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Source: American Museum Novitates, 2005(3473) : 1-25

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2005)473[0001:GMFTLP]2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3473, 25 pp., 11 figures, 2 tables May 11, 2005

Glires (Mammalia) from the Late Paleocene Bayan Ulan Locality of Inner Mongolia

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ABSTRACT

Two new early diverging members of Glires, *Eomylus bayanulanensis*, n.sp. and *Palaeomylus lii*, n.gen. and n.sp., are described from the late Paleocene Bayan Ulan Fauna, Inner Mongolia, China. These species add significantly to the diversity of Glires known from the early Paleogene of Asia. *E. bayanulanensis* and *Palaeomylus* sp. come from the lowest level of the Bayan Ulan section, from which the classic Bayan Ulan Fauna was collected. *Palaeomylus lii* and specimens belonging to two other genera of mammals, *Pseudictops* and *Palaeostylops*, are found from a horizon about 8 m above strata yielding the Bayan Ulan Fauna. These taxa are tentatively regarded as constituting a distinct faunal assemblage, which may prove to be of biostratigraphic utility within the region. Two calcanea tentatively assigned to *Gomphos* from a stratigraphic horizon slightly above the bed producing *P. lii* suggest the presence of strata of Early Eocene age in the Bayan Ulan section.

INTRODUCTION

Paleontological investigation in the Bayan Ulan area traces back to the 1920s, when a field party of the Central Asiatic Expeditions (CAE) of the American Museum of Natural History visited the Nom Khong Shireh of In-

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ISSN 0003-0082

ner Mongolia while making its way northeast from Shara Murun to Erlian. Nom Khong Shireh (also known as Nomogen today, meaning ''holy'') is an isolated mesa in the middle of a vast basin (see Meng et al., 1998, for a review of the research history). The Bayan Ulan Fauna was discovered at the northern foot of the mesa several decades later. First reported by Qi (1979), the fauna has recently been described (Meng et al., 1998). Fossils from Bayan Ulan have figured in numerous other recent studies (Miao, 1988; Meng, 1992; Meng et al., 1994, 1998; Meng and Wyss, 1994, 1995, 1997, 2001; Meng and McKenna, 1998). Current consensus places the Bayan Ulan Fauna in the late Paleocene Gashatan Asian Land Mammal Age, making it one of the earliest Tertiary mammal faunas known from the Mongolian Plateau (Meng et al., 1998; Meng and McKenna, 1998; Ting, 1998).

Early diverging members of Glires are known primarily from Paleocene and Eocene localities of Asia, Bayan Ulan included. Many of these forms are commonly termed eurymylids (or eurymyloids) and mimotonids. Eurymylids are regarded as those members of Glires, exclusive of rodents, characterized by having one pair of enlarged incisors in the lower and upper jaws. This concept changed recently with the discovery of a eurymylid taxon, *Sinomylus*, which has two pairs of lower and one pair of upper incisors (Kondrashov and Lopatin, 2003; Lopatin and Kondrashow, 2003). Mimotonids are generally regarded as those members of Glires, exclusive of Lagomorpha, having two pairs of incisors in both the upper and lower jaws. Eurymylids and mimotonids are quite diverse in the Paleogene of Asia and are pivotal to understanding the origin of rodents and lagomorphs on the continent. In addition, these fossils are useful in biostratigraphic correlations across the region because of their restricted stratigraphic distribution and distinctive morphology.

Since Russell and Zhai's (1987) compilation of the Bayan Ulan Fauna, additional collecting has been carried out at the locality, primarily by Meng and Wyss during field seasons in 1987 and 1992–1995. This work yielded several new taxa and additional material of previously known taxa, most of which have been published (Meng et al., 1998). Three taxa of Glires have been previously reported from Bayan Ulan: *Eomylus borealis*, ?*Khaychina elongata*, and *Tribosphenomys minutus*, of which only *T. minutus* has been described in detail (Meng et al., 1994; Meng and Wyss, 1994, 2001). Efforts to understand the fauna and the stratigraphic sequence hosting it have been continuously made, particularly in the context of exploring biotic and environmental changes across the Paleocene–Eocene boundary (Bowen et al., 2003, 2005). This interval coincides with a critical period of global warming and the first appearances of several major modern clades of eutherian mammals in the evolutionary history of mammals (Koch et al., 1992; Bowen et al., 2001, 2002). New specimens were collected from the Bayan Ulan locality in 2002–2004. In addition to those pertaining to the classic Bayan Ulan Fauna, a small sample of fossils was collected from a stratigraphic horizon 8 m above the one containing the typical Bayan Ulan Fauna. As these specimens are associated with precise stratigraphic and paleomagnetic data, they enhance understanding of the biostratigraphy at Bayan Ulan considerably (Bowen et al., 2005). Herein we describe the specimens of Glires from Bayan Ulan section, except *Tribosphenomys*, and briefly comment on current controversies regarding their phylogenetic relationships and taxonomy as well as their biochronologic implications.

MATERIAL AND METHODS

Specimens referred to *Eomylus borealis*, ?*Khaychina elongata*, and *Tribosphenomys minutus* (Meng et al., 1998) were either surface collected or acid prepared from coprolites originating from the beds, which have produced the other elements of the Bayan Ulan Fauna. Treatment in dilute formic acid revealed the fragmentary bones, isolated teeth, and jaws of small mammals contained in these nodules. The producers of these nodules remain uncertain, but they were likely carnivorous mammals, birds, or both (Meng et al., 1994, 1998). Several jaw fragments of members of Glires bear tooth marks and appear etched by stomach acid. Other taxa recovered from these nodules include *Palaeos-*

tylops sp., *Lambdopsalis bulla*, and at least two ‘‘insectivorans’’ (Meng et al., 1998).

In describing molars and molariform premolars we follow the dental terminology used for *Tribosphenomys* (Meng and Wyss, 2001). Because there is no consistent terminology for nonmolariform premolars, we use general, descriptive terms, such as labial or lingual cusp, instead of terms that imply homology, such as protocone and paracone, in describing these teeth.

Photographs of most teeth are taken from casts. Measurements were taken using digital calipers. IVPP is the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

STRATIGRAPHY AND FAUNAL LIST

The stratigraphic section measured at the Bayan Ulan site is presented below. This section represents only the lower portion of the entire Bayan Ulan sequence. The upper part of the stratigraphic sequence in this area consists of sedimentary rocks of the Irdin Manha and Sharamurum formations which make up the Nomogen mesa about 3 km south of the Bayan Ulan site. The total thickness of the measured section is 48 m. An updated list of the Bayan Ulan Fauna is incorporated in the description of the section. Additional lithological description of the sequence is provided in Bowen et al. (2005).

Starting point (bottom): N43°08.527′, E111°35.255′.

1. Reddish muddy siltstone (thickness: 3 m; the base of the sequence is covered by flat grasslands of the Mongolian steppe); fossil mammals (updated) include: *Bayanulanius tenuis*, *Dissacus serratus*, *Pachyaena* sp., *Tribosphenomys minutus*, *Eomylus bayanulanensis*, n.sp., *Palaeomylus*, n.gen., *Pseudictops lophiodon*, *Gashatostylops macrodon*, *Palaeostylops iturus*, *Hyracolestes ermineus*, *Lambdopsalis bulla*, *Prionessus* cf., *P. lucifer*, *Pastoralodon lacustris*, *Prodinoceras xinjiangensis*, *Prolimnocyon chowi*, *Sarcodon minor*, *Sarcodon pygmaeus*, *Viverravus* sp., Perissodactyla indet., Leptictida indet., and Cimolesta indet.
2. Light grayish green, blocky clay (mudstone) (thickness: 0.5 m).
3. Reddish brown mudstone, dense and blocky without bedding structures (thickness: 2.5 m).
4. Sandy grayish green siltstone. Fragments of fossils including *Prodinoceras* (thickness: 2 m).
5. Reddish brown mudstone, green nodules visible on fresh surfaces (thickness: 3 m). Fossil mammals including *Palaeostylops iturus*, *Pseudictops lophiodon*, and *Palaeomylus, lii* n.gen. and n.sp.
6. Thin layered grayish green siltstone (thickness: 1 m). Fragments of mammals including calcanea of *Gomphos*.
7. Light reddish brown siltstone (thickness: 1 m).
8. Deeply weathered, poorly exposed rock in an area of low relief (thickness: 4 m). Lateral variation in the color and texture of weathered rock suggests that this interval may include some younger rocks filling erosional channels. Fragments of fossil tapirs.
9. Light grayish green siltstone (thickness: 0.5 m).
10. Reddish brown mudstone and light brownish clay (thickness: 7.5 m).
11. Light brownish mudstone (thickness: 2.5 m).
12. Light grayish green siltstone (thickness: 4 m).
13. Light grayish brown sandy siltstone (thickness: 3 m).
14. Reddish brown blocky mudstone (thickness: 7 m).
15. Light grayish brown sandy siltstone (thickness: 1 m).
16. Reddish brown mudstone (thickness: 3 m).
17. Light grayish green muddy siltstone, with fossil tapirs (thickness: 2.5 m).

End of the section (top): N43°07.868′, E111°35.338′.

SYSTEMATIC PALEONTOLOGY

SIMPLICIDENTATA WEBER, 1904

Eomylus Dashzeveg and Russell, 1988

Eomylus bayanulanensis, new species

HOLOTYPE: V14126.1, a right M2 (fig. 1).

REFERRED SPECIMENS: V14126.2, a left maxilla with M1–3 in which the labial edges of the teeth are incomplete; V14127.1, a fragmentary right mandible with m1–3; V14127.2, a fragmentary left mandible with partial m2–3; V14127.3, a fragmentary right mandible with broken m2–3 and a separated anterior portion of a left mandible with incisor (from the same nodule containing V14126.2); V14127.4, a left m3 with little wear.

LOCALITY AND AGE: Upper Nomogen formation at Bayan Ulan (within the lower 3 m of the section), late Paleocene.

ETYMOLOGY: The trivial name is after that of the locality, Bayan Ulan.

