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Late Pleistocene Distribution and Diversity of Mammals in Northern Eurasia (PALEOFAUNA Database)

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INTRODUCTION

In order to study general changes in mammal communities during former geological times, to examine how their spatial dynamics were influenced by global climatic changes, and estimate intervals and rates of species' extinctions, one can do nothing without documenting the available primary data on the sites containing mammal remains. It is of special importance to include all possible data as concerning geographical position of the sites, their dating, and especially their taxa lists. At the present time numerous materials from Pleistocene sites, mainly these dated to the Late Pleistocene time, have been accumulated for the Northern Eurasia territories. This time interval is also described by numerous paleoclimatic data based mainly on pollen records, and in some cases resulting from the climatic models.

Mammals compose one of the most important biotic groups, changes in which during the geological past reveal general trends in environmental changes. Detailed analyses of the recent materials are given in literature (Chernov 1991; Zlotin & Yasny 1992; Shvarts & Pushkaryov 1994; Shvarts et al.,

1995; Curry 1991) which seeks to reveal the relationships between mammals' diversity (primarily, richness in species) and climatic changes.

Knowledge of contemporary mammal distribution and spatial evolution of mammal paleocommunities surely indicates main trends in climatic changes. The Late Pleistocene time surely represents one of the most distinguished by the climatic characteristics Pleistocene stages, showing significant warming during its first part, Mikulino (Kazantsevo) Interglacial, when the annual temperatures were much higher than those of today. On the contrary, the Late Pleistocene second half was the Valdai (Zyryanka and Sartan) Glaciation being the coldest period during the whole Late Pleistocene time. Now the majority of paleogeographical investigations of the Valdai time indicate to the most intricate character of this glacial time. In order to reconstruct the evolutionary changes of the Valdai ice sheet glaciological data were used together with results of the sea sediments' studies on both arctic isles and continental areas. These investigations were held under the protection of IGCP project (Quaternary Glaciation in the Northern Hemisphere). These studies permitted to describe the main features of the

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Valdai ice-sheet dynamics at the territories of the previous USSR, to confine the limits of the deglaciation stages, and to date them up. Thus, it was established that Scandinavian ice-sheet was of the largest dimensions between 24,000 and 17,000 yr B. P. Besides the Scandinavian ice sheet, during the Valdai time there existed the ice caps on the Novaya Zemlya and the Polar Urals, which were mostly developed about 37,000-39,000 yr B. P., and not simultaneous to the maximum spread of the Scandinavian sheet. Limited ice-massifs also covered the Byrrangha Mts., the Putorana Plato, parts of the Severnaya Zemlya and Spitsberghen Islands and the mountains of the Northeast (Faustova & Velichko, 1992; Frenzel 1992; Velichko et al. 1992; Velichko et al. 1993). Coast lines in the Northern Eurasia differed significantly from those in our days, as the world ocean level was much lower (to 100 m) thus creating vast land territories off the sea shelf, dry lands instead of the Bering's sea (so-called Beringia) and the English channel, dried-off Azov Sea, etc. (Flint 1973; Markov & Velichko 1973).

The late Valdai cold period was preceded by a time interval characterised by milder climatic conditions during an interstadial (some authors see this as an interglacial) which was named the Bryansk (Danube) interstadial in Eastern Europe and as the late-Karginy warming period in Siberia (Velichko et al. 1993). This warming period was radiocarbonated to approximately 35,000-24,000 years B. P. (Chichagova 1992; Chichagova & Cherkinsky 1993).

The ice-cover during the early Valdai time was imagined differently enough by various authors. Some proposed that during this time interval the Scandinavian ice sheet was limited to the Baltic Sea lines (Chebotaryova & Makarycheva 1974; Gerasimov & Velichko 1982). Other investigators concluded that it was during the early Valdai time when the Valdai ice sheet shown its maximum spread (Zarrina, Krasnov et al., 1989; Raukas & Serebryanny 1972; Serebryanny 1978 and etc.). The majority of authors, however, embrace the opinion by Velichko et al. (1993) who regard the early Valdai to be an iceless period.

At the present scientists have accumulated considerable data regarding other natural components of the Late Pleistocene in Northern Eurasia such as vegetation, fossil soils, criogenic phenomena, etc. These findings were summarised in several monographs, first of all in special editions, paleogeographical Atlas-monographs (1982, 1992, 1993). Thus the main features of paleoclimates and natural environments of those interesting times were described.

Investigators of the Late Pleistocene faunas in the territories of the previous USSR paid the most attention to species composition (taxa lists), morphological characteristics, and spatial distribution in the communities. These problems were discussed in the publications by V. I. Gromov, I. M. Gromov, I.

G. Pidoplichko, V. A. Topachevsky, K. K. Flerov, N. K. Vereshchaghin, L. I. Alekseeva, L. P. Alexandrova, E. A. Vangengeim, A. K. Agadjanyan, V. S. Zazhigin, L. I. Rekovets, G. F. Baryshnikov, A. V. Borodin, P. A. Kosintsev, P. F. Kalinovsky, V. A. Kochev, A.N. Motuzko, A. G. Maleeva, M. A. Erbaeva, N. A. Ermolova, V. I. Bibikova, V. E. Garutt, A. V. Sher, I. E. Kuz'mina, I. A. Dubrovo, M. N. Lozan, A. I. David, F. Khenzykhenova, authors of the present paper and many others. The Catalogue of Mammals of the USSR (1981) contained the data included mammal faunas from more than 90 sites dated to the Pliocene and Pleistocene.

Some publications are concerned with the problems of the origin of the Late Pleistocene periglacial faunas with regard to the features of their composition and spread over the territories (Pidoplichko 1954; Sher 1971; Vangengeim, 1977; Vereshchaghin & Baryshnikov 1977, 1980; Smirnov et al. 1986; 1990, etc.).

These data were integrated in the form of maps, distinguishing the main late Valdai mammal complexes of Europe, Northern Eurasia, and the whole Northern Hemisphere. These editions are: "Paleogeography of Europe during the last 100,000 years" (Moscow, Nauka 1982. Ed. I. P. Gerasimov; the unit on the mammal fauna was prepared by A. K. Markova); "Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere (Late Pleistocene-Holocene)", Budapest-Stuttgart 1992. Eds.

A. Frenzel, A. A. Velichko, and M. Pechi, the mammal unit was written by G. F. Baryshnikov and A. K. Markova; Atlas "Development of Landscapes and Climate of the Northern Eurasia", V. 2, Moscow, Nauka, in press, ed. A. A. Velichko, unit on mammal faunas prepared by G. F. Baryshnikov, A. K. Markova, and N. K. Vereshchaghin. These publications described the main characteristics of the species composition and distribution of mammal associations dated to the time interval 24,000-12,000 years B. P., i.e. to the period when the late Valdai ice sheet existed.

Yet the publications mentioned represented the data only in too generalised form and for a time interval exceeding 10,000 years, while no attention was paid to geographical features of mammal diversity. Besides that, the form of those publications excluded the possibility to analyse the relationships between mammals and climate and mammals and vegetation.

The main aim of the present publication was to reveal and describe the main factors affecting geography of diversity, species composition, and the distribution of Late Pleistocene mammals in the territories of the former SU, and, primarily, to understand the pattern of dependence of those characteristics upon paleoclimatic factors, by using the capabilities of the geographic information system (GIS). Description of these relationships will provide more valid approaches to derive forecasts for the future, for example, in accordance with the predicted human-

induced warming resulting from the increase in carbon-dioxide in the atmosphere.

Abundance of materials to characterize the Late Pleistocene dated mammal faunas of Northern Eurasia, together with the necessity to analyse those with the help of modern computers worked to arise the need to create a computer database of the Late Pleistocene sites of mammals which should contain all available information, with the data on species composition, dating, bibliography, etc.

Modern computers are able to transform this information into complex maps. The most advanced computer program for map-making is ARC/INFO. We considered it necessary to use this program to do the following:

- 1) to map the sites of isolated mammal species against the different time sections of the Late Pleistocene and reveal patterns of their areas' temporal dynamics;
- 2) to establish geographical distribution characteristics of the Late Pleistocene mammal communities;
- 3) to distinguish temporal and spatial gradations of mammal diversity;
- 4) to reconstruct and map the finds of the most interesting by their ecology plant species and to describe the main characteristics of plant communities directed at understanding relationships with mammal complexes.

One of the most important problems on the biotic changes during the Late Pleistocene is that of the mammal extinctions, their reasons, rates and scopes. In our opinion, analysis of the computer database on Late Pleistocene mammals has the best potential to resolve these questions. This information consists of a vast collection of materials that was compiled with regard to the revealed relationships between vegetational changes and the Late Pleistocene mammal (especially herbivorous) communities' collapse. It takes into account the changes in vegetation and mammals that are results of climatic changes.

Computer databases for fossil mammals are now been created in several countries. The most complete is the series by American paleontologists led by R. Graham and E. Lundelius who developed the database structure for the Late Wisconsin and Holocene sites of mammals younger than 40,000 years B. P. in the U.S.A. This base named FAUNMAP was constructed by means of PARADOX, V.3, 5;4. It includes the detailed information about the taxa lists, geographical and geological characteristics, dating, taphonomy and references. The authors also used the opportunities of the map-making program ARC/INFO to make the data described visible. This effect culminated in a two-volume reference edition including information for about 3,000 sites of mammals dated to the Late Wisconsin and Holocene in the U.S.A. The major part of the data

base, more than 2,500 sites, are Holocene-dated, and the rest of the sites are referred to as Late Wisconsin (FAUNMAP: A Database Documenting Late Quaternary Distributions of Mammal Species of the United States. Faunmap Working Group / Principal Authors R. W. Graham & E. L. Lundelius / Illinois State Museum, Sci. papers, Vol. XXV, no. 1 and 2, 1994).

In Western Europe the preparations to construct a similar database were also started. This work is guided by L. Werdelin and V. Koenigswald (Werdelin & Koenigswald 1994).

Thus we decided it is just the time to start the development of a database to describe the Late Pleistocene mammals' sites of the former SU, with the addition of information about paleoclimate and paleovegetation, and with the intention for its future integration with the developed databases for the U.S.A. and West European sites. The resulting database will cover the major part of the Northern Hemisphere.

The author's participation in this work was follows: Anastasia K. Markova was a initiator of this study as well as the leader of the team. She elaborated the PALEOFAUNA database structure, together with N. G. Smirnov and N. E. Kazantzeva gathered and entered data for Late Pleistocene mammal sites. She also wrote the texts of Introduction and the parts of Chapters 1, 2, 3 and 5, and Summary.

Nikolai G. Smirnov gathered and analysed the Urals and West Siberia materials. His special attention was in elaborating the approaches to the research of the past mammal species' richness. He wrote the parts of Chapters 1, 2 and 4.

Natalia E. Kazantzeva, in addition to the participating in gathering and entering the original materials for the territory of Former Soviet Union, wrote the part of Chapter 2 (about the small mammal distribution in Late Pleistocene) and compiled the major portion of the maps of mammal ranges.

Alexander V. Kozharinov elaborated the principal approaches in analysing the relationships between paleoclimatic parameters and Late Pleistocene mammal species richness. He wrote the parts in Chapters 2, 4 & 5. He also participated in developing (together with A. N. Simakova) the PALEO- FLORA database for Late Pleistocene floristic materials.

Alexandra N. Simakova was gathered and entered in database the palynological materials from the sites corresponding to late Valdai for the territory of Russian Plain. She wrote Chapter 4 (with the participating of A. V. Kozharinov) and the part of Chapter 5, and compiled the floristic maps.

Lev M. Kitaev carried out the digitising of paleoclimatic isolines, the icesheets and permafrost limits and also the boundaries of former and recent mammal and plant ranges. He wrote the part in Chapter 2 and compiled some maps of Late Pleistocene mammal ranges.

Galina V. Bykova translated some of the texts in English.

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Information and advices on mammal localities, their composition, absolute and relative dates, relevant literature were provide by L. D. Sulerzhitzkii (Geological Institute RAS), L. R. Serebryanny, S. A. Laukhin, E. M. Zelikson, M. A. Faustova, E. A. Shvarts, I. I. Spasskaya, E. I. Kurenkova (Institute of Geography RAS), L. V. Grekhova (State Historical Museum) and M. D. Gvozdover and M. V. Alexandrova (Archaeological Institute RAS). We wish to express our thanks to all of them. Dr. Andrei E. Kachalin (Institute of Geography RAS) helped us in digitising maps. Ivan V. Solntzev - El'be participated in entering data.

We also would like to thank very much our American colleagues - Dr. Russel Graham, Mary Ann Graham (Illinois State Museum, Springfield, USA) and Prof. Holmes Semken (Iowa University, Iowa, USA) who helped us by sending all the information concerning FAUNMAP database, as well as unpublished materials. We would also wish to thank Prof. Holmes Semken, Jr. (University of Iowa) and Dr. Terrance Martin (Illinois State Museum) for their careful edition of some parts of the English version of the paper.

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1. MATERIALS AND STRUCTURE OF PALEOFAUNA DATABASE

1.1. Materials from the territory of Former Soviet Union (FSU)

Anastasia K. Markova

The PALEOFAUNA database includes the materials from the mammal localities of the different taphonomical types:

1. the cultural layers of Paleolithic sites (**PL**);
2. alluvial deposits (**FL**);
3. fluvioglacial and glacial deposits (**GL**);
4. loess deposits (**LS**);
5. lake deposits (**LC**);
6. liman deposits (**LI**);
7. fossil soil horizons (**PA**);
8. zoogenetic cave deposits (**CZ**)

The most of the indexes were assumed after the FAUNMAP ones (Graham & Lundelius 1994).

The majority of localities are connected with the cultural layers of Paleolithic sites and with alluvial deposits. Another types of mammal sites are rather rare (Table 1.1).

TABLE 1.1. Taphonomical types of mammal localities used in PALEOFAUNA database

PL	FL	LI	GL	LC	PA	LS	CZ
280	235	2	1	7	2	6	25

The distribution of the mammal localities through the temporal intervals of Late Pleistocene is the following one:

Only two dozens of sites correspond to the Mikulino (Kazantsevo) Interglacial (130,000-100,000 yr B.P.). Most of them are presented by the findings from alluvial and lake-marsh deposits. These localities are distributed on the FSU territory very unevenly (Fig. 1.1). The majority of them are located in southern and central North Eurasia.

More materials (141 mammal sites) correspond to early Valdai (100,000-35,000 yr B.P.). These localities were found throughout all the territory of the former Soviet Union. Most of them are concentrated in Eastern Europe. The main part of mammal localities is related to the cultural layers of Moustierien Paleolithic sites. The Moustierien artefacts are the important dating materials for these findings. The youngest localities have also radiocarbon dates (Fig. 1.2).

The middle Valdai mammal localities (Bryansk = late Karginsky Interstadial) are related to relatively small temporal interval, 35,000-24,000 yr B.P. So only 110 mammal localities correspond to this Interstadial. The most of these findings have the radiocarbon dates. The majority of localities are connected with cultural layers of Late Paleolithic sites; some of them correspond to alluvial deposits. One locality (Arapovichi, Desna drainage basin) was found in the Bryansk fossil soil horizon (Markova 1982) (Fig. 1.3).

The main part of mammal localities (270) included in PALEOFAUNA database refers to late Valdai (24,000-10,000 yr B.P.). These sites are distributed first of all in the Russian Plain, Crimea, Caucasus, the Urals Mts. and southern Siberia.

About 190 mammal sites are related to the Last Glacial Maximum, 24,000-15,000 yr B.P. (Fig. 1.4).

More than 80 localities are dated at the Late Glacial, 15,000-10,000 yr B.P. (Fig. 1.5).

As well as in the middle Valdai the main part of late Valdai localities refers to the cultural layers of Late Paleolithic sites and to alluvial deposits.

The data for the Holocene mammal localities were still not collected systematically. Thus materials from only about 10 Holocene mammal sites are included in PALEOFAUNA database (Fig. 1.6).

All Late Pleistocene mammal sites included in PALEOFAUNA database (Appendix. Table 1) are shown on Figure 1.7.

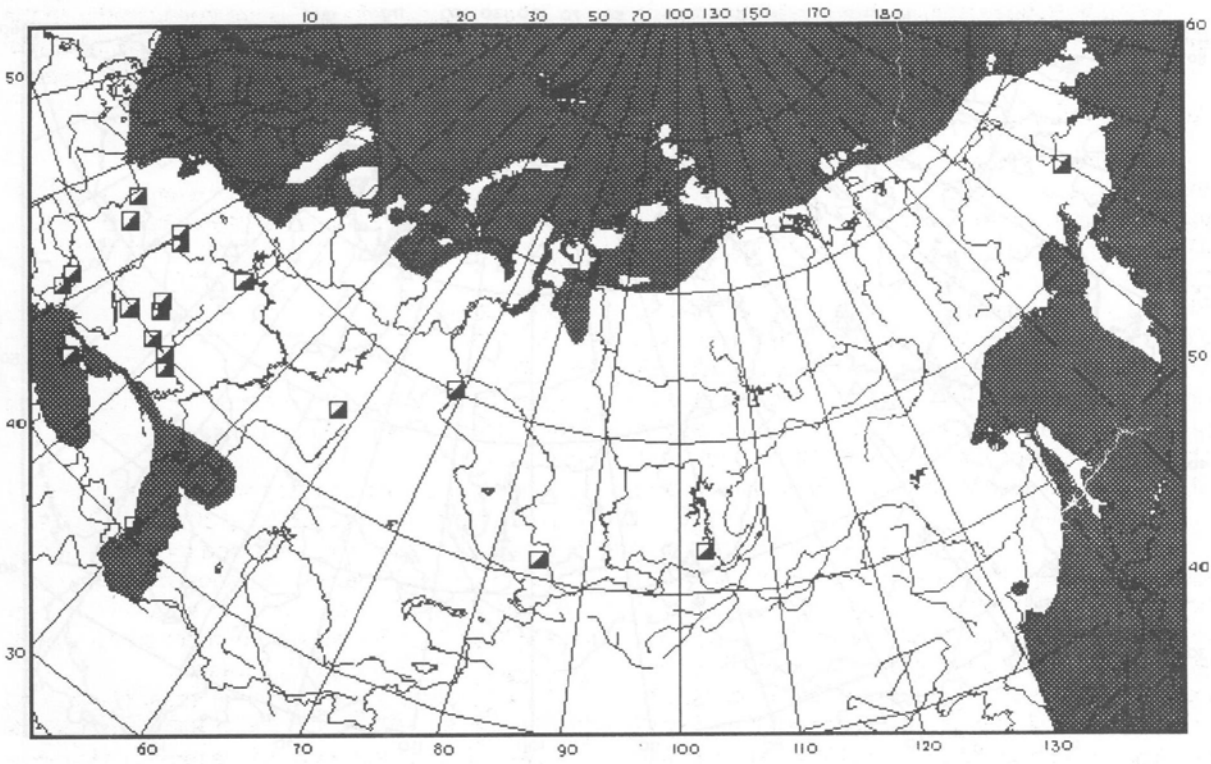


FIG. 1.1. Mammal localities of Mikiino Interglacial (130,000-100,000 yr B.P.)

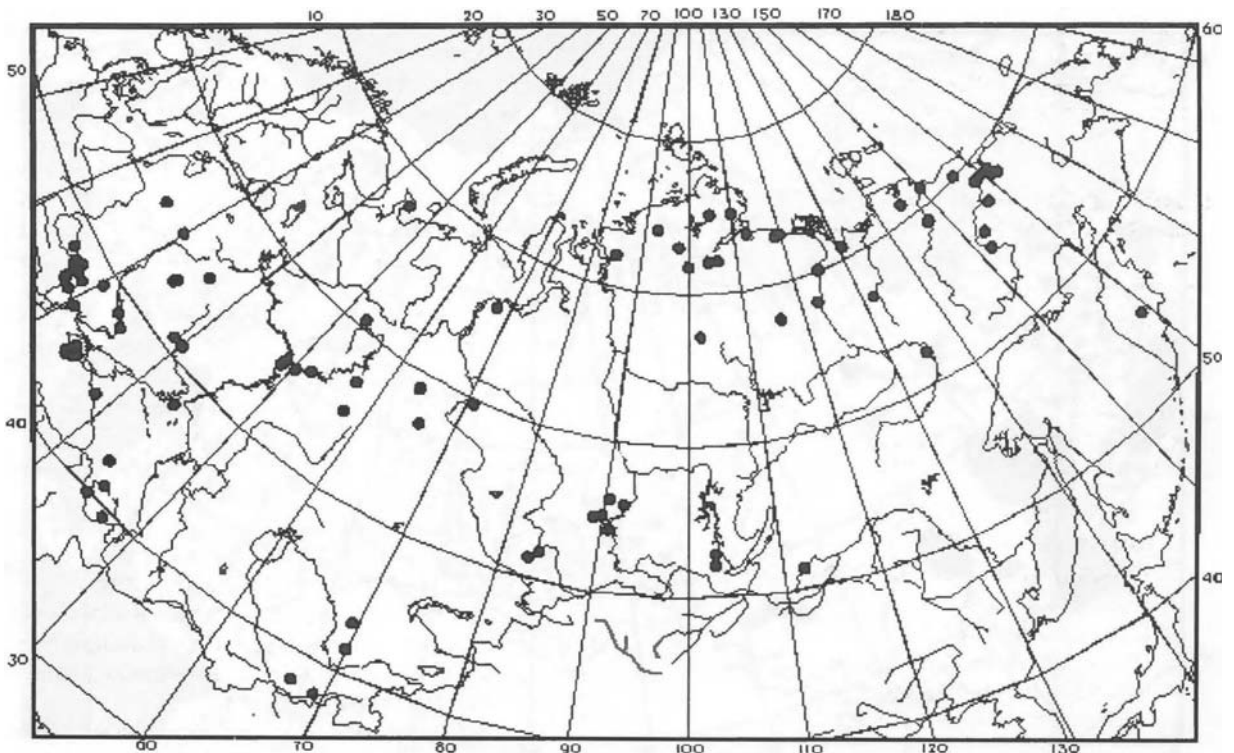


FIG. 1.2. Mammal localities of early Valdai time (100,000-35,000 yr B.P.)

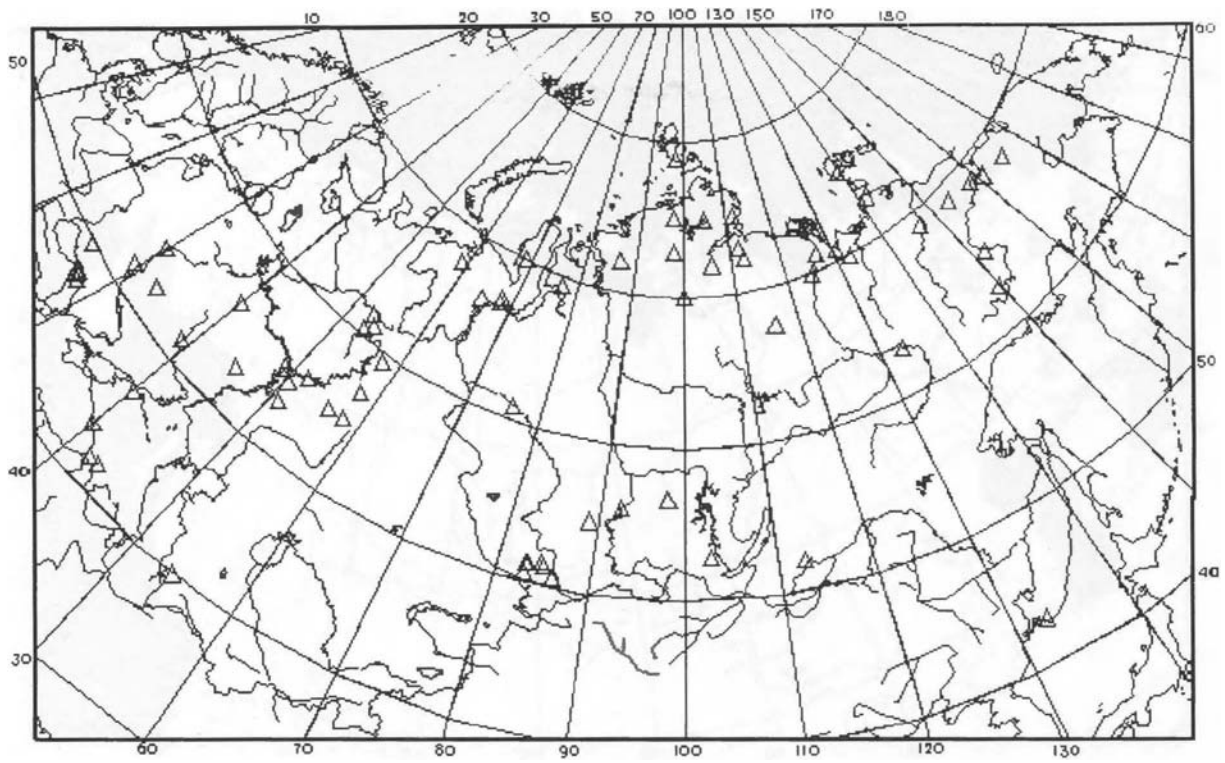


Fig. 1.3. Mammal localities of middle Valdai time (35,000-24,000 yr B.P.)

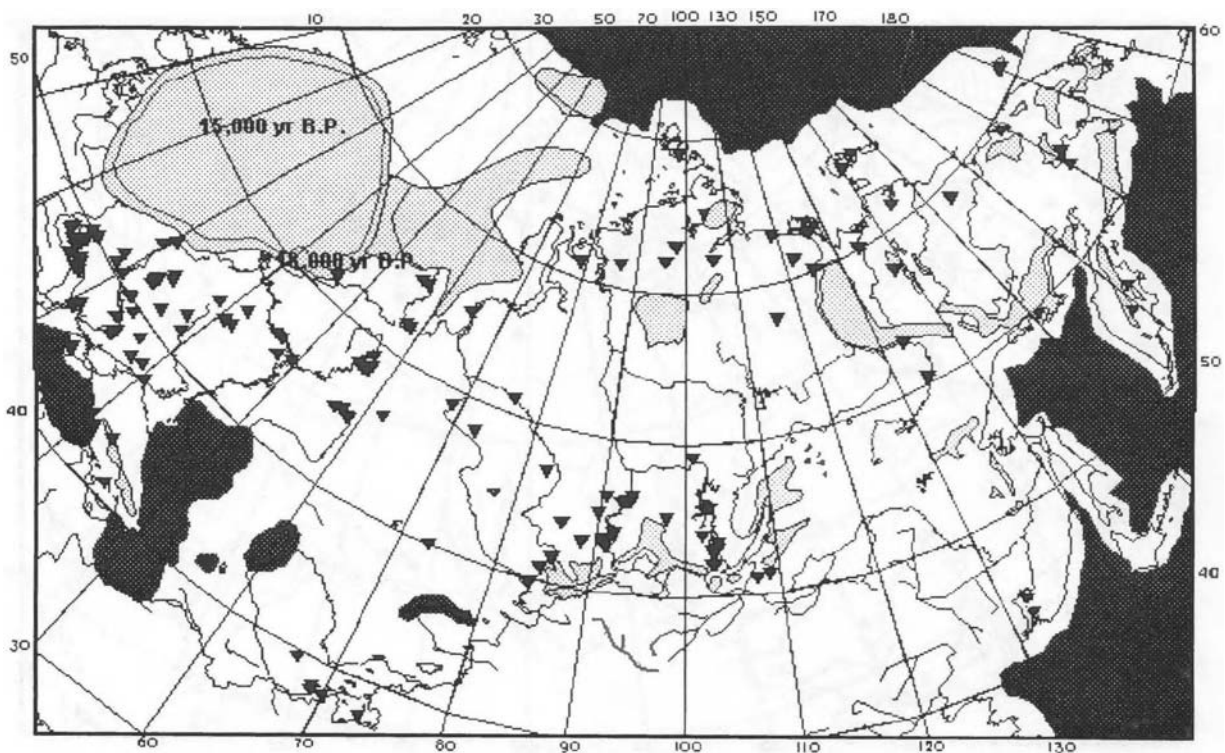


Fig. 1.4. Mammal localities of Glacial Maximum (24,000-15,000 yr B.P.)

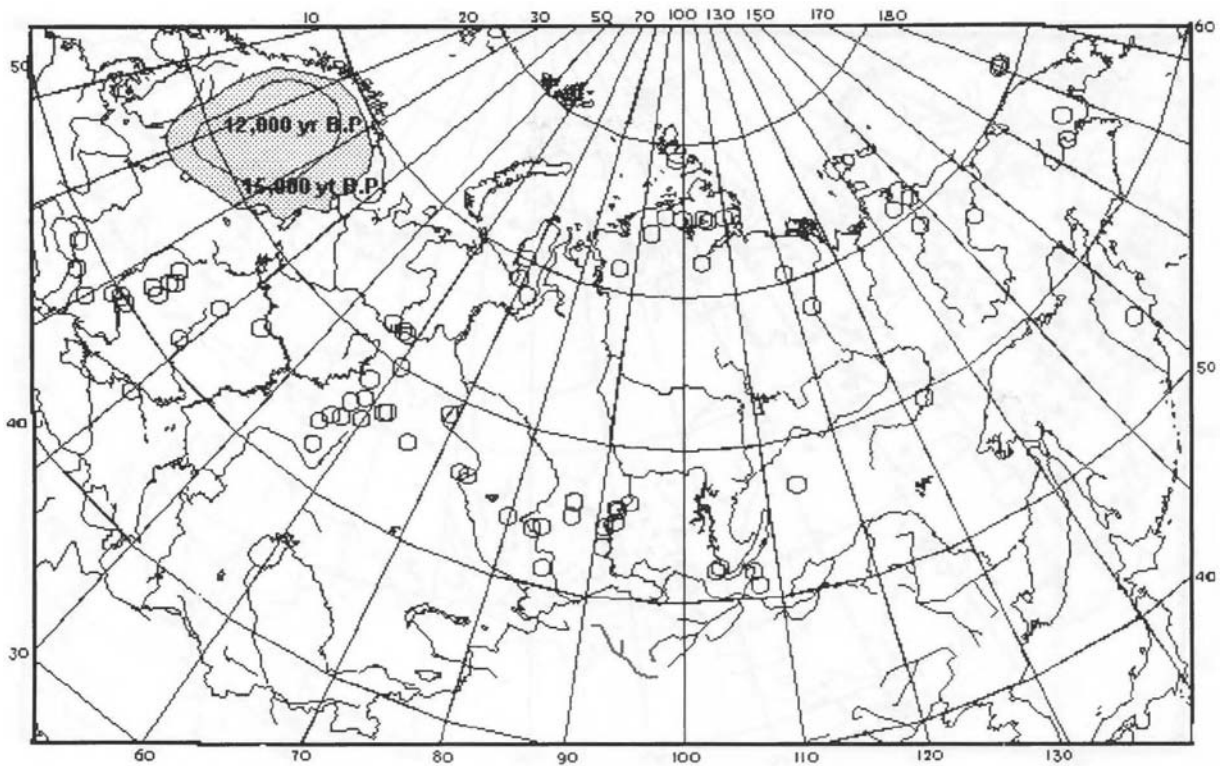


FIG. 1.5. Mammal localities of Late Glacial time (15,000-10,000 yr B.P.)

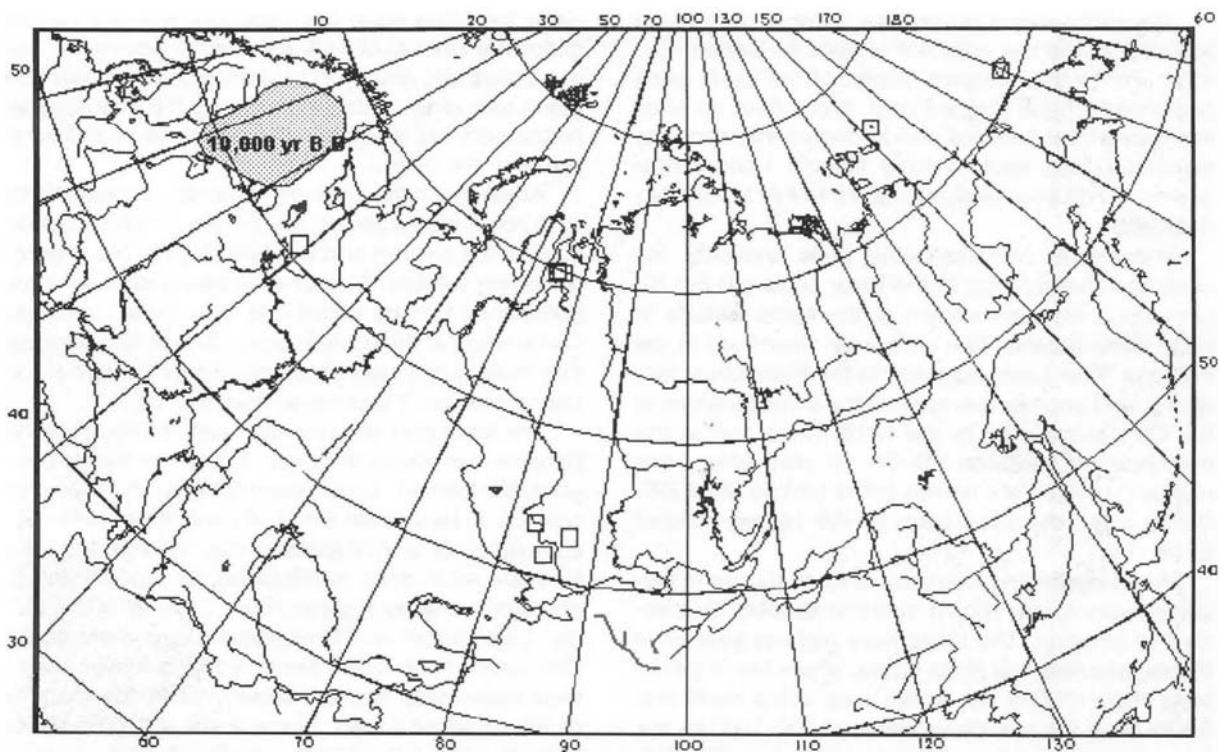


FIG. 1.6. Holocene mammal localities (<10,000 yr B.P.)

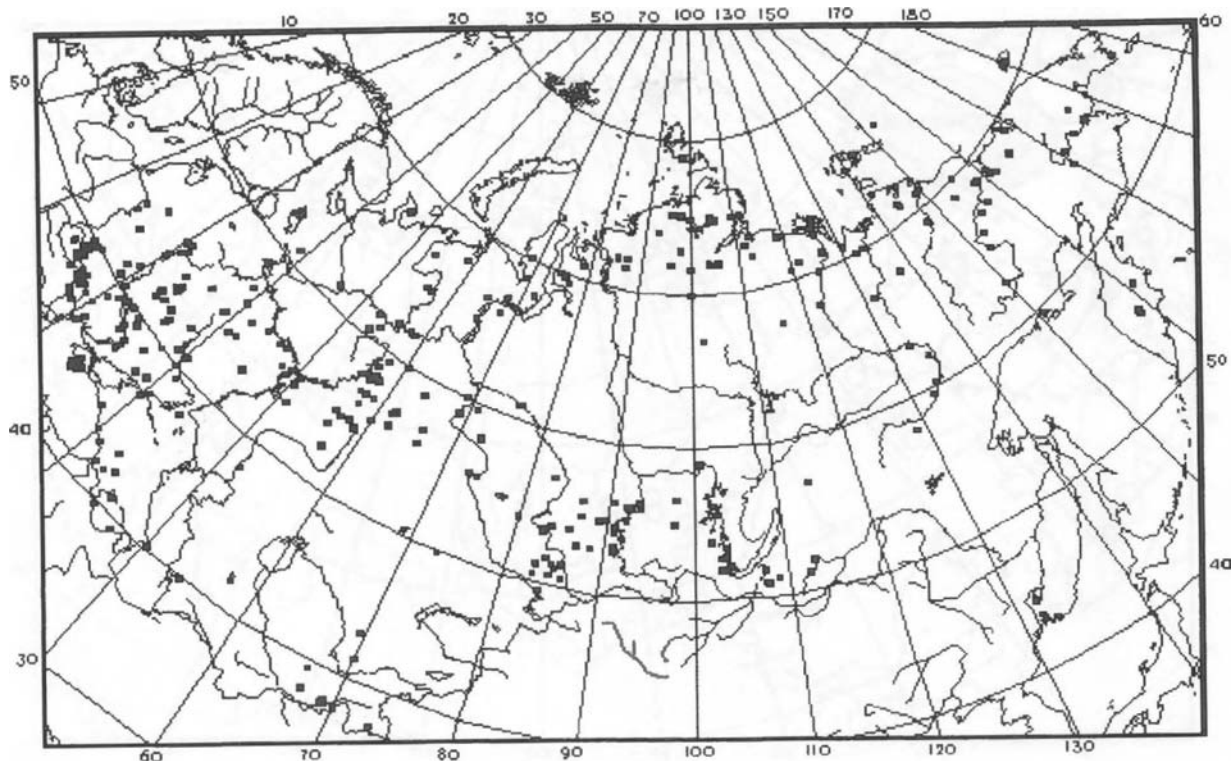


FIG. 1.7. Late Pleistocene and Holocene mammal localities (<130,000 yr B.P.)

1.2. Materials from the Urals localities

Nikolai G. Smirnov

The Urals region covers the territory of the Ural mountains and the adjacent regions of Eastern Europe (Pre-Urals = western slopes of the Urals Mts.) and West Siberia (Trans-Urals). More than 60 sites are known here, besides poorly-documented finds of isolated bones kept in local Natural History museums. So 63 sites were included into PALEOFAUNA database.

Those sites are distributed quite unevenly. No sites have been found in the Polar Urals (66-69° N), whereas 6 sites are known at the same latitude in north West Siberia. Two sites were described in the Pechora River basin adjacent to the Polar Urals (64- 66° N), and another two sites at the same latitudes in the Ob' River basin. In the North Urals and at the neighbouring lowlands (59-64° N) nine sites were marked. 14 sites are known in the Middle Urals (56- 59° N), and in the South Urals (51 -56° N) they number to 18.

When describing locations of fossil faunas in elevated regions, one should take into account their latitudinal position. The Urals have highest summit in the regions near the Polar Circle, where the ridge attains 1500-1700 m above sea level. In the North and South Urals the altitude values are 1000-1500 m, but the ridge is crossed by deep river valleys. In the Middle Urals the highest elevations reach 600-700 m, but

the most area is only slightly higher than the surrounding lowlands; thus, no altitudinal belts are distinguished at present. All the sites of Pleistocene fauna in the Urals have been found within the narrow altitudinal interval of 150-350 metres above the sea level, thus providing no opportunity to discuss the fauna altitudinal distribution during the Pleistocene. All the sites are located in the river valleys, and none just near the ridge.

Additional difficulties with analysis of paleofaunal data come from a certain asymmetry in natural conditions of the eastern and western slopes. The present prevailing western flow of air masses creates more continental climate conditions with lower precipitation amount at the eastern slope. Some data suggest that more aridity was characteristic for eastern slope during the Late Pleistocene time, too.

The most part of fauna sites with numerous bone remains was found in caves. Those are mainly zoogenically-formed bone assemblages in pre-entry cavities. In rare cases a role of ancient people in accumulation of animal remains was marked, too. The sites are most often multilayered, thus permitting to characterise several chronological stages of the Valdai, Late Glacial and Postglacial. Deep parts of the Ural caves have been examined to a lesser extent than those near the entrances. Yet in the majority of the explored caves, those of the labyrinth structure, situated in the Middle and South Urals, numerous congeries of cave bears remains were found.

Many of these sites were not dated with sufficient accuracy; they practically do not contain other species remains, and were not included into PALEOFAUNA database.

The sites with the Mikulino fauna are the most rare, and datings of that time are only preliminary. To our mind, the bottom layers in the rockshelter Bolshoi Glukhoi on the Tchusovaya River show the highest probability for being referred to this chronological stage. Materials from this most interesting site were described only in few publications (Guslitzer & Pavlov 1987; Kuz'mina & Sablin 1991; Smirnov 1993).

Sites referring to the early Valdai (100,000-35,000 yr B.P.), also are not absolutely reliable because they were dated only by stratigraphical evidences. In the South Urals, they include materials from the Ignatievsky and First Serpievsky caves; in the Middle Urals they correspond to several layers from the rockshelters Bobyliok and Bolshoi Glukhoi.

Also due to unreliable datings, we consider the middle Valdai, Bryansk (= late Karginsky) Interstadial (35,000-24,000 yr B.P.), to be poorly represented in the Urals. Sediments of this time should be identified only by absolute dating methods; other approaches are unreliable in the Urals, because doubts exist on the problem whether major climatic events occurred simultaneously in the Russian Plain and the Urals.

Information about the late Valdai, 24,000-10,000 yr B.P., was represented separately for the maximum cold time, late glacial and postglacial periods. The most abundant data belong to 16,000-13,000 yr B.P., i.e., the transition period to postglacial. Numerous bone remains were sampled at list in 8 caves located on the rivers Belaya, Sim, Yuryuzan' in the South Urals, Kapova, Kul'yurtamak, Ignatievsky, 1 and 2 Serpievsky caves, Idrisovsky, Prizhim 2. In the Middle Urals, the most abundant sample collection was found in the Bobyliok rockshelter, Arakaevo 8 cave, two caves of the same name "Dyrovaty Kamen", but located on diverse rivers, the Serga and Tchusovaya; shelters of Bezymyanny, Zotinsky, Bolshoi Glukhoi. In the North Urals, numerous data were obtained from three caves, namely, Medvezh'ya ("Bear"), Studenaya, Shaitansky.

The most interesting materials originate from the "Bear" Cave. For many years, it was used as a basic site for studies of Late Pleistocene sediments in the Urals. Results of those investigations have been published since 1959, but are discussed until now. First of all, it regards the dating of basic strata. In our work, we proceeded from the following: all the strata from the surface down to the layer "A" of brown loam ought to be regarded as Holocene-aged, the horizon "A" of the brown loam stratum was referred to the late glacial time, with the corresponding date of 12,230 yr B.P. (LA-3056), and the horizon "B" of the same brown loam stratum with the radiocarbon age determination 16,130 years, i.e. the most cold late Valdai stage. The datings were published (Guslitzer & Pavlov 1988), but the authors supposed the material to

be older. However, our recent view point is that the dates showed the real age of the sediments. Analysis of bone remains from the whole "brown loam layer", without distinction between the horizons A and B, has shown that integrated sample could not be used to characterise the Late Pleistocene fauna of the North Urals, because faunas of the two horizons differed significantly not only in their age but in the compositions, too. Rodent faunas from the "Bear Cave" from the collections of Institute of Geology, Komi Republic Scientific Centre, were studied by N. G. Smirnov.

Shaitansky cave, situated on the eastern slope of the North Urals, 60° 30' N, offered the unique data to study faunas of the late Valdai and early Holocene periods. It is this site, where the northernmost finds of many species were marked in the Urals, namely, steppe lemmings, grey hamster, russet souslik. Unfortunately, the most part of strata was not dated yet. Here we submit the materials from the bottom layers of the cave, systematic descriptions of which were not published yet. This part of sediments gave the date of 14,485 yr B.P. (Petrin 1992). However, these strata contained relatively low quantity of remains that could be analysed at the second level only.

Rodent faunas from the Middle and South Urals were described basing on numerous and previously published data (Smirnov 1990, 1993, 1995). For this report, we used only materials on the typical sites of some local faunas, treated at the third level; characteristics are submitted in the Table 5.1.

All the data on large mammals of the Urals were analysed at the first level.

1.3. PALEOFAUNA database structure *Anastasia K. Markova*

While developing the database structure in **PARADOX V.4** Databases Management Program we distinguished acronyms for four tables to present the following information:

- 1) "**GEO**" — geographical position of sites;
- 2) "**AGE**" — absolute or/and relative datings;
- 3) "**TAXA**" — lists of taxa (species composition);
- 4) "**REFER**" — references.

Each of these tables includes the site numbers, thus providing the possibility of their future use in complex analyses.

"**GEO**" database contains the detailed information about the geographical position of sites. Besides the number and name of sites, there are present latitude and longitude values (degrees and minutes), sometimes altitude in meters; names of the country (state), region, and district where the site is located; name of the river drainage basin; and the name of the nearest settlement (town, village, etc.).

In some cases, especially for the isolated bone finds dated to the Late Pleistocene time, the corre-

sponding reports contained only general information about the geographical position of the finds. It mostly concerns with the sites in the Subarctic and Northeast of Russia. We decided to include such locations in our database if they seemed to be significant from the paleogeographical view point. In this case, river basins were used as the main geographical location factor. However, the majority of Paleolithic sites possess exact geographical data.

“**AGE**” table includes the several fields to regard geochronological information: — stratigraphic units of different ranks: Quaternary: Pleistocene; sub-divisions of Pleistocene (for example, “Late”); Glacial or Interglacial period (for example, “Mikulino Interglacial”); stage of glaciation or interglacial (for example, “Bryansk Interstadial”).

Next fields contain dates obtained by absolute methods, firstly by radiocarbon methods with the standard errors, laboratory indexes and numbers, information about the sample quality, and, when available, the results of thermoluminescent and paleomagnetic datings.

Characteristics obtained by relative dating methods also included :

1. Geological context (for example, “alluvial deposits of the second terrace”, or “horizon of the Bryansk fossil soil”, etc.);
2. Archaeological context (i.e., “Magdalenian culture”);
3. Attachment to a certain faunal association (for example, “Shkurlat faunistic complex”);
4. Minimum and maximum dating values for a site and the methods of calculation;
5. The most reliable age resulting from the whole complex of methods ;
6. Information about the taphonomy of sites (i.e., “loess deposits”);
7. Possible redeposition of bones (“yes” — “no”-?)

“**TAXA**” table, besides the site numbers and names, contains special fields for each Late Pleistocene mammal species recovered from the territories of the former USSR. The pattern for these database fields was based on the “Catalogue of Mammals of the USSR” (Eds. I.M.Gromov & G.I.Baranova 1981). For each site special symbols were used for the species the remains of which were marked in the localities but without any quantitative data. The number of mammal remains that are indicated in the reference papers are marked in the table fields.

“**REFER**” table includes full references for each site indicating the authors’ names, the year, title and place of the publication, publishing house, pages number, and the names of the specialists who identified the bone materials (for example, “A.N.Motuzko — small mammals; N.K.Vereshchaghin — megamammals”).

While starting our work (PALEOFAUNA) we knew a little about the FAUNMAP database structure. Yet,

later on, thanks to Dr. Russel Graham from the Illinois State Museum, U.S.A., who is leading the FAUNMAP database creation, we receive information about these works regularly. In some tables we include the acronyms after FAUNMAP. However it is already too late for us to adopt the FAUNMAP approach in full extent.

Some problems of taphonomy and relative dating of sites.

Taphonomy of localities. When developing our database we included the results of taphonomical studies; these ones are essential for proper interpretation of bone remains from Pleistocene sites.

Bone remains of Late Pleistocene mammals are marked in the sites diverse by their taphonomy: those of alluvial, estuary, lake and marsh origin, those found in caves, and attached to the horizons of fossil soils and loess deposits, cultural layers of the ancient human sites. Recently some localities were found in the seashore deposits. In the majority of those sites concentration of mammal bone remains depended largely upon the processes of redeposition, the latter show to be the most intensive in alluvial and marine localities. Processes leading to the formation of sites were described in detail by I.A.Efremov (1950). He showed that after the organisms death living **biocenosis** turned into a **tanatocenosis**, which is an accumulation of remains not yet embedded, but thus still belongs in to the biosphere. Then, due to the transportation of bone remains, tanatocenosis transforms into a **taphocenosis**, that is, an accumulation of remains embedded but not yet fossilised. And lately, as a result of fossilisation, taphocenosis turns to become an **oryctocenosis**, which is an accumulation of the mineralised remains included inside the rock deposits. A site where the bone remains were embedded without any transportation from the animals’ burials is called as a **primary site**. These occur by several ways:

1. As a kind of natural trap, i.e. oil traps or puddles (Gromov 1952);
2. As embeddings in lake or marsh deposits similar to sapropels (Agadjanian, 1971);
3. Remains in mole-made tunnels in fossil soils (Markova 1982);
4. As a result of the predators’ activities, both birds and mammals (Andrews 1990; Gromov 1955, 1961; Gromov & Parfenova 1961; Smirnov et al. 1990; Vereshchaghin & Gromov, 1953);
5. As inclusions in loess deposits; where animals were buried with practically no transportation, being covered by eolic loess just at the place of death. Additional cases are known where such loess deposits and their organic matter were removed to some other place and redeposited there due to slope processes.

Secondary sites are the those where bones are concentrated away from places where animals died. These include:

1. Alluvial localities where mammal bones are concentrated in the sediments of river beds and flood-plains, being moved from the terraces or flood-plain surface by temporary streams, or by rain and flood waters. In this case the remains are spread depending upon their sizes and weights or due to the fluvial processes (Gromov 1957 a, b, c);

2. Estuary sites where bone remains are accumulated after being washed off the surfaces with further embedding in quiet water with no intensive redepositing;

3. Lake and marsh sites that are formed similarly to the previous type;

4. Localities in fluvioglacial and glacial sediments; the bone remains in such cases were intensively redeposited under the influence of meltwater streams, and the transportation processes were similar to those in alluvial sites. Redeposition also occurred when the underlying sediments containing organic matter were embedded in tills;

5. Localities connected with the cultural layers of the Paleolithic sites, where the bone remains were accumulated mainly in two ways: either resulting from hunting by ancient people or from natural mortality of some small mammals. On the whole, oryctocenoses of such localities correspond closely to the time when ancient people lived at a site, as the intervals of bone accumulation were relatively short. Actually this was confirmed by AMS (Accelerator Mass Spectrometer) dating of small bone samples (for example, separate rodent teeth) from cultural layers of archaeological sites in North America (Graham & Grimm 1990).

While the remains from the primary sites are synchronous to the time of accumulation of the sediments including them, secondary sites contain remains of different ages. Thus interpretation of such data must be done more carefully. Usually it is easy enough to reveal the strongly mixed local faunas containing mammal remains of different preservation, i.e. diverse in colour and damage extent, differently nodulized or discriminated by evolutionary levels. As for the latter, the most evolutionary young group of remains usually corresponds to the time of site formation. Analysis of bone preservation usually provides rather good discrimination of the redeposited remains in order to eliminate them from the further analysis. For this reason, the remains from archaeological cultural layers, though being concentrated in two ways, make one of the best subjects for studies and analyses as they are synchronous to the time when those people lived.

Geological and paleogeographical data. Sites of mammal remains included into the PALEOFAUNA database are dated to a long time interval exceeding

100.000 years. The earliest of them correspond to the deposits of the Mikulino (Kazantsevo-Eem) Interglacial which is estimated differently by duration. The older publications accepted significant duration of this period, from 130,000 till 70,000 years ago (Velichko 1973). Later on the concept of the duration of this warm period changed. Based on the studies of annual rings in diatomites, scientists came to narrow the limits of this warm time down to 11,000-12,000 years (Muller 1974). Now the majority of investigators are concerned that the Eem (Mikulino) Interglacial persisted for no longer than 15,000 years (Zaghwjin 1992; Frenzel et al. 1992). Still other points of view also exist. Thus, N.Morner (1977) concluded that this interval covered the time from 128,000 till 92,000 years ago, i.e. during ca. 35.000 years, and included the Blake's paleomagnetic episode dated to 114,000-108,000 yr B.P. The optimum of the Mikulino Interglacial was dated to 125,000 yr B.P. (Frenzel et al. 1992).

Scientists refer the Karanghat transgression of the Black Sea, Eem transgression of the Baltic Sea, Boreal transgression of the Arctic Ocean to the the Mikulino Interglacial (Fedorov 1978; Velichko et al. 1993); aggradation of the second terraces; and formation of the early Salynsk phase of the Mezin soil complex (Morozova 1981). All this information helped with the relative dating of the earliest mammal sites, some of which were registered in the second alluvial terraces, others with the Mezin soil complex, or with liman deposits made by the Karanghat transgression of the Black Sea, etc. The beginning of the Valdai Glaciation (= Veichselian in the Western Europe; Zyryanka and Sartan in Siberia) is dated to 115,000-92,000 yr B.P., as it was mentioned above. The Valdai glacial terminal is referred much more exactly, to 10,000 yr B.P.

The early Valdai-Zyryanka (early Veichselian) cold stage increased till 35,000 yr B.P., being interrupted sometimes by interstadial warmings. Judging from the West European data, the next earliest Veichselian interstadial named Ammersfort started about 80,000 years ago. The next Early Valdai warming was named as Krutitsa-Upper Volga Interstadial; it correlated with the Brarup Interstadial in Western Europe and dated to ca. 70,000-60,000 yr B.P. (Chebotaryova & Makarycheva 1974; Faustova & Velichko 1992). This time of warming corresponds to the formation of the Kru-titsky soil of the Mesinsky soil complex (Morozova 1981). Temperature decreases of the early Valdai were reflected in loess accumulation and marked by Sevsky and Khotylevsky loess horizons of the Russian Plain (Velichko et al. 1992 b).

The most expressed warming during the Valdai glacial epoch (Bryansk-Danube-Late Karginsky) corresponding to the Denecamp Interstadial in Western Europe persisted from ca. 35,000 to 24,000 yr B.P. (Velichko et al. 1992 b). Interzonal Bryansk fossil soil was formed during this time (Morozova, 1981).

The second cold period of the Valdai glacial time, Sartan Glaciation in Siberia, was the time when the thick loess cover on the Russian Plain was formed. This is marked by weakly expressed Trubchevsk fos-

sil soil having radiocarbon dates to about 17,000 yr B.P. (Velichko et al. 1992 b). It was also the time for aggradation of the first terraces.

Brief geological evidence provide the relative dating of available paleofaunal materials. This is of special importance for the early Valdai sites that are beyond the limits of resolution of radiocarbon dating which includes the time interval not exceeding the last 40,000-45,000 years.

Thermoluminescent and paleomagnetic methods provide additional information to establish these dates. The Blake paleomagnetic episode, as well as pollen evidence, malacological and pedological characteristics, and, surely, archaeological materials are examples.

Archaeological data. While the PALEOFAUNA database was developed the major information was received from archaeological reports. Complex studies from Paleolithic sites usually include examination of the paleontological remains found in the cultural layers. A total of ca. 300 sites were included in the database. These are situated in different regions of the former USSR and refer to different Paleolithic cultures.

As concluded by I. K. Ivanova, a well-known specialist for geological problems of the Paleolithic Age, the Mikulino Interglacial, or at least the terminal of the latter, and the first half of the Valdai period represent the interval corresponded to the Early Paleolithic Mousterian culture (Ivanova 1982). I. P. Boriskovsky (1979) refers the Mousterian cultures to the time interval of 100,000-35,000 years ago. It is known that Neanderthal people being the carriers of the Mousterian culture, spread from northwards, and with no regularity at the territories of the former USSR; thus the later Mousterian sites are usually situated in the central and northern regions of the territory under study.

Transition from the Mousterian culture to those of the late Paleolithic was not uniform either. The oldest Late Paleolithic sites are dated to 33,000 yr B.P.; at the territories of the former USSR they were found in the Don River basin, Kostenki 1 (layer 5), Kostenki 6, Kostenki 12, Kostenki 17, dated to 32,000-33,000 yr B.P. (Boriskovsky 1979; Ivanova 1982; Praslov & Rogachev 1982; Velichko et al. 1990). The youngest Late Paleolithic sites situated on the Russian Plain are dated to about 11,000-10,000 yr B.P. The succession and ages of archaeological cultures during the Early and Late Paleolithic time were established in many detail based on archaeological and associate data.

