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## EARLY MIOCENE BEAR *BALLUSIA* (CARNIVORA, URSIDAE) FROM THE LOCALITY KHIRGIS-NUR-I IN MONGOLIA

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### ABSTRACT

The maxillary fragment with two molars belonging to a small ursid from the locality of Khirgis-Nur-I in north-western part of Mongolia (MN3) was examined. Metrical and morphological comparison of the upper dentition in representatives of the genera *Ballusia* and *Ursavus* showed remarkable similarities between the Mongolian specimen and *B. elmensis* from the Early Miocene of Europe. This species is divided into two subspecies: *B. e. elmensis* (Europe) and *B. e. orientalis* (Eastern Asia). The tooth morphology of *Ballusia* demonstrates plesiomorphic states of characters, which became more advanced in representatives of *Ursavus*.

**Key-words:** *Ballusia*, Early Miocene, Mongolia, phylogeny, tooth morphology, *Ursavus*, Ursidae

## РАННЕМИОЦЕНОВЫЙ МЕДВЕДЬ *BALLUSIA* (CARNIVORA, URSIDAE) ИЗ МЕСТОНАХОЖДЕНИЯ ХИРГИЗ-НУР-И В МОНГОЛИИ

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### РЕЗЮМЕ

Изучен фрагмент верхней челюсти с двумя коренными зубами, принадлежащий маленькому медведю из местонахождения Хиргиз-Нур-И в северо-западной части Монголии (MN3). Сравнение размеров и строения верхних зубов у представителей родов *Ballusia* and *Ursavus* показало значительное сходство экземпляра из Монголии с *B. elmensis* из раннего миоцена Европы. Этот вид разделяется на два подвида: *B. e. elmensis* (Европа) и *B. e. orientalis* (Восточная Азия). Зубная морфология *Ballusia* демонстрирует плезиоморфные состояния признаков, которые стали более продвинутыми у представителей рода *Ursavus*.

**Ключевые слова:** *Ballusia*, ранний миоцен, Монголия, филогения, зубная морфология, *Ursavus*, Ursidae

## INTRODUCTION

Genus *Ursavus* Schlosser, 1899 (type species *Cephalogale brevirohinus* Hofmann, 1887) was traditionally understood as a paraphyletic taxon comprised of the earliest representatives of subfamily Ursinae Fischer, 1814 (*sensu* Baryshnikov, 2007). It includes small and medium size forms from Early to Late Miocene from Eurasia and North America. Assumed ancestors of all later ursine tribes (Ailuropodini Grevé, 1894, Agriotheriini Kretzoi, 1929, Arctotheriini F. Ameghino, 1903, and Ursini Fischer, 1814) are laid within *Ursavus*. The Early Miocene taxa are represented by small plantigrade arboreal animals. The later forms become terrestrial, reaching the size of a small brown bear (*Ursus arctos* Linnaeus, 1758) (Roth and Morlo 1997).

Recently, new genus *Ballusia* Ginsburg et Morales, 1998 (type species *Ursavus elmensis* Stehlin, 1917) was erected for Early Miocene archaic ursines incorporating two European species: *B. elmensis* (Stehlin, 1917) from the locality of Elmin, Germany (biozone MN3) and *B. hareni* (Ginsburg, 1989) from Les Beilleaux à Savigné-sur-Lathan in France (MN3a) (Ginsburg and Morales 1998). Subsequently (Baryshnikov 2007; Qiu and Qiu 2013; Qiu et al. 2014), it has been supplemented by *Ursavus orientalis* Qiu et al., 1985, which was described on the basis of the complete skeleton from Shanwan (Xiejiahe Fauna from Shanwang Formation) in Shandong Province, China (Qiu et al. 1985). The age of Shanwang Formation correlates with the European zones MN4 (Qiu et al. 1985) or MN5 (Zhang et al. 2003). Qiu and Qiu (2013) correlated the whole Shanwang Formation with MN3-5, but the Xiejiahe Fauna/Locality (which includes *U. orientalis*) was correlated more or less with MN4.

Baryshnikov (2007) adopted *Ballusia* only on a subgeneric level with a single species *U. elmensis* (including *U. e. orientalis* as a subspecies). Based on the revision of holotype (lower jaw fragment with m1) he assumed that *B. hareni* represents more advanced form and synonymized it with *U. brevirohinus*.

Cladistic analysis carried out by Qiu et al. (2014) predominantly on the basis of dental characters revealed that *B. elmensis* and *B. orientalis* occupy a basal position within ursine taxa and represent a sister group to other ursine taxa included into analyses [i.e. subf. Ursinae (including *Ursavus*) and Ailuropodinae *sensu* Qiu et al. 2014]. Thereby the validity of

the genus *Ballusia* has been proved. The material on *B. hareni*, which is known only by the isolated teeth, was not analyzed. However, this taxon was placed into the genus *Ballusia* in their final classification (Qiu et al. 2014).

Gagnaison (2006), studying maxilla with M1–M2 of a small ursid from Savigné-sur-Lathanin, France, referred this material to *B. hareni*. Taking into account this new data, we accept the previous generic level of *Ballusia*, which comprises three species: *B. elmensis*, *B. orientalis*, and *B. hareni*.

The genus *Ursavus* includes five species in Eurasia (Baryshnikov 2007, Qiu et al. 2014): *U. isorei* Ginsburg et Morales, 1998 from Denezé-sous-le-Ludein, France (MN3a), *U. brevirohinus* (Hofmann, 1887) from Voitsbergand Steyreggin, Austria (MN6), *U. primaevus* (Gaillard, 1899) from La Grive-Saint-Albanin, France (MN7-8), *U. depereti* Schlosser, 1902 from Melchingenin, Germany (MN10), and recently described *U. tedfordi* Qiu et al., 2014 from Liushu Formation in China (Late Bahean strata, around 8 Ma, which corresponds to the European zones MN11-12, see Vangengeim and Tesakov 2008).

