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EARLY PLIOCENE BEAR URSUS THIBETANUS (MAMMALIA, CARNIVORA) FROM PRIOZERNOE LOCALITY IN THE DNIESTER BASIN (MOLDOVA REPUBLIC)

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ABSTRACT

The upper molar of a small ursid from Priozernoe locality in Moldova (the Trans-Dniester Region) incorporating remains of Moldavian faunal vertebrate complex (MN15) was found to belong to the Asian black bear (*Ursus thibetanus*). This discovery ascertains the time of first appearance of *U. thibetanus* in Europe in the early Pliocene.

Keywords: biostratigraphy, early Pliocene, Moldova, Ursus

РАННЕПЛИОЦЕНОВЫЙ МЕДВЕДЬ *URSUS THIBETANUS* (MAMMALIA, CARNIVORA) ИЗ МЕСТОНАХОЖДЕНИЯ ПРИОЗЕРНОЕ В БАССЕЙНЕ ДНЕСТРА (МОЛДАВИЯ, ПРИДНЕСТРОВЬЕ)

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РЕЗЮМЕ

Показано, что верхний коренной зуб мелкого медвежьего из местонахождения Приозерное в Молдавии (Приднестровье), содержащего остатки позвоночных молдавского фаунистического комплекса (MN15), принадлежит гималайскому медведю (*Ursus thibetanus*). Эта находка относит время первого появления *U. thibetanus* в Европе к раннему плиоцену.

Ключевые слова: биостратиграфия, ранний плиоцен, Молдавия, Ursus

INTRODUCTION

At present time, the Asian black bear (*Ursus thibetanus* G. Cuvier, 1823) occurs in forests and mountains of Eastern and Southern Asia, from Iran southwestwards to southern parts of the Russian Far

East and Japan northeastwards. Its origin, evolution, and history of its dispersion remain unstudied.

The analyses of the mitochondrial DNA affiliate U. thibetanus with the American black bear (U. americanus Pallas, 1780), referring a time of splitting of their ancestor from the ursine lineage nearly to 6 Ma and the time of their divergence one from another

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approximately to 5 Ma (Talbot and Shields 1996). The analysis of nuclear genes provides the placement of the Asian black bear as a basal taxon with respect to the group involving American black bear, brown bear (*U. arctos* L., 1758), and polar bear (*U. maritimus* Phipps, 1774) (Pages et al. 2008). *U. thibetanus* was found to form two mitochondrial lineages (Japanese and Continental populations), which divided nearly 0.58 Ma (Yasukochi et al. 2009). Therefore, molecular data point out noticeably old age of the Asian black bear (even with regards to a probability of the earlier time of its origin) as well as the differentiation of this taxon to take place before the appearance of other recent species of the genus *Ursus*.

The fossil record of *U. thibetanus* is widely known in the middle and late Pleistocene of Europe, Caucasus, Ural, southern part of Siberia, China, and Japan Islands (Erdbrink 1953; Kurtén 1968; Crégut-Bonnoure 1997; Baryshnikov 2002, 2010). It is not quite clear if this species was constantly distributed throughout this vast range or came to Europe only from time to time.

The earlier paleontological history of *U. thibetanus* is open to discussion. There are finds of fossil bears (predominantly represented by isolated teeth) in the European Pliocene localities. Their unambiguous attribution to any species is difficult, since tooth morphology of *U. thibetanus* resembles that of the small bear *U. minimus* Devèze de Chabriol et Bouillet, 1827 (including *U. boecki* Schlosser, 1899) from the early and late Pliocene of Eurasia, which is regarded to be ancestral to all species of the genus *Ursus*.

Mazza and Rustioni (1994) suggested that a fraction of the ursid material from the locality Perpignan (Chefdebien) in France (MN15a) belongs to *U. thibetanus*. This opinion was also accepted by Baryshnikov (2002, 2007). Other researchers believe, on the contrary, that this Perpignan bear does not belong to *U. thibetanus* and should be referred to *U. minimus* (Morlo and Kundrat 2001; Wagner 2010). Wagner et al. (2011), having examined this and other early finds of black bears, came to the conclusion that there is no reliable Pliocene record of *U. thibetanus* in Europe.