On the Russian Plain the sites with Kostenki-Streletzkaya Paleolithic culture (32,000-30,000 yr B.P.) and Kostenki — Sungir' Paleolithic culture (27,000-24,000 yr B.P.) correspond to the beginning of the Late Paleolithic time. These were replaced by the sites with Kostenki-Avdeevo culture (23,000-21,000 yr B.P.). The more late sites containing dwellings from bones and earth are correlated to the late glacial time

(15,000-12,000 yr. B.P.). The first sites of the Mesolithic age appear about 12,000-10,000 years ago.

Many local cultures of the Late Paleolithic are distinguished in Siberia also. For example, in the Yenisey River basin, based on the studies of numerous Late Paleolithic sites, Z.A. Abramova (1979, 1989) described the Kokorevo and Afontovo lithic cultures, dated to 15,000-12,000 and 20,000-19,000 yr B.P. respectively.

Surely, the replacement of cultures was not simultaneous throughout the whole territory, many facts of retardation, overlapping or/and losses of Paleolithic cultures occurred. Yet the general picture of evolution of the main Paleolithic cultures exists, providing a valuable additional source for dating of associated materials, namely, synchronous deposits of mammal remains.

2. PRINCIPAL METHODS OF INVESTIGATIONS IN THE LATE PLEISTOCENE MAMMAL SPECIES RICHNESS

2.1. Methods of sampling and treatment

Nikolai G. Smirnov

Pattern of fauna analysis. Before discussing methods of the data analysis, it is necessary to clarify some terms and notions.

We used the term "site" to describe a location of remains being uniform in regard to age characteristics. One and the same point of sampling could contain several sites if it possessed several layers of different age. In this sense, this was fauna of a site that made the basis for creation of the PALEOFAUNA database. All the rest faunal characteristics were secondary, derivative from the initial notions. One of those was "local fauna".

We used the term "local fauna" to describe animal population of the relatively compact and uniform territory, commensurate to several dozens of square kilometers. Characteristics of a local fauna were reconstructed, based upon the samples belonging to the same interval (data from one or several sites). A typical site was selected for each local fauna, being determined on the basis of the largest quantity of the taxa listed. Characteristics of local faunas were used to examine geographical or temporal changes in biodiversity.

Information to be included into the PALEOFAUNA database can be of different quality and quantity. Absence of reliable dates of the needed accuracy was the most usual and, in the majority of cases, the only reason for not including the data into the database. A site could demonstrate any quantity of both remains and taxa involved. Based on these features of the initial paleofaunal data, different levels of analysis were provided.

FIRST LEVEL. This level of analysis may be used for sites of any kind of taphonomy, supplied with reliable information, that some quantity of remains

have been found. It is used for the sites with no data on the quantity of remains for each species marked. The data on these sites may be applied for description of the areas of separate mammal species, and to open taxa lists for local faunas. For the whole territory of the FSU, and by the present day, total of 210 sites were analysed at the first level, and were included into the database.

SECOND LEVEL is an intermediate one, preceding the most complicate third level. Analysis at the second level may be realized if we possess taxa lists with quantity of remains documented, but no data to distinguish skeleton elements or to estimate minimum number of individuals. Hence, it is impossible to be correct in appraisal of relative numbers of diverse species, but crude assessment is available, and that is sufficient to establish general structure of the fauna, while listing the most abundant species. This way may be used to analyse the sites showing low numbers of remains, surely insufficient to reveal full taxa lists of local faunas.

THIRD LEVEL of analysis allows to characterize compositions and structures of local faunas, using such quantitative parameters, as quantity of mammal species according to the certain taxonomical groups, index of the species diversity "d", and equi- tability index "e", showing the value of uniformity or disbalance of the proportions of minimum number of individuals attributed to different species. In order to calculate these indices, one should possess taxa lists, showing quantity of remains according to the skeleton elements or indicating minimum numbers of individuals. The total number of remains should be sufficient to characterize complete taxa lists and with high accuracy.

Estimation of data applicability for analysis.

Applicability of materials for the third level of analysis is determined according to the probability values, which should indicate, that the complete taxa lists have been established for local faunas at study. Hence, a problem arises to evaluate the quantity of remains being necessary (and sufficient) to reveal a certain number of the species. Numerical solution of the problem depends both on the number of species involved (for example, 5 or 20) in a fauna, and upon balanced or disbalanced proportions of remains attributed to the different species. Actually it is necessary to determine the quantity of remains being sufficient to reveal the most rare species. If the proportions of remains are equable enough, the sample volume (i.e. number of remains that ought to be identified in order to reveal the complete taxa list of a site) is significantly lower than that in the situation when the proportions of remains in a site are evidently non-uniform. Therefore, it is impossible to determine the sample volume needed to reveal the complete taxa list of a site, with no account to equitability of proportions of different species. In order to perform the latter estimate, we used equitability index "e" according to Pielou (1975), see formula [2] below.

Thus, three types of sites were distinguished. If equitability values ("e") composed 0.8 or more, a site was concerned as relatively uniform; the values being between 0.79 and 0.5, a site was referred to be non-uniform; and the third category included the sites showing extremely irregular (non-uniform, disbalanced) distribution of proportions of the species remains (e-values lower than 0.5). These gradations were established, basing on the analyses of natural paleofaunal data. Besides this criterion, crude estimates may be obtained from the following original information. If a site list includes about 10 taxa, and the proportion of remains of the first two (most abundant) species exceeds 79 %, this site shows the most disbalanced distribution of the remains shares. Distribution is considered as non-uniform, if the proportions mentioned make from 50 to 79 %. And in the cases, when the portion of remains of the two most abundant species does not exceed 49 %, the sites are usually referred to the category of those "even-distributed".

Let us revise an example of three sites, each with 10 taxa involved, and with 1,000 remains identified in each case, but different in the proportions of the species remains. In one of the sites proportions showed relatively uniform distribution, with "e" equal to 0.85, and the portion of remains referring to the first two most abundant species composed 45 %. The second one gave "e" value of 0.68 (non- uniform distribution), and 70 % of the remains found belonged to the first two species. The last of the sites demonstrated extremely unbalanced shares of the species remains ("e" = 0.43), and about 90 % of all the remains quantity was identified to the first two species. Calculations show, that sample of 20 molars is sufficient to establish the list of 7 taxa for the first site, but as many as 36 molars are needed to do the same in the second case, and 92 molars would be enough in the third one. In order to extend the list up to 9 taxa, the sample volumes should be increased, too, but 115 molars will be needed in the first case, 130 in the second, and even 255 in the third situation. To illustrate the relationship between the quantity of remains and list of the species revealed, we present the table 2.1, the data for which were obtained by means of "rarefaction" method, according to A. Magurran (1992).

TABLE 2.1. Number of species that can be revealed in the sites showing different uniformity of proportions of the species remains as dependent upon the actual quantity of remains

	Quality of remains				
	1000	600	200	50	12.5
	Number of species				
Site N 1	10	9.6	9.19	8.38	6.05
Site N 2	10	9.6	9.18	7.77	4.8
Site N 3	10	9.6	8.56	5.48	3.13

Surely, "number of remains" includes only those, which can be determined to the species level. Practically, for different species the quantity of those will depend both upon the investigator's qualification, and upon level of morphological elaborateness for the species, and, besides, upon some other factors. Practical investigations have shown that consistent characteristics of rodent local faunas, dated to the late Valdai time and situated at the middle latitudes, were obtained when the total number of buccal teeth approached to 1,000, and quantity of those designated to the species level was about 600, while the minimum number of individuals was no less than 100-150.

Selection of typical sites, description of local faunas and their structures. A typical site was selected for every relatively compact region, with account to the largest number of the taxa listed. Due to peculiarities of taphonomy, typical sites might differ in regard to the small or large mammals. Thus, in the southern part of the Middle Urals, west slope, 4 sites of the late Valdai time age, are known namely, Arakaevo 8, Boblyok, Dyrovaty Kamen' on the Serga- river, Alikaev Kamen'. The most distant of them are separated by 30 km south-north, and about 100 km east-west. In regard to megamammals, the rock- shelter Boblyok was selected as typical site, since the remains of 15 megamammal species were found there, while only three species of those were identified in Arakaevo 8, and 4 in the site of Dyrovaty Kamen'. As for micromammals, the cave Arakaevo 8 was selected for the typical site, because its taxa list included 14 species of rodents, whereas 11 species of small mammals were registered in the Boblyok rockshelter, 10 species in the site of Dyrovaty Kamen', and 6 rodent species in the Alikaev Kamen' site.

When the sample volumes show the same order of magnitude, criterion of similarity between the typical site and the others of the resembling taphonomy occurs to be close to 1. Usually, the taxa list of the typical site includes all the taxa of the local fauna. However, occasionally, some rare species might be not revealed in the typical site, but occur to be displayed in other sites lists. In this situation, those taxa names ought to be added to the typical site list, and frequencies of individuals for a local fauna are calculated as an average value between the typical site and those other sites where the additional species were found.

In order to calculate and compare qualitative characteristics of the faunas compositions and structures, in addition to PALEOFAUNA database, a special program "Fauna-analysis" was designed (by L. N. Smirnov), basing on "Paradox for Windows". The main processing in this program was filling in of the "key" form, including several steps.

A special form is opened for each new site, with a certain table structure to fill in the data on the site. Fields are provided to put in the following informa-

tion: the site name, number of the layer, name of the database where the data are to be filled in; at the same time the taxa list is created for the site, by selection of the corresponding taxa from the existing standard list of the species names. This is a moment of special importance, since afterwards the species names should be identified, and thus variations in the names' spellings are prohibitive. Another field of the form is intended for the list of bone remains, the number of which will be filled in the table. The form of this list is unrestricted. It may be formed either based on some initial variant, or new symbols may be entered every time. The form also provides a variant, when only the numbers of remains are given, with no identification of the remains.

When the form has been created and acknowledged, the basic form returns unattended. Then there opens the table to enter the data on the quantity of each type of bone remains for every species, and minimum quantity of individuals (if known, of course). When it has been filled, six resulting columns of the table occur to be filled by the command: total number of remains for every species, maximum quantity of one-type remains in every species, average quantity of the identified remains for each species; proportion of each species remains referred to the total number of remains, the same being referenced to the maximum quantity of one-type remains, and that referred to the average number of the identified remains. In different cases each of those indices may be used for further calculations; in our program we used the proportions of species calculated by the minimum numbers of individuals. If the field "minimum number of individuals" is filled in, all the next calculations start from those values; otherwise, we recognized the number of individuals as a half of the maximum quantity of one-type elements (with no regard to the right or left items).

At this stage one column in the table is left vacant, the probability of the species being detected; these values will be computed at the following step of work with the basic form.

After quitting the table, we return to the basic form, where the fields for the site treated appear to be completed unattended, those containing the following data: number of taxa involved; quantity of the identified bone remains; index of the species diversity "d"; equitability index "e"; Shannon index. All of them are calculated based on the proportions of minimum numbers of individuals.

Index of the species diversity "d" was computed by the formula:

$$[1] \quad d = \frac{S-1}{\ln N}$$

where **N** is the minimum number of individuals, and **S** is the number of species.

As the formula takes account of the number of individuals, thus reflecting the volume of the data obtained, this index may be also computed for the sites with significantly diverse quantities of material.

Equitability index according to E. Pietou (1975) was computed as:

$$[2] \quad e = \frac{H}{\ln S'}$$

where **S** is number of species; **H** — Shannon index, found by the formula:

$$[3] \quad H = - \sum P_i \ln P_i$$

where **P** is the proportion of the *i*-th species, being calculated from the minimum number of individuals.

In contrast to "d" index, equitability "e" neglects the material volume; therefore, one should think of the level of its stability as dependent upon the volume of the sample treated.

Two cells remain free at this stage. One of them is to receive the figure, showing to what volume the collection should be decreased to, in order to calculate the probability of detection of each species remains, while the second will contain the total number of taxa after that decrease. The results of those calculations by the separate species will appear in the table, while the taxa quantity after the "dilution" procedure — in the main form. Calculations of the species quantity after dilution procedure are performed by the formulae according to A. Magurran (1992), with such modifications, that probabilities of the species detection are calculated starting from the number of bone remains, but not from the number of individuals revealed. This seems to be more warrant for us, since in our studies it is a find of a single bone (from one animal) which ought to be regarded as an elementary event.

The same basic form provides an opportunity to estimate level of similarity for pairs of sites, using "r"-criterion. The latter is calculated, basing upon the proportions of individuals of the species found in both sites compared, by the formula:

$$[4] \quad r = \frac{\sum_{i=1}^m \sqrt{p_i q_i}}{m}$$

where **p** and **q** are the frequency values showing minimum numbers of individuals of the same species found in two compared sites, and *m* is the number of the species, being in common for both sites. The criterion values vary from 1 (full similarity of sites) to 0, when nothing in common is revealed. An important merit of this criterium is the possibility of statistical estimation, whether a value differs significantly from 1; statistical errors may be calculated, too; using those one can determine the significance of differences between the "r" values for diverse pairs of comparison (Zhivotovsky, 1979). The program also provides computing of the results of comparizon of the selected pairs, being demonstrated as "revalues, supplied with final conclusion whether they differ significantly from 1, and with error value for it.

2.2. Reconstruction of species richness in mammal local faunas Anastasia K. Markova

In order to analyse the relationships between the species richness values of mammals and paleoclimatic factors, the parameters for quantifying mammal species at Late Pleistocene sites had to be redefined. The PALEOFAUNA database in the main includes information about the sites of mammals of the first level (see Chapter 2, part 1). Thus, in this case it is impossible to apply the method proposed by N.G. Smirnov, which holds that structure and composition of the faunas should be determined on the basis of the number of remains and skeletal elements. Besides, the number of remains identified to the species level should consist of a minimum of 600 (Chapter 2, part 1).

The PALEOFAUNA database includes a limited number of sites described in a way that could satisfy these conditions, and the majority of those are from the Urals. In some cases, megamammal remains were given priority for identification, especially in the case of game species. At other sites, only small mammals such as rodents, lagomorphs, and insectivores were described.

In order to obtain the most accurate reconstructions of species richness for Late Pleistocene mammals we used the following approaches. For sites of the Mikulino Interglacial, where the complex information permits the reconstruction of the zonal structure of biotic components, we took into account the modern ratio of large and small mammal species. For sites from the period of the Valdai glaciation, we used the proportions of small and large mammals from the Late Pleistocene local faunas that were studied in detail. Transpositions of modern data with these proportions are objectionable since the faunal assemblages that existed during the glacial periods had species compositions and structures that have no modern analogues, thus making their comparisons to the modern assemblages impossible (Graham, 1976, 1985, 1986; Semken 1988; Smirnov 1990; Vangengeim 1977; Vereshchaghin & Baryshnikov 1985).

The number of small mammal species in the faunas of Northern Eurasia is significantly greater than that for megamammals. Based on the numbers of species in some mammalian orders given by "MAMMALS OF THE FAUNA OF THE USSR" (Eds. Gromov & Baranova 1981) and "MAMMALS OF THE FAUNA OF RUSSIA" (Eds. Skarlato, 1995), the proportion between the quantity of small mammal species (SM) (e.g., *Insectivora*, *Lagomorpha*, and *Rodentia*) and large mammals (LM) (e.g., *Perissodactyla*, *Artiodactyla*, and *Carnivora*) is: SM/LM = 3.25.

If bats (Order *Chiroptera*) are included with the small mammals, the value becomes: SM/LM = 3.84.

When calculating these proportions we did not include the orders *Pinnipedia* and *Cetecea* with the large mammals since their remains are absent from

the Late Pleistocene sites of former Soviet Union. The group of small mammals is taken into account without the order *Chiroptera*, since the remains of bats are rare in the Late Pleistocene localities.

Species richness of mammals was found to vary irregularly by the natural zones. Information available for Eastern Europe indicate that 25 species of mammals inhabit the tundra zone, 47 species occur in taiga, 60 species are recorded in the mixed forests, 59 species exist in the broad-leafed forests, 53 species are found in the steppes, and 35 are known for the deserts and semideserts (Tishkov 1993).

The ratios between the numbers of small mammal species and large mammal species were calculated from data obtained from reservations situated in different natural zones. The calculated values are as follows:

- 1.0 in tundra (Taimyr and Ust'-Lena reservations); 1.2 in forest-tundra (Putorana, Lapland, Magadan reservations);
- 1.5-2.0 in the forest zone (Bashkir reservation);
- 1.8-2.0 in the forest-steppes (Central-Chernozemny, Zhighuly, and Khoper reservations);
- 2.0-2.2 in the steppes (Askania-Nova, Lugansky, Ukrainian steppe reservations);
- 1.6 in the mountains in the southern portion of Eastern Europe (the Carpathian reserve).

One can see that SM/LM ratios vary irregularly in response to the geographical position of the territories and environmental conditions such as heat, duration of summer season, vegetation, etc.

As previously noted, these relationships could not be extended back to the Late Pleistocene faunas of the Valdai period. Yet we considered their use valid while reconstructing of actual species richness during the Mikulino Interglacial, with regard to the zonal structure of this time.

Analysis of relationships between large and small mammals in the local faunas described in most detail for the Valdai glaciation and situated in the zone adjacent to the ice sheet resulted in the following values of SM/LM:

- Eastern Europe
 - 1. In the zone near the ice-sheet (200-km belt along the ice sheet edge; 56-53° N) 1.0-1.2
 - 2. Regions 200-400 km distant from the ice sheet edge (53-51° N) 1.4
 - 3. Regions 400-700 km distant from the glacial edge (51-48° N) not good materials
 - 4. Those 700-1000 km distant from the glacial edge (48-45° N) 1.5
 - 5. The Crimea (45° N) ... 1.5
 - 6. Eastern foothills of Carpathians (46° N) ..0.9-1.0
 - 7. Western Caucasus (42° N) 0.95
- Asian part of former USSR
 - 8. Aldan upland (58° N) 0.9-1.0
 - 9. Altai (51-50°N) 1.4-2.0
 - 10. Eastern Transcaucasus (39° N) 0.8

There are no Valdai-dated sites with full identification of mammal remains for areas north of Siberia nor for regions of the Northeast.

The relationships presented are of the most interest. They indicate that during the Valdai Glaciation the proportions of small mammal species to those of large mammals were similar to those in modern tundra and forest-tundra zones over most of Eastern Europe.

Based on these indices we considered it possible to reconstruct the values of mammalian species richness for the other Valdai sites located in the corresponding belts where either large or small mammals were identified. If there were but few species of large or small mammals identified at a site, we did not use such sites for the species richness reconstructions and expelled them from further analyses.

These procedures were followed for the most Uralian sites containing Late Pleistocene mammals. The data on the reconstructed species richness values were then used to describe the relationships between species richness and paleoclimatic factors, e.g., temperatures, precipitation, humidity, permafrost thickness, etc.

2.3. GIS technique in biotic and climatic studies

Lev M. Kitaev

Character of initial information containing many variables, as well as the need to study spatial regularities and relationships of climatic factors and biodiversity in different time intervals (sections) made it necessary to develop a method of usage of geo-information technologies.

Any geo-information system should satisfy the general requirements for the products of this kind (Smieth 1987). Namely, a system is expected to be capable for operational treatment of the arrays of component-wise heterogeneous spatially-co-ordinated information. Besides, it ought to be able to maintain a database involving a significant number of characteristics and possess a feature of interactive work. The system should be set up flexibly to solve different problems within the scope of the general trend of investigations.

Starting from the above said, in the system development there were used the standard approaches of computer organisation of information (Kalchitz et al. 1987). Functioning of the system is based on a special complex of aids which includes:

- 1. Software: standard package to create GIS ARC/INFO (Environmental Systems Research Institute, New York, USA), standard package for database PARADOX V.4.
- 2. Hardware: digitizer of A4 format (input of map information), computer AT 486 DX (calculations), printer (output of hard copies).

Structure of data system includes information block, interactive management system, operational-assessment and decision-making block.

Information block. This block includes two inter-related parts. One of them contains data arrays, while the other — a set of electronic maps. Information base is integrated into the database access to which is gained by the management system represented by two program packages. One of those is PARADOX, a specialised package for data organisation, used to execute the input, structuring and primary treatment of initial information. Then the structured information was imported into the shell ARC / INFO, the DBF format, and was correlated with entities of electronic maps. As a negative consequence of duplication of initial information in two program packages came the necessity to increase (practically double) memory capacity for storage. On the other hand, the capability in data treatment appear to increase as legible properties of the both packages complement each other. Existence of the standardised blocks for export and import of packages made feasible an operational exchange of information after the data processing.

Total thematic information contained in the database may be divided into the following groups:

1. Data on geographical situation;
2. Information about the sites of animals and plants upon different time sections;
3. Data on the modern distribution of plant and animal species;
4. Data about age of finds;
5. Modern climatic data (temperature and precipitation, average annual and seasonal values);
6. Data about climatic characteristics during various time intervals of the past (reconstructed values of annual and seasonal temperatures and precipitation), data about the permafrost thickness during the time of the glaciation maximum (with reference to the Atlas of Paleoclimates and Paleoenvironments of Northern Hemisphere, 1992);
7. References.

Information is contained in the database both in numeric and text forms. The total quantity of fields (parameters) is about 400, the number of attributes is about 800.

When developing of GIS special attention was paid to the maps made in the ARC / INFO package. Maps are represented in vector format. Automated map-making is based on the main principles of mapping (Salishchev 1980), with regard to specifics computer construction (Serbenyuk & Tikunov 1984). For the background a topographical map of the former SU was used, plotted at a scale of 1:8,000,000 and done in the generally used for this scale normal conical equal-spaced projection after V. V. Kavraisky. In this projection no error occurs along the parallels of 49.4° N and 67.8° N, areas are not distorted

between the parallels of 48.2 and 67.8° N, and no deformation of angles is observed between the parallels of 50.6 and 66.80° N.

Electronic cartographic background is represented by the shore-line and isles shown with the accuracy corresponding to the scale used. It has the grid of parallels and meridians being standard for an Atlas, with mesh width equal to 10 degrees; density of river network corresponds to the scale. As a map of the former SU was used, the boundary line of the former SU is shown in the electronic map for better orientation. Besides that, authors used the maps of the Atlas of Paleoclimates and Paleoenvironments of Northern Hemisphere, 1992, polar projection at the scale of 1:35,000,000, and those from the Atlas of climates of the USSR, of the normal conical equidistant projection, at the scale of 1:8,000,000.

The main usually used entities of maps are points, lines, and polygons, each possessing its set of attributes (Burrough 1980; Linnik 1986). Based on the properties of initial materials, during the GIS development authors used all usual entities of the following sense:

- sites of plant and animal remains: points;
- areas occupied by the ice-sheets of mountain glaciations during different time intervals: polygons and lines;
- islines of permafrost thickness limiting the areas of certain depths of its occurrence during the glaciation maximum: polygons and lines;
- shore-lines during the different time intervals: lines;
- isolines of temperatures and precipitation limiting the areas characterised with certain values of those during the distinct time sections: polygons and lines;
- modern ranges of plant and animal species: polygons and lines.

Maximum information load at this stage of research is resided in the points. Information for them is divided into several groups and characterized in Chapter 1.

At this stage of research information load of the polygons and lines is lower than that of the points. There are the following data for them in the information system:

1. Area and linear dimensions.
2. For the ranges of animals and plants during the different time intervals, polygons are identified according to the species names.
3. For the isolines of temperatures, precipitation and permafrost, polygons and lines are identified according to the corresponding parameter values.
4. For the glaciers and shoreline during the different time sections, polygons and lines are identified according to the entity character: ice sheets, mountain or lowland glaciers, the shoreline.

At this stage of research the system blocks being connected with polygons and lines (climate charac-

teristics, condition of glaciers, modern ranges of animals) are of auxiliary significance, and thus their information maintenance compare unfavourably with that of the paleopoints (data about the finds of animals and plants).

To sum up, the map-making part represents a set of initial specialised component maps (strata) and a set of the derivative synthetical maps which will be described below.

Interactive management system; block of assessment and decision-making

Some problems arising in the course of work with information system show significant and moderate level of difficulties. Thus, some special skills are needed for operations of arrangement of thematic information and electronic map background. Assessment and decision-making block is simpler and may be operated by users of the average skills.

The system was developed for information and inquiry, and what is even more significant, as an analytical instrument to be used in temporal and spatial modelling. The information system represents a relational database in which organisation of information provides for the relationship between the objects and their attributes (Lorie & Meier 1984; Miller 1985; Shapiro & Haralick 1980]. All possible variants of the relations between the objects are sustained: "one-to-one", "one-to-many", "many-to-many" (Atre 1983). The developed apparatus of the data operational management, and, namely, multilevel sampling, provided to determine the sense relations between initial parameters of information system.

Resulting from the analysis, based on available initial and thematical information, and upon special electronic maps, synthetical maps were developed. According to the tasks of investigations, age of finds and quantitative species contents in those were taken for basic classifiers. Separate electronic maps were constructed for each species in six temporal sections using non-scale unified symbols. These pictures were combined with electronic maps (layers) of the ice cover condition during the corresponding time intervals, and in some cases, with maps of recent species areas. A large set of colours and shadings for the polygons present, there occurred the possibility to create electronic map variants suitable for monochromic and polychromatic hard copies.

Special attention should be paid to the block for possible usage of the developed information system in modelling. On one hand, availability of sampling, possibility to establish the relationships between the parameters, combination of several electronic maps (layers) may be considered as modelling. But, besides that, information system creates the conditions to pass on to statistical modelling.

One of the promising directions of the statistics usage for these studies is to reveal the relationships between the quantity of remains found in each point and climatic characteristics represented as electronic maps with isolines. Thus a method was developed to transform the corresponding electronic isoline maps into the regular grid, the nodes of which match the grade grid with projection component in view. Any step size may be used if not computer-limited. In our case we used the step equal to 1 degree which made the picture representative enough. A certain drawback of the method at this stage of investigation was impossibility of interpolation for the points lying between isolines thus decreasing accuracy of calculations. Probably, this may be neglected in some cases as isolines of seasonal temperatures are divided by a step of 4 degrees, those of annual temperatures — by a step of 2 degrees, and those of precipitation — by 50-mm steps. On the other hand, development of the software for interpolation is principally feasible, and this should be concerned as a part of promising methodical research.

By the present moment opportunity of quantitative estimation of the relationship between the number of the remains found and the distance of those from the ice-sheet edge was not realised, but the problem may be solved by means of the existing software and thus may be regarded for the future work.

Significant amount of information in GIS is represented as points with certain attributes. This determines one more direction of work, namely, transition from points to polygons characterising plant and animal areas with further quantitative analyses of their interrelations with climatical factors.

The information system described is an open one, and this offers to improve constantly the quality of information enclosed.

2.4. Models of Paleoclimate for Eastern Europe *Alexander V. Kozharinov*

Initial paleoclimatic information, figured from the "Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere (Late Pleistocene — Holocene)" was formatted in ARC / INFO. For the three temporal sections (130,000-100,000 yr B.P., 35,000-24,000 yr B.P., and 20,000-8,000 yr B.P.) the following characteristics were used as variables: deviations in the annual average temperatures of air, deviations in the annual average precipitation, permafrost thickness. Then, by the Kriging-method the initial paleoclimatic characteristics were interpolated in order to construct the corresponding isoline maps and to obtain grid information with a step one degree. Such step is warrant for the informativeness of the basic climatic characteristics and interpolation error.

As the development of the biotic cover is, to a large extent, a function of humidity, it is desirable to use one of the complex indicators, namely humidification coefficient after N. N. Ivanov (1941), the virtue of which were discussed in the previous publication (Kozharinov 1983). For the basic information we used the developed earlier database "CLIMATE", including long-term data for 170 climatic variables from 1200 meteorological stations (Reference Book on Climate of the USSR, v. 1-5, N 1-34, 1965-1968). Humidity coefficient after N. N. Ivanov (K) is the amount of precipitation (P) related to vap- orability (E). Formula of potential evaporation, after N. N. Ivanov, is as follows:

$$[5] E = 0.0018 * (25 + TY)^2 * (100-A),$$

where TY is annual average temperature of air, A — is relative humidity of air (using the method of Stepwise Regression based on modern data value of the air relative humidity was approximated with respect to annual average temperatures of air and annual average precipitation). In addition the model included latitude and longitude, to the great extent reflecting macroregional differences of circulation mechanisms (Table 2.2).

Analysis of variance (ANOVA) permitted to determine the input of each variable and the level of assurance (Table 2.3).

After the calculations empirical formula of the air relative potential evaporation turns to the following:

$$[6] A = -15.3416 + 3.3068*Lat - 0.0284* Lat^2 - 0.003343*Long^2 - 1.2832*TY + 0.0778*TY^2 - 0.0074TY^3 + 0.000899* TY^4 + 0.164866*P - 0.000836*P^2,$$

where **Lat** is geographical latitude value, and **Long** - is that of the longitude. Deviation values for paleoclimatic characteristics were concerned during the calculations of the absolute value. Formulas (5,6) were used to calculate the values of air relative humidity, potential evaporation, and coefficient of humidity for the three time intervals, and the corresponding maps were constructed.

Standard procedures of combination of several files by the two fields of geographical coordinates in PARADOX 4.5 made it possible to determine climatic characteristics rather easily for each site of mammalian remains. Further on, the relationship between paleofaunal species richness and climatic characteristics was also determined by means of the Stepwise Regression. In this case, normalised values of climatic indices were used for the independent variables. Normalisation was performed by indexing the initial i-values by the series variance. This is necessary as non-normalised values can result to the

TABLE 2.2. Model fitting results

Independent variable	Coefficient	Std. error	T-value	Sig. level
CONST.	-15.341637	13.295543	-1.1539	0.0491
LAT	3.306767	10503879	6.5662	0.0000
LAT ²	-0.028443	0.004588	-6.1990	0.0000
LONG ²	-0.003343	0.000254	-13.1776	0.0000
TY	-1.283204	0.20669	-6.2083	0.0000
TY ²	0.07779	0.013234	5.8781	0.0000
TY ³	-0.007401	0.002858	-2.5897	0.0099
TY ⁴	0.000899	0.000226	3.9677	0.0001
OSY	0.164866	0.024102	6.8404	0.0000
OSY ⁴	-0.000836	0.000167	-5.0141	0.0000

R-SQ (ADJ) = 0.8171; SE = 1.600993; MAE = 1.123485; DurbWat = 1.478491 observations fitted.

TABLE 2.3. Further ANOVA for Variables in the Order Fitted

Source	Sum of Squares	DF	Mean Sq.	F-Ratio	P-value
LAT	2735.07105	1	2735.0711	1067.06	.0000
LAT ²	51.22079	1	51.2208	19.98	.0000
LONG ²	1873.18728	1	1873.1873	730.81	.0000
TY	87.13456	1	87.1346	33.99	.0000
TY ²	600.35288	1	600.3529	234.22	.0000
TY ³	88.03967	1	88.0397	34.35	.0000
TY ⁴	30.55141	1	30.5514	11.92	.0000
OSY	103.91443	1	103.9144	40.54	.0000
OSY ²	64.44198	1	64.4420	25.14	.0000
Model	5633.91406	9			

wrong outcome, due to their different measures and absolute figures.

3. DISTRIBUTION OF THE MOST DIAGNOSTIC MAMMAL SPECIES OF NORTHERN EURASIA DURING THE LATE PLEISTOCENE

3.1. Megamammals

Anastasia K. Markova

A number of attempts to map the findings of the Late Pleistocene mammal remains at the territories of North Eurasia were made in the previous years. K. K. Flerov (1951) made one of the first generalizations. E. A. Vangengeim (1977) presented maps of sites for several Late Pleistocene mammal species, and, based upon the data on mammals, distinguished several periglacial subzones during the Late Pleistocene time: the northern subzone (tundra-steppe with forest-tundra patches), intermediate subzone (periglacial forest-steppe), and the southern one (periglacial steppe and semidesert). It should be noted, however, all the data on the Late Pleistocene time were given only in general, without further subdivision into smaller time intervals.

Some papers contained the maps of mammal sites, mainly for large animals, arranged according to the Late Pleistocene stages (Musil, 1985). The data for Western Europe were basically represented, while those on Eastern Europe concerned but few sites.

The monograph of R. Kahlke (1994) described the ranges of several large mammals in Northern Eurasia, on the basis of information from 54 sites dated to the last glaciation. The maps shows the ranges of ungulates, carnivores, and proboscidians (20 species in total).

The atlas-monograph "Paleogeography of Europe during the last 100,000 years" also contained maps of mammal remains locations, as well as the map of the main mammal assemblages dated to the second half of Valdai glaciation in Europe. The information from more than 200 sites dated to 24,000-12,000 yr B.P. has been analysed (Markova 1982).

The main mammal assemblages of the late Valdai-Weichselian-Wisconsin, of the Northern Hemisphere were reconstructed by G. F. Baryshnikov and A. K. Markova on the basis of materials from about 600 sites in the "Atlas of Paleoclimates and Paleoenvironments of the Northern Hemisphere (Late Pleistocene-Holocene)", Budapest-Stuttgart, 1992. The authors described chief characteristics of species composition and distributions of the main theriocomplexes dated to 24,000-12,000 yr B.P. and showed them on maps.

Modern computers provide a possibility to demonstrate on maps any information contained in the

PALEOFAUNA database on the Late Pleistocene mammals in any detail, namely: 1) to present a sample on any time section; 2) to represent any mammal species or needed combination of species; 3) to combine information on mammal finds with vegetation data; and/or with 4) paleoclimatic characteristics represented in the map form; 5) to compare paleoinformation with the present-day ranges of the species under study; etc.

Among chief applications of the research there were the following: 1) to map the sites of remains of the most characteristic mammal species dated to different stages of the Late Pleistocene; 2) to examine responses of certain mammal species to climatic changes and alterations in plant communities; 3) to define rates of the species ranges transformation; 4) to determine the time of extinction of the Late Pleistocene mammals; 5) to reveal the main refuge places of the Late Pleistocene mammals during the Valdai glaciation time.

Since in this chapter we could not review all 200 species of mammals included into the PALEOFAUNA database, we will describe only the most characteristic mammal species dated to the Late Pleistocene of Northern Eurasia.

Species that became extinct during the terminal Late Pleistocene and Holocene

It was marked in many publications that the Late Pleistocene extinction was global in character and affected primarily large mammals, the so-called megafauna (Barnosky 1990; Graham & Lundelius 1984; Vereshchagin & Baryshnikov 1980, 1985; Puchkov 1989; etc.). The body masses of animals included into this group ranges from 20 kg to more than 1000 kg. During the terminal Late Pleistocene, many of these animals disappeared from the Holarctic areas, too. They were especially numerous in Neoarctic (about 60 species), while in the Palearctic regions only ca. 20 (some authors number 30) species of megamammals became extinct. It should be noted yet, that some rodents and Lagomorphs identified as separate species on the Late Pleistocene data, made ancestors for the recent forms. Besides, clarity lacks about the problems of genetical relations between the domesticated animals and their ancestors, i.e. the Pleistocene and domestic horses, the primitive wild oxen and recent cattle. That may be the reason why different authors disagree in their estimates of the number of species that became extinct during the terminal Late Pleistocene.

Large mammals are especially vulnerable to climatic changes, due to their slow reproduction, low density of herds, high requirements for food. It seemed important to use computers in order to analyse pattern of distribution of some large mammals that became extinct during the terminal Late Pleistocene, in order to examine dynamics of their

ranges, and to ascertain the time of their extinction.

I. Mammoth — *Mammuthus primigenius* Blumenbach, 1799

Mammoth is one of the most characteristic Late Pleistocene species of the Northern Eurasia, that penetrated into the North America during the Valdai glaciation through the Beringian land. During the Late Pleistocene, the species *M. primigenius* was spread, which appeared first by the end of the Dnieper glaciation time (Dubrovo 1990). It was adapted to life in periglacial forest-steppes and forest-tundras, which were distinguished for high productivity. Its daily diet included up to 300 kg of succulent fodder, namely forbs with addition of branches of willows, birches, alder, larch (Vereshchagin & Baryshnikov 1980, 1985; Ukraintseva 1979).

PALEOFUANA database contains information on 339 Late Pleistocene sites with mammoth remains situated within the former SU territories.

The earliest Late Pleistocene remains of *Mammuthus primigenius*, early type, were described from the basins of the Dniestr and Don River middle reaches, and near the Baikal Lake (Appendix. Fig. 1). By the pollen records and geological and paleotheriological evidences, they were correlated to the Mikulin Interglacial. The associate fauna both of micro- and megamammals included mainly the steppe species (Alekseeva 1980; Markova 1986).

During the early Valdai time (100,000-35,000 yr B.P.), mammoth range embraced the major part of the former SU territory, from the Arctic Ocean down to the Crimea, Northern Caucasus, Altai and Sayan Mts., Transbaikalian. 103 sites of mammoth remains dated to this time have been found (Appendix. Fig. 1). The sites of the same age are also known farther south in Asia, namely, the Hwang Ho River basin and the Hokkaido Island (Kamei 1981). No reliable data exist regarding the Middle Asia and Transcaucasus regions (Baryshnikov & Markova 1992).

During the Bryansk Interstadial (the Karginsky warming), the mammoth range practically did not change. It is interesting that the remains of this age were found at Severnaya Zemlya and Novosibirsky Isles, where the animals migrated to by way of the dried shelf, and in the Far East (Appendix. Fig. 2). The sites of this age were not known in the Crimea, nor in the Caucasus. The total of 60 sites with mammoth bones dated to middle Valdai Interstadial are known.

The most part of sites with mammoth remains (117) corresponds to the time of the late Valdai (Sartan) glaciation (24,000-15,000 yr B.P.). At this time, the mammoth area spread from the border of the Scandinavian ice sheet and Arctic Ocean islands, down to the northern regions near the Black Sea and elevations in the south Siberia and the Far East. Mammoth sites attributed to this period are not

known from the Crimea, the Caucasus and Middle Asia. Compared to the early Valdai epoch, the mammoth area was reduced in its southern part, probably due to extermination of the large herbivorous animals by primitive hunters who were numerous in southern regions of the Russian Plain (Appendix. Fig. 3).

During the late glacial time (15,000-10,000 yr B.P.), the southern limit of the mammoth range retreated northwards, but the species still occupied the main part of North Eurasia (Appendix. Fig. 4.), though the animals density in herds decreased. Similar to the earlier periods of the Valdai glacial time, mammoth inhabited the Beringian land, and the remains of this age were found on arctic isles. 49 sites of the mammoth remains dated to this time are known.

The mammoth range size decreased significantly by the very end of the Late Pleistocene time. Bone remains of the species younger than 10,000 years were found only at the Ghydan and Taimyr Peninsulas and Wrangel Island (Vartanian, Garutt & Sher 1993). Sensational finds of the latest middle Holocene mammoth remains at the Wrangel Island showed the age of 4,000 years (Appendix. Fig. 4). After the elevation of the world ocean level in the beginning of Holocene, the animals remained completely isolated there and grew significantly smaller (Sulerzhitsky 1995).

Undoubtedly, catastrophic collapse of the mammoth range by the Late Pleistocene end and Holocene beginning was related, first of all, to degradation of the periglacial biome (hyperzone, by A. A. Velichko 1973) characterized by highly productive herbaceous vegetation of different types. According to the data presented by V. V. Ukraintseva (1991), during the Valdai time mammoth fed mainly on forbs, leaves and branches of different bushes, and in the cold seasons used the undersnow plants which were no worse in quality than hay. By the terminal late glaciation and the Holocene start, mammoth diet began to change, with plants of wet habitats dominating, whereas the contents of nutritive elements and mineral composition in those yielded significantly to the plants of dry biotopes (Ukraintseva 1991). Thus, the Holocene warming led to significant changes in vegetation on Eurasia vast territories, which appeared quite unfavourable for the mammoth. Co-evolutional equilibrium between the large herbivorous animals and vegetation mosaic communities was disturbed, and this probably became the main reason of the species extinction. Primitive hunters added considerably to the process of degradation of mammoth populations.

II. Large cave bear — *Ursus (Spelaearctos)* *spelaeus* Rosenmeller et Heinroth, 1794

Late Pleistocene sites of mammals contain a number of remains of cave predators, i.e. large and

smaller cave bears, cave lion, cave hyena. The large cave bear preferred karst regions with numerous caves and rock shelters. Plants made the most part of the bears' diet.

During the early Valdai time, the species range encompassed the Transcarpathians, the Crimea, Caucasus and Transcaucasus, southern part of the Urals (up to 58° N) (Appendix. Fig. 5). 26 sites of the bear remains are known in total.

During the middle Valdai warming, the western part of the species range did not change, but new sites dated to the same interval were found in the Altai Mts. (Appendix. Fig. 6).

During the late Valdai maximum, the large cave bear persisted mainly in the elevated regions of Transcarpathians, Crimea, Caucasus, and Altai. The bears migrated far northwards in the Urals reaching 62° N; this lends support to the opinion about limited dimensions of the North-Urals ice-sheet during this cold period. By the present day only 4 sites are known containing the bears remains dated to the late glacial time; they are situated in the Urals mountains (Kosintsev 1990).

III. Cave hyena — *Crocuta spelaea* Goldfuss, 1823

PALEOFAUNA data bank contains information about the only Mikulino-aged site with hyena bone remains, the Bynagady site in the eastern Transcaucasus. Rich associate mammalian fauna included mainly steppe and semidesert forms (Gromov 1951; Vereshchagin 1951).

During the early Valdai time, this carnivore was widely distributed in North Eurasia. Bone remains designated as *Crocuta spelaea* were found mainly in the southern highlands of Eastern Europe and Siberia, i.e. the Transcarpathians, the Crimea, Transcaucasus, Urals, Altai and Sayan Mts., Transbaikalian region (Appendix. Fig. 7)

All the known sites of the cave hyena dated to the middle Valdai warming, are situated in the south regions of the former SU territory. Some findings were marked in the Transcarpathians and in the Altai-Sayan mountains.

The hyena remains dated to the maximum of the Valdai glaciation were also located in the south regions of Eastern Europe and Siberia. Several sites were found in the Crimea, in the middle Dnieper basin, in the Transcaucasus, Altai and Sayan Mts., regions around the Baikal Lake (Appendix. Fig. 8). During the late glacial time, area of *Crocuta spelaea* broke into several separate areas; the remains corresponding to this period were found only in the Middle Don drainage basin, in the Urals and Altai Mts. The latest hyena remains were described from the Altai site of Kaminnaya (layers 6-9), they were dated to 10,000 yr B.P. The associate fauna included mammalian species differing in their ecological preferences, i.e. woolly rhinoceros, horse, elk, roe

deer, red deer, zokor, squirrel, souslik. One can see that cave hyena gave preference to habitats situated in the elevated regions. Probably those animals were not so tolerant to cold as compared to the cave lion, and during the whole Late Pleistocene its range was limited only to the southern regions of the former SU.

IV. Cave lion — *Panthera leo spelaea* Goldfuss

It was one of the large cave carnivores, with the body mass ca. 250-300 kg, sometimes up to 350 kg. The most complete data on the history, morphology and distribution of the cave lion during the Pleistocene time, supplied with the sketch map of the sites over the Northern Eurasia, were presented by N. K. Vereshchagin (1971). Having examined taphonomy of sites and their geography, the author came to the conclusion that these predators were perfectly adapted to the conditions of cold forest-steppes.

PALEOFAUNA database includes only materials dated reliably by means of absolute and relative methods. The following picture of the cave lion distributions during the Late Pleistocene time was based on such data only.

At the Late Pleistocene beginning, during Mikulino Interglacial, the cave lion was spread on the Russian Plain and in the Transcaucasus. Bones of the species were found in the Shkurlat site (Don River middle drainage basin) (Alekseeva 1980), and the Bynagady site (Vereshchagin 1951). There are no sufficient data of the Mikulino age, so we can not describe the lion range of that time.

In the first half of the Valdai glacial epoch, the area of the cave lion habitation increased in the Northern Eurasia (Appendix. Fig. 9). About 20 sites of this age are known. Most densely inhabited were the Russian Plain south, the Crimea, the Caucasus, the Urals, the Altai, Sayan and Middle Asia Mts. Sites with *Panthera leo spelaea* remains were found in Transbaikalian. Unique findings of this age are reported in the Subarctic, about 70° N.

During the Bryansk (Karginsky) warming, the species inhabited the centre of Russian Plain (Don River drainage basin), Transcaucasus, the South Urals, Sayan Mts. (Appendix. Fig. 7), primarily the elevated regions.

During the Valdai maximum phase (24,000-15,000 yr B.P.), the lion area changed insignificantly (Appendix. Fig. 8). In the Urals it reached 62° N. In the late glacial time, the area embraced the Russian Plain, mountains of the Urals, Altai and Sayan. The carnivore remains dated to this time were marked in the Subarctic, the Indigirka River basin, about 70° N (Appendix. Fig. 10).

Analysis of the cave lion distributions during the Late Pleistocene time argues for the species being highly eurybiotic, which allowed lions to live both in the mountains of Siberia and East European south, and in Subarctic regions. Abundance of her-

bivorous animals inhabiting highly-productive periglacial steppes and forest-steppes favoured wide spread of lions during the Valdai glaciation time.

The related north-american species, *Panthera leo atrox*, lived up to the late glacial period (Graham & Lundelius 1984).

V. Horses — *Equus latipes* V.Gromova, 1949; *Equus uralensis* Kuz'mina, 1975; *Equus lenensis* Russanov, 1968; *Equus ex gr.caballus* Linnaeus, 1978

Reconstructed area of distribution of the *Equus* subgenus embraces Western Europe, north of Africa, Asia Minor, centre and south of East Europe, Kazakhstan, Central Asia (Geptner et al. 1961).

Remains of caballoid horses dated to the Late Pleistocene beginning were found in the Crimea and at the Don River middle reaches (Appendix. Fig. 11). During the early Valdai, horses of the species mentioned were widely spread over the whole North Eurasia, from the Crimea, Transcaucasus, Middle Asia, Altai and Sayan Mts., up to the Taimyr Peninsula and lower reaches of the Kolyma River (Appendix. Fig. 11). Ecological requirements of all those horses were not totally identical. Thus, *Equus latipes* lived in the forest-steppes (Kuz'mina 1980), and *Equus uralensis* preferred habitats with more continental conditions (Kuz'mina 1989). Morphological characteristics of *Equus lenensis* skeleton argue for its adaptations to cold continental climate and feeding on forbs (Kuz'mina 1989; Egorova 1977). In the Ussuriysky region there lived another type of horse which showed adaptations to forest-steppe habitats. At that time, universally spread were various periglacial landscapes. They featured thin snow cover in winters and therefore were favourable for these herd ungulates.

During the Bryansk-Karginsky warming, the range practically did not change; the horses still lived in the central and south regions of the Russian Plain, in the Crimea, in the Urals, in the Altai and Sayan Mts., and east of the Baikal Lake. The horse remains have been recorded in the localities in Yakutia and the Taimyr peninsula (Appendix. Fig. 12). All these facts agree with the idea that middle Valdai Interstadial was insignificant enough, and, that the open landscapes which existed during the early Valdai time existed also during the later period in Northern Eurasia.

Finds of fossil horses remains were especially numerous during the late Valdai time. They were marked in the majority of cultural layers of Late Paleolithic sites, thus indicating that these mammals were intensively hunted. Numerous sites are situated in eastern Europe, and the northernmost of them lie at about 53° N, that is, some 100-200 km from the Valdai glacier limit. However, the majority of them are dated either to the beginning or to the end of the Valdai cold time. The associate fauna included

mammoth, woolly rhinoceros, reindeer, collared and true lemmings, *Lagurus*, forest voles. In the Urals, horses reached 62° N. In Siberia and North-East, bones of the horses were also found. The northernmost occurrences of these mammals have been reported from the Taimyr peninsula, 75° N, and the Ayon Island, 70° N. Horses also inhabited the centre of West Siberia, Middle Asia, Altai-Sayan Mountains, and the regions west of Baikal (Appendix. Fig. 13).

During the late glacial time, the range of the horses decreased. But their bone remains were found on the Russian Plain, in the Urals mountains, in West and East Siberia, Altai and Sayan Mts. No sites are known from the Siberian Subarctic (Appendix. Fig. 14). The main factors probably limiting the horses range were the coming warming and the consequent degradation of periglacial hyperzone with its highly-productive open landscapes, reinforced by intensive hunting activities of the Early Man.

VI. Pleistocene wild ass — *Equus hydruntinus* Regalia, 1907

During the Pleistocene time, *Equus hydruntinus* was widely spread in open landscapes of Mediterranean (Vereshchagin & Baryshnikov 1980 b; Batyrov & Kuz'mina 1991). It was a part of the Pontian-Kazakhstan steppe assemblage of mammals which existed during the late Valdai time (Baryshnikov & Markova 1992).

Mikulino sites with remains of wild ass were found in the Crimea (Kiik-Koba site, lower layer) and at the Apsheron peninsula (Binagady site), they also contained bones of numerous mammalian species, mainly the steppe forms (Appendix. Fig. 15).

During the early Valdai time, the wild asses inhabited the Crimea, Transcaucasus, mountains of Middle Asia and Altai (Appendix. Fig. 15). The associate mammalian fauna constantly included animals adapted to life in dry steppes and semideserts, as saiga, different horses, *Lagurus lagurus*, *Eolagurus luteus*, *Ellobius*, together with typical representatives of the mammoth complex, i.e. mammoth, woolly rhinoceros, reindeer, polar fox. Sites in Middle Asia contained ass bones together with those of the porcupine, in the Altai site "Proskuryakov's Cave" they were found together with bones of the black-tailed gazelle, and usually together with remains of cave carnivores, primarily the cave hyena.

During the Bryansk-Karginsky Interstadial, the wild ass inhabited the east foothills of Carpathians and Sayan Mts. (Appendix. Fig. 15). During the late Valdai time, the species continued to occupy the Crimea, where it co-existed both with the complex of steppe forms, and such representatives of the mammoth complex as the woolly rhinoceros, the reindeer, and the polar fox. Ass remains are also known in the Middle Asia (Appendix. Fig. 15). *Equus*

hydruntinus became extinct in the Crimea during Mesolithic time (Batyrov & Kuz'mina 1991), and persisted as late as the Middle Holocene in northern regions near the Black Sea (Bibikova 1975).

Analysis of all the available data on chorology of the Pleistocene ass revealed stability of the species area. The most favourable conditions for *Equus hydruntinus* were those in dry steppes and semideserts spread in south regions of North Eurasia, which remained there even during the cold periods.

VII. Woolly rhinoceros — *Coelodonta antiquitatis* Blumenbach, 1799

Judging by identifications of macrofossils reserved in teeth cavities of rhinoceros and its excrements, these large animals ate mainly graminids (89 %), *Compositae* plants (4.5 %), sagebrushes (2.5 %), as well as alder and willow branches (Vereshchagin & Baryshnikov 1980). The most favourable conditions for this species probably existed in dry southern steppes. Thus, EAVangengeim (1977) noted that rhinoceros were especially numerous in the Transbaikalian steppes and semideserts. As one can see from the sketch map drawn by N.K.Vereshchagin and G.F.Baryshnikov (1980-b), the Pleistocene range of *Coelodonta antiquitatis* occupied practically the whole North Eurasia. Information received with the help of the PALEOFAUNA data bank allowed to revise the species area alterations during the Late Pleistocene time in more details.

During the Mikulino Interglacial, the remains identified as the woolly rhinoceros were found in the Don River middle reaches, the site of Shkurlat (Alekseeva 1990). The remains dated to the early Valdai time were described from the central and southern regions of the Russian Plain, the Crimea, the Urals and Middle Asia Mts., Altai and Sayan mountains, Transbaikalian regions (Appendix. Fig. 18). No data indicate the species occurrence in the regions north of 55° N.

During the Bryansk-Karginsky warming, the remains of the woolly rhinoceros were found in the above mentioned places and, besides, in the Lena River middle reaches (63° N), and in the Middle Urals (60° N); thus the range spread towards the north (Appendix. Fig. 20).

During the last glacial maximum (24,000-15,000 yr B.P.), the area of the woolly rhinoceros covered practically the whole Russian Plain (except the Crimea), South and Middle Urals, eastern part of the lowland near the Caspian Sea, Kazakhstan uplands. The bone remains were found at the lower Irtysh River, in the Ob' River basin (south of 60° N), Altai and Sayan Mts., regions both east and west of the Baikal Lake, basin of the Aldan River. One-of-a-kind was the find at the Ayon Island (about 70° N) (Appendix. Fig. 20). Such trans-continental area occupied by the woolly rhinoceros offers the high ecological adaptability of the species, the main life demand of

which was perhaps presence of open lands with rich herbaceous vegetation.

During the late glacial time (15,000-10,000 yr B.P.), *Coelodonta* range changed significantly. The bone remains of this age are not known from the Crimea and Middle Asia, but they were found in polar Urals (69° N) and at the Indighirka River mouth (Appendix. Fig. 19).

The latest occurrence of the woolly rhinoceros were reported from the Altai sites, their age being estimated at about 10,000 years BP (Appendix. Fig. 19). Degradation of the late Valdai open periglacial tundra-steppes and steppes, together with the growing pressure of primitive hunters, led to abrupt devastation of the range of this large odd-toed animal, and to its subsequent extinction by the Late Pleistocene end.

VIII. Giant deer — *Megaloceros giganteus* Blumenbach, 1803.

First stages of evolution of *Megaloceros* species took place in Europe where its ancestor forms were known from the Villafrancian (Vereshchagin & Baryshnikov 1985).

During the Mikulino Interglacial, bones of the giant deer were identified only from the Crimea localities. The remains dated to the early Valdai were found in the Dniester basin, lower reaches of the Dnieper River, and Don middle-reaches, in numerous sites of the Crimea and Transcaucasus, in the mountains of southern Siberia. The total of 23 sites dated to this time are known (Appendix. Fig. 21). Associate fauna includes mammoth, woolly rhinoceros, bison, horse, badger, marmot, common and tundra voles, added with saiga and Pleistocene ass in the Crimea, and with *Lepus tolai* in the Altai sites.

During the Bryansk-late Karginsky warming, *Megaloceros* were spread in the Don basin, east foothills of Carpathians, and in the Caucasus (Appendix. Fig. 21). The co-existing species were mammoth (except in the Caucasus), bison, reindeer, common vole, etc. In the Caucasus, the Akhshtyrsky cave, *Megaloceros* bones were found together with those of the red deer, wild boar, cave bear, — i.e. the species complex indicative of the forest landscapes around the site.

Six sites with *Megaloceros giganteus* remains are dated to the late Valdai cold time. In the interval of 24,000-15,000 yr B.P., the species range encompassed the east foothills of Carpathians, Don River middle reaches, the Volga basin, the Crimea and the Altai. The giant deer bones were not recorded north of 53° N, thus the species is considered to be relatively mesophilic (Appendix. Fig. 22). In all the sites (except the Crimea) mammoth was found together with *Megaloceros*.

During the late glacial time this species practically disappeared from the territory of the former SU. Remnants of *Megaloceros* population persisted only

in the upper reaches of the Yenisey River and west regions near Baikal Lake, where they lived till 12,000-13,000 yr B.P. The associate fauna of this time included mammoth, reindeer, red deer, woolly rhinoceros, bison, cave lion, polar fox, alpine hare, etc.

