2

Why is evolution important to anthropologists?

This question is fundamental to contemporary anthropology and is a topic of great significance in wider scientific discussions. In this chapter, we will look at how the living world was understood before the nineteenth century, where Darwin's ideas came from, how they have been further elaborated since his time, and why evolutionary theory continues to be our most powerful tool for understanding biological processes today.

CHAPTER OUTLINE

Galapagos Darwin finch in the Galápagos Islands, Ecuador.

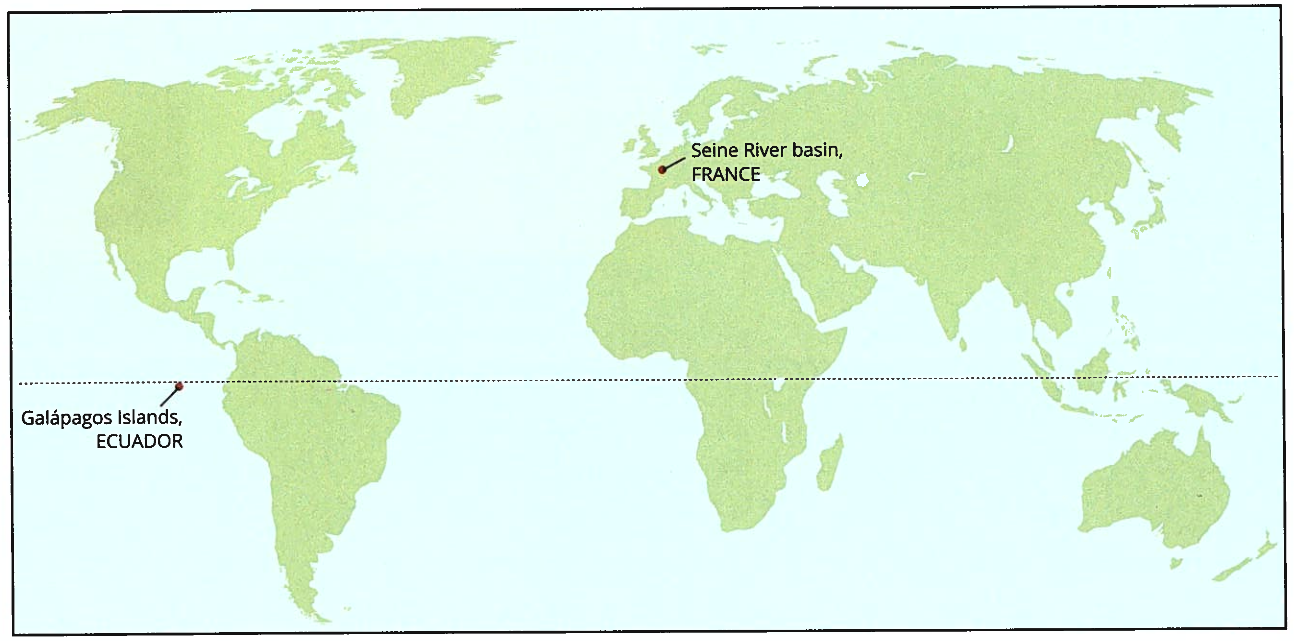


FIGURE 2.1 Major locations discussed in Chapter 2.

Philosopher of science Philip Kitcher (1982) has suggested that successful scientific theories are testable, unified, and fruitful. A theory is testable when its hypotheses can be independently matched up against nature. A theory is unified when it offers just one or a few basic problem-solving strategies that make sense of a wide range of material evidence. And a theory is fruitful when its central principles suggest new and promising possibilities for further research. The modern theory of biological evolution possesses all three characteristics. Evolutionary hypotheses are highly testable in a number of ways. As we shall see, material evidence from widely diverse sources has consistently fit evolutionary predictions. Because it is based on a few central concepts and assumptions, the evolutionary research program is also highly unified. Charles Darwin's *On the Origin of Species by Means of Natural Selection* appeared in 1859. As Kitcher (1982, 48) puts it, Darwin "gave structure to our ignorance." After that date, biologists could borrow Darwin's methods to guide them in new and promising directions. The study of life has not been the same since. As we begin our study of human evolution, you may be surprised at the number of terms and concepts that you are learning from biology, genetics, and ecology. The theory of evolution has engaged the efforts of many scientists for more than 150 years. Their work has produced a still-developing, powerful, multistranded theory. To understand the arguments made by modern evolutionary biologists, we must learn the language of evolution. The payoff will be a nuanced view of what the theory of evolution is really about and how powerful it really is.

What Is Evolutionary Theory?

Evolutionary theory claims that living species can change over time and give rise to new kinds of species, with the result that all organisms ultimately share a common ancestry. Because of this common ancestry, information about biological variation in finches or genetic transmission in fruit flies can help us understand the roles of biological variation and genetics in human evolution.

Eldredge and Tattersall (1982) observe that evolution "is as highly verified a thesis as can be found in science. Subjected to close scrutiny from all angles for over a century now, evolution emerges as the only naturalistic explanation we have of the twin patterns of similarity and diversity that pervade all life" (2). Steven Stanley (1981), another evolutionary biologist, states that "the theory of evolution is not just getting older, it is getting better. Like any scientific concept that has long withstood the test of time, this one has suffered setbacks, but, time and again, has rebounded to become richer and stronger" (xv). Thirty years later, evolutionary thinkers remain convinced that the story they propose to tell about the history of life on earth is more persuasive than any of its rivals. To what do they owe this sense of confidence?

evolutionary theory The set of testable hypotheses that assert that living organisms can change over time and give rise to new kinds of organisms, with the result that all organisms ultimately share a common ancestry.

What Material Evidence Is There for Evolution?

Two kinds of material evidence have been particularly important in the development of evolutionary theory: material evidence of change over time and material evidence of change across space. Geological research led to the discovery of the fossil record—the remains of life forms that had been preserved in the earth for a long time. When scientists compared these fossils with each other and with living organisms, they noted that the living organisms were quite different from the fossilized organisms. This was material evidence of change over time, or **evolution**, in the kinds of organisms that have lived on the earth. Any persuasive biological theory would have to find a way to explain this material evidence.

Equally important material evidence for the development of evolutionary theory came from the study of living organisms. Darwin himself was most interested in explaining the pattern of distribution of living species of organisms. In one of his best-known studies, Darwin noted that neighboring geographic areas on the islands of the Galápagos Archipelago were inhabited by species of finch different from the finch species found on the Ecuadorian mainland. At the same time, the various Galápagos species resembled one another closely and resembled mainland finch species (Figure 2.2). Species distribution patterns of this kind suggested change over space, which, again, any persuasive biological theory would have to explain.

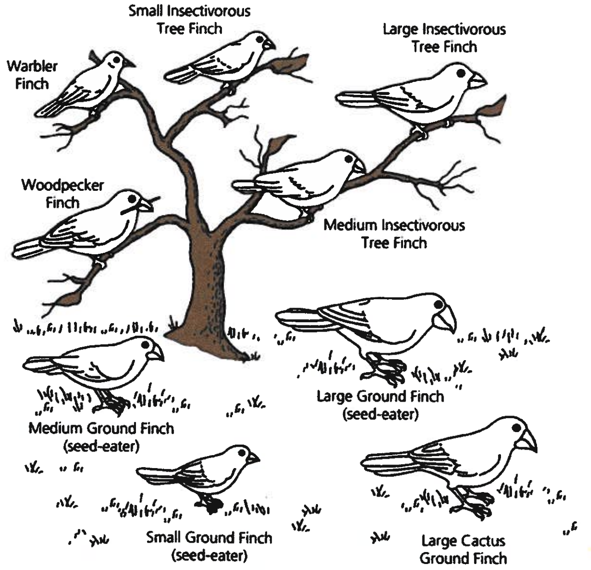


FIGURE 2.2 Charles Darwin and Alfred Russel Wallace explained the pattern of distribution of living species of organisms (such as the various species of finches living on the Galápagos Islands) by arguing that all the variants had evolved from a single ancestral species.

In the centuries before Darwin, however, the fossil record was mostly unknown, and many of those concerned with biology did not see the pattern of distribution of living species as evidence for past change. To understand why Darwin's ideas had such a powerful impact requires an understanding of pre-Darwinian views of the natural world (Table 2.1).

Pre-Darwinian Views of the Natural World

In the Western societies of antiquity, the Greeks thought the world had been, and would be, around forever; in the Judeo-Christian tradition, it was thought that the world was young and would end soon. Both traditions saw the world as fixed and unchanging.

Essentialism

If the world does not change, then the various forms of life that are part of that world also do not change. We can trace this view back to the ancient Greek philosopher Plato. A central element of Plato's philosophy was a belief in an ideal world of perfect, eternal, unchanging forms that exist apart from the imperfect, changeable, physical world of living things. Plato believed that these two worlds—ideal and material—were linked and that every ideal form—the ideal form of "cowness," for instance—was represented in the physical, material world by a number of imperfect but recognizable real cows of varying sizes, colors, temperaments, and so on. When observers looked at real cows and saw their similarities despite all this variation, Plato believed that what they were really seeing was the ideal form, or essence, of "cowness" that each individual cow incarnated.

According to Plato, all living things that share the same essence belong to the same "natural kind," and there are many natural kinds in the world, each of which is the result of the imperfect incarnation in the physical world of one or another eternal form or ideal ("cowness," "humanness," "ratness," and the like). This view is called **essentialism**. For essentialists, as Ernst Mayr (1982) explained, "each species is characterized by its unchanging essence . . . and separated from all other species by

evolution The process of change over time.

essentialism The belief, derived from Plato, in fixed ideas, or "forms," that exist perfect and unchanging in eternity. Actual objects in the temporal world, such as cows or horses, are seen as imperfect material realizations of the ideal form that defines their kind.

TABLE 2.1 Pre-Darwinian Views of the Natural World

VIEW	KEY FEATURES
Essentialism	Each "natural kind" of living thing is characterized by an unchanging core of features and separated from all other natural kinds by a sharp break.
Great Chain of Being	Based on three principles: 1. *Continuity:* Attributes of one kind of organism always overlap to some extent with the attributes of organisms closest to it in the classification. 2. *Plentitude:* A world of organisms created by a benevolent God can have no gaps but must include all logically conceivable organisms. 3. *Unilinear gradation:* All organisms can be arranged in a single hierarchy based on various degrees to which they depart from divine perfection.
Catastrophism	The notion that natural disasters, such as floods, are responsible for the extinction of species, which are then replaced by new species.
Uniformitarianism	The belief that the same gradual processes of erosion and uplift that change the earth's surface today had been at work in the past. Thus, we can use our understanding of current processes to reconstruct the history of the earth.
Transformational evolution	Assuming essentialist species and a uniformly changing environment, Lamarck argued that individual members of a species transform themselves in identical ways to adapt to commonly experienced changes in the environment. To explain why, Lamarck invoked (1) the law of use and disuse and (2) the inheritance of acquired characters.

a sharp discontinuity. Essentialism assumes that the diversity of inanimate as well as of organic nature is the reflection of a limited number of unchanging universals. . . . All those objects belong to the same species that share the same essence" (256). That essence is what made every individual cow a cow and not, say, a deer.

The Great Chain of Being

Greek ideas were adopted and adapted by thinkers in the Judeo-Christian religious tradition. By the Middle Ages, many scholars thought they could describe the organizing principles responsible for harmony in nature. According to Arthur Lovejoy ([1936] 1960), they reasoned as follows: the ancient Greek philosopher Aristotle suggested that kinds of organisms could be arranged in a single line from most primitive to most advanced. He further argued that the attributes of one kind of organism always overlap to some extent with the attributes of organisms closest to it in the classification, so that the differences between adjacent organisms were slight. Together, these ideas constituted a principle of continuity. Logically implied by the principle of continuity is the principle of plenitude, or fullness, which states that a world of organisms created by a benevolent God can have no gaps but must include all logically conceivable organisms. Finally, the ancient philosophers' assumption that God alone is self-sufficient and perfect implied that each of God's creatures must lack, to a greater or lesser degree, some part of divine perfection. As a result, the various kinds of organisms can be arranged in a single hierarchy, or unilinear gradation, like a ladder or a chain, based on the degrees to which they depart from the divine ideal.

When the notion of unilinear gradation was combined with the notions of continuity and plenitude, the result was called the **Great Chain of Being**, a comprehensive framework for interpreting the natural world. This framework suggested that the entire cosmos was composed "of an immense, or of an infinite, number of links . . . every one of them differing from that immediately above and that immediately below it by the 'least possible' degree of difference" (Lovejoy [1936] 1960, 59). Degrees of difference were understood in theological terms to be degrees of excellence. Creatures farthest away from divine perfection were lowest in the hierarchy, whereas creatures most like God (such as the angels) ranked highest. Human beings occupied a unique position in the chain. Their material bodies linked them to other material beings, but unlike other material creatures, they also possessed souls and were thereby linked to the spiritual realm by a God who had created them in his image.

For several hundred years—from the Middle Ages through the eighteenth century—the Great Chain of Being was the framework in the Western world within which all discussions of living organisms were set. As late as the mid-eighteenth century, Carolus Linnaeus (1707–1778), the father of modern biological **taxonomy** (or classification), operated within this framework. Linnaeus was committed to an essentialist definition of natural kinds. He focused on what modern taxonomists call the **genus** (plural *genera*) (Figure 2.3) and used the morphology of reproductive organs to define the "essence" of a genus (Mayr 1982, 178). (The term **species**, which modern biologists assign to subpopulations of the same genus that share certain specific attributes, was used more loosely in the past by essentialists and by nonessentialists.) Essentialists like Linnaeus knew that individuals sometimes differ markedly from what is considered "normal" for others of their kind. But these deviations were still thought of as accidents, or "degradations," that could not affect the unity of the natural kind.