Thus a time of the first appearance of *U. thibetanus* in Europe remains unclear. The examination of each finding of black-bear fossils is important. Here we describe the isolated tooth of this species collected in the locality of Priozernoe in the Dniester River basin

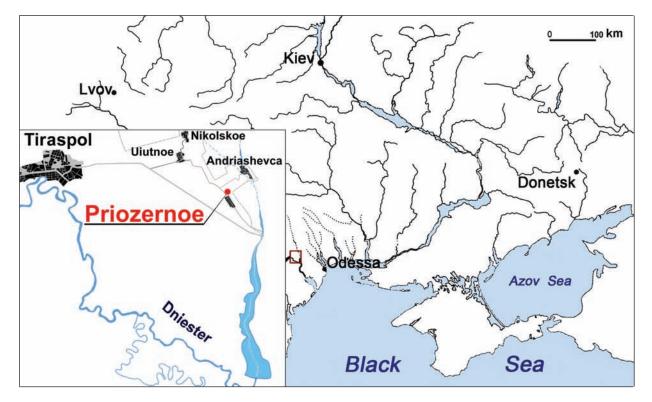


Fig. 1. Geographical position of Priozernoe locality.

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in Moldova (Fig. 1), provisionally referring it to *U*. *arvernensis* (Zakharov and Chepalyga 2012).

LOCALITY AND MATERIAL

Locality Priozernoe (46°48′13N, 29°55′39E) is situated near the settlement of the same name, 20 km southeastwards of Tiraspol. It represents a sand pit on the high fluvial terrace of Dniester River (Fig. 2); the altitude of its surface level is 110–130 m. The section reveals the strata of alluvial sediment divided into 4 layers (Chepalyga et al. 2011). The lower darkgray loamy-alluvial layer (thickness 2.0–3.5 m) is overlaid by yellow and yellow-gray sands (thickness 6.0–7.0 m) bearing the majority of mammal fossil remains. The geological unit situated above is formed by sandy-loam sediment (thickness 1.0–2.5 m) and by present-day soil (thickness 1.0–1.5 m).

Priozernoe is the southernmost among the localities found in the Dniester River valley predominantly involving fossils belonging to the Kuchurgan faunal complex, which corresponds to the early Pliocene (Ruscinium). The tentative faunal list from Priozernoe comprises more than 40 taxa of vertebrates (Chepalyga et al. 2011; Zakharov 2012; Zakharov and Redkozubov 2012): Pisces: Acipenser sp., Esox sp., Rutilus frisii (Nordmann, 1840), Scardinius sp., Tinca sp., Abramis sp., Silurus sp.; Amphibia: Anura gen.; Reptilia: Melanochelys pidoplickoi (Khosatzky, 1946), Melanochelys mossozyi (Mlinarski, 1964), Sakya riabinini (Khosatzky, 1946), Testudo cernovi Khosatzky, 1948, Testudo sp., Emys sp., Ophidia gen., Lacertidae gen.; Aves: Struthio sp.; Mammalia: Lipotyphla: Deinsdorfia sp., Talpidae gen., Desmaninae gen.; Primates: Dolichopithecus sp., Dolichopithecus cf. ruscinensis



Fig. 2. Sand pit of Priozernoe. Photo by D.S. Zakharov, September, 2009.

Depéret1889; Carnivora: Ursus thibetanus G. Cuvier, 1823, Mustelidae gen., Lynx issiodorensis (Croizet et Jobert, 1828), Mahairodontinae gen.; Lagomorpha: Trischizolagus dumitrescuae Radulesco et Samson, 1967, Ochotonidae gen.; Rodentia: Castoridae gen. (cf. Trogontherium sp.), Dryomimus cf. eliomyoides Kretzoi, 1959, Apodemus sp., Occitanomys cf. adroveri (Thaler, 1960), Promimomys ex gr. antiques Zazhigin, 1980 - moldavicus Kormos, 1932, cf. Nannospalax sp., Cricetidae gen., ?Kowalskia sp.; Proboscidea: Anancus arvernensis brevirostris Croizet et Jobert, 1828; Perissodactyla: Hipparion sp., Stephanorhinus megarhinus (De Christol, 1835); Artiodactyla: Cervidae gen., Procapreous sp., Eostyocerus sp., Muntjacus sp., Muntjacus pliocaenicus Korotkevich, 1965, Paracamelus ?alexejevi Havesson, 1950.

