

CHAPTER 20

Catarrhine Origins

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INTRODUCTION

Paleontological evidence demonstrates that early catarrhines (i.e., the clade comprising Old World monkeys, apes and humans) first occur in Afro-Arabia during the Early Oligocene (dating to about 29–32 Ma) and were restricted to this zoogeographic region until the Early Miocene (about 17–18 Ma) when they made their first appearance in Eurasia (Andrews et al. 1996; Harrison and Gu 1999; Harrison 2005). The estimated divergence date for catarrhines and platyrrhines, based on molecular evidence, indicates that catarrhines may have had an even earlier phylogenetic history that extends back to about 40–44 Ma into the Middle Eocene (Chatterjee et al. 2009). During this long period of isolation in Afro-Arabia several major clades of catarrhines originated, including the Propiopoithecoidea, Pliopithecoidea, Saadaniioidea, Dendropithecoidea, Cercopithecoidea and Hominoidea (see Table 20.1). The Cercopithecoidea (Old World monkeys) and the Hominoidea (apes and humans) comprise all of the extant catarrhines, and are referred to as crown catarrhines (Figure 20.1). The ancestral morphotype of crown catarrhines includes the following key hard-tissue features that can be potentially informative for interpreting the fossil record: lateral orbital fissure absent; postglenoid foramen highly reduced; tubular ectotympanic; dental formula 2.1.2.3, with reduction of number of premolars to two in each half of the upper and lower jaws; upper premolars with paracone much more elevated than the protocone; upper molars with an indistinct metaconule on the crista obliqua and a large hypocone; p3 modified into a single-cusped sectorial tooth, with a long and narrow crown and a moderately long honing face for occlusion with the upper canine; lower molars with a large hypoconulid, no paraconid and increase in size from m1 to m3; absence of an entepicondylar foramen and dorsal epitrochlear fossa on the distal humerus; and a saddle-like carpometacarpal joint of the thumb (Harrison 1987). Molecular evidence indicates that the cercopithecoid–hominoid divergence occurred in the Late Oligocene at about 27–30 Ma (Chatterjee et al. 2009). The earliest fossil evidence for an undoubted crown catarrhine is a single

Table 20.1 Family-group classification of the Catarrhini (after Harrison and Gu 1999; Harrison 2002, 2005, 2010; Andrews and Harrison 2005).

Order: Primates
Suborder: Anthropoidea
Infraorder: Catarrhini
Superfamily: Proploipithecoidea
Family: Proploipithecidae
Superfamily: Pliopithecoidea
Family: Pliopithecidae
Subfamily: Pliopithecinae
Subfamily: Crouzeliinae
Family: Dionysopithecidae
Superfamily: Saadanioidae
Family: Saadaniidae
Superfamily: Dendropithecoidea
Family: Dendropithecidae
Superfamily: Proconsuloidea or Hominoidea
Family: Proconsulidae
Subfamily: Proconsulinae
Subfamily: Afropithecinae
Subfamily: Nyanzapithecinae
Superfamily: Cercopithecoidea
Family: Cercopithecidae
Subfamily: Cercopithecinae
Subfamily: Colobinae
Superfamily: Hominoidea
Family: Hylobatidae
Family: Hominidae
Subfamily: Kenyapithecinae
Subfamily: Ponginae
Subfamily: Homininae

upper molar of a cercopithecoid from the Early Miocene of Napak in eastern Uganda dated to about 19 Ma. If the hominoid status and age of *Morotopithecus bishopi* from Moroto in Uganda are accepted, then this would push back the age of the oldest crown catarrhines to about 20.6 Ma (Gebo et al. 1997; MacLatchy et al. 2000; Young and MacLatchy 2004). Pickford et al. (2003) have also described several associated teeth of *Victoriapithecus macinnesi*, a stem cercopithecoid, from the same site. However, serious doubts have been raised about age of Moroto (faunal correlations suggest a late Early Miocene age of 17.0–17.5 Ma) and the taxonomic affinities of *Morotopithecus* have been questioned (Pickford 2002; Patel and Grossman 2006; Harrison 2002, 2010).

The Proploipithecoidea, Pliopithecoidea, Saadanioidae and Dendropithecoidea are extinct lineages of catarrhines that diverged prior to the last common ancestor of hominoids and cercopithecoids, and these are referred to as stem catarrhines (Figure 20.1). They range in age from 32 Ma to 7 Ma (late Oligocene to late Miocene) and all, except the Eurasian Pliopithecoidea, are restricted to Afro-Arabia. These taxa lack one or more of the specialized features detailed above that characterize the ancestral morphotype of crown catarrhines. Some authors also recognize the Proconsuloidea from the Early and Middle Miocene of Africa as stem catarrhines of modern aspect (Harrison

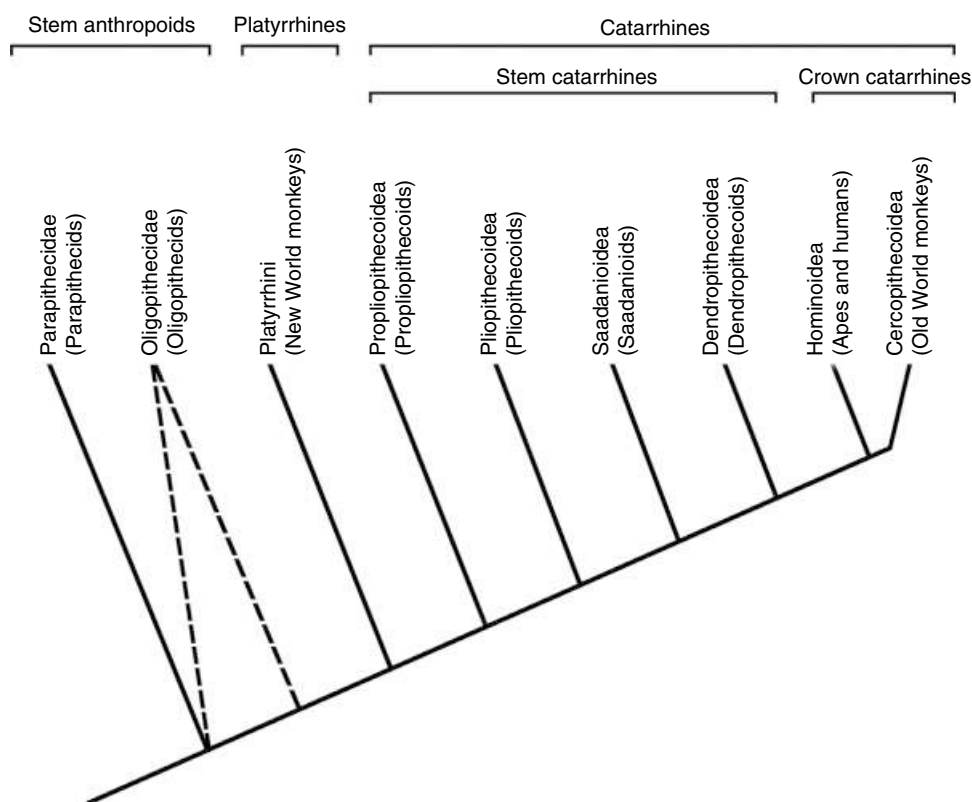


Figure 20.1 Cladogram showing the inferred phylogenetic relationships between the major groups of catarrhines.

1987, 1993, 2002, 2010), while others prefer to identify them as primitive hominoids (Andrews 1985, 1992; Begun et al. 1997; Kelley 1997; Walker 1997; Rae 1999). Regardless of their precise phylogenetic affinities, it is evident from their cranio-dental and postcranial anatomy that proconsuloids occupy an evolutionary grade close to the initial radiation of all extant catarrhines (see Harrison 1993, 2002, 2005, 2010).

Some Eocene and Early Oligocene anthropoids from Afro-Arabia have in the past been inferred to be early catarrhines (Rasmussen 2002). These include the parapithecoids, oligopithecids and several genera of anthropoids of uncertain taxonomic affinity, such as *Serapia* and *Proteopithecus*. However, the current evidence indicates that these taxa are stem anthropoids that diverged prior to the last common ancestor of platyrrhines+catarrhines (Fleagle and Kay 1987; Harrison 1987; Kay et al. 1997, 2004; Ross et al. 1998; Beard 2002; Seiffert et al. 2005, 2010; Figure 20.1).

