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Taxonomy and phylogenetic relationships of early Miocene catarrhines from Sihong, China

Paleontological investigations at sites in Sihong County, Jiangsu Province, China since 1981 have yielded a sizeable collection of previously undescribed fossil catarrhines from the Xiacaowan Formation. The associated vertebrate fauna indicates a late early Miocene age (correlating with MN 4, late Orleanian of Europe, ~17–18 Ma), which establishes the Sihong primates as the earliest known catarrhines from Eurasia. The fossil primates are assigned to two species: *Dionysopithecus shuangouensis* Li, 1978 and *Platodontopithecus jianghuaiensis* Gu & Lin, 1983. Although the new material from Sihong consists mainly of isolated teeth, it does provide important new information on the anatomy of *Dionysopithecus* and *Platodontopithecus* that helps to clarify their phylogenetic and taxonomic status. Previous studies have suggested that the Sihong catarrhines might be closely related to the proconsulids from the early Miocene of East Africa. However, with more extensive material available for comparison, the Sihong primates can now be shown to share a number of key derived features with pliopithecids. This new evidence helps to resolve a longstanding problem concerning the origins of the Pliopithecidae. It was previously considered that specialized pliopithecids migrated into Europe during MN 5, originating from an unknown antecedent and location in Africa. Recognition that the Sihong primates have affinities with pliopithecids, but are more primitive, suggests that the initial differentiation and diversification of the clade may have taken place in Asia rather than Africa. The earliest Eurasian catarrhines probably migrated into tropical Asia as part of a major faunal interchange with Africa that occurred during MN 3.

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Introduction

Since the late 1970s, paleontological investigations in the Xiacaowan Formation of Sihong County, Jiangsu Province, China, have yielded the remains of Miocene catarrhine primates. The first specimen was recovered by a local farmer while constructing a new pigsty from slabs of Xiacaowan sandstone. The specimen, a maxilla fragment with M^{1-3} , was described by Li (1978) as the holotype of a new genus and species of catarrhine, *Dionysopithecus shuangouensis*. The specimen was initially considered to be

a fossil gibbon (Li, 1978), but most subsequent workers have regarded it as having its closest affinities with the small catarrhines from the early Miocene of East Africa, especially *Micropithecus clarki* (Harrison, 1982, 1988; Fleagle, 1984, 1986, 1988; Bernor *et al.*, 1988; Etler, 1989; Harrison *et al.*, 1991). Continued research in the area, at the site of Songlinzhuang, under the direction of Gu Yumin and Lin Yipu from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) in Beijing, led to the recovery of additional fossil primates. These included several isolated teeth of a

second catarrhine species, *Platodontopithecus jianghuaiensis* (Gu & Lin, 1983). Again, this taxon was considered to have its closest affinities with East African proconsulids (Fleagle, 1988; Bernor *et al.*, 1988; Etlér, 1989; Harrison *et al.*, 1991). Excavations at Songlinzhuang in the summer of 1983, by a team from the Geological Museum of Nanjing, led to the recovery of further isolated teeth, of which three were designated by Lei (1985) as type specimens of *Pliopithecus wangi*, *Hylobates tianganhuensis*, and *Dryopithecus sihongensis*. Subsequently, *P. wangi* and *H. tianganhuensis* were subsumed into *D. shuangouensis* as junior synonyms, while “*Dryopithecus*” *sihongensis* was provisionally retained as a distinct species (Bernor *et al.*, 1988; Harrison *et al.*, 1991). However, a clear understanding of the taxonomic and phylogenetic relationships of the fossil primates from Sihong has in the past been severely hindered by the paucity of the available material—a total of only nine specimens representing the three purported species.

Between 1981 and 1986 paleontologists from IVPP recovered a sizeable collection of fossil primates from Sihong. This new material, comprising more than seventy specimens, is described here for the first time. Although most of these specimens consist of isolated teeth (apart from two mandibular fragments and three postcranial bones), they do provide important new information on the anatomy of the Sihong primates that helps to clarify their phylogenetic and taxonomic status. Moreover, the associated fauna correlates best with European Mammal Zone MN 4, indicating a late early Miocene age (late Orléanian, ~17–18 Ma). This serves to establish the Sihong primates as the earliest known catarrhines in Eurasia, making them of critical importance for understanding the timing and location of events that helped to shape the zoogeographic distribution of Miocene catarrhines.

The aim of this paper is to provide a descriptive account of the anatomy of the Sihong primates, based primarily on the new cranio-dental and postcranial material, and to present a revised assessment of their taxonomic and phylogenetic relationships. The results of this analysis have important implications for understanding the evolutionary history and zoogeography of Miocene catarrhines in Eurasia.

Geology, fauna, and biochronology

Sihong is located in the Jianghuai basin in the floodplain of the Chang Jiang (Yangtze) River, in northern Jiangsu Province, about 175 km north of Nanjing (Figure 1). The fossiliferous deposits of the Xiacaowan Formation consist of a thick series (up to 90 m) of fluviolacustrine sediments, comprising marly clays, sandstones, and calcareous conglomerates (Lin, 1980; Li *et al.*, 1983; Etlér, 1989). At Songlinzhuang and Zhengji, the main fossil-bearing horizon from which most of the primates have been recovered consists of a hard, light gray calcareous conglomerate (0.6–1.6 m in depth). The overlying soft, yellow-brown clays and the underlying gray-green clays are also fossiliferous, but primates are known only from the uppermost of these horizons.

Fossil mammals were first recovered from the Xiacaowan Formation in 1952. The small fauna was initially considered to be middle Pleistocene in age (Young, 1955; Young & Chow, 1955; Pei, 1957; Chow, 1959), but this estimation was later revised, and the fauna was generally recognized as belonging to the middle Miocene (Chow & Wang, 1964; Chow & Li, 1978; Li *et al.*, 1983). Since the 1970s geological and paleontological research at Sihong has been intensified, and the fossil vertebrate localities in the area are now among the most productive Miocene sites in China. Fossils have been recovered from more than ten different localities, but the key sites are

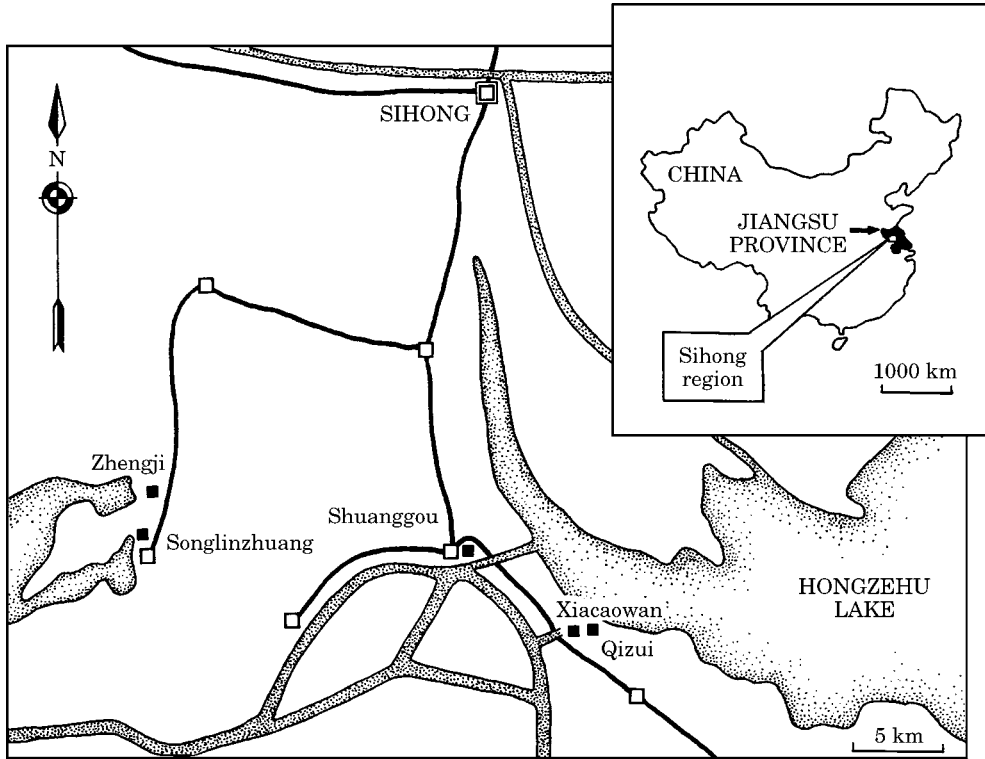


Figure 1. Map showing the location of the key fossil localities (black squares) in the vicinity of Sihong (after Li *et al.*, 1983). Towns are shown as open squares.

Songlinzhuang, Xiacaowan, Shuanggou, Qizui and Zhengji (see Figure 1). The fauna from the Xiacaowan Formation is now quite extensive and includes at least 38 species of mammals (Table 1), as well as freshwater fishes, frogs, turtles, monitor lizards, crocodiles, and birds. Fossil primates are known definitively only from Songlinzhuang and Zhengji, although Lin (1980) has noted the possible occurrence of *Dionysopithecus* from the Xiacaowan Formation at Huaguoshan in Xiji County to the southeast of Sihong.

The mammalian fauna has been used as a basis to correlate the Sihong sites with European Miocene localities (although we appreciate that such correlations on a continent-wide scale may prove unreliable). The cricetid and sciurid rodents are most similar in evolutionary level to those from European sites correlated with European Mammal

Zone MN 4 (early Orlanian) (Qiu & Lin, 1986; Qiu & Qiu, 1995). This correlation is also consistent with comparisons of other taxa in the Sihong fauna, including carnivores, tragulids, and ochotonids (Li *et al.*, 1983; Qiu & Gu, 1986, 1991; Wu, 1995). On a regional level, the Sihong fauna is inferred to be somewhat older than the Shanwang fauna (Shandong Province, China), which is reliably correlated with MN 5 (late Orlanian, ~15–17 Ma) (Li *et al.*, 1984; Qiu & Qiu, 1995). An age estimation of 16–17 Ma for the fossil-bearing sediments at Shanwang seems reasonable given the published radiometric and paleomagnetic dates (Li, 1981; Wang *et al.*, 1981; Jin, 1985; Etler, 1989; Liu & Leopold, 1992). The Sihong fauna contains a number of genera in common with Shanwang, although the taxa from Sihong

Table 1 List of fossil mammals from the Xiaocaowan Formation, Sihong

| | |
|-------------------|--|
| Mammalia | |
| Insectivora | |
| Erinaceidae | <i>Lanthanotherium</i> sp. |
| Talpidae | sp. indet. |
| Soricidae | <i>Crocidosorex</i> sp. |
| Chiroptera | |
| Vespertilionidae | <i>Myotis</i> sp. sp. indet. |
| Rodentia | |
| Castoridae | <i>Youngofiber sinensis</i> sp. indet. |
| Cricetidae | <i>Megacricetodon</i> sp. <i>Democricetodon</i> sp. <i>Spanocricetodon ningensis</i> <i>Neocometes</i> sp. <i>Primus</i> sp. |
| Aplodontidae | <i>Ansomys orientalis</i> |
| Gliridae | <i>Microdromys orientalis</i> |
| Ctenodactylidae | <i>Sayimys</i> sp. |
| Rhizomyidae | sp. indet. |
| Sciuridae | <i>Parapetaurista tenurugosa</i> <i>Shuanggouia lui</i> <i>Eutamias sihongensis</i> <i>Plesiosciurus sinensis</i> |
| Pedetidae | <i>Diatomys</i> cf. <i>shantungensis</i> |
| Lagomorpha | |
| Ochotonidae | <i>Alloptox sihongensis</i> |
| Carnivora | |
| Mustelidae | sp. indet. |
| Hyaenidae | ? <i>Protictitherium</i> sp. |
| Viverridae | <i>Semigenetta huaiheensis</i> |
| Amphicyonidae | sp. indet. |
| Felidae | <i>Pseudaelurus</i> cf. <i>lorteti</i> |
| Proboscidea | |
| Stegodontidae | <i>Stegolophodon hueiheensis</i> |
| Perissodactyla | |
| Equidae | ? <i>Anchitherium</i> sp. |
| Rhinocerotidae | sp. indet. |
| Artiodactyla | |
| Anthracotheriidae | <i>Sihongotherium sihongense</i> sp. indet. |
| Suidae | sp. indet. |
| Tragulidae | <i>Dorcatherium orientale</i> |
| Giraffidae | sp. indet. |
| Cervidae | <i>Stephanocemas</i> sp. |
| Cetacea | |
| Delphinidae | <i>Delphinus</i> sp. |
| Primates | |
| Pliopithecidae | <i>Dionysopithecus shuangouensis</i> <i>Platodontopithecus jianghuaiensis</i> |

Sources: Li *et al.*, 1983; Chow & Zhang, 1983; Qui & Lin, 1986; Qiu & Gu, 1986, 1991; Wu, 1986, 1995; Qiu, 1987; Zong, 1992; Liu & Zhang, 1993; Qiu & Qiu, 1995.

are generally more primitive. In sum, the faunal evidence indicates that the Xiaocaowan Formation can best be considered late early Miocene in age (=early Shanwangian, Faunal Unit II), tentatively correlated with MN 4 (=early Orleanian, ~17–18 Ma (Qiu, 1989; Qiu & Qiu, 1995) (see Figure 2).

Material

This paper presents the results of a detailed study of newly discovered and previously undescribed fossil primate specimens from Sihong (Harrison & Gu, 1996). Currently, there are 83 cranio-dental specimens known, of which 74 are described here for the first time. Of the nine previously published specimens, the authors examined and made direct comparisons with the five teeth that represent the type series of *Platodontopithecus jianghuaiensis* (Gu & Lin, 1983). The type specimen of *Dionysopithecus shuangouensis*, a maxilla with M¹⁻³, was available as a high-quality cast, while comparisons of the three isolated teeth described by Lei (1985) were restricted to published photographs and measurements only. The dental terminology adopted here generally follows that of Szalay & Delson (1979), with minor modifications (see Figure 3). In addition to the new cranio-dental specimens, three postcranial bones have been recovered: an almost entire right calcaneus, a proximal phalanx, and a partial proximal phalanx.

The specimens described here are from two sites—Songlinzhuang and Zhengji—of which the majority come from Songlinzhuang (Table 2). Of the specimens available, 50 are attributed to *Dionysopithecus shuangouensis* and 33 to *Platodontopithecus jianghuaiensis*. The difference in relative proportions of these species at the two sites (*D. shuangouensis* represents 63.0% of primates at Songlinzhuang and only 36.4% at Zhengji) may be of some ecologi-

| AGE (Ma) | EUROPEAN LAND MAMMAL AGES | MN ZONE | CHINESE LAND MAMMAL AGES | FAUN. UNIT | CHINESE LOCALITIES | OTHER ASIAN LOCALITIES |
|----------|---------------------------|-----------|--------------------------|------------|--------------------|-------------------------------------|
| 5 | Ruscinian | 14 | Jinglean | V | | |
| | Turolian | 13 | Baodean/ Lufengian | IV | Ertemte | Haritalyangar |
| | | 12 | | | | |
| | | 11 | | | | |
| 10 | Vallesian | 10 | | | | |
| | | 9 | | | | |
| | Astaracian | 7 8 | Tunggurian | III | Tongxin | Ban San Klang Kamlial Manchar |
| | | 6 | | | | |
| 15 | | Orleanian | | | | |
| | 4 | | | | | |
| | 3 | | Xiejiaan | I | | |
| 20 | | | | | | |

Figure 2. Biochronology of pliopithecids and other small catarrhines in Asia (after Harrison *et al.*, 1991; Qiu & Qiu, 1995; Steininger *et al.*, 1996; Andrews *et al.*, 1996).

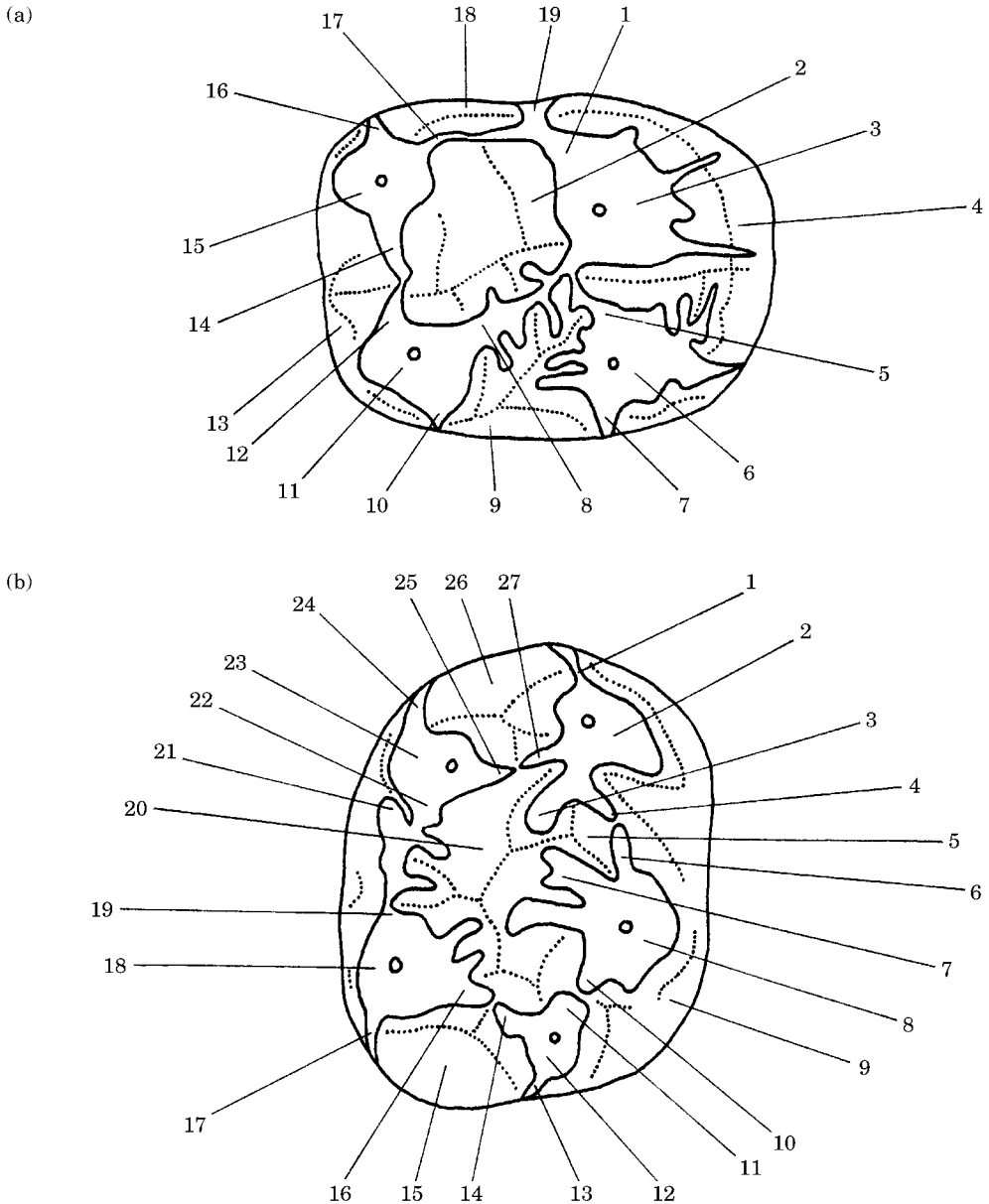


Figure 3. Molar terminology used in this study (adapted from Szalay & Delson, 1979). (a) Right M_2^2 (PA 1043) of *Dionysopithecus shuangouensis*: 1, preprotocrista; 2, trigon basin; 3, protocone; 4, lingual cingulum; 5, prehypocrista; 6, hypocone; 7, posthypocrista; 8, crista obliqua (=hypometacrista+postprotocrista); 9, distal fovea; 10, postmetacrista; 11, metacone; 12, premetacrista; 13, buccal cingulum; 14, postparacrista; 15, paracone; 16, preparacrista; 17, hypoparacrista; 18, mesial fovea; 19, paraconule. (b) Right M_2 (PA 1253) of *Dionysopithecus shuangouensis*: 1, preprotocristid; 2, protoconid; 3, mesial arm of pliopithecine triangle; 4, postprotocristid; 5, pliopithecine triangle; 6, prehypocristid; 7, distal arm of pliopithecine triangle; 8, hypoconid; 9, buccal cingulum; 10, posthypocristid; 11, prehypocristid; 12, hypoconulid; 13, posthypoconulid; 14, postcristid; 15, distal fovea; 16, hypopostcristid; 17, postentocristid; 18, entoconid; 19, pre-entocristid; 20, talonid basin; 21, mesostylid; 22, postmetacristid; 23, metaconid; 24, premetacristid; 25, hypometacristid; 26, mesial fovea (=trigon basin); 27, hypoprotocristid.

