

## GOMPHOS ELLAE, A NEW MIMOTONID FROM THE MIDDLE EOCENE OF MONGOLIA AND ITS IMPLICATIONS FOR THE ORIGIN OF LAGOMORPHA

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**ABSTRACT**—Mimotonids have recently been recognized as the likely ancestors to Lagomorpha (rabbits, hares, and pikas). Here a new species of mimotonid, *Gomphos ellae*, from Tsagaan Khutel locality, Valley of Lakes, Mongolia is described. This new material shows typical mimotonid features while also exhibiting important derived lagomorph features and helps to bridge the morphological and temporal gap between mimotonids and lagomorphs. The fossils comprise a right dentary, including cheek teeth and incisor, and a partial maxilla with two teeth. The dental features of *G. ellae* are similar to the mimotonid *G. elkema*, but *G. ellae* is distinguished from *G. elkema* and all other mimotonids by its long diastema. The diastema length of *G. ellae* is intermediate between all other mimotonids and all living and extinct lagomorphs. This feature distinguishes mimotonids from lagomorphs and the intermediate diastemal length of *G. ellae* further supports a strong pattern of lengthening of the diastema throughout Duplicidentata. Geologic and paleontological evidence suggest that the specimen is of Middle Eocene age, consistent with the notion that this taxon is an advanced mimotonid that likely lies near the ancestry of the lagomorphs.

### INTRODUCTION

Scientists have long debated the ancestry of lagomorphs (rabbits, hares, and pikas). Central to the debate has been the relationship between lagomorphs and rodents. The affinity of these two groups was first suggested by Linnaeus (1758), and the taxonomic group comprising rodents, lagomorphs and their ancestors became known as Glires. Within Glires, two main branches have been recognized: Duplicidentata (Mimotonidae + Lagomorpha) and Simplicidentata (Eurymylidae + Rodentia), although a sister group relationship between eurymylids and rodents is not unambiguously supported in all recent analyses (e.g., Asher et al., 2005). The Glires concept has fallen in and out of favor, but more recent molecular and morphologic studies strongly support the sister relationship of rodents and lagomorphs (Meng and Wyss, 2001; Huchon et al., 2002; Meng et al., 2003; Douzery and Huchon, 2004; Asher et al., 2005).

Recent discoveries of fossil material of a little known group of extinct mammals, mimotonids, from the Paleogene of Asia, have shed light on the evolutionary origin of lagomorphs, and in turn, the relationship between lagomorphs, rodents and their ancestors. The most recent phylogenetic treatments of Glires (Meng et al., 2003; Asher et al., 2005) suggest that Mimotonidae is a paraphyletic group, consisting of several stem taxa that branch before Lagomorpha (Rose et al., 2008). In this interpretation, Mimotonidae likely represents a grade of duplicidentates that show an evolutionary sequence from the most recent rodent-lagomorph ancestor to Lagomorpha *sensu strictu*. There remains, however, a significant temporal and morphologic gap between mimotonids and lagomorphs that prevents detailed understanding of the evolutionary transition from mimotonids to lagomorphs, if indeed mimotonids represent lagomorph ancestors. This study describes new mimotonid material from Mongolia

that helps to bridge this gap, and that strongly supports the idea that lagomorphs evolved from mimotonids.

### Taxonomic Background

Mimotonids are found in Late Paleocene and Eocene deposits of central Asia, and have been described from Mongolia (Shevyreva et al., 1975, Asher et al., 2005), northern China (Li, 1977; Li and Ting, 1985; Dashzeveg and Russell, 1988; Meng et al., 2004), and Kyrgystan (Averianov, 1994; Shevyreva, 1994). They are easily recognized as Glires due to the prominence of large, gnawing incisors. Their affinities to lagomorphs are most easily established by the presence of two pairs of upper incisors in contrast to the single pair of upper incisors found in rodents and their ancestors. Mimotonids also retain a second, reduced pair of lower incisors that distinguish them from lagomorphs.

Li (1977) erected the family Mimotonidae and at first included only *Mimotona* and *Mimolagus*. *Mimotona* was considered to typify the family from which Li (1977) suggested the lagomorphs might have evolved. The family was initially recognized, and distinguished from the eurymylids, based on a similarity in tooth formulae to Lagomorpha, the presence of unilateral hypsodonty in upper cheek teeth, and differences in the zygomatic arch with respect to both rodents and eurymylids. Particularly important was the anterior border of the arch within mimotonids, which originates more posteriorly than that of rodents and eurymylids. Li and Ting (1985) later revised these characteristics of Mimotonidae in a more detailed treatment, and at that time also included *Gomphos* and *Hypsomyilus* within the family. *Gomphos elkema* was first described from the early Eocene of Mongolia by Shevyreva et al. (1975), and has remained the only species within the genus. Dashzeveg and Russell (1988) later removed *Hypsomyilus* from the family based on the fragmentary nature of the material (two isolated lower cheek teeth) that did not show any features diagnostic of mimotonids. They also removed *Mimolagus* from this family (see discussion of this taxon below).

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Averianov (1994) described two new mimotonid genera from Kyrgyzstan, *Anatolimys* and *Aktashmys*, while also including *Zagmys* within Mimotonidae. *Aktashmys* was later removed from Mimotonidae and placed within a new family of Lagomorpha (Averianov and Lopatin, 2005). The lack of a second lower incisor supports the notion that this taxon is not a mimotonid. *Zagmys* was originally described as a eurymylid (Dashzeveg et al., 1987; Dashzeveg and Russell, 1988), but was placed in Mimotonidae by Averianov (1994) based on similarities to *Anatolimys*, including a deep jaw and short diastema. As neither of these features has been shown to be diagnostic for mimotonids, and because the second lower incisor is lacking in *Zagmys*, this taxon is not here considered a mimotonid.

