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The Primate Fossil Record

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CAMBRIDGE
UNIVERSITY PRESS
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DAVID R. BEGUN

Introduction

A primitive catarrhine group with no known descendants, pliopithecooids were a diverse and fascinating group of primates ranging from southwestern France to China, from about 17 to 7 million years ago. Equally impressive is the range of morphological diversity within the Pliopithecoidea. Pliopithecooids were highly diverse and successful, varying in size from approximately 3 to 20 kg, and spanning dietary adaptations from generalized frugivory to highly specialized folivory. Smaller taxa were probably more monkey-like in their positional behavior, moving along the tops of branches, while the larger forms appear to have been more suspensory. The fossil record of the Pliopithecoidea displays widespread homoplasy, or parallel evolution, and adaptive radiation. Pliopithecooids resemble South American monkeys in diversity and adaptation and, indeed, are an example of the "Splendid Isolation" phenomenon typified by the faunas of Australia and South America (Simpson, 1980). In contrast, the evolutionary relations remain unclear, both within the Pliopithecoidea and between it and other anthropoids.

History of discovery and debate

Pliopithecooids were among the first fossil primates to be discovered and described. The famous femur from Eppelsheim and the famous lower jaw from Sansan set the stage for both the catarrhine fossil record and the sciences of paleoprimatology and paleoanthropology. However, discovery of fossil catarrhines more closely resembling great apes and primatology and paleoanthropology. Howevet, discovery of the Pliopithecoidea displays widespread homoplasy, or parallel evolution, and adaptive radiation. Pliopithecooids resemble South American monkeys in diversity and adaptation and, indeed, are an example of the "Splendid Isolation" phenomenon typified by the faunas of Australia and South America (Simpson, 1980). In contrast, the evolutionary relations remain unclear, both within the Pliopithecoidea and between it and other anthropoids.

History of discovery and debate

Pliopithecooids were among the first fossil primates to be discovered and described. The famous femur from Eppelsheim and the famous lower jaw from Sansan set the stage for both the catarrhine fossil record and the sciences of paleoprimatology and paleoanthropology. However, discovery of fossil catarrhines more closely resembling great apes and humans shifted attention away from the Pliopithecoidea. After discovery and recognition of Pliopithecus antiquus only a few specimens from several localities, and a large collection of mostly isolated teeth from one (Göriach, Austria), were discovered in the next 100 years. Overall they attracted relatively little attention from the scientific community.

Paul Gervais (1849a) nominated Pliopithecus from discoveries first announced by Édouard Amand Isidore Hippolyte Lartet in 1837 and referred by Henri-Marie Ducrotay de Blainville (1839, 1840) to Pithecus antiquus. Several years later, a new and slightly larger species of Pliopithecus, P. platyodon, was described from collections in Switzerland by Biedermann (1863). A much larger collection of jaws and isolated teeth, first described by Hofmann (1863) from Göriach, was attributed to Pliopithecus antiquus, but eventually moved into P. platyodon (Hürzeler, 1954a; Harrison et al., 1991). More specimens were recovered from Sansan and another locality in France, La Grive St. Alban (Déperet, 1887). Isolated teeth were found in various localities in the Loire valley of central France (Gervais, 1867; Lecointre, 1912), in Germany near Augsburg and in Bavaria (Roger, 1898; Schlosser, 1900) and in Poland (Wegner, 1913). These highly fragmentary partial dentitions or isolated teeth expanded the known geographic range of Pliopithecus, but offered little insight into the nature of Pliopithecus. Researchers assumed with little doubt, based on the simple and primitive morphology of the teeth and their small size, that this taxon was directly ancestral to hyllobatids.

During the middle of the twentieth century the pace of discovery of, and scientific interest in, pliopithecoid fossils, continued to lag behind that of the hominoids. New isolated teeth from Switzerland (Stehlin, 1914) and an older specimen from Děvinská Nová Ves, known since the end of the previous century but only described in Glässner (1931), preceded the exceptional review monograph by Johannes Hürzeler (1954a). He referred to recent discoveries to be described elsewhere, including the remains of several skeletons of a pliopithecoid from the Děvinská Nová Ves fissures (Zapfě, 1952; Zapfě & Hürzeler, 1957). Eventual publication of these specimens would jump-start research and interest in this group.

The spectacular discoveries made by Helmuth Zapfě in the fissures of Děvinská Nová Ves culminated in what many consider the best monograph ever written on a fossil primate – Zapfě’s monumental treatise on Pliopithecus (Epipliopithecus) vindobonensis (Zapfě, 1960). These specimens include the first postcranial fossils described for a pliopithecoid, although Lartet (1837b) noted some in his announcement. Major portions of three individuals are preserved at Děvinská Nová Ves, including a well-preserved skull, associated limb bones, vertebrae, scapulae and an ilium, which indicated extreme primitiveness. While he stressed resemblances to gibbons, Zapfě (1960) noted numerous similarities to platyrhines, and even suggested that had they not been found in association, the humerus and the ear region of the temporal bone would scarcely have been recognized as anthropoid (Zapfě, 1958).

Along with more isolated specimens found at this time, a new type of pliopithecoid was discovered in 1959 and named Plesiopliopithecus (Zapfě, 1961; Bergounioux & Crouzel, 1965), which several authors have recognized as belonging to a distinct subfamily, the Crouzelinae (Ginsburg & Mein, 1980; Andrews et al., 1996). In fact, most of the more
recently discovered pliopithecoids have been placed in the Crouzeliniæ by these authors, though the justification for this is by no means clear (see below). This includes large samples of jaws, teeth and postcrania from Rudabánya, Hungary and Lufeng, Yunnan Province, China (Kretzoi, 1975; Pan, 1988). These latter specimens are also among the last surviving members of the Pliopithecidea, and dentally the most peculiar. Interestingly, these most recently discovered specimens may clear up one of the oldest controversies of paleoanthropology, the affinities of the famous femur from Eppelsheim (see below). Also discovered and described in this most recent phase of research are the oldest and most primitive pliopithecoids, Dionysopithecus and Platodontopithecus, from the early Miocene of China (Li, 1978; Gu & Lin, 1983), as well as a more advanced form, Pliopithecus zhanxiangi (Harrison et al., 1991).

Beginning with Cuvier and his apparent dismissal of the Eppelsheim femur, through the great breakthrough by Larjet, and up to the present, pliopithecoids have been in and out of the limelight. Hürzeler and Zapfe did much to revive interest in this group, as did the discovery of “gibbon-like” fossils from east Africa (Le Gros Clark & Thomas, 1951; Ferembach, 1958; Fleagle, 1975; Andrews & Simons, 1977). However, in the final analysis, pliopithecoids tell us more about the dynamics of macroevolution than about the evolutionary history of gibbons, which remains shrouded in mystery.

**Taxonomy**

**Systematic framework**

**The Pliopithecoida**

Because they are extinct, distant relatives of living catarrhines, a brief description of their defining features, assuming there are some, is appropriate before embarking on their systematics. Beyond the fact that they have only two premolars per quadrant in their adult dentitions, few characters define them as catarrhines and none offers convincing evidence that they are more closely related to modern catarrhines than are the earliest members of this group, the propliopithecoids of the Eocene and Oligocene of Egypt. In their recent review of the pliopithecoids, Harrison & Gu (1999) cite only three characters linking pliopithecoids to Old World monkeys and apes, and these are relatively unimpressive. They suggest that upper molars are narrower than those of Propliopithecus or Aegyptopithecus, lower molars are broader than Propliopithecus or Aegyptopithecus, and that the tubular ectotympanic is partially ossified. However, neither of the molar features is consistent in all pliopithecoids, and is also variable in propliopithecoids and platyrrhines. Worse still, the ectotympanic character is a presumed intermediate morphology and not an actual synapomorphy.

