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Late Pleistocene of Northern Asia

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Late Pleistocene mammals of Northern Asia and Eastern Europe. Vertebrate records

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Introduction

Late Pleistocene vertebrate records are mostly represented by mammalian data, on account of the long history of mammalian studies spanning several centuries. Information about birds (Aves), fish

(Pisces), reptiles (Reptilia), and amphibians (Amphibia) is fragmentary so this article will deal predominantly with Late Pleistocene mammalian evidence.

Late Pleistocene vertebrate localities occur within several different types of deposits, for example, fluvial, lacustrine, fossil soil horizons, cave deposits, and cultural layers in the Paleolithic sites (Figs. 1 and 2). Part of the bones may have been deposited as a result of the catastrophic death of animals during periods of flooding or drought (mammoth, large herbivores), whereas other remains may be the result of carnivore hunting activity. Still other remains may be present through the activities of Paleolithic humans. Special technical approaches such as screening and washing in sieves help to separate the bones of small animals and prepare them for analysis.

The age of the localities has been established primarily by a combination of geological and paleontological (palynological, carpological, and malacological) methods, as well as by absolute dates, including radiocarbon (^{14}C), radiometric (U-Th), optically stimulated luminescence (OSL), and electron spin resonance (ESR) methods. Paleomagnetic data may also help to distinguish the age of localities in some cases.

The Late Pleistocene in this region includes the following very different climatic intervals: Mikulino (=Kazantsevo, =Eemian) Interglacial (130-117 kyr BP) (Marine Isotope Stage (MIS) 5e), early Valdai (=early Zyryan, =early Weichselian) Glaciation (117-64 kyr BP) (MIS 5 d-a, MIS 4), middle Valdai (=Karga, =middle Weichselian) Glaciation (MIS 3) (64-25 kyr BP), late Valdai (=Sartan, =late Weichselian) Glaciation (MIS 2) (25-10 kyr BP) (Van Andel and Tzedakis, 1996; Velichko et al, 2002).



Figure 1 Mammal locality in cultural layer of Mezherich late Paleolithic site (Ukraine, Dniepr River drainage basin). The remnants of the hut, built from mammoth bones. Photo by A. K. Markova.



Figure 2 Mammal locality in the lacustrine-fluvial deposits in Eltigen site, dated as Mikulino Interglacial (Northern Black Sea coast, Eastern Crimea). Photo by A. K. Markova.

Mikulino (=Kazantsevo, =Eemian) Interglacial

The majority of Mikulino (= Kasantsevo, = Eemian) mammal faunas described here are known from Eastern Europe. Only a limited number of sites have been found in Northern Asia, mostly in the mountain regions of south Siberia. The characteristics of the Mikulino fauna have been inferred primarily from small mammal assemblages as only a few localities have yielded remains of large mammals (Vereshchagin, 1951; Alexeeva, 1980; Patou-Mathis, 2005; Markova, 2000, 2005; Baryshnikov and Markova, 2002).

During this period, a large number of forest mammals inhabited the zone between 60 and 52° N in Eastern Europe, including the red squirrel (*Sciurus vulgaris*), beaver (*Castor fiber*), forest lemming (*Myopus* sp.), wood mouse (*Apodemus* sp.), and pine vole (*Microtus (Terricola) subterraneus*). This assemblage indicates the presence of a mixed and broad-leaf forest community (III) (Fig. 3).

The distribution area of the so-called forest-steppe mammal assemblage (IV) was situated further south, between 52° N and 45° N. The steppe species (corsac fox (*Vulpes corsac*), woolly rhinoceros (*Coelodonta antiquitatis*), primitive bison (*Bison priscus*), steppe pika (*Ochotona pusilla*), ground squirrel (*Spermophilus* sp.), bobac marmot (*Marmota bobac*), northern mole-vole (*Ellobius talpinus*), steppe and yellow lemmings (*Lagurus* and *Eolagurus* spp.), narrow skulled vole (*Microtus (Stenocranius) gregalis*), and others) were found together with forest-adapted mammals (straight-tusked elephant (*Palaeoloxodon antiquus*), common [bank] vole (*Clethrionomys glareolus*), short-tailed field vole (*Microtus agrestis*) and others). The woolly mammoth (*Mammuthus primigenius*), lion (*Panthera (Leo) spelaea*), and spotted hyena

(*Crocota crocuta spelaea*) (early type) were also present in some regions.

A Steppe mammal assemblage (V) existed in the Northern Black Sea region and in steppic areas of the Crimean Peninsula. The species present include red fox (*Vulpes vulpes* and corsac fox), wild horse (*Equus* sp.), wild ass (*Equus hydruntinus*), (woolly rhinoceros), saiga antelope (*Saiga tatarica*), Bovidae (*Bos/Bison*), bicolored white-toothed shrew (*Crociodura leucodon*), steppe pika, ground squirrel, Russian mole rat (*Spalax microphthalmus*), southern birch mouse (*Sicista subtilis*), great jerboa (*Allactaga major*), northern mole-vole, grey hamster (*Cricetulus migratorius*), steppe remming, narrow skulled vole and Altayan vole (*Microtus (Microtus) obscurus*) (Fig. 3).

Most of the species mentioned above were distributed in the Crimean Mountains, but they include several forest species, including red deer (*Cervus elaphus*), forest mouse (*Apodemus flavicolis*), forest dormouse (*Dryomys nitedula*), and other species indicative of patches of forest, alternating with open, steppe-like habitats (Kabazi II middle Paleolithic site, Units VI-IV) (Patou-Mathis, 2005;

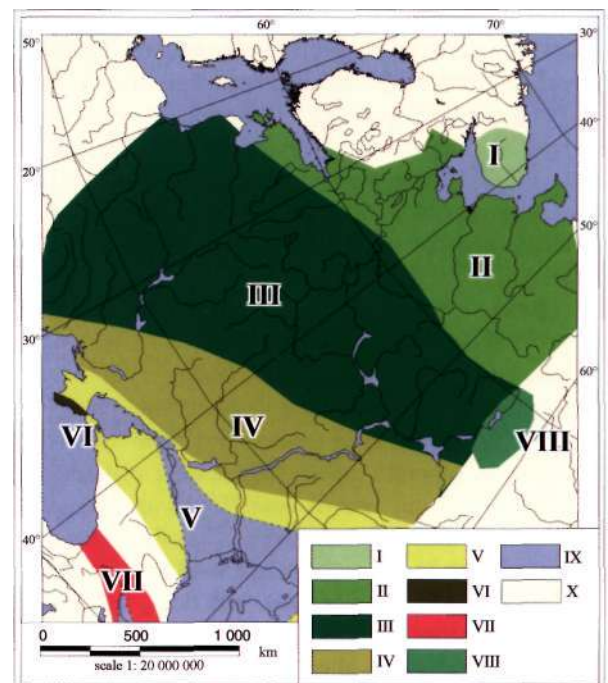


Figure 3 Mammal assemblages of Mikulino Interglacial (135-117kyrBP). I - birch and pine open woodland (after Grichuk (1989)). Mammal data are absent; II - fir/birch woodland with some oak and hornbeam in the south (Modified from Grichuk (1989)). Mammal data are absent. Mammal assemblages: III - assemblage of mixed and broad-leaved woodland, IV - forest-steppe assemblage; V - steppe assemblage; VI - Crimean montane assemblage; VII - Caucasian montane assemblage; VIII - the Urals montane assemblage; IX - water areas; X - data absent.

