

By P. Andrews and E. Delson

REPRINTED FROM:

*Encyclopedia of Human Evolution and Prehistory*, 2nd ed; E. Delson, I. Tattersall, J. A. Van Couvering and A. S. Brooks, eds. Garland: New York, 2000

WITH THE COMPLIMENTS OF:

Eric Delson  
Department of Vertebrate Paleontology  
American Museum of Natural History  
New York, NY 10024

### Hominoidea

Superfamily to which apes and humans belong. It can conveniently be divided for modern forms into the lesser apes, Hylobatidae, and the great apes and humans, Hominidae. Little is known about the evolution of the hylobatids, but the divisions within the hominids are better documented. Within this group, the orangutan was the first to branch off from the others, leaving a group comprising the African apes and humans, here called the Homininae. Thus, the nearest living relatives to humans are either or both of the African apes, but it is not clear yet whether chimpanzees and gorillas are more closely related to each other or whether one of them is more closely related to humans.

### Hominoid Origins

By comparing all of the living species of hominoid, we can make inferences about the morphology of their common ancestor. These inferences are based on the likelihood that if all or most of the living species possess the same character or state, then that character or state was probably also present in their common ancestor. The alternative is to suppose that

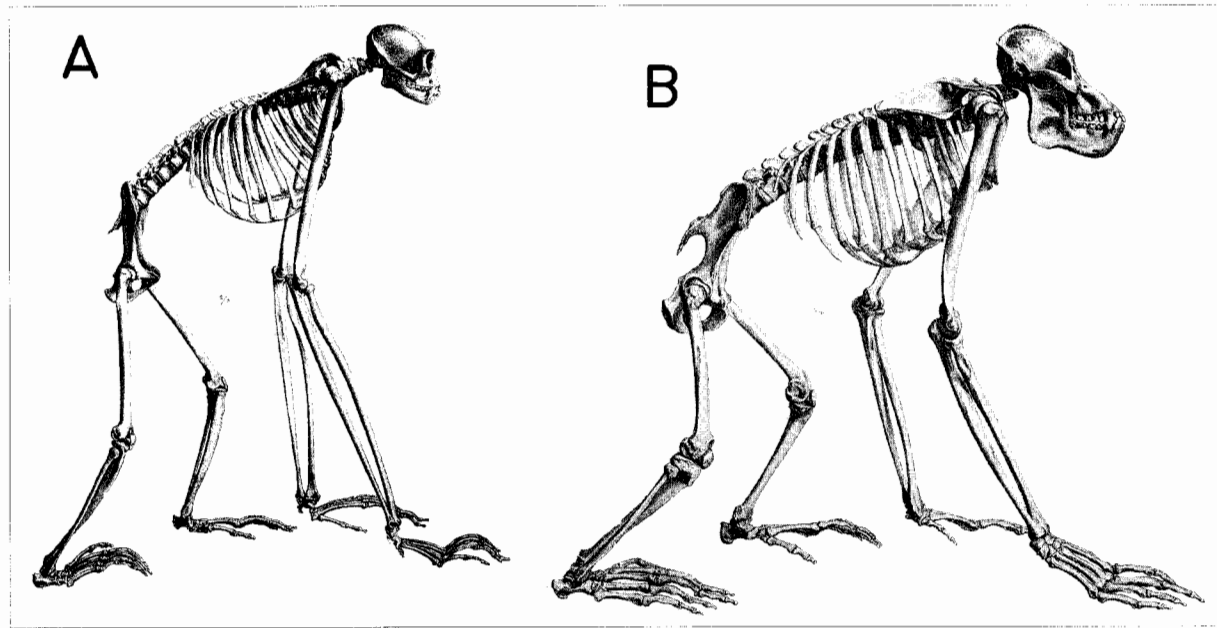
the character evolved independently in each of the living hominoids, and, while this might have occurred in some instances, it is not likely. The majority of characters present in every animal are inherited from more or less remote ancestors, ranging from basic characters like a backbone (in all vertebrates), warm-bloodedness (in all mammals), nails instead of claws on the hands and feet (in all euprimates), or a reduced number of premolars in the jaw (in all catarrhines).

