



Contents lists available at ScienceDirect

## Quaternary International

journal homepage: [www.elsevier.com/locate/quaint](http://www.elsevier.com/locate/quaint)

## The North Eurasian mammal assemblages during the end of MIS 3 (Brianskian–Late Karginian–Denekamp Interstadial)

Anastasia K. Markova<sup>a,\*</sup>, Andrei Yu. Puzachenko<sup>a</sup>, Thijs van Kolfschoten<sup>b</sup>

<sup>a</sup> Institute of Geography, Russian Academy of Sciences, Staromonetny 29, Moscow 119017, Russia

<sup>b</sup> Faculty of Archaeology, Leiden University, P.O. Box 9515, 2300 RA Leiden, The Netherlands

### ARTICLE INFO

#### Article history:

Available online 23 February 2009

### ABSTRACT

Abundant Northern Eurasian mammal data have been collected from deposits of the final part of MIS 3 (Brianskian–Late Karginian–Denekamp Interstadial). They indicate a period of some warming with respect to climates associated with the encompassing glacial deposits. The unique structure of mammal assemblages of this interval was distinguished during this study. All mammal assemblages of Northern Eurasia related to the end of MIS 3 are characterized by “mixed”, “non-analogue” species composition. The mammals which now inhabit different natural zones (tundra, steppe, forest) occurred together in different combinations over the huge territories of Northern Eurasia. The Northern Eurasian mammalian assemblages correlated with the end of MIS 3 were closer in the species composition to the faunas of cold stages of the Last Glaciation than to interglacial ones. Mathematical methods elucidate the principal and local characteristics of the structure and geographical position of mammal assemblages through most Eurasia between 33 and 24 ka BP.

© 2009 Elsevier Ltd and INQUA. All rights reserved.

### 1. Introduction

MIS 3 was the warmest part of the Last Glaciation (Van Andel, 2003). It is usually considered to be a mega-interstadial, with significant fluctuations of climate and several warmer and cooler intervals identified within it. According to materials obtained from Eastern Europe, the final part of MIS 3 mega-interstadial corresponds to the Briansk (Dunaevo–Dniester–Upper Vytachev (Vt-3b)) Interstadial, which preceded the Late Weichselian–Late Valdai Glaciation (Ivanova, 1980; Morozova, 1981; Velichko and Morozova, 1982, 2002; Bolikhovskaya, 1995; Rousseau et al., 2001; Glushankova, 2004; Gerasimenko, 2007; Sycheva et al., 2007; and others). In Western Europe, the Briansk Interstadial correlates with the Grudziadz (Poland), Denekamp (Netherlands), Schtilfried B (Austria), Krinides (Balkan Mountains), Grand Bya and Arcy (France), Tolsta (Scotland), and Sandnes/Alesund (Norway) Interstadials. Those are usually present in the sequences as fossil soils and various organic sediments (Fink, 1969; Kolstrup and Wijmstra, 1977; Nadachowski, 1984; Faustova and Velichko, 1992; Whittington and Hall, 2002; Granoszewski, 2003; and others). These data contradict to a certain degree to the oxygen-isotopic data, which

indicate the trend to cooling towards the end of MIS 3 (Van Andel and Davies, 2003). However, the  $\delta^{18}\text{O}$  curve (GRIP2—Greenland ice-core record) indicates very strong fluctuations between cold and warm conditions at the end of MIS 3 (Meese et al., 1997). Therefore, soil horizons could form during the warm phases of the latter part of MIS3, as has been confirmed by fossil soils found, described and dated in the different parts of Northern Eurasia. A large amount of fossil mammal localities, related to the end of MIS 3, was discovered in the different parts of this continent. These data could provide important information about environmental and climatic conditions of this interesting interval.

### 2. Deposits, geochronology and materials

The interstadial of the end of MIS 3 was complicated and included relatively cool and warm intervals. In Eastern Europe it is reflected in the wide distribution of the Briansk paleosol complex dated between 33 and 24 ka BP (Chichagova and Cherkinsky, 1993). Studies of the Central Russian Plain have shown the Briansk soil to be represented in some sections by two individual horizons. In the Upper Don basin, Sycheva described two paleosols related to the end of MIS 3: the lower “Monastyrshian” and the upper “Brianskian” soils, with respective radiocarbon dates of  $29,100 \pm 340$  ka BP and  $24,400 \pm 700$  ka BP (Sycheva et al., 2007).

In Siberia there was also distinguished the middle Valdai warm period, sometimes described as an Interstadial, and sometimes as

\* Corresponding author. Tel.: +7 495 939 0524; fax: +7 495 959 0033.

E-mail addresses: [nature@online.ru](mailto:nature@online.ru) (A.K. Markova), [puzak1@rambler.ru](mailto:puzak1@rambler.ru) (A.Yu. Puzachenko), [t.van.kolfschoten@arch.leidenuniv.nl](mailto:t.van.kolfschoten@arch.leidenuniv.nl) (T. van Kolfschoten).

an Interglacial. It was initially determined at Cape Karginy at the mouth of Yenisei River (Eastern Siberia) (Saks and Antonova, 1945). Later, the age of Karginian deposits from the Yenisei section was revised (on the basis of EPR dating) and the section lost its stratotype meaning, the deposits having been attributed to the Kazantsevo (=Eemian) age (Volkova, 2001). However, the name “Karginian” is still used frequently in stratigraphical literature. Thus, in the Lower Ob' River basin (West Siberia) the three horizons of alluvial and lake deposits (dated between 55 and 23 ka BP) are referred to as belonging to the Karginian Interstadial. The uppermost of these horizons dated between 30 and 25 ka BP is known as the Late Karginian Interstadial (Volkova, 2001). Palynological materials indicated the presence of northern taiga in the Lower Ob' basin at the beginning of Late Karginian time. Later, after 26 ka BP, the climate became cooler and birch open woodlands replaced the taiga forests in the region (Volkova, 2001). In the sections Kirias 1 and 2 (Lower Ob' basin, 60°51' N, 75°45' E) several radiocarbon dates have been obtained for a peat layer: 27,800 ± 210 (LU-5095) BP, 31,880 ± 290 (LU-5115) BP and 32,600 ± 200 (LU-5094) BP. In these sections three warming and two cooling episodes have been distinguished within the Karginian interval between 28 and 46 ka BP (Arslanov et al., 2007; Laukhin, 2007).

The Iskitim paleosol complex was described in the south part of Western Siberia (Ob' River basin, Novosibirsk region). The upper soil of this complex has <sup>14</sup>C dates between 24,900 ± 380 and 33,100 ± 1600 ka BP, which is very close to the <sup>14</sup>C age of the Briansk soil in Eastern Europe and Late Karginian horizon in the north of Western Siberia (Zykina 2006). The upper Iskitim soil developed during the interstadial and indicates forest–steppe environments in the Novosibirsk region at that time.

The Osinsky paleosol complex identified in the south of Central Siberia is also correlated with MIS 3. The upper Osinsky soils were similar to the modern ones (Vorob'eva and Zykina, 2002).

In Eastern Siberia there are also found organic soil deposits confined to the Late Pleistocene cryogenic “edoma” (“loess–ice”) complex. In the northeast of Yakutia there are four fossil soil horizons formed between 40 and 26 ka BP. The youngest two soils were dated between 33 and 26 ka BP (Gubin and Zanina, 2006). All four soils were referred to Karginian time. The upper soils could be compared with Briansk complicated soil of Eastern Europe and correlated to the Upper Karginian.

Therefore, the Brianskian interstadial corresponds to the Late Karginian–Iskitim–Osinsky warming in Siberia (Volkova, 2001; Vorob'eva and Zykina, 2002; Gubin and Zanina, 2006; Zykina, 2006) and to the Shtilfried B–Denekamp–Grand Bya–Tolsta–Sandnes/Alesund of Western Europe (Fink, 1969; Zykina, 2006; Kolstrup and Wilmstra, 1977; Faustova and Velichko, 1992; Whittington and Hall, 2002; and others). The Briansk interval in Eastern Europe (which was not homogeneous) was dated by <sup>14</sup>C between 33 ka BP and 24 ka BP (Chichagova and Cherkinsky, 1993). It was the last in a series of interstadials of the Middle Weichselian–Middle Valdai (MIS 3).

Pospelova (2007) revealed the close correlation between the Pleistocene paleomagnetic episodes and warm intervals. Paleomagnetic episode Yangiul I is dated between 29 and 27 ka BP, providing additional dating of this Interstadial. The position of coastline at the end of MIS 3 roughly corresponded to the present-day –50 m isobath (Porter, 1983).

There are more than 222 mammal localities in Northern Eurasia related to this time interval (Fig. 1). Most of the fossil remains have been recovered from cultural levels of Paleolithic sites and all have been dated by radiocarbon (uncalibrated dates). Some of the localities are related to the horizon of Briansk fossil soil (Fig. 2).

