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Catarrhini

Old World infraorder of Anthroidea, including the families Propliopithecidae, Pliopithecidae, Cercopithecidae, Proconsulidae, Hylobatidae, and Hominidae, as well as Miocene forms included here in the "*Dendropithecus*-group." Of these seven sets of Afro-Eurasian higher primates, four are extinct (three African and one Eurasian), while one is extant in Asia and two are extant in both Africa and Asia, with extinct European representatives (other than the worldwide *Homo* and the relict or introduced Gibraltar macaque). The last three named families appear to form a monophyletic superfamily Hominoidea as they are understood here.

Catarrhine Characteristics

Defining the catarrhines by means of uniquely shared characters depends upon which taxa are considered when such a list is developed. If only the living forms are examined, the list of such characters is long and includes numerous features not determinable for any fossils, as well as others known only for a few extinct forms. Such a list, of course, can yield information only about the last common ancestor of the living forms, and still earlier catarrhines, or even earlier ancestors, might present a different mosaic of character states. Nonetheless, an abbreviated version of such a list does provide a starting point for a survey of catarrhine morphology and evolution.

Research in the 1980s and 1990s suggests that the ancestor of living catarrhines (Cercopithecoidea and Hominoidea, here termed the Eucatarrhini) would have been characterized by the following dental features, which are derived by comparison with those of an ancestral anthropoid and are not known to have evolved in parallel among platyrrhines: dental formula of 2-1-2-3; singlecusped, bilaterally compressed P_3 , involved in honing C^1 ; and five-cusped lower molars with no paraconid, midline distal hypoconulid (not very large on M_3), talonid and trigonid of roughly equal height, and M_2 rather larger than M_1 but only slightly smaller than M_3 . The presence of a wear facet (termed facet x) caused by Phase 2 contact between the distolingual surface of the protoconid and the mesiobuccal aspect of the protocone has also been used as a diagnostic catarrhine feature, but it now appears that this may have been developed in parallel in several anthropoid lineages. Cranially, such characters might include a moderately prominent glabella, separate from the supraorbital tori; a tubular external auditory meatus; a moderately developed mandibular inferior transverse torus; a long mandibular ramus with nearly vertical anterior margin; a U-shaped mandibular arcade; and very reduced olfactory lobes of the brain. Postcranially, characters of this type might include humerus with low deltopectoral and supinator crests, a narrow brachialis flange, and a deep olecranon fossa, but with no entepicondylar foramen or dorsal epitrochlear fossa; ulna with weak pronator crest and round head; ischium with expanded tuberosity (and callosities); and a synovial distal joint between the tibia and the fibula.

Relationships of Major Catarrhine Subgroups

If we now examine a variety of fossils, it is possible to see which of these characters they share and, thus, how strongly

they are linked to the modern catarrhines. A number of Eocene and Oligocene Old World taxa have been previously included in the catarrhines, but, as discussed in ANTHROPOIDEA, few such referrals are accepted here. In brief, *Djebelmur*, *Pondaungia*, and *Amphipithecus* are best interpreted as adapiforms; *Eosimias* is a tarsioid; the oligopithecids are probably archaic anthropoids; and the parapithecids are likely advanced early anthropoids but probably not catarrhines. Only the last two of these taxa merit further discussion here.

The parapithecids include five genera from the Fayum Eo-Oligocene and probably three others from slightly earlier North African sites. E.L. Simons has long argued that they are the sister taxon to Cercopithecidae; E. Delson has considered them to be the sister of all other catarrhines and has formally termed them Paracatarrhini; R. Hoffstetter has proposed that they may be the African sister taxon of the platyrrhines; and in the late 1980s T. Harrison and then J.G. Fleagle and R.F. Kay suggested that parapithecids are the sister taxon to Platyrrhini plus Catarrhini, thus archaic anthropoids (the view accepted here). It is now widely agreed that parapithecids share no derived features with either cercopithecids or platyrrhines, the apparent similarities that do exist being best interpreted as parallelisms.

