

Primates

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GLOSSARY

Cathemeral Activity pattern of an animal wherein activity is distributed over the entire 24-hr cycle, rather than limited to the daytime (diurnal), night-time (nocturnal), or the times around dawn and dusk (crepuscular)

Morphology Visible attributes; anatomy

Phylogeny Evolutionary history; a statement of evolutionary relationships

Systematics Study of the diversity of life and of the relationships among taxa

Taxonomy Theory and practice of classifying organisms; derived from the noun "taxon" (pl. taxa), which denotes a named unit at any rank of the Linnean hierarchy

PRIMATES IS THE ORDER OF MAMMALS CONTAINING the lemurs, lorises, tarsier, monkeys of the Old and New Worlds, apes, and humans, totaling approximately 200 living species. Also usually regarded as primates, besides the fossil relatives of extant species, are the members of an early Tertiary group of "archaic" forms known as Paromomyiformes.

I. DEFINITION AND CLASSIFICATION

Attempts to define the order Primates in terms of morphological characteristics uniquely shared by all

of its members have routinely been frustrated by the fact that phylogeny, rather than morphology, gives the group its unity. However, if we disregard the archaic forms of the Paleocene and early Eocene, we can follow W. E. Le Gros Clark in identifying several "progressive trends" that have some value in demarcating developments in primate evolution from those in other mammalian lineages. These include a decreased significance of olfaction compared with stereoscopic vision; enhancement of grasping and manipulative capabilities, associated with the replacement of claws by nails on all or nearly all digits; and a tendency toward relative enlargement of the "higher" centers of the brain, notably the association areas of the cortex.

A diagram of primate evolutionary relationships at the family level is shown in Fig. 1. Many of its details, perhaps most importantly the affinities of the tarsier, are actively debated, and we do not regard this statement as definitive. However, it does serve as the basis for the outline classification presented in Table I. Geological ranges of the families identified in Fig. 1 are shown in Fig. 2.

II. "ARCHAIC" PRIMATES

The primate order originated prior to about 65 Myr (million years) ago, and early primates flourished in the northern continents during the Paleocene epoch, around 65–56 Myr ago. The most successful of these archaic forms were *Plesiadapis* (Figs. 3 and 4) and its relatives, which were characterized by small braincases, long faces, clawed feet, and an enlarged, specialized anterior dentition. "Archaic" primates lacked the postorbital bar, a strut that delineates the orbit laterally in all living primates, and are included in the

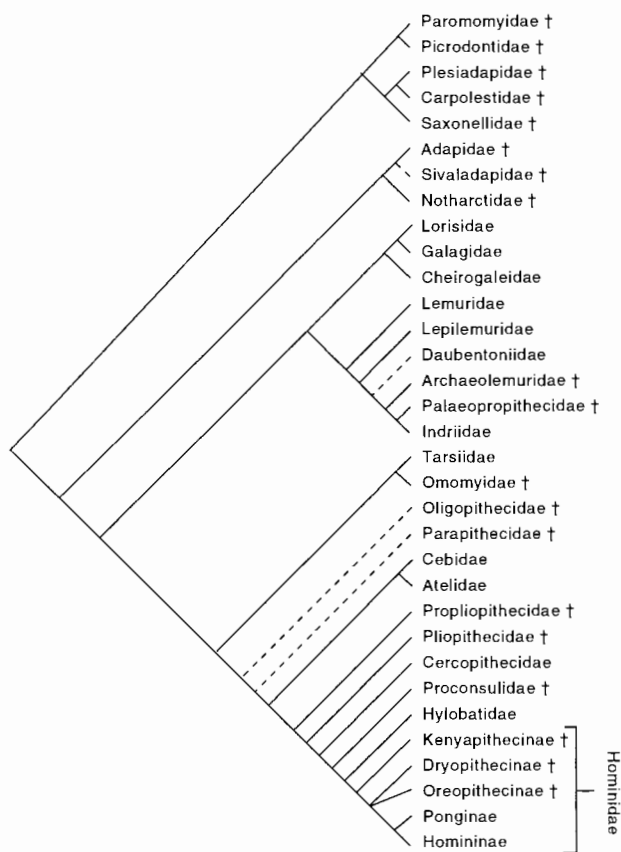


FIGURE 1 A provisional phylogeny of the primates. † denotes extinct taxon. Dotted lines indicate alternative placement of disputed taxa.

order principally on the bases of the structure of their bony ear and postcranial bones and their molar tooth morphology. Generally, in early primates, the molars show some lowering of cusp relief, which has been taken to suggest that the origin of the primate order lay in a dietary shift away from insects and toward plant foods. Postcranial remains are rare but indicate that *Plesiadapis* itself, though heavy-boned, was arboreal. Although some studies suggest that the paromyiforms were more closely related to other mammalian groups and should be removed from the primates, we retain them within this order at present.

III. "LOWER" PRIMATES OF MODERN ASPECT

A. The Living "Lower" Primates

The extant strepsirhine (or "lower") primates (suborder Strepsirhini; Fig. 3) are most abundantly repre-

sented on the island of Madagascar, where higher primates were absent before the recent arrival of humans. All living strepsirhines are united in possessing a "grooming claw" on the second pedal digit and a "tooth comb," in which the slender, elongated front lower teeth lie horizontally and are closely pressed together. They also retain a primitive form of the nasal apparatus, with a "tethered" upper lip (fixed to the upper jaw in the midline, rather than fully mobile) and a moist rhinarium (or "wet nose," as in dogs). In comparison with the "higher" primates, the sense of smell, as expressed by these anatomical retentions and the presence of olfactory marking behaviors using feces, urine, or the exudations of specialized glands, is relatively important. On the other hand, the diurnal visual sense is less developed, as reflected in weak or absent color vision. Notably, however, in contrast to the higher primates, many strepsirhines are nocturnal.

