

# 内蒙古额尔登敖包中始新世戈壁兔 (哺乳纲:兔形目)新材料<sup>1)</sup>

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**摘要:**描述了来自内蒙古二连盆地的戈壁兔新材料,并命名了一个戈壁兔新种 *Gobiolagus aliwusuensis* sp. nov.。化石产于额尔登敖包剖面中阿里乌苏地点,传统地层划分中的下红层,时代约为中始新世。该种具有中等个体,P3 主尖前壁具有小的附尖,P4 颊侧有两个明显的尖。这些化石材料保存了戈壁兔材料中仅有的完整上齿列,其中的 P2 和 M3 形态是首次报道,为了解亚洲早期兔形类的演化增加了新的信息。

**关键词:**内蒙古,始新世,兔形类干群,戈壁兔属,牙齿形态,进化

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## NEW *Gobiolagus* (MAMMALIA: LAGOMORPHA) MATERIAL FROM THE MIDDLE EOCENE OF ERDEN OBO (NEI MONGOL, CHINA)

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**Abstract** A new species of *Gobiolagus* (Lagomorpha: Palaeolagidae) from the Middle Eocene locality of Aliwusu (Erlian Basin, Nei Mongol, China) is described. *Gobiolagus aliwusuensis* sp. nov. is characterized by its medium size, accessory cusp on the anterior wall of P3 central lobe and by two distinct buccal cusps on P4. The material from Aliwusu constitutes the only record of *Gobiolagus* with complete upper dental rows, which contain previously unknown P2 and M3. This discovery adds new data on the morphology and diversification of Middle Eocene lagomorph fauna in Central Asia.

**Key words** Nei Mongol, Eocene, stem lagomorphs, *Gobiolagus*, dental morphology, evolution

### 1 Introduction

The Asian record of Lagomorpha, a group of duplicidentate Glires (Meng and Wyss,

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2001), dates back to the Early Eocene (Averianov and Lopatin, 2005; Li et al., 2007; Lopatin and Averianov, 2008; Rose et al., 2008). The earliest fossil remains referred to Lagomorpha come from China (Nei Mongol), India (Gujarat), Kyrgyzstan (Batken), and Mongolia (Ömnögovı). The fossil record from China is most abundant and complete, while the Indian specimens consist only of ankle bones, which, although undoubtedly lagomorph-like in morphology (Rose et al., 2008), cannot be attributed with certainty to any currently known lagomorph family.

There are six lagomorph genera known from the late Early and Middle Eocene of China. These are *Dawsonolagus*, *Desmatolagus*, *Gobiolagus*, *Hypsimylus*, *Lushilagus*, and *Shamolagus* (Meng et al., 2005; Li et al., 2007). Among them, *Dawsonolagus* exhibits the most primitive character array for the group and is known from the most complete material (Li et al., 2007). *Gobiolagus*, with six currently recognized species, is still one of the earliest lagomorphs appearing in the early Middle Eocene of Central Asia, but it is generally rare and not very numerous.

The new material described herein, adds important data on the dental morphology of *Gobiolagus*, because it includes some complete dental rows, with unknown so far P2 and M3. Furthermore, many of specimens express only light wear, thus giving an insight into the early stages of dental development, unknown from the previously studied samples (see Meng et al., 2005). Finally, the presence of a new species of *Gobiolagus* in the Middle Eocene of Erden Obo (Urdyn Obo), Nei Mongol, points to higher than previously thought, diversity of this early Asian lagomorph genus.

## 2 Material and methods

The newly described specimens (housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing) were collected during the IVPP field expedition in 2008. Measurements were taken with a Sylvac digital caliper to 0.01 mm accuracy for teeth and 0.1 mm for maxillary and mandibular remains. Dental measurements (Tables 1 and 2) reflect the dimensions of the upper crown. Length (L) is the antero-distal dimension of the occlusal surface, while width (W) was measured between the buccalmost part of the crown and the lingual edge of the tooth at the same level (in stronger worn specimens both points mark the edge of the occlusal surface). The relative height of the crown discussed in the text was referred to the maximum vertical extension of the enamel layer (at the lingual or antero-lingual side) and the total crown-to-root height of the tooth.

All comparative material was measured in this manner, apart from *Gobiolagus lii* (the holotype and only specimen) and *Gobiolagus major* (specimens IVPP V 14134 and V 14135), where measurements are after Zhang et al. (2001) and Meng and Hu (2004), respectively. Dental terminology is descriptive and follows Wood (1940) and Meng et al. (2005).

For the photographs, a Nikon Digital Sight DS-Fi1 camera attached to Nikon SMZ-U binocular microscope was used to acquire a Z-stack, which was then merged into a single image using Helicon Focus 5.1 (for Windows) software.

**Institutional abbreviation** AMNH, American Museum of Natural History, New York, USA.

## 3 Geological settings

Lagomorph specimens were collected from the “Lower Red” beds of Osborn (1929; see also Qi, 1990; Fig. 1). Osborn considered the “Middle Red” beds as a part of the Ulan Gochu Formation and the “Lower Red” beds as either the Ulan Gochu Formation or Shara Murun Formation. From the base of the “Middle Red” beds the holotype of *Embolotherium grangeri*

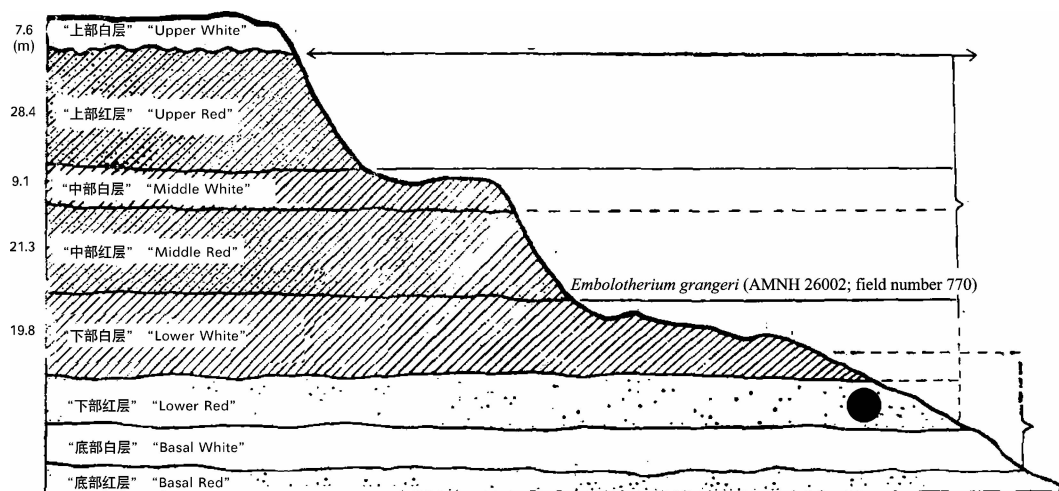


Fig. 1 The section of Erden Obo (Urtyn Obo), Erlian Basin, Nei Mongol, China

The sketch section was modified from Qi (1990), which is originally from Osborn (1929). The black dot indicates the occurrence of the lagomorph specimens reported in this work

(AMNH 26002; field number 770) was collected. The lithological division and correlation of the beds in Osborn (1929) have long been a matter of uncertainty (Jiang, 1983; Russell and Zhai, 1987; Qi, 1990; Wang, 2003), and a systematic treatment of the stratigraphy of the Erden Obo (Urtyn Obo) section is under way. For the present, we still use the term "Lower Red" of Osborn (1929), but we note that the lithological assignment and age estimate are different from those suggested by Osborn.

The preliminary study of the Erden Obo area points to the Middle Eocene age of the "Lower Red" beds. The fauna associated with the lagomorphs described here include rodents, *Yuomys* and *Gobiomys*, and perissodactyls, such as *Teilhardia pretiosa*, *Caenolophus promissus*, and *Triplopus progressus*. The underlying upper part of the "Basal White" beds yielded remains of two perissodactyls, *Triplopus proficiens* and *Pappaceras confluens*, and a rodent *Asiomys*, whereas from the overlying "Lower White", a perissodactyl, *Amynodontopsis*? and a rodent *Yuomys* were recovered. These mammal taxa indicate that the "Lower Red" is most likely Middle Eocene in age, ranging from the Irdinmanhan to Sharamurunian.