The vole *Promimomys* (identified by A.S. Tesakov) is closely related to the voles belonging to the evolutionary levels of P. antiquus Zazhigin – davakosi Van de Weerd, 1979 and P. moldavicus, which is pointed to the upper strata of the Lower Pliocene and biozone MN15 (Koenigswald and Heinrich 2007; Tesakov et al. 2007). Hence, the Priozernoe fauna is younger than Kuchurgan fauna, which involves more archaic species Promimomys insuliferus Kowalski, 1958 (MN14). It reveals more resemblance with the Moldavian faunal complex (MN15, 4.2–3.5 Ma) than with Kochurgan complex (MN14, 5.3-4.2 Ma). This assessment is in accordance with the species composition of the tortoise fauna, which also belongs to the Moldavian complex and comparable to that established in the localities of Lucheshty, Tatareshty, Etuliya, and Musait in Moldova (Zakharov and Redkozubov 2012).

The presence of pika (Ochotonidae), hare (*Trischizolagus*), and camel (*Paracamelus*), as well as remains of the egg-shell of ostrich (*Struthio*) and fragments of tortoise-shells (*Testudo*) indicate a wide distribution of steppe biotopes there in the past. At the same time, the occurrence of mastodon (*Anancus*), roe deer (*Procapreolus*), rhino (*Stephanorhinus*), and monkey (*Dolichoithecus*) suggests the existence of forest zones along river valleys.

Examined ursid material represents the isolated right upper molar tooth M1 from a young individual (only the crown is preserved). It was found in the autumn, 2011 and is described here for the first time.

For the comparison, we used collections of the Pliocene and Pleistocene small ursids from Europe and Caucasus *U. thibetanus* and *U. minimus* (including the type specimens of *U. minimus* and *U. wenzensis*

Stach, 1953). In addition, dental material on the recent *U. thibetanus* has been studied.

The definition of the Mammal Ages and their correlation with the chronostratigraphical scale as well as the MN-zones follows Fejfar and Heinrich (1990), Mein (1990), Fejfar et al. (1998), Koenigswald and Heinrich (2007) and Wagner et al. (2011).

Measurements of teeth were carried out using the scheme elaborated earlier (Baryshnikov 2006). The data were processed with the use of Factor Analysis from STATISTICA 6.0.

Institutional abbreviations. CBUL – Claude Bernard University Lyon 1, Villerbann, France; GPMT – Geological-Paleontological Museum, Pridnestrovsky University, Tiraspol, Republic of Moldova (the Trans-Dniester Region); IGB – Institute of Geology, Budapest, Hungary; IGF – Museo di Storia Naturale, Sezione Geologia e Paleontologia, Università di Firenze, Italy; ISEA – Institute of Systematics and Evolution of Animals, Krakow, Poland; IVPP – Institute of Vertebrate Paleontology, Beijing, China; MNHN – National d'Histoire Naturelle, Paris, France; NMM – Naturhistorisches Museum, Mainz, Germany; RMA – Muséum Requien d'Histoire Naturelle, Avignon, France; SMNS – Staatliches Museum für Naturkunde, Stuttgart, Germany; ZIN – Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Measurement abbreviations. L – greatest length, Lant – length of anterior part, Lme – length of metacone, Lpa – length of paracone, Lpost – length of posterior part, W – greatest width (see Table 1).

DESCRIPTION AND COMPARISONS

The examined upper molar GPMT, which is not provided with the collection number (n/n), shows no facets of wear. The enamel is colored brown, being partially paler, yellowish. Outlines of the tooth are rectangular; its anterior wall with a prominence at the buccal margin, the posterior wall is rounded. The angle formed by the anterior margin of the tooth crown and the lingual margin is nearly straight. The crown is somewhat wider in the posterior part than in the anterior part (Fig. 3).