### 3. Methods

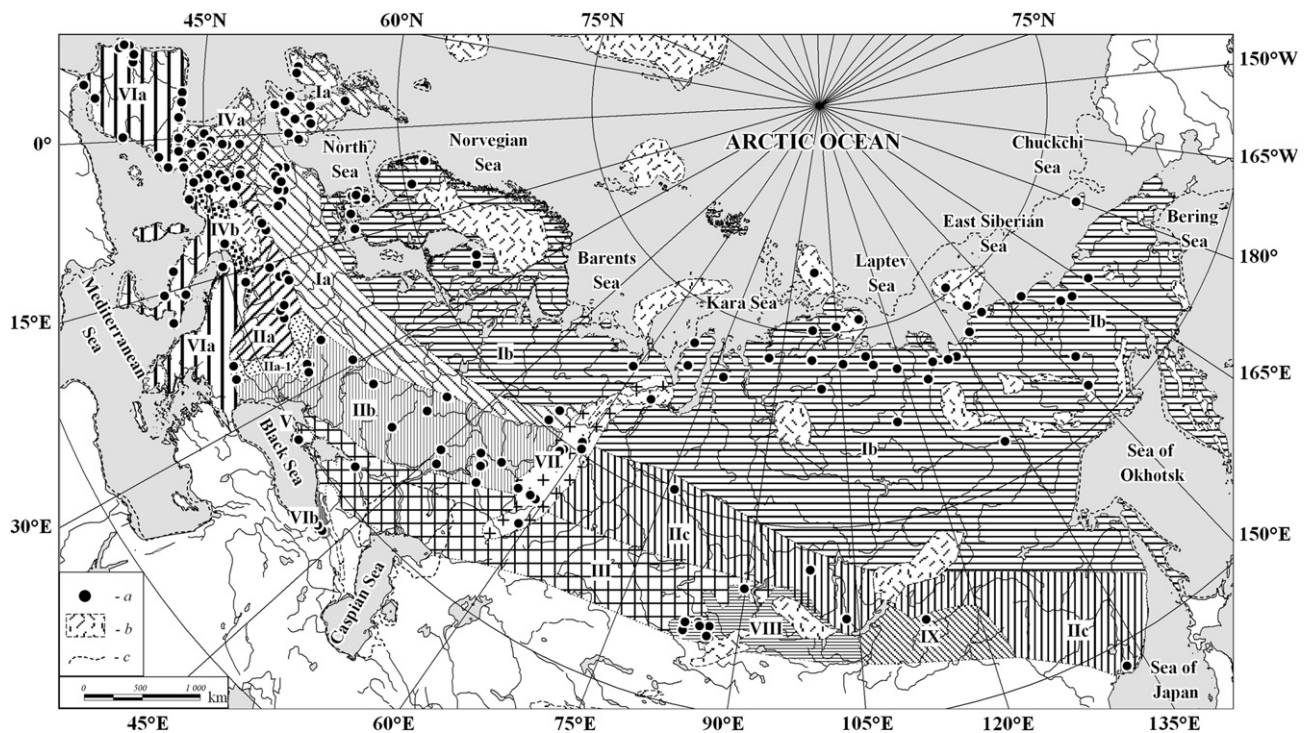
Analysis of the abundant mammalian material used GIS technology and a number of mathematical methods extensively employed in previous studies (Markova et al., 2002a,b,c; Markova and Puzachenko, 2007; Markova et al., 2008). Recently the distribution and species composition of mammal assemblages dated to the Briansk Interstadial have been reconstructed for the Russian Plain (Markova et al., 2002a,b). Collected and integrated data on mammals from other regions of Northern Eurasia allow reconstruction of the mammal distribution, diversity and community for the entire northern part of the continent.

Multivariate techniques were applied to the data analysis. At the first stage of the analysis, the mammalian materials were tabulated as a matrix of “presence–absence” of all species of mammals (more than 110 species), which have been found in Briansk–Karginian–Denekamp deposits. The square matrix of Jaccard's dichotomy coefficients among all the pairs of 222 localities was calculated. This matrix was used in the non-metric multidimensional scaling (MDS) technique, which visualizes proximity relations of localities by distances between points in a low dimensional Euclidian space (Shepard, 1962; Davison and Jones, 1983; James and McCulloch, 1990). The next stage of analysis involved hierarchic Unweighted Pair Group Averaging using Arithmetic Mean (UPGMA) classification (Sneath and Sokal, 1973) of localities by mammalian composition with MDS axes as variables. Localities from preliminary clusters have been mapped in the GIS MapInfo (MapInfo Corporation) and analyzed. The new Euclidian distances between 15 improved clusters and new classification tree were calculated (Figs. 1 and 3). Lists of indicative species (Table 1) were established for each cluster and indicative species were defined with the Maximum-Likelihood Chi-square test. This permits not only maps for indicative mammal species to be constructed, but also ecological groups of mammals (steppe, tundra, etc.) to be identified. This allows characterization of species composition and distribution of the principal mammal assemblages of Northern Eurasia using the general scheme of paleozoogeographical zonation of Eastern Europe and Northern Asia reconstructed earlier (Baryshnikov and Markova, 2002; Markova and Puzachenko, 2007).

### 4. Mammal assemblages

Between 33 and 24 ka BP, huge territories of Eastern Europe and Siberia were occupied by the mammals of Arctic sub-assemblage of mammoth assemblage (Ia and Ib; 83 localities). The assemblage includes mammoth, woolly rhinoceros, reindeer, wild horse, cave hyena, cave bear, collared and Siberian lemmings, and others (Table 1). The principal features of this assemblage were also described in earlier papers on the maximum cooling of the Last Glaciation (Baryshnikov and Markova, 1992, 2002). No forest animals were found. Mammoth localities were widely distributed (Fig. 4). Woolly rhinoceros (*Coelodonta antiquitatis*) is commonly found in the western part of area of this assemblage, though rare localities with this species were discovered also in northeast Eurasia (Fig. 5). Giant deer and red deer finds are practically unknown in Northern Siberia; their finds are concentrated in the British Isles and in western Europe, where the climate was milder (Figs. 10, 11). Typical forest animals, such as wild boar, were absent in this sub-assemblage (Fig. 12), but some steppe mammals existed in small amounts (Figs. 8, 9). The mammal composition suggests a noticeable cooling during the end of the Mega-interstadial.

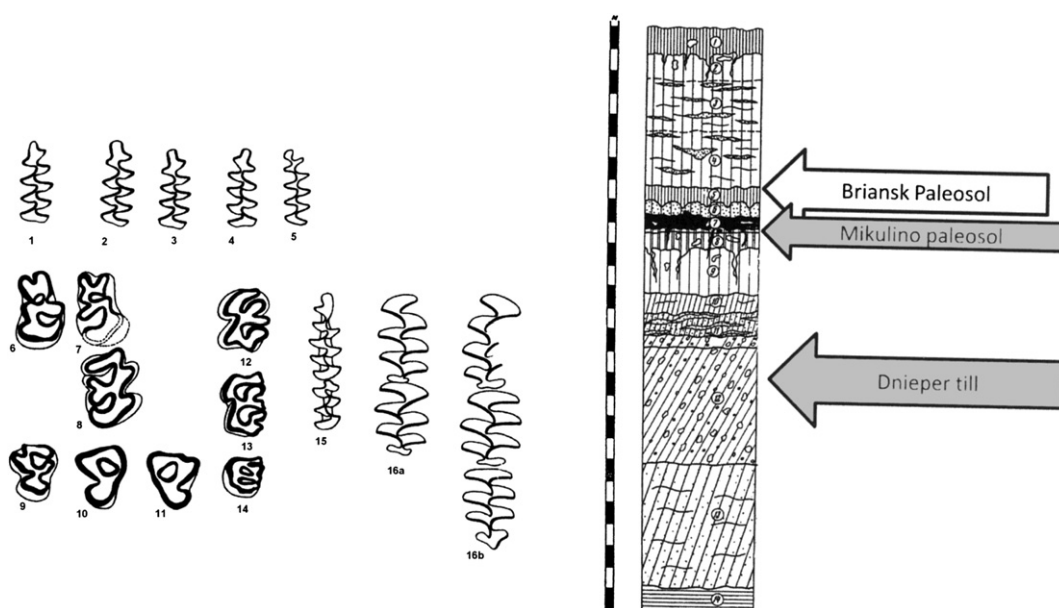
South of this zone the boreal type of mammoth assemblage occurred, with four variants distinguished. The first (IIa; 20 localities) was distributed in Western, Central and partly Eastern Europe and included *Sorex araneus*, *Talpa* sp., *Gulo gulo*, *Mammuthus*



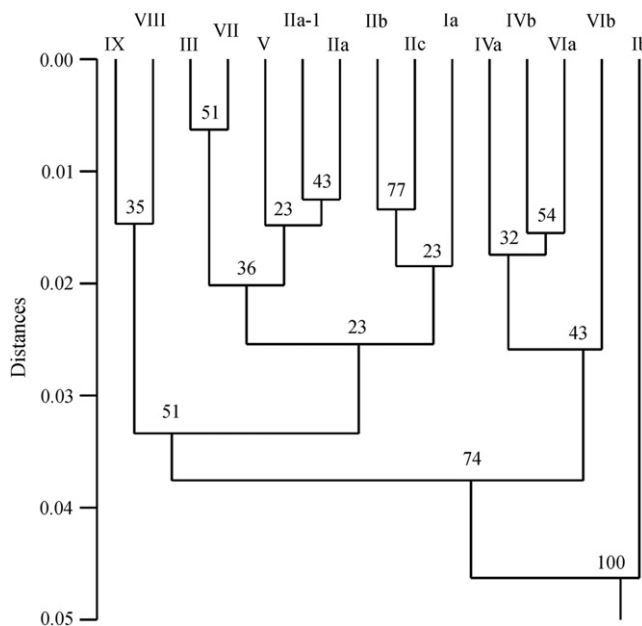
**Fig. 1.** Mammal localities and mammal assemblages (I–IX) between 33 and 24 ka BP. I: arctic sub-assemblage of mammoth assemblage. a, western variant; b, eastern variant. II: boreal sub-assemblage of mammoth assemblage. a, central European variant; a-1, Carpathian-Balkanian variant; b, Eastern European variant; c, Siberian variant. III: steppe sub-assemblage of mammoth assemblage. IV: Central European (IVa) and South Alpine (IVb) montane assemblage. V: Crimean montane mammoth assemblage. VI: Mediterranean (VIa) and Caucasian (VIb) montane assemblage. VII: The Urals montane mammoth assemblage. VIII: The Altayan montane assemblage. IX: Transbaikalian mammal assemblage. a, mammal localities; b, ice sheets and montane glaciers; c, coast line.

*primigenius*, *Lepus timidus*, *Ochotona pusilla*, *Dicrostonyx*, *Lemmus lemmus*, *Chionomys nivalis*, *Clethrionomys glareolus*, *Cricetus cricetus*, *Mesocricetus newtoni*, *Megaloceros giganteus*, *Microtus (Terricola) subterraneus*, *Mustela nivalis*, *Spermophilus suslicus*, and *Marmota marmota* (Fig. 1, Table 1). The number of forest species indicates the presence of forest areas together with widely

distributed open tundra–steppe. In Eastern Europe, east of the Dnieper (IIb; 14 localities, Table 1) this type of mammal assemblage was represented by mammoth, woolly rhinoceros, reindeer, primitive bison, red, roe and giant deer, saiga, wild horse, arctic fox, cave bear and cave lion, weasels, European polecat, steppe pika, steppe and yellow lemmings, red-backed vole, narrow-skulled vole and



**Fig. 2.** The structure of Arapovichi section (Upper Dnieper Basin) and the picture of the rodent teeth found in the Brianskian soil: *Lagurus ex gr. lagurus*: 1–5, M/1; *Allactaga major*: 6, 7, M1; 8, M2; 9–11, M3; 12, M1; 13, M2; 14, M3; *Microtus (Stenocranius) gregalis*: 15, M1 and M2; *Dicrostonyx guilelmi*: 11a, M1 and M2; 11b, M1, M2 and M3 (after Markova, 1982).



