Human Origins

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New discoveries combine to indicate that all the major steps in human evolution took place in Africa. Skeletal analysis of oldest human forbears around 3 million years ago reveal many anatomical similarities to African Great Apes. These and biochemical resemblances indicate a common ancestry for humans and apes, perhaps only a few million years earlier. Enlarged knowledge through recent recovery of skeletons of several successive stages in the line leading to modern peoples shows that many attributes or skills by which we define humanity arose much more recently in time than heretofore believed.

THE RECENT DEATH OF RAYMOND ARTHUR DART (1893–1988) draws attention to the end of the initial phase in the exploration of human origins. Ten to 20 years ago it was still possible to say that many of those who had made significant discoveries concerning our ancient ancestors were still living. Dart, who in 1925 described the early hominid *Australopithecus* (*1*), was one of these. In his long lifetime, he witnessed nothing less than a total revolution in our understanding of whence we came. For instance, at the time of his birth in 1893 the continent, time, and manner of our origin were quite unknown. Just then, however, Eugene DuBois, a Dutch surgeon, was in Java gathering evidence, that he published in 1894 (*2*), reporting the discovery of the Java ape man (now *Homo erectus*). The flattened skull-cap and low brain volume (approximately 900 cm^3) of *H. erectus* strongly pointed toward the derivation of humans from apes.

The view of the influential British anatomist Elliot Smith that a large brain appeared first in human origins, published in 1912 (*3*), coupled with the description a year later of the large-brained Piltdown man (*4*), started an alternative theory that creatures with big brains and apelike bodies would signal the beginning of mankind. Before the turn of the century the famous German biologist Ernst Haeckel stressed that both bipedal walking and the appearance of language must have characterized the earliest hominids (*5*). In 1915 Matthew (*6*) and in 1917 Barrell (*7*) suggested that man must have arisen in the great plateau of Central Asia. The rising Himalayas causing increasing aridity to the north would have reduced the forests to savanna and forced apes from the trees to become ape men. Later H. F. Osborn championed this "plateau origin" theory about our ancestors and encouraged the American Museum expeditions to Central Asia under R. C. Andrews that were undertaken in large part in order to discover earliest humans. Osborn also pressed the view that our ancestral line had split off early, perhaps in the Oligocene Epoch [now dated 37 to 26 million years ago (Ma)]. He championed the idea that the large brain posited for protohumans required that we not be derived from the apes (*8*). Thus were planted several ideas that led to much future misdirection. Searchers were looking in the wrong place, for the wrong ancestors, with the wrong anatomy, at the wrong time.

I have already touched on the reasons for human origins as having been due to some sort of behavioral change, coupled with an environmental change, to bring these creatures out of the forests. It is clear that both *Aegyptopithecus* and *Proconsul* (the earliest well-known ancestors of apes) were forest-living arboreal quadrupeds (*9, 10*), whereas *Australopithecus*, the first hominid, was a successful biped. What happened to bring about the change? The early theory of Matthew, Barrell, and Osborn that our forebears left the trees because of the increasing aridity and deforestation of Central Asia has failed because the differentiation of hominids did not occur there. A second hypothesis, with which I have been associated, was that the shift from trees to savanna was brought about through a dietary change in the Miocene that evoked the great thickening of cheek tooth enamel which characterizes *Sivapithecus* and *Ramapithecus*. Wrinkling on the cheek teeth of these hominoids resembled that of African apes and *Australopithecus*, not *Pongo*; *Ramapithecus* was seen as hominid-like or as a hominid because of reduced canines, reduced anterior dentition, and thick tooth enamel. Terrestrial feeding on roots and seeds and ranging away from forests was presented as a preadaptation to the evolution of bipedal walking (*11, 12*). Later some suggested that *Ramapithecus* specimens are either female *Sivapithecus* or closely related to *Sivapithecus* (*13, 14*). Earliest hominids of the genus *Australopithecus* had, unlike modern African apes, unusually thick cheek tooth enamel.

Defining earliest hominids from their dental mechanism failed in the early 1980s for several reasons. Cranial anatomy of *Sivapithecus*, reported first in this decade, allied it to the orangutan (*15*). Thus, the thick tooth enamel was only coincidentally like that of *Australopithecus*. Nothing then could be determined about the paleoenvironments or skeleton of *Sivapithecus* (*-Ramapithecus*) to prove that it had left the trees and forests. The date of the oldest *Sivapithecus* in Africa at Fort Ternan (14 Ma) was too early to satisfy biochemically determined times of 4 to 5 Ma posited for the time of splitting between the ancestors of *Pan* and *Homo* (*16, 17*). Microwear striations on *Sivapithecus* teeth did not indicate that the diet was other than as in modern forest-dwelling apes (*18*).

Australopithecus

In order to explain what we now think happened in human origins we must return to Raymond Dart, his discovery in South Africa of *Australopithecus*, and to the review of the most significant body of fossils relevant to human origins—those of *Australopithecus*. Dart's announcement in 1925 (*1*) of the Taung child as a new genus and species (*Australopithecus africanus*) related to, or in, human

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ancestry was not at first well received (*19*). Nevertheless, this hominid genus is now generally accepted as representing the first well-documented phase of human ancestry. Numerous discoveries from the 1930s right up to the present day from South Africa, and after 1958, increasingly from East Africa as well, have enormously enlarged knowledge of *Australopithecus* and a related subgenus, *Paranthropus*, considered by some, on weak taxonomic grounds, to be a separate genus (*20*). After many species names were proposed, two, *A. africanus* and *A. robustus*, became widely accepted. The former is smaller, more delicately built, and has relatively smaller cheek, teeth, and chewing musculature. These species came to be known as "gracile" and "robust" *Australopithecus*.