The row of buccal cusps (paracone and metacone) is tall, markedly exceeding in height the row of lingual cusps (protocone and metaconule). Both rows

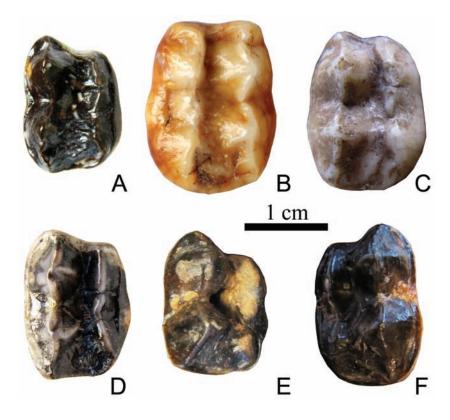


Fig. 3. Upper molar M1 of Ursus thibetanus (A–C) and U. minimus (Węże 1, Poland), right (A, C, D, E) and left (B, F); occlusal view: A –GPMT n/n, Priozernoe; B – ZIN 33179, Kudaro 3 Cave (middle Pleistocene), U. t. mediterraneus; C – ZIN 8808, Primorsky Krai (recent), U. t. ussuricus; D – ISEA n/n; E – ISEA MF/339/60 (type wenzensis); F – ISEA MF/833/67/1.

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Table 1. Measurements (in mm) of upper molar M1 in Ursus thibetanus and U. minimus. L – greatest length, Lant – length of anterior part,Lme – length of metacone, Lpa – length of paracone, Lpost – length of posterior part, W – greatest width.

| Localities | Museum number | L | Lant | Lpost | Lpa | Lme | W | |
|---|--|------|------|-------|-----|------|------|--|
| U. thibetanus | | | | | | | | |
| Priozernoe, Moldova (MN15) | GPMT n/n | | 8.2 | 8.8 | 6.0 | 5.8 | 12.5 | |
| Chefdebien, Perpignan, France (MN15a) | CBUL 41.326 | 18.6 | 9.0 | 9.7 | 6.1 | 5.9 | 14.4 | |
| | U. t. mediterraneus (middle Pleistocen | e) | | | | | | |
| Bruges, France | MNHN n/n | 19.2 | 9.2 | 9.7 | 7.0 | 6.9 | 14.8 | |
| Boule Cave, France | RMA n/n | 19.1 | 9.5 | 9.5 | 6.9 | 6.6 | 14.5 | |
| Cèdres Cave, France | RMA C6 | 19.8 | 9.5 | 9.8 | 6.4 | 5.9 | 15.8 | |
| Mauer, Germany | SMNS 31183 | _ | _ | 11.1 | 9.3 | 8.7 | 16.8 | |
| | NMM 1959/627 | 19.6 | 9.7 | 9.6 | 6.9 | 6.5 | 14.4 | |
| Kudaro 3 Cave, Georgia (Southern Ossetia) | ZIN 33179 | 20.9 | 9.4 | | 6.7 | | 16.0 | |
| | U. minimus | | | | | | | |
| Baróth-Köpecz, Hungary (MN14) | IGB Ob/2386 (Ryziewicz, 1969) | 18.5 | | | | | 16.0 | |
| Alcoy, Spain (MN14) | MNHN Alc 20 (Montoya et al. 2006) | 19.6 | | | | 16.6 | | |
| | ISEA MF/339/60 (type wenzensis) | 17.6 | 8.7 | 7.9 | 6.8 | 7.1 | 13.4 | |
| Węże 1, Poland (MN15b) | ISEA MF/833/67/1 | 19.5 | 9.5 | 10.5 | 8.9 | 7.7 | 14.6 | |
| | ISEA n/n | 18.3 | 8.9 | 9.5 | 6.9 | 8.5 | 13.4 | |
| Les Etouaires, Perrier, France (MN16b) | CBUL FSL 211227 (type minimus) | 18.9 | 8.9 | 10.3 | 7.7 | 7.5 | 15.1 | |
| | MNHN n/n (coll. Croizet 131) | 19.0 | 8.5 | 9.7 | 7.7 | 7.0 | 14.2 | |
| Gaville, Italy (MN16) | IGF 11568 | 21.0 | 10.1 | 11.1 | _ | _ | 16.9 | |
| Yinan, China (MN16) | IVPP V10320 (type <i>yinanensis</i>) (Qiu et al. 2009) | 17.7 | | | | | 13.8 | |

are parallel one another, being divided by the narrow longitudinal valley opened backwards. This valley is extended in the posterior part (behind metacone and metaconule) and its enamel is rugose.