Table 2 Number of cranio-dental specimens of *Dionysopithecus* and *Platodontopithecus* from Sihong

| | <i>Dionysopithecus</i> <i>shuangouensis</i> | <i>Platodontopithecus</i> <i>jianghuaiensis</i> | Total |
|---------------|--|--|-------|
| Songlinzhuang | 46 | 26 | 72 |
| Zhengji | 4 | 7 | 11 |
| Total | 50 | 33 | 83 |

cal or taphonomic importance, but this observation will need to be confirmed by the recovery of larger samples, especially from Zhengji.

The distinctive state of preservation of the material also merits comment. Bone is rarely preserved, and apart from one maxillary fragment (V5597), two mandibular fragments—both poorly preserved (PA 1054, PA 1273), and three postcranial bones (PA 1270, PA 1271, PA 1272), the entire sample of fossil primates from Sihong consists of isolated teeth. A close examination of the material provides some clues to help explain this unusual preservation. Almost all of the isolated teeth show evidence of having been damaged by exposure to an acidic medium. In many cases the roots of the teeth are partially or entirely dissolved, while the more resistant enamel caps show varying degrees of etching, pitting and thinning. This is most consistent with the teeth (and missing bone) having passed through the digestive tract of a large carnivore (Andrews, 1990). It is well-documented that modern spotted hyenas (*Crocuta crocuta*) can produce similar damage as a result of regurgitation of indigestible materials from the stomach (Kitching, 1963; Brain, 1981). However, since there are no specialized bone-eating hyaenids in the Sihong fauna, the most likely candidates are large amphicyonids. Alternatively, the primates may have been ingested by crocodiles, which are common elements in the fauna, although the type of damage observed is not compatible with patterns obtained from

actualistic experiments using modern species (Fisher, 1981).

Further support that the fossil primates were accumulated as a result of carnivore activity can be inferred from the reconstructed age profile of the sample (Craig & Oertel, 1966; Klein, 1982; Lyman, 1994). By assigning the deciduous and permanent cheek teeth to age classes on the basis of wear and the presence or absence of interstitial contact facets, it can be shown that 66.7% of all teeth belonged to individuals that can be categorized as neonates, infants or juveniles [i.e., up to and including individuals in which most of the deciduous teeth are retained, but only M1 of the permanent molars is in place; equivalent to *Macaca nemestrina* individuals younger than 3.5 years of age (Sirianni & Swindler, 1985)]. Since younger individuals might be expected to be more prone to predation than adults, carnivore activity could account for the disproportionate representation of the younger age classes in the Sihong sample.

Systematics

Order Primates Linnaeus, 1758

Infraorder Catarrhini Geoffroy, 1812

Superfamily Pliopithecoidea Zapfe, 1961

Family Pliopithecidae Zapfe, 1961

Subfamily *Dionysopithecinae subfam. nov.*

Genus *Dionysopithecus* Li, 1978

Emended diagnosis: Small catarrhine primates approximating to *Hylobates lar* in dental size (with an average estimated body weight of 5.5 kg—see below for details of

size estimation). I^1 is broad and spatulate, with an apex that recedes distally, slightly waisted towards the base of the crown, a pronounced lingual cingulum and the lingual pillar weakly developed or absent. The upper canine in presumed female individuals (canines of males unknown) is low-crowned, with a broad distal heel that gives the crown a triangular occlusal outline. Upper premolars are relatively narrow. M^1 and M^2 have the following characteristics: crown moderately broad, subrectangular in occlusal outline, with convex lingual and distal margins (M^1 distinctly narrower with more strongly convex lingual and distal margins than M^2); narrow occlusal basins in relation to the total breadth of the crown; lingual cingulum broad and well-developed; hypocone prominent, but distinctly smaller than the trigon cusps; transverse crest between the metacone and hypocone weakly developed or absent; buccal cingulum moderately well-developed. M^3 is relatively small, with rudimentary metacone and hypocone. $M^2 > M^1 \geq M^3$. Lower incisors are moderately high-crowned, the apex recedes distally, and they are slightly waisted towards the base of the crown. P_3 is mesio-distally short, with elevated protoconid, steep mesiobuccal face and minimal extension of enamel inferiorly onto the anterior root. P_4 has metaconid distinctly smaller than protoconid. Lower molars have the following characteristics: crown relatively long and moderately narrow; prominent paraconid usually retained; mesial transverse crest slightly obliquely directed in relation to the transverse axis of the crown; mesial fovea mesiodistally long, narrow in relation to the maximum breadth of the crown and more elevated than the talonid basin; mesostylid well-developed; cristid obliqua slightly obliquely oriented; pliopithecine triangle present; hypoconulid much smaller than the hypoconid; small, well-defined distal fovea; buccal cingulum generally well-developed. M_3 is relatively

small. $M_2 \geq M_3 > M_1$. Upper and lower molars are low-crowned with low, rounded cusps and crests. [Emended from Li (1978).] For characteristics that differentiate *Dionysopithecus* from other fossil catarrhines see Phylogenetic relationships.

Dionysopithecus shuangouensis
Li, 1978

Synonyms: *Pliopithecus wangi* Lei, 1985; *Hylobates tianganhuensis* Lei, 1985; = *Hylobates tianganhunensis*: Lei, 1985 (*lapsus*); *Pliopithecus wongi*: Etler, 1989 (*lapsus*).

Diagnosis: As for genus.

Holotype: IVPP V5597. Left maxillary fragment with M^1 – M^3 .

Type locality: Songlinzhuang, Sihong County, Jiangsu Province, People's Republic of China (see Figure 1).

Distribution: Latest early Miocene (late Shanwangian=late Orleanian, MN 4). Xiacowan Formation; localities (1) Songlinzhuang and (2) Zhengji, Sihong County, Jiangsu Province, People's Republic of China (see Figure 1).

Referred material: In addition to the holotype, the hypodigm includes 44 specimens from Songlinzhuang and four specimens from Zhenji. See Table 3 for a complete listing of referred specimens and Table 4 for a summary of dental measurements and abbreviations.

Description of material

Upper dentition

I^1 is spatulate in shape (Figure 4). In buccal view it is broadest at the apex, and becomes narrower and slightly waisted towards the base of the crown. The crown is slightly higher than it is broad, with an average breadth–height index ($MD \times 100/BHT$) of 89.5. The incisive apex is sharp and mesio-distally slightly convex, and in buccal view it is not aligned perpendicular to the apico-basal axis of the root, but tends to recede

Table 3 List of cranio-dental material assigned to *Dionysopithecus shuangouensis*

| Accession number* | Locality | Brief description |
|-------------------|---------------|---|
| V5597 | Songlinzhuang | Left maxilla with M ¹⁻³ (holotype of <i>D. shuangouensis</i> Li, 1978). |
| P83.3 | Songlinzhuang | Left M ¹ (holotype of <i>Hylobates tianganhuensis</i> Lei, 1985). |
| P83.4 | Songlinzhuang | Left M ₃ (holotype of <i>Pliopithecus wangi</i> Lei, 1985). |
| PA 1042 | Songlinzhuang | Left M ² . Heavily worn. |
| PA 1043 | Songlinzhuang | Right M ² . Unerupted crown. |
| PA 1044 | Songlinzhuang | Right M ² . Unerupted crown. |
| PA 1045 | Songlinzhuang | Left M ¹ . Moderately worn, slightly damaged. |
| PA 1046 | Songlinzhuang | Left M ¹ . Unerupted crown. |
| PA 1047 | Songlinzhuang | Right M ² . Moderately worn. |
| PA 1048 | Songlinzhuang | Right M ² . Heavily worn and damaged. |
| PA 1049 | Songlinzhuang | Left M ² . Unerupted germ. |
| PA 1051 | Songlinzhuang | Left P ₃ . Slightly worn. |
| PA 1052 | Songlinzhuang | Right dP ₃ . Slightly worn. |
| PA 1053 | Songlinzhuang | Right P ₄ . Unerupted germ. |
| PA 1054 | Songlinzhuang | Right mandibular fragment with M ₁₋₂ . Poorly preserved. Molars moderately worn. |
| PA 1211 | Songlinzhuang | Left dC ₁ . Unworn. |
| PA 1228 | Songlinzhuang | Right C ¹ . Female individual. Slightly worn. |
| PA 1230 | Songlinzhuang | Left I ¹ . Moderately worn. |
| PA 1231 | Songlinzhuang | Left I ¹ . Unworn. |
| PA 1232 | Songlinzhuang | Left P ⁴ . Unworn. |
| PA 1233 | Songlinzhuang | Right P ⁴ . Unerupted germ. |
| PA 1235 | Songlinzhuang | Right M ₁ . Unerupted germ. |
| PA 1236 | Songlinzhuang | Right P ⁴ . Heavily worn and damaged. |
| PA 1237a | Songlinzhuang | Right M ₂ . Buccal portion of crown only. Moderately worn. |
| PA 1237b | Songlinzhuang | Right M ₂ . Mesial portion of crown only. Unerupted germ. |
| PA 1238 | Songlinzhuang | Right I ¹ . Heavily worn. |
| PA 1239 | Songlinzhuang | Right dP ⁴ . Mesiobuccal corner of crown lacking. Unworn. |
| PA 1240 | Songlinzhuang | Left ?M ₂ . Poorly preserved and worn. |
| PA 1241 | Songlinzhuang | Right dP ₄ . Moderately worn. |
| PA 1242 | Songlinzhuang | Left I ₂ . Heavily worn. |
| PA 1243 | Songlinzhuang | Left M ₁ . Poorly preserved. |
| PA 1244 | Songlinzhuang | Left I ₂ . Unworn. |
| PA 1245 | Songlinzhuang | Left dP ₃ . Slightly damaged and heavily worn. |
| PA 1246 | Songlinzhuang | Left dP ₃ . Slightly worn. |
| PA 1247 | Songlinzhuang | Left dP ₃ . Unerupted germ. |
| PA 1248 | Songlinzhuang | Right M ₁ . Heavily worn. |
| PA 1249 | Songlinzhuang | Left M ₁ . Unerupted germ. |
| PA 1251 | Songlinzhuang | Right M ₁ . Slightly worn. |
| PA 1252 | Songlinzhuang | Right M ₂ . Unerupted germ. |
| PA 1253 | Songlinzhuang | Right M ₃ . Moderately worn, slightly damaged. |
| PA 1254 | Songlinzhuang | Left M ₁ . Unerupted germ. |
| PA 1255 | Songlinzhuang | Left dP ₄ . Moderately worn. |
| PA 1256 | Songlinzhuang | Left M ₁ . Mesiobuccal portion of crown only. Moderately worn. |
| PA 1257 | Songlinzhuang | Right P ₃ . Unerupted germ. |
| PA 1258 | Songlinzhuang | Left dC ¹ . Moderately worn. |
| PA 1259 | Songlinzhuang | Left M ¹ . Distal portion of crown only. Unworn. |
| PA 1262 | Zhengji | Left M ₂ . Unerupted crown. |
| PA 1265 | Zhengji | Right I ¹ . Moderately worn. |
| PA 1266 | Zhengji | Left dC ₁ . Poorly preserved. |
| PA 1267 | Zhengji | Left I ₂ . Slightly worn. |

*Accession numbers: P, collections of the Geological Museum of Nanjing; PA, Paleoanthropology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; V, Vertebrate Paleontology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

Table 4 Dimensions of the teeth of *Dionysopithecus shuangouensis*

| | Acc. no. | Lowers | | | Acc. no. | Uppers | | |
|-----|----------|--------|-----|--------|-------------|--------|-----|--------|
| | | MD | BL | BHT | | MD | BL | BHT |
| I1 | | | | | PA 1230 | 4.9 | 4.9 | 5.0(-) |
| | | | | | PA1231 | 5.0 | 3.8 | 5.5(-) |
| | | | | | PA 1238 | 4.9(-) | 4.4 | 5.6(-) |
| | | | | | PA 1265 | 4.9(-) | 4.4 | 6.0(-) |
| I2 | PA 1242 | 3.4(-) | 4.5 | — | | | | |
| | PA 1244 | 3.3 | 4.2 | 6.2 | | | | |
| | PA 1267 | 3.0 | 3.5 | 5.2(-) | | | | |
| C | | | | | PA 1228 (f) | 6.1 | 5.1 | 6.7 |
| P3 | PA 1051 | 5.5 | 3.6 | | | | | |
| P4 | PA 1053 | 4.6 | 3.9 | | PA 1232 | 4.2 | 6.1 | |
| | | | | | PA 1233 | 3.8 | 5.3 | |
| | | | | | PA 1236 | 3.5 | 5.5 | |
| M1 | PA 1235 | 5.5 | 4.7 | | PA 1045 | 5.4 | 6.1 | |
| | PA 1248 | 5.0 | 4.5 | | PA 1046 | 5.6 | 6.3 | |
| | PA 1249 | 5.8 | 5.1 | | P83.3* | 5.5 | 6.3 | |
| | PA 1251 | 6.0 | 5.4 | | V5597† | 4.9 | 5.7 | |
| | PA 1254 | 6.3 | 5.0 | | | | | |
| M2 | PA 1252 | 6.5 | 5.5 | | PA 1042 | 4.9 | 6.7 | |
| | PA 1262 | 6.7 | 5.5 | | PA 1043 | 5.2 | 6.5 | |
| | | | | | PA 1044 | 5.8 | 6.8 | |
| | | | | | PA 1047 | 4.7 | 6.3 | |
| | | | | | PA 1048 | 5.2 | 6.6 | |
| | | | | | PA 1049 | 5.5 | 6.7 | |
| | | | | | V5597† | 5.3 | 6.1 | |
| M3 | PA 1253 | 6.0 | 5.3 | | V5597† | 4.9 | 5.6 | |
| | P83.4* | 6.7 | 5.1 | | | | | |
| dC | PA 1211 | 4.0 | 3.0 | 4.8 | PA 1258 | 3.6 | 3.2 | 3.8 |
| dP3 | PA 1052 | 5.1 | 3.5 | | | | | |
| | PA 1245 | 4.5(-) | 3.3 | | | | | |
| | PA 1247 | 4.2(-) | 3.0 | | | | | |
| dP4 | PA 1241 | 4.9 | 3.9 | | | | | |
| | PA 1255 | 5.1 | 3.8 | | | | | |

Abbreviations: Acc. no., Accession number; BHT, buccal height; BL, buccolingual breadth; MD, mesiodistal length; P, collections of the Geological Museum of Nanjing; PA, Paleoanthropology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; V, Vertebrate Paleontology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

(f) Female individual; (-), minimum dimension.

*Data from Lei (1985); P83.4 originally identified as an M_2 or M_3 .

†Data from Li (1978).

distally. This latter feature suggests that the root of the tooth was implanted obliquely in the premaxilla so that the tip of the root was positioned more laterally than the base of the root. In the unworn state the apex bears three low, irregular mammilons. The mesial margin of the crown is straight to slightly convex, while the distal margin is more strongly convex. The lingual cingulum is broad, well-developed, and forms a continu-

ous shelf around the lingual aspect of the base of the crown. Originating from the lingual cingulum, in the midline of the crown, are one or more fine crests that extend towards the apex, but there is no distinct lingual pillar. The lingual face of the crown is finely wrinkled. The buccal face is biconvex and generally featureless, except for some minor wrinkling. In early stages of wear, a narrow strip of dentine is exposed

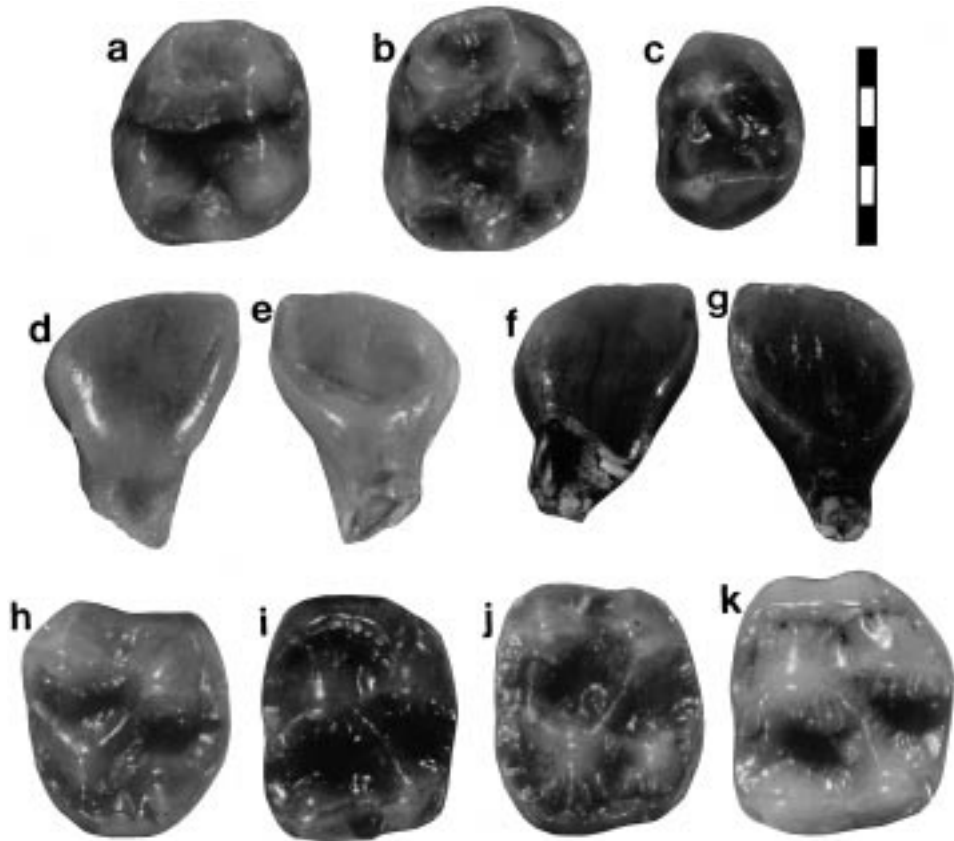


Figure 4. Upper and lower teeth of *Dionysopithecus shuangouensis*. (a) PA 1251, right M_1 , occlusal view; (b) PA 1253, right M_2 , occlusal view; (c) PA 1233, right P^4 , occlusal view; (d) PA 1230, left I^1 , buccal view; (e) lingual view; (f) PA 1231, left I^1 , buccal view; (g) lingual view; (h) PA 1046, left M^1 , occlusal view; (i) PA 1043, right M^2 , occlusal view; (j) PA 1049, left M^2 , occlusal view; (k) PA 1044, right M^2 , occlusal view. Scale bar=5 mm.

along the incisive apex and wear facets are produced on the lingual face of the crown. As wear advances, dentine is also exposed along the length of the lingual cingulum.