The giant deer failed to adapt to the conditions of the Valdai time opposed to other species of the mammoth complex, such as mammoth, woolly rhinoceros, primitive bison, aurochs and reindeer. During the Valdai glacial time its range was restricted to the southern regions of North Eurasia, probably being limited mainly to highly-productive periglacial forest-steppes and grasslands. Extinction resulted primarily from the devastation of relatively mesic herbaceous formations, and was aggravated by low reproduction in the species, and hunting pressure of early people. The Holocene-dated *Megaloceros* populations are known from Ireland (Vereshchagin & Baryshnikov 1985; Monaghan 1995).

IX. Aurochs, the wild ox — *Bos (Bos) primigenius* Bojanus, 1827

This ancestor of the European cattle with body mass reaching 600-800 kg existed as long as the 17th century (Tsalkin, 1956). Numerous paintings of this animal made by early people exist, some of those are known from Late Paleolithic cave sites in Spain and France. In the historic time, the species range included the Northern Africa, all parts of Europe (South, Centre, West and East), Asia Minor, Syria, Mesopotamia. In the pre-historic time, it occurred in West Siberia and Kazakhstan. Last primitive oxen were forced to the forests by people. However, the most optimal conditions for these animals were those of forest-steppes, and probably of steppes. These large ungulates fed on herbaceous vegetation and leaved tree branches. They were domesticated in Greece about 4,000 yr B.P. (Vereshchagin 1956; Geptner et al. 1961).

The earliest Late Pleistocene remains of the aurochs were found at the site Kiik-Koba in the Crimea (Appendix. Fig. 23). During the early Valdai time *Bos primigenius* occurred widely in the Dnieper and Don basins, in the Crimea, Transcaucasus, and in the mountains of Middle Asia (Appendix. Fig. 21).

During the Bryansk-late Karginy Interstadial (35,000-24,000 yr B.P.), the species inhabited regions near the Dnieper and Don middle reaches, regions east of the Volga River, and in the South Urals (Appendix. Fig. 23). The most favourable conditions for the species were those in periglacial forest-steppe landscapes.

During the Valdai glaciation maximum phase, the primitive ox range spread even more, and in Eastern Europe it covered the territory from the northern coasts of the Black Sea and the Crimea up to 55° N. This is an indication of the animals being indifferent to severe conditions of the time. Thin snow cover, characteristic of the late Valdai environments, was also

good for the animals. Existence of vast open periglacial landscapes with highly productive phytocoenoses made the conditions optimal for these mammals (Appendix. Fig. 24). Bones of the primitive oxen were found in the Middle Asia, Sayan and regions west of the Baikal Lake. Population density of the species was very high. The remains of these important hunted animals were found in the cultural layers of many Late Paleolithic sites in the Northern Eurasia. The species formed a part of the boreal variant of the mammoth complex and of the Pontian-Kazakhstan steppe complex (Baryshnikov & Markova 1992).

During the late glacial time *Bos primigenius* retreated from the Crimea, the Caucasus, and mountains of the Middle Asia. Bone remains of the species were found in the sites of the central Russian Plain (47-54° N), in the South Urals, and in the West Siberia (55° N) (Appendix. Fig. 24).

X. The Baikal yak — *Bos (Poephagus) baikalensis* N. Verestchagin, 1954

In our days range of the recent yak *Bos (Poephagus) mutus*, is restricted to stony deserts of the Tibet plateau. The animals feed mainly on forbs, they are indifferent to low winter temperatures.

Only few data are available as regards the distribution of yaks during the Late Pleistocene time. All the finds known are dated to the Late Pleistocene second half, Valdai glaciation time. The only site with yak bone remains in the Sayan Mts. was correlated to the early Valdai (Appendix. Fig. 16). During the middle Valdai warming the species range was probably wider, including the Altai and Sayan mountains, as well as Transbaikalian region (Appendix. Fig. 16). No sites of later age were found.

Together with yak remains, bones of other animals were found, those of woolly rhinoceros, onager, primitive bison, reindeer, giant deer, saiga, cave lion and cave hyena, ounce, leopard, dog fox, siberian ibex, black-tailed gazelle, tolai hare, pikas, narrow-skulled vole, sagebrush vole, etc. Besides, some sites contained the remains of the mammoth. The associate fauna lists are characteristic mainly for the open landscapes of mountains. Large number of presently extinct species (mammoth, woolly rhinoceros, etc.) were widely spread during the Late Pleistocene time in periglacial tundra-steppes and steppes all over the North Eurasia.

XI. Primitive bison — *Bison priscus* Bojanus, 1827

It was one of the most widely spread species of the Late Pleistocene megafauna, and one of the most important hunted animals of the time.

During the Mikulino Interglacial, it inhabited vast territories in the Russian Plain south, in the Crimea, being also marked in the upper reaches of the Ural

River (Appendix. Fig.) However, no sites with remains of this species were described east of the Ural Mts.

The early Valdai range of *Bison priscus* occupied an immense territory in Eastern Europe, from the Russian Plain south and the Crimea, to the upper Dnieper River. The species expansion followed the reduction of forest cover on the Russian Plain and wide development of open periglacial landscapes. Dated to this time interval are the bone remains of primitive bisons from the Urals (about 55° N), from the Middle Asia, Altai and Sayan Mts., the Transbaikalian. The northernmost site of this age is situated at 68° N, in the basin of the Raucha River (Appendix. Fig. 25).

During the Bryansk (Karginsky) warming, bisons also inhabited the whole territory of the Russian Plain. They were not noted north of 59° N in the Urals, probably due to the ice sheet from Novaya Zemlya which showed the maximum spread southwards about 39,000 yr B.P. (Faustova & Velichko 1992). The northernmost finds in Siberia are known from the Aldan River basin (Appendix. Fig. 25).

At the time of glaciation maximum in Eastern Europe, the northern limit of the range moved southwards, undoubtedly being forced by the Scandinavian ice sheet. However, in the Urals mountains *Bison priscus* occurred up to 62° N, the fact probably suggesting not so large dimensions of the Novaya Zemlya ice sheet during the late Valdai time. Bison bone remains were also found in West Siberia (middle streams of the Ob' River), in the Altai and Sayan Mts. Several sites of the same age are known from the Aldan River basin. The northernmost known site is situated at the Ayon Island (70° N), which at that time was a part of the continent. (Appendix. Fig. 26). Vast distribution of bisons during the Late Pleistocene maximum argues for favourable conditions existing for these herbivorous animals, whose fodder demands need wide highly-productive grasslands.

During the late glacial period (15,000-10,000 yr B.P.), the range of *Bison priscus* was also very extensive, but differed from that of the previous time, as it reached the Pechora River middle reaches in Eastern Europe, and the Enisey River mouth in Siberia. As before, bison bone remains were noted in the extreme North-East, i.e. basin of the Anadyr' River and Indighirka River mouth (Appendix. Fig. 26).

It is known that *Bison priscus* was spread in the Northern Eurasia till the Holocene time. Populations of the subspecies *Bison priscus athabasca* Rhoads, 1897, now remain in low numbers in Canada (Gromov, Baranova 1981). The only species of the genus, the wisent *Bison bonasus*, now persists only in reservations of the North Eurasia, and the conditions there (forest massives) are not optimal habitats for the animals. All the data available for this form, as well as for the ancestor form, *Bison priscus*, indicate that the best habitats for those were the steppe landscapes, including periglacial steppes.

XII. Extinct spiral-horned antelope — *Spiroceros kiakhtensis* M.Pavlova, 1910

This even-toed mammal inhabited south of Siberia and Northern China starting from the Middle Pleistocene time (Gromov & Baranova 1981). It was a typical species of the Central Asia.

Dated sites of this species remains are very rare. Only 4 sites are attributed to the Late Pleistocene time (Appendix. Fig. 17).

During the Karginsky warm period (35,000-24,000 yr B.P.), this large hooved animal occurred in the Altai and Transbaikalian regions (sites Sukhotino 4 and Kara-Bom). During the last glacial maximum (24,000-15,000 yr B.P.), it occupied the same regions (Appendix. Fig. 17). The species remains were found in the sites Sannyi Mys and Ust'-Kanskaya. The main associate fauna included woolly rhinoceros, mammoth, primitive bison, saiga, yak, horse, cave hyena, mufion, Siberian goat, black-tailed gazelle, tolai hare, long-tailed Siberian souslik. All these species are well adapted to living in various elevated xerophytic ecosystems, i.e. mountain steppes, semideserts, grassland-steppes. Such conditions were favourable for *Spiroceros kiakhtensis*, too.

Species reserved alive till now

Species inhabiting the tundra zone

XIII. Polar fox —*Alopex lagopus* Linnaeus, 1758

Alopex lagopus is one of the few carnivore animals, inhabiting tundra and forest-tundra zones up to the present moment.

Remains of this species, dated to the Late Pleistocene beginning, are known only from the Urals and western foothills of the Carpathians. During the early Valdai time, *Alopex* range increased; the bones of this age were found at many sites in the Crimea, Dniپر middle and upper reaches, in the Urals and Sayan Mts. Thus, the species southern limit was shifted about 2000 km southwards as compared to the recent range (Appendix. Fig. 27).

During the interstadial warming, 35,000-24,000 yr B.P., the polar fox range was reduced, and it did not include the Crimea. The southern boundary of the range passed east-west at about 48° N in the west regions of the Russian Plain, rising northwards until 52° N in the regions east of the Volga River. In the Urals, *Alopex* occupied the territory from the Ural River upper reaches up to 69° N (Appendix. Fig. 27). No finds of this time are known from Siberia.

Numerous bone remains of *Alopex lagopus* are dated to the late Valdai time, 24,000-15,000 yr B.P. At that time, the polar fox inhabited the Crimea, lower Dnieper basin, and the Don River middle reaches. Many sites were found in the South and Middle Urals; some *Alopex* bones were reported from the upper Ob' River reaches, Sayan Mts., west of the

Baikal Lake, and in the upper Aldan River basin (Appendix. Fig. 28). Such expansion was certainly the result of global cooling and wide spread of periglacial open landscapes with rich fauna of such small mammals as lemmings, voles, steppe lemmings, etc., that made a feedstuff of the polar foxes.

During the late glacial time, 15,000-10,000 yr B.P., the southern limit of *Alopex* area of habitation was about 48-50° N. The carnivore remains of this age are not known in the Crimea, but plenty of these were found in the Urals, between 50 and 65° N (Appendix. Fig. 28).

XIV. Reindeer — *Rangifer tarandus* Linneaus, 1758

During the historic time, the reindeer occurred all over the northern part of Eastern Europe, reaching 55° N, and the same latitude in West Siberia. Towards the east, the area expanded southwards, and the species range covered practically the whole territory of East Siberia and North-East (Geptner & et al. 1961). Hence, in the historical time, reindeers inhabited tundra, forest-tundra, and subzone of taiga forests, with small populations lasted out in south Siberia mountains. The most favourable conditions for recent reindeers were those of tundra and forest-tundra.

Reindeer is one of the most characteristic species of the mammoth complex. Late Pleistocene sites with bones of these ungulate mammals are widely spread in North Eurasia.

Reindeer remains, dated to Mikulino Interglacial, are very rare. They were found only in the Urals and Transcarpathians (Appendix. Fig. 29). Onset of the early Valdai cold time, and the following changes in nature zonation of the period, as well as wide distribution of open landscapes, led to the extreme expansion of the reindeer species over the whole territory of the former SU, embracing the regions immediately north of the Black Sea, the Crimea, Transcaucasus, mountains of Middle Asia, Altai, Sayan, and Transbaikalian regions. Early Valdai sites with reindeer remains were especially numerous in the Siberian Subarctic (Appendix. Fig. 29), but none of those were known from the Far East.

During the Bryansk (late Karginisky) Interstadial, the reindeer also occupied vast territories of the Russian Plain, in the Urals, Altai, and Transbaikalian. Sites of the species bone remains were in the Aldan River basin. The northernmost site is at the Ob' River mouth (Appendix. Fig. 30). This is perhaps an indication that warming was insignificant at this time, having no prominent effect upon vegetation cover, and, consequently, the reindeer range did not change.

During the Valdai glaciation maximum phase (24,000-15,000 yr B.P.), the reindeer was one of the most characteristic species of the mammoth complex, and one of the main hunted species. Sites with remains of those ungulates were numerous in the

Russian Plain, in the Urals, Altai and Sayan mountains. The northernmost site of this age was marked at the Ayon island, which formed then a part of the continent because of the dried shelf (Appendix. Fig. 31). Some data on the late Valdai reindeers in the Aldan River basin exist as well.

During the late glacial time, the density of reindeer sites in Eastern Europe was still high enough. However, the range southern limit shifted northwards, and no sites were found in the Crimea and in the Caucasus (Appendix. Fig. 32). At the same time, ca. 15,000-10,000 yr B.P., reindeers were numerous in the Urals mountains, reaching 65° N, i.e. there was probably no significant glaciation in the North Urals at that time. To compare, one would remember, that during the maximum cold period, the limit of *Rangifer tarandus* in the Urals was on 60° N (Appendix. Fig. 32). In Siberia, the reindeer bones were found in Altai and Sayan sites, the regions around the Baikal Lake, basin of the Aldan River, and Indigirka River mouth.

Of particular interest is finding of reindeer bones dated to 7,000-8,000 yr B.P., at the Zhokhov Island, 77° N. The reindeers came to this arctic island during the Late Pleistocene time, and persisted there till the Holocene (Pitul'ko et al. 1990).

Analysis of the reindeer area dynamics during the Valdai Glaciation time suggests that this mammal was a highly eurybiotic species, and it was adapted to periglacial landscapes of various types, from the arctic tundras to savanna-like ecosystems of the south regions of the Russian Plain, and mosaic mountain landscapes; there were no barriers like forest zone which could prevent the reindeers spread southwards.

XV. Musk ox — *Ovibos moschatus* Zimmermann, 1780

The musk ox is one of the most characteristic Subarctic species, demonstrating frost-tolerance to the temperatures as low as -50 -60° C, but not capable to ignore thick snow cover. Now they live only on Greenland, in the north of Canada, and on the isles of North-American archipelago. *Ovibos* inhabited North Siberia and Alaska till the historical time (Vereshchagin & Baryshnikov 1980).

This species formed a part of arctic subcomplex of the mammoth complex. During the Valdai time, it was not as abundant as the reindeer (Baryshnikov & Markova 1992).

No information exists on the *Ovibos* distribution during the Mikulino Interglacial. Probably the species area was restricted to the high latitudes. Sites dated to the early Valdai time are also very rare, being restricted to East Siberia (Appendix. Fig. 33). Middle Valdai aged sites were found in the Middle Urals (Appendix. Fig. 33). During the late Valdai maximum cold period, the musk oxen expanded far to the south, reaching 49° N in Eastern Europe, and

60° N in West Siberia. Their remains were marked in the Altai Mts., and the Aldan River upper reaches. No sites of this age are known in the European Subarctic, which was then covered by the ice sheet, but *Ovibos* bones were found in the Urals, ca. 62° N. The species was also widely spread in East Siberia and North-East (Appendix. Fig. 31). Being compared to the area of the permafrost during the late Valdai time, *Ovibos* range appeared to be practically identical to it. V.P.Nechaev (1986) studied paleo-cryogenic deformations and thus reconstructed the areas of the permafrost in Eastern Europe during the late Valdai time. Based on his data, the southern permafrost boundary in the west of the Russian Plain was established to lie on 47° N at that time, being shifted northwards in the eastern regions.

At the beginning of the late glacial time, *Ovibos moschatus* still inhabited the centre of the Russian Plain, the Middle and North Urals, Sayan Mts., Aldan River basin (Appendix. Fig. 33). During the Holocene period, periglacial biome was disintegrated, and the oxen range was reduced significantly; the species disappeared from many regions of the North Eurasia. At the territories of the former SU, the musk oxen lasted in the East Siberia until the historic time (before reacclimatization).

Analysis of distributions of the Subarctic mammals during the Late Pleistocene time lead us to the following conclusions:

1) no remains of the animals now inhabiting tundra and forest-tundra were found to correspond to the Mikulino Interglacial. Probably the ranges of these species during that warm period were restricted to the Subarctic regions only;

2) during the Valdai glaciation time, they expanded far to the south. Some of them reached the Crimea and other regions near the Black Sea, as reindeer and polar fox, while the others, namely *Ovibos*, reached the latitude of 47° N in Eastern Europe, which was just the permafrost southern borderline. Diverse mammal species now inhabiting the Subarctic regions are different in their responses to cooling, thus corroborating the correctness of Dr. Graham's idea about individualistic response of separate species, not associations of species, to climatic changes (Graham 1985; 1986).

Mammals now inhabiting forest and forest- steppe zones

XVI. Common (pine) marten — *Martes martes* Linnaeus, 1758

Now the common marten inhabits old coniferous, deciduous, and mixed forests with numerous wind-fallen trees. These carnivores prey mainly rodents, hares and birds.

Mikulino-dated remains of *Martes martes* were reported from the Southern Urals (Appendix. Fig. 34). During the early Valdai time, the marten inhabit

ed mountain forests of the Crimea, Caucasus, and the Urals (Appendix. Fig. 34). No remains of the species were found in flat country, which may indicate, that no significant patches of forest vegetation existed on the Russian Plain or in West Siberia during that time.

During the Bryansk interstadial, and until the late Valdai time, the marten range was also restricted mainly to the elevated regions of the Caucasus and Transcarpathians (Appendix. Fig. 34). In the Urals, during the late glacial time, *Martes martes* began to migrate northwards and reached 62° N, probably in response to the warming process (Appendix. Fig. 34).

On the whole, during the Valdai glaciation time, abrupt reduction of *Martes martes* range was marked, resulting perhaps from degradation of zonal forest biome, when forest massives remained only in mountain regions of North Eurasia.

XVII. Russian sable — *Martes zibellina* Linnaeus, 1758

The recent range of the sable occupies the Urals, East and West Siberia, the Far East; the sable inhabits dark-coniferous taiga forests. The diet includes small rodents, birds, pine nuts, berries, insects (Flint et al. 1970).

The sable remains, dated to the Late Pleistocene time, are known from few sites, and practically all of them were found in the Urals; one early Valdai site was described from the Altai (Appendix. Fig. 35).

Rare finds of this carnivore, attributed to the Valdai time, probably reflect destruction of the zonal forest vegetation, which was the case during the whole period of the last glaciation.

XVIII. Glutton (wolverine) — *Gulo gulo* Linnaeus, 1758

Wolverines now inhabit taiga and forest-tundras, penetrating to the tundra zone, too. It is a predatory species, attacking ungulates (reindeer, roe deer, musk deer), and preying birds, but it can also feed as a scavenger (Flint et al. 1970).

Dated to the Mikulino Interglacial, bone remains of *Gulo gulo* were found in the Transcarpathians, and in the Urals (Appendix. Fig. 36). During the early Valdai time (110,000-35,000 yr B.P.), this carnivore inhabited the Crimea and Caucasus, Middle and South Urals, Altai and Sayan Mts. (Appendix. Fig. 36). Probably it rarely occurred in the plain regions of Eurasia, although the animals making the species diet inhabited vast territories of periglacial forest-steppes and steppes in Europe and Siberia. On the other hand, here we might be faced with the shortage of data, needed to describe the species distribution pattern during the time period mentioned.

Information concerning the Bryansk-Karginsky Interstadial is also practically missing. The only site of this age with *Gulo gulo* remains is known from the Middle Urals (Appendix. Fig. 36). Dated to the second half of the Valdai epoch, the glutton bones were found at numerous sites situated in the Transcarpathians, Russian Plain centre, in the Urals, Altai, and regions west of the Baikal Lake (Appendix. Fig. 37). Concentration of sites with *Gulo gulo* remains in the centre of the Russian Plain, between 50 and 53° N, is of the particular interest. As it was mentioned above, forest-steppe periglacial associations were reconstructed for these regions (Simakova & Kozharinov, Chapter 4 of the present publication). The carnivorous species *Gulo gulo*, well fit to severe climatic conditions of the time, probably preyed numerous herbivores living there, primarily, reindeers and horses.

Dated to the late glacial time, numerous glutton remains were marked on the Russian Plain (north of 49° N), as well as in the Middle and North Urals, centre of the West-Siberian Plain, and in the Subarctic, namely at the mouth of the Indigirka River (Appendix. Fig. 37). Thus, the range evidently shifted northwards, following the forest-zone restoration onset during the terminal late glacial (Simakova & Kozharinov, Chapter 4 of the present publication).

XIX. Lynx — *Lynx lynx* Linnaeus, 1758

This large cat is now a typical inhabitant of wild forests with thick undergrowth, both in mountains and plain regions. The diet includes hares, rodents, birds; the lynx also hunted roe and musk deers.

Dated to the early Valdai time, lynx remains were found only at the sites situated in elevated regions of the Crimea, Caucasus, Urals, and Sayan (Appendix. Fig. 38). Variety of habitats in elevated regions provided reservation of forest vegetation plots, where the animals preyed by *Lynx lynx* probably were concentrated. Faunas of these regions showed significant increase in mammal species richness during the whole Valdai glacial epoch (Markova 1994; Markova Chapter 5 in the present publication).

Similar situation probably existed also at the time of the late Karginsky warming, although only few data are known related to this period (Appendix. Fig. 38). During the late Valdai time, lynx was spread in the Crimea, Transcarpathians, Russian Plain centre. The species remains of the same age registered at 52° N, in the Desna River drainage basin suggest that even during the late Valdai cold maximum there existed limited areas of forest vegetation, probably as remnants of the preceding forest zone.

During the late glacial time, the lynx range at the Russian Plain shifted northwards, up to 54° N, the

fact probably indicating some amelioration of climatic conditions, and the consequent restoration of biota natural structure (Appendix. Fig. 39).

XX. Wild boar (pig) — *Sus scrofa* Linnaeus, 1758

Now wild hogs live in different types of forests, inhabit forest-steppes, and sometimes are noted in steppe regions. They usually prefer wet biotopes. The northern limit of their range now lies at 55° N in Eastern Europe, and at about 50° N in Siberia and Far East. The species shows high ecological plasticity; though its area is situated in the southern regions mainly, the animals can tolerate low winter temperatures. The main limiting factor for them is thick snow cover (Geptner et al. 1961). In Eastern Europe, wild pigs usually inhabit deciduous and mixed forests, but their preferred biotopes are oak and beech forests with wetlands, and grasslands. In the elevated regions, pigs also inhabit mainly the mountain-forest belt. Their diet includes all kinds of food, i.e. plant roots, rhizomes, bulbs, fruits and seeds, green parts of herbs; insects, earthworms, mollusks, small mammals, etc.

Sites of the wild hog bone remains dated to the Mikulino Interglacial have been reported from the upper Dnieper basin, ca. 55° N and in the east of the Transcaucasus, thus indicating the existence of forest plots there (Appendix. Fig. 40). In the centre of the Russian Plain, forests showed probably the zonal character, which was confirmed by the finds of other forest mammals remains there. On the contrary, in the western regions near the Caspian Sea, forest biotopes showed but limited distribution, this being proved by steppe complex of associate mammalian fauna.

Sites with pig remains dated to the early Valdai time, were found only in the south of North Eurasia, namely, in the Crimea, Taman' peninsula, Transcaucasus, mountains of Middle Asia (Appendix. Fig. 40). Thus, the range evidently shifted significantly as compared to the previous period. That was probably a result of abrupt changes in climatic situation which lead to the forest zone degradation, with arboreal vegetation remaining only in the south regions.

Similar situation probably lasted out during the late Valdai glacial (Appendix. Fig. 40). Only during the late glacial time, pigs penetrated northwards along the forested regions of the Urals Mts (Appendix. Fig. 40).

Thus, cold epoch of the Valdai glaciation appeared to be critical for such moderate-mesic species as wild boar was, that persisted only in the forest ecosystems of southern mountains. Later, during the Holocene time, the species left these refuge places, and moved northwards once again, to populate recent forest and forest-steppe zones.

**XXI. Red deer — *Cervus (Cervus) elaphus*
Linnaeus, 1758**

Cervus elaphus is an ecologically plastic species, now living in different conditions, such as taiga and broad-leaved forests, steppes, tугai (riverine) forests of deserts and semideserts, and in subtropical regions. The most favourable conditions for the red deers are those in forest-steppes. In elevated regions, deers prefer forest belt, although they are noted in other altitudinal belts, too. Deers' diet includes mainly herbs, branches, and tree fruits (Geptner et al. 1961).

PALEOFAUNA data bank possesses no data on the *Cervus* spread during the Mikulino Interglacial. Finds from many sites are dated to the early Valdai time. They are situated in west foothills of the Carpathians, Desna drainage basin, the Dnieper and Don middle reaches. Many of them are located in the Crimea, in the Caucasus, and mountains of Middle Asia; several sites were also found in the South Urals, Altai and Sayan Mts. (Appendix. Fig. 42).

During the middle Valdai Interstadial, distribution of the red deer in Eastern Europe was similar to that during the early Valdai time. Asian part of the range was seen to change, since the red deer migrated far to the Subarctic. Bone remains were found in the lower reaches of the Kolyma River, and in Transbaikalian region (Appendix. Fig. 42).

During the Valdai glacial maximum, the red deer was also widely spread in periglacial landscapes of the Russian Plain, reaching 55° N. It was marked in all mountain systems of East Europe south, Middle Asia, and Siberia, as well as in the Far North (Appendix. Fig. 43). In Asia, the northern limit of the species range also reached 55° N. No finds of this age were marked in the Urals.

In the late glacial, *Cervus elaphus* also inhabited vast regions in the middle and south regions of North Eurasia. Red deers expanded significantly northwards in the Urals, having reached the upper Pechora River (Appendix. Fig. 43).

Analysis of spatial distribution of *Cervus elaphus* during the Valdai glacial epoch argues for its high adaptability to highly variable landscapes of that time, i.e. periglacial forest-steppes, steppes, and forest belts in mountain regions. However, red deers practically did not penetrate to the northern regions, thus being distinct from the typical representatives of the mammoth complex of mammals.

**XXII. Roe deer — *Capreolus capreolus* Linnaeus,
1758**

Roe deer now inhabits deciduous, mixed, and south-taiga forests. It is widely spread in forest-steppe zone, by the flood-plain forests penetrates into the steppe zone; in elevated regions prefers the forest belt. The diet includes mainly leaves and shoots of trees and bushes, as well as forbs. The

northern limit of the recent area lies at 60° N in East Europe, and at 55° N in Siberia (Flint et al. 1970).

Capreolus remains, dated to the early Valdai time, were reported only from Transcarpathians, Crimea, Transcaucasus, Altai and Sayan Mts. (Appendix. Fig. 44), that is, from the mountains of southern North Eurasia. The northern limit was at about 48° N in Europe, and somewhat farther north in East Siberia. For certain, the conditions of glaciation and lacking forest zone were unfavourable for spread of these thermophilic leaf-eating ungulates.

During the Bryansk-Karginsky Interstadial, the range of the roe deer increased. The species remains were registered up to 55° N. Sites with its bones were found in Transbaikalian (Appendix. Fig. 44).

The most part of the sites, dated to the Valdai glaciation second stage, was situated in the south elevated regions of North Eurasia. Several localities were found in the Urals, with the northernmost of them at the lower Pechora River (Appendix. Fig. 43). New data on distribution of the plant communities during that time gave an insight into the problem of trees as components of phytocoenoses at middle latitudes of the Russian Plain (Simakova & Kozhari- nov Chapter 4 of the present publication). Probably populations of the late Valdai roe deers were associated with patches of trees and bush vegetation in periglacial forest-steppes. However, only 11 sites with *Capreolus* remains of that age (24,000-15,000 yr B.P.) have been found, though we analysed information on about 185 sites, dated to the time mentioned. Hence, the species was not common during the second half of the Late Pleistocene, when its preferable habitats seemed to be absent.

During the late glacial time, these ungulates were not abundant, too. Several sites of *Capreolus* bones were found in the Urals, and South Siberia mountains (Appendix. Fig. 45). Only when the Holocene warming came, and the zones of forests and forest-steppes were restored on the plains of East Europe and Siberia, roe deers expanded northwards, and over the forest zone.

XXIII. Elk — *Alces alces* Linnaeus, 1758

The elk is now spread in the forests of Eurasia and North America, and partially in the forest-steppes. It inhabits different types of forests (taiga, mixed, and deciduous forests), keeps in the forested plots of forest-steppes and the flood-plain forests in steppes. In winter, elks feed on woody branches, while in summer they eat leaves of trees and forbs, especially those growing in wetlands, as well as water plants. It is one of the few mammals indifferent to thick snow cover, up to 80 cm (Geptner et al. 1961).

No bone remains of elks, dated to the early Valdai time (35,000-100,000 yr B.P.), are known from the Russian Plain. This perhaps argues for significantly different structure of natural zones at that

time. Bones of elks were found only in Transcarpathians, Altai Mts., and Transbaikalian (Appendix. Fig. 46). Finds of the species remains in the North-East are of especial interest.

Sites with *Alces alces* remains, dated to the Middle Valdai (Bryansk-Karginsky) interval, are also few. They are known from Transcaucasus regions, Sayan Mts., and Transbaikalian. Of the total 110 sites included into PALEOFAUNA data bank and dated to this time period, only 4 taxa lists mentioned the elk remains. Such ratio clearly indicates, that conditions were unfavourable for these mammals, probably due to degradation of forests, that held out mainly in the elevated regions of the south of Northern Eurasia.

Dated to the late Valdai time (24,000-15,000 yr B.P.), the number of sites with *Alces alces* remains was limited, too. They were found in Transcarpathians, in the Caucasus, Urals, Altai and Sayan Mts. (Appendix. Fig. 47), where forest plots still existed.

During the late glacial period (15,000-10,000 yr B.P.), the elk distribution showed the similar pattern (Appendix. Fig. 47). Only in the Urals it moved northwards, reaching latitude 53° N.

Alces remains dated to the second half of the Late Pleistocene practically lacked among mammal bones in the most part of sites; they were marked only in 30 cases of the total 522 sites listed. All this was perhaps due to unfavourable conditions of that time, which made elks to retreat to the south of North Eurasia.

Analyses of the Late Pleistocene distribution characteristics of some ungulates and carnivore mammals, which are now fit to live in the forest zone, gave an insight of the cardinal rearrangement of biota during the Valdai glacial time in North Eurasia. Thus, the forest zone was probably destroyed, and forest vegetation remained only in mountain regions and / or as small patches in the centre of the Russian Plain, probably located in the flood-plains. The picture began to change during the second half of late glacial, when many forest species moved northwards, following the formation of zonal forest ecosystems. This process ran differently in diverse species of this ecological group, which agrees with the Dr. Graham's idea about individualistic response of separate mammal species to changing climatic and biotic conditions (Graham & Lundelius 1984, Graham & Grimm 1990).

Species now inhabiting the steppe and semidesert zones

XXIV. Corsac fox — *Vulpes corsac* Linnaeus, 1768

The modern range of the species occupies steppes and deserts of the Middle Asia, Kazakhstan, the lower Volga River basin, south of West Siberia, and Transbaikalian region. In the historic time, cor

sac fox inhabited the Crimea, and areas between the rivers of Ural and Irtysh. Diet includes mainly small rodents, sometimes sousliks, hares, hedgehogs (Flint et al. 1970; Gromov & Baranova 1981).

The Late Pleistocene findings are rare. During the Mikulino Interglacial, corsac fox inhabited the Crimea and East Transcaucasus, together with several steppe and semidesert species (Appendix. Fig. 48). During the early Valdai cold time, it occurred in the Crimea, in the Altai and Sayan Mts. (Appendix. Fig. 48). The total of 11 sites are known, and 8 of those are situated in the Crimea. All the sites demonstrated the associate faunas, including the saiga and the reindeer, while in some of them, besides the species mentioned, mammoth and woolly rhinoceros remains were found, too. No corsac fox remains dated to the Bryansk-late Karginsky Interstadial are known.

During the late Valdai time (24,000-15,000 years ago), *Vulpes corsac* was widely spread on the Russian Plain, reaching 53° N (Appendix. Fig. 48). It was also noted in the Crimea, and mountains of the Middle Asia. During the late glacial, the Russian Plain was occupied, too, but the southern limit of the range probably retreated southwards, and no remains of that age were found in these regions to the north from 49° N. However, in the Urals the species remains were found up to 62° N. (Appendix. Fig. 48).

In faunas of different ages, the corsac fox was always found together with saiga, pikas, marmots, sousliks, jerboas, and, since the early Valdai time, — together with the reindeer and polar fox. Mammoth bones were marked in all early Valdai sites together with *Vulpes corsac*, but in the only one site, dated to the maximum glaciation (the site "Eliseevichi 2", in the Desna River basin). During the Valdai glaciation, vast treeless areas and abundant steppe small rodents made favourite conditions for propagation of these small carnivores, being well adapted to the arid open environments.

XXV. Onager (Asiatic wild ass) — *Equus hemionus* Pallas, 1775

Reconstructed onager range occupies the steppe regions of East Europe, West Siberia, Kazakhstan, and Transbaikalian regions, semideserts and deserts of Middle and Central Asia, Tibet, Asia Minor, and North-West India. Asses inhabited Eastern Europe probably until the 12th century. It is a typical inhabitant of deserts, semideserts and south steppes, where annual precipitation is as low as 100-200 mm per year. The diet includes herbs, preferably graminids, sedges, saltworts, onions, forbs. The snow cover thicker than 10 cm, makes difficult feeding in winter (Geptner et al. 1961; Bannikov 1981).

No bone remains of the Asiatic wild ass are known to be dated to the Mikulino Interglacial. The remains of the early Valdai time were found in the

cultural layers of the Altai Mousterian sites “Strashnaya” and “Proskuryakova” (Appendix. Fig. 41). The associate mammal fauna included woolly rhinoceros, cave hyena, lynx, glutton, cabaloid horse, Persian gazelle, steppe lemming, etc., with dominating species fit to habitation in steppe biogeocoenoses.

Onager remains, dated to the Bryansk-Karginsky Interstadial, occur significantly wider; they were found in the Caucasus, Middle Urals, and Altai Mts. (Appendix. Fig. 41). The associate faunas looked different in diverse parts of the range. In the Caucasus, the site Sakadziya, there were bones of a horse, the wild pig, bison, elk, red deer, cave bear, cave lion, — that is, the species of steppe and forest ecology, indicating mosaicity of landscapes in elevated regions, where onager lived in the mountain steppes. As for the Altai sites, the onager bones were found there together with those of mammoth, woolly rhinoceros, bison, yak, saiga, horses, cave bear and cave hyena, muflon, etc., that is, mainly animals of the open biotopes, both of elevated and flat regions. In the Urals, the onager remains were marked together with the bones of mammals designated primarily to steppe forms. Thus, during the Bryansk Interstadial, Asiatic wild ass inhabited various ecosystems, but in all cases the main limiting factor for the species was availability of open steppe or semidesert areas.

During the cold maximum of the Valdai glaciation epoch, the onager inhabited the Altai-Sayan Mts, and Transbaikalian region, together with mammoth, woolly rhinoceros, horses, reindeer, aurochs, bison, Persian gazelle, cave-dwelling carnivores, polar fox, etc., while the remains of the forest mammals were practically absent from these sites. The majority of species, making the bulk of the faunas, were those ecologically related to periglacial cold steppes.

Equus hemionus remains dated to the late glacial time (about 13,000 yr B.P.), have been found only in the upper Enisei drainage basin, at the sites of the “Kokorevsky” Paleolithic culture (Appendix. Fig. 41). The associate fauna of mammals included also mammoth, giant deer and reindeer, bison, and saiga. Besides, the remains of the roe deer, red deer, and the elk were found, too, probably indicating the climate growing warmer. Attributed to the Late Pleistocene terminal and Holocene beginning, mammal fauna from the site of “Kaminnyaya” contained woolly rhinoceros, cave hyena, roe deer, red deer, squirrel, thus indicating restoration of forests in the region. Probably the latter situation was not favourable for *Equus hemionus*.

There exist some data about the Late Pleistocene onager remains in Yakutia, and even at the Begichev Island, but their age is not clear enough (Kuz'mina 1989). Perhaps, the main environmental requirements of both saiga and onager concerned the presence of open territories with hard grounds and herbaceous vegetation. Highly-continental climate with low winter temperatures and low precipitation was favourable for *Equus hemionus*.

XXVI. Saiga — *Saiga tatarica* Linnaeus, 1766

Saiga is a typical specialized inhabitant of dry steppes and semideserts, and a perfect runner developing speeds up to 80 km/h. The species diet includes graminids, plant shoots, saltworts, forbs, ephemeral plants, sagebrushes, steppe lichens, etc. (Geptner et al. 1961). During the last glaciation period, saiga was a component of mammalian mammoth complex (Vangengeim 1977; Baryshnikov & Markova 1992). Till the historic time these ungulates inhabited the steppe zone of Eastern Europe, reaching the Prut River basin in the west, and 50° N in the northern part of the area.

The Mikulino saiga remains were found in the Crimea and East Transcaucasus (Binagady site at the Apsheon Peninsula) (Appendix. Fig. 49). The associate fauna included numerous mammalian remains, primarily of the steppe and semidesert species, i.e. wild ass, horse, corsac fox, different jerboas, mole-vole, and hamsters. In the East Transcaucasus, this complex contained gerbils, *Mesocricetus* golden hamsters, porcupines, together with remains of several cave carnivores, and giant deer. Besides, there were found bones of some species preferring the forest biotopes, as wild pigs, forest mice, and tree dormice (Gromov 1951; Vereshchagin 1951). “Binagady” species complex indicates arid climatic situation, with widely spread dry-steppe and semidesert landscapes. Woodlands and bush communities penetrated there along northern slopes of mountains, and through wet biotopes, providing life conditions for some forest animals.

31 sites of the saiga remains were dated to the early Valdai time (Appendix. Fig. 49). The most part of them referred to cultural layers of the Mousterian sites in the Crimea. Saiga bones of the same age were also noted in the Northwestern Black Sea region, in the Caucasus, Middle Urals, Middle Asia, Altai and Sayan Mts.

Interesting data have been obtained on the Bryansk-Karginsky warming. During that time, saiga expanded far northwards, having reached 56° N at the Russian Plain, and 59° N in the Urals. The species remains were also found in the South Siberia mountains, and in Transbaikalia (Appendix. Fig. 49). Such wide expansion could only occur at the conditions of vast open ecosystems, which were formed during the early Valdai time, and continued to exist during the Bryansk Interstadial, indicating minor warming intensity of the latter period.

During the cold maximum of the Valdai glacial time, the saiga range reached enormous expansion. The remains of the species were marked in the upper Pechora basin in Eastern Europe, and in the Chaun Bay of the North-East (Appendix. Fig. 50). As regards south regions of the former SU territory, saiga bones were found in the Crimea, Middle Asia (38° N), Sayan Mts., and Transbaikalian (Appendix. Fig. 50). The main limiting factors for the species were not environmental temperatures, but food available

and the thickness of snow cover. Rich herbaceous communities of the late Valdai time, the absence of the forest zone, and continental climate with low precipitation particularly in winter, were the factors to favour *Saiga tatarica* expansion all over the North Eurasia. At this time the ungulates migrated far to the west of Europe. The associate fauna included species of the mammoth complex, as mammoth, woolly rhinoceros, reindeer, horses, polar fox, *Lagu-rus*, added by lemmings and the musk ox in the northern part of the range.

Only few remains were found to correspond to the Valdai glaciation terminal (15,000-10,000 yr B.P.); all of them came from the Urals, West Siberia, and Sayan Mts. (Appendix. Fig. 50). However, we can propose, that the species had not completely retreated from the East Europe regions. Indirectly, it is suggested by the facts of deep penetration of the species into Western Europe. Unusual mobility of this ungulate permitted its distant migrations during the late glaciation cold intervals, reaching southwestern France and the British Isles. Thus, in Dryas I sediments (15,000-14,500 yr B.P.) saiga remains were found in the south-west of France, while those dated to Dryas II (12,000-13,000 yr B.P.) were documented in Germany, south-east of France, and in English site "Gough's cave" (Deplish 1983; Currant 1987; Kahlke 1992, 1994).

Analysis of ample information of the PALEO-FAUNA database reveals some general features in responses of individual indicator species of both large and small mammals to global climatic changes during the Late Pleistocene time; it permits to describe alternations of their ranges during the various Late Pleistocene time intervals, and to establish the time spans of extinction of several characteristic Late Pleistocene mammals of the mammoth complex.

For the Mikulino (Kazantsevo) Interglacial, we could fix zonal structure of distributions of small and large mammals in North Eurasia, though based upon few available data. Zonal forest faunas were distinguished clearly. Lack of information on the Arctic regions of the Northern Eurasia gave no opportunity to characterize the northernmost mammal faunas. Probably there existed some reduced variants of zonal tundra and forest-tundra ecosystems, located in Asian regions mainly.

South of the forest faunas range, a belt was revealed with dominating forest-steppe mammal assemblages, but with forest and steppe forms present in local faunas. This belt is natural forest-steppe zone, evidenced by materials from the Russian Plain regions. Previously, location of this zone was concluded from the fauna species composition, mainly by small mammals (Markova 1985, 1986). Position of the forest-steppes south edge is not clear enough due to the shortage of reliable data. However, it was shown that steppe landscapes were spread in the Eastern Crimea, and in the south of the East European Plain.

Species of different ecology inhabited highlands of the Crimea, Urals, Altai, Sayan, etc., since large variety of habitats could be found there in different altitudinal belts, differently facing slopes, and so on. Many endemic mammal species were shown to live in these regions.

Thus, materials on mammal remains from the Mikulino sites, with emphasis on the areas analyses, gave an insight into zonality of natural environments of the time. Although fragmented, the data permit to distinguish the forest, forest-steppe, and steppe zones on the Russian Plain.

Reconstructions of paleovegetation of the Mikulino Interglacial in Eastern Europe showed wide distribution of different nemoral communities between 50-52° N and 59° N, being replaced southwards by forest-steppe formations. The latter occupied the whole south of the Russian Plain, reaching the Black Sea (Grichuk 1982). In general, plant fossils and faunal data are in reasonable agreement. Nevertheless, information on mammals remains indicated that steppe ecosystems existed in the East European south, too. Paleoclimatic reconstructions argue for increase of annual temperatures during the Mikulino optimum by 4° C and more in the north of the Russian Plain, and by 2° C in the centre of the Plain. In the south of Eastern Europe, temperatures seemed not to differ from those of the present day. Annual precipitation values within the whole territory of East Europe were also in excess of the present-day values, by 100-200 mm in the north, and up to 300 mm in the south-west (Velichko et al. 1992). Such climatic situation accounts for wide propagation of nemoral plant communities, as well as of the forest and forest-steppe zonal mammal faunas.

During the Valdai Glaciation, the most part of both large and small mammals changed their ranges significantly. During the Mikulino Interglacial, some mammals showed allopatric distribution, but they became sympatric species during the early Valdai time. First of all, this concerned the species of the steppe and Subarctic zones. In some cases, apart from the remains of steppe and tundra species, the sites included those of the animals adapted to forest biotopes. Therefore, such faunas were named "mixed" or "disharmonious" faunas.

3.2. Small mammals

Natalia E. Kazantseva

The information about localities of small mammals remains is based mostly on fossil material from the ancient man sites and also from fluvial localities. For selection of imposing collections of small mammal remains the elaboration of methodically complicated actions, lead by qualified experts, is necessary. Such work was carried out extremely rare. That was one of the reason of limited lists of small mammals from human sites in comparison with the materials of megamammals. At present the situation is

being changed as the fossil small mammals specialists are being attracted to the work at Paleolithic sites.

The data, favourable for compiling up paleozoologic and paleoclimatologic reconstruction is based on the factual material, for the most part collected out from fluvial deposits. Small mammal remains from the fluvial sites characterise the diverse landscapes of vast territories from which the fossil materials enter into river valleys.

Faunal associations of small mammals of the centre of the Russian Plain (Dneper and Dnestr drainage basins), the Crimea Mts., the Urals Mts., southern part of West Siberian Lowland, and the Altai Mts. are studied the most extensively.

There is some few material from Middle Asia, the Central Kazakhstan, Middle and North-eastern Siberia. There are no data in fact on the Far East region.

Thus because of incomplete material, any reconstruction on form and size of small mammal ranges, it's dynamics during Late Pleistocene is rather approximate. Still definite principal and some particular regularities are succeeded to be marked by the materials arranged in database PALEOFAUNA.

Subarctic small mammals

XXVII. Pied (collared) lemmings — genus *Dicrostonyx* Gloger, 1841

The lemmings inhabit various environments of watersheds and slopes in lowlands and mountain tundra and forest-tundra, though prefer dry and well-drained habitats. They feed on leaves and bark of dwarf birch and willow, on sedges, cloudberry and cowberry (Flint, et al. 1970; Vereshchagin & Baryshnikov 1980). In the opinion of N. G. Smirnov, ancestral forms differed from the modern ones (*D. torquatus*) in ecological characteristics. *D. simplicior* inhabited temperate forest-steppes and tundras, while *D. gulielmi* lived in cold steppes with occasional trees (Smirnov et al. 1990).

Pied lemming remains dated to the Late Pleistocene interglacial have been found in the lower Irtysh basin, in the southern Urals mountains, and on the Chukchi Peninsula. In the last-named region the genus was common since the end of the Pliocene (Agadjanian & Erbaeva 1983).

During the Early Valdai time, the rodent expanded its range as far as 2,000 km south of its modern boundary (Dnestr, Zapadnaya Dvina, the head of the Desna River) (Markova 1984) (Appendix. Fig. 51). During the Bryansk (Karginsky) Interstadial time and the coldest time of the Late Pleistocene, it was distributed all over the territory, and occurred in Eastern Europe, in the Urals, in the lower reaches of the Ob' and Irtysh rivers, at the Angara, and farther eastward in the Aldan basin and on the Chukchi Penin-

sula. The lemmings were also widespread in the west as well, as indicated by numerous findings in Western and Central Europe (Sutcliffe & Kowalski 1976; Chaline 1972; Nadachowski & Wolsan 1987; et al.), where the lemmings formed a part of the Arctic mammoth assemblage, together with musk ox, mammoth, and woolly rhinoceros (Baryshnikov & Markova 1992). Northern boundaries of their ranges in the European part of the former Soviet Union coincided with the ice sheet margins, while in the south they reached as far as 52 to 49° N (Appendix. Fig. 52). In the Asian part of the country localities of *Dicrostonyx* are mostly found within areas of mountain glaciations, such as the Upper Angara drainage basin, between the glaciated regions of the Stanovoye Upland and the Sayans, and at the Aldan River in the immediate vicinity of glaciers of the southern Verkhoyansk Province (Appendix. Fig. 52).

The late glacial *Dicrostonyx* findings are rare, both in the European and Asian Russia; they are mostly restricted to the Urals. It seems likely that the collared lemmings penetrated to the Yamal Peninsula at that time (Appendix. Fig. 53)

XXVIII. True lemmings — genus *Lemmus* Link, 1795

The form is typical of the present-day tundra and forest-tundra (*L. sibiricus*); it is well adapted to life in moss and sod layer under conditions of low temperatures and permafrost (Vereshchagin & Baryshnikov 1980). Within the taiga zone it occurs occasionally in wetlands (*L. amurensis*).

At the beginning of the Late Pleistocene, in the Mikulino Interglacial, the lemming has been recorded in the Urals and in West Siberia (Appendix. Fig. 54), in the regions far south of its modern range. *Lemmus* dated to the Mikulino time is known also from the Borisova Gora locality in Byelarus' (Motuzko 1985); it is possible that it occurred, on a limited scale, in the Mikulino forest assemblages of Eastern Europe.

During the Valdai epoch, the range of *Lemmus* was identical to that of *Dicrostonyx* (Appendix. Fig. 55, 56). It should be noted that the Late Valdai *Lemmus* findings are most abundant in the Ural mountains (both in the north and in the south), and farther along the southern margin of the West Siberian Lowland, at the Upper Ob' and in the Kuznetsk-Salair province of southern Siberia (Appendix. Fig. 56). Such an abundance of the localities within the Asian part of the territory (while they are considerably reduced in number in Eastern Europe) could be a circumstantial evidence that the lemmings range shrank both northward and eastward at the late glacial time. Separate areas where the animal lives at present (in the Amur region, Verkhoyansky Range and eastern Transbaikalian region) are remnants of the vast territory inhabited by lemmings during the Valdai epoch.

Steppe small mammals

XXIX. Bobac marmot — *Marmota bobac* Muller, 1776

Presently, the bobac lives in the Kazakhstan plain steppes. During the historic time, it inhabited steppes and — more rarely — forest-steppes in the south-east of European Russia; there are still a few small colonies there. The bobac marmot somewhat differs in ecology from mountain species of *Marmota* (Zimina 1978). In the Kazakhstan hilly regions it prefers areas of low hills, with flattened moderately wet surface covered with herbs and grasses (Zimina & Gerasimov 1971).

It is typical of the Mikulino Interglacial assemblages. Numerous findings are known from the southern and south-eastern Russian Plain, the Dnestr valley, and from the Crimea (Appendix. Fig. 57).

The bobac marmot formed a part of periglacial faunas in Europe throughout the Valdai cold stage (Appendix. Fig 57, 58); it penetrated far west of its present range. Chalin (1972) notes that *Marmota primigenia* (similar to modern bobac in morphology) was abundant in France during the Wiirm glacial epoch. The marmots appeared in Western Europe before the Late Pleistocene glaciation; they are present in Riss-Wurmian faunas along with the ancestral form of root vole, hamster, and steppe lemming (Chalin 1972). With the onset of cooling and general aridization, decrease of forested areas and expansion of open landscapes, the bobac marmot gained in importance in the West European faunas (Zimina & Gerasimov 1971).

The range of the bobac marmot within the European part of the former Soviet Union probably varied insignificantly in size, and retained its general configuration (Appendix. Fig. 57, 58) since the Mikulino time. The only exception was its noticeable expansion northward along the Urals in the Valdai time (it reached as far north as 62° N). It is known that at present the rodent tends to avoid mountain landscapes (Zimina & Gerasimov 1971).

During the late glacial, the range of the marmot on the Russian Plain shifted north-eastward. No findings have been recorded east and south-east of the Urals. It seems probable that extremely cold and dry climate of the continental areas was limiting factor which inhibited the marmot penetration into Eastern Asia.

XXX. Great jerboa — *Allactaga major* Pallas, 1778

At present, the species is restricted to open spaces of steppes, forest-steppes, and semi-deserts, from south and southeast of Ukraine and European Russia to the Altai mountains. It prefers habitats with a low degree of vegetation coverage, though avoids unvegetated sands in deserts (Gromav & Baranova 1981).

It lives usually in holes and hibernates in winter.

During the Late Pleistocene, *A. major* penetrated farther west than other jerboas; its remains are known from Roumania, Hungary, Germany, and Bulgaria (Kowalski & Nadachowski 1982). Within the limits of the former Soviet Union, it was distributed much wider during the Valdai time than at present (Appendix. Fig. 59, 60). The range reached its maximum expansion at the time of maximum cooling; it covered the whole area from Dnester in the west to the upper Pechora in the north and the Enisei River in the east. The late glacial time shows a notable reduction in the range, and most of localities dated to that time are either within the present-day range, or near its limits (Appendix. Fig. 59, 60).

XXXI. Greater mole rat — *Spalax microphthalmus* Guldenstaedt, 1770

The burrowing species inhabits steppe and forest-steppe areas in the south of European Russia and Ukraine. It is adapted to seasonally frozen ground due to its ability to store food in quantities more than enough for winter (Formozov 1976).

Localities of the Mikulino age are restricted to the Central Russian Upland. The Valdai localities are scarce and occur some west of their present range (Appendix. Fig. 61). At the late glacial maximum the mole rat persisted at the Podolian Upland, at the Dnestr, and in the north of the Privolzhskaya Upland. Though it is difficult to understand, the geophilic species seems to have inhabited the area subjected to active cryogenic processes. The permafrost was up to 200 m deep in the middle reaches of the Volga and ice wedges and frost fissures were widely spread over the Dnieper province (Nechaev 1986).

In the Holocene, the west limit of mole rat range expanded westward beyond the Dnestr river; in the east and south-east the rodent moved into the area it inhabits at present.

XXXII. Eversmann's hamster — *Allocricetulus eversmanni* Brandt, 1859

The hibernating rodent inhabits dry steppes and clayey or sandy deserts in the south of European Russia and West Siberia.

During the Valdai epoch it had much wider distribution extending as far west and north as the Dnestr and Pechora basins; it has been found also in the Crimea. No finding is known, however, from other regions of Ukraine and European Russia. In Asia, it has been found no farther east than the Turgai Plateau. The Eversmann's hamster persisted in the Northern Urals and Pechora basin throughout the second half of the Late Pleistocene (Appendix. Fig. 63).

**XXXIII. Common hamster — *Cricetus cricetus*
Linnaeus, 1758**

The species has an extensive range including the southern part of European Russia and Ukraine, Moldova, Kazakhstan, and southern West Siberia. Its localities dated to the Mikulino Interglacial are known from European Russia and the Urals (Appendix. Fig. 64). Occasionally the species occurred in Central Europe throughout the Late Pleistocene (Kowalski & Nadachowski 1982). During the Early Valdai and the Bryansk (late Karginsky) Interstadial, the hamster was rather common within its present range. The area was however reduced at the time of the last glacial maximum (Appendix. Fig. 65), the hamster probably occurring no farther east than the Urals. A new wave of migration into West Siberia and Kazakhstan took place at the final stages of the Pleistocene and during the Holocene.

**XXXIV. Altai zokor — *Myospalax myospalax*
Laxmann, 1773**

The steppe geophilic form inhabits plains, foothills and low mountains in southern West Siberia and the Altai Mountains. At the beginning of the Pleistocene, the zokor lived in the European Russia (Krasnenkov, et al., 1984) and formed a part of steppe faunal assemblages of the Don region. By the Late Pleistocene, its range had reduced to its present size, and remained conservative throughout the whole Valdai time and the Holocene (Appendix. Fig. 62). The only exception was movement of the zokor eastward — as far as the Enisei region — into the Sayan province during the late Karginsky Interstadial. Such a limited distribution of the rodent (in spite of dominance of steppic landscapes during the second half of the Late Pleistocene) was probably due to the widespread permafrost; as the animal lives mostly in holes underground, the permafrost could be the most important factor inhibiting its activities.

**XXXV. Steppe lemming — *Lagurus lagurus* Pallas,
1842**

The steppe lemming is widely spread over steppes and semi-deserts and reaches far into forest-steppe along open biotops. It is rather tolerant to food quality and can get by without water for a long time. It feeds on a wide variety of plants, from lichens to grass and wormwoods, including essential oil plants unsuitable for cattle; it often eats underground parts of plants (Formozov 1976). It burrows holes of complicated configuration with winter nests.

Its range was extended eastward and westward from the modern boundaries during the Mikulino Interglacial. Fossil remains of the species are known

from the Dnieper Lowland to the Baikal region. They have been also found in the lower reaches of the Irtysh River (West Siberia) (Appendix. Fig. 66).

During the Early Valdai and the Bryansk Interstadial the steppe lemmings appeared in the Crimea and in the southern Caspian Lowland, as well as on the Moldova territory (Appendix. Fig. 67). Findings dated to the Vistulian 1/2 (the end of the Early Valdai) have been recorded in Poland (Nadachowski 1989).

