NEW MATERIAL OF ALAGOMYIDAE (MAMMALIA, GLIRES) FROM THE LATE PALEOCENE SUBENG LOCALITY, INNER MONGOLIA

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ABSTRACT

Newly discovered specimens of alagomyids, mostly isolated teeth collected by screenwashing at the Gashatan (Late Paleocene) Subeng locality in Inner Mongolia, document considerable intraspecific variation in *Tribosphenomys minutus* that has not been appreciated previously because of limited sample sizes. P4s of *Tribosphenomys* are described for the first time, which helps to clarify the posterior premolar identification of alagomyids. Some of the alagomyid specimens are referred to *Tribosphenomys* cf. *T. secundus* and *Neimengomys qii* gen. and sp. nov. Based on the new data, *Tribosphenomys borealis* from the Bumban Member of the Naran Bulak Formation, Mongolia, is considered to be a junior synonym of *Alagomys inopinatus*, and *T. tertius* from the Zhigden Member of the Naran Bulak Formation is regarded as a junior synonym of *T. minutus*. Alagomyidae, consisting of *Tribosphenomys*, *Alagomys* and *Neimengomys*, is maintained as a valid family. The presence of a diversity of alagomyids and other recently obtained fossils and stratigraphic evidence from the Erlian Basin suggest that the Gashatan and Bumbanian of Asia are probably correlative to the late Tiffanian–early Wasachian of North America. The faunal turnover during the Gashatan and Bumbanian in Asia is probably related to the Late Paleocene–Early Eocene global warming, but current evidence is insufficient to link any specific event with the Paleocene-Eocene Thermal Maximum.

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INTRODUCTION

Basal Glires, including mimotonids, eurymylids, stem lagomorphs, and stem rodents, were abundant and diverse during the Paleocene and Eocene in Asia, suggesting that Asia was the center of origin for this group (Dashzeveg and Russell, 1988; Meng et al., 2003; Asher et al., 2005). Among these early Glires, the family Alagomyidae is particularly pertinent to the origin of rodents. The family contains the genera *Tribosphenomys* and *Alagomys*, with a total of seven named species (Dashzeveg, 1990b, 2003; Meng et al., 1994; Meng and Wyss, 1994, 2001; Tong and Dawson, 1995; Dawson and Beard, 1996; Lopatin and Averianov, 2004a, 2004b). These species are minuscule mammals with gliriform, ever-growing upper and lower incisors typical of rodents. Their lower cheek teeth are rodentlike, but their upper cheek teeth are highly distinctive and less reminiscent of those of other rodents or Glires. Isolated upper cheek teeth of *Tribosphenomys* collected at the Subeng locality during the late 1970s proved to be enigmatic for several decades. In an unpublished manuscript written by Zhai (see Russell and Zhai, 1987: 71) these teeth were considered to pertain to a dermopteran (flying lemur) because the paracone and metacone are widely separated by a transverse valley on the upper molars. More nearly complete material of alagomyids collected from the Bumban Member of the Naran Bulak Formation, Mongolia (Dashzeveg, 1990b) and the Gashatan Bayan Ulan locality in Inner Mongolia (Meng et al., 1994) demonstrated that these tiny mammals are actually Glires.

To date, three species of *Alagomys* have been described: *Alagomys inopinatus* (Dashzeveg, 1990a), *A. oriensis* (Tong and Dawson, 1995) and *A. russelli* (Dawson and Beard, 1996). Four species of *Tribosphenomys* have been proposed: *T. minutus* (Meng et al., 1994), *T. borealis* (Dashzeveg, 2003), *T. secundus,* and *T. tertius* (Lopatin and Averianov, 2004a, 2004b). These species range in age from the Gashatan to Bumbanian and all occur in Asia, except for *A. russelli* from the Clarkforkian (latest Paleocene) of North America (Dawson and Beard, 1996).

Here we describe specimens of alagomyids collected by screenwashing at the Subeng locality in the Erlian Basin of Inner Mongolia. Some of these specimens were collected during the 1970s, but most were recovered by renewed fieldwork at Subeng over the past few years.

MATERIAL AND METHODS

All specimens described here were collected by screenwashing sediment from the Subeng locality. A few teeth were collected in 1978, and most were obtained during the field seasons of 2003–2004. Based on the known morphology of alagomyids, these isolated teeth can be identified with a high level of confidence. The specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing. The SEM photographs were taken from uncoated specimens using a Hitachi SEM machine at the American Museum of Natural History. We follow Meng and Wyss (2001) for terminology of dental features in the description. Because the dental morphology of *Tribosphenomys* and *Alagomys* has been described in detail (Dashzeveg, 1990b, 2003; Meng et al., 1994; Tong and Dawson, 1995; Meng and Wyss, 1998, 2001; Dawson and Beard, 1995; Lopatin and Averianov, 2004a, 2004b; Tong and Wang, 2006), our description will be brief and comparative, with a particular focus on intraspecific variation and structures that were previously unknown. Measurements of cheek teeth are taken for the maximum length and width.

SUBENG LOCALITY AND FAUNA

The Upper Paleocene of central Asia was first described from the Gashato (Khashat) Formation in the Ulan-Nur Basin of Mongolia during the 1920s by the Central Asiatic Expedition. Morris first studied the beds in 1923 (see Matthew and Granger, 1925; Russell and Zhai, 1987: 57), and Matthew and Granger (1925) employed the term Gashato in describing the Gashato fauna. The Gashato Formation was formally proposed in 1927 by

Berkey and Morris. The Gashato fauna derives from Member I of the formation, and is overlain by members II and III, which produced only one mammal taxon, *Gomphos elkema* (Dashzeveg, 1988).

Berkey and Morris (1927: 379) proposed the Gashato time as an interval in the Paleocene (their ''Eocene''). The Gashatan as an Asian land-mammal age was proposed by Romer (1966) without definition. Szalay and McKenna (1971) characterized Romer's Gashatan as the joint overlapping time ranges of *Palaeostylops, Pseudictops, Prionessus*, and *Eurymylus*. Russell and Zhai (1987: 412) attributed the Gashato, Nomogen, Zhigden, and Naran faunas, along with several other faunas from other parts of China, to the late Paleocene Nongshanian (= Nungshanian; Li and Ting, 1983) Land Mammal Age of Asia, thereby abandoning the Gashatan. In a tentative proposal of Chinese provincial land-mammal ages, Li and Ting (1983) considered the Nongshanian as Late Paleocene and correlated it to the North American Tiffanian. These authors also proposed ''Bayanulanian'' as a Paleocene-Eocene transitional age, correlating with the North Amerian Clarkforkian. Tong et al. (1995) further expanded the Nongshanian to correlate with both the Clarkforkian and Tiffanian. The Gashatan is now frequently used as the Latest Paleocene Asian Land Mammal Age (Meng and McKenna, 1998; Luterbacher et al., 2004). Local faunas typically attributed to the Gashatan interval include those from the Gashato and Naran localities of Mongolia, and the Nomogen, Bayan Ulan, Urdyn Obo, and Subeng localities in China (Russell and Zhai, 1987; Wang et al., 1998; Meng et al., 1998, 2004, 2005). However, intercontinental correlation of the Gashatan remains an open issue. It is usually correlated with the North American Clarkforkian (Ting, 1998; Luterbacher et al., 2004), the lowest part of the Wasatchian plus the Clarkforkian (McKenna and Bell, 1997), or the upper part of the Tiffanian plus the Clarkforkian (Wang et al., 1998; Beard, 1998; Beard and Dawson, 1999).

The Subeng locality was first discovered in the 1970s by the geological mapping team from the Geological Survey of Inner Mongolia and the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (Jiang, 1983; Qi, 1987; Russell and Zhai, 1987; BGMRNMAR, 1991; Meng et al., 1998). Primary fieldwork at this locality was conducted by Qi Tao from the IVPP during the late 1970s and early 1980s, and the authors of this paper have worked in the area since 1987. Additional investigation was also conducted by the Belgian-Inner Mongolian Dinosaur project during the late 1990s. Numerous fossils have been collected by surface collecting, and over 40 tons of matrix from Subeng have been screenwashed by personnel from the IVPP and its collaborators since the 1980s. Magnetostratigraphic and paleoisotopic works have also been carried out during the last few years.

A short faunal list for Subeng (provided by Zhai Renjie) was published by Jiang (1983), which included *Mongolotherium* sp., *Prionessus lucifer*, *Lambdopsalis bulla*, *Pastoralodon lacustris*, *Prodinoceras* sp., and *Palaeostylops iturus*. *Mongolotherium* is now regarded as a junior synonym of *Prodinoceras* (Dashzeveg, 1982). In an unpublished manuscript written by Zhai (see Russell and Zhai, 1987: 71) dermopteran teeth were identified among the specimens collected at Subeng by screenwashing. Similar teeth were subsequently found at Bayan Ulan and recognized as *Tribosphenomys minutus* (Meng et al., 1994; Meng and Wyss, 1994, 2001), a basal Glires, not a dermopteran. Other small mammals collected by screenwashing at Subeng include the carpolestid *Subengius mengi* (Smith et al., 2004) and *Asionyctia guoi* (Missiaen and Smith, 2005). As a result of the increased collecting efforts during the last three decades, the Subeng fauna now includes about 30 species (table 1).

SYSTEMATIC PALEONTOLOGY

Glires Linnaeus, 1758

Alagomyidae Dashzeveg, 1990b

Tribosphenomys minutus Meng, Wyss, Dawson and Zhai, 1994

HOLOTYPE: IVPP V10775, left maxilla with P3, DP4 and M1-2 and associated mandible

TABLE 1
Taxon list of the Late Paleocene Subeng fauna.

MULTITUBERCULATA
  Ptilodontidae gen. et sp. nov. (2)
  Taeniolabididae
    Lambdopsalis bulla
    Prionesus sp.

ANAGALIDA
  Pseudictopidae
    Pseudictops lophiodon

GLIRES
  Eurymylidae
    Eomylus bayanulanensis
    Palaeomylus lii
  Alagomyidae
    Tribosphenomys minutus
    Tribosphenomys cf. *T. secundus*
    Neimengomys qii gen. et sp. nov.

CIMOLESTA
  Pastoralodontidae
    Pastoralodon lacustris (from Jiang, 1983)
  Palaeoryctidae
    Palaeoryctes sp.
  Cimolestidae
    Gen. et sp. indet.
    Paleotomus sp.
    Tsaganius sp.

CREODONTA
  Hyaenodontidae
    Prolimnocyon chowi

CARNIVORA
  Viverravidae
    Viverravus sp.

ERINACEOMORPHA
  Incertae familiae
    Litocherus sp.

SORICOMORPH
  Micropternodontidae
    Hyracolestes sp. nov.
    Hyracolestes cf. *H. ermineus*
    Sarcodon minor
  Nyctitheriidae
    Plagioctenodon sp.
    Leptacodon sp.
    Bayanulanius sp. nov.
    Bumbanius aff. *B. rarus*
    Asionyctia guoi

PLESIADAPIFORMES
  Carpolestidae
    Subengius mengi

TABLE 1.
(*Continued*)

DINOCERATA
  Uintatheriidae
    Prodinoceras cf. *xinjiangensis*

ARCTOSTYLOPIDA
  Arctostylopidae
    Palaeostylops iturus

MESONYCHIA
  Mesonychidae
    Pachyaena sp.
  Hapalodectidae
    Hapalodectes sp. nov.

with dp4–m3 from Bayan Ulan, Inner Mongolia.

NEWLY REFERRED SPECIMENS: IVPP V14707.1–2, 2 right upper incisors; V14707.3–10, 8 isolated DP4s; IVPP V14707.11, a fragmentary maxilla with P4–M1; V14707.12–19, 8 isolated P4s; V14707.20-39, 20 isolated M1; V14707.40–54, 15 M2s; V14707.55–63, 12 M3s; V14708.1, fragmentary right mandible with p4; V14708.2, right p4; V14708.3–9, 7 dp4s; V14708.10–20, 11 m1s; V14708.21–44, 24 m2s; V14708.45–55, 11 ms. See tables 2 and 3 for measurements.

LOCALITY AND AGE: Subeng, about 25 km west of Erlian; Gashatan, Late Paleocene.

COMPARATIVE DESCRIPTION: Several isolated incisors can be referred to *Tribosphenomys* because of their similar size and morphology to those described from Bayan Ulan (Meng et al., 1994; Meng and Wyss, 2001). Two upper left incisors (V14707.1–2) are illustrated (fig. 1), which measure 0.68/1.12 mm and 0.62/1.3 mm (width/depth), respectively. The tip of the tooth is rounded buccally and has a straight medial edge of contact, and an elongated wear facet. The wear striations on the facet are parallel to its medial edge.