Markova, 2005). The Crimean montane mammal assemblage (VI) existed here (Fig. 3).

In the Caucasus Mountains, a fauna rich in endemic species existed at this time. Rich faunal assemblages were obtained from the Kudaro, Azykh and Binagady Paleolithic sites (Vereshchagin and Baryshnikov, 1980; Baryshnikov, 1987; Markova, 1982). The specific Caucasian montane assemblage (VII) has been reconstructed on the basis of these faunas. This montane assemblage includes such ancient species as Merck's rhinoceros, Kudaro's cave bear, both small and large porcupines, and the Caucasian mole-vole, that survived in the Caucasian mountain refuge (Baryshnikov and Markova, 2002).

Only one site of Mikulino age (Makhnevskaya cave) was discovered in the Urals (VIII), at ca. 59° N (Baryshnikov, 2001; Kosintsev, 2003) (Fig. 3). The species composition of this fauna includes Tanaitic hare (*Lepus tanaiticus*), small porcupine (*Hystrix vinogradovi*), common wolf (*Canis lupus*), Himalayan bear (*Ursus thibetanus*), lion, wild horse, red deer, elk (*Alces alces*), bison, and woolly mammoth. The presence of porcupine and Himalayan bear bones indicates warm climate.

Several sites of Mikulino = Kazantsevo (= Eemian) age were found in Northern Asia. Unique Paleolithic sites were recovered in the Altai Mountains (Denisova Cave, Ust-Karakol-1). Detailed faunal analysis of these sites suggested the correlation of some of their layers with the Mikulino (= Eemian) Interglacial (Derevianko *et al.*, 2003). These layers include a rich mammalian fauna, including the common shrew (*Sorex araneus*), Siberian mole (*Asioscalops* sp.), long-tailed suslik (*Spermophilus undulatus*), striped hamster (*Cricetulus barabensis*), Eversman's hamster (*Allocricetus eversmanni*), ruddy vole (*Clethrionomys rutilus*), red-backed vole (*C. rufocanus*), flat-headed vole (*Alticola strelzovi*), steppe lemming (*Lagurus lagurus*), narrow-skulled vole, root vole (*Microtus oeconomus*), Siberian zokor (*Myospalax myospalax*), pika, red fox, wolf, brown bear (*Ursus arctos*), small cave bear (*Ursus rossicus*), hyena, woolly mammoth, woolly rhinoceros, Pleistocene ass, wild horse, Siberian roe deer (*Capreolus pygargus*), red deer, Mongolian gazelle (*Procapra gutturosa*), Siberian ibex (*Capra sibirica*), and wild sheep (*Ovis ammon*). This mammalian community indicates the close proximity of forest. Some animals adapted to open landscapes are indicative of steppe-like biotopes. Several species are typical of the Asian province (*Asioscalops*, *Myospalax*, *Alticola*, *Capra sibirica*, and others). The bird fauna includes many Alpine-steppe species. These mosaic landscapes are typical of the mountain region with its many biotopes.

Until now we have lacked sufficient materials of Mikulino = Kazantsevo (= Eemian) age from sites in Northern Asia, and so our paleozoological spatial reconstructions have only been done for Eastern Europe.

Early Valdai = Zyrian (=Early Weichselian) Glaciation

Mammalian faunas of this age have been distinguished mostly on the basis of fossils from Mousterian Paleolithic sites. About 80 sites of this age from Northern Asia and Eastern Europe have yielded mammal assemblages. Because of the difficulties in dating most sites of this interval, we include here a discussion of faunas correlated with MIS 5 a-d, MIS 4, and the first part of MIS 3 (117-35 kyr BP). Seven mammal assemblages with several subcomplexes have been distinguished from this interval. The wide territories of Northern Asia and Eastern Europe have been occupied by the mammoth mammal assemblage, including four sub-assemblages: Arctic (I), European-Siberian boreal (Ha), North Caucasian boreal (Iib), and Altayan (III) (Fig. 4 and Tables 1 and 2) (Baryshnikov and Markova, 2002). The index mammal for all of these sub-assemblages was woolly mammoth (Fig. 5). The mammoth Transbaikalian assemblage (IV) also includes woolly rhinoceros, wild yak, and saiga antelope. Steppe animals (wild horse, saiga, primitive bison, steppe pika, marmot, ground squirrels, steppe and yellow lemmings, and others) dominated the Eurasian steppe assemblage (V). Reindeer and Pleistocene bison were also typical in this area. The desert assemblage included two variants: Caspian desert (Via) and Central Asian (VIb) desert assemblages (Fig. 5 and Table 2). The mountain assemblages contained characteristic faunas, including a number of endemic species. The Crimean mammal assemblage (VII) (Fig. 5 and Table 2) included woolly mammoth, woolly rhinoceros, wild horse, Pleistocene ass, saiga, red, roe and giant deer, mountain sheep and goat, cave bear, cave hyena, steppe and yellow lemmings, and 'obscurus' vole. The Caucasian mammal assemblage (VIII) included wild boar, red deer, roe deer, elk, Caucasian goat, leopard, cave lion, and Prometheus' mouse. Species indicative of warm climate include Kudaro's cave bear, small porcupine, forest dormouse, pine vole, and others. These animals inhabited the southern slopes of the main Caucasus mountain system. Species typical of steppe-like landscapes lived in the Northern Caucasus region, including northern pika, wild sheep, and mountain ground squirrel. Several now-extinct species survived in the Caucasian Mountains, including a species of bear