The glacial maximum featured most wide distribution of the taxon. It extended north and northwest almost to the ice sheet margin (Appendix. Fig. 68) (that was however not as far north as the lemmings penetrated); it reached as far as the Crimea in the south-west, and as far as Baikal — in the southeast. In Western Europe the steppe lemmings occurred in France (Chaline 1972).

The onset of warming about 15,000 yr B.P. left the steppe lemming ranges practically unchanged in size and configuration (Appendix. Fig. 68).

The reduction of its range down to its present dimensions did not take place until the Holocene.

**XXXVI. Yellow steppe lemming — *Eolagurus
luteus* Eversmann, 1946**

At present, the species is in the process of extinction over the former SU territory, and inhabits limited areas in the Zaisan Lake region. During the historical time, it existed on the Caspian Lowland and in the Central Kazakhstan (Gromov & Baranova 1981). It prefers sandy grounds, with scarce vegetation and groves of pea-shrub (*Caragana*), saxaul, and calligonum (Flint et al. 1970).

During the whole Pleistocene, it was characteristic member of steppe and forest-steppe assemblages in the southern European Russia, Kazakhstan, West Siberia (Gromov & Baranova 1981).

All the Mikulino localities of yellow steppe lemmings are restricted to the middle reaches of the Don River, on the Central Russian Upland (Appendix. Fig. 69). At the beginning of the Late Pleistocene cooling and during the Bryansk interval, they were present from the Dneestr, Crimea and the Urals to the Altai mountains (Appendix. Fig. 69). Under extremely severe conditions of the glacial maximum, the limits of the species in West Siberia were probably shifted westward. It is suggested by the fact that it was not found in rich collection from lower Irtysh sites (Smirnov 1990), nor from Transbaikalian region (Agadjanian & Erbaeva 1983) (Appendix. Fig. 70). With the beginning of the late glacial warming the yellow steppe lemmings once more become a typical form in the Lower Ob' faunal assemblages. During the Holocene, the range of the species underwent gradually a considerable reduction until it became restricted to the regions of the Caspian Lowland, northern Aral, southern West Siberia, and eastern Kazakhstan.

Forest small mammals

XXXVII. Bank (common red-backed) vole — *Clethrionomys glareolus* Schreber, 1780

The species presently inhabits forest zone of Eastern Europe, and taiga in Western and partly Central Siberia. It occurs also in riparian landscapes within tundra and steppe zones. It feeds on seeds, bark and buds of trees, on herbs and grasses, as well as on mushrooms and lichens (Flint, et al. 1970).

In Western and Eastern Europe it is considered to be a typical forest representative of the Late Pleistocene faunal assemblages, both of warm and cold epochs. An overwhelming majority of the bank vole localities (all over the former USSR territory) have been recorded within its present range (Appendix. Fig. 71,72). During the early Valdai and the Bryansk Interstadial the vole occurred from the modern Moldova and Byelorussia territory to the Ob' upper reaches. At the last glacial maximum its easternmost occurrence has been recorded in the lower Irtysh region, all the rest are confined to the European part of the country (Appendix. Fig. 72).

In the late glacial the range of the bank vole extended once more eastward, into the upper reaches of the Enisei River. In the north, its findings are known from the Pechora basin and the Northern Urals within the limits of its present-day range. It is evident that this forest-dwelling species was constantly present in the periglacial faunas in the immediate vicinity of the ice sheet (Appendix. Fig. 72), even under conditions of the most severe climates of the Valdai Glaciation. That is a further evidence indicating that some relict of forests could persist among the dominant open landscapes during the glacial epoch.

XXXVIII. Ruddy (northern red-backed) vole — *Clethrionomys rutilus* Pallas, 1799

The species inhabits forests, forest-tundra and forest-steppe and shows an extensive range — from the European North to the Northeast and Southeast of Russia.

The vole remains dated to the Valdai epoch have been found within its present-day range east of the Urals and to the Baikal Lake and the Vitim valley (Appendix. Fig. 73, 74). At the glacial maximum the remains are confined to the Ural mountains, with a few findings in the Baikal region.

XXXIX. Grey red-backed vole — *Clethrionomys rufocanus* Sundervall, 1846-1847

The species is an inhabitant of taiga and coniferous mountain forests, it occurs also in tundra in groves of dwarf willows and birches (Flint, et al. 1970).

Its localities dated to the early Valdai and Kargin-sky Interstadial are concentrated along the southwestern and southern limits of its modern range (the Southern Urals, lower reaches of the Irtysh River, the upper Ob' and Baikal). At the glacial maximum, the species inhabited the Ishim valley in the northern Kazakhstan and the Urals; no traces of its presence have been recorded east or west of those regions. It was probably the extremely dry climate and deficiency of forests in the southern West Siberia that caused the vole migration into the Kazakhstan hilly land and into the Ural mountains. *C. rufocanus* either did not penetrate into Europe at all, or penetrated only in limited amounts (Appendix. Fig. 75, 76).

With the beginning of warming in the late glacial, the species once more extended its range and reached as far east as the Stanovoy Range.

XL. Field vole — *Microtus agrestis* Linnaeus, 1761

The species is forest dweller, occasionally penetrates into steppe and tundra in forested sites. It was typical of the Mikulino Interglacial assemblages, being found in a number of localities of the Russian Plain, the Urals and West Siberia (Appendix. Fig. 77). In Western Europe it occurred throughout the whole Late Pleistocene, including the climatic minimum.

At the first stages of the glaciation, it occurred mostly within its present range over the territory under consideration (Appendix. Fig. 78). At the coldest time of the Valdai its range was probably reduced, all the findings of that age are confined to European Russia and not one is known east of the Urals. After the late glacial began, the vole extended its range once more eastward up to its present-day limits (Appendix. Fig. 78).

A collection of data for a data base and construction of electronic maps of mammal ranges on this basis provides a promising method for investigations of dynamics and characteristics of evolution of the Late Pleistocene faunal assemblages of Palearctic.

A scarcity of data on the Mikulino Interglacial and the lack of radiometric datings (with only a few exceptions) do not permit to analyse in full measure characteristics of the small mammals' distribution during that time. It should be noted however that a number of the species of Mikulino Interglacial featured wider ranges compared with those at present in the European part of the former USSR (it refers in particular to the collared and true lemmings, bobac marmot, and yellow steppe lemming). Almost no data are available on the Asian territory, and on the Kazakhstan in particular.

A great volume of data and relatively precise chronological calibration permits to analyse the Valdai faunas in terms of time and space in considerable detail. Analysis of data derived from electronic maps confirms a frequently cited in literature con-

clusion that some of the Valdai glacial assemblages have no modern analogues. The disharmonious or mixed faunas (V. Gromov 1948; Markov & et al., 1965; Vangengeim 1977; Hibbard & Taylor 1960) developed under periglacial conditions; they included allopatric at present forms which are opposite in their environmental requirements. A similarity in ranges did not determine, however, similarity in adaptation of different species to extreme environmental conditions.

Three groups of small mammals could be distinguished by responses of their ranges to global climatic changes during the Valdai glacial time: 1) ranges increased markedly; 2) ranges showed no changes; 3) ranges reduced. (The changes were defined with reference to modern range of the taxa and data on their ecology, with necessary corrections for what is known about the Mikulino time; (according to A. K. Markova the Mikulino Interglacial faunas have the zonal structure) (Markova 1992). The first group includes collared and true lemmings, arctic shrew, steppe lemming and yellow steppe lemming, great jerboa, susliks, Eversmann's hamster and grey hamster, steppe pika, narrow-skulled vole, Midden-dorf's vole, north Siberian vole (*Microtus hyperbo-reus*), arctic hare (*Lepus timidus*), and some others. Geographically, most widely distributed were species highly tolerant to cold and dry climate and well adapted to life in open spaces. Among those are mostly inhabitants of tundra and forest-tundra (such as lemmings and north Siberian vole), and steppe dwellers which are active throughout a year, can forage under snow and store food in burrows (narrow- skulled vole, steppe lemming, steppe pika) (Formozov 1976).

With the expansion of periglacial steppes, some hibernating species — susliks, marmots, hamsters, jerboas — extended their ranges considerably. They inhabited primarily foothills and mountain areas, and occurred in areas of highly dissected topography (where they could burrow holes in south-facing slopes of gullies), as well as on floodplains where soils thawed in summer to a maximum depth (Vereshchagin & Baryshnikov 1980).

The second group includes common hamster, zokor, field vole, bank vole, grey red-backed vole, and ruddy vole. Forest species were probably restricted to relict tree groves scattered over periglacial steppes and forest-steppes. Though in general their ranges remained unchanged during the Late Pleistocene, they were noticeably reduced in area at the Last Glacial Maximum. Low temperatures and treeless landscapes forced the Asian forest-dwellers to retreat to south and west towards mountains where climates were not so extreme. The same factors caused a reduction in ranges of Europe forest species.

The range of the Altai zokor kept its stability except for movement of the species into the Western Sayan region during the late Karginsky interstadial. The Central Asian mountains were not subject to the

glacial climate to such extent as the plains. Data cited by Boyarskaya (1965) indicate the mountain vegetation only slightly different from today's.

The third group includes the yellow-necked and wood mice, brown squirrel, shrews, dormice, mole rats, birch mice, mole voles, chipmunk, European hare and tolai hare, common moles. Dominant are forms connected closely with broad-leaved and other deciduous tree species (dormice, mice, and some shrews), as well as geophilic species (moles, mole rats, mole voles). For the former, vitally important was the presence of forested areas, for the latter — moderate depth of soil freezing in winter. Those animals persisted only in separate refugia within mountain regions.

Arctic forms most closely approached margins of ice sheets and alpine glaciers. The northern limit of steppe taxa was about 400 to 500 km farther south (which in all probability corresponds to the boundary between the tundra and periglacial tundra-steppe) (Markova 1994). In general, the plains of the European and Asian parts of the former Soviet Union featured less rich faunas than those of the present day; the same cannot be said, however, of mountains and foothill regions. At the time of the Valdai glaciation several specific centres of plants and animals conservation were formed. Such relict areas were in the Dnestr valley and in the Carpathians in the west, in the Crimea and Caucasus in the south, the Altai and Sayan mountains in Siberia.

Somewhat peculiar was the Uralian region where four migratory flows met: forest European and Asian species penetrated there from west and east, Arctic species retreated from the Novaya Zemlya ice sheet from the north, steppe animals actively penetrated from the south. Besides, geophilic species could find a refuge here, in highly variable mountain environments.

To summarise, it should be noted that in spite of the fact that the ranges of some presently allopatric species considerably overlapped each other during the Valdai glaciation, individual species differed in their response to the climatic changes. It shows advantage of Graham's hypothesis of the individualistic response of mammal species in comparison with the model of the whole community shifting in response to climatic changes (Graham 1985, 1986).

Some of the animals successfully adapted themselves to new environments and sometimes could change their ecological specialization (as narrow-skulled vole and, in the opinion of N. G. Smirnov, pied lemming have done). Others were reduced in number during extremely severe epochs and concentrated in relict forest areas from where they could recolonize their former territories under more favourable conditions (forest species of voles, squirrel, and others). The third group — dormice, mice, chipmunks, and others — became almost completely extinct in most of their habitats and persisted only within mountains during the whole Valdai time (with exception of the Bryansk = late Karginsky Interstadial).

Therefore, the history of small mammal ranges dynamics during the Late Pleistocene reveals an extremely complicated complex highly responsive to climatic fluctuations which induced catastrophic restructuring of the biocenoses of the past.

3.3. Distribution of indicator species of mammals and plants during the second half of the Late Pleistocene (based on data from the Russian Plain)

Anastasia K. Markova & Alexandra N. Simakova

In the course of our investigations two data bases have been developed: PALEOFAUNA, which includes materials on the Late Pleistocene mammals within the limits of the former Soviet Union, and PALEOFLORA which summarises East European data on the Late Pleistocene vegetation during the second half of the last glaciation. Having two sets of data at our disposal we considered it interesting to analyse the indicator species distribution for both animals and plants at the same chronological intervals on the territory of Russian Plain. For the analysis, we have chosen the most characteristic specialised species of mammals and plants typical for certain environments.

Among most typical inhabitants of subarctic tundra landscapes are lemmings of the genus *Dicrostonyx*; they range from southern Arctic tundra to northern forest-tundra, and occur in mountain tundra, usually choosing well drained sites. They feed primarily on twigs, bark, and leaves of dwarf birches, willows, bog bilberry, cloudberry, and dryad (Gromov & Erbaeva 1995). In the previous section materials are cited about the *Dicrostonyx* range during the Valdai time when the rodents were widely spread over the former USSR territory and reached as far south as 48° N. Other data on the pied lemming distribution during the Pleistocene show that their range expanded considerably during glacial epochs (Agadjanian 1973, 1976).

Among the plants indicative of severe environments, and of permafrost in particular, there are *Alnaster fruticosus*, *Selaginella selaginoides*, and a dwarf birch *Betula nana*. At the late Valdai time many representatives of Arctic and northern taiga flora expanded their range south up to 47° N. The plants named above form a part of a diet of mammals — inhabitants of tundra and forest-tundra. The lemmings of the genus *Dicrostonyx*, for example, feed on *Alnaster fruticosus* — low branching bush, often with contorted trunk and boughs. It is widely spread in the northern taiga and forest-tundra zones, inhabits mountain slopes, forest edges, occurs on alluvial sands and gravels. Being a microtherm, it is highly tolerant of winter cold, and may exist under conditions of summer temperatures about 14 to 18° C and the growth season about 2 to 3.5 months long (Sokolov, Svyaseva & Kubli 1978).

When superimposed, points of *Dicrostonyx* and

Alnaster fruticosus findings in localities of the same (late Valdai) age reveal similar changes in their ranges induced by the global cooling (Appendix. Fig. 79.). Both areas show a dramatic expansion toward south and Southeast, practically over the whole Russian Plain (from the ice sheet margin in the north to the southern regions of the plain). Later, during the second half of the late Valdai (17 to 12 ka B.P.) *Alnaster* reduced their ranges and retreated northwestward by about 1000 km. *Dicrostonyx* range reduced not so significantly, but its sites became very rare (Appendix. Fig. 80).

Another mammal equally typical of the recent tundra and forest-tundra is lemming of the genus *Lemmus* which is one of most abundant taxa of zonal tundra in Northern Eurasia. It occurs both on the continent and on islands, in mountains and on plains, being most frequent in hummocky and polygonal moss and sedge tundras. It feeds mostly on sedges, cotton grass, green moss, and tundra dwarf shrubs (Gromov & Erbaeva 1995).

A species indicative of the modern tundra zone is *Selaginella selaginoides*, a dweller of wet open habitats. Appendix. Fig. 81 -84 shows the late Valdai localities of *Lemmus* and *Selaginella selaginoides* belonging to 4 chronological intervals.

Findings of *Lemmus* and *Selaginella selaginoides* dated to the beginning of the late Valdai cooling (24,000-21,000 yr B.P.) are rather few in number. Nevertheless, they record a considerable expansion of the species ranges resulting from the global cooling of the late Valdai. *Lemmus* penetrated as far south as 53° N, and *Selaginella selaginoides* pollen was found at latitude 50° N in the Dnieper valley and even in the lower reaches of the Dnestr (Appendix. Fig. 81).

During the subsequent interval — from about 21,000-17,000 yr B.P. — those two taxa were still widespread (Appendix. Fig. 82). The findings increase in density, some of them are located farther south (50° N) than those dated to the previous interval. The southernmost occurrence of *Selaginella selaginoides* (about 48° N) are known from the eastern Carpathian foothills.

The localities attributed to interval between 17,000- 15,000 yr B.P. are less abundant, some of them occur within the recently deglaciated zone (Appendix. Fig. 83). At the end of the Valdai glaciation (15,000-12,000 yr B.P.) the areas occupied by those species become discontinuous. *Selaginella selaginoides* persists only in the Carpathian foothills, in the middle reaches of the Dnieper and north of the Upper Volga (Appendix. Fig. 84). *Lemmus* remains of that age have been found in the upper reaches of the Dnieper. In the late glacial time the taxon becomes rare. At that time, the landscape structure begins to change from hyperzonal to zonal one. Typical subarctic species of plants and animals retreat northward.

Not only the subarctic taxa but typical steppic mammals and plant underwent considerable changes

in their distribution. Appendix. Fig. 85 shows localities of saiga antelope — *Saiga tatarica* — and *Ephedra* dated to the LGM, as well as modern limits of their occurrence. Both of them belong to steppe ecosystems, and ephedra is one of essential components of the saiga diet. *Ephedra* is a dwarf shrub typical of steppe and semideserts. It is usually restricted to sandy soils on plains and in foothills, while in low mountains it inhabits rubbly slopes and gravel floors of valleys (Shmidt 1983). At the coldest time of the Valdai both saiga and ephedra considerably expanded their ranges toward west and north and penetrated into areas now covered by forests. The recorded change in the areas of steppic flora and fauna lends support to the notion that zonal forest environments did not exist during the Valdai glaciation, while open ecosystems — periglacial tundra-steppes and steppes — were widely spread over the plain.

We analysed also the range of a carnivorous mammal — wolverine *Gulo gulo* in relation to those of some conifer species: *Picea* and Siberian pine *Pinus sibirica*. At present wolverine inhabits taiga and forest-tundra, and occasionally migrates into tundra and forest-steppe zones. In Eastern Europe southern limit of the wolverine modern range is at latitude 58-57° N. Wolverines hunt reindeer, roe deer, birds, sometimes feed on carrion. At the coldest time of the Valdai, the wolverine range, as suggested by the data at hand, covered area from 55° N in the north to 50° N in the south. The whole range, therefore, shifted southwards as compared with that of today. At the late glacial time its limits did not change significantly.

The distribution of *Pinus sibirica* at the LGM also differs considerably from today's: fossil remains of this conifer tree have been found as far south as the Black Sea coastal lowland (Appendix. Fig. 86). The Siberian pine is mesophytic and microtherm plant growing well under conditions of moderate moisture and reduced heat supply. Its present-day range includes the whole Siberia and northeast of European Russia. It is highly tolerant of low temperatures and reduced insolation, and undemanding of soils.

Picea pollen dated to the late Valdai has been recorded from sections located north of 48° N. It is rather indifferent to soils, though requires sufficient moisture. Due to its high tolerance to frosts it can grow under severe climates like those of tundra. However, it is highly sensitive to droughts in early spring (between the onset of warm weather and the beginning of soil thawing) (Walter 1982). High summer temperatures are known to be principal limiting factor for this tree; it cannot grow in regions where summer temperatures exceed 22-24° C.

The late Valdai range of wolverine coincides closely enough with *Picea* findings and with most of the area inhabited by *Pinus sibirica*. A rather wide distribution of those species of plants and animals suggests that patches of forests and bush vegetation existed locally at the centre of the Russian Plain at the late Valdai maximum.

We made also an attempt to examine mammoth distribution in the late Valdai in the context of herb communities distribution. An analysis of subfossil pollen spectra shows that they correspond closely enough to the composition of plant communities in question (Grichuk 1946; Grichuk et al. 1973). Thus, non-arboreal pollen percentage in excess of 60 % of total pollen and spores quantity implies the presence of open ecosystems at the time when the sampled deposits were formed.

It is well known that mammoth was one of dominant species in the Late Pleistocene herbivorous mammal assemblage (Chapter 3.1). An analysis of pollen spectra included in the data base PALEO- FLORA permitted to identify those late Valdai sections where more than 60 % of pollen grains in the spectra were NAP which suggested open phytocoenoses (Appendix. Fig. 87).

During the interval 24,000 to 17,000 yr B.P., herb and grass communities prevailed on the most of the Russian Plain (from the ice sheet margin to the Black Sea coastal regions). The mammoth range at that time was broad enough (though reduced in comparison with the early Valdai) and covered most part of the Russian Plain (Appendix. Fig. 87). Practically all the locations of the mammoth (*Mammuthus primigenius*) remains are within the areas of dominant herb and grass communities.

Between 17,000 and 12,000 yr B.P. the mammoth range underwent a considerable reduction and became discontinuous (Appendix. Fig. 88). A majority of findings are clustered between 48° and 55° N. At that time the northern limit of grass communities shifted slightly southward. The end of this interval was marked by the onset of global warming and formation of the forest zone, which appeared unfavourable for large herbivorous mammals belonging to the mammoth faunal assemblage.

Dynamics of spatial distribution of indicator species of mammals during the second half of the Late Pleistocene when compared with that of plants revealed a synchronicity in areal changes of species similar in ecology. The data on the Valdai glacial epoch show a synchronous expansion of northern animals and plants southward, while steppe species expanded their ranges northward and westward. The facts have been cited in literature more than once, and our data corroborate them.

Special features of forest species distribution (both of animals and plants) during the glacial epochs were of less concern to paleogeographers. It has been usually emphasised that those species practically disappeared from the biocenoses of the central Russian Plain.

The materials from the PALEOFAUNA and PALEOFLORA data bases indicate, however, that a number of forest species persisted in regions close enough to the ice sheet. The forest species responded to the cooling in a variety of ways. Some of them practically disappeared from the middle latitudes of Northern Eurasia; among them are boar, forest mice

of the genus *Apodemus*, dormice *Glis*, *Dryomys*, *Eliomys*, and *Muscardinus*, beaver *Castor*, voles *Microtus (Terricola) subterraneus*, as well as oak, lime, maple which persisted only in southern mountain refugia of the Carpathians, the Crimea, and the Caucasus, and in the Donetsky Kryazh, at latitude 49° N.

Other forest species, such as wolverine, *Clethrionomys glareolus*, *Clethrionomys rutilus*, *Clethrionomys rufocanus*, *Microtus agrestis* voles did not change their ranges even at the time of the Valdai maximum cooling and continued to inhabit fairly close to the ice sheet, where they probably were restricted to local patches of shrubs and trees. The presence of such isolated forest communities is indicated by pollen of *Pinus sibirica* and *Picea*, as well as bush and dwarf shrub species recovered from deposits dated to the coldest interval of the glaciation. There is no question that those forested sites occurred only locally; the ecosystems of the central Russian Plain were mosaic in structure, the prevalent open landscapes with corresponding flora and fauna were interspersed with local forested biotops where a number of forest mammals indifferent to low temperatures and permafrost could persist.

On the whole, both floristic and faunistic data indicate that during the Valdai glaciation the system of natural zones underwent drastic restructuring. At the coldest time of the Valdai epoch the forest biome ceased to exist, and most part of the Russian Plain was occupied by various periglacial ecosystems having no analogues in the modern vegetation. They featured mosaic structure, with open herb and grass communities predominant; the latter were inhabited by diverse assemblage of herbivorous mammals and carnivores which hunted them; riparian environments still included patches of trees (mostly conifers) and shrubs where some mammals associated with this type of vegetation could exist. A majority of woodland mammals practically disappeared from the Russian Plain as a result of the forest biome disintegration and could only persist in southern mountains.

4. DYNAMICS OF THE INDICATOR PLANT SPECIES RANGES IN EASTERN EUROPE DURING THE LATE VALDAI

Alexandra N. Simakova & Alexander V. Kozharinov

Paleophytology as the science of stages and regularities of formation of the plant population paleoranges is still in the "juvenile" state of development, though theoretical and methodological bases for it were developed as long ago as the 50-ies, by A.I. Tolmachev and W. Safer. Paleophytological reconstructions are directed to determine the character and scales of migrations and refuges, and thus permit to approach solving of the flora and phylogenetical problems. By the present moment there exist many publications dealing with these problems (Serebryanny 1971, 1974; Ralska-

Jasiewiczowa 1983; Elina 1981; Grimm 1984; Graham & Grimm 1990; Grimm & Jacobson 1992; Kozharinov 1989, 1994; etc.). A majority of them, however, contain but fragmentary data on tree species ranges within regions, and thus the information is insufficient in order to reveal general zonal regularities of the areas formation.

Earlier we developed paleophytological reconstructions for Eastern Europe during the Late Glacial time and the Holocene (Kozharinov 1994). Pollen spectra recovered from 64 sites (in all 336 samples) of the European part of former Soviet Union provided the basis on which the PALEOFLOORA database in the Paradox V. 4.5 format was developed for the late Valdai time (Fig. 4.1; Appendix. Table 2).

In structure, the PALEOFLOORA database is similar to previously developed PALEO database (Kozharinov 1994). It includes three information blocks. The first one contains information about the geographical position of the sites (latitude, longitude, country, region, district, settlement, river basin, modern vegetation zone) and references, with the name of the author of pollen identifications. The second block includes information about number of samples for each pollen diagram, their position in the sequence, lithology, absolute dates obtained by radiocarbon and thermoluminescent methods or by microlayers counting in lake sediments, as well as the data about relative age correlations based upon geological, archaeological and pollen evidence; information about pollen redeposition. The third block concerns taphonomy, containing genera and species identifications with the corresponding pollen numbers (percentages).

The data properly selected made the actual base for a series of maps of the different plant species constructed in ARC / INFO cartographic software for the following intervals of the late Valdai: 24,000- 21,000; 21,000-17,000; 17,000-15,000; 15,000-12,000 yrB.P.

Analysis of the electronic maps made it possible to study temporal dynamics of distribution of individual representatives of the tundra and forest-tundra plant communities, coniferous and broad-leaved forests, and steppe ecosystems. Thus, *Alnaster fruticosus* Ldb. is a boreal-arctic and arcto-alpine Eurasian species being also a microthermic plant. Its modern range only partially, by its northern-western edge, covers some regions of the Russian Plain. At the glacial maximum this inhabitant of the northern- taiga forests occupied the whole European part of the of the FSU, reaching as far south as Rostov-na- Donu and Odessa. During the second half of late Valdai, 17,000-12,000 yr B.P., *Alnaster fruticosus* area shifted towards the north-west, by ca. 400- 500 km (Appendix. Fig. 89, 90).

A hypoarctic species, common in the forest-tundra and adjacent regions of the forest zone, the dwarf birch *Betula nana* L. was reported to response in similar way (Alekhin, Kudryashov & Govorukhin 1957). By now the southern limit of *Betula nana* L.

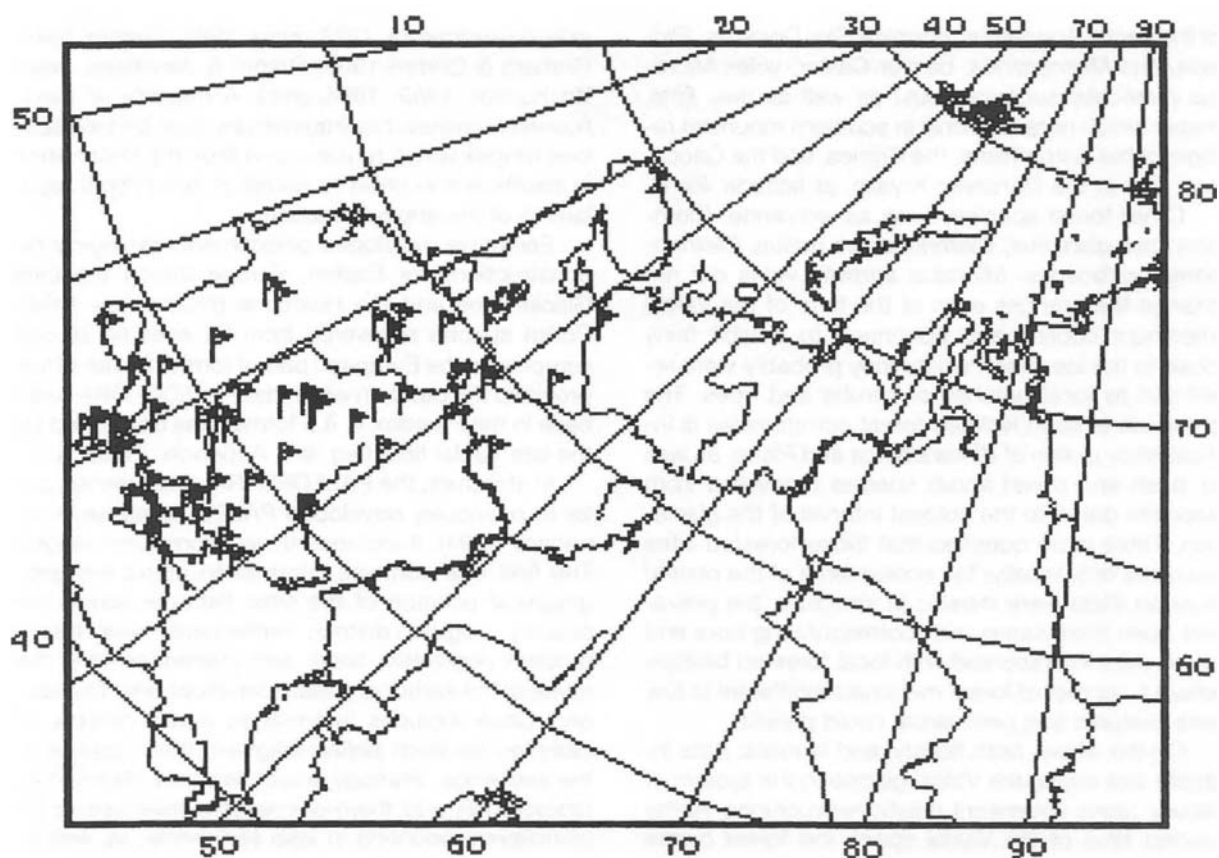


FIG. 4.1. Spore-pollen localities of the Late Valdai

reaches 54-55° N (Sokolov, Svyaseva, Kubli 1978). During the first half of the late Valdai maximum (24,000-17,000 yr B.P.) this limit shifted to 47° N. Later, (17,000-15,000 yr B.P.), it shifted 500-550 km to the north-west, and during the late glacial time by 200 km to the north—north-west (Appendix. Fig. 91, 92). *Selaginella selaginoides* Link., a typical tundra and north-boreal mesophyte, occurred far south, ca. 1500 km from its modern range (Appendix. Fig. 93, 94). Among the coniferous trees, *Picea* A. Dietr. is of the most interest, as a moderate-thermophilic forest mesophyte. During the initial and maximum glaciation stages spruce was spread in the west and north-west of Eastern Europe; and it grew along the coasts of the Black and Azov Seas. It has not been found in the south-east of the Russian Plain, with the exception of the Don middle reaches. During the 17,000-15,000 yr B.P. interval the range decreased, some 300 km to the north-west, and by the late glacial it was displaced to the north and approached to its modern limits (Appendix. Fig. 95, 96, 97, 98). The larch, *Larix* Mill., is also a forest mesophyte and a microthermic plant. At the time of the late Valdai larch pollen was founded about 52° N on the Russian Plain and in the south of Moldova, spreading probably from the Carpathian region. The fir, *Abies* Mill., is a mesophytic component of the spruce-and- fir or fir-and-beech coniferous forests in the boreal zone (Bobrov & et al. 1983). During the first half of

late Valdai it grew in the limits of 49-52° N and along the Azov Sea, i.e. about 1000 km more to the southwest as compared to its modern range. Yet, north of this zone *Abies* pollen was not marked, probably, due to the fact that the fir prefers moderate humidification, avoiding water-logged soils (Gammerman & Shass 1954), which is confirmed by paleopedological studies. According to T.D.Morozova (1981), starting from 22,000-23,000 years ago, evidences of forest pedogenesis become more pronounced which suggests more humid and cold climate. The active podzolic soil formation started soon after the loam-covered surface had been free of the meltwater and proceeded under colder and more humid climate conditions when coniferous forests with moss communities dominated the vegetation; at present it has partially stopped. During the second half of late Valdai *Abies* were persisted only around the Azov Sea, and at the end of the late Valdai it occurred in the Don middle reaches and in the Carpathians (Appendix. Fig. 99, 100). The Siberian pine, *Pinus sibirica* Du Tour, is a forest mesophyte and typical representative of the dark coniferous taiga. During the late Valdai it was spread up to 47° N, grew in the Carpathian region and along the Black and Azov Seas, in the middle Don drainage basin and in the upper Dnieper basin. During the interval of 17,000 —12,000 years ago the species range decreased significantly moving northwards, and no pine pollen

was found south of 53° N except in the Carpathians (Appendix. Fig. 101,102). A moderate-thermophilic species as the common pine, *Pinus silvestris* L, was also widely spread over the whole Eastern Europe territory during the late Valdai, gradually migrating towards the north and north-west following the retreat of the ice sheet, except the regions adjacent to the Carpathian Mts. and to the Azov Sea. All the coniferous tree species discussed were present, if in small quantities, in the plant cover over practically the whole Russian Plain during the first half of late Valdai. During the second half of late Valdai (17,000- 15,000 yr B.P.) their ranges decreased and in the majority of cases shifted towards north — northwest being thus distinct from those of the tundra and forest-tundra dwellers which were displaced to the north-west.

Up to the present moment scientists cannot agree on the broad-leaved trees occurrence during the late Valdai time. Many authors consider that presence of these species pollen in the sediments of this age is a result of redeposition (Grichuk, Mal'gina & Monoszon 1969; Pashkevich 1977, 1987; Semenenko & et al. 1981; Devyatova 1982; Zelikson 1986). Most probably, redeposition occurs in the places situated inside the limits of the ice sheet or near its margins. Analysis of maps showing pollen occurrence of a few broad leaved species (*Acer*, *Tilia*, *Carpinus*, *Corylus*, *Quercus*, *Fagus* and *Ulmus*) reveals certain regularities and makes more clear the overall picture of biota at that time.

At the beginning of the late Valdai (24,000-21,000 yr B.P.) pollen of elm, oak, hornbeam, maple, hazel, lime tree is found in the central and southwest regions of the Russian Plain, and near the Azov Sea, up to of 49° N. At the late Valdai maximum (21,000-17,000 yr B.P.) *Ulmus*, *Acer*, *Tilia*, *Corylus*, *Carpinus* pollen disappears from the spectra of the major portion of Eastern Europe. *Quercus*, *Tilia*, and *Acer* are reported in Moldova; *Quercus*, *Tilia*, and *Carpinus* — in the Azov coastal region, and *Quercus*, *Tilia*, and *Acer* — in the centre of the Russian Plain, at latitude 49-51° N. At the terminal stages of glaciation hazel pollen again occurred widely. The phenomenon may result from the situation when *Corylus* forming the shrubage, with no competition from other shrubs and without overshadowing trees, spread widely over the vast territories of the Russian Plain. Isolated oak, elm and hornbeam grains were founded, too. *Fagus* pollen was registered in the Middle Dnieper drainage basin, 49° N., only in deposits dated to the second part of late Valdai. Probably hazel spread from the Carpathian refuge of the broad-leaved flora. In the interval of 17,000-15,000 yr B.P., no *Tilia* pollen was registered, possibly due to relatively dry climate of that time.

It may be thought that during the glacial maximum of the late Valdai broad-leaved trees did not vanish but participated in the vegetation cover in south-west of Russian Plain, in the regions around the Azov Sea and at the Central Russian Upland (49-

51° N.). Beech is frost-tolerant to the temperatures -22-30° C. Frost tolerance of the other species showing more northern distribution is even higher. Thus *Tilia platyphyllos* is tolerant to -25° C, and *Tilia cordata* — to -35° C (Larher 1972; Walter 1982; Plotnikova 1989). Distinct from the coniferous trees, ranges of the broad-leaved forms were displaced along latitudes. They were persisted in refuges in the south and south-west of the Russian Plain during the late Valdai.

In second half of late Valdai time representatives of steppe phytocoenoses were spread over the whole territory of Eastern Europe, being included into tundra-steppe, forest-steppe, steppe, and semi-desert vegetation. For example, *Ephedra distachya* L. is a xerophytic and semixerophytic dwarf shrub growing in the steppe zone, deserts and open forests. The modern range of this Northern Mediterranean — Eurasian species covers the whole arid zone from south-western Russian Plain to the Altai Mts. and Tuva except the Karakum, northern Kysylkum and near-Balkhash sand massifs (Shmidt 1983). In the late Valdai it was distributed over the whole Russian Plain reaching 62° N. In the late Valdai its range decreased significantly being displaced towards south and south-east (Appendix. Fig. 103,104). *Eurotia ceratoides* (L) C. A. Mey, family *Chenopodiaceae*, a xerophytic and meso-microthermic plant, is an edicator of the sagebrush and saltwort dwarf semishrub deserts and steppe cenoses with xerophytic shrubs involved. In Eastern Europe it grows in the south regions, middle— and lower reaches of the Volga River, east of the Volga, in the Southern Urals, the Crimea and the Caucasus (Sokolov, Svyaseva & Kubli 1980). During the glacial maximum the species area of distribution was displaced to more than 1,000 km to north-west reaching the 62° N (Appendix. Fig. 105, 106). Steppe phytocenoses were the most widely represented at the territory of the Russian Plain during the late Valdai glacial maximum. While the late Valdai second half the steppe vegetation grew mainly north of 56° N or south of 51° N. The results were obtained based on pollen contents of the *Chenopodiaceae* family by the natural zones of European part of the USSR (Monoszon 1985).

The analysis of development and dynamics of paleoranges permitted to draw the following conclusions. At the development of the last ice-sheet on the Russian Plain, a radical restructuring of the existing vegetation zones took place. The arctic flora and that of the northern taiga expanded their ranges towards the south and south-east as far as 47° N, while steppe communities reached 62° N. During the glacial maximum forest zone deteriorated. The broad-leaved trees were not registered during this period, persisting only in the south of the Russian Plain and in the Carpathians. At the end of the late Valdai the vegetation cover began to show a distinct zonality, the zones being directed from southwest towards northeast unlike the modern — sub-latitudinal pattern.

5. MAMMAL SPECIES RICHNESS OVER THE FORMER USSR DURING THE LATE PLEISTOCENE

5.1. Geographical pattern of the mammal species richness during the Late Pleistocene

Anastasia K. Markova

The electronic PALEOFAUNA database not only reveals general biogeography and dynamics of Late Pleistocene mammals, but it also permits the preliminary reconstruction mammal species richness over the whole territory of the former Soviet Union during the Late Pleistocene.

To identify actual parameters of the species richness with reference to particular localities, we used the procedures described in Chapter 2.

Species diversity is known to increase from the poles towards the equator in parallel with the increase in temperature (Simpson 1964). It turns out, however, that the "temperature — species richness" relationship is most clearly pronounced within the colder latitudes and becomes attenuated southward (Shvarts 1991; Chernov 1975, 1991). Besides, near- polar ecosystems could now be biologically less diverse because of their younger geological age.

The higher tropical diversity of flora and fauna is also increased by a number of biotic factors most significant in tropics. Contrary to that, abiotic factors (e.g. permafrost) control partially biodiversity in polar landscapes (Buko 1979).

P. V. Terentyev (1963) has found that 80 to 90 % of the mammal species richness variability is related to climate, the most important factor being the July temperature.

Interesting patterns in spatial changes of species richness (both in mammals and other biotic groups) have been established for North America (Currie 1991). The main climatic factor which controls the mammal species richness in his model appears to be potential evapotranspiration (PET), that is the quantity of moisture that can evaporate from the land surface (which primarily depends, in turn, on the solar energy income). Currie (1991) ascertained that PET contributed about 81 % of the influence for the mammal species richness in North America.

Recent investigations into mammal biodiversity in Northern Eurasia have been based on superposition of modern range maps; these show that the species richness increases from north to south, but that richness reaches its peak within the primary forest-steppe regions, and then begins to decrease farther south. Zones of noticeable decrease in species richness have been outlined within arid regions of the former USSR, while mountains of Northern Eurasia show a sharp increase in the parameter (which could be due to highly variable habitats in mountains and, occasionally, to interpenetration of species belonging to different faunal-genetic complexes

(Shvarts E. & et al. 1995; Shvarts E. & Pushkaryov 1994). An exception is in the Ural Mountains where the mammal species richness is somewhat lower (Shvarts E. & et al. 1995).

This lends support to the significance of the aridity index developed by M. I. Budyko (R/LP , where R is yearly radiation budget, L is latent heat of evaporation, and P — total annual precipitation). The maximum values of the mammal species richness appear to be typical of regions where the aridity index is about 1 (e.g. forest-steppe and the southern part of broad-leaved and mixed coniferous broad- leaved forests). At index values above 3 (typical of deserts) species richness decreases. It appears, therefore, that climate continentality poses a direct relationship between species richness and yearly potential evapotranspiration.

Materials collected in the PALEOFAUNA database permit reconstruction of mammal species richness for the principal time increments of the Late Pleistocene. To accomplish this, materials from the most comprehensively studied localities have been used. First, some real parameters of the mammal species richness for each locality was reconstructed using procedures described in Chapter 2. The reconstructions are based on materials obtained from the **272** best documented Late Pleistocene localities with fossil mammals.

This was transformed into a series of schematic maps and three-dimensional diagrams showing relationships between species richness and geographic coordinates for the major subdivisions of the Late Pleistocene.

The data available for the earliest interval of the Late Pleistocene, the **Mikulino Interglacial (130,000-100,000 yr B.P.)**, is sparse. As a consequence, we could not present the values of the mammal species richness in cartographic form. However, the species richness in relation to the geographical coordinates has been shown in a 3-D diagram based on the material from Eastern Europe (Fig. 5.1.). The diagram clearly shows a regular increase in species richness southward. Thus, the species richness was 10 to 20 species at latitude 65° N, while at latitude 47° N a number of mammalian species was as high as 40 to 45. The most conspicuous rise in species number is recorded in mountain regions of the Carpathians and the Caucasus. A small peak in species richness is documented in the central Russian Plain: at latitude 50 to 51° N and longitude 30 to 32° E; paleobotanic data suggest that the southern boundary of the broad-leaved forests was located within that region during the Mikulino Interglacial (Grichuk 1992). The lack of adequate data leads to underestimating the species richness in the north-eastern part of Eastern Europe. On the whole, the predicted pattern of the mammal species richness during the Mikulino Interglacial shows a similarity to that of today. The number of species tends to increase southward, the species richness rises at the forest and steppe boundary, as well as within mountain regions.

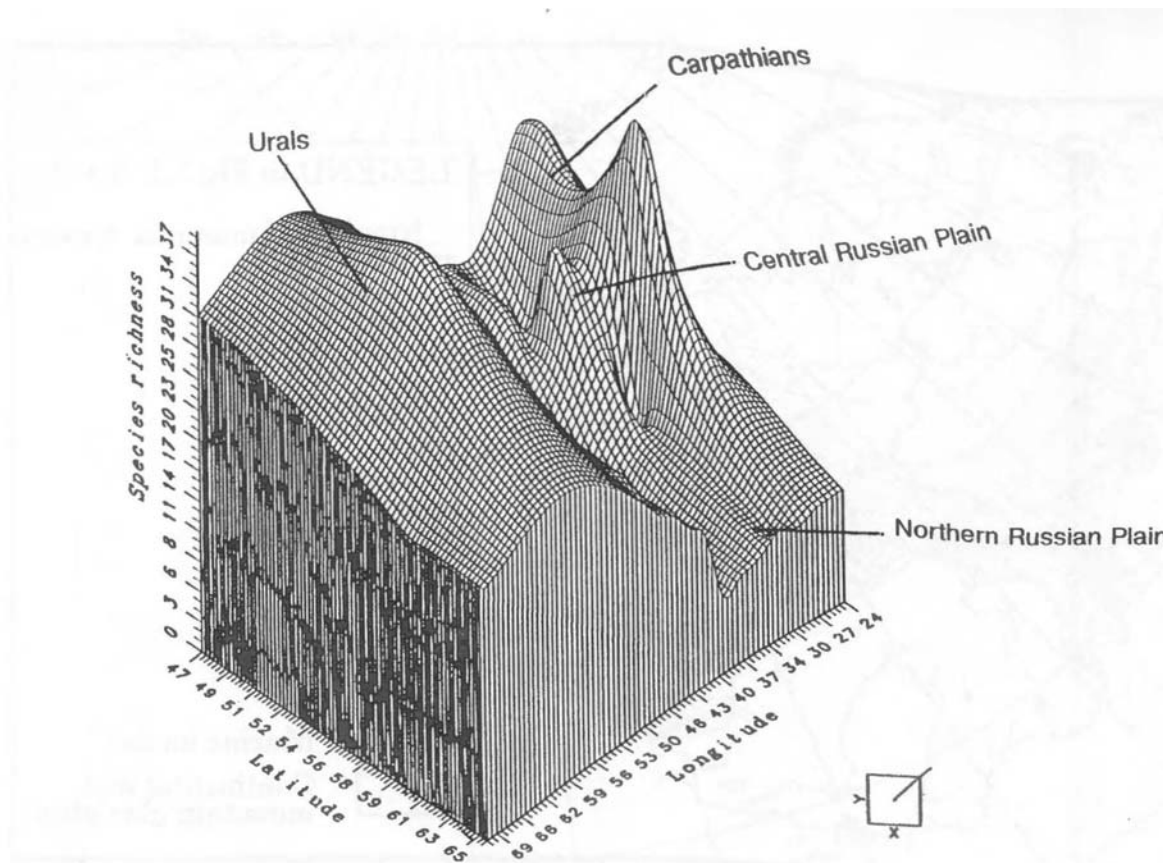


FIG. 5.1. Mammal species richness in the Mikulino Interglacial (100,000-130,000 yr B.p.)

Reliable data on fossil mammals is more dense for **the early Valdai (100,000 to 35,000 yr B.P.)** and it is possible to construct a schematic map of the mammalian richness for that period. As a majority of mammal localities dated to that time are restricted to either Eastern Europe or to Siberia west of the Yenisei River, no reconstruction could be made for Eastern Siberia and the Northeast of FSU.

Zones of low values of mammal species richness (less than 20 species) were located between latitudes 54 and 55° N in Eastern Europe and North of 60° N in Siberia (Fig. 5.2; Fig. 5.3). Low value zones were inhabited by the open landscape species, both subarctic and steppe; some of them exist at present, others died out at the end of the Pleistocene. These open landscape mammals were well adapted to life in the peculiar periglacial landscapes of tundra- steppe; they have been placed into the arctic variety of the mammoth faunal assemblage (Baryshnikov, Markova & Vereshchagin, in press), or to a northern variety of a disharmonious or mixed faunas for which no modern analogue exists. That region was typified by faunas dominated by a few species best suited to the extreme periglacial environments.

Farther south there was a region of higher species richness (20 to 30 species) distinguished by a mixture of characteristically steppe species (which dominated the faunas) and a few forest dwellers. This (disharmonious) faunal associations occupied vast areas of the Russian Plain and Siberia and reached as

far south as the Black Sea coast and 50° N (in West Siberia) Most of widely distributed large mammals in the regions at that time became extinct at the end of the Pleistocene (mammoths, woolly rhinoceros, bison and aurochs, giant deer, cave-dwelling predators, see Chapter 3). Extant arctic animals, such as lemmings and musk oxen, reached as far south as 47 to 48° N; the southern boundary of the arctic variety of the mammoth assemblage was determined by the southernmost occurrences of lemmings and musk oxen (Baryshnikov & Markova 1992). A certain uniformity in the species richness values over vast areas of the present day temperate zone in Northern Eurasia was probably a reflection of uniform climatic conditions within the early Valdai periglacial zone ("hyperzone", by A. A. Velichko 1973) and a destruction of zonal structure of the Northern Eurasia biotas during the Valdai glacial epoch. In their structure, the periglacial faunas resembled those of modern ecotones. It should be noted, however, that unlike the disharmonious glacial-age faunas of North America, the Valdai faunal assemblages of the Russian and Siberian plains never exceeded the modern values of species richness. This contrasts sharply with North America where near glacial regions featured equable climates and an increase in species richness during the Wisconsin (Graham 1976; Semken 1988). Different geographical position of the ice sheets and, accordingly, location of periglacial zones in Eurasia and North

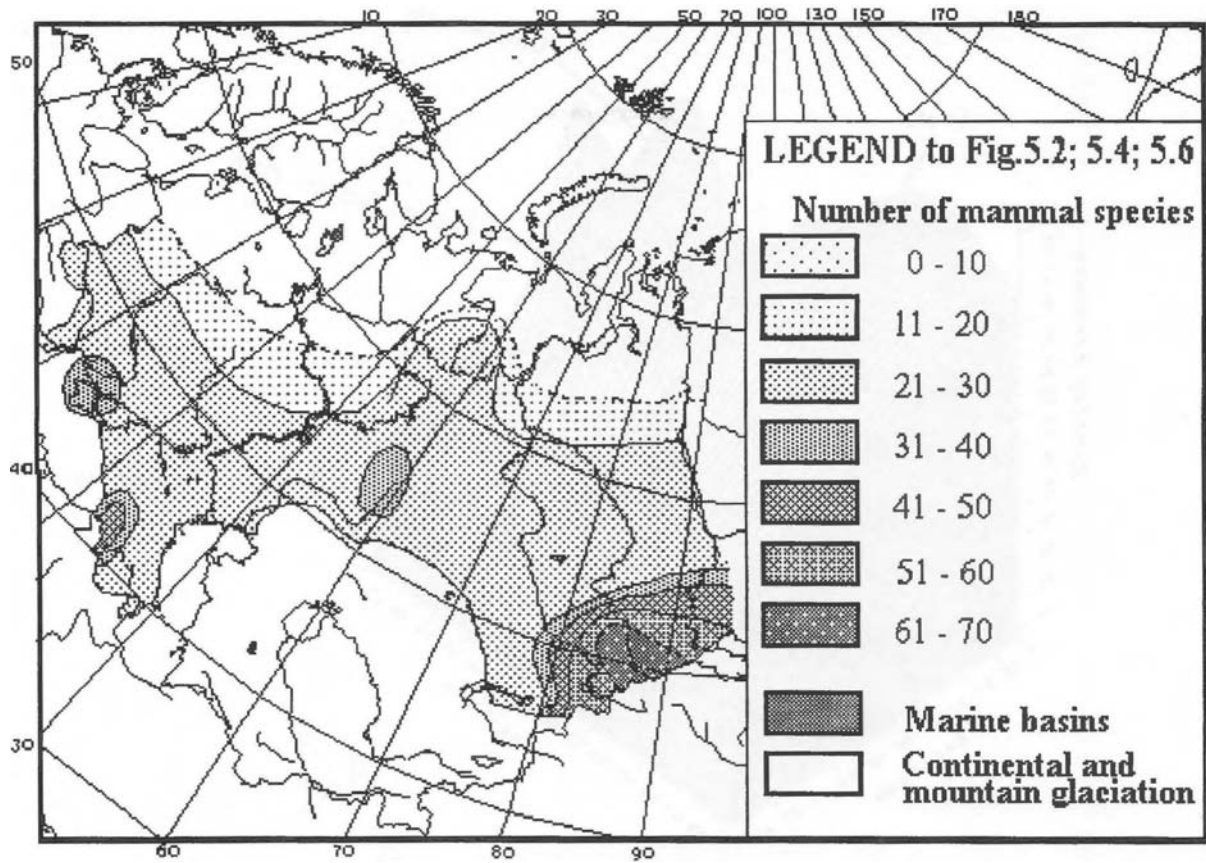


FIG. 5.2. Mammal species richness in early Valdai (100,000-35,000 yr B.P.)

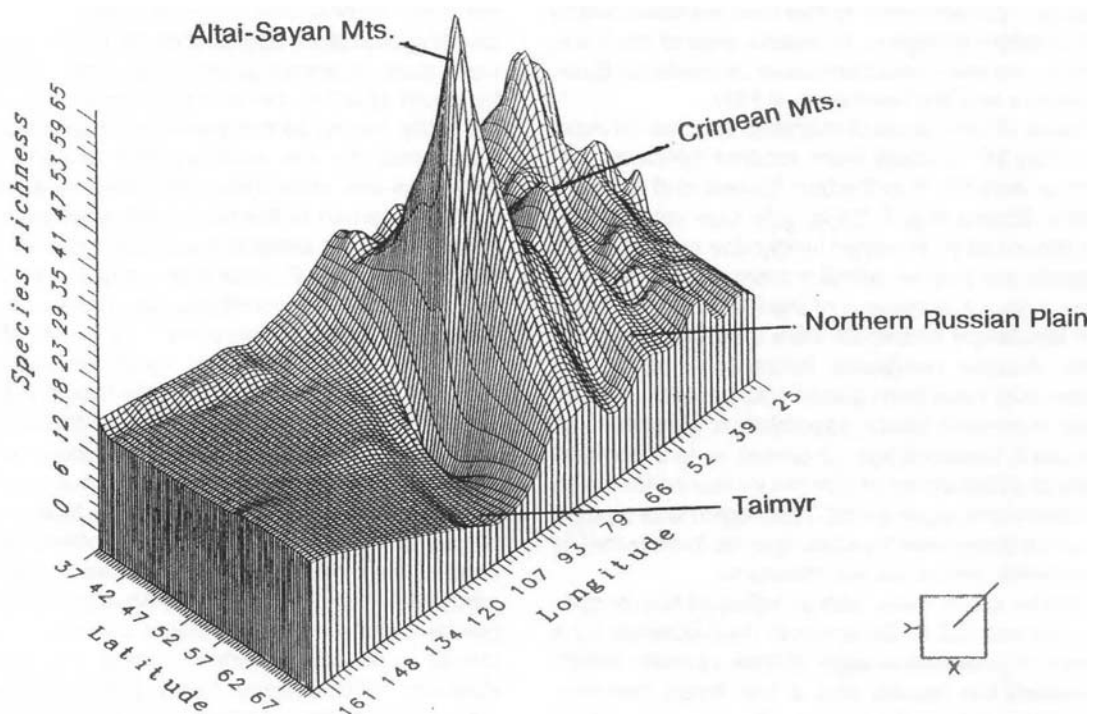


FIG. 5.3. Mammal species richness in the Early Valdai (35,001-100,000 yr B.P.)

America may account for the different values of species richness. While the Wisconsinian ice sheet reached as far south as 40° N, the Valdai ice sheet never penetrated south of latitude 54° N, even at its maximum. Besides, there was at West a narrow, perhaps spotty permafrost zone in North America, but permafrost was widely spread in Eastern Europe (up to 47° N) and occupied practically the whole Asian territory of the former Soviet Union. This distinction could not fail to imprint species richness of the Late Pleistocene faunal assemblages differently between the two continents.

The number of mammal species was considerably higher in mountains. Thus, as many as 40 early Valdai mammal species inhabited the Crimea and the Urals, and up to 50 species lived in the Caucasus. The most conspicuous rise in the mammal species number (between 60 and 70 species) is recorded in mountain sites of Southern Siberia. Such a sharp increase in the species richness in mountain regions may be explained by a greater diversity of habitats (due to altitudinal zonation, different orientation of slopes, etc.) which allows animals with different environmental requirements to find suitable ecological niches within smaller geographic areas. Mountain regions also provided refugia for many representatives of flora and fauna (forest-dwelling mammals, in particular) during glacial epochs.

As mentioned above, mountains are distinguished for their high species richness at present

too. Thus, materials collected from natural reserves on the former USSR territory show the highest values of mammal species richness (more than 75 species) in the Altai-Sayan mountains (Shvarts E. & Pushkaryov 1994).

The data available on species richness during the **Bryansk (= late Karginsky) Interstadial (35,000-24,000 yr B.P.)**, which is one of most important interstadials of the Valdai glacial epoch, is insufficient for construction of a map. However, the 3-D diagram (Fig. 5.4.) reveals a tendency for an increase in the species richness southward, from 10 mammal species in the north to 33 in the south. Maximum values again occur in the mountains.

