

Evolution of Old World monkeys

The group of higher primates called the Old World anthropoid primates, or catarrhines, is taxonomically more diverse today but morphologically more homogeneous than its sister taxon, the New World anthropoids or platyrrhines. Modern catarrhines are represented by only two superfamilies – the Cercopithecoidea (Old World monkeys) and Hominoidea (apes and humans). There is still controversy about the classification and evolutionary relationships of these subgroups.

Living Old World monkeys

The living Old World monkeys comprise a single family, Cercopithecidae, with two subfamilies, Cercopithecinae (cheek-pouched monkeys) and Colobinae (leaf monkeys) (see Box). All cercopithecids share several distinctive features that make it likely that they have a common ancestry, and they thus constitute a monophyletic group. As with other catarrhines (hominoids), they have only two premolars in each jaw. The three molars in each quadrant are long and have two crests (*lophs*) connecting transverse pairs of cusps (*bilophodont* condition). There is usually considerable sexual dimorphism, especially in the size and shape of the canines and the front lower premolar, and the upper canine has a deep groove that extends onto the root, particularly in males. Old World monkeys are not united by special features of the skull, but the rest of the skeleton does have some unique and diagnostic characters – such as the various structures that aid in rapid quadrupedal locomotion along branches or on the ground.

The two subfamilies also have diagnostic features, especially in diet, which are reflected in their vernacular names. The cercopithecines are cheek-pouched monkeys, and have buccal sacs used for storing food; they will eat almost anything, but often concentrate on fruit. The colobines eat leaves, which they digest in specialised guts convergently similar to those of ruminant artiodactyls such as cattle. Dietary preferences are also reflected in teeth. Cercopithecines retain more 'primitive', rounded bilophodont molars, with rather large incisors, the lower ones having completely lost the enamel on their inner surfaces. By contrast, colobines have relatively smaller incisors and sharper, high-cusped teeth.

Modern cercopithecines include both tree-climbing and terrestrial species, whereas living colobines almost all live, run and leap in trees and have reduced or almost absent thumbs. The skull of colobines has widely spaced orbits, a narrow nasal opening and a short face, whereas that of cercopithecines – especially in the long-snouted baboons – shows the opposite pattern.

A CLASSIFICATION OF LIVING AND FOSSIL OLD WORLD MONKEYS

- Superfamily Cercopithecoidea
 - Family Cercopithecidae (Old World monkeys)
 - Subfamily Cercopithecinae (cheek-pouched monkeys)
 - Tribe Cercopithecini
 - Subtribe Allenopithecina
 - Allenopithecus* (Allen's swamp monkey)
 - Subtribe Cercopithecina
 - Cercopithecus* (guenons)
 - Miopithecus* (talapoin)
 - Erythrocebus* (patas monkey)
 - Tribe Papionini
 - Subtribe Papionina
 - Papio*
 - P.* (*Papio*) (baboons)
 - P.* (*Mandrillus*) (drill/mandrill)
 - [†]*P.* (*Dinopithecus*)
 - Cercocebus*
 - C.* (*Cercocebus*) (terrestrial mangabeys)
 - C.* (*Lophocebus*) (arboreal mangabeys)
 - [†]*Parapapio*
 - [†]*Gorgopithecus*
 - Theropithecus* (gelada baboon)
 - Subtribe Macacina
 - [†]*Procynocephalus*
 - [†]*Paradoichopithecus*
 - Subfamily Colobinae
 - Subtribe Colobina
 - Colobus* (black colobus monkeys)
 - Procolobus*
 - P.* (*Procolobus*) (olive colobus monkey)
 - P.* (*Piliocolobus*) (red colobus monkey)
 - [†]*Libypithecus*
 - [†]*Cercopithecoides*
 - [‡]*Paracolobus*
 - [†]*Rhinocolobus*
 - [‡]*Microcolobus*
 - Subtribe Presbytina
 - Presbytis* (surelis)
 - Semnopithecus*
 - S.* (*Semnopithecus*) (langurs)
 - S.* (*Trachypithecus*) (leaf monkeys)
 - Pygathrix*
 - P.* (*Pygathrix*) (douc langur)
 - P.* (*Rhinopithecus*) (snub-nosed langurs)
 - Nasalis*
 - N.* (*Nasalis*) (proboscis monkey)
 - N.* (*Simias*) (Pagai Island langur)
 - Subfamily Colobinae (uncertain affinities)
 - [†]*Mesopithecus*
 - [†]*Dolichopithecus*
 - Subfamily Victoriapithecinae
 - [†]*Prohylobates*
 - [†]*Victoriapithecus*
- Family Oreopithecidae*
 - [†]*Oreopithecus*
 - [†]*Nyanzapithecus*
 - [†]*Rangwapithecus*

