

Fossil humans

All prehistoric skeletal remains of humans which are archeologically earlier than Neolithic (necessarily an imprecise limit), regardless of degree of mineralization or fossilization of bone, and regardless of whether the remains may be classed as *Homo sapiens sapiens*, anatomically modern humans. In this sense, the term “humans” is used broadly to mean all primates related to living people since the last common ancestor of people and African apes, thus all species currently included in the genera *Homo*, *Australopithecus*, *Ardipithecus*, and *Paranthropus*.

Discoveries began early in the nineteenth century, although their meaning and antiquity were not recognized before the finding of the Neanderthal specimen in 1856. Fossil human remains have come principally from Europe, Asia, China, Java, and Africa. Because of the rather late entry of humans into the New World, all American Indian remains are of relatively recent origin and recognizable as *H. s. sapiens*.

Dating fossils. The human lineage was once thought to have come into existence only at the beginning of the Pleistocene. It is now known to have been fully separate from the ancestry of the apes at least as far back as the early Pliocene or perhaps even the later Miocene (4–6 million years ago, or Ma). This view was widely held by anthropologists, on theoretical grounds, in the early part of the twentieth century. It was abandoned in the 1940s because of lack of supporting evidence. Discoveries in Pliocene and Miocene deposits since then have led to a reappraisal of the evidence (**Fig. 1**). Examples of fossil humans ranging from about 9.5 million years ago to 400,000 years ago are shown in **Figs. 2–11**.

Dating within the Pleistocene (and earlier) is accomplished by the methods of conventional paleontology and geology, by association with human implements, by several chemical and physical tests for relative age (such as the fluorine test for accumulation of this element in bone), and by geochronometric methods which provide an age in years. The latter usually involve determining the presence of radioactive substances such as radiocarbon and radiopotassium as well as other radioactivity-based methods such as electron spin resonance, thermoluminescence, and fission-track dating; all of these are broadly termed radiometric methods, as opposed to approaches such as amino acid racemization or dendrochronology (tree-ring dating). See RADIOCARBON DATING.

One of the most important methods of correlation between dated geological sequences is paleomagnetism, which does not itself provide a date because it is basically a boolean system with two states (so-called normal and reversed polarity of geomagnetism) of which all occurrences are indistinguishable. But if the pattern of reversals at any site can be matched against the global paleomagnetic time scale and even approximately dated by means of geochronology or paleontology, a sequence of

dates may result. See DATING METHODS; PALEOMAGNETISM.

Prehuman ancestry. Humans are catarrhine primates, part of a group including Old World monkeys, apes, and various extinct forms. Most evidence from both comparative morphology and molecular studies of proteins shows that humans' closest living relatives are the African apes: the chimpanzee and the gorilla. Less close is the Asian orangutan, and most distinctive of all apes are the gibbons. A classification which conforms to these relationships within the Hominoidea (apes, humans, and close extinct relatives) recognizes the family Hylobatidae for the gibbons and Hominidae for humans and great apes. The latter family is divided into Ponginae (orangs and extinct relatives) and Homininae. Many workers, however, continue to reject this view and place humans in the Hominidae as contrasted with the paraphyletic (multi-origined) apes in Pongidae. A few others have suggested that in fact orangutans are the closest living relatives of humans. No fossils of any modern ape are known, other than Pleistocene gibbon and orangutan teeth from southern Asia. See FOSSIL APES; FOSSIL PRIMATES; MOLECULAR ANTHROPOLOGY; MONKEY; PRIMATES.

The oldest certain representatives of the Catarrhini are fossils from the Fayum beds of northern Egypt dated around 34 Ma. The best known is *Propliopithecus* (= *Aegyptopithecus*) *zeuxis*, a species near the common ancestor of apes, humans, and Old World monkeys. Hominoid evolution took place only in Africa in the late Oligocene and early Miocene (26–17 Ma), as documented by the genera *Kamoyapithecus* and *Proconsul*, placed in the family Proconsulidae. Between 20 and 15 Ma, there are several more derived (“advanced”) African genera (for example, *Morotopithecus*, *Afropithecus*, and *Kenyaipithecus*) and one Eurasian form (*Griphopithecus*). If these are more closely related to living great apes than are gibbons, as has been proposed in the past, they may represent early members of the Hominidae. But if they are conservative (“primitive,” plesiomorphic) by comparison with the gibbons, then they should not be included in the hominid family.

In the latter case, several workers have argued that the origin of modern ape (and human) lineages must have occurred in Eurasia, where a number of derived genera occur between 14 and 8 Ma. These include *Dryopithecus*, which was probably close to the common ancestor of all great apes and humans; *Ankarapithecus* and *Sivapithecus*, which appear to represent two early stages in the orangutan lineage (Ponginae); and *Graecopithecus* (also termed *Ouranopithecus*), which has been suggested as a member of Homininae, that is on the lineage leading toward African apes and humans. Another early hominine is *Samburupithecus*, newly named in 1997 from a maxilla found in the Samburu Hills of Kenya and dated to 9.5 Ma. A possible biogeographic alternative is that a form such as *Morotopithecus*, with relatively derived but poorly known postcranial elements, might have given rise both to the early Eurasian hominids and to

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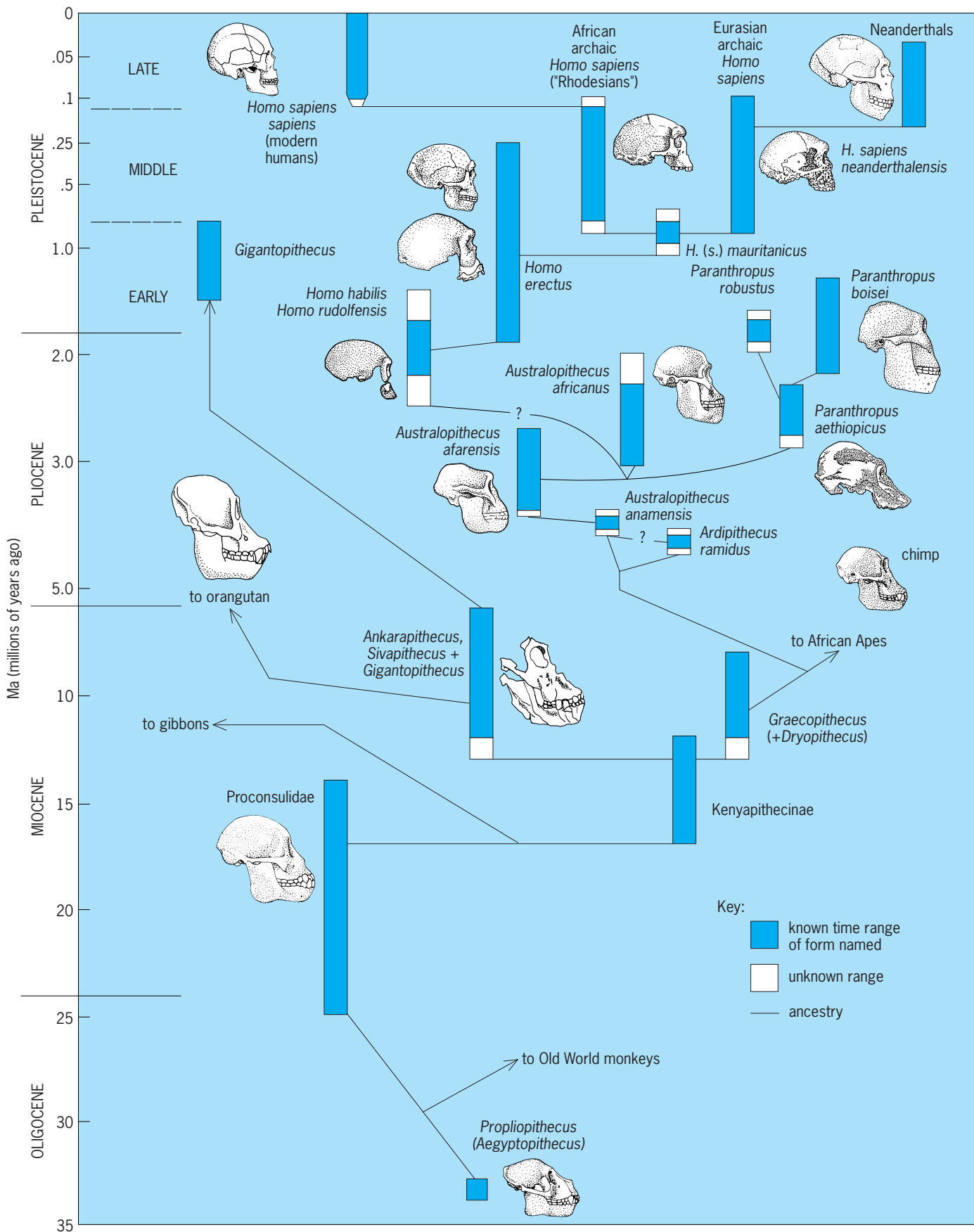


