

# 2. Evolution

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## Learning Objectives

### LEARNING OBJECTIVES

- Discuss differing perspectives about how the human species descended from a primate ancestor
- Discuss pre-Darwinian perspectives on the nature of the earth and evolution
- Explain the process of natural selection
- Describe what is meant by the “biopolitics of heredity”
- Examine and correct several misconceptions about human evolution
- Discuss Darwin’s theory and contributions to our understanding of evolution

## THE SCIENCE OF WHO WE ARE AND WHERE WE COME FROM

As we discussed at the end of Chapter 1, all peoples tell stories about their ancestors. Scientific stories about our ancestors are constrained by the assumptions of science, which developed out of 17th-century European philosophy. The first of these scientific assumptions is that the universe is divisible into (a) the natural world of matter and law and (b) the supernatural world of spirit and miracle, and we can focus our attention solely on the former. The second is that miracles, or capricious suspensions of the laws of nature, are not explanatory in the natural world; rather, historical processes are. The third is that we learn about nature by principally collecting data, under controlled circumstances, so that anyone, anywhere, can come to the same conclusions. We call such fundamental cultural assumptions like these **epistemes**, and we can label these as naturalism, rationalism, and empiricism, respectively. Our fourth assumption is that maximum accuracy is the only goal of a good scientific explanation. All of these are quite unusual cross-culturally; after all, the basis of most polite conversation universally is the assumption that maximum accuracy is *not* desirable. For example, when someone in the United States asks how you are, they generally *do not really want to know*, and if you insist on telling them, they will probably think you are a freak and not talk to you again.

Nevertheless, as these particular epistemic assumptions began to dominate European scholarly research in the 1600s, traditional ideas about how the world works began to fall away. Many of these ideas had theological implications. For example, it was generally believed by medieval European scholars that Heaven was a place up in the sky, and it was fundamentally different from Earth; after all, Heaven is where God lives. Things on Earth tend to move in straight lines, but in the sky they move in circles. Things on Earth decay; things in the sky seem to be eternal. Things here are ugly and uneven; things in the sky are perfect crystalline spheres. Things on Earth are made of four elements (earth, air, fire, and water), but things in the sky partake of a fifth element, the quintessence, which gives them those different properties. Nevertheless, by 1700 it was clear that the same basic rules of gravity and motion govern things up in Heaven and here on Earth. An apple falls from a tree by virtue of exactly the same laws of matter and motion that keep the moon revolving around the earth, as Isaac Newton showed.

The earth itself is a body in space revolving around the sun, just as the other planets in the solar system do. Things up in the sky and down here on Earth really aren't so different, after all.

Scholars began trying to reconstruct the history of the earth naturalistically. Around 1700 Thomas Burnet speculated that perhaps a comet smashed into the earth, which set off the Great Flood related in the Bible. At about the same time, the English anatomist Edward Tyson published the first anatomical study of the animal we now call a chimpanzee, demonstrating that it was physically more similar to us than to any other creature known. He even counted up its similarities: the chimpanzee resembled humans in 48 ways, but monkeys in only 34 ways (see Figure 2.1).

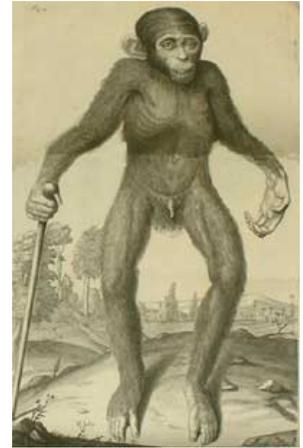


Figure 2.1 Tyson's "orang-outang".

## PRE-DARWINIAN INTELLECTUAL TRENDS

Three general problems were especially vexing to pious Christian biologists of the 1700s. First, **extinction**—the loss of a species from the face of the earth—became grudgingly accepted as a fact, even though it seemed to diminish the power and wisdom of God, by making His creation and plan more transient than had traditionally been imagined. Yet not only was there extinction in the present (notably, a bird known as the dodo, hunted and eaten by Dutch colonists on the island of Mauritius, the only place it lived), but there was extinction in the past as well—and a lot of it, the evidence of which was being recovered as fossils. Moreover, the extinctions implied by the fossils were not contemporaneous—the extinctions were patterned, as if different kinds of creatures had lived and died at different times, embedded in distinct geological formations. What might that mean?

The second problem involved a great discovery by the Swedish biologist Carl Linnaeus. Where animal species had traditionally been linearly conceptualized in terms of how similar to humans they are—forming a "Great Chain of Being"—Linnaeus identified a distinctly different pattern. After all, there was no clear basis on which to say that an elk is more like a human than a tiger or a walrus is. Linnaeus, rather, argued that species should be arranged not according to how similar they are to us but, rather, by how similar they are to one another. In so doing, Linnaeus found that warm-blooded, hairy, lactating vertebrates formed a natural group that he named "Mammalia" in 1758 (in contrast to, say, fish or birds). Within that group was a cluster of species he called "Primates," and among them, according to our physical features, was our own species, which he named *Homo sapiens*. These physical correspondences among diverse kinds of creatures later came to be known as **homology**. But why did such a pattern of nested similarities exist, and what did it mean?



Figure 2.2A Ring-tailed Lemur.



Figure 2.2B Ruffed Lemur.



Figure 2.2C Red Ruffed Lemur.



Figure 2.2D Blue-eyed black lemur.

The third problem involved the relationship between **adaptation** and biogeography. Even though the Bible doesn't exactly say so, it was understood that animals are adapted to their surroundings because God made them that way. The Bible does say that all living species of animals started out together in the same place—the mountains of Ararat, where

**Noah's Ark** landed. Yet those animals would not have been adapted to Ararat; so how did polar bears get to the Arctic, koalas to Australia, and bison to the Great Plains, where they are each well adapted, without going extinct first? How could all the lemurs have ended up in Madagascar and nowhere else (see Figure 2.2)? An explanation for adaptation that was historical, rather than miraculous, would be very valuable.

These were the questions that dominated the field of natural history by the beginning of the 1800s. But of course the big questions of the day weren't even about fossils or polar bears at all but, rather, about the biopolitics of slavery. Were all people of one stock, the descendants of **Adam and Eve**? That would seem to afford a moral argument against treating some people as property, if we are all brothers and sisters under the skin, and would seem to accord well with the biblical narrative as well. This position, however, required the development of a biological theory to explain how Adam and Eve's descendants could have morphed into the diverse peoples of the world. In other words, if you imagined Adam and Eve to be white, then how did black people arise? (Or vice versa.) This position, known as **monogenism**, was biblical, socially progressive, and generated the earliest modern evolutionary theories—microevolutionary, to be sure, but theories intended to explain the naturalistic production of difference, or what we would now call evolution.

Others believed that Africans and Europeans shared no common ancestry at all, being the products of separate creations by God. Perhaps in Adam and Eve, the Bible was merely recounting His most recent creation, but the peoples of the rest of the world were fundamentally and unalterably different and had always been so. This position, known as **polygenism**, was attractive to those looking to rationalize slavery as well as to radical intellectuals who did not feel constrained by biblical literalism. Paradoxically, however, in holding that peoples are as they always have been and could never change, the polygenists had more intellectual continuity with modern-day creationists.

By the mid-1800s, the discovery of stone tools in the ground implied a remote period in ancient Europe when the ancestors lived like the “**savages**” who still used stone tools, whom Europeans were encountering in more remote places of the world. This in turn implied an ancient European “stone age” before the invention of metals, which, like many of the new discoveries, was not part of the information in the Bible. It was increasingly becoming apparent that a long time ago, very primitive Europeans had lived with some extinct animals, like woolly mammoths. They even drew pictures of the extinct animals on the walls of their caves (see Figure 2.3).



Figure 2.3 Cave painting in the Grotte de Rouffignac.

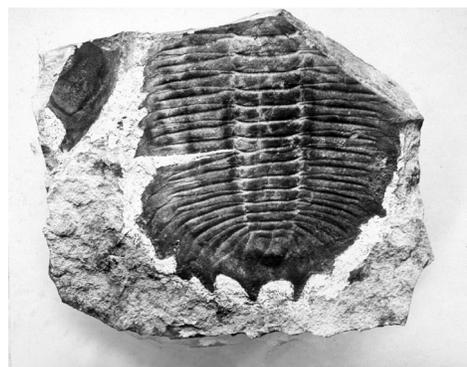


Figure 2.4 Trilobite fossil.

Further, even a Stone Age seemed relatively recent in the larger context of the new geology. All those extinct fossil remains were being found in geological formations far more ancient than any known human evidence (see Figure 2.4). Just how ancient was not very clear, but judging by the pace of geological processes we can see today, those processes seem to have been going on for a very, very long time. You simply can't get fossilization or fossil fuels made in the ground over the few thousands of years of biblical time. The most rational interpretation of the geological evidence, argued the pious Scottish lawyer/geologist Charles Lyell is that the earth is very, very old—thus stimulating a revolution in both geological and ethnological time. Lyell himself argued that the earth was very old in the 1830s but waffled on

how old the human species was until the 1860s.

Finally, educated Europeans were taking their biblical stories more and more loosely, as the field of biblical studies matured. The Bible was being understood as a collection of sacred Jewish and early Christian writings composed at different times and selected from a much larger corpus. Thomas Jefferson had privately distinguished between the things Jesus probably said and did and the things Jesus probably did not say and do. In 1835, a German biblical scholar

named David Strauss scandalously interpreted the life of Christ without miracles; his work was published in English in 1846, translated by the aspiring novelist Marian Evans (aka George Eliot). We should focus, argued Strauss, on the meaning of the stories of the Bible, not on whether they really happened or not, for their meaning lies in their narrative content, not in their historicity. This launched a revolution in the area of biblical scholarship.

## THE TRANSMUTATION HYPOTHESIS

The publication of *The Origin of Species* by Charles Darwin in 1859 became an intellectual flash point in European intellectual life (Darwin 1859). It was focused on a significantly narrow point: Where do new species, adapted to their surroundings, come from? The Bible says God made all species. However, the Bible also says that God made all languages at the foot of the **Tower of Babel**; and yet, half a century of historical linguistics had showed clearly that such was not the case (French and Spanish had only been different languages, having diverged from Vulgar Latin, for a matter of a few centuries), and nobody seemed to get too upset about it.