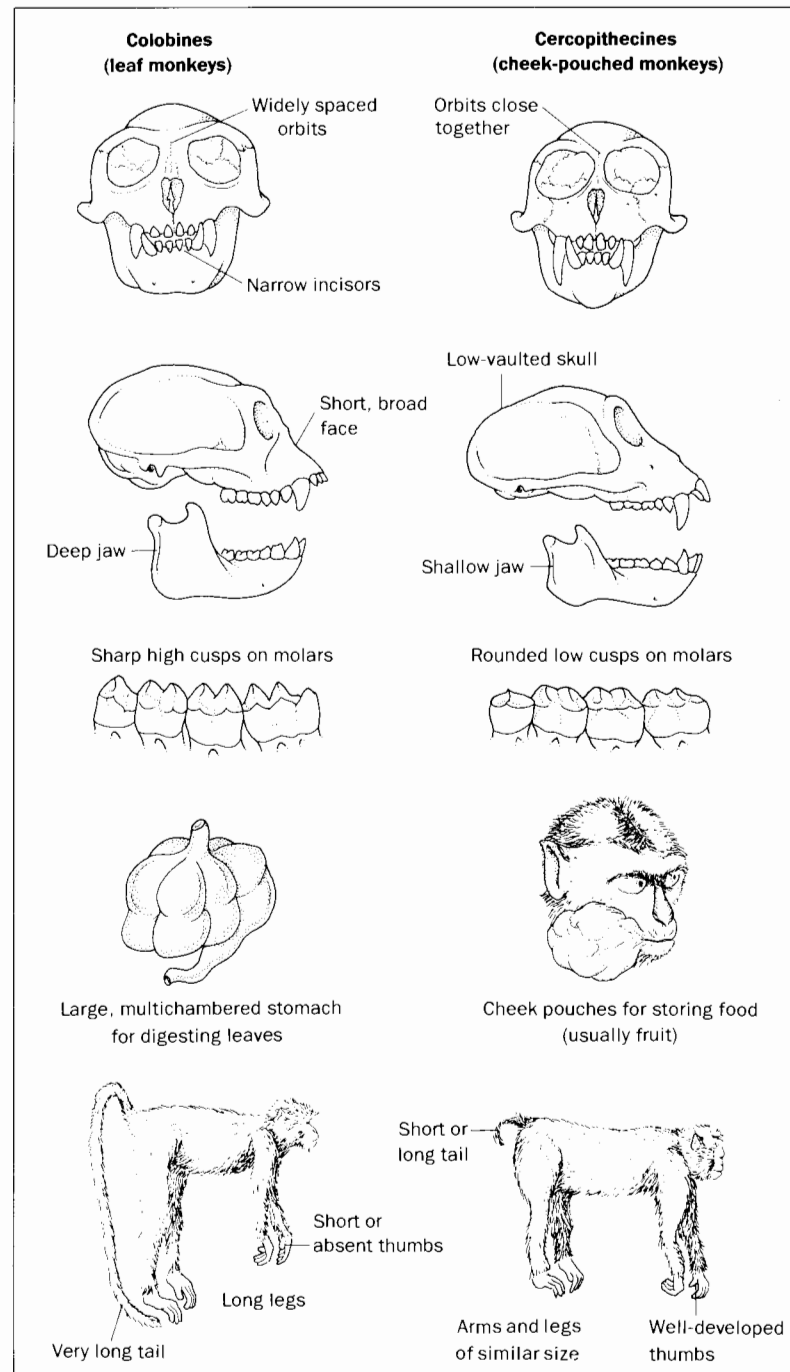
Subgenera (shown in parentheses) are called genera in some classifications. Fossil genera and subgenera are denoted by a dagger sign.