Fig. 1. Human phylogeny from the Oligocene to the present time, showing the skulls of the major known fossil relatives and possible ancestors of modern humans.



Fig. 2. Face (cast) of *Graecopithecus freybergi* from Xirochori, Greece, about 9.5 million years ago. (Courtesy of Lorraine Meeker/Eric Delson)



Fig. 3. Cranium of *Australopithecus afarensis* from Hadar, Ethiopia, about 3.1 million years ago. (Institute of Human Origins)

an as yet unknown African line which culminated in *Samburupithecus*.

Molecular anthropological studies of DNA sequences and other lines of evidence have suggested that chimpanzees are more closely related to humans than either is to gorillas. This would appear counterintuitive, given the morphological similarity between the two African apes, both of which are also derived in the knuckle-walking locomotion. But those similarities may be merely holdovers from the common ancestor of all three forms, while chimps and humans shared an intermediate common ancestor after the gorilla lineage split away. Paleontological evidence is sparse in Africa between 12 and 5 Ma, but it is possible that *Samburupithecus* (or *Graecopithecus*) represents a species near the base of that three-way split or already on the gorilla line. Their ages of 10–9 Ma fit reasonably well with the “molecular clock” estimates of 10–7 Ma for that divergence. The human-chimp split is molecularly estimated at

8–5 Ma or even less, but the human fossil record refutes a date younger than perhaps 5 Ma at the minimum.

Yves Coppens developed a hypothesis called the East Side Story to explain the history and distribution of African apes and early humans. Modern chimpanzees and gorillas occur only to the west of the great East African rift valleys, in areas that are now mainly rainforest, whereas the first clear human fossils are concentrated in sparsely forested rift valley localities and, rarely, to the east. Thus, Coppens suggests that an ecological-geographical division occurred during the late Miocene (8–6 Ma), with the apes being restricted to the west and early humans differentiating in more open country to the east of the western rift scarp. An *Australopithecus* jaw from Chad, 1500 mi (2500 km) west of the rift valley, weakens this hypothesis, but might represent a later migration.

Pliocene Homininae. *Australopithecus*, the first truly humanlike beings, appear in the fossil record in quantity some 4.5 Ma, during the early Pliocene.



Fig. 4. Cranium of adult (female?) *Australopithecus africanus* from Sterkfontein, South Africa, about 2.5 million years ago. (Courtesy of I. Tattersall)



Fig. 5. Cranium of adult (male?) *Paranthropus aethiopicus* from West Turkana, Kenya, about 2.5 million years ago. (Courtesy of A. Walker)

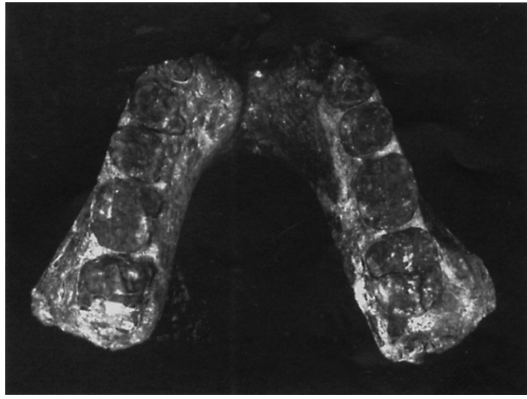


Fig. 6. Lower jaw of *Homo rudolfensis* from Uraha, Malawi, about 2.4 million years ago. (Courtesy of T. Bromage)



Fig. 7. Partial cranium of *Homo habilis* from Sterkfontein, South Africa, about 1.9 million years ago. (Courtesy of A. R. Hughes)

One partial jaw with a single tooth has been found that may be as old as 5 Ma, and another fragment with two teeth dates to about 4.5 Ma, but only in 1994 and 1995 were human fossils of this antiquity reported that were sufficiently complete to permit the naming of a new species. Pliocene humans have been grouped in various ways, but it now seems that four main types can be distinguished. Three of these, dating from 4.5–1 Ma, have often been assigned to the genus *Australopithecus* and can informally be termed australopiths; the fourth group includes early species of *Homo*, beginning about 2.5 Ma. The australopiths have previously been divided into gracile and robust varieties, but the former term really does not accurately describe the earliest species and thus is not used here. All australopith species appear to share a number of basic characteristics distinguishing them from living and fossil apes and also from later humans, although clearly linking them to the latter.