Most authors have assumed a unilinear direction in the evolutionary transformation (morphoclone) of the catarrhine ectotympanic (e.g., Szalay, 1975a; Szalay & Delson, 1979; Andrews et al., 1996). The scenario is as follows: the ectotympanic resembles a short bony tube fused to the outer surface of the auditory bulla in New World monkeys; it becomes an elongated tube, forming the canal of the outer ear (external auditory meatus). This occurs, it is assumed, through the intermediate step of a partially ossified tube, as seen in Epipliopithecus vindobonensis and superficially resembling some very young modern catarrhines. Direct evidence for this is lacking, however, and it is just as probable that the ectotympanic morphology of Epipliopithecus vindobonensis is either unique to that species or to the Pliopithecidea, and independent of the evolution of an ectotympanic tube in Old World monkeys and apes, or primitive for Anthropoidea. In fact, among anthropoids the external auditory meatus in Epipliopithecus resembles those of Tremacebus harringtoni, a primitive platyrrhine from the late Oligocene of Argentina (Hershkovitz, 1974), and Aegyptopithecus, from the Oligocene of Egypt (Szalay & Delson, 1979; Fleagle & Kay, 1983). These forms also resemble much more primitive primates or primitive relatives such as Ignacius and Shoshonius (Kay et al., 1992; Beard & MacPhee, 1994). While the inferior or ventral portions of the ectotympanic tube may be slightly more ossified in Epipliopithecus, convergence in the evolution of ectotympanics in fossil and living primatians, pleiadiforms and tarsiids is well noted (e.g., Szalay, 1975a; MacPhee, 1977, 1981; MacPhee & Cartmill, 1986; Kay et al., 1992; Beard & MacPhee, 1994) and there is no reason to think that anthropoids were immune to such phenomena.

In many ways pliopithecoid dental morphology is more similar to platyrrhines than to propliopithecoids. Pliopithecoids tend to have narrow lower incisors, occasionally waisted, or constricted at the junction of the crown and the root (the cervix), and this morphology is also found in a number of platyrrhines. In addition, one of the few defining traits that seems to be consistently present in pliopithecoids is a P3 with a tall crown, roughly triangular in outline, with a comparatively short, vertically oriented mesiobuccal face. The mesiobuccal face of the anterior premolar is not expanded to accommodate the upper canine, which in catarrhines is honed or sharpened by this structure (the sectorial premolar) (Andrews, 1978a; Harrison & Gu, 1999).

In most pliopithecoids the protoconid and metaconid are not transversely aligned, but slightly offset such that the protoconid is mesial to the metaconid. In some cases the fovea mesial to these cusps is also expanded and bears a small mesial cusp that may be homologous to the paraconid. These features are never found in even the most primitive hominoid or Old World monkey, but they are common in platyrrhines and many adapids and living prosimians (Begun, 1989b). Some pliopithecoids appear to have had shorter faces and larger brains than propliopithecoids, and these features are shared with catarrhines (Fleagle & Kay, 1983), but also with many platyrrhines. Ford (1994) found no unambiguous derived postcranial character shared between
Order Primates Linnaeus, 1758

Infraorder Catarrhini É. Geoffroy Saint-Hilaire, 1812

Superfamily Pliopithecoidea Zapfe, 1960

Family Pliopithecidae Zapfe, 1960

Subfamily Dionysopithecinae

Genus Dionysopithecus Li, 1978

Dionysopithecus shuangouensis Li, 1978

Dionysopithecus orientalis Suteethorn et al., 1990

Genus Platodontopithecus Li, 1978

Platodontopithecus jianguhuensis Li, 1978

Subfamily Pliopithecinae Zapfe, 1960

Genus Pliopithecus Gervais, 1849

Pliopithecus pivetaui Hürzeler, 1954

Pliopithecus antiquus Gervais, 1849

Pliopithecus platyodon Biedermann, 1863

Pliopithecus zhanxiangii Harrison et al., 1991

Pliopithecus sp.

Genus Epiplopiopithecus Zapfe & Hürzeler, 1957

Epiplopiopithecus vindobonensis Zapfe & Hürzeler, 1957

Genus Egarapithecus Moyà-Solà et al., 2001

Family Crouzeliidae

Genus Plesiopliopithecus Zapfe, 1961

Plesiopliopithecus lockeri Zapfe, 1961

Plesiopliopithecus ausciutensis Bergouinioux & Crouzel, 1965

Plesiopliopithecus rhodanica Ginsburg & Mein, 1980

Plesiopliopithecus priensis Welcomme et al., 1991

Genus Anapithecus Kretzoi, 1975

Anapithecus hernnykii Kretzoi, 1975

Genus Laccopithecus Wu & Pan, 1984

Laccopithecus robustus Wu & Pan, 1984

Family incertae sedis

Genus Pseudopithecus Pohlig, 1895

Pseudopithecus rhenanus Pohlig, 1895

Superfamily Pliopithecoidea

Family Pliopithecidae

Subfamily Dionysopithecinae

GENUS Dionysopithecus Li, 1978

A genus of small primitive catarrhine approximating the size of gibbons. Of the two species recognized here one is known only from a single lower molar. Thus, the genus is defined essentially by the morphology of the better-known species, Dionysopithecus shuangouensis. Four isolated teeth from Pakistan are also referred to Dionysopithecus but no species is defined, so these teeth are not described here (Bernor et al., 1988).

INCLUDED SPECIES D. orientalis, D. shuangouensis

SPECIES Dionysopithecus shuangouensis Li, 1978

TYPE SPECIMEN IVPP V5597 (from Songlinzhuang, Sihong County, Jiangsu Province, People’s Republic of China), a left maxillary fragment with M3–3.

AGE AND GEOGRAPHIC RANGE The earliest species of the genus, known from the Xiaocawan Formation at the type locality of Songlinzhuang, dated by faunal associations to between 17 and 18 Ma; also recognized from the Zhenji locality, thought to be of similar age (Harrison & Gu, 1999; Qiu et al., 1999).

ANATOMICAL DEFINITION Dionysopithecus shuangouensis is known only from isolated teeth. It has a broad I1 with a pronounced lingual cingulum and female upper canines that are triangular in horizontal cross-section. Upper premolars are narrow while upper molars are comparatively broad with well-developed lingual cingula and moderately developed buccal cingula. M3 has strongly reduced distal cusps. Incisors are tall-crowned, narrow and waisted. P3 is vertical and lacks the crown flare of a structurally sectorial P4 (see above). P4 has a lingual cusp (metaconid) that is lower in cusp height...
than the buccal cusp (protoconid), a feature not found in other currently recognized pliopithecoinds, but possibly present in one specimen from Kenya (see below). The lower molars are long and narrow, often preserving the paraconid, a mesial cusp otherwise only found in prosimians and the most primitive anthropoids. The other mesial cusps are not aligned transversely, as in most other catarrhines, but, common to pliopithecoinds, the buccal cusp (protoconid) is more anterior or mesial than the lingual cusp (metaconid). The cristid obliquid is obliquely oriented, again as in most pliopithecoinds and more primitive anthropoids, and unlike most other catarrhines. Finally, a pliopithecin triangle, one of the few defining characters of the Pliopithecinae, is present. This feature consists of a subtle set of ridges on the buccal side of the crown defining a small triangular shaped pit between the protocone and hypocone (Hürzeler, 1954a). Dionysopithecus shuangouensis (and Platodontopithecus jianghuaiensis) are distinguished from other pliopithecoinds in having relatively rounded molar cusps and moderately developed upper molar buccal cingula, narrow M1 with a distinctively convex lingual edge, and small M3 with reduced lingual cusps (Ginsburg & Mein, 1980; Harrison & Gu, 1999).

