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A new genus of stem lagomorph (Mammalia: Glires) from the Middle Eocene of the Erlian Basin, Nei Mongol, China

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Abstract. We report the discovery of *Erenlagus anielae*, a new genus and species of stem lagomorph from the lower part of the Middle Eocene Irdin Manha Formation at the Huheboerhe locality, Erlian Basin, Nei Mongol, China. The remains consist of isolated teeth; however, the material includes all loci except the incisors and P2. The new lagomorph is characterized by a small size and high degree of unilateral hypsodonty comparable to that of *Aktashmys* and slightly higher than that observed in the coeval and co-occurring *Stre-nulagus*. Further, it shows advanced root fusion, which exceeds even that in *Gobiolagus*. Although phylogenetic relationships of the Eocene lagomorphs from Asia are still not fully resolved, the dental characters of *Erenlagus anielae* suggest that it is most closely related to '*Lushilagus*' *danjingensis* from the Middle Eocene of Henan, China and *Aktashmys montealbus* from the late Early Eocene of Kyrgyzstan. This stratigraphically well-constrained finding represents one of the lagomorph genera that appeared in the Eocene Glires paleobiodiversity reservoir, the Erlian Basin in Nei Mongol.

Key words: Lagomorpha, Eocene, Irdinmanhan, Inner Mongolia, evolution, hypsodonty.

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I. INTRODUCTION

The earliest fossils considered to belong to Lagomorpha, a group of duplicidentate Glires with two extant families (Leporidae and Ochotonidae), were reported from the Early Eocene of Mongolia (LOPATIN & AVERIANOV 2008) and India (ROSE et al. 2008). The exact center of origin for lagomorphs is still uncertain as those findings come from two quite distant regions; furthermore, the remains are extremely scarce and fragmentary. The fossil record from China surpasses them in abundance and completeness; the oldest lagomorph of modern aspect *Dawsonolagus antiquus* LI et al., 2007 comes from the lowest beds

(AS-1) of the late Early Eocene Arshanto Formation of the Erlian Basin, Nei Mongol (LI et al. 2007) and may be of age comparable to the specimens from Vastan (India).

The Erlian Basin is an important fossiliferous area with well exposed Paleogene strata; it has been investigated since the 1920s by scientific expedition teams from the United States of America, China, and the former USSR (see CHOW & RO DESTVENSKIJ 1960; MENG et al. 2007; WANG et al. 2012). On the basis of Chinese Paleogene mammal faunas from the Erlian Basin, several Asian Land Mammal Ages (ALMAs) have been proposed (for details, see RUSSELL & ZHAI 1987; TONG et al. 1995; MENG et al. 2007; WANG et al. 2010, 2012), including the Irdinmanhan. As currently understood, the Irdinmanhan ALMA corresponds to the early Middle Eocene (MENG et al. 2007; WANG et al. 2010, 2012). With the beginning of this interval a more diverse assemblage of Glires appears (FOSTO-WICZ-FRELIK et al. in press; LI & MENG in press). In the case of lagomorphs, the Irdinmanhan witnessed the first significant increase in their taxonomical and morphological diversity. The fossil remains of the Middle Eocene Lagomorpha are known from several regions of China, but among them two are most important: Henan (TONG 1997), and Nei Mongol (MENG et al. 2005; FOSTOWICZ-FRELIK et al. in press). Currently, there are at least five genera with five species known from Henan (TONG 1997) and at least four lagomorph genera (including a new genus described here) with seven species known from Nei Mongol (MENG et al. 2005; FOSTOWICZ-FRELIK et al. 2012; FOSTOWICZ-FRELIK et al. in press).

Here we describe a new genus and species of lagomorph from the Middle Eocene Irdin Manha Formation of Nei Mongol, China that shows advanced unilateral hypsodonty, and a dentine junction between the trigonid and talonid of lower molars, a rare condition for the early stem lagomorphs. We also discuss the morphological and phylogenetic implications of this new lagomorph.

II. GEOLOGICAL SETTINGS

The Erlian Basin lies in the central Inner Mongolia (China), close to the China-Mongolia border (Fig. 1), and extends approximately between 42°-44°N and 110°-114°E (JIANG 1983; WANG et al. 2010, 2012). The Huheboerhe area is located in the northern part of the Erlian Basin, approximately 40 km southwest of Erenhot. The Huheboerhe section is roughly identified with the location called '10 Miles Southwest of Camp Margetts' within the operational area of Camp Margetts established during the Central Asiatic Expeditions (CAE) of the American Museum of Natural History (MENG et al. 2007; WANG et al. 2012). The sedimentological studies held in this section revealed that most of the series belongs to the Irdin Manha Formation and underlying Arshanto Formation, which is best exposed here (MENG et al. 2007; WANG et al. 2012).

