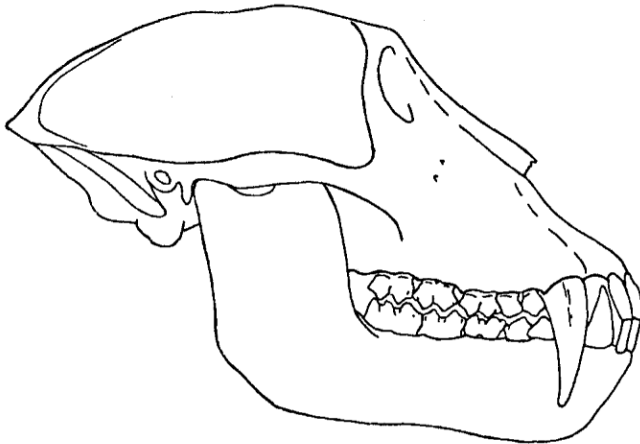


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Cercopithecidae and Parapithecidae

E. L. Simons and E. Delson



The higher primates of the suborder Anthroipoidea represent the more progressive division of the primate order related to and including man himself, as distinguished from the lower primates or suborder Prosimii. The New World monkeys or Ceboidea (Platyrrhini) today occur in South and Central America and apparently represent a radiation of the neotropical region that may well have been distinct from Old World forms (Catarrhini) at least since early Eocene times. The Old World Anthroipoidea, which includes monkeys, apes, and man, occurs as a range of both living and fossil species throughout Africa and Eurasia.

Both groups of Anthroipoidea share a number of readily identified features. The brain is large and convoluted, eye sockets are fully formed, the rostrum is typically foreshortened, and the jaw rami and frontal bones fuse together in embryonic or early juvenile stages. The front lower premolar (P_2 in New World monkeys and P_3 in Old World Anthroipoidea) is often but not always anterolaterally extended, bears comparatively thick enamel, and may serve as a hone that sharpens the posterior blade of the upper canine. In man and certain ceboids this function is reduced.

Following Simpson (1945), almost all authorities divide the catarrhine infraorder into two living superfamilies, Hominoidea, including three families—Hominidae, Pongidae, and Hylobatidae—and Cercopithecoidea, with a single family—Cercopithecidae. The extinct African Oligocene monkeys of the family Parapithecidae are here considered as possibly referable to Cercopithecoidea, Simons considering them closer and Delson further from living Old World monkeys. Delson and Andrews (1975) have revised the foregoing classification somewhat, but for this review we will remain taxonomically conservative. As a group the Old World higher primates show little or no expansion of the auditory bulla, but among all extant species the tympanic bone is drawn out into an elongated external auditory meatus, part of the roof of which is formed by the squamosal bone. The postorbital plate is composed of elements of the jugal, frontal, and alisphenoid bones, with maxillaries contributing a small portion to the medial orbital floor. The dental formula is typically $\frac{2.1.2.3}{2.1.2.3} \times 2$, but as would be expected for early forms, in *Apidium* and *Parapithecus* it is $\frac{2.1.3.3}{2.1.3.3} \times 2$. Postcranial adaptations vary with modes of locomotion (Simons 1972:86–92).

The history of monkeys in Africa is little understood but it is generally supposed that the earliest

phases of the development of cercopithecoids took place there (von Koenigswald 1969, Simons 1970, 1972, Delson 1975a). Nevertheless, these animals are not abundant in Miocene and earlier Pliocene deposits known from that continent. In addition, most of the African Plio-Pleistocene species described so far differ markedly from present-day African monkeys. Some North African fossil monkeys of the later Tertiary may well have had strong affinities with circum-Mediterranean faunas, while others are linked with those of sub-Saharan Africa (Delson 1973, 1975a, b).

Moreover, the only Oligocene monkeys known from Africa, species of *Parapithecus* and *Apidium*, are too disjunct in time from the much later occurring series of African fossil monkeys for their exact phyletic position, in relation to the latter, to be known. That is, one cannot be certain (without intermediate connecting links) whether the Egyptian Oligocene Parapithecidae gave rise directly to modern Cercopithecidae or are relatively distantly related to their ancestors. We can be definite, however, that the Parapithecidae had reached the grade of organization of higher primates and are not Prosimii (Simons 1974; Conroy, Simons, and Schwartz 1975; Delson 1975c; Conroy 1976).

Being approximately 28 to 30 m.y. old, *Parapithecus* and *Apidium* species naturally show a blend of "primitive" and "advanced" features that cause them to resemble in some respects the ceboid monkeys (Conroy 1976). Nevertheless, our view is that the ceboid-parapithecoid similarities—most are no more than retention of prosimian or ancestral anthropoidean features—reflect only their general level of organization. In terms of *grade*, the ceboids, cercopithecids, and parapithecids are monkeys, rather than prosimians or apes, but this might reflect nothing more than parallel advance from a common genotype last shared some time between early Eocene to late Eocene. Pending more complete analysis of not only parapithecids (under way by Simons) but also of ceboids by Rosenberger (e.g. 1977), relationships among the three monkey groups will continue to be uncertain.

The derivation of South American monkeys from an early Tertiary African stock is a hypothesis that has gained a certain fashion recently. The transit postulated to have occurred first for rodents and then for monkeys by rafting across the South Atlantic in Eocene times (Lavocat 1969, Hoffstetter 1972) is wholly untenable. The South Atlantic was then perhaps two-thirds as broad as it is now (see Phillips and Forsythe 1972). Any small Eocene primates in West Africa postulated to have been washed out to

sea clinging on masses of vegetation would surely have died of thirst and exposure long before the hypothetical slow transit to South America by ocean currents was completed: approximate crossing time today based on drift card transport in the South Equatorial Current is an absolute minimum of 60 days (Sheltima 1971). To this must be added an unknown time of random wandering between formation of rafts in rivers and their possible insertion into ocean currents. Even allowing mid-Tertiary South Atlantic widths of two-thirds to one-half the present and omitting time lost in random wandering, the corresponding 30 to 40 days minimum for current transport across would prevent small primate survival (see Simons 1977).

Several studies covering the fossil cercopithecoid monkeys of Africa have recently been completed. These include Delson (1973) on the circum-Mediterranean species with comments on the East African Miocene forms; Jolly (1970, 1972) on the genus *Theropithecus* (= *Simopithecus*) and on the adaptive significance of the *Theropithecus* functional complex; the various reviews of Freedman (1957–1976) and of Maier (1970–1972) on the South African fossil monkeys; studies by R. E. F. Leakey (1969), von Koenigswald (1969), M. G. Leakey (1976), M. G. and R. E. F. Leakey (1973a, b, 1976) and Eck (1976, 1977) on East African monkeys; and finally general reviews of all fossil monkeys by Simons (1970, 1972) and Delson (1975a).

Family Cercopithecidae—Miocene to Pleistocene Monkeys

The essential taxonomic characters of the cercopithecids have been summarized most recently by Delson (1975a), while more detailed anatomical treatments are presented by Hill (1966, 1970, 1974; see also Kingdon, 1977). In brief, the two subfamilies differ in such cranial features as relative interorbital width and facial length (nasal bone length, lacrimal relationships), the colobines having shorter and broader faces than cercopithecines. Dentally, the colobines are characterized by high relief on the molars, short trigonids on lowers, relatively straight-sided molars and narrow incisors, as well as several minor features; African forms often also show a reduction of the P³ protocone and/or the P₄ metaconid and may have the distal lophid on M₃ wider than the mesial. The cercopithecines fall into three groups dentally: most distinct are the African guenons and relatives, tribe Cercopithecini, which have lost the hypoconulid on M₃ as well as on dP₄-M₂, but share with other cercopithecines enlarged

incisors (related to a frugivorous diet), longer trigonids, and low molar relief; they also preserve enamel on the lingual surfaces of the lower incisors and share relatively straight-sided molars with colobines (except in *Allenopithecus*). The tribe Papionini includes both African and Eurasian forms that in a majority of cases appear to be dentally the most conservative among cercopithecids. Baboons and mangabeys, as well as macaques, typically have large M_3 hypoconulids, low relief, and moderate to long trigonids, as well as large incisors and more "flaring" or sloping-sided molars, but they also share a reduction (or complete lack) of enamel on the lingual face of the lower incisors, probably an adaptation to a gliriform "self-sharpening" incisor wear pattern. The genus *Theropithecus* has further converged on colobines from a "typical papionin" dental pattern. Cheek-tooth relief is increased and the trigonid is somewhat shortened. Postcranial differences among cercopithecids appear to reflect habitus more clearly than heritage. For example, moderate to extreme terrestriality has arisen several times in parallel. Brief comments on each genus are presented here: see Szalay and Delson (in press) for greater detail and documentation.

