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Small mammal fauna from Wulanhuxiu (Nei Mongol, China) implies the Irdinmanhan–Sharamurunian (Eocene) faunal turnover

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Wulanhuxiu, a middle Eocene locality in the Erlian Basin, Nei Mongol (China) has been commonly regarded as belonging to the Ulan Shireh Formation, equated with the Irdin Manha Formation. We recognized two separate mammalian faunas of different age from the beds exposed at Wulanhuxiu. The lower fossiliferous horizon contains an anagalid, uncommon duplicidentate representatives (*Gomphos progressus* sp. nov., *Mimolagus*, *Erenlagus*, and *Strenulagus*), and diverse perissodactyls. This combination of taxa points to an Irdinmanhan age, but one element of the fauna (*Schlosseria*) may represent an Arshantan relic. Overall, the assemblage comprises "paleoplacental" mammals mixed with "neoplacentals". The upper horizon is less species-rich and the only paleoplacentals present are scarce creodonts. However, this horizon is marked by abundant remains (including postcranial material) of the lagomorph *Gobiolagus* and by the presence of an advanced form of *Gobiomys* (Rodentia), and is most probably Sharamurunian in age. Thus, Wulanhuxiu documents replacement, albeit incomplete, of paleoplacentals by neoplacentals in the Chinese Eocene record.

Key words: Mammalia, Rodentia, Duplicidentata, Anagalidae, Eocene, Ulan Shireh Formation, China, Erlian Basin.

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Introduction

The Erlian Basin lies in northern China, in the central part of Nei Mongol (Inner Mongolia). Its Paleogene deposits have yielded rich fossil mammal assemblages, especially of Eocene age, providing the basis for several Paleogene Asian Land Mammal Ages or ALMAs (see Holroyd and Ciochon 1994; Meng and McKenna 1998; Luterbacher et al. 2004). The eastern part of the basin in the vicinity of Erenhot has been relatively well studied. However, the western part, including the area in the vicinity of the Shara Murun River, remains poorly known. The Central Asiatic Expeditions (CAEs) of the American Museum of Natural History surveyed Baron Sog Mesa and North Mesa west of the Shara Murun River in the 1920s. In 1925 they collected intensively at two localities in the area of North Mesa, described as "4 and 8 miles north of Tukhum Lamasery", and they returned to the locality "eight miles north of Tukhum" ("Chimney Butte") in 1928 (Radinsky 1964). The "Chimney Butte" locality (which includes the famous "Buckshot Quarry") is now called Wulanhuxiu (Wang et al. 2012). The most important CAE results concerning the "Chimney Butte" mammalian fauna include descriptions of pantodonts such as *Pantolambdodon inermis* and *P. fortis* (Granger and Gregory 1934), brontotheriids such as *Desmatotitan tukhumensis*, *Epimanteoceras formosus*, *Protitan grangeri* (= *bellus*), and *Microtitan mongoliensis* (Granger and Gregory 1943), small tapiroids such as *Breviodon* and *Rhodopagus* (Radinsky 1965), the creodont *Sarkastodon mongoliensis* (Granger 1938), the rodent *Advenimus bohlini* (Dawson 1964) and the lagomorph *Shamolagus grangeri* (Burke 1941), the mesonychid ?*Harpagolestes orientalis* (Szalay and Gould 1966), and the didymoconid *Kennatherium shirensis* (Mellet and Szalay 1968). More material was collected by a Sino-Soviet expedition in 1959, and by IVPP field-parties from 1975 onward (Chow and Rozhdestvensky 1960; Russell and Zhai 1987). However, no further infor-

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mation on the mammalian fauna from this region has been reported, apart from a review by Ye (1983).

Here we focus on the fossil assemblage of small mammals from Wulanhuxiu based on new material collected from that locality over the past decade. In particular, the Glires (rodents, lagomorphs, and their closest relatives) fauna from this locality provides new data on the age and paleoenvironment of the Ulan Shireh Formation (exposed only at North Mesa) and enhances our knowledge of the regional aspects of the middle Eocene mammal fauna in the western Erlian Basin. In analyzing the Wulanhuxiu assemblage we found Lucas's (2001: 230) proposed dichotomy between "paleoplacentals" and "neoplacentals", which stems directly from Osborn's concept of mesoplacentals and cenoplacentals (Osborn 1894; Osborn and Earle 1895), to be useful. The paleoplacentals were understood by Lucas (2001) as mammalian groups of a Paleogene radiation, all of which lack surviving descendants and were characterized by an archaic tooth structure and poorly developed brain. According to Lucas (2001) these groups included Anagalida, Condylarthra, Creodonta, Dinocerata, Mesonychia, Notoungulata, Pantodonta, and Tillodontia, whereas neoplacentals included all groups with extant representatives ("the placentals of modern aspect"). Neoplacentals would then include, for example, artiodactyls, carnivorans, chiropterans, lagomorphs, perissodactyls, primates, and rodents. Furthermore, a degree of parallelism existed between the paleoplacental and neoplacental radiations. Eurymylidae and Mimotonidae, for instance can be regarded as paleoplacental counterparts of modern Glires (Rodentia and Lagomorpha, respectively). The replacement of the paleoplacentals by neoplacentals in Asian faunas continued through the Eocene; thus, the two groups coexisted for some 20 million years, although the major turnover occurred most probably during the Arshantan–Irdinmanhan (Lucas 2001). At Wulanhuxiu, we document a remarkable replacement of some extinct "paleoplacental" clades (anagalids and mimotonids) by their modern "neoplacental" counterparts (lagomorphs and rodents), in addition to a decrease in ungulate diversity.

Institutional abbreviations.—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China.

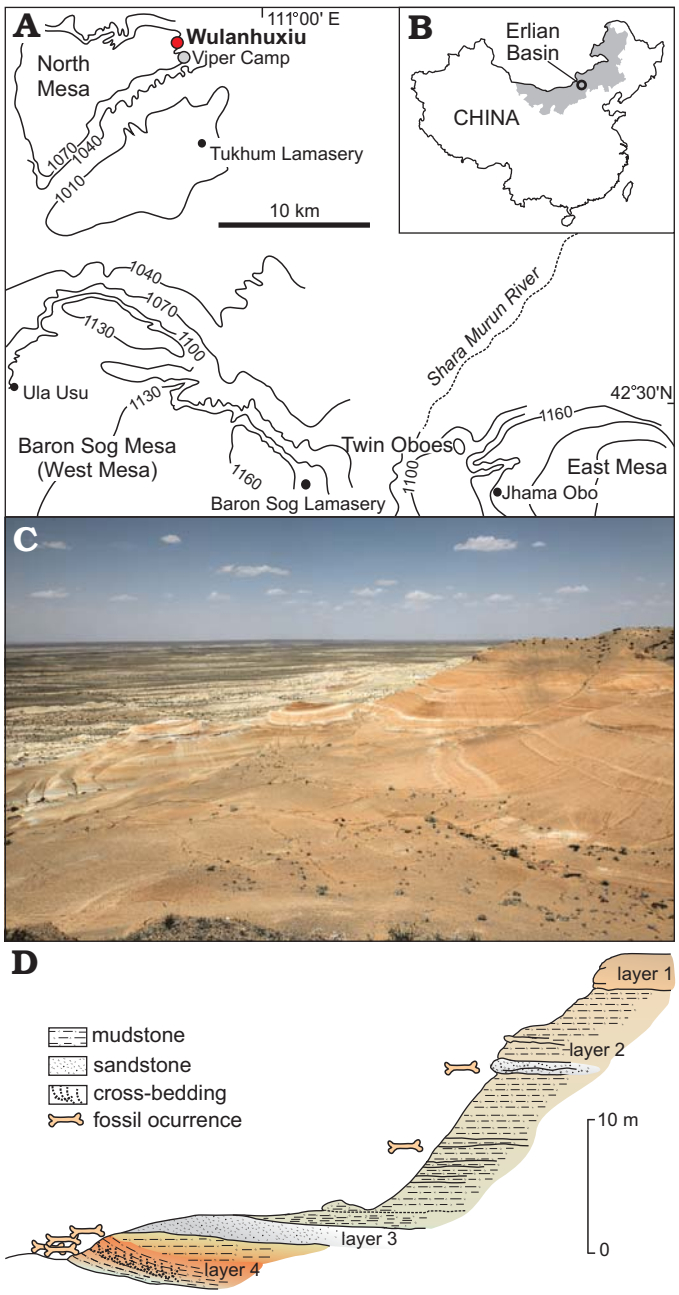

Fig. 1. **A**. Location of the Wulanhuxiu mammalian fossil site in the western part of the Erlian Basin (elevations given in meters; modified from Russell and Zhai 1987). **B**. Map of continental China (Nei Mongol Autonomous Region in gray). **C**. Typical landscape at the Wulanhuxiu locality showing fossiliferous beds with the Irdinmanhan–Sharamurunian transition. **D**. Stratigraphic section of the studied sediment series at Wulanhuxiu (after a field sketch by Bin Bai).

Geological setting

The Wulanhuxiu locality lies in the western part of the Erlian Basin on the northern side of the North Mesa (Fig. 1). According to Russell and Zhai (1987: fig. 54), a representative section of the Ulan Shireh Formation (note that a type section has not been formally specified) crops out east of Wulanhuxiu, at the easternmost part of the North Mesa (near Viper Camp; Fig. 1).

The current study encompasses the four uppermost sedimentary units exposed at Wulanhuxiu. The topmost unit (layer 1) lacks any fossil remains. Layer 2, located just below, is the thickest in the profile and contains fossil bones and teeth. It is composed of white mudstone, which become greenish towards the bottom. In the upper part of the layer a lens of white sandstone occurs. Layer 3 which is unfossiliferous, is much thinner and composed of grey-white sandstone. Layer 4, the lowermost considered in this study, consists of mudstone that is greenish in the upper part of the layer, red below and green-white at the very bottom. The faunal con-

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faunal content of layers 2 and 4, the only fossiliferous ones within the stratigraphic interval considered here, is listed in Table 1. No fossils have so far been reported in the beds below layer 4.

Material and methods

The fossil material used in this study was collected by IVPP field parties, by surface prospecting (ungulates and large Glires) or screen washing (small Glires); all specimens are housed at the IVPP. The material consists of isolated dental and postcranial elements, the latter dominated by tarsal bones, which due to their sturdier structure survive post-burial diagenesis and eventual weathering more readily than other bones. The specimens were studied under a scanning microscope JSM 6100 (IVPP), and some photos were taken with a DinoLite Pro digital microscope. Measurements were taken with Sylvac electronic calipers with an accuracy of 0.1 mm for bones and 0.01 mm for teeth. Dental terminology generally follows Meng and Wyss (2001: fig. 1) and directional terms for the teeth are after Ungar (2010: fig. 1.1). Anatomical terminology for long bones follows Evans (1993).

Systematic palaeontology

Class Mammalia Linnaeus, 1758

Superorder Anagalida Szalay and McKenna, 1971

Family Anagalidae Simpson, 1931

Anagalidae gen. et sp. indet.

Fig. 2A.

Material.—Right m1 in a fragment of the mandible (IVPP V20825) from Wulanhuxiu, Erlian Basin, Nei Mongol (China), horizon 4 (lower part), Irdinmanhan (middle Eocene).

Description.—The tooth shows a well-developed unilateral hypsodonty, the crown on the buccal side is about one-third higher (4.94 mm) than the crown on the lingual side (3.64 mm). The tooth stands upright and the anterior and posterior roots are straight and positioned close together. The total tooth height is 10.30 mm and the length of the crown is 4.44 mm. The trigonid and talonid are much more asymmetric than those of mimotonids, with trigonid wider (3.99 mm) than the talonid (3.48 mm). The occlusal surface is strongly worn but the trigonid and talonid are partly separate (by about 50% of the tooth width, including the depths of both the hypoflexid and the mesoflexid). The hypoflexid is shallower than the mesoflexid, which is delicately arched posteriorly and overall slightly more posterior. The trigonid is larger, oval, and with a gently concave occlusal surface; the bases of the main cusps are still discernible even in this strongly worn stage. The protoconid and metaconid are similar in size but the metaconid is much higher than the protoconid (Fig. 2A$_2$–A$_4$). The metaconid is the highest eminence on the occlusal surface, and is not quite aligned transversely with the protoconid, but rather shifted slightly posteriorly. There is no trace of a paraconid or paracristid and the anterior margin of the tooth is straight. The lingual side of the trigonid is no broader than the buccal one, indicating that the paraconid was absent or of negligible size.