In *Tribosphenomys minutus* DP4 is molariform and triangular in occlusal view, with distinctive protocone, paracone, metacone, and metaconule (fig. 2). Most of the isolated DP4s in our sample from Subeng are generally similar to that of the holotype from Bayan Ulan. They differ from that of *T. secundus* in being smaller and having slimmer cusps and weaker crests. There are no published measurements for the cheek teeth in the holotype

TABLE 2
Upper Tooth Measurements (mm) of *Tribosphenomys minutus* (Length/Width)

Specimens	L/W	Specimens	L/W
DP4 (V14707.3)	0.67/1.08	P4 (V14707.11)	0.46/1.17
DP4 (V14707.4)	0.85/1.12	P4 (V14707.12)	0.50/1.19
DP4 (V14707.5)	0.77/1.12	P4 (V14707.13)	0.41/1.13
DP4 (V14707.6)	0.73/1.10	P4 (V14707.14)	0.46/1.08
DP4 (V14707.7)	0.73/1.15	P4 (V14707.15)	0.42/1.06
DP4 (V14707.8)	0.71/1.06	P4 (V14707.16)	0.52/1.35
DP4 (V14707.9)	0.69/0.93	P4 (V14707.17)	0.42/1.27
DP4 (V14707.10)	0.65/1.00	P4 (V14707.18)	0.48/1.25
		P4 (V14707.19)	0.52/1.25
M1 (V14707.20)	0.77/1.38	M2 (V14707.40)	0.77/1.23
M1 (V14707.21)	0.79/1.38	M2 (V14707.41)	0.78/1.31
M1 (V14707.22)	0.75/1.48	M2 (V14707.42)	0.75/1.35
M1 (V14707.23)	0.77/1.31	M2 (V14707.43)	0.83/1.40
M1 (V14707.24)	0.83/1.29	M2 (V14707.44)	0.79/1.31
M1 (V14707.25)	0.78/1.44	M2 (V14707.45)	0.79/1.21
M1 (V14707.26)	0.83/1.44	M2 (V14707.46)	0.83/1.40
M1 (V14707.27)	0.87/1.56	M2 (V14707.47)	0.85/1.38
M1 (V14707.28)	0.87/1.48	M2 (V14707.48)	0.83/1.33
M1 (V14707.29)	0.77/1.56	M2 (V14707.49)	0.85/1.40
M1 (V14707.30)	0.88/1.44	M2 (V14707.50)	0.79/1.23
M1 (V14707.31)	0.85/1.44	M2 (V14707.51)	0.88/1.40
M1 (V14707.32)	0.81/1.58	M2 (V14707.52)	0.90/1.37
M1 (V14707.33)	0.83/1.58	M2 (V14707.53)	0.90/1.50
M1 (V14707.34)	0.83/1.40	M2 (V14707.54)	0.88/1.58
M1 (V14707.35)	0.85/1.59	M3 (V14707.55)	0.65/1.02
M1 (V14707.36)	0.81/1.48	M3 (V14707.56)	0.65/1.00
M1 (V14707.37)	0.88/1.52	M3 (V14707.57)	0.69/1.00
M1 (V14707.38)	0.87/1.48	M3 (V14707.58)	0.65/1.02
M1 (V14707.39)	0.83/1.56	M3 (V14707.59)	0.63/0.98
M1 (V14707.11)	0.92/1.58	M3 (V14707.60)	0.67/0.92
		M3 (V14707.61)	0.73/0.94
		M3 (V14707.62)	0.66/1.06
		M3 (V14707.63)	0.75/1.10

of *T. borealis* (Dashzeveg, 2003), but the DP4 described here appears to be proportionally larger relative to M1, particularly in the transverse dimension, and have a more prominent buccal shelf than that of *T. borealis.* One specimen (fig. 2h) is smaller, shorter, and simpler, which may indicate that it pertains to a different species.

The fragmentary maxilla (V14707.11; fig. 3a) is similar to that of the holotype of *Tribosphenomys minutus* in the position of the anterior zygomatic arch, the ridge on the ventral surface of the zygomatic root, the size and position of the infraorbital foramen and the smooth floor of the orbit dorsal to the cheek teeth. A partial alveolus anterior to P4 indicates that P3 was present, although

examples of this tooth locus have not been recovered by screenwashing at Subeng. P3 was described in the holotype of *Tribosphenomys minutus* (Meng et al., 1994; Meng and Wyss, 2001). It is a small, unicuspate tooth with two closely spaced roots arranged anteroposteriorly. A dP3 has been described for *T. secundus* (Lopatin and Averianov, 2004a), which has two roots that are more widely separated and a more complex crown morphology than P3 of *T. minutus*.

In the original description of *Tribosphenomys minutus* (Meng et al., 1994), the posterior premolars of the holotype (V10775) and referred specimen (V10776) were regarded as P4/p4. Additional material referred to *T. minutus* (V10778) clearly displays a nonmolari-

TABLE 3
Lower Tooth Measurements (mm) of *Tribosphenomys minutus* (Length/Width)

| Specimens	L/W	Specimens	L/W
p4 (V14708.1)	0.61/0.62	m1 (V14708.10)	1.00/0.81
p4 (V14708.2)	0.75/0.67	m1 (V14708.11)	0.96/0.88
dp4 (V14708.3)	0.73/0.73	m1 (V14708.12)	1.02/0.87
dp4 (V14708.4)	0.76/0.76	m1 (V14708.13)	0.94/0.81
dp4 (V14708.5)	0.78/0.78	m1 (V14708.14)	0.81/0.83
dp4 (V14708.6)	0.78/0.71	m1 (V14708.15)	0.92/0.81
dp4 (V14708.7)	0.88/0.82	m1 (V14708.16)	0.88/0.77
dp4 (V14708.8)	0.86/0.69	m1 (V14708.17)	0.90/0.85
dp4 (V14708.9)	0.86/0.78	m1 (V14708.18)	0.96/0.85
		m1 (V14708.19)	0.96/0.88
		m1 (V14708.20)	0.92/0.69
m2 (V14708.21)	0.92/0.88	m2 (V14708.39)	0.98/0.90
m2 (V14708.22)	0.96/0.88	m2 (V14708.40)	1.02/1.00
m2 (V14708.23)	0.92/0.94	m2 (V14708.41)	1.00/0.98
m2 (V14708.24)	1.01/0.94	m2 (V14708.42)	1.01/0.98
m2 (V14708.25)	0.88/0.90	m2 (V14708.43)	0.94/0.85
m2 (V14708.26)	1.02/0.94	m2 (V14708.44)	0.94/0.92
m2 (V14708.27)	0.96/0.92		
m2 (V14708.28)	1.02/0.88	m3 (V14708.45)	1.17/0.75
m2 (V14708.29)	0.88/0.83	m3 (V14708.46)	1.10/0.87
m2 (V14708.30)	0.96/0.83	m3 (V14708.47)	1.10/0.85
m2 (V14708.31)	0.96/0.83	m3 (V14708.48)	1.09/0.88
m2 (V14708.32)	0.98/0.92	m3 (V14708.49)	1.12/0.80
m2 (V14708.33)	1.00/0.96	m3 (V14708.50)	1.04/0.71
m2 (V14708.34)	0.96/0.98	m3 (V14708.51)	1.15/0.69
m2 (V14708.35)	0.98/0.98	m3 (V14708.52)	1.13/0.87
m2 (V14708.36)	1.00/0.83	m3 (V14708.53)	1.19/0.87
m2 (V14708.37)	1.04/0.98	m3 (V14708.54)	1.14/0.86
m2 (V14708.38)	1.00/0.92	m3 (V14708.55)	1.27/0.88
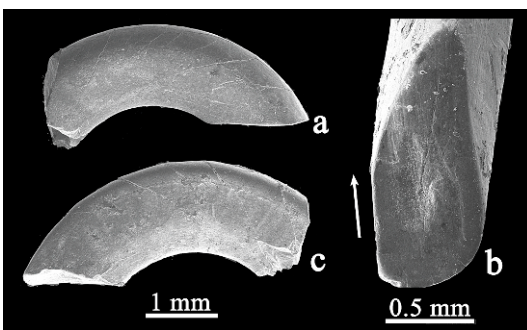
Fig. 1. Right upper incisors of *Tribosphenomys minutus* from late Paleocene Subeng locality. **a.** Buccal view (V14707.1). **b.** Wear facet of the incisor tip (V14707.1). **c.** Lingual view (V14707.2). Arrow indicates the direction of striations on the wear facet.

form p4, which led Meng and Wyss (2001) to regard the posterior premolars in V10775–6 as DP4/dp4. According to this interpretation, the permanent replacements for these deciduous teeth are delayed. Meng and Wyss (2001) also extended this interpretation to *Alagomys*. P4 of *Tribosphenomys* has not been described previously. Lopatin and Averianov (2004a) reported additional DP4 from *T. secundus*. Dashzeveg (2003) named *T. borealis* based on a fragmentary maxilla bearing two cheek teeth that he interpreted as P4 and M1. In our view, however, the more anterior tooth locus in the holotype of *T. borealis* is actually a DP4. P4 is only known in *A. inopinatus* (Dashzeveg, 1990b), although interpretation of this tooth in the species was confused (see below).

The fragmentary maxilla bearing P4 and M1 and the isolated P4s illustrated in fig. 3 are the first record of P4 in *Tribosphenomys*. As
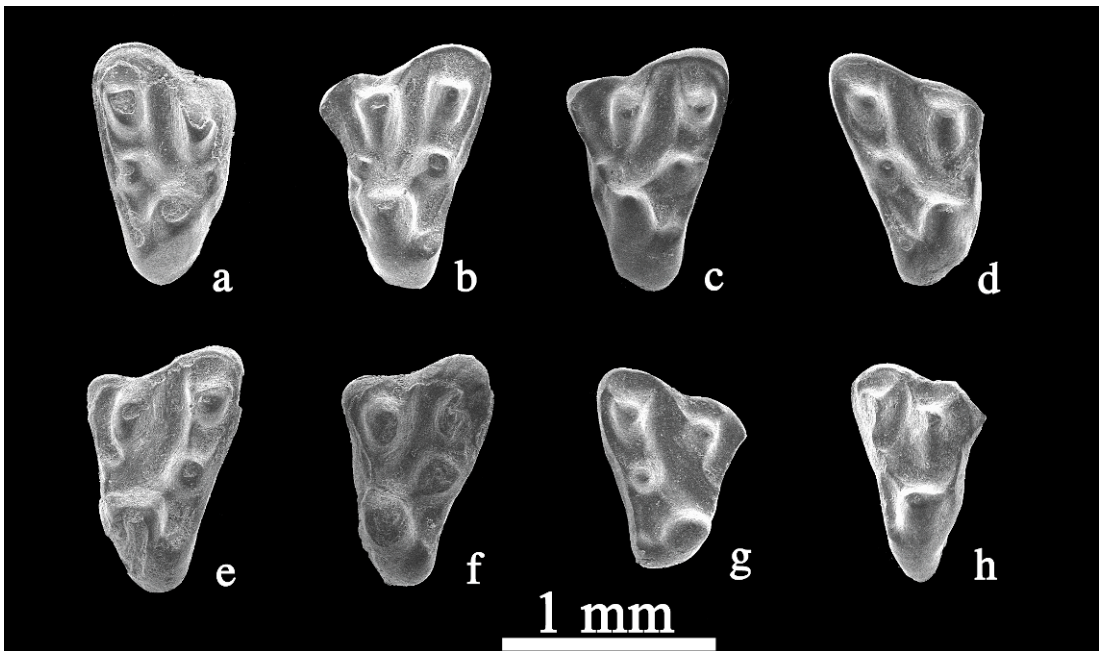
Fig. 2. **a–h.** Crown views of DP4 of *Tribosphenomys minutus* from late Paleocene Subeng locality (V14707.3–10). All images of specimens in figs. 2–13 are on the same scale.

predicted by Meng and Wyss (2001), the P4 is non-molariform, similar to but proportionally larger than that of *Alagomys inopinatus*. The P4 of *T. minutus* is relatively larger in comparison with M1, more lingually positioned, and has a wider buccal shelf than that of *A. inopinatus*. P4 is a short, transverse tooth bearing one lingual and one buccal cusp. It is double-rooted, with the lingual root being much stronger than its buccal counterpart (fig. 4a). The lingual cusp is lower than the buccal cusp and has a rounded lingual surface but a flat or concave buccal surface. In most of the specimens at hand, anterior and posterior ridges form the edges of the tooth. These ridges extend from the lingual cusp to the buccal shelf. In some cases, the posterior ridge is weak or absent. The buccal cusp is cresentic. In unworn specimens (fig. 3e), the buccal cusp forms an isolated island; in most cases, however, its anterior and posterior arms extend buccally to join the anterior and posterior edges of the tooth, respectively. The buccal shelf is broad, varying from one-fifth to one-third of the tooth width. As shown (fig. 3a), there is little if any interstitial contact

between P4 and M1; therefore, interstitial facets are typically absent on the posterior surface of P4 and the anterior surface of M1.

All upper molars have a strong lingual root and two small labial ones (fig. 4b, c). Compared to the holotype of *T. minutus*, M1 in the maxilla (fig. 3a) is heavily worn, indicating that it derives from an older individual. This observation supports the interpretation that the eruption of P4 was ontogenetically delayed in alagomyids. Among the 20 isolated M1 illustrated (fig. 5; some poorly preserved specimens are not figured), only one (fig. 5s) is in a similar wear stage as that of V14707.11. This perhaps indicates a minority of older individuals in the population.