Only a single upper canine is represented (Figure 5). On the basis of size and morphological characteristics this is assumed to have belonged to a female individual. The crown is relatively short and quite robust. The apex is recurved distally and lingually. The mesial crest is short, and it terminates basally at a well-developed lingual cingulum. On the lingual face of the crown, just distal to the mesial crest, is a shallow, but quite well-

defined groove. The groove is broadest and deepest at the level of the lingual cingulum. Just distal to the mesial groove is a prominent lingual pillar, which extends from the cingulum to the apex of the crown. Distally, there is a broad heel that gives the crown a distinctive triangular shape in occlusal outline. A broad, but irregular, cingulum passes lingually around the base of the crown. The buccal face of the crown is evenly biconvex and finely wrinkled. Mesially, there is a slight trace of a buccal cingulum. The root is almost complete, lacking only its tip. The base of the root is distinctively triangular in

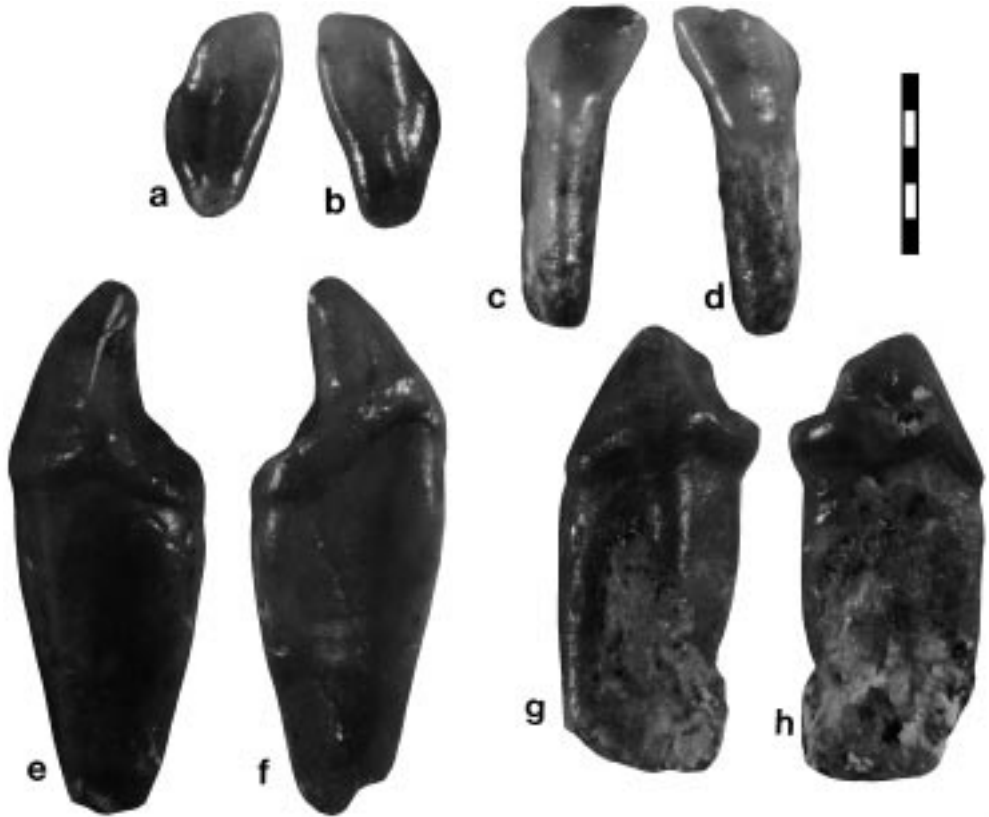


Figure 5. Upper and lower teeth of *Dionysopithecus shuangouensis*. (a) PA 1244, left I_2 , lingual view; (b) buccal view; (c) PA 1242, left I_2 , lingual view; (d) buccal view; (e) PA 1228, left upper canine, buccal view; (f) lingual view; (g) PA 1051, left P_3 , buccal view; (h) lingual view. Scale bar=5 mm.

cross-section, concordant with the shape of the crown. Towards the apex, the root becomes more elliptical in cross-section and bilaterally compressed.

P^4 is oval in occlusal outline, narrowing lingually, with a strongly convex distal margin (Figure 4). The crown is relatively narrow, with an average length–breadth index ($MD \times 100/BL$) of 68.1. The buccal moiety of the crown is slightly longer mesiodistally than the lingual moiety. The protocone is low and conical, and is situated slightly closer to the mesial margin than to the distal margin. The paracone is more elevated than the protocone and is buccolingually compressed. A hypoparacrista passed lingually from the apex of the paracone to terminate

at the base of the protocone. The preparacrista is short and sharp. It terminates mesially at an elevated portion of the mesial marginal ridge. The postparacrista is longer than the preparacrista and terminates at the distal marginal crest. By comparison, the preprotocrista and postprotocrista are low and rounded, and less well-developed. A fine crest, the hypoprotocrista, usually descends from the apex of the protocone and passes distobuccally to terminate close to the base of the postprotocrista. However, in PA 1232 this crest is lacking. Mesial to the hypoparacrista is a broad and well-defined transverse fissure that represents the mesial fovea. A shallow triangular fovea in the center of the crown is delimited by the

hypoparacrista and hypoprotocrista (when present). Distal to the hypoprotocrista is a large and finely wrinkled distal fovea. The lingual margin of the protocone is bordered by a narrow lingual cingulum. Traces of a buccal cingulum are evident mesially and distally.

M^1 is subrectangular in occlusal outline (Figure 4). The lingual and distal margins are both convex, giving the distolingual corner of the crown a rounded contour. The crown is mesiodistally slightly shorter in the lingual moiety than in the buccal moiety, and the buccal margin tends to exhibit a slight degree of waisting between the paracone and metacone. The crown is relatively narrow, with an average length–breadth index ($MD \times 100/BL$) of 87.7. The four main cusps are low and rounded. The protocone is the most voluminous cusp, but it is less elevated than the paracone and metacone. The preprotocrista is well-developed. It passes mesiobuccally to the margin of the crown where it becomes continuous with the mesial marginal ridge. Midway along its length there is a slight swelling to indicate the location of the paraconule. The postprotocrista is less prominent than the preprotocrista. It passes distobuccally to meet the hypometacrista, and together they form the crista obliqua. There is no metaconule. The paracone is more elevated than or subequal in height to the metacone. A short crest passes mesially, the preparacrista, to terminate at the mesial margin. The postparacrista passes distally to make contact with the premetacrista. The hypoparacrista is a narrow, irregular crest that passes lingually to terminate at the paraconule. Mesial to the hypoparacrista is a well-defined mesial fovea. The metacone is pyramidal in shape, and the premetacrista and hypometacrista sharply defined. In PA 1045 the postmetacrista is short and passes distally to terminate at the distal margin of the crown. In PA 1046, by contrast, it passes directly lingually to terminate within the distal basin.

The hypocone is small and conical. A fine prehypocrista passes mesially to terminate at the base of the protocone. An ill-defined posthypocrista passes distobuccally to join the distal marginal ridge. The lingual cingulum is broad and well-developed, forming a C-shaped ledge around the mesial and lingual margins of the protocone, but not generally continuing around the hypocone. The lingual cingulum tends to be disrupted by fine crests that radiate from the base of the protocone. The trigon basin is relatively narrow (the distance between the apices of the protocone and paracone is only 38% of the total buccolingual breadth of the tooth), but quite deep and well-defined. The groove system within the basin is simple, with little or no development of secondary wrinkling of the enamel surface. The distal fovea is quite extensive, with an area approximately equal to that of the trigon, due mainly to the marked convexity of the distal margin of the crown. In V5597 and PA 1045 the distal basin is transected by a crest that runs from the hypocone to the metacone. The distal fovea may be disrupted by fine crests that originate from the crista obliqua and the base of the hypocone. The buccal cingulum is poorly developed or entirely absent.

M^2 is similar to M^1 , but differs in the following characteristics: (1) it is slightly larger in size; (2) the crown is relatively broader, with an average length–breadth index ($MD \times 100/BL$) of 80.1; (3) the crown is more rectangular in shape, with a less rounded distolingual margin; (4) the mesial fovea is relatively broader; (5) the distal fovea is smaller than the trigon basin (subequal in M^1); (6) the trigon basin is relatively broader, although still quite narrow (the distance between the apices of the protocone and paracone averages 46% of the total buccolingual breadth of the crown); (7) the lingual cingulum is better developed (which contributes to the greater overall breadth of the crown), and it continues distally around the hypocone; (8) the

crown tends to be mesiodistally longest in the lingual moiety, and narrows slightly buccally (in M^1 the crown is longest in the midline); and (9) the buccal cingulum is better developed, consisting of a discontinuous ledge along the distobuccal margin of the metacone, at the junction between the metacone and paracone, and on the mesiobuccal margin of the paracone (Figures 4 and 6).

M^3 is known only from the holotype. It is considerably smaller than M^2 . The subrectangular crown narrows slightly distally, especially along the buccal side. The protocone is voluminous, being much larger than the paracone. The preprotocrista is well-developed, and terminates close to the mesial marginal ridge at a small but distinct paraconule. The crista obliqua, which originates from the tip of the protocone, is well-developed lingually, but recedes as it arcs distobuccally to meet the metacone. The paracone is high and conical, and buccolingually compressed. The preparacrista is sharp and arcs mesiolingually to become confluent with the mesial marginal ridge. A fine, sinuous crest, the hypoparacrista, passes lingually from the apex of the paracone to connect with the paraconule. This crest defines the distal margin of a broad, crescent-shaped mesial fovea. The metacone is rudimentary, being represented only by a small tubercle located at the junction of the postparacrista and the crista obliqua. The trigon basin is shallow and well-defined, with minimal secondary wrinkling. The hypocone is represented by a small conule just distal to the protocone, which is only slightly more prominent than the metacone. It is linked by a fine crest to the crista obliqua, as well as to two smaller subsidiary tubercles located within the distal fovea. In addition, the distal fovea is further disrupted by fine wrinkles. The lingual cingulum forms a broad, C-shaped ledge around the lingual aspect of the protocone, and, as in M^1 and M^2 , it is disrupted by crests that

radiate from the base of the protocone. Traces of a buccal cingulum are present on the mesial and distal aspects of the buccal face of the crown.

The upper deciduous canine is a stout, low-crowned tooth in which the apico-basal height is only slightly greater than the mesiodistal length. In buccal view the crown is conical, with the mesial and distal crests subequal in length. Like the permanent upper canine, dC^1 is triangular in occlusal outline with a broad distal heel. On the lingual face of the crown, just distal to the mesial crest, is a shallow groove. This is bordered distally by a swollen lingual pillar. A narrow cingulum extends around the lingual aspect of the base of the crown.

The dP^4 is generally similar in morphology to M^1 , but is smaller in size, relatively narrower, and has a simple occlusal plan. The main cusps are small and conical, and the connecting crests are relatively low, but sharp. The crown tends to narrow slightly towards the lingual side. The hypocone is much smaller than the trigon cusps, although it is linked to the protocone by a sharp, obliquely directed crest. The lingual cingulum forms a narrow C-shaped ledge around the mesial and lingual aspects of the protocone. The talonid is narrow, and its floor is smooth and featureless. The distal basin is quite large by comparison, and devoid of secondary wrinkling.

Lower dentition

I_2 is a slender and moderately high-crowned tooth (Figure 5). The mesial margin of the crown is long and slightly convex. The distal margin has an angulation midway along its length, making the crown bilaterally asymmetrical. The distal margin is shorter than the mesial margin, so that the narrow incisive apex recedes somewhat distally—an unusual feature among Miocene catarrhines noted also in the upper central incisors. The lingual cingulum is well-developed, forming

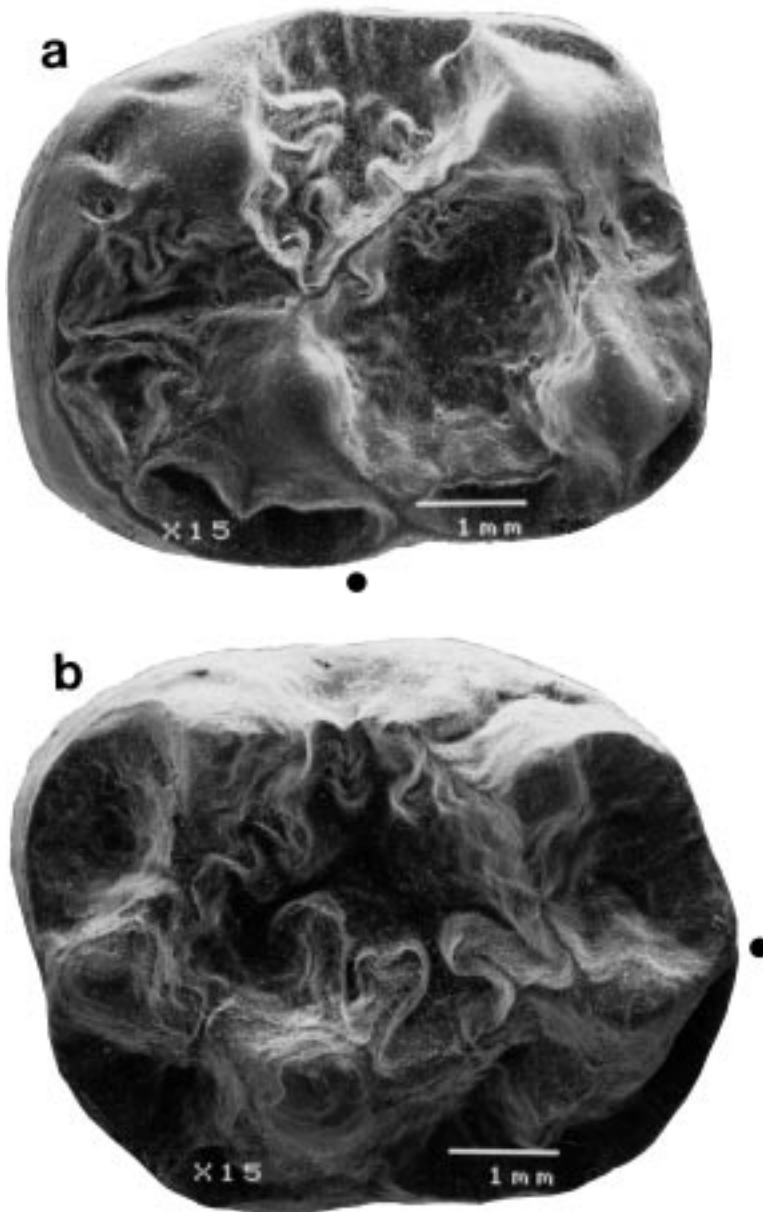


Figure 6. Scanning electron micrograph showing the detailed morphology of the upper and lower molars of *Dionysopithecus shuangouensis*: (a) PA 1043, right M_2^u , occlusal view; (b) PA 1253, right M_2^l , occlusal view. Dot indicates mesial margin. Scale bar=1 mm.

a continuous ledge around the base of the lingual face of the crown. Where the lingual cingulum meets the distal margin a distinct tubercle is developed. Originating from the

lingual cingulum is a narrow crest, the lingual pillar, which extends about two-thirds along the crown towards the apex. The buccal face of the crown is smoothly

convex and featureless. As in the upper central incisor, the crown narrows basally with a slight degree of waisting, giving it a distinctive flask-shaped appearance.

P_3 is a mesiodistally short and relatively high-crowned tooth (Figure 5). The protoconid is elevated and conical in shape. Three crests originate from its apex. The preprotocristid descends midway down the crown to terminate at the mesial junction of the lingual cingulum. The postprotocristid, which is low and rounded, ends distally at the marginal ridge. The hypoprotocristid arcs distolingually to terminate in the distal basin. In PA 1051 this latter crest bears a well-developed metaconid, whereas in PA 1257 there is only a minor protuberance towards the apex, but no distinct cusp. The mesiobuccal face of the crown is steeply inclined, with only a slight degree of extension of enamel inferiorly onto the mesial root of the tooth. There is a slight trace of a buccal cingulum. The distal heel is relatively long and surrounded by a raised marginal ridge which encloses a shallow basin. The lingual cingulum forms a narrow ledge along the entire length of the lingual face, and is continuous distally with the marginal ridge.

P_4 is suboval in occlusal outline, with an obliquely oriented long axis that passes mesiobuccally. There are two main cusps, the protoconid and metaconid, of which the former is distinctly larger and more elevated. The protoconid is pyramidal in shape, with three crests originating from its apex. The preprotocristid is long and narrow, and terminates at the mesial marginal ridge, while the postprotocristid is irregular and bifurcates midway along its length. The buccal arm of the postprotocristid descends into the buccal cingulum, while the lingual arm terminates at a small tubercle on the rim of the distal margin. The metaconid is linked to the protoconid by a transverse crest. The premetacristid originates from the base of the metaconid and passes mesially to end at the margin of the crown. The mesial fovea is

represented by a narrow triangular basin. The postmetacristid descends from the apex of the metaconid to end at a small tubercle on the distal margin. The distal marginal ridge is elevated and encloses a relatively long and narrow talonid.

M_1 is suboval in occlusal outline, being slightly broader in its distal moiety than its mesial moiety, and with a slight degree of waisting on the buccal side of the crown (Figure 4). The crown is moderately narrow, with an average breadth-length index (BL \times 100/MD) of 86.6. The protoconid is low and conical. The preprotocristid, the hypoprotocristid and the postprotocristid are short, low and rounded. The hypoconid is similar in size to the protoconid. It has two main crests, the prehypocristid and the posthypocristid, both of which are low and rounded. The prehypocristid and the postprotocristid form the cristid obliqua, which is slightly obliquely oriented in relation to the long axis of the crown. A narrow subsidiary crest generally originates from near the apex of the hypocone and descends mesiolingually into the talonid basin. This crest is the homologue of the distal arm of the pliopithecine triangle. The mesial arm of the pliopithecine triangle, originating from the protoconid, is variably developed on M_1 , but is present in PA 1235, PA 1249, and PA 1256. The hypoconulid is the smallest of the main cusps. It is positioned on the distal margin, usually slightly towards the buccal side of the midline of the crown. The mesiobuccal crest of the hypoconulid is poorly developed. The mesiolingual crest is better defined, and it meets the hypoentocristid to delimit the mesial margin of a small, triangular distal fovea. The metaconid and entoconid are subequal in size to the protoconid and hypoconid, but are somewhat more elevated. The premetacristid arcs buccally to become continuous with the mesial marginal ridge. In several specimens the latter terminates just mesial to the protoconid in a small tubercle: the vestige of a

paraconid. The postmetacristid is relatively short and rounded. At its junction it bears a distinct mesostylid; an unusual feature, but one seen in almost all of the unworn lower molars. The hypometacristid passes buccally and slightly mesially to meet with the hypoprotocristid in the midline. The two crests define the distal wall of the trigonid basin (=mesial fovea). This mesial transverse crest is obliquely oriented because the metaconid is slightly distally offset from the protoconid. The mesial fovea is relatively long and rectangular, and its floor is only slightly more elevated than that of the talonid basin. The entoconid is pyramidal in shape, with three ill-defined crests, the pre-entocristid, the hypoentocristid and the postentocristid. The talonid basin is longer than it is broad. It has a simple Y-shaped groove system, with subsidiary grooves that pass between each of the main cusps. The buccal cingulum is well-developed, although not usually continuous. A narrow ledge occurs on the mesiobuccal face of the protoconid and a second portion of the cingulum occurs between the protoconid and hypoconid. A small fovea between the hypoconid and hypoconulid represents the distalmost portion of the cingulum.

M_2 is similar in morphology to M_1 , but differs in the following respects: (1) it is slightly larger in size; (2) the crown is relatively longer (with an average breadth-length index of 83.3), and more rectangular in occlusal outline; (3) there is no trace of a paraconid; (4) the pliopithecine triangle is always well-defined, forming a small V-shaped fovea within the talonid basin; and (5) the buccal cingulum is generally better developed, although still not forming a continuous ledge around the buccal margin of the crown (Figures 4 and 6).

M_3 is moderately long and narrow (with an average breadth-length of 82.2), and the crown tapers slightly distally. Although only known from two isolated teeth, both M_3 s are

relatively small by comparison to M_2 (the average occlusal area of M_3 is only 90.9% of that of M_2), and this may prove to be a distinctive feature of the species when associated material is eventually recovered. As noted above for the preceding molars, M_3 is characterized by: (1) a relatively elongated mesial fovea; (2) a slightly oblique mesial transverse crest (but the obliquity is less marked than in M_1 and M_2); (3) a well-developed pliopithecine triangle; (4) a long and narrow talonid basin; (5) a slightly oblique cristid obliqua; (6) a small hypoconulid placed towards the buccal side of the midline of the crown; (7) a small, well-defined distal fovea; and (8) a broad, but discontinuous buccal cingulum. All of the cheek teeth are low-crowned and, judging by their pattern of wear, they have relatively thin enamel.

The dC_1 is moderately high-crowned and bilaterally compressed. The apex of the crown is located in the midline, somewhat towards the mesial end of the tooth. The mesial crest is short, and terminates midway down the crown at a raised portion of the lingual cingulum. The distal crest is longer and descends into the shallow distal basin. The lingual face is triangular in shape and has a slight crenulation of its enamel surface. It is bordered basally by a low, rounded lingual cingulum. The distal margin is raised and it passes around the basal termination of the distal crest to end at a small, but distinct tubercle. The latter gives rise to a slender crest that passes towards, but does not quite reach, the distal crest. The buccal face of the tooth is generally smooth and featureless, apart from a slight trace of a buccal cingulum on its mesial aspect.