Surviving strepsirhines in Africa and Asia are all classified as lorisooids, belonging to the families Lorisidae (the quadrumanous lorises and pottos) and Galagidae (the leaping bushbabies); so also are the dwarf lemurs of Madagascar (family Cheirogaleidae). All lorisooids are nocturnal primates, which, although social, are relatively nongregarious; as noted, scent-marking provides an important channel for intraspecific communication among these forms.

The Malagasy families Lemuridae (the lemurs, ruffed lemurs, and bamboo lemurs), Indriidae (the sifakas, babakotos, and woolly lemurs), Daubentoniidae (the aye-aye), and Lepilemuridae (sportive lemurs) are more diverse. Of these families, the latter two are exclusively nocturnal, and the last probably lost a diurnal genus only recently; the other two (the principally quadrupedal Lemuridae and the vertical-clinging and leaping Indriidae) are chiefly composed of diurnal or cathemeral species and show a great deal of variation in social organization. Groups range from bonded pairs (permanent associations of an adult male with an adult female) with immature offspring through small multimale, multifemale units to large heterosexual groups of 30 individuals or more. These groups, as in most higher primates, appear to be based around female nuclei, and male exchange is common, especially during the brief annual breeding season. Diets appear to vary widely by season and locality, and despite their generally lower ratios of brain to body size, these diurnal strepsirhines seem to be every bit as opportunistic in the exploitation of their habitats as are the higher primates.

TABLE I
Partial Classification of the Order Primates

Rank	Taxon	"Common" name
Semiorder	Paromomyiformes†	"Archaic" forms
Suborder	Plesiadapiformes†	"Archaic" forms
Superfamily	Paromomyoidea†	"Archaic" forms
Superfamily	Plesiadapoidea†	"Archaic" forms
Genus	<i>Plesiadapis</i> †	
Semiorder	Euprimates	"Primates of modern aspect"
Suborder	Strepsirhini	"Lower" primates, strepsirhines
Infraorder	Adapiformes†	Extinct "lemur-like" forms
Genus	<i>Notharctus</i> †	
Genus	<i>Smilodectes</i> †	
Genus	<i>Leptadapis</i> †	
Infraorder	Lemuriformes	Lemurs, lorises
Superfamily	Lemuroidea	"True" lemurs
Family	Lemuridae	
Superfamily	Indrioidea	Sifakas, aye-aye, etc.
Family	Indriidae	Sifakas
Family	Daubentoniidae	Aye-aye
Family	Lepilemuridae	Sportive lemurs
Superfamily	Lorisoidea	Lorises, galagos, mouse lemurs
Family	Lorisiidae	Lorises
Family	Galagidae	Galagos, bushbabies
Family	Cheirogaleidae	Mouse and dwarf lemurs
Suborder	Haplorhini	"Higher" primates and tarsiers
Hyporder	Tarsiiformes	Tarsier, fossil relatives
Family	Tarsiidae	Tarsiers
Family	Omomyidae†	Extinct "tarsier-like" forms
Genus	<i>Necrolemur</i> †	
Hyporder	Anthropeoidea	"Higher" primates
Infraorder	Paracatarrhini†	"Archaic" anthropoids
Family	Oligopithecidae†	"Archaic" protoanthropoids
Genus	<i>Catopithecus</i> †	
Family	Parapithecidae†	Extinct Oligocene monkeys
Genus	<i>Apidium</i> †	
Infraorder	Platyrrhini	New World anthropoids
Superfamily	Ateloidea	New World monkeys
Family	Atelidae	Howler, spider, saki
Subfamily	Atelinae	Howler, spider monkeys
Subfamily	Pitheciinae	Saki, titis, owl monkeys
Family	Cebidae	Marmosets, capuchins, squirrel monkeys
Subfamily	Cebinae	Squirrel, capuchin monkeys
Subfamily	Callitrichinae	Marmosets, tamarins
Subfamily	Branisellinae†	Extinct early platyrrhines
Infraorder	Catarrhini	Old World anthropoids
Parvorder	Eocatarrhini†	"Archaic" catarrhines
Family	Propliopithecidae†	Extinct common ancestors of eucatarrhines
Genus	<i>Propliopithecus</i> †	
Family	Pliopithecidae†	Extinct early catarrhines
Genus	<i>Pliopithecus</i> †	
Parvorder	Eucatarrhini	Advanced Catarrhines
Superfamily	Cercopithecoidea	Old World monkeys
Family	Cercopithecidae	Old World monkeys
Subfamily	Cercopithecinae	Cheek-pouched Old World monkeys
Subfamily	Colobinae	Leaf-eating Old World monkeys
Genus	<i>Mesopithecus</i> †	
Subfamily	Victoriapithecinae	Extinct early cercopithecids
Superfamily	Hominoidea	Apes and humans
Family	Proconsulidae	Extinct early apes
Family	Hylobatidae	Lesser apes, gibbons
Genus	<i>Hylobates</i>	

(continues)

TABLE I (Continued)

Rank	Taxon	"Common" name
Family	Hominidae	Great apes, humans and extinct relatives
Subfamily	Kenyapithecinae	Extinct "archaic" great apes
Subfamily	Dryopithecinae	Extinct early great apes
Subfamily	Oreopithecinae	<i>Oreopithecus</i>
Subfamily	Ponginae	Orangutans and extinct relatives
Genus	<i>Pongo</i>	
Genus	<i>Sivapithecus</i> †	
Subfamily	Homininae	African apes, humans, and extinct relatives
Genus	<i>Ardipithecus</i> †	
Genus	<i>Australopithecus</i> †	
Genus	<i>Paranthropus</i> †	
Genus	<i>Homo</i>	
Genus	<i>Graecopithecus</i> †	
Genus	<i>Gorilla</i>	
Genus	<i>Pan</i>	

†Denotes extinct taxon; genera listed are those illustrated or mentioned in the text.