M1 differs from DP4 mainly in having a more rectangular occlusal outline, with the lingual side being slightly shorter than its buccal counterpart, and by its greater width (fig. 5). Reflecting this difference in width, all cusps and crests on M1 are transversely more extended than the corresponding structures on DP4. All the M1s have a distinct buccal shelf, which differs from that of *Alagomys*.
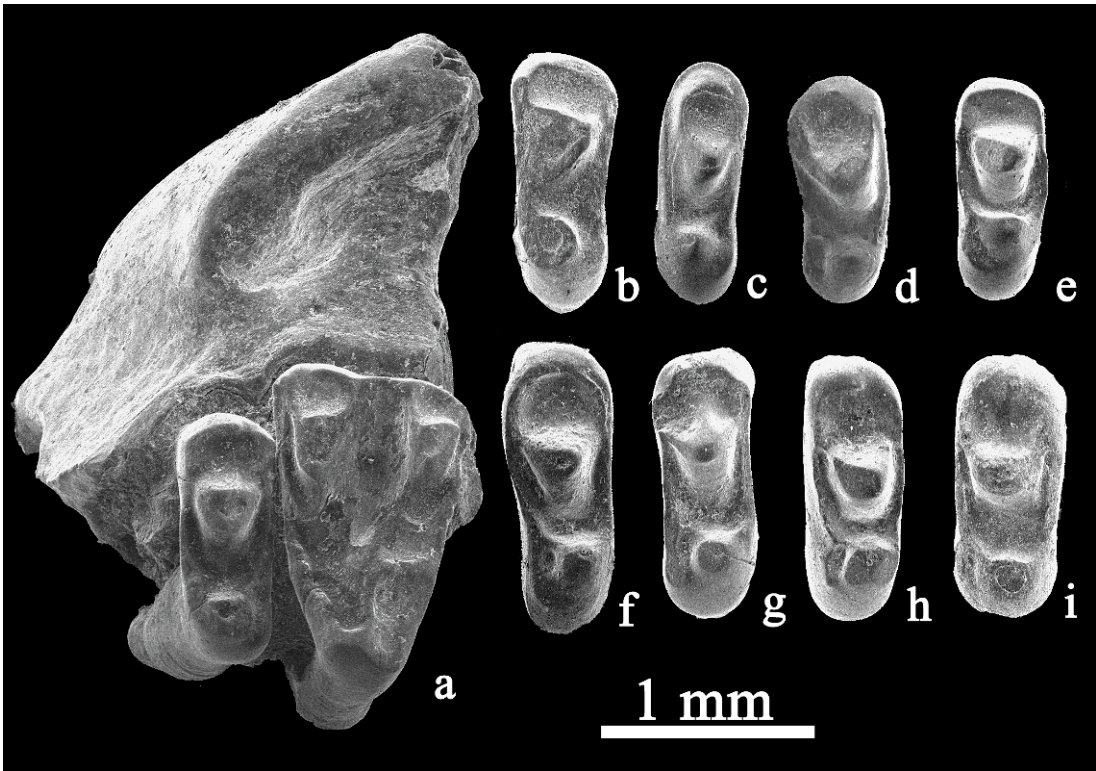
Fig. 3. **a.** Ventral view of a fragmentary left maxilla with P4–M1 of *Tribosphenomys minutus* (V14707.11). **b–i.** Crown views of P4s of *Tribosphenomys minutus* (V14707.12–19) from late Paleocene Subeng locality.

However, these teeth vary slightly in size and their width/length proportions. Minor morphological variation is also evident within the M1 collection. Examples include rounded vs. squared anterobuccal and posterobuccal corners, straight vs. concave buccal margins, and variable development of the buccal shelf, the hypocone, the postcingulum, and conules. In general, M1 cusps of *Tribosphenomys* are more transverse than those of *Alagomys*.

M2 is less symmetrical than M1 in that it reduces in width posteriorly (fig. 6). It is narrower and has a less pronounced buccal shelf, particularly the part buccal to the metacone, than is the case for M1. M2 generally lacks any trace of the hypocone. In tooth width, they range from 0.75 to 0.9 mm (table 2). However, because of the continuous variation within the sample in terms of both size and morphology, we regard these differences as intraspecific variation. In most cases

the anterior and posterior surfaces of M2 do not have interstitial facets.

M3 is the smallest, simplest, and least transverse of the upper molars (fig. 7). The posterior half of M3 is further reduced over the condition seen in M2, and the buccal shelf is narrower. The metacone is reduced to a tiny accessory cuspule or a crest on the posterobuccal side of the metaconule, or else it disappears completely. The protoconule is absent.

A fragmentary right mandible bearing a p4 is preserved (fig. 8a). The diastema between the posterior edge of the incisor alveolus and p4 root is 1.8 mm. A large mental foramen occurs below p4. Several dp4s are present in the sample from Subeng (fig. 8c–i). These teeth lack interstitial facets on their anterior surfaces. Some of the teeth are severely worn, so that their original morphologies are obscured. Two dp4 are unworn and have
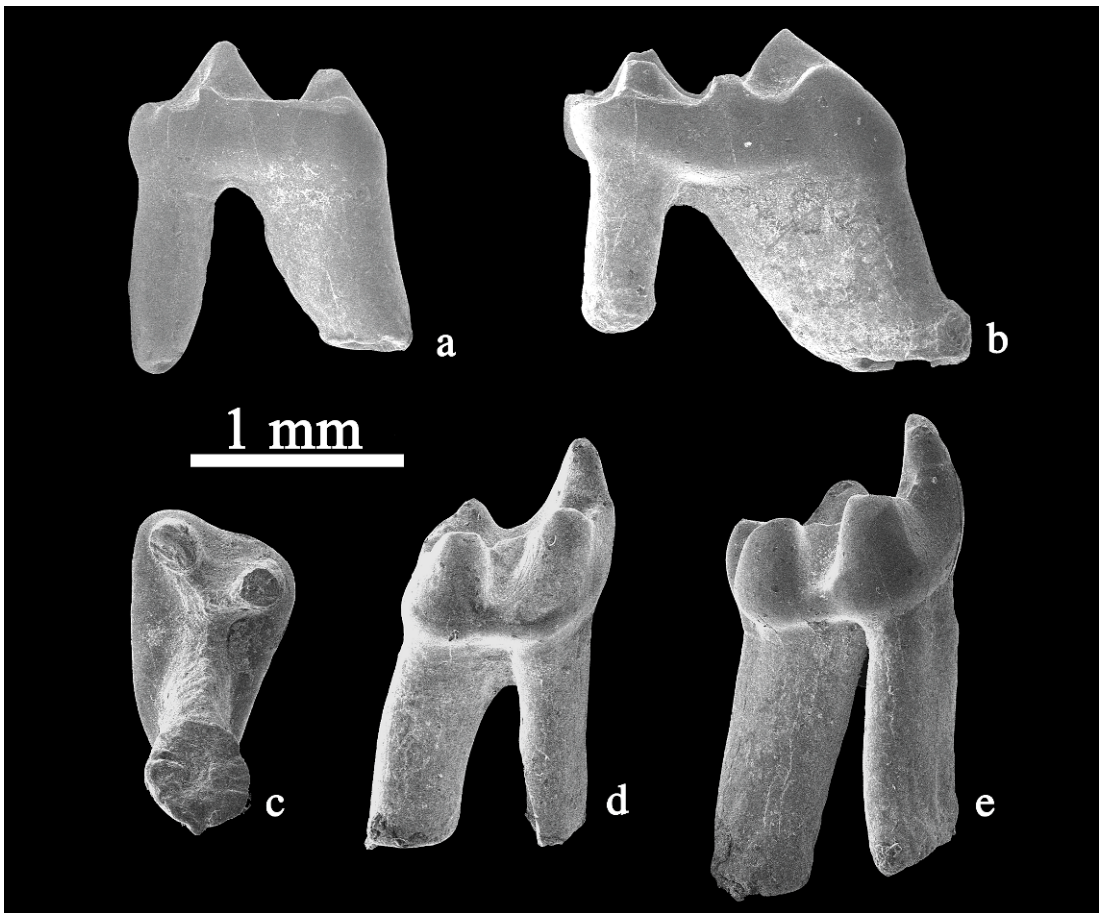
Fig. 4. Root conditions of *Tribosphenomys minutus* from Subeng. **a.** Anterior view of P4. **b.** Posterior view of M1. **c.** Dorsal view of M2. **d.** Buccal view of m2. **e.** Buccal view of m3.

a rudimentary cusp at the anterior end of the trigonid, which is called the paraconid for convenience of description (fig. 8c, d). The dp4 is similar to m1 except being smaller and having the paraconid.

Two p4 are in the collection; one is an isolated tooth and the other is preserved in the fragmentary mandible (fig. 8a, b). These two p4s are similar in morphology but differ slightly in size. The p4 has a wider trigonid that consists of two subequal cusps that may be interpreted as protoconid and metaconid. The talonid is a transverse ridge that is more lingually positioned, posterior to the metaconid. These p4s are similar to that of *T. minutus* from Bayan Ulan (Meng and Wyss, 2001: fig. 7b–d).

The m1 bears an interstitial contact facet on its anterior surface and lacks the paraconid. The protoconid and metaconid are closely appressed, with the metaconid being more anteriorly extended (fig. 9). The m2 differs from m1 in having a wider trigonid and the metaconid less anteriorly extended (fig. 10). The protocristid and mesoconid are usually present, but weak. The paraconid is absent. Unlike m3, the hypoconulid is transverse.

The m3 differs from m1–2 in having the metaconid more anteriorly extended and a prominent hypoconulid that forms the third lobe of the tooth (fig. 11). The size of the hypoconulid varies considerably and the ridges connecting it to the hypoconid and entoconid also take different shapes. The
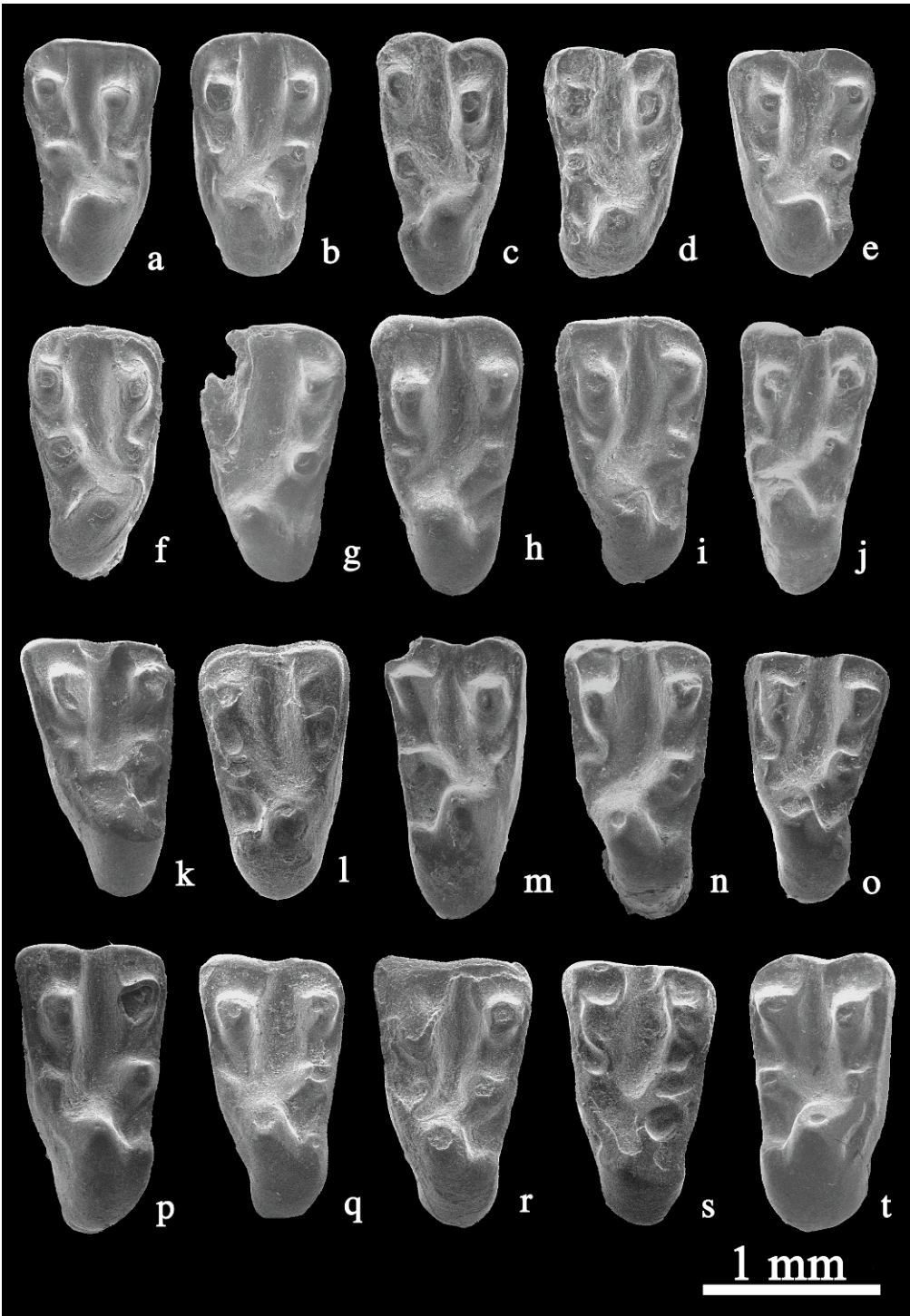
Fig. 5. **a–t.** Crown views of M1s of *Tribosphenomys minutus* (V14707.20–39) from late Paleocene Subeng locality.
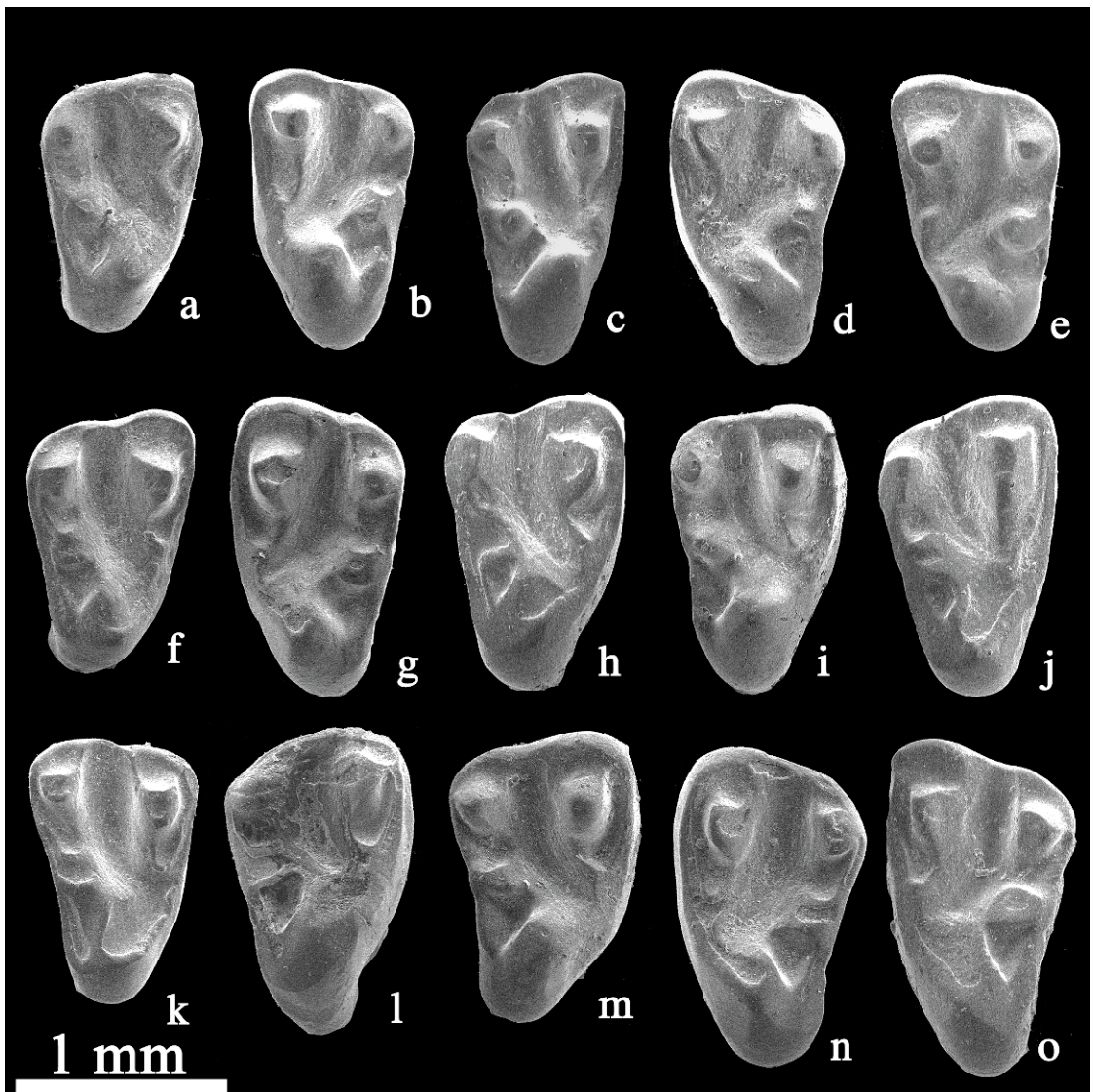
Fig. 6. **a–o.** Crown views of M2s of *Tribosphenomys minutus* (V14707.40–54) from late Paleocene Subeng locality.