The parastyle is well developed. The paracone exhibits three edges arising from its apex. The metacone is also three-edged and is markedly lower as compared to the paracone. The metastyle, which is larger than parastyle, is located behind the metacone. Protocone is ridge-shaped. Poorly defined mesocone adjoins to the protocone posteriorly. The former is clearly separated from the metaconule which is looking like a solitary cusp nearly of the same height with the protocone. The distinct buccal cingulum stretches nearly along the whole crown, being interrupted only at the base of metacone. The lingual cingulum is pronounced as well; it is slightly indented and extends from the anterior margin of protocone to the posterior margin of metaconule.

The Priozernoe tooth is characterized by the small size. Its length and width are pronouncedly smaller than those in the fossil teeth of *U. thibetanus*

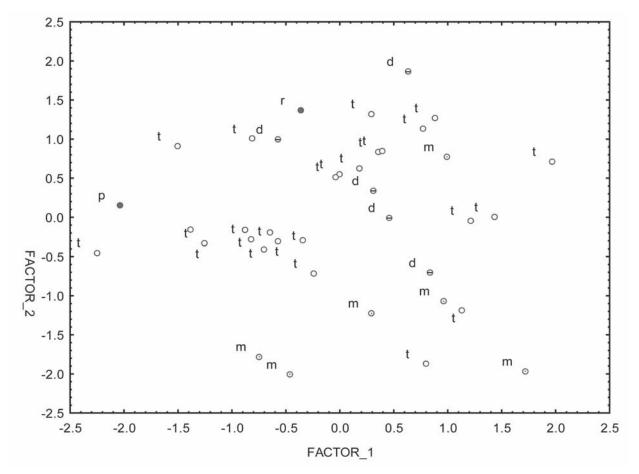


Fig. 4. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of upper molar M1 in *Ursus thibetanus* and *U. minimus*. Designations: *U. thibetanus*: d - U. *thibetanus mediterraneus*, middle Pleistocene; p - Priozernoe, early Pliocene; r - Perpignan, early Pliocene; t - Recent; m - U. *minimus*, early Pliocene.

from the middle Pleistocene European localities and in the teeth of *U. minimus* (Table 1). It also does not reach in these dimensions the ursid from Perpignan (CBUL 41.326). At the same time, GPMT n/n falls into the limits of M1 measurements in the recent continental populations of the Asian black bear, whose greatest tooth length varies from 16.4 mm to 21.2 mm (M=18.44 mm, n=51). The insular, Japanese, sample (*U. t. japonicus* Schlegel, 1857) is characterized by this length pronouncedly less, constituting 15.0–18.2 mm (M=16.44 mm, n=29).

The principal components analysis has been carried out on the basis of 6 measurements. It involved measurements of M1 of the small fossil ursid from Perpignan, *U. minimus* from Les Etouaires in France, Gaville in Italy, and Węże 1 in Poland (originally described as *U. wenzensis* Stach, 1953) as well as *U.* *thibetanus* (including fossil teeth from various European and Caucasian localities referring to the subspecies *U. t. mediterraneus* Forsyth Major, 1873, and recent teeth from continental populations) (Table 1).

The scatterplot of Factor 1 and Factor 2 demonstrates that a difference between *U. minimus* and *U. thibetanus* is observed in Factor 1, which includes most tooth measurements (L, Lant, Lpost, W; 55.1% of dispersion), and in Factor 2 (Lme, 18.6% of dispersion). Priozernoe and Perpignan specimens are distributed within *U. thibetanus* and are well separated from *U. minimus*, despite the tooth samples of both species are partially overlapped (Fig. 4).

