

Pliocene bear *Ursus minimus* Devèze de Chabriol et Bouillet, 1827 (Carnivora, Ursidae) in Russia and Kazakhstan

Gennady F. Baryshnikov & Alexander V. Lavrov

ABSTRACT. Mandibular fragments of the small Pliocene bear from Kosyakino in Northern Caucasus, Russia (MN15) and from Moiseevka in Irtysh River basin, Kazakhstan (MN14) revealed morphological similarity with the specimens of *Ursus minimus*. During the evolution of this species, the enlargement of molars and equalization of the m1 and m2 in length took place. Our study ascertained the presence of geographical variability of *U. minimus* in Eurasia in the Early Pliocene (*U. m. boeckhi* in Europe and *U. m. ssp.* in Kazakhstan) as well as in the Late Pliocene (*U. m. minimus* in Europe and *U. m. yinanensis* in China).

KEY WORDS: *Ursus minimus*, Ursidae, Pliocene, Caucasus, Kazakhstan.

Gennady F. Baryshnikov [G_Baryshnikov@mail.ru], Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, Saint Petersburg 199034, Russia; Alexander V. Lavrov [lavrov@paleo.ru], A. A. Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow 117647, Russia.

Плиоценовый медведь *Ursus minimus* Devèze de Chabriol et Bouillet, 1827 (Carnivora, Ursidae) в России и Казахстане

Г.Ф. Барышников, А.В. Лавров

РЕЗЮМЕ. Фрагменты нижнечелюстных костей маленького плиоценового медведя из местонахождений Косякино на Северном Кавказе, Россия (MN15), и Моисеевка в бассейне реки Иртыш, Казахстан (MN14), обнаружили морфологическое сходство с образцами *Ursus minimus*. В процессе эволюции вида происходило увеличение размеров коренных зубов и имело место выравнивание длины m1 и m2. Наше исследование подтвердило существование у *U. minimus* в Евразии географической изменчивости как в раннем плиоцене (*U. m. boeckhi* in Europe and *U. m. ssp.* in Kazakhstan), так и в позднем плиоцене (*U. m. minimus* in Europe and *U. m. yinanensis* in China).

КЛЮЧЕВЫЕ СЛОВА: *Ursus minimus*, Ursidae, плиоцен, Кавказ, Казахстан.

Introduction

All recent bears of the Old World (except of bamboo bear, *Ailuropoda melanoleuca* (David, 1869) belong to the tribe Ursini Fischer, 1814 and derive (according to the data of mitochondrial phylogeny) from bears of the New World (tribe Arctotheriini F. Ameghino, 1903) at the beginning of the Late Miocene (Tortonian), near 12.86 Ma (Krause *et al.*, 2008). The ancestor of ursine bears is regarded to be a member of the genus *Ursavus* Schlosser, 1899, presumably *U. primaevus* (Gaillard, 1899) (Baryshnikov, 2007).

Ursine bears radiation occurred at the time corresponding to the time period near the Miocene-Pliocene boundary (5.39 Ma by molecular data). The basal position by molecular phylogeny (see Krause *et al.*, 2008) is occupied by the sloth bear, *Melursus ursinus* (Shaw, 1791). The appearance of the genus *Ursus* L., 1758, is referred to the beginning of the Pliocene (5.05 Ma). The time of divergence of the two species of black bears (*Ursus thibetanus* G. Cuvier, 1823 and *U. americanus* Pallas, 1780) was determinate as 4.08 Ma.

The earliest member of the genus *Ursus* is regarded to be the fossil bear *U. minimus* Devèze de Chabriol et Bouillet, 1827 (= *U. arvernensis* Croizet et Jobert, 1828), which presumably was the ancestral taxon for black bears, cave bears, and brown bears of Eurasia and North America (Baryshnikov, 2007). The greatest similarity of *U. minimus* to the Asian black bear (*U. thibetanus*) is expressed in their dental morphology. Hence, the findings of the teeth of Pliocene ursids in Europe are often determined as *U. ex gr. minimus-thibetanus* (Wagner, 2010).

U. minimus is represented by cranial fragments, lower jaws, isolated teeth and some bones of postcranial skeleton (Croizet & Jobert, 1828; Depéret, 1890; Maier von Mayerfels, 1929; Roshchin, 1956; Ryziewicz, 1969; Berzi, 1966; Jánossy, 1978; etc.). However, its taxonomic position remains questionable. Some researchers divide *U. minimus* for several taxa: *U. boeckhi* Schlosser, 1899 (Early Pliocene, Europe), *U. minimus* s.str. (Late Pliocene, Europe), *U. yinanensis* Li, 1993 (Late Pliocene, China) and *U. abstrusus* Bjork, 1970 (Early Pliocene, North America) (Li, 1993; Tedford & Harington, 2003; Wagner, 2010). The others

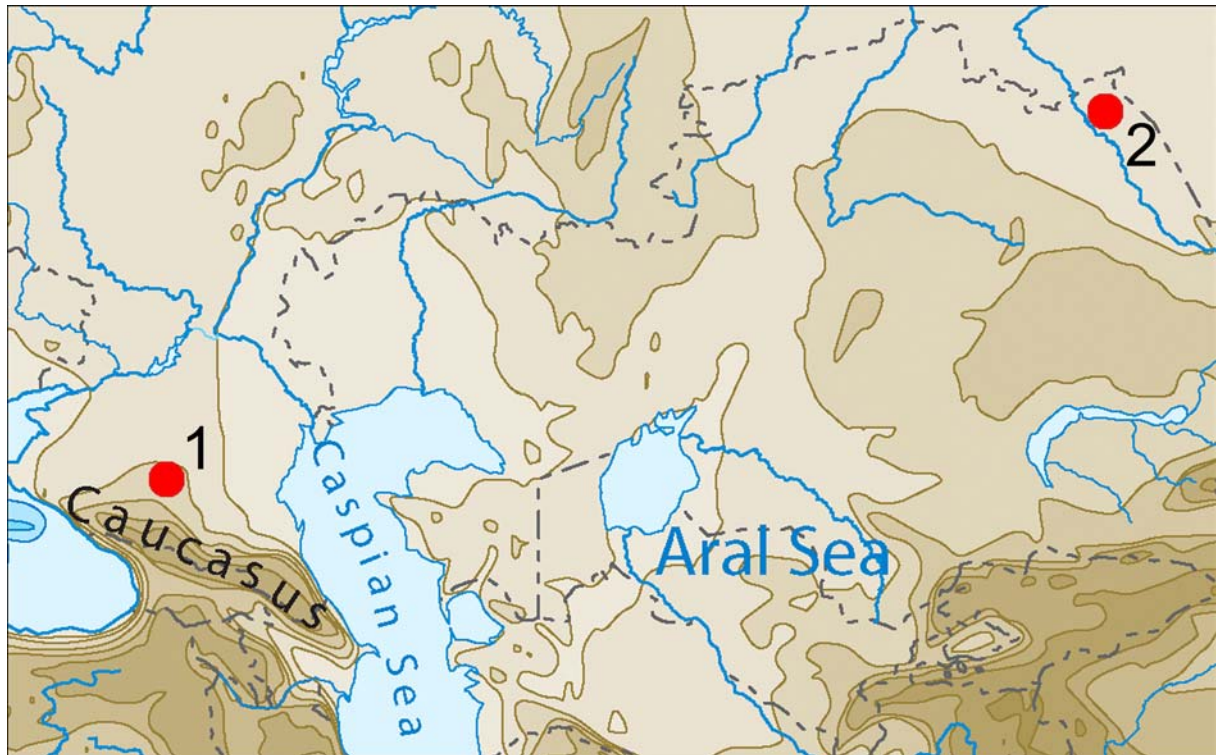


Figure 1. The geographic positions of the localities of *Ursus minimus* considered in the paper.

