

## **HUMAN EVOLUTION**

In order to evaluate the scientific stories told about human origins, people need to become more knowledgeable about the kinds of material evidence and the interpretations of that evidence that scientists use. This chapter provides a brief introduction to both matters, offering an overview of the basic elements of modern evolutionary theory, presenting some of the key evidence that evolutionary biologists have collected to support their hypotheses, and illustrating the ways in which biological anthropologists have used evolutionary approaches in their studies of the human species. We will sketch out the ways in which scientific inquiry into the biology of living primates, the analysis of fossils, the interpretation of archaeological remains, and the study of a wide range of contemporary human societies provide a vast body of evidence in support of an evolutionary story about human origins, the origin of culture, and the development of human cultural diversity. But one short chapter can only skim the surface of these exciting topics. For treatments at greater depth, we recommend you take a course or two in biological anthropology or archaeology! Even students interested only in cultural anthropology need to know what makes the theory of evolution so compelling.

### **WHY IS EVOLUTION IMPORTANT TO ANTHROPOLOGISTS?**

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. After that date, biologists could borrow Darwin's methods to guide them in new and promising directions. As Kitcher puts it, Darwin "gave structure to our ignorance" (48). The study of life has not been the same since. The theory of evolution has engaged the efforts of many scientists for nearly a century. Their work has produced a still-developing, powerful, multistranded theory. To understand the arguments made by modern evolutionary biologists, we have to 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.

## **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 origin. Because of this common origin, 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 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" (1982, 2). Evolutionary thinkers are convinced that the story they propose to tell about the history of life on earth is more persuasive than any rival stories. To what do they owe this confidence?

## **MATERIAL EVIDENCE 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 also resembled mainland finch species (Figure 1).

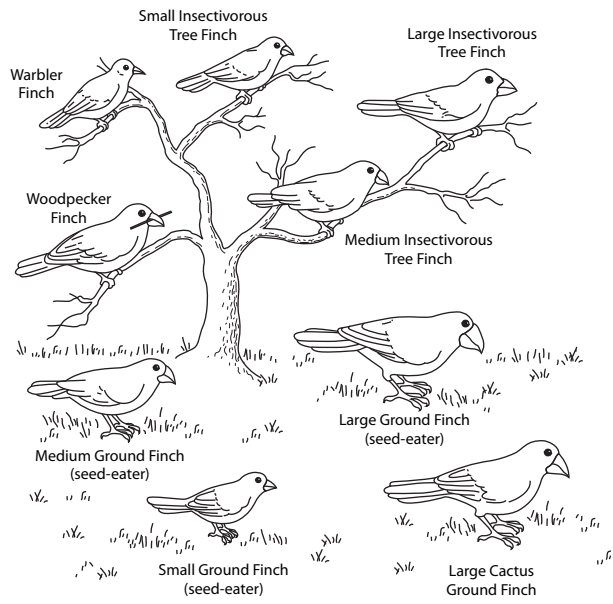


Figure 1. Charles Darwin and Alfred Russel Wallace explained the pattern of distribution of living species of organisms (such as the various species of finches living on the Galapagos Islands) by arguing that all the variants had evolved from a single ancestral species.

Species distribution patterns of this kind suggested change over space, which, again, any persuasive biological theory would have to explain.

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 1).

TABLE 1 PRE-DARWINIAN VIEWS OF THE NATURAL WORLD

View	Key Features
Essentialism	<ul style="list-style-type: none"><li>•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.</li></ul>
Great Chain of Being	<p>Based on three principles:</p> <ol style="list-style-type: none"><li>1. Continuity: Attributes of one kind of organism always overlap to some extent with the attributes of organisms closest to it in the classification.</li><li>2. Plenitude: A world of organisms created by a benevolent God can have no gaps but must include all logically conceivable organisms.</li><li>3. Unilinear gradation: All organisms can be arranged in a single hierarchy based on various degrees to which they depart from divine perfection.</li></ol>
Catastrophism	<ul style="list-style-type: none"><li>•The notion that natural disasters, such as floods, are responsible for the extinction of species, which are then replaced by new species.</li></ul>
Uniformitarianism	<ul style="list-style-type: none"><li>•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.</li></ul>
Transformational evolution	<ul style="list-style-type: none"><li>•Assuming essentialist species and a uniformly changing environment, Lamarck argued that individual members of a species transform themselves in identical ways in order 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.</li></ul>

## PRE-DARWINIAN VIEWS OF THE NATURAL WORLD

### The Great Chain of Being

The idea that the world is fixed and unchanging—and that the various forms of life that are part of that world also do not change—was present in ancient Greek philosophy. Greek ideas were adopted and adapted by thinkers in the Judeo-Christian religious traditions of Western Europe. By the Middle Ages, many scholars thought they could describe the organizing principles responsible for harmony in nature. According to Arthur Lovejoy (1936), 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 very 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, 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, 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. For example, Carolus Linnaeus (1707–1778), the inventor of modern biological **taxonomy** (or classification), operated within this framework.

### **Transformational Evolution**

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. One of the most serious challenges was the problem of extinction. For example, French naturalist Georges Cuvier (1768–1832) carried out some of the first important excavations of fossils in the Seine River Basin near Paris. This research suggested that certain species that had once lived in the Seine Basin had disappeared in what appeared to be mass extinctions and were replaced later by species introduced from elsewhere. Cuvier's colleague Jean-Baptiste de Monet de Lamarck (1744–1829), attempted to grapple with this problem. 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.

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. This was the law of inheritance of acquired characteristics.

Consider the following example: Modern pandas possess an oversized, elongated wrist bone that aids them in stripping bamboo leaves, their favorite food, from bamboo stalks (Figure 2).

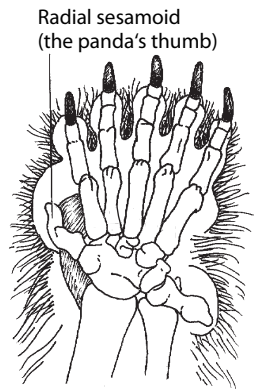


Figure 2. Lamarckian transformational evolution and Darwinian variational evolution offer two different explanations for how the panda got its “thumb.” This thumb is actually an elongated wristbone that aids pandas in stripping bamboo leaves, their favorite food, from bamboo stalks.

This bone has been called the panda's "thumb," although pandas retain all of the usual 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 wrist bones 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) in order to remove enough bamboo leaves to satisfy their appetite. Continual exercise of their wrists caused the wrist bone to enlarge and lengthen into a shape resembling a thumb. After acquiring "thumbs" through strenuous activity, pandas gave birth to offspring with elongated wrist bones (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."

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.

## **THE THEORY OF NATURAL SELECTION**

Lamarck had argued that a species could vary over time. Contemporaries of Lamarck, observing living organisms in the wild in Europe, America, 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) 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 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, on the basis of the very slow rate of natural processes such as erosion and the uplift of mountains, that the earth was much more than 6,000 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.

The theory of **common origin**—“the first Darwinian revolution” (Mayr 1982, 116)—was in itself scandalous, for 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 he also 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, for it has been tested and

reformulated for over a century and remains the best explanation we have today for the diversity of life on earth.

Charles Darwin's theory of evolution was only possible because he was able to think about species in a new way. 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 is the ground condition of life. This is why it is called **variational evolution**, in contrast to the *transformational evolution* of Lamarck (see, for example, Lewontin 1982). Variational evolution depends on what Ernst Mayr (1980) called *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.

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**.

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, intelligence, and so on.
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 wrist bones 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 wrist bones of different lengths (the principle of variation). Because offspring tend to resemble their parents, pandas with long wrist bones gave birth to offspring with long wrist bones, and pandas with short wrist bones gave birth to offspring with short wrist bones (the principle of heredity). When the climate changed such that pandas became dependent on bamboo leaves for food, pandas with wrist bones 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 wrist bones 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 wrist bones made them fitter than pandas with short wrist bones. Thus, pandas with “thumbs” survived and

left more offspring than did those without “thumbs.” As a result, the proportion of pandas with elongated wrist bones in the next generation was larger than it had been in the previous generation and the proportion of pandas with short wrist bones was smaller. If these selective pressures were severe enough, pandas with short wrist bones might not leave any offspring at all, resulting at some point in a population made up entirely of pandas with “thumbs.”

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. 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 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” (1982, 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.

## UNLOCKING THE SECRETS OF HEREDITY

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 particulate theory of inheritance, 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**

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 ( $F_1$ ) generation (Figure 3).