Moreover, the suggestion that species came from other species was not all that radical. The celebrated French naturalist Lamarck had said as much in 1809 and an anonymous 1844 English bestseller called *Vestiges of the Natural History of Creation* had sensationalized it—to the consternation of both theologians and naturalists. Indeed, by the 1850s European biologists were very confident that cells were fundamental units of life and that the only way you could get new cells was from old cells. While this begged the question of where the first cell came from, it nevertheless was not too much of a stretch to see species as fundamental units of life as well and to ask whether new ones arose miraculously, or just from older species. The idea that species had their beginnings in other, older, similar species was known as “**the transmutation hypothesis**.”

Charles Darwin had come to think about the origin of species upon returning from a long voyage around the world in the early 1830s on the *H.M.S. Beagle*. In South America, Darwin had observed that the unusual species he saw alive there were very similar to the unusual extinct animals in the same area. This suggested some sort of historical continuity between them—**descent with modification**, he called it. The problem was how to make sense historically, rather than miraculously, of the particular adaptations that differentiate species. The engine of adaptation, Darwin realized, was competition. This did not necessarily entail face-to-face competition but simply the fact that not all members of a species are equally likely to survive and breed. Which ones are more likely? The ones that randomly are a bit more in sync with their environment. Those creatures will disproportionately thrive and breed, and the next generation of the species will come to look just a bit more like them, on the average. The core of Darwin's thought is thus a two-step process: the random generation of variation, and the nonrandom process by which the environment subtly favors organisms with certain features to thrive and breed.

The biology that Darwin learned in college had invoked a famous simile: a species is like a watch, meticulously crafted by a wise watchmaker, implying a heavenly species-maker. Darwin substituted a more powerful simile, arguing that a species is actually like a breed or strain of animals, rather than like a watch. But we know that a breed or strain of animals arises naturally, historically, by the actions of breeders who select certain features to characterize populations.

Whether dogs, pigeons, or roses, the properties of living beings can change, and have changed, in quite dramatic ways by virtue of human activity in rather short periods of time. If people could make beagles and greyhounds and bulldogs by selecting the progenitors of particular stocks, then maybe nature could work to select progenitors as well, although more subtly and over vastly longer periods of time (see Figure 2.5).

Darwin called this principle “**natural selection**” and planned to write a long book about it someday. But in 1858 he received a manuscript from a fellow naturalist, Alfred Russel Wallace, who had come up



Figure 2.5A Beagle.



Figure 2.5B Bulldog.



Figure 2.5C Greyhound.

with quite similar ideas to his own while working in the Malay archipelago. Darwin’s friend, the geologist Charles Lyell, had papers by Darwin and Wallace read into the record, *The Transactions of the Linnaean Society*, July 1, 1858, so they could share credit for the discovery, and Darwin set about to publish the work he had done on natural selection. The result was called *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, published on November 24, 1859.

Darwin’s central thesis was that the differences among breeds or strains or varieties of animals and plants were the same kinds of differences that exist between species, only smaller and formed over short periods of time. The origin of new species lay in the long-term biases of survival and reproduction in older species. The result was a convincing naturalistic explanation for adaptation. Moreover, it finally explained the nested pattern of similarities among species that Linnaeus had discovered a century earlier but couldn’t explain. Those nested patterns were the legacy of common ancestries; they were literally family resemblances.

Darwin was especially careful to omit any discussion of people from his book. He wanted the discussion to be about the general process; consequently he wrote just a single line, near the end, about people: “Light will be thrown on the origin of man and his history” (Darwin 1859, 488). He was willing to acknowledge the possibility that life had “been originally breathed into a few forms or into one,” but he was satisfied with having described the mechanism by which adaptive change has taken place in the organic world since then—in parallel with Isaac Newton, who famously refused to speculate on where gravity came from, focusing instead only on how it works (Darwin 1859, 490).

People, however, were bound to be the central issue. A British scholar named Herbert Spencer had also come up with a similar idea, which he called “survival of the fittest” and he convinced Darwin that his phrase was synonymous with “natural selection.” And of course, who was more fit than wealthy, British white men? This confusion of human history (that is, the construction of social and political hierarchies) for evolutionary biology would prove to be a consistent irritation for students of human diversity and ancestry. Indeed, this issue eventually led Darwin and Wallace to part ways. Wallace asked: if natural selection does not produce useless organs, then why does the “savage” have a brain as big as a civilized European’s, if the savage doesn’t use it? This seeming paradox led Wallace into spiritualism and the possibility that all species of organisms had evolved...but human intelligence had had a little divine help. Darwin wrote him, “I hope you have not murdered too completely your own and my child” (Darwin, 1869). In 1871, the early British anthropologist Edward Tylor formally separated the evolution and study of “culture” from the biological properties of people. Of course the so-called “savage’s” brain was as good as the European’s, and he does use it fully, but it was filled with different information—“knowledge, belief, art, morals, law, custom, and any other capabilities and habits acquired by man as a member of society” (Tylor 1871, 1). Furthermore, this cultural information was the product of historical process, not miracle. This understanding marks the beginning of modern anthropology.

Within the academy, there was not too much reaction against the proposition that humans had descended with modification from an ape stock, and had then differentiated from that stock over the eons as a result of the differential preservation of favorable variations. The heart of Darwinism as applied to humans is simply ape ancestry and adaptive divergence.

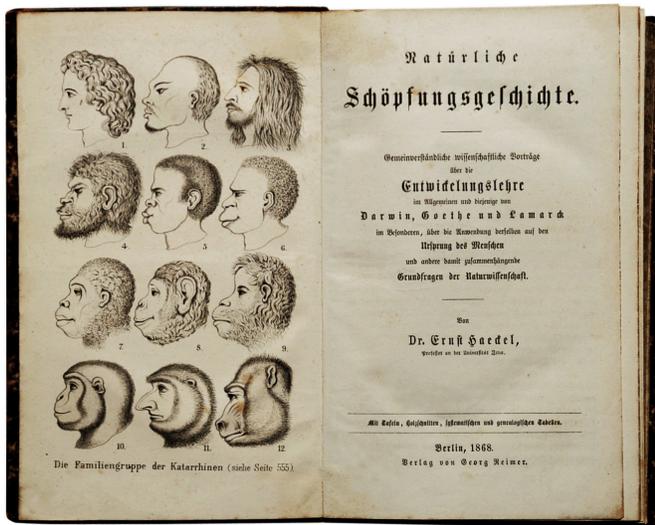


Figure 2.6 The frontispiece to Ernst Haeckel's (1868) popular German book on Darwinism. The English translation lacked this illustration.

But the early Darwinians were faced with a dilemma—in 1860, there was no fossil evidence linking humans to apes. The German biologist Ernst Haeckel solved this problem by fatefully arguing that we don't need a fossil record to link us to the apes, because Europeans are linked to the apes through the nonwhite peoples of the world. He envisioned 12 different species of living peoples, each at different distances from the apes, thus sacrificing the full humanity of most people on the altar of Darwinism (see Figure 2.6). Scientists of the 1860s thought the full humanity of Africans was less important than evolution. Today that is morally repugnant. While Darwin and his English colleagues did not agree with these details, they nevertheless saw Haeckel as an ally in the broader struggle to get evolution accepted. With hindsight, we can judge this to be a morally questionable decision: Today we would hopefully universally consider the full

humanity of Africans to be more important than whether humans are descended from apes, and thoroughly repudiate anyone who denied it.

## POST-DARWINIAN THEORIES AND DISPUTES

The immediate theoretical weakness of Darwinism lay in its reliance upon a pool of undirected variation for nature to select from. The dominant theory of heredity at the time was known as **blending inheritance**, in which a child is a blend of the parents—like paint, if mom is red and dad is blue, then the child is purple (see Figure 2.7). The problem is that any descendants of purple child will never be as different as blue mom and red dad. You can't recover the original blue and red from purple paint—which simply means that for people, variation is lost every generation. How can natural selection work if you lose variation every generation?

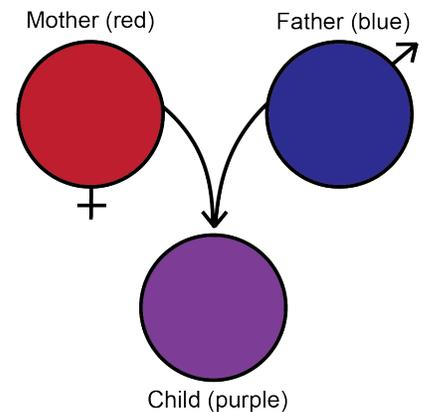


Figure 2.7 Blending inheritance in color.

Darwin fell back on a principle developed by Lamarck known as the “**inheritance of acquired characteristics**” or “use and disuse of organs.” Here, whatever attributes you develop over the course of your life—muscles, a tan, compassion, bad breath—can be stably passed on to your children, somehow. That way, variation can be reintroduced every generation, by virtue of this new pool of acquired characters. Unfortunately, an influential school of German biologists in the 1880s, led by August Weismann, had identified just two types of cells in bodies: reproductive or germ cells, and somatic or body cells. It was the germ cells that formed the next generation; the somatic cells, which form the body, comprise merely an evolutionary dead-end to aid in the transmission of the germ-line. Life could thus be seen as a continuous series of germ-cells, with adult bodies as transient receptacles grown up around them every generation. (On this basis, the English writer Samuel Butler quipped that a hen is just an egg's way of making another egg.) But how, then, could information about your elbow or your cerebral cortex during the course of your life get into your germ cells? There didn't seem to be a way, so that generation called themselves “neoDarwinians” to express their belief in natural selection minus the inheritance of acquired characteristics.

