

» Paleontology: » Human fossils



## Fossil apes

**A**pes and humans are closely related primates in the superfamily Hominoidea. The living hominoids are subdivided into the families Hylobatidae and Hominidae. The hylobatids or lesser apes (genus *Hylobates*) are represented by approximately nine species found throughout Southeast Asia. Humans and the great apes—the orangutan (*Pongo pygmaeus*), the gorilla (*Gorilla gorilla*), the common chimpanzee (*Pan troglodytes*), and the pygmy chimpanzee (*Pan paniscus*)—are grouped in the Hominidae. In the past, the great apes were included in a separate family, the Pongidae, but subsequent anatomical and molecular studies showed that the African apes (*Gorilla* and *Pan*) are more closely related to humans than they are to the Asian orangutan.

The classification of fossil and living apes, along with their geological ages and geographical regions, is shown below. The asterisk indicates extinct apes.

- Superfamily Hominoidea
  - Family Hylobatidae
    - *Hylobates* (Pleistocene to Recent, Southeast Asia)
  - Family Hominidae
    - Subfamily Kenyapithecinae
      - *Griphopithecus*\* (middle Miocene, Turkey and Austria)
      - *Kenyapithecus*\* (middle Miocene, East Africa)
    - Subfamily Dryopithecinae
      - *Dryopithecus*\* (middle to late Miocene, Europe)
      - *Oreopithecus*\* (late Miocene, Italy)
    - Subfamily Ponginae
      - *Ankarapithecus*\* (late Miocene, Turkey)
      - *Gigantopithecus*\* (late Miocene to Pleistocene, Asia)
      - *Lufengpithecus*\* (late Miocene, China)
      - *Pongo* (Pleistocene to Recent, Southeast Asia)
      - *Sivapithecus*\* (middle to late Miocene, Indo-Pakistan)
    - Subfamily Homininae
      - *Ardipithecus*\* (early Pliocene, Ethiopia)
      - *Australopithecus*\* (Pliocene, Africa)
      - *Gorilla* (Recent, Africa)
      - *Graecopithecus* (= *Ouranopithecus*)\* (late Miocene, Greece)
      - *Homo* (late Pliocene to Recent, cosmopolitan)
      - *Pan* (Recent, Africa)
      - *Paranthropus*\* (Pliocene to Pleistocene, Africa)
      - *Samburupithecus*\* (late Miocene, Kenya)
  - Uncertain family status
    - *Morotopithecus*\* (early Miocene, Uganda)
    - *Otavipithecus*\* (middle Miocene, Namibia)
- Uncertain superfamily status
  - Family Proconsulidae
    - *Afropithecus*\* (early Miocene, Kenya)
    - *Dendropithecus*\* (early Miocene, East Africa)
    - *Heliopithecus*\* (early Miocene, Saudi Arabia)
    - *Kalepithecus*\* (early Miocene, East Africa)
    - *Kamoyapithecus*\* (late Oligocene, Kenya)

- *Limnopithecus*\* (early to middle Miocene, East Africa)
- *Mabokopithecus*\* (middle Miocene, Kenya)
- *Micropithecus*\* (early and middle Miocene, East Africa)
- *Nyanzapithecus*\* (early and middle Miocene, East Africa)
- *Proconsul*\* (early and middle Miocene, East Africa)
- *Rangwapithecus*\* (early Miocene, East Africa)
- *Simiolus*\* (early Miocene, Kenya)
- *Turkanapithecus*\* (early Miocene, Kenya)

