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*An Australopithecus africanus skull*

21

# Human Evolution and Human Behavior

A universal human desire is for knowledge of our ancestry, to learn about ourselves from learning about our ancestors. The study of human evolution promises to supply such knowledge in abundance. But have scientists actually revealed the “mysteries of mysteries” concerning our ancestry?

The answer is yes and no. Yes, we have discovered a great deal of information about human evolution, as a series of historical events. Despite long odds, intrepid fossil hunters have found numerous fossil bones that might have come from our ancestors, or their cousins (a picture of such fossilized bone is on this page). We will summarize this history of human evolution, but no—we do not have a complete accounting for our ancestry. Dark areas remain.

Yes, we know a great deal about human population genetics and human molecular genetics. Some of this recently collected information is staggering in its implications. But no, we are still very much in the dark as to why humans evolved. We know some of the story, but we don’t know the motives behind the plot. The *causes* of human evolution remain open to debate. We will explore this controversy.

Finally, there is the evolutionary interpretation of present-day human behavior. This question has been the source of sputtering controversy, with biologists of various ideologies calling each other names. But beyond the rhetoric, there are issues of great importance. ♦

# THE HOMINID PHYLOGENY

## 21.1 Humans evolved from Old World apes, which split from the rest of the primates about 20 million years ago

Humans are **primates**. The evolutionary tree of the primates is shown in Figure 21.1A. The primate evolutionary tree has two main branches: prosimian and anthropoid. **Prosimians** include tarsiers, lorises, lemurs, and pottos. These species have a variety of features in common with non-primate mammals, especially the insectivores. Prosimians cannot manipulate objects as well as other primates can, and they have relatively small brains. For these reasons, they are often thought to be similar to the earliest primates of 60 million years ago. However, it is also possible that contemporaneous species of prosimian have undergone some reverse evolution to adapt them to their way of life. We don't know.

Of more interest for human evolution is the **anthropoid** group, made up of monkeys, apes, and humans. There are three living anthropoid branches: New World monkeys, Old World monkeys, and the **hominoids** (apes and humans), this last group also being Old World in its distribution. The split between New World and Old World monkeys provides a wonderful example of biogeography. New World monkeys have prehensile tails, which function as a kind of fifth arm—very handy for animals that live in trees. Old World monkeys lack prehensile tails. This is almost certainly due to long-standing separate evolution in the two groups.

The hominoid branch of primate evolution is shown in more detail in Figure 21.1B (this figure corresponds to the rightmost branch in Figure 21.1A). Within the hominoids, the apes are represented by four genera: *Hylobates* (gibbons), *Pongo* (orangutans), *Gorilla* (gorillas), and *Pan* (chimpanzees). The apes are a very interesting group. None have tails, and they all have powerful arms and shoulders. The gibbons and orangutans are the most arboreal (tree living) in their behavioral ecology. Gibbons are not very good at walking, but they are extremely good at swinging from tree to tree. Gibbons exhibit a dramatic form of sexual dimorphism: Adult males and females have completely different colors in some species. There are 12 species of gibbon, also called the hylobatids. The other three ape genera have only one or two species. Gorillas and chimps share a very rare adaptation, **knuckle walking**. They use the knuckles of one hand to shuffle along the ground, leaving the other hand free to carry something. Humans are the upright hominoids; we walk on two legs only. All hominoids are apes. The **great apes** are the orangutans, gorillas, chimpanzees, and humans, together grouped as members of the taxonomic family Hominidae, the hominids. Of course, some people do not like to be called great apes.

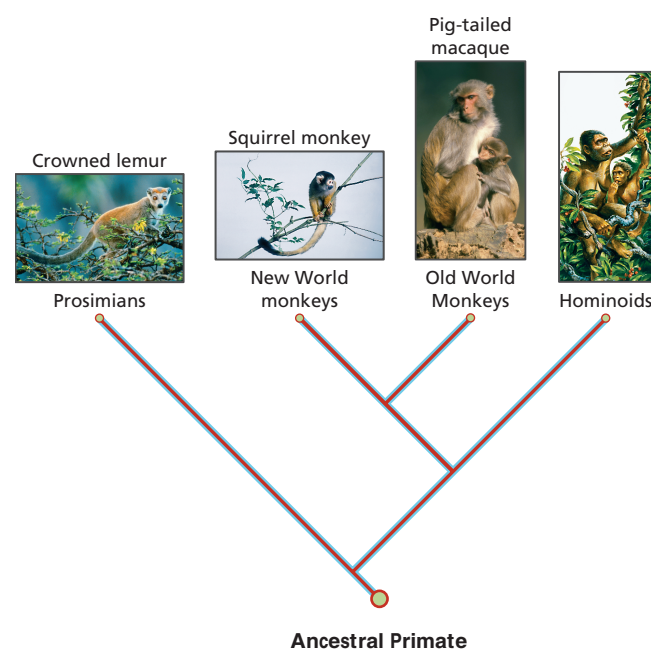


FIGURE 21.1A The Primate Evolutionary Tree

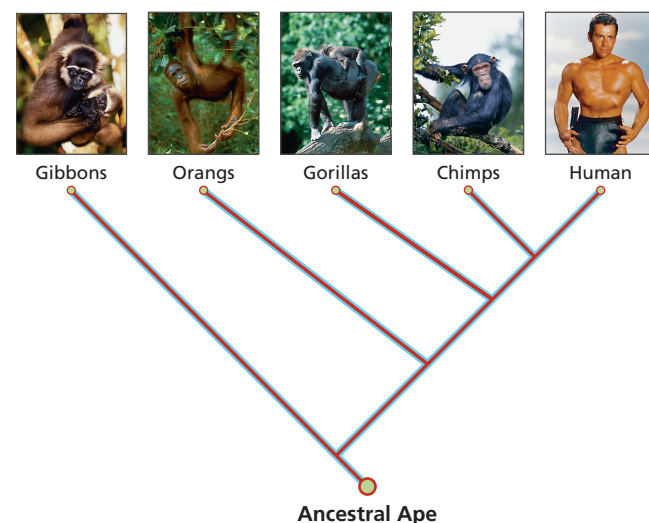


FIGURE 21.1B Evolution of the Apes





## 21.2 Chimpanzees are our closest living relatives, followed by gorillas

If you weren't human, you would be hard pressed to see the fundamental difference between gorillas, chimps, and humans. All share large brains, very dexterous hands, and excellent vision. All three are fairly large by the standards of most terrestrial animals—which are, indeed, insects. Perhaps the most obvious difference is that humans have relatively hairless bodies.

Molecular evidence suggests that upright hominids first evolved only 4–8 million years ago. However, fossil evidence indicates that our hominid ancestors were a distinct group as far back as 6–8 million years ago, suggesting that the earlier date for molecular divergence is likely the correct one.

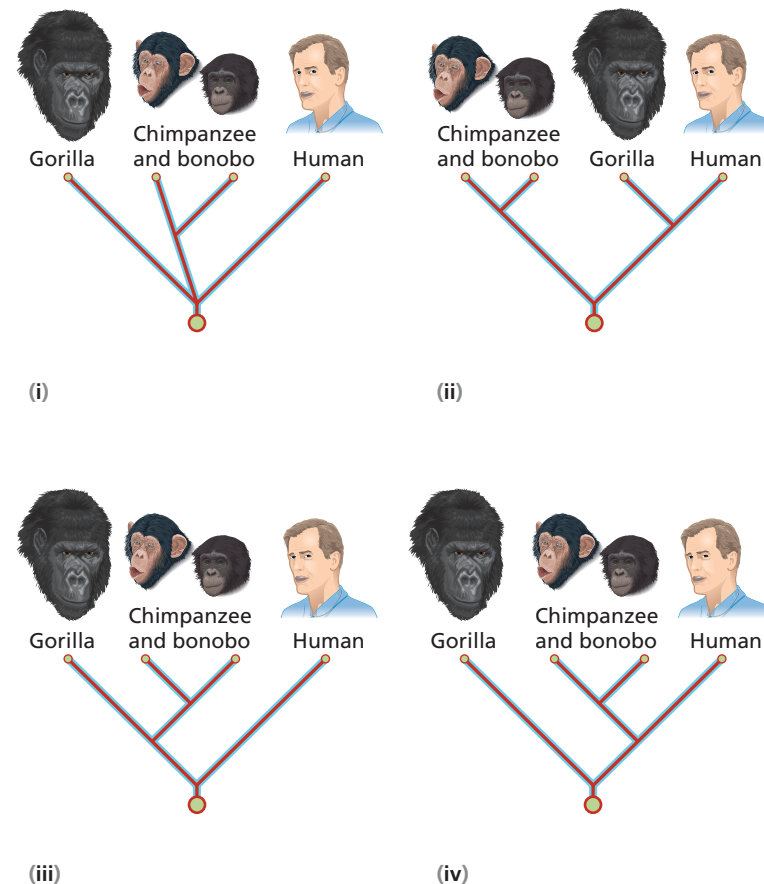
There has been some controversy as to the order of divergence among the three hominid groups. The alternative possible phylogenies are shown in Figure 21.2A. In the absence of data, there is no reason to prefer one over any of the others. One of the confusing features of this evolutionary radiation is that both chimps and gorillas are knuckle walkers. If knuckle walking evolved only once, then the gorilla and chimp species must have branched off from the pathway of hominid evolution before they evolved knuckle walking, by the principle of parsimony, described in Chapter 2. However, many morphological characters are shared by chimps

and humans, but not gorillas. These include skeletal structure as well as sexual maturation and anatomy.

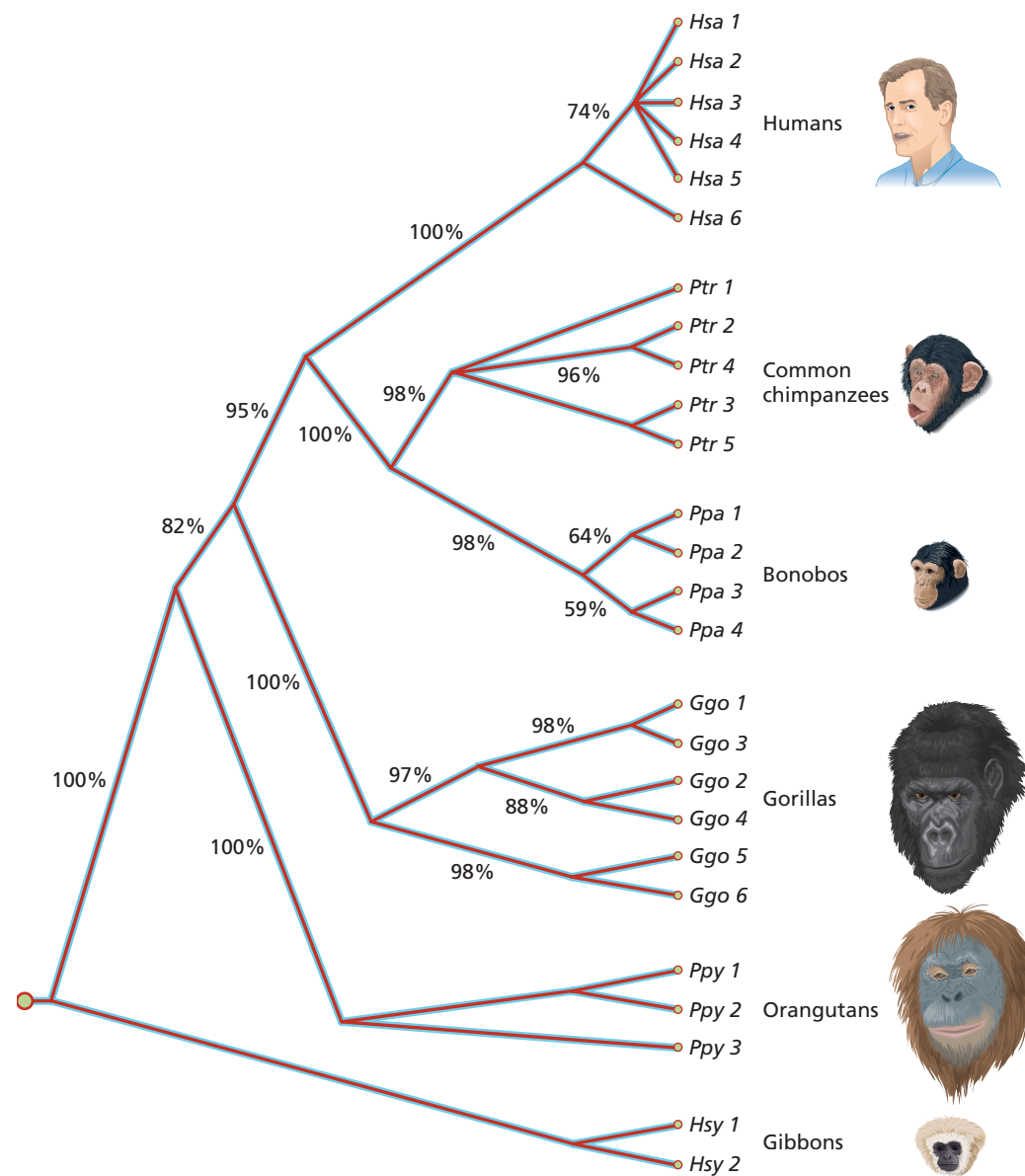
Molecular data have provided the most consistent results. One body of data is shown in Figure 21.2B. Molecular studies concur in finding humans and chimps more closely related to each other than either of them are to gorillas. This suggests that knuckle walking either evolved separately in gorillas and chimps or that it was lost in the ancestral hominids, having evolved in the ancestors of all three groups. In any case, the molecular results support the following evolutionary scenario. Great apes diverged from the other primates around 20 million years ago. Orangutans split from the other great apes about 15 million years ago. Gorillas split from the ancestors of hominids and chimps about 10 million years ago. Chimps and hominids diverged from each other about 8 million years ago.