Great Chain of Being A comprehensive framework for interpreting the world, based on Aristotelian principles and elaborated during the Middle Ages, in which every kind of living organism was linked to every other kind in an enormous, divinely created chain. An organism differed from the kinds immediately above it and below it on the chain by the least possible degree.

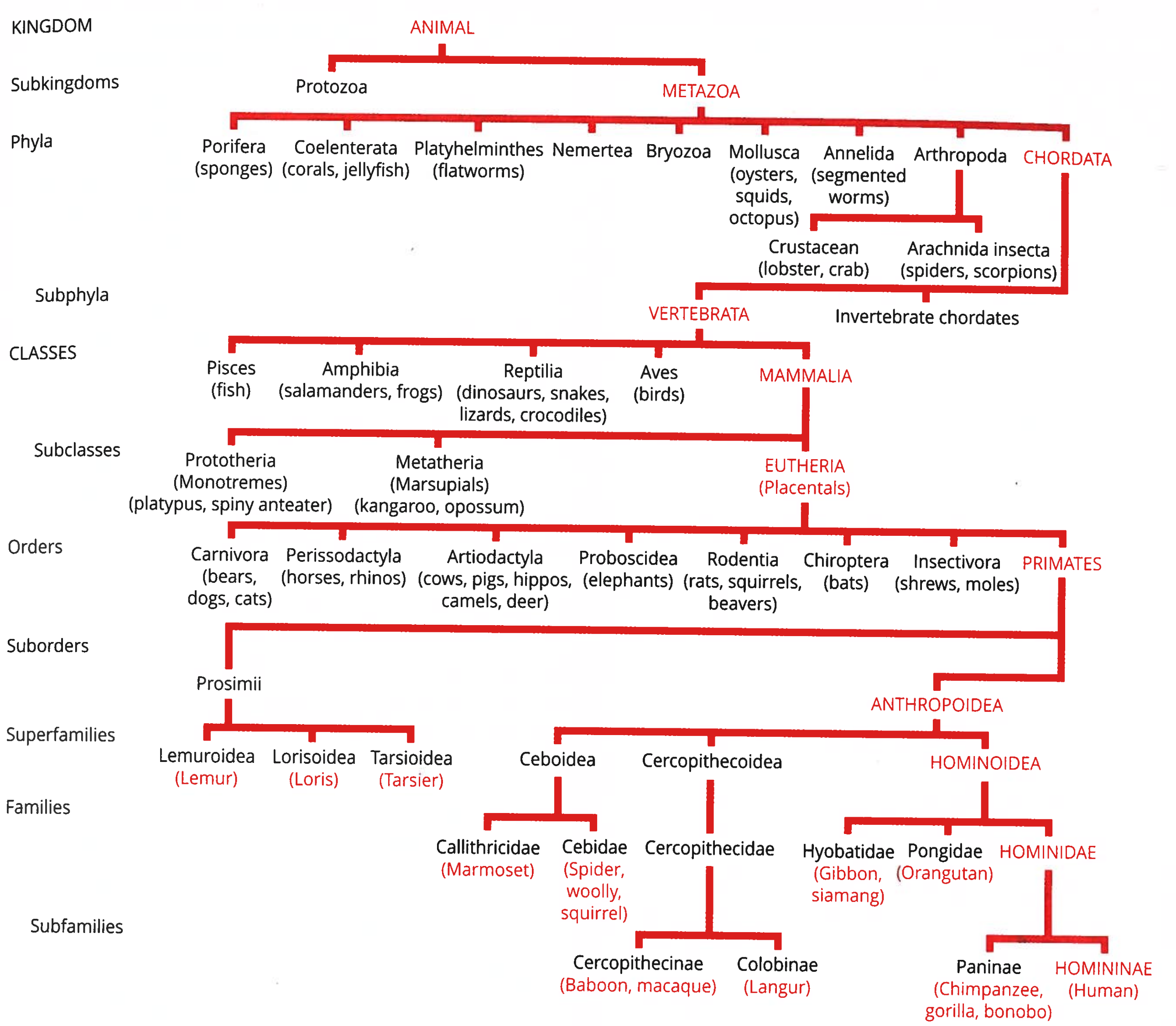


FIGURE 2.3 A modern biological taxonomy based on the Linnaean classification (popular names are in parentheses). Organisms sharing structural similarities are still grouped together, but their similarities are understood to be the result of common ancestry, indicated by the horizontal line connecting them. Thus, Paninae (chimpanzees, gorillas, and bonobos) and Homininae (human beings) all share a recent common ancestor.

taxonomy A classification; in biology, the classification of various kinds of organisms.

genus The level of the Linnaean taxonomy in which different species are grouped together on the basis of their similarities to one another.

species (1) For Linnaeus, a Platonic "natural kind" defined in terms of its essence. (2) For modern biologists, a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.

Catastrophism and Uniformitarianism

The unprecedented social and scientific changes brought about by the eighteenth-century Enlightenment in Europe gradually raised doubts about the Great Chain of Being. The principle of continuity was criticized by the French scientist Georges Cuvier (1769–1832), a pioneer in modern anatomy who also carried out some of the first important excavations of fossils in the Seine River basin near Paris. He was a firm believer in the essentialist definition of natural kinds, but his anatomical studies convinced him that there were only four natural categories of living things. Each category was excellently adapted to its way of life but had no connection to any of the others. Cuvier's studies of the fossil record convinced him that, over time, some species had been abruptly wiped out and replaced, equally abruptly, by new species from somewhere else. He called these abrupt transitions "revolutions," although this term was translated into English as "catastrophe." Hence, the term **catastrophism** came to refer to the notion that natural disasters, such as floods, are responsible for the extinction of some natural kinds, which are later replaced by new natural kinds.

In some ways, Cuvier's ideas were perfectly traditional: he did not reject the essentialist understanding of species and never suggested that new species were simply old species that had changed. Yet, his idea that some species might disappear in mass extinctions was quite radical because, according to Judeo-Christian theology, God had created all possible forms of life only once. In the same way, Cuvier's assertion in 1812 that there were no connections whatsoever among the four basic categories of living things seriously undermined the principle of unilinear gradation. That is, if the four categories had nothing in common with one another, then they could not be arranged in a simple chain of natural kinds, each precisely placed between the one slightly less advanced and the one slightly more advanced. Ernst Mayr (1982, 201) concluded that this argument dealt the Great Chain of Being its death blow.

But the Great Chain of Being did not die gently because its principles had become inextricably intertwined with Judeo-Christian beliefs about the natural world. By the late eighteenth and early nineteenth centuries, one result of this process of amalgamation was the development of an approach arguing that the perfection of each organism's adaptation could only be the result of intentional design by a benevolent creator. One group of thinkers, known as "catastrophists," modified Cuvier's theory and argued that the new species that replaced old ones had been specially created by God. Others subscribed to a position known as **uniformitarianism**, which stressed nature's overall harmonious integration as evidence for God's handiwork. These "uniformitarians" criticized the ideas of Cuvier and the catastrophists. God might allow the world to change, they admitted, but a benevolent God's blueprint for creation could not include sharp breaks between different forms of life and the abrupt disappearance of species through extinction. The uniformitarian position gained powerful support from the book *Principles of Geology* by Charles Lyell (1797–1875), published between 1830 and 1833. Lyell argued that the same gradual processes of erosion and uplift that change the earth's surface today had also been at work in the past. Assuming the uniformity of these processes, he contended that our understanding of current processes could be used to reconstruct the past history of the earth.

The quarrel between catastrophists and uniformitarians has often been portrayed as a conflict between narrow-minded dogmatism (identified with the catastrophists) and open-minded, empirical science (identified with the uniformitarians). But, as Stephen Jay Gould (1987) demonstrated, this portrayal misrepresents the nature of their disagreement. Both Cuvier and Lyell were empirical scientists: the former, a leading anatomist and excavator of fossils; the latter, a fieldworking geologist. Both confronted much of the same material evidence; however, as Gould points out, they interpreted that evidence in very different ways. Catastrophists were willing to accept a view of earth's history that permitted ruptures of harmony to preserve their belief that history, guided by divine intervention, was going somewhere. By contrast, the harmonious, nondirectional view of the uniformitarians was rooted in their belief that time was cyclic, like the changing seasons. Uniformitarians promoted the view that God's creation was the "incarnation of rationality"—that is, that God's creation unfolded in accordance with God's laws, without requiring subsequent divine intervention or a fixed historical trajectory.

Transformational Evolution

Thus, by the early years of the nineteenth century, traditional ideas about the natural world had been challenged by new material evidence and conflicting interpretations of that evidence. In the ferment of this period, the French naturalist Jean-Baptiste de Monet de Lamarck (1744–1829) grappled with the inconsistencies described above, dealing the first serious blow against essentialism (Figure 2.4). Lamarck wanted to preserve the traditional view of a harmonious living world. One of the most serious challenges to that view was the problem of extinction. How could perfectly adapted creatures suddenly be wiped out, and where did their replacements come from? Some suggested that the extinctions were the result of Noah's flood, but this could not explain how aquatic animals had become extinct. Others suggested that extinctions were the result of human hunting, possibly explaining why mastodons no longer roamed the earth. Some hoped that natural kinds believed to be extinct might yet be found inhabiting an unexplored area of the globe.

Lamarck suggested an original interpretation of the material evidence that had been used to argue in favor of extinction. Noticing that many fossil species bore a close resemblance to living species, he suggested in 1809 that perhaps fossil forms were the ancestors of living forms. Fossil forms looked different from their descendants, he believed, because ancestral features had been modified over time to suit their descendants to changing climate and geography. Such a process would prove that nature was harmonious after all—that, although the world was a changing world, living organisms possessed the capacity to change along with it.

catastrophism The notion that natural disasters, such as floods, are responsible for the extinction of species, which are then replaced by new species.

uniformitarianism The notion that an understanding of current processes can be used to reconstruct the past history of the earth, based on the assumption that the same gradual processes of erosion and uplift that change the earth's surface today had also been at work in the past.

FIGURE 2.4 Jean-Baptiste de Monet de Lamarck. Lamarck wanted to preserve the traditional view of a harmonious living world, but his interpretation of the evidence of fossils eventually undermined exactly the view he was trying to defend.

Many elements of the Great Chain of Being could be made to fit with Lamarck's scheme. Lamarck believed that once a natural kind had come into existence, it had the capacity to evolve over time into increasingly complex (or "perfect") forms. This could happen, Lamarck suggested, because all organisms have two attributes: (1) the ability to change physically in response to environmental demands and (2) the capacity to activate this ability whenever environmental change makes the organism's previous response obsolete. Otherwise, the resulting lack of fit between organisms and environment would create disharmony in nature. Lamarck never suggested that a species might adapt to change by splitting into two or more new species; rather, every member of every species is engaged in its own individual adaptive transformation over time. This is why Lamarckian evolution has also been called **transformational evolution**.

Lamarck proposed two "laws" to explain how such transformation occurs. First, he said, an organ is strengthened by use and weakened by disuse (an early statement of "use it or lose it"). If environmental changes cause members of a species to rely more heavily on some organs than on others, the former will become enhanced and the latter reduced. But the law of use and disuse had evolutionary consequences, Lamarck argued, because the physical result of use or disuse could be passed from one generation to the next. Lamarck's second law was the law of inheritance of acquired characteristics.

Consider the following example: modern pandas possess an oversized, elongated wristbone that aids them in stripping bamboo leaves, their favorite food, from bamboo stalks (Figure 2.5). This bone has been called the panda's "thumb," although pandas retain all five digits on each paw. Had Lamarck known about the panda's thumb, he might have explained its origin as follows: suppose that pandas originally had wristbones like other bears. Then the environment changed, obliging pandas to become dependent on bamboo for food. Pandas, unable to survive on bamboo unless they found an efficient way to strip the leaves off the stalk, were forced to use their forepaws more intensively (the law of use and disuse) to remove enough bamboo leaves to

transformational evolution Also called *Lamarckian evolution*, it assumes essentialist species and a uniform environment. Each individual member of a species transforms itself to meet the challenges of a changed environment through the laws of use and disuse and the inheritance of acquired characters.

FIGURE 2.5 Lamarckian transformational evolution and Darwinian variational evolution offer two different explanations for how the panda got its "thumb." The thumb is actually an elongated wristbone that aids pandas in stripping bamboo leaves, their favorite food, from bamboo stalks.

satisfy their appetite. Continual exercise of their wrists caused the wristbone to enlarge and lengthen into a shape resembling a thumb. After acquiring "thumbs" through strenuous activity, pandas gave birth to offspring with elongated wristbones (the law of inheritance of acquired characters). Thus, Lamarck's laws could explain how each species builds up new, more complex organs and attains, over many generations, increasingly higher levels of "perfection."

Because transformational evolution works through the efforts of individual members of a species, what would prevent different individuals from transforming themselves in different directions? Part of the answer is that Lamarck expected a changing environment to affect all individuals of the same species in the same way, leading to identical responses in terms of use and disuse. But the rest of the answer lies with the fact that Lamarck still accepted the view that every individual member of a species was identical in essence to every other member. Only if this were so could all members of the same species respond in the same ways to the same environmental pressures and retain their species identity over time.

Lamarck's transformational theory of biological evolution was rejected by biologists in the early twentieth century, when geneticists were able to demonstrate that neither the law of use and disuse nor the law of inheritance of acquired characters applied to genes. In the early nineteenth century, however, Lamarck's speculations opened the door for Darwin.

What Is Natural Selection?

Lamarck had argued that a species could vary over time. Contemporaries of Lamarck, observing living organisms in the wild in Europe, the Americas, Africa, and Asia, had demonstrated that species could vary over space as well. Where did all this mutually coexisting but previously unknown living variation come from?