Although all lagomorph specimens reported here derive from the "Lower Red" beds, they have slightly different position within the strata. Specimens with numbers IVPP V 18501 – 18508 come from the lower part (site 1) of the "Lower Red" beds, whereas those numbered V 18500, 18509 – 18530 are from the slightly higher middle part (site 2) of the "Lower Red" beds.

#### 4 Systematic paleontology

##### Lagomorpha Brandt, 1855

##### Palaeolagidae Dice, 1929

##### *Gobiolagus* Burke, 1941

##### *Gobiolagus aliwusuensis* sp. nov.

(Figs. 2-6)

**Holotype** Right maxilla with P3-M3 (IVPP V 18500) (Fig. 2).

**Referred specimens** Fragmentary right maxilla with P3-M2 (IVPP V 18501), fragmentary right maxilla with P2-M1 (V 18502), fragmentary left maxilla with P3-M2 and root of M3

(V 18503), fragmentary, strongly eroded, right maxilla with P3-M3 (V 18504), fragmentary right mandible with p4-m3 (V 18505), fragmentary right mandible with p4-m2 (V 18506), fragmentary left mandible with p4-m3 (V 18507), fragmentary left mandible with m2 (V 18508), fragmentary right maxilla with P3-M3 and anterior root of zygoma (V 18509), fragmentary left maxilla with P3-M3 and anterior root of zygoma (V 18510), fragmentary left juvenile maxilla with remains of the root of P2, DP3, DP4 and M1-M2 (V 18511.1) associated with fragmentary left mandible with roots of dp3, dp4, and m1-m3 (V 18511.2), fragmentary right maxilla with P3-M3 and anterior root of zygoma (V 18512), fragmentary right maxilla with P4-M2 (V 18513), fragmentary left maxilla with P3-M2 (V 18514), fragmentary right maxilla with P3-M2 (V 18515), fragmentary left maxilla with P4-M2 (V 18516), fragmentary right mandible with p3-m3 and most of diastema preserved (V 18517), fragmentary right mandible with p3-m3 (V 18518), fragmentary right mandible with p3-m1 (V 18519), fragmentary right mandible with p4-m3, part of diastema and lower incisor preserved (V 18520), fragmentary left mandible with p4-m3 (V 18521), fragmentary left mandible with p4-m2 (V 18522), fragmentary right mandible with p4-m3 (V 18523), fragmentary left mandible with p4-m3 (V 18524), fragmentary right mandible with lower incisor (di2), fragment of p3, root of p4, and m1 (V 18525), fragmentary right mandible with partly preserved lower incisor (di2) and p3-p4 (V 18526), fragmentary left mandible with roots of p3-p4 (V 18527), fragment of the diastema of the right mandible with partly preserved lower incisor (V 18528), fragmentary right mandible with m2-m3 (V 18529), a fragment of isolated molar (V 18530).

**Etymology** The specific name is derived from Aliwusu, the type locality of the species.

**Locality and horizon** Aliwusu, Naomugeng, Siziwang Qi, Nei Mongol, China (Meng et al., 2007:fig. 1), “Lower Red” beds of Osborn (1929). The age is Middle Eocene, probably Irdinmanhan to Sharamurian.

**Diagnosis** Medium size *Gobiolagus*, smaller than *G. major* but larger than *G. burkei*, *G. hekkeri*, and *G. lii*. From all species of *Gobiolagus* it differs in an accessory cusp on the anterior wall of the central lobe of P3, which merges at more advanced dental stages with anteroloph. From *G. tolmachovi* it differs in less persistent paraflexia on P3 and distinct antero-buccal cusp on P4 separated from the buccal lobe. From *G. lii* it differs in lack of the premolar foramen. From *G. andrewsi* it differs in lower mandible body and proportionally wider p3 with a shorter trigonid. From *G. burkei*, apart from the markedly larger size, it differs in stronger pronounced pear-shaped p4 trigonid, more reduced p4 talonid and longer talonids of m1 and m2.

**Description and comparisons** Material consists of fragmentary maxillae (Figs. 2-5) and mandibles (Fig. 6) with partly preserved dentition. Most specimens are permanent dentition but some deciduous teeth are preserved in the associated maxilla-mandible pair (V 18511.1-2, Fig. 5). The material represents all dental loci, apart from the upper incisors (DI2 and I3), and a range of dental stages, from lightly to very strongly worn teeth, thus covering juvenile to mature ontogenetic stages (measurements in Table 1, 2).

The dental row is arched and a portion housing the molars (especially M2-M3) is directed postero-lingually (Figs. 2B, 3A,B, 4C,I, 5A). This feature was considered to be a generic character for *Gobiolagus* (Lopatin and Averianov, 2006), although the degree of the postero-lingual flexion is variable within the genus, from fairly well bent in *G. tolmachovi* and *G. lii* to relatively weakly bent in *G. major* (compare Zhang et al., 2001:fig. 1; Meng and Hu, 2004:fig. 1E; Meng et al., 2005:fig. 4.1). Such condition is different from that in *Strenulagus*, which has rather a straight course of the dental row (Tong, 1997; Lopatin and Averianov, 2006). On the other hand, it resembles the maxillary architecture of *Dawsonolagus* (Li et al., 2007:fig. 1C, D), where the postero-lingual bending of the tooth row is very well expressed. The dental row in *Lushilagus* and *Shamolagus* is evenly arched along the whole length (Li, 1965:pl. 1, figs. 1-3), however, to a lesser extent than in *Gobiolagus*.

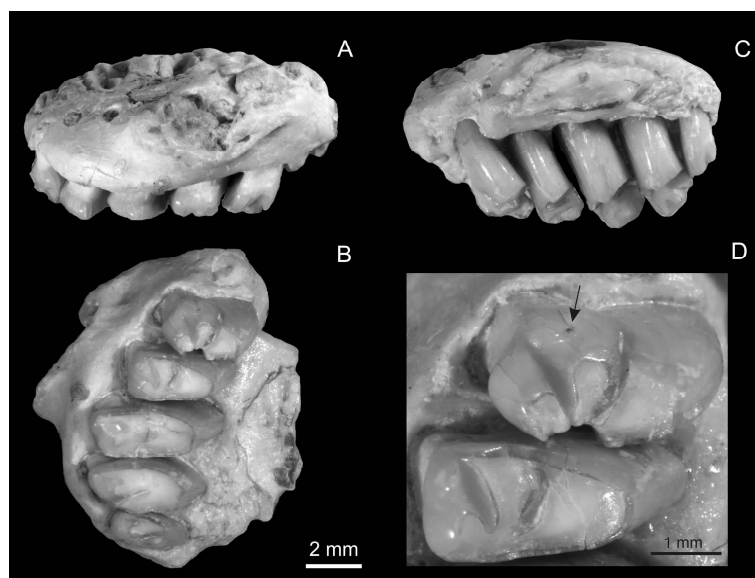


Fig. 2 Right maxilla with P3-M3 of *Gobiolagus aliwusuensis* sp. nov. (IVPP V 18500 the holotype) from the Middle Eocene Erden Obo site of Nei Mongol, China

A-C. buccal, occlusal, and lingual views; D. magnification of P3-P4, note accessory cusp on P3 (arrow)

**Table 1** Measurements of the upper dentition of *Gobiolagus aliwusuensis* sp. nov. (mm)

Specimen	P2		P3		P4		M1		M2		M3	
	L	W	L	W	L	W	L	W	L	W	L	W
V 18500			1.90	3.25	2.04	3.42	1.96	4.02	1.86	3.64	1.28	2.47
V 18501			1.67	3.13	2.02	3.27	2.08	3.62	1.86	3.15		
V 18502	1.18	1.5	1.75	3.12	2.17	3.35	2.08	3.45				
V 18503			1.71	3.16	2.20	3.20	1.88	3.93	1.95	3.55	<i>1.87</i>	<i>2.49</i>
V 18504			1.87	2.73	2.22	3.80	2.37	4.49	2.08	4.16	1.33	2.30
V 18509			1.97	2.82	1.85	3.03	2.03	3.38	2.01	2.98	1.43	2.27
V 18510			1.83	2.90	1.80	3.07	2.16	3.47	1.94	3.54	1.41	2.48
V 18511.1							2.07	3.07	2.01	3.29		
V 18512			1.75	3.09	1.82	3.87	1.93	4.73	2.00	3.43	1.19	2.56
V 18513					1.73	3.05	1.94	3.59	1.85	3.56		
V 18514			1.73	2.86	1.89	3.50	2.07	4.09	1.80	3.68		
V 18516					2.21	3.23	2.13	3.75	1.70	3.16		

Note: Values for alveolus in broken tooth are italicized.