The parapithecoids represent a diverse group (i.e., *Apidium*, *Abuqatrania*, *Arsinoea*, *Biretia*, *Parapithecus*, *Qatrania*, and *Simonsius*) of small anthropoids from the Late Eocene and Early Oligocene of Egypt and Algeria (Seiffert et al. 2010). Parapithecoids are well represented in the collections from the Fayum in Egypt, dating from about 29–37 Ma. They combine a suite of primitive anthropoid features of the cranium, dentition and postcranium with specialized molars (at least in later taxa) that share derived features with crown catarrhines. The latter features include

banodonty, weakly developed crests and poorly developed cingula, the presence of wear facet X on m2 (in some species), a large hypocone on upper molars, and a well-developed midline hypoconulid on lower molars (in some species). However, parapithecoids lack several key synapomorphies of extant anthropoids (i.e., they primitively retain a p4 with a relatively small and distally positioned metaconid separated from the protoconid by a longitudinal fissure; well-developed paraconids on the lower molars (in some species); possible retention of an unfused mandibular symphysis in *Biretia* and *Arsinoea*; shallow mandibular corpus with relatively short ramus; less advanced frontation and convergence of the orbits; deep femoral condyles, and a narrow tibial shaft with extensive distal tibio-fibular appression) that indicate that they are the sister group of platyrrhines+catarrhines (Fleagle and Kay 1987; Harrison 1987; Simons 1992, 2001; Kay et al. 1997; Ross et al. 1998; Simons et al. 2001; Seiffert et al. 2010). The most parsimonious explanation is that the parapithecoids represent primitive anthropoids that diverged prior to the last common ancestor of catarrhines and platyrrhines, but developed dental feature in parallel to catarrhines as a result of similar dietary adaptations. Some authors have suggested that the proteopithecids (comprising *Proteopithecus* and *Serapia*) might represent the sister taxon to parapithecoids (Kay et al. 2004; Seiffert et al. 2005), but the morphology of the p4, with a large metaconid transversely aligned opposite the protoconid, more closely allies the former with oligopithecids and crown anthropoids (Seiffert et al. 2010).

The oligopithecids (i.e., *Oligopithecus* and *Catopithecus*) from the Late Eocene and Early Oligocene of Egypt and Oman (about 33–34 Ma) are still considered by some authors (e.g., Rasmussen 2002; Seiffert et al. 2005, 2010) to be stem catarrhines because they possess one important specialization that is the hallmark of catarrhines – loss of the second premolar. However, the p3 of oligopithecids has been remodeled in quite a different fashion from the sectorial tooth of all undoubted catarrhines, having a short and narrow crown, lacking an elongated mesial honing face. In oligopithecids the upper canine occludes with the mesial ridge of p3 rather than with the extended mesiobuccal face of p3 as in extant catarrhines. This presumably implies that P2/p2 loss was not accompanied by the same structural-functional modifications to p3 that is seen in extant catarrhines. It should also be noted that the second premolar has been lost independently in unrelated primate lineages (i.e., indriids, palaeopropithecids, *Afradapis*). In most other respects oligopithecids retain a morphology that is close to the primitive anthropoid morphotype (Simons and Rasmussen 1996), and in the absence of definitive synapomorphies linking oligopithecids with catarrhines (beyond the simple loss of P2/p2) a close relationship is not strongly supported (Figure 20.1). Although similarities in the postcranial morphology of *Catopithecus* and *Propithecus* have been suggested to support the catarrhine affinities of oligopithecids, the phylogenetic significance of these features is equivocal (Seiffert et al. 2000; Seiffert and Simons 2001). On the other hand, the presence of a small paraconid on m1 and m2, an elevated trigonid on the lower molars, an unfused mandibular symphysis, and a shallow mandibular corpus are primitive features that indicate that oligopithecids diverged prior to the last common ancestor of crown anthropoids. Oligopithecids have a p4 with a large metaconid placed transversely opposite the protoconid, as in modern anthropoids, implying that they are possibly more closely related to crown anthropoids than are parapithecoids (Figure 20.1). The balance of evidence favors the conclusion that oligopithecids are stem anthropoids, somewhat

more derived than parapiithecoids, that originated prior to the divergence of platyrrhines and catarrhines (Kay et al. 1997; Ross et al. 1998).

PROPLIOPITHECOIDEA

The earliest definitive members of the Catarrhini, the Propliopithecoidea, are from the Early Oligocene of Afro-Arabia (Seiffert et al. 2010). The propliopithecids are best known from Early Oligocene (about 29–32 Ma) sediments in the Fayum of Egypt (Seiffert et al. 2010). More fragmentary material has been recovered from Taqah in Oman and Malembe in Angola. The family includes five species, which are often included in two or three genera (i.e., *Propliopithecus*, *Moeripithecus* and *Aegyptopithecus*) (Seiffert et al. 2010; Table 20.2). However, the species are certainly closely related and the morphological distinctions between them are probably best accommodated within a single genus, *Propliopithecus* (Szalay and Delson 1979; Andrews 1985; Harrison 1987).

The best-known species is *Propl. zeuxis* from the Early Oligocene (about 30 Ma) of Egypt (Simons et al. 2007; Seiffert et al. 2010; Figure 20.2). The absence of P2/p2, a dental formula of 2.1.2.3, development of a specialized upper canine/p3 honing complex, the detailed morphology of the molars, and a reduced postglenoid foramen are derived anthropoid features that link *Propliopithecus* with later catarrhines (Fleagle and Kay 1987; Harrison 1987; Seiffert et al. 2010). On the other hand, *Propliopithecus* retains several primitive anthropoid features not seen in extant catarrhines (i.e., an annular ectotympanic, an extensive ascending wing of the premaxilla, an atrioturbinal in the nasal cavity, and an entepicondylar foramen and dorsal epitrochlear fossa in the distal humerus). This combination of features establishes the propliopithecoids as stem catarrhines (Fleagle and Kay 1987; Harrison 1987; Seiffert et al. 2010; Figure 20.1).

The average body mass of *Propl. zeuxis*, the largest of the propliopithecids, is estimated to be 6–8 kg, while the smaller species averaged about 4–6 kg (similar in size to living howler monkeys) (Fleagle 1999). The cranial morphology of *Propl. zeuxis* is known from two relatively complete crania and several faces (see Figure 20.2). The face is relatively deep, with a moderately projecting rostrum, short and broad premaxilla with a large ascending wing, relatively narrow pear-shaped nasal aperture, small subcircular orbits, wide interorbital distance, relatively long nasal bones, extensive maxillary sinuses and slight development of supraorbital costae. Orbital convergence and frontation are similar to modern anthropoids. The postorbital septum is fully enclosed, except

Table 20.2 Classification of the Propliopithecoidea from the Oligocene of Afro-Arabia.

Superfamily: Propliopithecoidea
Family: Propliopithecidae
<i>Propliopithecus</i> (incl. <i>Aegyptopithecus</i> , <i>Moeripithecus</i> , <i>Aeolopithecus</i>)
<i>Propl. ankelae</i>
<i>Propl. chirobates</i>
<i>Propl. haeckeli</i>
<i>Propl. markgrafi</i>
<i>Propl. zeuxis</i>

