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SHORT COMMUNICATION

A NEW EUHARAMIYIDAN MAMMALIAFORM FROM THE LOWER CRETACEOUS OF YAKUTIA, RUSSIA

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Euharamiyida represent a clade of Mesozoic mammaliaforms with gliriform-like dentition and a dental formula of 1–2.0.2.2/1.0.1.2. By having a high triangular last premolar, only two molars, two rows of multiple cusps on the molars, and a vertically oriented mandibular condyle, euharamiyidans are similar to advanced multituberculates. However, they differ from early multituberculates of the paulchoffatiid and plagiulacid lines by having only one lower premolar, whereas in these multituberculate groups there are four lower premolars. In addition, M2 is one cusp row lingually positioned in relation to M1, whereas in euharamiyidans the cusp rows in M1 and M2 are aligned. At least some euharamiyidans were gliders (Han et al., 2017; Meng et al., 2017).

Although being known from complete skeletons, the phylogenetic position of Euharamiyida is under debate. Currently, there are two alternative phylogenetic hypotheses for Euharamiyida: (1) Euharamiyida belongs to the mammalian crown group Altheria that includes also Haramiyidae and Multituberculata (Zheng et al., 2013; Bi et al., 2014; Meng et al., 2014, 2018; Han et al., 2017; Mao et al., 2017; Mao and Meng, 2019b); and (2) Euharamiyida and Haramiyidae form the clade Haramiyida outside crown mammals (Mammalia) (Zhou et al., 2013; Luo et al., 2015, 2017; Huttenlocker et al., 2018; Martin, 2018).

The uncertainty in the phylogenetic placement of Euharamiyida is caused mostly by alternative interpretations of the mandible and middle ear morphology. One group of authors advocates that the mandible lacks a postdentary trough, with the postdentary bones detached from the mandible and forming a three-boned middle ear (Bi et al., 2014; Meng et al., 2014, 2018, 2019; Han et al., 2017; Mao and Meng, 2019b). According to other authors, euharamiyidans possess a postdentary trough with the postdentary bones attached to the mandible (Luo et al., 2015, 2017; Huttenlocker et al., 2018).

All current records of Euharamiyida are confined to Asia. This group is known by numerous complete skeletons from the Middle–Late Jurassic Yanliao Biota in northwestern China (Zheng et al., 2013; Bi et al., 2014; Meng et al., 2014, 2017; Han

et al., 2017; Luo et al., 2017; Mao and Meng, 2019a, 2019b; Mao et al., 2019). Isolated euharamiyidan teeth were found in the Middle Jurassic (Bathonian) Itat Formation of the Berezovsk coal mine, Krasnoyarsk Territory, Russia, and in the Upper Jurassic (Oxfordian) Qigu Formation of the Liuhuanggou locality in Xinjiang, China (Maisch et al., 2005; Martin et al., 2010; Averianov et al., 2011, 2019).

Here, we describe a new euharamiyidan taxon from the Lower Cretaceous of Yakutia, East Siberia, Russia. This new taxon extends significantly the stratigraphic and geographic ranges for Euharamiyida.

Institutional Abbreviation—PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

MATERIALS AND METHODS

PIN 5614/4 was recovered during screen-washing of 500 kg of fossiliferous matrix from the Teete locality in Yakutia, Russia, 545 km west of Yakutsk (Fig. 1), in 2017 by P. P. Skutschas, R. Schellhorn, and D. D. Vitenko. The sample from screen-washing contained numerous vertebrate microfossils, including remains of fishes, salamanders, turtles, choristoderes, lizards, dinosaurs, tritylodontids, and mammals (Averianov et al., 2018).

The tooth was scanned with a resolution of 2.39 μm using the 180 kV X-ray tube of the v|tome|x s micro-computed tomography (μCT) device (GE Sensing & Inspection Technologies phoenix|x-ray) housed in the Institute for Geosciences, University of Bonn, Bonn, Germany. Scan settings were 80 kV and 80 μA with a shutter speed of 500 ms per capture. The instrument produced isotropic voxels, and the single image size is 2024 × 2024 pixels. Avizo 8 (Thermo Fisher Scientific) was used for segmentation.