B. The Fossil Record of Lower Primates

By the end of the Paleocene, new kinds of primates were beginning to appear alongside the archaic forms, and in the following Eocene epoch, between about 56 and 34 Myr ago, these more modern-looking forms rapidly replaced the archaic types. The fossil record, as currently known, provides no clear ancestry within the Paleocene primate radiation for that of the Eocene; it is possible that the African record, still poorly known, holds the key to this relationship. Eocene primates are generally classified into the lemur-like Adapiformes and the tarsier-like Omomyidae, although this simple division probably obscures a situation of considerably greater complexity, and some of today's lemurs may bear more than general affinities to elements of the Eocene primate fauna. Whatever the exact geometry of the relationships between the lower primates of today and those of the Eocene may ultimately prove to be, however, as functioning organisms, the latter were already clearly similar to today's lower primates. Undoubtedly arboreal in habit, Eocene primates had grasping hands and feet, with an opposed hallux and sensitive digital pads backed by flat nails; braincases were relatively large whereas the face was reduced, presumably in correlation with a deemphasis of the sense of smell. Conversely, the eyes faced forward to enhance overlap of the visual fields, thus promoting stereoscopic vision, and were ringed by bone (Figs. 4 and 5).

As climates cooled subsequent to the Eocene, primates began to disappear from the northern conti-

nents, and later fossil evidence, principally from the Miocene of Africa and Asia, reveals strepsirhine primates closely related to those that now live in those areas. Late Holocene deposits in Madagascar indicate the survival until recently, on that island, of a much more varied lemur fauna than exists there today; extinct genera include several large-bodied and specialized forms.

IV. "HIGHER" PRIMATES AND TARSIERS

The living primates have been subdivided alternatively into the Prosimii (=Plesiadapiformes, Strepsirhini, and Tarsiiformes here) versus Anthropoidea or into the Strepsirhini versus Haplorhini, with the main difference involving the position of the tarsier. Most current research, both genetic and morphological, supports the phylogenetic linkage of tarsiers to the other "dry-nosed" or haplorhine primates (monkeys, apes, and humans), as opposed to the "wet-nosed" strepsirhines characterized, as noted earlier, by a tethered upper lip and greater sensory emphasis on olfaction. The resulting division is usually recognized at the taxonomic level of the suborder, as in our classification. However, as universally accepted today, the platyrrhines (New World monkeys) and the catarrhines (Old World monkeys, apes, humans, and their extinct relatives) shared a common ancestry distinct from all other primates, thus forming a natural

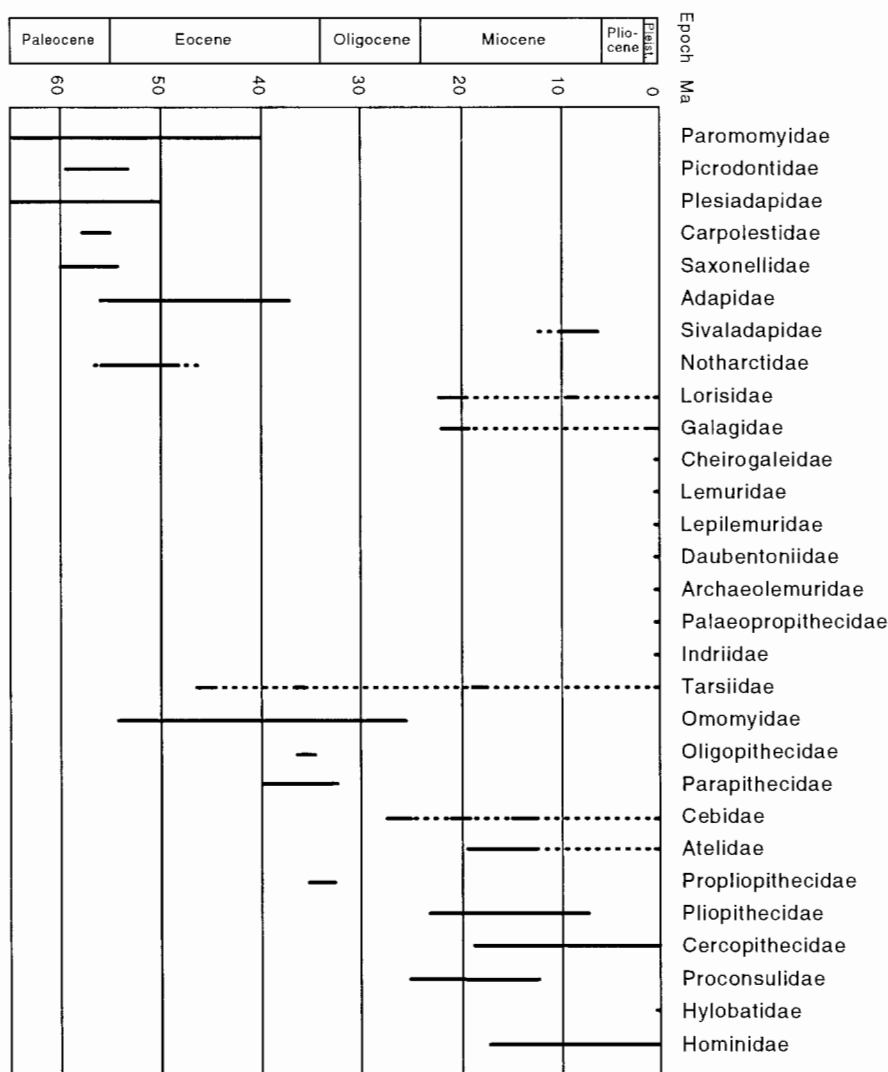


FIGURE 2 Temporal distribution of the primate families shown in Fig. 1. Dotted lines represent presumed range continuity between known occurrences.

group—the “higher” primates, or anthropoids. This group is formally recognized as the Anthropoidea and was previously ranked as a suborder, when tarsiers were considered prosimians. To recognize both of these important systematic evolutionary concepts, we include the Anthropoidea as a subunit within the Haplorhini, giving it the rank of hyporder.

