

Arnebolagus, the oldest eulagomorph, and phylogenetic relationships within the Eocene Eulagomorpha new clade (Mammalia, Duplicidentata)

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Abstract.—*Arnebolagus leporinus* Lopatin and Averianov, 2008, known previously from a single tooth (P3) from the early Eocene Bumban Member of Naran Bulak Formation at Tsagan-Khushu locality in Mongolia, is redescribed based on additional specimens from the type locality. Phylogenetic relationships of Eocene stem lagomorphs from Asia and North America are reconstructed for the first time based on a parsimony analysis of 54 morphological characters and 32 taxa. Two new node-based clades are proposed, stemming from the most-recent common ancestor of *Lepus* Linnaeus, 1758 and *Dawsonolagus* Li, Meng, and Wang, 2007 (Eulagomorpha new clade, ‘lagomorphs of the modern aspect’) and from the most-recent common ancestor of *Lepus* and *Gobiolagus* Burke, 1941 (Epilagomorpha new clade). *Arnebolagus* Lopatin and Averianov, 2008 is geologically oldest and the most plesiomorphic eulagomorph, similar to *Dawsonolagus* from the early Eocene Arshanto Formation of China in its weakly pronounced, unilateral hypsodonty of the upper cheek teeth and its brachyodont lower cheek teeth with separate roots. *Arnebolagus* is more plesiomorphic than *Dawsonolagus* in having two roots of P4. *Arnebolagus* is the oldest known eulagomorph, the only taxon known from the earliest Eocene Bumbanian Asiatic Land Mammal Age (ALMA). The other Asiatic early Eocene eulagomorphs (*Dawsonolagus*, *Aktashmys* Averianov, 1994, and *Romanolagus* Shevyreva, 1995) come from the Arshantan ALMA.

Introduction

The order Lagomorpha includes the modern hares and rabbits (Leporidae) and pikas (*Ochotona* Link, 1795, the only Recent genus of Ochotonidae). Lagomorphs have a long history dating back to the Eocene. The Paleogene stem lagomorphs have been referred previously to Leporidae (Matthew and Granger, 1923; Burke, 1934, 1941; Wood, 1940; Dawson, 1958, 1967, 1970, 2007; Meng and Hu, 2004; Meng et al., 2005; Fostowicz-Frelik and Tabrum, 2009; Korth and Dharmapuri, 2017), to Palaeolagidae within Lagomorpha (Gureev, 1964; Fostowicz-Frelik et al., 2012; Fostowicz-Frelik, 2013), or to Lagomorpha incertae sedis (Li et al., 2007; Lopatin and Averianov, 2008; Fostowicz-Frelik and Li, 2014). Averianov and Lopatin (2005) placed some Asiatic Eocene taxa into the family Strenulagidae within Lagomorpha.

With the advent of phylogenetic systematics, the term Lagomorpha was restricted to the crown group stemming from the most common ancestor of *Ochotona* and Leporidae. Duplicidentata is the total group defined as all members of Glires sharing a more recent common ancestor with Lagomorpha than with Rodentia (Wyss and Meng, 1996; Meng and Wyss, 2005). Two clades were proposed within the stem Lagomorpha: Lagomorphomorpha, the clade stemming from the most common ancestor of *Mimotona* Li, 1977 and Lagomorpha; and Leporomorpha, the clade including all lagomorphs sharing a more recent common ancestor with Leporidae than with *Ochotona* (Meng and Wyss, 2001). However, there is a considerable morphological gap between the Paleocene stem lagomorphs (Mimotonidae) and the Eocene stem lagomorphs, which shares numerous dental similarities with modern lagomorphs and often regarded as

‘lagomorphs of modern aspect’ (Li et al., 2007; Fostowicz-Frelik and Li, 2014; Fostowicz-Frelik et al., 2015a; Fostowicz-Frelik, 2017; Ruedas et al., 2018). This morphological similarity was the main reason for the referral of these Eocene taxa to Lagomorpha and even Leporidae in the previous literature. The tarsal bones of the early Eocene stem lagomorphs are so similar with the bones in modern lagomorphs that Rose et al. (2008) supposed the presence of the crown Lagomorpha and even Leporidae in the early Eocene. In this report, we propose a new clade, Eulagomorpha new clade, uniting these Eocene stem lagomorphs and the crown group Lagomorpha. This clade is based on the phylogenetic analysis presented herein and is defined in the Systematic paleontology section.

Materials and methods

Dental measurements.—The measurements are the tooth crown length (L) and width (W). All measurements are in mm.

Phylogenetic analysis.—We used characters mostly employed in the diagnostics of Eocene stem lagomorphs (Burke, 1934, 1941; Dawson, 1970; Zhang et al., 2001; Meng and Hu, 2004; Averianov and Lopatin, 2005; Meng et al., 2005; Lopatin and Averianov, 2006; Li et al., 2007; Fostowicz-Frelik and Tabrum, 2009; Fostowicz-Frelik et al., 2012; Fostowicz-Frelik and Li, 2014), as well as some new characters recognized in this study. Because most of the Eocene stem lagomorphs are represented by jaw fragments and dentitions, we utilized mostly dental characters and those of cranial characters that can be checked at least in some Eocene taxa.