DIAGNOSIS: *Eomylus* differs from other genera of basal Glires in having a large metaconule, a distinct hypoconulid on lower mo-

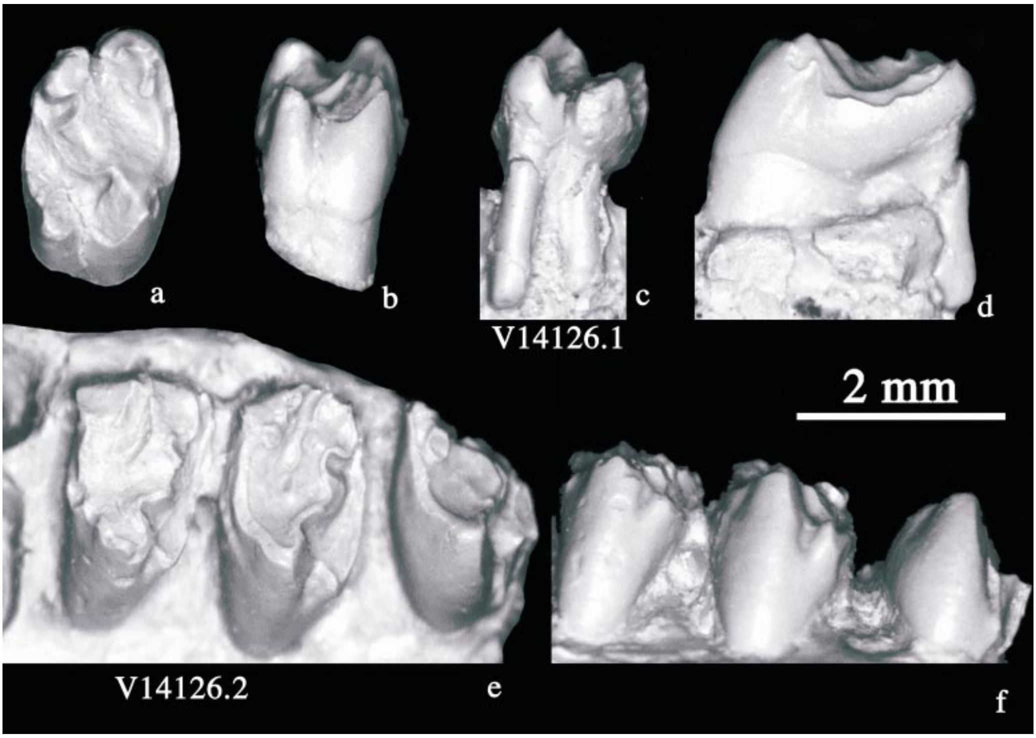

Fig. 1. Upper cheek teeth of *Eomylus bayanulanensis*, n.sp. **a–d,** occlusal, lingual, labial, and anterior views of a right M2 (V14126.1, holotype); **e, f,** occlusal and lingual views of left M1–3 (V14126.2).

lars, and a diagonal wear trough on the talonid. Further differs from *Rhombomylus*, *Matutinia*, *Mimotona*, *Heomys*, *Eurymylus*, *Gomphos*, and *Amar* by its anteroposteriorly shortened upper cheek teeth and less expanded hypocone shelf. Further differs from *Sinomylus* in having a stronger hypocone, more marginally positioned paracone and metacone and more lingually positioned protocone. Further differs from *Tribosphenomys* in having more lophate cheek teeth. The new species differs from *Eomylus zhigdenensis* in having upper cheek teeth less anteroposteriorly shortened and less unilaterally hyspodont; the hypocone and metaconule more prominent; M2 with the paracone and metacone separated by a labial notch; lower cheek teeth less transversely extended; the mandible proportionally shallower. Differs from *E. borealis* in being smaller and molars less transversely extended, and in having a partial anterior cingulid on the lower molars and a relatively smaller hypoconulid.

DESCRIPTION: Association of the upper and lower teeth is based on their comparable sizes (tables 1, 2) and morphology. This association is supported by the fact that the left maxilla with M1–3 (V14126.2) and the fragmentary right mandible with broken m2–3 (V14127.3) were prepared from a single coprolitic nodule. The fragmentary maxilla shows that the posterior border of the hard palate is even with M2. The posterior margin of the palate bears a blunt, rounded lip, the postpalatine torus. This lip continues posteriorly as a ridge that bounds the choanal orifice. Lateral to the ridge is a broad, shallow trough in which a small foramen of unknown function resides. Two small palatine foramina occur within the palatine opposite M1.

Upper premolars are unknown. The alveolus of P4 indicates a large (as wide as M1) double-rooted tooth (fig. 1). The external edges of M1–3 (V14126.2), prepared from a coprolitic nodule in which V14126.2 is also contained, are seemingly etched by acid (fig.

TABLE 1
Measurements of Lower Teeth (in mm)
L = length; W = width; tri = trigonid; tal = talonid; * = nonavailable measurement.

	L	L/W (tri)	L/W (tal)
Palaeomylus lii			
V14132			
p3	1.71		1.55
m1	2.27	0.87/1.86	1.35/2.06
m2	2.26	0.85/1.97	1.35/2.38
m3	3.05	0.82/1.99	2.15/2.07
V14129.1			
m1	1.87	0.91/1.87	0.93/2.11
m2	2.04	0.89/2.03	1.14/2.41
m3	2.85	0.74/1.93	2.10/2.23
V14129.2			
m1	1.98	0.91/*	0.96/1.98
m2	1.93	0.82/*	1.11/2.27
m3	2.92	0.69/1.96	2.28/2.08
V14130.1			
p3	1.30	*/1.17	
p4	1.93		
m1	2.12	1.04/1.77	1.16/1.96
m2	2.44	1.03/2.07	1.37/2.17
V14130.2			
p4	2.05	1.01/1.79	1.03/1.66
m1	1.89	1.12/1.83	0.78/*
m3	3.06	0.98/2.21	2.15/2.26
V14129.3			
m3	3.11	1.02/2.08	2.06/2.32
V14129.5			
m3	3.08	0.90/2.11	2.16/2.26
V14129.4			
m2	2.14	0.85/1.94	1.34/2.24
V14131			
m1	2.27	0.98/1.88	1.20/2.02
m2	2.19	0.98/1.95	1.18/2.21
Palaeomylus sp.			
V14125.1			
p4	2.00	1.08/1.73	0.98/1.42
m1	2.25	0.94/*	1.27/*
V14125.2			
m1	1.96	0.91/1.65	1.04/1.94
Eomylus bayanulanensis			
V14127.1			
m1	1.73	0.83/1.18	0.91/1.53
m2	1.74	0.76/1.43	1.02/1.74
m3	2.22	0.75/1.39	1.67/1.63
Eomylus bayanulanensis			
V14127.2			
m2	1.92	0.82/1.57	1.10/1.76
m3	2.41	0.56/*	1.86/1.56 (est)
V14127.3			
m3	2.59	0.69/1.46 (est)	1.88/165

TABLE 2
Measurements of Upper Teeth (in mm)

	Length	Width
Palaeomylus lii		
V14128		
P4	1.43	3.32
M1	1.84	3.75
Eomylus bayanulanensis		
V14126.1		
M2	1.53	2.51
V14126.2		
M1	1.44	2.70 (est)
M2	1.45	2.80 (est)
M3	1.43	2.40 (est)

1). The first upper molar resembles M2 except in being slightly shorter lingually. The description of the upper molar is based primarily on V14126.1 (the holotype; fig. 1). The tooth is low crowned, wider anteriorly than posteriorly, and has one large lingual and two small labial roots. The protocone is the largest cusp of the tooth and is more lingually extended than the hypocone, although the tips of the two cusps are aligned anteroposteriorly. Lingually, the protocone and hypocone are separated by a shallow valley that deepens toward the hypocone. In occlusal view, the protocone has a large wear facet on its posterior surface; this aligns with the orientation of a wear facet on the posterior surface of the metaconule. The protocone connects with the paracone by a low, strong preprotocrista that forms a curved anterior edge of the tooth. A small, transverse enamel lake is present at the labial end of the preprotocrista and is lingual to the paracone; this suggests the presence of a small paraconule on an unworn tooth. The paracone and metacone are placed on the labial margin of the tooth. The paracone is larger and more labially positioned than the metacone. The two cusps are separated by a notch at the labial edge of the tooth. A small cuspule is at the posterolabial base of the paracone, probably representing the mesostyle. The metaconule is larger than the paracone or metacone. It is connected lingually with the protocone by a short postprotocrista and labially with the metacone by the premetaconule crista. Between the swollen metaconule and the metacone, an enamel bay is formed. The anterior surface of the metaconule is bare dentine, forming part of the concave trigon basin. The hypocone is distinct and separated from the protocone by a narrow valley. It merges labially with the postcingulum, forming the hypocone shelf. The hypocone shelf forms an oblique valley that parallels the plane aligning the wear facets on the posterior sides of the protocone and metaconule. This concave area is covered with thin enamel between the protocone and metaconule, whereas the rest of the shelf is bare dentine. This oblique orientation and the wear facets on the hypocone shelf fit well against the oblique wear facets on the lower molars (see below). The last upper molar is narrower than M1 and M2 and retains the basic molar pattern (fig. 1).

The mandible (V14127.2) is 4.82 mm deep at m1 and 2.42 mm thick at m2. Tooth marks occur on the medial surface of two mandibles (V14127.1–2). Breakages in the mandibles (V14127.1–2), both in cross section and along the lingual surface, reveal no incisor under the molars. The narrow space ventral to roots of molars also indicates that the incisor probably ends anterior to the first molar. The incisor preserved in V14127.3 shows that it probably extends posteriorly to the level of p4. On the lateral surface of the mandible the anterior edge of the masseteric fossa is aligned with the talonid of m3.

No lower premolar is preserved. The molars are all double-rooted. The m1 and m2 differ mainly in m2 being larger (fig. 2). The trigonid is short and has a steep posterior wall. A partial anterior cingulid occurs labially below the protoconid. The protoconid and metaconid are subequal in size, the latter cusp being higher and more anteriorly placed. A wear facet is present on the anterolabial side of the protoconid. A similar facet, having the same orientation, occurs on the hypoconid. The paracristid and protocristid are complete and straight, enclosing the trigonid basin anteriorly and posteriorly. The talonid is longer and wider than the trigonid. All talonid cusps are high. The hypoconid, the largest talonid cusp, is elongated labially. The cristid obliqua is strong and extends anterolingually from the hypoconid to join the posterior wall of the trigonid near its midpoint. In little worn specimens, the mesoconid is distinct. Following wear the cristid obliqua becomes a sharp ridge; the lingual surface of the cristid obliqua forms a flat wear facet that merges posteriorly with the facet on the posterolingual side of the hypoconid, obliterating the mesoconid. The entoconid is anterior to the hypoconid and separated from the hypoconulid by a narrow gap. The gap is deeper on m2 than on m1. The wear facets on the anterolabial surfaces of the entoconid and hypoconulid are extensive, forming the lingual wall of a V-shaped talonid basin that slants from a point between the hypoconid and hypoconulid to the point between the metaconid and entoconid. The valley is oriented diagonally, as indicated by the arrow in figure 2c. Orientations of the valley and the wear facets indicate anterolingual movement of the tooth row during mastication. The hypoconulid is widely and deeply separated from the hypoconid. The cusps are more robust on m3 than on m2; nevertheless, the basic pattern of the two teeth is comparable except that the hypoconulid forms a distinct third lobe on m3. The posterolingual surface of the hypoconulid bears a large wear facet. Unworn m3 in V14127.4 exhibits a distinct mesoconid. A small enamel peak rises between the hypoconid and hypoconulid in V14127.1 (fig. 2e).

COMPARISON: *Eomylus* was named based on specimens from the late Paleocene of Mongolia (Dashzeveg and Russell, 1988), including *E. zhegdenensis* and *E. borealis*. In the same study, another taxon, *Khaychina elongata*, was proposed based on a fragmentary mandible with molars from the Naran Member of the Naran-Bulak Formation. Based on a larger sample of specimens including articulated dentitions from the late Paleocene Zhigden Member of the Naran Bulak Formation at Tsagan Khushu, Kondrashov and Lopatin (2003) were able to recognize that the holotype of *E. zhigdenensis*, a fragmentary maxilla with M1–2, and the holotype of *Khaychina elongata* (PSS 30-3, Dashzeveg and Russell, 1988) are conspecific; thus, *Khaychina* and *K. elongata* are junior synonyms of *Eomylus* and *E. zhigdenensis*, respectively.

