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FOSSIL *OVIBOS MOSCHATUS* (ARTIODACTYLA, BOVIDAE) FROM BURYN, WITH REFERENCE TO MUSKOCOX DISPERSAL IN THE LATE PLEISTOCENE OF UKRAINE

T. V. Krakhmalnaya¹, O. M. Kovalchuk^{1,2}

¹National Museum of Natural History NAS of Ukraine,
B. Khmelnytsky st., 15, Kyiv, 01030 Ukraine

²National University of Life and Environmental Sciences,
General Rodimtsev st., 19, Kyiv, 03041 Ukraine
E-mail: tvkrakhmalnaya@gmail.com, biologist@ukr.net

Fossil *Ovibos moschatus* (Artiodactyla, Bovidae) from Buryn, with Reference to Muskocox Dispersal in the Late Pleistocene of Ukraine. Krakhmalnaya, T. V., Kovalchuk, O. M. — The skull fragment of muskocox *Ovibos moschatus* (Artiodactyla, Bovidae) obtained from Chasha River bed alluvium near the Buryn (Sumy Region, North-Eastern Ukraine) is described here in detail. It belongs to a young male, and presumably dates back to Late Pleistocene. This new find slightly extends the known Ukrainian range of the species to the east. Taxonomic attribution of extinct muskocox and dispersal of *Ovibos moschatus* within the territory of Ukraine during the Late Pleistocene are also discussed in the paper.

Key words: muskocox, skull, morphology, species range, periglacial zone, Eastern Europe.

Introduction

The muskocox, *Ovibos moschatus* (Zimmermann, 1780), is a characteristic component of subarctic fauna being well adapted to cold climatic conditions with low snow cover (Lent, 1988). The natural range of this species is currently restricted to areas of open tundra with permafrost in Greenland, northern Canada, Alaska, and some isles of the American archipelago, while muskocoxen were widely distributed throughout the Holarctic during cold phases of the Pleistocene (Raufuss & Koenigswald, 1999; Markova et al., 2015). Fossil muskocox remains are rather scarce compared to those of other herbivores of the “mammoth steppe” mammalian assemblage. This may be due to relatively smaller populations of this species (fig. 1) which seems to be ecologically intolerant and was not able to adapt to increasing humidity and average annual temperatures during the Holocene (Lent, 1988; Markova et al., 1995, 2015).



Fig. 1. Localities with fossil muskox remains on the territory of Ukraine.

To date, more than 200 localities with fossil remains of *O. moschatus* in Europe and Siberia are known and mapped (Raufuss & Koenigswald, 1999; Markova et al., 2015; Marciszak et al., 2018); however only two of them from the territory of Ukraine (Dobranychivka and Mezyn) were included to the list. The aim of the present study is to describe in detail a new find of muskox remains of the Late Pleistocene age from the Buryń (Ukraine), compare it with relevant fossils from other localities, and to find out how it fits into the known past range of the species. Such data are necessary for precise reconstruction of muskox dispersal within the territory of Eastern Europe during the last cooling stage at the end of Pleistocene.

History of the study of muskox in Ukraine

Fossil muskox remains of Pleistocene age were found for the first time near the Zbranky village (51°17' N, 28°39' E) in the Zhytomyr Region, Ukraine (fig. 1). Pidoplichko (1933) noted five skulls belonging to *Ovibos moschatus* from this locality within the specimens representing at the exhibition "Quaternary period in Ukraine". Gromova (1935) also mentioned the complete skull and a series of muskox bones from Zbranky, pointing Kyiv and Leningrad as depositaries of these specimens. Later these remains were disappeared, apparently during the World War II (Krakhmalnaya, 2007 a). Muskox skull from Zbranky discovered in Pleistocene clay deposits in 1897 was described by Ryziewicz (1955). Somewhat later, Khan (1966) also mentioned it in his publication with measurements.

Frontal-occipital part of the skull of *Ovibos moschatus* was found on July 1951 in Kyiv (50°29' N, 30°32' E) during the operation of a hydraulic monitor (Pidoplichko, 1952). Further fate of this find is obscure — the specimen is recently absent in the collection of National Museum of Natural History, National Academy of Sciences of Ukraine (NMNHU-P). Only photos and a brief description of the skull without measurements were presented in the original publication.

