

Fossil primates

Extinct members of the order of mammals to which humans belong. All current classifications divide the living primates into two major groups (suborders), but zoologists differ as to whether the tarsier (*Tarsius*) should be classified with the lower primates (lemurs, lorises, and bushbabies) or the higher primates (New and Old World monkeys, greater and lesser apes, and humans).

All primates have a common origin which, however, is not reflected in the universal possession of a suite of diagnostic features. The order as a whole has been characterized in terms of showing a group of progressive evolutionary trends, notably toward the predominance of the visual sense, the reduction of the sense of smell and associated structures, improved grasping and manipulative capacities, and enlargement of the higher centers of the brain. Among the extant primates, the lower primates more closely resemble forms that evolved relatively early in the history of the order, while the higher primates represent a group more recently evolved (**Fig. 1**). A classification of the primates, as accepted here, is as follows:

Primates

- Semiorder Plesiadapiformes (archaic extinct primates)
 - Superfamily Paromomyoidea (paromomyids, picrodontids)
 - Superfamily Plesiadapoidea (plesiadapids, carpolestids)
- Semiorder Euprimates (modern primates)
 - Suborder Strepsirhini (toothcombed “prosimians” and extinct allies)
 - Infraorder Adapiformes (extinct early strepsirhines)
 - Superfamily Adapoidea (extinct early strepsirhines)
 - Infraorder Lemuriformes (modern strepsirhines)
 - Superfamily Lemuroidea (typical lemurs)
 - Superfamily Indrioidea (indris, aye-ayes, and subfossil relatives)
 - Superfamily Lorisioidea (lorises, bushbabies, mouse and dwarf lemurs)
 - Suborder Haplorhini (tarsiers and higher primates)
 - Hyporder Tarsiiformes (tarsiers and extinct relatives)
 - Superfamily Tarsioidea (tarsiers and close relatives)
 - Superfamily Omomyoidea (extinct early haplorhines)
 - Hyporder Anthropoidea (higher primates)
 - Infraorder Paracatarrhini (archaic anthropoids)
 - Family Oligopithecidae (archaic protoanthropoids)

- Family Parapithecidae (extinct Oligocene monkeys)
- Infraorder Platyrrhini (New World anthropoids)
 - Superfamily Ateloidea (New World monkeys)
 - Family Atelidae (howler, spider, saki, titi, and owl monkeys)
 - Family Cebidae (squirrel, capuchin, and marmoset monkeys)
- Infraorder Catarrhini (Old World anthropoids)
 - Parvorder Eocatarrhini (archaic catarrhines)
 - Family Propliopithecidae (extinct common ancestors of hominoids and cercopithecoids)
 - Family Pliopithecidae (extinct early catarrhines)
 - Parvorder Eucatarrhini (advanced catarrhines)
 - Superfamily Hominoidea (apes and humans)
 - Family Proconsulidae (extinct early apes)
 - Family Hylobatidae (gibbons, lesser apes)
 - Family Hominidae (great apes, humans, and extinct relatives)
 - Superfamily Cercopithecoidea (Old World monkeys)
 - Family Cercopithecidae (Old World monkeys)

Early primates. The earliest primates are placed in their own suborder, Plesiadapiformes, because they have no direct evolutionary links with, and bear no adaptive resemblances to, any group of living primates. However, the chewing teeth and the locomotor anatomy of these fossil forms sufficiently resemble those of later primates to demonstrate the common origin of the two groups. Best known from the Paleocene Epoch, around 66–54 million years ago (Ma), and found in both the Old World and the New World, the plesiadapiforms retained clawed hands and feet, had rather small brains compared to their body size, possessed large specialized front teeth, and were probably arboreal in habit (**Fig. 2**). These animals are also known from fossil deposits on Ellesmere Island, in Arctic Canada, which was then covered by the subtropical forest stretching continuously from western North America across a landlocked North Atlantic into western Europe.

Eocene primates. There is no known plesiadapiform that is a satisfactory candidate for the ancestry of the fossil primates of modern aspect typical of the succeeding epoch, the Eocene (54–34 Ma). Often termed euprimates, they are divided broadly into lemurlike forms, usually grouped into the superfamily Adapoidea, and tarsierlike forms (Omomyoidea), although this division may prove to be oversimplified. Eocene primates of both the Old