In the previous study of the Bayan Ulan

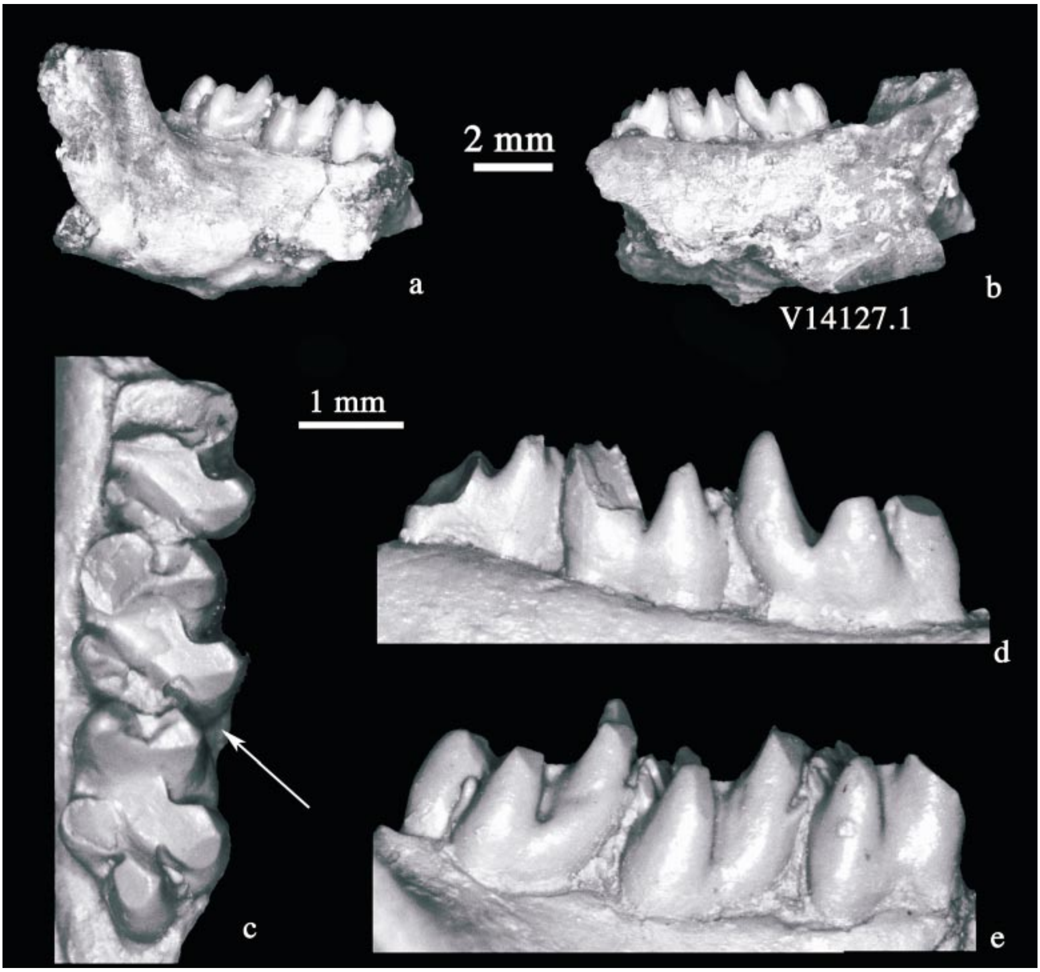

Fig. 2. Lower cheek teeth of *Eomylus bayanulanensis*, n.sp. **a, b,** lateral and medial views of a partial right mandible with m1–3 (V14127.1); **c–e,** occlusal, lingual, and labial views of m1–3. Arrow indicates the direction of trough created by wear.

Fauna, Meng et al. (1998) tentatively referred some specimens that have the incisor ventral to the cheek teeth and ending at the first molar to ?*Khaychina elongata*, although the possibility that these specimens represent a new taxon was also entertained. The diastema on the fragmentary mandible (V14127.3) appears long, which is the main reason for the tentative referral, but the lower cheek teeth resemble those of *Khaychina elongata* (Dashzeveg and Russell, 1988). For instance, as recognized by Dashzeveg and Russell (1988: 143), an oblique groove crosses the talonid basin of *Eomylus* from the notch between the metaconid and entoconid to another notch between the hypoconid and hypoconulid; the hypoconulid is well separated from both the entoconid and hypoconid and on m3 forms a distinct third lobe. Given the observations of Kondrashov and Lopatin (2003), however, *Khaychina* should be a junior synonym of *Eomylus*. With additional specimens, particularly upper cheek teeth collected since 1998, we here regard these Bayan Ulan specimens as a new species.

Eomylus bayanulanensis differs from *E. zhigdenensis* in having upper cheek teeth less anteroposteriorly shortened and less unilaterally hyspodont. In addition, the molar hypocone and metoconule are more distinct and there is a labial notch between the paracone and metacone on M2. The lower cheek teeth of the two species are similar in size and shape. The m1 and m2 of *Eomylus bayanulanensis* are less transversely extended. In contrast, these teeth are wider than long in *E. zhigdenensis*. The partial anterior cingulid on the lower molars of *E. bayanulanensis* is not seen in *E. zhigdenensis*. In addition, the mandible of *E. bayanulanensis* is proportionally shallower than that of *E. zhigdenensis*.

Eomylus borealis was originally referred to *Mimotona* and distinguished from other species of *Mimotona* by the presence of a single incisor in the mandible (Chow and Qi, 1978). This difference was considered sufficient to place the specimen in the eurymylid genus *Eomylus* (Dashzeveg and Russell, 1988). *Eomylus borealis* differed from *E. zhigdenensis* ‘‘by its greater size and by the presence of a deep groove in the lower molars between the hypoconid and the hypoconulid’’ (Dashzeveg and Russell, 1988: 138). However, the lower dentition referred to *E. zhigdenensis* is now considered to be from an unnamed species of *Sinomylus* and the lower jaw originally referred to *Khaychina elongata* (PSS 30-3) is now transferred to *E. zhigdenensis* (Kondrashov and Lopatin, 2003). Dashzeveg and Russell (1988) did not make comparisons between the lower jaw of *E. borealis* and PSS 30-3. Although *E. borealis* is larger than *E. zhigdenensis* (based on PSS 30-3) in terms of lower cheek tooth dimensions, the ‘‘deep groove in the lower molars between the hypoconid and the hypoconulid’’ is no longer diagnostic of *E. borealis*. This condition is present in the three species currently recognized in the genus. The features that are unique to PSS 30-3 include a long diastema between the incisor and p3, the proclivity of the incisor, and shallow anterior part of the mandible (Dashzeveg and Russell, 1988). These features are not preserved in the holotype of *E. borealis*. Dashzeveg and Russell (1988: 141), however, recognized that PSS 30-3 further differs ‘‘from *Eomylus* by having lower crowned molars with a smaller hypoconulid’’. Thus, it can be rephrased that *E. borealis* differs from *E. zhigdenensis* in being larger and having higher crowned molars with larger hypoconulids.

Eomylus bayanulanensis is the smallest of the three species, although the size differences between these species are not significant. Its m1 and m2 are less transversely extended than those of *E. borealis*. The partial anterior cingulid on the lower molars and relatively smaller hypoconulid of *E. bayanulanensis* also distinguish it from *E. borealis*.

Palaeomylus, new genus

TYPE SPECIES: *Palaeomylus lii*, n.sp., the only species of the genus.

DIAGNOSIS: Differs from other early diverging members of Glires in having on upper molars a weak centrocrista between the paracone and metacone, distinct conules close to the paracone and metacone but distant from the protocone, and a distinct hypolophid connecting the pointed entoconid and the hypoconid on m3. Further differs from *Mimotona*, *Gomphos*, and *Sinomylus* in possessing only a single, evergrowing lower incisor (presumably di2) in each lower jaw. Further differs from *Sinomylus* in being larger, cheek teeth less unilaterally hypsodont, the apex of the protocone more lingual and confluent with the hypocone, weaker lophs but more distinct conules, lack of a mesostyle, a simpler p4 (the p4 of *Sinomylus* illustrated in Dashzeveg and Russell, 1988, has a better developed trigonid), and stronger hypolophid. Further differs from *Tribosphenomys* in being much larger, having a stronger hypocone shelf, more labially positioned conules, lack of an external cingulum, lower teeth more lophate than cuspate, and better developed posterior lobe on m3. Further differs from *Eurymylus*, *Rhombomylus*, and *Matutinia* in being smaller and having more cuspate cheek teeth that possess a less developed hypocone shelf. Further differs from *Eomylus* in having a low, transverse hypoconulid on m1–2, in lacking a diagonal shearing pattern, in having a broader third lobe on m3. Further differs from *Heomys* in having less inflated cusps.

Palaeomylus lii, new species

HOLOTYPE: IVPP V14128, a fragmentary right maxilla with P4 and M1 (fig. 3).

REFERRED SPECIMENS: V14129.1, a fragmentary left mandible with m1–3; V14129.2,

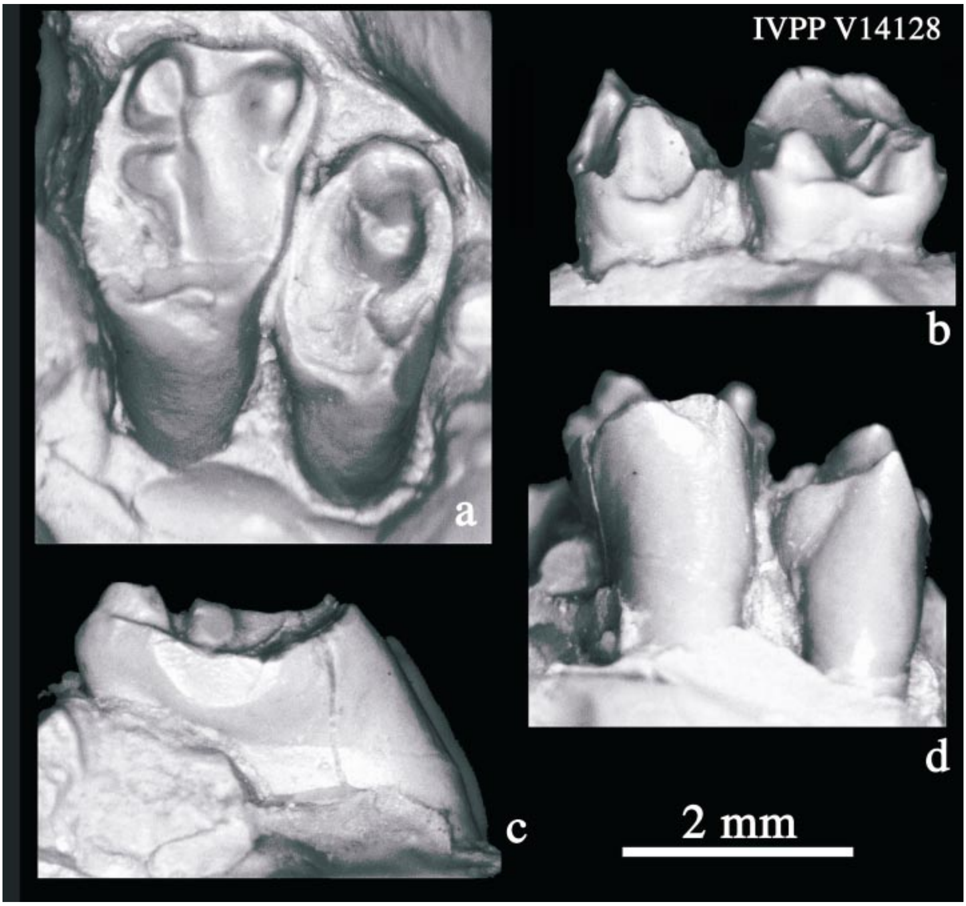

Fig. 3. Occlusal, labial, posterior, and lingual views of P4–M1 of *Palaeomylus lii*, n.gen. and n.sp. IVPP V14128, holotype.

a fragmentary left mandible with m1–3; V14129.3, a fragmentary right mandible with m3; V14129.4, a fragmentary left mandible with m2; V14129.5, a fragmentary right mandible with m3; V14129.6, a fragmentary left mandible with talonid of m2 (a young individual); V14130.1, a fragmentary left mandible with p4, m3, and partial m1–2 (from the same individual of V14130.2); V14130.2, a fragmentary right mandible with p3–m2 (p4 and m1 broken); V14130.3, a left partial femur and innominate (associated with V14130.1–2); V14131, a fragmentary right mandible with m1–2; V14132, a left mandible with erupting p4 and m1–3. Numerous fragmentary mandibles with broken teeth are not numbered. See tables 1 and 2 for measurements.