At first, dating was uncertain and authorities thought that perhaps *Australopithecus* lived too recently in time to be ancestral to ancient humans such as *H. erectus*. Dart's first enthusiasm for *A. africanus* as a human ancestor was occasioned by his misidentification of the lambdoid suture as the lunate sulcus and thus reading a human-like sulcal pattern in the natural cast of the brain of the Taung child. After exposing the child's teeth, he saw that they were human-like as well (*21*). Much later, with many additional finds by Broom, Robinson, Tobias, and others, it became clear that the hip bones of *Australopithecus* showed that the creature was an upright bipedal walker (*22–24*). This fact brought forward support of *Australopithecus* as a true hominid from LeGros Clark in 1947 and, after that, increasingly from others (*25–29*). Evidence of a bipedal stance was indicated even though bones of the lower extremities were then poorly known.

On the assumption that the environment in South Africa at the time of *Australopithecus* was essentially as it is today, Dart postulated that the origin of *Australopithecus* and thus of hominids was an adaptation to the open savanna where fruit, succulent vegetation, and water would all be scarce. Dart and early writers generally called these creatures "man apes." The South African *Australopithecus* fossils all came from cave sites in the Transvaal that were full of broken rocks and bones of antelopes, baboons and many other mammals. Being aware of carnivorous feeding among modern chacma baboons of the same region Dart, in the late 1950s, suggested that *Australopithecus* was a hunter, whose ape ancestors had been selected for intelligence and manual dexterity (with concomitant bipedality) by the demands of savanna living (*30–33*). About the same time, John Robinson proposed the idea that the diets of robust and gracile *Australopithecus* were different: *A. africanus* was an omnivore, *A. robustus* a plant feeder (*34*).

Knowledge of the hierarchical and ordered social organization of savanna baboons increasingly led scholars such as Washburn (*35*), Oakley (*36*), and Washburn and Lancaster (*37*) to see hominid origins in terms of primate analogs. They inferred that greater intelligence and society were ultimately derived from a successful hunting adaptation. Dart's arguments went further. Individual *Australopithecus* were not only killing a variety of animals to eat, but he proposed that there were traumatically formed breaks in the Taung child skull, as well as in several other specimens [SK 54, TM 1517, STS 60 (*38*)], suggesting to Dart that these hominids were killing each other with weapons of stone and bone. Hence, he termed these creatures "killer apes." In retrospect, Dart may have been overreacting to the early rejection of *Australopithecus* as a human ancestor by attributing to it various unquestionably human-like features, particularly predatory hunting methods. His enthusiasm was understandable, but today more stringent requirements are necessary to confirm systematic hunting.

These new standards come partly from the rise of taphonomy (the study of death assemblages), especially as exemplified by the work of Brain beginning in 1970 (*39–41*). Brain studied the bone accumulations that result after baboons, antelope and other mammals have been eaten by carnivores and scavengers such as porcupines, leopards, and hyenas. He also analyzed the possible traumatic breaks of various skulls of *Australopithecus* studied by Dart. These breaks could easily have been caused by rock falls or compaction of rocks against skulls as they washed or fell in and accumulated in caves. The broken mammal bones, rather than being weapons, were like those broken by leopards, who perhaps had eaten their prey in trees at or above ancient cave entrances. Brain was effective in showing that paired holes and eyesockets in the skull of one young *Australopithecus* from Swartkrans exactly fit the gape of jaws and canines of a fossil leopard skull, so that a leopard could have hauled this individual to a feeding tree above the cave entrance. In sum, Brain's work, and that of others later, now makes *Australopithecus* look like the prey, not the predator. More recently, Shipman, Potts, and Bunn (*42–46*) have analyzed bones from various hominid sites in East Africa, mainly Olduvai, in order to understand the meaning of breaks, cuts, and scratches on them. Their work indicates that early hominids were not hunting and killing animals on a large scale but were instead scavenging mainly on meat and marrow of artiodactyl limbs, which were perhaps often the remnants of carnivore kills.

At about the same time as Brain's work, Mann (*47, 48*) compared the pattern of tooth formation and eruption in South African *Australopithecus* with teeth of both humans and apes. His observations led him to the conclusion that maturation in the man-apes was human, not ape-like, in schedule of development. Mann inferred that the distinctively long period of childhood maturation seen in modern humans had already evolved, perhaps in conjunction with the origin of Hominidae. Under Mann's procedures the Taung child was estimated as having died at about 6 years of age. Bromage and Dean (*49*) endeavored to establish age at death for several young *Australopithecus* specimens by counting incremental growth lines on the teeth. Although some part of the age also had to be estimated, they still could not come up with ages greater than about 3 years. This finding put *Australopithecus* on an ape schedule of development. In 1986 Smith (*50*) argued that the pattern of dental development in *Australopithecus*, as well as in other early hominid fossils, was like that of apes and that Bromage and Dean had been correct in proposing short, ape-like maturation times. In the last 2 years Conroy and Vannier (*51, 52*) have also supported an ape-like dental eruption pattern on the basis of x-rays and CT scans (*38*) of the Taung child.

Primitiveness of *Australopithecus*

The real significance of these various arguments is not at what age a particular tooth erupted, but the evident discovery that these early hominids did not have prolonged maturation as do modern human beings; rather they grew up rapidly like apes. Considerably before these arguments, it was realized that *Australopithecus* was certainly in existence long before stone tools had appeared and had probably not left tools at the South African sites (*41, 53*). Discoveries in East Africa brought new light to the understanding of *Australopithecus* by showing us more about its age and anatomy. The majority of these finds came from Laetolil and Olduvai in Tanzania, East and West Turkana in Kenya, and from Omo and Hadar in Ethiopia (*20*). They supplemented what was known from South Africa, because new parts of the skeleton were found and, in general, the East African sites could be better dated by the potassium-argon method. These discoveries showed that, as in South Africa, East Africa had small *Australopithecus* as well as robust forms (*53–55*). Species names now widely accepted are *A. africanus* and *A. robustus* in South Africa and *A. afarensis* and *A. boisei* in East Africa. For a long time some researchers (*56, 57*) held that hominids had always existed as a single species at any one time. However, it was evident at Olduvai that one or more species had overlapped in time with primitive species of *Homo* (*54, 58*). The "single species hypothesis" implying that humans were so aggressive or so overwhelming in their use of the environment that two types could not coexist had "died" on the shores of an ancient East African lake (Lake Turkana today). If not "killer apes," what were they?