While there is still some controversy, the consensus among evolutionary biologists is that human ancestors diverged most recently from a common ancestor shared with chimpanzee species, though we are quite closely related to the other great apes. The greater controversies involve human evolution itself, to which we now turn.

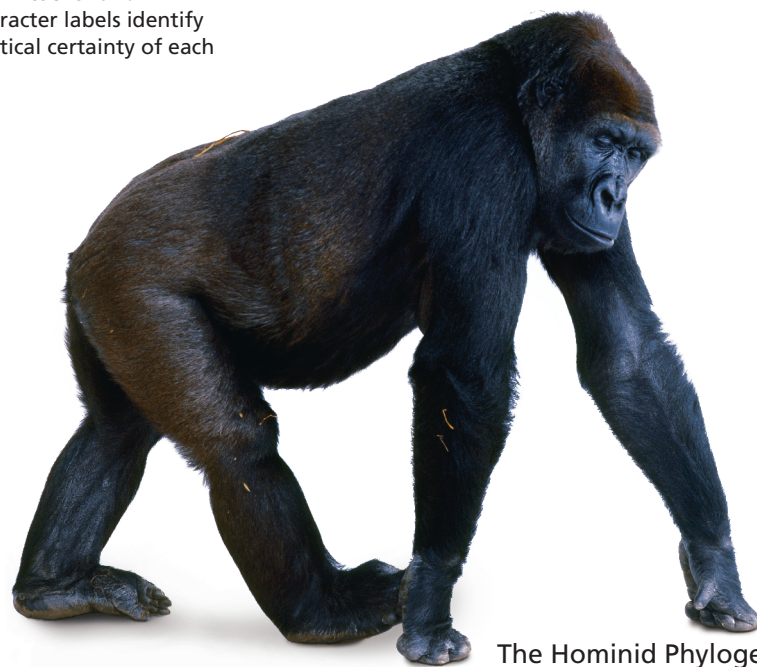
*There has been some controversy as to the order of divergence among the three hominid groups.*



**FIGURE 21.2A** Four Possible Human-Ape Phylogenies



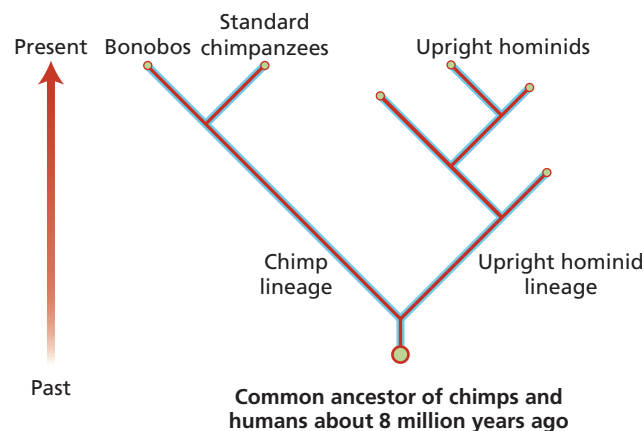
**FIGURE 21.2B Human-Ape Phylogeny Based on Mitochondrial Cytochrome Oxidase II Sequence** The three-character labels identify different alleles. The percentages give the statistical certainty of each branch of the evolutionary tree.



## 21.3 There were at least two major upright hominid lineages, which may have included multiple species each

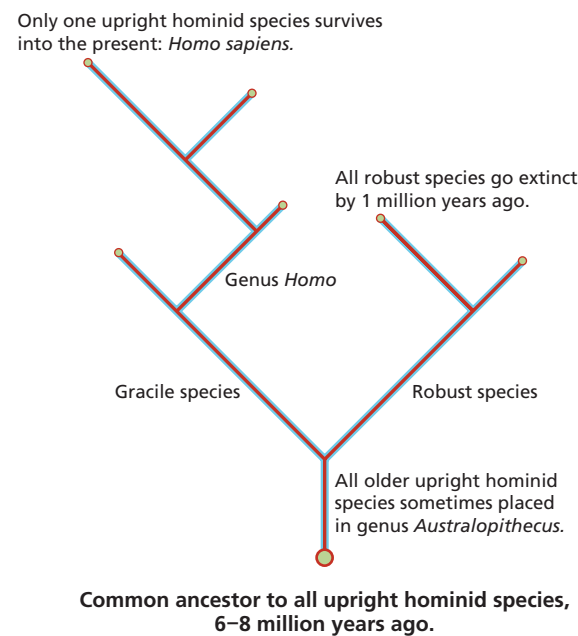
It is difficult to learn hominid phylogeny, because it seems to change every other week with the announcement of a new hominid species or genus, based on a fossil found in or near Ethiopia. But this difficulty is more apparent than real. Hominid paleontologists as a group are almost certainly discovering less than they usually claim. Three major themes can be reliably derived from hominid paleontology.

1. The recent evolution of the genus *Homo* is being documented in greater detail, including important contributions from molecular biology. Some of this work is featured in this chapter. We are learning about human evolution in considerable, satisfying detail.
2. The hominid fossil record is being pushed farther and farther back in time, approaching the point where humans share a common ancestor with the chimpanzees. We have not yet reached that point in time, but we are getting closer; recent fossil finds are dated at more than 4 million years ago. Once we have 7- or 8-million-year-old fossils, they should be intermediate between chimpanzee and upright hominid species, roughly speaking. This creeping-backward pattern is shown in Figure 21.3A.
3. For several million years, multiple upright hominid species coexisted in the continent of Africa, possibly with more species in Europe and Asia. This finding came as some surprise in hominid paleontology, because many paleontologists had assumed that human evolution followed a "ladder" pattern, with larger-brained species superseding smaller-brained species, only one species being dominant at any one time. We now know without any doubt that the ladder model for hominid evolution is not correct.



**FIGURE 21.3A** Back to the Missing Link? The rough outlines of human evolution relative to that of the two chimpanzee species.

The truth is that after the evolution of efficient bipedal locomotion, but some time before the evolution of modern humans, there were usually at least two distinct groups of upright hominids. This split began early in hominid evolution. How long it continued after that point is unclear. In any case, beginning about 3 million years ago, hominids were split into the **gracile** and **robust** lineages. (These lineages are sometimes put together in the *Australopithecus* genus, but sometimes they are placed in separate genera.)



(i) A crude phylogeny

These three species are thought to have coexisted 1.9 million years ago. From left to right are *Homo rudolfensis*, *Homo ergaster*, and *Paranthropus boisei*.



**Three hominid species from East Turkana, Kenya**  
(ii) Coexistence of multiple upright hominid species

**FIGURE 21.3B** Human Evolution Simplified



The gracile lineage appears to have contained species with relatively omnivorous diets, with smaller teeth and smaller jaws. The robust lineage had species with large molars and large jaws; they consumed a great deal of plant matter. Some paleontologists identify multiple coexisting gracile species, and other paleontologists find multiple robust species. There is little doubt that both types of lineage coexisted for

a million years or more. But after that, the robust lineage(s) died out. The genus *Homo* is generally thought to have been derived from the gracile lineage,—or a gracile lineage, if there was more than one. This general scenario is depicted in Figure 21.3B. Many details of our ancestry have generated controversy, but the existence of separate gracile and robust lineages is not disputed. ♦





## 21.4 Human evolution featured expansion of the braincase, reduction in the jaws, and changes to the rest of the skeleton

How have upright hominids changed over the past several million years? The highlights of hominid morphological evolution are easy to understand. Three main types of morphological change took place, affecting the brain, feeding, and locomotion.

The obvious change during the last few million years of human evolution is a dramatic expansion in the **braincase**. Several million years ago, the braincase volume of upright hominids was around 400–500 cubic centimeters (cc). In modern humans, braincase volume ranges from 1000 cc to 2000 cc. Various hominid braincases are shown in Figure 21.4A.

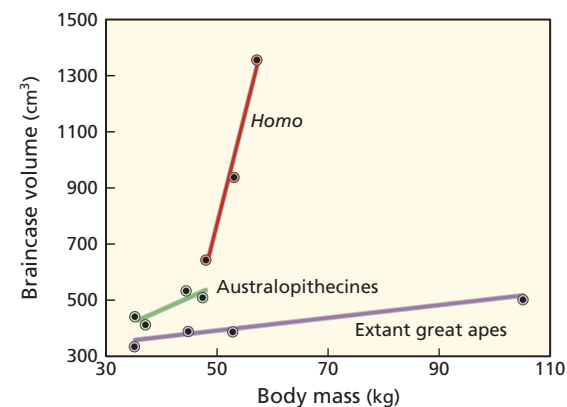
At first sight, this change seems like a spectacular evolutionary increase in brain size. But the estimated body sizes of early hominids are much smaller than those of modern humans. Early hominid females, like the famous Lucy from several million years ago—a fairly complete *Australopithecus afarensis* skeleton—might grow to 40–48 inches tall. Brain size generally scales with body size in the mammals. The huge brains of whales do not necessarily indicate greater intelligence, because larger brains are required to animate larger bodies.

This argument almost implies that humans are not intelligent at all. But there are two additional factors to bear in mind. The first is that all the australopithecine species, whatever their size or diet, had brain sizes in the same range as that of gorillas and chimps. A reasonable interpretation is that the australopithecines were about as smart as these ape species. The second point is that over the last few million years, the size of the braincases of our ancestors increased faster than body size. This increase is shown in Figure 21.4B. If hominid brain size increased only because hominid body size increased, then the *Homo* data should have followed the same pattern as the data for other hominids. But *Homo* data are off this scale. Our ancestors' brains increased in size substantially more than body size would have required. We did get smarter.

The second major change that took place in upright hominids during the last 4 million years is a considerable reduction in the size of the upper and lower jaws. Basically, we evolved flatter faces that look less apelike. This evolutionary

change may have occurred because of dietary changes, or it may have occurred because of morphological constraints imposed by the expanding braincase. Conceivably, sexual selection might have been involved. We don't know.

