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WITH THE COMPLIMENTS OF:

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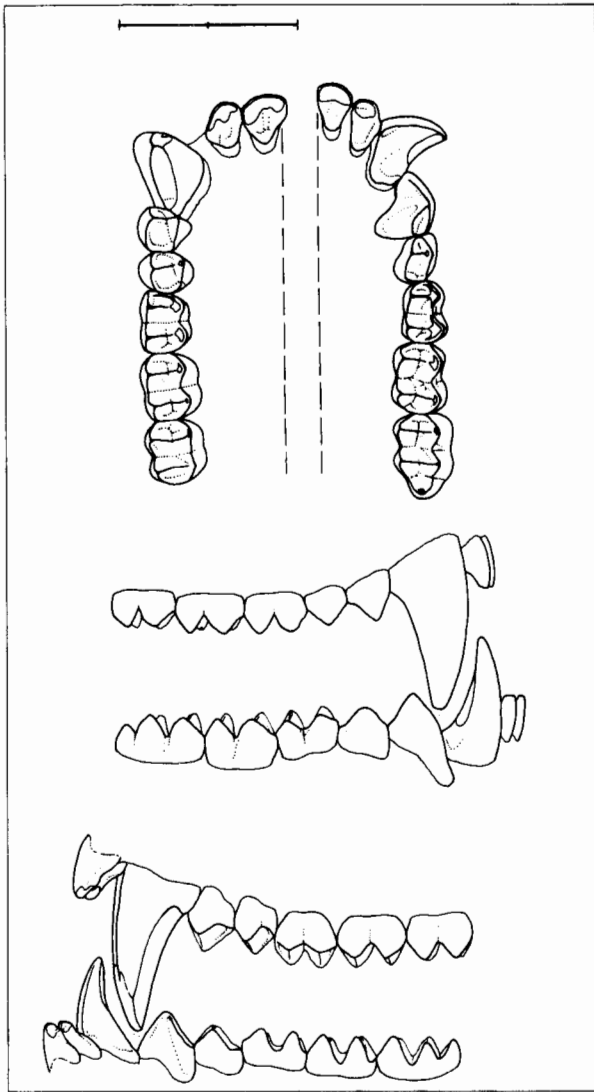
Colobinae

Subfamily of Old World monkeys including the leaf-eating cercopithecids, such as langurs (*Presbytis* and *Semnopithecus*), doucs (*Pygathrix*), proboscis monkeys (*Nasalis*), guerezas (*Colobus*), and their extant and extinct relatives. In adapting to the high proportion of leaves and other low-quality foods in their diet, colobines have evolved a number of derived conditions as compared with the cercopithecoid morphotype.

These include extra chambers in the stomach to enhance fermentation and digestion of cellulose; increased cheek-tooth crown relief (between cusp tips and notch bases) but reduced flare and short lower molar trigonids (possibly conservative); reduction in incisor size (and greater frequency of underbite); a mandible with expanded gonial region but shallowing mesially. As part of their adaptation to arboreal running and leaping, colobines have relatively longer limbs, hands, and feet than do cercopithecines of similar weight. In addition, the external thumb is reduced in length, in some cases lost entirely, and the tarsal region is shortened; the latter is best seen in the cuboid-entocuneiform contacts, where the distal facet is lengthened while the proximal is reduced or lost. Although in most catarrhines the major weight-bearing axis of the foot passes through the middle digit, which is longer than the fourth, in colobines these two are equal, signaling the shift of the axis of the foot to between these two rays. In concert with this, a number of related muscle functions have been modified and a groove developed on the proximal astragalus. Colobines generally have retained the ancestral cercopithecoid conditions of a short, broad face with wide interorbital distance, short nasal bones, and a lacrimal fossa extending onto the maxilla; a relatively high-vaulted skull; fully enamel covered lower incisors; and a simple cerebral sulcal pattern.

Within the modern Colobinae, both morphological and (rare) molecular evidence suggests a division into subtaxa according to geography. Because the number of diagnostic features separating them is low, these groups have been ranked as subtribes rather than full tribes; they seem to be about as distinct from one another as the subtribes of the Cercopithecinae.

