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Authors: MENG, JIN, LI, CHUANKUI, NI, XIJUN, WANG, YUANQING, and BEARD, K. CHRISTOPHER

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A New Eocene Rodent from the Lower Arshanto Formation in the Nuhetingboerhe (Camp Margetts) Area, Inner Mongolia

JIN MENG,¹ CHUANKUI LI,² XIJUN NI,² YUANQING WANG,² AND
K. CHRISTOPHER BEARD³

ABSTRACT

A new miniscule rodent represented by isolated cheek teeth is reported from the lower part of the late Early Eocene Arshanto Formation, Nuhetingboerhe (Camp Margetts) area, Inner Mongolia. A new family, based on the new genus and species, is proposed. The new taxon resembles alagomyids but differs from early rodents in having a partial buccal cingulum, a distinct metacone that merges posteriorly with the postcingulum, a transversely oriented trigon basin that widely separates the paracone and metacone, a prominent hypoconulid on lower molars, and in lacking the hypocone and protocristid. It differs from alagomyids in having a greater length/width ratio of upper cheek teeth, a neomorphic cusp termed as the preprotoconule, a preprotoconule crista that projects anteriorly, an anteroconid on dp4, an oblique cristid obliqua bearing a distinct mesoconid, and the hypoconid more posteriorly extended (or hypoconulid less posteriorly extended) on m3. The dental morphology of the new taxon is derivable from an alagomyid dental pattern and is intermediate between alagomyids and rodents of modern aspect; it casts new light on the evolution of dentition of early rodents.

INTRODUCTION

The Nuhetingboerhe (Camp Margetts) area of Nei Mongol (Inner Mongolia) was first

explored by the Central Asiatic Expeditions (CAE) of the American Museum of Natural History in the 1920s. In 1930, the CAE team set up a base named "Camp Margetts" in this

¹ Division of Paleontology, American Museum of Natural History (jmeng@amnh.org).

² Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China (lichuankui@ivpp.ac.cn).

³ Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Ave., Pittsburgh, PA 15213 (beardc@CarnegieMNH.org).

area. Camp Margetts, in turn, served as a geographic waypoint that was used to designate several other nearby localities (Radinsky, 1964; Meng, 1990; Meng et al.; 1998; Meng et al., in press). Numerous fossils were collected from this area at the time, but specimens of rodents and other micromammals were rare, partly because their small size rendered surface collecting difficult (Dawson, 1964; Qi, 1987). During the past few years, several fossil localities have been found in this area, which significantly expanded the fossil record, particularly micromammals, of this region. Most notable among them is the Early Eocene *Gomphos* bed, which has been correlated with the Bumban beds of Mongolia (Meng et al., 2004; Bowen et al., 2005). The *Gomphos* bed is in the upper part of the Nomogen Formation (Meng et al., in press), underneath the Arshanto Formation. In addition to *G. elkema*, a typical species from the Bumbanian fauna, small rodents that appear to be similar to the Bumban ctenodactyls (Dashzeveg, 1990a) have been collected from the *Gomphos* bed. A euprimate closely similar to *Teilhardina brandti* from the earliest Eocene Wa0 fauna of Wyoming (Gingerich, 1993) has also been reported from the *Gomphos* bed (Ni et al., in press).

In the Nuhetingboerhe area, the lower boundary of the Arshanto Formation has now been identified and defined for the first time (Meng et al., in press). Immediately above the lithological boundary the basal beds of the Arshanto Formation have yielded a large number of fossil mammals, including numerous specimens of Glires that are dominated with ctenodactyls. Of the Glires specimens a new lagomorph, probably the most primitive species currently known for the order, has been described (Li et al., in press). A new myodont rodent is likewise among the most primitive representatives of that diverse group recovered to date. Biostratigraphic correlations suggest that the lower part of the Arshanto Formation is probably late Early Eocene rather than Middle Eocene as previously considered (Meng et al., in press).

Here we report a new, primitive rodent that comes from the same beds and localities that yielded the primitive lagomorph and myodont rodent. The specimens were collected by

screenwashing matrix from the lower beds of the Arshanto Formation during the field seasons of 2004–2005. Additional information about the locality and stratigraphy can be found in Meng et al. (in press). The new rodent described here is among the smallest rodents known and displays dental morphology intermediate between alagomyids and rodents of modern aspect, which warrants family-level taxonomic recognition and casts new light on the origin and early evolution of rodents.

MATERIALS AND METHODS

The teeth described here are assigned to a single species based on their similar size and unique morphology. This new species is the smallest rodent from the locality and perhaps the smallest Eocene rodent yet described. The SEM photographs of teeth were taken from uncoated specimens using a Hitachi SEM at the American Museum of Natural History. To help with comparisons, we include in each feature tooth images of *Tribosphenomys*, based on specimens collected from the Late Paleocene Subeng locality, Inner Mongolia. The specimens are housed in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. We follow Meng and Wyss (2001) for terminology of dental features in the description.

SYSTEMATIC PALEONTOLOGY

RODENTIA BOWDICH, 1821
ARCHETYPOMYIDAE, NEW FAMILY

TYPE GENUS: *Archetypomys*, gen. nov.

DIAGNOSIS: A minuscule Glires having a combination of dental features found in alagomyids and rodents of modern aspect (see table 1 for measurements). Similar to alagomyids but differing from early rodents in having a partial buccal cingulum, a distinct metaconule that merges posteriorly with the postcingulum, a transversely oriented trigon basin that widely separates the paracone and metacone, a prominent hypoconulid on lower molars, and in lacking the hypocone and the protocristid. Differs from alagomyids in having greater length/width ratio of upper cheek teeth, a preprotoconule, a preprotoconule

TABLE 1
Tooth Measurements (mm) of *Archetypomys erlianensis* (Length/Width)

P4 (V14623.2)	0.60/0.85	m1 (V14622.18)	0.81/0.75
M1 (V14622.1)	0.75/0.90	m1 (V14622.19)	0.90/0.77
M1 (V14622.2)	0.77/0.97	m1 (V14622.20)	0.82/0.72
M1 (V14622.3)	0.79/0.79	m1 (V14622.21)	0.94/0.78
M1 (V14622.4)	0.77/0.99	m1 (V14622.22)	0.90/0.77
M1 (V14622.5)	0.79/0.80	m1 (V14623.10)	0.77/0.73
M1 (V14623.1)	0.77/0.85	m1 (V14623.11)	0.86/0.84
M2 (V14622.6)	0.79/0.92	m1 (V14623.12)	0.83/0.63
M2 (V14622.7)	0.87/1.00	m1 (V14623.13)	0.85/0.73
M2 (V14622.8)	0.77/0.94	m2 (V14622.23)	0.87/0.74
M2 (V14622.9)	0.79/0.96	m2 (V14622.24)	0.87/0.77
M2 (V14623.3)	0.81/0.96	m2 (V14622.25)	0.80/0.71
M2 (V14623.4)	0.85/0.92	m2 (V14622.26)	0.79/0.65
M2 (V14623.5)	0.81/1.00	m2 (V14622.27)	0.91/0.72
M3 (V14623.6)	0.71/0.87	m2 (V14622.28)	0.77/0.67
dp4 (V14622.10)	0.73/0.48	m2 (V14623.14)	0.86/0.85
dp4 (V14622.11)	0.85/0.65	m2 (V14623.15)	0.96/0.83
dp4 (V14622.12)	0.83/0.42	m2 (V14623.16)	0.80/0.69
dp4 (V14622.13)	0.82/0.77	m2 (V14623.17)	0.87/0.71
dp4 (V14622.14)	0.85/0.76	m3 (V14622.29)	0.95/0.72
dp4 (V14622.15)	0.89/0.74	m3 (V14622.30)	1.00/0.73
dp4 (V14622.16)	0.84/0.75	m3 (V14622.31)	0.87/0.67
dp4 (V14622.17)	0.75/0.71	m3 (V14622.32)	0.98/0.75
dp4 (V14623.7)	0.85/0.71	m3 (V14622.33)	0.91/0.80
dp4 (V14623.8)	0.88/0.73		
dp4 (V14623.9)	0.81/0.79		

crista that projects anteriorly, an anteroconid on dp4, an oblique cristid obliqua bearing a distinct mesoconid, and the hypoconid more posteriorly extended (or hypoconulid less posteriorly extended) on m3.

Archetypomys erlianensis, sp. nov.

HOLOTYPE: IVPP V14623.1, an upper M1.

