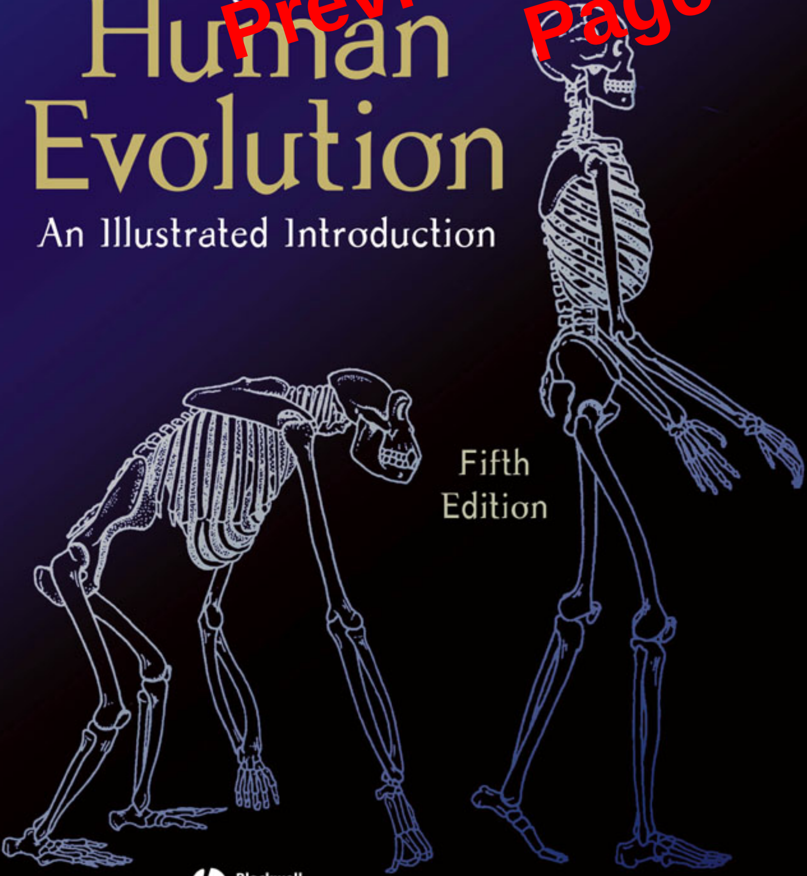
Roger Lewin

# Human Evolution

## An Illustrated Introduction



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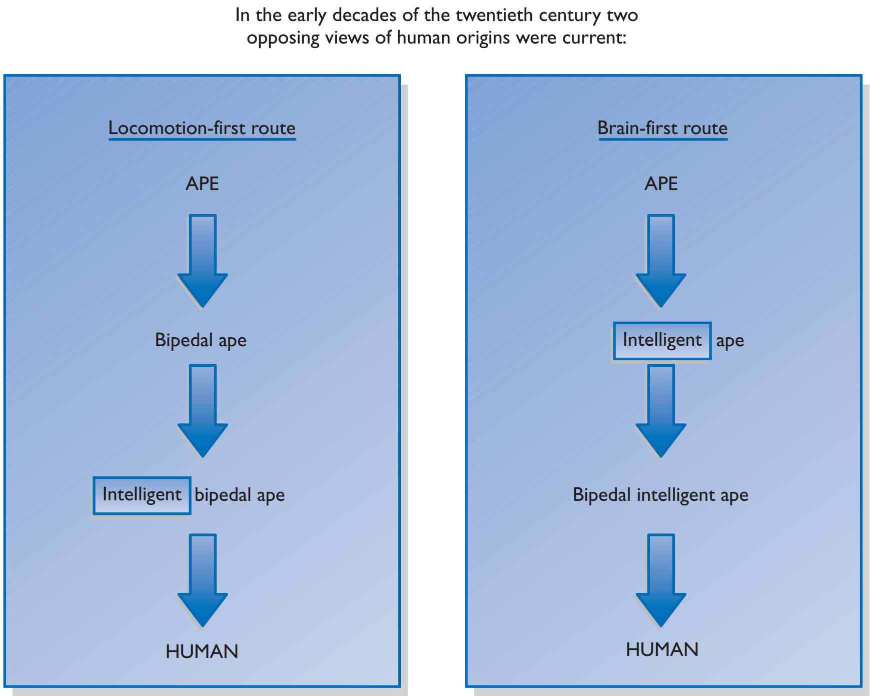

**FIGURE 3.3 Conflicting views:** One of the key differences of opinion regarding the history of human evolution was the role of the expanded brain: was it an early or a late development? The "brain-first" notion, promoted by Elliot Smith, was important in paving the way for the acceptance of the Piltdown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

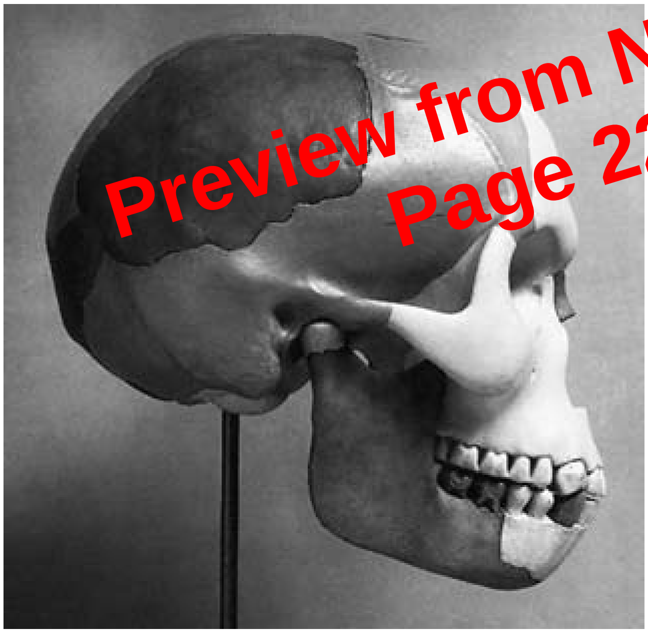

**FIGURE 3.4 A fossil chimera:** A cast of the Piltdown reconstruction, based on lower jaw, canine tooth, and skull fragments (shaded dark). The ready acceptance of the Piltdown forgery—a chimera of a modern human cranium and the jaw of an orangutan—derived from the British establishment's adherence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

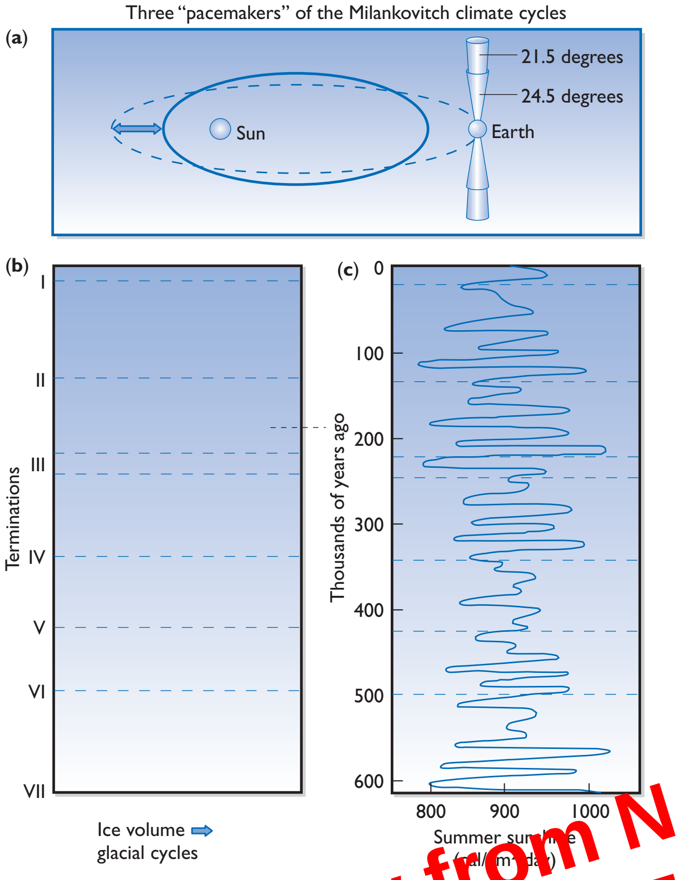

**FIGURE 5.3 Milankovitch climate cycles of the past 600,000 years:** Superimposed on long-term global climate change are regular cycles driven by three pacemakers: (a) changes in orbital eccentricity, and tilt and orientation of the Earth's spin axis, which results in a 100,000-year cycle; (b) changes in the volume of the Earth's ice sheets, giving a 41,000-year cycle; and (c) the effect of the intensity of summer sunshine at northern latitudes, yielding a 23,000-year cycle.

ticularly for the time period most relevant to human evolution, the last 5 million years. The climatic picture is one of continual and sometimes dramatic change within a net cooling trend. Superimposed on this pattern are global cooling and warming cycles, the so-called Milankovitch cycles, with periodicities of approximately 100,000, 41,000, and 23,000 years. (See figure 5.3.) Each of these cycles dominates climate fluctuation at different times in Earth history. For example, prior to 2.8 million years ago, the shortest cycle was dominant; between 2.8 and 1 million years ago, the 41,000-year cycle prevailed; from 1 million years onward, the dominant cycle has been 100,000 years.

During the 5 million years since the first appearance of the hominin clade, several major global cooling episodes have occurred within this overall trend and against the background of the frequent Milankovitch cycles; the existence of these episodes has been inferred from oxygen isotope data and more recently from measures of wind-blown dust in the oceans around Africa. The first event, appearing at 5 million years, involved significant cooling. The second, between 3.5 and 2.5 million years ago, was associated with the first major buildup of Arctic ice and substantial expansion of Antarctic ice. The modern Sahara's roots lie at this point, too. This beginning of the modern Ice Age may have been initiated by a change in circulation patterns in the atmosphere and oceans as a result of the rise of the Panamanian Isthmus, which joined North and South America some 3.5 million years ago. The third event occurred nearly 1.7 million years ago. The fourth, arising approximately 0.9 million years ago, was possibly caused by uplift in western North America and of the Himalayan range and the Tibetan Plateau. Of the four events, the second was largest in extent. The overall pattern of climate change is therefore extremely complicated, driven by several different forcing agents.

Inevitably, species and the ecosystems of which they are a part do not remain immune to climate change of this magnitude. The temperature extremes of the Milankovitch cycles exceed the habitat tolerances of virtually all species, turning a once suitable habitat into an inhospitable one; the larger shifts have an even more dramatic impact. The average lifespan of a terrestrial mammal species, for instance, is several million years; the periodicity of the cycles is just a fraction of that average. Thus, it is obvious that most species are able to survive these repeated climatic fluctuations. The principal response of species to climate is dispersal, tracking the change so as to remain in hospitable habitats. During global cooling, dispersal moves toward lower latitudes; during warm periods, it takes the reverse direction. Because different species have different tolerance limits, ecosystems do not migrate en masse, but rather become fragmented, eventually forming new communities.

Other biotic responses to climate change are possible as well, particularly when a threshold of tolerance is exceeded—namely extinction and speciation. These trends are central to the **habitat hypothesis**, which has been promoted principally by Yale University biologist Elisabeth Vrba. Although it has many components, the habitat hypothesis can be stated simply: species' responses to climate change represent the principal engine of evolutionary change. The major mechanism of such change is **vicariance**, or the creation of allopatric populations from once continuous populations, either by the establishment of physical barriers or the dispersal of populations across such barriers. Geographical areas with high topographical variation inevitably have a greater tendency to create vicariant populations when climate changes. (See figure 5.4.) After such populations become established, they are both vulnerable to extinction and have an opportunity for speciation (see unit 4).

**FIGURE 6.3 The smoking gun:** The suggestion that the end-Cretaceous extinction might have been caused by asteroid impact was first made in 1979, based on the discovery of the rare element iridium at the Cretaceous/Tertiary boundary. Since then, much evidence has been amassed in support of the proposal, including the recent discovery of a huge impact crater in the Yucatan Peninsula dated at 65 million years.

found patterns similar in *form*, but not in *magnitude*, to the contents of the fossil record. In other words, species numbers fluctuated significantly with no external driving force, but only rarely crashed in a way that could be termed a mass extinction. Thus, bad luck cannot be the sole cause of a species' demise in a mass extinction event. This research also partly inspired the realization that bad genes could not provide the sole explanation of the pattern of life. Instead, some combination of selection and bad luck operated in tandem.

## MASS EXTINCTIONS ARE QUALITATIVELY DIFFERENT

The University of Chicago paleontologist David Jablonski has investigated the nature of that selection by comparing the pattern in background and mass extinction periods. During background extinction, several factors contribute to the protection of a species from extinction. Species that are geographically widespread resist extinction, for instance. Likewise, marine species that send their larvae far and wide (drifting with the currents) resist extinction, for similar reasons. A group of related species, a clade, resists extinction if it contains many species rather than only a few. Thus, the chance disappearance of a few species is more likely to threaten the survival of a clade that includes only three species, for example, than one that has 20.

When Jablonski examined the fate of mollusc species and species' clades across the end-Cretaceous extinction, he saw a very different picture. Most of the above rules applied. The only rule he could discern was valid for groups of related species, or clades. Once again, geographic distribution played a part in survival. If a group of species occurred over a wide geographic range, then they fared better in the biotic crisis than those that were geographically restricted, no matter how many species made up the clade. "During mass extinctions, quality of adaptation or fitness values . . . are far less important than membership in the particular communities, provinces, or distributional categories that suffer minimal disturbance during mass extinction events," wrote Jablonski. This finding was a landmark result, because it was the first to clearly indicate that the rules changed between background

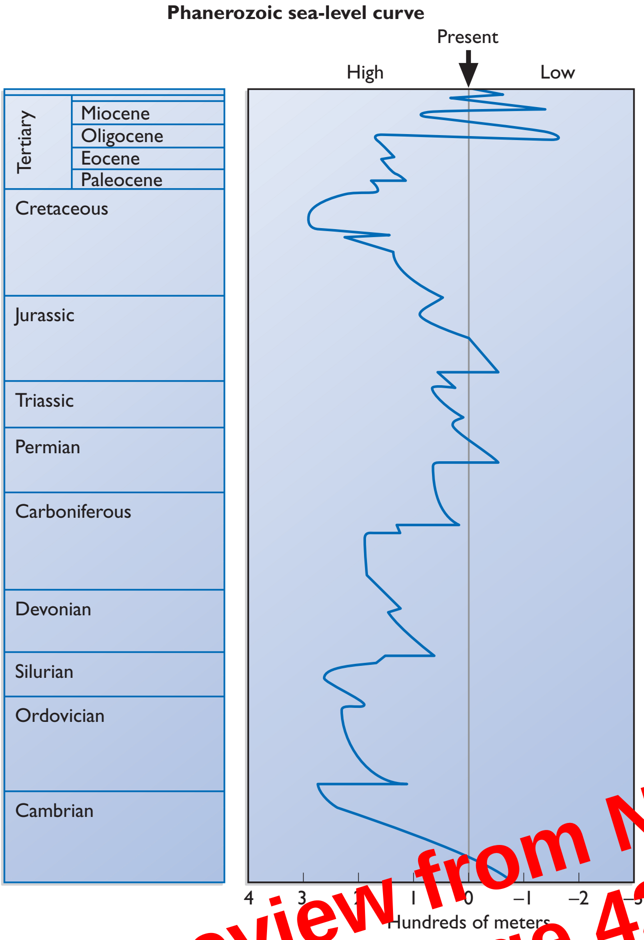

**FIGURE 6.[illegible] Sea-level changes:** Sea-level regression is a probable factor in some extinctions, and is associated with many of them. Many falls do not coincide with extinction, however, indicating that some mass extinctions are complex events, involving the interplay of several agencies.

and mass extinction. Biotic crises are *not* simply background extinctions writ large.

This idea makes sense because, in the history of life, many successful species or groups of species have met abrupt ends in mass extinctions. The dinosaurs dominated their realms for more than 100 million years and were as diverse as they had ever been toward the end of the Cretaceous. Some authorities argue that the diversity of dinosaur species was already in decline when they vanished completely at the end-Cretaceous extinction. No evidence suggests that the mammals were better adapted in any way than dinosaurs, which they subsequently replaced as the major terrestrial tetrapod group.

Natural selection operates cogently at the level of the individual, in relation to local conditions, reflecting the impact of competitors and prevailing physical conditions. It is a powerful response to immediate biological experience, but it cannot anticipate future events. And it certainly cannot anticipate rare events. The average longevity of an animal species is about 2 million years, and extinction bursts occur on average no more than every 27 million years or so. Consequently, most species never experience such bursts. The mass extinction episodes are rarer still, making them invisible to natural selection. Species cannot adapt to conditions they do not experience. The Darwinian view that the history of life is one of continual improvement through adaptation led by natural selection is therefore incomplete.

Mass extinctions, then, restructure the biosphere, with an unpredictable set of survivors finding themselves in a world of greatly reduced biological diversity. With at least 15 percent and as much as 95 percent of species wiped out, ecological niches are opened or at least made much less crowded. This time provides an evolutionary opportunity offered to a lucky few.

*Homo sapiens* evolved amid a high point of global biodiversity. We are but one of millions of species here on Earth, the product of half a billion years of life's flow, lucky survivors of at least 20 biotic crises, including the catastrophic Big Five. If the ancestral primate species had been among the mammalian lineages that became extinct at the end-Cretaceous event, there would be no prosimians, no monkeys, no apes, and no *Homo sapiens* today. Its survival, and our subsequent existence, was largely a matter of factors having nothing to do with adaptive qualities.

## KEY QUESTIONS

- Why did Uniformitarianism become so powerful a force in late-nineteenth- and twentieth-century scientific thinking?
- How might mass extinction be explained as a consequence of natural selection?
- How does mass extinction influence the history of life?
- How can the hypothesis of asteroid impact be tested?

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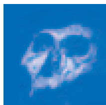

# 7

# DATING METHODS

*Paleoanthropologists have a suite of techniques available to them for inferring the age of fossils and artifacts. Typically, the techniques depend on determining the age of material associated with the relics in question, such as the strata in which they are found or other fossils of known age. Many of the techniques are based on the decay of radioactive isotopes.*

An accurate time scale is a crucial aspect of reconstructing the pattern of evolution of the anatomical and behavioral characteristics of early hominins. At least half a dozen methods of dating are now available that have the potential to cover events from 1000 years ago to many billions of years, albeit with some frustrating gaps. Paleoanthropologists' focus is on the last 10 million years or so, which includes some of those gaps.