The sediment series of the Irdin Manha Fm. cropping out at the Huheboerhe area comprises two mammal-bearing horizons, abbreviated IM-1 and IM-2 (WANG et al. 2010). The lower horizon (IM-1) yielded abundant mammal fauna including the early primate *Tarkops mckennai* NI et al., 2010, hyenodontid *Propterodon morrisi* (MATTHEW & GRANGER 1924), mesonychids *Harpagolestes leei* JIN, 2005 (JIN 2012) and *Andrewsarchus mongoliensis* OSBORN, 1924, tapiroids *Lophialetes expeditus* MATTHEW & GRANGER, 1925 and *Deperetella* sp., the mimotonid *Gomphos shevyrevae* MENG et al. 2009, the lagomorph



Fig. 1. Stratigraphy and location of the Huheboerhe area. A: generalized stratigraphic section of sediment series cropping out in early to middle Eocene vertebrate fossil localities of the Erlian Basin (after WANG et al. 2010, modified); B: schematic map of China showing Nei Mongol, Erenhot and Huheboerhe area (H); C: map of Erenhot vicinity, the Huheboerhe area marked with blue star; D: photograph of the Huheboerhe area; the Irdin Manha Formation beds (at the top) are light gray and yellowish and overlay the sediment series of the upper Arshanto Formation (reddish deposits). Photo by Xun JIN (IVPP).

Strenulagus solaris LOPATIN & AVERIANOV, 2006 (FOSTOWICZ-FRELIK et al. in press), ctenodactyloid rodents *Tamquammys wilsoni* DAWSON et al. 1984, *Tamquammys* new species, *Yuomys* new species, *Yuomys* sp. A, *Yuomys* sp. B, and *Yuomys* sp. C, and two new genera with two species (LI & MENG in press), some cricetids, *Pappocricetodon neimon-golensis* LI, 2012, *Pappocricetodon* sp., *Pappocricetodon* cf. *zhongtiaensis* TONG, 1997, and the ischyromyid *Asiomys dawsonae* QI, 1987 (LI 2012, LI & MENG 2013). All lagomorph specimens described herein come from that horizon. The upper horizon (IM-2), consisting mostly of grayish white sandy conglomerates, yielded much scarcer fauna, including remains of *Lophialetes expeditus* and *Protitan* sp. (WANG et al. 2012).

III. MATERIAL AND METHODS

The material described herein is housed in the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) of the Chinese Academy of Sciences (Beijing).

We accept the dental terminology for the molars after MENG & WYSS (2001) and KRAATZ et al. (2010). In case of the premolars, due to the lack of universally accepted homologies of the transformed tribosphenic dentition we used a descriptive terminology (MENG et al. 2005; FOSTOWICZ-FRELIK & TABRUM 2009; FOSTOWICZ-FRELIK et al. 2012; FOSTOWICZ-FRELIK 2013). The photos were made using the DinoLite PRO digital microscope with adjustable polarization filter; drawings were performed under a binocular microscope (Olympus) with a camera lucida, and measurements were taken using a Sylvac digital caliper with an accuracy of 0.01 mm. Dental measurements are given in Table I and II.

Table I

Tooth	Specimen No.	Length	Width	Max. crown height	Total tooth height	
P3	IVPP V20187.1	0.98	2.08	_	_	
	IVPP V20187.3	1.36	2.09	3.44	_	
M1	IVPP V20187.4	1.32	_	2.88	4.14	
	IVPP V20187.5	1.23	_	2.0	4.32	
M2	IVPP V20187.6	1.45	2.37	3.04	_	
М3	IVPP V20187.7	1.02	1.73	1.6	3.06	
	IVPP V20187.8	1.07	1.63	1.34	2.43	
	IVPP V20187.9	1.0	1.56	_	_	
	IVPP V20187.10	0.99	1.54	1.17	2.42	
	IVPP V20187.11	1.06	1.69	_	_	
	IVPP V20187.12	1.0	1.57	1.55	2.76	
	IVPP V20187.13	_	_	1.47	2.65	

Measurements (in mm) of upper teeth of *Erenlagus anielae* gen. et sp. nov.