Most hominid paleontology focuses on the skull. But in the background of hominid evolution is considerable change in the skeleton below the skull. Present thinking is that all known upright hominids were efficient bipeds and probably held simple implements in their hands. But that does not mean that all hominids were equally adept at walking or using tools. Between 4 and 8 million years ago, a period mostly unknown due to lack of fossils, the earliest upright hominids began to evolve bipedal locomotion and manual dexterity. The last 4 million years of hominid evolution may have seen further improvements in these central hominid adaptations. Upright walking, not a large brain, is the quintessential adaptation of our ancestors. ♦



**FIGURE 21.4B** Brain Size versus Body Size in Hominids Note that the slope becomes much steeper in the genus *Homo*.



**FIGURE 21.4A** New Caption T/K

# HUMAN POPULATION GENETICS

## Molecular genetic tools are crucial to unraveling the patterns of human evolution 21.5

The fossil record has helped us to understand some aspects of human evolution. There are, however, limits to what we can infer from the fossil record. Fossils, after all, are the phenotypic expression of only part of the genome. Genes shape many characteristics that are unseen or not preserved in fossils. In addition, the fossil record may reflect the influence of the environment in ways that have sometimes been hard to determine. For example, the size and shape of some bones can be affected by the environment. These facts have had major consequences for the study of human evolution.

For instance, when the first **Neanderthal** fossil was discovered in Europe in 1857, not all scientists were willing to acknowledge that these bones were from a hominid quite different from modern humans. Figure 21.5A shows the contrast between a Neanderthal skull and that of a member of our species. The bones were inspected by Professor **August Mayer**. He was convinced that the remains came from a Cossack soldier who died after deserting his troops. The curvatures of the leg bones and pelvis were attributed to riding horses. According to Mayer, these minor deformities may have been accentuated by a bad case of rickets, a vitamin D deficiency that can affect bone growth. Professor Mayer also noticed a badly healed fracture of the left arm. This injury, he implied, caused constant pain and the resultant frowning ultimately created the skull's thick browridge.

Nevertheless, scientists eventually became convinced that Neanderthals were ancient hominids. There were too many anatomical differences between Neanderthals and all modern

humans (we will give one example shortly). Eventually, the definitive data supporting this view came from the extraction of small samples of DNA from the Neanderthal bones. For the first time, DNA from an extinct hominid was compared to DNA from contemporary human populations. We will review those results.

The recognition that Neanderthals were ancient hominids did not end the controversy surrounding them. It was still not clear if modern humans were direct descendants of Neanderthals, or whether Neanderthals were contemporaries of modern man and simply went extinct.

Neanderthals notwithstanding, it is usually not possible to obtain genetic samples from our ancestors to chart the pattern of evolution. However, several clever studies with modern human populations have been useful for making inferences about this problem, which we will also review.

One of the more controversial topics in human genetics has been the study of race. Well before we knew the principles of genetics, humankind was acutely aware of differences in the physical appearances of members of different populations. These physical differences were used by racist groups to formulate systems of classification for humans. These classifications were used in turn to persecute members of other so-called races. This history has made many uneasy with the concept of race. There is no doubt that some human populations have become differentiated for genetic characteristics that affect physical features as well as biochemical and physiological features. These genetic differences arose because of isolation and random genetic drift, sometimes even natural selection (e.g., sickle-cell anemia).

But it is more important to understand that there is extensive overlap in the genetic constitution of human populations. Even at loci that show differentiation between populations, we often see the same alleles in different populations—though their frequencies differ. As we shall see shortly, interesting patterns also come out of human genetic variation and can help us understand important aspects of genetic and cultural evolution. ♦

*Genes shape many characteristics that are unseen or not preserved in fossils.*



**FIGURE 21.5A** The first Cro-Magnon skull (right) found in the Dordogne region of western France in 1868, next to a Neanderthal skull (left).



## 21.6 Genetic evidence suggests that the Neanderthals belonged to a different species from the lineage that was ancestral to modern humans

There is little doubt that most of us could pick out a Neanderthal in a crowd. He would have a long trunk and powerful

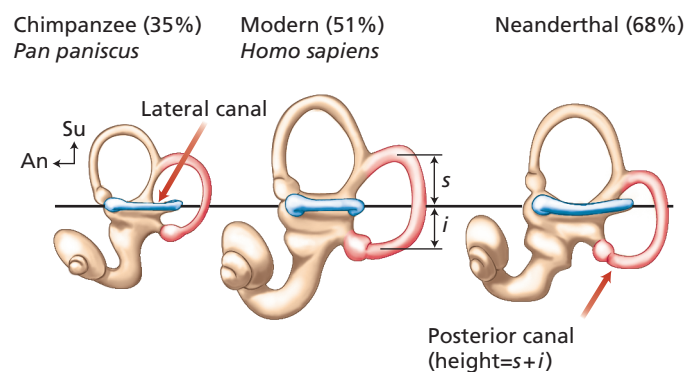
arms and shoulders. His head would be large relative to the rest of his body. He would have big eye sockets and a massive

brow. Fossils of Neanderthals have been found in a variety of locations throughout Europe and the Middle East. Some of these fossils have been estimated to be only 34,000 years old, although Neanderthals were probably in Europe for a total of 100,000 years. One theory is that modern humans are direct descendants of Neanderthals, or at least exchanged genes freely with their populations. Recent evidence has cast doubt on this idea and supports the idea that Neanderthals were a separate subspecies, or even a separate species, that was eventually displaced by modern humans.

The differences between modern humans and Neanderthals are pervasive. Consider the bones of the **ear canal**. In Figure 21.6A, we see that a structure called the posterior canal (red) is situated well below a second structure called the lateral canal (blue) relative to its position in modern humans and chimpanzees. The Neanderthal ear structure is quite different from that of hominids like *Australopithecus* and *Homo erectus*. In France, samples of Neanderthals showing this type of ear canal have been found that are only 34,000 years old. It is unlikely that Neanderthals were exchanging genes with our immediate ancestors at any significant rate yet could still be so different from modern humans 34,000 years ago.

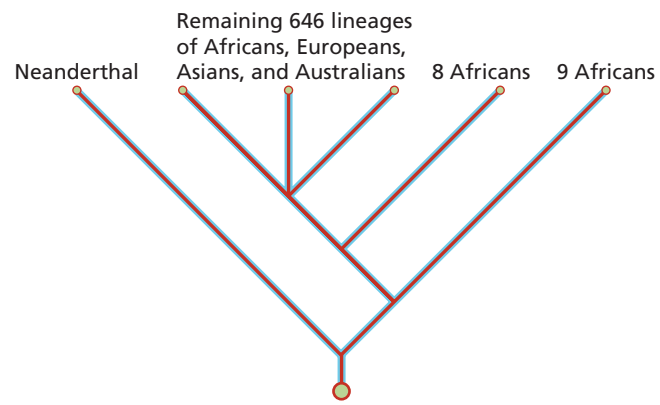
These conclusions have been strengthened by the recent analysis of **mitochondrial DNA** from Neanderthal fossils. The ability to get DNA from these samples is made possible by the relative stability of DNA as a molecule, the fact that single cells often contain many mitochondria and thus many copies of the same genome, and finally the polymerase chain reaction (PCR) that permits scientists to amplify DNA from very small samples. Recently (Figure 21.6B), mitochondrial samples from one Neanderthal and 663 humans have been compared. These data support the idea that Neanderthals separated from the human lineage well before modern populations of humans differentiated. Although these results are based on only a single gene region, they are consistent with the idea that Neanderthals were a distinct evolutionary unit, possibly even a species.

So what happened to Neanderthals? They probably coexisted in Europe with modern humans for 100,000 years. The numbers of both Neanderthals and modern humans could not have been very great during this period. However, during the period of coexistence,

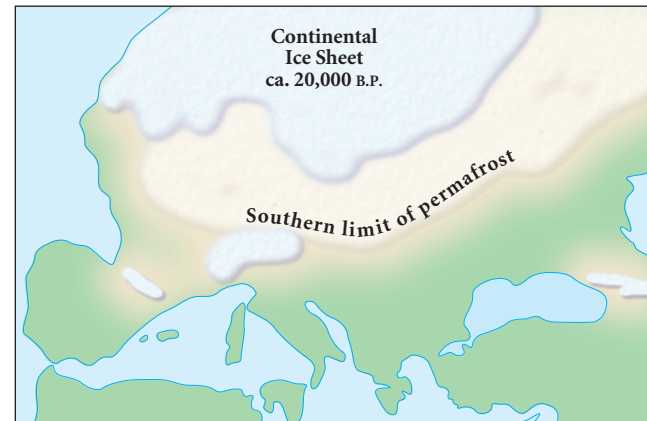


**FIGURE 21.6A** Neanderthal ears differed morphologically from the ears of modern humans. The Neanderthal posterior ear canal is lower than that of chimpanzees or humans.





**FIGURE 21.6B** Genetic evidence shows that Neanderthals were different from modern humans. Mitochondrial DNA sequences from Neanderthals, humans, and chimpanzees show that Neanderthals are on a different evolutionary branch from all human populations. Human and Neanderthal mitochondrial genes shared a common ancestor between 300,000 and 800,000 years ago.



**FIGURE 21.6C** The spread of ice and permafrost during the last glacier advance in Europe, 20,000 years ago. Such dramatic climate changes may have earlier restricted the territories available to humans and Neanderthals.

there were periods of climate change when glaciers spread south and almost certainly forced any hominids to move to the most southern regions of Europe (Figure 21.6C). These climatic changes may have made it more likely for modern

human populations and Neanderthals to interact, either competitively for resources or as combatants. These interactions could then have led to the decline and ultimate extinction of the Neanderthals. ❖





## 21.7 There are two main theories concerning the ancestry of modern human populations

In 1868, railroad workers in the Dordogne region of western France uncovered a burial ground for ancient humans now called **Cro-Magnon**. These humans had the features of modern humans but were about 30,000 years old. Since that time, many other hominid fossils have been found and modern dating techniques have helped establish their age. As a result it has become clear that numerous hominid species coexisted for periods of time (Figure 21.7A). Of course, our interpretation of the fossil record would have been much easier if there was no overlap in the appearance of these fossils and there was a gradual progression from apelike hominids to modern humans. But life is not always simple. To explain these features of the fossil record, two major hypotheses about human evolution have been proposed.

One theory, called the **multiregional theory**, suggests that hominid evolution began in Africa; but perhaps 1 million years ago hominids radiated out of Africa and into other regions of the world (Figure 21.7B). Evolution continued giving rise to changing features of hominid fossils found in

Europe, for instance, but there was appreciable genetic exchange among hominid populations then extant. This genetic exchange ensured that the features of modern humans would be fairly uniform around the world.

A second theory, called **out-of-Africa**, suggests there were several hominid lineages that had more or less independent histories from the one that gave rise to modern humans. The ancestors of modern humans left Africa more recently, perhaps as recently as 100,000 years ago. At that time they encountered other hominids, like Neanderthals, and these other lineages went extinct (see Figure 21.7B).