Such features include an apparently humanlike body form and upright posture, with relatively long legs; a foramen magnum placed rather forward under the skull; a large brain relative to body size; a pelvis

adapted to bipedalism, of a human if not fully modern type; and teeth of human form, especially with small canines in both sexes. The species of australopith also broadly share a smaller body size than modern humans with surprisingly little difference among the known forms. Estimates of body size based on analysis of weight-bearing joint surfaces and bone lengths

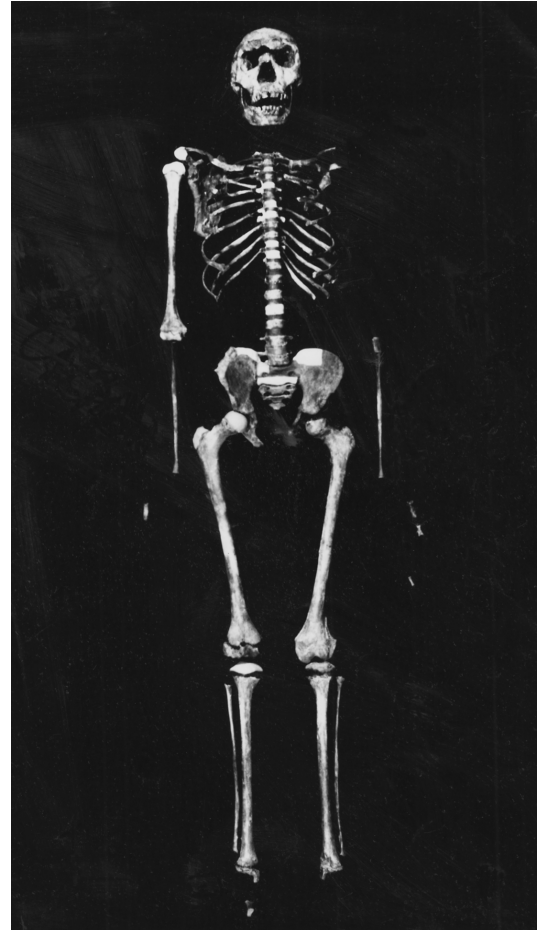


Fig. 8. Partial skeleton of adolescent male *Homo erectus* from West Turkana, Kenya, about 1.5 million years ago. (National Museums of Kenya)



Fig. 9. Lower jaw of *Homo erectus* from Dmanisi, Georgia, possibly about 1.7 million years ago. (Courtesy of E. Delson)

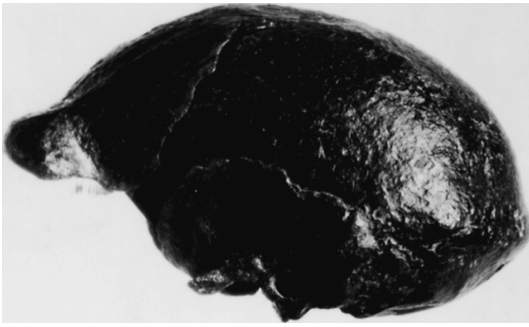


Fig. 10. Skullcap of Java *Homo erectus*, about 700,000 years ago. (American Museum of Natural History)



Fig. 11. Face of European "archaic *Homo sapiens*" from Arago, France, about 400,000 years ago. (J. Oster/MHP)

suggest average weights around 130 lb (59 kg), with females often under 77 lb (35 kg) and males over 155 lb (70 kg). This quite high sexual dimorphism is also typical of australopiths, as are back teeth that are large for the estimated body size, although the actual sizes and tooth proportions are among the features distinguishing the seven species from one another. In light of the diversity now recognized, many researchers are coming to accept a division into at least the two genera *Australopithecus* and *Paranthropus*, and one species has been placed in its own genus, *Ardipithecus*, but others continue to recognize only a single genus, *Australopithecus*. See AUSTRALOPITHECINE.

Distribution. The fossils of these early humans were first found in South Africa in 1924, but the most recent major discoveries and the best evidence of their age come from East Africa. The South African fossils come from five main sites, which are the remains of

ancient cave systems. The australopiths did not live in caves, but their carcasses may have been dropped there by leopards or other carnivores. In two sites especially, many fossils are known from a relatively short span of time (perhaps less than 100 thousand years ago, Ka), but the evidence for dating is not definite.

In 1959 Mary Leakey and L. S. B. Leakey discovered a nearly complete australopith skull at Olduvai Gorge, Tanzania; and colleagues dated it at about 1.75 Ma, far older than previously thought. Since then, American and joint American-French expeditions have found hundreds of human fossils in the Omo and Afar areas of Ethiopia, while a Kenyan team has worked around the shores of Lake Turkana (formerly Lake Rudolf), Kenya, and various studies have continued at Olduvai and nearby Laetoli. These regions have yielded smaller numbers of specimens at many separate subsites, but the age of each site can usually be estimated closely by potassium-argon and paleomagnetic dating. Also, many specimens are more complete and show less distortion than their contemporaries from South Africa. Until 1993, no definite examples of *Australopithecus* or *Paranthropus* were known outside these areas, although some claims have been made. The recovery of australopith specimens from Chad (and of early *Homo* from Malawi) suggests that new productive regions remain to be explored. It is not clear whether australopiths made stone tools, although they were probably collectors of plant foods, using wooden sticks and skin bags, and perhaps scavengers of small game animals.

Earliest humans. The oldest known probable human species, *Ardipithecus ramidus*, is known from a small group of fossils found at the Aramis locality in the Middle Awash Valley, Ethiopia. These fossils were recovered since 1993 from rocks just above a layer dated to 4.4 Ma, which also yielded animal and plant fossils suggesting a relatively wooded environment. The remains of *Ard. ramidus* include teeth, part of a skull base, and the nearly complete long bones of a forelimb, as well as nearly 100 pieces of a fragmented adult skeleton, including parts of almost all regions of the body; as of early 2001, this skeleton had not yet been described or illustrated. The elements described so far document a mosaic pattern combining features similar to those of younger humans (for example, the anterior position of the foramen magnum and nearby structures, implying upright posture and presumably bipedalism; partial reduction of the canines combined with partial transformation toward an incisorlike shape) with others reflecting retention of apelike conditions (for example, thin enamel covering on molars and incisors; lack of a second cusp, or metaconid, on the lower anterior premolar; relatively large size of canines; and apelike shape of the lower anterior deciduous premolar or "milk molar"). It has been suggested that their presence in a wooded environment implies that australopiths may have differentiated from apelike ancestors in forests rather than open savannahs. But an alternative

view might be that this species represents a “failed” human lineage, one which returned to the forest and secondarily developed thinner enamel convergently with African apes.

The remaining components of the *Ard. ramidus* mosaic are all reasonably interpreted as ancestral conditions, to be expected in an ancient human ancestor. Analysis of the partial skeleton should permit determination of the locomotor abilities of this species and of the need for this distinct genus. It is not yet clear whether the still older but more fragmentary fossils from Lothagam and Tabarin (Kenya) can be placed within the same species as those from Aramis, but the Tabarin jaw was prematurely named *Aus. praegens*, a species name which would have to be applied to the Aramis specimens should they prove conspecific.

Slightly younger hominin fossils named *Aus. anamensis* have been found since 1994 at sites in the southern Lake Turkana region of Kenya. From Kanapoi, in a layer dated to 4.2–4.1 Ma, come several jaws that differ only slightly from other *Australopithecus* species. A partial knee joint from a younger layer, and a partial elbow joint that was collected in 1965, look relatively modern and confirm upright walking around 4 Ma. It seems likely that *Aus. anamensis* may be closer to the ancestry of later species than is *Ard. ramidus*.