The celebrated series of various finds of hominids from Olduvai collected by Louis and Mary Leakey between 1959 and 1971 included fossils as old as 1.75 to 1.8 (Ma) (*59*). Proving any hominid to be that old was then a revelation. A few of the early Olduvai finds were *Australopithecus*, but many others were eventually referred to a then, 1964, new species *H. habilis* (*58*). Perhaps the most striking specimen was the remarkable large skull of *A. boisei* found by Mary Leakey in 1959, a specimen that combined enormous cheek teeth with a small brain and a large face (*54, 60*). By analogy with South African species, *A. boisei* came to be described as "hyperrobust." Much later R. E. F. Leakey and Walker (*61*) confirmed that *Homo habilis, H. erectus*, and *A. boisei* all also occur in ancient deposits surrounding Lake Turkana.

The site of Laetolil in Tanzania grew in importance with renewed research by Mary Leakey. A series of *Australopithecus* mandibles were found there as well as a trackway showing numerous footprints of three bipedal hominids imprinted in an ashfall that has been dated to 3.6 Ma (*62, 63*). Meanwhile Johanson's expeditions to the Hadar-Afar region of Ethiopia between 1973 and 1983 yielded an extensive assemblage of *Australopithecus* fossils that appear to date to around 3 Ma (*64*). Older hominids exist in Africa back to 5.6 Ma or before, but the specimens are fragmentary (*65*).

Lucy

The best find in the Afar, the celebrated skeleton called "Lucy" (AL 288-1), recovered in 1974, is the oldest relatively complete skeleton of a hominid and one of the most important hominid fossils ever found (Fig. 1). After initially suggesting (*66, 67*) that the Ethiopian fossils represented three species, Johanson and White decided to combine these fossils from the Afar triangle with those recovered at Laetolil, Tanzania, as one new species, *A. afarensis* (*55*). This taxonomic decision brought immediate criticism. Scholars questioned that the Laetolil and Hadar samples could be the same species and some, especially Tobias, suggested that *A. afarensis* and *A. africanus* were the same (*68, 69*). At first, the K-Ar dating of the Afar sites was not fully accepted and that of the South African sites has always been uncertain. Therefore, it was not clear, initially, that the Hadar fossils were probably 0.5 to 1 million years older than those from the Transvaal, except perhaps those of Makapansgat that could also be as old as 3.2 Ma. Although the rather incomplete cranial fragments from Ethiopia were reported to be chimpanzee-like in many ways (*53, 64*), Lovejoy, who had analyzed the excellent pelvic and lower limb material, judged *A. afarensis* to be an effective, well-adapted biped. It was clear to him, writing in 1979, that the exact shapes of pelvis and proximal femur were different from *Homo* but not in a way that would inhibit the bipedal gait. Johanson and others (*53, 64*) presented an interpretation of the Afar hominids that did little to distinguish them from *A. africanus*, either in degree of primitiveness or in supposed adaptation as open country bipeds. Meanwhile, other theories as to bipedal origins were emerging. For instance, bipedal walking might have started through balancing erect on branches or vines in the trees, as gibbons sometimes do. In 1983 Stern and Susman (*70*) presented a detailed study of the Hadar postcrania and concluded that these hominids had continued to frequent trees even after they began to evolve longer lower limbs, a human-like foot with broadened heel and great toe in line, with straightened lateral toes and concomitant low broadened ilia. Frequent recourse to the trees for safety and frugivorous and folivorous feeding would explain why the microwear patterns on *Australopithecus* molars do not show differences from those of the frugivorous-folivorous African apes (*71*), as well as indicate how these small creatures could protect themselves from nocturnal predators.

Cranial parts recovered with Lucy are inadequate to determine a brain volume. In 1985 Falk (*72*) analyzed the three best Hadar specimens (AL 333-45, 333-105, and 162-28) and calculated that the mean brain volume was much lower than the original estimate of 500 cm^3, in fact below 400 cm^3. It is also her view that the Hadar fragments are "consistent with an ape-like external cortical morphology"; she saw "no evidence for expansion or reorganization of parietal-occipital areas." Falk concluded that in hominid evolution "the trend toward brain enlargement preceded cortical reorganization." If correct, both of Falk's points are of great importance. Although her position was immediately challenged by Holloway and Kimbel (*73*), who considered AL 162-28 more hominid-like in pattern, the main problems of interpretation appear to come from the extremely fragmentary nature of the Hadar crania.