A. The Living Haplorhines

Modern tarsiers (Tarsiidae) occur as four species of the genus *Tarsius*. They are among the smallest primates, restricted to islands of Southeast Asia and

the Philippines, where they live in pair-bonded groups. Their huge eyes are an adaptation to their principally nocturnal activity pattern, and their elongated leg and foot bones allow a rapid-leaping locomotion (see Fig. 3).

The South American platyrrhines are considered by many to be the most diverse primate superfamily, in terms of diet, locomotion, and morphology. The family Cebidae includes the subfamilies Callitrichinae (marmosets and tamarins) and Cebinae, both characterized by a short face and lightly built masticatory system designed for a diet of insects, fruits, and gums. The marmosets are the smallest living anthropoids;

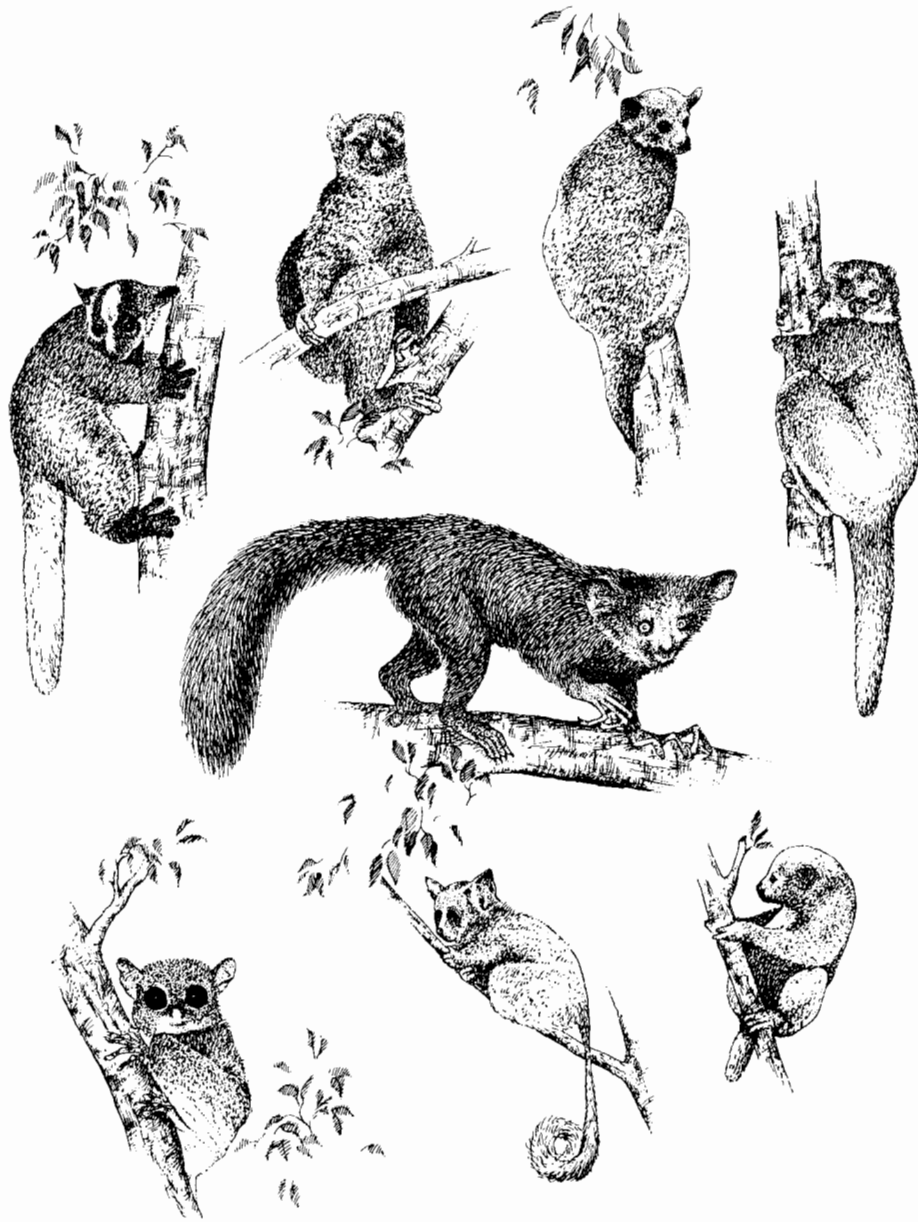


FIGURE 3 Representative living lower primates. Clockwise from top left: forkmarked lemur (Cheirogaleidae), bamboo lemur (Lemuridae), sportive lemur (Lepilemuridae), avahy (Indriidae), potto (Lorisidae), bushbaby (Galagidae), tarsier (Tarsiidae). Center: aye-aye (Daubentoniidae). Not to scale. (Illustration by Don McGranaghan.)

they are generally pair-bonded, and the male takes an active role in the care of the young, often twins. The cebines include both large- (capuchins) and small-bodied (squirrel monkey) species, which live in large groups and have relatively large brains for platyrrhines. The family Atelidae includes mostly larger platyrrhines with a heavily built masticatory apparatus

(jaws, teeth, projecting face, chewing muscles) adapted to a frugivorous (fruit-eating) or folivorous (leaf-eating) diet. The uniformly large atelines (including the spider and howler monkeys) are characterized by prehensile (grasping) tails and suspensory locomotion and feeding postures, although some species are acrobatic, whereas others move cautiously; most atelines live in