All of these characters are present in the hominoids, but they are not diagnostic of the group, since they are present in other animals as well. What we want is to identify those characters present only in (living) hominoids, and the following abbreviated description includes just such characters. These are the defining characters for the superfamily that were present in its common ancestor, by comparison to earlier catarrhines: The middle part of the skull is expanded, although overall size is no greater than in other catarrhines; the palate is deep and the sinuses are enlarged; the incisors are broader, the molars longer, and the differences between the premolars are reduced; the clavicle is elongated; the trapezius muscle inserts onto the clavicle; the humeral head is rounded, more medially oriented, and larger than the femoral head; the deltoid insertion is low on the humerus; the elbow joint is adapted for stability and for mobility in the articular surfaces for the ulna and radius; the wrist joint is adapted for mobility; the femur has asymmetrical condyles; the iliac blade of the pelvis is expanded; the talus neck and calcaneus are short and broad; the metacarpals have broad distal ends; numbers of vertebrae are lumbar 5, sacral 4–5, caudal 6 (tail is lost); a vermiform appendix is developed.

Having established the probable morphology of the ancestral hominoid on the basis of the comparative method, we can now look at the fossil record to see if any fossils fit this pattern. In the Early Miocene of East Africa is a group of fossil species with the generic name *Proconsul*. Several species are known from partial skulls and limb bones, and these show that *Proconsul* had acquired a number of the defining hominoid characters listed above. For instance, they have expanded skulls, reduced heteromorphy of the premolars, rounded and enlarged humeral heads, and the adaptations for stability of the joints (although not the ones for mobility). These lead to the conclusion that *Proconsul* was a hominoid, and we can now say a little about hominoid origins on the basis of what we know about these species.

*Proconsul* species lived in Africa in the Early Miocene. The earliest record is ca. 23 Ma, although fragmentary jaws of a similar form (*Kamoyapithecus*) are known back to ca. 26 Ma. The origin of the hominoids was, therefore, somewhat earlier than that. Such an age also makes sense in terms of the time of highest diversity of African hominoids, between 20 and 17 Ma, when there were more species present than anywhere today; this diversity would have taken at least several million years to develop, suggesting an origin perhaps 28–25 Ma. Moreover, this date closely corresponds to estimates of hominoid divergence based on the molecular clock.

The place of origin of the hominoids is difficult to determine based on the comparative method alone, because living hominoids are divided equally between Africa and Asia. The fossil evidence, however, is exclusively African for about the



Male skeletons in right lateral view of (A) gibbon, and (B) orangutan. From H.M.D. de Blainville, *Ostéographie. I: Primates*, 1839, Baillière.

first 10–12 Myr of hominoid history, with no reliable evidence for fossil hominoids in Europe or Asia until ca. 16–15 Ma.

#### Gibbon Divergence and Hominid Origins

The earliest branching point within the living hominoids is that dividing the gibbons from the rest of the apes and humans. The fossil species of *Proconsul* just discussed branched off earlier than the divergence of the gibbons, because the former lack several postcranial features shared by both gibbons and great apes, such as those related to adaptations for mobility in the forearm and wrist joint. Thus, *Proconsul* provides no information on gibbon origins. The gibbons themselves are a highly derived group, with many distinctive features; despite this, no fossil taxon has been found that shares any of these distinctive characters. The latter include characters of the forelimb related to the gibbons' brachiating mode of locomotion (characters not present in the great apes), the lack of sexual dimorphism in body size and in such aspects of their skull and jaws that are related to this (e.g., equal-size and large canine teeth), and their distinctive social structure and complex vocalizations. The branching event that gave rise to the gibbons also produced the great apes and humans—hominids, as defined here—and evidence for this split would also provide some indirect evidence for gibbon origins.

The ancestral morphotype for the hominid clade can be defined as follows: The skull has distinct mastoid processes, large medial pterygoids, lengthened premaxilla and increased alveolar prognathism, and reduced incisive foramen; the dentition has spatulate lateral incisors, robust canines, elongated premolars, and molars with thick enamel; the tooth rows are wide apart, the maxillary and mandibular bodies deep; the elbow joint has increased adaptations for stability in the trochlear region; the ulnar styloid process does not contact carpal bones; the hindlimb is reduced in length so that the intermembral index (the relationship of forelimbs to hindlimbs) is high; the deltoid

muscle is greatly developed; and the pectoralis abdominis is missing.