The mystery of geographical variation in living organisms was particularly vexing to Charles Darwin (1809–1882, Figure 2.6) and Alfred Russel Wallace (1823–1913), whose field observations made it impossible to ignore. Wallace reasoned that the relationship between similar but distinct species in the wild could be explained if all the similar species were related to one another biologically—that is, if they were considered daughter (or sibling) species of some other parental species. Darwin, comparing the finches on the Galápagos Islands with finches on the Ecuadorian mainland, reasoned that the similarities linking the finches could be explained if all of them had descended from a single parental finch population. Both men concluded independently that similar species must descend from a common ancestor, meaning that any species might split into a number of new species given enough time. But how much time? In the 1650s, James Ussher, the Anglican archbishop of Ireland, used information in the Bible to calculate that God created the earth on October 23, 4004 B.C., a date that was still widely accepted. Charles Lyell and other geologists, however, claimed that the earth was much more than 6000 years old (indeed, it is about 4.5 billion years old). If the geologists were right, there had been ample time for what Darwin called "descent with modification" to have produced the high degree of species diversity we find in the world today.

Darwin had refrained from publishing his work on evolution for years but was moved to action when Lyell warned him that Wallace was ready to publish his ideas. As a result, Darwin and Wallace first published their views in a scientific paper carrying both their names. Darwin became better known than Wallace in later years, in part because of the mass of material evidence he collected in support of his theory together with his refined theoretical interpretations of that evidence.

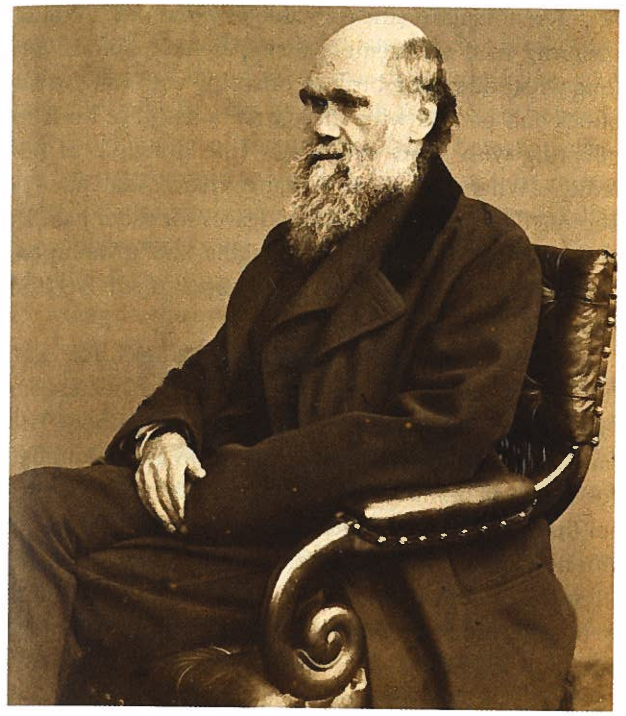


FIGURE 2.6 Charles Darwin (1809–1882).

The theory of **common ancestry**—"the first Darwinian revolution" (Mayr 1982, 116)—was in itself scandalous because it went far beyond Lamarck's modest suggestion that species can change without losing their essential integrity. Not only did Darwin propose that similar species can be traced to a common ancestor, but also he offered a straightforward, mechanistic explanation of how such descent with modification takes place. His explanation, the theory of **natural selection**, was "the second Darwinian revolution." That natural selection remains central to modern evolutionary theory is testimony to the power of Darwin's insight because it has been tested and reformulated for more than 150 years and remains the best explanation we have today for the diversity of life on earth.

Charles Darwin's theory of evolution was possible only because he was able to think about species in a new way. Although Lamarck had begun to do this when he suggested that species could change, Darwin completed the job. If organisms could change, then they did not have a fixed essence. This, in turn, meant that variation—or differences—among individual members of a species might be extremely important.

Thus, Darwin turned the essentialist definition of *species* on its head. He argued that the important thing about individual members of a species is not what they have in common but how they are different. The Darwinian theory of evolution by natural selection argued that variation, not a unitary essence, is the ground condition of life. This is why it is called **variational evolution**, in contrast to the transformational evolution of Lamarck (see, e.g., Lewontin 1982). The idea of variational evolution depends on what Ernst Mayr (1982) calls "population thinking"—that is, seeing the populations that make up a species as composed of biological individuals whose differences from one another are genuine and important.

Population Thinking

Darwin combined this new view of species with other observations about the natural world. Consider, for example, frogs in a pond. Nobody would deny that new frogs hatch from hundreds of eggs laid by mature females every breeding season, yet the size of the population of adult frogs in a given pond rarely changes much from one season to the next. Clearly, the great potential fertility represented by all those eggs is never realized or the pond would shortly be overrun by frogs. Something must keep all those eggs from maturing into adults. Darwin (following Thomas Malthus) attributed this to the limited food supply in the pond, which means that the hatchlings are forced to struggle with one another for food and that the losers do not survive to reproduce. Darwin wondered what factors determined which competitors win and which lose. Pointing to the variation among all individuals of the species, he argued that those individuals whose variant traits better equip them to compete in the struggle for existence are more likely to survive and reproduce than those who lack such traits. Individuals who leave greater numbers of offspring are said to have superior **fitness**.

Such an argument makes no sense, of course, unless species are understood in variational terms. For an essentialist, the individual members of a species are identical

common ancestry Darwin's claim that similar living species must all have had a common ancestor.

natural selection A two-step, mechanistic explanation of how descent with modification takes place: (1) every generation, variant individuals are generated within a species because of genetic mutation, and (2) those variant individuals best suited to the current environment survive and produce more offspring than other variants.

variational evolution The Darwinian theory of evolution, which assumes that variant members of a species respond differently to environmental challenges. Those variants that are more successful ("fitter") survive and reproduce more offspring, who inherit the traits that made their parents fit.

fitness A measure of an organism's ability to compete in the struggle for existence. Those individuals whose variant traits better equip them to compete with other members of their species for limited resources are more likely to survive and reproduce than individuals who lack such traits.

to one another because they share the same essence; it makes no difference which or how many of them survive and reproduce. From an essentialist point of view, therefore, competition can only occur between different species because only the differences between entire species (not between a species' individual members) matter. Once we think of a species in variational terms, however, the notion that competition for resources "is 'dog eat dog' rather than 'dog eat cat'" begins to make sense (Depew and Weber 1989, 257).

When Darwin interpreted his observations, he came up with the following explanation of how biological evolution occurs. Levins and Lewontin (1985, 31ff.) summarize his theory in three principles and one driving force that sets the process in motion:

1. The principle of variation. No two individuals in a species are identical in all respects; they vary in such features as size, color, and intelligence.
2. The principle of heredity. Offspring tend to resemble their parents.
3. The principle of natural selection. Different variants leave different numbers of offspring.

The driving force, Darwin suggested, was the struggle for existence. In a later edition of *On the Origin of Species*, he borrowed a phrase coined by sociologist Herbert Spencer and described the outcome of the struggle for existence as "survival of the fittest."

Natural Selection in Action

To illustrate the operation of natural selection, let us return to the problem of how pandas got their "thumbs." Lamarck would explain this phenomenon by arguing that individual pandas all used their wrists intensively to obtain enough bamboo leaves to survive, causing their wristbones to lengthen, a trait they passed on to their offspring. Darwin, by contrast, would explain this phenomenon by focusing attention not on individual pandas, but on a *population* of pandas and the ways in which members of that population differed from one another. He would argue that originally there must have been a population of pandas with wristbones of different lengths (the principle of variation). Because offspring tend to resemble their parents, pandas with long wristbones gave birth to offspring with long wristbones and pandas with short wristbones gave birth to offspring with short wristbones (the principle of heredity). When the climate changed such that pandas became dependent on bamboo leaves for food, pandas with wristbones of different lengths had to compete with one another to get enough leaves to survive (the struggle for existence).

Note that, in this example, "the struggle for existence" does not imply that the pandas were necessarily *fighting* with one another over access to bamboo. The pandas with long wristbones functioning as "thumbs" for stripping bamboo stalks were simply more successful than pandas who lacked such a "thumb"; that is, in this new environment, their elongated wristbones made them fitter than pandas with short wristbones. Thus, pandas in the population with "thumbs" survived and left more offspring than did those without "thumbs." As a result, the proportion of pandas in the population with elongated wristbones in the next generation was larger than it had been in the previous generation and the proportion of pandas in the population with short wristbones was smaller. If these selective pressures were severe enough, pandas with short wristbones might not leave any offspring at all, resulting at some point in a population made up entirely of pandas with "thumbs."

In Darwinian terms, adaptation has been traditionally understood as the process by which an organism "is engineered to be in harmony with the natural environment" as a result of natural selection (Little 1995, 123). However, this concept contains ambiguities that can confuse the *process* of adaptation with its *outcomes* (also often called "adaptations"). In 1982, paleontologists Stephen Jay Gould and Elisabeth Vrba helped to resolve this confusion by distinguishing among aptation, adaptation, and exaptation. An **aptation** refers to any useful feature of an organism, regardless of its origin. An **adaptation** refers to a useful feature of an organism that was shaped by natural selection for the function it now performs. An **exaptation**, by contrast, refers to a useful feature of an organism that was originally shaped by natural selection to perform one function but later reshaped by different selection pressures to perform a new function.

The distinction between adaptation and exaptation is important because mistaking one for the other can lead to evolutionary misinterpretations. For example, it has been standard practice to explain an organism's current form (e.g., an insect's wing shape) as an adaptation for the function it currently carries out (i.e., flight). This kind of explanation, however, raises problems. If insect wings evolved gradually via natural selection, then the first modest appendages on which selection would operate could not have looked like—or worked like—the wings of living insects. As a result, those early appendages could not have been used for flying. But what adaptive advantage could something that was not yet a wing confer on insect ancestors? Gould and Vrba showed that appendages that were not yet wings could have been adaptive for reasons having nothing to do with flying. For example, the original adaptive function of insect appendages was body cooling, but these appendages were later exapted for the function of flying, once they had reached a certain size or shape (Figure 2.7). Specialists in human evolution like Ian Tattersall (2012, 44) use the concepts of adaptation and exaptation to explain some of the twists and turns in human evolutionary history.

Darwin's theory of evolution by natural selection is elegant and dramatic. As generations of biologists have tested its components in their own research, they have come to examine it critically. For example, much debate has been generated about the concept of fitness.

aptation The shaping of any useful feature of an organism, regardless of its origin.

adaptation The shaping of useful features of an organism by natural selection for the function they now perform.

exaptation The shaping of a useful feature of an organism by natural selection to perform one function and the later reshaping of it by different selection pressures to perform a new function.

FIGURE 2.7 How did wings evolve for flight? Gould and Vrba (1982) suggest that appendages on early insects were for body cooling but later exapted for flying once they had reached a certain size or shape.

Some people have assumed that the biggest, strongest, toughest individuals must be, by definition, fitter than the smaller, weaker, gentler members of their species. Strictly speaking, however, Darwinian, or biological, fitness is nothing more (and nothing less) than an individual's ability to survive and leave offspring. There is no such thing as "absolute" fitness. In a given environment, those who leave more offspring behind are fitter than those who leave fewer offspring behind. But any organism that manages to reproduce in that environment is fit. As geneticist Richard Lewontin (1982) puts it, "In evolutionary terms, an Olympic athlete who never has any children has a fitness of zero, whereas J. S. Bach, who was sedentary and very much overweight, had an unusually high Darwinian fitness by virtue of his having been the father of twenty children" (150).

Clearly, Darwinian theory has been challenged to show that biological heredity operates to produce ever-renewing variation and to explain how such variation is generated and passed on from parents to offspring. Darwin's original formulation of the theory of evolution by natural selection was virtually silent about these matters. Darwin was convinced on the basis of considerable evidence that heritable variation must exist, but he and his colleagues were completely ignorant about the sources of variation. Not until the beginning of the twentieth century did knowledge about these matters begin to accumulate, and not until the 1930s did a new evolutionary synthesis of Darwinian principles and genetics become established.

How Did Biologists Learn about Genes?

Offspring tend to look like their parents, which suggests that something unchanging is passed on from one generation to the next. At the same time, offspring are not identical to their parents, which raises the possibility that whatever the parents pass on may be modified by environmental forces. Whether biological inheritance was stable or modifiable, or both, challenged Darwin and his contemporaries.

In the absence of scientific knowledge about heredity, Darwin and many of his contemporaries adopted a theory of heredity that had roots in antiquity: the theory of pangenesis. **Pangenesis** was a theory of inheritance

pangenesis A theory of heredity suggesting that an organism's physical traits are passed on from one generation to the next in the form of multiple distinct particles given off by all parts of the organism, different proportions of which get passed on to offspring via sperm or egg.