Subfamily Cercopithecinae Gray 1825

Tribe Cercopithecini

Genus *Cercopithecus* Linnaeus 1758

Although the Early Miocene African fauna mainly represents a forest biotype, this environment is poorly sampled in the later Neogene. Modern *Cercopithecus* is represented by numerous species, of which most are restricted to forest; it is likely that members of the genus would rarely be found as fossils. Only one set of *Cercopithecus* fossils has been described in any detail, by Eck and Howell (1972). They recovered a partial mandible and isolated teeth from several levels in the Omo Group ranging in age from ca 3.0–1.5 m.y., but were unable to associate these remains clearly with any modern species. Additional fossils referable to *Cercopithecus* have been recovered from the East Rudolf area (see M. G. Leakey 1976). The group of sites to the east of Lake Turkana (formerly Lake Rudolf) will continue to be denoted here by their original East Rudolf locality designations now embedded in the paleontological literature and should not, in our opinion, be subject to fluctuating name changes. *Cercopithecus* also occurs at Kanam East (Delson, unpublished). No fossils referable to either *Allenopithecus* (which would be recognizable from its distinctive dental morphol-

ogy) or *Erythrocebus* (also with distinctive large teeth and postcrania) have been reported.

Tribe Papionini Burnett 1828

Genus *Macaca* Lacépède 1799

Fossil finds indicate that the genus *Macaca* was European or perhaps circum-Mediterranean in origin. Today it has achieved what appears to be the most widespread distribution of any Old World monkey, ranging discontinuously from Gibraltar and North Africa across India and Southeast Asia to the northern island of Japan. The Japanese macaque, *Macaca fuscata*, is adapted to the most rigorous environment tolerated in the wild by any living non-human primate.

Although *Macaca* has an extensive fossil record in Europe, it is scarce in Asia and only poorly known in North Africa. Two important collections from the latter region which are provisionally referred to the genus (about as much on geography as on morphology) represent its earliest occurrences. Stromer (1920) described a group of fragmentary gnathic specimens from Wadi Natrun, Egypt (6? m.y.) which he termed *Aulaxinus libycus*, employing as the generic name a term previously applied to some European fossils (Cocchi 1872) but which had been shown to be synonymous with *Macaca* (Ristori 1890). This locality has also yielded the colobine *Libypithecus* and a small assemblage of other mammals, including *Lutra*, *Sivachoerus* (*Nyanzachoerus*), a distinctive rodent and other taxa, discussed in more detail under *Libypithecus*. *Macaca* is essentially a highly conservative papionin, so that its identification in the fossil record is fraught with probable error, but no characters in the known sample (about five partial mandibles, two maxillae, and a dozen isolated teeth) preclude assignment to this genus, as a probably distinct species *M. libyca*.

Perhaps slightly earlier than the Natrun local fauna (7? m.y.) is one from Marceau, Algeria, which is strangely dominated by cercopithecids. Arambourg (1959) reported these fossils, but he both confused the age of Marceau with that of the much older Oued el Hammam and named only a single cercopithecoid species, *Macaca flandrini*. Delson (1973, 1975a) showed that the type and several other teeth of this form were colobine, possibly sharing certain dental features with other African forms, and he referred the species to "*?Colobus*," employing the modern name as a "form-genus" pending further data. The remainder of the sample, about forty mainly isolated teeth, are clearly papionin but are otherwise indeterminate. Pending their more detailed study

by Delson (in progress), at least one species of cf. *Macaca* may be recognized here. The single M_3 from Ongoliba, Zaïre, described by Hooijer (1963, 1970) as "cf. *Mesopithecus* c.q. *Macaca*" is very similar in size and morphology to those from Marceau and might represent the same taxon, being probably of similar age as well. Delson (1975b) has suggested that the Marceau and Ongoliba populations might be part of one or more widespread species of early papionin which ranged across the Sahara region before it suffered Final Miocene dessication and the macaques differentiated from sub-Saharan papionins.

Genus *Parapapio* Jones 1937

Of the six papionin genera represented in the Plio-Pleistocene of sub-Saharan Africa, *Parapapio* is certainly the most "primitive," providing something of a model for the origin of the group. It is difficult to differentiate it from *Macaca* morphologically, as each has retained many of the characters that probably were present in Late Miocene ancestral papionins. The bulk of known *Parapapio* specimens is from southern Africa (South Africa, also Angola), but recently some fragmentary remains have been recognized in eastern Africa as well.

Among the major distinguishing characters of *Parapapio* are rather straight profile of the muzzle dorsum in both sexes from nasion to rhinion (or to nasospinale), rather than the steeper anteorbital drop seen in *Papio* and *Cercocebus*; glabella and supraorbital tori not projecting; weak development of temporal lines and slender cheek bones, suggesting gracile masticatory musculature; lack of strongly developed maxillary or mandibular fossae (in most cases); and lack of sexual dimorphism in teeth (other

than the canine- P_3 complex) or in skull shape. Many of the features that distinguish *Parapapio* and *Papio* cranially can be seen in figure 7.1. Muzzle shape may vary individually, but there does appear to be a fairly uniform pattern of distinction from *Papio* and *Cercocebus* overall, although both these genera might conceivably have evolved from early species of *Parapapio*-like animals.

Some three hundred to five hundred specimens of *Parapapio* are now known from South African sites, which include Sterkfontein, Makapansgat, Bolt's Farm, and Taung. Specimens of the genus have also been reported at Swartkrans, Kromdraai, and at Leba, Angola, but the amount of material from these latter sites is very small. Studies so far have divided *Parapapio* into four species—*P. broomi*, *P. jonesi*, *P. whitei*, and *P. antiquus*. However, it is not always entirely possible to decide to which of these species an individual specimen belongs (compare, e.g., Maier 1971a and Freedman 1976). Much of the definition of species at Sterkfontein (type site for all species but *P. antiquus*) and Makapan has rested on absolute tooth size, but recent studies emphasizing cranial (and dental) proportions arrive at differing conclusions. Although the known variation appears to require several species, their precise differentiation is still unclear. *Parapapio antiquus* is known only from Taung and appears cranially somewhat more distinctive.

In eastern Africa, at least one (perhaps two) species of small to medium-sized papionin is known from several sites in the 3–4 m.y. range: Kanapoi, Lothagam-3, Laetolil, Hadar, and perhaps Kubi Algi. Later, generally even more fragmentary material has been reported from Omo, the Koobi Fora



Figure 7.1 Comparison of casts of (A) male *Parapapio* cf. *broomi* and (B) female *Papio wellsi* from South African Pleistocene deposits. Both genera often occur in association with *Australopithecus*. The profile of the nasal bones in *Parapapio* is much less concave than in *Papio*. (Scale $\times \frac{1}{2}$ approximately.) (Photo by A. H. Coleman.)

Formation at East Rudolf, and perhaps Olduvai. Patterson (1968) originally referred the Kanapoi jaw to *P. jonesi*, but M. G. and R. Leakey (1976) thought the specimen indeterminate, while describing others from the noted sites as *Cercocebus* sp. (see also M. G. Leakey 1976, Eck 1976). It would seem that most of the earlier fossils, at least, are best referred to *Parapapio* at present, but detailed analysis is badly needed. The genus *Parapapio* should have great potential as a transcontinental indicator of stratigraphic age in sub-Saharan Africa. Unfortunately, its paleobiology is less certain, as no postcranial elements have yet been unquestionably allocated, but there is some suggestion of greater arboreality than among *Papio* species.

Genus *Cercocebus* E. Geoffroy 1812

The living mangabeys are divided into two main groups that appear to differ minimally in characters of dental wear and development of facial fossae. They are basically arboreal, although some forms come to the ground regularly. Species of this genus are, as expected from their arboreality, rare in the fossil record. Specimens from Makapan previously identified as *Parapapio jonesi* have recently been suggested to be *Cercocebus* sp. (Eisenhart 1975), while other small papionins from Omo and Koobi Fora may also represent this genus, as do probably some isolated teeth from Kanam.

Genus *Papio* Müller 1773

Typical baboons, usually considered to represent the genus *Papio*, are the dominant open-country cercopithecoid in modern Africa. Their close relatives in West African forests, the mandrills and drills, are often termed *Mandrillus*, but Delson and Napier (1976) have shown that the term *Papio* was applied to a mandrill before being used for a "savanna" baboon. They requested the International Commission on Zoological Nomenclature to rule on this problem. Pending such a ruling, the generic term *Papio* will be used here for both groups of baboons, which may well be congeneric (Delson 1975a). Studies of behavior, genetics, and morphology show that all the "savannah" baboons are quite closely related, but it appears that two species may be recognized today: *P. cynocephalus* in most of sub-Saharan Africa and *P. hamadryas* in eastern Ethiopia and Arabia, probably in the final phases of speciating from the former.

Papio is rather rarer than might be expected in the fossil record, especially in eastern Africa. This is probably due to the past widespread presence of *Theropithecus*, which Jolly (1970, 1972) suggested may have inhabited wetter grasslands. In the latter

environment it may only recently have been replaced by *Papio*, species of which may now, in turn, be adapting to drier savanna from a previous forest-fringe habitat. Fossils apparently referable to the modern species have been reported from Olduvai (horizon uncertain) and occur throughout the Omo sequence (Eck 1976, 1977), while *Papio robinsoni* from numerous South African sites is probably best considered at most a temporal subspecies of *P. cynocephalus*. The characters utilized by Freedman (1957) in diagnosing *P. robinsoni* are minimal compared to the range of variation seen in the modern polytypic biospecies. On the other hand, *Papio baringensis* R. Leakey (1969), may well represent a distinctive species whose most diagnostic characters are small incisors, marked postorbital constriction, and some differences in facial proportions (see M. G. and R. Leakey 1976).