Researchers who want to know the age of particular hominin fossils and/or artifacts in principle have two options for dating them: direct methods and indirect methods.

Direct methods apply the dating techniques to the objects. Two types of problem arise with this approach, however. First, for most objects of interest, no methods are as yet available for direct dating. Ancient fossils and most stone tools, for example, remain inaccessible to direct dating. Some methods, such as **carbon-14 dating** and **electron spin resonance**, may be applied directly to teeth or young fossils, and indeed to the pigments of rock shelter and cave paintings; in addition, **thermoluminescence dating** may be applied directly to ancient pots, flint, and sand grains. Second, fossils and artifacts are often too precious to risk destroying any part of them in the dating process.

In practice, indirect dating methods represent the typical approach. Here, an age for the fossil or artifact is obtained by dating something that is associated with them. This strategy may involve direct dating on nonhuman fossil teeth that occur in the same **stratigraphic layer**, by electron spin resonance, for instance, or by thermoluminescence dating of flints associated with human fossils. Both these approaches have been applied in recent years to fossils relating to the origin of modern humans (see unit 27). Fossils or artifacts may be attributed an age through information about the evolutionary stage of nonhuman fossils associated with them, a technique known as faunal correlation.

The most common indirect approach, where feasible, is to date stratigraphic layers that lie below and above the object in question. Stratigraphic layers accumulate from the bottom up, so that the lower layers are oldest and the upper layers youngest. The two dates, taken from below and above the object, provide brackets that include the date at which the object became buried in the stratigraphic system.

This unit will survey briefly the principal techniques available and identify where they are best applicable. The techniques may be classified into two types: those that provide relative dates and those that provide absolute dates. **Relative dating** techniques give information about the site in question by referring to what is known at other sites or other sources of information. **Absolute dating** techniques provide information by some kind of physical measurement of the age of material at the site in question.

## RELATIVE DATING TECHNIQUES

Relative dating techniques include **faunal correlation** and **paleomagnetism**. Geologists and paleontologists have long used fossils to structure prehistory. For instance, the geological time scale for the history of life on Earth is built upon major changes in fossil populations, such as appearances and disappearances of groups. Because they are interested in a finer-scale approach, archeologists and anthropologists often look for evolutionary changes *within* groups. Among the most important species for paleoanthropologists are elephants, pigs, and horses.

The principle behind the faunal correlation is simple. If a hominin fossil is found in sedimentary layers which also include fossil pigs that are known to have lived, for instance, between 2 million and 1.6 million years ago (as assessed, say, by tooth size or morphology), then this provides a bracket for the date of the hominin. (See figure 7.1.)

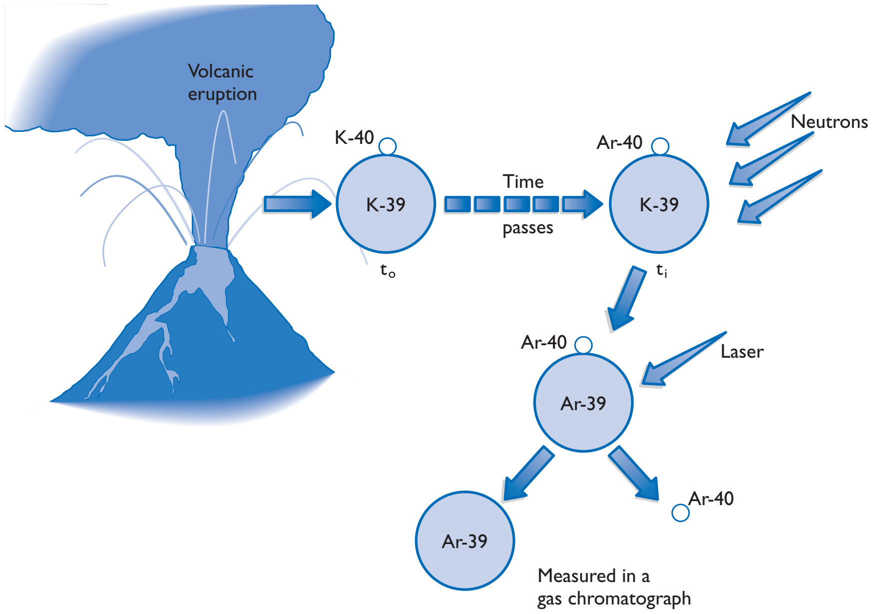

**FIGURE 7.3 Argon-39/argon-40 dating:** Volcanic ash contains potassium-rich minerals, such as feldspar. A small percentage of the potassium exists as a radioisotope, potassium-40, which has argon-40 as one of its decay products. In the laboratory, crystals of feldspar are irradiated with neutrons, which converts the stable potassium-39 isotope to argon-39. The crystals can then be individually heated by laser beam, and the emitted argon-39 and argon-40 measured separately in a gas chromatograph. The argon-39 represents a measure of the total amount of potassium that was present in the crystal, and the argon-40 provides a measure of the time since eruption.

sets a radiometric "clock" to zero, such as the heating that rock experiences during volcanic eruption or burial in the Earth. Second, the products of radioactive decay steadily accumulate, thus recording the passage of time.

The most important radiometric technique that has been applied in paleoanthropology is **radiopotassium (potassium/argon) dating**. This technique is based on the fact that potassium-40, a radioactive isotope of potassium that makes up 0.01 percent of all naturally occurring potassium, slowly decays to argon-40, an inert gas. Rocks that contain potassium, such as volcanic rocks, slowly accumulate argon-40 in their crystal lattices. The high temperature experienced during eruption drives out the argon (and other gases) from the mineral, and the clock is set to zero—the time of the eruption. As time passes, argon-40 builds up, with the amount in any particular rock depending on the initial potassium concentration and the time since the eruption. The age calculation is based on measurements of the potassium concentration and the accumulated argon-40 in potassium-rich minerals, such as feldspar.

A common problem is that a sample may be contaminated with older rock, which may happen when ash is erupting from a volcano, for instance, or mixing with other minerals as it accumulates on the landscape. Even a few crystals of, for example, Cambrian-age rock in a gram of 2-million-year-old ash can produce an erroneously old date.

The first major application of the potassium/argon technique to paleoanthropology occurred in 1960, in an assessment of ash layers at Olduvai Gorge. In 1959, Mary Leakey found the famous *Zinjanthropus* fossil (see unit 19), the first early hominin discovered in East Africa, at this site. The date produced for the fossil, 1.75 million years, was double the age inferred by indirect means. Both the discovery of the fossil and the application of the dating technique represented major milestones for paleoanthropology.

Since that time two important advances have taken place with radiopotassium-based dating. The first, developed in the 1970s, allows measurements to be taken in one sample rather than in two separate samples (one to measure potassium, the second to measure argon-40). The rock is initially irradiated with neutrons, which transforms the stable potassium-39 into argon-39; when the rock is then heated, the two argon isotopes, 39 and 40, are released together and can be measured simultaneously on a gas chromatograph. The potassium-39 level provides a vicarious measure of the potassium originally in the rock, and the argon-40 measures the decay of potassium-40 since the rock was ejected from the volcano. This technique is known as argon-39/argon-40 dating. (See figure 7.3.)

The second advance, developed during the 1980s, allows the technique to be applied to single crystals taken from volcanic ash, compared with the several grams required for the conventional technique. The advantages of the new technique, known as single-crystal laser fusion, are several, including avoiding the problem of contamination. Until recently the youngest rocks that could be dated with radiopotassium techniques were approximately 0.5 million years old. Recent work, however, has shown that rocks containing potassium-rich minerals can be accurately dated with ages as young as 10,000 years—a range that overlaps with the limits of radiocarbon dating. There is no effective upper limit of age estimation.

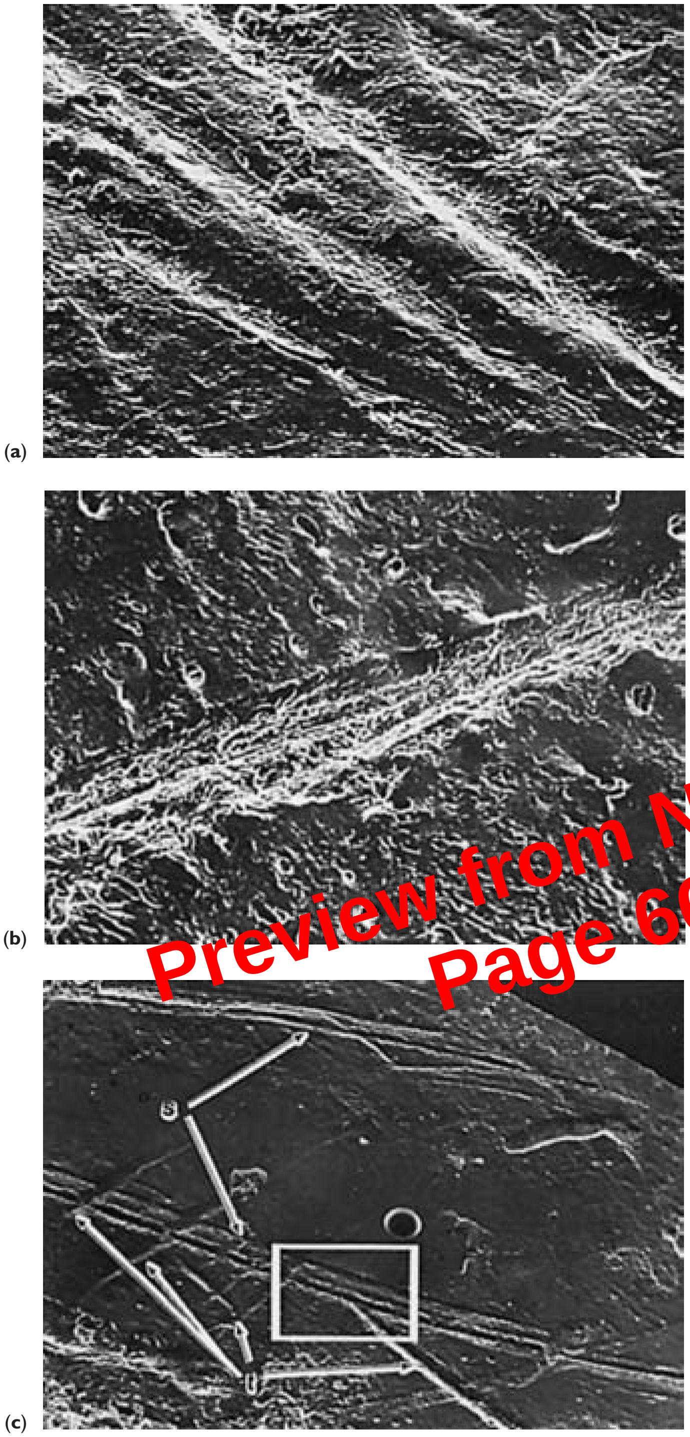

**FIGURE 9.2** **Bone surfaces under the electron microscope:** (a) The surface shows the round-bottomed groove made by a hyena gnawing at a modern bone. (b) A sharp stone flake makes a V-shaped groove in a bone surface (modern). (c) This fossil bone from the Olduvai Gorge carries carnivore tooth marks (t) and stone flake grooves (s); the scavenger activity followed the hominin's activity on this occasion. (Courtesy of Pat Shipman and Richard Potts.)

## CLUES FROM MARKS ON BONES

In the late 1970s and early 1980s, several researchers discovered on the surface of a small percentage of the Olduvai bones what appeared to be marks made by stone tools. Thus, although the sites might not have been typical hunter-gatherer home bases, it did appear that a connection existed between the bones and the stones: the hominins almost certainly were eating meat. By looking at the pattern of distribution of cutmarks over a bone—on the shaft as compared with the articular ends, for example—investigators can obtain some idea of whether the marks were made during the disarticulation of a carcass or during the removal of meat or skin from the bone.

Determining the identity of marks on the surface of fossil bones is an important taphonomic activity: gnawing carnivores and nibbling porcupines can all leave their signatures. Likewise, sand grains can leave behind tell-tale signs. In 1986, Behrensmeyer and two colleagues from the Smithsonian Institution reported that bones trampled in sandy sediment can sustain abrasions that are virtually indistinguishable from genuine stone-tool cutmarks. "Microscopic features of individual marks alone provide insufficient evidence for tool use versus trampling," warn Behrensmeyer and her colleagues. "If such evidence is combined with criteria based on context, pattern of multiple marks and placement on bones, however, it should be possible to distinguish the two processes in at least some cases bearing on early human behavior." (See figure 9.2.)

Not all taphonomists agree about the difficulty of distinguishing between the effects of trampling and genuine cutmarks, however. For instance, Sandra Olsen and Pat Shipman have examined the problem experimentally and stated: "Macroscopic and microscopic comparison of experimentally trampled bones and those which have had soft tissue removed with a flint tool demonstrate significant differences between the surface modifications produced by the two processes."

## KEY QUESTIONS

- What is implied by the fact that the great majority of hominin fossil remains have been recovered from sediments laid down near sources of water, such as streams and lakes?
- Why is the fossil record of the African great apes virtually nonexistent for the past 5 million years—during which time the hominin record is relatively good?
- Fossil fragments from almost 500 hominid individuals representing perhaps four species over a period of 4 million years ago to 1 million years ago have been recovered from the Lake Turkana region of Kenya. What percentage does this amount represent of the original populations?
- What is the single most important factor in shaping the life history of a fossil?

smell or hearing, so that visual predation by itself is not sufficient to explain this suite of primate adaptations. He also argues that the earliest primates evolved at a time when flowering plants were in the midst of an evolutionary diversification. Grasping hands and feet would have enabled small primate species to move with agility in terminal branches rich with fruit; keen visual acuity would allow fine discrimination of small food items. Sussman's hypothesis is obviously similar in some ways to the earlier arboreal hypothesis. Cartmill's hypothesis remains the most cogent explanation of primate adaptations. In any case, a 2002 report in *Science* of a 55-million-year-old primate fossil from Wyoming points to an ancestor adapted to hanging tightly onto tree branches.

Living primates do not follow a single "primate diet." Insects, gums, fruit, leaves, eggs, and even other primates—all are found on the menu of one primate species or another, and most species regularly consume items from two or more of these categories. The key factor that determines what any individual species will principally subsist on is body size. Small species have high energy requirements per unit of body weight (because of a high relative metabolic rate), and they therefore require food in small, rich packets. Leaves, for instance, are simply too bulky and require too much digestive processing to satisfy small primates. Because of their reduced relative energy demands, large species have the luxury of being able to subsist on bulky, low-quality resources, which are usually more abundant. From the small to the large species, the preferred foods shift, roughly speaking, from insects and gums, to fruit, to leaves.

A good deal of variation around this basic equation exists, however. As the University of Cambridge primatologist Alison Richard points out, "Almost all primates, regardless of size, meet part of their energy requirements with fruit, which provides a ready source of simple sugars." What sets the basic equation, she says, is "how they make up the difference in energy and how they meet their protein requirements." This issue is where body size is crucial, and why, for instance, the bushbaby's staple is insects and the gorilla's is leaves.

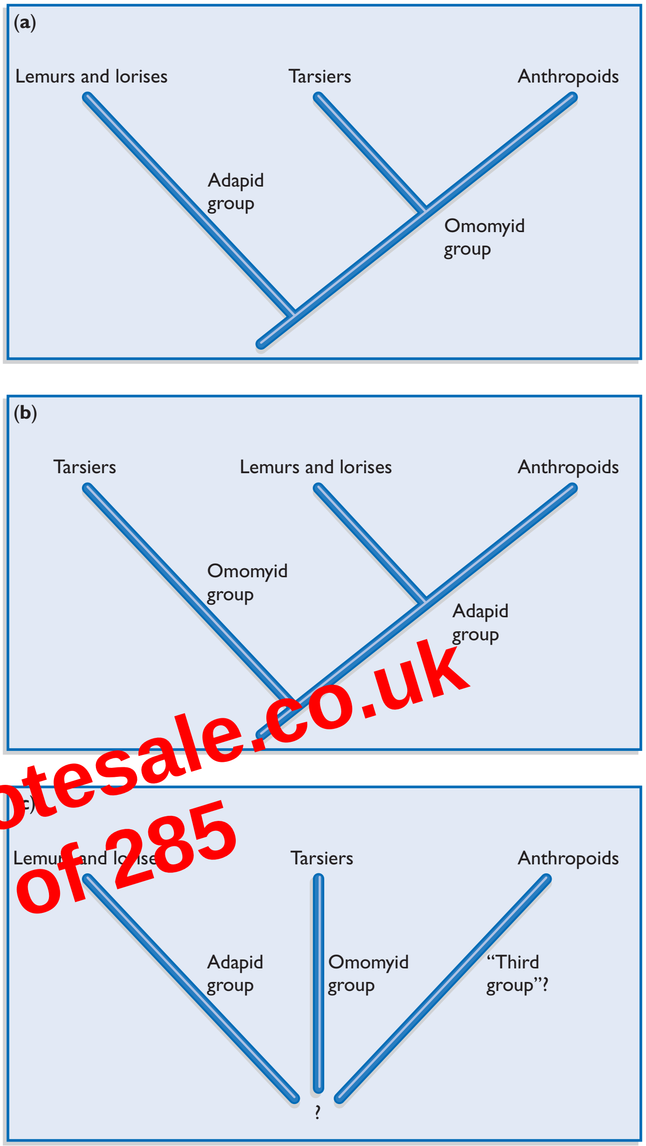

**FIGURE 10.5 Three views of primate evolution:** A good deal of uncertainty exists over the pattern of primate evolution. Until recently most opinion was divided between schemes (a) and (b), which show differences over the origin of anthropoids. A third view (c) has also been proposed, which postulates a third, early group of primates that was ancestral to modern anthropoids. Based on the most recently discovered fossil evidence, however, scheme (a) is now most strongly supported.

