

# The zoogeographic and phylogenetic relationships of early catarrhine primates in Asia

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**Abstract** Catarrhines originated in Afro-Arabia during the Paleogene, and were restricted to this zoogeographic province until the early Miocene. During this period of isolation, several major clades of catarrhines originated. The pliopithecoids were the first catarrhines to migrate out of Africa at ~18–20 Ma, while contemporary proconsulids and dendropithecids may have been restricted to Afro-Arabia. Hominoids and Old World monkeys originated in Africa prior to 20 Ma, but neither clade became an important component of the catarrhine fauna until the middle to late Miocene. At ~15–17 Ma, hominoids expanded into Eurasia, while cercopithecids arrived somewhat later, during the late Miocene. The earliest catarrhines in Eurasia, *Dionysopithecus* and *Platodontopithecus* from Sihong in China (~17–18 Ma), represent the primitive sister group of all other pliopithecoids. From this ancestral stock in Asia, the more specialized pliopithecines extended their range westwards into Europe by ~16–17 Ma, where a pliopithecine-like common ancestor gave rise to the crouzeliines. The only known crouzeliine from Asia, *Laccopithecus*, from the late Miocene of China, points to a late arrival of this clade in the region. Small catarrhines from the middle Miocene of Pakistan (~16–17 Ma), and new material from China, may possibly have closer ties with dendropithecids, proconsulids, or hylobatids.

**Key words:** catarrhines, Miocene, Africa, China, phylogeny

## Introduction

Paleontological investigations over the past century have demonstrated conclusively that the major clades of catarrhines originated and diversified in Afro-Arabia. However, since their origins in the Paleogene, catarrhines have repeatedly expanded their geographic range into Eurasia. The collision of the Afro-Arabian plate with Eurasia during the early Orlanian (MN 3–4, ~17–20 Ma) established a land bridge between Arabia and Southwest Asia that permitted a major influx of endemic African mammals into Eurasia, including the first catarrhines (Thomas, 1985; Andrews et al., 1996; Rögl and Daxner-Höck, 1996; Rögl, 1999; van der Made, 1999). Subsequent immigrations into Eurasia brought the first hominoids (at ~16–17 Ma), colobines (possibly as early as ~10–11 Ma, but certainly by ~9 Ma), cercopithecines (~5–6 Ma), hominins (~1.9 Ma), and modern humans (~40 ka). Catarrhine evolution has been very much an 'Out of Africa' story. Nevertheless, the evolution and diversification of Eurasian catarrhines has been a significant chapter in this story, and their fossil record during the later part of the Miocene is much better known than that from Africa. Consequently, reconstructing the phylogenetic and zoogeographic relationships of the Eurasian radiation is of crucial

importance for understanding catarrhine evolution in general during this critical time period. Moreover, the dramatic increase in both the quantity and quality of fossil finds from the Miocene of Asia over the past decade has been especially important in improving our understanding of early catarrhine diversity, distribution, and evolutionary history. This paper reviews the phylogenetic and zoogeographic relationships of early fossil catarrhines from Asia and their origins in Africa.

## African Origins

Catarrhines originated in Afro-Arabia during the Paleogene, and were restricted to this zoogeographic province until the early Miocene (Bernor, 1983; Andrews et al., 1996; Harrison and Gu, 1999). During this period of isolation, several major clades of catarrhines originated, including the Propliopithecidae, Pliopithecidae, Proconsulidae, Dendropithecidae, Cercopithecidae, and Hominoidea (see Table 1). The earliest definitive members of the Catarrhini, the Propliopithecidae, are from the early Oligocene of Egypt, Oman, and Angola (Kay et al., 1981; Pickford, 1986; Thomas et al., 1991; Rasmussen, 2002). Formerly, other late Eocene and early Oligocene anthropoids from Egypt, Algeria, and Oman, including the parapithecids (i.e. *Parapithecus*, *Apidium*, *Simonsius*, *Qatrania*, *Serapia*, *Arsinoea*, and *Biretia*), oligopithecids (i.e. *Oligopithecus* and *Catopithecus*), and several genera of uncertain taxonomic affinity (i.e. *Algeripithecus*, *Tabelia*, and *Proteopithecus*), have been

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Table 1. Classification of the Catarrhini