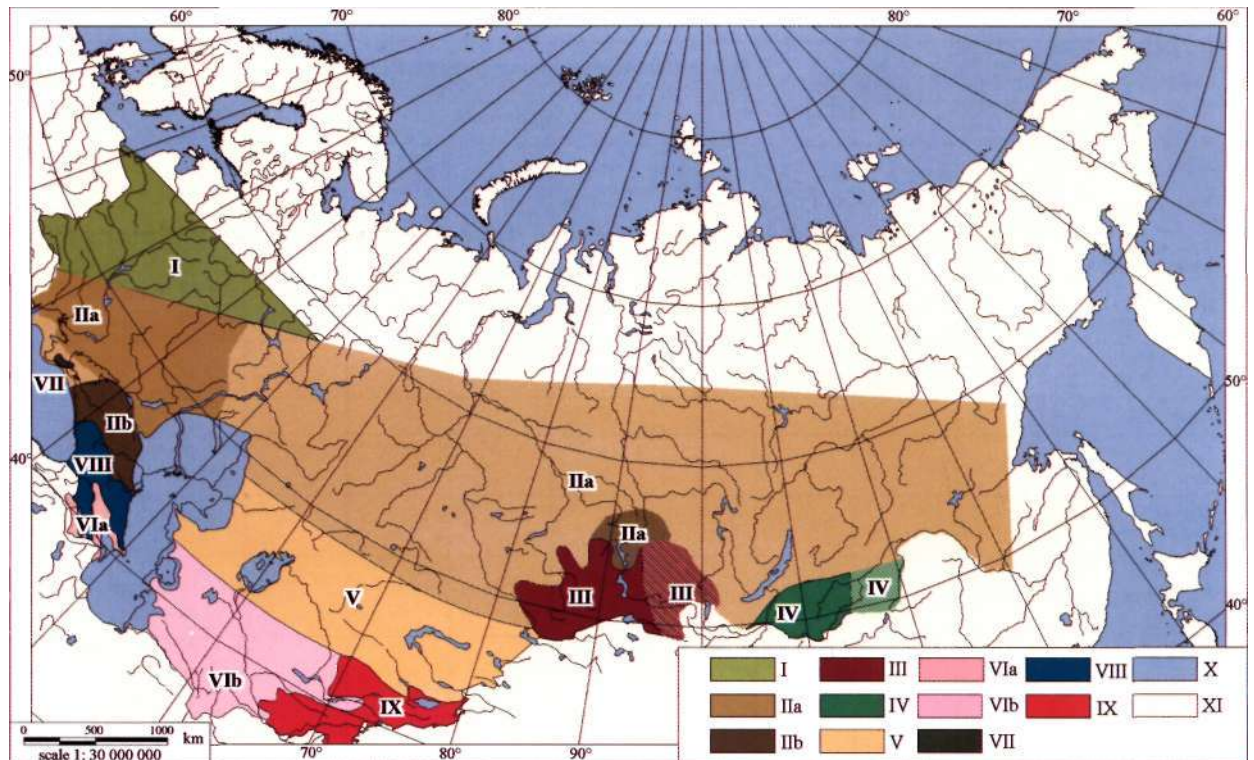


Figure 4 Mammal assemblages during the early and first part of the Valdai glaciation (117-33 kyr BP). I - Mammoth assemblage (Arctic subassemblage); IIa - Mammoth assemblage (European-Siberian boreal subassemblage); IIb - Mammoth assemblage (North Caucasian boreal subassemblage); III - Mammoth Altayan montane assemblage; IV - Mammoth Transbaikalian assemblage; V - Eurasian steppe assemblage; VIa - Caspian desert assemblage; VIb - Central Asian desert assemblage; VII - Crimean montane assemblage; VIII - Caucasian montane assemblage; IX - Central Asian montane assemblage; X - water areas; XI - data absent. Reproduced from Baryshnikov GF and Markova AK (2002) Animal world (mammal assemblages of the Late Valdai). Chapter 7. In: Velichko AA (ed.) *Dynamics of Terrestrial Landscape Components and Inner Marine Basins of Northern Eurasia during the Last 130 000 years*, pp. 123-137. Moscow: GEOS, with permission from GEOS.

that is similar to Deninger's bear, Merck's rhinoceros, and a small porcupine. This indicates that the Caucasian Mountains were a biotic refuge during the Late Pleistocene (**Fig. 5** and **Table 2**) (Baryshnikov and Markova, 2002). The Central Asian mammal assemblage (IX) includes Asiatic wild ass (*Equus hemionus*), red deer, Siberian roe deer, primitive bison, Siberian goat, snow leopard, and large porcupine (**Fig. 5** and **Table 2**).

The Early Valdai mammal fossils indicate the unique structure of mammalian assemblages of this time. Most of the faunal assemblages include species associated with a variety of habitats, **but** they are dominated by tundra and steppe species, now found in different ecosystems. The overlap of their ranges during the Pleistocene produced assemblages of mammal species for which there is no modern analog. Forest animals lived mostly in mountain regions, including endemic species in different mountain systems. The rarity of localities containing forest mammal remains indicates the absence of a continuous forest zone during this

interval. This allowed Arctic animals to range farther south, and steppe mammals to range farther north and west. These nonanalog, 'mixed' faunas reflect the strong influence of the Scandinavian and Ural ice sheets and some Siberian smaller glacial caps over Eastern Europe and northwest Asia, in combination with decreased annual temperatures and precipitation, and a wide distribution periglacial landscapes. These unique mammal assemblages from the last glaciation have been described in many papers (Vereshchagin and Baryshnikov, 1980; Vangengeim, 1977; Smirnov, 1996; Sher, 1971; Markova *et al.*, 1995, and others).

Briansk (= Late Karga, =Denekamp) Interstadial Mammal Assemblages

Abundant mammal fossils have been collected from deposits of the Middle Valdai Briansk Interstadial from localities in Eastern Europe and Northern Asia. These faunas indicate a warm interval situated between glacial intervals. This was the Briansk

Table 1 Mammoth mammal assemblage. Early Valdai = Zyrian (= Weichselian) glaciation

Index mammal species	Sub-assemblages of mammoth assemblage										North Caucasian	Altayan
	Arctic		Boreal									
	Neumas River drainage basin	Desna River drainage basin	Prut and Dniester River basins	Dnieper drainage basin	Don River drainage basin	Volga River drainage basin	Northern Black Sea Coast	Northern Azov Sea				
Lagomorpha												
<i>Ochotona pusilla</i> Pall.		+	+									+
<i>Ochotona alpina</i> Pall.												+
Rodentia												
<i>Eutamias sibiricus</i> Laxm.												+
<i>Marmota bobac</i> Mull.		+	+									
<i>Marmota baibacina</i> Kastsch.												+
<i>Hystrix vinogradovi</i> Arg.								+				
<i>Myospalax myospalax</i> Laxm.								+				
<i>Clethrionomys rufocanus</i> Sundevall.								+				
<i>Lagurus lagurus</i> Pall.		+	+	+	+	+						+
<i>Dicrostonyx guillemi</i> Sanford	+	+	+									
<i>Microtus (Stenocranius) gregalis</i> Pall.	+	+	+	+	+							+
Carnivora												
<i>Alopex lagopus</i> L.		+	+									+
<i>Ursus spelaeus</i> Rosenm.			+					+			+	
<i>Ursus rossicus</i> Boris.												+
<i>Crocota crocuta spelaea</i> Goldf.			+	+	+						+	+
<i>Panthera (Leo) spelaea</i> Goldf.			+	+	+						+	+
Proboscidea												
<i>Mammuthus primigenius</i> Blum.	+	+	+	+	+	+	+	+	+	+	+	+
Perissodactyla												
<i>Equus ferus</i> Bodd.	+	+	+	+	+	+	+	+	+	+	+	+

(Continued)

Table 1 (Continued)

