A New Species of Gomphos (Glires, Mammalia) from the Eocene of the Erlian Basin, Nei Mongol, China

Authors: Meng, Jin, Kraatz, Brian P., Wang, Yuanqing, Ni, Xijun, Gebo, Daniel L, et al.

Source: American Museum Novitates, 2009(3670) : 1-11

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/673.1

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3670, 11 pp., 4 figures, 1 table November 30, 2009

A New Species of *Gomphos* (Glires, Mammalia) from the Eocene of the Erlian Basin, Nei Mongol, China

JIN MENG,[1] BRIAN P. KRAATZ,[1] YUANQING WANG,[2] XIJUN NI,[2]
DANIEL L. GEBO,[3] AND K. CHRISTOPHER BEARD[4]

ABSTRACT

Dental and postcranial specimens of *Gomphos shevyrevae*, sp. nov., from the lower part of the Irdin Manha Formation at the Huheboerhe locality, Erlian Basin, Nei Mongol (Inner Mongolia), are described. The new species differs from *G. elkema* and *G. ellae* in having more robust teeth with inflated cusps and stronger lophs and a calcaneus with extra articulation for the astragalus and navicular. The new species is stratigraphically well constrained and probably represents the youngest known species of the genus, extending its geological record into the Middle Eocene. It also shows that mimotonids coexisted for millions of years as a side branch of duplicidentates with the earliest stem lagomorphs, including *Dawsonolagus*.

INTRODUCTION

Glires consists of two modern groups: rodents and lagomorphs. Although the monophyly of Glires has been a matter of debate, recent morphological and molecular evidence strongly supports the recognition of Glires as a clade (Meng and Wyss, 2001; Huchon et al., 2002; Meng et al., 2003; Douzery and Huchon, 2004; Asher et al., 2005; Bininda-Emonds et al., 2007). Within Glires, Simplicidentata is defined as all Glires sharing a more recent common ancestor with Rodentia than with Lagomorpha. It is the stem-based counterpart to Rodentia. Duplicidentata is defined as all members of Glires sharing a more recent common ancestor with Lagomorpha than with Rodentia (Meng and Wyss, 2005).

Mimotonidae has been recognized as a paraphyletic group, within which a monophy-

---

[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, P.R. China.
[3] Department of Anthropology, Northern Illinois University, DeKalb, IL 60115.
[4] Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, PA 15213.

ISSN 0003-0082

letic Lagomorpha is nested. *Gomphos* has been shown to be a late-branching mimotonid and the sister group of Lagomorpha based on morphological evidence (Meng et al., 2003, 2004; Asher et al., 2005). Mimotonids are typical as gliriform mammals in having a pair of enlarged and ever-growing upper and lower incisors. In addition, they bear a minor pair of incisors in their upper and lower jaws, easily distinguishing them from most other Glires and mammals.

Gomphos elkema, the type species of the genus, has been described from Mongolia (Shevyreva et al., 1975; Asher et al., 2005) and China (Meng et al., 2004, 2005) and is considered to be a characteristic fossil for the earliest Eocene Bumbanian faunas in central Asia (Dashzeveg, 1988; Dashzeveg and Russell, 1988). The initial species identification was based on a fragmentary lower jaw, which was first named by Shevyreva (Shevyreva et al., 1975) and redescribed by Zhegallo and Shevyreva (1976) and by Dashzeveg and Russell (1988). This specimen was from members II and III of the Gashato (Khashat) Formation at the Ulan-Nur Basin (Dashzeveg, 1988). More complete *G. elkema* material was reported by Asher et al. (2005) from the Bumban Member of the Naran-Bulak Formation in Tsagan-Khushu, Nemegt Basin. Recently, a second species of the genus, *G. ellae*, was reported from Tsagaan Khutel, Mongolia. The age of *G. ellae* is poorly constrained, but this species probably dates to the late Early Eocene (Kraatz et al., 2009), younger than *G. elkema*.

MATERIALS AND METHODS

All specimens reported here were collected from the Huheboerhe locality either by surface collecting or by screen washing. Each specimen has its own GPS log from the specific site collected. A large number of mammals have been collected from the same level, though only a handful of *Gomphos* specimens were recovered. Similarities in foot bones to those of *G. elkema* (Meng et al., 2004; Asher et al., 2005) help to associate two tarsal elements with the teeth.

In describing molar structures we follow the dental terminology used for *Tribosphenomys* (Meng and Wyss, 2001), considering that a consistent terminology with tribosphenic tooth pattern, wherever it can be established, will aid in understanding the phylogenetic relationships of Glires within Mammalia. However, because there is no consistent terminology for nonmolariform premolars, we use descriptive, noncommittal terms, such as a labial or lingual cusp, instead of terms that imply homology, such as the protocone and paracone, in describing these teeth. Measurements were taken using digital calipers. SEM photographs of teeth were taken from uncoated specimens using a Hitachi SEM at the American Museum of Natural History.

Institutional abbreviation: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, where the original specimens will reside.

GEOLOGICAL SETTING

The Tertiary beds in the Erlian Basin, Nei Mongol (Inner Mongolia), China, were first explored by the Central Asiatic Expeditions (CAE) in the 1920s (Granger and Berkey, 1922; Berkey and Granger, 1923; Berkey and Morris, 1924, 1927; Matthew and Granger, 1926). The stratigraphy and vertebrate fossils from this area have formed the bases for several Eocene Asian Land Mammal ages, such as the Arshantan and Irdinmanhan. However, the stratigraphy of this region remained unclear (Radinsky, 1964) until more recent investigations revealed lithological and biostratigraphic relationships for several key sections in this area (Meng et al., 2004, 2007c; Bowen et al., 2005).