Information about the Early Miocene genera *Ballusia* and *Ursavus* is rather scarce, especially for the Asian localities. Therefore it seems to be principally important to study all available findings. One of them, originating from the territory of Mongolia, has not been examined so far. The maxillary fragment and isolated P4 from Khirgis-Nur-I locality have been provisionally designate in museum label as *Amphicyon* sp. However, this maxillary fragment seems to belong to a small bear (Ursavini Kretzoi, 1945). Its description and taxonomical determination is the main subject of the present paper. This specimen is kept in the collection of Borissiak Paleontological Institute of Russian Academy of Science, Moscow, Russia (PIN).

## LOCALITY, MATERIALS AND METHODS

The examined left maxillary fragment with upper teeth M1 and M2 (PIN 3380/56) was discovered in the locality of Khirgis-Nur-I (= Hyargas, Khyargas) in Western Mongolia (49°10'N, 93°20'E) (Fig. 1). This locality is situated on the northern side of the saline Khirgis-Nur Lake in the central part of Great Lake basin and located at 1028 m above sea level. This specimen is labeled: outcrop Oshin, second bone-bearing horizon, collector V. Zhegalov, 1979.

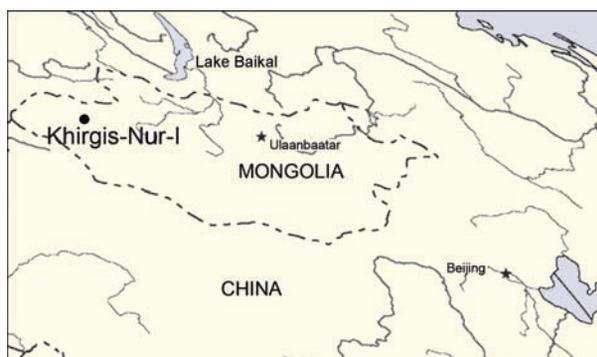


Fig. 1. Location of the examined locality.

The lacustrine and alluvial deposits of the lower suite Oshin are overlapped by those of the suite Khirgis-Nur. According to V. Zhegallo (1978) there are several bone-bearing distinguished.

The second bone-bearing layer enters into the composition of the horizon 5 of locality deposits – the horizons 2–6 affiliate to suite Oshin (Fig. 2; Deviatkin and Zhegallo 1974). The described specimen of *Ballusia* was found here in second bone-bearing layer together with the bones of rhinoceros *Begertherium* sp. By opinion of V. Zhegallo, this layer belongs to lower subsuite of suite Oshin.

The layers of suite Oshin also contain the bones of cervids *Procerovulus gracilis* Vislobokova, 1983 and *Asiagenes ceratinus* Vislobokova, 1983. The age of suite Oshin corresponds to the later part of Early Miocene (Deviatkin and Zhegallo 1974; Zhegallo 1978; Vislobokova 1983). According to later opinion of I. A. Vislobokova (1990) the age of deposits could correlate with European zone MN3.

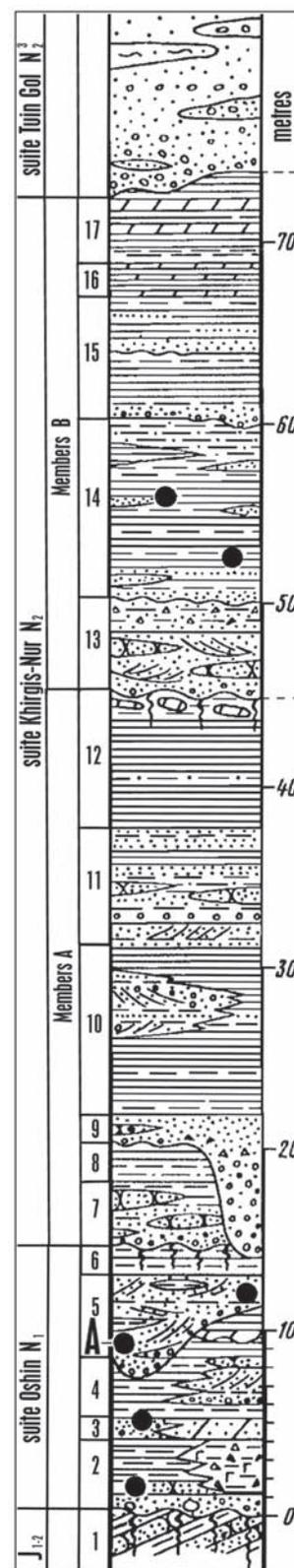
For the comparison, we studied upper dentition of *Ballusia* and *Ursavus*, collected at the European museums (see Institutes Abbreviations). In total, material on 4 species has been examined: *Ballusia harenii* (MNHNP, M1: M4840 cast, M2: Fs1693, M4918 cast), *Ursavus isorei* (MNHNP, M1: Fs5149, M3938 cast, M4011 cast, M4221 cast, M2: Fs1691, holotype, MD31 cast, MD32 cast, MD33 cast, M3861 cast), *U. breverhinus* (MNB, M1–M2: MB.Ma.29321; SMNS, P4–M2: 10326, referred to *Ursavus cf. intermedius*; BMG, P4–M2: 1433, M1–M2: 598781; MNHNP, M2: n/n, Baigneaux, referred to *U. cf. breverhinus*) and *U. primaevus* (NHML, M2: 5318; MNHNP, M1913-21 cast, M1 and M2; CBUL, M1: F.S.L.213748). We also managed to briefly examine (without special study) the unpublished collections of Prof. O. Fejfar (NMP)