Fossils from sites in Ethiopia and Tanzania reveal far more details about a still younger species, *Aus. afarensis*. The most complete material is known from Hadar, about 50 km (30 mi) north of Aramis, where deposits yielded fossils dating between 3.4 and 2.9 Ma. In 1974 a partial skeleton was found and identified as a female by its pelvic bones (and small size compared to other fossils) and nicknamed Lucy. This individual would have stood only 3.5 ft (106 cm) tall and weighed perhaps 65 lb (30 kg). The leg bones of this skeleton indicate that Lucy’s legs would have been rather short for a modern human of comparable body weight, but they were in proportion for her estimated stature; this observation supports other evidence that most australopiths were more robustly built than modern humans. Larger males, perhaps 130–175 lb (59–80 kg), are known from more fragmentary remains, and a skull (not found with Lucy) has been reconstructed from isolated parts.

A more complete skull was found at Hadar in 1993 which substantiates most of the inferences drawn from the earlier reconstruction. Mandibles and postcranial elements from Maka (across the Awash River from Aramis) and Laetoli (Tanzania) dating around 3.4–3.7 Ma confirm the sexually dimorphic but taxonomically unified nature of the species, while a frontal bone from Belohdelie (3.8 Ma, near Maka) and teeth from the Lake Turkana Basin (3–2.7 Ma) define its temporal range.

Lucy’s pelvis and leg bones, as well as remarkably preserved footprints from Laetoli, clearly demonstrate that upright bipedal walking was well developed by 3.6 Ma, along with a brain somewhat larger than in modern apes of similar body size. Brain size

in *Aus. afarensis* might have been between 350 and 450 ml, as compared to 365 ml in a 100-lb (45-kg) chimpanzee, 500 ml in a 300-lb (135-kg) gorilla, or 1400 ml in a 150-lb (67-kg) living human. Arguments as to the priority of brain expansion or walking ability in human evolution thus have yet to be resolved. *Australopithecus afarensis* combines both of these advanced, human characteristics with numerous other features reminiscent of later Miocene hominids and modern apes. The lower face is rather projecting (prognathic), the canines project slightly beyond the level of the neighboring teeth, the anterior lower premolar sometimes has only one major cusp, the tooth row is elongated and nearly parallel-sided, and the forehead is low and retreating. However, the mastoid region (below and behind the bony ear opening in the skull) projects inferiorly more than in either living apes or modern humans.

The youngest of the early australopiths is actually the first to have been recognized. *Australopithecus africanus* was named by R. Dart in 1925 on the basis of a juvenile specimen from Taung (South Africa). It appears to have lived from 3 to 2.3 Ma, but so far it is known only from four sites in South Africa; by far the most numerous specimens come from the middle levels (Member 4) of Sterkfontein, dated about 2.8–2.6 Ma. It may have stood 4–5 ft (120–150 cm) tall, weighed 65–150 lb (30–68 kg), and had an average brain size of some 450 ml. The skull seems more lightly built than in *Aus. afarensis*, with a rounded vault but more projecting face. The teeth are more humanlike as well, especially in the presence of two cusps on all anterior lower premolars (like all younger hominins) and less projecting canines. Although the absolute tooth size of *Aus. africanus* is nearly equal to that of small gorillas, the proportions are human, with a smooth decrease in size from molars through incisors. Thus, it was perhaps little changed from its putative ancestor, but those few changes are roughly in the direction of later humans. Some workers have gone so far as to suggest including this species in the genus *Homo*, but pending clearer evidence for its phyletic position, that step is not taken here.

In 1995 researchers described bones of a partial foot from the lower levels (Member 2) of Sterkfontein, contemporaneous with *Aus. afarensis*. These bones were interpreted as indicating a foot adapted to grasping, and perhaps tree climbing, rather than only to bipedal walking. In late 1998 the find of additional parts of the same skeleton was reported, including both legs, some arm bones, and what appears to be most of the skull. All of these elements must be fully removed from the encasing rock and reconstructed before they can be accurately analyzed, but much more of the skeleton may be preserved, in which case it might surpass Lucy in its completeness. Preliminary paleomagnetic correlation suggests that the specimen may date between 3.6 and 3.2 Ma, and it has not yet been determined if it should be identified as *Aus. africanus*, *Aus. afarensis*, or a new species of australopith.

In 1999, Ethiopian and American researchers described *Aus. garhi* from deposits in the Awash valley of Ethiopia, dated about 2.5 Ma. A partial face and uncertainly associated limb bones were said to represent a new species close to the origin of *Homo*, but other workers have suggested alternative interpretations, such as that these fossils represented a late population of *Aus. afarensis* or female individuals of *Par. aethiopicus*.

Robust varieties. Until 1986, robust australopiths were known from two forms, usually accepted as distinct species and increasingly given generic status as *Paranthropus*: *P. robustus* in South Africa and the more extreme *P. boisei* in East Africa. These species lived between about 2.3 and 1.4 Ma (the age of *P. robustus* is known with less certainty, perhaps 1.9–1.6 Ma) and are distinguished from the other australopiths by their larger size and craniodental specializations. They may have been 4 ft 6 in. to 5 ft 9 in. (135–175 cm) tall, weighed 80 to 190 lb (36 to 86 kg), had a heavy muscular body build, and a brain size of about 525 ml. The skull is robust, with deep cheekbones and thick lower jaw and often a slightly raised sagittal (midline) crest in the middle part of the skull roof from back to front. These features indicate strong chewing muscles and perhaps a diet of tough foods. The teeth themselves are distinctive: the back teeth (molars and premolars) are large to huge; the front teeth (incisors and canines) are quite small and run nearly straight across the front of the mouth. This difference from other hominins, including apes (which generally have large front teeth and small back teeth), combined with a low forehead and a concave, nearly upright face, further suggests adaptation to powerful chewing. The anterior teeth were probably used as much for grinding as for cutting.

A small group of more ancient fossils presents a combination of many of these *Paranthropus* features plus others that appear to be holdovers from an *Aus. afarensis*-like ancestry. Here, large molars lie behind sockets for rather large incisors and canines; a concave upper face with low forehead sits above a projecting snout; and the sagittal crest extends back to meet the large nuchal (neck muscle) crest. Brain size was small, near 400 ml. This combination indicates that the creature emphasized both large front and back teeth, occupying an evolutionary position intermediate between *Aus. afarensis* and the two previously known robust australopiths. It is also intermediate in time, ranging from 2.7 to 2.3 Ma in age. Based on the apparent equivalence of a well-preserved cranium and partial mandible to a toothless lower jaw found in the late 1960s, this species has been called *P. aethiopicus*.

Australopith relationships. The widely accepted view before 1978 was that *Aus. africanus* represented the common ancestor of the robust forms and *Homo*. The discovery of *Aus. afarensis* led to its placement as the basal hominin, with several alternative views of its descendants. In the 1990s the newly recovered *Aus. anamensis* was usually ranked

as a still older common ancestor, with *Ard. ramidus* held off to the side, in suspense. Early analyses of *P. aethiopicus* considered it as close to the common ancestor of *P. boisei* and *P. robustus*, but some later studies argued that the three robust species were “only” linked by their common possession of a heavily built chewing apparatus, which might have evolved convergently in two or more disparate lineages. These studies proposed (as had earlier workers on other grounds) that *Aus. africanus* might have been ancestral to *P. robustus* in South Africa or that *P. aethiopicus* might have been an early experiment unrelated to later robust species. Such views seem poorly founded, for if the three robust species are in fact linked by the adaptive complex of “heavy chewing” composed of a number of closely similar elements in each form, it is far more likely that they developed from a single common ancestor than that they were convergently comparable but unrelated. Here the robust clade or lineage is recognized as an evolutionary unit, the genus *Paranthropus*, which was thus long-lived but seems to have had no later descendants.