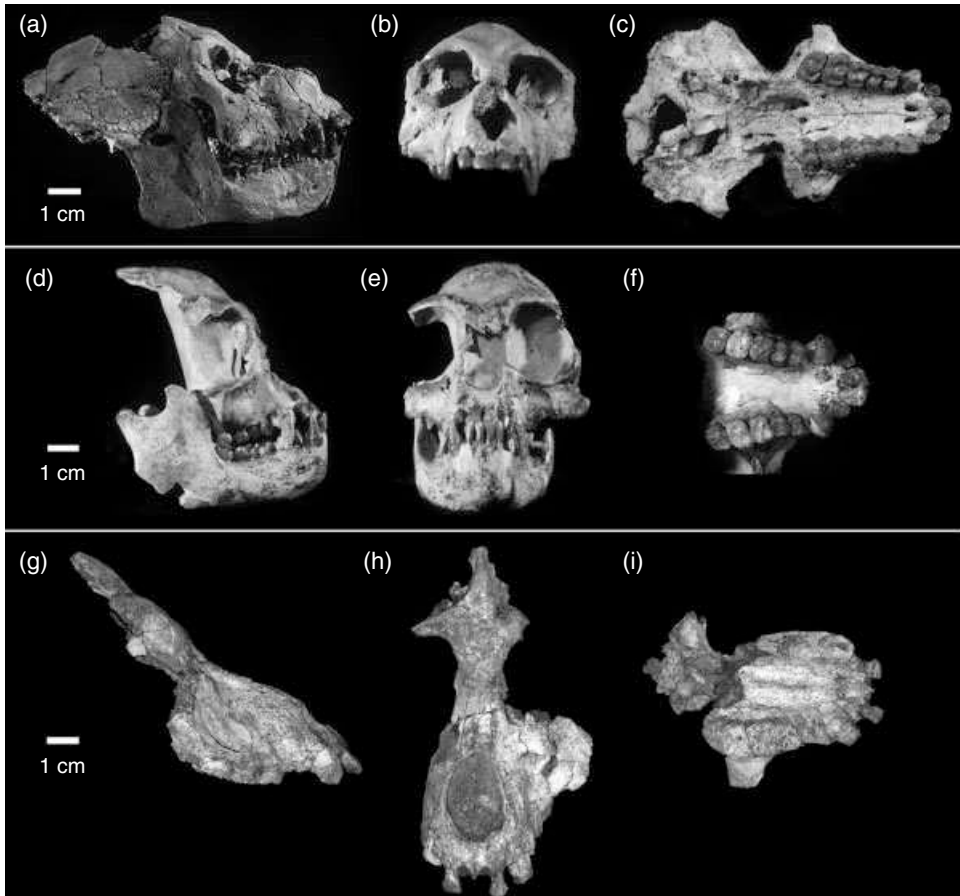


Figure 20.2 Comparison of crania of stem catarrhines. (a–c) Cranium of *Propithecus zeuxis* (CGM 40237) from the Early Oligocene of the Fayum, Egypt. (a) right lateral view (with unassociated mandible); (b) anterior view; (c) ventral view. Courtesy of and © Eric Delson. (d–f) Partial skull of *Pliopithecus vindobonensis* from the Middle Miocene locality of Neudorf-Spalte, Devínská Nová Ves, Slovakia. (d) right lateral view; (e) frontal view; (f) palatal view. Courtesy of and © Eric Delson. (g–h) Partial cranium of *Saadanius hijazensis* (SGS-UM 2009-002) from the mid-Oligocene locality of Harrat Al Ujayfa, Saudi Arabia. (g) left lateral view (image reversed); (h) oblique antero-dorsal view; (i) ventral view. Courtesy of Iyad Zalmout and William J. Sanders.

for a relatively small inferior orbital fissure. The size of the neurocranium indicates a small brain compared with modern anthropoids of similar body size, being most comparable to those of extant strepsirrhines. Compared with extant anthropoids, the frontal lobe of the brain was small, while the olfactory bulbs were relatively large. Postorbital constriction was marked. The metopic suture in the midline of the frontal bone is fully fused, and a frontal sinus was variably developed. The ectotypanic is annular in form, rather than tubular as in extant catarrhines. The palate is long and narrow, and tapers anteriorly. There is a pair of large incisive fenestrae located just posterior to the incisors (see Figure 20.2). The mandibular corpus is relatively deep and quite robust. The cranium exhibits strong sexually dimorphism, in which males have a longer rostrum and

deeper face, more pronounced frontal trigon, temporal lines that converge just posterior to the supraorbital costae to form a prominent sagittal crest, and a strongly developed flange-like nuchal crest. Females have a shorter rostrum, a more globular neurocranium on which the temporal lines converge posteriorly but do not meet to form a sagittal crest, and the nuchal crest is less developed (Simons et al. 2007).

The incisors are relatively small by comparison to the cheek teeth. The canines are highly sexually dimorphic, with the canines in males being much larger than those of females. A specialized sectorial p3 occludes with the upper canine. The molars are short and broad, with strong buccolingual flare, low rounded cusps and crests, and relatively small occlusal basins (see Figure 20.2). The lower molars increase in size from m1 to m3 in *Propl. zeuxis*, whereas in the other species m3 is subequal in size or smaller than m2. The morphology of the dentition, in conjunction with the length of the molar shearing crests and microwear, indicates that the diet of *Propliopithecus* consisted primarily of fruits and young leaves.

Isolated postcranial remains have been referred to the two most common species of *Propliopithecus*, *Propl. zeuxis* and *Propl. chirobates* (Seiffert et al. 2010). The limb bones of *Propl. zeuxis* indicate a heavy-bodied primate, with forelimbs that are slightly shorter than the hind limbs. Distally, the humerus has an entepicondylar foramen and a large dorsal epitrochlear fossa, both of which are absent in extant catarrhines. The foot bones indicate a powerful grasping hallux and mobile ankle joint that permitted a wide range of rotational ability. The first metatarsal has a small facet for the prehallux, a primitive anthropoid feature lost in extant catarrhines (except for gibbons). The phalanges are relatively long and curved with well-developed ridges for attachment of the flexor sheaths and collateral ligaments. These features are consistent with cheiridia adapted for arboreal quadrupedal locomotion involving powerful digital grasping. Overall, the morphology of the postcranial skeleton indicates arboreal above-branch palmigrade quadrupedalism dominated by cautious climbing and clambering, probably most similar in its positional behavior to *Alouatta* or *Varecia* among extant primates.

PLIOPITHECOIDEA

The pliopithecoids are a group of primitive catarrhines with a wide geographical distribution throughout much of Eurasia during the Miocene (Andrews et al. 1996; Harrison and Gu 1999; Begun 2002; Alba et al. 2010). Pliopithecoids presumably originated in Africa some time during the Oligocene, although their occurrence outside of Eurasia is entirely unknown (*contra* Rossie and MacLatchy 2006). The occurrence of primitive pliopithecoids in China during the Early Miocene at about 17–18 Ma establishes them as the first catarrhines to migrate out of Africa, slightly earlier than or broadly contemporaneous with the first appearance of Eurasian hominoids (about 17 Ma), and well before the arrival of cercopithecoids (about 8–11 Ma) (Andrews et al. 1996; Heizmann and Begun 2001; Böhme et al. 2011). The collision of the Afro-Arabian plate with Eurasia during the Early Miocene, in conjunction with lowered sea-levels, led to a temporary closure of the Tethys seaway at 17–19 Ma and the establishment of a land bridge between Arabia and southwest Asia that permitted an influx of African mammals into Eurasia (Andrews et al. 1996; Rögl 1999). The warmer climate at this time facilitated the migration of pliopithecoids out of Africa

and into subtropical and tropical regions of Asia. During the Middle and Late Miocene (about 16–7 Ma) pliopithecoids diversified regionally, with at least 13 species being represented across Eurasia from northern Spain to eastern China. In Europe, few pliopithecoids survived the mid-Vallesian crisis at 9.6 Ma, when gradual global cooling led to greater seasonality and a shift from subtropical evergreen woodlands to predominantly deciduous broadleaved woodlands. Pliopithecoids eventually became extinct in Europe at about 9 Ma, but continued to survive in the subtropical woodlands and forests of eastern Asia until about 7 Ma (Andrews et al. 1996). Further climatic deterioration and possibly the arrival of cercopithecoids from Africa may have been contributing factors in their final extinction.

Unfortunately, the cranial and postcranial morphology is poorly known for many species of pliopithecoids. Partial crania are known for *Pliopithecus vindobonensis* from Slovakia (Figure 20.2), *Anapithecus hernyaki* from Hungary, and *Laccopithecus robustus* from China, and good cranio-mandibular specimens of *Pliopithecus zhangxiangi* and *Plio. canmatensis* are known from China and Spain respectively (Zapfe 1960; Wu and Pan 1985; Harrison et al. 1991; Begun 2002; Alba et al. 2010). Several partial skeletons of *Pliopithecus vindobonensis* are known (Zapfe 1960), while other pliopithecoids are represented only by a few isolated postcranial elements (Begun 2002).

Pliopithecoids are more derived than propliopithecoids in having a short, partially enclosed tubular ectotympanic, but they are more primitive than all other catarrhines in having an incomplete ectotympanic tube, an entepicondylar foramen in the distal humerus and a simple hinge-like carpometacarpal joint of the thumb (Harrison 1987). They represent a group of stem catarrhines that originated later than the propliopithecoids, but prior to the divergence of crown catarrhines (Figure 20.1).

Despite their taxonomic diversity, based primarily on difference in their dentitions, pliopithecoids are remarkably uniform in their cranial morphology. The face is relatively short and quite broad. The lower face is shallow, with a substantial vertical overlap of the orbits and nasal aperture. The subnasal clivus is short and the premaxilla is relatively narrow. The palate narrows anteriorly, with strongly converging tooth rows. The palate has large paired incisive fenestrae. The orbits are subcircular, frontally directed and situated anteriorly above the upper premolars, with slightly protruding inferior rims. The infraorbital foramen is placed close to the inferior margin of the orbit. The interorbital region is relatively wide. The anterior root of the zygomatic arch originates low on the face, close to the maxillary alveolar margin. There is a small frontal sinus and an extensive maxillary sinus. The postorbital plate is complete, except for a broad inferior orbital fissure, but there is no lateral orbital fissure. The neurocranium is globular and relatively large in relation to the size of the facial skeleton. The temporal lines are quite strongly marked and converge posteriorly, but do not meet in the midline to form a sagittal crest, even in male individuals (Zapfe 1960; Wu and Pan 1985; Harrison et al. 1991; Andrews et al. 1996; Begun 2002; see Figure 20.2).