## THE ORIGIN AND EVOLUTION OF PRIMATES

The overall evolutionary pattern of primates remains unsettled (see figure 10.5), although the origin of the order has recently been estimated at close to 85 million years rather than the 65 million that has generally been assumed. Some kind (or kinds) of species ancestral to all primates survived the mass extinction 65 million years ago that spelled the end of the Age of Reptiles, with the dinosaurs being the most notorious of the extinctions. Soon into the subsequent Age of Mammals, "primates of modern aspect" appeared approximately 50 million years ago, beginning an adaptive radiation that included an increase in range of body size and a concomitant broadening of diet. The 200 modern species represent the remains of that adaptive radiation, which, in total, probably gave rise to some 6000 species.

The known fossil record provides only the briefest of glimpses of this radiation, a sketchy outline at best; somewhere between 60 and 180 fossil primate species can be recognized. Some researchers consider the earliest primate group to be the plesiadapiforms, the best-known specimen

The earliest known fossil of the superfamily Hominoidea, which includes all living and extinct species of humans and apes, is some 20 million years old; it was found in Africa (see unit 16).

## KEY QUESTIONS

- What general trends did the primate order follow through evolutionary time that are common in other mammalian orders?
- What are the most important problems in trying to reconstruct the phylogeny of primates?
- What key adaptations do humans share with nonhuman primates?
- How great a departure is bipedalism from the mode of locomotion of monkeys and apes?

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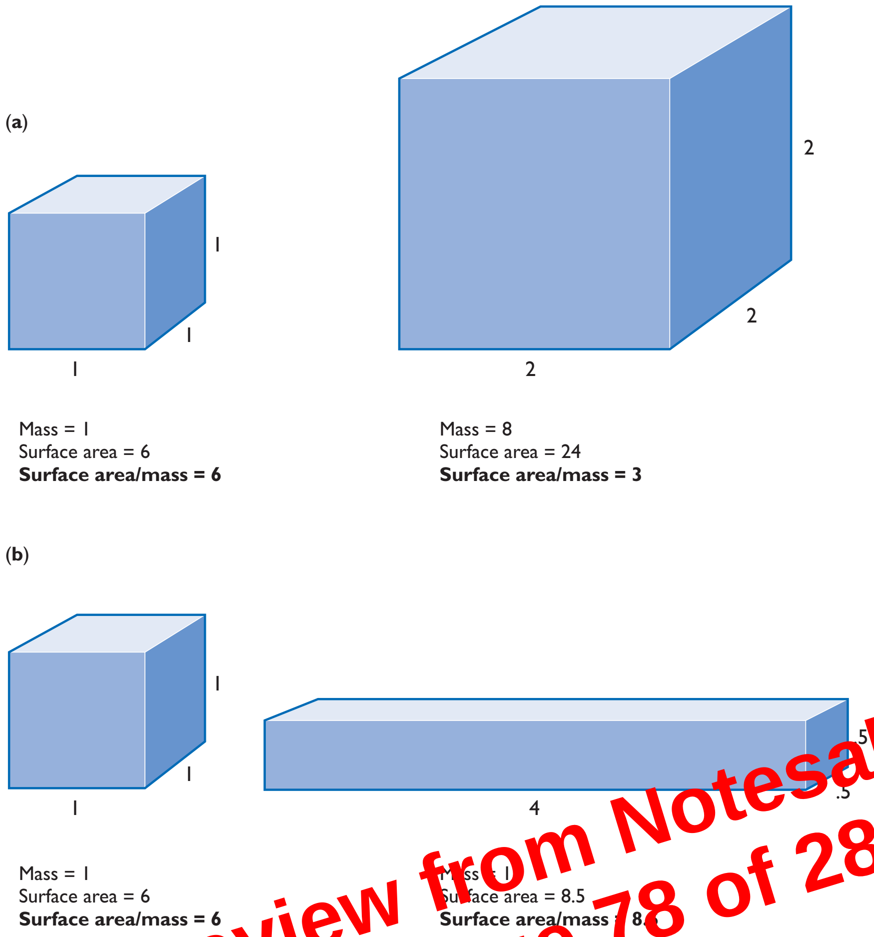

**FIGURE 11.1 Geometric basis of Bergmann's and Allen's rules:** (a) Bergmann's rule: An increase in size decreases the ratio of surface area to mass; in humans, this relationship is reflected in the breadth of the trunk. (b) Allen's rule: An elongated shape increases the ratio of surface area to mass; in humans, this relationship is reflected in limb length.

height is more than six feet, and Mbuti Pygmies, who are two feet shorter on average. Why the difference in stature? (See figure 11.5.)

The answer is related to efficiency of heat dissipation. Humans rely heavily on sweating to cool their bodies. Nilotics live in open environments, where sweating is efficient; in contrast, Mbuti Pygmies, like most Pygmy populations, live in moist, humid forests, where the air is still and sweating is an inefficient cooling mechanism. Under these environmental conditions, the best strategy is to limit the amount of heat generated during physical exertion, which is achieved by reducing the volume of the cylinder. With the width of the cylinder remaining constant, this requirement implies a reduction of its length—in other words, reduced stature.

This insight may have implications for the lifestyles of both Lucy (*Australopithecus afarensis*, short in stature) and the Turkana boy (*Homo erectus*, tall in stature), whose differences in stature are similar to the differences observed between Nilotics and Pygmies (see figure 11.6). Despite their varying statures, Lucy and the Turkana boy had very similar body widths, comparable with the width of modern tropical populations. This observation makes sense because, living in East Africa as they did, they were exposed to a tropical climate (albeit more than a million years apart). Ruff speculates that, like the Nilotics of today, the Turkana boy and his fellow *Homo erectus* people lived an active life in open environments. Lucy and her companions, by contrast, may have inhabited more closed, forested environments, comparable with the environment of modern Pygmies.

Climatic adaptation of body form can also be seen in Neanderthals, who lived in Europe between 250,000 and 27,000 years ago—a time when, for the most part, the Pleistocene Ice Age still held the continent in its grip (see unit 30). The frigid conditions under which the Neanderthals evolved is reflected in their wide bodies and their relatively short limbs, characteristics comparable to those seen in modern Eskimos.

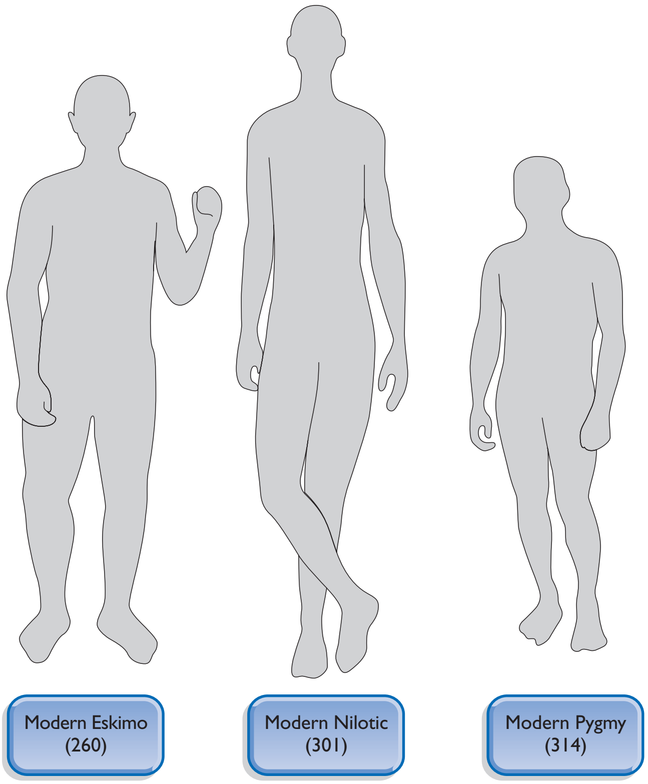

**FIGURE 11.5 Body outlines of modern populations:** Figures below the outlines give the surface area to body mass ratio ($cm^2/kg$). Note the broad body and short stature of the Eskimo, and a low ratio; the Nilotic body is narrow and taller, with a high ratio. The Pygmy has the same body breadth as the Nilotic and a similar ratio. (Courtesy of C. B. Ruff.)

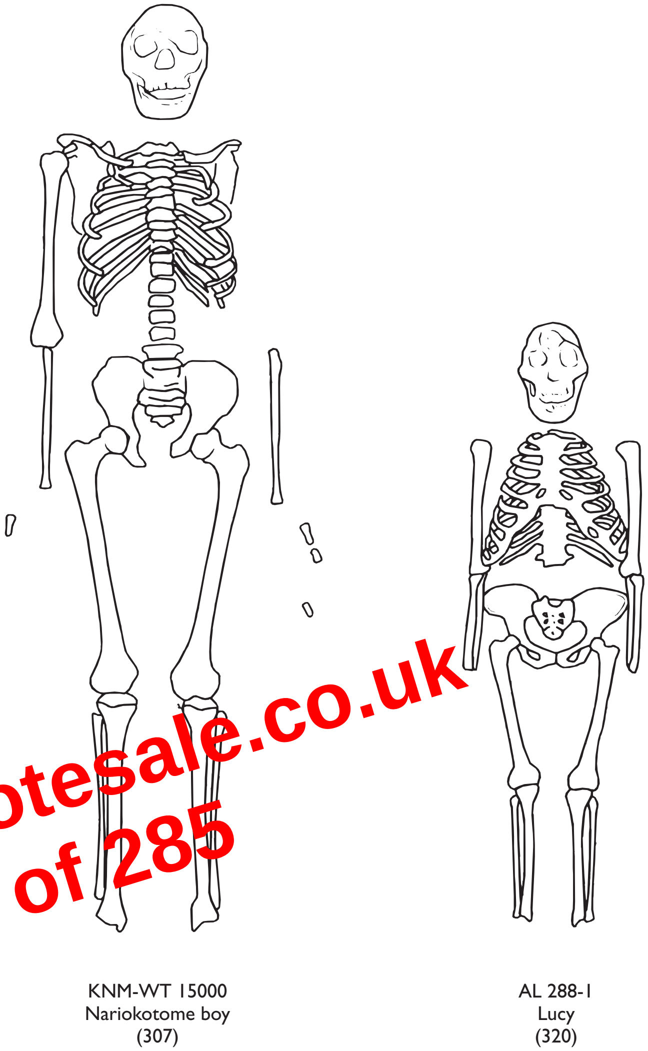

**FIGURE 11.6 Body proportions in fossil humans:** Despite their different statures, the Nariokotome (Turkana) boy and Lucy have very similar body breadths and surface area to body mass ratios. (Courtesy of C. B. Ruff.)

For instance, in his studies of Australian populations, Peter Brown, of the University of New England, Armidale, found the following changes in the five millennia after the Ice Age: tooth reduction, 4.5 percent; facial size reduction, 6–12 percent; brain size reduction, 9.5 percent; and stature reduction, 7 percent. Where data exist in other parts of the world, such as in Europe and Southeast and West Asia, similar changes are observed, although paleoanthropologists disagree on whether, for instance, significant brain shrinkage began as early as 30,000 years ago or only 10,000 years ago. Whatever the details of the timing of events in these later stages, it seems irrefutable that, until the nutritional effects of the last century or so kicked in, modern people were comparative midgets on the human evolutionary stage. (See figure 11.7.)

What overall pattern held, beginning with the increase in robusticity until archaic *sapiens* arrived? Subsistence was strenuous in those days, as our ancestors plied a life of hunting and gathering with only rudimentary technology to aid them. Muscles—not missiles—were their weapons. Other explanations for this trend have been suggested, too. For instance, Robert Foley, of Cambridge University, speculates that people became stronger because they were embroiled in increasing conflict between neighboring groups. The conflicts arose, he says, because the groups were dominated by bands of males, probably closely related, who sought to appropriate the plentiful resources in their area, including females from other groups.

Why, then, did robusticity decline with the origin of anatomically modern humans, and continue to diminish for tens of millennia? Not because these humans changed their social structure and became more peaceable, says Foley, but because technological inventions usurped the role previously played by sheer strength. One key invention involved projectiles, spears in which stone points were hafted onto wooden *into account*. That is, all figures for each life-history variable would fall on the appropriate straight lines. In fact, individual figures often fall above or below the line, indicating a good deal of life-history variation. This variation reveals an individual species' (or, more usually, a group of related species') adaptive strategy.

Researchers now know that, in addition to body size, brain size is also highly correlated with certain life-history factors, in some cases much more so than is body size.

## ALTRICIAL AND PRECOCIAL STRATEGIES

Among mammals as a whole, a key dichotomy exists in developmental strategy that has important implications for life-history measures: the altricial/precocial dichotomy. **Altricial** species produce extremely immature young that are unable to feed or care for themselves. The young of **precocial** species, on the other hand, are relatively mature and can fend for themselves to a certain degree.

Life-history factors critically associated with altriciality and precociality include gestation length. In altricial species, gestation is short and neonatal brain size is small. Gestation in precocial species is relatively long, and neonatal brain size is large. There is, however, no consistent difference in *adult* brain size between altricial and precocial species. Primates as a group are relatively precocial with the exception of *Homo sapiens*, which has developed a secondary altriciality and an unusually large brain (see unit 31).

In addition to the distinction between fast and slow lives based on absolute body size, some species' lives may be fast or slow *for their body sizes*. Such deviations have traditionally been explained in terms of classic *r*- and *K*-selection theory. According to this theory, environments that are unstable in terms of food supply (that is, are subject to booms and busts) encourage *r*-selection: fast lives, with high potential reproductive output. Alternatively, stable environments (which are close to carrying capacity and in which competition is therefore keen) favor *K*-selection: slow lives with low potential reproductive output and high competitive efficiency.

As mentioned earlier, primates are close to the *K*-selection end of the spectrum among mammals as a whole, but some primates are less *K*-selected than others. For instance, Caroline Ross has shown that, when body size is taken into account, primate species that live in unpredictable environments have higher potential reproductive output than species residing in more stable environments.

A second factor that influences whether a species might live relatively fast or slow for its body size has been identified by Paul Harvey and Daniel Promislow. In a survey of 48 mammal species, the two found that "those species with higher rates of mortality than expected had shorter gestation lengths, smaller neonates, larger litters, as well as earlier ages at weaning and maturity." In other words, species that suffer high natural rates of mortality live fast. "The reason is that species with higher rates of mortality are less likely to survive to the following breeding season and will therefore be selected to pay the higher costs associated with the earlier reproduction."

Again, does the very slow life lived by *Homo sapiens* imply evolution from an ancestor that experienced very low levels of mortality?

Given that most mammals measure less than 32 centimeters in length, hominins—even the early, small species—must be classified as large mammals. One of the earliest known hominin species, *Australopithecus afarensis*, stood 1 meter (females) to 1.7 meters (males) tall, and weighed some 30 to 65 kilograms (see unit 19). These general proportions persisted until approximately 1.5 million years ago and the evolution of *Homo erectus*, which stood close to 1.8 meters (with a much reduced difference between males and females). (See unit 24.)

## PREDICTIONS FOR EARLY HOMININ SPECIES

With a knowledge of these general body proportions and the estimates of brain size, it becomes possible to make estimates of various life-history factors for the early hominin species, given what is known of the only extant hominin, *Homo sapiens*. Surely, hominins lived slow lives in the terms of life-history variables, with a vastly increased brain capacity eventually distorting some of them.

In addition, we can identify several behavioral ecology traits that would be associated with large body size, as Cambridge University anthropologist Robert Foley has done. For instance, dietary scope could be broad; day and home ranges could be large; mobility could be high; predator–prey relations would be shifted from that of smaller primates; thermoregulatory efficiency would be improved; sociality would be extended; and enhanced encephalization would be energetically possible.

In sum, studies of life-history strategies have identified body size, brain size, environmental variability, and mortality rates as being crucial to the rate at which a species will live. Much of human evolution may therefore be explained in terms of a large hominoid exploiting a relatively stable food supply, its stability perhaps being enhanced by virtue of its breadth. Technology may eventually have contributed to this stability by permitting more efficient exploitation of meat and certain plant foods, thus broadening the diet even further. A reduction in mortality, perhaps through improved antipredator defense, would further encourage a "slow" life-history strategy. The selection pressure leading to increased body size remains to be identified.

15

# APE AND HUMAN RELATIONS: MORPHOLOGICAL AND MOLECULAR VIEWS

*Anthropologists have for years argued over the relationship between humans and great apes. Until relatively recently, the great apes were considered each other's closest relatives, with humans being separate. Now, however, based on anatomical and especially molecular evidence, it has become apparent that humans and chimpanzees are each other's closest relatives, with gorillas being separate.*

The superfamily **Hominoidea** (colloquially, hominoids) includes all living and extinct ape and human (hominin) species. This unit will address the relationships among living hominoids and their formal classification, the timing of the evolutionary divergence between the human and ape lineages, and the probable anatomical characteristics of the ancestor of humans common to both humans and apes. Unit 16 will examine our knowledge of extinct ape species and their possible relationship to living hominoids.

## MORPHOLOGICAL INTERPRETATIONS

Since the time of Darwin and Huxley, anthropologists have recognized that humans' closest relatives are the African great apes, the chimpanzee and gorilla, with the Asian great ape, the orangutan, more distant. This conclusion is based principally on comparative anatomy of the hominoids. For a long time the question of the evolutionary relationship between humans, chimpanzees, and gorillas was debated. (It seems now to have been resolved, principally based on molecular evidence.)

For instance, the African apes share many anatomical similarities, particularly in their forelimbs, which show adaptations to their knuckle-walking mode of locomotion (see figures 15.1 and 15.2) and in their dentition (see figure 15.3) which has a thin layer of enamel on the cheek teeth. Modern humans and (most of) their extinct relatives have thick enamel (but see unit 19 for a qualification), as do many fossil apes. In several cladistic analyses of living hominoids (by, for example, Lawrence Martin of the State University of New York at Stony Brook and Peter Andrews of the Natural History Museum, London), the shared limb anatomy and dental features of African apes were judged to be derived characters that linked chimpanzees and gorillas as a separate clade from humans. Under this scheme, humans were seen as having diverged first from the hominoid lineage, with gorillas and chimpanzees sharing a common ancestor in which knuckle-walking and thin tooth enamel evolved. A second scheme—a trichotomy in which African apes and humans diverged simultaneously from a common ancestor—was also said to be possible, though less likely.