Some of the maxillary fragments described here, show part of the hard palate with dominating the palatine portion which wedges sharply into the maxilla. The anteriormost projecting part of the palatine-maxillary suture is even with the P3/P4 alveolar transition area.

The premolar foramen is absent in all specimens unlike in *G. lii* and a specimen of *G. tolmachovi* (V 8430) reported by Qi (1988). The major palatine foramina are relatively large and

embedded in the palatine. They are close to the palatine-maxillary suture, medial to P4. There are two other paired palatine foramina located distally to the major pair. Their exact position is variable; the second pair, which can be equally large as the first one, is located mostly at the M1, while the third, smaller, is either medial to it or located further distally, medially to the M1/M2.

In some specimens (V 18509, 18510, and 18512) the anterior roots of the zygomatic arch are preserved. In ventral view they are rounded laterally; the masseteric spine is not strongly pronounced, but defined better than in *Dawsonolagus* (Li et al., 2007:fig. 1) and semilunar in its course. The structure of the anterior root of the zygomatic arch resembles that in *Mytonolagus* (see Fostowicz-Frelik and Tabrum, 2009:fig. 3B, E, H) with even more pronounced lateral projection (Fig. 3). The position and shape of the maxillary root of the zygomatic arch indicate that the arch might be a relatively wide laterally flared structure, similar to that in *Dawsonolagus*. Such architecture of the zygomatic arch is probably typical for the most primitive lagomorphs, while in more derived genera, such as *Megalagus*, *Palaeolagus* or *Chadrolagus* (Wood, 1940; Dawson, 1958; Gawne, 1978), the zygomatic bone tends to be more parallel to the skull. The anterior margin of the maxillary root of the zygomatic arch is directed laterally to the P4 (mostly its mid-length), while the posterior margin occurs laterally to the M1 (mid-length or distal part of the tooth). This position is slightly posterior to that mentioned by Meng et al. (2005) for the *Gobiolagus tolmachovi* from Ula Usu, but this character is variable, as noted by Lopatin and Averianov (2006).

There is a relatively shallow, but extensive and well-defined, antorbital fossa located anteriorly to the zygomatic arch, laterally to the place occupied by P3 and anterior part of P4, similar to *Dawsonolagus*. This differentiates *Gobiolagus* from *Mytonolagus*, in which the antorbital fossa is located more anteriorly and does not extend farther back than the distal margin of P3 (Fostowicz-Frelik and Tabrum, 2009). The exact position of the distal margin of the incisive foramen and posterior edge of the hard palate cannot be ascertained in the studied material because these parts are damaged.

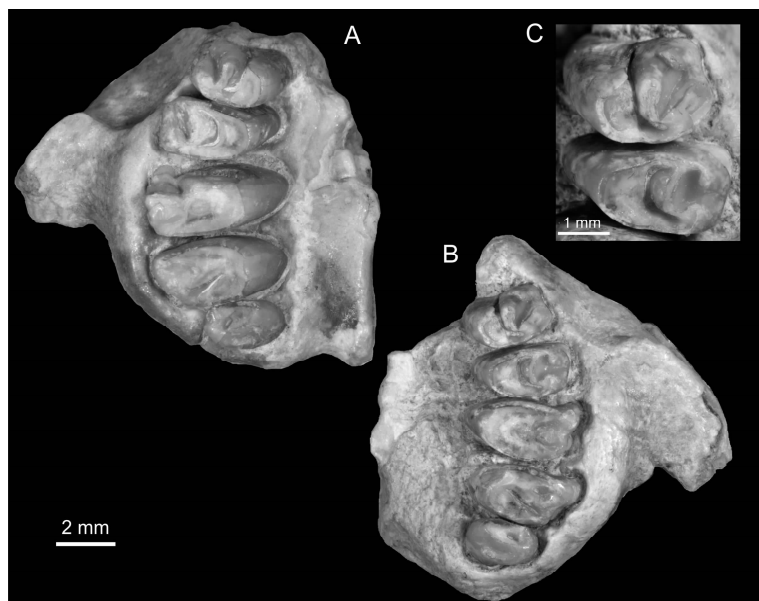


Fig. 3 Maxilla and upper dentition of *Gobiolagus aliwusuensis* sp. nov. from the Middle Eocene Erden Obo site of Nei Mongol, China

A. right maxilla with P3-M3 (IVPP V 18509) in occlusal view; B-C. left maxilla (V 18510) with well-developed accessory cusp of P3 and two cusps on buccal wall of P4 (C. magnification of the P3-P4), in occlusal view

P2 is known only in one specimen V 18502 (Fig. 4E-G), showing an early stage of wear. The crown is almost equally high along the entire circumference and relatively low, occupying ca. 38% of the total tooth height. The tooth is smaller than P3, and its width is approximately half the width of P3, similarly to *Strenulagus* (see Lopatin and Averianov, 2006) and slightly smaller than in *Shamolagus medius* (see Li, 1965). It is trilobate and similar in shape and proportions of the lobes to P3 at an early stage of wear. In occlusal view, the tooth is oval, but the antero-distal compression is not very strong ( $L/W = 0.75$ ), comparable to that in *Shamolagus medius* (V. 3010;  $L/W = 0.75$ , see Li, 1965:28 for metric data), and *Mytonolagus ashcrafti* ( $L/W = 0.71$ , Fostowicz-Frelik and Tabrum, 2009), but slightly greater than in *Mytonolagus wyomingensis* and *Mytonolagus* near *petersoni* sensu Dawson (1970). There are two anterior reentrants, the antero-lingual reentrant (paraflexia), slightly more persistent, and cutting deeper into the crown, and the antero-buccal reentrant (mesoflexia). The lingual lobe is the largest, semilunar in outline, and can increase its area as wear progresses. The central lobe is well-rounded and has thicker enamel layer, but it is not so strongly protruded anteriorly as in *Mytonolagus* (LFF personal observation). The tooth has a single root, round in cross-section. In this respect, it resembles Asian genera, such as *Lushilagus*, *Shamolagus*, and *Strenulagus* more than the early representatives of *Mytonolagus* from Badwater (Wyoming, USA), which have mostly two roots showing different stages of fusion (LFF personal observation). The buccal lobe is the smallest lobe on P2, with elongated, spindle-like occlusal surface directed slightly obliquely anteriorly. The buccal reentrant separating it from the central lobe is rather persistent, thus the buccal lobe most probably will be distinguishable until the senile stage of wear.

P3 at the light and moderate stages of wear is well represented within the sample, thus allowing us to study the intra-and interspecific variability. In fact, morphology of P3 and P4 provides most characters differentiating the material described herein from *Gobiolagus tolmachovi* of the Shara Murun Formation, Ula Usu, (Nei Mongol) in Meng et al. (2005), which is the most abundant material of that species reported so far. Generally, the P3 morphology is typical of the most primitive lagomorphs, grouped in Strenulagidae sensu Averianov and Lopatin (2005). The unmolarized tooth is trilobate, semihypsodont and has a single buccal root, similarly to *Aktashmys*, *Dawsonolagus*, *Lushilagus*, *Strenulagus*, *Shamolagus* (Li, 1965; Tong and Lei, 1987; Averianov and Lopatin, 2005; Lopatin and Averianov, 2006), and partly *Mytonolagus* (see Dawson, 1970; Fostowicz-Frelik and Tabrum, 2009), but unlike *Desmatolagus*, including "*Procaprolagus*" (Meng and Hu, 2004; Meng et al., 2005).

The lingual lobe is enlarged, occupying about one half of the tooth width. Its outline is semicircular and gains in width as wear progresses. It is slightly wider than in *G. tolmachovi* at the comparable stages of wear. The lingual margin of the lobe has no trace of the hypostria, but is slightly flattened in less worn specimens. This condition is probably typical for *Gobiolagus tolmachovi*, observed also in the specimens at moderate stage of wear (Meng et al., 2005:fig. 5. 1, 2), and was noticed also in *Dawsonolagus* (Li et al., 2007:fig. 4B) and *Strenulagus* (Lopatin and Averianov, 2006:fig. 2a).