The pliopithecoids are characterized by a number of specialized dental features that distinguish the clade. These include: lower central incisors waisted towards the base of the crown, giving the tooth a distinctive flask-shaped outline when viewed from the buccal aspect; p3 mesiodistally short and high-crowned, with a steeply inclined mesiobuccal honing face; p4 and lower molars relatively long and narrow; lower molars have a pliopithecine triangle (i.e., a small triangular fovea on the buccal side of the talonid basin delimited by crests linking the protoconid and hypoconid and crests

Table 20.3 Classification of the Pliopithecoidea from the Miocene of Eurasia (updated from Harrison and Gu 1999).

Superfamily: Pliopithecoidea
Family: Dionysopithecidae
<i>Dionysopithecus</i>
<i>Dio. shuangouensis</i>
<i>Dio. orientalis</i>
<i>Platodontopithecus</i>
<i>Plat. jianghuaiensis</i>
Family: Pliopithecidae
Subfamily: Pliopithecinae
<i>Pliopithecus</i>
<i>Plio. antiquus</i>
<i>Plio. bii</i>
<i>Plio. canmatensis</i>
<i>Plio. platyodon</i>
<i>Plio. vindobonensis</i>
<i>Plio. zhanxiangi</i>
Subfamily: Crouzeliinae
<i>Plesiopliopithecus</i>
<i>Plesio. auscitanensis</i>
<i>Plesio. lockeri</i>
<i>Plesio. priensis</i>
<i>Plesio. rhodanica</i>
<i>Anapithecus</i>
<i>A. bernyaki</i>
<i>Laccopithecus</i>
<i>Lac. robustus</i>
<i>Egarapithecus</i>
<i>E. narcissi</i>

that descend from the apices of these two cusps and converge in the talonid basin – a feature lacking, and presumably secondarily lost, in *Pliopithecus vindobonensis*); lower molars with marked size increase from m1 to m3; upper premolars and molars relatively broad; and M2 and M3 considerably larger than M1 (Andrews et al. 1996).

The Pliopithecoidea are divided into two families, the Dionysopithecidae and Pliopithecidae, of which the latter is divided into two subfamilies, the Pliopithecinae and Crouzeliinae (Harrison and Gu 1999; Begun 2002; Table 20.3). The earliest known pliopithecoids are from the Xiacaowan Formation, Sihong, China (about 17–18 Ma), where two species are represented – *Dionysopithecus shuangouensis* and *Platodontopithecus jianghuaiensis* (Harrison and Gu 1999). Initially, *Dionysopithecus* was suggested to be related to the dendropithecoids from the Early Miocene of East Africa (Bernor et al. 1988; Harrison et al. 1991), but the Sihong catarrhines have a suite of specialized features that link them uniquely with the pliopithecoids. However, they are more primitive than all other pliopithecoids, and presumably represent closely related stem pliopithecoids that can be included together in their own family, the Dionysopithecidae (Harrison and Gu 1999).

An isolated lower molar from Ban San Klang in northern Thailand (about 15–17 Ma), originally described as *Dendropithecus orientalis* (Suteethorn et al. 1990),

is similar to the smaller dionysopithecine from China, but can be recognized as a distinct species, *Dionysopithecus orientalis* (see Harrison and Gu 1999). In addition, several teeth of a small catarrhine primate from the Middle Miocene Kamliang and Manchar Formations of Pakistan (about 16–17 Ma) (Bernor et al. 1988) have previously been considered to be closely related to *Dionysopithecus* or to East African dendropithecoids (Bernor et al. 1988). However, Harrison and Gu (1999) have suggested that the specimens are unlikely to be pliopithecoids, and are possibly dendropithecoids or hylobatids. An isolated and worn M3 of a small catarrhine from the Late Miocene locality of Haritalyangar in northern India (dated to about 8–9 Ma) has been referred to *Krishnapithecus krishnai*, but the specimen is inadequate to determine its taxonomic or phylogenetic placement (Chopra and Kaul 1979).

A more specialized clade of pliopithecoids, the Pliopithecidae, originated from the dionysopithecines presumably somewhere in Asia. Early in their evolutionary history pliopithecids diverged into two distinct lineages – the Pliopithecinae and the Crouzeliinae. Paleobiogeographic evidence suggests that the two groups originated in Asia, and then successively extended their range westwards into Europe at about 13–17 Ma, at a time when warmer climates prevailed.

The pliopithecines comprise six species, referable to a single genus, *Pliopithecus* (although some authors recognize *Pliopithecus vindobonensis* as a separate genus, *Epipliopithecus*) (Andrews et al. 1996; Harrison and Gu 1999; Begun 2002; Table 20.2). The cheek teeth of pliopithecines conform to the generalized pliopithecoid bauplan, similar in most respects to those of the earlier dionysopithecines, but individual species are distinguished from one another on the basis of size and detailed features of the dentition. *Pliopithecus* is best known from the Middle Miocene of Europe, where *Plio. canmatensis* is recorded from northern Spain, *Plio. antiquus* is broadly distributed throughout western and central Europe, and *Plio. platyodon* and *Plio. vindobonensis* are restricted to central Europe (Andrews et al. 1996; Begun 2002; Alba et al. 2010). The subfamily is also represented in the Middle Miocene (about 14–15 Ma) of China by a number of jaw fragments belonging to *Plio. zhanxiangji* from Tongxin, Ningxia Hui Autonomous Region, as well as isolated teeth of *Plio. bii* and *Pliopithecus* sp. from Tiersihabahe, Junggar, Xinjiang and Laogou, Gansu Province respectively (Harrison et al. 1991; Harrison 2005).

The partial skeletons of *Plio. vindobonensis* provide a remarkably complete picture of pliopithecoid postcranial morphology (Zapfe 1960; Fleagle 1983, Rose 1983, 1993). The limb bones indicate that *Pliopithecus* had relative long and slender limbs. The hind limbs are slightly longer than the forelimbs, with an intermembral index of 94, as in many cercopithecoids. The individual limb bones are morphologically most similar to arboreal cercopithecids, large platyrrhines and lemurids. As noted above, the distal humerus has a large entepicondylar foramen, a primitive anthropoid feature lost in all extant catarrhines. The hand was relatively narrow, with long and curved lateral digits and a large, and a well-developed thumb that had a hinge-like carpometacarpal joint. The foot was long and mobile with good grasping capabilities that facilitated arboreal climbing and hind limb suspension. The torso was long, with a flexible lumbar region composed of at least 6 and probably 7 vertebrae. The sacrum contains three fused vertebral elements as in most non-hominoid primates. No caudal vertebrae are known, but the morphology of the sacrum indicates that there was probably a relatively long tail. The morphology of the skeleton is most similar to that of colobines, atelids and lemurids,

and indicates that *Pliopithecus* was an agile quadruped capable of above-branch running and walking, climbing, forelimb and hind limb suspension, and leaping.

The more specialized crouzeliines apparently originated in Asia from a pliopithecine-like ancestor. Stem crouzeliines have recently been reported from the mid-Miocene of China. The locality of Fanchang in Anhui Province (about 16.5–17 Ma) has yielded a large sample of isolated teeth of a new genus and species of pliopithecoid and an isolated molar of a different species has been recovered from Damiao in Inner Mongolia (Zhang and Harrison 2008). These taxa share derived features of the dentition that indicate a close relationship with crouzeliines, but retain a number of primitive traits that indicate that they are stem members of the clade. The occurrence of stem crouzeliines in China implies that the Pliopithecinae and Crouzeliinae probably diverged in Asia prior to their arrival in Europe.

Crouzeliines can be distinguished from pliopithecines in the following features: relatively broader and lower crowned incisors; elongated p4 with mesial fovea that opens mesiolingually; upper premolars with buccolingually compressed paracone; m1 crown narrows mesially; m1 and m2 crowns very long with buccolingual waisting, elongated mesial fovea, strongly oblique crest connecting the protoconid and metaconid, more elevated trigonid relative to the talonid basin, oblique cristid obliqua, hypoconulids reduced in size and situated in the midline or slightly lingually to the midline of the crown, and restricted distal fovea; m3 with slightly oblique mesial fovea and hypoconulid more lingually placed relative to the protoconid and hypoconid; lower molars with high, conical and well-spaced cusps; M1 crown narrows lingually; M1 and M2 with narrower crowns, relatively narrower trigon, weaker development of the lingual cingulum and more pronounced buccal cingulum (Andrews et al. 1996).