No known australopith clearly shows features which link it to later human species of the genus *Homo*, but many workers have suggested that *Aus. africanus* might represent the closest approach to such an ancestry yet recovered. However, some have thought that several shared features of the skull point to a common ancestry of *Homo* and *Paranthropus* to the exclusion of *Aus. africanus* (see also below). If *Aus. afarensis* is eventually determined to have been (close to) the common ancestor of both *Paranthropus* and *Homo* (plus *Aus. africanus*?), then it will probably be wise to provide a new genus name for *afarensis* (and also *anamensis*), but for the moment all three species are retained in the genus *Australopithecus*. See AUSTRALOPITHECINE.

Early Homo. The only other genus of the Hominini is *Homo*, true humans, into which all later forms are placed. The identification of the earliest specimens of *Homo* is a subject of debate among paleoanthropologists. In the late 1970s the scientific pendulum had swung back to an idea proposed on less secure grounds by L. S. B. Leakey and colleagues in 1964. They named the species *H. habilis*, based on several finds from Olduvai. Especially significant was the discovery of the remains of a juvenile’s lower jaw, with teeth much like those of *Aus. africanus*, and its partial skull, with an estimated cranial capacity of about 685 ml, dated about 1.8 Ma. After much argument over the “reality” and distinctiveness of the new species, it was made clear from additional finds at Olduvai, Lake Turkana, and probably an upper level at Sterkfontein that a relatively small-brained (510–700 ml) and small-toothed *Homo* was present in the 2.0–1.5 Ma time period. This was thought to be younger than *Australopithecus*, older than (most) *H. erectus*, and contemporaneous with *P. boisei*. A partial skeleton discovered at Olduvai in 1986 has similar teeth and an estimated body size comparable to Lucy; this was reported as remarkable but should

have been expected, given the similarity in skull size to those of the smaller australopiths.

Several fossils, especially from the Lake Turkana region, appeared to represent a different “morph” or structural pattern. These were typified by skull KNM-ER-1470 (its catalog number in the Kenya National Museum) which has a brain size of about 750 ml, a high rounded vault and probably large teeth (the crowns are broken off), but a relatively protruding face. This (and a few more fragmentary specimens) were suggested to represent male individuals, while the far smaller group were females. Leg bones suggesting a size of 4 ft 9 in. (155 cm) and 110 lb (50 kg) were at first thought to go with these cranial parts, but it later became clear that early *H. erectus* overlapped in time with the more archaic fossils and had comparable leg bones. Unassociated postcranial elements have had to be set aside pending the recovery of such bones clearly linked to crania.

These two sets of early human fossils pose an acute problem in paleoanthropology: either *H. habilis* had greater sexual dimorphism (especially in brain size) than any known primate, or two (rather homogeneous) species were masquerading under a single name, with the smaller set (the supposed females) most similar in facial morphology to both *Aus. africanus* and later *Homo*. There are at least two opposing solutions to this problem. One view holds that all the known specimens from Olduvai, the Turkana Basin, and South Africa represent the single species *H. habilis*, a larger-brained and bigger creature than *Aus. africanus*, but one with essentially the same dental apparatus—another example of mosaic evolution. It would have had as much sexual dimorphism as did *Aus. afarensis*, perhaps more than in modern gorillas or orangutans, in both form and size of teeth, face, and brain.

Another suggestion is that the known variation in brain size and other aspects of craniofacial morphology is too great to represent merely the sexes of even a strongly dimorphic species. All of the Olduvai fossils, the smaller Turkana region specimens and some from South Africa, are recognized as *H. habilis*, while the 1470 specimen and other larger (non-*Paranthropus*) individuals from Turkana are considered as *H. rudolfensis*, a name first applied to the 1470 specimen in the 1980s without sufficient justification. This two-species view is gaining adherents and is accepted here. In 1992 a partial mandible was found at Uraha in Malawi that is extremely similar to a Turkana *H. rudolfensis* specimen. Not only is Malawi geographically intermediate between the known eastern and southern African site regions, but preliminary age estimates based on associated fossil mammals place the find at about 2.5–2.3 Ma, making it one of the oldest representatives of the genus *Homo*. A temporal bone (the lower middle part of the cranium, where the mandible hinges and the ear is housed) of similar age from central Kenya might also represent this species, and some authorities have even suggested that a few Olduvai specimens belong here as well.

Although australopiths were fully bipedal, limb bones attributed to *H. habilis* and possibly to *H. rudolfensis* indicate a wider pelvis to permit the birth of larger-headed (because larger-brained) infants, which resulted also in the leg bones themselves appearing more modern. It is this combination of apparently significant change in the two major human adaptations of locomotion and intelligence that leads most authors to classify these species as *Homo*, but some have placed both of them in *Australopithecus*.

It is also not clear which species of early *Homo* might have been ancestral in turn to *H. erectus*. Both early forms have been found in the 2.0–1.6 Ma time range in the Turkana Basin, where they overlapped with *P. boisei* and *H. erectus*, but *H. habilis* apparently persisted in the Olduvai region until at least 1.6 Ma, without *H. erectus* or *H. rudolfensis*. But neither *H. habilis* nor *H. rudolfensis* as known are morphologically very close to early *H. erectus*. The former species differs not only in small brain and body size but also in limb proportions, although its facial morphology is potentially acceptable in an ancestor of *H. erectus*. The brain of *H. rudolfensis* is large, as might be expected in an ancestor of *H. erectus*, but its teeth are large and distinctive, its face is unique, and its limb bones have not been satisfactorily identified. One wonders if there might not be an as yet undiscovered early species of *Homo* which combined smaller teeth and face with a larger brain. Perhaps the upper jaw from Makaamitalu (found in 1994 high in the Hadar sequence) dated about 2.35 Ma might be a step toward fulfilling this prediction.

Evidence of archeological activity has been found with these specimens, mostly flakes and choppers or “pebble tools” of the Oldowan stone-tool industry (see **table**), and also the remains of small animal prey. It is not possible to tell which types of humans made the tools, but at present the oldest evidence is from Ethiopia, in the Hadar region and the Omo valley, about 2.5 Ma. The close time and space concordance of Oldowan tools and early *Homo* suggests that at least one of these species was the actual toolmaker; whichever it was may have been an active hunter of small game, collector of plant and insect food items, and scavenger of larger mammals. See PALEOLITHIC; PREHISTORIC TECHNOLOGY.

