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A new species of *Pliopithecus* from the middle Miocene of China and its implications for early catarrhine zoogeography

Eight cranio-dental specimens of a small catarrhine primate have been recovered recently from the locality of Maerzuizigou and nearby sites in Tongxin County, Ningxia Hui Autonomous Region, northcentral China. This area has yielded a diverse mammalian fauna which is estimated to date to about 15 m.y.a. (early Tunggurian, Faunal Unit 1), broadly comparable to the Sansan and Byelometchetskaya local faunas of Europe (early Astaracian, MN 6). The present study has confirmed the initial assessment of Qiu & Guan (1986) that the primate material should be referred to *Pliopithecus*. It is generally similar to *Pliopithecus* from Europe, but differs from the three currently recognized species in being considerably larger in size and in the details of its dental morphology. On the basis of these differences, there is sufficient evidence to recognize a new species of *Pliopithecus*. The new species confirms that the pliopithecids extended their range eastwards into Asia during the early middle Miocene soon after their earliest appearance in Europe. The diversity of pliopithecids in Eurasia at this time suggests that the initial migration may have involved multiple species derived from a diverse community established in Africa prior to their arrival in Europe. The distribution of early pliopithecids and Eurasian proconsulids during the middle Miocene indicates that the two groups may have occupied geographically and ecologically distinct provinces. The pliopithecids in China document two episodes of faunal contact between Europe and Asia during the Miocene.

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Introduction

Since the late 1970s, palaeontological research by the Institute of Vertebrate Paleontology and Palaeoanthropology (IVPP), the Bureau of Geology, Ningxia (BGN) and the Beijing Natural History Museum, Section of Vertebrate Paleontology (BPV) has yielded well-preserved fossil material of a rich vertebrate fauna from the middle Miocene deposits of Tongxin, Ningxia Hui Autonomous Region, People's Republic of China (Li *et al.*, 1984; Ye & Jia, 1986; Qiu *et al.*, 1988a,b). Qiu & Guan (1986) described an isolated lower molar (BPV-261) of a small catarrhine primate from the site of Maerzuizigou (or Maerzuizi Valley) in Tongxin County. On the basis of the presence of a pliopithecine triangle and a number of conservative characteristics typical of European pliopithecids, the authors referred the molar to *Pliopithecus* sp. The specimen had been purchased in 1985 from a local farmer at the site of discovery. The farmers in the area traditionally supplement their income by excavating deep tunnels into the Miocene sediments in order to obtain fossils, which they then sell as medicinal "dragon bones". In 1987, excavations at the site of Maerzuizigou (Beijing Natural History locality number BN 87021), by a team from the Beijing Natural History Museum, recovered three upper jaw fragments (BPV-1021, BPV-1022 and BPV-1023) of a fossil catarrhine primate, in association with a diverse vertebrate fauna (Guan, 1988). In addition, three further fossil primate specimens, a maxillary fragment (BPV-1024), a mandibular fragment (BGN mandible) and a lower molar in a mandibular fragment (BGN molar), were obtained from local farmers. The precise provenience of these latter specimens is unknown, but it is likely that they came from a locality (perhaps BN 8204) in Bianchiangou (Bianchian Valley), near Yujiali Village, which is about 10 km south of Maerzuizigou (Figure 1).

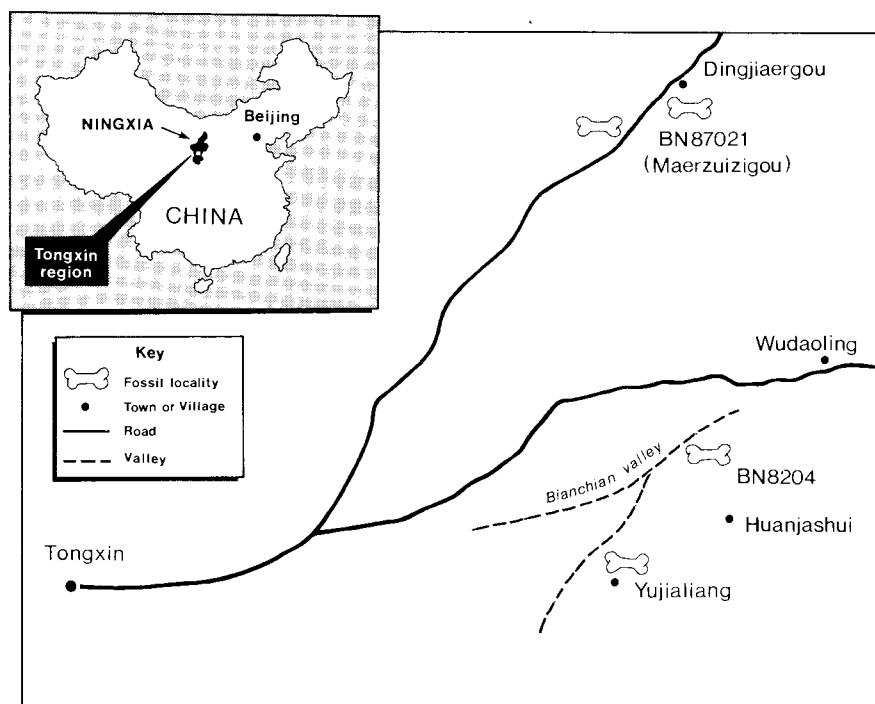


Figure 1. Location map of Tongxin region, including major villages and fossil localities. Most of the *Pliopithecus* specimens described here come from the Maerzuizigou (BN 87021) locality, while the nearby site has yielded no primates, but provides evidence that several fossiliferous horizons occur in the Tongxin faunal sequence. Farther south, in the Bianchian Valley is located BN 8204 and various other sites, including those yielding three other *Pliopithecus* specimens described here.

A detailed study of the fossil primate material from Tongxin shows that all of the specimens can be assigned to a single species. The range of metrical and morphological variation seen in the material is no greater than would be expected in a single species of extant anthropoid primate exhibiting a moderately high degree of sexual dimorphism. The present study has also confirmed the initial assessment by Qiu & Guan (1986) that the material should be referred to the genus *Pliopithecus* (Delson *et al.*, 1990). It demonstrates evident morphological similarities in its dental specializations and its facial morphology to *Pliopithecus* from the middle Miocene of Europe. However, the material differs from the three currently recognized species of *Pliopithecus* (Harrison, in prep.) in being considerably larger in size, and also in the details of its dental morphology. On the basis of these differences there is sufficient evidence to support the formal recognition of a new species. The aim of this paper, therefore, is to provide detailed descriptions and illustrations of the fossil primate material from Tongxin, and to discuss the systematic, biochronological and zoogeographical implications of the new species of *Pliopithecus*.

Taxonomic notes

When originally proposed, the Pliopithecidae included *Propliopithecus* from the Oligocene deposits of the Fayum in Egypt, as well as European Miocene representatives (Zapfe, 1961a).

This scheme was widely adopted and expanded upon by subsequent workers (Remane, 1965; Groves, 1972, 1974; Delson & Andrews, 1975; Szalay & Delson, 1979; Andrews, 1980; Fleagle, 1986). However, Harrison (1982, 1987) has argued that the Pliopithecidae, as traditionally conceived, is a paraphyletic taxonomic grouping comprising unrelated conservative early catarrhines. As a consequence, Harrison recognized two distinct family-groups: the Pliopithecidae Zapfe, 1961a, comprising the Eurasian Miocene genera *Pliopithecus*, *Crouzelia*, *Plesiopliopithecus*, *Anapithecus* and *Laccopithecus*; and the Propliopithecidae, comprising *Propliopithecus* (including *Aegyptopithecus*). This latter view has received support from other recent workers (Andrews, 1985; Delson, 1988; Tattersall *et al.*, 1988; Fleagle, 1988), and is used here in this more restrictive sense.

Harrison (1982, 1987, 1989a) has also suggested that most of the non-cercopithecoid catarrhines from the early Miocene of East Africa should all be tentatively assigned to a single family, the Proconsulidae Leakey, 1963. The family would include *Limnopithecus*, *Micropithecus*, *Dendropithecus*, *Simiolus*, *Kalepithecus*, *Proconsul*, *Afropithecus* and *Turkanapithecus*, and possibly also *Rangwapithecus*. The Proconsulidae is regarded as a patristic grouping of undifferentiated basal catarrhines of modern aspect, in which the inter-relationships of its constituent members are, as yet, undetermined (Harrison, 1989a). The Proconsulidae is used throughout the text in this sense. Delson (1988), however, prefers to include the early Miocene catarrhines from East Africa in a number of separate family groups in accordance with their inferred cladistic affinities.

Geology, fauna and biochronology

The Tongxin basin is located geographically in the northeastern sector of the Northwest Plateau of China. The Miocene sediments are exposed in a limited area, about 350 km² in extent, situated about 15 km to the northeast of Tongxin, the county capital (Figure 1; Guan & Rice, 1990). At a site west of Maerzuizigou, three fossiliferous horizons have been recognized in the Miocene deposits (Guan, 1988). They consist of fluviolacustrine sediments comprising a series of medium- to fine-grained yellowish-grey sandstones, intercalated with layers of gypsum sandstone and brownish clays and gravels. The *Pliopithecus* specimens of known provenience were all recovered from the uppermost fossiliferous horizon, along with an associated fauna listed in Table 1. The geological sequence at Bianchiangou, the probable area of origin for the remaining *Pliopithecus* specimens, also includes several fossiliferous horizons. It is not clear which horizon(s) may have yielded the remains of *Pliopithecus*, but it is worth noting that the differences in coloration of BPV-1024 (white bone with yellow teeth, similar to the material from Maerzuizigou) and the BGN mandible (reddish-brown bone and teeth), imply that they were recovered from several horizons within the Bianchiangou sequence. Based on stratigraphic correlation and the general similarity of the faunas, the *Pliopithecus*-bearing sites at Tongxin can be considered to be essentially contemporaneous.

The vertebrate fauna from Tongxin (Table 1) is similar to, but may be a little older than, the extensive fauna from Tung Gur, Nei Monggol, and correlates well with other faunas of broadly comparable age, such as Lengshuigou, Shanxi and Chetuoguo, Qinghai, from the northwest China faunal province (Li *et al.*, 1984; Guan, 1988; Qiu, 1990). On this basis, the Tongxin fauna can be considered to be early Tunggurian (= Faunal Unit III, early middle Miocene) in age (see also Qiu, 1990). There are also distinct faunal similarities between Tongxin and major European localities, such as Kuban (Byelometchetskaya), U.S.S.R. and

Table 1 Associated vertebrate fauna from Maerzuizigou, Tongxin

Reptilia
Chelonia
Testudinidae
<i>Testudo</i> sp.
Mammalia
Lagomorpha
Ochotonidae
<i>Alloptox</i> sp.
Carnivora
Hyaenidae
<i>Protictitherium</i> sp.
<i>Miohyaena</i> sp.
<i>Percrocuta primordialis</i>
Canidae?
<i>Gobicyon</i> sp.
Primates
Pliopithecidae
<i>Pliopithecus</i> nov. sp.
Artiodactyla
Cervoidea
<i>Stephanocemas</i> sp.
Cervidae indet.
Suidae
<i>Kubanochoerus lantianensis</i>
<i>Kubanochoerus</i> sp.
<i>Listriodon</i> sp.
Perissodactyla
Rhinocerotidae
<i>Aceratherium</i> sp.
<i>Caementodon tongxinensis</i>
<i>Huaqingtherium giui</i>
Proboscidea
Amebelodontidae
<i>Platybelodon tongxinensis</i>
Rodentia
Castoridae
<i>Monosaulax</i> sp.
Rodentia indet.

Sansan, France, which support a tentative correlation with MN6 (early Astaracian, ca. 15 m.y.a.) (Qiu *et al.*, 1988a,b; Guan, 1988).