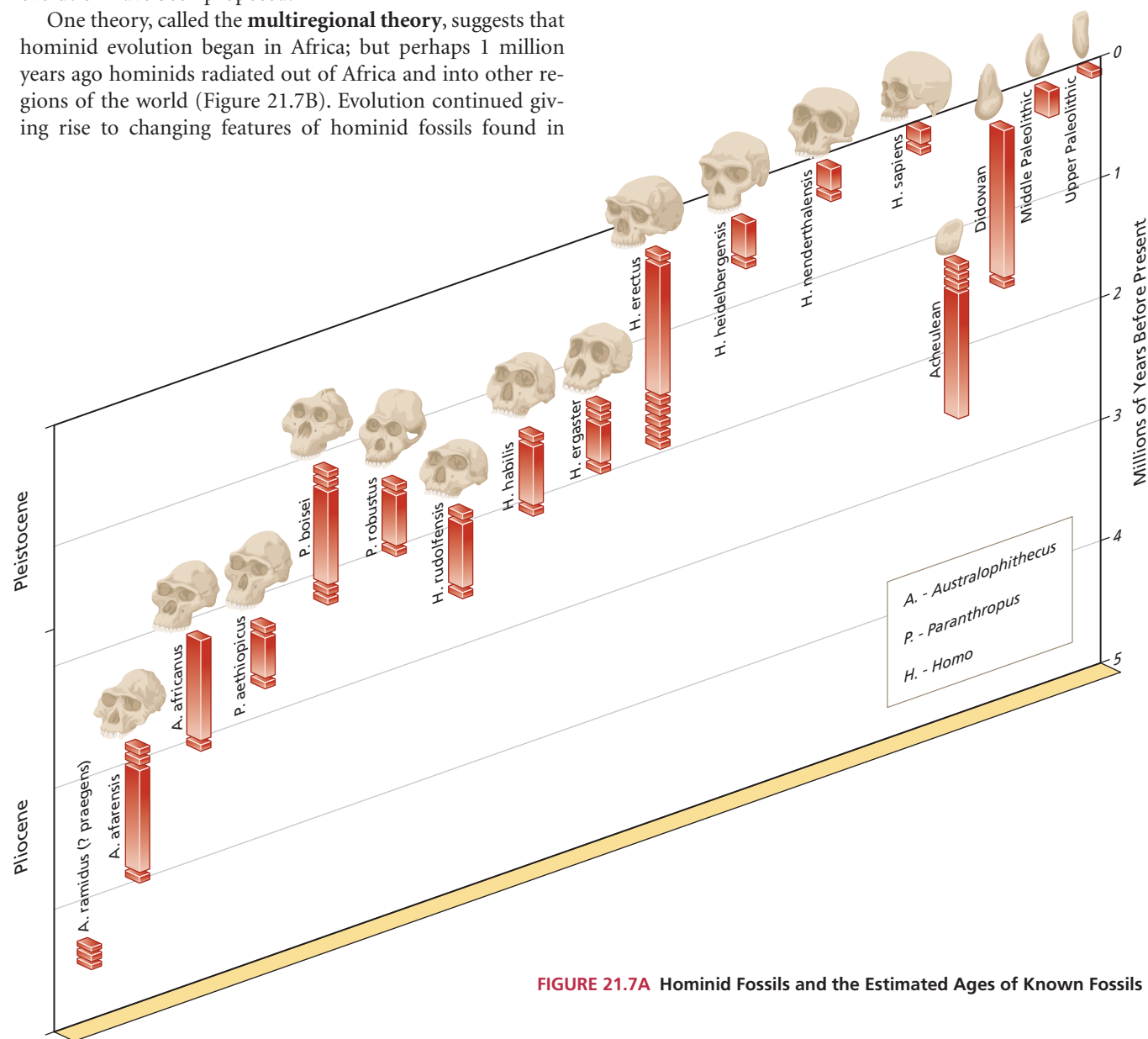
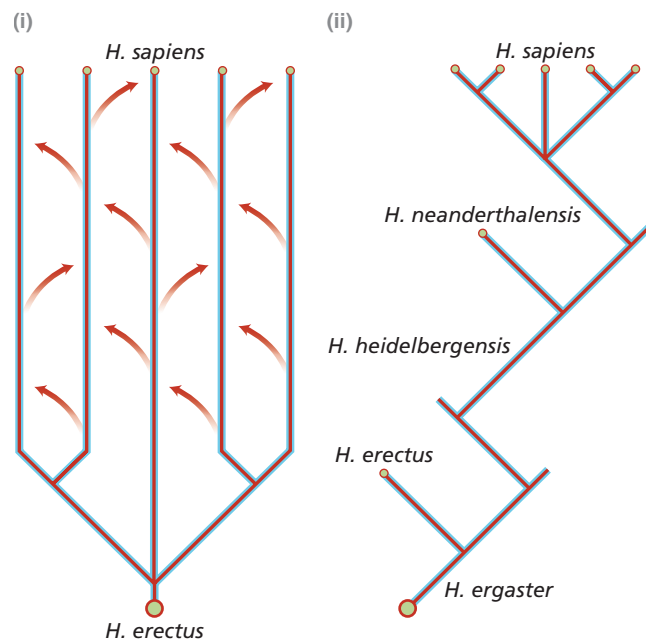


FIGURE 21.7A Hominid Fossils and the Estimated Ages of Known Fossils





**FIGURE 21.7B** The Multiregional Theory of Human Evolution (i) and the Out-of-Africa Theory (ii)

These hypotheses lead to some general predictions about current levels of genetic variation in human populations. If we can estimate the divergence time between African and non-African populations, we would expect that number to be about 1 million years for the multiregional model, but 200,000 years or less for the out-of-Africa model. Genetic diversity should be greatest in African populations under the out-of-Africa model because that theory assumes that all other populations were derived from them. Under the multiregional model, the long period of evolution with gene exchange would be more likely to give equal levels of genetic diversity between regions. A corollary of this idea is that non-African populations should have subsets of the alleles present in Africa under the out-of-Africa model. Again this follows from the derived nature of the other populations.

The strength of these predictions is not tremendous, because the two theories of human evolution depend on events that we don't know with any precision. For instance, under the multiregional theory, because we are certain that hominid evolution began in Africa, it might still be the case that the African population of *H. sapiens* will have greater genetic diversity. In any event, genetic data can be examined to test these ideas, as we will see in the next module. ♦

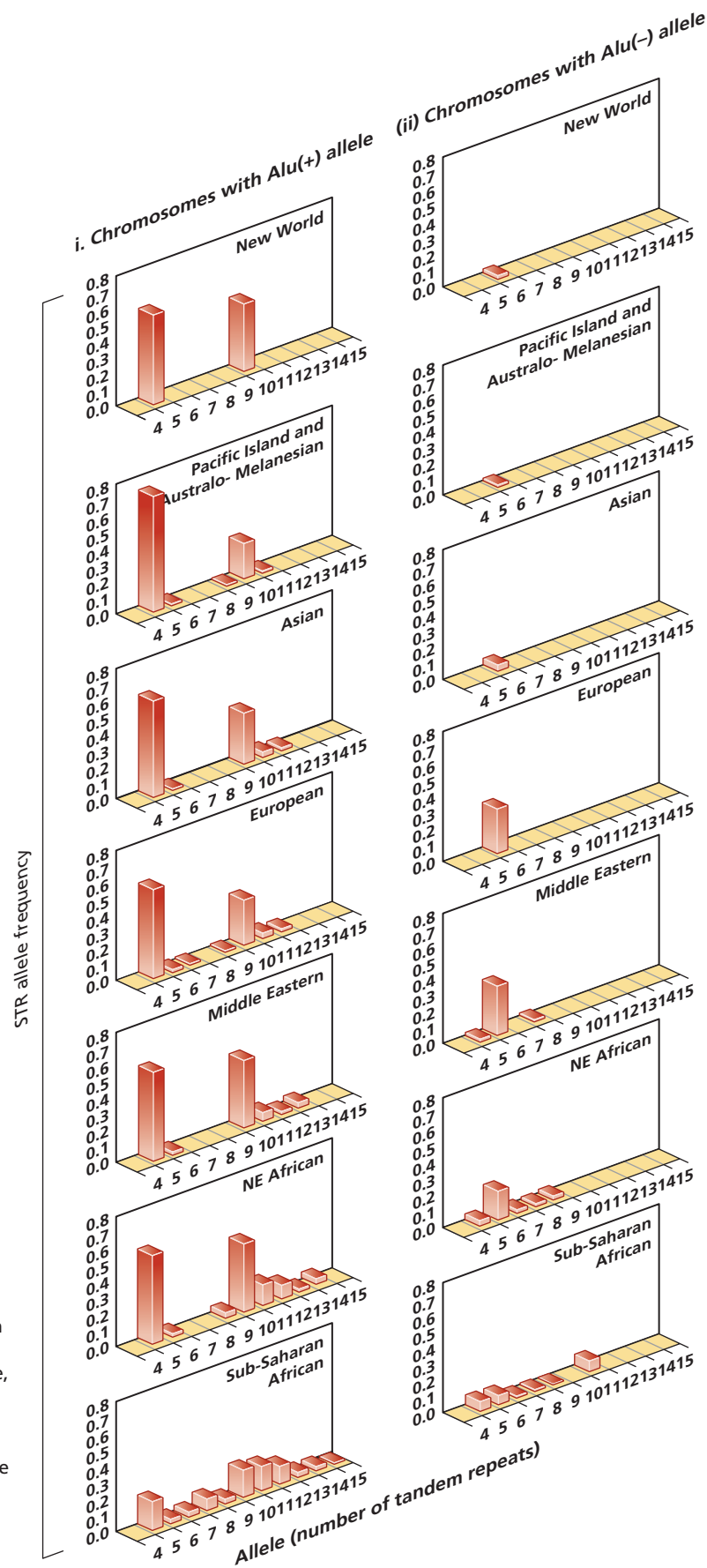


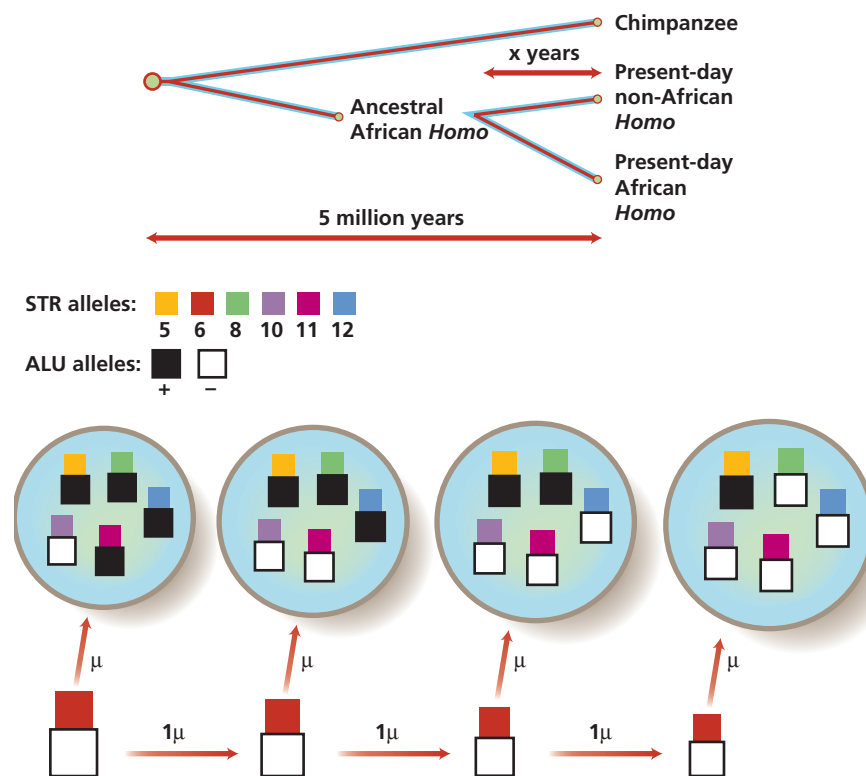
## 21.8 The latest data strongly support recent African proliferation of modern humans

A recent study of genetic variation in modern human populations looked at genetic variation in a large number of African populations and populations in Asia, Europe, South America, and Australia. They studied a gene on chromosome 12 that falls into a class of genes known as **short tandem repeats (STR)**. The genes have small sequences of DNA that are repeated a variable number of times, giving rise to alleles that are different sizes. The different alleles found are distinguished with integers indicating the number of repeated units (Figure 21.8A). There is also a second gene within 9,800 base pairs of the **STR** gene that has two alleles. The more common allele at the second locus is called *Alu*(+). The less common allele is called *Alu*(-) and represents a 256-base-pair deletion (the transposable element) of *Alu*. The *Alu*(-) allele is not found in the great apes, and is presumed to be a rare event that probably occurred 4–6 million years ago, after our lineage diverged from the apes.

If we focus on just the variation at the STR locus, we find two key observations that support the out-of-Africa hypothesis. The first is that the levels of genetic variation are greatest in the sub-Saharan African populations. The second observation is that the types of alleles found in the non-African populations tend to be small subsets of the alleles that are found in sub-Saharan African populations. These observations are consistent with the idea that the human populations that colonized the non-African continents were small founding groups that ultimately came from the African continent, and therefore contained only a portion of the total genetic variability present in Africa.

