interbreeding) between regions kept the geographical varieties united in a single species at any one time. Although most researchers reject a significant contribution from Neanderthals or *H. erectus* to the modern human gene pool, there was apparently a small amount of interbreeding among the species. In order to avoid postulating the evolution of modern *H. sapiens* several times independently from the same ancestor, adherents of the “multiregional” view often collapse *H. erectus* and all later species into *H. sapiens*, so only intraspecific evolution would have occurred, despite the strong morphological (and genetic) differences among the several species that we have recognized above. See EArLY MODERN HUMANS; PALEOLITHIC; PREHISTORIC TECHNOLOGY.

Eric Delson; Karen L. Baab


---

**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): the Strepsirhini or “lower” primates (lemurs, lorises, and bushbabies) and the Haplorhini or “higher” primates (tarsiers and anthropoids (New and Old World monkeys, greater and lesser apes, and humans)). Some fossil groups (omomyiforms and adapiforms) can be placed with or near these two extant groupings; however, there is contention whether the Plesiadapiformes represent the earliest relatives of primates and are best placed within the order (as here) or outside it. See FOSSIL; MAMMALIA; PHYLOGENY; PHYSICAL ANTHROPOLOGY; PRIMATES.

Vast evidence suggests that the order Primates is a monophyletic group, that is, the primates have a common genetic origin. Although several peculiarities of the primate bauplan (body plan) appear to be inherited from an inferred common ancestor, it seems that the order as a whole is characterized by showing a variety of parallel adaptations in different groups to a predominantly arboreal lifestyle, including anatomical and behavioral complexes related to improved grasping and manipulative capacities, a variety of locomotor styles, 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, whereas the higher primates represent a group that evolved more recently (Fig. 1).

A classification of the primates, as accepted here, appears on page 515 at top.

**Early primates.** The earliest primates are placed in their own semiorder, Plesiadapiformes (as contrasted with the semiorder Euprimates for all living forms), because they have no direct evolutionary links with, and bear few adaptive resemblances to, any group of living primates. Moreover, there is strong evidence suggesting that only some plesiadapiforms might be related directly to the euprimates. Nonetheless, the chewing teeth and the locomotor anatomy of these fossil forms sufficiently resemble those of later primates to suggest a common origin of the two groups to the exclusion of members of other extant orders in most cases. Best known from the Paleocene Epoch, around 65–55 million years ago (Ma), and found in both the Old World and the New World, most known plesiadapiforms retained clawed hands and feet. However, at least one species, *Carpopotes simpsoni* (Fig. 2), appears to have possessed an opposable great toe with a nail, as in euprimates. Plesiadapiforms also lacked the bony postorbital bar that closed off the eye socket laterally (possibly to aid in stabilizing the eyeball during chewing), had

---

**Fig. 1.** Representatives of living primate families.
Order Primates
  Suborder Haplorhini (higher primates; tarsiers and anthropoids)
    Family Tarsiidae (tarsiers and close relatives)
    Family Omomyidae (extinct early haplorhines)
  Suborder Anthropoidea (anthropoids)
    Family Haplorhini (archaic anthropoids)
      Family Oligopithecidae (archaic proconsuloids)
    Family Platyrrhini (New World anthropoids)
      Family Atelidae (howlers, spider, saki, titi, and owl monkeys)
       Cebidae (squirrel, capuchin, and marmoset monkeys)
      Family Cataclini (Old World anthropoids)
    Family Eutheria (archaic eutherians)
      Family Propithecidae (extinct ancestral stock of hominoids and cercopithecoids)
       Propithecidae (extinct Eurasian early catarrhines)
       Dendropithecidae (extinct African early catarrhines)
    Family Platyrrhini (advanced catarrhines)
      Superfamily Hominioidea (apes and humans)
       Family Proconsulidae (extinct early apes)
       Hylobatidae (gibbons [lesser apes])
       Homiidae (great apes, humans, and extinct relatives)
      Superfamily Cercopithecoidae (Old World monkeys)
       Family Cercopithecidae (Old World monkeys)

rather small brains compared to their body size, mostly possessed large projecting front teeth, and were probably arboreal in habit. Known skeletons suggest a diversity of arboreal niches. Most appear to bear adaptations for vertical clinging, yet their prehensile hands (and, in some cases, prehensile feet) suggest adaptation for terminal-branch feeding. As currently understood, there were some 6–11 families of plesiadapiforms, whose precise relationships to each other and to euprimates are still controversial. These animals are known from fossil deposits as far north as Ellesmere Island, in Arctic Canada.