Index mammal species	Sub-assemblages of mammoth assemblage									
	Arctic		Boreal						North Caucasian	Altayan
	Neumas River drainage basin	Desna River drainage basin	Prut and Dniester River basins	Dnieper drainage basin	Don River drainage basin	Volga River drainage basin	Northern Black Sea Coast	Northern Azov Sea		
<i>Equus hydruntinus</i> Regel.			+					+	+	+
<i>Equus hemionus</i> Pall.										+
<i>Coelodonta antiquitatis</i> Blum.	+	+	+	+	+					+
Artiodactyla										
<i>Cervus elaphus</i> L.	+	+	+	+		+			+	+
<i>Megaloceros giganteus</i> Blum.		+	+	+					+	+
<i>Rangifer tarandus</i> L.		+	+	+	+	+				
<i>Poepagus baikalensis</i> N. Vre.										+
<i>Bison priscus</i> Boj.			+	+		+	+	+	+	+
<i>Procapra gutturosa</i> Pall.										+
<i>Saiga tatarica</i> L.			+			+	+		+	+
<i>Capra sibirica</i> Pall.										+
<i>Ovis orientalis</i> Gmel.									+	
<i>Ovis ammon</i> L.										+

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(= Dunaevo, = Dniester) Interstadial, which preceded the late Valdai glaciation. The interstadial was complicated, and included both cool and warm intervals. This is reflected in the wide distribution of the Briansk paleosol. This unit corresponds to the Upper Karga (Karginsky Interstadial) warming in Siberia, and to the Shtilfried B = Denekamp = Grand Bay of Western Europe (Faustova and Velichko, 1992). The Briansk interval is radiocarbon dated between 33 and 24 kyrBP (Chichagova and Cherkinsky, 1993), and is the last in a series of Middle Valdai Interstadials (MIS 3). There are 45 radiocarbon-dated Briansk mammal localities in Eastern Europe, 43 of which are referred to cultural levels of Paleolithic sites. There are also 48 dated faunal assemblage sites from Siberia.

The huge territories of Eastern Europe and Siberia was occupied by the mammals of the Arctic sub-

assemblage of the mammoth mammal assemblage (I) (43 localities) including woolly mammoth, woolly rhinoceros, reindeer, Pleistocene bison, wild horse, rare saiga, arctic fox, cave hyena, cave bear, steppe pika, arctic hare, collared and Siberian lemmings, rare steppe lemming, and the narrow-skulled vole. There were no forest animals found here (Fig. 6). South of this zone, the boreal type of mammoth assemblage was dominant. It includes two variants: the Eastern Europe (Ha) fauna included woolly 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, and narrow-skulled vole. In Siberia (Iib), this assemblage also included North Siberian vole and Siberian chipmunk. The presence of forest animals of this sub-assemblage indicates more moderate

Table 2 Early Valdai (early Weichselian) montane assemblages

<i>Index species</i>	Crimean montane Assemblage (Adzhi-Koba, Kiik-Koba, Kabazi II & V, Starosele, Chokurcha 1, and others)	Caucasian montane assemblages		Central Asian montane assemblage
		The Main Caucasus montane sub-assemblage (Barakaevskaia, Akhshtyrskaya, Vorontsovskaja, Kudaro 1 & 3, Navalishenskaya, Tsona, Tsutskhvati)	The Tran-Caucasian sub-assemblage (Taglar)	
Lagomorpha				
<i>Ochotona pusilla</i> Pall.	+	+		
<i>Ochotona azerica</i> Gadz.			+	
<i>Ochotona transcaucazica</i> Vekua		+	+	
Rodentia				
<i>Sciurus anomalis</i> Gmel.		+		
<i>Spermophilus muscicus</i> Menetr.		+		
<i>Spermophilus pygmaeus</i> Pall.	+			
<i>Marmota bobac</i> Mull.	+	+		
<i>Marmota caudata</i> Geoffr.				+
<i>Hystrix vinogradovi</i> Argyr.		+		
<i>Hystrix indica</i> Ken.			?	+
<i>Dryomys nitedula</i> Pall.		+		
<i>Apodemys flavicollis</i> Melchior	+	+		
<i>Rattus turkestanicus</i> Satun.				+
<i>Mesocricetus raddei</i> Nehr.		+		
<i>Cricetus cricetus</i> L.	+	+		
<i>Prometheomys schaposhnicovi</i> Satun.		+		
<i>Eolagurus luteus</i> Eversm.	+			
<i>Lagurus lagurus</i> Pall.	+			
<i>Microtus (Terricola) majori</i> Thom.		+		
<i>Microtus (Microtus) obscurus</i> Eversm.	+		+	
<i>Microtus (Pallasianus) oeconomus</i> Pall.	+			
<i>Chionomys gud</i> Satun.		+		
Carnivora				
<i>Vulpes corsac</i> L.	+			+
<i>Alopex lagopus</i> L.	+			
<i>Cuon alpinus</i> Pall.		+		?
<i>Ursus deningeri kudarensis</i> Baryshn.		+	+	

(Continued)

Table 2 (Continued)

Index species	Crimean montane Assemblage (Adzhi-Koba, Kiik-Koba, Kabazi II & V, Starosele, Chokurcha 1, and others)	Caucasian montane assemblages		Central Asian montane assemblage
		The Main Caucasus montane sub-assemblage (Barakaevskaia, Akhshtyrskaya, Vorontsovskaya, Kudaro 1 & 3, Navalishenskaya, Tsona, Tsutskhvatii)	The Trans-Caucasian sub-assemblage (Taglar)	
<i>Ursus spelaeus</i> Rosenm. Et Hein	+			
<i>Panthera (Leo) spelaea</i> Goldt.	+	+	+	
<i>Panthera pardus</i> L.		+		
<i>Uncia uncia</i> Schreb.				+
Proboscidea				
<i>Mammuthus primigenius</i> Blum.	+	+?		
Perissodactyla				
<i>Equus hemionus</i> Pall.				+
<i>Equus hydruntinus</i> Reg.	+	+	+	+
<i>Stephanorhinus kirchbergensis</i> Jager		?	+	
<i>Coelodonta antiquitatis</i> Blum.	+			
Artiodactyla				
<i>Sus scrota</i> L.	+	+	+	+
<i>Cervus elaphus</i> L.	+	+	+	+
<i>Dama dama mesopotamica</i> Brooke			+	
<i>Capreolus capreolus</i> Pall.	+	+	+	
<i>Capreolus pygargus</i> Pall.				+
<i>Alces alces</i> L.		+		
<i>Megaloceros giganteus</i> Blum.	+	+	+?	
<i>Rangifer tarandus</i> L.	+			
<i>Saiga tatarica</i> L.	+			+
<i>Rupicapra rupicapra</i> L.	+	+		
<i>Capra sibirica</i> Pall.				+
<i>Capra caucasica</i> Guld. et Pall.		+		
<i>Capra aegagrus</i> Erxl.			+	
<i>Ovis orientalis</i> Gmel.	?	+	+	+

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conditions and the presence of periglacial forest-steppe habitats (Fig. 6). The steppe variant of the boreal sub-assemblage of the mammoth assemblage occurred to the south (III). Typical steppe mammals

(wild horse, saiga, bobac marmot, steppe pika, and others) were found in association with woolly mammoth, giant deer, reindeer, cave bear, and other Late Pleistocene species.