The talonid is triangular, narrowing lingually towards a well-defined hypoconid that is slightly smaller than the protoconid (Fig. 2A$_1$, A$_2$). The hypoconid is located more lingually than the protoconid. The entoconid is well defined and is almost in line (transversely) with the hypoconid. Furthermore, the entoconid does not align with the metaconid which protrudes farther lingually. The posterobuccal part of the talonid is angled, which suggests the presence of a well-developed, asymmetrically positioned hypoconulid that is shifted strongly buccally.

Remarks.—Anagalidae are an endemic Asian group known mostly from the Paleocene of China. Only *Anagale gobiensis* (Ulan Gochu Formation, Nei Mongol) and *Anagalopsis kansuensis* (Baiyanghe Formation, western Gansu) are known to have survived to the late Eocene–early Oligocene (Simpson 1931; Bohlin 1951; McKenna 1963). The molars of anagalids share some similarities with those of mimotonids and eurymylids, but differ in being larger and frequently more hypsodont, and in showing a slightly different cusp arrangement and overall geometry of the occlusal surface.

The described m1 is bigger than that of any known mimotonid, lagomorph or eurymylid. However, the tooth is closest in size to the m1 of *Hsiuannania* (see Hu 1993), being slightly smaller than that of *Anagalopsis* (Bohlin 1951) and larger than that of *Anagale* (Simpson 1931). The talonid

Table 1. Mammals of the Wulanhuxiu locality. Note that horizon 2 is younger than horizon 4.

Taxon		Horizon 2	Horizon 4
Creodonta indet.		+	+
Mesonychidae indet.		+	
Pantodonta	*Pantolambdodon* sp.		+
Perissodactyla	*Breviodon* sp.		+
	Lophialetes?		+
	Deperetellidae indet.		+
	Teleolophus sp.	+	+
	Schlosseria sp.		+
	Rhodopagus sp.		+
	Heleletidae indet.		+
Artiodactyla, Helohyidae	*Gobiohyus* sp.		+
Glires, Duplicidentata, Mimotonidae	*Gomphos progressus* sp. nov.		+
	Mimolagus aurorae		+
Rodentia	*Asiomys dawsoni*		+
	Gobiomys exiguus	+	
	Yuomys sp.		+
Lagomorpha	*Erenlagus anielae*		+
	Gobiolagus aliwusuensis	+	
	Strenulagus solaris		+
Anagalidae	Gen. et sp. indet.		+

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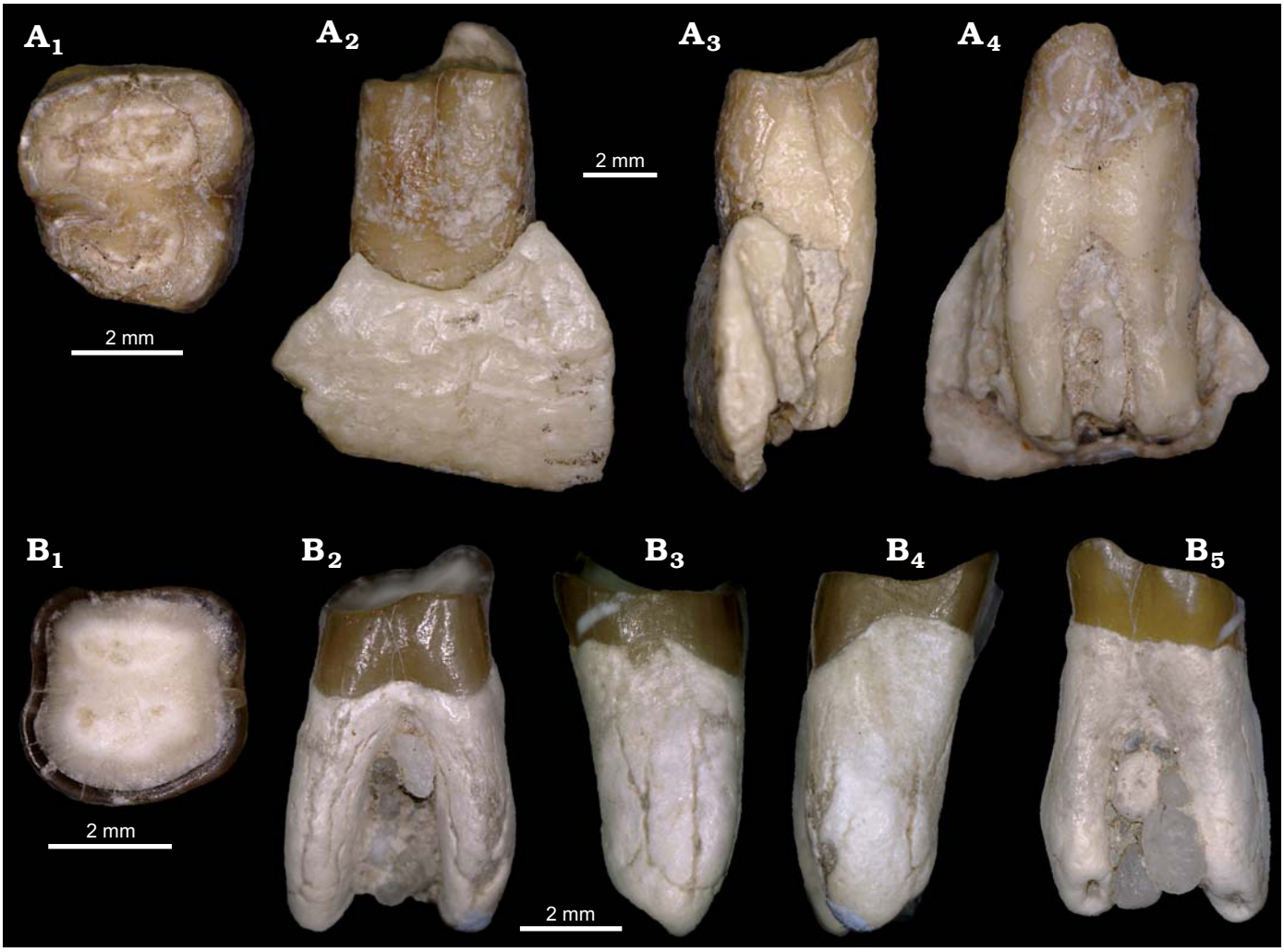

Fig. 2. Anagalid and mimotonid from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Anagalidae gen. et sp. indet., left m1 (IVPP V20825) in occlusal (A_1), buccal (A_2), anterior (A_3), and lingual (A_4) views. **B**. *Mimolagus aurorae* Fostowicz-Frelik, Li, Mao, Meng, and Wang, 2015, right m1 (IVPP V20826) in occlusal (B_1), buccal (B_2), posterior (B_3), anterior (B_4), and lingual (B_5) views.

is narrower than the trigonid, whereas in the p4–m3 of the coeval taxa *Gomphos* and *Mimolagus* the occlusal planes of the crowns have square, symmetric outlines with wide talonids, and the cusps are generally aligned. Anagalid teeth frequently show asymmetry and lack precise cusp alignment. In both molars and premolars, the talonid is either wider (e.g., *Anagale*; see Simpson 1931; McKenna 1963) or narrower (e.g., *Huaiyangale*, *Hsiuannania*, *Qipania* or *Eosigale*; Xu 1976; Hu 1993) than the trigonid or may be shifted lingually.

The trigonid shows no trace of a paraconid or paracristid, but these features are variably present in anagalids, as in basal Glires. They may be present in all cheek teeth in reduced or normal form, but may also be absent in at least some teeth; in general, the paraconid and paracristid are much less persistent than the metaconid, and in heavily worn teeth may not be visible. The paraconid is lacking, for example, in molars of *Hsiuannania*. Moreover, the talonid of the described m1 is not typical of duplicidentates, being generally triangular, with an anteroposteriorly short lingual side and longer buccal side. The talonid narrows buccally in lagomorphs, but does not narrow lingually, and is roughly square in mimotonids. On the other hand, narrowing of the lingual margin of the talonid and lengthening of the buccal margin can be observed in some anagalids, such as *Hsiuannania*.

Although the described tooth is strongly worn, it is still markedly unilaterally hypsodont. The degree of hypsodonty in the Wulanhuxiu specimen is markedly increased in comparison with *Mimolagus*, and especially with *Gomphos*. Some Anagalidae show distinctly higher crowns than are present in most derived mimotonids, beeing comparable in this feature even to some primitive lagomorphs of modern aspect, such as *Hypsimylus* (Meng and Hu 2004). By contrast, mimotonids have poorly expressed hypsodonty (see Dashzeveg and Russell 1988).

The specimen from Wulanhuxiu resembles *Hsiuannania* in the overall tooth morphology and in having a high degree of hypsodonty, although *Hsiuannania* is known only from the late Paleocene of Anhui and Jiangxi, China (Hu 1993).

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Glires Linnaeus, 1758

Family Mimotonidae Li, 1977

Genus *Mimolagus* Bohlin, 1951

Type species: *Mimolagus rodens* Bohlin, 1951; early Oligocene, Baiyanghe Formation, Shanmacheng, western Gansu, China.

Mimolagus aurorae Fostowicz-Frelik, Li, Mao, Meng, and Wang, 2015

Fig. 2B.

Material.—Right m1 (IVPP V20826) from Wulanhuxiu, Erlian Basin, Nei Mongol, China, horizon 4 (lower part), Irdinmanhan (middle Eocene).

Description.—The tooth is strongly worn, and the trigonid and talonid form a continuous square, gently concave occlusal surface (Fig. 2). The protoconid is aligned with both the metaconid and the hypoconid, while the entoconid protrudes slightly lingually. The metaconid is the highest cusp. The enamel layer maintains a uniform thickness around the entire perimeter of the crown. Because of the heavy wear, the tooth crown is not very high, and the difference in crown height between the buccal and lingual sides of the tooth is not very pronounced. The mesial and distal roots are complete, robust and relatively divergent. Each root has a small apical aperture. The tooth closely resembles other specimens of *Mimolagus aurorae* from the eastern part of the Erlian Basin (Fostowicz-Frelik et al. 2015b). Such strong crown wear, leaving a gently concave and obliterated occlusal surface, is characteristic of this species, and was probably achieved relatively early in ontogeny (similar wear can be seen in two of three lower teeth found in the Huheboerhe area; Fostowicz-Frelik et al. 2015b: fig. 5).

Stratigraphic and geographic range.—Irdin Manha Formation, Irdinmanhan, middle Eocene, Erlian Basin, Nei Mongol, China.

Genus *Gomphos* Shevyreva in Shevyreva et al., 1975

Type species: *Gomphos elkema* Shevyreva, 1975; early Eocene, Gashato, Mongolia.

Gomphos progressus sp. nov.

Figs. 3, 4.

Etymology: From Latin *progressus*, progressive; in relation to the derived dental morphology seen in this species.

Type material: Holotype: left m2 (IVPP V20259), paratypes: right M3 (IVPP V20824); right m3 (IVPP V20259.1).

Type locality: Layer 4 (lower to middle part), Wulanhuxiu, Ulan Shireh Formation, Erlian Basin, Nei Mongol, China.

Type horizon: Irdinmanhan, middle Eocene.

Other material.—DI2 (IVPP V20259.2), di2 (IVPP V20259.3) from the type locality and horizon.

Diagnosis.—Derived *Gomphos* characterized by fusion of lower molar cusps to form continuous crests. Differs from all other *Gomphos* species in lacking mesoconid, cristid obliqua and mesostylid. Entoconid and hypoconulid form a ridge instead of separate cusps. Further differs from *G. elkema* in having reduced hypoconal shelf on M3 and lacking mesostyle. Further differs from *G. shevyrevae* in being less hypsodont and in having buccally shifted entoconid on m3.