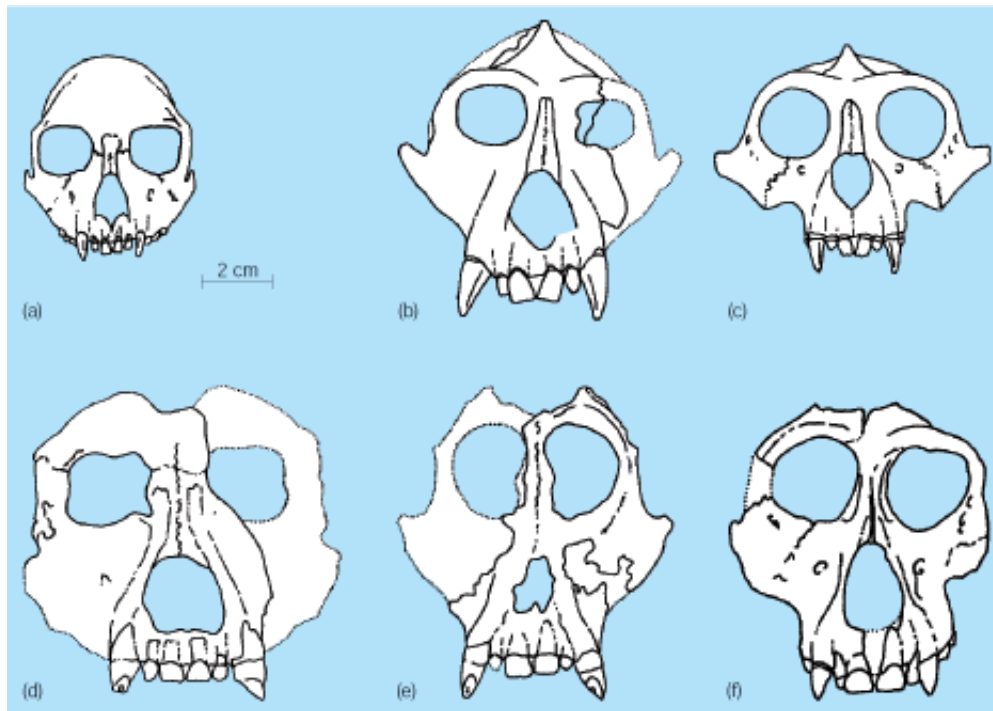
## Evolutionary history

The evolutionary history of the extant hominoids is poorly known, with the notable exception of humans, which have a relatively complete fossil record extending back more than 4 million years. The earliest fossil apes that can be definitively linked to the modern hylobatids are known from sites in China dated to less than 1.5 million years ago (Ma), while the fossil record for the African apes is entirely unknown. The evolution of the orangutan is, by comparison, much better documented. Fossil teeth from cave sites in Asia dating back more than 1 million years show that orangutans in the past were considerably larger than they are today, and that unlike their living relatives, which are found only on Sumatra and Borneo, they once had a wider distribution in Southeast Asia that extended as far north as China. In contrast to the paucity of fossils available to trace the evolutionary history of hominoids over the past 5 million years, there is a wealth of evidence from the Miocene Period (23-5 Ma). This evidence shows that apes were once much more common and more diverse than they are today.

## Proconsulids

The remains of apelike fossil primates, commonly known as proconsulids, have been recovered from sites in Kenya, Uganda, and Saudi Arabia dating to the early Miocene (23-16 Ma). There are 15 species of proconsulids, ranging in size from the tiny *Micropithecus clarki* (4 kg; 9 lb) to the chimpanzee-sized *Proconsul major* (50 kg; 110 lb). Comparisons of their teeth, jaws, and skeletons indicate that proconsulids exhibited a wide diversity of dietary and locomotor behaviors, but they were typically arboreal and ate various combinations of soft fruits and are *Proconsul heseloni*, *Turkanapithecus kalakolensis*, and *Afropithecus turkanensis* (Fig. 1). Studies have shown that proconsulids represent either the earliest known hominoids or primitive stem catarrhines (the group which gave rise to both Old World monkeys and apes). They are certainly more primitive than any of the living apes, retaining generalized skulls and teeth, and monkeylike postcranial skeletons. However, during the early Miocene there was at least one species of hominoid living in East Africa, *Morotopithecus bishopi*, which had already acquired some of the unique features of modern apes. This species, from Moroto in Uganda (dated to more than 20 Ma), had specializations of the lumbar vertebrae and scapula, not found in the contemporary proconsulids, that indicate that it had developed the stiff-backed, partially upright posture and suspensory forelimbs that are characteristic of modern hominoids.