INCLUDED SPECIMENS: V14623.2, left P4 (or dP4); V14622.1, right M1 with metacone broken; V14622.2, left M1; V14622.3, right M1; V14622.4, left M1; V14622.5, right M1; V14622.6, right M2; V14622.7, right M2; V14622.8, left M2; V14622.9, left M2; V14623.3, left M2; V14623.4, left M2; V14623.5, left M2; V14623.6, right M3; V14622.10, left dp4; V14622.11, right dp4; V14622.12, right dp4; V14622.13, left dp4; V14622.14, right dp4; V14622.15, right dp4; V14622.16, right dp4; V14622.17, left dp4; V14623.7, left dp4; V14623.8, left dp4; V14623.9, right dp4; V14622.18, left m1; V14622.19, right m1; V14622.20, left m1;

V14622.21, right m1; V14622.22, right m1; V14623.10, right m1; V14623.11, right m1; V14623.12, left m1; V14623.13, right m1; V14622.23, right m2; V14622.24, left m2; V14622.25, left m2; V14622.26, left m2; V14622.27, left m2; V14622.28, right m2; V14623.14, right m2; V14623.15, left m2; V14623.16, left m2; V14623.17, left m2; V14622.29, right m3; V14622.30, right m3; V14622.31, left m3; V14622.32, right m3; V14622.33, left m3.

ETYMOLOGY: *Archetypus* (L.), original; species name from Erlian, Nei Mongol (Inner Mongolia), the nearest city to the outcrops where the specimens were collected.

DIAGNOSIS: Same as for the family.

TYPE LOCALITY AND HORIZON: Nuhtingboerhe (Camp Margetts area), Erlian Basin, Nei Mongol (Inner Mongolia); lower part of the Arshanto Formation; late Early Eocene. Specimens were collected from two sites that are geographically separated by about 200 m, with the "chalicothere pit" being slightly lower stratigraphically than the other, unnamed site.

Those from the chalicothere pit were cataloged with the number V14622, and the others from the unnamed site bear the number V14623.

DESCRIPTION: Because the current sample consists only of isolated teeth showing unique morphology unknown previously, the orientation of the teeth is problematic. Based on the similar occlusal pattern in *Tribosphenomys* and *Alagomys*, we interpret upper cheek teeth of *Archetypomys* as having a protocone that tapers anterobuccally and is separated from a large metaconule by a talon basin (Meng and Wyss, 2001) or hypocone basin (Lopatin and Averianov, 2004a), while the protoconule (paraconule) joins the preprotocrista. Without better material to show the upper dentition in serial association, we cannot rule out the possibility that the anteroposterior tooth orientation we currently recognize is reversed.

All upper cheek teeth have one major lingual and two minor buccal roots. Upper and lower teeth have distinct cusps but weak crests; they are small and low-crowned. P4 (or DP4) is identified as such because of its relatively simple occlusal pattern (fig. 1a). It is basically triangular in shape, with the protocone forming the lingual apex. The protocone is tilted anterobuccally and is connected with the large paracone by a crest. A weak crest is anterior to the paracone. There is no paraconule. An oval, transversely oriented trigon basin occupies the central part of the tooth and opens buccally. The metacone occurs at the posterobuccal corner of the tooth and is much smaller than the paracone. The metaconule is subequal to the metacone in size and is separated from the latter by a small basin. A more distinct basin separates the metaconule from the protocone.

Six teeth are identified as M1 (fig. 1b–g) because of their relatively narrow anterior margins. These teeth are somewhat triangular in occlusal view, with all apexes rounded, and are anteroposteriorly longer than P4. The protocone is somewhat comma-shaped with the preprotocrista being its tail. The anterolingual surface of the protocone bears an inclined wear facet in V14622.1 (fig. 1b), on which there are microstriations indicating a primarily transverse movement of mastication. A neomorphic cusp occurs on the preprotocrista

between the protocone and protoconule (paraconule). Because this cusp is unique among early rodents with which we are familiar, we designate it as the preprotoconule (see below). Buccal to the preprotoconule is a distinct protoconule, and between them is a short, weak ridge, which we consider to be the buccal part of the preprotocrista. A wear facet occurs on the anterolingual side of the preprotoconule in V14622.1, parallel to that on the protocone. The paracone is conical and connects to the paraconule by a short and low postparaconule crista. The buccal surface of the paracone forms the anterobuccal margin of the tooth, but a vestigial buccal cingulum occurs in some specimens. Anterior to the paracone and protoconule is a transverse crest that projects anteriorly and is similar in position to the precingulum of rodents. Because of its relationship with the preprotoconule and its similarity with those of alagomyids, we regard it as the preprotoconule crista, which may be homologous with the precingulum of rodents (see below). Posterobuccal to the paracone is a small cusp that may be called the mesostyle. The central basin of the tooth is long and curved, starting from the region between the protocone and preprotoconule and ending at the buccal edge of the tooth between the mesostyle and the metacone. Wear striations within the basin are roughly parallel to the long axis of the basin, indicating primarily transverse movements of the lower jaw during mastication. The metaconule, which is as large as the metacone, is connected to the protocone by a low postprotocrista lingually, and to the metacone by a low premetaconule crista buccally. The posterior part of the metaconule merges with the postcingulum, which is low but more distinctive between the metacone and metaconule than it is farther lingually. Between the protocone and metaconule is a conspicuous basin, which was homologized with the talon basin of a tribosphenic tooth (Meng and Wyss, 2001). A smaller basin is present between the metaconule and metacone. The metacone is smaller than the paracone and occupies the posterobuccal corner of the tooth; there is no cingulum buccal to the metacone.

Seven teeth are identified as M2 (fig. 2a–g). M2 is basically similar to M1 in general morphology. They are, however, relatively

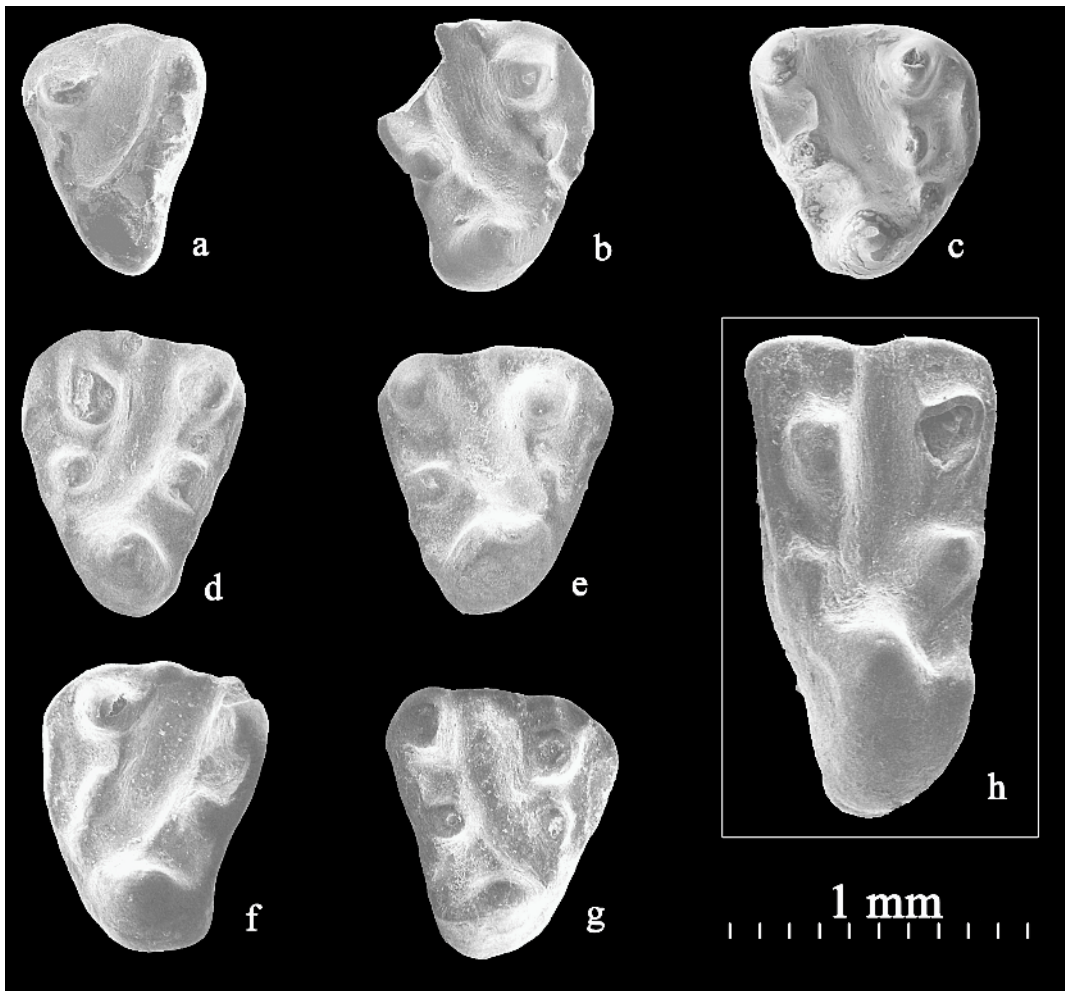


Fig. 1. P4 and M1 of *Archetypomys erlianensis*. a, V14623.2, left P4 (or dP4); b, V14622.1, right M1 with metacone broken; c, V14623.1, right M1 (holotype); d, V14622.2, left M1; e, V14622.3, right M1; f, V14622.4, left M1; g, V14622.5, right M1; h, left M1 of *Tribosphenomys minutus* from the Late Paleocene Subeng locality, Inner Mongolia. All teeth in figures 1–6 are on the same scale.