In Europe, crouzeliines diversify regionally into several distinct genera – *Anapithecus* in central Europe, *Plesiopliopithecus* in western and central Europe, and *Egarapithecus* in Spain (Table 20.3). They are first recorded at European localities dating to about 14–15 Ma and become extinct by about 9 Ma. The best-known crouzeliine in Europe is *Anapithecus hernyaki* from Rudabánya in Hungary and other localities in central Europe (about 10–11 Ma). It is a relatively large pliopithecoid with cheek teeth that are somewhat larger than those of the extant siamang, with an estimated body mass of about 15 kg (Begun 2002). The upper and lower incisors are relatively low-crowned and broad and the lower incisors lack the waisting seen in other pliopithecoids. I2 is much smaller than I1. The lower molars are long, and increase markedly in size from m1 to m3, and they possess the suite of specialized features of crouzeliines briefly described above. A late-surviving crouzeliine, *Laccopithecus robustus*, is known from the Late Miocene (about 7 Ma) of Shihuiba, Yunnan, China. It is represented by a partial cranium, numerous jaw fragments, isolated teeth and a single manual phalanx (Wu and Pan 1985).

Pliopithecoids are small to medium-size catarrhines with estimated average body weights ranging from about 6 kg to 15 kg. The occlusal morphology of the cheek teeth, the relative proportions of the incisors and molars, and the length of the molar shearing crests indicate that the diet of dionysopithecines and pliopithecines consisted primarily of fruits, supplemented by young leaves, while crouzeliines were specialist folivores. The postcranial remains indicate that pliopithecoids were agile arboreal quadrupedal primates adapted for above-branch running and walking, climbing, leaping and suspensory postures.

SAADANIOIDEA

During the later part of the Oligocene (32–23 Ma), between the Early Oligocene sediments of the Fayum and the fossil-rich Early Miocene deposits in East Africa, the catarrhine fossil record is exceedingly sparse. However, a recent important discovery in Saudi Arabia and fossil finds from a Late Oligocene locality in northern Kenya have helped to fill the gap.

A partial cranium of an adult male individual of an early catarrhine has been recovered from Harrat Al Ujayfa in western Saudi Arabia dated to 28–29 Ma (Figure 20.2). The specimen has recently been described as a new genus and species, *Saadanius hijazensis* (Zalmout et al. 2010). Based on the size of the teeth and cranium it was a relatively large catarrhine (15–20 kg), about the size of a male proboscis monkey. The main features of the cranium include: short and broad premaxilla; short subnasal clivus; large paired incisive fenestrae; palate long and narrow, and tapering anteriorly; moderately long rostrum with strong midfacial prognathism; maxillary sinus present, but relatively restricted in its extent; nasal aperture large and ovoid; orbits probably slightly higher than wide; interorbital region relatively broad; nasal bones long and narrow; very slender supraorbital costae; temporal lines strongly developed and converge just behind the orbits to form a frontal trigon; a distinct sagittal crest would have been present in the midline for much of the length of the neurocranium; frontal bone more elevated than the superior margin of the orbits; no frontal sinus; and tubular ectotympanic. The upper incisors and canines are relatively small. The upper canine is ovoid in cross-section, with a relatively stout root. The premolar crowns are not preserved, but the roots demonstrate that there were only two premolars in each half of the maxilla. The upper molars are relatively broad and increase in size from M1 to M3 (Zalmout et al. 2010) (see Figure 20.2). *Saadanius* is the oldest catarrhine primate to exhibit a tubular ectotympanic and this feature clearly demonstrates that it is more derived in the direction of crown catarrhines than the propliopithecoids and pliopithecoids (Figure 20.1). It is likely that *Saadanius* represents the sister taxon to Dendropithecoidae+Proconsuloidae+crown catarrhines, and for this reason it has been placed in its own superfamily, the Saadanioidae (Zalmout et al. 2010).

Propliopithecoids and pliopithecoids primitively retain relative broad upper molars, with a progressive tendency to become narrower in more advanced catarrhines. *Saadanius* has relatively broad molars, intermediate between propliopithecoids+pliopithecoids and dendropithecoids+proconsuloids. This feature places *Saadanius* as the sister taxon to Dendropithecoidae+Proconsuloidae+crown catarrhines. In addition, Zalmout et al. (2010) indicate that dendropithecoids and proconsuloids share several derived features with hominoids that are lacking in *Saadanius*, including the presence of a frontal sinus and relatively large male canines. However, the phylogenetic significance of both of these features is incorrectly interpreted. Frontal sinuses are ubiquitous in extant strepsirrhines and platyrrhines, and occur in propliopithecoids, pliopithecoids, and proconsuloids, but only occur in African apes and humans among extant hominoids. Given the distribution of frontal sinuses in extant and fossil primates it can be presumed that the presence of a frontal sinus is a primitive feature of anthropoids (and unquestionably a developmentally labile feature that is highly prone to homoplasy) and not a synapomorphy that defines the Hominoidea. Similarly, comparative

data on relative canine size do not support the contention that dendropithecoids, proconsuloids and hominoids can be distinguished from cercopithecoids and primitive catarrhines in having relatively larger canines in males.

More fragmentary material of a large catarrhine primate, *Kamoyapithecus hamiltoni*, is known from the Late Oligocene (about 24–27 Ma) locality of Losodok in northern Kenya (Leakey et al. 1995; Rasmussen and Gutierrez 2009). Based on the size of its teeth, *Kamoyapithecus* was much larger than *Propliopithecus* and *Saadanius*, with an estimated body mass of about 30–40 kg (Harrison 2010). Comparisons show that *Kamoyapithecus* retains features of its dentition that are more primitive than those of Early Miocene dendropithecoids and proconsuloids. These include a short stout canine with a robust root, broad upper molars with strong buccolingual flare, low rounded cusps, a relatively narrow trigon, and a broad lingual cingulum (Leakey et al. 1995; Rasmussen 2002; Rasmussen and Gutierrez 2009; Harrison 2002, 2010). The primitiveness of *Kamoyapithecus* is consistent with its antiquity, and, like *Saadanius*, it probably represents the sister taxon of dendropithecoids+proconsuloids+crown catarrhines (see Figure 20.1). *Kamoyapithecus* may eventually prove to be a member of the Saadaniioidea, but additional material is needed to determine its precise phylogenetic and taxonomic status.

DENDROPITHECOIDEA

The dendropithecoids are stem catarrhines of modern aspect from the Miocene of Africa (Harrison 2002, 2010). The taxon consists of a single family of three closely related genera – *Micropithecus*, *Dendropithecus*, and *Simiolus* (Table 20.4). They are all small catarrhines with an average body mass of 4–8 kg. Their primitive dental and postcranial features indicate that they are the sister taxon to Proconsuloidea+Hominioidea+Cercopithecoidea (Figure 20.1).

Dendropithecoids are known only from localities in East Africa, and it is likely that they were restricted to the Afro-Arabian province throughout their evolutionary history. They are characterized by the following distinctive features: rostrum relatively abbreviated, with a short subnasal clivus; upper and lower canines strongly bilaterally compressed; p3 moderately to strongly sectorial; limb bones long and slender; distal humerus with large medially directed medial epicondyle, a well-developed dorsal epitrochlear fossa, trochlea with minimal spooling, a weak lateral trochlear keel, and a shallow olecranon fossa (Harrison 2010). Most of these characters can be interpreted as the primitive condition for catarrhines, while the distinctive C/p3 honing complex probably corresponds closely to the primitive condition for catarrhines of modern aspect (Harrison and Gu 1999). It is conceivable that the dendropithecoids represent a paraphyletic group, but their close morphological similarity, especially in their postcranial morphology, makes it more likely that they represent a distinct clade. The loss of the entepicondylar foramen in the distal humerus is a synapomorphy that links them with later catarrhines, but they primitively retain a dorsal epitrochlear fossa that has been lost in crown catarrhines. Unfortunately, the cranial material is inadequate to determine whether they possessed a tubular ectotympanic typical of modern catarrhines.

Dendropithecus macinnesi is a small catarrhine from the Early Miocene (about 17–20 Ma) of western Kenya with an estimated average body weight of about 6–8 kg.

Table 20.4 Taxonomy of Saadaniioidea, Dendropithecoidea and early catarrhines of uncertain affinity from the Oligocene and Miocene of Afro-Arabia (after Harrison 2002, 2010; Pickford et al. 2010; Zalmout et al. 2010).

