HUMAN EVOLUTION

FIFTH EDITION

HUMAN EVOLUTION: AN ILLUSTRATED INTRODUCTION

Roger Lewin

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PREFACE

The pattern of treatment of issues in this new edition follows that established with the fourth edition; nevertheless there are important changes. For instance, in the preface to the previous edition I wrote, "The five years since the third edition of *Human Evolution: An Illustrated Introduction* have been an extraordinarily productive time for paleoanthropology," not least because of the number of new species of early humans that had been discovered. The same can be said of the period between the fourth and fifth editions. Since 1999 four new species of hominin have been announced. (Hominin is the term now used for members of the human family.)

Of the four new species, three have been assigned to new genera. Two of them are older than anything known previously, dated at 6 to 7 million years old. One of them was found in Chad, rather than in East Africa. And another, *Kenyanthropus platyops* (3.5 million years old, from Kenya), has the kind of flat face that was thought to have arisen much later in hominin history. Clearly, hominin history is turning out to be much more complex than previously assumed. Description and discussion of these finds represents one of the major changes from the fourth edition, which involves a thorough reorganization of units dealing with this period.

The origin of modern humans continues to be a major topic in paleoanthropology, as Curtis Marean and Jessica Thompson noted in their report of the 2002 meeting of the Paleoanthropology Society.* The debate over the mode of the origin of modern humans—was it a single, recent origin or global and gradual—continues, but new genetic evidence adds further support to the notion of a single, recent origin. Some of this evidence comes in the form of mitochondrial DNA analysis of a Neanderthal specimen from the northern Caucasus. The announcement, in mid-2003, of a 160,000-year-old specimen of early *Homo sapiens* from Ethiopia also strengthens the argument for a single, recent origin, in Africa. Becoming more center stage in discussions over modern human origins, however, is the evolution of modern human behavior. Was it recent and dramatic, or more gradual, with deeper roots? Evidence for the latter is growing. All these aspects of the debate are updated in this edition in what remains a strong contribution to *Human Evolution*.

The trend continues in paleoanthropology from viewing human evolution as having occurred under special circumstances to accepting humans as animals and having evolved in ways similar to other animals. Humans are special in many ways, of course, but this specialness is a feature that emerges relatively late in our evolutionary history. This is recognized here in discussions of life-history factors and the impact of body size and shape.

Many new finds and insights are included in this new edition, including, among others, the redating of an important specimen in Australia, at Lake Mungo. Previously thought to be 25,000 years old, the Lake Mungo cranium is now shown to be 42,000 years old, and tools at a nearby site are close to 50,000 years old, establishing a relatively early occupation of the continent. Another important change is the realization that *Homo ergaster* may not, after all, have experienced prolonged infancy. That change in human development appears to have occurred later in the lineage. And Morris Goodman continues to tweak paleoanthropologists' tails by suggesting that both humans and chimpanzees be placed in the same genus, *Homo*.

Obviously, paleoanthropology continues to be a healthy, robust science, embracing new facts and reinterpretations in the search for the pattern of human history. As always, however, it is worth remembering that when the subject of scientific scrutiny is ourselves and how we came to be who we are, subjectivity is a constant trap. As I noted in the previous edition, "Armed with this knowledge, the student is better prepared to assess what is being said in one debate or another in the science."

Christopher Ruff, Ian Tattersall, and Alan Walker were kind enough to comment on new material in the book. The responsibility for the final product is, of course, mine.

Roger Lewin
Cambridge, Massachusetts

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* Marean CW, Thompson JC. Research on the origin of modern humans continues to dominate paleoanthropology. *Evol Anthropol* 2003;12:165–167.

PART 1

HUMAN EVOLUTION IN PERSPECTIVE

1 OUR PLACE IN NATURE

The Darwinian revolution forced people to face the fact that humans are part of nature, not above nature. Nevertheless, anthropologists struggled with explaining the special features of Homo sapiens, *such as our great intelligence, our sense of right and wrong, our esthetic sensibilities. Only since the latter part of the twentieth century have anthropologists fully embraced naturalistic explanations of our special qualities.*

In 1863 Charles Darwin's friend and champion, Thomas Henry Huxley, published a landmark book, titled *Evidences as to Man's Place in Nature*. The book, which appeared a little more than three years after Darwin's *Origin of Species*, was based principally on evidence from comparative anatomy and embryology among apes and humans. (There was essentially no fossil evidence of early humans available at that time, apart from the early Neanderthal finds, which were not yet accepted as early humans by most anthropologists; see unit 27.) Huxley's conclusion—that humans share a close evolutionary relationship with the great apes, particularly the African apes—was a key element in a revolution in the history of Western philosophy: humans were to be seen as being *a part of* nature, no longer as *apart from* nature.

Although Huxley was committed to the idea of the evolution of *Homo sapiens* from some type of ancestral ape, he nevertheless considered humans to be a very special kind of animal. "No one is more strongly convinced than I am of the vastness of the gulf between . . . man and the brutes," wrote Huxley, "for, he alone possesses the marvellous endowment of intelligible and rational speech [and] . . . stands raised upon it as on a mountain top, far above the level of his humble fellows, and transfigured from his grosser nature by reflecting, here and there, a ray from the infinite source of truth."

EXPLAINING THE "GAP" BETWEEN HUMANS AND ANIMALS

The explanation of this "gap" between humans and the rest of animate nature has always exercised the minds of Western intellectuals, in both pre- and post-evolutionary eras. One difference between the two eras was that, after Darwin, naturalistic explanations had to account not only for the human physical form but also for humans' exceptional intellectual, spiritual, and moral qualities. Previously, these qualities had been regarded as God-given.

As a result, said the late archeologist Glynn Isaac, "Understanding the literature on human evolution calls for the recognition of special problems that confront scientists who report on this topic." He made the remark at the 1982 centenary celebration of Darwin's death. "Regardless of how scientists present them, accounts of human origins are read as replacement materials for Genesis. They . . . do more than cope with curiosity, they have allegorical content, and they convey values, ethics and attitudes." In other words, in addition to reconstructing phylogenies—or evolutionary family trees—paleoanthropological research also addresses "Man's place in nature" in more than just the physical sense. As we shall see, that "place" has long been regarded as being special in some sense.

The revolution wrought by Darwin's work was, in fact, the second of two such intellectual upheavals within the history of Western philosophy. The first revolution occurred three centuries earlier, when Nicholaus Copernicus replaced the geocentric model of the universe (see figure 1.1) with a heliocentric model. Although the Copernican revolution deposed humans from being the cosmic center of all of God's creation and transformed humans into the occupants of a small planet cycling in a vast universe, humans nevertheless remained the pinnacle of God's works. From the sixteenth through the mid-nineteenth centuries, those who studied humans and nature as a whole were coming close to the wonder of those works.

This pursuit—known as **natural philosophy**—positioned science and religion in close harmony, with the remarkable design so clearly manifested in creatures great and small being seen as evidence of God's hand. In addition to design, a second feature of God's created world was natural hierarchy, from the lowest to the highest, with humans being near the

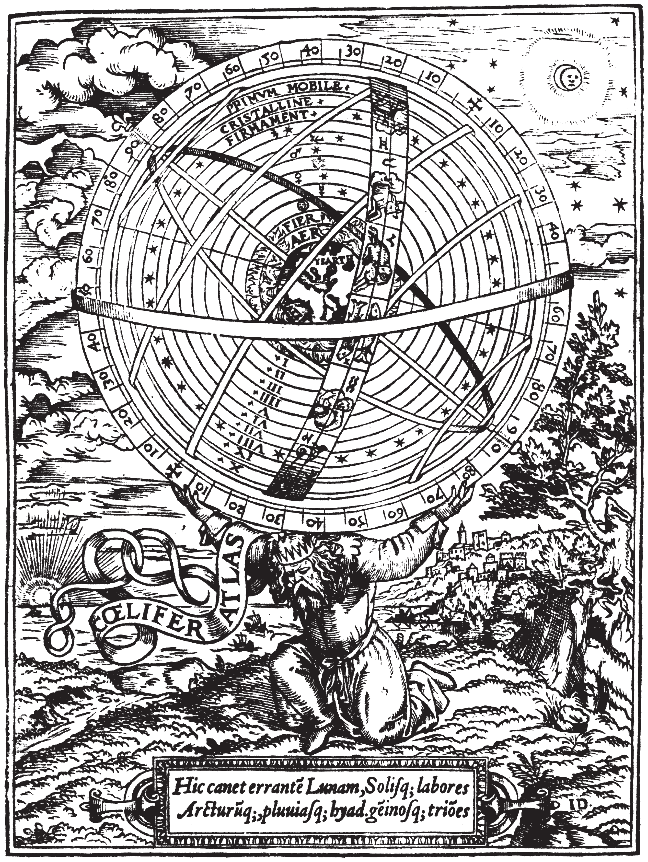


FIGURE 1.1 Ptolemy's universe: Before the Copernican revolution in the sixteenth century, scholars' views of the universe were based on ideas of Aristotle. The Earth was seen as the center of the universe, with the Sun, Moon, stars, and planets fixed in concentric crystalline spheres circling it.

FIGURE 1.2 The anthropomorpha of Linnaeus: In the mid-eighteenth century, when Linnaeus compiled his *Systema Naturae*, Western scientific knowledge about the apes of Asia and Africa was sketchy at best. Based on tales of sea captains and other transient visitors, fanciful images of these creatures were created. Here, produced from a dissertation of Linnaeus' student Hoppius, are four supposed "manlike apes," some of which became species of *Homo* in Linnaeus' *Systema Naturae*. From left to right: *Troglodyta bontii*, or *Homo troglodytes*, in Linnaeus; *Lucifer aldrovandii*, or *Homo caudatus*; *Satyrus tulpii*, a chimpanzee; and *Pygmaeus edwardi*, an orangutan.

very top, just a little lower than the angels. This continuum —known as the **Chain of Being**—was not a statement of evolutionary relationships between organisms, reflecting historical connections and evolutionary derivations. Instead, noted the late Stephen Jay Gould, "The chain is a static ordering of unchanging, created entities, a set of creatures placed by God in fixed positions of an ascending hierarchy."

Powerful though it was, the theory faced problems—specifically, some unexplained gaps. One such discontinuity appeared between the world of plants and the world of animals. Another separated humans and apes.

Knowing that the gap between apes and humans should be filled, eighteenth- and early-nineteenth-century scientists tended to exaggerate the humanness of the apes while overstating the simianness of some of the so-called "lower" races. For instance, some apes were "known" to walk upright, to carry off humans for slaves, and even to produce offspring after mating with humans. By the same token, some humans were "known" to be brutal savages, equipped with neither culture nor language.

This perception of the natural world inevitably became encompassed within the formal classification system, which was developed by Carolus Linnaeus in the mid-eighteenth century. In his *Systema Naturae*, published first in 1736 with a tenth edition in 1758, Linnaeus included not only *Homo sapiens*—the species to which we all belong—but also the little-known *Homo troglodytes*, which was said to be active only at night and to speak in hisses, and the even rarer *Homo caudatus*, which was known to possess a tail. (See figure 1.2.) "Linnaeus worked with a theory that anticipated such creatures," noted Gould; "since they should exist anyway, imperfect evidence becomes acceptable." This concept did not represent scientific finagling, but rather proved that honest scientists saw what they expected to see. This human weakness has always operated in science—in all sciences—and always will.