Thus, the Priozernoe specimen differs from *U. minimus* by the more miniature size and by proportions of the crown. Meantime it reveals morphometric resemblance with *U. thibetanus*. The principal

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Table 2. Comparative characteristics of upper molar M1 in Ursus thibetanus and U. minimus.

| Characters | U. thibetanus, Priozernoe | U. thibetanus, recent | U. minimus |
|------------------|---------------------------|-----------------------|--------------------|
| Anterior margin | with projection | straight | with projection |
| Parastile | distinct | distinct | small or absent |
| Metacone | small | small | large |
| Metastile | large | large | small |
| Mesocone | indistinct | distinct | indistinct |
| Lingual cingulum | long | short | long, rarely short |

components analysis produced provides the possibility to regard the bear from Perpignan also to belonging to this species.

At the same time, the ursid from Priozernoe demonstrates characters affiliating it with *U. minimus* (presence of prominence on the anterior margin of the M1 crown, weakly developed mesostyle, etc., see Table 2). In spite of these characters are found to vary in *U. minimus*, as shows the examined sample from Węże 1 (Fig. 3) and published images (e. g. Berzi 1966; Ryziewicz 1969; Montoya et al. 2006; Wagner et al. 2011), these indicate the stage of modification of the masticatory surface in M1, which may be regarded as an ancestral of the bears of the genus *Ursus*.

Therefore, in the Pliocene, *U. thibetanus* yielded plesiomorphic characters of tooth morphology inherited from *U. minimus*; at the same time, it acquired features of specialization (distinctive parastyle, moderate metacone, and large metastyle), which acquire further development in the course of evolution of the Asian black bear from the Pleistocene and Recent.

CONCLUSIONS

This study assigns the isolated upper molar M1 from Priozernoe locality in Moldova Republic (the Trans-Dniester Region) to *Ursus thibetanus*. Accompanying fauna allows dating of this locality by the early Pliocene (MN15). Our data maintain the view by Mazza and Rustioni (1994) on the assignment of the small ursid from Perpignan (Chefdebien), whose taxonomic status was not clearly defined (see above), to *Ursus thibetanus*. Its geological age approaches to that of the ursid from Priozernoe.

Discrepancy in the species attribution of the small ursid from Perpignan may be explained (after our study of the Priozernoe tooth) that the Pliocene *U. thibetanus* maintains archaic morphological characters approaching it to the ancestral species *U. minimus*. However, *U. thibetanus* has already acquired modifications determining specialization of its dental apparatus. In a course of evolution of this species, the role of these modifications increased, the archaic traits, meantime, were lost.

Thus, examination of fossils from Priozernoe and Perpignan provides possibility to refer the time of the first appearance of *U. thibetanus* in Eastern and Western Europe to the early Pliocene (late Ruscinium). In spite of the available data are scant, these correspond to a time of origin of *U. thibetanus* evaluated by molecular clock (nearly 5 Ma).

Paleontological record on the Asian black bear leading predominantly semi-arboreal life is accumulated slowly; therefore, even fragmentary fossil material, such as the new find from Priozernoe locality, provides the important information on the early stages of the evolution of *U. thibetanus*.

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REFERENCES

Baryshnikov G. 2002. The Pleistocene black bear (Ursus thibetanus) from the Urals (Russia). Lynx (Praha), n. s., 2001, 32: 33–43.