Several fossil groups must be considered as potential hominids in relation to this list of characters. The earliest of these are the late Early Miocene (17 Ma) hominoids from Buluk and Kaloditr (Kenya) named *Afropithecus turkanensis*. Their hominid characters include a very deep mandibular body and symphysis, as well as molar teeth with thick enamel. The material is relatively complete, with parts of a skull, several jaws, and postcrania little different from *Proconsul*, but the descriptions published so far (1999) do not allow any further conclusions to be drawn. Another recently described fossil comes from the Ad Dabtiyah site (Saudi Arabia, which at this stage of the Miocene was connected with Africa and separate from Eurasia). This is about the same age as Buluk, and the fossil hominoid from there, *Heliopithecus leakeyi*, has at least one hominid character in its upper premolar elongation. It also has slightly thicker molar enamel than in the ancestral hominoid state, but it has not reached the full thickness seen in all other early hominids. These hominid taxa are placed in the tribe Afropithecini, and three other taxa of probably somewhat younger date may also belong to this group.

*Otaviopithecus* from Namibia is known by a single partial mandible and is smaller than the other species, while a group of large specimens from Moroto (Uganda) recently named *Morotopithecus* are like *Afropithecus* but appear to have more modern postcrania. Specimens from Maboko and especially Nachola (both Kenya) previously termed *Kenyapithecus africanus* probably do not belong to that genus but are more like *Afropithecus* and its allies.

*Kenyapithecus wickeri* from Fort Ternan (Kenya) and species of *Griphopithecus* from sites in Turkey and central Europe date between 15 and 14 Ma. They have thick molar tooth enamel like *Afropithecus* (thicker than some other afropithecines) but more modern postcrania. On the other hand, they have less advanced postcrania than the European

*Dryopithecus*, whose enamel is thin. Given the uncertainty surrounding the determination of polarity for enamel thickness, it seems most reasonable to place *Griphopithecus* and *Kenya-pithecus* together in the tribe Kenyapithecini, in turn linked with the Afropithecini in the subfamily Kenyapithecinae.

Placing greater weight on the postcranial evidence and some questionable cranial features, *Dryopithecus* is placed in its own subfamily, Dryopithecinae, probably near the origin of the two modern hominid subfamilies. *Dryopithecus* fossils from Rudábánya (Hungary) and Can Llobateres (Spain) show adaptations of the elbow joint and other limb elements very close to those of the living hominid species, and the naso-alveolar region, while not as developed as any of the living great apes, is more derived than the condition seen in *Proconsul* or the kenyapithecines. Some workers argue that *Dryopithecus* shares the klinorhynch condition with the African apes (see below), while others have suggested that it shares facial morphology with pongines. *Dryopithecus* species are known from Spain through Georgia ca. 13–8 Ma, and rare thin-enameled fossils from eastern Asia have also been referred to this genus. Two other more derived European genera, *Oreopithecus* and *Graecopithecus*, are here placed in different subfamilies but might instead be included in the Dryopithecinae.

The evidence from these fossils indicates that the divergence of the hylobatid and hominid clades occurred at least 17 Ma, probably in Africa. The initial changes leading to the hominid clade included enlargement of the premolars, deepening of the jaws, thickening of molar enamel, and stabilizing of the elbow joint. It is likely that in all of these characters the ancestral gibbons, which by definition must have been present alongside the hominids, would have retained the primitive condition. It is, in fact, possible that the early gibbon ancestors retained ancestral characters in most respects, making them difficult to identify in the fossil record, for they would have been little different from the ancestral hominoids. Generalized catarrhines that have been identified under a variety of names are known from Middle and Late Miocene sites as far apart as Kenya and China (e.g., *Micropithecus* from Africa and “cf. *Dionysopithecus*” from eastern Asia). Since these lack any defining hominoid characters, they are here included with *Dendropithecus* in a poorly defined grouping intermediate between pliopithecids and proconsulids. If further evidence revealed the presence of either hylobatid or hominid characters, they might eventually be included in one of these two clades.