CATASTROPHISM GIVES WAY TO UNIFORMITARIANISM

The notion of evolution—the transmutation of species—had been in the air for a long time when, in 1859, the power of data and argument in the *Origin of Species* proved decisive. Geological ideas had been changing as well. In 1808 Baron Georges Cuvier, a zoologist and paleontologist at the Paris Natural History Museum, suggested that there had been a series of great deluges throughout Earth history, each of which wiped out all existing species. Following each catastrophe, the Earth was repopulated in a wave of creation. This theory, which came to be known as **Catastrophism**, was warmly embraced by intellectuals in Europe, as it accepted scientific observation while maintaining much of the biblical account, including the Noachim flood. (See also unit 6.)

The theory of Catastrophism soon found itself in competition with a new hypothesis: **Uniformitarianism**, which views the major geological features of the Earth as the outcome of everyday, gradual processes, not occasional violent events. James Hutton, a Scotsman, seeded the ideas of Uniformitarianism, but it was Charles Lyell, another Scotsman, who solidified the ideas, effectively becoming the founder of modern geology. Both men were impressed by the power of erosion they observed in their studies, and reasoned that with sufficient time major geological features could be fashioned by such forces.

Lyell published his work in three volumes, *The Principles of Geology*, the first of which appeared in 1830. One of the conclusions of Uniformitarianism was that the Earth is unimaginably old, not the 6000 years that was commonly believed at that time. This was important for Charles Darwin's development of the theory of natural selection, which is based on the accumulation of small changes over long periods of time.

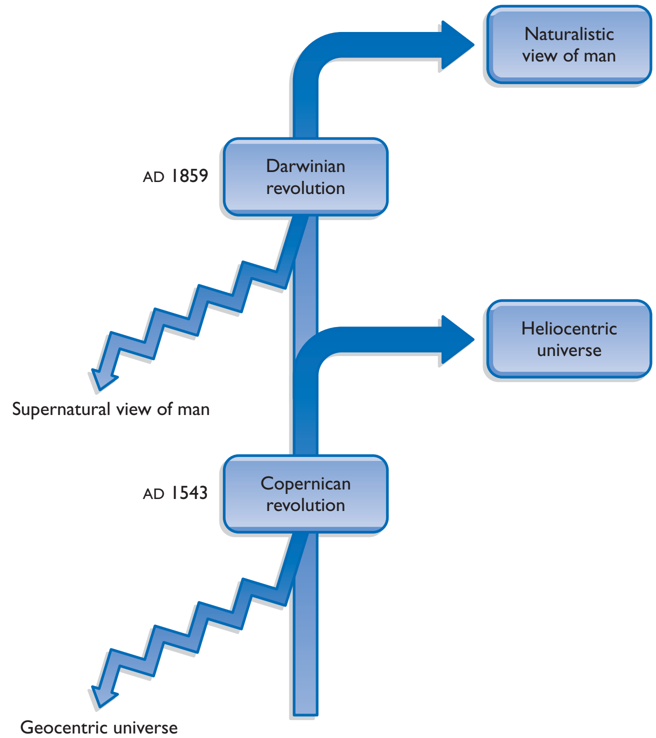


FIGURE 1.3 Two great intellectual revolutions: In the mid-sixteenth century the Polish mathematician Nicolaus Copernicus proposed a heliocentric rather than a geocentric view of the universe. "The Earth was not the center of all things celestial," he said, "but instead was one of several planets circling a sun, which was one of many suns in the universe." Three centuries later, in 1859, Charles Darwin further changed Man's view of himself, arguing that humans were a part of nature, not apart from nature.

SAME OBSERVATION, DIFFERENT EXPLANATION

The impact of, first, the Copernican revolution, and, second, the Darwinian revolution, was to place humans in a naturalistic context. (See figure 1.3.) Interestingly, although the advent of the evolutionary era brought an enormous shift in intellectual perceptions of the *origin* of humankind, many elements concerning the *nature* of mankind remained unassailed. For instance, humans were still regarded as being "above" other animals and endowed with special qualities—those of intelligence, spirituality, and moral judgment. And the gradation from the so-called "lower" races to "higher" races that had been part of the Chain of Being was now explained by the process of evolution.

"The progress of the different races was unequal," noted Roy Chapman Andrews, a researcher at the American Museum of Natural History in the 1920s and 1930s. "Some developed into masters of the world at an incredible speed. But the Tasmanians . . . and the existing Australian aborigines lagged far behind, not much advanced beyond the stages of Neanderthal man." Such overtly racist comments were echoed frequently in literature of the time and were reflected in the evolutionary trees published then. (See, for example, figure 1.4.)

In other words, inequality of races—with blacks on the bottom and whites on the top—was explained away as the natural order of things: before 1859 as the product of God's creation, and after 1859 as the product of natural selection.

In the same vein, nineteenth-century discussions of human evolution incorporated the notion of progress, and specifically the inevitability of *Homo sapiens* as the ultimate aim of evolutionary trends. "Much of evolution looks as if it had been planned to result in man, and in other animals and plants to make the world a suitable place for him to dwell in," observed Robert Broom in 1933. (Broom, a Scottish paleontologist, was responsible for some of the more important early human fossil finds in South Africa during the 1930s and 1940s.)

EVOLUTION AS PROGRESS

Evolution as progress—the inexorable improvement to more complex, more intelligent life—has always been a seductive notion. "Progress—or what is the same thing, Evolution—is [Nature's] religion," wrote Britain's Sir Arthur Keith in 1927. The notion of progress as a driving ethos of nature—and society—has been a characteristic of Western philosophy,

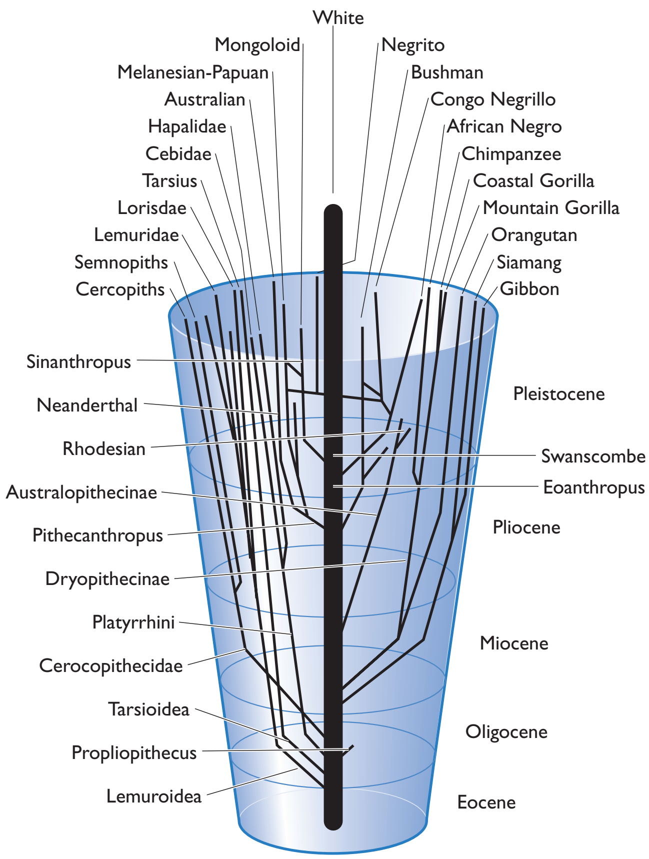


FIGURE 1.4 Racism in anthropology: In the early decades of the twentieth century, racism was an implicit part of anthropology, with "white" races considered to be superior to "black" races, through greater effort and struggle in the evolutionary race. Here, the supposed ascendancy of the "white" races is shown explicitly, in Earnest Hooton's *Up from the Ape* (2nd ed., 1946).

but not of all intellectual thought. "The myth of progress" is how Niles Eldredge and Ian Tattersall characterize this idea. "Once evolved, species with their own peculiar adaptations, behaviors, and genetic systems are remarkably conservative, often remaining unchanged for several million years. In this light it is wrong to see evolution, or for that matter human history, as a constant progression, slow or otherwise."

Some species later in evolutionary time are clearly more complex in certain ways than many found earlier in time. This development can, however, be explained simply as the ratchet effect—the fact that evolution builds on what existed before. For the most part, the world has not become a strikingly more complex place biologically as a whole. Although most organisms remain simple, we remain blinded by the exceptions, particularly the one with which we are most familiar.

Even this brief historical sketch clearly illustrates the **anthropocentric** spectacles through which paleoanthropologists have viewed the natural world in which we evolved. Such a perception is probably inescapable to some degree, as Glynn Isaac's earlier remark implied. In 1958, for instance, Julian Huxley, grandson of Thomas Henry, suggested that mankind's special intellectual and social qualities should be recognized formally by assigning *Homo sapiens* to a new grade, the Psychozoan. "The new grade is of very large extent, at least equal in magnitude to all the rest of the animal Kingdom," he wrote, "though I prefer to regard it as covering an entirely new sector of the evolutionary process, the psychosocial, as against the entire non-human biological sector."

The ultimate issue is "the long-held view that humans are unique, a totally new type of organism," as Cambridge University's Robert Foley points out. This type of thinking leads to the notion that human origin therefore "requires a special type of explanation, different from that used in understanding the rest of the biological world." That, of course, is untrue, but it has been only since the latter part of the twentieth century that paleoanthropology has become fully committed to finding purely biological explanations for the origin of the undoubtedly special features possessed by *Homo sapiens*. But, as the following unit shows, the nature of the science and its quest makes complete objectivity difficult.

KEY QUESTIONS

- Did the intellectual framework provided by the great Chain of Being lead naturally to the idea of the evolution of species?
- Why did the perception of Man's place in nature not change much in some ways between pre- and post-Darwinian eras?
- Why has the notion of progress become such an integral part of evolutionary thinking within Western philosophy, particularly in relation to human evolution?
- Does the evolution of qualitatively novel characteristics require qualitatively novel explanations?

KEY REFERENCES

Cartmill M. Human uniqueness and theoretical content in paleoanthropology. *Int J Primatol* 1990;11:173–192.

Dawkins R. The blind watchmaker. Harlow: Longman, 1986.

Eldredge N, Tattersall I. The myths of human evolution. New York: Columbia University Press, 1982.

Gould SJ. Vision with a vengeance. *Natural History* Sept 1980:16–20.

———. Bound by the great chain. *Natural History* Nov 1983:20–24.

———. Chimp on a chain. *Natural History* Dec 1983:18–26.

———. Spin doctoring Darwin. *Natural History* July 1995:6–9, 69–71.

Lewin R. Chapter 2, Bones of contention. Chicago: The University of Chicago Press, 1997.

Lovejoy AO. The great chain of being. Cambridge, MA: Harvard University Press, 1970.

Richards RJ. The meaning of evolution. Chicago: The University of Chicago Press, 1992.

Tattersall I. Becoming human: evolution and human uniqueness. New York: Harcourt Brace and Company, 1998.

2 HUMAN EVOLUTION AS NARRATIVE

In the early twentieth century, explanations of human evolution were often constructed as stories, particularly hero myths. Human ancestors were seen as overcoming great challenges, and finally triumphing. Part of the story was an implicit inevitability, that Homo sapiens *was an inevitable outcome of evolution. Even today, because the narrative form is so powerful and seductive, it is hard to avoid.*

"One of the species specific characteristics of *Homo sapiens* is a love of stories," noted Glynn Isaac, "so that narrative reports of human evolution are demanded by society and even tend toward a common form." Isaac was referring to the work of Boston University anthropologist Misia Landau, who has analyzed the **narrative** component of professional—not just popular—accounts of human origins.