At the **maximum cooling of the last (late Valdai) glaciation (24,000 to 15,000 yr B.P.)**, the most severe climatic conditions documented deeply influenced the characteristics of the mammal species richness. Near the ice sheet (within 200 km of the ice margin), no more than 10 species of mammals have been recorded, among them mammoth, reindeer, polar fox, musk ox, two genera of lemmings, narrow-skulled voles (Fig. 5.5; Fig. 5.6), but up to 20 may be present in others. Farther south, within 200 to 400 km from the ice sheet, about 20 species occurred including a noticeable number of steppe animals, such as horse, saiga, bison and auroch, marmots, ground squirrels, steppe lemming, yellow lemming, and others. Still farther south, on the Russian Plain and in Siberia, a zone inhabited by as many as 30 species existed. It was represented primarily

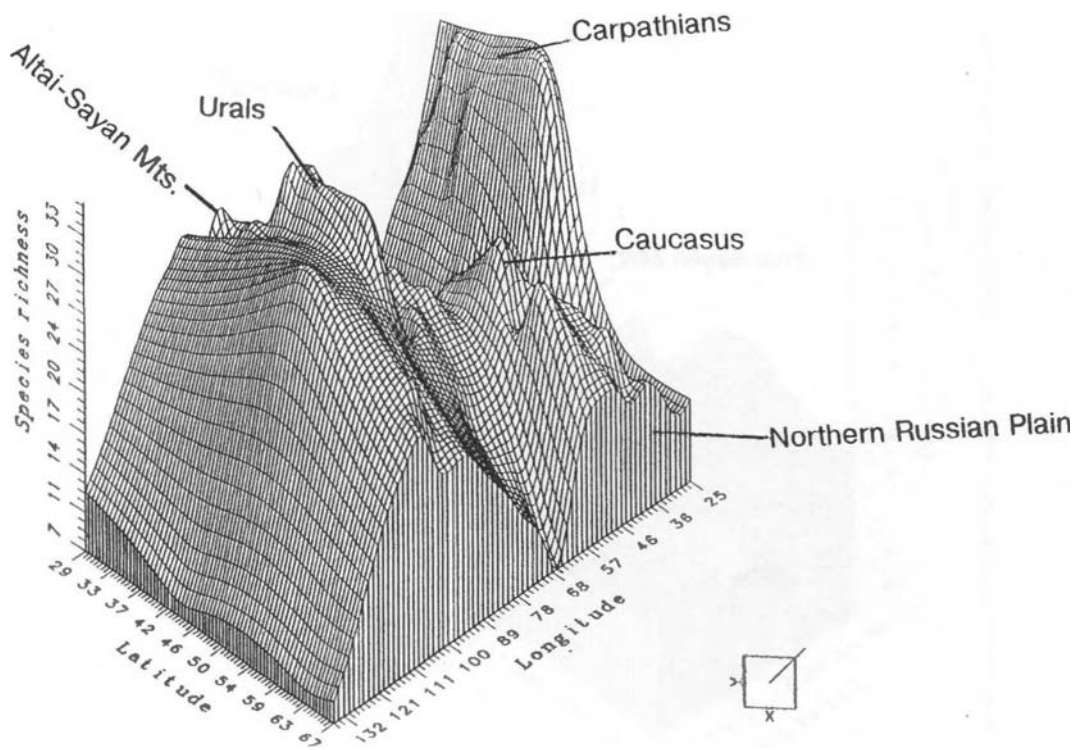


FIG. 5.4. Mammal species richness in the Middle Valdai Interstade (24,001-35,000 yr B.P.)

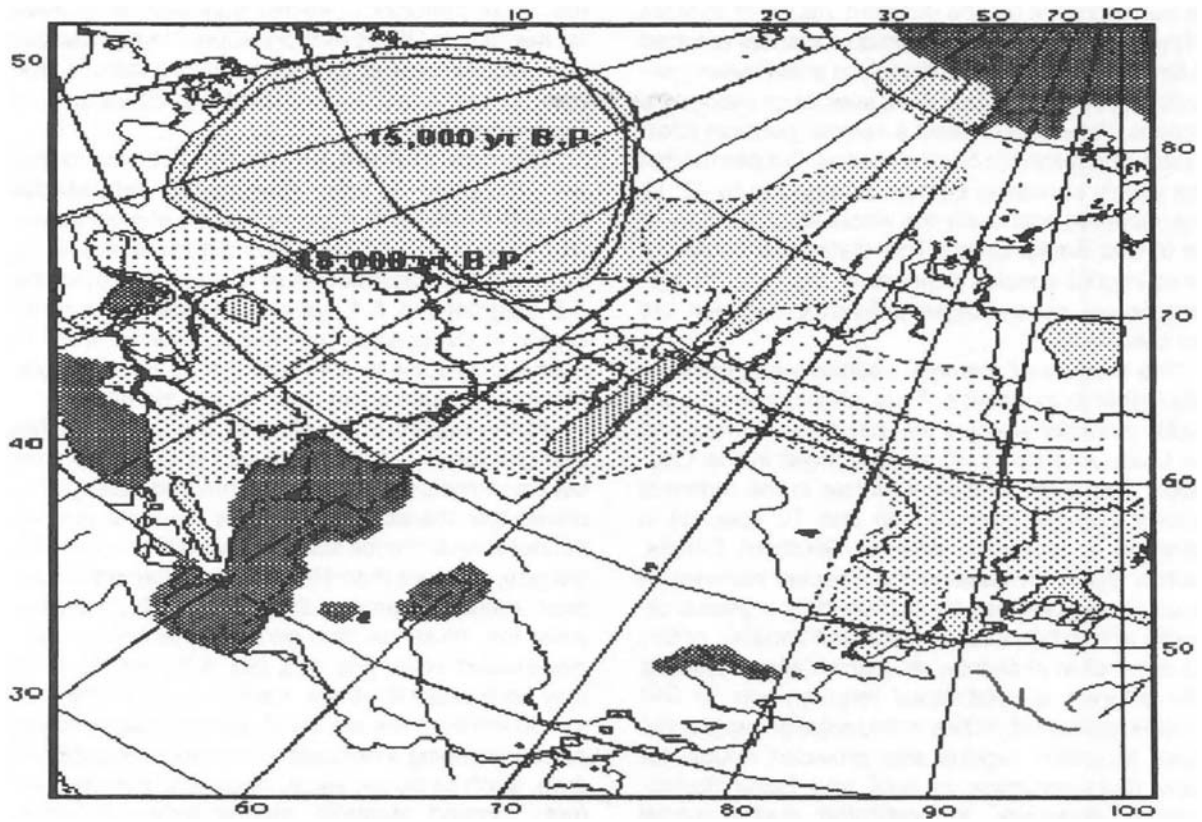


FIG. 5.5. Mammal species richness in Glacial Maximum (24,000-15,000 yr B.P.)

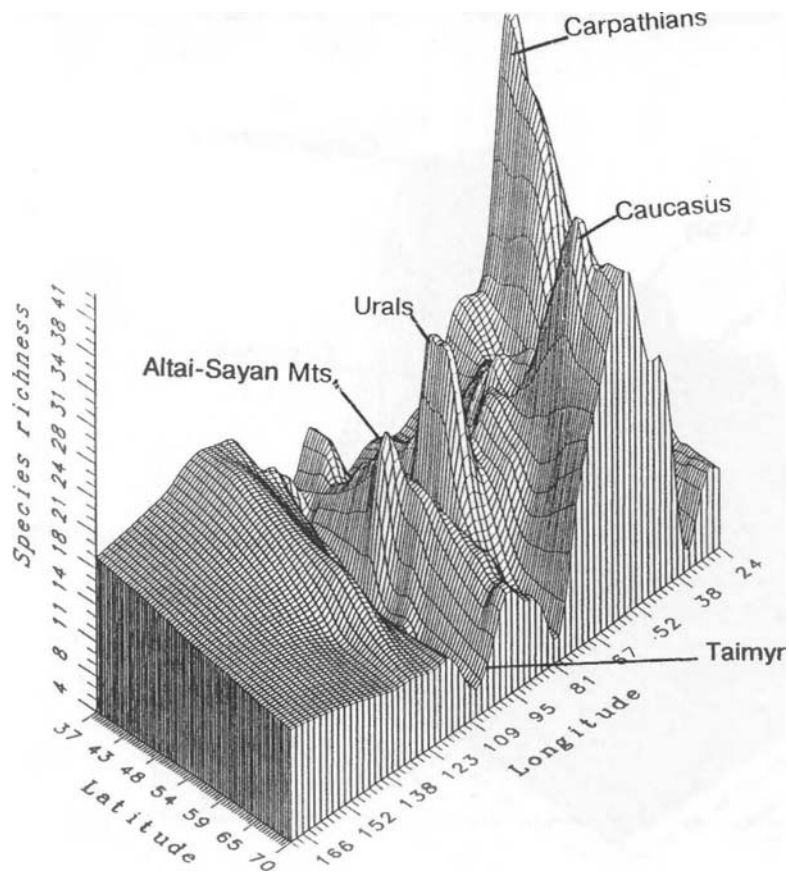


FIG. 5.6. Late Valdai mammal species richness (15,001-24,000 yr B.P.)

by steppe mammals, to a lesser extent by subarctic ones, but it included a few forest dwellers. A slight decrease in mammal species quantity is recorded in the South of the Russian Plain (Fig. 5.5) that could be a result of dryer climate and reduced potential evapotranspiration in the regions. As with the previous time interval, the highest values of mammal species richness are found in mountains (as many as 40 species in the Urals and up to 56 species in the Carpathians). Unfortunately, we have no reliable data for either the Caucasus or the mountains of southern Siberia for this interval.

At the **end of the Valdai glacial epoch** (15,000 to 10,000 yr B.P.) species richness values on the plains of Eastern Europe were kept at a low level. Between 10 and 20 species are documented be

tween latitudes 50° and 60° N and up to 30 species coexist south of 50° N. Such low values of species richness are indicative of rather severe environments during the late glacial (especially, at its beginning). In the Ural mountains mammalian species increased in number up to **40**, similar to that at the glacial maximum, at that time (Fig. 5.7). We have practically no material to describe species richness for the south of Eastern Europe and Asia. Therefore, only a fragment of total pattern of the species richness during the late glacial can be reconstructed.

The materials analysed on the Late Pleistocene mammal species richness within the limits of the former USSR permit to draw some conclusions:

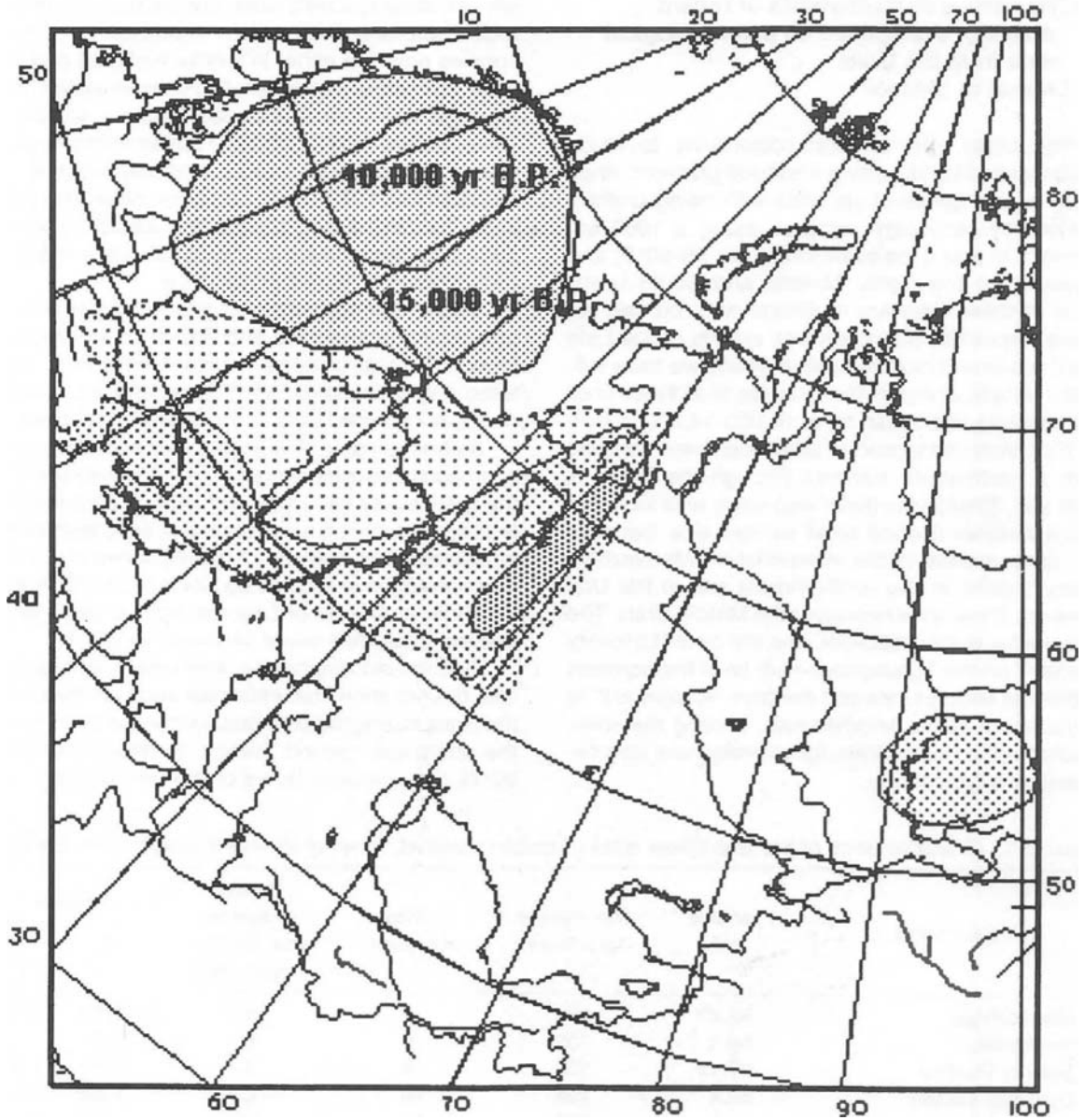


FIG. 5.7. Mammal species richness in Late Glacial (15,000-10,000 yr B.P.)

1. Mammal species richness values increased from north to south both during the Mikulino Interglacial and at four intervals of the Valdai epoch, this shows a distinct dependence between the heat supply and species richness.

2. The Valdai glacial time was typified by a certain equability of the species richness characteristics; vast areas of the Russian Plain and Siberia were occupied by mammal assemblages similar in their rather low parameters of the species richness.

3. The highest values of species richness have been found within mountain regions where highly variable environments allow higher numbers of suitable ecological niches. Many mammalian taxa survived the extremely severe glacial epochs in the diverse mountain environments.

5.2. Numerical characteristics of rodent diversity, exemplified on paleontological data from the Urals

Nikolai G. Smirnov

The Urals offer a good opportunity to study mammalian diversity along a latitude gradient, since there exist a series of six sites with being uniform taphonomy, abundant remains, along a 1000 km transect, at about the same longitude, 58-60° E, and representing the North, Middle, and South Urals. Most of these sites are multilayer and, contain remains deposited during diverse stages of the Late Pleistocene and Holocene. At present, we have sufficient data to compare the faunas of all these sites representing late Valdai time, 16,000-14,000 yr B.P.

Five sites composed of small mammals remains form a north-south transect through the Urals. A sixth site, Shaitansky (Ivdel'sky) cave, was included in the analysis despite small sample size, because this cave assists in the interpretation Medvezh'ya ("Bear") cave, in the northernmost site in the Ural transect. Three sites represent the Middle Urals. The rockshelter Bolshoi Glukhoi, and the cave "Dyrovaty Kamen" on the Tchusovaya-river lie in the northern part of the Middle Urals and the cave "Arakaevo 8" is in the south of the Middle Urals. Among the sites, studied in the South Urals, Ignatievsky cave was selected as a typical one.

It is clear that quantity of rodent species decreased linearly towards the north (Table 5.1). It would be interesting to find out, due to what species this regularity was observed. The species found in all sites were *Microtus gregalis*, *Dicrostonyx gulielmi*, *Lemmus sibiricus*, *Clethrionomys ex gr. rutilus-glareolus*. The remains of *Ochotonapusilla* were recorded everywhere, but as non-rodent they were not included into the quantitative analysis. The remains of *Clethrionomys rufocanus* were missing only in Shaitansky cave, probably due to small sample volume. They were noted in all the neighbouring caves, both northwards and southwards from the latter site, but as a very rare species. After "diluting" the quantity of remains collected in Medvezh'ya cave, down to the number of remains found in the Shaitansky cave, the probability of finding this species in that sample is 0.1. Therefore, we can be sure that within the 1000 km latitudinal gradient there were at least 6 common rodent species. The modern descendants of these species now live either in tundra (collared and Siberian lemmings, narrow-skulled vole), in taiga (*Clethrionomys voles*), or in steppes (*Lagurus sagebrush voles*, narrow-skulled voles). Faunas of this kind are usually called mixed faunas or disharmonious faunas (Semken 1988). Species composition and ratios in the examined local faunas also varied by the latitude and permit description of latitude variants of disharmonious faunas in the Urals.

Only in the northernmost site, were the remains of *Myopus schisticolor* and *Microtus middendorffi* found. The first of these two species is now registered only in the taiga, and the second, *M. middendorffii*, is recorded only in the present-day tundra.

Jerboa remains (*Allactaga major* and *Alactagulus pygmaeus*) were registered only in the very south, in the Ignatievsky cave site. Remains of *Eolagurus leuteus* and *Allocricetulus eversmanni* were identified in Ignatievsky and Arakaevo 8 (56° N), those of *Cricetulus migratorius* in all sites up North to 58° N (Bolshoi Glukhoi), and finds of *Lagurus lagurus* were documented in all sites except Medvezh'ya (60° N).

One should emphasise, that recent steppe species did not show maximum advance northwards in the Urals during the late Valdai time, but later, during the postglacial period. Hence, in Shaitansky cave, 60° N, the Holocene layers of this time not only con-

TABLE 5.1. Characteristics of the late Valdai sites of rodent remains, forming the north-south Urals transect

Cave name	Latitude (°N)	Min. number of animals	Number of species	Number of species after "diluting" N till 170	Indices	
					"d"	"e"
1. Medvezh'ya	62.03	196	7	5.7	1.14	0.43
2. Shaitansky	60.1	32	6	6	1.45	—
3. Bolshoi Glukhoi	58.15	105	9	8.7	1.72	0.71
4. Dyrovaty Kamen'	57.4	424	10	6.7	1.49	0.57
5. Arakaevo 8	56.1	339	14	10.3	2.23	0.68
6. Ignatievsky	55.07	299	14	12	2.45	0.47

tained the remains of the steppe pika, but, also, those of *Eolagurus luteus* and *Cricetulus migratorius*. This location was so distant from all of those previously known for the late Valdai time, and particularly, from the present-day species ranges, that it I regarded (Smirnov 1994) the eastern slope of the Middle Urals as a kind of a corridor with a peculiar arid climate, along which the steppe biota immigrated to the far north. During the postglacial and early Holocene time both the northernmost expansion of the steppe animals, and the maximum proportion of the steppe species remains are recorded in contemporaneous in layers of several sites of fossil local faunas in the Middle Urals (Smirnov 1994, 1995).

Dynamics of the species richness along the Ural transect could not be interpreted without grouping the species according to their ecological preferences (Table 5.2).

In the most cases, each species can be assigned to a category. However, the narrow-skulled vole, the most abundant fossil in the late Valdai local faunas of the Urals, is now known to inhabit two natural zones: tundra and steppes. Previous authors have regarded the Late Pleistocene representatives of this species from different positions. Some considered them to inhabit steppe biotopes, while others rate these animals as tundra-dwellers, still other investigators referred them, together with fossil *Dicrostonyx* lemmings, to represent a peculiar group of animals that occupied special periglacial biotopes with no analogue in the present-day natural environments. Different approaches to this problem are based upon morphological similarity of fossil narrow-skulled

voles to different modern subspecies, including multivariate analysis (Smirnov 1992). Table 5.2 submitting the number of species inhabiting different biotopes, the narrow-skulled vole was listed in two columns simultaneously, both with the steppe and tundra forms; in Table 5.3, the proportion of minimum number of individuals of this species was given as a separate column.

Species diversity of the rodent local faunas showed general increase southwards, mainly due to growth of the steppe-associated species. The quantity of tundra-dwelling species practically did not change along this transect. Only in the deposits of the Medvezhya cave (North Urals), the remains were recorded being assigned to *M. middendorffii*, which may not be reliable. The greatest number of the species inhabiting grasslands was observed in the south Middle Urals; the most common was *Microtus oeconomus*, as in most sites, and, followed by the water vole and the common hamster. The quantity of the forest species within the transect varied but weakly (discounting Shaitansky). However, the species composition of this group changed. This might be a result of the fact that all the forest species during the late Valdai time were either rare or very rare. However, their presence must be significant because the remains of squirrels and forest mice were recorded in the Middle Urals, whereas in the North and South Urals this group was represented only by *Clethrionomys* voles.

To characterise biodiversity, it would be useful, in addition to the index of the species diversity, to apply another indicator of the community structure, the equitability index "e". (Table 5.1) . The latter is calculated

TABLE 5.2. Numbers of the species assigned by ecological preferences in the sites along the Urals north-south transect

Caves	Steppe species	Tundra species	Grassland species	Forest species
1. Medvezh'ya	1	4	0	3
2. Shaitansky	3	3	1	1
3. Bolshoi Glukhoi	4	3	1	3
4. Dyrovaty Karmen'	4	3	1	4
5. Arakaevo 8	6	3	3	4
6. Ignatievsky cave	8	3	2	3

TABLE 5.3. Proportions of individuals assigned to the species of diverse ecological preferences in the late Valdai site along the Urals transect north-south (%)

Caves	<i>M. gregalis</i> (other steppe species)	Tundra species	Grassland species	Forest species
1. Medvezh'ya	14(0)	84	0	2
2. Shaitansky	29(5)	62	2	3
3. Bolshoi Glukhoi	29(5)	48	8	10
4. Dyrovaty Karmen'	30 (17)	50	2	1
5. Arakaevo 8	37 (28)	17	11	6
6. Ignatievsky cave	68 (10)	3	14	4

based upon minimum number of individuals with respect to the species numbers, by the formulas [2,3], According to the accepted classification, we distinguished three groups of sites: (1) those showing relatively uniform distribution of the species proportions, (2) those with unbalanced distribution and (3) those — with extremely disbalanced proportions. Among the late Valdai rodent local faunas in the Urals, neither revealed uniform shares of animals of different species. Uniform proportions, however, are characteristic of the present-day zonal faunas which were recorded in the Urals since middle Holocene time. Unbalanced and extremely disbalanced species diversity was typical of the late Valdai disharmonious faunas. The quality of the local faunas, as described by equitability index “e”. In contrast to the index of species diversity, “e” varied non-linearly. In the very south and northernmost sites studied, its values were significantly lower than those in the Middle Urals. This means, that one or two species dominated all the rest by the proportions of individuals. In the north, the collared lemming was such a dominant species, while in the southern sites, the narrow-skulled vole dominated.

The proportions of individuals, assigned by ecological presence supplement the insight of a latitude gradient in the structure of disharmonious faunas. One can see, that by the relative abundance of individuals, show that the bulk of all local faunas examined consisted of steppe and tundra species and that there is a clearly expressed north-south gradient with regard to proportions of individuals of tundra species, whereas species diversity in this group practically did not change. The share of individuals of the grassland-dwelling species showed significant increase southwards. The greatest equitability values were observed in the local faunas of the Middle Ural (Dyrovaty Karmen¹ expected), where collared lemmings and narrow-skulled voles were less dominate, and proportions of animals assigned to the grassland and forest species were noticeably increased. This situation in the middle Ural, with the best developed disharmonious faunas, could be a result of the ratio of heat and moisture being equally favourable for the species of both steppe and tundra habitats and suitable for more species of grasslands and forest ecosystems as well. Northwards from this area, cold became a limiting factor, whereas toward the south, it was aridity.

Level of similarity between disharmonious faunas located on the same latitude, with an account to their compositions and structures, may be as estimated by means of “r”-criterion (Table 5.4).

Neighbouring local faunas showed high similarity with each other, and the index values for diverse pairs differed insignificantly. A regression equation was calculated, in order to establish the significance of the relationship between the similarity index values (when each local fauna was compared to the northernmost one) and the site latitudes. The equation appeared to satisfy a linear pattern; that is, similarity decreased uniformly. This conclusion was substantiated by the high value of correlation coefficient (0.92). This perhaps

TABLE 5.4. Coefficients of similarity between the late Valdai rodent local faunas of the North, Middle, and South Urals

Caves	1	12	3	4	5	6
1. Medvzh'ya	1					
2. Shaitansky	0.92	1				
3. Bolshoi Glukhoi	0.86	0.92	1			
4. Dyrovaty Kamen'	0.85	0.9	0.92	1		
5. Arakaevo 8	0.62	0.8	0.87	0.89	1	
6. Ignatievsky	0.49	0.7	0.79	0.77	0.91	1

dicates, that factors determining differences between the local faunas, are dependent directly upon latitudinal characteristics, and that no sharp boundaries can be seen within the transect. One should note that the present-day biota also changes gradationally in these regions; but to a greater degree. For example, the similarity index for the late Valdai local fauna of the South North Urals equalled to 0.7; while the recent faunas between the same regions showed $r = 0.43$. Values of the species diversity indices, describing rodent local faunas, from the late Valdai time until now vary insignificantly, though their structures and compositions revealed considerable changes. Similarity index values were estimated for several late Valdai and recent local faunas, based on taphonomically uniform data from the South Urals; they appeared to be low enough, about 0.2. This might be due to the fact, that among the total of 24 species in the combined taxonomic list for the late Valdai and the present-day faunas, only 5 are in common, and moreover show quite different relative numbers.

It would be interesting to compare spatial dynamics of the rodent fauna diversity with vegetation characteristics along the same transect. Pollen spectra from the deposits associated with the late Valdai faunules show an unusually high content spores of ferns and mosses, as is usual with cave sediments in this region. That is why we are apprehensive of plant community reconstruction based only on the pollen data upon trees, bushes and herbs.

The general composition of vegetation deduced from pollen evidence is in good agreement with biotope ratios drawn from the proportions of rodent remains. For example, in the South Urals, the pollen ratio of trees to herbs is about 1:85, and only isolated birch and willow grains were identified. In the late Valdai deposits in the Middle Urals, those proportions equaled to about 1:60, and variety of tree pollen increased, i.e. *Picea*, *Pinus*, *Betula*, and *Abies* grains were recorded.

To conclude the analysis of data on the late Valdai rodent faunas from the Urals north-south transect, I can mark the following important interpretations. Within the 62-55° N transect only disharmonious local faunas were recorded. Species diversity in these local faunas was reduced northwards to about half of that in the south. This decrease is a result of non-uniform

TABLE 5.5. Further ANOVA for Variables in the Order Fitted

Source	Sum of Squares	DF	Mean Sq.	F-Ratio
TY	4843.75832	1	4843.7583	27.79
TY ²	11.61964	1	11.6196	0.07
TY ³	93.57832	1	93.5783	0.54
TY ⁿ	65.82121	1	65.8212	0.38
PY	0.19129	1	0.1913	0.001
PY ²	119.86808	1	119.8681	0.69
K	1.80424	1	1.8042	0.01
K ⁵	15.53394	1	15.5339	0.09
Model	5152.17505	8		

northern expansion of steppe related species. Animals of forest and grassland habitats were most numerous in the centre of the region (the Middle Urals) where the most uniform proportions of tundra, grassland and forest species occurred, while steppe species were concentrated at the south and tundra species at the north. The rodent representatives of late Valdai time in each region differed from those of the present day, primarily, by the species composition and still higher concentration of species confined to a single modern biotope. General species diversity values of the late Valdai rodent faunas, however, differed little the values of corresponding characteristics of modern communities. communities.

TABLE 5.6. Model fitting results

Independent variable	Coefficient	Std. error	T-value
TY	-220.453616	802.482461	-0.2747
TY ²	70.742964	175.805427	0.4024
TY ³	-5.729224	12.970061	-0.4417
TY ⁴	0.146003	0.315448	0.4628
PY	-1815.554317	4302.169577	-0.4220
PY ²	935.420864	2169.170356	0.4312
K	9.987055	34.832468	0.2867
K ²	-0.109138	0.365553	-0.2986

5.3. Climate and mammal species richness in Eastern Europe during the Late Pleistocene

Alexander V. Kozharinov, Anastasia K. Markova

Studies of fossil mammal species richness of in relation to climatic factors has not been adequately elucidated in literature, a situation primarily attributed to the lack of detailed paleoclimatic maps and to incompleteness of the paleontological records. The gaps were partially closed after publication of the Palaeogeographic Atlas of the Northern Hemisphere (Frenzel, Pecsí, Velichko, 1992), which made it possible to relate mammal species richness to climatic variables. These small-scale paleoclimatic maps, however, can only give a rough idea of the climatic distinction between plains and mountainous regions within the same latitudinal zone. It could help to achieve relationship of the mammal species richness fluctuations related to paleoclimates during various intervals of the Late Pleistocene. The mammal species richness appears to depend of many climatic factors which are attributed to sectorial climatic differences. In western regions of Eastern Europe, where humidity values are moderate, the principal limiting factor is the mean annual temperature; in the eastern regions of insufficient humidity the annual precipitation increases in importance while the temperature factor becomes less significant.

We used empirical equations to calculate some new climatic characteristics — potential evaporation, mean annual values of air humidity, the humidity index — for three time intervals (the Mikulino Interglacial, the middle and the late Valdai Glacial).

During the **Mikulino Interglacial** the principal factor controlling the mammal species richness was mean annual air temperature. Results of the analysis of variance are given in the Table 5.5. where TY-mean annual air temperature, PY-total annual precipitation, K-yearly humidity index. Evidently, climatic dependence of the mammal species richness is non-linear. Therefore we applied regression analysis to approximate mammal species richness values by climatic parameters. Table 5.6 gives the results of the regression analysis (method of Stepwise Regression).

In the chosen regression model (R-SQ) the R² correlation coefficient is high enough to suggest that mammal species richness is climatically dependent to a

R-SQ. (ADJ.) = 0.6929; SE = 13.2; MAE = 5.15; DurbWat = 3.144;

considerable degree. To calculate the potential value of the mammal species richness (Rt) as a function of climate, the regression equation used:

$$[7] \quad R_t = -220.454 \cdot TY + 70.743 \cdot TY^2 - 5.729 \cdot TY^3 + 0.146 \cdot TY^4 - 1815.554 \cdot PY + 935.42 \cdot PY^2 + 9.987 \cdot K - 0.109 \cdot K^2$$

The mammal species richness during the Mikulino was primarily controlled by the mean annual air temperature: the species number increases exponentially with rise in temperature (Fig. 5.7). The maximum number of species has been recorded within regions where mean annual temperatures exceeded 9.2° C.

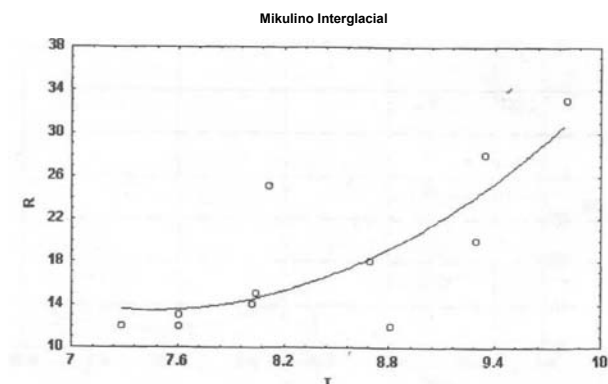


FIG. 5.7. The mammal species richness (R) versus mean annual air temperature (T° C)

The relationship between the mammal species richness and the total annual precipitation is more complicated; on average, the latter was somewhat above the today's level in Eastern Europe.

As shown in Figure 5.8, the maximum species richness falls in regions where mean precipitation ranges from 640 to 700 mm. Both increase and decrease in precipitation values results in reduction in species number.

On the whole, the mammal species richness — humidity index relationship is similar to that of total annual precipitation; the principal difference is that the curve rises slightly as values equal to 1 are approached (Fig. 5.9). The maximum mammal species richness in Eastern Europe corresponds to areas where the humidity index is less than 0.55 (five sites) and reaches a peak at 0.5. There are at least two — peaks of the mammal species richness (0.4, 0.5); they correspond to regions belonging to mega-ecotones in the natural zonality system, such as the forest-tundra and forest-steppe.

In Eastern Europe the climatic conditions of the Mikulino Interglacial were the most favourable throughout the Late Pleistocene for mammalian communities. A large share of the territory was optimum in climatic conditions. Abundant rainfall when mean annual temperature is low is unfavourable for the diversity of the mammal species (Fig. 5.10).

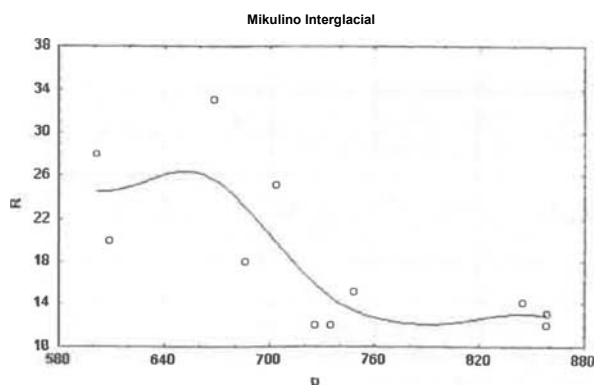


FIG. 5.8. Mammal species richness (R) versus total annual precipitation (P, mm)

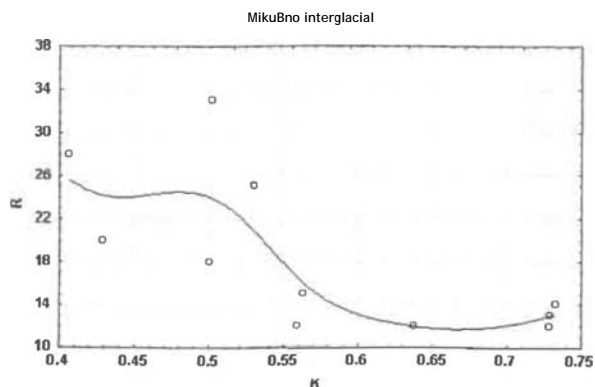


FIG. 5.9. Mammal species richness (R) versus humidity index (K)

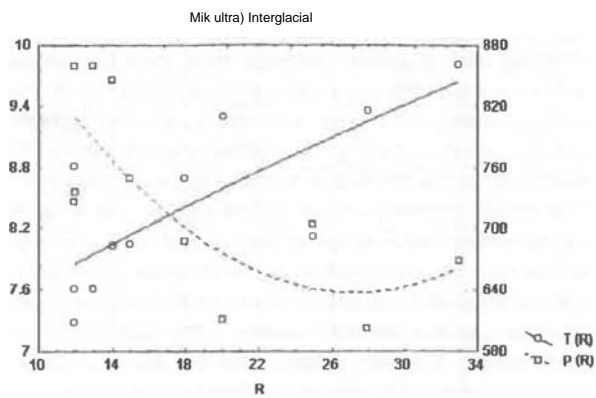


FIG. 5.10 The relation between mammal species richness (R) and mean annual temperature (T) and precipitation (P)

The middle Valdai (Bryansk-Late Karginsky) Interstadial featured, on the average, positive annual temperatures but insufficient humidity (Frenzel, 1992) for a variety of plants. That substantially affected the relation between the species richness and climatic factors. Under unique combinations of Bryansk environments, the humidity index became more important (compared with the Mikulino Interglacial); the analysis of variance, however, indicates that both annual precipitation and mean annual temperature contribute almost equally (Table 5.7).

TABLE 5.7. Further ANOVA for Variables in the Order Fitted

Source	Sum of Squares	DF	Mean Sq.	F-Ratio
TY	1007.02654	1	1007.0265	12.11
TY ²	651.06116	1	651.0612	7.83
TY ³	789.75216	1	789.7522	9.50
TY ⁴	1986.907	1	1986.9070	23.90
PY	2383.88772	1	2383.8877	28.68
PY ²	666.52649	1	666.5265	8.02
OVY	2324.81418	1	2324.8142	27.97
K	20.68747	1	20.7875	0.25
K ²	66.38037	1	66.3804	0.80
Model	9897.04310	9		

Where OYV is mean annual relative air humidity (%).

The results of the regression analysis reflect relationships more complicated in structure (Table 5.8). In spite of the leading role of the mean annual temperature during the Bryansk interstadial the mammal species richness in Eastern Europe was tangibly influenced by humidity. The moisture deficit limited the growth of the mammal species diversity.

The high value of the squared correlation coefficient (R-SQ) permits to calculate the equation of the potential species richness (Rt) as a function of various climatic parameters on the basis of the results of the analysis of regression:

$$[8] \quad Rt = 36.484 \cdot TY + 106.449 \cdot TY^2 - 236.843 \cdot TY^3 - 0.214 \cdot TY^4 - 8403.569 \cdot PY + 0.0000735 \cdot PY^2 - 4.796 \cdot OYV + 16.544 \cdot K - 1.444 \cdot K^2$$

TABLE 5.8. Model fitting results

Independent variable	Coefficient	Std. error	T-value
TY	36.483537	38.916512	0.9375
TY ²	106.449199	76.186143	1.3972
TY ³	-246.843113	462.02888	-0.5343
TY ⁴	-0.211379	0.40659	-0.5258
PY	-8403.568947	2.426181E4	-0.3464
PY ²	7.349286E5	2.459036E6	0.2989
OVI	-4.795756	9.00707	-0.5324
K	16.543944	16.221545	1.0199
K ²	-1.443763	1.61567	-0.8936

R-SQ. (ADJ.) = 0.82846; SE = 9.118; MAE = 4.769; DurWat = 2.774;

Mammal species richness depends exponentially on the mean annual air temperature, and its maximum falls on regions with annual temperature about 2.5 to 3° C (Fig. 5.11).

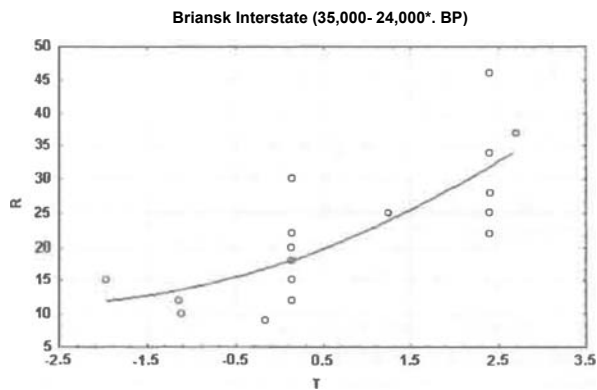


FIG. 5.11. The mammal species richness (R) versus mean annual air temperature (T° C)

A non-linear relationship has been found between the mammal species richness and total annual precipitation (Fig. 5.12) Maximum mammal species richness values are typical of the regions where the rainfall amount does not exceed 370 mm. An analysis of the geographic position of the regions revealed, however, that they are restricted to the south of Eastern Europe where annual temperatures were high enough. The temperature was precisely the dominant climatic factor which accounted for relatively high values of the species richness.

More informative results are presented in fig. 5.13, where mammal species richness values are plotted against the regional humidity index. The maximum number of the mammal species is restricted to the areas with humidity index about 0.3 to 0.35; it decreases gradually with increase in the humidity index and rises again when the latter exceeds 0.6. At present, the species richness maximum is located in the regions where K = 1, that is within the forest-steppe zone (Shvarts et al., 1994).

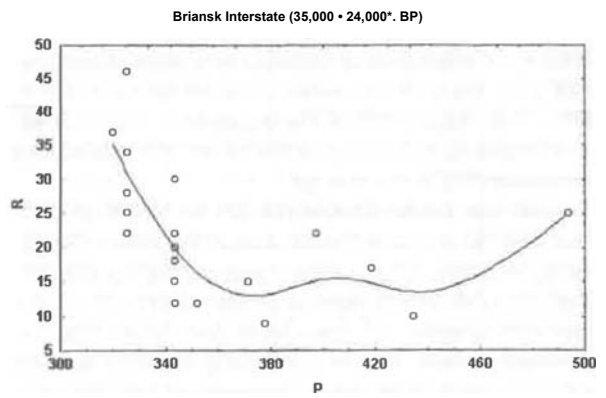


FIG. 5.12. The mammal species richness (R) versus total annual precipitation (P, mm)

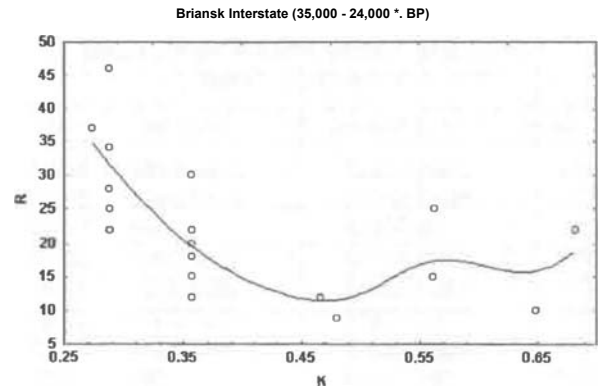


FIG. 5.13. The mammal species richness (R) versus humidity index (K)

A radically different distribution of the humidity values over the Russian Plain has been reconstructed for the Bryansk — late Karginsky Interstadial. The reconstruction shows no region on the Russian Plain with the humidity index values in excess of 0.65. In figure 5.13., sites showing relatively low values of species richness (less than 20) and corresponding to the humidity index more than 0.45 are concentrated in northern regions of Eastern Europe where mean annual temperatures are low.

The net effect of the mean annual temperature and total precipitation is shown in figure 5.14. On the whole,

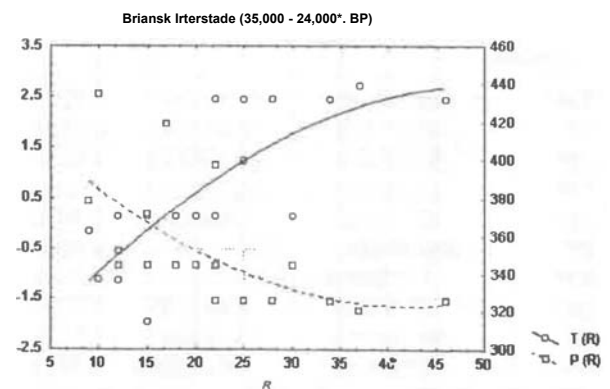


FIG. 5.14. The relation between mammal species richness (R) and mean annual temperature (T) and precipitation (P)

the curves showing the mammal species richness relationship to mean annual values of temperature and precipitation are similar to those obtained for the Mikulino time. That suggests that the response of mammal assemblages to increasing temperature and decreasing precipitation did not change.

The late Valdai Glacial (24,000 to 15,000 yr B.P.) featured the most severe climates of the whole Pleistocene (Velichko 1993). Under these conditions the permafrost (VM) would have a profound impact on the mammal species richness (Table 5.9). As before, the principal climatic factors controlling mammal species richness parameters were mean annual temperatures and precipitation, the contribution from the latter being more significant.

TABLE 5.9. Further ANOVA for Variables in the Order Fitted

Source	Sum of Squares	DF	Mean Sq.	F-Ratio
VM	3586.57857	1	3586.5786	30.25
TY	6048.60925	1	6048.6092	51.01
TY ²	8.40857	1	8.4086	0.07
TY ³	2790.60639	1	2790.6064	23.53
TY ⁴	1827.33576	1	1827.3358	15.41
PY	6765.83214	1	6765.8321	57.06
p _Y ²	1680.93245	1	1680.9324	14.18
OVY	125.71844	1	125.7184	1.06
K	338.08426	1	338.0843	2.85
K ²	89.99934	1	89.9993	0.76
Model	23262.1052	10		

The results of the regression analysis are presented in table 5.10. When all the climatic factors are considered together, it appears that most pronounced effects on the mammal species richness are those of the humidity index (K) and of the moisture deficiency (OVY). The mean annual temperatures and rainfall are of lesser importance.

TABLE 5.10. Model fitting results

Independent variable	Coefficient	Std. error	T-value
VM	-49.331223	404.12334	-0.1221
TY	-3.371561	16.418585	-0.2054
TY ²	33.296404	25.745373	1.2933
TY ³	17.876197	43.795292	0.4082
TY ⁴	0.012487	0.030634	0.4076
PY	855.80662	2622.0858	0.3264
PY ²	-1.758986E45	2.85479E4	-0.3328
OVY	9.293099	8.641455	1.0754
K	-54.505694	36.024992	-1.5130
K ²	22.884052	26.269964	0.8711

R-SQ. (ADJ.) = 0.7761 SE = 10.89; MAE = 6.58
DurbWat = 1.659;

Potential values of the mammal species richness controlled by the late Valdai climatic factors for Eastern Europe may be calculated using the following equation:

$$[9] Rt = -49.331'VM - 3.372'TY + 33.296'TY^2 + 17.876'TY^3 + 0.0125'TY^4 + 855.807'PY - 0.0001176'PY^2 + 9.293'OVY - 54.506'K + 22.884'K^2$$

With an increase in the mean annual air temperature, mammal species richness value rose exponentially, though its increase at that time proceeded much more slowly than during the Mikulino Interglacial and the Bryansk Interstadial (Fig. 5.15). The maximum mammal species richness is characteristic for regions where mean annual temperatures are above 4° C.

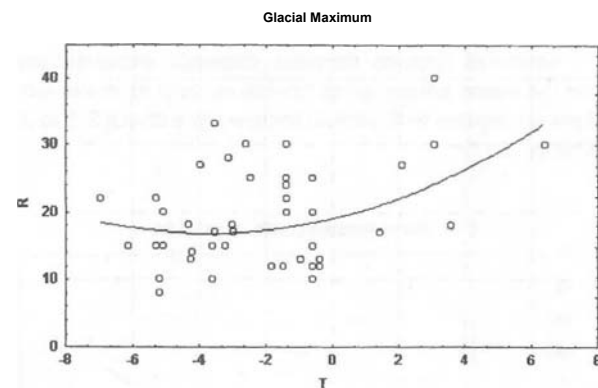


FIG. 5.15. The mammal species richness (R) versus mean annual air temperature (T° C)

The precipitation-dependence of the mammal species richness appeared to be more intricate. It was most likely due to the fact that at the coldest time of the Valdai, the ice sheet exerted not only cooling, but primarily a desiccating effect upon the climate (and therefore, the biota) of the adjacent regions (Fig. 5.16).

The mammal species richness plotted against the humidity index shows an almost linear relationship, with a two slightly pronounced peaks (Fig. 5.17). A certain equability of the mammal species richness values

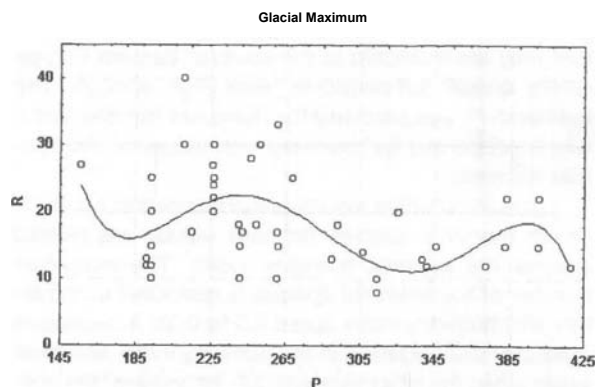


FIG. 5.16. The mammal species richness (R) versus total annual precipitation (P, mm)

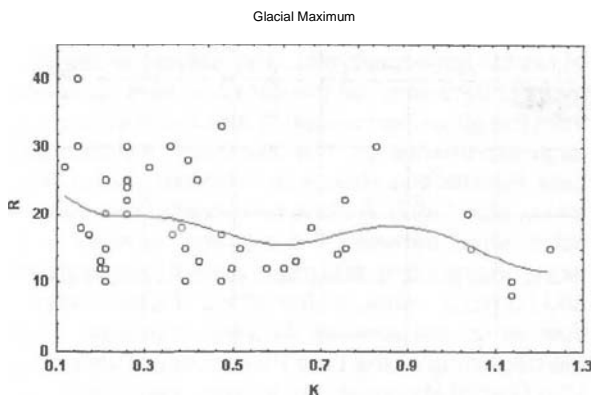


FIG. 5.17. The mammal species richness (R) versus humidity index (K)

with reference to the degree of humidity is typical of the East European territory. The maximum number of mammal species is found in the regions where the humidity index equals 0.40 and 0.90. The first peak ($K = 0.40$) characterises the central Russian Plain, the other one (0.90) falls on the northern regions of Eastern Europe.

On the whole, during the coldest stage of the Valdai the climatic conditions over the most part of Eastern Europe (and the heat and moisture supply in particular) did not favour development of biotic diversity. Maximum values of the mammal species richness are established in the plains regions where the mean annual temperatures exceeded 2°C and the humidity index equalled either 0.40 or 0.90 (Fig. 5.18). We do not consider data on mammal species richness in mountains because of specific characteristics of highland climates and therefore different type of relation between the mammal diversity and the paleoclimates in these regions.

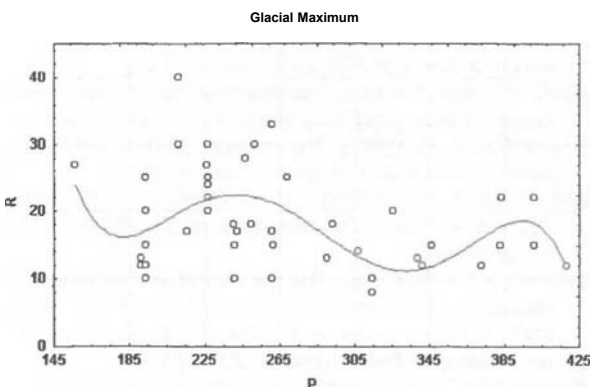


FIG. 5.18. The relation between mammal species richness (R) and mean annual temperature (t) and precipitation (P)

The analysis performed permits to draw the following conclusions:

1. The mammal species richness both during the Mikulino Interglacial and the Valdai Glacial time was primarily controlled by mean annual air temperatures; the

relation was exponential. The same — exponential dependence is found for the climatic conditions of today.

2. Since the beginning of the Late Pleistocene time through the coldest time of last glacial epoch the influence of humidity on the mammal species richness increases in importance.

3. Total annual precipitation was most significant for regional mammal species richness in the middle Valdai interstadial.

4. The mammal species richness varied inversely with the permafrost thickness at the late Valdai time.

CONCLUSIONS

A great deal of materials on fossil mammals of Northern Eurasia has been amassed to date. The most abundant subset consists of theriological data obtained from the Late Pleistocene and the Holocene localities. The data, however, have not yet been analysed and summarised adequately, using up-to-date methods.

The authors are the first to accomplish a computerised synthesis of this database. For this purpose, the database PALEOFAUNA has been devised which includes four blocks of information. Within the blocks, each of the Late Pleistocene mammal sites is characterised by its geographic position, age span, species composition, and abundance of remains of individual species; bibliographic references are supplied. The database structure is developed using the Paradox V.4 package; it is compatible with related databases already in use, such as FAUNMAP which was designed for theriological materials of North America (FAUNMAP. A database Documenting Late Quaternary Distributions of Mammal Species in the United States, 1994).

To accomplish a cartographic presentation of the materials, we use software ARC / INFO and ARC A/IEW which permitted compilation of maps of mammal remain findings and species richness of component taxa for different intervals of the Late Pleistocene (including the Mikulino Interglacial, early Valdai, the Bryansk Interstadial, the glacial maximum, the coldest interval of the late Valdai, and the late glacial time); climatic characteristics of each interval varies over a wide range.

The cartographic programs and the first variant of the geoinformation system permitted quantification of responses of ecologically different mammal species to climatic change. The responses are found to be highly diversified, and the data obtained thus far seem to corroborate the "individualistic response" theory (Graham 1986; Fromozov 1976). During the last glacial epoch, a majority of northern subarctic mammals considerably extended their ranges to the south, at the same time steppic species penetrated further north. Forest mammals responded variously: a number of more warm-loving mammals drastically reduced their ranges and persisted only in mountains in the south of Northern Eurasia; forest animals less sensitive

to cooling continued to inhabit central regions of Eastern Europe and Siberia, though they were restricted to local forested biocenoses. On the whole, the mammalian faunas underwent drastic restructuring during the period of the last glaciation. Most characteristic feature of the new structure was joint habitation within the same areas of mammals which at present are geographically separated and belong to different modern natural zones. As a result, so called "mixed" or "disharmonious" faunas were formed; no analogues of those faunas are known at present, and none have been recorded from any interglacial in the past.

The PALEOFAUNA database also permitted to locate more precise definition of the time and the place of extinction for many characteristic species of the mammoth assemblage which did not survive the Holocene warming, changes in plant communities, and probably the pressing of early hunters.

To analyse relationship between the faunal assemblages and plant communities, an electronic PALEOFLORA database has been established simultaneously; it comprises palynological materials on Eastern Europe dated back to the second half of the Valdai glacial epoch (the geographic and chronological span of the database will be extended to earlier sites). Using materials of the two databases jointly it is possible to document both the simultaneous response of indicator species of plants and mammals to global climatic changes, and the dramatic cooling of the late Valdai.

An essential part of the work was to reveal the Late Pleistocene climate impact on the mammal species richness. To make the paleoclimatic data usable for the analysis, we had to transform into digital form and introduce into electronic database

isolines of temperatures (paleoisotherms), isolines of rainfall (paleoisohyets), and isolines of the permafrost thickness; all the data had been obtained from the atlas-monograph "Paleoclimates and paleoenvironments of the Northern Hemisphere. Late Pleistocene-Holocene" (Frenzel, Pecs, Velichko, eds. 1992). A close relationship can now be established between the mammal species richness, on one hand, and mean annual temperatures and humidity index, on the other. The humidity influence on the species diversity increases since the beginning of the Late Pleistocene towards the Last Glacial Maximum. An inverse relationship appears to exist between the permafrost thickness and mammal species richness during the Late Pleistocene.

The revealed relationships between the parameters of paleoclimates during various intervals of the Late Pleistocene and the mammal species richness over the vast areas of Northern Eurasia allowed estimation of principal trends in the mammal species richness fluctuations over hundred of thousands years and compilation of maps showing the species richness at different chronological intervals of the Late Pleistocene. The distribution of the mammal species richness of the Valdai epoch shows marked distinctions from that of the present day.

The work on the electronic PALEOFAUNA database opened up new possibilities for analysis of the Late Pleistocene mammalian faunas distribution and species richness over the whole territory of the former Soviet Union. It would not be no less interesting to follow the subsequent transformation of the mammal faunas induced by the Holocene warming. The authors contemplate to cover these issues in their further publications.