**Fig. 1** Reconstructions and partial reconstructions of the skulls of fossil apes: (a) *Proconsul*, (b) *Afropithecus*, (c) *Oreopithecus*, (d) *Graecopithecus*, (e) *Sivapithecus*, and (f) *Ankarapithecus*.

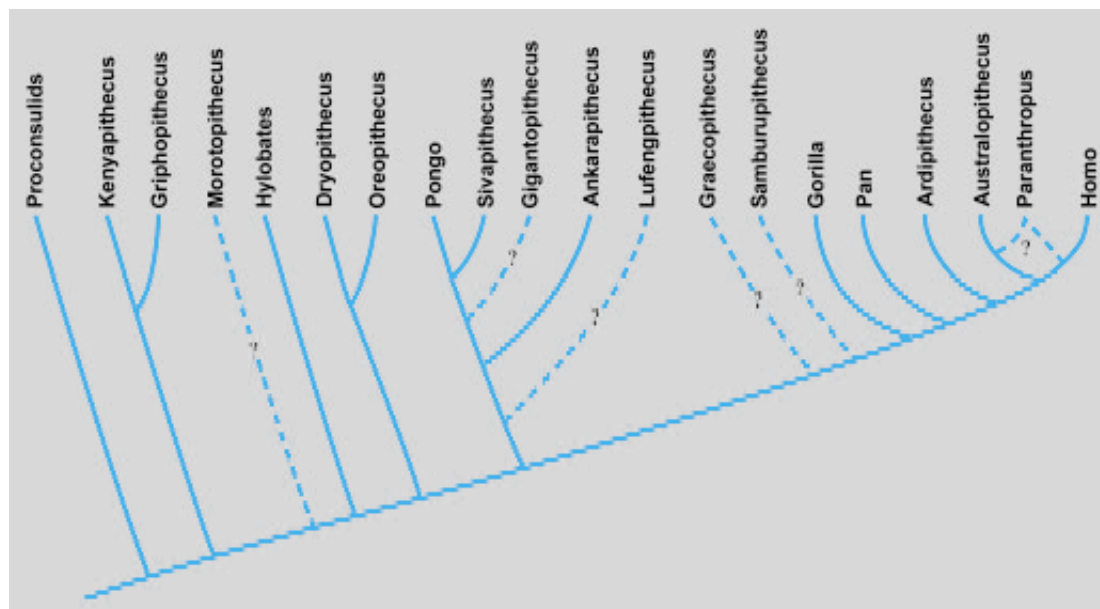


During the middle Miocene (16-10 Ma), conditions in East Africa became somewhat drier, cooler, and more seasonal, and open woodland habitats replaced the humid tropical forests that were typical of the early Miocene. These ecological changes coincided with the appearance in East Africa of a more advanced type of hominoid, *Kenyapithecus*. This ape is derived relative to the proconsulids in having thickened enamel on its cheek teeth, more robust jaws, and relatively larger upper premolars. The limb bones indicate that *Kenyapithecus* was more terrestrially adapted than proconsulids and exhibited a number of specialized features that link it more closely to extant hominoids. Another intriguing fossil ape from this time period is *Otavipithecus* from Namibia, dated to approximately 13 Ma, and the only Miocene hominoid recorded from southern Africa. Until recently, it was known only by a single jaw fragment, so its relationships to other fossil and extant hominoids have been difficult to establish. However, additional cranial and postcranial specimens of *Otavipithecus* have now been discovered, and it is hoped that these will shed further light on its affinities.