Description.—The M3 of *Gomphos* has not previously been described in detail. The tooth is strongly asymmetrical with a buccolingually wide anterior part and a posterior part which is roughly 40% narrower. Both individual cusps and the crown as a whole seem more inflated than in *G. elkema* (the M3 is unknown in *G. ellae* and *G. shevyrevae*). The tooth resembles the M3 of *G. elkema* in lacking strong unilateral hypsodonty. The roots have been broken away. The protocone is large and prominent, being larger overall than the paracone. As in other *Gomphos* and *Mimolagus aurorae*, the protocone produces two arms (lophs), the preprotocrista and postprotocrista, which diverge anteroposteriorly, and extend buccally to delineate the trigon. The anterior and posterior lophs meet at an acute angle, that is slightly wider than in *G. elkema*. The preprotocrista surrounds the paracone anteriorly and continues to the anterobuccal corner of the tooth (Fig. 3), while the postprotocrista joins with the metacone. The postprotocrista is shorter than in *G. elkema*, and deviates more posteriorly from the paracone. The metacone therefore is located more posterolingually than in *G. elkema*. The metaconule is small and marked only by a slight broadening of the postprotocrista, whereas in *G. elkema* the metaconule is larger than the metacone. The specimen from Wulanhuxiu lacks a mesostyle, although this feature is quite prominent in *G. elkema*. The trigon basin is wider than in *G. elkema* and is open buccally, forming a relatively flat, triangular valley. The small, oval hypoconal shelf, and buccolingually shorter than in *G. elkema*, and more similar to the equivalent structure in *Mimolagus aurorae*. The hypoconal shelf is positioned, slightly askew, at the posterolingual side of the tooth. The hypocone is aligned with the protocone, and the posterobuccal end of the hypoconal shelf is aligned with the metacone (Fig. 3). Between the metacone and hypoconal shelf is a deep narrow groove.

The lower molars (Table 2) are slightly larger than those of *Gomphos shevyrevae* (see Meng et al. 2009), and the crowns are even more swollen than in that species. The unilateral hypsodonty of the crown is very poorly expressed and is slightly weaker than in *G. shevyrevae*.

Table 2. Measurements (in mm) of *Gomphos progressus* teeth.

Locus	Collection number	Length	Width	Trigonid width	Talonid width	Crown height (lingual)	Crown height (buccal)
DI2	V20259.2	4.0	2.47				
di2	V20259.3	3.35	2.76				
M3	V20824	2.68	3.59			2.87	
m2	V20259	3.52		3.49	2.98		3.46
m3	V20259.1	3.25		3.32	2.95		3.04

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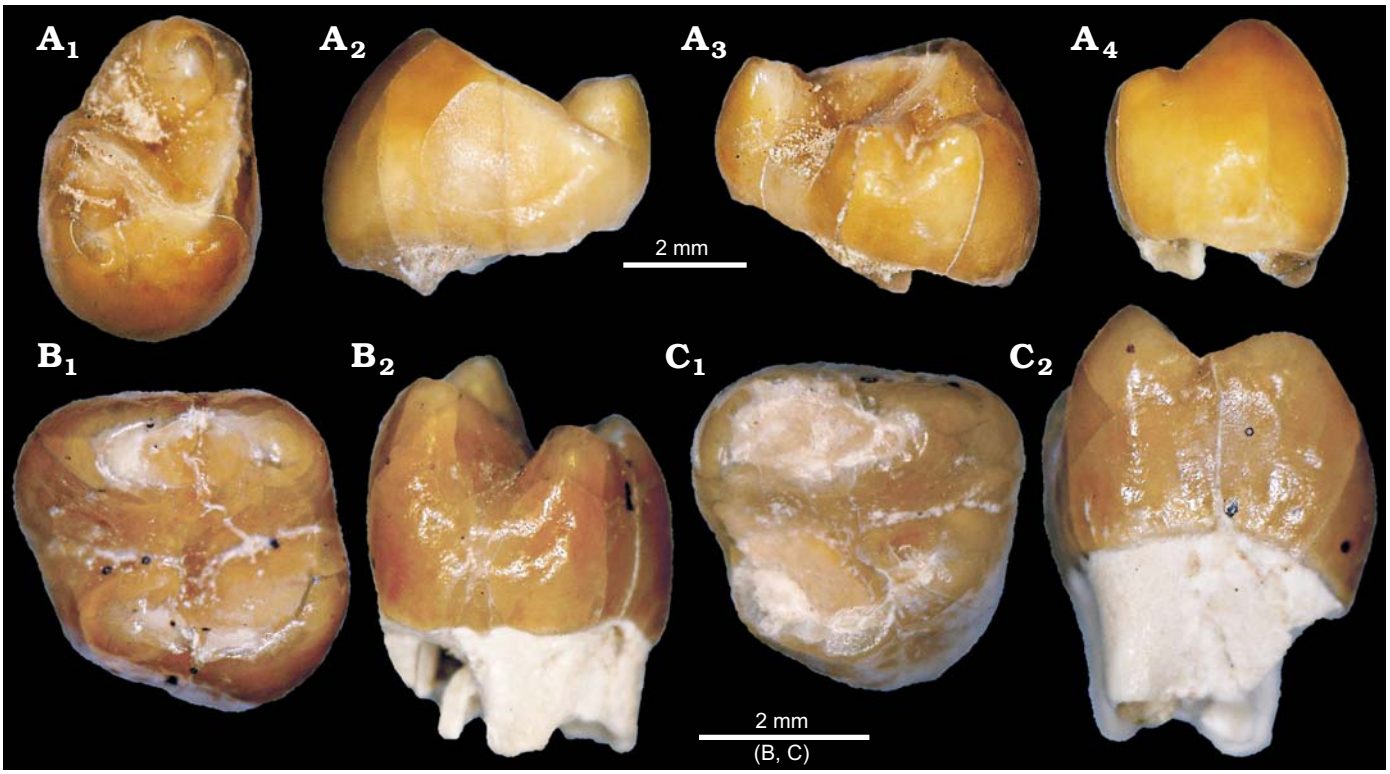

Fig. 3. Mimotonid *Gomphos progressus* sp. nov. from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Left M3 (IVPP V20824) in occlusal (A_1), anterior (A_2), posterior (A_3), and lingual (A_4) views. **B**. Left m2, holotype (IVPP V20259) in occlusal (B_1) and buccal (B_2) views. **C**. Right m3 (IVPP V20259.1) in occlusal (C_1) and anterior (C_2) views.

The tooth crowns also differ slightly in occlusal outline from those of *G. shevyrevae*, being less perfectly square; instead, the trigonid is slightly wider than the talonid and this difference seems to persist as the crown swells towards the base. In both specimens from Wulanhuxiu the hypoconulid lies at the distal edge of the talonid. In the specimen IVPP V20259.1 (Fig. 3C) the hypoconulid is slightly larger, and more central, than in the holotype. For this reason, we are inclined to regard V20259.1 as m3. The holotype specimen, in which the hypoconulid is shifted more lingually, can be identified as m2. The distal margin of the talonid between the hypoconulid and entoconid is straight. This feature is more clearly visible in m3, which is the more worn of the two lower molars, although wear in both cases is light. In both lower molars, the trigonid has two large cusps, the protoconid and the metaconid. The metaconid is visibly higher, although both cusps have a similar base radius. There is no trace of a paraconid or paracristid, as is typical of *Gomphos* (Zhegallo and Shevyreva 1976; Dashzeveg and Russell 1988; Meng et al. 2004, 2009). Between the cusps of the trigonid a deep and wide V-shaped trigonid basin is formed. In both molars the protoconid and metaconid are aligned.

In the less heavily worn left m2, the talonid forms a large basin surrounded by a perimeter of almost totally merged cusps, namely the entoconid, hypoconulid, and hypoconid. The hypoconid is particularly prominent on the m2, although it is hard to determine the exact boundary of each talonid cusp. In m3, which is slightly more worn, the hypoconid is more isolated and forms its own wear facet (Figs. 3, 4). The posterior rim connecting the hypoconulid with entoconid is slightly indented where it intersects with the hypoconid. The hypoconulid is similar to that of *Gomphos shevyrevae* but smaller than in *G. elkema*. The hypoconulid forms most distally pronounced portion, which is gently rounded, of the distal rim of the talonid (Fig. $3B_1$, C_1). The edge between the entoconid and hypoconulid tends to be flat (Fig. $3B_1$, C_1). During the early stages of wear, the hypoconid is aligned with the protoconid, although as wear progresses this alignment becomes distorted because the protoconid "shifts" more buccally as the whole trigonid is more extended buccally, rather unlike in *G. shevyrevae* and other *Gomphos* species (see Meng et al. 2004, 2009). The hypoconid and entoconid are aligned in both molars. However, the metaconid and entoconid are aligned in m2 (Fig. $3B_1$) but not in m3, in which the entoconid is shifted buccally (Fig. $3C_1$).

The lower molars of *Gomphos* from Wulanhuxiu show no trace of the mesostylid, which is well developed in *G. elkema* and *G. ellae* (Meng et al. 2004; Kraatz et al. 2009). The Wulanhuxiu specimens also lack a mesoconid, a feature present in all other *Gomphos* species including *G. shevyrevae* (Meng et al. 2009).

Stratigraphic and geographic range.—Ulan Shireh Formation, Irdinmanhan, middle Eocene, Erlian Basin, Nei Mongol, China.

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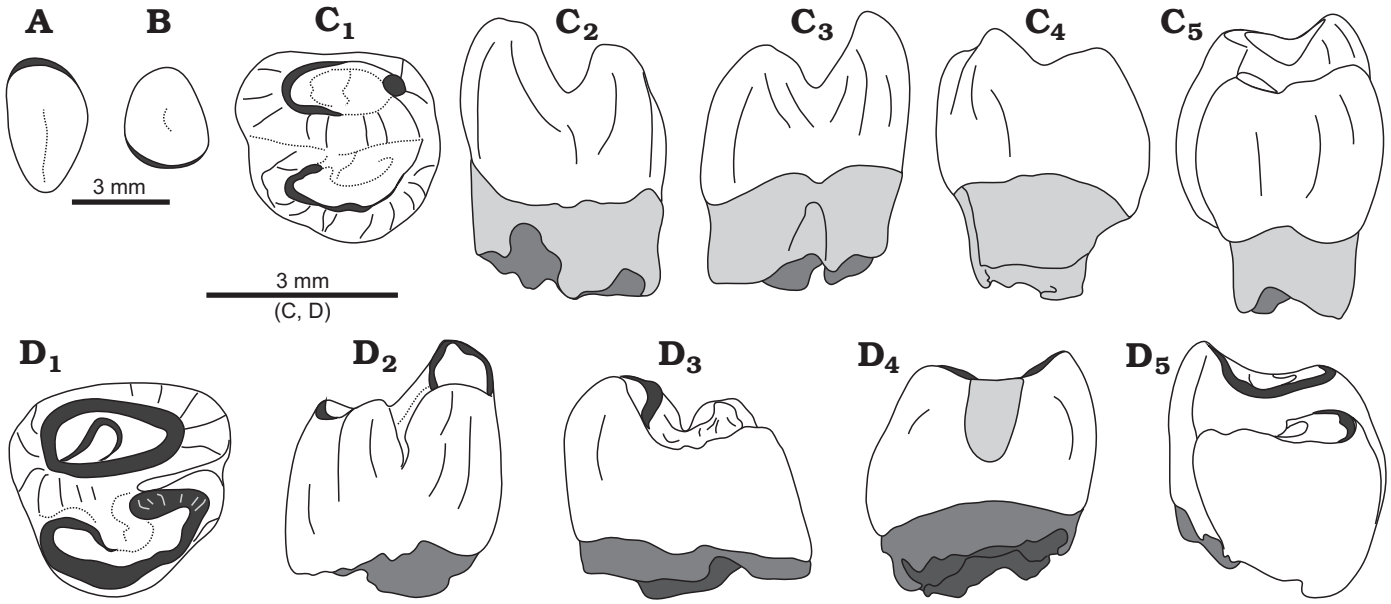

Fig. 4. Morphology of tooth of *Gomphos progressus* sp. nov. **A**. Cross-section of the left upper incisor (IVPP V20259.2). **B**. Cross-section of the left lower incisor (IVPP V20259.3). **C**. Left m2, holotype (IVPP V20259) in occlusal (C_1), buccal (C_2), lingual (C_3), anterior (C_4), and posterior (C_5) views. **D**. Right m3 (IVPP V20259.1) in occlusal (D_1), buccal (D_2), lingual (D_3), anterior (D_4), and posterior (D_5) views.

Order Lagomorpha Brandt, 1855

Family indet.

Genus *Erenlagus* Fostowicz-Frelik and Li, 2014

Type species: *Erenlagus anielae* Fostowicz-Frelik and Li, 2014; middle Eocene, Huheboerhe, Nei Mongol, China.

Erenlagus anielae Fostowicz-Frelik and Li, 2014

Figs. 5, 6.

