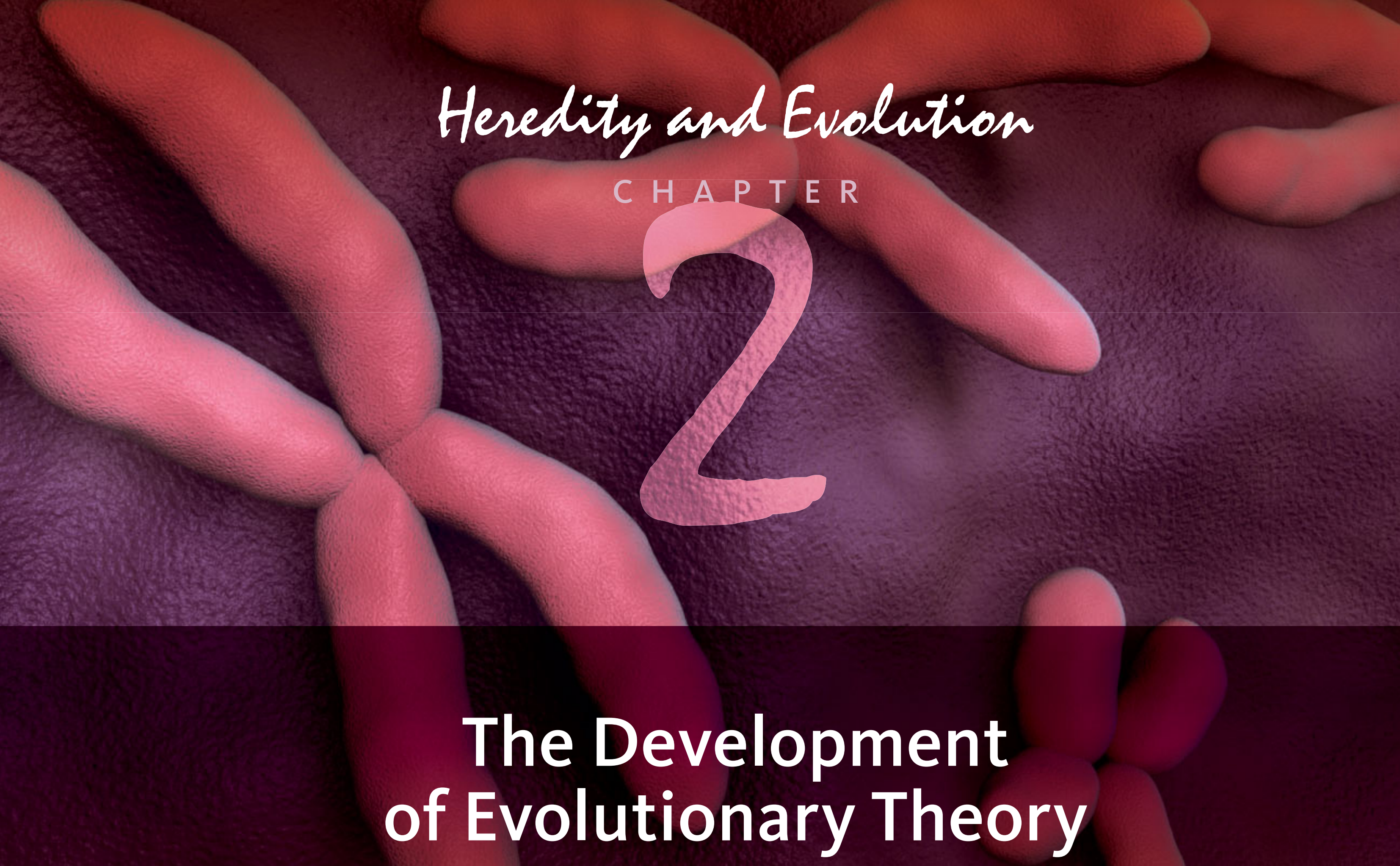

CHAPTER 2

The Development of Evolutionary Theory

OUTLINE

CHAPTER 2

Focus Questions

What are the basic premises of natural selection?

What were the technological and philosophical changes that led people to accept notions of evolutionary change?

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Introduction

Has anyone ever asked you, "If humans evolved from monkeys, then why do we still have monkeys?" Or perhaps, "If evolution happens, then why don't we ever see new species?" These are the kinds of questions people sometimes ask if they don't understand evolutionary processes or they don't believe those processes exist. Evolution is one of the most fundamental of biological processes, and yet it's one of the most misunderstood. The explanation for the misunderstanding is simple. Evolution isn't taught in most primary and secondary schools, and in fact, it's frequently avoided. In colleges and universities, evolution is covered only in classes that directly relate to it. Indeed, if you're not an anthropology or biology major and you're taking a class in biological anthropology mainly to fill a science requirement, you'll probably never study evolution again.

By the end of this course, you'll know the answers to the questions that opened the previous paragraph. Briefly, no one who studies evolution would ever say that humans evolved from monkeys, because they didn't. They didn't evolve from chimpanzees either. The earliest human ancestors evolved from a species that lived some 5 to 8 million years ago (mya). That ancestral species was the *last common ancestor* we share with chimpanzees. In turn, the lineage that led to the apes and ourselves separated from a monkey-like ancestor some 20 mya, and monkeys are still around because as lineages diverged from a common ancestor, each group went its separate way. Over time, some of these groups became extinct, while others evolved into the species we see today. Therefore, each living species is the current product of processes that go back millions of years. Because evolution takes time, and lots of it, we rarely witness the appearance of new species except in microorganisms. But we do see *microevolutionary* changes in many species.

The subject of evolution is controversial, especially in the United States, because some people think that evolutionary statements run counter to biblical teachings. Indeed, as you're probably aware, there is strong opposition to the teaching of evolution in public schools.

People who deny that evolution happens often say that "evolution is only a theory," implying that evolution is nothing more than supposition. Actually, referring to a concept as "theory" supports it. As we discussed in Chapter 1, theories are hypotheses that have been tested and subjected to verification through accumulated evidence. Evolution *is* a theory, one that has increasingly been supported by a mounting body of genetic evidence. It's a theory that has stood the test of time, and today it stands as the most fundamental unifying force in biological science.

Because physical anthropology is concerned with all aspects of how humans came to be and how we adapt physiologically to the external environment, understanding the details of the evolutionary process is crucial. Therefore, it's beneficial to know how the mechanics of the process came to be discovered. Also, if we want to appreciate the nature of the controversy that still surrounds the issue, we need to see how social and political events influenced the discovery of evolutionary principles.

A Brief History of Evolutionary Thought

The discovery of evolutionary principles first took place in western Europe and was made possible by advances in scientific thinking that date back to the sixteenth century. Having said this, we must recognize that Western science could not have developed without writings from other cultures, especially the Arabs, Indians, and Chinese. In fact, intellectuals in these cultures and in ancient Greece had notions of biological evolution (Teresi, 2002), but they never formulated them into a cohesive theory.

Charles Darwin was the first person to explain the basic mechanics of the evolutionary process. But while he was developing his theory of **natural selection**, a Scottish naturalist named Alfred Russel Wallace independently reached the same conclusion. The fact that natural selection, the single most important force of evolutionary change, should be proposed at more or less the same time by two British men in the mid-nineteenth century may seem like a strange coincidence. But if Darwin and Wallace hadn't made their simultaneous discoveries, someone else soon would have, and that someone would probably have been British or French. That's because the groundwork had already been laid in Britain and France, and many scientists there were prepared to accept explanations of biological change that would have been unacceptable even 25 years before.