The dP_3 has a long elliptical crown. The single main cusp, the protoconid, is conical and somewhat buccolingually compressed. It is located in the midline of the crown, slightly off-center towards the mesial margin. A sharp preprotocristid passes mesially to terminate at the mesial junction of the

lingual cingulum. The mesiolingual face of the crown bears a narrow cingulum. The hypoprotocristid passes distolingually to meet the small metaconid. The postprotocristid terminates distally at a prominent tubercle (=hypoconid) on the distal margin of the crown. A sharp crest originates from the apex of the metaconid and arcs distally and then buccally to join the hypoconid. Midway along the length of the crest there is a well-developed tubercle (indistinct in PA 1247) that presumably represents the equivalent of the entoconid. Distally there is a shallow, pyriform basin delimited by the postprotocristid, the postmetacristid and the distal marginal ridge. Traces of the buccal cingulum occur on the mesial margin of the crown and on the buccal aspect of the hypoconid, respectively.

The dP_4 is similar in general morphology to M_1 . However, it differs in that: (1) the crown is relatively longer (with an average breadth-length index of 77.1, as opposed to 86.6), with a more pronounced mesial narrowing; (2) the mesial fovea is relatively longer, (3) a distinctive subsidiary crest originates from the protoconid and passes obliquely across the mesial fovea; (4) the trigonid is somewhat more elevated relative to the floor of the talonid; (5) the mesial transverse crest is more obliquely oriented; (6) the paraconid is more prominent; (7) there is no development of a pliopithecine triangle; (8) the cristid obliqua is relatively long and more obliquely directed; (9) the hypoconulid is diminutive; (10) the distal fovea is smaller and less clearly demarcated from the talonid basin (in PA 1255 the fovea communicates directly with the talonid basin); and (11) the buccal cingulum is generally less well-developed.

Genus *Platodontopithecus*
Gu & Lin, 1983

Emended diagnosis: Medium-sized catarrhine primate, slightly larger in dental size than

Hylobates syndactylus and *Nasalis larvatus* (with an estimated average body weight of approximately 15 kg—see below for details on size estimation). The upper canine in presumed male individuals (canines of female unknown) is moderately high-crowned and strongly bilaterally compressed. Upper premolars are relatively broad. Upper molars have rounded cusps and low occlusal relief, broad and well-developed lingual cingulum usually disrupted by subsidiary crests originating from the base of the protocone, and moderately well-developed buccal cingulum. M^1 and M^2 have the following characteristics: crown broad and subrectangular in shape with convex lingual and distal margins; hypocone prominent, but distinctly smaller than the trigon cusps; transverse crest(s) between the metacone and hypocone generally well-developed. M^3 has rudimentary hypocone and metacone. $M^2 > M^3 > M^1$. P_3 is mesiodistally short, with elevated protoconid, steep mesiobuccal face, and minimal extension of enamel inferiorly onto the anterior root. Lower molars have the following characteristics: crown long and moderately narrow; low, rounded cusps and crests; small paraconid usually retained; mesial transverse crest incompletely formed, but obliquely directed in relation to the long-axis of the crown; mesial fovea mesiodistally long, often with accessory crests, and wide communication with the talonid basin; mesostylid well-developed; cristid obliqua slightly obliquely oriented; pliopithecine triangle present; hypoconulid slightly smaller than the hypoconid; well-defined distal fovea; buccal cingulum generally well-developed, and commonly beaded with small accessory cusps. M_3 is relatively small. $M_2 \geq M_3 > M_1$. [Emended from Gu & Lin (1983).] For characteristics that differentiate *Platodontopithecus* from other fossil catarrhines see Phylogenetic relationships.

Platodontopithecus jianghuaiensis
Gu & Lin, 1983

Synonyms: *Dryopithecus sichongensis* Lei, 1985.

Lectotype: PA 870 (IVPP). Left M₃. Originally part of a *type series* described by Gu & Lin (1983) which also included PA 849, PA 850, PA 851 and PA 871. However, as noted by Harrison *et al.* (1991) these five specimens almost certainly do not constitute teeth from a single individual, and it was considered in the best interests of taxonomic stability to identify PA 870 (the least worn and morphologically the most distinctive tooth) as a lectotype [following Article 74(a) of the International Code of Zoological Nomenclature, Ride *et al.*, 1985].

Type locality: Songlinzhuang, Sihong County, Jiangsu Province, People's Republic of China (see Figure 1).

Distribution: Latest early Miocene (late Shanwangian=late Orleanian, MN 4). Xiaocaowan Formation; localities (1) Songlinzhuang and (2) Zhengji, Sihong County, Jiangsu Province, People's Republic of China.

Referred material: In addition to the lectotype, the hypodigm includes 25 specimens from Songlinzhuang and 7 specimens from Zhengji. See Table 5 for a complete listing of referred specimens and Table 6 for a summary of dental measurements.

Description of material

Upper dentition

Only two upper canines are known, PA 1218 and PA 1219, of which only the latter is well enough preserved for adequate description (Figure 7). Based on their morphology and size, both specimens can be presumed to be canines of male individuals. The tooth is relatively high-crowned and strongly bilaterally compressed. The apex of the crown is recurved distally and slightly lingually. The sharp and convex mesial crest

is bordered lingually by a deep mesial groove that extends almost to the tip of the crown. Mesiolingually there is a pronounced lingual pillar. Distal to the lingual pillar the lingual face of the crown is slightly concave and finely crenulated. There appears to be no development of a lingual cingulum. The distal margin of the crown is formed by a long, blade-like crest. The buccal surface of the crown is mesiodistally convex and featureless apart from a series of fine striations that run apico-basally. The mesial crest is bordered buccally by a shallow groove. In PA 1219, occlusion with the lower canine has produced flattened wear facets along the mesial crest and the mesial face of the lingual pillar. In addition, occlusion with the mesiobuccal honing face of P₃ has produced an extensive strip of dentine exposure along the length of the lingual face of the distal crest, and this serves to maintain a sharp edge to the distal margin.

P³ is relatively broad, with an average length-breadth index (MD × 100/BL) of 72.6. The tooth is triangular in occlusal outline, with a crown that is mesiodistally longest along its buccal side and narrows towards its lingual side. There are two main cusps of which the paracone is much more elevated than the protocone. Both cusps are conical in shape. The preparacrista and postparacrista are sharp, subequal in length and terminate at the margin of the crown. A hypoparacrista originates from the apex of the paracone and passes lingually to meet the preprotocrista midway along its length. The transversely aligned hypoparacrista forms the distal wall of the mesial fovea. The preprotocrista arcs mesially and buccally after it originates from the protocone, to become continuous with the mesial margin of the crown. The postprotocrista is more irregular in contour, but generally meets the distal margin of the crown. In PA 1227, a sharp crest originates midway along the length of the postparacrista and passes lingually, but does not quite reach the post-

Table 5 List of cranio-dental material assigned to *Platodontopithecus jianghuaiensis*

| Accession number* | Locality | Brief description |
|-------------------|---------------|---|
| P83.3 | Songlinzhuang | Left M ₃ (holotype of <i>Dryopithecus sichongensis</i> Lei, 1985). |
| PA 849† | Songlinzhuang | Right M ¹ . Heavily worn and slightly damaged. |
| PA 850† | Songlinzhuang | Left M ² . Heavily worn. |
| PA 851† | Songlinzhuang | Right M ³ . Slightly worn. |
| | | Left M ₃ . Moderately worn. (Lectotype of <i>Platodontopithecus jianghuaiensis</i> Gu & Lin, 1983)‡. |
| PA 870† | Songlinzhuang | Left M ₂ . Mesial and distal margins lacking. Moderately worn. |
| PA 871† | Songlinzhuang | Right dP ³ . Buccal margin of crown missing. Unerupted germ. |
| PA 1050 | Songlinzhuang | Right P ³ . Unerupted crown. |
| PA 1212 | Songlinzhuang | Left P ⁴ . Moderately worn and slightly damaged. |
| PA 1213 | Songlinzhuang | Right P ⁴ . Moderately worn. |
| PA 1214 | Songlinzhuang | Left M ³ . Slightly worn. |
| PA 1215 | Songlinzhuang | Left M ³ . Slightly worn. |
| PA 1216 | Songlinzhuang | Right P ³ . Distobuccal portion of crown missing. Germ. |
| PA 1217 | Songlinzhuang | Left C ¹ . Male individual. Poorly preserved. |
| PA 1218 | Songlinzhuang | Left C ¹ . Male individual. Slightly worn. |
| PA 1219 | Songlinzhuang | Left M ₂ . Unerupted crown. |
| PA 1220 | Songlinzhuang | Right M ₂ . Moderately worn. |
| PA 1221 | Songlinzhuang | Right M ₂ . Mesiobuccal portion of crown only. Moderately worn. |
| PA 1222 | Songlinzhuang | Right M ₂ . Unerupted crown. |
| PA 1223 | Songlinzhuang | Left M ₁ . Moderately worn. |
| PA 1224 | Songlinzhuang | Right M ₁ . Slightly worn. |
| PA 1225 | Songlinzhuang | Right M ₁ . Unerupted crown. |
| PA 1226 | Songlinzhuang | Left P ³ . Unerupted germ. |
| PA 1227 | Songlinzhuang | Left P ₃ . Unerupted germ. |
| PA 1229 | Songlinzhuang | Right M ₁ . Slightly worn, damaged. |
| PA 1234 | Songlinzhuang | Right M ¹ . Lingual half of crown only. Slightly worn. |
| PA 1250 | Zhengji | Right M ¹ . Moderately worn. |
| PA 1260 | Zhengji | Left M ¹ . Moderately worn and damaged. |
| PA 1261 | Zhengji | Right M ₁ . Poorly preserved. |
| PA 1263 | Zhengji | Right P ₃ . Moderately worn. |
| PA 1264 | Zhengji | Left dC ¹ . Slightly worn. |
| PA 1268 | Zhengji | Right dC ₁ . Slightly worn. |
| PA 1269 | Zhengji | Right mandibular fragment preserving the germ of P ₄ . |
| PA 1273 | Songlinzhuang | |

*Accession numbers: P, collections of the Geological Museum of Nanjing; PA, Paleoanthropology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; V, Vertebrate Paleontology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

†Type series of Gu & Lin (1983).

‡Lectotype attribution following Harrison *et al.* (1991).

protocrista. As a result, the distal basin is partially subdivided into a small distal fovea and a larger central fovea. In other examples (PA 1212 and PA 1217), however, this distal transverse crest is lacking and the distal basin is extensive. There is no lingual cingulum, and the buccal cingulum is restricted to traces along the mesial and distal aspects only.

P⁴ is relatively broad, with a length-breadth index ($MD \times 100/BL$) of 59.5, and the crown is subovoid in occlusal outline. The paracone is more elevated than the protocone, but the difference in height between the two main cusps is much less than in P³. The preparacrista and postparacrista are short, sharp crests that terminate at the marginal ridge. A mesial transverse

Table 6 Dimensions of the teeth of *Platodontopithecus jianghuaiensis*

| | Acc. no. | Lowers | | | Acc. no. | Uppers | | |
|-----|----------|--------|-----|-----|-------------|--------|--------|------|
| | | MD | BL | BHT | | MD | BL | BHT |
| C | | | | | PA 1219 (m) | 9.1 | 7.6 | 11.8 |
| P3 | PA 1229 | 6.6 | 4.9 | | PA 1212 | 4.5 | 6.3 | |
| | PA 1264 | 6.3 | 4.2 | | PA 1227 | 4.8 | 6.5 | |
| P4 | PA 1273 | 6.4 | 5.5 | | PA 1213 | 4.6 | 6.4(-) | |
| | | | | | PA 1214 | 4.4 | 7.4 | |
| M1 | PA 1224 | 7.3 | 6.4 | | PA 1260 | 6.8 | 8.1 | |
| | PA 1225 | 7.9 | 6.6 | | PA 1261 | 6.5 | 8.2 | |
| | PA 1226 | 8.4 | 7.0 | | PA 849 | 6.4 | 8.6 | |
| M2 | PA 1220 | 9.2 | 7.6 | | PA 850 | 7.1 | 9.2 | |
| | PA 1221 | 9.0 | 7.6 | | | | | |
| | PA 1223 | 9.3 | 8.0 | | | | | |
| M3 | PA 870 | 8.6 | 7.5 | | PA851 | 7.8 | 9.0 | |
| | P83.5* | 8.7 | 7.1 | | PA 1215 | 7.0 | 9.0 | |
| | | | | | PA 1216 | 6.7 | 8.2 | |
| dC | PA 1269 | 4.3 | 2.9 | 5.3 | PA 1268 | 4.2 | 3.6 | 5.0 |
| dP3 | | | | | PA 1050 | 4.2 | 4.8(-) | |

Abbreviations: Acc. no., Accession number; BHT, buccal height; BL, buccolingual breadth; MD, mesiodistal length; P, collections of the Geological Museum of Nanjing; PA, Paleoanthropology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; V, Vertebrate Paleontology collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

(m) Male individual; (-), minimum dimension.

*Data from Lei (1985); possibly an M_2 .

crest passes from the apex of the paracone to end midway along the preprotocrista. This latter crest delimits a well-defined, fissure-like mesial fovea. A low, irregular crest originates from the apex of the protocone and loops buccolingually across the crown to the base of the paracone. This distal transverse crest, which occurs in both examples of P^4 , subdivides the distal basin into distal and central foveae. The lingual cingulum is well-developed. The buccal cingulum consists of narrow traces along the mesial and distal aspects of the buccal face of the crown.

M^1 is a relatively broad, rectangular tooth, usually with convex lingual and distal margins (Figure 8). Of the four main cusps, the paracone is the most elevated, but it is somewhat less voluminous than the metacone and protocone. The hypocone is distinctly smaller than the trigon cusps. One of the most remarkable features of the upper molars is the relatively low relief of the occlusal surface, even in unworn or lightly

worn specimens. The cusps and occlusal crests are generally low and rounded. The hypoparacrista is well-developed, forming the posterior border of a broad, fissure-like mesial fovea. The crista obliqua is also relatively pronounced, and along with the latter crest, delimits a well-defined trigon basin. The basin is slightly broader than it is long, with a simple Y-shaped groove system. On the best preserved example of M^1 , PA 1260, a fine crest passes from the apex of the hypocone to the base of the metacone, and an equivalent crest passes from the metacone to the hypocone. These two crests define a small triangular fovea within the confines of the talon basin. In PA 1261, however, only a single transverse crest links the hypocone and metacone (as seen in M^2). The lingual cingulum is well-developed, forming a broad ledge around the mesial and lingual aspects of the protocone, and even continuing around on to the distal margin of the hypocone. The lingual



Figure 7. PA 1219, left upper canine of *Platodontopithecus jianghuaiensis*. (a) Lingual view; (b) buccal view. Scale bar=5 mm.



Figure 8. Upper molars of *Platodontopithecus jianhuaiensis*: (a) PA 849, right M^1 ; (b) PA 850, left M^2 ; (c) PA 851, right M^3 ; (d) PA 1215, left M^3 . All occlusal views. Scale bar=5 mm.

cingulum may be disrupted by secondary crests that radiate from the base of the protocone. The buccal cingulum is represented by narrow ledges on the mesial and distal aspects of the buccal face of the crown, and by a small depression at the marginal junction of the groove that passes between the paracone and metacone.

M^2 is known only from a single specimen, PA 850, which is quite heavily worn (Figure 8). It is similar in morphology to M^1 , but differs in being larger in size (with an occlusal area 18.6% greater than the largest M^1) and in having a more regularly rectangular occlusal outline. Moreover, PA 850 has a small tubercle at the mesial junction of the preprotocrista corresponding to the paracone. This is not observed on any of the

M^1 s and it is uncertain whether this feature is typical of M^2 or merely represents an individual variant.

M^3 is subovoid to triangular in shape, narrowing distally (Figure 8). As in M^1 and M^2 occlusal relief is low. The protocone is generally more voluminous and somewhat more elevated than the paracone. The pre-para-crista is prominent, with a bulbous swelling, the paraconule, located midway along its length. The hypopara-crista follows an irregular course, but usually passes lingually to meet the preprotocrista at or just distal to the paraconule. The pre-para-crista is short and it arcs mesially and lingually to become continuous with the mesial marginal ridge. The mesial fovea is represented by a short crescentic fissure just mesial to the

hypoparacrista. The crista obliqua generally forms a continuous crest. The postparacrista passes distolingually from the paracone, where it converges with the crista obliqua. The metacone is restricted to a tiny cuspule. The trigon basin is well-defined, but relatively shallow. There is usually some degree of secondary wrinkling in the basin. The hypocone is small by comparison to the mesial cusps, but is usually larger than the metacone. It is connected to the protocone by a narrow crest, but there is no connection with the metacone. The hypocone is somewhat removed from the distal margin of the crown, and in some cases a short crest descends from its apex to join the distal marginal crest. The distal fovea is a large triangular basin, often disrupted by secondary wrinkling. The lingual cingulum is broad and it forms a continuous shelf around the lingual aspects of the protocone and hypocone. As in M^2 , fine crests originate from the base of the protocone and radiate out onto the cingular shelf. The buccal cingulum is variably developed.

The dC^1 is oval in occlusal outline with a single cusp located close to the center of the crown. The mesial and distal crests are sharp and subequal in length. A shallow mesial groove is present, bordered by a low, rounded lingual pillar that extends almost to the apex of the crown. Distal to the lingual pillar is a broad, but shallow basin. The lingual cingulum is continuous around the base of the lingual face. Traces of a buccal cingulum can be seen mesially and distally.

The dP^3 is known only from a partially complete tooth. The crown is buccolingually broader than it is long, narrows lingually, and is triangular in shape. As in the permanent cheek teeth the occlusal relief is relatively low. The protocone is voluminous, but is less elevated than the paracone. The preprotocrista arcs mesiobuccally to join the mesial margin of the crown. The postprotocrista is a narrow crest that terminates distally at a small tubercle (a rudimentary

hypocone). The preparacrista and postparacrista are sharp, well-defined and subequal in length. A hypoprotocrista originates from the base of the protocone and passes buccally and slightly distally to join the postparacrista close to the apex of the paracone. Similarly, an ill-defined crest, the hypoparacrista, passes lingually from the paracone, but does not quite reach the preprotocrista. The tooth is therefore similar to P^4 s and some P^3 s in having a double transverse crest that isolates a small central fovea. The mesial fovea is a shallow triangular basin. The distal basin is quite extensive, and a short subsidiary crest descends from the base of the paracone into the center of the basin.

Lower dentition

P_3 is oval in occlusal outline. The tooth is mesiodistally relatively short and high-crowned, with only a limited extension of enamel onto the mesiobuccal face of the anterior root. As a consequence, the honing face for occlusion with the upper canine is relatively high and steep, but it does not extend inferiorly much below the general level of the cementum–enamel junction of the other lower cheek teeth. The single main cusp, the protoconid, is elevated and pyramidal in shape. Its mesial crest terminates basally at the mesial margin of the lingual cingulum. A sharp crest passes mesiodistally from the apex of the protoconid and ends at a small cuspule, the metaconid, close to the margin of the tooth at the junction of the lingual cingulum and the distal marginal crest. The distal crest of the protoconid is low and rounded, meeting the distal margin at a small styloid, and the lingual cingulum is relatively narrow. A small triangular distal fovea is enclosed by the distal and distolingual crests of the protoconid and by the distal marginal crest. The buccal cingulum can be identified as rounded ledges on the mesial and distal aspect of the buccal face of the crown.