Material.—left M1 (IVPP V20260), right m2 (IVPP V20258) from Wulanhuxiu, Erlian Basin, Nei Mongol, China, horizon 4, Irdinmanhan (middle Eocene).

Description.—The M1 matches in size that of the type sample (the crown width is 2.37 mm and the crown length 1.47 mm; see Fostowicz-Frelik and Li 2014). The upper molar is worn and the buccal roots are broken (Fig. 5). The occlusal surface is symmetrical and roughly rectangular, which indicates M1 rather than M2. The remains of an almost vanished crescent are asymmetrical (with the anterior arm larger) and shifted anteriorly. There is a narrow and small hypostrial lake positioned diagonally, separating the trigon from the hypoconal shelf. The hypostria is only a shallow indentation. The protocone is slightly larger than the hypocone, and it protrudes farther lingually then the latter. The hypoconal shelf is not inflated, covering roughly 30% of the occlusal surface, it is relatively extended buccolingually but short anteroposteriorly. The tooth curvature is slightly greater than in the upper molars of *Erenlagus* from Huheboerhe.

The m2 is close (apart from the more strongly bent roots) to the holotype specimen (Fig. 6; see also Fostowicz-Frelik and Li 2014: fig. 2A–J). The occlusal surfaces of the trigonid and talonid are lingually confluent as in the holotype. The length of the occlusal surface is 1.65 mm and the maximum crown height equals 1.98 mm; the trigonid (1.88 mm in width) is oval with flattened anterior and posterior edges. The metaconid is higher than the protoconid, even at this strongly worn stage, and both cusps are aligned. The enamel layer surrounding the protocone is thickened markedly. The anterior wall of the trigonid is concave and displays a wide enamel-less hiatus. The occlusal surface of the talonid (1.41 mm in width) is placed lower than the trigonid one; it is generally rectangular with a tapering buccal side. The entoconid is placed more distally than the hypoconid, but both have a similar height. The poorly distinguished hypoconulid is aligned with the entoconid and both cusps form a straight flat distal margin of the talonid. The anterior margin of the talonid is irregular curving anteriorly. The whole tooth column is slightly bent distally, which is typical of m2 in lagomorphs. The roots are broken apically. The part which is preserved shows a fused condition, with the apical trigonid and talonid part dis-

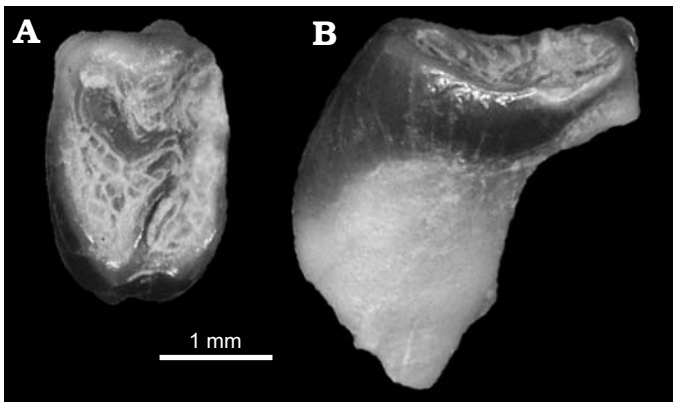

Fig. 5. Lagomorph *Erenlagus anielae* Fostowicz-Frelik and Li, 2014 from the Eocene of Wulanhuxiu, Nei Mongol, China. Left M1 (IVPP V20260) in occlusal (**A**) and posterior (**B**) views.

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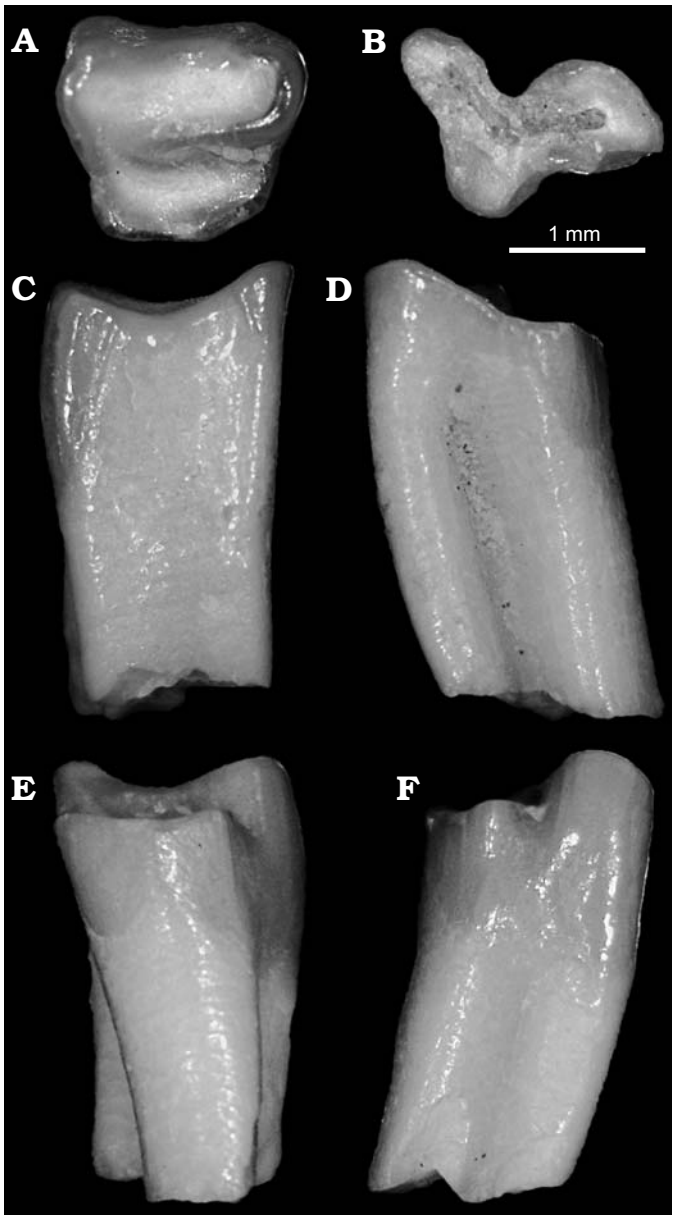

Fig. 6. Lagomorph *Erenlagus anielae* Fostowicz-Frelik and Li, 2014 from the Eocene of Wulanhuxiu, Nei Mongol, China. Right m2 (IVPP V20258) in occlusal (**A**), apical (**B**), mesial (**C**), lingual (**D**), distal (**E**), and buccal (**F**) views.

tinct, but having a common root chamber. In this respect the Wulanhuxiu specimen is different from the type specimen, in which the roots have separate dental chambers.

Stratigraphic and geographic range.—Irdin Manha Formation and Ulan Shireh Formation, Irdinmanhan, middle Eocene, Erlian Basin, Nei Mongol, China.

Genus *Strenulagus* Tong and Lei, 1987

Type species: *Strenulagus shipigouensis* Tong and Lei, 1987; middle Eocene, Shipigou, Henan, China.

Strenulagus solaris Lopatin and Averianov, 2006

Fig. 7.

Material.—Right m1 (IVPP V20256.1), fragment of left M2 (IVPP V20264), left calcaneus (IVPP V20256.2), from Wulanhuxiu, Erlian Basin, Nei Mongol, China, horizon 4, Irdinmanhan (middle Eocene).

Description.—The M2 (V20264) is partly damaged and worn. The overall dental structure and size is consistent with the morphology and measurements of M2 of *Strenulagus solaris* from the Erenhot area (Fostowicz-Frelik et al. 2015a). The total tooth height is 4.24 mm and the dimensions of the crown are length 1.37 mm and width 2.5 mm. The occlusal surface is oval and almost totally obliterated, apart from the buccally situated remnants of the groove dividing the trigon from the hypoconal shelf.

The m1 (V20256.1) also shows morphology typical of this species (see Fostowicz-Frelik et al. 2015a: fig. 6). The total length of the occlusal surface is 1.93 mm. The crown is moderately high (crown height is 2.80 mm at 5.76 mm of the total tooth height) and the roots fused, displaying a common dental chamber (Fig. 7). The trigonid (1.86 mm in width) is elliptical and shorter than the talonid (1.43 mm in width),

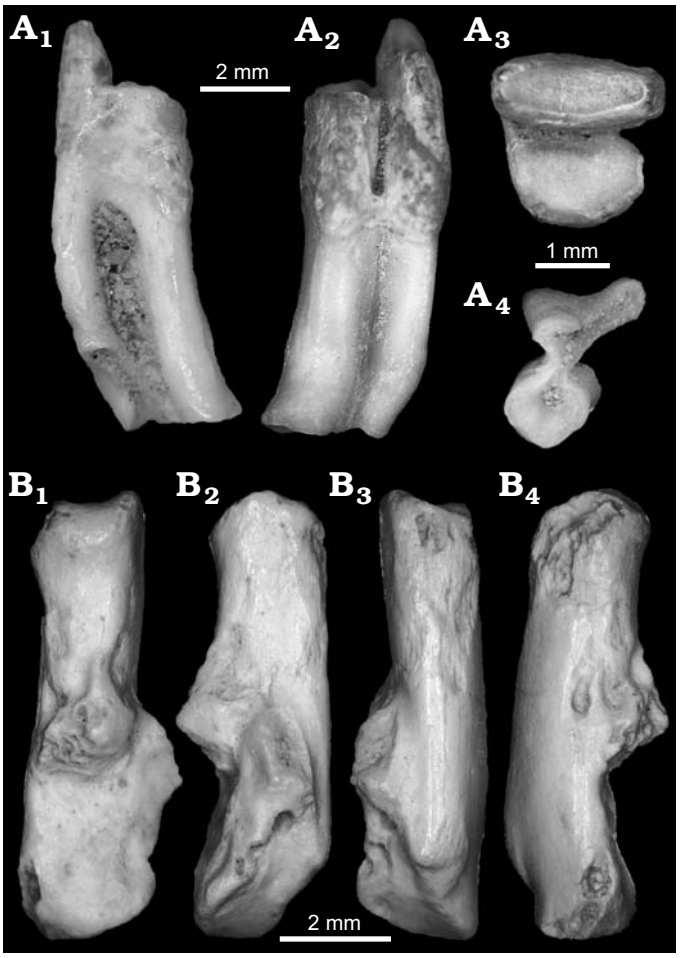

Fig. 7. Lagomorph *Strenulagus solaris* Lopatin and Averianov, 2006 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Right m1 (IVPP V20256.1) in lingual (A_1), buccal (A_2), occlusal (A_3), and apical (A_4) views. **B**. Left calcaneus (IVPP V20256.2) in dorsal (B_1), medial (B_2), plantar (B_3), and lateral (B_4) views.

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which is subrectangular in outline. The metaconid is sharp and higher than the protoconid. The occlusal surface of the talonid is much lower than that of the trigonid.

A right calcaneus (V20256.2) with a damaged sustentaculum tali was found together with the right m1 (V20256.1), and the same species attribution is presumed for the bone. The calcaneus total length is 8.1 mm, closely matching the size of the bones from the Irdin Manha Escarpment (Fostowicz-Frelik et al. 2015a: fig. 7, table 5) assigned to *Strenulagus solaris*. The bone is slender and the length of the calcaneal body (3.1 mm) is only slightly shorter than the tuber calcanei (3.9 mm). The ratio of the length of the calcaneal body to the length of the calcaneal tuber (0.80) resembles that of the specimen from the Irdin Manha Escarpment (0.75). Also, the length of the calcaneal eminence bearing the calcaneo-astragalar facet and the calcaneo-fibular facet is relatively short, again resembling the specimens from Irdin Manha. Both apertures of the calcaneal canal are well developed, similar to those of *Ochotona* (Bleefeld and Bock 2002) rather than those of leporids, in which they are much smaller (Fostowicz-Frelik 2007: fig. 12).

Stratigraphic and geographic range.—Middle Eocene, Khaychin Formation, Mongolia and Irdin Manha Formation, Nei Mongol, China.

Genus *Gobiolagus* Burke, 1941

Type species: *Gobiolagus tolmachovi* Burke, 1941; middle Eocene, Erden Obo, Nei Mongol, China.

Gobiolagus aliwusuensis Fostowicz-Frelik, Li, Meng, and Wang, 2012

Figs. 8–11.