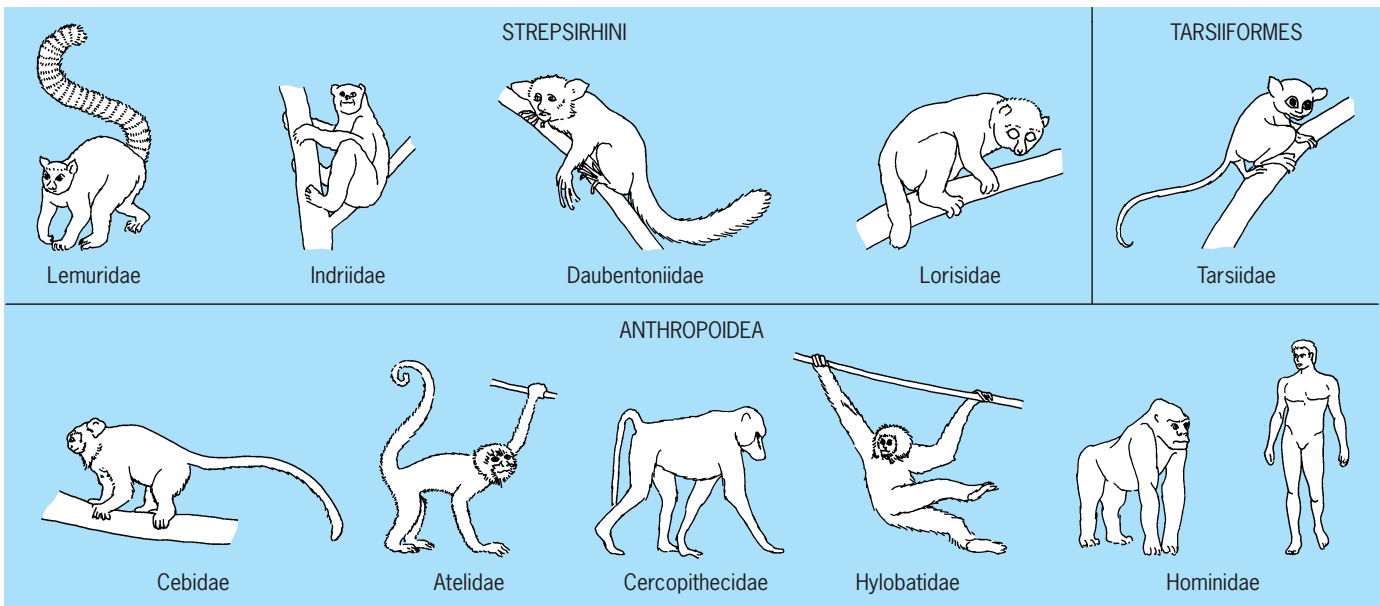


Fig. 1. Representatives of living primate families.

and New Worlds already display the trends that mark modern primates as a whole: These arboreal animals possessed grasping hands and feet in which sharp claws were replaced by flat nails backing sensitive pads; the snout was reduced, suggesting a deemphasis of smell, while the bone-ringed eyes faced more forward, producing stereoscopic vision and suggesting primary reliance on the sense of sight; and the brain was somewhat enlarged relative to body size when compared to those of other mammals of the period.

It is possible that the origins of some specific groups of extant lower primates may be traced back to or through certain known primate genera of the Eocene. Even if this is not the case, however, it is universally accepted that the antecedents of these living forms are to be sought somewhere within the Eocene primate radiation, though the details of this ancestry may remain unclear. In North America and Europe, lower primates had nearly disappeared by the close of the Eocene, while virtually all known fossil lower primates of later epochs in Africa and

