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The Gashatan (late Paleocene) mammal fauna from Subeng, Inner Mongolia, China

PIETER MISSIAEN and THIERRY SMITH



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The Paleocene–Eocene boundary is of particular importance for the evolution of mammals and the poorly known Asian mammal faunas from this period have received much attention. The late Paleocene Subeng site in Inner Mongolia (China) has come under study only recently, and here we present the first complete description of its mammal fauna. Two new species are described, the neoplagiaulacid multituberculate *Mesodmops tenuis* sp. nov. and the praolestine nyctitheriid *Bumbanius ningi* sp. nov., representing stratigraphic range extensions of the respective genera into the Paleocene. Previously unknown parts of the dentition are described here for the eumylid *Eomylus bayanulanensis*, the sarcodontid *Hyracolestes ermineus*, the cimolestid *Tsaganium ambiguus*, the carpolestid *Subengius mengi*, as well as the femur of the mesonychid *Dissacus serratus*. For most taxa, the new specimens from Subeng provide new phylogenetic and/or biostratigraphic information. We confirm the inclusion of *Hyracolestes* in the Sarcodontinae and elevate this group to the rank of family, the Sarcodontidae, separate from Micropternodontidae. In the case of *Subengius mengi* an updated cladistic analysis of carpolestids supports the hypothesis that *Subengius* is derived from an evolved *Elphidotarsius*-like ancestor in the early to middle Tiffanian of North America. A total of 17 species is identified, including well-known biostratigraphic markers for the late Paleocene Gashatan Asian Land Mammal Age such as *Lambdopsalis bulla*, *Prionessus* sp., *Palaeostylops iturus*, *Pseudictops lophiodon*, *Tribosphenomys minutus*, and *Dissacus serratus*. We propose that the Gashatan faunas are less endemic than previously thought, and result from a significant exchange with North American faunas from the late Paleocene.

Key words: Mammalia, “Insectivora”, Multituberculata, Glires, Carpolestidae, late Paleocene, Gashatan, Subeng, China.

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Introduction

The Paleocene–Eocene Boundary (PEB) was a major turning point in Earth history, one that was characterized by sudden global climatologic and biotic changes. The Paleocene–Eocene Thermal Maximum (PETM) was a short-lived climate pulse marked by global temperatures increasing by 5–10°C, superimposed on an already warm background climate (Zachos et al. 2001; Wing et al. 2005). Presumably in association with these climatic changes, a wave of modern mammal groups appeared and dispersed throughout the northern hemisphere, taking advantage of the new possibilities for migratory routes (Bowen et al. 2002; Smith et al. 2006). The evolution of mammal faunas at the PEB has been fairly well documented in North America and Europe (Gingerich 2003; Hooker 1998). Although the Asian fossil mammal record near the Paleocene–Eocene boundary is still poorly known, it has figured prominently in many hypotheses on the origin of modern mammals (Krause and Maas 1990; Beard 1998; Smith et al. 2006). In Asia, the PEB is traditionally placed at the boundary between the Gashatan and the Bumbanian Asian Land Mammal Ages (ALMAs) and this seems to be supported by recent isotope

analyses of both the Nomogen Formation in Inner Mongolia and the Lingcha Formation in southern China (Bowen et al. 2002, 2005). The classic Gashatan faunas are the Gashato, Zhigden, Naran, and the Khaychin-Ula faunas in Mongolia, and the Nomogen and Bayan Ulan faunas in China. However, it has recently been suggested that the Nomogen Formation extends into the Bumbanian based on the presence of the so-called “*Gomphos* fauna” (Meng et al. 2004; Meng, Wang et al. 2007). Typical examples of the Bumbanian ALMA are the Mongolian Bumban fauna and the Chinese Wutu and Upper Lingcha faunas (Meng and McKenna 1998; Bowen et al. 2002).

The late Paleocene Subeng fauna in Inner Mongolia (China) has only recently come under scientific study. Although the locality was discovered in 1976 by a team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) and the Inner Mongolian Museum (IMM), specimens have remained unpublished to date. In their overview of Asian Paleogene mammal sites, Russell and Zhai (1987: 71) mentioned the Subeng locality, noting the presence of “*Arctostylops*, *Pseudictops*, multituberculates, a primitive uintathere and dermopteran teeth”. In 1995,

2000, 2001, and 2004, the site was re-sampled by a multi-disciplinary team from the IMM and the Royal Belgian Institute of Natural Sciences (RBINS), resulting in the discovery of a new genus and species of carpolestid plesiadapiiform and the first geological interpretation of the locality (Smith et al. 2004). Publication of some of the more abundant fossil taxa followed, providing new insights in the phylogenetic and biogeographic relations between Asian and North American mammal faunas (Missiaen and Smith 2005; Missiaen et al. 2006). In addition, a preliminary list of the Subeng fossil mammal fauna, together with an integrated study of sedimentology, palynomorphs, charophytes, ostracods, molluscs, and other vertebrate fossils, has been published, providing further paleoenvironmental insights for this site (Van Itterbeeck et al. 2007). Here we give an overview of the fossil mammal fauna from Subeng, including detailed illustrations of previously unpublished specimens, and discuss the possible phylogenetic and biogeographic implications of the assemblage.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; IMM, Inner Mongolian Museum, Hohhot, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Materials and methods

The fossils described and figured in this report are from the Subeng locality in Inner Mongolia, China (N 43°31'50", E 111°44'04"), and were collected in the upper part of the Nomogen Formation ("Bayan Ulan Beds"), of Gashatan, late Paleocene age (Van Itterbeeck et al. 2007). The fossils were mainly obtained by underwater screen-washing of approximately 1650 kg of sediment through screens with a mesh of 1 mm.

Systematic classification is modified from Rose (2006).

Systematic paleontology

Class Mammalia Linnaeus, 1785

Subclass Allotheria Marsh, 1880

Order Multituberculata Cope, 1884

Superfamily Ptilodontoidea Cope, 1887

Family Neoplagiaulacidae Ameghino, 1890

Genus *Mesodmops* Tong and Wang, 1994

Type species: *Mesodmops dawsonae* Tong and Wang, 1994; Bumbanian (early Eocene), Wutu (Shandong Province, China).

Mesodmops tenuis sp. nov.

Fig. 1A–E; Table 1.

Etymology: From Latin *tenuis* = thin, fine, slender, for the overall more slender, anteroposteriorly elongate shape of the molars.

Holotype: IMM-2004-SB-013, right m1.

Type locality: Subeng, Inner Mongolia, China.

Type horizon: Upper part of the Nomogen Formation, Gashatan (late Paleocene).

Referred material: IMM-2001-SB-016, left M1; IMM-2001-SB-017, right DP3?; IMM-2001-SB-018, left m1; IMM-2004-SB-014, left M2; IMM-2004-SB-015, left m1; IMM-2004-SB-016, left m2; IMM-2004-SB-017, left m1; IMM-2004-SB-018, left M1.

Diagnosis.—Neoplagiaulacid multituberculate similar in size to *Mesodmops dawsonae*. Differs from *M. dawsonae* in having less inflated, less rounded lower molars with a more irregular outline, and in the 6:5 and 3:2 cusp formulae of m1 and m2, respectively. The M1 differs from the M1 of *M. dawsonae* in having smaller anterior-most cusps and square cusps in the middle cusp row, instead of rectangular cusps as in *M. dawsonae*. *M. tenuis* is further generally characterized by slightly longer but narrower, less inflated molars.

Description.—Five tooth loci are known for *M. tenuis*. The cusp formula of M1 (Fig. 1A) is 8:10:5, with the cusps of M1 become gradually larger toward the posterior end of the tooth. The middle cusp row has very small, subpyramidal cusps anteriorly that become larger and more crescentic posteriorly. The cusp formula of M2 (Fig. 1B) is 1:3:3, and M2 has a trapezoidal shape, tapering toward the posterior end. The anterior-most cusp of the middle row has an antero-posteriorly compressed shape due to the presence of the preceding M1.

The m1 (Fig. 1D) is rectangular in shape with the lingual and labial rows roughly parallel. The labial and lingual sides of the crown are, however, somewhat irregular and undulating. The cusp formula of m1 is 6:5, with cusps bearing grooves on their valley-facing sides and with the anterior cusps of both rows notably smaller. The anterior cusps of the labial row are subpyramidal, becoming crescentic posteriorly. The posterior cusp of the lingual row forms a large crest. The m2 (Fig. 1E) has a simple, slender shape with a cusp formula of 3:2. The cusps bear grooves on their valley-facing sides and become slightly less crescentic posteriorly.

IMM-2001-SB-017 (Fig. 1C) is tentatively identified here as a right DP3. The cusp formula of 2:3 matches that of DP3 shown in *M. dawsonae* (Tong and Wang 1994) and the general shape is similar, although it is notably smaller and relatively more slender.

Table 1. Measurements of *Mesodmops tenuis* sp. nov. from the Gashatan of Subeng. Hyphen designates dimensions that could not be measured.

	Position	Length (mm)	Width (mm)
IMM-2001-SB-017	dP3?	0.73	0.50
IMM-2001-SB-016	M1	3.28	1.30
IMM-2004-SB-014	M2	1.30	1.20
IMM-2001-SB-018	m1	—	0.93
IMM-2004-SB-013	m1	2.15	0.90
IMM-2004-SB-017	m1	—	0.93
IMM-2004-SB-016	m2	1.20	0.98

Discussion.—The teeth of *Mesodmops tenuis* from Subeng closely resemble those of the type-species *M. dawsonae* from the Bumbanian of Wutu (Shandong Province, China) in size and general morphology. The lower molars of *M. dawsonae* differ in having a more rounded outline in occlusal view with smooth labial and lingual sides. The m1 of *M. dawsonae* is not rectangular, as in *M. tenuis*, but the cusp rows in *M. dawsonae* curve toward the midline of the tooth anteriorly and posteriorly, and the greatest transverse length is situated at the height of the fifth labial cusp. The cusp formulae of m1 and m2 in *M. tenuis* are 6:5 and 3:2, respectively, but 7:5 and 4:2 respectively for *M. dawsonae*. On M1, the anterior-most cusps are relatively smaller compared to the posterior cusps in *M. tenuis* than in *M. dawsonae*. The cusps of the middle cusp row of M1 are rectangular and wider than long in *M. dawsonae*, not square as in *M. tenuis*.

M. tenuis further differs in having generally more slender teeth, with a higher length-width ratio. Although these differences may seem limited or based on few specimens, they are consistently present in all specimens, allowing to distinguish them from *M. dawsonae*, and we therefore to allocate them to the new, closely related species *M. tenuis*.

Tong and Wang (1994) suggested that *Mesodmops*, then known only from the Eocene, could have been present already in the Paleocene of Asia; the discovery of *M. tenuis* confirms this idea. They also suggested that *M. dawsonae* from the Eocene of China could be derived from the North American *Mesodma*, noting similarity in the P4 cusp formula similar to that of *Mesodma thompsoni* (Tong and Wang 1994). Neoplagiaulacid phylogeny is mainly based on the highly diagnostic P4 and p4, and because both loci are unknown for *M. tenuis*, the possibilities for phylogenetic analysis are limited. Nevertheless, the lower molar cusp formulae of *Mesodmops tenuis* (6:5 for m1, 3:2 for m2) are intermediate between *Mesodma thompsoni* (6:4 and 3:2) (Sloan 1987) and *Mesodmops dawsonae* (7:5 and 4:2), and therefore seem to corroborate the ideas of Tong and Wang (1994).

Superfamily Taeniolabidoidea Granger and Simpson, 1929

Family Taeniolabididae Granger and Simpson, 1929

Genus *Lambdopsalis* Chow and Qi, 1978

Type species: *Lambdopsalis bulla* Chow and Qi, 1978; Gashatan (late Paleocene), Nomogen (Inner Mongolia, China).

Lambdopsalis bulla Chow and Qi, 1978

Fig. 1F–I.

Referred material: 108 complete and partial molars.

Discussion.—Numerous molars of *Lambdopsalis bulla* have been identified in the Subeng fauna, making the species one of the best-represented taxa in the assemblage, as it is in the nearby Bayan Ulan and Nomogen faunas (Meng et al. 1998; Ting 1998). This taxon has been extensively studied in earlier works (Miao 1986, 1988; Kielan-Jaworowska and Qi 1990).

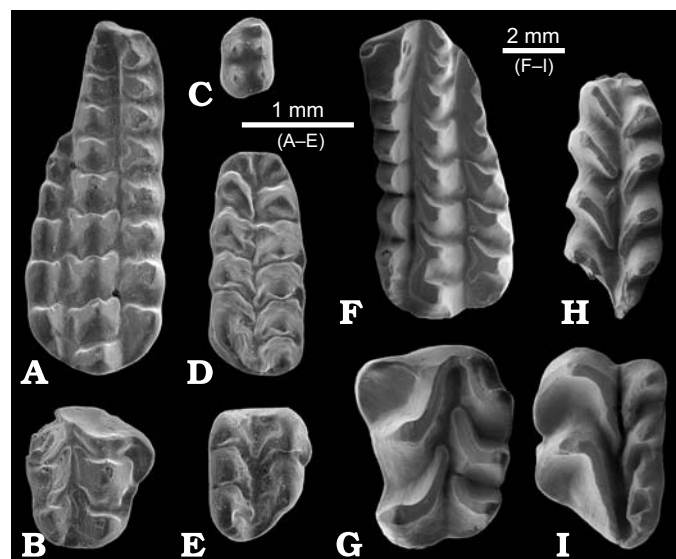


Fig. 1. Multituberculates from the Gashatan (Paleocene) of Subeng, China, in occlusal view (SEM micrographs). A–E. *Mesodmops tenuis* sp. nov. A. IMM-2001-SB-016, LM1. B. IMM-2004-SB-014, LM2. C. IMM-2001-SB-017, RDP3. D. IMM-2004-SB-013, Rm1 (holotype). E. IMM-2004-SB-016, Lm2. F–I. *Lambdopsalis bulla* Chow and Qi, 1978. F. IMM-2001-SB-019, RM1. G. IMM-2001-SB-020, RM2. H. IMM-2001-SB-021, Rm1. I. IMM-2001-SB-022, Rm2.

Stratigraphic and geographic range.—*Lambdopsalis bulla* is known from the Gashatan (late Paleocene) Nomogen Formation at Nomogen, Bayan Ulan, Subeng and Nuheting-boerhe in Inner Mongolia, China.

Genus *Prionessus* Matthew and Granger, 1925

Prionessus sp.

Referred material: IMM-2004-SB-019, fragmentary right M1.