Dates from the molecular clock are in general accord with the dates from the fossil evidence. DNA-DNA hybridization data give an age range of 22–18 Ma for gibbon divergence, based on assumed divergence dates for the orangutan of 16–13 Ma. A similar, if slightly younger date, is given by the clock from nuclear DNA-sequencing data, whereas sequencing of mtDNA indicates a younger divergence date still.

### Orangutan Divergence

Probably the most solid evidence for any of the branching points within the Hominoidea is available for the orangutan lineage. The orangutan is highly derived, in both its morphology and its molecules. For these characters, the African apes and humans (the Homininae) share the same character

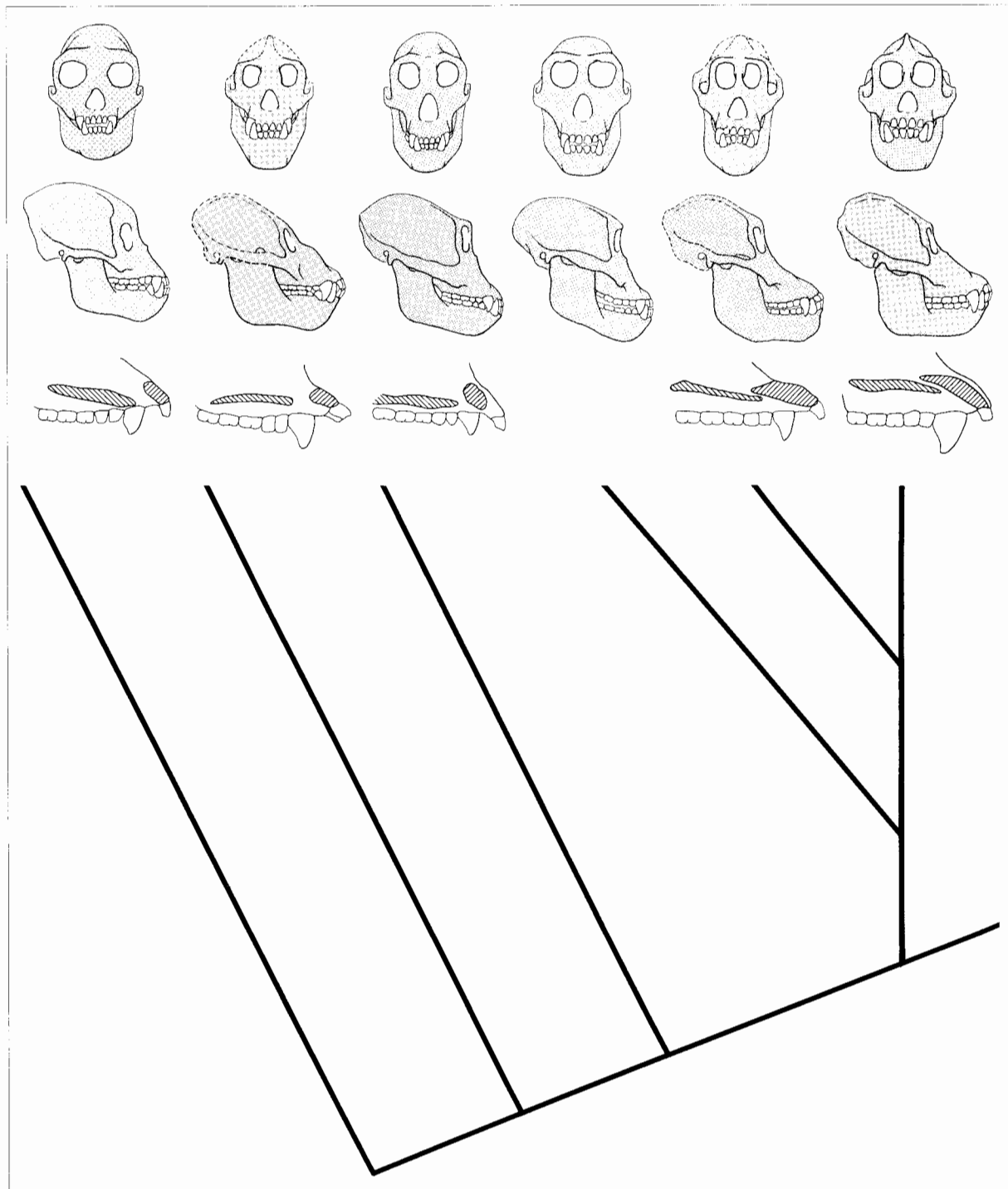
states as gibbons, and often with cercopithecoid monkeys as well, so that they are assumed to retain the ancestral condition for hominoids or catarrhines, respectively. In fact, within Hominoidea the hominines are characterized mostly by retention of ancestral characters, and this makes them a difficult clade to define. Among the defining characters of the pongine clade (based on modern *Pongo*) are these: The skull has an expanded and flattened zygomatic region, giving the face a concave aspect, no glabellar thickening, narrow distance between the eyes, no browridges, and a rotated premaxilla giving a smooth floor to the nasal cavity and an extremely reduced incisive canal with no incisive fossa; in the dentition, the upper lateral incisors are very small relative to the central, the molar enamel is of intermediate thickness, and the molars have a flattened dentine surface and deeply wrinkled enamel; and the articular surfaces of the limb bones are adapted for extreme mobility at the elbow, wrist, and hip joints. None of the fossils so far discussed (with the possible exception of *Dryopithecus*) share any of these pongine characters. They all retain the ancestral condition, where it is known, in these characters and, therefore, have no direct link with the pongine clade.