The Martin/Andrews view of human/African ape affinity won wide support, although different views were expressed as well. For instance, one cladistic analysis grouped the orangutan with the African apes in a clade separate from humans, while another identified an African ape clade and a human/orangutan clade. In this plethora of morphological analyses, only one, published in 1986 by the Australian anatomist Colin Groves, concluded (weakly) that humans and chimpanzees are one another's closest relatives; this assessment was based on forelimb anatomy, particularly the wrist. That is, gorillas were suggested to have diverged first from the hominoid ancestor, with humans and chimpanzees sharing a common ancestor from which they later diverged. (A later, more detailed study, reached the same conclusion; see figure 15.4) As we shall see, this counterintuitive view was also emerging from molecular studies of the time, and it became ever more strongly supported throughout the following decade.

Morphologists resisted this latter interpretation, because the many anatomical similarities between gorillas and chimpanzees were assumed to be shared derived characters. If the human/chimpanzee association was indeed correct, then morphologists faced awkward puzzles. For instance, the many striking anatomical similarities of gorillas and chimpanzees must be explained either as homoplasies (independent, parallel evolution), which seems unlikely, or as shared primitive characters that were present in the common ancestor of apes and humans (see below). Furthermore, why have the development of thick enameled teeth among hominoids might be interpreted in the context of the cooling Miocene climate, but no universal trend in this direction occurred through time—that is, thick and thin enamels are seen both early and late. For instance, *Kenyapithecus* (an archaic Kenyan species that lived from 12 million years ago) and *Dryopithecus* (a modern form that lived between 13 and 8 million years ago) have thick and thin enamel, respectively.

The 1999 announcement of a 15-million-year-old partial skeleton of an ape from the Lake Baringo region of Kenya clarified what had been a somewhat confused picture of *Kenyapithecus*. Until that time two species of *Kenyapithecus* had been recognized, the 15-million-year-old *K. africanus* and a somewhat younger *K. wickeri*. The former displayed a rather primitive anatomy, while the latter had a more modern, great-ape pattern. The Baringo fossil closely resembles *K. africanus*, and its discoverers suggest that a new genus be named, *Equatorius*, that would include the new material and the existing *K. africanus*. This new arrangement leaves *K. wickeri* as a stronger contender for ancestry of hominoids. In addition, it is anatomically similar to so far unnamed fossil specimens from Pasolar, in Turkey.

Other archaic hominoids include *Ouranopithecus* (Greece), *Lufengpithecus* (China), *Sivapithecus*, the recently discovered *Otavipithecus* (a Namibian species from 15 million years ago), and *Ankarapithecus* (a Turkish species, dated at 9.8 million years). The first two lived approximately 8 million years ago. *Ouranopithecus* (also called *Graecopithecus*) had extremely thick enamel, whereas *Otavipithecus* had thin enamel. *Ankarapithecus*, details of which were published late in 1996, exhibited a mix of gorillalike and orangutanlike features in its cranial anatomy. A very large archaic hominoid, *Gigantopithecus*, lived in China, India, and Viet Nam from 8.6 to 0.2 million years ago, but for different periods of time in these parts of Asia. It had large, thickly enameled molar teeth, stood as high as 8 feet tall, and weighed as much as 640 to 650 pounds, making it the biggest hominoid ever.

Of all the Miocene hominoids, *Sivapithecus* holds the strongest claim to being ancestral to a living hominoid, the orangutan. This relationship is based on anatomical similarities in the structure of the face and palate.

Hominoids of modern aspect are rare in the fossil record. They include *Oreopithecus* (from Italy), *Morotopithecus bishopi* (from Uganda), and *Dryopithecus*.

*Oreopithecus*, the first specimens of which were found in the late nineteenth century, lived approximately 8 million years ago. Its dentition represents a mix of primitive and derived characters (but not like those of living hominoids); its trunk was short and the thorax broad, with long arms and short legs. Its elbow joints resembled those of modern apes. Its evolutionary relationships are unknown. Aspects of its lumbar, pelvic, and foot anatomy have recently been interpreted as implying a significant degree of habitual bipedal locomotion.

The Ugandan fossil, first found in the 1960s and recently dated to at least 20.6 million years, was similar to *Proconsul* and *Afropithecus* in terms of dentition and cranial anatomy. Parts of its postcranial anatomy, including shoulder and lumbar vertebrae, were derived in the direction of living apes and humans. Its evolutionary relationships are unclear.

*Dryopithecus* specimens have been found in Spain, Greece, Germany, and Hungary. They display a combination of primitive dentition and advanced postcranial anatomy that places them in the group of hominoids of modern aspect. *Dryopithecus* has been subject to many different phylogenetic interpretations since its discovery.

The January 1996 announcement of the discovery of an extraordinary partial skeleton of *Dryopithecus laietanus* from the site of Can Llobateres in Spain greatly increases our understanding of the species' postcranial anatomy and locomotor pattern, but it does not solve its phylogenetic affiliation. The newly discovered postcranial material is interpreted as reflecting more suspensory adaptation and orthograde posture (similar to living apes) than are seen in any Miocene ape. For instance, the lumbar vertebrae are proportionally shorter than in monkeys and most Miocene apes; the arms are powerful and capable of a wide range of movement; the hand is large and adapted for powerful grasping. The ratio of arm length to leg length (**intermembral index**) is larger than in living African apes and similar to that in the orangutan. The Spanish species is dated at 9.5 million years, indicating that the postcranial adaptations of living apes might have evolved by that date, depending on the still unsettled evolutionary relationship between *Dryopithecus* and the living apes.

This conservative discussion of the phylogenetic relationships of fossil hominoids leaves us with a tree with many branches; few, if any, of these branches appear to be joined to any other branches. Undoubtedly, the hominoid radiation was diverse and successful, and the later fossil species lived in drier, more open woodland habitats than either living hominoids or the early Miocene species. The African hominoid clade evolved at a time when climatic conditions were deteriorating in terms of preferred habitat for apes and when ape diversity was decreasing, perhaps as different adaptations or as reactions to that change. Today's African apes are woodland and forest creatures, while early hominins lived in more open environments. Open environments were once posited to be influential in the origin of the hominin clade, but recent fossil discoveries show the earliest known hominins lived in forest environments (see unit 19).

A recent study of fossil anatomy and of DNA from living anthropoids has led to a novel scenario for the history of the group. Caro-Beth Stewart, of the State University of New York at Albany, and Todd Disotell, of New York University, suggest that around 18 million years ago, when ape species were plentiful in Africa, at least one ape species migrated into Asia. It underwent a rapid adaptive radiation, giving rise to

A hypothesis developed by Kevin Hunt, of Indiana University, shifts the focus away from foraging efficiency to feeding efficiency. From more than 600 hours of field observations of chimpanzees and their bipedal behavior—which included stationary feeding of fruits from bushes and low branches in small trees, and locomotion from one spot to another—Hunt made the following observations: 80 percent of bipedal behavior was related to stationary feeding; only 4 percent was observed during direct locomotion. Hunt suggests, therefore, that the hominin bipedal adaptation was primarily a feeding adaptation; only later in hominin history did it become a specifically locomotor adaptation.

The plethora of hypotheses offered to explain the evolution of bipedalism reflects both a fertility of ideas among anthropologists and the difficulty of using available evidence to discriminate between them. Any attempt to test hypotheses must encompass the possibility that hominin bipedalism arose in a heavily wooded or forested environment, rather than in open woodland or grassland savannah as was once thought to be the case.

## KEY QUESTIONS

- What does the rarity of primate bipedalism imply, other than that it is “difficult” to evolve?
- Given the energetic differences between hominoid quadrupedalism and human bipedalism, would an evolutionary transformation be *necessarily* fast or slow?
- Which hypotheses would suffer adversely if bipedalism evolved in a wooded or even forested context?
- Could a hominoid that was completely apelike apart from being bipedal be classified as a hominin?

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# 18

# JAWS AND TEETH

*Jaws and teeth are a rich source of information about a species' subsistence and behavior. In hominoids there was an evolutionary trend toward shorter jaws and a deeper face, giving a less snout-like aspect. This trend was particularly exaggerated in hominins. Eruption patterns give insight into a species' life history. And microwear patterns on the surface of teeth give strong clues to a species' diet.*

Jaws—particularly lower jaws—and teeth are by far the most common elements recovered from the fossil record. The reason is that, compared with much of the rest of the skeleton, jaws and teeth are very dense (and teeth very tough), which increases the likelihood that they will survive long enough to become fossilized.

Because jaws usually serve as an animal's principal food-processing machine, the nature of a species' dentition can yield important clues about its mode of subsistence and behavior. Overall, however, the dental apparatus is evolutionarily rather conservative, with dramatic changes rarely appearing. For instance, human and ape dentition retains roughly the basic hominoid pattern established more than 20 million years ago. Moreover, different species facing similar selection pressures related to their feeding habits may evolve superficially similar dental characteristics, as we shall see, for example, in the matter of enamel thickness. Similar sets of jaws and teeth may therefore arise in species with very different biological repertoires.

In this unit we will examine four facets of hominoid dentition: the overall structure of jaws and teeth; the pattern of eruption; the characteristics of tooth enamel; and the indications of diet that are to be found in microwear patterns on tooth surfaces.

## BASIC ANATOMY

Perhaps the most obvious trend in the structure of the primate jaw (and face) throughout evolution is its shortening from front to back and its deepening from top to bottom, going from the pointed snout of lemurs to the flat face of *Homo sapiens*. Structurally, this change involved the progressive tucking of the jaws under the brain case, which steadily reduced the angle of the lower jaw bone (mandible) until it reached the virtual "L" shape seen in humans. (See figures 18.1 and 18.2.) Functionally, the change involved a shift from an "insect trap" in prosimians to a "grinding machine" in hominoids. Grinding efficiency increases as the distance between the pivot of the jaw and the tooth row decreases, with hominins being closest to this position.

The primitive dental pattern for anthropoids includes (in a half-jaw) two incisors, one canine, three premolars, and three molars, giving a total of 36 teeth. This pattern is seen in modern-day New World anthropoids, while Old World

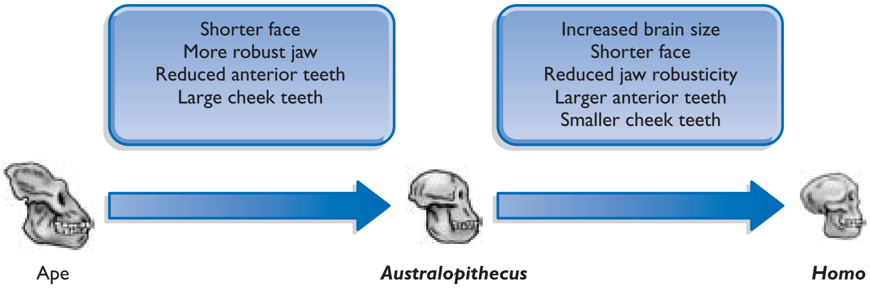


**FIGURE 18.1 Evolutionary trends in dentition:** The transition from ape to *Australopithecus* and from *Australopithecus* to *Homo* involved some changes that were continuous and others that were not. For instance, the face became increasingly shorter throughout hominid evolution, while robusticity of the jaw first increased and then decreased. The combined increase in cheek tooth size and decrease in anterior tooth size that occurred between apes and *Australopithecus* was also reversed with the advent of *Homo*.

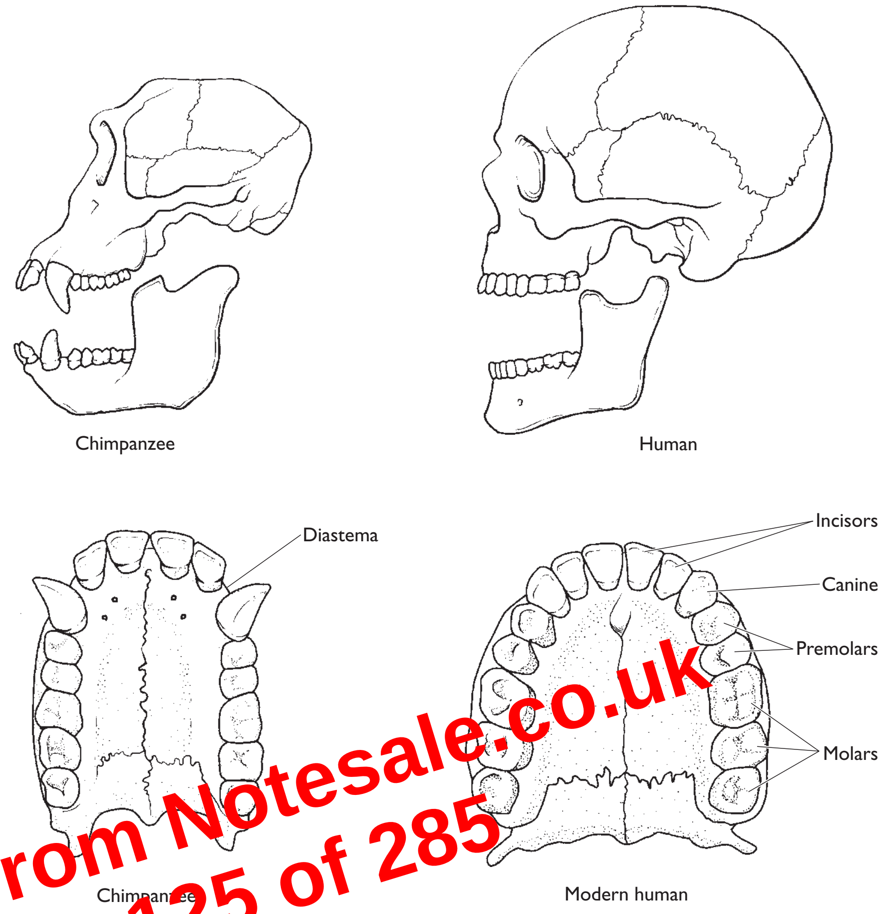


**FIGURE 18.2 Jaws and teeth:** Note the longer jaw and more projecting face in the chimpanzee, the protruding incisors, and large canines.

anthropoids possess two premolars (not three), giving them a total of 32 teeth. Overall, the modern ape jaw is rather rectangular in shape, while the human jaw more closely resembles a parabola. One of the most striking differences, however, is that apes' conical and somewhat blade-shaped canine teeth are very large and project far beyond the level of the tooth row; in these animals, males' canines are substantially larger than those found in females, an aspect of sexual dimorphism with significant behavioral consequences (see unit 13).

When an ape closes its jaws, the large canines are accommodated in gaps (diastemata) in the tooth rows: between the incisor and canine in the upper jaw, and between the canine and first premolar in the lower jaw. As a result of the canines' large size, an ape's jaw is effectively "locked" when closed, with side-to-side movement being limited. By contrast, human canines—in both males and females—are small and barely extend beyond the level of the tooth row. As a result, the tooth rows have no diastemata, and a side-to-side "milling" motion is possible, which further increases grinding efficiency. (See figure 18.2.) The upper incisors of apes are large and spatulalike, which is a frugivore adaptation. In contrast, human upper incisors are smaller and more vertical, and, with the small, relatively flat canines, they form a slicing row with the lower teeth.

The single-cusped first premolar of apes is highly characteristic of the clade, particularly the lower premolar against which the huge upper canine slides. Ape molar teeth are larger than the premolars and include high, conical cusps. In humans, the two premolars assume the same shape and have become somewhat "molarized." The molars themselves are large and relatively flat, with low, rounded cusps—characteristics that are extremely exaggerated in some of the earlier hominins (see unit 20).

The hominin dental package as a whole can therefore be regarded as an extension of a trend toward a more effective grinding adaptation. In some of the earliest known hominins —*Ardipithecus ramidus* and *Australopithecus anamensis* from more than 4 million years ago (see unit 19)—the dentition remains strikingly apelike, with a significant degree of sexual dimorphism. (See figures 18.3 and 18.4.) Within 2 million years, however, the canines in several hominin species have become smaller and flattened, looking very much like incisors (see unit 20).

PART 5

# THE HOMININ ADAPTATION

**20** *The Australopithecines*
**21** *Early* Homo
**22** *Hominin Relations*
**23** *Early Tool Technologies*

**FIGURE 20.3 Crania compared:** These profiles of human, *afarensis*, and chimpanzee crania show how very apelike the first known hominid was. (Courtesy of the Cleveland Museum of Natural History.)

lower limbs. The pelvis of *A. afarensis* is undoubtedly more like that of a hominin than that of an ape, being squatter and broader, but significant differences exist as well, such as the angle of the iliac blades (hip bones). These differences were not functionally significant in terms of achieving the balance required for bipedal locomotion, concluded Lovejoy. Combined with the architecture of the femoral neck and the pronounced valgus angle of the knee, Lovejoy concluded, this character would permit a full, striding gait, essentially like modern humans in overall pattern if not in every detail. In other words, *A. afarensis* was said to be a fully committed terrestrial biped, with any apelike anatomy being genetic baggage and not functionally significant.

Meanwhile, other researchers began to see indications of arboreal adaptation in the *A. afarensis* anatomy. French researchers Christine Tardieu and Brigitte Senut studied the lower limb and upper limb, respectively, and inferred a degree of mobility that would be consistent with arboreality. Russell Tuttle, of the University of Chicago, pointed out that the bones of the hands and feet were curved like those of an ape, which could be taken as indicative of climbing activity. William Jungers reported that although the arms of *A. afarensis* are hominin in terms of length, its legs remain short, like those of an ape, which favors a climbing adaptation. Examining certain *A. afarensis* wrist bones, Henry McHenry concluded that the joint would have been much more mobile than in modern humans, a character consistent with arboreality. (See figure 20.4.)

Following a more wide-ranging survey, Jungers, Jack Stern, and Randall Susman (all of SUNY, Stony Brook) argued that the full suite of postcranial anatomical adaptations indicated that, although *A. afarensis* was bipedal while on the ground, it spent a significant amount of time climbing trees, for sleeping, escaping predators, and foraging. Moreover, they concluded, while the animal was moving on the ground it could not achieve a full striding gait, as Lovejoy had argued, but instead adopted a bent knee, bent hip (BKBH) gait. Such a mode of locomotion would clearly have important biomechanical and energetic implications for *A. afarensis*. Specifically, such a gait is considerably less energy-efficient than a striding gait. The selective advantage of a BKBH gait would therefore have had to have been considerable, given the energy costs of this form of walking (see unit 17).