The entire problem was rendered moot with the discovery in 1900 of Gregor Mendel's work on heredity in peas from 35 years earlier. Mendel showed that heredity didn't actually work like the blending of paints at all. When you isolated particular traits, you saw that offspring were not midway between their parents; rather, they were like one or the other parent. The offspring of a plant with green peas and one with yellow peas was green, not chartreuse. The offspring of a plant with wrinkled peas and one with round peas was round, not wrinkly-round. This suggested, rather, that heredity worked like interacting particles that came into new combinations but fundamentally retained their structural integrity every generation. Unlike paints, you could indeed recover the original variants under this model; variation wasn't lost every generation.

Mendelian genetics soon created new problems for Darwinism, however. The new geneticists were focused on discrete binary states of existence, like Mendel's peas: green/yellow, wrinkled/round, tall/short, in experimental populations. But the old Darwinian naturalists were working with quantitative variations in real populations—many of them intermediate, not extreme, in form. So, the Mendelians had a robust theory of heredity that had difficulty explaining natural patterns of variation, and the Darwinians had a robust theory of biological change that had difficulty accommodating discontinuous variation. One solution might be to reconceptualize all variation as fundamentally binary; the American geneticist Charles Davenport, for example, argued with considerable success that there were two kinds of people—smart and stupid—and that the stupid people simply had the **allele** for “feeble-mindedness.” This actually had a major and regrettable impact on American science and social policy in the 1920s.

A better solution came with the invention of population genetics, in works published around 1930 by the British geneticists Ronald Fisher and J. B. S. Haldane and the American geneticist Sewall Wright. In this model, a **gene** has small but cumulative effects. If we reduce a body to its genetic composition or **genotype**, and we reduce a species to its cumulative genetic composition, or **gene pool**, we can mathematically model the ways in which the gene pool can be transformed. There are rather few ways to accomplish it, and each has characteristic and predictable effects.



Figure 2.8 George Gaylord Simpson (1983).  
Photo courtesy of Jonathan Marks.

This became the first part of the **Synthetic Theory of Evolution**, the extension of Mendelian genetics to population genetics and the formal mathematical study of how gene pools may be transformed through time. The second part involved the study of how species diversify in addition to simply changing, and it entailed integrating speciation and geography in the story of how animal species have come to be. The primary scholars involved were the Russian-American fruit fly geneticist Theodosius Dobzhansky, the German-American ornithologist Ernst Mayr, and the American paleontologist George Gaylord Simpson (see Figure 2.8).

By the 1960s, then, biologists had a robust theory to explain the history of life. Genetic or genotypic changes (known to be encoded in molecules of DNA) cause changes in the physical appearance or **phenotype**. The environment sorts out these changes, and their proportion within a species rises or falls with the nature and stringency of the environment. Selection could now be reduced to the favoring of certain genotypes over alternatives, which can make populations genetically adaptively different from one another. **Genetic drift**, or stochastic (random) changes to the gene pool, makes populations genetically different from one another nonadaptively—that is to say, in ways that don't track the environment. The genetic contact of populations, or **gene flow**, makes populations more similar to one another. Disrupting gene flow acts to divide gene pools, which is in turn stabilized by the development of reproductive barriers between the populations. These processes can be directly studied within living species and can be extrapolated and can adequately explain the differences we find among species.

## MOLECULAR EVOLUTION

The Evolutionary Synthesis successfully reduced evolution to genetics, but until the 1980s it was not possible to study the DNA sequence of the genes directly. Various surrogate measures had been employed for decades. For example, not only is blood a powerful metaphor for heredity, but also it contains genetically controlled immunological properties that can be used to study evolution. It was known in this way by the 1920s that the blood of human and chimpanzee were more similar to one another than were the blood of horse and donkey (see Figure 2.9). By the mid-1960s, it was well established that the blood of human and chimpanzee were more similar to one another than either was to the blood of an orangutan. With greater precision, the actual amino acid sequences of some proteins could be established and compared across species.

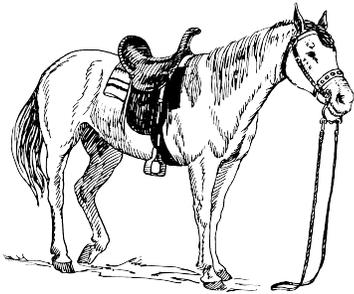


Figure 2.9A Horse.

It quickly became clear that while genetic differences appear generally to track anatomical differences—that is, the closest relatives of species inferred from their hemoglobin (the blood protein that carries gases) are generally the same as those inferred from their teeth—they nevertheless don't match well quantitatively. Thus, while humans are very easily distinguishable from gorillas physically and mentally, their hemoglobins only have two differences—the other 285 amino acids composing

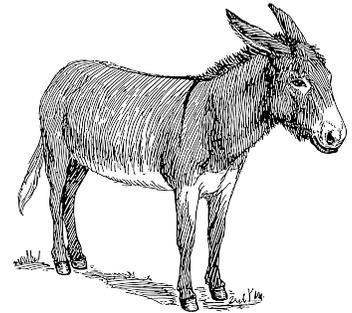


Figure 2.9B Donkey.

the protein match up perfectly. With less than one percent difference in the structure of their hemoglobin, yet striking differences in anatomical form, communication, and behavior, there seems to be a paradox in their biochemical versus anatomical relationships. This led to some thoughtless early inferences from biochemists, such as suggesting that humans are merely variant gorillas, from the viewpoint of hemoglobin. (But if we do not appear to be variant gorillas from any other viewpoint, then perhaps the viewpoint of hemoglobin—or molecular genetics more broadly, so went the counter-argument—is a foolish one to adopt.)

We now appreciate that anatomical variation tracks adaptive divergence of the species (obvious differences between humans and apes relate to locomotion, cognition, sound production, heat dissipation, etc.). But genetic variation more closely tracks the time since the species diverged from one another. By the late 1960s, molecular data were being used to test an important hypothesis about human evolution. Where physical anthropologist Sherwood Washburn thought that humans and African apes probably shared a common ancestor as recently as three to five million years ago, paleoanthropologist David Pilbeam felt that they had separated far earlier than that. Armed with the well-dated (but poorly reconstructed) dental remains of a 14-million-year-old fossil called *Ramapithecus*, Pilbeam argued that



Figure 2.10 Dentition of *Ramapithecus*.

*Ramapithecus* was a part of the human lineage, which in turn had to be at least that old (Figure 2.10). But Washburn's colleagues, Allan Wilson and Vincent Sarich, showed in 1967 that (1) the biochemical changes they measured were changing in a clocklike manner and (2) given the small amount of biochemical difference detectable between human and chimpanzee, the species separated no more than five million years ago. Thus, (3) *Ramapithecus* could not be on the human line 14 million years ago, because there was no separate human line 14 million years ago!

We now see *Ramapithecus* differently, as part of the orangutan lineage, and we find that genetic or molecular evolution does indeed tend to track time, rather than adaptive divergence. The reason is that most of the genome's DNA falls between genes and does not actually code for anything. Consequently, **mutations** that occur to most of the DNA do not have discernible effects on the body and are thus nonadaptive. Only a small bit of the DNA, it seems, actually builds the organism and encodes its adaptations; and even today, the processes by which it does so are vaguely understood.

When we compare actual DNA sequences across species, we consequently find striking patterns. Notably, we almost always find more difference across species in DNA *between* genes than in DNA *within* genes (see Figure 2.11). Where you might find two percent difference between species in the base sequence of a gene, you will find three percent difference in the DNA outside of that gene. Mutations are just as likely to arise within a gene as outside of a gene, yet when you compare species, you find more differences between genes. This suggests that the DNA between genes can tolerate changes without significantly harming the organism, because that DNA is not expressed, while DNA within genes cannot tolerate mutations quite as readily, so they get weeded out. Why? Because the genes do indeed function; consequently, random changes in a gene are far more likely to compromise that function than to improve it. Imagine trying to adjust the fuel injector in your car with a hammer. There is a small probability that you might hit it in just the right way to improve its performance, but chances are good that you would make it worse. Similarly, a random change to an already-functioning molecule is far more likely to make it work worse than to make it work better. That is why mutations can give you cancer, not superpowers. And by compromising the health of its bearer, such a mutation would be “weeded out” by natural selection (See the discussion in Chapters 3 and 4).

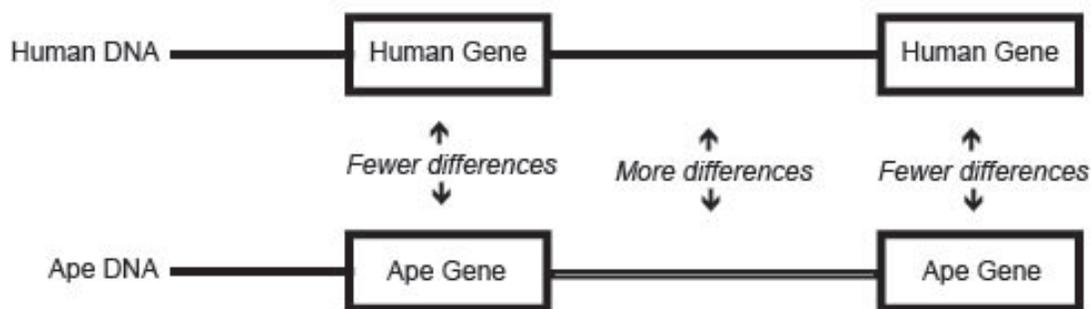


Figure 2.11 DNA comparisons yield more difference between than within genes.

This interpretation is supported when we examine the DNA differences simply *within* genes across species. While most mutations to the gene's coding sequence must affect the structure of the protein it codes for, a few do not. We call these “**synonymous mutations**,” and when we compare genes across species, we almost always find far more of them than we find of the mutations that do indeed change the structure of the gene product. So even though synonymous mutations are a small proportion of mutations, they predominate in cross-species comparisons of genes. And for exactly the same reason: synonymous DNA mutations are less likely to be weeded out, because they are unexpressed and are thus invisible to the environment.