The new *Gomphos* specimens were collected from the Huheboerhe locality, Erlian Basin. At this locality the section consists of the Nomogen, Arshanto, and Irdin Manha formations, from oldest to youngest. The new *Gomphos* fossils came from level 10 of the section, equivalent to the lower portion of the Irdin Manha Formation (fig. 1). Specimens of *Gomphos elkema* have been collected from level one of the same section, in the upper part of the Nomogen Formation. The stratigraphic occurrences for these two species of *Gomphos* are clear, thus providing a solid superpositional basis for discussing the evolutionary relationship of the two species.

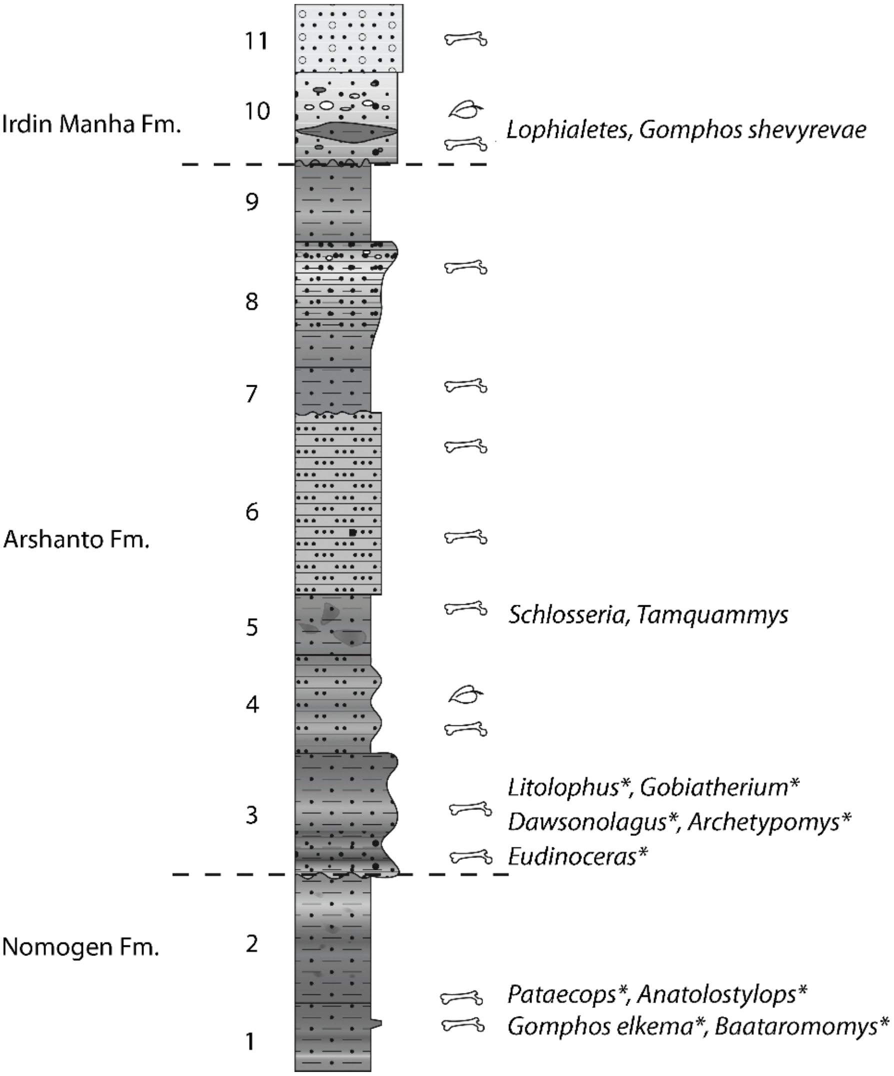

Fig. 1. Section at Huheboerhe, Erlian (modified from Meng et al., 2007c), showing stratigraphic occurences of *Gomphos elkema*, *G. shevyrevae*, and some associated species. Asterisks show species currently known from Nuhetingboerhe.

SYSTEMATIC PALEONTOLOGY

Mammalia Linnaeus, 1758

Glires Linnaeus, 1758

Mimotonidae Li, 1977

Gomphos Shevyreva, 1975

Type Species: *Gomphos elkema* Shevyreva, 1975.

Included Species: *Gomphos ellae* and *G. shevyrevae*, new species.

Revised Diagnosis: Similar to other mimotonids but differing from other Glires in having two pairs of lower incisors. Differs from *Mimotona* (Li, 1977) in its larger size, less transversely extended and more unilaterally hypsodont upper teeth, stronger lophs, a mesostyle usually present, lower molars with a longer trigonid, and a mesoconid on lower molars. Differs from *Anatolmylus* (Averianov, 1994; Averianov and Godinot, 1998) in having a shallow horizontal ramus. Differs from *Mimolagus* (Bolin, 1951) in its smaller size and higher-crowned cheek teeth with distinctive cusps and ridges.

LOCALITIES AND AGE: *Gomphos elkema* is known from Bumbanian faunas in Tsagan-Khushu, Nemegt Basin, and Ulan-Nur Basin of Mongolia (Dashzeveg and Russell, 1988; Dashzeveg, 1988); Huheboerhe, Wulanboerhe, and Nuhetingboerhe (Meng et al., 2004), and Bayan Ulan (Meng et al., 2005) in the Erlian Basin of Nei-Mongol (Inner Mongolia), China. *G. ellae* is from Tsagaan Khutel, Mongolia (Kraatz et al., 2009). *G. shevyrevae* is from the Irdin Manha Formation at Huheboerhe, Erlian. Early to Middle Eocene.