Of the list of catarrhine features noted above, parapithecids share a moderate glabella, molar trigonids and talonids of nearly equal height, and a well-developed midline distal hypoconulid with a generally large distal fovea. They are clearly less derived than any other catarrhine in the following

features (and conservative by comparison with platyrrhines in those marked with *): retention of P2 (which may show honing contact with the canine), molar paraconids (at least in some species), lingually open P₄ trigonid, small P₄ metaconid placed distolingual to protoconid*, a weak mandibular inferior torus, shallow corpus, short ramus with sloping anterior margin, narrow tibial shaft*, and a fibrous distal joint between the tibia and the fibula. They share with the propliopithecids (see below) an annular auditory meatus, large olfactory bulb*, and numerous conservative postcranial features, such as humerus with prominent deltopectoral crest, high supinator crest, elongate capitulum, shallow olecranon fossa, moderate brachialis flange, entepicondylar foramen, and dorsal epitrochlear fossa; and ulna with prominent pronator crest. Two conservative parapithecid features cannot be determined in propliopithecids: ulna with narrow head* and ischium with narrow tuberosity* (and presumably no callosities). Unique derived features shared by at least several parapithecids are apparently restricted to a central conule on the upper premolars and a sulcus separating the metaconid from the protoconid on P₄. Despite a few derived similarities with catarrhines, it now appears most likely that the parapithecid clade split away from a common anthropoid ancestral "stock" before the platyrrhines and the catarrhines diverged. This situation is even more true for the oligopithecids, now well represented by *Catopithecus*. Although Simons and D.T. Rasmussen have included this group as a subfamily of Propliopithecidae, only the two-premolared condition is a shared derived feature, but one that does not appear to be homologous. Dentally, cranially, and postcranially, oligopithecids are marginally acceptable as anthropoids, but the most primitive ones now known.

Eocatarrhini: The Archaic Catarrhines

The Oligocene and many Miocene catarrhines are not specially related to the modern eucatarrhines. Instead, they appear to form a "comb" of successive clades or radiations, each with a larger frequency of eucatarrhine character states. Of these, the Propliopithecidae includes only one genus with several species; the Pliopithecidae is a monophyletic group of six to eight genera; and the "*Dendropithecus*-group" is a paraphyletic group of six Early-to-Middle Miocene East African genera intermediate in morphology between pliopithecids and eucatarrhines.

Propliopithecus of the Fayum and Omani Early Oligocene is known by fragments of up to five species, but the most complete remains are those of *P. zeuxis*, sometimes placed in the genus *Aegyptopithecus*. This species, and presumably its congeners, is derived by comparison with the parapithecids in such features as having lost P2 and possessing a bilaterally compressed P₃ that hones C₁; P₄ with lingually closed trigonid and metaconid subequal in size to directly buccal protoconid; lower molars lacking paraconids but with facet x; inferior transverse torus of mandible moderately developed; long ramus with vertical anterior border; corpus deep under M₁; no contact between zygomatic and parietal bones in temporal fossa and clearly closed rear of orbit; and a moderately broad tibial shaft with synovial joint between tibia and fibula distally. A number of conservative conditions are shared with pliopithecids and listed below. It

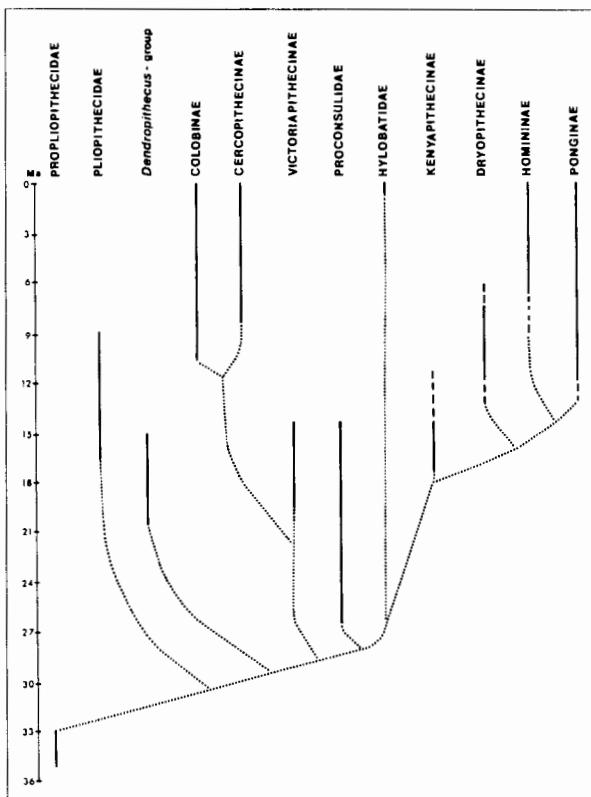
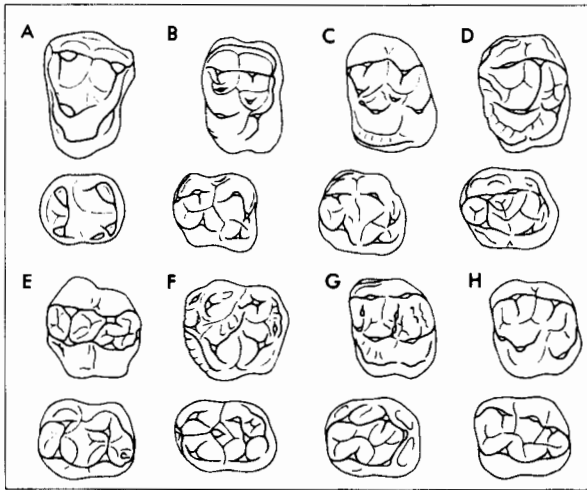