1 — Kosyakino, 2 — Moiseevka.

consider these taxa to be subspecies of the single polytypical species of *U. minimus*, which formed the Pan-Holarctic distribution (Baryshnikov, 2007). Some paleontologists consider that all bear fossils from Europe of this age belong to a single species — *U. minimus* (Morlo & Kundrát, 2001). Moreover, the idea has been put forward on separating of black bears in two genera: *Protarctos* Kretzoi, 1945 (*P. boeckhi*, MN14; *P. ruscinensis* Depéret, 1890, MN15; *P. yinanensis*, MN16–17), and *Euarctos* Gray, 1864 (*E. pyrenaicus* Depéret, 1892, MN15; *E. minimus*, MN16–17; and recent species: *E. thibetanus* and American baribal *E. americanus*), was suggested by Qui *et al.* (2009). Thus the species *U. thibetanus* and *U. americanus* are excluded from the genus *Ursus*. However, this opinion is based mainly on the morphology of one tooth m1 only. This point of view is disputable by the reasons of the significant variability of dental characters in bears as well as molecular studies supporting the monophyly of the genus *Ursus* (Pagés *et al.*, 2008).

European findings of *U. minimus* in the Early Ruscinian (MN14) are known from Alcoy in Spain, Montpellier in France (MN14a), Kuchurganian beds (Trudomirovka) in Ukraine, Baraolt-Căpeni in Romania (=Barót-Köpecz in Hungary), and Dorkovo in Bulgaria (Schlosser, 1899; Maier von Mayerfels, 1929; Korotkevich, 1967; Dubrovo & Kapelist, 1979; Spassov, 2003; Montoya *et al.*, 2006; Wagner, 2006). In the late Ruscinian and early Villanyian localities, the species was recorded in Perpignan, France (MN15a), Layna,

Spain and Weże 1, Poland (MN 15b), Wölfersheim, Germany (MN15b), Odessa Catacombs, Ukraine (MN 15/16), Gaville, Triversa, Arondelli, Ponzano, Italy (MN16), Les Etouaires, France (MN16b), Včeláre 2, Slovakia (probably MN16), and Osztramos 7, Hungary (MN16b) (Roshchin, 1956; Berzi, 1966; Ryziewicz, 1969; Soria & Morales, 1976; Jánossy, 1978; Mazza & Rustioni, 1994; Alberdi *et al.*, 1997; Morlo & Kundrát, 2001; Sabol *et al.*, 2008; Wagner, 2010; Wagner *et al.*, 2012). Bears from aforementioned localities had been referred to different taxa, but later were assigned to *U. minimus* (synonymy see in Baryshnikov, 2007).

In Asia, *U. minimus* was discovered in Kvabebi, Georgia (MN16, Vekua, 1972), Kosyakino and Udunga (MN15) in Russia (Vereshchagin, 1959; Sotnikova & Kalmykov, 1991; Baryshnikov, 2007; Sotnikova, 2008), as well as in Yushe (as *Ursus* sp.), Liang-Chia-Ho [as *U. cf. boeckhi*; assigned to *Helarctos sinomalayanus* by Thenius (1947)] and Yinan (as *U. yinanensis*, MN16/17) in China (Zdansky, 1927; Teilhard de Chardin, 1940; Qiu *et al.*, 2009). In North America, there are several findings (as *U. abstrusus*) in the Early Blancanian sites (Hagerman, White Bluffs, Buckeye Creek) and Late Blancanian sites (Cita Canyon) in the USA (Kurtén & Andersen, 1980; Kelly, 1994) and in Canadian Arctic (Elsmere Island; Tedford & Harington, 2003).

Though the remains of *Ursus minimus* are known from numerous localities, the findings of this species are rather rare. The evolutionary changes of teeth and

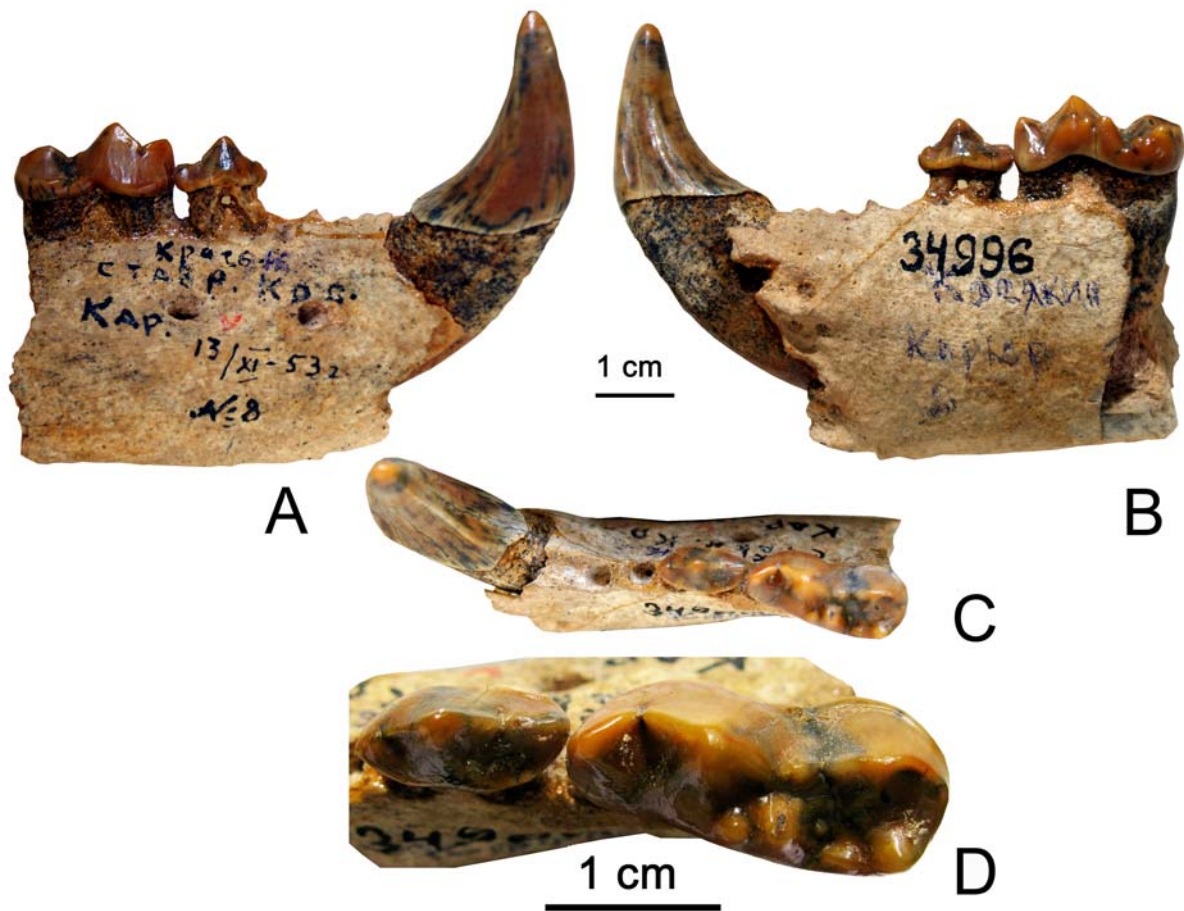


Figure 2. The fragment of the right mandibular ramus of *Ursus minimus* from Kosyakino, Northern Caucasus (ZIN 34996); labial (A), lingual (B) and occlusal (C, D) views.

skull characters of this species, as well as its variability, remain unclear. Therefore, the prior attention was given to the complete description of the material from the territories of Russia and Kazakhstan. This material makes possible estimating of morphological changes throughout all specific range of *U. minimus* from West European to Chinese localities.