We follow Van Valen (2002) and Meng et al. (2004) in including *Gomphos*, *Mimotona*, *Anatolimys*, and *Mimolagus* in Mimotonidae. Three species of *Mimotona* have been described from Paleocene deposits within China. *Mimolagus* is known from questionable Oligocene deposits in China (Bohlin, 1951) and *Anatolimys rozhdestvenskii* is known from middle Eocene deposits of Kyrgyzstan (Averianov, 1994, see Table 1 for a summary of all mimotonid species). After the original description of *G. elkema* from Mongolia, the species was also described from China (Meng et al., 2004). Based on taxa recognized here, mimotonids can be considered to share several important features, including two pairs of upper and lower incisors, unilateral hypsodonty in upper cheek teeth, and variably developed mesocoincids on lower cheek teeth. Both the depth of the ramus and the diastema length are important features that vary within the family and that will be discussed further.

*Mimolagus rodens* is an enigmatic taxon questionably dated to the Early Oligocene of China (Bohlin, 1951). No lower jaw material is known, but nicely preserved partial skulls as well as tarsals were described. Bohlin (1951) considered the skull material to be that of a lagomorph. He was hesitant to associate the tarsals found at the same locality to the individual from which the skull came, as he noted that the lack of a fibular-calcaneal articulation suggested that they were not from a lagomorph. The skull of *M. rodens* exhibits two pairs of upper incisors and unilateral hypsodonty within the cheek teeth, features of both mimotonids and lagomorphs. Wood (1962) suggested that the tarsals were indeed from *M. rodens*, which was supported by Meng et al. (2004) in a detailed study of *Gomphos elkema*. In that study, Meng et al. (2004) showed a strong similarity between calcanei of *Gomphos* and those purported to be from *Mimolagus*. Based on skull features that show similarity to both mimotonids and lagomorphs, it is clear that *M. rodens* is a duplicidentate. The similarity in tarsal morphology to *G. elkema* suggests that *M. rodens* is a mimotonid. The age, however, of this taxon should be regarded as extremely questionable as the locality has only produced one other taxon, the anagalid *Anagalopsis kansuensis*, and neither that nor *Mimolagus* are diagnostic of age. Previous authors have also suggested that the material may be of Paleocene age, and this is at least partially supported by the fact that all other members of the Anagalidae have an almost exclusively Paleocene distribution (McKenna and Bell, 1997).

## Geologic Context

The specimens described here come from the Kholboldchi Formation, Tsagaan Khutel locality of the Valley of Lakes depression, which was visited three consecutive field seasons (2004–2006). This basin is bordered to the north by the Khangai Dome and to the south by the Gobi Altai Mountains (Fig. 1). The area is well known for Oligocene mammal fossils found in the Hsanda Gol formation, but only limited Eocene discoveries have been described (see Russell and Zhai, 1987 for summary). The exposures discussed here are situated on western bank of the Tuin Gol 2 km to the NE of Bogd. The Central Asiatic Expeditions originally visited the area (Berkey et al., 1929) and described the Kholboldchi Formation as Eocene in age. Much later, the Soviet-Mongolian Geological and Paleontological Expeditions visited the area and Badamgarav (1975) described the local geologic section and formally named the Kholboldchi Formation and designated its age as Late Eocene. Dashzeveg (1979) first described the mammalian locality of Tsagaan Khutel, and Deveyatkin (1981) provided a more complete faunal list. Despite these previous studies, the faunal list from Tsagaan Khutel is limited, and to date no gliriform mammals have been reported (Table 2). Based on this fauna, early workers suggested an Irдин Manha age (EALMA) for the locality (Russell and Zhai, 1987), but more recently the fauna has been tentatively referred to the Arshantan EALMA (Dashzeveg and Hooker, 1997; Lucas, 2001).

The Eocene sediments at Tsagaan Khutel are the earliest Cenozoic deposits in the Valley of Lakes, and directly overlie Paleozoic rocks. The local section (Fig. 2) spans nearly 32 meters, and the Kholboldchi Formation is differentiated into two series. The lower series consists mainly of siltstones and mudstones, sometimes fine-grained sandstones. These sediments form beds varying in thickness from a few tens of centimeters to 3.5 m. The mudstones are green in color, while the sandstones are of white-grey color. The thickness of the lower series at the Tsagaan Khutel locality is about 17 m and is devoid of vertebrate fossils. Coarse and medium-grained sands that are often poorly sorted characterize the upper series. The sands are often greenish-grey in color, and may contain intercalations of gravels, silts, and muds. The thickness of the lower series of the Kholboldchi at Tsagaan Khutel is about 13.5 m. Fossils come from the two levels of poorly sorted sand, as denoted in Figure 2.

## MATERIALS AND METHODS

Tooth dimensions were measured under a microscope at 64X magnification (Wild MC3). Diastemata were measured with Mitutoya calipers and measurements rounded to the nearest 0.01mm. To assess the transitional morphology of *Gomphos ellae*, diastemal lengths were measured for numerous mimotonid and lagomorph taxa. Diastemal lengths were measured for each specimen along with m1 area (length x width, abbreviated m1A), and a metric of diastemal length/m1A (DL/m1A) was used to normalize diastemal length with regard to size. Much previous

TABLE 1. List of known mimotonid species, including age, locality, and citations of original descriptions from relevant localities.