Gomphos shevyrevae, new species

HOLOTYPE: A right M1 (IVPP V14669).

PARATYPE: A right m1 (IVPP V14670).

INCLUDED SPECIMENS: A right P4 (or P3) (V14671.1), a right M1 (V14671.2), a right M2 (V14671.3), a left M2 (V14671.4), a right m1 (V14672.1), a right m2 (V14672.2), a left m3 (V14672.3), a left calcaneus (V14673), and a left astragalus (V14674).

ETYMOLOGY: The species name is in honor of N.S. Shevyreva who named *Gomphos elkema*.

DIAGNOSIS: Differs from *Gomphos elkema* and *G. ellae* in having more robust teeth with higher crowns, inflated cusps; upper molars with more posteriorly expanded hypocone and shelf; absence of the ridge connecting the lingual and labial cusps on P4; lower molars with relatively long trigonid and short talonid, reduced mesoconid and hypoconulid, and absence of the mesostylid; further differs from *G. elkema* in having extra facets on the calcaneus for articulation with the astragalus and navicular (unknown for *G. ellae*).

TYPE LOCALITY AND AGE: Huheboerhe escarpment, Erlian Basin of Nei-Mongol, Middle Eocene lower beds of the Irdin Manha Formation.

COMPARATIVE DESCRIPTION: Measurements of all teeth are in table 1. The tooth we identified as a P4 could also be a P3 (fig. 2). However, the anterior border of P3 is usually narrower than the posterior border in *Gomphos*. This tooth has its anterior portion as wide as the posterior and bears a tiny posterolingual cusp, suggesting that it is likely a right P4. The P4 is a recently erupted tooth that bears no wear. As is typical of *Gomphos*, the P4 is unilaterally hypsodont and consists of a lingual main cusp, presumably the protocone, and a labial cusp. The lingual cusp is crescent shaped, and its two lophs form the anterior and posterior edges of the tooth. The labial cusp is conical, having a steeper labial surface and a more rounded lingual surface. Unlike P4 of *Gomphos elkema*, in which P4 is known (Meng et al., 2004; Asher et al., 2005), the ridge connecting the two cusps is absent in *G. shevyrevae*; instead, there is a weak ridge extending from the labial cusp anterolingually to join the midpoint of the anterior loph. The absence of a connection between the lingual and labial cusps of P4 recalls the condition found in *Mimotona* (Li, 1977; Li and Ting, 1993).

TABLE 1

Tooth measurements of *Gomphos shevyrevae* (in mm)

	Length	Width	Field site
P4 (V14671.1)	2.22	3.38	(H2A)
M1 (V14669)	2.87	4.57	(H2A, holotype)
M1 (V14671.2)	2.74	4.30	(H2)
M2 (V14671.3)	3.38	4.08	(H2A)
M2 (V14671.4)	3.56	4.03	(060722WYQ01)
m1 (V14670)	3.30	3.30	(H2)
m1 (V14672.1)	2.84	2.70	(060720BB01)
m2 (V14672.2)	3.31	3.24	(H2A)
m3 (V14672.3)	3.46	3.32	(H2)

Upper molars have one major lingual and two minor labial roots. The enamel is thick. M1 is so assigned because its hypocone and shelf are less expanded posteriorly than those of M2, and M1 is usually proportionally shorter than M2 (fig. 2). M1 of *G. shevyrevae* is similar to that of *G. elkema* in general morphology. However, the M1 and other upper cheek teeth of *G. shevyrevae* are more robust with more inflated cusps and stronger lophs. The protocone and its anterior and posterior lophs form a V-shaped structure with a slightly rounded apex (the lingual side of the protocone). The angle created by the lophs is about 45°. The lingual portion of the anterior loph may be homologized with the