In this publication we describe the morphological features of the lower jaws from Northern Caucasus (Kosyakino) and from the northern part of Kazakhstan (Moiseevka) for the first time (Fig. 1). Examined material is stored in Zoological Institute, Russian Academy of Sciences in St. Petersburg (ZIN) and in A.A. Borissiak Paleontological Institute, Russian Academy of Sciences in Moscow (PIN). For comparative analysis, we used the collections of several European depositories (see Institutional abbreviations).

In the definition of the mammal ages and their correlation with the chronostratigraphical scale as well as the MN-zones we follow Mein (1990), Fejfar & Heinrich (1990), Fejfar *et al.* (1998), and Wagner *et al.* (2012).

Institutional abbreviations. CBUL — Claude Bernard University Lyon 1, Villerbann, France; IGF — Museo di Storia Naturale, Sezione Geologia e Paleon-

tologia, Università di Firenze, Italy; ISEA — Institute of Systematics and Evolution of Animals, Krakow, Poland; SNMB — Slovak National Museum, Bratislava, Slovakia; NHMN — Muséum National d'Histoire Naturelle, Paris, France; PIN — A. A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; ZIN — Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Localities and material

Kosyakino. This locality (sand quarry) is situated near Stavropol city in Northern Caucasus, Russia (45°03'N, 41°57'E). The mammalian fossils were located in the sandy alluvial deposits and were redeposited by the ancient river (Vereshchagin, 1959).

Originally the list of mammalian taxa from this locality included: *Ursus cf. arvernensis* Croiz. et Job., *Dinocyon cf. thenardi* Jourd., *Felis cf. issiodorensis* Croiz. et Job., *Ochotona cf. antiqua* Pidopl., *Lepus sp.*, *Amblicastor caucasicus* Argirop., *Steneofiber sp.*, *Ananacus arvernensis* Aymard, *Dinotherium sp.*, *Hipparion gracile* Kaup, *Tapirus cf. arvernensis* Croiz. et Job.,

Dicerorhinus orientalis Schlosser, *Aceratotherium* cf. *incisivum* Kaup, *Propotamochoerus provincialis* Gervais, *Procapreolus* sp., *Pliocervus* sp., *Pseudalces* sp., *Gazella* sp., etc. (Argiropulo, 1939, 1940; Beliaeva, 1940, 1944; Vereshchagin, 1959).

Later some of these taxa were redefined. The beaver *Amblicastor caucasicus* was determined as porcupine *Hystrix caucasicus* (Lopatin *et al.*, 2003); hemicyonid *Dinocyon* cf. *thenardi* as ursid *Agriotherium sivalense minutum* Gerv. (Baryshnikov, 2007). The list of the lagomorph species was also modified: *Prolagus caucasicus* Averianov et Tesakov, *Ochotona* cf. *antiqua*, *Hypolagus* cf. *igromovi* Gureev (Averianov & Tesakov, 1998).

The geological age of Kosyakino is determined as Early Ruscinian (MN14) based on lagomorphs (Averianov & Tesakov, 1998) or as Late Ruscinian (MN15) according to carnivores' data (Vislobokova *et al.*, 2001).

Ursid findings from Kosyakino were represented by two right mandible fragments. The specimen ZIN 34996 (Fig. 2) includes the lower canine, alveoli p1–p3 and also cheek teeth p4 and m1. The color of bone is light gray. Tooth enamel is light brown, with indistinct dark spots (collected by N.K. Vereshchagin in September 13, 1953). The specimen PIN No.225/253 (Fig. 3) includes the fragment of the lower canine, alveoli p1–p3 and molars m1–m2. The bone is dense; its color is beige turning to light brown. Tooth enamel is colored as that of the specimen ZIN 34996. The bone mineralization is high. Vereshchagin (1959: Fig. 24, 1, 3) identified the lower jaw fragments from Kosyakino as *Ursus* cf. *arvernensis* but not described it. This paper includes illustrations of both lower jaw fragments of ursids from Kosyakino. Vereshchagin (1959) reported that 12 ursid bones totally were collected in the locality.

Moiseevka. The locality is situated at the right bank of the Irtysh River near Moiseevka village in Zhelezinsky District of Pavlodar Region, Kazakhstan (53°27'N, 75°28'E). The age of the finding is not precise, but Pliocene age is mentioned in the museum label.

The member of green clay is located at the left bank of the Irtysh River; these clays were dated as Oligocene – Middle Miocene. The same type of deposits is present at the right bank of the Irtysh River. This member is overlain by Late Miocene and Pliocene deposits (Nikiforova, 1953). Near from the village Moiseevka the member sandy (psammitic) and marlaceous clays was established as Moiseevskaya svita, in which were found fossils of *Equus stenorhinus* Cocchi fossils (Kostenko, 1963). Zinova (1982) included Moiseevskaya svita as a member within the compound of Podpusk-Lebiazhinskaya svita characterized by presence of *Archidiskodon gromovi* Garutt et Alex., *Equus stenorhinus* Cocchi, *Elasmotherium* sp., *Gazella* cf. *sinensis* Teih. et Piv., “*Vulpes*” *odessanus* Odinz. (= *Eocyon odessanus*, see Sotnikova & Rock, 2010). E. Vangengeim (1977) considered that Podpusk-Lebiazhinskaya svita is analogous to Khaprovian age (Middle Villafranchian) of Eastern Europe. Vislobokova (1996) noted a presence

of faunal horizons dated earlier than Middle Villafranchian in the Moiseevskaya svita.

Deposits of Novostanychnaya svita (stratum) in the neighborhood of the Moiseevka village are of Middle Pliocene age (Zinova, 1982: 44). In the deposits of this unit the bones of small mammals Desmanidae gen.?, *Steneofiber*, *Prosiphneus*, and *Baranomys* had been collected. According to the opinion of Zazhigin (1980) the presence of *Baranomys* and degree of evolutionary development of beaver *Steneofiber* teeth makes possible attribution of Novostanychnaya svita to the horizon directly below the Akchaghylian beds. It's very likely that described lower jaw originates from these deposits. The deposits of this svita have been later attributed by V. Zazhigin to the Late Miocene (MN13; Zykina *et al.*, 2007). We determine the age of the ursid lower jaw from Moiseevka approximately as Early Pliocene (Early Ruscinian, MN14). This suggestion confirmed by the ursids morphological features described below.