Discussion.—*Prionessus lucifer* is known from all classic Gashatan faunas (Ting 1998), and one fragmentary molar from Subeng is assignable to this taxon. Meng et al. (1998) tentatively distinguished a possible second morphotype of *Prionessus*, *Prionessus* cf. *P. lucifer*, at Bayan Ulan, based on the possession of a double-rooted p4. Given this uncertainty, IMM-2004-SB-019 is here referred to *Prionessus* sp.

Subclass Boreosphenida Luo, Cifelli, and Kielan-Jaworowska, 2001

Cohort Placentalia Owen, 1837

Superorder Gliriformes Wyss and Meng, 1996

Comment.—The superorder “Anagalida” traditionally comprises the Macroscelidea (elephant shrews) and the Glires (rodents, lagomorphs and related forms), as well as a number of extinct families of uncertain affinities (McKenna and Bell 1997). Because several studies suggest Macroscelidea do not have close affinities with Glires (Zack et al. 2005; Tabuce et al. 2006), we prefer to use the term Gliriformes (Meng and Wyss 2001) to designate Glires and a number of closely related, extinct families. The latter traditionally include Zalambdalestidae, Anagalidae, and Pseudictopidae (McKenna and

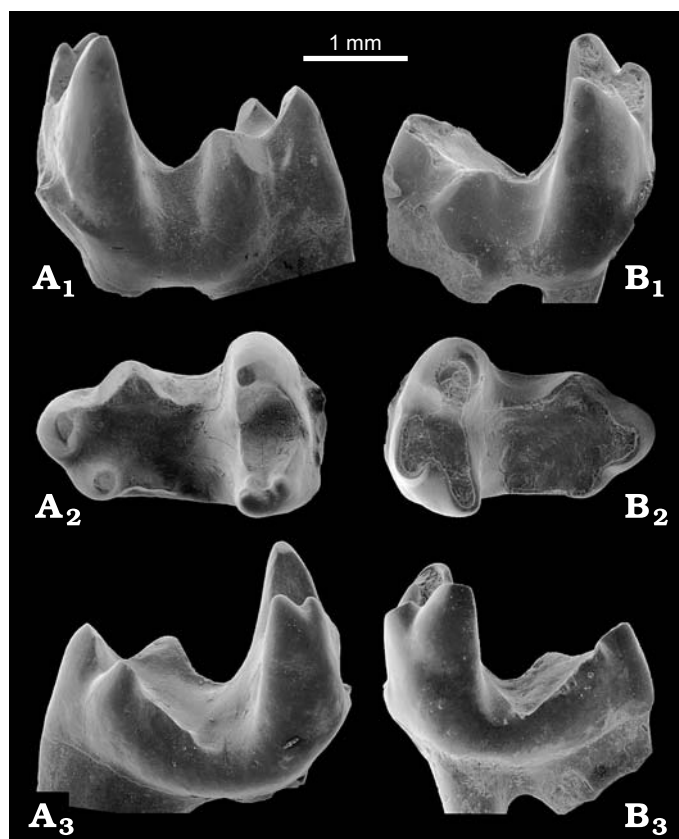


Fig. 2. The gliriform Astigalidae gen. et sp. indet. from the Gashatan (Paleocene) of Subeng, China, in labial (A₁, B₁), occlusal (A₂, B₂), and lingual (A₃, B₃) views. **A.** IMM-2001-SB-023, Lm3. **B.** IMM-2004-SB-020, Rm3. SEM micrographs.

Bell 1997), but probably also Astigalidae (Hu 1993; Tong and Wang 2006) and Arctostylopidae (Missiaen et al. 2006).

Family Astigalidae Zhang and Tong, 1981

Astigalidae gen. et sp. indet.

Fig. 2.

Referred material: IMM-2001-SB-023, left m3; IMM-2004-SB-020, right m3.

Description.—The two referred specimens are similar in having an anteroposteriorly compressed, high trigonid with a nearly connate paraconid and metaconid, and with a weak precingulid. The talonid is much narrower than the trigonid, is strongly elongate and bears a prominent hypoconulid lobe. The lophs connecting different cusps are only weakly developed. The oblique crest is low, and directed toward the lingual part of the base of the protoconid. The entocristid is reduced, leaving the talonid basin open lingually. Although the cusps are high in unworn specimens, the crown is apparently quickly lowered by wear. Both teeth display a limited unilateral hypsodonty. Although there is some difference in the shape of the paraconid between the two specimens, we consider this partly as a difference in wear stage, and partly as intraspecific morphological variability.

Discussion.—The referred specimens possess many characters that have been recognised as diagnostic of “Anagalida”: an anteroposteriorly compressed trigonid with partially or completely united paraconid and metaconid, an unreduced m3, and a tendency towards unilateral hypsodonty (Szalay and McKenna 1971; Tong and Wang 2006). Within the “Anagalida”, the Subeng specimens are closest to the enigmatic family Astigalidae, based on a trigonid that is much taller and anteroposteriorly shorter than the talonid, the limited development of lophs, the strong cusps and the lingually open talonid basin. Currently, three different genera of astigalids have been described: *Astigale* and *Zhujegale* from the early Paleocene of South China (Zhang and Tong 1981) and the recently described, more derived *Yupingale* from the early Eocene of Wutu (Shandong Province, China) (Tong and Wang 2006). The new Subeng specimens thus partly fill in the temporal gap between both previously described occurrences. Because of their lower crowned, less lophodont morphology, the new late Paleocene specimens from Subeng are morphologically closer to early Paleocene taxa than to the early Eocene *Yupingale*.

Family Arctostylopidae Schlosser, 1923

Genus *Palaeostylops* Matthew and Granger, 1925

Type species: *Palaeostylops iturus* Matthew and Granger, 1925; Gashatan (late Paleocene), Gashato (Mongolia).

Palaeostylops iturus Matthew and Granger, 1925

Figs. 3, 4; Table 2.

Referred material: 204 jaw fragments, isolated teeth and identifiable fragmentary teeth.

Discussion.—*Palaeostylops* is a typical taxon at Gashatan fossil mammal sites, and is by far the most abundant taxon in the Subeng fauna. Originally, two species of *Palaeostylops* were described, *P. iturus* and *P. macrodon*, with the latter differing from the former by the larger size of the cheek teeth, and the comparatively enlarged second molars (Matthew et al. 1929). Cifelli et al. (1989) reported that *P. macrodon* differed further from *P. iturus* by having cusps on the lingual cingula of the upper molars, by the weakness or absence of a sulcus separating the lingual cusps on M1, and by the number of upper incisors and the curvature of the snout; these authors placed *P. macrodon* in a new monotypic genus “*Gashatostylops*”. However, the cusps on the lingual cingulum are variably developed in both *P. iturus* and *P. macrodon*, and a strong sulcus separating the lingual cusps is known in only one specimen of *P. iturus* (AMNH 20415). Moreover, the alleged differences in the number of upper incisors and the curvature of the snout cannot be evaluated because well-preserved complete rostra are unavailable for both species, and thus their value as a generic difference is limited (Kondrashov and Lucas 2004a). Several authors have since suggested that the validity of “*Gashatostylops*” is weakly supported and considered it a junior subjective synonym (Meng et al. 1998; Kondrashov and Lucas 2004a).

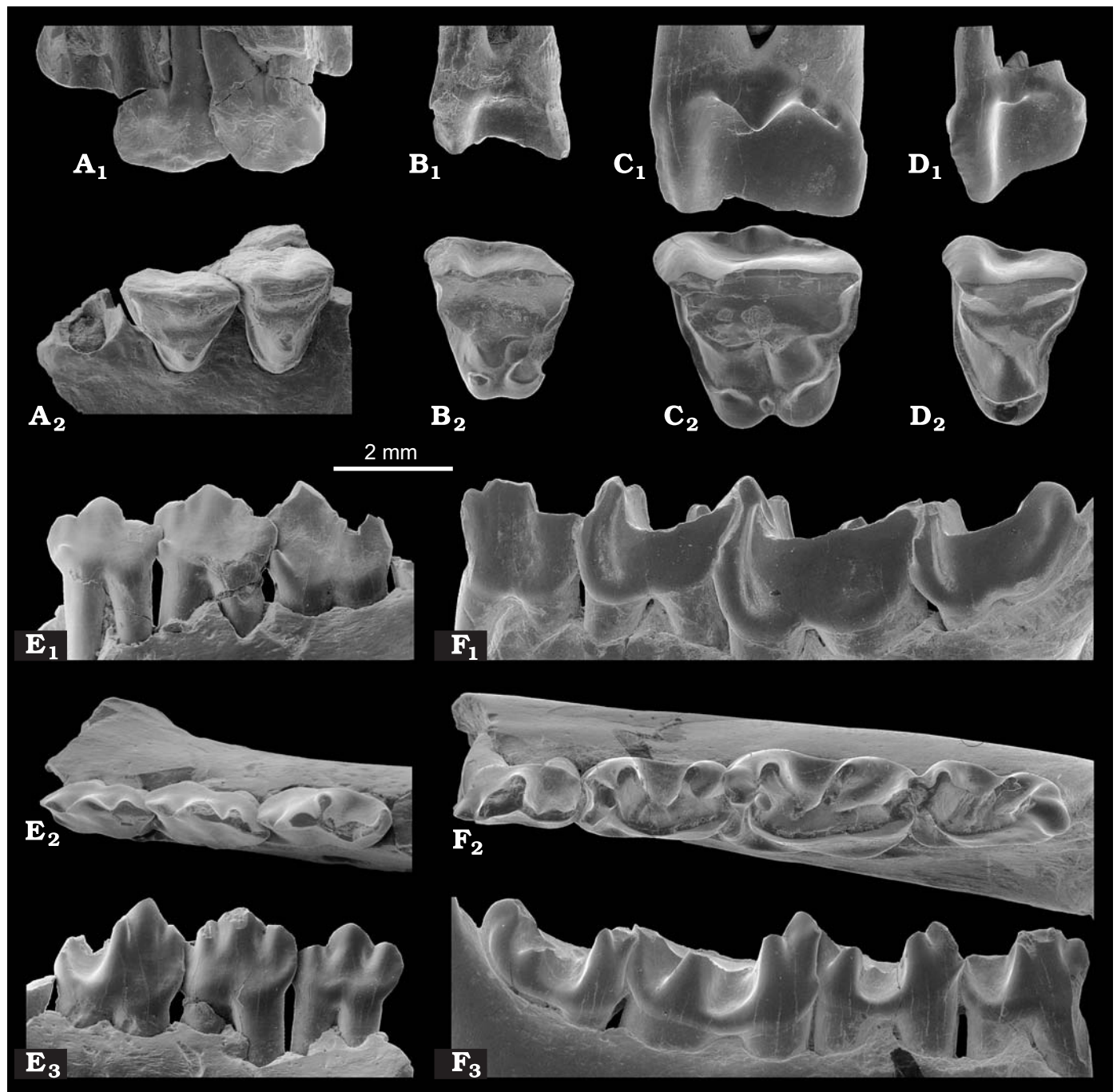


Fig. 3. The gliriform *Palaeostylops iturus* Matthew and Granger, 1925, from the Gashatan (Paleocene) of Subeng, China, in labial (A_1 – F_1), occlusal (A_2 – F_2), and lingual (A_3 – F_3) views. **A.** IMM-2004-SB-021, left maxillary fragment with P3–4. **B.** IMM-2001-SB-024, LM1. **C.** IMM-2004-SB-022, LM2. **D.** IMM-2004-SB-023, LM3. **E.** IMM-2004-SB-024, left incomplete dentary with p2–4. **F.** IMM-2004-SB-025, left incomplete dentary with p4–m3. SEM micrographs.

At the Subeng site, both morphology and size indicate that only a single form is present. Comparisons with the type specimens of both species clearly support referral of all Subeng arctostylopid specimens to *P. iturus*, and none of the available specimens shows the relatively enlarged second molar typical of *P. macrodon*. Table 2 and Fig. 4 show the measurements of the *Palaeostylops* cheek teeth from Subeng, and compare these to the extensive measurements

modified after Kondrashov and Lucas (2004; personal communication with Peter Kondrashov, 27/07/2007). The mean values and the size ranges of the Subeng *Palaeostylops* teeth are very close to those reported for *P. iturus*, and are clearly different from those reported for *P. macrodon*. The low variation of measurements within the Subeng sample indicates the presence of only one species. Nevertheless, we note the presence of variably developed lingual cuspules on M1 and

Table 2. Measurements in mm of *Palaeostylops iturus* cheek teeth from Subeng, and their comparison with those of *P. iturus* and *P. macrodon* from other sites (modified after Kondrashov and Lucas 2004a; personal communication with Peter Kondrashov, 27/07/2007). Note similarities in dimensions at each locus among the specimens referred to *P. iturus*, and differences with dimensions at homologous loci in *P. macrodon*. Abbreviations: L, anteroposterior length; W, transverse width; min., minimum value; max., maximum value; n, number of measured specimens.