The differences of opinion in the *A. afarensis* locomotor debate stem partly from a lack of agreement over how to define the anatomy in certain instances and partly from differences in functional interpretation of other aspects of the anatomy. The opposing views were aired on an equal footing at a scientific symposium organized by the Institute of Human Origins in Berkeley in 1983. Since then, most publications have favored the partially arboreal, BKBH bipedal locomotor posture.

The key anatomical features cited in support of a partially arboreal adaptation include the following:

- Curved hand and foot bones;
- Great mobility in the wrist and ankle;
- A shoulder joint (the glenoid fossa) that is oriented toward the head more than in humans; and
- Short hindlimbs.

Opponents of arboreal adaptation dispute the degree of

**FIGURE 20.9 The black skull:** Found by Alan Walker in 1985, the skull shows extreme features of australopithecine robusticity, but is dated at 2.6 million years. It is considered by some to be a member of *Australopithecus aethiopicus*. (Courtesy of Alan Walker.)

australopithecine traits had become extremely exaggerated: specifically the chewing apparatus became increasingly robust. If true, then the fossil record should have revealed a steady increase through time in dental, facial, and jaw robusticity.

The 1985 discovery of the *Australopithecus aethiopicus* cranium KNM-WT 17,000 from the west side of Lake Turkana finally put to rest this simple relationship. The cranium was as robust as any yet known, but was 2.5 million years old. Clearly, the huge molars, flared cheek bones, and dished face could not be the end-product of an evolutionary line if it were present at the origin of that supposed line. How this discovery affects the shape of the hominin family tree remains under discussion (see unit 22).

This cranium, known colloquially as the "black skull," was surprising not only because of its great age but also because it contained an unexpected combination of anatomical characteristics (see figure 20.9). Although the face was distinctly like that of that most robust of robust australopithecines, *Australopithecus boisei*, the cranium—particularly the top and back—were not: they were similar to those of *Australopithecus afarensis*. Such anatomical combinations in these species surprised many people, and remind us that hominin biology of 3 to 2 million years ago was more complicated than current hypotheses have allowed. Similarly, the mosaic set of features seen in the *A. boisei* specimen from Konso, Ethiopia, cautions against simple categorizations.

## AUSTRALOPITHECUS, A TOOL MAKER?

The identity of the maker of the stone tools in the archeological record is a constant question, although many paleoanthropologists assign this role to *Homo*—not *Australopithecus*. Evidence on this issue is necessarily indirect, such as the anatomy of the hands. No hands of *A. africanus* have been discovered. The hand bones of *Australopithecus afarensis* (as known from the Hadar) were strikingly apelike, having curved phalanges, thin tips to the fingers, and a short thumb. By contrast, recent analysis of robust australopithecine hand bones from the Swartkrans site indicates that they were much more humanlike. Randall Susman reports that the thumb is longer and more mobile and the fingertips much broader (the latter is a feature thought to be associated with the supply of blood vessels and nerve endings to the sensitive fingerpads). According to Susman, the robust australopithecines' anatomy probably allowed sufficient manipulative skills to enable stone tool making, an ability that has usually been thought of as strictly within the domain of *Homo*.

Differences of opinion have arisen over these conclusions, however. The recently discovered simple bone tools—digging sticks—may be taken as support for Susman's hypothesis. Nevertheless the tools could have been made by a species of *Homo*, whose fossils are also known at Swartkrans. Furthermore, some scholars question whether the fossil hand bones that Susman studied might have been those of *Homo* and not *A. robustus*, as he believes.

Perhaps the strongest evidence of tool making by an australopithecine comes from Ethiopia, where Tim White and his colleagues found the cranial and dental remains of a hominin they named *Australopithecus garhi*. Associated with the hominin fossils were antelope bones that showed signs of having been cut and broken with sharp stone implements. The researchers point out that stone tools which are the same age as *A. garhi* have been found at another site, Gona. No remains of *Homo* have been recovered from the area.

## KEY QUESTIONS

- What is the likely locomotor pattern in australopithecines?
- Why do evolutionary biologists not favor reversals, such as would be the case in a progression from *afarensis* to *africanus* to *Homo*, with respect to the robusticity of the joints of the arm?
- What kind of evidence might settle the issue of whether australopithecines made and used stone tools?
- What is the likely relationship between robust and gracile australopithecines?

**FIGURE 21.2 Type specimen of *Homo habilis*:** The establishment of the species *Homo habilis* in 1964 involved a redefinition of the genus *Homo*. This development, among other things, provoked a strong reaction to its validity. (Courtesy of John Reader.)

lumping. Splitters see many species in the record; lumpers see few.

For *Homo habilis* to be a valid species, it would have to be intermediate between *A. africanus* and *Homo erectus*, because it was of intermediate age. Lumpers expected considerable anatomical variation in both *africanus* and *erectus*, which left little or no room for an equally variable intermediate. The putative *Homo habilis* fossils therefore had to be either *Australopithecus africanus* or *Homo erectus*. Unfortunately, the critics of *habilis* could not decide to which species it belonged; some said that it was a large *africanus*, while others argued that it was a small *erectus*.

Eventually, *Homo habilis* was accepted by most anthropologists as a valid species, partly through the discovery of other, similar specimens, and partly because of a recognition of the excessive lumping tendency. Nevertheless, the species' history in the science has been rocky, principally because of the large degree of anatomical variation found among specimens that are intermediate between *africanus* and *erectus*, which are therefore putative members of *habilis*. Ironically, a current resolution of this dilemma that is gaining much favor involves a recognition of *two* species of *Homo* at this early time (close to 2 million years ago), not just one—the point to which earlier workers objected so stridently.

## FURTHER FINDS, MORE PUZZLES

In 1972 Richard Leakey announced the discovery of a fossil that was to make him world-famous. That fossil, KNM-ER 1470, was the larger part of a cranium pieced together from hundreds of fragments, and has been dated at 1.9 million years old. The face was large and flat, the palate was blunt and wide, and, judging by their roots, the absent teeth would have been large. These features are reminiscent of australopithecines. Nevertheless, the cranium was large, estimated at 750 cubic centimeters, which betokened *Homo*. Eventually, the fossil was described in a *Nature* publication as *Homo*, but with its species undetermined.

A year after the announcement of 1470's discovery, a second cranium was found at Lake Turkana, which was to play an important role in the resolution of early *Homo*. Known as KNM-ER 1813, its face and palate are similar to those of *Homo habilis* from Olduvai and different from those of 1470; the brain is small, however—not much more than 500 cubic centimeters. (See figure 21.3.) Despite this disparity, 1813 has been described by some as a female *Homo habilis*, though Leakey himself has not made this claim.

In 1986, Donald Johanson, Tim White, and a large team of colleagues discovered an extremely fragmented hominin skeleton at Olduvai Gorge, comprising part of the upper jaw, some cranial fragments, most of the right arm, and parts of both legs. The following year they published details of the fossils, code-named OH 62 (and nicknamed "Lucy's child"), which they attributed to *Homo habilis*, and dated at between 1.85 and 1.75 million years old. An influential reason why they designated the specimen as *Homo habilis* was the resemblance of the palate to that of a skull found at Sterkfontein a decade earlier, code-named Stw 53, which was assigned to *habilis*. Cranial remains were insufficient to estimate a brain size. The limb proportions, however, were both interesting and surprising.

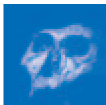
OH 62 was a small, mature female, comparable to Lucy in being approximately 1 meter tall. As with Lucy, the arms were long and the legs short, compared with later *Homo*. The unexpected aspect, as shown by Robert Martin of the Field Museum, Chicago, and Sigrid Hartwig-Scherer of the Anthropological Institute in Zurich, was that OH 62's arms were even longer than those possessed by Lucy, and its legs shorter. Thus, the specimen was even more apelike than *afarensis*, its presumed ancestor. (See figure 21.4.)

The year before OH 62 was found, the *Homo erectus* (*ergaster*) youth had been unearthed on the west side of Lake Turkana (see unit 24). This specimen was tall (almost 2 meters) and had very humanlike limb proportions, but lived

## PART 6

# *HOMO ERECTUS*: BIOLOGY AND BEHAVIOR

**24** *The Changing Position of* Homo erectus
**25** *New Technologies*
**26** *Hunter or Scavenger?*



# 24

# THE CHANGING POSITION OF *HOMO ERECTUS*

Homo erectus *was long assumed to be the species intermediate between early* Homo *and* Homo sapiens. *Now, however, many scholars believe that the specimens assigned to* Homo erectus *in fact represent two species*, Homo erectus *and* Homo ergaster, *with* ergaster *being the precursor of* erectus. *Whatever the true interpretation, it is clear that the emergence of* erectus/ergaster *represented a new grade of hominin, with a very different behavioral repertoire that included the ability to expand its range beyond Africa, a first for hominins.*

This unit deals with the species of *Homo* that has been assumed to be intermediate between early *Homo* (*habilis*, *rudolfensis*) and modern-day humans, *Homo sapiens*. Until recently, the story would have been portrayed as relatively straightforward: Early *Homo* gave rise to a larger-bodied, larger-brained species, *Homo erectus*, approximately 2 million years ago, in Africa. Roughly 1 million years ago, *Homo erectus* expanded its range beyond Africa, first into Asia and then into Europe, developing geographically variable populations. *Homo erectus* then became the direct ancestor of *Homo sapiens*, either by a speciation event in a single population in Africa, which then spread throughout the Old World and replaced established populations of *Homo erectus* (the "out of Africa" or single-origin model), or by a gradual, worldwide (excluding the Americas and Australia) evolutionary transformation of all populations of *Homo erectus* (the multiregional evolution model). (See units 27 through 30.)

Much that was assumed to have been settled about the earlier events in this scenario has been overturned in recent years, through the discovery of new fossils and the redating and reinterpretation of known fossils. It will be helpful to give a snapshot of evolutionary events as currently viewed by most anthropologists.

Early *Homo* gave rise to a large-bodied, large-brained species in Africa approximately 2 million years ago, but this species is now called *Homo ergaster* by some anthropologists. *Homo ergaster* expanded its range beyond Africa and into Asia soon after its origin and at least by 1.8 million years ago; it then gave rise to *Homo erectus* in those areas. *Homo erectus* expanded its range throughout Asia, back into Africa, and presumably into Europe, although few unequivocal fossils have been found (most evidence takes the form of the stone-tool technology often associated with the species). Approximately 150,000 years ago, a speciation event in Africa gave rise to *Homo sapiens* (probably from *Homo ergaster* but possibly from *Homo erectus*), which then spread into the rest of the Old World, and subsequently into Australia and the Americas.

## A BRIEF HISTORY OF DISCOVERY

The first discoveries of *Homo erectus* were made in 1891 and 1892 in Java, Indonesia, by Eugene Dubois, a Dutch medical doctor, who had gone there specifically to search for "the missing link." The specimens were of a skull cap and a complete thigh bone, or femur, which indicated that the creature had walked upright. Although he was initially ambivalent over the human nature of his fossil find, Dubois eventually came to name the species *Pithecanthropus erectus*, or upright ape man, inspired in part by Ernst Haeckel's speculations on human ancestry (see unit 3). (See figure 24.1.) Great controversy greeted Dubois's announcement, and no agreement could be reached as to whether *Pithecanthropus* was human, ape, or something in between.

The rehabilitation of *Pithecanthropus erectus* as an important discovery in human evolution coincided with discoveries in China, at the Choukoutien (now Zoukoutien) site near Peking (now Beijing). In 1927, Davidson Black, the Canadian-born director of the Peking Medical College, recognized the human affinities of a tooth that had been found at the site. He named it *Sinanthropus pekinensis*, or Chinese man from Peking. An immense effort was mounted toward uncovering more fossils. Within a decade a rich haul had accumulated, including 14 partial or fragmentary crania, 14 mandibles, more than 100 teeth, and many other fragments. Black concluded that *Sinanthropus* and *Pithecanthropus* were similar creatures, having a long, low, thick-boned skull, with a brain

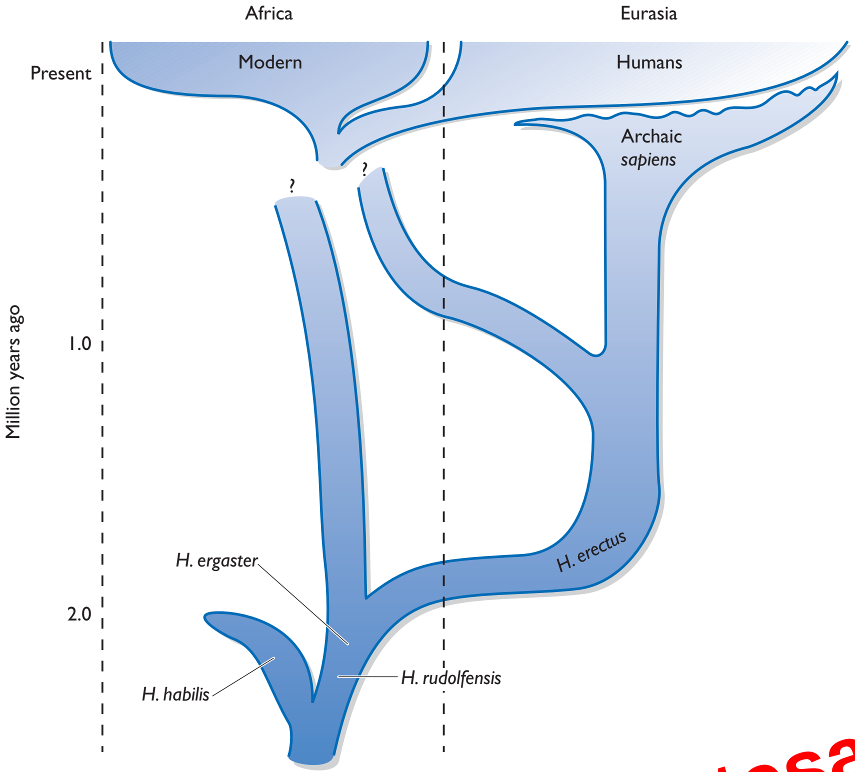


**FIGURE 24.7 A postulated phylogeny:** *Homo ergaster* is seen here as being the descendant of *H. rudolfensis* in Africa approximately 2 million years ago, and immediately expanding its range into Asia, where it gives rise to classic *H. erectus*. *Homo erectus* persists in Eurasia, where it gives rise to archaic *sapiens* species, including Neanderthals; it also enters Africa, where it or *H. ergaster* gives rise to modern humans, which replace established archaic populations.

which is significantly smaller than actually develops. Continued brain growth at a high rate for a time after birth would be necessary to achieve the observed adult brain capacity of at least 850 cubic centimeters—the pattern seen in *Homo sapiens*. Infant helplessness and prolonged childhood might therefore have already begun in *Homo ergaster*, thus giving an opportunity for more cultural learning. However, a recent analysis of the tooth development pattern in the Turkana boy throws doubt on this conclusion (see below).

In an analysis of tooth development as an indicator of life-history patterns, Holly Smith, of the University of Michigan, has also produced evidence for a shift to a life-history pattern similar to that seen in modern humans (see unit 12). In apes, first molar eruption occurs at a little over 3 years, and lifespan is about 40 years; in humans, the corresponding figures are 5.9 years and 66 years, respectively. In other words, human life-history patterns have slowed relative to those of the great apes, including factors such as age at weaning, age at sexual maturity, and effective gestation length. While late *Homo erectus* fit the modern human pattern, as do Neanderthals and other archaic *sapiens*, *Homo ergaster* was somewhat intermediate between humans and apes; its first molar eruption occurred at 4.6 years, and its lifespan averaged 52 years.

For the Turkana boy, a recent analysis of tooth development shows that it is fast paced, giving the boy's age at death to have been around 8 years. This implies that development in *Homo ergaster* had not moved very far in the human direction. Walker, who was one of the authors of the study, together with Christopher Dean and others, concludes that this calls into question his earlier conclusion about brain growth and prolonged childhood. Many assumptions went into his earlier analysis, and he now says that while the conclusion may be correct, it is no longer strongly supported.

The accumulations of bones and stones that appear in the archeological record coincidentally with the origin of the genus *Homo* become more frequent through *ergaster* and *erectus* times, giving an increasingly clear putative signal of some hunting activity (see unit 26). Some investigators speculate that a more broadly based diet, which included a greater proportion of meat than was eaten by earlier hominin species, was a factor in the population expansion out of Africa. Whatever the niceties of taxonomy, the evolution of *ergaster/erectus* signals the appearance of a new grade of hominin evolution.

## CHANGING PATTERNS OF BEHAVIOR

A number of important "firsts" were recorded in human prehistory with the appearance of *ergaster/erectus*:

- The first appearance of hominins outside Africa;
- The first appearance of systematic hunting;
- The first appearance of anything like "home bases";
- The first systematic tool making;

## 26

# HUNTER OR SCAVENGER?

*Interpretations of the lifestyle of early* Homo *have undergone many changes. Initially, they were seen as primitive versions of modern hunter-gatherers. These days, their lifestyle is regarded as considerably less "human" than this implied. Nevertheless, there is still considerable debate over the degree to which these hominins hunted or scavenged.*

Some time between the beginning of the hominin lineage and the evolution of *Homo sapiens*, an essentially apelike behavioral adaptation was replaced by what we would recognize as human behavior—namely, the hunter-gatherer way of life. How and when this development occurred is central to paleoanthropological concerns. As we have seen, fossil evidence reveals the fundamental anatomical changes during this period, but it is to archeology that one turns for direct evidence of behavior.

The earliest stone artifacts recognized in the record are dated to approximately 2.6 million years ago (see unit 23), which coincides closely with the earliest evidence of the genus *Homo*. From their earliest appearance in the record, stone tools occur both as isolated scatters and, significantly, in association with concentrations of animal bones. What this association between bones and stones means in terms of early hominin behavior has become the subject of heated debate among archeologists.

Until recently, some archeologists argued by analogy with modern hunter-gatherer societies that the associations represented remains of ancient campsites, or fossil home bases, to which meat and plant food were brought to be shared and consumed amidst a complex social environment. Others have countered by suggesting that these combinations merely indicated that hominins used the stones to scavenge for meat scraps and marrow bones at carnivores' kill sites; according to this hypothesis, the associations had no social implications. Hence the debate, which has often been characterized as "hunting versus scavenging," is being fought over how "human" was the behavior of hominins 2 million years ago.