Describing material from Kazakhstan presented by right ramus of the lower jaw with m1–m2 (PIN No.5332/1). It was found at the right bank of Irtysh River (outcrop number 130, specimen 207) in 2.5 km upstream from the Moiseevka village, Omsk Region (now Pavlodar region, Kazakhstan), collected by K. Nikiforova, Institute of Geological Sciences of Academy of Sciences of USSR, Moscow, September 7, 1948. The bone color is dark gray. Teeth are well preserved, the enamel is brown colored. The specimen was identified and labeled as *Ursus arvernensis*. This specimen was neither described nor figured earlier.

Systematic Paleontology

Order Carnivora Bowdich, 1821
Family Ursidae Fischer, 1814
Genus *Ursus* Linnaeus, 1758

Ursus minimus Devèze de Chabriol et Bouillet, 1827

Description. *Kosyakino* (ZIN 34996, PIN No.225/253; Figs. 2, 3). The lower margin of the mandible is straight. The ramus is high; its height is decreasing forward. The mandibular symphysis is short, reaches the level of the premolar p3; a “chin” prominent at the ventro-caudal symphyseal edge is relatively small, but it's well expressed. The masseteric fossa is rather shallow and extends anteriorly to the level of the posterior margin of m3. Judging by the preserved part of the coronoid process, its anterior margin should be gradually upraised over the tooth row. There are two mental foramina: the anterior one is located at the level between p2/p3 and posterior one is located directly below the contact between p4 and m1.

The axis of the tooth row is slightly curved in dorsal projection. There is an angle between the axes of premolar and molar rows. The masticatory surface of m3 is inclined anteriorly.

The shape of the canine is typical for bears. There are two carnassial ridges on the enamel surface (anteriorly).

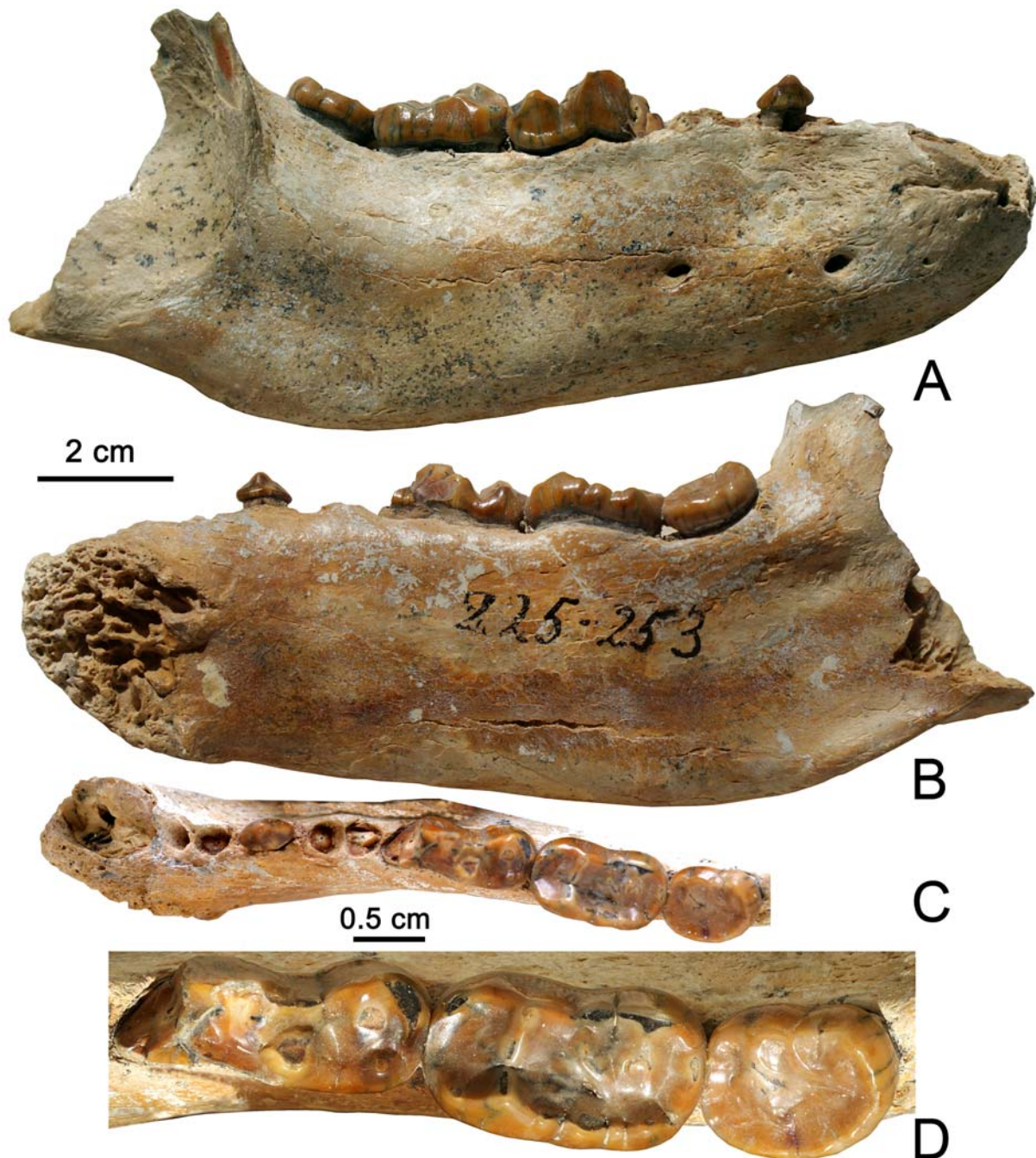


Figure 3. The right mandibular ramus of *Ursus minimus* from Kosyakino, Northern Caucasus (PIN No.225/253); labial (A), lingual (B) and occlusal (C, D) views.

or and posterior one). These ridges are slightly notched and run from the basis of the crown toward the canine apex. Also, a weakly developed ridge runs along the middle line of the lingual side of the crown. The tooth is somewhat turned along the longitudinal axis, so that the longitudinal axis is directed lingual from the row of cheek teeth.

The row of anterior premolars p1–p3 is crowded towards the canine. The postcanine diastema is absent.

The teeth p1 and p2 were single-rooted. The premolar p3 in ZIN 34996 is single-rooted as well. In the specimen PIN No.225/253 p3 is completely preserved, it's a small, single-cusped, and double-rooted tooth. In the recent species of the genus *Ursus*, the premolar p3 is single-rooted and frequently absent (in *U. arctos* L., *U. maritimus* Phipps).

The premolar p4 has two separated roots. There are two longitudinal enamel crests run nearly from basis of

the crown to the apex of the main cusp. The anterior keel runs from a small cuspid near the crown margin. The posterior keel passes into elongated horizontal ridge. There is a slender buccal cingulid, which is better developed in the posterior portion of the tooth crown. The lingual cingulid is well expressed. It is looks like to a ridge in the posterior portion of the crown. It is upraised directly behind the base of the main cusp and forms separated cuspid (probably "metaconid").