protocristid (posterior arm of the protoconid) varies from being completely absent to a weakly developed crest. As is the case for the upper molars, deeply worn lower cheek teeth, such as the one shown in fig. 11k, are rare.

Tribosphenomys cf. *T. secundus* Lopatin and Averianov, 2004a

HOLOTYPE: PIN3104/435, A fragmentary maxilla with alveolus of DP2, Dp3, Dp4 and M1 from the Zhigden Member of the upper Naran-Bulak Formation, Tsagan-Khushu, Mongolia.

REFERRED SPECIMENS: V14709.1, left M1; V14709.2, left M2; V14709.3–5, three left M3s; V14710.1–2, two left dp4s; V14710.3, right m1 or m2; V14710.4, right m2; V14710.5, left m3. See table 4 for measurements.

LOCALITY AND AGE: Subeng, about 25 km west of Erlian; Gashatan, Late Paleocene.

COMPARATIVE DESCRIPTION: The M1 (fig. 12a) is 20% larger than those referred to
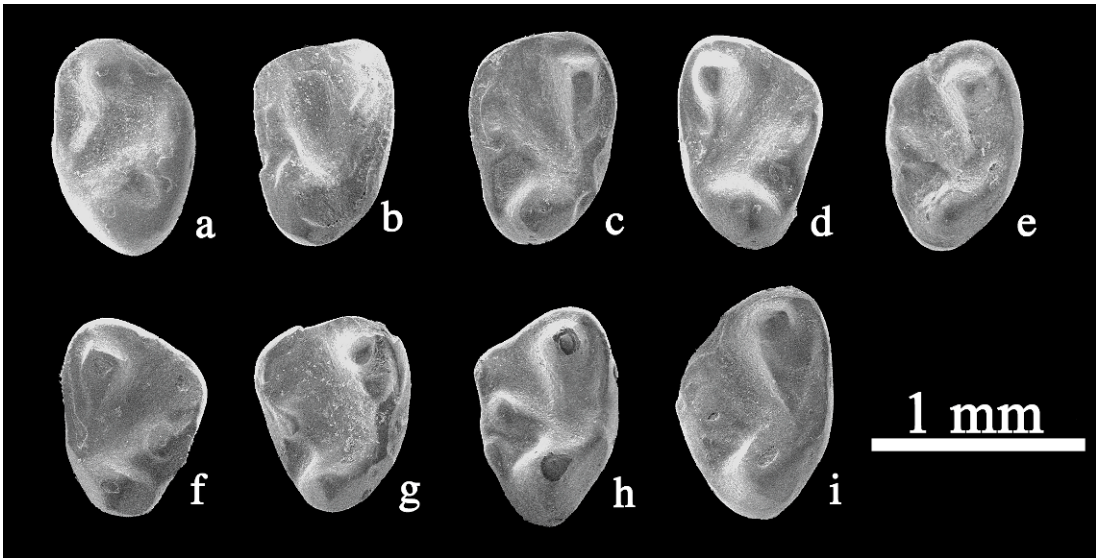
Fig. 7.   **a–i.** Crown views of M3s of *Tribosphenomys minutus* (V14707.55–66) from late Paleocene Subeng locality.
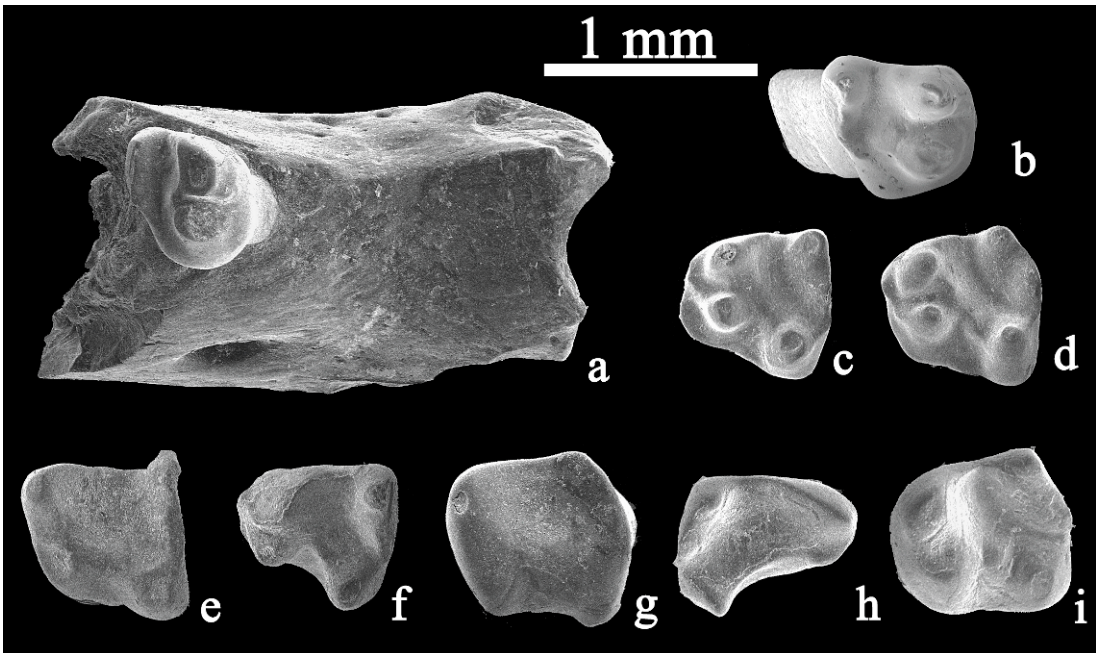

Fig. 8.   **a.** A fragmentary right mandible with p4 of *Tribosphenomys minutus* (V14708.1). **b.** Crown view of a right p4 of *T. minutus* (V14708.2). **c–i.** Crown views of dp4s of *Tribosphenomys minutus* (V14708.3–9) from late Paleocene Subeng locality.
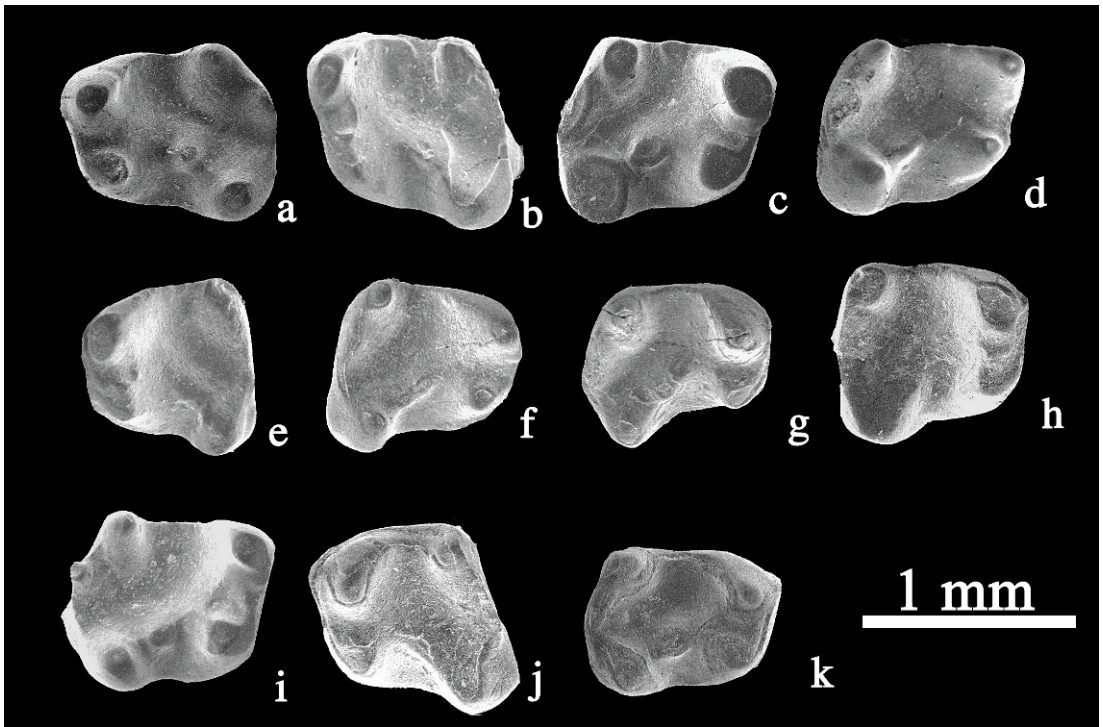
Fig. 9. **a–k,** Crown views of m1s of *Tribosphenomys minutus* (V14708.10–20) from late Paleocene Subeng locality.

T. minutus (table 4; figs. 14, 15), being similar in size to that of *T. secundus* (Lopatin and Averianov, 2004a). Moreover, the buccal shelf is decorated with cuspules, a condition that also occurs in *T. secundus.* This tooth represents an old individual, but the degree of wear is similar to that of V14707.38 (fig. 5s); therefore, its larger size cannot be attributed to its age.

The M2 (fig. 12b) is larger than any known M2 of alagomyids but closely matches the M1 of *T.* cf. *T. secundus*. M2 of *T. secundus* has not previously been documented. The M2 cusps appear slimmer than those of the M1 referred to *T.* cf. *T. secundus*, so that the central basin is relatively broader. The weathered surface of the M2 may have altered its morphology.

Like M2, M3 has not previously been described for *T. secundus*. Here we refer three M3s to *Tribosphenomys* cf. *T. secundus* because of their relatively larger sizes. These teeth also differ from those of *T. minutus* in

having a large metacone and accessory cuspules on the buccal shelf, although these structures are heavily worn in one of the teeth (fig. 12e).

Two dp4 are assigned to *Tribosphenomys* cf. *T. secundus* because of their size (fig. 12f, g). Of the two, one is little worn and shows a distinct cusp anterior to the metaconid, the so-called paraconid, so that the trigonid is relatively complete; the other is heavily worn and the paraconid is absent.