Material.—Fragment of right maxilla with M1–M2 (IVPP V20262), fragment of left maxilla with M1–M2 (IVPP V20263.1), m2 in fragment of mandible (IVPP V20263.2), DI2 (IVPP V20265.1), Di2 (IVPP V20265.2), P3 (IVPP V20265.3), fragmentary P3 (IVPP V20265.4), fragmentary P4 (IVPP V20265.5–6), M1 (IVPP V20265.7), M2 juv. (IVPP V20265.8), M2 (IVPP V20265.9–10), M3 (IVPP V20265.11–12), p3 (IVPP V20265.13), p4 (IVPP V20261), m1 (IVPP V20265.14), m2 (IVPP V20265.15–16, IVPP V20257.3), m3 (IVPP V20265.17), humerus fragments (IVPP V20265.18–19), radius (IVPP V20265.20), ulna (IVPP V20265.21), right calcaneus (IVPP V20265.22), fragment of right calcaneus (IVPP V20265.23), fragment of right calcaneus (IVPP V20257.1), fragment of left calcaneus (IVPP V20257.2), fragment of left pelvic bone (IVPP V20265.24), proximal part of left metatarsus III (IVPP V20265.25), distal part of metatarsus III (IVPP V20257.4). All material from Wulanhuxiu, Erlian Basin, Nei Mongol, China, horizon 2, Sharamurunian (late middle Eocene).

Description.—*Gobiolagus* is by far the most abundant lagomorph at the Wulanhuxiu locality. The cranial elements are fragmentary; a specimen V20262 (Fig. 8) is a maxillary part showing the characteristic *Gobiolagus* morphology of having a lingually bent distal part of the tooth row (see Meng et al. 2005, Lopatin and Averianov 2006; Fostowicz-Frelik et al. 2012). The zygomatic process is well-defined with an anteriorly pointed masseteric spine. The jugal, detached from the specimen, shows a clear suture reaching far anteriorly beyond the anterior margin of the zygomatic process

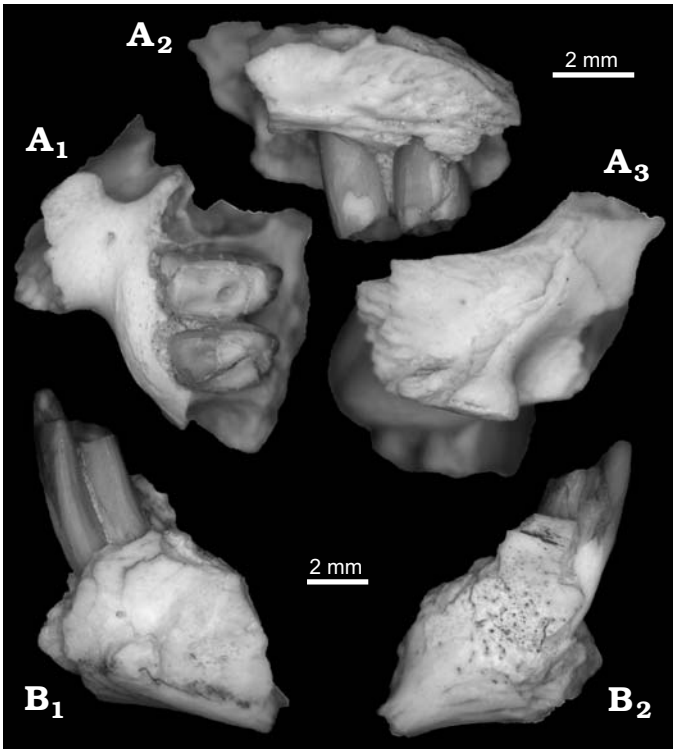

Fig. 8. Lagomorph *Gobiolagus aliwusuensis* Fostowicz-Frelik, Li, Meng, and Wang, 2012 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Fragment of the right maxilla with M1–M2 (IVPP V20262) in ventral (A_1), medial (A_2), and lateral (A_3) views. **B**. Left m2 in mandible fragment (IVPP V20263.2) in buccal (B_1, note the knob-like masseteric tubercle under the trigonid) and lingual (B_2) views.

Table 3. Measurements (in mm) of incisors and upper teeth of *Gobiolagus aliwusuensis*.

Locus	Collection number	Length	Width	Crown height	Total tooth height
DI2	V20265.1	1.70	1.84		
Di2	V20265.2	1.65	1.35		
P3	V20265.3	1.46	2.55	3.96	4.88
P3	V20265.4	1.32			
P4	V20265.5	1.64		3.99	5.53
P4 fragmentary	V20265.6	1.53		3.95	5.36
M1 fragmentary	V20265.7			4.59	
M1 associated	V20262	1.98	2.95		
M2 associated	V20262	2.27	2.83		
M1 associated	V20263	1.92	3.43		
M2 associated	V20263	1.89	3.36		
M2	V20265.8	2.04	3.12		
M2	V20265.9	1.96	3.69	4.37	5.06
M2	V20265.10	1.82	3.44		
M3	V20265.11	1.35	2.24	2.59	3.61
M3	V20265.12	1.28	2.28	2.47	3.66

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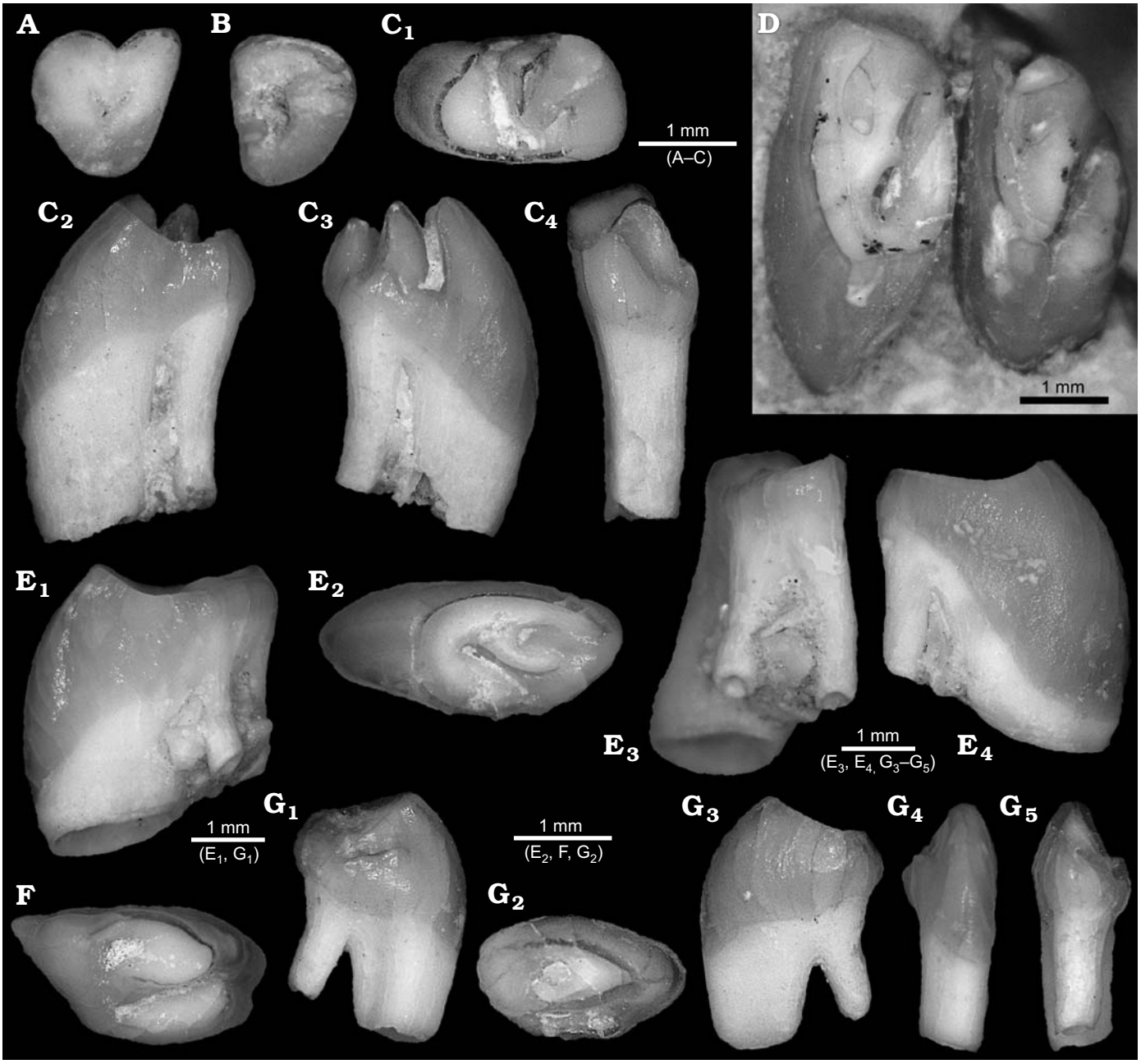

Fig. 9. Lagomorph *Gobiolagus aliwusuensis* Fostowicz-Frelik, Li, Meng, and Wang, 2012 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Cross section of the right DI2 (IVPP V20265.1). **B**. Cross section of the right di2 (IVPP V20265.1). **C**. Left P3 (IVPP V20265.3) in occlusal (C_1), posterior (C_2), anterior (C_3), and lingual (C_4) views. **D**. Associated left M1–M2 (IVPP V20263.1) in occlusal view. **E**. Left M2 (IVPP V20265.9) in posterior (E_1), occlusal (E_2), buccal (E_3), and anterior (E_4) views. **F**. Right juvenile M2 (IVPP V20265.8) in occlusal view. **G**. Right M3 (IVPP V20265.11) in posterior (G_1), occlusal (G_2), anterior (G_3), lingual (G_4), and buccal (G_5) views.

of the maxilla. The anterior margin of the zygomatic falls at mid-length of P4, while its distal margin is at the M1–M2 interseptum. The remains of the mandible are even more fragmentary; the specimen IVPP V20263.2 displays a knob-like masseteric tubercle under the trigonid of m2 (Fig. 8).

The dental remains of *Gobiolagus* found in Wulanhuxiu (Figs. 9, 10) closely resemble in morphology and size (Table 3) *G. aliwusuensis* from the Aliwusu locality in the Erden Obo area (Fostowicz-Frelik et al. 2012) in the western part of the Erlian Basin.

There are upper and lower incisors (dI2 and di2) present in this sample, tooth loci that has not been described previously for this species. The DI2 is typical of stem lagomorphs in having a heart-shaped cross-section (Fig. 9). However, the tooth is relatively longer (labiolingual measurement, see Table 3) than *Strenulagus* from the Irdin Manha Fm. (Fostowicz-Frelik et al. 2015a). The mesial lobe is narrower and protrudes slightly labially. The lower incisor is roughly triangular in cross-section and slightly longer than wide. The labial border is gently rounded, while the lingual one is