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Table II

?m2

m3

IVPP V20188.6

IVPP V20188.7

IVPP V20188.8

Tooth	Specimen No.	Length	Trigonid width	Talonid width	Max. crown height	Total tooth height		
р3	IVPP V20186	1.45	_	1.0	2.77	5.12		
p4	IVPP V20188.1	1.36	1.37	1.04	2.51	4.96		
	IVPP V20189.1	1.54	1.38	1.08	3.09	4.45		
m 1	IVPP V20188. 2	1.60	1.74	1.13	3.15	-		
	IVPP V20188.3	1.71	1.57	1.28	4.20	4.98		
	IVPP V20188.4	1.80	1.58	1.34	_	-		
	IVPP V20188.5	1.45	1.71	1.38	_	-		
	IVPP V20185 (holotype)	1.63	1.80	1.33	1.74	5.10		

Measurements (in mm) of lower teeth of *Erenlagus anielae* gen. et sp. nov.

1.40

1.33

1.11

IV. SYSTEMATIC PALEONTOLOGY

1.44

1.01

0.99

1.16

2.78

1.75

4.26

Order: Lagomorpha BRANDT, 1855

Family: Indeterminate

Genus: Erenlagus gen. nov.

Type species: Erenlagus anielae sp. nov., the only species.

E t y m o l o g y. The generic name refers to Erenhot (Mongolian Eren Khot; Erlianhaote in Chinese pinyin), the city in Inner Mongolia Autonomous Region (China) near the type locality; and Greek *lagos*, hare.

D i a g n o s i s. Small lagomorph of highly developed unilateral hypsodonty. Differs from *Aktashmys montealbus* AVERIANOV & LOPATIN, 2005 in M2 more buccolingually elongated with less persistent buccal groove, lack of any trace of paracristid on p4 and greater reduction of talonid in that tooth, stronger fusion of roots in lower molars and reduction of bony bridges joining them. Differs from *Dawsonolagus antiquus* in having markedly higher degree of hypsodonty, fused roots in lower cheek teeth, less persistent occlusal structures, and formation of dentine connection between trigonid and talonid in lower molars. Differs from *Dituberolagus venustus* TONG, 1997 in being larger and having more complex talonid of p3, protoconid of p3 trigonid enlarged, later formation of occlusal connection between trigonid and talonid asymmetrically placed. Differs from *Gobiolagus* species in being smaller (except from *G. burkei* MENG et al., 2005), in having relatively less reduced p4 talonid and oval (not pear-shaped) p4 trigonid, lack of lingual bridges, but

present occlusal connection between trigonid and talonid on m1 and m2. Differs from *Lushilagus lohoensis* LI, 1965 in greater unilateral hypsodonty and strong fusion of roots on p3-m3. Differs from *Strenulagus* in having smaller size, slightly higher unilateral hypsodonty, narrower p3, lower and less spiky main cusp of p3 trigonid, and slightly more developed metaconid, more reduced M3 with buccal root largely fused with main shaft, more closely joined roots of lower cheek teeth and virtual lack of bony bridges between roots of upper and lower molars. Differs from *Shamolagus* in being smaller, higher unilateral hypsodonty, strong fusion of roots on p3-m3, trigonid and talonid of p4-m2 of similar length, and m1 nearly equal in size to m2.

Erenlagus anielae sp. nov.

(Fig. 2-4)

D i a g n o s i s: the same as for the genus.

E t y mo l o g y. The specific name honors Mrs. Aniela KUNC-GŁĄBIŃSKA (1918-2002), the first author's grandmother, who instilled in her granddaughter a love of nature.

Material examined. Holotype: right m1 (IVPP V20185) (Fig. 2). Paratype: left p3 (IVPP V20186).

Referred material: left P3 (IVPP V20187.1), fragment of left P3 or P4 (IVPP V20187.2), right juv. M1 (IVPP V20187.3), two left fragmentary M1 (IVPP V20187.4, 5), left M2 (IVPP V20187.6), seven M3 (IVPP V20187.7-13), two left p4 (IVPP V20188.1, IVPP V20189.1), right juv. ?m1 (IVPP V20188.2), left juv. m1 (IVPP V20188.3), two right m1 (IVPP V20188.4, V20188.5), right m2 strongly worn (IVPP V20188.6), right m2 (IVPP V20189.2), right m3 (IVPP V20188.7), two left m3 (IVPP V20188.8, IVPP V20190).