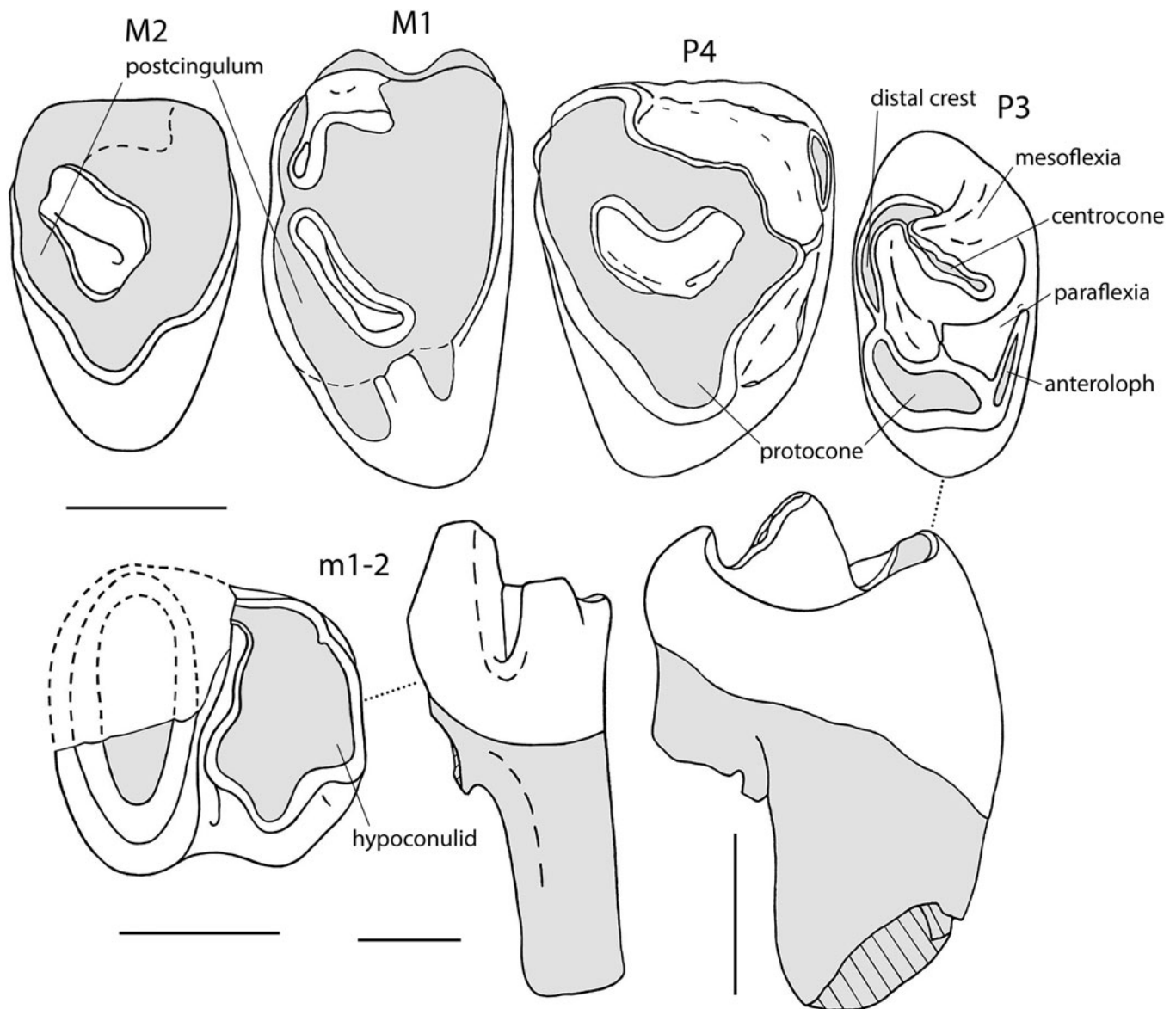


Figure 1. Known dentition of *Arnebolagus leporinus* Lopatin and Averianov, 2008, Tsagan-Khushu locality, Nemegt Depression, Mongolia, basal Eocene, Bum-ban Member of Naran Bulak Formation: right M2 (PIN 3104/918), occlusal view; right M1 (PIN 3104/917), occlusal view; left P4 (PIN 3104/915), occlusal view (reversed); right P3 (PIN 3104/914, holotype), occlusal and distal views; m1-2, left (PIN 3104/920), occlusal and labial views. Scale bars = 1 mm.

A total of 32 taxa and 54 characters (Appendices 1, 2), formed the data matrix (Appendix 3), assembled using Mesquite 3.61 (Maddison and Maddison, 2019). Three multistate characters (3, 19, and 20) were ordered. The eurymylid *Rhombomylus turpanensis* Zhai, 1978 from the early Eocene of China and Mongolia (Dashzeveg and Russell, 1988; Meng et al., 2003) was used as an outgroup. The scoring of this taxon was based on the detailed description provided by Meng et al. (2003). The ingroup taxa were scored based on the specimens and casts from the AMNH, PIN, and ZIN collections and from the literature (Appendix 1). For obtaining the tree statistics, consensus tree, and distribution of characters, we used WinClada 1.00.08 (Nixon, 1999). The character-taxon matrix was analyzed using PRAP, parsimony ratchet analysis using PAUP (Müller, 2007), and PAUP* 4.0b10 (Swofford, 2002).

To increase tree resolution and recover better phylogenetic signal, we performed a second analysis, including a successive weighting for various characters (Farris, 1969). Using PAUP, the characters were reweighted by the maximum value of rescaled consistency indices (RC), and a heuristic search with 10,000 random sequence addition replicates, and TBR (tree bisection and reconnection) branch swapping was performed. Thirty-one characters got a weight of < 1 during the reweighting.

Repositories and institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZIN, Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia.

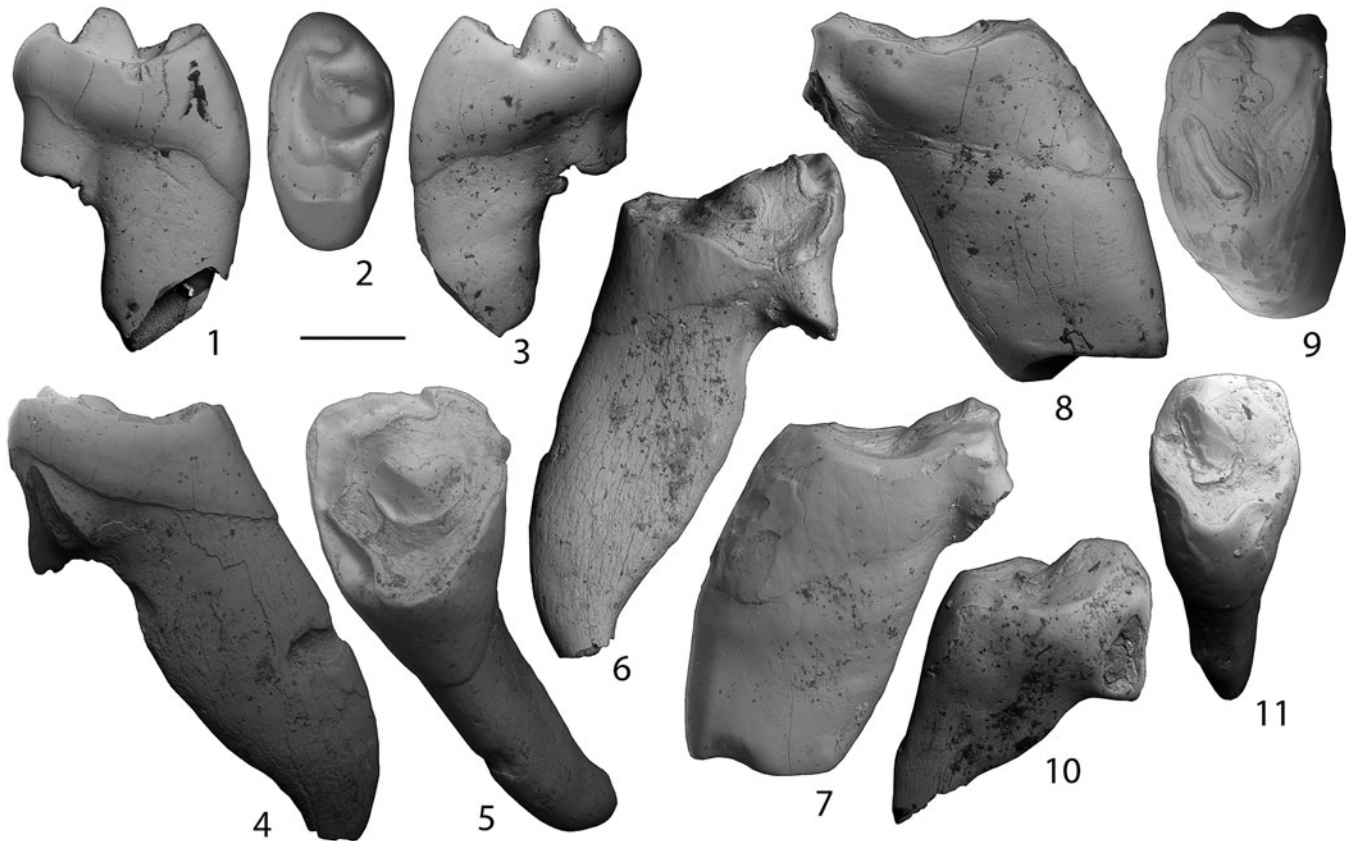


Figure 2. Upper dentition of *Arnebolagus leporinus* Lopatin and Averianov, 2008, Tsagan-Khushu locality, Nemegt Depression, Mongolia, basal Eocene, Bumban Member of Naran Bulak Formation: (1–3) PIN 3104/914, holotype, right P3 in distal (1), occlusal (2), and mesial (3) views; (4–6) PIN 3104/915, left P4 in mesial (4), occlusal (5), and distal (6) views; (7–9) PIN 3104/917, right M1 in mesial (7), distal (8), and occlusal (9) views; (10, 11) PIN 3104/918, right M2 in mesial (10) and occlusal (11) views. Scale bar = 1 mm.

Systematic paleontology

Mammalia Linnaeus, 1758

Glires Linnaeus, 1758

Duplicidentata Illiger, 1811

Lagomorphomorpha Meng and Wyss, 2001

Eulagomorpha new clade

Remarks.—Eulagomorpha n. clade is here defined as a node-based clade that contains the most-recent common ancestor of *Lepus* Linnaeus, 1758 and *Dawsonolagus* Li, Meng, and Wang, 2007 and all of its descendants.