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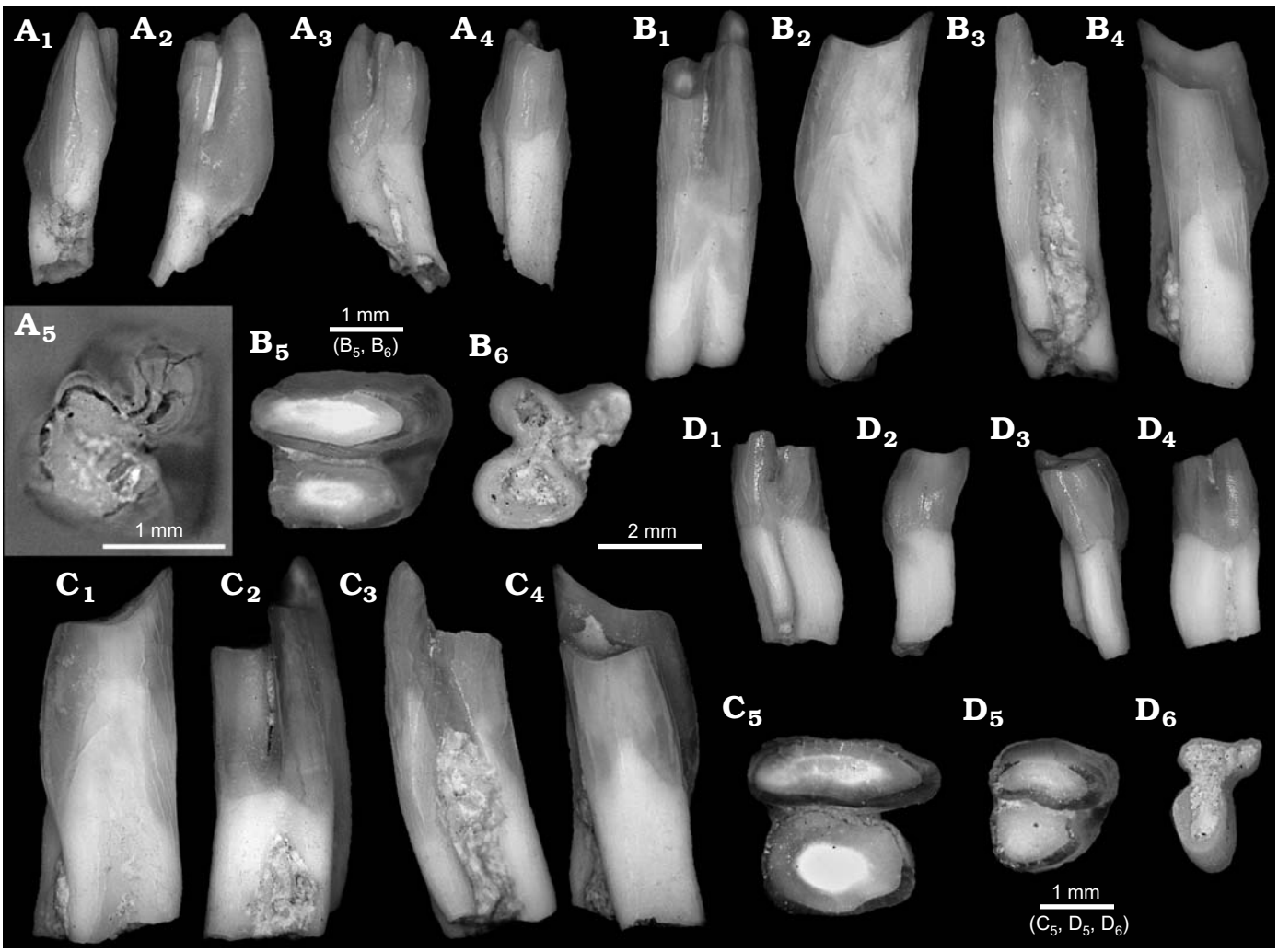

Fig. 10. Lower cheek dentition of the lagomorph *Gobiolagus aliwusuensis* Fostowicz-Frelik, Li, Meng, and Wang, 2012 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Right p3 (IVPP V20265.13) in anterior (A_1), buccal (A_2), lingual (A_3), posterior (A_4), and occlusal (A_5) views. **B**. Right m1 (IVPP V20265.14) in buccal (B_1), anterior (B_2), lingual (B_3), posterior (B_4), occlusal (B_5), and apical (B_6) views. **C**. Right m2 (IVPP V20265.16) in anterior (C_1), buccal (C_2), lingual (C_3), posterior (C_4), and occlusal (C_5) views. **D**. Right m3 (IVPP V20265.17) in lingual (D_1), anterior (D_2), posterior (D_3), buccal (D_4), occlusal (D_5), and apical (D_6) views.

straight. In both incisors the enamel layer is restricted to the labial side of the tooth.

The P3 is derived from a relatively young individual, thus the central and buccal lobes are almost unworn (Fig. 8). The buccal lobe is semicircular. The anterior margin of the P3 has a slight trace of a small additional cuspule which may appear in *Gobiolagus aliwusuensis*, but is unknown for other *Gobiolagus* species from Nei Mongol.

Two P4 are fragmentary but their occlusal surfaces indicate that there was a fully formed anteroloph and it was coalesced with the central lobe, thereby being more advanced than that of *Strenulagus*.

The M2 is represented by teeth at different stages of wear. The juvenile poorly worn specimen show a deep hypostria separating the trigon from talon. The trigon has a deep and round trigon basin in the center. The paracone is the highest cusp, but it is poorly defined and joined with protocone by the anterior loph (an anterior arm of the protocone–preprotocrista). The metacone is slightly smaller and placed more lingually, closer to the tooth center. The hypocone and the hypoconal shelf are placed more dorsally than the trigon, and these structures fail to protrude lingually more than the protocone. The hypoconal shelf is elongated and oval, and it is approximately as long as the "anterior loph" of the protocone. The M2 has two roots slightly asymmetrically placed on the shaft (distal root is more strongly attached to the shaft).

The M3 has one buccal root of roughly circular cross-section, clearly detached from the main shaft and slightly shorter than it. The trigon is well-developed, triangular and has a deeply excavated basin in the center (Fig. 9). The protocone is more prominent than the paracone or metacone, but is not well defined because of its strong anterior and posterior arms, which together define the trigon. The hypoconal shelf is much more reduced than in M2. It is strongly compressed mesiodistally and matches only about 40% of the total width of the trigon; its occlusal surface is not on the

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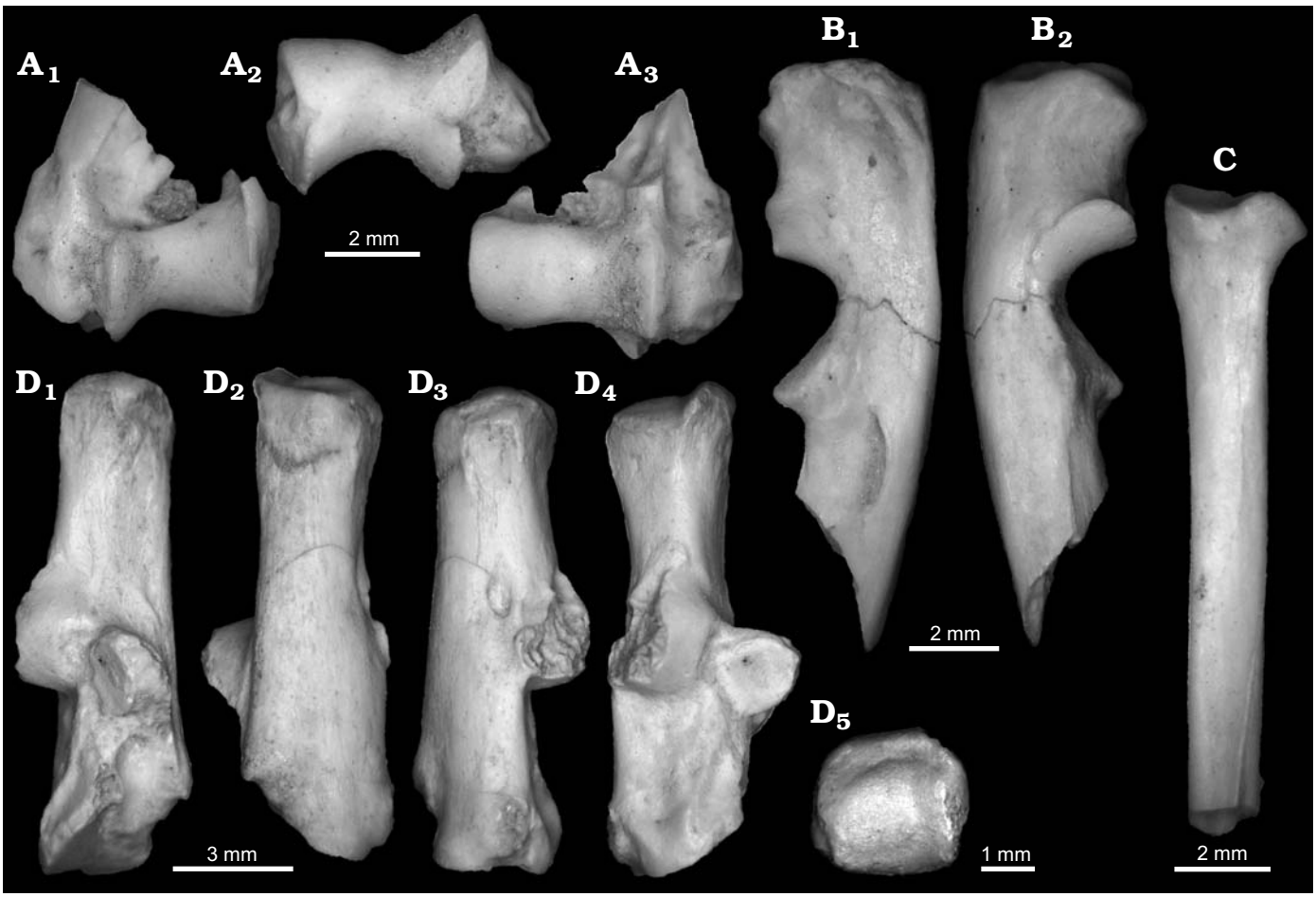

Fig. 11. Limb bones of the lagomorph *Gobiolagus aliwusuensis* Fostowicz-Frelik, Li, Meng, and Wang, 2012 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Distal part of left humerus (IVPP V20265.19) in ventral (A_2), cranial (A_1), and caudal (A_3) views. **B**. Proximal part of right ulna (IVPP V20265.21) in medial (B_1) and lateral (B_2) views. **C**. Proximal part of radius (IVPP V20265.20) in cranial view. **D**. Right calcaneus (IVPP V20265.22) in medial (D_1), plantar (D_2), lateral (D_3), dorsal (D_4), and caudal (D_5) views.

same plane as the occlusal surface of the trigon. The hypocone is placed more buccally than the protocone and is much weaker and smaller than it.

The p3 trigonid has two cusps of which the protoconid is larger and protrudes more anteriorly, while the metaconid is placed close to the talonid (entoconid). The entoconid and hypoconid form slightly higher eminences of the enamel rim enclosing the talonid basin. The entoconid is higher than the hypoconid. The hypoconulid is absent. The talonid basin at this early stage of development is filled with small dentine rugosities.

The lower dentition includes worn p4 with almost obliterated talonid and a large pear-shaped trigonid, the feature characteristic for the genus (Meng et al. 2005). The size and shape match *Gobiolagus aliwusuensis*, although none of the specimens from the Aliwusu sample is worn to such a degree (Fostowicz-Frelik et al. 2012).

The m1 and m2 are similar in structure. They differ subtly by the distal bending of the fused roots and in the size of the talonid, which is more rounded and larger in m2 (Table 4). The occlusal surface of the talonid is not joined to that of the trigonid until the buccal bridge is formed which is slightly later in ontogeny than in *Gobiolagus tolmachovi*.

The m3 is similar to but smaller than m2. The trigonid is compressed mesiodistally and the talonid longer and rounder (Fig. 10D_5), the roots are fully fused and have a joint root chamber (Fig. 10D_1–D_4, D_6). The talonid portion of the root is extended mesiodistally in comparison to its counterpart in m2, which is rounded (Fig. 10B_6, D_6).

Table 4. Measurements (in mm) of lower teeth of *Gobiolagus aliwusuensis*.

Locus	Collection number	Length	Trigonid width	Talonid width	Crown height	Total tooth height
p3	V20265.13	1.84	1.17	1.35	3.88	
p4	V20261	1.60	1.42	1.18		
m1	V20265.14	2.13	2.41	1.53	3.61	7.09
m2 juvenile	V20265.15	2.48	2.33	1.97		
m2	V20265.16	2.39	2.63	1.96	6.29	7.35
m3	V20265.17	1.71	1.50	1.26	2.43	4.15

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The postcranial elements were found associated with the dentition of *Gobiolagus aliwusuensis*, thus such attribution is the most plausible for these fragmentary remains.

The humerus fragments preserve the complete distal articular surface. The proximal extremity of the humerus is strongly weathered specimen. The head is rather short and relatively wide; it tapers slightly caudally, thus it is less round than in *Ochotona*. The overall morphology of the proximal extremity of the humerus resembles that of *Rhombomylus*, especially in dorsal view (see Meng et al. 2003: fig. 57A$_3$). The greater tubercle is low, similar to the condition in *Ochotona*. On the other hand, the lesser tubercle is slightly larger and thicker than in *Ochotona*. The distal extremity of the humerus is narrower than in *Ochotona* and closely resembles that of *Rhombomylus*. The medial epicondyle is large and prominent, although it is less extended medio-laterally and much thicker (craniocaudally) than in *Rhombomylus*, the latter feature being characteristic for lagomorphs. The trochlea is wide and generally larger and thicker than in *Rhombomylus*, with a prominent medial crista, which however does not protrude so strongly distally. The radial fossa is deep and large and the supratrochlear foramen is open and relatively large.

The proximal part of the radius (V20265.20) with a half of the shaft preserved, has a relatively wide head (width 3.3 mm, length 1.85 measured craniocaudally) and a thick neck. The articular circumference is weaker developed than in leporids and the whole head is flatter than in leporids, although the fovea is well developed.