**FIGURE 21.8A Genetic Variation in Modern Human Populations** Sarah Tishkoff and colleagues studied genetic variation for short tandem repeat (STR) alleles (numbered 4–15) found at a particular locus on human chromosome 12. Part (i) shows frequencies of alleles that are found on chromosomes with the *Alu*(+) allele, a very close linked locus. Part (ii) shows similar information for alleles on chromosomes with the alternative *Alu* allele, *Alu*(-). Two features of these data support the out-of-Africa theory: (1) There is more variation in the sub-Saharan African populations than in the others. (2) The variation found in the other populations appears to be subsets of genetic variation found in the sub-Saharan African populations.





**FIGURE 21.8B** Estimating the Time Since Leaving Africa Every generation some fraction,  $\mu$ , of the gametes with the 6/- genotype (the gametes with the red box and the hollow box together) will mutate to one of the other STR alleles. This rate can be estimated from the accumulation of other gamete types in the present-day African populations under the assumption of 5 million years elapsing since the origin of the first 6/- gamete. Once the mutation rate has been estimated it can be used to estimate the time since non-African populations left Africa,  $x$ . This time estimate will depend on the frequency of non-6 STR alleles found in combination with *Alu*(-).

An approximate date for the departure of the hominid populations that left Africa has been estimated (Figure 21.8B). The first *Alu*(-) mutant is assumed to have occurred on a chromosome with the STR at allele 6. After the *Alu*(-) mutation event, perhaps 5 million years ago, unequal crossing over generated new STR alleles, like 5/- and 11/- (see Chapter 5). The *Alu*(-) allele is unlikely to mutate back to the *Alu*(+) allele, and recombination between the two loci will contribute little to the new gametes observed. The frequency of *Alu*(-) alleles that are found with STR alleles other than 6 in the sub-Saharan populations can be used to estimate the STR locus mutation rate, assuming the first *Alu*(-) allele appeared 5 million years ago (Figure 21.8B).

We next assume that the migrants from Africa to other regions of the world always brought the *Alu*(-) allele on a chromosome with the 6 allele at the STR locus. Then the frequency of *Alu*(-) alleles associated with non-6 alleles in these non-African regions allows us to estimate how long the non-African populations have been isolated from Africa. This procedure produces an estimate of time since leaving Africa of 102,000 years. These estimates are subject to substantial statistical error, and the true value may be as high as 700,000 years ago. Even so, this higher time estimate is also consistent with a recent movement of *Homo* populations from Africa to the other continents. ♦

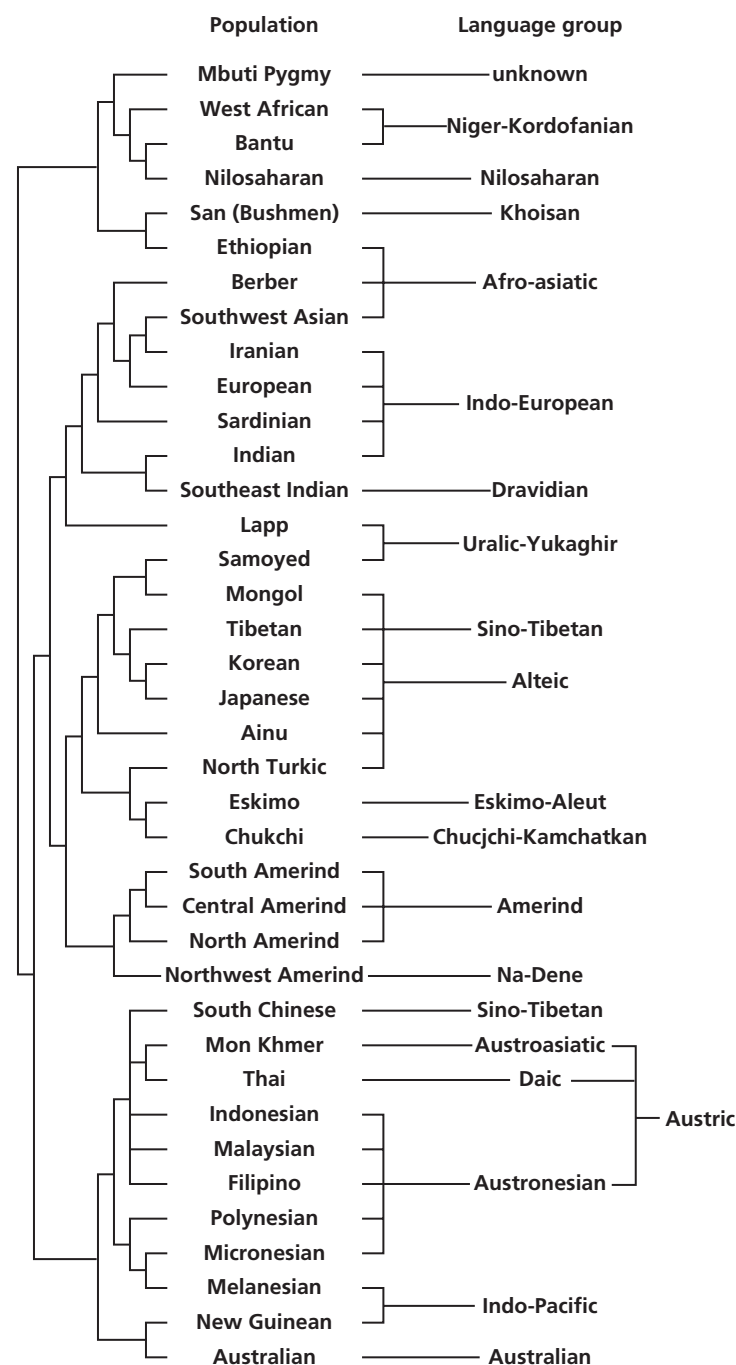




## 21.9 Modern human populations seem to be a patchwork of local differentiation, with little racial differentiation

It should come as no surprise that the rules of evolution and population genetics apply to humans in the same way they do to other organisms. Thus drift, mutation, natural selection, and inbreeding have historically played an important role in determining human population genetic structure, just as they do in other species. Many of the genetic differences among

people are completely invisible to us. Thus, with respect to the *Alu* polymorphisms discussed in the previous pages, most of us have no idea whether we or our neighbors are *Alu*(+) or *Alu*(-) for that STR region. However, we probably can describe the phenotypic effects of the genes that affect our hair and skin color.



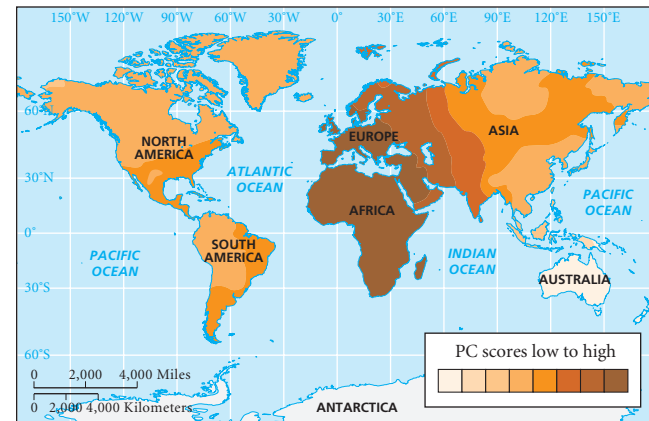
**FIGURE 21.9A The Concordance between Genes and Language** A genetic tree based on 120 loci corresponds fairly well to linguistic diversity. This suggests that the same factors that lead to genetic differentiation can also lead to linguistic differentiation.

Genetic differences between human populations have arisen as a consequence of many factors, but isolation and lack of gene exchange with other populations are probably the most important factors. Using genetic data from many loci, we can develop genetic trees for the human population (Figure 21.9A). These tend to group populations that are either geographically close or have historically had gene flow between them.

The boundaries between human populations are not absolute. After all, we are all members of the same species, and the genetic data used to develop the trees in Figure 21.9A show there are always loci where different populations share some alleles. Thus in human population genetics there is little interest in developing categories or races into which people can be placed and more interest in studying patterns of genetic variation. For instance, there is a close association between the genetic trees of populations and the relationships between language groups (Figure 21.9A). The most reasonable explanation for this association is that when human populations become isolated, this isolation can lead to both genetic differentiation and language evolution.

Occasionally these patterns break down. For instance, when populations or nations conquer territory, the resident languages may be virtually replaced by the language of the conquering population, except for isolated redoubts. This explains relic languages in marginal areas, such as the Basque language in Europe or the Dravidian languages in India. In other instances, the genes of a population may be replaced by exchange with a group that does not reflect the origins of the language of interest. This type of gene replacement can happen quite quickly. For instance, U.S. blacks in northern states obtained 25–30 percent of their genes from European sources. This gene flow has occurred over just 300 years since Africans were brought to the United States as slaves.

We can also find genetic patterns over geographic regions that parallel the movement of people out of Africa



**FIGURE 21.9B Genetic Map Showing Regions of Similarity** For this map, a genetic distance measure was used to distill genetic information from 120 genes into a single number (the PC score) that represents the genetic differentiation of indigenous populations. The samples from the indigenous populations of Africa all have a similar value of this number. As we move eastward into Asia, the value of this number changes gradually, indicating greater homogeneity. These values are consistent with movement of human populations out of Africa.

(Figure 21.9B). In another study of human population genetics, 120 polymorphic genes were used to characterize the genetic variation in the worldwide human population. As Figure 21.9B shows, populations in Africa are similar to each other, as we would expect. The non-African populations most similar to those from Africa are the populations just to the north and east of Africa—the European and Middle Eastern. This pattern continues across Asia and into North America. The populations least similar to those of Africa are found in Australian aboriginal populations. The out-of-Africa model is supported well by these results. ♦

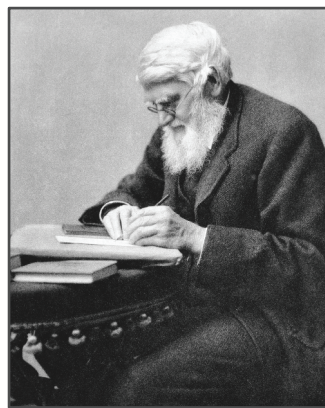




# WHY DID EVOLUTION PRODUCE HUMANS?

## 21.10 The puzzle of our evolution has generated both intellectual aversion and gratuitous speculation

Why did humans evolve? This is different from asking *how* humans evolved. The earlier modules of this chapter tell a fairly detailed story concerning the anatomical and molecular evolution of humans and our immediate ancestors. As that story makes clear, there is no lack of evidence concerning how humans evolved. Compared to the evolution of most forms of life, the human evolutionary record, both fossil and molecular, is quite good.



**FIGURE 21.10A** Alfred Russel Wallace (1823–1913)

But the “why question” remains a source of trouble. Even **Alfred Russell Wallace** (Figure 21.10A), the codiscoverer of evolution by natural selection, felt that human evolution required the intervention of spiritual forces, above and beyond mere natural selection.

Problems like Wallace’s spiritualist views have tended to make evolutionary biologists somewhat averse to treating the question of why evolution produced humans. As a result, anthropologists,

zoologists, and popular writers have tended to fill the void left by this aversion, and their speculations have been the most frequent statements addressing selection on humans.

One popular explanation of human evolution is based on the assumption that our evolution is a kind of straight line from chimpanzees to the **hunter-gatherer** societies of modern Africa to the suburbs of Chicago. Sometimes the favored explanation is that we became smart because of selection to be hunters. The problem with this sort of explanation is that a lot of other species are carnivores without being particularly intelligent. A variant of this hypothesis is that we had to become smart in order to hunt using tools. A problem with this theory is that ants use fairly complex technologies to find, devour, store, or otherwise exploit other species. Yet ants are not intelligent. Still other writers think that bad weather was important in making humans evolve, as if there aren’t millions of other species on the planet that suffer through bad weather.

The problem with these stories is that they have a storybook quality, like Kipling’s *Just-So Stories*, in which plausible explanations of peculiar things are given to children who have no way to check these explanations, test them, or even doubt them. Human evolution took place over the last few million

years, and we were not there to observe it. This lets uninhibited writers, with few fears of contradiction, create stories about the African **savanna** 2 million years ago. But these stories have little scientific value because they are based on specific evolutionary scenarios that we cannot test directly. This problem arises because we can’t test *any* very specific scenario for the evolution of any species millions of years ago. We don’t have time machines, contrary to the stories of **H. G. Wells**.