Type locality and horizon. Huheboerhe, Erlian Basin, Nei Mongol, China; lower Irdin Manha Fm., Middle Eocene.

D e s c r i p t i o n. The material of *Erenlagus anielae* sp. nov. consists of isolated teeth only, but teeth from almost all loci (except the incisors and P2) are present in the collection.

A single P3 has a broken root part, but it is clear that there was only a single buccal root present. The tooth is trilobate and the outline of the occlusal surface is narrow oval (Fig. 3). The lingual lobe is the largest and semicircular, typical of the Eocene lagomorphs, although it is not very enlarged, forming about 35% of the occlusal surface and it does not encircle any part of the central lobe. The central lobe is smaller but similarly extended anteriorly and compressed buccolingually, while the buccal lobe is smaller and placed distally. The deep reentrant between the lingual and central lobes is placed slightly askew in the buccal direction. A valley between the central and buccal lobes is much shallower and forms a round depression sloping anterobuccally.

The upper molars are scarce and some are broken. Their occlusal surface relatively early in ontogeny becomes completely obliterated and lacks enamel structures such as the crescent or lakes. In that respect *Erenlagus* resembles *Aktashmys* (which however has much more persistent the buccal groove on M2), and specimens referred as *?Lushilagus*



Fig. 2. Type material of *Erenlagus anielae* gen. et sp. nov. A-J: holotype right m1 (IVPP V20185); L-Q: paratype left p3 (IVPP V20186). A, F, N: distal view. B, G, P: buccal view. C, H, Q: lingual view. I, O: anterior view. D, E, K, L: occlusal view. J, M: morphology of the root aperture. The hatched areas indicate the wear surfaces resulted from interdental friction. Scale bar: upper for D, E; middle for A-C, F-J, M-Q; lower for K, L.



Fig. 3. Upper cheek teeth of *Erenlagus anielae* gen. et sp. nov. A: left P3 (IVPP V20187.1); B: right juv. M1 (IVPP V20187.3); C, D: left M2 (IVPP V20187.6); E-G: left M3 (IVPP V20187.7), note fused roots; H-J: right M3 (IVPP V20187.8), buccal root separated from the main shaft. A-C, F, I: occlusal view; D, G-H: anterior view; E, J: distal view. Scale bar: upper for A-D, lower for E-J.

danjingensis by TONG (1997), presenting completely obliterated surfaces of the upper molars (especially M1 and M2).

M1 had two relatively delicate buccal roots placed high on the shaft just below the buccal base of the crown. The occlusal surface of M1 is almost square in a juvenile specimen (Fig. 3B) and becomes oval with a flattened lingual edge in mature individuals. In the shape of the upper molars adult specimens of *Erenlagus anielae* resemble closer *Strenulagus* than *Aktashmys*, the latter having molars compressed much more buccolingually. A juvenile specimen (V20187.3) has a well developed and relatively narrow, but shallow hypostria, of weak persistency. In more worn specimens, the hypostria disappears leaving a lingual flattening or gentle concavity. In a juvenile specimen the paracone and metacone are well-distinguishable; the latter is surrounded by a large crescent lake, which closes at the anterior side, leaving a narrow isolated lake. The crescentic valley is extended at the linguodis-

tal side of the metacone forming an oblique enamel surface. The postcingulum is narrower than the anteroloph. The protocone and hypocone are similar in size, the latter is more rounded lingually, and both are lower than the paracone and metacone. More worn specimens of M1 (IVPP V20187.4, 5) have completely obliterated and gently concave occlusal surface.

M2 is similar in size to M1 but more asymmetric. Its buccal edge is oblique, thus the tooth is wider anteriorly than distally. It has also two buccal roots developed as in M1, but placed more asymmetrically on the shaft; the distal one detaches slightly more dorsally. There is a shallow but well-defined hypostria between the protocone and hypocone; the latter is slightly smaller, positioned more buccally, and rounder. The paracone is higher than the metacone but the latter has a more roundish and larger occlusal surface. Between these cusps a moderately deep buccal basin is present. The buccal groove is partly closed and preserved in two parts: the buccodistal one and the elongated lake in the center of the tooth. The postcingulum is relatively narrow.