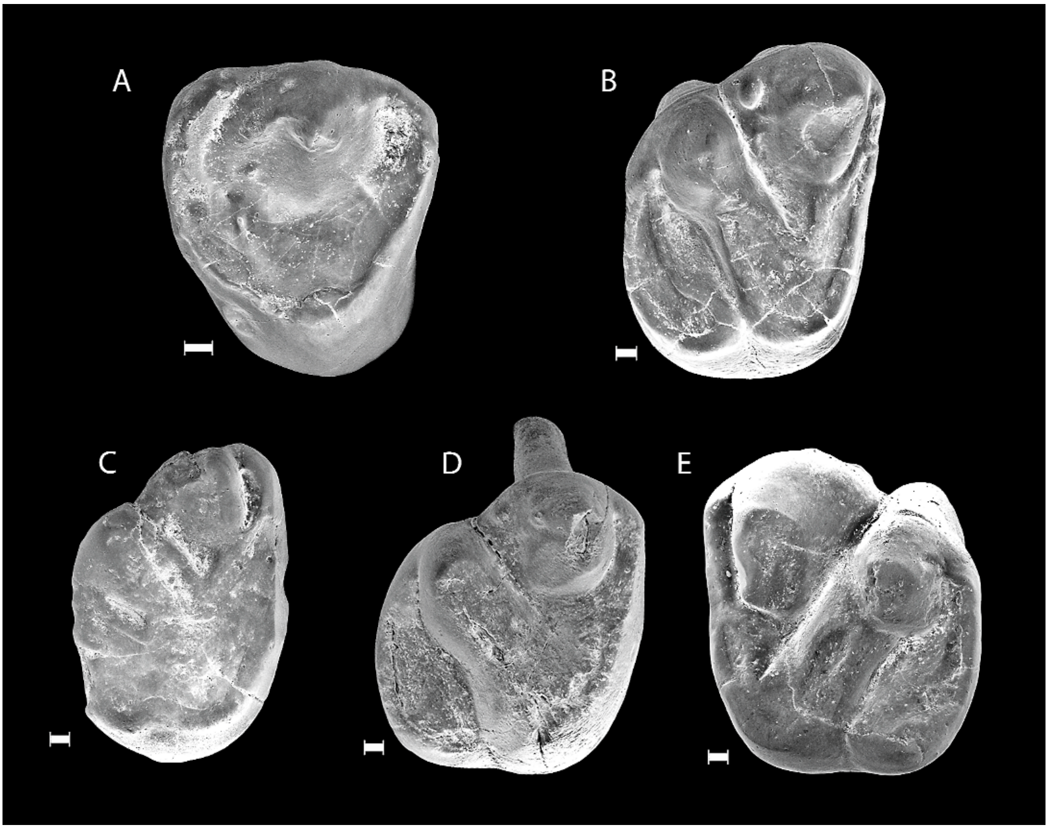

Fig. 2. Crown views of upper cheek teeth of *Gomphos shevyrevae* from the lower Irdin Manha Formation, Huheboerhe at Erlian, Nei Mongol. **A,** right P4 (or P3) (V14671.1); **B,** right M1 (V14669, holotype); **C,** right M1 (V14671.2); **D,** right M2 (V14671.3); **E,** left M2 (V14671.4). Scale bars are 200 µm.

preprotocrista and the labial portion, which is much thinner, with the preparaconule crista. A paraconule (protoconule) is not distinct, but is indicated by a slight inflation where the postparaconule crista joins the anterior loph. Absence of the paraconule is common in basal Glires, both in simplicidentates, such as *Matutinia* and *Rhombomylus* (Ting et al., 2002; Meng et al., 2003), and duplicidentates, such as *Mimotona* and *Gomphos* (Li, 1977; Li and Ting, 1993; Meng et al., 2004), but it is usually present in taxa that are more closely related to rodents and in basal rodents, such as *Tribosphenomys* (Meng et al., 1994, 2007b; Meng and Wyss, 2001), *Neimengomys* (Meng et al., 2007b), *Archetypomys* (Meng et al., 2007a), and *Cocomys* (Li et al., 1989).

There is a weak ridge between the paracone and the anterior loph, which is probably the postparaconule crista. The metacone is smaller and more lingually positioned than the paracone. It is connected with the protocone by the posterior loph of the protocone. The latter loph is strong, almost as wide as the metacone. A mesostyle occurs at the posterior base of the paracone, which blocks the labial exit of the narrow trigon basin. The metaconule is present, but is difficult to distinguish in heavily worn specimens. In lightly worn specimens (fig. 2E) a broader wear facet indicates the metaconule that must be higher and broader than the crista in order for such a wear pattern to be created. In *G. elkema* the posterior loph of the protocone is relatively slimmer and there is usually a restriction labial to the protocone.

The hypocone and the postcingulum are well developed, and both structures are expanded

Fig. 3. Lower molars of *Gomphos shevyrevae* from the lower Irdin Manha Formation at Huheboerhe, Erlian, Nei Mongol. **A1–2,** crown and lingual views of right m1 (V14670, paratype); **B,** right m1 (V14672.1); **C1–2,** crown and labial views of right m2 (V14672.2); **D,** left m3 (V14672.3). Scale bars are 200 µm.

posteriorly. The hypocone is separated from the protocone by a transverse groove, and a similar condition occurs on M2. This condition appears to differ from the morphology prevailing in *G. elkema* and *G. ellae*. In well-worn specimens (fig. 2C), however, the protocone and hypocone become confluent. On the lingual surface of the tooth, a vertical groove between the protocone and hypocone exists near the occlusal surface of the tooth, and this feature also seems more pronounced than on upper molars of *G. elkema* and *G. ellae*.

M2 is similar to M1 in general morphology, but it is proportionally longer. The mesostyle is reduced, either being incorporated into the posterior base of the paracone or entirely absent. No M3 was collected.

The lower molars have an anterior and a posterior root. The tooth crown is somewhat higher than that of *G. elkema* and *G. ellae*. As in the upper molars, the enamel appears thicker than that of *G. elkema* and *G. ellae*. The m1 is identified as such because it has a transversely oriented, ridgelike hypoconulid (fig 3). In *Gomphos*, the lower molar hypoconulid becomes more pronounced posteriorly. The m1 and m2 are very similar except that m2 has a more posteriorly projecting hypoconulid. The lower molars are proportionally wider, and therefore relatively shorter, than those of other species of the genus. Lower molar trigonids are proportionally longer in relation to their corresponding talonid than is the case in other species of the genus. As is typical of *Gomphos*, the protoconid and metaconid are transversely aligned, and the trigonid has nearly vertical anterior and posterior walls. The protoconid and the metaconid are subequal in size. The protoconid is worn more extensively and is therefore