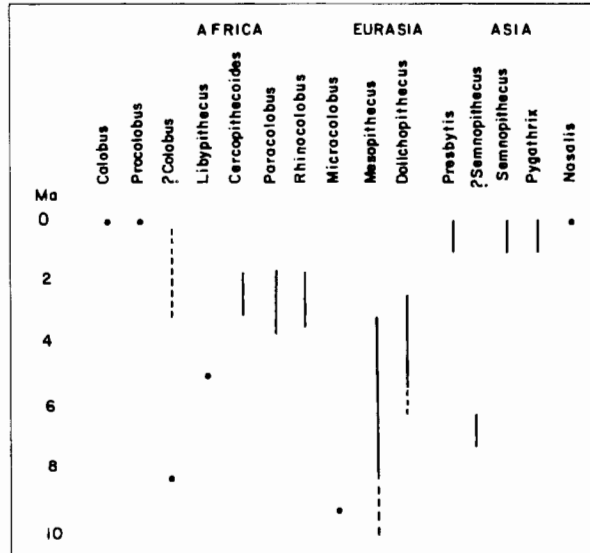
The African colobinans have completely lost the external thumb and the proximal cuboid-entocuneiform contact, while these features are only reduced in the Asian presbytinans. Two living genera are recognized in Africa: *Colobus* (the guerezas, or black[♂]-and-white colobus) with four species, characterized by the derived loss of female sexual swellings and the development of a large larynx and subhyoid sac; and *Procolobus* (for olive colobus and red or bay colobus) with perhaps three to four species, typified by a four-chambered stomach (other colobines have only three chambers), a sagittal crest (perhaps implying a relatively small brain), a male perineal organ, and discontinuous male ischial callosities (also in Asian *Pygathrix*). The Asian colobines are more numerous and their interrelationships more complex; in fact, it is possible that they may not form a natural (holophyletic) group. For the present, four genera are recognized, most with subgeneric divisions. *Semnopithecus* may be the most conservative, *Presbytis* intermediate



Dentition (right side) of male *Nasalis*, in occlusal (upper on left, lower on right), buccal, and lingual views. Scale is 2 cm. From Szalay and Delson, 1979.

(possibly dwarfed, according to N. Jablonski), and *Nasalis* and *Pygathrix* the most derived, at least in terms of facial shape.

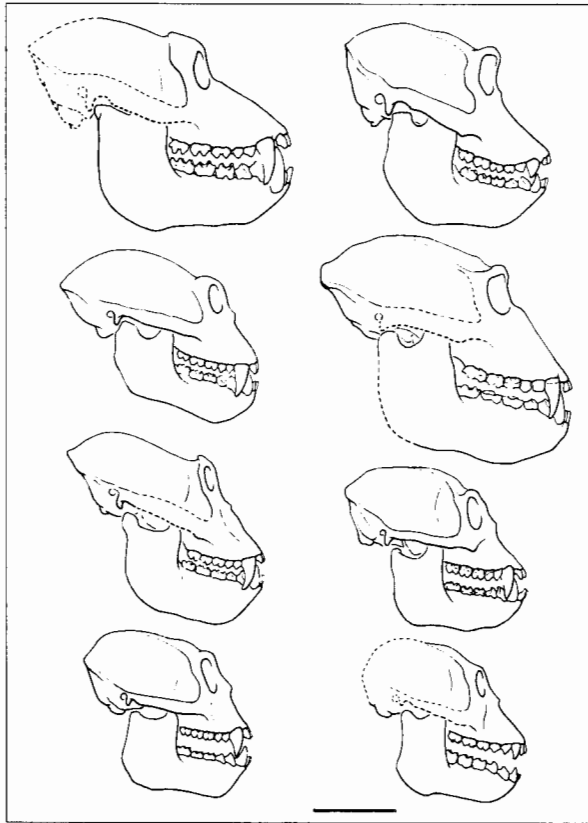
The colobine diet includes not only leaves but a variety of fruits, flowers, buds, shoots, seeds, insects, gums, and earth (for minerals). Their enlarged stomach permits the ingestion of foods high in toxic substances (*secondary compounds*), which can be detoxified through the action of the same bacteria that break down the cellulose in leaves. Most living colobines are active arboreal leapers and runners, with only one species, *Semnopithecus entellus*, spending much time on the ground; several fossil colobines have independently become terrestrial, however. Group composition is mainly multimale, with troop sizes up to 100 (e.g., *Procolobus badius*) but more commonly 20–40. Some species live in small groups with a single adult male (most *Colobus* and *Presbytis*, among others), and at least *Presbytis potenziani* is apparently monogamous. In *S. entellus*, among other species, coalitions of peripheral males may attack the primary male of a troop and kill or expel him, at which time they, or a new leader, may attack and kill juveniles. Among colobines, juveniles are