Arnebolagus Lopatin and Averianov, 2008

Type species.—*Arnebolagus leporinus* Lopatin and Averianov, 2008.

Other species.—Type species only.

Revised diagnosis.—Referred to Eulagomorpha n. clade because of one labial root of P3 and trigonid and talonid of lower cheek teeth connected by lingual bridge on worn teeth. Similar to *Dawsonolagus* and differs from other Eulagomorpha n. clade by less pronounced unilateral hypsodonty of upper cheek teeth, separate roots of lower

cheek teeth, and m1-2 hypoconulid separated from the rest of talonid by labial fold only. Similar to *Dawsonolagus* and *Lushilagus danjiangensis* Tong and Lei, 1987 and differing from other Eulagomorpha n. clade by brachyodont lower cheek teeth. Differs from *Dawsonolagus* by two labial roots of P4.

Arnebolagus leporinus Lopatin and Averianov, 2008

Figures 1–3

2008 *Arnebolagus leporinus* Lopatin and Averianov, p. 131, fig. 1.

Holotype.—PIN 3104/914, a right P3.

Occurrence.—Tsagan-Khushu locality, Nemegt Depression, Ömnögovi Aimag, Mongolia; base of Bumban member, Naran Bulak Formation, earliest Eocene.

Description.—The upper cheek teeth are unilaterally hypsodont, with the lingual crown side approximately two times as high as the labial crown side on little worn teeth. The P3–4 are nonmolariform.

The P3 is oval in crown outline, approximately twice in transverse width than in mesiodistal length (Figs. 1, 2.1–2.3). The centrocone is high and massive, positioned closer to the

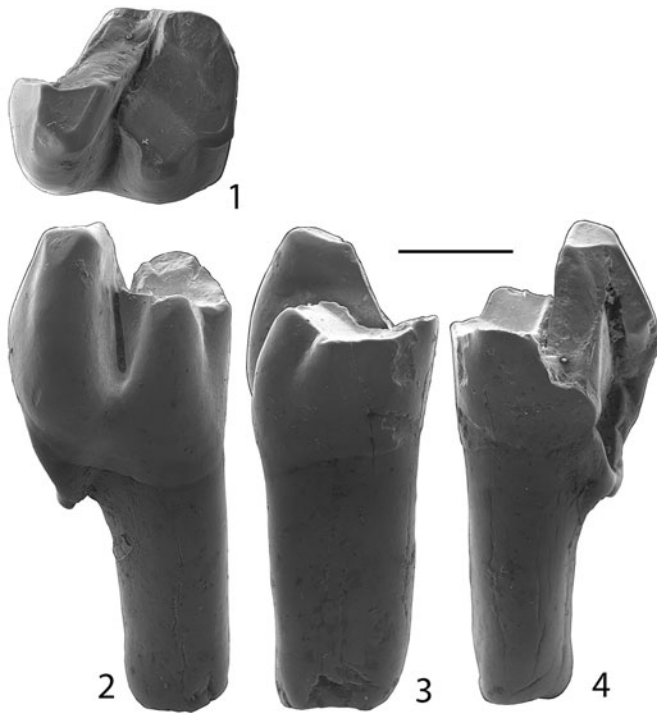


Figure 3. Left lower molar (m1 or m2, PIN 3104/920) of *Arnebolagus leporinus* Lopatin and Averianov, 2008, Tsagan-Khushu locality, Nemegt Depression, Mongolia, basal Eocene, Bumban Member of Naran Bulak Formation: in occlusal (1), labial (2), distal (3), and lingual (4) views. Scale bar = 1 mm.

labial margin of the crown. The anteroloph is short, straight, and terminates slightly labial to the line of the lingual wall of the centrocone. At the early wear stage, the anteroloph and posterior crest are separated from the wear facet on the protocone. The mesoflexia is half as long as the paraflexia. The paraflexia is divided in the middle by a narrow crest formed by projections of the lingual wall of the centrocone and the labial wall of the protocone. One labial root is present.

The P4 is subtriangular, with a flattened labial side and a pointed lingual side (Figs. 1, 2.4–2.6). The crown is dominated by a large centrocone, which is compressed labiolingually. The protocone is small and flattened mesiodistally. PIN 3104/915 is moderately worn, with wear facets on the centrocone, protocone, and posterior crest. Also, there is a transverse wear facet mesial to the centrocone and protocone that connects these cusps. This wear facet closes the paraflexia mesially. The mesoflexia is slightly shorter than the paraflexia. The anteroloph is in shape of a weak cingulum extending along the whole mesial margin of the crown and connecting with the labial cingulum. The labial

cingulum is interrupted mesial to the worn distal crest. There are two labial roots. The large lingual root is swollen in the middle part and tapers toward the distal end.

The labial roots of M1 and M2 are well separated. M1 is transversely wide, 1.4 times labiolingually wider than mesiodistally long (Figs. 1; 2.7–2.9). The lingual part is similar in width with the labial part. PIN 3104/917 is heavily worn, with most of the crown structures obliterated by wear. The fold separating the trigon and the postcingulum is still present but closed distally. Unworn enamel is present in the distolabial corner of the crown. Two wear facets extend on the lingual side at the postcingulum and protocone.

M2 is smaller than M1, with crown width:length ratio of 1.3, similar to that of M1. The labial crown margin is straight, and the lingual part is compressed mesiodistally (Figs. 1; 2.10, 2.11). In PIN 3104/919, most of the crown is heavily worn. Enamel remains only on the distal side of the trigon and partially within the fold separating the trigon and postcingulum.

The single known lower molar (PIN 3104/920, m1 or m2; Figs. 1, 3) is broken at the mesiolingual corner of the trigonid. The crown is brachyodont, with the labial crown side only a little deeper than the labial one. The trigonid is higher and wider than the talonid. The crown is moderately worn and the trigonid and talonid are connected lingually by a relatively wide bone bridge. The labial fold, separating the trigonid and talonid, extends deeply for more than half of the preserved crown height. There is a remnant of the hypoconulid separated from the rest of the talonid by a shallow labial fold. On the distal side of the hypoconulid, there is a polished surface likely representing the contact facet with the trigonid of the succeeding molar. There are two well-separated roots. The mesial root is mostly missing. The distal root is higher than the preserved talonid and somewhat compressed mesiodistally.

Materials.—PIN 3104/915, left P4; 3104/917, right M1; 3104/918, right M2; 3104/920, left lower molar (m1 or m2).

Measurements.—PIN 3104/914 (holotype, P3): L = 1.2, W = 2.3; PIN 3104/915 (P4): L = 1.4, W = 2.2; PIN 3104/917 (M1): L = 1.5, W = 2.1; PIN 3104/918 (M2): L = 1.5, W = 1.9.

Remarks.—PIN 3104/915 differs from the P4 typical for the stem lagomorphs by the crown shape, which is not oval, and by a very large lingual root. The latter character is more appropriate for a molar. An M1 with centrocone is present in *Dawsonolagus* (Li et al., 2007: fig. 4A). However, PIN 3104/915 lacks the postcingulum and thus could not be interpreted as a molar.

Table 1. Statistics for equal weight (PRAP and PAUP) and reweight (PAUP) analyses.