Anatomical Abbreviations—L, crown length; W, crown width.

GEOLOGICAL SETTING

The Vilyuy River Basin is part of the Vilyuy syncline, a depression within the Siberian Platform that was formed in the Middle Jurassic to Early Cretaceous (Callovian–Albian). The infill of the Vilyuy syncline represents a sequence of partly coal-bearing, but laterally highly variable terrestrial sediments such as sandstones, siltstones, and clays (Trushkov, 1975), formally named the Sangar Series. The Sangar Series is about 1,500 m thick and is

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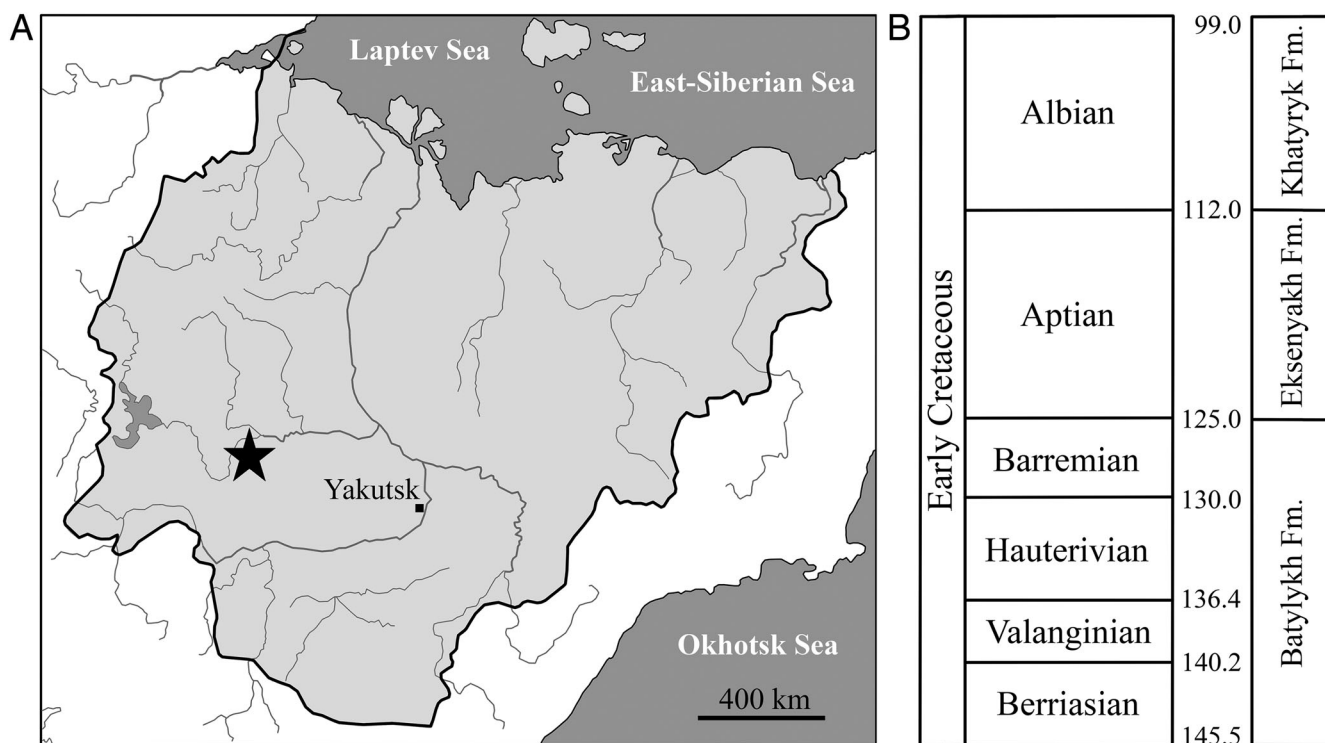


FIGURE 1. **A**, map of Yakutia showing the position of the Teete locality (star); **B**, the approximate stratigraphic positions of the formations of the Sangar Series in Yakutia.

divided from oldest to youngest into the Batylykh, Eksenyakh, and Khatyryk formations (Grinenko and Devyatov, 2017). The Teete locality, located in the southwestern part of the Vilyuy syncline at the junction of the Suntar uplift and the Kempendyay depression, is placed within the Batylykh Formation, the stratigraphically lowermost formation of the Sangar Series (Fig. 1).