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APPENDIX

TABLE 1. Mammal locality data

No.	Site name	Latitude	Longitude	References
1	Veselaya Gora	48.50	39.14	Loktyushov S. A., 1940
2	Amvrosievka	47.45	38.20	Boriskovskii P. I., Praslov N. D., 1964
3	Donskoe	47.20	40.05	Boriskovskii, P. I., Praslov N. D., 1964
4	Byzovaya	65.10	57.20	Guslits'er V. I., Kanivets V. I., 1965
5	Vladimirovka 1	48.30	30.50	Chernysh A. P., 1973
6	Dneprovo-Kamenka	48.35	33.55	Turusova S. A., 1940
7	Pristenskaya	49.10	37.10	Sobinev N. V., 1946
8	Gagarino	52.25	38.50	Zamyatin S. N., 1935
9	Monastyrek	48.45	25.50	Chernysh A. P., 1973
10	Grushevatyi	48.20	35.30	Chernysh A. P., 1954
11	Viasovka	50.00	33.05	Proceedings of III Archeol. Conference, 1878
12	Poltava	49.38	34.35	Chernysh A. P., 1954
13	Pol'noe-Yaltunovo	54.00	41.50	Milonov I. P., 1958
14	Karacharovo	55.35	42.00	Boriskovskii P. I., 1937
15	Podsosenka Verkhnya	54.12	41.58	Milonov I. P., 1958
16	Talitzkogo	58.05	56.40	Bader O. N., 1961
17	Zolotovka	47.32	40.33	Pralov N. D. et al., 1980
18	Syngir	56.08	40.20	Bader O. N., 1961
19	Borshevo-2	51.29	39.00	Vereshchagin N. K., Kuz'mina I. E., 1977
20	Kostenki-8	51.29	39.00	Vereshchagin N. K., Kuz'mina I. E., 1977
21	Kostenki-13	51.29	39.00	Vereshchagin N. K., Kuz'mina I. E., 1977
22	Medvezhia peshera	62.40	56.10	Kanivets V. P., 1962
23	Suren'-1	44.55	34.00	Mereshkovskii K. S., 1879
24	Kostenki-1 (layer 1)	51.29	39.00	Rogachev A. N. et al., 1981
25	Kostenki-1 (layer 2)	51.29	39.00	Rogachev A. N. et al., 1981
26	Kostenki-1 (layer 3)	51.29	39.00	Rogachev A. N. et al., 1981
27	Kostenki-1 (layer 4)	51.29	39.00	Rogachev A. N. et al., 1981
28	Kostenki-1 (layer 5)	51.29	39.00	Rogachev A. N. et al., 1981
29	Kostenki-17 (upper layer)	51.29	39.00	Boriskovskii P. I. et al., 1981
30	Kostenki-17 (lower layer)	51.29	39.00	Boriskovskii P. I. et al., 1981
31	Kostenki-11 (layer 1)	51.29	39.00	Rogachev A. N. et al., 1981
32	Kostenki-11 (layer 2)	51.29	39.00	Rogachev A. N. et al., 1981
33	Kostenki-11 (layer 3)	51.29	39.00	Rogachev A. N. et al., 1981
34	Kostenki-11 (layer 4)	51.29	39.00	Rogachev A. N. et al., 1981
35	Kostenki-11 (layer 5)	51.29	39.00	Rogachev A. N. et al., 1981
36	Kostenki-21	51.29	39.00	Pralov N. D., 1981
37	Kosoutza (layer 2)	48.07	28.10	Borziyak I. A., David A. I., 1986
38	Kosoutza (layer 3)	48.07	28.10	Borziyak I. A., David A. I., 1986
39	Kosoutza (layer 4)	48.07	28.10	Borziyak I. A., David A. I., 1986
40	Kosoutza (layer 5)	48.07	28.10	Borziyak I. A., David A. I., 1986
41	Kosoutza (layer 6)	48.07	28.10	Borziyak I. A., David A. I., 1986
42	Kosoutza (layer 7)	48.07	28.10	Borziyak I. A., David A. I., 1986
43	Kosoutza (layer 8)	48.07	28.10	Borziyak I. A., David A. I., 1986
44	Kosoutza (layer 9)	48.07	28.10	Borziyak I. A., David A. I., 1986
45	Kosoutza (layer 10)	48.07	28.10	Borziyak I. A., David A. I., 1986
46	Kostenki-14 (layer 2)	51.29	39.00	Rogachev A. N., 1957
47	Kostenki-14 (layer 3)	51.29	39.00	Rogachev A. N., 1957
48	Kostenki-14 (layer 4)	51.29	39.00	Rogachev A. N., 1957

No.	Site name	Latitude	Longitude	References
49	Osokirevka I	47.35	35.20	Boriskovskii P. I., 1953
50	Mysy	49.45	55.25	Panichkina Z. A., 1953
51	Ulyank	55.30	47.58	Bryusov D. Ya., 1940
52	Yunga-Kusherga	46.30	56.10	Khalikov A. Kh., 1950
53	Perevoloki	48.15	51.55	Abramova Z. A., 1958
54	Kamennaya Balka II	47.00	40.00	Pralov N. D., 1964
55	Adzhi-Koba	44.50	34.05	Vekilova E. A., 1971
56	Avdeevo	51.15	36.00	Gvozdover M. D., Grigor'ev G. P., 1977
57	Drychaluki	55.36	30.43	Kalinovskii P. F., 1983
58	Pashino	54.35	30.38	Kalinovskii P. F., 1983
59	Rumlovka	53.31	24.09	Kalinovskii P. F., 1983
60	Suponevo	53.27	34.10	Gromov V. I., 1948
61	Kulichivka (lower layer)	50.05	25.44	Savich V. P., 1975
62	Kulichivka (upper layer)	50.05	25.44	Savich V. P., 1975
63	Khotylevo II	53.20	34.10	Velichko A. A. et al., 1977
64	Lipa VI	50.19	26.30	Tatarinov K. A., 1969
65	Korman IV (layer 11)	48.27	27.28	Goretskii G. I., Tseitlin S. M. (eds.), 1977
66	Korman IV (layer 7)	48.27	27.28	Goretskii G. I., Tseitlin S. M. (eds.), 1977
67	Korman IV (layer 6)	48.27	27.80	Goretskii G. I., Tseitlin S. M. (eds.), 1977
68	Korman IV (layer 5)	48.27	27.80	Goretskii G. I., Tseitlin S. M. (eds.), 1977
69	Korman IV (layer 5a)	48.27	27.28	Goretskii G. I., Tseitlin S. M. (eds.), 1977
70	Eliseevichi II	53.19	33.46	Markova A. K., 1994
71	Shapkina I	67.00	54.00	Kochev V. A., 1993
72	Kur'yador	61.45	53.30	Kochev V. A., 1993
73	Ryabovo	61.25	46.15	Kochev V. A., 1993
74	Lipa IX (Pustel'skaia)	50.50	25.40	Ostrovski M. I., 1964
75	Volchkov	48.55	24.40	Chernysh A. P., 1973
76	Velikii Goluboček	49.32	25.35	Chernysh A. P., 1973
77	Staryi Vyshnivetz	49.40	25.45	Chernysh A. P., 1973
78	Lisichniki	49.25	25.30	Boriskovski P. I., 1953
79	Bila	48.42	25.45	Timashchuk B. A., 1952
80	Neporotovo	48.25	27.28	Chernysh A. P., 1954
81	Molodovo I (layer 3)	48.27	27.28	Ivanova I. K. et al., 1982
82	Molodovo I (layer 2)	48.27	27.28	Ivanova I. K. et al., 1982
83	Molodovo V (layer 10)	48.27	27.28	Chernysh A. P., 1959
84	Molodova V (layer 8)	48.27	27.28	Chernysh A. P., 1959
85	Molodova V (layer 7)	48.27	27.28	Chernysh A. P., 1973
86	Molodova V (layer 6)	48.27	27.28	Chernysh A. P., 1973
87	Molodova V (layer 5)	48.27	27.28	Chernysh A. P., 1973
88	Molodova V (layer 4)	48.27	27.28	Chernysh A. P., 1973
89	Molodova V (layer 3)	48.27	27.28	Chernysh A. P., 1973
90	Molodova V (layer 2)	48.27	27.28	Chernysh A. P., 1973
91	Ataki I	48.27	27.28	Chernysh A. P., 1968
92	Starye Duruitory (layer 2)	47.59	27.30	David A. I., Ketraru N. A., 1970
93	Trinka II (layers 2 & 3)	48.10	28.20	Anisyutkin N. K., Borziyak I. A., Ketraru N. A., 1986
94	Kosteshty I	48.00	27.35	Ketraru N. A., 1973
95	Roshkov IV	48.05	28.30	Chernysh A. P., 1973
96	Akkarzha	46.40	30.45	Boriskovskii P. I., Pralov N. D., 1964
97	Klintzy	51.15	28.47	Mesyats V. A., 1956
98	Diskeninovo	55.17	30.20	Kalinovskii P. F., 1983

No.	Site name	Latitude	Longitude	References
99	Berdyzh	53.00	30.48	Voznyachuk L. N., Kalechits E. G., 1969
100	Kurovo	52.30	33.00	Gromov V. I., 1948
101	Timonovka II	53.27	34.10	Gromov V. I., 1948
102	Anetovka II	47.40	31.10	Stanko V. H., Grigor'eva G. V., Shvaiko, T. N. 1989
103	Pushkari I (Paseka)	52.20	33.20	Boriskovskii P. I., 1953
104	Kosoutzy (layer 1)	48.07	28.10	Borziyak I. A., David A. I., 1986
105	Chulatovo I	54.50	33.07	Boriskovskii P. I., 1953
106	Novgorod Severskaya	52.00	33.16	Rekovets L. I., 1985
107	Mesin	51.45	33.05	Boriskovskii P. I., 1953
108	Kirillovskaya	50.26	30.31	Gromov V. I., 1948
109	Dobranuchevka	50.02	32.40	Pidoplichko I. G., 1969
110	Meshirich	49.38	31.24	Pidoplichko I. G., 1969
111	Gontsy	50.10	32.49	Pidoplichko I. G., 1969
112	Fastov	50.05	32.49	Soffer O., 1985
113	Radomyshl'	50.33	29.14	Softer O., 1985
114	Voronovitz 1	48.30	26.50	Chernysh A. P., 1959
115	Roshnev	49.00	24.50	Chernysh A. P., 1973
116	Sevsk	52.05	34.20	Lavrov A. V., 1992; Mashchenko E. N., 1992
117	Yudinovo	52.40	33.10	Abramova Z. A., 1993; Markova A. K., 1995
118	Ignat'eva	54.53	56.48	Smirnov N. G., Bol'shakov V. N. et al., 1990
119	Serpievskaya	54.53	56.48	Smirnov N. G., Bol'shakov V. N. et al., 1990
120	Sakadgia	42.20	42.40	Paleolithic of West Baikalian, 1957
121	Oshurkovo	51.52	107.38	Tseitlin S. M., Golubeva L. V., 1977
122	Logovo Gieny	51.25	83.12	Derevyanko A. P. et al., 1990
123	Geograph icheskogo obshestva	43.20	133.05	Derevyanko A. P. et al., 1990
124	Tigrovyi	42.53	132.05	Fauna i Systematika pozvonochnykh Sibiri, 1977
125	list' Mil'	59.37	133.10	Mochanov Yu. A., 1977
126	Ikhine I	63.05	133.18	Mochanov Yu. A., 1977
127	Ikhine II	63.05	133.18	Mochanov Yu. A., 1977
128	Ayion	69.50	169.00	Agadjanian A. K., 1980
129	Dyuktaiskaya	58.00	129.00	Mochanov Yu. A., 1970
130	Berelekh	70.55	149.05	Vereschagin N. K., 1972
131	Sannyo mys	51.50	107.42	Tseitlin S. M., 1979
132	Stolbovoi	58.25	57.35	Kuz'mina I. E., 1975
133	Kokorevo I (Zabochka)	54.42	91.00	Tseitlin S. M., 1979
134	Kikorevo II (Telejnyi log)	56.27	93.41	Tseitlin S. M., 1979
135	Kokorevo III	56.27	93.41	Tseitlin S. M., 1979
136	Kokorevo IV-1 (Kipernyi log)	56.27	93.41	Tseitlin S. M., 1979
137	Kokorevo IV-2 (Kipernyi log)	56.27	93.41	Tseitlin S. M., 1979
138	Chernoozer'e II	55.42	74.30	Tseitlin S. M., 1979
139	Sukhotino 4	52.05	113.30	Kasparov A. K., 1986
140	Kharol'	44.35	132.09	Korotkii A. M. et al., 1981
141	Malyi Anyui	68.00	162.30	Sher A. V., 1971
142	Akhtyrskaya	43.30	40.00	Boriskovskii P. I., 1978
143	Shikaevka	65.40	56.00	Tseitlin S. M., 1979
144	Tolbaga	51.13	109.20	Tseitlin S. M., 1979
145	Kashtanka I (layer 1)	56.20	93.30	Derevyanko A. P., Drozdov N. I., Chekha V. P. (eds.), 1990
146	Us'e Bukhtarma	49.47	84.05	Kozhamkulova B. S., 1969

No.	Site name	Latitude	Longitude	References
147	Kachkari II	54.45	58.54	Bibikov S. I., 1950
148	Katavskii naves	54.47	58.45	Bibikov S. I., 1950
149	Batpak 7	50.40	73.07	Kozhamkulova B.S., 1969
150	Samarkandskaya	39.38	66.56	Lev D. N., 1955
151	Strashnaya	51.24	83.10	Ovodov N. D., 1980
152	Ust'Kanskaya	50.53	84.45	Tseitlin S. M., 1979
153	Denisova	51.23	85.05	Ovodov N. D., 1980
154	Razboinichaya	51.23	85.05	Ovodov N. D., 1980
155	Bol'shaya Kyrkylinskaya	51.38	85.45	Ovodov N. D., 1980
156	Peschera	49.45	84.10	Chernikov S. S., 1950
157	Achinskaya	56.15	90.36	Tseitlin S. M., 1979
158	Afontova gora II	56.20	93.30	Larichev V. E., 1969
159	Tonnel'naya	55.50	92.24	Drozdov N. I. et al., 1990
160	Listvenka	55.55	92.24	Drozdov N. I. et al., 1990
161	Kurtak-4	56.30	93.38	Drozdov N. I. et al., 1990
162	Ui-I	53.00	91.25	Drozdov N. I. et al., 1990
163	Main (layer B)	53.00	91.25	Drozdov N. I. et al., 1990
164	Mal'ta	52.50	103.23	Tseitlin S. M., 1979
165	Buret'	53.02	103.35	Tseitlin S. M., 1979
166	Sosnovyi bor I	52.50	103.29	Tseitlin S. M., 1979
167	Sosnovyi bor II	52.50	103.29	Tseitlin S. M., 1979
168	Verkhne-T roitzkoe	60.25	134.30	Mochanov Yu. A., 1977
169	Volchya Griva	54.50	80.20	Tseitlin S. M., 1979
170	Ushbas	38.20	69.05	Ranov V. A., Nesmeyanov S. A., 1973
171	Turlanskii pereval	38.15	69.05	Ranov V. A., Nesmeyanov S. A., 1973
172	Shugnou	38.20	70.06	Ranov V. A., Nesmeyanov S. A., 1973
173	Alichur	37.45	73.25	Nikonov A. A., 1977
174	Nikolaevskaya	53.20	88.36	Ovodov N. D., 1980
175	Verkholenskaya gora	52.21	104.20	Aksenov M. P., Medvedev S. A., 1973
176	Kranyi yar	53.25	103.45	Tseitlin S. M., 1979
177	Ogzi-Kichik	38.10	69.15	Stal'makova V. A., Kireev V. I., 1986
178	Damdzhily	41.05	45.05	Aliev S. D., 1969
179	Wrangel Island (Mamont. R. 1)	71.30	180.00	Vartanian S. L., Gamut V. E., Sher A. V., 1993.
180	Wrangel Island (Mamont. R. 2)	71.30	180.00	Vartanian S. L., Gamut V. E., Sher A. V., 1993.
181	Wrangel Island (Goosinaya R.)	71.30	180.00	Vartanian S. L., Gamut V. E., Sher A. V., 1993.
182	Wrangel Island (Tundrovaya R.)	71.30	180.00	Vartanian S. L., Gamut V. E., Sher A. V., 1993.
183	Wrangel Island (Krasny Flag R.)	71.30	180.00	Vartanian S. L., Gamut V. E., Sher A. V., 1993.
184	Wrangel Island (Neizvestnaya R.)	71.30	180.00	Vartanian S. L., Gamut V. E., Sher A. V., 1993.
185	Dzudzuana (layer 2)	42.20	43.10	Bendukidze O. G., 1978
186	Kep-Bogaz (layer D)	43.00	41.30	Bendukidze O. G., 1978
187	Bolshoi Jakor' (layers 4-7)	57.30	114.00	Belousov V. M., Ineshin E. M. et al., 1990
188	Bolshoi Jakor' (layers 8-9)	57.30	114.00	Belousov V. M., Ineshin E. M. et al., 1990
189	Zhokhov Island	76.03	153.00	Pitul'ko V. V., Makeev V. M., Samarskii M. B., 1990
190	Apiancha (layer 5)	43.00	43.25	Vekya A. K., 1990

No.	Site name	Latitude	Longitude	References
191	Korman IY (layer 12)	48.27	27.28	Goretskii G. I., Tseitlin S. M. (eds.), 1977
192	Korman IY (layer 9)	48.27	27.28	Goretskii G. I., Tseitlin S. M. (eds.), 1977
193	Molodova 1 (layer 4)	48.27	27.28	Agadjanian A. K., 1982
194	Molodova 1 (layer 11)	48.27	27.28	Agadjanian A. K., 1982
195	Arta 2	51.18	112.18	Kirillov I. I., Kasparov A. K., 1990
196	German-Dumeny	47.07	28.00	Ketraru N. A., 1973
197	Vasilika	47.14	27.51	Ketraru N. A., 1973
198	Starye Kokuneshty	47.15	27.55	Ketraru N. A., 1973
199	Skulyany	47.10	27.58	Ketraru N. A., 1973
200	Buteshty	47.40	27.40	Ketraru N. A., 1970
201	Trinka 1 (layer 4)	48.10	28.20	Anisyutkin N. K., Borziyak I. A., Ketraru N. A., 1986
202	Trinka 2 (layers 4 & 5)	48.10	28.20	Anisyutkin N. K., Borziyak I. A., Ketraru N. A., 1986
203	Buzduzhany 1	48.05	27.18	Chernysk A. P., 1973
204	Naslavcha 1	48.12	27.40	Chernysh A. P., 1973
205	Vyhvatintzy	47.45	28.56	Ketraru N. A., 1973
206	Starye Duruntory (layers 3 & 4)	47.59	27.30	David A. i., Ketraru N. A., 1970
207	Kasperovtzy	48.38	25.45	Beregovaya N. A., 1972
208	Kodak 1	48.25	35.10	Pidoplichko I. G., 1936
209	Grigor'evka	48.55	33.42	Boriskovskii P. I., 1953
210	Betovo	53.16	34.07	Tarasov L. I., 1977
211	Kudaro 1	42.28	43.57	Vereshchagin N. K., Baryshnikov G. F., Gromov I. M., Fokanov V. A., 1978
212	Kudaro 3	42.28	43.57	Vereshchagin N. K., Baryshnikov G. F., 1978
213	Adgin-Koba	44.50	34.05	Kolosov Ya. G., 1995
214	Brynzeny 1	48.12	27.26	Losan M. N., 1970
215	Il'inka	46.43	30.51	Chernysh A. P., 1954
216	Starosel'e	44.45	33.52	Vereshchagin N. K., Baryshnikov G. F., 1980
217	Chokurcha	44.53	34.08	Vereshchagin N. K., Baryshnikov G. F., 1980
218	Mamat-Koba (layer 2)	44.48	34.34	Vereshchagin N. K., Baryshnikov G. F., 1980
219	Kiik-Koba	44.58	34.25	Efimenko P. P., 1953
220	Kosh-Koba	45.00	34.24	Efimenko P. P., 1953
221	Chagorak-Koba	44.53	34.08	Efimenko P. P., 1953
222	Shaitan-Koba (Bodrak)	44.53	34.04	Bonch-Osmolovskii G. A., 1930
223	Volchii grot	45.01	34.30	Bader O. N., 1940
224	Bahchisaraiskaya	44.46	33.51	Bonch-Osmolovskii G. A., 1947
225	Shubnoe	50.53	39.00	Gromov V. I., 1936
226	Il'skaya	44.50	38.35	Zamyatin S. N., 1934
227	Taglar	39.33	47.00	Aliev S. D., 1969
228	Azyh (layer 3)	39.35	46.59	Aliev S. D., 1969
229	Erevanskaya peschera	40.10	44.36	Boriskovskii P. I., 1979
230	Ahtyrskaya peschera	41.30	40.00	Boriskovskii P. I., 1979
231	Prolom	45.05	34.43	Boriskovskii P. I., 1979
232	Khotylevo 1	53.20	34.10	Gromov V. I., 1948
233	Dvuglazka	54.15	90.55	Abramova Z. A., Eritsyanyan B. G., Ermolova N. M., 1976
234	Valikhanova	43.18	69.32	Alpystaev X. A., 1977

No.	Site name	Latitude	Longitude	References
235	Machaïskii	38.15	67.09	
236	Bol'shaya Glukhaya (layer 6)	57.30	57.00	History of Usb. SSR, 1955 Softer O. & Praslov N. D., (eds.), 1993
237	Proskuryakova	54.55	89.50	Ovodov N. D., 1975
238	Malaya Syya	54.53	89.50	Ovodov N. D., 1975
239	Strashnaya	51.24	83.10	Ovodov N. D., 1975
240	Achinskaya	56.15	90.36	Ovodov N. D., 1975
241	Maloyalomanskaya	50.45	86.10	Archeology of Altai Mts., 1990 ~
242	Obi-Rakhmat	41.35	70.00	Suleimanov R. X., 1968
243	Dashsalakhly	41.05	45.17	Aliev S. D., 1969
244	Sukhaya Mechetka	48.40	44.30	Vereshchagin N. K., Kolbutov A. D., 1957
245	Troitza 2	40.06	54.20	Markova A. K., 1985
246	Yurovichi	29.33	51.55	Gromov V. I., 1948
247	Khar'yaska 2 (layer 4)	51.00	108.00	
248	Eliseevichi 1	53.08	33.37	Khenzykhenova F. I., Endrikhinskii A. S., Dergausova M. I., 1991 Vereshchagin N. K., Kuz'mina I. E., 1977
249	Malyutino	51.35	36.00	Markova A. K., 1985
250	Chemianka	50.40	37.55	Markova A. K., 1985
251	Gadiach	50.20	34.00	Markova A. K., 1985
252	Shkurlat	50.05	40.03	Markova A. K., 1985
253	Novonekrasovka (upper layer)	47.30	28.35	Markova A. K., Mikhailets K. D., 1990
254	Novonekrasovka (lower layer)	47.30	28.35	Markova A. K., Mikhailets K. D., 1990
255	Cheremoshnya	57.07	39.20	Agadjanian A. K., Erbaeva m. A., 1983
256	Nyatesos	54.15	24.10	Motuzko A. N., 1992
257	Konevich	55.40	31.05	Motuzko A. N., 1992
258	Mikhailovka 5	52.20	35.18	Agadjanian A. K., Glushankova N. I., 1986
259	Borisova Gora	55.27	30.40	San'ko A. F., Motuzko A. N., 1991
260	Timoshkovichi	53.40	26.05	Motuzko a. N., 1985
261	Arapovichi	52.00	33.15	Markova A. K., 1985
262	Gralevo 2	55.15	30.05	San'ko A. F., Motuzko A. N., 1982
263	Kobelyaki	54.30	30.20	Motuzko A. N., 1992
264	Jar	56.45	98.40	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
265	Ust'-Odinskoe (layer 3)	52.55	103.30	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
266	Ust'-Odinskoe (layer 6)	52.55	103.30	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
267	Ust'-Odinskoe (layers 7-11)	52.55	103.30	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
268	Ust'-Odinskoe (layer 13)	52.55	103.30	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
269	Kitoiskii Most (layer 5)	52.54	103.30	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
270	Pisarevo	53.57	102.03	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995
271	Ozemaya Balya	55.45	102.55	Filippov A. G., Erbaeva M. A., Khenzykhenova F. I., 1995

No.	Site name	Latitude	Longitude	References
272	Ingashet	55.45	102.55	Filippov A. G., Erbaeva M. A., Khenzynkhenova F. I., 1995
273	Odinskii	52.54	103.29	Filippov A. G., Erbaeva M. A., Khenzynkhenova F. I., 1995
274	Okladnikova	51.57	84.82	Derevyanko A. P., Markin S. V., 1992
275	Kaminnaya (layers 6-9)	51.37	84.48	Derevyanko A. P., Markin S. V., 1990
276	Kaminnaya (layers 10-14)	51.37	84.48	Derevyanko A. P., Markin S. V., 1990
277	Ust'Karakol	51.23	85.05	Maloletko A. M., Panychev V. A., 1990
278	Kara-Bom	50.45	83.10	Okladnikov A. P., 1983
279	Gydan	70.00	76.00	Sulerzhitsky L. D., 1995
280	Taimyr (Engel'gardt)	75.10	110.30	Sulerzhitsky L. D., 1995
281	Taimyr (Engel'gardt)	75.10	110.30	Sulerzhitsky L. D., 1995
282	Taimyr (Engel'gardt)	75.10	110.30	Sulerzhitsky L. D., 1995
283	Taimyr (Engel'gardt)	75.30	100.00	Sulerzhitsky L. D., 1995
284	P. Yamal	70.15	69.00	Sulerzhitsky L. D., 1995
285	P. Yamal	70.15	69.00	Sulerzhitsky L. D., 1995
286	Taimyr (Baikura-Neru)	74.05	93.10	Sulerzhitsky L. D., 1995
287	Taimyr (Baikura-Neru)	74.05	93.10	Sulerzhitsky L. D., 1995
288	Taimyr (Baikura-Neru)	74.05	93.10	Sulerzhitsky L. D., 1995
289	Taimyr (Baikura-Neru)	74.05	93.10	Sulerzhitsky L. D., 1995
290	Taimyr (Baikura-Neru)	74.05	93.10	Sulerzhitsky L. D., 1995
291	Taimyr (Mamonta)	75.15	96.00	Sulerzhitsky L. D., 1995
292	L. Oktyabr'skoi Revolyutsii	79.30	98.00	Sulerzhitsky L. D., 1995
293	L. Oktyabr'skoi Revolyutsii	79.30	98.00	Sulerzhitsky L. D., 1995
294	L. Oktyabr'skoi Revolyutsii	79.30	98.00	Sulerzhitsky L. D., 1995
295	Berelekh	71.00	145.00	Sulerzhitsky L. D., 1995
296	Berelekh	71.00	145.00	Sulerzhitsky L. D., 1995
297	Berelekh	71.00	145.00	Sulerzhitsky L. D., 1995
298	Taimyr (Severnaya)	75.50	112.00	Sulerzhitsky L. D., 1995
299	Taimyr (Severnaya)	75.50	112.00	Sulerzhitsky L. D., 1995
300	Achchygyi-Alaikha	69.00	147.30	Sulerzhitsky L. D., 1995
301	Achchygyi-Alaikha	69.00	147.30	Sulerzhitsky L. D., 1995
302	Achchygyi-Alaikha	69.00	147.30	Sulerzhitsky L. D., 1995
303	Kamchatka	55.00	159.00	Sulerzhitsky L. D., 1995
304	Kamchatka	55.00	159.00	Sulerzhitsky L. D., 1995
305	Wrangel Island	71.00	181.00	Sulerzhitsky L. D., 1995
306	Taimyr (Bikada)	74.53	106.30	Sulerzhitsky L. D., 1995
307	Yar Berezovski	59.00	69.00	Sulerzhitsky L. D., 1995
308	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
309	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
310	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
311	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
312	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
313	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
314	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
315	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
316	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
317	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
318	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
319	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
320	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
321	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
322	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
323	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995

No.	Site name	Latitude	Longitude	References
324	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
325	Taimyr (B. Balakhnaya)	75.30	105.00	Sulerzhitsky L. D., 1995
326	Krasnoyarsk	56.10	92.50	Sulerzhitsky L. D., 1995
327	Bashkiriya	54.30	56.30	Sulerzhitsky L. D., 1995
328	Lena	68.00	123.00	Sulerzhitsky L. D., 1995
329	Len	68.00	123.00	Sulerzhitsky L. D., 1995
330	Shatrishe	54.45	39.15	Sulerzhitsky L. D., 1995
331	Chukotka	66.30	177.00	Sulerzhitsky L. D., 1995
332	Kintu	56.10	44.00	Sulerzhitsky L. D., 1995
333	Ulahan-Yuryakh	72.12	104.00	Sulerzhitsky L. D., 1995
334	Kotel'nyi	75.30	140.00	Sulerzhitsky L. D., 1995
335	Kotel'nyi	75.30	140.00	Sulerzhitsky L. D., 1995
336	Kotel'nyi	75.30	140.00	Sulerzhitsky L. D., 1995
337	Gydan	71.30	76.00	Sulerzhitsky L. D., 1995
338	Main (Anadyr)	65.00	171.00	Sulerzhitsky L. D., 1995
339	Lena	70.00	125.00	Sulerzhitsky L. D., 1995
340	Lena	70.00	125.00	Sulerzhitsky L. D., 1995
341	Lena	70.00	125.00	Sulerzhitsky L. D., 1995
342	Lena	70.00	125.00	Sulerzhitsky L. D., 1995
343	Zaraisk	54.37	38.55	Sulerzhitsky L. D., 1995
344	Zaraisk	54.37	38.55	Sulerzhitsky L. D., 1995
345	Enisei	53.55	92.00	Sulerzhitsky L. D., 1995
346	Enisei	53.55	92.00	Sulerzhitsky L. D., 1995
347	Enisei	53.55	92.00	Sulerzhitsky L. D., 1995
348	Bur	71.40	119.00	Sulerzhitsky L. D., 1995
349	Amydai	73.00	119.00	Sulerzhitsky L. D., 1995
350	Amydai	73.00	119.00	Sulerzhitsky L. D., 1995
351	Amydai	73.00	119.00	Sulerzhitsky L. D., 1995
352	Amydai	73.00	119.00	Sulerzhitsky L. D., 1995
353	Minusinskaya Hollow	53.30	91.40	Sulerzhitsky L. D., 1995
354	Chulym	55.05	90.00	Sulerzhitsky L. D., 1995
355	Chulym	55.05	90.00	Sulerzhitsky L. D., 1995
356	Chulym	55.05	90.00	Sulerzhitsky L. D., 1995
357	Taimyr (Dudypta)	72.00	96.00	Sulerzhitsky L. D., 1995
358	Belaya	52.50	103.10	Sulerzhitsky L. D., 1995
359	Belaya	52.50	103.10	Sulerzhitsky L. D., 1995
360	Belaya	52.50	103.10	Sulerzhitsky L. D., 1995
361	Island Fadeevskii	75.25	144.00	Sulerzhitsky L. D., 1995
362	Island Fadeevskii	75.25	144.00	Sulerzhitsky L. D., 1995
363	Island Fadeevskii	75.25	144.00	Sulerzhitsky L. D., 1995
364	Island Fadeevskii	75.25	144.00	Sulerzhitsky L. D., 1995
365	Pakhcha	56.35	161.00	Sulerzhitsky L. D., 1995
366	Tanton	59.45	150.55	Sulerzhitsky L. D., 1995
367	Bykovskaya Protoka	72.25	127.00	Sulerzhitsky L. D., 1995
368	Yar Generalka	55.00	159.15	Sulerzhitsky L. D., 1995
369	Popigai	72.40	106.00	Sulerzhitsky L. D., 1995
370	Popigai	72.40	106.00	Sulerzhitsky L. D., 1995
371	Tyung	67.35	116.00	Sulerzhitsky L. D., 1995
372	Tyung	67.35	116.00	Sulerzhitsky L. D., 1995
373	Tyung	67.35	116.00	Sulerzhitsky L. D., 1995
374	Tyung	67.35	116.00	Sulerzhitsky L. D., 1995
375	Tyung	67.35	116.00	Sulerzhitsky L. D., 1995
376	Tyung	67.35	116.00	Sulerzhitsky L. D., 1995
377	Angara	59.00	101.30	Sulerzhitsky L. D., 1995
378	Kular	70.50	134.23	Sulerzhitsky L. D., 1995
379	Taimyr (Pyasina)	72.50	87.00	Sulerzhitsky L. D., 1995
380	Kama	55.43	52.00	Sulerzhitsky L. D., 1995
381	Kama	55.43	52.00	Sulerzhitsky L. D., 1995

No.	Site name	Latitude	Longitude	References
382	Kama	55.43	52.00	Sulerzhitsky L. D., 1995
383	Kama	55.43	52.00	Sulerzhitsky L. D., 1995
384	Kama	55.43	52.00	Sulerzhitsky L. D., 1995
385	Kama	55.43	52.00	Sulerzhitsky L. D., 1995
386	Coast of Laptevykh Sea	70.45	131.00	Sulerzhitsky L. D., 1995
387	Coast of Laptevykh Sea	70.45	131.00	Sulerzhitsky L. D., 1995
388	Coast of Laptevykh Sea	70.45	131.00	Sulerzhitsky L. D., 1995
389	Coast of Laptevykh Sea	70.45	131.00	Sulerzhitsky L. D., 1995
390	Chekurovka	71.05	127.30	Sulerzhitsky L. D., 1995
391	Gulya	70.05	100.30	Sulerzhitsky L. D., 1995
392	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
393	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
394	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
395	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
396	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
397	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
398	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
399	Taimyr (Logata River)	73.00	98.00	Sulerzhitsky L. D., 1995
400	Srednekan	62.45	150.30	Sulerzhitsky L. D., 1995
401	Yar Duvannyi	68.45	150.45	Sulerzhitsky L. D., 1995
402	Yar Duvannyi	68.45	150.45	Sulerzhitsky L. D., 1995
403	Yar Duvannyi	68.45	150.45	Sulerzhitsky L. D., 1995
404	Taimyr (Shrenk)	75.15	98.00	Sulerzhitsky L. D., 1995
405	Anabarka	72.40	106.00	Sulerzhitsky L. D., 1995
406	Anabarka	72.40	106.00	Sulerzhitsky L. D., 1995
407	Anabarka	72.40	106.00	Sulerzhitsky L. D., 1995
408	Anabarka	72.40	106.00	Sulerzhitsky L. D., 1995
409	Anabarka	72.40	106.00	Sulerzhitsky L. D., 1995
410	Bol'shezemel'skaya Tundra	68.00	59.00	Sulerzhitsky L. D., 1995
411	Anabar	72.15	113.30	Sulerzhitsky L. D., 1995
412	Bol. Hamus-Yuryakh	65.00	152.30	Sulerzhitsky L. D., 1995
413	Bol. Hamus-Yuryakh	65.00	152.30	Sulerzhitsky L. D., 1995
414	Sualema	73.00	112.00	Sulerzhitsky L. D., 1995
415	Island Bol. Lyakhovskii	73.30	142.00	Sulerzhitsky L. D., 1995
416	Bilibino	68.03	166.00	Sulerzhitsky L. D., 1995
417	Gydan	70.30	77.30	Sulerzhitsky L. D., 1995
418	P. Yamal	67.10	68.00	Sulerzhitsky L. D., 1995
419	Mokhovaya	72.00	85.30	Sulerzhitsky L. D., 1995
420	Kanin	68.00	46.00	Sulerzhitsky L. D., 1995
421	Viliya	54.74	26.00	Sulerzhitsky L. D., 1995
422	Taimyr (Khatanga)	72.30	104.30	Sulerzhitsky L. D., 1995
423	Kirgilyakh	68.45	158.30	Sulerzhitsky L. D., 1995
424	Anabar Bay	73.00	113.35	Sulerzhitsky L. D., 1995
425	Shandrin	71.20	150.30	Sulerzhitsky L. D., 1995
426	Tavda	59.00	64.00	Sulerzhitsky L. D., 1995
427	Novopetrovskoe	55.30	36.30	Sulerzhitsky L. D., 1995
428	Massonov Stream	72.30	104.30	Sulerzhitsky L. D., 1995
429	Berezovskaya	67.15	157.30	Sulerzhitsky L. D., 1995
430	Terektyakh	69.30	147.15	Sulerzhitsky L. D., 1995
431	Taimyr (Kheta)	71.45	100.00	Sulerzhitsky L. D., 1995
432	Pavlovsk	50.55	40.15	Sulerzhitsky L. D., 1995
433	Nekyu	73.00	120.00	Sulerzhitsky L. D., 1995
434	Maimecha	71.00	100.45	Sulerzhitsky L. D., 1995
435	Cherski	68.45	161.15	Sulerzhitsky L. D., 1995
436	Bol'shaya Slizneva	55.59	92.31	Derevyanko A. P. et al., 1992
437	Kammennyi Log	55.58	92.29	Derevyanko A. P. et al., 1992
438	Berezhkovo	55.58	92.29	Derevyanko A. P. et al., 1992
439	Mamontova Gora	62.40	135.20	Sulerzhitsky L. D., 1995

No.	Site name	Latitude	Longitude	References
440	Mamontova Gora	62.40	135.20	Sulerzhitsky L. D., 1995
441	Mamontova Gora	62.40	135.20	Sulerzhitsky L. D., 1995
442	Taimyr (Agara River)	71.32	87.00	Sulerzhitsky L. D., 1995
443	Taimyr (Agara River)	71.32	87.00	Sulerzhitsky L. D., 1995
444	Mal'kovo	57.00	66.00	Sulerzhitsky L. D., 1995
445	Ust'Belay	65.30	173.56	Sulerzhitsky L. D., 1995
446	Beresovka	67.00	155.50	Sulerzhitsky L. D., 1995
447	Bol'shaya Chukoch'ya	70.30	156.30	Sulerzhitsky L. D., 1995
448	Targana	66.00	132.56	Sulerzhitsky L. D., 1995
449	Omoloi	70.40	133.00	Sulerzhitsky L. D., 1995
450	Khetchan	68.16	160.58	Sulerzhitsky L. D., 1995
451	Khetchan	68.16	160.58	Sulerzhitsky L. D., 1995
452	Baltatai	66.50	153.10	Sulerzhitsky L. D., 1995
453	M. Anui	68.24	161.20	Sulerzhitsky L. D., 1995
454	Tirekhtyakh	67.38	138.00	Sulerzhitsky L. D., 1995
455	Khromya	71.12	144.28	Sulerzhitsky L. D., 1995
456	Bol. Khomus-Yuryakh	71.16	153.45	Sulerzhitsky L. D., 1995
457	Bol. Kholzhe-Yuryakh	71.16	153.45	Sulerzhitsky L. D., 1995
458	Bol. Kholzhe-Yuryakh	71.16	153.45	Sulerzhitsky L. D., 1995
459	Bol. Kholzhe-Yuryakh	71.16	153.45	Sulerzhitsky L. D., 1995
460	Oienek	70.38	119.59	Sulerzhitsky L. D., 1995
461	Sida	67.07	102.05	Sulerzhitsky L. D., 1995
462	Lacha	61.10	39.10	Sulerzhitsky L. D., 1995
463	Ghistopol	55.13	50.33	Sulerzhitsky L. D., 1995
464	Mezha	54.42	50.23	Sulerzhitsky L. D., 1995
465	Tetyushi	54.47	48.53	Sulerzhitsky L. D., 1995
466	Krasnovidovo	55.16	49.05	Sulerzhitsky L. D., 1995
467	Krasnovidovo	55.16	49.05	Sulerzhitsky L. D., 1995
468	Mysy	60.38	53.07	Sulerzhitsky L. D., 1995
469	Mysy	60.38	53.07	Sulerzhitsky L. D., 1995
470	Mysy	60.38	53.07	Sulerzhitsky L. D., 1995
471	Cheboksary	56.04	47.03	Sulerzhitsky L. D., 1995
472	Penza	53.10	45.10	Sulerzhitsky L. D., 1995
473	Vyatkinskaya Guba	53.24	51.30	Sulerzhitsky L. D., 1995
474	Ak-kaya III	45.08	34.42	Kolosov Yu. G. et al., 1995
475	Zaskalnaya Y (layer 1)	45.06	34.43	Kolosov Yu. G. et al., 1995
476	Zaskalnaya Y (layer 2-3)	45.06	34.43	Kolosov Yu. G. et al., 1995
477	Zaskalnaya Y (layer 4-7)	45.06	34.43	Kolosov Yu. G. et al., 1995
478	Zaskalnaya YI (layer 1)	45.06	34.43	Kolosov Yu. G. et al., 1995
479	Zaskalnaya YI (layer 2-3)	45.06	34.43	Kolosov Yu. G. et al., 1995
480	Zaskalnaya YI (layer 4-5)	45.06	34.43	Kolosov Yu. G. et al., 1995
481	Zaskalnaya IX (lower layer)	45.06	34.43	Kolosov Yu. G. et al., 1995
482	Prolom II (layer 1)	45.05	34.43	Kolosov Yu. G. et al., 1995
483	Prolom II (layer 4)	45.05	34.43	Kolosov Yu. G. et al., 1995
484	Kiik-Koba (lower layer)	44.58	34.25	Kolosov Yu. G. et al., 1995
485	Denisova Cave (entrance)	51.23	85.05	Agadjanian A. K., per. com.
486	Volchi Grot (lower layer)	45.03	34.05	Kolosov Yu. G. et al., 1995
487	Adgi-Koba (lower layer)	44.50	34.30	Kolosov Yu. G. et al., 1995
488	Veshinskaya	49.32	41.30	Kazantseva N. E., per. com
489	Kapova	52.38	57.03	Shelinsky V. E., 1989
490	Kuljurtamak	52.37	57.01	Nekhoroshev P. E., 1989
491	Gornova	55.00	56.00	Pleistocene Predural'ya, 1987
492	Shaitansky	60.10	60.21	Smirnov N. G. et al., 1981
493	Stolbovoi	58.09	57.34	Kuz'mina I. E., 1989
494	Bliznetsova	59.35	57.49	Kuz'mina I. E., 1989
495	Talitskogo	58.10	57.00	Gromov V. I., 1948
496	Tchernoozerye	55.45	73.50	Gening V. F., Petrin V. T., 1985

No.	Site name	Latitude	Longitude	References
497	Shikaevka	56.00	66.00	Petrin V. T., Smirnov N. G., 1975
498	Bezemyanny	57.08	62.04	Petrin V. T., Smirnov N. G., 1977
499	Zotinsky	56.57	61.42	Petrin V. T., Smirnov N. G., 1977
500	Arakaevo 8	56.08	62.04	Smirnov N. G., 1993
501	Site 430a	65.30	65.40	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
502	Ignatievsky (layer 2.2)	55.07	57.47	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
503	Prizhim 2 (layer 2)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
504	Bobyliok	56.19	57.38	Smirnov N. G., 1993
505	Serpievsky 2-3	55.10	57.52	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
506	Ustinovo	55.48	59.58	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
507	Dyrovaty Kamen' (Tchusov)	57.40	58.53	Smirnov N. G., Ulitko A. I., 1994
508	Bolshoi Glukhoi	58.15	58.10	Smirnov N. G., 1993
509	Mogochino	57.50	83.30	Petrin V. T., Smirnov N. G. 1976
510	Serpievsky 1-2	55.10	57.52	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
511	Tchernie Kosty	59.30	57.50	Kuz'mina I. E., 1989
512	Prizhim 2 (layer 6)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
513	Prizhim 2 (layer 1)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
514	Prizhim 2 (layer 3)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
515	Prizhim 2 (layer 4)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
516	Prizhim 2 (layer 5)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
517	Prizhim 2 (layer 7)	55.06	57.46	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
518	Serpievsky 1 (layer 3.1)	55.10	57.52	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
519	Serpievsky 1 (layer 3.2)	55.10	57.52	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
520	Serpievsky 2 (layer 2)	55.10	57.52	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
521	Serpievsky 2 (layer 4)	55.10	57.52	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990

No.	Site name	Latitude	Longitude	References
522	Ignatievsky (layer 3)	55.07	57.47	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
523	Ignatievsky (layer 4)	55.07	57.47	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
524	Kur'yador	61.40	54.50	Kochev V. A., 1993
525	Medvezh'ya 5a	62.03	58.10	Guslitser P. B., Pavlov P. Yu., 1988
526	Medvezh'ya 5b	62.03	58.10	Guslitser P. B., Pavlov P. Yu., 1988
527	Idrisovsky (layer 4)	55.15	58.05	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
528	Idrisovsky (layer 6)	55.15	58.05	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
529	Ignatievsky (layer 8)	55.07	57.47	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
530	Ignatievsky (layer 9)	55.07	57.47	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
531	Ignatievsky (layer 3.5)	55.07	57.47	Smirnov N. G., Bol'shakov V. N., Kosintsev P. A. et al., 1990
532	Agansky Uval-1290	61.30	76.15	Borodin A. V., Zinov'ev E. V., Bykova G. V. et al., 1994
533	Nyamuyu-nado	68.53	69.10	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
534	Gornokazym'sk	66.40	68.20	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
535	Pel'yakh-Yugan	66.35	65.40	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
536	Chembakchino	60.15	69.50	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
537	Yarsino	59.00	71.45	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
538	Shakhmatovka 1	58.50	73.00	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
539	Shakhmatovka 2	58.50	73.00	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
540	Mega	61.00	76.10	Smirnov N. G., Bol'shakov V. N., Borodin A. V., 1986
541	Ngoyun	68.30	72.10	Borodin A. V., 1988
542	Lyabtosyo	67.15	68.50	Borodin A. V., 1988
543	Marininsk	56.10	87.50	Zazhigin V. S., 1980
544	2-Pristan'	56.00	87.50	Zazhigin V. S., 1980
545	Alekseevskiy	55.50	87.30	Zazhigin V. S., 1980
546	Shumikha	53.50	87.20	Zazhigin V. S., 1980
547	Tal'menka	53.45	83.30	Zazhigin V. S., 1980
548	Shadrintsevo	54.00	84.00	Zazhigin V. S., 1980
549	Kazachyi	53.35	83.40	Zazhigin V. S., 1980
550	Yuribei	70.30	75.50	Yuribei Mammoth, 1982
551	Batchatsky	54.20	86.10	Smirnov N. G., per. com.
552	Yurovsky	59.30	69.30	Bobkovskaya N. E., 1989

TABLE 2. Plant locality data

No.	Site name	Latitude	Longitude	References
1	Molodovo V	48.30	26.45	Pashkevich G. A., 1987
2	Molodovo I	48.30	26.45	Bolikhovskaya N. S., Pashkevich G. A., 1982
3	Korman IV	49.24	27.22	Pashkevich G. A., 1977
4	Ketrosy	48.33	26.45	Bolikhovskaya N. S., 1981
5	Avdeevo	51.15	36.00	Velichko A. A., Gvozdoder M. D., Grigor'ev G. P. et al., 1981
6	Puchka	59.30	39.33	Chebotareva N. S., Makarycheva I. A., 1974
7	Sitno	57.29	33.25	Kotlukov I.V., 1972
8	Karachizh	53.25	34.30	Serebryannaya T. A., 1972
9	Arapovichi	52.00	33.10	Grichuk V. P., Monoszon M. M., Grichuk M. P., 1972
10	Aktash	45.33	35.29	Nikonov A. A., Pakhomov M. M., Cherkinsky A. E. et al., 1993
11	Ivanovo	57.00	40.30	Grichuk V. P., 1982
12	Beloomut	54.29	39.30	Grichuk V. P., 1982
13	Khotylevo II	53.30	33.25	Zelikson E. M., 1986
14	Fabrika 1 Maya	56.35	37.12	Semenenko L. T., Aleshinskaya Z. V., Arslanov Ch. A. et al., 1981
15	Timonovka II	53.40	34.24	Velichko A. A., Grechova L. V., Gubonina Z. P. et al., 1981
16	Dobranichevka	50.10	31.48	Shovkoplyas I. G., Korniets N. L., Pashkevich G. A. et al., 1981
17	Kubenskoe	59.24	39.42	Grichuk V. P., Mal'gina E. A., Monoszon M. M., 1969
18	Antavilyai	54.36	25.24	Grichuk V. P., Mal'gina E. A., Monoszon M. M., 1969
19	Edazi	58.20	32.00	Grichuk V. P., Mal'gina E. A., Monoszon M. M., 1969
20	Veselo-Voznesenskoe	47.20	38.24	Markov K. K., 1976
21	Mouralovka	47.19	38.50	Spiridonova E. A., 1991
22	Kostenki 1	50.50	39.48	Spiridonova E. A., 1991
23	Kostenki 21	50.51	39.30	Praslov N. D., Ivanova M. A., Malyasova E. S. et al., 1981
24	Kostenki 21 (south pit)	50.51	39.30	Praslov N. D., Ivanova M. A., Malyasova E. S. et al., 1981
25	Molochny Kamen'	48.18	23.30	Gladilin V. N., Pashkevich G. A., 1977
26	Mezhirich	49.40	31.25	Korniets N. L., Gladkikh M. I., Zelikson E. M. et al., 1981
27	Eliseevichi	52.50	32.60	Zelikson E. M., 1986
28	Kolkotova Balka	46.35	29.40	Veklich M. F., 1982
29	Koty	51.20	31.10	Veklich M. F., 1982
30	Vasilievka	46.40	33.10	Veklich M. F., 1982
31	Zaporozh'e	47.47	35.15	Veklich M. F., 1982
32	Taromsky Ovrage	48.25	35.00	Veklich M. F., 1982
33	Hotimlya	58.45	32.05	Zarrina E. P., 1991
34	Zhdanov	48.05	37.30	Artyushenko A. T., 1970
35	Primorskoe	46.05	30.25	Artyushenko A. T., 1970
36	Zagorodnee	49.40	36.25	Artyushenko A. T., 1970
37	Mironovka	46.35	35.20	Artyushenko A. T., 1970
38	Kuyalnik Liman	46.40	30.50	Artyushenko A. T., 1970
39	Priluki	50.20	32.30	Artyushenko A. T., 1970
40	Berislav	46.35	33.10	Artyushenko A. T., 1970

No.	Site name	Latitude	Longitude	References
41	Kryzhanovka	46.38	33.05	Artyushenko A. T., 1970
42	Etylia Noue	45.33	28.25	Medyanik S. I., Mikhailesku K. D., 1992
43	Khadzhimus	46.40	29.50	Medyanik S. I., Mikhailesku K. D., 1992
44	Chichmykey	45.30	28.20	Medyanik S. I., Mikhailesku K. D., 1992
45	Varnitsa	46.50	29.20	Medyanik S. I., Mikhailesku K. D., 1992
46	Varnitsa 1	46.50	29.20	Medyanik S. I., Mikhailesku K. D., 1992
47	Speya	46.55	29.15	Medyanik S. I., Mikhailesku K. D., 1992
48	Khrushka	48.05	29.40	Medyanik S. I., Mikhailesku K. D., 1992
49	Vladicheny	45.27	28.30	Medyanik S. I., Mikhailesku K. D., 1992
50	Parkan'	46.40	29.45	Medyanik S. I., Mikhailesku K. D., 1992
51	Karagash	46.30	29.44	Medyanik S. I., Mikhailesku K. D., 1992
52	Tyrnauka	46.40	29.48	Medyanik S. I., Mikhailesku K. D., 1992
53	Naroch'	54.55	26.20	Makhnach N. A., 1971
54	Pas'va	61.15	43.05	Devyatova E. I., 1982
55	Pervomaysky	64.25	41.50	Devyatova E. I., 1982
56	Pikalevo	59.35	34.00	Grichuk V. P., Mal'gina E. A., Monoszon M. Kh., 1969
57	Koposa	57.20	31.15	Grichuk V. P., Mal'gina E. A., Monoszon M. Kh., 1969
58	Dvoretz	57.50	32.20	Grichuk V. P., Mal'gina E. A., Monoszon M. Kh., 1969
59	Voznesenie	61.05	35.15	Grichuk V. P., Mal'gina E. A., Monoszon M. Kh., 1969
60	Shapurovo	55.35	36.25	Chebotareva N. S., Makarycheva I. A., 1974
61	Likhvin	54.15	36.50	Sudakova n. G., Rengarten N. V., Basilevskaya LI., 1977
62	Tutaevo	57.50	44.30	Paramonova N. N., Vvedenskaya A. I., Sudakova N. G. et al., 1977
63	Mezin	51.50	33.05	Grichuk V. P., 1969
64	Or'ya	56.10	55.05	Yakhimovich V. L., Nemkova V. K., 1981

MAPS OF LARGE MAMMAL LOCALITIES

LEGEND TO THE MAPS OF MAMMAL LOCALITIES

MAMMAL LOCALITIES

HOLOCENE <10,000 yr B.P.



VALDAI GLACIAL

LATE VALDAI (SARTAN)

a. Late glacial 10,001 - 15,000 yr B.P.



b. Glacial maximum 15,001 - 24,000 yr B.P.



MIDDLE VALDAI (BRYANSK= LATE KARGINSKY)

INTERSTADIAL 24,001 - 35,000 yr B.P.



EARLY VALDAI (ZYRYAN) 35,001 - 100,000 yr B.P.



MIKULINO (KAZANTSEVO) INTERGLACIAL

about 100,000 - 130,000 yr B.P.



MODERN SPECIES DISTRIBUTION



CONTINENTAL AND MOUNTAIN GLACIATION



ICE SHEETS BOUNDARIES

a. proved



b. approximate



MARINE BASINS OF THE GLACIAL MAXIMUM



MARINE BASINS OF THE LAST INTERGLACIAL



PROBOSCIDEA: *Mammuthus primigenius*

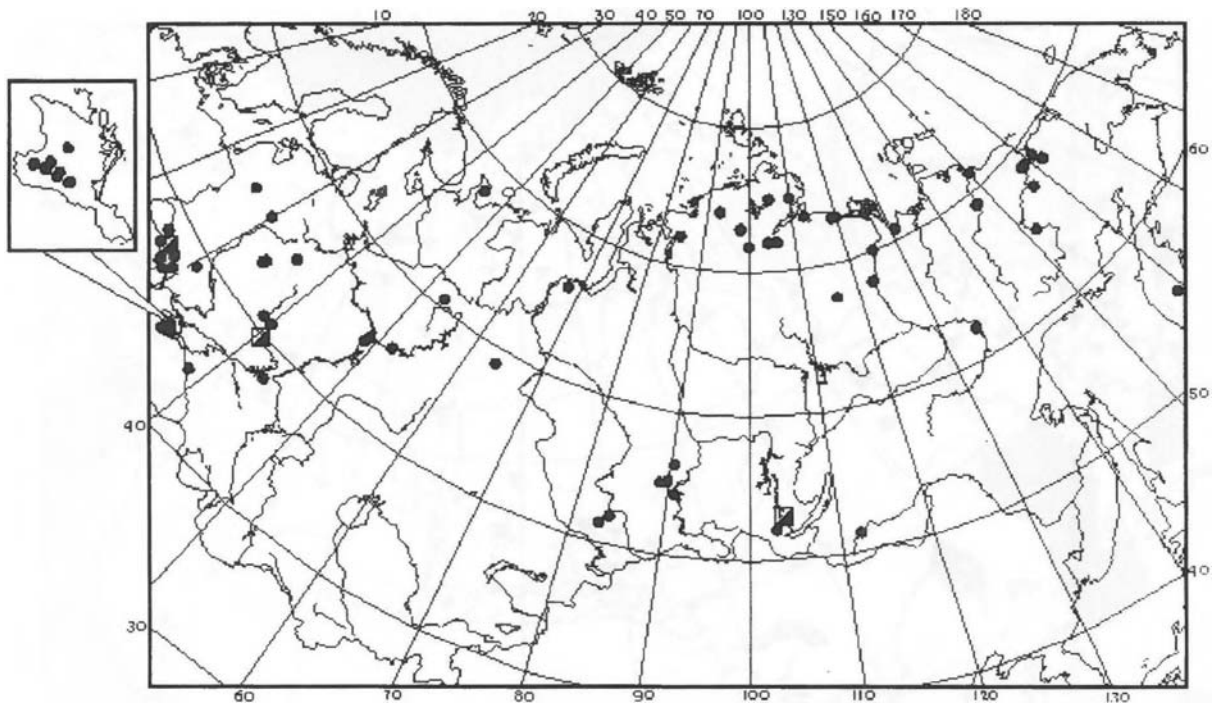


FIGURE 1. Localities of mammoth (35,000-130,000 yr B.P.).