Homo erectus. While *H. habilis* and *H. rudolfensis* apparently were short-lived and relatively rare African species, their likely successor, *H. erectus*, was common, widespread, and long-surviving. The first fossils were found in Java in 1893 and termed *Pithecanthropus erectus*. Each of the later finds in China and across Africa were given distinctive generic and specific names, but all are now usually considered local variants or subspecies of the single species *H. erectus*. The major anatomical characteristics of this form are the following: a body of nearly modern form and proportions below the neck, topped by a low and slightly elongated skull with cranial capacity averaging 1100 ml (with a range of about 800–1300 ml), smaller teeth in a less projecting face than *Aus. africanus* or *H. rudolfensis*,

Old World archeological variants before 10,000 years ago			
Technological		Paleolithic subdivisions	Selected regional industries*
Mode	Description		
4	Blade cores, to produce scrapers, points, burins; bone harpoons, art	Late (Upper) Paleolithic	Later Stone Age [sub-Saharan Africa, >40 to <5 Ka (mode 5, microlithic)] Upper Paleolithic of Europe, including Perigordian, Solutrean, Magdalenian Aurignacian (Europe, SW Asia?, >40 to 27 Ka)
3	Widespread use of prepared cores to obtain variety of flake forms, used as scrapers and projectile points	Middle Paleolithic	Chatelperronian (western Europe, 36 to 30 Ka) Aterian (northern Africa, 100 to 30 Ka) Mousterian (many variants; western Eurasia and northwestern Africa, 200 to 35 Ka) Middle Stone Age (many variants; sub-Saharan Africa and southern Asia, 250 to 40 Ka)
2	Large bifaces (handaxes and cleavers), also simple cores and retouched flakes	Early (Lower) Paleolithic	In late stages, use of prepared cores and wooden throwing spears Acheulean (Africa 1.5 to <0.2 Ma; Europe, western/southern Asia, 0.4 to <0.2 Ma)
1	Simple cores and "casual" flakes	Early (Lower) Paleolithic	Zhoukoudian (China, 1 to 0.25 Ma) Various (Europe, >1 to <0.4 Ma) Oldowan (Africa, 2.5 to <1.5 Ma)

*Ka = thousand years ago; Ma = million years ago.

large solid brow ridges, thick cranial bones, and no chin.

African populations. The earliest specimens are probably from East Africa, dating to as much as 1.9 Ma. According to some researchers, the earlier African forms should be termed *H. ergaster*, but that division is not followed here. These populations might have continued to make simple Oldowan artifacts, as no other form of stone tools is known at this time. There is evidence of the use of fire as early as 1.8 Ma and in scattered sites thereafter. Acheulean bifaces (handaxes and cleavers) appear by 1.5 Ma, though only rarely in direct association with *H. erectus* fossils; evidence for group hunting of large animals is rarer still and has been questioned by some scholars. In addition, the eventual extinction of *P. boisei* in this time interval may have been caused by direct or indirect competition with the more advanced *H. erectus*.

The most important African *H. erectus* find of recent decades is a mostly complete skeleton of an adolescent male (its sex judged by pelvic bones as well as relative cranial robusticity), recovered on the west side of Lake Turkana in 1984. Judging by the pattern of dental eruption, he was probably 9–10 years old at death, although an age of 11–12 has also been suggested. One still ambiguously answered question is whether this species underwent the adolescent growth spurt which occurs in modern children of 12–14. Using formulas based on limb bone lengths of modern human adults and children, it was estimated that the “Turkana boy” might have reached an adult height of nearly 6 ft (183 cm) and a body weight of 150 lb (68 kg). Moreover, his body shape would have been slender or elongate, much as seen in living people of the same region, as a result of similar adaptation to a warm and dry climate. The development

of brow ridges and other cranial structures in the adolescent male and a larger skull from Olduvai contrasts markedly with other Turkana skulls, indicating the persistence of strong sexual dimorphism.

Eurasian representatives. *Homo erectus* (presumably as a result of increasing population size) spread into Eurasia through the Middle East, perhaps earlier than has previously been thought. Dates for some long-known Javanese fossils suggested ages around 1.7 Ma, and a lower jaw and two crania associated with Mode 1 (Oldowan-like) tools from Dmanisi (Georgia) reported in 1995 and 2000 may date to 1.8–1.6 Ma. Mode 1 and early Mode 2 artifacts from Israel (as yet not found with human fossils) are slightly younger. A similar age was claimed for some southern Chinese fossil fragments in late 1995, but several workers have suggested that these represent apes rather than early human teeth. All of these age estimates have been questioned, moreover, and further confirmation is required. Nonetheless, *H. erectus* must have been the first human species to leave Africa in large numbers.

Fossils of this species may extend in Asia to nearly 200,000 years ago, mostly associated with fauna from the warmer intervals in this time of alternating glacial climate. From central Java, Indonesia, come a series of cranial and dental remains spanning from perhaps 1.7 Ma to possibly 30 Ka. The earlier range of time yielded several groups of skulls known popularly as Java man, including the first found members of this species; these specimens (and also those from China) tend to be more derived or extreme in their morphology than most African specimens, including the common presence of an especially thickened vault bone in the midline from front to back, known as a sagittal keel. A dozen younger partial skulls from Ngandong, Java, known as Solo man lack the face (as is true of

most of the earlier specimens) and have been said to show evidence of ritualized brain eating. These specimens were long thought to be quite recent in age and placed in *H. sapiens*, but later study indicated close similarity to earlier Indonesian *H. erectus*, as they are now classified. Their age remains uncertain, with some evidence suggesting a range between 400 and 100 Ka, while the dating attempt in 1996 arrived at the astoundingly young age of 50–25 Ka, which has been questioned on several grounds. If indeed a correct date for these fossils, this would be the first demonstration of the coexistence of *H. erectus* with anatomically modern humans.

In 1999, a partial cranium of *Homo erectus* was recognized in a New York City shop selling natural history specimens. Originally of unknown origin, it was determined that it had been found in Indonesia some years earlier and illegally removed from that country; the shop's owner, Henry Galiano, returned it to Indonesian authorities. The specimen presents the highest forehead of any *H. erectus* and shows other differences from most Indonesian specimens which place it in some ways intermediate between them and more modern humans; unfortunately, its age is unknown.

The first Chinese *H. erectus*, called Beijing (Peking) man, was found at Zhoukoudian, near Beijing, where they occupied a large cave during most of the period between 500 and 250 Ka. Additional fossils of this form are known from Yuanmou and perhaps Wushan in the southwest, Lantian and Yunxian in the center, and Hexian and Tongshan (Nanjing) in eastern China; some may be as old as 1–1.2 Ma. Archeological remains found with these fossils are of the simple, Mode 1 variety, with only a few isolated finds of Mode 2 bifaces anywhere in eastern Asia. No stone tools are unambiguously known from layers with human fossils in Java. Two current interpretations of this difference from the contemporary archeological pattern in Africa are either that most East Asian stone tools are simple because they were used mainly to work bamboo into more precise (but now decayed) tools, or that the earliest humans had arrived in East Asia before the Acheulean was “invented” in Africa and thus continued to make Mode 1 tool kits.

Although there have been claims, no definite *H. erectus* fossils are yet known from Europe, nor are archeological remains or more modern humans unambiguously documented there as older than about 800,000 years. The Dmanisi specimens from Georgia are the most ancient human representatives in the region, but the lack of further remains over the succeeding million years may indicate that *Homo* required further physical or cultural adaptations in order to survive in Europe proper.