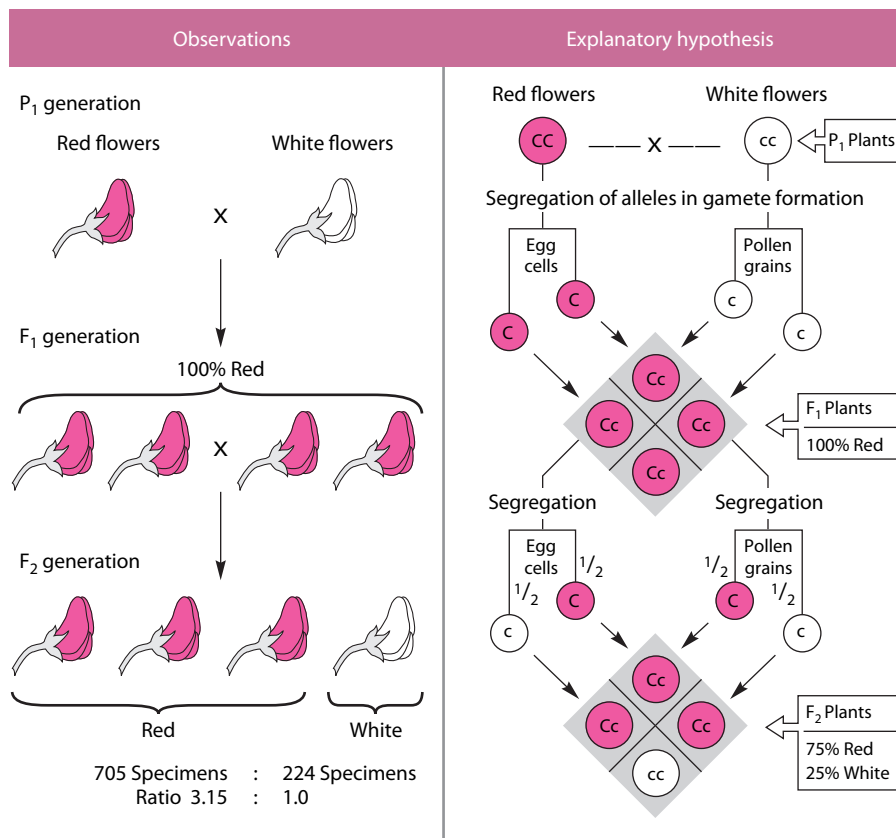


Figure 3. Mendel crossbred peas with red flowers and peas with white flowers (the parental, or P<sub>1</sub>, generation). This produced a generation (F<sub>1</sub>) of only red flowers. When Mendel crossed red-flowered peas from the F<sub>1</sub> generation, they produced the F<sub>2</sub> generation 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.

They did, however, reappear in their original form in the next ( $F_2$ ) generation. 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).

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 (that is, one-half of the pair) from each parent. This is the **principle of segregation**. Mendel further argued that each pair of particles separates independent 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 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.

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).

## **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 4a). The process is different, however, when the sex cells (sperm and eggs) are formed. This process is **meiosis**, or reduction division (Figure 4b).

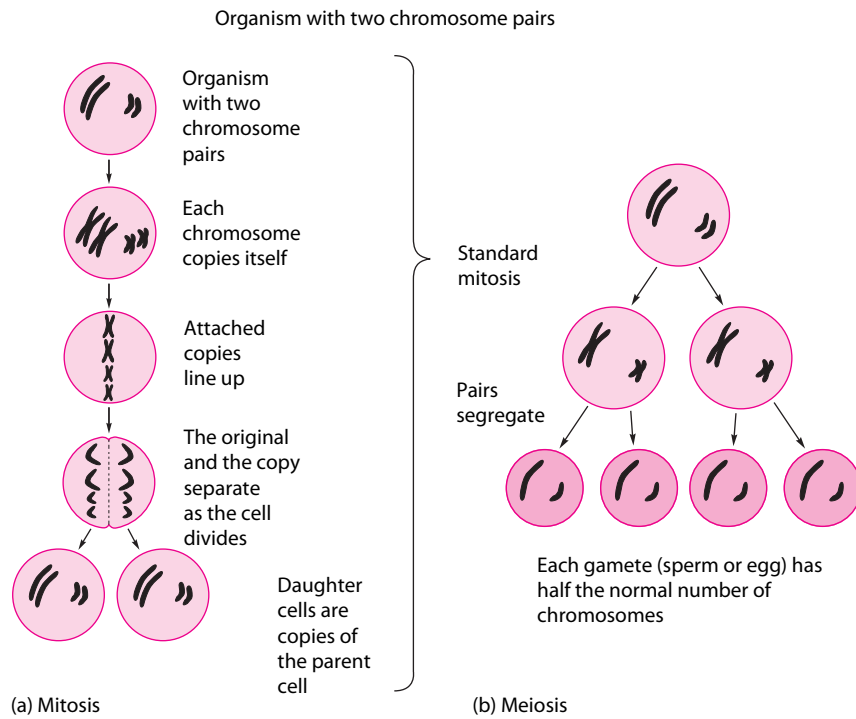


Figure 4. Cells divide in two different ways. (a) In mitosis, ordinary body cells double the number of chromosomes they contain before dividing so that each daughter cell carries a full copy of the genetic information in the mother cell. (b) Meiosis occurs only when sex cells (sperm or eggs) are produced. 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.

The behavior of the chromosomes during meiosis intrigued geneticists. Slides of cells made at different stages in the process of reduction division 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).

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 5a). 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 5b).

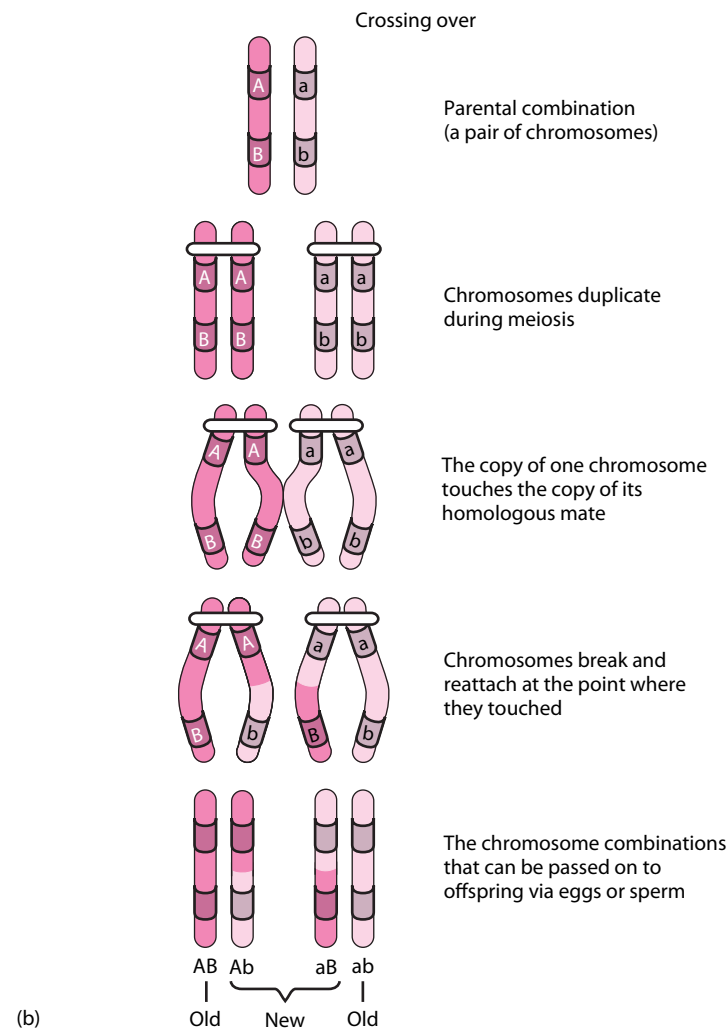
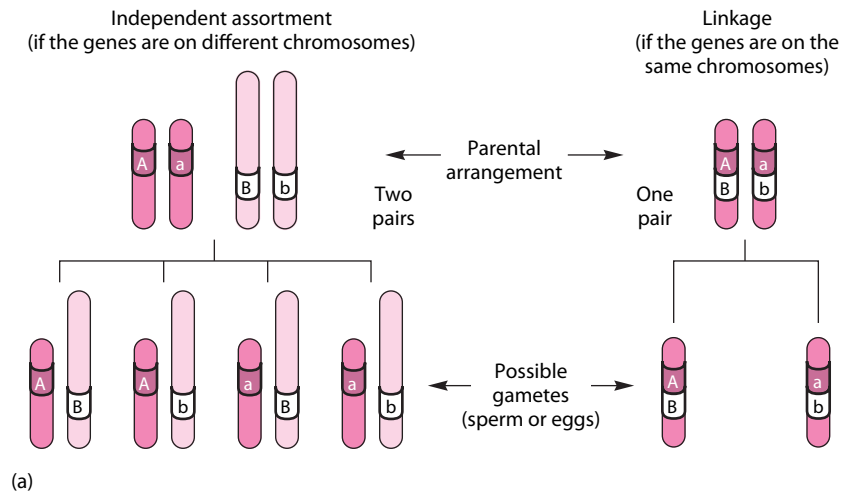


Figure 5. The principle of independent assortment predicts that genetic factors on different chromosomes will not be passed on together; each will be passed on to a different sex cell during meiosis. (a) Linkage predicts that genetic factors on the same chromosome will tend to be passed on together because 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.