Like other human endeavors, scientific knowledge is usually gained through a series of small steps rather than giant leaps, and just as technological change is based on past achievements, scientific knowledge builds on previously developed theories. For this reason, it's informative to examine the development of ideas that led Darwin and Wallace to independently develop the theory of evolution by natural selection.

Throughout the Middle Ages, one predominant feature of the European worldview was that all aspects of nature, including all forms of life and their relationships to one another, never changed. This view was partly shaped by a feudal society that was itself a hierarchical, rigid class system that hadn't changed much for centuries. It was also influenced by an extremely powerful religious system, and the teachings of Christianity were taken literally. Consequently, it was generally accepted that all life on earth had been created by God exactly as it existed in the present, and the belief that life-forms couldn't change came to be known as **fixity of species**.

The plan of the entire universe was viewed as God's design. In what is called the "argument from design," anatomical structures were engineered to meet the purpose for which they were required. Wings, arms, and eyes fit the functions they performed, and nature was a deliberate plan of the Grand Designer who was believed to have completed his works fairly recently. In fact, an Irish archbishop named James Ussher (1581–1656) analyzed the "begat" chapter of Genesis and concluded that the earth was created in 4004 B.C. Archbishop Ussher wasn't the first person to suggest a recent origin of the earth, but he was the first to propose a precise date for it.

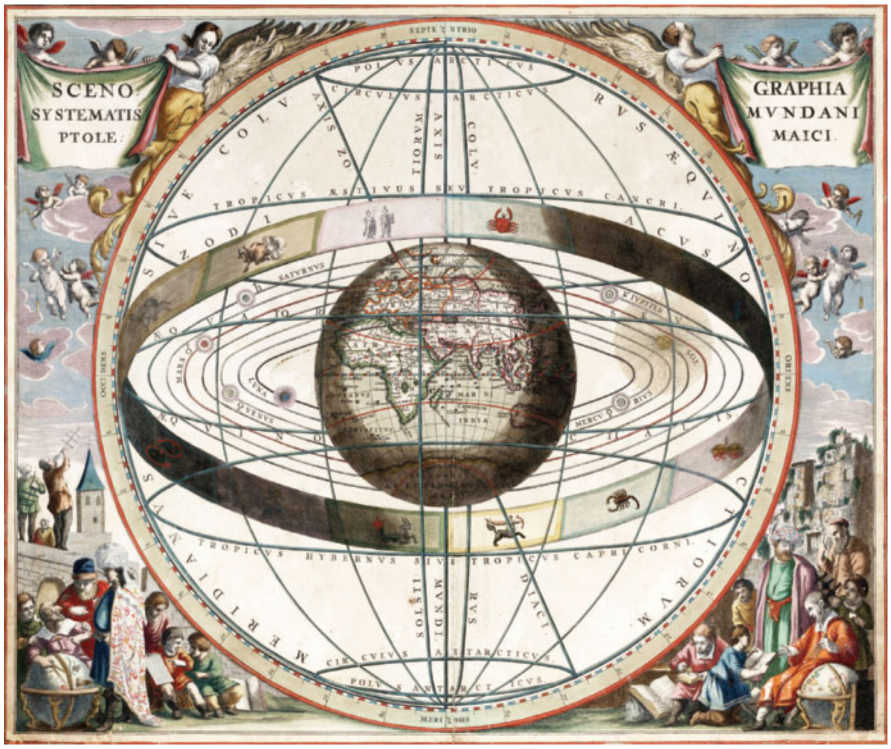
The prevailing notion of the earth's brief existence, together with fixity of species, posed a huge obstacle to the development of evolutionary theory because evolution requires time, and the idea of immense geological time, which today we take for granted, simply didn't exist. In fact, until the concepts of fixity and time were fundamentally altered, it was impossible to conceive of evolution by means of natural selection.

THE SCIENTIFIC REVOLUTION

So, what transformed centuries-old beliefs in a rigid, static universe to a view of worlds in continuous motion? How did the earth's brief history become an immense expanse of incomprehensible time? How did the scientific method as we know it today develop? These are important questions, but it would be equally appropriate to ask why it took so

natural selection The most critical mechanism of evolutionary change, first articulated by Charles Darwin; refers to genetic change or changes in the frequencies of certain traits in populations due to differential reproductive success between individuals.

fixity of species The notion that species, once created, can never change; an idea diametrically opposed to theories of biological evolution.



J. van (Johannes) Loon/Wikimedia Commons

Figure **2-1**
This beautifully illustrated seventeenth-century map shows the earth at the center of the solar system. Around it are seven concentric circles depicting the orbits of the moon, the sun, and the five planets that were known at the time. (Note also the signs of the zodiac.)

long for Europe to break from traditional belief systems when Arab and Indian scholars had developed concepts of planetary motion centuries earlier.

For Europeans, the discovery of the New World and circumnavigation of the globe in the fifteenth century overturned some very basic ideas about the planet. For one thing, the earth could no longer be thought of as flat. Also, as Europeans began to explore the New World, their awareness of biological diversity was greatly expanded as they became aware of plants and animals they hadn't seen before.

There were other attacks on traditional beliefs. In 1514, a Polish mathematician named Copernicus challenged the notion, proposed more than 1,800 years earlier by the Greek philosopher Aristotle, that the earth, circled by the sun, moon, and stars, was the center of the universe (Fig. 2-1). In fact, Indian scholars had figured out that the sun was the center of the solar system long before Copernicus did; but Copernicus is generally credited with removing the earth as the center of all things.

Copernicus' theory didn't attract much attention at the time; however, in the early 1600s, it was restated by an Italian mathematician named Galileo Galilei. To his misfortune, Galileo came into confrontation with the Pope over his publications, and he spent the last nine years of his life under house arrest. Still, in intellectual circles, the universe had changed from earth-centered to sun-centered. Throughout the sixteenth and seventeenth centuries, European scholars developed methods and theories that revolutionized scientific thought. Their technological advances, such as the invention of the telescope, permitted investigations of natural phenomena and opened up entire new worlds for discoveries such as never before had been imagined. But even with these advances, the idea that living forms could change over time simply didn't occur to people.

PRECURSORS TO THE THEORY OF EVOLUTION

Before early naturalists could begin to understand the many forms of organic life, it was necessary to list and describe them. And as research progressed, scholars were increasingly impressed with the amount of biological diversity they saw.

John Ray It wasn't until the seventeenth century that John Ray (1627–1705), a minister educated at Cambridge University, developed the concept of species. He was the first person to recognize that groups of plants and animals could be distinguished from other groups by their ability to mate with one another and produce offspring. He placed such groups of reproductively isolated organisms into a single category, which he called the *species* (*pl*., species). Thus, by the late 1600s, the biological criterion of reproduction was used to define species, much as it is today (Young, 1992). Ray also recognized that species frequently shared similarities with other species, and he grouped these together in a second level of classification he called the *genus* (*pl*., genera). He was the first to use the labels *genus* and *species* in this way, and they're the terms we still use today.