Fig. 2. *Carpolestes simpsoni*, a 55.5-million-year-old plesiadapiform from Wyoming. (a) Skeleton as recovered, laid out in approximate anatomical position. (b) Reconstruction in life stance on tree branch; elements in dark gray are known. (c) External restoration. (Courtesy of and copyright © Jon Bloch and Doug Boyer; artwork by Doug Boyer)
which, during the Paleocene, was covered by a subtropical forest stretching continuously from western North America across a landlocked North Atlantic into western Europe.

Several alternative hypotheses have been proposed to explain the morphological characteristics related to the origin of primates. Building on an earlier simplistic model of arboreality as the major primate feature, some paleontologists suggested that it was the ability to both grasp small branches and leap between them that enabled primates to be among the first successful arboreal mammals; in addition, their teeth were adapted for eating fruit in this arboreal setting. Anatomists focusing on living primates argued instead that the earliest primates were insectivores who hunted their prey at night in an arboreal setting, requiring improved vision to aid their search, and thus leading to larger and more frontally directed eyes (nocturnal visual predation). Researchers who studied primate ecology suggested that the rise of angiosperm plants (which emphasized flowers and fruits) led ancestral primates to enter the terminal branches to seek these foods, evolving grasping hands and feet to better move securely in trees and pick the dietary items, and later improving their vision to better locate fruit and determine its ripeness. Comparison of these models in the light of new fossils reveals that the first two probably focused on successive stages of primate evolution (grasping in some plesiadapiforms, and improved vision and postorbital bars in early euprimates), supporting the third, integrative view as most reasonable.

Eocene primates. There is no well-known plesiadapiform that is a satisfactory candidate for the ancestry of the fossil primates of modern aspect typical of the succeeding epoch, the Eocene (55–34 Ma). These succeeding euprimates are divided broadly into lemuriform like forms, grouped in the hyopdor Adapiformes, and tarsierlike forms (superfamily Omomyoidea), although this division is somewhat oversimplified. Eocene primates of both the Old World and New World already display the patterns 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 variably reduced, suggesting a de-emphasis of smell, whereas 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 in comparison to that of other mammals of the Eocene. The adapiforms are generally large-bodied and diurnal, with representatives in North America, Europe, Asia (some extending to as young as 10–8 Ma), and Africa. At least one group of European species shares detailed similarities of the foot and other regions with the later lemuriforms. On the other hand, the omomyoids are mainly small-bodied, with mostly nocturnal (large-eyed) and some diurnal species, widely distributed in North America, with one group of species restricted to Europe and a few forms in Asia. The genus *Teilhardina* (Fig. 3) may be among the earliest omomyoids, occurring at the very beginning of the Eocene in China, Europe, and western and southern North America; its relatively small orbits suggested that it was diurnal. Other European forms may be close to the ancestry of tarsiers, as are some Chinese species also of Eocene age.

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. Two distinct dentitions bearing the toothcomb characteristic of all modern strepsirhines (see below) were recovered in Eocene deposits dated to approximately 37 Ma. It has been suggested that one of these forms is related to the living bushbabies and the other to the lorises; other dental fossils reported from 30-Ma deposits in Pakistan have been identified as lemuroids. In North America and Europe, lower primates had nearly disappeared by the close of the Eocene, whereas virtually all known fossil lower primates of later epochs in Africa and most in Asia are closely related to modern primates of these areas.

Modern lower primates. The extant lower primates are included in the suborder Strepsirhini. All extant strepsirhines possess dental scrapers (toothcombs), 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 (via Jacobson’s organ) than is typical of higher primates. Furthermore, all possess a toilet claw (used for self-cleaning) on the

![Fig. 3. Cranium of the omomyoid tarsiform *Teilhardina asiatica*, from deposits dated approximately 55 Ma in China. (a) Dorsal (top) view as found. (b) Left lateral reconstruction. (Courtesy of and copyright © Xijun Ni)](image-url)
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 smaller.