"Scientists are generally aware of the influence of theory on observation," concludes Landau. "Seldom do they recognize, however, that many scientific theories are essentially narratives." Although this comment applies to all sciences, Landau identifies several elements in **paleoanthropology** that make it particularly susceptible to being cast in narrative form, both by those who tell the stories and by those who listen to them.

First, in seeking to explain human origins, paleoanthropology is apparently faced with a sequence of events through time that transformed apes into humans. The description of such a sequence falls naturally into narrative form. Second, the subject of that transformation is ourselves. Being egotistical creatures, we tend to find stories about ourselves more interesting than stories about, for instance, the behavior of arthropods or the origin of flowering plants.

SAME STORY, DIFFERENT SEQUENCES

Traditionally, paleoanthropologists have recognized four key events in human evolution: the origin of **terrestriality** (coming to the ground from the trees), **bipedality** (upright walking), **encephalization** (brain expansion in relation to body size), and **culture** (or civilization). While these four events have usually featured in accounts of human origins, paleoanthropologists have disagreed about the order in which they were thought to have occurred. (See figure 2.1.)

For instance, Henry Fairfield Osborn, director of the American Museum of Natural History in the early decades of the twentieth century, considered the order to be that given above, which, incidentally, coincides closely with Darwin's view. Sir Arthur Keith, a prominent figure in British anthropology in the 1920s, considered bipedalism to have been the first event, with terrestriality following. In other words, Keith's ancestral ape began walking on two legs while it was still a tree dweller; only subsequently did it descend to the ground. For Sir Grafton Elliot Smith (figure 2.2), a contemporary of Keith, encephalization led the way. His student, Frederic Wood Jones, agreed with Smith that encephalization and bipedalism developed while our ancestor lived in trees, but thought that bipedalism preceded rather than followed brain expansion. William King Gregory, like his colleague Osborn, argued for terrestriality first, but suggested that the adoption of culture (tool use) preceded significant brain expansion. And so on.

Thus, we see these four common elements linked together in different ways, with each narrative scheme purporting to tell the story of human origins. And "story" is the operative word here. "If you analyze the way in which Osborn, Keith and others explained the relation of these four events, you see clearly a narrative structure," says Landau, "but they are more than just stories. They conform to the structure of the hero folk tale." In her analysis of paleoanthropological literature, Landau drew upon a system devised in 1925 by the Russian literary scholar Vladimir Propp. This system, published in Propp's *Morphology of the Folk Tale*, included a series of 31 stages that encompassed the basic elements of the hero myth. Landau reduced the number of stages to nine, but kept the same overall structure: hero enters; hero is challenged; hero triumphs. (See figure 2.3.)

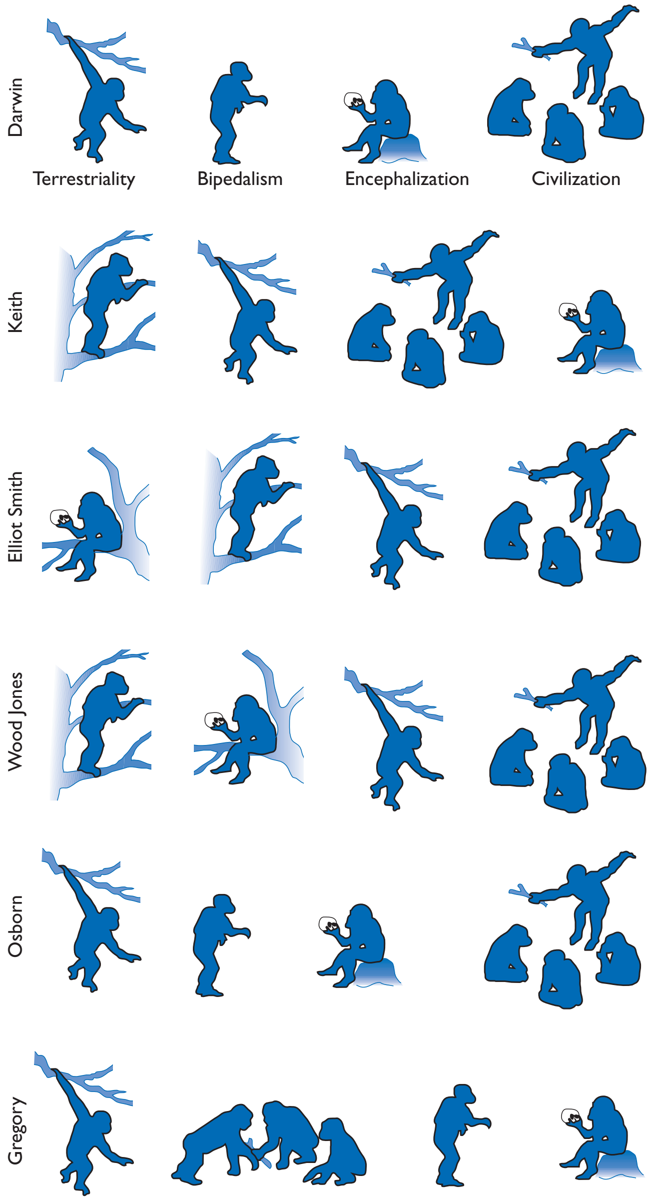


FIGURE 2.1 Different views of the story: Even though anthropologists saw the human journey as involving the same fundamental events—terrestriality, bipedalism, encephalization, and civilization—different authorities sometimes placed these steps in slightly different orders. For instance, although Charles Darwin envisaged an ancient ape first coming to the ground and then developing bipedalism, Sir Arthur Keith believed that the ape became bipedal before leaving the trees. (Courtesy of Misia Landau/*American Scientist*.)

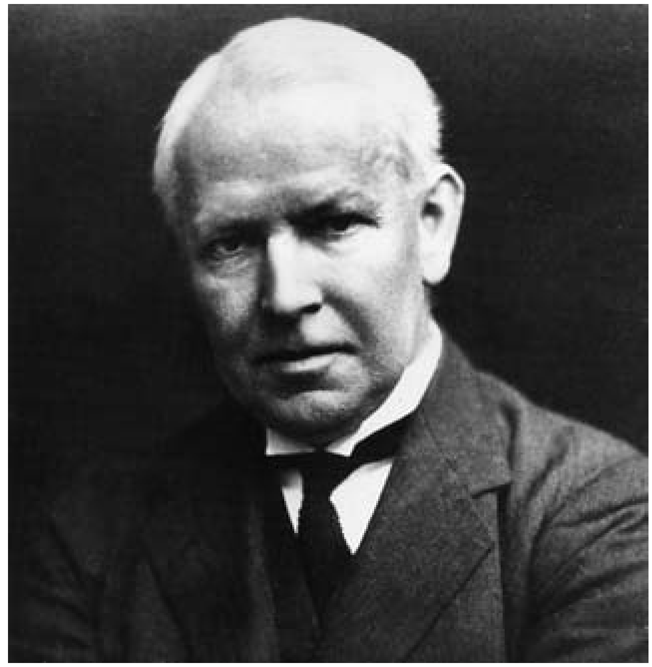


FIGURE 2.2 Sir Grafton Elliot Smith: A leading anatomist and anthropologist in early-twentieth-century England, Elliot Smith often wrote in florid prose about human evolution. (See figure 2.4.) (Courtesy of University College, London.)

In the case of human origins, the hero is the ape in the forest, who is "destined" to become us. The climate changes, the forests shrink, and the hero is cast out on the savannah where he faces new and terrible dangers. He struggles to overcome them, by developing intelligence, learning to use tools, and so on, and eventually emerges triumphant, recognizably you and me.

"When you read the literature you immediately notice not only the structure of the hero myth, but also the language," explains Landau. For instance, Elliot Smith writes about ". . . the wonderful story of Man's journeyings towards his ultimate goal . . ." and ". . . Man's ceaseless struggle to achieve his destiny." (See figure 2.4.) Roy Chapman Andrews, Osborn's colleague at the American Museum, writes of the pioneer spirit of our hero: "Hurry has always been the tempo of human evolution. Hurry to get out of the primordial ape stage, to change body, brains, hands and feet faster than it had ever been done in the history of creation. Hurry on to the time when man could conquer the land and the sea and the air; when he could stand as Lord of all the Earth."

Osborn wrote in similar tone: "Why, then, has evolutionary fate treated ape and man so differently? The one has been left in the obscurity of its native jungle, while the other has been given a glorious exodus leading to the domination of earth, sea, and sky." Indeed, many of Osborn's writings explicitly embodied the notion of drama: "The great drama of the prehistory of man . . . ," he wrote, and "the prologue and opening acts of the human drama . . . ," and so on.

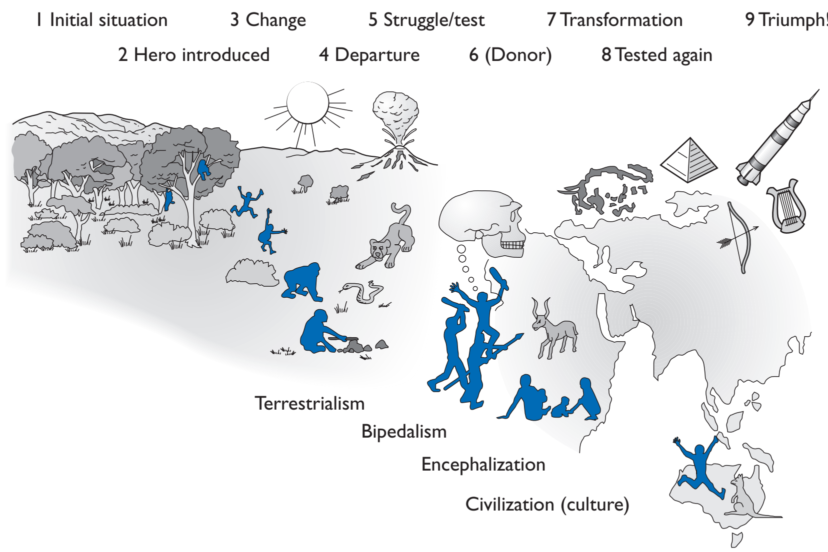
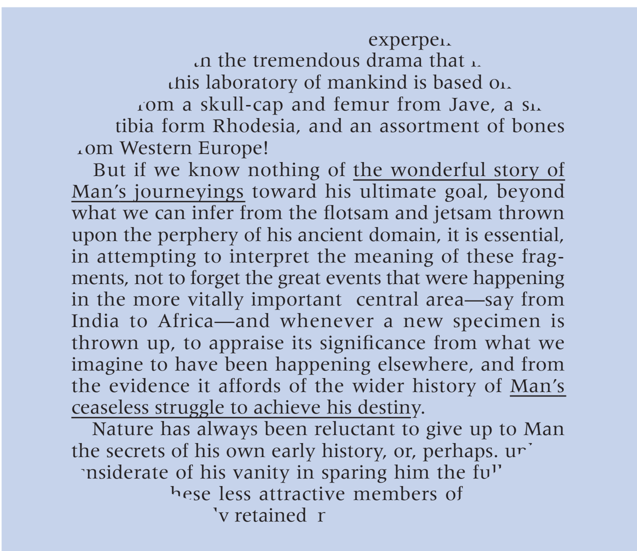


FIGURE 2.3 The hero-myth framework: Like folk tales ancient and modern, accounts of human origins have often followed the structure of hero myth. The hero (an ancient ape) sets off on a journey, during which he faces a series of challenges and opportunities that shape his final triumph (civilization). Recounting the evolution of any species is, of course, equivalent to telling a tale of a series of historical events. The effect, in the case of *Homo sapiens*, is to see the events as if, from the beginning, the journey was inevitable. (Courtesy of Misia Landau.)



experpe.
.n the tremendous drama that .
.his laboratory of mankind is based o.
.om a skull-cap and femur from Jave, a s.
tibia form Rhodesia, and an assortment of bones
.om Western Europe!