Carolus Linnaeus The Swedish naturalist Carolus Linnaeus (1707–1778) is best known for developing a method of classifying plants and animals. In his famous work, *Systema Naturae* (Systems of Nature), first published in 1735, he standardized Ray's use of genus and species terminology and established the system of **binomial nomenclature**. He also added two more categories: class and order. Linnaeus' four-level system became the basis for **taxonomy**, the system of classification we continue to use today.

Another of Linnaeus' innovations was to include humans in his classification of animals, placing them in the genus *Homo* and species *sapiens*. Including humans in this scheme was controversial because it defied contemporary thought that humans, made in God's image, should be considered unique and separate from the animal kingdom.

Linnaeus also believed in fixity of species, although in later years, faced with mounting evidence to the contrary, he came to question it. Indeed, fixity was being challenged on many fronts, especially in France, where voices were being raised in favor of a universe based on change—and, more to the point, in favor of a biological relationship between similar species based on descent from a common ancestor.

binomial nomenclature (*binomial*, meaning "two names") In taxonomy, the convention established by Carolus Linnaeus whereby genus and species names are used to refer to species. For example, *Homo sapiens* refers to human beings.

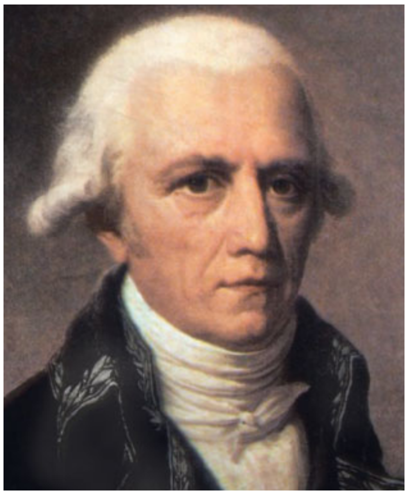
taxonomy The branch of science concerned with the rules of classifying organisms on the basis of evolutionary relationships.

Georges-Louis Leclerc de Buffon Buffon (1707–1788) was Keeper of the King's Gardens in Paris. Unlike others, he recognized the dynamic relationship between the external environment and living forms. In his *Natural History*, first published in 1749, he repeatedly stressed the importance of change in the universe and in the changing nature of species.

Buffon believed that when groups of organisms migrated to new areas, they were gradually altered as a result of adaptation to a somewhat different environment. Buffon's recognition of the external environment as an agent of change in species was an important innovation; however, he rejected the idea that one species could give rise to another.

Erasmus Darwin Today, Erasmus Darwin (1731–1802) is best known as Charles Darwin's grandfather. But he was also a physician, inventor, naturalist, philosopher, poet, and leading member of a well-known intellectual community in Lichfield, England. Living in the English midlands, birthplace of the industrial revolution—which was in full swing—Darwin counted among his friends some of the leading figures of this time of rapid technological and social change.

During his lifetime, Erasmus Darwin became famous as a poet. In his most famous work, he publicly expressed his views that life had originated in the seas and that all species had descended from a common ancestor. From letters and other sources, we know that Charles Darwin read his grandfather's writings; but the degree to which his theories were influenced by Erasmus isn't known.



American Museum of Natural History

Figure 2-2

Lamarck believed that species change was influenced by environmental change. He is best known for his theory of the inheritance of acquired characteristics.

Jean-Baptiste Lamarck Neither Buffon nor Erasmus Darwin attempted to *explain* the evolutionary process. The first scientist to do this was a French naturalist named Jean-Baptiste Lamarck (1744–1829). Lamarck (Fig. 2-2), like Buffon, suggested a dynamic relationship between species and the environment such that if the external environment changed, an animal's activity patterns would also change to accommodate the new

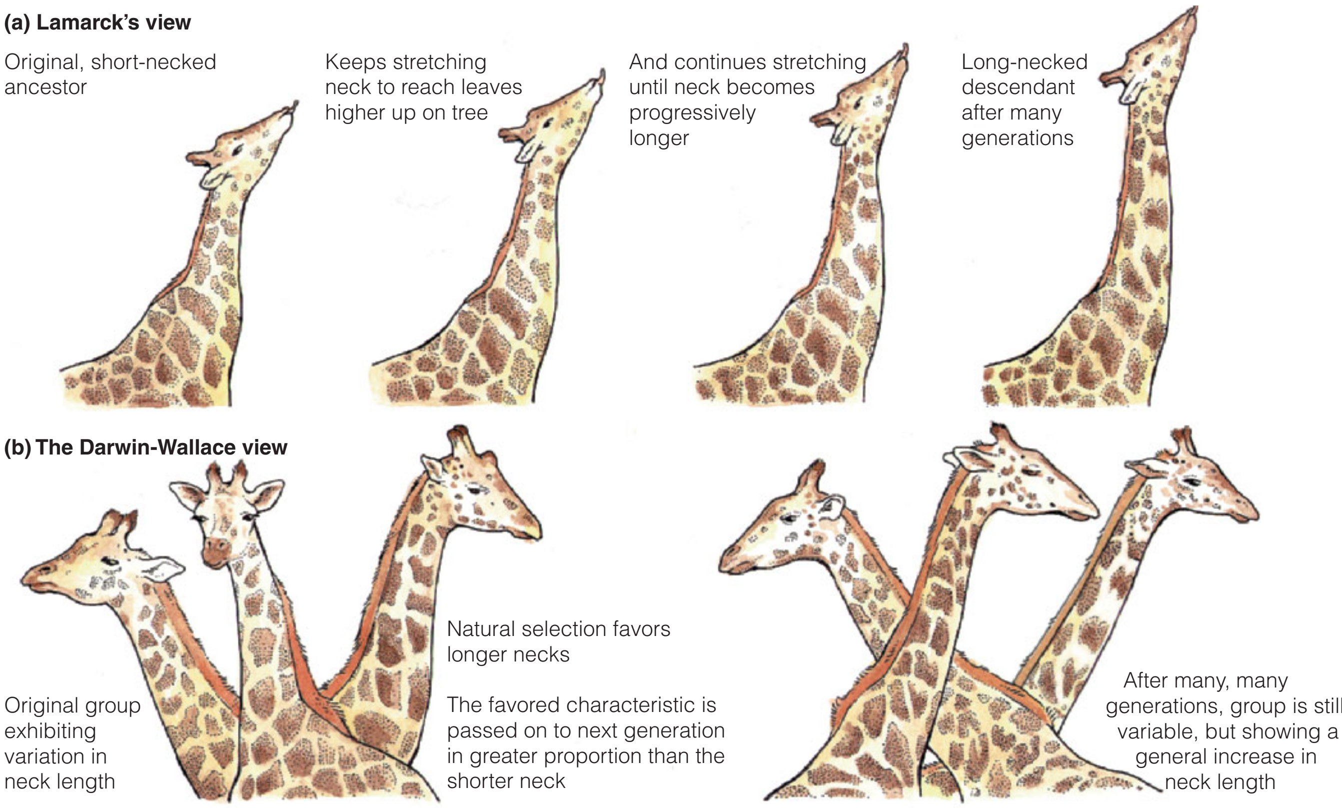


Figure **2-3**

Contrasting ideas about the mechanism of evolution. (a) Lamarck's theory holds that acquired characteristics can be passed to subsequent generations. Short-necked giraffes stretched their necks to reach higher into trees for food. Consequently their necks became longer and, according to Lamarck, this acquired trait was passed on to offspring, who were born with longer necks. (b) The Darwin-Wallace theory of natural selection states that among giraffes there is variation in neck length. If having a longer neck provides an advantage for feeding, the trait will be passed on to a greater number of offspring, leading to an overall increase in the length of giraffe necks over many generations.

circumstances. This would result in the increased or decreased use of certain body parts, and consequently, those body parts would be modified. According to Lamarck, these physical changes would occur in response to bodily "needs," so that if a particular part of the body felt a certain need, "fluids and forces" would be directed to that point and the structure would be modified. Because the alteration would make the animal better suited to its habitat, the new trait would be passed on to its offspring. This theory is known as the *inheritance of acquired characteristics*, or the *use-disuse* theory.