* Many authorities classify the oreopithecids among the Hominoidea (or even as a distinct superfamily).

Within the Cercopithecoinae, the African guenons and their relatives make up the tribe Cercopithecini, and the baboons, mangabeys and macaques form the Papionini. The latter all have an essentially similar chromosome complement (karyotype) with a diploid number of 42. The Cercopithecini have lost the distal (hindmost) cusp on the third molar, and their diploid chromosome numbers range between 48 and 72, often in groups separated by multiples of 6. This diversity of karyotypes might reflect a pattern of speciation in closely adjacent populations.



Representative living Old World monkeys: a cercopithecine (below), the chacma baboon (*Papio hamadryas ursinus* (or *P. ursinus*)), from the savannas of southern Africa; and a colobine (above), the Asian proboscis monkey (*Nasalis larvatus*), from the mangrove forests of Borneo.



Features characterising the modern subfamilies of Old World monkeys, the Colobinae and Cercopithecoinae.

The taxonomy of living colobines fits well with their geographical distribution (see p. 34). However, the differences between African and Asian forms are not as strong as between cercopithecine tribes, with only minor contrasts in teeth and limbs.

Molecular primatologists have concentrated on analysing the relationships among relatively distantly related primates and among hominoids. Little is known of the genetics of cercopithecine genera. The difference between

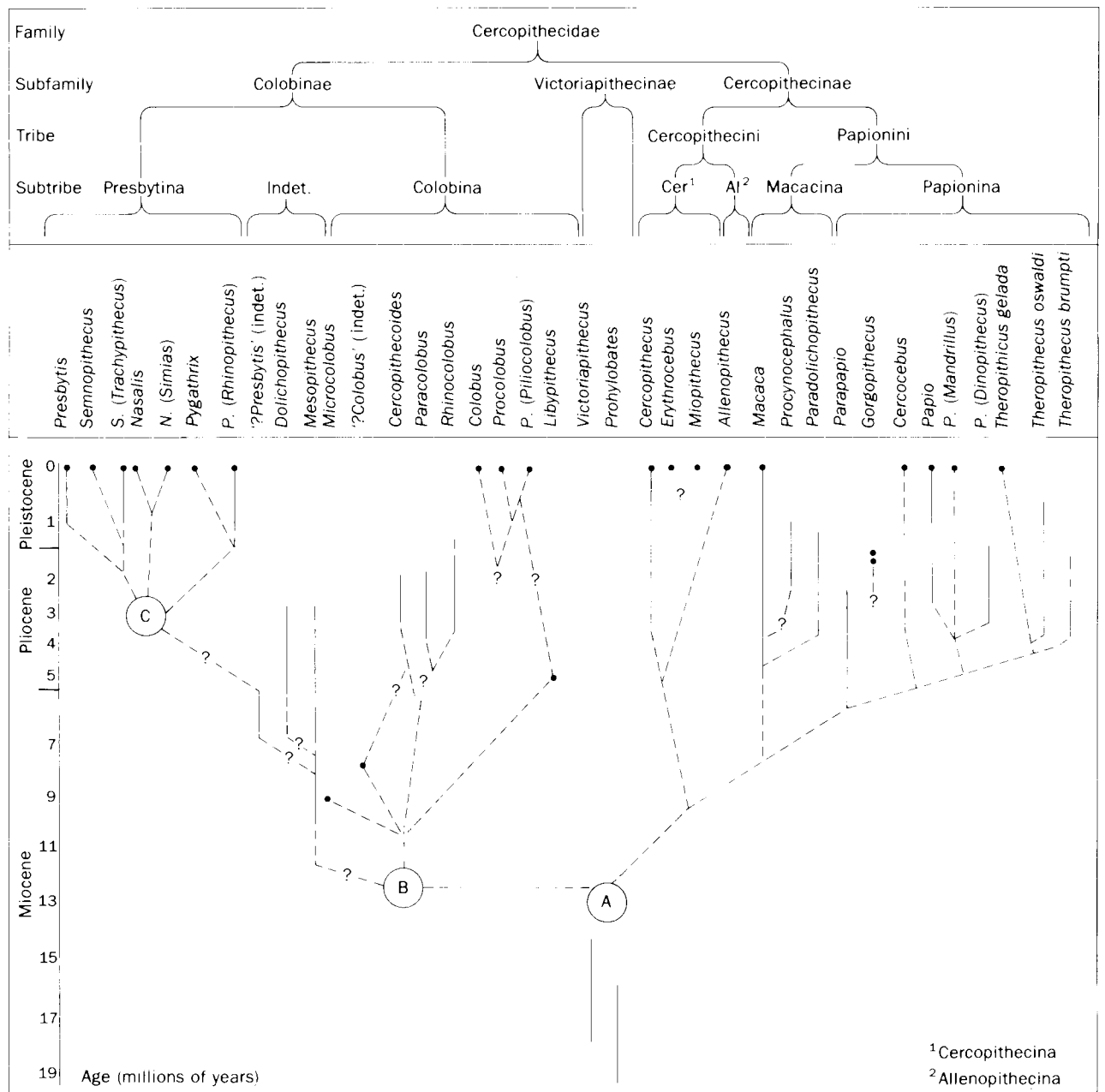
colobines and cercopithecines is comparable in several ways to that between orang-utans and African apes, so that these two phyletic splits may have occurred at about the same time.