But if we know nothing of the wonderful story of Man's journeyings toward his ultimate goal, beyond what we can infer from the flotsam and jetsam thrown upon the perphery of his ancient domain, it is essential, in attempting to interpret the meaning of these fragments, not to forget the great events that were happening in the more vitally important central area—say from India to Africa—and whenever a new specimen is thrown up, to appraise its significance from what we imagine to have been happening elsewhere, and from the evidence it affords of the wider history of Man's ceaseless struggle to achieve his destiny.

Nature has always been reluctant to give up to Man the secrets of his own early history, or, perhaps. ur
.nsiderate of his vanity in sparing him the fu
.hese less attractive members of
.y retained r

FIGURE 2.4 Adventures in anthropology: Here, a short passage from Sir Grafton Elliot Smith's *Essays on the Evolution of Man*, published in 1924, illustrates the storytelling tone in which anthropological writing was often couched. Even modern prose is not always entirely free of this influence.

HUMANS AS INEVITABLE PRODUCTS OF EVOLUTION

Of course, it is possible to tell stories with similar gusto about nonhuman animals, such as the "triumph of the reptiles in conquering the land" or "the triumph of birds in conquering the air." Such stirring tales are readily found in accounts of evolutionary history—look no further than every child's hero, the dinosaur. The fact that the hero of the paleoanthropology tale is *Homo sapiens*—ourselves—makes a significant difference, however. Although dinosaurs may be lauded as lords of the land in their time, only humans have been regarded as the inevitable product of evolution—indeed, the ultimate purpose of evolution, as we saw in the previous unit. Not everyone was as explicit about this as Broom was (see unit 1), but most authorities betrayed the sentiment in the hero worship of their prose.

These stories were not just accounts of the ultimate triumph of our hero; they carried a moral tale, too—namely, triumph demands effort. "The struggle for existence was severe and evoked all the inventive and resourceful faculties and encouraged [Dawn Man] to the fashioning and first use of wooden and then stone weapons for the chase," wrote Osborn. "It compelled Dawn Man . . . to develop strength of limb to make long journeys on foot, strength of lungs for running, and quick vision and stealth for the chase."

According to Elliot Smith, our ancestors ". . . were impelled to issue forth from their forests, and seek new sources of food and new surroundings on hill and plain, where they could obtain the sustenance they needed." The penalty for indolence and lack of effort was plain for all to see, because the apes had fallen into this trap: "While man was evolved amidst the strife with adverse conditions, the ancestors of the Gorilla and Chimpanzee gave up the struggle for mental supremacy because they were satisfied with their circumstances."

In the literature of Elliot Smith's time, the apes were usually viewed as evolutionary failures, left behind in the evolutionary race. This sentiment prevailed for several decades, but eventually became transformed. Instead of evolutionary failures, the apes came to be viewed as evolutionarily primitive, or relatively unchanged from the common ancestor they shared with humans. In contrast, humans were regarded as much more advanced. Today, anthropologists recognize that both humans and apes display advanced evolutionary features, and differ equally (but in separate ways) from their common ancestor.

Although modern accounts of human origins usually avoid purple prose and implicit moralizing, one aspect of the narrative structure lingers in current literature. Paleoanthropologists still tend to describe the events in the "transformation of ape into human" as if each event were somehow a preparation for the next. "Our ancestors became bipedal in order to make and use tools and weapons . . . tool-use enabled brain expansion and the evolution of language . . . thus endowed, sophisticated societal interactions were finally made possible . . ." Crudely put, to be sure, but this kind of reasoning was common in Osborn's day and persists in some current narratives.

Origins Defined in Terms of Endings

Why does it happen? "Telling a story does not consist simply in adding episodes to one another," explains Landau. "It consists in creating relations between events." Consider, for instance, our ancestor's supposed "coming to the ground"—the first and crucial advance on the long road toward becoming human. It is easy to imagine how such an event might be perceived as a courageous first step on the long journey to civilization: the defenseless ape faces the unknown predatory hazards of the savannah. "There is nothing inherently transitional about the descent to the ground, however momentous the occasion," says Landau. "It only acquires such value in relation to our overall conception of the course of human evolution."

If evolution were steadily progressive, forming a program of constant improvement, the transformation of ape to human could be viewed as a series of novel adaptations, each one naturally preparing for and leading to the next. Such a scenario would involve continual progress through time, going in a particular direction. From our vantage point, where we can view the end-product, it is tempting to view the process in that way because we can actually see that all those steps did actually take place. This slant, however, ignores the fact that evolution tends to work in a rather halting, unpredictable fashion, shifting abruptly from one "adaptive plateau" to another. These adaptive plateaux are species, of course, and each was adaptively successful and persisted for a considerable time (several million years in some cases) before a rapid evolutionary shift, perhaps propelled by external forces, yielded a new species with a new adaptation (see unit 4).

For instance, one cannot say that the first bipedal ape would inevitably become a stone-tool maker. In fact, if the current archeological record serves as any guide, those two events—bipedality and the advent of stone-tool making—were separated by approximately 2.5 million years (see unit 23). The brain expanded from about 2.5 million years onwards (see unit 21). In addition, a more humanlike body structure emerged abruptly at this time (see unit 24). The origin of anatomically modern humans after another 2 million or so years was also probably a punctuational event (see units 27 through 30). Thus, although many writers proclaim that our ancestors were propelled inexorably along an evolutionary trajectory that ended with *Homo sapiens*, that scenario simply describes what did happen; it ignores the many other possibilities that did not transpire. As Landau remarks: "There is a tendency in theories of hominid evolution to define origins in terms of endings."

For paleoanthropology, language represents an important scientific tool that is used for the technical description of fossils and for the serious explication of evolutionary scenarios. All scientists should step back and scrutinize the language they use, because intertwined within it will be the elements of many unspoken assumptions. For human origins research, where narrative becomes a particularly seductive vehicle for assumptions, it is especially important that one carefully examines what one says and the way one says it.

Landau's focus on language in the context of anthropology made some researchers defensive, because it seems to threaten the legitimacy of the science. But this is partly because of the idealized image that science projects: complete objectivity in the search for truth. The telling of stories had no place in this construction of how science works. But, as Niles Eldredge and Ian Tattersall have put it, "Science *is* storytelling, albeit of a very special kind." And paleoanthropology is a science of a special kind, too, partly because it is historical, and therefore susceptible to storytelling, but mostly because it is meant to explain how we came to be here. Not everyone would agree with the way that John Durant, of Imperial College, London, puts it, but it is at least worth thinking about: "Like the Judeo-Christian myths they so largely replaced, theories of human evolution are first and foremost stories about the appearance of man on earth and the institution of society."

Key Questions

- What is implied by the fact that, although paleoanthropologists in Osborn's time employed the same set of events to describe the transformation of ape to human, those events were linked in many different combinations?
- Is paleoanthropology particularly susceptible to the invocation of the hero myth?
- Why do evolutionary scenarios tend to lend themselves to narrative treatment?
- In what context were apes considered to be evolutionary failures?

KEY REFERENCES

Durant J. The myth of human evolution. *New Universities Quarterly* 1981;35:425–438.

Eldredge N, Tattersall I. The myths of human evolution. New York: Columbia University Press, 1982.

Isaac G. Aspects of human evolution. In: Bendall D. Evolution from molecules to men. Cambridge, UK: Cambridge University Press, 1983:509–543.

Landau M. Human evolution as narrative. *Am Scientist* 1984;72:262–268.

———. Paradise lost: the theme of terrestriality in human evolution. In: Nelson JS, Megill A, McClosky DN. The rhetoric of the human sciences. Madison: University of Wisconsin Press, 1987:111–124.

———. Narratives of human evolution. New Haven: Yale University Press, 1991.

Lewin R. Chapter 2, Bones of contention. Chicago: The University of Chicago Press, 1997.

Medawar P. Pluto's Republic. Oxford: Oxford University Press, 1984.

3 HISTORICAL VIEWS

Two principal themes have been recurrent in paleoanthropology in the twentieth century. First is the relationship between humans and apes: how close, how distant? The second concerns the "humanness" of our direct ancestors. Anthropologists have come to recognize a very close relationship between humans and African apes; and they see our early ancestors as much less humanlike than was once the case.

During the past hundred-plus years, the issue of our relatedness to the apes has gone full circle. From the time of Darwin, Huxley, and Haeckel until soon after the turn of the twentieth century, humans' closest relatives were regarded as being the African apes, the chimpanzee and gorilla, with the Asian great ape, the orangutan, being considered to be somewhat separate. From the 1920s until the 1960s, humans were distanced from the great apes, which were said to be an evolutionarily closely knit group. Since the 1960s, however, conventional wisdom has returned to its Darwinian cast. (See figure 3.1.)

This shift of opinions has, incidentally, been paralleled by a related shift in ideas on the location of the "cradle of mankind." Darwin plumped for Africa, because that's where our closest relatives, the chimpanzee and gorilla, live; Asia became popular in the early decades of the twentieth century; and Africa has once again emerged as the focus.

While this human/African ape wheel has gone through one complete revolution, the question of the humanness of the hominin lineage has been changing as well—albeit in a single direction. (*Hominin* is the term now generally used to describe species in the human family, or clade; until recently, the term hominid was used, as discussed in unit 8.) Specifically, hominins—with the exception of *Homo sapiens* itself—have been gradually perceived as less humanlike in the eyes of paleoanthropologists, particularly in the last three decades. The different views on the origin of modern humans are, however, imbued with different perspectives of this issue (see unit 27).

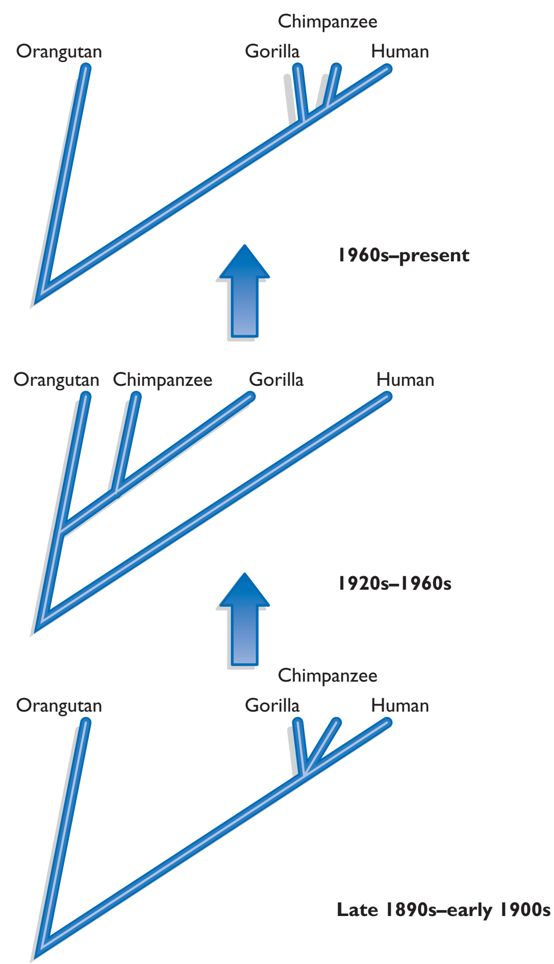


FIGURE 3.1 Shifting patterns: Between the beginning of the twentieth century and today, ideas about the relationships among apes and humans have moved full circle.