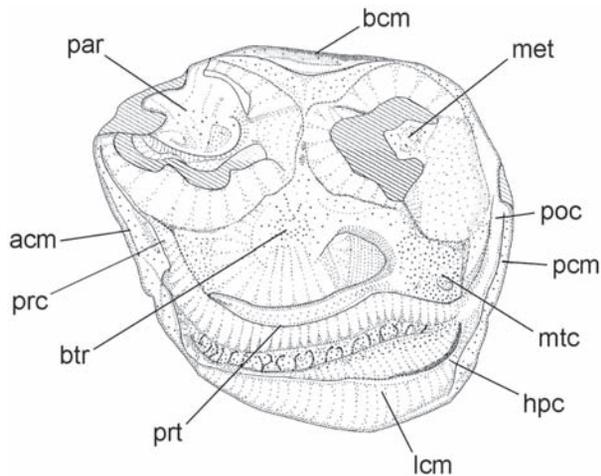
on *Ballusia elmensis* from the North Bohemia (Ahnikov 1, 2, Merkur mine, MN3) in the Czech Republic.

Measurements were carried out using the standard scheme of tooth dimensions for bears, which has been published earlier (Baryshnikov 2007). Measurements were taken by calipers with 0.5 mm accuracy. Terminology of the tooth crown elements is shown in Fig. 3. Photos were produced by G. Baryshnikov. He also elaborated the dental nomenclature (Fig. 3), which is graphically performed by Leonid Voyta. Fig. 2 is drawn by A. Lavrov.

**Institutional abbreviations.** MBLJG, Museum für Bergbau, Geologie und Technikam Landesmuseum Joanneum, Graz, Austria; MNB, Museum für Naturkunde, Humboldt Universität, Berlin, Germany; MNHNP, Museum National d'Histoire Naturelle Paris,

Fig. 2. The outcrop of Neogene lacustrine-alluvial deposits in the western part of the Khirgis-Nur-I locality (after Zhegallo 1978, with changes). The big spots mark the bone bearing layers. The capital letter "A" marks the second bone bearing layer with *Balussia elmensis* and *Begertherium* sp.





**Fig. 3.** The dental cusp nomenclature of ursavine M1. Abbreviations: acm – anterior cingulum; bcm – buccal cingulum; btr – basin of trigon; hpc – hypocone; lcm – lingual cingulum; met – metacone; mtc – metaconule; par – paracone; pcm – postcingulum; poc – postprotocrista; prc – preprotocrista; prt – protocone.

France; NHML, Natural History Museum, London, UK; NMP, National Museum, Prague, Czech Republic; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SMNHS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UCBL, Université Claud Bernard Lyon 1, Lyon, France.

**Dimensional abbreviations.** L, greatest length, W, greatest width.

## SYSTEMATICS

**Order Carnivora Bowdich, 1821**

**Family Ursidae Fischer, 1814**

**Subfamily Ursinae Fischer, 1814**

**Tribus Ursavini Kretzoi, 1945**

***Ballusia* Ginsburg et Morales, 1998**

***Ballusia elmensis* (Stehlin, 1917)**

***Ballusia elmensis* ssp.**

(Fig. 4, Table 1)

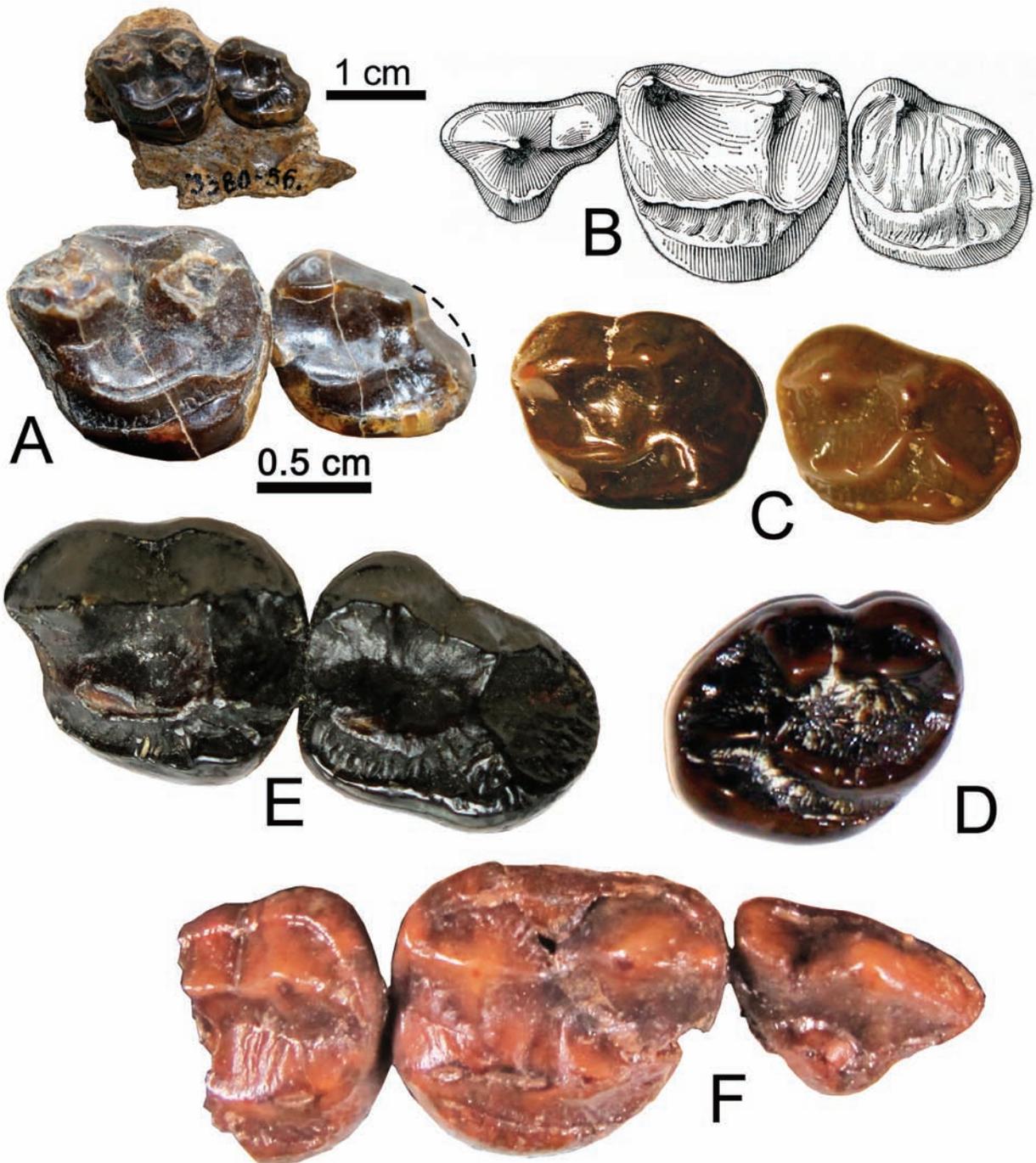
**Description.** The specimen PIN 3380/56 is characterized by small molar teeth. Its tooth row length (M1–M2) is markedly shorter than that of *Ursavus breverhinus* (Table 1, 2).