## EARLY HYPOTHESES AND RECENT DEVELOPMENTS

During the 1960s and early 1970s, paleoanthropologists considered hunting to be the primary human adaptation, a notion that has deep intellectual roots, reaching back as far as Darwin's *Descent of Man*. The apogee of the "hunting hypothesis" was marked by a Wenner-Gren Foundation conference in Chicago in 1966 titled "Man the Hunter." The conference not only stressed the idyllic nature of the hunter-gatherer existence—"the first affluent society" as one authority termed it—but also firmly identified the technical and organizational demands of hunting as the driving force of hominin evolution.

A shift of paradigms occurred in the mid- to late 1970s, when the late Glynn Isaac proposed the "food-sharing hypothesis." Cooperation was what made us human, argued Isaac—specifically, cooperation in the sharing of meat and plant food resources that routinely were brought back to a social focus, the home base. In this system, the males did the hunting while the females were responsible for gathering plant foods. As for "Man the Hunter," Isaac claimed that it was not possible to evaluate the importance of hunting relative to that of scavenging. "For the present it seems less reasonable to assume that protohumans, armed primitively if at all, would be particularly effective hunters," he concluded in 1978.

Although the shift from the hunting hypothesis to the food-sharing hypothesis changed what was perceived to be the principal evolutionary force in early hominins, it nevertheless left them recognizably human. Specifically, the conclusion that the coexistence of bones and stones on Plio/Pleistocene landscapes implied a hominin home base immediately invoked a hunter-gatherer social package. Although the food-sharing hypothesis was often described by proponents as merely one of many possible candidates for explaining the evolution of human behavior, it proved very seductive. As Smithsonian Institution paleoanthropologist Richard Potts has observed: "The home base/food sharing

PART 7

# THE ORIGIN OF MODERN HUMANS

**27** *The Neanderthal Enigma*
**28** *Anatomical Evidence*
**29** *Genetic Evidence*
**30** *Archeological Evidence*

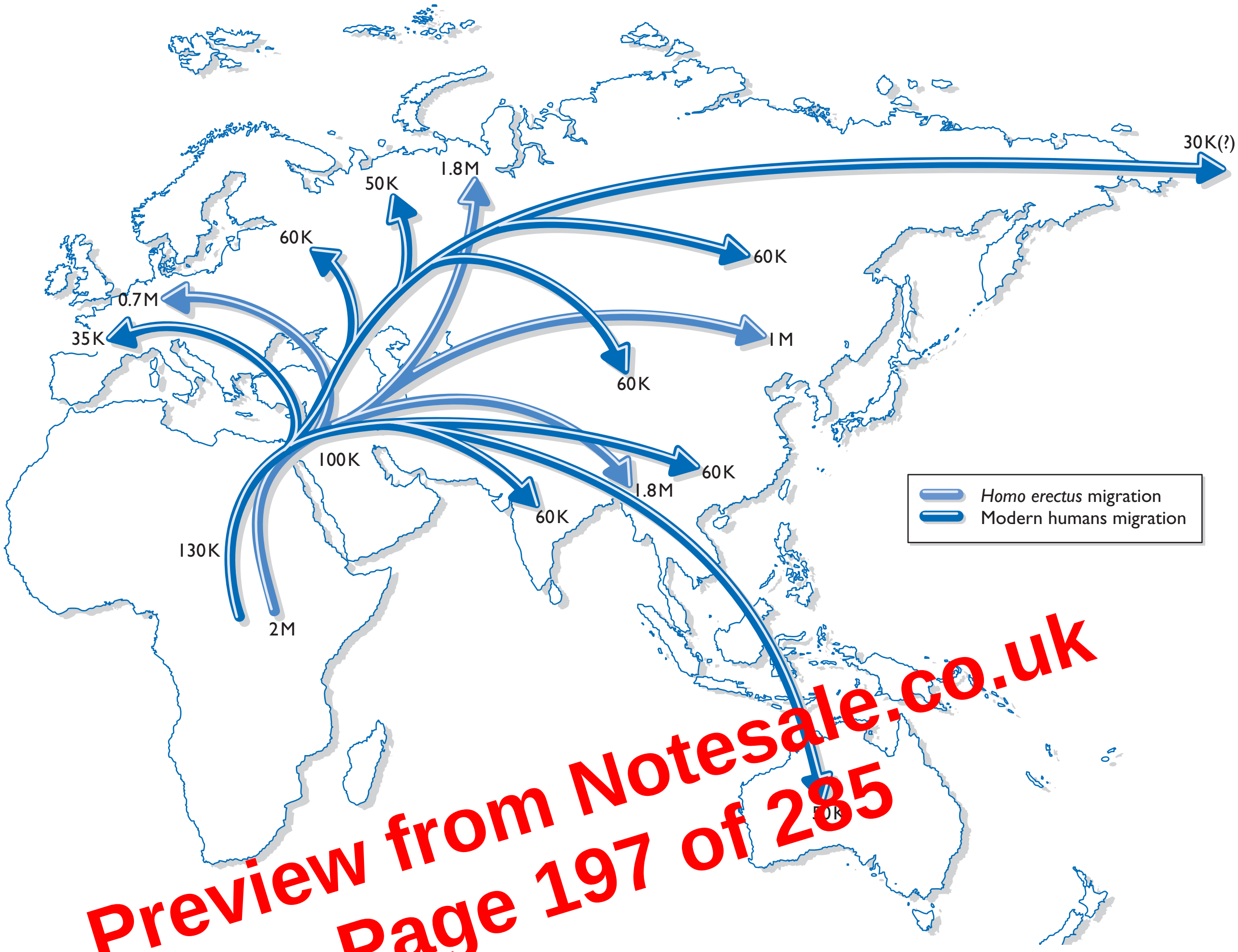


**FIGURE 28.2 Two migrations:** If the single, recent-origin model is correct, then the original expansion of *Homo erectus* from Africa into the rest of the Old World would have been followed much later by a similar expansion of modern people. This presentation is certain to be an oversimplification because it implies two discrete events. In fact, multiple population movements must have occurred at different times and in different places. (K, thousand years ago; M, million years ago).

fossils led some anthropologists to suggest a North African origin for modern humans, with the Middle East as part of the same ecological zone. Others left open the possibility that the Middle East itself was the region of origin. The strikingly modern form of the Omo 1 (Kibish) brain case dated at as much as 130,000 years old, and the 160,000-year-old Herto fossils, described in June 2003, provide sub-Saharan Africa's strongest claim to being the region of origin. (See figure 28.3.)

## THE QUESTION OF REGIONAL CONTINUITY

Regional continuity of anatomical traits from ancient to modern populations represents the cornerstone of the multiregional evolution hypothesis. The extreme form of the single-origin hypothesis denies such continuity, particularly through to the present day. The identification of such putative regional continuity in the Far East, in fact, led Weidenreich to formulate the multiregional hypothesis half a century ago. Modern proponents of the hypothesis claim to find such continuity in Asia, Africa, the Middle East, and Europe, as well as the Far East. The issue of regional continuity remains the most contentious aspect of the current debate, however, with little agreement between proponents of competing hypotheses over interpretation of relevant fossil anatomy in these geographical regions.

### Australasia

Proponents of multiregionalism argue that Australasia offers

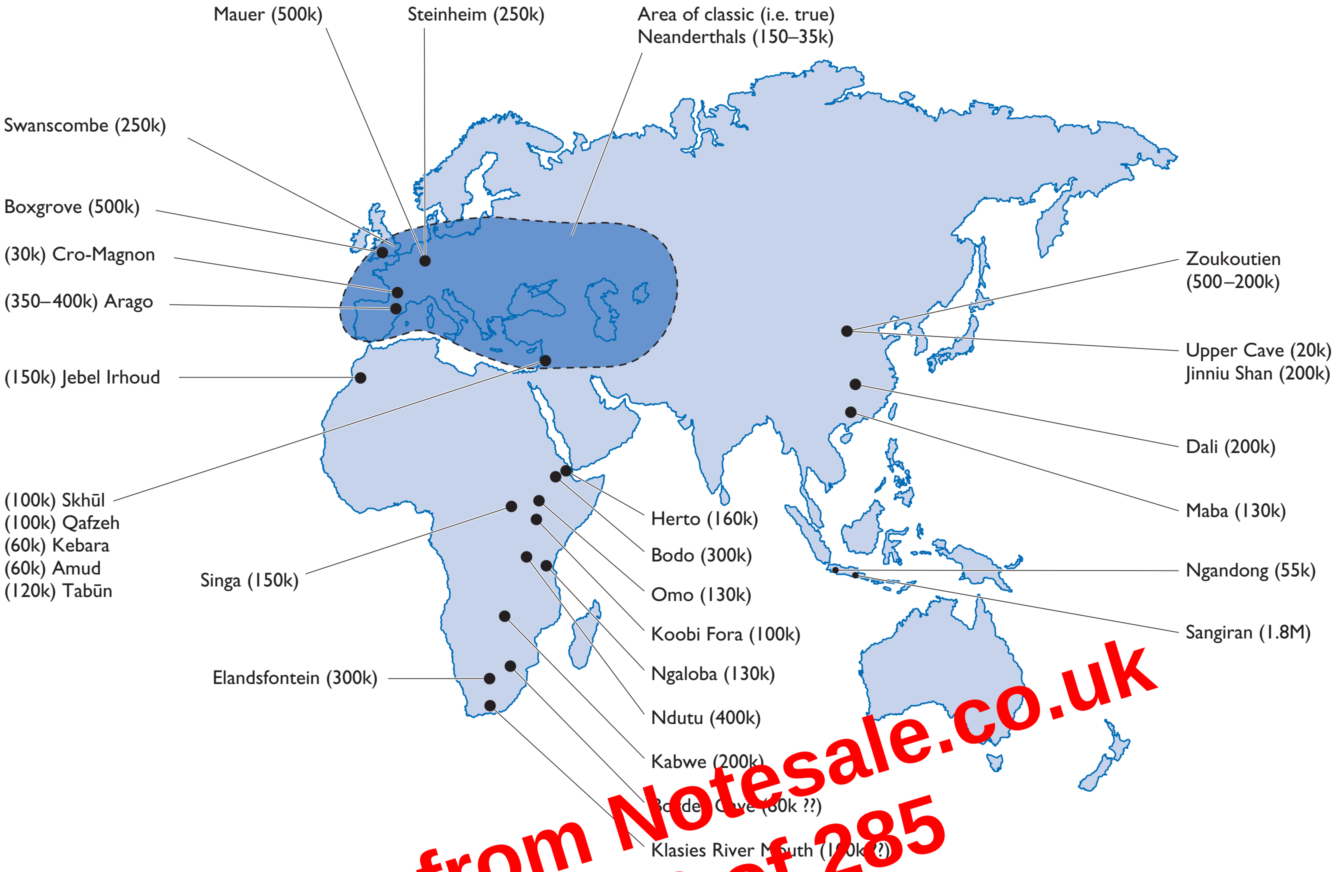


**FIGURE 28.3 Map showing some of the most important sites.** (k, thousand years ago; M, million years ago.)

one of the strongest sets of evidence in favor of regional continuity. The argument is based on essentially three data points: the earliest inhabitants of Java, much more recent archaic forms in Java, and modern Australians. The earliest Javan inhabitants, *Homo erectus*, possessed especially thick skull bones, strong and continuous brow ridges, and a well-developed shelf of bones at the back of the skull. Their foreheads were flat and retreating, and the large, projecting faces sported massive cheek bones. Indeed, the teeth are the largest known in *Homo erectus*. As noted in unit 24, these people may have lived in Java as long as 1.8 million years ago.

The next data point is taken from a dozen brain cases found in 1936 at Ngandong, in western Java. Colloquially known as Solo Man, these specimens have many *Homo erectus* features. Multiregionalists see them as descendants of the earlier Javan *Homo erectus* people, displaying many of the same anatomical features mentioned above, but with enlarged brain cases. The age of the Ngandong fossils is surprising. Until recently, they had been estimated to have been more than 100,000 years old, but dates newly obtained at the Berkeley Geochronology Center place them between 27,000 and 53,000 years old. If correct, it means that the archaic Ngandong population lived long after modern humans had appeared elsewhere in the Old World and were contemporaries of the earliest *Homo sapiens* in the region. This development is parallel to the situation in Europe, where Neanderthals and modern humans coexisted for a while.

The earliest inhabitants of Australia constitute the third data point. Archeological evidence indicates that humans first reached Australia approximately 60,000 years ago, although fossil evidence is considerably younger (see unit 34). According to multiregionalists, the earliest Australian fossils “show the Javan complex of features.”

Can the features cited as evidence of regional continuity truly be traced from ancient Javan *Homo erectus* (1.8 million years old), to the Ngandong specimens (50,000 years), to modern Australians (60,000 years)? The very large time span over which these three points are distributed, and the clumping of the two most recent dates, makes the proposition unlikely. More particularly, are these features truly unique (that is, derived) to this region of the world?

A general anatomical similarity undoubtedly exists in these three populations, particularly in terms of their robusticity. Unfortunately, the comparison of facial and dental

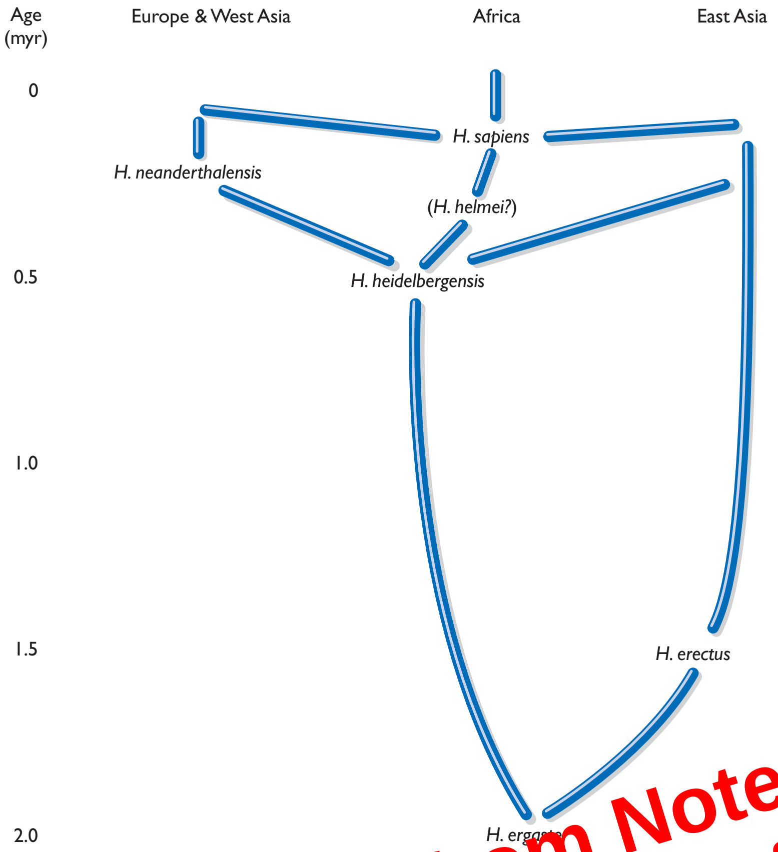


**FIGURE 28.14 A phylogenetic scheme, reflecting the single-origin model.**

from a variable source population in Africa at different times and via different routes may help explain how morphological variability developed in the modern world. In any case, the weight of evidence offers more support for some form of single-origin hypothesis than for the multiregional evolution hypothesis. (See figure 28.14.)

## KEY QUESTIONS

- How has the history of the interpretation of Neanderthals' place in human evolution influenced the modern debate over the origin of modern humans?
- Why is the same fossil evidence often interpreted differently by different anthropologists?
- What is the strongest evidence in favor of (1) the multiregional evolution hypothesis and (2) the single-origin hypothesis?
- What additional fossil evidence would help to resolve the current debate?

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29

# GENETIC EVIDENCE

*Modern human origin has come under the scrutiny of molecular genetic analysis more than any other topic in anthropology, including the origin of the hominin clade, which was its first target. In the two decades of work on this topic, two things have become clear. First, the analysis of genetic data is more challenging than was once thought. Second, the picture that emerges from several realms of genetic analysis shows the pattern of origin and dispersal of modern humans was probably more complex than is inferred from anatomical evidence. Nevertheless, the weight of genetic evidence favors the out-of-Africa model, but probably with multiple dispersals rather than one.*

The first application of genetic data to the question of the origin of modern humans took place in the early 1980s, but not until 1987 did it become highly visible in this field. The initial work, conducted first in Douglas Wallace's laboratory at Emory University and later at the University of California, Berkeley, laboratory of Allan Wilson, focused on mitochondrial DNA. It inspired the so-called **mitochondrial Eve hypothesis**, which posited that the mitochondrial DNA in all living people could be traced back to a single female who lived in Africa approximately 200,000 years ago (hence the inclusion of the term "Eve"). This female was a member of a population of an estimated 10,000 individuals, all of whom were related to the founding population of modern humans; descendants of this population spread into the rest of the Old World, and replaced existing populations of various species of archaic *sapiens* and *Homo erectus*. Thus, the mitochondrial Eve hypothesis was consistent with the recent, single-origin (out of Africa) model and gave no support for the multiregional evolution model (see unit 28).

A decade after the Berkeley group's conclusions were published, it was recognized that the analysis had been less than adequate, and that the conclusion was not as solid as had been supposed. Recent work has concentrated on two lines of inquiry. First, evidence from other forms of DNA, including nuclear genes and the Y chromosome, has been added to the mitochondrial work of attempting to elucidate the origin of modern humans. Second, genetic data have been used to infer the population dynamics of early populations of modern humans. Although less clear cut than the original conclusions, the out-of-Africa model is still the most strongly favored, with little or no support for the multiregional model.

## THE MITOCHONDRIAL EVE STORY: BRIEFLY TOLD

Most of the DNA in our cells is packaged within the 23 pairs of chromosomes in the nucleus, which in total measures about 3 billion base pairs in length; this structure is known as the **nuclear genome**. The cell also contains many copies of a second, much smaller genome that consists of a circular molecule of DNA 16,569 base pairs long, called the **mitochondrial genome**. Mitochondria are the organelles responsible for the cell's energy metabolism, and each cell contains several hundred of these structures. (See figure 29.1.)