In Yakutia, the climatic and environmental conditions changed very little from the Late Jurassic to the Early Cretaceous (Tuchkov, 1973). Because the faunistic and floristic changes occurred gradually, the age determination of the Teete locality is difficult (Kolosov et al., 2009). Two levels with rich assemblages of freshwater mollusks have been reported from the Sangar Series, of which one is similar to that from the Valanginian of Transbaikalia and the other to the assemblages from the Hauterivian–Barremian of Transbaikalia and Mongolia (Martinson, 1956; Chumakov, 1959; Grinenko and Devyatov, 2017). Some of the freshwater mollusks from the fossiliferous level at the Teete locality correspond to the Valanginian assemblage. An early study of plant macrofossils suggested a Neocomian age for the Batylykh Formation in the lower reaches of the Vilyuy River (Vakhrameev, 1957). An Early Cretaceous age of the Teete locality is supported by the pollen assemblage collected from Teete sections, which contains typical Neocomian (Early Cretaceous) taxa with some Late Jurassic elements (Kolosov et al., 2009). Therefore, the age of the Teete vertebrate locality is considered here the early part of the Early Cretaceous (Berriasian–Barremian).

SYSTEMATIC PALEONTOLOGY

Clade MAMMALIAFORMES Rowe, 1988
 Order HARAMIYIDA Hahn et al., 1989
 Suborder EUHARAMIYIDA Bi et al., 2014
 EUHARAMIYIDA incertae sedis
 Genus *CRYOHARAMIYA*, gen. nov.

Type Species—*Cryoharamiya tarda*, sp. nov.

Etymology—From Greek ‘κρύος,’ cold, and genus *Haramiya* Simpson, 1947.

Diagnosis—As for the type and only known species.

Included Species—Type species only.

CRYOHARAMIYA TARDA, sp. nov.
 (Fig. 2)

Eleutherodontidae indet. cf. *Sineleutherus* sp.: Averianov et al. (2018):fig. 2f, g.

Etymology—After Latin ‘tardus,’ late.

Holotype—PIN 5614/4, right M1.

Type Locality and Horizon—Teete locality, Yakutia, Russia; Batylykh Formation, Sangar Series, Lower Cretaceous.

Diagnosis—Differs from *Maiopatagium* and *Shenshou* by upper molar cusps not coalesced. Differs from *Arboroharamiya* and *Sharypovoia* by two intermediate cusps in the labial cusp row of M1. Differs from *Vilevolodon*, *Arboroharamiya*, and *Qishou* by three lingual cusps on M1. Differs from *Vilevolodon* and *Arboroharamiya* by the central cusp in the lingual cusp row of M1 larger and well separated from the side cusps, and by the longitudinal furrow of the central valley labially convex. Differs from *Arboroharamiya*, *Xianshou*, and *Sharypovoia* by a long mesial ridge lacking cusps. Differs from *Arboroharamiya* by upper molar cusps lacking enamel sculpture. Differs from *Arboroharamiya*, *Vilevolodon*, and *Sharypovoia* by the central valley open mesially. Differs from *Arboroharamiya*, *Vilevolodon*, and *Xianshou* by the central valley open distally. Differs from *Xianshou* by distolabial cusp A1 of M1 not hypertrophied.