Parameters	Equal weight analysis	Reweight analysis 1	Reweight analysis 2	Reweight analysis 3
N, number of trees	131	197	203	202
L, tree length	135	51.79	48.20	48.20
CI, consistency index	0.4889	0.7233	0.7509	0.7509
HI, homoplasy index	0.5111	0.2767	0.2491	0.2491
RI, retention index	0.7335	0.8939	0.9071	0.9071
RC, rescaled consistency index	0.3635	0.6466	0.6812	0.6812

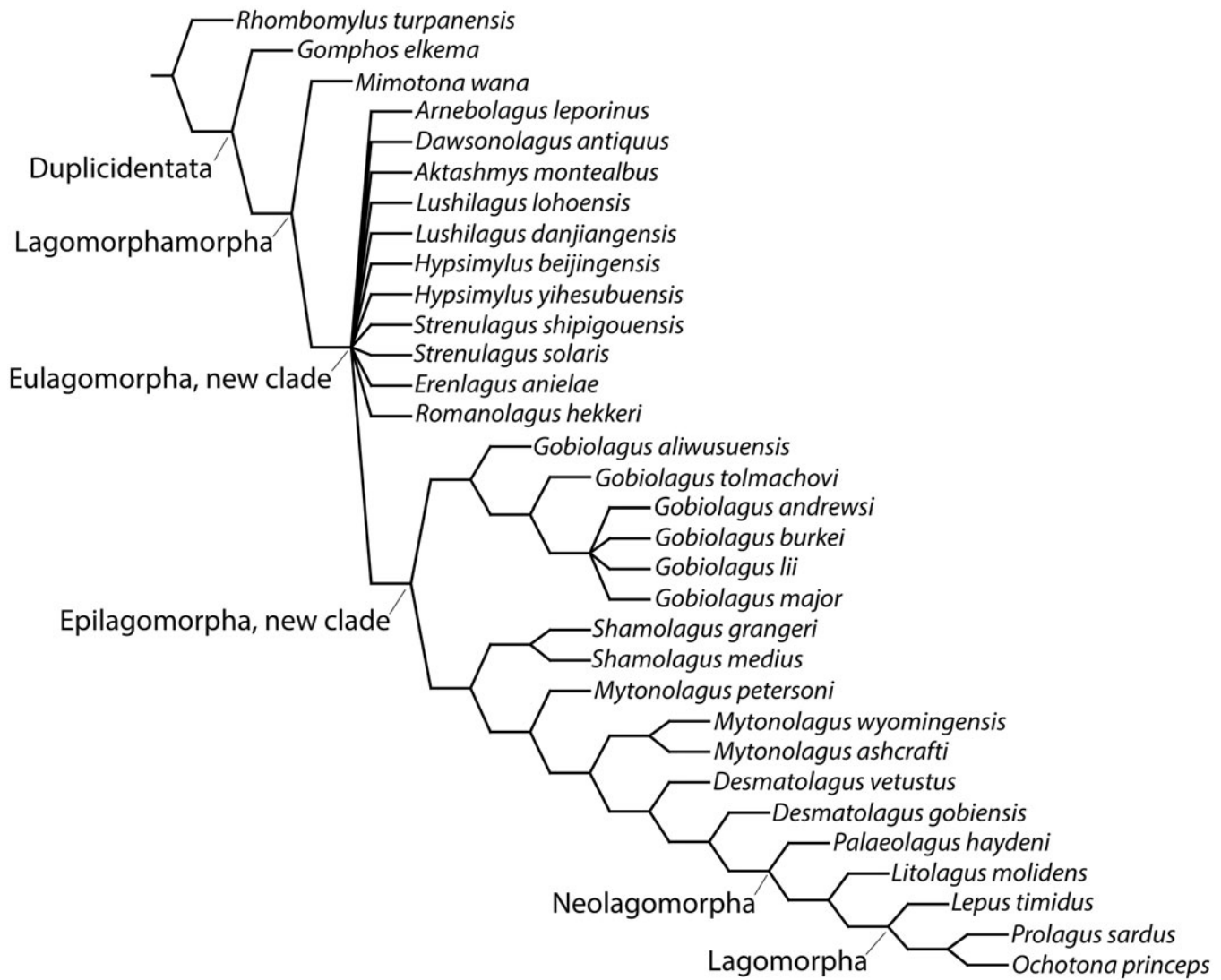


Figure 4. The strict consensus tree of 202 trees produced by PAUP reweighted analysis. See Appendices 1, 2 and 3 for taxon list, character list, and data matrix, respectively.

Phylogenetic analysis

The phylogenetic analysis presented here focuses on the interrelationships among the Asiatic Eocene stem lagomorphs. Fostowicz-Frelik (2013) provided a thorough phylogenetic analysis of Paleogene North American stem lagomorphs based on distribution of 44 morphological characters. Most of the cranial characters used in that analysis cannot be checked for more fragmentary materials on Asiatic Eocene stem lagomorphs and some dental characters require considerable ontogenetic series of the dentition that are not available for most of the Asiatic taxa.

This analysis produced 968 most-parsimonious trees (see Table 1 for tree statistics). The strict consensus tree has poor resolution. The relationships within the crown Lagomorpha are fully resolved and *Palaeolagus haydeni* Leidy, 1856 is the sister taxon to that group. Most other Paleogene stem lagomorph taxa are collapsed to a polytomy. This result is largely affected by incomplete nature of the majority of Eocene stem lagomorphs. In the successive weighting analysis, tree statistics

stabilized after three successive runs (Table 1). The strict consensus of 202 trees obtained in the last and preferred analysis is illustrated in Figure 4.

Lagomorpha, the node-based clade stemming from the most-recent common ancestor of *Mimotona* and Lagomorpha (Meng and Wyss, 2001), is supported in our analysis by two new unambiguously optimized synapomorphies: dI2 groove present [13(1)] and p3 single-rooted [41(1)]. In the analysis by Meng and Wyss (2001), it was supported by nine characters. The node is a polytomy consisting of the Eocene Asiatic and North American stem lagomorphs that have been traditionally referred to the Lagomorpha or even Leporidae (see Introduction) and more derived Oligocene to Recent lagomorphs. This cluster of lagomorphs ‘of the modern aspect’ (Li et al., 2007) is supported in our analysis by ten unambiguously optimized synapomorphies: P3 with one labial root [23(1)]; P4 with one labial root [25(1)]; M3 double-rooted [32(1)]; p4, m1–3 roots fused or connected by a bony bridge [36(1)]; p3 trigonid narrower than talonid [38(1)]; p4 paracristid absent [44(1)]; p4