Order: Primates Linnaeus, 1758
Suborder: Anthropoidea Mivart, 1864
Infraorder: Catarrhini E. Geoffroy Saint Hilaire, 1812
Superfamily: Propliopithecoidea Straus, 1961
Family: Propliopithecidae Straus, 1961
Superfamily: Pliopithecoidea Zapfe, 1961
Family: Pliopithecidae Zapfe, 1961
Subfamily: Pliopithecinae Zapfe, 1961
Subfamily: Crouzeliinae Ginsburg and Mein, 1980
Family: Dionysopithecidae Harrison and Gu, 1999
Superfamily: Dendropithecoidea Harrison, 2002
Family: Dendropithecidae Harrison, 2002
Superfamily: Proconsuloidea Leakey, 1963
Family: Proconsulidae Leakey, 1963
Subfamily: Proconsulinae Leakey, 1963
Subfamily: Afropithecinae Andrews, 1992
Subfamily: Nyanzapithecinae Harrison, 2002
Superfamily: Cercopithecoidea Gray, 1821
Family: Cercopithecidae Gray, 1821
Subfamily: Cercopithecinae Gray, 1821
Subfamily: Colobinae Jerdon, 1867
Superfamily: Hominoidea Gray, 1825
Family: Hylobatidae Gray, 1870
Family: Hominidae Gray, 1825
Subfamily: Ponginae Elliot, 1913
Subfamily: Homininae Gray, 1825

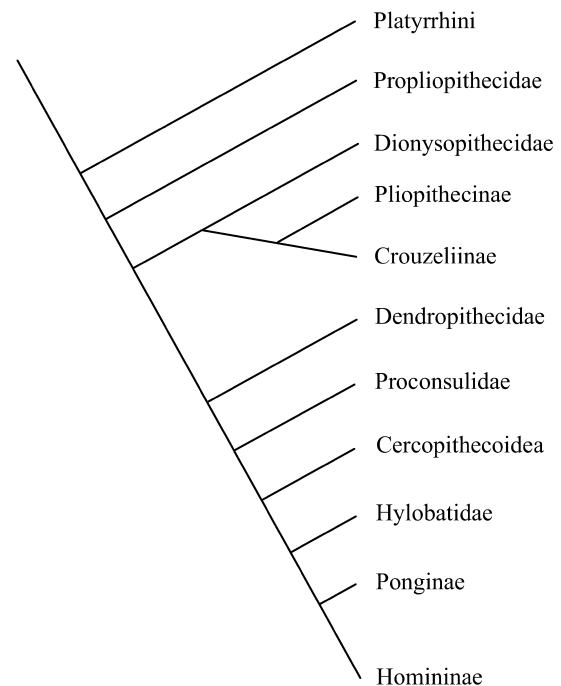


Figure 1. Cladogram showing the inferred relationships between the major groups of catarrhines.

inferred to be early catarrhines (Szalay and Delson, 1979; Fleagle, 1986, 1999; Godinot, 1994; Rasmussen, 2002), but current evidence suggests that these taxa are most probably stem anthropoids (or even stem haplorhines) that diverged prior to the last common ancestor of platyrrhines and catarrhines (Fleagle and Kay, 1987; Harrison, 1987, 1996; Kay et al., 1997; Ross et al., 1998; Delson, 2000; Kay, 2000; Beard, 2002).

The propliopithecids are best known from early Oligocene (~33–34 Ma) sediments in the Fayum of Egypt, although more fragmentary material has also been recovered from Taqah in Oman (Thomas et al., 1991) and Malembe in Angola (Pickford, 1986). The family includes five species, which are generally included in two or three genera (i.e. *Propliopithecus*, *Moeripithecus*, and *Aegyptopithecus*) (Simons, 1972, 1992, 1995; Kay et al., 1981; Fleagle and Kay, 1983; Fleagle, 1986; Simons et al., 1987; Simons and Rasmussen, 1991; Thomas et al., 1991; Rasmussen, 2002). However, the species are certainly closely related, and the morphological distinctions between them can best be accommodated within a single genus, *Propliopithecus* (Szalay and Delson, 1979; Andrews, 1980, 1985; Harrison, 1987). The absence of P2, development of a specialized C/P3 honing complex, morphology of the molars, and reduced postglenoid foramen are derived anthropoid features that link *Propliopithecus* with later catarrhines (Harrison, 1987). However, they retain several primitive features (i.e. an annular ectotympanic, and an entepicondylar foramen and dorsal epitrochlear fossa in the distal humerus) not seen in extant catarrhines, which establish them as stem catarrhines (Harrison, 1987) (see Figure 1).