Figure 5 Woolly mammoth *Mammuthus primigenius*. Painted by Elizaveta Pylenkova. Reproduced with permission from Elizaveta Pylenkova.

Various kinds of mammalian assemblages have been found in the different mountain ranges of Eurasia. The Carpathian and Transcarpathian mammoth mammal assemblage (IV) includes a large number of mammal

species from various ecological groups: steppe, forest, and tundra. This assemblage includes woolly mammoth, woolly rhinoceros, reindeer, red and giant deer, wild horse, saiga, Pleistocene bison, arctic fox, cave hyena, cave bear, short-tailed weasel, yellow-throated marten, steppe pika, bobac marmot, steppe lemming, and narrow-skulled vole. (Fig. 6). The Crimean mammoth montane assemblage (V) includes woolly 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 the 'obscurus' vole (Fig. 6). There was little influence of glacial ice in this region. The Caucasian montane assemblage (VI) was also characterized by montane species (montane goat and sheep), but included forest dwellers (red deer, wild boar, common dormice). This assemblage also included cave lion, cave bear, Pleistocene bison, and ox. The Urals mammoth montane assemblage (VII) includes a large number of species associated with forest, steppe, and tundra habitats. Pleistocene large herbivores, including mammoth, woolly rhinoceros, and giant deer, were also widely

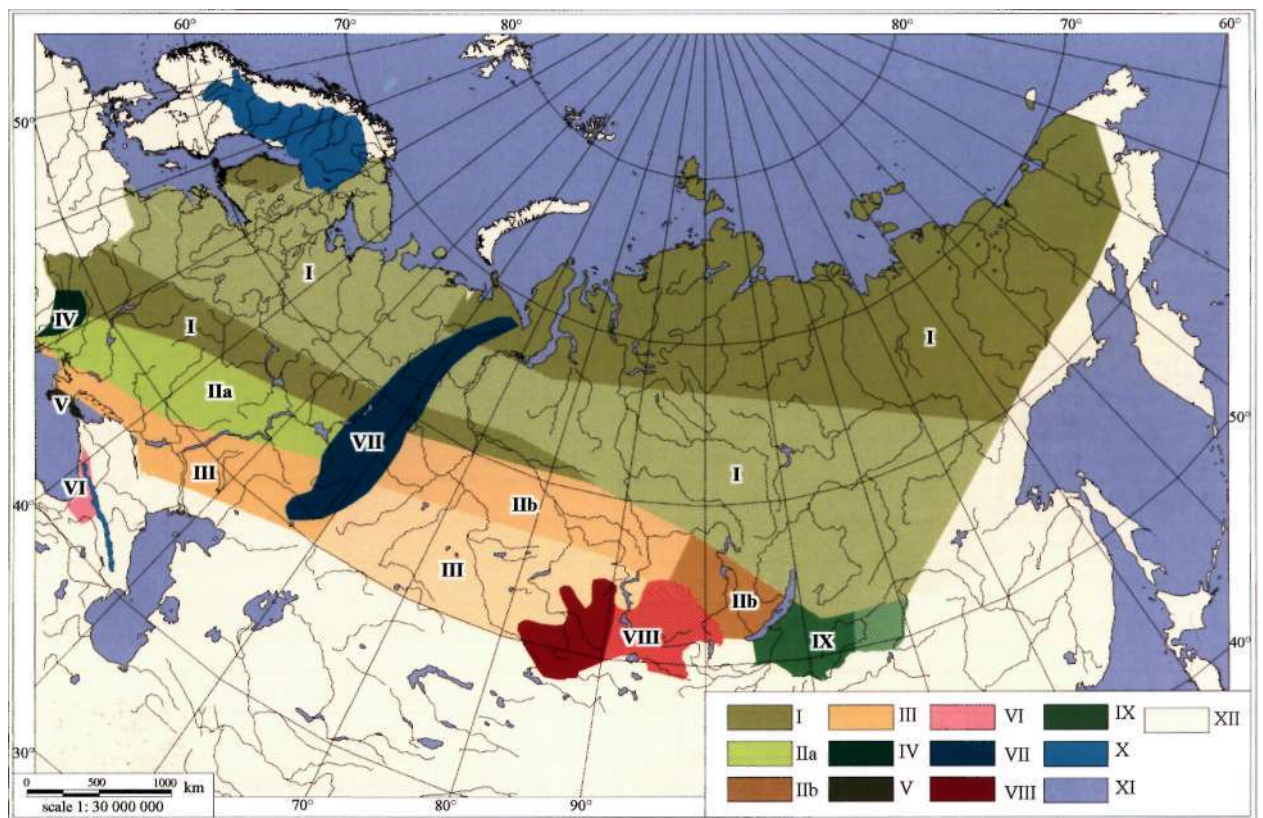


Figure 6 Mammal assemblages during Briansk Interstadial (33-24 kyrBP). I - Mammoth assemblage (Arctic sub-assemblage); Ma - Mammoth assemblage, European boreal sub-assemblage; Iib - Mammoth assemblage, Siberian boreal sub-assemblage; III - Mammoth assemblage, periglacial forest-steppe sub-assemblage; IV - Carpathian montane assemblage (periglacial montane forest steppe); V - Crimean montane assemblage (periglacial montane forest-steppe); VI - Caucasian montane assemblage; VII - Mammoth assemblage, the Urals montane sub-assemblage; VIII - Mammoth Altayan - Sayan montane assemblage; IX - Transbaikalian assemblage. White stripes indicate areas of hypothetical reconstructions. X - oceans; XI - inner seas; XII - unreconstructed areas.

distributed here. The Altayan mammoth montane assemblage (VIII) was characterized by a very high diversity of mammals. More than 50 species have been identified from fossil assemblages in this region. These include mammoth, woolly rhinoceros, Pleistocene bison, red and Siberian roe deer, reindeer, argali sheep, snow leopard, and many others. The Transbaikalian mammal assemblage (IX) does not include mammoth, but it does contain woolly rhinoceros, Pleistocene bison, wild yak, reindeer, red and Siberian roe deer, saiga, wild horse, alpine ibex, northern lynx, and reed vole (Fig. 6). In summary, the distribution and composition of mammal assemblages during the Briansk Interstadial differed significantly from the modern faunas, reflecting the colder climate. Range extensions, contractions, and continuations at different scales resulted in mammalian communities that were quite different from the modern ones. The presence of the extinct terminal Pleistocene large

herbivores (woolly mammoth, woolly rhinoceros, giant deer, bovids) and cave carnivores added to their eccentricity.