larger and have a more transversely extended preprotoconule crista. These teeth show that a narrow cingulum usually exists buccal to the paracone but not the metacone; the metaconule is subequal to the metacone in occlusal view, but is lower than the latter (fig. 2f1); the preprotoconule crista is low, along the anterior edge of the tooth (fig. 2d1). The buccal margin of M2 can be quite uneven, depending on the development of the buccal cingulum and mesostyle.

A single M3 (V14623.6, fig. 2h) is identified, and its metacone is broken. It is smaller than

the other molars and is narrower posteriorly than anteriorly; its metaconule is not so pronounced as in M1–2, and the central basin is shorter than in the other upper cheek teeth. The preprotoconule is relatively indistinct, and there is no connection between it and the paraconule.

In identifying the lower cheek teeth, we consider those bearing an anteroconid (we do not assume homology between this cusp and those in, for instance, myodont rodents) as terminal teeth because the anteroconid usually occurs on the anteriormost cheek tooth in

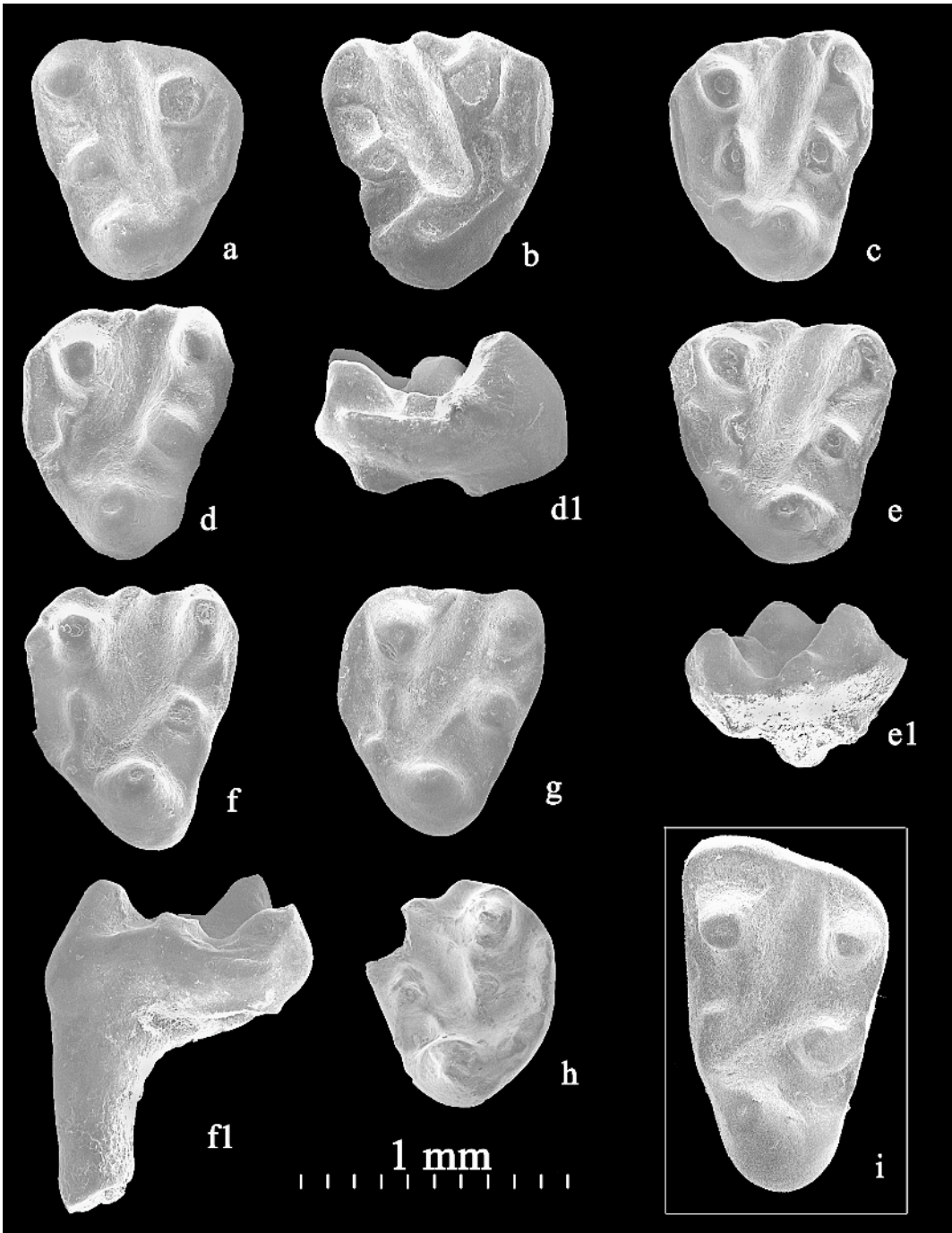


Fig. 2. M2–3 of *Archetypomys erlianensis*. **a**, V14622.6, right M2; **b**, V14622.7, right M2; **c**, V14622.8, left M2; **d**, V14623.3, left M2; **d1**, anterior view of V14623.3; **e**, V14623.4, left M2; **e1**, buccal view of V14623.4; **f**, V14623.5, left M2; **f1**, posterior view of V14623.5; **g**, V14622.9, left M2; **h**, V14623.6, right M3; **i**, left M2 of *Tribosphenomys minutus* from the Late Paleocene Subeng locality, Inner Mongolia.

rodents, such as the m1 in early myodont rodents (Emry and Korth, 1989; Emry et al., 1998; Tong, 1992, 1997; Wang and Dawson, 1994; Dawson and Tong, 1998) and because there is no contact facet on the anterior surface of any of these teeth. We interpret these teeth as dp4 (fig. 3), although other possibilities, such as their being p4 or m1, cannot be absolutely ruled out. However, if they are p4s, then these teeth are quite molariform, which is inconsistent with the general trend in mammal tooth replacement for a successive tooth to be simpler than its deciduous precursor. In particular, it has been shown that p4 is much simpler than dp4 of *Tribosphenomys* (Meng and Wyss, 2001; Lopatin and Averianov, 2004a, b). Similar p4–dp4 morphologies are also present in rodents of modern aspect, such as *Paramys adamus* (Dawson and Beard, 1996). Given the similarity between the molars of *Archetypomys* and *Tribosphenomys*, it seems that similar p4–dp4 morphologies can be inferred for *Archetypomys*. Although a molariform p4 was recognized in *Alagomys* (Tong and Dawson, 1995; Dawson and Beard, 1996), Meng and Wyss (2001) have pointed out that these molariform teeth probably represent delayed or nonreplaced deciduous teeth, a view that is supported by additional evidence (Lopatin and Averianov, 2004a).

These teeth are unlikely to be m1s, because this would imply that the lower dentition consists of only three molars, which is inconsistent with both the primitive structure of these teeth and the identification of the P4. A myodont rodent from the same quarries retains a p4 or dp4 (unpubl. data); suppression of the last lower premolar therefore seems unlikely for *Archetypomys*. Moreover, m1 and m2 seem to be recognizable within the current sample, inasmuch as the m1 trigonid is relatively narrower than that of m2, although the difference is not dramatic.