Unfortunately, catarrhine evolution in Africa is poorly documented for much of the Oligocene, with a 10 million

year gap between the fossil record from the Fayum and that from East Africa. It is during this temporal hiatus that the pliopithecoids diverged, presumably in Africa, although their occurrence outside of Eurasia is entirely unknown. The pliopithecoids are a group of primitive catarrhines with a wide geographical distribution throughout much of Eurasia during the Miocene (Ginsburg and Mein, 1980; Ginsburg, 1986; Harrison, 1987; Andrews et al., 1996; Harrison and Gu, 1999; Begun, 2002; Harrison et al., 2002a). Following Harrison and Gu (1999) and Begun (2002), the superfamily is divided here into two families, the Dionysopithecidae and Pliopithecidae, of which the latter is divided into two subfamilies, the Pliopithecinae and Crouzeliinae (see Table 2). Although pliopithecoids are more derived than the propliopithecids in having a partially formed tubular ectotympanic, they are more primitive than all other catarrhines in retaining an entepicondylar foramen in the distal humerus (see Figure 1). The appearance of pliopithecoids in Eurasia during the early Miocene at ~17–18 Ma establishes them as the earliest catarrhines to migrate out of Africa.

Proconsulids and dendropithecids are stem catarrhines of modern aspect from the late Oligocene to mid-Miocene of Africa (Table 3, Figure 1) (see Harrison, 2002 and references therein). They are characterized by the following shared derived features linking them with later catarrhines: fully formed tubular ectotympanic (unknown in dendropithecids) and loss of the entepicondylar foramen in the distal humerus (although dendropithecids primitively retain a dorsal epitrochlear fossa which has generally been lost in proconsulids and crown catarrhines). Proconsulids and dendropithecids are best known from localities in East Africa, but additional finds from Saudi Arabia, Namibia, and South Africa show

Table 2. Classification of the Pliopithecoidea (after Harrison and Gu, 1999)

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Superfamily: Pliopithecoidea Zapfe, 1961  
 Family: Dionysopithecidae Harrison and Gu, 1999  
*Dionysopithecus* Li, 1978  
*D. shuangouensis* Li, 1978  
*D. orientalis* Suteethorn et al., 1990  
*Platodontopithecus* Gu and Lin, 1983  
*Plat. jianghuaiensis* Gu and Lin, 1983  
 Family: Pliopithecidae Zapfe, 1961  
 Subfamily: Pliopithecinae Zapfe, 1961  
*Pliopithecus* Gervais, 1849  
*Plio. antiquus* (de Blainville, 1839)  
*Plio. platyodon* Biedermann, 1863  
*Plio. vindobonensis* Zapfe and Hürzeler, 1957  
*Plio. zhanxiangi* Harrison et al., 1991  
 Subfamily: Crouzeliinae Ginsburg and Mein, 1980  
*Plesiopliopithecus* Zapfe, 1961a  
*Plesio. lockeri* Zapfe, 1961a  
*Plesio. auscitanensis* (Ginsburg, 1975)  
*Plesio. rhodanica* (Ginsburg and Mein, 1980)  
*Plesio. priensis* (Welcomme et al., 1991)  
*Anapithecus* Kretzoi, 1975  
*A. hernyaki* Kretzoi, 1975  
*Laccopithecus* Wu and Pan, 1984  
*L. robustus* Wu and Pan, 1984  
*Egarapithecus* Moyà-Solà et al., 2001  
*E. narcisoi* Moyà-Solà et al., 2001

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Table 3. Taxonomy of stem catarrhine primates from that late Oligocene to middle Miocene of Afro-Arabia (after Harrison, 2002)