Late Valdai Glaciation

Arctic and boreal types of the mammoth assemblage occupied northern Eurasia during the early and late Valdai intervals. The late Valdai (= Sartan, = Late Weichselian) was marked by the most severe climate of the Pleistocene, with extensive ice sheets and periglacial landscapes spread extensively over the middle and high latitudes of the Northern Hemisphere. Analysis of the fossil mammal assemblages associated with the Late Glacial Maximum (LGM) interval have yielded seven distinct types of mammal assemblages with several sub-assemblages. The huge territories of Eurasia were occupied by the different variants of the mammoth mammal assemblage (Fig. 7, Tables 3 and 4). The Arctic

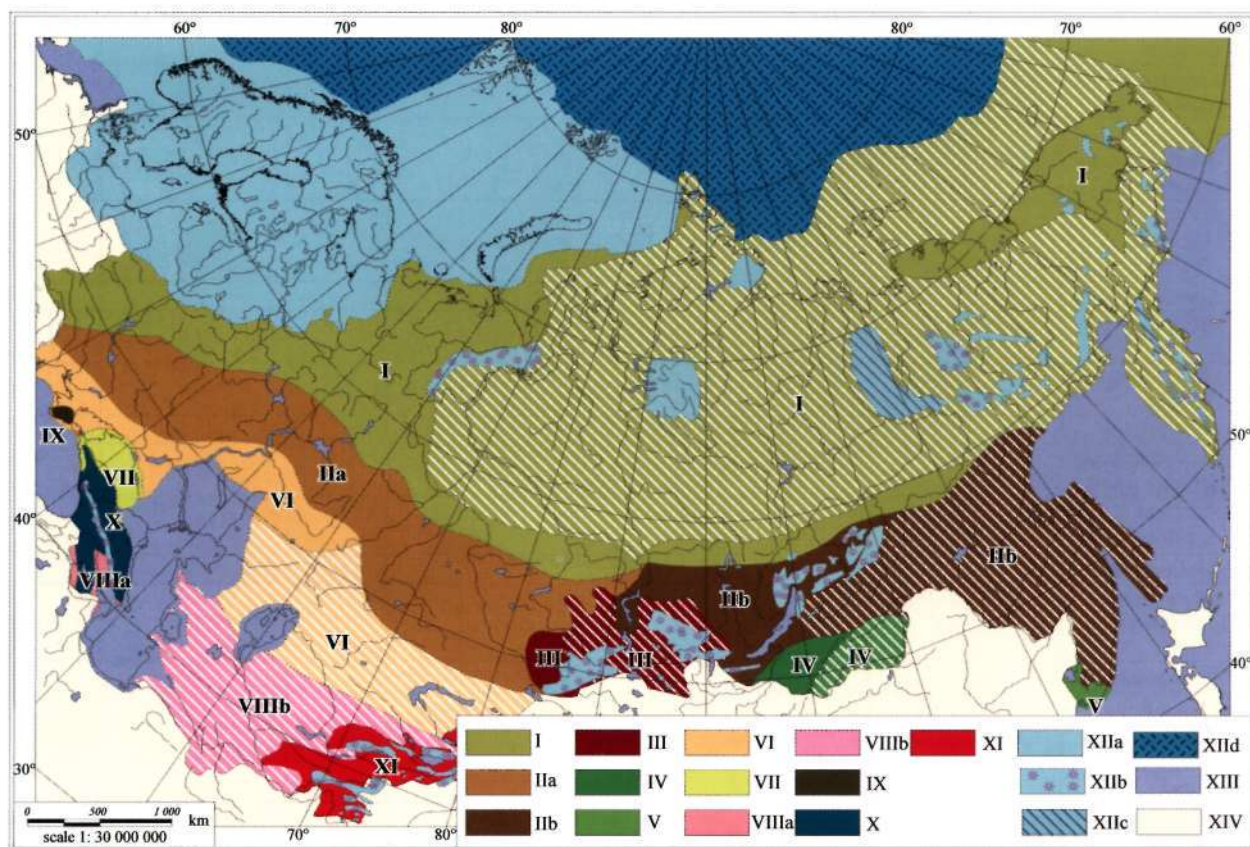


Figure 7 Mammal assemblages during the late Valdai (24-12 kyrBP). I - Mammoth Arctic assemblage; II - Mammoth boreal assemblage (IIa - western variant; IIb eastern variant); III - Mammoth Altayan assemblage; IV - Mammoth Transbaikalian assemblage; V - Far-East forest-steppe assemblage; VI - Euro-Kazakhstan assemblage; VII - North Caucasian assemblage; VIII - Caspian desert assemblage (VIIIa - Transcaucasian; VIIIb - Central Asian); IX - Crimean montane assemblage; X - Caucasian montane assemblage; XI - Central Asian montane assemblage. Other symbols: XIIa - Ice sheets and ice domes, XIIb - Extensive valley glaciers, XIIc - Reticulated glaciers and ice fields, XIIId - Perennial pack ice, XIII - Sea and lake pools, XIV - Mammal assemblages not reconstructed. White stripes indicate areas of hypothetical reconstructions. Reproduced from Baryshnikov GF and Markova AK (2002) Animal world (mammal assemblages of the Late Valdai). Chapter 7. In: Velichko AA (ed.) *Dynamics of Terrestrial Landscape Components and Inner Marine Basins of Northern Eurasia during the Last 130 000 years*, pp. 123-137. Moscow: GEOS, with permission from GEOS.

Table 3 Late Valdai. Mammoth assemblage (Arctic sub-assemblage)

Index species	Eastern Europe						Siberia				
	Belarus	Upper Dniester basin, Volyn-Podolia	Dnieper and Desna basins	Oka and Don basins	Pechora basin	Middle Ural Mountains	Aldan basin	Indigirka basin	Kolyma basin	Chukotka	Anui basin
Lagomorpha											
<i>Lepus tanaiticus</i> Gureev					+	+?		+	+		
<i>Ochotona pusilla</i> Pall			+	+	+						
<i>Ochotona alpina</i> Pall.							+				
Rodentia											
<i>Spermophilus undulatus</i> Pall.							+				
<i>Allactaga major</i> Kerr.	+		+	+							
<i>Lemmus sibiricus</i> Kerr.	+	+	+	+	+		+				
<i>Dicrostonyx guillemi</i> Sanford	+	+	+	+	+	+	+				
<i>Lagurus lagurus</i> Pall.		+	+	+		+					
<i>Microtus (Stenocranius) gregalis</i> Pall.	+	+	+	+	+	+					
<i>Microtus (Microtus) agrestis</i> L.	+										
Carnivora											
<i>Alopex lagopus</i> L.		+	+	+	+	+	+		+		
<i>Ursus spelaeus</i> Rosemn.					+	+					
<i>Gulo gulo</i> L.		+	+		+	+		+			
<i>Crocota crocuta spelaea</i> Goldf.		+	+								
<i>Panthera (Leo) spelaea</i> Goldf			+		+	+		+	+		
Proboscidea											
<i>Mammuthus primigenius</i> Blum	+	+	+	+	+	+	+	+	+	+	+
Perissodactyla											
<i>Equus ferus</i> L.		+	+	+	+	+	+	+	+	+	+
<i>Coelodonta antiquitatis</i> Blum.		+	+	+	+	+	+	+	+	+	+
Artiodactyla											
<i>Rangifer tarandus</i> L.		+	+	+	+	+	+	+	+	+	+
<i>Bison priscus</i> Boj.			+	+	+	+	+	+	+	+	
<i>Saiga tatarica</i> L.					+	+					
<i>Ovibos pallantis</i> H. Smith		+	+		+	+	+	+	+	+	+