This helps to explain why the genetics seems to track time while the anatomy seems to track adaptation. If most mutations are neutral, with no net effect on the fitness of the organisms that possess them, then (as statisticians calculated in the 1960s) they will spread through a population rarely and in proportion to the rate at which they arise. The mutation rate is a constant, so consequently, over time, neutral mutations will spread and come to differentiate populations in proportion to the time since those gene pools have been separated from one another. Bodily difference,

by contrast, interacts with the environment in important ways, and its evolution will track that interaction. Thus, biologists often envision evolution working on different hierarchical “levels”: a genetic or molecular level and an anatomical level.

Yet how do we simultaneously accommodate the knowledge that (1) genetics and anatomy are different levels, with one tracking time and the other adaptive divergence, and that (2) the genes somehow cause the anatomy? The disconnect lies in the recognition that we still do not know how our one-dimensional DNA nucleotide sequence encodes a four-dimensional animal. This was the unfulfilled promise of the Human Genome Project in the 1990s: This Project produced the complete DNA sequence of a human cell in the hopes that it would reveal how human bodies are built and how to cure them when they are built poorly; however, that information has remained elusive. Presumably the knowledge of how organisms are produced from DNA sequences will one day permit us to reconcile the discrepancies between the patterns we see in anatomical and molecular evolution.

## ORGANISMAL AND MULTILEVEL EVOLUTION

By the 1980s, the acknowledgment that even though genes cause bodies, genes and bodies evolve with different rates and patterns, led to a renewed focus on how bodies change. The Evolutionary Synthesis of the 1930s–1970s had reduced organisms to their genotypes and species to their gene pools, which provided valuable insights about the processes of biological change, but it was only a first approximation. Animals are in fact reactive and adaptable beings, not passive and inert genotypes. Nor are species simply gene pools; rather, they are clusters of socially interacting and reproductively compatible organisms.

So, accepting that evolutionary change is fundamentally genetic change, how do bodies nevertheless function and evolve? And accepting that speciation is ultimately a division of the gene pool, how do groups of animals nevertheless come to see one another as potential mates or competitors for mates, as opposed to just other creatures in the environment? Are there evolutionary processes that are not explicable by population genetics? These questions were raised in the 1980s by paleontologist Stephen Jay Gould, the leading evolutionary biologist of the late 20th century, to progress beyond the reductive assumptions that had guided the earlier generation.

Gould spearheaded a movement to identify and examine higher-order processes and features of evolution that were not adequately explained by population genetics. For example, extinction, which was such a problem for biologists of the 1600s, could now be seen as playing a more complex role in the history of life than population genetics had been able to model. The crucial recognition was that there are two kinds of extinctions, each with different consequences: background extinctions and mass extinctions. Background extinctions are those that reflect the balance of nature, because in a competitive Darwinian world, some things go extinct and other things take their place. Ecologically, your species may be adapted to its niche, but if another species comes along that's better adapted to the same niche, eventually your species will go extinct. It sucks, but it is the way of all life: you come into existence, you endure, and you pass out of existence. But mass extinctions are quite different. They reflect not so much the balance of nature as the wholesale disruption of nature: many species from many different lineages dying off at roughly the same time—presumably as the result of some kind of rare ecological disaster. The situation may not be survival of the fittest as much as survival of the luckiest. The result, then, would be an ecological scramble among the survivors. Having made it through the worst, the survivors could now simply divide up the new ecosystem amongst themselves, since their competitors were gone. Something like this may well have happened about 65 million years ago, with mammals surviving and dinosaurs not. Something like this may be happening now, due to human expansion and environmental degradation. Note, though, that there is only a limited descriptive role here for population genetics: the phenomena we are describing are about organisms and species in ecosystems.

Another question involved the properties of species that might not be reducible to the properties of their gene pools. For example, there are upwards of 15 species of gibbons but only two of chimpanzees. Why? There are upwards of 20 species of guenons but fewer than ten of baboons. Why? Are there genes for that? It seems unlikely. Gould suggested that species, as analytic units of nature, might have properties that are not reducible to the genes in their cells. For example, characteristic rates of speciation and extinction might be emergent properties of their ecologies and histories, and not properties of the genes. Consistent biases of speciation rates might well produce patterns of macroevolutionary diversity that are difficult to explain genetically and that need to be understood ecologically. Gould called such biases in speciation rates **species selection**—a higher-order process that invokes competition between species, in addition to the classic Darwinian competition between individuals.

One of Gould’s most important studies involved the very nature of species. In the classical view, a species is continually adapting to its environment until it changes so much that it is a different species than it was at the beginning of this sentence (Eldredge and Gould 1972). That implies that the species is a fundamentally unstable entity through time, continuously changing to fit in. But suppose, argued Gould along with paleontologist Niles Eldredge, a species is more fundamentally stable through time and only really adapts as it is being founded? Then we might expect to find in the fossil record long equilibrium periods—a few million years or so—in which species don’t seem to change much, punctuated by relatively brief periods in which they change a bit and then stabilize again as new species. They called this idea **punctuated equilibria**, and it helps to explain certain features of the fossil record, notably the existence of small anatomical “gaps” between closely related fossil forms (see Figure 2.12). Its significance, once again, lies in the fact that although it incorporates genetics, it is not really a theory of genetics but a theory of groups of bodies in deep time.

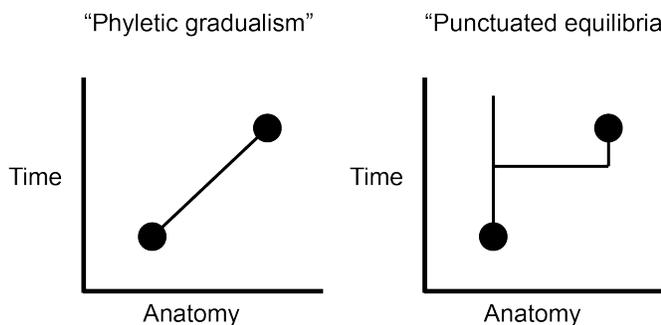


Figure 2.12 Different ways of conceptualizing the evolutionary relationship between an earlier and a later species.

In response to the call for a theory of the evolution of form, the field of **evo-devo**—the intersection of evolutionary and developmental biology—arose. The central focus here is on how changes in form and shape arise. An embryo matures by the stimulation of certain cells to divide, forming growth fields. The interactions and relationships among these growth fields generate the structures of the body. The genes that regulate these growth fields turn out to be very highly conserved across the animal kingdom. This is because they repeatedly turn on and off the most basic genes guiding the animal’s

development, and thus any changes to them would be catastrophic. Indeed, these genes were first identified by producing a bizarre mutant fruit fly that grew a pair of legs where its antennae were supposed to be.

Certain genetic changes can alter the fates of cells and the body parts that they build; meanwhile, other genetic changes can simply affect the rates at which neighboring groups of cells grow and divide, thus producing physical bumps or dents in the developing body. The result of altering the relationships among these fields of cellular proliferation in the growing embryo is allometry, or the differential growth of body parts. As an animal gets larger—either over the course of its life or over the course of macroevolution—it often has to change shape in order to live at a different size. Many important physiological functions depend on properties of geometric area: the strength of a bone, for example, is proportional to its cross-sectional area. But area is a two-dimensional quality, while growing takes place in three dimensions—as an increase in mass or volume. As an animal expands, its bones necessarily weaken, because volume expands faster than area does. Consequently a bigger animal has more stress on its bones than a smaller animal does and must evolve bones even thicker than they would be by simply scaling the animal up proportionally. In other words, if you expand a mouse to the size of an elephant, it will nevertheless still have much thinner bones than the elephant does. But those giant mouse bones will unfortunately not be adequate to the task. Thus, a giant mouse would have to change aspects of its form to maintain function at a larger size (see Figure 2.13).

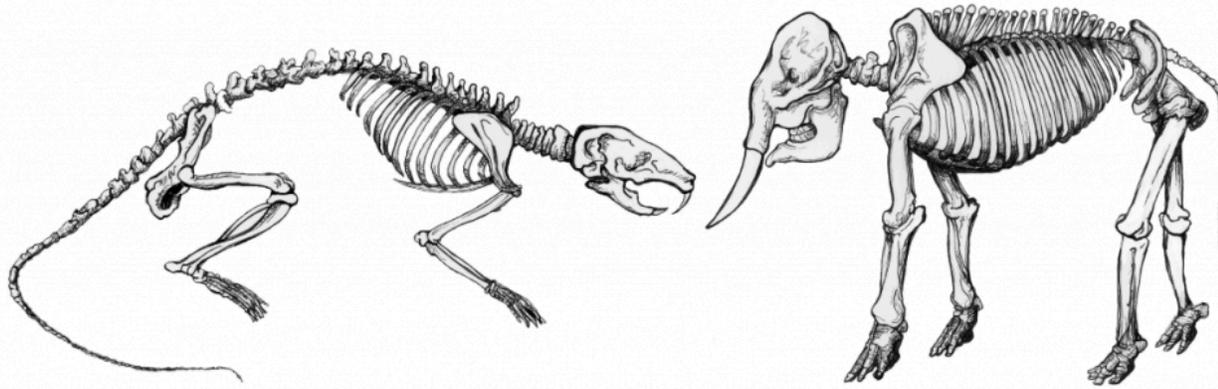


Figure 2.13 Mouse (left) and elephant skeletons (right). Notice the elephant's bones are more robust when the two animals are the same size.

Physiologically, we would like to know how the body “knows” when to turn on and off the genes that regulate growth to produce a normal animal. Evolutionarily, we would like to know how the body “learns” to alter the genetic on/off switch (or the genetic “slow down/speed up” switch) to produce an animal that looks different. Moreover, since organisms differ from one another, we would like to know how the developing body distinguishes a range of normal variation from abnormal, pathological variation. And finally, how does abnormal variation eventually become normal in a descendant species?

Gould here invoked the work of a British geneticist named Conrad H. Waddington, who thought about genetics less reductively than his colleagues. Without isolating specific DNA sites and analyzing their function, Waddington instead studied the inheritance of an organism's reactivity—its ability to adapt to the circumstances of its life. In a famous experiment, he grew fruit fly eggs in an atmosphere containing ether. Most died, but a few survived somehow by developing a weird physical feature: a second thorax, with a second pair of wings. Waddington bred these flies and soon developed a stable line of flies who would reliably develop a second thorax when grown in ether. Then he began to lower the concentration of ether, while continuing to selectively breed the flies that developed the strange appearance. Eventually he had a line of flies that would stably develop the “bithorax” phenotype even when there was no ether; it had become the “new normal.” The flies had genetically assimilated the bithorax condition.