Three bones belonging to *O. moschatus* were identified in materials of the Late Paleolithic site Dobranychivka (50°10' N, 31°48' E) in the Kyiv Region (Pidoplichko, 1969; Shovkoplyas et al., 1981), however only one heel bone (calcaneus) was described in detail (Belan, 1985). A single muskox skull comes from the Bugorok camp (52°13' N, 33°18' E) near the Pushkari village in the Chernihiv Region (Velichko, 1961). Another skull was found in 2006 near the Khodoriv village, 49°55' N, 31°14' E (Krakhmalnaya, 2007 b). To date, this is the southernmost find of this species. There is also some information about the finds of muskox remains at the Paleolithic sites of Korman IV and Molodovo I (Chernivtsi Region). However, this material was not noted in rich museum collections from the Dniester region after the World War II (Belan, 1985). The most numerous muskox remains at the territory of Ukraine were obtained during excavations of the Late Paleolithic site Mezyn, 51°50' N, 33°05' E (fig. 1). In total, 188 bones including 14 skulls were collected (Pidoplichko, 1969), while only a fragment of the neurocranium, lower jaw and several postcranial bones are represented in the NMNHU-P.

Absolute dates of the osteological material accompanying the fossil remains of muskoxen are known only for two aforementioned localities: Mezyn — 27 500 ± 800, 21 600 ± 2200, 15 100 ± 200 years, and Dobranychivka — 12 700 ± 200 years (Sinitsyn et al., 1997).

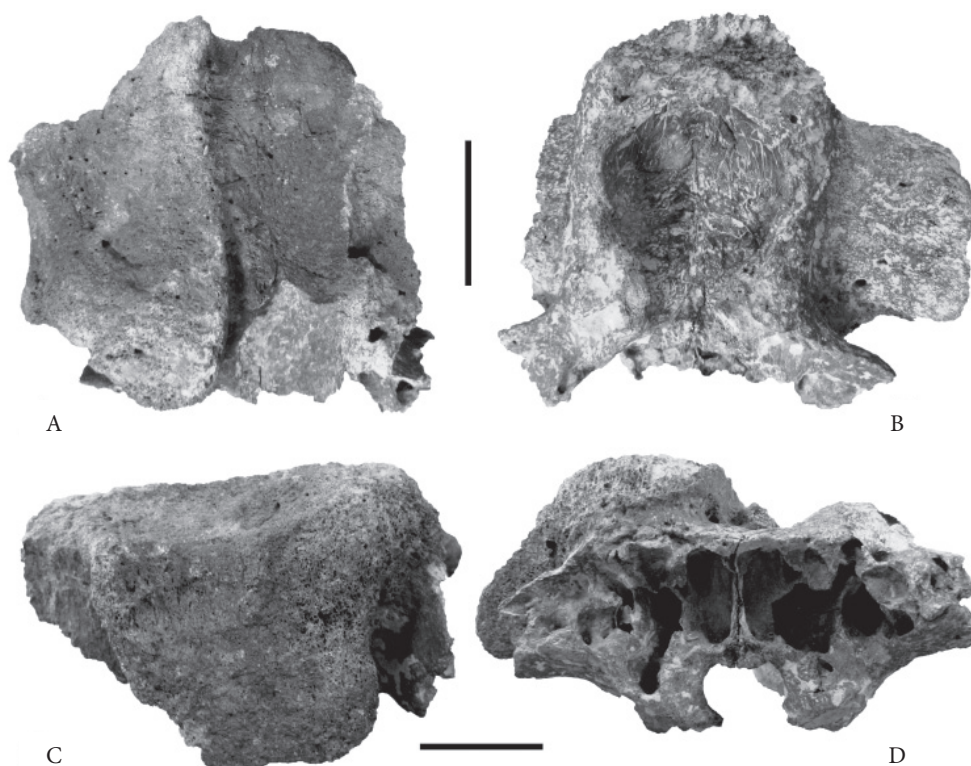
Systematic paleontology**Family BOVIDAE** Gray, 1821**Subfamily Caprinae** Gray, 1821**Tribe Ovibovini** Simpson, 1945**Genus *Ovibos*** Blainville, 1816***Ovibos moschatus* (Zimmermann, 1780)****Material.** Skull fragment, Buryn district local history museum.**Locality and geological age.** Chasha River bed alluvium (51°10' N, 33°52' E), near Buryn, Sumy Region, Ukraine; Late Pleistocene.**Description.** The skull (fig. 2) belongs to a young, probably 4-year-old individual, which is evidenced by the presence of thickened horncores whose bases not yet fused together (according to the scheme in Henrichsen & Grue, 1980). Only cranium cerebrale with unequally preserved horncores is available for the study. Basis cranii as well as occipital part of the skull are completely destroyed; however jugular processes are preserved. Imprint of the brain is well pronounced on the inner surface of calvaria. The skull is dark brown in colour, which is usual for the fossil material that has been in water for a long time. The horncores are wide, compressed dorso-ventrally; they come down almost vertically, slightly deviating laterally in lower part. Their surface is rather loose and bears the traces of exostoses.**Measurements** (according to Walker, 1982). See table 1.**Comparison.** The muskox skull from Buryn as compared to those of adult individuals of *O. moschatus* from the Pleistocene (Vangengeim, 1961; Sher, 1971; Krakhmalnaya, 2007 b) is characterized by well-developed cerebral part, high occiput and large foramen