The lower carnassial tooth m1 is comparatively small in contrast to other bears. The habitus of m1 is rather compact: its length is approximately twice the tooth width. The paraconid is short, shaped as a sharp tubercle; its anterior margin is parallel to the dorso-ventral axis. The paraconid is approximately equal to metaconid in height. The protoconid is robust, high and has a trenchant anterior margin. The carnassials notch between paraconid and protoconid is rather shallow. The metaconid is massive, well separated from the protoconid. It is shifted posteriorly far from the caudal margin of the protoconid. In the specimen PIN No.225/253, the metaconid has a single apex (Fig. 3D), whereas the specimen ZIN 34996 has an accessorial cusp (premetaconid) in front of the metaconid (Fig. 2D), similar to recent black bears and brown bears. The talonid portion is comparatively short (the length being nearly equal to the width) and doesn't have the inner basin. The talonid is slightly wider than the trigonid, and there is a slightly expressed constriction between them. The greater part of the talonid is formed by the hypoconid which looks like a high three-edged cusp. The hypoconid possesses no separated inner structure in contrast to cave bears and brown bears. The entoconid is divided from the hypoconid. The entoconid has a single apex and is significantly smaller and lower than the hypoconid. There is a small entoconulid (ZIN 34996) in front of the entoconid. It is necessary to note that the entoconulid is absent on the specimen PIN No.225/253. The hypoconulid is absent in ZIN 34996. The posterior part of the crown has a distinct buccal cingulid. The lingual cingulid is absent.

The molar of m2 is slightly smaller in length than m1. The masticatory surface is subrectangular, without a distinct constriction. The trigonid and talonid are nearly equal in width. The anterior margin of the crown has an arched ridge. The paraconid is not developed. The protoconid has a single apex and it is rather low. The metaconid do not have an additional tubercles and it is noticeably higher than the protoconid. The inner ridges, running from the protoconid and metaconid merge together. These ridges divide anterior (the trigonid) and posterior (the talonid) parts of the interior region of the crown. The anterior part of the crown is cup-shaped and comparatively small. The posterior part is more extensive, spreading onto the talonid and displaying enamel folds. The hypoconid is single-cusped

and it tends to form an inner lobe. The entoconid is ridge-shaped and exceeds hypoconid in height, being composed of two tubercles divided by a small cuspid. The distal ridge runs along the posterior margin of the crown, linking the hypoconid and entoconid; there are no clear traces of the hypoconulid. The buccal and lingual cingulids are absent.

The molar m3 is comparatively small and oviform. A slight separation of the talonid from the trigonid is traced on the buccal side of the tooth (this separation is especially well developed in the cave bears). The outer margin of the crown is upraised like a ridge with slightly expressed protoconid and hypoconid. The lingual surface of the tooth is somewhat wrinkled.

Moiseevka. The lower margin of the mandible fragment (PIN No.5332/1, Fig. 4) is nearly straight with a slight concavity below m1; as a result, the height of the mandibular ramus decreases from the diaphysis towards the level of m1, increasing again at the level of m2. The symphyseal part is large in regard to the mandible size; it extends backwards up to the level of p2. The "chin" (the ventral prominent) is absent. There are two approximated mental foramina distanced from each other at 6.3 mm. The posterior opening is located below the alveolus of p3.

The postcanine diastema is absent. The canine is broken; its remaining part implies its size was somewhat smaller than that in ZIN 34996 (Kosyakino). The area between the canine and the molar m1 is occupied by three alveoli from anterior premolars p1–p3, which were single-rooted, as well as by two alveoli from the premolar p4.

The lower carnassial tooth is similar by proportions and shape to the specimen from ZIN 34996 (Kosyakino), being, however, somewhat smaller. The metaconid is single-cusped, less robust than that in the specimen from Kosyakino. The hypoconid is large; there is no accessorial tubercle between it and the protoconid. The entoconid is shaped like a ridge formed by two closely spaced cuspids (the first one being higher). The additional, tiny cuspid (entoconulid) is located in front of the entoconid, and closes the inner area of talonid from the lingual side.

The proportions and shape of the molar m2 are similar to those in PIN No.225/253 from Kosyakino, but, in contrast to the latter, the tooth is markedly shorter than m1. The metaconid is robust and single-cusped. The hypoconid is pronouncedly higher as compared to the entoconid (unlike in PIN No.225/253). The entoconid is ridge-like, and only two poorly expressed and widely spaced cuspids are present. The buccal cingulid is well developed.

Comparison. The comparison of a tooth sizes of *U. minimus* from various geological ages (horizons) shows that tooth sizes increased during the species evolution. The latest members of the species possess the largest

Figure 4. The fragment of right mandibular ramus of *Ursus minimus* (PIN No.5332/1) from Moiseevka, Kazakhstan; labial (A), lingual (B) and occlusal (C, D) views.



2 cm



1 cm



Table 1. Sizes of the mandibles of *Ursus minimus*.

Measurements, mm	<i>U. m. boeckhi</i>		<i>U. m. minimus</i>				
	Baraolt-Căpeni, Romania (=Baróth-Köpec, Hungary)	Moiseevka, Kazakhstan	Kosyakino, Russia		Perpignan, France	France (locality unknown)	Gaville, Italy
	CBUL 3302, cast	PIN 5332-1	PIN 225-253	ZIN 34996	CBUL 41.326	NHMN, coll. Bravard 12q, cast	IGF 11568, sin
Length c1–m3			ca109		125.3	125.1	136.0
Length c1–m2		ca83.9	ca94				
Length alvp4–m3			66.3		66.1	76.1	76.5
Length alvp4–m2		49.2	52.9				
Length m1–m3	53.2		ca56		54.7	63.1	64.5
Length m1–m2		38.2	ca42				
Height behind m1		29.9	37.3			36.7	49.5
Height behind p4	39.5				42.6	42.4	49.0
Height behind p2		33.6	35.7	32.8			
Teeth							
c1 L	14.5	ca17.1		18.7	26.3	23.5	25.0
c1 W	12.6	ca10.0		11.5	13.8	13.8	14.5
p3 L			7.6		7.0		
p3 W			4.2		4.5		
p4 L				11.9	12.1	13.3	11.4
p4 W				6.1	6.9	7.7	6.9
m1 L	20.9	20.4	ca22.1	21.0	20.4	23.6	25.1
m1 W	9.4	9.4	9.3	9.7	9.1	12.5	11.5
m2 L	17.9	17.9	20.0		20.0	22.5	22.7
m2 W	10.6	11.3	11.2		11.8	15.5	13.8
m3 L	14.5		14.3		15.1	16.3	
m3 W	11.6		11.1		11.6	13.5	

cheek teeth (Tabs. 1–3). The increasing of m2 is notably expressed: in the specimens from the Early Ruscinian of Europe (Baraolt-Căpeni, Moiseevka, MN14) the length of m2 is significantly smaller than that of m1. However m1 and m2 from the Late Ruscinian specimens (Perpignan, Kosyakino, MN15) are approximately equal in length. The lower jaw from the Late Villányian (Gaville, MN16) has m1 which is significantly longer than m2. Moreover, tooth sizes are notably larger than those in the bears from the Early Ruscinian. Length ratio of m1/m2 of *U. minimus yinanensis* from China (Dongxiang, Yinan) are similar to those from the Early Ruscinian, although the geological age of the Chinese taxon is more late (it is equal to MN16–17; Qiu *et al.*, 2009). In recent *U. thibetanus* m1 and m2 are approximately equal in length. It may be hypothesized that Asian black bear diverged from the Late Ruscinian ursids. This proposal was confirmed by the results of the molecular studies (Talbot & Shields, 1996) and paleontological data (Baryshnikov & Zakharov, 2013).