### Eurasian hominoids

Until the middle Miocene, hominoids were restricted to Africa, but during this period they migrated into Eurasia. The earliest Eurasian hominoid, dated to 16-15 Ma, is *Griphopithecus*, which is known from Turkey and central Europe. The teeth and jaws are similar to those of *Kenyapithecus* from East Africa, to which it is probably closely related. Once in Eurasia, hominoids became established over a wide geographical region, extending from Spain in western Europe to eastern China, and they became increasingly diversified during the middle and late Miocene (16-5 Ma). The best-known fossil Eurasian hominoids are *Dryopithecus* (western and central Europe), *Oreopithecus* (Italy), *Graecopithecus* or *Ouranopithecus* (Greece), *Ankarapithecus* (Turkey), *Sivapithecus* (Indo-Pakistan), and *Lufengpithecus* (China) [Fig. 1]. Of these forms, *Sivapithecus* is evidently closely related to the living orangutan, but the relationships of the other Eurasian Miocene hominoids remain contentious. A number of alternative hypotheses about the interrelationships of Eurasian Miocene hominoids have been proposed: (1) that they form a closely related group with the living orangutan, all being derived from a common ancestor that migrated into Europe from Africa sometime during the middle Miocene; (2) that some of the Eurasian hominoids, such as *Dryopithecus* and *Graecopithecus*, are more closely related to the African apes and humans than they are to *Sivapithecus* and the orangutan; and (3) that they represent a diverse group containing primitive hominoids, as well as forms belonging to the orangutan and African great ape lineages (Fig. 2).

**Fig. 2** Cladogram of the evolutionary relationships of fossil and living apes. Broken lines indicate uncertain relationships.



An ecological shift from moist temperate woodlands to drier, more seasonal habitats during the later Miocene coincided with a sharp decline in the diversity of hominoids in Eurasia. The only was *Oreopithecus*, a highly specialized relative of *Dryopithecus* that was isolated on a group of islands in the northern Mediterranean which today form part of Italy (Fig. 1). *Lufengpithecus* and *Sivapithecus*, along with *Gigantopithecus*, are found in the late Miocene of Asia. The ape *Gigantopithecus* was the largest known hominoid, with massive jaws and teeth specialized for eating tough, fibrous vegetation, and with an estimated body weight that may have exceeded 200 kg (440 lb) [living male gorillas average only 170 kg or 375 lb]. All of these Eurasian hominoids became extinct by the close of the Miocene, except for *Gigantopithecus*, whose remains have been recovered from Pleistocene cave sites in China dated to less than 1 Ma.

Hominoids also became extremely rare in Africa during the late Miocene. A large hominoid, *Samburupithecus*, known only by a single maxilla from Kenya (dated to 10-8 Ma), may represent a close relative of the African apes and humans. A few isolated teeth and a lower jaw fragment of fossil hominoids from the late Miocene sites of Lukeino and Lothagam (dated to 7-5 Ma) in northern Kenya have been suggested to be the earliest known occurrence of the human lineage, but the remains are too scrappy to be certain of their taxonomic affinities. The earliest definitive record of fossil hominoids that are more closely related to humans than they are to the African great apes is known from the Pliocene (5.2-1.6 Ma) with the appearance of *Ardipithecus ramidus* from Ethiopia (4.4 Ma), *Australopithecus anamensis* from Kenya (4.2-3.9 Ma) and *Australopithecus afarensis* from Ethiopia and Tanzania (4-3 Ma). See also: [Apes](#); [Fossil humans](#); [Mammalia](#); [Monkey](#)

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## Bibliography

- D. R. Begun, C. V. Ward, and M. D. Rose, *Function, Phylogeny, and Fossils: Miocene Adaptations*, 1997
- R. L. Ciochon and R. S. Corruccini, *New Interpretations of Ape and Human Ancestry*, 1983
- J. G. Fleagle, *Primate Adaptation and Evolution*, 2d ed., 1998
- R. G. Klein, *The Human Career*, 1989
- B. Wood, L. B. Martin, and P. Andrews, *Major Topics in Primate and Human Evolution*, 1986



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