The skeleton of Lucy has been analyzed by many scientists (*64, 70, 74, 75*). The rib cage shows an ape-like conical thorax. Jungers, however, has shown that Lucy's limb proportions are distinctive (*75*). The forelimb relative to body proportions is comparable to that of modern humans. The humerus is 85.1% of the length of the

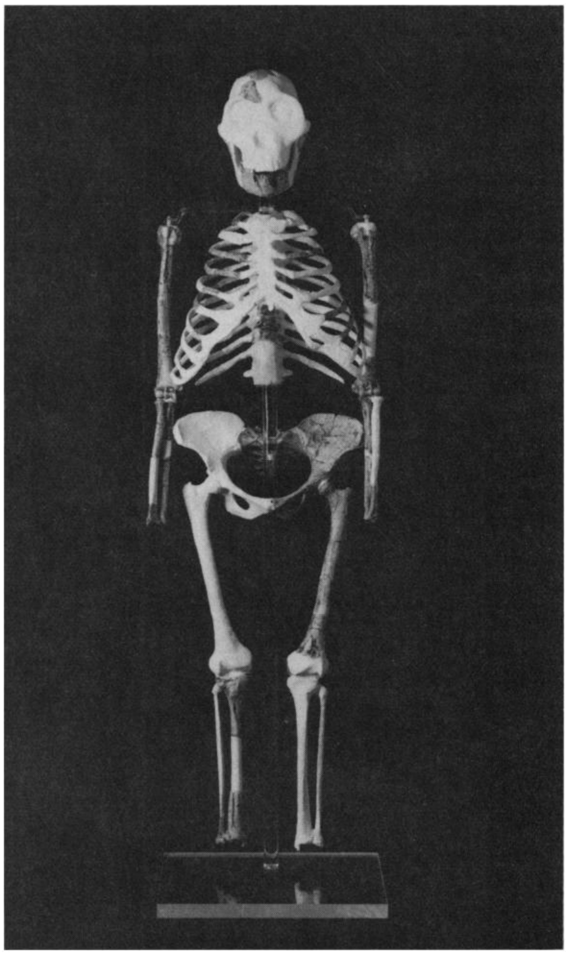

Fig. 1. Reconstructed skeleton of "Lucy," a 3-million-year-old human forerunner: AL 288-1, from the Hadar region of Ethiopia. [Photo courtesy of Peter Schmid, University of Zurich; from *Folia Primatol.* **40**, 4 (1983) with permission of S. Karger AG, Basel]

femur, a condition intermediate between that of humans and apes. He shows, further, that the hindlimbs, compared to body size as a whole, are much shorter than in modern humans and are closer in length to those of similar-sized apes. Although bipedal locomotion was surely possible, Lucy's relatively short stride most likely raised the energetic cost of walking and lowered speed in running. Her discoverers (*76*) estimated Lucy as about 60 pounds body weight (27.3 kg). Her height was set at about 3.5 feet (about 1 meter). Males could be up to 5 feet tall (1.52 m) and weigh 150 pounds or 68.2 kg (*53*). New estimates by Jungers (*77*) confirmed a height of 1 meter for Lucy and raised the weight to about 30 kg. Thus, the range of fossils from Hadar show that a marked size dimorphism existed there.

Some of the other differences did not involve only size. If one considers the joint at the top of the ankle where the tibia and talus join, the back is higher and the front lower in apes because apes can flex their foot downward better than humans can. In humans the front of this joint is higher so that the foot can better be flexed upward. At Hadar the larger tali indicate a joint opening forward; in the smaller individuals such as Lucy the back is lower, as in apes. This and other differences led Stern and Susman (*70*) to suggest that the two sexes at Hadar differed in their tree-climbing ability so that the anatomy of the skeleton was more ape-like in females, and better suited to climbing. Meanwhile two French scientists, Senut (*78*) and Tardieu (*79*), had suggested that the larger Afar hominids were more like *Homo* in their limb joints and the smaller ones were more like *Australopithecus*. Many experts doubt that there were two species or two genera at Hadar, but the evident differences are worrisome and may even show that there were two species (*80*). A marked sexual size dimorphism has been demonstrated for almost all Oligocene and Miocene apes and characterizes two of the five living hominoid species. Since a striking dimorphism seems likely for *A. afarensis*, this should affect how we interpret its lifestyle and breeding behavior. If two or more differently adapted species (perhaps of different genera) were there at the beginning, then the time of their separation must have been much further back.

In correlation with possible tree climbing or living propensities, *A. afarensis* shows curved finger bones and a conformation of certain wrist bones that is distinctly ape-like. Likewise, the toe bones of the foot show curvature (*65, 70*). There is no evidence whatever of tool use or of the building of habitations. It is not clear whether, or to what extent, there could have been scavenging of meat or marrow. Regardless of how primitive the Hadar fossils may be, whether they had smaller brains or a propensity to share bipedal walking with tree living, there now seems to be general agreement that these are the oldest members of the human lineage. A favored family tree, just a few years ago was to have *A. afarensis* give rise to two later species: *A. africanus* and *A. robustus*, with *A. africanus* then leading through *H. habilis* to *H. erectus* and *A. robustus* to *A. boisei*. In an impressive study of australopithecine crania, Rak (*81*) demonstrated a possible morphocline by which to derive the robust (*A. robustus*) and hyper-robust (*A. boisei*) from *A. africanus*. Both of these latter two arrangements have been altered by new finds such as the next specimen.

The Black Skull

In 1985, west of Lake Turkana, Kenya, in 2.5-Ma, sediments at a site called Lomekwi I, a large, dark (manganese stained) *Australopithecus* skull, KNM-WT 17000, was found by Walker (*82*). This massive skull has an extremely large facial skeleton joined to a small brain case. The skull combines primitive features such as a forward jutting, ape-like lower face with large overall size, an extremely large palate, large teeth, and a low placement of the cheek arch. This combination suggests that KNM-WT 17000 could represent a new species ancestral to *A. boisei* (and perhaps descended from *A. afarensis*). Either *A. robustus* is derived independently from something like KNM-WT 17000 or it arose separately from *A. africanus* in South Africa (*83*). Walker *et al.* (*82*) also suggest that if this fossil and a similarly large mandible found at a nearby site should be a distinct species, then a prior name is available. In 1967 Arambourg and Coppens (*84*) described as *Paraustralopithecus aethiopicus* a mandible from the same sedimentary basis and same time period (Omo 1967–78, Shungura Formation) whose name should go with KNM-WT 17000. Since a generic distinction cannot be sustained, the name for these fossils would become *A. aethiopicus*.