There is no ancient [older than 10,000 years ago (10 ka)] primate fossil record in Madagascar, home of the most diverse group of modern lower primates, but fossils of now-extinct species document a much wider adaptive radiation before the arrival of humans on the island less than 2000 years ago. Notable among those extinct lemurs are *Palaeopropithecus*, a large-bodied under-branch hanger, somewhat sloth-like in its locomotion (Fig. 4); the semi-terrestrial and dentally specialized members of the family Archaeolemuridae, 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.

**Tarsiers.** The tiny *Tarsius*, which lives today in Southeast Asia, is a surviving member of a very old lineage and has also evolved nocturnal predatory adaptations. It has thus conserved some features that tend to resemble those of strepsirhines, in general structurally more primitive than anthropoids, to which the tarsier appears more closely related. Like anthropoids, tarsiers have acute eyesight, a dry-nosed snout, and a specialized form of placentation; they lack a toothcomb and their DNA is more similar to that of anthropoids than to strepsirhines. The extinct Eocene omomyoids are close to tarsiers morphologically; some have small eye sockets, whereas others have large orbits, suggesting nocturnality; and there are other skeletal similarities. They are often considered broadly ancestral to the anthropoids as well. Tarsierlike fossils have been recovered in Egypt and China from deposits of early Oligocene and middle Eocene age, respectively (30 and 45 Ma, respectively); in 2006, new material of the Chinese form supported a closer link to living tarsiers. In late 2010, an extinct species of *Tarsius* was described from Thailand. Another Chinese Eocene form, *Eosimias*, has been claimed to be an early anthropoid (higher primate), but some researchers argue that it is also a tarsier relative, although more distant than the three preceding forms.

Living tarsiers with their sharply crested teeth eat insects and small vertebrates. They are dramatically adapted to vertical clinging and leaping, exhibiting long hind limbs relative to forelimbs, a fused tibia and fibula in the lower leg, and two greatly elongated bones of the foot (calcaneus and navicular). Their nocturnal habit is shown by their relatively huge eyes, which, however, lack the reflective layer (tapetum lucidum) retained by strepsirhines, suggesting evolution of nocturnality from a diurnal lineage. They appear to live mainly in pairs, but they may form larger associations in some regions.

**Anthropoids.** The anthropoids include three main groups of living animals and their extinct relatives; their divergence from an ancestral stock that may have resembled some primitive omomyids probably took place approximately 55–50 Ma. The monkeys of the New World and those of the Old World are not as closely related as once thought, because the latter share a much more recent common ancestry with apes and humans, with which they are grouped in the infraorder Catarrhini. They are called monkeys by default: Both are higher primates, and neither is an ape. See MONKEY.

There is significant disagreement about the identity of the earliest known anthropoids. As noted previously, some researchers claim that the Eocene eosiomids (and/or the amphipithecids) of eastern Asia (mainly India, Myanmar, Thailand, and China) may represent early anthropoids, but others reject that claim because of their lack of morphological features found in later anthropoids. For some years, it was conjectured that the earliest African anthropoids might be represented by a few teeth (of *Algeripithecus*) from Algeria about 45 million years old, but a study published in late 2009 demonstrated that this animal was actually an early strepsirhine, perhaps even a lemuriform with a toothcomb. An even older Moroccan form (*Altit taxis*, perhaps dating to 55 Ma), known by fewer teeth, has also been suggested as a potential euprimate or anthropoid, but it is hard to determine its true affinities without additional specimens.

There is general agreement that definitive early anthropoids appear in the Fayum region of Egypt between 37 and 30 Ma, with new finds reported almost every year. Although it is now a desert, this area was once a lush tropical forest through which the sluggish proto-Nile river meandered. Four main groups of early higher primates are represented: the prolopithecids, the oligopithecids, the parapithecids, and the propithecids. The former three 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 New World monkeys. The propliopithecids (species of *Propliopithecus*, including what is usually called *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 large quadrupedal and acrobatic South American howler monkeys. Slightly more "advanced" in the direction of living catarrhines are the pliopithecids, known in Europe and eastern Asia from 18–8 Ma. Interestingly, there is a long gap of over 10 million years between the latest propliopithecids and the earliest definite pliopithecids, which had already exited Africa for Eurasia; the dendropithecids of eastern Africa (20–14 Ma) are less well known but appear to be more "advanced" than pliopithecids, implying that the latter group may have existed in Africa for millions of years before their first appearance in the fossil record. In 2010, a new primate was reported from Saudi Arabia that may illuminate the diversity of these early catarrhines. *Saadantius* is known from a partial face with upper teeth and part of the bone containing the ear region. The teeth are most similar to those of pliopithecids, but the ear is more "advanced" because it has a complete bony tube connecting the inner and middle ear (where hearing takes place) to the "outside world," as in later catarrhines. *Saadantius*, dating to about 29 Ma, may be intermediate between pliopithecids and dendropithecids, at a time when the Arabian peninsula was essentially a part of northeastern Africa.