- Baryshnikov G. 2007. The bears family (Ursidae). Nauka, Sant-Petersburg, 542 p. (Fauna of Russia and neighbouring countries, n. ser., 147). [In Russian]
- Baryshnikov G. 2010. Middle Pleistocene Ursus thibetanus (Mammalia, Carnivora) from Kudaro caves in the Caucasus. Proceeding of the Zoological Institute RAS, 314: 67–79.
- Berzi A. 1966. L'orso di Gaville nel Valdarno Superiore. Palaeontographia Italica, 1965, 40: 19–32.
- Chepalyga A.L., Tesakov A.S., Zakharov D.S., Marareskul V.F. and Chepalyga R.Yu. 2011. Priozernoe – new locality of Riscimium mammal fauna (early Pliocene) in Kuchurgan allivium of Dniester. In: I. Trombitsky (Ed.). Academician Leo Berg – 135. Collection of Scientific Articles. Bendery, Eco-TIRAS: 392–395. [In Russian]
- Crégut-Bonnoure E. 1997. The Saalian Ursus thibetanus from France and Italy. Geobios, 30: 285–294.
- Erdbrink D.P. 1953. A review of fossil and recent bears of the Old World, with remarks on their phylogeny based upon their dentition. Drukkerij Jan de Lange, Deventer, 597 p.
- Fejfar O. and Heinrich W.-D. 1990. Proposed biochronical division of the European continental Neogene and Quaternary based on Muroid rodents (Rodentia, Mammalia). In: O. Fejfar and W.-D. Heinrich (Eds.) International symposium Evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia). Verlag Dr. Friedrich Pfeil, München: 115–124.
- Fejfar O., Heinrich W.-D. and Lindsay E.H. 1998. Updating the Neogene rodent biochronology in Europe. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO, 60: 533–554.
- Koenigswald W. Von and Heinrich W.-D. 2007. Biostratigraphische Begriffe aus der Säugetierpaläontologie für das Pliozän und Pleistozän Deutschlands. *Eiszeitalter* und Gegenwart, 56: 96–115.
- Kurtén B. 1968. Pleistocene Mammals of Europe. Weidenfeld and Nicolson, London, 317 p.
- Mazza P. and Rustioni M. 1994. On the phylogeny of Eurasian bears. *Palaeontographica*. Abr. A., 230: 1–38.
- Mein P. 1990. Updating of MN zones. In: E.H. Lindsay et al. (Eds) European Neogene mammal chronology. Plenium Press, New York: 73–90.
- Pages M., Calvignac S., Klein C., Paris M., Hughes S. and Hänni C. 2008. Combined analysis of fourteen nuclear genes refines the Ursidae phylogeny. *Molecular Phylogenetics and Evolution*, 47: 73–83.

- Ryziewicz Z., 1969. Badania nad niedźwiedziami plioceńskimi. Acta Palaeontologica Polonica, 14: 199–243.
- Talbot S.L. and Shields G.F. 1996. A phylogeny of the bears (Ursidae) inferred from complete sequences of three mitochondrial genes. *Molecular Phylogenetics and Evolution*, 5: 567–575.
- Tesakov A.S., Vangengeim E.A. and Pevzner M.A. 2007. Arvicolid zonation of continental Pliocene deposits. Courier Forschungsinstitut Senckenberg, 259: 227–236.
- Wagner J. 2004. A taxonomic revision of bears from selected Biharian localities of the Czech Republic. A preliminary report: I. C 718, Chlum I, Chlum IV. Cahiers scientifiques, Hors série, 2: 139–144.
- Wagner J. 2010. Pliocene to early middle Pleistocene ursine bears in Europe: a taxonomic overview. *Journal of the National Museum (Prague)*, Natural History Series, 179: 197–215.
- Wagner J., Čermak S. and Horaček I. 2011. 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 série, 4: 39–58.
- Yasukochi Y., Nishida S., Han S.-H., Kurosaki T., Yoneda M. and Koike H. 2009. Genetic structure of the Asiatic black bear in Japan using mitochondrial DNA analysis. *Journal of Heredity*, 100: 297–308.
- Zakharov D.S. 2012. New data on Ruscinium vertebrate fauna from locality near Priozernoe village. Paleontologicheskie issledovaniya v usoverschenstvovanii stratigraphicheskikh skhem fanerozoiskikh otlozhenii. Materialy XXXIV sessii Paleontologicheskogo obshchestva NAN Ukrainy, Kiev: 130–132. [In Russian]
- Zakharov D.S. and Chepalyga A.L. 2012. Problems of the earliest stages of Dniester valley evolution: Alluvial of Kuchurganian sections. In: S.I. Philipenko, V.G.Phomenko and I.I. Ignatiev (Eds). Geoecological and Bioecological Problems of the north Black See coast. Proceedind of the international conference. Tiraspol, Nomember 9–10, 2012. PGU publ., Tiraspol: 109–111. [In Russian]
- Zakharov D.S. and Redkozubov O.I. 2012. Early Pliocene turtles from Priozernoe site (Dniester valley). In: S.I. Philipenko, V.G. Phomenko and I.I. Ignatiev (Eds). Geoecological and Bioecological Problems of the north Black See coast. Proceedings of the International Conference. Tiraspol, November 9–10, 2012. PGU publ., Tiraspol: 108–109. [In Russian]

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