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Human origins

The combined evidence from molecular systematics, comparative morphology, and primatology has established that the African great apes — gorillas and chimpanzees — are more closely related to humans than they are to the Asian orangutan and other extant primates. Since our closest primate relatives are restricted today to Equatorial Africa, it can be deduced (as Charles Darwin and Thomas Huxley did more than a century ago) that humans are descended from a last common ancestor that also lived in Africa. Using a "molecular clock" model, in which the time scale of genetic change is calibrated against the fossil record, and based on the degree of genetic similarity between humans and chimpanzees (we share about 98% of our genomes), scientists can infer that humans diverged from the African apes about 6-7 million years ago (Ma).

Paleontologists searching for the fossil remains of human ancestors or hominins (that is, the taxonomic group to which modern humans and all extinct members of the human lineage belong) have been extraordinarily successful in piecing together the early stages of human evolutionary history. The fossil evidence shows that a diverse group of primitive hominins, comprising at least six species belonging to the genera *Australopithecus* and *Kenyanthropus*, were present in Africa 4-2 Ma. After 2.5 Ma, following climatic and ecological changes, more specialized hominins appeared in Africa, better adapted to exploiting drier, more seasonal habitats. These new kinds of hominins, belonging to the genera *Paranthropus* and *Homo*, replaced *Australopithecus* and *Kenyanthropus. Paranthropus* eventually became extinct 1.4 Ma, leaving *Homo erectus* (sometimes referred to as *Homo ergaster*) as the sole surviving hominin in Africa, and this eventually gave rise to our own species — *Homo sapiens*.

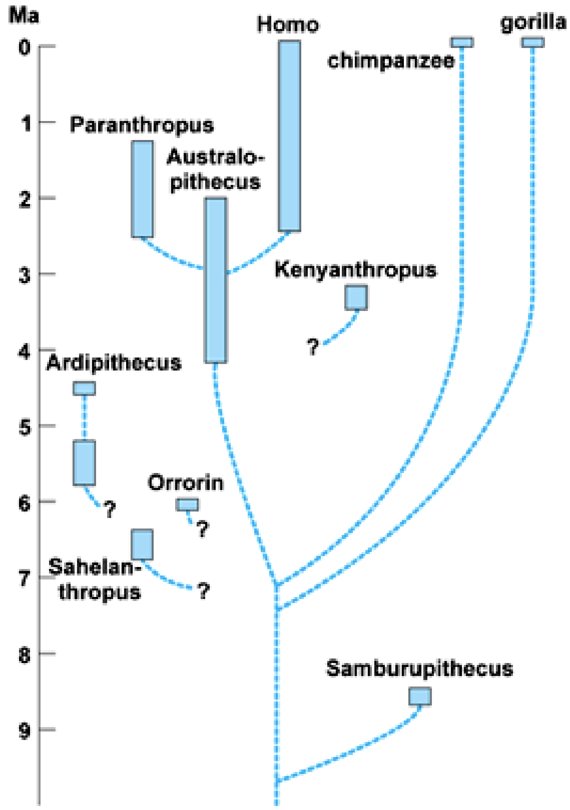
Australopithecus

One consequence of these discoveries is that scientists have been able to partially reconstruct the initial evolutionary steps taken by humans subsequent to their divergence from the last common ancestor with chimpanzees. Hominins 3-4 Ma, belonging to *Australopithecus*, were much more apelike than modern humans in many regards, but they had already acquired a suite of specialized characteristics unique to humans: (1) There is a slight increase in relative brain size (judging from the capacity of the braincase of the cranium, which is large in relation to that of chimpanzees, but less than one-third of an average modern human braincase). (2) The upper and lower canines are reduced in size compared with great apes and have a tip-to-tip bite pattern, functionally more similar to incisor teeth (whereas great apes have large tusklike canines, in which the upper canine slices down the outer side of the lower canine and the first lower premolar so that with wear they maintain sharp edges), and the canines are much less sexually dimorphic (that is, the sexes have canines that do not differ much in size, as in humans, whereas in all great apes the canines of males are much larger and more projecting than those of females). (3) The skeleton exhibits numerous distinctive specializations, especially of the hip, hindlimb, and foot, indicating that *Australopithecus*, when on the ground, traveled in an upright posture on two legs, similar to the striding bipedal gait of modern humans (whereas extant great apes are more specialized for arboreal activities, and primarily move along the ground quadrupedally, using all four limbs).

Fossil hominids

However, pertinent fossils from 5-7 Ma, the crucial time period for documenting the earliest representatives of the human lineage, have proved frustratingly elusive. Fossil hominids (the taxonomic group to which the great apes and humans belong) are extremely rare in Africa during the late Miocene (10-5 Ma). In fact, the fossil record of chimpanzees and gorillas, in contrast to that of humans, is entirely unknown. A large hominid, *Samburupithecus*, known only from a single upper jaw fragment from the site of Namurungule in Kenya (dated to 8-9 Ma), may represent a stem member of the African ape-human lineage. Until recently, a few isolated teeth of fossil hominids from the late Miocene sites of Lukeino and Lothagam in Kenya (dated at 5.0-6.5 Ma) were all that were available to document the earliest known occurrence of the human lineage prior to 5 Ma, but the remains were too fragmentary to be confident about their phylogenetic affinities or tell us much about their anatomy. Then, beginning in the mid-1990s, intrepid paleontologists working in Ethiopia, Kenya, and Chad made some remarkable discoveries that have helped to fill this critical gap in the fossil record (see illus.).