Mitochondrial DNA is useful for tracking relatively recent evolutionary events for two reasons. First, the DNA, which codes for 37 genes, accumulates mutations on average 10 times faster than occurs in nuclear DNA. Even in short periods of time, therefore, the DNA will accumulate mutations that can be counted. As mutations represent the equivalent of information, mitochondrial DNA provides more information over the short term than does nuclear DNA. Second, unlike an individual's nuclear genome, which consists of a combination of genes from both parents, the mitochondrial genome comes only from the mother (except under unusual circumstances). Because of this maternal mode of inheritance, no recombination of maternal and paternal genes occurs; such a mixture may sometimes blur the history of the genome as read by geneticists. Potentially, therefore, mitochondrial DNA offers a powerful way of inferring population history, unhindered by the genetic fog of recombination.

One of the first significant observations to emerge from this work was that the amount of variation of mitochondrial DNA types in the modern human population throughout the world is surprisingly low—just one-tenth of that known among chimpanzees, for instance. One explanation is that modern humans evolved very recently, a view that Wallace and Wilson independently supported. A calculation based

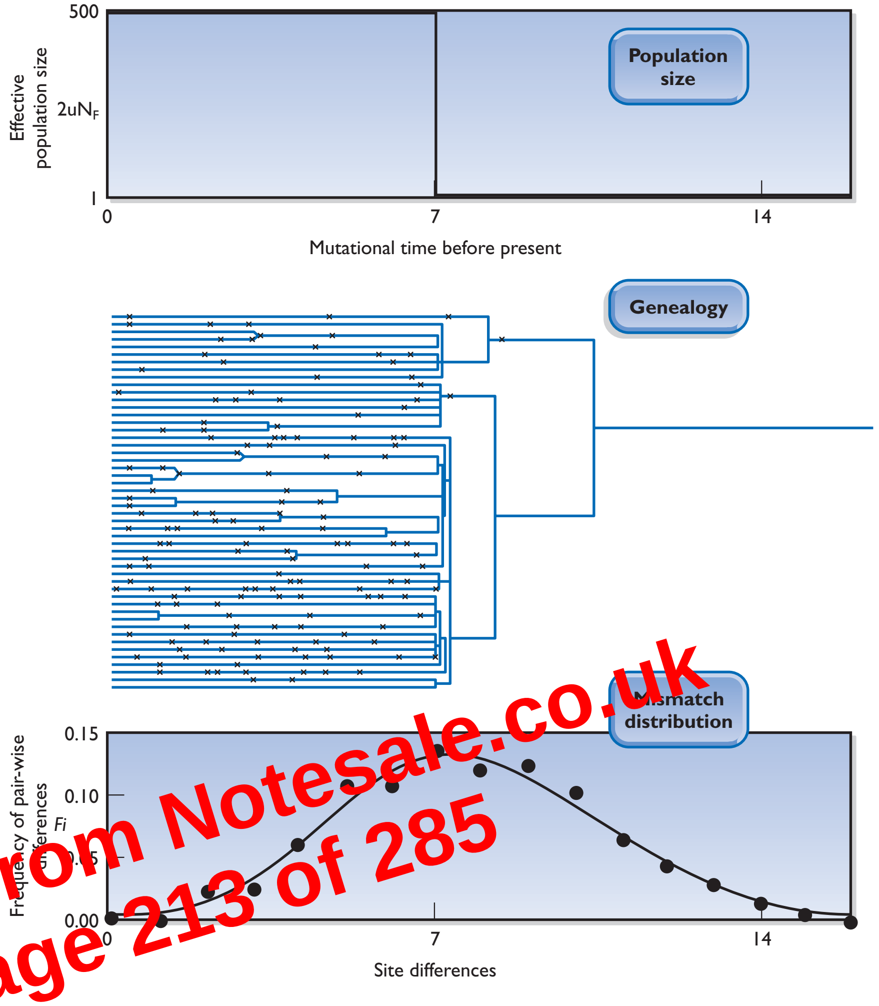

**FIGURE 29.7 Mismatch distribution:** This method uses genetic variation in modern populations to infer population events in the past. (See text for details.) (Courtesy of Alan Rogers and Lynn Jorde.)

bers, the timing of which was centered around 60,000 years ago. Further analysis revealed that the expansion took place at different times for different geographical populations. The African population expanded first, followed later by expansions in the European and Asian populations. This conclusion came from a mismatch distribution analysis conducted *within* each geographical population, followed by a similar analysis performed *between* pairs of populations (this latter technique is termed **intermatch distribution**).

Several possible scenarios exist to explain what happened here, the most persuasive of which is the weak Garden of Eden hypothesis. Remember that the recent, single-origin hypothesis posits that modern humans arose as a small, isolated population, and that descendants of this population spread throughout the Old World, replacing existing populations of archaic *sapiens*. This concept is also called the **Garden of Eden hypothesis**. The intermatch distribution analysis implies a little more complicated history. According to this hypothesis, once established (some 100,000 years ago), the founding population of modern humans fragmented into separate populations; these groups later spread out geographically to form the modern populations of Africa, Europe, and Asia. The genetic distinctiveness of these populations was therefore established prior to the expansion; the mismatch and intermatch distribution data indicate that these separate expansions took place at different times. Thus, replacement of archaic *sapiens* populations would still have occurred, but would not have involved the same dynamics as envisaged with the original Garden of Eden hypothesis. (See figure 29.8.)

According to this new line of investigation, the low level of mitochondrial DNA diversity reflects a population bottleneck after the establishment of the modern human population; this bottleneck was followed by sequential population expansions in different parts of the world. Several questions arise here, the most important of which is, What was the severity of the bottleneck?

The complicated calculation required to answer this question is based on the current genetic diversity of mitochondrial

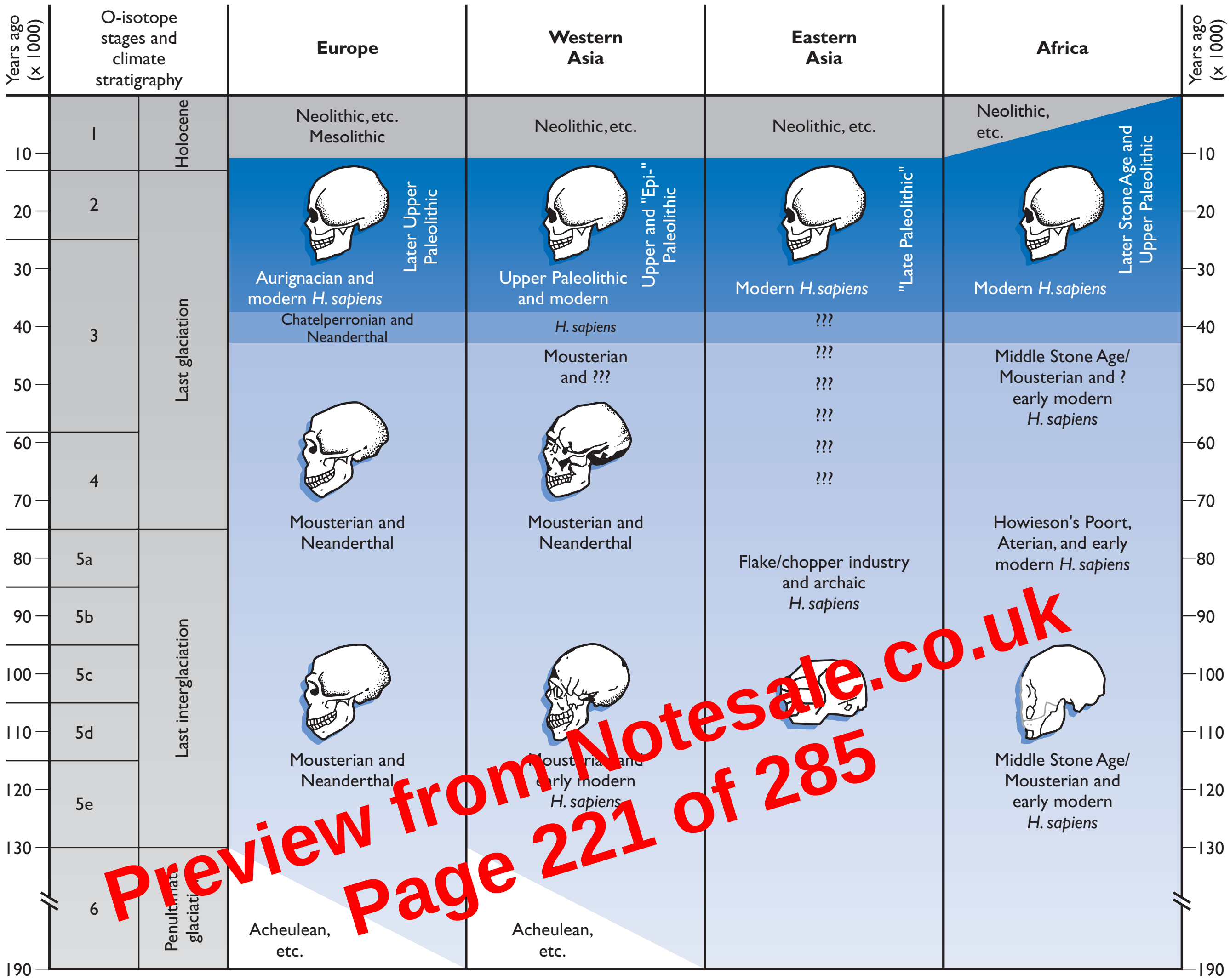

**FIGURE 30.7 Continents compared:** The picture of modern human origins derived from archeological evidence is at best incomplete. In Europe, where the evidence is most plentiful, the picture is quite sharp, showing a sharp transition approximately 40,000 years ago that reflects the inward migration of anatomically modern humans carrying modern cultural behavior. In Asia, the picture is less clear. In Africa, new evidence suggests that modern human behavior begins to appear early in the Middle Stone Age, congruent with the early appearance of anatomically modern humans in that continent. (Courtesy of Richard Klein/*Evolutionary Anthropology*.)

Upper Paleolithic and Later Stone Age. That explosion was a cultural change, however, not a biological one. By contrast, Klein and others have argued that only with a critical biological change—such as facilitation of linguistic ability—did modern human behavior become possible; they define modern human behavior as including the ability to produce the entire range of activities, not just one of them at different times and different places. Undoubtedly this issue will continue to inspire debate for some time to come. (See figure 30.7.)

## HYPOTHESES TESTED

As a test of competing hypotheses—the “out of Africa” and multiregional evolution hypotheses—the archeological evidence is equivocal, and certainly not as strong as the anatomical and genetic evidence. Nevertheless, it can be argued that a signal of modernity appears first in Africa, representing a chronological precursor of what later appears in Eurasia. The appearance of modern cultural activities in Europe seems to coincide with the first appearance of anatomically modern

## PART 8

# THE HUMAN MILIEU

**31** *Evolution of the Brain, Intelligence, and Consciousness*
**32** *The Evolution of Language*
**33** *Art in Prehistory*

31

# EVOLUTION OF THE BRAIN, INTELLIGENCE, AND CONSCIOUSNESS

*Humans have brains far larger than other large primates. Theories explaining the evolutionary background to brain expansion centered for a long time on practical factors, such as tool making and use, and the needs of operating a hunter-gatherer way of life. More recently, the cognitive demands of a highly complex social context have come to the fore.*

The brain is a very expensive organ to maintain. In adult humans, for instance, even though it represents just 2 percent of the total body weight, the brain consumes some 18 percent of the energy budget. Given the fact that the human brain is three times larger than it would be if humans were apes, we have to ask, Why and how did brain expansion occur in the human lineage? And what were the selection pressures that produced a cognitive capacity that surely far outstripped the day to day practical demands of a hunter-gatherer way of life? (See figure 31.1)

As we saw in unit 12, life-history factors—gestation length, metabolic rate, precociality versus altriciality, and so on—have an important impact on the size of brain that a species can develop. In this context, two major ideas have been advanced in recent years that bear on the special problem faced by hominins in brain expansion.

The first, proposed by Robert Martin of the Field Museum, Chicago, is that the mother's metabolic rate is the key to the size of brain a species can afford—the higher the metabolic rate, the bigger the relative brain size. The second, proposed by Mark Pagel and Paul Harvey of Oxford University, is that gestation time and litter size represent the determining factors—long gestation, with a litter of one, is optimal for a large-brained species. Although both hypotheses are said by their authors to have empirical support, debate continues as to which is the more germane. Whichever case proves to be correct, both pathways require the same kind of environmental context: a stable, high-energy food supply, with minimum predation pressure.

**FIGURE 31.1 Expanded human brain:** The human brain is three times bigger than an ape's brain would be, given the same body size.

In being well endowed mentally, humans and other primates are a part of a very clear pattern among vertebrates as a whole. Depending somewhat on the measure used, mammals are approximately 10 times "brainier" than reptiles and amphibians. Underlying this stepwise progression, which takes into account successive major evolutionary innovations and radiations, is the building of more and more sophisticated "reality" in species' heads.

By being mammals, primates are therefore better equipped mentally than any reptile. Two orders of mammal have significantly larger brains than the rest of mammalian life: primates and cetaceans (toothed whales). And among primates, the anthropoids (monkeys and apes) are brainier still. Only humans are outliers from the monkey/ape axis: the brain of *Homo sapiens* is three times bigger than that of an ape of the same body size.

The need to grow such a large brain has distorted several basic life-history characteristics seen in other primates. For instance, the adult ape brain is nearly 2.3 times bigger than the brain in the newborn (neonate); in humans, this difference is 3.5 times. More dramatic, however, is the size of the human neonate compared with ape newborns. Even though humans are of similar body size to apes (57 kilograms for humans, compared with 30 to 100 kilograms for apes) and have a similar gestation period (270 days versus 245 to 270 days), human neonates are approximately twice as large and have brains twice as large as ape newborns. "From this it can be concluded that human mothers devote a relatively greater quantity of energy and other resources to fetal brain and body development over a standard time than do our closest relative, the great apes," notes Martin.

Another major difference is the pattern of growth. In mammals with precocial young—which includes primates—brain growth proceeds rapidly until birth, whereupon a slower phase ensues for roughly a year. In humans, the prenatal phase of rapid brain growth continues for a longer period after birth, a pattern that is seen in altricial species. Compared with other altricial species, however, the rapid postnatal phase (at a fetal rate) of brain growth continues for a relatively longer period in humans. This extension effectively gives humans the equivalent of a 21-month gestation period (9 months in the uterus and 12 months outside). This unique pattern of development has been called secondary altriciality. One important consequence is that human infants are far more helpless, and for a much longer time, than the young of the great apes. This extended period of infant care and subsequent "schooling" must have had a major impact on the social life of hominins.

## FOSSIL EVIDENCE

Two types of fossil evidence are related to brain evolution: indications of absolute size, and information about the surface features—convolutions and fissures—of the brain. Both pieces of evidence can be obtained from either natural or man-made endocasts, which show the convolutions of the brain as they became impressed on the inner surface of the cranium.

Brain size is the first and most obvious piece of information to be gleaned, and it can often be gained even with partial crania. Measured at a little less than 400 cubic centimeters, the early australopithecine brain is often said to be roughly the same size as modern gorilla and chimpanzee brains. This interpretation is misleading, however, for two reasons: (1) early australopithecines were smaller in body size than modern gorillas, and (2) modern ape brains almost certainly are larger than those of their 3-million-year-old ancestors. It is therefore safe to say that brain expansion had already been established by the time *Australopithecus afarensis* appeared.

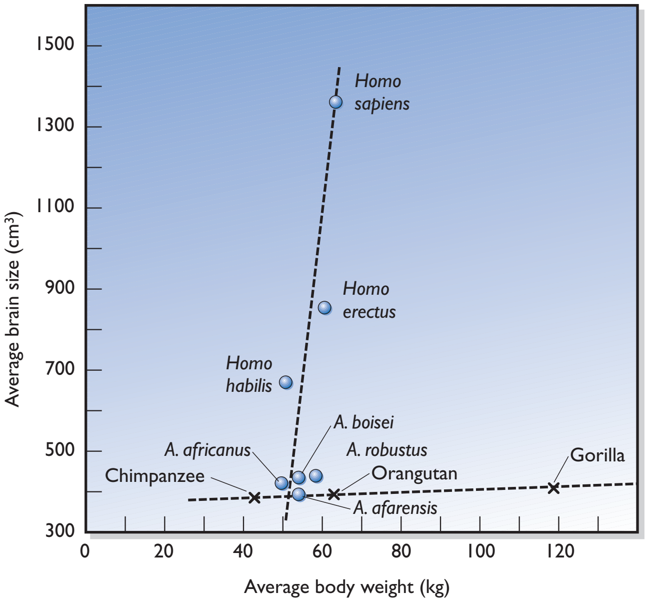

**FIGURE 31.2 Brains and bodies:** Even though a dramatic increase in body size did not occur in the *Homo* lineage, absolute (and therefore relative) brain size expanded significantly from *habilis* to *erectus* to *sapiens*. Brain size did not change significantly among the australopithecines or the modern apes, despite a large body size difference in the latter.

Marked brain expansion is seen with the origin of the genus *Homo*, specifically *Homo habilis/rudolfensis*, which existed from 2.5 to 1.8 million years ago and had a range of brain size of 650 to 800 cubic centimeters. The size range for *Homo ergaster/erectus*, dated at 1.8 million to 300,000 years ago, is 850 to slightly more than 1000 cubic centimeters, although the concomitant increase in body size means that encephalization was not commensurately increased. The comparable measurements for archaic *Homo sapiens*, including Neanderthals, range from 1100 to more than 1400 cubic centimeters, or larger than in modern humans. Using the **encephalization quotient** (E.Q.), a measure of brain size in relation to body size, this progression can be discerned more objectively. The australopithecine species have E.Q.s in the region of 2.5, compared with 2 for the common chimpanzee, 3.1 for early *Homo*, 3.3 for early *Homo ergaster/erectus*, and 5.8 for modern humans. (See figures 31.2 and 31.3.)