LOCALITY AND AGE: Upper part of the Nomogen Formation at Bayan Ulan, Inner Mongolia; late Paleocene.

ETYMOLOGY: *Palaeo* (Greek), ancient; *mylos* (Greek), grinder or millstone, in analogy with *Eurymylus*, *Eomylus*, *Rhombomylus*, and *Sinomylus*. The trivial name honors Professor Chuankui Li for his landmark contributions to the study of Glires.

DESCRIPTION: The posterior edge of the anterior root of the zygoma lies lateral to the anterior half of M2. The tips of the P4–M1 roots are exposed in the floor of the orbit. The third upper premolar is not preserved; its alveolus indicates a double-rooted tooth that is narrower than P4. The nonmolariform P4 is also double-rooted and has an oval outline in occlusal view (fig. 3). One cusp occurs at the anterolingual corner of the tooth; its anterior surface bears a flat wear facet. No contact facet for P3 occurs on the anterior surface of P4. Three ridges emanate from the lingual cusp. The anterior ridge (anteroloph) extends labially, forming the anterior edge of the tooth. The central one of the three ridges curves to meet the lingual base of the labial cusp. A small depression occurs between this ridge and the anteroloph. The third ridge (posteroloph) runs posteriorly from the lingual cusp, and bends labially at the posterolingual corner of the tooth, extending in a gentle curve to reach the labial margin of the tooth. The extended posterolingual corner suggests a hypocone. An elongate basin is formed between the posterior and the middle ridges. The labial cusp is conical and a short ridge projects from it posterolabially to join the posteroloph.

A large lingual root and two small labial ones occur on M1. The tooth's lingual surface bears a shallow depression bordering the protocone and hypocone. The protocone forms a curved ridge that is continuous anteriorly with the preprotocrista and posteriorly with a crescentic hypocone (fig. 3). The preprotocrista, made up of thick enamel, is low and curved; it ends labially at the small paraconule. Because the paraconule is positioned labially very near the paracone, the preprotocrista is unusally long. A short, curved postparaconule crista connects the paraconule and the base of the paracone. The preparaconule crista extends anterolabially to the anterolabial base of the paracone. The boundary between the protocone and hypocone is indistinct in occlusal view. The latter is slightly more lingually positioned. The metaconule is as large as the metacone and is situated much nearer the metacone than the protocone. The long postprotocrista is faint near the protocone but strengthens toward the metoconule. The metaconule's posterior surface is rounded and covered by enamel. Light wear is reflected on the posterior surfaces of the metaconule and metacone. In contrast, the anterior surface of the metaconule is a heavily worn facet of bare dentine, which slopes into the large, transversely oriented trigon basin. A short premetaconule crista connects the metaconule and metacone. The paracone and metacone are roughly equal in size and are connected by a weak centrocrista. The paracone is the transversely wider of the two cusps and tapers lingually. A narrow cingulum is present at the labial base of the paracone. The metacone is roughly conical, but its tip is broken. There is no cingulum on the external side of the metacone. The postcingulum is low, long, and convex posteriorly. The hypocone shelf is sizable and concave. The thin enamel that covered the shelf has been eliminated by wear; the area adjacent to the metaconule still bears enamel. A contact facet for M2 is present on the posterior surface of M1.

Several fragmentary mandibles bear tooth marks. The best preserved mandibles are V14132 and V14130.1–2 (figs. 4, 5). V14132 is from a relatively young individual because its p4 is not erupted and the molars are little worn, whereas V14130.1–2 are from an old individual, of which the teeth are deeply worn. The symphysis of V14132 is partially preserved and is an inclined, simple articular surface. In V14130.1–2 the symphysis is much more extensive with uneven articular surface, the morphology being possibly age related. The lower diastema is 4.6 mm long in V14130.1 and 3.2 mm in V14132; the mandible is 6.7 mm deep at m1 and 3.48 mm thick at m2 in V14130.1 and 4.8 and 3.0 at the same positions in V14132. There are two mental foramina on the lateral surface of the mandible, a large one under p3 and a small one under p4. One or two very small foramina are also present lateral to the diastema. Ventrally the mandible bears numerous small fenestrations. The anterior edge of the masseteric fossa is even with the m3 trigonid and ends at a knob.

The lower dental formula is 1-0-2-3. The incisor is slender, measuring 1.39 mm wide and 1.75 mm thick in V14130.1, and 1.1 by 1.36 mm in V14132, again a difference due to age. It extends posteriorly to the talonid of m3 and is positioned ventromedial to the roots of the cheek teeth. Therefore, a protuberance is created on the lingual surface below the molars. In V14132, the incisor is complete and is 15.7 mm long, of which the exposed tip is a small portion (2.2 mm). The entire lingual surface of this exposed tip bears a wear facet. The wear facet is oval and forms a step at its base. The tip of the incisor is at a position slightly lower than the

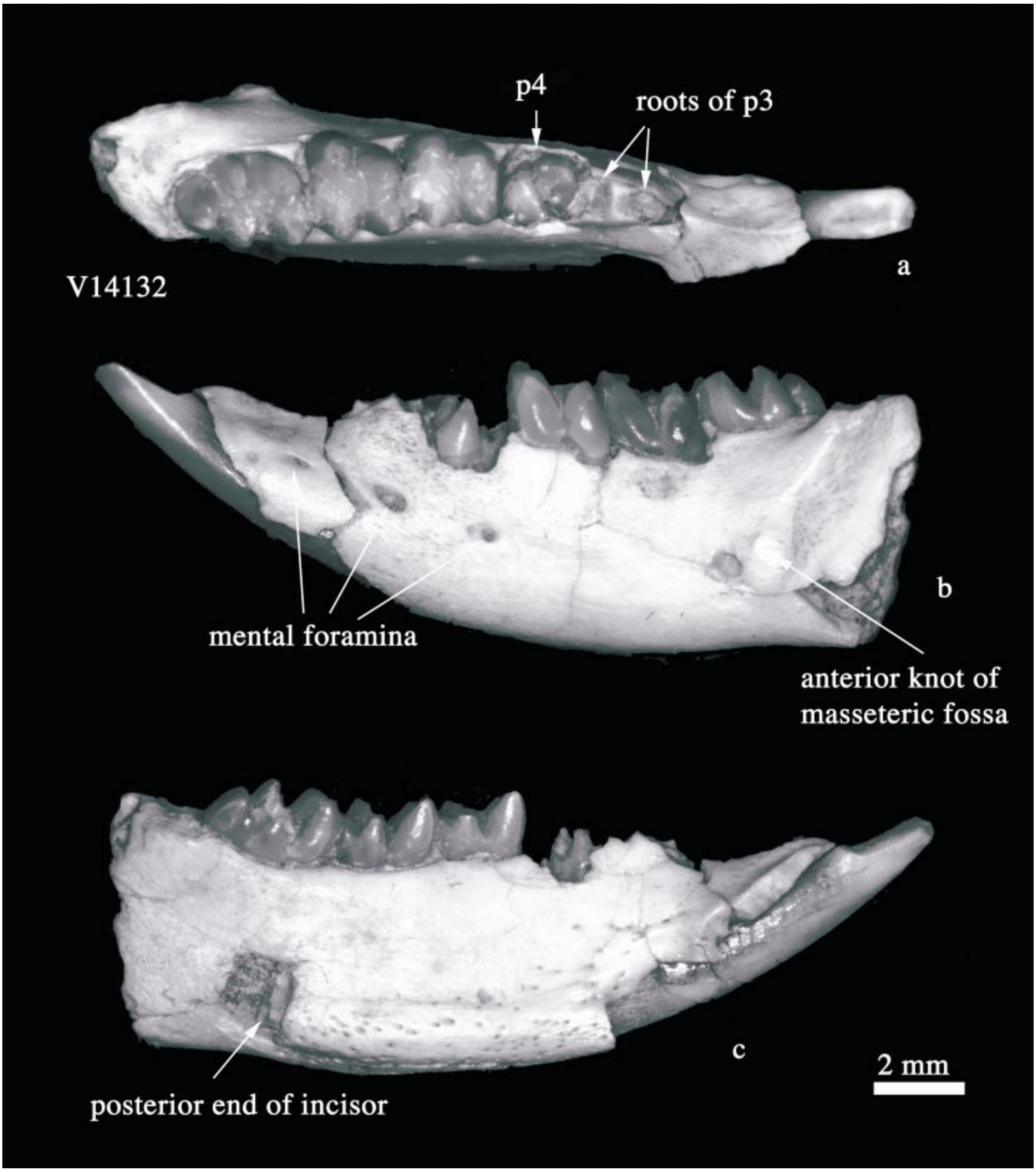

Fig. 4. Occlusal, labial, and lingual views of the left mandible of *Palaeomylus lii* (V14132).

occlusal surface of the cheek teeth (fig. 4). The incisor enamel is thin. As in other Glires, it is distributed along the entire tooth longitudinally but mainly on the labial surface of the tooth. The incisor increases in width posteriorly.

The p3 is preserved only in the right mandible (V14130.2). It is small, nonmolariform, and double-rooted (figs. 5, 6). The trigonid consists of only one large cusp, of which the posterior surface bears a flat wear facet. A cingulid cusp lies at the anteromedial base of the main cusp. The talonid is a simple, low and transverse ridge.

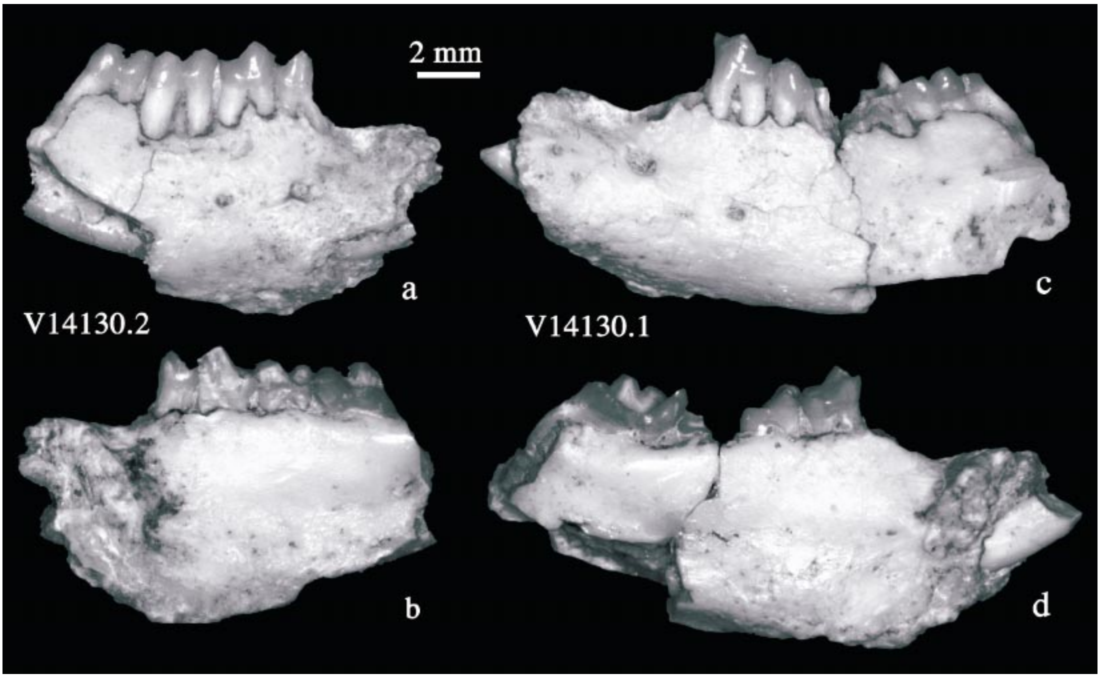

Fig. 5. **a, b,** Labial and lingual views of a fragmentary right mandible with p3–m2 of *Palaeomylus lii* (p4 and m1 broken) (V14130.2); **c, d,** labial and lingual views of a fragmentary left mandible with p4, m3, and partial m1–2 (V14130.1). The jaws are from the same individual.