Diagram of evolutionary relationships and temporal ranges of the higher taxa of catarrhine primates. Solid vertical lines indicate known ranges, heavy dashed lines indicate probable range extensions, and dots represent phyletic relationships.



Idealized drawings of left M^2 above right M_2 of representative catarrhines and early anthropoids. (A) Catopithecus; (B) Parapithecus; (C) Propliopithecus; (D) Pliopithecus; (E) Victoriapithecus; (F) Oreopithecus; (G) Proconsul; (H) Sivapithecus.

is as yet unknown whether propliopithecids are derived compared with parapithecids in the shape of the ulnar head, development of the ischial tuberosity, size of the femoral lesser trochanter, or depth of the femoral distal condyles. If not, the derived state(s) would have been evolved independently in platyrrhines and later catarrhines; in turn, this would strengthen a parapithecid link to catarrhines. The Propliopithecidae now represent the most ancient known catarrhines and provide a tentative model for the eucatarrhine common ancestor.

Pliopithecus, known from several European Middle Miocene partial skeletons, is, in turn, further derived than *Propliopithecus* in having a P_4 somewhat longer than broad, a prominent glabellar region, and a hallux with a modified saddle joint, as well as having lost the dorsal epitrochlear fossa on the distal humerus. Both genera retain such ancestral anthropoid conditions as a ringlike external auditory meatus (partly tubular in *Pliopithecus*, as in juvenile eucatarrhines); distinct prehallux bone in the foot; humerus with entepicondylar foramen, moderately broad brachialis flange, high supinator crest, shallow olecranon fossa, and elongate capitulum; ulna with prominent pronator crest and narrow head; and narrow ischial tuberosity (the latter two are unknown in propliopithecids). The other genera of pliopithecids are less well known but agree with *Pliopithecus* in most of these conditions where determination is possible. Among the most fascinating aspects of the pliopithecids is their presence in the fossil record contemporaneous with, or younger than, a number of far more derived taxa; they must have diverged from propliopithecidlike ancestors by mid-Oligocene time and then remained relatively rare in some as yet unsampled region or habitat of Africa. When that island continent finally contacted Eurasia by ca. 19 Ma, pliopithecids were among the first mammals to leave, entering eastern Asia, whence they seem to have reached Europe perhaps twice.

The generally older Early-Middle Miocene small catarrhines from Africa are more derived than pliopithecids when character states can be observed. The best known of

these forms is *Dendropithecus*, whose humerus has low deltopectoral and supinator crests and a narrow bicipital groove and lacks an entepicondylar foramen, although the olecranon fossa is conservatively deep. *Simiolus* also presents postcranial elements that may place it closer to the last common ancestor of Hominoidea and Cercopithecoidea. *Micropithecus*, *Kalepithecus*, *Nyanzapithecus* (a possible *Oreopithecus* relative), *Limnopithecus*, and *Turkanapithecus* (the last two possibly proconsulids) are generally less fully preserved, but the last form may be the most derived of all. Most of these genera (especially the pliopithecids) have at various times been allied with the Hylobatidae, but that was mainly on the basis of small size and relatively gracile limb bones, rather than any sharing of the distinctive derived postcranial features of gibbons. Based on subjective considerations, it appears reasonable to suggest that *Dendropithecus* and any species monophyletically linked to it merit placement in a family distinct from any so far named, but that step is not taken here. Instead, the “*Dendropithecus*-group” is used as an informal cluster of taxa between the pliopithecids and the common eucatarrhine ancestor.