		Subeng		Kondrashov and Lucas (2004a)			
		<i>Palaeostylops iturus</i>		<i>Palaeostylops iturus</i>		<i>Palaeostylops macrodon</i>	
		L	W	L	W	L	W
p4	min.	2.0	1.0	2.1	1.0	2.4	1.1
	mean	2.25	1.10	2.35	1.13	2.67	1.36
	max.	2.4	1.4	2.7	1.3	2.9	1.7
	n	21	21	21	18	7	6
m1	min.	2.3	1.1	2.4	1.0	3.2	1.2
	mean	2.65	1.38	2.78	1.33	3.46	1.54
	max.	2.8	1.5	3.2	1.5	3.8	1.8
	n	21	20	19	18	8	6
m2	min.	3.3	1.6	3.0	1.4	4.1	1.7
	mean	3.50	1.75	3.39	1.74	4.69	1.96
	max.	3.7	1.9	3.7	2.1	5.2	2.2
	n	10	11	21	21	20	20
m3	min.	2.5	1.2	2.3	1.2	2.5	6
	mean	2.76	1.35	2.74	1.37	2.93	6
	max.	3.0	1.5	3.3	1.6	3.4	6
	n	8	8	17	17	6	6
P4	min.	1.9	2.1	1.6	1.5	2.0	6
	mean	2.04	2.24	2.06	2.17	2.13	6
	max.	2.2	2.5	2.5	2.6	2.2	6
	n	7	7	18	18	6	6
M1	min.	2.5	2.8	2.2	2.3	2.6	6
	mean	2.60	2.90	2.75	2.92	3.01	6
	max.	2.8	3.0	3.1	3.3	3.4	6
	n	7	7	21	21	9	6
M2	min.	3.5	3.6	3.1	2.9	4.4	6
	mean	3.73	3.78	3.67	3.58	4.62	6
	max.	3.9	4.0	4.1	4.1	5.3	6
	n	6	6	20	19	10	6
M3	min.	2.1	2.7	1.9	2.3	2.2	6
	mean	2.27	3.04	2.17	3.00	2.40	6
	max.	2.6	3.4	2.5	3.5	2.6	6
	n	7	5	14	15	6	6

M2, and the absence or weak development of a sulcus separating the lingual cusps on M1. The Subeng specimens therefore weaken morphological distinctions between *Palaeo-*

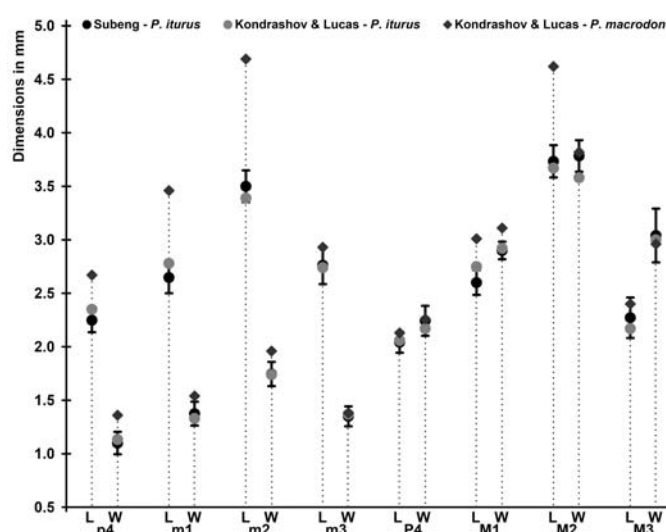


Fig. 4. Dental measurements of *Palaeostylops iturus* Matthew and Granger, 1929, from the Gashatan of Subeng (black circles) compared to those of *P. iturus* (light grey circles) and *Palaeostylops macrodon* Matthew, Granger, and Simpson, 1929 (dark grey diamonds), modified after Kondrashov and Lucas (2004a). The graph illustrates the similar sizes of both *P. iturus* samples, and their size difference from *P. macrodon*. L, anteroposterior length. W, transverse width. Error bars on the Subeng measurements are 1 standard deviation.

stylops iturus and *P. macrodon* suggested by Cifelli et al. (1989) to justify generic distinctions, and we continue to consider both species member of one genus *Palaeostylops*.

Stratigraphic and geographic range.—*Palaeostylops iturus* is typical for the Gashatan (late Paleocene). *P. iturus* is known from Member I of the Gashato Formation and from the Zhigden and Naran Member of the Naran Bulak Formation (Mongolia); and from the Nomogen Formation at Nomogen, Bayan Ulan and Subeng (Inner Mongolia, China).

Family Pseudictopidae Sulimski, 1968

Genus *Pseudictops* Matthew, Granger, and Simpson, 1929

Type species: *Pseudictops lophiodon* Matthew, Granger and Simpson, 1929; Gashatan (late Paleocene), Gashato (Mongolia).

Pseudictops lophiodon Matthew, Granger, and Simpson, 1929

Figs. 5, 6.

Referred material: IMM-2001-SB-025, right I3; IMM-2001-SB-026, left calcaneum; IMM-2004-SB-026, right P1; IMM-2004-SB-027, left calcaneum.

Discussion.—Specimens of *P. lophiodon* are common in Gashatan mammal faunas, and Russell and Zhai (1987) have previously reported *P. lophiodon* at Subeng. Although *P. lophiodon* is not abundant in our collection, we can confirm its presence at the Subeng site. Sulimski (1968) provided a comprehensive overview of the morphology of *Pseudictops*. Based on our specimens, we concur with his description and

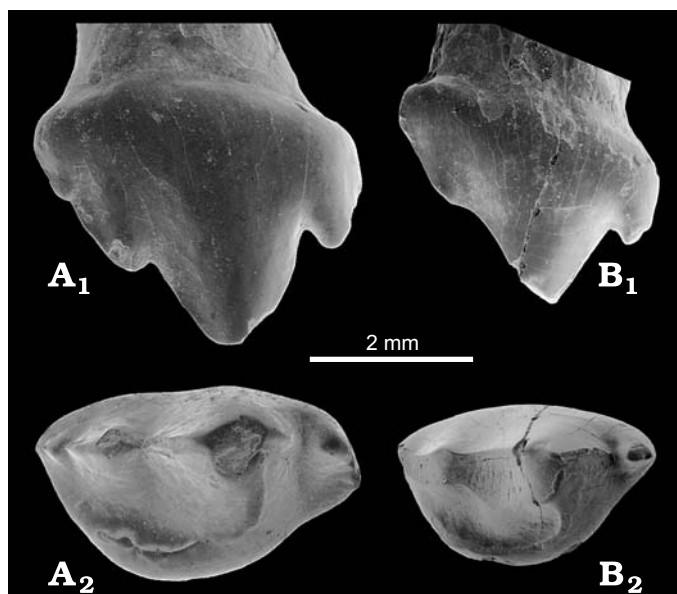


Fig. 5. The gliriform *Pseudictops lophiodon* Matthew, Granger, and Simpson, 1929, from the Gashatan (Paleocene) of Subeng, China, in labial (A₁, B₁) and occlusal (A₂, B₂) views. A. IMM-2004-SB-026, RP1. B. IMM-2001-SB-025, RI3. SEM micrographs.

interpretation, and provide further illustrations of the new specimens of this much discussed taxon.

Stratigraphic and geographic range.—*Pseudictops lophiodon* is typical for the Gashatan (late Paleocene). *P. lophiodon* is known from Member I of the Gashato Formation and from the Zhigden and Naran Member of the Naran Bulak Formation (Mongolia); and from the Nomogen Formation (Inner Mongolia, China).

Grandorder Glires Linnaeus, 1758

Mirorder Simplicidentata Weber, 1904

Order Mixodontia Sych, 1971

Family Eurymylidae Matthew, Granger, and Simpson, 1929

Genus *Eomylus* Dashzeveg and Russell, 1988

Type species: *Eomylus zhigdenensis* Dashzeveg and Russell, 1988; Gashatan (late Paleocene), Tsagan Khushu (Mongolia).

Eomylus bayanulanensis Meng, Wyss, Hu, Wang, Bowen, and Koch, 2005

Fig. 7.

Referred material: IMM-2001-SB-027, right m1; IMM-2001-SB-028, right m1; IMM-2001-SB-029, left M2; IMM-2001-SB-030, left m3; IMM-2001-SB-031, left M2; IMM-2001-SB-032, right m2; IMM-2001-SB-033; right DP4; IMM-2004-SB-028, left M1; IMM-2004-SB-029, left P3; IMM-2004-SB-030, right dp4; IMM-2004-SB-031, left P3; IMM-2004-SB-032, right M2.

Description.—Based on comparable size and morphology, and on comparison with related taxa, we were able to identify the previously unknown P3, DP4 and dp4 of *Eomylus bayanulanensis*. The P3 (Fig. 7A) has a simple, ellipsoid shape with two roots and two main cusps of subequal size in unworn specimens. A low ectocingulum with two weak stylar cusps, and a small hypocone can also be distinguished. A similar P3 morphology is known for other basal Glires such as *Mimotona*, *Eurymylus*, *Heomys*, and *Sinomylus* (Dashzeveg and Russell 1988; Meng et al. 2003), but the antero-posteriorly short crown, the little expanded hypoconal shelf, and the lingual position of the hypocone are more typical of the upper molars of *Eomylus*.

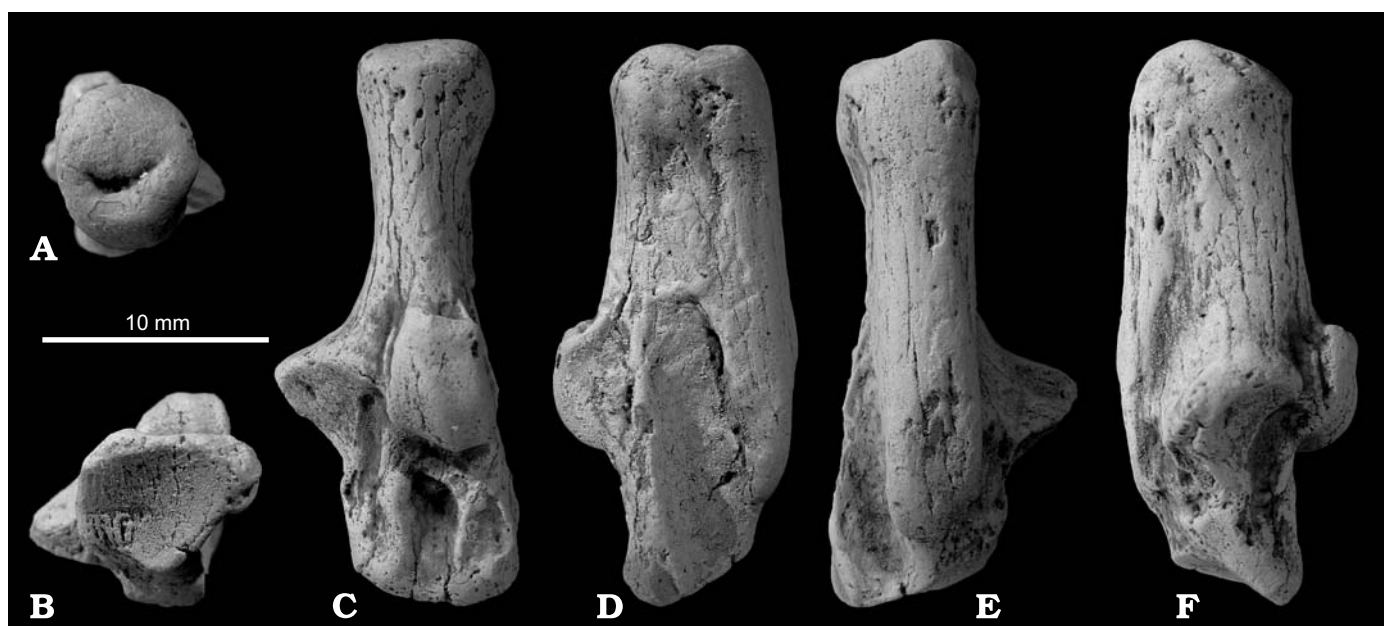


Fig. 6. The gliriform *Pseudictops lophiodon* Matthew, Granger, and Simpson, 1929, from the Gashatan (Paleocene) of Subeng, China. IMM-2004-SB-027, left calcaneum in proximal (A), distal (B), dorsal (C), lateral (D), ventral (E), and medial (F) views.

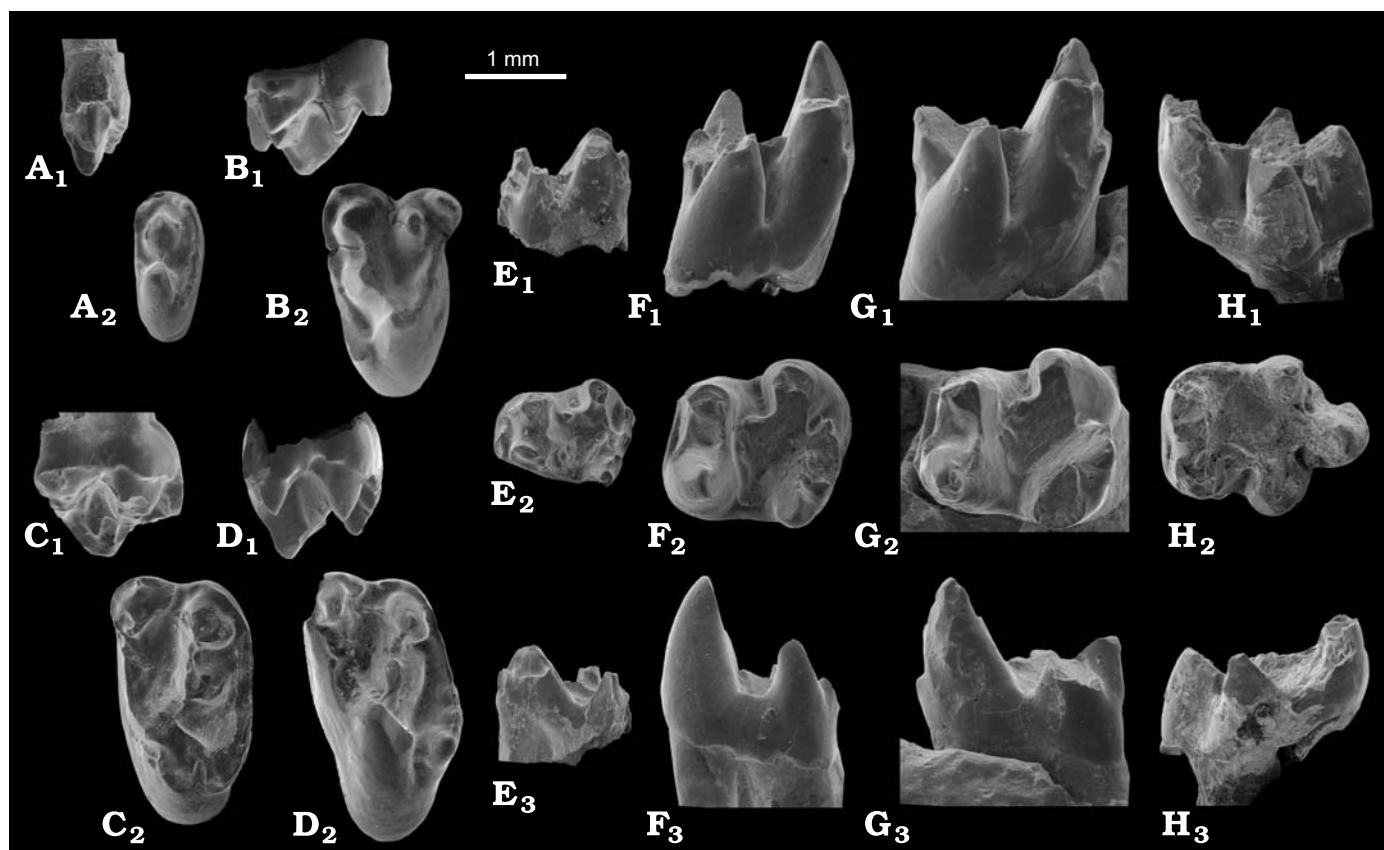


Fig. 7. The eurymylid *Eomylus bayanulanensis* Meng, Wyss, Hu, Wang, Bowen, and Koch, 2005, from the Gashatan (Paleocene) of Subeng, China, in labial (A₁–H₁), occlusal (A₂–H₂), and lingual (A₃–H₃) views. A. IMM-2004-SB-031, LP3. B. IMM-2001-SB-033, RDP4. C. IMM-2004-SB-028, LM1. D. IMM-2001-SB-031, LM2. E. IMM-2004-SB-030, Rdp4. F. IMM-2001-SB-028, Rm1. G. IMM-2001-SB-032, right dentary fragment with m2. H. IMM-2001-SB-030, Lm3. SEM micrographs.