Among the 11 dp4s, three specimens are poorly preserved, with the enamel layer largely gone (fig. 3a–c). Because they are considerably worn, owing to postmortem preservation, these specimens look relatively small and lack an anteroconid. The remaining specimens are quite molariform in having the major cusps of a lower molar. The dp4 is significantly

narrower anteriorly than posteriorly. It has a small anteroconid at its anterior tip, situated near the longitudinal axis of the tooth, as is the case on m1 in some Eocene myodonts, such as *Pappocricetodon* (Tong, 1992, 1997; Wang and Dawson, 1994), but there is no anterior cingulid. There is no contact facet on the anterior surface of the tooth. The protoconid and metaconid are conical and closely spaced; they are separated by a longitudinal groove. The metaconid is larger than the protoconid and extends posteriorly as a crest that forms the lingual border of the tooth. The cristid obliqua is distinct and quite diagonally oriented. The anterior end of the cristid obliqua extends to the posterolingual base of the protoconid. A mesoconid is present on the cristid obliqua. Because of the orientation of the cristid obliqua, there is a deep sinusid. The hypoconid is the largest cusp on the tooth and is more posterobuccally extended than the hypoconulid; the latter is transversely extended. The entoconid occupies the posterolingual corner of the tooth. There is no crest developed from the main cusps of the tooth.

The differences between what we regard as m1 and m2 are comparatively trivial. The trigonid of m1 (fig. 4) is slightly narrower than that of m2 (fig. 5), as is the case in *Tribosphenomys* (Meng and Wyss, 2001; Lopatin and Averianov, 2004a, 2004b) and *Alagomys* (Tong and Dawson, 1995; Dawson and Beard, 1996). Each of the specimens identified as m2 has a contact facet on its posterior surface, excluding it from being an m3. Because of their similarity, we describe m1 and m2 collectively. The crown tapers anteriorly, but to a lesser degree than that of dp4, and it lacks the anteroconid. It is double-rooted, with the posterior root being more robust (fig. 4b1). The metaconid extends more anteriorly than the protoconid and is the highest cusp of the tooth. The anterior margin of the tooth is raised to form a low ridge; otherwise, there is no crest between the protoconid and metaconid. The posterior wall of the metaconid is a large sloping surface that descends to the central basin of the tooth. A ridge from the metaconid is developed to a variable degree among the specimens at hand and extends posteriorly to form the lingual edge of the tooth. In some specimens,

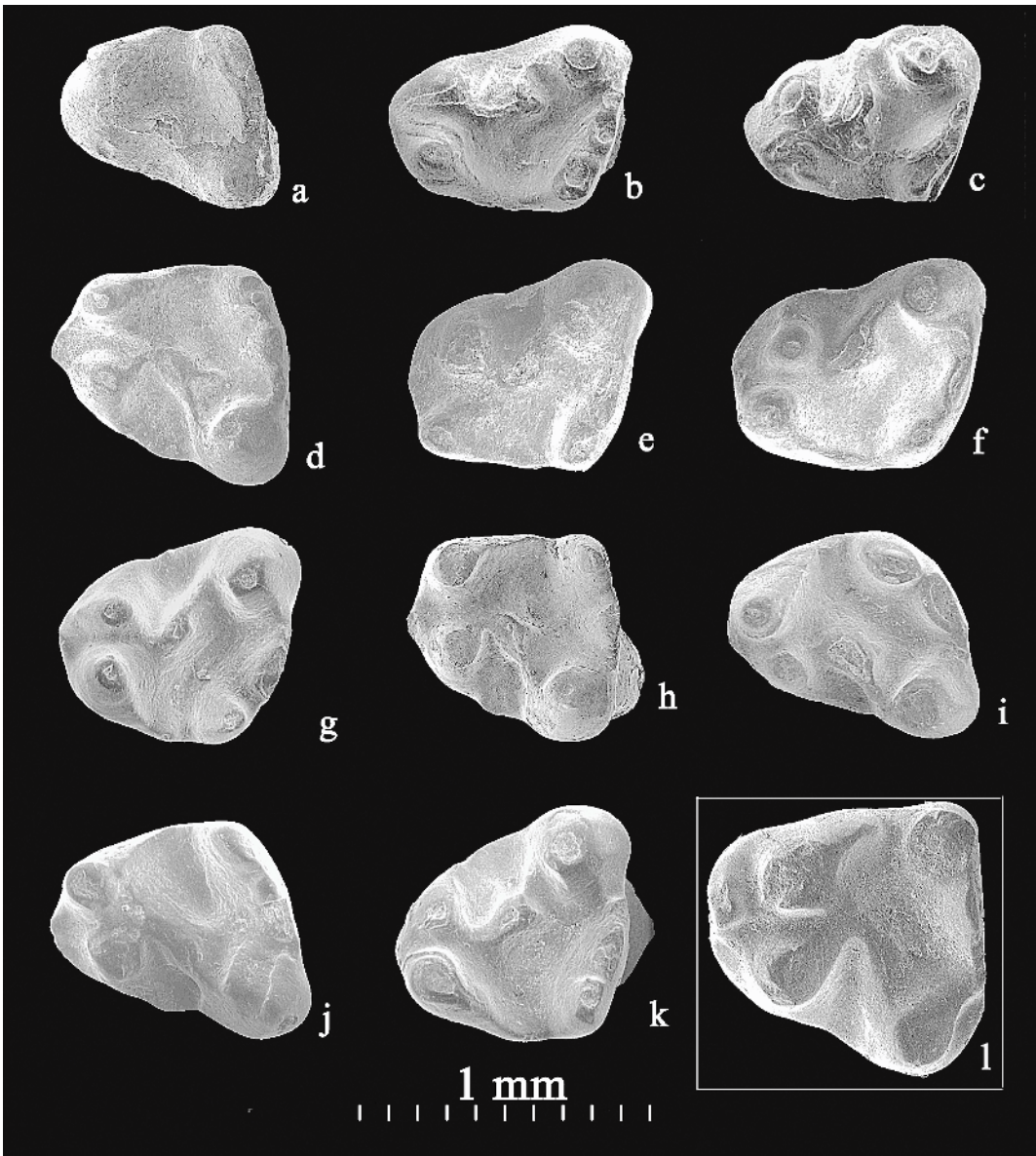


Fig. 3. The dp4 of *Archetypomys erlianensis*. **a**, V14622.10, left dp4; **b**, V14622.11, right dp4; **c**, V14622.12, right dp4; **d**, V14622.13, left dp4; **e**, V14622.14, right dp4; **f**, V14622.15, right dp4; **g**, V14622.16, right dp4; **h**, V14622.17, left dp4; **i**, V14623.7, left dp4; **j**, V14623.8, left dp4; **k**, V14623.9, right dp4; **l**, left dp4 of *Tribosphenomys minutus* from the Late Paleocene Subeng locality, Inner Mongolia.

a small cuspid at the posterior end of the ridge may be called the mesostylid. The cristid obliqua is diagonally oriented. Its anterior end terminates at the posterolingual base of the protoconid, either merging with the base or being separated from the base by a narrow

notch. Posteriorly, it develops from the anterobuccal side of the hypoconid. The anterior part of the cristid obliqua inflates to form a sizable, elongated mesoconid. Because of the orientation of the cristid obliqua, the sinusid is narrow and lingually deep. Similar to the