Known time ranges of colobine genera; solid lines indicate well-preserved fossils, dotted lines indicate fragmentary remains, less clear allocations, or dating uncertainty. The relationships among these taxa are still relatively unclear, and thus no attempt is made to present a cladogram, but see the diagram of living genera in the entry *CERCOPITHECIDAE*.

often carried by females other than the mother—known as *aunting* behavior, this may serve to speed independence of the infant from its mother and protect it from infanticide during male takeovers. Home-range size averages ca. 30 ha but is variable both between species (e.g., 130 ha in *Nasalis larvatus*) and even within species, depending on environmental factors (e.g., from 5 to 1,300 ha in *S. entellus*). Numerous species are endangered, often as the result of human hunting and expansion of cultivated land.

The fossil record of the colobines is quite good in both Africa and Europe but poor in Asia. The earliest African colobine, *Microcolobus*, is known by a single mandible from Ngeringerowa (Kenya), estimated to date to ca. 10–9 Ma. This is the smallest known colobine, slightly smaller in tooth size than *Procolobus verus* but larger than the cercopithecine *Miopithecus talapoin*. Tooth relief is low for a colobine, and the inferior transverse torus of the symphysis is poorly developed, as in cercopithecines but no other colobine. A larger colobine is known by isolated teeth from the Late Miocene (ca. 8 Ma) of Marceau (Algeria). Originally identified as a macaque, then termed “*Colobus*” in the sense of an African colobine, these teeth show some similarities to the Pliocene *Cercopithecoides*. Late Miocene sites in Libya and Egypt have yielded a nearly complete cranium, some teeth, and perhaps fragmentary limb bones of *Libypithecus*, a form broadly similar to the red colobus. The Pliocene of southern and especially eastern Africa saw a great flowering of colobine diversity. *Cercopithecoides* was long known by skulls and teeth in South African sites dating between 3 and 1.5 Ma (e.g., Makapansgat, Sterkfontein, Kromdraai), but an associated partial skeleton from Koobi Fora (Kenya) demonstrated that it was the most terrestrially adapted colobine known. Isolated limb bones of this 20–25 kg species (male estimate only) can be mistaken for those of *Theropithecus* baboons. The teeth of *Cercopithecoides* are often heavily worn, suggest-



Drawings, in right lateral view, of representative colobines; M = male, F = female. Top row: †*Paracolobus chemeroni* (M), †*Rhinocolobus turkanaensis* (F). Second row: †*Cercopithecoides williamsi* (M), †*C. kimeui* (M). Third row: †*Libypithecus markgrafi* (M), *Colobus guereza* (F—note large canine). Bottom row: †*Mesopithecus pentelicus* (M), †*Dolichopithecus ruscinensis* (F). Scale bar = 5 cm; † indicates extinct species. By Lorraine Meeker.

