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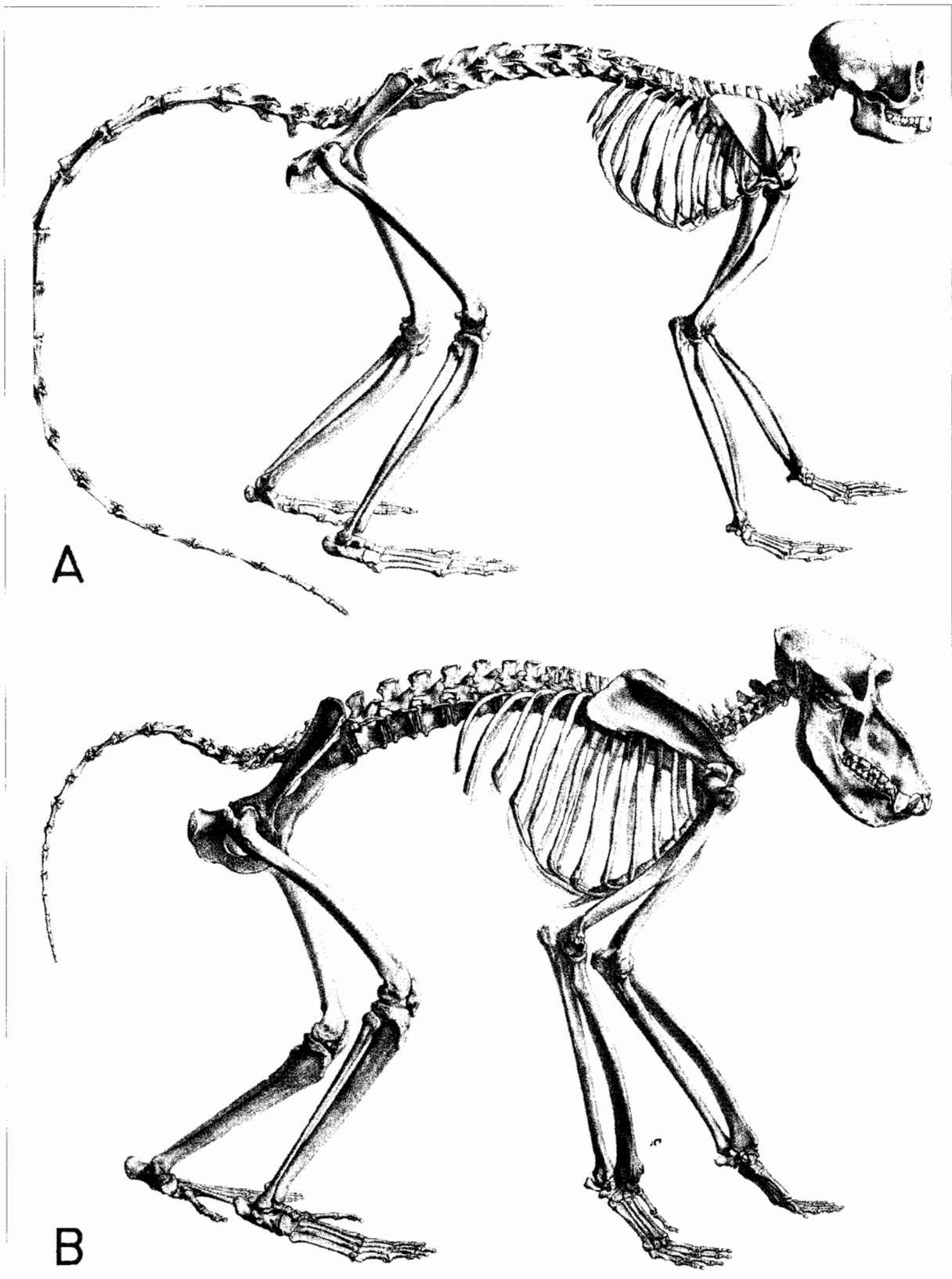
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WITH THE COMPLIMENTS OF:

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Cercopithecinae

Subfamily of Old World monkeys including the cheek-pouched cercopithecids, such as guenons (*Cercopithecus* and allies), baboons (*Papio*), macaques (*Macaca*), and mangabeys (*Cercocebus*) and their extant and extinct relatives. The underlying adaptation of the cercopithecines appears to be their increased reliance on the terrestrial environment for feeding and social activities, although some members of the subfamily are highly arboreal. As part of a general increase in terrestriality by comparison with ancestral cercopithecids, the earliest cercopithecines apparently evolved several novel features that continue to characterize all of their descendants, whatever their current mode of life. The derived conditions of Cercopithecinae are essentially craniodental and include large pouches in the cheeks for temporary storage of food; relatively enlarged I²; loss of enamel on the lingual surfaces of both lower incisors; facial elongation, linked with narrow interorbital distance, long nasal bones, the lacrimal bone often extending beyond the anteroinferior border of the orbit with the lacrimal fossa wholly enclosed within that bone, the vomer expanded to form part of the medial wall of the orbit, and the ethmoid apparently expanded anteriorly; a low-vaulted and long neurocranium; mandibular corpus deepening mesially and symphysis with poorly developed inferior torus; brain modification involving rostral expansion of the occipital region and increase of the associa-



Skeletons of representative cercopithecids: above, arboreal Cercopithecus; below, terrestrial Papio. From H.M.D. de Blainville, Ostéographie. I: Primates, 1839, Baillière.

tion and the visual cortex, documented on the surface by numerous sulcal modifications. Postcranially, cercopithecines differ from colobines in several consistent ways. The majority of these are conservative retentions from the common cercopithecoid ancestor, while in others morphocline polarity is uncertain (e.g., robust and straight-shafted limbs, subequal supratrochlear and supracapitular fossae on the distal humerus, and doubled radial articular surface on the proximal ulna). Most of these locomotor-related features are probably retained from an increasingly terrestrial ancestral cercopithecine, which was also the interpretation offered for cheek pouches: filled with food while an animal was foraging terrestrially, then emptied if the animal fled to the security of upper branches. Carefully designed studies revealed, to the contrary, that terrestrial species have reduced pouches, implying less terrestriality at the origin of this feature. Cercopithecines have a varied diet, including fruit as its usual central focus, and their generally large incisors and especially the reduction of enamel on the lowers are adaptations for scraping and cutting the outer covering of tough fruits prior to reduction of pieces by the molars. Cercopithecine cheek teeth appear to be broadly conservative, with low relief compared with those of colobines, as well as greater flare, or basal broadening, and longer trigonids; the last feature may, in fact, be derived. It appears that this dentition was originally evolved for a mixed leaf-and-fruit diet, by comparison with the more frugivorous ancestral catarrhine diet, and that cercopithecines, especially the baboon-macaque group, hardly modified it subsequently.

Within the Cercopithecinae, there are two major subdivisions, or tribes, that each can be further divided into subtribes; the characters of these groups can be reviewed, although they are not emphasized here. The tribe Cercopithecini includes the mainly arboreal guenons (*Cercopithecus*) and talapoin (*Miopithecus*), the perhaps semiterrestrial swamp monkey *Allenopithecus*, and the very terrestrial patas (*Erythrocebus*). All of these share loss of the hypoconulid on M_3 (lost on anterior cheek teeth in ancestral cercopithecids) and an increase in chromosome number above 42.