Superfamily Saadaniioidea
Family: Saadaniidae
<i>Saadanius</i>
<i>Saad. hijazensis</i>
Superfamily: Dendropithecoidea
Family: Dendropithecidae
<i>Dendropithecus</i>
<i>Den. macinnesi</i>
<i>Den. ugandensis</i>
<i>Micropithecus</i>
<i>M. clarki</i>
<i>M. leakeyorum</i>
<i>Simiolus</i>
<i>Sim. andrewsi</i>
<i>Sim. cheptumuae</i>
<i>Sim. enjiessi</i>
Superfamily: <i>incertae sedis</i>
Family: <i>incertae sedis</i>
<i>Iriripithecus</i>
<i>I. alekileki</i>
<i>Limnopithecus</i>
<i>Lim. legetet</i>
<i>Lomorpithecus</i>
<i>Lom. evansi</i>
<i>Kalepithecus</i>
<i>Kal. songhorensis</i>
<i>Kamoyapithecus</i>
<i>Kam. hamiltoni</i>
<i>Karamojapithecus</i>
<i>Kar. akisimia</i>
<i>Kogolepithecus</i>
<i>Kog. morotoensis</i>

A second smaller species of the genus, *Den. ugandensis*, has recently been described from the Early Miocene locality of Napak in Uganda (about 19 Ma), (Pickford et al. 2010). *Dendropithecus* has high-crowned and narrow incisors that are small in relation to the size of the molars. The canines are strongly sexually dimorphic. They are high-crowned and bilaterally compressed in males and lower crowned and less compressed in females. The upper canine in males is unusual in having a double mesial groove. The upper premolars are broad, and the paraconid is much more elevated than the protoconid. The p3 is sectorial with a bilaterally compressed crown and a long mesiobuccal honing face. The upper molars are broad and rectangular, with high and voluminous cusps, well-developed crests, and a broad lingual cingulum. The lower molars are relatively long, with high conical cusps, sharp occlusal crests, expansive foveae and talonid basin, and moderately well developed buccal cingulum. The lower molars exhibit a marked increase in size from m1 to m3. The palate is long and narrow with large paired incisive foramina. The nasal aperture is narrow and tapers

inferiorly, and the subnasal clivus is very short. The maxillary sinus is extensive. The mandibular corpus is low and robust, and the symphyseal region is buttressed by moderately well developed superior and inferior transverse tori (Harrison 2002, 2010). Several partial skeletons of *Den. macinnesi* are known from Rusinga Island in Kenya (Le Gros Clark and Thomas 1951). As noted above, the distal humerus has a dorsal epitrochlear fossa, but lacks an entepicondylar foramen. The limb bones are long and slender, with joints that are capable of wide ranges of excursion. *Dendropithecus* was clearly an active, arboreal quadrupedal palmigrade primate, capable of powerful climbing, and at least some degree of forelimb suspension. It was probably most similar in its locomotor capabilities to extant atelid platyrrhines.

Micropithecus is the smallest of the dendropithecoids, with an estimated average body weight of about 3–4 kg. *Micropithecus clarki* is from the Early Miocene (about 19–20 Ma) of Uganda and Kenya (Harrison 1988, 2002, 2010), while a later species, *M. leakeyorum*, is known from the Middle Miocene (about 15–16 Ma) of Kenya (Harrison 1989). The dentition of *M. clarki* is characterized by high crowned incisors that are large relative to the size of the cheek teeth; high-crowned and bilaterally compressed canines that are markedly sexually dimorphic; relatively narrow upper molars, with hypocone more lingually placed than protocone, and weak to moderately developed lingual cingulum; lower molars with low rounded crests, and reduced M3. The mandibular corpus is tall and slender. The cranium exhibits the following key features: face short and broad; premaxilla probably did not make contact with the nasals; subnasal clivus short; nasal aperture broad, and narrows inferiorly; orbits relatively large and subcircular; broad interorbital region; inferior orbital fissure extensive; no supraorbital torus or glabellar eminence; temporal lines widely spaced and weakly developed; anterior root of zygomatic arch posteriorly placed, originating above M2, and situated close to the alveolar margin; maxillary sinus extensive; palate broad and shallow; large paired incisive foramina; and sulcal pattern on endocranial surface of the frontal bone similar to extant platyrrhines.

Simiolus is represented by three species from the Early and Middle Miocene of East Africa – *S. enjiessi* from the Early Miocene (about 16.8–17.5 Ma) of Kalodirr and Locherangan in northern Kenya (Leakey and Leakey 1987), *S. cheptumoe* from the Middle Miocene (about 14.5 Ma) of Kipsaraman in Kenya (Pickford and Kunimatsu 2005), and *S. andrewsi* from the Middle Miocene (about 13.7 Ma) locality of Fort Ternan in Kenya (Harrison 2010). *Simiolus* is a small catarrhine primate (4–6 kg) with the following combination of features: lower face relatively short with orbits positioned far anteriorly; large paired incisive fenestrae; mandible with high and slender corpus, and well developed superior and inferior transverse tori; lower incisors narrow, and small in relation to the size of the molars; upper canine moderately high-crowned and buccolingually compressed; p3 moderately bilaterally compressed with a long and steep honing face; P3 triangular in occlusal outline; upper molars relatively long mesiodistally, with elevated cusps and crests, and a strong transverse crest linking the metacone and hypocone; lower molars relatively long and narrow, ovoid in occlusal outline, with moderately high and sharp cusps and crests, and well-defined basins (Leakey and Leakey 1987; Harrison 2002, 2010).

A number of postcranial specimens of *Simiolus* are known from Kalodirr (Leakey and Leakey 1987; Rose et al. 1992; Rose 1993). They are comparable in morphology to those of *Dendropithecus*, but slightly smaller in size. The most important features

are as follows: humerus with slender and slightly retroflexed shaft, distinct dorsal epitrochlear fossa, no entepicondylar foramen, and distal articulation with modest lateral trochlear keel; femur with relatively small head and high neck angle; talus similar to that of other dendropithecids and to proconsulids; metacarpals and phalanges indicating a narrow hand with good grasping capabilities. *Simiolus*, like *Dendropithecus*, is inferred to have been an agile arboreal quadruped most similar in its positional behavior to the larger extant platyrrhines.

OTHER STEM CATARRHINES FROM THE MIOCENE OF EAST AFRICA

Among the remarkable diversity of small primitive catarrhines from the Early Miocene (about 17–20 Ma) of Kenya and Uganda are several genera that are too inadequately known anatomically to confidently establish their taxonomic or phylogenetic relationships. These taxa, each represented by a single species, include *Kalepithecus*, *Limnopithecus*, *Kogolepithecus*, *Lomorupithecus*, *Iriripithecus* and *Karamojapithecus* (Pickford et al. 2003, 2010; Rossie and MacLatchy 2006; Harrison 2010; Table 20.4). *Lomorupithecus* has been suggested to be a member of the Pliopithecidae (Rossie and MacLatchy 2006), but it lacks the derived dental features that unite the Eurasian members of this clade (Harrison 2010), and it is much more likely that *Lomorupithecus* represents a dendropithecoid.

They are all relatively small catarrhines that differ from each other in the detailed morphology of their dentition. *Limnopithecus*, *Lomorupithecus*, *Iriripithecus* and *Karamojapithecus* have an estimated average body weight of 4–5 kg, while *Kalepithecus* and *Kogolepithecus* are slightly larger with estimated body weights of 5–6 kg and 8–10 kg respectively. Where the cranial anatomy is known, they are short faced catarrhines, with a shallow subnasal clivus (deeper in *Kalepithecus*), narrow nasal aperture (broad in *Kalepithecus*), orbits positioned far anteriorly and situated low on the face, a relatively extensive maxillary sinus, anterior root of the zygomatic arch situated close to the alveolar margin of the maxilla; relatively large incisive fenestrae; narrow and shallow palate, with tooth rows that taper anteriorly; mandibular corpus slender and shallowing posteriorly, usually with a well-developed superior transverse torus and weak to absent inferior transverse torus. The incisors are generally small in relation to the size of the molars. The canines are sexually dimorphic in size and morphology, with those of males being larger and more bilaterally compressed than in females. The p3 is usually long and narrow, with a moderately long mesiobuccal honing face, at least in male individuals (but not in *Limnopithecus*). The upper premolars and molars are relatively broad with well-developed lingual cingula. The lower molars are ovoid to rectangular in occlusal outline with well-developed buccal cingulum, and they increase in size from m1 to m3 (Harrison 1988, 2002, 2010). Unassociated postcranial remains referred to *Limnopithecus* are morphologically similar to the corresponding elements in *Dendropithecus* and *Simiolus*.

Given the quality of material available it is not possible to determine the precise phylogenetic relationships of these small catarrhine primates from the Early Miocene of East Africa, but when better material becomes available it is likely that they will prove to represent additional dendropithecoids or possibly small species of proconsuloids. Regardless of their affinities, they do show that there was a remarkably diverse

community of early catarrhines in East Africa during the early part of the Miocene (Harrison 2010). The nine species of dendropithecoids and small early catarrhines of uncertain taxonomic status discussed above coexisted with at least ten species of proconsulids and one species of cercopithecoid. By the Middle Miocene (16–10 Ma), non-cercopithecoid catarrhine diversity in East Africa was reduced to only 12 species, but still included three species of dendropithecoids and at least one other small catarrhine. Although the record of fossil non-cercopithecoid catarrhines from the Late Miocene of East Africa is poor, and relatively few species have been named from this time period, evidence from the site of Nakali in Kenya confirms that small, primitive catarrhines survived in the region until at least about 10 Ma (Kunimatsu et al. 2007).