Taxon	Age	Locality	Reference
<i>Mimotona wana</i>	Late Paleocene	Qianshan Basin (Wanghudun Fm.), Anhui Pr., China	Li, 1977
<i>M. robustus</i>	Late Paleocene	Qianshan Basin (Doumu Fm.), China	Li, 1977
<i>M. lii</i>	Late Paleocene	Qianshan Basin (Wanghudun Fm.), China	Dashzeveg and Russell, 1988
<i>Anatolimys rozhdestvenskii</i>	Middle Eocene	Andarak 2, Kyrgyzstan	Averianov, 1994
<i>Gomphos elkema</i>	Early Eocene	Gashato, Mongolia; Tsagan Khushu, Mongolia; Huheboerhe, Inner Mongolia Pr., China	Shevyreva, 1975, Dashzeveg and Russell, 1988, Meng et al., 2004
<i>G. ellae</i>	Middle Eocene	Tsagan Khutel, Mongolia	This report
<i>Mimolagus rodens</i>	?Early Oligocene	Shih-her-ma-ch'eng, Gansu Pr., China	Bohlin, 1951

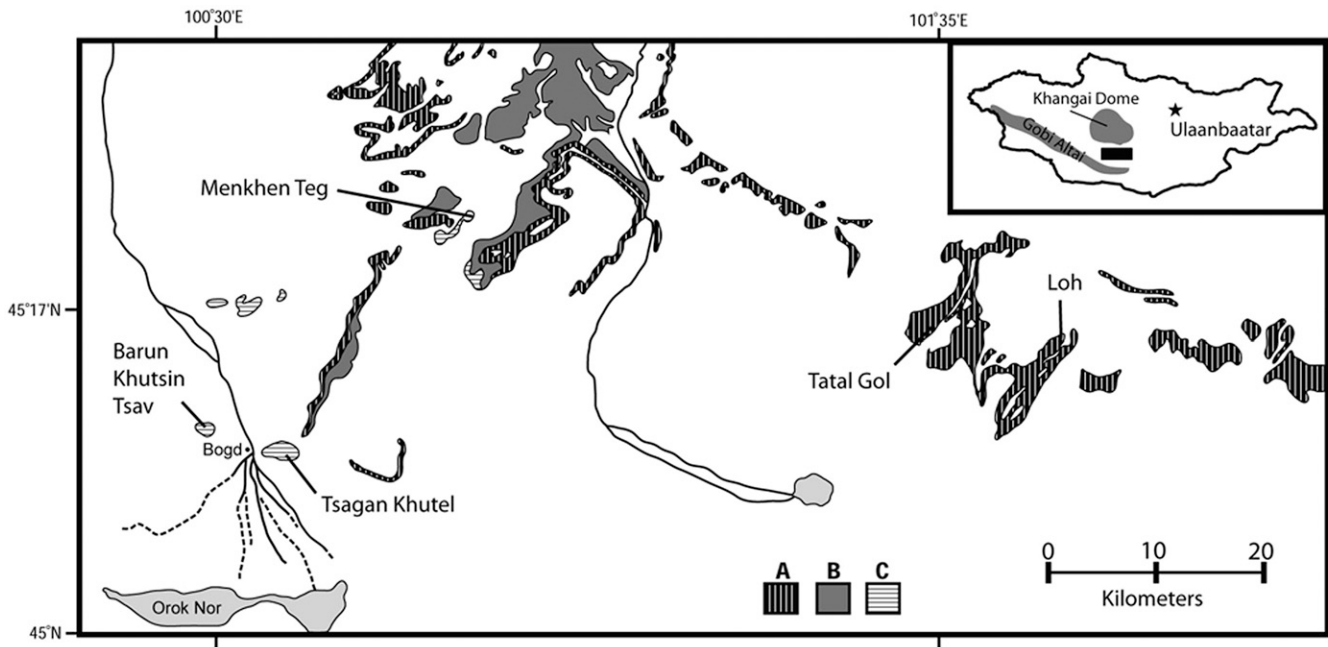


FIGURE 1. Tsagaan Khutel locality map. Solid black rectangle in upper-right inset map shows location within Mongolia. **A** represents the Hsanda Gol Formation, **B** represents the Elegen Formation, and **C** represents the Kholboldchi Formation. Map modified from Russell and Zhai (1987).

work has shown that m1 area is an adequate proxy for body size (Gingerich and Schoeninger, 1979, LeGendre, 1986, Damuth and MacFadden, 1990, among others). A recent study of variation in size of the leporid *Oryctolagus cuniculus* has shown that an area measurement of any cheek tooth besides p3 will accurately predict body size (Calzada et al., 2003). The first molar was used here for consistency with the many other studies that estimate body size in fossils. Statistical analyses were conducted using JMP IN 5.1 (SAS Institute). Tooth cusp terminology follows Meng and Wyss (2001) and Meng et al. (2004), and is illustrated in Figure 3.

**Abbreviations**—Tooth abbreviations, with capitals denoting upper teeth and small letters lower teeth, are as follows: **P/p**, premolar; **M/m**, molar; **I/i**, incisor; **d**, deciduous. **MVZ**, University of California, Berkeley, Museum of Zoology; **UCMP**, University of California, Berkeley, Museum of Paleontology; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology; **MAE**, Mongolian Academy of Sciences-American Museum of Natural History Expeditions; **MPC**, Mongolian Paleontological Center; **ZIN**, Zoological Institute of the Russian Academy of Sciences, Moscow, Russia; **EALMA**, East Asian Land Mammal Age; **BU**, Bumban Formation; **McK**, collections of Malcolm C. McKenna.

#### SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

GLIRES Linnaeus, 1758

MIMOTONIDAE Li, 1977

**Included Genera**—*Anatolimys*, *Gomphos*, *Mimolagus*, and *Mimotona*. Table 1.

*GOMPHOS* Shevyreva, 1975

**Type**—*Gomphos elkema* Shevyreva et al., 1975, Gashato Locality, Mongolia, Gashato Fm., Early Eocene.

*GOMPHOS ELLAE*, sp. nov.  
(Figs. 3, 4)

**Holotype**—MPC 30/1, right dentary fragment (Fig. 3) with p4–m3, i3, alveolus for p3, partial alveolus for di2 and right maxilla with M1 and M2 (Fig. 4).