The p4 is partially erupted in V14132, and in occlusal view its crown pattern is visible (fig. 7). The trigonid of the nonmolariform tooth consists of two cusps, with the lingual one (presumably the metaconid) being higher than the labial one (presumably the protoconid). Anterior and posterior ridges extend from the labial cusp to the anterior and posterior bases of the lingual cusp, respectively, defining a closed trigonid basin. The bases of the two cusps meet at the center of the trigonid basin. The talonid is narrower and lower than the trigonid. The lingual cusp (presumably the entoconid) on the talonid is conical and from it a narrow crest extends to a ridgelike cusp (presumably the hypoconid) at the labial side of the talonid. The trigonid and talonid are separated by a broad transverse valley in which there is no trace of the cristid obliqua. The p4 in V14130.1 (fig. 6) was worn. A crescentic trigonid basin develops between the trigonid cusps; the posterior wall of the trigonid forms a steeply sloping surface that sweeps posteriorly into the concave, structureless talonid basin.

The m1 and m2 are similar except that m2 is larger (figs. 7–8). They differ from p4 in that the talonid is wider and longer than the trigonid and has more differentiated cusps. The protoconid is much lower than the metaconid and has a wear facet on its tip that continues to its labial surface. The paracristid extends to the anterior side of the metaconid and is separated from the latter by a narrow groove. The paraconid is absent. The metaconid is pointed and extends anterolabially toward the paracristid. An extensive wear facet covers the anterolabial surface of the cusp. The protocristid is lower but thicker than the paracristid. Diverging from the condition seen in *E. bayanulanensis*, where the protocristid directly joins the metaconid, the protocristid curves around and reaches to the posterolingual side of the metaconid. Following moderate wear, the trigonid basin takes on the shape of a crescentic enamel lake between the metaconid and protocristid. The posterior wall of the trigonid is inclined anteriorly and bears a large wear facet. The trigonid becomes shaped by two major facets,

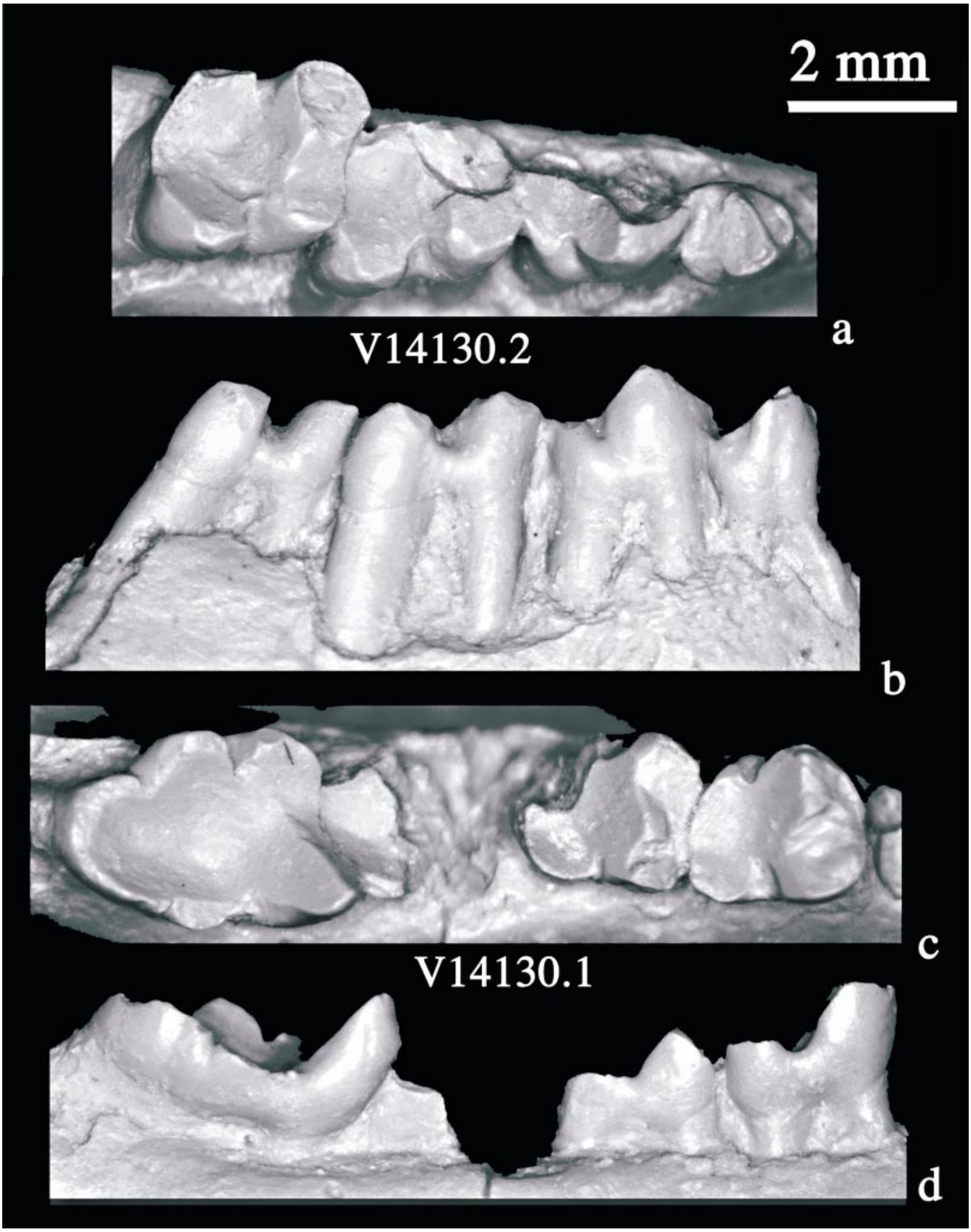

Fig. 6. **a, b,** Occlusal and labial views of p3–m2 of *Palaeomylus lii* (p4 and m1 broken) (V14130.2); **c, d,** occlusal and lingual views of p4, m3, and partial m1–2 (V14130.1). The jaws are from the same individual.

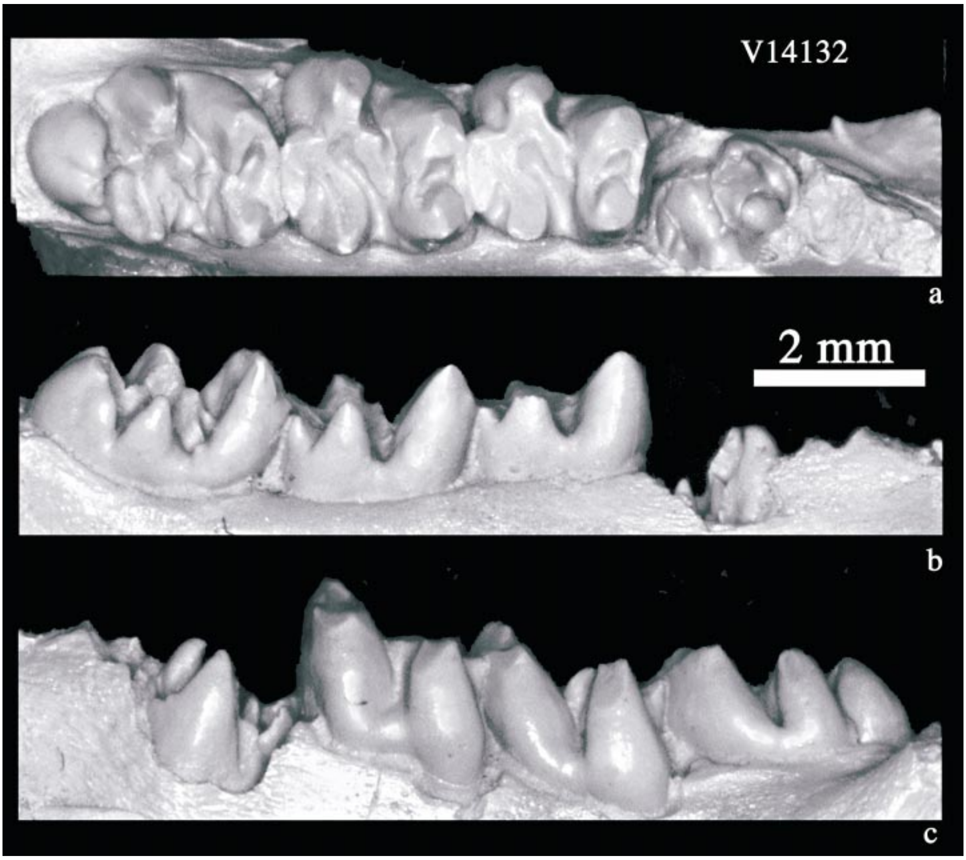

Fig. 7. Occlusal, lingual, and labial views of left lower cheek teeth of *Palaeomylus lii* (V14132).

a horizontal (occlusal) anterior one and a sloped posterior one, in later wear stages. The occlusal trigonid wear surface is level with the hypoconulid of the preceding tooth, thus forming a posterior functional extension of the talonid of the preceding tooth.

Specimen V14129.6 (not illustrated) is an unworn m2 talonid from a young individual. It shows that the cusps were originally pointed and the ridges sharp. Other specimens show various degrees of wear. The hypoconid is the largest cusp of the talonid and is labially extended. As with the protoconid, a wear facet marks the labial surface of the hypoconid. The cristid obliqua is short but broad, bears a mesoconid, and merges to the posterior wall of the trigonid at the midpoint. The entoconid is the highest cusp of the talonid, from which the well-developed hypolophid extends posterolabially to join the hypoconulid. It is eradicated early in wear and all cusps become confluent with the talonid basin. The hypoconulid is transversely stretched and becomes either completely obliterated or is recognizable only as a small notch separating it lingually from the entoconid. At this stage of wear the flat hypoconulid abuts the protoconid of the following tooth. The talonid basin is broad, concave, and smoothly polished after wear.