Most scholars argue that they know that the robust forms of *Australopithecus* were not in the ancestry of later humans. Consequently, the information they give to our reading of the stages of human ancestry is only tangential, but yet relates importantly to our understanding of other early hominids. The brain volume of robust *Australopithecus* in both East and South Africa ranges from approximately 410 to 530 cm^3 (*85–87*) and is not significantly different from the *A. africanus* average of about 450 cm^3 (*85*). From the study of the postcranial bones of *A. boisei*, it appears that the females are similar to *A. africanus* and *A. afarensis* and are unlike both chimpanzees and modern humans (*88*). Of particular interest is a talus from Ileret, KBS Member, Area 6A, associated with mandibles and teeth of at least four individuals of *A. boisei*. This talus is extremely similar to that in the supposed *H. habilis* foot recovered from Olduvai, OH 8 (*89*), but is larger. OH 35, a tibia and fibula, may also belong with OH 8. Grausz *et al.* (*88*) now agree with Wood (*90*) that all these bones should be referred to *A. boisei*. Another possibility is that lower limb bones of *A. boisei* and *H. habilis* are not easy to distinguish.

What is known overall of the *Australopithecus* group—creatures that are often called australopithecines or "man apes"? Although relatively large in relation to body size, their brains, ranging from about 350 to 530 cm^3, are small when contrasted to those of humans. With large, long-fingered hands, having arms shorter in relation to torso length than in comparable sized apes, but with lower limbs seemingly only a little longer than those of similar-sized apes, their overall anatomy forms a connecting link. Although foot and hip are adapted to bipedal walking, the stride was short and walking and running slowed. Almost certainly they did not talk or use fire (*91*). If they took strength from numbers they could probably have driven off the great African carnivores by screaming, charging, and throwing objects as apes do. Like virtually all terrestrial primates they probably slept in trees or on cliffs.

When speculating about the behavior and habits of early hominids it seems imperative to draw analogies from the range of excellent data now available on the behavior of living primates and to limit the reading of modern human attributes into these early creatures. Foley and Lee (*92*) have summarized recent efforts to reconstruct early hominid behavior. In their view, these first hominids may have associated as mixed sex groups containing multiple males linked by kinship with females forming bonds, either with individual males or with all the males. This interpretation, however, supports the view that earliest *Australopithecus* included both large and small body-sized species.

The Emergence of *Homo*

Largely contemporary with *A. boisei* is another species, *H. habilis*, that was named in 1964 by Leakey, Tobias, and Napier (*58*). This species has recently been under much discussion for there seems to have been at least two kinds of "handy man," as its species name is translated. From the time of its discovery the validity of this species was strongly questioned, much as was *A. afarensis*, but for different reasons. The type and referred specimens were not very similar in comparable parts. They were from both Olduvai Beds I and II, then thought to span a broad time range; therefore it seemed they might not belong together. Initially about a dozen fossil hominids from Olduvai Gorge were assigned to *H. habilis*, the type being OH 7 (*58*). This group of fossils consists of a mandible, parietals, hand bones of a juvenile, and a possibly associated upper molar later numbered OH 45. The species was characterized as having a mean brain volume intermediate between that of *Australopithecus* and that of *H. erectus*. The upper and lower jaws are less robust than those in *Australopithecus* and the anterior teeth are relatively large. Breadth across the cheek teeth is narrower from inside to out, particularly across the lower premolars, and the external sagittal curvature of the occipital region of the skull is much slighter.

Beginning in 1968 Richard Leakey's collecting teams at Koobi Fora, east of Lake Turkana, secured numerous fossils relevant to determining the status of *H. habilis* (*93*). The large number of possible *H. habilis* specimens from both Olduvai and Koobi Fora appear to date from between about 2.2 and 1.6 Ma. A considerable number of only partially complete specimens have been included in the taxon by Howell (*94*). Cranial remains include OH 7, 13, 16, and 24 and KNM-ER 1470, 1590, 1805, and 1813. Some workers argue that the latter two may be *Australopithecus*. None of these finds preserves associated skeletal parts from upper and lower limbs, but isolated and sometimes questionably referred skeletal elements of *H. habilis* have generally been described as resembling those of *H. sapiens* (for instance, two femora from East Turkana KNM-ER 1472 and KNM-ER 1481a). As previously discussed, OH 8 and 35 (formerly ranked as *H. habilis*) may belong to *A. boisei* (*76*).

In 1987, Johanson *et al.* (*95*) described a highly broken and fragmented skeleton from Olduvai (OH 62) as being *H. habilis*. Their estimated humerofemoral index of 95 for this specimen resembles that of *Pan* and is 10% higher than in Lucy (AL 288-1), but perhaps this index should be revised downward as the specimen is very fragmentary. An elongated forelimb like this was quite unexpected for a skeleton referred to genus *Homo*, because the forearm can be interpreted as even more chimpanzee-like than that of *Australopithecus*. It is therefore significant that Leakey *et al.* (*96*) report similar findings from an associated partial skeleton, KNM-ER 3735, a gracile *H. habilis*-like specimen from the Upper Burgi member of the Koobi Fora Formation of an age estimated at 1.9 Ma. The cranial fragments indicate a small gracile skull with a thin-boned brain case without cresting and having small temporomandibular joints. In a comparative series of measurements on the limb skeleton, KNM-ER 3735 was found to differ from *H. sapiens* in a manner similar to that of Lucy (*96*). The large thick scapular spine fragment, the distal humeral fragment and the proximal radius all suggest that the climbing abilities of this species were as developed as in *Pan*. Leakey *et al.* (*96*) speculate that the species represented by OH 62 and KNM-ER 3735 may not have been ancestral to *H. erectus*. Could this species have been the East African equivalent of *A. africanus*? The other kind of *H. habilis* (not yet documented by a good skeleton) may have been more *Homo*-like and have therefore made a smoother transition to *H. erectus*.