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, possibly mangrove-like vegetation to reach the isolated island continent.

**New World primates.** The platyrhine or ateloid monkeys of South America and Central America are divided into two or three families, of which the contents vary according to researcher. Here, the small marmosets and the common squirrel and capuchin monkeys are grouped into the family Ceboidea, whereas the generally large-bodied spiderhowler and saki–uakari groups are linked to the smaller titis and (probably) owl monkeys in the Atelidae. These two families differ in the shapes of their jaws and reduction of their last molars. 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 apparent antiquity of the extant lineages, which is reflected by the close relationships of most of the few known fossils to modern genera.

The earliest fossil platyrhine, the 26-million-year-old *Brevisella* 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. Two slightly later (about 20 Ma) species from Patagonia and Chile are also probable cebids, close to the ancestry of the living *Saimiri*, whereas a new Patagonian species described in 2006 is younger (16.4 Ma) and shows precocious brain size enlargement in the cebine lineage. Several forms dated 18–17 Ma represent early atelids, close to the living pithecinines (the saki–uakari and titi–owl monkey groups).

The largest number of fossil platyrhines 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 the results of another blossoming of extinct platyrhine lineages. The Toca da Boa Vista cave site in eastern Brazil has yielded partial skeletons of "giant" relatives of the howler and spider monkeys, whereas several localities in the Caribbean dated less than 10,000 years ago produced controversial fossils perhaps related to howlers, owl monkeys, and squirrel monkeys (or possibly representing a distinct lineage whose members came to resemble those other groups). The origin of these several lineages must be many millions of years old, but there is no evidence for them until late in the Pleistocene. In 2011, three new finds greatly expanded the knowledge of these Caribbean monkeys. Divers recovered a partial skeleton with skull, and another separate skull, in underwater cave sites in the Dominican Republic. A new genus from Haiti, known mainly from teeth, along with earlier finds of a related Jamaican species, support suggested links to the owl monkeys. These geologically young species seem to have entered the Caribbean region at the same time that their relatives were deploying across northern South America more than 10 Ma.

**Old World monkeys.** The living Cercopithecidae are divided into two subfamilies: Colobinae and Cercopithecinae. The oldest cercopithecids are found in Africa, with a few fossil forms such as *ViCTORIAPITHECUS* of 15 Ma probably predating the divergence of the modern subfamilies. The cercopithecines include a wide variety of forms; all share cheek pouches for temporary food storage and usually large incisors, reflecting a fruit diet. In contrast, colobines 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 cercopithecids possess ischial callosities (rump-sitting pads), which have been lost to a greater or lesser extent in apes and humans (note that gibbons have not lost the ischial callosities).

The earliest members of the two living subfamilies also are mainly African. One colobine jaw, associated with arboreally adapted limb bones described in 2010, is known by 9 Ma, and species of both cercopithecines and colobines became more abundant from 7 to 4 Ma. 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. Papionins (baboons and their relatives) are represented first
by *Parapapio*, which was a semiterrestrial animal probably closer to the common ancestor of later forms, and then by several extinct 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 their living relatives. For example, the biggest colobine may have weighed close to 50 kg (110 lb) [Fig. 5], whereas a *Theropithecus* dated about 1 Ma has been estimated to be nearly twice that weight. 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 8–6-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 and Bulgaria. 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 (and possibly Japan) from about 4.5 to 2.5 Ma. It was even more terrestrially adapted, more so than any living colobine. The living macaques (*Macaca*) are widespread across eastern Asia and 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 80,000 years ago (80 ka). Large and highly terrestrial relatives, such as *Paradolichopithecus*, inhabited Europe, central Asia, and eastern Asia from about 3 to 1 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 placental 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 researchers (as here), whereas others place only humans in the Hominidae and class all great apes in the Pongidae. See APES.