Tooth crown of M1 in occlusal view is nearly square. Its buccal length only slightly exceeds the lingual length; the tooth width is almost equal to its length. Buccal crown outline is straight; the posterior margin is slightly convex. Apices of cusps and ridges, as well as buccal walls of the crown are partly worn or cracked. Three roots are present; the lingual root, under the protocone, is the most robust. Buccal roots vary in their size only inconspicuously, but the posterior root is slightly larger, similarly to *Ballusia orientalis* (Qiu et al. 1985).

Paracone and metacone form a high three-edged pyramid. The buccal edge of this pyramid is convex and steeply descends to the base. Both tubercles occupy nearly a half of the tooth-crown, with the paracone being somewhat larger than metacone. Metastyle is absent, the area of potential parastyle is broken. Protocone forms an elongated ridge slightly convex lingually and exhibiting a narrow facet of wear, which run along the protocone upper margin. The anterior end of this ridge turns to the paracone. The protocone inner slope is steep, and its surface is rugose (with distinct vertical enamel folds). Metaconule is entirely worn. It is connected with the metacone by a short transverse ridge bordering a deep trigon basin. The surface of this basin is smooth. The buccal cingulum is distinctive. The lingual cingulum is pronounced and short. It is crowded with the protocone and takes place from the anterior margin of protocone to the metaconule basis, forming there a cuspid. The anterior cingulum is shaped as a narrow strip. Posterior cingulum is not expressed.

M2 is placed in the tooth row lingually with regards to M1 (in the recent *Ursus arctos* buccal margins of both molars are situated nearly on one line). Outline of the crown resembles an irregular oval, which is narrowed in its posterior part. The crown is partly broken posteriorly, which produces a false effect the M2 posterior margin in occlusal view. There are three roots, the lingual one is the largest.

The length of M2 is smaller than that of M1. The length of M2 slightly exceeds its width. The morphology of the occlusal surface is similar to that of M1. Paracone and metacone are smaller and markedly lower than in M1; the metacone is smaller than paracone. Longitudinal ridges connect paracone with metacone. Protocone is ridge-like; it is merged anteriorly with the preprotocrista running to the antero-buccal margin of M2 and approaches posteriorly to the poorly expressed metaconule. The latter



**Fig. 4.** Upper teeth of *Ballusia* (A–B) and *Ursavus* (C–F); occlusal views: A – *Ballusia elmensis*, Khirgis-Nur-I (MN3), Mongolia (M1–M2 left, PIN 3380/56); B – *B. elmensis orientalis*, Shanwang (MN5), Shandong Province, China (P4–M2 left, IVPPB 820846, holotype; Qiu et al. 1985); C – *Ursavus isorei*, Dénézé-sous-le-Lude (MN3a), France (M1 left, MNHN Fs5149 and M2 left, MNHN Fs1691); D – *Ballusia hareni*, Dénézé-sous-le-Lude, France (MN3a) (MN3a), France (M2 right, MNHN Fs1693); E – *Ursavus breverhinus*, Győrny Śląsk (=Kieferstädte), Poland (M1–M2 left, MNHUB 29321a); F – *U. breverhinus*, Goriach (MN6), Austria (P4–M1 and def. M2 right, BMUG 1433).