The central lobe is separated from the lingual lobe by a deep curved paraflexia, which is much deeper in both antero-posterior and vertical aspects than the mesoflexia separating the central lobe from the buccal one. The central lobe is tear-shaped to rounded in outline and has a thickened enamel layer at the antero-lingual margin. In a weakly worn specimen V 18510 it is strongly compressed linguo-buccally, similarly to the holotype of *Strenulagus solaris* (Lopatin and Averianov, 2006:fig. 1a) but this condition is only due to an early ontogenetic stage of the specimen.

The buccal lobe is compressed linguo-buccally and occupies bucco-distal part of the occlusal surface. The mesostria is positioned obliquely, slightly antero-buccally and shallows toward the base of the crown. Thus, as wear progresses, the buccal lobe merges with the central lobe,

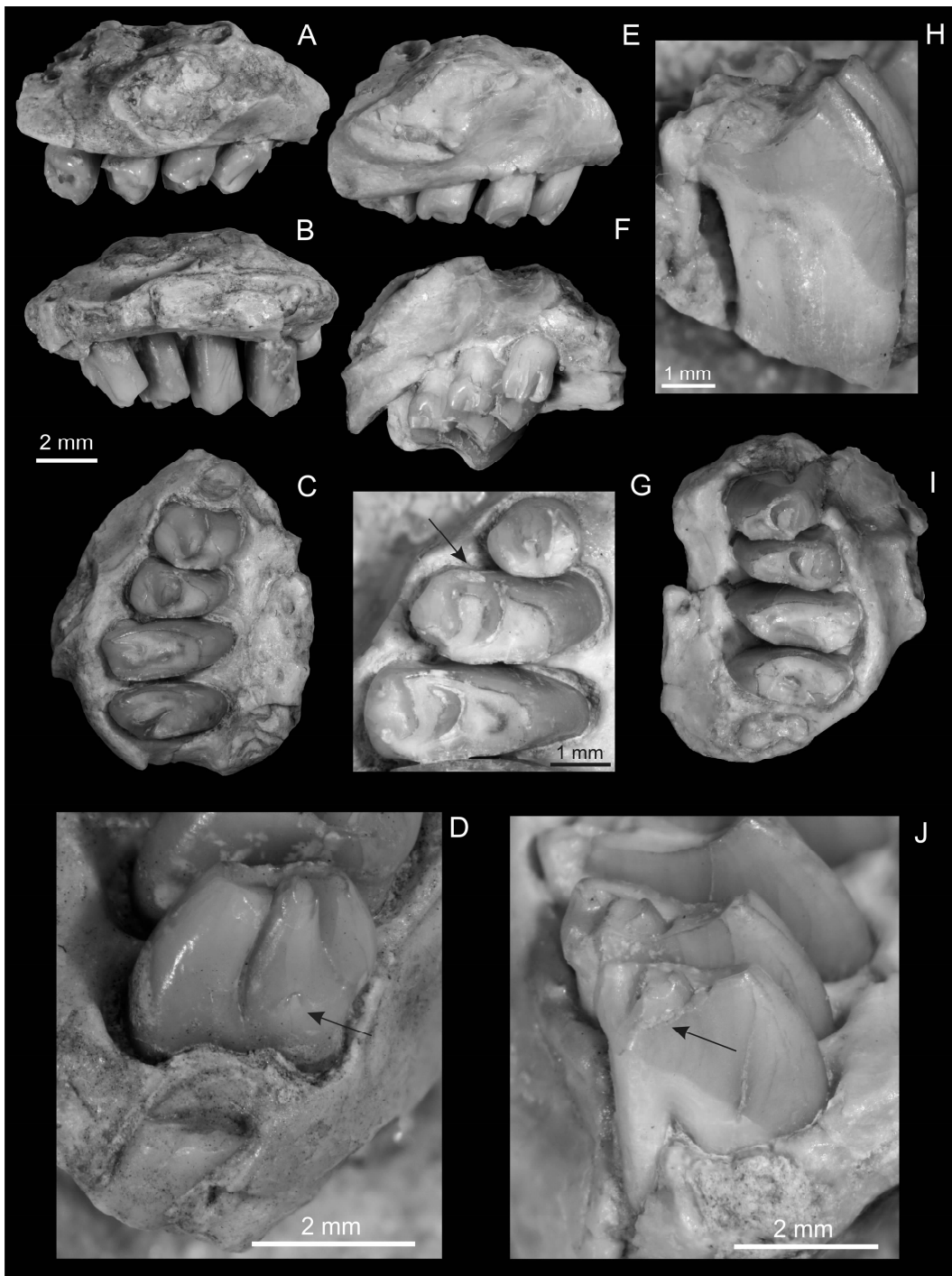


Fig. 4 Variability in morphology of maxilla and upper dentition of *Gobiolagus aliwusuensis* sp. nov. from the Middle Eocene Erden Obo site of Nei Mongol, China

A-D. right maxilla with P3-M2 (IVPP V 18501) in buccal, lingual, occlusal, and anterior views, respectively, D. magnification of P3 in anterior view; E-H. right maxilla with P2-M1 (V 18502) in buccal (E), anterior (F), and occlusal (G, magnification of P2-P4) views, H. P4 in distal aspect; I-J. left maxilla (V 18503) in occlusal and anterior views, J. magnified (note merged accessory cusp and anteroloph)



and eventually it can be completely obliterated. The parastria and mesostria in most of the specimens are less persistent than in *G. tolmachovi* from Ula Usu (Shara Murun Region), although the morphology and arrangement of these folds show some variability and specimens V 18509 – 18510 have parastria and mesostria persistent and almost vertical as in *G. tolmachovi*.

The base of the crown at the buccal lobe and central lobe, just ventrally to the root, is strongly swollen and pronounced, which differs the specimens described here from *G. tolmachovi* described by Meng et al. (2005). There is a small accessory cusp on the anterior part of this swelling at the base of the central lobe, anteriorly and level with the dorsal reach of the mesostria (Fig. 2D, 3B, C, 4A, C, D, G). The cusp is present in three specimens (V 18501 – 18503) from site 1 and in two specimens from site 2 (V 18500 and V 18510). All of them are lightly to moderately worn. The rest of the specimens have either damaged P3 (V 18504, V 18512 and V 18513) or no such cusp (V 18509, V 18514 and V 18515). Among the latter group, specimens V 18514 and V 18515 have marked buccal swelling of the base of the crown and less persistent mesostria directed more buccally in comparison to *G. tolmachovi* (e. g., AMNH 141281 or AMNH 141283), whereas specimen V 18509 resembles closely *G. tolmachovi*.

The specimens from site 1 show an intriguing sequence of wear stages, that is a gradual connection of the lingual lobe and the base of the accessory cusp, which leads to the formation of a thin buccal extension of the lingual lobe and virtually closes the crescentic valley at the anterior side (Fig. 4C-D, G, I-J). Such sequence suggests that the accessory cusp of P3 may have had a functional role in increasing the buccal reach of the lingual lobe, and therefore can be interpreted as an early attempt toward molarization, the process which among others includes buccal extension of the lingual lobe (in this case, the anteroloph).

The exact homology of the accessory cusp described here is not certain. In most specimens (apart from V 18510, Fig. 3B, C) it appears attached rather to the anterior wall of the central lobe in cingulum-like manner, than more buccally at the base of the buccal lobe, as in the case of V 18510, and as the cusp referred to as the parastyle by Tong (1997:206, table 8, fig. 27A) in *Strenulagus shipigouensis* from the Irindmanhan beds of the Hetaoyuan Formation, Xichuan County, Henan Province (China). In most *Gobiolagus* species such structure was not observed. The “antero-labial cusp” of P3 was mentioned by Lopatin and Averianov (2006) as differing *Gobiolagus lii* from *G. hekkeri*. In fact, original description of *Gobiolagus lii* does not mention the presence of such cusp (Zhang et al. 2001). However, the anterior margin of the buccal cusp of P3 in *G. lii* shows a small anterior extension which, most probably, represents the remains of the worn down antero-labial cusp which merged with the buccal cusp (see Zhang et al., 2001:fig. 1). The similarly positioned accessory cusps referred to as “pLE-hinteres Labialelement” by Tobien (1974) are quite common in some Oligocene lagomorphs from Europe (e. g. *Amphilagus* and *Titanomys*). The most similar (and probably homologous to the described here accessory cusp of P3) structure was observed in “*Amphilagus ulmensis*” from the Oligocene of Germany, a poorly known lagomorph species of uncertain taxonomic affiliations, where it was referred to as a “mLE-mitteres Labialelement” (Tobien, 1974). Interestingly, a similar cingulum-like extension of the anteroloph was observed in *Arnebolagus leporinus* from the Early Eocene of Mongolia (Lopatin and Averianov, 2008), although this species lacks an accessory cusp.