All the fossil remains discussed above have about the cranial size found in most living baboon populations, but a group of smaller specimens is also known from several South African sites. These fossils show the diagnostic facial features of *Papio* (such as deep facial fossae, steep anteorbital drop, and relatively projecting brows), but are smaller than or comparable to individuals of the smallest modern subspecies *P. cynocephalus* "*kindae*." *P. izodi* and *P. wellsi* have been reported from Taung, while *P. angusticeps* is known from several of the younger sites (Swartkrans, Kromdraai, and others), and one juvenile skull was reported from Sterkfontein (Eisenhart 1975). The relationships among these nominal species are still uncertain.

Modern *Papio* species, excluding drills and mandrills (of whom there is no definite fossil record), are highly terrestrial animals, presumably like their fossil congeners. Unfortunately, the presence of numerous species of similar size in the South African cave deposits (where direct associations of skeletal elements are almost unknown) makes it difficult to allocate the few limb bones reported there to specific species or even to particular genera.

Genus *Dinopithecus* Broom 1937

This monotypic genus is known essentially from only Swartkrans, South Africa. It was among the largest of known cercopithecoids; only the biggest *Theropithecus* species of the past and perhaps some modern *Papio* (mandrills) are larger. The type specimen of *Dinopithecus ingens*, and perhaps one other fossil, is from Schurweberg, but the several dozen other specimens are from Swartkrans (see Freedman 1957); additional undescribed remains may be present at Leba, Angola. Arambourg (1947) named

some teeth from Omo *D. brumpti*, but most of these are now known to be referable to *Theropithecus*. The morphology of the skull and teeth of *Dinopithecus ingens* is most like that of *Papio*, from which it is hard to separate. Like *Papio*, but unlike *Parapapio*, the skull was very large and rugged, and the female at least had a rather long muzzle somewhat reminiscent of large "savanna" baboons; maxillary fossae are lacking. In females, the upper tooth row is arranged in a U-shaped outline narrowing somewhat to the rear. The males may have been similar but with less posterior narrowing. The tooth morphology of *D. ingens* most closely resembles that of *Gorgopithecus major*, but the latter species is smaller and apparently shows little or no sexual dimorphism in tooth size. Cresting on the skull of *Dinopithecus* is pronounced: both sexes show a large nuchal crest, and the temporal lines are strong. The males have well-developed sagittal crests and large postglenoid processes. The large molars often show many accessory cuspules, and the genus is characterized in general by a tendency to show large, broad cheek teeth coupled with a relatively short lower front pre-molar possessing a particularly large anterior fovea (Freedman 1957).

Genus *Gorgopithecus* Broom and Robinson 1949

The one species now placed in the genus *Gorgopithecus* was originally described by Broom in 1940 as *Parapapio major*; later Broom and Robinson (1949) elevated it to generic level. The type consists of only two teeth, an upper second and third molar that are considerably worn and of unidentifiable sex. However, there seems to be no other South African fossil monkey species that falls into the same size range as *Gorgopithecus*. Skulls of this genus are about the size of those of male *Papio cynocephalus ursinus*. Freedman (1957) pointed out that the type of *Gorgopithecus* is a particularly unfortunate specimen because of its incompleteness, but concluded that two other Kromdraai specimens, on which most of the diagnosis of this animal is based, presumably belonged to the same species as the type. *Gorgopithecus* appears to be restricted to the Kromdraai "faunal" site, or Kromdraai A; the only cranium of this species is illustrated in figure 7.2.

Compared with modern *Papio*, the muzzle of *Gorgopithecus* is short and the brain case is rather longer. Another significant difference is that in *Gorgopithecus* the anterior insertion of the zygomatic processes has an almost vertical face, whereas that of *Papio cynocephalus ursinus* slopes backward, giving the impression of a shorter snout in the latter than would otherwise be apparent. Even so, with the

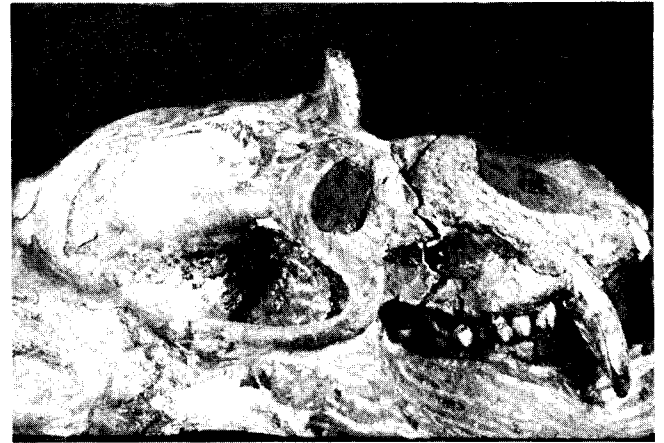


Figure 7.2 Oblique view of the cranium of *Gorgopithecus major*, a large *Papio*-like baboon from Kromdraai (A), South Africa. The middle part of the face in this unique skull has been largely reconstructed in plaster. (Scale $\times \frac{1}{3}$ approximately.) (Photo by R. Ciochon.)

muzzle starting more or less directly under the orbit in *Gorgopithecus*, the snout appears short; this feature is combined with a vertically high and transversely narrow rostrum. Other important characteristics of *G. major* include an apparent lack of sexual dimorphism in either skull or tooth size (but only a few specimens are known and not all can be sexed by the dimorphic canine- P_3 complex) and the presence of strong supraorbital ridges and deep maxillary fossae, without mandibular fossae. Only one skull is known, and although this is nearly complete, the facial region has been badly "reconstructed" in plaster (Delson 1975a), a point not mentioned by either of the major describers which has confused interpretations by later workers. Delson (1975a) suggested placing *Gorgopithecus* as a subgenus of *Dinopithecus*, mainly on grounds of size, but this view cannot yet be substantiated by shared derived morphological features—that is, by "characters of common descent." *Gorgopithecus* is retained here as a full genus, pending revision. Both *Gorgopithecus* and *Dinopithecus* are probably most closely related to *Papio*, and Maier (1971b; also Eisenhart, pers. comm.) suggested that they may be synonyms of the modern genus, but until this view can be documented, it need not be accepted. Freedman (1957, 1976), on the other hand, has suggested that both large extinct forms have some dental features specially in common with *Theropithecus*, but Delson (1973, 1975a; also Jolly 1972) has refuted this opinion. Allocation of postcranial elements to these two taxa would go far toward clarifying their mode of life as well, perhaps, as their phyletic affinities.

Genus *Theropithecus* I. Geoffroy 1843

Theropithecus today is represented by a single species, *T. gelada*, occupying a relict distribution in the Ethiopian highlands where it feeds extensively on dry grass blades, seeds, and rhizomes. Relatives of the gelada have long been known from the fossil record of the African Plio-Pleistocene, under the name *Simopithecus* Andrews 1916. Jolly (1972, 1970) has recently revised these forms. He has suggested that they should best be ranked as a subgenus of *Theropithecus*, a view we and most, but not all, primatologists now accept (compare, for instance, M. G. and R. Leakey 1973a, Freedman 1976).

In addition to dental morphology, the major special features that link the modern and fossil forms include reduction of the anterior dentition (which grows proportionally smaller in larger populations); upright mandibular ramus, higher in larger forms and, in turn, linked to a deep and short face; sagittal crest placed relatively anteriorly if present; elongate forelimb, especially humerus; elbow complex with expanded, back-tilted ulnar olecranon and small, retroflected medial epicondyle of the humerus; and short, stout phalanges. These characters reflect the dietary and postural-locomotor adaptations of *Theropithecus*: a concentration on tough foods, requiring little incisal preparation, but prolonged trituration by complex cheek teeth (see figure 7.3A) in turn necessitating a musculature that brings the greatest pressure to bear on the distal teeth. These monkeys present an extreme terrestriality—living geladas hardly ever enter trees but instead walk long distances in search of food and then eat it in a sit-

ting posture, passing small food items to the mouth with the prehensile hands. The presence of most of the same morphological features in the larger fossil races or species suggests that they, too, were strongly terrestrial graminivores. Jolly (1972) was further able to demonstrate that most *Theropithecus* (*Simopithecus*) remains occur in waterside habitats, where seasonal rainfall fluctuations would have produced extensive open grasslands.