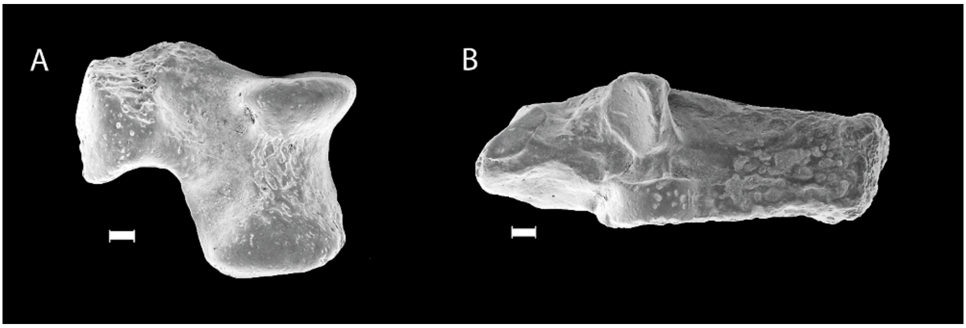

Fig. 4. Tarsal bones of *Gomphos shevyrevae* from the lower Irdin Manha Formation at Huheboerhe, Erlian, Nei Mongol. **A,** dorsal view of left astragalus (V14673); **B,** dorsal view of left calcaneus (V14674). Scale bar is 1 mm.

lower than the metaconid. The protoconid sends the paralophid (paracristid) to the anterolingual base of the metaconid and the protolophid (protocristid) to the posterior base of the metaconid. A crescentic trigonid basin is enclosed by the trigonid cusps and lophids.

Lower molar talonids are as wide as the trigonid and are longer than their corresponding trigonid. The hypoconid is as large as the protoconid and is very close to the posterior wall of the trigonid, so that the hypoflexid becomes a narrow groove. The cristid obliqua (ectolophid) is short and the mesoconid appears very weak relative to other mimotonids. The entoconid is low. Unlike the condition in *G. elkema* and *G. ellae*, in which a mesostylid is present (Meng et al., 2004; Kraatz et al., 2009), the mesostylid is absent in the new species. Because of the reduction of the mesoconid and cristid obliqua, the talonid basin is a broad, featureless concavity. The hypoconulid is a transverse ridge at the rear of the tooth, being connected with the entoconid by a strong postcristid.

The m3 is little worn and displays several additional minor cuspules on the occlusal surface; these structures would be quickly removed with wear (fig. 3). The m3 differs from m1 and m2 in having a longer talonid and a more pronounced hypoconulid. However, compared to those of *G. elkema* and *G. ellae*, the talonid of *G. shevyrevae* is relatively shorter and the hypoconulid is reduced; it does not form a projection at the posterior end of the tooth.

The astragalus measures 11.34 mm long and 8.82 mm wide (maximum dimensions) and is partly broken at its head (fig. 4A). The morphology of the preserved portion is identical to that of *Gomphos elkema* (Meng et al., 2004). The bone is ventrodorsally (or anteroposteriorly) flat. The trochlea is transversely broad and shallow. In *G. elkema*, the lateral and medial rims of the astragalar trochlea appear to be more asymmetrical, with the lateral much larger than the medial (Meng et al., 2004).

The calcaneus measures 20.8 mm long and 8.93 mm wide (maximum dimensions; fig. 4B). It is typical of *Gomphos* in that the calcaneoastragalar and sustentacular facets are aligned at the same level, similar to that of lagomorphs (Bleefeld and McKenna, 1985), but the bone lacks a calcaneal canal that is characteristic of lagomorphs (Bleefeld and Bock, 2002). The calcaneoastragalar facet is a narrow, long and convex surface in a proximodistal orientation, nearly parallel to the long axis of the bone, whereas the sustentacular facet is rounded and concave. Although the general morphology of the calcaneus is similar to that of *G. elkema*, it differs from the latter in having a facet on the distal side of the bone, which probably articulates with the navicular and astragalus. This feature does not occur in known astragali of *G. elkema* (Meng et al., 2004, 2005; Asher et al., 2005), and is most likely a derived feature of *G. shevyrevae.* However, in *Mimolagus*, a similar facet is present on the calcaneus, which is in articulation with the astragalus (Bohlin, 1951).

DISCUSSION

TAXONOMY: The specimens described here clearly represent a new species of *Gomphos* and the youngest species of the genus, and perhaps, the youngest representative of Mimotonidae. It differs from *G. elkema* and *G. ellae* in having more robust teeth that are higher crowned with more inflated cusps, upper molars with more posteriorly expanded hypocones and posterolophs, and lower molars that are proportionally shorter, lack mesostylids, and have reduced hypoconulids. In addition, an extra articular facet is developed on the calcaneus.

G. shevyrevae is more similar to *G. elkema* than to *G. ellae* in general morphology. The major difference from *G. elkema* is inflation of cusps and lophs in *G. shevyrevae*. *G. ellae* has shorter, therefore transversely longer upper molars, which may be partly attributable to the advanced wear of the known specimen. The M1 (fig. 2B, C) of *G. shevyrevae* also shows significant wear, but does not display the tendency of transverse elongation present in upper molars of *G. ellae*. Although worn, which suggests an adult individual, the tooth enamel layer of *G. ellae* remains thinner than that of *G. shevyrevae*. Thickened tooth enamel confers a greater resistance to wear, suggesting an ability to process tougher food.

G. shevyrevae indicates that *Gomphos*, the sister taxon of lagomorphs of modern aspect, was more diverse and has a longer stratigraphic range than was previously thought. The earliest lagomorphs of modern aspect are known from the Early Eocene (Li et al., 2007; Rose et al., 2008; Lopatin and Averianov, 2006), as are the earliest representatives of *Gomphos*. The fossil record indicates that the divergence between the *Gomphos* and modern lagomorph lineages was no younger than the Early Eocene. In addition, *G. shevyrevae* further suggests that a branch of mimotonids coexisted with the earliest lagomorphs at least up to the Middle Eocene. This is further supported by the description of both mimotonids and lagomorphs from the Andarak 2 locality in Kyrgyzstan (Averianov, 1994). The *Gomphos* lineage may have extended into still younger age if *Mimolagus* proves to be more closely related to *Gomphos* than to any other Glires.