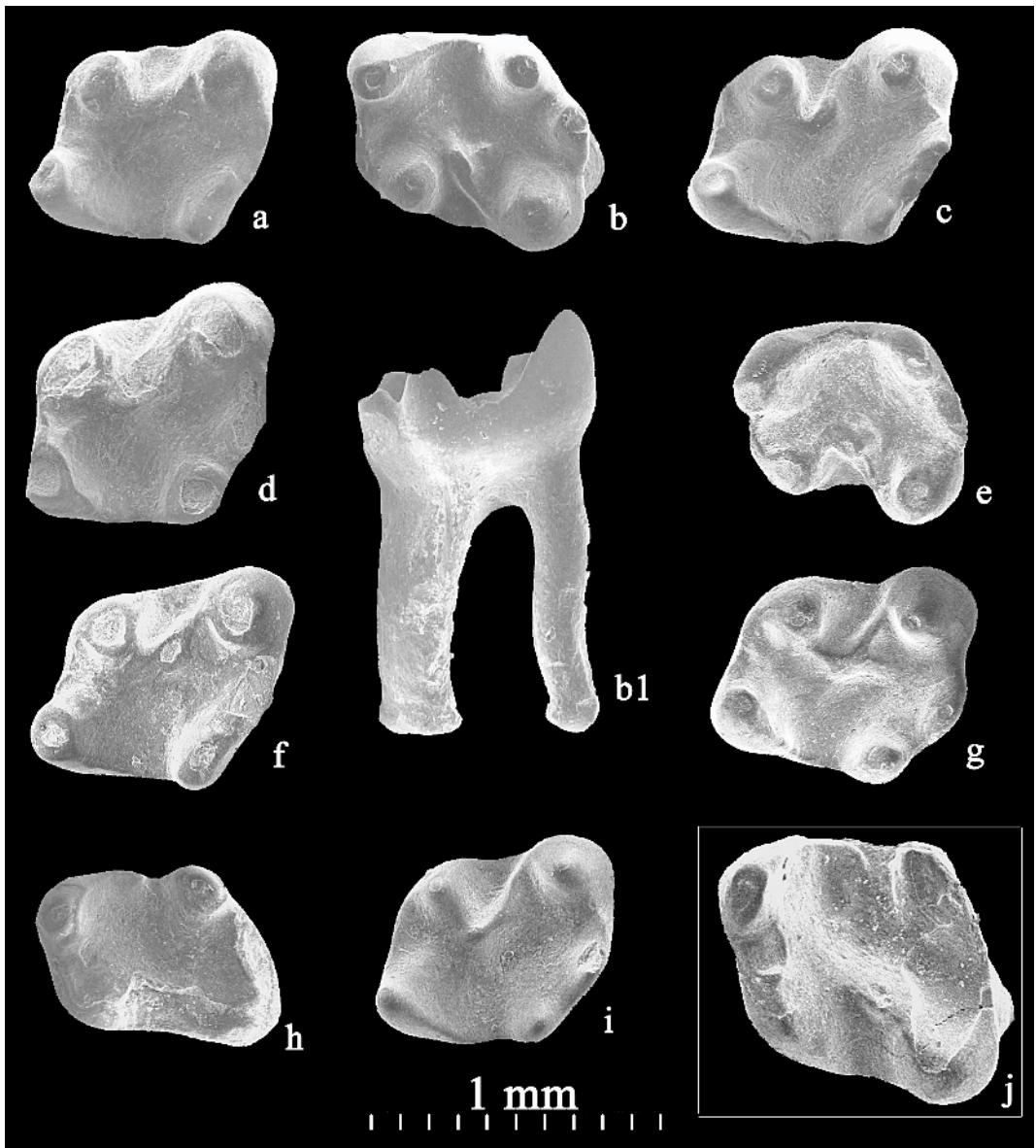


Fig. 4. The m1 of *Archetypomys erlianensis*. **a**, V14623.10, right m1; **b**, V14622.18, left m1; **b1**, buccal view of V14622.18; **c**, V14622.19, right m1; **d**, V14623.11, right m1; **e**, V14622.20, left m1; **f**, V14622.21, right m1; **g**, V14622.22, right m1; **h**, V14623.12, left m1; **i**, V14623.13, right m1; **j**, left m1 of *Tribosphenomys minutus* from the Late Paleocene Subeng locality, Inner Mongolia.

metaconid, the entoconid is more anterior than the hypoconid so that the tooth is more or less diamond-shaped in occlusal view. The hypoconid projects posterobuccally and is the most robust cuspid of the tooth. The hypoculid is prominent and transversely oriented.

The postcingulid or postlophid is weak between these cuspid. No other crest is developed from these talonid cuspid. V14623.13 (fig. 4i) is a tooth that had not fully erupted in life; its cuspid are not fully developed and bear no wear; it could also be an m2.

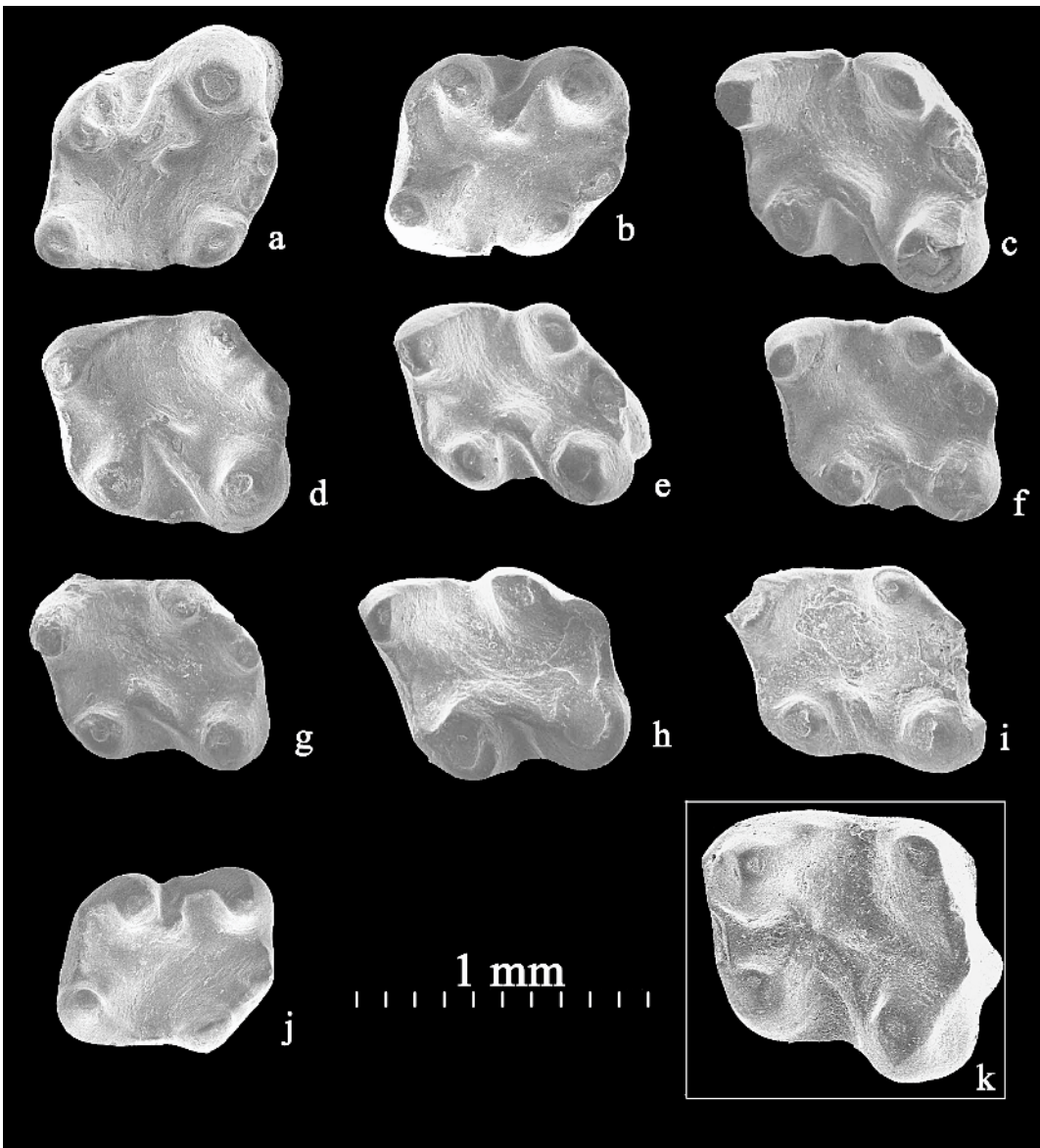


Fig. 5. The m2 of *Archetypomys erlianensis*. **a**, V14623.14, right m2; **b**, V14622.23, right m2; **c**, V14623.15, left m2; **d**, V14622.24, left m2; **e**, V14623.16, left m2; **f**, V14622.25, left m2; **g**, V14622.26, left m2; **h**, V14622.27, left m2; **i**, V14623.17, left m2; **j**, V14622.28, right m2; **k**, left m2 of *Tribosphenomys minutus* from the Late Paleocene Subeng locality, Inner Mongolia.