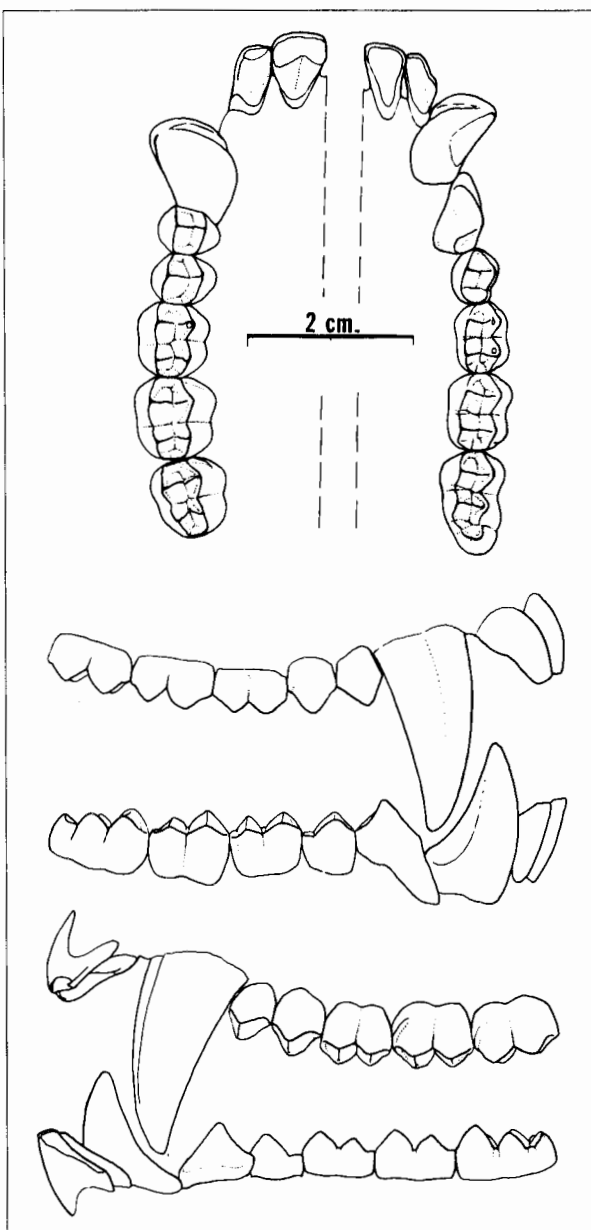
Allenopithecus is conservative, and the other three genera derived, in having reduced molar flare and the male ischial callosities separated by a strip of hairy skin. *Cercopithecus* further presents a greatly increased diploid chromosome number over the 48 of *Allenopithecus* and the 54 seen in *Miopithecus* and *Erythrocebus*, and it shares with *Erythrocebus* loss of a roughly monthly cycle in its female sexual swellings. This suggests that *Allenopithecus* is most similar to the common ancestor of all cercopithecines and its lineage diverged first, followed, in turn, by those of talapoin, patas, and the many guenons. The swamp-living adaptations of the first two of these clades may suggest this as the original environment to which the tribe was adapted.

Patas monkeys live in open woodlands with acacia trees between the Sahara and the rain forests of Central Africa. Small troops led by a single adult male have large ranges. Different authorities recognize between one dozen and two dozen species within *Cercopithecus*, but there are only about six to eight ecological-behavioral patterns. *C. aethiops* and *C. lhoesti* are quite terrestrial, living in gallery forests along watercourses

or denser forest, respectively, but most other species are highly arboreal. Members of four to six species may inhabit a single grove of trees, at different canopy levels or concentrating on complementary foods. Multispecies associations are common in generally unimale troops. The fossil record of this tribe is scarce, but characteristic teeth are known from Kenyan and Ethiopian localities as far back as 3 Ma.

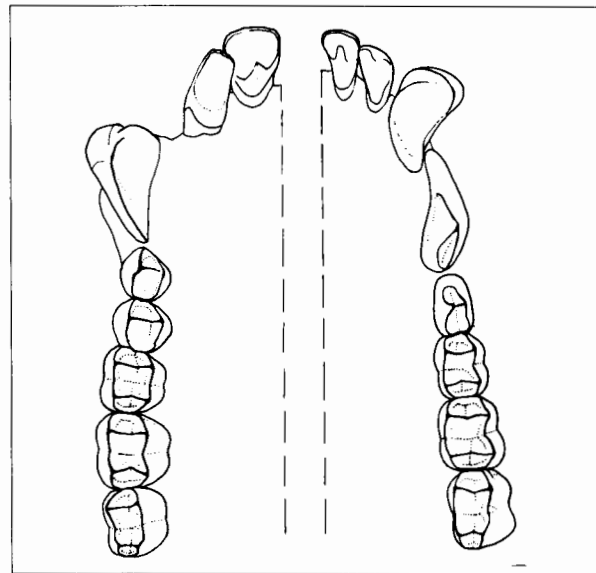
The second, far more diverse and widespread, cercopithecine tribe is Papionini, including the macaques of North Africa and eastern Asia and the baboons, mandrills (*Mandrillus*), mangabeys, and geladas (*Theropithecus*) of sub-Saharan Africa. There may be only one distinct derived character of this tribe, a secondary increase in the maximum width of the nasal aperture, but papionins are characterized by further development of such cercopithecine tendencies as increased molar flare, accessory cuspules in molar clefts, an elongated face, posterior inclination of the mandibular ramus, and a generally high degree of terrestriality. It has been suggested that the two geographic divisions of Papionini represent true clades, separated by the development of the Sahara Desert as an ecological barrier to continued north-south migration and gene flow during the Late Miocene (ca. 10–7 Ma). No clear and consistent morphological features characterize these two, but the African genera do share a steep drop in facial profile in front of the orbits and often hollows or fossae on the maxilla and the lateral surfaces of the mandible (facial fossae). Chromosome number is constant at 42, and the dentition of almost all papionins is identical, although some mangabeys have especially high flare, while geladas, which at times have been considered to represent a third subtribe, have uniquely derived dental and cranial form.