IMM-2001-SB-033 is identified as a DP4 (Fig. 7B). The general shape of the crown is triangular, and the tooth bears two labial roots and one lingual root. A narrow, bilobed stylar shelf is present, with a large anterior and small posterior stylar cusp. The paracone is small and anteroposteriorly compressed, whereas the metacone is more massive and slightly taller. The preprotocrista forms the anterior border of the tooth and runs toward the anterior stylar cusp. The paraconule is only weakly developed. The postprotocrista is directed toward the metacone and supports a prominent metaconule. The protocone is well developed. The protocone, hypocone and metaconule all exhibit the posterior wear facets also seen in *Eomylus zhigdenensis* and *E. bayanulanensis*. The hypocone is small and is slightly more lingually placed than the protocone.

IMM-2004-SB-030 (Fig. 7E) is identifiable as the dp4 of *E. bayanulanensis*. It is similar to the p4 of *E. borealis*, but differs in having a small, anterior paraconid and a wider, fully developed talonid with a mesoconid and much better developed hypoconid.

Discussion.—The identification of the species of the Gashatan genus *Eomylus* has been problematic (Kondrashov and Lopatin 2003), but three species are currently recognized (Meng et al. 2005). *E. borealis* and *E. bayanulanensis* come from two sites in Inner Mongolia, Nomogen and Bayan Ulan

respectively, while the type species, *E. zhigdenensis*, comes from the Mongolian Tsagan Khushu locality. The new specimens from Subeng more closely resemble the teeth of *E. bayanulanensis*, clearly demonstrating its presence at the Subeng site. The lower molars from Subeng have the marked hypoconid and diagonal wear trough typical of *Eomylus* (Meng et al. 2005), and the partial anterior cingulid and the less transverse crown typical of *E. bayanulanensis*. The upper molars possess a large hypocone and metaconule, and weak unilateral hypsodonty, features that are characteristic of the upper teeth of *E. bayanulanensis* (Meng et al. 2005).

Stratigraphic and geographic range.—*Eomylus bayanulanensis* is known from the Gashatan (late Paleocene) Nomogen Formation at Bayan Ulan and Subeng in Inner Mongolia, China.

Order Rodentia Bowdich, 1821

Family Alagomyidae Dashzeveg, 1990

Genus *Tribosphenomys* Meng, Wyss, Dawson, and Zhai, 1994

Type species: *Tribosphenomys minutus* Meng, Wyss, Dawson, and Zhai, 1994; Gashatan (late Paleocene), Bayan Ulan (Inner Mongolia, China).

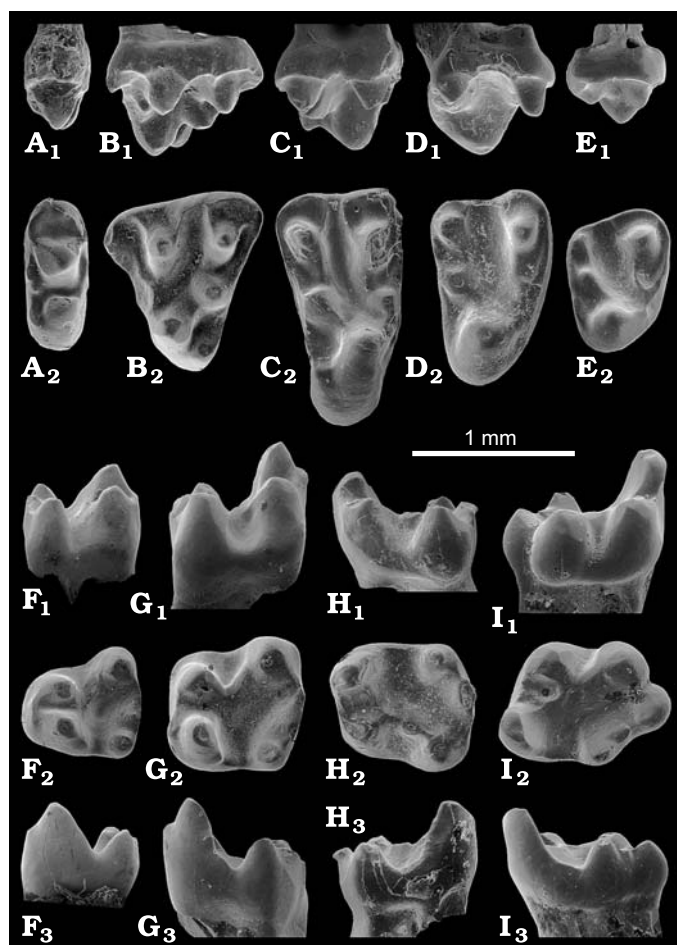


Fig. 8. The alagomyid *Tribosphenomys minutus* Meng, Wyss, Dawson, and Zhai, 1994, from the Gashatan (Paleocene) of Subeng, China, in labial (A₁–I₁), occlusal (A₂–I₂), and lingual (A₃–I₃) views. A. IMM-2001-SB-036, RP4. B. IMM-2001-SB-037, LDP4. C. IMM-2004-SB-033, RM1. D. IMM-2001-SB-035, RM2. E. IMM-2001-SB-034, RM3. F. IMM-2001-SB-038, Rdp4. G. IMM-2001-SB-039, Rm1. H. IMM-2001-SB-040, Lm2. I. IMM-2001-SB-041, Rm3. SEM micrographs.

Tribosphenomys minutus Meng, Wyss, Dawson, and Zhai, 1994

Fig. 8.

Referred material: 39 isolated teeth and identifiable fragmentary teeth.

Discussion.—Recently, an exhaustive study of the Alagomyidae from Subeng was published (Meng, Ni et al. 2007), identifying three different alagomyids at Subeng: *Tribosphenomys minutus*, *Tribosphenomys* cf. *T. secundus* and the new taxon *Neimengomys qii*. Based on both morphology and size, all material collected by us is identified here as *T. minutus* and our observations on the dental morphology and variability of *T. minutus* from Subeng confirms their results. However, not a single specimen in our collections can be attributed to one of the other alagomyids reported from Subeng. This difference is possibly because our specimens were collected from a single, precise level (Van Itterbeeck et al. 2007) which may be different than that screen-washed by Meng

and co-workers, although no detailed information was published on this (Meng, Ni et al. 2007).

Stratigraphic and geographic range.—*Tribosphenomys minutus* is known from the Gashatan (late Paleocene) Nomogen Formation at Bayan Ulan and Subeng and the Zhigden Member of the Naran Bulak Formation at Tsagan Khushu (Mongolia).

Superorder Insectivora Bowdich, 1821

Order Lipotyphla Haeckel, 1866

Suborder Soricomorpha Gregory, 1910

Family Nyctitheriidae Simpson, 1928

Subfamily Asionyctiinae Missiaen and Smith, 2005

Genus *Asionyctia* Missiaen and Smith, 2005

Type species: *Asionyctia guoi* Missiaen and Smith, 2005; Gashatan (late Paleocene), Subeng (Inner Mongolia, China).

Asionyctia guoi Missiaen and Smith, 2005

Referred material: 132 jaw fragments, isolated teeth, and identifiable fragmentary teeth.

Discussion.—The nyctitheriid *Asionyctia guoi*, previously described from Subeng, is the type genus for the Asionyctiinae, an endemic Asian subfamily of Nyctitheriidae (Missiaen and Smith 2005). Since its publication, a few additional specimens have been identified, yielding a new total of 132 specimens. This makes *A. guoi* one of the most abundant species at Subeng, second only to *Palaeostylops iturus*, but does not add significant new morphological information.

Stratigraphic and geographic range.—*Asionyctia guoi* is currently only known from the Gashatan (late Paleocene) Nomogen Formation at Subeng (Inner Mongolia, China).

Subfamily Praolestinae Lopatin, 2006

Genus *Bumbanius* Russell and Dashzeveg, 1986

Type species: *Bumbanius rarus* Russell and Dashzeveg, 1986; Bumbanian (early Eocene), Tsagan Khushu (Mongolia).

Bumbanius ningi sp. nov.

Fig. 9; Table 3.

Etymology: In honour of Ning Pei Jie, manager of the Erlian Dinosaur Museum, in Erlianhot (Inner Mongolia, China), who guided and assisted us during fieldwork in the Subeng area since 1995.

Holotype: IMM-2004-SB-034, right M1?

Type locality: Subeng, Inner Mongolia, China.

Type horizon: upper part of the Nomogen Formation, Gashatan (late Paleocene).

Referred material: IMM-2001-SB-042, right p4; IMM-2001-SB-043, left m2; IMM-2001-SB-044, right m3; IMM-2001-SB-045, left m1; IMM-2001-SB-046, left m3; IMM-2001-SB-047, left m3; IMM-2001-SB-048, right M1 or M2; IMM-2001-SB-049, fragmentary right M2?; IMM-2001-SB-050, right M1 or M2; IMM-2004-SB-035, right M1 or M2; IMM-2004-SB-036, right M3; IMM-2004-SB-037, right p4; IMM-2004-SB-038, right p4; IMM-2004-SB-039, right m1; IMM-2004-SB-040, left m3; IMM-2004-SB-041, right m2; IMM-2004-SB-042, right m2; IMM-2004-SB-043, left M1?; IMM-2004-SB-044, right p4.

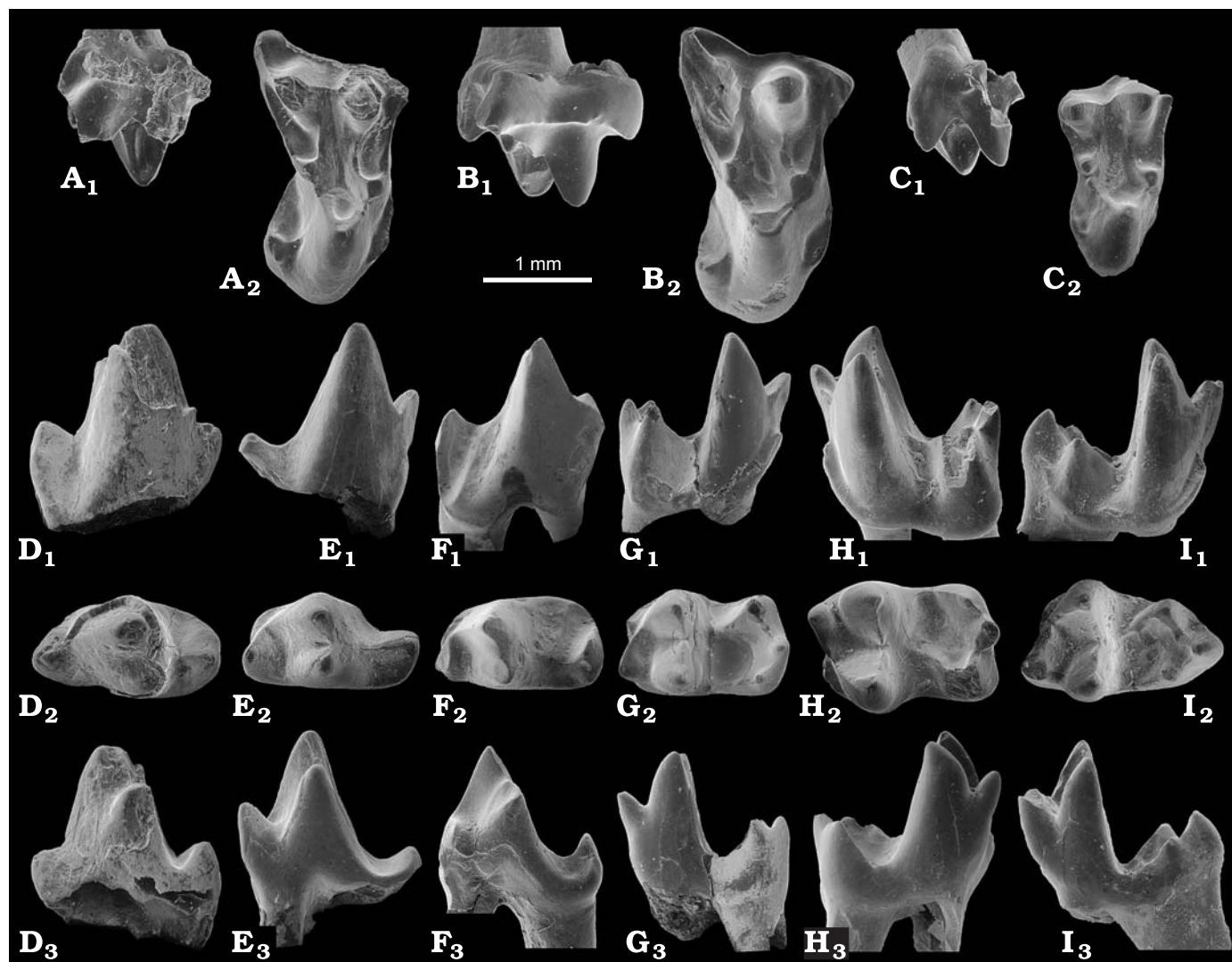


Fig. 9. The nyctitheriid *Bumbanius ningi* sp. nov., from the Gashatan (Paleocene) of Subeng, China, in labial (A₁–I₁), occlusal (A₂–I₂), and lingual (A₃–I₃) views. A. IMM-2004-SB-035, RM1 or M2. B. IMM-2004-SB-034 (holotype), RM1?. C. IMM-2004-SB-036, RM3. D. IMM-2004-SB-037, Rp4. E. IMM-2004-SB-038, Rp4. F. IMM-2001-SB-042, Rp4. G. IMM-2004-SB-039, Rm1. H. IMM-2001-SB-043, Lm2. I. IMM-2001-SB-044, Rm3. SEM micrographs.