Fig. 2. Skull fragment of muskox from the Buryn district local history museum in dorsal (A), ventral (B), lateral (C), and posterior view (D). Scale bar equals 10 cm in A and B, 5 cm in C and D.

Table 1. Skull measurements of Pleistocene *Ovibos moschatus* from Europe and Siberia

Locality	Measurements ¹ , in mm								Reference
	1	2	3	4	5	6	7	8	
Europe (Ukraine*, Germany**, Poland***)									
Buryn*	~150.0	>200.0	165.0	113.0	102.0	133.0	7.2	~40.1	Our data
Zbranky*	–	195.0	–	–	–	100.0	8.5	–	Ryziewicz, 1955
Mezyn*	–	145.0	–	101.5	80.5	72.5	–	–	Belan, 1985
Khodoriv*	168.2	168.0	133.2	126.0	113.0	186.4	7.2	35.2	Krakhmalnaya, 2007
Rhine**	–	174.0	–	–	–	106.0	16.0	–	Khan, 1966
Splawie***	–	–	–	–	–	142.0	14.0	–	Chubur, 2015
Siberia (Russian Federation)									
Yenisei River	–	188.0	–	–	–	173.0	–	–	Tchersky, 1891
Yana River	–	205.0	–	–	–	206.0	–	–	Tchersky, 1891
Bolshoy Lyakhovsky Island	–	–	–	–	–	168.0	–	–	Tchersky, 1891
Lena River	–	192.0	–	–	–	226.0	–	–	Tchersky, 1891
Bolshoy Lyakhovsky Island	–	175.0	–	–	–	187.0	–	–	Vangengeim, 1961
Mamontova Gora	–	175.0	–	–	–	137.0	–	–	Rusanov, 1968
Far North-East of the USSR ²	–	177.0	–	–	–	188.5	–	30.6	Sher, 1971
Far North-East of the USSR ³	–	151.0	–	–	–	83.6	–	32.3	Sher, 1971
Khaptashynsky Yar	–	–	–	–	–	78.0	–	–	Lazarev & Tomskaya, 1987
Alazeia	–	–	–	–	–	144.0	–	–	Lazarev & Tomskaya, 1987
Tomsk Region	–	203.0	164.0	–	–	–	–	–	Shpansky, 2000
Minusinsk	–	174.0	105.0	–	–	–	–	–	Malikov, 2015

¹Measurements: 1 — skull breadth at the anterior margin level of orbits; 2 — maximum occipital breadth; 3 — minimum occipital breadth; 4 — akrocranium-basion height; 5 — height of akrocranium-upper margin of foramen magnum; 6 — diameter of horncore base; 7 — distance between inner margins of horncore processes; 8 — breadth of foramen magnum. ²Skulls of males, mean values. ³Skulls of females, mean values.

magnum. Maximum occipital breadth of the studied specimen is comparable to those in skulls obtained from the Yana River (Tchersky, 1891), Tomsk Region (Shpansky, 2000), and to a lesser extent — to those from Zbranky (Ryziewicz, 1995). These four skulls have the widest occipital region in comparison with others, whose measurements are presented in table 1. According to the minimum occipital breadth, the specimen from Buryn is also similar to those from the Tomsk.