All examined specimens have similar proportions of m1. Height of the paraconid and metaconid is approximately equal (in the ancestral Miocene *Ursavus primaevus* the metaconid is higher than paraconid). The dimensions of these cusps changed during the evolution, therefore in the recent *Ursus thibetanus* the

paraconid is pronouncedly higher than metaconid. The metaconid, in general, is single-cusped (Baraolt-Căpeni, Perpignan, Včeláre). However, many specimens from Odessa Catacombs and Gaville have premetaconid (Roshchin, 1956; Berzi, 1966; Ryziewicz, 1969; Vekua, 1972). Even in the same series of specimens this feature may be rather variable (Kosyakino, Weže 1). Recent Asian black bear (*U. thibetanus*) has smaller double-cusped metaconid connected to protoconid (in some cases, it can be formed only by a single cusp of the metaconid).

Evolutionary changes of m1 morphology also include the increasing of the talonid size, which is enlarged transversally in the latest representatives of the species (Tab. 1). In *Ursus minimus* the talonid and trigonid are separated by the large transversal groove facing the lingual side of the crown. The same peculiarities are typical for recent *U. thibetanus*. This groove may be of exposed type (ZIN 34996, Kosyakino) or closed type, in the latter the groove is overlapped by enamel cuspid close to the tooth border (the specimen from Moiseevka). The hypoconid of all described specimens is large, its inner lobe is not separated. The entoconid morphology in described specimens is variable. The entoconid of the most specimens (Baraolt-Căpeni, Weže 1, Perpignan, Včeláre, Odessa Cata-

Table 2. Measurements (mm) of lower molar m1 of *Ursus minimus*.

Localities	Museum number	Greatest length	Buccal length of trigonid	Width of trigonid	Width of talonid	Width of constriction
<i>U. minimus boeckhi</i>						
Baraolt-Căpeni, Romania (MN14)	CBUL 3302, cast	20.9	ca14.4	9.0	9.4	8.7
Moiseevka, Kazakhstan (early MN15)	PIN 5332-1	20.4	13.2	7.9	9.4	8.1
<i>U. minimus minimus</i>						
Kosyakino, Russia (MN15)	PIN 225-253	ca22.1	-	7.6	9.3	7.8
	ZIN 34996	21.0	14.1	8.0	9.7	8.0
Perpignan, France (MN15)	CBUL 41.326	20.4	13.0	8.0	9.1	7.7
Weże 1, Poland (MN15)	ISEA MF/833/67/5	21.0	13.0	7.5	8.8	7.6
	ISEA MF/833/67/9	22.8	14.3	8.5	10.9	9.4
	ISEA MF/833/67/13	21.2	12.9	7.8	9.1	7.5
	ISEA MF/833/67/15	19.2	12.3	7.7	8.5	6.8
	ISEA MF/833/67/17	19.4	13.1	8.1	9.0	8.3
Včeláre, Slovakia (MN16)	SNMB Z26702	21.4	14.5	8.5	9.3	8.3
France (locality unknown)	NHMN, coll. Bravard 12q, cast	23.6	14.4	9.8	12.5	10.2
Gaville, Italy (MN16)	IGF 11568, sin	25.1	15.2	10.4	11.5	9.2
	IGF 11568, dex	24.8	16.6	9.7	10.3	8.9

Table 3. Measurements (mm) of lower molar m2 of *Ursus minimus*.

Localities	Museum number	Greatest length	Buccal length of trigonid	Lingual length of trigonid	Width of trigonid	Width of talonid
<i>U. minimus boeckhi</i>						
Baraolt-Căpeni, Romania (MN14)	CBUL 3302, cast	17.9	12.0	-	10.6	10.5
Moiseevka, Kazakhstan (MN14)	PIN 5332-1	17.9	11.2	9.7	11.3	10.5
<i>U. minimus minimus</i>						
Kosyakino, Russia (MN15)	PIN 225-253	20.0	12.6	10.0	11.0	11.2
Weże 1, Poland (MN15)	ISEA MF/833/67/6	20.4	12.4	10.4	11.0	11.5
	ISEA MF/833/67/7	21.2	12.3	11.5	12.3	11.8
	ISEA MF/833/67/8	20.6	13.1	11.8	11.2	11.3
	ISEA MF/833/67/21	20.5	11.9	11.1	10.9	11.6
Perpignan, France (MN15)	CBUL 41.326	20.7	11.6	10.5	11.6	11.8
France (locality unknown)	NHMN, coll. Bravard 12q, cast	22.5	14.8	12.5	15.5	15.0
Gaville, Italy (MN16)	IGF 11568, sin	22.7	13.2	12.5	12.8	13.8
	IGF 11568, dex	22.4	13.1	12.8	11.8	12.7

combs, Gaville, and PIN No.225/253, Kosyakino) is single-cusped and displaced to the caudal side of the crown. Sometimes there is an accessory cuspid, located anteriorly from the entoconid (ZIN 34996, Kosyakino). The entoconid may be ridge-shaped or double-cusped (Moiseevka specimen). It is necessary to note that the entoconid of *Ursavus primaevus* is double-cusped (Baryshnikov, 2007: Fig. 59). In recent *Ursus thibetanus*, as a rule, the entoconid is single-cusped.

The structure of the metaconid of m2 is rather different in *U. minimus*. The metaconid is single-cusped

and nearly equal in height to protoconid (in the specimen from Moiseevka locality). Frequently the metaconid is considerably higher than protoconid (Baraolt-Căpeni, Kosyakino, Perpignan, Odessa Catacombs). Sometimes there are accessory cuspids, located anteriorly and posteriorly from the main cusp of metaconid (Weże 1, Odessa Catacombs, Kvabebi). The entoconid is regularly double-cusped and shifted backwards (in CBUL 3302 from Baraolt-Căpeni it is single-cusped). It looks like weakly serrated ridge with more expressed posterior cuspid (Moiseevka, Perpignan). The ento-

conid of m2 is double-cusped in recent *Ursus thibetanus*, similar to the aforementioned specimen of *U. minimus*.

Conclusion

This study takes the opportunity to determinate the main trends of teeth morphological changes of the *Ursus minimus*. The specimens of this species from the Early Ruscinian (Baróth-Köpec, Moiseevka) are characterized by archaic tooth morphology and small size. The members of *U. minimus* from the Late Ruscinian are characterized by larger size of the teeth in comparison to the Early Ruscinian ursids. All specimens of *U. minimus* from the Late Ruscinian are very close to each other in tooth sizes and their morphology (Kosyakino, Weže 1, Perpignan and possible Odessa Catacombs). The largest tooth sizes are correlated with maximum number of structures at the masticatory surface in the *U. minimus* specimens from the Early Villányian (MN16; Gaville and Kvabebi localities).

Despite considerable intraspecific variability of the tooth features in bears, studied specimens of *U. minimus* are morphologically similar. All variations observed are typical for intraspecific variability in bears and other omnivorous carnivores. Therefore there are no solid reasons for subdivision of *Ursus minimus* into a different species.