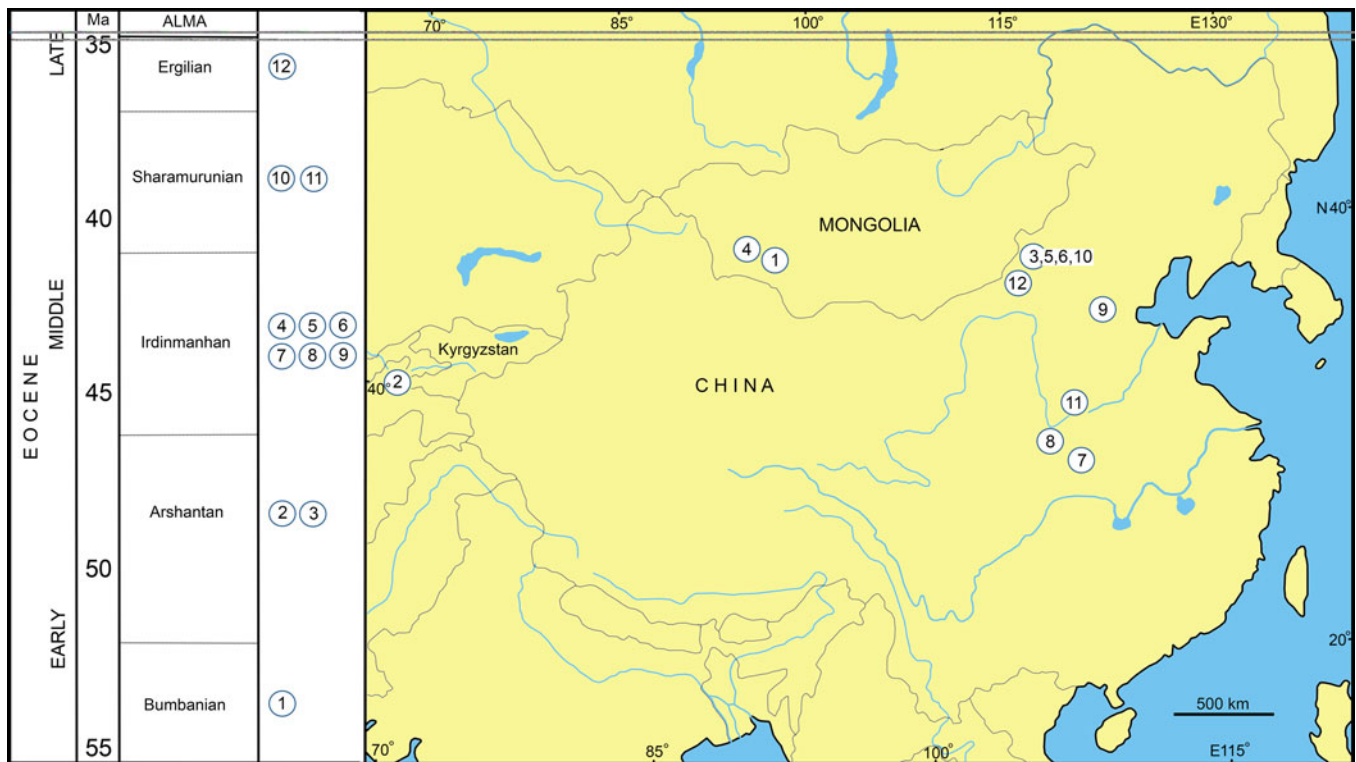


Figure 5. Stratigraphic (left) and geographic (right) positions of the main occurrences of the Eocene Eulagomorpha n. clade in Asia: Occurrences: 1 = Bumban Member, Naran Bulak Formation, Mongolia; 2 = Alay beds, Kyrgyzstan; 3 = Arshanto Formation, Inner Mongolia, China; 4 = Khaychin Formation, Mongolia; 5 = Irdin Manha Formation, Inner Mongolia, China; 6 = Ulan Shireh Formation, Inner Mongolia, China; 7 = Hetaoyan Formation, Henan, China; 8 = Lushi Formation, Henan, China; 9 = Changxiandian Formation, Beijing, China; 10 = Shara Murun Formation, Inner Mongolia, China; 11 = Heti Formation, Shanxi, China; 12 = Ulan Gochu Formation, Inner Mongolia, China.

and m1-3 trigonid and talonid connected lingually on worn teeth [45(1) and 47(1)]; m1-2 hypoconulid separated by labial and lingual folds [49(1)]; and m1-2 similar in size [50(1)].

However, there are no sufficient characters to resolve the relationship of these taxa. Under the current topology, some of these characters are reversed in a number of Asiatic Eocene taxa. Two labial roots of P3 and P4 [23(0) and 25(0)] are present in *Hypsomyilus yihesubuensis* Meng and Hu, 2004, *Strenulagus shipigouensis* Tong and Lei, 1987, and *Gobiolagus major* Burke, 1941; the latter character is also found in *Gobiolagus lii* Zhang, Dawson, and Huang, 2001. M3 is three-rooted [32(0)] in *Dawsonolagus antiquus* Li, Meng, and Wang, 2007, according to the original description (Li et al. 2007: p. 102) but only two roots are evident on the published photograph (Li et al., 2007: fig. 4A). The roots of lower molars are separate [36(0)] in *D. antiquus* and *Arnebolagus leporinus*. The p3 trigonid is subequal to the talonid [38(0)] in *Lushilagus danjiangensis*. The p4 paracristid present [44(0)] in *Aktashmys montealbus* Averianov, 1994. The labial and lingual folds separating trigonid and talonid are of similar depth [45(0)] in *Aktashmys montealbus*, *H. beijingensis* Zhai, 1977, and *Strenulagus shipigouensis*. A similar character regarding the trigonid and talonid separation on lower molars [47(0)] is present in *Lushilagus danjiangensis* and *H. beijingensis*. The hypoconulid of m1-2 is separated by the labial fold only [49(0)] in *Arnebolagus leporinus* and *D. antiquus*. The m2 is larger than m1 [50(1)] in *D. antiquus*, *Shamolagus* Burke, 1941, and three species of *Gobiolagus* Burke, 1941. The largest number of reversals (four) is

found in *D. antiquus*. This could indicate a more basal position of this taxon related to other Eocene stem lagomorphs under the alternative tree topology. Here we propose a new name, Eulagomorpha n. clade, for the clade containing these lagomorphs 'of the modern aspect.' This is a node-based clade defined as the most-recent common ancestor of *Lepus* and *Dawsonolagus* and all of its descendants.

Our analysis did not reveal monophyly for the two genera of Asiatic Eocene eulagomorphs: *Hypsomyilus* Zhai, 1977 and *Strenulagus* Tong and Lei, 1987. *Hypsomyilus beijingensis*, based on a dentary fragment with two cheek teeth from the middle Eocene of China, was initially referred to Eurymylidae (Zhai, 1977; Dashzeveg and Russell, 1988) or Mimotonidae (Li and Ting, 1985), but later was considered a lagomorph (Averianov, 1998; Meng and Hu, 2004). The cheek teeth, originally interpreted as dp4, m1, are likely p4, m1 (Dashzeveg and Russell, 1988). The second species, *H. yihesubuensis*, is known from jaw fragments from the late Eocene of China (Meng and Hu, 2004). Both species of *Hypsomyilus* are similar in their large size, high tooth crowns, and very large hypoconulid on p4, m1-2, which is well separated from the rest of the talonid by deep labial and lingual folds. By a combination of these characters, *Hypsomyilus* is clearly different from other Asiatic Eocene Eulagomorpha n. clade. However, at least high tooth crowns and large hypoconulid might be related to the juvenile nature of the known specimens of *Hypsomyilus*. More worn teeth of this taxon could be more similar to the other Asiatic Eocene eulagomorphs.

The type species of the genus *Strenulagus*, *Strenulagus shipigouensis*, is represented by jaw fragments and isolated teeth from the middle Eocene of China (Tong and Lei, 1987; Tong, 1997). The second species, *Strenulagus solaris* Lopatin and Averianov, 2006 is known from similar specimens from the middle Eocene of Mongolia and China (Lopatin and Averianov, 2006; Fostowicz-Frelik et al., 2015b). The original diagnosis of *Strenulagus* is somewhat misleading because M2 was confused with P3 (Lopatin and Averianov, 2006). Most of the characters listed in the revised diagnosis of *Strenulagus* by Lopatin and Averianov (2006) were not included in our phylogenetic analysis and we could not test their utility. More complete specimens of *Strenulagus shipigouensis* are needed to confirm the monophyly of *Strenulagus*.

Among the Asiatic Eocene stem lagomorphs, two previously recognized genera received support in our analysis: *Gobiolagus* and *Shamolagus*. *Gobiolagus* includes all species previously referred to that genus except for *Gobiolagus hekkeri* (Shevyreva, 1995) from the early Eocene of Kyrgyzstan. The latter species was originally referred to a distinct monotypic genus *Romanolagus* Shevyreva, 1995 (Shevyreva, 1995) but later transferred to *Gobiolagus* by Lopatin and Averianov (2006). As it is evident now, *Romanolagus hekkeri* is a more primitive eulagomorph with the crescentic valley open mesially on both P3-4 [20(0)], double-rooted M3 [32(1)], and hypoconulid on p4, m1-2 [46(0) and 48(0)].

The genus *Gobiolagus* is supported in our analysis by two unambiguously optimized synapomorphies: pear-shaped trigonid of p4 [43(1)]; and m3 hypoconulid absent [54(1)]. The pear-shaped trigonid of p4 was previously considered diagnostic for *Gobiolagus tolmachovi* Burke, 1941 (Burke, 1941; Meng et al., 2005), but is also found in *Gobiolagus aliwusuensis* Fostowicz-Frelik et al., 2012 (Fostowicz-Frelik et al., 2012) and variously expressed in other species. Two species of *Shamolagus* are united in our analysis by a single unambiguously optimized synapomorphy, m1-2 similar in size [50(0)]. This is reversal from the basal eulagomorph condition, also found in some species of *Gobiolagus*.