M3 is well represented within the sample by specimens at the different stages of wear. The M3 has one buccal root which is attached to the main shaft. In some specimens (IVPP V20187.7, IVPP V20187.10, 11) it is completely fused, forming only a keel-like structure at the buccal side of the shaft (Fig. 3E, G), whereas in others the buccal root is detached from the shaft in its mid-length and forms a separate rootlet, slightly compressed buccolingually (Fig. 3H, J). The degree of the buccal root reduction in M3 of *Erenlagus anielae* resembles that found in *Aktashmys* (AVERIANOV & LOPATIN 2005). The occlusal surface of M3 shows a relatively well-developed trigon with the paracone and metacone similarly shaped and divided by a narrow buccal valley, which, as wear progresses, forms an isolated lake. A greatly reduced postcingulum forms a short narrow shelf, relatively quickly merging with the occlusal surface of the trigon. The protocone is large and in unworn or lightly worn specimens is much higher than the paracone and metacone.

The lower premolars and molars express a high degree of the unilateral hypsodonty. In lightly worn teeth the enamel layer covering the crown at the trigonid portion reaches almost the opening of a root (Fig. 4L, M). The roots are fused in lower cheek teeth to a degree comparable to that observed in *Aktashmys* (see AVERIANOV & LOPATIN 2005) and some specimens of '*Lushilagus*' *danjingensis* (see TONG 1997). The anterior and distal roots of p3 and p4 are fused completely and form a joint root chamber with an oval or 8-shaped opening (Fig. 2M). In m1 the lingual part of the root, which lies under the trigonid portion, forms a lingual extension in the form of a loblet (Fig. 4N), but the roots still have a joint root chamber. The root chambers in mature specimens may be separate, but roots are closely joined (Fig. 2J). The m3 are similar in root structure to premolars and display virtually single root (Fig. 4Q).

The basic morphology of p3 is similar to that observed in *Strenulagus* and *Gobiolagus* (Fig. 2K-Q). The proportions and general structure of p3 in *Erenlagus* closely resembles those found in specimens referred to as '*Lushilagus*' *danjingensis*. They are slightly narrower and anterodistally elongated than those of *Strenulagus shipigouensis* TONG & LEI, 1987 and *S. solaris* LOPATIN & AVERIANOV, 2006, and have a stronger vertical domination of the trigonid over the talonid than in *Gobiolagus*. The trigonid has two cusps, of which the protoconid is significantly larger and dominates over the metaconid located

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Fig. 4. Lower cheek teeth of *Erenlagus anielae* gen. et sp. nov. A-E: right juv. m1 (IVPP V20188.2); F-J: left p4 (IVPP V20188.1); K-P: left juv. m1 (IVPP V20188.3); Q, R: right m3 (IVPP V20188.7); S-U: right m2 (IVPP V20188.6). A, F, K, R, S: occlusal view; B, I, P: distal view; C, H, O, U: lingual view; D, G, L, Q, T: buccal view; E, M, J: anterior view; N: root view. Scale bar: upper for B-E,G-J, L, M, O, P, T, U; lower for A, F, K, N, Q-S.

more distally at the lingual side of the trigonid. The anterobuccal cusp of the trigonid is the highest of all cusps of p3 and forms an oblique occlusal surface sloping distally along the p3. There are two reentrants in p3, of different persistence; a less persistent anterolingual reentrant, between the two cusps of the trigonid and a more persistent hypoflexid, between the trigonid and talonid, at the buccal side.

A well-preserved p4 (Fig. 4F-J) is moderately worn. The crown shows reduction of the talonid similar to that of *Strenulagus*; the lingual side of the talonid tapers lingually and

narrows towards the root portion, thus at more advanced wear stages the occlusal surface of the talonid becomes smaller than that of the trigonid, although this disparity is relatively smaller than in most *Gobiolagus* species (see MENG et al. 2005; FOSTOWICZ-FRELIK et al. 2012). There is no trace of the paralophid unlike in *Aktashmys montealbus* on p4 (AVERIANOV & LOPATIN 2005).