A number of fossil populations have been recovered and numerous taxa named, mostly reviewed in the cited papers. The oldest specimens are isolated lower molars: one from Lothagam-3, Kenya (Patterson et al. 1970), about 4 m.y. old, has a morphology rather typical of early *Theropithecus*. Another find is from Aïn Jourdel, Algeria, probably slightly younger and morphologically more distinctive than at Lothagam (this was described as *Cynocephalus atlanticus* by Thomas 1884; see also Delson 1975a, and in preparation). Two species of *Theropithecus* (*Simopithecus*) can be recognized from the later Pliocene through the Pleistocene. *T. (S.) darti* occurs at Makapan South Africa, and perhaps also at Hadar and East Rudolf in eastern Africa. It is somewhat larger than the modern species (in turn smaller than most *Papio* species) and shows only slight incisor reduction. Of the foregoing numerous dental-gnathic elements are known, but no postcranials have been reported. Relatively recently, juvenile and adult female skulls from Makapan were described by Maier (1972) and Freedman (1976), respectively (see figure 7.3B). *T. (S.) oswaldi* was described first from Kanjera, Kenya, but is now known as several sub-

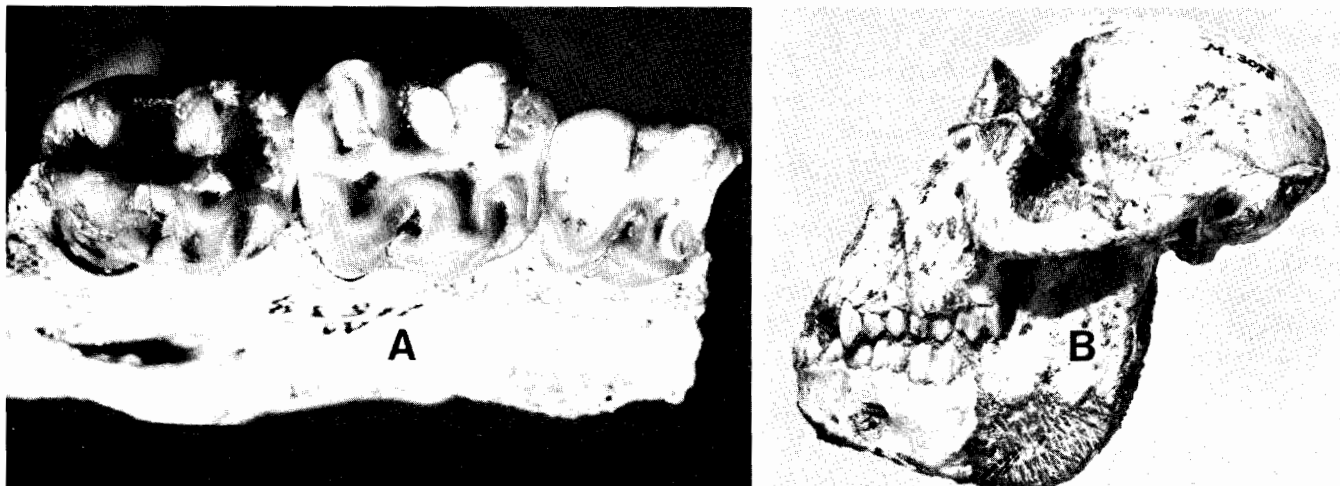


Figure 7.3 (A) *Theropithecus oswaldi*, female, upper right molars from Kanjera, Kenya, East Africa, with thick, in-folded enamel and differential wear on successive molars (scale $\times 2$). (B) *Theropithecus darti*, lateral view of the skull of a female juvenile from Makpansgat, South Africa, showing the flattened face and elongated ascending mandibular ramus characteristic of members of this genus (scale $\times \frac{4}{9}$ approximately). (Photos by E. Delson and W. Eisenhart.)

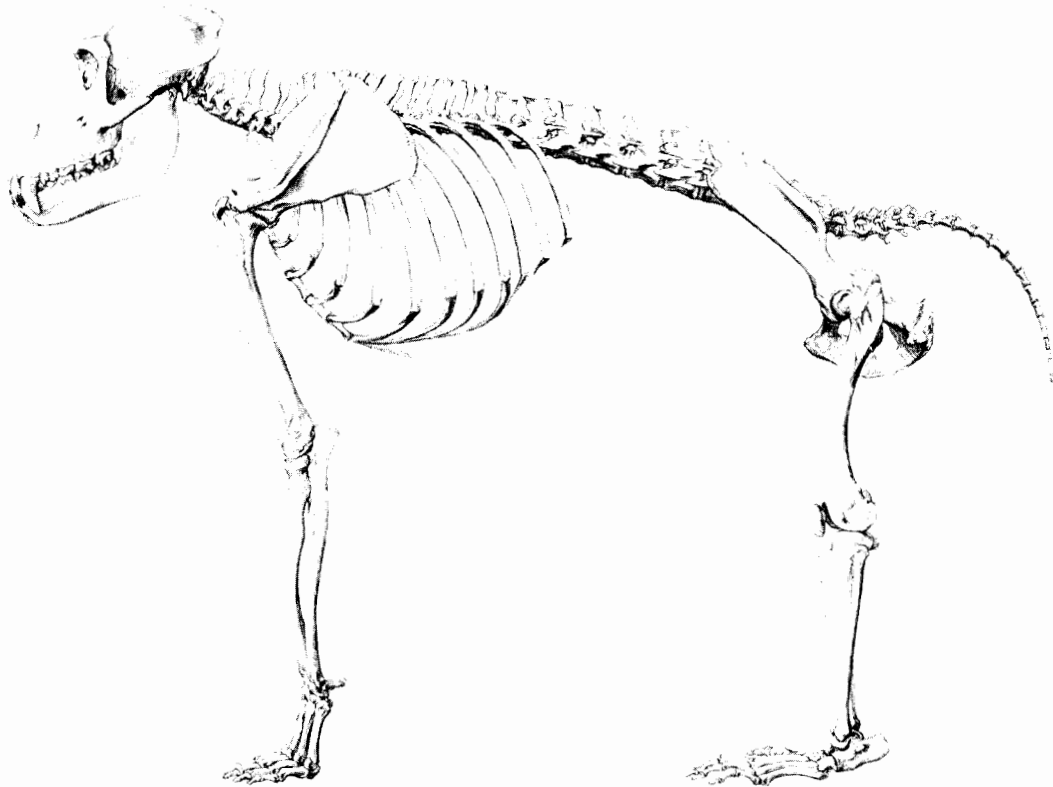


Figure 7.4 Reconstruction of the skeleton of an extinct "giant" species of *Theropithecus* (*Simopithecus*) found at Olduvai Gorge, Tanzania. At least in part for allometric reasons the forelimbs are distinctly longer than the hind-limbs. The skull has been restored with too much resemblance to *Papio*; the canines should be smaller, the face shorter and deeper, and the ascending ramus of the jaw should be at more of a right angle to the horizontal. (Scale $\times \frac{1}{8}$.) (Drawing by Jay H. Matternes, © National Geographic Society.)

species from numerous East African localities, as well as in at least one site each in northern and southern Africa. The several populations vary greatly in size, and a number of allometric (and possibly temporal) trends can be discerned, mostly from teeth, but also from the cranial and postcranial material known from Kanjera, Ologesailie, and Olduvai, especially. In the largest forms, the cheek teeth increase in size in proportion to the mandible and cranium, but the anterior dentition is hardly if at all larger than in much smaller individuals of the modern species.

To illustrate this pattern, the modern *T. gelada* has molars (and canines) about equal in size to those of neighboring *Papio hamadryas*, but rather smaller incisors. In *T. darti* from Makapan, the molars are larger, while the incisors are about the same size, but the male canines are still tall and compressed. In the smaller *T. (S.) oswaldi*, the incisors are smaller still, while in the larger forms, the cheek teeth are very long, the incisors even smaller and the canines robust but short, with reduced P_3 mesio-buccal flange for honing the upper canine. The most

extreme case is the mandible from the lower Ndutu Beds at Olduvai Gorge (above Bed IV, perhaps 300,000 years old; Hay 1976). It was termed *Simopithecus jonathoni* by Leakey and Whitworth (1958). Although previously considered a female, M. G. and R. Leakey (1973a) suggested that it may have been a male with canines even more reduced and turned somewhat laterally, away from occlusion with P_3 ; this specimen is nearly the size of a female gorilla mandible and may represent the maximum size of any known cercopithecoid. Eck (1977) has also discussed a cranially distinctive species from the earlier Omo deposits as *Theropithecus brumpti* (Arambourg 1947).

Jolly (1972) has described a number of complete and partial postcranial elements that underline the affinities and adaptations of *T. (Simopithecus)*. A nearly complete male skeleton has more recently been recovered in Bed II at Olduvai, (M. and R. Leakey 1973a), but never fully described. A reconstruction of it has been attempted by J. Matternes (figure 7.4), but the canine and skull are probably too *Papio*-like. The great elongation of the forelimb was

used by Jolly as evidence of extreme terrestrial adaptation, like that seen in *Gorilla*, in turn suggesting postural ability comparable to *Theropithecus gelada*. Moreover, the phalanges are about the length of those in much smaller male *Papio*, but considerably more thick or robust, and the elbow and shoulder joints are constructed as in geladas and other terrestrial primates.

The extinction of such a successful and widespread taxon is always a problem of some interest, and in this case, several suggestions have been put forward. In a number of localities, especially Olorge-sailie, there is evidence for *Theropithecus* having been extensively hunted by humans with an Acheulean culture. In addition, changing climatic conditions may have at once reduced the extent of wet grassland and extended drier savanna, to which previously forest-fringe *Papio* species became better adapted. Eventually, only the relict and probably ancient population of *T. gelada* survived in upland Ethiopia. Interestingly, *Theropithecus* individuals appear behaviorally subordinate to *Papio* in their infrequent interactions.