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; 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 alters 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.

Perhaps even more surprising than polygenic gene 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 showed that genes do not produce traits in isolation. Many geneticists came to focus attention on what the Russian geneticist Chetverikov called the *genetic milieu*, investigating the effects that different genes could have on one another (Figure 6).

Gene effects

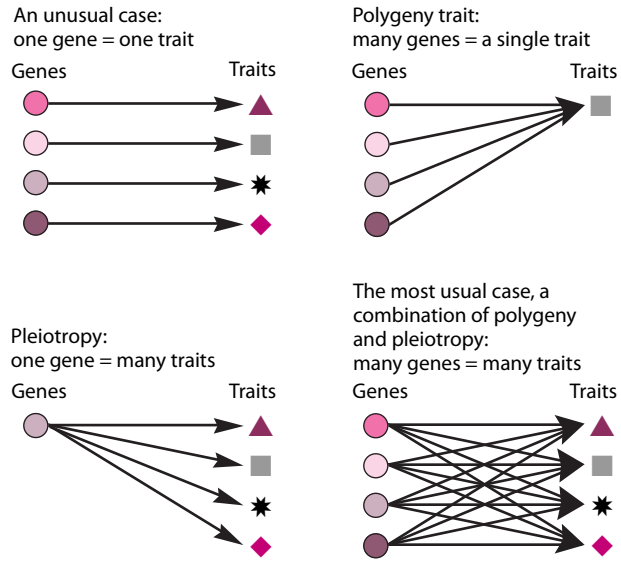


Figure 6. Only rarely is a single physical trait the result of the action of a single gene. Many traits are the result of gene interaction, involving polygeny, or pleiotropy or, as is usually the case, both.



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).

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 egg or sperm of that organism, reshaping the information it contains, thereby allowing an adaptation to be passed on to offspring.

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* 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.

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*. Faithful copies of DNA molecules are made when chromosomes are copied prior to cell division. 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 7).

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**.

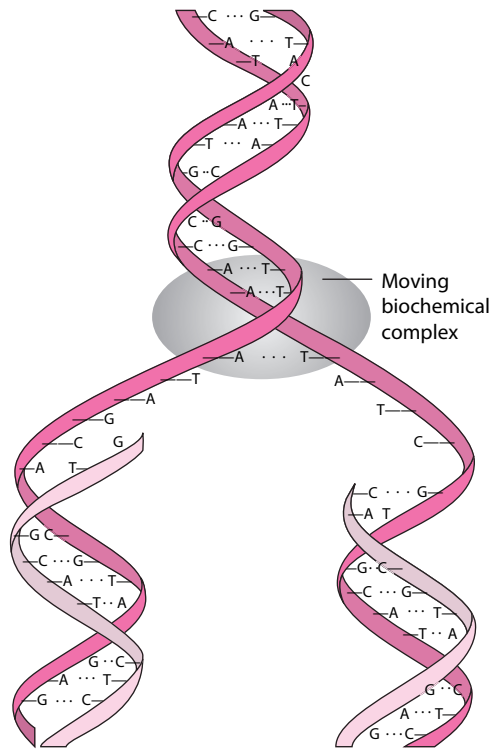


Figure 7. For DNA to replicate, a biochemical complex moves along the molecule and “unzips” the double helix, and two complete copies are rebuilt from appropriate molecules floating in the nucleus. Adenine (A) always attracts thymine (T), and cytosine (C) always attracts guanine (G).

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 transmitted directly through that organism's tissues and cells in order to restructure the organism's DNA in a more "adaptive" form. 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. 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. 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 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 (2003, 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.

### **“There Is No ‘Race Memory’ in Biology, Only in Books”**

“Genetic inheritance is unchanging inheritance,” which means that a Lamarckian inheritance of acquired characteristics is impossible via genetic mechanisms. Because of the overwhelming evidence we now possess to support this statement, evolutionary biologists have rejected the notion that something experienced by individuals in one generation can be genetically transmitted to their offspring and become a permanent part of their genetic heritage, a notion sometimes referred to as *race memory*. Science fiction writers often use the concept of race memory in their plots, but they are not alone. We still encounter popular explanations of human behavior that appeal to race memory. One well-known example is the following: Our ancestors killed animals for food, and this habit somehow sent a message to their genes to produce descendants who were born with an instinctive appetite for murder.

As you can see, genetic race memory is scientific nonsense. There is no biological mechanism that transforms an organism’s experiences into messages that penetrate the eggs and sperm and restructure the genes inside them. Evolutionary history can only be inferred on the basis of information about the way a species, or its ancestors, lived at particular times in its past. None of that information is genetic; it is behavioral, ecological, and—in the human case—cultural. As Lewontin puts it, “The history of a species’ biological evolution . . . is stored nowhere in the individual members of the species. Their present state is, indeed, a consequence of their history, but the genes currently possessed by the species are all that matter for its evolutionary future, irrespective of how it acquired those genes. There is no ‘race memory’ in biology, only in books” (1982, 148). The way experience affects people is through memory, not genetics—people remember what they have experienced and reflect on it, either through oral tradition or, eventually, through writing.

## **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 and 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 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 general, a genotype cannot be characterized by a unique phenotype” (1985, 90–91).

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 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” (1982, 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 argue that organisms play two roles in evolution: carrying genes and interacting with environments. **Niche construction** is understood to occur either when an organism actively perturbs the environment or when it actively moves into a different environment (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. Odling-Smee et al. 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 (2003, 50–115). Their most controversial proposal is that 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 (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. 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” (2003, 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 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., 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 (2003, 3). Odling-Smee and his colleagues regard human beings as “virtuoso niche constructors” (2003, 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. Humans are never free to do exactly as they please, but we 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.



## **EVOLUTIONARY STUDIES IN BIOLOGICAL ANTHROPOLOGY**

Evolutionary research can be divided into two major subfields. **Microevolution** concentrates on short-term evolutionary changes that occur within a given species over relatively few generations. It involves what is sometimes called *ecological time*, or the pace of time as experienced by organisms living in and adapting to their ecological settings. **Macroevolution**, by contrast, focuses on long-term evolutionary changes, especially the origins of new species and their diversification across space and over millions of years. Macroevolutionary events, which span many generations and the growth and decay of many different ecological settings, are measured in geological time.

### **Microevolutionary Studies in Biological Anthropology**

Microevolutionary studies in evolutionary biology were made possible by the *modern evolutionary synthesis*, a major theoretical innovation accomplished in the 1930s and 1940s that integrated genetics and natural selection into the expanded framework of population genetics. After World War II, biological anthropologists discarded the old “race”-based physical anthropology and began to use concepts and methods drawn from population genetics to address questions about human biological variation.

The modern synthesis defined a **species** as “a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature” (Mayr 1982, 273). The ability of human beings from anywhere in the world to interbreed successfully is one measure of our membership in a single species. In addition, as we saw earlier, geneticists had demonstrated that most genes come in a variety of forms, called *alleles*. Population genetics has shown that genetic variation in human populations is mostly a matter of differences in the relative proportions of the same sets of alleles and that the distribution of particular phenotypes shifts gradually from place to place across populations, as the frequencies of some alleles increase while others decrease or stay the same. These observations lead to an inescapable conclusion: “humankind . . . is not divided into a series of genetically distinct units” (Jones 1986, 324). Put

another way, the boundaries said to define human “races” have been culturally imposed on shifting and unstable clusters of alleles (Marks 1995, 117). In addition, the distributions of some traits (like skin color) do not match the distributions of other traits (like hair type). The pattern of gradually shifting geographic frequency of a phenotypic trait across human populations is called a **cline**. Clines can be represented on maps such as Figure 8, which shows the gradually shifting distribution of differences in human skin color from the equator to the poles.