Our inability to describe exactly why we evolved over the last 2 million years does not preclude useful scientific analysis of this question. Physicists commonly treat such difficult problems as the origin and early development of the universe, even though they are unlikely ever to go back in time to find out exactly what happened. Instead, they develop more general theories for the history of the universe, asking such basic questions as whether the universe has been expanding, whether there was a “big bang” at its origin, and so on. By reducing the specificity of their theories, physicists have been able to propose, examine, and test theories for the development of the universe.

In the same way, although evolutionary biologists will never know exactly what our ancestors were doing 2 million years ago, we can address very broad questions about human evolution. Questions of this kind approach a level at which human evolution can be discussed scientifically. That is, theories about human evolution that are general enough to be tested *without* a time machine are worth considering. The problem is, what type of theories are these? What do robust theories of human evolution look like?

At least two general questions about human evolution can be formulated to the point where we have some possibility of considering them scientifically. The first is whether or not the evolution of distinctive human attributes, such as a large brain, was driven by selection, or instead occurred primarily because of genetic drift. This is a central question for any discussion of human evolution. If selection did not drive our evolution, then we do not need to invent selection scenarios to solve the problem. We will address this question next.

The second general question about human evolution’s distinctive features is as follows: If it *was* driven by selection, what kind of selection forced our evolution? And the *kind of selection* cannot be as specific as bad weather, a particular predator, or a new type of plant food. Kinds of selection worth comparing must instead be broad in nature, with significant consequences for data that we might some day obtain. These hypotheses are available, and we have at least some empirical information with which to test them, as we will see. ♦

## Humans must have evolved by intense directional selection for abilities derived from increased brain sizes **21.11**

Evolutionary change does not require natural selection. As we saw in Chapter 3, evolution can change gene frequencies by processes like genetic drift alone. Therefore, the many evolutionary changes in humans relative to the other great apes do not prove, by themselves, that selection drove human evolution.

But other aspects of human biology suggest that intense selection shaped the evolution of our ancestors. What must be understood is that when considerable fitness costs are associated with the evolution of a feature, then genetic drift is unlikely to be a valid explanation of that feature's evolution. Under these conditions, stabilizing selection will prevent directional change. Therefore, the role of selection in human evolution depends on whether there is evidence of purifying or stabilizing selection against change in the characters involved.

And there certainly is. One of the best-known examples of stabilizing selection is on the birth weight of the human newborn (See Module 4.11.). Babies with very large or very small weights are selected against. One of the biggest determinants of weight in the human newborn is the size of its brain. And brain size is by far the biggest problem in human birth. Once the head is through the birth canal, the rest is comparatively easy. Both child and mother are subject to relatively high levels of mortality in human childbirth. And the newborn human is a highly dependent, immobile, vulnerable mammal. Furthermore, it remains that way for more than a year, during which it is not even able to walk. One interpretation of the human pattern of child development is that the human infant is really

a fetus for its first 12–18 months. The problem is probably the difficulty of giving birth to a 1-year-old human. Human pelvises are simply not big enough.

Overall, it seems as if the processes of human gestation, birth, and early infancy have been radically modified to accommodate the development of the large human brain. Even the female pelvis has been evolutionarily remodeled to accommodate the human infant, rendering it less efficient for running. The many costs associated with the expanded

brain of the human infant are diagrammed in Figure 21.11A.

Yet other costs are associated with the human brain. At rest, the brain generates a large fraction of the metabolism of the human body. Programming the human brain, or “learning,” has considerable costs in missed opportunities for feeding or reproduction, as every bored high school student knows. Yet there is little point in having a powerful brain if it is not educated. Complex human languages are in large measure tools for instruction of the young, and massive amounts of neural processing underlie language.

Note that there are alternative lifestyles among other species. Even fairly sophisticated animals, like the other great apes, get by on very simple utterances and social signals, and their knowledge of biology and engineering is rarely impressive. The bonobos (*Pan paniscus*), for example, make do with a simple lifestyle, centered around an omnivorous diet and a very active sex life. Our failure to pursue such a way of life must have compensating selective advantages. In other words, increased brain size must have conferred abilities that provided advantages that outweighed its costs. ♦

### *One of the best-known examples of stabilizing selection is on the birth weight of the human newborn.*

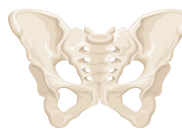
(i) Prolonged gestational building of brain



(ii) Metabolic costs of brain construction



(iii) Difficulty with birth



(iv) Cost of programming brain



(v) Prolonged period of dependency



**FIGURE 21.11A** The Costs of Being Smart



## 21.12 The hypothesis that we were selected only to use technology is undermined by the material simplicity of some cultures relative to their social complexity

So what are the advantages of a larger brain? The traditional proposal is the **tool-use theory** of human evolution—that natural selection favored human intelligence, and thus a large brain, because humans used that intelligence to develop useful technology, tool use first among these technologies. This is an old theory. One of its first proponents was **Friedrich Engels**, Karl Marx's collaborator, who wrote about it in the nineteenth century. This concept has been epitomized by the phrase, "man the tool-user." This phrase implies that we evolved to use tools, and that tool use is at the center of human nature.

In support of this tool-use theory is the vast technology associated with modern human civilizations. No other animal comes remotely close to this technological level. It takes significant intelligence to create, sustain, and use modern technologies. Yet this point of reference reveals a weakness in the

argument. For almost all of human evolution, including the entire period during which the human brain evolved its present size—which was the last 2 million years, *excluding* the last 200,000 years—we had nothing like modern technology. We didn't even have extensive agriculture. The fact is that we evolved our intelligence before we developed modern technologies. Hominid life was quite simple two million years ago, when we started to evolve larger brains (Figure 21.12A).

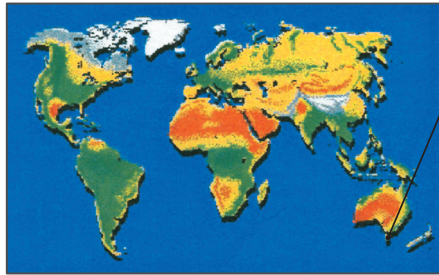
A further complication is that some recent human societies have had minimal levels of technology. Many hunter-gatherer societies that have been studied in the last two centuries use extremely simple tools. Furthermore, historically recent human populations show wide differences in technology, yet there are no clear differences in intelligence. If technology were the driving force of selection that remodeled the human development pattern, the female pelvis, and human language,



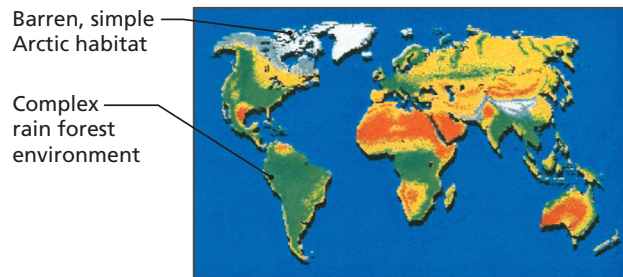
**FIGURE 21.12A** Artist's conception of *Paranthropus robustus* in South Africa 1.7 million years ago.



(i) Very low levels of tool use in some humans



- (ii) Homogeneity among human populations for average intelligence, despite wide variation in opportunities for tool use with environment



Complex —  
rain forest  
environment

why wouldn't large differences in the use of technology over tens of thousands of years be associated with systematic, qualitative differences in intelligence? Figure 21.12B summarizes the main weaknesses in the tool-use theory.

Adding to these anomalies is the universality of complex human social behavior. Human societies generally invent elaborate social systems that give family and social status. Humans create complex rituals for coming of age, marriage, childbirth, and death. Humans spend vast amounts of time on gossip and rumor that is technologically unproductive. The individuals who spend their time making tools are usually a minority in human societies. Large numbers of people do not watch television shows about tractors. They watch television shows about love affairs, families, and heroes. Is this the behavioral pattern to be expected of a species that is supposed to have evolved to make and use tools?

Probably not. Instead, anthropologists have been interested in very different models for the evolutionary enlargement of the human brain—models based on social behavior, as we will see in the next module.

**FIGURE 21.12B** Problems with the Tool-Use Theory of Human Evolution



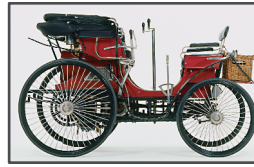
## 21.13 The hypothesis that we were selected only for social calculation is undermined by our facility with complex material technologies

The main alternative theory for human evolution is the **social intelligence theory**: that we evolved “Machiavelian” intelligence in order to obtain relative social advantage. The idea is that being a little bit smarter gave some hominids an advantage in social competitions for mates or access to resources. This is a **mental arms race** because it is an individual’s relative standing that matters. In some versions of this theory, it is supposed that such selection for social intelligence is virtually universal and relentless. Theories of this kind, at first sight, would seem to have all the features required to explain the evolution of human intelligence.

In conformity with this theory, humans spend a great deal of time and ingenuity outwitting each other, rather than doing real work. All human societies are notable for their maneuvering and back-stabbing. And humans are very interested in such behavior. Today, lawyers, politicians, and criminals are more popular subjects of fiction and drama, compared to scientists, engineers, and mathematicians. Social intelligence theories of human evolution have been popular among academics for the last 25 years. However, it might be noted that Charles Darwin proposed a version of this theory in his book, *The Descent of Man*, more than a century ago.

But this theory faces major problems too. The first problem is that, while humans are not the hardwired engineers that the technology selection model suggests, they aren’t completely hopeless where tools are concerned. Figure 21.13A summarizes aspects of this problem. Humans of all cultures invent new technologies and adopt them when they have been invented in other cultures. Humans do not seem widely deficient in the ability to handle technology, unlike a species that has evolved intelligence only for social purposes. Furthermore, humans seem to delight in inventing new forms of technology, even technologies whose utilitarian value is not immediately obvious. Scientists and engineers seem to be on an endless quest to invent, from electron microscopes to rockets. Humans have had an enduring relationship with technology. Stone tools have been found in fossil strata more than 2 million years old. It is hard to believe that the evolution of human intelligence did not involve selection for the capacity to use tools efficiently.

The second major problem with the social intelligence theory is that this theory is too strong. Why shouldn’t every social animal have higher intelligence? Birds, for example, often live in large social groups called colonies. These colonies are characterized by squabbles over nesting space, food, and sex. Birds have social interactions that achieve considerable complexity, with behavior patterns that resemble such human practices as ownership, marriage, adultery, and so on (see Figure 21.13B). Why haven’t large brain sizes evolved in birds,



(i) Humans have the capacity to develop elaborate technologies as the last 200 years have shown.



(ii) Once a technology is developed in one human culture, there appear to be few intellectual barriers to its adoption by other human cultures.



(iii) Humans even develop novel technologies of little immediate practical value, as illustrated by the electron microscope, shown at the right; we almost seem to have a technological drive.

**FIGURE 21.13A Problems with the Social Intelligence Theory of Human Evolution**

thanks to selection for increased social intelligence? Indeed, some proponents of the social intelligence theory apply it to the social evolution of various primate species. Yet none of these non-human primates has evolved a level of intelligence like that of humans. If selection for social intelligence is so common, why do humans uniquely possess complex language and other features of intelligence?

Selection for social intelligence cannot explain why humans, and only humans, have evolved such powerful intelligence. As with the tool-use theory, the social intelligence theory appears to be lacking as an explanation of the unprecedented phenomenon of human intelligence. ♦



There are many other highly social species, such as birds that live in colonies. Wouldn’t they benefit from social intelligence too?

**FIGURE 21.13B Another Problem for the Social Intelligence Theory of Human Evolution**



## Human evolution probably involved a combination of selection pressures favoring both technology and social behavior 21.14

Human intelligence is probably one of those characters that has been subjected to a combination of selection pressures. We exhibit high levels of both social and technological intelligence. It makes sense to suppose that the evolution of humans involved selection for both of these types of intelligence.