One of the earliest probable members of Hominidea 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. 6). Several species ranged in size from a small chimpanzee to a 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 were not always recognized as such. Thus, several researchers have removed *Proconsul* from the Hominidea and placed it and several relatives as an advanced archaic catarrhine. 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 aforementioned Eurasian Pliohipithecidae and the African dendropithecids) are clearly more primitive than *Proconsul*, although at times they have wrongly been included in Hominidea, 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 time as early Hominidae did. A small group of teeth from southwestern China dating to about 6 Ma and named *Yuanmoupithecus* may belong to an early gibbon relative.

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. However, most of these
species have recently been questioned as hominids because they lack apelike features of the postcranial skeleton (especially in the elbow, shoulder, hip, and knee joints). 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 17 and 13 Ma. None of these fossils is 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. Two other groups are related to living Asian and African great apes.

**Spread of modern ape ancestors.** Most scientists today agree that, of the great apes, the orangutan is evolutionarily farthest from humans. This view is 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, 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, whereas 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 genus was also present as far north as southern China. See MOLECULAR ANTHROPOLOGY.

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 to be 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. However, 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 that the absence of this feature denies *Sivapithecus* close relationship with orangs, or that Asian and African great apes independently evolved these features long thought to document their shared ancestry. Alternatively, the lack of this feature may merely represent a secondary specialization of *Sivapithecus* that happens to be similar to what is seen in more archaic apes such as the kenyapithecines. This last option makes the most 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 that probably belong to the Ponginae are placed in the genus *Gigantopithecus*. One dates to about 9–6 Ma from India and Pakistan, whereas the other lived approximately 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 that was probably the largest primate that ever lived [perhaps weighing 200–400 kg (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 that expanded into moist forested environments. Such a habitat would have provided an abundance of fruit plus gritty and tough food objects (such as fibrous and thick-skinned fruits or nuts), to which this group’s dentition appears to be 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. As with orangutans and some early humans, they share 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 incisor-like elements, but no Miocene fossils yet known show this feature clearly. See DENTAL ANTHROPOLOGY; DENTITION; FOSSIL HUMANS.

The origin of the Homininae is more problematic. The fossil ape *Oouranopithecus* (also termed *Graecopithecus*) is known from several Greek localities estimated to date between 9.6 and 8.7 Ma. Well-preserved fossil 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 may lie 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. *Oouranopithecus* shows more evidence of the downwardly bent face typical of African apes (a pattern termed klinorhynchy) and also very
thick molar enamel (as expected in an early hominin), whereas *Dryopithecus* has thin enamel. Some of the differences between them may then reflect the far larger size of *Ouranopithecus*, but at present this genus appears more derived in the direction of later hominines. The first known ape fossil dated to about the same time in Africa was a single upper jaw found by a Japanese team in 1982 and named *Samburupithecus* in 1997. Then, in 2007, two additional Japanese-led teams recovered dental remains of similar age in Kenya (*Nakaliopithecus*) and Ethiopia (*Chororapithecus*). All of these fragmentary fossils are large and may represent early, gorillalike members of Homininae.

Some researchers have suggested that hominines may have evolved in Eurasia and then returned to Africa about 10 Ma. Previous workers often thought that the hominine lineage could be traced purely within Africa, and some of them now point to the aforementioned three large (if poorly known) fossils as supporting evidence. On the other hand, there is still a significant "gap" in Africa between the kenya- 

- pithecines of 15–13 Ma and the apparently more modern jaws from 10 Ma, whereas that time interval in Eurasia has yielded a number of fossils that appear to fill this gap and document a radiation of forms potentially ancestral to both pongines and hominines in Eurasia. In mid-2011, this conflict remained unresolved. The later ancestry of the African apes is still a mystery: Until mid-2005, no fossils had been found that clearly represent their lineage before or after separation from humans. However, a few teeth reported from a Kenyan archeological site appear to represent a form of chimpanzee, but so far these say little about the history of African ape adaptations, and some researchers have suggested that they are in fact teehs of human relatives.

**Human evolution.** During the last few decades, three new African genera have been described that have been claimed to throw new light on the origin of the Hominini, the lineage including living humans but postdating the last common ancestor of humans and apes. Potentially the oldest of these is *Sabelanopithecus*, found in 2002 in Chad, and dated in the range of 7–6 Ma. Slightly younger is *Orrorin*, from Kenya, at about 6 Ma, and the youngest is *Ardipithecus*, reported from sites in Ethiopia dating between 5.8 and 4.3 Ma and described in detail in 2010. Each of these is known from essentially different skeletal elements, and each has been disputed in one way or another, reflecting the fact that there is as yet no adequate conception of what the earliest hominins might be expected to look like. All, however, have been claimed, on the basis of tenuous evidence, to have been upright bipeds.