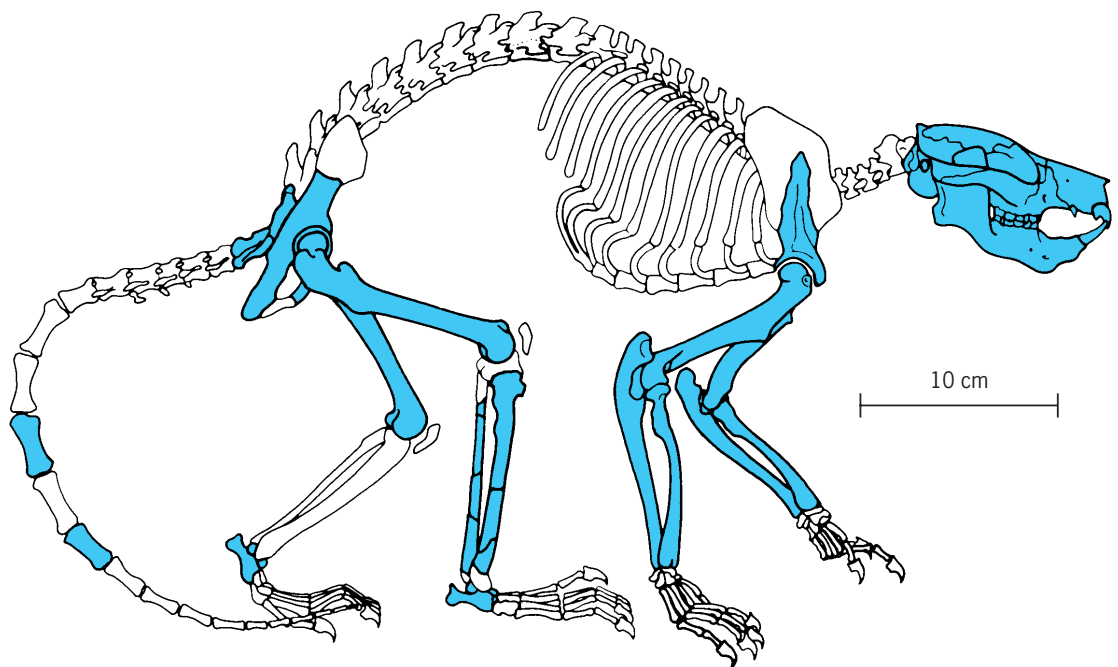


Fig. 2. Reconstructed skeleton of *Plesiadapis tricuspidens*, a Eurasian plesiadapiform from about 60 Ma. Known parts are shaded.

Asia are closely related to modern primates of these areas.

Modern lower primates. The extant lower primates are allocated to the suborder Prosimii if *Tarsius* is included, and to the suborder Strepsirhini if this strange primate is excluded, as is provisionally done here. All extant strepsirhines possess dental scrapers (tooth-combs), in which the lower front teeth are elongated, closely approximated, and forwardly projecting. These specialized structures are used both in feeding and in social grooming. Additionally, all living strepsirhines retain a moist, naked rhinarium (wet nose, as in a dog) and related structures, reflecting a greater reliance on the sense of smell than is typical of higher primates. All are also united by possessing a toilet claw (used for self-cleaning) on the second digit of the foot. Although all strepsirhines possess grasping hands and feet, their manual dexterity is generally inferior to that of higher primates; their brains are also relatively small.

There is no ancient primate fossil record in Madagascar, home of the most diverse group of modern lower primates, but extinct species little more than a thousand years old document a much wider adaptive radiation before the arrival of humans on the island. Notable among those extinct lemurs are *Paleopropithecus*, a large-bodied climber-hanger somewhat like the orangutan in its locomotion (Fig. 3); the semiterrestrial and dentally specialized members of the subfamily Archaeolemurinae, related to the living indriids but adapted somewhat like baboons; and *Megaladapis*, a very large, vertically postured, short-limbed, and probably slow-moving climber with adaptive resemblances to the koala of Australia. Fragmentary remains of lorisooid strepsirhines are known from the Miocene of East Africa and Pakistan.

Tarsiers. The tiny *Tarsius*, which lives today in Southeast Asia, represents a link between the tooth-combed strepsirhines and the anthropoids (monkeys, apes, and humans). In many respects (such as lack of toothcomb, dry nasal area, molecular biology, and placentation), it is related to the anthropoids, but dentally it is usually thought primitive, although some authors have found similarities to some strepsirhines. The extinct Eocene omomyoids are close to tarsiers skeletally; they are often considered broadly ancestral to the anthropoids for that reason and also because some have monkeylike front teeth. A tarsier-like fossil has been recovered in Egypt from deposits of early Oligocene age (35 Ma). Living tarsiers eat insects and small vertebrates, and are vertical clingers and leapers; their nocturnal habit is shown by their relatively huge eyes. They appear to live mainly in pairs, but they may form larger associations in some regions.

Higher primates. The anthropoids include three main groups of living animals and their extinct relatives; their divergence from a possibly omomyoid stock probably took place some 50 Ma. The monkeys of the New World and those of the Old are of similar evolutionary grade, but the latter share a much