Fig. Evolutionary tree showing the relationships between humans, African great apes (chimpanzees and gorillas), and fossil hominids from the late Miocene onward. Bars depict the known time range of each genus. Broken lines represent inferred relationships. Question marks indicate uncertain relationships.



Ardipithecus ramidus

In 1994, Tim White and colleagues described important new fossil hominids from the early Pliocene site of Aramis in the Middle Awash region of Ethiopia. The specimens consist of a mandible fragment of an infant, an associated dental series, some isolated teeth, cranial fragments, and several bones of the forelimb. The material, reliably dated to 4.4 Ma, was described as a new genus and species of hominin—*Ardipithecus ramidus*. White and colleagues suggested that *Ardipithecus* was the earliest known hominin and a member of the stem group from which all later hominins were derived. *Ardipithecus* is certainly more primitive than *Australopithecus*, but it does share several specialized features that link it with these later hominins. For example, the canines are relatively small and more incisiform, and they exhibit reduced sexual dimorphism compared with those of great apes. *Ardipithecus* also has a more forward-positioned foramen magnum (the large aperture in the base of the cranium that connects the spinal cord and brain), and this indicates perhaps a more upright posture than is typical of extant apes. Unfortunately, hip and hindlimb bones, which are critical for confirming not *Ardipithecus* was bipedal, have not yet been described from the site.

More recently, Yohannes Haile-Selassie reported *Ardipithecus* specimens from several sites in the Middle Awash that are significantly older than those from Aramis, being dated to 5.2-5.8 Ma. These finds share the same tendency toward small, incisiform lower canines as the Aramis material, but since they differ in other details of their dental anatomy, Haile-Selassie recognized them as a separate subspecies, *Ardipithecus ramidus kadabba*. One of the new specimens is a toe bone that is strongly curved as in apes, but the joint surface for articulation with the metatarsal is orientated in a fashion that resembles that seen in later bipedal hominins.

Orrorin tugenensis

In 2000, a French-Kenyan team directed by Brigitte Senut and Martin Pickford resumed work at sites in the Lukeino Formation of the Tugen Hills of Kenya that had previously yielded an isolated tooth of a hominin dated to 6 Ma. They recovered additional finds that formed the basis for the description of a new genus and species of hominin—*Orrorin tugenensis*. The teeth are generally similar to those of middle and late Miocene apes from Africa and Eurasia, with no dental specializations that link the species uniquely with hominins. Although the forelimb bones suggest that *Orrorin* was a good arboreal climber like modern apes, Senut and colleagues have argued that the structure of the upper part of the femur (the thighbone) indicates that it was a terrestrial biped. The discoverers suggest that *Orrorin* is a direct ancestor of *Homo* with *Australopithecus* being an earlier evolutionary offshoot, whereas *Ardipithecus* is relegated to the ancestry of the African great apes. Critics, however, question the interpretation that *Orrorin* was bipedal, preferring instead to view it as an ape, possibly a primitive member of the African ape-human lineage.

Sahelanthropus tchadensis

The most recent, and arguably the most spectacular, contender for the title of the earliest hominin is *Sahelanthropus tchadensis* from the wind-swept deserts of northern Chad in central Africa. The fossils, from the late Miocene locality of

Toros-Menalla, dated to 6-7 Ma, were recovered in 2001-2002 by a team of scientists led by French paleontologist Michel Brunet. The best specimen, a crushed but relatively complete cranium, is characterized by a short face, an ape-sized braincase, widely spaced eye sockets, a broad nasal aperture, a thick bony bar that runs across the top of the eyes (as in gorillas, but even more pronounced), and a small crest along the midline of the rear of the cranium for the attachment of large chewing muscles. The teeth of *Sahelanthropus* are generally apelike, although it does have relatively small canines with tip-to-tip wear as in later hominins. Unfortunately, no postcranial bones of *Sahelanthropus* have been recovered, so it is not possible to deduce anything about its locomotor behavior. Brunet and colleagues proposed that *Sahelanthropus* is the oldest and most primitive known hominin, very close to the divergence of the human and chimpanzee lineages, although other scientists have suggested that it may be a stem member of the African ape-human lineage.

Conclusion

It is evident from preliminary assessments of the evolutionary relationships of these new fossil finds that it will take some time to resolve ongoing debates about their hominin status. Part of the difficulty is that the further back in time the human lineage is traced, the fewer humanlike specializations would have been accrued by human ancestors, and these could well have been quite subtle anatomical and behavioral shifts initially, not easily recognizable based on fragmentary fossils. Nevertheless, the recent fossil hominid remains discovered from the late Miocene and early Pliocene of Africa certainly offer tantalizing clues to suggest that aspects of their anatomy foreshadow the more specialized pattern seen in later hominins. Even so, given the fragmentary nature of the available fossil record and the inherently mosaic fashion in which characters evolve, it is possible that at least some of these contenders may eventually turn out to be fossil apes rather than hominins. Regardless of the final outcome, researchers agree that these exciting discoveries contribute an important new dimension to the understanding of early hominid diversity, one that will profoundly influence the way in which scientists perceive and interpret the critical events and factors that led to the origin and subsequent divergence of the human lineage.

See also: Australopithecine; Early modern humans; Fossil apes; Fossil humans; Physical anthropology

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