Early diversification

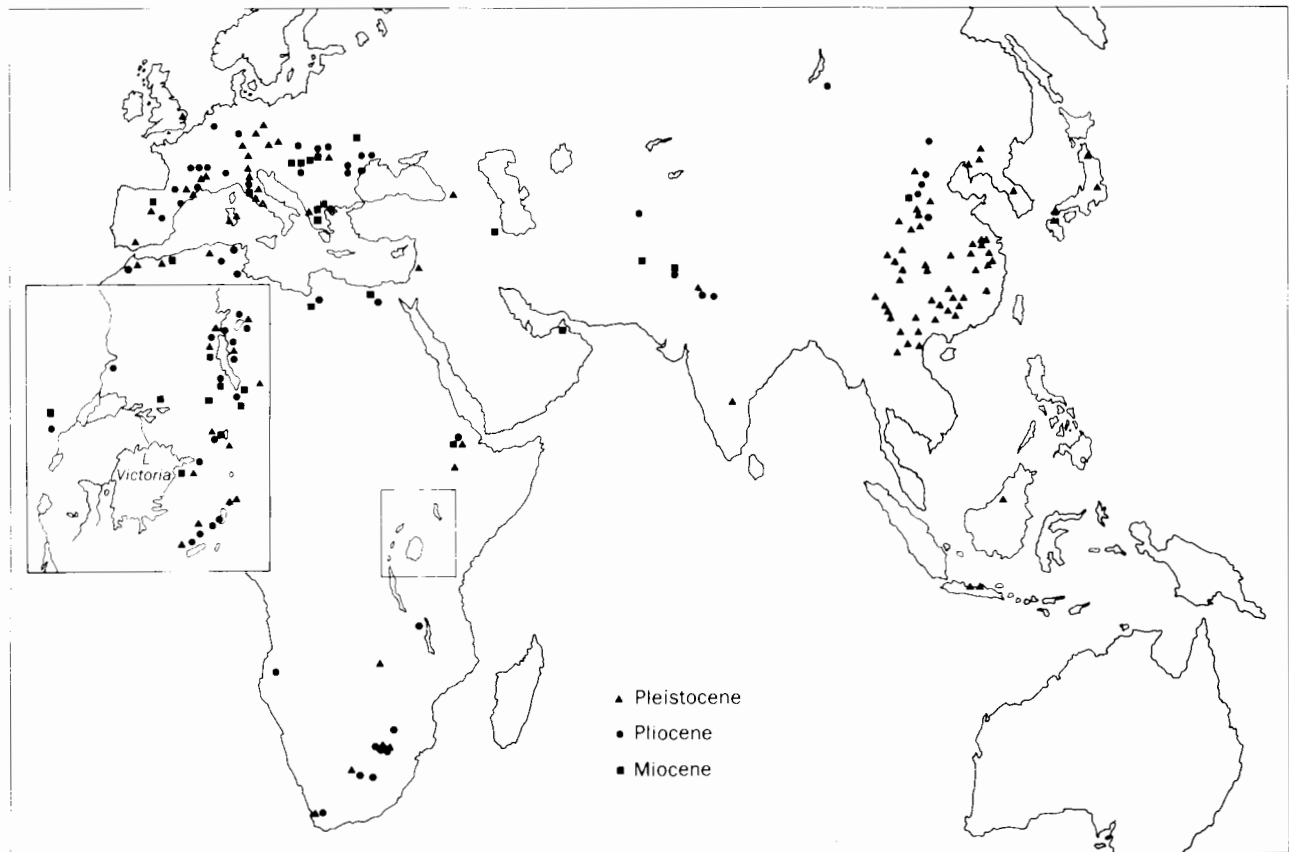
The origin of the Old World monkeys is not well reflected in the fossil record. A form called *Propliopithecus*, known from early Oligocene deposits in Egypt around 33 million years old, may have been close to the common ancestry of all modern catarrhines. With the exception of a single upper tooth from Uganda, however, no fossil with clear ties to the cercopithecids is known from Oligocene or early Miocene deposits.