The m3 is slightly wider anteriorly than posteriorly and has a hypoconulid that is more conical than transverse, although in one tooth (fig. 6b) the hypoconulid is not distinct. In addition, there is no contact fact on the posterior surface of the tooth and the poste-

rior root is more posteriorly flared than those of m1–2. The metaconid of m3 is relatively higher and even more anteriorly extended than that of m1–2. A peculiar cuspid is developed between the protoconid and metaconid in two specimens (fig. 6a, d); it sends a weak ridge to

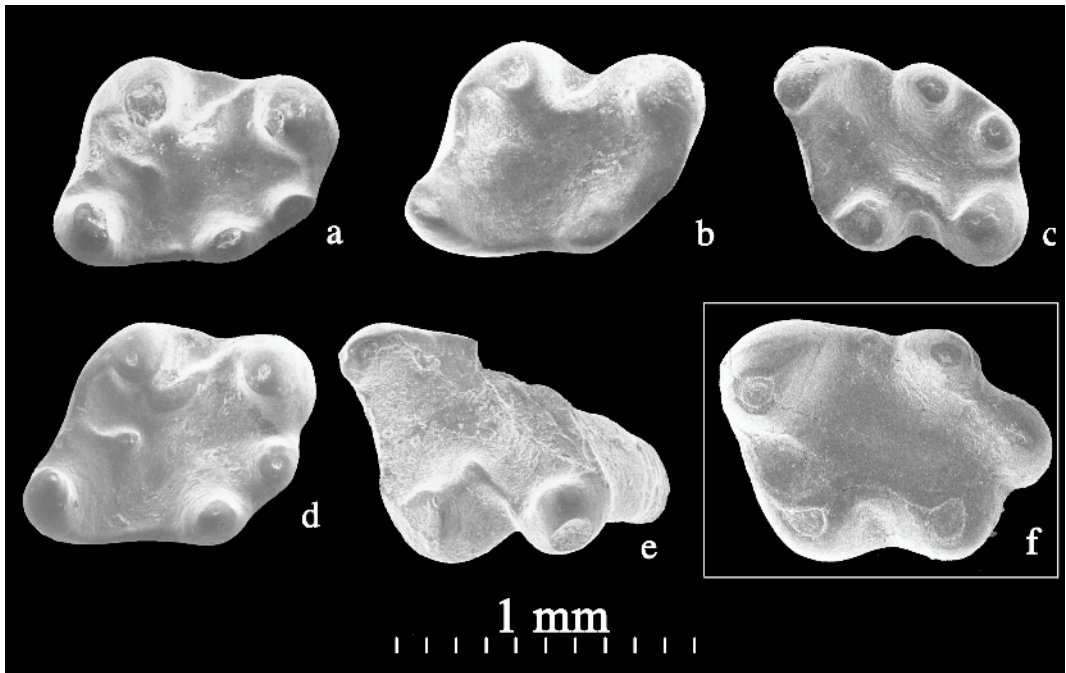


Fig. 6. The m3 of *Archetypomys erlianensis*. a, V14622.29, right m3; b, V14622.30, right m3; c, V14622.31, left m3; d, V14622.32, right m3; e, V14622.33, left m3; f, left m3 of *Tribosphenomys minutus* from the Late Paleocene Subeng locality, Inner Mongolia.

the anterior edge of the tooth. As in m1–2, the m3 hypoconid is the largest talonid cusp and is slightly more posterior than the hypoconulid.

CHARACTER ANALYSES

Because of their similar morphology and temporal distributions, we compared *Archetypomys erlianensis* primarily with alagomyids and some early rodents of modern aspect, such as *Cocomys* and *Paramys*. As in alagomyids, the lower cheek teeth of *Archetypomys erlianensis* are rodentlike, whereas the uppers are less so. Therefore, *Archetypomys erlianensis* shares some features with either alagomyids or rodents. *Archetypomys* is in the size range of alagomyids and has more distinct cusps but weaker crests than any of the other forms with which it was compared; its upper molars are also more triangular than is the case among the other forms. The following analyses detail some of the dental features and discuss those that have general implications in understand-

ing the early evolution of rodent dental morphology.

TOOTH DIMENSIONS: The primary difference between *A. erlianensis* and alagomyids is that the upper cheek teeth of *A. erlianensis* are transversely narrower than those of alagomyids, thereby being more similar to those of rodents of modern aspect. In alagomyids, the upper cheek teeth are transversely wide (figs. 1h, 2i), whereas in early rodents, such as cocomyids (Li et al., 1989; Dashzeveg, 1990a) and paramyines (Wood, 1962; Dawson and Beard, 1996), the upper cheek teeth are quadrate. Table 2 compares M1 dimensions and length/width ratios among selected early rodents and alagomyids where M1 measurements are available. It shows that from *Tribosphenomys* to more advanced rodents, M1 changes from being wider transversely to being longer anteroposteriorly. Because of its narrower tooth dimensions, cheek tooth cusps of *A. erlianensis* are more conical, whereas those of alagomyids are more transverse. The absolute length of the upper molar of *A.*

TABLE 2
M1 Measurements (mm) in Selected Glires Taxa

	L/W (no.) ^a	Ratio
<i>Tribosphenomys minutus</i> (V10775)	0.86/1.56 (1)	0.55
<i>T. secundus</i> (PIN 3104/435)	1.0/1.8 (1)	0.56
<i>Alagomys inopinatus</i> (PSS N20-176)	0.7/1.1 (1)	0.63
<i>A. russelli</i> (CM 69771)	0.64/1.01 (1)	0.63
<i>Archetypomys erlianensis</i> (M1)	0.77/0.88 (6)	0.88
<i>Archetypomys erlianensis</i> (M2)	0.81/0.96 (7)	0.84
<i>Cocomys lingchaensis</i>	1.40/1.79 (8)	0.78
<i>Bandaomys zhonghuaensis</i> (V10689)	1.44/1.68 (1)	0.86
<i>Paramys adamus</i> (CM 68765)	1.56/1.90 (1)	0.82
<i>Petrokozlovica</i> cf. <i>P. notos</i>	3.17/3.33 (3)	0.95
New myodont rodent from 7 same locality of <i>A. erlianensis</i>	1.00/1.03 (1)	0.97
<i>Pappocricetodon antiquus</i>	1.24/1.10 (62)	1.12

^aLength/width (mm) and (number of specimens).

erlianensis is similar to or slightly smaller than that of *Tribosphenomys* (figs. 1, 2; table 2) but its width is relatively much smaller. This suggests that in relation to the wider tooth of *Tribosphenomys* the nearly quadrate tooth of *A. erlianensis* is achieved by narrowing the tooth instead of increasing its anteroposterior length. The difference in tooth dimensions probably reflects a functional transition in mastication, in which the transverse component of the masticatory stroke may have been reduced in *A. erlianensis* compared with alagomyids.

PREPROTOCONULE: The preprotoconule is a unique feature of *A. erlianensis*. In *Tribosphenomys minutus*, the cusp that occurs on the anterior margin of the upper molar and connects lingually with the preprotocrista is identified as the protoconule (Meng and Wyss, 2001). In other alagomyid species for which the upper molar is known, the protoconule is always recognized, although in *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996) this cusp is more prominent and less anteriorly marginal than in *Tribosphenomys* (Lopatin and Averianov, 2004a). In contrast, there are two cuspules between the protocone and paracone in *A. erlianensis*: a smaller one on the preprotocrista and a larger one lingual to the paracone. The cuspule lingual to the paracone is more appropriately homologized with the protoconule, judging from its position and relationship with the paracone, whereas the one on the

preprotocrista is here called the preprotoconule. The preprotoconule of *A. erlianensis*, however, is positionally similar to what has been identified as the protoconule in *Tribosphenomys minutus* (Meng and Wyss, 2001; fig. 1m) and *T. secundus* (Lopatin and Averianov, 2004a), whereas the protoconule of *A. erlianensis* is positionally more similar to that of *Alagomys* (Dashzeveg, 1990b; Tong and Dawson, 1995; Dawson and Beard, 1996), although in *A. russelli* the protoconule is closer to the protocone than to the paracone (Dawson and Beard, 1996: pl. 1F), and in *A. oriensis* the position of this cuspule is not very clear because of damage (Tong and Dawson, 1995: fig. 3A). Several interpretations are possible for the homologies of these cusps. First, the protoconule in either *Tribosphenomys* or *Alagomys* is actually homologous with the preprotoconule of *A. erlianensis*, so that the protoconule is not developed in *Tribosphenomys* and *Alagomys*, but it is developed in *Archetypomys*. Second, the protoconule in *Tribosphenomys* is homologous with the preprotoconule of *A. erlianensis*, and the protoconule in *Alagomys* is equivalent to the same cuspule of *A. erlianensis*. If so, then *Tribosphenomys* develops the preprotoconule but not the protoconule, whereas *Alagomys* has the reversed condition. Third, the cuspule in question is the protoconule in both *Tribosphenomys* and *Alagomys*, which is homologous with that of *A. erlianensis*; the latter is the cusp designation we prefer here. It follows that the preprotoconule is an apomorphic feature of *A. erlianensis*, and the protoconule has shifted buccally toward the paracone compared to the condition in *Tribosphenomys* and *Alagomys*. Given that the protoconule is a common feature in mammals, we consider its presence in *Tribosphenomys* and *Alagomys* as a primitive feature, as currently recognized in studies on alagomyids. Butler (1985: 386) stated that “rodent molars have passed through a tribosphenic stage in their evolution, and the Osbornian names can be applied confidently to their cusps.” This is evidenced by the dental morphology of *Tribosphenomys* and again by *Archetypomys*, although homology of finer-scale structures, such as the preprotoconule in the latter, remain uncertain.