Macaques inhabit a wide range of environments, including rain forest, woodland, steppe, and snow-covered regions, and their diets are concomitantly varied. Some of the dozen or so recognized species are highly arboreal, others semiterrestrial; most live in multimale troops with female as well as male hierarchies and maternally inherited social status. Mangabeys are ecological equivalents of macaques in the African forests, with some species making much more use of the ground than others. Two groups are now often recognized as full genera, and some evidence suggests that they are not each other's closest relatives (i.e., that mangabeys as a group are paraphyletic). Savannah baboons form a single widespread species ranging from Guinea (West African coast) to Ethiopia and southern Saudi Arabia, down to South Africa and into Angola. At least six subgroups may be recognized; each used to be thought full species but have since been observed to interbreed in overlap zones, confirming the genetic unity of the species. Multimale troops are the rule, especially in open country, but in forest habitats the structured social hierarchies are less evident. Mandrills are deep-forest baboons, with brightly colored faces in the male to serve as signals in unimale troops. The living gelada is the last remnant of a once widespread lineage, now restricted to the dry uplands of Ethiopia. There *Theropithecus* individuals live in unimale harems, which may come together in associations of several hundred for sleeping on scattered cliffs and for feeding in certain seasons. They are the most terrestrially adapted of living monkeys, with short digits

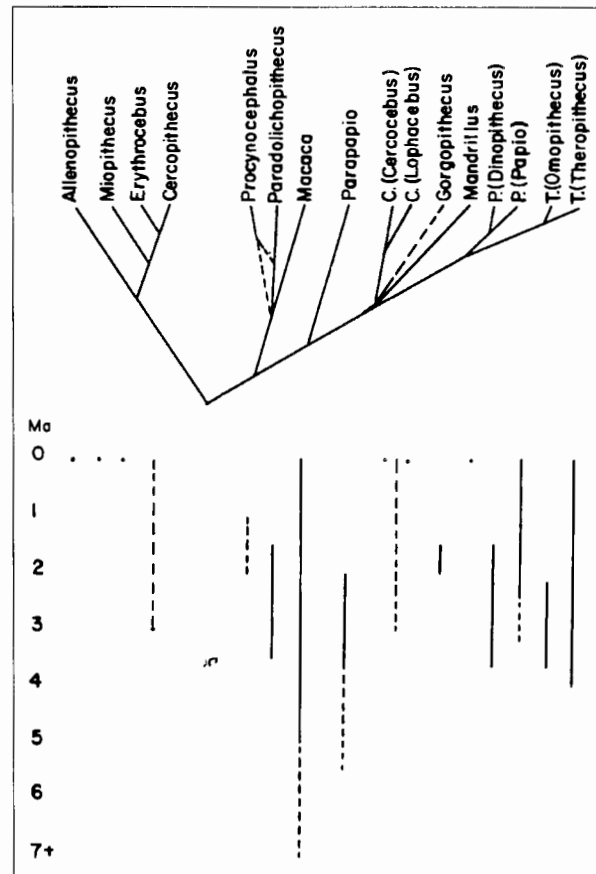


Dentition (right side) of male Macaca, in occlusal (upper on left, lower on right), buccal, and lingual views. These teeth are typical for Papionini. From Szalay and Delson, 1979.

for better walking and for manipulation of the grass blades and stems that form their dietary staple. Their teeth have converged on those of colobines in having high relief (deep notches and elevated cusp tips), but they also have thick enamel and a characteristic wear pattern to prolong tooth life while grinding up their low-quality gritty diet. Morphological and molecular studies of the relationships among the African genera have yielded conflicting views: Skull form suggests that mandrills might belong to the genus *Papio*, with *Theropithecus* close but derived and *Cercocebus* unified; DNA sequencing and other genetic evidence, on the other hand, indicates that *Theropithecus* and *Papio* are closest, with *Cercocebus* related, while *Mandrillus* and *Lophocebus* seem to form a separate clade. In 1999 J.G. Fleagle and W.S. McGraw described a complex of derived postcranial features (and one



Dentition (right side) of male Erythrocebus, in occlusal (upper on left, lower on right) view, for comparison with those of Macaca at the left. From Szalay and Delson, 1979.