Diagnosis.—Praolestine nyctitheriid similar in size to *Bumbanius rarus*. Differs from *B. rarus* by the taller trigonid on lower molars, the more pronounced hypoconulid on m3 and the more transversely expanded upper molars. Differs from *Praolestes* by the lower position of the paraconid on p4 and by the less transversely expanded upper molars with strong conules and conule crests. Differs from all other Praolestinae by the expanded talon shelf with large hypocone.

Description.—The upper molars (Fig. 9A, B) have a transversely expanded crown with generally well-developed cusps and crests. The stylar shelf is narrow and lacks cusps. The paracone and metacone are equally robust, closely spaced and slightly fused at the base. The paraconule and metaconule are both well developed, with the paraconule slightly the more robust. The conule wings and pre- and postprotocrista all are clearly present on the upper molars. The protocone is about the same height as the paracone and metacone, but is the most massive molar cusp. A narrow precingulum is present, as well

as a relatively wide postcingulum with a rounded posterior border and a prominent hypocone. Because the M1 and M2 of Praolestinae have a similar structure (Lopatin 2006), and the upper molars available to us are all isolated and similar in form, it is difficult to differentiate M1 and M2 with certainty, although the holotype specimen probably represents an M1 based on the anteriorly directed parastyle and the shallow ectoflexus.

The M3 (Fig. 9C) is moderately smaller than the preceding molars, with a reduced stylar shelf and lower paracone and metacone. The conules and associated crests are reduced, the precingulum is absent and the postcingulum is much smaller with only a faint trace of a hypocone.

None of the referred p4s is complete, but the available specimens (Fig. 9D–F) suggest that p4 is relatively large and semimolariform. The paraconid projects anteriorly and bears a small precingulid. The protoconid is the main trigonid cusp, with the smaller metaconid closely appressed to it and

somewhat more posterior in position. The talonid is simple, consisting only of a single talonid cusp.

The m1 (Fig. 9G) has a moderately tall trigonid in which the metaconid is slightly more robust and higher than the protoconid. The paraconid arises from high on the metaconid and slightly labial to it, and is connected to the protoconid by a strong paracristid. The anterior side of the paracristid bears a moderate precingulid. The oblique crest connects the hypoconid to the middle of the trigonid wall, but does not rise high onto it. All three talonid cusps are subequal in height but the hypoconid is the most robust. The apex of the entoconid is displaced slightly posterolabially toward the hypoconulid, forming a more rounded posterolingual edge to the talonid. In contrast, the labially protruding hypoconid forms a more acute angle.

The m2 (Fig. 9H) is the largest lower molar, with a more anteroposteriorly compressed trigonid than m1. The m3 (Fig. 9I) is narrower than m2 and only slightly longer; it supports a small hypoconulid lobe, and the crests running from the hypoconid and entoconid toward the hypoconulid variably curve toward one another and fuse before reaching the hypoconulid.

Discussion.—*Bumbanius ningi* sp. nov. described here strongly resembles the type species *Bumbanius rarus* from the early Eocene of Mongolia in having well-developed cusps and crests on the upper molars, a narrow labial cingulum, and in the presence of both a pre- and postcingulum. The lower cheek teeth of *B. ningi* resemble those of *B. rarus* in the precingulid, the large metaconid, the strong hypoconid and the U-shaped notch in the entocristid. *B. ningi* differs from *B. rarus*, however, in having more transversely elongated upper molars and a better-developed postcingulum and hypocone, in the slightly taller molar trigonids, with a higher

positioned paraconid, and in the stronger hypoconulid lobe on m3 (Russell and Dashzeveg 1986).

The genera *Bumbanius* and *Praolestes* have been grouped in the subfamily Praolestinae (Lopatin 2006). *B. ningi* resembles *Praolestes* in the semimolariform p4, in the anteroposteriorly short molar trigonids that are dominated by the high, large protoconid and metaconid, and in the shape of the postcristid on m3. Important features distinguishing *B. ningi* from *Praolestes* are the strong conules and the large talon and hypocone on the upper molars, and the large p4. Because of the clear and discrete nature of the latter differences, we assign our new specimens to a new species of *Bumbanius* rather than a new species of *Praolestes*. However, *B. ningi* is a morphological intermediate between *B. rarus* and *Praolestes*, considering the transverse length of the upper molars, the position of the paraconid on p4, the height of the lower molar trigonid and the expression of the hypoconulid lobe on m3. The discovery of such an intermediate form is an additional reason for grouping the two genera together and we suggest that *B. ningi* is more primitive predecessor to the Eocene *B. rarus*.

Superorder Ferae Linnaeus, 1785

Mirorder Cimolesta McKenna, 1975

Family Sarcodontidae Lopatin and Kondrashov, 2004 new rank

Type genus: *Sarcodon* Matthew and Granger, 1925.

Genera included: *Carnilestes* Wang and Zhai, 1995; *Hyracolestes* Matthew and Granger, 1925; *Metasarcodon* Lopatin, 2006; *Prosarcodon* McKenna, Xue, and Zhou 1984.

Revised diagnosis.—Small to medium-sized insectivores, characterised by the presence of only two lower and two upper molars with a straight centrocrista, and by a dentition with a carnassial tendency. Incisors small, canines large and caniniform. Premolariform p4, with a relatively strong metaconid and a short talonid with only one cusp. The p4 and lower molars characterised by a high trigonid with a strong paracristid and a weak to absent precingulid. Premolariform P4. Long, prominent metastylar crest on P4 and M1. Postcingulum very small to absent on P4 and M2, but relatively well-developed on M1. Upper molars transversely elongated, with twinned paracone and metacone, and developed conules.

Remarks.—The subfamily Sarcodontinae was named by Lopatin and Kondrashov (2004) to include *Sarcodon*, *Prosarcodon*, *Metasarcodon*, *Carnilestes* and, tentatively, *Hyracolestes*. We confirm the inclusion of *Hyracolestes* in this group, and moreover we elevate Sarcodontinae to family rank. We consider Sarcodontidae a natural group, clearly different from Micropternodontidae with which they were previously allied (Van Valen 1967; McKenna and Bell 1997). Sarcodontidae are present in Asia from the earliest Paleocene until the middle Eocene, and are characterised by having only two molars and by the absence of a hypocone shelf on P4 and M2. Conversely, Micropternodontidae only appear in the middle Eocene, and have three molars and a hypocone shelf on P4 and the upper molars. After their separation from micropternodontids, we

Table 3. Measurements of *Bumbanius ningi* sp. nov. from the Gashatan of Subeng. Hyphen designates dimensions that could not be measured.

	Position	Length (mm)	Width (mm)
IMM-2004-SB-034	M1?	1.70	2.75
IMM-2004-SB-043	M1?	1.65	2.55
IMM-2001-SB-049	M(1.2)	1.50	—
IMM-2001-SB-050	M(1.2)	—	2.40
IMM-2004-SB-035	M(1.2)	—	2.55
IMM-2001-SB-042	p4	1.60	0.80
IMM-2004-SB-037	p4	1.88	1.03
IMM-2004-SB-038	p4	1.70	0.90
IMM-2001-SB-045	m1	1.90	1.13
IMM-2004-SB-039	m1	1.70	0.97
IMM-2001-SB-043	m2	1.75	1.25
IMM-2004-SB-041	m2	1.70	1.20
IMM-2004-SB-042	m2	—	1.20
IMM-2001-SB-044	m3	1.86	1.11
IMM-2001-SB-046	m3	1.85	1.10
IMM-2001-SB-047	m3	1.90	1.20
IMM-2004-SB-040	m3	1.78	1.08

see no reason to continue to place sarcodontids in Soricomorpha. Instead, Sarcodontidae resemble cimolestans such as didymoconids, wyolestids, cimolestids and palaeoryctids, in the large, caniniform canines, in the transversely elongated upper molars with partially fused paracone and metacone, and in the high trigonid on the lower molars. They specifically resemble Didymoconidae in having only two molars. The lower molars of sarcodontids resemble those of Wyolestidae in the anteriorly placed paraconid, and those of Wyolestidae and Cimolestidae in the well-developed talonid cusps. Finally, they also resemble Palaeoryctidae by the strong metastylar crest on the upper cheek teeth, and by basicranial characters already noted by Butler (1988). Based on this, we consider Sarcodontidae as members of Cimolesta, with uncertain ordinal affinities.

Genus *Hyracolestes* Matthew and Granger, 1925

Type species: Hyracolestes ermineus Matthew and Granger, 1925; Gashatan (late Paleocene), Gashato (Mongolia).

Hyracolestes ermineus Matthew and Granger, 1925

Fig. 10.

Referred material: IMM-2001-SB-051, right m2; IMM-2004-SB-045, right m1; IMM-2004-SB-046, right m2 fragment; IMM-2004-SB-047 left m2.

Description.—*Hyracolestes* is a poorly known taxon, based on very sparse material. The lower jaw has only six post-canine tooth loci, usually interpreted as p4 to m2, but only the supposed p3–m1 positions have been published (Szalay and McKenna 1971; Meng et al. 1998; Lopatin and Kondrashov 2004; Lopatin 2006). Collectively, the specimens from Subeng document the m1 position of *Hyracolestes ermineus* (Fig. 10A), and the previously unpublished ultimate tooth.

The m2 of *H. ermineus* (Fig. 10B) is markedly larger than m1, as would be expected based on the size of the alveoli for this position in the holotype. It resembles m1 in having a high trigonid, an anteriorly projecting paraconid with a strong paracristid, and a trigonid that is wide open lingually. The anterolabial cingulum is poorly developed. Although the protoconid is broken, it was clearly taller than the metaconid, and in this respect the morphology of m2 is closer to that of p4 than to that of m1. The m2 metaconid is positioned slightly more anteriorly than it is in m1. The talonid is low, shorter and narrower than the trigonid, and the oblique crest is very low. The entoconid is the smallest talonid cusp, the hypoconid and hypoconulid have about the same width but the hypoconulid is notably taller. The hypoconulid is set off posteriorly, but does not form a separate lobe. The talonid basin is open lingually.

Discussion.—*Hyracolestes* has had a confusing taxonomic history, but the genus was recently tentatively placed in an endemic Asian subfamily, the Sarcodontinae, based on its similarities to *Sarcodon* (Lopatin and Kondrashov 2004). The m2 of *Hyracolestes* is similar to that of *S. pygmaeus* and thus supports this phylogenetic placement. As is the case for m1, the m2 of *Hyracolestes* differs from that of *S. pygmaeus*

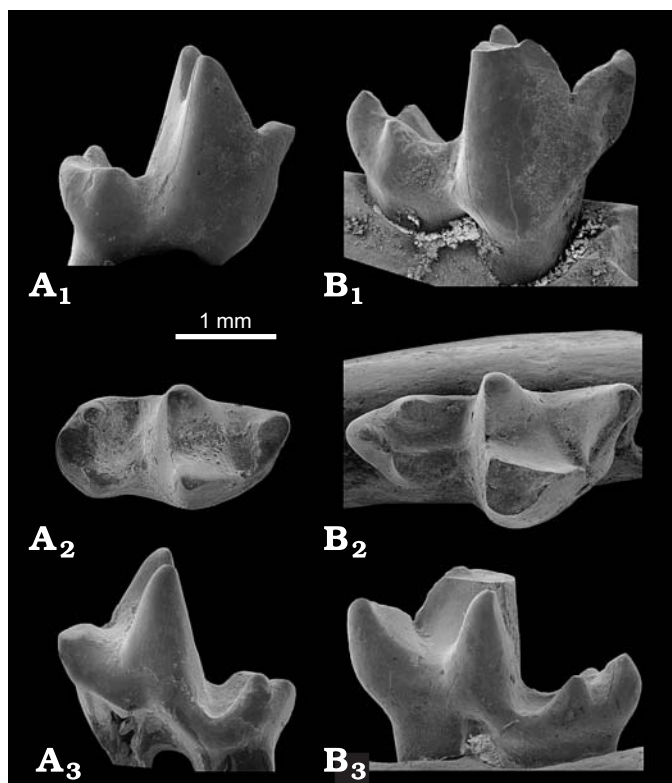


Fig. 10. The sarcodontid *Hyracolestes ermineus* Matthew and Granger, 1925, from the Gashatan (Paleocene) of Subeng, China, in labial (A₁, B₁), occlusal (A₂, B₂), and lingual (A₃, B₃) views. A. IMM-2004-SB-032, Rm1. B. IMM-2001-SB-051, right dentary fragment with m2. SEM micrographs.

by the more anteroposteriorly expanded trigonid and the lingually open talonid, and from other Sarcodontinae also by the very weak anterolabial cingulum.

Stratigraphic and geographic range.—*Hyracolestes ermineus* is typical for the Gashatan (late Paleocene), and is known from Member I of the Gashato Formation and from the Zhigden Member of the Naran Bulak Formation (Mongolia); and from the Nomogen Formation at Bayan Ulan and Subeng (Inner Mongolia, China).

Order Didelphodonta McKenna, 1975

Family Cimolestidae Marsh, 1889

Genus *Tsaganianus* Russell and Dashzeveg, 1986

Fig. 11.

Type species: Tsaganianus ambiguus Russell and Dashzeveg, 1986; Bumbanian (early Eocene), Tsagan Khushu (Mongolia).

Tsaganianus ambiguus Russell and Dashzeveg, 1986

Referred material: IMM-2001-SB-052, partial right M1 or M2; IMM-2001-SB-053, right P4; IMM-2001-SB-054, partial right M1 or M2; IMM-2001-SB-055, partial left P4; IMM-2001-SB-056, partial right M1 or M2; IMM-2001-SB-057, right M1 or M2; IMM-2001-SB-058, left p4; IMM-2004-SB-048, right dp4; IMM-2004-SB-049, left jaw fragment with partial m2 and complete m3; IMM-2004-SB-050, right m3.