If there was only one species of *Homo habilis* after all, these new discoveries show that it was much more primitive and ape-like than originally supposed. Were there two species, one must have been more close to the ancestry of *H. erectus*. Before it was realized that two species might be involved, it was suggested that the life style of *H. habilis* differed from that of earlier and contemporary *Australopithecus*, with many assuming that this species was the first to manufacture tools, such as Oldowan pebble tools. These conceivably were used to break into and retrieve the bone marrow from leg bones of hoofed mammals remaining from carnivore kills. Because this tool kit does not enlarge or diversify for about 1 million years (*97*), the extent of use of first tools seems to have been limited. Susman (*98*), from work on the hand of *A. robustus* from Swartkrans, South Africa, suggested the possible existence of precision gripping, but the manufacturing of such early, crude tools requires power, not precision. From the start then, there has been much indecision about variation within this supposed species, as well as whether to transfer specimens others had assigned to it to *A. boisei*, *H. erectus*, or *A. africanus*. Stringer (*99*) reviewed the many referred specimens and concluded that one skull, KNM-ER 1813, represents a small-bodied species allied to both archaic *H. erectus* and *H. sapiens*. He considered KNM-ER 1470 and 1805, together with OH 24, as representing another contemporaneous species that was larger with a greater endocranial volume and *Homo*-like postcranium but with facial resemblances to *Australopithecus*. Recently Lieberman, Pilbeam, and Wood (*100*) considered the probability that KNM-ER 1470 (presumed to be a large male) and KNM-ER 1813 (presumed to be a small female) could be in the same species by comparing these with randomly sampled but markedly dimorphic male and female gorillas. Their analysis suggests that the two could not be in the same species unless *H. habilis* was considerably more dimorphic than the gorilla or had dimorphism unlike that of living higher primates in some other way. Like Stringer, these authors concluded that another species related to *H. habilis* needs to be named. The name *H. ergaster* was proposed by Groves and Mazak (*101*) for a mandible, KNM-ER 992, that some have considered as possibly being suitable for one of these two species. That this is not so has been recently proposed by Leakey and Walker (*102*) who show that KNM-ER 992 is referable to early *H. erectus*. Another possibility is that KNM-ER 1813 is a gracile *Australopithecus*.

Many important things relating to human origins happened in East and South Africa between 2.3 and 17 Ma: significant brain enlargement occurred, tool manufacture began, and the first post-cranial bones closely similar to those of modern *H. sapiens* initially appeared. Nevertheless, because three contemporary hominids (*A. boisei* and two kinds of "*H. habilis*") then existed, none of which is known from a good associated skeleton, we yet have much to learn about the course of human development in that period.

Nariokotome

In 1984, at a site called Nariokotome III in Kenya, Kamoya Kimeu discovered the first skull parts of what, with continued excavation during the succeeding 4 years, has proven to be by far the most complete early hominid skeleton ever found. The skeleton has been identified (*103*) as an early representative of *H. erectus* with an age of about 1.6 million years. This find, KNM-WT 15000, is immensely important, not only for its great age, but for its completeness (Fig. 2). Because much of the skeleton is preserved, accurate estimates of height, weight, age at death, brain volume, and limb proportions can be made. Leakey and Walker (*102*) suggest that there was considerable stasis throughout the long period of existence of this kind of human forerunner. The teeth of KNM-WT 15000, combined with others nearly contemporary with it, average close to those from Zhoukoudian, China, measured by Weidenreich (*104*). This similarity, together with other close cranial and skeletal resemblances to Asian ape men, satisfy Leakey and Walker (*102*) that, even though over a million years separate Peking and Nariokotome man, they are of the same species. These two authors share the view, recently proposed by Rose and Bown (*105*), that dividing documented and relatively unchanging lineages into many time-successive species is often unwarranted and misleading. Taxonomic decisions should be based on structural, not temporal, differences.

This young *H. erectus* is identified as a male because of the robustness of the face and of the masculine shape of the pelvic bones. Estimating age in humans from degree of closure of epiphyses on long bones and from tooth eruption is well known. Application of these methods to the Nariokotome youth gives an age, according to Leakey and Walker, of 12 ± 1 years in modern human terms. Consideration of the work of Smith (*50*) on estimation of the dental ages of *Australopithecus* and early *Homo*, which revised downward the age in years, might make this individual even younger. Being even less than 12 is the more striking because his height would be remarkable in a modern 12-year-old. If the regression equations worked out for stature based on long bone length of modern human adult males are applied to this skeleton, stature would have been close to 1.64 to 1.68 meters (*106*). The youth would have been somewhat shorter than this estimate because *H. sapiens* crania are several centimeters taller than are *H. erectus* skulls. The height as a sub-adult would have then been between about 5′3″ and 5′6″. The brain volume estimated by these authors (*103*) is 900 cm^3, just slightly above the mean for Indonesian *H. erectus*. Although many of the bones of *H. erectus*, here seen for the first time, resemble those of present-day humans, those that differ are useful in reconstructing phylogeny. The spinal canal is unusually small in diameter, correlating with smaller brain size. Lower cervical and upper thoracic vertebrae have nearly horizontal spines, arranged as they typically are in both African apes and Neandertals rather than inclined downward as is more characteristic of modern humans. Most interestingly, when the ribs are arranged as an articulated cage, the shape of the thorax is conical like that of Lucy and of African apes, and not barrel-shaped as in later humans.