PRECINGULUM: The transverse ridge anterior to the paracone and protoconule in *A. erlianensis* is described as the preprotoconule crista, which is somewhat inflated and protrudes farther anteriorly than that of alagomyids. The condition in *A. erlianensis* is to some extent similar to the precingulum in rodents of modern aspect, such as cocomyids and paramyines. This raises the issues of whether such a ridge should be called the precingulum and whether the precingulum in rodents is homologous with that of a typical tribosphenic tooth pattern.

The precingulum in eutherians is usually at the anterior base of the protocone and is primitively weak and incomplete, or absent; it has nothing to do with the crests derived from the protocone, such as the preprotocrista and preparaconule crista. In describing *Tribosphenomys minutus*, Meng and Wyss (2001) homologized the anterobuccal crest from the protoconule with the preparaconule crista of a typical tribosphenic molar and the posterobuccal crest from the protoconule with the postparaconule crista that connects the paracone buccally; they considered the precingulum as being absent in *T. minutus*, *Alagomys*, and most basal Glires. In describing *A. russelli*, Dawson and Beard (1996) employed descriptive, unambiguous yet non-committal terms for those tooth crests. However, Meng and Wyss (2001) accepted that a distinctive precingulum is present in early rodents, which is also called anteroloph or anterior cingulum, as used in previous studies (Wood, 1962; Li et al., 1989; Dashzeveg, 1990a; Tong and Dawson, 1995; Averianov, 1996; Dawson and Beard, 1996; Shevyreva, 1996) and considered to be similar to that of anagalids and pseudictopids (Hu, 1993). Meng and Wyss (2001) further noted that in later rodents, the precingulum may join the protoloph (Dashzeveg and Meng, 1998) and is usually called the anteroloph (Flynn et al., 1986).

In its position, the ridge anterior to the paracone and protoconule in *A. erlianensis* is similar to the preparaconule crista of *T. minutus*, even though the preprotoconule has replaced the protoconule. The origin of this ridge differs from the precingulum in typical tribosphenic teeth. Therefore, we consider this

ridge in *A. erlianensis* as the preprotoconule crista, instead of the precingulum. The close structural similarity between *A. erlianensis* and other rodents suggests that the precingulum of early rodents could be a modified preprotoconule crista. This may explain why the precingulum in early rodents is restricted to the anterobuccal edge of the upper molars and is rarely on the anterior base of the protocone. If this is correct, it follows that the so-called precingulum in rodents is not homologous with that on the typical tribosphenic tooth.

BUCCAL CINGULUM: A buccal cingulum (or buccal shelf of Lopatin and Averianov, 2004a) is present on the upper molars of *Tribosphenomys* (figs. 1h, 2i) but this structure is usually absent in rodents, so that the paracone and metacone are marginally positioned, forming the buccal border of a molar. In *Tribosphenomys*, the cingulum buccal to the paracone is always wider than its counterpart buccal to the metacone. The condition in *Alagomys* varies from being more distinctive in *A. oriensis*, narrow in *A. inopinatus* (Lopatin and Averianov, 2004a), to being absent in *A. russelli* (Dawson and Beard, 1996: pl. 1F, G). In *Archetypomys erlianensis* a vestige of the cingulum can be observed buccal to the paracone, being more similar to that of *Alagomys* than to *Tribosphenomys*.

HYPOCONE: The hypocone is absent on upper cheek teeth of *Archetypomys*, as is the case in *Alagomys* but in contrast to *Tribosphenomys*, which bears a tiny hypocone (Meng et al., 1994; Meng and Wyss, 2001; fig. 1m). However, *Archetypomys* is more similar to *Tribosphenomys* in having a distinctive, well-defined basin between the protocone and metaconule; the same basin is less developed in *Alagomys*. Absence of the hypocone gives the molar a triangular outline in occlusal view. This differs from the more quadrate teeth of early rodents, such as cocomyids and paramyines, in which a hypocone is usually developed.

TRIGON BASIN: It was pointed out by Meng and Wyss (2001) that a shared derived feature for *Alagomys* and *Tribosphenomys* is that the trigon basins (the central basin) of their upper molars form a broad, transversely oriented valley, which distinctly separates the paracone and metacone; the cusp surfaces

facing the basin are steep and flat. The absence of the centrocrista between the paracone and metacone also contributes to the distinctive trigon basin configuration of alagomyids. Lopatin and Averianov (2004a) disagreed with previous workers (Meng et al., 1994; Dawson and Beard, 1996) who regarded *Tribosphenomys* and *Alagomys* as being closely related members of the same family Alagomyidae. Apparently, Lopatin and Averianov (2004a) were unaware of the work by Meng and Wyss (2001) at the time, but soon published a short paper proposing the new species *T. tertius* (Lopatin and Averianov, 2004b), in which they cited Meng and Wyss (2001). In the later paper, the authors still maintained their earlier opinion that *Tribosphenomys* and *Alagomys* belong to separate families. We are not convinced by the argumentation of Lopatin and Averianov (2004a, 2004b) for separating *Tribosphenomys* and *Alagomys* at the family level. Meng and Wyss (2001) considered the upper molar trigon basin condition described above as a unique feature for *Tribosphenomys* and *Alagomys*, but Lopatin and Averianov (2004b: 337) presented an alternative view on the structure and stated: "Actually, 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 structure of the trigon basin in alagomyids differs appreciably from that of *Cocomys* and *Ischyromyidae* (moreover, the trigon basin in various species of *Ischyromyidae* varies considerably). In early rodents such as *Cocomys* (Li et al., 1989), the cheek tooth is square-shaped in occlusal outline, so that its trigon basin is proportionally not comparable to that of alagomyids. Moreover, the surfaces of adjacent cusps and cuspules are more rounded and in most cases the bases of the paracone and metacone are in contact, or nearly so (Li et al., 1989: fig. 5a); therefore, the trigon basin in these forms does not have the peculiar cleft shape that occurs in alagomyids. In fact, in an unpublished study by Zhai (see Russell and Zhai, 1987: 71), teeth of *Tribosphenomys* from the Late Paleocene Subeng locality, Inner Mongolia, were initially

considered to pertain to a dermopteran because the paracone and metacone are widely separated by a transverse valley. Thus, we still regard the trigon basin condition in *Tribosphenomys* and *Alagomys* as a good indicator of their relationship. *Archetypomys* is quite similar to alagomyids in the trigon basin condition, although the basin in *Archetypomys* is transversely narrower because of its modified occlusal outline.

METACONULE: The metaconule is distinct in alagomyids, in which this cusp is connected to the protocone and metacone by weak crests, if at all. Moreover, the metaconule in alagomyids merges posteriorly with the postcingulum, so that basins are formed on the lingual and buccal side of the metaconule, respectively (figs. 1h, 2i). This condition is more pronounced in *Tribosphenomys* than in *Alagomys*. *Archetypomys* compares better with *Tribosphenomys* than with *Alagomys* in the development of the metaconule and its connections with other cusps. In rodents of modern aspect, the metaconule is often prominent, but it is less isolated from the metacone and protocone and is separated from the postcingulum (posteroloph) by a transverse valley that varies in depth among different species.

PROTOCRISTID: The crest extending from the protoconid toward the metaconid in rodents is homologized with the protocristid (Meng and Wyss, 2001). This crest has been given different names, such as metalophid (Wood, 1962), metalophulid II (Flynn et al., 1986; Li et al., 1989; Korth, 1994), and posterior arm of the protoconid (Dawson et al., 1984), in various studies of rodent dental anatomy and evolution. A weak protocristid is present on some lower molars of *Tribosphenomys minutus* (Meng et al., 1994; Meng and Wyss, 2001; figs. 4j, 5k) and *T. secundus* (Lopatin and Averianov, 2004a), but this structure is unclear in *T. tertius* because of wear (Lopatin and Averianov, 2004b). Lopatin and Averianov (2004a) regarded the protocristid as being absent in *Alagomys*, although the lower cheek teeth of *A. russelli* appear to have some indication of a crest between the protoconid and metaconid (Dawson and Beard, 1996: pl. 1A–D). *A. erlianensis* is similar to *Alagomys* in lacking

the protocristid, so that a continuous, broad basin extends from the anterior edge of the tooth to the hypoconulid. However, in some teeth of *Archetypomys* (fig. 6a, d), a cuspid and its associated crests occur between the protoconid and metaconid.