One of the most frequently given hypothetical examples of Lamarck's theory is that of the giraffe, which, having stripped all the leaves from the lower branches of a tree (environmental change), tries to reach leaves on upper branches. As "vital forces" move to tissues of the neck, it becomes slightly longer, and the giraffe can reach higher. The longer neck is then passed on to offspring, with the eventual result that all giraffes have longer necks than their predecessors had (Fig. 2-3). Thus, according to this theory, *a trait acquired by an animal during its lifetime can be passed on to offspring*. Today we know that this explanation is wrong, because only those traits that are influenced by genetic information contained within sex cells (eggs and sperm) can be inherited (see Chapter 3).

Because Lamarck's explanation of species change isn't genetically correct, it's been made fun of and dismissed. But actually, Lamarck deserves a lot of credit because he emphasized the importance of interactions between organisms and the external environment and tried to explain them. Moreover, he coined the term *biology* to refer to studies of living organisms.

Georges Cuvier Georges Cuvier (1769–1832), the most vehement opponent of Lamarck, was a French vertebrate paleontologist who introduced the concept of extinction to explain the disappearance of animals represented by fossils (Fig. 2-4). Although a brilliant anatomist, Cuvier never grasped the dynamic concept of nature, and he insisted on the fixity of species. So, rather than assume that similarities between certain fossil forms and living species indicated evolutionary relationships, he suggested a variation of a theory known as **catastrophism**.

Catastrophism was the belief that the earth's geological features are the results of sudden, worldwide cataclysmic events like the Noah flood. Cuvier's version of catastrophism suggested that a series of regional disasters had destroyed most or all of the plant and animal life in various places. These areas were then restocked with new, similar forms that migrated in from unaffected regions. But Cuvier needed to be consistent with emerging fossil evidence that indicated organisms had become more complex over time, so he suggested that after each disaster, the incoming migrants had a more modern appearance because they were the results of more recent creation events. (The last of these events was the one described in Genesis.) So Cuvier's explanation of increased complexity over time avoided any notion of evolution while still being able to account for the evidence for change that was preserved in the fossil record.

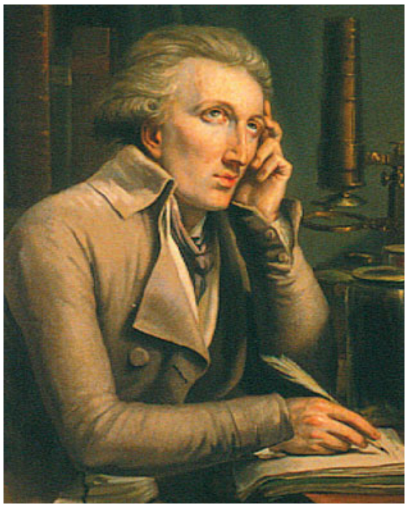

Wikipedia

Figure 2-4
Cuvier explained the fossil record as the result of a succession of catastrophes followed by new creation events.

Thomas Malthus In 1798, Thomas Malthus (1766–1834), an English clergyman and economist, wrote *An Essay on the Principle of Population*, which inspired both Charles Darwin and Alfred Wallace in their separate discoveries of natural selection (Fig. 2-5). In his essay, Malthus argued for limits to human population growth and pointed out that human populations could double in size every 25 years if they weren't kept in check by limited food supplies. Of course, humans, unlike other species, can increase their food supplies and aren't dependent on natural sources, but Malthus warned that increased numbers of humans would eventually lead to famine.

Darwin and Wallace accepted Malthus' proposition that population size increases exponentially while food supplies remain relatively constant, and they extended it to all organisms. But what impressed them the most was something Malthus hadn't written about. They both recognized the important fact that when population size is limited by the availability of resources, there must be constant competition for food and water. And competition between individuals is the ultimate key to understanding natural selection.


With permission from the Master of Haileybury

Figure 2-5
Thomas Malthus' *Essay on the Principle of Population* led both Darwin and Wallace to the principle of natural selection.

Charles Lyell Charles Lyell (1797–1875), the son of Scottish landowners, is considered the founder of modern geology (Fig. 2-6). He was a barrister, a geologist, and for many years Charles Darwin's friend and mentor. Before meeting Darwin in 1836, Lyell had earned acceptance in Europe's most prestigious scientific circles, thanks to his highly praised *Principles of Geology*, first published during the years 1830–1833.

In this immensely important work, Lyell argued that the geological processes observed in the present are the same as those that occurred in the past. This theory, called **uniformitarianism**, didn't originate entirely with Lyell, having been proposed by James Hutton in the late 1700s. Even so, it was Lyell who demonstrated that such forces as wind, water erosion, local flooding, frost, decomposition of vegetation, volcanoes, earthquakes, and glacial movements had all contributed in the past to produce the geological landscape that exists in the present. What's more, the fact that these processes still occurred indicated that geological change was still happening and that the forces driving such change were consistent, or *uniform*, over time. In other words, although various aspects of the earth's surface (for example, climate, plants, animals, and land surfaces) are variable through time, the *underlying processes* that influence them are constant.

catastrophism The view that the earth's geological landscape is the result of violent cataclysmic events. This view was promoted by Cuvier, especially in opposition to Lamarck.

uniformitarianism The theory that the earth's features are the result of long-term processes that continue to operate in the present as they did in the past. Elaborated on by Lyell, this theory opposed catastrophism and contributed strongly to the concept of immense geological time.

© National Portrait Gallery, London

Figure **2-6**
Portrait of Charles Lyell.

The theory of uniformitarianism flew in the face of Cuvier's catastrophism. Additionally, Lyell emphasized the obvious: namely, that for such slow-acting forces to produce momentous change, the earth would have to be far older than anyone had previously suspected. By providing an immense time scale and thereby altering perceptions of earth's history from a few thousand to many millions of years, Lyell changed the framework within which scientists viewed the geological past. Thus, the concept of "deep time" (Gould, 1987) remains one of Lyell's most significant contributions to the discovery of evolutionary principles. The immensity of geological time permitted the necessary time depth for the inherently slow process of evolutionary change.

THE DISCOVERY OF NATURAL SELECTION

Charles Darwin Having already been introduced to Erasmus Darwin, you shouldn't be surprised that his grandson Charles grew up in an educated family with ties to intellectual circles. Charles Darwin (1809–1882) was one of six children of Dr. Robert and Susanna Darwin (Fig. 2-7). Being the grandson not only of Erasmus Darwin but also of the wealthy Josiah Wedgwood (of Wedgwood china fame), Charles grew up enjoying the comfortable lifestyle of the landed gentry in rural England.

As a boy, he had a keen interest in nature and spent his days fishing and collecting shells, birds' eggs, rocks, and so forth. However, this interest in natural history didn't dispel the generally held view of family and friends that he was in no way remarkable. In fact, his performance at school was no more than ordinary.