Several species of the genus *Australopithecus* are known from sites dating between 4.2 and 1.8 Ma in South Africa, Chad, and the Rift Valley from Tanzania through Ethiopia. They have crania with internal volumes (brain size) of 400–500 cm$^3$, in the range of living gorillas; body weight, however, is far smaller, being about 30 kg (66 lb) for females and up to 60 kg (132 lb) for males. The jaw musculature was small enough that it did not require strong crests on the outer surface of the skull. The dentition had moderately large incisors, relatively small and partly incisivized canines, thick-enameded 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 animal protein. There is no definitive evidence for toolmaking. However, in 2010, one team described animal bones from older than 3 Ma and claimed that these bones showed cut marks made by stone tools; other scholars rejected this claim. See AUSTROLOPIETH.

### Fossil seeds and fruits

The organic remains, traces, or imprint of seeds and fruits. Seeds, ovules containing a fertilized egg and ready to be shed from the plant, are reproductive organs characteristic of both gymnospermous and angiospermous plants. In angiosperms (Magnoliophyta), an additional structure, the matured ovary, encloses one or more seeds to form a fruit. See FOSSIL; FRUIT; MAGNOLIOPHYTA; SEED.

Seeds and fruits are less commonly found as fossils than as vegetative remains. They may be preserved structurally as casts, or as compressions which are sometimes found with leaf compressions. Seeds and fruits often occur in lignites. See LIGNITE.

The oldest known seed plants are of Mississippian age. Carboniferous seed plants include the extinct Cordaitales, probable conifer ancestors, and Pteridospermae, seed plants with fernlike foliage. Both groups had similar seeds, basically like those of modern cycads. No embryos have been found in Paleozoic seeds. See CORDATALES; PTERIDOSPERMS.

During the Mesozoic Era, all major modern groups of seed plants were represented, along with members of the declining cordaitalean and pteridospermous stocks. Among the most completely known Mesozoic seeds are those of the cycadeoids, extinct cycad relatives. Their silicified, beehive-shaped trunks may include shoots bearing numerous small seeds between thick scales. The Mesozoic Caytoniales, whose small seeds were borne in fleshy enclosures, were thought at one time to be ancestral angiosperms. Now they are recognized as gymnospermous forms, probably related to the pteridosperms. See CAYTONIALES; CYCAEOIDEALES.

Angiosperm fruits are rare in Lower Cretaceous beds; Upper Cretaceous fruits are known from northern Africa; Long Island, New York; and elsewhere. Tertiary fruits and seeds have been found in numbers in the United States in the Brandon lignite of Vermont (see illustration) and in the Clarno Formation of central Oregon. Silicified cones of araucarian conifers are known from Patagonia. The best-known European Tertiary fruits and seeds are from the brown coals of Germany and the Eocene London Clay Formation of England.

Important paleobotanical findings resulting from the study of fossil seeds and fruits include the knowledge obtained of the independent evolution of the seed habit in unrelated groups; the discovery that much Carboniferous fernlike foliage was borne on seed plants rather than on ferns; and the discovery that Glossopteris, an important plant in widespread Permian floras of the Southern Hemisphere, was a seed plant. Pyritized fruits from the London Clay Formation reveal the presence of many extinct genera along with modern genera in early Tertiary time. Morphological changes in herbaceous angiosperm seeds from sequences of Tertiary beds furnish data on rates of evolution in plants. Because plant classification is based primarily upon reproductive structures, fossil seeds and fruits provide highly reliable evidence for

---

*Early Tertiary fruits and seeds which were found in the Brandon lignite of Vermont. (a) Endocarps of Symlocos. (b) Seeds of grape (Vitis). (c) Seeds of Rubus. (d) Endocarp of extinct species of Nyssa. (e) Seeds of fossil genus of family Rutaceae, which are related to Phellodendron. (f) Endocarps of a species of Alangium. (g) Acorn cups, Quercus sp. (Courtesy of Elsea S. Bergstrom)