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

PIETER MISSIAEN and THIERRY SMITH


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 tenais sp. nov. and the praoestine 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 eumylylid Eomylus bayanulanensis, the sarcodontid Hyracolestes ermineus, the cimolestid Tsaganius ambiguus, the carpolesid 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 carpolesids 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 bula, 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, Carpolesidae, late Paleocene, Gashatan, Subeng, China.

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 Khaychun-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 Buman 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), 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 uintathera and dermopteran teeth”. In 1995,
2000, 2001, and 2004, the site was re-sampled by a multidisciplinary team from the IMM and the Royal Belgian Institute of Natural Sciences (RBINS), resulting in the discovery of a new genus and species of carpopod plesiadapiform 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 apertate Paleocene age (Van Itterbeeck et al. 2007). 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). 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.

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.

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

<table>
<thead>
<tr>
<th>Position</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
</tr>
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<tbody>
<tr>
<td>IMM-2001-SB-017</td>
<td>dP3?</td>
<td>0.73</td>
</tr>
<tr>
<td>IMM-2001-SB-016</td>
<td>M1</td>
<td>3.28</td>
</tr>
<tr>
<td>IMM-2004-SB-014</td>
<td>M2</td>
<td>1.30</td>
</tr>
<tr>
<td>IMM-2001-SB-018</td>
<td>m1</td>
<td>–</td>
</tr>
<tr>
<td>IMM-2004-SB-013</td>
<td>m1</td>
<td>2.15</td>
</tr>
<tr>
<td>IMM-2004-SB-017</td>
<td>m1</td>
<td>–</td>
</tr>
<tr>
<td>IMM-2004-SB-016</td>
<td>m2</td>
<td>1.20</td>
</tr>
</tbody>
</table>

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-017, 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 anteroposteriorly 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.
Discussion.—The teeth of *Mesodmops tenuis* from Subeng closely resemble those of the type-species *M. dawsonae* from the Bumbian of Wuwu (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. dawsonae* confirms this idea. They also suggested that *M. tenuis* were ready in the Paleocene of Asia; the discovery of *M. tenuis* 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; Kielen-Jaworowska and Qi 1990).

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; Kielen-Jaworowska and Qi 1990).
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 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 cuspules 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 cuspules 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).
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 arctostyloid 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 cuspsules on M1 and

M2, and the absence or weak development of a sulcus separating the lingual cusps on M1. The Subeng specimens therefore weaken morphological distinctions between Palaeostylops iturus and Palaeostylops macrodon suggested by Cifelli et al. (1989) to justify generic distinctions, and we continue to consider both species members 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

### 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.

<table>
<thead>
<tr>
<th></th>
<th>Subeng</th>
<th>Kondrashov and Lucas (2004a)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Palaeostylops iturus</td>
<td>Palaeostylops iturus</td>
</tr>
<tr>
<td></td>
<td>L</td>
<td>W</td>
</tr>
<tr>
<td><strong>p4</strong></td>
<td>min.</td>
<td>2.0</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>2.25</td>
</tr>
<tr>
<td></td>
<td>max.</td>
<td>2.4</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>21</td>
</tr>
<tr>
<td><strong>m1</strong></td>
<td>min.</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>2.65</td>
</tr>
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<td></td>
<td>max.</td>
<td>2.8</td>
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<td></td>
<td>n</td>
<td>21</td>
</tr>
<tr>
<td><strong>m2</strong></td>
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<tr>
<td></td>
<td>mean</td>
<td>3.50</td>
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<td></td>
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<td>3.7</td>
</tr>
<tr>
<td></td>
<td>n</td>
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<tr>
<td><strong>m3</strong></td>
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<tr>
<td></td>
<td>mean</td>
<td>2.76</td>
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<tr>
<td></td>
<td>max.</td>
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<td></td>
<td>n</td>
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<tr>
<td><strong>M1</strong></td>
<td>min.</td>
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</tr>
<tr>
<td></td>
<td>mean</td>
<td>2.04</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>n</td>
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<td></td>
<td>mean</td>
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</tr>
<tr>
<td></td>
<td>max.</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>n</td>
<td>7</td>
</tr>
<tr>
<td><strong>M3</strong></td>
<td>min.</td>
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<tr>
<td></td>
<td>mean</td>
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<td>max.</td>
<td>3.9</td>
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<tr>
<td></td>
<td>n</td>
<td>6</td>
</tr>
</tbody>
</table>

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.
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).

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**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 Khusu (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*.
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).
Tribosphenomys minutus Meng, Wyss, Dawson, and Zhai, 1994

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.