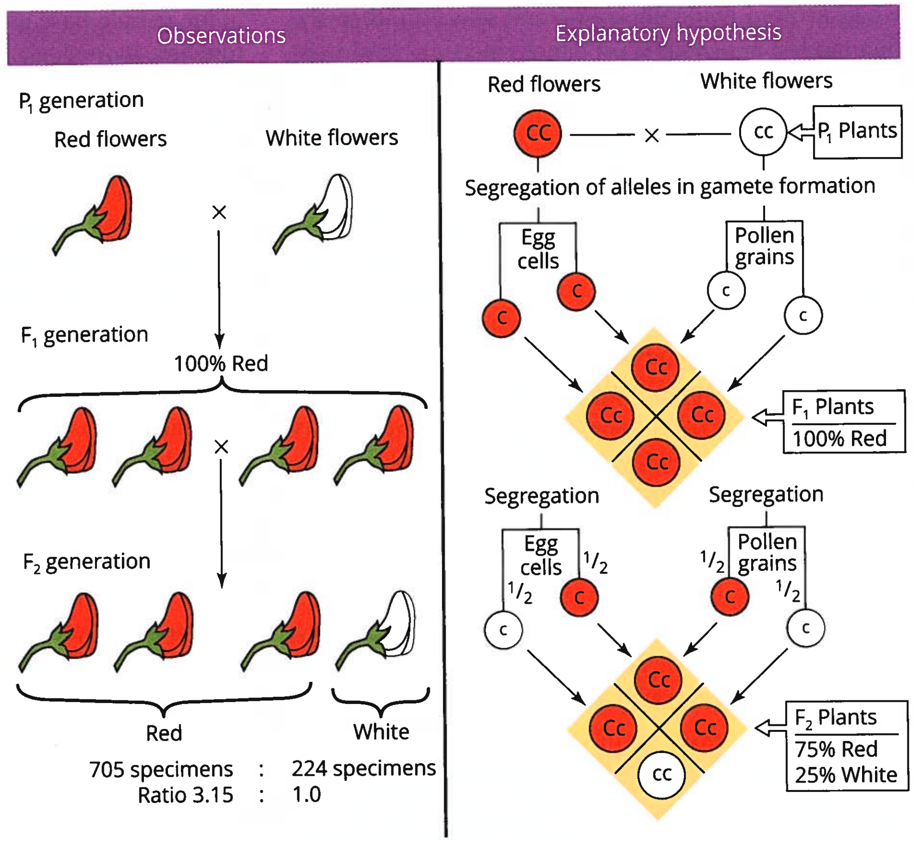


FIGURE 2.8 Mendel crossbred peas with red flowers and peas with white flowers (the parental, or P_1, generation). This produced a generation (F_1) of only red flowers. When Mendel crossed red-flowered peas from the F_1 generation, they produced the F_2 generation of peas, in which there were approximately three red-flowered plants for every one plant with white flowers. This 3:1 ratio of red to white flowers, together with the reappearance of white flowers, could be explained if each plant had two genetic factors and the factor for red flowers was dominant. Only a plant with two factors for white flowers would produce white flowers, whereas red flowers would appear in every plant that had at least one factor for red.

in which multiple particles from both parents blended in their offspring. That is, it claimed that an organism's physical traits are passed on from one generation to the next in the form of distinct particles. Supporters of pangenesis argued that all the organs of both mother and father gave off multiple particles that were somehow transmitted, in different proportions, to each of their offspring. For example, suppose that a child resembled her father more than her mother in a particular trait (say, hair color). Pangenesis explained this by arguing that the child had received more "hair color particles" from her father than from her mother. The particles inherited from both parents were believed to blend in their offspring. Thus, the child's hair color would be closer to her father's shade than to her mother's.

Mendel's Experiments

The notion of particulate inheritance was already common in the middle of the nineteenth century when the Austrian monk Gregor Mendel (1822–1884) began conducting plant-breeding experiments in the garden of his monastery. His great contribution was to provide evidence in favor of nonblending, single-particle inheritance, called **Mendelian inheritance**. When Mendel crossed peas with strikingly different traits, some of those traits did not appear in offspring of the first generation (F_1) (Figure 2.8). They did, however, reappear in their original form in the next generation (F_2). Had the particles blended, all the offspring of plants with red flowers and plants with white flowers should have been some shade of pink, but this did not happen, providing strong evidence that the particles responsible for the trait did not blend in offspring but remained discrete.

When Mendel carefully counted the number of offspring in the F_2 generation that showed each trait, he consistently came up with a 3:1 ratio of one form to the other, a factor nobody before him had noticed. This ratio recurred whenever Mendel repeated his experiments. If pangenesis were correct, no such ratios would have occurred because each individual would have inherited an unpredictable number of particles from each parent. However, the 3:1 ratio made excellent sense if, as Mendel assumed, each individual inherited only one particle from each parent (Mayr 1982, 721).

Mendelian inheritance The view that heredity is based on nonblending, single-particle genetic inheritance.

The results of his breeding experiments suggested to Mendel something else as well—that the particle responsible for one form of a particular trait (flower color, for example) could be present in an organism but go unexpressed. Those particles whose traits are expressed in an organism are said to be *dominant*; those whose traits are not expressed are said to be *recessive*. (We now know that sometimes both traits can be expressed, in which case they are said to be *codominant*.) Mendel thus concluded that the particles responsible for a particular trait, such as the pea's flower color, occur in pairs. An individual gets one particle for each trait (i.e., one-half of the pair) from each parent. This is the **principle of segregation**. Mendel further argued that each pair of particles separates independently of every other pair when what he called "germ cells" (egg and sperm) are formed. This is the **principle of independent assortment**. As a result, each sperm and ovum is virtually guaranteed to be different from all others produced by an individual because the collection of particles that each contains will be distinct. Moreover, the pairs of particles that come together in any individual offspring are random, depending on which egg and which sperm happened to unite to form that individual.

The Emergence of Genetics

Mendel's insights were ignored for nearly 35 years until three biologists rediscovered them at the beginning of the twentieth century, resulting in an explosion of research and vast growth of scientific knowledge about heredity. The British scientist William Bateson coined the term **genetics** in 1908 to describe the new science being built on Mendelian principles. He invented the term **homozygous** to describe a fertilized egg that receives the same particle from both parents for a particular trait and the term **heterozygous** to describe a fertilized egg that receives a different particle from each parent for the same trait. In 1909, the Danish geneticist W. L. Johannsen suggested the term **gene** to refer to the particle itself. Although genes occur in pairs in any individual, geneticists discovered that there might be many more than two forms of a given gene. Bateson used the term **alleles** to refer to all the different forms that a particular gene might take.

At first, nobody knew what physical structures corresponded to the genes and alleles they had been describing. However, advances in cell biology led some scientists to suggest that the **chromosomes** in the cell nucleus might play an important role. These sets of paired bodies were easy to see under the microscope because they accepted a colored stain very well (hence their name, from Greek, meaning "colored bodies"). Animals of different species have different numbers of chromosomes (humans have 46), but all chromosomes are found in pairs (humans have 23 pairs).

What Are the Basics of Contemporary Genetics?

Biologists learned that living cells undergo two different kinds of division. The first kind, **mitosis**, is simply the way cells make copies of themselves (Figure 2.9a).

The process is different, however, when the sex cells (sperm and eggs) are formed. This process is **meiosis**, or reduction division (Figure 2.9b).

The behavior of the chromosomes during meiosis intrigued geneticists. Slides of cells made at different stages in the process showed that chromosomes obey the principles of segregation and independent assortment, just like Mendelian genes. This fact led geneticists, early in the twentieth century, to hypothesize that genes and chromosomes are connected. The first real test of this hypothesis came when a number of geneticists looked at the ratio of males to females among the offspring of sexually reproducing species. They found that this 1:1 ratio is the same as "the ratio resulting from the cross of a heterozygote (*Aa*) and a homozygous recessive (*aa*). Mendel himself had already suggested this possibility" (Mayr 1982, 750).

principle of segregation A principle of Mendelian inheritance in which an individual gets one particle (gene) for each trait (i.e., one-half of the required pair) from each parent.

principle of independent assortment A principle of Mendelian inheritance in which each pair of particles (genes) separates independently of every other pair when germ cells (egg and sperm) are formed.

genetics The scientific study of biological heredity.

homozygous Describes a fertilized egg that receives the same particle (or allele) from each parent for a particular trait.

heterozygous Describes a fertilized egg that receives a different particle (or allele) from each parent for the same trait.

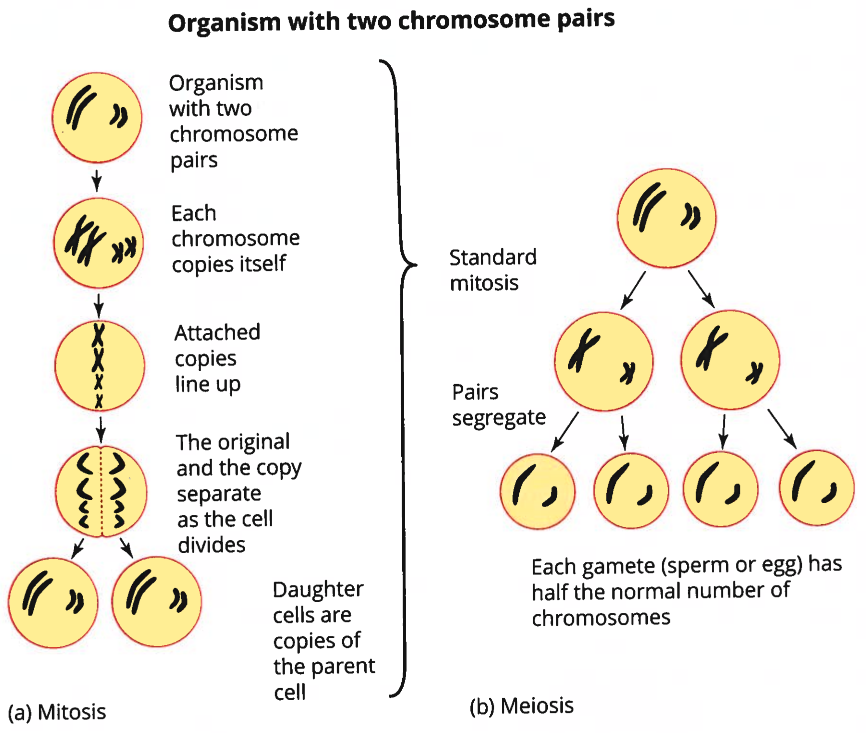
gene Portion or portions of the DNA molecule that code for proteins that shape phenotypic traits.

alleles All the different forms that a particular gene might take.

chromosomes Sets of paired bodies in the nucleus of cells that are made of DNA and contain the hereditary genetic information that organisms pass on to their offspring.

mitosis The way body cells make copies of themselves. The pairs of chromosomes in the nucleus of the cell duplicate and line up along the center of the cell. The cell then divides, each daughter cell taking one full set of paired chromosomes.

meiosis The way sex cells make copies of themselves, which begins like mitosis, with chromosome duplication and the formation of two daughter cells. However, each daughter cell then divides again without chromosome duplication and, as a result, contains only a single set of chromosomes rather than the paired set typical of body cells.



(a) Mitosis (b) Meiosis

FIGURE 2.9 Cells divide in two different ways. (*a*) In mitosis, ordinary body cells double the number of chromosomes they contain before dividing so that each daughter cell carries a full copy of the genetic information in the mother cell. (*b*) Meiosis occurs only when sex cells (sperm or eggs) are produced. In meiosis, each daughter cell retains only half the genetic material of the mother cell; the other half will be supplied when sperm and egg join in fertilization.

A gene was understood as a unit occupying a particular position, or **locus** (plural, *loci*), on the chromosome. Early geneticists discovered that frequently one trait appears in an organism only when another trait is also present. This discovery suggested that the genes responsible for those traits must, for some reason, always be passed on together, a phenomenon called **linkage**. We now know that linkage occurs when genes for different traits occur on the same chromosome (Figure 2.10a). However, in some cases, the expected linkages do not occur. Geneticists eventually discovered that part of a chromosome can break off and reattach itself to a different chromosome during meiosis, a phenomenon known as **crossing over**, or incomplete linkage (Figure 2.10b).

Genes and Traits

Geneticists originally thought (and many nonscientists still believe) that one gene equals one trait. Sometimes a single allele does appear to govern a single physical trait. This may be true of many physical traits that show **discontinuous variation**, that is, sharp breaks from one individual to the next. Recall that the flowers on Mendel's pea plants were either red or white; they did not come in various shades of pink. This observation led Mendel to conclude that a single dominant particle (or two identical recessive particles) determines flower color.

Early research, however, showed that one gene–one trait was too simplistic an explanation for many hereditary traits. Sometimes many genes are responsible for producing a single trait, such as skin color (Figure 2.12); such traits are thus said to be the result of **polygeny**. Traits like skin color in human beings are different from traits like flower color in Mendel's peas because they show **continuous variation**. That is, the expression of the trait grades imperceptibly from one individual to another, without sharp breaks. The discovery of polygenic inheritance showed that Mendelian concepts could be used to explain discontinuous and continuous variation alike.

locus A portion of the DNA strand responsible for encoding specific parts of an organism's biological makeup.

linkage An inheritance pattern in which unrelated phenotypic traits regularly occur together because the genes responsible for those co-occurring traits are passed on together on the same chromosome.

crossing over The phenomenon that occurs when part of one chromosome breaks off and reattaches itself to a different chromosome during meiosis; also called *incomplete linkage*.

discontinuous variation A pattern of phenotypic variation in which the phenotype (e.g., flower color) exhibits sharp breaks from one member of the population to the next.

polygeny The phenomenon whereby many genes are responsible for producing a phenotypic trait, such as skin color.

continuous variation A pattern of variation involving polygeny in which phenotypic traits grade imperceptibly from one member of the population to another without sharp breaks.