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Table 4 Late Valdai. Mammoth mammal assemblage

Index species	Mammoth boreal sub-assemblage							Mammoth Altain assemblage	Mammoth Transbaicalian assemblage
	Eastern Europe			The Southern Urals	West Siberia	Eastern Siberia			
	Prut, Dniester, and Yuzhny Bug drainage basins	Dnieper, Don, Oka basins	Middle Volga drainage basin			Upper Enisei drainage basin	Angara drainage basin		
Lagomorpha									
<i>Lepus tanaiticus</i> Gureev		+							
<i>Ochotona alpina</i> Pall.								+	
Rodentia									
<i>Spermophilus undulatus</i> Pall.									+
<i>Marmota bobac</i> Mull.	+	+		+					
<i>Marmota baibacina</i> Kasitch.								+	
<i>Allactaga major</i> Kerr.		+		+					
<i>Pygerethmus zhitkovi</i> Kuznetsov								+	
<i>Myospalax myospalax</i> Laxm.								+	
<i>Clethrionomys rufocanus</i> Sundervall								+	
<i>Lagurus lagurus</i> Pall.	+	+	+	+				+	
<i>Microtus (Stenocranius) gregalis</i> Pall.									
<i>Lasiopodomys (Lasiopodomys) brandi</i> Radde									+
Carnivora									
<i>Alopex lagopus</i> L.	+	+		+	+	+	+		
<i>Cuon alpinus</i> Pall.				?			+		
<i>Ursus spelaeus</i> Rosenm.			+	+					
<i>Gulo gulo</i> L.		+				+	+		
<i>Crocuta crocuta spelaea</i> Goldf.	+							+	+
<i>Panthera (Leo) spelaea</i> Goldf.		+				+	+		
Proboscidea									
<i>Mammuthus primigenius</i> Blum.	+	+	+	+	+	+	+	+	+
Perrissodactyla									
<i>Equus ferus</i> L.	+	+	+	+	+	+	+	+	+
<i>Equus hemionus</i> Pall.						+	+	+	

(Continued)

Table 4 (Continued)

Index species	Mammoth boreal sub-assemblage							Mammoth Attain assemblage	Mammoth Transbaicalian assemblage
	Eastern Europe			The Southern Urals	West Siberia	Eastern Siberia			
	Prut, Dniester, and Yuzhny Bug drain- age basins	Dnieper, Don, Oka basins	Middle Volga drainage basin			Upper Enisei drainage basin	Angara drainage basin		
<i>Coelodonta antiquitatis</i> Blum.	+	+	+	+			+	+	+
Artiodactyla									
<i>Cervus elaphus</i> L.	+	+	+	+		+	+	+	+
<i>Capreolus capreolus</i> L.	+	+							
<i>Capreolus pygargus</i> Pall.						+		+	+
<i>Alces alces</i> L.	+	+	+	+	+	+	+	+	+
<i>Rangifer tarandus</i> L.	+	+	+	+		+	+		+
<i>Bison priscus</i> Boj.	+	+	+	+	+	+	+	+	+
<i>Poephagus baikalensis</i> N. Ver.								+	
<i>Spiroceros kjakhtensis</i> M. Pavl.								+	+
<i>Saiga tatarica</i> L.	+	+	+	+		+		+	+
<i>Capra sibirica</i> Pall.								+	
<i>Ovis ammon</i> L.					+	+		+	+
<i>Ovis nivicola</i> Eschsch.							+		

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subassemblage (I) occupied all of northern Eurasia (Fig. 7 and Table 3). The index species of this assemblage include woolly mammoth, woolly rhinoceros, reindeer, bison, wild ox, collared and Siberian lemmings (Table 3). This sub-assemblage was rather homogeneous in species composition. Northern pika, long-tailed suslik, and the Kamchatkan marmot lived east of the Urals. All the species of the Arctic sub-assemblage were adapted to severe continental climatic conditions, and to open landscapes with low snow cover in winter time (Vereshchagin and Baryshnikov, 1980). The Boreal sub-assemblage (II) also included a very wide range of territory in Eastern Europe and Northern Asia and included several variants (Fig. 7, Table 4). Besides the woolly mammoth and woolly rhinoceros this sub-assemblage includes horse, saiga, cave lion, and hyena, and also several

forest animals (red and roe deer, elk, and very rarely the wild boar). The tablelands and highlands of Eastern Siberia were home to a specific mammalian community that included several Asiatic animals, such as Asiatic wild ass, Siberian musk deer, and red deer (Table 4). Faunas of the Altai Mountains (III) were characterized by Asian wild ass, wild yak, Siberian ibex, argali, flat-headed vole, and others (Table 4). A different faunal community, with Mongolian marmot, wild yak, Mongolian gazelle, and others, lived in Transbaikalia (rV) (Table 4). The animals of Manchurian fauna (V) were distributed in the Far East. Forest species were also typical of this province (Table 5).

To the south, steppe and desert habitats prevailed during the LGM. Steppe Eurasian mammal assemblages occupied the southern regions of the Russian

Table 5 Late Valdai. The Far East forest-steppe mammal assemblage

Index species	Partizanskaia River drainage basin	
	Geographicheskogo Obshchestva cave, layers 4-5	Tigrovyi grotto
Lagomorpha		
<i>Lepus (Allolagus) mandshuricus</i> Radde	+	
Rodentia		
<i>Myopus</i> sp.	+	+
<i>Microtus (Alexandromys) fortis</i> Buchn.	+	+
Carnivora		
<i>Nyctereutes procyonoides</i> Gray	+	+
<i>Cuon alpinus</i> Pall.	+	
<i>Ursus arctos</i> L.	+	
<i>Gulo gulo</i> L.	+	
<i>Meles meles</i> L.	+	+
<i>Crocuta crocuta spelaea</i> Goldf.	+	
<i>Lynx lynx</i> L.	+	
<i>Panthera (Leo) spelaea</i> Goldf.	+	
<i>Panthera tigris</i> L.	+	
<i>Panthera pardus</i> L.	+	+
Proboscidea		
<i>Mammuthus primigenius</i> Blum.	+	
Perissodactyla		
<i>Equus ferus</i> L.	+	+
<i>Coelodonta antiquitatis</i> Blum.	+	
Artiodactyla		
<i>Sus scrota</i> L.	+	
<i>Moschus moschiferus</i> L.	+	
<i>Capreolus pygargus</i> Pall.	+	+
<i>Cervus elaphus</i> L.	+	+
<i>Cervus nippon</i> Temm.	+	
<i>Alces alces</i> L.	+	
<i>Bison priscus</i> Boj.	+	
<i>Nemorhaedus caudatus</i> Milne-Edw.	+	

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Plain and Kazakhstan. Index species of this community include horse, saiga antelope, Pleistocene bison, corsac fox, ground squirrels, marmot, and hamster (Fig. 7, Table 6). Besides a large amount of steppe species the Euro-Kazakhstanian assemblage (VI) includes also arctic fox and reindeer. Only steppe species lived in

the north Caucasus region (Table 6). In central Asia (Villa), semi-desert and desert animals were dominant, including horse, camel, Afgan uriel (*Ovis vignei*), and others). Semi-desert animals inhabited the Transcaucasian region (VIIIb) (Table 6). Mammoth remains have not been found in late Valdai deposits