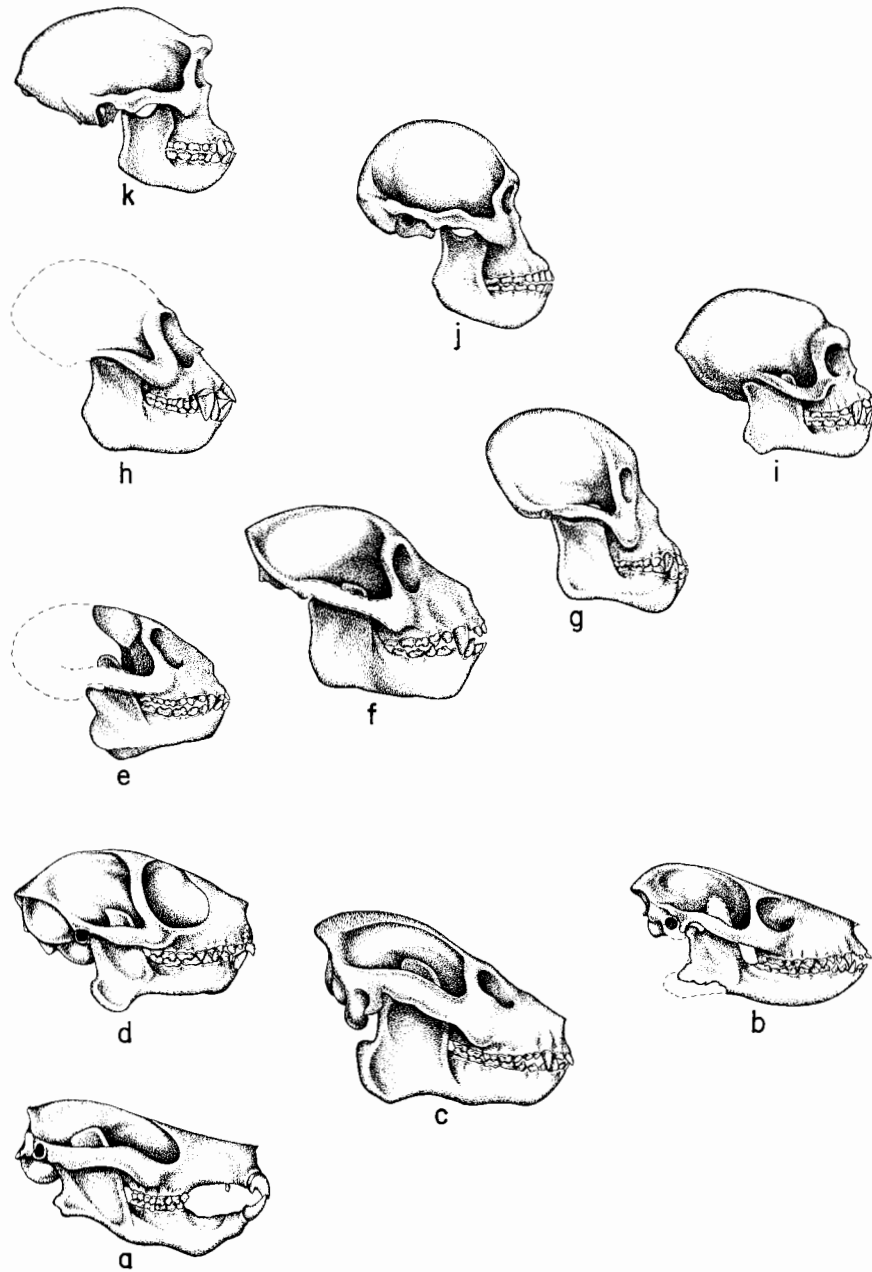


FIGURE 4 Skulls in lateral view of various extinct primates. a, *Plesiadapis tricuspidens*; b, *Notharctus tenebrosus*; c, *Leptadapis magnus*; d, *Necrolemur antiquus*; e, *Apidium phiomense*; f, *Propithecus* (= *Aegyptopithecus*) *zeuxis*; g, *Proconsul heseloni*; h, *Cebupithecus sarmientoi*; i, *Pliopithecus vindobonensis*; j, *Australopithecus africanus*; k, *Homo erectus*. Not to scale. (Illustration by Don McGranaghan.)

moderately large social units. By contrast, the pitheciines may form pair-bonded social groups (the titi and the nocturnal-cathemeral owl monkey) or small heterosexual units (the somewhat larger-bodied sakis and uakaris). The latter forms have adapted to a diet of

hard-shelled or hard-seeded fruits, for which they have developed a specialized dentition (Fig. 6).

The Old World monkeys (superfamily Cercopithecoidea) are the most numerous living primate group, with some 75 species in about 15 genera,