ing that its diet included grit taken in with terrestrial foods and that enamel had not been thickened to prolong tooth life. Somewhat larger (at 43–50 kg for males) was *Paracolobus*, whose fossils span from 3.5 to 1.9 Ma at such East African sites as Laetoli (Tanzania), Koobi Fora (Kenya), and Omo (Ethiopia). A nearly complete skeleton reveals a forelimb that looks like those of more terrestrial monkeys, but a scapula and a foot that indicate a relatively arboreal adaptation. A third genus, *Rhinocolobus*, from Koobi Fora, Omo, and Hadar (Ethiopia) localities between 3.5 and perhaps 1.3 Ma, was intermediate in size, and fragmentary limb bones suggest a degree of arboreality comparable to that in living colobinans. This is unexpected for such a large-bodied species. A medium-sized colobine is known by a partial skull and skeleton from the Hadar region and from isolated teeth in other deposits, and small teeth of *Colobus* size have also been found at Laetoli, Omo, and Koobi Fora. Most of these species seem to have survived Late Pliocene climatic cooling but had disappeared by the start of the Pleistocene.

The earliest Eurasian colobine, *Mesopithecus pentelicus*, ranged over a wide area from Yugoslavian Macedonia to Afghanistan ca. 8–7 Ma, and a tooth from central Germany may date to 11–10 Ma. This species, known from dozens of skulls and numerous limb bones, was probably a semiterrestrial inhabitant of gallery forests bordering open steppe,

comparable in its morphological features to the modern *Semnopithecus entellus*, the Hanuman langur. Body size is estimated at ca. 11–15 kg for males, 7–10 kg for females. At the end of the Miocene, although southern Europe was rather arid, northern Central Europe retained forested regions, which may have served as a refuge for a flora that spread rapidly from Spain to Ukraine with the return of moist conditions at the start of the Pliocene.

Another terrestrial colobine, *Dolichopithecus*, is common in Early Pliocene sites over this wide range of monsoon forest. Larger than *Mesopithecus* (20–30 kg for males, 12–18 females), with a long face and numerous postcranial adaptations to life on the ground, *Dolichopithecus* was in some ways a colobine “mandrill” or forest baboon. It has been thought to be a direct descendant of *M. pentelicus*, but that view was somewhat weakened by the finding that, while the latter species has the derived African colobinelike loss of the proximal cuboid-entocuneiform contact, *Dolichopithecus* presents the less-derived small facet. This pattern is variable in the living species, however. A second, less terrestrial, species of *Mesopithecus* coexisted with *Dolichopithecus* through most of the Pliocene. A current problem in colobine systematics is the relationship of this group (if, indeed, it is a unified clade) to the eastern Asian species.

Asian colobine fossils are quite rare, but a number of teeth have been recovered from levels in the Pakistan Siwaliks dated ca. 7–6 Ma. These might represent a late extension eastward of *Mesopithecus*, but, as most colobine teeth are similar, it is difficult to make a comparison without cranial or postcranial material. An isolated M₃ from a latest Miocene level in the Yushe Basin of east-central China (ca. 5.5 Ma) represents the earliest colobine in eastern Asia. Several partial dentitions, cranial fragments, and a partial elbow joint from Shamar (Mongolia) and Udunga (Siberian Russia), dated to ca. 3–2.5 Ma, have been named *Parapresbytis eohanuman*, but they might represent an East Asian species of *Dolichopithecus*. A colobine face from Atsugi, Japan (near Yokohama), estimated to date to 2.5 Ma, has only been announced in the popular press. It appears similar to the previous species, but also to some African forms. Fossils of the modern *Pygathrix* (*Rhinopithecus*) are known from several Pleistocene sites in China, while *Semnopithecus* and *Presbytis* species have been recovered in Java.