P4 morphology is less variable than P3 and this tooth similarly, displays a single buccal root. The reach of the P4 anteroloph and development of the buccal lobe is variable; similarly to P3 it has no hypostris. The length of the anteroloph is mostly related to the stage of wear, thus in some of the specimens showing lighter wear the anteroloph does not extend all the way to the buccal lobe. Instead, it surrounds the central lobe (V 18501) and then merges with it as wear progresses leaving a gap between its buccalmost part and the anterior buccal cusp (V 18500, 18502 – 18503, V 18513), although a lightly worn specimen (V 18510) has the anteroloph joining the anterior side of the buccal wall. In all specimens showing more advanced wear the

anteroloph is complete and its buccalmost part merges the anterior buccal cusp (Fig. 4I-J). The most specimens with well-preserved P4 have two separated buccal cusps (V 18500, 18502 – 18503, V 18510, V 18512 – 18513; Figs. 2D, 3C, 4G), similarly to *G. hekkeri* (Lopatin and Averianov, 2006:fig. 5C) and unlike *G. lii* (Zhang et al., 2001:fig. 1) and most of *G. tolmachovi* specimens (Meng et al., 2005) apart from specimen V 8430 (Qi, 1988:fig. 1). In the material studied herein, lightly worn teeth show that the anterior cusp is an independent structure from both the buccal lobe (metastyle sensu Wood, 1940), forming the posterior buccal cusp, and anteroloph, with which it can be merged as the wear progresses. The appearance of the anterior cusp is slightly delayed in relation to the posterior buccal cusp. Specimen V 18501 has an unworn buccal lobe which is positioned somewhat askew and slopes anteriorly, so it is not clear whether the anterior cusp was still to have been erupted or not. On the other hand, specimen V 18510 shows similarly shaped buccal lobe but in the tooth with more advanced wear. In this specimen the division into two cusps is not visible but rather the buccal lobe is extended and forms a ridge cutting out a relatively shallow, antero-posteriorly extended, valley (most probably, homologous to P3 mesoflexia), the morphology more similar to some specimens of *G. tolmachovi* (AMNH 141283 and 141285), although the ridge is smaller in these specimens.

The bicuspid buccal lobe of P4 is known in *Dawsonolagus antiquus* (Li et al., 2007:100), *Aktashmys montealbus* (Averianov and Lopatin, 2005:312, figs. 2a, 3e, f, h), and *Strenulagus shipigouensis* (Tong, 1997:fig. 27A), but such division is absent from *Gobiolagus tolmachovi* (Meng et al., 2005).

The development of the antero-labial cusp and anteroloph in *Gobiolagus* is closely related to the molarization of P4, which has been discussed since the discovery of the maxilla fragment ascribed to *Gobiolagus tolmachovi* by Qi (1988). Meng et al. (2005:11) in their revision of *Gobiolagus* material give an explanation of what should be regarded as a molarized P4. They state that because P4 of *G. tolmachovi*, despite the presence of the complete anteroloph, has “neither the division of the trigon and talon, nor division of cusps on the labial side of the tooth”, it should be considered as nonmolariform. It is debatable whether the P4 teeth described here are already molarized or not. In most of the undamaged specimens studied here, there are two clearly defined cusps on the labial (here buccal) side. On the other hand, the completion of the anteroloph is delayed in ontogeny and the trigon and talon could not be clearly identified. Thus, in agreement with Meng et al. (2005), the new material does not display fully molarized P4, although it can be said that in comparison with *G. tolmachovi* the molarization of teeth of *G. aliwusuensis* n. sp. is more advanced.

M1 is the largest and widest tooth in the upper tooth row and has two buccal roots. It is significantly larger than in *Gobiolagus hekkeri* and smaller than in *G. major*, and the size range of the M1 described here is similar to that of *G. tolmachovi* and *G. lii*. The M1 morphology also does not differ markedly from the specimens assigned to *Gobiolagus tolmachovi*, and the L/W index is different only than in *G. hekkeri* which has the relatively longer (less transversely extended) tooth. The associated specimens V 18511.1–2 give an insight into early stages of wear of the molars (Fig. 5C). At this stage, M1 and M2 do not differ much. The hypostria is shallow but visible, forming a sharp indentation in the lingual margin of the tooth. The occlusal surface is divided into trigon and the hypocone shelf (postcingulum sensu Lopatin and Averianov, 2006), which occupies ca. one-third of the occlusal surface, by a deep valley cutting across almost a whole tooth diagonally from the postero-buccal side. This valley at its lingual end points at the innermost part of the hypostria with which it was confluent at the earlier stage. The remains of the crescentic valley occupy the antero-buccal part of the occlusal surface of the tooth and centro-buccal part of the trigon. Judging from the already vanishing crescentic valley it is obvious that the enamel lake appearing on the occlusal surface in the stronger worn M1 specimens is the remnant of the posterior valley separating trigon from the hypocone shelf rather

than the remnant of the crescentic valley. Similarly, the “hypofosette” of M1 in *Dawsonolagus* interpreted by Li et al. (2007) as a remnant of the hypostria is most probably of the same origin.

The enamel elements at the occlusal surface of M1 are relatively quickly obliterated in comparison with other upper cheek teeth, which is not surprising since M1 is the first erupted permanent tooth.

M2 is slightly smaller than M1 and also has two buccal roots. It is more strongly asymmetrical, with narrower hypocone shelf. The unworn or lightly worn teeth show the reduced crescentic valley displayed as a deep funnel or a pit at the occlusal surface. The valley separating trigon from the hypocone shelf cuts across the occlusal surface, completely separating the two parts of the tooth. The valley begins to close from the lingual side. It persists as a cleft, then as an elongated enamel islet, to be finally divided into two small enamel islets (V 18503) and disappear.