Two lower teeth are identified as m2s of *Tribosphenomys* cf. *T. secundus* because of their relatively large size (fig. 12h, i), although one (fig. 12h) could be m1. In addition, these teeth have a small cusp (the so-called paraconid) at the lingual end of the paracristid and bear a small mesostylid on the lingual margin of the talonid basin between the metaconid and entoconid. These features are absent in Subeng lower cheek teeth referred to *T. minutus*. A vestige of the paraconid, however, is present in some less worn m1–2s of *T.*
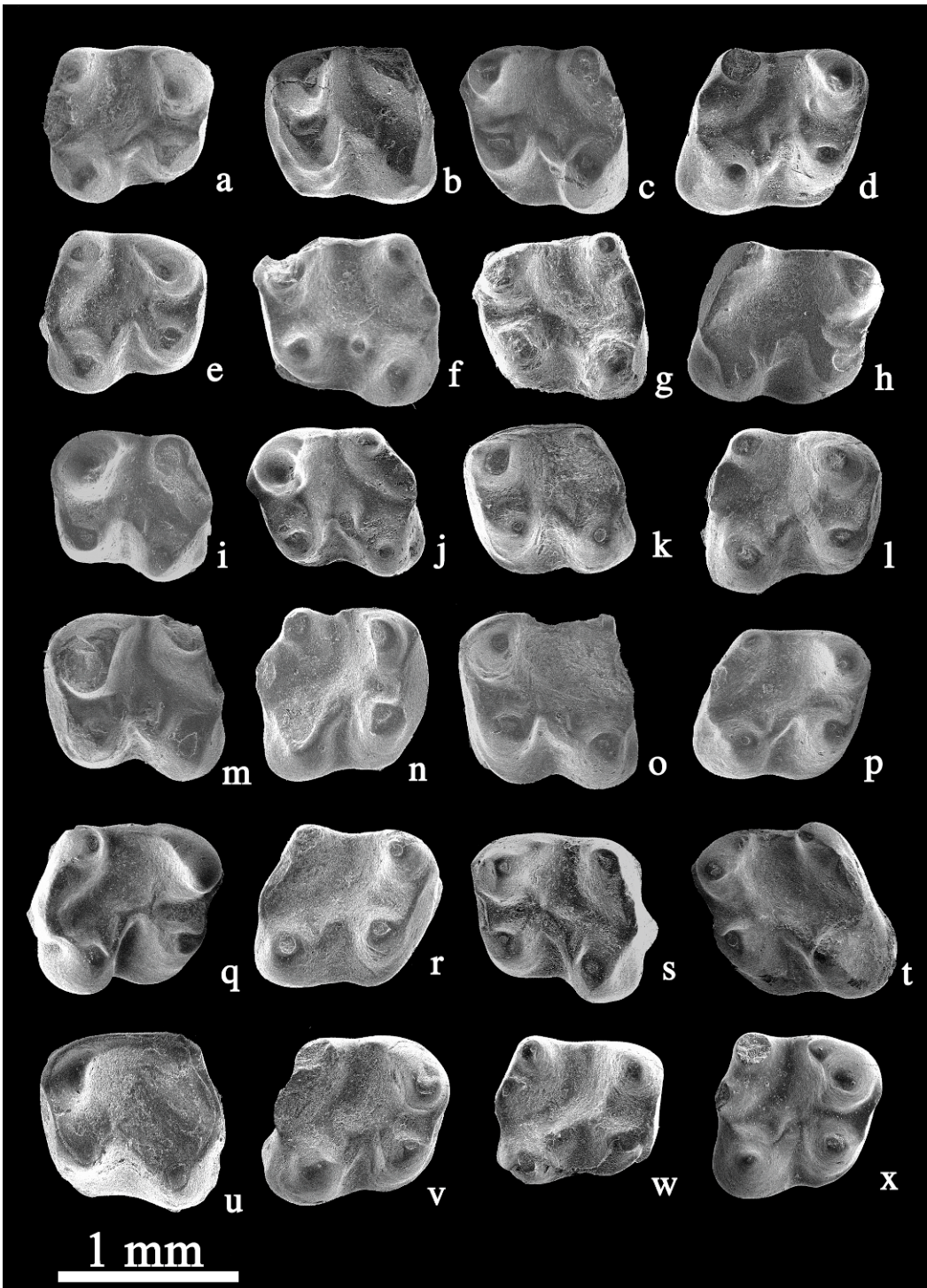
Fig. 10. **a–x.** Crown views of m2 of *Tribosphenomys minutus* (V14708.21–44) from late Paleocene Subeng locality.
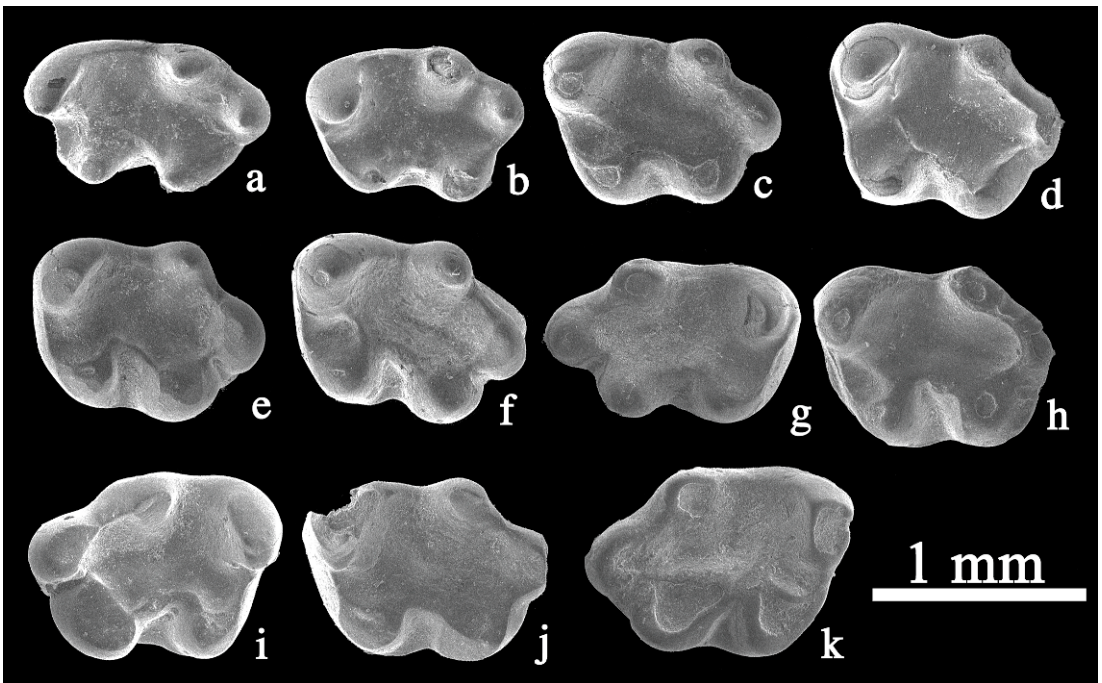
Fig. 11. **a–k.** Crown views of m3s of *Tribosphenomys minutus* (V14708.45–55) from late Paleocene Subeng locality.

minutus from Bayan Ulan (Meng and Wyss, 2001). The paraconid is absent in previously described specimens of *T. secundus*, but because the only known lower teeth are from an old individual with teeth that are heavily worn and p4 fully erupted; the apparent absence of a paraconid in *T. secundus* may be caused by wear, as in *T. minutus*. The lower m2s from Subeng are longer than wide, contrasting with those described previously for *T. secundus*, which are slightly wider than long (Lopatin and Averianov, 2004a).

The m3 is previously unknown for *T. secundus*. Here we refer an m3 (fig. 12j) to

Tribosphenomys cf. *T. secundus* because it is distinctly larger than those of *T. minutus*. This m3 is 22% longer than that in the holotype of *T. minutus*.

Similarities and differences are present between the Subeng specimens and the type specimen of *T. secundus*. Given the fragmentary nature of both samples, we tentatively recognize the Subeng specimens as *Tribosphenomys* cf. *T. secundus*.

Neimengomys, new genus

TYPE SPECIES: *Neimengomys qii*, new species

ETYMOLOGY: *Nei-Meng* is Chinese (in pinyin) for "Inner Mongolia"; *mys* is Greek for "mouse", in analogy with *Alagomys* and *Tribosphenomys*.

DIAGNOSIS: Differs from *Alagomys* but resembles *Tribosphenomys* in having a buccal shelf and a hypocone on upper molars, a more transverse M3 with conical cusps, and a narrower talonid basin. Differs from *Tribosphenomys* in having a P4 with a weak buccal

TABLE 4
Tooth Measurements (mm) of *Tribosphenomys* cf. *T. secundus* (Length/Width)

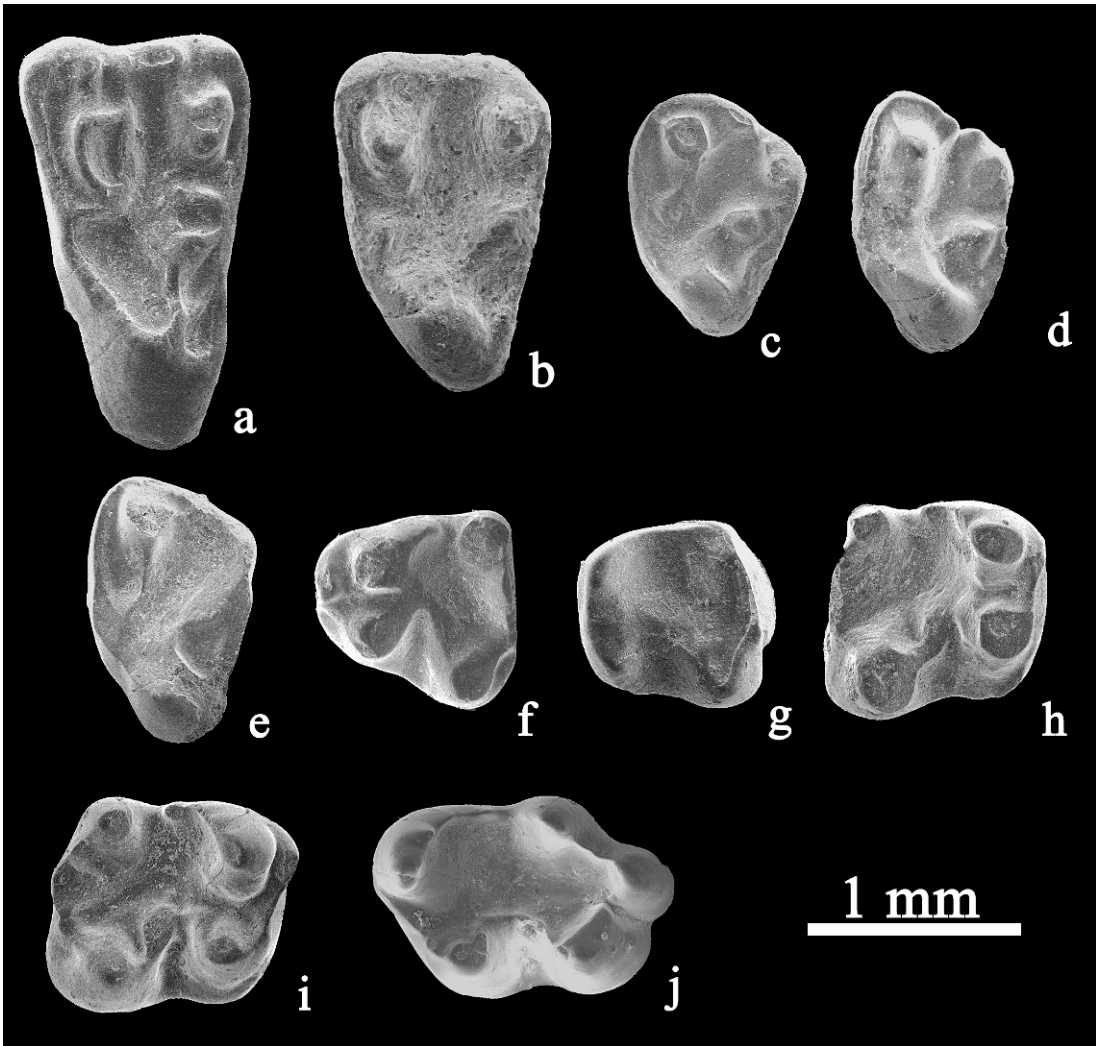| Specimens	L/W	Specimens	L/W
M1 (V14709.1)	1.08/1.94	dp4 (V14710.1)	0.98/0.94
M2 (V14709.2)	1.02/1.60	dp4 (V14710.2)	0.90/0.89
M3 (V14709.3)	0.79/1.27	m2 (V14710.3)	1.06/1.00
M3 (V14709.4)	0.80/0.96	m2 (V14710.4)	1.19/1.00
M3 (V14709.5)	0.79/1.24	m3 (V14710.5)	1.43/0.98

Fig. 12. Crown views of cheek teeth of *Tribosphenomys* cf. *T. secundus* from late Paleocene Subeng locality. **a.** Left M1 (V14709.1). **b.** Left M2 (V14709.2). **c–e.** Left M3s (V14709.3-5); **f–g.** Left dp4 (V14710.1–2). **h.** Right m1 or m2 (V14710.3). **i.** Right m2 (V14710.4). **j.** Left m3 (V14710.5).

shelf, a more inflated protocone on upper molars, a more inflated and buccally positioned hypocone, and a smaller hypoconulid on lower molars.

Neimengomys qii, new spesies

HOLOTYPE: IVPP V14711.1, a right M1 (or M2) (fig. 13b).

INCLUDED SPECIMENS: V14711.2, left P4; V14711.3–10, 8 M1s and/or M2s; V14711.11–14, 4 M3s (or M2s); V14712.1, right p4; V14712.2, right m1; V14712.3–5, 14712.3–5, 3 m3s (fig. 13). See table 5 for measurements.

ETYMOLOGY: The trivial name is after Qi Tao (IVPP), who made the first discovery of *Tribosphenomys* specimens by screenwashing at Subeng in the 1980s.

DIAGNOSIS: Same as for the genus.