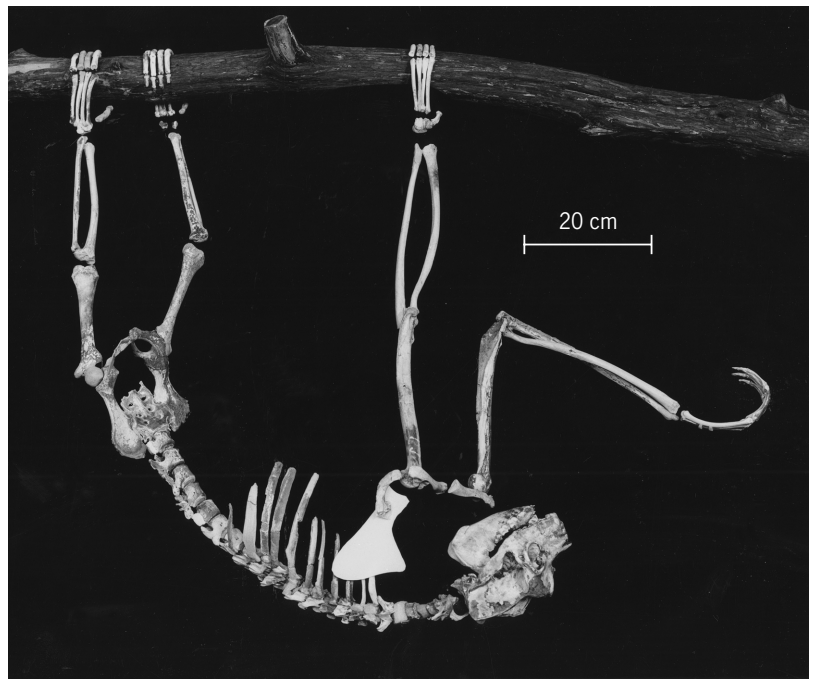


Fig. 3. Anjohibe specimen of *Paleopropithecus ingens*, mounted in probable habitat posture. (Photo courtesy of American Geological Institute)

more recent common ancestry with apes and humans, with which they are grouped in the infraorder Catarrhini.

The earliest known anthropoids may be represented by a few teeth (of *Algeripithecus*) from Algeria about 45 million years old, but better-preserved forms appear in the Fayum region of Egypt between 35 and 33 Ma. Although now a desert, at the time this was a lush tropical forest through which meandered the sluggish proto-Nile river. Three main groups of early higher primates are represented: the oligopithecids, the parapithecids, and the propliopithecids. The former two appear to be only distantly related to any of the living monkeys or apes, although they may be termed monkeys in the broad sense, as their adaptations are similar to those of modern monkeys. The propliopithecids (species of *Propliopithecus*, including *Aegyptopithecus*) may be close to the common ancestry of later catarrhines (Old World anthropoids). These arboreal animals were the size of small cats, with apelike teeth, small brain, and limbs similar to those of the acrobatic South American atelines. Representatives of modern lineages begin to occur in the fossil record by about 28–20 Ma in both hemispheres. Most scholars subscribe to a colonization of South America by Fayum-age African anthropoids that crossed a then-narrower South Atlantic ocean on rafts of natural vegetation to reach the isolated island continent.

New World primates. The platyrrhine or ateloid monkeys of South and Central America are divided into two families, of which the contents vary according to author. All living (and well-known extinct) forms are arboreal and occupy forested areas between Argentina and southern Mexico. A distinctive

evolutionary pattern observed in this group is the antiquity of the extant lineages as reflected by the close relationships of most of the few known fossils to modern genera. The small marmosets and the common squirrel and capuchin monkeys are grouped into the family Cebidae, while the generally large-bodied spider-howler and saki-uakari groups are linked to the smaller titis and (probably) owl monkeys in the Atelidae. These two families differ in the relative robustness of their jaws and reduction of last molars.

The earliest fossil platyrrhine, 26-million-year-old *Branisella* from Bolivia, is as yet known only by teeth and jaw fragments. A probable size reduction of its last molars may suggest an evolutionary relationship to the Cebidae. It has also been suggested that *Branisella* might have lived in a savannahlike environment and been adapted to life at least partly on the ground, as opposed to all later platyrrhines. Two slightly later (about 20 Ma) species from Patagonia and Chile are also probable cebids, close to the ancestry of the living *Saimiri*, and several forms of 18–17 Ma represent early atelids, close to the living pitheciines (the saki-uakari and titi-owl monkey groups).

The largest number of fossil platyrrhines comes from the La Venta beds of Colombia, dated about 13 Ma. These include one or two species in each subfamily of Cebidae (Callitrichinae and Cebinae), one relative each of owl and howler monkeys, and four early members of the saki-uakari group. The last 100,000 years saw another flowering of extinct platyrrhine lineages. A cave site in eastern Brazil has yielded partial skeletons of “giant” relatives of the howler and spider monkeys, while several localities

in the Caribbean produced controversial fossils perhaps related to howlers, saki-uakaris, and squirrel monkeys (or possibly representing a distinct lineage whose members came to resemble those other groups). See MONKEY.