Subfamily Colobinae

Tribe Colobini

Subtribe Colobina

Colobus

Procolobus

P. (*Procolobus*)

P. (*Piliocolobus*)

†*Libypithecus*

†*Cercopithecoides*

†*Paracolobus*

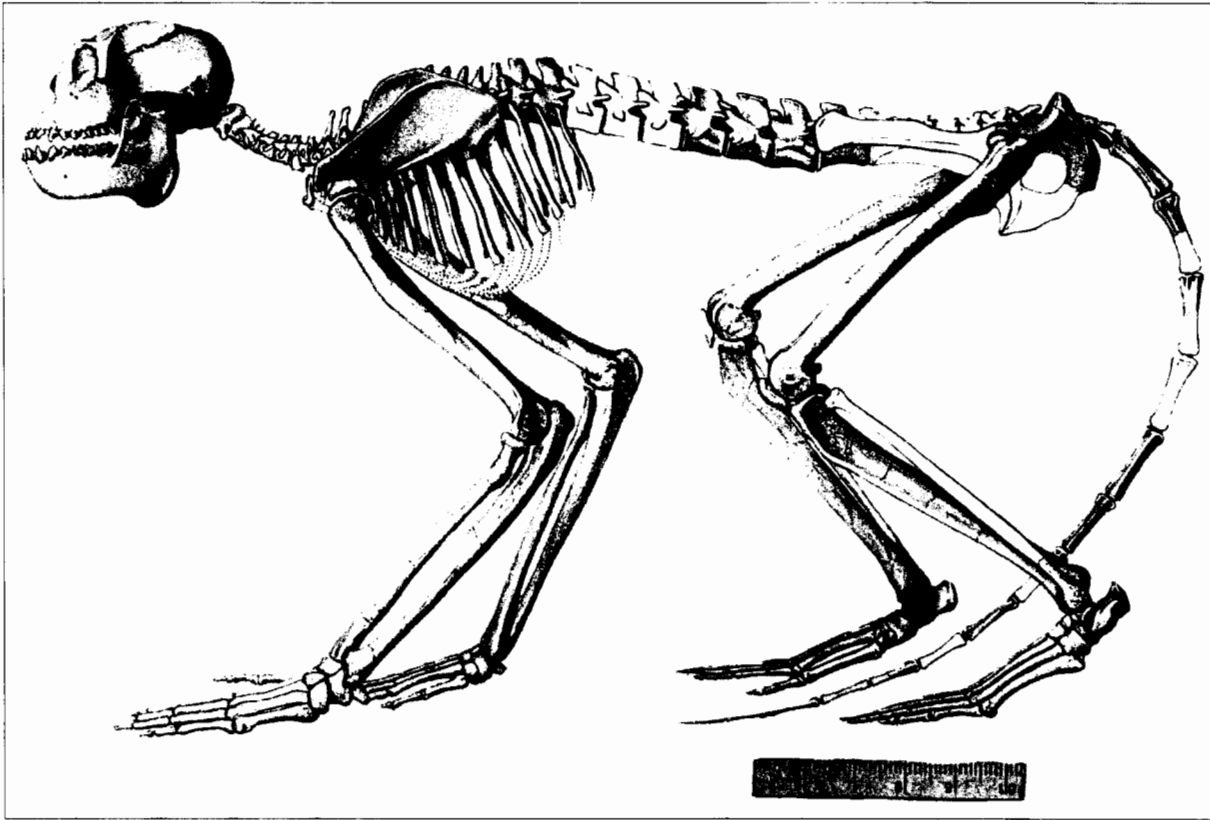
†*Rhinocolobus*

?†*Microcolobus*

Subtribe Presbytina

Presbytis

Semnopithecus



Reconstruction of female skeleton of *Mesopithecus*, from Pikermi (Greece), ca. 8.5 Ma. A medium-sized, semi-terrestrial colobine, *Mesopithecus* is known from England through Afghanistan at times between 10 and 3 Ma. From A. Gaudry, *Animaux Fossiles et Géologie de l'Attique*, 1862, F. Savy. Three cm on scale = 7cm of actual size.

- S. (Semnopithecus)*
- S. (Trachypithecus)*
- Pygathrix*
- P. (Pygathrix)*
- P. (Rhinopithecus)*
- Nasalis*
- N. (Nasalis)*
- N. (Simias)*

Subfamily Colobinae, incertae sedis

- †*Mesopithecus*
- †*Dolichopithecus* (?including †*Parapresbytis*)

†extinct

See also Africa; Asia, Eastern and Southern; Cercopithecidae; Cercopithecinae; Diet; Europe; Hadar; Kromdraai; Laetoli; Makapansgat; Miocene; Monkey; Pliocene; Primate Ecology; Primate Societies; Siwaliks; Skull; Sociobiology; Sterkfontein; Teeth. [E.D.]

Further Readings

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