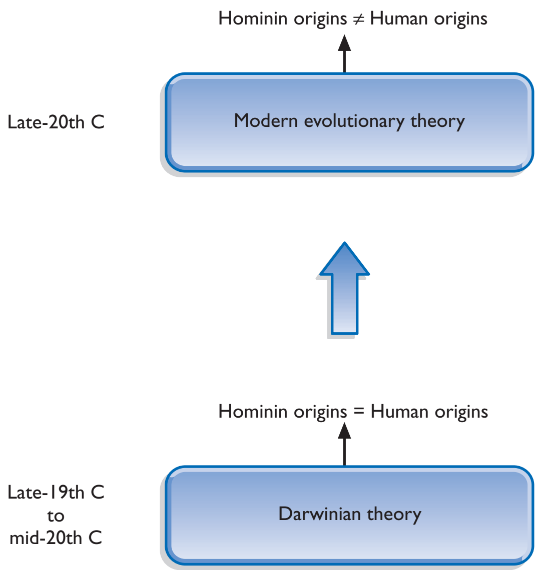


FIGURE 3.2 Hominins as humans: Until quite recently anthropologists frequently thought about humanlike characteristics while considering hominin origins, a habit that can be traced back to Darwin. The humanity of hominins is now seen as a rather recent evolutionary development.

HOMININ ORIGINS IN TERMS OF HUMAN QUALITIES

Once Darwin's work firmly established evolution as part of mainstream nineteenth-century intellectual life, scientists had to account for human origins in naturalistic rather than supernatural terms. More importantly, as we saw in the previous two units, they had to account for the evolutionary origin of special qualities of humankind, those that appear to separate us from the world of nature. This issue posed a formidable challenge—and the response to it set the intellectual tone in paleoanthropology for a very long time.

In his *Descent of Man*, Darwin identified those characteristics that apparently make humans special—intelligence, manual dexterity, technology, and uprightness of posture—and argued that an ape endowed with minor amounts of each of these qualities would surely possess an advantage over other apes. Once the earliest human forebear became established upon this evolutionary trajectory, the eventual emergence of *Homo sapiens* appeared almost inevitable because of the continued power of natural selection. In other words, hominin origins became explicable in terms of human qualities, and *hominin* origins therefore equated with *human* origins. (See figure 3.2.) It was a seductive formula, and one that persisted until quite recently.

THE STAGE IS SET FOR THE PILTDOWN FORGERY

At the turn of the century several interrelated intellectual debates were brewing, one of which focused on the order in which the major anatomical changes occurred in the human lineage. One notion was that the first step on the road to humanity was the adoption of upright locomotion. A second held that the brain led the way, producing an intelligent but still arboreal creature. (See figure 3.3.) It was into this intellectual climate that the perpetrator of the famous Piltdown hoax—a chimera of fragments from a modern human cranium and an orangutan's jaw, both doctored to make them look like ancient fossils—made his play from 1908 to 1913. (See figure 3.4.) (In mid-1996 the first material clues as to the identity of the Piltdown forger came to light, pointing to Martin Hinton, Arthur Smith Woodward's colleague at the Natural History Museum, London.)

The Piltdown "fossils" appeared to confirm not only that the brain did indeed lead the way, but also that something close to the modern *sapiens* form was extremely ancient in human history. The apparent confirmation of this latter fact —extreme human antiquity—was important to both the prominent British anthropologist Sir Arthur Keith and Henry Fairfield Osborn, because their theories demanded it. (See figure 3.5.) One consequence of Piltdown was that Neanderthal —one of the few genuine fossils of the time—was disqualified from direct ancestry to *Homo sapiens*, because it apparently came later in time than Piltdown and yet was more primitive (see unit 27). British anthropologists were of course happy to believe that Britain was now firmly on the anthropological map, apparently overshadowing German and French claims. (See figure 3.6.)

For Osborn, Piltdown represented strong support for his Dawn Man theory, which stated that mankind originated on the high plateaux of Central Asia, not in the jungles of Africa. During the 1920s and 1930s, Osborn was locked in constant but gentlemanly debate with his colleague, William King Gregory, who carried the increasingly unpopular Darwin/Huxley/Haeckel torch for a close relationship between humans and African apes—the Ape Man theory.

Although Osborn was never very clear about what the earliest human **progenitors** might have looked like, his ally Frederic Wood Jones espoused firmer ideas. Wood Jones, a British anatomist, interpreted key features of ape and monkey anatomy as specializations that were completely absent in human anatomy. In 1919, he proposed his "tarsioid hypothesis," which sought human antecedents very low down in the primate tree, with a creature like the modern tarsier. In today's terms, this proposal would place human origins in the region of 50 to 60 million years ago, close to the origin of the primate radiation, while Keith's notion of some kind of early ape would date this development to approximately 30 million years ago.

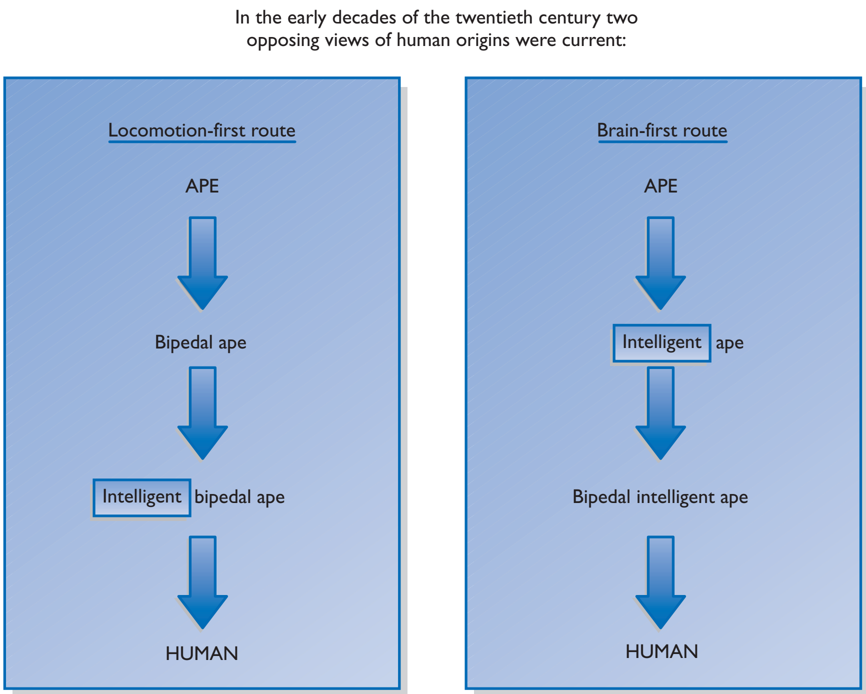


FIGURE 3.3 Conflicting views: One of the key differences of opinion regarding the history of human evolution was the role of the expanded brain: was it an early or a late development? The "brain-first" notion, promoted by Elliot Smith, was important in paving the way for the acceptance of the Piltdown man fraud.

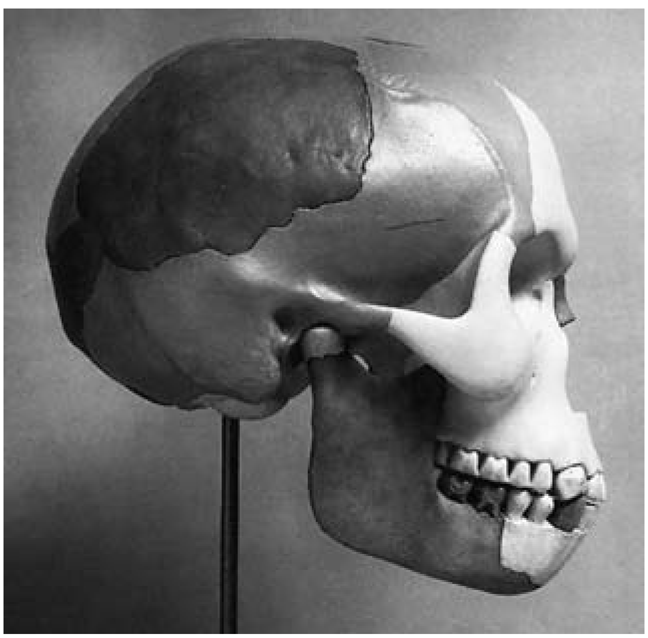


FIGURE 3.4 A fossil chimera: A cast of the Piltdown reconstruction, based on lower jaw, canine tooth, and skull fragments (shaded dark). The ready acceptance of the Piltdown forgery—a chimera of a modern human cranium and the jaw of an orangutan—derived from the British establishment's adherence to the brain-first route. (Courtesy of the American Museum of Natural History.)

APES BECOME ACCEPTABLE AS ANCESTORS

During the 1930s and 1940s, the anti-ape arguments of Osborn and Wood Jones were lost, but Gregory's position did not immediately prevail. Gregory had argued for a close link between humans and the African apes on the basis of shared anatomical features. Others, including Adolph Schultz and D. J. Morton, claimed that although humans probably derived from apelike stock, the similarities between humans and modern African apes were the result of convergent evolution. That is, two separate lines evolved similar adaptations, and therefore look alike, although they are not closely related evolutionarily (see unit 4). This position remained dominant through the 1960s, firmly supported by Sir Wilfrid Le Gros Clark, Britain's most prominent primate anatomist of the time. Humans, it was argued, came from the base of the ape stock, not later in evolution.