Subfamily Colobinae Blyth 1875

Genus *Colobus* Illiger 1811

Colobus is the only living African colobine, including four main species in three groups, often ranked as subgenera. Fossil remains are rare and most fragmentary. A skull of uncertain age of the modern *C. guereza* was reported by Simons (1967) from Sudan, and partial dentitions are known from the Omo, East Rudolf, and Kanam deposits. As indicated above, Delson (1975a, 1973) showed that the type and several other isolated teeth of *Macaca flandri* Arambourg, 1959, from Marceau, Algeria, were colobine in morphology. These specimens are similar in size and shape to *Cercopithecoides williamsi*, but are also morphologically close to certain living colobine species. To emphasize their uncertain allocation, they may be termed ?*Colobus flandri*. Except for unpublished remains from the Ngorora Formation, central Kenya, these constitute the oldest known colobine in Africa.

Genus *Libypithecus* Stromer 1913

The most completely preserved skull of a North African late Tertiary monkey is that of *Libypithecus markgrafi* Stromer (1913) from a probably late Turolian faunal equivalent (age estimated at 6 m.y. by Cooke and Maglio 1972) at Gar Maluk, Wadi Natrun, northern Egypt (see figure 7.5). With it at the same site have been found a lower M_1 probably of

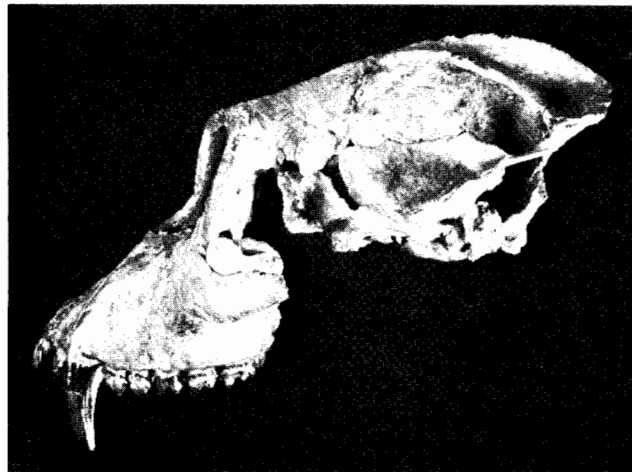


Figure 7.5 Left lateral view of the cranium of the holotype of *Libypithecus markgrafi*, a colobine with possibly semiterrestrial habits from the Latest Miocene Wadi Natrun deposits of northern Egypt. (Scale $\times 0.6$.) (Photo by E. Delson.)

the same species, as well as mandibular and maxillary fragments of a species of *Macaca*. Because of its completeness and its unique combination of anatomical features the relationships of this species have been much discussed (see Stromer 1913, Edinger 1938, Jolly 1967, Hill 1970, and Simons 1970, 1972). Delson (1973, 1975a) has reviewed the history of study and the anatomy of this single skull in detail and has added some interesting clarification of the animal.

The male skull is nearly complete, although because of missing parts the mid and lower face is insecurely joined to the neurocranium. Moreover, the basicranium is extensively damaged, and there was antemortem trauma to the right canine and premaxilla. The dentition is anatomically colobine, the incisors small, but the molars increase in size to the rear. The face is projecting and somewhat narrow for a colobine, the supraorbital torus weak, and the sagittal and nuchal crests strong, meeting at the raisedinion. The size and shape of the skull is quite similar to that of *Colobus badius* (as suggested by Jolly 1967), but also close in form to the larger genus *Cercopithecoides* and in dental size to those of *Mesopithecus*. The similarity to *Dolichopithecus ruscinensis* suggested by Jolly (1967) was refuted by Delson, as were past considerations by various authors of relationships to *Papio* (partly based on incorrect assessment of its size) and to *Theropithecus* (Hill 1970). The endocranial cast was studied by Edinger (1938) and Radinsky (1974), who found basic resemblances to other colobines.

There are no postcranial elements known, so that

locomotor adaptation is uncertain, and the dental evidence is inconsistent. The rearward placement of temporal musculature suggests, following Jolly (1970), an emphasis on incisal food preparation, as in mandrills; but the incisors are small, as is typical for colobines, while the largest molar is the third, suggesting cheek tooth emphasis on crushing or slicing. Thus, the diet was probably different from that of modern colobines. Delson (1975a, 1973) was unable to determine the direction of that difference, although in some ways it parallels the dental adaptation of *Theropithecus*. The paleoecology of Wadi Natrun indicates that the region (although much better watered 6 m.y. ago than at present) was surrounded by open country inhabited by ostrich, mastodon, and *Hipparion*, as well as macaque. The aridity that produced the aeolian excavation of the Egyptian Western Depressions (Qattara, Natrun, Fayum) was probably underway by this time, as a continuation of the longer term Saharan aridity. Thus, although the shores of Natrun Lake were probably wooded, the open country might have been suited to some sort of terrestrial feeding, possibly on small objects by *Libypithecus*. On the other hand, despite the generally circum-Mediterranean nature of the associated mammals, the affinities of this species are clearly with the African colobines *Colobus*, *Cercopithecoides*, and *Paracolobus*, none of which was terrestrial. Therefore a strong terrestrial adaptation appears to be unlikely.

Genus *Cercopithecoides* Mollett 1947

Cercopithecoides is one of the most widespread African monkeys, occurring in almost all the southern African localities from Makapan (the type site) through Kromdraai to Swartkrans "b," as well as at East Rudolf (Freedman 1957, 1976; M. G. and R. Leakey 1973b). The South African species, *C. williamsi* (figure 7.6), is larger than any modern colobine, with a slightly long and narrow face, short premaxilla, deep ophryonic groove, and pronounced sexual dimorphism in cranial shape (including the face). The temporal musculature is weak, with no evidence of sagittal cresting, and the nuchal muscles are also poorly developed. The mandibular ramus is slightly back tilted, with no enlargement of the gonial region. No postcranial elements have yet been allocated to *C. williamsi*, as is also the case with most other South African cercopithecoid species. Specimens previously termed *C. molletti*, as well as the neurocranium made the holotype of *Parapapio coronatus*, are now referred to *Cercopithecoides williamsi*, which may be clearly placed in Colobinae on



Figure 7.6 Dorsal view of the most completely preserved skull of *Cercopithecoides williamsi*, a male specimen from Makapansgat, South Africa. (Photo by W. Eisenhart.)

both cranial and dental morphology, despite previous uncertainty.

The affinities of *Cercopithecoides* within Colobinae are not completely certain, however. There appears to be little evolutionary change in the South African species over a long time range, despite some variability at Makapansgat. M. G. and R. Leakey (1973b) referred to the genus a skull and mandible from East Rudolf that are certainly distinct specifically but could well be close to *C. williamsi* phylogenetically. Overall dental and facial morphology appears to relate it most closely to *Paracolobus* (Delson 1973), but detailed comparative studies remain to be undertaken.

Genus *Paracolobus* R. Leakey 1969

The type species of the genus *Paracolobus*, *P. chemeroni*, was described by Richard Leakey (1969) from a find of a remarkably well-preserved skeleton in the Chemeron Beds west of Lake Baringo, Kenya. The partial skull of this specimen is illustrated in figure 7.7. Geological evidence from this succession indicates that the skeleton is about 4 m.y. old, while the associated fauna is comparable to 2-m.y.-old levels at Omo, suggesting a channel filling.

Paracolobus is a comparatively large form showing definite ties with the colobine monkeys. An estimate of skull length is that it probably exceeded 16 cm, and length of the hindlimb from the head of the femur to the distal extremities of the toes would have been approximately 0.75 m. These measurements exceed those of any other known colobine and



Figure 7.7 Lateral view of the cranium of *Paracolobus*, a large extinct colobine monkey from late Pliocene deposits in the Baringo Basin, Kenya. (Courtesy Kenya Nat. Mus.)

are comparable with the general gigantism of many East African Pleistocene and Pliocene mammals.

Considering dental function, mandibular anatomy of *Paracolobus* corresponds well with what would be expected of a large folivorous monkey. In *Paracolobus*, the face is deep, the horizontal line of the tooth row is dropped well below the basicranium, and the axis of the high mandibular ramus is at right angles to the corpus.

In these features, among several others, the probable male of *Paracolobus* resembles males of the genus *Colobus*. It differs from the latter cranially in having a longer snout and very broad face, comparable to *Pygathrix* species; laterally, the face has a smoothly rounded outline that is little like that of *Papio* (figure 7.7). Another difference from most modern *Colobus* is that the nasal aperture is transversely quite narrow and vertically unusually high. R. E. F. Leakey (1969) appears to believe that, in general, South African *Cercopithecoides* is more similar to some modern *Colobus* than is *Paracolobus chemeroni*, but the two are probably closely related.

The postcranial skeleton of this unusual find still awaits comprehensive analysis, but a few notes can be added. The olecranon process of the ulna is curved anteriorly to a line drawn through the long axis of the remaining shaft, which, together with a humero-femoral index below 100, could suggest that this was an arboreally adapted species; even so, a similar low index can be found in the patas monkey, a terrestrial form. Despite the retroflected humeral medial epicondyle, the long phalanges seem to confirm probable arboreality.

Additional colobine material has been recovered from several localities in both eastern and southern Africa which may be referable to *Paracolobus* or a similar genus. Fragmentary remains from Makapan are larger than *Cercopithecoides* from that site, while several mandibles and teeth from Laetolil are quite similar to *P. chemeroni*. A cranium and mandible from Omo was described by M. G. and R. Leakey (1973b) as a new, unnamed genus, but it and more recently recovered specimens from Omo (Eck 1977), East Rudolf, and Hadar indicate the presence of two or three colobine species of differing size during the Plio-Pleistocene interval, whose full analysis is awaited.