**Species** Dionysopithecus orientalis Suteethorn et al., 1990

**Type Specimen** TF 2451, an M1

**Age and Geographic Range** Known only from a single tooth dated by faunal association to between 16 and 17 Ma (Ducrocq et al., 1994; Qiu et al., 1999), from Ban San Klang, northern Thailand.

**Anatomical Definition** Though originally referred to the east African genus Dendropithecus, Dionysopithecus orientalis is referred to Dionysopithecus in Harrison & Gu (1999) based on strong similarities to the type species, D. shuangouensis. These include size and basic morphological attributes of the occlusal surface typical of pliopithecoinds. For example, D. orientalis has mesial cusps that are offset, such that the buccal cusp is more mesial than the lingual cusp, as in most pliopithecoinds, but unlike Dendropithecus and hominoids. It should be noted however, that while the morphology of the Ban San Klang molar is clearly pliopithecoind, its distinctiveness from the type species of Dionysopithecus remains to be proven. Harrison & Gu (1999) are cautious in recognizing a separate species, and this is wise given the known range of variation in molar morphology among pliopithecoinds.

**Genus** Platodontopithecus Li, 1978

**Included Species** P. antiquus, P. piveteaui, P. platyodon, P. zhanxiangi

**Species** Platodontopithecus jianghuaiensis Li, 1978

**Type Specimen** PA 870, currently in the collections of the IVPP, Beijing, PRC. a left M3

**Age and Geographic Range** Known from the Xiacaowan Formation at the type locality of Songlinzhuang, Sihong County, Jiangsu Province, PRC, dated by faunal associations to between 17 and 18 Ma; also recognized from the Zhenji locality, thought to be of similar age (Harrison & Gu, 1999; Qiu et al., 1999)

**Anatomical Definition** Platodontopithecus jianghuaiensis is known only from isolated teeth, which are considerably larger than those of D. shuangouensis, being somewhat larger than siamang teeth. Harrison & Gu (1999) estimate the body mass at about 15 kg. Presumed male upper canines are tall and bilaterally compressed. The upper premolars are broader than in Dionysopithecus, and the lower P3 has subequal mesial cusps unlike Dionysopithecus. The molars are like Dionysopithecus but slightly narrower, with higher cusps and crests, including a better developed pliopithecin triangle.

**Subfamily Pliopithecinae**

**Genus** Pliothecus Gervais, 1849

A genus of small primitive catarrhine approximating the size range of hylobatids. Pliothecines share with dionysopithecines a suite of dental characters that are almost all primitive for anthropoids. These include incisors that are tall-crowned, narrow and waisted, spatulate but labiobuccolingually flat upper central incisors, narrow, pointed and asymmetrical upper lateral incisors, tall, broad P3, crown lacking a truly sectorial morphology, long and narrow lower molars, often preserving a paraconid, mesial cusps that are aligned obliquely, an obliquely oriented cristid obliquid, and a pliopithecin triangle. In most species of Pliothecus the P3 and lower molars tend to be long and narrow with large anterior or mesial pits (fovea) and well-developed buccal cingula. Though most species can have teeth close in size to Hylobates, the mandibles tend to be more massive. Upper premolars and molars tend to be broad and short. The premolars have heteromorphic cusps, the buccal ones always the more prominent. The upper molars usually have well-developed, shelf-like lingual cingula, and commonly buccal cingula or stylar shelves. Upper molars commonly lack a distal transverse ridge between the hypocone and metacone, but have a ridge connecting the hypocone to the protocone or the cristal obliqua (this is true of crouzelines as well, in contrast to the opinion of Andrews et al. (1996)).

**Included Species** P. antiquus, P. piveteaui, P. platyodon, P. zhanxiangi

**Species** Pliothecus antiquus Gervais, 1849 (Fig. 15.1)

**Type Specimen** From the E. Lartet collection from Sansan at the Museum National d'Histoire Naturelle, Paris, a mandible lacking only the rami and portions of the right canine and left I3 crowns.
Fig. 15.1 Pliopithecus antiquus. (A) The type mandible in occlusal view; (B) buccal and lingual view of the type; (C) occlusal drawings of the type (both appear to be from the left side, but in fact the row on the left is a photographically reversed image of the right side dentition, for ease of comparison with the left side and with other dentitions). Adapted from Simons (1972) and Hürzeler (1954a).
**Fig. 15.2** *Pliopithecus piveteaui.* (A) Three views of the type and only specimen, a right mandible photographically reversed here; (B) studies of the M₃ (left) and M₄ (right). Adapted from Hürzeler (1954a).

**AGE AND GEOGRAPHIC RANGE** *Pliopithecus antiquus* is definitively identified only at Sansan and La Grive, both in France and dated to MN 6 (about 15 Ma). Hürzeler (1954a) was of the view that the species is only known from Sansan, but most subsequent authors also include the La Grive specimen, which comes from older sediments than the *Dryopithecus* teeth from the same site (Ginsburg, 1975, 1986). *Pliopithecus antiquus* may also be known from other MN 6 localities in Germany (Diessen am Ammersee, Stützling, Ziemetshausen, Gallenboch) and Switzerland (Kreuzlingen and Rümlikon), though these are isolated teeth and their species attribution is uncertain. Similarly, *P. antiquus* has been tentatively identified at later localities in Poland (MN 7 of Opole, Poland; MN 8 of Castel de Barbera, Spain and Przeworno II, Poland; MN 9 of Doué-la-fontaine and Meigné-le-vicomte, France), though again only on the basis of isolated teeth. In a number of cases however, authors note similarities to the sample from Góriach referred previously to *P. antiquus* but here, following Andrews et al. (1996), referred to *P. platyodon*. In addition, one of these samples, from Castel de Barbera, is recognized here as a distinct species (see below). Conservatively, we can conclude that *P. antiquus* is an MN 6 taxon from France that may have persisted into later periods (MN 6–9) in more central areas of Europe.

**ANATOMICAL DEFINITION**

*Pliopithecus antiquus* is dentally among the smallest species of *Pliopithecus*, though there is extensive overlap among the European species (Fig. 15.1). In addition to size, *P. antiquus* can be distinguished from some other species only by a number of subtle dental characters. To avoid repetition, these are listed in the anatomical definitions of the other species.

**SPECIES** *Pliopithecus piveteaui* Hürzeler, 1954 (Fig. 15.2)

**TYPE SPECIMEN** In the Lecointre collections at la Chapelle-Blanche, Manthelan (Indre et Loire), a right mandibular fragment with M₂–₃ and alveoli for the roots of the P₄ and M₄.

**AGE AND GEOGRAPHIC RANGE** Dated to MN 5 (16–17 Ma), only from the Loire valley of France (Faluns de Touraine, Anjou, Pontevoy-Thenay, Manthelan) (Ginsburg & Mein, 1980; Ginsburg, 1986).