During the 1950s and 1960s, the growing body of fossil evidence related to early apes appeared to show that these creatures were not simply early versions of modern apes, as had been tacitly assumed. This idea meant that those authorities who accepted an evolutionary link between humans and apes, but rejected a close human/African ape link, did not have to retreat back in the history of the group to "avoid" the specialization of the modern species. At the same time, those who insisted that the similarities between African apes and humans reflected a common heritage, not convergent evolution, were forced to argue for a very recent origin of the human line. Prominent among proponents of this latter

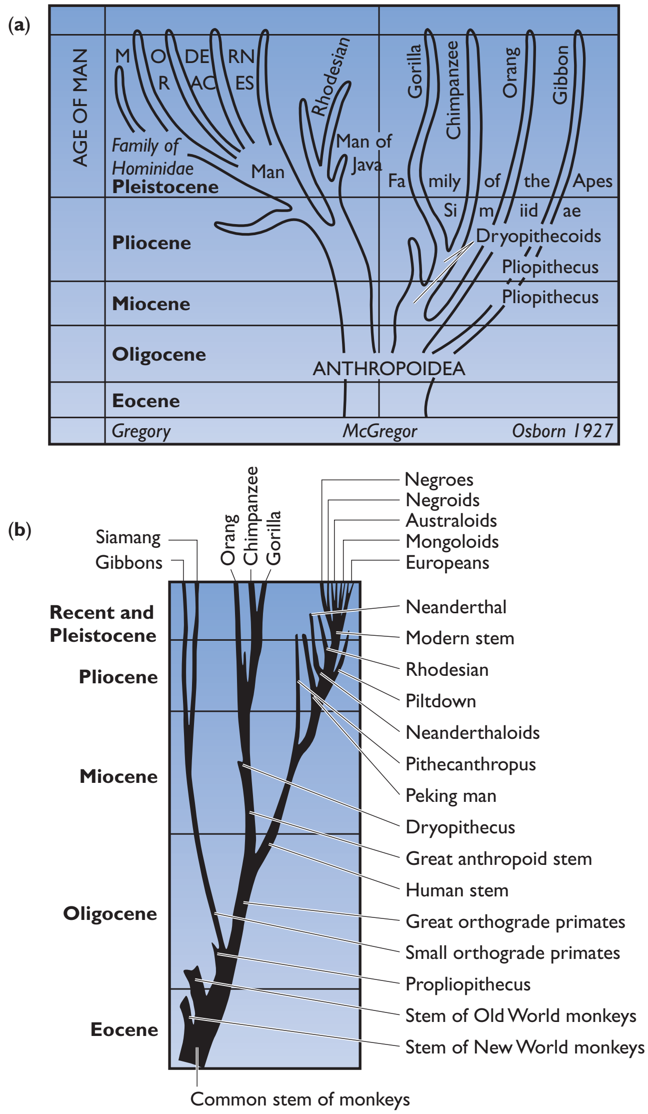


FIGURE 3.5 Two phylogenetic trees: (a) Henry Fairfield Osborn's 1927 view of human evolution shows a very early division between humans and apes (in today's geological scale, this division would be about 30 million years ago). (b) Sir Arthur Keith's slightly earlier rendition also shows a very early human/ape division. Long lines link modern species with supposed ancestral stock, a habit that was to persist until quite recently. Note also the purported very long history of modern human races.

argument was Sherwood Washburn, of the University of California, Berkeley.

One of the fossil discoveries of the 1960s—in fact, a rediscovery of a specimen unearthed three decades earlier—that appeared to confirm the notion of parallel evolution to explain human/African ape similarities was made by Elwyn Simons, then of Yale University. The fossil specimen was *Ramapithecus*, an apelike creature that lived in Eurasia approximately 15 million years ago and appeared to share many anatomical features (in the teeth and jaws) with hominins. Simons, later supported closely by David Pilbeam, proposed *Ramapithecus* as the beginning of the hominin line, thus excluding a human/African ape connection.

RELATIONSHIP AMONG THE GREAT APES RECONSIDERED

Arguments about the relatedness between humans and African apes were mirrored by a reconsideration of the relatedness among the apes themselves. In 1927, G. E. Pilgrim had suggested that the great apes be treated as a natural group (that is, evolutionarily closely related), with humans viewed as more distant. This idea eventually became popular and remained the accepted wisdom until molecular biological evidence undermined it in 1963, via the work of Morris Goodman at Wayne State University. Goodman's molecular biology data on blood proteins indicated that humans and the African apes formed a natural group, with the orangutan more distant (see unit 15).

As a result, the Darwin/Huxley/Haeckel position returned to prominence, with first Gregory and then Washburn emerging as its champion. Subsequent molecular biological—and fossil—evidence appeared to confirm Washburn's original suggestion that the origin of the human line is quite recent, close to 5 million years ago. *Ramapithecus* was no longer regarded as the first hominin, but simply one of many early apes. (The nomenclature and evolutionary assignment of *Ramapithecus* subsequently was modified, too, as described in unit 16.)

THE SINGLE-SPECIES HYPOTHESIS, AND ITS DEMISE

Meanwhile, discoveries of fossil hominins, and the stone tools they apparently made, had been accumulating at a rapid pace from the 1940s through 1970s, first in South Africa and then in East Africa. Culture—specifically, stone-tool making and tool use in butchering animals—became a dominant theme, so much so that hominin was considered to imply a hunter-gatherer lifeway. The most extreme expression of culture's importance as *the* hominin characteristic consisted of the single-species hypothesis, promulgated during the 1960s principally by C. Loring Brace and Milford Wolpoff, both of the University of Michigan.

According to this hypothesis, only one species of hominin existed at any one time; human history was viewed as progressing by steady improvement up a single evolutionary ladder. The rationale relied upon a supposed rule of ecology: the principle of competitive exclusion, which states that two species with very similar adaptations cannot coexist. In this

FIGURE 3.6 A discussion of the Piltdown skull: Back row, left to right: F. G. Barlow, Grafton Elliot Smith, Charles Dawson, and Arthur Smith Woodward. Front row, left to right: A. S. Underwood, Arthur Keith (examining the skull), W. P. Pycraft, and Ray Lankester. The Piltdown man fossil, discovered in 1912 and exposed as a fraud in 1953, fitted so closely with British anthropologists' views of human origins that it was accepted uncritically as being genuine. (Courtesy of the American Museum of Natural History.)

case, culture was viewed as such a novel and powerful behavioral adaptation that two cultural species simply could not thrive side by side. Thus, because all hominins are cultural by definition, only one hominin species could exist at any one time.

The single-species hypothesis collapsed in the mid-1970s, after fossil discoveries from Kenya undisputedly demonstrated the coexistence of two very different species of hominin: *Homo erectus*, a large-brained species that apparently was ancestral to *Homo sapiens*, and *Australopithecus boisei*, a small-brained species that eventually became extinct. Subsequent discoveries and analyses implied that several species of hominin coexisted in Africa some 2 million or so years ago (see unit 22), suggesting that several different ecological niches were being successfully exploited. These findings implied that to be hominin did not necessarily mean being cultural. Thus, no longer could hominin origins be equated with human origins (see figure 3.2). (Foley, 2001, and Tattersall, 2000, provide interesting—and opposing—ideas about why anthropologists embraced this unilinear view of human evolution.)

During the past decade, not only has an appreciation of a spectrum of hominin adaptations—including the simple notion of a bipedal ape—emerged, but the lineage that eventually led to *Homo sapiens* has also come to be perceived as much less human. Gone is the notion of a scaled-down version of a modern hunter-gatherer way of life. In its place has appeared a rather unusual African ape adopting some novel, un-apelike modes of subsistence (see unit 26).

Today, hominin origins are completely divorced from any notion of human origins. Questions about the beginning of the hominin lineage are now firmly within the territory of behavioral ecology and do not draw upon those qualities that we might perceive as separating us from the rest of animate nature. Questions of hominin origins must now be posed within the context of primate biology.

KEY QUESTIONS

- Why were post-evolutionary theory explanations of human origins considered "self-explanatory"?
- What is the effect of sparse fossil evidence on theories of human evolution?
- Was the notion of parallel evolution of similar anatomical features among humans and African apes a reasonable explanation?
- Why was "culture" so dominant a theme in explanations of human origins?

KEY REFERENCES

Bowler PJ. Theories of human evolution. Baltimore: Johns Hopkins Press, 1986.

Cartmill M. Human uniqueness and theoretical content in paleoanthropology. *Int J Primatol* 1990;11:173–192.

Cartmill M, Pilbeam DR, Isaac GL. One hundred years of paleoanthropology. *Am Scientist* 1986;74:410–420.

Fleagle JG, Jungers WL. Fifty years of higher primate phylogeny. In: Spencer F, ed. A history of American physical anthropology. New York: Academic Press, 1982.

Foley RA. In the shadow of the modern synthesis: alternative perspectives on the last 50 years of paleoanthropology. *Evol Anthropol* 2001;10:5–15.

Gee H. Box of bones "clinches" identity of Piltdown palaeontology hoaxer. *Nature* 1996;381:261–262.

Lewin R. Chapters 4–6, Bones of contention. Chicago: The University of Chicago Press, 1997.

Sacket J. Human antiquity and the old Stone Age: the nineteenth century background to paleoanthropology. *Evol Anthropol* 2000;9:37–49.

Spencer, F. Piltdown: A scientific forgery. Oxford: Oxford University Press, 1990.

Tattersall I. Paleoanthropology: the last half-century. *Evol Anthropol* 2000;9:2–16.

Tobias PV. An appraisal of the case against Sir Arthur Keith. *Curr Anthropol* 1992;33:243–294.

4 MODERN EVOLUTIONARY THEORY

Evolutionary theory is concerned principally with explanations of species' adaptation to their environment, the origin of species, and the origin of trends within groups of related species, such as the increase in brain size among certain hominins. Some evolutionary biologists argue that all evolutionary change is the outcome of the accumulation of small changes through natural selection. Others see different mechanisms as being important, too.

One of the most important phenomena that a successful theory of evolution must explain is **adaptation**—that is, the way that species' anatomy, physiology, and behavior appear to be well suited to the demands of their environments. Adaptation is pervasive in nature, and in pre-Darwinian times it was viewed as the product of divine creation. Moreover, once created, species were believed to change little, if at all, through time. In his *Origin of Species*, published in November 1859, Darwin explained the purpose of the book as follows: "I had two distinct objects in view; firstly to show that species had not been separately created, and secondly, that natural selection had been the chief agent of change." **Natural selection**, Darwin believed, explained how species became adapted to their environments.

The notion that species do, in fact, change through time was already in the air in 1859. Consequently, Darwin readily succeeded with his first goal, given the volume of evidence he presented in the *Origin* in support of the reality of evolution. The second goal, showing that natural selection was an important engine of evolutionary change, remained elusive until the 1930s, when it became the central pillar of newly established evolutionary thinking, known as **NeoDarwinism**.

In addition to adaptation, evolutionary theory must explain the origin of new species and major trends within groups of related species: trends such as the increase in body size and the reduction of the number of toes among horses in that group's 50 million years of evolution, and the increase in the size of the brain in human evolution. The origin of species and the pattern of trends among groups of species are collectively known as **macroevolution**. Despite the title of his most famous book, Darwin did not address the origin of species in detail in the *Origin*. As stated above, his principal focus was directed toward change within species, through natural selection, which was viewed as a slow, steady process built on minute modifications through time. This process is known as **microevolution**. Macroevolution was assumed to represent the outcome of microevolutionary processes accumulating over very long periods of time within populations, an assumption that was central to NeoDarwinism as well.

During the past several decades, the validity of this assumption has been challenged. Although adaptation through natural selection remains an important part of modern evolutionary theory, the patterns of change at levels higher than the individual organism (that is, at the level of species and groups of species) are now viewed as being more complex. This unit will address the mechanisms of microevolution and macroevolution and their roles in the overall pattern of life as seen in the fossil record. Unit 6 will discuss the role of extinctions—particularly mass extinctions—in creating this pattern.

THE POWER OF NATURAL SELECTION

Natural selection, as enunciated by Darwin, is a simple and powerful process that depends on three conditions. First, members of a species differ from one another, and this variation is heritable. Second, all organisms produce more offspring than can survive. (Although some organisms, most notably large-bodied species and those that bestow a lot of parental care, produce few offspring while others may produce thousands or even millions, the same rule applies.) Third, given that not all offspring survive, those that do are, on average, likely to have an anatomy, physiology, or behavior that best prepares them for the demands of the prevailing environment. The principle of natural selection came to be known (inaccurately) as **survival of the fittest**, even though Darwin did not use that term.