Premodern *Homo sapiens*. It has been suggested that the increased rigor of the glacial climate in Europe at this time was the impetus leading to the evolution of humans who seem to be physically more “modern” in several ways than Afro-Asian *H. erectus*. These people are often termed early or archaic *H. sapiens*, or sometimes placed in their own species,

H. heidelbergensis. This view was acceptable so long as the most ancient African representatives of this group were poorly dated or younger, but studies in the later 1990s suggested some modification. The earliest human fossils in Europe were thought to date to about 500 Ka in England (a tibia from Boxgrove) and Germany (the mandible from Mauer near Heidelberg found in 1908). The long-known human fossils from Tighenif (previously called Ternifine, in Algeria), dated to 800–700 Ka, were transferred out of *H. erectus* by some workers because they present at least one derived feature of the lower jaw. Moreover, the partial skull from Bodo (Ethiopia) was also dated older than 600 Ka, and similar South African fossils were estimated to be of comparable age. These dates suggested that the earliest representatives of “archaic *H. sapiens*” may have lived in the northern half of Africa and perhaps evolved there from local *H. erectus* populations.

Then, in 1995, fragmentary human fossils and associated stone tools from the older levels at Atapuerca (Spain) were dated to about 800 Ka, implying that archaic *H. sapiens* appeared at about this date all over the western Old World. These specimens were named *H. antecessor* in 1997, and it was suggested that they represented the common ancestor of all later human varieties. Meanwhile, in 1996, a cranium lacking the face was described from Ceprano, Italy, in a context suggestive of a date of about 700 Ka or more. A revised reconstruction claims strong similarity to *H. erectus*, otherwise unknown in Europe. Finally, in mid-1998, most of a cranium from Buya (Eritrea), dated about 1 Ma, was described as being intermediate between *H. erectus* and archaic *H. sapiens*.

All of these finds, combined with theoretical arguments about the best way to recognize and delimit species in the fossil record, have led to competing interpretations of the number of species of *Homo* known in the past million years. Some workers continue to place all post-*erectus* fossils in archaic *Homo sapiens*, sometimes recognizing a variety of temporal and geographic subspecies (such as the Neanderthals and anatomically modern humans). A few have gone so far as to include *H. erectus* within an over-enlarged *H. sapiens*. At the other extreme, some researchers accept between three and six species in the same time period: *H. antecessor*; *H. heidelbergensis* (either restricted to Europe or extended to Africa and even East Asia), *H. rhodesiensis* (for early African “archaics”), *H. neanderthalensis*, *H. sapiens* (restricted to anatomically modern humans), and perhaps others. A possible middle ground would be to (1) include the earliest of these African and European populations in one named group [for example, *antecessor*, or perhaps *mauritanicus* (the name originally given to the Tighenif fossils), as suggested by J.-J. Hublin]; (2) combine all post-500 Ka nonmodern European fossils in *neanderthalensis* (including *heidelbergensis* here); (3) group nonmodern African fossils younger than Tighenif in *rhodesiensis*; and (4) restrict *sapiens* to anatomically

modern humans worldwide. At least the last three groups, and perhaps also the first, could be recognized as subspecies of *H. sapiens* under certain theoretical models, and this interpretation is followed here. As yet, it is not possible to even suggest where this species may have originated from a *H. erectus* ancestor.

Early representatives of *H. s. neanderthalensis* and *H. s. rhodesiensis* occur in Europe and Africa between 500 (or even 600) and 250 Ka, thus contemporaneous with *H. erectus* populations in eastern Asia. They share somewhat larger brains (for body size), smaller teeth, more expanded facial sinuses and occiput (rear of the skull), but less robustness than in *H. erectus*. All these features are found in more extreme form in modern humans and in the late “classic” Neanderthals (see below). In most areas, these people still used Acheulean tools, but perhaps with greater efficiency. It is likely that these archaic *H. sapiens* spread gradually eastward across the Old World, replacing late-surviving populations of the broadly ancestral *H. erectus* everywhere by 200 Ka, when a poorly known (and here unnamed) variant occurs in northern China.

These three geographic variants (subspecies?) were not only distinct from *H. erectus* but also from each other to a greater degree than is true among living varieties or “races” of anatomically modern humans. In southern Africa, one cranium was found at Broken Hill, now Kabwe, Zambia (formerly Northern Rhodesia, hence the name Rhodesian man), and broadly similar specimens are known in South Africa (Saldanha and Florisbad), Tanzania (Ndutu), Ethiopia (Bodo), and Morocco (Salé and Thomas quarries). These people made Acheulean or equivalent Mode 2 tools and apparently hunted big game, between 650 and 250 Ka. Rare specimens from China appear to be younger, mainly dating to about 250–150 Ka. These include a nearly complete cranium from Dali, in central China, and a partial skull and skeleton from Jinniushan (or Yingkou), in the northeast, as well as scattered, less complete remains. All of these fossils, especially Dali, are quite similar to the African specimens just mentioned, as well as to some of the earliest European *H. s. neanderthalensis*. Other Chinese specimens, such as Maba (from the southeast), and the central Indian Hathnora (or Narmada) fossil, are partial crania which are both younger (perhaps about 150–75 Ka) and more derived morphologically, although not in the direction of either early anatomically modern people or the contemporaneous Neanderthals.

Neanderthals. The best known of the archaic varieties are the Neanderthals, from Europe and western Asia. It now seems likely that this group evolved locally in Europe from earliest *H. sapiens* via intermediate forms (“pre-Neanderthals” or “ante-Neanderthals”) such as those known from England (Swanscombe), Spain (Atapuerca), France (Arago, Montmaurin), Germany (Steinheim), and Greece (Petalona). They became adapted to the cold climates of glaciated Europe, with prototypical Neanderthal

anatomy well established by about 200 Ka. During the warm interval about 120 Ka, they may have spread into the Near East and central Asia. In the cold glacial phase between 110 and 35 Ka, “classic” (or extreme), cold-adapted Neanderthals were abundant in cold northern parts of western and central Europe, while less extreme forms (perhaps more like their immediate predecessors) inhabited areas to the south and east. They were essentially stocky humans, but had long, low skulls with a projecting occipital region, large faces, teeth, and brow ridges; and brains averaging 1500 ml in volume. Their limbs and trunks were heavily muscled, indicating great strength, but many bones were broken and healed during life. They made Mousterian tools (a variant of Middle Paleolithic or Mode 3 flake-based tool kits), often lived in caves or wooden shelters where they controlled fire, hunted big game, and had primitive religious beliefs, including burial of the dead with grave goods.