As reconstructed, the sacrum and pelvis of KNM-WT 15000 has a small interacetabular diameter. Since sacral diameters are not known to vary much between the sexes of modern humans, it may be inferred that female *H. erectus* might have had a similarly small interacetabular diameter and birth canal. Leakey and Walker (*102*) speculate that head size at birth may well have been small and therefore that a uniquely modern human characteristic of extending a high rate of brain growth into infancy may also have characterized *H. erectus* at 1.6 Ma (*107*). Analysis of the femora of KNM-WT 15000 shows an extremely long neck with very low femoral neck angle of 110 degrees. This is apparently far outside the range of *H. sapiens*. These structural distinctions of the proximal femur resemble *Australopithecus* and thus reflect the ancestral derivation of *H. erectus*.

In sum, the Nariokotome youth qualifies beautifully as a connecting link. In its skeletal anatomy it reflects retentions from its *Australopithecus* and earlier ape ancestors, whereas in other features it foreshadows what was to come.

Hominids Leave Africa

After the time of Nariokotome man, hominids continued to evolve only in Africa for a period of about 0.6 million years. Although the process is far from well documented, *H. erectus* groups eventually wandered out of Africa about 1 Ma and eventually reached Southeast Asia (*108*). Regional populations became established throughout Eurasia and gradually evolved into what has been called archaic *H. sapiens*. In Europe and Western Asia from this archaic form the creatures we call classic Neandertal man, or *H. sapiens neanderthalensis* differentiated (*109*). Recently the work of Trinkaus (*109*) and others has shown that typical Neandertalers differed from later, or "modern" *H. sapiens*, often called *H. sapiens sapiens*, in several striking ways. Nevertheless, Neandertalers buried their dead, had brain volumes comparable to or exceeding those of early modern *H. sapiens* (*111*), and seem to have shared with them the same "tool kit" (middle Paleolithic) in Israel and probably elsewhere about 50,000 to 100,000 years ago (*110*). The view is growing that the two kinds of late hominids may have differentiated allopatrically: Neandertals having arisen in the north and modern *H. sapiens* entering Eurasia from Africa relatively recently (*112*, *113*). Like earlier *H. erectus*, Neandertalers have extremely dense skeletal bones and thick skulls with projecting brow ridges, and both sexes are extraordinarily muscular (*114*). The face juts forward and holds large front teeth, that become heavily worn with age. If recently determined dates (*115*) are correct, evidence from Israel indicates that Neandertal man and early modern *H. sapiens* alternated at various sites without anatomical intermediates. Falk (*116*) has shown by restudying cranial anatomy that the proposal of Lieberman *et al.* (*117*) that structurally Neandertal man was not capable of speech is in error. Both Tobias (*118*) and Falk (*119*) have also stressed that Broca's area of the brain is already well developed in KNM-ER 1470, which dates to somewhat older than 1.8 Ma. Enlargement of this area, it is agreed, could be a structural indication of the development of speech. In contrast to this, some authors, such as Cavalli-Sforza et al. (*120*), reason that language is a late development, perhaps arising first in early modern humans, only a few tens of thousands of years ago. Both Neandertals and early modern humans, from 90,000 to 40,000 years ago, have simple tool

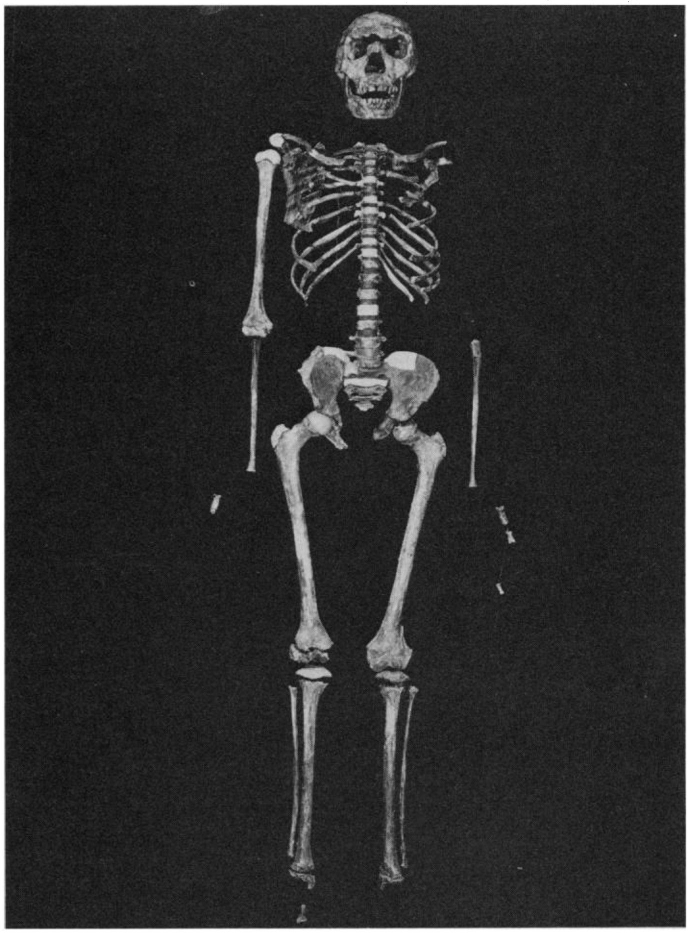

Fig. 2. Nearly complete skeleton of very early *Homo erectus* youth from the Nariokotome III site west of Lake Turkana, Kenya. Estimated age 1.6 million years. [Photo courtesy of Alan Walker and the National Museums of Kenya]

kits and no art. Some think that the appearance of elaborately made and diversified stone tools, as well as carving, painting and sculpture, about 30,000 to 40,000 years ago, signifies the appearance, among humans that were not Neandertal, of fully developed language. A generalization about study of the distant past, however, is that first appearances and last occurrences are never the real times of the beginning or ending of a species or artifact type.