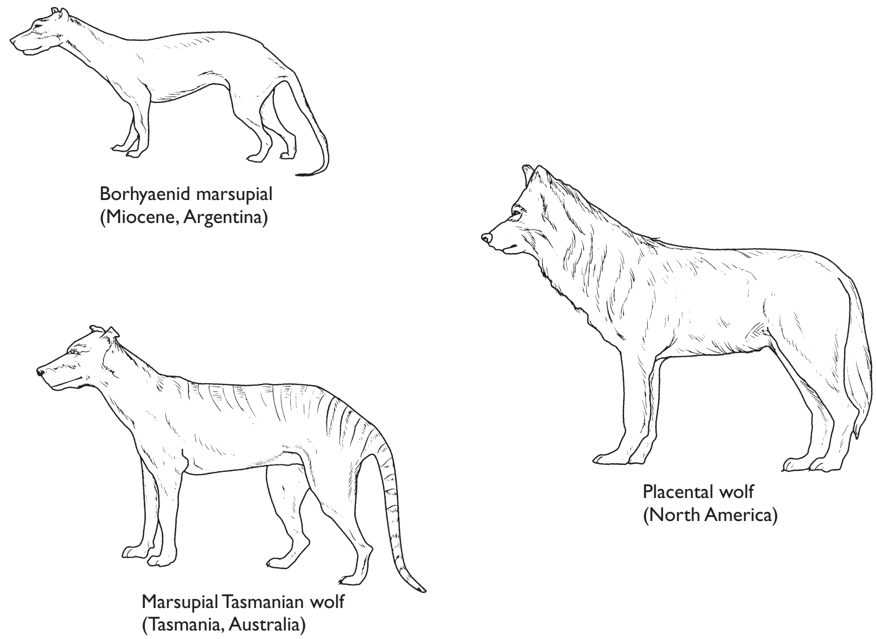


FIGURE 4.1 Convergent evolution: The power of natural selection is seen in its ability to produce similar morphologies in widely different species. Here we see a Miocene hyena from South America (a marsupial mammal), the Tasmanian wolf (a marsupial mammal), and the North American wolf (a placental mammal). Although marsupial and placental mammals diverged more than 100 million years ago, their morphologies have become very similar through similar adaptations as large, terrestrial carnivores. The Tasmanian wolf is closer evolutionarily to the kangaroo than it is to the North American wolf.

Natural selection, then, is **differential reproductive success**, with heritable favorable **traits** bestowing a survival advantage on those individuals that possess them. Generation by generation, favorable traits will become ever more common in the population, causing a microevolutionary shift in the species. Such traits will remain favored, however, only if prevailing conditions remain the same. A species' environment usually does not remain constant in nature. A change in a species' physical or biological environment (see unit 5) may alter a population's **adaptive landscape**, perhaps rendering a previously advantageous trait less beneficial or making a less advantageous trait more favorable. Natural selection, or an individual's "struggle for existence" as Darwin put it, is a local process, consisting of a generation-by-generation adjustment to local conditions.

The power of natural selection can be seen in the phenomenon of **convergent** (or **parallel**) **evolution**, in which distantly related species come to resemble one another very closely by adapting to similar ecological **niches**. The anatomical similarity of the North American wolf and the Tasmanian wolf is a good example. (See figure 4.1.) The former is a placental mammal and the latter is a marsupial, making the two species extremely distant genetically, having been evolutionarily separate for at least 100 million years. The anatomical similarities between the two distant species of wolf reflect convergent evolution, or **analogy**, not shared ancestry. Anatomical similarities that result from shared ancestry are examples of **homology**. Homologous structures are especially important in the reconstruction of evolutionary history based on morphological characters (see unit 8).

ESTABLISHMENT OF POPULATION GENETICS

Darwin was well aware that members of a species vary, and that these variations are heritable: his observations of natural populations and experiments with domestic breeding were proof of that ability. He was not familiar with the basis of inheritance, however. Although the rules of inheritance were discovered by the Austrian monk Gregor Mendel in the early 1860s, the results of his work remained generally unknown until two decades after Darwin's death, in 1882.

From observations on the progeny from experimental crossing of pea plants, Mendel discovered that physical traits are determined by stable inheritance factors (what we now call genes). He also found that each plant has two genes for each trait, one from the female parent and one from the male. The variants of each gene, or **alleles**, may be identical (in which case the individual is **homozygous**) or different (the individual is **heterozygous**). When the two alleles differ, one form may be **dominant** and the other **recessive** (in humans, for instance, the allele for brown eyes is dominant relative to the blue allele). Gametes, or sex cells, receive one or the other of the two alleles with equal probability.

Mendel's experiments were very simple from a genetic standpoint, with just one or two genes affecting one trait. Before long it became apparent that most traits are influenced by many genes, not just one or two. Nevertheless, the system was amenable to mathematical analysis, and the selection of favored physical, physiological, or behavioral traits (the **phenotype**) could be studied in terms of the selection of genes that underlay them (the **genotype**).

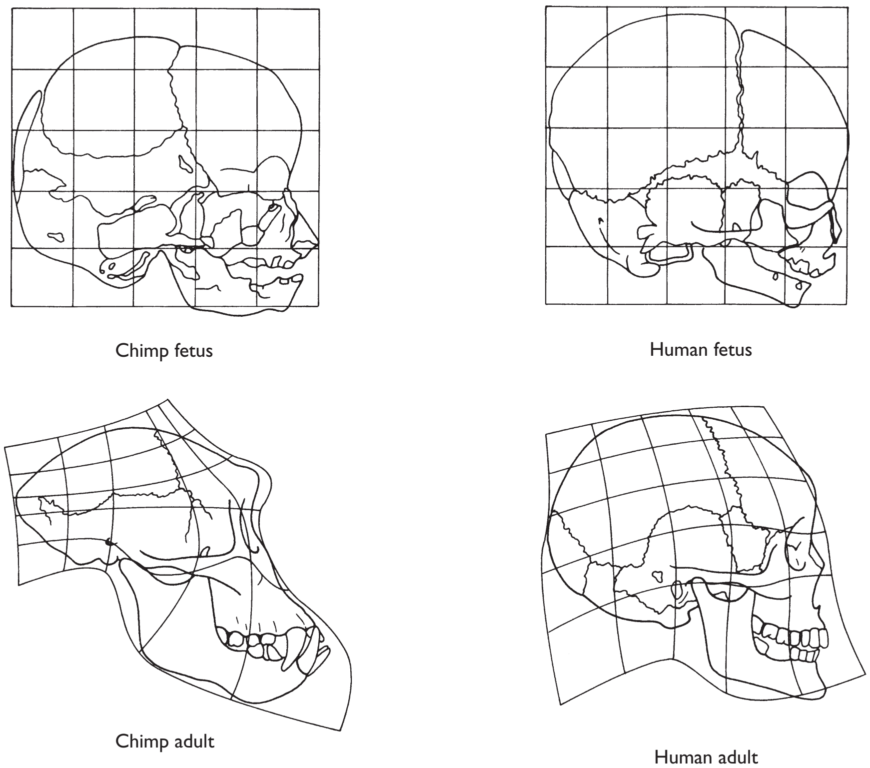


FIGURE 4.2 Neoteny in human evolution: Although the shape of the cranium in human and chimpanzee fetuses is very similar, a slowdown in development through human evolution has produced adult crania of very different forms, varying principally in the shape of the face and the size of the brain case. The changes in grid shapes indicate the orientation of growth.

THE EMERGENCE OF THE MODERN SYNTHESIS

The change in frequency of particular alleles within a population as a result of natural selection on them provides the basis of microevolution. From time to time, however, the DNA sequence that represents the information encoded in a gene becomes changed, often when a "mistake" occurs as the gene is copied within the **germline**. Such a **mutation** introduces the potential for further genetic variation within the population.

No simple relationship exists between a mutation and the degree of phenotypic change it might produce. For instance, a single base mutation in the gene of a serum albumin might marginally modify the physical chemistry of the blood, perhaps with some impact on adaptation or perhaps not. On the other hand, a similar mutation in a gene that affects the timing of the program of embryological development might have dramatic consequences for the mature organism. The slowing of embryological development and subsequent prolongation of the growth period, a phenomenon known as **neoteny**, was apparently important in the evolution of humans from apes. (See figure 4.2.)

The fate of mutations, and therefore their importance in future evolution, was the topic of intense debate in the early years of population genetics. (In this discipline, it is important to distinguish between the mutation rate of a gene, which may be quite common, and the retention, or fixation, of those mutations in the species' populations, which is much less common.) In Darwinian evolution, natural selection was viewed as retaining beneficial traits (alleles) and was therefore a creative process, not just a cleaning-up process that eliminated disadvantageous traits.

Until the mid-1940s, evolutionary theory remained distinctly at odds with strict Darwinism, and many different views were put forth to explain how the pattern of life was shaped. Then, following the creative melding of natural history, population genetics, and paleontology, a consensus of sorts appeared, known as the **modern synthesis**. This theory encompassed three principal tenets. First, evolution proceeds in a gradual manner, with the accumulation of small changes over long periods of time. Second, this change results from natural selection, with the differential reproductive success founded on favorable traits, as described earlier. Third, these processes explain not only changes within species but also higher-level processes, such as the origin of new species, producing the great diversity of life, extant and extinct. Darwinism had triumphed.

MECHANISMS OF MACROEVOLUTION

Our discussion so far has focused on microevolution, or changes within species. We will now turn to macroevolution

—that is, the origin of new species and trends among groups of related species.

New species may arise in two ways. First, an existing species may be transformed by gradual change through time, so that the descendant individuals are sufficiently differentiated from their ancestors as to be recognized as a separate species. This mode is known as **anagenesis**, and it results in one species evolving into another over time. In this case there is no increase in the diversity of species. In the second case, a population of an existing species may become reproductively isolated from the parent species, producing a second, distinct species. This mode is known as **cladogenesis**, and comprises a splitting event that yields two species where previously only one existed. This process has obviously been important in the history of life because the fossil record shows that biodiversity has increased steadily (with fluctuations and occasional mass extinctions, as discussed in unit 6) since complex forms of life evolved, a little more than half a billion years ago. (Cladogenesis is also called **speciation**.)

On a shorter time scale, cladogenesis plays an important role in **adaptive radiation**. Adaptive radiation is a characteristic pattern of evolution following the origin of an evolutionary novelty, such as feathered flight (for birds), placental gestation (for eutherian mammals), or bipedal locomotion (in hominins). The original species bearing the evolutionary novelty very quickly yields descendant species, each representing a variant on the new adaptation. The result, drawn graphically, is an evolutionary bush, with an increasing number of coexisting species through time that have all descended from the same ancestor. The sum total of descendants of that common ancestor is known as a **clade** (see unit 8)—hence the term "cladogenesis."

Cladogenesis is most likely to occur when a small, peripheral population of a species is separated from the parental population. Such small populations, which contain less genetic variation and are less stable genetically than large populations, may become established in one of several ways, such as through the origin of new physical barriers, the colonization of islands, or the rapid crash of a subpopulation to small numbers. When a small population becomes established in one of these ways and then expands, it exhibits what is termed a **founder effect**. A founder population that gives rise to a new species in separation from other populations of the same species produces **allopatric speciation** ("allopatric" means "in another place"). Allopatric speciation is the most common means by which new vertebrate species arise. When a new species arises from a subpopulation that is not separated from the main population, the process is termed **sympatric speciation** ("sympatric" means "in the same place").