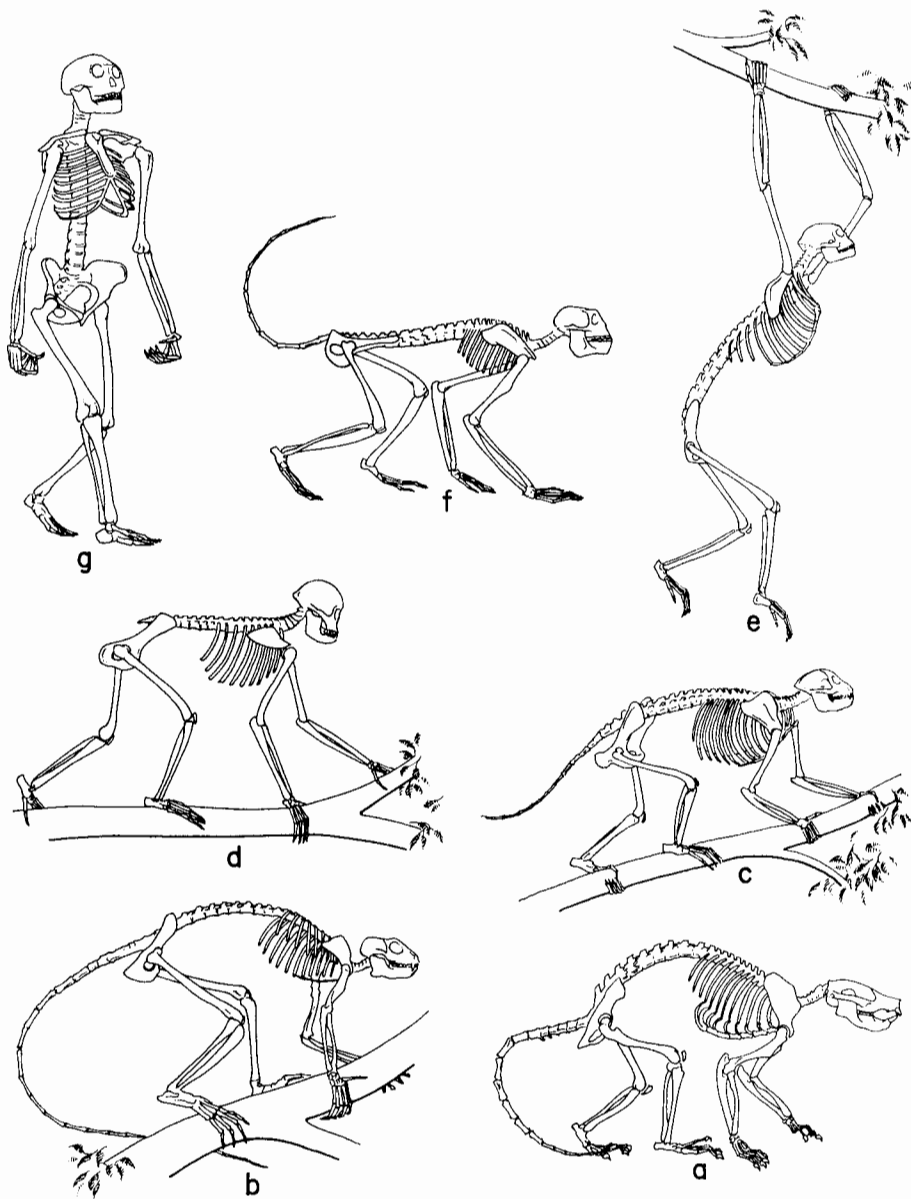


FIGURE 5 Skeletons of various extinct primates. a, *Plesiadapis tricuspidens*; b, *Smilodectes gracilis*; c, *Propithecus* (= *Aegyptopithecus*) *zeuxis*; d, *Proconsul heseloni*; e, *Pliopithecus vindobonensis*; f, *Mesopithecus pentelicus*; g, *Australopithecus afarensis*. Not to scale. (Illustration by Don Mc-Granaghan.)

and among the most widely distributed. They share a distinctive dental pattern and the presence of ischial callosities, tough rump patches on which they sit in trees (also found in gibbons and possibly an ancient catarrhine feature). One family, Cercopithecidae, is divided into two subfamilies, Cercopithecinae and Colobinae. The former is characterized by cheek

pouches for temporary food storage, a simple stomach, and generally a somewhat to greatly elongated snout; the diet is eclectic, including fruits, some leaves and shoots, nuts, insects, and even rare vertebrate prey. A partly terrestrial quadrupedal pattern of locomotion probably is typical for the cercopithecines, with several groups independently either