The m3, the longest lower molar, displays considerable variation (figs. 6–8) between specimens. The metaconid remains a tall cusp even after the tooth is deeply worn, but is frequently broken. The talonid is slightly narrower but is much longer than on m2, owing to the presence of the third lobe formed of a large hypoconulid. In some specimens the m3 hypoconulid lobe consists of a single cusp, but in V14129.1 and V14132 it is bifurcated into two, relatively smaller cusps (figs. 7, 8). The entoconid is distinct and is

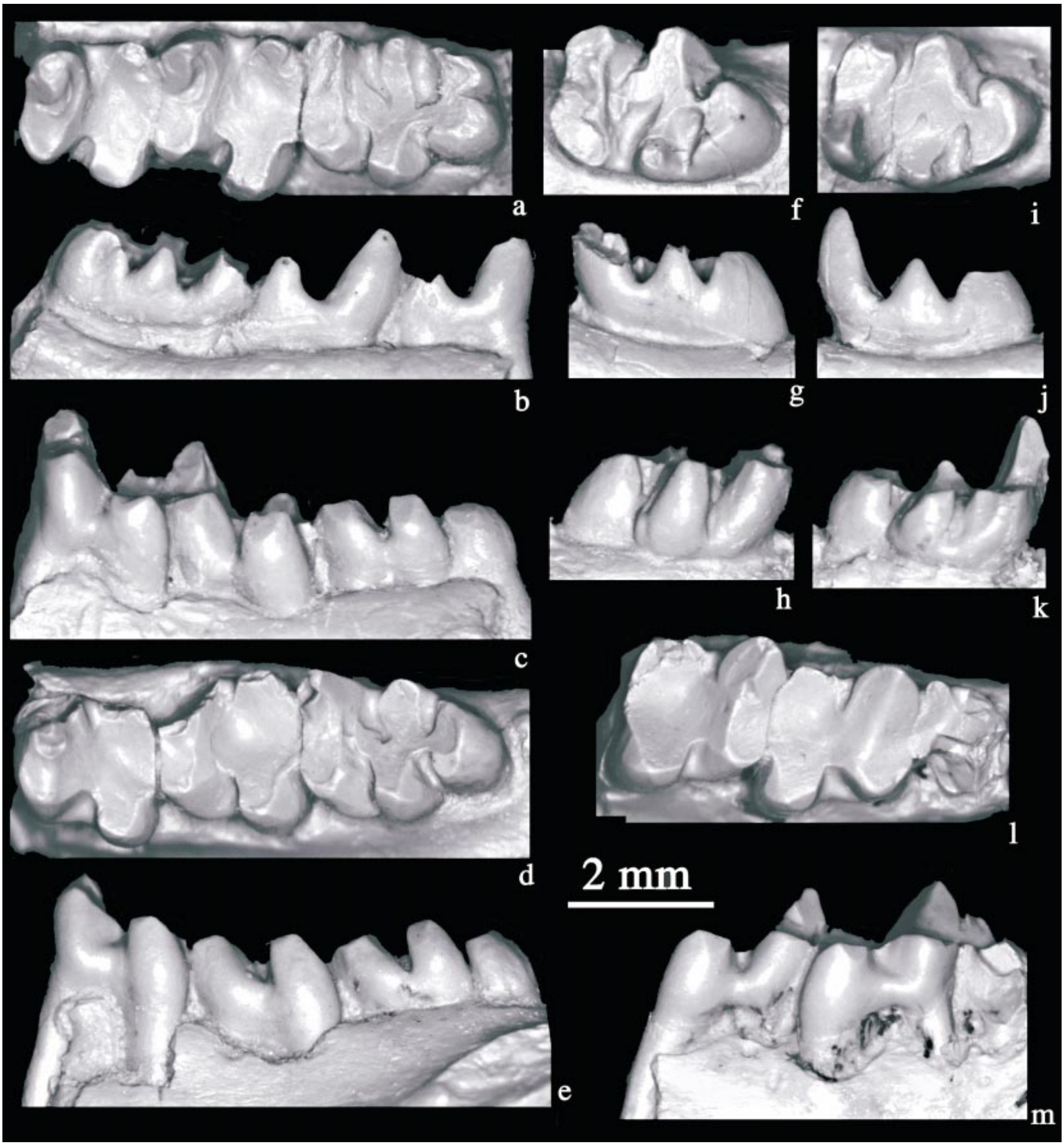

Fig. 8. Lower cheek teeth of *Palaeomylus lii*. **a–c,** Occlusal, lingual, and labial views of left m1–3 (V14129.1); **d, e,** Occlusal and labial views of left m1–3 (V14129.2); **f–h,** Occlusal, lingual, and labial views of right m3 (V14129.3); **i–k,** Occlusal, lingual, and labial views of right m3 (V14129.5); **l, m,** Occlusal and labial views of right m1–2 (V14131).

aligned transversely with the hypoconid. It is separated from the hypoconulid by a broad, deep valley. Unlike in m1–2, the m3 hypolophid does not merge to the hypoconulid directly; instead, it joins the ridge that connects the hypoconid and hypoconulid. Following wear, the cusps and crests from flat surfaces with low, wide outer edges. Further wear erases all structures within the talonid, leaving only a broad, concave basin that is deepest lingually as shown in V14130.1 (fig. 6).

A left partial femur and pelvis (V14131.3; fig. 9) were recovered from the same nodule containing V14130.1–2, indicating the likely

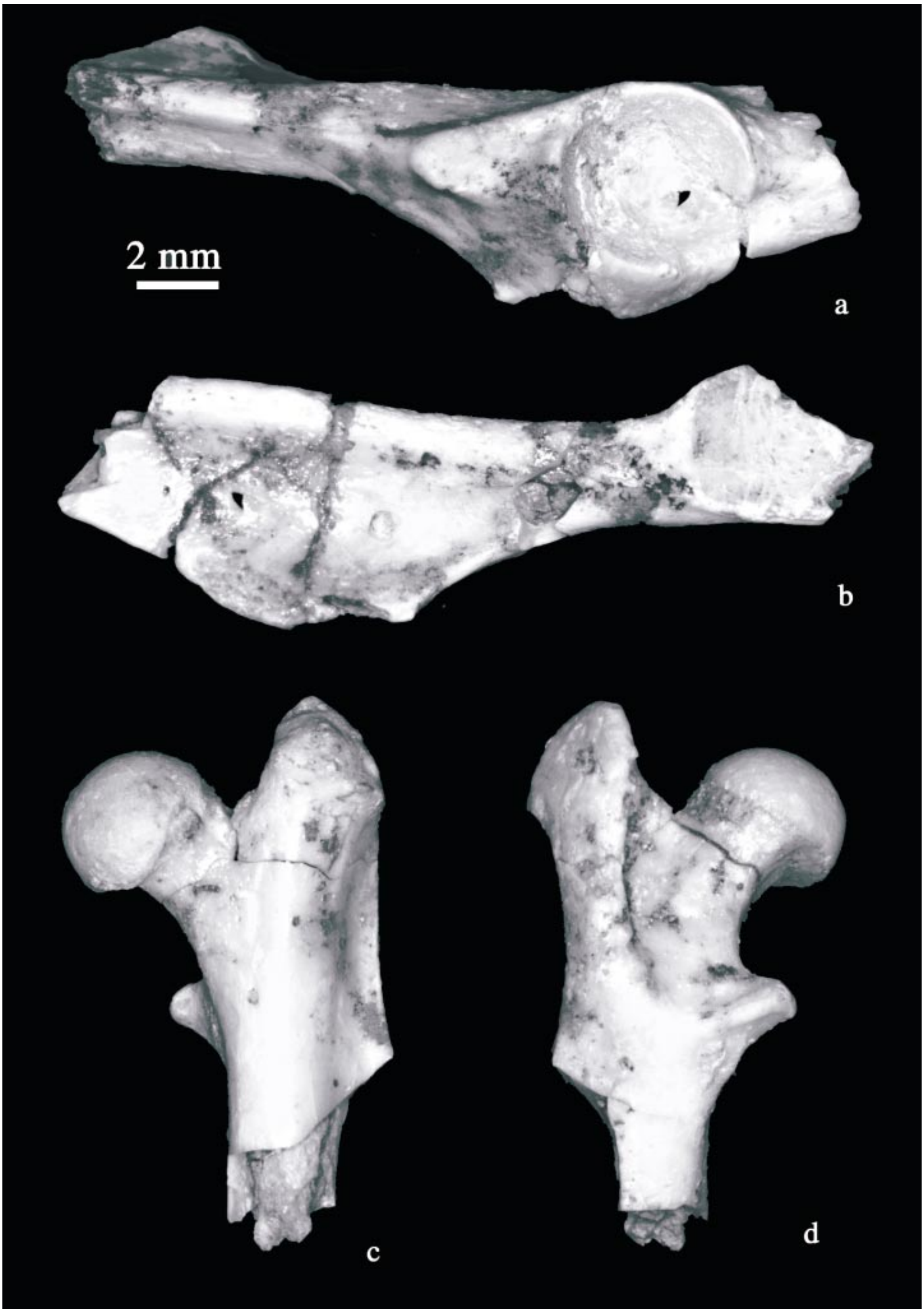

Fig. 9. **a, b,** Lateral and medial views of a left partial pelvis; **c, d,** anterior and posterior views of the proximal portion of a left partial femur of *Palaeomylus lii* (V14132; associated with V14130.1–2).

association of these specimens. The anterior portion of the ilium is broken but a prominent posterior iliac spine, forming the anterior edge of a greater sciatic notch, is preserved. The medial surface preserves a partial, shallowly concave articular facet for the sacrum. A prominent femoral process lies anterior to the acetabulum that is deep and nearly hemispherical in shape and bears a well-defined rim except posteroventrally, where it is indented by the acetabular notch. The notch is deep and extends as a groove anterodorsally onto the upper surface of the acetabulum. The groove divides the lunate surface into two portions. The posterodorsal band of the lunate surface is narrow and bears a prominent ventral process that bounds the deep acetabular notch laterally. The rest of the lunate surface surrounds the nonarticular surface in the center of the acetabulum except at the acetabular notch. The medial surface of the innominate is a large, concave area. The sutures between ilium, ischium, and pubis are completely fused and no longer visible. The proximal portion of the left femur is preserved. The femoral head is well defined and has a globular articular surface. The greater trochanter is robust and is more proximally extended than the femoral head. The lateral surface of the greater trochanter is a low, curved ridge, which would extend distally to the third trochanter. The greater trochanter is marked posteriorly by a prominent trochanteric crest that overhangs a deep, pocketlike trochanteric fossa. The lesser trochanter forms a low triangular flange, projecting posteromedially from the shaft. A rounded ridge runs laterally from the lesser trochanter to meet the trochanteric crest of the greater trochanter.

COMPARISON: The collection from the late Paleocene Zhigden Member of the Naran Bulak Formation at Tsagan Khushu also includes articulated upper and lower dentitions of a new species of *Sinomylus* (Kondrashov and Lopatin, 2003; Lopatin and Kondrashov, 2003). According to Kondrashov and Lopatin (2003), the lower jaws and teeth of the unnamed species are identical to those tentatively referred to *Eomylus zhigdenensis* by Dashzeveg and Russell (1988). Moreover, the mandible of the unnamed species of *Sinomylus* has an i3, leading Kondrashov and Lopatin (2003) to assign *Sinomylus* a dental formula intermediate between Mimotonidae and typical Eurymyloidea (since mimotonids have two pairs of incisors in both upper and lower jaws whereas eurymylids have single incisors in each jaw). Whether *Sinomylus zhaii* (McKenna and Meng, 2001) also has an i3 is unknown.

Although the lower cheek teeth resemble those originally referred to *E. zhigdenensis* by Dashzeveg and Russell (1988), now allocated to a new species of *Sinomylus* (Kondrashov and Lopatin, 2003), the new taxon from Bayan Ulan certainly lacks i3, which distinguishes *Palaeomylus* from *Sinomylus*. In addition to absence of i3, cheek teeth of the new taxon also differ from those of ''*E. zhigdenensis*'' in several respects, as indicated in the diagnosis.