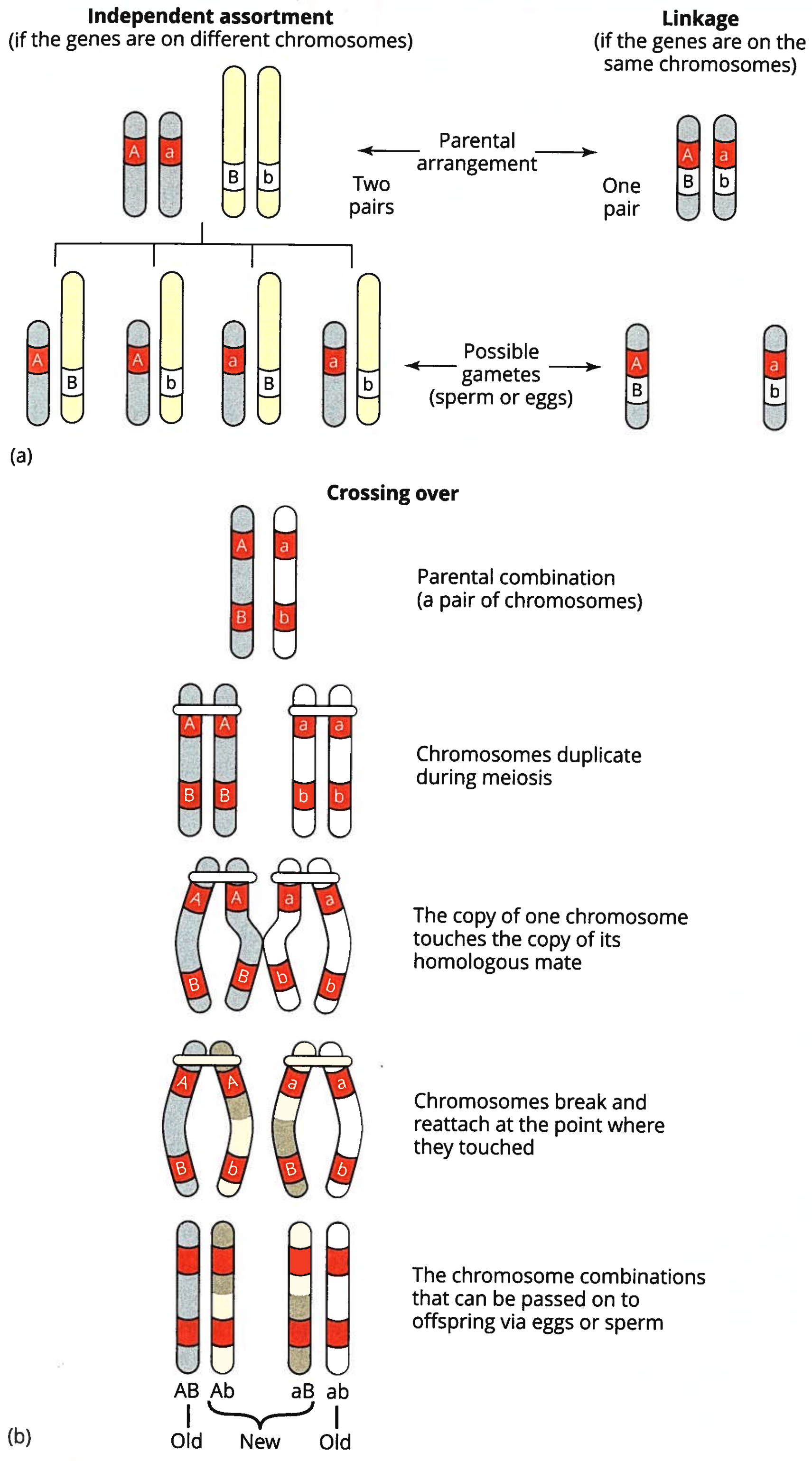


FIGURE 2.10 The principle of independent assortment predicts that genetic factors on different chromosomes will not be passed on together; each will be passed on to a different sex cell during meiosis. (*a*) Linkage predicts that genetic factors on the same chromosome will tend to be passed on together because it is the chromosomes that separate during meiosis, not individual genes. (*b*) The predictions about independent assortment and linkage do not hold if chromosomes cross over prior to meiosis. When this occurs, chromosomes break and reattach to their mates, leading to new combinations of genes on each chromosome that can then be passed on to offspring.

Perhaps even more surprising than polygenic activity was the discovery that a single gene may affect more than one trait, a phenomenon called **pleiotropy**. For example, the *S* allele that gives human red blood cells increased resistance to malarial parasites also reduces the amount of oxygen these cells can carry (Rothwell 1977, 18). Similarly, the allele that causes the feathers of chickens to be white also works to slow down their body growth (Lerner and Libby 1976). The discovery of

pleiotropy The phenomenon whereby a single gene may affect more than one phenotypic trait.

ANTHROPOLOGY *in Everyday Life*

Investigating Human-Rights Violations and Identifying Remains

In Argentina between 1976 and 1983, more than 10,000 people disappeared during the "dirty war" waged by the Argentine military government against supposed subversives. A not-for-profit nongovernmental organization called the *Equipo Argentino de Antropología Forense* (EAAF, Argentine Forensic Anthropology Team; Figures 1.6 and 2.11) was established in 1984 to investigate the cases of the disappeared. This organization, which notable anthropologist Clyde Snow helped found, has gone on to investigate human-rights violations in more than forty countries, from Bolivia, Bosnia, and Brazil to Guatemala, Venezuela, Kosovo, and Zimbabwe. They have also trained similar forensic teams in Chile, Guatemala, Peru, and elsewhere. The EAAF takes a multidisciplinary approach to its work, drawing on both forensic and cultural anthropology, archaeology, dental analysis, human genetics, pathology, ballistics, and computer science. Their formal mission includes six objectives:

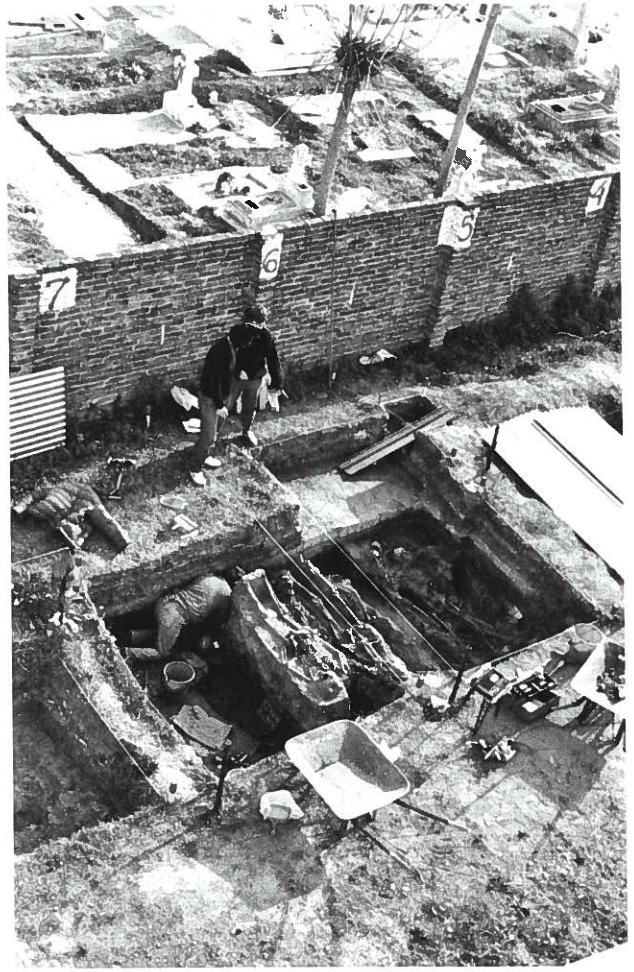


FIGURE 2.11 Members of the Argentine Forensic Anthropology Team excavating in the Avellaneda cemetery, sector 134, where Karina's family was secretly buried.

1. Apply forensic scientific methodology to the investigation and documentation of human-rights violations.
2. Give testimony of our findings in trials and other judicial inquiries in human-rights cases.
3. Provide identification of the victims, providing closure for victims' families.
4. Train new teams in other countries where investigations into human-rights violations are necessary.
5. Conduct seminars on the applications of forensic science to the investigation of human-rights violations in cooperation with human-rights organizations, judicial systems, and forensic institutes.
6. Collect and analyze scientific evidence of massive human-rights violations, providing data to reconstruct the often distorted or hidden histories of repressive regimes (Doretti and Snow 2009, 306).

One example of their work, which Doretti and Snow (2009) call the Manfil Case, illustrates both the multidisciplinary skills of the EAAF and the profound human drama that human-rights violations generate. In 1991, the EAAF team was working in Sector 134, a small, walled-off area inside a huge municipal cemetery in Avellaneda, a suburb of Buenos Aires, Argentina. One day, an eighteen-year-old woman named Karina Manfil approached them and informed them of her search for her family, who had disappeared fifteen years earlier during a death-squad raid on their home on October 27, 1976. Someone had told her that her parents and little brother might be buried in Sector 134.

At that time, the EAAF had been working in Sector 134 for three years using their regular four-step approach: (1) historical research, (2) collection of antemortem (predeath) data, (3) archaeology, and (4) laboratory analysis (Doretti and Snow 2009, 308). In conducting historical research, they collected information from written records and through interviews with witnesses toward the goal of answering questions such as "Why was the grave made, and how long was it used to bury bodies? Who made the grave? How was it made? How many people may be buried there?" (308). The researchers discovered that the death squads who operated during the dirty war had created a network of clandestine detention centers (CDCs) throughout the country and that CDCs tended to use the same cemetery for disposing of the remains of their victims. This meant that the remains of people who were swept up together in raids (members of the same political party, student group, union, or occupation) at times ended up in the same cemetery, sometimes in the same grave. This pattern also applied to families who were arrested together.

Once the historical investigation gave some sense of who might be buried in the Avellaneda cemetery, the team collected antemortem data—such as age at death, sex, height, handedness, dental work, and any old injuries—through interviews with family members, doctors, and dentists. As DNA testing became more sophisticated, they also took DNA samples from relatives. They could then apply these data to the analysis of skeletal material recovered.

Third, the team used archaeological techniques to excavate the cemetery. In Sector 134, they found nineteen mass graves, eleven single burials, and more than 300 bullets. In the mass graves, the number of skeletons ranged from ten to twenty-eight. Nearly all had been buried without clothing or jewelry. Laboratory analysis, the fourth step in EAAF's approach, indicated the remains of 324 individuals—104 more than cemetery records indicated. About three-quarters of the skeletons were male, about a third elderly, but most of the female skeletons were of women who were between the ages of 21 and 35 at the time of death. The elderly seemed to have died of natural causes. Almost all of the much larger group of younger individuals (male and female) had died of gunshot wounds.

Through their work, the EAAF team who took on Karina's quest were able to reconstruct what had happened on the night of October 27. A joint police-army death squad had broken into the Manfil family's third-floor apartment, where most of the family members were asleep: 35-year-old Carlos Manfil, a politically active member of the party that had been overthrown by the military; his 28-year-old wife, Angélica; and three of their four children—Carlitos, age 9; Karina herself, age 4; and 6-month-old Cristian. Also asleep in the apartment were guests of the Manfils, Rosario Ramírez, her husband José Vega, and their two children. As the attack began, 9-year-old Carlitos leaned out the window to see what was happening and was shot in the forehead. The other children hid under the bed and were wounded when the attackers sprayed the room with bullets.

The EAAF team determined that Karina's mother, Angélica, was killed inside the apartment. The other three adults tried to escape by climbing down the drainpipes. Carlos Manfil and Rosario Ramirez fell, fracturing their legs, and were shot and killed on the spot. Karina, her infant sibling Cristian, and the two Vega children, apparently overlooked by the death squad, were the only survivors. José Vega escaped but was caught about a year later and disappeared. The bodies of Carlos and Angélica, their son Carlitos, and Rosario Ramirez were not returned to their families, and the families were not even informed of their deaths. Some family members heard rumors that they were buried in Sector 134. The team interviewed family members about the antemortem details of the people who had disappeared and searched the official records, where they discovered the death certificates that showed that the bodies had, in fact, been buried in Sector 134.

The only skeleton of a young boy recovered from this sector had a gunshot entrance wound in the frontal bone of the skull. The archaeological records showed that this particular skeleton came from a mass grave containing several adult skeletons, including three that matched the sex, age, height, and dental information that family members had provided about Carlos, Angélica, and Rosario. The male and one of the females had perimortem (meaning from around or at the time of death) fractures of the long bones of the legs. In 1991, the EAAF group found a file on the Manfil case from a military court that included an autopsy report, which described gunshot wounds and leg fractures corresponding to those of the skeletons.

The EAAF team felt that they could provisionally identify the skeletons but were not yet able to make a positive identification. So they sent bone samples to a lab at Oxford University, where nuclear DNA was extracted, and they sent teeth from each skull, along with blood samples from family members, to a lab at the University of California Berkeley for mitochondrial DNA (mtDNA) testing. By August 1992, the geneticists had connected the DNA of two of the skeletons—those of Carlitos and his mother, Angélica. Furthermore, the mtDNA testing of a tooth from the skeleton believed to be Angélica's matched the mtDNA from the blood of her daughter Karina, and the mtDNA of the male presumed to be Carlos Manfil matched mtDNA from the blood of his mother. The genetic analyses confirmed the historical and anthropological results, and the Argentine Federal Court of Appeals accepted the EAAF report on the Manfil case, releasing the remains to the family. This case marked the first time that the court had accepted DNA evidence for skeletal identification. It took several more years to locate relatives of Rosario Ramirez, but once found, DNA analysis established a positive identification of the remaining skeleton. "In December 1992, Karina's sixteen-year quest finally ended when she was able to inter the long-lost bones of her father, mother, and little brother Carlitos in a modest family crypt. Ironically, it stands in the cemetery of Avellaneda, not far from Sector 134" (Doretti and Snow 2009, 311).

Despite the difficulty in resolving such cases, the EAAF continues its work. They point out that their work benefits from the four-field anthropological approach: their skills as biological anthropologists are complemented by their training in archaeology, which allows them to excavate properly and to interpret the burials they find, and their training in cultural anthropology, which provides them "with some insight and sensitivity in dealing with families and communities oppressed by the violence" (Doretti and Snow 2009, 329). The EAAF's website is www.eaaf.org.