By early middle Miocene times, 17 to 15 million years ago, several varieties of early cercopithecoid existed in northeastern Africa. *Prohylobates* is represented by parts of four lower jaws from Egypt and Libya, and *Victoriapithecus* left a few jaws, some limb bones and hundreds of isolated teeth at Maboko, Kenya. Specimens from other sites have

Evolutionary relationships, time ranges and major groupings of Old World monkeys. The genera and subgenera (and species groups for *Theropithecus*) are along the top, together with their classificatory subdivisions. Solid lines represent the time ranges of fossils, dashed lines the estimated ranges, large dots are forms known today or from single sites in the past, and dotted lines indicate hypothesised evolutionary relationships; question marks indicate especially uncertain links. Large circles (marked A, B and C) represent uncertainty of branching sequence among specific groups: A, the original division between colobines and cercopithecines; B, the split between African and Asian colobines; and C, the split among living Asian colobines.



¹ Cercopithecoina
² Allenopithecoina



Principal sites of discovery of Old World monkey fossils in the Miocene, Pliocene and Pleistocene.

been assigned to one or the other genus, and it has been suggested that the two may not really be different.

These early cercopithecids, best termed the subfamily Victoriapithecinae, show that monkeys were present in more open habitats than those dominated by hominoids. They moved on the ground to some extent, and ate more leaves than hominoids. Modern species have a similar way of life, and this may have promoted the divergence of the first cercopithecoids from their ancestors.