HYPOCONULID: A distinct hypoconulid is present on all lower molars of *Archetypomys*, but this cuspid is most prominent on m3. This condition recalls that of alagomyids, although some differences exist. The hypoconulid of *Archetypomys* is more conical and isolated on m1 and m2. Unlike the condition in alagomyids, the hypoconulid of m3 in *Archetypomys* does not form the rearmost part of the tooth; instead, its hypoconid extends slightly farther posteriorly than the hypoconulid, which is actually comparable to that of *Cocomys* (Li et al., 1989: fig. 5d). If the hypoconulid is small or absent, as in V14622.30 (fig. 6b), the m3 is quite similar to that of *Cocomys*. Dawson and Beard (1996) considered that the m3 hypoconulid forming a narrow lobe on the tooth is a shared feature of *Alagomys* and *Tribosphenomys*, a view that was adopted by Meng and Wyss (2001). Lopatin and Averianov (2004b) considered it impossible to designate the m3 hypoconulid of *Alagomys* as a narrow third lobe; these authors stated (p. 337) "On the contrary, its hypoconulid is similar in structure to that Ctenodactylidae and substantially differs from the plesiomorphic condition characteristic of *Tribosphenomys*." Dawson and Beard (1996) and Meng and Wyss (2001) compared alagomyids only with the ctenodactyloid *Cocomys*, not with any species of Ctenodactylidae. In *Cocomys*, the hypoconulid is reduced and incorporated into the posterior cingulid, as recognized by Dawson and Beard (1996), which is undoubtedly different from the condition of alagomyids. Given that species of Ctenodactylidae have diverse and quite derived tooth morphologies, we are not sure which species Lopatin and Averianov (2004b) used to compare with *Alagomys*.

ANTEROCONID: A small anteroconid on dp4 in *Archetypomys* distinguished it from alagomyids. The dp4, as interpreted by Meng and Wyss (2001), in *Alagomys orientis* (Tong and Dawson, 1995) and *A. russelli* (Dawson and Beard, 1996) is molariform but lacks an

anteroconid; the anterior end of those dp4s is relatively flat. In *Tribosphenomys minutus* (Meng et al., 1994; Meng and Wyss, 2001), the dp4 does not have any anterior cuspid when worn. However, in an unworn dp4 (Meng and Wyss, 2001: fig. 6a), a small projection at the anterolingual tip of the tooth was interpreted as representing a rudimentary paraconid. A similar condition is present in some unworn dp4s from the Late Paleocene Subeng locality (fig. 3l). In contrast, the anteroconid of *Archetypomys* lies on the longitudinal midline of the tooth.

An anteroconid is a characteristic feature of m1 in early myodont rodents (Emry and Korth, 1989; Emry et al., 1998; Tong, 1992, 1997; Wang and Dawson, 1994; Dawson and Tong, 1998), although the cuspid is usually more prominent and often transversely extended. These cusps are similar in their positions but are unlikely to be homologous. In the early rodents that have p4, such as ctenodactyloids and paramyines, preservation of the dp4 is usually uncommon. One specimen from the Bumban beds, which was named *Boromys grandis* (Dashzeveg, 1990a: fig. 13), has a dp4 (it was originally described as a p4). The dp4 was deeply worn, judging from the illustration, but it is elongated anteroposteriorly and probably has a sizable anteroconid. A definitive anteroconid is on the dp4 of *Paramys adamus* (Dawson and Beard, 1996: pl. II D), more distinct than that of *Archetypomys*. Development of the dp4 anteroconid may be a derived feature compared to those of alagomyids, but retaining the dp4 is probably a primitive feature similar to that of alagomyids.

CRISTID OBLIQUA: The cristid obliqua (ectolophid) is buccal on the lower molars of alagomyids, and is relatively shorter in *Tribosphenomys* than in *Alagomys* (Lopatin and Averianov, 2004a). A small mesoconid is either present or absent; for those that have a small mesoconid, wear may eradicate the mesoconid. Because of the relatively buccal position of the cristid obliqua, small or absent mesoconid, marginally positioned cusps, anteriorly extended metaconid, and reduced or absent protocristid, the talonid basin of alagomyids is broad (Meng and Wyss, 2001). The talonid basin of *Archetypomys* is also

quite open, but its cristid obliqua is more oblique in that it initiates posteriorly at the anterolabial base of the hypoconid and terminates anteriorly at the posterolingual base of the protoconid; its anterior portion is inflated to form an obliquely oriented mesoconid, which differs from those of either alagomyids or early rodents.

DISCUSSION

A diversity of Glires, including eurymylids, mimotonids, and stem rodents and lagomorphs, have been known from Asia since the 1920s, when *Eurymylus* was first described by Matthew and Granger (1925). Numerous fossils have been recovered from the early Tertiary of Asia during the last few decades. The discovery of *Heomys* and the proposal of its relationship with rodents (Li, 1977), a view followed by many authors thereafter (Chaline and Mein, 1979; Hartenberger, 1980; Dawson et al., 1984; Li et al., 1987), have focused attention on Asia for the origin of Glires, and recent phylogenetic analyses that involved many of these newly discovered Glires have supported the hypothesis that Asia is the center of origin for Glires (Meng et al., 2003; Asher et al., 2005).

Among these early Glires, Alagomyidae is particularly pertinent to the origin of rodents. This family contains two genera, *Alagomys* and *Tribosphenomys*. So far, three species have been described for *Alagomys*: *Alagomys inopinatus* (Dashzeveg, 1990a), *A. oriensis* (Tong and Dawson, 1995), and *A. russelli* (Dawson and Beard, 1996); and four species of *Tribosphenomys* have been named: *T. minutus* (Meng et al., 1994), *T. borealis* (Dashzeveg, 2003), *T. secundus*, and *T. tertius* (Lopatin and Averianov, 2004a, 2004b). These species range from the Upper Paleocene to Lower Eocene of Asia, except for *A. russelli*, the only species discovered from the Upper Paleocene of North America. *Alagomys* and *Tribosphenomys* are miniscule animals that have enlarged, evergrowing upper and lower incisors typical of rodents and rodentlike lower cheek teeth, but their upper cheek teeth are not so characteristic of rodents. Unlike other eurymylids and mimotonids, the cheek teeth of alagomyids are low-crowned with distinct

cusps but weak crests. As the name *Tribosphenomys* implies, the cheek teeth of this genus display some aspects of the tribosphenic molar pattern of primitive therians (Meng et al., 1994), which therefore narrows the morphological gap between a typical tribosphenic tooth pattern and a typical rodent molar. However, a conspicuous feature of alagomyid molars is their transverse occlusal outline, which differs from the more quadrate condition in rodents of modern aspect. The most speciose groups among the earliest rodents of modern aspect are the ctenodactyloids in Asia and the paramyines in North America, both of which bear upper molars that are somewhat square-shaped with a precingulum and a hypocone.

Archetypomys reported here has a tooth pattern combining features that are found separately in alagomyids and rodents of modern aspect. As discussed above, *Archetypomys* is similar to alagomyids in having a partial buccal cingulum, a distinct metaconule that merges posteriorly with the postcingulum, a transversely oriented trigon basin that widely separates the paracone and metacone, a prominent hypoconulid on lower molars, and in lacking the hypocone and the protocristid. These features distinguish *Archetypomys* from rodents of modern aspect. On the other hand, *Archetypomys* differs from alagomyids in having upper cheek teeth that are transversely narrower, a preprotoconule, a preprotoconule crista that projects anteriorly, an anteroconid on dp4, an oblique cristid obliqua bearing a distinct mesoconid, and the hypoconid more posteriorly extended (or hypoconulid less posteriorly extended) on m3. The narrow upper cheek teeth are more comparable to those of rodents than to alagomyids. If the preprotoconule crista of *Archetypomys* is homologous with the precingulum of rodents, then this feature is also more similar to that of rodents than to alagomyids. The presence of the preprotoconule is probably an autapomorphy of *Archetypomys*. Given the fragmentary nature of available material, a phylogenetic analysis may not be meaningful, but the dental features discussed here suggest that *Archetypomys* occupies an intermediate phylogenetic position between alagomyids and rodents of

modern aspect. The discovery of *Archetypomys* shows that rodents were more diverse than previously appreciated during the Early Eocene. Some of them are unquestionably miniscule species that might be discovered in other areas using appropriate collecting methods.

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