The detection of tendencies of the tooth apparatus evolution in *U. minimus* was made on the basis of European fossils material. However, the tendencies and peculiarities of the evolutionary process in the Asiatic part of the specific range stay indistinctive. The specimens of *U. minimus* from Caucasus (Kosyakino, Kvabebi) correspond to the European trends. The specimen from Kazakhstan (Moiseevka) possesses some peculiarities in morphology of m1 talonid in contrast to the specimens from Europe. The available specimens of *U. minimus* from China (Dongxiang, Yinan) are characterized by retaining of plesiomorphic features (small tooth sizes and the m1/m2 length ratio; Qiu *et al.*, 2009).

Thus *U. minimus* is characterized by geographic variability in its large specific range which covered the most part of Eurasia. The geographic variability of the species was well expressed during both the Early Pliocene (*U. m. boeckhi* in Europe and *U. m. ssp.* in Kazakhstan) and the Late Pliocene (*U. m. minimus* in Europe and *U. m. yinanensis* in China).

ACKNOWLEDGEMENTS. The material for examination and comparison has been provided by Dr. V. Eisenmann (NHMN), Prof. C. Guérin (CBUL), Dr. E. Crégut-Bonnoure (RMA), Dr. L. Rook (IGF), Prof. R. Ziegler (SMNS), Dr. H. Lutz (NMM), Prof. A. Nadachowski, Dr. P. Wojtal and Dr. G. Lipecki (ISEA), Dr. M. Sabol and Dr. A. Durisova (SNMB). Dr. J. Wagner (Prague) and G. Nazimbetova (Almaty) gave us valuable advices in preparing the paper and Dr. S. Baryshnikova (ZIN) assisted us in this study.

References

- Alberdi M.T., Azanza B., Cerdeño E. & Prado J.L. 1997. Similarity relationship between mammal faunas and biochronology from latest Miocene to Pleistocene in western Mediterranean area // *Eclogae Geologicae Helveticae*. T.90. P.115–132.
- Argiropulo A.I. 1939. [Remains of beaver *Amblycastor caucasicus* sp. n. from Ciscaucasia Pliocene] // *Doklady Akademii Nauk SSSR*. Vol.25. No.7. P.638–640 [in Russian].
- Argiropulo A.I. 1940. [Review of Tertiary rodent findings from USSR and adjoining territory of Asia] // *Priroda*. No.12. P.74–82 [in Russian].
- Averianov A.O. & Tesakov A.S. 1998. [The Lagomorpha (Mammalia) from the Early Pliocene Kosyakino locality of the Northern Caucasus] // *Paleontologicheskii Zhurnal*. No.3. P.91–96 [in Russian].
- Baryshnikov G.F. 2003. Late Miocene *Indarctos punjabiensis atticus* (Carnivora, Ursidae) in Ukraine with survey of *Indarctos* records from the former USSR // *Russian Journal of Theriology*. Vol.1 (for 2002). No.2. P.83–89.
- Baryshnikov G.F. 2007. [Mammals. The Bears Family (Ursidae)] // *Fauna of Russia and Neighbouring Countries*. N.ser. 147. Nauka: Sankt-Peterburg. 542 p. [in Russian].
- Baryshnikov G.F. & Zakharov D.S. 2013. Early Pliocene *Ursus thibetanus* (Mammalia, Carnivora) from Priozernoe locality in the Dniester basin (Moldova Republic) // *Proceedings of the Zoological Institute RAS*. Vol.317. No.1. P.3–10.
- Beliaeva E.I. 1940. [New Upper Tertiary mammal fauna from Northern Caucasus] // *Priroda*. No.2. P.82 [in Russian].
- Beliaeva E.I. 1944. [New material by Upper Tertiary mammals from Northern Caucasus] // *Priroda*. No.3. P.76–77 [in Russian].
- Berzi A. 1966. L'orso di Gaville nel Valdarno Superiore // *Palaeontographia Italica*. Vol.40 (for 1965). P.19–32 + VI–XIX Tav.
- Croizet A. & Jobert A. 1828. *Recherches Sur Les Ossemens Fossils du Département du Puy-de-Dôme*. Paris: Chez les Princip. Library. 224 p.
- Depéret Ch. 1890. Les animaux pliocènes du Roussillon // *Mémoires de la Société Géologique de France. Paléontologie*. Mém. 3. P.1–88.
- Dubrovo I.A. & Kapelist K.V. 1979. [Catalogus of Tertiary Vertebrate Localities in Ukraine]. Moskva: Nauka. 160 p. [in Russian].
- Fejfar O. & Heinrich W.-D. 1990. Proposed biochronical division of the European continental Neogene and Quaternary based on muroid rodents (Rodentia, Mammalia) // Fejfar O. & Heinrich W.-D. (eds.). *International Symposium "Evolution, Phylogeny and Biostratigraphy of Arvicolids (Rodentia, Mammalia)"*. München: Verlag Dr. Friedrich Pfeil. P.115–124.
- Fejfar O., Heinrich W.-D. & Lindsay E.H. 1998. Updating the Neogene rodent biochronology in Europe // *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*. Vol.60. P.533–554.
- Jánossy D. 1978. Larger mammals from the lowermost Pleistocene fauna Osztramos, Loc. 7 (Hungary) // *Annales*