BIOSTRATIGRAPHIC IMPLICATION: Two Asian Land Mammal ages, the Arshantan and Irdinmanhan, have been widely accepted, but their definition and recognition have not always been clear (Meng et al., 2007c). Dashzeveg and Hooker (1997: 136) suggested that the Arshantan "predates the Irdinmanhan and belongs to the earliest Middle or latest Early Eocene." Lucas and Emry (2001) considered the Irdinmanhan and Arshantan ages as collectively correlative with the Bridgerian, although Luterbacher et al. (2004) correlated the Arshantan with the entire Bridgerian and the Irdinmanhan with the Uintan. Lucas (2001) also regarded the Arshantan land mammal age to be older than the North American middle Bridgerian.

One example of the difficulty in distinguishing these two ages is found in the fauna from the Kholboldchi Formation of Mongolia. Localities that supposedly expose the same formation have produced different fossils, and most of the fossils were typical of both Arshantan and Irdinmanhan faunas. These localities have been considered either Irdinmanhan or Arshantan (Russell and Zhai, 1987; Dashzeveg and Hooker, 1997; Lucas, 2001; Meng et al., 2007c; Kraatz et al., 2009). Similarly, Averianov and Godinot (2005) considered the Andarak fauna to be Irdinmanhan in age, following the definition of the Arshantan and Irdinmanhan (Lucas, 2001). However, because the Andarak mammals are found within a marine section that yields a selachian fauna, Averianov and Godinot (1998, 2005) argued that the Andarak fauna, and thus the Irdinmanhan, be correlated with the latest Early Eocene (late Ypresian).

Part of the current confusion may have stemmed from the original collections of Arshantan and Irdinmanhan faunas, which appear to have been mixed assemblages of fossils from different ages, as pointed out by Meng et al. (2007c). With new stratigraphic and faunal data, clarification of both the Arshantan and Irdinmanhan faunas can be expected. Here, the stratigraphic relationships of *Gomphos elkema*, *G. shevyrevae*, and many other associated fossils, are clear (fig. 1).

Between the occurrence of *Gomphos elkema* and *G. shevyrevae* lies an interval of strata that represents a considerable amount of time and faunal evolution. It is clear that *G. shevyrevae* is dentally more derived than both *G. elkema* and *G. ellae*. This is consistent with the stratigraphic occurrences of *G. elkema* and *G. shevyrevae* in the Huheboerhe section. Morphological polarities in the dentition also suggest that *G. ellae* is older than *G. shevyrevae*, supporting the view that the Kholboldchi Formation may contain fossils of Arshantan age (Dashzeveg and Hooker, 1997; Meng et al., 2007c; Kraatz et al., 2009).

Mimolagus rodens is an enigmatic member of the Glires that is thought to be from the Early Oligocene of China (Bohlin, 1951). Meng et al. (2004) recognized the similarity between calcanei and astragali of *Gomphos* and those purported to pertain to *Mimolagus*, noting that all were more lagomorphlike than rodentlike. A source of uncertainty regarding the possible mimotonid relationships of *Mimolagus* pertains to its age, because all other mimotonids have been recovered from Middle Eocene or older beds. However, with a revised placement of the Eocene-Oligocene boundary in Asian terrestrial strata (Meng and McKenna, 1998), it seems likely that *Mimolagus* may be older than previously thought. Considered in light of the discovery of the Irdinmanhan *Gomphos* at Huheboerhe described here, the apparent temporal gap between *Mimolagus* and other mimotonids may be significantly less, if not entirely absent.

ACKNOWLEDGMENTS

We thank Bin Bai, Qiang Cao, Wei Gao, Chun Li, Ping Li, Qiang Li, Shijie Li, and Wei Zhou for field assistance; Lawrence J. Flynn (Peabody Museum of Archaeology and Ethnology, Harvard University) and Chuankui Li (Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences) for comments on the manuscript. This project has been supported by the National Natural Science Foundation of China (40532010), U.S. National Science Foundation grants (BCS 0820603 to J.M.), and the Major Basic Research Projects of MST of China (2006CB806400).

REFERENCES

Asher, R.J., J. Meng, M.C. McKenna, J.R. Wible, D. Dashzeveg, G. Rougier, and M.J. Novacek. 2005. Stem Lagomorpha and the antiquity of Glires. Science 307: 1091–1094.

Averianov, A.O. 1994. Early Eocene mimotonids of Kyrgyzstan and the problem of Mixodontia. Acta Palaeontologica Polonica 39: 393–411.

Averianov, A.O., and M. Godinot. 1998. A report on the Eocene Andarak mammal fauna of Kyrgyzstan. *In* K.C. Beard and M.R. Dawson (editors), Dawn of the age of mammals in Asia. Bulletin of Carnegie Museum of National History 34: 124–147.

Averianov, A.O., and M. Godinot. 2005. Ceratomorphs (Mammalia, Perissodactyla) from the early Eocene Andarak 2 locality in Kyrgystan. Geodiversitas 27: 221–234.

Averianov, A.O., and A.V. Lopatin. 2005. Eocene Lagomorphs (Mammalia) of Asia: 1. *Aktashmys* (Strenulagidae fam. nov.). Paleontological Journal 39: 308–317. [Translated from Paleontoliicheskii Zhurnal 3: 81–90]

Bai, B. 2006. New materials of Eocene Dinocerata (Mammalia) from the Erlian Basin, Nei Mongol (Inner Mongolia). Vertebrata Palasiatica 44: 250–261.