The height of the occipital region can only be compared with material from Ukraine. It is smaller than those in the specimen from Khodoriv. The breadth of foramen magnum in the studied specimen slightly exceeds those few measurements, which are indicated in table 1.

Diameter of horncore base is greater than those in an adult female from Mezyn (Belan, 1985) and male from Zbranky, but considerably smaller than in the skull from Khodoriv (Krakhmalnaya & Kovalchuk, 2017). Minimum distance between inner margins of horn processes does not exceed 10 mm which is typical for muskox males (Tchersky, 1891; Sher, 1971). Muskoxen from Siberia have more powerful horns, especially males from the Yana and Lena Rivers (Tchersky, 1891), as well as from other localities of this region, except of the skull from the Mamontova Gora (Rusanov, 1968) and some female skulls (Sher, 1971; Lazarev & Tomskaya, 1987).

Remarks. Late Pleistocene muskox of Eurasia has uncertain taxonomic status in the scientific literature. Recently, this species is increasingly referred to *O. moschatus* (Zimmer-

mann, 1780), emphasizing its relatedness with the extant American muskox. However, not all the researchers agreed with the unification of the extinct representative of the genus with the living one. There is no doubt that they differ significantly in a number of morphological characters noted in the comparative analysis of their skulls (Ryziewicz, 1955; Sher, 1971; Tikhonov, 1994; Chubur, 2015). These differences allowed C. H. Smith to describe the extinct muskox as *O. pallantis* in 1827. However, “the Fossil Musk Ox, *O. pallantis*, with the horns pressed against the temples behind the orbits, found on the coasts of Siberia, is not definitively ascertained to be a separate species” (Smith, 1827, p. 370).

Recognizing the close proximity of the two species, but wanting to confirm the significance of the morphological differences between them, a number of researchers considered the extinct Late Pleistocene muskox as a sub-species of the extant *O. moschatus* and identified it as *O. moschatus pallantis* (Lydekker, 1900; Andréé, 1933; Gromova, 1935; Baryshnikov, 1981; Belan, 1985; Krakhmalnaya, 2007 a; Krakhmalnaya & Kovalchuk, 2017). Khant (1996) described a new subspecies *Ovibos pallantis rhenanus* from the Rhine Valley, Germany. Using modern research methods, e. g. ancient DNA analysis supports the attribution of the Late Pleistocene and extant muskoxen to the same species (MacPhee et al., 2005; Campos et al., 2010). Taking these data into account, researchers began to recognize the species name *O. moschatus* for the Pleistocene muskox instead of *O. pallantis* or *O. moschatus pallantis*.

Discussion

The skull of a young muskox male from Buryn is quite comparable in size (e. g. in maximum occipital breadth) with the skulls of adult individuals from Siberia and exceeds by this value all known specimens from the territory of Ukraine. However, according to maximum diameter of horncore base, the skull described herein is smaller than those from other localities.

Muskox was a typical component of the periglacial fauna. This species, along with other large mammals of the “mammoth” fauna, was an object of hunting for an ancient man. The Late Pleistocene muskox is represented on the territory of Ukraine in materials from seven localities, four of which are archaeological sites. It allows us to assume that these animals