There is intense argument among paleoanthropologists as to how “modern” the Neanderthals were behaviorally, in terms of their stoneworking and hunting techniques and modes of foraging, whether planned or merely ad hoc. Such controversies feed back into the question of whether the Neanderthals are a distinct species or, as accepted here, a distinctive subspecies of *H. sapiens*. A related question is whether the Neanderthals were in any way ancestral to anatomically modern humans, especially of Europe. Recognition of a separate Neanderthal species implies an almost absolute reproductive isolation and lack of genealogical continuity, while the opposite is true for most interpretations of Neanderthals as members of *H. sapiens*. Here, however, another intermediate position is taken: *H. sapiens neanderthalensis* is considered to have been geographically and culturally isolated from early anatomically modern humans and their ancestors, two independent but closely related lineages evolving in parallel until they finally met, after which the former group soon became extinct. *See NEANDERTALS.*

Spread of modern humans. One of the major foci of recent paleoanthropological research is the clarification of the area of origin and early history of anatomically modern humans, *H. s. sapiens*. The skull of this form is characterized by a small, upright face; small teeth and brow ridges; chin; and high, rounded braincase. There are no specimens of this type known (or even hinted at) anywhere in the world earlier than about 150 Ka. But from about 150–100 Ka, in eastern and southern Africa, some fossils suggest the persistence of a “Rhodesian-like” morphology, while others (for example, at Kibish, in the Omo valley of Ethiopia, or at Djebel Irhoud, Morocco) are often considered to be nearly modern. Two somewhat younger sites in South Africa have produced the most important evidence. At Border Cave, a partial cranium and other fragments may date to nearly 90 Ka; they are clearly modern in form, but their date is questionable. The Klasies River Mouth caves, on the southern coast, have yielded a

sequence of layers with good dates and archeological context; the human remains dated about 100 Ka are scrappy but appear modern, with a chin, small brow ridges, and overall gracility. In combination, these remains and other, less complete fossils indicate that early moderns were living in sub-Saharan Africa by about 100 Ka. Archeological remains of comparable antiquity in South Africa and Zaire indicate that at least some of these people were making Mode 3 (MSA) tool kits with elements (such as bone harpoons) which do not appear in Europe until after 20 Ka. See EARLY MODERN HUMANS; PALEOLITHIC; PREHISTORIC TECHNOLOGY.

From such a possible sub-Saharan origin, anatomically modern *H. s. sapiens* may have spread across the Old World, differentiating into local races by 80–50 Ka. This view of human dispersal has received support from studies of the distribution pattern of human mitochondrial deoxyribonucleic acid (DNA) haplotypes (variants) and other genetic evidence. The majority of these studies suggest that the major dichotomy in modern human population genetics is between Eurasians and Africans. Such results fit well with the fossil evidence for African versus Eurasian divergence about 100 Ka. Moreover, dates on early anatomically modern remains from Israel (Djebel Qafzeh and Skhul) documented the presence of the ancestors of Eurasians outside Africa by about 110–90 Ka. This is especially intriguing because most Israeli Neanderthals have been dated to about 65–45 Ka, significantly younger than the early moderns. Even more complexity is implied by the near-identity of Mousterian tool kits associated with the Neanderthals of Europe and Israel (and farther east), the early moderns from Israel, and the “pre-moderns” from Jebel Irhoud (Morocco), but the implications of this cultural similarity are as yet unclear.

The youngest known Neanderthal skull, found in the late 1970s, comes from southern France and is associated with tools of the Châtelperronian industry, a Mode 3 or 4 variety previously thought to have been made by *H. s. sapiens*. This specimen dated to 34 Ka has been alternatively interpreted as the maker of these tools (possibly after contact with Late Paleolithic moderns); as evidence for direct Neanderthal ancestry of moderns; or as a Neanderthal “captive” of moderns who made the tools. In some cases, more fossils do not solve problems but create new ones. Sites in southern Spain and Portugal have yielded less complete Neanderthal fossils and Mousterian tools dated about 30 Ka, after which modern *H. s. sapiens* was the sole form of human to be found anywhere. One reason for the success of *H. s. sapiens* may have been their greater tool-making efficiency, as documented by the Late (or Upper) Paleolithic Mode 4 blade-and-burin industries. These people included large quantities of worked bone in their tool kits (using burins to carve and engrave the bone), constructed dwellings of wood or of already fossilized animal bone, hunted large game, fished with harpoons, and in general behaved much like their living descendants. In many parts of the world, they

also engaged in artistic pursuits, including carving small animal statues and perhaps calendars, as well as painting on the walls of rock overhangs and deep caves. See PALEOLITHIC; PREHISTORIC TECHNOLOGY.

In 1999, Portuguese and American paleoanthropologists described the remains of a 4-year-old child, buried near Lagar Velho, Portugal, about 24 Ka. The burial pattern and most of the child’s morphology indicated links to the Gravettian culture, made by Cro-Magnon people elsewhere in Europe at this time. However, features of the lower leg bone (tibia) and lower jaw (the cranium was crushed and being reconstructed as of early 2001) suggested similarity to Neanderthals. The describers hypothesized that this individual might have been the result of hybridization between Neanderthals and Cro-Magnons, but other researchers argued that the morphology was not that different from what could be expected in a robust anatomically modern child and that hybridization would have resulted in features intermediate between Neanderthals and moderns, not clear features of each.

In contrast to the “Out of Africa” view of human dispersal (based on the idea that modern humans evolved in sub-Saharan Africa more than 100,000 years ago from Neanderthal populations) hypothesis accepted here, a minority view (the “Multiregional” hypothesis) interprets the fossil record to document the nearly parallel origin of modern humans in different regions of the Old World from a *H. erectus* ancestry. Each regional variety is said to present morphological characteristics linking archaic to modern populations, while gene flow between regions kept the geographical varieties united in a single species at any one time. Most scholars reject the implication that Neanderthals, for example, were ancestral to modern Europeans, or Chinese *H. erectus* to modern north Asians.

Many names have been given to early modern humans, especially in Europe, but these indicate only minor differences. The term Cro-Magnon derives from several skeletons found in 1868 in Les Eyzies, France. They gave their name to a “race” said to occur either just in France or across most of Europe. In fact, Cro-Magnon people were already essentially Europeans, while early Africans are known from sites in eastern and southern Africa. Australasia was colonized over water after about 70 Ka, with important finds at Keilor and Lake Mungo. New World Indians certainly originated from Siberia, by means of crossing a land bridge over what is now the Bering Strait. Many human fossil remains are known in the Americas as far back as 12 Ka, but some dates as old as 35 Ka have been obtained on archeological sites, indicating that perhaps several crossings of the land bridge occurred. See EARLY MODERN HUMANS; PALEOLITHIC; PREHISTORIC TECHNOLOGY. Eric Delson

Bibliography. D. R. Begun, C. V. Ward, and M. D. Rose (eds.), *Miocene Hominoid Fossils: Functional and Phylogenetic Implications*, 1997; E. Delson (ed.), *Ancestors: The Hard Evidence*, 1985; E. Delson et al. (eds.), *Encyclopedia of Human*

Evolution and Prehistory, 2d ed., 2000; J. G. Fleagle, *Primate Evolution and Adaptation*, 2d ed., 1998; R. G. Klein, *The Human Career: Human Biological and Cultural Origins*, 2d ed., 1999; F. Schrenck and T. Bromage (eds.), *African Biogeography, Cli-*

matic Change and Early Hominid Evolution, 1999; A. Walker and R. Leakey (eds.), *The Nariokotome Homo erectus Skeleton*, 1993; B. A. Wood, *Koobi Fora Research Project*, vol. 4.: *Hominid Cranial Remains*, 1991.

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