Cladogram of relationships among the living and extinct genera and subgenera (in parentheses) of Cercopithecinae. Dotted lines indicate uncertain links. Note that some molecular and new morphological data contradict this older morphological interpretation, suggesting instead that *Theropithecus* and *Lophocebus* are farther removed. Below the cladogram are indicated the known time ranges of these genera; solid lines indicate well-preserved fossils, dotted lines indicate fragmentary remains, less clear allocations or dating uncertainty.

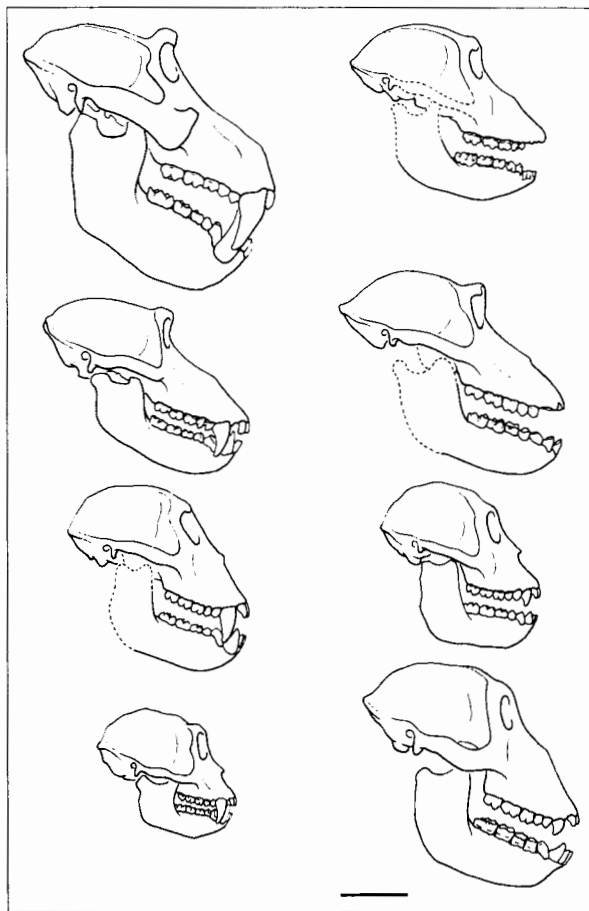
dental similarity) which link *Lophocebus* and *Mandrillus*, strongly supporting the genetic viewpoint.

The fossil record of Papionini is rich, especially in Africa. The earliest members of the tribe are known by teeth from North Africa and Kenya late in the Miocene (8–6 Ma), perhaps, from geological evidence, after the Sahara had formed an ecological barrier. In the Pliocene (4–2 Ma) of eastern and southern Africa, the conservative *Parapapio* is fairly common. It has a similar facial conformation to macaques and mangabeys (but may share some anteorbital deepening with *Papio*), and rare postcranial elements suggest a semiterrestrial adaptation. *Parapapio* may represent a form close to the common ancestor of later African papionins.

At least four varieties of *Theropithecus* are frequent, especially at waterside sites. Three of these form a lineage known across Africa, from southern South Africa to Morocco, from the Early Pliocene to the later Middle Pleistocene. They are characterized by a gradual size increase and anterior tooth reduction through time, and the late large forms (up to 70–100 kg) probably were hunted by Acheulean peoples, perhaps to extinction. There is controversy over taxonomic ranking, but here they are recognized as three subspecies of *T. oswaldi*. Several teeth suggest that this group also reached Spain and the Siwaliks of India ca. 2–1 Ma. The living *T. gelada* is more conservative than even the earliest fossil form (although it is placed in the same subgenus) and probably separated from them by 4–3.5 Myr. Another lineage (the subgenus *Omopithecus*) is represented only in the Lake Turkana region, at Koobi Fora (Kenya) and Omo (Ethiopia) between ca. 3.5 and 2 Ma: The moderately well known *T. brumpti* had *Papio*-like large incisors and a low, flat muzzle with typical gelada molars and flaring zygomatic arches, but its putative ancestor ?*T. baringensis* had smaller incisors and less-complex molars, suggesting that molar form evolved in parallel in the two lineages.