Berkey, C.P., and W. Granger. 1923. Later sediments of the desert basins of central Mongolia. American Museum Novitates 77: 1–16.

Berkey, C.P., and F.K. Morris. 1924. Basin structures in Mongolia. Bulletin of the American Museum of Natural History 51(5): 103–127.

Berkey, C.P., and F.K. Morris. 1927. Geology of Mongolia: a reconnaissance report based on the investigations of the years 1922–1923. Natural History of Central Asia, Vol. 2. New York: American Museum of Natural History.

Bininda-Emonds, O.R.P., M. Cardillo, K.E. Jones, R.D.E. MacPhee, R.M.D. Beck, R. Grenyer, S.A. Price, R.A. Vos, J.L. Gittleman, and A. Purvis. 2007. The delayed rise of present-day mammals. Nature 449: 507–512.

Bleefeld, A.R., and W.J. Bock. 2002. Unique anatomy of lagomorph calcaneus. Acta Palaeontologica Polonica 47: 181–183.

Bleefeld, A.R., and M.C. McKenna. 1985. Skeletal integrity of *Mimolagus rodens* (Lagomorpha, Mammalia). American Museum Novitates 2806: 1–5.

Bohlin, B. 1951. Some mammalian remains from Shi-her-ma-cheng, Hui-hui-pu area, western Kansu. Report from the scientific expedition to the northwestern provinces of China under leadership of Dr. Sven Hedin. Vertebrate Palaeontology 5: 1–47.

Bowen, G.J., P.L. Koch, J. Meng, J. Ye, and S.-Y. Ting. 2005. Age and correlation of fossiliferous Late Paleocene-Early Eocene strata of the Erlian Basin, Inner Mongolia, China. American Museum Novitates 3474: 1–26.

Dashzeveg, D. 1988. Holarctic correlation of non-marine Palaeocene-Eocene boundary strata using mammals. Journal of the Geological Society (London) 145: 473–478.

Dashzeveg, D., and J.J. Hooker. 1997. New ceratomorph perissodactyls (Mammalia) from the Middle and Late Eocene of Mongolia: their implications for phylogeny and dating. Zoological Journal of the Linnean Society 120: 105–138.

Dashzeveg, D., and D.E. Russell. 1988. Palaeocene and Eocene Mixodontia (Mammalia, Glires) of Mongolia and China. Palaeontology 31: 129–164.

Douzery, E.J.P., and D. Huchon. 2004. Rabbits, if anything, are likely Glires. Molecular Phylogenetics and Evolution 33: 922–935.

Granger, W., and C.P. Berkey. 1922. Discovery of Cretaceous and older Tertiary strata in Mongolia. American Museum Novitates 42: 1–7.

Huchon, D., O. Madsen, M.J.J.B. Sibbald, K. Ament, M.J. Stanhope, F. Catzeflis, W.W. de Jong, and E.J.P. Douzery E. 2002. Rodent phylogeny and a timescale for the evolution of Glires: evidence from an extensive taxon sampling using three nuclear genes. Molecular Biology and Evolution 19: 1053–1065.

Kraatz, B.P., D. Badamgarav, and F. Bibi. 2009. *Gomphos ellae*, a new mimotonid from the Middle Eocene of Mongolia and its implications for the origin of Lagomorpha. Journal of Vertebrate Paleontology 29: 576–583.

Li, C.-K. 1977. Paleocene eurymyloids (Anagalida, Mammalia) of Quianshan, Anhui. Vertebrata Palasiatica 15: 103–118.

Li, C.-K., and S.-Y. Ting. 1993. New cranial and postcranial evidence for the affinities of the eurymylids (Rodentia) and mimotonids (Lagomorpha). *In*: F.S. Szalay, M.J. Novacek, and M.C. McKenna (editors), Mammal phylogeny: placentals: 151–158. New York: Springer.

Li, C.-K., J.-J. Zheng, and S.-Y. Ting. 1989. The skull of *Cocomys lingchaensis*, an Early Eocene Ctenodactyloid Rodent of Asia. *In* C.C. Black and M.R. Dawson (editors), Papers on fossil rodents in honour of Albert Elmer Wood. Natural History Museum of Los Angeles County Science Series 33: 179–192.

Li, C.-K., J. Meng, and Y.-Q. Wang. 2007. *Dawsonolagus antiquus*, a primitive lagomorph from the Eocene Arshanto Formation, Inner Mongolia, China. Bulletin of Carnegie Museum of National History 39: 97–110.

Lopatin, A.V., and A.O. Averianov. 2006. Eocene Lagomorpha (Mammalia) of Asia: 2. *Strenulagus* and *Gobiolagus* (Strenulagidae). Paleontological Journal 40: 198–206.

Lucas, S.G. 2001. *Gobiatherium* (Mammalia: Dinocerata) from the Middle Eocene of Asia: taxonomy and biochronological significance. Paläontologische Zeitschrift 74: 591–600.

Lucas, S.G., and R.J. Emry. 2001. *Sharamynodon* (Mammalia: Perissodactyla) from the Eocene of the Ily basin, Kazakstan and the antiquity of Asian amynodonts. Proceedings of the Biological Society of Washington 114: 517–525.

Luterbacher, H.P., et al. 2004. The Paleogene period. *In*: F. Gradstein, J. Ogg, and A. Smith (editors), A geological time scale 2004: 384–408. Cambridge: Cambridge University Press.