**Fig. 3.** Dendrogram of mammal assemblages (see Fig. 1): distances: Euclid; method: UPGMA. The number of times of each branch was supported in the bootstrap replication (100) is shown as a percentage.

others (Figs. 1, 6, 7). In Siberia (IIc; 5 localities, Table 1) this assemblage included also North Siberian vole, Siberian chipmunk, and others. A high proportion of steppe tundra mammals, along with forest animals in all three variants of this sub-assemblage indicate more moderate climatic conditions and the presence of periglacial forest–steppes.

The Carpathian-Balkanian assemblage (IIa-1; 6 localities) is based on the materials of Bacho-Kiro cave (Layers 6a,b and 7) (Kozłowski, 1982; Nadachowski, 1984); Temnata cave (Popov, 1986); La Adam Cave (Dumitresku et al., 1963); Trinka 2 (Layers 2 and 3) (Anisiutkin et al., 1986) and others. Small mammals include *Spermophilus* sp., *Marmota bobac*, *Allactaga major*, *Cricetulus migratorius*, *Cricetus cricetus*, *Mesocricetus newtoni*, *Nannospalax leucodon*, *Spalax polonicus*, *Sicista subtilis*, *Muscardinus avellanarius*, *Mus musculus*, *Glis glis*, *Dryomys nitedula*, *Silvaemus flavicollis*, *Clethrionomys* (=Myodes) *glareolus*, *Arvicola terrestris*, *Eolagurus luteus*, *Lagurus lagurus*, *Microtus cf. arvalis*, *M. cf. agrestis*, *Microtus* (*Terricola*) *grafi* (*subterraneus* group), *Chionomys nivalis*, *Ochotona pusilla*, and others (Fig. 1, Table 1). Large mammals are represented by *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus caballus*, *Equus hydruntinus*, *Rangifer tarandus*, *Cervus elaphus*, *Megaloceros giganteus*, *Crocota crocota spelaea*, *Martes flavigula*, *Mustela erminea*, *Mustela nivalis*, *Ursus spelaeus*, *Vulpes vulpes* and others. This rich mammal assemblage reflects the numerous local habitats related to the mountains and highlands. Pleistocene large herbivorous and cave carnivorous, steppe, forest and hydrogenous mammals were

**Table 1**  
Indicative species for each cluster.

Clusters	Indicative species
I la	<i>Mammuthus primigenius</i> , <i>Coelodonta antiquitatis</i> , <i>Rangifer tarandus</i> , <i>Megaloceros giganteus</i> , <i>Equus caballus</i> , <i>Alopecurus lagopus</i> , <i>Canis lupus</i> , <i>Crocota crocota spelaea</i> , <i>Panthera spelaea</i> , <i>Ursus spelaeus</i> , <i>Ursus arctos</i> , <i>Vulpes vulpes</i> , <i>Lepus timidus</i> , <i>Dicrostonyx</i> , <i>Lemmus</i>
I lb	<i>Mammuthus primigenius</i> , <i>Equus caballus</i> , <i>Rangifer tarandus</i> , <i>Alopecurus lagopus</i> , <i>Dicrostonyx</i> , <i>Lemmus</i>
II IIa	<i>Mammuthus primigenius</i> , <i>Coelodonta antiquitatis</i> , <i>Rangifer tarandus</i> , <i>Megaloceros giganteus</i> , <i>Cervus elaphus</i> , <i>Equus caballus</i> , <i>Rupicapra rupicapra</i> , <i>Alloicricetus bursae</i> , <i>Alopecurus lagopus</i> , <i>Crocota crocota spelaea</i> , <i>Bison priscus</i> , <i>Canis lupus</i> , <i>Martes flavigula</i> , <i>Mustela nivalis</i> <i>Chionomys nivalis</i> , <i>Felis silvestris</i> , <i>Felis</i> ( <i>Lynx</i> ) <i>lynx</i> , <i>Gulo gulo</i> , <i>Spermophilus suslicus</i> , <i>Clethrionomys</i> (=Myodes) <i>glareolus</i> , <i>Dicrostonyx gulielmi</i> , <i>Lemmus lemmus</i> , <i>Marmota marmota</i> , <i>Meles meles</i> , <i>Ursus savini</i> , <i>Ursus spelaeus</i> , <i>Ursus arctos</i> , <i>Vulpes vulpes</i> , <i>Panthera spelaea</i> , <i>Sorex araneus</i> , <i>Talpa europaea</i> , <i>Neomys fodiens</i> , <i>Silvaemus sylvaticus</i> , <i>Arvicola terrestris</i> , <i>Microtus agrestis</i> , <i>Microtus oeconomus</i> , <i>Microtus</i> ( <i>Terricola</i> ) <i>grafi</i> , <i>Lepus europaeus</i> , <i>Lepus timidus</i>
IIa-1	<i>Mammuthus primigenius</i> , <i>Coelodonta antiquitatis</i> , <i>Rangifer tarandus</i> , <i>Megaloceros giganteus</i> , <i>Equus hydruntinus</i> , <i>Crocota crocota spelaea</i> , <i>Martes flavigula</i> , <i>Mustela erminea</i> , <i>Mustela nivalis</i> , <i>Ursus spelaeus</i> , <i>Vulpes vulpes</i> , <i>Sorex araneus</i> , <i>Sorex alpinus</i> , <i>Spermophilus suslicus</i> , <i>Marmota bobac</i> , <i>Allactaga major</i> , <i>Nannospalax leucodon</i> , <i>Silvaemus flavicollis</i> , <i>Silvaemus sylvaticus</i> , <i>Cricetulus migratorius</i> , <i>Cricetus cricetus</i> , <i>Mesocricetus newtoni</i> , <i>Arvicola terrestris</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys</i> (=Myodes) <i>glareolus</i> , <i>Eolagurus luteus</i> , <i>Lagurus lagurus</i> , <i>Microtus arvalis</i> , <i>Microtus</i> ( <i>Terricola</i> ) <i>grafi</i> ("subterraneus" group), <i>Lepus timidus</i> , <i>Ochotona pusilla</i>
IIb	<i>Mammuthus primigenius</i> , <i>Rangifer tarandus</i> , <i>Megaloceros giganteus</i> , <i>Saiga tatarica</i> , <i>Ursus spelaeus</i> , <i>Marmota bobac</i> , <i>Dicrostonyx gulielmi</i> , <i>Lagurus lagurus</i> , <i>Microtus arvalis</i> , <i>Microtus oeconomus</i> , <i>Lepus timidus</i> , <i>Ochotona pusilla</i>
IIc	<i>Equus caballus</i> , <i>Hyaena hyaena</i> , <i>Eutamias sibirica</i> , <i>Myopus sp.</i> , <i>Lagurus lagurus</i> , <i>Microtus hyperboreus</i> , <i>Microtus middendorffi</i> , <i>Microtus oeconomus</i> , <i>Microtus gregalis</i>
III	<i>Mammuthus primigenius</i> , <i>Coelodonta antiquitatis</i> , <i>Rangifer tarandus</i> , <i>Cervus elaphus</i> , <i>Capreolus pygargus</i> , <i>Alces alces</i> , <i>Equus caballus</i> , <i>Equus hemionus</i> , <i>Antelope sp.</i> , <i>Saiga tatarica</i> , <i>Capra sibirica</i> , <i>Ovis ammon</i> , <i>Sus scrofa</i> , <i>Crocota crocota spelaea</i> , <i>Felis</i> ( <i>Lynx</i> ) <i>lynx</i> , <i>Ursus arctos</i> , <i>Spermophilus undulatus</i> , <i>Marmota baibacina</i> , <i>Alticola sp.</i> , <i>Clethrionomys</i> (=Myodes) <i>rufocanus</i> , <i>Clethrionomys</i> (=Myodes) <i>rutillus</i> , <i>Microtus arvalis</i> , <i>Microtus oeconomus</i> , <i>Microtus gregalis</i> , <i>Lepus timidus</i>
IV IVa	<i>Equus caballus</i> , <i>Equus hydruntinus</i> , <i>Rangifer tarandus</i> , <i>Cervus elaphus</i> , <i>Capreolus capreolus</i> , <i>Bison priscus</i> , <i>Bos primigenius</i> , <i>Rupicapra rupicapra</i> , <i>Felis</i> ( <i>Lynx</i> ) <i>pardina</i> , <i>Crocota crocota spelaea</i> , <i>Ursus spelaeus</i> , <i>Vulpes vulpes</i> , <i>Eliomys quercinus</i> , <i>Microtus brecciensis</i>
IVb	<i>Equus caballus</i> , <i>Rangifer tarandus</i> , <i>Cervus elaphus</i> , <i>Capreolus capreolus</i> , <i>Dama dama</i> , <i>Bos primigenius</i> , <i>Capra ibex</i> , <i>Rupicapra rupicapra</i> , <i>Sus scrofa</i> , <i>Crocota crocota spelaea</i> , <i>Panthera spelaea</i> , <i>Panthera pardus</i> , <i>Felis</i> ( <i>Lynx</i> ) <i>lynx</i> , <i>Felis silvestris</i> , <i>Cuon alpinus</i> , <i>Canis lupus</i> , <i>Vulpes vulpes</i> , <i>Meles meles</i> , <i>Ursus spelaeus</i> , <i>Ursus arctos</i> , <i>Erinaceus europaeus</i> , <i>Sorex araneus</i> , <i>Eliomys quercinus</i> , <i>Glis glis</i> , <i>Castor fiber</i> , <i>Spermophilus citellus</i> , <i>Spermophilus suslicus</i> , <i>Marmota marmota</i> , <i>Silvaemus sylvaticus</i> , <i>Arvicola terrestris</i> , <i>Chionomys nivalis</i> , <i>Microtus agrestis</i> , <i>Microtus arvalis</i> , <i>Oryctolagus cuniculus</i> , <i>Lepus europaeus</i>
V	<i>Mammuthus primigenius</i> , <i>Coelodonta antiquitatis</i> , <i>Equus caballus</i> , <i>Rangifer tarandus</i> , <i>Cervus elaphus</i> , <i>Capreolus pygargus</i> , <i>Saiga tatarica</i> , <i>Sus scrofa</i> , <i>Sorex araneus</i> , <i>Crocota crocota spelaea</i> , <i>Panthera spelaea</i> , <i>Ursus spelaeus</i> , <i>Vulpes vulpes</i> , <i>Marmota bobac</i> , <i>Allactaga major</i> , <i>Ellobius talpinus</i> , <i>Silvaemus flavicollis</i> , <i>Arvicola terrestris</i> , <i>Cricetulus migratorius</i> , <i>Lagurus lagurus</i> , <i>Microtus agrestis</i> , <i>Microtus arvalis</i> , <i>Microtus oeconomus</i> , <i>Microtus gregalis</i> , <i>Ochotona pusilla</i> , <i>Lepus timidus</i>
VI VIa	<i>Dicerorhinus kirchbergensis</i> , <i>Equus hydruntinus</i> , <i>Equus caballus</i> , <i>Cervus elaphus</i> , <i>Capreolus capreolus</i> , <i>Bos primigenius</i> , <i>Capra ibex</i> , <i>Ovis orientalis musimon</i> , <i>Rupicapra rupicapra</i> , <i>Sus scrofa</i> , <i>Crocota crocota spelaea</i> , <i>Panthera pardus</i> , <i>Felis silvestris</i> , <i>Canis lupus</i> , <i>Ursus spelaeus</i> , <i>Erinaceus europaeus</i> , <i>Hystrix vinogradovi</i> , <i>Alloicricetus bursae</i> , <i>Silvaemus sylvaticus</i> , <i>Arvicola sapidus</i> , <i>Microtus</i> ( <i>Terricola</i> ) <i>duodecimcostatus</i> , <i>Lepus europaeus</i> , <i>Oryctolagus cuniculus</i>
VIb	<i>Equus caballus</i> , <i>Cervus elaphus</i> , <i>Capreolus capreolus</i> , <i>Alces alces</i> , <i>Bison priscus</i> , <i>Bos primigenius</i> , <i>Capra sp.</i> , <i>Sus scrofa</i> , <i>Panthera spelaea</i> , <i>Ursus spelaeus</i> , <i>Ursus arctos</i> , <i>Castor fiber</i> , <i>Glis glis</i> , <i>Mus musculus</i>
VII	<i>Coelodonta antiquitatis</i> , <i>Equus caballus</i> , <i>Rangifer tarandus</i> , <i>Bison priscus</i> , <i>Ovibos pallantis</i> , <i>Saiga tatarica</i> , <i>Panthera spelaea</i> , <i>Alopecurus lagopus</i> , <i>Canis lupus</i> , <i>Vulpes vulpes</i> , <i>Mustela erminea</i> , <i>Mustela eversmanni</i> , <i>Ursus spelaeus</i> , <i>Spermophilus superciliosus</i> , <i>Marmota bobac</i> , <i>Alloicricetus eversmanni</i> , <i>Arvicola terrestris</i> <i>Clethrionomys</i> (=Myodes) <i>glareolus</i> , <i>Clethrionomys</i> (=Myodes) <i>rufocanus</i> , <i>Clethrionomys</i> (=Myodes) <i>rutillus</i> , <i>Cricetulus migratorius</i> , <i>Dicrostonyx gulielmi</i> , <i>Lemmus sibiricus</i> , <i>Eolagurus luteus</i> , <i>Lagurus lagurus</i> , <i>Microtus agrestis</i> , <i>Microtus middendorffi</i> , <i>Microtus oeconomus</i> , <i>Microtus gregalis</i> , <i>Lepus tanaiticus</i> , <i>Ochotona pusilla</i>
VIII	<i>Coelodonta antiquitatis</i> , <i>Equus hemionus</i> , <i>Equus caballus</i> , <i>Cervus elaphus</i> , <i>Capreolus pygargus</i> , <i>Bison priscus</i> , <i>Bos</i> ( <i>Poephagus</i> ) <i>baicalensis</i> , <i>Spiroceros kiakhtensis</i> , <i>Capra sibirica</i> , <i>Ovis ammon</i> , <i>Crocota crocota spelaea</i> , <i>Felis manul</i> , <i>Uncia uncia</i> , <i>Meles leucurus</i> , <i>Mustela erminea</i> , <i>Mustela eversmanni</i> , <i>Mustela nivalis</i> , <i>Canis lupus</i> , <i>Ursus savini</i> <i>rossicus</i> , <i>Ursus spelaeus</i> , <i>Ursus arctos</i> , <i>Vulpes vulpes</i> , <i>Spermophilus undulatus</i> , <i>Marmota baibacina</i> , <i>Pteromys volans</i> , <i>Allactaga sp.</i> , <i>Alticola sp.</i> , <i>Cricetus cricetus</i> , <i>Lagurus lagurus</i> , <i>Ochotona alpina</i>
IX	<i>Coelodonta antiquitatis</i> , <i>Equus caballus</i> , <i>Rangifer tarandus</i> , <i>Cervus elaphus</i> , <i>Capreolus pygargus</i> , <i>Alces alces</i> , <i>Bison priscus</i> , <i>Bos</i> ( <i>Poephagus</i> ) <i>baicalensis</i> , <i>Ovis ammon</i> , <i>Capra sibirica</i> , <i>Procavia gutturosa</i> , <i>Spiroceros kiakhtensis</i> , <i>Felis</i> ( <i>Lynx</i> ) <i>lynx</i> , <i>Canis lupus</i> , <i>Microtus fortis</i>