CONCLUSIONS

The earliest definitive record of fossil catarrhines, the propliopithecoids, comes from the Early Oligocene (about 29–32 Ma) of Egypt. Earlier anthropoids from the Late Eocene and Early Oligocene (about 29–37 Ma) of northern Africa and the Arabian Peninsula, including the parapithecoids, oligopithecoids and proteopithecoids, have been regarded in the past to be early catarrhines, but the evidence suggests that they are best identified as stem anthropoids that originated prior to the divergence of platyrrhines and catarrhines. The pliopithecoids are a diverse group of stem catarrhines widely distributed throughout Eurasia during much of the Miocene (18–7 Ma). Although pliopithecoids are currently only known from Eurasia, the clade presumably originated in Africa some time during the Oligocene and migrated into Asia during the Early Miocene (about 17–18 Ma). They are more derived than propliopithecoids in a number of features and represent the sister taxon of all other catarrhines. The recent discovery of a partial cranium of *Saadanius* from the Late Oligocene of Saudi Arabia (about 28–29 Ma) has helped to fill the gap in the fossil catarrhine record between the Early Oligocene of the Fayum, Egypt and the Early Miocene localities in East Africa. *Saadanius* is the earliest catarrhine with a tubular ectotympanic, being more derived in its ear region than propliopithecoids and pliopithecoids. It can be placed as the sister taxon to dendropithecoids+proconsuloids+crown catarrhines. The Dendropithecoidea is a group of stem catarrhines of modern aspect from the Miocene of East Africa that shares a closer relationship with crown catarrhines than do the propliopithecoids, pliopithecoids and saadanioids. Contemporary with the dendropithecoids in East Africa are a number of poorly known genera of small catarrhines of uncertain phylogenetic relationships. These are likely to be additional dendropithecoids, but it cannot be entirely ruled out that they represent small proconsuloids or even stem hominoids.

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REFERENCES

- Alba, D. M., S. Moyà-Solà, A. Malgosa, I. Casanovas-Vilar, J. M. Robles, S. Almécija, J. Galindo, C. Rotgers, and J. V. B. Mengual, 2010 A New Species of *Pliopithecus* Gervais, 1849 (Primates: Pliopithecidae) from the Middle Miocene (MN8) of Abocador de Can Mata (els Hostalets de Pierola, Catalonia, Spain). *American Journal of Physical Anthropology* 141:52–75.
- Andrews P., 1985 Family Group Systematics and Evolution among Catarrhine Primates. *In* *Ancestors: The Hard Evidence*. E. Delson, ed. pp. 14–22. New York: Alan R. Liss.
- Andrews, P., 1992 Evolution and Environment in the Hominoidea. *Nature* 360:641–647.
- Andrews, P., and T. Harrison, 2005 The Last Common Ancestor of Apes and Humans. *In* *Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam*. D.E. Lieberman, R.J. Smith, and J. Kelley, eds. pp. 103–121. Boston: Brill Academic Publishers.
- Andrews, P., T. Harrison, E. Delson, R. L. Bernor, and L. Martin, 1996 Distribution and Biochronology of European and Southwest Asian Miocene Catarrhines. *In* *The Evolution of Western Eurasian Neogene Mammal Faunas*. R. L. Bernor, V. Fahlbusch, and H.-W. Mittmann, eds. pp. 168–207. New York: Columbia University Press.
- Beard, K. C., 2002 Basal Anthropoids. *In* *The Primate Fossil Record*. W. C. Hartwig, ed. pp. 133–149. Cambridge: Cambridge University Press.
- Begun, D. R., 2002 The Pliopithecidae. *In* *The Primate Fossil Record*. W. C. Hartwig, ed. pp. 221–240. Cambridge: Cambridge University Press.
- Begun, D. R., C. V. Ward, and M. D. Rose, 1997 Events in Hominoid Evolution; *In* *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*. D. R. Begun, C. V. Ward, and M. D. Rose, eds. pp. 389–415. New York: Plenum Press.
- Bernor, R., L. Flynn, T. Harrison, S. T. Hussain, and J. Kelley, 1988 *Dionysopithecus* from Southern Pakistan and the Biochronology and Biogeography of Early Eurasian Catarrhines. *Journal of Human Evolution* 17:339–358.
- Böhme, M., H. A. Aziz, J. Prieto, V. Bachtadse, and G. Schweigert, 2011 Bio-magnetostratigraphy and Environment of the Oldest Eurasian Hominoid from the Early Miocene of Engelswies (Germany). *Journal of Human Evolution* 61(3):332–9.
- Chatterjee, H. J., S. Y. W. Ho, I. Barnes, and C. Groves, 2009 Estimating the Phylogeny and Divergence Times of Primates Using a Supermatrix Approach. *BMC Evolutionary Biology* 2009, 9:259.
- Chopra, S. R. K., and S. Kaul, 1979 A New Species of *Pliopithecus* from the Indian Sivaliks. *Journal of Human Evolution* 8:475–477.
- Fleagle, J. G., 1983 Locomotor Adaptations of Oligocene and Miocene Hominoids and their Phyletic Implications. *In* *New Interpretations of Ape and Human Ancestry*. R. L. Ciochon and R. S. Corruccini, eds. pp. 301–324. New York: Plenum Press.

- Fleagle, J. G., 1999 Primate Adaptation and Evolution. New York: Academic Press.
- Fleagle, J. G., and R. F. Kay, 1987 The Phyletic Position of the Parapithecidae. *Journal of Human Evolution* 16:483–532.
- Gebo, D. L., L. MacLatchy, R. Kityo, A. Deino, J. Kingston, and D. Pilbeam, 1997 A Hominoid Genus from the Early Miocene of Uganda. *Science* 276:401–404.
- Harrison, T., 1987 The Phylogenetic Relationships of the Early Catarrhine Primates: A Review of the Current Evidence. *Journal of Human Evolution* 16:41–80.
- Harrison, T., 1988 A Taxonomic Revision of the Small Catarrhine Primates from the early Miocene of East Africa. *Folia Primatologica* 50:59–108.
- Harrison, T., 1989 A New Species of *Micropithecus* from the Middle Miocene of Kenya. *Journal of Human Evolution* 18:537–557.
- Harrison, T., 1993 Cladistic Concepts and the Species Problem in Hominoid Evolution. *In* Species, Species Concepts, and Primate Evolution. W. H. Kimbel and L. B. Martin, eds. pp. 345–371. New York: Plenum Press.
- Harrison, T., 2002 Late Oligocene to Middle Miocene Catarrhines from Afro-Arabia. *In* The Primate Fossil Record. W. C. Hartwig, ed. pp. 311–338. Cambridge: Cambridge University Press.
- Harrison, T., 2005 The Zoogeographic and Phylogenetic Relationships of Early Catarrhine Primates in Asia. *Anthropological Science* 113:43–51.
- Harrison, T., 2010 Dendropithecoidea, Proconsuloidea and Hominoidea. *In* Cenozoic Mammals of Africa. L. Werdelin and W. J. Sanders, eds. pp. 429–469. Berkeley: University of California Press.
- Harrison, T., E. Delson, and J. Guan, 1991 A New Species of *Pliopithecus* from the Middle Miocene of China and its Implications for Early Catarrhine Zoogeography. *Journal of Human Evolution* 21:329–361.
- Harrison, T., and Y. Gu, 1999 Taxonomy and Phylogenetic Relationships of Early Miocene Catarrhines from Sihong, China. *Journal of Human Evolution*, 37:225–277.
- Heizmann, E. P. J., and D. R. Begun, 2001 The Oldest Eurasian Hominoid. *Journal of Human Evolution* 41:463–481.
- Kay, R. F., C. Ross, and B. A. Williams, 1997 Anthropoid Origins. *Science* 275:797–803.
- Kay, R. F., B. A. Williams, C. F. Ross, M. Takai, and N. Shigehara, 2004 Anthropoid Origins: A Phylogenetic Analysis. *In* Anthropoid Origins: New Visions. C. F. Ross and R. F. Kay, eds. pp. 91–135. New York: Kluwer Academic/Plenum Press.
- Kelley, J., 1997 Paleobiological and Phylogenetic Significance of Life History in Miocene Hominoids. *In* Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation. D. R. Begun, C. V. Ward, and M. D. Rose, eds. pp. 173–208. New York: Plenum Press.
- Kunimatsu, Y., M. Nakatsukasa, Y. Sawada, T. Sakai, M. Hyodo, H. Hyodo, T. Itaya, H. Nakaya, H. Saegusa, A. Mazurier, M. Saneyoshi, H. Tsujikawa, A. Yamamoto, and E. Mbua, 2007 A New Late Miocene Great Ape from Kenya and its Implications for the Origins of African Great Apes and Humans. *Proceedings of the National Academy of Sciences of the USA* 104:19220–19225.
- Leakey, M. G., P. S. Ungar, and A. Walker, 1995 A New Genus of Large Primate from the Late Oligocene of Lothidok, Turkana District, Kenya. *Journal of Human Evolution* 28:519–531.
- Leakey, R. E., and M. G. Leakey, 1987 A New Miocene Small-Bodied Ape from Kenya. *Journal of Human Evolution*, 16:369–387.
- Le Gros Clark, W. E., and D. P. Thomas, 1951 Associated Jaws and Limb Bones of *Limnopithecus macinnesi*. Fossil Mammals of Africa No. 3. London: British Museum (Natural History).
- MacLatchy, L., D. Gebo, R. Kityo, and D. Pilbeam, 2000 Postcranial Functional Morphology of *Morotopithecus bishopi*, with Implications for the Evolution of Modern Ape Locomotion. *Journal of Human Evolution* 39:159–183.
- Patel, B. A., and A. Grossman, 2006 Dental Metric Comparisons of *Morotopithecus* and *Afropithecus*: Implications for the Validity of the Genus *Morotopithecus*. *Journal of Human Evolution* 51:506–512.