Systematics

Order Primates Linnaeus, 1758

Suborder Euprimates Hoffstetter, 1977

Hyporder Anthroidea Mivart, 1864

Infraorder Catarrhini Geoffroy, 1812

Superfamily Pliopithecoidea Zapfe, 1961a

Family Pliopithecidae Zapfe, 1961a

Subfamily Pliopithecinae Zapfe, 1961a

Genus *Pliopithecus* Gervais, 1849

Emended diagnosis: Lower incisors moderately high-crowned and quite narrow. Lower canine high-crowned and bilaterally compressed. P_3 relatively mesiodistally short, high-crowned and narrow; mesiobuccal face for occlusion with the upper canine is steeply inclined, and little or no extension of enamel onto the mesial root. P_4 slightly broader than long, with talonid basin and mesial fovea subequal in size. Lower molars relatively long and narrow, increasing in size from M_1 to M_3 ; M_2 and M_3 with well-developed pliopithecine triangle (except *P. vindobonensis*); mesial fovea short and broad; talonid quite long and narrow; distal fovea broad and well-defined; buccal cingulum moderately well-developed; hypoconulid relatively large and positioned buccally to the midline; cristid obliqua mesially directed or slightly oblique; cusps and occlusal crests quite low and rounded; M_3 with buccal cusps arranged in a line. Upper incisors relatively high-crowned and quite narrow, with a distinct lingual cingulum. Upper canine high-crowned and bilaterally compressed. Canines with marked sexual dimorphism in size and morphology. Upper premolars relatively broad, with the paracone much more elevated than the protocone. Upper molars relatively broad, with a well-developed lingual cingulum and moderate to well-developed buccal cingulum; trigon basin much broader than long; M^2 much larger than M^1 ; M^3 large (similar in size to M^2) and morphologically well-developed. Cranium with a short face; narrow, ovoid nasal aperture; shallow subnasal clivus; circular orbits with slightly raised circumorbital rim; broad inter-orbital region; short and broad incisive canal; long and narrow palate, that tapers anteriorly to a narrow incisive region; globular neurocranium, lacking a sagittal crest; incomplete enclosure of the ectotympanic tube (after Harrison, in prep., which should be consulted for family group diagnoses).

Content: Four species—*P. antiquus* (Blainville, 1839), type species; *P. platyodon* Biedermann, 1863; *P. vindobonensis* Zapfe & Hürzeler, 1957; and *P. zhanxiangi* sp. nov.

Pliopithecus platyodon Biedermann, 1863 is resurrected as a valid species to include the holotype from Elgg, Switzerland, and the extensive material from Göriach, Austria. This species can be readily distinguished from *P. antiquus* on the basis of its larger size and the details of its dentition (Harrison, in prep.). In addition, *Pliopithecus pivoteaui* Hürzeler, 1954 is considered here to be a junior synonym of *Pliopithecus antiquus*.

***Pliopithecus zhanxiangi* sp. nov.**

Diagnosis: A large species of *Pliopithecus* (larger than all other included species), similar in cranio-dental size to the extant *Hylobates hoolock*. Lower molars with marked size increase from M_1 to M_3 . Upper canine relatively low-crowned and stout. Upper premolars and molars very broad with well-developed cingula. High incidence of secondary wrinkling on upper and lower premolars and molars.

Differential diagnosis: Differs from *P. antiquus* Blainville, 1839, the type species, in (1) being considerably larger in size (the lower molar row is 32% longer on average in *P. zhanxiangi*; see Table 2 and Figure 2); (2) having more elongated posterior molars with a slight degree of buccolingual waisting (Table 2); (3) having a more marked size differential between the lower molars (Table 2); (4) having lower molars with shorter and broader distal foveae; and (5) having a higher incidence of secondary enamel folding on the molars.

Differs from *P. platyodon* Biedermann, 1863 in: (1) being larger in size (the lower and upper molar rows are 12% and 11% longer on average respectively in *P. zhanxiangi*; see Table 2 and

Table 2 Comparative measurements of *Pliopithecus* spp.

	Molar row length ¹		Length-breadth proportions ²		Molar size differential ³	
	Upper M ₁₋₄	Lower M ₁₋₄	Upper M ₂	Lower M ₂	Upper M 1:2:3	Lower M 1:2:3
<i>P. zhanxiangi</i>						
Mean	21.0	25.5	73.9	83.6	86:100:96	76:100:114
Sample size	3	1	3	3	3	1
Range	21.0-21.1	25.5	71.0-77.6	77.2-92.8		
<i>P. antiquus</i>						
Mean		19.4		93.9		78:100:108
Sample size		2		1		1
Range		18.6-20.1		93.9		
<i>P. platyodon</i>						
Mean	19.0	22.7	78.4	88.9	90:100:89	86:100:116
Sample size	5	8	6	10	6	9
Range	18.3-19.8	20.9-24.6	75.6-82.1	83.8-97.1		
<i>P. vindobonensis</i>						
Mean	19.0	21.3	73.2	86.4	81:100:102	76:100:109
Sample size	2	2	2	3	2	3
Range	18.7-19.3	20.3-22.3	72.2-74.1	78.7-95.7		

¹Mesiodistal length of molar row.

$$^2\text{Uppers} = \frac{\text{Mesiodistal length} \times 100}{\text{Buccolingual breadth}}; \text{Lowers} = \frac{\text{Buccolingual breadth} \times 100}{\text{Mesiodistal length}}$$

$$^3\frac{\text{Mesiodistal length} \times \text{Buccolingual breadth} \times 100}{\text{Mesiodistal length} \times \text{Buccolingual breadth of } M_2}$$

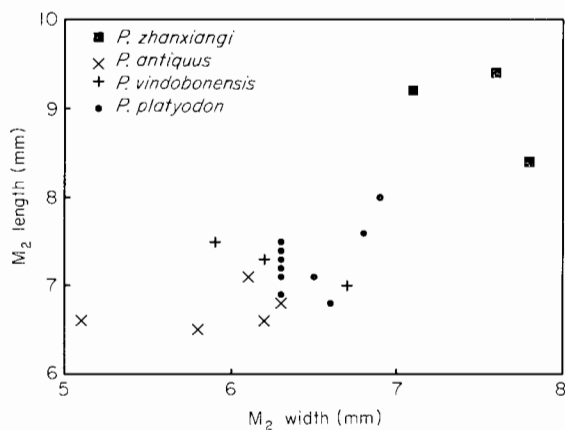


Figure 2. Scatterplot of lower second molar width and length for all known specimens of *Pliopithecus* spp. The three Tongxin specimens are clearly larger than all others.

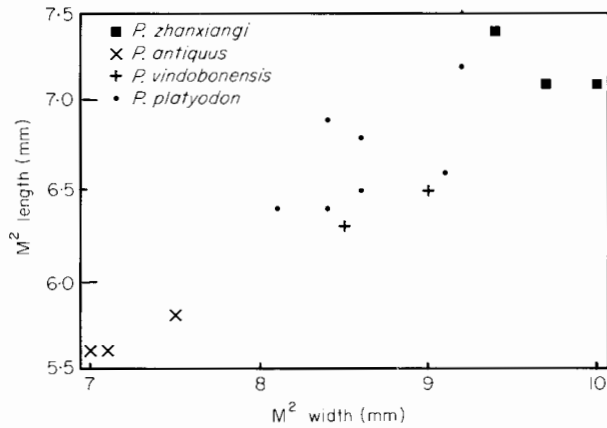


Figure 3. Scatterplot of upper second molar for all known specimens of *Pliopithecus* spp. The three Tongxin specimens are generally larger than all others, but are approximated by one *P. platyodon*.

Figures 2 & 3); (2) having relatively broader upper and lower molars (Table 2; Figures 2 & 3); having a more marked size differential between the lower molars (Table 2); and (4) having a higher incidence of secondary wrinkling on the premolars and molars.

Differs from *P. vindobonensis* Zapfe & Hürzeler, 1957 in: (1) being larger in size (the lower and upper molar rows are 19% and 11% longer on average respectively in *P. zhanxiangi*; see Table 2 and Figures 2 & 3); (2) having broader lower molars (Table 2; Figure 2); (3) the presence of a well-defined pliopithecine triangle (absent or restricted to a vestigial enamel fold in *P. vindobonensis*); (4) having a shorter, stouter and less recurved upper canine, at least in males; (5) having slightly broader upper premolars; (6) having more pronounced lingual cingulum and lacking a posterior transverse crest on P⁴; and (7) having upper molars with a more strongly developed buccal cingulum.

Holotype: BPV-1021. A crushed partial cranium, still embedded in matrix superiorly, comprising the almost complete palate, the facial and postorbital regions of the maxillae, and the entire left malar. The dentition, which is moderately to heavily worn, includes the left P³–M³ and the right P⁴–M³ (the right P⁴ and M¹ are broken). The palate also preserves the partial or entire alveoli for left I¹–C and right P³. The size of the canine alveolus suggests that the specimen belonged to a female individual (Figure 4).

Type locality: BN 87021 (Beijing Natural History Museum Locality), Maerzuizigou, near Dingjiaergou Village, Tongxin County, Ningxia Hui Autonomous Region, People's Republic of China (see Figure 1).

Distribution: Middle Miocene (early Tunggurian = early Astaracian, MN 6), Tongxin, People's Republic of China.

Referred material: BPV 261. Isolated left M₂. Lightly worn and well-preserved. Previously described by Qiu & Guan (1986). Locality: BN 87021, Maerzuizigou, Tongxin.

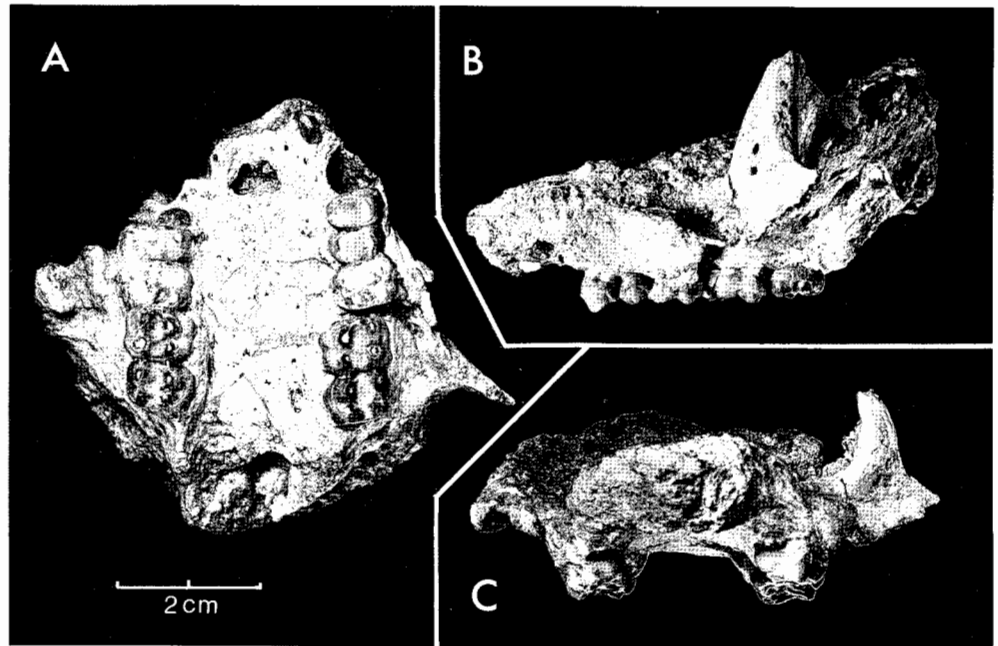


Figure 4. *Pliopithecus zhanxiangi* from Maerzuizigou, China. Holotype palate, BPV-1021: (A) occlusal view; (B) left lateral view; (C) anterior view.

BPV-1022. Badly crushed and poorly preserved cranial fragment consisting of the posterior half of the palate, with left M^2 – M^3 and right P^2 – M^3 , and the postorbital region on the left side. The dentition is moderately to heavily worn, and the left M^2 , right M^2 and right M^3 are damaged. Locality: BN 87021, Maerzuizigou, Tongxin.

BPV-1023. Left premaxilla and maxilla with C^1 – P^4 , the roots of M^1 and the partial alveoli of I^1 , I^2 and M^2 . The dentition is slightly worn and well-preserved. The canine is relatively high-crowned, which suggests that this represents a male individual. Locality: BN 87021, Maerzuizigou, Tongxin.

BPV-1024. Left maxillary fragment, consisting of the alveolar process only, with P^3 – M^3 . The dentition is moderately to heavily worn. Locality: Uncertain, but probably BN 8204, Bianchiangou, Tongxin.

BGN mandible. Right mandibular fragment with M_1 – M_3 . The mandibular corpus is complete in the region of the molars and extends posteriorly to include the anterior root of the ramus. The molars are moderately worn and the enamel surface appears to be damaged by erosion. Locality: Uncertain, but in Bianchiangou Valley, Tongxin.

BGN molar. Right M_2 in a mandibular fragment still encased in matrix. Very slightly worn, and lacking a distal contact facet for M_3 . The mesiolingual margin of the crown is slightly damaged. Locality: Uncertain, but in Bianchiangou Valley, Tongxin.

Measurements of the specimens are presented in Table 3.

Etymology: The new species is named in honor of Qiu Zhanxiang for his outstanding contribution to the study of Neogene mammals from China.