**ANATOMICAL DEFINITION**

The combination of subtle morphological differences, more primitive morphology, geography and greater age suggest that *P. piveteaui* is a distinct species, as originally recognized by Hürzeler (1954a) and more recently by Ginsburg (1975, 1986) and Ginsburg & Mein (1980). The type specimen is unusual for *pliopithecinidae* in having a very small M₃ in relation to M₂. The teeth are small but within the range of *P. antiquus*. They are considerably smaller than in other most species, but close to those of the small species from Castel de Barbera (see below). Both teeth narrow distally, a feature common in M₃ but unusual in M₂. The M₃ of the type has an even more tapered morphology than is typical for the genus. The M₄ has a very reduced entoconid (the distal lingual cusp) and the M₄ has a smooth and flared, or bulging buccal surface lacking the buccal cingulum typical of *P. antiquus*. Finally, the cusps on both molars are more bilaterally compressed, the crests that connect them more strongly defined, and the fovea and basins that separate them are larger, all compared to *P. antiquus*. These latter features are found in a number of other *pliopithecoids*, including *P. platyodon*, *P. sp.* from Spain and in most *crouzelii*, and thus may be primitive for the superfamily. The right P₄ is broad and also has a more bulging buccal surface than in *P. antiquus*, with a larger talonid basin, a lower protoconid and a more strongly developed hypoconid (Ginsburg, 1975). Ginsburg (1975)
also described additional lower molars that resemble the type. Finally, two upper teeth are known, a P³ and M³, which cannot be compared directly to P. antiquus from Sansan. Compared to an isolated P³ from Poland that may belong to P. antiquus or P. platyodon (Kowalski & Zapfe, 1974) the P. piveteaui P³ is smaller, and relatively broader or shorter, with a relatively larger protocone, a pronounced lingual cingulum, and a much shorter talon. Both upper teeth more closely resemble P. platyodon P³ specimens from Gòriach, though again they are much smaller (Fig. 15.4).

A number of researchers have recently suggested that P. piveteaui is indistinguishable from P. antiquus (Harrison et al., 1991; Andrews et al., 1996). Andrews et al. (1996) consider the relative size of the M₁ and its unusual morphology, which distinguishes P. piveteaui from P. antiquus, to be unreliable given known ranges of variability in this tooth. They do not comment on other aspects of the dental morphology of P. piveteaui. In light of the number of differences from P. antiquus and the consistency of those differences in the larger samples described by Ginsburg (1975), P. piveteaui is recognized here as a separate species. Its apparently primitive morphology may be an important hint to understanding some aspects of the evolutionary history of the Pliopithecoidae (Ginsburg & Mein, 1980, and see below).

**SPECIES** Pliopithecus platyodon Biedermann, 1863 (Fig. 15.3)

**TYPE SPECIMEN** In the collections of the Museum of Winterthur, Zurich, a damaged female maxilla with heavily worn dentition

**AGE AND GEOGRAPHIC RANGE** Pliopithecus platyodon from Elgg (near Zurich) is considered to be MN 5 in age, based on biostratigraphic correlations (Ginsburg, 1986); however, the bulk of the sample currently attributed to this taxon is from the MN 6 locality of Gòriach, Austria

**ANATOMICAL DEFINITION** Pliopithecus platyodon, based on the sample from Gòriach, is dentally larger on average than P. antiquus. According to Andrews et al. (1996), P. platyodon has a relatively broader P₃ and slightly longer, more rectangular lower molars that increase in size from M₁ to M₃, more than in P. antiquus. However, these characters are very variable in the Gòriach sample. It is safe to say that P. antiquus and P. platyodon are very similar and essentially differ only in size (Fig. 15.3).

Hürzeler (1954) and Zapfe (1960) both suggested that the Elgg and Gòriach samples may represent the same species, but were reluctant to attribute the Gòriach material to P. platyodon due to the poorly preserved occlusal morphology of the type. Harrison et al. (1991) formally combined the two samples. Andrews et al. (1996) cite a number of differences between the Gòriach and Sansan samples as evidence of their taxonomic distinction (see below). Of course, it remains unclear if Elgg and Gòriach are really the same taxon or if another species of Pliopithecus, P. goriiuenesis (Sera, 1917) should be recognized. Here I follow Harrison et al. (1991). As noted above, a number of other specimens usually attributed to P. antiquus may in fact belong to P. platyodon (Hürzeler, 1954).

**SPECIES** Pliopithecus zhuxiangei Harrison et al., 1991

**TYPE SPECIMEN** BPV-1021 (found at Maerzuizigou (BN 87021), Tongxin County, People’s Republic of China, and in the collections of the IVPP, Beijing), a damaged female cranium

**AGE AND GEOGRAPHIC RANGE** Considered to be contemporary with Sansan (MN 6), based on faunal similarities (Harrison et al., 1991; Qiu et al., 1999), China

**ANATOMICAL DEFINITION** Pliopithecus zhuxiangei is the largest species of the genus. Lower molars, which bear pliopithecid triangles, increase markedly in size from M₁ to M₃. They commonly show secondary wrinkling of the occlusal surface. The mandible is robust with a large extramolar sulcus. The upper canine is thick and relatively low-crowned, and the upper premolars and molars are very broad with strong buccal cingula (Harrison et al., 1991). On the buccal sides of the M₁₃ there is a depression or notch that gives the tooth a waisted appearance.

Unlike other species of the genus, P. zhuxiangei is also known from a partial cranium, distinguished from E. vindobonensis primarily by size. The anterior palate is somewhat more complete in P. zhuxiangei, revealing large, broad incisive foramina, similar to those of hyllobatids and other non-hominid primates. The inferior orbital fissure is large, a feature also more typical of non-catarhine primates (e.g., Hershkovitz, 1974). Pliopithecus zhuxiangei shares with E. vindobonensis a short face with narrow premaxilla, broad incisive foramina, narrow, oval-shaped nasal apertures, broad orbits with mildly projecting rims, low cheek bones (zygoma), and restricted maxillary sinuses.

**GENUS** Epipliopithecus Zapfe & Hürzeler, 1957

**INCLUDED SPECIES** E. vindobonensis

**SPECIES** Epipliopithecus vindobonensis Zapfe & Hürzeler, 1957 (Figs. 15.4–15.6; see also Fig. 20.1)

**TYPE SPECIMEN** In the collections of the Naturhistorische Museum, Vienna, Individual III from the Děvinská Nová Ves fissures (Harrison et al. (1991) describe a palate as part of the holotype, but this is from Individual II (Zapfe, 1960); their Figure 9 with a view of the type (Individual III) is correct), portions of a mandible, maxilla, cranial fragments, vertebrae, a left clavicle, left humerus, distal left ulna, carpal, metacarpals and phalanges

**AGE AND GEOGRAPHIC RANGE** Based on faunal comparisons, generally considered to be lower MN 6 or upper MN 5 in age, about 15 to 15.5 Ma (Zapfe, 1958; Ginsburg, 1986; Rögl, 1999), eastern Europe

**ANATOMICAL DEFINITION** Epipliopithecus vindobonensis was originally named as a subgenus of Pliopithecus, P. (Epipliopithecus) vindobonensis (Zapfe &
Hürzeler, 1957). In addition to the impressive type specimen, *E. vindobonensis* is known from two more partial skeletons and a number of isolated remains, all from the same fissure deposit. Dentally *E. vindobonensis* can be distinguished from *Pliopithecus* by a number of features. These include differences from *P. antiquus* in overall larger dental size, higher-crowned lower incisors, upper central incisor broad with a notched lingual cingulum, *P*. and lower molars slightly narrower, indistinct or missing plopiithecine triangle, slightly broader upper molars, small trigone basin on molars, less well-developed buccal cingulum on upper molars, and greater size differences between molars. It is due to this more impressive suite of dental differences, particularly the absence of a
Fig. 15.4 (A) Epipliopithecus: basicranial (left) and intracranial (right) views of a petrous bone. M.a.e = external auditory meatus; A.e.c.c = external carotid canal aperture; M.a.i = internal auditory meatus; F.a = subarcuate fossa. Note the flanges of bone forming a partially ossified ectotympanic tube around the external meatus. This condition is similar to that seen in some other primates, but unlike that of any cetarrhine. Adapted from Zapfe (1960). (B) Pliopithecus, upper (right) and lower (left) molars, illustrating the general occlusal pattern. Adapted from Hürzeler (1954a). (C) Epipliopithecus hemipalate, illustrating the basic pattern of the upper adult dentition. Note the broad molars with massive lingual cingula and the small premolars with poorly developed lingual cusps. (D) Epipliopithecus, occlusal and lateral views of the mandible. Note the short, high-crowned P1, long molars with prominent buccal cingula, obliquely oriented mesial cusps and relatively robust mandible. Adapted from Zapfe (1960).
Epipliopithecus vindobonensis has a fairly large and globular braincase with well-developed temporal lines (in one specimen meeting in the midline to form a low sagittal crest), a relatively projecting snout (though less than in *Aegyptopithecus*), orbits slightly laterally deviated with a prominent, projecting glabellar region, supraorbital costae that do not meet in the midline to form a torus, depressed frontal trigon, relatively short but vertical frontal squama, broad interorbital space, prominent lacrimal crest obscuring the lacrimal fossa from anterior view, petrous bones with a large subarcuate fossa, and an incompletely ossified ectotympanic tube. The mandibles are long and have robust corpora and broad rami with prominent, flared gonial angles. Postcranially *E. vindobonensis* most closely resembles long-limbed New World monkeys but also relatively leggy Old World monkeys. In brachial index it is more like suspensory New World monkeys and prosimians, but hindlimb overall length and the crural index are closer to Old World monkeys (Zapfe, 1960). However, the crural index of *E. vindobonensis* is also very close to gibbons and chimpanzees, and within the human range (Zapfe, 1960). Unlike apes, however, the forelimb was slightly shorter than the hindlimb, being most comparable to howling monkeys but also baboons (Zapfe, 1960). The trunk was long and slender, and probably had seven lumbar vertebrae, a long sacrum and possibly a tail (Zapfe, 1960; Ankel, 1965). *Epipliopithecus vindobonensis* had comparatively long hands and feet, and long, curved fingers, and was mostly likely an agile climber. This is also suggested by the morphology of the joint surfaces of the limb bones (Fig. 15.6).