Eucatarrhini: The “Modern” Catarrhines

HOMINOIDEA

Recent finds have pushed the first occurrence of hominoid eucatarrhines back into the final Oligocene, where they are older than any other catarrhine but *Propliopithecus*. The hominoids comprise mainly the hylobatids and the hominids, the latter including *Pongo* and its extinct allies, African apes plus humans, and a group of mostly fragmentary Miocene taxa that share with later hominids such derived features as thick molar enamel, elongated premolars, robust P_3 and canines, spatulate I^2 , subparallel tooth rows, deep mandibular symphysis with superior torus less pronounced than inferior, enlarged maxillary sinus, and/or prominent keels on humeral trochlea. The Early Miocene *Proconsul* appears to fall between this latter group and *Dendropithecus*, in that it presents such ancestral hominoid features as P_3 with low crown, upper premolars with reduced cusp heteromorphy, development of the maxillary jugum, frontal bone wider at bregma than anteriorly, strong humeral trochlear keels but without sulci bordering the lateral keel, humeral head medially oriented, rounded and larger than the femoral head, and scapula with elongated vertebral border and robust acromion (the last several not known for *Dendropithecus*). On this basis, the family Proconsulidae is included in the Hominoidea. In addition to several species of mainly Early Miocene *Proconsul* and the poorly known *Rangwapithecus*, the Oligocene *Kamoyapithecus* is also placed in the Proconsulidae.

By the end of the Early Miocene (ca. 17 Ma), the first hominoids appear with features that link them to the living hominids. *Afropithecus* has thick molar enamel and relatively large upper premolars compared to its molars. The slightly younger *Kenyapithecus* also had somewhat more modern postcranial elements. About the same time (ca. 15 Ma), the broadly similar *Griphopithecus* is found in Turkey and Central Europe. *Morotopithecus* (ca. 20 Myr old) may also differ from *Afropithecus* in its more advanced postcranium. These kenyapithecines represent

an early radiation of archaic hominids not clearly linked to any living forms. Although there is no fossil record, it is likely that this time interval saw the divergence of the hylobatids from ancestral hominoids, perhaps in Eurasia.

The Middle-to-Late Miocene dryopithecines are on the border of relationship to the living great apes but still cannot be definitively included in either modern subfamily. *Dryopithecus* is known from Europe between ca. 13 and 8 Ma and is represented by crania in Hungary and Spain, the latter associated with a partial skeleton. Molar enamel is thin, but the subnasal region and the limb bones appear somewhat more like modern apes than those of the kenyapithecines. Some authors have suggested that *Dryopithecus* be included in Homininae and others in Ponginae, but both views appear overstated. Instead, the genus represents a reasonable approach to the last common ancestor of those later clades (although its thin enamel seems to be a reversal that sets it off from direct ancestry). *Oreopithecus* of the Italian Late Miocene is broadly similar to *Dryopithecus* postcranially, but its highly distinctive dentition leads to its continued placement in a separate subfamily. Its previously suggested affiliation with Cercopithecidae has been rejected.

Sivapithecus from the Siwaliks of Pakistan and India appears to be the first hominoid with derived similarities to a modern genus. In its narrow interorbital pillar, ovoid orbits, expanded and flattened zygomatic region, well-developed airorhynch, lack of glabellar thickening or browridges, a rotated premaxilla giving a smooth floor to the nasal cavity, an extremely reduced incisive canal with no incisive fossa, and small upper lateral incisors very small relative to the central and relatively thick molar enamel, *Sivapithecus* presents a complex of character states otherwise found only in *Pongo*, the orangutan. Most of its postcranium is also rather modern, although the proximal humerus is more conservative than in any living hominoid (including hylobatids); this latter feature may reflect habitus more than heritage, however. *Sivapithecus* specimens with these diagnostic features appear as early as 12 Ma, providing a solid minimum age for the hominine-pongine divergence. *Ankarapithecus* (ca. 10 Ma in Turkey) may be a less-derived representative of Ponginae, with somewhat intermediate upper facial morphology and a conservative palate; it is too late to be an actual ancestor for *Sivapithecus* but (like *Pliopithecus*) presumably lasted well after its descendants became widespread.