**Table 1.** Measurements of the upper cheek teeth of *Ballusia* and *Ursavus* from the Early Miocene of Eurasia.

Measurements (mm) and indexes (%)	<i>B. elmensis</i>	<i>B. e. orientalis</i>	<i>B. hareni</i>		<i>U. isorei</i>	
	Khirgis-Nur-I, Mongolia (MN3)	Shangwang, China (MN4)	Dénezè-sous-le-Lude, France (MN3a)	Les Billeaux á Savigné-sur-Lathan, France (MN3)	Dénezè-sous-Lude, France (MN3a)	
	PIN 3380-56	Qiu et al. 1985	MNHNP Fs1693	Gagnaison 2006	MNHNP Fs5149	MNHNP Fs1691, holotype
Length M1-M2	21.3					
LP4		8.5				
WP4		5.3				
LM1	11.5	9.9		13.2	11.4	
WM1	10.9	9.2		12.0	8.9	
LM2	9.6	9.0	13.3	11.4		11.4
WM2	8.7	8.1	10.9	10.9		8.0
Indexes						
LM1/LM2	120	110		116		
LM1/WM1	105	127		110	128	
LM2/WM2	110	111	122	105		142

is crowded with the metacone, being linked with it by a rather low ridge, which borders posteriorly the wide trigon basin. The surface of the latter is smooth and slightly concave. The posterior keel of metaconule extends postero-lingually, reaching the edge of the crown. Talon is small. Its surface is smooth. The buccal cingulum is narrow; the anterior cingulum is not present. The lingual cingulum is distinct, taking place from the anterior end of protocone to the posterior end of metaconule and forming a relatively small enamel shelf with the poorly marked hypocone.

**Comparison.** Tooth size increases in the representatives of the genera *Ballusia* and *Ursavus* from geologically older species of *Ballusia* (*B. elmensis*, *B. orientalis*) to younger ones belonging to *Ursavus* (*U. primaevus*, *U. depereti*, *U. tedfordi*). PIN 3380/56 falls into the small-sized group.

M1 of PIN 3380/56 is noticeably longer than M2. By the ratio between their lengths, the examined specimen is similar to *Ballusia orientalis*, *B. hareni* and earlier representatives of *Ursavus breverhinus* (MN6). Meanwhile, later specimens of *U. breverhinus* (MN7) as well as *U. primaevus* and *U. tedfordi* have M1 shorter than M2. The recent *Ursus arctos* is characterized by M2 being markedly longer than M1, both teeth having nearly the equal width. All examined specimens of the geologically earlier bears as well as *U. tedfordi* (see Qiu et al. 2014) have M1 wider than M2 (Table 1, 2).

The specimen PIN 3380/56 corresponds by the length of M1 to *Ballusia elmensis*, *B. orientalis*, and *Ursavus isorei*. The length of this tooth in the taxa not exceeding 11.5 mm (among the M1 teeth of *B. elmensis* recovered at the locality of Wintershof-West in Germany, one specimen has the length 12.3 mm; see Dehm 1950). *Ballusia hareni* is found to have the larger M1 (M4840, cast: LM1 = 13.2 mm, WM1 = 12.5 mm). It is still longer in *Ursavus breverhinus* and *U. primaevus*.

The tooth crown of M1 in PIN 3380/56 as well as that in *Ballusia elmensis* and *B. hareni* is nearly square, whereas it is elongated in *B. orientalis* and *Ursavus isorei* (with regards to the tooth width). Similar proportions with *Ballusia elmensis* are found in *Ursavus breverhinus* and *U. primaevus*.

The structure of occlusal surface of M1 in PIN 3380/56 resembles that of *Ballusia elmensis* and *B. orientalis*. Buccal slopes of paracone and metacone of these species are steep. M1 of *B. elmensis* is known to have the buccal cingulum but reveals no metastyle, which is characteristic of *B. orientalis* (Qiu et al. 1985). In contrast to PIN 3380/56, *B. elmensis* and *B. orientalis* show the metaconule markedly distanced from metacone. The trigon basin of *B. elmensis* is wider and exhibits fine enamel tubercles and folds on its surface. The area between the protocone and the lingual cingulum is wider in *B. elmensis* and *B. orientalis* as compared to that in the examined specimen.

**Table 2.** Measurements of the upper cheek teeth of *Ursavus breverhinus* and *U. primaevus*.

Measurements (mm) and indexes (%)	<i>U. breverhinus</i>					<i>U. primaevus</i>		
	Göriach, Austria (MN6)	Steyeregg, Austria (MN6)	Steinheim, Germany (MN7)	Górny Śląsk (= Kieferstädte), Poland		La Grive Saint-Alban, France (MN7-8)		
	MBLJG 1433	MBLJG 58781	SMNHS 10326	MNHUB 29321a	MNHUB 29322	MNHNP 1913-21, cast	NHML M5318	UCBL 213748
Length P4-M2			37.1			ca 43.5		
Length M1-M2		23.9	26.5	25.2		29.7		
LP4	9.7		11.2			13.3		
WP4	6.6		8.0			11.5		
LM1	11.8	11.9	12.8	12.1	10.9	12.5		13.4
WM1	11.1	10.5	11.2	11.3	10.4	11.6		12.0
LM2		10.9	13.6	13.0		16.6	16.1	
WM2		8.6	9.9	10.3		10.1	12.4	
Indexes								
LM1/LM2		109	94	93		75		
LM1/WM1	106	113	114	107	105	108		112
LM2/WM2		127	137	126		164	130	

In both comprised species the anterior cingulum is developed. The area beyond the ridge linking metaconule with metacone is larger in *B. elmensis* and *B. orientalis* than in the specimen-in-study. This area is found to be more extensive in *Ursavus isorei* and *U. breverhinus*.

The buccal walls of paracone and metacone of M1 slope slightly in *Ursavus breverhinus* and *U. primaevus*. Rather small metastyle is developed. Metaconule is shifted lingually, occupying the position beyond the protocone. These cusps form the lingual edge running parallel to the buccal ones (paracone and metacone). It is the important characteristic of Ursinae (Beaumont 1982). In *U. breverhinus*, the trigon basin remains to be clearly closed backwards. In *U. primaevus* the area between the lingual and buccal rows of cusps becomes wider and forms a longitudinal valley, which is well expressed in the recent bears of the genus *Ursus*. The lingual cingulum of both *Ursavus breverhinus* and *U. primaevus* is more massive as compared to that of PIN 3380/56. It extends more posteriorly and is broader.