**GENUS** Egarapithecus Moyà-Solà et al., 2001

**INCLUDED SPECIES** E. narcisoi

**SPECIES** Egarapithecus narcisoi Moyà-Solà et al., 2001

**TYPE SPECIMEN** IPS 2943, a fragmentary mandible

**AGE AND GEOGRAPHIC RANGE** Torrent de Febulines, in the Vallès Penedés basin of Catalonia near Barcelona, is biostratigraphically dated to MN 10 and is placed in Chron C4An of the Geomagnetic Polarity Time Scale, indicating an age of about 9 Ma (Moya-Solà et al., 2001).

**ANATOMICAL DEFINITION**

The type specimen and an associated palatal fragment with a right P3 have been mentioned in the literature by Golpe-Posse (1982) and Andrews et al. (1996), and recently named to a new genus by Moyà-Solà et al. (2001). *Egarapithecus* has a very distinctive occlusal morphology that surely merits a genus-level distinction. The lower teeth are narrow and elongated with sharply defined occlusal crests and large talonid basins. The P3 has a strong metaconid and the P4 an exceptionally elongated talonid with well-formed distal cusps. The molars have small mesial fovea and large talonid basins. The M3 is exceptional long and narrow. The mandible is extremely deep relative to transverse breadth compared to *Epipliopithecus*, *Anapithecus* and *Pliopithecus*. Moyà-Solà et al. (2001) suggest that the small canines in the symphyseal fragment are unerupted, despite the wear on the M3 (canines almost always erupt before the M3 in catarrhines). However, unerupted canines lack root apical closure, while the canines in the *Egarapithecus* type have completed roots. The fact that the canines in *Egarapithecus* remain embedded in the mandible probably results from a pathology, another possibility suggested by Moyà-Solà et al. (2001). The incisors (based on the exposed roots) and canines are very small, even for a female, but it is not clear to what extent this is normal for the genus. The palatal fragment preserves the distal surface of the canine alveolus indicating the presence of a large upper canine, probably of a male. Thus it is unlikely to have come from the same individual as the type. The P3 is also unusual in being rectangular with roughly equal mesial and distal moieties, unlike most other pliopithecoids.

As noted by Andrews et al. (1996) and Moyà-Solà et al. (2001), *Egarapithecus* has some crouzeliniine similarities, and indeed these authors assign this taxon to the Crouzeliniinae. These similarities mainly involve lower dental elongation and sharply developed occlusal crests, which, while more strongly developed in crouzeliniines, are nevertheless present...
Fig. 15.6 Epipliopithecus vindobonensis. (A–H) The best preserved cranium and limbs. The limb bones of Epipliopithecus (A–C) are compared to those of a gibbon (D,E); (F) lateral view of the skull; (G) frontal and (H) palatal views. (I) (overleaf) Lower dentitions. Note the tall, narrow, heteromorphic lower incisors (top) and the absent or poorly defined pliopithecine triangle on the lower molars. (J) Upper limb bones (humerus left, radius right). (K) Study of the ulna. Note the prominent olecranon process, unkeeled trochlear notch, small, anteriorly placed and facing radial facet and the deep shaft (top row). Note also the very prominent and robust ulnar styloid (bottom row). (L) Hands and feet. Top row, articulated left hand skeleton and dorsal, left lateral, right lateral and palmar views of a 2nd hand proximal phalanx. Bottom row, same views of a hallucal proximal phalanx and a 3rd proximal phalanx of the foot, and an articulated left foot. (M) Cranial (top) and caudal (bottom) views of the sacrum. Note the large sacral canal, suggesting the presence of a long tail (Ankel, 1965). Adapted from Zapfe (1960).
in some pliopithecids, including those from the nearby and somewhat older locality of Castel de Barbera (see below). However, Egarapithecus lacks key features, such as large mesial basins, and has unique characters, such as very long molars and premolars, $P_4$ with large distal cusps, very obliquely oriented oblique crests and very small lower anterior teeth, suggesting that this taxon evolved independently from the crouzelines, the view adopted here. It may be a descendant of the Castel de Barbera taxon, which has some similar characteristics but in a less well-developed state.

**New pliopithecine**

At least one new taxon belonging to this subfamily is probably present in Spain, but given the scope of this work it is not formally named here. A new species of *Pliopithecus* is represented by specimens from two other localities in the Vallés Penedès basin. The most informative specimen is an associated upper and lower dentition of a small crouzeline from the MN 8 locality of Castel de Barbera. Recognition of a new but unnamed species here contrasts with the view of Andrews et al. (1996), who consider these teeth to belong to *P. antiquus*. However, the Castel de Barbera specimens are smaller on average than *P. antiquus*, and are morphologically distinctive. They have bilaterally compressed cusps with well-developed crests and large occlusal basins. In some respects these are similarities with *P. piveteaui*, but they are more strongly developed in the Spanish taxon. In addition, a right $dP_4$ is known from Can Feliu, also considered to be of MN 8 age (Ginsburg, 1986). Andrews et al. (1996) consider this specimen to be a crouzeline based on the fact that in size it is more consistent with *Egarapithecus*, which they consider to be a crouzeline. As noted above, *Egarapithecus* lacks diagnostic crouzeline characters. In addition, the Can Feliu specimen is morphologically closer to homologous *Pliopithecus* teeth from Görzach than to crouzeline specimens from Rudabánya. It is long compared to breadth and has a narrower talonid, a more mesial protoconid and a distinctive trigonid with a long basin divided by a transverse ridge ending mesiolingually at a small paraconid. It is probably from a larger individual of the same taxon as the Castel de Barbera dentitions. An isolated male canine from Castel de Barbera (IPS 1823), considerably larger than that from the associated dentitions, may also represent this taxon.

**Family Crouzeliidae**

**Subfamily Crouzeliinae**

Ginsburg & Mein (1980) defined Crouzeliinae based on the type genus Crouzela. Subsequent authors (e.g., Andrews et al., 1996) have recognized that Crouzela cannot be distinguished from *Plesiopithecus*, but the suprageneric taxon remains valid. Here it is elevated to a family based on the numerous differences from the Pliopithecidae.