Waddington was thus able to mimic the inheritance of acquired characteristics: what had been a trait stimulated by ether a few generations ago was now a normal part of the development of the descendants. Waddington recognized that he had performed a selection experiment on genetic variants, yet he had not selected for particular traits but, rather, for the physiological tendency to develop particular traits when appropriately stimulated. He called that tendency **plasticity** and its converse, the tendency to stay the same even under weird environmental circumstances, **canalization**. Waddington had initially selected for plasticity, the tendency to develop the bithorax phenotype under weird conditions, and then, later, for canalization, the developmental normalization of that weird physical trait. Although Waddington had high stature in the community of geneticists, evolutionary biologists of the 1950s and 1960s regarded him with suspicion because he was not working within the standard mindset of reductionism, which saw evolution as the spread of genetic variants that coded for favorable traits.

Waddington also recognized that cells had two types of inheritance patterns. Through mitosis, one cell becomes two cells that contain the same genetic information as one another and as the original cell. The faithful transmission of the DNA base sequences is genetic transmission. And yet, genetically identical nerve cells, skin cells, and white blood cells faithfully transmit their identities as nerve cells, skin cells, and white blood cells to their descendant cells, in spite of

being genetically identical (see Figure 2.14). White blood cells only make more white blood cells, never nerve cells—even though they have exactly the same DNA sequence. Waddington called this kind of cellular inheritance **epigenetic**.

Figure 2.14 Five kinds of cells that all have the same DNA sequence yet look different.

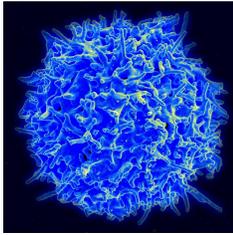


Figure 2.14A Healthy Human T cell.

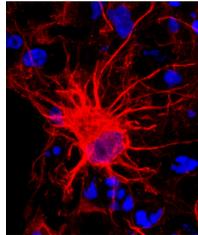


Figure 2.14B Human brain cell.

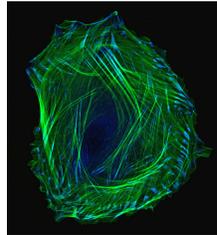


Figure 2.14C Embryonic smooth muscle.

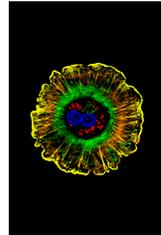


Figure 2.14D Human liver cell.

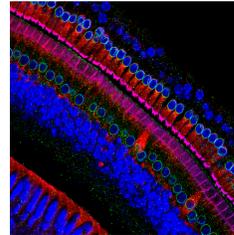


Figure 2.14E Human hair cells in the ear.

The Human Genome Project in the 1990s generated a great deal of public interest in analyzing the human DNA sequence from the standpoint of medical genetics. Some of the rhetoric was extravagant in trying to sell the public on the idea of investing a lot of money and resources in sequencing the human genome: showing the genetic basis of heritable traits, curing genetic diseases, and learning what it means ultimately to be biologically human. However, the human DNA sequence was not actually able to answer those questions, and interest began to shift from genetic information to epigenetic information: the modification of DNA structure, but not the base sequence, and the stable multi-generational inheritance of that modification.

This interest in genetics built upon decades of research in human biology, which saw the human body as highly adaptable, as controlled anthropometric studies of immigrant communities begun by anthropologists like Franz Boas and Harry Shapiro had been showing since the early 20th century. The growing human body adjusts itself to the conditions of life, such as diet, sunshine, high altitude, hard labor, population density, how babies are carried—any and all of which can have subtle but consistent effects upon its development. There can thus be no normal human form, only a context-specific range of human forms. What the human biologists called human adaptability, evolutionary biologists called developmental plasticity, and evidence quickly began to mount for its cause being epigenetic modifications to DNA.

Evolution is about how descendants come to differ from ancestors. Inheritance from parent to offspring is still the critical elementary process. But in the 21st century, the intimate relationship between evolution and inheritance has been broadened to include not merely genetic inheritance patterns but epigenetic inheritance patterns as well. We also recognize two other forms of intergenerational transmission and inheritance, which also have consequences for evolution. In addition to genetic and epigenetic variation as sources of heritable physical differences among organisms that can lead to biases in survival and reproduction, we can also model the effects of behavioral variation. Here the transmitted information is not in the DNA at all and is thus not transmitted across generations (intergenerationally). Instead, this information is transmitted horizontally (intragenerationally), permitting more rapid ways for organisms to adjust to the environment. Finally, humans are unique in that we are the only species that horizontally transmits an arbitrary set of rules to govern communication, social interaction, and thought. This shared information is symbolic and has resulted in what we recognize as “culture”: an imaginary world of names, words, pictures, classifications, revered pasts, possible futures, spirits, dead ancestors, unborn descendants, in-laws, politeness, taboo, justice, beauty, and story, all accompanied by a material world of tools. This is a fourth, symbolic or cultural mode of transmission.

Consequently our post-Synthesis ideas about evolution tend to see the evolutionary processes as hierarchically organized and not restricted to simply the differential transmission of DNA sequences into the next generation. While that is indeed a significant part of evolution, the organism and species are nevertheless crucial to understanding how those DNA sequences get transmitted and cannot be taken for granted. Nor can we take for granted the complex roles

played by the transmission of epigenetic, behavioral, and symbolic information in perpetuating our genes, bodies, and species. In the case of human evolution, one can readily see that symbolic information and cultural adaptation are far more central to our lives and our survival today than DNA and genetic adaptation. It is thus misleading to think of humans passively occupying an environmental niche. Rather, humans are actively engaged in constructing our own niches, as well as adapting to them and using them to adapt. The complex interplay between a species and its active engagement in creating its own ecology is known as **niche construction**.

## THE BIOPOLITICS OF HEREDITY

Perhaps the hardest lesson about human evolution to learn is that it is intensely political. Indeed, to see it from the opposite side, as it were, the history of creationism is essentially a history of legal decisions: most famously, *Tennessee vs. John T. Scopes* (1925), in which a schoolteacher was prosecuted for violating a law in Tennessee that prohibited the teaching of human evolution in public schools, where public school teachers were required by law to teach creationism. More recently, *McLean vs. Arkansas* (1982) dispatched “scientific creationism”; and *Kitzmiller vs. Dover (Pennsylvania) Area School District* (2005), dispatched “intelligent design.” In some cases, people see unbiblical things in evolution, although most Christian theologians are easily able to reconcile science to the Bible. In other cases, people see immoral things in evolution, although there is morality and its opposite everywhere. And some people see evolution as an aspect of alt-religion, usurping the authority of science in schools to teach the rejection of the Christian faith, which would be unconstitutional.

Clearly, the position that there is no politics here is untenable. But is the politics in evolution an aberration or is it somehow embedded in the science, even if we don’t see it? In the early 20th century, scientists commonly promoted the view that science and politics were separate—science was a pure activity, only rarely corrupted by politics. And yet as early as World War I, the politics of nationalism made a hero of the German chemist Fritz Haber for inventing poison gas. And of course in World War II, German doctors and American physicists were recruited to the war effort and helped to end many civilian lives for different sides. So we now think of the apolitical scientist as a self-serving myth that functions merely to absolve scientists of responsibility for their politics. The history of science shows how every generation of scientists has used evolutionary theory to rationalize political and moral positions. In the very first generation of evolutionary science, Darwin’s *Origin of Species* (1859) is today far more readable than his *Descent of Man* (1871). The reason is that Darwin consciously purged *The Origin of Species* of any discussion of people, as we noted earlier. And when he finally got around to people, in *The Descent of Man*, he simply imbued them with the quaint Victorian prejudices of his age, and the result often makes you want to cringe every few pages. There is plenty of politics in there—sexism, racism, and colonialism at the very least—and that is simply because *you cannot talk about people apolitically*.

One immediate faddish deduction from Darwinism, popularized by Herbert Spencer as “survival of the fittest,” held that unfettered competition led to advancement in nature, and also in human history, and since the poor were losers in that struggle, anything that made their lives easier would go against the natural order. This position later came to be known ironically as “Social Darwinism.” Spencer was challenged by fellow Darwinian Thomas Huxley (“Man’s Place in Nature”), who agreed that struggle was the law of the jungle but observed that we don’t live in jungles any more. The obligation to make lives better for others is a moral, not a natural, fact. We simultaneously inhabit a natural universe of descent from apes and a moral universe of injustice and inequality, and science is not well served by ignoring the latter.

Concurrently, the German biologist Ernst Haeckel’s 1868 popularization of Darwinism was translated into English a few years later as *The History of Creation*. As we saw earlier, Haeckel was determined to convince his readers that they were descended from apes, even in the absence of fossil evidence attesting to it. When he made non-Europeans into the missing links that connected his readers to the apes, and depicted them as ugly caricatures, he knew precisely what he

was doing. Indeed, when the degrading racial drawings were deleted from the English translation of his book, the text nevertheless made his arguments quite clear. And a generation later, when the Americans had not yet entered the Great War in 1916, a biologist named Vernon Kellogg visited the German High Command as a neutral observer and found that the officers knew a lot about evolutionary biology, which they had gotten from Haeckel and which rationalized their military aggressions. Kellogg went home and wrote a bestseller about it, called *Headquarters Nights* (1917). World War I would have been fought with or without evolutionary theory, but as a source of scientific authority, evolution—even if a perversion of the Darwinian theory—had very quickly attained global geopolitical relevance.

Scientific racism, the recruitment of science for the evil political ends of racism, proved remarkably impervious to evolution. Before Darwin, there was creationist scientific racism, and after Darwin, there was evolutionist scientific racism. And there is still scientific racism, self-justified by recourse to evolution, which means that scientists have to be politically astute and sensitive to the uses of their work.