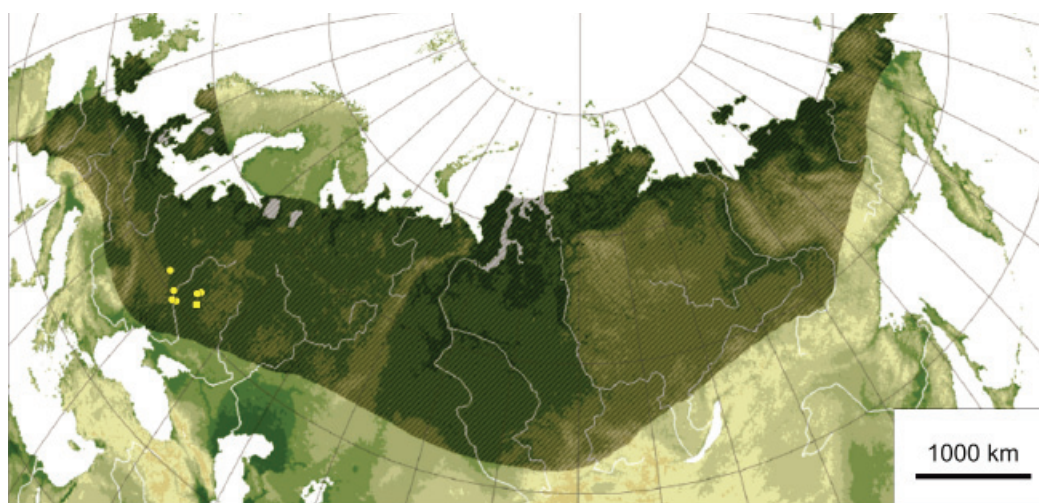


Fig. 3. Last Glacial maximum distribution of *Ovibos moschatus* (after Kahlke, 2014, with modifications). Previously known localities with fossil muskox remains within the territory of Ukraine are indicated by circles. The find described herein is indicated by square.

in the Dnipro region were extracted by Late Paleolithic hunters. Most likely, during Late Pleistocene muskoxen appeared there sporadically in winter time. The new find of the fossil remains belonging to this species from river alluvium near Buryn allows us to extend the known range of *O. moschatus* in Ukraine to the east (fig. 3) thereby clarifying the data on its former distribution (Kahlke, 2014).

Although territories occupied by man and muskox during the Late Pleistocene were partially overlaid in many regions, people probably did not cause the significant decrease of the former range of this species. In some areas, the number of people and muskoxen grew almost simultaneously (Lent, 1999). According to the latest data aiming to check the human impact on species dynamics based on the study of the DNA of *Ovibos moschatus* from all parts of its previous range (Campos et al., 2010), muskoxen survived several periods when the flowering of populations of these animals was alternated with a decrease in their number. We assume that the decline in population numbers of this species was due to unfavorable climate changes, primarily the significant increasing humidity and progressive warming during the Holocene.

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References

- Andrée, J. 1933. Über diluviale Moschusochsen. *Abhandlungen aus dem Westfälischen Provinzial-Museum für Naturkunde*, **4**, 5–34.
- Baryshnikov, G. F. 1981. Order Artiodactyla. *Catalog mlekopitaiushikh SSSR (pliocen — sovremennost')*. [Mammal catalogue of USSR (Pliocene — modern time)]. Nauka Press, Leningrad, 343–408.
- Belan, N. G. 1985. Muskox in the Pleistocene of Ukraine. *Vestnik Zoologii*, **2**, 31–34 [In Russian].
- Blainville, H. de. 1816. Sur plusieurs espèces d'animaux mammifères, de l'ordre des ruminants. *Bulletin des Sciences, par la Société Philomathique de Paris, année 1816*, 73–82.
- Campos, P., Willerslev, E., Sher, A., Orlando, L., Axelsson, E., Tikhonov, A., Aaris-Sørensen, K., Greenwood, A., Kahlke, R.-D., Kosintsev, P., Krakhmalnaya, T., Kuznetsova, T., Lemey, P., MacPhee, R., Norris, C. A., Shephard, K., Suchard, M. A., Zazula, G. D., Shapiro, B., Gilbert, M. T. P. 2010. Ancient DNA analyses exclude humans as the driving force behind late Pleistocene musk ox (*Ovibos moschatus*) population dynamics. *PNAS*, **105**, 8327–8332.
- Chubur, A. A. 2015. The muskox of locality Splawie (Wielkopolska). In: Antiukhov, A. V. et al., eds. *Yearbook of the Institute for Fundamental and Applied Research (2015)*. Bryansk, 90–92 [In Russian].
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *The London Medical Repository Monthly Journal and Review*, **15**, 296–310.
- Gromova, V. I. 1935. About the distribution of musk ox remains in the Eastern Europe and Northern Asia. *Izvestiya AN SSSR*, **8** (1), 101–114 [In Russian].
- Henrichsen, P., Grue, H. 1980. Age criteria in the muskox (*Ovibos moschatus*) from Greenland. *Danish Review of Game Biology*, **11**, 1–18.
- Kahlke, R.-D. 2014. The origin of Eurasian Mammoth Faunas (*Mammuthus–Coelodonta* Faunal Complex). *Quaternary Science Reviews*, **96**, 32–49.
- Khan, E. 1966. *Ovibus pallantis rhenanus* nov. subsp., an extinct *Ovibos* of Weinheim, Rhine Valley, Germany. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **6**, 133–142.
- Krakhmalnaya, T. 2007 a. Late Pleistocene musk-ox of Ukraine: the state of study. In: Boeskorov, G. G., Lazarev, P. A., eds. *Abstracts of the IV International Mammoth conference (18–22 June 2007)*. Yakutsk, 142–143.
- Krakhmalnaya, T. V. 2007 b. The southernmost finding of musk ox in the Late Pleistocene of Ukraine. In: Lavrushin, Yu. A., Khoreva, I. M., Chistyakova, I. A., eds. *V All-Russian Conference on Quaternary Research "Fundamental problems of Quaternary, results and main trends of future studies"*: Collection of papers (Moscow, 7–9 November 2007). GEOS, Moscow, 195–198 [In Russian].
- Krakhmalnaya, T. V., Kovalchuk, O. M. 2017. A new finding of the fossil remains of musk ox in Ukraine. In: Toderas, I. et al., eds. *Actual problems of zoology and parasitology: achievements and prospects: materials*