Crouzeliids in general differ from pliopithecids in having sharper, more bilaterally compressed cusps more displaced toward the margins of the crowns, resulting in larger, relatively deep occlusal basins (except the distal basin, which is restricted and lingually offset) (Ginsburg & Mein, 1980; Begun, 1989b; Andrews et al., 1996). These traits are similar to those in pliopithecines from Spain, but more strongly expressed. Crouzeliids also differ in having elongated molars and premolars with sharp, well-developed crests, particularly between the trigonids and talonids and along the crown margins.

**GENUS** Plesiopithecus Zapfe, 1961

*Plesiopithecus* is a small primitive catarrhine, most of the species of which are, on average, smaller in dental size than *Pliopithecus*. Like *Epipliopithecus*, *Plesiopithecus* was originally recognized as a subgenus of *Pliopithecus* by Zapfe (1961). I follow Ginsburg & Mein (1980) in elevating *Plesiopithecus* to genus status here. *Plesiopithecus* species are only known from lower teeth. They are distinguished from other crouzelines in being much smaller and in having very reduced hypoconulids. In addition to their crouzeline characters, they retain typical features of the pliopithecoidea including a variably expressed pliopithecine triangle, obliquely oriented oblique crest and a protoconid that is mesial to the metaconid.

**INCLUDED SPECIES** *P. auscitans*, *P. lockeri*, *P. priensis*, *P. rhodanica*

**SPECIES** *Plesiopithecus lockeri* Zapfe, 1961 (Fig. 15.7)

**TYPE SPECIMEN** In the collections of the Naturhistorische Museum, Vienna, a left mandibular fragment from Trimmelkam, Austria

**AGE AND GEOGRAPHIC RANGE** Trimmelkam is considered to date to MN 6, but the fauna from the site is poor (Ginsburg, 1986); the only other taxon definitively identified at the site, *Palaeanomys eminus*, is generally considered to be an MN 7/8 taxon (Gentry et al., 1999)

**ANATOMICAL DEFINITION**

Like all the species of *Plesiopithecus*, *P. lockeri* is known from one individual. The $P_3$ is long and oval with a small distal fovea, compared to the other crouzelines *Anapithecus* and *Laccopithecus*. The $P_4$ is like other crouzelines in being elongated with a particularly large talonid surrounded by tall, sharp crests (Zapfe, 1961; Ginsburg & Mein, 1980). Like *P. auscitans* the $P_4$ has a distinct entoconid. Like *P. auscitans* and *Laccopithecus*, but unlike *Anapithecus*, the $M_1$ is broader distally due to the presence of a large, buccally displaced hypoconid. The lower incisors are tall-crowned and narrow. The $I_1$ is flared or wider at the occlusal edge than at the cervix and the $I_2$ is asymmetrical (Fig. 15.7).

**SPECIES** *Plesiopithecus auscitans* Bergounioux & Crouzel, 1965 (Fig. 15.8C, D)

**TYPE SPECIMEN** Sa 999 (MNHN), a left mandibular fragment with $P_4$–$M_1$. 

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**Fig. 15.7** Plesiopliopithecus lockeri. (A) Lingual and (B) buccal views of P\textsubscript{3} to M\textsubscript{1} and the impression in the matrix of the canine. (C) Lower incisors and (D) an occlusal view of the postcanine dentition. Note the oblique cristid oblique between the protoconid and hypoconid and the broad, distally flared talonid basin, and reduced hypoconulid. Adapted from Zapfe (1961).

**AGE AND GEOGRAPHIC RANGE** Sansan, France is in MN 6 (by definition, since it is the reference locality for this zone); it is considered to date to about the middle of this zone, roughly 14.5 Ma

**ANATOMICAL DEFINITION**

Plesiopliopithecus auscitens\textsubscript{i}s is very difficult to distinguish from P. lockeri. According to Ginsburg & Mein (1980) it has a somewhat smaller P\textsubscript{4} talonid and an M\textsubscript{1} with compressed mesial cusps and a reduced hypoconulid. According to Andrews et al. (1996) it has a less well-developed M\textsubscript{1} buccal cingulum and a less well-defined distal fovea, lacking the ridge that separates this basin from the talonid in P. lockeri. Unfortunately, these apparently distinct morphologies are found together in larger single species samples of pliopithecoids, such as Anapite\textsubscript{i}lus heryaki and Pliopithecus platyodon. Plesiopliopithecus auscitensis is dentally smaller than P. lockeri, but the only specimen of P. lockeri is a male, which can be expected to have been in the upper end of the range of variation in dental size. Reluctantly, two separate species are recognized here (Fig. 15.8).

**SPECIES** Plesiopliopithecus rhodanica Ginsburg & Mein, 1980 (Fig. 15.8A, B)

**TYPE SPECIMEN** FSL 65626, collections of the Facult\textsubscript{e} des Science, Université Claude-Bernard, Lyon, an M\textsubscript{1}

**AGE AND GEOGRAPHIC RANGE** La Grive Saint Alban, Isère, France, has primate-bearing sediments of differing ages; Fissure L7 is dated to MN 7 (Ginsburg, 1986). Many authors currently combine MN 7 and MN 8, so that the ages of the crouzeliine and hominid from La Grive may in fact be quite close. This would be an interesting combination of primates, already known from a number of localities (Salmendingen, Austria, Rudab\textsubscript{a}nya, Hungary and Lufeng, China)

**ANATOMICAL DEFINITION**

Plesiopliopithecus rhodanica is even more difficult to distinguish because it is only known from one tooth. Differences include smaller size, slightly narrower crown, elongated crests, reduced buccal cingulum, smaller mesial fovea and very small hypoconulid (Andrews et al., 1996), but again, a similar range of variation is easy to match in larger samples of other pliopithecoids. Ginsburg & Mein (1980) consider these characters, which tend to distinguish pliopithecids from crouzelines, better developed in P. rhodanica (apart from size). Given this evidence of an evolutionary change, and given the temporal separation of the samples, this
**Fig. 15.8** Plesiopliopithecus. (A, B) *P. rhodanica* in occlusal (A) and buccal (B) views. (C, D) *P. ausitanensis* in occlusal (C) and buccal (D) views. Adapted from Ginsburg and Mein (1980).

**Fig. 15.9** Plesiopliopithecus priensis. Occlusal view.

**Fig. 15.10** Anapithecus hernyaki. (A) Palatal view from a partial cranium of a female with a heavily worn and damaged dentition, and, bottom, well-preserved lower (B) and upper (C) dentitions of a subadult female.

Species is recognized here as distinct as well (Fig. 15.8).

**SPECIES** Plesiopliopithecus priensis Welcomme et al., 1991 (Fig. 15.9)

**TYPE SPECIMEN** Specimen in the collections of the Muséum Nationale d’Histoire Naturelle, Paris, a right mandibular fragment

**AGE AND GEOGRAPHIC RANGE** Priay (Ain, France) contains a good micromammal assemblage that unambiguously dates the locality to the upper part of MN 9, or about 9.5 Ma, considerably younger than other species of the genus (Welcomme et al., 1991)

**ANATOMICAL DEFINITION**
Plesiopliopithecus priensis can be distinguished by its much larger size, but it retains the typical morphology of the genus with its broad talonid and reduced hypoconulid. The buccal cingulum is also more strongly developed than is typical for Anapithecus. This specimen has been attributed to Pliopithecus in Welcomme et al. (1991) and Andrews et al. (1996), but it is clearly distinct as described in general for crouzelelines and more specifically for Plesiopliopithecus (see above).