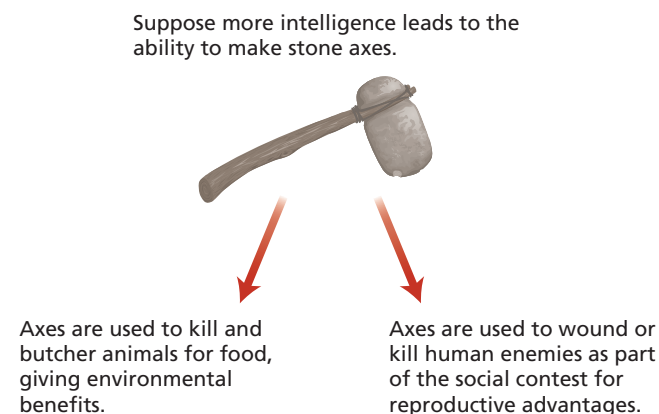
This idea still leaves the question of why humans should have been subjected to a uniquely powerful combination of these two selection mechanisms. One possible answer is that our ancestors, at some point in their evolution as upright tool-users, may have achieved hunting technologies that constituted deadly force for other hominids. Under these conditions, the normal type of strategy selection may have been superseded.

Consider the consequences for evolution of a stone axe blade tied to a wooden handle. Possession of such a weapon together with an understanding of how to use it would give its owner the status of a warrior. Invention of better weapons and weapon-using tactics would give a fitness advantage. But it would also destroy the evolutionary game rules that determine the best behavioral strategy in most animal species. For example, lions and eagles and spiders have evolved relatively simple behavior because their weapons are built in. In facing other lions, a lion is facing a predictable enemy. Standard reactions, tactics, and strategies are fine. But an armed hominid facing other armed hominids does not have a biologically standardized enemy. In this way, novel technology destroyed the social stability of hominid life (see Figures 21.14A and 21.14B).

Without evolutionary stability of social behavior, one possible characteristic for selection to favor is the ability to calculate immediately the best combination of social tactics and technology. In other words, hominid technology may have created an environment that selected for both social and technological intelligence.

An interesting feature of this type of selection is that brain mechanisms that foster both social and technological intelligence can give rise to a “free” arms race. If having a more generalized type of intelligence is roughly “paid for” at the level of food gathering, or in some other ecological context, then the use of that same intelligence in social competition is free. But since social competition is a selective process of relative advantage, natural selection will push for higher and higher levels of intelligence generalized enough to be of use in both social and technological arenas.

This unusual situation has no doubt arisen only rarely in the history of life on Earth, if indeed it does apply to human evolution. But such uniqueness is required to explain the historically unprecedented evolution of the human mind. That is, a theory of human evolution cannot be so general that it explains the evolution of higher intelligence in numerous species, because that never happened. An additional attractive feature of this theory is that it is based on a biological adaptation, learned and proficient tool-use, that is uniquely associated with hominids in the fossil record. That is, there are good reasons for supposing that this type of combined selection mechanism would have arisen only among upright hominids of the last few million years. ♦



**FIGURE 21.14A** Mental arms races are expensive unless there are spin-offs that pay for the costs of the arms race.



**FIGURE 21.14B** How Did Free Mental Arms Races Start? Consider the evolutionary game situation of an animal that does not use tools. The parameters of its evolutionary games are fixed by its body. But humans that use tools are not limited to the weaponry built into their bodies; their intelligence will be a major limiting factor in their success in conflicts because it limits their tools and their tool use.

# HUMAN BEHAVIOR FROM AN EVOLUTIONARY PERSPECTIVE

## 21.15 There is a long tradition of Darwinian analysis of human behavior, despite controversy about it

The importance of the Darwinian theory of evolution for our understanding of human behavior has been a perennial concern. However, it has received particularly intense attention since 1975. That year, the entomologist **E. O. Wilson** published a book, *Sociobiology*, that attempted to unite behavioral research on all animals, from insects to humans (E. O. Wilson is shown in Figure 21.15A). He explicitly connected selection on social behavior in insects with parallel selection on human behavior. A great many biologists and social scientists found Wilson's ideas interesting. We have summarized this type of thinking in Chapter 20, albeit without the application to humans.

But another large group of biologists, social scientists, and philosophers found Wilson's ideas repugnant. Not only did they object to his use of Darwinian thinking in reasoning about human social behavior, but they also found his scientific analyses of other animals inadequate. They were especially concerned about what they saw as a "reductionist" attempt to explain all behavior in terms of genes and natural selection. They regarded this view of behavior as grossly distorted. This difference of opinion generated one of the more rancorous Darwinian controversies.

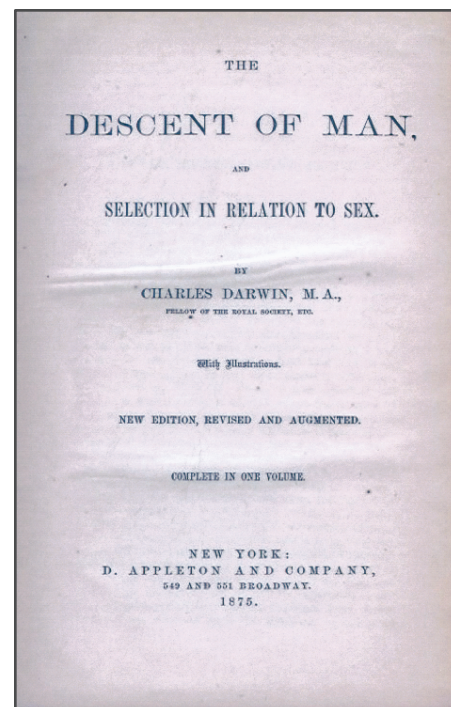
One aftermath of this controversy was the avoidance of the term **sociobiology**. It was nonetheless reborn as a new academic movement, **evolutionary psychology**, which hardly differs from Wilson's original proposal. Evolutionary psychology has been very influential in the general culture, from articles in popular magazines to evolutionary "self-help" books. It is important to understand how much scientific support this discipline has received. This is our primary concern here.



**FIGURE 21.15A** E. O. Wilson

As much as evolutionary psychology has attracted attention and criticism, there is nothing new about it. Its first practitioner was Charles Darwin, who made remarks about the evolution of human behavior in two books, *The Descent of Man* and *The Expression of the Emotions in Man and Animals* (see Figure 21.15B). Darwin's main interest was in showing the plausibility of human evolution from other mammals, especially from a common ancestor shared with the apes of Africa. Unlike Wallace, his co-inventor of the principle of natural selection, Darwin was unwilling to make a special case of human evolution, human behavior included.

Ever since Darwin, there have been many speculations about the causes of human evolution and the results of that evolution. Ethologist **Desmond Morris** wrote *The Naked Ape*, presenting humans as animals, which caused a sensation in the late 1960s (see Figures 21.15C and 21.15D). Even a playwright, **Robert Ardrey**, weighed in with speculative theories about the causes of human evolution and our resulting behavior. Like some others, Ardrey blamed the evolution of hunting behavior in the genus *Homo* for our continued aggression in the twentieth century.



**FIGURE 21.15B** Title Page of *The Descent of Man* by Charles Darwin



**FIGURE 21.15C** Desmond Morris

Before the sociobiology controversy, the controversies about the evolution of human behavior were not highly focused. Although quite a few scientists, especially evolutionary biologists, deplored the rampant speculation of some popular works, these works were generally considered harmless.

Since the sociobiology controversy, the discussion of the evolution of human behavior has become more intense. Ironically, even though Engels speculated about human evolution and Marx was a fan of Darwin, the left wing has disparaged attempts to analyze the evolution of human behavior. They have not presented much in the way of an alternative Darwinian analysis. Their main interest seems to be to stop the use of Darwinian foundations as an alternative to Marxist analysis of human behavior. As a final twist, the religious right wing doesn't like the Darwinian analysis of human evolution any more than the left wing does.

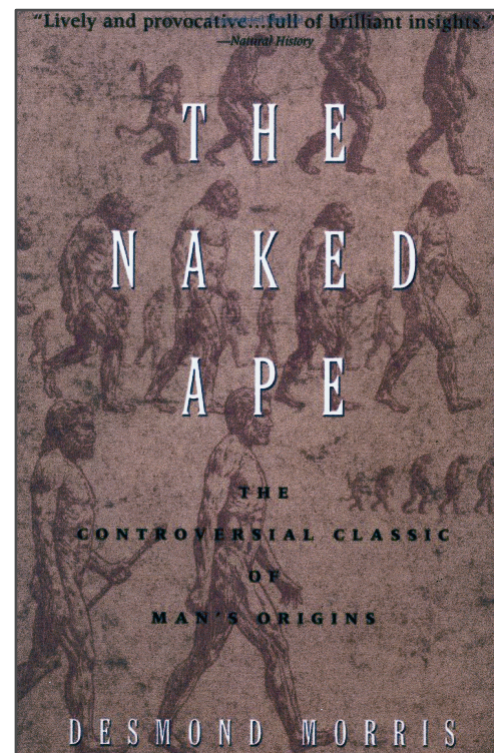
There is nothing new about Darwinian ideas coming under attack for ideological or religious reasons. It should be noted that ideologues have often used Darwinian thinking to support their causes. Darwinism was used as an ideological support for nineteenth-century opposition to welfare. Even worse, in the twentieth century it was used as a buttress for fascism and the extermination of minorities, homosexuals, and defective babies. There is nothing inherently benign about the extrapolation of science. It can be actively evil in its consequences.

Where does that leave the modern evaluation of evolutionary psychology? Should its Darwinian credentials be accepted, and political concerns dismissed? If present-day left-wing and right-wing groups are trying to censor discussions of the Darwinian basis of human behavior, should they be allowed to do so?

A few principles might provide useful guidelines.

1. We cannot assume that any particular group is infallible. Evolutionary psychologists who ally themselves with Charles Darwin are not necessarily correct. Even though both the left wing and right wing think they have ideological infallibility, they have no greater claim to the truth. Any of these groups could be right, and any of them could be wrong.
2. Because no one is infallible, the discussion of human evolution should be based on logic and evidence. Ideas that evolutionary biologists have assumed for decades might be wrong. Political consequences that might have been important in 1930 might no longer matter. But other societal consequences, never before significant, might now be devastating in their impact.
3. Because any discussion of human evolution is likely to be provisional at best, it seems useful to approach the issues tentatively.

All together, these three principles might be summarized as, "Try to be reasonable, and reasonably cautious, when considering the significance of evolution for human behavior." ❖



**FIGURE 21.15D** Cover of *The Naked Ape*



## 21.16 Some human behavior can be analyzed by the same methods used to study animal behavior

At the root of the debate about sociobiology and evolutionary psychology lies the fact that some human behavior can be analyzed using methods that are very similar to those used in the evolutionary analysis of animal behavior. There are two aspects to this situation.

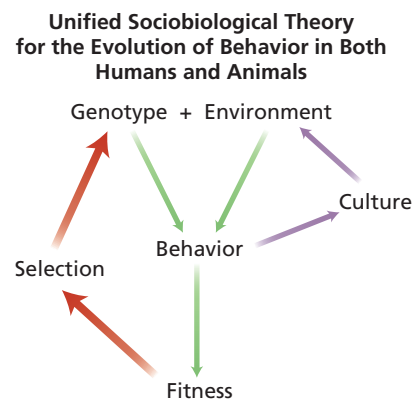
First, evolutionary biology and the related field of quantitative genetics offer some of the best scientific tools for analyzing behavior in any species. In particular, using the tools of quantitative genetics, it is possible to transcend simple dichotomies like “nature vs. nurture.” Though some erroneous publications have misused quantitative genetics to make polemical hay with issues like race and IQ, quantitative genetic methods themselves are the best tools for cleaning up such messes.

Figure 21.16A offers a brief overview of the causal complexity underlying human behavior. Here are some of the most important points. Few characters are completely free of genetic influence. And virtually no behavioral characters are completely free of environmental influences—including environmental influences like learning in species that learn, such as humans. Therefore, almost all behavior results from a combination of genes and environment. Sometimes this combination is “additive”; that is, a particular environmental change might always have the same kind of effect. But sometimes the combination of genes and environment will be nonadditive, and not particularly predictable. All of this was introduced in Chapter 3. Many genes are likely to shape any particular behavior, and many environments. Despite this complexity, behavior is not totally unpredictable. Much of it seems well organized.