Old World monkeys. The living Cercopithecoidea are divided into two subfamilies, Colobinae and Cercopithecoidea. The oldest cercopithecoidea are found in Africa, with a few fossil forms such as *Victoriapithecus* of 20–15 Ma probably predating the divergence of the modern subfamilies. The cercopithecoidea include a wide variety of forms, all of which share cheek pouches for temporary food storage and usually large incisors reflecting a fruit diet; colobines, by contrast, are more restricted in morphology, range, and behavior pattern, and all are leaf eaters with a complicated digestive tract to facilitate the low-nutrition diet. All cercopithecoidea possess ischial callosities, or rump sitting pads, which have been lost to a greater or lesser extent in apes and humans.

The earliest members of the two living subfamilies also are mainly African. One colobine jaw is known by 9 Ma, and from 7 to 5 Ma species of both cercopithecoidea and colobines become more abundant. Large collections of Old World monkey fossils have been recovered from East and South African sites (often in association with early human remains) in the 4–1.5 Ma interval. Cercopithecoidea are represented first by *Parapapio*, which was a semiterrestrial animal probably closer to the common ancestor of later forms, and then by several species of the highly terrestrial living *Theropithecus*. At least three types of large colobine monkeys were also common, ranging from arboreal to terrestrial in adaptation. Many of these species were significantly larger than

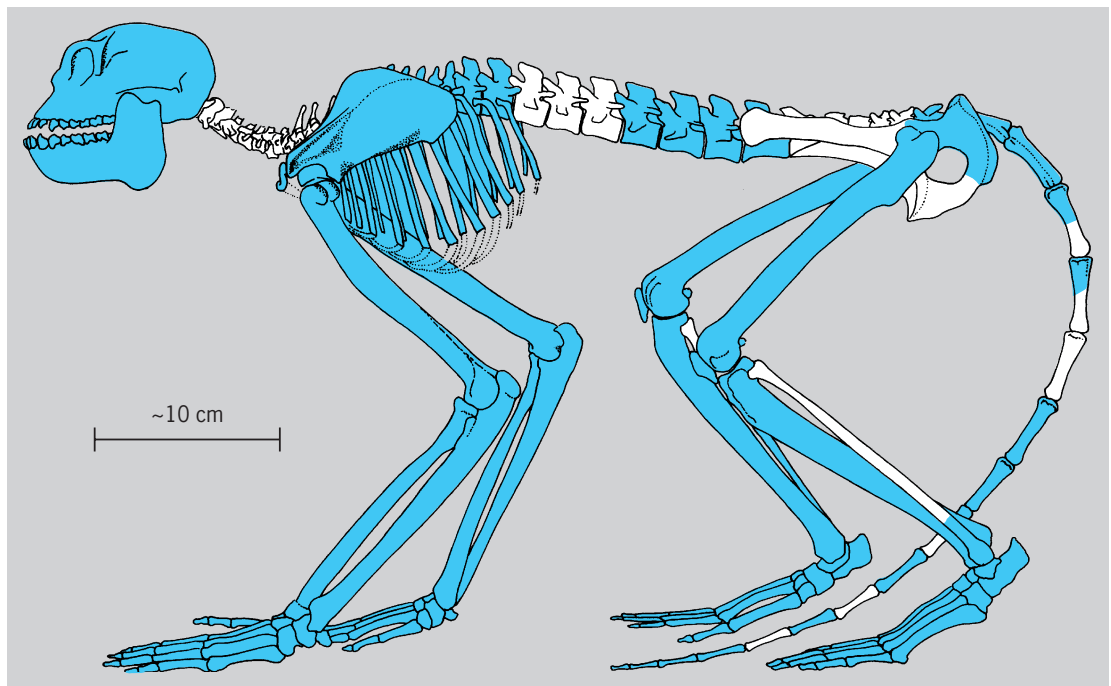


Fig. 4. Reconstructed skeleton of *Mesopithecus pentelicus*, an 11- to 8-million-year-old colobine monkey. Known parts are shaded. (After A. Gaudry, *Animaux Fossiles et Géologie de l'Attique*, Savy, Paris, 1862)

their living relatives: The biggest colobine may have weighed close to 50 kg (110 lb), while a *Theropithecus* dated about 1 Ma has been estimated nearly twice that large. Some of these large and slow-moving species may have been hunted and perhaps driven to extinction by early humans.