**Type Locality**—Tsagaan Khutel, Mongolia.

**Diagnosis**—*Gomphos ellae* is distinguished from *G. elkema* by a deeper ramus (based on the height from the dorsal surface of the alveoli of di2 to the base of the m1 alveolus 5.96mm in *G. ellae* vs. 4.54mm at m1 in *G. elkema* (IVPP 13509.3)). *G. ellae* differs from all other mimotonids by having a diastema that is

TABLE 2. Faunal List of Tsagan Khutel Locality, Order and Family designations from McKenna and Bell (1997).

Order	Family	Taxon	Reference
Cimolesta	Pantolestidae	<i>Bogdia orientalis</i>	Dashzeveg and Russell, 1975
Cimolesta	Pantolambdodontidae	<i>Archaeolambda prima</i>	Dashzeveg, 1980
Cimolesta	Coryphodontidae	<i>Eudinoceras kholbolchiensis</i>	Osborn and Granger, 1931
Perissodactyla	Lophialetidae	<i>Schlosseria</i> sp.	Russell and Zhai, 1987
Perissodactyla	Lophialetidae	<i>Lophialates?</i> sp.	Russell and Zhai, 1987
Perissodactyla	Hyracodontidae	<i>Rhodophagus</i> sp.	Reshetov, 1975
Perissodactyla	Deperetellidae	? <i>Irdinolophus tuiensis</i>	Dashzeveg and Hooker, 1997
Mixodontia	Mimotonidae	<i>Gomphos ellae</i>	This paper

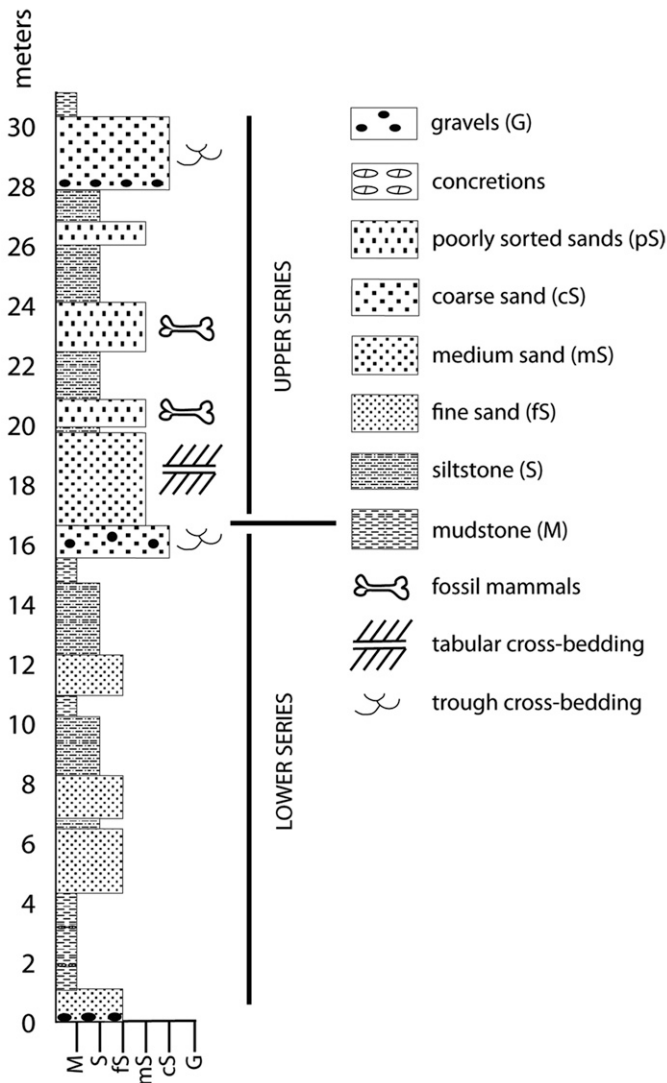


FIGURE 2. Stratigraphic section of the Kholboldchi formation as it occurs at Tsagaan Khutel, Mongolia.

proportionally longer than any known mimotonid, yet shorter than fossil and extant lagomorphs.

**Age and Distribution**—Known only from Middle Eocene Kholboldchi Formation, Mongolia.

**Etymology**—Named for Ella Margaret Lund Andersen, the future world explorer.

**Description**—On the lingual surface of the dentary, much of the compact bone has been worn away. The entire ventral surface of the mandible is missing, although the dorsal surface of the alveolus for the di2 remains. The dentary is broken just posterior to the anterior border of the masseteric fossa and along the anterior border of the alveolus for i3 (Fig. 3). Four mental foramina are present on the lateral side of the dentary. Two small foramina are found immediately ventral to the posterior border of the alveolus for i3. The largest mental foramen is found half way from the dorsal surface of the diastema to the alveolus of the di2, and approximately half way between the alveoli for p3 and i3. Another foramen is present above the alveolus of di2, below p4. The anterior border of the masseteric fossa extends to a point below the anterior portion of m3, similar to the condition seen in *Gomphos elkema*, *Mimotona*, and *Anatolimys*. All known mimotonids have a tuberosity at the