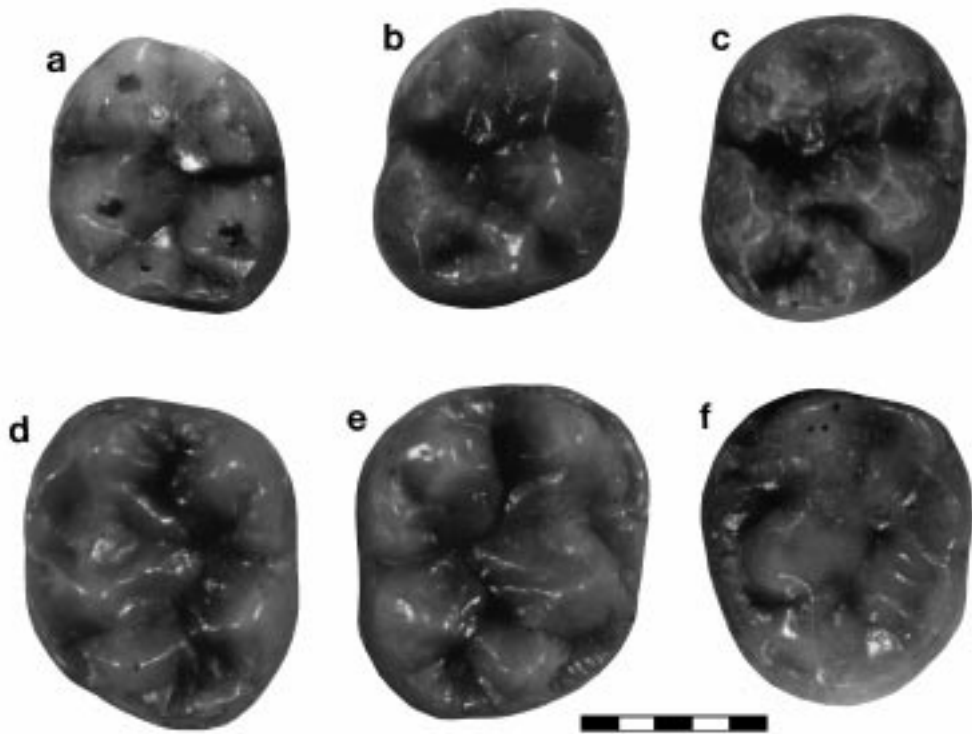


Figure 9. Lower molars of *Platodontopithecus jianghuaiensis*. (a) PA 1224, left M_1 ; (b) PA 1225, right M_1 ; (c) PA 1226, right M_1 ; (d) PA 1220, left, M_2 ; (e) PA 1223, right M_2 ; (f) PA 870, left M_3 . All occlusal views. Scale bar=5 mm.

P_4 is suboval in occlusal outline, with a distinct mesiobuccal flare. It is a bicuspid tooth in which the protoconid is slightly larger and more elevated than the metaconid. The transverse crest between the two cusps, comprising the hypoprotocristid and the hypometacristid, is divided in the midline by a fine longitudinal groove, and it is slightly obliquely oriented in relation to the transverse axis of the crown. Both of the main cusps have sharply defined mesial crests that delimit a long and narrow mesial fovea. The postprotocristid is rounded, and it terminates distally at a prominent stylid. The corresponding crest derived from the metaconid lacks a stylid. The distal basin (=talonid) is deep and well-defined, and much larger than the mesial fovea. A narrow

and irregular cingulum extends around most of the base of the buccal face of the crown.

M_1 is long and moderately narrow, subrectangular in outline, and exhibits a slight degree of buccolingual waisting midway along its length (Figures 9 and 10). The main cusps are conical in shape, quite high, and are generally subequal in size, except the hypoconulid, which is smaller than the others. The preprotocristid is short and sharp, while the postprotocristid is low and rounded. The hypoprotocristid and hypometacristid meet to form the mesial transverse crest, which is slightly obliquely oriented in relation to the buccolingual axis of the crown. The premetacristid arcs mesiobuccally to become continuous with the mesial marginal ridge. In all examples

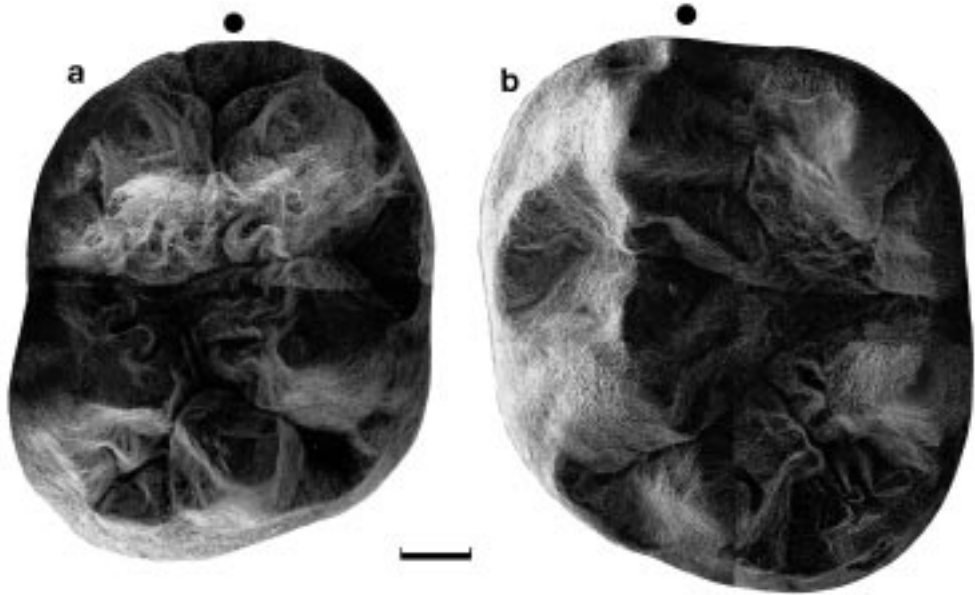


Figure 10. Composite scanning electron micrographs showing detailed morphology of the lower molars of *Platodontopithecus jianghuaiensis*: (a) PA 1225, right M_1 ; (b) PA 1220, left M_2 . Occlusal views. Dot indicates the mesial margin. Scale bar=1 mm.

available, there is a small tubercle located on the mesial margin of the crown either in the midline or slightly towards the lingual side. This presumably represents a vestige of the paraconid. The trigonid basin (=mesial fovea) is mesiodistally elongated. In PA 1225, subsidiary crests originate midway along the premetacristid and preprotocristid and converge to subdivide the trigonid basin. The postmetacristid is short and terminates at a distinct mesostylid. The postprotocristid divides midway along its length to give rise to the mesial arm of a pliopithecine triangle. The distal arm, which originates from the hypocone, is present on only two of the three well-preserved specimens available. The two arms of the pliopithecine triangle are relatively short and are connivent, so that the small triangular fovea delimited by them communicates broadly with the talonid basin. The prehypocristid is relatively long and it joins the postprotocristid mesially to form a slightly obliquely directed cristid obliqua. The pre-entocristid is quite

short, and is separated from the postmetacristid by a deep groove. The postentocristid passes mesiobuccally to become continuous with the distal marginal ridge. The hypoentocristid converges with a similar crest from the hypoconulid to define a small distal fovea. In some specimens subsidiary crests originate from the hypoconulid and entocristid, or from their attendant distal crests, and descend into the distal basin. The hypoconulid is smaller and lower than the other main cusps. It is situated on the distal margin, just to the buccal side of the midline of the crown. The talonid basin is long and quite narrow. Apart from the pliopithecine triangle, the talonid basin has a basic Y-shaped groove pattern with only a moderate degree of secondary wrinkling. The buccal cingulum forms a discontinuous ledge around the buccal aspect of the crown.

M_2 is similar in morphology to M_1 (Figures 9 and 10). It differs in the following respects: (1) it is larger in size; (2) the crown is relatively slightly broader; (3) the mesial

fovea is broader, more transversely aligned, and less well-defined (i.e., the hypoparacristid and hypoprotocristid do not meet, so that there is a wide communication between the mesial fovea and the talonid basin); (4) the paraconid (seen on two of the three well-preserved specimens) is larger; (5) the distal fovea is broader, and accommodates a *tuberculum sextum* or accessory crest; (6) the pliopithecine triangle is generally better developed; (7) the mesostylid is more prominent; (8) the hypoconulid is larger and more buccally placed; and (9) the buccal cingulum is better developed (but still discontinuous), and usually beaded with accessory cusps.

The crown of M_3 is subrectangular, longer than broad, and it narrows slightly distally (Figure 9). Both known examples of M_3 are smaller than all of the isolated M_2 s (the average area of M_3 is only 89.1% that of M_2), so it is possible that a reduced M_3 is a characteristic of the species. However, there is no corresponding reduction in the upper molar series, so the apparent small size of M_3 might simply be due to inadequate sampling. In fact, as noted by Gu & Lin (1983) in their initial diagnosis of the species, M^3 is actually relatively large in relation to M^2 (the average area of M^3 is 96.0% that of M^2). At present, with such small samples of unassociated material available, it may not be possible to reliably predict the size relationships of upper and lower molars.

M_3 exhibits the same key morphological characteristics as M_2 (and M_1), namely: (1) the cusps are low and rounded; (2) the mesial fovea is mesiodistally relatively long; (3) the hypoparacristid and hypoprotocristid do not meet, and the mesial fovea and the talonid basin have a wide communication; (4) accessory transverse crests are developed mesial to the hypoparacristid and hypoprotocristid; (5) the pliopithecine triangle is fully developed; (6) a prominent mesostylid is present on the lingual margin of the

crown; (7) the buccal cingulum is well-developed (it forms an almost continuous ledge along the buccal margin of the crown), and shows some degree of beading; (8) the hypoconulid is relatively small and buccally placed; and (9) the talonid basin has a simple Y-shaped groove system, with minimal secondary wrinkling.

The dC_1 is relatively high-crowned and exhibits a moderate degree of buccolingual compression. The apex of the crown is situated in the midline, somewhat towards the mesial end of the tooth. The mesial crest is short and terminates basally at an elevated region of the lingual cingulum. The lingual cingulum is rounded, but well-developed, forming a continuous rim around the lingual aspect of the base of the crown. The distal crest bifurcates close to the apex; the buccal arm of which terminates at a small marginal tubercle, while the lingual arm descends onto the short distal heel.

Mandible

A single mandibular fragment (PA 1273) is known, but unfortunately it provides little useful anatomical information. The specimen consists of a right mandibular fragment of an immature individual preserving the alveoli or partial alveoli (but no crowns) of dP_{3-4} and M_{1-2} . When originally recovered the P_4 was retained in its crypt, but the crown was removed during preparation of the specimen in order to facilitate its description. *Platodontopithecus* retains the plesiomorphic anthropoid sequence of dental eruption, in which M_2 emerges before P_4 , a pattern seen almost universally among extant catarrhines (Swindler, 1985). The corpus appears to be low and robust, as is typical of catarrhines at this stage of dental eruption. The mental foramen is represented by a single small elliptical aperture located midway down the lateral face of the corpus below dP_3 .



Figure 11. PA 1270, right calcaneus of *Platodontopithecus jianghuaiensis*. (a) Superior view; (b) medial view. Scale bar=5 mm.

Postcranials

Three isolated postcranial bones of primates have been recovered from the Xiacaowan Formation at Sihong. Based on their size, all three are assignable to *Platodontopithecus jianghuaiensis*.

PA 1270 consists of a partial right calcaneus lacking most of the calcaneal tuberosity (Figure 11). The articular facet for the cuboid is damaged, and a large flake of bone has been detached and glued in place on the lateral side. The peroneal tuberosity and the tip of the sustentaculum tali are both badly abraded.

The cuboid facet is poorly preserved, but the shallow depression for the beak of the

cuboid and the sharply defined dorso-lateral margin are generally similar to the pattern seen in Old World monkeys. The anterior portion of the calcaneus distal to the posterior articular facet is roughened for the attachment of strong interosseus ligaments and for extensor digitorum brevis. This prearticular region is moderately long (107.6% of the length of the posterior facet) when compared with that of extant apes, and most resembles the proportions seen in some platyrrhines and cercopithecids (Figure 11, Table 7). The anterior articular surface consists of a single flask-shaped facet. It is not as broad as in hominoids, nor does it form the double facet that is typically

Table 7 Relative length of prearticular region of the calcaneus in *Platodontopithecus* and extant anthropoids*

| Taxon | N | Range | Mean | S.D. |
|--|---|-------------|-------|-------|
| <i>Cercopithecus aethiops</i> | 9 | 134.2–169.5 | 149.1 | 9.42 |
| <i>Colobus guereza</i> | 6 | 123.7–135.8 | 129.6 | 4.35 |
| <i>Presbytis</i> spp. | 5 | 113.2–141.0 | 124.2 | 11.96 |
| <i>Papio anubus</i> | 6 | 104.5–131.5 | 120.0 | 8.47 |
| <i>Platodontopithecus juanghuaiensis</i> | 1 | | 107.6 | |
| <i>Ateles</i> spp. | 5 | 77.9–114.1 | 97.4 | 13.45 |
| <i>Alouatta seniculus</i> | 8 | 77.0–102.0 | 89.3 | 8.60 |
| <i>Pongo pygmaeus</i> | 6 | 63.4–96.1 | 76.8 | 9.94 |
| <i>Pan troglodytes</i> | 6 | 55.3–74.5 | 64.5 | 6.13 |
| <i>Gorilla gorilla</i> | 6 | 46.6–73.0 | 62.1 | 8.74 |

*Index=length from distal margin of calcaneus to distal margin of posterior articular facet \times 100/length of posterior articular facet.

Source: Harrison (1982, unpublished data).

seen in Old World monkeys (Harrison, 1982, 1986a, 1989a; Strasser, 1988; Gebo, 1989). The calcaneal sulcus is relatively wide, with a minimum distance between the anterior and posterior facets of 4.7. The posterior facet is proximodistally relatively long (length, 13.1; breadth, 8.8), with a low dorsoventral convexity. It lacks the specialized talo-calcaneal joint morphology characteristic of Old World monkeys (Szalay, 1975; Langdon, 1986; Strasser, 1988). The sustentaculum tali is relatively wide. The base of the calcaneal tuberosity is dorsoventrally deep, with a slight degree of waisting, and most resembles the condition seen in hominoids and large platyrrhine monkeys. Although the posterior portion of the calcaneal tuberosity is missing, the contour of its inferior surface indicates that the plantar tubercle was not well-developed, unlike the condition seen in anthropoids specialized for climbing and hindlimb suspension, such as the extant hominoids and some of the platyrrhines (Sarmiento, 1983). Inferiorly, the anterior tubercle for attachment of the short plantar ligament is weakly developed, while the groove for the flexor hallucis longus is deep and well-defined.

The calcaneus in *Platodontopithecus* is more primitive than the patterns seen in

either extant hominoids or cercopithecids. Hominoids are more derived in having a broader and more deeply pitted cuboid facet with a flattened dorsolateral margin, a shorter prearticular region, a broader anterior articular facet, a relatively narrow calcaneal sulcus between the two articular facets, and a well-developed plantar tubercle. The Sihong calcaneus is more similar to that in cercopithecids, but the latter group is derived in having a relatively longer prearticular region, a tendency to develop a double anterior articular facet, a short and steeply inclined posterior articular facet, and a shallow calcaneal tuberosity with a deeply excavated superior border. The calcaneus of *Platodontopithecus* is most similar to those of other early catarrhines, including the proconsulids from the early Miocene of East Africa and *Pliopithecus* from the later Miocene of Europe (Zapfe, 1961; Lewis, 1980; Harrison, 1982; Langdon, 1986; Rose, 1993). In fact, the Sihong calcaneus is closely comparable in size and morphology to *Pliopithecus vindobonensis*; the main differences are that in the latter the calcaneal tuberosity appears to be relatively shorter with a well-developed plantar tubercle (Zapfe, 1958, 1961; Sarmiento, 1983).



Figure 12. Phalanges of *Platodontopithecus jianghuaiensis*: (a) PA 1271, partial proximal phalanx, dorsal view (left), ventral view (right); (b) PA 1272, proximal pollicial phalanx, dorsal view (left), ventral view (right). Scale bar=5 mm.

PA 1271 is a partial proximal phalanx, lacking the proximal end (Figure 12). Judging from the proportions of the head it is probably a pedal phalanx. Unfortunately, it is not possible to estimate the original length of the bone, but it appears to have been relatively long and slender with a marked degree of dorsoventral curvature. The distal articular surface is relatively narrow, with symmetrical condyles separated by a shallow trochlear groove. The plantar surface bears well-developed keels laterally and medially for the insertion of the flexor sheath.

PA 1272 is a complete proximal pollicial phalanx, most probably from the left side (Figure 12). The phalanx is quite long and slender, indicating a well-developed thumb. Using an index of phalanx length in relation to estimated body weight (mean phalanx

length³/mean body weight) it can be shown that the pollicial phalanx in *Platodontopithecus* is relatively longer (index=94.1) than in all extant nonhuman catarrhines (index=49.9–88.5), with the exception of the hylobatids (106.8–113.9) (Table 8). Since most strepsirhines and platyrrhines have relatively long pollicial phalanges (index=100 ± 15) it is reasonable to assume that the pattern seen in *Platodontopithecus* represents the ancestral condition for catarrhines. A similarly high index value (91.6) for *Proconsul heseloni* (KNM-RU 2036) provides further support for this inference.

In terms of its degree of robusticity, the midshaft diameter of the pollicial phalanx is 21.1% of the total length of the bone. This value falls within the lower end of the range for extant catarrhines ($n=47$; mean=23.8 ±

Table 8 Relative length of proximal pollicial phalanx in extant primates and *Platodontopithecus**

| Relative length of phalanx | Taxon (<i>n</i>) | Index | |
|---------------------------------|---|-----------------------------------|------|
| Very long (120–140) | <i>Tarsius bancanus</i> (2) | 127.0 | |
| | <i>Hylobates agilis</i> (5) | 113.9 | |
| Long (100–120) | <i>Cebus albifrons</i> (5) | 107.8 | |
| | <i>Propithecus verreauxi</i> (2) | 107.8 | |
| | <i>Hylobates hoolock</i> (2) | 106.8 | |
| | <i>Cebus olivaceus</i> (5) | 106.5 | |
| | <i>Platodontopithecus jianghuaiensis</i> (1)† | 94.1 | |
| Moderately long (80–100) | <i>Lemur fulvus</i> (6) | 93.9 | |
| | <i>Nycticebus coucang</i> (3) | 90.9 | |
| | <i>Otolemur crassicaudatus</i> (3) | 90.4 | |
| | <i>Saimiri sciureus</i> (11) | 89.2 | |
| | <i>Avahi laniger</i> (2) | 89.1 | |
| | <i>Haplemur griseus</i> (3) | 88.8 | |
| | <i>Mandrillus sphinx</i> (2) | 88.5 | |
| | <i>Pan troglodytes</i> (9) | 83.5 | |
| | <i>Lepilemur</i> spp. (9) | 83.2 | |
| | <i>Cercopithecus cephus</i> (2) | 83.2 | |
| | <i>Loris tardigradus</i> (2) | 82.4 | |
| | <i>Macaca nemestrina</i> (4) | 80.9 | |
| | <i>Alouatta seniculus</i> (3) | 80.4 | |
| | Moderately short (60–80) | <i>Cercopithecus aethiops</i> (6) | 79.1 |
| | | <i>Cercopithecus mitis</i> (4) | 76.5 |
| | | <i>Macaca fascicularis</i> (7) | 75.5 |
| <i>Lophocebus albigena</i> (5) | | 71.9 | |
| <i>Papio anubis</i> (3) | | 71.4 | |
| <i>Pygathrix nemaeus</i> (2) | | 70.7 | |
| <i>Pongo pygmaeus</i> (6) | | 70.1 | |
| <i>Macaca mulatta</i> (10) | | 69.8 | |
| <i>Papio hamadryas</i> (6) | | 69.3 | |
| <i>Miopithecus talapoin</i> (7) | | 67.3 | |
| <i>Presbytis rubicunda</i> (6) | | 62.0 | |
| <i>Presbytis hosei</i> (2) | | 60.5 | |
| Short (40–60) | <i>Gorilla gorilla</i> (10) | 58.8 | |
| | <i>Trachypithecus obscurus</i> (2) | 55.3 | |
| | <i>Theropithecus gelada</i> (5) | 50.4 | |
| | <i>Presbytis comata</i> (1) | 49.9 | |

*Index of relative phalanx length = mean length of phalanx (mm)³√mean body weight (g). Body weight data from Smith & Jungers (1997). Phalangeal data from Sarlo (1996, unpublished) and Harrison (unpublished).

†Phalanx length = 23.2. Estimated body weight = 15,000 g.