By the length of M2, PIN 3380/56 resembles *Ballusia elmensis* and *B. orientalis* (see Crusafont Pairy and Kurtén 1976; Qiu et al. 1985), having this parameter not exceeding 10 mm whereas in *B. hareni* and in the representatives of the genus *Ursavus* the greatest length of M2 most often surpasses 11 mm.

The length of this tooth slightly exceeds its width. The ratio between the length and width of M2 in PIN 3380/56 is similar to that of *Ballusia orientalis* as well as to the sample of *Ballusia elmensis* from Wintershof-West locality (Dehm 1950). M2 in *B. hareni*, *Ursavus isorei*, and *U. breverhinus* are longer and this tooth is even more elongated in *U. primaevus* (Table 1, 2).

Morphology of the occlusal surface of M2 in PIN 3380/56 resembles that of *B. elmensis* and *B. orientalis*: the ridge between the metacone and metaconule is slightly developed. As a result, trigon basin is weakly separated from the basin of small talon. Surfaces of both basins of *B. elmensis* are finely tuberculous. The buccal cingulum of *B. elmensis* is better developed, whereas the lingual cingulum is well separated from the protocone and forms a shelf with the expressed hypocone. In *B. orientalis*, paracone and metacone are located closer to the buccal side of the crown. The talon and the lingual shelf are rather small.

In *Ballusia hareni*, paracone and metacone have steep buccal walls. Metaconule is crowded with the metacone. The basin of trigon is wide. The talon of M2 in this species is undeveloped or small; a cutting ridge runs along its outer margin. Buccal cingulum is distinct. Lingual cingulum is spaced from the protocone, forming a shelf with the hypocone. *U. isorei* is characterized by crowded metaconule and metacone. Talon is enlarged, which determines a general

elongation of the tooth crown in this species. *Ursavus breverhinus* reveals talon well developed; its surface is rugose. Lingual cingulum is well expressed; it is separated from protocone, forming a wide shelf with the hypocone. The longer talon of M2 is characteristic for *U. primaevus*.

**Discussion.** The study shows that the examined specimen PIN 3380/56 from Khirgis-Nur-I, Mongolia may be referred to the genus *Ballusia* by the shape, size, and proportions of the upper molars M1 and M2. This determination is based on the small tooth size, the ratio between the length of M1 and of M2 (the length of M2 is smaller than the length of M1), nearly square shape of the M1 crown (tooth length is equal to its width), vertical position of the buccal walls of paracone and metacone, the position of metaconule relatively to the protocone, slightly developed cingular shelf on M1, proportions of the M2 crown and its poorly expressed talon (the talon length constitutes less than 120% of its width). The listed features of *Ballusia* differ from those of the genus *Ursavus*. These features may be regarded as ancestral (plesiomorphic) ones in the evolutionary direction of the earlier Ursinae. The tooth morphology of *Ballusia* has no apomorphic features supporting the separation of this taxon from *Ursavus* and its distinctiveness at the genera level.

Within the genus *Ballusia*, specimen PIN 3380/56 demonstrates the great similarity to *B. elmensis* by dimensions, proportions, and the structure of upper molars. This species has been erected on the basis of left ramus of the mandible with p3-m2 from the Early Miocene, locality Elmin, Germany (Stehlin 1917). Later, it was found in many European localities: Les Bailleaux á Savigné-sur-Lathan (MN3a) and Vieux-Collonges (MN5) in France, Wintershof-West (MN3), Petersbuch 62 (MN3), Petersbuch 2 (MN4a), Petersbuch 4 (MN4b) and Hambach 6C (MN5) in Germany, Merkur-Ahnikov (MN3a) and Tuchořice (MN3b) in the Czech Republic, and probably in Leiding near Pitten (MN5) in Austria (Dehm 1950, Mein 1958, Thenius 1991, Fejfar and Kvaček 1993, Roth and Morlo 1997, Ginsburg and Morales 1998, Mörs et al. 2000, Fejfar et al. 2003, Dvořák et al. 2010, Rossina and Rummel 2012). The European material is known by isolated teeth, which makes determination of this species difficult. The difference between the Mongolian specimen and typical *B. elmensis* seems to be in following: in *B. elmensis* the metaconule of M1 separated from the

metacone; the masticatory surface of the tooth has tiny folds of enamel; on the contrary, PIN 3380/56 is characterized by the metaconule of M1 being more crowded with the metacone and by smooth trigon basin without an enamel folds (probably it is a result of the partial tooth wearing). Therefore, taking into account small differences between these specimens we determined the specimen from Khirgis-Nur-I as *B. elmensis*.

*B. orientalis* was described on the basis of the complete skeleton from the locality of Shanwang (MN4-5) in China (Qiu et al. 1985). Teeth of this taxon are smaller and definitely differ morphologically (M1 is extended and having metastyle, M2 is more elongated in contrast to M1) in comparison with those of PIN 3380/56.

There is a great similarity between *B. elmensis* (Europe, MN3-5) and *B. orientalis* (China, MN4-5) in the dentition, both taxa may be considered as subspecies of a single species, which had a wide range in the Early Miocene of Eurasia. This hypothesis has been already put forward (Baryshnikov 2007).