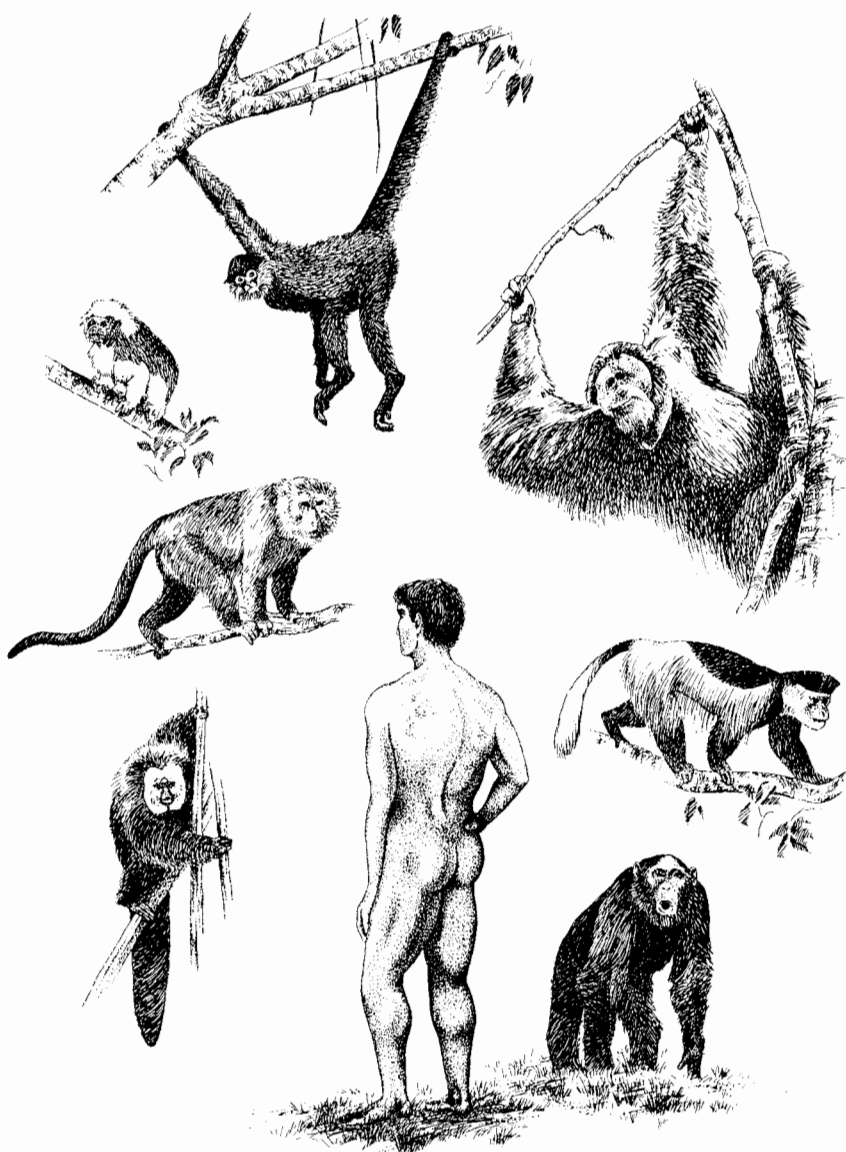


FIGURE 6 Representative living higher primates. Clockwise from upper left: tamarin (*Callitrichinae*), spider monkey (*Atelinae*), orangutan (*Ponginae*), colobus (*Colobinae*), chimpanzee, human (*Homininae*), saki (*Pitheciinae*), macaque (*Cercopithecinae*). Not to scale. (Illustration by Don McGranaghan.)

strongly terrestrial or more fully arboreal. The colobines, on the other hand, are more acrobatic arboreal runners and leapers, with only one living species spending much time on the ground. Their diet is concentrated on leaves and shoots, as mirrored in their enlarged and sacculated stomach. Social organization varies widely among the cercopithecids, including bonded pairs, unimale “harems” with sev-

eral females, and groups with roughly equal numbers of both sexes and between 15 and 200 members. African cercopithecines include mangabeys, baboons, mandrills, guenons, and patas monkeys, whereas the macaques occur in Northwest Africa and range from Pakistan to Japan and Indonesia; they live in environments from desert fringe through savannah, rain forest, deciduous forest to high moun-

tains. Colobines are less tolerant, with the African colobus varieties and the Asian langurs and doucs found mainly in deciduous or evergreen forest, although “golden monkeys” range to high elevations in China and proboscis monkeys live in mangrove swamps.

To humans, the most intriguing primates are the apes, grouped (along with people) in the superfamily Hominoidea. The lesser apes, or gibbons (*Hylobates*), form one family found only in Southeast Asia. These pair-bonded fruit-eaters are most famous for their brachiating pattern of locomotion, involving ricochetal arm-swinging and below-branch suspension, as contrasted with the above-branch running of most monkeys. Gibbon males and females both defend their home ranges or territories by means of “song” calls of several types, which indicate their position to neighbors and cement the pair bond.

In the past, great apes (Asian orangutan, African chimpanzee and gorilla) were often classified together in the family Pongidae, as opposed to humans in Hominidae, but a variety of mainly genetic studies have demonstrated that humans and great apes are extremely close to each other in evolutionary terms and that African apes and humans form a phyletic unit or evolutionary subgroup as contrasted with orangutans. Thus, by analogy to other primates (and mammals in general), only a single family Hominidae is recognized to reflect the low diversity of this group, and it is in turn divided into the subfamilies Ponginae for the orangutan and its extinct relatives and Homininae for humans, chimpanzees, and gorillas. The orangutan is, almost like lorisoids, relatively nongregarious: the large adult males patrol broad ranges overlapping those of females and their offspring, but the two sexes seldom travel together. Gorillas live in social groups with one or two adult males and several females, whereas chimpanzees usually form small groups of males, females, and young or consort pairs, which fluidly “fuse” into larger bisexual groups and divide again every few days. Diets of most hominoids consist mainly of fruits, although gorillas also eat other plant parts, and chimpanzees have been seen to actively hunt various animals including monkeys. Chimpanzees also use twigs to obtain termites from their mounds, stones to break open nutshells, and leaves to get water from tree cavities; thus, they are considered to make and use tools on a regular basis, and they teach this behavior to their offspring. Great apes do not truly brachiate (like gibbons do) as adults: orangutans use hands and feet interchange-

ably when climbing and walk quadrupedally on the ground; chimpanzees and gorillas “knuckle-walk” on the ground but also climb actively and swing manually in trees (except for adult gorillas).

B. The Fossil Record

The living tarsiers represent only a small fraction of the past diversity of the Tarsiiformes. The earliest tarsier-like primates, known as the Omomyidae, first appeared in the early Eocene, along with the lemur-like adapiforms (see earlier). This group was diverse throughout the Eocene in North America, with several species often found together. Additional species, including several in a distinct subfamily, occurred in Europe, and rare fossils possibly belonging to the Omomyidae have been recognized in Asia and northern Africa. Recently, fragmentary remains of possible close relatives of *Tarsioides* itself have been recovered from the Eocene of China, Oligocene of Egypt, and Miocene of Thailand. Most likely, an animal broadly similar to the Eocene omomyids was ancestral to the anthropoids, but no known form is a good candidate for such an ancestor. A variety of poorly known species from eastern Asia (45–40 Myr ago) and northern Africa (55–40 Myr ago) have been suggested as documenting a previously unknown major radiation of protoanthropoids. The fragmentary nature of these fossils makes it difficult to test this hypothesis.