Table 3 Dental measurements of the *Pliopithecus* material from Tongxin¹

	C			P3		P4		M1		M2		M3	
	Max L	BR	BHT	MD	BL	MD	BL	MD	BL	MD	BL	MD	BL
Uppers													
BPV 1021				5.1	8.0	4.5	7.9	6.6	8.9	7.1	9.7	7.3	9.4
BPV 1022						4.4	8.0	6.9	9.3	7.1	10.0	7.1	9.3
BPV 1023	9.4	7.1	11.8 ²	5.5	7.9	6.1	9.2						
BPV 1024				4.5	6.5	4.7	7.3	6.4	8.8	7.3	9.4	7.3	9.0
Lowers													
BPV 261										9.2	7.1		
BGN													
Mandible								7.3	6.8	8.4	7.8	9.8	7.7
BGN molar										9.4	7.6		

¹Abbreviations: Max L, Maximum length; BR, perpendicular breadth; BHT, buccal height; MD, mesiodistal length; BL, buccolingual breadth.

²Minimum measurement due to wear. Estimated unworn height is 14.0.

Description of material

Cranium

The premaxilla is relatively short antero-posteriorly and quite narrow. The upper incisors of *Pliopithecus zhanxiangi* are not known, but their alveoli are preserved, at least partially, in BPV-1021 and BPV-1023. The alveolus for I¹ is too incomplete to determine its shape, but that of the upper lateral incisor was buccolingually longer than broad, and elliptical in outline. The difference in maximum mesio-distal diameter of the alveoli of I¹ (3.5 mm) and I² (3.1 mm) in BPV-1023 suggests that there was probably a quite marked size discrepancy between the two upper incisors. In addition, the lateral incisor appears to have been positioned markedly posteriorly in relation to the central incisor, which is concordant with the indication that the incisor row was set in a relatively narrow premaxilla. The diastema between I² and the upper canine appears to have been extremely small, even in males. The roots of I² and C¹ are separated by a thin lamina of bone, only 1.2 mm wide in BPV-1023 (a male individual) and 2.3 mm wide in BPV-1021 (considered to be a female individual) (Figures 4 & 5).

The facial portion of the premaxilla is not preserved in any of the specimens, so useful information on the height and construction of the subnasal clivus and the morphology of the nasal aperture is lacking.

The palatal surface of the premaxilla is perforated by numerous minute vascular canals. Just posterior to the level of the lingual margin of the I¹ alveolus, the midline of the premaxilla is interrupted by a large incisive fossa. In BPV-1021, the fossa is relatively short and broad (7.5 mm long × 7.7 mm wide), and is placed far anteriorly on the palate, only 1.7 mm behind the posterior limit of the central incisor alveoli. Posteriorly, the fossa extends back in the midline as far as the level of the distal margin of the canine alveolus. The sloping internal wall of the incisive canal, visible in ventral view, is produced by the posterior extension of the subnasal portion of the premaxilla superiorly, which then serves to restrict direct communication between the oral cavity and the nasal passage to a non-overlapping area only 3.7 mm

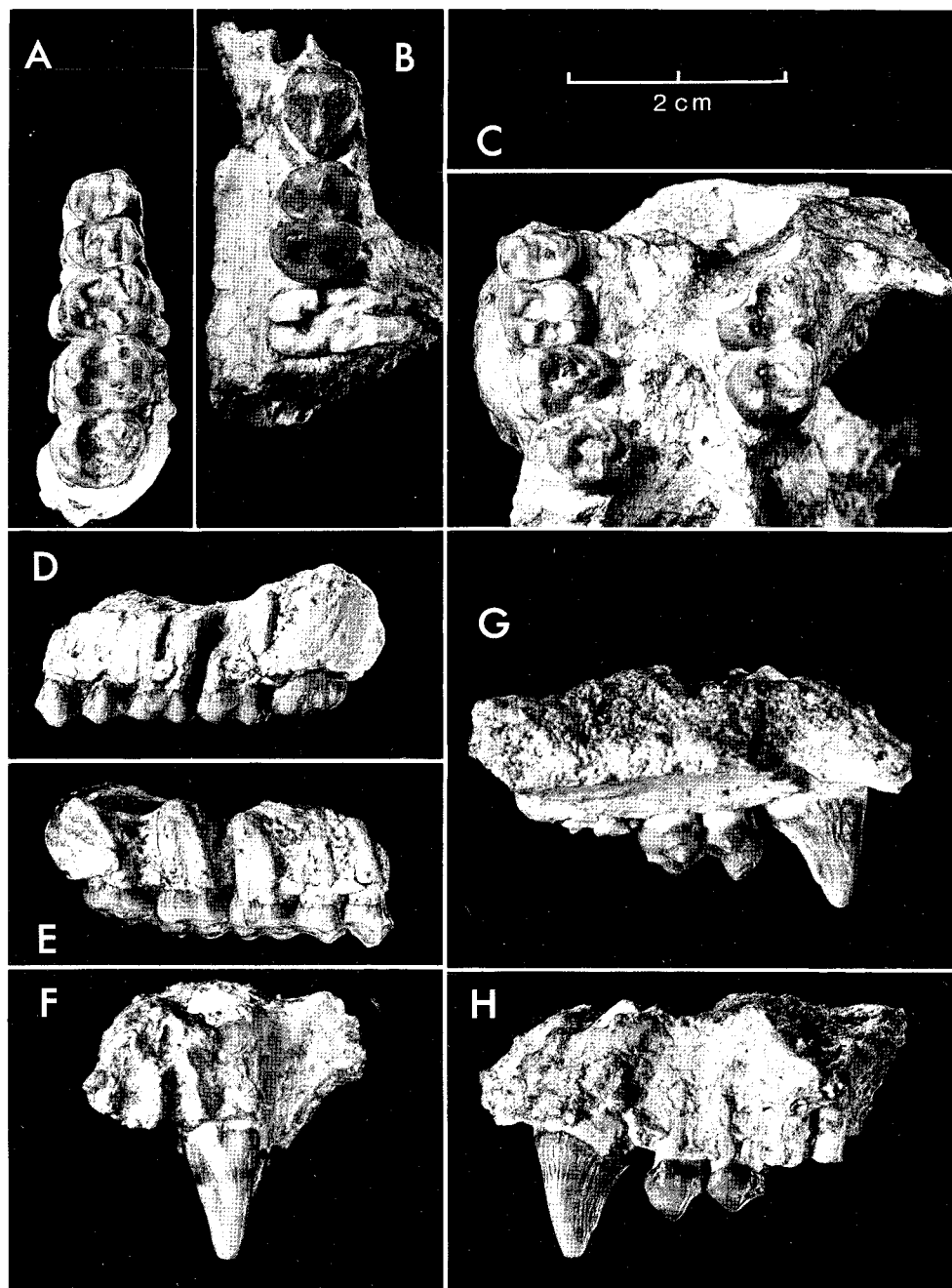


Figure 5. *Pliopithecus zhanxiangi* from Tongxin area, China. BPV-1024 (Bianchiangou), ?female L P¹-M³ in fragment of alveolar process: (A) occlusal view; (D) buccal view; (E) lingual view. BPV-1023 (Maerzuizigou), male L premaxilla and maxillary fragment with C¹-P¹, roots of M¹ and some alveoli: (B) occlusal view; (F) anterior view; (G) lingual view; (H) buccal view. BPV-1022, posterior palate with L M²⁻³, R P¹-M²: (C) occlusal view.

long. The anterior margin of the incisive fossa bears the remains of a slender sagittal septum which subdivided the canal into a pair of bilaterally arranged openings.

The palate appears to be relatively long and narrow, and is quite shallow with a slight degree of transverse arching. The toothrows apparently converged slightly as they approached the narrow incisive region. The posterior margin of the palate is poorly preserved, but it appears to have had a shallow double-arched configuration with a small midline tubercle. This is a pattern common to most extant anthropoids. Opposite the lingual margin of M^3 the palate bears a small aperture for the greater palatine foramen, which opens anteriorly into a narrow groove on the palate running beside M^2 and M^3 (Figure 4).

Posteriorly, the alveolar process of the maxilla ends abruptly behind M^3 , and there is little or no development of a distinct posterior tubercle. Its posterior face bears a sharp crest that ascends the process to become continuous with the pterygoid wing of the sphenoid. Posterior to the palatine in BPV-1021, a small fragment of the sphenoid has been dislodged and crushed anteriorly and slightly medially into the posterior opening of the nasal passage. The fragment preserves a large elliptical aperture, which presumably represents the remains of the *foramen ovale*. The anterior margin of the *foramen ovale* is also preserved in place in BPV-1022. Interestingly, in both specimens the foramen is located entirely within the corpus of the sphenoid, and not placed peripherally as in many anthropoids, in which the medial border is provided by the petrosal.

The facial portion of the maxilla is inflated anteriorly, at least in males, to form a distinct canine juga, which accommodates the large canine root. Posteriorly, above the upper premolars, the maxilla is depressed to form a shallow canine fossa. The maxillary corpus is quite robustly constructed and the enclosed maxillary sinus does not appear to have been extensive. The floor of the sinus does not penetrate deeply between the roots of the cheek teeth. Instead, the roots are solidly embedded in the alveolar body of the maxilla, and the floor of the sinus does not descend much below the level of the apices of the tooth roots. However, in BPV-1023, at least, the sinus does extend laterally into the anterior root of the zygomatic arch.

The anterior root of the zygomatic arch originates above M^1 . Its inferior border is located relatively low on the face, only about 8 mm above the cementum-enamel junction of M^1 . The junction of the maxilla and malar bears a distinct tubercle inferiorly to mark the anterior origin of the masseter. The zygomatic arch is relatively deep infero-superiorly, but extremely slender. When viewed anteriorly, the superior margin of the zygomatic arch has a substantial overlap with the orbit in the dorsoventral plane (Figure 4).

In BPV-1021 the left malar is preserved virtually intact. The facial portion preserves the infero-lateral quadrant of the orbit. The orbit appears to have been moderately large, concordant in size with extant anthropoids of similar cranio-dental size, and subcircular in outline. The outer orbital margin is smoothly rounded and projects slightly to form an incipiently developed circumorbital rim. The floor and lateral wall of the orbit are confluent with the orbital margin, and there is no distinct step-down from the face into the orbital cavity. The internal wall of the orbit is perforated laterally by a relatively large foramen which exits onto the anterior face of the malar as a pair of small elliptical zygomatic foramina (Figure 4).

The anterior root of the zygomatic arch gives rise to two ill-defined crests that pass superiorly around the lateral wall of the frontal process of the malar. The low and rounded anterior crest defines the limit of attachment for the temporalis muscle behind the orbit. It is separated from the posterior crest by a flattened plateau approximately 4 mm wide. As a

result, the facial and postorbital planes of the malar meet at a relatively obtuse angle. The postorbital plate fully encloses the orbit posteriorly, except for a large inferior orbital fissure, which in BPV-1022 forms a transversely-oriented slit almost 17 mm long.

Mandible

The mandible of *Pliopithecus zhanxiangi* is known only from a single specimen, the BGN mandible (Figure 6). The mandibular corpus beneath the molars is relatively stoutly constructed. Externally, the line leading to the anterior margin of the ascending ramus originates midway down the mandible below M_1 . The external surface of the corpus is strongly convex dorsoventrally. The ramus partially obscures the posterior portion of M_3 when the mandible is viewed from the lateral aspect. The mandibular corpus shallows slightly as it passes posteriorly, but becomes increasingly more robust. The inferior margin of the mandible is thick and rounded. Internally, the mandibular corpus is steep and only slightly convex. The anterior root of the ramus bears an almost circular mandibular foramen on its internal aspect. The opening of the foramen, which is located horizontally just below the occlusal plane of M_3 , is oriented obliquely in an antero-inferior direction.

Dentition

Lower teeth. The lower dentition of *Pliopithecus zhanxiangi* is known only from the BGN mandible, which preserves M_1 – M_3 , and two M_2 s, BPV-261 and the BGN molar (Figure 6). As M_2 is best known it therefore provides the primary basis for the following description of lower molar morphology in *Pliopithecus zhanxiangi*.*

M_2 is relatively elongated and rectangular in shape, with a slight degree of buccolingual waisting midway along its length. The crown is slightly broader in its mesial moiety than in its distal moiety. The protoconid, metaconid and hypoconid are large and subequal in size. The hypoconulid and entoconid are both slightly smaller. The protoconid is conical in shape and voluminous, and is situated close to the mesial margin of the crown. Four low and rounded crests originate from its apex. The preprotocristid is short and terminates mesially at the margin of the crown. There is no trace of a paraconid. A well-developed crest, the hypoprotocristid, passes lingually and slightly distally to meet a reciprocal crest from the metaconid. The postprotocristid is arranged mesio-distally in line with the preprotocristid. It is relatively short, and is continuous with the cristid obliqua which originates from the hypoconid. In the angle formed by the hypoprotocristid and the postprotocristid an ill-defined crest descends distobuccally from the apex of the protoconid to terminate in the talonid basin. The metaconid is pyramidal in form, and is situated slightly more distally than the protoconid. The premetacristid is relatively sharp and arcs buccally to become continuous with the mesial marginal crest. The hypometacristid passes slightly mesially to meet the hypoprotocristid, and together they form a slightly oblique distal trigonid crest. The trigonid basin is a relatively large, quite deep and well-defined triangular depression, finely intersected by a Y-shaped groove. The postmetacristid is short and rounded.