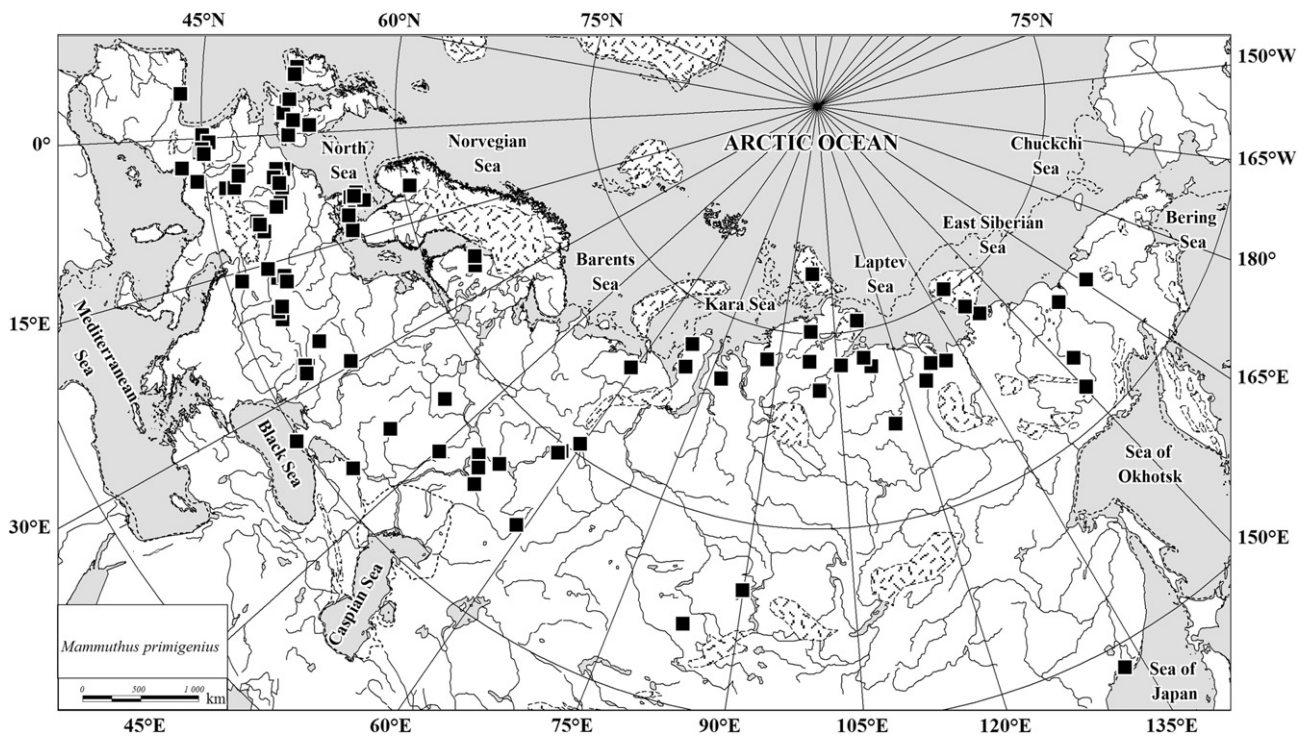


Fig. 4. The woolly mammoth *Mammuthus primigenius* localities (33–24 ka BP).

represented in this assemblage. Interesting findings were recovered in Brynzeny 1 and Starye Durutory (Transcarpathians), where *Dicrostonyx* bones have been distinguished at 48° N (Lozan, 1970).

The steppe sub-assemblage of mammoth assemblage occurred farther south (III; 3 localities, Table 1). Typical steppe mammals (wild horse, saiga, bobac marmot, steppe pika and others)

inhabited the territory together with mammoth, reindeer, cave bear and other Late Pleistocene species.

West European montane assemblages (IVa, IVb; 44 localities, Fig. 1, Table 1) includes a large quantity of mammal species, belonging to different ecological groups: steppe, forest and tundra. Mammoth, woolly rhinoceros, reindeer, red and giant deer, wild