*Ballusia* and *Ursavus* demonstrate an evolutionary trend to elongation of the talon of M2 from geologically older *Balusia* towards younger one *Ursavus*. The talon is formed as a result of the lingual and posterior cingula growing backwards. Such elongation occurred in ursins in the process of the increase of herbivore specialization. The enlarged talon of M2 compensates the absence of M3 in ursids (while M3 is well-developed in many phytophagous mammals: rodents, artiodactyls, and perissodactyls). In the Ursinae, the longest talon of M2 is observed in the recent species of *Tremarctos* and *Ursus*. Different herbivore specialization of dentition has developed in the lineage to the extant *Ailuropoda melanoleuca* (David, 1869). Its M2 is less elongated, whereas the reinforcement of masticatory function is a result of M1 width increase (tooth width exceeds its length) and of molarization of posterior premolars. Our study led us to presume that that bears possessing these specializations diverged from the common lineage in the Early Miocene. Representatives of the first lineage seem to be descendants of the later species of *Ursavus*, whereas the second lineage split earlier from *Ballusia*. This hypothesis is confirmed by the results of karyological and molecular analyses evaluating the time of splitting the lineage of *Ailuropoda* (Nash and O'Brien 1987, Talbot and Shields 1996, Yu et al. 2004, Krause et al. 2008).

*Ballusia elmensis* (including PIN 3380/56 and *B. orientalis*) is characterized by short talon of M2. The tooth length only slightly exceeds its width (the ratio of  $w$  and  $l$  varies from 100% to 116%,  $n = 8$ ). *B. hareni* exhibits considerable enlargement of the talon, with the ratio between the length and width of the tooth crown 105–122% ( $n = 2$ ). M2 is noticeably elongated as a result of further talon development in *Ursavus isorei* (127–142%,  $n = 2$ ), *U. breverhinus* (126–137%,  $n = 3$ ), *U. tedfordi* (132%,  $n = 1$ ), and especially in *U. primaevus* (130–164%,  $n = 2$ ). Baryshnikov (2007) used this index for the separation of *Ballusia* (index below 120%) from *Ursavus* (index exceeding 120%).

*Ballusia hareni*, which is known mainly by the isolated teeth from the French localities of Les Beilleaux à Savigné-sur-Lathan (MN3a) and La Guimardière (MN3) (Ginsburg and Morales 1998, Gagnaison 2006, 2013), resembles *B. elmensis* by the shape and proportions of upper molars; however, several features affiliate it with the early representatives of *Ursavus*. The taxonomic position of *Ballusia hareni* remains unclear.

## CONCLUSION

The Ursavini remains are recorded in Asia in the range 19 to 9 Ma (European biozones MN 3-13), our knowledge on the earlier stages of the evolution of this taxon being, however, rather scant. The specimen of a small ursavin from Khirgis-Nur-I in Mongolia (MN3) is the oldest for the Asian localities, since the oldest record of Ursavini in China is Shanwang (ca. 16 Ma; approximately equal to European MN4) (Qiu et al. 2013, Qiu and Qiu 2013). The latest finding from China seems to be *Ursavus silvestris* from Lufeng locality (MN13, see Dong and Qi 2013).

The maxillary fragment from Khirgis-Nur-I, which is referred to *Ballusia elmensis*, allows us to improve our knowledge about the tooth morphology and distribution of this species. It points to a wide range of *B. elmensis* in the Early Miocene of Eurasia from Europe to Mongolia and China, which suggests its geographical variability. We recognize two subspecies: *B. e. elmensis* in Europe and *B. e. orientalis* in Eastern Asia, which existed during biozones MN3-5. A scarcity of material provides no possibility to carry out the subspecies attribution of the fossil bear from Mongolia. This bear is geographically distant from *B. e. elmensis* and seems to be evolutionary more primitive than *B. e. orientalis*. In this time ursids migrated

from Eurasia to the North America, where the earliest *Ursavus*-like findings are recorded from the Early Hemingfordian – Running water Chronofauna (Hunt 2004). This formation is comparable to the European biozone MN3. *B. elmensis* may be reconstructed as small arboreal animal with the omnivorous diet.

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## REFERENCES

- Baryshnikov G.F. 2007.** Bears Family (Carnivora, Ursidae). In: Fauna of Russia and neighbouring countries. New series, Vol. 147. Nauka, St. Petersburg, 541 p. [In Russian].
- Beaumont G. de. 1982.** Brèves remarques sur la dentition de certains ursides (mammifères). *Archives des Sciences Physiques et Naturelles, Genève*, **35**: 153–156.
- Crusafont Pairy M. and Kurtén B. 1976.** Bears and bears-dogs from the Vallesian of the Vallés-Penedés Basin, Spain. *Acta Zoologica Fennica* **144**: 1–29.
- Dehm R. 1950.** Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, neue Folge*, **58**: 1–141.
- Deviatkin E.V. and Zhegallo V.I. 1974.** New data on the localities of Neogene faunas of North-West Mongolia. In: Fauna and biostratigraphy of Mesozoic and Cenozoic of Mongolia. Nauka, Moscow: 330–355. [In Russian].
- Dong W. and Qi G-Q. 2013.** Hominoid-Producing Localities and Biostratigraphy in Yunnan. In: X. Wang, L.J. Flynn and M. Fortelius (Eds.). *Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, Chichester: 293–313.
- Dvořák Z., Mack K., Prokop J. and Knor S. 2010.** Třetihorní fauna severočeské hnědouhelné pánve [Tertiary Fauna of North Bohemian brown coal basin]. *Granit, Praha*, 175 p.