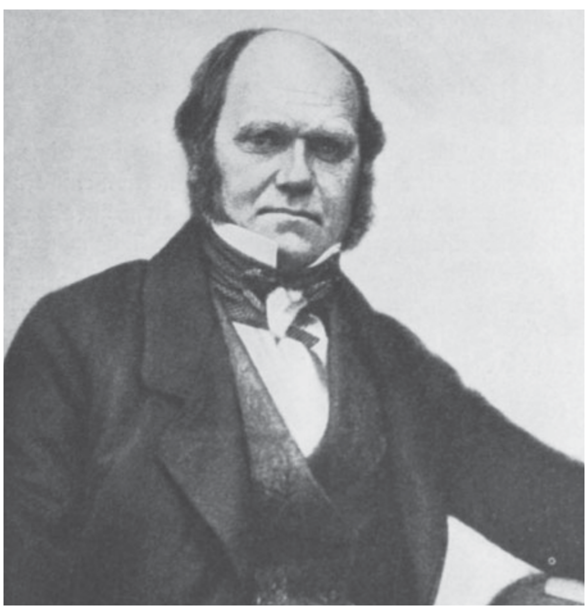
After the death of his mother when he was eight years old, Darwin was raised by his father and his older sisters. Because he showed little interest in anything except hunting, shooting, and perhaps science, his father sent him to Edinburgh University to study medicine. It was there that Darwin first became acquainted with the evolutionary theories of Lamarck and others.

transmutation The change of one species to another. The term *evolution* did not assume its current meaning until the late nineteenth century.

During that time (the 1820s), notions of evolution were becoming feared in England and elsewhere. Anything identifiable with postrevolutionary France was viewed with suspicion by the established order in England. Lamarck, partly because he was French, was especially vilified by British scientists.

It was also a time of growing political unrest in Britain. The Reform Movement, which sought to undo many of the wrongs of the traditional class system, was under way; and like most social movements, this one had a radical faction. Because many of the radicals were atheists and socialists who also supported Lamarck's ideas, many people came to associate evolution with atheism and political subversion. Such was the growing fear of evolutionary ideas that many believed that if they were generally accepted, "the Church would crash, the moral fabric of society would be torn apart, and civilized man would return to savagery" (Desmond and Moore, 1991, p. 34). It's unfortunate that some of the most outspoken early proponents of **transmutation** were so vehemently anti-Christian, because their rhetoric helped establish the entrenched suspicion and misunderstanding of evolutionary theory that persist today.

Figure **2-7**
Black-and-white photograph of Charles Darwin taken five years before the publication of *Origin of Species*.



© Bettmann/Corbis

While at Edinburgh, young Darwin studied with professors who were outspoken supporters of Lamarck. Therefore, although he hated medicine and left Edinburgh after two years, his experience there was a formative period in his intellectual development.

Even though Darwin was fairly indifferent to religion, he next went to Christ's College, Cambridge, to study theology. It was during his Cambridge years that he seriously cultivated his interests in natural science, immersing himself in botany and geology. It's no wonder that following his graduation in 1831, he was invited to join a scientific expedition that would circle the globe. And so it was that Darwin set sail aboard

Figure 2-8
The route of HMS *Beagle*.

the HMS *Beagle* on December 17, 1831. The famous voyage of the *Beagle* would take almost five years and would forever change not only the course of Darwin's life but also the history of biological science.

Darwin went aboard the *Beagle* believing in fixity of species. But during the voyage, he privately began to have doubts. For example, he came across fossils of ancient giant animals that, except for size, looked very much like species that still lived in the same vicinity, and he wondered if the fossils represented ancestors of those living forms.

During the famous stopover at the Galápagos Islands (Fig. 2-8), Darwin noticed that the vegetation and animals (especially birds) shared many similarities with those on the mainland of South America. But they weren't identical to them. What's more, the birds on one island were somewhat different from those living on another. Darwin collected 13 different varieties of Galápagos finches, and it was clear that they represented a closely affiliated group; but they differed with regard to certain physical traits, particularly the shape and size of their beaks (Fig. 2-9). He also collected finches from the mainland, and these appeared to represent only one group, or species.

The insight that Darwin gained from the finches is legendary. He recognized that the various Galápagos finches had all descended from a common mainland ancestor and had been modified over time in response to different island habitats and dietary preferences.

Figure 2-9
Beak variation in Darwin's Galápagos finches.

(a) Ground finch
Main food: seeds
Beak: heavy

(b) Tree finch
Main food: leaves, buds, blossoms, fruits
Beak: thick, short

(c) Tree finch (called woodpecker finch)
Main food: insects
Beak: stout, straight

(d) Ground finch (known as warbler finch)
Main food: insects
Beak: slender

Figure 2-10
All domestic dog breeds share a common ancestor, the wolf. The extreme variation exhibited by dog breeds today has been achieved in a relatively short time through artificial selection. In this situation, humans allow only certain dogs to breed to emphasize specific characteristics. (We should note that not all traits desired by human breeders are advantageous to the dogs themselves.)

But actually, it wasn't until *after* he returned to England that he recognized the significance of the variation in beak structure. In fact, during the voyage, he had paid little attention to the finches. It was only later that he considered the factors that could lead to the modification of one species into 13 (Gould, 1985; Desmond and Moore, 1991).

Darwin arrived back in England in October 1836 and was immediately accepted into the most prestigious scientific circles. He married his cousin, Emma Wedgwood, and moved to the village of Down, near London, where he spent the rest of his life writing on topics ranging from fossils to orchids. But the question of species change was his overriding passion.

At Down, Darwin began to develop his views on what he called *natural selection*. This concept was borrowed from animal breeders, who choose, or "select," as breeding stock those animals that possess certain traits they want to emphasize in offspring. Animals with undesirable traits are "selected against," or prevented from breeding. A dramatic example of the effects of selective breeding can be seen in the various domestic dog breeds shown in Figure 2-10. Darwin applied his knowledge of domesticated species to naturally occurring ones, recognizing that in undomesticated organisms, the selective agent is nature, not humans.

By the late 1830s, Darwin had realized that biological variation within a species (that is, differences among individuals) was crucial. Furthermore, he recognized that sexual reproduction increased variation, although he didn't know why. Then, in 1838, he read Malthus' essay, and there he found the answer to the question of how new species came to be. He accepted from Malthus that populations increase at a faster rate than do resources, and he recognized that in nonhuman animals, increase in population size is continuously restricted by limited food supplies. He also accepted that in nature there is a constant "struggle for existence." The idea that in each generation more offspring are born than survive to adulthood, coupled with the notions of competition for resources and biological diversity, was all Darwin needed to develop his theory of natural selection. He wrote: "It at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of a new species" (F. Darwin, 1950, pp. 53–54). Basically, this quotation summarizes the entire theory of natural selection.

By 1844, Darwin had written a short summary of his views on natural selection, but he didn't think he had enough data to support his hypothesis, so he continued his research without publishing. He also had other reasons for not publishing what he knew would be, to say the least, a highly controversial work. He was deeply troubled by the fact that his wife, Emma, saw his ideas as running counter to her strong religious convictions (Keynes, 2001). Also, as a member of the established order, he knew that many of his friends and associates were concerned with threats to the status quo, and evolutionary theory was viewed as a very serious threat. So he waited.