The proximal part of the ulna (V20265.21) is well preserved with a large and slightly elongated (height 4.5 mm, width 4.0 mm) olecranon (Fig. 11). In general morphology it does not differ significantly from the bone of the European rabbit. The trochlear notch (incisura trochlearis) is well-developed, in lateral view, open about 80°, which is slightly less than in leporids. The lateral and medial coronoid processes are also well developed and unreduced.

The calcaneus of *Gobiolagus* closely resembles that of *Strenulagus*, but the bone is larger (length 12.4 mm). The length of the tuber is 5.8 mm and the length of the body, 4.9 mm, yielding a slightly shorter tuber in relation to the body than in known *Strenulagus* specimens (Fostowicz-Frelik et al. 2015a), although the difference is not significant. The calcaneal eminence seems to be more robust and slightly longer than in *Strenulagus*, but the most important difference in the morphology of the calcaneus is the diameter of the calcaneal canal, which is very large in *Gobiolagus* (Fig. 11D), larger than in any other Eocene lagomorph.

Stratigraphic and geographic range.—Middle Eocene, ?Irdinmanhan to Sharamurunian, Nei Mongol, China.

Order Rodentia Bowdich, 1821

Family Ischyromyidae Alston, 1876

Genus *Asiomys* Qi, 1987

Type species: *Asiomys dawsoni* Qi, 1987; middle Eocene, Irdin Manha area, Nei Mongol, China.

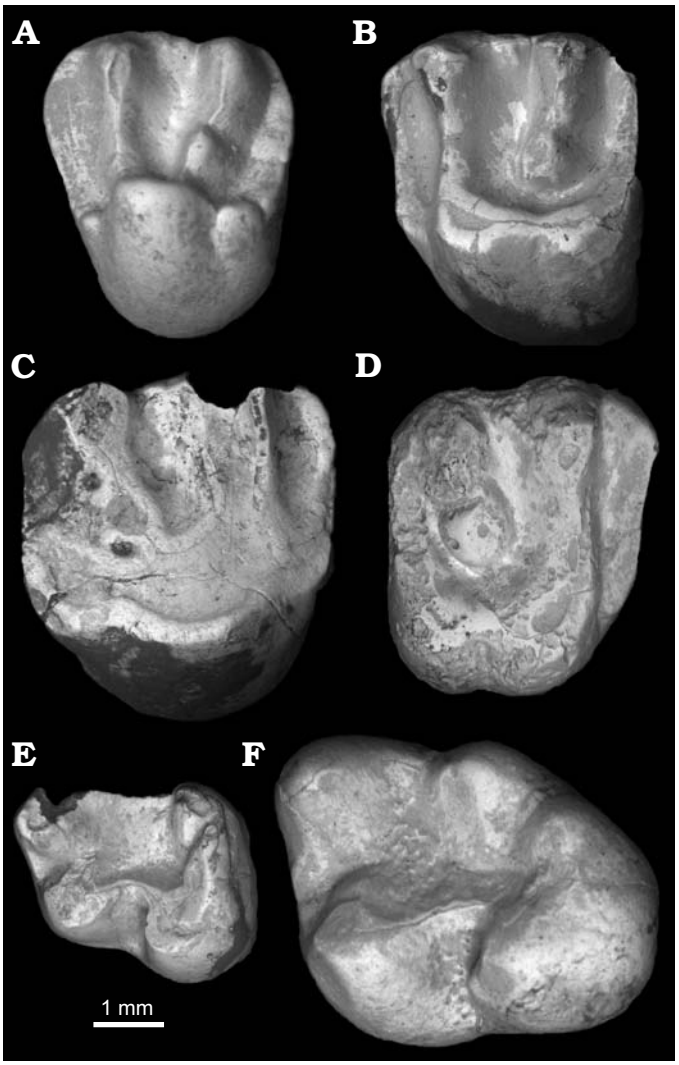

Fig. 12. Ischyromyid rodent *Asiomys dawsoni* Qi, 1987 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Left P4 (IVPP V20828.1). **B**. Left M1 (IVPP V20828.2). **C**. Right M1 (IVPP V20828.4). **D**. Right M2 (IVPP V20828.5). **E**. Left dp4 (IVPP V20828.6). **F**. Left m3 (IVPP V20828.7). All in occlusal view.

Asiomys dawsoni Qi, 1987

Fig. 12.

Material.—Left P4 (V20828.1), left M1 (V20828.2–3), right M1 (V20828.4), right M2 (V20828.5), left dp4 (V20828.6), left m3 (V20828.7) from Wulanhuxiu, Erlian Basin, Nei Mongol, China, middle and upper part of horizon 4, middle Eocene.

Description.—P4 (Fig. 12A) lacks the hypocone, but has a prominent protocone. On M1 (Fig. 12B, C) and M2 (Fig. 12D) the four main cusps are prominent, the crests are low, and the paracone and metacone are subequal in size and widely separated from one another. The hypocone is less-developed, being smaller than the protocone. The protoloph is complete, and the metaloph is weaker than the protoloph. The metaconule is large and V20828.5 has two metaconules (Fig. 12D). The anterior and posterior cingula

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Table 5. Measurements (in mm) of cheek teeth of *Asiomys dawsoni*.

Locus	Collection number	Length	Width
P4	V20828.1	3.60	4.40
M1	V20828.2	3.80	4.50
M1	V20828.3	3.90	4.40
M1	V20828.4	3.90	4.60
M2	V20828.5	4.50	5.00
dp4	V20828.6	3.50	2.90
m3	V20828.7	5.50	4.50

on M1 and M2 are prominent, and the entoloph is distinct. The sinus is shallow.

The trigonid of dp4 is narrower than the talonid. In dp4 (Fig. 12E) the metaconid is close to the protoconid and is slightly anteriorly placed, the entoconid is separated from the hypoconulid by a notch, the distinct hypoconulid extends transversely along the posterior margin of the tooth, and the short hypolophid extends from the entoconid. The m3 (Fig. 12F) has a weak hypoconulid, and a short hypolophid. The protocristid on m3 is absent, so that the trigonid basin is open posteriorly.

Asiomys dawsoni was first described by Qi (1987) based on three teeth from the Irdin Manha area. Li and Meng (2013) reported many specimens of *Asiomys* from the Irdin Manha Formation of the Huheboerhe area, which adds substantially to our knowledge of this ischyromyid. The new specimens from Wulanhuxiu show several diagnostic features, including the absence of a hypocone on P4, the presence of a small hypocone on M1–M2, a complete protoloph, an enlarged (or dual) metaconule on M1–M2, and a short hypolophid on dp4 and m3. All of these features identify these specimens as *Asiomys dawsoni*. The size of the new specimens also falls within the range of variation of *A. dawsoni* (Li and Meng, 2013) (see Table 5).

Stratigraphic and geographic range.—Middle Eocene, Irdinmanhan, Nei Mongol, China.

Superfamily Ctenodactyloidea Simpson, 1945

Family Gobiomyidae Wang, 2001

Genus *Gobiomys* Wang, 2001

Type species: *Gobiomys neimongolensis* (Meng, Ye, and Huang, 1999); middle Eocene (Sharamurunian), Bayan Ulan, Nei Mongol, China.

Gobiomys exiguus Wang, 2001

Fig. 13.

Material.—Right M2 (V20827.1), right M3 (V20827.2), left lower jaw with m1 (V20827.3), right m2 (V20827.4) from Wulanhuxiu, Erlian Basin, Nei Mongol, China, upper and middle part of horizon 2, middle Eocene.

Description.—The M2 is square (length 1.50 mm, width 1.50 mm) in crown outline (Fig. 13A). The protocone, paracone, and metacone are all well-developed. A distinct hypocone is present but smaller than the protocone. The metaconule is subequal and anterolingual to the metacone. The protoloph is complete and the protoconule is absent. A weak metaloph extends from the metacone to the metaconule, whereas the metaconule and protocone are isolated from one another. The anterior cingulum is well developed and reaches the protoloph lingually. The entoloph is absent.

M3 (length 1.60 mm, width 1.50 mm) has a rounded triangular outline in occlusal view (Fig. 13B). The metacone is reduced, and the hypocone is slightly buccally displaced and smaller than that of M2. The metaconule is absent and the well-developed metaloph extends to the protocone. The anterior and posterior cingula are distinct.

The m1 (length 1.30 mm, width 1.20 mm) is oval in occlusal view, with wider posterior side (Fig. 13C). The m2 (length 1.80 mm, width 1.60 mm) is larger than m1 (Fig. 13D). The protoconid and metaconid of m1 and m2 are prominent and connected by a low but complete preprotocristid. The protoconid and hypoconid are larger than the two lingual cuspids. The postprotocristid is short and extends rather posteriorly. In m1 and m2 a distinct hypoconulid is situated at the mid-point of the posterior margin of the talonid. The hypolophid of m1 and m2 is absent. The ectolophid is complete and located buccally with respect to the middle longitudinal line.

Gobiomys was described by Wang (2001), and includes three species, *G. neimongolensis*, *G. exiguus*, and *G. asiaticus*. The new specimen differs from *G. neimongolensis* in being smaller, in having a weaker metaloph on M2, and a more buccally located ectolophid on m1. In *G. asiaticus* the lower molars have a complete arm of the entoconid reaching to the hypoconid, but in the new specimens the hypolophid of m1–m2 is absent. Moreover, *G. asiaticus* differs from the new specimen in having wider and shorter upper molars. The new specimen shares the following features

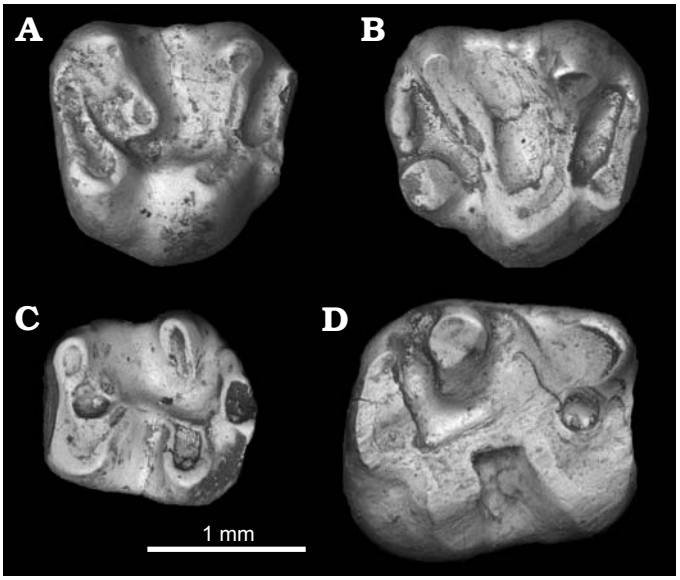

Fig. 13. Ctenodactyloid rodent *Gobiomys exiguus* Wang, 2001 from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Right M2 (IVPP V20827.1). **B**. Right M3 (IVPP V20827.2). **C**. Left m1 (IVPP V20827.3). **D**. Right m2 (IVPP V20827.4). All in occlusal view.

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with *G. exiguus*: small size, absence of protoconule, distinct metaconule and short metaloph on M2, and the absence of the lingual part of the postprotocristid and of entoconid arm on the lower molars. Compared to the holotype of *G. exiguus*, the specimens reported here are slightly larger.

Stratigraphic and geographic range.—Middle Eocene, Nei Mongol, China.

Family Yuomyidae Dawson, Li, and Qi, 1984

Genus *Yuomys* Li, 1975

Type species: *Yuomys cavioides* Li, 1975; middle Eocene, Rencun, Mianchi, Henan, China.

Yuomys sp.

Fig. 14.

Material.—Fragmentary right maxilla with M1 (V20829.1), fragmentary right mandible with m2–m3 (V20829.2) from Wulanhuxiu, Erlian Basin, Nei Mongol, China, upper part of horizon 4, middle Eocene.

Description.—The M1 (length 3.00 mm, width 3.50 mm; Fig. 14A) has a well-developed hypocone and metaloph directed toward but never in contact with the protocone. On M1 there is no paraconule, but the metaconule is distinct, being larger than the metacone. On m2–m3 (m2, length 2.90 mm, width 2.50 mm; m3, length 3.70 mm, width 2.80 mm; Fig. 14B) the postprotocristid is short, the trigonid basin is open posteriorly, and the transverse hypolophid extends to the complete ectolophid. All these features are similar to those of *Yuomys*.