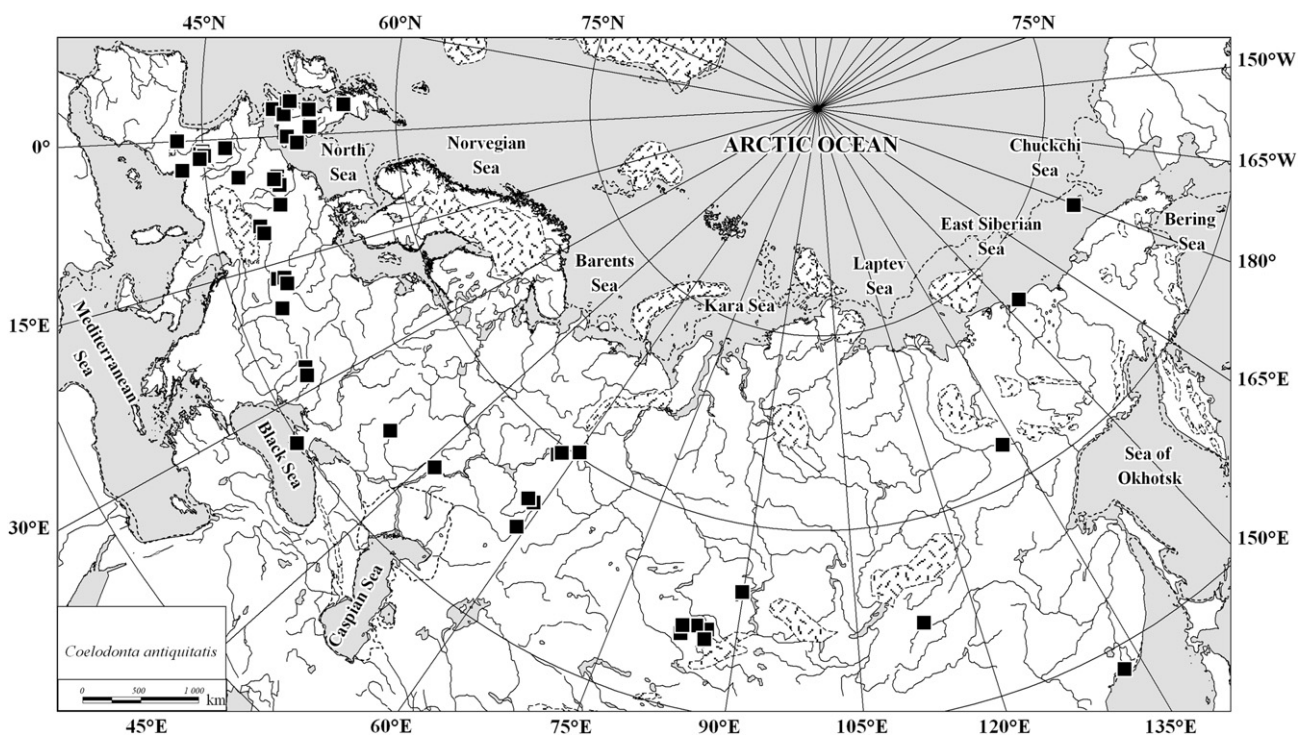


Fig. 5. The woolly rhinoceros *Coelodonta antiquitatis* localities (33–24 ka BP).

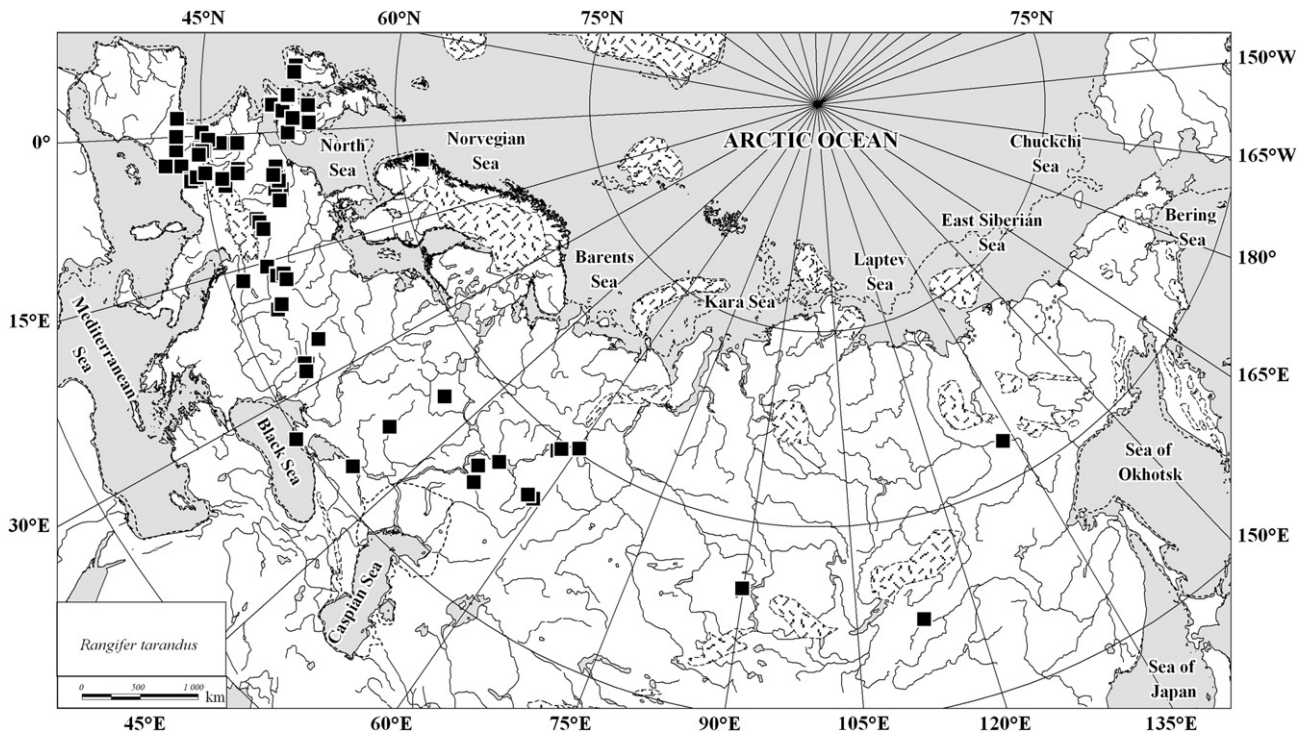


Fig. 6. The reindeer *Rangifer tarandus* localities (33–24 ka BP).

horse, saiga, primitive bison, arctic fox, cave hyena, cave bear, short-tailed weasel, yellow-throated marten, steppe pika, marmot bobac, steppe lemming, narrow-skulled vole and other mammals were distributed in this region (Figs. 2, 8, 9).

The Crimean montane mammoth assemblage (V; 3 localities) includes mammoth, woolly rhinoceros, reindeer, red and giant

deer, wild horse, Pleistocene ass, saiga, cave lion, cave bear, cave hyena, yellow-necked field mouse, steppe and yellow lemmings, and Altayan vole (Fig. 2). The ice-sheet influence was rather weak here and cold-adapted species were not found (Figs. 1, 11, 12).

The Mediterranean (VIa) and Caucasian (VIb) montane assemblages (29 localities, Table 1) were characterized by the presence of

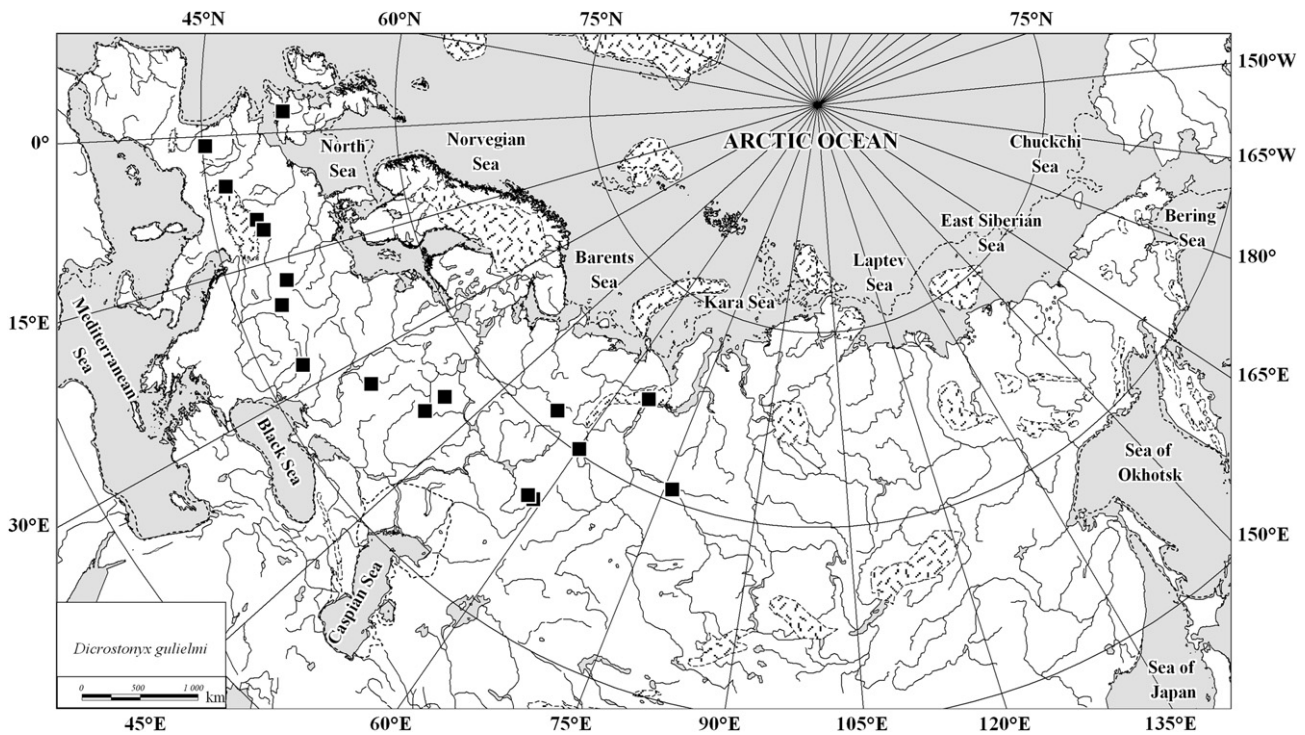


Fig. 7. The collar lemming *Dicrostonyx gulielmi* localities (33–24 ka BP).