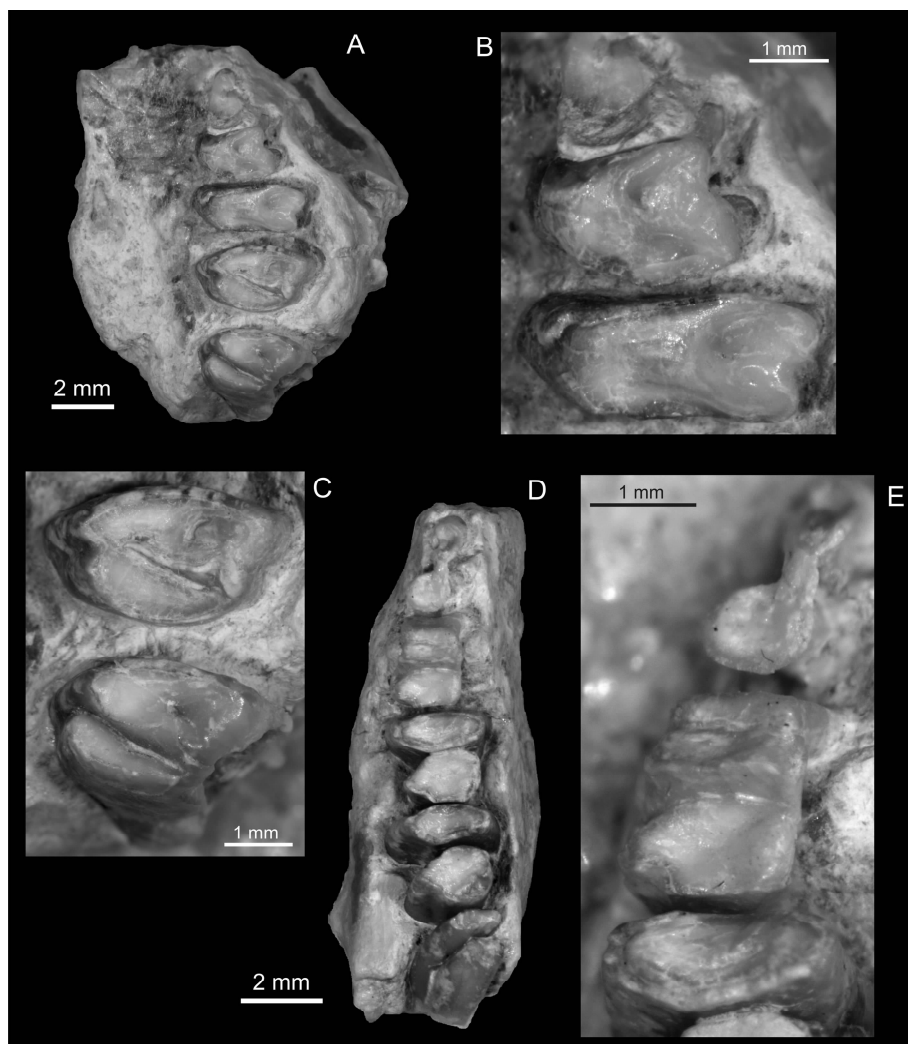


Fig. 5 Juvenile dental morphology of *Gobiolagus alivusuensis* sp. nov. from the Middle Eocene Erden Obo site of Nei Mongol, China

A-C. juvenile maxilla (IVPP V 18511.1) with P2 root, DP3, DP4 and M1-M2 in occlusal view, B. and C. magnification of deciduous premolars (DP3-DP4) and lightly worn molars (M1-M2), respectively; D-E. juvenile mandible (V 18511.2) with root of dp3, dp4 and m1-m3 in occlusal views, E. magnification of dp4

The comparative material of *Gobiolagus tolmachovi* contains only strongly worn specimens, with a single or double enamel islet, and at this stage there is no significant difference between *G. tolmachovi* and the specimens described here.

M3 was not previously reported for any *Gobiolagus* species apart from a single specimen of *G. tolmachovi* V 8430 (Qi, 1988:fig. 1). It is unknown for *G. hekkeri*, *G. major*, *G. lii*, *G. andrewsi* and *G. burkei*, the last two species are known only from the mandible material (Burke, 1941; Qi, 1988; Meng and Hu, 2004; Meng et al., 2005; Lopatin and Averianov, 2006). Its width relative to M2 (for *G. tolmachovi*) was calculated as ca. 65%, on the basis of its preserved alveolus (Tong, 1997:table 8). In our sample the arithmetic mean for this ratio is 66% and the observed range is 47%~76%.

In the material studied here, there are five M3, embedded in the dental rows and showing different stages of wear. M3 is reduced to the two-thirds of the M2 width and has a single buccal root, similarly to *Strenulagus* (see Lopatin and Averianov, 2006). The occlusal surface is composed of the trigon, triangular in outline with two buccal cusps separated by a deep buccal valley (in lightly worn specimens appearing as a funnel on the occlusal surface), and a narrow postcingulum located more dorsally than the trigon. In the holotype specimen (V 18500), the occlusal surface of the postcingulum is a narrow triangle with its base on the lingual side. It transforms into a ridge and then obliterated concavity at the posterior wall of the tooth, as the wear progresses.

The mandibular material consists of 18 fragments of mandible body with variably preserved dentition (see Table 2 for measurements). The mandible body is deeper than in *Shamolagus* and slightly deeper than in *Strenulagus solaris*, equally deep as in *Gobiolagus tolmachovi* and "*Procaprolagus*" *vetustus*, but slightly lower than in *Gobiolagus andrewsi*. The ventral line of the mandible is relatively flat, especially in the alveolar part, similar to other *Gobiolagus* species, and not visibly curved as in *Dawsonolagus* and *Strenulagus*. The alveolus for the lower incisor is well visible at the medial side of the mandible and ends under the mid-length of m2, similarly to other *Gobiolagus* species, *Strenulagus*, and "*Procaprolagus*". The lower incisor is flat at the lingual side and gently rounded at the buccal side, with a slightly flattened ventral margin. The enamel is thin and covers only the ventro-buccal area.

The anterior mental foramen is located in the middle of the diastemal portion and the posterior mental foramen occurs below p4 or p4-m1. In specimen V 18506 there are two mental foramina in the alveolar portion, one below p3 and another below p4. It is not certain if the anterior mental foramen moved back or an additional foramen appeared, because the diastemal portion is partly broken.

Similar to *Gobiolagus tolmachovi*, the roots of the lower teeth are mainly fused, showing shared, although very irregular and branching, dental chamber for p4-m2 (Fig. 6D), with wider parts under the trigonids (see Meng et al., 2005). The complete root of p3 is unknown in our material, but the specimen V 18505 shows a rounded posterior part of the root, which appears to have a separate chamber and was attached to the anterior part of the root by a bony bridge.

The p3 is preserved in four mandibles (V 18517 – 18519, V 18526; Fig. 6G, I-K). All teeth are less worn than in the holotype of *Gobiolagus tolmachovi*, but stronger than in *G. andrewsi*. Size range of the p3 falls between relatively shorter *G. tolmachovi* and more elongated *G. andrewsi*. The smallest and least worn tooth (V 18517) has slightly different proportions than the remainder of the specimens, being relatively wide. It is also the only specimen having a second, directed posteriorly lingual reentrant, which is probably a juvenile character for *Gobiolagus*. Other specimens are moderately elongated, with round trigonid, partly separated from the talonid by two reentrants: the lingual one, deeper, but less persistent, and shallower, but very persistent, buccal reentrant. The buccal reentrant is directed slightly posteriorly in comparison to the lingual fold. At the moderate stage of wear, the new material does not show any

marked differences from *G. tolmachovi*, especially specimen AMNH 141288. The p3 of the holotype of *Gobiolagus tolmachovi* is strongly worn, with the lingual reentrant obliterated and the trigonid considerably enlarged. Such stage of wear is unknown from the specimens described here. The only comparable specimen (V 18524) has the tooth broken in the alveolus near the level of the alveolar margin. It is distinctly elongated with moderately deep single buccal reentrant, cutting across ca. one-third of the tooth surface.

**Table 2** Measurements of the lower dentition of *Gobiolagus aliwusuensis* sp. nov. (mm)

Specimen	P3		P4		m1		m2		m3	
	L	W tri/tal	L	W tri/tal	L	W tri/tal	L	W tri/tal	L	W tri/tal
V 18505			1.94	2.14/1.65	2.23	2.63/1.70	2.27	2.74/2.12	1.84	1.78/1.35
V 18506			1.78	1.99/1.37	2.56	— /1.55	2.52	2.68/1.81		
V 18507			2.08	1.92/1.56	2.1	2.48/1.99	2.36	2.57/2.05	1.99	1.60/1.39
V 18508							2.35	2.69/1.82		
V 18517	1.21	0.87/1.38	1.70	1.75/1.54	2.08	2.18/1.92	2.39	2.42/2.06	1.61	1.50/1.05
V 18518	1.70	0.95/1.39	1.86	1.72/1.58	1.70	2.11/1.84	2.17	2.24/1.92	1.39	1.56/1.25
V 18519	1.83	1.02/1.35	1.82	1.81/1.42	2.13	2.27/1.65				
V 18520			1.80	1.70/1.57	2.18	2.40/1.70	2.50	2.70/1.93	1.90	1.66/1.42
V 18521			1.89	1.97/1.45	1.99	2.57/1.76	2.45	2.75/2.17	1.75	1.7/1.29
V 18522			1.66	1.83/1.50	1.97	2.22/1.83	2.40	2.60/2.00		
V 18523			1.96		1.85		1.73	2.53/1.82	1.66	1.56/1.33
V 18524			1.80	1.78/1.82	1.87	2.10/1.84	2.30	2.42/2.07	1.39	1.54/1.37
V 18526			1.81	1.82/1.42						
V 18529							2.44	2.65/2.06	1.63	1.63/1.33

The differences with *G. andrewsi* are more pronounced, although two available for us to study specimens ascribed to this species (AMNH 26091 and 26092) are young individuals, one with almost unworn p3 (AMNH 26092). The p3 of *G. andrewsi* is more elongated than the tooth in the Aliwusu sample and in *G. tolmachovi* which was already observed by Meng et al. (2005). Moreover, the p3 trigonid in *G. andrewsi* is proportionally longer than in any of the two species. In lingual view, the p3 trigonids in both specimens of *G. andrewsi* are visibly cone-shaped, strongly increasing the antero-posterior dimension at the base. This can lead to a significant gain in length as wear progresses. None of the specimens studied herein and of those of *G. tolmachovi* described by Meng et al. (2005) show such strong increase of the p3 trigonid length at its base.