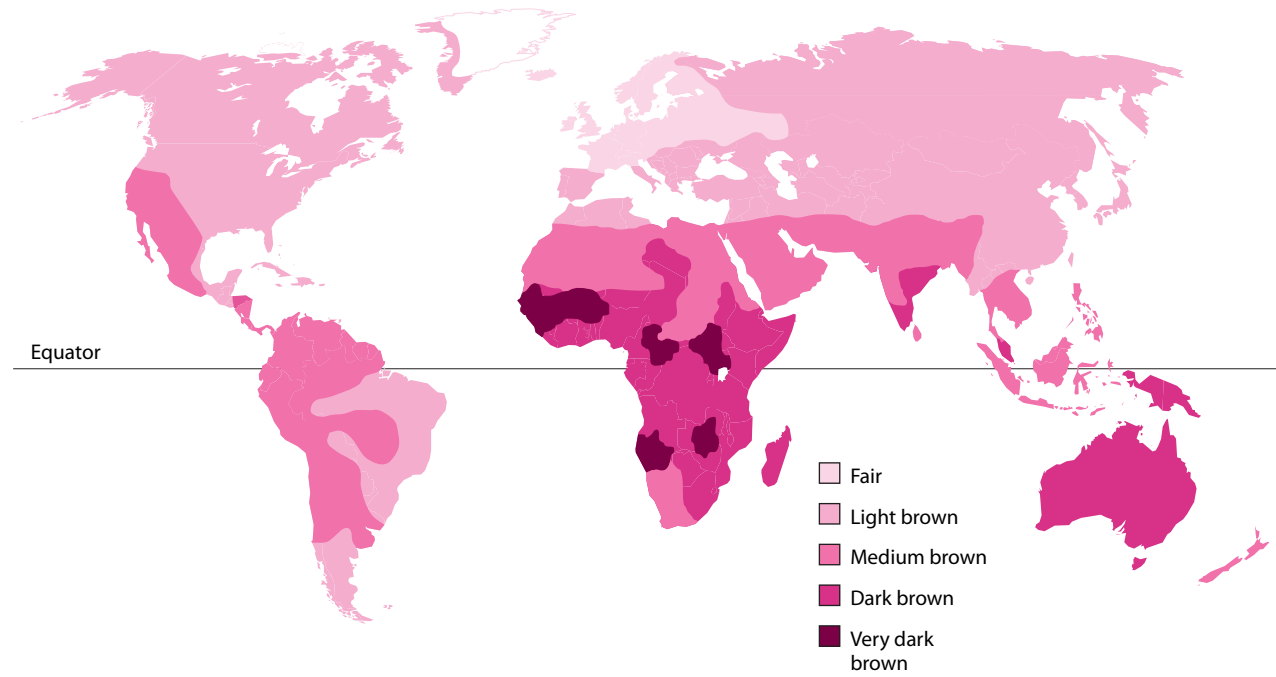


Figure 8. When the unexposed skin of indigenous peoples is measured and mapped according to the degree of pigmentation, skin shades tend to grow progressively lighter the farther one moves from the equator.

Phenotypic contrasts are greatest when people from very different places are brought together and compared while ignoring the populations that connect them (Marks 1995, 161). This is what happened when Europeans arrived in the New World, conquered the indigenous peoples, and imported slaves from Africa to work on their plantations. But if you were to walk from Stockholm, Sweden, to Cape Town, South Africa (or from Singapore to Beijing, China), you would perceive gradual changes in average skin color as you moved from north to south (or vice versa). Evolutionary biologists argue that skin pigmentation is distributed in this way as a consequence of natural selection: Individuals in tropical populations with darker skin pigmentation had a selective advantage in equatorial habitats over individuals with light pigmentation. By contrast, populations further away from the equator faced less intense selection pressure for darkly pigmented skin and perhaps even selective pressures in favor of lighter skins. But *different* selection pressures would have been at work on other traits, such as stature and hair type, within the same population, which is why the geographical distributions of these traits do *not* match up neatly with the distribution of skin pigmentation. To make things even more complex, different genes may be involved in the production of similar phenotypic traits in different populations. For example, although different ancestral populations of humans living near the equator all have dark skin, the identity and the number of alleles involved in the production of this phenotypic trait may be different in different populations (see later).

Evidence of intergradation in human phenotypes led biological anthropologist Frank Livingstone to declare 40 years ago that “There are no races, there are only clines” (1964, 279). Clinal variation explains why people searching for “races” have never been able to agree on how many there are or how they can be identified. *Clines are not groups*. The only group involved in clinal mapping is the entire human species. Each cline is a map of the distribution of a *single* trait. Biologists might compare the clinal maps of trait A and trait B to see if they overlap and, if so, by how much. But the more clines they superimpose, the more obvious it becomes that the trait distributions they map *do not coincide* in ways that neatly subdivide into distinct human

subpopulations. Since the biological concept of race predicts exactly such overlap, the biological concept of race cannot be correct. In other words, *clinal analysis tests the biological concept of race and finds nothing in nature to match it*. And if biological races cannot be found, then the so-called “races” identified over the years can only be symbolic constructs, based on cultural elaboration of a few superficial phenotypic differences—skin color, hair type and quantity, skin folds, lip shape, and the like. In short, early race theorists “weren’t extracting races from their set of data, they were imposing races upon it” (Marks 1995, 132).

Many anthropologists hoped that the cultural category of “race” would disappear once its supposed biological underpinnings were exposed as false. During the 1960s and 1970s, anthropologists and others replaced racial explanations for social differences with cultural explanations. In the last 30 years, however, we have witnessed in the United States and elsewhere a resurgence of attempts to explain group differences in terms of race. Sometimes it is the powerful who engage in such practices, in controversial books like *The Bell Curve* (Herrnstein and Murray, 1994). Sometimes it is members of politically and economically marginalized groups who do so, as a calculated move in political struggles with those who dominate them (see Chapter 15).

Genetic and other biological evidence alone cannot dismantle oppressive sociopolitical structures, but it can provide an important component in the struggle to eliminate racist practices from our societies. As we show in Chapter 14, anthropologists can make a strong case when they combine the lack of biological justification for racial categories with powerful ethnographic evidence to show how racial categories have been socially, culturally, and politically constructed in the course of human history. Of course, to deny the existence of biological race is not to deny the existence of human biological or genetic diversity. It is, rather, to deny that the patterns of human diversity can be usefully sorted into a handful of mutually exclusive categories. As Jonathan Marks reminds us, it was the recognition that human variation did not come in neat

divisions called races that “began to convert racial studies into studies of human microevolution” (1995, 117).

### **Macroevolutionary Studies in Biological Anthropology**

As we noted earlier, macroevolutionary studies focus on long-term evolutionary changes, especially the origins of new species and their diversification across space and over millions of years. **Paleoanthropology** attempts to answer questions about macroevolutionary events in the human past by studying fossils that help us reconstruct the evolutionary origin of our own species, *Homo sapiens*. But our species is only one of many species of monkeys, apes, and prosimians that are classified together in the same taxonomic order, Primates. This means that tracing the evolution of our own lineage also involves attempting to identify common ancestors that we share with other living primates. By combining knowledge from **primatology**, the study of living primates species, with an understanding of primate fossils, we may be able to reconstruct the family tree linking all primate species to a common ancestral species that appears to have emerged around 65 million years ago.

Very little is known about primates that lived 65 million years ago, although a few suggestive fossils have been found. Fossils about 55 million years old, however, are similar, but not identical to, the skeletons of some living primates, such as lemurs and tarsiers. Between 38 million and 23 million years ago, the ancestors of lemurs made it to the island of Madagascar, which buffered them from evolutionary competition. Elsewhere, however, evolutionary processes produced a group of organisms known as *anthropoideans*. Some anthropoidean fossils found in Egypt may be ancestral to New World monkeys, whereas other anthropoidean fossils may be ancestral to Old World monkeys and apes. Fossils of hominoids—primates that appear to be ancestors of Old World apes—first appear between 26 million and 23 million years ago in Africa. Hominoid evolution was confined to the African continent, until about 16 million years ago, when a land bridge connected Africa to Eurasia, making it possible for hominoids to migrate into the rest of the Old World, from Europe to China. About 10 million years ago, the numbers of hominoid fossils began to decline, whereas between 9 million and 5

million years ago, the fossils of Old World monkeys started to increase. Between 6 million and 5 million years ago, many hominoid species became extinct, but it was during this same period that the first members of our own lineage appeared.

### **Hominid Evolution**

Taxonomists separate the earliest fossil hominids from all other hominoids and group them together with living human beings because of a set of skeletal features that indicates habitual **bipedalism**, a feature that seems to be the first of our distinctive anatomical traits to have appeared (Figure 9).