Comments—As was discussed in Averianov et al. (2019), all Asiatic euharamiyidan taxa, except *Maiopatagium*, are referable

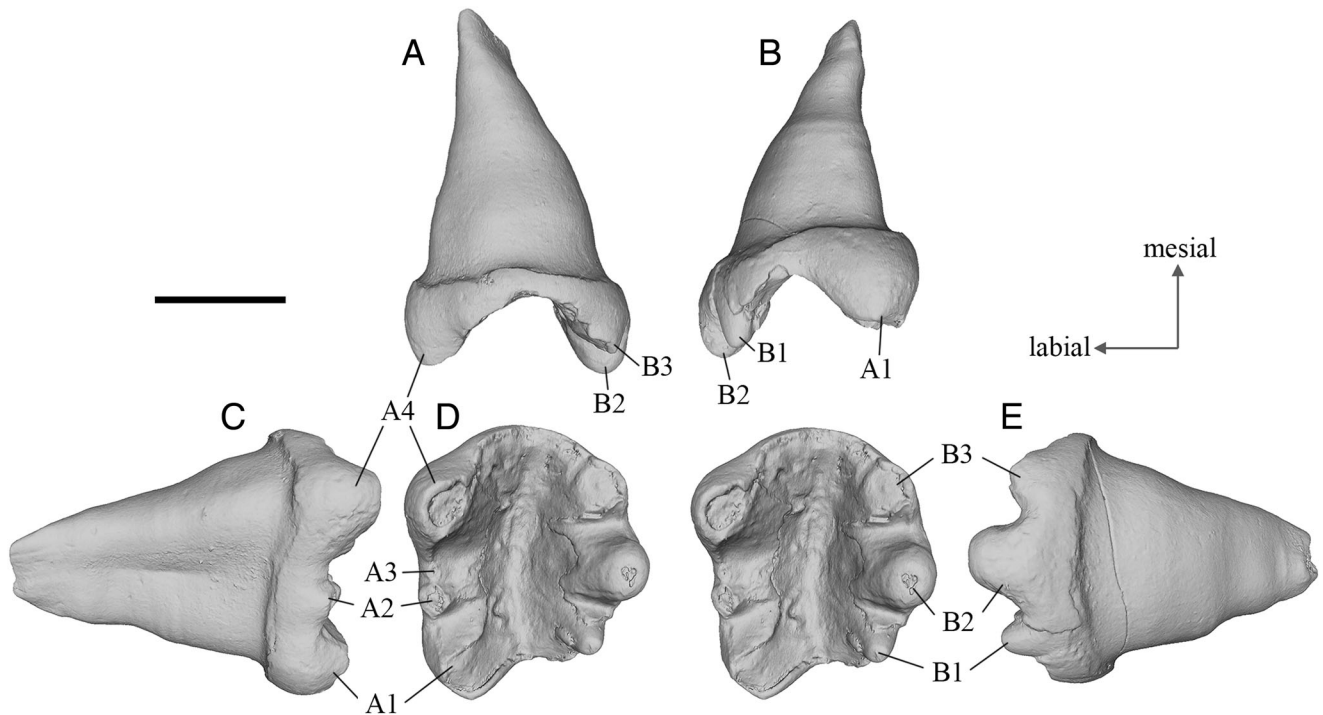


FIGURE 2. *Cryoharamiya tarda*, gen. et sp. nov., PIN 5614/4, holotype, right M1, in **A**, mesial, **B**, distal, **C**, labial, **D**, occlusal (stereopair), and **E**, lingual views. Teete locality, Yakutia, Russia; Batylykh Formation, Lower Cretaceous. Scale bar equals 1 mm.

to either Arboroharamiyidae or Shenshouidae, but not to Eleutherodontidae. Arboroharamiyidae and Shenshouidae differ mostly in the structure of p4 (Mao and Meng, 2019b): in arboroharamiyids, the p4 is high and triangular, whereas in shenshouids this tooth is molariform, with the main cusp and talonid basin surrounded by two rows of cusps. Among Shenshouidae, the intermediate cusps between the main marginal cusps in the labial cusp row of M1 can be absent (*Shenshou*, *Sharypovoia*) or two cusps may be present (*Qishou*) (Bi et al., 2014; Averianov et al., 2019; Mao and Meng, 2019b). Among Arboroharamiyidae, there may occur two (*Xianshou*, *Vilevolodon*) or three (*Arboroharamiya*) intermediate cusps in the labial cusp row of M1 (Bi et al., 2014; Meng et al., 2014; Luo et al., 2017). In *Cryoharamiya*, gen. nov., there are two intermediate cusps, one of which is minute. In this respect, the new genus holds an intermediate position between Shenshouidae, where there is a tendency toward reduction of the intermediate cusps, and Arboroharamiyidae, where these cusps are normally developed. Because of this, we do not attribute the new genus to a particular family of Euharamiyida. By crown proportions, it is very similar to the arboroharamiyid *Vilevolodon*, which would support affinities with Arboroharamiyidae.