PROBOSCIDEA: *Mammuthus primigenius*

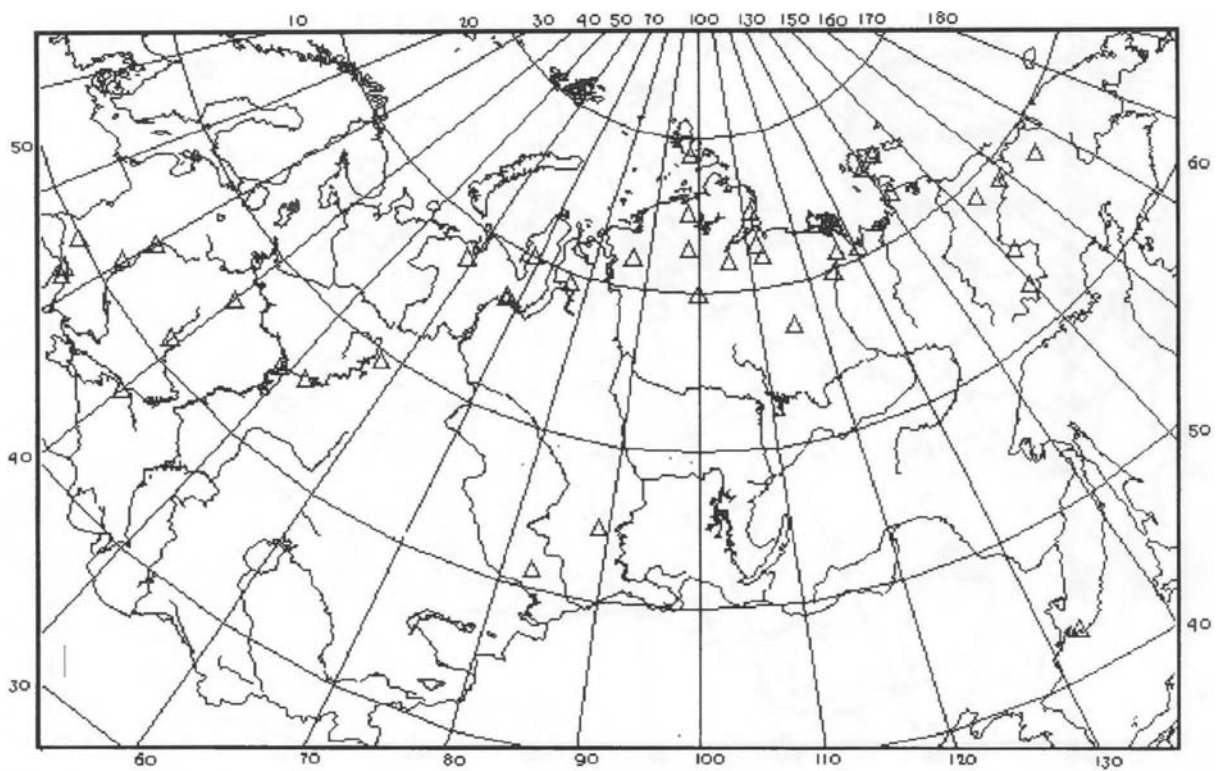


FIGURE 2. Localities of mammoth (24,000-35,000 yr B.P.).

PROBOSCIDEA: *Mammuthus primigenius*

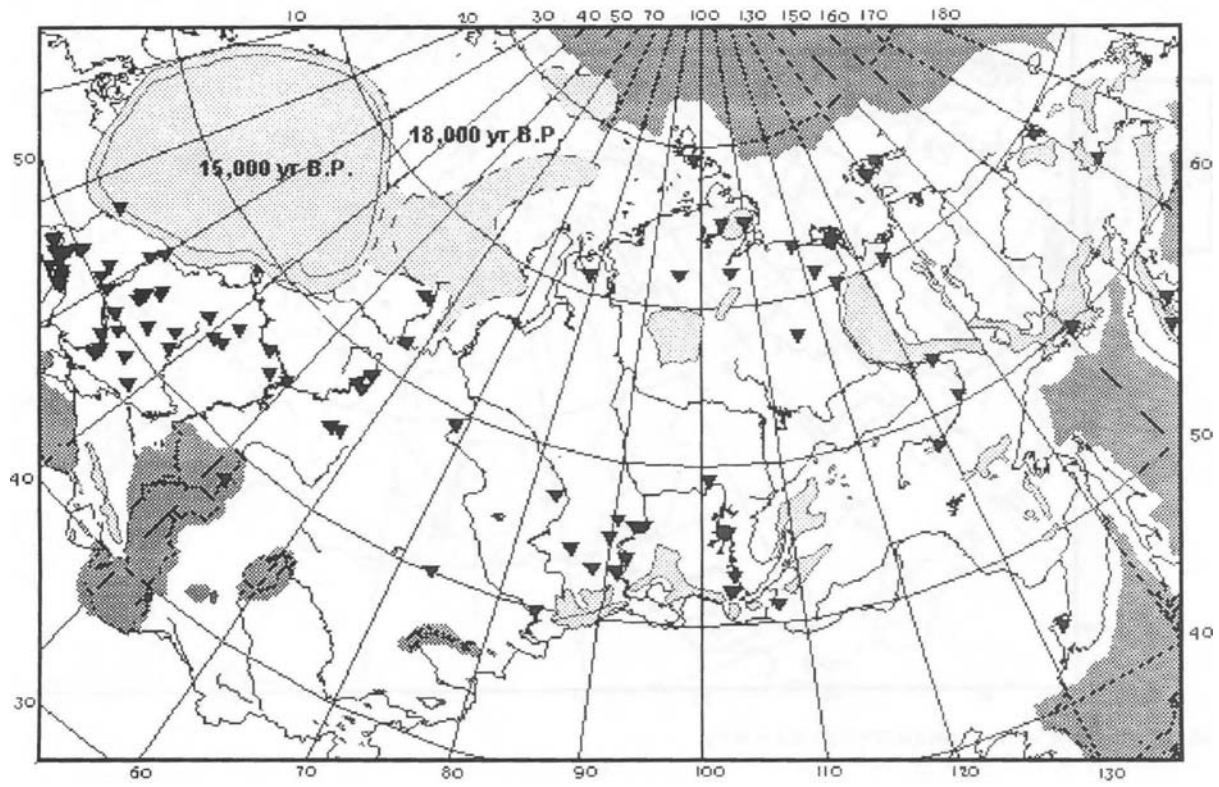


FIGURE 3. Localities of mammoth (15,000-24,000 yr B.P.).

PROBOSCIDEA: *Mammuthus primigenius*

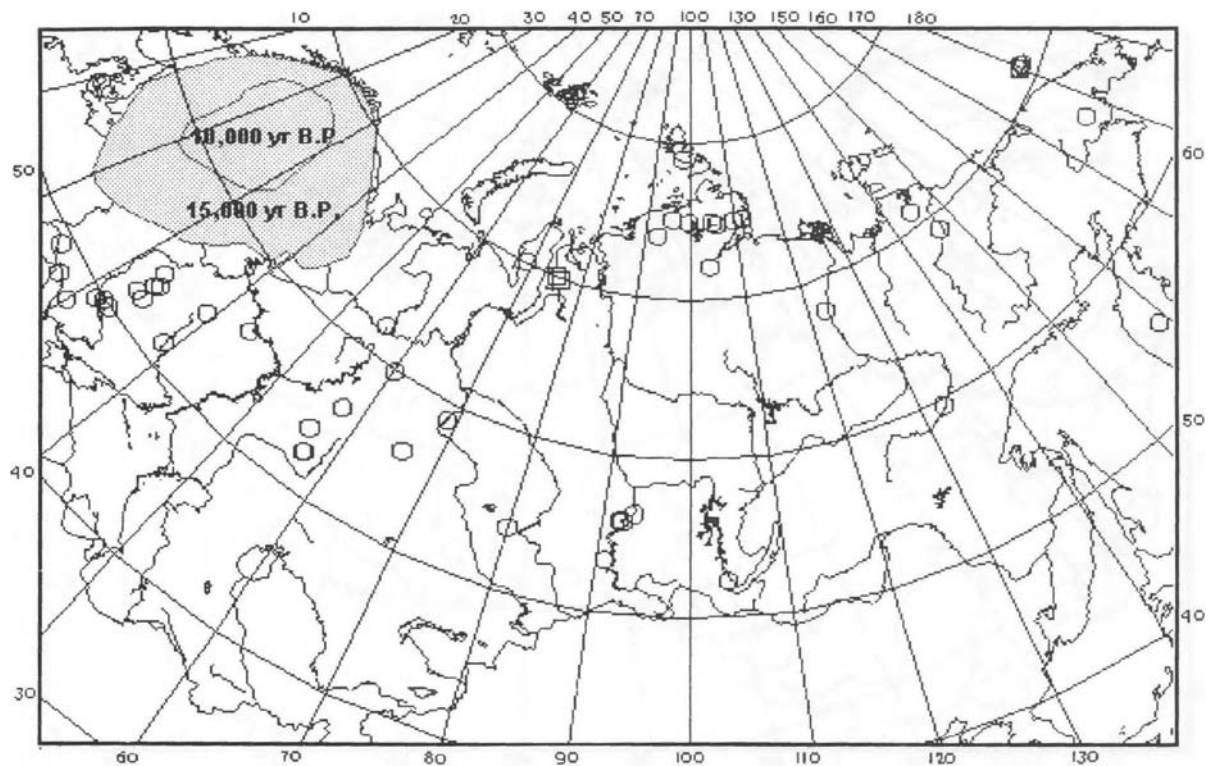


FIGURE 4. Localities of mammoth (<15,000 yr B.P.).

CARNIVORA: *Ursus (Spelaearctos) spelaeus*

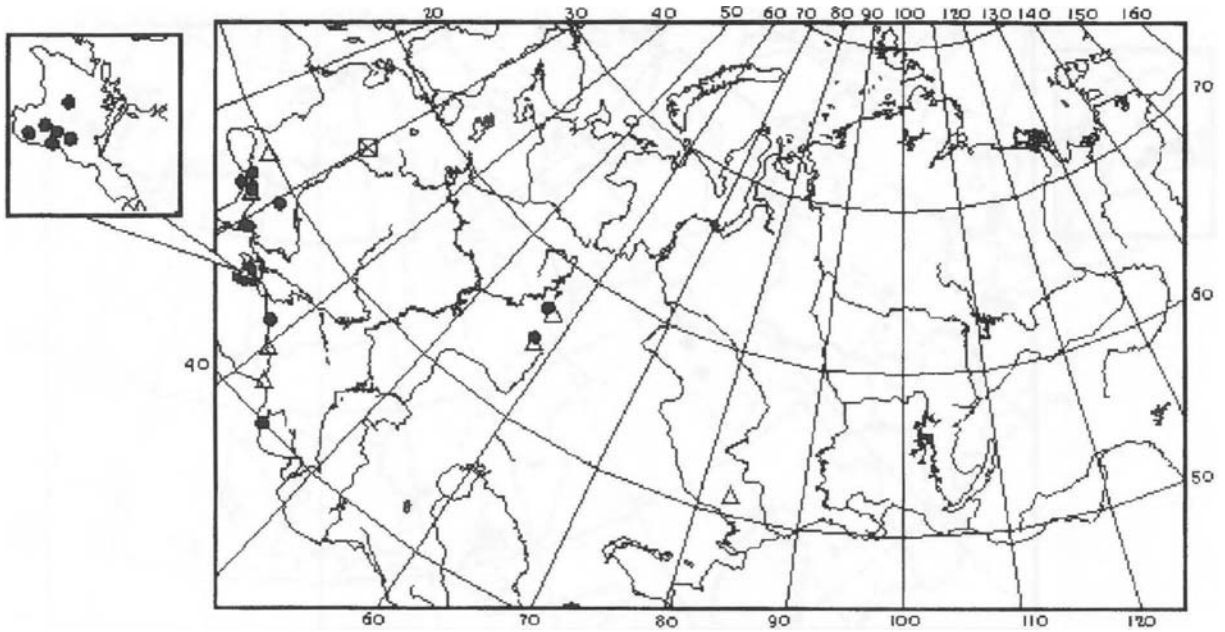


FIGURE 5. Localities of large cave bear (24,000-130,000 yr B.P.).

CARNIVORA: *Ursus (Spelaearctos) spelaeus*

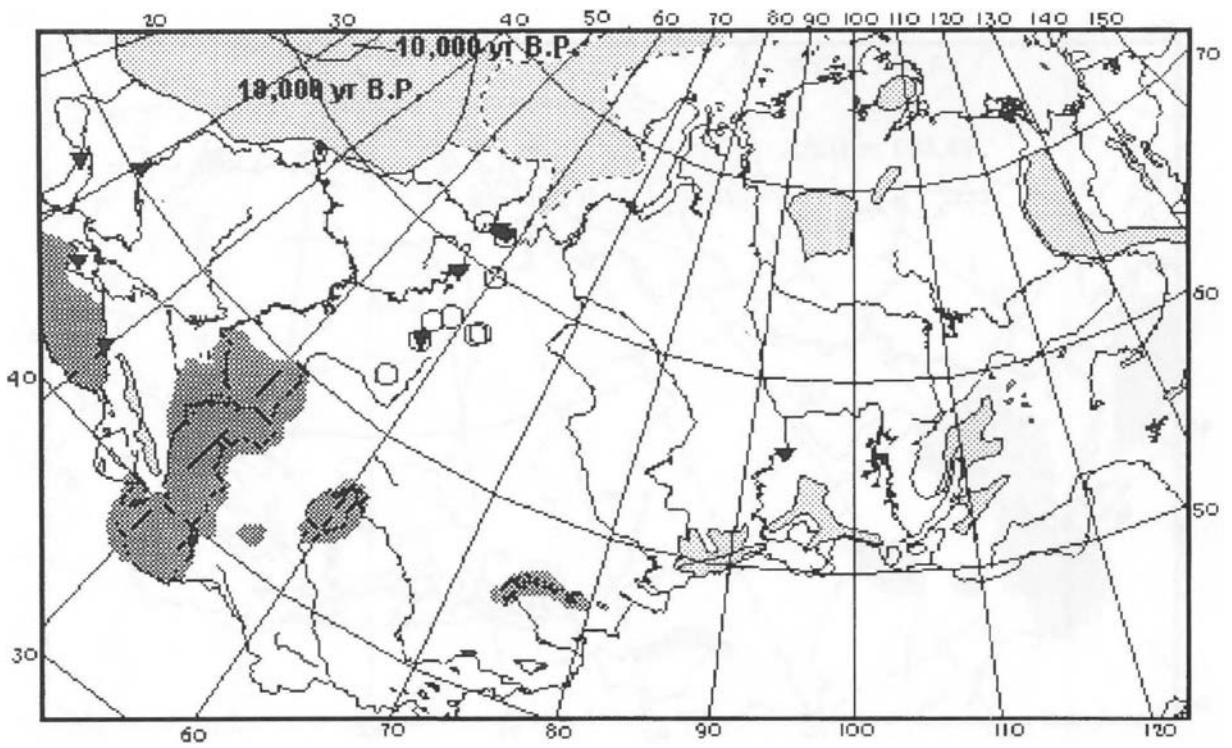


FIGURE 6. Localities of large cave bear (10,000-24,000 yr B.P.).

CARNIVORA: *Crocota spelaea*

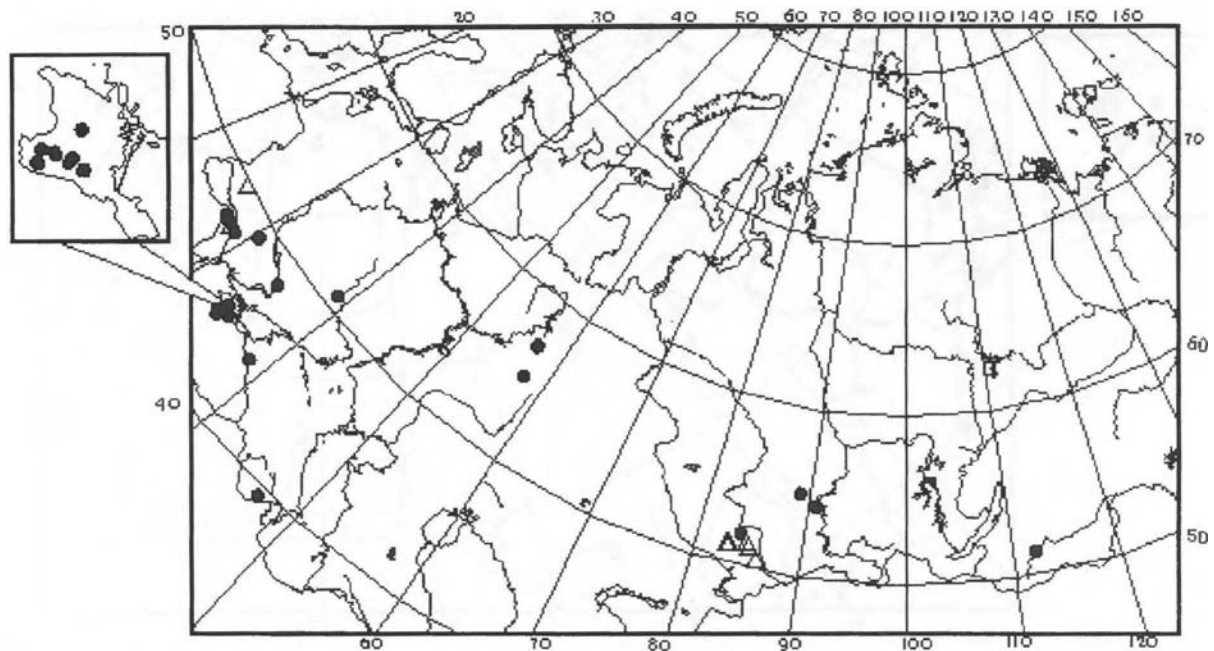


FIGURE 7. Localities of cave hyena (35,000-100,000 yr B.P.).

CARNIVORA: *Crocota spelaea*

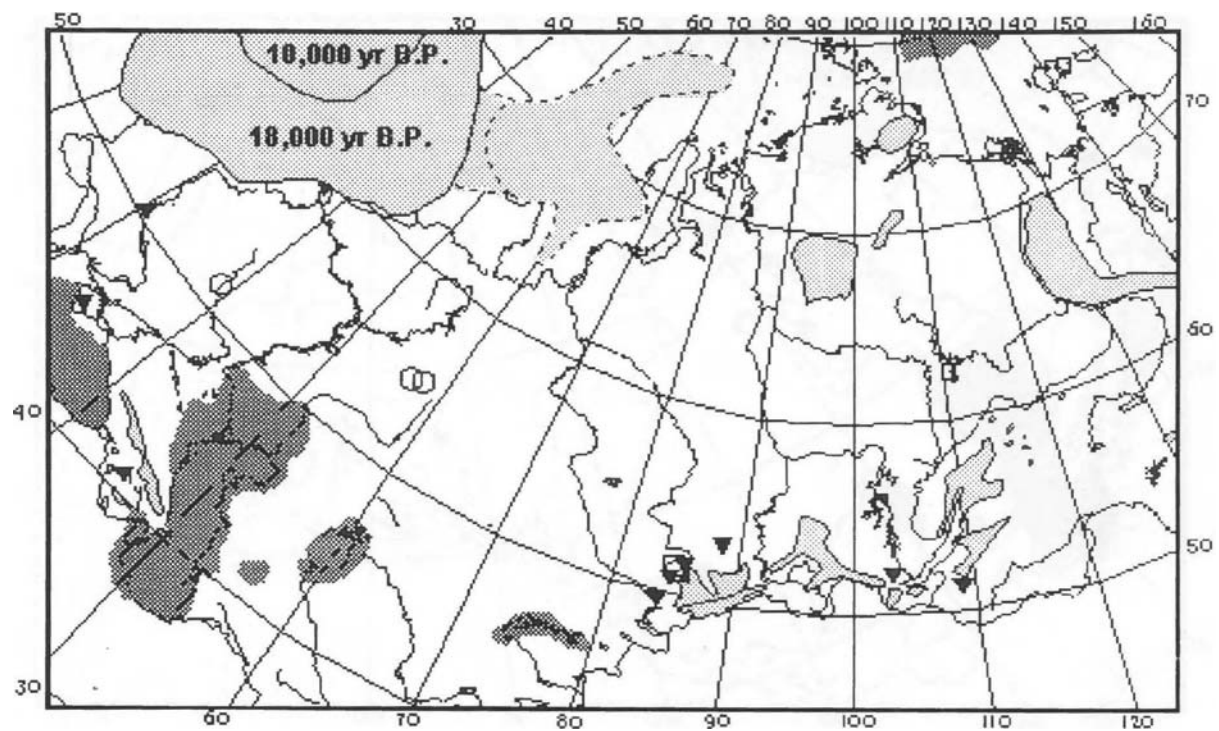


FIGURE 8. Localities of cave hyena (10,000-35,000 yr B.P.).

CARNIVORA: *Panthera leo spelaea*

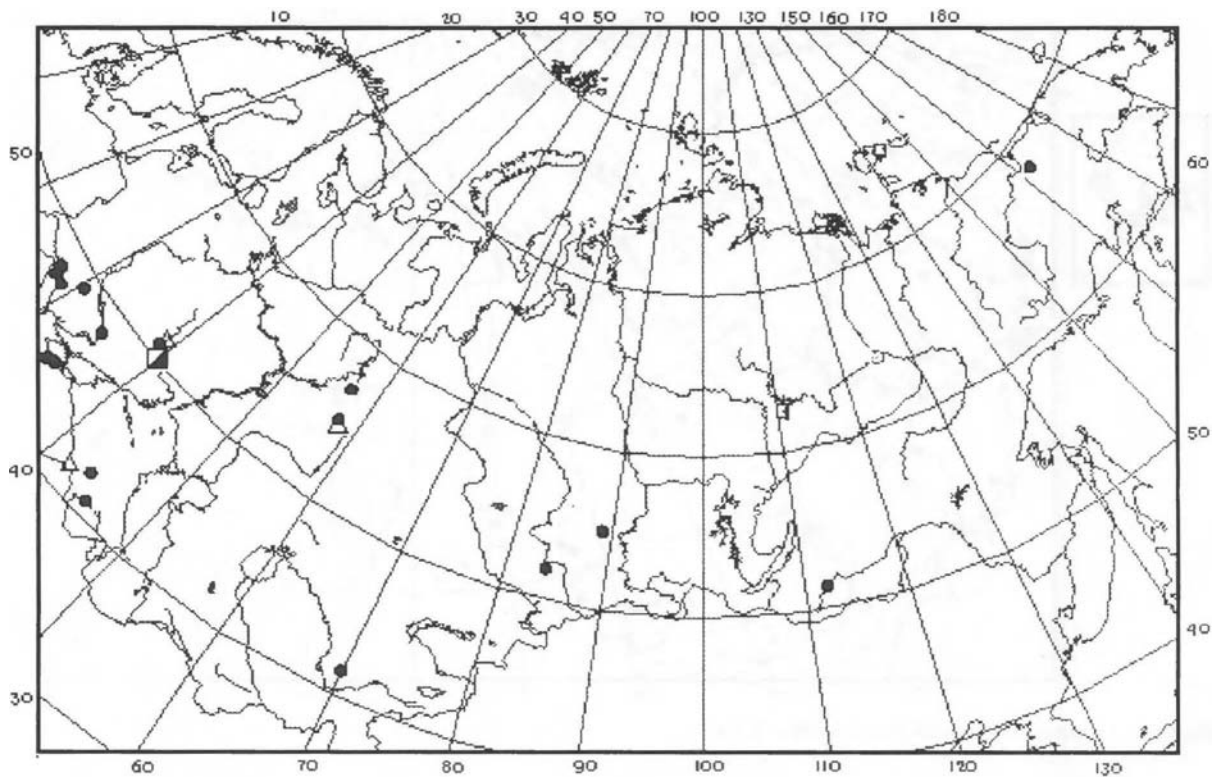


FIGURE 9. Localities of cave lion (24,000-130,000 yr B.P.).

CARNIVORA: *Panthera leo spelaea*

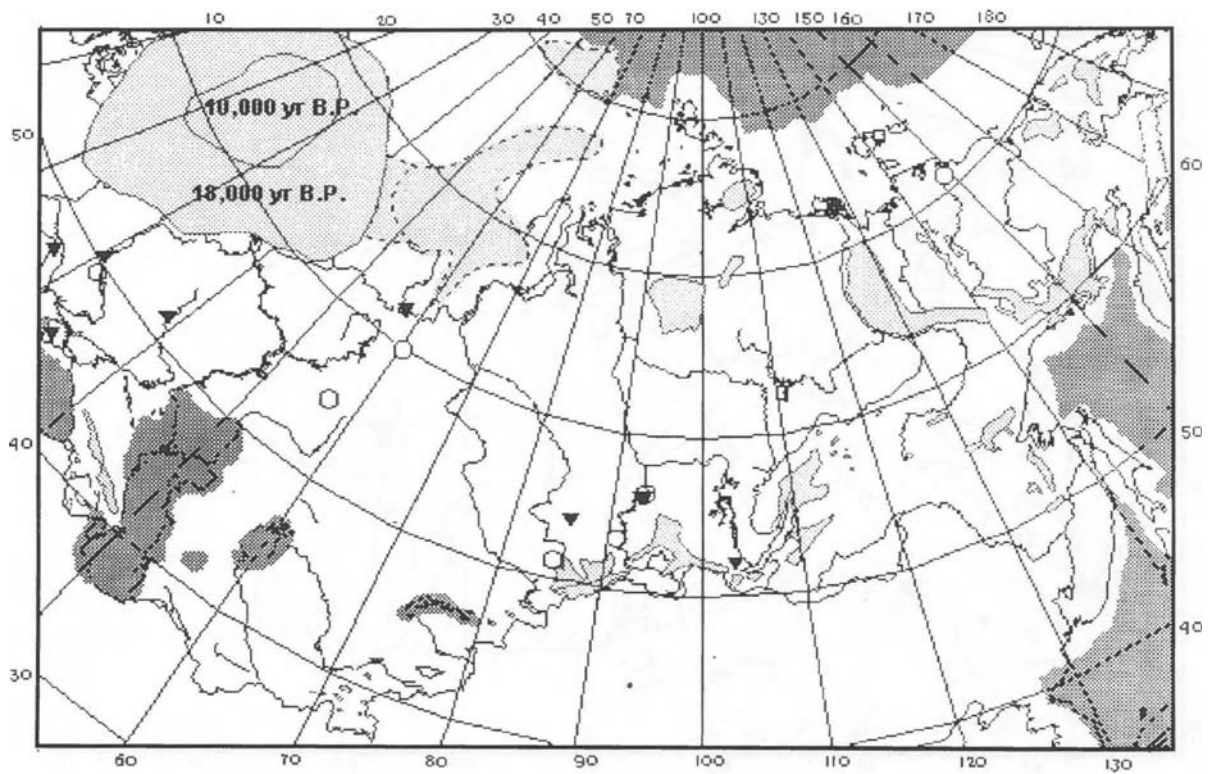


FIGURE 10. Localities of cave lion (10,000-24,000 yr B.P.).

PERISSODACTYLA: *Equus*

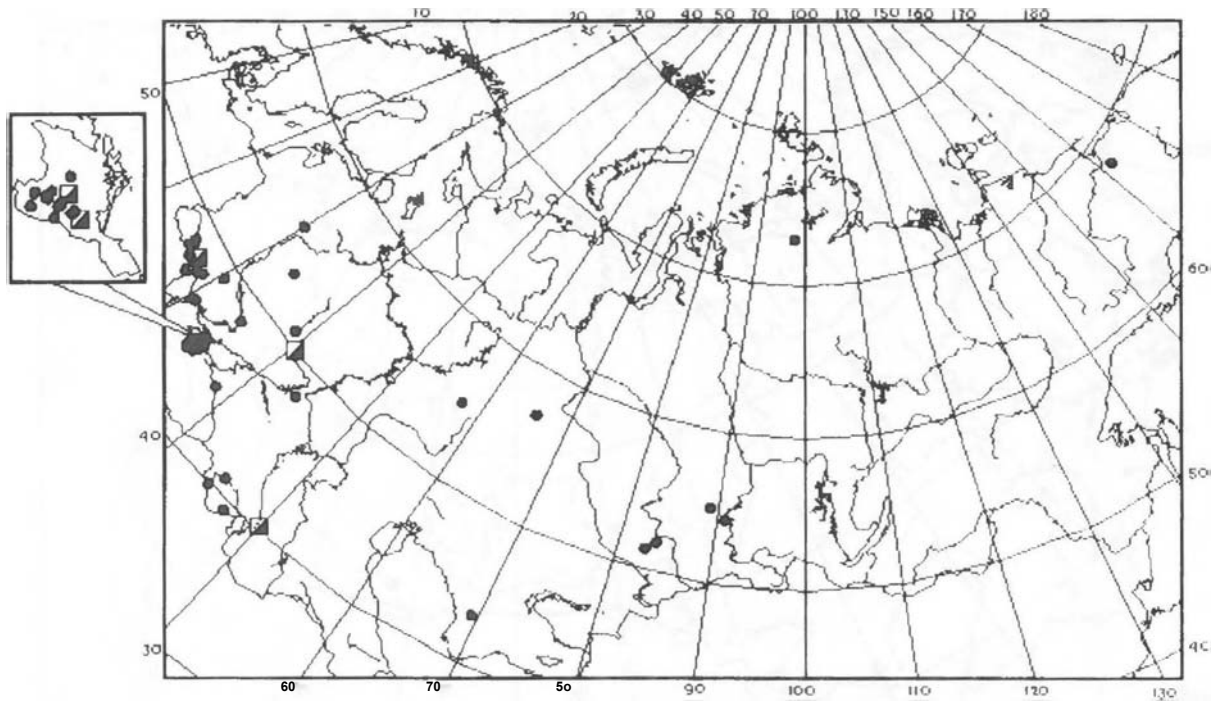


FIGURE 11. Localities of horses (35,000-130,000 yr B.P.).

PERISSODACTYLA: *Equus*

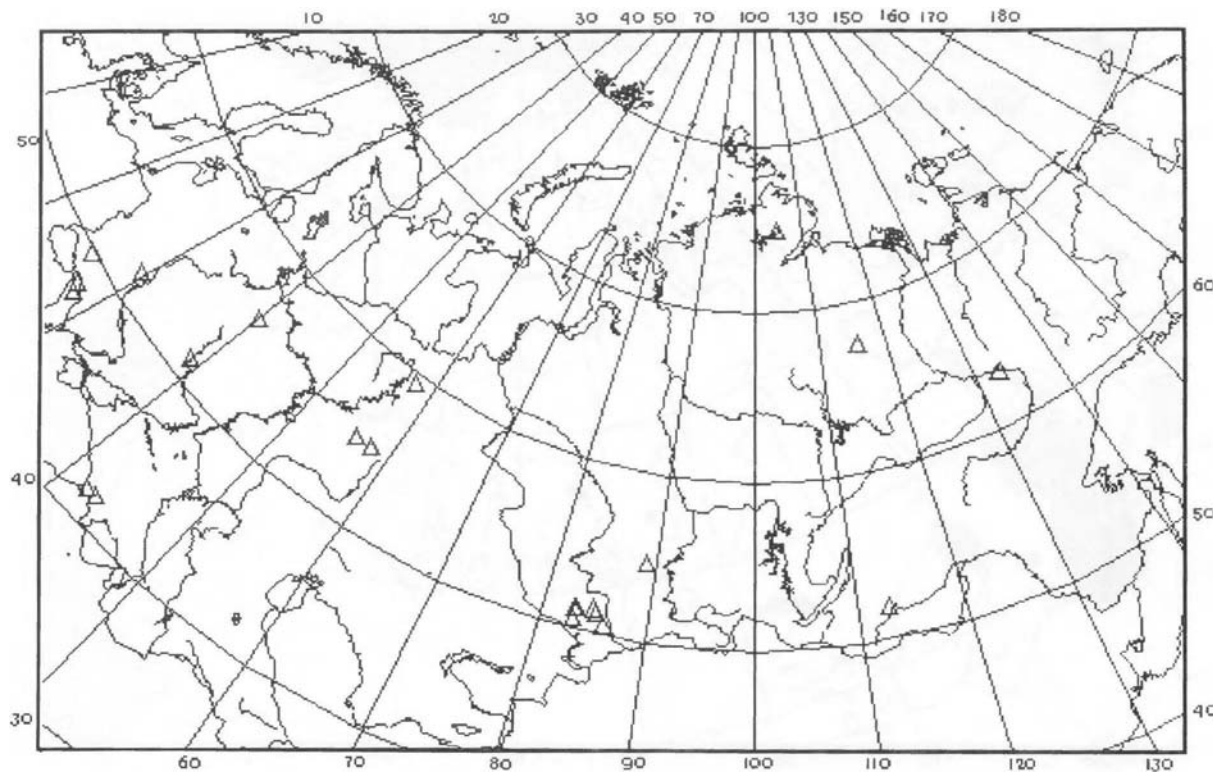


FIGURE 12. Localities of horses (14,000-35,000 yr B.P.).

PERISSODACTYLA: *Equus*

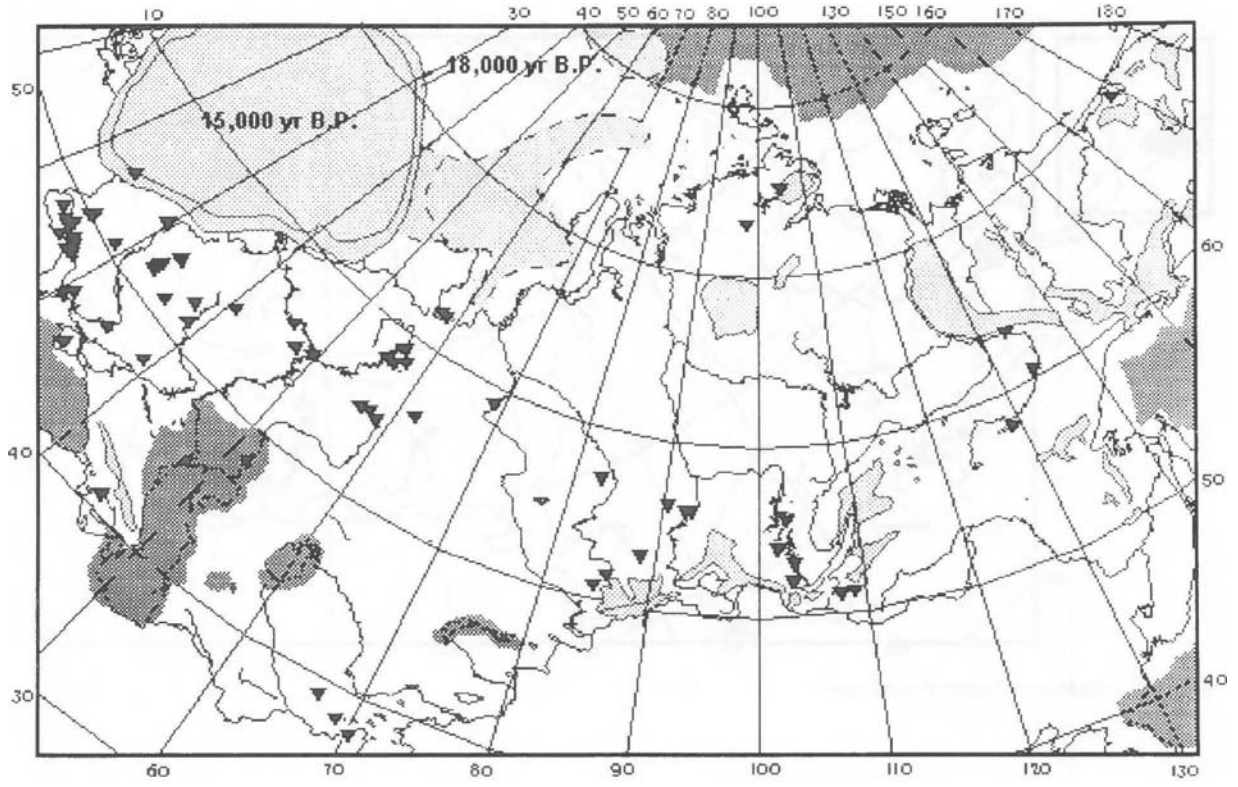


FIGURE 13. Localities of horses (15,000-24,000 yr B.P.).

PERISSODACTYLA: *Equus*

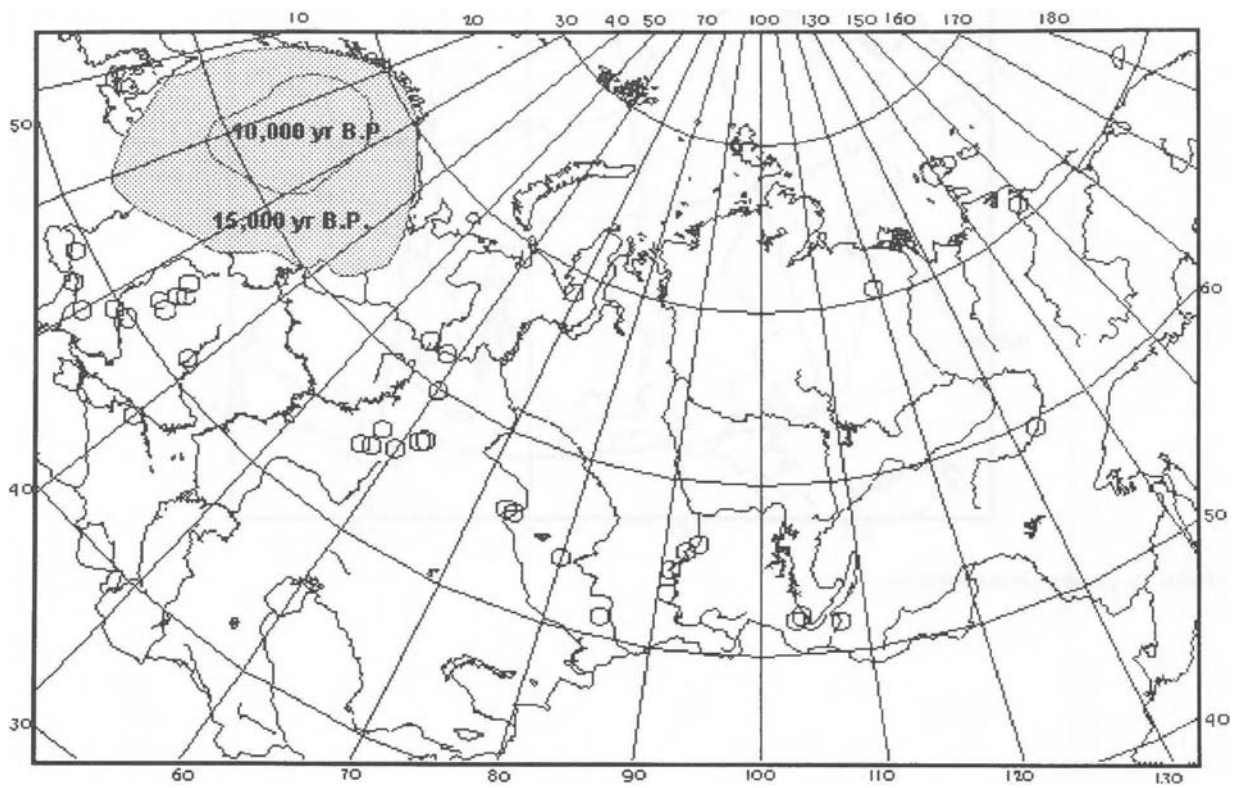


FIGURE 14. Localities of horses (10,000-15,000 yr B.P.).

PERISSODACTYLA: *Equus hydruntinus*

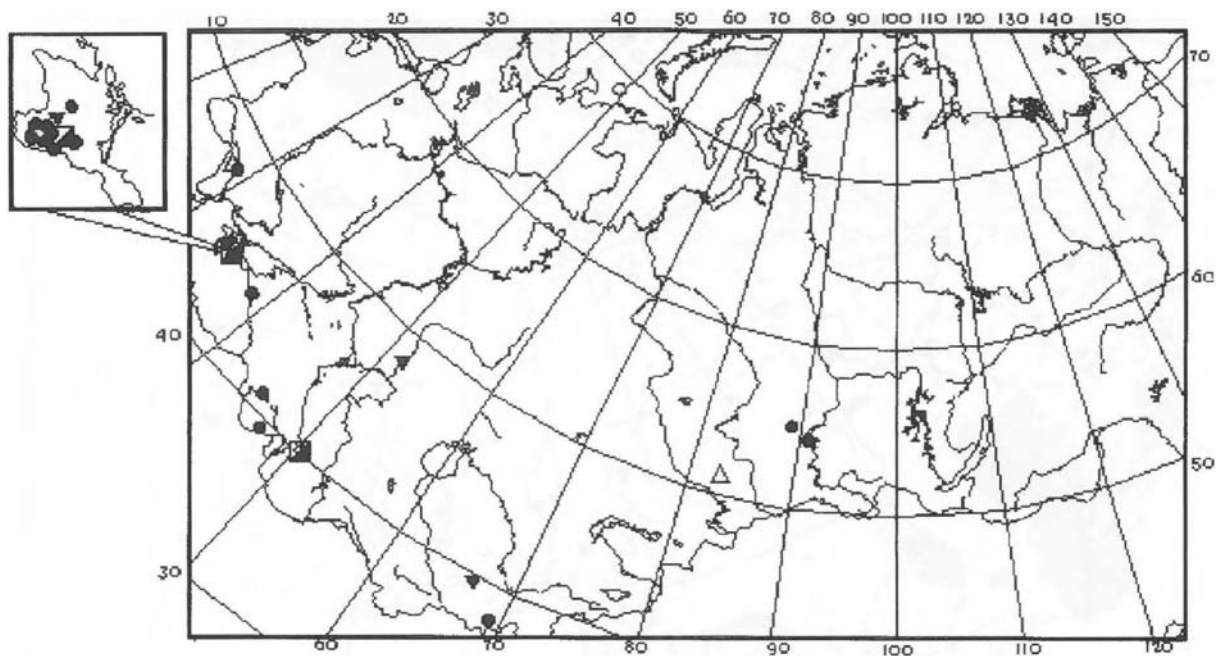


FIGURE 15. Localities of Pleistocene wild ass.

ARTIODACTYLA: *Bos (Poephagus) baikalensis*

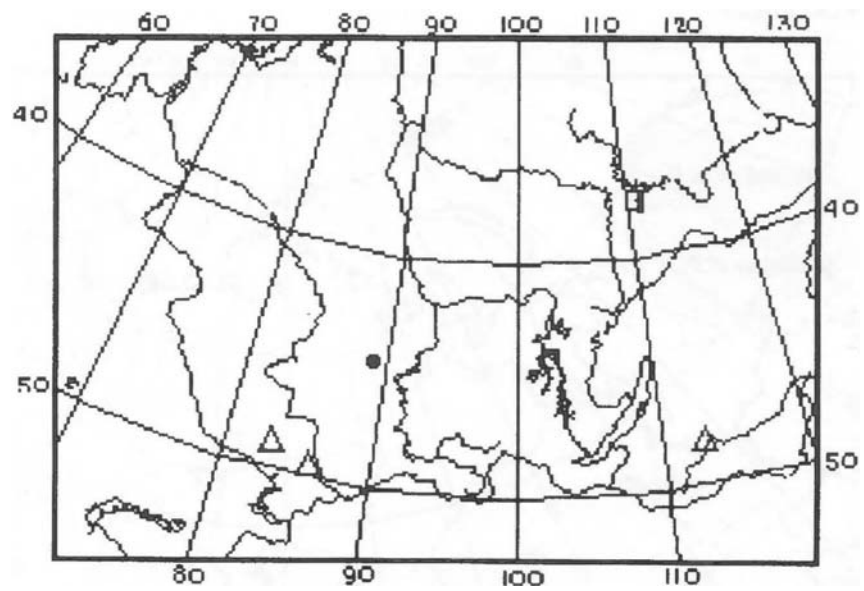


FIGURE 16. Localities of the Baikal yak.

ARTIODACTYLA: *Spirocerus kiakhtensis*

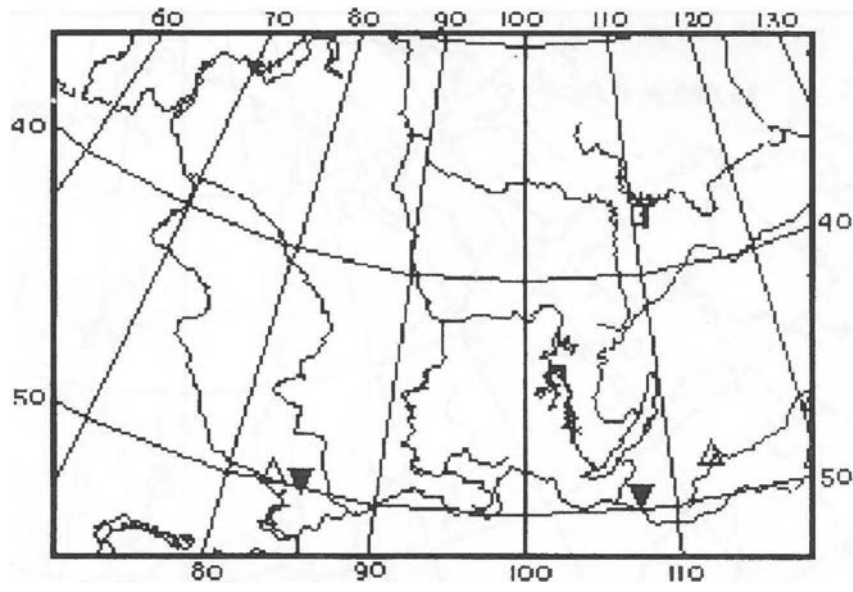


FIGURE 17. Localities of extinct spiral-homed antelope.

PERISSODACTYLA: *Coelodonta antiquitatis*

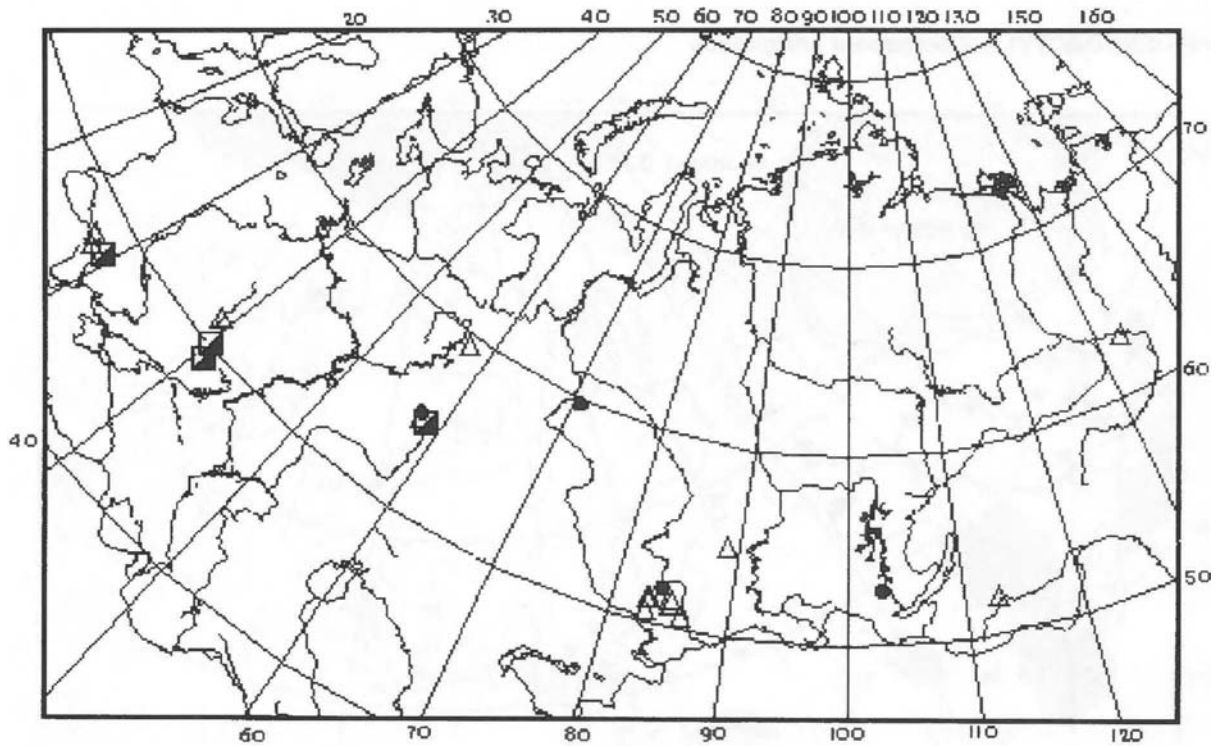


FIGURE 18. Localities of woolly rhinoceros (24,000-130,000 yr B.P.).

PERISSODACTYLA: *Coelodonta antiquitatis*

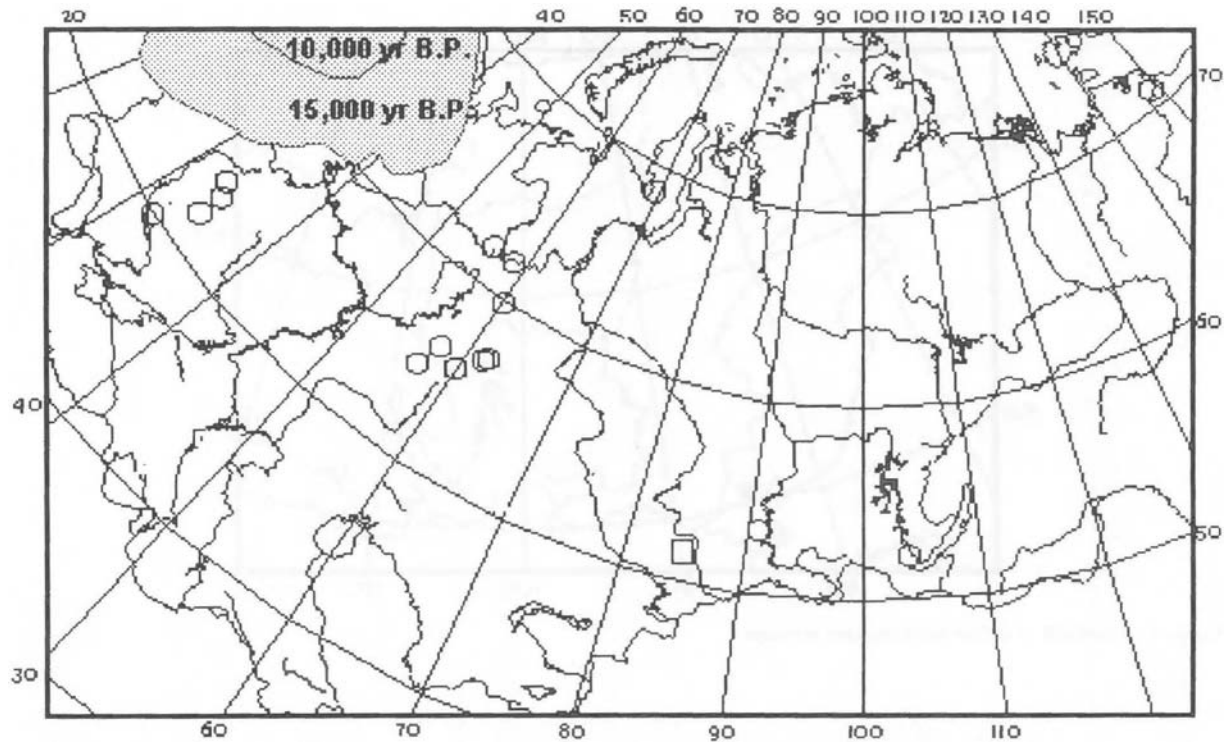


FIGURE 19. Localities of woolly rhinoceros (10,000-15,000 yr B.P.).

PERISSODACTYLA: *Coelodonta antiquitatis*

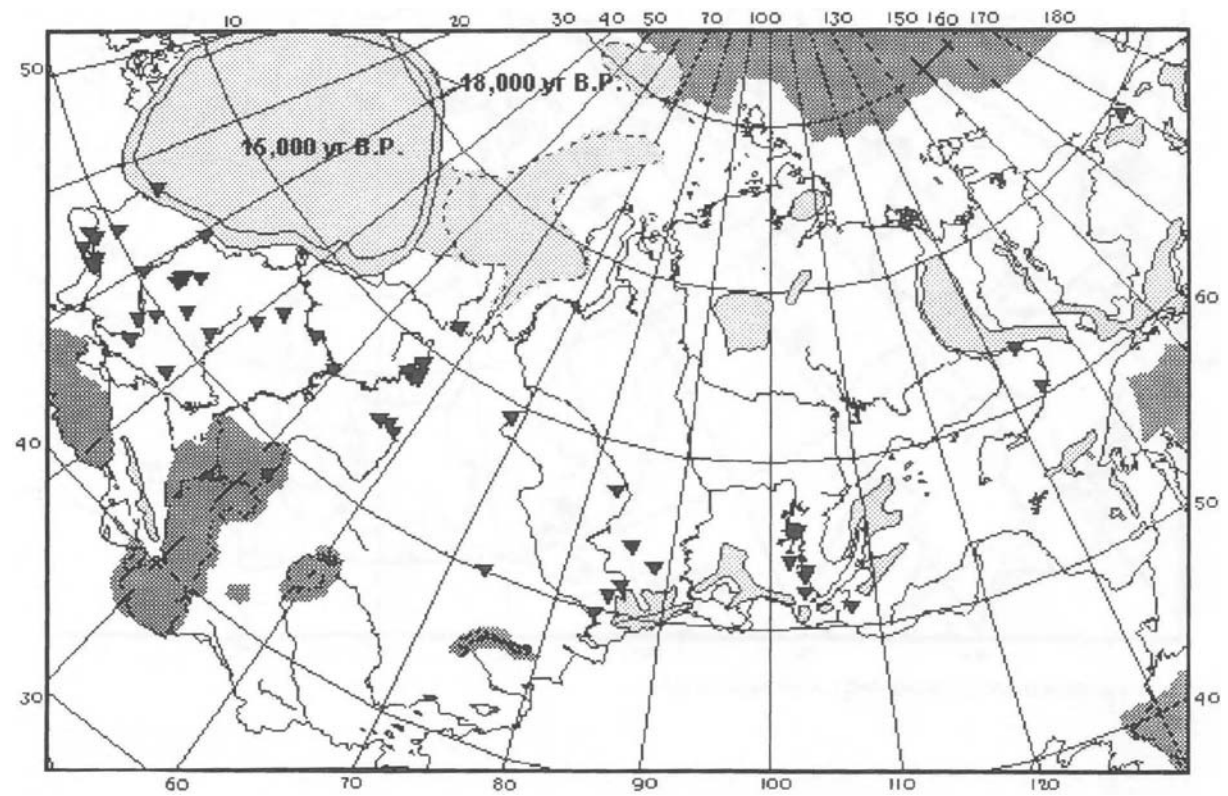


FIGURE 20. Localities of woolly rhinoceros (15,000-24,000 yr B.P.).