Mangabeys are poorly represented paleontologically, probably because forest soils are notoriously acid rich (bone thus deteriorates quickly), but some East African Pleistocene specimens have diagnostic facial features of the group. *Papio* is known by large-bodied populations probably referable to the living savannah baboon species in southern (and more rarely eastern) Africa after 3 Ma, but they were almost always less common than *Theropithecus*. It has been suggested that they were then more forest-fringe dwellers, while geladas were more successful in open country, the pattern changing only in the later Pleistocene. Small-bodied *Papio* is also known in South Africa between 2.5 and 1.5 Ma, and a very large form known as *P. (Dinopithecus)* is common at sites in South Africa, Angola, and Ethiopia from 3 to 1.5 Ma. Although this group has previously been given its own genus, it differs from *Papio* only in lacking facial fossae and is now considered a baboon subgenus, possibly related to the ancestors of mandrills. The large-bodied *Gorgopithecus* is represented only at one group of South African sites between 1.9 and 1.5 Ma, but its distinctive facial conformation, deep fossae, and reduced dental sexual dimorphism justify its generic identity.

Macaque fossils are known in North Africa and across Europe from Spain and Britain to Israel and the Caucasus



Drawings, in right lateral view, of representative cercopithecines; left column males, right column females. Top row: †Theropithecus (*O.*) brumpti, †*T. (T.) oswaldi darti*. Second row: *Papio (P.) hamadryas*, †*P. (Dinopithecus) quadratiostris*. Third row: †*Parapapio broomi (both)*. Bottom row: *Macaca fascicularis*, †*Paradolichopithecus senensis*. Scale bar = 5 cm; † indicates extinct species. By Lorraine Meeker.

throughout the Pliocene and the Pleistocene (5.5 Ma onward). The living “Barbary ape” (*Macaca sylvanus*) of Algeria and Gibraltar probably represents the remaining relic of this far wider distribution. Living macaques have been divided into four to six subgroups, all of which show independent reduction in tail length and have overlapping distributions in eastern Asia. Fossil teeth document their arrival in China by 5.5 Ma and India by ca. 2.5 Ma, and a variety of populations are known from the Pleistocene of China and Indonesia. The extinct *Paradolichopithecus* was larger bodied than any macaque (males ca. 35 kg), far more terrestrially adapted, and less sex-dimorphic in cranial size, but had similar facial morphology. It is known from Spain through Central Asia in the later Pliocene (ca. 3–1.8 Ma) and probably represents a baboonlike macaque derivative. A similar form, *Procycephalus*, is represented by fragmentary remains from the later Pliocene of India and China; it is kept taxonomically distinct because its limb bones do not appear to present the reduced dimorphism of its western “cousin.”

Subfamily Cercopithecinae
Tribe Cercopithecini

- Subtribe Allenopithecina
 - Allenopithecus*
- Subtribe Cercopithecina
 - Cercopithecus*
 - Miopithecus*
 - Erythrocebus*
- Tribe Papionini
 - Subtribe Papionina
 - Papio*
 - P.* (*Papio*)
 - † *P.* (*Dinopithecus*)
 - Mandrillus*
 - Cercocebus*
 - C.* (*Cercocebus*)
 - ? *C.* (*Lophocebus*)
 - † *Gorgopithecus*
 - Theropithecus*
 - T.* (*Theropithecus*)
 - † *T.* (*Omopithecus*)
 - † *Parapapio*
 - Subtribe Macacina
 - Macaca*
 - † *Procynocephalus*
 - † *Paradolichopithecus*

†extinct

See also Africa; Asia, Eastern and Southern; Cercopithecidae; Colobinae; Diet; Europe; Extinction; Miocene; Molecular "vs." Morphological Approaches to Systematics; Monkey; Paleobiogeography; Pleistocene; Pliocene; Primate Ecology; Primate Societies; Skull; Teeth. [E.D.]

Further Readings

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