Cercopithecids entered Eurasia from Africa. *Mesopithecus pentelicus*, an 11- to 8-million-year-old colobine known in a geographical range from Germany through Afghanistan, is the best-represented Eurasian fossil monkey, with dozens of individuals recovered from sites in Greece (Fig. 4). It was semiterrestrial, perhaps like the living hanuman langur *Semnopithecus entellus*, sleeping in trees and feeding on the ground along watercourses. A possible descendant is *Dolichopithecus*, which lived in Europe from about 4.5 to 2.5 Ma and perhaps in Mongolia and Siberia as well. It was even more terrestrially adapted, more so than any living colobine. The living macaques (*Macaca*) are widespread across eastern Asia and in North Africa, and their fossil record adds to that large range. Scattered specimens are known from North Africa after 7 Ma, and populations have been recovered across Europe from 5.5 Ma to about 100,000 years ago. A large and highly terrestrial relative, *Paradolichopithecus*, inhabited Europe, central Asia, and perhaps eastern Asia from about 3 to 1.5 Ma.

Hominoids. The most humanlike of all primates are the apes, which form a group distinguished by generally large body size, relatively large brain, lack of an external tail, and advanced placentation pattern. Living forms include the lesser apes, or gibbons (*Hylobates*), placed in their own family Hylobatidae, and the several great apes: orangutan (*Pongo*), chimpanzee (*Pan*), and gorilla (*Gorilla*). The great apes and humans, along with some extinct relatives, are grouped as the Hominidae by some authors, while others place only humans in the Hominidae and class all great apes in the Pongidae.

One of the earliest probable members of Hominoidea is *Proconsul*, of the East African Miocene, 23–14 million years old; a few teeth of a similar form date to 26 Ma. *Proconsul* is well known by most of its skeleton (Fig. 5). Several species ranged in size from small chimpanzee to small gorilla, with a somewhat chimplike skull, large projecting canine teeth, and limb bones seemingly adapted to quadrupedal running. However, *Proconsul* has few of the defining features of the ape group. It lacks the mobile shoulder characteristic of all living species, and there is some controversy over its tail: some workers believe that tail bones have been found but not always recognized as such. For the present, *Proconsul* is retained as a hominoid belonging to a distinct archaic family of its own. Two other groups of roughly contemporaneous species (the Eurasian Pliopithecidae and the African “*Dendropithecus*-group”) are clearly more “primitive” than *Proconsul*, although they have at times wrongly been included in Hominoidea, usually as purported relatives of the gibbons. The oldest fossil gibbons date only to about 1 Ma; presumably, their ancestors lived after *Proconsul* and

entered Eurasia about the same times as did early Hominidae.

Several fossil apes from Africa dating to 20–14 Ma are often placed in the Hominidae because they appear to share “advanced” dental features with the modern great apes. But most of these species have recently been questioned as hominids because they lack apelike features of the postcranial skeleton (in the elbow, shoulder, hip, and knee joints, especially). Surprisingly, the oldest of these, *Morotopithecus*, may be the most “modern,” although only fragmentary postcranial elements are known. The youngest, *Kenyapithecus*, is similar to the first Eurasian hominoid, *Griphopithecus*, found in Turkey, Germany, Slovakia, and Austria between 16 and 13 Ma. None of these fossils are specially related to any living great ape, and they are often placed in the hominid subfamily Kenyapithecinae or even outside Hominidae.

Although interpretations vary, there appear to be three groups of Eurasian hominids between 13 and 7 Ma. *Dryopithecus* is characteristic of the Dryopithecinae, which may include the common ancestors of all later great apes (and humans). This animal has been known since the 1850s, but only in the 1990s were partial crania and skeletons described. These show several similarities to living apes in general but not to any specific forms.

Spread of modern ape ancestors. Most scientists today agree that, of the great apes, the orangutan is evolutionarily farthest from humans. This view is