- of the International symposium dedicated to the 100th anniversary from the birth of Alexei Spassky (13 October 2017). Elan Poligraf, Chişinău, 389–390.
- Lazarev, P. A., Tomskaya, A. I. 1987. *Mlekopitajushchie i biostratigrafija pozdnego kajnozoja Severnoj Yakutii* (Mammals and biostratigraphy of the late Cenozoic of Northern Yakutia). YaF SO AN SSSR, Yakutsk, 1–170 [In Russian].
- Lent, P. C. 1988. *Ovibos moschatus*. *Mammalian Species*, **302**, 1–9.
- Lent, P. C. 1999. *Muskoxen and their hunters: a history*. University of Oklahoma Press, Norman, Oklahoma, 1–324.
- Lydekker, R. 1900. A new race of musk-ox. *Nature*, **63**, 157.
- MacPhee, R. D. E., Tikhonov, A. N., Mol, D., Greenwood, A. D. 2005. Late Quaternary loss of genetic diversity in muskox (*Ovibos*). *BMC Evolutionary Biology*, **5**, 49.
- Malikov, D. G. 2015. The first find of *Ovibos moschatus* Zimmermann, 1780 on the territory of Minusinsk basin. In: Bogdanova, T. N. et al., eds. *Current problems in paleontology: Materials of LXI session of Paleontological Society of the Russian Academy of Sciences* (April 13–17, 2015, St. Petersburg). St. Petersburg, 158–160 [In Russian].
- Marciszak, A., Kotowski, A., Przybylski, B., Badura, J., Wiśniewski, A., Stefaniak, K. 2018. Large mammals from historical collections of open-air sites of Silesia (southern Poland) with special reference to carnivores and rhinoceros. *Historical Biology*, <https://doi.org/10.1080/08912963.2017.1388377>.
- Markova, A. K., Smimov, N. G., Kozhovinov, A. Y., Kazantseva, N. E., Simankova, A. E., Kitaev, A. N. 1995. Late Pleistocene distribution and diversity of Mammals in Northern Eurasia. *Paleontologia i Evolucio*, **28-29**, 5–143.
- Markova, A. K., Puzachenko, A. Yu., Kolfshoten, T.v., Kosintsev, P. A., Kuznetsova, T. V., Tikhonov, A. N., Bachura, O. P., Ponomarev, D. V., Plicht, J. van der, Kuitems, M. 2015. Changes in the Eurasian distribution of the musk ox (*Ovibos moschatus*) and the extinct bison (*Bison priscus*) during the last 50 ka BP. *Quaternary International*, **378**, 99–110.
- Pidoplichko, I. G. 1933. Exhibition “Quaternary period in Ukraine” held in VUAN. *Chetvertynnyi period*, **5**, 113–119 [In Ukrainian].
- Pidoplichko, I. G. 1952. The finding of the fossil remains of musk ox. *Priroda*, **5**, 114–116 [In Russian].
- Pidoplichko, I. G. 1969. *Pozdnepaleoliticheskie zhilishcha iz kostej mamonta na Ukraine* (Late Paleolithic dwellings of mammoth bones in Ukraine). Naukova Dumka, Kiev, 1–163 [In Russian].
- Raufuss, I., Koenigswald, W. V. 1999. New remains of Pleistocene *Ovibos moschatus* from Germany and its geographic and stratigraphic occurrence in Europe. *Geologie en Mijnbouw*, **78** (3), 383–394.
- Rusanov, B. S. 1968. *Biostratigrafija otlozhenij Yuzhnoj Yakutii* (Biostratigraphy of Southern Yakutia deposits). Nauka, Moscow, 1–459 [In Russian].
- Ryziewicz, Z. 1955. Systematic place of the fossil musk-ox from the Eurasian diluvium. *Prace Wroclawskiego Towarzystwa Naukowego. Series B*, **49**, 1–74.