Table 6 Late Valdai. Steppe, desert and mountain mammal assemblages

Index species	Mammal assemblages								
	Euro-Kazakhstanian steppe assemblage			North Caucasian assemblage	Caspian desert assemblage		Montane assemblages		
	Northern Black Sea coast	Azov Sea coast	Volga River drainage basin		Transcaucasian sub-assemblage	Central Asian sub-ass-semblage	Crimean assem- blage	Caucasian assem- blage	Central Asian assem- blage
Lagomorpha									
<i>Ochotona pusilla</i> Pall.	+						+		
Rodentia									
<i>Sciurus cf. anomalis</i> Guld.									
<i>Marmota bobac</i> Mull.	+		+				+		
<i>Spermophilus superciliosus</i> Kaup.							+		
<i>Spalax microphthalmus</i> Guld.				+					
<i>Spalax</i> sp.			+						
<i>Allactaga major</i> Kerr.							+		
<i>Stylodipus telum</i> Licht.							+		
<i>Apodemys sylvaticus</i> L.							+	+	
<i>Ellobius talpinus</i> Pall.							+		
<i>Ellobius fuscocapillus</i>					+				
<i>Allocricetulus eversmanni</i> Brandt.							+		
<i>Cricetus cricetus</i> L.				+			+	+	
<i>Promethomys schaposhnikovi</i> Satun.								+	
<i>Lagurus lagurus</i> Pall.	+	+	+	+			+		
<i>Eolagurus luteus</i> Eversm.	+	+	+				+		
<i>Chionomys gud</i> Satun.								+	
<i>Microtus (Stenocranius) gregalis</i> Pall.	+	+	+				+		
<i>Microtus (Sumeriomys) socialis</i> Pall.	+	+							
<i>Microtus obscurus</i> Eversm.					+		+		
Carnivora									
<i>Vulpes corsac</i> L.							+		
<i>Alopex lagopus</i> L.							+		

(Continued)

Table 6 (Continued)

Index species	Mammal assemblages								
	Euro-Kazakhstanian steppe assemblage			North Caucasian assemblage	Caspian desert assemblage		Montane assemblages		
	Northern Black Sea coast	Azov Sea coast	Volga River drainage basin		Transcaucasian sub-assemblage	Central Asian sub-assemblage	Crimean assemblage	Caucasian assemblage	Central Asian assemblage
<i>Ursus arctos</i> L.		+						+	
<i>Ursus deningeri kudarensis</i> Baryshn.								+	
<i>Ursus spelaeus</i> Rosemn							+		
<i>Gulo gulo</i> L.									
<i>Crocuta crocuta spelaea</i> Goldf.									
<i>Felis silvestris</i> Schreb.									
Perissodactyla									
<i>Equus ferus</i> L.	+	+		+	+	+	+	+	+
<i>Equus hydruntinus</i> Regal.					+	+	+		
<i>Equus hemionus</i> Pall.						+			
Artiodactyla									
<i>Sus scrofa</i> L.				+	+		+	+	
<i>Camelus</i> sp.							+		
<i>Cervus elaphus</i> L.					+	+		+	
<i>Capreolus capreolus</i> L.				+			+	+	+
<i>Megaloceros giganteus</i> Blum.							+		
<i>Rangifer tarandus</i> L.	+	+					+		
<i>Alces alces</i> L.								+	
<i>Bison priscus</i> Boj	+	+					+	+	
<i>Bison</i> cf. <i>bonasus</i> L.								+	
<i>Bos</i> sp.					+				
<i>Saiga tatarica</i> L.					+	+	+		
<i>Rupicapra rupicapra</i> L.								+	
<i>Capra aegagrus</i> Exl.					+			+	
<i>Capra caucasica</i> Guld. et Pall.								+	
<i>Ovis orientalis</i> Gmel.					+				
<i>Ovis vignei</i> Blyth.						+			

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from the Crimean, Caucasian, and Central Asian Mountains. By this time, this animal it had already shifted its range northward. The fauna of the Crimean Mountains (IX) included European ass, wild boar, red and giant deer, saiga, northern mole-vole, steppe and yellow lemmings. The Caucasian montane mammal assemblage (X) included a large number of mountain and forest species. Remains of reindeer have not been recovered from the Caucasus (Table 6). The Central Asian montane assemblage (XI) includes red deer, Siberian roe deer, primitive bison, corsac fox, and others (Table 6).

Extinctions

The end of the Late Pleistocene is marked by the extensive extinctions of large herbivores and cave carnivores. Large herbivores became extinct under the influence of climatic warming, and also because of human hunting. Climatic warming induced a rapid change in the so-called mammoth steppe, as forested areas expanded into Northern Eurasia, at the expense of steppe-tundra. Many large mammal species did not survive these climatic and environmental changes.

Mammoth became extinct in Eastern Europe by 9.7 kyr BP. However, sensational finds of the late middle Holocene mammoth remains on Wrangel Island show that this species persisted there until after 4 kyr BP. Woolly rhinoceros was extinct in Eastern Europe by 12.3 kyr BP. The latest occurrence of woolly rhinoceros in Northern Asia was reported from the Altai Mountains and dated about 10 kyr BP. The youngest remains of giant deer were recovered in the Urals and dated 6.8 kyr BP. Musk ox probably disappeared from Eastern Europe in the early Holocene; in Eastern Siberia it survived until historic times. The youngest fossils of large cave bear are about 14 kyr BP. Deninger's bear probably became extinct during the Pleistocene-Holocene transition. Cave lion died out at the end of Pleistocene. Cave hyena became extinct during the LGM (Kosintsev, in press; Stuart, 1993; Stuart *et al.*, 2004).

Conclusions

The main characteristics of the Eastern European and Northern Asian mammalian faunas during late Valdai are the following: most of the late Valdai mammal assemblages had a unique structure, and were sharply different from interglacial faunas. The late Valdai species composition includes the animals found in different ecosystems, including the Arctic, steppe, and sometimes semi-desert zones.

Forest animals were rather rare on the Russian and Western Siberian Plains, indicating the absence of continuous forest there. The destruction of the continuous forest zone opened the way for southward migration of cold-adapted animals, and allowed steppe-adapted mammals shift to north and west. The responses of mammals to climatic changes were individualistic. Their dispersal events had different scales and directions. The re-organization of these various animal communities produced new types of nonanalog faunas. These mixed, periglacial-landscape mammal communities, distributed throughout most of Northern Eurasia, inhabited the so-called 'mammoth steppe.' Forest animals survived in southern and western refuges, associated with mountain and highland regions with highly variable local biotopes. The mountain mammal communities were characteristic of more ancient Pleistocene faunas.

See also: **Vertebrate Overview. Vertebrate Records:** Early Pleistocene; Late Pleistocene of Southeast Asia; Late Pleistocene Mummified Mammals.

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