Palaeomylus sp.

Eomylus borealis; Dashzeveg and Russell, 1988: 138.

Eomylus borealis; Meng, Zhai and Wyss, 1998: 168.

REFERRED SPECIMENS: V14125.1, fragmentary left mandible with erupting p4 and partial m1; V14125.2, an isolated right m1; V14125.3, a talonid of left m3; V14125.4, a talonid of right m2; V14125.5, a fragmentary right mandible with broken incisor and roots of p3–m2 are preserved.

LOCALITY AND AGE: Upper part of the Nomogen Formation at Bayan Ulan (within the lower 3 m of the section), Inner Mongolia; late Paleocene.

DESCRIPTION: The fragmentary mandible (V14125.5) has two mental foramina, one below p3 and the other below the trigonid of m1. The mandible is 5.84 mm deep at m1. The incisor extends posteriorly to at least below m2. Breakage near m2 reveals that the incisor lies ventromedial to the root of the tooth. Because of the position of the incisor, the mandible is quite thick (3.65 mm at m2).

The p4 in V14125.1 is well preserved (fig. 10a–c). It is partially erupted and is unworn. The tooth is nonmolariform. The trigonid consists of two cusps of roughly equal size. The lingual cusp is higher than the labial one. Anterior and posterior ridges extend from the labial cusp to the anterior and posterior bases

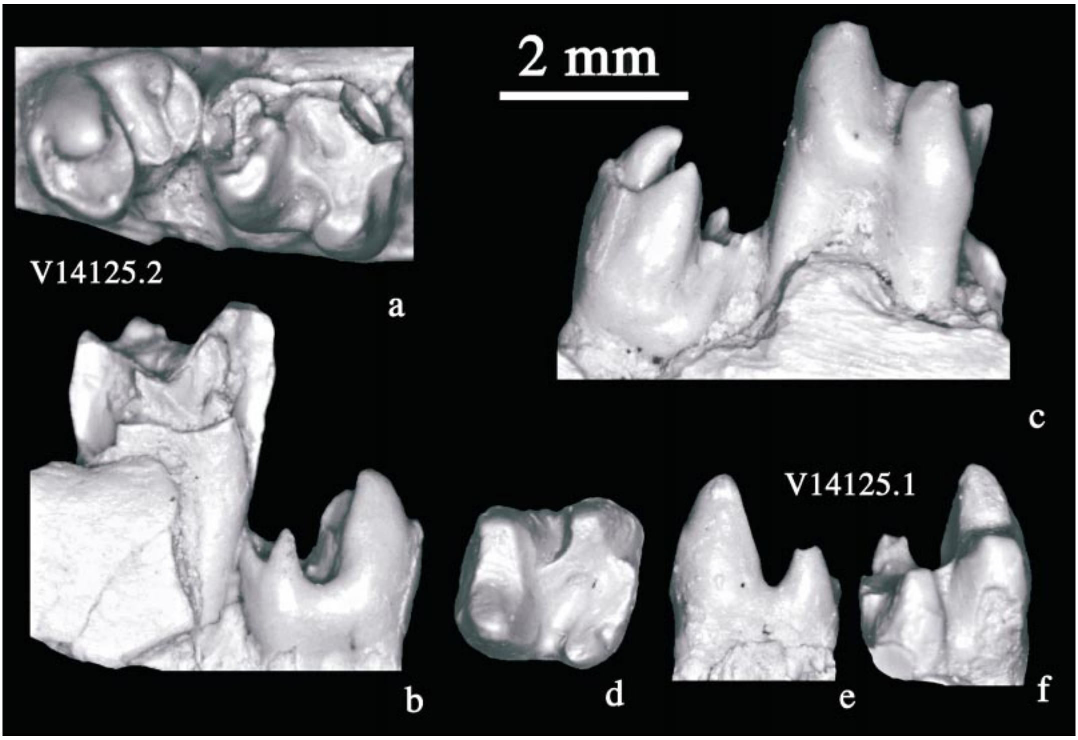

Fig. 10. **a–c,** Occlusal, lingual, and labial views of left p4–m1 of *Palaeomylus* sp. (V14125.1). **d–f,** Occlusal, lingual, and labial views of a right m1 of *Palaeomylus* sp. (V14125.2).

of the lingual cusp, defining a closed trigonid basin. In the center of the basin, the bases of the two cusps merge. The talonid is narrower and lower than the trigonid. The only distinct cusp occurs lingually; from it a narrow ridge extends across the talonid to the labial border of the tooth. The lateral and posterior borders of the talonid are ridgelike and do not form a cusp.

The trigonid of m1 (V14125.2) is anteroposteriorly compressed, and the metaconid is higher than the protoconid (fig. 10d–f). The anterior and posterior arms of the protoconid are weak, and join the anterior and posterior bases of the metaconid to enclose a small, crescentic trigonid basin. The talonid is longer and wider than the trigonid. The hypoconid is the largest talonid cusp and projects labially. A strong cristid obliqua extends from the hypoconid to the posterior base of the trigonid at the midpoint. There seems to be no mesoconid. The entoconid is conical and is connected to a low, transverse hypoconulid. The talonid of m3 (V14125.3) is heavily worn. It has the third lobe formed by the hypoconulid, similar to that of *Palaeomylus lii* (V14130.1).

COMMENTS: These specimens were collected from the lowest 3 m within the Bayan Ulan section in the 1970s. They were previously referred to *Eomylus borealis* (Dashzeveg and Russell, 1988; Meng et al., 1998). Meng et al. (1998) cautioned, however, that referral of the specimens from Bayan Ulan to *Eomylus* was provisional, inasmuch as the diagnosis for *Eomylus* (Dashzeveg and Russell, 1988) was based exclusively on the upper dentition, while the Bayan Ulan specimens then available (to Dashzeveg and Russell) consisted solely of lower teeth. These specimens are certainly different from those assigned to *Eomylus bayanulanensis* in being larger and with the incisor extending posteriorly beyond and ventrolateral to the roots of the molars. The p4 in V14125.1 is similar to that of *Palaeomylus lii* but is larger and more robust. The general morphology of these specimens is comparable to that of *P.*

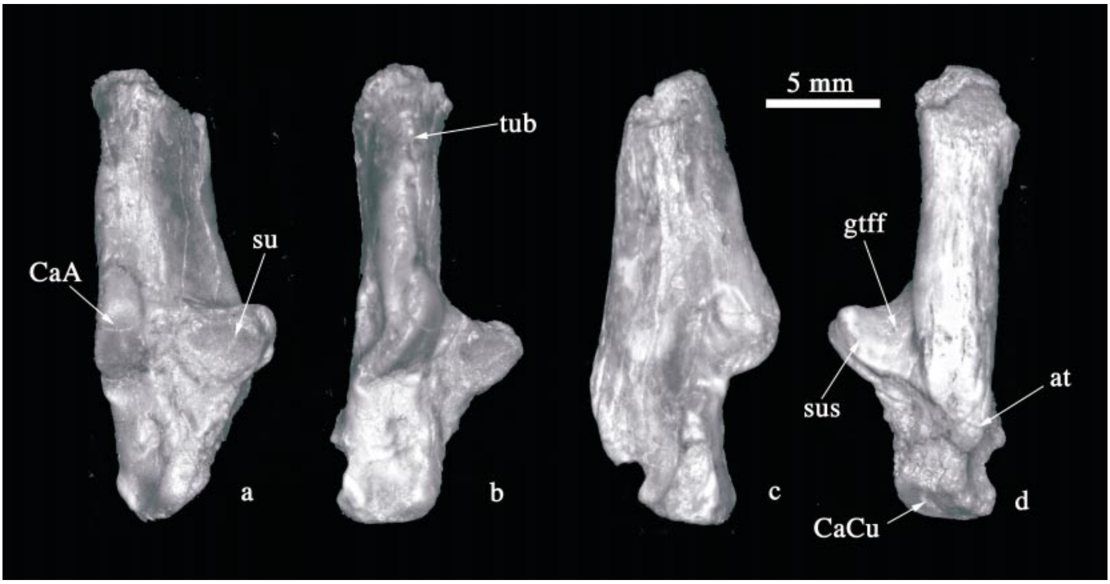

Fig. 11. **a–d,** Dorsal, lateral, ventral, and medial views of the right calcaneus of *Gomphos* (V14133.1). Abbreviations: **at,** anterior plantar tubercle; **CaA,** calcaneoastragalar facet; **CaCu,** calcaneocuboid facet; **gtff,** groove for the tendon of **M.** flexor fibularis; **su,** sustentacular facet; **sus,** sustentaculum talus; and **tub,** tuber of the calcaneus.

lii, but they are too fragmentary to warrant more precise identification.

DUPLICIDENTATA ILLIGER, 1811

Gomphos sp.

REFERRED SPECIMENS: Two calcanea (V14133.1–2).

LOCALITY AND AGE: Bed 6 of the Bayan Ulan section, possibly early Eocene.

DESCRIPTION: Of the two calcanea, one lacks the epiphysis and the other is broken at the sustentacular talus. The calcaneus has a long, strong tuber, which is about half of the total length of the bone (measured from the posterior edge of the calcaneoastragalar facet) (fig. 11). In dorsal view, the calcaneoastragalar facet and the sustentacular facet are aligned roughly at the same level. The calcaneoastragalar facet is a narrow convex band extended in a proximodistal direction, nearly parallel to the long axis of the bone. The sustentacular facet is somewhat rounded and concave. A narrow sulcus calcanei separates the two facets. In plantar view, the anterior plantar tubercle is low and blunt. The peroneal process is strong. Between the process and the anterior plantar tubercle is a broad, concave area. A distinct pit is present on the plantar side of the peroneal process. The dorsal side of the peroneal process bears the calcaneoastragalar facet. In distal view (not shown), the calcaneocuboid facet is large, concave, and oblique, with the lateral edge extending more distally than the medial one; the medial edge is notched. Between the notch and the broad groove for the tendon of the flexor fibularis—on the plantar side of the process bearing the sustentacular facet—is a concave area with a rough surface, in which resides a small foramen of unknown function. There is no calcaneal canal.

COMPARISON: Thus far there is only one named species of *Gomphos*, *G. elkema*, from the Lower Eocene of Asia. The species was first known from the Bumban beds of the Naran Bulak Formation, Mongolia (Shevyreva et al., 1975; Zhegallo and Shevyreva, 1976; Dashzeveg and Russell, 1988). Additional material assigned to this species was discovered recently from the Huheboerhe section of Inner Mongolia (Meng et al., 2004) and from the Bumban beds of the Naran Bulak Formation, Mongolia (Meng et al., 1999). The calcaneus of *Gomphos* is similar to that of *Mimolagus* (Bohlin, 1951; Bleefeld and McKenna, 1985; Szalay, 1985) but is significantly smaller. In both genera, the calcaneus shares several unique features: the tuber of the calcaneus gradually expanding distally; the calcaneoastragalar and the sustentacular facets being aligned at the same level; the calcaneoastragalar facet being a narrow convex band in a distoproximal orientation, nearly parallel to the long axis of the bone; a distinctive pit being present on the plantar side of the process bearing the calcaneoastragalar facet; astragalonavicular facet on the head of the calcaneus with similar orientation; and the astragalus being ventrodorsally (or anteroposteriorly) narrow (Meng et al., 2004). The calcaneus of *Gomphos* is therefore distinctive from those of other Paleocene–Eocene Glires. In general shape, the calcaneus of *Gomphos* and *Mimolagus* is most comparable to that of lagomorphs, but in both genera some primitive calcaneal features, such as absence of a calcaneofibular facet on the calcaneus and the distal portion of the calcaneus not elongated, differentiate them from lagomorphs.