The close relationships between the Asiatic *Shamolagus* and *Gobiolagus* on the one hand and the North American *Mytonolagus* Burke, 1934 on the other was first noted by Burke (1941), who united these three genera into the subfamily Mytonolaginae within Leporidae. This conclusion is also supported by our analysis (Fig. 4). *Gobiolagus* is the sister taxon for the more derived Eulagomorpha n. clade, including *Shamolagus*. *Shamolagus* is the sister taxon for the clade including *Mytonolagus* and more derived taxa. *Mytonolagus* is paraphyletic in our analysis: *Mytonolagus petersoni* Burke, 1934 is the sister taxon for the clade of more derived eulagomorphs including the clade *Mytonolagus wyomingensis* Wood, 1949 and *Mytonolagus ashcrafti* Fostowicz-Frelik and Tabrum, 2009. This result is in line with the previous conclusion that *Mytonolagus petersoni* is less advanced compared with *Mytonolagus wyomingensis* (Dawson, 1970; Fostowicz-Frelik and Tabrum, 2009). The clade including *Gobiolagus*, *Shamolagus*, and more derived eulagomorph taxa is named here Epilagomorpha new clade. This is a node-based clade defined as the most-recent common ancestor of *Lepus* and *Gobiolagus* and all of its descendants.

The interrelationships of the Oligocene to Recent eulagomorphs are fully resolved in our analysis (Fig. 4) but our taxonomic sample was limited to few taxa and cannot demonstrate the split between the Leporidae and Ochotonidae. In particular, the Oligocene North American *Litolagus molidens* Dawson, 1958 is outside the crown group Lagomorpha on our cladogram (Fig. 4), but it is distinctly more related to the modern leporids than to *Ochotona* (Dawson, 1958; Fostowicz-Frelik, 2013) and should belong to the crown group Lagomorpha (to the Leporomorpha sensu Meng and Wyss [2001]). *Palaeolagus haydeni* in our analysis is the sister taxon to the crown group Lagomorpha. The clade containing the most-recent common ancestor of *Lepus*, *Ochotona*, and *Palaeolagus* Leidy, 1856, and all of its descendants, was previously named Neolagomorpha (Averianov, 1999).

Discussion

Arnebolagus leporinus comes from the base of the Bumban Member of Naran Bulak Formation (Fig. 5). The fauna from this stratigraphic unit forms the biological basis for the early Eocene Bumbanian Asiatic Land Mammal Age (ALMA) (Russell and Zhai, 1987; Dashzeveg, 1988; Ting, 1998). The Bumban Member represents the *Orientalophus* Interval Zone, the first biozone of the Bumbanian ALMA (Ting, 1998). *Arnebolagus* was the first lagomorph ‘of the modern aspect’ reported from the Bumbanian ALMA (Lopatin and Averianov, 2008) and it remains the oldest known eulagomorph. The next oldest eulagomorph is *Dawsonolagus* from the lower part of the Arshanto Formation in Inner Mongolia, China (Li et al., 2007; Fig. 5). Now, most of the Arshanto Formation is regarded as late early Eocene in age (Meng et al., 2007; Sun et al., 2009). The Bumbanian and Arshantan ALMAs correlate with the Ypresian stage in Europe and with the Wasatchian North American Land Mammal Age (NALMA) (Wang et al., 2010). According to Beard (1998), the Bumbanian ALMA could correlate with the late Clarkforkian–early Wasatchian NALMAs. *Aktashmys* Averianov, 1994 and *Romanolagus* from the Alay beds in Kyrgyzstan are late Ypresian in age (Averianov and Udovichenko, 1993; Averianov and Godinot, 1998) and slightly younger than *Arnebolagus* and *Dawsonolagus*. Rose et al. (2008) reported some tarsal bones similar to those of modern lagomorphs from the early Eocene (middle Ypresian) Cambay Shale at the Vastan lignite mine in Gujarat, India. These bones could belong to a eulagomorph similar in age with *Dawsonolagus*. All other Eocene eulagomorphs from Asia are middle–late Eocene in age (Appendix 1). ‘*Procaprolagus*’ *vusillus* Storer, 1984 and three species of *Mytonolagus*, the oldest stem lagomorphs of North America, come from the middle Eocene deposits (Uintan-Ducheshnian) (Burke, 1934; Wood, 1949; Gazin, 1956; Dawson, 1970, 2007; Storer, 1984; Fostowicz-Frelik and Tabrum, 2009). This spatial distribution of taxa and our phylogenetic analysis support origin of the lagomorphs ‘of the modern aspect’ (Eulagomorpha n. clade) in Asia and their subsequent migration to North America at the beginning of the middle Eocene. Eulagomorpha n. clade likely appeared in Asia shortly before the Paleocene/Eocene boundary together with some other important mammalian groups (Bowen et al., 2002).

The assemblage of small mammals from the Bumban Member of Naran Bulak Formation is dominated by eurymylids, mimotonids, and diverse ctenodactyloid rodents and ‘insectivores’ (Dashzeveg et al., 1987; Dashzeveg and Russell, 1988; Shevyreva, 1989; Dashzeveg, 1990a, b; Lopatin, 2006). The abundance of ctenoactyloid rodents and rodent-like eurymylids on the one hand and the rarity of primates compared with the contemporaneous Bumbanian faunas of China (Beard, 1998) on the other hand, suggest a predominance of open landscapes in Tsagan-Khushu area during Bumbanian times. These open landscapes were likely favorable for radiation of the earliest eulagomorphs.

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Appendix 1. Taxa used in the phylogenetic analysis.

Aktashmys montealbus Averianov, 1994—Represented by isolated teeth and jaw fragments from the early Eocene Alai beds at Andarak 2 locality in Kyrgyzstan (Averianov, 1994; Averianov and Lopatin, 2005). *Valerilagus reshetovi* Shevyreva, 1995, based on the maxillary fragment from this locality (Shevyreva, 1995), is a junior subjective synonym of *Aktashmys montealbus* (see Averianov and Lopatin, 2005).

Arnebolagus leporinus Lopatin and Averianov, 2008—The species is known from the holotype (PIN 3104/914), an isolated P3 (Lopatin and Averianov, 2008), and additional upper cheek teeth described in this report from the earliest Eocene Bumbanian Member of Naran Bulak Formation at Tsagan-Khushu locality in Mongolia.