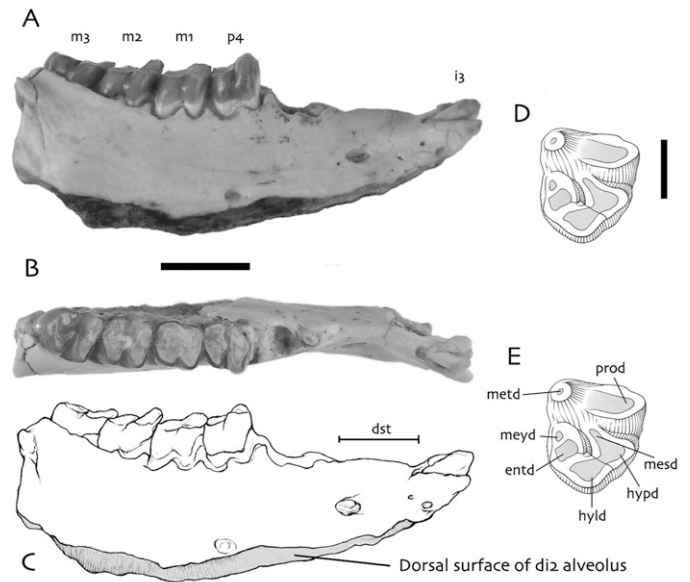


FIGURE 3. Right dentary of *Gomphos ellae*, MPC 30/1. **A**, lateral view; **B**, occlusal view; **C**, lateral view line drawing; **D**, illustration of m3, anterior towards top, lateral towards right; and **E**, illustration of m3 with cusps labeled as follows; **prod**, protoconid; **metd**, metaconid; **mesd**, mesoconid; **meyd**, mesostylid; **entd**, entoconid; **hypd**, hypoconid; **hyld**, hypoconulid. In drawing **C**, **dst** shows area measured for diastemal lengths. Scale bar for **A–C** equals 5 mm, scale bar for **D** equals 1 mm.

anterior border of the masseteric fossa. The tuberosity in MPC 30/1 is reduced relative to that of *G. elkema* and *Mimotona*. The extent of the tuberosity in *Anatolimys* is not known. Although much of the dentary is missing from *G. ellae*, the dentary beneath the cheek is narrower than in *G. elkema*. Based on the height from the dorsal surface of the alveoli of di2 to the base of the m1 alveolus (5.96 mm in *G. ellae*), the dentary of *G. ellae* is

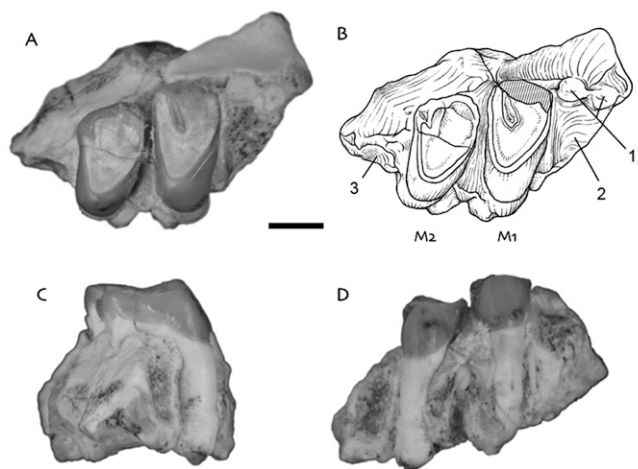


FIGURE 4. Images and line drawing of *Gomphos ellae* maxilla, MPC 30/1. **A** shows occlusal view with anterior to right and lingual down, and **B** is a line drawing of the same. **C** and **D** show posterior (labial to left) and lingual views, respectively. In **B**, 1 equals buccal alveoli for P4, 2 equals lingual alveolus for P4, and 3 equals lingual alveoli for M3. Scale bar equals 1 mm.

deeper than *G. elkema* (4.54 mm at m1 in *G. elkema*, IVPP 13509.3) and is similar to *Anatolimys rozhdestvenskii*. Most jaw specimens of *Gomphos* exhibit nutritive foramina medially, particularly in a discrete region along the bone near the base of di2, which are perhaps related to the continued growth of their incisors. This region is not preserved in *G. ellae*, but the nature of the fracture along the dorsal border of the alveoli for the di2 suggests that the dentary was weak in that area, possibly due to the presence of nutritive foramina.

The dental formula for the lower dentition of *Gomphos ellae* is 2-0-2-3. The p4–m3 are present, as well as the i3; the presence of p3 and di2 are inferred from alveoli. The di2 extends at least to the posterior border of the m3, similar to other mimotonids. A second incisor, i3, is present and a break on the medial surface the dentary shows much of the root of this tooth. The tooth emerges slightly posterior and dorsal to the di2. The tooth is reduced in size relative to di2, as in other mimotonids. In contrast to *Mimotona* where i3 erupts along the lateral side of the dentary, the i3 in *G. ellae* erupts more towards the dorsal surface of the dentary.

Based on its alveoli, p3 was rooted and perhaps narrower than other cheek teeth, but similar in length. Two alveoli are present, aligned antero-posteriorly, and the anterior alveolus contains a broken root. The small size of the anterior alveolus suggests that the trigonid of this tooth was reduced in size relative to the talonid.

The fourth premolar is similar in length and width to m1 and m2 (Table 3) and is double rooted. *Gomphos elkema* material from Hueheboerhe has been described as having a slightly narrower p4 relative to m1 (Meng, et al., 2004). This is in contrast to *Mimotona*, which shows a much-reduced p4 relative to m1 and m2 (see Table 3). The trigonid of p4 is higher than the talonid in *G. ellae*. The metaconid of p4 is elongated anteroposteriorly relative to the protoconid and is the highest cusp of the tooth. No paraconid is present. The trigonid has a shallow basin between the metaconid and protoconid. The talonid of p4 is worn, but there are remnants of a mesoconid and the mesostylid on its anterior border. The molariform cusp pattern of p4 of *G. ellae* resembles the condition in *G. elkema* and *Anatolimys*.

The m1 and m2 of *Gomphos ellae* in most regards resembles p4, although these molars are at a more advanced wear stage. The trigonids of m1 and m2 are slightly higher than the talonids only on their lingual sides, which is a function of the advanced wear stage of this individual. The m1 is most advanced in wear and no enamel boundary exists between the trigonid and talonid. An enamel boundary is evident between these structures in the less worn m2. A line drawn through the metaconid and proto-

conid of m1 would parallel a line drawn through the hypoconid and entoconid, giving the tooth an overall square shape. The talonid is longer than the trigonid in both m1 and m2, which are approximately the same size. The protoconid and the hypoconid of m2 are shifted slightly posteriorly from the metaconid and entoconid, respectively. The talonid of m2 shows two accessory lobes that are correlated to the mesoconid and mesostylid, although they are not as pronounced as similar structures on p4. There is a slight fold on the lingual side of the talonid of m2 tooth that may correlate to the separation of an entoconid and mesostylid. The m2 also shows a small lobe on the posterior part of the talonid in the position of a hypoconulid.