More commonly, however, the politics in the evolutionary science is subtle. This is in large part an expression of the advancement of science. We recognize the biases of our academic ancestors and modify our scientific stories accordingly. But we can never be free of our own cultural biases, which are invisible to us, as much as our predecessors' biases were invisible to them. In some cases, the most important cultural issues resurface in different guises each generation, like scientific racism.

Consider this: Are you just your ancestry, or can you transcend it? If that sounds like a weird question, it was actually quite important to a turn-of-the-20th-century European society in which an old hereditary aristocracy was under increasing threat from a rising middle class. And that is why the very first English textbook of Mendelian genetics concluded with the thought that “permanent progress is a question of breeding rather than of pedagogics; a matter of gametes, not of training ... the creature is not made but born.” (Punnett 1905, 60). *Translation: Not only do we now know a bit about how heredity works, but it's also the most important thing about you. Trust me, I'm a scientist.*

Yet evolution is about how descendants come to differ from ancestors. Do we really know that your heredity, your DNA, your ancestry, is the most important thing about you? That you were born, not made? After all, we do know that you could be born a slave or a peasant, and come from a long line of slaves or peasants, and yet not have slavery or peasantry be the most important thing about you. Whatever your ancestors were may constrain what you can be but probably should not, as a moral precept. But now we can also begin to see that ancestry is not a strictly biological concept. Human ancestry is biopolitics, not biology.

Evolution is fundamentally a theory about ancestry and yet ancestors are, in the broad anthropological sense, sacred—and often far more meaningful symbolically than biologically. Just a few years after *The Origin of Species*, the British politician and writer Benjamin Disraeli declared himself to be on the side of the angels, not the apes, and to “repudiate with indignation and abhorrence those new-fangled theories” (Monypenny 1920, 105) He turned his back on an ape ancestry and looked to the angel; yet, he did so as a prominent Jew-turned-Anglican, who had personally transcended his humble roots and risen to the pinnacle of the Empire. Ancestry was certainly important, and Disraeli was famously proud of his, but it was also certainly not the most important thing, not the primary determinant of his place in the world. Indeed, quite the opposite: Disraeli's life was built on the transcendence of many centuries of Jewish poverty and oppression in Europe. Humble ancestry was there to be superseded and nobility was there to be earned; Disraeli would later become the Earl of Beaconsfield. Clearly, “are you just your ancestry” is not a value-neutral question, and “the creature is not made, but born” is not a value-neutral answer.

The idea that the most important thing about you is your ancestry became popular twice in 20th century science. The first time was at the beginning of the century, when the **eugenics** movement in America called attention to feeble-minded stocks—which usually referred to the poor or immigrants (see Figure 2.15). This movement culminated in Congress restricting the immigration of feeble-minded races (notably Jews and Italians) in 1924, and the Supreme Court declaring it acceptable for states to sterilize their feeble-minded citizens involuntarily in 1927. When the Nazis picked up and embellished these ideas, Americans fell away from them during World War II.



Figure 2.15 Eugenic and Health Exhibit, Fitter Families exhibit and examination building, Kansas State Free Fair.

The second time that ancestry became paramount was as part of a successful attempt to drum up public support for the Human Genome Project in the 1990s. Public support for sequencing the human genome was encouraged by a popular science campaign that featured books titled *The Book of Man*, *The Human Blueprint*, and *The Code of Codes*. These books generally promised cures for genetic diseases and a deeper understanding of the human condition. We can certainly identify progress in molecular genetics over the last couple of decades since the human genome was sequenced, but that progress has notably not been accompanied by cures for genetic diseases, nor by deeper understandings of the human condition.

Even at the most detailed and refined levels of genetic analysis, we still don't have much of an understanding of the actual basis by which things seem to "run in families." While the genetic basis of simple, if tragic, genetic diseases have become well-known—such as sickle-cell anemia, cystic fibrosis, and Tay-Sachs' Disease—we still haven't found the ostensible genetic basis for traits that are thought to have a strong genetic component. For example, a recent genetic summary found over 600 genetic sites that contributed to height, yet nevertheless still explained only about 16 percent of the variation in height, which we know strongly runs in families (Wood et al., 2014).

Partly in reaction to the reductionistic hype of the Human Genome Project, the study of epigenetics has now become the subject of great clinical and evolutionary interest. One famous natural experiment involves a Nazi-imposed famine in Holland over the winter of 1944–1945. Children born during and shortly after the famine experienced a higher incidence of certain health problems as adults, many decades later. Apparently, certain genes had been down-regulated early in development and remained that way throughout the course of life. Indeed, this modified regulation of the genes in response to the severe environmental conditions may have been passed on to their children.

Obviously one's particular genetic constitution may play an important role in one's life trajectory. But overvaluing that role may have important social and political consequences. In the first place, genotypes are rendered meaningful in a cultural universe. Thus, if you live in a strongly patriarchal society and are born without a Y chromosome (since human males are chromosomally XY and females XX), your genotype will indeed have a strong effect upon your life course. So even though the variation is natural, the consequences are political. The mediating factors are the cultural ideas about how people ought to be treated, and the role of the state in permitting people to develop and thrive. More broadly, there are implications for public education if variation in intelligence is genetic. There are implications for the legal system if criminality is genetic. There are implications for the justice system if sexual preference, or sexual identity, is genetic. There are implications for the development of sports talent if that is genetic. And yet, even for the human traits that are more straightforward to measure and that are known to be strongly heritable, the DNA base sequence variation only seems to explain a little.

Genetic determinism or **hereditarianism** is the idea that "the creature is made, not born"—or, in a more recent

formulation by James Watson, that “our fate is in our genes.” One of the major implications drawn from genetic determinism is that the feature in question must inevitably express itself; therefore, we can’t do anything about it. Therefore, we might as well not fund the social programs designed to ameliorate economic inequality and improve people’s lives, because their courses are fated genetically. And therefore, they don’t deserve better lives.

All of the “therefores” in the preceding paragraph are open to debate. What is important is that the argument relies on a very narrow understanding of the role of genetics in human life, and it misdirects the causes of inequality from cultural to natural processes. By contrast, instead of focusing on the genes and imagining them to place an invisible limit upon social progress, we can study the ways in which your DNA sequence does *not* limit your capability for self-improvement or fix your place in a social hierarchy. In general, two such avenues exist. First, we can examine the ways in which the human body responds and reacts to environmental variation: human adaptability and plasticity. This line of research began with the anthropometric studies of immigrants by Franz Boas in the early 20th century and has now expanded to incorporate the epigenetic inheritance of modified human DNA. And second, we can consider how human lives are shaped by the social histories, and especially the structural inequalities within the societies in which they grow up.

Although it arises and is refuted every generation, the radical hereditarian position (genetic determinism) perennially claims to speak for both science and evolution. It does not. It is the voice of a radical fringe—perhaps naive, perhaps evil. It is not the authentic voice of science or of evolution. Indeed, keeping Charles Darwin’s name unsullied by protecting it from association with bad science often seems like a full-time job. Culture and epigenetics are very much a part of the human condition, and their roles are significant parts of the complete story of human evolution.

## ADAPTATION AND ADAPTATIONISM

Charles Darwin explained in material, naturalistic terms how animals adapt to their environments. The most fit, it seems, have survived over eons of the history of life on earth to co-create ecosystems full of animals and plants. Our own bodies are full of evident adaptations: eyes for seeing, ears for hearing, feet for walking on.

But what about hands? Feet are adapted to be primarily weight-bearing structures (rather than grasping structures, as in the apes) and that is what we primarily use them for. But we use our hands in many ways: for fine-scale manipulation, greeting, pointing, stimulating a sexual partner, writing, throwing, and cooking, among other uses. So which of these uses express what hands are “for,” when all of them express what hands do?

There is an important lesson in recognizing that what things do in the present is not a good guide to understand why they came to exist. Gunpowder was invented for entertainment—and only later adopted for killing people. The Internet was invented to decentralize computers in case of a nuclear attack—and only later adopted for social media. The apes have short thumbs and use their hands in locomotion; our ancestors stopped using their hands in locomotion by about six million years ago and had fairly modern-looking hands by about two million years ago. We can speculate that a combination of selection for abstract thought and dexterity led to evolution of the human hand, with its capability for tool-making that exceeds what apes can do (see Figure 2.16). But let’s face it—how many tools have you made today?

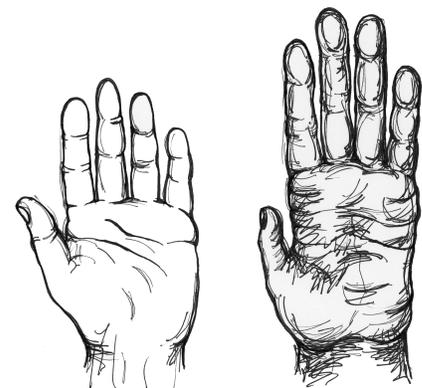


Figure 2.16 Chimpanzee hand (right) compared to a human hand (left).

Consequently, we are obliged to see the human foot as having a purpose to which it is adapted and the human hand as having multiple purposes, most of which are different from what it originally evolved for. Paleontologists Stephen Jay Gould and Elisabeth Vrba suggested that an original use be regarded as an



And third, the possibility of knowing what the reason for any particular feature is, assuming that it has one, is a challenge for evolutionary epistemology (the theory of how we know things). Consider the big adaptations of our lineage: bipedalism and language. Nobody doubts that they are good and they evolved by natural selection, and we know how they work. But why did they evolve? If talking and walking are simply better than not talking and not walking, then why did they evolve in just a single branch of the ape lineage in the primate family tree? We don't know what bipedalism evolved for, although there are plenty of speculations: walking long distances, running long distances, cooling the head, seeing over tall grass, carrying babies, carrying food, wading, threatening, counting calories, sexual display. Neither do we know what language evolved for, although there are speculations: coordinating hunting, gossiping, manipulating others. But it also possible that bipedality is simply the way that a small arboreal ape travels on the ground, if it isn't in the treetops. Or that language is simply the way that a primate with small canine teeth and certain mental propensities comes to communicate. If that were true, then there might be no reason for bipedality or language: having the unique suite of preconditions and a fortuitous set of circumstances simply set them in motion, and natural selection elaborated and explored their potentials. Possibly, walking and talking solved problems that no other lineage had ever solved; but even if so, the fact remains that rest of the species in the history of life have done pretty well without having solved them.