- Dawsonolagus antiquus* Li, Meng, and Wang, 2007—Based on a fragmentary skull with mandibles and isolated teeth and tarsal bones from the early Eocene Arshanto Formation of Inner Mongolia, China (Li et al., 2007).
- Desmatolagus gobiensis* Matthew and Granger, 1923—The species is represented by abundant jaw fragments and isolated teeth from the middle Oligocene Shand-Gol Formation at several localities within Valley of Lakes Depression, Mongolia (Matthew and Granger, 1923; Sych, 1975).
- Desmatolagus vetustus* Burke, 1941—The species is known from the late Eocene Ulan Gochu Formation, Inner Mongolia, China (Burke, 1941; Meng and Hu, 2004; Meng et al., 2005).
- Erenlagus anielae* Fostowicz-Frelik and Li, 2014—Based on isolated teeth from the middle Eocene Irдин Manha Formation at Huheboerhe locality, Erlian Basin, Inner Mongolia, China (Fostowicz-Frelik and Li, 2014).
- Gobiolagus aliwusuensis* Fostowicz-Frelik et al., 2012—The species is represented by abundant fragments from the middle Eocene deposits at Aliwusu, Inner Mongolia, China (Fostowicz-Frelik et al., 2012).
- Gobiolagus andrewsi* Burke, 1941—The species is known from two mandibles from the late Eocene Ulan Gochu Beds, Inner Mongolia, China (Burke, 1941; Meng et al., 2005).
- Gobiolagus burkei* Meng, Hu, and Li, 2005—The species is known by jaw fragments from the middle Eocene Shara Murun Formation, Inner Mongolia, China (Meng et al., 2005).
- Gobiolagus lii* Zhang, Dawson, and Huang, 2001—Represented by a single maxilla from the middle Eocene Heti Formation; Shanxi Province, China (Zhang et al., 2001).
- Gobiolagus major* Burke, 1941—The species is known from maxillary and dentary fragments from the late Eocene of Ulan Gochu Beds, Inner Mongolia, China (Burke, 1941; Meng et al., 2005).
- Gobiolagus tolmachovi* Burke, 1941—The species is known from maxillary and dentary fragments from the middle Eocene Shara Murun Formation at Ula Usu (= Baron Sog Mesa), Shara Murun Region, Inner Mongolia, China (Burke, 1941; Qi, 1988; Meng et al., 2005).
- Gomphos elkema* Shevyreva in Shevyreva et al., 1975—The species is represented by a skeleton and jaw fragments from several early Eocene localities in Mongolia and China (Shevyreva et al., 1975; Dashzeveg and Russell, 1988; Meng et al., 2004; Asher et al., 2005).
- Hypsomyilus beijingensis* Zhai, 1977—The species is based on a dentary fragment from the middle Eocene Changxiandian Formation in Beijing, China (Zhai, 1977; Dashzeveg and Russell, 1988).
- Hypsomyilus yihesubuensis* Meng and Hu, 2004—The species is known from maxillary and dentary fragments from unnamed upper Eocene beds at Yihesubu locality, Inner Mongolia, China (Meng and Hu, 2004).
- Lepus timidus* Linnaeus, 1758—The Recent mountain hare is widely distributed across Europe and Asia; scoring is based on specimens in the ZIN collection.
- Litolagus molidens* Dawson, 1958—A rare species known from rather complete materials, including skulls and a postcranial skeleton from the early Oligocene (Orellan) deposits of Wyoming, USA (Dawson, 1958; Fostowicz-Frelik, 2013).
- Lushilagus danjiangensis* Tong and Lei, 1987—The species is based on isolated teeth from the middle Eocene lower part of the Hetaoyuan Formation in Henan Province, China (Tong and Lei, 1987; Tong, 1997).
- Lushilagus lohoensis* Li, 1965—The species is represented by upper dentition from the middle Eocene Lushi Formation, Henan Province, China, and karstic fillings in the Triassic Shanghuang Limestone, Jiangsu Province, China (Li, 1965; Qi et al., 1991; Tong, 1997).
- Mimotona wana* Li, 1977—The species is known from cranial and postcranial material from the middle Paleocene Wanghudun Formation, Qianshan Basin, Anhui Province, China (Li, 1977; Li and Ting, 1985, 1993; Dashzeveg and Russell, 1988).
- Mytonolagus ashcrafti* Fostowicz-Frelik and Tabrum, 2009—The species is represented by jaw fragments and isolated teeth from the middle Eocene (Duchesnean) Renova Formation at Diamond O Ranch No. 1 locality, Montana, USA (Fostowicz-Frelik and Tabrum, 2009).
- Mytonolagus petersoni* Burke, 1934—The species is known from a fragmentary skeleton, jaw fragments, and isolated teeth from the middle Eocene (Uintan) Uinta Formation, Utah, USA (Burke, 1934; Dawson, 1970).
- Mytonolagus wyomingensis* Wood, 1949—The species is represented by a maxillary fragment and isolated teeth from the middle Eocene (Uintan) of Wyoming and Montana, USA (Wood, 1949; Gazin, 1956).
- Ochotona princeps* Richardson, 1828—The Recent American pika is distributed in western North America; scoring is based on specimens in the ZIN collection and on Wible (2007).
- Palaeolagus haydeni* Leidy, 1856—The species is represented by abundant cranial and postcranial material from the late Eocene (Chadronian) of Nebraska, USA (Leidy, 1856; Troxell, 1921; Wood, 1940; Dawson, 1958; Korth and Dharmapuri, 2017).
- Prolagus sardus* Wagner, 1832—The recently extinct Sardinia pika lived on Sardinia, Corsica and neighboring Mediterranean islands (Dawson, 1969).
- Rhombomyilus turpanensis* Zhai, 1978—This species was used as the outgroup taxon in the phylogenetic analysis. It is known

from numerous cranial and postcranial specimens from several early Eocene formations in China and Mongolia (Zhai, 1978; Dashzeveg and Russell, 1988; Meng et al., 2003).

Romanolagus hekkeri Shevyreva, 1995—The species is known from maxillary fragments and isolated teeth from the early Eocene Alai beds at Andarak 2 locality, Kyrgyzstan (Shevyreva, 1995; Lopatin and Averianov, 2006).

Shamolagus grangeri Burke, 1941—The species is based on a dentary fragment with p4, m1–3 (AMNH 26289) from the middle Eocene Ulan Shireh Formation at Wulanhuxiu (= Chimney Butte), Shara Murun region, Inner Mongolia, China (Burke, 1941; Meng et al., 2005).

Shamolagus medius Burke, 1941—The species is known from a dentary fragment and fragmentary skeleton from the middle Eocene Shara Murun Formation at Ula Usu (= Baron Sog Mesa), Shara Murun region, Inner Mongolia, China (Burke, 1941; Li, 1965; Meng et al., 2005).

Strenulagus shipigouensis Tong and Lei, 1987—The species is represented by jaw fragments and isolated teeth from the middle Eocene lower part of the Hetaoyuan Formation, Henan Province, China (Tong and Lei, 1987; Tong, 1997).

Strenulagus solaris Lopatin and Averianov, 2006—The species is known from jaw fragments and isolated teeth from the middle Eocene Khaychin Formation at Khaychin-Ula 3 locality, Mongolia (Lopatin and Averianov, 2006) and isolated teeth from the middle Eocene Irдин Manha Formation at the Irдин Manha and Huheboerhe localities, Erlian Basin, Inner Mongolia, China (Fostowicz-Frelik et al., 2015b).

Appendix 2. Character list.