Matthew, W.D., and W. Granger. 1926. Two new perissodactyls from the Arshanto Eocene of Mongolia. American Museum Novitates 208: 1–5.

Meng, J., G.J. Bowen, J. Ye, P.L. Koch, S.-Y. Ting, Q. Li, and X. Jin. 2004. *Gomphos elkema* (Glires, Mammalia) from the Erlian Basin: evidence for the Early Tertiary Bumbanian Land Mammal Age in Nei-Mongol, China. American Museum Novitates 3425: 1–24.

Meng, J., Y.-M. Hu, and C.-K. Li. 2003. The osteology of *Rhombomylus* (Mammalia, Glires): implications for phylogeny and evolution of Glires. Bulletin of the American Museum of Natural History 275: 1–247.

Meng, J., C.-K. Li, X.-J. Ni, Y.-Q. Wang, and K.C. Beard. 2007a. A new Eocene rodent from the lower Arshanto Formation in the Nuhetingboerhe (Camp Margetts) area, Inner Mongolia. American Museum Novitates 3569: 1–18.

Meng, J., and M.C. McKenna. 1998. Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. Nature 394: 364–367.

Meng, J., X.-J. Ni, C.-K. Li, K.C. Beard, D.L. Gebo, Y.-Q. Wang, and H.-J. Wang. 2007b. New material of Alagomyidae (Mammalia, Glires) from the late Paleocene Subeng locality, Inner Mongolia. American Museum Novitates 3597: 1–29.

Meng, J., Y.-Q. Wang, X.-J. Ni, K.C. Beard, C.-K. Sun, Q. Li, X. Jin, and B. Bai. 2007c. New Stratigraphic data from the Erlian Basin: definitions, divisions and correlations of Paleogene stratigraphic units in Inner Mongolia. American Museum Novitates 3570: 1–31.

Meng, J., and A.R. Wyss. 2001. The morphology of *Tribosphenomys* (Rodentiaformes, Mammalia):

phylogenetic implications for basal Glires. Journal of Mammalian Evolution 8: 1–71.

Meng, J., and A.R. Wyss. 2005. Glires (Lagomorpha, Rodentia). *In*: D. Archibald and K. Rose (editors), The rise of placental mammals: origins and relationships of major extant clades: 145–158. Baltimore, MD: Johns Hopkins University Press.

Meng, J., A.R. Wyss, M.R. Dawson, and R.-J. Zhai. 1994. Primitive fossil rodent from Inner Mongolia and its implications for mammalian phylogeny. Nature 370: 134–136.

Meng, J., A.R. Wyss, Y.-M. Hu, Y.-Q. Wang, G.J. Bowen, and P.L. Koch. 2005. Glires (Mammalia) from the late Paleocene Bayan Ulan locality of Inner Mongolia. American Museum Novitates 3473: 1–25.

Ni, X.-J., C.K. Beard, J. Meng, Y.-Q. Wang, and D. Gebo. 2007. Discovery of the first early Cenozoic euprimate (Mammalia) from Inner Mongolia. American Museum Novitates 3571: 1–11.

Qi, T. 1987. The Middle Eocene Arshanto fauna (Mammalia) of Inner Mongolia. Annals of Carnegie Museum 56: 1–73.

Radinsky, L.B. 1964. Notes on Eocene and Oligocene fossil localities in Inner Mongolia. American Museum Novitates 2180: 1–11.

Rose, K.D., V. Burke DeLeon, P. Missiaen, R.S. Rana, A. Sahni, L. Singh, and T. Smith. 2008. Early Eocene lagomorph (Mammalia) from western India and the early diversification of Lagomorpha. Proceedings of the Royal Society Biological Sciences Series B 275: 1203–1208.

Russell, D.E., and R.-J. Zhai. 1987. The Palaeogene of Asia: mammals and stratigraphy. Mémoires du Muséum National d'Histoire Naturelle, Sciences de la Terre Series C52: 1–488.

Shevyreva, N.S., V.M. Chkhikvadze, and V.I. Zhegallo. 1975. New data on the vertebrate fauna of the Gashato Formation, Mongolian People's Republic. Bulletin of the Georgian Academy of Science 77: 225–228.

Ting, S.-Y., J. Meng, M.C. McKenna, and C.-K. Li. 2002. The osteology of *Matutinia* (Simplicidentata, Mammalia) and its relationship to *Rhombomylus*. American Museum Novitates 3371: 1–33.

Wang, Y.-Q., Y.-M. Hu, M.-C. Chow, and C.-K. Li. 1998. Chinese Paleocene mammal faunas and their correlation. Special volume of the Symposium on Cretaceous and Early Tertiary Mammals of Asia. Bulletin of Carnegie Museum of Natural History 34: 148–185.

Wang, Y.-Q., J. Meng, X.-J. Ni, and K.C. Beard. 2008. A new early Eocene arctostylopid (Arctostylopida, Mammalia) from Erlian Basin, Nei Mongol (Inner Mongolia), China. Journal of Vertebrate Paleontology 28(2): 553–558.

Zhegallo, V.I., and N.S. Sheryreva. 1976. Revision of the geological structure and new data on the fauna of Gashato (Paleocene, M.P.R.). *In* N.N. Kramarenko, B. Luvsandansan, Y.I. Voronin, R. Barshold, A.K. Rozhdestvensky, B.A. Trofinov, and V.Y. Reshetov (editors), Paleontology and biostratigraphy of Mongolia. Joint Soviet-Mongolian Paleontological Expedition Transactions 3: 269–279.

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site http://library.amnh.org/pubs. Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.