In BPV-261, a small tubercle on the lingual margin of the crown presumably represent a derivative of this latter crest. The hypoconid is large and is well-separated from the protoconid mesially. The cristid obliqua (= the prehypocristid) is very long, but low and rounded, and only slightly obliquely oriented with respect to the long axis of the crown. A fine crest

*The terminology for upper and lower molar morphology used throughout the paper essentially follows that of Szalay & Delson (1979).

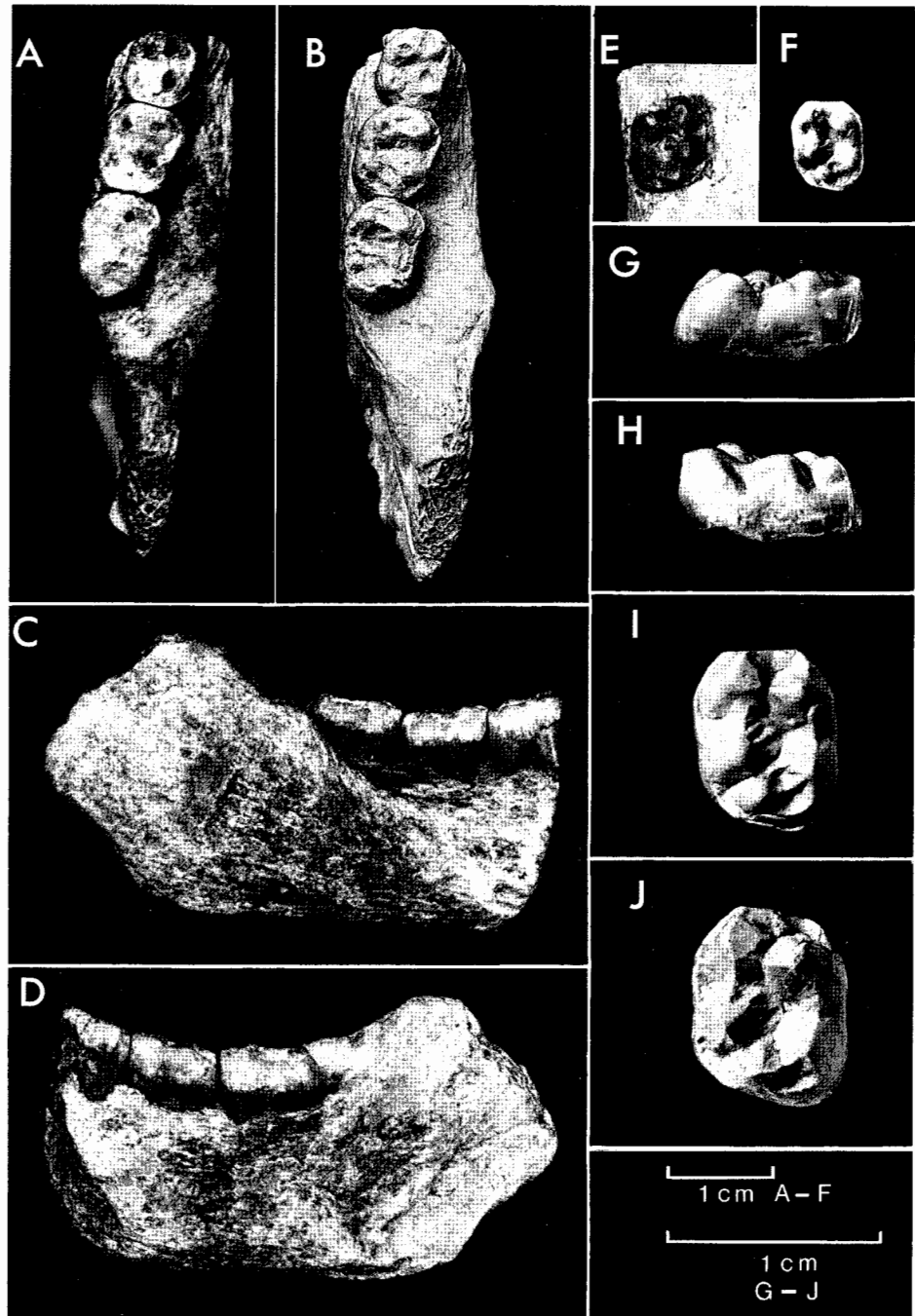


Figure 6. *Pliopithecus zhanxiangi* from Tongxin area, China. BGN mandible (Bianchiangou), fragment of right corpus with M₁; (A) occlusal view; (B) occlusal view of cast; (C) buccal view; (D) lingual view. BGN molar, R M₂ in jaw fragment and matrix: (E) occlusal view; (J) occlusal view of cast (photographically reversed). BPV-261 (Maerzuizigou), L M₂ crown; (F) occlusal view; (G) buccal view; (H) lingual view; (I) occlusal view of cast.

originates from the apex of the hypoconid and passes mesiolingually to terminate almost in the center of the talonid basin. This crest, along with the distolingual crest of the protoconid, defines a small triangular fovea, the pliopithecine triangle, located entirely within the confines of the talonid basin. The connivent arrangement of these two crests allows a wide communication lingually between the enclosed fovea and the main talonid basin. The posthypocristid passes distally and slightly lingually from the apex of the hypoconid to terminate at the base of the hypoconulid. The hypoconulid is the smallest of the five main cusps. It is located slightly buccally to the midline of the crown in close association with the hypoconid. A short crest passes mesio buccally to the base of the hypoconulid where it meets the posthypocristid. The entoconid is small in size, but is quite elevated. The preentoconid cristid is sharp and well-defined. It is separated from the distal termination of the postmetaconid cristid by a deep lingual talonid notch. A fine crest also passes obliquely distobuccally from the apex of the entoconid to meet the hypoconulid. This defines a broad D-shaped distal fovea which bulges distally beyond the level of the hypoconulid. The talonid basin is long and narrow, and quite shallow, being only slightly less elevated than the trigonid basin. The talonid basin is usually simple in construction, and apart from the development of a distinctive pliopithecine triangle, the groove system conforms to the basic *Dryopithecus* Y-5 pattern. However, BPV-261 does exhibit subsidiary crest formation along the cristid obliqua and between the entoconid and hypoconulid. The buccal cingulum is well-developed and is represented by a narrow enamel ledge about midway up the buccal aspect of the crown. The cingulum is continuous, apart from a short break below the apex of the hypoconid.

M_1 is similar in general morphology and proportions to M_2 , but differs mainly in being much smaller in size (M_1 is only 76% of the occlusal area of M_2). Other differences include: relatively smaller mesial and distal foveae, a less well-developed buccal cingulum, a more restricted talonid basin, and probably no development of a pliopithecine triangle.

M_3 is larger than M_2 (M_3 is 114% of the occlusal area of M_2) and relatively much longer. The crown is long and narrow, and tapers distally. The metaconid and protoconid are both large in size, with the latter being the most voluminous. They are transversely aligned and are connected by a short crest. The mesial fovea is relatively broad, being more expansive than M_1 or M_2 . The protoconid, hypoconid and hypoconulid are arranged almost in line and are connected by a series of well-developed crests. The cristid obliqua is short and almost perfectly longitudinally aligned. The pliopithecine triangle is small, but well-defined. The hypoconid and hypoconulid are slightly smaller than the mesial pair of cusps, but they are still well-developed. The entoconid is very small and is perched on the marginal rim of the tooth, and is widely separated from the hypoconulid. There is no development of a hypoconulid-entoconid crest, and as a result the distal fovea is not delimited from the talonid basin. The talonid basin is long and narrow and is disrupted by the development of a number of subsidiary crests. The buccal cingulum is prominent, forming a continuous, but irregular shelf around the buccal margin of the crown.

Upper teeth. The only upper canine known, associated with the maxilla BPV-1023, is presumably that of a male individual, judging from its large size and relative crown height (Figure 7). The canine is quite robust, moderately high-crowned and strongly bilaterally compressed. It exhibits a slight degree of distal and lingual recurvature. The crown is moderately worn, and this has probably reduced the apico-basal height of the crown by as much as several millimeters. The crown is set on a very thick root, which also exhibits a moderate degree of distal recurvature. The lingual face of the crown is dominated by a prominent

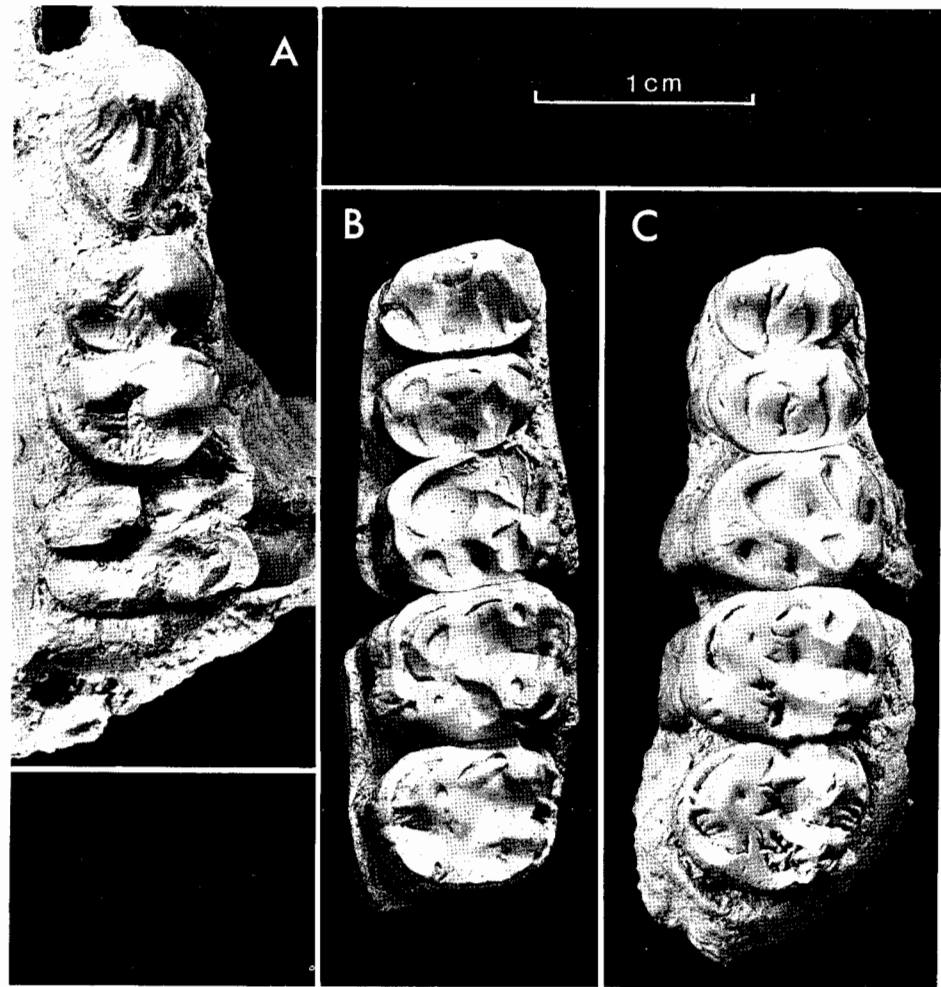


Figure 7. *Pliopithecus zhanxiangi* from Tongxin area, China. Occlusal view of maxillary teeth (photographs of casts). (A) BPV-1023 (Maerzuizigou), male L C¹-P¹; (B) BPV-1024 (Bianchiangou), ?female L P³-M¹; (C) BPV-1021, holotype (Maerzuizigou), female L P³-M¹ (M^{2 3} reset against M¹ by approximating contact facets).

lingual pillar, which is broadest basally and tapers towards the apex. Mesially, the lingual pillar is separated from the mesial crest of the crown by a deeply incised groove, which does not continue past the base of the crown onto the root. Originating from the base of the mesial ridge, an irregular and poorly-defined lingual cingulum passes distally around the lingual face of the crown. Just posterior to the lingual pillar, the lingual face of the crown is concave, producing a sharp, rather blade-like distal margin. The buccal surface is convex and featureless, apart from a shallow depression disto-basally, which accentuates the blade-like configuration of the distal crest. The distal crest is long and concave, and terminates basally at a small distal heel. The enamel surface of the crown is disrupted by a series of fine apico-basal striations. Wear, produced by occlusion with the distal margin of the lower canine, has flattened the mesial crest along its entire length, and has even cut through to the dentine at

the base of the crown. A wear facet also occurs on the apical aspect of the lingual pillar. The distal crest is moderately worn, with a narrow strip of dentine exposure along its lingual margin from the apex to the distal heel. This has been produced by occlusion with the mesiobuccal face of P_3 . The upper canine alveolus in BPV-1021, which measures 7.0×5.9 mm, is 38% smaller than the basal cross-sectional area of the upper canine in BPV-1023. This confirms that *Pliopithecus zhanxiangi*, like other pliopithecids from Eurasia, exhibits a moderately high degree of sexual dimorphism in canine size (Hürzeler, 1954; Harrison, 1982; Pan *et al.*, 1989).