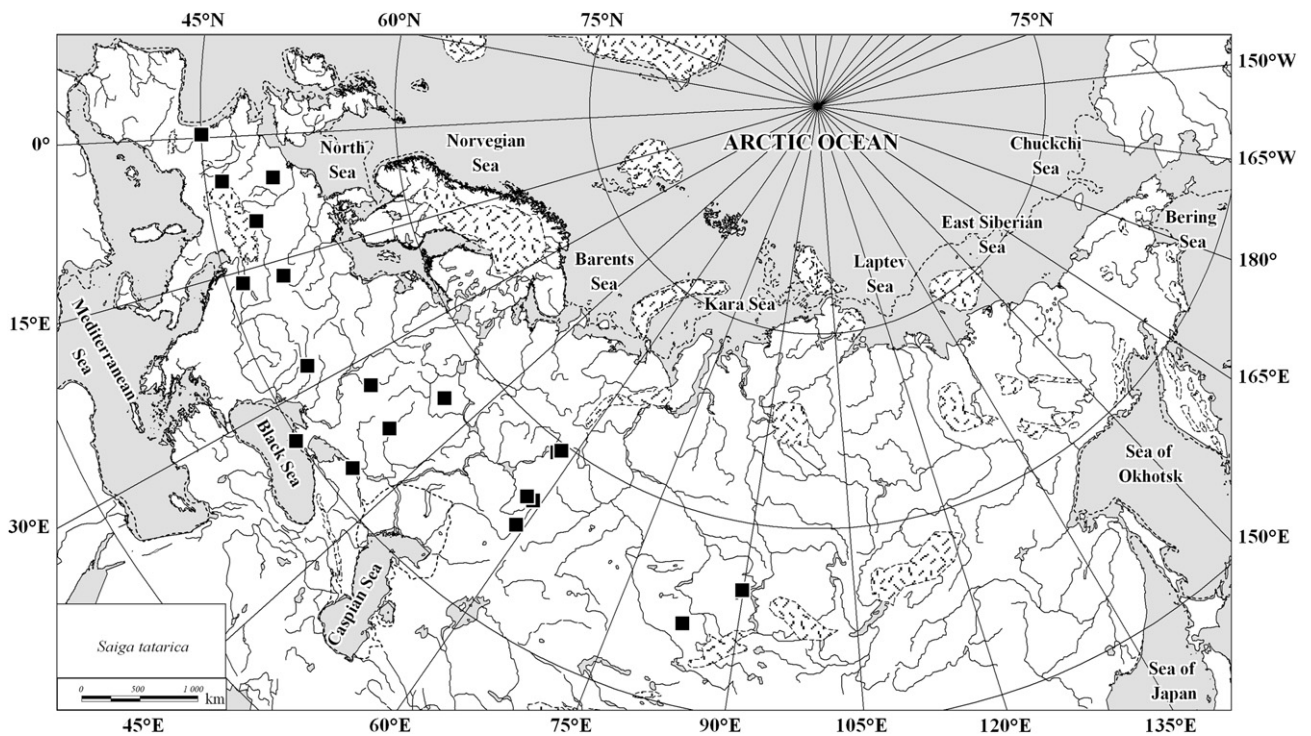


Fig. 8. The saiga antelope *Saiga tatarica* localities (33–24 ka BP).

both montane species (montane goat and sheep), and forest ones (red deer, wild boar, common dormouse). Cave lion, leopard, dhole, cave bear, leopard, primitive bison and wild ox were also found here.

The Urals montane mammoth assemblage (VII; 9 localities, Fig. 1, Table 1) includes a large number of adapted, steppe-

adapted and tundra-adapted species. Pleistocene large herbivores (mammoth, woolly rhinoceros, giant deer) also occurred in abundance.

The Altayan montane mammoth assemblage (VIII; 6 localities, Fig. 1, Table 1) was characterized by very high diversity of mammals. More than 50 species were identified from this region,

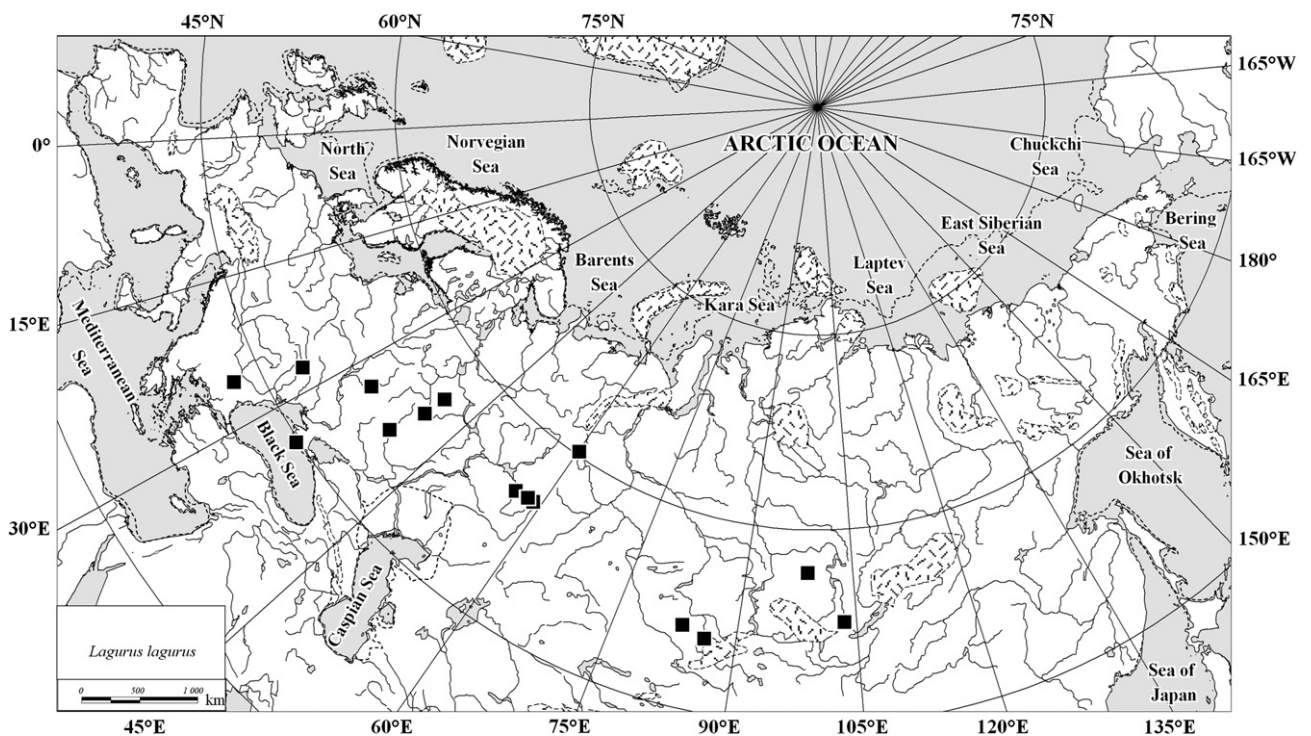


Fig. 9. The steppe lemming *Lagurus lagurus* localities (33–24 ka BP).

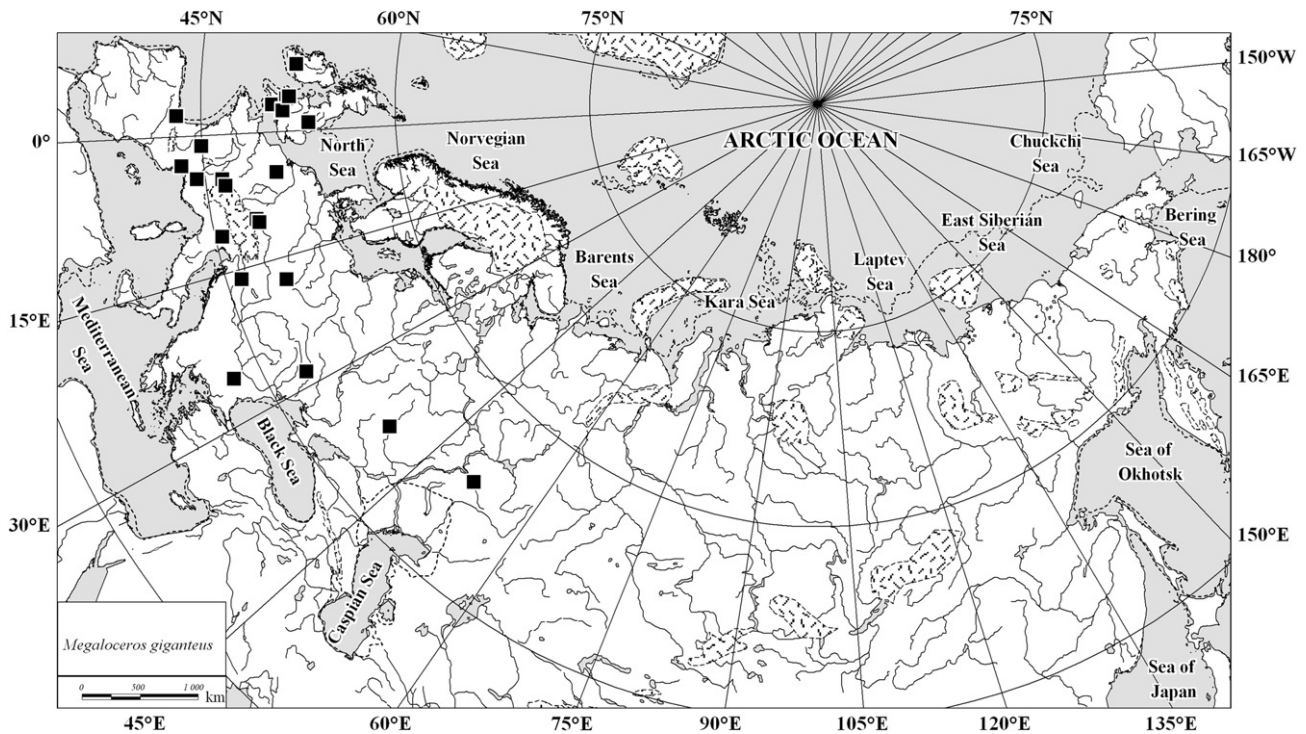


Fig. 10. The giant deer *Megaloceros giganteus* localities (33–24 ka BP).

including mammoth, woolly rhinoceros, primitive bison, red and Siberian roe deer, reindeer, argali sheep, snow leopard and many others.

The Transbaikalian mammal assemblage (IX; 1 locality, Fig. 1, Table 1) does not include mammoth, but woolly rhinoceros inhabited this region. Very typical were primitive bison, Baikalian yak, reindeer, red and Siberian roe deer, antelope (*Spiroceros*

*kiakhtensis*), Mongolian gazelle, wild horse, alpine ibex, Northern lynx, red vole and others.