- Pickford, M., 2002 New Reconstruction of the Moroto Hominoid Palate and a Reassessment of Its Affinities to *Afropithecus turkanensis*. *Human Evolution* 17:1–19.
- Pickford, M., and Y. Kunimatsu, 2005 Catarrhines from the Middle Miocene (ca. 14.5 Ma) of Kipsaraman, Tugen Hills, Kenya. *Anthropological Science* 113:189–224.
- Pickford, M., S. Musalizi, B. Senut, D. Gommery, and E. Musiime, 2010 Small Apes from the Early Miocene of Napak, Uganda. *Geo-Pal Uganda* 3:1–111.
- Pickford, M., B. Senut, D. Gommery, and E. Musiime, 2003 New Catarrhine Fossils from Moroto II, Early Middle Miocene (ca 17.5 Ma) Uganda. *Comptes Rendus Palevol* 2:649–662.
- Rae, T. C., 1999 Mosaic Evolution in the Origin of the Hominoidea. *Folia Primatologica* 70:125–135.
- Rasmussen, D. T., 2002 Early Catarrhines of the African Eocene and Oligocene. *In* The Primate Fossil Record. W. C. Hartwig, ed. pp. 203–220. Cambridge: Cambridge University Press.
- Rasmussen, D. T., and M. Gutierrez, 2009 A Mammalian Fauna from the Late Oligocene of Northwestern Kenya. *Palaeontographica, Abt. A*, 288:1–52.
- Rögl, F., 1999 Circum-Mediterranean Miocene Paleogeography. *In* The Miocene Land Mammals of Europe. G. E. Rössner and K. Heissig K., eds. pp. 39–48. Munich: Verlag Dr. Friedrich Pfeil.
- Rose, M. D., 1983 Miocene Hominoid Postcranial Morphology: Monkey-like, Ape-Like, Neither, or Both? *In* New Interpretations of Ape and Human Ancestry. R. L. Ciochon and R. S. Corruccini, eds. pp. 405–420. New York: Plenum Press.
- Rose, M. D., 1993 Locomotor Anatomy of Miocene Hominoids. *In* Postcranial Adaptation in Nonhuman Primates. D. L. Gebo, ed. pp. 252–272. DeKalb: Northern Illinois University Press.
- Rose, M. D., M. G. Leakey, R. E. F. Leakey, and A. C. Walker, 1992 Postcranial Specimens of *Simiolus enjessi* and Other Primitive Catarrhines from the Early Miocene of Lake Turkana, Kenya. *Journal of Human Evolution* 22:171–237.
- Ross, C. F., B. Williams, and R. F. Kay, 1998 Phylogenetic Analysis of Anthropoid Relationships. *Journal of Human Evolution* 35:221–306.
- Rossie, J. B., and L. MacLatchy, 2006 A New Pliopithecoid Genus from the Early Miocene of Uganda. *Journal of Human Evolution* 50:568–586.
- Seiffert, E. R., and E. L. Simons, 2001 Astragalar Morphology of Late Eocene Anthropoids from the Fayum Depression (Egypt) and the Origin of Catarrhine Primates. *Journal of Human Evolution* 41:577–606.
- Seiffert, E. R., E. L. Simons, W. C. Clyde, J. B. Rossie, Y. Attia, T. M. Bown, P. Chatrath, and M. Mathison, 2005 Basal Anthropoids from Egypt and the Antiquity of Africa's Higher Primate Radiation. *Science* 310:300–304.
- Seiffert, E. R., E. L. Simons, and J. G. Fleagle, 2000 Anthropoid Humeri from the Late Eocene of Egypt. *Proceedings of the National Academy of Sciences of the USA* 97:10062–10067.
- Seiffert, E. R., E. L. Simons, J. G. Fleagle, and M. Godinot, 2010 Paleogene Anthropoids. *In* Cenozoic Mammals of Africa. L. Werdelin and W. J. Sanders, eds. pp. 369–391. Berkeley: University of California Press.
- Simons, E. L., 1992 Diversity in the Early Tertiary Anthropean Radiation in Africa. *Proceedings of the National Academy of Sciences of the USA* 89:10743–10747.
- Simons, E. L., 2001 The Cranium of *Parapithecus grangeri*, and Egyptian Oligocene Anthropoid Primate. *Proceedings of the National Academy of Sciences of the USA* 98:7892–7897.
- Simons, E. L., and D. T. Rasmussen, 1996 Skull of *Catopithecus browni*, an Early Tertiary Catarrhine. *American Journal of Physical Anthropology* 100:261–292.
- Simons, E. L., E. R. Seiffert, P. S. Chatrath, and Y. Attia, 2001 Earliest Record of a Parapithecoid Anthropoid from the Jebel Qatrani Formation, Northern Egypt. *Folia Primatologica* 72:316–331.

- Simons, E. L., E. R. Seiffert, T. M. Ryan, and Y. Artia, 2007 A Remarkable Female Cranium of the Early Oligocene Anthropoid *Aegyptopithecus zeuxis* (Catarrhini, Propliopithecidae). *Proceedings of the National Academy of Sciences of the USA* 104:8731–8736.
- Suteethorn V., E. Buffetaut, H. Buffetaut-Tong, S. Ducrocq, R. Helmcke-Ingavat, J.-J. Jaeger, and Y. Jongkanjanasontorn, 1990 A Hominoid Locality in the Middle Miocene of Thailand. *Comptes Rendus de l'Académie des Sciences, Paris*, 311, Sér. II:1449–1454.
- Szalay F.S., and E. Delson, 1979 *Evolutionary History of the Primates*. New York: Academic Press.
- Walker, A., 1997 *Proconsul* Function and Phylogeny. *In* *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptation*. D. R. Begun, C. V. Ward, and M. D. Rose, eds. pp. 209–224. New York: Plenum Press.
- Wu, R., and Y. Pan, 1985 Preliminary Observation on the Cranium of *Laccopithecus robustus* from Lufeng, Yunnan with Reference to its Phylogenetic Relationship. *Acta Anthropologica Sinica* 4:7–12.
- Young, N. M., and L. MacLachy, 2004 The Phylogenetic Position of *Morotopithecus*. *Journal of Human Evolution* 46:163–184.
- Zalmout, I. S., W. J. Sanders, L. M. MacLachy, G. F. Gunnell, Y. A. Al-Mufarreh, M. A. Ali, A.-A. H. Nasser, A. M. Al-Masari, A. A. Al-Sobhi, A. O. Nadhra, A. H. Matari, J. A. Wilson, and P. D. Gingerich, 2010 New Oligocene Primate from Saudi Arabia and the Divergence of Apes and Old World Monkeys. *Nature* 466:360–364.
- Zapfe, H., 1960 Die Primatenfunde aus der miozänen Spaltenfüllung von Neudorf an der March (Devínská Nová Ves), Tschechoslowakei. *Schweizerische Palaeontologische Abhandlungen* 78:1–293.
- Zhang, Z., and T. Harrison, 2008 A New Middle Miocene Pliopithecoid from Inner Mongolia, China. *Journal of Human Evolution* 54:444–447.