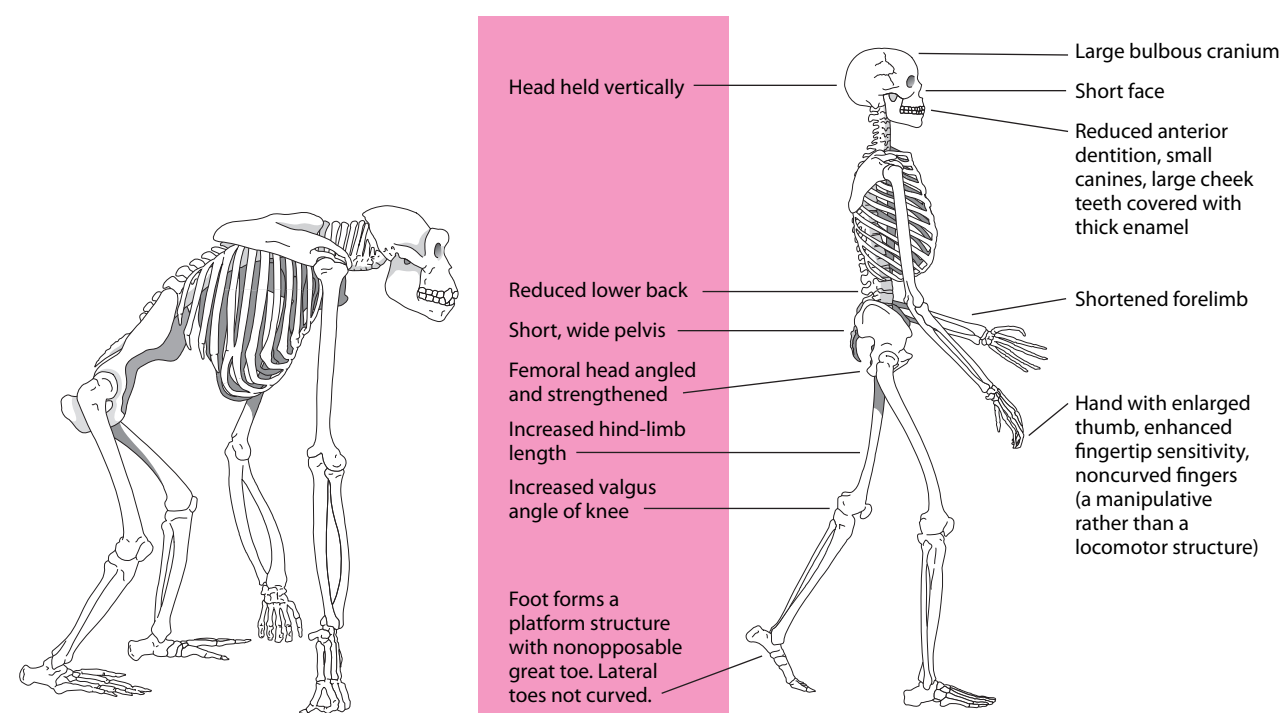


Figure 9. Apes (left) are adapted anatomically for a form of quadrupedal locomotion called knuckle walking, although they often stand upright and occasionally may even walk on their hind limbs for short distances. A human skeleton (right) shows the kinds of reshaping natural selection performed in order to produce the hominid anatomy, which is adapted to habitual bipedalism.



Most of these hominids are assigned to the genus *Australopithecus* and are often called *australopithecines*. Hominid evolution has also been marked by additional evolutionary changes in dentition. Finally, some hominids developed an expanded brain and ultimately came to depend on tools and language—that is, on culture—for their survival (Table 2). These developments did not all occur at once but were the result of **mosaic evolution** (different traits evolving at different rates).

TABLE 2

## FOUR MAJOR TRENDS IN HOMINID EVOLUTION

Trend	Development	Dates
Bipedalism	Evidence of bipedalism marks the appearance of the hominid line.	Between 10 and 5 mya
Distinctive dentition	The development of huge cheek teeth (molars) and much smaller front teeth was characteristic of the australopithecines.	4 to 2 mya
Expanded brain	Brain expansion beyond 400 to 500 cm <sup>3</sup> of the australopithecines was characteristic of the genus Homo.	Beginning 2.4 mya
Culture	Greater reliance on learned patterns of behavior and thought, on tools, and on language became important for Homo.	Beginning 2.5 mya

All the oldest-known hominid fossils come from Africa (Figure 10). The oldest remains are fragmentary, however, and their significance for later hominid evolution is still being debated. The most noteworthy of the recent finds are *Sahelanthropus tchadensis*, from Chad, in central Africa (6 million to 7 million years old) (Brunet et al. 2002, 6); *Orrorin tugenensis*, from Kenya (6 million years old) (Senut et al. 2001); and *Ardipithecus kadabba* (5.8 million to 5.2 million years old) and *Ardipithecus ramidus* (5.8 million to 4.4 million years old) (Haile Selassie et al. 2004; Haile Selassie, 2001; White et al. 1994, 1995). The earliest direct evidence of hominid bipedalism is 3.6 million years old. It comes from a trail of footprints that extends over 70 feet, preserved in a layer of hardened volcanic ash laid down during the middle Pliocene at the site of Laetoli, Tanzania. When compared to footprints made by modern apes and human beings, experts agree, the shapes of the Laetoli prints were definitely produced by hominid bipedal locomotion (Day 1985, 92; Day 1986, 191; Feibel et al. 1995/96).

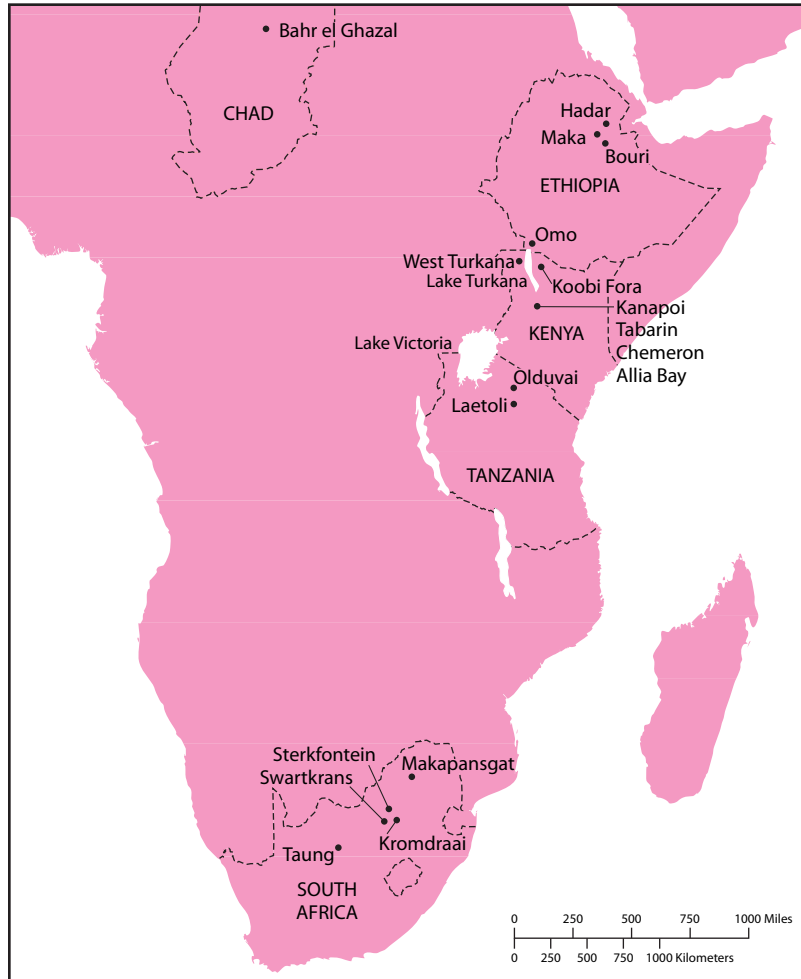


Figure 10. Major sites in eastern and southern Africa from which fossils of australopithecines and early Homo have been recovered.

As noted earlier, most early hominid fossils showing skeletal evidence of bipedalism have been placed in the genus *Australopithecus*. The oldest of these is *Australopithecus anamensis*, whose fossils come from Kanapoi and Allia Bay in Kenya. *A. anamensis* dates from 4.2 to 3.9 million years ago (mya). The remaining early hominid fossils have been assigned to the species *Australopithecus afarensis*. Fossils assigned to this taxon have also been found at Laetoli and in a region of Ethiopia known as the Afar Depression—hence the species name *afarensis*. These fossils, which are quite numerous, range between 3.9 million and 3.0 million years in age (Johanson and Edey 1981; Kimbel et al. 1994; T. White et al. 1993). The famous *A. afarensis* fossil Lucy (named after the Beatles song “Lucy in the Sky with Diamonds”) was found 40 percent intact and undisturbed where she had died, which allowed Donald Johanson and his colleagues to reconstruct her postcranial skeleton in great detail. The first fairly complete adult skull of *A. afarensis*, found in the early 1990s, confirmed its small-brained, apelike features.