### 5. Summary

As follows from the above, the distribution and composition of mammal assemblages of Northern Eurasia at the end of MIS 3

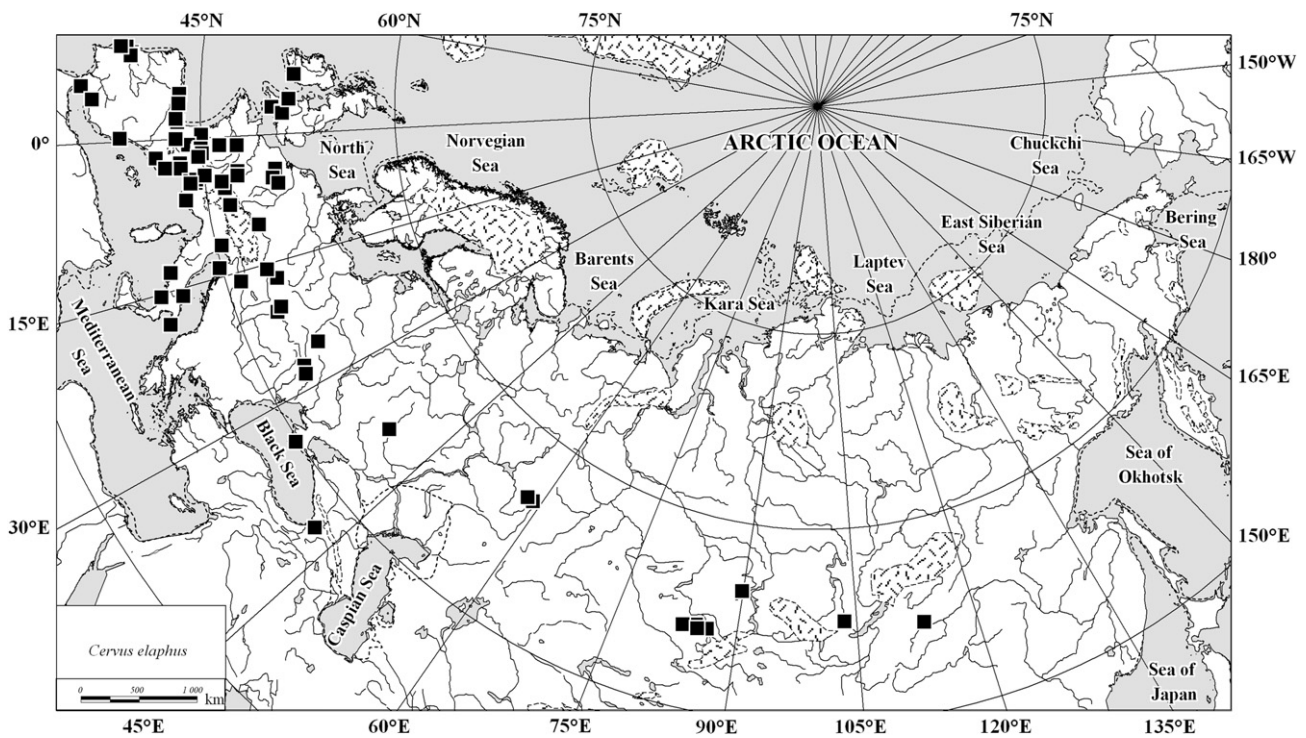


Fig. 11. The red deer *Cervus elaphus* localities (33–24 ka BP).



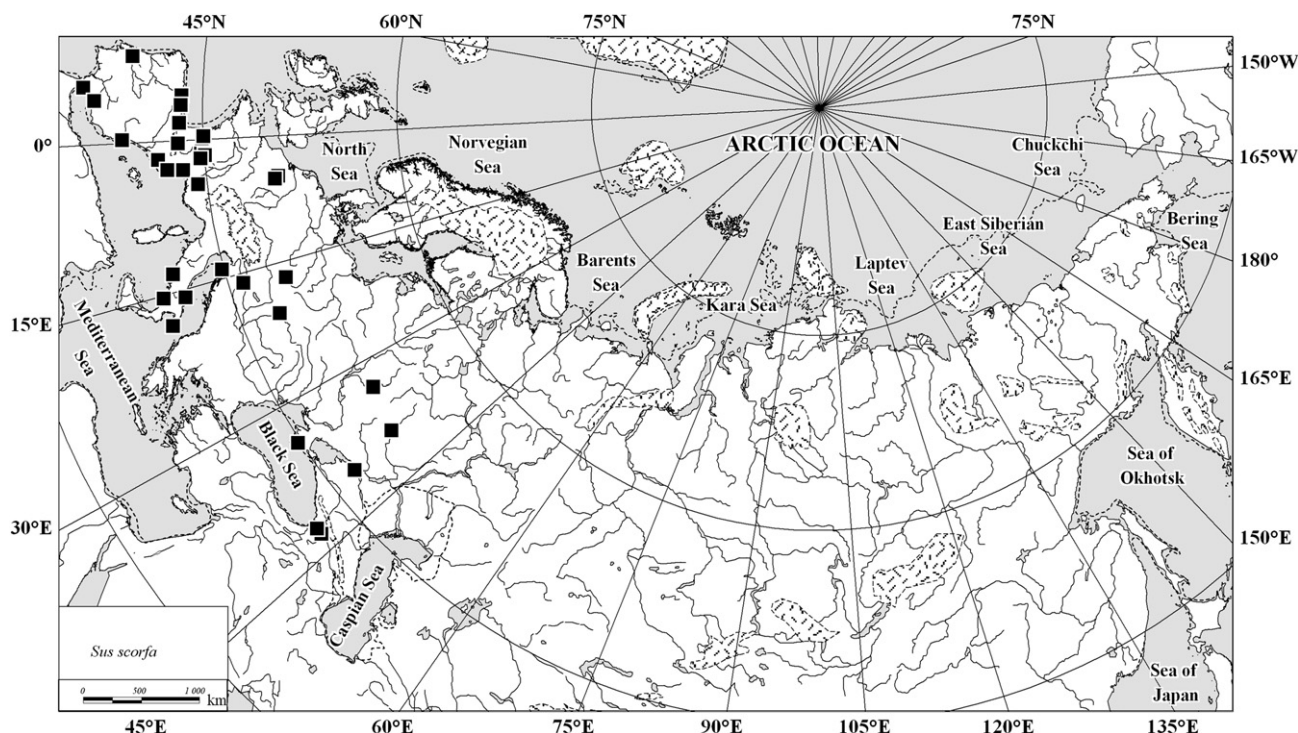


Fig. 12. The wild boar *Sus scrofa* localities (33–24 ka BP).

differed significantly from the modern ones and reflected the colder climate. Wide areas of continent were occupied by the mammals belonging to the mammoth assemblage. Several large herbivores (mammoth, woolly rhinoceros, giant deer, reindeer, wild ox, primitive bison and some others) made up the core of this assemblage. These animals become extinct during the end of the Pleistocene and the Holocene. The steppe mammals were also quite common. They enlarged their ranges to the north and to the west very actively. Forest animals were present in the mammoth assemblage, but in low quantities. Most typical forest mammals were concentrated in the southern part of Northern Eurasia in mountain and hill regions. They were also found in the forested “islands” confined to elevated areas or to river valleys in the northern latitudes. Different mountain regions had specific mammal communities with many endemic forms. Range extensions, contractions and continuations on different scales resulted in mammalian communities, which differed strongly from the modern ones. The presence of the extinct terminal Pleistocene large herbivores (mammoth, woolly rhinoceros, giant deer, bovids) and cave carnivores added to their eccentricity.

The arctic and the boreal types of mammoth assemblages that occupied the northern part of Eurasia were similar to the assemblages of the Early and Late Weichselian–Late Valdai. Therefore, the mammal assemblages of the end of MIS 3 belonged to the type which was characteristic of the glaciations and differed very strongly from the interglacial type. The typical forest communities were practically absent during 33–24 ka BP, which indicates the absence of the continuous forest zone. Most of the mammal assemblages include animals of different ecology. Such a “mixture” was a result of the reorganization of all of the mammal ranges under climatic changes that happened during the first half of the Last Glaciation. Thus, mammal communities during the Last Glaciation maintained a stable structure over a long geological time span. These mammal assemblages were described in many papers based on materials from different parts of the Northern

Hemisphere. They are often referred to as “non-analogous”, “disharmonious” and “mixed” (Graham, 1985; Musil, 1985; Vereshchagin and Baryshnikov, 1985; Semken, 1988; Markova et al., 1995, 2008). The abundant mammalian materials related to the end of MIS 3 indicate that the last interstadial of this stage was rather cool and the mammal assemblages of that age were not unlike the glacial ones.

#### Acknowledgments

This study was supported by grants of Dutch Science Foundation (NWO) No. 47.009.004, No. 047.017.2006.014 and RFBS grant No. 07-05-92312 NWO\_a.

#### References

- Anisiutkin, N.K., Borziyay, I.A., Ketrary, N.A., 1986. Pervobytny chelovek v grotakh Trinka 1–3. (The ancient man in Trinka 1–3 grottos). Shtiintsa, Kishinev (in Russian)
- Arslanov, Kh A., Maksimov, F.E., Laykhin, S.A., Kuznetsov, V.Yu., Chernov, S.B., Ter-tychnaya, T.V., Firsov, A.M., 2007. The using of the advanced variants  $^{14}\text{C}$  and  $^{230}\text{Th}/\text{U}$  methods for substantiation of Late Pleistocene chronology of Western Siberian deposits. In: Lavrushin, Yu.A., Khoreva, I.M., Chistyakova, I.A. (Eds.), *Fundamental'nye problemy kvartera: itogi izucheniya i osnovnye napravleniya dal'neishikh issledovaniy. Materialy Vserossiiskogo soveshchaniya po izucheniu chetvertichnogo perioda*: Moskva, pp. 18–20 (in Russian)
- Baryshnikov, G.F., Markova, A.K., 1992. Main mammal assemblages between 24,000 and 12,000 yr B.P. In: Frenzel, B., Pesci, M., Velichko, A. (Eds.), *Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere (Late Pleistocene–Holocene)*. Gustav Fischer, Budapest/Stuttgart, pp. 127–129 (map on p. 61).
- Baryshnikov, G.F., Markova, A.K., 2002. Animal world (mammal assemblages of Late Valdai). In: Velichko, A. (Ed.), *Dinamika landshaftnykh komponentov i vnutrennikh basseinov Severnoi Evrazii za poslednie 130 tysiach let (Dynamics of Landscapes and Inner Sea Basins of Northern Eurasia during Last 130 ka BP)*. GEOS, Moskva, Chapter 7, pp. 123–137 (maps on pp. 40–47) (in Russian).
- Bolikhovskaya, N.S., 1995. Evolution of loess-soil formation of Northern Eurasia (*Evolutsiya lessovo-pochvennoi formatsii Severnoi Evrazii*). Moscow State University Press, Moscow, 268 pp. (in Russian).
- Chichagova, O.A., Cherkinsky, A.E., 1993. Problems in radiocarbon dating of soils. *Radiocarbon* 35 (3), 351–362.