- Historico-Naturales Musei Nationalis Hungarici. Vol.70. P.69–79.
- Kelly Th. 1994. Two Pliocene (Blancan) vertebrate faunas from Douglas County, Nevada // *PaleoBios*. Vol.16. No.1. P.1–23.
- Korotkevich M.L. 1967. [Large mammals from the Pliocene layers of Kuèrgan River] // *Mesto i znachenie Iskopayemykh Mlekopitayushchikh Moldavii v Kainozoe SSSR*. Kishinev: Shtiintsa. P.77–84 [in Russian].
- Kostenko N.N. 1963. [Stratigraphical Foundation of Anthropogene of Kazakhstan]. Alma-Ata: Izdatelstvo Akademii Nauk KazSSR. 74 p. [in Russian].
- Krause J., Unger T., Noçon A., Malaspina A.-S., Kolokotronis S.-O., Stiller M., Soibelzon L., Spriggs H., Dear P.H., Briggs A.W., Bray S.C.E., O'Brien S.J., Rabeder G., Mathews P., Cooper A., Slatkin M., Pääbo S. & Hofreiter M. 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary // *BMC Evolutionary Biology*. Vol.8: 220. DOI 10.1186/1471-2148-8-220.
- Kurtén B. & Anderson E. 1980. *Pleistocene Mammals of North America*. New York: Columbia University Press. 443 p.
- Li Y. 1993. On a new species of Pliocene *Ursus* (Carnivora: Ursidae) from Yinan, Shandong Province // *Vertebrata Palasiatica*. Vol.31. No.1. P.44–60 + Pl.I–II.
- Lopatin A.V., Tesakov A.S. & Titov V.V. 2003. Late Miocene – early Pliocene porcupines (Rodentia, Hystricidae) from south European Russia // *Russian Journal of Theriology*. Vol.2. No.1. P.26–32.
- Maier von Mayerfels S. 1929. Zur Stammesgeschichte der europäischen Bären // *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilagen-Band 72*. S.325–332.
- Mazza P. & Rustioni M. 1994. On the phylogeny of Eurasian bears // *Palaeontographica*. Abt.A. Vol.230. P.1–38.
- Mein P. 1990. Updating of MN zones // Lindsay E.H., Fahlbusch V. & Mein P. (eds.). *European Neogene Mammal Chronology*. New York: Plenum Press. P.73–90.
- Montoya P., Ginsburg L., Alberdi M.T., Van Der Made J., Morales J. & Soria M.D. 2006. Fossil large mammals from the early Pliocene locality of Alcoy (Spain) and their importance in biostratigraphy // *Geodiversitas*. T.28. No.1. P.137–173.
- Morlo M. & Kundrát M. 2001. The first carnivoran fauna from the Ruscium (Early Pliocene, MN 15) of Germany // *Paläontologische Zeitschrift*. Bd.75. No.2. P.163–187.
- Nikiforova K.V. 1953. [Geomorphology and geological situation in Irtysh River depression] // *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*. T.141. P.3–33 [in Russian].
- Pagés M., Calvignac S., Klein C., Paris M., Hughes S. & Hänni C. 2008. Combined analysis of fourteen nuclear genes refines the Ursidae phylogeny // *Molecular Phylogenetics and Evolution*. Vol.47. P.73–83.
- Qiu Z.-X., Deng T. & Wang B.-Y. 2009. First ursine bear material from Dongxiang, Gansu – Addition to the Longdan mammalian fauna // *Vertebrata Palasiatica*. Vol.47. No.4. P.245–264.
- Roshchin A.D. 1956. [Upper Pliocene fauna of south part of Ukraine] // *Naukovye Zapiski Geographicheskogo Fakulteta Odesskogo Pedagogicheskogo Instituta*. Ö.14. P.33–83 + V Tabls [in Ukrainian].
- Ryziewicz Z. 1969. Badania nad niedŹwiedziami plioceñskimi // *Acta Palaeontologica Polonica*. Vol.14. No.2. P.199–243 + VI Pls. [with English and Russian summary].
- Sabol M., Holec P. & Wagner J. 2008. Late Pliocene Carnivores from Vèelàre 2 (Southeastern Slovakia) // *Paleontological Journal*. Vol.42. P.531–543.
- Schlosser M. 1899. *Parailurus anglicus* und *Ursus boeckhi* aus den Ligniten von Baróth-Köpecz // *Mitteilungen aus dem Jahrbuche der Königlich Ungarische Geologische Anstalt*. Bd.13. S.67–95 + X–XIII Pls.
- Soria D. & Morales J. 1976. Hallazgo de un Ursido en el yacimiento de Layna (Soria) // *Trabajos Sobre Neogeno Cuaternario*. T.5. P.129–140.
- Sotnikova M.V. & Kalmykov N.P. 1991. [Pliocene associate of carnivore mammals at locality Udunga (western Transbaikalia)] // Vangengeim E.A. (ed.). *Paleogeografiya i Biostratigrafiya Pliotsena i Antropogena*. Moskva: Geologicheskii Institut Akademii Nauk SSSR. P.146–160 [in Russian].
- Sotnikova M.V. 2008. Carnivora assemblages of the Ruscian – Early Villafranchian transition: Eastern Europe (Ukraine) and Russia (Transbaikalia) – similarity and distinctions // *Abstracts of 6th Meeting of the European Association of Vertebrate Palaeontologists*, 30 June – 5 July, 2008. Spišská Nová Ves, Slovak Republic. P.85–87.
- Sotnikova M. & Rook L. 2010. Dispersal of the Canini (Mammalia, Canidae: Caninae) across Eurasia during the Late Miocene to Early Pleistocene // *Quaternary International*. Vol.212. P.86–97.
- Spassov N. 2003. The Plio-Pleistocene vertebrate fauna in South-Eastern Europe and the megafaunal migratory waves from the east to Europe // *Revue de Paléobiologie, Genève*. Vol.22. No.1. P.197–229.
- Talbot S.L. & Shields G.F. 1996. A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes // *Molecular Phylogenetics and Evolution*. Vol.5. P.567–575.
- Tedford R. & Harington R. 2003. An Arctic mammal fauna from the Early Pliocene of North America // *Nature*. Vol.425. P.388–390.
- Teilhard de Chardin P. 1940. The fossils from Locality 18 near Peking // *Palaeontologica Sinica*. Ser.C. Vol.9. P.1–100.
- Thenius E. 1947. Bemerkungen über fossile Ursiden (Mamm.) // *Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse*. Abt.1. Bd.156. Hf.3-4. S.201–208.
- Vangengeim E.A. 1977. [Paleontological Foundation of the Anthropogene Stratigraphy of Northern Asia (On Mammals)]. Moskva: Nauka. 170 p. [in Russian].
- Vangengeim E.A., Pevzner M.A. & Tesakov A.S. 2005. [Age of boundary and position in magnitochronology scale of Ruscian and lower Villafranchian] // *Stratigrafiya. Geologicheskaya Korrelyatsiya*. Vol.13. No.5. P.78–95 [in Russian].

- Vekua A.K. 1972. [Akchagyl Vertebrates of Kvabebi Locality]. Moskva: Nauka. 351 p. + XXXVI Tabs. [in Russian].
- Vereshchagin N.K. 1959. [Mammals of Caucasus. History of Fauna Origin]. Moskva-Leningrad: Izdatelstvo Akademii Nauk SSSR. 704 p. [in Russian].
- Vislobokova I.A. 1996. The Podpusk-Lebyazh'e mammalian faunas assemblage, Western Siberia // *Palaeontographia Italica*. Vol.83. P.1–23.
- Vislobokova I., Sotnikova M. & Dodonov A. 2001. Late Miocene-Pliocene mammalian faunas of Russia and neighbouring countries // *Bollettino della Società Paleontologica Italiana*. Vol.40. No.2. P.307–313.
- Wagner J. 2010. A list of craniodental material of Pliocene ursids (genus *Ursus*) in the collection of Naturhistorisches Museum Basel // *Scientific Annals, School of Geology Aristotle University of Thessaloniki*. Special Vol.98. P.127–139.
- Wagner J. 2010. Pliocene to early Middle Pleistocene ursine bears in Europe: a taxonomic overview // *Journal of the National Museum (Prague)*, Natural History Series. Vol.179. No.20. P.197–215.
- Wagner J., Čermak S. & Horaček I. 2012. The presence of *Ursus ex gr. minimus-thibetanus* in the Late Villanyian and its position among the Pliocene and Pleistocene black bears Europe // *Quaternaire, Hors Ser.* Vol.4 (for 2011). P.39–58.
- Zazhigin V.S. 1980. [Late Pliocene and Anthropogene rodents of the south of Western Siberia] // *Trudy Geologicheskogo Instituta Akademii Nauk SSSR*. T.339. P.1–156 [in Russian].
- Zdansky O. 1927. Weitere Bemerkungen über fossile Carnivoren und Cerviden aus China // *Palaeontologica Sinica*. Ser. C. Vol.4. Fasc.4. P.1–30 + II Taf.
- Zinova R.A. 1982. [Pliocene of North Part of Central Kazakhstan]. Minsk: Nauka i Tekhnika. 149 p. [in Russian].
- Zykin V.S., Zykina V.S. & Zazhigin V.S. 2007. [Problems of difference and correlation of Pliocene and Quaternary sediments of south part of Western Siberia] // *Arkheologiya, Etnografiya i Antropologiya Evrazii*. No.2. P.24–40 [in Russian].