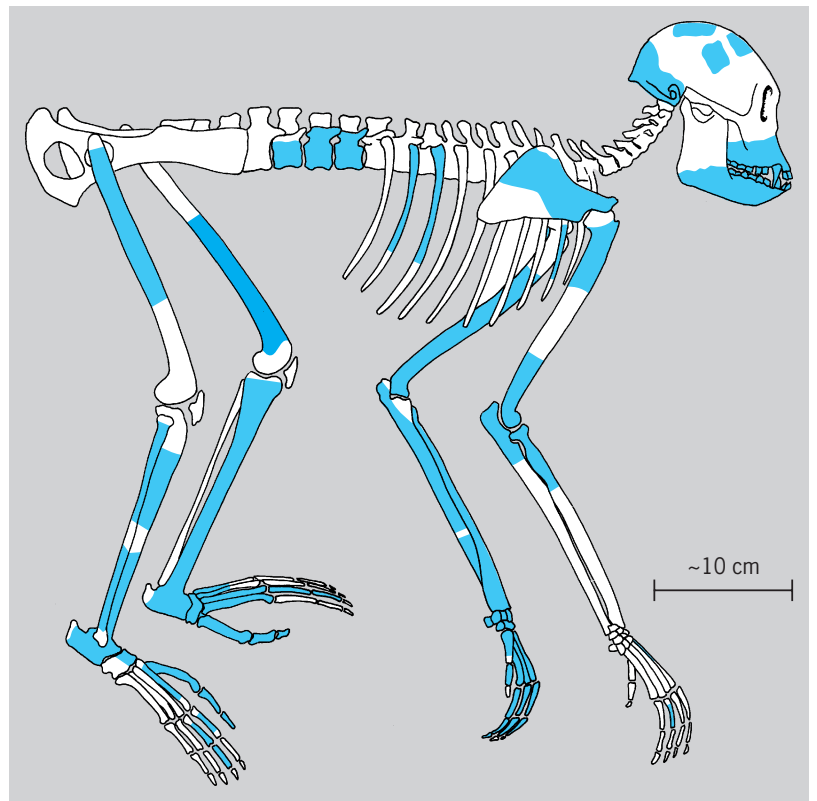


Fig. 5. Reconstructed skeleton of *Proconsul africanus*, an early hominoid (23–14 Ma) from East Africa. Known parts are shaded. (After R. L. Ciochon and R. S. Corruccini, eds., *New Interpretations of Ape and Human Evolution*, Plenum Press, 1983)

based mainly on the results of numerous studies of proteins and DNA sequences, which reveal great similarity among the genes of gorillas, chimpanzees, and humans; and with orangutans, gibbons, and monkeys successively farther from that close-knit group. As a result, orangutans and their extinct relatives are here placed in the subfamily Ponginae, while African apes, humans, and their relatives are included in Homininae. The living orangutans (*Pongo*) inhabit a small range in the deep forests of Borneo and Sumatra; less than 1 Ma, the same species was also present as far north as southern China. See APES.

The orangutan lineage is, however, the oldest well-documented one among all catarrhines. Fossils from Pakistan and India known as *Sivapithecus* show facial, palatal, and dental architectures clearly specialized in the orang direction as far back as 13–12 Ma. Although slightly younger in time, *Ankarapithecus* from Turkey at approximately 10 Ma appears intermediate between *Sivapithecus* and *Dryopithecus* in facial morphology. These three genera seem to form a transformation series representing the approximate manner in which orang ancestry evolved from dryopithecines, and both *Ankarapithecus* and *Sivapithecus* are usually included in Ponginae. But whereas the living great apes (and human ancestors) share a complex of arm-bone features related to suspensory behavior and forelimb flexibility, the upper arm of *Sivapithecus* lacks at least one part of this complex. Thus, it is possible either that this lack denies *Sivapithecus* close relationship with orangs or other apes, or that Asian and African great apes independently evolved these features long thought to document their shared ancestry. However, the lack may merely represent a secondary specialization of *Sivapithecus* which happens to be (convergently) similar to more archaic apes like the kenyapithecines. This last option makes sense, as *Sivapithecus* in other ways appears to be somewhat more adapted to quadrupedal life on the ground than is the living orangutan.

Two larger species which probably belong to the Ponginae are placed in the genus *Gigantopithecus*: One dates to about 9–6 Ma from India and Pakistan, the other lived about 1.5–0.5 Ma in China and perhaps Vietnam. Hundreds of specimens, mostly isolated teeth, are known from China, and these document a species which was probably the largest primate that ever lived (perhaps weighing 200–400 kg or 440–880 lb, although teeth are not the best body part from which to estimate weight). *Gigantopithecus* was once thought to be near the ancestry of humans, but today it is usually considered a collateral descendant of *Sivapithecus*.

The pongines probably evolved in Asia from an arboreal dryopithecine (or even kenyapithecine) ancestry which expanded into less forested environments. Such a habitat would have provided an abundance of gritty and tough food objects, to which this group's dentition appears adapted. It was at first thought that these creatures might have spent significantly more time walking and feeding on the ground than modern or earlier apes, but partial limb

bones suggest overall similarity of structure, and thus probably of behavioral function, to living arboreal and partly ground-living apes. They share with orangutans and some early humans a complex of dental-related features, including a thick molar enamel covering (to prolong tooth life with heavy wear), large molars in relation to estimated body size, strongly buttressed jaws (to take up stresses of heavy chewing), and some reorientation of the front teeth. A major factor in human dental evolution was facial shortening combined with reduction of the canine teeth and their transformation into incisorlike elements, but no Miocene fossils yet known show this feature clearly.