Description—The M1 is mesiodistally slightly longer than transversely wide. In occlusal view, the crown is strongly convex mesially, convex lingually, strongly concave distally, and slightly concave labially. There are four cusps in the labial row and three cusps in the lingual row. The hook-like distolabial cusp A1 is mostly eliminated by wear. As it is preserved, it is lower than the mesiolabial cusp A4, but it is typically the largest crown cusp in unworn euharamiyidan M1s. Cusps A1 and A4 are separated by a considerable space and connected by a longitudinal ridge. There are two cusps on this ridge between the large marginal cusps. Cusp A2 is much lower and about three times smaller than the mesiolabial cusp A4. Cusp A3 is minute, nearly one-third the size of cusp A2, and not much elevated above the longitudinal ridge (its apex is worn, as in the other

labial cusps). There is a distinct ridge extending lingually from cusp A2. The mesiolabial cusp A4 is placed somewhat labially to the distolabial cusp A1. There are no cusps mesial to cusp A4, and it is connected to the mesiolingual cusp B3 by a ‘U’-shaped mesial ridge. In the lingual cusp row, central cusp B2 is the largest cusp. It projects vertically. The distolingual cusp B1 is about half as high and distinctly smaller. It is directed ventrodistally. There is a shoulder-like distal ridge descending from the base of cusp B1. The mesiolingual cusp B3 is mostly removed by wear. It is larger than cusp B1 but was undoubtedly lower than cusp B2. Central cusp B2 is separated from the side cusps B1 and B3 by deep and wide transverse grooves. The deepest part of the central valley forms a longitudinal furrow, which is convex labially and extends between the mesial and distal crown margins. This furrow is deepest in the middle of the central valley. The central valley is not closed mesially or distally by an elevated ridge. In the central valley, enamel is mostly chipped off postmortem and the exposed dentine is sculptured by short ridges, suggesting that the enamel was also sculptured. However, the enamel remaining on some cusps is smooth. The single root is conical and rapidly tapers toward the end. It is subdivided on the labial side by a shallow groove. The labial side of the root is perpendicular to the crown plane.

Comparison—PIN 5614/4 matches very closely the proportions of M1 of the arboroharamiyid *Vilevolodon diplomylos* (Luo et al., 2017:figs. 1d, 4a–d): it is 1.12 times longer than wide (1.13 in M1 of *V. diplomylos*), whereas M2 in *V. diplomylos* is 1.43 times longer than wide. In PIN 5614/4, the mesial half of the crown is distinctly wider transversely than the distal half, as in M1 of *V. diplomylos*, whereas in M2 of that taxon the difference in transverse width between the mesial and distal parts of the crown is much less pronounced. In PIN 5614/4 and M1 of *V. diplomylos*, the deepest part of the crown basin is in the middle of the tooth, whereas in M2 it is placed closer to the mesial margin of the crown. This allows identification of PIN 5614/4 as an M1. The cusp morphology in