On the other hand, many of these characters are present in a widespread group of fossils generally placed in the Middle to Late Miocene Asian genus *Sivapithecus*, which is thus grouped with the orangutan clade. Included in *Sivapithecus* are a number of forms that used to be separated as distinct genera, including particularly *Ramapithecus*, which at one time was thought to be directly ancestral to humans. The Turkish fossils known as *Ankarapithecus* were previously included in *Sivapithecus* but they are distinct from the Indo-Pakistani material. Both share at least some of the facial characters detailed above for the pongine clade, and where they differ they retain the ancestral hominoid condition. They can thus be interpreted as within the pongine clade but as less advanced than the living orangutan. Their age range is from 12.5 to ca. 7 Ma, with the earliest good evidence for pongine affinities coming from Pakistan. Some researchers have assigned a number of other fossils to *Sivapithecus* (or to the pongine clade in general), such as those from Lufeng (China), Ravin de la Pluie (Greece), and Rudábánya (Hungary), but there appears to be little justification for this.

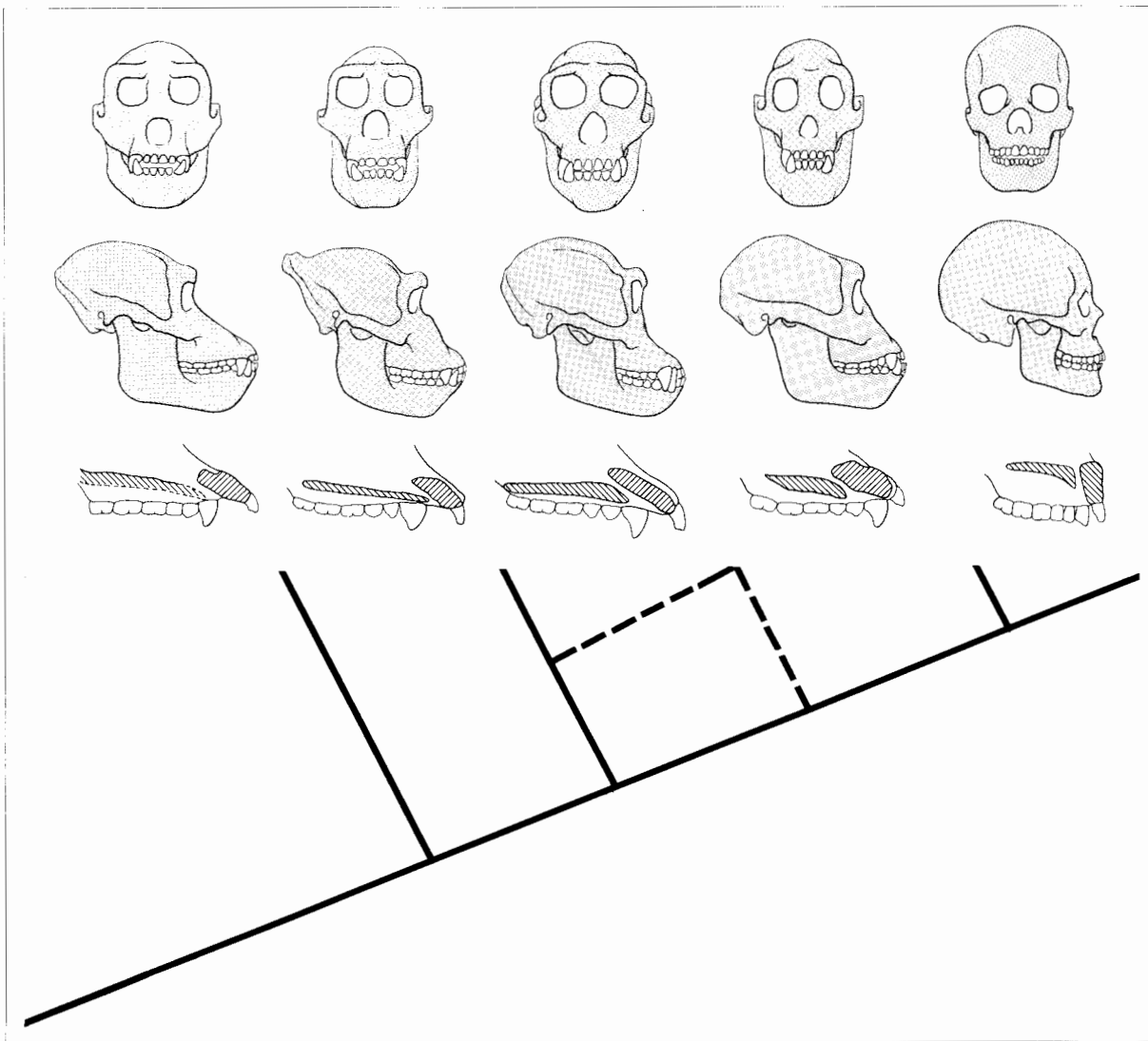
The conclusion from the fossils, therefore, is that the branching point of the pongine clade was at least 13–12 Ma and maybe more, if the Turkish *Griphopithecus* proves to be near the ancestry of this group. No specimen known from Africa can be included in this clade, but since the earliest hominoids are all African, it appears likely that