The Homininae is perhaps the least well known hominoid clade in the Miocene. Cranially, hominines are relatively conservative, with a stepped premaxillary-maxillary contact in the subnasal area (a condition likely ancestral to the pongine state), wide interorbital pillar, and moderately sized I². The only diagnostic facial complex seems to be increased klinorhynch, including well-developed browridges and glabella. Thus, recognition of early hominines requires relatively complete fossil material. As of the late 1990s, the only reasonable candidate for such a role was *Graecopithecus*, known from Greece between ca. 10 and 8 Ma. It also has extremely thick molar enamel and reduced canine height, as well as a rather gorillalike face. *Samburupithecus* from Kenya may be a contemporaneous African equivalent. The next several million years are nearly void of potential hominine fos-

sils, although this is the very time that the molecular clock predicts divergence of the gorilla and then the chimpanzee clades from the early human lineage. During the Pliocene, the latter diversified into *Australopithecus*, *Ardipithecus*, *Paranthropus*, and eventually *Homo*. In turn, during the Pleistocene, *Homo* spread out of Africa and across the Old World, probably in several successive migrations, coming to dominate the natural environment through technology.

CERCOPITHECOIDEA

Views of Old World monkey evolutionary history generally agree that the postcranium and perhaps skull, as well as the teeth, of cercopithecoids are derived by comparison to the eucatarrhine morphotype. Previously, it was thought that monkeys were primitive, but detailed study demonstrated that in addition to the derived bilophodont dentition, the terrestrially adapted postcranium is about as different from the common ancestor as is that of the hominoids. B.R. Benefit and M.L. McCrossin have further argued that facial remains of early cercopithecoids share a relatively narrow interorbital pillar, frontal trigone (depression bounded by raised temporal lines), and elongated muzzle with faces of *Propliopithecus* and *Afropithecus*. They have suggested that this implies that such a pattern was ancestral for catarrhines, in opposition to the previous view that a relatively short face, widely spaced orbits, and rounded vault (as in colobines and gibbons and, to a lesser degree, humans, *Oreopithecus*, and *Pliopithecus*) were ancestral. This question has not been resolved.

The later Early and Middle Miocene African *Victoriapithecus* and *Prohylobates* document the earliest definite cercopithecoids, albeit less completely bilophodont than later monkeys. These forms present a variable expression of the hypoconulid on lower dP₄-M₂ (lost entirely in later cercopithecoids) and an incomplete formation of the distal transverse loph combined with variable expression of a crista obliqua on upper molars. These and other features have led Benefit to place the two genera in the family Victoriapithecidae, but here this taxon is ranked as a subfamily.

The first occurrence of colobines is nearly contemporaneous in East Africa and Europe, ca. 10 Ma, but cercopithecines do not appear until several Myr later (North Africa). The European colobines form a terrestrial clade that may also extend into northern Asia in the Pliocene, while the numerous modern genera of southern Asian colobines are poorly represented in the fossil record. A variety of macaques and more terrestrial relatives occur across Eurasia. In Africa, there is a radiation of large colobines in the Pliocene, alongside a long-lived lineage of *Theropithecus* which shows continuing size increase into the Middle Pleistocene.

See also Africa; *Afropithecus*; Anthropoidea; Asia, Eastern and Southern; *Australopithecus*; Cercopithecidae; Cercopithecinae; Colobinae; "Dendropithecus-Group"; Diet; Dryopithecinae; Europe; Fayum; Griphopithecus; Hominidae; Homininae; Hominoidea; *Homo*; Kenyapithecinae; *Kenyapithecus*; Locomotion; Miocene; Molecular Clock; *Morotopithecus*; Oligocene; Oligopithecidae; *Oreopithecus*; *Paranthropus*; Parapithecidae; Pleistocene; Pliocene;

Pliopithecidae; Ponginae; Proconsulidae; Propliopithecidae; Samburupithecus; Sivapithecus; Skeleton; Skull; Teeth; Victoriapithecinae. [E.D.]

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