P^3 is relatively broad and ovoid in shape, being slightly shorter in its lingual moiety than its buccal moiety. The two main cusps, the paracone and protocone, are positioned slightly mesial of the mid-transverse line. The paracone is very elevated and pyramidal in form. Although worn in all specimens, the mesio-distally aligned preparacrista and postparacrista were apparently sharp and well-developed. The preparacrista descends steeply from the apex of the paracone to terminate mesially at a parastyle situated on the narrow cingular shelf. The preparacrista bifurcates close to its apex to give rise to a hypoparacrista. In BPV-1023 the latter crest passes obliquely mesio-lingually to terminate at a well-developed paraconule perched on the mesial margin of the crown. In BPV-1021, by contrast, the hypoparacrista passes directly transversely to the base of the protocone, and there is no development of a distinct paraconule. The preparacrista, the hypoparacrista and the mesial marginal crest delimit a narrow but well-defined mesial fovea. The postparacrista is similar in length to the preparacrista, but it is more steeply inclined. It terminates distally at a style on the marginal ridge of the crown. The protocone is low and rounded, being much smaller and less elevated than the paracone. In addition, the protocone is located slightly more mesially than the paracone. In BPV-1021 and BPV-1024 the preprotocrista arcs buccally to become continuous with the mesial marginal ridge, while in BPV-1023 the crest is indistinct, and the protocone is separated from the closely associated paraconule by a shallow groove. A postprotocrista was present, but is heavily worn in all specimens, and its development cannot be ascertained. A second transverse crest linking the cusps distally is lacking. As a result, the distal basin is expansive. It is subdivided bilaterally by a deep mesiodistal groove. In BPV-1023 the enamel surface of the distal basin is disrupted by a series of fine wrinkles, and there is evidence from the other more worn specimens that some degree of wrinkling or secondary enamel folding is a characteristic feature of the upper premolars of this species. In BPV-1023 a narrow lingual cingulum originates from the paraconule and passes around the protocone as an irregular enamel ledge to become continuous with the distal marginal ridge. A lingual cingulum on P^3 is a rare feature in fossil catarrhines, except among oreopithecids (Harrison, 1986). However, a lingual cingulum appears to be lacking in the other P^3 s from Tongxin, and is probably not typical of the species. In all specimens the buccal face of the crown bears a narrow cingular shelf. In BPV-1021, the buccal cingulum is well-developed and forms an almost continuous, but irregular, rim around the base of the crown. In BPV-1023 and BPV-1024 the buccal cingulum is represented by a narrow ledge of enamel originating mesially at the parastyle and ascending the buccal face almost to the base of the crown (Figure 7).

P^4 is generally similar in its morphology to P^3 . It is comparable in occlusal area with P^3 , being slightly smaller in size in BPV-1021 and slightly larger in size in BPV-1023 and BPV-1024. P^4 differs from P^3 in the following details: the crown is more regularly ovoid in occlusal outline; the protocone is larger and more elevated, while the paracone is lower; there is always a well-developed lingual cingulum; and the buccal cingulum is more pronounced in

its development. The upper premolars of BPV 1023 are unusual in a number of respects, and when compared with the other Tongxin specimens they appear to be atypical. For example, the presence of a large protoconule, the very small size of the protocone, and the occurrence of a lingual cingulum on P^3 , the low rounded cusps and the irregular outline of the crown in P^4 , as well as the obvious size discrepancy between P^3 and P^4 (P^4 occlusal area is 129% that of P^3 , compared with 87% in BPV-1021 and 117% in BPV-1024) are certainly unusual characters among early catarrhine primates. These features are presumably due to normal populational variation that should be taken into account when attempting to identify the typical morphological pattern of *Pliopithecus zhanxiangi* (Figures 5 & 7).

All the upper molars are moderately to heavily worn, so the occlusal morphology, particularly that of M^1 , cannot be determined in any detail. Nevertheless, the M^2 s are sufficiently unworn to provide the basis for a general review of the morphology of the upper molars.

M^2 is relatively broad and is rectangular in occlusal outline, with a slight degree of buccolingual waisting. The protocone is the most voluminous of the four main cusps. A prominent crest, the preprotocone crista, passes mesiobuccally from the apex of the protocone to terminate at a low rounded paraconule. This crest continues mesially as the preparaconule crista, which blends in with the marginal crest almost midway across the mesial margin of the crown. The postprotocone crista passes distobuccally and meets with the hypometacrista to form a well-developed crista obliqua. There is no evidence of a distinct metaconule. Also originating from the protocone is a short, robust crest that passes distally to meet with a similar crest from the hypocone, the prehypocone crista. These latter two crests are separated by a fine groove, connecting the talonid basin with the lingual cingulum. The paracone and metacone are subequal in size, being slightly more elevated and more conical than the protocone, but somewhat less voluminous. The paracone has a short mesial crest, the preparacrista, which terminates at the mesial margin of the crown in a small parastyle. The paracone also gives rise to a lingual crest, the hypoparacrista, which passes transversely across the crown to terminate at the paraconule. This crest forms the distal wall of a narrow, fissure-like mesial fovea. The premetacrista and the postmetacrista of the metacone are mesio-distally oriented and sharply defined. The latter crest terminates distally at a small metastyle on the marginal ridge. The trigon basin is well-defined and is much broader than it is long. The basin is intersected by a Y-shaped groove in which the arms pass mesially and lingually around the protocone, while the stem passes buccally between the postparacrista and the premetacrista to terminate at the cingular shelf. In addition, the remnants of other fine grooves in the talon basin indicate that some degree of secondary enamel wrinkling may have been a common feature of the upper molars in the unworn state. The hypocone is the smallest of the main cusps, but is still well-developed. It is positioned slightly more lingually than the protocone, and is located very close to the distolingual margin of the crown. The prehypocone crista and the posthypocone crista are both short, low, rounded crests originating from the apex of the hypocone. The distal basin, delimited mesially by the crista obliqua, is relatively restricted, due to the large size of the hypocone. In BPV-1022 and BPV-1024, the distal basin is disrupted by heavy wrinkling, while in the holotype, BPV-1021, the enamel surface of the basin appears to be relatively smooth. The lingual cingulum forms a prominent L-shaped ledge around the mesial and lingual margins of the protocone, but it does not continue distally around the hypocone. The buccal cingulum is generally well-developed. It forms a distinct but discontinuous shelf linking the parastyle with the metastyle about midway up the crown (Figures 5 & 7).

M¹ conforms to the general morphological pattern of M², but differs in being smaller in size (M¹ is only 86% of the occlusal area of M²) and having less well-developed lingual and buccal cingula. The associated upper dentitions also demonstrate a strong wear differential between M¹ and M². In BPV-1021, for example, dentine exposure on M¹ exceeds 50% of the occlusal surface area, while that on M² is less than 3%.

M³ is slightly smaller than M² (being 96% of the occlusal area of M²), but larger than M¹. The crown is broad and D-shaped, with a rounded distal margin. The arrangement of the cusps and crests is essentially the same as on M², although the distal portion of the crown has undergone morphological regression. The protocone and paracone are comparable in size and shape to those on M², while the metacone is slightly reduced and the hypocone is very small. A distinct parastyle and metastyle are present on the mesial and distal margins of the crown respectively. The mesial fovea is represented by a broad transverse groove. The trigon basin is broader than long, well-defined, but relatively shallow. The crista obliqua is relatively low, presumably related to the reduction in size of the metacone. The distal basin is short and broad, with extensive secondary wrinkling of the enamel surface. The lingual cingulum forms a broad C-shaped ledge around the mesial and lingual aspects of the protocone. The cingulum is disrupted by a number of fine crests that radiate out lingually from the base of the protocone. The buccal cingulum is better developed than on M². It forms a narrow, almost continuous ledge located midway up the buccal face of the crown (Figures 5 & 7).

One remarkable feature of the upper and lower molars is the prominent degree of interstitial wear that has occurred, especially on the mesial faces of the crowns. This is quite striking, particularly when compared with other small Miocene catarrhines from East Africa and Eurasia, which rarely exhibit such advanced stages of interstitial wear, even in more senile individuals. In view of the relative degree of occlusal wear on the molars from Tongxin, this phenomenon is unlikely to be explained purely by ontogenetic processes. In BPV-261, for example, the crown is very lightly worn, and yet marked interstitial wear has almost entirely removed the enamel from the mesial face of the crown (see Figure 6I). It seems more likely, therefore, that the exaggerated interstitial wear in relation to the degree of occlusal wear in the Tongxin sample may be a response to dietary or biomechanical factors.

Comparison

The following comparisons serve to establish the distinctiveness of the new species of *Pliopithecus* from other small catarrhine primates from the Miocene of Eurasia. The comparisons are organized, so as to form a nested set of outgroups of increasing relatedness. In this way, the comparisons not only set out diagnostic criteria for the new species, but also provide our justification for the generic and higher-order rankings adopted here.

Sihong catarrhines

The Xiacaowan Formation at Sihong, Jiangsu Province (eastern China) has yielded the remains of at least three species of catarrhine primates. The precise age of the formation is uncertain, but faunal correlations and radiometric age determinations of underlying and overlying deposits support an age of 16–17 m.y.a. (Upper Shanwangian, Faunal Unit II, equivalent to MN 4b or MN 5) (Li *et al.*, 1983; Jin, 1985; Qiu *et al.*, 1986; Qiu & Gu, 1986; Qiu & Lin, 1986; Bernor *et al.*, 1988; Qiu, 1990). The Xiacaowan primates are therefore among the oldest recorded catarrhines in Eurasia and are somewhat older than the material from Tongxin (see Figure 10 below).

The best known taxon from Sihong is *Dionysopithecus shuangouensis*, which is represented by a left maxillary fragment with M^1 – M^3 (Li, 1978), and other as yet unpublished specimens (Gu Yumin, personal communication). In addition, several isolated teeth from the Kamli Formation of northern Pakistan and the Manchar Formation of southern Pakistan, dated at about 16–17 m.y.a., have tentatively been referred to this genus (Raza *et al.*, 1984; Barry *et al.*, 1987; Bernor *et al.*, 1988). Four further species of fossil primates have been described from Sihong. Gu & Lin (1983) named *Platodontopithecus jianghuaiensis* on the basis of five isolated molars, while Lei (1985) described *Hylobates tianganhuensis*, *Pliopithecus wangi* and *Dryopithecus sihongensis* based on single isolated molars. *Platodontopithecus jianghuaiensis* and “*Dryopithecus*” *sihongensis* are both larger and morphologically distinct from *Dionysopithecus shuangouensis*, and clearly represent different species. However, *Hylobates tianganhuensis* and *Pliopithecus wangi* are considered to be junior synonyms of *Dionysopithecus shuangouensis* (see Bernor *et al.*, 1988, for further discussion).

The Xiacaowan primates appear to be closely related to the catarrhine primates from the Miocene of East Africa, which apparently extended their range into subtropical and tropical parts of Asia during the late early Miocene (Bernor *et al.*, 1988). They are most similar in their molar morphology to the proconsulids, and they can be distinguished from *Pliopithecus zhanxiangi* and other pliopithecids in the following respects: (1) the lower molars are generally relatively broader; (2) the lower molars lack a pliopithecine triangle; (3) the cristid obliqua is shorter and less obliquely directed; (4) the mesial fovea of the lower molars is relatively shorter; (5) the hypoconulid is larger in relation to the other main cusps; (6) the hypoconulid is displaced lingually in relation to the other buccal cusps on M_3 , such that the buccal cusps are not linearly arranged; (7) the size differential between the lower molars is much less marked; (8) the upper molars are usually relatively narrower; (9) M^1 is more similar in size to M^2 , and M^3 is relatively much smaller; and (10) the crests and cusps on the upper and lower molars are less elevated and more rounded.