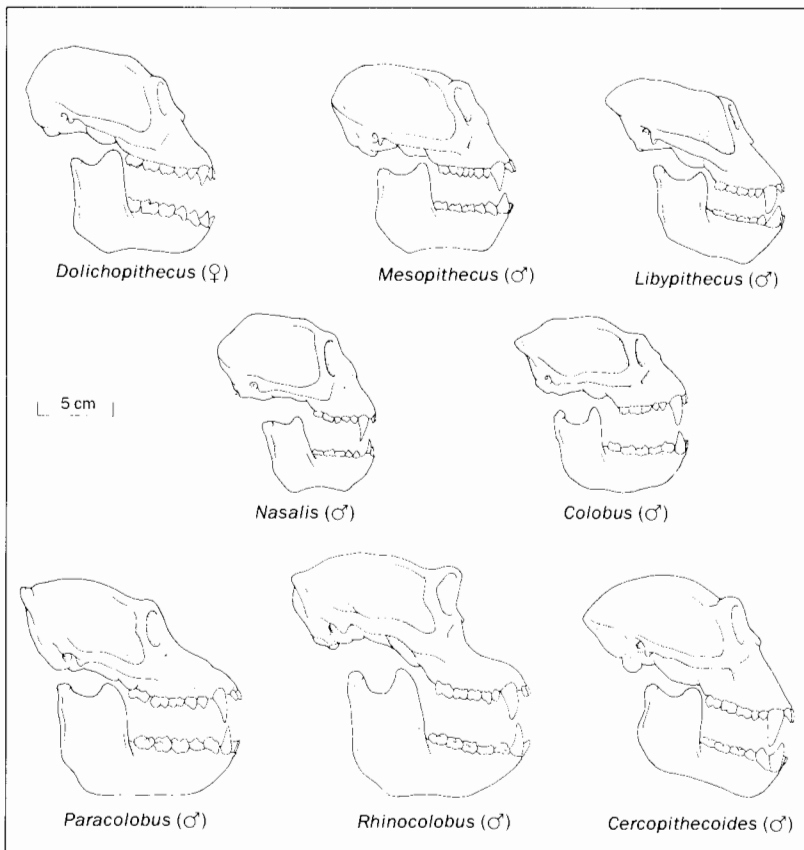
By the late Miocene (8 to 9 million years ago), cercopithecoids were present across the Old World and had replaced most of the hominoid and early catarrhine lineages that had dominated the earlier Miocene. At least six and perhaps as many as 10 independent lineages developed a strong commitment to life on the ground, and monkeys invaded all types of habitat from the fringes of deserts to snowy forests.

The enigmatic European catarrhine *Oreopithecus bambolii* is known from a crushed skeleton and some jaws and limb bones from 8 to 9 million-year-old sites in Italy (see p. 225). Its teeth are highly distinctive, but some authors see certain dental similarities to cercopithecids, suggesting that the two lineages shared a common ancestor. However, the postcranium is more like that of hominoids. Some African species dating to between 19 and 14 million years old resemble *Oreopithecus* and are placed with it in the family Oreopithecidae. It is unclear whether this unique group should be placed in the Cercopithecoidea, in the Hominoidea or even in its own superfamily.

African monkeys of the Miocene and Plio-Pleistocene

Monkeys from late Miocene times are rare in Africa, but a very small colobine is known from Kenya, and both colobines and macaque-like cercopithecines are present across the continent's northern fringe. It is likely that the Sahara desert had become a barrier to north-south movement of mammals by 7 million years ago, leading to the separation of the Papionini into sub-Saharan baboons and mangabeys on one side of the desert and North African and Eurasian macaques on the other. African and Eurasian colobines may also have been separated at this time. There is no fossil evidence, but the Cercopithecini probably diverged from ancestral cercopithecines even earlier, entering the high canopies of the rain forest perhaps around 10 million years ago.

The African Pliocene was a time of great diversification of Old World monkeys. Wide expanses of plains alternated with forests in the east and south, offering numerous habitats for both colobines and cercopithecines. The radiation of the colobines is perhaps the most impressive, with up to seven species present in late Pliocene times, 2 million years ago, around Lake Turkana in Kenya. *Cercopithecoides* species were terrestrial, medium-sized to large colobine monkeys of Kenya and South Africa; their heavily worn



Right side views of reconstructed skulls of extinct colobine monkeys, accompanied (centre) by the skulls of two modern species (*Colobus polykomos* and *Nasalis larvatus*) for comparison (drawn approximately to the same scale). Notice the difference in size between the living and extinct forms.