TYPE LOCALITY AND AGE: Subeng, about 25 km west of Erlian, Gashatan, Late Paleocene.
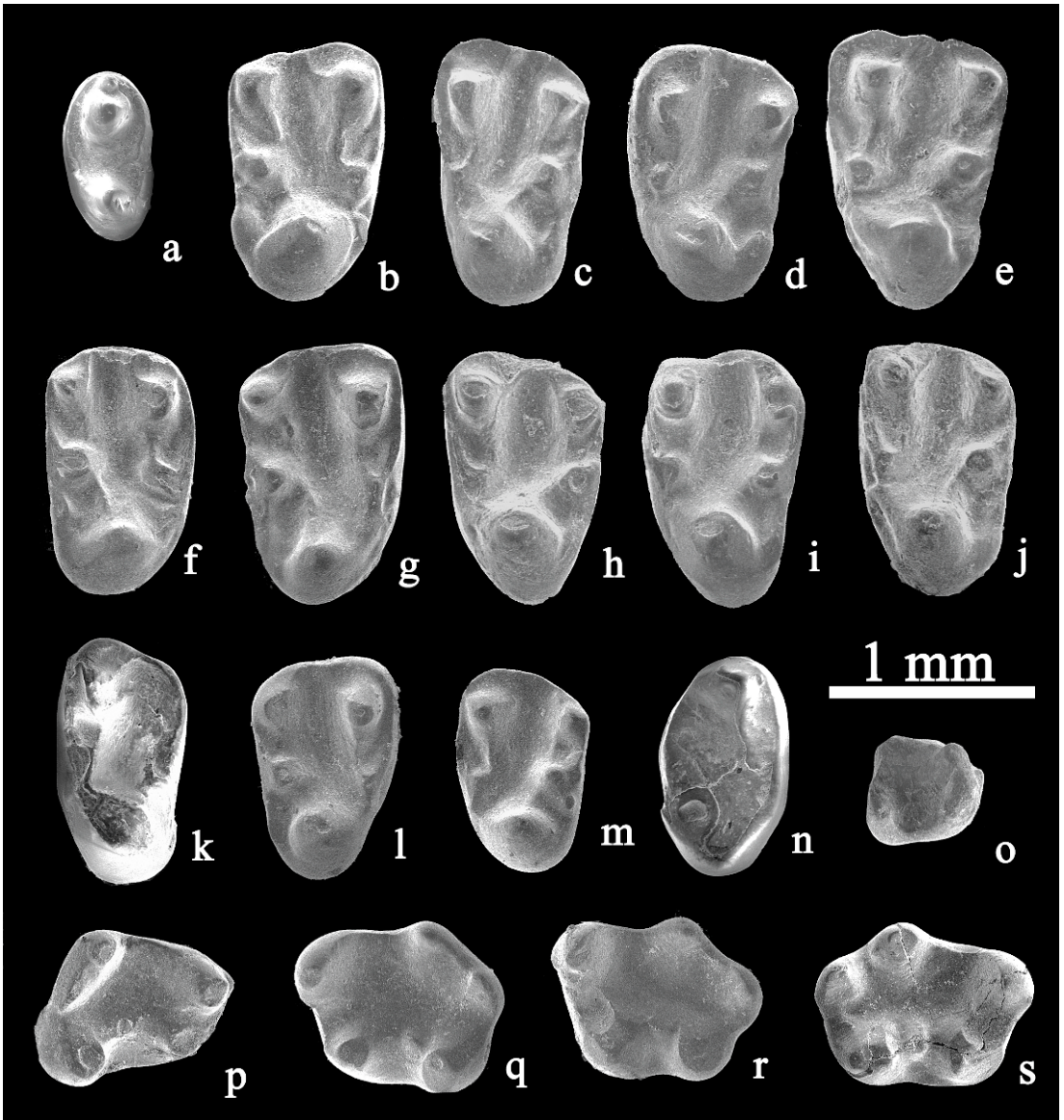
Fig. 13. Crown views of cheek teeth of *Neimengomys qii* from late Paleocene Subeng locality. **a.** Left P4 (V14711.2). **b.** Right M2 (or M1, the holotype, V14711.1). **c–j.** M1s and/or M2 (V14711.3–10). **k–n.** M3 (or M2s, V14711.11–14). **o.** Right p4 (V14712.1). **p.** Right m1 (V14712.2). **q–s.** m3s (14712.3–5).

COMPARATIVE DESCRIPTION: A P4 is identified for this species (fig. 13a). This tooth is smaller than those of *T. minutus* and transversely oval-shaped. The P4 buccal shelf is much narrower than that of *T. minutus* and is similar to that of *A. inopinatus* (Dashzeveg, 1990b). It differs from both *Tribosphenomys* and *Alagomys* in bearing a very small cuspule on the buccal shelf.

Nine upper cheek teeth are considered to be either M1 or M2 (fig. 13b–j), which we cannot yet distinguish with confidence. These teeth have an oval shape in occlusal view. Compared to M1 of *Tribosphenomys minutus*

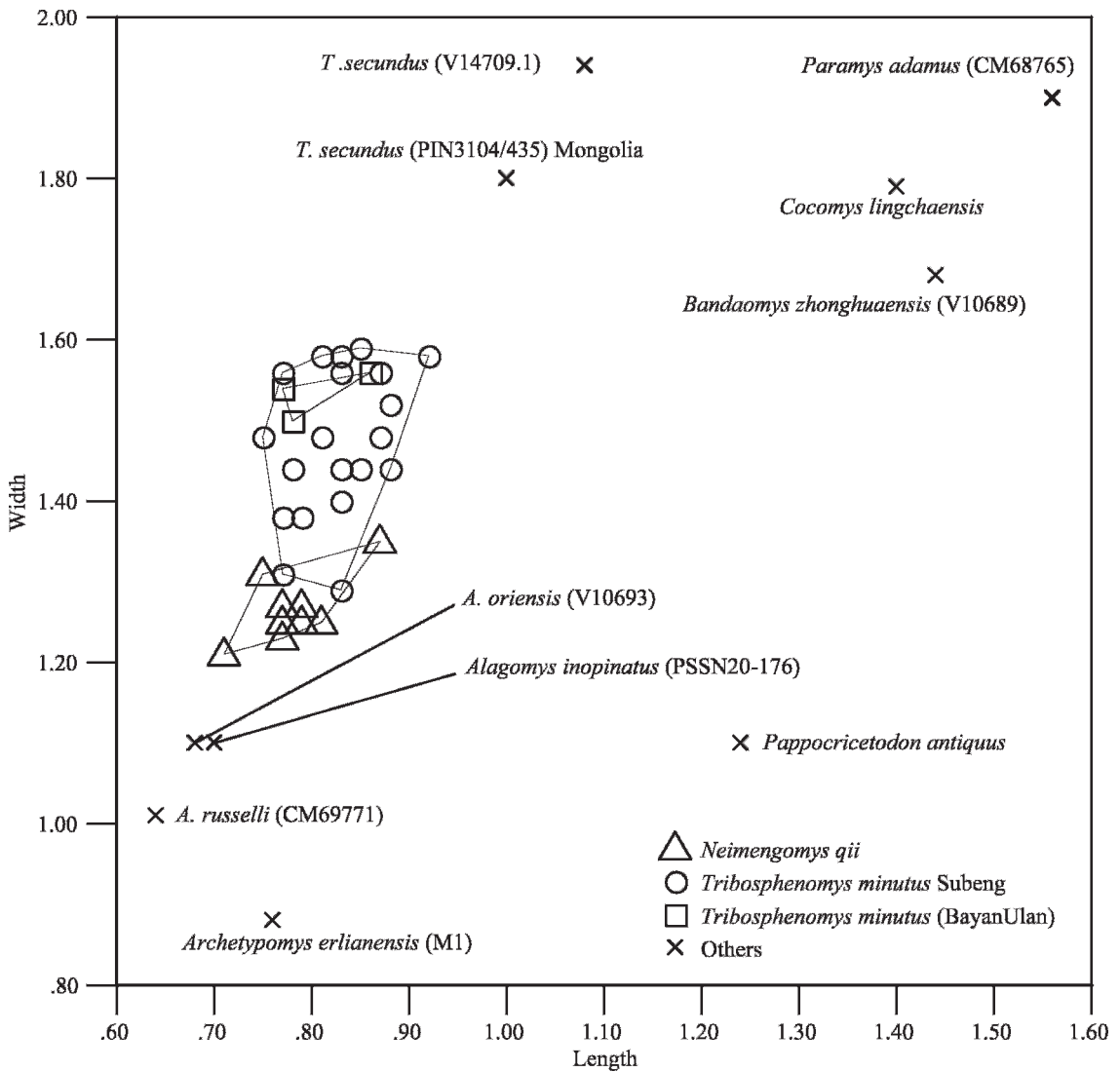Fig. 14.   M1 size distributions of alagomyids and some early rodents. See tables 2, 4–6 for measurements. Data from non-Subeng specimens for this and fig. 15 are adopted from Meng and Wyss (2001, *Tribosphenomys minutus*); Lopatin and Averianov (2004a, 2004b *T. secundus*, *T. tertius*); Dashzeveg (1990b, *Alagomys inopinatus*); Dawson and Beard (1996, *A. russelli*, *Paramys adamus*); Tong and Dawson (1995, *A. oriensis*); Meng et al. (2007, *Archetypomys erlianensis*); Li et al. (1989, *Cocomys lingchaensis*); Tong and Dawson (1995, *Bandaomys zhonghuaensis*); Averianov (1996, *Petrokozlovia* cf. *P. notos*), and Wang and Dawson (1994, *Pappocricetodon antiquus*).

these teeth are narrower and less symmetrical along the transverse axis, the protocone is more inflated, the hypocone is more inflated and buccally positioned, and the buccal shelf of the tooth is distinctly narrower. The width/ length ratio of these teeth is similar to that of

M2 of *T. minutus*, but M2 of *T. minutus* is more triangular in occlusal view, the anterior edge of the tooth is much wider than its posterior counterpart, the protocone is ante-roposteriorly more compressed, and the hy-pocone is usually absent. These teeth are also
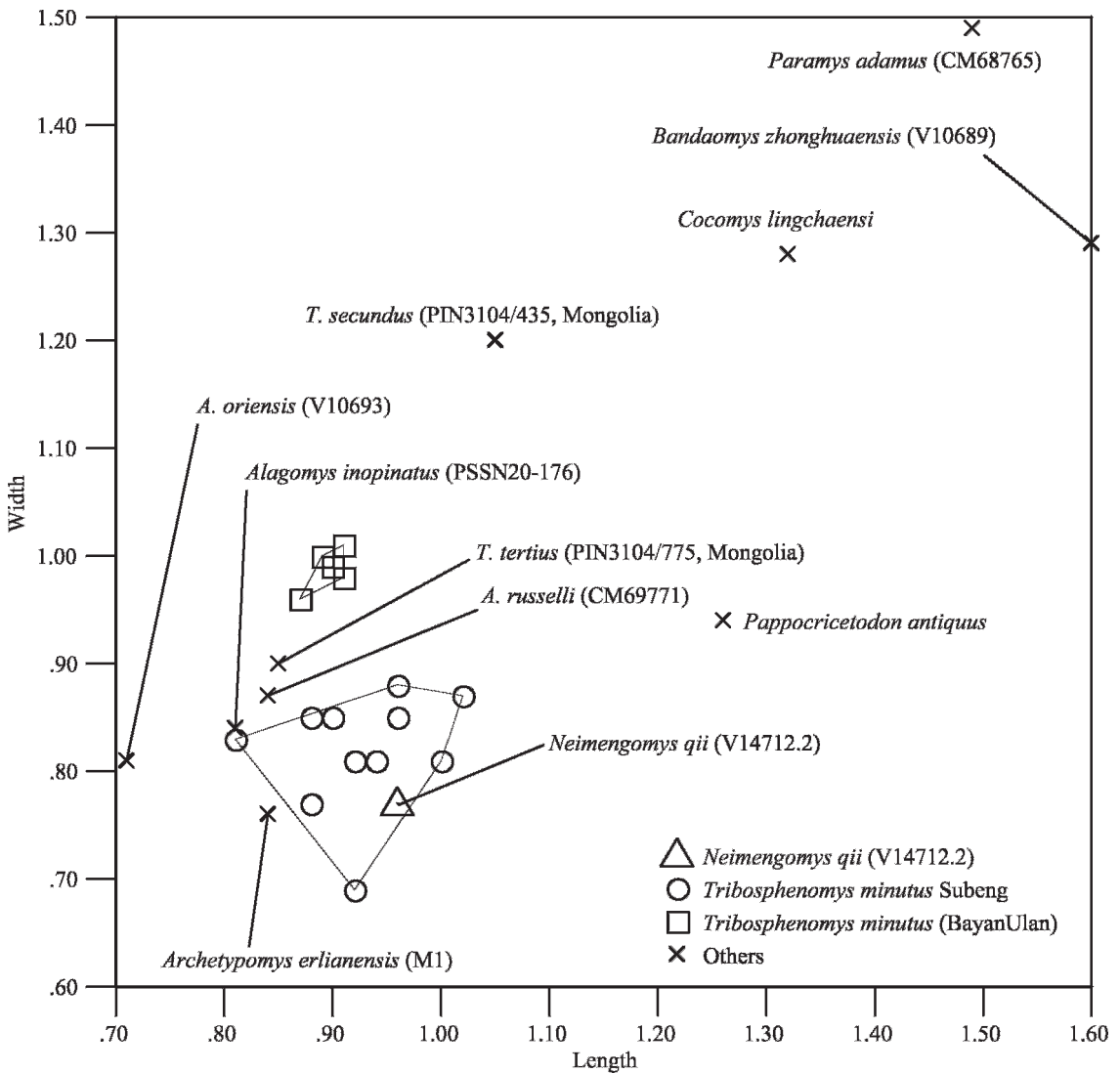
Fig. 15. The m1 size distributions of alagomyids and some early rodents. See tables 3–6 for measurements and fig. 14 for source of data.

distinctive in size and morphology from upper molars of *T. secundus* (Lopatin and Averianov, 2004a).