Description.—The P4 (Fig. 11A) of *Tsaganianus* was previously unknown. The crown is semimolariform, with a slen-

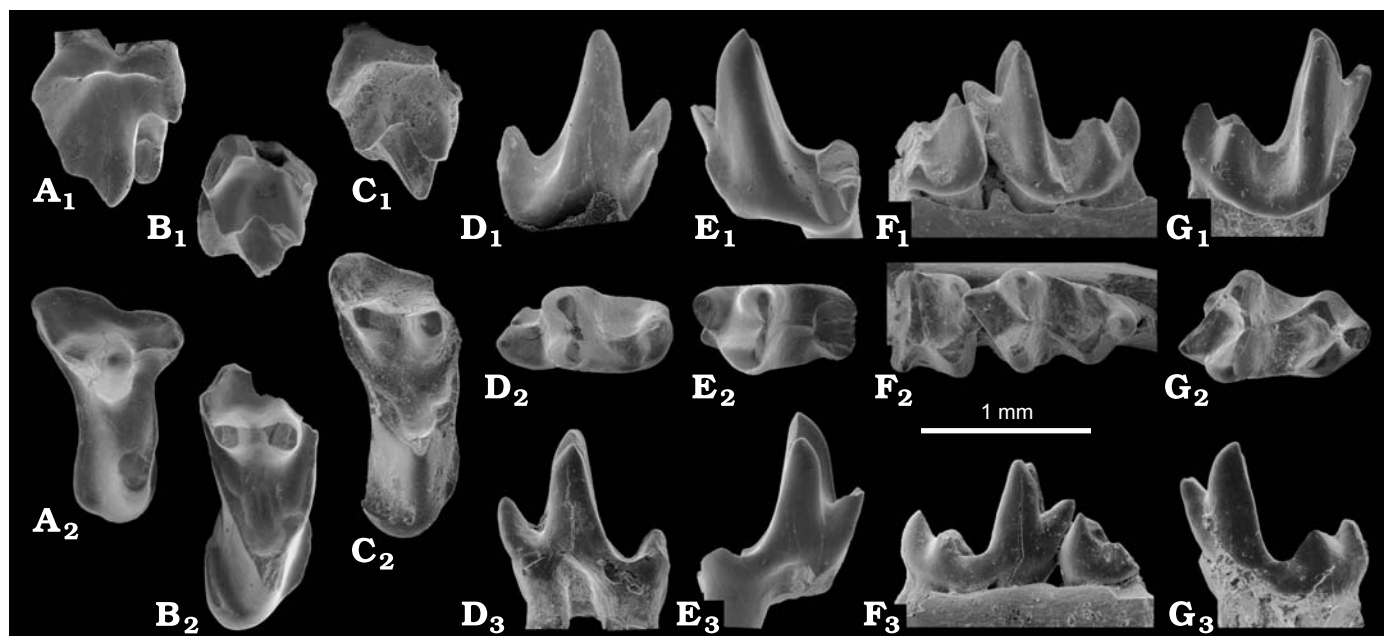


Fig. 11. The cimolestid *Tsaganianus ambiguus* Russell and Dashzeveg, 1986, from the Gashatan (Paleocene) of Subeng, China, in labial (A₁–G₁), occlusal (A₂–G₂), and lingual (A₃–G₃) views. **A.** IMM-2001-SB-053, RP4. **B.** IMM-2001-SB-052, RM1 or M2. **C.** IMM-2001-SB-054, RM1 or M2. **D.** IMM-2004-SB-048, Rdp4. **E.** IMM-2001-SB-058, Lp4. **F.** IMM-2004-SB-049, left dentary fragment with m3 and incomplete m2. **G.** IMM-2004-SB-050, Rm3. SEM micrographs.

der metacone that is connate with the paracone. The metacone is lower than the paracone, but taller than the protocone. The styler shelf is narrower than that of the molars, but has a well-differentiated parastyle and metacrista. The P4 shows no conules or associated conule wings. The precingulum is narrow, whereas the postcingulum is somewhat wider but lacks a hypocone.

The upper molars (Fig. 11B, C) assigned here to *Tsaganianus* are fragmentary and/or heavily worn, but together provide an overall idea of the upper molar morphology. The crowns are strongly elongated transversely, with a narrow trigon basin. The paracone is slightly taller than the metacone, and the cusps are closely approximated. The styler shelf is moderately developed, with a small parastyle and a strong metacrista. The paraconule is prominent, with robust pre- and postparaconule cristae, but the metaconule is weaker and the premetaconule crista is reduced. The pre- and postcingulum are transversely long and relatively wide, and a small hypocone is developed on the postcingulum, lingual of the level of the protocone.

IMM-2004-SB-048 (Fig. 11D) is here identified as a dp4 of *T. ambiguus*: it differs from the p4 in the stronger, more anteriorly projecting paraconid and anterolabial cingulum. The protoconid and metaconid are more gracile than in p4, with the metaconid slightly higher than in p4, but still lower than the protoconid. The oblique crest runs from the base of the trigonid wall towards the single talonid cusp, probably equivalent to the hypoconid, and a small talonid basin is present lingually of this cusp.

Discussion.—Although several of these specimens were preliminarily identified as belonging to “*Naranius*” (Missiaen

and Smith 2004) and “*Tsaganianus* sp. nov.” (Van Itterbeeck et al. 2007), additional specimens and comparison with topotypic material clearly indicate that the referred specimens are best identified as pertaining to *T. ambiguus*.

Among Cimolestidae, the upper molar morphology reported here for *Tsaganianus* is close to that of *Naranius*. Morphological similarities include the transversely expanded crown with broad styler shelf, the reduced premetaconule crista, and the wide pre- and postcingulum. Differences include the shallower ectoflexus and the unreduced postparaconule crista in *Tsaganianus*. The semimolariform P4 of *Tsaganianus* is clearly different from the premolariform P4 of *Naranius* reported by Lopatin (2006); this is not surprising, considering that the p4 is also semimolariform in *Tsaganianus* but premolariform in *Naranius* (Russell and Dashzeveg 1986). Moreover, a semimolariform P4/p4 is also seen in other Paleocene Cimolestidae such as *Procerberus* and *Aboletylestes*. However, the overall similarity of these taxa to *Tsaganianus* is low and the semimolariform P4/p4 in *Tsaganianus* does not indicate a special relationship to the latter taxa.

Stratigraphic and geographic range.—*Tsaganianus ambiguus* is known from the Gashatan (late Paleocene) of the Nomogen Formation at Subeng (Inner Mongolia, China) and from the Bumbanian (early Eocene) of the Bumban Member of the Naran Bulak Formation at Tsagan Khushu (Mongolia).

Superorder Archonta Gregory, 1910

Order Proprimates Gingerich, 1989

Infraorder Plesiadapiformes Simons, 1972

Family Carpolestidae Simpson, 1935

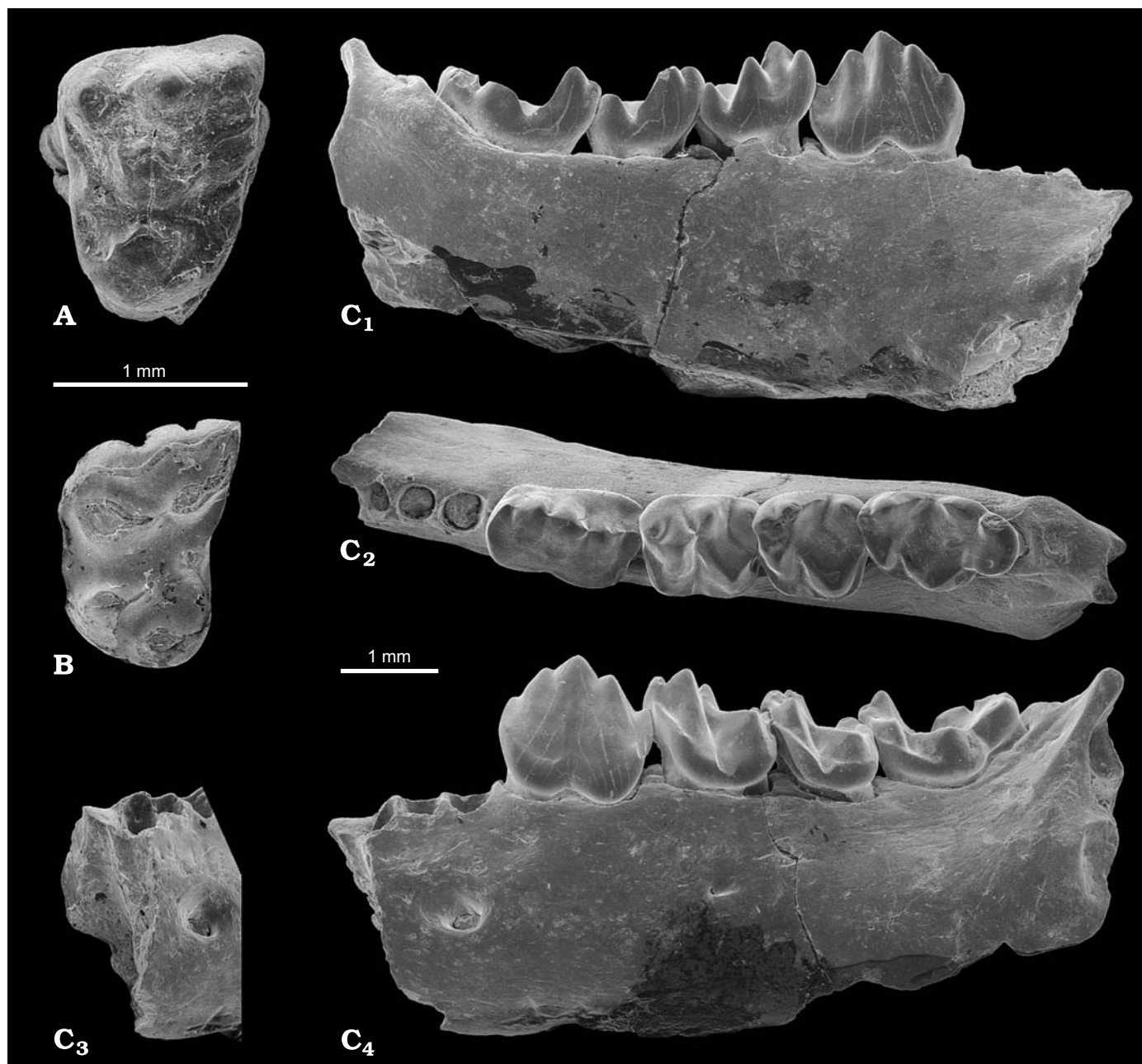


Fig. 12. The carpolestid *Subengius mengi* Smith, Van Itterbeeck, and Missiaen, 2004, from the Gashatan (Paleocene) of Subeng, China. **A.** IMM-2004-SB-052, LP3 in occlusal view. **B.** IMM-2001-SB-059, LP3 in occlusal view. **C.** IMM-2004-SB-053, left dentary with p4-m3, in lingual (**C**₁), occlusal (**C**₂), anterolabial (**C**₃), and labial (**C**₄) views. SEM micrographs.

Genus *Subengius* Smith, Van Itterbeeck, and Missiaen, 2004

Type species: *Subengius mengi* Smith, Van Itterbeeck and Missiaen, 2004; Gashatan (late Paleocene), Subeng (Inner Mongolia, China).

Subengius mengi Smith, Van Itterbeeck, and Missiaen, 2004

Figs. 12, 13.

Referred material: IMM 2001-SB-001, partial right p4; IMM 2001-SB-002, left m1; IMM 2001-SB-003, right m2; IMM 2001-SB-004, right m3; IMM 2001-SB-005, right I1; IMM 2001-SB-006 left P4

(holotype); IMM 2001-SB-007, right M2; IMM 2001-SB-008, left M3; IMM 2001-SB-059, left P3; IMM-2004-SB-051, left P3; IMM-2004-SB-052, left P3; IMM-2004-SB-053, left jaw fragment with p4-m3 in place; IMM-2004-SB-054, partial right p4.

Description.—Since the description of *Subengius mengi* (see Smith et al. 2004), additional specimens have been collected at the type locality. The previously unknown P3 (Fig. 12A, B) of *S. mengi* seems to be slightly smaller than P4, but the available specimens have suffered wear and breakage, obscuring their original dimensions. Three cusps are present labially. The paraconule is prominent, forming part of a single median crest.

The lingual side of the crown is moderately developed, with a marked talon basin and a posterolingual hypocone. A crest runs from the hypocone to the labial side, forming the posterior border of the crown; a swelling is developed halfway between the hypocone and the median crest.

IMM-2004-SB-053 (Fig. 12C) is a left jaw fragment containing p4–m3, and four anterior alveoli. The first of these is large and anteriorly aligned, the other three are of similar size and placed in a single row. These four alveoli probably correspond to those for the enlarged medial incisor, the reduced lateral incisor, the canine and p3. Therefore, the dental formula of the *Subengius mengi* lower jaw is 2.1.2.3. A mental foramen is present below the alveolus of p3. IMM-2004-SB-053 also contains a complete p4, showing that the talonid portion of p4 in *S. mengi* bears a single small cusp aligned with the four apical cusps.

Discussion.—In their original description, Smith et al. (2004) suggested that *S. mengi* had a strong mosaic pattern of autapomorphic, primitive and derived characters, and based on this they created the new carpolestid genus *Subengius*, but placed it at an evolutionary stage slightly before the transition between the primitive genus *Elphidotarsius* and the more advanced genus *Carpodactes* (Smith et al. 2004). The new specimens presented here support this hypothesis. The small size of P3 and the presence of only three labial cusps are features seen in the most primitive *Elphidotarsius* species. The p4 with only four apical cusps is typical of *Elphidotarsius* (Rose 1975). The absence of p2, the alignment of the apical cusps on p4 and the limited development of the lingual border of P3 is seen both in more advanced species of *Elphidotarsius* and primitive species of *Carpodactes* (Rose 1975; Silcox et al. 2001).

To test the original hypothesis of Smith et al. (2004) on the phylogenetic position of *Subengius*, we performed a cladistic analysis by adding *Subengius* to the analysis of carpolestids published by Bloch et al. (2001), to specifically resolve the relations of taxa within the family Carpolestidae. To this, we also added the new morphological data on *Elphidotarsius russelli* presented by Silcox et al. (2001) (see Table 4 for codelines). We do not consider the Asian Eocene *Chronolestes* to be a member of the Carpolestidae (Bloch et al. 2001; Silcox et al. 2001), and follow Fox (2002) in restricting the genus *Carpocristes* to its Asian Eocene type species *C. oriens*.