the pongines originated from a sivapith-like form somewhere in Africa. The age range for the divergence of the orangutan is 16.4–12.7 Ma based on sequencing of nuclear DNA, while a younger date of 12.1–9.7 Ma is given by sequencing of mtDNA.

### Hominines

The last group of hominoids, and the sister group to the pongines, is that containing the African apes and humans. This is a hard group to define because it has so few shared derived characters, particularly of features likely to be preserved as fossils. Chimpanzees, gorillas, and humans share



A cladogram of relationships of the Hominoidea, with illustrations of the frontal and right lateral views and nasopalatal sections of selected genera. From left to right: Proconsul, Afropithecus, Dryopithecus, Ankarapithecus (nasopalatal details unclear), Sivapithecus, Pongo, Graccopithecus, Gorilla, Pan, Australopithecus, and Homo. Not to scale. Reconstructions of fossils modified by L. Meeke and E. Delson after various sources. Afropithecus based on sketch by A. Walker; its nasopalatal section is taken from the Moroto palate, now placed in Mototopithecus, while the Afropithecus face may show a pattern more like that of Sivapithecus. Nasopalatal sketches represent cross-section through midline of palate and nasal cavity, showing dental outlines, body of premaxilla (||||) and maxillary surface (|||||) on either side of incisive canal. In Homo, the "premaxilla" is fused with the maxilla. See text for discussion of the details of this region. Dashes indicate tentative reconstruction when remains unknown.