More specifically, the upper molars of *Dionysopithecus shuangouensis* can be distinguished from those of *Pliopithecus zhanxiangi* in the following features: (1) they are much smaller in size (the upper molar row is only 72% of the average upper molar row length in *Pliopithecus zhanxiangi*); (2) they are buccolingually narrower, with more rounded corners to the crowns; (3) M^1 is more comparable in size to M^2 , while M^3 is much more reduced; (4) the main cusps are less voluminous and more discrete; (5) the hypocone is relatively larger, being more similar in size to the trigon cusps; (6) the trigon is smaller in relation to the size of the talon; (7) the lingual cingulum continues around the hypocone on M^2 and M^3 ; and (8) the buccal cingulum is less well-developed.

Unfortunately, detailed comparisons with *Platodontopithecus jianghuaiensis* are made difficult by the inadequacy of the material. Only five isolated molars are known: two heavily worn upper molars (IVPP PA 849 and PA 850); a broken and poorly preserved lower molar (IVPP PA 871); an unworn M^3 (IVPP PA 851) and a lightly worn, well-preserved M_3 (IVPP PA 870). The best sources of comparison are the two posterior molars (IVPP PA 851 and PA 870), which, being notoriously variable, may not provide a fair representation of typical molar morphology in *Platodontopithecus*. Nevertheless, there are sufficient grounds to be able to distinguish the molars of *Platodontopithecus* from *Pliopithecus zhanxiangi*. The M^1 and M^2 of *Platodontopithecus* differ in: (1) being slightly smaller in size; (2) being relatively narrower; (3) being less rectangular in occlusal outline, with more rounded corners; (4) being mesiodistally longest in the lingual moiety, and narrowing buccally (the inverse relationship is typical in *Pliopithecus zhanxiangi*); (5) having less pronounced occlusal relief at comparable stages of

wear (PA 850 has a much flatter occlusal table than the M^2 in BPV 1021, although they are similar in having small areas of dentine exposure at the apex of each of their four main cusps); and (6) having the paracone and metacone more marginally placed, and the associated styles more weakly expressed. The M^3 of *Platodontopithecus* differs from *Pliopithecus zhanxiangi* in: (1) being more mesiodistally elongated; (2) having a more massively developed lingual cingulum; (3) having a more strongly reduced paracone, metacone and hypocone; (4) having a lower occlusal topography; and (5) having a greater degree of secondary wrinkling of the enamel surface. The M_3 of *Platodontopithecus* is much more readily distinguishable from *Pliopithecus zhanxiangi* than the other molars, and in fact represents the most diagnostic tooth of *Platodontopithecus*. It differs from that of *Pliopithecus zhanxiangi* in: (1) being relatively mesiodistally shorter; (2) in having a relatively shorter and less well-defined mesial fovea; (3) the talonid basin being broader, shallower and more open, with no development of transverse crests; (4) the buccal cingulum being better developed, forming a continuous beaded ledge around the buccal aspect of the crown; (5) the hypoconulid being more lingually placed relative to the hypoconid, such that the three buccal cusps are not linearly arranged; (6) having a better developed entoconid, subequal in size to the hypoconid and hypoconulid; (7) having the entoconid and hypoconulid more closely approximated; (8) lacking a pliopithecine triangle; (9) having a larger, but less well-delimited distal fovea; (10) having more weakly developed crests; and (11) having a lower occlusal topography.

A problem with the original description of *Platodontopithecus jianghuaiensis* by Gu & Lin (1983), that may impinge on the discussion of *Pliopithecus zhanxiangi*, is the fact that the authors list four isolated molars as the holotype. However, it is evident from the size and relative state of wear of these molars that they do not comprise a dental series from a single individual. Although it is reasonable to assume on present evidence that these belong to a single species, it is not inconceivable that they may later prove to belong to different taxa. In order to circumvent this possibility, it would be prudent and in the interests of taxonomic stability to identify a single molar as a type specimen. As the M_3 (IVPP PA 870) is well-preserved, and is the most easily distinguishable from other Miocene catarrhines, including *Pliopithecus zhanxiangi*, we propose to nominate it as the lectotype of *Platodontopithecus jianghuaiensis* (see Article 74(a) of the International Code of Zoological Nomenclature, Ride *et al.*, 1985).

The relationships of “*Dryopithecus*” *sihongensis*, represented by an isolated molar only, are difficult to determine, but it may have closer affinities with the more conservative East African genera, *Proconsul* and *Afropithecus*, or possibly even *Kenyapithecus*, than with European *Dryopithecus* (Bernor *et al.*, 1988). The specimen differs from the lower molars of *Pliopithecus zhanxiangi* in: (1) being considerably larger in size; (2) being relatively broader; (3) lacking a pliopithecine triangle; (4) having a shorter and less oblique cristid obliqua; (5) having a relatively larger hypoconulid; and (6) having more voluminous main cusps.

“*Krishnapithecus*”

In 1924 Schlosser described and figured a heavily worn left upper third molar from Ertemte, Nei Monggol, for which he named a new species, *Pliopithecus posthumus*. Based on faunal evidence the site is considerably younger than that from Tongxin, probably latest Miocene in age, being best correlated with MN 13 (Li *et al.*, 1984; Qiu, 1990). Unfortunately, however, the specimen is much too worn to be certain of its taxonomic affinities, and several authors have even questioned whether it belongs to a primate at all (Hürzeler, 1954; Simons, 1972; Simons & Fleagle, 1973; Fleagle, 1983). Certainly the configuration of the roots is unusual for

a primate, but apart from this, there is little evidence either to confirm or to refute its primate status. The specimen is a little larger and relatively narrower than the upper third molars from Tongxin, being closer in size and proportions to those of small dryopithecines, such as *Dryopithecus laietanus* from Spain. Until more fossil primate material is recovered from the deposits at Ertemte, it is impossible to make any definitive statements about the taxonomic status of this specimen. It is, perhaps, best to regard it as of indeterminate status and unlikely, on the basis of its age, size and proportions, to enter into synonymy with *P. zhanxiangi*.

Chopra & Kaul (1979) assigned an isolated and rather worn M^3 from Haritalyengar in northern India to a new species, *Pliopithecus krishnani*. The site of Haritalyengar is late Miocene in age, dated by magnetic polarity stratigraphy to 7.4 m.y.a. (Johnson *et al.*, 1983; Barry, 1986). The taxonomic affinities of the specimen are uncertain, because of the difficulties of identifying species on the basis of isolated and worn upper third molars. In the shape of the crown, the distribution and relative size of the cusps, and the configuration of the narrow lingual cingulum, the specimen is most reminiscent of M^3 s in the Sihong primates and the small catarrhine primates from the early Miocene of East Africa, and contrasts with the broader and more rectangular crown in *Pliopithecus*. The specimen is also much smaller than *Pliopithecus zhanxiangi* (the occlusal area is only 60% that of M^3 in *P. zhanxiangi*), and is more similar in size to *Pliopithecus antiquus*, or even *Dionysopithecus shuangouensis*.

More recently, Ginsburg & Mein (1980) have included *Pliopithecus posthumus* and *Pliopithecus krishnani* in a separate genus, *Krishnapithecus*. However, this seems an unjustified move in view of the paucity and the uncertain taxonomic status of the included material.

"*Kansupithecus*"

An edentulous mandibular symphysis of a small catarrhine primate is known from Hsi Shui, Taben Buluk area, Gansu Province, northern China. The site is probably early Miocene in age (Thenius, 1958; Conroy & Bown, 1974; Li *et al.*, 1984; Russell & Zhai, 1987; Qiu, 1990), and is therefore broadly comparable in age to Tongxin. Bohlin (1946) originally referred the specimen to a new genus, "*Kansupithecus*", but the name remains unavailable (under Article 11 of the International Code of Zoological Nomenclature, Ride *et al.*, 1985) because he failed to provide a species name for the taxon (Szalay & Delson, 1979; Bernor *et al.*, 1988). The configuration of the symphyseal region of the mandible is not available for comparison in the Tongxin material, but the specimen from Taben Buluk is consistent in its general morphology with other small catarrhine primates from the Miocene of East Africa and Europe, including *Pliopithecus* (Szalay & Delson, 1979; Harrison, 1982). Nevertheless, the Taben Buluk mandibular fragment clearly represents a much smaller species than *P. zhanxiangi*, being comparable in size to *Dionysopithecus shuangouensis* (Bernor *et al.*, 1988). A second specimen, consisting of a fragmentary molar, was also referred to "*Kansupithecus*" by Bohlin (1946). It was recovered from the neighboring site of Yindirte in the Taben Buluk region, which is estimated to be late Oligocene in age (Li *et al.*, 1984; Thomas, 1985; Russell & Zhai, 1987). However, the molar is too incomplete to determine its taxonomic affinities, and it may not even belong to a primate (Bernor *et al.*, 1988).

Laccopithecus

A large collection of small fossil catarrhines has been recovered from the late Miocene locality of Shihuiba, Lufeng County, Yunnan, southern China, dated at about 7–8 m.y.a. (Qi, 1979, 1985; Flynn & Qi, 1982; Li *et al.*, 1984; Qiu *et al.*, 1985; Han, 1985; Qiu, 1990). The material, which has been named *Laccopithecus robustus* Wu & Pan, 1984, is evidently closely related to

the European pliopithecids (Wu & Pan, 1984, 1985; Harrison, 1987; Pan, 1988; Pan *et al.*, 1989; Fleagle, 1988). Furthermore, in its lower dentition,* *Laccopithecus* exhibits specializations which are characteristic of the crouzeliine pliopithecids (Harrison, in prep.), and as a result it can be assigned, along with *Plesiopithecus* (including *Crouzelia*) and *Anapithecus*, to the subfamily Crouzeliinae. Although *Laccopithecus robustus* and *Pliopithecus zhanxiangi* are similar in overall dental size, they are readily distinguishable on the basis of a number of morphological criteria, including those that separate the Crouzeliinae from the Pliopithecinae (Ginsburg & Mein, 1980; Harrison, in prep.). The lower molars of *Laccopithecus* differ from those of *Pliopithecus zhanxiangi* in the following respects: (1) the mesial transverse crest (formed by the hypometacristid and the hypoprotocristid) is more obliquely oriented in relation to the transverse axis of the crown; (2) the mesial fovea is relatively more elongated; (3) the mesial moiety of the crown is relatively narrower than the distal moiety in M_1 and M_2 (the crown is more rectangular in *P. zhanxiangi*); (4) the cristid obliqua is slightly more obliquely directed; (5) the crown exhibits a more pronounced buccolingual waisting; (6) the trigonid is slightly more elevated in relation to the height of the talonid basin; (7) the hypoconulid on M_1 and M_2 is positioned in the midline or slightly lingually to the midline of the crown (in *P. zhanxiangi* the hypoconulid is more buccally placed); (8) the hypoconulid on M_3 is more lingually placed than the protoconid and hypoconid (in *P. zhanxiangi* the buccal cusps on M_3 are arranged almost in line); (9) the hypoconulid and entoconid are closely associated, and the distal fovea is small or indistinct (it is broad and well-defined in *P. zhanxiangi*); (10) the buccal cingulum is much less pronounced; (11) the size differential between the lower molars is less marked; and (12) the enamel surface is simple, lacking fine crenulation and secondary wrinkling. The upper premolars of *Laccopithecus* differ in having a pair of transverse crests (only a single mesial transverse crest occurs in *P. zhanxiangi*), and in lacking a lingual cingulum on P^1 , as well as on P^3 . The upper molars of *Laccopithecus* can be distinguished from those on *P. zhanxiangi* in: (1) being relatively slightly narrower; (2) having a trigon that is only slightly broader than long (it is much broader than long in *P. zhanxiangi*); (3) having a trigon that forms a larger component of the crown, with a relatively restricted distal basin; (4) having the hypocone separated from the trigon by a deep groove (a crest connects the hypocone with the protocone in *P. zhanxiangi*), thereby emphasizing the distinction between the trigon and talon; (5) the lingual and buccal cingula being much less pronounced; and (6) the enamel surface being free from secondary wrinkling.

European Pliopithecus

The general morphology of the dentition establishes the pliopithecoid affinities of the Tongxin material. The lower molars are relatively elongated with a marked size increase from M_1 to M_3 ; M_2 and M_3 have a pliopithecine triangle; the lower molars have a well-developed buccal cingulum; the upper molars and premolars are relatively broad, with a prominent lingual cingulum, at least on P^4 – M^3 ; and M^3 is relatively large in size.