5.8%); only hylobatids, with relatively slender phalanges ($n=3$; mean = 12.1%), and *Theropithecus*, with short, stout phalanges ($n=4$; mean = 33.9%), fall outside this range. The shaft exhibits dorsoventral curvature comparable to that found in extant African apes and large platyrrhines. It is mediolaterally expanded midway along its

length to accommodate well-developed crests for the attachment of the flexor sheath. The distal end of the phalanx is broad, with widely diverging condyles and a deep trochlear groove. The medial condyle is somewhat larger than the lateral condyle, but it does not extend as far distally. This gives the head a slightly obliquely oriented

transverse axis relative to the long axis of the shaft. The proximal end of the phalanx has an elliptical, saddle-shaped depression for articulation with the head of the first metacarpal. The proximal end is bilaterally asymmetrical, with the articular depression placed eccentrically towards the lateral side, and the medial lip more strongly protruding than the lateral lip.

Unfortunately, these few postcranial remains do not allow much of an insight into the locomotor capabilities of *Platodontopithecus*, but it is reasonable to conclude that it was a generalized quadrupedal arboreal primate, probably favoring above-branch walking and running on relatively large diameter supports. This finding is of some interest given that the estimate of average body weight for *Platodontopithecus* (~15 kg) places it at the upper limit of the mean body weight range for extant arboreal cercopithecids (i.e., 15.0 kg for *Nasalis larvatus* and 15.6 kg for *Rhinopithecus roxellana*; Smith & Jungers, 1997). Only some of the terrestrial and semi-terrestrial papionins (i.e., *Papio ursinus* and *Mandrillus sphinx*) and the great apes are significantly heavier among extant nonhuman primates.

Phylogenetic relationships

Previous studies have drawn attention to the morphological similarities and possible phylogenetic affinities of the Sihong catarrhines to certain proconsulids from the early Miocene of East Africa. In particular, *Dionysopithecus* has been shown to be similar in its upper molar morphology to *Micropithecus clarki*, while the isolated molars of *Platodontopithecus* have been compared in more general terms to those of *Proconsul* (Li, 1978; Harrison, 1982, 1988; Gu & Lin, 1983; Fleagle, 1984, 1986, 1988; Bernor *et al.*, 1988; Etler, 1989; Harrison *et al.*, 1991). However, the enlarged sample of specimens now available makes it possible to present a more detailed assessment of the

phylogenetic and taxonomic relationships of the fossil primates from Sihong.

In this study, comparisons have been made with other early catarrhines from the Miocene of Eurasia and Africa belonging to the Pliopithecidae and Proconsulidae respectively. In addition, a number of Asian Miocene catarrhines of uncertain taxonomic status, pertinent to the discussion of the relationships of the Sihong primates, have also been included in the analysis. These include "*Dendropithecus*" *orientalis*, *Krishnapithecus krishnaii*, "*Pliopithecus*" *posthumus*, "*Kansupithecus*," *Dianopithecus progressus*, and specimens from Pakistan tentatively referred to *Dionysopithecus*. The aims of these comparisons are twofold: (1) to establish the morphological similarity or distinctiveness of the Sihong primates, and (2) to serve as the basis for establishing the phylogenetic and taxonomic affinities of the Sihong primates.

Dionysopithecus shuangouensis and *Platodontopithecus jianghuaiensis*

As discussed above, the enlarged sample of material now available from Sihong confirms that only two species are represented at the site—*Dionysopithecus shuangouensis* and *Platodontopithecus jianghuaiensis*. Three additional species from Sihong described by Lei (1985) on the basis of single isolated teeth are considered to be junior synonyms. We agree with the earlier assessment of Harrison *et al.* (1991) that the type and only specimens of *Pliopithecus wangi* (P 83.4) and *Hylobates tianganhuensis* (P 83.3) are morphologically and metrically indistinguishable from *Dionysopithecus shuangouensis*, while *Dryopithecus sihongensis*, previously considered to be distinct (Bernor *et al.*, 1988; Harrison *et al.*, 1991), can, in the light of further comparisons, be readily accommodated within the hypodigm of *Platodontopithecus jianghuaiensis*.

The two currently recognized species from Sihong can be distinguished from each

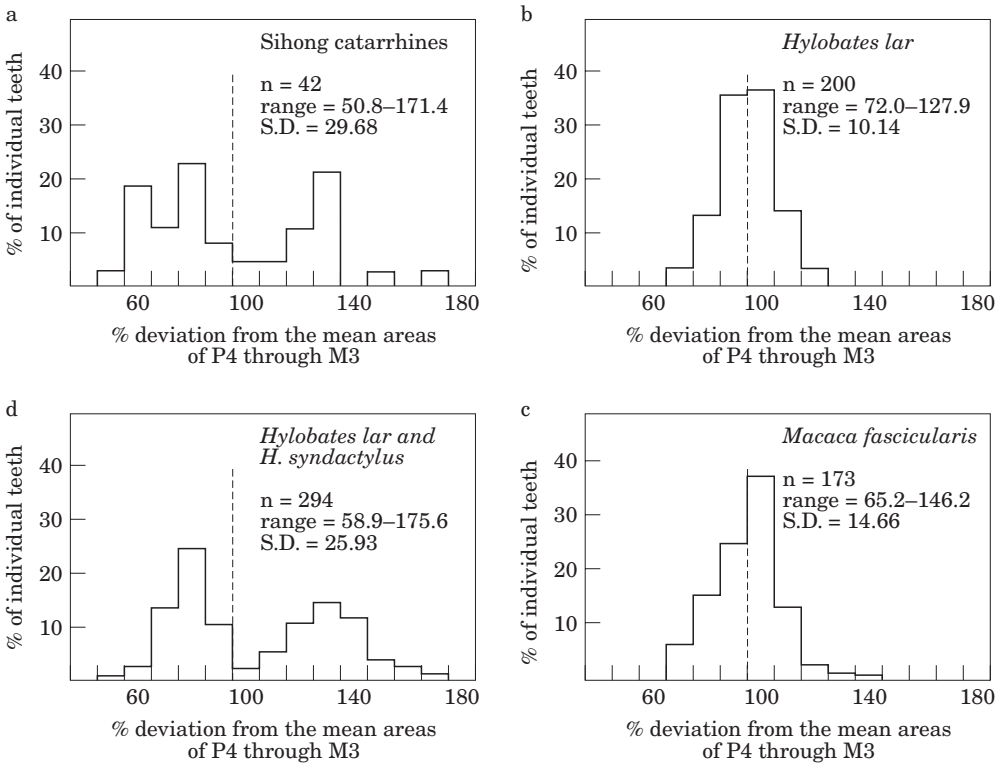


Figure 13. Size distribution of the cheek teeth (upper and lower P4 through M3) from Sihong compared with those of extant catarrhines. Areas (mesiodistal length \times buccolingual breadth) of individual cheek teeth calculated as the percentage deviation from the mean area of its particular class of tooth. Dashed lines represent the dividing line between specimens that are less than or greater than the mean value. Note the bimodal distribution and greater range of variation in the Sihong sample (a), compared with that seen in *Hylobates lar* (b) and *Macaca fascicularis* (c). The pattern is closely comparable to (d), the distribution seen when samples from two species of different size, in this case *Hylobates lar* and *Hylobates syndactylus*, are combined.

other on the basis of overall size and differences in the detailed morphology of their cheek teeth. In fact, dental size was used as the primary basis for sorting the material. To illustrate this difference, the size distribution of the combined sample of cheek teeth from Sihong was analyzed and compared with data from modern catarrhines of similar size (i.e., *Hylobates lar* and *Macaca fascicularis*). The area (mesiodistal length \times buccolingual breadth) of individual cheek teeth was calculated as the percentage deviation from the mean area for that particular tooth and the data were then com-

bined and plotted as a histogram (Figure 13). As one would expect, both extant species exhibit a unimodal distribution with a peak at the mean and a narrow total range of variation [Figure 13(a,b)]. By contrast, the distribution of the Sihong sample is clearly bimodal, with a range of variation that exceeds that of the modern species [Figure 13(c)]. In fact, the size distribution of cheek teeth from Sihong is closely similar to that observed when data from two extant species of different size, in this case *Hylobates lar* and *Hylobates syndactylus*, are combined [Figure 13(d)]. On the basis of size

alone there is good evidence to indicate that at least two species are represented at Sihong; a conclusion confirmed by morphological criteria. Moreover, the close morphological similarity of the teeth within each of these size categories further indicates that *only* two species are represented.

The smaller species from Sihong is *Dionysopithecus shuangouensis*, and this includes the type specimens of *Pliopithecus wangi* and *Hylobates tianganhuensis*, which are morphologically and metrically indistinguishable. *Platodontopithecus jianghuaiensis* has cheek teeth that are on average 35.7% larger (in terms of linear dimensions) than those of *Dionysopithecus shuangouensis*. The size of the cheek teeth (combined areas of the lower molars) suggests that *D. shuangouensis* is similar in size to *Hylobates lar* and *Trachypithecus cristata*, and slightly larger than *Cercopithecus aethiops*, while *P. jianghuaiensis* is slightly larger in size than *Cercocebus torquatus*, *Macaca nemestrina*, *Hylobates syndactylus* and *Nasalis larvatus*. Comparative body weight data for these extant primates (Smith & Jungers, 1997) provide a crude estimation of average body weight for *Dionysopithecus* and *Platodontopithecus* of approximately 5–6 kg and 12–15 kg respectively. Using Conroy's (1987) regression formula for the relationship between M_1 area and body weight in extant anthropoids, body weights for the Sihong primates are calculated at 5.5 kg and 14.9 kg respectively.

Apart from being considerably smaller than *Platodontopithecus*, *Dionysopithecus* differs in the following morphological features: (1) the P_4 metaconid is lower than the protoconid, rather than subequal; (2) the upper premolars are relatively narrower; (3) the upper and lower molars have slightly higher cusps and greater occlusal relief; (4) the lower molars are mesiodistally longer and have a better defined mesial fovea, a more pronounced pliopithecine triangle, a smaller hypoconulid, and a buccal cingulum

that lacks beading; and (5) the upper molars are slightly narrower, with a smaller metacone, and lack a crest (or crests) linking the metacone and hypocone. These distinguishing characteristics provide sufficient justification to maintain at least a species distinction. However, in view of the unique features that the two species share (see below), one could contend that they should be placed together in a single genus. At present, we favor retaining the species in separate genera because, even with the limited range of comparisons available, there are discernible and consistent differences throughout the dentition that serve to distinguish the two taxa.

One of the most significant findings of the present study is that *Dionysopithecus* and *Platodontopithecus* share a number of distinctive morphological characters that imply that they are closely related to one another. The features they share include: (1) upper and lower molars with rounded cusps and crests and low occlusal relief; (2) lower molars characterized by a moderately narrow crown (see Table 9), long and narrow mesial fovea, small paraconid, mesial transverse crest slightly oblique, well-developed mesostylid, distinct pliopithecine triangle, cristid obliqua slightly obliquely directed in relation to the long axis of the crown, relatively small hypoconulid and distinct buccal cingulum; (3) upper molars broad to moderately broad and rectangular in shape, with a relatively small hypocone; (4) upper and lower M_3 possibly small in relation to M_2 , with highly reduced posterior cusps on M_3 ; and (5) P_3 mesiodistally short and relatively high-crowned, with only a slight extension inferiorly of the mesiobuccal face of the crown. As discussed below, many of these features are not unique to *Dionysopithecus* and *Platodontopithecus*, and, in fact, they represent part of a more extensive suite of synapomorphies that link the Sihong primates with Eurasian pliopithecids. Even so, the Sihong primates do share a more

primitive molar morphology than all other Eurasian Miocene catarrhines, which implies at least a gradistic association between them. More compelling evidence of a close phyletic relationship is based on what can be inferred to be derived features (based on outgroup comparisons with proconsulids and propliopithecids) shared uniquely by *Dionysopithecus* and *Platodontopithecus*. These include: (1) upper and lower molars with low occlusal relief; (2) lower molars with a high incidence of a well-developed mesostylid (this feature is variably developed in *Pliopithecus*, rare in crouzeliines and most proconsulids, but quite common in *Proconsul*); (3) M^1 contrasts with M^2 in being relatively narrower and less rectangular in shape with a more rounded lingual and distal margin; and (4) upper and lower $M3$ possibly small in relation to $M2$, with highly reduced posterior cusps on M^3 . On this basis, *Dionysopithecus* and *Platodontopithecus* are considered to be members of a clade distinct from other Eurasian catarrhines. We therefore include them here in a separate subfamily, the Dionysopithecinae.

Pliopithecidae

The Pliopithecidae is a group of primitive catarrhines with a wide geographical distribution throughout much of Eurasia during the Miocene (Ginsburg & Mein, 1980; Ginsburg, 1986; Harrison, 1987, 1991; Harrison *et al.*, 1991; Harrison in Andrews *et al.*, 1996). The family, as currently conceived, is divided into two subfamilies: the Pliopithecinae, which includes five species of *Pliopithecus* (i.e., *P. antiquus*, *P. platyodon*, *P. priensis*, *P. vindobonensis*, and *P. zhanxiangi*), and the Crouzeliinae, which comprises *Plesiopliopithecus lockeri*, *Plesiopliopithecus auscitanensis*, *Plesiopliopithecus rhodanica*, *Anapithecus hernyaki*, and *Laccopithecus robustus* (Harrison, 1991; Harrison *et al.*, 1991; Harrison in Andrews *et al.*, 1996). The two species of pliopithecids known from China are somewhat younger

than the primates from Sihong; *Laccopithecus robustus* from the site of Shihuiba, Lufeng County, Yunnan, southern China is late Miocene in age (~7–8 Ma), while *Pliopithecus zhanxiangi* from Tongxin, Ningxia Hui Autonomous Region, northern China is early middle Miocene in age (~15 Ma) (Qiu, 1989; Harrison *et al.*, 1991; Qiu & Qiu, 1995).

A number of authors have argued that the pliopithecids (either as a group or as individual genera) are closely related to extant hylobatids (Hürzeler, 1954; Zapfe, 1958, 1961; Simons, 1972; Simons & Fleagle, 1973; Wu & Pan, 1985; Meldrum & Pan, 1988; Fleagle, 1988). However, a critical reappraisal of the morphological evidence indicates that the characteristics linking the two groups are due to similarities in size and the retention of plesiomorphic characters (Remane, 1965; Groves, 1972, 1974; Delson & Andrews, 1975; Ciochon & Corruccini, 1977; Szalay & Delson, 1979; Ginsburg & Mein, 1980; Harrison, 1982, 1987, 1991; Fleagle, 1988; Harrison *et al.*, 1991; Andrews, 1985; Andrews *et al.*, 1996). Cranially and postcranially pliopithecids appear to conform closely to the inferred ancestral catarrhine morphotype, and the possession of several primitive characters (i.e., a partially enclosed tubular ectotympanic, an entepicondylar foramen in the distal humerus, relatively very broad upper molars, and detailed occlusal morphology of the lower molars) not seen in proconsulids clearly establishes the pliopithecids as the sister taxon to proconsulids plus all contemporary and later catarrhines (Andrews, 1985; Harrison, 1987; Fleagle, 1988; Harrison *et al.*, 1991; Andrews *et al.*, 1996).

Despite their degree of primitiveness, pliopithecids are distinguished as a monophyletic group by a number of dental specializations. These include: (1) lower incisors (and to some extent the upper central incisor) mesiodistally waisted towards the base of the crown, giving the

Table 9 Comparison of molar proportions in fossil and extant catarrhines*

| | Length-breadth proportions of upper M2+ | | Representative modern catarrhines |
|---------------------------|---|--|---|
| | Pliopithecids and propithecids | Proconsulids | |
| Narrow (>90) | | <p><i>Nyanzapithecus pickfordi</i> (115.3)</p> <p><i>Nyanzapithecus vancouveriorum</i> (104.1)</p> <p><i>Nyanzapithecus harrisoni</i> (98.2)</p> <p><i>Rangwapithecus gondoni</i> (94.9)</p> <p><i>Turkanapithecus kalakolensis</i> (94.4)</p> | <p><i>Cercopithecus aethiops</i> (103.0)</p> <p><i>Colobus guereza</i> (102.6)</p> <p><i>Macaca fascicularis</i> (101.6)</p> <p><i>Hylobates syndactylus</i> (98.5)</p> <p><i>Gorilla gorilla</i> (97.8)</p> <p><i>Trachypithecus cristatus</i> (96.9)</p> <p><i>Hylobates lar</i> (94.4)</p> |
| Moderately narrow (85-90) | | <p><i>Proconsul nyanzae</i> (88.2)</p> <p><i>Limnopithecus legeret</i> (87.5)</p> <p><i>Micropithecus clarki</i> (87.4)</p> <p><i>Proconsul major</i> (86.9)</p> | <p><i>Pan troglodytes</i> (87.6)</p> |
| Moderately broad (80-85) | | <p><i>Micropithecus leakeyorum</i> (85.4)</p> <p><i>Afropithecus turkanensis</i> (83.8)</p> <p><i>Kalepithecus songhorensis</i> (83.7)</p> <p><i>Proconsul heseloni</i> (83.7)</p> | |
| Broad (75-80) | <p><i>Laccopithecus robustus</i> (82.8)</p> <p><i>Dionyssopithecus shuangouensis</i> (80.1)</p> <p><i>Pliopithecus antiquus</i> (79.9)</p> <p><i>Pliopithecus platyodon</i> (78.4)</p> | <p><i>Dendropithecus macinnesi</i> (82.1)</p> <p><i>Proconsul africanus</i> (80.6)</p> <p><i>Limnopithecus evansi</i> (79.9)</p> <p><i>Kamoyapithecus hamiltoni</i> (77.1)</p> | |
| Very broad (<75) | <p><i>Platodontopithecus jianghuaiensis</i> (77.2)</p> <p><i>Pliopithecus zhanxiangi</i> (74.0)</p> <p><i>Pliopithecus windobonensis</i> (73.2)</p> <p><i>Propithecus chiobates</i> (70.6)</p> <p><i>Prophopithecus zeuxis</i> (66.6)</p> | | |

Table 9 Continued

| Breadth-length proportions of lower M ₂ † | | | |
|--|---|---|--|
| | Pliopithecids and propiopithecids | Proconsulids | Representative modern catarrhines |
| Very narrow (<=75) | <i>Plesiopithecus rhodanica</i> (75.0) | <i>Nyanzapithecus pickfordi</i> (73.4) | |
| Narrow (75-80) | <i>Plesiopithecus ausitanensis</i> (79.7) | <i>Nyanzapithecus vancouveringorum</i> (75.6) | <i>Macaca fascicularis</i> (79.1) |
| Moderately narrow (80-85) | <i>Anapithecus hemyaki</i> (79.9) | <i>Micropithecus leakeyorum</i> (77.8) | <i>Hylobates syndactylus</i> (79.6) |
| | <i>Pliopithecus vindobonensis</i> (81.7) | <i>Nyanzapithecus harrisoni</i> (79.4) | <i>Cercopithecus aethiops</i> (82.0) |
| | <i>Dionysopithecus shuangouensis</i> (83.3) | <i>Rangevapithecus gordonii</i> (81.0) | |
| | <i>Laccopithecus robustus</i> (83.6) | <i>Dendropithecus macinnesi</i> (83.6) | <i>Colobus guereza</i> (83.4) |
| | <i>Pliopithecus zhanxiangi</i> (83.7) | | |
| Broad (85-90) | <i>Platodontopithecus jianghuatensis</i> (84.3) | <i>Proconsul heseloni</i> (84.3) | |
| | | <i>Linnopithecus evansi</i> (85.8) | <i>Trachypithecus cristatus</i> (85.9) |
| | <i>Pliopithecus antiquus</i> (87.9) | <i>Micropithecus clarki</i> (87.1) | <i>Gorilla gorilla</i> (87.2) |
| | <i>Pliopithecus playodon</i> (88.9) | <i>Linnopithecus legatet</i> (87.3) | <i>Hylobates lar</i> (87.8) |
| Very broad (>90) | | <i>Proconsul nyanzae</i> (88.1) | |
| | | <i>Afropithecus turkanensis</i> (89.0) | |
| | | <i>Proconsul major</i> (91.3) | <i>Pan troglodytes</i> (92.0) |
| | <i>Propliopithecus zeuxis</i> (95.1) | <i>Kalepithecus songhorensis</i> (93.8) | |
| | <i>Propliopithecus chirobates</i> (99.9) | | |

*Sources: Harrison (1982), Harrison *et al.* (1991), Leakey *et al.* (1995), Andrews *et al.* (1996), Kunimatsu (1997), Harrison, unpublished data.