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Superfamily: Proconsuloidea Leakey, 1963  
 Family: Proconsulidae Leakey, 1963  
 Subfamily: Proconsulinae Leakey, 1963  
*Proconsul* Hopwood, 1933  
 Subfamily: Afropithecinae Andrews, 1992  
*Afropithecus* Leakey and Leakey, 1986a  
*Heliopithecus* Andrews and Martin, 1987  
 Subfamily: Nyanzapithecinae Harrison, 2002  
*Mabokopithecus* von Koenigswald, 1969  
*Rangwapithecus* Andrews, 1974  
*Nyanzapithecus* Harrison, 1986  
*Turkanapithecus* Leakey and Leakey, 1986b  
 Superfamily: Dendropithecoidea Harrison, 2002  
 Family: Dendropithecidae Harrison, 2002  
*Dendropithecus* Andrews and Simons, 1977  
*Micropithecus* Fleagle and Simons, 1978  
*Simiolus* Leakey and Leakey, 1987  
 Superfamily: *incertae sedis*  
 Family: *incertae sedis*  
*Limnopithecus* Hopwood, 1933  
*Kalepithecus* Harrison, 1988  
*Otavipithecus* Conroy et al., 1992  
*Kamoyapithecus* Leakey et al., 1995  
*Kogolepithecus* Pickford et al., 2003

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that they were widely distributed throughout the Afro-Arabian province during the early and middle Miocene (Andrews and Martin, 1987; Conroy et al., 1992; Senut et al., 1997). Even though they are the most taxonomically and adaptively diverse groups of Miocene catarrhines, no definitive proconsulids or dendropithecids have been recovered from Eurasia (although, as discussed below, some Eurasian

taxa have been phyletically linked with them in the past), and it is possible that they were entirely restricted to Afro-Arabia. It may well be that their specialized morphology and relatively narrow niches limited their ability to extend their geographic range into Eurasia.

This hypothesis is supported by evidence of marked zoogeographic provinciality in East Africa during the early Miocene. For example, early Miocene sites in East Africa dated at 16.6–18.5 Ma are characterized by endemic catarrhine faunas in northern and western Kenya respectively. At Rusinga and Mfangano Islands in western Kenya, the fauna includes *Proconsul heseloni*, *P. nyanzae*, *Nyanzapithecus vancoveringorum*, *Dendropithecus macinnesi*, and *Limnopithecus legetet*, while contemporary sites in northern Kenya, such as Kalodirr, Buluk, and Locherangan, have *Afropithecus turkanensis*, *Turkanapithecus kalakolensis*, and *Simiolus enjiessi* (Andrews, 1978; Leakey and Leakey, 1986a, b, 1987; Harrison, 1988, 2002; Leakey et al., 1988a, b; Anyonge, 1991). Such small-scale provinciality implies that early Miocene East African primate communities were tied to relatively narrow habitats, and that their ability to disperse may have been quite limited. Another factor that could have impeded the immigration of dendropithecids and proconsulids into Eurasia during the early Miocene relates to differences in carnivore community structure between Eurasia and Africa. African faunas at this time were dominated by creodonts, while large felids, which entered Africa from Eurasia at the start of the Miocene, comprise a relatively minor component of the overall carnivore fauna (Savage, 1978; Schmidt-Kittler, 1987; Morales et al., 1998; Ginsburg, 1999). By contrast, Eurasia was dominated by fissioned carnivores, including large felids that were capable of preying on arboreally adapted catarrhines. This diverse guild of predators in Eurasia might have proved too skilled for dendropithecids and proconsulids, which had coevolved with the slower, less encephalized, and more terrestrially adapted creodonts. Harrison and Sanders (2004) have speculated that an important factor in the decline of dendropithecids and proconsulids at the end of the early Miocene, and subsequent success and diversification of cercopithecoids and hominoids, may be associated with a faunal turnover of the carnivores in Africa, in which creodonts were replaced by large felids and hyaenids (Morales et al., 1998).

Crown catarrhines belonging to Hominoidea and Cercopithecoidea appear to have originated in Africa prior to 20 Ma (see Figure 1), but neither clade becomes an important component of the catarrhine fauna until the middle Miocene (~11–16 Ma), and even then their taxonomic diversity remains relatively low. The earliest purported hominoid, *Morotopithecus bishopi*, has been recovered from the early Miocene site of Moroto in eastern Uganda. Recently published  $^{40}\text{Ar}/^{39}\text{Ar}$  dates indicate an age of 20.6 Ma (Gebo et al., 1997), although Pickford (1998) and Pickford et al. (1999, 2003) claim that Moroto may be younger, possibly late early Miocene (~17.0–17.5 Ma) or early middle Miocene, based on faunal correlations. *Morotopithecus* is recognized as a stem hominoid based on the presence of synapomorphies of the postcranium (particularly the lumbar vertebrae) that link it with extant hominoids (Ward, 1993; Sanders and Bodenbender, 1994; Gebo et al., 1997;