The m1 and m2 are similar in structure; they have anterodistally compressed trigonids (weaker than in *Shamolagus*) and longer but narrower talonids, which in juvenile specimens have a well-developed hypoconulid, separated from the hypoconid by a wide reentrant. In lightly worn specimens the trigonid is distinctly bicuspid, with higher and more pointy metaconid aligned with the protoconid. In strongly worn specimens a wear surface forms an area which stretches over the distal margin of the trigonid and anterior part of the talonid, joining both conids. Such a structure is rarely observed in Eocene lagomorphs and is more typical for some mimotonids. It was also reported from strongly worn specimens of *Aktashmys montealbus* (AVERIANOV & LOPATIN 2005: fig. 4d) and is observed in some specimens of '*Lushilagus*' danjingensis (see TONG 1997: fig. 29h, pl. 4:7). In *Erenlagus* this merging surface is developed more lingually than in '*Lushilagus*' danjingensis and in m1 of *Aktashmys montealbus* (see AVERIANOV & LOPATIN 2005: fig. 4d).

The trigonid of m3 is similarly anterodistally compressed as in m1 and m2. The hypoconulid is slightly smaller than in '*Lushilagus*' *danjingensis*. The enamel layer covering the distal edge of the trigonid is relatively thick and it remains even in strongly worn specimens as the only eminent structure at the occlusal surface (Fig. 4Q, R).

V. DISCUSSION

The evolution of Lagomorpha since its very beginning is characterized by a mosaicity of dental and cranial characters that obscures phylogenetic relationships within this group. Nevertheless, features such as increase of the crown height, strong fusion of the roots, and lesser differences in size and shape between trigonids and talonids in the lower cheek teeth are considered progressive in Lagomorpha (MENG et al. 2005; AVERIANOV & LOPATIN 2005; LOPATIN & AVERIANOV 2006; FOSTOWICZ-FRELIK et al. 2012; FOSTOWICZ-FRE-LIK 2013). In that respect, *Erenlagus anielae* sp. nov. can be considered as one of the most advanced species of the Middle Eocene stem lagomorphs. The dental morphology and degree of hypsodonty in *Erenlagus* closely resemble those of *Aktashmys* and specimens from Shipigou (Henan, China) described as ?Lushilagus danjingensis by TONG (1997). The latter form most probably belongs to *Erenlagus*, as it is more hypsodont and overall more progressive than Lushilagus lohoensis (the type species of Lushilagus). 'Lushilagus' danjingensis was originally described by TONG & LEI (1987) based on a limited material. TONG (1997) described a much more abundant sample from Henan and noted that the form differs from *Lushilagus* at the generic level, but left the specimens in open nomenclature. The revision of the Henan material is beyond the scope of this paper; however, we note that our new genus may have been phylogenetically close to the lagomorphs from the Middle Eocene (Irdinmanhan) of Henan, which could have migrated north to Nei Mongol. The northward fauna migration is implied also by another lagomorph taxon from the Huheboerhe area, that is Strenulagus solaris found in the same beds, which shows some more

advanced dental characters (e.g. a stronger curvature of the upper cheek teeth) than *Strenulagus shipigouensis* from Henan (FOSTOWICZ-FRELIK et al. in press). A possibility arises that the Henan lagomorph-bearing deposits are slightly older than currently accepted, probably closer to the Arshantan/Irdinmanhan boundary.

The exact phylogenetic relations of the Eocene stem lagomorphs are still a matter of debate. AVERIANOV & LOPATIN (2005) erected Strenulagidae composed of *Aktashmys*, *Gobiolagus*, *Lushilagus*, *Shamolagus*, and *Strenulagus*; the type genus at the moment of family name creation consisted of a single species, *Strenulagus shipigouensis*. Among included taxa, *Shamolagus* and *Lushilagus* represent the most primitive dental morphotype (e.g., relatively low crowned cheek teeth and M3 not significantly reduced), thus it is probable that they are more closely related to *Dawsonolagus antiquus* than to other members of 'Strenulagidae'. *Gobiolagus* and *Strenulagus* indeed may form a closely related group; they share a set of dental characters that are progressive in lagomorphs, such as root fusion and the increase in the crown height. Furthermore, they share a peculiar structure of p4, with a reduced talonid and a pear-shaped trigonid (characters more strongly expressed in the *Gobiolagus* lineage; see MENG et al. 2005, FOSTOWICZ-FRELIK et al. 2012).