Subfamily *incertae sedis*

Genus *Victoriapithecus* von Koenigswald, 1969

Victoriapithecus is now known by a sample of over one-hundred mostly isolated teeth, but including several partial mandibles and about a dozen postcranial elements, almost all from a Middle Miocene East African locality on Maboko Island, Lake Victoria, Kenya. Five of these mandibular fragments are illustrated in figure 7.8. Although von Koenigswald (1969) stated that the holotype of *V. macinnesi* was from Rusinga, its attached matrix and the lack of additional specimens from anywhere on that island make this improbable; instead, this mandible may have also come from Maboko. Macinnes (1943) described and figured it, mentioning also some other teeth and indicating that at least one specimen was from Rusinga, without being more specific; he tentatively referred the jaw to *Mesopithecus* sp., then the oldest known cercopithecoid. Unfortunately, several recent authors have continued to employ uncritically this mistaken generic allocation. As Delson (1975a) indicated, von Koenigswald only described part of the original collection available to him, and numerous additional specimens have been recovered more recently on Maboko Island by Pilbeam, Andrews, and others.

In his report, von Koenigswald (1969) established

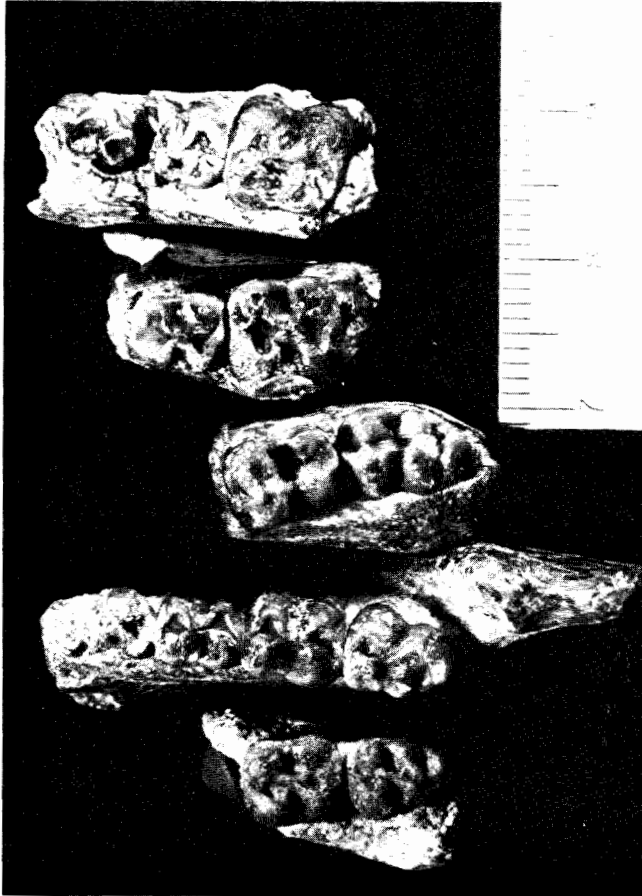


Figure 7.8 Occlusal views of *Victoriapithecus* mandibles from the Miocene of Maboko Island, Lake Victoria, Kenya. Center specimen is "*V.*" *leakeyi*. (Photo by E. Delson.)

two species of *Victoriapithecus*, *V. macinnesi*, based on the mandible mentioned above, and *V. leakeyi*, based on an isolated upper molar. Delson (1974, 1975a) reviewed the finds, suggesting that von Koenigswald's allocations were confusing, but that two different morphologies could be recognized on grounds other than size. *V. macinnesi* includes most of the dental remains, with both large and small individuals characterized by squarish molars with short trigonids (like colobines) but shallow lingual notches (like cercopithecines) and also with P_4 turned slightly oblique to the molar row. One lower jaw and perhaps some additional isolated teeth present narrower, more elongate molar crowns, also with shallow notches but longer trigonids, more like the macaque type of tooth thought to be ancestral for Cercopithecidae. The upper molar holotype of "*V.*" *leakeyi* (which, along with one other tooth, preserves the crista obliqua) appears to occlude with some of these, rather than with *V. macinnesi* of any size. It may be suggested (following Delson) that the latter

species had begun to develop a colobine tooth pattern, and it is possible that the two "morphs" represent different genera, if not subfamilies (in a vertical classification), but further analysis of sample variability in size and wear pattern is required. Both morphologies (species, genera?) are nearly fully bilophodont and are probably near the ancestry of later cercopithecids.

The several postcranial elements mostly derive from one species showing phalangeal robusticity and a macaque-like adaptation of its elbow joint. One humerus and perhaps one phalanx appear more "arboreal" in function, and are somewhat similar to those of modern *Colobus*. Delson has attributed the former, larger elements to "*V.*" *leakeyi* and the latter to *V. macinnesi*, but without better association, such allocation is uncertain.

Additional specimens possibly referable to *Victoriapithecus* are known from Ombo, Loperot, and perhaps Napak, Uganda. From the latter site, Pilbeam and Walker (1968) described one upper molar of cercopithecine aspect and a frontal bone of uncertain allocation.

Genus *Prohylobates* Fourtau 1918

The species *Prohylobates tandyi* was described in 1918 by the French geologist René Fourtau. It was one of a series of species of Miocene vertebrate fossils collected from the ridges north of Hatayet al Moghara, on the northwest side of Wadi Moghara, Egypt, U.A.R. In addition to the type specimen of *P. tandyi*, Fourtau described two other mandibular fragments under the name ?*Dryopithecus mogharensis*. In recent years Remane (1965) and Le Gros Clark and Leakey (1951) have recognized that the molars of the three Wadi Moghara primates resemble those of cercopithecoid monkeys but, because they had not seen the originals, their remarks were cautious. Simons (1969) recently restudied these three finds and showed that they are not apes, but all have the mandibular anatomy of cercopithecoid monkeys. It seems reasonable to conclude that they all belong to the same species because insofar as they can be compared there seems to be no anatomical difference between the three, the size disparity is not great, and they come from the same general locality and age. *Prohylobates tandyi* should thus be sustained as a taxonomically valid name for what seems to be the oldest monkey described to date.

Initially, Remane (1924), who considered the significance of Fourtau's Miocene Egyptian primates at some length, believed that *Prohylobates* was rather closely related to *Propliopithecus*. Nevertheless Remane was the first to point out that the entire set of

characteristics by which Fourtau attempted to relate *Prohylobates* to *Hylobates* was not taxonomically important and that they do not indicate in any way that the two held an ancestor-descendant relationship. On the other hand, Remane himself, working from Fourtau's poor photographic plates, did not realize that the external border of the mandible had been broken away anteriorly so that the mesial alveolus and root of P_3 had been lost. Concluding instead that P_3 of *Prohylobates* was single-rooted, he considered the form quite distinctive, because this feature is found commonly elsewhere among higher primates only in *Homo*. By 1965, however, he had reversed his position that *Prohylobates* was related to the ape *Propliopithecus*, concluding instead that its affinities might lie with the colobines.

The molar teeth of *Prohylobates tandyi* are not as completely bilophodont as those of *Victoriapithecus* or later cercopithecids, but the basic pattern is present. It may be best seen on M_2 of the holotype, despite its wear: the mesial lophid is worn away (if ever present), the distal one is poorly developed, and a low crest links the metaconid and hypoconid—the ancient cristid obliqua. In addition, there may have been a small median hypoconulid on M_2 , but this cuspule could also have been a variable minor accessory feature, as sometimes occurs in *Theropithecus* species. The M_3 in *Prohylobates tandyi* is shorter than M_2 but damaged distally, and the P_4 is somewhat oblique to the molar row, as in *Victoriapithecus macinnesi* and also some modern colobines. The corpus is somewhat deep compared to crown height, suggesting possible colobine affinities to Simons (1969). Recently, a new specimen from Jebel Zelten, Libya, has been identified as a possible *Prohylobates*, differing from *P. tandyi* in larger size and elongate M_3 (Delson, 1977).

Oligocene Monkeys

Superfamily ?Cercopithecoidea or Parapithecoidea

Family Parapithecidae Schlosser 1911

Catarrhine primates from the Oligocene and Early Miocene have been found only in Africa. Many sites for fossil mammals in Europe and Asia date to this period (from about 16 to about 37 m.y. ago) but none have yielded any cercopithecoid monkey fossils. This suggests that before the later Miocene about 12 m.y. ago no monkeys had reached Eurasia (von Koenigswald 1969; Simons 1970, 1972; Delson 1975b).

Monkeys are not well known either from most

Miocene localities in Africa, while in these numerous sites fossil apes are quite common. Only at Maboko Island in Lake Victoria do apes and monkeys occur together abundantly. Today in most parts of forested Africa monkeys are quite common while apes are absent or rare. The lack of monkeys in the earlier Miocene of Africa may have been caused by the fact that, like bovids, their adaptive radiation had not yet come. Evidently monkeys were not adapted to the habitats represented in the earlier Miocene of Kenya and Uganda.