1. Postorbital process of frontal: present (0); absent (1).
2. Posterior end of zygomatic root: at M1 (0); more posterior, at P4 (1).
3. Incisive foramen posterior margin (ordered): anterior to the cheek teeth (0); at P2 (1); at P3 or more posterior (2).
4. Premolar foramen on maxilla: absent (0); present (1).
5. Posterior margin of palate: at M2 or more posterior (0); at M1 or more anterior (1).
6. Masseteric fossa anterior end: at m3 or more posterior (0); at m2 (1).
7. Tubercle on masseteric crest: absent (0); present (1).
8. Coronoid process of dentary: large (0); small (1).
9. Coronoid canal on mandible posterior to m3: absent (0); present (1).
10. Anterior mental foramen: at p3 (0); at diastema (1).
11. Posterior mental foramen: at p4–m1 (0); at m2 (1). Taxa without posterior mental foramen were coded as inapplicable.
12. Cement on teeth: absent (0); present (1).
13. di2 groove: absent (0); present (1).
14. di2 cross section: heart-shaped, distal side narrow (0); subrectangular (1). Taxa without groove were coded as inapplicable.
15. di2 medial and lateral lobes relative width: similar (0); medial lobe wider (1); medial lobe narrower (2). Taxa without groove were coded as inapplicable.
16. di2 medial lobe position: projecting anteriorly (0); level with the lateral lobe (1). Taxa without groove were coded as inapplicable.
17. Upper cheek teeth: unilaterally hypsodont (0); hypsodont (roots absent) (1).
18. P2 crown shape: round (0); mesiodistally compressed (1).
19. P2 mesial folds (ordered): one (0); two (1); three (2).
20. P3–4 crescentic valley (paraflexia) (ordered): open mesially on both P3 and P4 (0); open on P3, closed on P4 (1); open on P3, absent on P4 (2); absent on both P3 and P4 (3).
21. P3 anteroloph: short (0); long, extending labially at least to the middle of centrocone (1). Taxa without anteroloph were coded as inapplicable.
22. P3 hypostria: absent (0); shallow, forming lake (1); deep, not forming lake (2).
23. P3 labial roots: two (0); one (1). Taxa without roots were coded as inapplicable.
24. P4 hypostria: absent (0); present (1).
25. P4 labial roots: two (0); one (1). Taxa without roots were coded as inapplicable.
26. M1–2 crescent: absent (0); present (1).
27. M1–2 postcingulum: present (0); absent (0).
28. M1–2 hypostria: absent or shallow (0); short, enamel lake on late wear (1); present for most of crown width (2).
29. M3: present (0); absent (1).
30. M3 size: wider than M2 (0); 50–100% of M2 width (1); < 50% of M2 width (2). Taxa without M3 were coded as inapplicable.
31. M3 postcingulum: present (0); absent (0). Taxa without M3 were coded as inapplicable.
32. M3 roots: three (0); two (1); one (2). Taxa without M3 or roots were coded as inapplicable.
33. i3: present (0); absent (1).
34. Origin of di2: posterior to m3 (0); at m1–2 (1); more anterior (2).
35. Lower cheek teeth: brachydont (0); unilaterally hypsodont (1); hypsodont (roots absent) (2).
36. p4, m1–3 roots: separate (0); fused or connected by a bony bridge (1). Taxa without roots were coded as inapplicable.
37. p4, m1–2 trigonid height to talonid: larger (0); subequal (1).
38. p3 trigonid to talonid width: larger or subequal (0); smaller (1).
39. p3 trigonid and talonid separation: labial and lingual folds (0); labial fold only (1); lingual fold closed in enamel lake on late wear (2).
40. p3 mesiolingual fold on trigonid: absent (0); present (1).
41. p3 roots: two (0); one (1). Taxa without roots were coded as inapplicable.
42. p4 trigonid width to talonid: larger (0); subequal (1).
43. p4 pear-shaped trigonid: absent (0); present (1).
44. p4 paracristid: present (0); absent (1).
45. p4 labial and lingual folds separating trigonid and talonid: of similar depth (0); lingual fold shallower, trigonid and talonid connected lingually on worn teeth (1).
46. p4 hypoconulid (little worn teeth): present (0); absent (1).
47. m1–3 labial and lingual folds separating trigonid and talonid: of similar depth (0); lingual fold shallower, trigonid and talonid connected lingually on worn teeth (1).

48. m1–2 hypoconulid (little worn teeth): present (0); absent (1).
 49. m1–2 hypoconulid separated from talonid: by labial fold (0); by both labial and lingual folds (1). Taxa without hypoconulid were coded as inapplicable.
 50. m1–2 relative size: m2 larger (0); similar (1).
 51. m1 trigonid length to talonid: larger (0); similar (1).
 52. m2 trigonid length to talonid: larger (0); similar (1).
 53. m3 trigonid height to talonid: larger (0); subequal (1).
 54. m3 hypoconulid (little worn teeth): present (0); absent (1).

Appendix 3. Data matrix. A = [01].

Taxon	12345	1 67890	11111 12345	11112 67890	22222 12345	22223 67890	33333 12345	33334 67890	44444 12345	44445 67890	5555 1234
<i>Rhombomylus turpanensis</i> (outgroup)	00000	00000	000??	?0???	?0000	00000	00101	00000	00000	00000	00000
<i>Aktashmys montealbus</i>	?0?1?	?????	?0101	00??0	00101	00001	01??1	10???	?0000	0A011	00000
<i>Arnebolagus leporinus</i>	?????	?????	?0???	?0???	00100	000??	????0	00???	?????	?100?	????
<i>Dawsonolagus antiquus</i>	00000	00001	?0100	00??0	00101	00001	?0110	00???	?????	?1000	?000
<i>Desmatolagus vetustus</i>	?0101	00??1	?????	?0011	?0000	?1102	?2111	10111	10010	111?1	0011
<i>Desmatolagus gobiensis</i>	?1211	01?01	01???	?0011	11010	11102	12121	10110	10010	101?1	1101
<i>Erenlagus anielae</i>	?????	?????	?????	?0???	?01??	00001	01??1	10100	10011	110??	0001
<i>Gobiolagus andrewsi</i>	?????	11???	00???	?????	?????	?????	???	10100	10111	111?0	1011
<i>Gobiolagus tolmachovi</i>	?0111	11??1	00???	?0??1	?0101	00001	??111	10100	10111	111?0	1001
<i>Gobiolagus aliwusuensis</i>	?0?1?	????1	00102	10011	?0101	00001	02111	10100	10111	111?1	0001
<i>Gobiolagus burkei</i>	?????	?????	0???	?????	?????	?????	???	10111	10111	111?0	1011
<i>Gobiolagus lii</i>	?011?	?????	?????	?0??1	?0100	00001	?2???	?????	?????	?????	?????
<i>Gobiolagus major</i>	?0101	11???	?0???	?0??1	?0000	00001	???	10???	?0111	111?1	1011
<i>Gomphos elkema</i>	10100	00000	000??	?0???	?0000	00001	00001	00000	01000	?0000	0000
<i>Hypsomylyus beijingensis</i>	?????	?????	?????	?????	?????	?????	???	10???	?0010	0001?	0???
<i>Hypsomylyus yiheesubuensis</i>	?????	?????	?0???	?010?	?0000	?????	???	10???	?????	?1011	00??
<i>Lepus timidus</i>	01101	00111	?1112	01123	?2?1?	01202	1?122	?1110	?0011	111?1	1111
<i>Litolagus molidens</i>	00101	00101	?1111	11103	?2?1?	01202	1?122	?110	?0011	111?1	1111
<i>Lushilagus lohoensis</i>	?0???	?????	?0???	?0??0	?0101	??001	?????	?????	?????	?????	?????
<i>Lushilagus danjiangensis</i>	?????	?????	?0???	?0??0	?0101	00001	0???	10000	100?1	10011	00??
<i>Mimotona wana</i>	?000?	00?00	?0100	00???	?0000	0001	0001	0000	10000	10000	0000
<i>Mytonolagus petersoni</i>	?1101	01??1	00100	00011	10111	11101	0?111	10A20	10011	111?1	0010
<i>Mytonolagus wyomingensis</i>	?0???	?????	?1100	000A1	10111	11101	1??11	1?A20	10010	101??	0???
<i>Mytonolagus ashcrafti</i>	?1101	?1??1	01100	00011	10A1A	11101	12111	1010A	10010	001?1	0010
<i>Ochotona princeps</i>	10211	0011?	11112	01102	10?1?	0121?	??122	?1111	?1010	101?1	11??
<i>Palaeolagus haydeni</i>	011?1	00101	01112	011A1	11?1?	11102	1?112	?0A21	?0011	01011	1111
<i>Prolagus sardus</i>	10211	00111	11112	01011	10?1?	0121?	??122	?1101	?1010	101?1	11??
<i>Romanolagus hekkeri</i>	?0???	?????	??100	00??0	??101	00001	1???1	10???	?0011	0101?	000?
<i>Shamolagus granger</i>	?????	01?01	?0???	?????	?????	?????	??111	10???	?0011	111?0	1010
<i>Shamolagus medius</i>	?0?0?	01?01	00???	?0011	?0?0?	?1001	1?111	10101	10011	111?0	0010
<i>Strenulagus shipigouensis</i>	?????	?????	?0???	?0???	???	00001	0???	10101	10010	011?1	0000
<i>Strenulagus solari</i>	??10?	01100	00???	?0??0	?0101	00001	01111	10101	10011	011??	0000