MacLatchy et al., 2000). However, Harrison (2002) has raised the possibility that *Morotopithecus* might be a large orthograde afropithecine proconsulid that developed its own unique adaptations in the vertebral column in parallel with extant Hominoidea (see also Pickford, 2002). The next oldest indisputable hominoids in Africa, *Equatorius* and *Kenyanthropus*, dated at ~14–16 Ma, are considerably younger than *Morotopithecus* (McCrossin and Benefit, 1994; Ward et al., 1999; Ward and Duren, 2002). During MN 5 and basal MN 6 (~14–17 Ma), *Griphopithecus*, a primitive hominoid similar in dental morphology and probably closely related to *Equatorius*, expanded its range into Eurasia, soon after the arrival of pliopithecids (Andrews et al., 1996; Heizmann and Begun, 2001).

The earliest known cercopithecoidea is represented by a single isolated upper molar from Napak in eastern Uganda, dated at ~19 Ma (Pilbeam and Walker, 1968; Pickford et al., 1986). Stem cercopithecoidea belonging to *Victoriapithecus* and *Prohylobates* occur at late early Miocene through late Miocene localities in Kenya, Libya, and Egypt, ranging in age from ~12.5–17.5 Ma (Benefit and McCrossin, 2002; Hill et al., 2002). Recently, Pickford et al. (2003) have described several associated teeth of *Prohylobates macinnesi* from Moroto, which may date to as old as ~20.6 Ma (Gebo et al., 1997), but faunal correlations suggest a late early Miocene age of 17.0–17.5 Ma (Pickford et al., 2003).

The earliest indisputable crown cercopithecoidea, referable to either the Colobinae or Cercopithecinae, appear in Africa during the early late Miocene. *Microcolobus tugenensis*, the earliest colobine in Africa, is known from Ngeringerowa and Nakali in Kenya dated to ~9 Ma (Benefit and Pickford, 1986; Hill, 1999), almost contemporary with the earliest arrival of the clade in Eurasia (correlated with MN 11, dated at ~8.0–8.7 Ma; although an isolated upper premolar from Wissberg, Germany may indicate an earlier first appearance of MN 9, 9.7–11.1 Ma, but the stratigraphic association of this specimen is insecure) (Andrews et al., 1996). Similarly, the earliest known cercopithecoidea is *Parapapio lothagamensis*, a stem papionin from the Upper and Lower Nawata Formation at Lothagam in northern Kenya, dated at ~5.0–7.4 Ma (Leakey et al., 2003). A collection of isolated teeth of a primitive papionin from Marceau, Algeria, possibly referable to *Macaca*, might be slightly older than the material from Lothagam (Arambourg, 1959; Delson, 1975; Szalay and Delson, 1979). In Europe, the only cercopithecoidea from the late Miocene is a mandibular fragment of *Macaca* sp. from Casablanca M (correlated with late MN 13, ~5–6 Ma) (Moyà-Solà et al., 1992; Andrews et al., 1996).

### Early Catarrhines in Asia: Zoogeographic and Phylogenetic Relationships

The earliest known catarrhines in Eurasia are recorded from the Xiacaowan Formation, Sihong, China (from several localities correlated with MN 4, ~17–18 Ma) (Harrison and Gu, 1999), where two species are represented—*Dionysopithecus shuangouensis* and *Platodontopithecus jianghuaiensis* (Li, 1978; Gu and Lin, 1983; Harrison and Gu, 1999)(see Table 4). In the past, *Dionysopithecus* has been inferred to be related to *Micropithecus*, a dendropithe-

Table 4. Timing of catarrhine immigration events from Africa into Eurasia

	Earliest representative in Afro-Arabia	Earliest representative in Eurasia
Propliopithecidae	early Oligocene, ~33–34 Ma	unknown
Pliopithecidae	unknown	early Miocene, ~17–18 Ma
Dendropithecidae	early Miocene, ~20 Ma	unknown?
Proconsulidae	early Miocene, 22.5 Ma	unknown?
Cercopithecoidea	early Miocene, ~19 Ma	late Miocene, ~10–11 Ma?
Hominoidea	early Miocene, 20.6 Ma?	middle Miocene, ~16.5–17.0 Ma

Sources: Andrews et al. (1996); Harrison and Gu (1999); Gebo et al. (1997); Heizmann and Begun (2001); Harrison (1988, 2002).