It is certainly very optimistic to think that all three assumptions (that organisms can be meaningfully atomized, that everything has a reason, and that we can know the reason) would be simultaneously in effect. Indeed, just as there are many ways of adapting (genetically, epigenetically, behaviorally, culturally), there are also many ways of being nonadaptive, which would imply that there is no reason at all for the feature in question.

First, there is the element of randomness of population histories. There are more cases of sickle-cell anemia among sub-Saharan Africans than other peoples, and there is a reason for it: carriers of sickle-cell anemia have a resistance to malaria, which is more frequent in parts of Africa (as discussed in Chapters 4 and 14). But there are more cases of a blood disease called variegated porphyria, a rare genetic metabolic disorder, in the Afrikaners of South Africa (descendants of mostly Dutch settlers in the 17th century) than in other peoples, and there is no reason for it. Yet we know the cause: One of the founding Dutch colonial settlers had the allele, and everyone in South Africa with it today is her descendant. But that is not a reason, that is simply an accident of history.

Second, there is the potential mismatch between the past and the present. The value of a particular feature in the past may be changed as the environmental circumstances change. Our species is diurnal, and our ancestors were diurnal. But beginning around a few hundred thousand years ago, our ancestors could build fires, which extended the light period, which was subsequently further amplified by lamps and candles. And over the course of the 20th century, electrical power has made it possible for people to stay up very late when it is dark—working, partying, worrying—to a greater extent than any other closely related species. In other words, we evolved to be diurnal, yet we are now far more nocturnal than any of our recent ancestors or close relatives. Are we adapting to nocturnality? If so, why? Does it even make any sense to speak of the human occupation of a nocturnal ape niche, despite the fact that we empirically seem to be doing just that? And if so, does it make sense to ask what the reason for it is?

Third, there is a genetic phenomenon known as a selective sweep, or the hitchhiker effect. Imagine three genes—A, B, and C—located very closely together on a chromosome. They each have several variants, or alleles, in the population. Now, for whatever reason, it becomes beneficial to have one of the B alleles, say B4; this B4 allele is now under strong positive selection. Obviously, we will expect future generations to be characterized by mostly B4. But what was B4 attached to? Because whatever A and C alleles were adjacent to it will also be quickly spread, simply by virtue of the selection for B4. Even if the A and C alleles are not very good, they will spread because of the good B4 allele between them. Eventually the linkage groups will break up because of genetic crossing-over in future generations. But in the meantime, some random version of genes A and C are proliferating in the species simply because they are joined to superior allele B4. And clearly, the A and C alleles are there because of selection—but not because of selection for them!

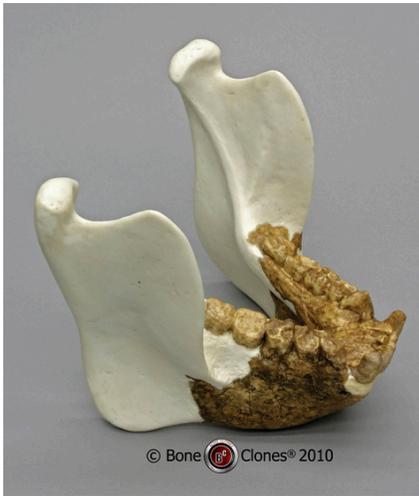


Figure 2.19 Lower jaw of *Gigantopithecus*.

Fourth, why does the jaw of the Miocene ape *Gigantopithecus* contain a first molar the size of a quarter? Was there something special about the enlarged molar? No, it had enormous jaws and teeth, and the first molar is simply one of them. This is the correlation of parts, the problem with atomizing the organism and imagining the parts to be existing and evolving independently. There is no reason for *Gigantopithecus* to have a large molar; there may well have been a reason that *Gigantopithecus*'s jaws (and, inferentially, head and body) were huge, but framing questions about the size of one tooth will never produce the correct answer (see Figure 2.19).

Fifth, some features are simply consequences of other properties rather than adaptations to external conditions. We already have noted the phenomenon of allometric growth, in which some physical features have to outgrow others simply to maintain function at an increased size. Can we ask the reason for the massive brow ridges of *Homo erectus*, or are brow ridges simply what you get when you have a conjunction of thick skull bones, a large face, and a sloping forehead—and, thus, again would have a cause but no reason?

Sixth, some features may be underutilized and on the way out. What is the reason for our two outer toes? They aren't propulsive, they don't do anything, and sometimes they're just in the way. Obviously they are there because we are descended from pentadactyl tetrapod ancestors. Is it possible that a million years from now, we will just have our three largest toes, just as the ancestors of the horse lost their digits in favor of a single hoof per limb? Or will our outer toes find another use, such as stabilizing the landings in our personal jet-packs? For the time being, we can just recognize vestigiality as another nonadaptive explanation for the presence of a given feature.

Finally, Darwin himself recognized that many obvious features do not help an animal survive. Some things may instead help an animal breed. The peacock's tail feathers do not help it eat, but they do help it mate. There is competition, but only against half of the species; Darwin called this **sexual selection**. Its result is not a fit to the environment but, rather, a fit to the opposite sex. In some species, that is literally the case, as the male and female genitalia have specific ways of anatomically fitting together. The specific form is less important than the specific match, so inquiring about the reason for a particular form of the reproductive anatomy may be misleading. The specific form may be effectively random, as long as it fits the opposite sex and is different from the anatomies of other species. Nor is sexual selection the only form of selection that can affect the body differently from natural selection. Competition might also take place between biological units other than organisms—perhaps genes, perhaps cells, or populations, or species. The spread of cultural things, such as head-binding or cheap refined fructose or forced labor, can have significant effects upon bodies, which are also not adaptations produced by natural selection. They are often adaptive physiological responses to stresses but not the products of natural selection.

Clearly, with so many paths available by which a physical feature might have naturalistically arisen without specifically having been the object of natural selection, it is unwise to simply assume that any individual trait is an adaptation. And that generalization applies to the best-known, best-studied, and most materially based evolutionary adaptations of our lineage. But our cultural behaviors are also highly adaptive, so what about our most familiar social behaviors? Patriarchy, hierarchy, warfare—are these adaptations? Do they have reasons? Are they good for something?

This is where some sloppy thinking has been troublesome. What would it mean to say that patriarchy evolved by natural selection in the human species? If, on the one hand, it means that the human mind evolved by natural selection to be able to create and survive in many different kinds of social and political regimes, of which patriarchy is one (or several), then biological anthropologists will readily agree. If, on the other hand, it means that patriarchy itself evolved by natural selection, that implies that patriarchy is genetically determined (since natural selection is a genetic process) and out-reproduced the alleles for other, more egalitarian, social forms. This in turn would imply that patriarchy is an adaptation

and therefore of some beneficial value in the past as well as an ingrained part of human nature today. This would be bad news, say, if you harbored ambitions of dismantling it. Dismantling patriarchy in that case would be to go against nature, a futile gesture. In other words, this latter interpretation would be a naturalistic manifesto for a conservative political platform: don't try to dismantle the patriarchy, because it is within us, the product of evolution—suck it up and live with it.

Here, evolution is being used simply as a political instrument for transforming the human genome into an imaginary glass ceiling against equality. There is thus a convergence between the pseudo-biology of crude adaptationism (the idea that everything is the product of natural selection) and the pseudo-biology of hereditarianism. Naturalizing inequality is not the business of evolutionary theory, and it represents a difficult moral position for a scientist to adopt, as well as a poor scientific position.

## MISCONCEPTIONS ABOUT HUMAN EVOLUTION

At root, human evolutionary theory consists of two propositions: (1) that the human species is descended from other similar species and (2) that natural selection has been the primary agency of biological adaptation. Pretty much everything else is subject to some degree of contestation. To conclude this chapter, let us call attention to some of the major corrections we would like to apply to popular misunderstandings of human micro- and macroevolution.

- There is no separation of culture from science, or facts from values, in human evolution.

As we have seen, the scientific study of who we are and where we come from is not biology. It is a branch of anthropology that overlaps in crucial ways with biology, and yet it also traffics in the world of politics, cultures, moral codes, and histories. This is not to say that other sciences can necessarily be free of culture but simply that it is easier to be objective about boron than about your ancestors. Narratives about ancestors are invariably sacred stories, and biological anthropologists incur an unusual responsibility in being the scientific custodians of our ancestors' stories—writing and validating their stories, shepherding them through history.

- Equality is not identity.

The great geneticist Theodosius Dobzhansky emphasized the distinction between equality (a political state) and identity (a biological state). Sameness/difference is unrelated to equal/unequal, under our system of government. No matter what kind of person you are, you are entitled to equality. Consequently all discussions of race or sex are irrelevant to questions of rights: All citizens are entitled to equal rights. The difficulty is how to guarantee that all receive them, which is a political issue, because obviously there is a great deal of inequality in America. Patterns of social inequality are not grounded in human biological variation. It has become a moral challenge for the nation and for science to better understand this fact, particularly as critiques of equality are too often accompanied by pseudo-biological arguments.

- All humans are equally close to apes, despite the attempt of some people to question the essential humanity of certain populations by suggesting that some people are more apelike than others.

The suggestion that some groups of humans are more naturally apelike than others is a recurrent slander of the modern age. Apelike is obviously a synonym for subhuman; and the symbolic association of apes with African peoples is actually a pre-Darwinian slur, from centuries before evolutionary theory was developed. All humans are equally distantly related from the chimpanzee, but some humans, especially people of color, have

been symbolically dehumanized throughout modern history by associating them with apes. Consequently, such a comparison is no longer considered funny.

- Competition can take many forms other than overt aggression.