- Davison, M.L., Jones, L.E., 1983. Special issue: multidimensional scaling and its applications. *Applications of Psychological Measurements* 7, 373–514.
- Dumitrescu, M., Samson, P., Terzea, E., Radulescu, C., Ghica, M., 1963. Pestera "La Adam", statiune pleistocena. *Lucrarile Institutului de Speologie "Emile Racovitză"* 1–2, 229–284.
- Gerasimenko, N., 2007. Environmental changes in the Crimean Mountains during the Last Interglacial - Middle Pleniglacial as recorded by pollen and lithopedology. *Quaternary International* 164–165, 207–220.
- Glushankova, N.I., 2004. In: Kasimov, N.S. (Ed.), *Structure, Dynamics and Evolution of Natural Geosystems. Soil cover evolution during the Pleistocene*, Vol. 1. Gorodets Press, Moscow, pp. 538–560.
- Gubin, S.V., Zanina, O.G., 2006. The fossil soils of Late Pleistocene cryogenic complex (edoma) on the North-East of Russia. *Problemy korreliatsii pleistotsenovykh sobytii na russkom severe* (The Problems of Correlation of the Pleistocene Events on the Russian North). *Tezisy dokladov mezhdunarodnogo soveshania, St.-Petersburg*, 35 (in Russian)
- Graham, R.W., 1985. Diversity and community structure of the late Pleistocene mammal fauna of North America. *Acta Zoologica Fennica* 170, 181–192.
- Granoszewski, W., 2003. Late Pleistocene vegetation history and climatic changes at Horoski Duze, Eastern Poland: a palaeobotanical study. *Acta Paleobotanica. Suppl* 4, 3–95.
- Faustova, M.A., Velichko, A.A., 1992. Dynamics of the last glaciation in Northern Eurasia. *Sveriges Geologiska Undersokning, Ser. Ca* 81, 113–118.
- Fink, J., 1969. Le loess en Autriche. La stratigraphie des loess d'Europeane, 123–141
- Ivanova, I.K., 1980. Geochronology and stratigraphy of Late Pleistocene (by the materials of Middle Dniester basin). *Geokhronologia chetvertichnogo perioda* (Geochronology of Quaternary). *Nauka Press, Moscow* (in Russian) 102–115.
- James, F.C., McCulloch, Ch.E., 1990. Multivariate analysis in ecology and systematic: panacea or Pandora's box? *Annual Review Ecological Systematics* 21, 129–166.
- Kolstrup, E., Wijmstra, T.A., 1977. A palynological investigation of the Moershoofd, Hengelo and Denekamp Interstadials in Netherlands. *Geologische Mijnbouw* 56 (2), 85–102.
- Kozłowski, J.K. (Ed.), 1982. *Excavation in the Bacho Kiro Cave (Bulgaria)*. Final report. PWN, Warszawa.
- Laukhin, S.A., 2007. Palaeovegetation and palaeoclimates during the early interstadial of Zyrian Glaciation in boreal zone of the Western-Siberian Plain. *Vestnik arheologii, antropologii i ethnographii* 8, 188–205 (in Russian).
- Lozan, M.N., 1970. The rodents of Moldavia (Gryzuny Moldavii), Vol. 1. Shtiintza, Kishinev (in Russian)
- Markova, A.K., 1982. *Pleistotsenovye gryzuny Russkoi ravniny (Pleistocene rodents of the Russian Plain)*. *Nauka, Moskva*, 182 pp. (In Russian)
- Markova, A.K., Puzachenko, A.Yu., 2007. In: Elias, S.A. (Ed.), *Vertebrate Records. Encyclopedia of Quaternary Science. Late Pleistocene mammals of Northern Asia and Eastern Europe*, Vol. 4. Elsevier, pp. 3158–3174.
- Markova, A.K., Smirnov, N.G., Kozharinov, A.V., Kazantseva, N.E., Simakova, A.N., Kitaev, L.M., 1995. Late Pleistocene distribution and diversity of mammals in Northern Eurasia (PALEOFAUNA database). *Paleontologia i Evolucio* 28–29, 5–143.
- Markova, A.K., Simakova, A.N., Puzachenko, A.Yu., Kitaev, L.M., 2002a. Environments of the Russian Plain during the Middle Valdai Brianskian Interstade (33,000–24,000 yr B.P.) indicated by fossil mammals and plants. *Quaternary Research* 57, 391–400.
- Markova, A.K., Simakova, A.N., Puzachenko, A.Yu., Kitaev, L.M., 2002b. Reconstruction of natural zonality of Russian Plain during Brianskian Interstadial (33–24 th.yr.ago). *Seria geographicheskaya* 4, 45–57 (in Russian).
- Markova, A.K., Simakova, A.N., Puzachenko, A.Yu., 2002c. Ecosystems of Eastern Europe during the Last Glacial Maximum by floristic and mammalian data. *Doklady Akademii Nauk* 389 (5), 681–685.
- Markova, A.K., Kolfshoten, T.van, Bohncke, S., Kosintsev, P.A., Mol, J., Puzachenko, A.Yu., Simakova, A.N., Smirnov, N.G., Verpoorte, A., Golovachev, I.B., 2008. In: Markova, A.K., van Kolfshoten, T. (Eds.), *Evolution of European Ecosystems during Pleistocene–Holocene Transition (24–8 kyr BP)*. KMK, Moscow, 556 pp. (in Russian).
- Meese, D.A., Gow, A.J., Alley, R.B., Zielinsky, G.A., Grootes, P.M., Ram, M., Taylor, K.C., Mayewski, P.A., Bolzan, J.F., 1997. The Greenland Ice Sheet Project 2 depth-age scale: methods and results. *Journal of Geophysical Research* 102 (26), 411–423.
- Morozova, T.D., 1981. *Razvitiye pochvennogo pokrova Evropy v pozdnem Pleistocene (Late Pleistocene development of soil cover in Europe)*. *Nauka, Moskva*, 282 pp. (in Russian).
- Musil, R., 1985. In: Cejka, J. (Ed.), *Acta Musei Nationalis Pragae. Paleobiography of terrestrial communities in Europe during the Last Glacial*. *Sbornik Narodniho Muzea v Praze*, Vol. XLI, 1/2, 83 pp.
- Nadachowski, A., 1984. Morphometric variability of dentition of the Late Palistocene voles (Arvicolidae, Rodentia) from Bacho Kiro Cave (Bulgaria). *Acta Zoologica Cracovensis* 27 (9), 149–176.
- Popov, V.V., 1986. Early Pleistocene Rodentia (Mammalia) from the "Temnata Dupka" Cave near Karkulovo (North Bulgaria). *Acta Zoologica Bulgarica* 30, 3–14.
- Porter, S., 1983. *Late Quaternary Environments of the United States*, Vol. 1. University of Minnesota Press, Minneapolis.
- Pospelova, G.A., 2007. The global fluctuations of palaeoclimate and the characteristic changes of the main magnetic field during the Neopleistocene. *Bulleten ispytatelei prirody. Otdelenie geologicheskoe* 82 (4), 3–11 (in Russian).
- Rousseau, D.-D., Gerasimenko, N., Maviischina, Zh, Kukla, G., 2001. Late Pleistocene Environments of the Central Ukraine. *Quaternary International* 56, 349–356.
- Saks, V.N., Antonova, K.V., 1945. *The Quaternary deposits and geomorphology of Ust'-Enisei* port. Leningrad, 117 pp. (in Russian)
- Semken Jr., H.A., 1988. In: Laub, R.S., Miller, N.G., Steadman, D.W. (Eds.), *Late Pleistocene and Early Holocene Paleoecology and Archeology of the Eastern Great Lakes Region. Environmental interpretations of the "disharmonious" Late Wisconsinian biome of South-eastern North America*, 33. *Bulletin of Buffalo Society of Natural Sciences*, pp. 185–194.
- Shepard, B.N., 1962. The analysis of proximities: multidimensional scaling with unknown distance function. *Psychometrika* 27, 125–140.
- Sneath, P.H.A., Sokal, R.R., 1973. *Numerical Taxonomy*. W.H. Freeman and Co., San Francisco.
- Sycheva, S.A., Gunova, V.S., Simakova, A.N., 2007. Two variants of structure of Late Pleistocene cover thickness of periglacial region of the Russian Plain. In: Lavrushin, Yu.A., Khoreva, I.M., Chistyakova, I.A. (Eds.), *Fundamental'nye problemy kvartera: itogi izucheniya i osnovnye napravleniya dal'neishikh issledovaniy. Materialy V srossiiskogo soveshchaniya po izucheniu chetvertichnogo perioda: Moskva*, pp. 404–407 (in Russian).
- Van Andel, T.H., 2003. *Glacial Environments I: the Weichselian Climate in Europe between the End of OIS-5 Interglacial and the Last Glacial Maximum*. In: Van Andel, T.H., Davies, W. (Eds.), *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*. McDonald Institute monographs, Cambridge, pp. 9–19.
- VanAndel, T.H., Davies, W. (Eds.), 2003. *Neanderthals and Modern Humans in the European Landscape during the Last Glaciation*. McDonald Institute monographs, Cambridge.
- Velichko, A.A., Morozova, T.D., 1982. Soil cover during the Brianskian Interval. Map 8. In: Gerasimov, I.P., Velichko, A. (Eds.), *Paleogeography of Europe during Last 100,000 yr. (atlas-monography)*. *Nauka, Moskva*, pp. 81–91 (in Russian).
- Velichko, A.A., Morozova, T.D., 2002. Soil cover. In: Velichko, A.A. (Ed.), *Dinamika landshaftnykh komponentov i vnutrennikh basseinov Severnoi Evrazii za poslednie 130 tysiach let (Dynamics of Landscapes and Inner Sea Basins of Northern Eurasia during Last 130 ka BP)*. GEOS, Moskva, Chapter 6, pp. 105–117 (in Russian).
- Vereshchagin, N.K., Baryshnikov, G.F., 1985. Mammal extinction in the Quaternary of Northern Eurasia. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR (The proceedings of the Zoological Institute of Academy of Sciences of Soviet Union)* 131, 3–38.
- Volkova, V.S., 2001. Palaeogeography of Karginian Interglacial (Interstadial) in the Western Siberia 50(55)–23 ka BP. *Bulleten Komissii po Izucheniu chetvertichnogo perioda* 64, 89–93.
- Vorob'eva, G.A., Zykina, V.S., 2002. Reconstruction of the soil cover of Siberia (South of West Siberia and Central Siberia). In: Velichko, A.A. (Ed.), *Dinamika landshaftnykh komponentov i vnutrennikh basseinov Severnoi Evrazii za poslednie 130 tysiach let (Dynamics of Landscapes and Inner Sea Basins of Northern Eurasia during Last 130 ka BP)*. GEOS, Moskva, pp. 114–117 (map 9B on p. 33) (in Russian).
- Whittington, G., Hall, A.M., 2002. The Tolsta Interstadial, Scotland: correlation with D-O cycles GI-8 to GI-5? *Quaternary Science Reviews* 21 (8–9), 901–915.
- Zykina, V.S., 2006. *The loess-paleosol sequences structure and evolution of pedological genesis in Pleistocene of Western Siberia*. Aftoreferat of doctor of sciences thesis. Novosibirsk, 33 pp. (in Russian).