The molars of *Neimengomys qii* differ from M1 and/or M2 of *Alagomys* in having a hypocone and a more prominent buccal shelf. Among species of *Alagomys*, *N. qii* is more comparable with the North American *A. russelli* than the Asian *A. inopinatus* and *A. oriensis*. The Asian species are similar in have an anteroposteriorly compressed protocone,

while *A. russelli* has an inflated protocone and a somewhat oval-shaped occlusal outline (Dawson and Beard, 1996: plate 1F). Subeng specimens differ from *A. russelli* in having a distinct buccal shelf on the upper molars, whereas the same structure is completely absent in *A. russelli*. In addition, the molar cusps of *A. russelli* are less isolated, the lophs are stronger, the protocone is more inflated, and the trigon basin is deeper. In addition, the basin and postcingulum between the proto-

TABLE 5
Tooth Measurements (mm) of *Neimengomys qii* (Length/Width)

Specimens	L/W	Specimens	L/W
P4 (V14711.2) a	0.45/0.84	M3 (V14711.11) k	0.65/1.22
M1 (V14711.1 b	0.77/1.27	M3 (V14711.13) m	0.63/1.00
M1 (V14711.3) c	0.75/1.31	M3 (V14711.14) n	0.63/1.08
M1 (V14711.4) d	0.81/1.25	p4 (V14712.1) o	0.57/0.53
M1 (V14711.5 e	0.87/1.35	m1 (V14712.2) p	0.96/0.77
M1 (V14711.6) f	0.71/1.21	m3 (V14712.3) q	1.02/0.84
M1 (V14711.7) g	0.79/1.27	m3 (V14712.4) r	1.07/0.81
M1 (V14711.8) h	0.77/1.25	m3 (V14712.5) s	1.02/0.81
M1 (V14711.9) i	0.79/1.25		
M1 (V14711.10) j	0.77/1.23		

cone and metaconule are more prominent in Subeng specimens.

Four specimens are identified as M3s (fig. 13k–n) of *Neimengomys qii* because of their small size and reduced metacone. Compared to M3 of *T. minutus*, the M3 of *N. qii* is also oval-shaped and has a more inflated, conical protocone. The M3 of *N. qii* is more transverse and cuspate than those of *Alagomys* (Dawson and Beard, 1996; Tong and Dawson, 1995). However, we cannot rule out the possibility that these teeth are M2.

One p4 is identified as *N. qii* because of its smaller size and unique morphology. Unlike those referred to *T. minutus*, the p4 (fig. 13o)

has a narrow trigonid consisting of two closely appressed cusps. In contrast, the talonid is wider than the trigonid and formed by two transverse, ridgelike cuspids. The p4 is similar in morphology to that of *T. secundus* (Lopatin and Averianov, 2004a), but differs in being much smaller.

The m1 of *N. qii* (fig. 13p) has a narrower trigonid than those of *T. minutus* and a hypoconulid that is aligned with the entoconid as a ridge. Three m3s are referred to *T. qii* (fig. 13q–s). The hypoconulid on these m3s is more transverse than conical, differing from those referred to *T. minutus*. The trigonid basin of the lower molar is somewhat re-

TABLE 6
M1 and m1 Length/width (mm) and L/W ratios (R) in Selected Glires Taxa

		M1	R	m1	R
Tribosphenomys minutus V10775		0.86/1.56	0.55	0.90/0.99	0.91
(Bayan Ulan)	V10776	0.78/1.50	0.52	0.91/1.01	0.90
	V10778	/		0.91/0.98	0.93
	V10779	0.77/1.54	0.50	/	
	V10780a	/		0.87/0.96	0.91
	V10780b	/		0.89/1.00	0.89
T. secundus (PIN 3104/435)		1.00/1.80	0.56	1.05/1.20	0.88
T. tertius (PIN 3104/775)		/		0.85/0.90	0.94
Alagomys inopinatus (PSS N20-176)		0.70/1.10	0.63	0.81/0.84	0.96
A. russelli (CM 69771)		0.64/1.01	0.63	0.84/0.87	0.97
A. oriensis (V10693)		0.68/1.10*	0.62	0.71/0.81	0.88
Archetypomys erlianensis		0.77/0.88(6)	0.88	0.84/0.76(7)	1.11
Cocomys lingchaensis		1.40/1.79(8)	0.78	1.32/1.28(3)	1.03
Bandaomys zhonghuaensis (V10689)		1.44/1.68	0.86	1.60/1.29(2)	1.24
Paramys adamus (CM 68765)		1.56/1.90	0.82	1.49/1.49(2)	1.00
Petrokozlovia cf. *P. notos*		3.17/3.33(3)	0.95	3.33/3.33(4)	1.00
New myodont rodent (V14615.1)		1.00/1.03	0.97	1.03/0.81(5)	1.27
Pappocricetodon antiquus		1.24/1.10(62)	1.12	1.26/0.94(54)	1.34

stricted, similar to that of *T. minutus*. In contrast, the trigonid basin in *Alagomys* is more open.

Although the material is fragmentary, the morphologies of these teeth show that they must be from a previously unknown taxon. Based on these specimens, we propose a new genus and species of alagomyid.

DISCUSSION

ALAGOMYS: Three species have been reported for the genus: *A. inopinatus* (Dashzeveg, 1990b), *A. oriensis* (Tong and Dawson, 1995), and *A. russelli* (Dawson and Beard, 1996). The holotype of *A. inopinatus* is a fragmentary maxilla bearing three teeth. In the original description, these teeth were interpreted as P4–M2 (Dashzeveg, 1990b), but the upper tooth loci were identifed as P3–M1 in a more recent work (Dashzeveg, 2003), based on a personal communication from J.-L Hartenberger. In the original description (Dashzeveg, 1990b: 38) it was noted that "P3 not preserved but remains of its posterior alveole[alveolus] present." Presence of the P3 alveolus was also cited by Meng and Wyss (2001: 34) as a personal communication from Dashzeveg, although the alveolus in question could also pertain to DP3. Interpreting these teeth as P3–M1, as did Dashzeveg (2003), would make the anterior alveolus, if it is present, attributable to P2 (or DP2). However, the latter alveolus was not mentioned in the recent study (Dashzeveg, 2003), and it was never properly illustrated or described in the original study. The new interpretation of the holotype by Dashzeveg (2003) creates a large and fully molariform "P4" for *A. inopinatus*, which is unsupported by evidence from other alagomyids. We did not have a chance to examine the holotype of *A. inopinatus*, but judging from tooth morphology we think the teeth in question are P4–M2; this view is supported by P4 morphology of *Tribosphenomys* described here. We think the original tooth assignment of the holotype of *A. inopinatus* by Dashzeveg (1990b) is correct. It remains uncertain whether there is an alveolus for P3 or DP3 in the holotype of *A. inopinatus*. There is no convincing evidence that P3 or DP3 is present in any species of *Alagomys*. Because P4 in the holotype of *A. inopinatus* is significantly reduced in comparison to that of *T. minutus* from Subeng, it is probable that P3 has been lost in *Alagomys*, although a DP3 could occur.

The questionable assignment of the teeth in the holotype of *A. inopinatus* leads to the problematic identification of *Tribosphenomys borealis* (Dashzeveg, 2003). The holotype, the only known specimen of the species, is a fragmentary maxilla with two teeth, interpreted as P4 and M1. This specimen came from the Lower Eocene Bumban member of the Naran Bulak Formation, the same bed and locality that yielded the holotype of *A. inopinatus*. This record, if correct, would extend the known stratigraphic range of *Tribosphenomys* from the Gashatan to the Bumbanian. Dashzeveg (2003: 54) diagnosed the species as "differs from *T. minutus* in its absence of P3, lack of hypocone on P4 and M1 and clearly triangular shape of the crown of M1." However, the M1 of *T. borealis* appears more similar to that of *A. inopinatus* than to those of *Tribosphenomys* in possessing the following features: absence of the hypocone, a more distinct metaconule, more conical and inflated cusps, a comma-shaped protocone, absence of the postcingulum between the protocone and metaconule, and narrower buccal shelf. The "P4" of *T. borealis* is almost certainly a DP4, which is similar to but, in relation to M1, proportionally smaller than that of *Tribosphenomys* (measurements of individual teeth were not provided in the original study). A smaller DP4 is consistent with a proportionally smaller P4 in the holotype of *A. inopinatus*. We think that the holotype of *T. borealis* is probably derived from a relatively young individual of *A. inopinatus* and that *T. borealis* is therefore a junior synonym of *A. inopinatus*.

A. oriensis (Tong and Dawson, 1995) is similar to *A. inopinatus* in upper molar morphology but has a broader trigonid basin on its lower cheek teeth. In contrast, *A. russelli* (Dawson and Beard, 1996) displays some significant differences from the Asian species. In the upper molars of *A. russelli*, the hypocone is more inflated, the lophs are more developed, there is no trace of the buccal shelf, and the trigon basin is deeper, suggesting

a relatively higher crown. Its lower molar trigonid basin is not as open as that of *A. oriensis*. These features indicate that *A. russelli* may be placed in a different genus. *A. russelli* appears to have more derived features than other species of the genus and the general shape of the upper molars suggests that *A. russelli* is more closely related to *Neimengomys qii* than it is to other species of alagomyids.

TRIBOSPHENOMYS: With *T. borealis* being synonymized to *A. inopinatus*, the genus *Tribosphenomys* contains three species: *T. minutus* (Meng et al., 1994), *T. secundus* (Lopatin and Averianov, 2004a), and *T. tertius* (Lopatin and Averianov, 2004b); the latter two species came from the Late Paleocene Zhigden Member of the Naran Bulak Formation at Tsagan-Khushu, Mongolia.

Lopatin and Averianov (2004a: 170) diagnosed *T. secundus* as "Differs from the type species of the genus by size somewhat larger, small DP2 present (judging from the alveolus), DP3 with two separate roots and rudimentary protocone, m1-2 without a paraconid." Apparently being unaware of the work by Meng and Wyss (2001), who interpreted the anterior upper premolar of *T. minutus* as P3, not DP3, Lopatin and Averianov (2004a) considered the presence of DP2 as a feature that distinguishes *T. secundus* from *T. minutus* as well as indicating that the former species could be older than *T. minutus*. Lopatin and Averianov (2004a) incorrectly concluded that *Heomys* is the only eurymylid that possesses a DP2. In fact, the Paleocene *Sinomylus* has a P2 (McKenna and Meng, 2001). The holotype of *T. secundus* is from a young individual, younger than any known specimen of *T. minutus*, in which M1 has little wear and was not even fully erupted, judging from its relationship with the DP4 in the maxilla (Lopatin and Averianov, 2004a: fig. 2a). The DP3 of *T. secundus* is already reduced; DP2 is even smaller and may not have persisted in adult individuals. Whether the anterior premolar is DP3 or P3 in the holotype of *T. minutus* (Meng et al., 1994; Meng and Wyss, 2001), the possible presence of DP2 at a younger ontogenetic stage of *T. minutus* cannot be ruled out. Nonetheless, we think *T. secundus* does differ from *T. minutus* in being

larger, having more complex cuspules on the buccal shelf (or cingulum of Lopatin and Averianov, 2004a) of upper cheek teeth, and having a relatively wider p4 talonid (or narrower trigonid).

T. tertius is based on a left dentary with p4-m3 (Lopatin and Averianov, 2004b). There is no diagnosis specified for the species. According to these authors (ibid.: 336), "The new species is similar in measurements to *T. minutus* Meng *et al.,* 1994 and differs from it in the reduced P_4, which has a longer talonid and a low protoconid and lacks metaconid. It differs from *T. secundus* Lopatin et Averianov, 2004 in the 20% smaller measurements and the simple unicusped trigonid of P_4."

According to our observations, the p4 dimensions (width/length) for *T. minutus* (Meng and Wyss, 2001) and *T. tertius* (Lopatin and Averianov, 2004b: 336) are 0.57/0.63m and 0.45/0.65m, respectively. There seems to be no statistically meaningful difference in size between the p4s of the two species. Regarding the interpretation of the cuspid homology, we think Lopatin and Averianov (2004b) misinterpreted the lingual cuspid on the p4 trigonid as a protoconid; that cusp should be the metaconid by position. The possible absence of the p4 protoconid (or the metaconid of Lopatin and Averianov, 2004b) in *T. tertius* is not fully established, because the anterobuccal corner of the tooth was broken (Lopatin and Averianov, 2004b). The simple and narrow talonid of p4 in *T. tertius*, which is relatively lingual in position, is similar to that of *T. minutus* from Bayan Ulan (Meng and Wyss, 2001: fig. 7) and Subeng (fig. 8a–b). The p4 morphology in *T. minutus* may vary considerably, as is demonstrated by the Subeng sample described here. Taking into account the level of dental variation shown within the Subeng collection leaves no sufficient morphological criteria to distinguish *T. tertius* from *T. minutus*. Thus, we regard *T. tertius* as a junior synonym of *T. minutus*. The specimen referred to *T. tertius* came from the same level of *T. secundus* and represents an adult individual—its smaller size and p4 morphology distinguish it from *T. secundus*.

ALAGOMYIDAE: *Alagomys* and *Tribosphenomys* were previously the only two genera that

were placed in Alagomyidae under Rodentiaformes (Wyss and Meng, 1996). These small mammals have a dental morphology, typical for rodents, that bridges the gap between the typical tribosphenic eutherian tooth pattern (Meng and Wyss, 2001). In general, the incisors and lower cheek teeth of alagomyids are closely comparable to those of typical rodents whereas the upper cheek teeth, which are cuspate and transversely wide, are less so. *Alagomys* and *Tribosphenomys* were placed within the same family because they share some similar derived features (Dawson and Beard, 1996; Meng and Wyss, 2001) and because there is currently no other group that shows evidence of having a closer relationship to either of them.

Lopatin and Averianov (2004a: table 1) disagreed with Meng et al. (1994) and Dawson and Beard (1996) regarding their allocation of *Tribophenomys* and *Alagomys* to Alagomyidae; rather, they thought these two genera differ so markedly that they can no longer be placed in the same family. Although they failed to identify any third taxon that is more closely related to either genus, Lopatin and Averianov (ibid.) treated *Tribosphenomys* as Rodentiaformes incertae sedis, and not a member of Alagomyidae. It appears that Lopatin and Averianov (2004a) were unaware of the work by Meng and Wyss (2001). They pointed out that similarities used by others (Meng et al., 1994; Dawson and Beard, 1996) for referring the two genera to the same family are primitive; they listed several differences between *Tribosphenomys* and *Alagomys* to justify their argument against the placement of the two genera in the same family. Lopatin and Averianov (2004a) considered a non-molariform p4 in *Tribosphenomys* and a molariform p4 in *Alagomys* as one of the features that distinguishes the two taxa. These authors interpret the p4 condition of *Tribosphenomys* as secondarily simplified and the molariform p4 of *Alagomys* as plesiomorphic, representing the primitive condition for rodents. Again, these authors overlooked the possibility that the anteriormost lower cheek tooth known for *Alagomys* could be a delayed dp4, as suggested by Meng and Wyss (2001); this is particularly convincing when P4 of *Alagomys inopinatus* is non-molariform, as also noted by Lopatin and

Averianov (2004a). Lopatin and Averianov (2004a) suggested that the presence of a hypocone and postcingulum (the ridge between the metaconule and protocone) in *Tribosphenomys* distinguish it from *Alagomys*. However, the Subeng specimens demonstrate that these features vary within the population.