Some biologists use Darwinism as a way of rationalizing war, arguing that even though war sucks, it is the very competition among political entities that leads to social advances in human history. But even Darwin knew that it wasn't necessarily the case, and it remains a problematic moral position. Darwin's intellectual inspiration here was actually the Scottish economist Adam Smith, whose 1776 book *The Wealth of Nations* is the foundation of modern capitalism. Smith argued that people simply acting in their own best interests in competition with one another would naturally form complex thriving economic systems, which would function to the mutual prosperity of all, as if guided by an "invisible hand." The competition was neither cutthroat nor physical. Today we recognize competition as potentially occurring in many ways and between several different kinds of things, from DNA segments to cultural artifacts. Physical aggression is one way humans have interacted competitively, but there is nothing particularly Darwinian in the attempt to identify merit in war. A conscientious scientist is more interested in ways to avert it.

- There is no "person of the future."

We do the great bulk of our adapting culturally, although our gene pool is continually being tweaked by diseases and demographic trends. But of course we cannot predict future environments for our descendants to adapt to, culturally or naturally. The idea that our species is simply a way station for the next great step in evolution betrays teleological thinking about history—that is, the idea that history is preset and that there is a path down which we are proceeding. But there is no path; there is only the present and possible solutions to the problems of the present. Consequently, there is no way to know what a "person of the future" might look like. No lateral toes? Maybe. No wisdom teeth? Maybe. A brain the size of a basketball? Not without radically restructuring the maternal anatomy and the birth process. Perhaps with the colonization of other planets, our own species will undergo novel forms of selection and a great deal of founder effect or genetic drift. But their products are inherently unpredictable.

- Evolution is more like a tree than like an escalator.

Darwin thought of evolution as producing separate branches, like those of a tree, with the tips representing living species. But the word *evolution* implies to many people an unfolding, a development along a path—this is what the word meant initially to Darwin, who avoided it in the first edition of *The Origin of Species*. Teleological theories of evolution have indeed been proposed from time to time, but if we see evolution as divergence rather than improvement, then we reject teleology. When creationists ask, "If we evolved from monkeys, then why are there still monkeys?" they are imagining evolution as a teleological process. The pre-Darwinian evolutionist Lamarck imagined that in the face of extinction a species could survive by changing into something a little higher up on the Great Chain of Being. In such a world, monkeys might constantly be evolving into people, but that is not a branching, Darwinian world. Rather, we would say that our monkey ancestor diverged and eventually became an ape-like creature but did so without necessarily exterminating monkeys in the process. Interestingly, genomics is now revealing that speciation is commonly less complete than we used to imagine, and ostensibly discrete branches sometimes come together. This might call for a new metaphor to describe human evolution, such as the roots of a tree, rather than its branches.

- Bible scholarship does not conflict with science.

Contemporary scholars recognize that the Bible is a collection of traditional stories and tales, culled from a larger

set of writings from various times and places and later collected into a single volume. They have meant, and continue to mean, different things to different communities. For many centuries, scholars have studied what the texts mean, assuming that the Bible's meanings are neither obvious nor literal but relevant to the lives of worshippers in any specific time and place and denomination. Consequently, there can be no "true meaning" of the Bible, only the most useful and appropriate meaning for the particular community. Biblical literalism is a very recent phenomenon, independent of the centuries-old humanistic traditions of biblical scholarship, and it demands a very selective and arbitrary approach to the texts chosen to be taken literally. The creationist today thus rejects not merely modern scientific scholarship but modern biblical scholarship as well. Nevertheless, many Jewish, Catholic, and Protestant scholars, as well as scholars from other religious traditions in the modern age, are actively engaged in understanding what it means to lead a fulfilled life in a post-Darwinian world.

Now that you've finished this chapter on evolution, you are equipped to go into the post-Darwinian world armed with an understanding of the true intentions of Darwin's work, and where his findings part from past and current racist misinterpretations of his theories. You understand that politics is often inseparable from biology, no matter the best intentions toward objectivity of the scientist.

## Review Questions

- How is the study of your ancestors biopolitical, not just biological? Does that make it less scientific or differently scientific?
- What was gained by reducing organisms to genotypes and species to gene pools? What is gained by reintroducing bodies and species into evolutionary studies?
- How do genetic or molecular studies complement anatomical studies of evolution?
- How are you reducible to your ancestry? If you could meet your ancestors from the year 1700 (and you would have well over a thousand of them!), would their lives be meaningfully similar to yours? Would you even be able to communicate with them?
- The molecular biologist François Jacob argued that evolution is more like a tinkerer than like an engineer. In what ways do we seem like precisely engineered machinery, and in what ways do we seem like jerry-rigged or improvised contraptions?

## Key Terms

**Adam and Eve:** According to the Bible (Genesis 2–3), the first two people are Adam (man) and Eve (life). They inhabit The Garden of Eden, with a Tree of Life and a Tree of the Knowledge of Good and Evil in the center. They are instructed not to eat the fruit of the latter tree, but they do so anyway and are subsequently cursed and expelled from the garden. This forms the basis for the traditional origin myth of Jews, Muslims and Christians.

**Adaptation:** A fit between the organism and environment.

**Allele:** A genetic variant.

**Blending Inheritance:** Heredity conceptualized as a mixture of fluids. Its opposite would be particulate inheritance, where heredity is regarded as the interaction of discrete elements and provides the basis of Mendelian genetics.

**Canalization:** The tendency of a growing organism to be buffered toward normal development.

**Descent with Modification:** Darwin's term for what we now call "evolution," in which animals and plants look different from their ancestors.

**Epigenetics:** The study of how genetically identical cells and organisms (with the same DNA base sequence) can nevertheless differ in stably inherited ways.

**Epistemes:** Fundamental cultural ideas, which organize the world and help to render it meaningful. Similar to paradigm.

**Eugenics:** An idea that was popular in the 1920s that society should be improved by breeding better kinds of people.

**Evo-devo:** The study of the origin of form; a contraction of "evolutionary developmental biology."

**Exaptation:** An additional beneficial use for a biological feature.

**Extinction:** The loss of a species from the face of the earth.

**Founder Effect:** The reduced genetic diversity that results when a population is descended from a small number of ancestors.

**Gene:** A stretch of DNA with an identifiable function (sometimes broadened to include any DNA with recognizable structural features as well).

**Gene Flow:** Geographical movement of genes, due to the contact of populations.

**Gene Pool:** Hypothetical summation of the entire genetic composition of population or species.

**Genetic Drift:** Random, short-term perturbations to the gene pool, with nonadaptive effects.

**Genotype:** Genetic constitution of an individual organism.

**Hereditarianism:** The idea that genes or ancestry is the most crucial or salient element in a human life. Generally associated with an argument for natural inequality on pseudo-genetic grounds.

**Homology:** Correspondence of parts between species due to the mutual inheritance of a primordial form from a common ancestor.

**Inheritance of Acquired Characteristics:** The idea that you pass on the features that developed during your lifetime, not just your genes; also known as Lamarckian inheritance.

**Monogenism:** The idea that all people share a common single origin.

**Mutation:** An alteration to the base sequence of DNA.

**Natural Selection:** A consistent bias in survival and fertility, leading to the over-representation of certain features in future generations and an improved fit between an average member of the population and the environment.

**Niche Construction:** The active engagement by which species transform their surroundings in favorable ways, rather than passively inhabiting them.

**Noah's Ark:** According to the Bible (Genesis 6–9), God decides to destroy all life because of the wickedness of people,

but he saves a righteous man named Noah, his three sons, and their wives. They build a large boat and preserve pairs of all the animals; the boat eventually lands “on the mountains of Ararat” and the world is subsequently repopulated. Other ancient cultures also have cognate myths about a flood, boat-builder, and animal-saver, with differing details.

**Phenotype:** Observable manifestation of a genetic constitution, expressed in a particular set of circumstances.

**Plasticity:** The tendency of a growing organism to react developmentally to its particular conditions of life.

**Polygenism:** The idea that different peoples have different origins.

**Phrenology:** The 19<sup>th</sup> century anatomical study of bumps on the head as an indication of personality and mental abilities.

**Punctuated Equilibria:** The idea that species are stable through time and are formed very rapidly relative to their duration. (The opposite, that species are unstable and constantly changing through time, is called phyletic gradualism.)

**Savage:** A dehumanizing term used by pre-modern European scholars to suggest that other cultures were primitive, violent, immoral, and illogical.

**Sexual Selection:** Natural selection arising through preference by one sex for certain characteristics in individuals of the other sex.

**Synonymous Mutation:** A change in the DNA sequence that codes for amino acids in a protein sequence, but does not change the encoded amino acid.

**Synthetic Theory of Evolution:** Explains the evolution of life in terms of genetic changes occurring in the population that leads to the formation of new species.

**Species Selection:** A postulated evolutionary process in which selection acts on an entire species population, rather than individuals.

**Teleological:** The explanation of phenomena in terms of the purpose they serve rather than of the cause by which they arise.

**Tower of Babel:** According to the Bible (Genesis 11), all people once spoke a single language and decided to cooperate to build a giant tower that would stretch into the heavens. For this arrogance, they are made to speak different languages and must give up building the tower. The story’s setting is generally thought to refer to the ancient ziggurats of Babylonia.

**Transmutation Hypothesis:** The nineteenth century idea that life forms were spontaneously generated and not descended from a common ancestor.

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Jonathan Marks is Professor of Anthropology at the University of North Carolina at Charlotte. He has published many books and articles on broad aspects of biological anthropology. In 2006 he was elected a Fellow of the American Association for the Advancement of Science. In 2012 he was awarded the First Citizen's Bank Scholar's Medal from UNC Charlotte. In recent years he has been a Visiting Research Fellow at the ESRC Genomics Forum in Edinburgh, at the Max Planck Institute for the History of Science in Berlin, and a Templeton Fellow at the Institute for Advanced Study at Notre Dame. His work has received the W. W. Howells Book Prize and the General Anthropology Division Prize for Exemplary Cross-Field Scholarship from the American Anthropological Association as well as the J. I. Staley Prize from the School for Advanced Research. Two of his books are called *What It Means to Be 98% Chimpanzee* and *Why I Am Not a Scientist*, but actually he is about 98 percent scientist and not a chimpanzee.

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