Compared to *G. burkei*, specimens from Aliwusu, apart from being larger, show also relatively wider p3 with larger and more rounded trigonid, separated from the talonid by deeper reentrants. The p3 in the reminder species of *Gobiolagus* is not known (see Zhang et al., 2001; Meng and Hu, 2004; Meng et al., 2005; Lopatin and Averianov, 2006).

The p4, relatively small tooth with an easily recognizable pear-shaped trigonid and distinctly smaller talonid (narrower and shorter) is characteristic for *Gobiolagus*, allowing to distinguish this genus from other Eocene lagomorphs (Meng et al., 2005; Lopatin and Averianov, 2006; Li et al., 2007). The pear-shaped trigonid and the reduced talonid are especially well-expressed in *Gobiolagus tolmachovi* (Meng et al., 2005), and in the material described here. The p4 assumes its most typical form at the more worn stages, although even in a lightly worn specimen (V 18522), the pear-shaped trigonid is already recognizable (Fig. 6C, G, I-K).

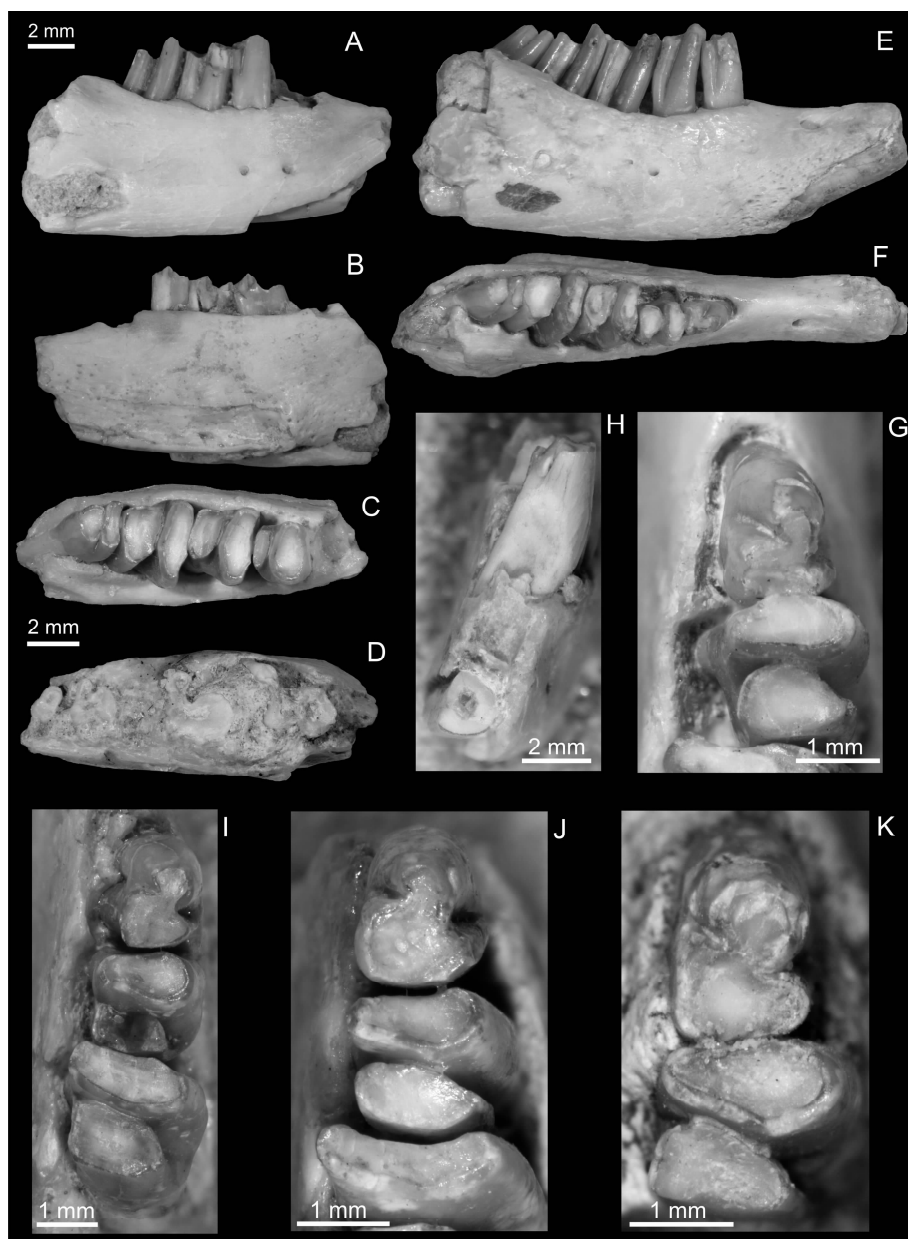


Fig. 6 Mandible and lower dentition of *Gobiolagus aliwusuensis* sp. nov. from the Middle Eocene Erden Obo site of Nei Mongol, China

A-B. right mandible (IVPP V 18506) with p4-m2, in buccal and lingual views; C-D. right mandible (V 18505) with p4-m3, in occlusal and ventral views, D. broken mandible body, visible fused roots; E-G. right mandible (V 18517) with p3-m3 in buccal and occlusal views, G. magnification of p3; H. left mandible (V 18507) showing di2 in cross-section (in anterior view); I. right p3-m1 (V 18519) in occlusal view; J. right p3-p4 (V 18518) in occlusal view; K. right p3-p4 (V 18526) in occlusal view

The m1 is noticeably larger than p4 and smaller only than m2. The trigonids of both m1 and m2 are oval in outline, compressed antero-posteriorly, and wider than the talonids. The difference in width between the trigonid and talonid of m1 and m2 is stronger expressed in *Gobiolagus*

than in *Aktashmys*, *Dawsonolagus*, *Lushilagus*, *Shamolagus*, and *Strenulagus* (Li, 1965; Meng et al., 2005; Averianov and Lopatin, 2005; Lopatin and Averianov, 2006; Li et al., 2007). In the material described here, the proportion of the talonid to trigonid width for m1 is similar to that of *Gobiolagus tolmachovi*, and slightly higher than that for *G. major* and *G. burkei*. The talonid of m1 in the newly described material is similar in length or slightly shorter than the trigonid, similarly to *Gobiolagus tolmachovi* from the Shara Murun Formation (Meng et al., 2005).

The m2 is the largest tooth in the lower row; the proportions of the trigonid and talonid are different than in m1, which is typical for most of the late Early and Middle Eocene Asian lagomorphs. The trigonid is strongly compressed antero-posteriorly and the talonid has greatly expanded and rounded occlusal surface, located much lower than that of the trigonid, which indicates the main grinding surface.

The talonids of m1 and m2 do not display the hypoconulids. A vestigial hypoconulid can be traced only in one specimen (V 18511.2), which still has the deciduous premolars, thus these structures were present only in a freshly erupted tooth and were worn down rapidly.

The m3 is slightly reduced; the width of its trigonid equals 61%~69% of the m2 trigonid width. Similarly to m1 and m2, the trigonid of m3 is antero-posteriorly compressed, with the buccal side slightly longer than the lingual one. The talonid is longer and more round than the trigonid, with smooth and rounded posterior margin.

The molarized lower premolars and molars form lingual enamel bridges, joining up trigonids and talonids, at the relatively early stage. The observation of the lower dental row at different stages of wear shows that m1 is the first tooth forming an enamel bridge, which is not unexpected, taking into account the sequence of eruption of the permanent teeth. The m1 is followed by p4, and then by m2 and m3, which form enamel bridges approximately at the same time.