Going farther back to the Oligocene sites of the Old World the whole of our knowledge of Anthropoidea comes from the Fayum of Egypt. No primates are known definitely from the Oligocene of Europe and the sole variety reported from this epoch in Asia, "Kansupithecus" is now dated much younger by associated fauna. In the later Eocene deposits of Burma, however, fossils of two genera, *Pondaungia* and *Amhipithecus*, show various resemblances to Egyptian Fayum primates but are so incompletely known that the exact degree of this relationship is uncertain. Insofar as the affinity is real, their similarities do suggest some sort of Eocene faunal interconnections between Africa and Asia.

The origin of the Cercopithecidae has been considered in several recent papers (e.g., Simons 1969, 1972, 1974; Delson 1975c). Although we differ on their interpretation, the Fayum parapithecids clearly are relevant to solution of this problem. Before indicating the possible alternative viewpoints, it is useful to review parapithecoid morphology and adaptations.

The Parapithecidae as currently understood includes two genera, *Parapithecus* and *Apidium*, each with two known species, one from the middle and one from the upper Fayum fossiliferous horizons. As a result of the six Yale expeditions to Egypt directed by Simons from 1961 to 1967, a large series of new specimens has been found. These make it clear that parapithecids are animals of primitive anthropoid grade, thus monkeys in adaptive terms, whether or not they are so in a phyletic sense. Among the shared features that define the family are dental formula of 2.1.3.3, as in most cebids; early fusion of mandibular symphysis (and metopic suture); P_2 semicaniniform, smaller and simpler than P_{3-4} ; upper molars with well-developed hypocone and large bulbous conules, not linked by crests to the main cusps; upper premolars probably with central conule; lower molars waisted, with reduced buccal cingulum, hypoconulid on midline; P_{3-4} with small metaconid; mandible shallowing slightly anteriorly. This combination of features demonstrates

both the monkey grade of parapithecids and their taxonomic distinction from cercopithecoid or ceboid monkeys.

One of the more important new facts about species of these two genera is that *Apidium* and *Parapithecus* are shown to be the most common African Oligocene primates. Including isolated teeth, there are about two hundred finds of *Apidium* and about a fifth as many of *Parapithecus*. All the Fayum ape specimens put together do not equal as many specimens as those of *Parapithecus* alone. Parapithecids are, in fact, the commonest Fayum mammals. They differ in a number of their features from the modern African monkeys, but on the other hand they do not have many specializations that would distinguish them from what would be hypothetically expected stages in the ancestry of Old World monkeys. In this regard they are unlike such abundant earlier primates as *Plesiadapis*, where extreme crossing specializations such as incisor, canine, and premolar loss—coupled with hypertrophy of remaining incisors—renders ancestral status to later primates impossible. The parapithecids also have several distinctive, but presumably “primitive,” features that resemble tooth morphology in a broad range of Paleocene and Eocene primates. *Parapithecus* especially bears many resemblances to Miocene-Recent Cercopithecoidea. Unlike all the other Fayum primates, *Parapithecus* has the principal cusps of the upper and lower molars arranged in a quadrate pattern that could be a foreshadowing of the quadrate teeth of Miocene-Recent cercopithecoids, but its one or two specialized or derived characters might eliminate it as an immediate ancestor. Of course, no Oligocene mammal species can be proved to be directly ancestral to a living mammal species. What is of interest regarding *Parapithecus* is whether it is possible to take it as broadly representing a stage in the ancestry of the Old World monkeys. Recovery of forms intermediate in age between *Parapithecus* at about 30 m.y. and *Victoriapithecus* at 15 m.y. might aid in resolving this question. Undue stressing of the parapithecids as direct Old World monkey ancestors is as unwise as similar emphasis on the view that they cannot be so related. Because we have approximated these extremes in the past and because this is a review article, we will summarize a middle view.

Genus *Apidium* Osborn 1908

Apidium was the first Oligocene “monkey” to be discovered. When it was described Osborn was not certain even of its ordinal affinities. The name, meaning “Little Apis” (the Ptolemaic sacred bull) suggests that at least when the name was coined, he

considered it an artiodactyl. The type specimen of *Apidium phiomense* was found by Richard Markgraf in the upper fossil wood zone of the Jebel el Qatrani Formation, but the exact locality was not recorded except as northeast of Quarry A. Extensive prospecting by Yale University expeditions in this zone has demonstrated that fossils in the upper Fayum levels are so rare, except in Quarries I and M—the only known places where *A. phiomense* occurs—that the type specimen probably came from one or the other of these quarry areas, or from their same level “to the N. E. of Quarry A.”

Simons (1962) described a smaller and older *Apidium* species, *A. moustafai*, known from a hypodigm of a few dozen jaws found in Quarry G. This site is located stratigraphically between the two fossil wood zones. During the several Yale expeditions, *A. phiomense* proved to be the most common mammal found at Quarry I. The material now available includes many limb bones, scores of teeth and mandibles, three partial frontals, petrosals, and several maxillae. The lower molars increase in length from M1 to M3, and all show the centroconid (mesoconid) on the cristid obliqua between hypoconid and metaconid. The upper molars are also polycuspidate, with strong conules, often a pericone and a “protoconule” (called cusp *a* by Kay 1977) mesial to the paraconule; all cusps are nearly the same size, although the protocone is generally larger. The eruption pattern has been described by Conroy, Simons, and Schwartz (1975).

A partial cranial reconstruction of *A. phiomense* made possible by the discoveries of Simons' expeditions, is illustrated in figure 7.9.

Preliminary cranial and postcranial studies suggest that *A. phiomense* had a short, rather marmosetlike face with small canines relative to those of *Parapithecus* and similar to those of *Callithrix* (see figure 7.9). Like *Aegyptopithecus* ear structure was at approximately the ceboid grade of organization (see Gingerich 1973). Postcranials indicate that the hind feet were adapted for springing. The olecranon process is not retroflexed but rather the ulna is bowed forward as in highly arboreal primates. *Apidium phiomense* was apparently about the size of the present-day owl monkey, *Aotus trivirgatus*. Conroy (1976) implied that the general locomotor adaptation may have been similar to *Samiri* or *Cebus*.

The affinities of *Apidium* were much discussed when there was but one specimen. It seemed condylarthlike to some (e.g., Hürzeler 1968), but condylarths have not otherwise been found in Africa. Simons (1960) stressed that in its polycuspidation



Figure 7.9 Photo reconstruction of the lateral view of the face of *Apidium phiomense*, primitive catarrhine from the Oligocene deposits of Egypt. The view is based on the American Museum frontal, Cairo Museum maxilla, and a mandible at Yale (rostrum and posterior mandible restored from other specimens at Yale). (Scale $\times 2.5$.) (Photo by A. H. Coleman.)

and possession of a lower molar centroconid *Apidium* resembles *Oreopithecus* from the late Miocene of Tuscany (but see below). Hürzeler (1968) suggested that *Apidium* is not a primate, giving as reasons the facts that the molar tooth structure resembles that of nonprimates and that the mandibular ramus is low or shallow, a nonprimate characteristic. Nevertheless, he has admitted a striking resemblance between *Apidium* and *Oreopithecus*. Inspection of the type of *Apidium phiomense* shows that it is a juvenile; it has M_3 unerupted and the characteristic juvenile striated bone—indicating that the animal's immaturity was the reason for the shallowness of the horizontal ramus of this mandible. It would have deepened with increasing age, as demonstrated now by numerous adult specimens of both species.

Scores of jaws of *Apidium* and *Parapithecus* have been found in the Fayum by recent Yale expeditions. These new materials resolve without doubt the affinities of *Apidium*. In January 1967, at Fayum Quarry I, a possibly associated group of skull fragments of *A. phiomense* was found by Simons, together with palatal fragments and upper teeth. One of the fragments of this find is a partial frontal bone

preserving the interorbital pillar. The frontals are completely fused, showing no trace of the metopic suture between bilateral frontals commonly present in prosimians and nonprimates. This frontal fragment is exactly like that from the Fayum described by Simons (1959), and consequently the latter more complete frontal, which gives evidence of the presence of postorbital closure can be assigned to *A. phiomense*. The upper teeth of *Apidium* are anteroposteriorly short and have well-delineated separate cusps with distinct paraconule and metaconule. These teeth admit the possibility, just as the lower teeth do, of a topological conversion into those of *Oreopithecus*, particularly because those of *Oreopithecus* (unlike any other later member of the Catarrhini) retain well-defined paraconule and metaconule cusps. Nevertheless, about 20 m.y. separate *Apidium* and *Oreopithecus*. The analogies in the upper and lower tooth structure may thus be parallelisms, primitive retentions, or indications of real phyletic affinity.