The 36- to 33-Myr-old Fayum fossil beds in northern Egypt provide an important “window” onto both anthropoid and catarrhine origins. Of the three families known from there, two may belong to an archaic anthropoid infraorder, the Paracatarrhini; some authors consider these animals to be members of the catarrhine radiation, but they appear too conservative to be retained in that group. The Oligopithecidae includes the recently discovered *Catopithecus*, for which a skull and jaws are known. These reveal a mosaic pattern of derived and conservative features: for example, the orbits appear to have been closed off as in anthropoids, whereas the mandibular symphysis was probably unfused and the teeth are like those of lower primates. The oligopithecids may represent a late-surviving member of the protoanthropoid radiation. Somewhat more derived are the Parapithecidae, which were morphologically monkey-like, sharing general features of locomotor ability, relative brain size, and probably lifeways with living monkeys of both the Old and New Worlds. Although once proposed as ancestors

of the cercopithecoids, they are today viewed as an early side-branch radiation of either the catarrhines or the anthropoids as a whole. They were mainly arboreal fruit-eaters; at least one species was unique among primates in having lost all lower incisor (front) teeth (see Figs. 4 and 5).

The earliest New World monkeys appeared in South America late in the Oligocene, about 27 Myr ago, with no trace of earlier primates south of Texas. During the early Cenozoic, South America was an island continent, isolated from Africa by the expanding South Atlantic Ocean and from North and Central America by a broad Caribbean–Pacific connection, and the source area of the platyrrhines is, thus, a continuing problem in primate evolution. Both North America (with Eocene omomyids) and Africa (with somewhat earlier anthropoids; see the following) have been championed, with the latter view more widely but not universally accepted. In one of the most fascinating aspects of New World monkey evolution, fossils that can be readily identified as belonging to each of the two living families occur by 20 Myr ago, and by 15 Myr ago, fossils that belong to each of the four living subfamilies have been identified; some of those fossils can even be identified as close evolutionary relatives or ancestors of certain living genera. This very early diversification of living lineages is uncommon among primates (see Figs. 1, 4, and 5).

By contrast, the history of catarrhine primates is best seen as a series of radiations, each replacing its antecedents after a brief overlap interval. The third group of anthropoids represented in the Egyptian Fayum, contemporary with the parapithecids, includes several species of the undoubted archaic catarrhine *Propliopithecus* (one is often called *Aegyptopithecus*). In tooth and skull morphology, these animals are more similar to the living catarrhines and may be similar to the common ancestor of all later Old World anthropoids. Additional genera of “primitive” catarrhines, not closely related to either monkeys or apes, are known from the Miocene of Africa, Europe, and Asia. These forms, along with the older *Propliopithecus*, offer insight into the morphology and diversity of early catarrhines.

The oldest definite Old World monkeys (cercopithecoids), recognized by their distinctive tooth morphology, are known from the earlier Miocene (15–20 Myr) of eastern and northeastern Africa. The two modern subfamilies possibly differentiated in Africa by 12 Myr ago, but they are not documented until about 10 Myr ago. Today, the leaf-eating colobines

are almost entirely arboreal and generally of rather small size, but large, terrestrially active forms lived in Europe and Africa between 5 and 2 Myr ago and briefly extended into Mongolia. The same interval (the Pliocene) saw a great radiation of cercopithecine monkeys in Africa, the spread of macaques across Eurasia, and the development of a number of apparently independent terrestrial lineages.

The ape and human superfamily Hominoidea is first represented in the late Oligocene of Africa, where *Proconsul* and related forms occur between 26 and 14 Myr ago. This group is now usually thought to be similar to the common ancestor of the two living hominoid families: the gibbons (Hylobatidae) and the humans and great apes (Hominidae). No gibbon ancestors have been discerned in the fossil record, although previous researchers suggested certain pliopithecoids for that role; a major problem is that modern gibbons combine very conservative craniodental morphology with (secondarily?) small body size and unique locomotor adaptations, so that recognizing a “proto-gibbon” that lacks these unique features is operationally difficult.

The earliest members of Hominidae (the kenyanthropines) appeared in Africa and Arabia between about 20 and 14 Myr ago, and closely related species inhabited Turkey and central Europe slightly later; none of them can be clearly linked with either modern subfamily. The dryopithecines of Europe and eastern Asia lived between 13 and 8 Myr ago; they are somewhat more like modern hominids in their faces and limb bones especially, but they still do not show any characters linking them unequivocally to either living subfamily. The orangutan lineage is the first to be documented in the fossil record, with members of the genus *Sivapithecus* known from Turkey, Pakistan, and India between 12 and 7 Myr ago. *Sivapithecus* shares with orangutans several specialized features of the face and teeth [such as frontal sinuses derived from the maxillary sinus, narrow interorbital region, ovoid orbits, outwardly rotated upper canines, and constricted incisive canals (the passageway linking the floor of the nose to the roof of the mouth)], which can be readily recognized in even fragmentary fossils.

The hominine lineage is far less well documented in the 10- to 4-Myr interval, with only a few teeth or jaws in eastern Africa and perhaps the European *Graecopithecus* (10–8 Myr) representing potential early relatives of the African apes and humans. No later fossils are linked to the chimpanzee or gorilla, but human evolution is rather well known after 4

Myr ago. *Australopithecus*, *Paranthropus*, and *Ardipithecus* include eight species characterized by brains slightly expanded relative to body size as compared with those of apes, small canine teeth incorporated into the incisor complex, and a variety of features related to their bipedal locomotor adaptation. By about 2.5 Myr ago, the earliest members of the genus *Homo* can be diagnosed by an increase in brain size, an apparently more modern postcranium and locomotor system, and the presence of stone tools. Humans occupied Eurasia by at least 1 Myr ago, but anatomically modern fossils are not known until around 100,000 years ago, in Africa and then the Near East. By about 30,000 years ago, modern humans had spread over the Old World including Australia, replacing more archaic varieties such as the European Neanderthals, and reached the New World by at least 12,000 years ago. [See Comparative Anatomy; Evolving Hominid Strategies; Human Evolution.]

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