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 M1 or M2; IMM-2004-SB-037, right m1; 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.  

http://app.pan.pl/acta53/app53-357.pdf
Diagnosis.—Praolestine nyctitheriid similar in size to *Bumbanius rarus*. Diffe...
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 hypococonid 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 hypococonid.

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 precingulum, 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 hypococone, 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 antero-posteriorly 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 hypococone 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 Micropteromodontidae 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, Micropteromodontidae only appear in the middle Eocene, and have three molars and a hypocone shelf on P4 and the upper molars. After their separation from micropteromodontids, we
see no reason to continue to place sarcodontids in Soricomorpha. Instead, Sarcodontidae resemble cimolestans such as didymoconids, wyolestids, cimolestids and palaebryctids, in the large, caniform 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 Palaebryctidae 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* 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 Tsaganius Russell and Dashzeveg, 1986

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

**Tsaganius 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, partial right M1 or M2; IMM−2001−SB−058, left p4; IMM−2004−SB−048, right dp4; IMM−2004−SB−049, right jaw fragment with partial m2 and complete m3; IMM−2004−SB−050, right m3.

*Description.*—The P4 (Fig. 11A) of *Tsaganius* was previously unknown. The crown is semimolariform, with a slen-
der metacone that is connate with the paracone. The metacone is lower than the paracone, but taller than the protocone. The stylar 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 *Tsaganius* 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 stylar 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 “*Tsaganius 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 *Tsaganius* is close to that of *Naranius*. Morphological similarities include the transversely expanded crown with broad stylar shelf, the reduced premetaconule crista, and the wide pre- and postcingulum. Differences include the shallower ectoflexus and the unreduced postparaconule crista in *Tsaganius*. The semimolariform P4 of *Tsaganius* 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 *Tsaganius* but premolariform in *Naranius* (Russell and Dashzeveg 1986). Moreover, a semimolariform P4/p4 is also seen in other Paleocene Cimolestidae such as *Procerberus* and *Abolylestes*. However, the overall similarity of these taxa to *Tsaganius* is low and the semimolariform P4/p4 in *Tsaganius* does not indicate a special relationship to the latter taxa.

Stratigraphic and geographic range.—*Tsaganius ambiguus* is known from the Gashatan (late Paleocene) of 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 Carolestidae Simpson, 1935
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 11; 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.

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 (C1), occlusal (C2), anterolabial (C3), and labial (C4) views. SEM micrographs.
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 carolestid genus *Subengius*, but placed it at an evolutionary stage slightly before the transition between the primitive genus *Elphidotarsius* and the more advanced genus *Carpodaptes* (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 *Carpodaptes* (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 carolestids published by Bloch et al. (2001), to specifically resolve the relations of taxa within the family Carolestidae. 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 *Chromolestes* to be a member of the Carolestidae (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 *Carpodaptes* that it in fact obscures the generic distinction between *Elphidotarsius* and *Carpodaptes* (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 *Carpodaptes* 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 carolestids 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.
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 carpolestids thus represent two independent dispersal events, although it is not impossible these occurred simultaneously. 

**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.

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**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.
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 dentary 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 posteromedially. 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 is 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

http://app.pan.pl/acta53/app53-357.pdf
Table 5. List of all fossil mammals known from the Gashatan of Subeng.

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<thead>
<tr>
<th>Family</th>
<th>Order</th>
<th>Superorder</th>
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<tr>
<td>Mesonychidae</td>
<td>Mesonychia</td>
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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 *Asionycia guoi* (Smith et al. 2004; Missiaen et al. 2005). Van Itterbeeck et al. (2007) made an integrated study of the Gashatan 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*, *Astrocnemius 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 faunus*” as opposed to the typical Gashatan “*Lambdopsalis faunus*” (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 Carpoolestidae, 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 onomyid 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 *Baataromomys ulaanus*, the perissodactyl *Pataecops parvus* and the dinoceratan *Uintatherium* sp. in the *Gomphos* fauna (Ni et al. 2007; Meng, Wang et al. 2007) 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 excurs 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 Shanghuans 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, Taeniolabididae, Arctostylopidae, Alagomyidae, Nycitheriidae, Carpocestidae, 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, nycitheriids and carpocestids, are North American immigrants into Asia, while other groups such as lagomorphs 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. Alagomyiidae probably dispersed at the Tiffanian–Clarkforkian boundary and Arctostylopidae and Dinocerata possibly during the late Tiffanian (Beard 1998). But for Nycitheriidae and Carpodaptes cygneus 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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References


Kondrashov, P. and Lopatin, A. 2003. Late Paleocene mixodonts from the