The m3 is less worn than the other cheek teeth due to its late eruption. The protoconid of m3 is shifted posteriorly relative to the metaconid. The tip of the metaconid has been worn to expose dentine, although much of the base of this cusp remains. The trigonid is more oblique to the longitudinal axis of the tooth than is the case in the other cheek teeth. Both the mesoconid and hypoconid are present on m3, and the mesoconid appears as an enamel lobe projecting lingually and anteriorly from the hypoconid. Mesoconids are also present on m2, and perhaps m1 in *Gomphos ellae*, as in *G. elkema*. The m2 of *Mimotona robustus* shows minimal development of a mesoconid, as do the m1 and m2 of *M. wana* (IVPP V4325.2). *Anatolimys* shows a small mesoconid in m1.

On the lingual portion of the talonid of *Gomphos ellae*, both a mesostylid and an entoconid can be differentiated. The mesostylid is smaller than the entoconid. The cheek tooth row has a pronounced concavity along the occlusal surface causing m3 and p4 to be higher than m1 and m2.

A left maxilla containing M1 and M2, both in advanced wear stage, is shown in Figure 4. Measurements for these teeth are as follows: M1, L = 2.42mm and W = 3.45mm, and M2, L = 2.61mm and W = 3.64mm. Both teeth have two small buccal roots, and one large lingual root. The teeth show unilateral hypsodonty, where the lingual portion of the crown is about twice as high as the buccal. The palatine portion of the specimen is broken, fully exposing the lingual roots of both teeth. The lingual roots show a small concentric bulge near their bases. The anterior portion of the alveolus of lingual root of M3 is present as is the posterior portion of the alveolus of the lingual root for P4. Two small buccal roots of P4 remain.

In M1 and M2, the posterior border of the occlusal surface is more perpendicular to the longitudinal axis of the tooth than the anterior border. Although this suggests that a small hypocone may have been present in these teeth, its prominence, or even its presence, is unclear due to the advanced wear stage. *Gomphos*

TABLE 3. Tooth and jaw measurement comparisons among mimotonid species.

Taxon	m3		m2		m1		p4		p3		Diastema Length
	L	W	L	W	L	W	L	W	L	W	
<i>Gomphos ellae</i> MPC 30/1	3.33	3.03	2.97	3.05	2.83	2.75	2.76	3.06			5.46
<i>G. elkema</i> (R) MAE BU.91.5976	3.47	2.92	3.02	3.07	3.23	2.81					
<i>G. elkema</i> (L) MAE BU.91.5976			3.09	2.72	3.09	2.80	2.61				
<i>G. elkema</i> (R) MAE BU.14425	3.40	2.65	3.08	2.68	2.97	2.66	3.16	2.21	2.19	1.69	
<i>G. elkema</i> (L) MAE BU.14425	3.58	2.59	3.26	2.97	3.5	3.17	2.91	2.30	2.06	1.54	2.57
<i>G. elkema</i> IVPP 13509.1	4.56	3.42	3.30	3.28	3.32	3.12					
<i>G. elkema</i> IVPP 13509.2	4.55	3.35	3.50	3.12							
<i>G. elkema</i> IVPP 13509.3	4.22	3.10	3.30	3.15							
<i>Anatolimys rozhdestvenskii</i> * ZIN 79158	4.3	3.3	3.7	3.5				3.4			
<i>A. rozhdestvenskii</i> * ZIN 79159					3.6	3.7					
<i>A. rozhdestvenskii</i> * ZIN 79160			3.8	3.3							
<i>Mimotona wana</i> * IVPP 4325.1	2.54	1.82	2.00	1.82	1.95	1.82	1.69	1.36	1.30	1.10	1.51
<i>M. robustus</i> * IVPP 4329			2.25	2.35	2.15	2.35	1.80	1.65			
<i>M. lii</i> * IVPP 4327	2.06	1.43	1.95	1.56	1.82	1.43	1.43	1.30	1.10	0.78	

All measurements taken by the author, except where indicated (\*) otherwise. (R) or (L) denotes measurements from right or left jaw. All measurements are maximums in millimeters.

*elkema* shows a well-developed hypocone on the molars, but not on the premolars. Both M1 and M2 show a minor enamel fold that originates on the posterior portion of the buccal side of the teeth and extends roughly one-fourth of the width of the tooth. Much of the lingual portion of M1 has been broken. The advanced wear stage of these teeth makes it difficult to discern any identifiable characteristics of individual cusps.

This maxilla was collected from the surface about 1 meter from the dentary described here. Although the dentary and maxilla were not found in articulation, they are assumed to have come from the same individual. Both specimens exhibit similar coloration and overall weathering. Both the teeth in the mandible and maxilla are at a similar wear stage (advanced) and can be tightly articulated when held together.

## DISCUSSION

The absence of canines and some premolars in duplicitentates is related to the presence of a diastema throughout this group. Figure 5 shows differences in diastemal lengths among extant and fossil duplicitentate species. Diastemal length comparison between mimotonids and extant and fossil lagomorphs is complicated by the retention of an additional lower incisor (i3) in mimotonids. Diastemal lengths for mimotonids were measured from the anterior part of the alveolus of p3 to the posterior part of the alveolus of i3. Within the lagomorphs, the anterior measurement was taken from the posterior portion of the alveolus for di2. Although these measurements are taken from non-homologous points (i.e. i3 vs. di2), it is a valid comparison as the *diastema* is represented by space between the anterior most cheek teeth and the incisors. Additionally, in several fossil specimens the di2 as well as its alveolus have been broken or lost. By measuring to the i3 instead of the di2, a larger sample number was obtained.