DISCUSSION

HIGHER LEVEL TAXONOMY: Glires refers to the least inclusive clade that consists of extant rodents and lagomorphs and their stem taxa usually termed eurymylids, mimotonids, or mixodonts (Li and Ting, 1985, 1993; Dashzeveg et al., 1987, 1998; Li et al., 1987; Dashzeveg and Russell, 1988; Wilson, 1989; Averianov, 1994; Meng et al., 1994, 2003, 2004; Tong and Dawson, 1995; Dawson and Beard, 1996; Wyss and Meng, 1996; McKenna and Meng, 2001; Meng and Wyss, 2001). The view that rodents and lagomorphs share an exclusive common ancestry with eurymylids and mimotonids (a more inclusive conception of Glires than has been traditional) is advocated by many morphological workers (see Meng and Wyss, 2005, for a recent review). A basal dichotomy within the Glires occurs between rodents plus eurymylids—the Simplicidentata—and lagomorphs plus mimotonids—the Duplicidentata (Li and Ting, 1985, 1993; Flynn et al., 1986, 1987; Dashzeveg et al., 1987; Dashzeveg and Russell, 1988; Luckett and Hartenberger, 1993; Meng et al., 1994, 2003; McKenna and Meng, 2001; Meng and Wyss, 2001). Simplicidentata is diagnosed by a single pair of incisors in the upper jaws whereas the Duplicidentata is characterized by two upper pairs. In early forms of Duplicidentata there are two pairs of lower incisors, which are reduced to a single pair in the later members, that is, Lagomorpha.

Based primarily on the incisor condition, the following genera are considered nonrodent simplicidentates (conventionally termed eurymylids): *Zagmys*, *Nikolomylus*, *Aktashmys*, *Asiaparamys*, *Kazygurtia*, *Eomylus*, *Eurymylus*, *Amar*, *Matutinia*, *Rhombomylus*, *Decipomys*, and *Sinomylus*. *Palaeomylus* is now added to this list. Of these taxa, *Zagmys* (Dashzeveg et al., 1987) was referred to the Mimotonidae by Averianov (1994). However, McKenna and Meng (2001) questioned this assignment because the original description does not show the mandible of *Zagmys* to bear the i3 (Dashzeveg and Russell, 1988).

As discussed above, *Khaychina* (Dashzeveg and Russell, 1988) is no longer a valid name according to Kondrashov and Lopatin (2003), nor is Khaychininae (Dashzeveg and Russell, 1988; McKenna and Bell, 1997).

Hypsimylus beijingensis was questionably considered a eurymylid (Zhai, 1977; Dashzeveg and Russell, 1988) whereas Li and Ting (1985) placed it in Mimotonidae. Wilson (1989: 4) thought *Hypsimylus* ‘‘as likely to be a genuine lagomorph as otherwise.’’ McKenna and Bell (1997) considered *Hypsimylus* a palaeolagine lagomorph and placed it within Leporidae. The latter view is followed in a study on new *Hypsimylus* specimens from a late Eocene locality, Yihesubu, of Inner Mongolia (Meng and Hu, 2004). Averianov (1998) considered *Hypsimylus* a lagomorph but assigned it as Lagomorpha incertae familiae. Thus, the current consensus is that *Hypsimylus* is a lagomorph, not a eurymylid.

Gomphos was considered a eurymylid (McKenna and Bell, 1997), but more recent studies show this taxon to be a member of the Duplicidentata because of its two pairs of lower incisors (McKenna and Meng, 2001; Meng et al., 2004). The condition of the upper incisors is unknown in published specimens of *Gomphos*, but new specimens of *Gomphos* or a related taxon from the Bumban Member of Naran-Bulak Formation display two pairs of upper incisors (Meng et al., 1999).

The incisors of *Sinomylus* are intriguing. As mentioned above, although the lower incisors of *Sinomylus zhaii* are unknown (McKenna and Meng, 2001), recent discoveries show that an unnamed species of *Sinomylus* from the Naran Bulak Formation at Tsagan Khushu has one pair of upper incisors but two pairs of lower incisors (Kondrashov and Lopatin, 2003; Lopatin and Kondrashow, 2003). In addition, the unnamed species displays similarities with both mimotonids and eurymylids. For instance, a longitudinal groove on the labial surface of the upper incisor is typical of mimotonids and lagomorphs, whereas absence of I3 is diagnositic of eurymylids and rodents. Based on the new specimens of *Sinomylus*, Lopatin and Kondrashov (2003: 72A–73A) concluded that ‘‘[t]his data confirms the referral of *Sinomylus* to Eurymyloidea and supports the evidence of close relationship between Eurymyloidea and Mimotonida and of the monophyly of the group Mixodontia + Lagomorpha. We suggest including eurymyloids and mimotonids in the order Mixodontia as either suborders or superfamilies. I2/2 C0/0 P3/2-3 M3/3 is a possible initial dental condition in Mixodontia, so such characters as the presence of I3, P2 and i3 in mimotonids, P2 and i3 in *Sinomylus* and i3 in ‘gomphostids’ are plesiomorphic, and so is the single-layered enamel. The mimotonids gave rise to lagomorphs. A group that includes *Sinomylus* and ‘gomphostids’ developed parallel to mimotonids. Rhombomylidae and Eurymylidae (including *Eomylus* and *Heomys*) lost the P2 and I3 and were developing in a different direction, converging with rodents.’’ This view is problematic in several respects. First, it advocates inconsistently at least two sets of incompatible relationships simultaneously: (Rhombomylidae + Eurymylidae) ((*Sinomylus* + ‘‘gomphostids’’)(mimotonids + lagomorphs)) or ((Rhombomylidae + Eurymylidae)(*Sinomylus* + ‘‘gomphostids’’)) (mimotonids + lagomorphs). The monophyletic group of Mixodontia + Lagomorpha is likely the sister group of Rodentia. Based on the statement that the group including *Sinomylus* and ‘‘gomphostids’’ developed parallel to mimotonids, one may choose the first relationship. If endorsing the referral of *Sinomylus* to Eurymyloidea, then one may prefer the second relationship. In each case, the following points require attention. First, the dental formula I2/2–C0/0–P3/2-3–M3/3 is not only an initial dental condition in Mixodontia, but it is applicable to the clade Glires. Second, the order Mixodontia in Lopatin and Kondrashov’s (2003) usage, similar to that of Averianov (1994), is obviously a paraphyletic grouping. We agree with Lopatin and Kondrashov (2003) that the early Glires display a mosaic pattern in their morphologies, so that their relationships are far from conclusively known. Nevertheless, we are not aware of a single shared derived character supporting the grouping of Mixotontia. Third, it is unclear why Lopatin and Kondrashov (2003) argue for a close relationship between *Sinomylus* and ‘‘gomphostids’’. As mentioned, new specimens of ‘‘gomphostids’’ display two pairs of upper and lower incisors but *Sinomylus* has only one pair of upper incisors. Given that fact, the grouping of *Sinomylus* and ‘‘gomphostids’’ in each of the two relationships will inevitably add extra steps of incisor transformation.

BIOSTRATIGRAPHY: The holotype of *Eomylus zhigdenensis* (Dashzeveg and Russell, 1988) and additional specimens of the same species (Kondrashov and Lopatin, 2003; Lopatin and Kondrashov, 2003) come from the late Paleocene Zhigden Member of the Naran Bulak Formation at Tsagan Khushu. The mandible (PSS 30-3; Dashzeveg and Russell, 1988) that has been referred to *E. zhigdenensis* by Kondrashov and Lopatin (2003) is from the Naran Member of the Naran-Bulak Formation (Dashzeveg and Russell, 1988). The Naran Member occurs above the Zhigden Member within the Naran Bulak Foramation and both members are considered late Paleocene (Dashzeveg, 1988). *E. borealis* is from the late Paleocene Nomogen fauna (Chow and Qi, 1978), and now *E. bayanulanensis* and *Palaeomylus* sp. are known from the conventional Bayan Ulan Fauna.

Palaeomylus lii, however, is collected from a bed approximately 8 m above the horizon producing the typical Bayan Ulan Fauna. Co-occurring with *Palaeomylus lii* are two common taxa of the Bayan Ulan Fauna: *Palaeostylops* and *Pseudictops*. *Lambdopsalis bulla*, a multituberculate that is the most abundantly preserved taxon in the Bayan Ulan Fauna, does not occur in the beds hosting *Palaeomylus lii*. Given the superpositional and compositional differences of these faunas, we here refer the *Palaeomylus* assemblage as Bayan Ulan Fauna II, which, pending further field investigation, may prove to be a significant biostratigraphic level in the Bayan Ulan section.

From slightly above the beds that yield the specimens of *Palaeomylus lii*, two calcanea referable to *Gomphos* were recovered. *Gomphos* specimens have been reported from the Bumban Member of the Naran-Bulak Formation in Tsagan-Khushu, Nemegt Basin, from Bumban equivalent beds (members II and III) of the Gashato Formation, Ulan-Nur Basin of Mongolia (Dashzeveg, 1988; Dashzeveg and Russell, 1988), and recently from the Huheboerhe section in the Erlian Basin (Meng et al., 2004). At the Huheboerhe section, *Prodinoceras martyr*, a typical late Paleocene Gashatan taxon, was found in beds stratigraphically below the level producing dental and foot elements of *Gomphos*. Fossils referable to the Arshantan and Irdinmanhan Asian Land Mammal Ages are found from the upper part of the section. This sequence of fossil occurrences is similar to that of Bayan Ulan.

Gomphos is so far known only from Bumbanian faunas; on this basis, the beds containing *Gomphos* in Huheboerhe are considered temporally correlative to rocks bearing Bumbanian fossils elsewhere on the Mongolian Plateau (Meng et al., 2004). The fauna contained in the Bumban Member is conventionally considered earliest Eocene (Dashzeveg, 1988; Ting, 1998; Bowen et al., 2003), although an alternative hypothesis that the Bumbanian fauna is of Late Paleocene age has been proposed (Beard, 1998). Presence of *Gomphos* pedal elements indicates that beds correlative with the *Gomphos*-bearing strata in the Huheboerhe section and in Mongolia are probably present in the section at Bayan Ulan; therefore, the lower part of the Bayan Ulan section may actually contain Paleocene–Eocene transitional sediments. Recognition of a Bumbanian-equivalent level at the Bayan Ulan section, where some of the thickest and most continuous exposures of early Paleogene sediments on the Mongolian Plateau are present, may prove important in future biostratigraphic work in central Asia.

ACKNOWLEDGMENTS

We thank Professor Renjie Zhai for his contribution to the early study of the Bayan Ulan Fauna. We acknowledge the field assistance by Suyin Ting, Jie Ye, Xijun Ni, Xun Jin, Qian Li, Bing Wang, Rui Li, Wei Gao, and Wei Zhou. We thank Drs. Mary R. Dawson and Lawrence J. Flynn for comments on the manuscript. This project has been supported by the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), the American Museum of Natural History, and the University of California. Most of the fieldwork was supported by the IVPP, the Chinese Academy of Sciences, the National Natural Science Foundation of China (special funds for major state basic research projects of China [G200007707] and an CAS grant [49928202] to Meng), and a U.S. National Science Foundation grant to Meng, Koch, and collaborators (EAR-0120727). Bowen was supported by the National Science Foundation Graduate Research Fellowship Program.

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