Soon after the work describing *T. secundus*, Lopatin and Averianov (2004b) published a short note to name *T. tertius*, in which they cited Meng and Wyss (2001) but continued to maintain their earlier opinion against placing *Tribosphenomys* and *Alagomys* in the same family. The doubt raised by Lopatin and Averianov (2004a, 2004b) on the family level relationship between *Tribosphenomys* and *Alagomys* could ultimately prove to be appropriate, but their current argument appears to be weak. For instance, Meng and Wyss (2001) considered the trigon basin a transverse cleft that separates the paracone and metacone as a unique feature for *Tribosphenomys* and *Alagomys* within Glires, but Lopatin and Averianov (2004b) presented an alternative view on the structure and stated that "[a]ctually, the trigon basin of *Tribosphenomys* and *Alagomys* is wide; however, it is also wide in other early rodents, for example, *Cocomys* and Ischyromyidae, which were encoded by the plesiomorphic condition of this character". We think that the trigon basin condition in alagomyids is different from those of *Cocomys* and Ischyromyidae. As mentioned above, upper cheek teeth of *Tribosphenomys* from Subeng were originally considered to pertain to a dermopteran precisely because their paracone and metacone are distantly separated by a transverse valley (Russell and Zhai, 1987). In early rodents, such as *Cocomys* (Li et al., 1989), the upper cheek teeth are square-shaped, making the trigon basin proportionally unlike that of alagomyids. Moreover, upper molar cusps and cuspules are more rounded and in most cases the bases of the paracone and metacone are in contact, or nearly so, among early rodents; therefore, the trigon basin in these forms does not have a cleft shape as it does in alagomyids. The trigon basin in various species of Ischyromyidae varies, but we are unaware of any species in that family in which the trigon basin is similar to that of alagomyids. Without

proposing a closer relationship for either *Alagomys* or *Tribosphenomys* to any third taxon, we think there is no reason to remove *Tribosphenomys* from Alagomyidae. We still regard the trigon basin condition in *Tribosphenomys*, *Alagomys*, and now *Neimengomys* as a good indicator of their close relationship and retain Alagomyidae as a valid taxon.

CORRELATION: The Subeng fauna is closely correlative to that of Bayan Ulan and other Gashatan sites in sharing many taxa, including *Prodinoceras*, *Sarcodon*, *Prolimnocyon*, *Pseudictops, Palaeostylops,* and *Lambdopsalis.* Alagomyids from the Subeng locality also support this correlation. However, the Subeng fauna contains some taxa, such as the carpolestid *Subengius* and ptilodontid multituberculates, that have not been found at Bayan Ulan or other Gashatan localities. The difference in faunal composition between Subeng and Bayan Ulan is partly taphonomic. The beds that yield the Bayan Ulan fauna are primarily reddish clays, and many fossils, such as *Lambdopsalis bulla*, were found as articulated skeletons; they were probably buried in their burrows. The beds yielding the Subeng fauna consist primarily of fluvial sediments, which are dominated by light colored clay, sandstones, and conglomerates. Fossils from this locality are fragmentary and most of them were collected by screenwashing. Another factor that contributes to the discrepancy between the Bayan Ulan and Subeng faunas is that a greater effort of screenwashing has been made at the Subeng locality during the past few years. In contrast, fossils from Bayan Ulan were obtained primarily by surface collecting and acid preparation of coprolites. In addition to the taphonomic and collecting biases, it is also possible that the ages of Bayan Ulan and Subeng are slightly different. If this is true, it implies that the subdivision of the Gashatan is more complex than previously thought. Until a full-scale study of these faunas is conducted, we tentatively consider the Subeng and Bayan Ulan faunas as temporally undifferentiable.

The Asian Paleogene biochronological units, such as Gashatan and Bumbanian that are pertinent in this discussion, were established by faunal correlations to North America. Age controls independent of fossils are generally weak. Paleomagnetic and isotopic works at Subeng and its vicinity have provided preliminary, but not conclusive, evidence for intercontinental correlation (Bowen et al., 2005). The correlation of the Gashatan remains an open issue. It is usually correlated with either the North American Clarkforkian (Ting, 1998; Luterbacher et al., 2004), the lowest part of the Wasatchian plus Clarkforkian (McKenna and Bell, 1997), or the upper part of the Tiffanian plus Clarkforkian (Wang et al., 1998; Beard, 1998; Beard and Dawson, 1999). A related problem concerns the correlation of the succeeding Bumbanian, which is usually considered as early Eocene, correlated with the North American Wasatchian (Dashzeveg, 1988; Ting, 1998; Luterbacher et al., 2004) or Wasatchian and the lower part of Bridgerian (McKenna and Bell, 1997), but an alternative view argues for an earlier correlation (Beard, 1998; Beard and Dawson, 1999). The age determinations for the Gashatan and Bumbanian become increasingly critical because they bear on interpretations of the biogeographic origins and dispersal history of several key mammalian groups, such as primates and rodents (see below). Alagomyids are one of the few taxa that are shared by Asia and North America during the Gashatan-Bumbanian interval and are relevant for intercontinental faunal correlation.

Among the known alagomyids, only *Alagomys russelli* occurs outside of Asia. *A russelli* has been recovered from the late Paleocene (early Clarkforkian or Cf1) Big Multi Quarry, Washakie Basin, Wyoming (Dawson and Beard, 1996). Asia has been considered the most probable center of origin for Glires because of the diversity of basal taxa on that continent during the early Tertiary. Given that *Tribosphenomys* is more primitive than *Alagomys*, *Alagomys russelli* was considered an immigrant from Asia and thus Asian Gashatan faunas that contain *Tribosphenomys* should antedate the North American Clarkforkian (Dawson and Beard, 1996; Beard, 1998). Although *A. russelli* possibly belongs to a different genus, this does not change the fact that it is more derived than *Tribosphenomys*, *Neimengomys,* or even Asian

species of *Alagomys. A. russelli* and Asian *Alagomys* may be derived independently from *Tribosphenomys* or *Neimengomys*. From the evidence of alagomyids alone, it is logical to assume that Asian faunas containing *Tribosphenomys* and *Neimengomys* antedate the North American Cf1 fauna that yields *A. russelli*. Although this supports the notion that the Gashatan may extend partly into the late Tiffanian (Wang et al., 1998; Beard, 1998), it does little for the age correlation of the Bumbanian because the duration of the Gashatan is unclear.

The recent discovery of a euprimate, *Baataromomys ulaanus* (Ni et al., 2007), from the *Gomphos* bed of the Nuhetingboerhe-Huheboerhe (Camp Margetts) area of the Erlian Basin, Inner Mongolia, casts new light on Bumbanian correlation. The *Gomphos* bed was considered as Bumbanian (Meng et al., 2004, 2007; Bowen et al., 2005). Interestingly, *Baataromomys*, represented by a single m2, is more similar to the North American species *B. brandti* (= "*Teilhardina*" *brandti* [Gingerich, 1993]) than to any other euprimate known to date (Ni et al., 2007). *B. brandti* was previously represented also by a single m2, but additional specimens have recently been referred to this taxon (Smith et al., 2006). Because *Baataromomys ulaanus* is morphologically as primitive as *Teilhardina asiatica* (Ni et al., 2004; Ni et al., 2007; Smith et al., 2006), co-existence of *Baataromomys* in Asia and North American suggests that the *Gomphos* bed and fauna should be no earlier than the Lingcha fauna that produces *T. asiatica* (Bowen et al., 2002) and no later than Wa0 faunas from North America. *B. brandti* came from the Wa0 beds that are immediately above the Paleocene-Eocene global carbon isotope excursion (CIE) and was estimated to be about 19–25 Kyr above the Paleocene-Eocene boundary (Bowen et al., 2001; Bains et al., 2003). Therefore, it is most probable that the *Gomphos* fauna occurs either at the Paleocene-Eocene boundary or immediately above it. Unfortunately, recent stratigraphic work in the Erlian Basin has failed to identify the CIE, and paleomagnetic results are not decisive in pinpointing the Paleocene-Eocene boundary there (Bowen et al., 2005). Given the super-positional relationship of a Subeng-equivalent

fauna and the Bumbanian *Gomphos* fauna in the Nuhetingboerhe-Huheboerhe area (Meng et al., 2007), it is probable that Gashatan and Bumbanian faunas in the Erlian Basin may be collectively correlated to the late Tiffanian-Clarkforkian–early Wasatchian of North America. In other words, the *Gomphos* fauna may be correlative only to the early part of Wasatchian. This notion gains support from a recent study in which the lower beds and fauna of the redefined Arshanto Formation are considered to be probably late early Eocene (Meng et al., 2007). However, the correlation of the *Gomphos* fauna may not apply to other Bumbanian faunas, such as the Bumban fauna yielding *Altanius* (Dashzeveg and McKenna, 1977) or the Wutu fauna yielding *Alagomys oriensis* (Tong amd Wang, 2006).

Given the preceding correlation, the occurrence of *Paramys adamus* from the late Paleocene, early Clarkforkian (Cf1), Big Multi Quarry, Washakie Basin, Wyoming (Dawson and Beard, 1996) remains a problem, at least for Glires. This species is currently the earliest known rodent of modern aspect, and its record is inconsistent with the scenario that Asia is the center of origin for Glires and rodents. The earliest Asian rodents are known from Lingcha (Li et al., 1989) and the *Gomphos* bed in the Nuhetingboerhe-Huheboerhe area (Meng et al., 2007). Although these forms are morphologically more primitive, at least in terms of their dentition, than *Paramys adamus*, their ages are all considered to be earliest Eocene. This problem may be attributed to either of at least two possibilities. First, older rodents of modern aspect occurred in Asia, but simply have not yet been found there. Second, our current understanding of intercontinental correlations for the Bumbanian are incorrect (cf. Beard and Dawson, 1999). Additional work is needed to settle these issues.

FAUNAL EVOLUTION AND ENVIRONMENT: The composition of Gashatan faunas is distinctively different from that of the Bumbanian (Meng and McKenna, 1998; Ting, 1998; Bowen et al., 2002), a conclusion that gains further support from this and other recent studies (Meng et al., 2004, 2005, 2007). Archaic taxa commonly seen in Gashatan

faunas, such as multituberculates, mesonychids, *Pseudictops, Palaeostylops*, and *Prodinoceras*, either become much more rare or disappear in Bumbanian faunas. For Glires, Gashatan faunas are dominated by *Neimengomys, Tribosphenomys, Eomylus*, and *Palaeomylus*, but these taxa have not been convincingly reported from Bumbanian faunas. In contrast, Bumbanian faunas witness the first Asian occurrences of euprimates, rodents of modern aspect, and undoubted perissodactyls. In addition, *Gomphos* and *Alagomys* are other distinctive representatives of Glires in Bumbanian faunas.

The Gashatan-Bumbanian faunal turnover took place during the global warming from the late Palecene to early Eocene Climatic Optimum (Zachos et al., 2001). Higher annual temperature may have allowed a forested condition on the Mongolian Plateau that has relatively high latitudes. It was previously proposed that the paleoenvironment of the Mongolian Plateau during the early Cenozoic probably lacked dense forests (Berkey and Morris, 1927), in part because of the apparent absence of forest-related taxa such as primates and bats in collections previously made from the region (Meng and McKenna, 1998). However, the discoveries of the carpolestid *Subengius* from Subeng and the euprimate *Baataromomys* from the Nuhetingboerhe-Huheboerhe area suggest that forested habitats did occur, at least sporadically, on the Mongolian Plateau during the early Cenozoic (Ni et al., 2007). This is also supported by additional records of petrified wood in the Nomogen and Irdin Manha formations (Meng et al., 2007).

The preceding correlations suggest that the faunal turnover across the Gashatan-Bumbanian interval is near the Paleocene-Eocene boundary and may be coeval with the Paleocene-Eocene Thermal Maximum (PETM), characterized by the CIE that has been recognized from terrestrial deposits of northern continents (Koch et al., 1992; Steurbaut et al., 1999; Bowen et al., 2002). But direct evidence to link the biotic change in Asia with the PETM remains questionable because of inadequate sampling of fossils across the Paleocene-Eocene boundary and because of imprecise age determinations for key Asian faunas. Nonetheless, some general conclusions can be drawn based on current data. First, the Gashatan-Bumbanian faunal turnover does not seem to be caused by invasion of species from other continents. At least the Glires show a certain degree of phylogenetic relationships and continuity that are recognized only in Asia. The faunal turnover is thus more likely attributable to changing environments than to other physical factors. Second, forested habitats probably occurred in the late Paleocene and persisted at least until the middle Eocene on the Mongolian Plateau, which is consistent with the global climatic warming during this interval. Finally, if *B. ulaanus* and *B. brandti* prove to be closely related (Ni et al., 2007), it supports the hypothesis that euprimates originated in Asia and dispersed eastward to North America and westward to Europe (Beard and Dawson, 1999; Ni et al., 2005), not the hypothesis for a westward Asia-to-Europe-to-North America dispersal for early omomyids (Smith et al., 2006).

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