Alfred Russel Wallace Unlike Darwin, Alfred Russel Wallace (1823–1913) was born into a family of modest means (Fig. 2-11). He went to work at the age of 14, and with little formal education, he moved from one job to the next. He became interested in collecting plants and animals, and in 1848 he joined an expedition to the Amazon, where he acquired firsthand knowledge of many natural phenomena. Then, in 1854, he sailed for Southeast Asia and the Malay Peninsula to collect bird and insect specimens.

In 1855, Wallace published a paper suggesting that species were descended from other species and that the appearance of new species was influenced by environmental factors. The Wallace paper caused Lyell and others to urge Darwin to publish, but still he hesitated.

Then, in 1858, Wallace sent Darwin another paper, "On the Tendency of Varieties to Depart Indefinitely from the Original Type." In it, Wallace described evolution as a process driven by competition and natural selection. Once he read it Darwin feared that Wallace might get credit for a theory (natural selection) that he himself had developed. He quickly wrote a paper presenting his ideas, and both papers were read before the Linnean Society of London. Neither author was present. Wallace was out of the country, and Darwin was mourning the recent death of his young son.

The papers received little notice at the time; but when Darwin completed and published his greatest work, *On the Origin of Species*,* in December 1859, the storm broke, and it still hasn't abated. Although public opinion was negative, there was much scholarly praise for the book, and scientific opinion gradually came to Darwin's support. The riddle of species was now explained: Species were mutable, not fixed; and they evolved from other species through the mechanism of natural selection.

Figure 2-11
Alfred Russel Wallace independently discovered the key to the evolutionary process.

NATURAL SELECTION

Early in his research, Darwin had realized that natural selection was the key to evolution. With the help of Malthus' ideas, he saw *how* selection in nature could be explained. In the struggle for existence, those *individuals* with favorable variations would survive and reproduce, but those with unfavorable variations wouldn't. For Darwin, the explanation of evolution was simple. The basic processes, as he understood them, are as follows:

1. All species are capable of producing offspring at a faster rate than food supplies increase.
2. There is biological variation within all species. (Today we know that except for identical twins, no two individuals are genetically the same.)

*The full title is *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*.

3. Since in each generation more offspring are produced than can survive, and owing to limited resources, there is competition between individuals. (*Note*: This statement doesn't mean that there is constant fierce fighting.)
4. Individuals who possess favorable variations or traits (for example, speed, resistance to disease, protective coloration) have an advantage over those who don't have them. In other words, favorable traits increase the likelihood of survival and reproduction.
5. The environmental context determines whether or not a trait is beneficial. What is favorable in one setting may be a liability in another. Consequently, the traits that become most advantageous are the result of a natural process.
6. Traits are inherited and passed on to the next generation. Because individuals who possess favorable traits contribute more offspring to the next generation than individuals who don't, over time, such characteristics become more common in the population; less favorable traits aren't passed on as frequently, and they become less common, or are "weeded out." Individuals who produce more offspring in comparison to others are said to have greater **reproductive success**.
7. Over long periods of geological time, successful variations accumulate in a population, so that later generations may be distinct from ancestral ones. Thus, in time, a new species may appear.
8. Geographical isolation also contributes to the formation of new species. As populations of a species become geographically isolated from one another, for whatever reasons, they begin to adapt to different environments. Over time, as populations continue to respond to different **selective pressures** (that is, different ecological circumstances), they may become distinct species. The 13 species of Galápagos finches are presumably all descended from a common ancestor on the South American mainland, and they provide an example of the role of geographical isolation.

Before Darwin, individual members of species weren't considered important, so they weren't studied. But as we've seen, Darwin recognized the uniqueness of individuals and realized that variation among them could explain how selection occurs. Favorable variations are selected, or chosen, for survival by nature; unfavorable ones are eliminated. *Natural selection operates on individuals*, favorably or unfavorably, but *it's the population that evolves*. The unit of natural selection is the individual; the unit of evolution is the population (because individuals don't change genetically, but over time, populations do).

Natural Selection in Action

The most frequently cited example of natural selection concerns changes in the coloration of "peppered" moths around Manchester, England. In recent years, the moth story has come under some criticism; but the basic premise remains valid, so we use it to illustrate how natural selection works.

Before the nineteenth century, the most common variety of the peppered moth was a mottled gray color. During the day, as moths rested on lichen-covered tree trunks, their coloration provided camouflage (Fig. 2-12). There was also a dark gray variety of the same species, but since the dark moths weren't camouflaged, they were eaten by birds more frequently and so they were less common. (In this example, the birds are the *selective agent*, and they apply *selective pressure* on the moths.) Therefore, the dark moths produced fewer offspring than the camouflaged moths. Yet, by the end of the nineteenth century, the common gray form had been almost completely replaced by the darker one.

The cause of this change was the changing environment of industrialized nineteenth-century England. Coal dust from factories and fireplaces settled on trees, turning them dark gray and killing the lichen. The moths continued to rest on the trees, but the light gray ones became more conspicuous as the trees became darker, and they were

reproductive success The number of offspring an individual produces and rears to reproductive age; an individual's genetic contribution to the next generation.

selective pressures Factors in the environment that influence reproductive success in individuals.

Michael Tweedie/Photo Researchers

Breck P. Kent/Animals Animals

(a) (b)

Figure **2-12**

Variation in the peppered moth. (a) The dark form is more visible on the light, lichen-covered tree. (b) On trees darkened by pollution, the lighter form is more visible.

increasingly targeted by birds. Since fewer of the light gray moths were living long enough to reproduce, they contributed fewer genes to the next generation than the darker moths did, and the proportion of lighter moths decreased while the dark moths became more common. A similar color shift had also occurred in North America. But when the advent of clean air acts in both Britain and the United States reduced the amount of air pollution (at least from coal), the predominant color of the peppered moth once again became the light mottled gray. This kind of evolutionary shift in response to environmental change is called *adaptation*.

Another example of natural selection is provided by the medium ground finch of the Galápagos Islands. In 1977, drought killed many of the plants that produced the smaller, softer seeds favored by these birds. This forced a population of finches on one of the islands to feed on larger, harder seeds. Even before 1977, some birds had smaller, less robust beaks than others (that is, there was variation); and during the drought, because they were less able to process the larger seeds, more smaller-beaked birds died than larger-beaked birds. Therefore, although overall population size declined, average beak thickness in the survivors and their offspring increased, simply because thicker-beaked individuals were surviving in greater numbers and producing more offspring. In other words, they had greater reproductive success. But during heavy rains in 1982–1983, smaller seeds became more plentiful again and the pattern in beak size reversed itself, demonstrating how reproductive success is related to environmental conditions (Grant, 1975, 1986; Ridley, 1993).

The best illustration of natural selection, however, and certainly one with potentially grave consequences for humans, is the recent increase in resistant strains of disease-causing microorganisms. When antibiotics were first introduced in the 1940s, they were hailed as the cure for bacterial disease. But that optimistic view didn't take into account the fact that bacteria, like other organisms, possess genetic variability. Although an antibiotic will kill most bacteria in an infected person, any bacterium with an inherited resistance to that particular therapy will survive. Subsequently, the survivors reproduce and pass their drug resistance to future generations, so that eventually, the population is mostly made up of bacteria that don't respond to treatment. What's more, because bacteria produce new generations every few hours, antibiotic-resistant strains are continuously being produced. As a result, many types of infection no longer respond to treatment. For example, tuberculosis was once thought to be well controlled, but it has seen a resurgence in recent years because the bacterium that causes it is now resistant to many antibiotics.