Some features of the skeleton of *A. afarensis* reveal its adaptation to habitual bipedalism, especially when we compare it to the skeletons of modern humans and apes. The spinal column of a chimpanzee joins its head at the back of the skull, as is normally the case in quadrupedal animals. This is revealed by the position of a large hole, called the *foramen magnum*, through which the spinal cord passes on its way to the brain. The ape pelvis is long and broad and the knee is almost directly in line with the femur (or thigh bone) and is therefore ill adapted to support the ape’s center of gravity when it tries to move on its hind legs. As a result, when apes walk bipedally, they appear to waddle in an awkward attempt to stay upright. Finally, the great toe of the ape foot diverges like a thumb from the rest of the digits, a feature that allows apes to use their feet for grasping but inhibits their ability to use this toe for the “push-off” so important for effective bipedalism.

By contrast, the modern human head balances on the top of the spinal column. The foramen magnum in humans is located directly beneath the skull rather than at its back. The basin-shaped human pelvis is the body’s center of gravity, supporting and balancing the torso above it. Finally,

the bones of human legs have a knock-kneed appearance, with the femur pointing inward toward the knee joint at what is called the *valgus angle*. As a result, humans can easily transfer their center of gravity directly over the stepping foot in the course of bipedal walking.

The skeleton of *A. afarensis* more closely resembles that of modern human beings than that of apes. As Figure 11 shows, the great toe does not diverge from the rest of the digits on the foot; the femur bends inward toward the knee joint at the valgus angle; and the pelvis is short and basinlike.

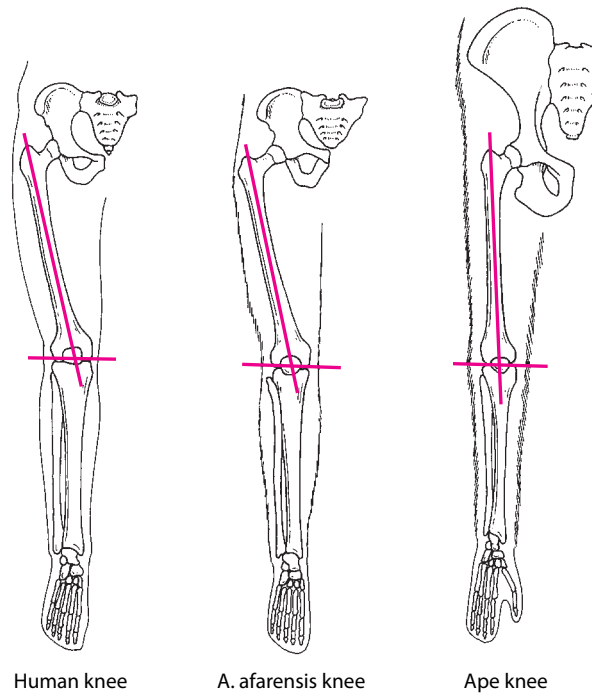


Figure 11. The bones of human legs have a somewhat knock-kneed appearance, with the femur pointing inward toward the knee joint at the valgus angle. This allows human beings to easily transfer the center of gravity directly over the foot in the course of bipedal walking. Ape femurs do not angle inward in this manner, so apes waddle when they try to walk bipedally. Because *A. afarensis* is humanlike in its valgus angle and in the shape of its pelvis, we conclude that, like us, it walked bipedally.

In addition, the skull of *A. afarensis* balanced on the top of the spinal column, as shown by the position of its foramen magnum. Nevertheless, elements of the postcranial skeleton of *A. afarensis* clearly recall its recent ape ancestry (Figure 12). It has longer arms, in proportion to its legs, than any other hominid. Also, the bones of its fingers and toes are slightly curved, and the toes are much longer, resembling the finger and toe bones of apes. Because these features are related to the typical tree-climbing adaptation of most hominoids, some paleoanthropologists have concluded that *A. afarensis* must have had significant tree-climbing ability along with bipedalism. (Klein 1989, 143–47; Lewin 1989, 77; Susman, Stern, and Jungers 1985). A 3.5-million-year-old australopithecine fossil found in Chad, in central Africa, is contemporaneous with *A. afarensis*. Called *Australopithecus bahrelghazali*, this specimen extends the geographic range of australopithecines far beyond southern and eastern Africa (Brunet et al. 1995).

Once the first bipedal hominids ventured regularly down from the trees and into a variety of new habitats, new diets appear to have created a set of selective pressures that led to important changes in hominid dentition, first evident in the teeth of *A. afarensis*. Fossils of 3-million-year-old bipedal hominids with rounded dental arcades, no gaps between teeth, small front teeth, and large cheek teeth were found first in southern Africa and later in eastern Africa. Some had faces that were small and lightly built and came to be known as the **gracile australopithecines**. Others, with more rugged jaws, flatter faces, and enormous molars, came to be known as the **robust australopithecines**.



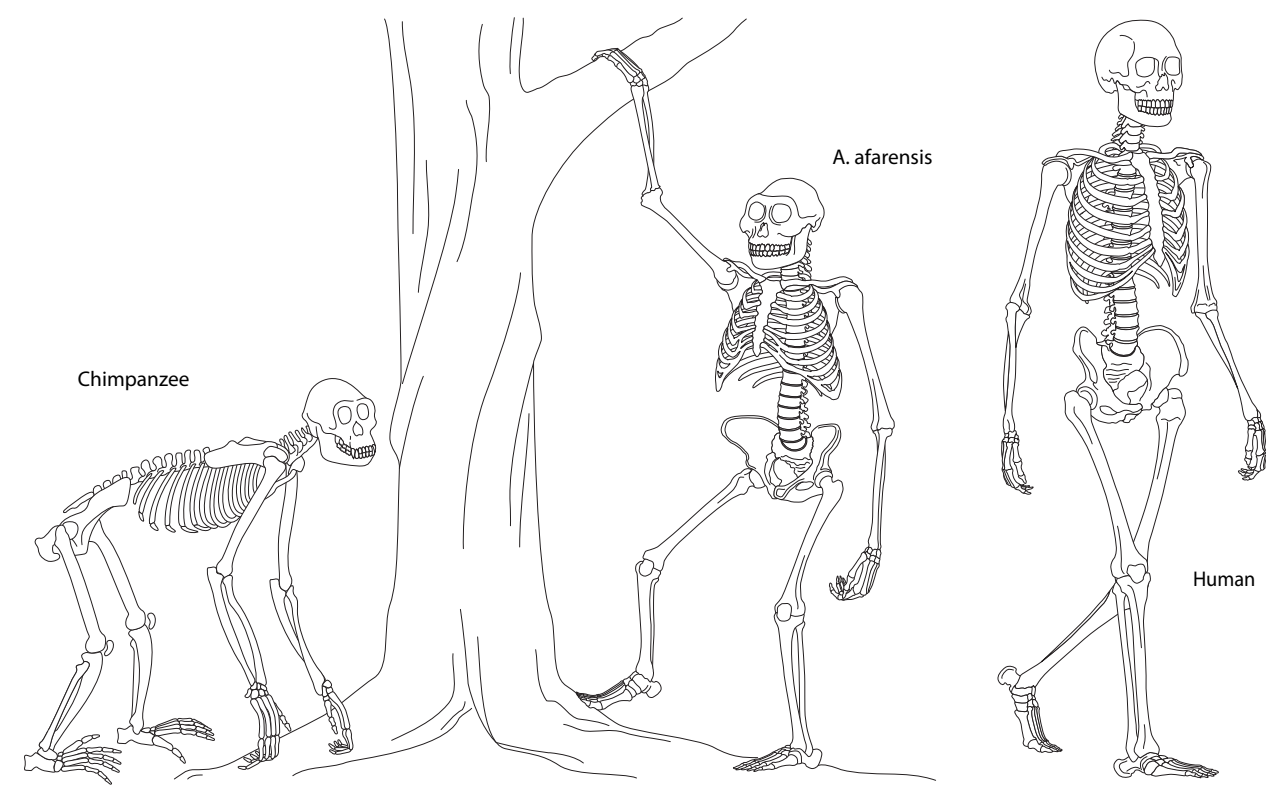


Figure 12. Although *A. afarensis* was humanlike in some respects, in other respects its skeleton retained adaptations to life in the trees.

About 2.5 to 2 mya, a drying trend in Africa became more pronounced, possibly causing a wave of extinction as well as the appearance of new species. During this period, the gracile australopithecines disappeared either by evolving into or being replaced by a new kind of hominid. These hominids had brains almost twice the size of australopithecines, and Louis Leakey, who found the fossil cranium of one of them, decided that it ought to be classified in the genus *Homo*, as *Homo habilis*. Today, it is widely believed that several species belonging to the genus *Homo* coexisted in eastern Africa in the early Pleistocene (Tattersall 1995). Which of these early species of *Homo* might be ancestral to later humans, however, is still being debated.