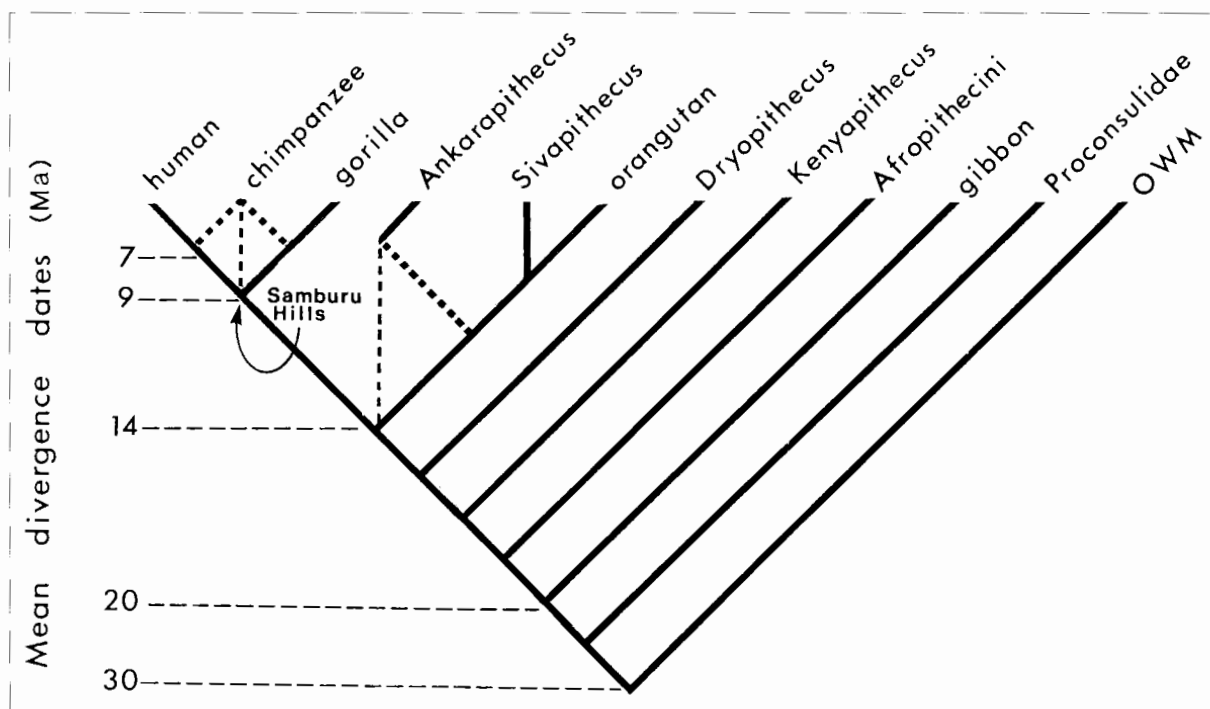
Continued.

the following list of characters, which are taken to define the node: The skull has a true frontal sinus developed; the browridges form a continuous bar across glabella, and a post-orbital sulcus is developed; middle-ear depth is increased; two of the wrist bones (os centrale and scaphoid) are fused; the prostate is subdivided; apocrine glands are scarce and eccrine glands abundant; there is a large axillary organ; and the aorta type is distinctive. At the molecular level, several amino-acid residue substitutions are uniquely shared in this clade, as are large numbers of DNA substitutions. Weak as this evidence is, it is still much stronger than that linking any other hominoid species with humans. The evidence put forward suggesting that humans are specially related to either orangutans or chimpanzees is poor in both cases, and the same applies to the evidence, or lack of it, linking the three great apes together.

The situation is not made any easier by the lack of any early fossils that can be definitively assigned to this clade. A frontal sinus has been reported for some of the genera mentioned earlier, but it is not certain if these structures are homologous with the hominine frontal sinus. It has been observed in *Dryopithecus* and it may be present in *Graecopithe-*

*cus*, where it has been claimed to be associated with development of African-ape-like browridges, but the presence of the latter and the significance of the former are both uncertain. The latter genus apparently shares one hominine character in the presence of a narrow incisive canal due to the overriding of the premaxilla above the maxilla, giving this region an African-ape type of morphology in *Graecopithecus*, but this character is not present (or is at best incipient) in *Dryopithecus*. It is possible that either or both of these European forms may be early hominines, but a more conservative view places them both in a more primitive subfamily, Dryopithecinae.