These three examples provide the following insights into the fundamentals of evolutionary change produced by natural selection:

1. *A trait must be inherited if natural selection is to act on it.* A characteristic that isn't hereditary (such as a temporary change in hair color produced by the hairdresser)

won't be passed on to succeeding generations. In finches, for example, beak size is a hereditary trait.

2. *Natural selection can't occur without population variation in inherited characteristics.* If, for example, all the peppered moths had initially been gray (you will recall that some dark forms were always present) and the trees had become darker, the survival and reproduction of all moths could have been so low that the population might have become extinct. *Selection can work only with variation that already exists.*
3. **Fitness** *is a relative measure that changes as the environment changes.* Fitness is simply *differential reproductive success*. In the initial stage, the lighter moths were more fit because they produced more offspring. But as the environment changed, the dark gray moths became more fit, and a further change reversed the adaptive pattern. Likewise, the majority of Galápagos finches will have larger or smaller beaks, depending on external conditions. So it should be obvious that statements regarding the "most fit" mean nothing without reference to specific environments.
4. *Natural selection can act only on traits that affect reproduction.* If a characteristic isn't expressed until later in life, after organisms have reproduced, then natural selection can't influence it. This is because the inherited components of the trait have already been passed on to offspring. Many forms of cancer and cardiovascular disease are influenced by hereditary factors, but because these diseases usually affect people after they've had children, natural selection can't act against them. By the same token, if a condition usually kills or compromises the individual before he or she reproduces, natural selection acts against it because the trait won't be passed on.

So far, our examples have shown how different death rates influence natural selection (for example, moths or finches that die early leave fewer offspring). But mortality isn't the complete picture. Another important aspect of natural selection is fertility, because an animal that gives birth to more young passes its genes on at a faster rate than one that bears fewer offspring. However, fertility isn't the entire story either, because the crucial element is the number of young raised successfully to the point at which they themselves reproduce. We call this *differential net reproductive success*. The way this mechanism works can be demonstrated through yet another example.

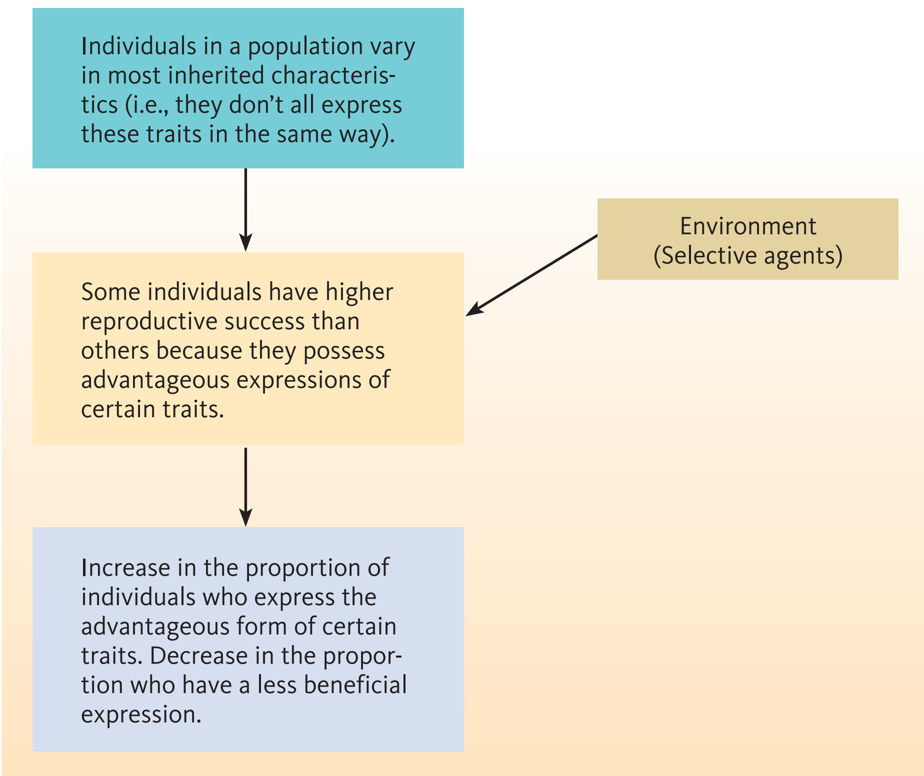
In swifts (small birds that resemble swallows), data show that producing more offspring doesn't necessarily guarantee that more young will be successfully raised. The number of eggs hatched in a breeding season is a measure of fertility. The number of birds that mature and are eventually able to leave the nest is a measure of net reproductive success, or offspring successfully raised. The following table shows the correlation between the number of eggs hatched (fertility) and the number of young that leave the nest (reproductive success), averaged over four breeding seasons (Lack, 1966):

Number of eggs hatched (fertility)	2 eggs	3 eggs	4 eggs
Average number of young raised (reproductive success)	1.92	2.54	1.76
Sample size (number of nests)	72	20	16

As you can see, the most efficient number of eggs is three, because that number yields the highest reproductive success. Raising two offspring is less beneficial to the parents, since the end result isn't as successful as with three eggs. Trying to raise more than three is actually detrimental, since the parents may not be able to provide enough nourishment for any of the offspring. In evolutionary terms, offspring that die before reaching reproductive age are equivalent to never being born. Actually, death of an offspring can be a minus to the parents, because before it dies, it drains parental resources. It may even inhibit their ability to raise other offspring, thereby reducing their reproductive success even further. Selection favors those genetic traits that yield the maximum net reproductive success. If the number of eggs laid is a genetic trait in birds (and it seems to be), natural selection in swifts should act to favor the laying of three eggs as opposed to two or four.

fitness Pertaining to natural selection, a measure of the *relative* reproductive success of individuals. Fitness can be measured by an individual's genetic contribution to the next generation compared to that of other individuals. The terms *genetic fitness*, *reproductive fitness*, and *differential reproductive success* are also used.

At a Glance
The Mechanism of Natural Selection



Constraints on Nineteenth-Century Evolutionary Theory

Darwin argued for the concept of evolution in general and the role of natural selection in particular, but he didn't understand the mechanisms of evolutionary change. As we have seen, natural selection acts on variation within species. But neither Darwin nor anyone else in the nineteenth century understood the actual source of variation. Also, no one understood how parents pass traits to offspring. Almost without exception, nineteenth-century scholars believed that inheritance was a *blending* process in which parental characteristics were mixed together to produce intermediate expressions in offspring. Given this notion, we can see why the true nature of genes was unimaginable, and with no alternative explanations, Darwin accepted it. As it turns out, a contemporary of Darwin's had actually worked out the rules of heredity. However, the work of this Augustinian monk named Gregor Mendel (whom you will meet in Chapter 3) wasn't recognized until the beginning of the twentieth century.

The first three decades of the twentieth century saw the merger of Mendel's discoveries and natural selection. This was a crucial development because until then, scientists thought that these concepts were unrelated. Then, in 1953, the structure of **deoxyribonucleic acid (DNA)** was discovered. This landmark achievement has been followed by even more amazing advances in the field of genetics, including the sequencing of the human **genome**. We may finally be on the threshold of revealing the remaining secrets of the evolutionary process. If only Darwin could know!

deoxyribonucleic acid (DNA) The double-stranded molecule that contains the genetic code.

genome The entire genetic makeup of an individual or species.