FIGURE 2.12 Skin color in human populations shows continuous variation, that is, different skin shades grade imperceptibly into one another without sharp breaks. Geneticists have shown that such continuous variation is produced by polygeny, the interaction of many genes to produce a single, observable trait.

pleiotropy showed that genes do not produce traits in isolation. Many geneticists came to focus attention on what the Russian geneticist Sergei Chetverikov called the "genetic milieu," investigating the effects that different genes could have on one another (Figure 2.13). For example, Theodosius Dobzhansky was able to demonstrate that "certain genes or chromosomes could convey superior fitness in some combinations, and be lethal in combination with other chromosomes" (Mayr 1982, 580).

Mutation

Early in the twentieth century, geneticists discovered that very occasionally a new allele can result when the old form of a gene suddenly changes (or undergoes a **mutation**) but that, otherwise, genes are stable. Mutation thus explains how genetic inheritance can be unchanging and still produce the variation that makes evolutionary change possible (Mayr 1982, 755). Being part of a process of stable inheritance means, however, that the occurrence of genetic mutations is random with respect to the adaptive challenges facing the organism in which it occurs: mutations do not occur because the organism "needs" them. Thus, modern geneticists rejected Lamarckian transformational evolution because it assumes a theory of modifiable inheritance. That is, to put it in modern terms, Lamarck assumed that information about the adaptive needs of an organism can somehow be fed back directly into the eggs or sperm cells of that organism, reshaping the information they contain, thereby allowing an adaptation to be passed on to offspring.

mutation The creation of a new allele for a gene when the portion of the DNA molecule to which it corresponds is suddenly altered.

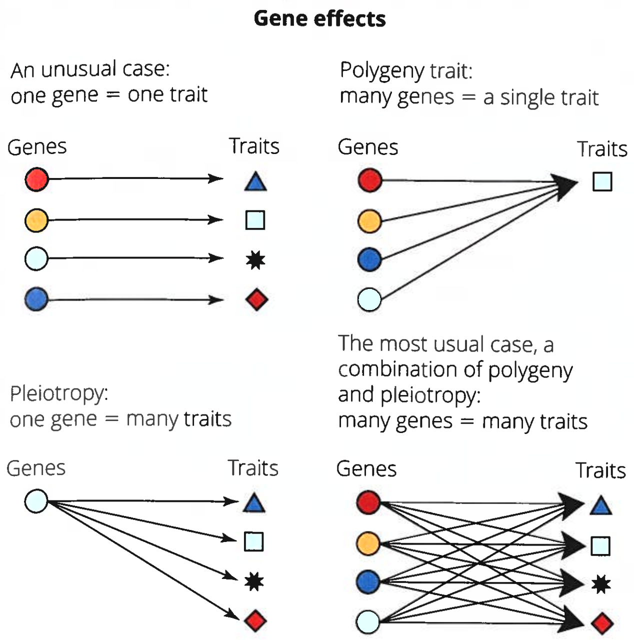


FIGURE 2.13 Only rarely is a single physical trait the result of the action of a single gene. Many traits are the result of gene interaction, involving polygeny or pleiotropy or, as is usually the case, both.

Modern genetics, by contrast, assumes that, apart from mutation, genes are inherited unchanged from parent organisms and that it is impossible for an organism's experiences or "needs" to feed back and reshape the genetic information in the sex cells. Natural selection can act only on randomly produced variation, which makes evolution by natural selection a two-step process. First, random genetic variation is produced. Second, those organisms whose variant traits better equip them to meet environmental challenges survive and produce more offspring than those whose traits equip them less well.

It is important to emphasize that, from a Darwinian point of view, *individual organisms* do not evolve genetically. Barring mutations (or the interventions of genetic engineering), individual organisms are stuck with the genes they are born with. However, the *populations* to which individuals belong *can evolve* as each generation contributes different numbers of offspring to the generation that comes after it. Put another way, from a Darwinian perspective, the only *biological* effect an individual can have on its population's evolution is in terms of the *number of offspring* that it bequeaths to the next generation. More (or fewer) offspring mean more (or fewer) copies of parental genes in the next generation. This is why Darwinian population biologists traditionally track evolutionary change by measuring changes in gene frequencies over time.

DNA and the Genome

The discovery in the early 1950s of the structure of chromosomes greatly expanded our understanding of genetic mutation. We now know that chromosomes are made up largely of long molecules of deoxyribonucleic acid, or **DNA**, parts of which are used by living cells as templates for the construction, or *synthesis*, of proteins that make up most of the tissues and organs of any living organism. The DNA molecule, assembled in the shape of a double helix, resembles a twisted ladder, the rungs of which are made up of chemical components called "bases." Although there are many bases, DNA ordinarily makes use of only four: guanine, cytosine, adenine, and thymine. Each rung of the DNA ladder is made up of two of these bases: guanine always links to cytosine, and adenine always links to thymine. Faithful copies of DNA molecules are made when chromosomes are copied prior to mitosis or meiosis. The biochemical machinery of the cell breaks the chemical bonds holding the bases together and the DNA ladder splits apart, like a zipper unzipping (Figure 2.14). The absent half of each separated strand of DNA is then rebuilt from appropriate complementary bases that float freely within the nucleus of a cell. When this process is complete, two identical copies of the same DNA molecule are produced.

The sum total of all the genetic material in the cell nucleus is called the **genome**. We know today that the human genome contains approximately 20,000 genes, but these account for less than 2% of the entire genome. Geneticists know that some noncoding DNA in the genome is involved in regulatory functions, but we remain ignorant of the functions played by much of it.

Discovery of the structure and operation of DNA solidified the rejection of Lamarckian views by geneticists. Simply put, no matter how useful or valuable a particular adaptation might be to an organism, genetic inheritance provides no mechanism whereby such information could be directly transmitted through that organism's tissues and cells to restructure the organism's DNA in a more "adaptive" form. At the same time, knowledge of DNA explained what mutations were: changes in the structure of the DNA molecule. Cosmic radiation, heat, and chemicals can all alter the structure of DNA; when these alterations occur in the sex cells, they can be passed on to offspring.

DNA (deoxyribonucleic acid) The structure that carries the genetic heritage of an organism as a kind of blueprint for the organism's construction and development.

genome The sum total of all the genetic information about an organism, carried on the chromosomes in the cell nucleus.

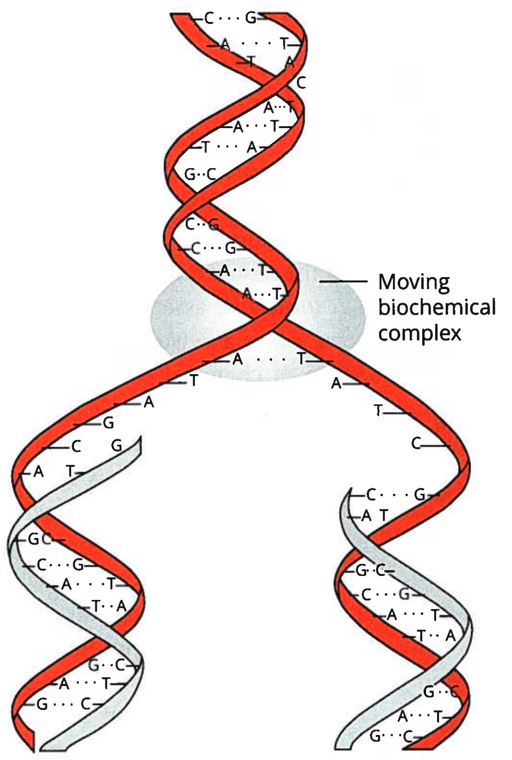


FIGURE 2.14 For DNA to replicate, a biochemical complex moves along the molecule and "unzips" the double helix, and two complete copies are rebuilt from appropriate molecules floating in the nucleus. Adenine (A) always attracts thymine (T), and cytosine (C) always attracts guanine (G).

Mutations can be harmful or helpful, but they may also have no effect at all. Mutations that neither help nor harm an organism are called "neutral" mutations. Molecular biologists have found an enormous amount of variation in those portions of the DNA molecule involved in protein synthesis, much of which appears to be neutral, although this is controversial.

When segments of the DNA molecule are required for particular cellular processes, parts of the cellular machinery enter the cell nucleus, unwind the relevant portion of a chromosome, and make copies of (or *transcribe*) relevant portions of the DNA molecule. These transcriptions are then transported into the cytoplasm of the cell and used to construct proteins, molecules that are basic to an organism's life processes (Figure 2.15). But this process is far from simple. Ironically perhaps, the more molecular biologists have learned about the way DNA functions in cells, the more difficult it has become for them to provide an unambiguous definition of what a "gene" is and what it does. As biologist Henry Plotkin (2008) observes, until the 1950s, geneticists assumed that genes occupied discrete positions on chromosomes, "like beads on a string."

> This image has had to be radically revised. Genes, it turns out, are structurally complex, almost messy. They are smeared across chromosomes, with large reaches of DNA not coding for anything as far as currently known. Genes also form complex families of spatially widespread units. . . . Far from being rather dull, inert, passive stores of information, genes interact in dynamic ways with other cellular molecules, including their own products. (38)

Many popular accounts of genes portray DNA as an all-powerful "master molecule" that determines an organism's physical appearance, with the added assumption that unless genes mutate, new physical traits will never appear. This is incorrect. Biologist Mary Jane West-Eberhard (2003) points out that most of the genetic variation in multicellular organisms comes from the shuffling of *existing* genetic sequences at different stages of the developmental process, rather than from mutation (334). Moreover, when more and more *different* developmental events become dependent on the *same* DNA sequences, these sequences become more resistant to evolutionary change, a phenomenon known as *generative entrenchment* (West-Eberhard 2003, 326; Wimsatt and Schank 1988). For these reasons, many biologists argue that an exclusive focus on the role of DNA in evolution must give way to a more complex view that situates genes as one component in the biological processes of living cells, playing different roles at different stages in the life cycles of developing organisms and in the evolutionary histories of living species. This is why developmental biologist Anne Fausto-Sterling urges us not to "get stuck trying to divide nature from nurture," and never to forget "that living bodies are dynamic systems that develop and change in response to their social and historical contexts" (2012, xii). On the contrary, she says, we should "think developmentally and appreciate biological diversity," remembering above all that "bodies are not bounded" (2012, xxi, 119).

Genotype, Phenotype, and the Norm of Reaction

Geneticists realized long ago that the molecular structure of genes (or **genotype**) had to be distinguished from the observable, measurable overt characteristics of an organism which genes help to produce (its **phenotype**). For example, the sequences of bases on a stretch of DNA (genotypes) are used by living cells to assemble strings of amino acids that bond to form proteins (phenotypes), but bases are not the same thing as protein molecules. How does a genotype get realized in a phenotype? The question is not idle because fertilized eggs do not turn into organisms in a vacuum. Living organisms grow in a physical environment that provides them with nourishment, protection, and other vital resources to support their development over time until they are mature and able to reproduce their own offspring. Without the raw materials for protein synthesis supplied by the ovum, and later by food, genotypes can do nothing. At the same time, just as one gene does not equal one trait, different genotypes may be associated with the same phenotype. Mendel first showed this when he was able to demonstrate the existence of recessive genes. That is, red flowers could be produced by homozygous dominant parents (i.e., both red) as well as by heterozygous parents (i.e., one red and one white), but only one in every four offspring of heterozygous parents would have the chance of producing white flowers (i.e., if it received a recessive white gene from each parent). Nevertheless, individuals with the same genotype—twins, for example, or cuttings from a single plant or cloned animals—may also develop a range of different phenotypes.

To understand how we get from an organism's genotype to its phenotype, we must consider both genotype and phenotype in relation to the environment in which that organism developed. Biologists compare the phenotypic outcomes of organisms with the same genotype in different environments and with different genotypes in the same environment, and they plot these outcomes on what is called a **norm of reaction**. Levins and Lewontin (1985) define the norm of reaction as "a table or graph of correspondence between the phenotypic outcome of development and the environment in which the development took place. Each genotype has its own norm of reaction, specifying how the developing organism will respond to various environments. In

genotype The genetic information about particular biological traits encoded in an organism's DNA.