One fossil that is of interest to the hominine branching event is *Samburupithecus* from Samburu Hills (Kenya), which raises the question of the relationships within the hominine clade. The Samburu fossil is dated at 9.5 Ma, and it has a morphology very close to that of gorillas. Only a single upper jaw is known, but the molar and premolar proportions and shape, and the cusp morphology of the molars, are all similar to the condition in gorillas. The polarity of these characters is hard to determine, but it is possible that they are gorilla synapomorphies.



Relationships of the hominoids. Both recent and fossil hominoid taxa are included on this cladogram, and estimated ages are assigned to several of the major branching points based on the oldest record of the fossils contained within the respective clades. Where multiple possible relationships are indicated by interrupted lines, the heavier (diagonal) line is judged more likely than the lighter (vertical) alternative. DNA sequencing and hybridization studies suggest a date between 27 and 25 Ma for the hominoid-cercopithecoïd divergence.

Evidence from comparative morphology supports the existence of an African-ape clade distinct from humans. Chimpanzees and gorillas share a major complex of characters relating to knuckle-walking, with about 10 characters of the elbow, wrist, and hand, depending upon how they are counted. They also share some characters of the chromosomes and DNA at the molecular level. In contrast to this is the abundant molecular evidence that indicates a closer link between humans and chimpanzees and that is supported by some morphological evidence: broad lower incisors, spatulate  $P^2$ , broad lower molars, vertical mandibular ramus, and the anterior edge of the incisive fossa posterior to  $P^3$ . These morphological characters shared between chimpanzees and humans are not very convincing, however, when set against the knuckle-walking complex of characters shared by chimpanzees and gorillas. As far as it goes, the single fossil from Samburu Hills supports the chimp-human relationship, if its gorilla affinities are correct, for it might imply the early separation of the gorilla clade from that linking humans and chimpanzees. Similarly, the European *Graecopithecus* (ca. 10–8 Ma) has been suggested as most similar to gorillas in certain characters, but these features may be hominine sympleisomorphies.

The scarcity of fossils makes it hard to say anything about the time and place of the origin of the hominine clade. Since humans and African apes have Africa as the only common geographical factor, that seems the likely place of origin, and this fits with *Samburupithecus*. On the other hand, if *Graecopithecus* and/or *Dryopithecus* are, in fact, hominines, the clade could have originated in Eurasia and then returned to Africa. Early human ancestors of the genus *Australopithe-*

*cus* are known only from Africa, but their fossil record starts long after the (human-chimpanzee) branching times indicated by the molecular clock. The latter are 10–6 Ma (DNA-DNA hybridization) and 8.1–6.3 Ma (DNA sequencing), and since these dates have been shown to be concordant with fossil evidence, where available, it seems reasonable to accept them where fossil evidence is lacking.

See also Africa; Africa, East; Afropithecus; Ape; Buluk; Catarrhini; Dryopithecinae; Dryopithecus; Hominidae; Homininae; Hominini; Kenyapithecinae; Kenyapithecus; Molecular Clock; Ponginae; Proconsulidae; Samburupithecus; Sivapithecus; Teeth. [P.A., E.D.]

#### Further Readings

- Andrews, P. (1992) Evolution and environment in the Hominoidea. *Nature* 360:641–646.
- Begun, D.R. (1994) Relations among the great apes and humans: New interpretations based on the fossil great ape *Dryopithecus*. *Yrbk. Phys. Anthropol.* 37:11–63.
- Begun, D., Ward, C., and Rose, M., eds. (1997) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*. New York: Plenum.
- Ciochon, R.L., and Corruccini, R.S. (1983) *New Interpretations of Ape and Human Ancestry*. New York: Plenum.
- Patterson, C., ed. (1987) *Molecules and Morphology in Evolution: Conflict or Compromise?* Cambridge: Cambridge University Press.
- Szalay, F.S., and Delson, E. (1979) *Evolutionary History of the Primates*. New York: Academic.