cid from the early Miocene of East Africa (Harrison, 1982, 1988; Fleagle, 1984, 1986; Bernor et al., 1988; Harrison et al., 1991). However, following Harrison and Gu (1999), the two species from Sihong are now considered to be closely related stem pliopithecids, included together in their own family, the Dionysopithecidae. An isolated lower molar from Ban San Klang in northern Thailand (~15–17 Ma) was originally described as *Dendropithecus orientalis* (Suteethorn et al., 1990), but it can be readily distinguished morphologically from *Dendropithecus* and other dendropithecoidea (Harrison and Gu, 1999). The specimen is identical in size and quite close in morphology to *Dionysopithecus shuangouensis* from southern China. The relatively minor differences are sufficient, perhaps, to recognize a distinct species, but the Thai specimen should certainly be included in the same genus. Consequently, the Ban San Klang specimen is provisionally recognized as *Dionysopithecus orientalis* (see Harrison and Gu, 1999).

The occurrence of stem pliopithecoidea in China and Thailand at this early date suggests that the European representatives of the clade (which make their first appearance during early MN 5 at ~16–17 Ma) may have been derived from an Asian source. Dionysopithecoidea probably entered tropical and subtropical Asia from Africa during MN 3 (~20–18 Ma), and diversified locally (Harrison and Gu, 1999). Although *Dionysopithecus* and *Platodontopithecus* are too specialized in their molar morphology to be the actual ancestors of later pliopithecoidea (Harrison and Gu, 1999), they are generalized enough to approximate closely to the ancestral morphotype of the clade. From these stem pliopithecoidea, a more specialized clade, the Pliopithecidae, originated, presumably in East Asia, and then extended its range westwards into Europe by ~16–17 Ma, at a time when warmer climatic conditions prevailed. The relatively early occurrence of pliopithecoidea in China, represented by *Pliopithecus zhanxiangi* from Tongxin and *Pliopithecus* sp. from the Halamagai Formation (both correlated with MN 6, ~15 Ma), tends to support this scenario (Qiu and Guan, 1986; Harrison et al., 1991; Ye et al., 2000). The more specialized crouzeiines appear, however, to have originated in Europe from a pliopithecoidea-like ancestor, where they are first recorded at

localities corresponding with MN 6 (~13.5–15.0 Ma). The only known crouzeliine from Asia, *Laccopithecus robustus* from the late Miocene (~7–8 Ma) of Shihuiba, Lufeng, China (Wu and Pan, 1984, 1985; Pan, 1988, 1998; Pan et al., 1989; Harrison et al., 1991; Harrison and Gu, 1999), points to a relatively late arrival of this clade into the region. Nevertheless, the extinction of pliopithecids in Europe by the close of the Vallesian (at ~8.7 Ma) would indicate that late surviving crouzeliines reached East Asia before 9 Ma, possible at the same time that hominoids arrived in the region (the earliest occurrence of which is recorded at Xiaolongtan, China, best correlated with MN 9, ~10–11 Ma; Qiu and Qiu, 1995; Pickford and Liu, 2001; Harrison et al., 2002b).

A number of early catarrhine finds from Asia are too poorly preserved to determine their phylogenetic relationships. Schlosser (1924) described an  $M^3$  from Ertemte, Nei Mongol, northern China (correlated with MN 13, ~5–6 Ma) as *Pliopithecus posthumus*, but this specimen is much too heavily worn to determine its taxonomic affinities, and several authors have even questioned its primate status (Hürzeler, 1954; Simons, 1972; Simons and Fleagle, 1973; Fleagle, 1984; Harrison et al., 1991; Harrison and Gu, 1999). Similarly, an  $M^3$  from the late Miocene locality of Haritalyangan in northern India, has been referred to *Pliopithecus krishnaii* or *Krishnapithecus krishnaii* (Chopra and Kaul, 1979; Ginsburg and Mein, 1980), but, because it is heavily worn, it is impossible to assess its taxonomic affinities (Harrison et al., 1991; Harrison and Gu, 1999). An edentulous mandibular symphysis of an anthropoid primate from the early Miocene locality of Hsi-shui, Taben Buluk in northern China, and a molar fragment from the neighboring late Oligocene locality of Yindirte (Bohlin, 1946), are too incomplete to establish their precise relationships (Harrison et al., 1991; Harrison and Gu, 1999).