Our analysis yielded a single most parsimonious tree of 67 steps, with CI 0.90 and RI 0.92, and places *Subengius* between *E. shotgunensis* and *E. russelli* (Fig. 13). Because *E. russelli* is so close to *Carpodactes* that it in fact obscures the generic distinction between *Elphidotarsius* and *Carpodactes*

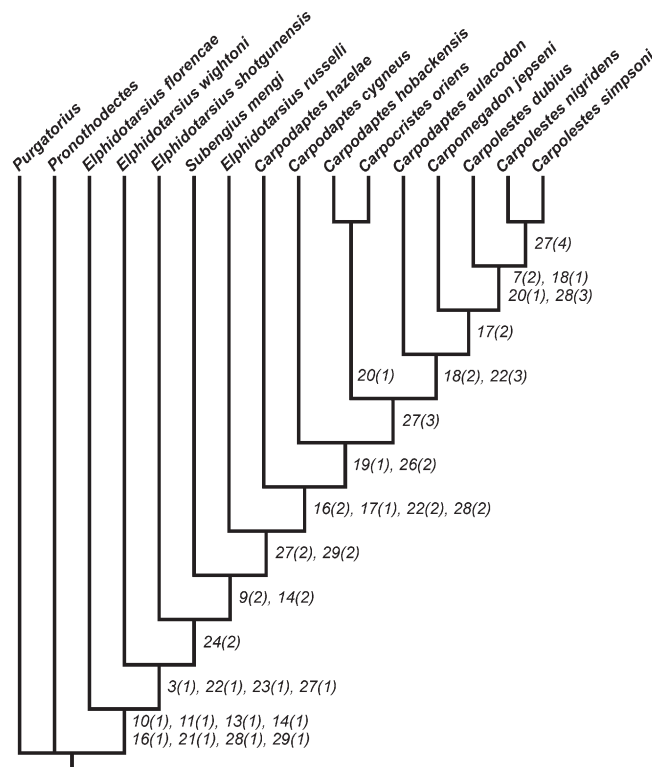


Fig. 13. Single most parsimonious tree of carpolestid relationships (CI 0.90, RI 0.92) based on the matrix of Bloch et al. (2001) and modified as noted in the appendix, with indication of unambiguous synapomorphies, i.e., invariable with respect to optimisation criteria.

(Silcox et al. 2001), we consider that the results of this analysis support the initial hypothesis relatively well. Detailed analysis of the character matrix shows that the morphology of *Subengius* is in fact closest to *E. russelli*, and that its slightly more primitive position is due to the lower number of labial cusps on P3 and P4. However, because of the very strong mosaic pattern of primitive and advanced characters, and because of the unique presence of two isolated median spurs on P4, we continue to place *S. mengi* in a separate genus, apart from *Elphidotarsius*. As in previous studies (Bloch et al. 2001; Silcox et al. 2001), our analysis shows that *Elphidotarsius* and *Carpodactes* are not monophyletic genera, and even the alternative of attributing *Subengius* to the genus *Elphidotarsius* would not change this taxonomic problem. A complete study of all known carpolestids might help to resolve this situation, but is obviously beyond the scope of this paper.

Our analysis suggests that *Subengius* and *Carpocristes* evolved independently from their North American ancestors.

Table 4. New character coding for *Subengius mengi* and *Elphidotarsius russelli* as used in our updated cladistic analysis of carpolestid plesiadapiforms (modified after Silcox et al. 2001, based on the original characters and matrix of Bloch et al. 2001).

	1				5					10					15					20					25					30		
<i>Subengius mengi</i>	0	1	?	?	0	1	1	?	2	1	1	?	1	2	0	1	0	0	1	0	1	1	0	2	2	1	1	1	1	2	1	1
<i>Elphidotarsius russelli</i>	0	1	?	?	0	1	1	?	2	1	1	?	1	2	0	1	0	0	0	0	1	1	1	2	2	1	2	1	2	1	1	1

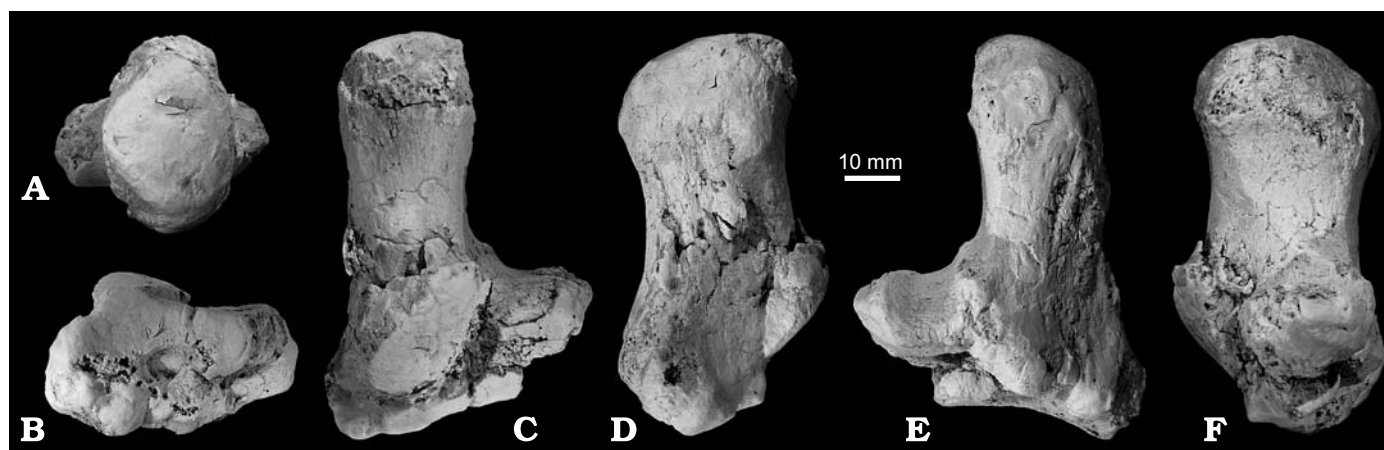


Fig. 14. The dinoceratan *Prodinoceras efremovi* (Flerov, 1957), from the Gashatan (Paleocene) of Subeng, China. IMM-2001-SB-060, right calcaneum in proximal (A), distal (B), dorsal (C), lateral (D), ventral (E), and medial (F) views.

The taxon that is morphologically closest to *Subengius*, *Elphidotarsius russelli*, is known from the North American Tiffanian 1–2, while *Elphidotarsius shotgunensis* and *Carpodaptes hazelae*, that are also morphologically close to *Subengius*, are known from Tiffanian 1–3 (Bloch et al. 2001; Silcox et al. 2001). The ancestor of *Subengius* thus probably migrated into Asia during the early Tiffanian. The closest relatives to *Carpocristes oriens*, *Carpodaptes hobackensis*, and *C. cygneus* are known from the late Tiffanian (Ti5) and middle Tiffanian (Ti3–4), respectively (Bloch et al. 2001). Asian carpolesids thus represent two independent dispersal events, although it is not impossible these occurred simultaneously. *Chronolestes simul* from the early Eocene of Wutu (Shandong Province, China) represents yet another dispersal of plesiadapiforms into Asia, but the timing of this is more problematic (see Silcox et al. 2001).

Stratigraphic and geographic range.—*Subengius mengi* is currently only known from the Gashatan (late Paleocene) Nomogen Formation at Subeng (Inner Mongolia, China).

Superorder Ungulatomorpha Archibald, 1996

Grandorder Ungulata Linnaeus, 1766

Order Dinocerata Marsh, 1873

Family Prodinoceratidae Flerov, 1952

Genus *Prodinoceras* Matthew, Granger, and Simpson, 1929

Type species: *Prodinoceras martyr* Matthew, Granger and Simpson, 1929; Gashatan (late Paleocene), Gashato (Mongolia).

Prodinoceras efremovi (Flerov, 1957)

Fig. 14.

Referred material: IMM-2001-SB-060, right calcaneum; possibly IMM-2004-SB-055, incisor.

Discussion.—Dinoceratans are important biogeographic markers for the early Paleogene of Asia (Ting 1998), and they have been reported from the Subeng locality (Russell and Zhai 1987).

A moderately well preserved calcaneum (Fig. 14) is the only specimen in our Subeng collection that can be confidently assigned to Dinocerata. The calcaneum from Subeng very closely matches the calcaneum of “*Mongolotherium*” *efremovi* in size and morphology, as described and illustrated by Flerov (1957). These similarities include the anterodorsally facing ectal and sustentacular facets and the relatively long tuber with a constricted anterior portion, an expanded posterior part, and a large posteroventrally facing posterior end. In later reviews, the genus “*Mongolotherium*” was considered a subgenus of *Prodinoceras* (Tong 1978; Dashzeveg 1982; Schoch and Lucas 1985). In non-taxonomic literature, “*M.*” *efremovi* has even been synonymised with *P. martyr* (Russell and Zhai 1987; Ting 1998; Bowen et al. 2002), but without justification by a species level review of *Prodinoceras*. Based on available information, we identify the dinoceratan calcaneum from Subeng as pertaining to *P. efremovi*.

Based on the presence of *Prodinoceras efremovi* at Subeng, and the similarity of a large incisor with the tip of the crown broken off, IMM-2004-SB-055, to one of the isolated incisors of the type specimen of *P. martyr*, AMNH 21714, (Matthew et al. 1929), we here tentatively assign IMM-2004-SB-055 also to *P. efremovi*.

There seems to be considerable size and morphological variation in species attributed to Prodinoceratidae, and sexual dimorphism has been suggested for many prodinoceratids (Schoch and Lucas 1985; Thewissen and Gingerich 1987). The possibility that many, or even all *Prodinoceras* specimens from Naran Bulak and Gashato (Mongolia) and from Subeng and Bayan Ulan (Inner Mongolia, China), represent one species cannot be ruled out. A revision of Asian prodinoceratids is definitely needed both at both generic and specific levels, and may have biogeographic implications.

Stratigraphic and geographic range.—*Prodinoceras efremovi* is known from the Gashatan (late Paleocene) in the Naran Member of the Naran Bulak Formation at Ulan Bulak (Mongolia) and in the Nomogen Formation at Subeng.

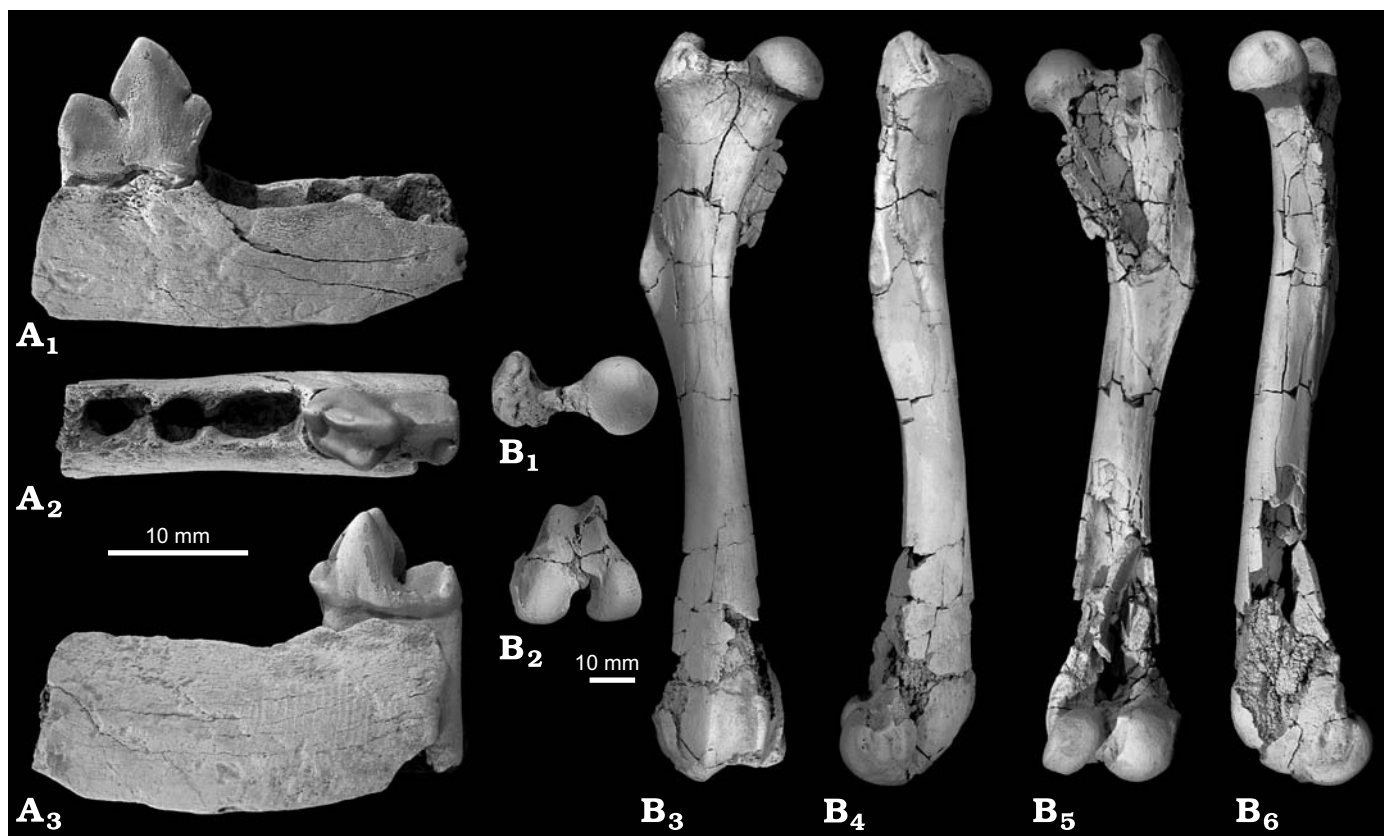


Fig. 15. The mesonychid *Dissacus serratus* (Chow and Qi, 1978), from the Gashatan (Paleocene) of Subeng, China. **A.** IMM-2004-SB-056, right dentary fragment with m1 in labial (A₁), occlusal (A₂), and lingual (A₃) view. **B.** IMM-2001-SB-061, right femur in proximal (B₁), distal (B₂), anterior (B₃), lateral (B₄), posterior (B₅), and medial (B₆) view.

Order Mesonychia Matthew, 1937

Family Mesonychidae Cope, 1875

Genus *Dissacus* Cope, 1881

Type species: *Dissacus navajovius* Cope, 1881; Torrejonian (early Paleocene), San Juan Basin (New Mexico, USA).

Dissacus serratus (Chow and Qi 1978)

Fig. 15.

Referred material: IMM-2004-SB-056, right jaw fragment with m1; IMM-2001-SB-061, right femur.

Description.—A lower jaw fragment with m1 (Fig. 15A) found at Subeng can be readily identified as *Dissacus serratus*, a small species of *Dissacus* previously reported from the nearby Nomogen and Bayan Ulan fauna (Chow and Qi 1978; Meng et al. 1998).