The second aspect of human behavior to think about is that some specific patterns of human behavior are parallel to the patterns of animal behavior. These parallels are of two

kinds. The first kind of parallel is the extent to which modern human behavior emulates adaptive behavior in animals. For example, animals often forage (look for food) very efficiently, maximizing their intake of calories and miscellaneous nutrients. Humans also seem to maximize their intake of calories per unit time; eating fast food is one example. But an animal species may have fed on a particular food, such as a hummingbird feeding on the nectar of a flower, for millions of years. It is reasonable to suppose that the feeding behavior of hummingbirds evolves by natural selection acting on genetic variation. Humans have had fast-food restaurants since the late 1940s, thanks particularly to the brothers McDonald. Our fast-food dining could not possibly have evolved by natural selection.

A second parallel between human and animal behavior might have involved evolution by natural selection. In a few contexts, the behavior of humans and animals has similar and devastating consequences for fitness. One example of this is incest. Incestuously produced human offspring are known to have reduced fitness, on average, and the production of even one human child is very costly. Many, but not all, animals systematically avoid incest. Often it is difficult to get siblings to mate with each other in animal colonies. As discussed in the box, “Incest,” there is significant evidence that humans also avoid incest, and they do so in ways that suggest genetic determination of behavioral patterns. On the other hand, there are many known cases of human incest, sometimes with social approval. Both the ancient Egyptians (e.g., Ramses the Great) and Cleopatra’s Ptolemy Dynasty routinely practiced incest, probably with adverse medical effects. So if humans avoid incest, they do not do so invariably (see box).



**FIGURE 21.16A** Sociobiology treats the evolution of all animal species as a process of natural selection in which genotype and environment determine behavior, which in turn determines both culture and the outcome of selection, which then mold the environment and the genotype, respectively.

### Incest

The most revealing examples of human **incest avoidance** arise in pseudo-families. Israeli **kibbutzim** live together communally, with children raised together in day-care settings. The parents of these communally raised children encourage the children to date and marry each other, within the kibbutz; but they rarely do so.

In some Chinese families, the future brides of their sons are adopted into the family as young children, long before the wedding. Once the wedding occurs, many of these marriages have problems with sexual compatibility. The couples often divorce.

In both of these cases, the behavioral pattern can be explained on the basis of a genetically built-in incest avoidance, which interferes with socially condoned mating despite the absence of a real genetic problem. Apparently, young children imprint on peers raised with them as siblings, and therefore reject them as mates. This example is widely regarded as the single best illustration of sociobiological theory.

## Human behavior may be organized to Darwinian ends without genetic specification, perhaps unconsciously 21.17

The apparently Darwinian avoidance of incest by humans suggests that human behavior might be straightforwardly organized along evolutionary genetic lines, like the behavior of social insects. But incest is one of the very few contexts in which this might be true. Most human behavior is organized in ways that seem difficult to explain genetically. For example, consider the ability of humans to navigate the modern world, with its many evolutionary novelties. Possums and deer face carnage crossing roads. Adult humans do not. We can even figure out ATM machines and Internet access.

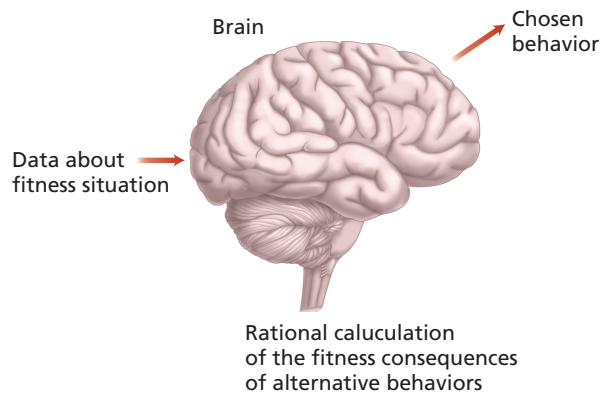
An alternative approach to the flexibility of adult human behavior is to suppose that humans rationally, consciously organize their behavior to Darwinian ends. In this context, humans can be seen as immediate bearers of the Darwinian imperative to survive and reproduce. We would thus be expected to organize our behavior to maximize our Darwinian fitness with few genetic constraints. Notably, this “gene-free” behavior fits well with the theory that humans evolved large brains to be able to calculate the consequences of our behavior in both social and technological realms. That is, the immediate calculation of the consequences of our behavior for our Darwinian fitness fits both a plausible model of our evolution and a plausible interpretation of our present-day behavior. This basic model is shown in Figure 21.17A. One way to think of this theory is that it supposes that, unlike the

brains of virtually all other animals, the human brain has replaced the genome as the controller for our behavior.

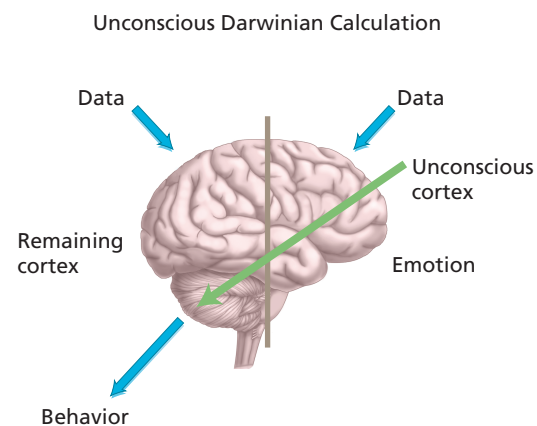
There is a huge problem facing this theory, however. Aside from a few committed sociobiologists, most of us do not consciously make decisions based on their impact on our Darwinian fitness. Indeed, many of us are quite uncertain as to our motives or desires. Therefore, it seems unlikely that human behavior is consciously and rationally organized toward the maximization of Darwinian fitness in our present environment, if not all environments.

But there is an alternative other than returning to gene-oriented sociobiology: To suppose that our thoughts, emotions, and behaviors are shaped to Darwinian ends as a result of the combined operation of both unconscious and conscious parts of the mind. Specifically, if some unconscious segment of our brain were to calculate consequences for fitness, it could then shape the motivations of the conscious segment toward enhancing fitness. This idea, sketched in Figure 21.17B, is admittedly more cumbersome than any of the theories considered so far. But it does allow the possibility of flexible, open-ended human behavior. At the same time, it explains our lack of the subjective experience of Darwinian thinking. These ideas need to be developed further before they can be considered proper scientific theories. But they indicate the diverse possibilities for the application of evolutionary thinking to human behavior. ❖

**A Rational Processing Model for Adaptive Human Behavior**



**FIGURE 21.17A** It might be imagined that the human brain directly, and as a matter of conscious experience, calculates the fitness consequences of each important action and chooses the behavior accordingly.



**FIGURE 21.17B** This model supposes that part of the cortex calculates the relative merits of alternative behaviors regarding their impact on fitness. That part of the cortex then signals the “conscious” part of the brain using emotion and biased perception to motivate behavior.



## SUMMARY

1. Humans are primates. We belong to the apes of the old world, none of whom have tails. Our closest ape relatives are the gorillas and the chimpanzees, with the chimpanzees probably closer to us than the gorillas. Our ancestors were upright hominids that probably first evolved 7–8 million years ago. At first our evolution was dominated by selection for efficient upright walking and simple forms of tool use. Multiple upright hominid lineages have coexisted in evolutionary time. In the last 2 million years, at least one upright hominid lineage underwent a massive increase in brain size.
2. The population genetics of our species has been complex. We have coexisted with at least one other very similar species in the last 100,000 years: *Homo neanderthalensis*. *Homo sapiens*, our own species, probably spread out from Africa in the last few hundred thousand years. This recent diffusion from Africa means that there are no radical differences between human populations, only patchwork differentiation.
3. The why of human evolution remains unknown. We probably evolved for reasons more complex than hunting or bad weather. One popular theory is that we evolved for tool use, but our elaborate social behavior does not fit that model. The alternative is that we evolved for social cunning, but this model has the difficulty that it does not uniquely fit human evolution. Many animals seemingly ought to evolve high levels of social calculation, but do not. There are reasons for supposing that instead our evolution may have involved selection for both technological and social acumen.
4. The theory of evolution is a plausible contender for preeminence in the theoretical explanation of human behavior, at first sight. But human behavior does not fit evolutionary genetic models well, especially with respect to our ability to invent novel behavior that is apparently adaptive. Therefore we need theories of human behavior that are not like those developed for other animals. One idea is that we can directly calculate the fitness consequences of our behavior and develop behavior accordingly. That is, the human brain may have replaced the genome as the ultimate arbiter of our behavior.

## REVIEW QUESTIONS

1. How can we be sure that humans are apes and not monkeys?
2. Since the upright hominids split off from the common ancestor of upright hominids and knuckle-walking chimpanzees, what is the minimum number of periods when more than one upright hominid species was alive?
3. Were Neanderthals members of our species?
4. Are human “races” biological groups of long standing, or are they evolutionarily recent?
5. Why do human languages show similar geography to human genetic differentiation?
6. Give at least one piece of evidence suggesting that the evolution of the large human brain involved strong directional selection.
7. Why is it reasonable to say that the social intelligence theory is too strong to explain human evolution?
8. Why should organisms avoid incest?
9. Why is it unlikely that most of our behavior is genetically encoded in the same way that insect behavior is genetically encoded?
10. Do you think that you possess free will?

## KEY TERMS

<i>Alu</i>	great ape	mental arms race	short tandem repeat (STR)
anthropoid	hominid	mitochondrial DNA	social intelligence
Ardrey, Robert	hominoid	Morris, Desmond	sociobiology
<i>Australopithecus</i>	<i>Homo</i>	multiregional theory	tool use
braincase	hunter-gatherer	Neanderthal	Wallace, Alfred Russell
Cro-Magnon man	incest avoidance	out-of-Africa theory	Wells, H. G.
ear canal	<i>Just-So Stories</i>	primate	Wilson, E. O.
Engels, Friedrich	kibbutzim	prosimian	
evolutionary psychology	knuckle walking	robust lineage	
gracile lineage	Mayer, August	savanna	

## FURTHER READINGS

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Barkow, J. H., L. Cosmides, and J. Tooby, eds. 1992. *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*. New York: Oxford University Press.

Byrne, R., and A. Whiten, eds. 1988. *Machiavellian Intelligence, Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford, UK: Clarendon Press.

Cavalli-Sforza, L. L. 1997. "Genes, Peoples, and Languages." *Proceedings of the National Academy of Sciences, USA*, 94:7719–24.

Cavalli-Sforza, L. L., P. Menozzi, and A. Piazza. 1994. *The History and Geography of Human Genes*. Princeton, NJ: Princeton University Press.

Hublin, J., F. Spoor, M. Braun, F. Zonneveld, and S. Condemi. 1996. "A Late Neanderthal Associated with Upper Palaeolithic Artefacts." *Nature* 381:224–26.

Kitcher, P. 1985. *Vaulting Ambition, Sociobiology and the Quest for Human Nature*. Cambridge, MA: MIT Press.

Krings, M., H. Geisert, R. W. Schmitz, H. Krainitzki, and S. Paabo. 1999. "DNA sequence of the Mitochondrial Hypervariable Region II from the Neanderthal Type Specimen." *Proceedings of the National Academy of Sciences, USA*, 96:5581–85.

Rose, M. R. 1998. *Darwin's Spectre: Evolutionary Biology in the Modern World*. Princeton, NJ: Princeton University Press.

Tattersall, I. 1999. *The Last Neanderthal*. New York: Nevramount.

Tishkoff, S. A., E. Dietzsch, W. Speed, A. J. Pakstis, J. R. Kidd, K. Cheung, B. Bonne-Tamir, A. S. Santachiara-Benerecetti, T. Jenkins, and K. K. Kidd. 1996. "Global Patterns of Linkage Disequilibrium at the CD4 Locus and Modern Human Origins." *Science* 271:1380–87.

Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Cambridge, MA: Belknap Press.

———. 1978. *On Human Nature*. Cambridge, MA: Harvard University Press.

Wolpoff, M. H. 1997. *Paleoanthropology*. New York: McGraw-Hill.