One-way ANOVA results showed that mean variations in DL/m1A among extant leporids, fossil leporids, ochotonids, mimotonids, and *Gomphos ellae* were significantly different ( $P < .0001$ ). Pair-wise (*t*-test) comparisons were not made in respect to *G. ellae* as only one specimen is known. However, the DL/m1A of *G. ellae* (0.70) falls outside the 96th percentile confidence interval for all of the groups to which it was compared (Leporidae, Ochotonidae, fossil Leporidae, and Mimotonidae). The diastemal length of *G. ellae* is intermediate between all other mimotonids and all living and extinct lagomorphs and its diastemal length is the longest known for any mimotonid (Fig. 5). This difference is important because diastemal length is a prominent distinguishing character between these two major groups established over 45 million years ago during the Middle Eocene. If lagomorphs evolved from mimotonids, the evolutionary transition must have included an elongation of the diastema, a character that has been maintained and advanced throughout the history of lagomorphs. Within lagomorphs, there exists a trend toward elongation of the diastema through time, as supported by recent molecular phylogenies (Matthee et al., 2004; Robinson and Matthee, 2005), whereas ochotonids have maintained a shorter diastema that is similar in length to the earliest lagomorph fossils. The molecular leporid phylogenies show that the earliest branching taxa (e.g. *Romerolagus*) often have short diastema, and the derived taxa (e.g. *Pronolagus*) often have elongated diastema. *Gomphos ellae* exhibits an intermediate diastemal length between all other mimotonids and all living and extinct lagomorphs, and combined with patterns observed in the crown group, gives evidence of a pattern of cranial morphology that has lasted for nearly 50 million years.

### Biostratigraphic Significance

The fauna of the Kholboldchi Formation is considered to be of Middle Eocene age (Dashzeveg and Hooker, 1997). Shevyreva

et al. (1975) described *Gomphos elkema* and Meng et al. (2004) have used that taxon as an index species for the Early Eocene Bumbanian East Asian Land Mammal Age (EALMA). The Middle Eocene of Asia is currently divided into two EALMAs, the earlier Arshantan and the later Irдинmanhan. Three fossil localities have been recognized from the Kholboldchi Formation: Tsagaan Khutel, Menkhen Teg, and Barun Khutsin Tsav (Fig. 1). These localities were jointly considered to be of Irдинmanhan age by Russell and Zhai (1987). Dashzeveg and Hooker (1997) later described the first deperetellid from Tsagaan Khutel, *?Irdinolophus tuiensis*, which they considered to be primitive relative to the more regionally abundant *Teleolophus*. Based on the primitive nature of *?Irdinolophus*, and the use of *Teleolophus* as an index taxon for the Irдинmanhan, Dashzeveg and Hooker (1997) suggested that Tsagaan Khutel and other localities within the Kholboldchi Formation might be attributable to the Arshatan EALMA.

Lucas (2001) proposed a system of first and last occurrences of various genera to distinguish the Arshantan and Irдинmanhan within central Asia. Unfortunately, all the taxa previously described from Tsagaan Khutel (Table 3) span both the Arshantan and the Irдинmanhan based on the scheme of Lucas (2001). Two genera described from Barun Khutsin Tsav, *Pantolamdodon* and *Haplodectes?* (Dashzeveg 1979, 1980, respectively), are considered to be last occurrences of the Arshantan, and Lucas (2001) used the presence of the Arshantan index taxon *Pantolamdodon* at Barun Khutsin Tsav to assign an Arshantan age to the Kholboldchi Formation. This age is consistent with the appearance of the mimotonid *Gomphos ellae* at this locality. As *G. elkema* is considered to be an index taxon of the Bumbanian EALMA (latest Paleocene–Early Eocene), the derived features of *G. ellae* relative to *G. elkema* are consistent with the younger age attributed to this locality. Based on the conclusion of Dashzeveg and Hooker (1997), and the system suggested by Lucas (2001), it is likely that the Kholboldchi Formation contains fossils of Arshantan age but more material is needed to determine its age more precisely.

The Andarak locality of Kyrgyzstan is the only other locality that has produced a Middle Eocene mimotonid (*Anatolimys*). Averianov and Godinot (1998) conducted a family-level parsimony analysis of endemism to compare various Middle Eocene faunas throughout central Asia. Their analysis showed that the Andarak fauna was most similar to Khaychin Ula (Irдинmanhan), although they did reference that Khaychin Ula was more derived relative to Andarak and that this may be due to the older age of Andarak. After describing new ceratomorphs from Andarak, Averianov and Godinot (2005) suggested that Andarak was Irдинmanhan using Lucas' (2001) system and the appearance of *Teleolophus* at Andarak. Although it is clear that there are distinct Arshantan and Irдинmanhan faunas within Asia, the unique faunas at both Tsagaan Khutel and Andarak suggest that more work is needed to determine their age, and in turn the age of the latest appearances of Mimotonidae. It is also clear that a revision of the deperetellids is needed (e.g. *Teleolophus* and *?Irdinolophus*) to better understand the biostratigraphic utility of this Middle Eocene group.