An isolated femur (Fig. 15B) found in association with the jaw shows a morphology also seen in the femora other of Mesonychidae (O'Leary and Rose 1995; Geisler and McKenna 2007), and is therefore also assigned to *Dissacus serratus*. The previously unknown femur of *D. serratus* is long and relatively slender. The diaphysis presents a slight S-shaped curve in an anteroposterior plane, and in cross section the depth is 1.5 times the width. The fovea on the femoral head is extensive but not open. The neck is very narrow in

proximal view. The greater trochanter is slightly higher than the head and the trochanteric fossa is deep. On the lateral side of the shaft, a slight crest descends from the greater trochanter to the third trochanter. The third trochanter is prominent but less robust than in *Pachyaena* (see O'Leary and Rose 1995); it is situated at about one third of the way down the length of the shaft, but a robust crest continues farther from it to just past the midpoint of the shaft. The lesser trochanter is not well preserved, but seems to have been thin and moderately large, and projecting medially or postero-medially. The distal femur is as deep as it is wide. The patellar groove is long, narrow and well defined with the medial crest markedly higher than the lateral.

Discussion.—Geisler and McKenna (2007) recently described the new *D. zanabazari* from the Bumbanian of Naran Bulak, based on a partial skeleton. To their comparison of the dental morphology of *D. zanabazari* and *D. serratus*, we add that the lower molars of *D. serratus* can be further distinguished from *D. zanabazari* by the relatively lower paraconid and higher protoconid, the better-developed labial shearing crests and the presence of a small entoconid.

The femoral morphology of *D. zanabazari* and *D. serratus* seems closely similar. *D. serratus* possibly had a somewhat larger lesser trochanter, a less deep distal femur but a deeper and narrower distal trochlae than *D. zanabazari*, but

Table 5. List of all fossil mammals known from the Gashatan of Subeng.

Order Multituberculata Cope, 1884
Family Neoplagiaulacidae Ameghino, 1890
<i>Mesodmops tenuis</i> sp. nov.
Family Taeniolabidae Granger and Simpson, 1929
<i>Lambdopsalis bulla</i> Chow and Qi, 1978
<i>Prionessus</i> sp.
Cohort Placentalia Owen, 1837
Superorder Gliriformes Wyss and Meng, 1996
Family Astigalidae Zhang and Tong, 1981
Astigalidae indet.
Family Arctostylopidae Schlosser, 1923
<i>Palaeostylops iturus</i> Matthew and Granger, 1925
Family Pseudictopidae Sulimski, 1969
<i>Pseudictops lophiodon</i> Matthew, Granger, and Simpson, 1929
Grandorder Glires Linnaeus, 1758
Order Mixodontia Sych, 1971
Family Eurymyliidae Matthew, Granger, and Simpson, 1929
<i>Eomytus bayanulanensis</i> Meng, Wyss, Hu, Wang, Bowen, and Koch, 2005
Order Rodentia Bowdich, 1821
Family Alagomyidae Dashzeveg, 1990
<i>Tribosphenomys minutus</i> Meng, Wyss, Dawson, and Zhai, 1994
<i>Tribosphenomys</i> cf. <i>T. secundus</i> Meng, Ni, Li, Beard, Gebo, Wang, and Wang, 2007
<i>Neimengomys qii</i> Meng, Ni, Li, Beard, Gebo, Wang, and Wang, 2007
Superorder Insectivora Bowdich, 1821
Order Lipotyphla Haeckel, 1866
Suborder Soricomorpha Gregory, 1910
Family Nyctitheriidae Simpson, 1928
<i>Asionyctia guoi</i> Missiaen and Smith, 2005
<i>Bumbanius ningi</i> sp. nov.
Superorder Ferae Linnaeus, 1758
Mirorder Cimolesta McKenna, 1975
Family Sarcodontidae Lopatin and Kondrashov, 2004 new rank
<i>Hyracolestes ermineus</i> Matthew and Granger, 1925
Order Didelphodonta McKenna, 1975
Family Cimolestidae McKenna, 1975
<i>Tsganius ambiguus</i> Russell and Dashzeveg, 1986
Superorder Archonta Gregory, 1910
Order Proprimates Gingerich, 1989
Infraorder Plesiadapiformes Simons, 1972
Family Carpolestidae Simpson, 1935
<i>Subengius mengi</i> Smith, Van Itterbeeck, and Missiaen, 2004
Superorder Ungulatomorpha Archibald, 1996
Order Dinocerata Marsh, 1873
Family Prodinoceratidae Flerov, 1952
<i>Prodinoceras efremovi</i> (Flerov, 1957)
Order Mesonychia Matthew, 1937
Family Mesonychidae Cope, 1875
<i>Dissacus serratus</i> (Chow and Qi, 1978)

preservation of the femur in *Dissacus zanabazari* does not allow a closer comparison.

Mesonychids are generally regarded as cursorially adapted, carnivorous ungulates, with *Dissacus* as the most basal genus (Szalay 1969; O'Leary and Rose 1995; Geisler and McKenna 2007). The generally slender femur of *Dissacus serratus* has well-developed trochanters, transversely compressed shaft, and a deep distal epiphysis with a long, narrow patellar groove. These features indicate a cursorial mode of life (O'Leary and Rose 1995), and the overall anatomy of the femur of *D. serratus* is closer to the cursorially specialised *Mesonyx* than to the generalised, subcursorial *Pachyaena* (see O'Leary and Rose 1995). Dental and femoral morphology of *D. serratus* thus clearly indicate carnivorous and cursorial adaptations. As *D. serratus* is the only large carnivore found at the Subeng site, and is also the only large carnivore described from the Nomogen site and the most abundant large carnivore at Bayan Ulan (Meng et al. 1998), we consider *D. serratus*, an important, possibly the most important, carnivore of the Gashatan Subeng local environment.

Stratigraphic and geographic range.—*Dissacus serratus* is known from the Gashatan (late Paleocene) Nomogen Formation at Nomogen, Bayan Ulan and Inner Mongolia, China.

Concluding discussion

Although Jiang (1983, not seen) and Russell and Zhai (1987) briefly mentioned the Subeng mammal site, neither a comprehensive discussion of the locality, nor a complete faunal listing was ever provided. The study of the Gashatan mammals from Subeng only started with the description of *Subengius mengi* and *Asionyctia guoi* (Smith et al. 2004; Missiaen et al. 2005). Van Itterbeeck et al. (2007) made an integrated study of the Subeng site based on sedimentology, charophytes, ostracods, palynomorphs, molluscs, amphibians, lizards and mammals. They concluded that the Nomogen Formation at Subeng was late Paleocene, Gashatan in age, and that the site was a relatively humid, closed environment during the late Paleocene, most probably an isolated woodland on the supposedly dry Mongolian Plateau. These authors suggested that, because the Subeng site was more humid and forested than the other known Gashatan sites, this explained the higher similarity of the Subeng fauna with the North American late Paleocene mammal faunas which are known to have inhabited a forested environment (see Van Itterbeeck et al. 2007). An exhaustive study of the Alagomyidae from Subeng (Meng, Ni et al. 2007) also gives a faunal list for the Gashatan mammals of Subeng, although it only provides supporting evidence for the alagomyids.

This paper is the first to discuss the complete Subeng mammal fauna in some detail and to provide full illustration of the specimens. The fossil fauna listed here (Table 5) is

dominated by small to medium-sized mammals, which were collected by screenwashing. The fact that most taxa are only represented by small, isolated elements, mainly isolated teeth, suggests that fluvial action caused a size bias favouring small elements. The excellent preservation of the often fragile specimens recovered by screenwashing nevertheless indicates that they only underwent limited transport. Therefore the faunal list provided here most probably does not represent the complete Gashatan fauna from the Subeng environment, but lacks a part of the medium and large-sized mammals, as exemplified by the few fossils from the larger taxa *Prodinoceras* and *Dissacus* which were recovered during quarrying.

Five new species have been recognized at Subeng, of which *Mesodmops tenuis* sp. nov. and *Bumbanius ningi* sp. nov. are described in this paper, and *Subengius mengi*, *Asionyctia guoi* and *Neimengomys qii* were described previously (Smith et al. 2004; Missiaen and Smith 2005; Meng, Ni et al. 2007). This study of the Subeng mammals provides additional morphological information for *Palaeostylops iturus*, *Eomylus bayanulanensis*, *Hyracolestes ermineus*, *Tsaganius ambiguus*, and *Dissacus serratus*, which in some cases has significant phylogenetic importance for these groups. Subeng is also the only Gashatan site where only one of two species of *Palaeostylops* has been found; in all other Gashatan sites both species have been found together. Considering the high abundance of *Palaeostylops iturus* at Subeng, we find the absence of *P. macrodon* significant. Although we do not offer a phylogenetic, biostratigraphic or paleoenvironmental interpretation of this, we do believe it may be of interest for future studies.

Lambdopsalis bulla, *Prionessus* sp., *Palaeostylops iturus*, *Pseudictops lophiodon*, *Tribosphenomys minutus*, and *Dissacus serratus* are all characteristic taxa for the Gashatan ALMA (Ting 1998), leaving no doubt that the Subeng fauna is Gashatan in age. It has been suggested that the uppermost part of the Nomogen Formation extends into the Bumbanian, based on the presence of the so-called “*Gomphos* fauna” as opposed to the typical Gashatan “*Lambdopsalis* fauna” (Meng et al. 2004; Meng, Ni et al. 2007; Meng, Wang et al. 2007). Because the mimotonid *Gomphos elkema* was previously known only from the Bumbanian of Mongolia, it was taken as evidence for a Bumbanian age of the faunas concerned. In contrast, the Subeng site is shown here to be of definite Gashatan age and does not contain *Gomphos*, but does contain the species *Tsaganius ambiguus*, the genera *Bumbanius* and *Mesodmops* and the family Carpolestidae, all of which were previously also only from the Bumbanian. We thus do not consider the presence of archaic taxa such as *Gomphos elkema* or *Tsaganius ambiguus* good evidence for a Bumbanian, Eocene age.

The presence of the new omomyid primate *Baataromomys ulaanus*, the perissodactyl *Pataecops parvus* and the dinoceratan *Uintatherium* sp. in the *Gomphos* fauna (Ni et al. 2007; Meng, Wang et al. 2007) is clearly evidence for an Eocene age of this fauna. In fact, the authors of *Baata-*

romomys suggest that it is the ancestor of *Teilhardina brandti* from the Wasatchian-0 in North America, and that *B. ulaanus* is as primitive as *T. asiatica* from the earliest Eocene upper Lingcha fauna. Based on this, they argue that the *Gomphos* fauna occurred at the PEB or during the first 25.000 years of the Eocene (Ni et al. 2007; Meng, Ni et al. 2007). However, the single specimen known for *B. ulaanus*, an isolated m2, is clearly more square and inflated than in the gracile *T. asiatica*, indicating to us a more derived phylogenetic position than *T. asiatica*, and probably a younger age. Moreover, the same *Gomphos* beds also yielded *Pataecops parvus* and *Uintatherium* sp., taxa that are otherwise only known from the middle Eocene Arshantan ALMA (Bowen et al. 2002). We therefore doubt the correlation of the *Gomphos* fauna with the earliest Eocene and find the correlation of the *Gomphos* fauna with the Bumbanian ALMA unsatisfactorily supported. Because some doubts exist that the Eocene *Gomphos* levels are truly continuous with the underlying late Paleocene Nomogen Formation (Meng, Wang et al. 2007: 11–13, 19), and because both isotope and paleomagnetic studies of the sections concerned failed to identify the carbon isotope excursion or to precisely locate the PEB (Bowen et al. 2005; Meng, Ni et al. 2007), we believe that the base of the Eocene might be missing in the Erlian Basin of Inner Mongolia. We therefore suggest that the *Gomphos* levels are not continuous with the Nomogen Formation, but instead belong to a previously unknown formation of limited exposure, with an early, but not earliest Eocene age.

Traditionally the Asian Paleocene faunas are considered to be strongly endemic, with limited exchanges occurring only in the late Paleocene and at the Paleocene–Eocene boundary (Ting 1998; Wang et al. 2007). During the Shanguan and Nongshanian ALMAs only pantodonts, mesonychids and possibly carnivores are shared between Asia and North America (Ting 1998; Kondrashov and Lucas 2004b; Wang et al. 2007). However, the Gashatan mammal fauna from Subeng shares considerably more taxa with North American faunas. At the family level, Cimolestidae, Neoplagiaulacidae, Taeniolabidae, Arctostylopidae, Alagomyidae, Nyctitheriidae, Carpolestidae, and Prodinoceratidae are all shared between Asia and North America during the Gashatan. In the case of Prodinoceratidae, it has even been proposed that the genus *Prodinoceras* is shared between the two continents (McKenna and Bell 1997). However, a biogeographic link at the generic level is more clearly established by *Dissacus*, even if this genus has an exceptionally long biostratigraphic range and a Holarctic distribution during the late Paleocene. Our own observations on the Subeng assemblage, as well as other published Gashatan faunas (see Ting 1998; Wang et al. 2007), therefore unmistakably show an increased number of mammal groups shared with the late Paleocene of North America. Some of these shared taxa, such as multituberculates, nyctitheriids and carpolestids, are North American immigrants into Asia, while other groups such as alagomyids and arctostylopids dispersed in the oppo-

site direction, from Asia into North America. We therefore suggest that the Nongshanian–Gashatan boundary coincides with a migration wave of mammal groups between Asia and North America. Whether this migration took place during a limited period at the Nongshanian–Gashatan boundary, or if migration remained possible throughout the Gashatan, can currently not be determined. Although Asia has been suggested as the place of origin for the modern primates, perissodactyls and artiodactyls (Beard 1998), no modern mammals have been unambiguously reported from the Asian Gashatan faunas. Subsequently, the Gashatan–Bumbanian boundary seems to coincide with the arrival of modern taxa on all Holarctic continents, and in this period migration was also possible directly between Asia and Europe (Smith et al. 2006).

The timing of the Nongshanian–Gashatan boundary is difficult to establish, although most recent studies correlate the Gashatan with a part of the late Tiffanian and the Clarkforkian from North America (Bowen et al. 2005; Wang et al. 2007; Meng, Ni et al. 2007). Biostratigraphic correlations are not precise because they mostly involve mammal exchanges at the family level. Alagomyidae probably dispersed at the Tiffanian–Clarkforkian boundary and Arctostylopidae and Dinocerata possibly during the late Tiffanian (Beard 1998). But for Nyctitheriidae and Carpoolestidae data suggest an earlier dispersal, in the early to middle Tiffanian (Missiaen and Smith 2005, this paper). We therefore suggest that the Asian Shanghuan and Nongshanian faunas had an endemic, isolated evolution, but that the Gashatan faunas are less endemic, because of the exchange of at least eight mammal families with the late Paleocene of North America.

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