Genus *Parapithecus* Schlosser 1910

The genera *Parapithecus* and *Propithecus* (and *Moeripithecus*) were described briefly by Schlosser in 1910 and then analysed in detail by him in 1911. *Parapithecus fraasi* Schlosser has the most complete type specimen of all the African Oligocene primates described in the early part of this century. It consists of a mandible that preserved both bodies and part of the rami at the back. In the type dentition were preserved a pair of central incisors and posterior to these seven teeth on the left, and six on the right (one anterior premolar had fallen out). As long as the type was the sole specimen of *Parapithecus*, it remained problematical because the dental formula was subject to various interpretations, while the morphology of the cheek teeth was somewhat unlike anything else among primates. Apart from a vague and distinct resemblance to the contemporary Fayum ape *Propithecus*, little tallying of affinities was possible, other than that this was definitely a primate dentition. Nevertheless, the specimen was endlessly discussed and associations ranging from ties with the modern prosimian *Tarsius* to an ancestral relationship for present-day man were proposed. At the anterior midline of this mandible, still the only specimen of this species, two small incisors are preserved. Their very small size showed finally that they are the central pair, but this was also accepted from the start. Lateral to these were two much larger teeth which were variously interpreted as large lateral incisors or as canines (see figure 7.10). Few if any students who wrote about it had access to the original speci-

men, depending instead on crown-view photographs that did not show the extreme size disparity between the two seemingly most anterior pairs of lower teeth. Had this discrepancy been understood at the start, the problem of what were the canines of this animal would have been solved before new finds were made. In writing the original description of this mandible, Schlosser wavered somewhat as to whether the lower dental formula was 1.1.3.3 as in the living tarsier or 2.1.2.3 as in the present-day catarrhines. This set the stage for the two principal interpretations of *Parapithecus*: (1) that it was a tarsioïd prosimian, or (2) that it was a higher primate. Gregory (1920) even went so far as to suggest it for hominid ancestry.

In fact, neither of these interpretations can be supported because neither of the dental formulas was correct. The new finds of *Parapithecus* and *Apidium* show them to be closely related forms, although generically distinct. Moreover, all the jaws that preserve part of the symphyseal region show sockets for two pairs of lower incisors. In Schlosser's type specimen the delicate alveolar border in the symphyseal region must have been broken away at or before the time of collection, and the two horizontal rami as well as the two central incisors were glued together in such a way as to suggest that the specimen did not have lateral incisors. This in turn led to the errors in interpreting the dental formula that continued to be perpetrated up to and including Kálin's monograph (1961) on the Fayum primates. Also, it was believed that the symphysis was unfused—because the damaged area had destroyed evidence of the incisor alveoli, the two central incisors were simply glued to the front of the mandible. Because the mandibular bodies were glued together with a central fragment missing, they diverged



Figure 7.10 Anterior face of the symphysis of the type mandible of *Parapithecus fraasi*, primitive catarrhine from the Oligocene Fayum of Egypt. There are no contacts between the two sides of the lower jaw or with the anterior teeth. (Scale $\times 2.5$.) (Photo by E. Delson.)

markedly to the rear. This pronounced V-shaped arrangement of the tooth rows was taken to be a tarsioïd resemblance. Actually, the new jaws, with their fused symphyses, are slightly more U-shaped.

Most of the new *Parapithecus* finds are 15 to 20% larger than the type specimen of *Parapithecus fraasi*, which was evidently found at a lower level than Quarry I, where the new species occurs. This new parapithecoid has been named *P. grangeri* (Simons 1974). In addition to size, it appears to differ from *P. fraasi* in having slightly smaller M_3 , larger metaconids on P_{3-4} , cusps slightly less bulbous on lower molars, and mandibular corpus relatively deeper distally.

Parapithecus shares with *Apidium* the basic dental features listed above as characterizing the family. It differs from *Apidium* in the short M_3 , relatively larger canine and premolars (compared to molars), presence of paraconid variable, and lack of the centroconid. A few isolated upper teeth appear to be referable to *P. grangeri*, as they occlude with the lowers and differ from those of *Apidium* in such features as lack of pericone and "protoconule," smaller paraconule and stronger buccal cingulum on the molars, and smaller conule and relatively taller paracone on the premolars. The presence of strong, relatively bulbous, isolated conules on these upper cheek teeth does suggest enough similarity with *Apidium* for them to be referred to *Parapithecus* pending final revision of the family. In dental and mandibular size, *P. grangeri* is comparable to the smallest living cercopithecoid, *Cercopithecus (Miopithecus) talapoin*, with which it shares some dental similarities (relative M_3 size, essentially four-cusped lower molars). The known postcranial elements from Yale Fayum Quarry I are homogeneous (except for a few large bones referred to *Aegyptopithecus*), and all have been referred to *Apidium*, as the frequency of isolated teeth and jaws shows that this is the most common small mammal at Quarry I (Conroy 1976). In consequence, no limb elements of *Parapithecus grangeri* have yet been definitely separated out from those presumed to be of *Apidium*.

Relationships of the Parapithecids

Most previous authors have each interpreted differently the phyletic position of *Parapithecus* and *Apidium* and thus we have refrained from commenting on this matter above. In addition to the shared monkey grade features of the two genera, the several detailed morphological resemblances outlined previously convince us that they are each other's closest relatives (or sister taxa), requiring that they be classified in a single higher taxon, to which family rank

is usually assigned (see Kälin, 1961, Simons 1974). This view contrasts with that of Kay (1977) who has tentatively suggested that *Apidium* may be more closely related to the *Aegyptopithecus* group of Fayum primates.

Two major phyletic linkages have been suggested for the parapithecids: *Apidium* with *Oreopithecus* and *Parapithecus* with Cercopithecidae. As noted briefly above, *Apidium* does share with *Oreopithecus* the presence of a centroconid on the lower molars, which moreover are waisted somewhat in both genera; in addition, conules are present on upper molars in both (Gregory 1922; Simons 1960, 1972; Delson and Andrews 1975). On the other hand, the placement and relative size of conules are different in both, and the presence of premolar conules in *Apidium*, which tends to link it strongly with *Parapithecus*, further separates it from the enigmatic Tuscan primate. At present Delson considers it unlikely that there was a common ancestor shared by *Apidium* and *Oreopithecus* more recently than the ancestor of all catarrhines, while Simons is prepared to stand by his 1960 assessment that a structural similarity exists but that in view of the great time separation and the lack of any intervening relevant fossils, that a relationship is hinted at but by no means confirmed. Simons was mainly concerned with refuting doubts, when there was only one very incomplete specimen, that *Apidium* was a primate, by showing structural analogies with undoubted primates such as *Oreopithecus* (Piveteau 1957, Hürzeler 1958).

Turning to the question of cercopithecoid origins introduced at the beginning of this section, both authors have presented their views recently (Simons 1974, Delson 1975c). Simons has suggested that the observed similarities between *Parapithecus grangeri* and *C. talapoin* are too strong to be merely convergence, while Delson argued that the latter was indeed the case, especially as the talapoin is a probably derived member of a dentally clearly derived group of monkeys. The presence of three premolars in parapithecids and of a tympanic without ossified external meatus in *Aegyptopithecus* would imply convergent development of both tubular tympanic and C/P₃ honing in living cercopithecids and hominoids. Simons (1974) has accepted these implications, while Delson has argued that there is no evidence for either case of nonhomology of these complexes in modern forms. However, the primate fossil record documents six cases of independent P₂ loss and at least three of separate development of a tubular auditory meatus (although none are as simi-

lar as are those of modern hominoids and cercopithecoids). More recently, Gingerich (1975) reported a structural "sequence" of gradual reduction of anterior premolars and distal shifting of upper canine honing in the adapid genera *Adapis* (with P₁ of moderate size, smaller than P₂, and honing upper C) *Lepidadapis* (P₁ quite small, the upper C honing on lower C, P₁, and the front of P₂) and *Cercamoni* (known only from P₄ to M₂, but with P₂ single-rooted and P₃ probably enlarged and obliquely implanted, suggesting upper C honing). This might offer an analog to the way some parapithecoid might have reduced P₂, even if that tooth were involved in canine honing already, as tentatively suggested by Delson (1975c). A possible counter to this argument might rest on the fact that although smaller and simpler than P₃₋₄, P₂ in parapithecids has not yet been reduced in height to the extent of indicating its probable subsequent loss. Moreover, the presence of large conules on the upper molars and especially premolars allocated to *Parapithecus* could represent an autapomorphic condition or "crossing specialization" not now seen in cercopithecoids were it not for the fact that we do not know the starting point for these tooth structures in basal Old World monkey ancestors. That is, like many Paleocene and Eocene forms that show accessory conules, these structures in *Parapithecus* and *Apidium* could have been derived from their ancestors and later lost in their descendants. Just because modern cercopithecoids have such extremely simplified tooth crowns, one cannot safely rule out that their ancestors had more complex tooth-crown anatomy.

The interpretation of the possibility of relationship between parapithecids and cercopithecids thus rests on variant interpretations of characters and character complexes. Clearly, no known parapithecoid can be proven to be directly ancestral to Neogene Old World monkeys, and we know so little of African Oligocene mammals generally that it seems improbable that exact ancestors for later forms have been found. It is still possible, but not proven that parapithecids more or less broadly represent a stage in the ancestry of such monkeys, or of catarrhines in general. For resolution of the question of cercopithecoid origins we are concerned not only with the nature of the early parapithecids but also require knowledge of temporally intermediate (or Oligocene alternate) possible ancestors. If cercopithecids shared a common ancestor with the parapithecids more recently than they did with the forerunners of living apes, either before some of the distinctive parapithecoid morphology appeared or after it was

lost, then a number of characters developed in parallel. On the other hand, if parapithecids are a side branch of catarrhine evolution, with no living close relatives, the similarities between the teeth of *Parapithecus* and *Cercopithecus* may best be viewed as adaptations to similar ecologies. As yet, this dilemma can not be fully resolved.¹

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