†Index = mesiodistal length of M₂ × 100/buccolingual breadth of M₂; numbers in parentheses are mean values for the species.

‡Index = buccolingual breadth of M₂ × 100/mesiodistal length of M₂; numbers in parentheses are mean values for the species.

tooth a flask-shaped outline when viewed from the buccal aspect; (2) P_3 mesiodistally short and relatively high-crowned, with a steeply inclined mesiobuccal face that does not extend much inferiorly to form a sectorial flange; and (3) lower molars generally narrow (see Table 9), with well-developed occlusal crests and a pliopithecine triangle (Harrison in Andrews *et al.*, 1996).

Several of these synapomorphies of pliopithecids are also found in *Dionysopithecus* and *Platodontopithecus*, and indicate a close phyletic relationship.¹ Comparisons of the incisors are limited to the lower lateral and upper central incisors of *Dionysopithecus*. These are similar to those of European pliopithecids in having the distinctive mesiodistal waisting of the crown. In addition, I^1 of *Dionysopithecus* resembles pliopithecids, rather than proconsulids, in lacking a strongly developed lingual pillar and in having a distally receding incisive apex. Compared to the P_3 s of proconsulids (with the notable exception of *Limnopithecus legetet*), those of *Dionysopithecus* and *Platodontopithecus* are similar to pliopithecids in being high-crowned with a relatively short and steep sectorial flange (see Figure 14). P_3 in *Propliopithecus*, from the Oligocene of Egypt, appears to be intermediate in morphology, and probably represents a pattern close to the primitive catarrhine morphotype (Robinson, 1996; Robinson & Harrison, 1997). In addition, the lower molars of *Platodontopithecus* and *Dionysopithecus* possess a pliopithecine triangle—a feature unique to pliopithecids.

Other features shared by the Sihong primates and pliopithecids include: (1) the lower incisors of *Dionysopithecus* are similar in relative height to those of pliopithecids, as well as proconsulids (except for the high-

crowned incisors in *Micropithecus clarki* and *Proconsul* spp.), whereas in *Propliopithecus* the incisors are somewhat higher-crowned. (2) The morphology of the upper canine in females of *Dionysopithecus* is quite distinctive (i.e., low-crowned, with a triangular occlusal outline, and a broad distal heel), but it does closely resemble the canines of female pliopithecids (as well as those of the middle Miocene cercopithecoid *Victoriapithecus*), rather than the conical, bilaterally compressed canines of female proconsulids. In addition, the male upper canine of *Platodontopithecus* is morphologically similar to those of *Pliopithecus*. (3) The size of the metaconid on P_3 appears to be variable in the Sihong primates, but, in *Dionysopithecus* at least, it can be quite large. A metaconid on P_3 is generally absent or relatively small in proconsulids and *Pliopithecus*, but is often quite prominent in crouzeliines (Harrison in Andrews *et al.*, 1996). (4) The lower molars of *Dionysopithecus* and *Platodontopithecus* share the following features with pliopithecids that are not generally found in proconsulids: a relatively long trigonid that is narrower than the talonid, at least on M_1 ; paraconids variably retained; the mesial transverse crest linking the protoconid and metaconid is obliquely oriented; the cristid obliqua (=prehypocristid) is slightly obliquely aligned relative to the long-axis of the crown; presence of a distinct pliopithecine triangle, at least on M_2 and M_3 ; the distal fovea is relatively small; and the hypoconulid is small and more distally placed relative to the hypoconid.

Although *Dionysopithecus* and *Platodontopithecus* share important derived features and some general similarities with pliopithecids, as detailed above, they can be distinguished from them as a group by various aspects of their dental morphology. The upper molars of the Sihong primates differ from those of pliopithecids in having narrower occlusal basins, a less lingually positioned protocone, and a less pronounced buccal cingulum.

¹It should be noted that the phylogenetic inferences presented in this paper represent the views of TH only. GY still prefers her earlier published assessment (Gu & Lin, 1983) that *Dionysopithecus* and *Platodontopithecus* are closely related to the East African Miocene catarrhines that she includes in the Hominoidea.

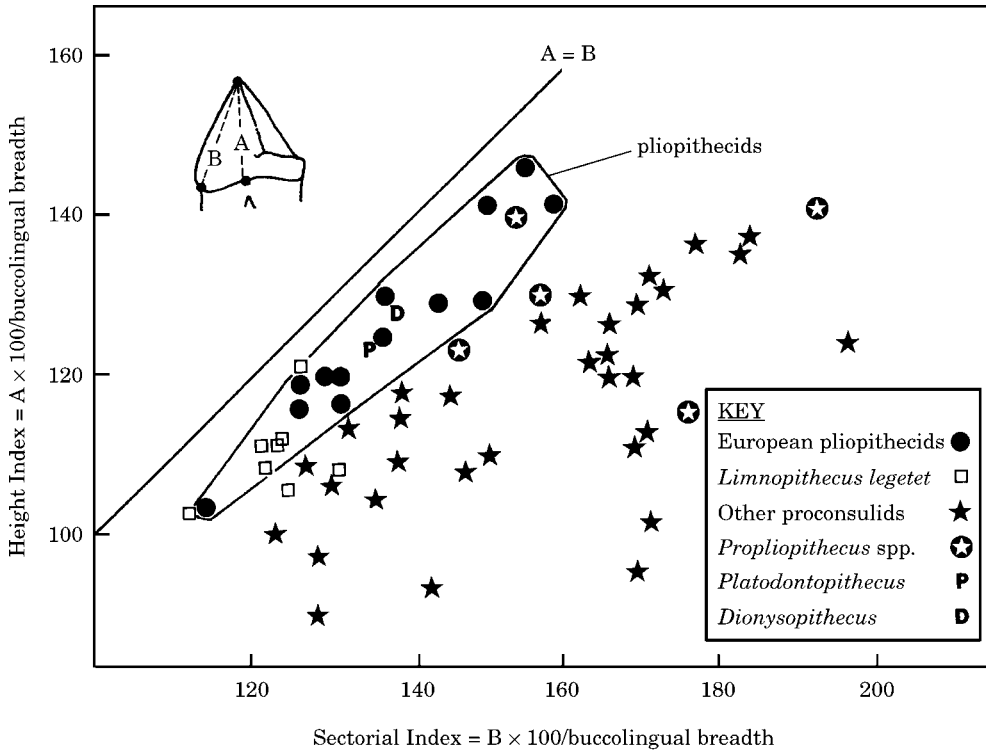


Figure 14. Bivariate plot comparing the proportions of the P_3 in *Propliopithecus* spp., European pliopithecids (*Pliopithecus antiquus*, *P. vindobonensis*, and *P. platyodon*), proconsulids (*Proconsul* spp., *Limnopithecus legetet*, *L. evansi*, *Micropithecus clarki*, *Dendropithecus macinnesi*, and *Kalepithecus songhorensis*), and the Sihong catarrhines. *Dionysopithecus* and *Platodontopithecus* resemble European pliopithecids in having a high-crowned P_3 with a relatively short mesial honing face. By comparison, proconsulids, except for *Limnopithecus legetet*, have lower crowned P_3 s with a relatively longer honing face. A=buccal height of crown; B=length of mesiobuccal face.

The M^1 is also narrower and less rectangular in shape (with convex distal and lingual margins). In these respects the upper molars from Sihong are more reminiscent of proconsulids, and this is why previous analyses of the material, when few specimens were available for study, tended to emphasize taxonomic affinities with proconsulids rather than pliopithecids. Also, compared with pliopithecids, *Dionysopithecus* and *Platodontopithecus* appear to have last molars that are reduced in size. In pliopithecids, proconsulids (*Micropithecus clarki* is the notable exception), and *Propliopithecus zeuxis*, M_3 is significantly larger on average than M_2 (with mean occlusal areas of M_3 ranging from

106–139% of M_2 area), whereas in both species from Sihong, at least as determined on the basis of isolated teeth, M_3 is smaller than M_2 (92% for *Dionysopithecus* and 89% for *Platodontopithecus*). A similar pattern emerges from comparisons of the upper molars. In most pliopithecids and proconsulids the mean area of M^3 is subequal ($100 \pm 10\%$) to that of M^2 , except for *Pliopithecus platyodon* (89%) and *Micropithecus clarki* (68%). *Platodontopithecus* fits this general range (96%), while *Dionysopithecus* has a relatively small M^3 (80% based on the entire sample, including isolated teeth, or 85% calculated from the associated molars in the holotype).

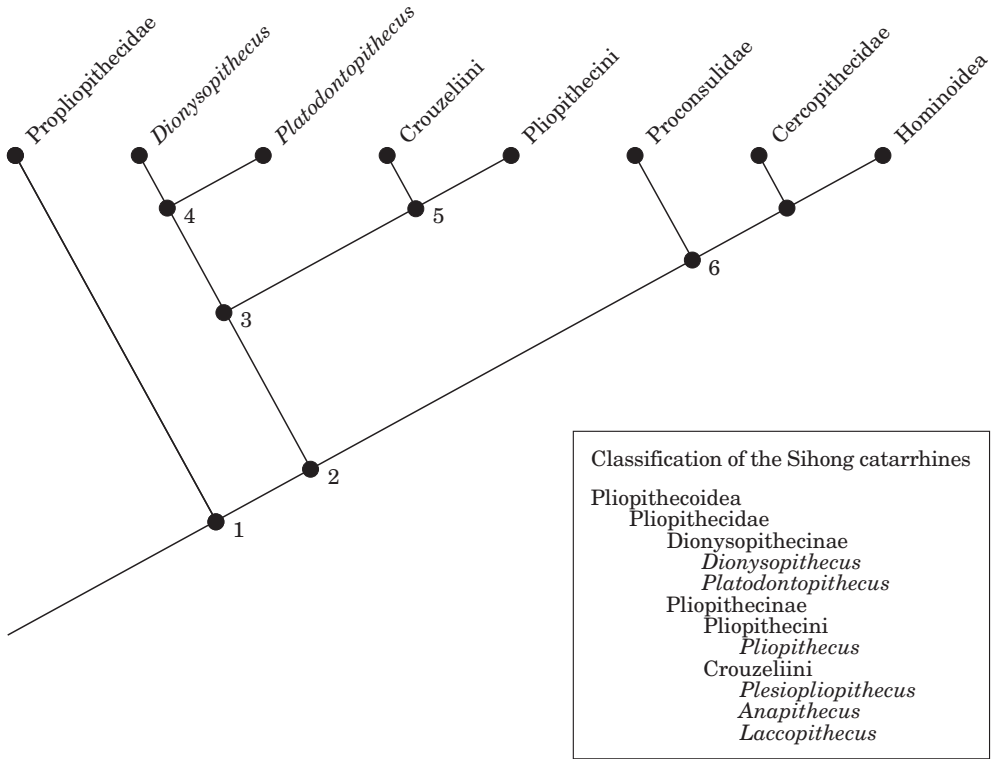


Figure 15. Cladogram depicting the inferred phylogenetic relationships of the Sihong catarrhines (see Table 10 for list of characters defining numbered nodes). See text for further discussion of the classification.

The morphological evidence presented above indicates that the Sihong primates are the primitive sister-group of all previously recognized pliopithecids. As a consequence, it is tempting to make the taxonomy of this clade mirror the inferred relationships by creating two separate families, the Dionysopithecidae and the Pliopithecidae (=Pliopithecinae+Crouzeliinae). However, in order to avoid unnecessary inflation of rank and to maintain a close congruence with the taxonomy of extant primates, we feel that the level of diversity among the fossils can be reasonably encompassed within a single family. We therefore recognize two separate subfamilies of equal rank within the Pliopithecidae, the Dionysopithecinae and the Pliopithecinae, and subdivide the latter taxon into two tribes, the

Pliopithecini and Crouzeliini (see Figure 15, Table 10).

Proconsulidae

The proconsulids represent a group of basal catarrhines of modern aspect from the late Oligocene to mid-Miocene of East Africa (Harrison, 1987, 1993). The family, as currently construed, includes *Limnopithecus*, *Dendropithecus*, *Micropithecus*, *Simiolus*, *Kalepithecus*, *Proconsul*, *Nyanzapithecus*, *Rangwapithecus*, *Afropithecus*, *Turkana-pithecus*, and possibly *Kamoyapithecus* (Andrews, 1978; Harrison, 1982, 1986b, 1987, 1989b, 1993; Leakey *et al.*, 1988a,b, 1995). Some of these taxa, such as *Proconsul*, *Limnopithecus*, *Rangwapithecus*, and *Afropithecus*, have, in the past, been linked phyletically to the Hominoidea (e.g.,

Table 10 Characters defining the numbered nodes in **Figure 15*****Node 1**

- (1) Annular ectotympanic
- (2) Lower incisors taper towards the base of the crown, but lack distinct mesiodistal waisting
- (3) P₃ sexually dimorphic with a quite long and obliquely inclined mesiobuccal face and a moderately developed sectorial flange in males (see [Figure 14](#))
- (4) Lower molars
- (a) very broad (see [Table 9](#))
 - (b) with short and narrow mesial fovea
 - (c) with obliquely oriented mesial transverse crest
 - (d) protoconid more mesially placed than metaconid
 - (e) slightly oblique cristid obliqua
 - (f) lacking a mesostylid
 - (g) with relatively small hypoconulid on M₁₋₂
 - (h) with moderately well-developed occlusal crests
 - (i) lacking a pliopithecine triangle on M₂₋₃
- (5) M₃ larger in area than M₂
- (6) Upper central incisors lack mesiodistal waisting of the crown
- (7) M² similar to M¹ in being relatively broad and rectangular in shape
- (8) M³ subequal (100 ± 10%) in area to M², with moderately reduced posterior cusps
- (9) Upper molars:
- (a) very broad (see [Table 9](#))
 - (b) with narrow trigon basin
 - (c) with relatively small hypocone
- (10) Upper and lower molars with moderately well-developed crests and occlusal relief
- (11) Entepicondylar foramen in the distal humerus

Node 2

- (1) Partially formed tubular ectotympanic
- (4) Lower molars:
- (a) broad (see [Table 9](#))
- (9) Upper molars:
- (a) slightly narrower (see [Table 9](#))

Node 3

- (2) Lower incisors mesiodistally waisted towards the base of the crown
- (3) P₃ mesiodistally short and relatively high-crowned, with a steeply inclined mesiobuccal face that does not extend far inferiorly to form a sectorial flange even in males (see [Figure 14](#))
- (4) Lower molars:
- (b) with long mesial fovea
 - (i) with a pliopithecine triangle on M₂₋₃
- (6) Upper central incisors slightly mesiodistally waisted

Node 4

- (4) Lower molars:
- (a) moderately narrow (see [Table 9](#))
 - (f) with a high incidence of a well-developed mesostylid
- (5) M₃ smaller in area than M₂
- (7) M² much broader and more rectangular in shape than M¹
- (8) M³ possibly small in relation to M², with highly reduced posterior cusps
- (9) Upper molars:
- (a) broad (see [Table 9](#))
- (10) Upper and lower molars with rounded cusps and low occlusal relief

Node 5

- (4) Lower molars:
- (h) with well-developed occlusal crests
- (9) Upper molars:
- (b) with relatively wide trigon basin

Table 10 Continued

Node 6

-
- | | |
|------|---|
| (1) | Tubular ectotympanic fully-developed |
| (3) | P ₃ markedly sexually dimorphic with long, obliquely inclined mesiobuccal face that forms a well-developed sectorial flange in males (see Figure 14) |
| (4) | Lower molars: |
| | (b) with relatively broad mesial fovea |
| | (c) with more transversely oriented mesial transverse crest |
| | (d) with protoconid and metaconid transversely aligned |
| | (e) cristid oblique aligned almost in line with the long axis of the crown |
| | (g) with relatively large hypoconulid |
| (9) | Upper molars: |
| | (a) broad (see Table 9) |
| | (c) with relatively large hypocone |
| (11) | Entepicondylar foramen absent |
-

*Includes only those characters mentioned or discussed in the text.

Andrews, 1978, 1985, 1992; Szalay & Delson, 1979; Fleagle, 1986, 1988; Rae, 1997; Ward, 1997; Kelley, 1997; Walker, 1997), but few morphological features can be identified to provide convincing support for such an inferred relationship (Harrison, 1987, 1993; Harrison & Rook, 1997). In fact, recent comparisons of *Proconsul* and other early Miocene catarrhines from East Africa provide additional support for the contention that proconsulids represent the sister-taxon of all extant catarrhines (Harrison & Sanders, 1999; Harrison, in preparation). In addition, it has been argued that *Nyanzapithecus* may be closely related to *Oreopithecus*, an undoubted hominoid from the late Miocene of Italy (Harrison, 1986a,b; Harrison & Rook, 1997). However, further analyses have demonstrated that *Oreopithecus* is a hominid, perhaps closely related to *Dryopithecus*, and that the unique dental specializations that it shares with *Nyanzapithecus* are convergently derived (Harrison & Rook, 1997). Consequently, *Nyanzapithecus* is now best considered as a specialized member of the Proconsulidae.

The Sihong primates differ from proconsulids in the following respects: upper incisors of *Dionysopithecus* are relatively larger (based on isolated teeth only) by compari-

son to the size of the molars (except *Micropithecus clarki*); I¹ is slightly waisted towards the base of the crown, lacks a lingual pillar or swelling, and has an incisive apex that recedes distally; lower incisors with distinct waisting towards the base of the crown; upper canine in female individuals of *Dionysopithecus* lower crowned, triangular in cross-section, with a broad distal heel; P₃ is mesiodistally shorter and relatively higher crowned, without pronounced inferior extension of the mesiobuccal face of the crown; P₄ with metaconid distinctly smaller than the protoconid; P⁴ in *Dionysopithecus* relatively narrower (except *Limnopithecus*, *Kalepithecus*, *Rangwapithecus* and *Nyanzapithecus*); M² is relatively broader (except *Limnopithecus evansi* and *Kamoyapithecus hamiltoni*; see Table 9); upper and lower M3 is apparently smaller than the corresponding M2 (except *Micropithecus clarki*); upper molars in *Dionysopithecus* lack a crest connecting the metacone and hypocone (occurs variably in proconsulids, but is generally well-developed); lower molars with a longer and narrower mesial fovea, obliquely-oriented mesial transverse crest with the protoconid more mesially placed than the metaconid, pliopithecine triangle present, well-developed mesostylid (rare in most proconsulids, although relatively common in

Proconsul), slightly oblique cristid obliqua, and smaller hypoconulid; dP_4 with distinct paraconid (sometimes also on permanent molars, particularly in *Platodontopithecus*), small hypoconulid, and no crest linking the hypoconulid and entoconid so that the distal fovea communicates directly with the talonid basin.

The Dionysopithecinae and the origins of the Pliopithecidae

With the larger sample of material now available from Sihong, it has been possible to demonstrate, contrary to previous opinion, that *Dionysopithecus* and *Platodontopithecus* are morphologically distinct from the East African Miocene proconsulids. The superficial similarities that they share in their molar morphology are probably primitive characters retained from the last common ancestor of pliopithecids, proconsulids, and all later catarrhines. We deduce from this that the distinctive molar morphology typical of European pliopithecids was derived from a pattern closer to that seen in proconsulids. If this is the case, then there are two important implications for understanding the evolutionary relationships of pliopithecids.