**GENUS** Anapithecus Kretzoi, 1975

**INCLUDED SPECIES** *A. hernyaki*

**SPECIES** Anapithecus hernyaki Kretzoi, 1975 (Fig. 15.10)

**TYPE SPECIMEN** RUD 9, in the collections of the Geological Museum of Hungary but currently stored in the National Museum of Hungary, a mandibular fragment

**AGE AND GEOGRAPHIC RANGE** Anapithecus hernyaki is known from several localities at Rudabánya, Hungary, the ages of which are essentially contemporaneous at MN 9. Unlike other pliopithecoids, *Anapithecus* appears to have had a broad distribution. It is identified at Salmendingen and Götzendorf, in the Vienna basin of Austria. Götzendorf is considered to be slightly younger than Rudabánya although
ANATOMICL DEFINITION

Anapithecus hemyaki is medium-sized primitive catarrhine that is larger than all other pliopithecoïds on average. It was originally recognized as a subgenus of Pliopithecus. Ginsburg & Mein (1980) elevated it to a distinct genus assigned to the crouzelines. A distinctive system of crests between the mesial cusps and the M1, hypoconid unambiguously identifies Anapithecus. These crests form a Y, with the vertical component represented by the cristid obliquid and the arms represented by crests going to the protoconid and metaconid (Begun, 1989a). While this looks superficially like catarrhine deciduous molar morphology there are fundamental differences in crest development, orientation and in overall crown morphology (Begun, 1991). In contrast to the opinion of Andrews et al. (1996), a careful examination of the original specimens from all three localities clearly reveals their morphological similarities.

Anapithecus hemyaki is dentally somewhat larger than a siamang and probably weighed about 15 kg. The specimens suggest little body-mass sexual dimorphism but substantial canine dimorphism. Lower incisors are tall-crowned but also relatively robust transversely (long), and lack the ”waisting” of other pliopithecoïds. Upper central incisors are broad and low-crowned with marked lingual cingula. Upper lateral incisors are very distinctive, being much smaller than the centrals, pointed, symmetrical and relatively flat labio-lingually, resembling miniature upper female canines. Lower premolars and molars are long with very large mesial fovea and talonids and small, lingually displaced distal fovea. The M1 is especially long and tapered distally. These characters are more strongly developed in A. hemyaki than in other crouzelines. In addition, lower molars have typical crouzeline and pliopithecoïd characters including mesially placed protoconids, obliquely oriented oblique crests, bilaterally compressed, marginalized cusps and prominent occusal crests. Many specimens preserve either remnants or well-developed pliopithecoïde triangles. Upper molars and premolars are broad with large basins as well. Premolars have substantial cusp heteromorphy, the buccal cusps being taller than the lingual ones, and a distinctive, hexagonal shape (L. Kordos, pers. comm.). The upper molars have strong lingual and buccal cingula, relatively large talons, and well-developed ridges connecting the hypocone to the protocone. Though poorly preserved it is clear that the mandible was transversely robust, as in many pliopithecoïds.

One cranial specimen is broadly similar to Pliopithecus zhuxiaangi and Epipliopithecus vindobonensis but much larger. Shared characters include short faces with short premaxilla, fenestrated palates, narrow, oval shaped nasal apertures, broad orbits with projecting rims, low cheek bones (zygoma), and restricted maxillary sinuses (Kordos & Begun, 2000). Like E. vindobonensis, Anapithecus hemyaki has a fairly large and globular neurocranium. The orbits also face slightly laterally and are surrounded laterally by prominent, projecting supraorbital costae and infraorbital rims, and the frontal bone has a depressed frontal trigon and a relatively short but vertical frontal squama, and broad interorbital space. Reconstruction suggests that the interorbital region was relatively somewhat narrower than in E. vindobonensis, and that the medial ends of the supraorbital costae dipped down toward glabella, as in E. vindobonensis and hylobatids. Compared to E. vindobonensis the temporal lines are less well-developed and the snout relatively less projecting. The orbits are more elongated, the root of the zygomatic on the maxilla is higher and positioned more anteriorly, the postorbital breadth is relatively greater, and the frontal is shorter and more vertical (Kordos & Begun, 2000). Compared to Pliopithecus zhuxiaangi and Epipliopithecus vindobonensis the anterior palate is broad. The few postcranial fragments include phalanges and some foot bones that are also broadly similar to Epipliopithecus vindobonensis, but with features that suggest more suspensory postures (e.g., more strongly curved phalanges) (Begun, 1988a, 1993a).

GENUS Laccopithecus Wu & Pan, 1984

INCLUDED SPECIES L. robustus

SPECIES Laccopithecus robustus Wu & Pan, 1984 (Fig. 15.11)

TYPE SPECIMEN PA 880, a nearly complete female lower dentition and fragmentary mandible, and PA 876, two halves of a badly damaged maxilla. Wu & Pan (1984) interpreted these specimens to be parts of a single individual, but PA 876 is clearly a male, based on canine size and morphology (Pan et al., 1989). Technically these specimens are thus syntypes rather than a holotype, because they are different specimens and different individuals. In view of the fact that PA 880 has a better preserved dentition, was figured first in the original publication, has been figured elsewhere in a higher-quality image (Pan et al., 1989), and is more directly comparable to most other type specimens of pliopithecoïds, it should be designated as the lectotype. All specimens are from Lufeng County, Yunnan Province, and are in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, PRC.

AGE AND GEOGRAPHIC RANGE Lufeng appears to be one of the latest occurrences of non-cercopithecid primates in Eurasia, and has been correlated to NMU 10, the Chinese mammal unit equivalent to MN 11–12 of Europe (Qiu, 1990; Qiu & Storch, 1990; Qiu et al., 1999), about 8 Ma; only Oreopithecus persists beyond this time in Eurasia.

ANATOMICL DEFINITION

Laccopithecus robustus is known from a rich sample of about 90 specimens, including a partial cranium with a well-preserved face and palate, as well as a number of more fragmentary jaws, associated dentitions, isolated teeth and a proximal phalanx (Pan, 1998). Laccopithecus robustus is a
medium-sized primitive catarrhine, in most dimensions dentally smaller than *Anapithecus*. Females are close in molar size to siamangs, whereas males are somewhat larger. It has a number of typical crouzeline characters such as large occlusal basins, compressed, marginalized cusps, and obliquely oriented oblique crests. Like *Anapithecus*, *L. robustus* has a fairly broad P3, but like *Plesiopliopithecus* the molars and premolars are less elongated than in *Anapithecus*, the occlusal basins are less expanded, especially the mesial fovea, and the hypoconulid is rather small, though not with the degree of reduction seen in *Plesiopliopithecus*. There are no pliopithecine triangles on any of the lower molars and the buccal cingula are minimally developed. The lower canines are more massive than in *Anapithecus* while the lower incisors more closely resemble *P. lockeri* in that they are mesiodistally shorter. Two damaged mandibular symphyses suggest that the anterior part of the mandible was robust with well-developed transverse tori while the posterior portion appears to have been relatively gracile in transverse dimensions. Upper incisors lack the strong size differential of *Anapithecus*, the I1 being a very short tooth barely longer than the I2. Both upper incisors are labiolingually robust. The male upper canine is very large and strongly bilaterally compressed. All three upper anterior teeth in fact closely resemble their homologues in hyllobatids, though this is not the case for the lower incisors, which are lower-crowned and broader in hyllobatids. Another important distinction from hyllobatids is the presence of sexual dimorphism in canine morphology, as in nearly all other anthropoids. The upper premolars are longer or less broad than in *Anapithecus*, and lack the degree of cusp heteromorphy of this taxon. The upper molars are also less broad than in *Anapithecus* with minimally developed lingual cingula and no stylar shelves. The talons tend to be smaller and the cusps more rounded.