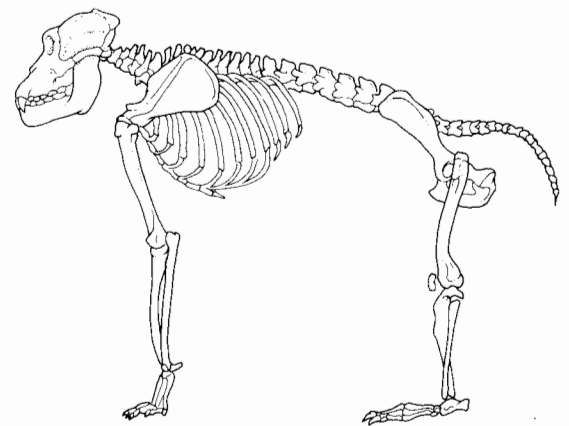
teeth probably reflect an abundance of grit in their diet, from foraging on the ground where living colobines seldom stay. Even larger were the highly arboreal *Rhinocolobus* and less 'specialised' *Paracolobus* of the Turkana Basin. All three forms were larger than any living colobine, in the range of mid- to large-sized baboons. Fossils of several species of smaller colobines, some probably belonging to the living genera, are also known.

At the same time, papionins were represented by members of several lineages. *Parapapio* from southern and eastern Africa was partly terrestrial and had a little derived skull. It was perhaps close to the common ancestry of later papionins and was somewhat like Eurasian macaques. Fossils of mangabeys and guenons are rare, but the extant baboons *Papio* and *Theropithecus* are well represented in the Pliocene and Pleistocene. All populations of the common savanna baboons living today appear to interbreed and are thus best grouped in a single species, *Papio hamadryas*. This includes not only the maned Hamadryas baboon but also the guinea, olive, yellow and chacma baboons, which previously were regarded as separate species. Fossil populations of this species first appear by about 2.5 million years ago, alongside a smaller species that persisted for 0.5 to 1 million years.

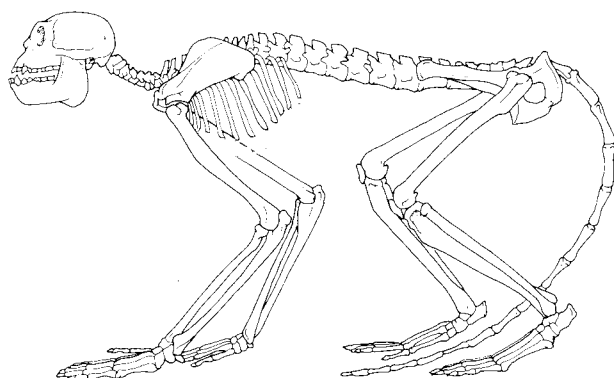
Although *P. hamadryas* (in its broad sense) is widespread today in Africa, it was not common in Plio-Pleistocene times, except in South Africa between 2 and 1.5 million years ago. Another large form was previously placed in its own genus *Dinopithecus*, but is now assigned to a subgenus of *Papio*; it is known only between 3 and 1.5 million years ago.

The gelada (*Theropithecus gelada*) lives today only in the Ethiopian highlands, but in the past it had a much wider distribution. The living gelada, a specialised ground-dweller, feeds mainly on grass blades and seeds; its incisors are relatively small as it uses its fingers for food preparation. The first specimens showing distinctive gelada-like molars appeared by 4 million years ago, and at least three extinct species are known.

Theropithecus darti is present in eastern and southern sites older than 2.5 million years and has a fully terrestrial skeleton and somewhat reduced incisors. Populations of *T. oswaldi* increase in size after about 2 million years ago, spreading into northwestern Africa and even India. The large, later Pleistocene animals have very small incisors and short, stout canines. In this, they show parallels to hominids. The distinction between *T. oswaldi* and its probable ancestor, *T. darti*, is fairly arbitrary, but the latter has larger front teeth. *Theropithecus brumpti*, which has even larger incisors and a distinctive facial shape, is known only in the Lake Turkana region between 3.3 and 2.3 million years ago.