Erenlagus shares root fusion and crown height increase with *Gobiolagus* and *Strenulagus*, its p4 structure also resembles that of *Strenulagus*, but it shares reduction of M3 buccal roots and formation of the central occlusal isthmus in lower cheek teeth with *Aktashmys*, *?Lushilagus danjingensis*, and an enigmatic Middle Eocene genus, *Dituberolagus*. The formation of the central occlusal isthmus between the trigonid and talonid is slightly different in all three forms (more lingual in *Erenlagus*), but in general such a feature is rare among stem lagomorphs and resembles the condition found in some mimotonids. This feature is most probably is a plesiomorphic character. Whether such differences merit the distinction at the family or subfamily level should become clearer after comprehensive phylogenetic analysis.

CONCLUSIONS

A new stem lagomorph *Erenlagus anielae* sp. nov. from Nei Mongol represents a minute and highly semihypsodont species closer related to '*Lushilagus*' *danjingensis* from Henan (China) and *Aktashmys montealbus* (Kyrgyzstan). This finding, along with other recently discovered lagomorph fossils from the Erlian Basin suggests that the region was important for early diversification of stem lagomorphs, and at the same time probably an area in connection with other regions of Central and East Asia.

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REFERENCES

- AVERIANOV A. O., LOPATIN A. V. 2005. Eocene Lagomorpha of Asia: 1. Aktashmys (Strenulagidae fam. nov.). Paleontological Journal, **39**: 308-317.
- CHOW M., ROŽDESTVENSKIJ A. K. 1960. Exploration in Inner Mongolia a preliminary account of the 1959 fieldwork of the Sino-Soviet Paleontological Expedition (SSPE). *Vertebrata Palasiatica*, **4**: 1-10.
- DAWSON M. R., LI C., QI T. 1984. Eocene ctenodactyloid rodents (Mammalia) of eastern central Asia. Carnegie Museum of Natural History Special Publication, 9: 138-150.
- FOSTOWICZ-FRELIK Ł. 2013. Reassessment of *Chadrolagus* and *Litolagus* (Mammalia: Lagomorpha) and a new genus of North American Eocene Lagomorpha from Wyoming. *American Museum Novitates*, **3773**: 1-76.
- FOSTOWICZ-FRELIK Ł., LI C., LI Q., MENG J., WANG Y. (in press). *Strenulagus* (Mammalia: Lagomorpha) from the Middle Eocene Irdin Manha Formation of the Erlian Basin, Nei Mongol, China. *Acta Geologica Sinica* (*English Edition*).
- FOSTOWICZ-FRELIK Ł., LI C., MENG J., WANG Y. 2012. New *Gobiolagus* (Mammalia: Lagomorpha) material from the middle Eocene of Erden Obo (Nei Mongol, China). *Vertebrata PalAsiatica*, **50**: 219-236.
- FOSTOWICZ-FRELIK Ł., TABRUM A. R. 2009. Leporids (Mammalia, Lagomorpha) from the Diamond O Ranch Local Fauna, latest Middle Eocene of southwestern Montana. *Annals of Carnegie Museum*, **78**: 253-271.
- JIANG H. 1983. Division of the Paleogene strata in the Erlian Basin of Inner Mongolia. *Nei Mongol Geology*, **55**: 18-36. [In Chinese].
- JIN X. 2005. Mesonychids from Lushi Basin, Henan Province, China. Vertebrata PalAsiatica, 43: 151-164.
- JIN X. 2012. New mesonychid (Mammalia) material from the lower Paleogene of the Erlian Basin, Nei Mongol, China. Vertebrata PalAsiatica, 50: 245-257.
- KRAATZ B. P., MENG J., WEKSLER M., LI C. 2010. Evolutionary patterns in the dentition of Duplicidentata (Mammalia) and a novel trend in the molarization of premolars. *PLoS ONE* 5: e12838.
- LI C. 1965. Eocene leporids of North China. Vertebrata PalAsiatica, 9: 23-36. [In Chinese and English].
- LI C., MENG J., WANG Y. 2007. *Dawsonolagus antiquus*, a primitive lagomorph from the Eocene Arshanto Formation, Nei Mongol, China. *Bulletin of Carnegie Museum*, **39**: 97-110.
- LI Q. 2012. Middle Eocene cricetids (Rodentia, Mammalia) from the Erlian Basin, Nei Mongol, China. Vertebrata PalAsiatica, **50**: 237-244.
- LI Q., MENG J. 2013. Eocene ischyromyids (Rodentia, Mammalia) from the Erlian Basin, Nei Mongol, China. *Vertebrata PalAsiatica*, **51**: 289-304.
- LI Q., MENG J. (in press). New ctenodactyloid rodents from the Erlian Basin, Nei Mongol, China and the phylogenic relationships of Eocene Asian ctenodactyloids. *American Museum Novitates*.
- LOPATIN A. V., AVERIANOV A. O. 2006. Eocene Lagomorpha (Mammalia) of Asia: 2. Strenulagus and Gobiolagus (Strenulagidae). Paleontological Journal, 40: 198-206.
- LOPATIN A. V., AVERIANOV A. O. 2008. The earliest lagomorph (Lagomorpha, Mammalia) from the basal Eocene of Mongolia. *Doklady Biological Sciences*, **419**: 131-132.
- MATTHEW W. D., GRANGER W. 1924. New Carnivora from the Tertiary of Mongolia. American Museum Novitates, 104: 1-9.
- MATTHEW W. D., GRANGER W. 1925. New mammals from the Shara Murun Eocene of Mongolia. *American Museum Novitates*, **196**: 1-11.