By looking at overall brain structure as revealed in endocasts, it is possible to differentiate between an apelike and a humanlike brain organization. Each hemisphere contains four lobes: frontal, temporal, parietal, and occipital. Very briefly, a brain in which the parietal and temporal lobes predominate is considered humanlike, whereas apelike brains

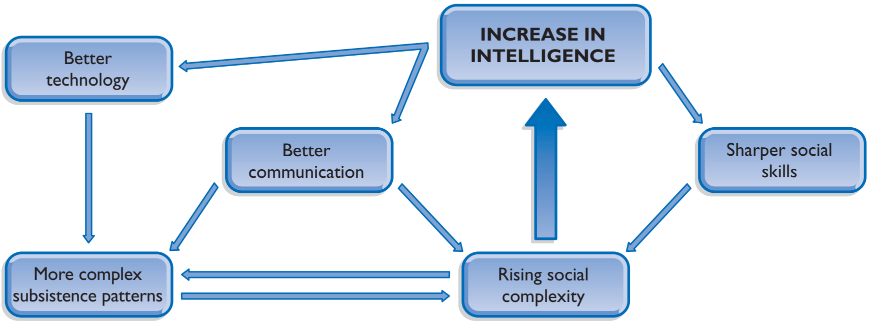

**FIGURE 31.6 Social complexity and increased intelligence:** The need to cope with rising social complexity—including increasingly demanding subsistence patterns but particularly a more ramified social structure and unpredictable social interactions—may have represented a key selection pressure for increased intelligence.

social intelligence, Dorothy Cheney, Robert Seyfarth, both of the University of Pennsylvania, and Barbara Smutts, of the University of Michigan, posed the following question: “Are [primates] capable of some of the higher cognitive processes that are central to human social interactions?” This question is important, because if anthropoid intellect, honed by complex social interaction, is merely sharper than that of the average mammal and more adept at solving psychologist’s puzzles, then it does not qualify as *creative* intelligence.

Cheney and her colleagues had no difficulty in finding many examples of primate behavior that appear to reflect humanlike social cognition. The researchers conclude that “primates can predict the consequences of their behavior for others and they understand enough about the motives of others to be able to be capable of deceit and other subtle forms of manipulation.” Supporting this hypothesis, known as the Machiavellian intelligence hypothesis, the British anthropologist Robin Dunbar has found that primate species with more complex social interaction have larger cerebral cortexes.

If nonhuman primate intellect has truly been honed, not in the realm of practical affairs, but in the hard school of social interaction, one is still left to explain why this situation has arisen. Why have primates found it advantageous to indulge in alliance building and manipulation? The answer, again gleaned from field studies, is that individuals that are adept at building and maintaining alliances are also reproductively more successful: making alliances opens up potential mating opportunities.

Once a lineage takes the evolutionary step of using social alliances to bolster reproductive success, it finds itself in what Nicholas Humphrey, a Cambridge University psychologist, calls an evolutionary ratchet. “Once a society has reached a certain level of complexity, then new internal pressures must arise which act to increase its complexity still further,” he explains. “For, in a society [of this kind], an animal’s intellectual ‘adversaries’ are members of his own breeding community. And in these circumstances there can be no going back.”

Where does consciousness fit into this mix? Humphrey describes it as an “inner eye,” with pun intended. Consciousness is a tool—the ultimate tool—of the social animal. By being able to look into one’s own mind and “see” one’s reactions to things and other individuals, one can more precisely predict how others will react to those same things and individuals. Consciousness builds a better reality—one that is attuned to the highly social world that humans inhabit. (See figure 31.6.)

## KEY QUESTIONS

- What limitations arise when measuring differences in intelligence from differences in brain size and overall organization?
- How might one infer levels of intelligence from different stone-tool technologies?
- What key pieces of information might lend support to the “Man the Social Animal” hypothesis?
- How would one test whether nonhuman primates possessed a humanlike consciousness?

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## ARCHEOLOGICAL EVIDENCE: TOOLS

Some anthropologists have argued that the pattern of tool manufacture and language production—essentially, a series of individual steps—implies a common cognitive basis. If true, then following the trajectory of the complexity of stone-tool technology through time should reveal something about the change in language capabilities.

Thomas Wynn, of the University of Colorado, has used psychological theory to examine the validity of this argument. "It is true," he says, "that language and tool making are sequential behaviors, but the relationship is more likely to be one of analogy rather than homology." In other words, only a superficial similarity connects the two, and their cognitive underpinnings remain quite separate. Thus, one cannot look at the complexity of a tool assemblage on one hand and learn anything *directly* about language abilities on the other.

Glynn Isaac has also searched for indications of language function in ancient tool technologies, albeit via a different approach. He has argued that the complexity of a tool assemblage might provide some information about social complexity, not cognitive complexity, relating to mechanical or verbal processes. Beyond a certain degree of social complexity there is an arbitrary imposition of standards and patterns. Discerning such a relationship is to some extent an abstract exercise, which would be impossible in the complete absence of language. (See figure 32.3.)

As we saw in units 23, 25, and 30, the trajectory of technological change through hominin history falls into two phases: an incredibly slow phase leading from the earliest artifacts some 2.5 million years ago to approximately 250,000 years ago, following by an ever-accelerating phase.

What lessons do we learn from this basic archeological evidence, in relation to origins of language? Writ on the large scale, it seems reasonable to infer that a language complex enough to conjure the abstract elements of social rules, myths, and ritual is a rather late development in hominin history; that is, it began only with archaic *Homo sapiens*, and became fully expressed only with anatomically modern humans. If one adds the economic and social organization necessary in hunting and gathering activities, which ultimately would involve the need for efficient verbal communication, then the archeological record shows the same pattern. Only in the later stages of hominin history does this organization take on a degree of sophistication that would seem to demand language skills.

## ARCHEOLOGICAL EVIDENCE: ART

Australian scholars Iain Davidson and William Noble argue that spoken language is a very recent evolutionary development, closely tied to the cognitive processes of the development of imagery and art.

Painting or engraving an image of, for example, a bison does not necessarily imply anything mystical about the motives in the artist's mind. Nevertheless, the creation of art represents an abstraction of the real world into a different form, a process that demands highly refined cognitive skills. But the art created in the Ice Age was not simply a series of

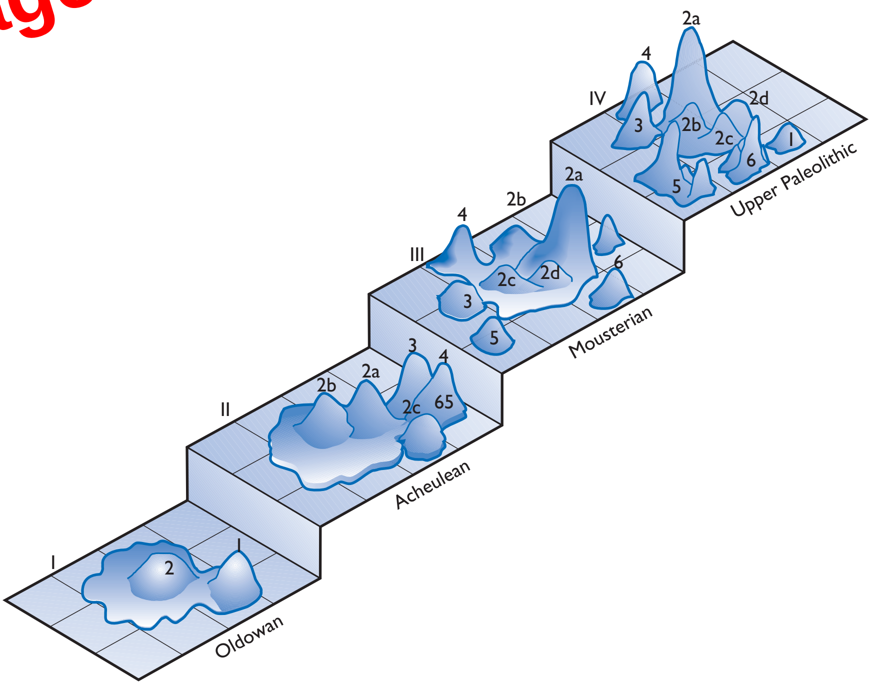

**FIGURE 32.3 Sharpening the mind, sharpening the tongue:** With the passage of time and the emergence of new species along the *Homo* lineage, stone-tool making became even more systematic and orderly. Peaks in the diagram represent identifiable artifact modes, with tall, narrow peaks implying highly standardized products. The increased orderliness in stone-tool manufacture must, argued archeologist Glynn Isaac, reflect an increasingly ordered set of cognitive processes that eventually involved spoken language. (I) Oldowan: 1 = core choppers; 2 = casual scrapers. (II) Acheulean (Olorgesailie): 2a = scrapers; 2b = nosed scrapers; 2c = large scrapers; 3 = handaxes; 4 = cleavers; 5 = picks; 6 = discoids. (III) Mousterian: 2a = racloir; 2b = grattoir; 2c = convergent; 3 = percoir; 4 = point; 5 = burin; 6 = biface. (IV) Upper Paleolithic: 2a = grattoir; 2b = nosed scraper; 2c = raclette; 3 = percoir; 4 = point; 5 = burins; 6 = backed blades. (Courtesy of Glynn Isaac.)

simple abstractions of images to be seen in the real world (see unit 33); rather, it was a highly selective abstraction. Whether it represented hunting magic or an encapsulation of social structure, this art speaks of a world created by introspective consciousness and complex language. It was, in fact, a world like ours, just technologically more primitive.

If artistic expression can inform us about the possession of complex language, the question is, How far back in prehistory did it stretch? Not very far, it seems. Although claims of some form of abstract artistic expression date back to 300,000 years ago, it is not until a little more than 30,000 years ago that artistic expression really began to blossom (see unit 33). Earlier than about 32,000 years ago, however, very little art has been recovered. Two pendants—one from reindeer bone, the other from a fox tooth—were discovered at the 35,000-year-old Neanderthal site of La Quina, France; an antelope shoulder blade etched with geometric pattern was also found at another French site, La Ferrassie. Elsewhere in Europe, bones and elephant teeth with distinct zigzag markings have been discovered that were carved by Neanderthals at least 50,000 years ago. The engraved pieces of ochre found in the Blombos Cave, South Africa, date a little earlier, to almost 80,000 years.

Bearing in mind the probable imperfections in the archeological record—in Europe, but especially in Africa—the inference to be drawn from artistic, abstract expression is that something important happened in the cultural milieu of hominins late in their history. The late British anthropologist Kenneth Oakley was one of the first to suggest, in 1951, that this “something important” was best explained by a quantum jump in the evolution of language. This development occurred, suggest Davidson and Noble, some 50,000 years ago.

Thus, the line of evidence from artistic expression suggests that the dynamic of language evolution was rapid and recent.

Finally, a novel line of evidence has come to light recently, which doesn’t fit into any of the three categories above. It concerns a gene that is linked to the ability to produce articulate speech. Svante Pääbo and his colleagues at the Max Planck Institute, Leipzig, have recently analyzed the gene, known as FOXP2, and estimate that it first appeared in its modern form less than 120,000 years ago. Richard Klein, of Stanford University, has long argued that language appeared as a result of a relatively recent mutation affecting brain wiring in relation to speech, perhaps 50,000 years ago. These genetic data fit with his hypothesis.

## WHAT CAUSED THE EVOLUTION OF LANGUAGE?

The most obvious cause for the evolution of language was its development within the context in which it is so obviously proficient: communication. For a long time, this line of argument was pursued by a variety of anthropologists. The shift from the essentially individualistic subsistence activities of higher primates to the complex, cooperative venture of hunting and gathering surely demanded proficient communication. A popular hypothesis of language evolution included the notion that a first stage would have been a gesture language—gesturing, remember, is something humans do frequently, especially when lost for words.

In recent years, however, the explanatory emphasis has shifted, paralleling the shift in explanation for the evolution of intelligence. From the practical world of communication, explanation of language origins now turns to the inner mental world and social context.

“The role of language in communication first evolved as a side effect of its basic role in the construction of reality,” argues Harry Jerison. “We can think of language as being an expression of another neural contribution to the construction of mental imagery. . . . We need language more to tell stories than to direct actions.” As we saw in unit 31, anthropologists are beginning to recognize the importance of social interaction as the engine of the evolution of hominin intelligence. Consciousness and language go hand in hand with that view.

More recently, Robin Dunbar has suggested that language may have evolved as a way of facilitating social interaction in human groups, the equivalent of grooming in nonhuman primates. Beyond a certain group size, he argues, grooming becomes inefficient for maintaining social ties. Language is

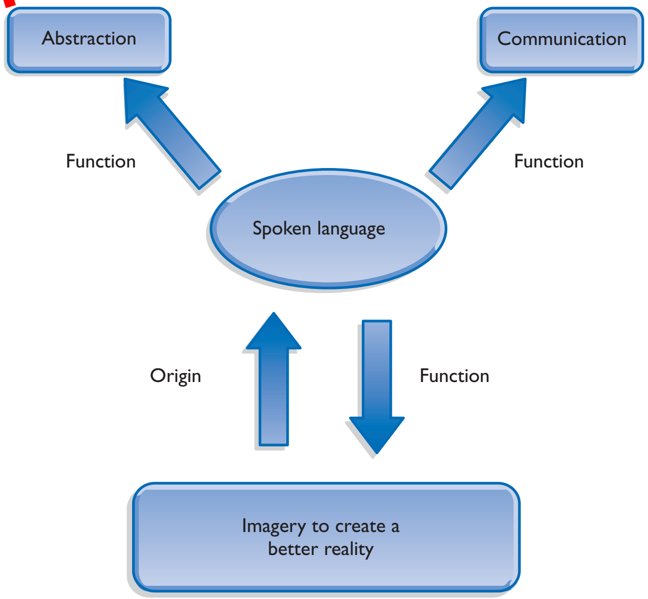

**FIGURE 32.4 Origin and function of language:** Although communication is clearly an important function of spoken language, its origins (and continued functions) probably centered on creating a better image of our ancestors’ social and material worlds.

prehistory, despite existing archeological and ethnographic evidence to the contrary.

For more than a decade, the !Kung model of the hunter-gatherer lifeway dominated anthropological thought. By the early 1980s, however, its shortcomings had been gradually exposed. This shift in perception was driven by new historical, archeological, and behavioral ecology evidence. It indicated that a great deal more variability existed in the hunting and gathering lifeway of prehistoric peoples than had been allowed for in the !Kung model; this variability included a degree of social and economic complexity that hitherto had been associated exclusively with agricultural societies. "Many characteristics previously associated solely with farmers—sedentism, elaborate burial and substantial tombs, social inequality, occupational specialization, long-distance exchange, technological innovation, warfare—are to be found among many foraging societies," concluded anthropologists James Brown and T. Douglas Price in 1984, in a classic reassessment of hunters and gatherers.

In other words, the Agricultural Revolution was recognized to be neither a revolution nor a movement primarily focused on the adoption of agriculture. Instead, the Neolithic transition involved increasing sedentism and social complexity, which was usually followed by the gradual adoption of plant and animal domestication. In some cases, however, plant domestication preceded sedentism, particularly in the New World. For instance, Kent Flannery of the University of Michigan has shown that the first plant domesticated in the New World, the bottle gourd, which was grown about 9000 years BP in the southern highlands of Mexico, preceded sedentism by at least 1000 years. Clearly, the Neolithic was a complex period and must have been influenced substantially by both local and global factors.

One long-standing question of interest in Europe, for instance, has been the mode by which agriculture spread. Was it carried by farmers moving into the region from the Middle East? Or did it develop locally, with the idea spreading throughout the continent, not the farming-oriented people? This question is amenable to genetic as well as archeological research. Work with classic genetic markers and, more recently, DNA sequences from nuclear genes suggested that population migration was important in the spread of agriculture. This conclusion, known as the demic expansion model, has been challenged by a recent survey of mitochondrial DNA patterns throughout the continent. This work implies that it was principally the idea of agriculture that spread, not a migration of people. The difference of opinion remains unresolved.

## CAUSES OF THE TRANSITION

Because the transition to food production occurred within a few thousand years independently in several different parts of the world, anthropologists have long sought a global cause. Two factors have been candidates for this single, prime mover: population pressure and climate change. (See figure 35.5.)

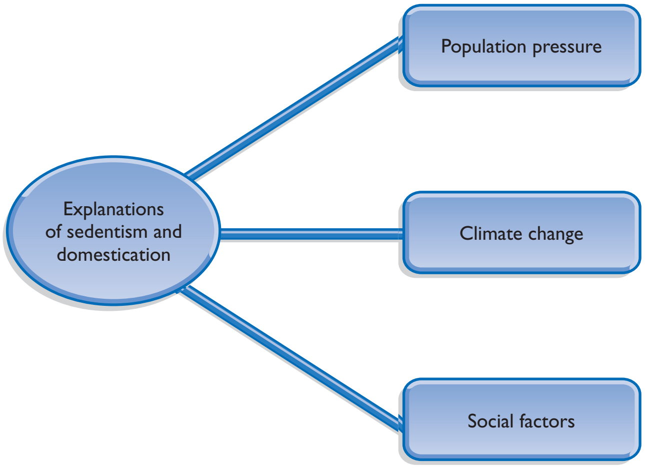

**FIGURE 35.5 Hypotheses of agricultural origins:** Population pressure and climate change have long vied as the most persuasive potential candidates for initiating sedentism and domestication. In recent times, attention has turned to factors concerning internal social complexity.

Although a dramatic rise in population numbers undoubtedly accompanied the Neolithic transition, the question of whether this relationship was one of cause or effect remains unanswered. Mark Cohen, of the State University of New York, Plattsburgh, is the principal proponent of the population pressure hypothesis. He argues that it was causal, and adduces signs of nutritional stress in skeletal remains from the late Paleolithic to support his case. In contrast, many anthropologists argue that numerous examples of the adoption of sedentism and agriculture can be found in the apparent absence of high population numbers—such as in the southern highlands of Mexico. For these researchers, including Flannery, the population pressure hypothesis remains unconvincing.

The second major candidate—climatic change—appears more persuasive, as the Neolithic transition coincides with the end of the Pleistocene glaciation. The shift from glacial to interglacial conditions would have driven extensive environmental restructuring, bringing plant and animal communities into areas where they did not previously exist. For instance, warmer, moister climes in the Levant 12,000 years ago likely encouraged the abundant growth of wild cereals on the steppe, allowing foragers to collect them in great numbers and subsequently domesticate these plants. Moore considers this step to have been important in the early establishment of Abu Hureyra and other similar settlements.

Evidence is lacking to prove that climate-driven floral

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