## CONCLUSIONS

The precise age of *Gomphos ellae* is unclear, but it likely represents one of the youngest known species of mimotonids. *Anatolimys*, from the Middle Eocene Andarak locality of Kyrgyzstan, also represents a late occurrence. The specimens described here represent a mimotonid exhibiting important features that place it close to the ancestry of lagomorphs. *Gomphos ellae* shows many typical mimotonid features including mesoconids on the lower cheek teeth, an extra set of lower incisors, and a well-developed hypoconulid on m3. *G. ellae* also

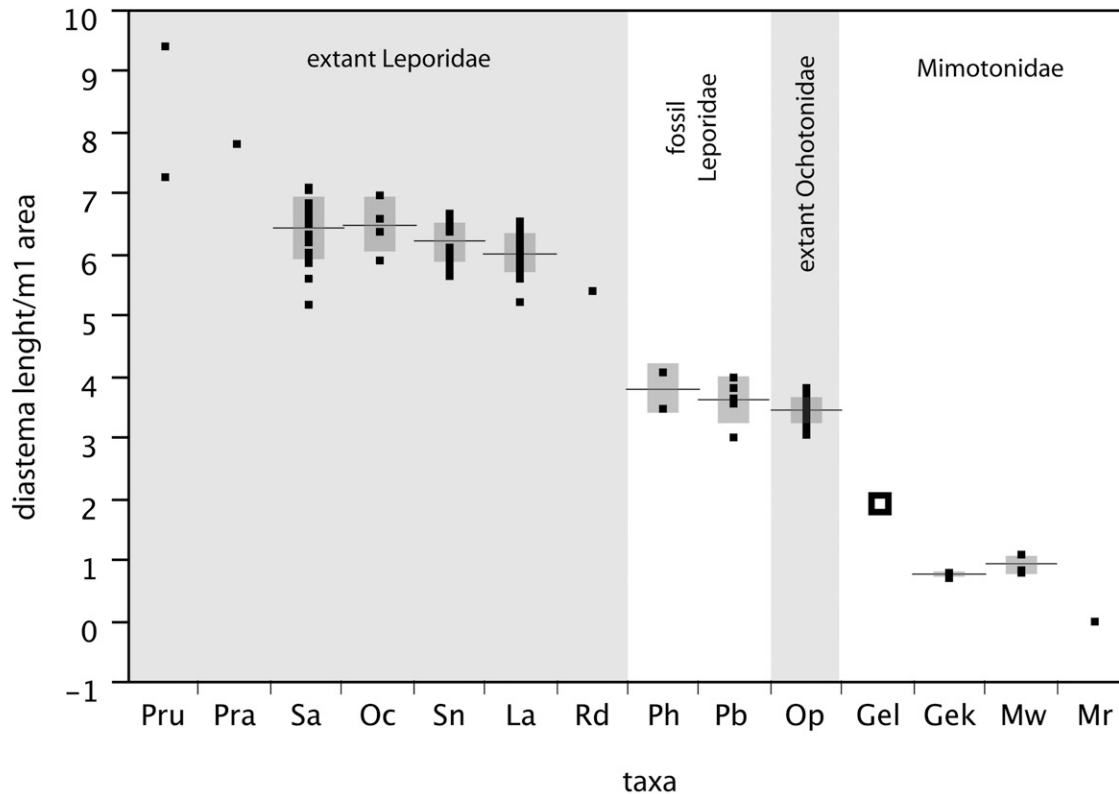


FIGURE 5. Relative diastemal lengths of various extant and fossil duplicitentates. Relative length is determined by diastema length/m1 area to normalize for size (see text for discussion). Standard deviations are shown with grey rectangles; means are shown with horizontal lines. Groupings for statistical comparisons to *Gomphos ellae* are shown with alternating grey and white shading. Taxonomic names are indicated by the following abbreviations: **Pru**, *Pronolagus rupestris*; **Pra**, *Pronolagus randensis*; **Sn**, *Sylvilagus nuttallii*; **Sa**, *Sylvilagus auduboni*; **Oc**, *Oryctolagus cuniculus*; **La**, *Lepus americanus*; **Rd**, *Romerlagus daizi*; **Ph**, *Palaeolagus burkei*; **Ph**, *Palaeolagus haydeni*; **Op**, *Ochotona princeps*; **Gel**, *Gomphos ellae*; **Gek**, *Gomphos elkema*; **Mw**, *Mimotona wana*; **Mr**, *Mimotona robustus*.

has a deep ramus that is similar only to *Anatolimys* among mimotonids. Most striking is the elongate diastema of *G. ellae* that is intermediate in length between all other mimotonids and living and extinct lagomorphs. The diastemal length of *G. ellae* shows transitional morphology that supports the hypothesis that lagomorphs evolved from mimotonids. Given the age and morphology of these specimens, it is likely that they represent an advanced form of an evolutionary grade that gave rise to Lagomorpha.

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APPENDIX 1. Specimens examined for analysis of diastemal length/ml area shown in figure 4. *Lepus americanus*, MVZ 43877, 43878, 40295, 40296, 40298, 40300, 32777, 32765, 32766, 32776, 32778, 32779, 32780, 32767, 32768, 32770, 32771, 32772; *Sylvilagus auduboni* MVZ 86080, 106142, 76212, 148866, 148862, 148861, 86079, 76213, 76216, 76215, 76217, 76214, 128259, 128258, 126487, 109681, 76979, 128257, 76978, 121727, 124800, 124798, 124797, 124799; *Sylvilagus nuttallii* MVZ 84044, 79592, 96781, 96780, 96779, 96774, 96773, 8264, 8263, 8262, 8268, 8267, 31710, 74279, 74277, 74281, 74280; *Romerolagus diazi* MVZ 92377; *Pronolagus rupestris* MVZ 118077, 118078; *Pronolagus randensis* MVZ 117272; *Oryctolagus cuniculus* MVZ 118078, 133289, 129757, 129756, 184550; *Ochotona princeps* MVZ 135163, 135162, 135069, 135164, 135068, 135060, 135160, 135085, 135082, 135081, 22911, 22909, 22907, 135217, 22906; *Palaeolagus haydeni* UCMP 152670, 152669; *Palaeolagus burkei* UCMP 152671, 152665, 152666, 152667, 152668; *Mimotona wana* IVPP 7416, 4325.1; *Mimotona robustus* IVPP 4329; *Gomphos elkema* MAE MN 95x2030-2088, MAE BU 14425, MAE MCK 174, MAE 14426.