Reconstruction of the skeleton of a large male *Theropithecus oswaldi*, a terrestrial 'giant baboon' of the East African Pleistocene. The separate skull, a female, is from South Africa.



Reconstruction of the skeleton of *Mesopithecus pentelicus*, a semiterrestrial colobine of the late Miocene and Pliocene of Europe. This female specimen (assembled from many unassociated parts) was found in Greece and is about 8 million years old. The separate skulls are male (left) and female (right).

The oldest members of this lineage have skulls and teeth similar to those of *Papio*, suggesting a close phyletic link between these genera, as well as much parallel evolution within *Theropithecus*. The *T. brumpti* lineage probably diverged early from the common ancestor of *T. gelada*, *T. darti* and *T. oswaldi*.

Eurasian monkeys of the Miocene to Pleistocene

The colobines entered Eurasia long before the cercopithecines, and diverged into European and Asian subgroups. Dozens of skulls and postcranial elements of *Mesopithecus* have been found, especially in the Balkans in deposits dating to between 9 and 8 million years ago. Other populations extended as far east as Afghanistan and perhaps India, and westwards to France and England as recently as 3 million years ago.

Mesopithecus was probably similar to the living Hanuman langur (*Semnopithecus* or *Presbytis entellus*) in its adaptation to life in forests and on the ground; its thumb is less reduced than in any other colobine, but more than in cercopithecines. A possible descendant of *Mesopithecus* is *Dolichopithecus*, a larger, longer-faced and more terrestrial colobine from

deposits in central and southern Europe dating to between 6 and 3 million years ago, and perhaps somewhat later in Mongolia. Other Asian fossil colobines are mainly members of the living genera, whose relationships are still unclear.

The only Eurasian cercopithecines (other than a single *Theropithecus maxilla*) are the macaques and their extinct relatives. There are four main groups of macaque species: the North African (and extinct European) Barbary macaque (*Macaca sylvanus*); the lion-tailed macaque (*M. silenus*) group of India and Southeast Asia; the Toque macaque (*M. sinica*) group of South and East Asia; and the widespread group of crab-eating macaques (*M. fascicularis*).

Both morphology and biochemistry agree in distinguishing these groups, although the details of their relationships are not yet clear. Macaque-like papionins first appear in North Africa in the late Miocene when the Mediterranean Sea dried up, and had entered Europe by the earliest Pliocene, when it had refilled. Many European populations between England and the Caucasus have been named, but none can readily be distinguished from *M. sylvanus*. Macaques persisted in Europe until the last interglacial, about 100 000 years ago, after which they were restricted to North Africa.

In Asia, macaques spread to India by around 3 million years ago; two Chinese teeth may be 5 million years old. Crania from the Pleistocene of China probably represent a member of the *sinica* group, and the several living species on Sulawesi are probably derived from a *silenus* group population that crossed from Borneo on a land bridge when sea levels were lower, and then speciated in isolated parts of the island.

Macaques are not particularly specialised for life on the ground. In this, they are comparable to mangabeys and to *Parapapio*. In the late Pliocene and early Pleistocene of Europe, a larger, more terrestrial lineage flourished as the genus *Paradolichopithecus*. Less well-preserved specimens from China and India may represent a second macaque 'experiment', or an extension of the range of *Paradolichopithecus*, which is also known from Central Asia.

The entry of humans into Asia by 1 million years ago may have driven these large monkeys to extinction, perhaps because they, like the large geladas of Africa, were hunted for food.

Eric Delson

See also 'Classification and evolutionary relationships' (p. 17), 'Non-human primates' (p. 24), 'Conservation of primates' (p. 33), 'Jaws and teeth' (p. 56), 'Diets and guts' (p. 60), 'Primate locomotion and posture' (p. 75), 'Land movements and species dispersal' (p. 169), 'Reconstructing past environments' (p. 191), 'The fossil history of primates' (p. 199), 'Evolution of apes' (p. 223) and Part 8 'Genetic clues of relatedness' (pp. 293–321).