Long ago the Neandertalers were seen as having been abruptly replaced in Europe by men of modern sort such as Cro-Magnon (*121*). This was followed by a period when some investigators provided evidence that there were progressive, gradualistic trends seen in younger and younger fossils throughout Eurasia that led up, through Neandertals, to modern humans (*121*). For instance, average size of teeth decreased successively with time and the face became smaller (*122*, *123*). Recent touting of punctuated equilibrium, cladistic branching, and ideas of saltational allopatric speciation have pushed the pendulum back toward the idea that modern *H. sapiens* spread relatively recently over Eurasia, outcompeted and replaced what must have been numerous and widespread archaic *H. sapiens* (*112*, *124*).

For me it is difficult to see how two genetically isolated species of humans could have so recently arisen. Primates often produce hybrids in the wild when two species or subspecies come into contact. Humans in conflict typically capture and incorporate unrelated women and children into their bands. Hunting and eating a species that is vastly different, as far as intelligence is concerned, might explain the disappearance in Africa of *A. boisei* at the hands of *Homo*, but Neandertals and modern humans shared equal brain size, tool kits, and other advanced practices. Nevertheless, there appears to be a change over between about 40,000 and 30,000 or 35,000 years ago, at least in Europe, from Neandertalers to early modern *H. s. sapiens*.

Appearance of Modern Humans

Trinkaus (*109*, *110*, *125*) has shown that there was a decrease in the muscularity of the arm with concomitant changes in shoulder, elbow, wrist, and hand as early modern man emerged. The Neandertalers seem to have needed more durable teeth and much more muscular limbs to subsist than did later humans. Although difficult to prove, the change in early modern humans most probably came through evolution favoring more mechanically efficient limb and weapon use and more successful dependence on manufactured tools, rather than use of the jaws as an implement. As with the forelimb and face, Neandertalers have extremely robust hind limbs with very dense bone suggesting exaggerated levels of endurance and an adaptation to long hours of walking and scrambling about. Whether or not the Neandertals were abruptly replaced, Trinkaus suggests that they may be taken in their general anatomy as fairly representative of earlier, less well-known transitional stages from *H. erectus* into the archaic varieties of *H. sapiens.* He suggests that the subsistence efficiency of the Neandertals and their ancestors was less developed than that seen in early modern humans, presumably because of the lack of certain hunting weapons. Early modern humans in Europe have longer distal limb segments than do Neandertals which might imply relatively recent equatorial ancestry or greater thermal protection in the form of better clothes. Allen's rule, a principle of zoology, predicts that mammals generally have longer extremities in warm climates.

Recently Stringer and Andrews (*112*) summarized work that suggests that a wave of early modern humans arising in Africa reached and swept over Eurasia where they either outbred, outcompeted, outlasted, or exterminated the populations that they found there. These older populations had been evolving for a long time and showed regional continuity (*126*, *127*). Writing in the winter of 1987, Cann, Stoneking, and Wilson (*128*) urged that the biological marker for this wave of modern humans is an extraordinarily high level of similarity in mitochondrial DNA (mtDNA). The European, Asian, New Guinean, Australian, as well as part of the African, mtDNA's analyzed are said to "stem from one woman who is postulated to have lived about 200,000 years ago" (*128*).

For several reasons there are almost certainly major difficulties in assigning a date to the time of first origin of modern Eurasian mtDNA. Latorre *et al.* (*129*) question the reasoning that deduces that populations can or do trace back through single individuals or even restricted populations. Gingerich (*130*) critically reviews weaknesses in the procedure of assigning dates derived from molecular data. The evidence for the origin and spread of modern humans has been much debated with the degree of replacement being unclear (*112*, *113*, *119–128*). It is hard to grasp how replacement could have been absolutely total, a result necessitated by this interpretation of the meaning of mtDNA (*131*). If the calibration of the mtDNA clock is off by a significant factor, then perhaps this procedure only documents the spread of *H. erectus* out of Africa (*132*). Spuhler (*133*) criticizes the calibration of the mtDNA clock of Stringer and Andrews (*112*). On the basis of more reliable rates of mtDNA evolution he calculates that the commonality of mtDNA in Eurasia only documents the original migration out of Africa about 1 Ma. Although one could say that the commonality of mtDNA reaffirms the "sisterhood" of humankind, if the kind of mtDNA we share arose only very late, it also points toward a genocide of Neandertals and all other archaic forms outside Africa.

Today, mainly because of recent discoveries, we know several points of the greatest significance about our origins. The major characteristics of humans: bipedal walking, tool use, large complex brains, use of fire, big game hunting, speech, art, and symbolization all appear to have originated more or less independently and at different times. Other than the first of these developments, bipedal walking, there never was a "human origin" but instead, a process.

Ideas that the multiple phases of human origin took 15 million to 40 million years have collapsed. Few now suggest that the appearance of bipedality, the first hominid feature, need have arisen much more than 1 million or 2 million years before its first demonstrated existence in the Laetolil trackways. Studies of later early modern *H. sapiens* show that much of what we hold "near and dear" about ourselves—our very anatomical proportions, our ability to create art and symbols, sophisticated tool manufacture, and construction and use of house and home may have appeared only a few tens of thousands of years ago.

The extreme novelty of humans as the dominant force on this planet is as surprising as is our current rate of destruction of our own habitat and that of the earth's other life forms. This disregard is all the more striking since, in geological terms, our species has only recently departed from its "place in nature." The full implications of our derivation by the random processes of biological evolution in a mere 5 million to 7 million years from an animal much like a chimpanzee have yet to be incorporated in any manner into the fundamental beliefs or institutions of our own, or in fact, any society. In its very success, our species has raised grave problems that demand new kinds of solutions. Will we, by better understanding the processes that made us what we are, grow in capacity to solve the frightening problems of the future arising from our very selves?

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