Opposition to Evolution

Almost 150 years after the publication of *Origin of Species*, the debate over evolution is far from over. For the vast majority of scientists today, evolution is indisputable. The genetic evidence for it is solid and accumulating daily. Anyone who appreciates and understands genetic mechanisms can't avoid the conclusion that populations and species evolve. But surveys consistently show that about half of all Americans don't believe that evolution occurs. There are a number of reasons for this.

The mechanisms of evolution are complex and don't lend themselves to simple explanations. Understanding them requires some familiarity with genetics and biology—a familiarity that people don't have unless they took related courses in school. What's more, people tend to want definitive, clear-cut answers to complex questions. But as you learned in Chapter 1, science doesn't always provide definitive answers to questions, nor does it establish absolute truths. Another thing to consider is that regardless of their culture, most people are raised in belief systems that don't emphasize **biological continuity** between species.

As we said at the beginning of this chapter, much of the opposition to evolutionary concepts is based in certain religious views. The relationship between science and religion has never been easy (remember Galileo). Even though both systems serve, in their own ways, to explain various phenomena, scientific explanations are based in data analysis, hypothesis testing, and interpretation. Religion, meanwhile, is a system of beliefs based in faith, and it isn't amenable to scientific testing. Religion and science concern different aspects of the human experience and we should remember that they aren't mutually exclusive approaches. Belief in God doesn't exclude the possibility of biological evolution; and acknowledgment of evolutionary processes doesn't preclude the existence of God. What's more, not all forms of Christianity or other religions are opposed to evolutionary concepts. Some years ago, the Vatican hosted an international conference on human evolution; and in 1996, Pope John Paul II issued a statement that "fresh knowledge leads to recognition of the theory of evolution as more than just a hypothesis." Today, the official position of the Catholic Church is that evolutionary processes occur, but that the human soul is of divine creation and not subject to evolutionary processes. Likewise, mainstream Protestants don't generally see a conflict. But those who believe absolutely in a literal interpretation of the bible (called fundamentalists) accept no compromise.

In 1925, a law banning the teaching of evolution in public schools was passed in Tennessee. To test the validity of the law, the American Civil Liberties Union persuaded a high school teacher named John Scopes to allow himself to be arrested and tried for teaching evolution. The subsequent trial (called the Scopes Monkey Trial) was a 1920s equivalent of current celebrity trials, and in the end, Scopes was convicted and fined $100. In the more than 80 years since that trial, Christian fundamentalists have continued to try to remove evolution from public school curricula. Known as "creationists" because they explain the existence of the universe as the result of a sudden creation event that occurred no more than 10,000 years ago, they are determined either to eliminate the teaching of evolution or to introduce antievolutionary material into public school classes. In the past 20 years, creationists have insisted that what they used to call "creation science" is as valid a scientific endeavor as is the study of evolution. They argue that in the interest of fairness, a balanced view should be offered: If evolution is taught as science, then creationism should also be taught as science. Superficially, this argument would sound fair to most people, but "creation science" is not science for the simple reason that creationists insist that their view is absolute and infallible. Consequently, creationism isn't a hypothesis that can be tested, nor is it amenable to falsification. Because hypothesis testing is the basis of all science, creationism, by its very nature, cannot be considered science.

Still, creationists remain active in state legislatures, promoting laws that mandate the teaching of creationism in public schools. In 1981, the Arkansas state legislature passed

biological continuity Refers to a biological continuum—the idea that organisms are related through common ancestry and that traits present in one species are also seen to varying degrees in others. When expressions of a phenomenon continuously grade into one another so that there are no discrete categories, they exist on a continuum. Color is one such phenomenon, and life-forms are another.

one such law but it was overturned in 1982. In his ruling against the state, the judge stated that “a theory that is by its own terms dogmatic, absolutist and never subject to revision is not a scientific theory.” And he added: “Since creation is not science, the conclusion is inescapable that the only real effect of [this law] is the advancement of religion.”

Since that time, numerous similar laws have been passed, only to be overturned because they violate the principle of separation of church and state as provided in the First Amendment to the U.S. Constitution. The First Amendment states, “Congress shall make no law respecting an establishment of religion, or prohibiting the free exercise thereof. . . .” This “establishment clause” was initially proposed to ensure that the government could neither promote nor restrict any particular religious view, as it did in England at the time the Constitution was written. Since then, state and federal courts have consistently interpreted this sentence to mean that institutions (such as public schools) that are funded by public money, which is derived from taxes, cannot be used to promote religion. Of course, this doesn’t mean that people can’t pray in public buildings, but it does prohibit organized events that promote a particular religion in such places. (It’s worth mentioning that the establishment clause also exempts churches from paying property taxes.)

But court rulings haven’t stopped the creationists, who encourage teachers to claim “academic freedom” to teach creationism. They’ve also dropped the word *creationism* in favor of the less religious-sounding term *intelligent design theory*, which harkens back to the argument from design (see p. 21). The term *intelligent design* is based on the notion that most biological functions and anatomical traits (for example, the eye) are too complex to be explained by a theory that doesn’t include the presence of a creator or designer. To avoid objections based on the guarantee of separation of church and state, proponents of intelligent design claim that they don’t emphasize any particular religion. But this argument still doesn’t speak to the essential point that promoting *any* religious view in a publicly funded school constitutes a violation of the U.S. Constitution.

Antievolution feeling also remains strong among many politicians, particularly those with strong support from Christian fundamentalists. The president of the United States (as of this writing) has publicly supported teaching intelligent design in public schools; and in 1999, one very powerful former U.S. congressman went so far as to state that the teaching of evolution is one of the factors behind violence in America today! Now, that’s a stretch!

Summary

Our current understanding of evolutionary processes is directly traceable to developments in intellectual thought in western Europe over the last 300 years. Many people contributed to this shift in perspective, and we’ve named only a few. Linnaeus placed humans in the same taxonomic scheme as all other animals. Importantly, Lamarck and Buffon both recognized that species could change in response to environmental circumstances, but Lamarck also attempted to explain *how* the changes occurred. He proposed the idea of *inheritance of acquired characteristics*, which was later discredited. Lyell, in his theory of uniformitarianism, provided the necessary expanse of time for evolution to occur, and Malthus discussed how population size is kept in check by the availability of resources. Darwin and Wallace, influenced by their predecessors, independently recognized that because of competition for resources, individuals with favorable characteristics tend to survive and pass those traits on to offspring. Those lacking beneficial traits produce fewer offspring, if they survive to reproductive age at all. That is, they have lower reproductive success and reduced fitness. Thus, over time, advantageous characteristics accumulate in a population (because they have been selected for) while disadvantageous ones are eliminated (selected against). This, in a nutshell, is the theory of evolution by means of natural selection.

Critical Thinking Questions

1. After having read this chapter, how would you respond to the question, "If humans evolved from monkeys, why do we still have monkeys?"
2. What are selective agents? Can you think of some examples we didn't discuss? Why did Darwin look at domesticated species as models for natural selection, and what is the selective agent in artificial selection? List some examples of artificial selection that we didn't discuss.
3. Given what you've read about the scientific method, how would you explain the differences between science and religion as methods of explaining natural phenomena? Do you personally see a conflict between evolutionary and religious explanations of how species came to be? Why or why not?