So much for the mode of the origin of new species; what of the tempo and its mechanism? The modern synthesis argued that macroevolution was simply an extrapolation of microevolutionary processes: an accumulation of small changes over a long period of time, leading to large resulting changes. This process is known as **phyletic gradualism**, which, given a large enough resultant change, may yield a new species. (See figure 4.3.)

Because phyletic gradualism is driven by the gradual process of natural selection, it creates new adaptations that, when sufficiently different from those in the ancestral species, may lead to a new species that is characterized by those adaptations. In principle, this gradual change should be evident in the fossil record, whether anagenesis or cladogenesis is the end-result. Typically, gradual change is *not* seen in the record, however. Instead, the new species usually appears abruptly, either replacing the parental species (anagenesis) or appearing concurrently with it (cladogenesis), with no transitional forms present.

Proponents of the modern synthesis adopted Darwin's explanation for the absence of transitional forms, which was that the fossil record is incomplete. In the early 1970s, Niles Eldredge, of the American Museum of Natural History, and the late Stephen Jay Gould, of Harvard University, challenged this interpretation. They argued that, incomplete though the fossil record may be, it presents an accurate view of the tempo of evolutionary change. Instead of undergoing continual, gradual change, species remain relatively static for long periods of time; when change comes, it occurs rapidly ("rapidly" means a few thousand years). Apart from rare occasions in unusual geological circumstances, the bursts of change go unrecorded in the fossil record. Eldredge and Gould gave this tempo of evolution—that is, long periods of stasis interspersed with brief intervals of rapid change—the name of **punctuated equilibrium**. (See figure 4.3.)

An important difference between punctuated equilibrium and the traditional explanation of species formation relates to the nature of change that occurs at that time. The modern synthesis saw adaptation as the *cause* of speciation, through the accumulation of such changes through time, whereas punctuated equilibrium sees it as a potential *consequence*, as changes accumulate after populations are separated geographically and genetically.

THE ORIGIN OF EVOLUTIONARY TRENDS

Punctuated equilibrium leads to another insight of macroevolution, that of trends within groups of species. Mentioned earlier was the evolutionary history of the horse clade, in which body size increased and the number of toes decreased. A second example involves the increase in brain size during human evolution, at least once the genus *Homo* had evolved, some 2-plus million years ago.

With horses, the evolutionary trend was long interpreted as a progressive improvement, as if increased body size and a reduced number of toes represented a more efficient way of being a horse. Similarly, the increase in brain size that was

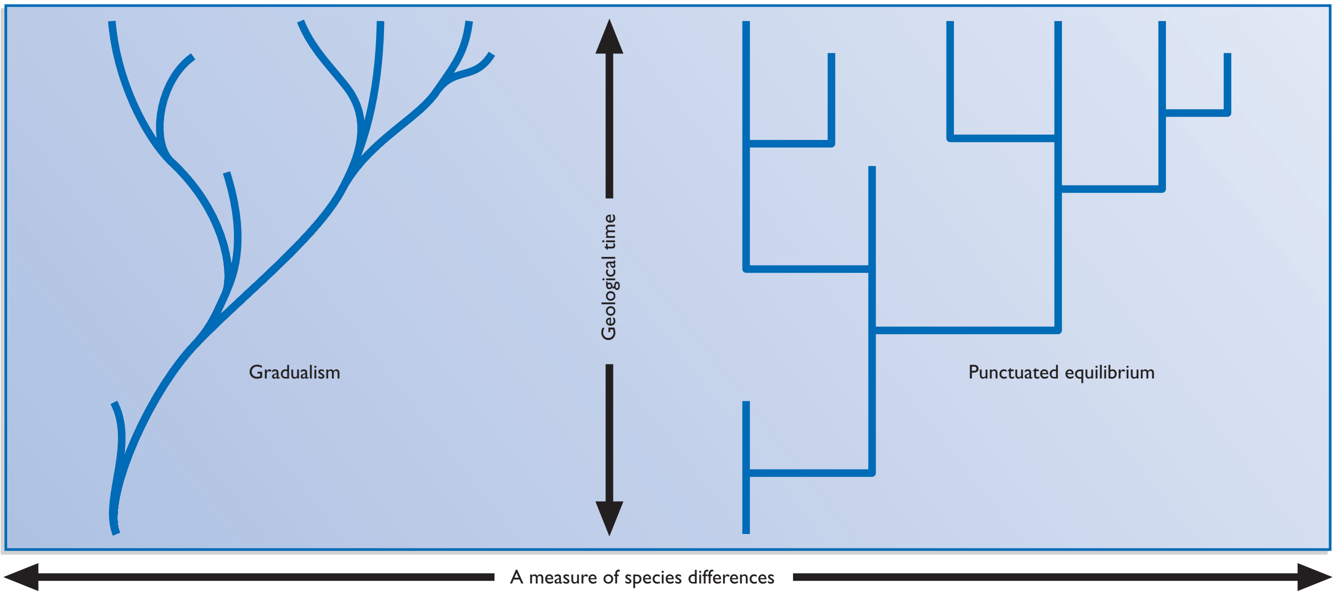


FIGURE 4.3 Two modes of evolution: Gradualism and punctuated equilibrium. Gradualism views evolution as proceeding by the steady accumulation of small changes over long periods of time. In contrast, punctuated equilibrium sees morphological change as being concentrated in "brief" bursts of change, usually associated with the origin of a new species. Evolutionary history reflects the outcome of a combination of these two modes of change, although considerable debate has arisen as to which mode is the more important.

evident with the appearance of the first species of *Homo* is often described as the beginning of brain enlargement, as if it were a progressive process that was nurtured steadily by natural selection. Through the lens of the modern synthesis, the trends could be explained as progressions that resulted from directional natural selection. Punctuated equilibrium, however, provides a different explanation.

If, as noted earlier, species persist unchanged for most of their duration, then evolution is *not* directional in this sense. Trends may occur within groups when member species with a certain characteristic are less likely to go extinct. Many factors can influence species' tendencies for extinction (and speciation), because the two trends are linked (see units 5 and 6, and figure 4.4).

One such factor is the nature of a species' adaptation. The fossil record shows that species with highly specialized environmental and subsistence requirements are more likely to speciate and become extinct than those with much broader adaptations. The reason is that any change in the prevailing environment is likely to push specialists beyond the limits of their tolerances, promoting both speciation and extinction. Clearly, generalists can accommodate much broader shifts in conditions, making speciation and extinction rarer for them.

Suppose, for example, that horse species with large body size survive longer, for some reason. The differential survival rates of species along these lines would produce a trend toward larger horses, not because it made better horses in the sense of adaptation but as a consequence of the properties of species. Similarly for hominin species and large brain size: there is no persuasive evidence to indicate an increase in encephalization within species; rather, there is a trend toward larger brain size within the clade as a whole. If large brain size endowed species with greater longevity, a history of increased brain size within the group would result.

In thinking about the shape of human evolution, an interesting question is this: how many hominin species might have existed at any one time, and how many in total? Adaptive radiation leads to a bushy family tree, with multiple species existing at any point, rather than a linear one, with just one species existing at any one time. Hominins and horses are unusual in nature in that each group is represented in today's world by a single genus. The fossil record of horses has shown, however, that this group was once a luxuriant evolutionary bush, with multiple species coexisting at any one time.

How bushy human history was remains to be established, but calculations based on the estimated number of fossil primate species imply that in the 5-plus million years that the hominin group has existed, at least 16 species would have arisen. As a result of a flurry in the discovery of new hominin species, the total number of species throughout human

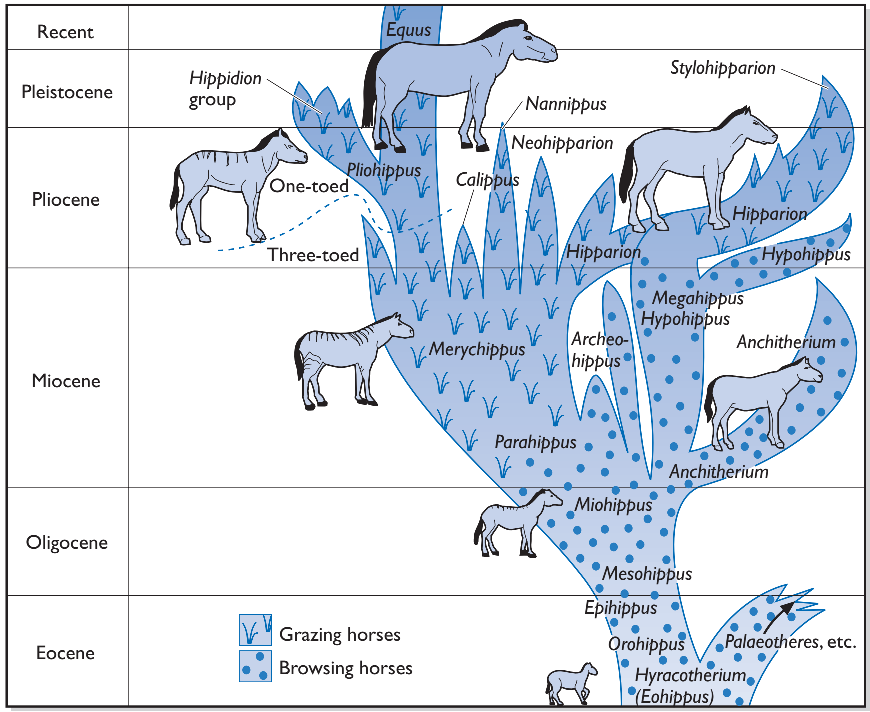


FIGURE 4.4 Evolutionary trends: The evolutionary history of horses was once considered as a series of evolutionary trends (to larger body size, more complex teeth, and fewer toes) that marked steady, directional progression. In fact, the evolution of horses is more like a bush than a directional ladder. The differential survival rate of certain species with certain characters merely gives the impression of steady progression, but does not represent reality.

history now approaches the theoretical prediction. And it is clear that until relatively recently, several different hominin species lived side by side throughout our history, once the adaptive radiation of bipedal apes was under way.

KEY QUESTIONS

- Why are mutations important in evolution, and how do they become fixed in a population?
- Why is macroevolution not considered to be merely an extrapolation of microevolutionary processes operating over long periods of time?
- Why is adaptive radiation so common a pattern in evolution?
- What evolutionary factors are most important in shaping the history of human evolution?

KEY REFERENCES

Fitch W, Ayala FJ, eds. Tempo and mode in evolution. Washington, DC: National Academy Press, 1995.

Foley RA. In the shadow of the modern synthesis: alternative perspectives on the last 50 years of paleoanthropology. *Evol Anthropol* 2001;10:5–15.

Gould SJ. Darwinism and the expansion of evolutionary theory. *Science* 1982;216:380–387.

Gould SJ, Eldredge N. Punctuated equilibrium comes of age. *Nature* 1993;366:223–227.

Somit A, Peterson SA, eds. The dynamics of evolution. Ithaca: Cornell University Press, 1992.

Stebbins GL, Ayala FJ. The evolution of Darwinism. *Sci Am* July 1985:72–80.

Tattersall I. How does evolution work? *Evol Anthropol* 1994;3:2–3.

———. Paleoanthropology: the last half-century. *Evol Anthropol* 2000;9:2–16.

Weiner J. The beak of the finch. New York: Alfred A. Knopf, 1994.