The origin of the Homininae is more problematic. The fossil ape *Graecopithecus* (also termed *Ouranopithecus*) is known from several Greek localities estimated to date between 10 and 8 Ma. Well-preserved facial material of this animal and of *Dryopithecus* recovered or reanalyzed in the 1990s has led different workers to suggest that one or both forms may lie near the split between Ponginae and Homininae or already on the hominine lineage, effectively close to the common ancestor of African apes and humans. This would agree well with the date of about 13–12 Ma for the earliest pongines on the assumption that both branches of the split would have developed their derived features contemporaneously. *Graecopithecus* shows more evidence of the downwardly bent face typical of African apes (a pattern termed klinorhynch) and also very thick molar enamel (as expected in an early hominine), while *Dryopithecus* has thin enamel. Some of the differences between them may just reflect the far larger size of *Graecopithecus*, but at present this genus appears more derived in the direction of later hominines. At about the same time in Africa, the only known ape fossil is a single upper jaw which was named *Samburupithecus* in 1997 and which may also represent an early, gorillalike member of Homininae. These fossils imply that the hominines may have evolved in Eurasia and then returned to Africa after about 10 Ma. Previous workers often thought that the hominine lineage could be traced purely within Africa, but that hypothesis now appears less likely. The ancestry of the African apes is still a mystery, as no fossils have yet been found which clearly represent their lineage before or after separation from humans.

Human evolution. After about 5 Ma, evidence for the human clade is increasingly common. The name *Ardipithecus ramidus* has been given to a small group of fossils dated about 4.4 Ma at the site of Aramis in the Awash Valley of Ethiopia. This species appears to be the most conservative (“primitive”) member of the Hominini, the lineage including living humans but postdating the last common ancestors of humans and other apes. *Ardipithecus ramidus* is characterized by teeth which combine some apelike morphology with reduced, incisiform canines, and also by an anterior placement of the foramen magnum (through which the spinal cord connects to the brain) indicating that the head was balanced atop

the trunk in the manner of bipedal humans rather than quadrupedal apes. A partial skeleton has been recovered, but not described as of early 2001.

Several species of the genus *Australopithecus* are known from sites dating between 4.2 and 2.3 Ma in South Africa, Chad, and the Rift Valley from Tanzania through Ethiopia. They have crania with internal volumes ("brain size") of 400–500 ml, in the range of living gorillas; body weight, however, is far smaller, about 30 kg for females, up to 60 kg for males. The jaw musculature was small enough not to require strong crests on the outer surface of the skull. The dentition had moderately large incisors, relatively small and partly incisivized canines, thick-enameled molars, and a broadly "humanlike" arcade shape. The postcranial skeleton was clearly adapted to upright bipedalism (also indicated by footprint trails), although it differed in detail from modern humans, with relatively short legs. The diet of these forms was probably omnivorous, including fruits, seeds, and perhaps scavenged animal protein; there is no evidence for toolmaking. See AUSTRALOPITHECINE.

The "robust" australopithecines, genus *Paranthropus*, were generally younger (about 2.6–1.4 Ma) and more derived craniofacially. Their postcanine teeth were greatly enlarged and adapted to crushing and grinding hard food items, while the canines and incisors were strongly reduced except in the earliest species, *P. aethiopicus*. Sagittal and nuchal crests served as anchors for the large temporal musculature covering a vault enclosing an only slightly larger brain than in *Australopithecus*; the postcranial skeleton is poorly known, but body structure and size were probably not much different from that of its predecessor.

The earliest toolmakers probably belonged to species included in the living genus *Homo*, first appearing 2.5–2.2 Ma in Malawi, Kenya, and Ethiopia, soon after the oldest stone tools. There is some debate over the number of early *Homo* species, but it seems likely that at least three were contemporaneous if not actual neighbors in eastern Africa around 2 Ma. Soon afterward, *Homo erectus* (or according to some authors, a closely related species named *H. ergaster*) emigrated from Africa to eastern Eurasia where *H. erectus* persisted until at least 300 Ka (thousand years ago). Continental Europe may not have been colonized until about 1 Ma; almost all younger populations there appear to be part of a lineage which led eventually to the Neanderthals, most common from 200 to 30 Ka between Spain and central Asia. African populations of the last half million years evolved less directly into anatomically modern humans (*Homo sapiens sapiens*), some of whom dispersed via southwestern Asia to colonize the rest of the Earth after 150 Ka. See FOSSIL HUMANS; MAMMALIA.

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