- Sher, A. V. 1971. *Mlekopitajushchie i stratigrafija plejstocena krajnego Severo-Vostoka SSSR i Severnoj Ameriki* (Pleistocene mammals and stratigraphy of the Far North-East of USSR and North America). Nauka, Moscow, 1–310 [In Russian].
- Shovkoplyas, I. G., Korniets, N. L., Pashkevich, G. A. 1981. Dobranichevka camp. In: Velichko, A. A. et al., eds., *Late Palaeolithic archaeology and palaeogeography of the Russian Plain*. Nauka, Moscow, 97–106 [In Russian].
- Shpansky, A. V. 2000. *Kopytnye srednego-pozdnego neoplejstocena jugo-vostoka Zapadno-Sibirskoj ravniny (stratigraficheskoe znachenie, paleoekologija i paleozoogeografija)* [Ungulates of the Middle-Late Neopleistocene of the southeast of the West Siberian Plain (stratigraphic significance, paleoecology and paleozoogeography)]. PhD Thesis. Tomsk, 1–25 [In Russian].
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, **85**, 1–350.
- Sinitsyn, A. A., Praslov, N. D., Svezhentsev, Yu. S., Sulerzhickiy, L. D. 1997. Radiocarbon chronology of the Upper Paleolithic of Eastern Europe. In: Sinitsyn, A. A., Praslov, N. D., eds. *Radiocarbon chronology of the Paleolithic of Eastern Europe and North Asia: problems and prospects*. St. Petersburg, 21–66 [In Russian].
- Smith, C. H. 1827. Synopsis of the species of the class Mammalia, as arranged with reference to their organization. Genus II. — *Ovibos*. In: Griffith, E., Smith, C. H., Pidgeon, E., eds. *The animal kingdom, arranged in conformity with its organization, by the Baron Cuvier. Vol. V*. Printed for G. B. Whittaker. London, United Kingdom, 370.
- Tchersky, I. D. 1891. *Opisanie kollekcij posletretichnyh mlekopitajushchih, sobrannyh Novo-Sibirskoj ekspedicii* (Description of the collection of post-Tertiary mammals, collected by the Novo-Sibirsk expedition in 1885–1886). Petersburg, 1–706 [In Russian].
- Tikhonov, A. N. 1994. Pleistocene muskox (*Ovibos pallantis*) of the Urals and western Siberia. *Proceedings of Zoological Institute RAS*, **256**, 92–110 [In Russian].

- Vangengeim, E. A. 1961. *Paleontologicheskoe obosnovanie stratigrafii antropogenovyh otlozhenij severa Vostochnoj Sibiri* (Palaeontological substantiation of stratigraphy of Anthropogene deposits on the north of Eastern Siberia). AN SSSR Publishing, Moscow, 1–182 [In Russian].
- Velichko, A. A. 1961. *Geologicheskij vozrast verhnego paleolita centralnyh rajonov Russkoj ravniny* (Geological age of the Upper Palaeolithic of central regions of the Russian Plain). AN SSSR Publishing, Moscow, 1–296 [In Russian].
- Walker, D. N. 1982. A Late Pleistocene *Ovibos* from Southeastern Wyoming. *Journal of Paleontology*, **56** (2), 486–491.
- Zimmermann, F. A. W. 1780. *Geographische Geschichte des Menschen, und der allgemein verbreiteten vierfüßigen Thiere. 2. Band: Enthält ein vollständiges Verzeichniß aller bekannten Quadrupeden*. Weygand, Leipzig, 1–450.

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