PIN 5614/4 is generally similar to that in M1 of *V. diplomylos*: there are two small cusps between the two marginal labial cusps A1 and A4, and in the lingual cusp row there is a large central cusp B2 flanked by lower cusps B1 and B3. However, details of the cusp morphology are different, especially in the lingual cusp row. The labial cusp A3 is much smaller than the adjacent cusp A2 in PIN 5614/4, whereas in *V. diplomylos* it is only half the size of A2. In the lingual cusp row of M1 of *V. diplomylos*, there are four distinct cusps, whereas only three are present in PIN 5614/4. In *V. diplomylos*, all lingual cusps are directed ventromesially, but in PIN 5614/4 the main cusp (B2) is directed ventrally and the side cusps are diverging from it, ventromesially (B3) and ventrodistally (B1). In PIN 5614/4, the main lingual cusp B2 is clearly separated from the side cusps by deep and wide grooves. In contrast, in *V. diplomylos*, cusps B1 and B2 have nearly coalesced and cusps B2 and B3 are separated by a shallow and narrow groove. In PIN 5614/4, cusp B2 is positioned more lingually compared with the side cusps. In *V. diplomylos*, the cusps B1–B3 are on the same line. The longitudinal furrow of the central valley is straight in *V. diplomylos* but labially convex in PIN 5614/4.

In *Arboroharamiya jenkinsi*, M1 has similar length and width (L/W ratio = 1.16) and the widest crown part is distal (Meng et al., 2014:fig. 9), whereas in PIN 5614/4 the widest crown part is mesial. The distal margin of M1 is not concave, in contrast to PIN 5614/4. The M1 of *A. jenkinsi* clearly differs from PIN 5614/4 by a much larger number of cusps, seven in each row. In particular, there are three intermediate cusps between the large marginal labial cusps A1 and A5 and two cusps mesial to cusp A5. In the middle of the lingual row of M1 of *A. jenkinsi*, there are several relatively small cusps of similar height, whereas in PIN 5614/4 there is a central cusp that is much larger than the side cusps. The mesial ridge of M1 is cusped in *A. jenkinsi* and has no cusps in PIN 5614/4. In *A. jenkinsi*, the enamel is heavily sculptured, including the cusps, whereas in PIN 5614/4 the sculpture was confined to the central valley.

In *Xianshou songae*, M1 is slightly longer than M2 (Bi et al., 2014:figs. 2f, 6a). The distal margin is convex and almost entirely occupied by the large distolabial cusp A1, which closes the central valley distally. In PIN 5614/4, the distal margin of M1 is concave and the central valley is open distally. There is a short space between the mesiolabial and mesiolingual cusps filled by two small cusps (long mesial ridge without cusps in PIN 5614/4). In the lingual cusp row of M1, there are three cusps, as in PIN 5614/4, but the central cusp is not much taller than the side cusps and poorly separated from the other cusps, in contrast to PIN 5614/4. The furrow of the central valley is straight (labially convex in PIN 5614/4).

In *Xianshou linglong* (Bi et al., 2014:figs. 2e, 5d), the distolabial cusp A1 is hypertrophied, larger than in M1 of *X. songae*. Two small cusps fill all the space between the closely placed marginal cusps in the labial row (A1 and A4), whereas in PIN 5614/4 these marginal cusps are widely separated and the intermediate cusps (A2 and A3) are much smaller.

In *Shenshou lui*, M1 is longer than M2 (Bi et al., 2014:fig. 2d; Mao and Meng, 2019a:fig. 10a, 2019b:fig. 4h). In *S. lui*, there are only two cusps in the labial row and the cusps in the lingual row are of equal height and coalesced. In PIN 5614/4, all cusps are well separated.

In *Qishou jizantang*, M1 is almost as long as M2 (Mao and Meng, 2019a:figs. 3, 4, 2019b:figs. 3a, b, 4a–e) and has a L/W ratio of 1.30 (1.12 in PIN 5614/4). The crown of M1 is convex both labially and lingually (concave labially and convex lingually in PIN 5614/4). The intermediate cusps in the labial cusp row, A2 and A3, are of similar size (cusp A3 is much smaller in PIN 5614/4). There is a distinct lingual ridge connecting cusps A3 and A4 (absent in PIN 5614/4). The main cusp in the lingual cusp row (B2) is vertical and widely separated from

the side cusps, as in PIN 5614/4. The longitudinal furrow of the central valley is convex labially, as in PIN 5614/4. The root has two longitudinal grooves on the labial side (one groove in PIN 5614/4).