This is also the period during which the first reliably dated stone tools—cultural remains—are found. With their appearance, archaeologists and paleoanthropologists begin to collaborate in reconstructing the story of human evolution. Stone tools are the most enduring evidence we have of culturally created human artifacts. The oldest undisputed stone tools, found at Hadar in Ethiopia, are at least 2.5 million years old (Semaw et al. 1997). This style of stone-tool-making is called the **Oldowan tradition**, after the Olduvai Gorge, where the first specimens were found.

Fossils of early *Homo* disappear around the beginning of the Pleistocene, about 1.8 mya, either by evolving into or being replaced by large-brained, robust hominids called *Homo erectus*. *H. erectus* seems to have coexisted in eastern Africa with the robust australopithecines until between 1.2 and 0.7 mya, when the australopithecines became extinct, and was the first hominid species to migrate out of Africa, apparently shortly after it first appeared. The cranial capacity of *H. erectus* averages around 1,000 cm<sup>3</sup>, a significant advance over early *Homo*, for whom cranial capacity ranged between 610 and 750 cm<sup>3</sup>. The postcranial skeleton of *H. erectus* is somewhat more robust than modern human skeletons but is otherwise like our own. In addition, *H. erectus* males are only 20–30 percent larger than females. What reduced sexual dimorphism may have meant for *H. erectus* is still an open question.

*Homo erectus* left a wider set of cultural remains than did the australopithecines. In terms of stone tools, *Homo erectus* is associated with the **Acheulean tradition** (named after the site in

France where the first such tools were found), in which the biface, or “hand ax,” is the most characteristic tool. Researchers have found African stone-tool assemblages between 1.5 million and 1.4 million years old that contain both Oldowan and larger biface tools, and typical Acheulean tools appear in African sites containing fossils of early *H. sapiens* over a million years later. The conclusion seems to be that more than one hominid species may have made and used tools that we assign to a single archaeological culture.

*H. erectus* also used fire, evidence for which comes from 500,000-year-old fossil hearths at Zhoukoudian, China (Klein 1999, 238). Burned cobbles and bones from a southern African site suggest that African *H. erectus* (*H. ergaster*) may have had intermittent control of fire a million years earlier than this (Tattersall 1998, 139–40). But many anthropologists are not convinced that *H. erectus* was primarily a big-game hunter dependent on meat.

*Homo erectus* flourished for over a million years. But about 500,000 years ago, the relatively rich and reasonably uniform fossil record associated with *Homo erectus* disappears, to be replaced by a far patchier and more varied fossil record. Some 30 sites in Africa, Europe, and Asia have yielded a collection of fossils sometimes called early or **archaic *Homo sapiens*** (Figure 13). Perhaps the most famous archaic human population is probably the **Neandertals**. The first Neandertals appeared about 130,000 years ago. The most recent Neandertal fossil from France is about 35,000 years old, and another from Spain may be even younger, at 27,000 years of age (Hublin et al. 1996). After this date, Neandertals disappear from the fossil record. The average Neandertal cranial capacity (1,520 cm<sup>3</sup>) is actually larger than that of modern human populations (1,400 cm<sup>3</sup>); however, the braincase is elongated, with a receding forehead, unlike the rounded crania and domed foreheads of modern humans. Neandertal postcranial skeletons are not significantly different from those of modern human beings, but their pelvis and femur are quite distinct (Aiello 1993, 82). This is why taxonomists continue to argue about whether Neandertals ought to be classified as a separate species (*H. neandertalensis*) or as a subspecies of *H. sapiens* (*H. sapiens neandertalensis*).

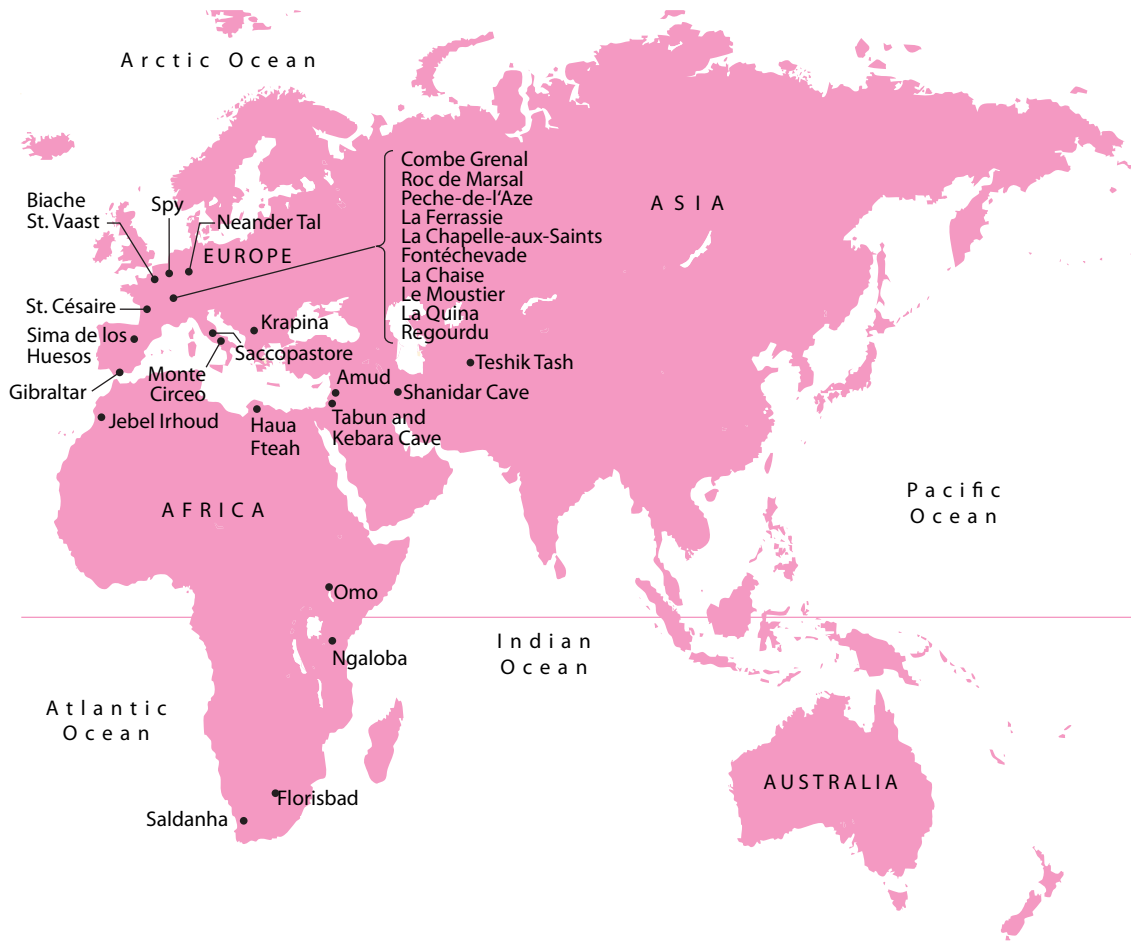


Figure 13. Major Neandertal sites, indicating the concentration of these hominids in Europe and southwestern Asia.

During the period when classic Neandertal populations appeared in Europe and western Asia, a different kind of hominid appeared to the south that possessed an anatomy like that of modern human beings. The postcranial skeleton of these **anatomically modern** people was much more lightly built than that of the Neandertals. New dating methods applied to remains from southwest Asia suggest that anatomically modern humans were living there between about 105,000 and 92,000 years ago, whereas Neandertal finds from the same region date from between about 105,000 and 60,000 years ago, and both groups were apparently using the same kinds of stone tools (Bar-Yosef 1989, 604; Mellars and Stringer 1989, 7). These dates suggest that modern human beings might have moved into southwestern Asia several thousand years before Neandertals. Because of the considerable morphological and cultural similarities shared by Neandertals and anatomically modern human beings, it seems reasonable to wonder whether they interbred. The matter remains unresolved.

These late archaic human populations in Europe, Africa, and southwestern Asia are associated with a new stone-tool tradition, called the **Mousterian tradition** in Europe and assigned to the **Middle Stone Age (MSA)** in Africa. Despite differing names and a distribution that covers more than one continent, most Mousterian/MSA stone-tool assemblages are surprisingly similar, consisting of flake tools that were retouched to make scrapers and points. Mousterian/MSA tools are more varied than the Lower Paleolithic/ESA tools that preceded them. Archaeologist Paul Mellars reviewed the evidence and concluded that this variation shows “a real element of cultural patterning” (1996, 355). In western Europe, Neandertals left traces of hearths (indicating a regular use of fire), although their sites were not centered around hearths, as is typical of the Upper Paleolithic. The evidence for stone walls is ambiguous, but there is good evidence for pits and even a post hole, especially at Combe-Grenal in France, where Bordes excavated (Mellars 1996, 295). Moreover, we know that Neandertals deliberately buried their dead, often with arms and legs folded against their upper bodies. All the data indicate that Neandertals lived hard lives in a difficult habitat, and many Neandertal bones show evidence of

injuries, disease, and premature aging. To survive as long as they did, the individuals to whom these bones belonged would have needed to rely on others to care for them (Chase 1989, 330). Klein observes, “The implicit group concern for the old and sick may have permitted Neandertals to live longer than any of their predecessors, and it is the most recognizably human, nonmaterial aspect of their behavior that can be directly inferred from the archaeological record” (1999, 476).