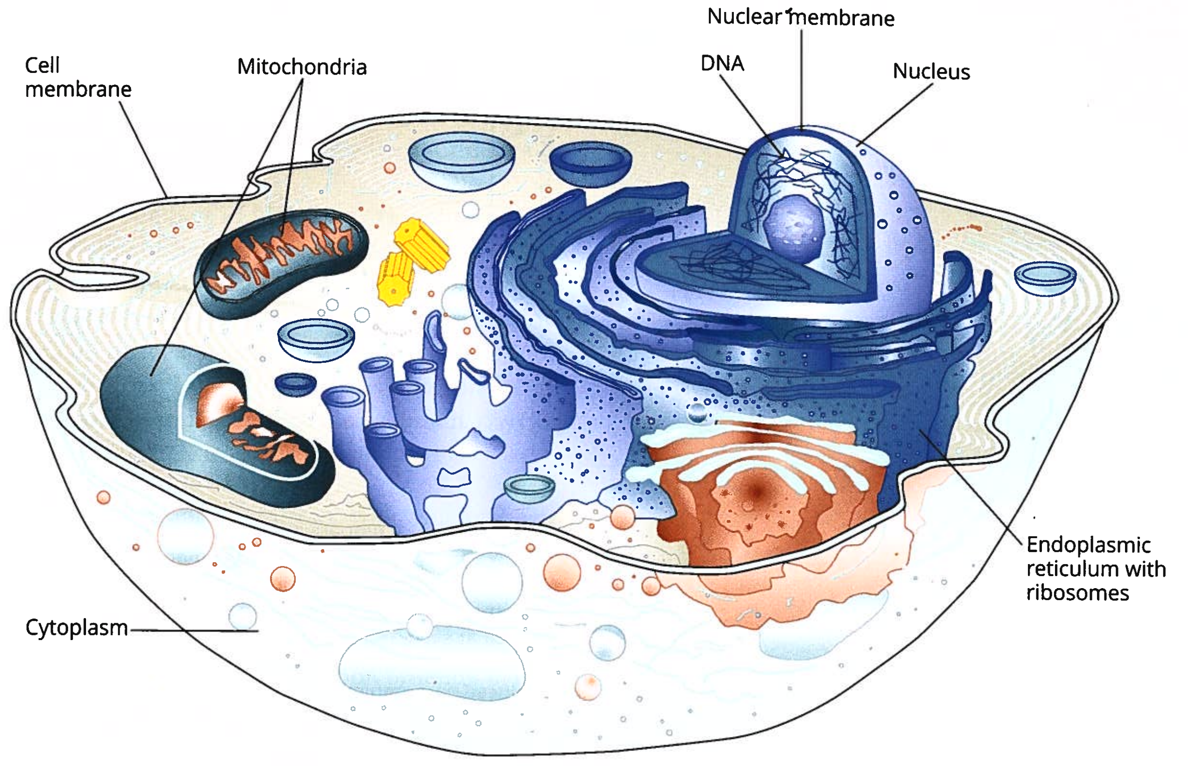


FIGURE 2.15 A nucleated cell is a complex system involving many components. DNA replication and protein synthesis are cellular processes that both involve and affect many cellular components.

phenotype The observable, measurable overt characteristics of an organism.

norm of reaction A table or graph that displays the possible range of phenotypic outcomes for a given genotype in different environments.

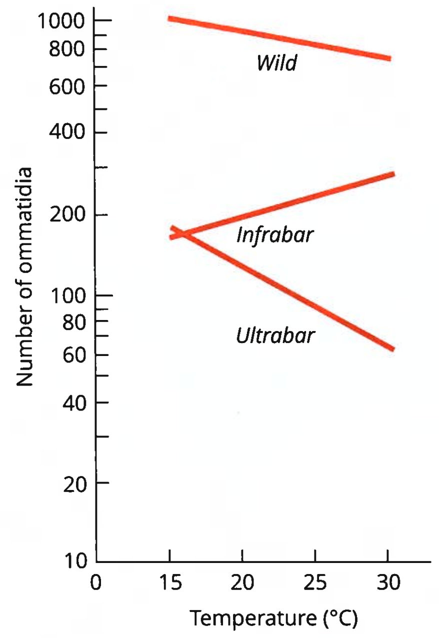


FIGURE 2.16 Each genotype has its own norm of reaction, specifying how the developing organism will respond to various environments. How many eye cells (*ommatidia*) a fruit fly develops depends both on that fly's genotype and on the environmental temperature at which development takes place. Not only does the same genotype produce different phenotypes at different temperatures, but also different genotypes may produce the same phenotype at the same temperatures (Levins and Lewontin 1985, 91).

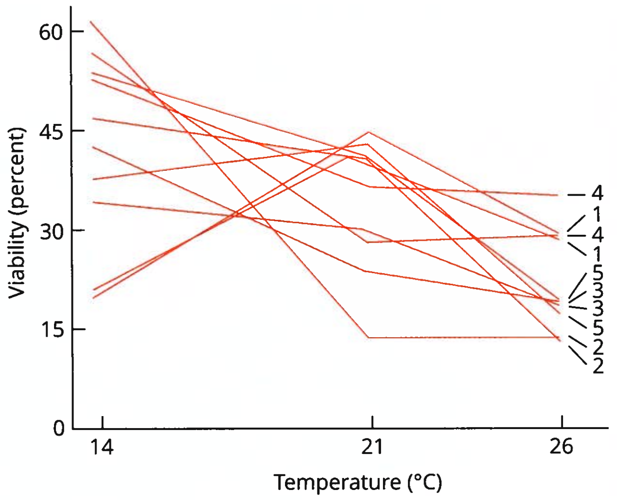


FIGURE 2.17 Comparison of norms of reaction for variant fruit fly genotypes in variant environments shows two things: (1) some genotypes always do better than others at any temperature and (2) no single genotype does better than all the rest at every temperature. Such evidence argues against the concept of a single, ideal genotype that is supposed to be produced deterministically by the genes (Levins and Lewontin 1985, 92).

general, a genotype cannot be characterized by a unique phenotype" (90–91).

Figure 2.16 shows the norms of reaction for three different genotypes for a particular trait in *Drosophila*, the fruit fly. The genotype in question controls the number of ommatidia, or light-receptor cells, that a particular individual will have in its compound eye. Flies carrying the Wild genotype usually have about 1,000 ommatidia in their eyes, whereas those with the Ultrabar and Infrabar genotypes have far fewer. However, as the graph shows, the number of ommatidia a fly develops depends not only on that fly's genotype but also on the environment (in this case, the temperature) at which development takes place—that is, the same genotype produces different phenotypes at different temperatures.

Figure 2.16 demonstrates yet another surprising fact about the relationship of genes to the environment: at about 15°C, both Ultrabar and Infrabar genotypes develop about the same number of ommatidia! In other words, different genotypes may also produce the same phenotype in a particular environment. This fact illustrates what Levins and Lewontin (1985) call the "many-to-many relationship among gene and organism" (94) and shows that the fitness of a particular genotype can vary depending on the environment. Figure 2.17 displays norms of reaction for the survival at different temperatures of immature fruit flies with different genotypes, all of which were taken from natural populations. As the graph illustrates, some genotypes always do better than others at any given temperature, but there is no single genotype that does better than all the rest at every temperature. The complexity of the relationship among genes, organism, and environment does not mean "that the organism is infinitely plastic, or that any genotype can correspond to any phenotype. Norms of reaction for different genotypes are different, but it is the norms of reaction that are the proper object of study for developmental biologists rather than some ideal organism that is supposed to be produced deterministically by the genes" (Levins and Lewontin 1985, 94).

The principles apply to humans as well. Different genotypes can produce the same phenotype in some environments, and the same genotype can produce different phenotypes in different environments. Despite very different genotypes, the eyes of newborn babies all tend to be the same color, as does hair color as we age. Indeed, the phenotype of a single individual can vary markedly from one environment to the next. As Lewontin (1982) points out, "People who 'tend to be fat' on 5,500 calories a day 'tend to be thin' on 2,000. Families with both 'tendencies' will be found living in the same towns in Northeastern Brazil, where two thirds of the families live on less than what is considered a minimum subsistence diet by the World Health Organization" (20).

Increasing numbers of biologists are addressing not only the ways in which the organism's phenotype is shaped by the environment in which it develops, but also how organisms shape the environments in which they develop. For example, in their book *Niche Construction*, F. John Odling-Smee, Kevin Laland, and Marcus Feldman (2003) argue that organisms play two roles in evolution, carrying genes and interacting with environments.

> Specifically, organisms interact with environments, take energy and resources from environments, make micro- and macrohabitat choices with respect to environments, construct artifacts, emit detritus and die in environments, and by doing all these things, modify at least some of the natural selection pressures in their own and in each other's local environments. This second role for phenotypes in evolution is not well described or understood by evolutionary biologists and has not been subject to a great deal of investigation. We call it "niche construction." . . . (1)

Niche construction is understood to occur either when an organism actively perturbs the environment or when it actively moves into a different environment (Odling-Smee et al. 2003, 41). If the physical, environmental consequences of niche construction are erased between generations, this process can have no long-term effects on evolution. But if these consequences endure, they feed back into the evolutionary process, *modifying the selection pressures* experienced by subsequent generations of organisms (Figure 2.18). Odling-Smee et al. (2003) provide numerous examples taken from all taxonomic groups of living organisms, including blue-green algae, earthworms, dam-building beavers, burrowing rodents, and nest-building birds (50–115). Their most controversial proposal is that niche construction be incorporated into evolutionary theory as an additional adaptive process alongside natural selection and that nongenetic "legacies of modified natural selection pressures" be recognized in addition to the genetic legacies passed on in the egg and sperm. In their view, a suitably extended evolutionary theory would recognize both niche construction and natural selection as evolutionary processes contributing together to the dynamic adaptive match between organisms and environments (Odling-Smee et al. 2003, 2–3).

Taking niche construction into account encourages biologists to look at organisms in a new way. Rather than picturing them as passively staying in place, subject to selection pressures they cannot affect, organisms are now seen as sometimes capable of actively intervening in their evolutionary fate by *modifying the environment:* Odling-Smee et al. (2003) predict that "those members of the population that are least fit relative to the imposed selective regime will be the individuals that exhibit the strongest evidence for niche construction" (298). Alternatively, organisms that *move into a new environment* with different selection pressures can no longer be automatically identified as the unquestionable losers in evolutionary competition in their

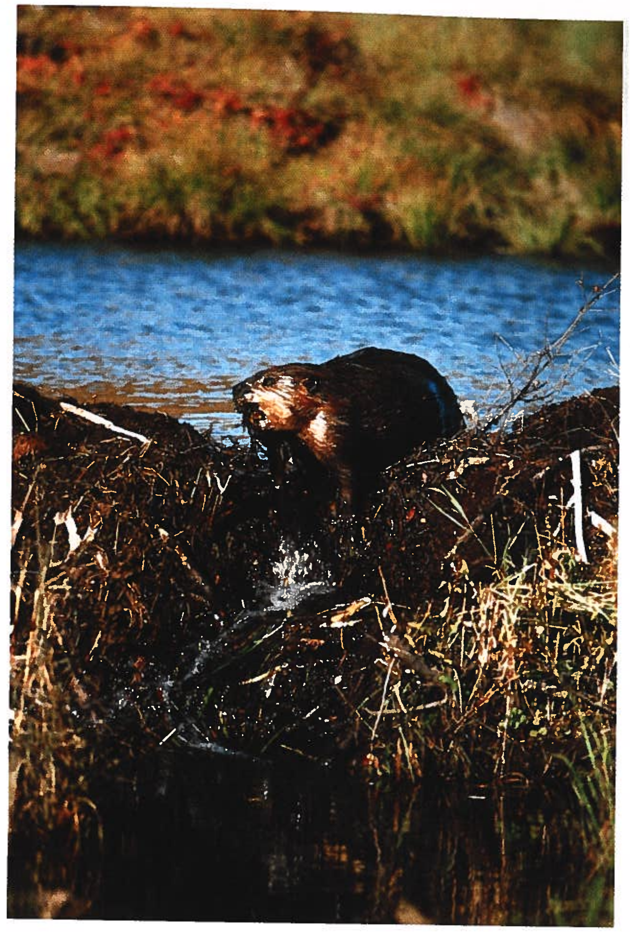


FIGURE 2.18 Many species, including beavers, construct key features of their own ecological niches. Beaver dams modify selection pressures experienced by beavers, but they also alter selection pressures experienced by neighboring species whose own niches are altered by the presence of the beaver dam in their habitats.

niche construction When organisms actively perturb the environment in ways that modify the selection pressures experienced by subsequent generations of organisms.

IN THEIR OWN WORDS

How Living Organisms Construct Their Environments

Geneticist Richard Lewontin rejects the notion that living organisms are passively molded by the "environment," thereby challenging us to rethink exactly what an environment is.

We must replace the adaptationist view of life with a constructionist one. It is not that organisms find environments and either adapt themselves to the environments or die. They actually *construct* their environment out of bits and pieces. In this sense, the environment of organisms is coded in their DNA and we find ourselves in a kind of reverse Lamarckian position. Whereas Lamarck supposed that changes in the external world would cause changes in the internal structures, we see that the reverse is true. An organism's genes, to the extent that they influence what that organism does in its behavior, physiology, and morphology, are at the same time helping to construct an environment. So, if genes change in evolution, the environment of the organism will change, too.

Consider the immediate environment of a human being. If one takes motion pictures of a person, using schlieren optics that detect differences in the refractive index of the air, one can see that a layer of warm, moist air completely surrounds each one of us and is slowly rising from our legs and bodies and going off the top of our heads. In fact, every living organism including trees has this boundary layer of warm air that is created by the organism's metabolism. The result is that we are encapsulated in a little atmosphere created by our own metabolic activities. One consequence is what is called the wind-chill factor. The reason that it gets much colder when the wind blows across us is because the wind is blowing away the boundary layer and our skins are then exposed to a different set of temperatures and humidities. Consider a mosquito feeding on the surface of the human body. That mosquito is completely immersed in the boundary layer that we have constructed. It is living in a warm, moist world. Yet one of the most common evolutionary changes for all organisms is a change in size, and over and over again organisms have evolved to be larger. If the mosquito species begins to evolve to a larger size, it may in fact find itself with its back in the "stratosphere" and only up to its knees in the warm, moist boundary layer while it is feeding. The consequence will be that the mosquito's evolution has put it into an entirely different world. Moreover, as human beings early in their evolution lost hair and the distribution of sweat glands over their bodies changed, the thickness of the boundary layer changed and so changed the micro-world that they carry with them, making it rather less hospitable for fleas, mosquitoes, and other parasites that live on hairy animals. The first rule of the real relation between organisms and environment is that environments do not exist in the absence of organisms but are constructed by them out of bits and pieces of the external world.