- MENG J., HU Y., LI C. 2005. Gobiolagus (Lagomorpha, Mammalia) from Eocene Ula Usu, Inner Mongolia, and comments on Eocene lagomorphs of Asia. Palaeontologia Electronica, 8(1): 7A: 23p.; http://palaeoelectronica.org/2005_1/meng7/meng7.pdf
- MENG J., KRAATZ B. P., WANG Y., NI X., GEBO D. L., BEARD K. C. 2009. A new species of Gomphos (Glires, Mammalia) from the Eocene of the Erlian Basin, Nei Mongol, China. American Museum Novitates, 3670: 1-11.
- MENG J., WANG Y., NI X., BEARD K. C., SUN C., LI Q., JIN X., BAI B. 2007. New stratigraphic data from the Erlian Basin: implications for the division, correlation, and definition of Paleogene lithological units in Nei Mongol (Inner Mongolia). American Museum Novitates, 3570: 1-31.
- MENG J., WYSS A. R. 2001. The morphology of *Tribosphenomys* (Rodentiaformes, Mammalia): phylogenetic implications for basal Glires. *Journal of Mammalian Evolution*, **8**: 1-71.
- NIX, MENG J., BEARD K. C., GEBO D. L., WANG Y., LI C. 2010. A new tarkadectine primate from the Eocene of Inner Mongolia, China: phylogenetic and biogeographic implications. *Proceedings of the Royal Society B: Biological Sciences*, 277: 247-256.
- OSBORN H. F. 1924. Andrewsarchus, giant mesonychid of Mongolia. American Museum Novitates, 146: 1-5.
- QIT. 1987. The Middle Eocene Arshanto Fauna (Mammalia) of Inner Mongolia. *Annals of Carnegie Museum*, **56**: 1-73.
- ROSE K. D., BURKE DELEON V., MISSIAEN P., RANA R. S., SAHNI A., SINGH L., SMITH T. 2008. Early Eocene lagomorph (Mammalia) from Western India and the early diversification of Lagomorpha. *Proceedings of the Royal Society Series B*, **275**: 1203-1208.
- RUSSELL D. E., ZHAI R. 1987. The Paleogene of Asia: mammals and stratigraphy. *Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre*, **52**: 1-488.
- TONG Y. 1997. Middle Eocene small mammals from Liguanqiao Basin of Henan Province and Yuanqu Basin of Shanxi Province, Central China. *Palaeontologia Sinica, New Series C*, **26**: 1-256. [In Chinese with English summary].
- TONG Y., LEI Y. 1987. Fossil lagomorphs (Mammalia) from the Hetaoyuan Eocene of Xichuan, Henan. Vertebrata PalAsiatica, 25: 208-221. [In Chinese with English summary].
- TONG Y., ZHENG S., QIU Z. 1995. Cenozoic mammal ages of China. *Vertebrata PalAsiatica*, **33**: 290-314. [In Chinese with English summary].
- WANG Y., MENG J., BEARD K. C., LI Q., NI X., GEBO D. L., BAI B., JIN X., LI P. 2010. Early Paleogene stratigraphic sequences, mammalian evolution and its response to environmental changes in Erlian Basin, Inner Mongolia, China. Science in China Earth Sciences, 53: 1918-1926.
- WANG Y., MENG J., JIN X. 2012. Comments on Paleogene localities and stratigraphy in the Erlian Basin, Nei Mongol, China. Vertebrata PalAsiatica, 50: 181-203. [In Chinese with English summary].