The cranium of *L. robustus* is badly damaged, as is the case for most specimens from Lufeng. The palate is narrow anteriorly, as in *Epipliopithecus* and it appears to have been fenestrated. As in *Epipliopithecus*, *Anapithecus* and *Hylobates*, the nasal aperture is tall but small and narrow overall, with a narrow base and an apex that reaches above the lower level of the orbits. As in *Epipliopithecus* the orbits appear to have been more squared, or less elongated than in *Anapithecus*, though they are distorted. Relative to orbital dimensions the interorbital space is similar to that of *Epipliopithecus*. The root of the zygomatic is placed fairly high on the maxilla, and the zygomatic bone itself is robust and separated from the body of the maxilla by a prominent malar notch, all more like *Anapithecus* than *Epipliopithecus*, while the orbital rims are less prominent than in *Anapithecus*, more like the condition in *Epipliopithecus* (Fig. 15.11). Finally, the single proximal phalanx of *Laccopithecus* is long and curved, with strong muscle markings suggestive of suspensory positional behavior (Meldrum & Pan, 1988).

**Family incertae sedis**

**GENUS** Paidopithex Pohlig, 1895

**INCLUDED SPECIES** *P. rhenanus*

**SPECIES** Paidopithex rhenanus Pohlig, 1895 (Fig. 15.12; see also Fig. 20.1)

**TYPE SPECIMEN** The Eppelsheim femur, a nearly complete specimen first described in Kaup (1861), in the collections of the Hessisches Landesmuseum, Darmstadt, Germany

**AGE AND GEOGRAPHIC RANGE** Known only from
Eppelsheim, dated securely to MN 9 based on its rich associated fauna (Mein, 1986)

**ANATOMICAL DEFINITION**

*Paidopithecus rhenanus* is a large primitive catarrhine known from the type femur and an upper male canine (Fig. 15.12). Both specimens resemble *Epipithecus* but are much larger. The femur routinely is attributed to *Dryopithecus*, but is different from any fossil or living hominoid (Begun, 1992a) as confirmed by the recent discovery of femoral fragments of *Dryopithecus* from Spain (Moyá-Solà & Köhler, 1996). Recently recovered femora from Rudábanya possibly attributable to *Anapithecus* based mostly on size, are very different in morphology from *Paidopithecus rhenanus* (Kordos & Begun, 1999). *Paidopithecus rhenanus* can be distinguished morphologically from hominoids but in terms of size it is consistent with a number of pliopithecoids. Here it is considered to be pliopithecoid but left unassigned beyond the superfamily level.

The femur of *Paidopithecus rhenanus* is long and gracile with a comparatively short neck with a lower neck–shaft angle than in hominoids generally, including *Dryopithecus*, and in comparison to the Rudábanya femora (Kordos & Begun, 1999). The shaft is straight and the condyles are shallow and separated by a broad patella groove. The canine is long and dagger-like, closely resembling the canines of *Epipithecus* and *Lacopithecus*. The root and cervix are similar in dimensions to the single upper male canine specimen of *Anapithecus*, which unfortunately does not preserve much of the crown. It is smaller and less robust than *Dryopithecus* upper male canines (Fig. 15.12).

**Evolution of European Miocene catarrhines**

What if anything is a pliopithecoid?

Distinguishing among many of the species of pliopithecoids is difficult due to their exceptionally primitive and conservative dental morphology. It is possible that the dionysopithecines are broadly ancestral to all other pliopithecoids, though more fossils are required to establish the affinities of these primitive Asian catarrhines. Within the Pliopithecinae it appears that *Pliopithecus platyodon* and *P. antiquus* are most closely related, differing essentially only in size. *Pliopithecus piveteau* is smaller and more primitive than the other European species, and may be their ancestor. Technically this should require a new genus name for the older sample to distinguish it from the more closely related descendants. *Pliopithecus zhanxiangi* and *Epipithecus vindobonensis* are more distinctive, and it may be justified to recognize separate genera for both of these taxa. Because *E. vindobonensis* lacks one of the few diagnostic characters of the pliopithecines, a pliopithecine triangle on the lower molars, it is recognized here as a distinct genus. In fact, *E. vindobonensis* is no more morphologically like *Pliopithecus* than are some specimens attributed tentatively to Limnopithecus, such as KNM-FT 20 from Fort Ternan, Kenya (Andrews, 1978a).

Within the Crouzeliinae a morphological gradient is apparent from the more conservative *Plesiopithecus lockeri* to the more derived *Anapithecus bernuyi*. *Lacopithecus* does not fit clearly with this trend and may have diverged early in the evolutionary history of the crouzelines. The dionysopithecines are most similar to early Miocene African taxa (Bernor et al., 1988; Harrison & Gu, 1999).

The early Miocene of Africa seems the most likely origin for the pliopithecoids (Thomas, 1985; Made, 1999). *Limnopithecus* shares the distinctive P₃ morphology with the Pliopithecidea. In addition, the lower P₄ of the specimen tentatively identified as *Limnopithecus* from Fort Ternan, Kenya has a metaconid that is much lower than the buccal cusp, as in *Dionysopithecus* (see above). This however is not true of other *Limnopithecus*, and it may well be that the specimen from Fort Ternan is not *Limnopithecus* but a pliopithecoid. If this is the case, the Fort Ternan specimen may represent the dispersal of a pliopithecoid into Africa, since Fort Ternan is considerably younger than much of the record of pliopithecoids in Europe and China (Pickford, 1986a). A number of Fort Ternan taxa, including rodents, ruminants and carnivores, are also thought to be Eurasian in origin (Tong & Jaeger, 1993; Gentry & Heizmann, 1996; Werdelin & Solounias, 1996; Made, 1999). At Wadi Moghara in Egypt, a humerus is known with a relatively modern elbow joint, as in proconsulids and more modern hominoids, and an entepicondylar foramen, reminiscent of prosimians, many New World monkeys, Oligocene catarrhines and, of course, *Epipithecus* (Simons, 1994a). This early Miocene specimen may also be associated with the ancestry of the Pliopithecidea. At any rate, these fossil samples suggest a complex connection between the Miocene primate faunas of Asia and Africa. It may be, as suggested by Harrison et al. (1991) that the earliest pliopithecoids lived in East Asia. They seem to diversify however in Europe. If the taxonomy proposed here is
correct, then it appears that on two separate occasions the pliopithecoids sent representatives to Asia, once in the form of the pliopithecine P. zu-xiangi and another time the crouzeline Laccopithecus. The evolutionary relations within the Pliopithecoidea are so poorly defined that it is possible that the Asian taxa evolved independently from the European taxa. However, given the evidence of migration of other mammalian genera between Asia and Europe during the middle and late Miocene (Flynn et al., 1986; Bernor et al., 1988; Qiu, 1990; Pickford, 1993b; Qiu & Qiu, 1995; Qiu et al., 1999; Made, 1999), a similarly complex pattern of biogeography in the Pliopithecoidea is certainly possible.

In conclusion, the systematics and evolutionary history of the Pliopithecoidea are about as simple as those of the Platyrrhini. This is no coincidence. The histories of both groups are remarkably similar. Both emerge from a primitive ancestor on a new land mass devoid of anthropoids, and both diverge into their respective major groups very shortly after their first appearance. Both undergo evolutionary changes that seem to be emergent or structurally inevitable in anthropoids: molarization, encephalization, reduction of the snout, limb gracilization and the development of suspensory positional behavior. Pliopithecoids were unable to maintain their splendid isolation, having been joined first by hominoids and then by cercopithecoids during the Miocene. Like the hominoids, they were unable to adapt to changing climates. It may be this more than anything else that led to the extinction of both groups at practically the same moment at the end of the Miocene.

**Primary References**

*Anapithecus*


*Dionysopithecus*


Egarapithecus


**Epipliopithecus**


Laccopithecus


Paidopithex

Platodontopithecus

Plesiopliopithecus


Pliopithecus


Pliopithecinae gen. et sp. indet.