Further comparisons demonstrate that the Tongxin material is most similar in its overall dental morphology to the pliopithecine primates, comprising the three currently recognized species of *Pliopithecus* from Europe, *P. antiquus*, *P. platyodon* and *P. vindobonensis*. When compared with the lower molars of crouzeliinae, those from Tongxin are more similar to European *Pliopithecus* in having: (1) more rounded and voluminous cusps and occlusal crests; (2) a

*Unfortunately, the upper teeth of species of the Crouzeliinae from Europe are unknown (except for an isolated canine of *Anapithecus*). This severely limits the extent of the comparisons that can be made with the upper dentition of *Laccopithecus* and with members of the Pliopithecinae.

relatively shorter mesial fovea; (3) a less obliquely oriented hypoparacristid-hypoprotocristid in relation to the transverse axis of the crown; (4) a relatively broader talonid, which is only slightly less elevated than the trigonid; (5) a shorter and more mesially oriented cristid obliqua; (6) a larger hypoconulid, situated on the buccal side of the midline of the crown; (7) a distinct and well-defined distal fovea; and (8) a linear arrangement of the buccal cusps on M_3 . In addition, the fragmentary cranial specimens from Tongxin show that the construction of the palate and lower face is remarkably similar to that of *Pliopithecus vindobonensis*, which is the only species of *Pliopithecus* in which the cranial morphology is adequately known (Zapfe, 1958, 1961b; Simons & Fleagle, 1973; Szalay & Delson, 1979).* The cranium of *P. zhanxiangi* resembles that of *P. vindobonensis* in having a relatively very short face, a lateral incisor positioned markedly posteriorly relative to the central incisor, a small diastema between I^2 and C^1 , a long and narrow palate that converges slightly anteriorly, a well-developed canine fossa on the facial aspect of the maxilla, the anterior root of the zygomatic arch located low down on the face above M^1 , and a subcircular orbit with a slightly projecting outer rim (Figures 4, 8 & 9).

There is, therefore, good evidence from the dentition and from the cranial remains to support the assignment of the Tongxin material to the genus *Pliopithecus* (see the generic diagnosis presented above for a summary of the characters defining *Pliopithecus*). The Tongxin species can be distinguished morphologically from the other species of *Pliopithecus* by a number of minor details of the dentition, such as the relative proportions and size differentials of the molars, the development of the cingula, and the high incidence of secondary wrinkling on the cheek teeth (see the differential diagnosis for more specific details). However, the major distinguishing characteristic of the Tongxin material is its much larger size. It is this combination of large size and differences in the morphology of the dentition that serves to establish the distinctiveness of the Tongxin material as a new species of *Pliopithecus*.

Discussion

The discovery of a new species of *Pliopithecus* from the early middle Miocene of China has important biochronological and biogeographical implications. Previously, the only undoubted pliopithecid from Asia was *Laccopithecus robustus* from Lufeng in southwestern China. The late Miocene age of *Laccopithecus*, which is the latest surviving pliopithecid in Eurasia (Figure 10), has led previous workers to speculate that pliopithecids may have appeared for the first time in Asia at a relatively late date (Bernor *et al.*, 1988). However, the present study of the Tongxin material has confirmed that pliopithecids extended their range eastwards into Asia during the early middle Miocene, soon after their earliest appearance in Europe.

The collision of the Afro-Arabian plate with Eurasia during the Agenian-Orleanian established a land corridor across the Arabian Peninsula from Ethiopia to Southwest Asia (Adams *et al.*, 1983; Bernor, 1983; Whybrow, 1984; Thomas, 1985; Steininger *et al.*, 1985). This allowed extensive faunal interchange, which included successive migrations of African catarrhines into Europe and Asia (Thomas, 1985; Barry *et al.*, 1985, 1987; Bernor *et al.*, 1988). Among the earliest catarrhines to appear in Eurasia are members of the Proconsulidae (*sensu*

*It is worth noting that the new material of *Pliopithecus* from China contributes new information on cranial morphology that is otherwise lacking in *Pliopithecus vindobonensis*. For example, the Tongxin specimens provide, for the first time, evidence regarding the morphology of the incisive canal, the postorbital plate, the *foramen ovale* and the inferior orbital fissure.

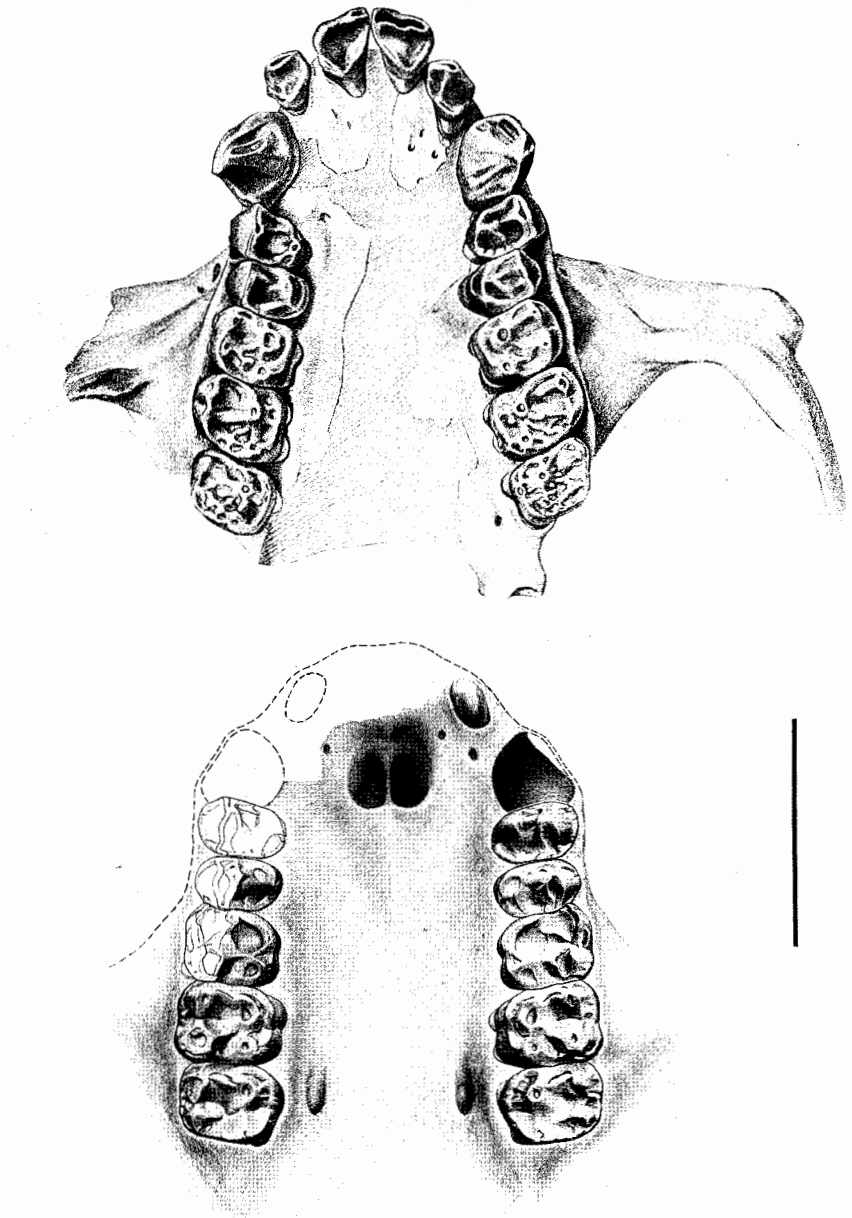


Figure 8. Comparisons of reconstructed palates of *Pliopithecus* spp. Below, BPV-1021, neotype of *P. zhanxiangi*, female individual from Maerzuizigou. Above, NMB (Naturhistorisches Museum, Basel) O.F. 303 (Individual III), holotype of *P. vindobonensis*, male individual from Neudorf-Spalte (from Zapfe, 1961b). Scale bar represents 2 cm.

Harrison, see taxonomic notes above), which presumably migrated from East Africa into subtropical and tropical parts of Asia during the early middle Miocene (17–16 m.y.a.; Upper Shanwangian, Faunal Unit II or MN 5). They probably entered Asia from Arabia via

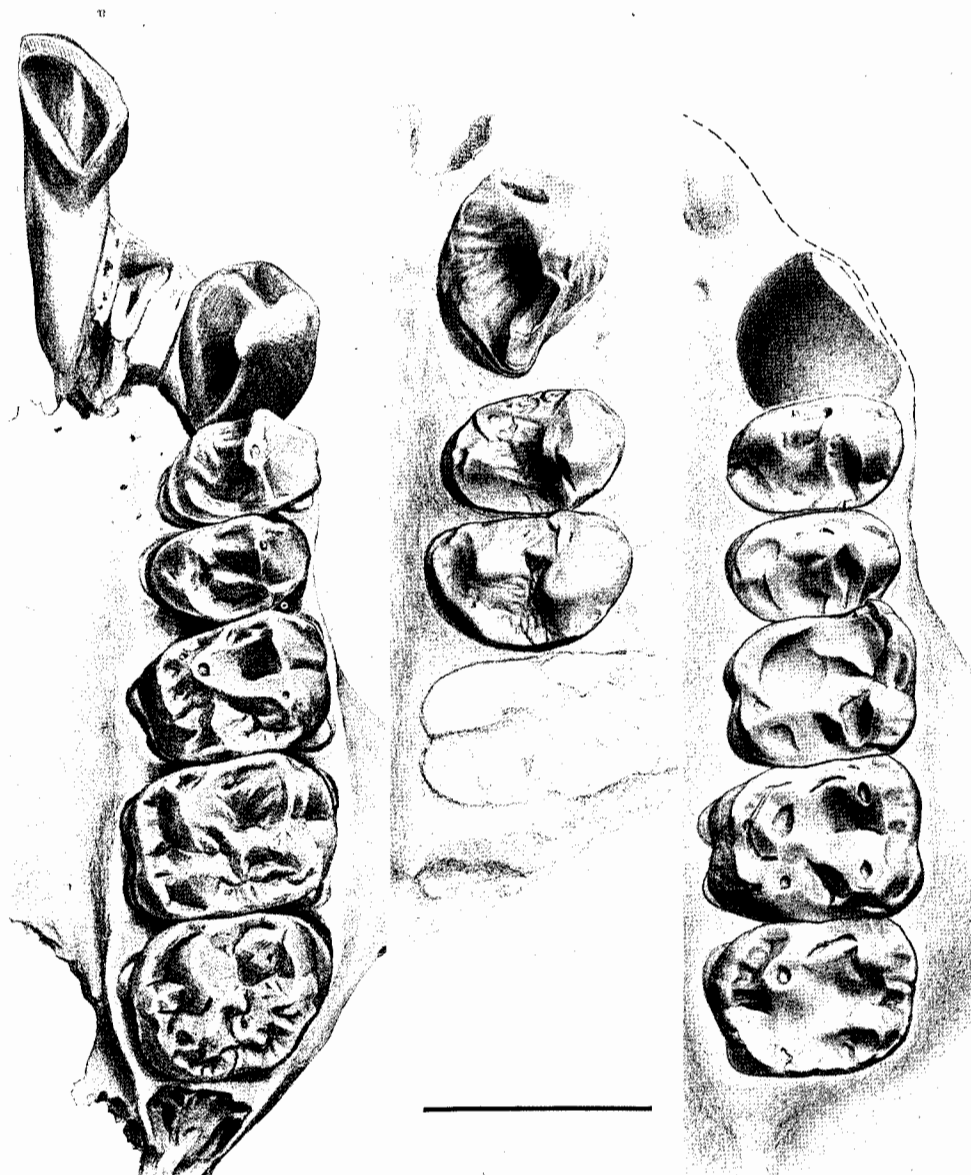


Figure 9. Comparison of reconstructed left maxillary toothrows of *Pliopithecus* spp. Left, NMB O.E. 303 (individual III), holotype of *P. vindobonensis*, male individual from Neudorf-Spalte (from Zapfe, 1961b). Center, BPV-1023, male *P. zhanxiangi* from Maerzuizigou. Right, BPV-1021, holotype of *P. zhanxiangi*, female individual from Maerzuizigou. Scale bar represents 1 cm for *P. zhanxiangi* specimens, *P. vindobensis* specimen is shown slightly more enlarged.

northern Iran through the narrow sub-Paratethyan isthmus between the present-day Caspian Sea and the Gulf of Arabia, and then followed a circum-Indian Ocean route through Indo-Pakistan into southern and eastern China (Bernor *et al.*, 1988). Representatives of this community of proconsulids have been found at several localities in Pakistan, in

AGE (Ma)	European Land Mammal Ages	MN Zone	Chinese Land Mammal Ages	Faun. Units	European Localities	Asian Localities	
5	Ruscinian	MN14	Jinglean	V			
6	Turolian	MN 13	Baodean	IV	Terrassa	Ertemte	
7		MN 12				Haritalyangar [?]	
8		MN 11				Shihuiba (Lufeng) U D U U ?	
9	Vallesian	MN 10	Bahean	IV	Terrassa	[Xiaolongtan]	
10		MN 9					Eppelsheim Rudábanya Doué-la-Fontaine Meigné-le-Vicomte Castel de Barbera Can Feliu
11	Astaracian	MN 8	Tunggurian	III	La Grive L7 Opole Przeworno II	[Xiaolongtan]	
12		MN 7					Tongxin
13		MN 6					
14	Orleanian	MN 5	Shanwangian	II		Kamlial ?	
15		MN 4				Manchar Hsi Shui	
16		MN 3				Xiacaowan (Sihong) (Taben Buluk) ?	
17				I			

Figure 10. Biochronology of pliopithecids and other, mainly small, catarrhines in Eurasia. { groups localities of similar age; | | surround two important Asian sites with large but not small catarrhines.

northern Thailand and at Sihong in eastern China (Li, 1978; Gu & Lin, 1983; Raza *et al.*, 1984; Lei, 1985; Barry *et al.*, 1987; Bernor *et al.*, 1988; Suteethorn *et al.*, 1990).