## 5 Discussion

The new material described here represents a considerably numerous sample of *Gobiolagus*, the lagomorph genus known mainly from the Shara Murun region of Nei Mongol (Inner Mongolia), China, from which four out of six hitherto recognized species were known. Two remaining species, *G. lii* and *G. hekkeri*, were described from Shanxi Province (China), and Kyrgyzstan (Batken Region, Andarak 2 locality) respectively. The new specimens reported here show all features characteristic for *Gobiolagus* listed by Meng et al. (2005) and Lopatin and Averianov (2006), such as: strong postero-lingual flexion of the buccal margin of the alveolar process of the maxilla in the molar portion, position of the maxillary root of the zygomatic arch between P4 and M1, the teeth more hypsodont than in *Shamolagus* and *Lushilagus*, but less than in *Desmatolagus* (with the exception of *D. vetustus*), lower incisor ending below m2, p4 significantly smaller than m1, with a pear-shaped trigonid and a strongly reduced talonid, m2 largest tooth in the lower row, with strongly laterally extended trigonid and enlarged talonid, lower molars forming lingual dental bridges relatively quickly and losing hypoconulids very early in ontogeny, not fully molarized P4 and moderately reduced M3. In size and general morphology they resemble most closely *Gobiolagus tolmachovi*, but they show also some characters unknown for this species or not noted for any other species of *Gobiolagus*. Interestingly, the mandibles and lower dentition, especially the premolars, are morphologically closer to *Gobiolagus tolmachovi* than the upper dentition is. The only difference is a slightly smaller reduction of the p4 talonid length observed in the new specimens. However, this character is strongly dependent upon wear stage and material described by Meng et al. (2005) generally consists of more strongly worn specimens than in the sample discussed herein.

The new characters described here are an accessory cusp on the anterior wall of the P3 central lobe (homologous or not with the antero-labial cusp of P4), and two well-defined buccal

cusps on P4. Although the new characters in the upper dentition are clearly present, their distribution within the sample varies and the relation to the wear stages is a factor worth noticing. Among 15 described maxillary fragments, the P3, at different stage of preservation, is present only in nine and only five of them display an accessory cusp. Most specimens that have an accessory cusp show generally light stage of wear, although the specimen V 18503 (with a cusp) is approximately at the similar stage of wear as V 18509 (without a cusp), thus this character is not entirely age-related, but rather polymorphic in our sample. The same applies to the P4 showing two distinct buccal cusps; not all specimens in the sample have this character well-developed (e. g., very weak anterobuccal cusp of P4 in V 18513).

Concluding, the new characters in the upper premolars are variable and mosaic within the material presented here. This may be a result of either the intra-specific variability (two morphotypes) or specific diversity (two coeval species). The polymorphism of dental characters in lagomorphs is a well-known phenomenon, and concerns many aspects of root and crown morphology (Dawson, 1970; Fostowicz-Frelik and Tabrum, 2009), thus we prefer the former possibility. Nevertheless, the greater morphological diversity can be observed in the geologically younger sample, which is also more abundant. Among specimens from this sample there are some that strongly resemble *G. tolmachovi* from the Shara Murun region (e. g., V 18509 or V 18512). Thus, we do not preclude that some of the specimens studied here, which do not have the accessory cusp on P3, can be reclassified as cf. *Gobiolagus tolmachovi*, especially if more material is recovered. According to the stratigraphic data, the material described herein is most probably older than that of *Gobiolagus tolmachovi* studied by Burke (1941) and Meng et al. (2005) from Shara Murun. The age of the new specimens detailed here is preliminary set to the Middle Eocene, from the Irдинmanhan to Sharamurunian, while the type material of *G. tolmachovi* and the rest of specimens from Shara Murun region are of late Middle Eocene age (Sharamurunian only; Qi, 1988; Meng et al., 1999, 2005).

The important morphological differences merit establishing a new species, but its overall morphological similarity to *G. tolmachovi* suggests that *G. aliwusuensis* may be regarded as an ancestral (or sister) group for this species.

The intrageneric relationships of *Gobiolagus* have not been discussed in details so far. It appears that this genus, as currently understood, may be paraphyletic, with *Gobiolagus major*, a distinctively larger species, most probably representing a separate lineage (Meng and Hu, 2004; Meng et al., 2005). The earliest *Gobiolagus* is represented currently by three species of Irдинmanhan age: *Gobiolagus lii*, *G. hekkeri*, and *G. aliwusuensis* sp. nov. All these species come from different geographic regions, Shanxi (China), Kyrgyzstan, and Nei Mongol (China) respectively, and most probably are not closely related. However, they have one character in common, which can be best described as related to the cuspal development of the buccal region in upper premolars, resulting in appearance of anterior buccal cusps. The character is poorly expressed in *G. lii*, the tooth of which is strongly worn, but *G. hekkeri* shows an anterior buccal cusp on P4 and *G. aliwusuensis* sp. nov. has accessory cusps on P3 and anterior buccal cusps on P4 well-expressed. This character can be viewed twofold. First, as a primitive condition for lagomorphs, because of overall simplification of the occlusal dental pattern in phylogeny. Secondly, as an early attempt toward molarization of the premolars. This is an important evolutionary trend in Lagomorpha, however, it had not been attained before the Oligocene in any lineage, and, in the case of P3, never attained by ochotonids (Dawson, 2008).

On the basis of dental (especially the lower dentition), limited cranial and mandibular morphology, and size, *Gobiolagus aliwusuensis* sp. nov. is probably more closely related to *G. tolmachovi* than any other species of *Gobiolagus*. Significantly smaller *G. burkei* known from the same beds as *G. tolmachovi* differs markedly in size and tooth structure and probably represents a different lineage. Phylogenetic affiliation of *G. andrewsi* is not certain, due to its scarcity and



overall similarity to *G. tolmachovi* (see Meng et al., 2005:11 for discussion).

The broader relationships of *Gobiolagus* are not resolved, the same is true for other Eocene lagomorph taxa. Among the late Early and Middle Eocene Asian taxa, *Gobiolagus* shows some progressive trends in hypsodonty surpassed only by *Hypsilylus* (Meng et al., 2005), and was probably one of the most advanced genera at that time.

Tong (1997) suggested possible phylogenetic relationships for *Lushilagus*, *Strenulagus*, and *Gobiolagus*, excluding *Shamolagus* as the immediate ancestor, on the basis of its two-rooted p3, although *Shamolagus* shares structure of the lower cheek teeth with similar occlusal shape of p3, distinctly wider trigonids of molars, and enlarged talonid of m2. On the other hand, *Gobiolagus* shares some characters in the dental morphology with *Mytonolagus* from the Middle Eocene (late Uintan) of Utah and Wyoming, USA, one of the two earliest North American lagomorphs. The immediate ancestor of *Mytonolagus* lineage has not been named so far. Dawson (2008) stated that *Mytonolagus* and *Desmatolagus* (“*Procaprolagus*”) *vusillus* represent most probably two distinct migration events from Asia, but Tong (1997) suggested the possible closer relationship between the Asian Irudinmanhan taxa and *Mytonolagus*. New data provided by the material studied here do support possibility of close phylogenetic relationships between *Gobiolagus* and *Mytonolagus*.

The lagomorph taxonomy at the infraordinal level is still open to debate. Among the authors, we can distinguish two opposite approaches; either they recognize only two families (Leporidae and Ochotonidae with living representatives; Dawson, 2008), thus extending the “crown group” concept to even the Early Eocene representatives of Lagomorpha, or they propose many, mostly paraphyletic, stem groups in order to apportion among the new families observed considerable variability. Five Asian taxa (*Aktashmys*, *Gobiolagus*, *Lushilagus*, *Shamolagus*, and *Strenulagus*) were recently grouped into Strenulagidae (Averianov and Lopatin, 2005). However, Li et al. (2007) disagree and recognize “Strenulagidae” as a grade, united by their primitive morphology. To us, the array of morphologies observed among the Early and Middle Eocene genera indicates a more complex picture, where *Dawsonolagus* (probably with *Arnebolagus*), *Aktashmys*, and a group consisting of *Gobiolagus*, *Lushilagus*, *Shamolagus*, and *Strenulagus* represent three independent lineages of basal lagomorphs. Thus, in the present work, we include the newly described material into “Palaeolagidae” *sensu lato*, a traditional ‘waste-basket’ family for stem groups (e. g., Fostowicz-Frelik et al., 2012), until a proper phylogenetic analysis is performed.

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