Compared to *Yuomys cavioides* (Li, 1975), the new specimens from Wulanhuxiu are smaller, have a weaker postprotocristid, and lack a conule on the hypolophid on m2–m3. The new specimens differ from *Y. eleganes* (Wang, 1978) in being smaller, and having a short anterior cingulum on M1 and with the metaconid located no farther anteriorly than the protoconid on m2–m3. Differences from *Y. weijingensis* (Ye, 1983) include weaker parastyle and metaloph on M1, and lack of mesostylid and conule on the hypolophid. *Y. yunnanensis* (Huang and Zhang, 1990) differs from the new specimens in larger size, and longer postprotocristid that contacts the base of the metaconid on m2. Differences from *Y. huangzhuangensis* (Shi, 1989) are: smaller size and smaller ratio of length to width of M1 (length/width 0.86 in new specimens, 1.07 in *Y. huangzhuangensis*).

In general, the new specimens have morphologically simpler teeth that lack a mesoconid on m2–m3, a mesostylid and a conule on the hypolophid. Among all the known species, the new specimens are most similar to *Y. huheboerhensis* from the Irdin Manha Formation of the Huheboerhe section, Erlian Basin (Li and Meng 2015) morphologically, but *Y. huheboerhensis* is smaller than the new specimens, and its M1 and M2 are both approximately as long as wide in occlusal view, and sometimes m3 has an ectomesolophid.

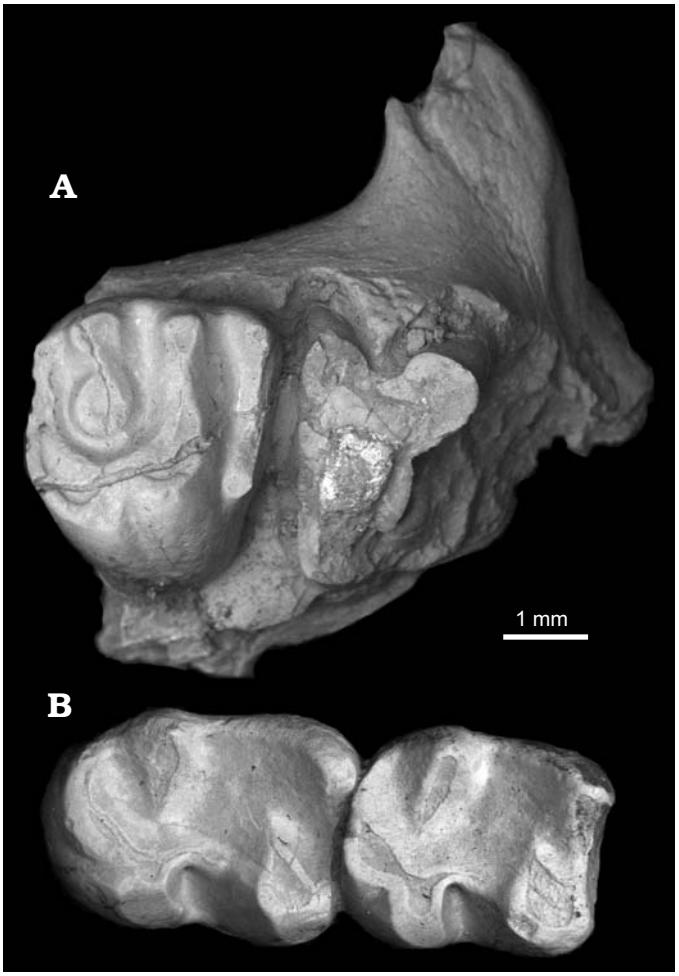

Fig. 14. Ctenodactyloid rodent *Yuomys* sp. from the Eocene of Wulanhuxiu, Nei Mongol, China. **A**. Right maxilla with M1 (IVPP V20829.1). **B**. Right mandible with m2–m3 (IVPP V20829.2). All in occlusal view.

Discussion and concluding remarks

The Wulanhuxiu stratigraphic section is considered to belong to the Ulan Shireh Formation (Wang et al. 2012), which is usually regarded as correlative with the Irdin Manha Formation in the eastern part of the Erlian Basin (Granger and Gregory 1934; Burke 1941; Radinsky 1964). The most recent review of the Ulan Shireh fauna was conducted by Ye (1983), who also proposed an Irdinmanhan age for the Ulan Shireh fauna.

The Wulanhuxiu section shows a dual character; the lower interval (horizon 4) contains a typical Irdinmanhan fauna, while the higher and thicker interval (horizon 2) contains more derived Glires taxa (e.g., *Gobiolagus* and *Gobiomys*) that are typical of younger temporal intervals, chiefly the Sharamurunian (Wang 2001; Meng et al. 2005; Fostowicz-Frelik et al. 2012). The intermediate interval (horizon 3) lacks fossils entirely, which seems to reflect a relatively short period of changed sedimentary conditions.

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The Irdinmanhan fauna of horizon 4 contains a typical assemblage of perissodactyls including deperetellids, lophialetids, *Breviodon*, and *Rhodopagus* (Table 1). Furthermore, this horizon yields small lagomorphs such as *Erenlagus* and *Strenulagus* that are also known from Irdinmanhan strata at Huheboerhe (Fostowicz-Frelik and Li 2014; Fostowicz-Frelik et al. 2015b). Also present are the rodents *Asiomys* and *Yuomys*, which are typical of Irdinmanhan assemblages from the eastern part of the Erlian Basin (Li and Meng 2015; Li 2016). Moreover, horizon 4 has produced some taxa pertaining to basal clades situated within or slightly outside Glires. These include the mimotonids *Gomphos* and *Mimolagus*, the latter of which is unknown from rocks of pre-Irdinmanhan age (Bohlin 1951; Fostowicz-Frelik et al. 2015a), and an anagalid, a rare faunal element in post-Paleocene sites in China. The only other record of Anagalidae in Nei Mongol is *Anagale gobiensis* from the lower part of the Ulan Gochu Formation at Twin Oboes (Simpson 1931).

In general, the fauna of horizon 4, which is dominated by perissodactyls and Glires, agrees in content with the Irdinmanhan mammal assemblage from the eastern part of the Erlian Basin as typified at such localities as Huheboerhe or the Irdin Manha Escarpment (Wang et al. 2010; Fostowicz-Frelik and Li 2014; Fostowicz-Frelik et al. 2015a, b; Li and Meng 2015; Li 2016). However, there are some faunal differences which could reflect either regional paleoenvironmental differences or a slightly later age for horizon 4, compared to the fossil rich IM-1 layer of the typical Irdin Manha Formation (see Wang et al. 2010).

The newly described *Gomphos progressus* shows some distinctive, advanced characters reflecting the simplification of its dental structure, alonside other features that imply descent from *Gomphos shevyrevae*. Similarly, *Yuomys* sp. from Wulanhuxiu also shows a more simplified (derived) occlusal pattern than either *Y. cavioides* and *Y. weijingensis*. The occlusal pattern of the Wulanhuxiu *Yuomys* is most similar to the smaller species *Y. huheboerhensis*. Nevertheless, the general trend towards simplification of the occlusal pattern in Glires and particularly in rodents, which commenced at the beginning of the Eocene in Asia and involved a reduction of different cusps (conules, etc.) and favored formation of ridges (Meng and McKenna 1998), continued in the middle Eocene. In that light the dental morphology of Glires from horizon 4 seems more derived than that of Glires from comparable Irdinmanhan beds in the eastern part of the Erlian Basin, suggesting a slightly younger age for the Wulanhuxiu assemblage. Horizon 4 may then represent either the latest phase of the early Irdinmanhan (IM-1) or even pertain to the late Irdinmanhan (IM-2). However, IM-2 is poorly defined in faunal terms in the eastern part of the Erlian Basin, being distinguished only by *Lophialetes expeditus* and *Protitan* (Wang et al. 2010). Notably, the latter taxon remains unknown from Wulanhuxiu.

The presence of *Schlosseria* in horizon 4 at Wulanhuxiu (as well as in deposits of Ulan Shireh), a genus otherwise considered to be characteristic of the Arshantan, is hard to explain. *Schlosseria* was initially interpreted as a possible admixture from underlying layers (Wang et al. 2012), but may be also an Arshantan relic. Ye (1983) stated that the Ulan Shireh fossil assemblage was more similar to the Arshanto faunas than to Shara Murun faunas, a conclusion with which we concur in the case of layer 4. Wang et al. (2012) pointed to a possible correlation between the upper part of the Ulan Shireh Formation and the Tukhum Formation. However, the latter is still poorly understood and has yielded only scarce fossil material (see Russell and Zhai 1987).

Horizon 2 contains abundant remains of *Gobiolagus aliwusuensis* known also from the Irdinmanhan to Sharamurunian "Lower red" beds of Erden Obo (Fostowicz-Frelik et al. 2012). None of the typically Irdinmanhan localities in the eastern part of the Erlian Basin has yielded *Gobiolagus*, whereas this genus is quite abundant in the Sharamurunian strata of Nei Mongol (Meng et al. 2005). Horizon 2 also yielded remains of *Gobiomys exiguus*, a rodent species typical of post-Irdinmanhan deposits (Wang 2001). This species has been recorded from the "Lower White" beds of Erden Obo and east of the railway station of Erenhot, Houldjin Formation. Wang (2001) suggested that the "Lower White" beds represented the upper part of the Shara Murun Formation. The age of the Houldjin Formation was subsequently estimated as most probably late Eocene (Wang et al. 2009), although Wang (2001) suggested that some taxa from the Houldjin Formation might be middle Eocene admixtures from underlying deposits.

On a broader scale, the mammal assemblage from Wulanhuxiu (and especially from the older horizon 4), is most similar to the fossil fauna from Khaychin-Ula II of the Western Gobi Desert of Mongolia, particularly in the composition of the perissodactyl and artiodactyl faunas (Badamgarav and Reshetov 1985: table 4) and the presence of *Strenulagus solaris* in all these localities (see Fostowicz-Frelik et al. 2015a and references therein). The tapiroid *Teleolophus*, recorded from both Khaychin-Ula III and horizon 2 at Wulanhuxiu suggests that the former locality may be somewhat younger than Khaychin-Ula II. Badamgarav and Reshetov (1985: table 5) correlated Khaychin-Ula II, III, and V collectively with Ulan Shireh. Furthermore, the presence of *Lophialetes*, *Yuomys*, and *Gobiolagus* (and possibly *Shamolagus*, known from "Chimney Butte") suggests that Wulanhuxiu (especially horizon 2) is close in age to the middle Eocene Mergen and Tsagan Tsav localities of the Eastern Gobi Desert in Mongolia (see Dashzeveg and Meng 1998).

The Wulanhuxiu section and its fossil fauna provide some clues to biotic changes occurring at the end of the middle Eocene in the western part of the Erlian Basin (Nei Mongol, China). There is a definite change in the faunal content between the older (horizon 4) assemblage at Wulanhuxiu and the younger (horizon 2) assemblage (see Table 1), manifested by a marked decrease in biodiversity. For example, the perissodactyl fauna of horizon 4 is quite diverse and typically Irdinmanhan (Wang et al. 2010, 2012), whereas in layer 2 the only perissodactyl present is *Teleolophus*, which

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has a wider (middle Eocene to early Oligocene) stratigraphic range (Tong and Lei 1984; Wang 2007).

More importantly, all but one species belonging to groups classified as paleoplacentals by Lucas (2001), such as pantodonts, anagalids, and mimotonids, appear to have gone at least locally extinct sometime after this horizon was deposited. They are not present in the assemblage from horizon 2, which yielded more derived ("neoplacental") species belonging to taxa such as the speciose stem-lagomorph *Gobiolagus* (Meng et al. 2005; Fostowicz-Frelik et al. 2012) and the rodent *Gobiomys*. *Gobiolagus* in particular was a successful and abundant genus, its prevalence contrasting with the sparser fossil record of Lagomorpha from typical Irdinmanhan deposits (e.g., Fostowicz-Frelik and Li 2014). *Gobiolagus* is larger and more derived than Irdinmanhan lagomorphs with regard to dental hypsodonty and root fusion, and its concentration in some field samples indicates quite high abundance. The presence of such an advanced lagomorph suggests an environmental shift from the typical post-PETM forest dominated habitat of the Irdinmanhan towards the drier and probably more open environment of the Sharamurunian.

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