Middle Paleolithic/MSA tools disappear in Africa and southwestern Asia by 40,000 years ago at the latest and in Europe after about 35,000 years ago. What replaces them are far more elaborate artifacts that signal the beginning of the **Upper Paleolithic** in Europe and southwestern Asia and the **Late Stone Age (LSA)** in Africa. The stone-tool industries of the Upper Paleolithic/LSA are traditionally identified by the high proportion of blades they contain, when compared with the Middle Paleolithic/MSA assemblages that preceded them. A **blade** is defined as any flake that is at least twice as long as it is wide. However, a recent survey by Ofer Bar-Yosef and Steven L. Kuhn challenges this understanding of blades (1999). Bar-Yosef and Kuhn identify over a dozen sites in western Eurasia and Africa that contain Middle Paleolithic or MSA stone-tool assemblages rich in blades. They conclude from this that there are no grounds for assuming that the presence of blades indicates the presence of anatomically modern humans. At the same time, blade-based technologies spread rapidly in the Upper Paleolithic/LSA, and this is a new development. During the Upper Paleolithic, blades were also regularly attached to wood, bone, antler, or ivory in order to form composite tools such as bows and arrows. Evidence for regular hunting of large game is better in Upper Paleolithic sites than in sites from earlier periods, especially in Europe and Asia.

The most striking evidence for a modern human capacity for culture comes from the extraordinary explosion of cultural creativity we call Upper Paleolithic/LSA art, including cave paintings, clay sculptures, and beads, found throughout the Old World. The oldest examples may be rock paintings in Australia that were made 60,000 years ago. The richness and sophistication of Upper Paleolithic culture is documented in many other ways. Upper Paleolithic burials are

more elaborate than Mousterian/MSA burials, and some of them contain several bodies (Klein 1999, 550–551). Finally, although Mousterian/MSA tool types persist with little change for over 100,000 years, several different Upper Paleolithic/LSA tool traditions replace one another over the 20,000 years or so of the Upper Paleolithic/LSA. Many experts believe this burst of innovation was due to a reorganization of the brain that produced the modern capacity for culture. If it occurred, however, this anatomical change left no fossil evidence.

Some archaeologists believe that Neandertals may have borrowed elements of Upper Paleolithic technology from a culturally more advanced population of southwestern Asian immigrants. But what happened to them afterwards? There is no evidence that the replacement of Neandertals by modern people involved conquest and extermination, although this has been proposed from time to time. It is possible that Neandertals were at an adaptive disadvantage for reasons not well understood but perhaps related to reproduction rates. Neandertals may have retreated as modern people spread throughout Europe, decreasing in number until, around 30,000 years ago, they simply died out.

Physically and culturally modern human beings were the first hominids to occupy the coldest, harshest climates in Asia. They were in central Asia about 40,000 to 30,000 years ago (Fagan 1990, 195), in Siberia are between 35,000 and 20,000 years ago (Klein 1999, 558), and in Alaska between 15,000 and 12,000 years ago. Between 25,000 and 14,000 years ago, land passage south would have been blocked by continuous ice. The earliest known evidence of human presence in the Americas comes after 14,000 years ago (Fagan 1990, 205–10; Klein 1999, 560 ff.) The first anatomically modern human beings in North America, called Paleoindians, apparently were successful hunting peoples. In 1997, the “Clovis barrier” of 11,200 years was finally broken when a group of archaeologists and other scientists formally announced that the South American site of Monte Verde, in Chile, was 12,500 years old (Dillehay 2000; Suplee 1997). The Americas may have been colonized more than once (Dillehay 2000). Anatomically modern human beings first arrived in Australia between 60,000 and 40,000 years ago and spread throughout the Australian

interior by 25,000 to 20,000 years ago. Thus, by 12,000 years ago, modern human beings had spread to every continent except Antarctica. Experts differ, for example, on how to reconstruct the human family tree.

Paleoanthropologists and archaeologists have assembled many of the pieces of the human evolutionary puzzle, but many questions remain. We want to emphasize in conclusion that one of the signs of the strength of evolutionary theory and the story it tells about human evolution is precisely that it is ongoing. You may well be confused about the several places where we have had to indicate that there are varying interpretations of the fossil data or even that there is not enough fossil data to make interpretation possible, wishing that we would take a stand and let you know “the facts.” You may even think that these are weaknesses in evolutionary theory—that it should be able to tell us clearly and unambiguously the entire story of our past. But our reply is that these are not weaknesses or deficiencies; they are signs that the theory is alive. These places where we don’t know everything yet are the growth points of evolutionary theory, the places that draw the attention of newer generations of scientists to areas that require more research. This is science in the making.



## Glossary

**Acheulean tradition** A Lower Paleolithic stone-tool tradition associated with *Homo erectus* and characterized by stone bifaces, or “hand axes.”

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

**anatomically modern *Homo sapiens*** Hominid fossils assigned to the species *Homo sapiens* with anatomical features similar to those of living human populations: short, round skulls, small brow ridges and faces, prominent chins, and light skeletal build.

**archaic *Homo sapiens*** Hominids dating from 500,000 to 200,000 years ago that possessed morphological features found in both *Homo erectus* and *Homo sapiens*.

**bipedalism** Walking on two feet rather than four.

**blade** A stone tool that is at least twice as long as it is wide.

**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.

**cline** The gradual intergradation of genetic variation from population to population.

**common origin** Darwin’s claim that similar living species must all have had a common ancestor.

**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.

**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 (for example, flower color) exhibits sharp breaks from one member of the population to the next.

**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.

**evolution** The process of change over time.

**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.

**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 are individuals who lack such traits.

**gene** A particle carrying hereditary information from parent to offspring. (With the discovery of the structure of DNA, *gene* is no longer viewed as a particle, but now refers to that section of the DNA molecule carrying hereditary information for a particular phenotypic trait.)

**genetics** The scientific study of biological heredity.

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

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

**gracile australopithecines** Members of the species *Australopithecus africanus* that had small and lightly built faces.

**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 of difference.

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

***Homo erectus*** The species of large-brained, robust hominids that lived between 1.8 and 0.4 mya.

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

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

**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.

**macroevolution** A subfield of evolutionary studies that focuses on long-term evolutionary changes, especially the origins of new species and their diversification across space and over millions of years of geological time.

**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.

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

**microevolution** A subfield of evolutionary studies that devotes attention to short-term evolutionary changes that occur within a given species over relatively few generations of ecological time.

**Middle Stone Age (MSA)** The name given to the period of Mousterian stone-tool tradition in Africa; 200,000 to 40,000 years ago.

**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.

**mosaic evolution** A phenotypic pattern that shows how different traits of an organism, responding to different selection pressures, may evolve at different rates.

**Mousterian tradition** A Middle Paleolithic stone-tool tradition associated with Neandertals in Europe and southwestern Asia and with anatomically modern human beings in Africa.

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

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

**Neandertals** A subspecies of *Homo sapiens* that lived in Europe and western Asia from 130,000 to 35,000 years ago.

**niche construction** When an organism actively perturbs the environment or when it actively moves into a different environment.

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

**Oldowan tradition** A stone-tool tradition named after the Olduvai Gorge (Tanzania), where the first specimens of the oldest human tools (2 to 2.5 mya) were found.

**paleoanthropology** The search for fossilized remains of humanity's earliest ancestors.

**pangeneses** 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 an organism, different proportions of which get passed on to offspring via sperm or egg.

**phenotype** The observable, measurable overt characteristics of an organism.

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

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

**primatology** The study of nonhuman primates, the closest living relatives of human beings.

**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.

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

**robust australopithecines** Members of several australopithecine species, dating from about 2.5 to 0.7 mya, that had rugged jaws, flat faces, and enormous molars.

**species** A reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature.

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

**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.

**Upper Paleolithic/Late Stone Age (LSA)** The name given to the period of highly elaborate stone-tool traditions in Europe in which blades were important; 40,000 to 10,300 years ago.

**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 (are fitter) survive and reproduce more offspring, who inherit the traits that made their parents fit.