First, one of the most intriguing problems in primate evolution has been to provide an explanation for the geographic and phylogenetic origins of the pliopithecids. Most researchers have assumed that the clade originated in Afro-Arabia, since early catarrhines are apparently restricted to this region until the start of the Miocene.² However,

²This should not be confused with the current debate concerning the inferred geographical origins of the Anthropoidea. The improved fossil record and diversity of purported early anthropoids from this region in recent years (i.e., *Eosimias sinensis* and *E. centemicus* from the middle Eocene of China; *Amphipithecus mogaungensis* and *Pondaungia cotteri* from the later Eocene of Myanmar; and *Siamopithecus eocaenus* and *Wailekia orientalis* from the late Eocene of Thailand) has led a number of authors to consider the possibility that the clade may have differentiated in Asia, rather than in Africa as once believed (Beard *et al.*, 1994, 1996;

the East African proconsulids which antedate the oldest known pliopithecids, are too derived (at least based on those whose anatomy is adequately known) to be potential candidates for ancestry or close relationship to the pliopithecids (see Harrison, 1987). Even so, it should be borne in mind that proconsulids are known almost exclusively from a relatively restricted region in East Africa, presumably providing only a limited perspective on total catarrhine diversity in Africa during the early Miocene. It has been assumed quite reasonably, therefore, that pliopithecids may have originated from a geographic and taxonomic source that is not well-sampled in the fossil record, such as in North Africa or West Africa. This general scenario is still sound, but the new evidence from Sihong adds a further complicating factor. In the past, we have been looking for pliopithecid-like representatives in Africa to provide the source of European pliopithecids. Now, with the realization that pliopithecids first migrated into Eurasia with molars that were superficially like proconsulids, the problem is introduced that the African sister-group of pliopithecids may be difficult to discern from contemporary proconsulids, at least on the basis of limited dental remains. It is conceivable, therefore,

Ciochon & Holroyd, 1994; Ducrocq *et al.*, 1995; Chaimanee *et al.*, 1997). However, these Asian Eocene taxa are at best basal anthropoids (or possibly even basal haplorhines; see Harrison, 1996), and clearly do not represent stem catarrhines. Fossil anthropoids antedating the earliest appearance of pliopithecids (including the dionysopithecines) with indisputable synapomorphies that link them uniquely to modern catarrhines are entirely Afro-Arabian in distribution [e.g., the propiopithecids from the early Oligocene of Egypt and Oman which share reduction in premolar count and molar morphology with later catarrhines (including the pliopithecids), and the proconsulids from the Miocene of East Africa which, in addition to these characters, share with modern catarrhines loss of the entepicondylar foramen and development of a fully developed tubular ectotympanic (see Harrison, 1987; Table 10)]. For these reasons the Eocene anthropoids from Asia are not relevant to the immediate ancestry of the pliopithecids, and further comparisons and discussions of their relationships need not be entertained at this juncture.

that a primitive sister-taxon of pliopithecids is already known, and lurking undetected among the poorly-known smaller proconsulids from East Africa. However, based on our current knowledge of this material we do not think that this is likely. We suspect that evidence of stem pliopithecids will eventually be found elsewhere in Africa, although it will require a careful comparative anatomist with a good eye for morphological detail to determine that they are not simply new varieties of proconsulids.

Second, the Sihong primates help to establish the polarities of dental character transformations among pliopithecids. The issue of whether or not the pliopithecins or crouzeliins are closest in their molar morphology to the pliopithecid ancestral morphotype has been the subject of some debate (Andrews, 1980; Harrison, 1987; Andrews *et al.*, 1996). Harrison (1987) has previously suggested that the crouzeliin dental pattern may be more primitive than that of pliopithecins in retaining several features of the lower molars characteristic of the inferred ancestral anthropoid morphotype. The long narrow crowns, the high and sharp occlusal crests and cusps, the relatively elongated mesial fovea, the small size of the hypoconulid, the long and obliquely directed cristid obliqua, and the absence of a well-defined distal fovea in the lower molars of crouzeliins are all characters that could be interpreted as primitive anthropoid features (Harrison in Andrews *et al.*, 1996). However, the absence of this suite of features in the Sihong catarrhines, which apparently represent the sister-group of crouzeliins and pliopithecins, suggests that the crouzeliin molar morphology is probably derived relative to the primitive pliopithecid pattern. This further supports the proposal by Harrison (in Andrews *et al.*, 1996) that the crouzeliin molar pattern is secondarily convergent on the ancestral anthropoid morphotype as a result of dietary specialization.

Other small catarrhine primates from Asia

In addition to the well-known pliopithecids from Lufeng and Tongxin, China (Wu & Pan, 1984, 1985; Qiu & Guan, 1986; Pan, 1988; Pan *et al.*, 1989; Harrison *et al.*, 1991), a number of isolated teeth and jaw fragments of small catarrhine primates have been recovered from other fossil localities in Asia. These include "*Pliopithecus*" *posthumus* from Ertemte, China; *Krishnapithecus krishnaii* from Haritalyangar, India; "*Kansupithecus*" from Taben Buluk, China; isolated teeth from the Kamliar and Manchar Formations, Pakistan, tentatively referred to *Dionysopithecus* sp.; and "*Dendropithecus*" *orientalis* from Ban San Klang, northern Thailand.³

Schlosser (1924) described a heavily worn left M³ from Ertemte, Nei Monggol (Inner Mongolia) northern China, as belonging to a new species of primate, *Pliopithecus posthumus*. The site is probably terminal Miocene in age, correlated with MN 13 (Fahlbusch *et al.*, 1983; Li *et al.*, 1983; Storch, 1987; Qiu, 1989; Qiu & Qiu, 1995). Unfortunately, the tooth is much too worn to be certain of its taxonomic affinities, and there are no justifiable grounds to include it within the Pliopithecidae. In fact, several authors have even questioned whether it belongs to a primate at all (Hürzeler, 1954; Simons, 1972; Simons & Fleagle, 1973; Fleagle, 1984; Harrison *et al.*, 1991). The crown is

³Pan (1996) recently described a collection of 36 isolated teeth recovered from three late Miocene localities in the Xiaohe region of the Yuanmou Basin, Yunnan Province, China. She described these as belonging to a new genus and species of small catarrhine primate, *Dianopithecus progressus*. However, it is evident from the accompanying plates that the sample is based almost entirely on deciduous teeth of the large hominoid primate which is known from these and neighboring localities. In a recent review of the evolutionary history of small catarrhines from China, Pan (1998), it seems, has reached a similar conclusion. The large hominoid from Yuanmou has been variously named *Homo orientalis*, *Ramapithecus hudiensis*, and *Lufengpithecus yuanmouensis*, all of which have priority over *Dianopithecus progressus*, but the case will require careful scrutiny in order to establish the valid name(s).

similar in size to the M^3 of *Platodontopithecus*, but differs in being relatively narrower. Unfortunately, until more material is recovered from Ertemte it is impossible to make any definitive statements about the affinities of this isolated specimen.

The same applies to a worn M^3 from the late Miocene locality of Haritalyangar in northern India (Johnson *et al.*, 1983; Barry *et al.*, 1986). Chopra & Kaul (1979) described the specimen as *Pliopithecus krishnaini*, and later Ginsburg & Mein (1980) included it, along with *Pliopithecus posthumus*, in a separate genus, *Krishnapithecus*. The Haritalyangar molar is similar in its general morphology to the Sihong catarrhines, and intermediate in size between the M^3 s of *D. shuangouensis* and *P. jianghuaiensis*. However, as noted previously by Harrison *et al.* (1991), it is extremely difficult to differentiate fossil catarrhines on the basis of isolated and worn upper molars. The size of the tooth alone probably precludes it from belonging to either of the two species from Sihong, but beyond this it is difficult to say much about its broader taxonomic affinities.

An edentulous mandibular symphysis from the early Miocene site of Hsi-shui, Taben Buluk, Gansu Province, northern China (Bohlin, 1946; Russell & Zhai, 1987; Qiu, 1989) is of the approximate size to be appropriate for *D. shuangouensis*. Since the symphyseal region of the mandible of *D. shuangouensis* is not preserved, direct comparisons are impossible. Nevertheless, broader comparisons show that the Taben Buluk specimen is generally similar in morphology to other small catarrhine primates from East Africa and Europe (Harrison *et al.*, 1991). A molar fragment from the neighboring site of Yindirte, estimated to be late Oligocene in age (Russell & Zhai, 1987), is too incomplete to determine its taxonomic affinities (Harrison *et al.*, 1991). Bohlin (1946) originally described these two specimens as belonging to a new genus,

“Kansupithecus”, but the nomen remains unavailable because he failed to provide a species name (Szalay & Delson, 1979; Bernor *et al.*, 1988; Harrison *et al.*, 1991).

Several isolated teeth of a small catarrhine primate have been recovered from the early middle Miocene Kamlial and Manchar Formations in Pakistan (associated with faunas that are correlated magnetostratigraphically in the Potwar Plateau to ~16–17 Ma) (Raza *et al.*, 1984; Barry *et al.*, 1986; Bernor *et al.*, 1988; Barry & Flynn, 1989). These specimens have previously been considered to have their closest affinities with *Dionysopithecus* and *Micropithecus* on the basis of their general similarity in size and molar morphology (Fleagle, 1984; Barry *et al.*, 1986; Bernor *et al.*, 1988). However, comparisons with the larger sample of *Dionysopithecus* specimens now available from Sihong indicates that the differences are greater than were initially believed. The upper canine (GSP S-76) from Pakistan is smaller in overall dimensions than PA 1228, and it is relatively higher-crowned and more bilaterally compressed, with a narrower distal heel. The isolated upper molar (GSP 24307) from the Kamlial Formation, described as an M^1 , or possibly M^2 , is considerably smaller than the molars of *D. shuangouensis* (its occlusal area is 27.8% smaller than the smallest M^1 of *D. shuangouensis* from Sihong), and the crown is relatively narrower. However, it is possible that the Kamlial specimen may represent a dP^4 , in which case the size of the crown, proportions, and general morphology would be consistent with the corresponding tooth of *D. shuangouensis*. The P^4 (H-GSP 8114/3690) from the Manchar Formation is consistent in size and morphology to those of *D. shuangouensis* from Sihong, but it is also generally similar to those of proconsulids and European pliopithecids.

The M_1 (H-GSP 8114/609) from the Manchar Formation provides the most informative comparison. It is distinct from

D. shuangouensis in the following respects: (1) the crown is shorter and broader (with breadth-length proportions of 90:7); (2) the cusps tend to be higher and more conical in shape; (3) the trigonid is shorter and broader; (4) the metaconid and protoconid are more transversely aligned, so that the mesial transverse crest is not obliquely oriented; (5) the prehypocristid is not obliquely directed in relation to the long axis of the crown; (6) the floor of the trigonid is similar in depth to that of the talonid basin; (7) the buccal cingulum is better developed, being more or less continuous along the buccal aspect of the crown; (8) there is no trace of a pliopithecine triangle (although this feature is incompletely expressed or absent on the M_1 of *D. shuangouensis* and other pliopithecids); (9) the paraconid is lacking; and (10) the hypoconulid is subequal in size to the hypoconid (the former is much smaller in *D. shuangouensis*). These are significant differences that indicate that the Manchar and Sihong catarrhines should be separated at least at the species level. Moreover, several of the features (i.e., characters 3, 4, 5, 6, 9, 10) are best considered as derived characters that link the Manchar specimen with proconsulids and other late catarrhines, rather than with pliopithecids (see Table 10). The implication is that the taxon from Pakistan may be more distantly related to *Dionysopithecus* than has been considered previously (Bernor *et al.*, 1988).

With the limited material available it is difficult to draw any definitive conclusions about the relationships of the small catarrhine primates from Pakistan. However, we offer the following tentative assessment. (1) The isolated teeth from the Manchar and Kamlial Formations are consistent in size and morphology and probably belong to a single species (Bernor *et al.*, 1988), although the possibility should not be discounted that multiple species may be represented. (2) The morphological differences in the upper canines and lower molars from Pakistan and

Sihong are sufficient to indicate that the South Asian material should not be allocated to *Dionysopithecus* (*contra* Bernor *et al.*, 1988). Until further material is recovered from Pakistan it is probably best to leave the Kamlial and Manchar specimens taxonomically unassigned. (3) There is no indication that the specimens are closely related to pliopithecids. In fact, in terms of their molar morphology they appear to be at least patristically (and probably also cladistically) more closely related to the East African proconsulids.

Finally, an isolated M_1 (TF 2451) of a small catarrhine primate has been recovered from the early middle Miocene locality of Ban San Klang in the Pong Basin of northern Thailand. The associated fauna from this locality indicates an age equivalent to or somewhat younger than the fauna from the Xiacaowan Formation, and is best correlated to ~15–17 Ma (Ducrocq *et al.*, 1994). Suteethorn *et al.* (1990) have suggested that the specimen is most closely similar to the East African proconsulid, *Dendropithecus macinnesi*, and have referred it to a new species, *Dendropithecus orientalis*. However, the Ban San Klang specimen can be distinguished from *Dendropithecus* and from other small proconsulids in the following respects: (1) the crown narrows more strongly mesially; (2) the mesial fovea is relatively longer; (3) the protoconid and metaconid are more distinctly mesiodistally off-set, so that the transverse crest connecting the two cusps is obliquely oriented relative to the transverse axis of the crown; (4) the talonid basin is shallower; (5) the prehypocristid is more obliquely oriented in relation to the long-axis of the crown; (6) the distal fovea is quite small; and (7) the hypoconulid is distinctly smaller than the hypoconid. As noted above, these make up an important suite of features that characterizes the lower molars of Eurasian pliopithecids, including the Sihong primates. The absence of a pliopithecine triangle on the Ban San Klang

molar is probably not significant given the fact that this feature is variably developed or absent on M_1 s of pliopithecids. On this basis, it is reasonable to infer that the Thai specimen has its closest affinities with the pliopithecids, rather than with the proconsulids, and we can confidently assume that it should *not* be assigned to *Dendropithecus*. Comparisons show that “*Dendropithecus*” *orientalis* is identical in size and similar in morphology to *Dionysopithecus shuangouensis*. The Ban San Klang specimen can be distinguished in several features (i.e., slightly larger distal fovea, more obliquely oriented mesial transverse crest, and more peripheralized lingual cusps), but these are relatively minor differences. Given the limited material available from Ban San Klang, several alternative options are possible—the specimen can be assigned to *D. shuangouensis*, allocated to a separate species in the same genus, or distinguished at the generic level. Obviously, further material from Thailand is needed to settle this question, but given the overall morphological similarity of the isolated molar to *D. shuangouensis*, in conjunction with discernible (although rather minor) differences, we favor referring the Ban San Klang specimen to a separate species within *Dionysopithecus*. We therefore recognize it, at least provisionally, as *Dionysopithecus orientalis*.

Zoogeography and paleoecology

The Sihong primates are of particular importance from a zoogeographic perspective because they likely represent the oldest known catarrhines from Eurasia. The fauna from the Xiacaowan Formation is considered to be late early Miocene in age, tentatively correlated with European Mammal Zone MN 4 (~17–18 Ma) (Qiu, 1989; Qiu & Qiu, 1995) (see Figure 2). Other sites of similar age in Asia with small catarrhines, such as Ban San Klang in Thailand, the

Kamlial and Manchar Formations in Pakistan, and Tongxin in China, are considered to be slightly younger (correlated with MN 5–6, ~15–17 Ma). The catarrhine primate from Hsi-shui may be equivalent in age or slightly older than Sihong, but unfortunately the taxonomic affinities of this specimen remain uncertain. The earliest known catarrhines in Europe are pliopithecines and dryopithecine hominoids from localities correlated with MN 5 (~16–17 Ma) (Andrews *et al.*, 1996).

The collision of the Afro-Arabian plate with Eurasia during the Agenian–Orleanian established an intermittent land connection between Arabia and Southwest Asia that allowed successive migrations of African mammals, including catarrhine primates, into Europe and Asia during the early part of the Miocene (Adams *et al.*, 1983; Rögl & Steininger, 1983; Bernor, 1983; Thomas, 1985; Andrews *et al.*, 1996). The fossil record of Miocene catarrhines in Eurasia is still meager, so any attempt to reconstruct their biogeography is likely to prove problematic. Nevertheless, the revised interpretation of the affinities of the Sihong material presented here does require a rethinking of previously proposed zoogeographic models. The first major wave of mammalian immigrants from Africa (“Neogene Dispersal Phase 1” of Thomas, 1985) included creodonts and, most notably, proboscideans. The sudden arrival of proboscideans in Europe (the “Proboscidean Datum Event” of Madden & Van Couvering, 1976) is correlated with MN 4 (~17–18 Ma) (Mein, 1989; Bulot & Ginsburg, 1993; Tassy, 1989, 1996), but evidence from Pakistan and China indicates that primitive elephants were already present in Asia prior to this date (Barry *et al.*, 1985; Barry & Flynn, 1989; Qiu, 1989; Tassy, 1989, 1996). It may be of some significance, therefore, that contemporary pliopithecids occur in Asia before making their appearance in Europe at MN 5.

Harrison *et al.* (1991) surmised that the sudden appearance and taxonomic diversity of pliopithecines in Europe during MN 5 (including three species of *Pliopithecus*) indicates that their initial migration from Africa involved multiple species originating from a diverse stem-community prior to their arrival in Europe. However, with stem pliopithecids in China during the early Miocene, it now seems more plausible to infer that the pliopithecins and crouzeliins were derived from an Asian rather than an African source. The scenario that best fits the evidence is that dionysopithecines entered Asia from Africa during the early Miocene, probably during MN 3 (~18–20 Ma), and diversified locally. From this source, a more specialized group, the pliopithecins, extended their range westwards into Europe by ~16–17 Ma. Although the earliest pliopithecins are recorded from Europe, it seems likely that the clade originated in Asia since there are no dionysopithecine antecedents in Europe, and a primitive pliopithecine, only slightly younger than the earliest representatives in Europe, is known from Tongxin in China (correlated with MN 6, ~15 Ma) (Harrison *et al.*, 1991). Crouzeliins, however, appear to have originated in Europe, where their first record is at localities correlated with MN 6 (Andrews *et al.*, 1996). The earliest representatives were apparently derived from a pliopithecine-like ancestor, and the group demonstrates increasing dental specialization through time. The only known crouzeliin from Asia, *Laccopithecus robustus*, from the late Miocene (~7–8 Ma) locality of Shihuiba, China, points to a relatively late arrival of this clade into the region. One potential complication with this scenario is that there is a major hiatus in the fossil record of small catarrhine primates in Asia from ~15 Ma to ~8 Ma (see Figure 2), which could lead to invalid assumptions concerning the timing of first appearances in Asia. It is possible, for example, that the absence of crouzeliins (and other small

catarrhines) from this time period is simply due to inadequate sampling of localities, but it is pertinent to note that small catarrhines have not been found in the intensively studied and productive sedimentary sequences of the appropriate age in Indo-Pakistan and China (Barry & Flynn, 1989; Harrison *et al.*, 1991; Qiu & Qiu, 1995). The current evidence, therefore, supports the inference that crouzeliins made their first appearance in Asia during the late Miocene, although the apparent extinction of pliopithecids in Europe by the close of the Vallesian (Andrews *et al.*, 1996), would indicate that late surviving crouzeliins reached Asia before ~11 Ma.

Summary

- (1) Paleontological investigations at Songlinzhuang and Zhengji in Sihong County, Jiangsu Province, China since 1981 have yielded a sizeable collection of previously undescribed fossil catarrhines from the Xiacaowan Formation.
- (2) The vertebrate fauna indicates a late early Miocene age (correlating with MN4, late Orleanian of Europe, ~17–18 Ma), which establishes the Sihong primates as the earliest known catarrhines from Eurasia.
- (3) The fossil primates are assigned to two species, *Dionysopithecus shuangouensis* Li, 1978 and *Platodontopithecus jianghuaiensis* Gu & Lin, 1983, which differ in size and dental morphology. Three additional species from the Xiacaowan Formation described by Lei (1985) are considered to be junior synonyms. The new collections from Sihong provide important new information on *Dionysopithecus* and *Platodontopithecus* which helps to clarify their phylogenetic and taxonomic status.
- (4) Previous studies have suggested that the Sihong catarrhines might be

closely related to the proconsulids from the Miocene of East Africa. However, the Sihong primates share a number of key derived features of their dentition with pliopithecids, and can be inferred to be the primitive sister taxon. As a consequence, *Dionysopithecus* and *Platodontopithecus* are included in the Pliopithecidae, within a separate subfamily, the Dionysopithecinae.

- (5) Recognition that the Sihong primates have affinities with pliopithecids, but are more primitive, suggests that the initial differentiation and diversification of the clade may have taken place in Asia rather than in Africa. The evidence suggests that the earliest Eurasian catarrhines probably migrated into tropical East Asia as part of a major faunal interchange with Africa that occurred during MN 3 (~18–22 Ma).

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