The M1s in *Sharypovoia arimasporum* (Averianov et al., 2019:figs. 3a–c, 4a–c) and *S. magna* (Averianov et al., 2019:fig. 4d–f) are similar in proportions to PIN 5614/4 but differ in having convex labial sides, less concave distal sides, no cusps between the large marginal cusps in the labial cusp rows, and in having mesial cusps. In *Sharypovoia*, the largest cusp in the lingual cusp row of M1 is B1 (*S. arimasporum*) or B2 (*S. magna*). The latter variant is similar to PIN 5614/4, but in *S. magna* the side cusps in the lingual cusp row are less separated from the central cusp than in PIN 5614/4. In *Sharypovoia*, all lingual cusps are longitudinally aligned, whereas in PIN 5614/4 the central cusp B2 is placed more lingually compared with the side cusps. In *Sharypovoia*, the longitudinal furrow of the central valley is convex labially, as in PIN 5614/4. The central valley is closed mesially (open mesially in PIN 5614/4).

Measurements—PIN 5614/4: L = 2.10 mm, W = 1.71 mm.

DISCUSSION

The new euharamiyidan taxon *Cryoharamiya* increases the taxonomic and morphological diversity of Euharamiyida. By similarity in crown proportions to the M1 of *Vilevolodon*, *Cryoharamiya* likely belongs to Arboroharamiyidae. However, the reduction of the intermediate cusps in the labial cusp row is a tendency found in Shenshouidae. The long mesial cingulum lacking cusps on M1 of *Cryoharamiya* may indicate that the mesial part of this tooth was overhung by a large P4, which played an essential role in mastication.

The Teete locality in Yakutia is the northernmost occurrence of Euharamiyida (62°N latitude). The exact paleolatitude for the Teete locality cannot be estimated because of its uncertain geological age. However, in any case, it was not much different from the Recent latitude. The other northern record for Haramiyidae is the Upper Triassic Fleming Fjord Formation of central East Greenland at 71°N modern latitude (Jenkins et al., 1997). The paleolatitude for this locality is estimated as 40°N (Kent and Tauxe, 2005), which is significantly lower than the Teete locality. The next northern occurrence for the Euharamiyida is the Berezovsk coal mine in Krasnoyarsk Territory, West Siberia, Russia (55°N modern latitude and likely a similar paleolatitude) (Averianov et al., 2011, 2019). The possible euharamiyidan *Baidabaty*r was found at a similar latitude (56°N latitude) (Averianov et al., 2017). The Chinese records of Euharamiyida are confined to North China. In the well-sampled assemblage of the Lower Jurassic Lower Lufeng Formation, Yunnan, China, there are no haramiyidan mammals, although the mammal fauna is similar in composition to the Late Triassic to Early Jurassic faunas of Europe, in which haramiyidans were abundant (Kielan-Jaworowska et al., 2004). In contrast, in Africa haramiyidans were found in a near-tropical assemblage (Heinrich, 1999, 2001). Thus, the Teete locality is the northernmost record for the Haramiyida.

The Early Cretaceous *Cryoharamiya* is the youngest representative of Euharamiyida in the fossil record. The geological age of the Batylykh Formation is not well constrained and estimated as Berriasian–Barremian (Averianov et al., 2018). The next youngest records are from the Upper Jurassic (Oxfordian) Tiaojschan Formation (Yanliao Biota) and Qigu Formation in northern China. The oldest record of Euharamiyida is from the Middle Jurassic Itat Formation in West Siberia, Russia. The possible euharamiyidan *Baidabaty*r from the Lower Cretaceous (Barremian–Aptian) Ilel Formation in Krasnoyarsk Territory, Russia (Averianov et al., 2017, 2019), may represent

another late occurrence of Euharamiyida in the fossil record. Discovery of euharamiyidans in the Lower Cretaceous of Siberia supports the idea that this region served as a refugium for many vertebrate taxa during Jurassic–Cretaceous transition (Averianov et al., 2018).

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