- Fejfar O. and Kvaček Z. 1993.** Excursion Nr. 3. Tertiary basins in Northwest Bohemia. *Paläontologische Gesellschaft*, **63**: 1–35.
- Fejfar O., Dvůrák Z. and Kadlecová E. 2003.** New record of Early Miocene (MN3a) mammals in the open brown coal pit Merkur, North Bohemia, Czech Republic. In: J.W.F. Reumer and W. Wessels (Eds.). Distribution and migration of Tertiary mammals in Eurasia. *Deinsea*, **10**: 163–182.
- Gagnaison C. 2006.** Découverte d'un maxillaire de *Ballusia hareni* dans le Miocène de Savigné-sur-Lathan (37, France). *Bulletin de la Société d'Etudes Scientifiques de l'Anjou. Nouvelle Série*, **20**: 79–82.
- Gagnaison C. 2013.** Les assemblages de vertébrés dans deux sites paléontologiques du bassin miocène de Savigné-sur-Lathan/Noyant-sous-le-Lude: La Guimardière et Pelmer (Maine-et-Loire, France). *Geodiversitas*, **35**: 67–103.
- Ginsburg L. and Morales J. 1998.** Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale. *Annales de Paléontologie*, **84**: 71–123.
- Hunt R.M. Jr. 2004.** Global Climate and the Evolution of Large Mammalian Carnivores during the Later Cenozoic in North America. *Bulletin of the American Museum of Natural History*, **285**: 139–156.
- Krause J., Unger T., Noçon A., Malaspinas A.-S., Kolokotronis S.-O., Stiller M., Soibelzon L., Spriggs H., Dear P.H., Briggs A.W., Bray S.C., O'Brien A.J., Rabeder G., Matheus P., Cooper A., Slatkin M., Pääbo S. and Hofreiter M. 2008.** Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. *BMC Evolutionary Biology*, **8**: 220 doi: 10.1186/1471-2148-8-220.
- Mein P. 1958.** Les Mammifères de la faune sidérolithique de Vieux-Collognes. Nouvelles *Archives du Muséum d'Histoire Naturelle de Lyon*, **5**: 1–122.
- Mörs T., Hocht F. von der and Wutzler B. 2000.** Die erste Wirbeltierfauna aus der miozänen Braunkohle der Niederrheinischen Bucht (Ville-Schichten, Tagebau Hambach). *Paläontologische Zeitschrift*, **74**: 145–170.
- Nash W.G. and O'Brien S.J. 1987.** A comparative chromosome banding analysis of the Ursidae and their relationship to other carnivores. *Cytogenetics and Cell Genetics*, **45**: 206–212.
- Qiu Z-D. and Qiu Z-X. 2013.** Early Miocene Xiejiahe and Sihong Fossil Localities and Their Faunas, Eastern China. In: X. Wang, L.J. Flynn, and M. Fortelius (Eds.). Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology. Columbia University Press, New York, Chichester: 142–154.
- Qiu Z-X., Deng T. and Wang B.-Y. 2014.** A Late Miocene *Ursavus* skull from Guanghe, Gansu, China. *Vertebrata Palasiatica*, **52**: 265–302.
- Qiu Z-X., Qiu Z-D, Deng T., Li C-K., Zhang Z-Q., Wang B-Y. and Wang X. 2013.** Neogene Land Mammal Stages/Ages of China. Towards the Goal to Establish an Asian Land Mammal Stage/Age Schema. In: X. Wang, L.J. Flynn and M. Fortelius (Eds.). Fossil Mammals of Asia. Neogene Biostratigraphy and Chronology. Columbia University Press, New York, Chichester: 29–90.
- Qiu Z., Yan D. and Jia H. 1985.** Dentition of the *Ursavus* skeleton from Shanwangm, Shandong Province. *Vertebrata Palasiatica*, **23**: 264–275.
- Rosina V.V. and Rummel M. 2012.** The bats (Chiroptera, Mammalia) from the Early Miocene of Petersbuch (Bavaria, Southern Germany). *Geobios*, **45**: 463–478.
- Roth C.H., and Morlo M. 1997.** Die Raubtiere (Mammalia, Carnivora) aus dem Turolium von Dorn-Dürkheim 1 (Rheinessen). Teil 2: Ursidae. *Courier Forschungs-Institut Senckenberg*, **197**: 49–71.
- Stehlin H.G. 1917.** Miocäne Säugetier reste aus der Gegend von Elm (Prov. Hessen). *Verhandlungen der Naturforschenden Gesellschaft in Basel*, **28**: 191–205.
- Talbot S. and Shields G. 1996.** A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes. *Molecular Phylogenetics and Evolution*, **5**: 567–575.
- Thenius E. 1991.** Über das Vorkommen von *Ursavus elmenensis* (Mammalia, Carnivora) im Miozän von Niederösterreich (Austria). *RAD Harvatske akademije znanosti I umjetnosti* (Knj. 458), *Razred za prirodne znanosti*, Knj., **25**: 91–101.
- Vangengein E.A. and Tesakov A.S. 2008.** Maeotian Mammalian localities of Eastern Paratethys: Magnetochronology and position in European continental scales. *Stratigraphy and Geological Correlation*, **16**: 437–450.
- Vislobokova I.A. 1983.** The fossil deer of Mongolia. Nauka, Moscow, 78 p. [In Russian].
- Vislobokova I.A. 1990.** The fossil deer of Eurasia. Nauka, Moscow, 208 p. [In Russian].
- Yu L., Li Q., Ryder O.A. and Zhang Y. 2004.** Phylogeny of the bears (Ursidae) based on nuclear and mitochondrial genes. *Molecular Phylogenetics and Evolution*, **32**: 480–494.
- Zhang W., Chen P.-J., and Paler A.R. 2003.** Biostratigraphy of China. Science Press, Beijing, 603 p.
- Zhegallo V.I. 1978.** The hipparions of Central Asia. *The joint Soviet-Mongolian paleontological expedition*, **7**: 1–156. [In Russian].