The second rule is that the environment of organisms is constantly being remade during the life of those living beings. When plants send down roots, they change the physical nature of the soil, breaking it up and aerating it. They exude organic molecules, humic acids, that change the soil's chemical nature as well. They make it possible for various beneficial fungi to live together with them and penetrate their root systems. They change the height of the water table by removing water. They alter the humidity in their immediate neighborhood, and the upper leaves of a plant change the amount of light that is available to the lower leaves. When the Canadian Department of Agriculture takes weather records for agricultural purposes, they do not set up a weather station in an open field or on the roof of a building. They take measurements of temperature and humidity at various levels above the ground in a field of growing plants because the plants are constantly changing the physical conditions that are relevant to agriculture. Moles burrow in the soil. Earthworms through their castings completely change the local topology. Beavers have had at least as important an effect on the landscape in North America as humans did until the beginning of the last century. Every breath you take removes oxygen and adds carbon dioxide to the world. Mort Sahl once said, "Remember, no matter how cruel and nasty and evil you may be, every time you take a breath you make a flower happy."

Source: Lewontin 1991, 112–14.

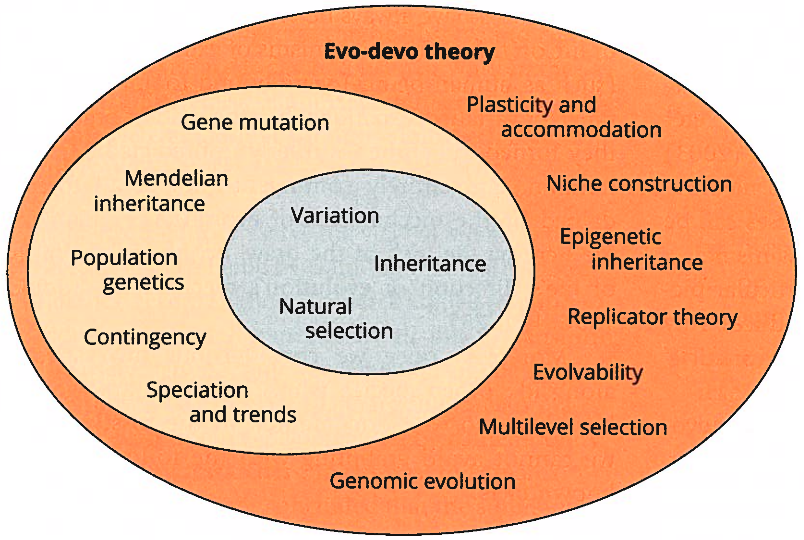


FIGURE 2.19 The scope of evolutionary theory has broadened and deepened over time. Evolutionary theorists Massimo Pigliucci and Gerd Müller represent these changes in this graphic. Darwin's original views are within the inner oval; the features added by the Modern Synthesis are encompassed within the middle oval, and new developments in evolutionary biology that may presage a new, extended synthesis, are included in the outermost oval.

Source: Pigliucci and Müller, 2010.

former environment. Niche construction portrays all organisms (not just human organisms) as active agents living in environments that are vulnerable to the consequences of their activities, contributing in potentially significant ways to the evolutionary histories of their own and other species.

According to Odling-Smee et al. (2003), acknowledging niche construction as an adaptive process offers a way to link evolutionary theory and ecosystem ecology, and it also alters the relationship between evolutionary theory and the human sciences (3). Odling-Smee and colleagues regard human beings as "virtuoso niche constructors" (367), and their arguments should be of great interest to anthropologists, especially cultural anthropologists who insist that any explanation of social and culture change must make room for **human agency**: the way people struggle, often against great odds, to exercise some control over their lives. At the same time, niche construction theorists remind us that humans are not the only agents at work: other organisms and the ecological artifacts they (and we) have created also play roles in shaping evolutionary outcomes. The agency of organisms as niche constructors matters in evolution "because it introduces feedback into the evolutionary dynamic [which] significantly modifies the selection pressures [on organisms]" (Odling-Smee et al. 2003, 2; see also Deacon 2003). As we will see in later chapters, we as humans are never free to do exactly as we please but always have options for action. And the actions we choose to undertake can sometimes reshape the selective pressures we experience, exactly as niche construction theorists would predict.

What Does Evolution Mean?

Ever since Darwin, evolutionary theory has been subjected to repeated testing. Although the results of those tests have led to modifications of the theory in certain respects, none of them has ever called the concept of evolution itself into question. Indeed, the power of evolutionary theory is illustrated by how the work of Linnaeus, Darwin, and Mendel meshes together so beautifully, although each of them worked independently. Modern biologists agree that no process other than evolution can explain nearly as much about the history of life on earth.

The study of evolution in contemporary biology is very lively. New evidence and new ways of interpreting evidence have led many evolutionists to question the adequacy of their old ways of understanding and to develop different perspectives on the evolutionary process (Figure 2.19). They are keenly aware that a phenomenon as complex as evolution requires theoretical

human agency The way people struggle, often against great odds, to exercise some control over their lives.

pluralism—that is, the recognition that a variety of processes operating at different levels work together to produce the similarities and differences that characterize the living world. As evolutionary theorists Peter Richerson, Robert Boyd, and Joseph Henrich (2003) remind us, "Evolutionary theory prescribes a method, not an answer, and a wide range of hypotheses can be cast in an evolutionary framework. . . . Darwinism as a method is not at all committed to any particular picture of how evolution works or what it produces. Any sentence that starts with 'evolutionary theory predicts' should be regarded with caution" (366).

Life has a comprehensible history for modern evolutionists. How it is likely to change next, however, cannot be predicted with any certainty because random factors continue to play an important evolutionary role. Human biologists have been forced to rethink the place of their own species in the web of life. Unquestionably, the result has been to dislodge human beings from the center. Most contemporary evolutionists would probably agree with Steven Stanley (1981) that "not all paths lead toward *Homo sapiens*, and possibly no persistent path led directly toward him" (151). Indeed, the very notion that organisms are "going somewhere" along a linear evolutionary "path" has been questioned. Stephen Jay Gould (1996) has argued that apparent directional trends in evolution such as increasing body size are "really random evolution away from small size, not directed evolution toward large size" (162). He suggests that a more appropriate way to think of the history of life is in terms of expansion or contraction over time in the total range of variation in living forms (i.e., life's "full house"). To do so is to recognize that bacteria have always been the most common form of life on this planet. Organisms of extreme complexity (such as human beings) were bound to appear as the range of variation expanded, but the kind of organisms they turned out to be "is utterly unpredictable, partly random, and entirely contingent—not at all foreordained by the mechanisms of evolution. . . . Humans are here by the luck of the draw, not the inevitability of life's direction or evolution's mechanism" (Gould 1996, 174–75).

Moreover, once we consider our own species alongside other species whose comings and goings have been so well documented in the fossil record, we cannot avoid grappling with the following well-known facts:

> The only certainty about the future of our species is that it is limited. Of all the species that have ever existed 99.999% are extinct. The average lifetime of a carnivore genus is only 10 million years, and the average lifetime of a species is much shorter. Indeed, life on earth is nearly half over: Fossil evidence shows that life began about 3 billion years ago, and the sun is due to become a red giant about 4 billion years from now, consuming life (and eventually the whole earth) in its fire. (Lewontin 1982, 169)

Our species' story is far from over. Who knows? Perhaps we will find a way to spread beyond our solar system, and our descendants may escape the grim fate that awaits our planet in 4 billion years. In the meantime, we remain on earth, searching for answers about who we are and how we are to live our lives.

Chapter Summary

1. Evolutionary theory is a testable, unified, and fruitful scientific theory. Material evidence of evolutionary change over time can be found in the fossil record and in the pattern of distribution of living species of organisms.
2. Before Darwin, European thinkers divided living things into natural kinds, each of which was thought to have its own unchanging essence. The Great Chain of Being was understood as God's creation, naturally harmonious and without gaps, and it inspired Linnaeus's important eighteenth-century taxonomy of living organisms.
3. In the nineteenth century, catastrophism and uniformitarianism undermined the Great Chain of Being. Catastrophism was based on the ideas of Georges Cuvier, who argued that some species had become extinct in massive natural disasters, after which new species were introduced from elsewhere. Uniformitarianism was promoted by geologist Charles Lyell, who argued that the same processes of erosion and uplift that can be observed to change the earth's surface today had been at work in the past. Uniformitarianism implied that changes in life forms were as gradual and reversible as changes in the earth's surface.
4. Lamarck tried to preserve the view of a harmonious Great Chain of Being by claiming that fossil species had not become extinct. Lamarck argued that individual members of a species are all able to transform themselves in the same way when facing the same environmental pressures. Lamarckian transformational evolution has been rejected by contemporary evolutionary researchers. In contrast to Lamarck, Darwin and Wallace concluded that the similarities shared by distinct living species could be explained if all such species had descended from a single parental species that had lived in the past. In addition, Darwin proposed that such "descent with modification" could occur as a result of the straightforward, mechanistic process of natural selection.
5. Darwin's theory of evolution by natural selection (or variational evolution) was based on the principle of variation, the principle of heredity, and the principle of natural selection. Variational evolution was driven by what Darwin called the "struggle for existence" between individuals of the same species to survive and reproduce. In a given environment, those variant individuals who survive and leave greater numbers of offspring are said to have greater fitness than other members of their species who leave fewer offspring. There is no such thing as "absolute" fitness. Today, evolutionists recognize four evolutionary processes, including natural selection, that can determine which variant individuals in a population will leave greater numbers of offspring than others.
6. Evolutionary theorists use the concept of adaptation to refer both to a process of mutual adjustment between organisms and their environments and to the phenotypic features of organisms that are produced by this process. Reconstructing accurate evolutionary histories of organisms requires distinguishing adaptations from exaptations.
7. Darwin did not know why offspring tend to resemble their parents, nor did he understand how variation was introduced into populations. Answers to these questions were developed in the field of genetics. Genes are associated with particular portions of the DNA molecules located on the chromosomes in the cell nucleus. The machinery of the cell uses DNA to synthesize proteins necessary for life processes and makes it possible for chromosomes to be copied before cells divide. Gene interaction helps explain how continuous traits, such as skin color or hair color, are the result of unchanging inheritance. Different genotypes may produce the same phenotype, and the same genotype may produce different phenotypes, depending on the kinds of environments in which organisms possessing these genotypes live and grow. That is, each genotype has its own norm of reaction.
8. The study of evolution in contemporary biology is very lively. Modern biologists agree that life on earth has evolved, but they have different views about how evolutionary processes work. Many evolutionary thinkers are increasingly convinced that a phenomenon as complex as biological evolution requires theoretical pluralism.

For Review

1. Define evolution.
2. Explain the kinds of material evidence that have been important in the development of evolutionary theory.
3. Define essentialism and the Great Chain of Being.
4. Explain the difference between transformational (Lamarckian) evolution and variational (Darwinian) evolution.
5. Describe the basic principles and driving force of natural selection.
6. Distinguish among aptation, adaptation, and exaptation.
7. Why is variation so important in evolutionary theory?
8. Explain nonblending, single-particle inheritance (Mendelian inheritance).

9. What is the difference between discontinuous and continuous variation?

10. Explain how, from a Darwinian perspective, it is populations (not individual organisms) that can evolve.

11. Explain what Richard Lewontin meant when he wrote "There is no 'race memory' in biology, only in books."

12. What are the differences between genotype and phenotype, and why are they important?

13. What is a norm of reaction? Explain its significance for the evolution of human populations.

14. Summarize the main components of niche construction.

Key Terms

adaptation	40
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aptation	40
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common ancestry	39
continuous variation	44
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Suggested Readings

Ayala, Francisco J., and John C. Avise (eds.). 2014. *Essential readings in evolutionary biology*. Baltimore: Johns Hopkins University Press. *This book is a bit challenging for students new to evolutionary biology, but it is a marvelous compendium of forty-eight excerpts by influential evolutionary thinkers, from Darwin until the present day, including theoretical developments connected with the rise of genetics, the negotiation of the evolutionary synthesis, the discovery of the structure of DNA, and more.*

Gould, Stephen Jay. 1987. *Time's arrow, time's cycle: Myth and metaphor in the discovery of geological time*. Cambridge, MA: Harvard University Press. *A fascinating account of the historical and cultural context out of which catastrophism and uniformitarianism were forged in the nineteenth century.*

——. 1996. *Full house: The spread of excellence from Plato to Darwin*. New York: Harmony Books. *An eloquent and entertaining defense of the view that human beings were not the end point of biological evolution and that bacteria are more properly regarded as the dominant life forms on earth.*

Kevles, Daniel J., and Leroy Hood. 1992. *The code of codes: Scientific and social issues in the Human Genome Project*. Cambridge, MA: Harvard University Press. *This edited collection contains a wide range of articles by geneticists, molecular biologists, biochemists, historians of science, and social scientists who examine the prospects and consequences of mapping all the genes in the human body. The book offers a range of opinions on how fully we will know what it means to be human if we learn one day all there is to know about our genes.*

Lewontin, Richard. 1991. *Biology as ideology: The doctrine of DNA*. New York: Harper Perennial. *The text of this book began as a series of radio broadcasts for the Canadian Broadcasting Company and is supplemented with an article Lewontin published in the* New York Review of Books. *Lewontin's accessible and hard-hitting essay addresses excessive claims that are sometimes made in the name of human genetics and offers incisive criticism of current efforts by geneticists to map all the genes in the human body.*

——. 2001. *The triple helix: Gene, organism, and environment*. Cambridge, MA: Harvard University Press. *Lewontin reminds biologists not to forget the role of organisms and environment in discussions of evolution; these are often ignored in discussions that attribute everything to genes.*

Lovejoy, Arthur O. [1936] 1960. *The Great Chain of Being*. New York: Harper Torchbooks. *Originally published in 1936, this classic is as fresh and relevant as anything being written about evolution today. A marvelously clear and detailed account of pre-Darwinian thinking about life on earth.*

Marks, Jonathan. 1995. *Human biodiversity*. New York: Aldine. *Marks is a biological anthropologist with a strong commitment to a biocultural approach to human nature. This book is an excellent introduction to biological anthropology.*