At about the same time, the Pliopithecidae entered Europe (Ginsburg, 1986; Mein, 1986; Steininger, 1986; Bernor *et al.*, 1988). Although the pliopithecids presumably originated in Africa, probably during the Oligocene, their early evolutionary history is obscure, with no identifiable antecedents in Africa during the early part of the Miocene (Harrison, 1987; Bernor *et al.*, 1988). The pliopithecids probably entered Europe from Southwest Asia during MN 5, penetrating as far west as central France via the Sub-Alpine Arch (Antunes, 1979; Bernor, 1983; Bernor *et al.*, 1988) and dispersing into the emergent areas of the Paratethys in Central and Eastern Europe (Steininger *et al.*, 1985; Steininger, 1986). The earliest pliopithecid-bearing localities in Europe, correlated with MN 5, have yielded the remains of at least four species of pliopithecid. All three European species of *Pliopithecus* are represented during this time period (*P. antiquus* from sites in France, *P. platyodon* from Elgg, Switzerland, and *P. vindobonensis* from Neudorf-Spalte, Czechoslovakia), in addition to the crouzeliine *Plesiopliopithecus lockeri* from Trimmelkam, Austria (Ginsburg & Mein, 1980; Ginsburg, 1986; Mein, 1986; Steininger, 1986; Harrison, in prep.; Figure 10). This level of taxonomic diversity at the time of their earliest occurrence in Europe is unlikely to be the result of rapid *in situ* radiation as a response to the increased availability of niche opportunities in Europe. Given the fact that the pliopithecids had already differentiated into two distinct clades at this time, it seems more probable that their initial migration involved multiple species derived from a diverse community established (perhaps in Africa) prior to their arrival in Europe.

While the pliopithecids became established and geographically widespread in Europe during the early Astaracian (MN 6), they made their first appearance in Asia at the site of Tongxin in northern China. This eastward dispersion of the pliopithecids may, in fact, have been penecontemporaneous with their initial migration into Europe, rather than as a result of a slightly later migratory episode from a secondary European center. If this proves to be the case, then pliopithecids could have extended their range into Asia at about the same time as the proconsulids. The fossil record from the Miocene of Asia is still too meager to attempt to fully reconstruct the geographic distribution of early catarrhines at this time. Nevertheless, it is undoubtedly of some significance that pliopithecids and proconsulids do not co-occur in Asian localities, despite their probable contemporaneity, while proconsulids are entirely absent from European Miocene localities where pliopithecids are so abundant.* With this in mind, and the fact that these two catarrhine families seem to have originated from different centers in Africa and are associated with different faunal communities in Eurasia, there is sufficient justification to suggest that Eurasian pliopithecids and proconsulids occupied geographically and ecologically distinct provinces.

The proconsulids from the early Miocene of East Africa are found primarily at sites associated with tropical rainforest and dense woodland (Bishop, 1967, 1968; Andrews & Van Couvering, 1975; Van Couvering & Van Couvering, 1976; Andrews, 1980; Harrison & Martin, 1980; Pickford & Andrews, 1981; Pickford, 1982, 1983, 1986; Harrison, 1989*b*). As they dispersed into Asia, during the early middle Miocene, they took advantage of the availability of tropical and subtropical forests and woodlands in Indo-Pakistan and southern China (Ramanujam, 1966; Lakhanpal, 1970; Prasad, 1971; Nandi, 1975; Sun & Wu, 1980; Chen *et al.*, 1986). By contrast, in the more northern latitudes of Europe, where pliopithecids were widely distributed, the landscape was dominated during the middle Miocene by warm temperate woodlands (Nagy, 1962; Meon-Vilain, 1968; Leopold, 1969; Ziembinska-Tworzydło, 1974; Planderova, 1978; Andrews, 1980; Artemiou, 1983, 1984). Similar vegetation also existed at corresponding latitudes in Asia (Wang, 1961), thereby providing suitable ecological conditions for pliopithecids in northern China. *Pliopithecus* probably gained access to China from Southwest Asia or Central Europe by means of a route around the Paratethys seaway, which at that time extended as far as the present-day Aral Sea, and then via a lowland corridor just north of the developing Himalayan orogenic belt (Bernor *et al.*, 1988). These inferred differences in habitat preference between the pliopithecids and proconsulids translate into a geographical and ecological partitioning of the two groups in China during the middle Miocene. The Pliopithecidae were apparently restricted to temperate woodland habitats in northern China, while the Proconsulidae were probably limited geographically to subtropical and tropical regions of southern and eastern China.

Although there is a general decline in their abundance and taxonomic diversity during the middle and late Miocene, pliopithecids remained widespread in Europe throughout the Astaracian and Vallesian. The pliopithecines were the first to decline in Europe. Until recently, the latest surviving member of the subfamily was recorded from Castel de Barbera in northern Spain, correlated with MN 8, or possibly MN 9 (Crusafont-Pairo & Golpe-Posse, 1973; Crusafont-Pairo, 1978; Agustí, 1982; Mein, 1986). However, Ginsburg (1986, 1989) has recently described a mandible with M_1 – M_3 from Meigné-le-Vicomte and some isolated

*Kretzoi (1984) has recently suggested that material from Rudabanya in Hungary may represent a new species of proconsulid, which he has referred to *Rangwapithecus* (*Ataxopithecus*) *sericus*. However, the isolated teeth that comprise the hypodigm are insufficiently distinct from the dryopithecine hominid *Dryopithecus brancoi* (= *Rudapithecus hungaricus*) to merit separate taxonomic status (see Begun, 1988).

check teeth from Dou -la-Fontaine, which he attributes to *Pliopithecus antiquus*. These finds confirm that the temporal range of the pliopithecines extended into the earliest Vallesian (MN 9). The Crouzeliinae, by contrast, continue well into the late Miocene of Europe, being represented during the Vallesian by abundant remains of *Anapithecus hemyaki* from Rud banya (MN 9) in Hungary (Kretzoi, 1975), and an undescribed species of pliopithecoid from Terrassa (MN 10) in Spain (Golpe-Posse, 1982; Moy -Sola, in prep.). However, the absence of pliopithecids from Turolian sites in Europe would suggest that the family had become extinct by the close of the Vallesian.

In Asia, there is a major hiatus in the fossil record of small catarrhine primates during the late Tunggurian (= late Astaracian) to early Baodean (= early Turolian) (Figure 10). This is certainly due in large part to the inadequacy of the sites sampled from the appropriate time period. Nevertheless, it is worth noting that small catarrhines have not been recovered from the intensively studied sediments of the Chinji and Nagri Formations of Indo-Pakistan, or from several paleontologically productive sites of broadly equivalent age in China (i.e., Xiaolongtan, Tung-Gur, Bulong, Bahe and Qingyang). Based on this evidence it would appear that the proconsulids were a relatively short-lived group in Asia, at least in Indo-Pakistan, and that other small catarrhines in Asia, including the pliopithecids, became extinct or maintained relatively low levels of abundance and diversity throughout the middle Miocene. The occurrence of a pliopithecoid at the late Miocene (Baodean) locality of Lufeng, associated with a warm temperate woodland setting (Sun & Wu, 1980; Andrews, 1983; Chen *et al.*, 1986), is particularly interesting in this regard. However, *Laccopithecus robustus* is unlikely to represent a late-surviving member of a long-established Asian pliopithecoid lineage dating back to the early Astaracian. A critical issue here is the fact that *Laccopithecus* has closer affinities with the European crouzeliines than it does with the Tongxin material assigned to *Pliopithecus*. This would suggest that *Laccopithecus* is part of a separate dispersal event, occurring much later in time than that which introduced *Pliopithecus zhanxiangi* into China.

Summary

Pliopithecus zhanxiangi is named on the basis of a female palate and seven other gnathic specimens from the early middle Miocene Tongxin fauna (*ca.* 15 m.y.a.), Ningxia Hui Autonomous Region, northcentral China. This species shares all observable morphological features with the three recognized European species of the genus, but differs in its larger size and other minor details. Based on the work of Harrison (in prep.), *P. piveteaui* is synonymized with the type species, *P. antiquus*, while *P. platyodon* is resurrected for the Elgg holotype and the G riach sample previously included in *P. antiquus*.

Following a detailed description of the Tongxin specimens, they are compared in turn to all of the known smaller catarrhines of eastern Asia. At least three catarrhine species are known from Sihong (Jiangsu Province, eastern China), dating to about 16–17 m.y.a. *Dionysopithecus shuangouensis*, also known from the deposits of similar age in Pakistan, is most similar to the catarrhines of the East African Miocene, termed proconsulids by Harrison (but not by Delson). *Platodontopithecus jianghuaiensis* also resembles the proconsulids but is harder to characterize because only isolated (and mostly worn) teeth have been described. The M₃ (IVPP PA 870) is here selected as the lectotype, given that it is unlikely that all five known teeth belong to a single individual. “*Dryopithecus*” *sihongensis* is known only by a single lower molar, but it too is most similar to the African proconsulids.

“*Pliopithecus*” *posthumus* from the latest Miocene of Ertemte (Nei Monggol), China, is based on an upper third molar which is too worn to allow certainty about its systematic position, although it could still be primate. “*P.*” *krishnii* from the late Miocene of Haritalyangar, India, is also based on a worn M³, but it may tentatively be linked with the proconsulids. The grouping of these two species in the genus *Krishnapithecus* by Ginsburg & Mein (1980) is considered premature.

Represented by much better material is *Laccopithecus robustus* from the late Miocene of Shihuiba (Lufeng County, Yunnan Province, southwestern China). Although it is similar to *Pliopithecus zhangxiangi* in overall size, *L. robustus* is readily referable to the crouzeliine pliopithecids on the basis of dental morphology.

The Tongxin specimens, in addition to providing some new details about facial morphology in *Pliopithecus*, demonstrate that members of this family arrived in Asia only shortly after they appeared in Europe and the proconsulids did in eastern Asia. This leads to two important implications for early catarrhine adaptation and diversification. First, the high level of diversity seen among the Eurasian pliopithecids at or just after their first appearance (three pliopithecine species in Europe and one in China, plus one crouzeliine in Europe) militates against a rapid local radiation, but suggests multiple invasions from stocks or lineages already established outside Europe (perhaps in Africa). It is not clear whether the pliopithecines entered eastern Asia from Europe or from Africa/western Asia at the same time as they reached western Europe.

Second, pliopithecids and proconsulids do not co-occur at any locality yet known in Eurasia (or, of course, in Africa), which suggests that the two groups differed in ecological requirements. East African and east Asian proconsulids both appear effectively restricted to tropical or subtropical forests and woodlands. The pliopithecids, on the other hand, inhabited more northerly regions covered by warm temperate woodlands across Eurasia. In Europe, the pliopithecines were apparently more common than the crouzeliines in the middle Miocene, although both are rare late in the subepoch. The latest pliopithecines occurred early in the French Vallesian, contemporary with a large crouzeliine in Hungary, but a small crouzeliine persisted in Spain until the end of the Vallesian age and *Laccopithecus* documents the presence of the subfamily into the mid-Turolian/Baodean.

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Meeker. Photographs for Figures 4–7 were taken by Lorraine Meeker, who mounted them as well, and by David Dean. The illustrations of Tongxin specimens in Figures 8 & 9 were prepared by Chester Tarka in his usual perfectionist manner, and Prof. Dr H. Zapfe gave permission to reprint comparative drawings made for him by Mr O. Garraux. We thank all of them for their help. The authors have benefitted greatly from discussions about Eurasian catarrhine systematics and paleoecology with the following colleagues: Peter Andrews, David Begun, Ray Bernor, John Fleagle, Terri Harrison, Jay Kelley, Salvador Moyá-Sola and Gu Yumin.

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