Several isolated teeth of a small catarrhine primate from the early Middle Miocene Kamlial and Manchar Formations of Pakistan (~16–17 Ma) (Raza et al., 1984; Barry et al., 1986; Bernor et al., 1988; Barry and Flynn, 1989) have previously been considered to be closely related to *Dionysopithecus* and to East African dendropithecids (Fleagle 1984; Barry et al., 1986; Bernor et al., 1988). Unfortunately, the limited material available does not provide adequate evidence to firmly establish their relationships, but Harrison and Gu (1999) have indicated that the Pakistani specimens are unlikely to be closely related to *Dionysopithecus* or other pliopithecoids. By contrast, they appear to share a few derived features of the upper and lower molars that might link them with the proconsulids or dendropithecids (Harrison and Gu, 1999), but more complete specimens will be needed to confirm this suggestion. Until further specimens are recovered from South Asia or elsewhere, it is probably best to leave the Kamlial and Manchar specimens taxonomically unassigned. Nevertheless, several important collections of small catarrhine primates from China are likely to be pertinent to resolving this problem in the near future when the material has been fully described and analyzed. These include a remarkable collection of small fossil catarrhines collected by Jin Changzhu at the middle Miocene locality of Fanchang in Anhui Province, and an equally important collection, currently being described by Pan Yuerong, from late

Miocene localities in the Yuanmou basin, Yunnan Province (Y. Pan, personal communication; C. Jin, personal communication). A preliminary assessment suggests that the material from Yuanmou and Fanchang represent two previously unknown genera. It would seem that there is no evidence to link them to pliopithecoids, but further detailed comparative analyses are needed to determine whether they are more closely related to dendropithecids, proconsulids or hylobatids.

Finally, mention should be made of the mandibular specimen from Wudu in Gansu Province, China described as *Dryopithecus wuduensis* (Xue and Delson, 1989). Unfortunately, the teeth are poorly preserved and worn, making any assessment of its taxonomic and phylogenetic relationships exceedingly difficult. However, major differences in the mandible and dentition (in addition to its overall smaller size) serve to distinguish the Wudu specimen from European representatives of *Dryopithecus*. Distinguishing features include: (1) mandibular corpus relatively more slender, especially below the molars; (2) anterior margin of the ramus more anteriorly placed, such that it would have overlapped with  $M_3$  to a greater extent in lateral view; (3) anterior margin of the ramus more sharply defined at its inferolateral origin; (4) superior transverse torus more weakly developed; (5) corpus exhibits a more marked posterior shallowing; (6) symphyseal region relatively narrower, with a more strongly convex external surface; (7) roots of the incisors suggest that they were relatively narrower; (8) canine root slender and more bilaterally compressed; (9)  $P_3$  relatively short mesiodistally, with a steep mesiobuccal face, and very slight extension of the enamel margin onto the base of the mesial root; (9)  $P_4$  more elongated, with a relatively long talonid; (10) molars probably with relatively small hypoconulids; and (11)  $M_3$  much longer than  $M_2$ , with a long, distally tapering heel. The evidence suggests that the Wudu mandible does not belong to *Dryopithecus* (or to any other genus of Eurasian hominid for that matter), and in my opinion, if the specimen were better preserved, there would probably be adequate grounds to recognize a distinct genus. Intriguingly, some of the distinctive characteristics of the Wudu specimen, such as the relatively narrow incisors, the slender and bilaterally compressed canine root, the short  $P_3$  with a steep mesiobuccal face, the elongated  $P_4$ , and the relatively long and distally tapering  $M_3$ , are features more typically found in pliopithecoids. Until we have more material, the best that we can conclude about the specimen from Wudu is that it almost certainly belongs to a previously unnamed genus of non-cercopithecoid catarrhine.

In conclusion, important discoveries of fossil primates have been made in China and Southeast Asia in the past decade that have added significantly to our appreciation of the zoogeographic and phylogenetic relationships of early catarrhine primates. It is clear from these findings, however, that we have sampled only a small fraction of the taxonomic diversity that occurred in this region during the Miocene and Pliocene. Without a better representation of these taxa in time and space it will prove exceedingly difficult to realistically reconstruct the zoogeography of Eurasian catarrhine primates. Nevertheless, I am confident that the rapidly expanding pace of exploration and paleontological research

by my colleagues in Asia will yield many exciting new finds in the near future, and hopefully will prove that we have made a good start on building a sound foundation for understanding the evolutionary history of early catarrhine primates.

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