ARTIODACTYLA: *Megaloceros qiqanteus*

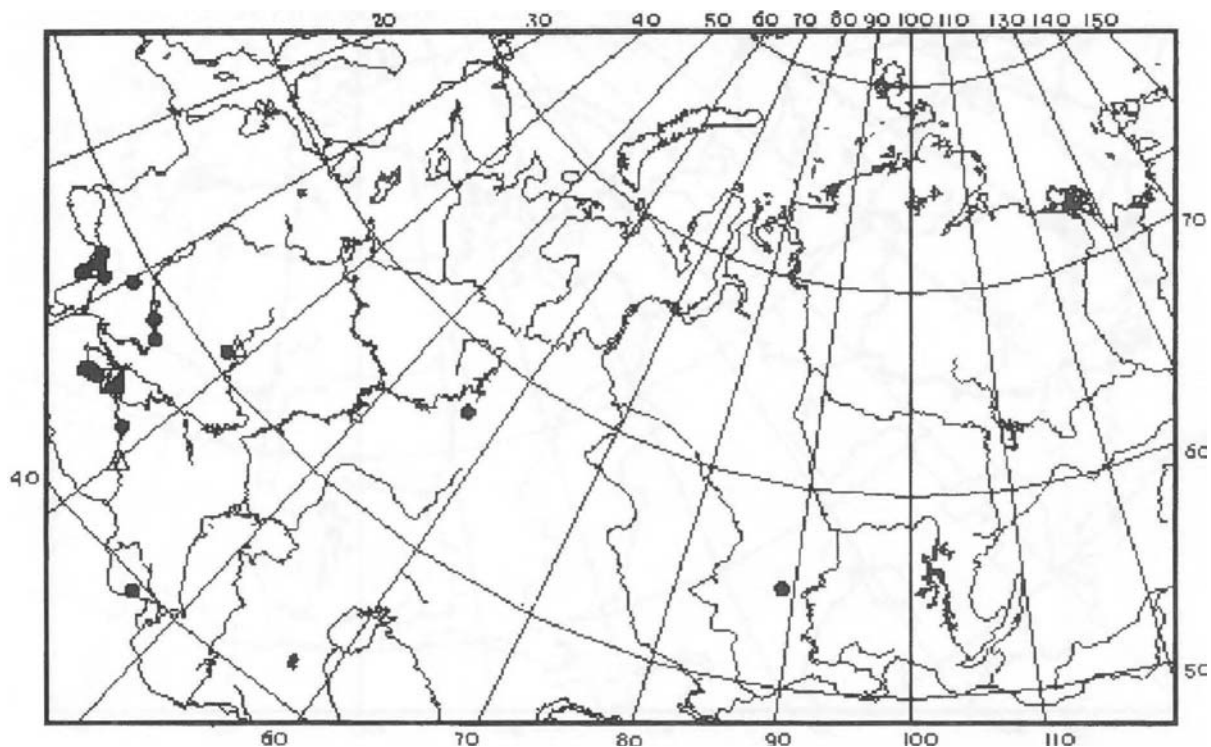


FIGURE 21. Localities of giant deer (24,000-130,000 yr B.P.).

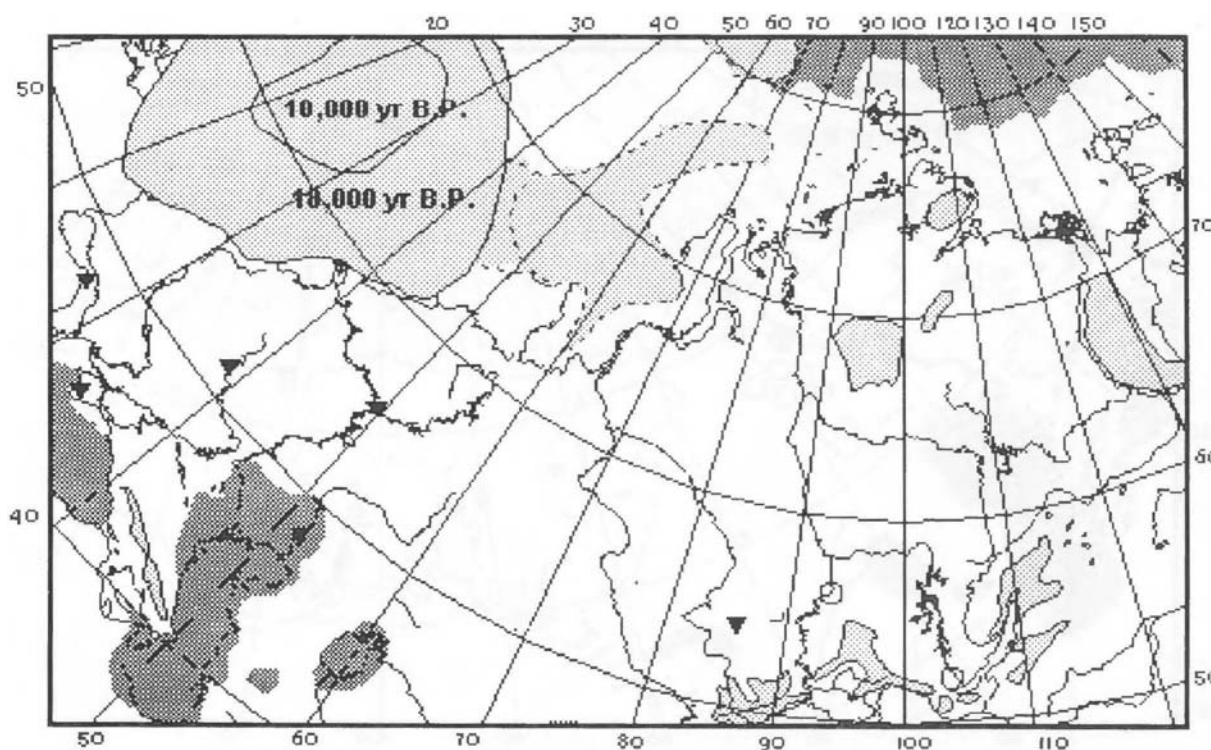


FIGURE 22. Localities of giant deer (10,000-24,000 yr B.P.)

ARTIODACTYLA: *Bos (Bos) primigenius*

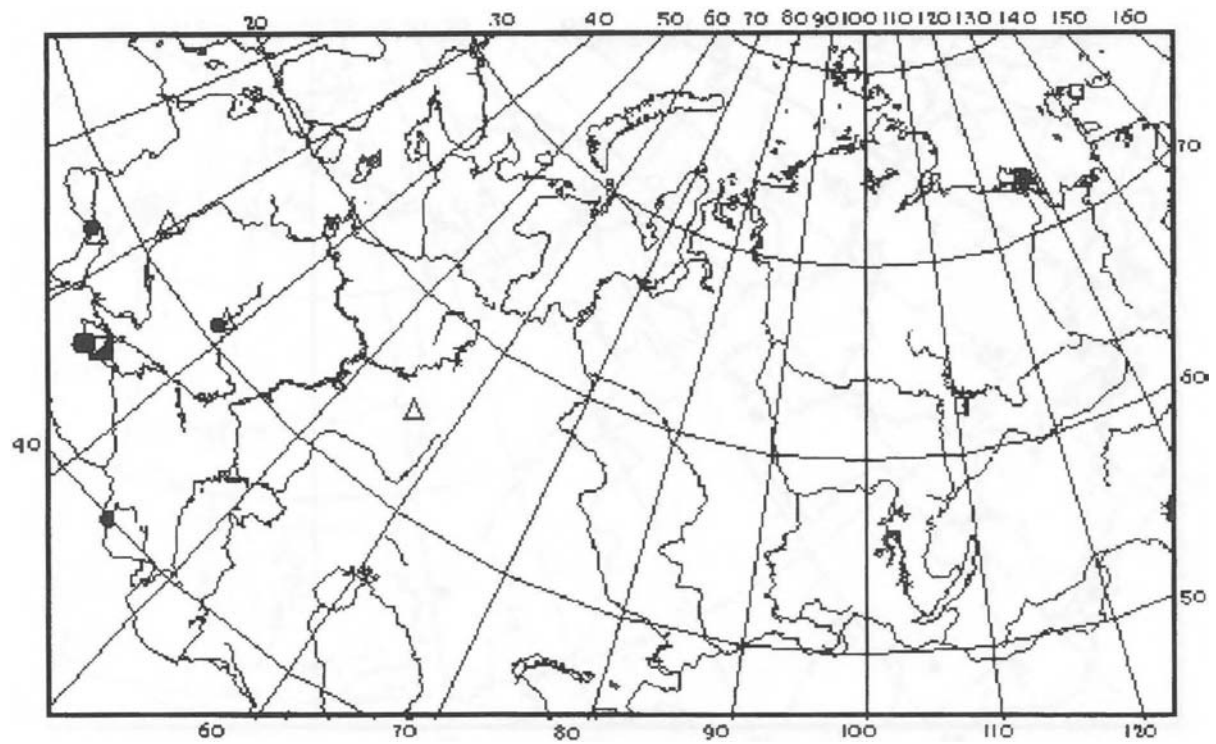


FIGURE 23. Localities of aurochs, the wild ox (24,000-130,000 yr B.P.).

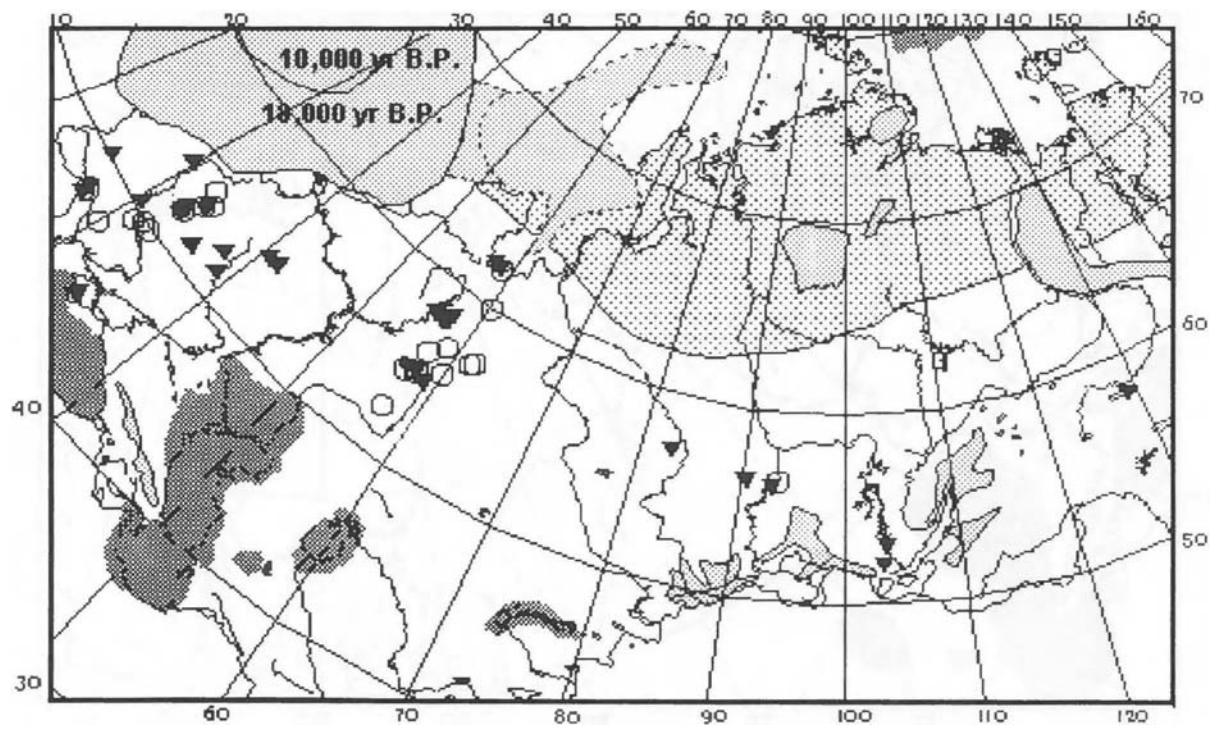


FIGURE 24. Localities of aurochs, the wild ox (10,000-24,000 yr B.P.).

ARTIODACTYLA: *Bison (Bison) priscus*

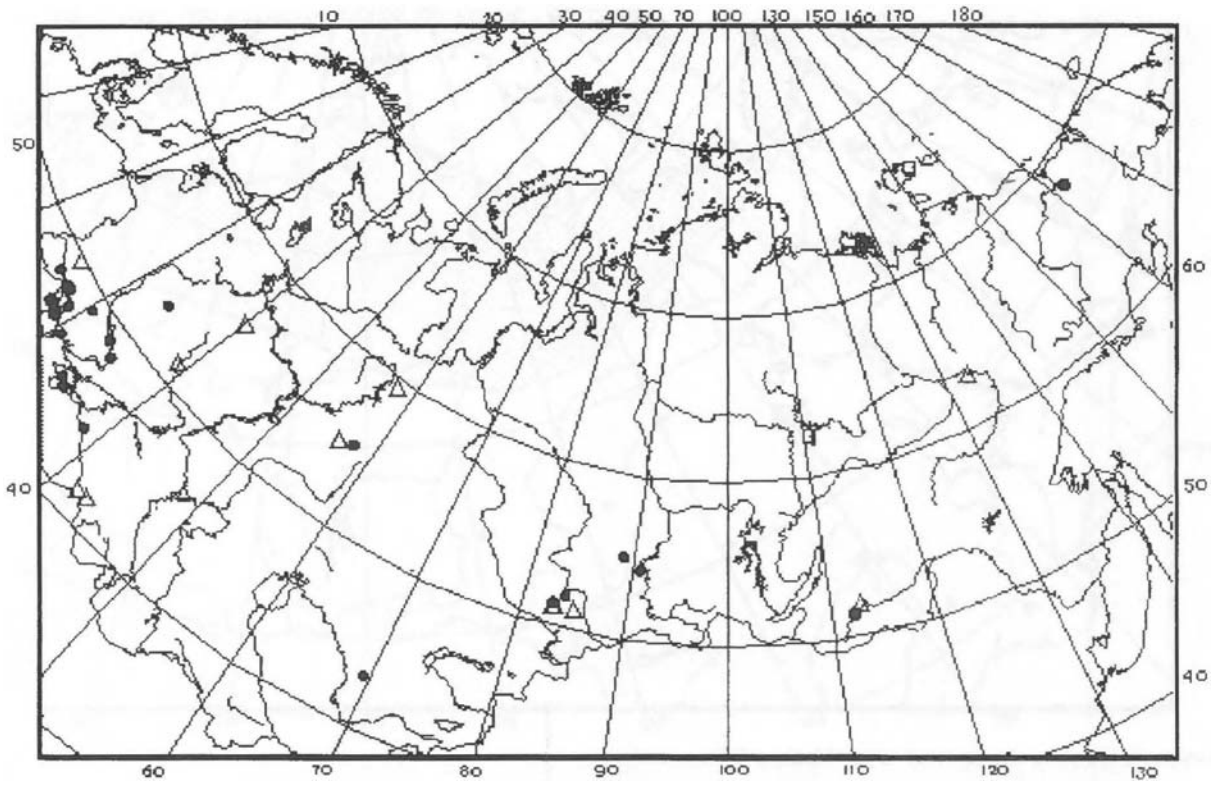


FIGURE 25. Localities of primitive bison (24,000-100,000 yr B.P.).

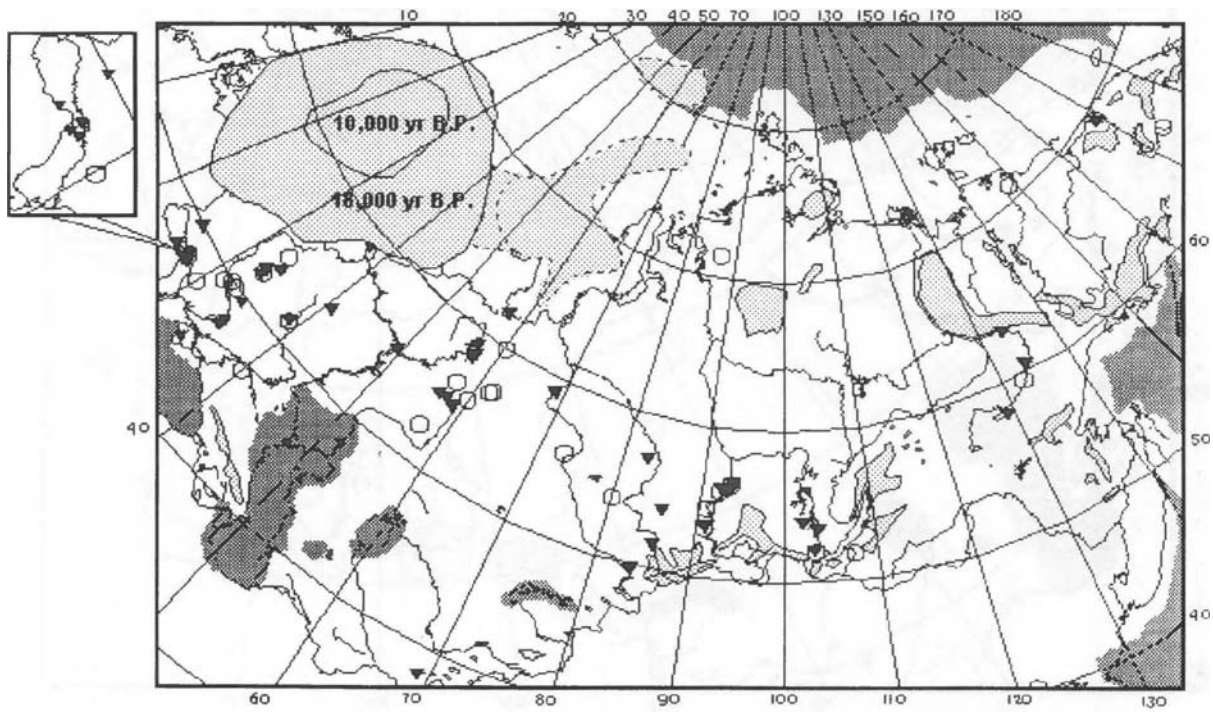


FIGURE 26. Localities of primitive bison (10,000-24,000 yr B.P.).

CARNIVORA: *Alopex lagopus*

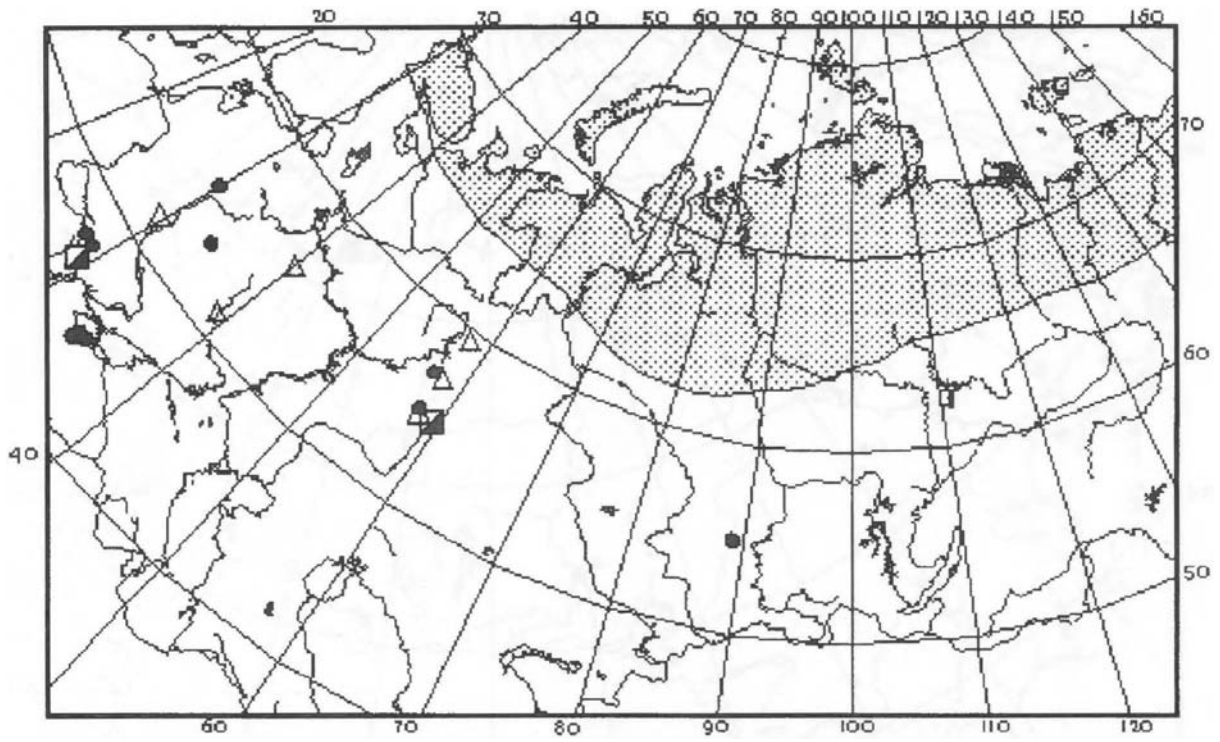


FIGURE 27. Localities of polar fox (24,000-130,000 yr B.P.).

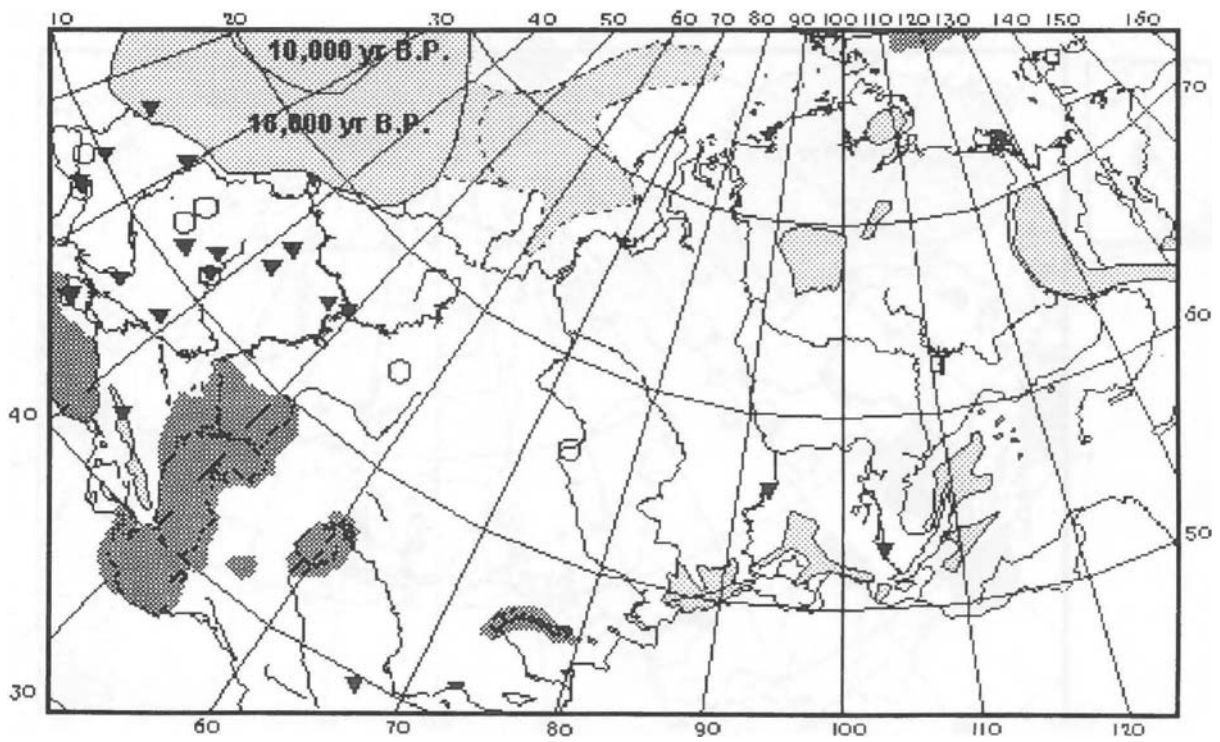


FIGURE 28. Localities of polar fox (10,000-24,000 yr B.P.).

ARTIODACTYLA: Rangifer tarandus

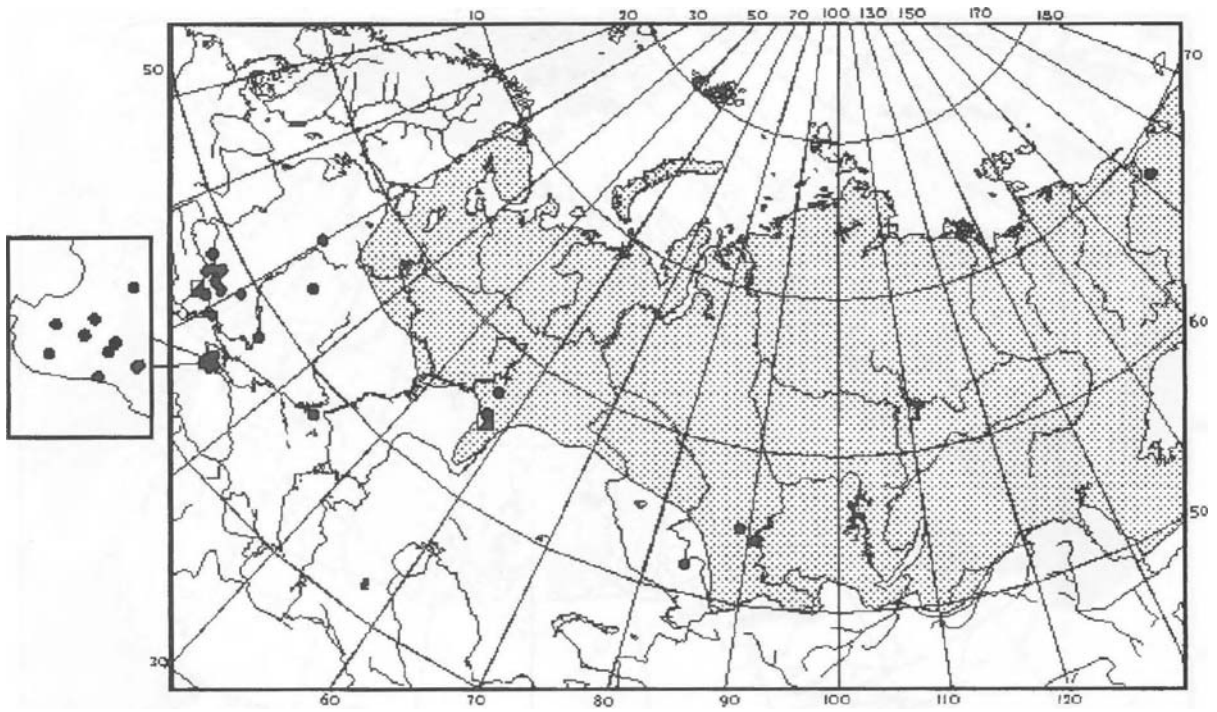


FIGURE 29. Localities of reindeer (35,000-130,000 yr B.P.).

ARTIODACTYLA: Rangifer tarandus

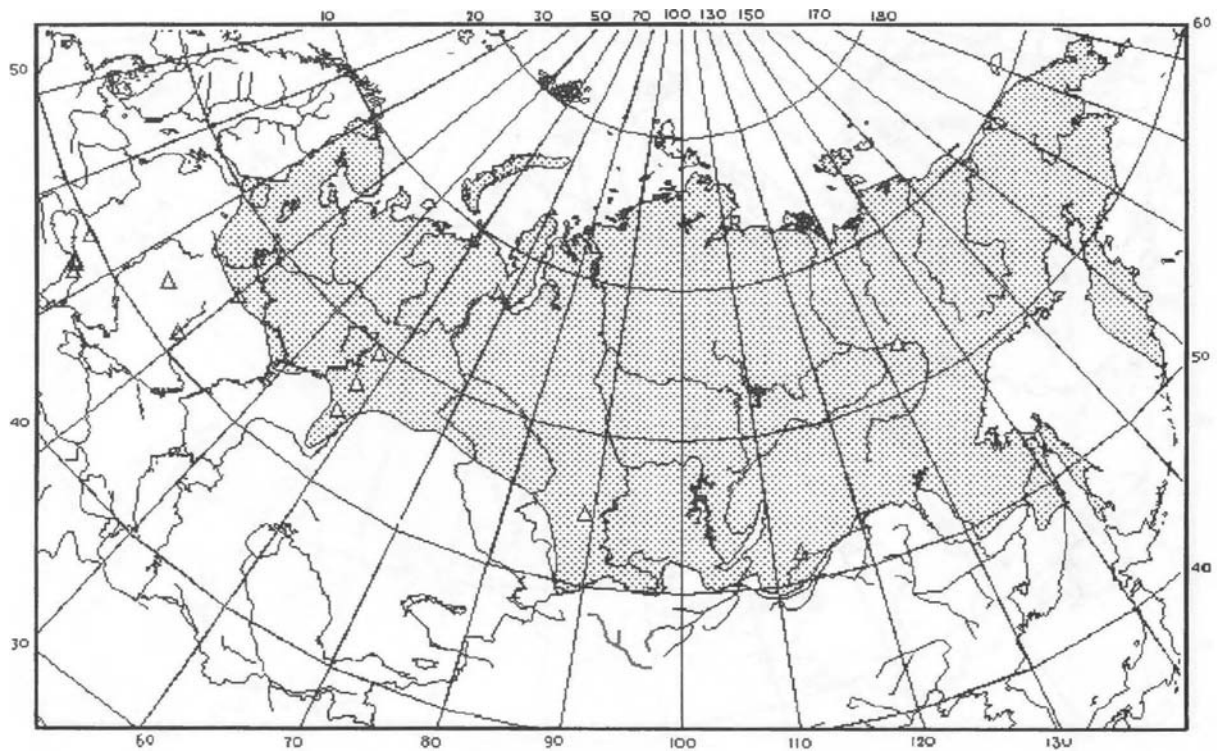


FIGURE 30. Localities of reindeer (24,000-35,000 yr B.P.).

ARTIODACTYLA: Rangifer tarandus

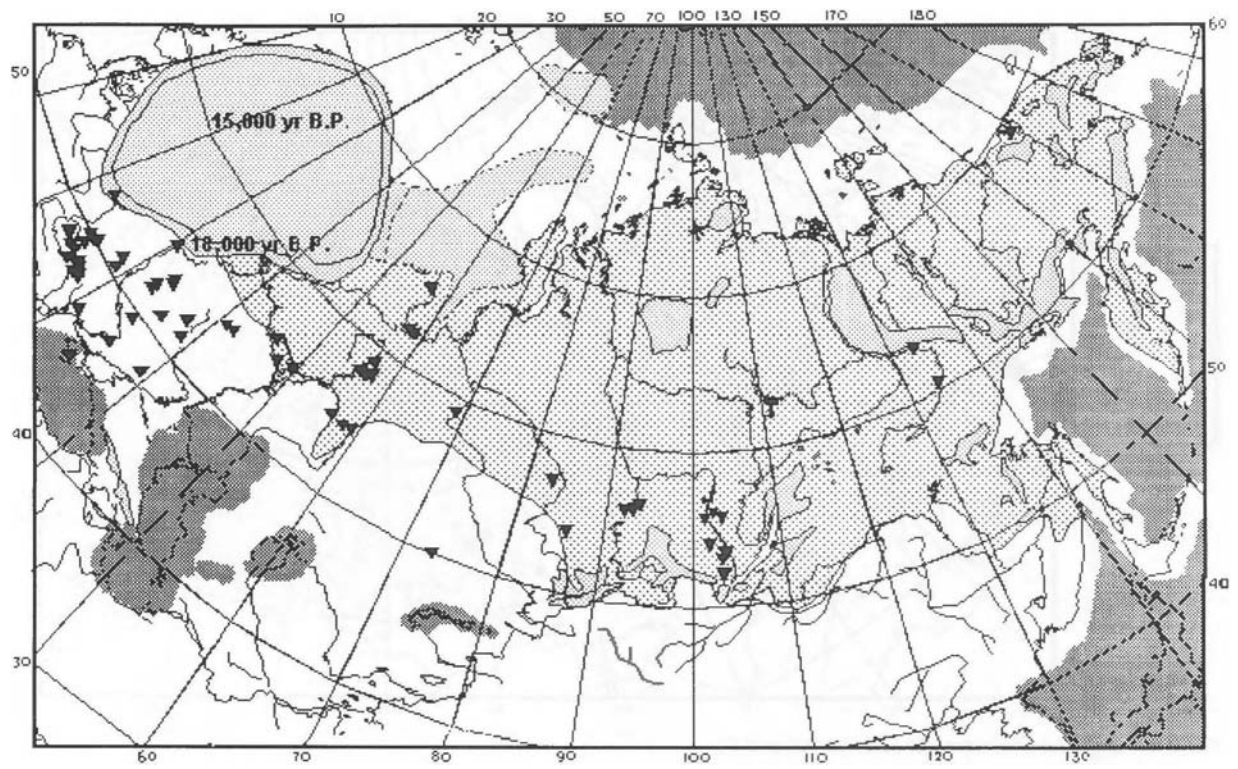


FIGURE 31. Localities of reindeer (15,000-24,000 yr B.P.).

ARTIODACTYLA: Rangifer tarandus

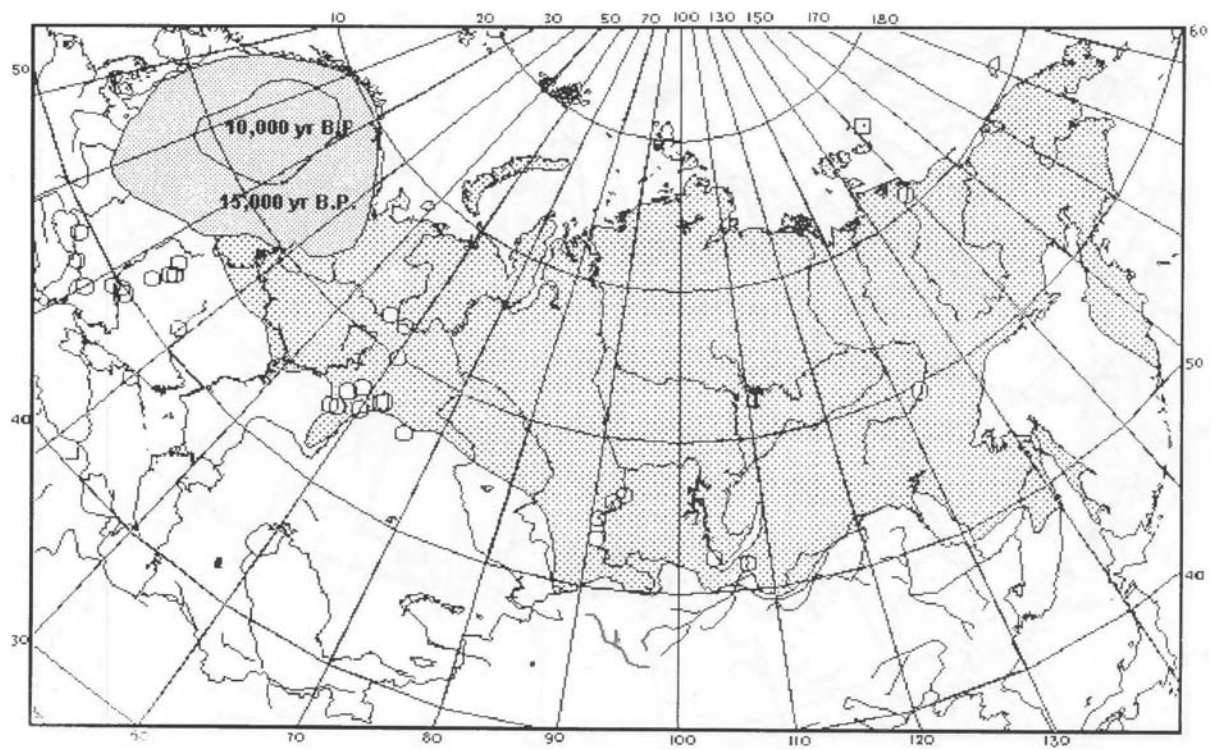


FIGURE 32. Localities of reindeer (<15,000 yr B.P.).

ARTIODACTYLA: *Ovibos moschatus*

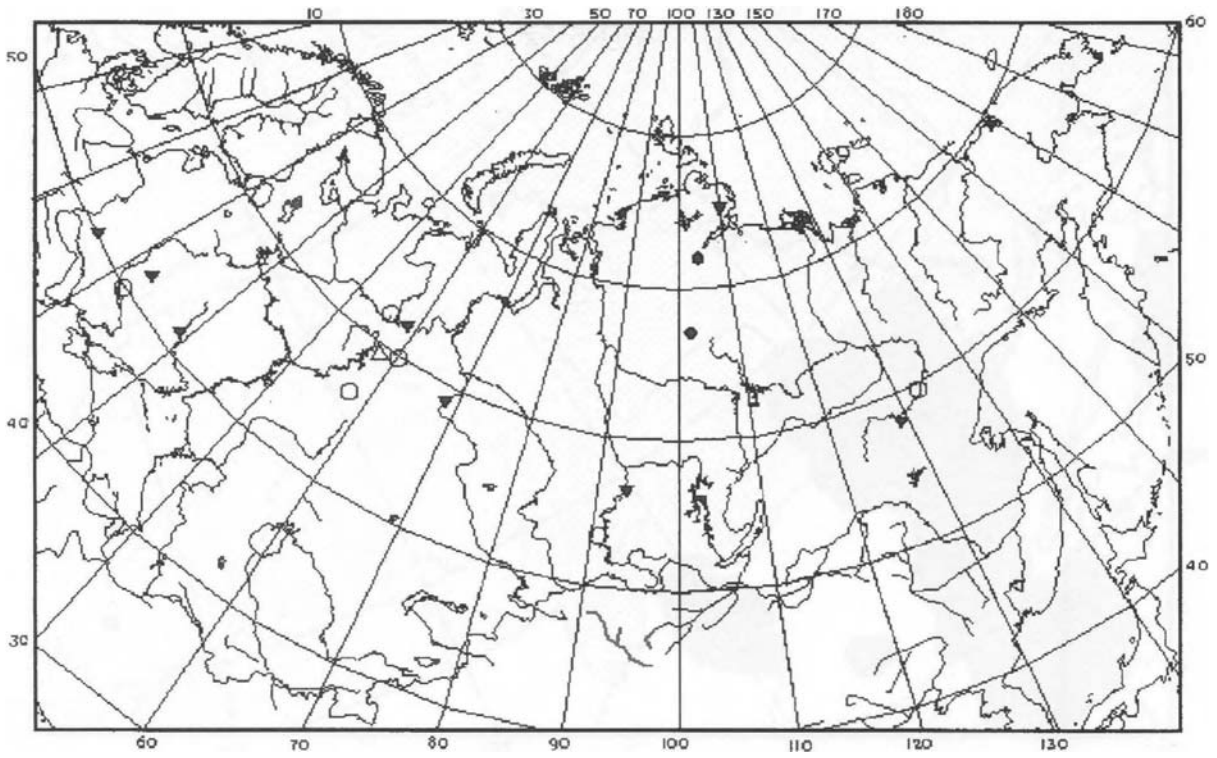


FIGURE 33. Localities of musk ox (10,000-100,000 yr B.P.).

CARNIVORA: *Maries (Maries) martes*

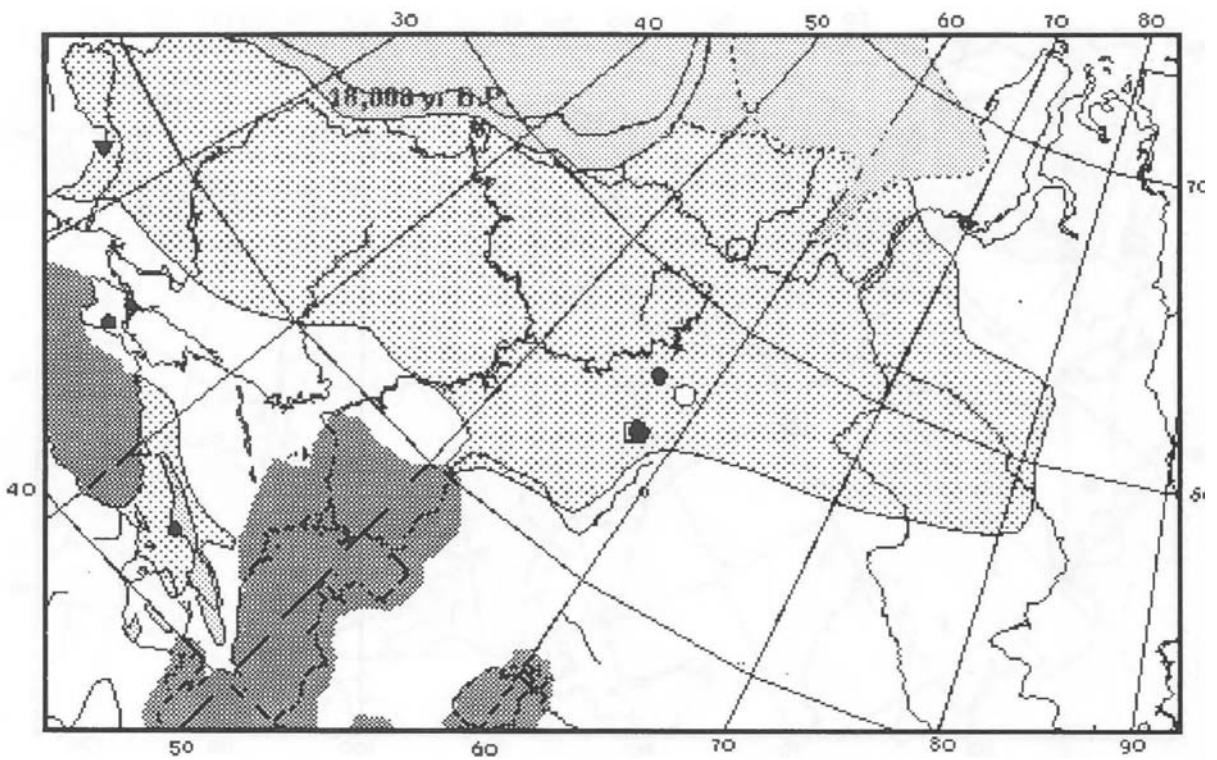


FIGURE 34. Localities of common (pine) marten (10,000-130,000 yr B.P.).

CARNIVORA: *Maries (Maries) zibellina*

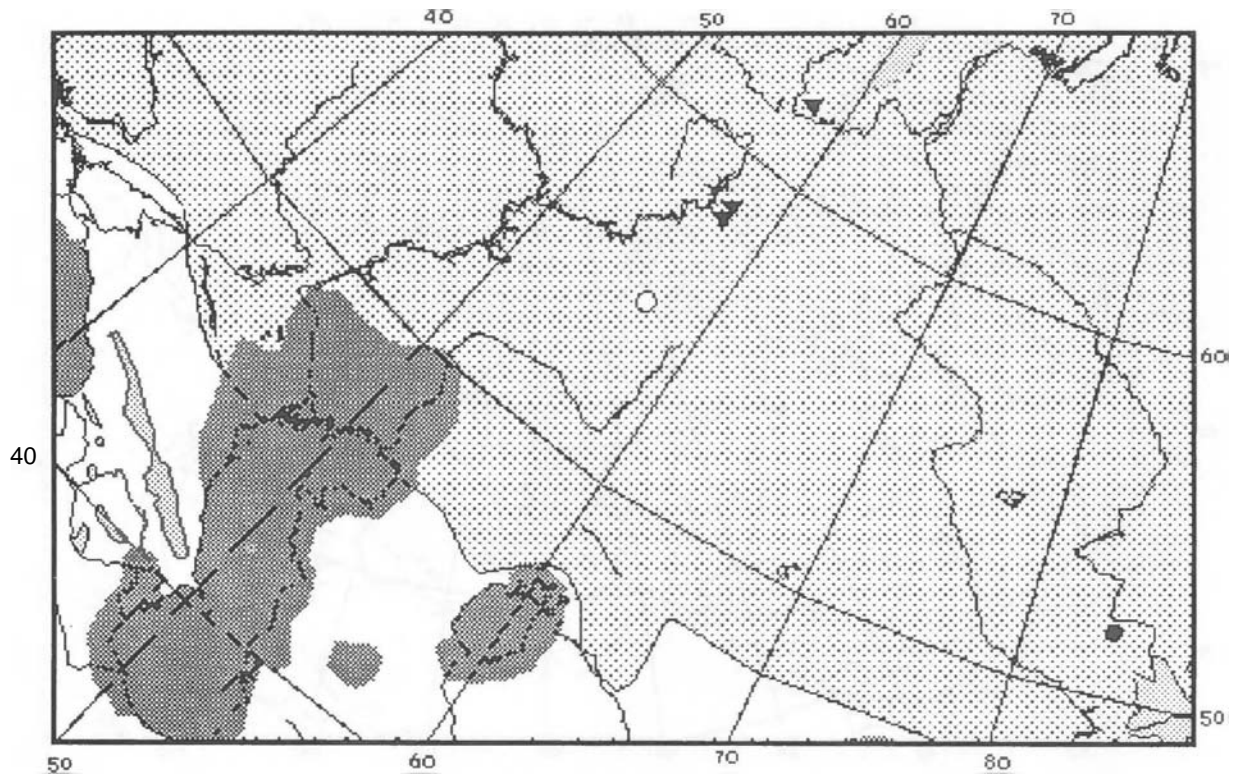


FIGURE 35. Localities of Russian sable (10,000-100,000 yr B.P.).

CARNIVORA: *Gulo gulo*

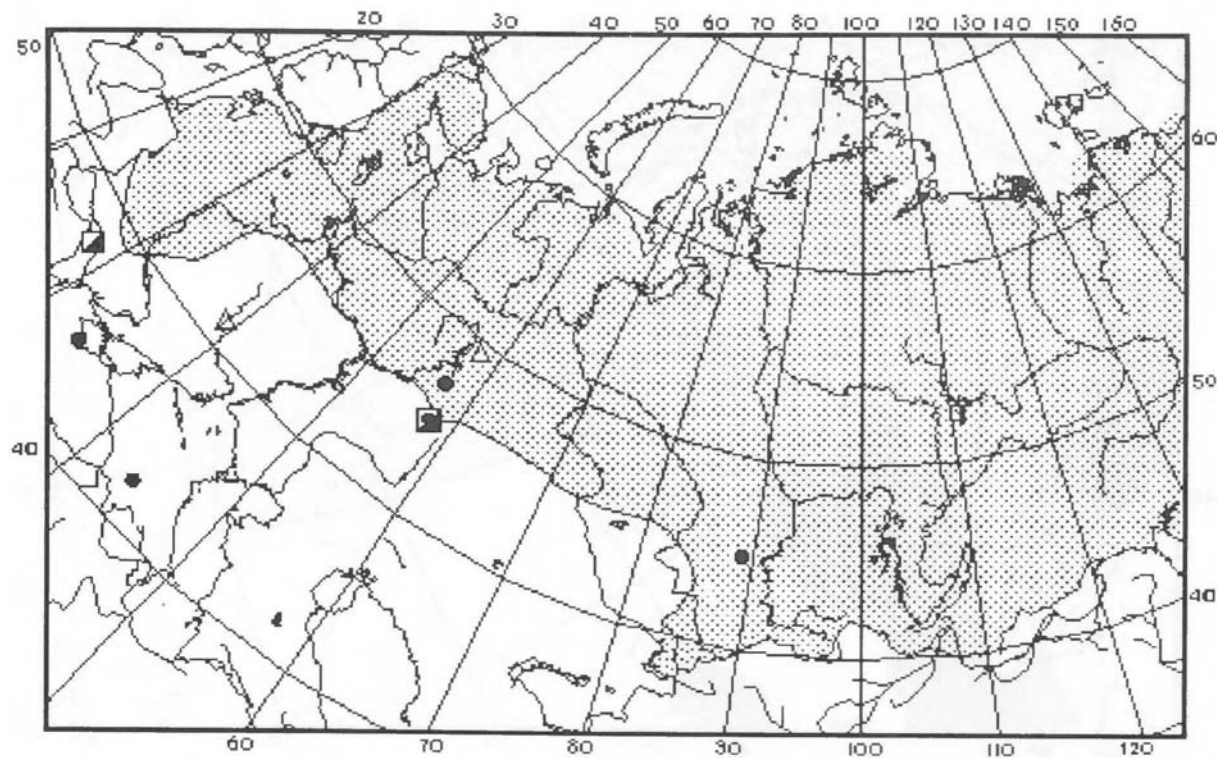


FIGURE 36. Localities of glutton (wolverine) (24,000-130,000 yr B.P.).

CARNIVORA: *Gulo gulo*

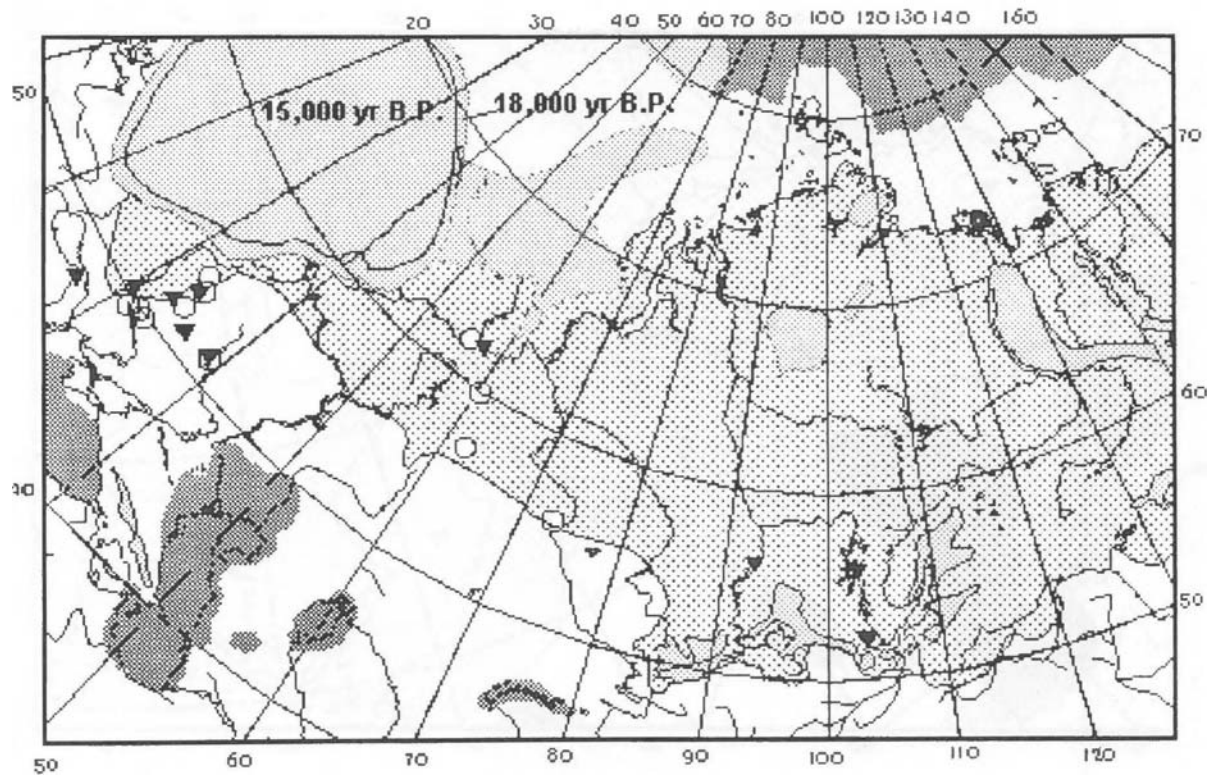


FIGURE 37. Localities of glutton (wolverine) (10,000-24,000 yr B.P.).

CARNIVORA: *Lynx (Lynx) lynx*

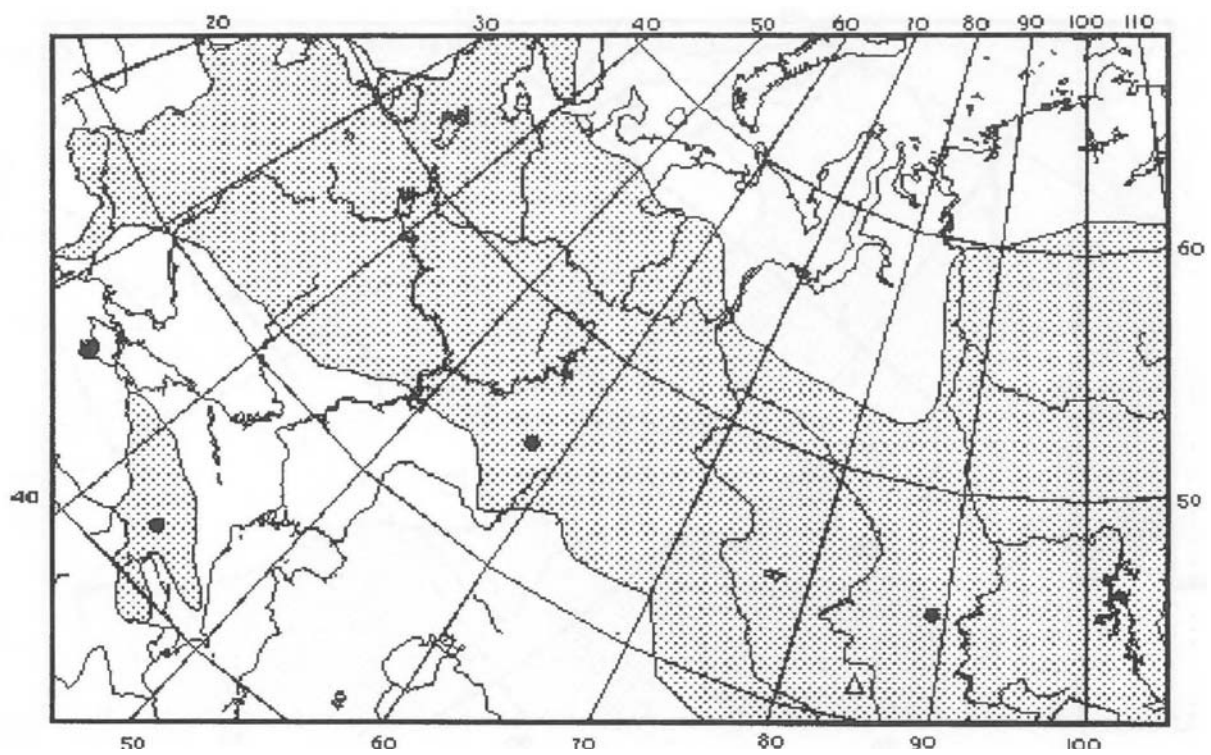


FIGURE 38. Localities of lynx (24,000-100,000 yr B.P.).

CARNIVORA: *Lynx (Lynx) lynx*

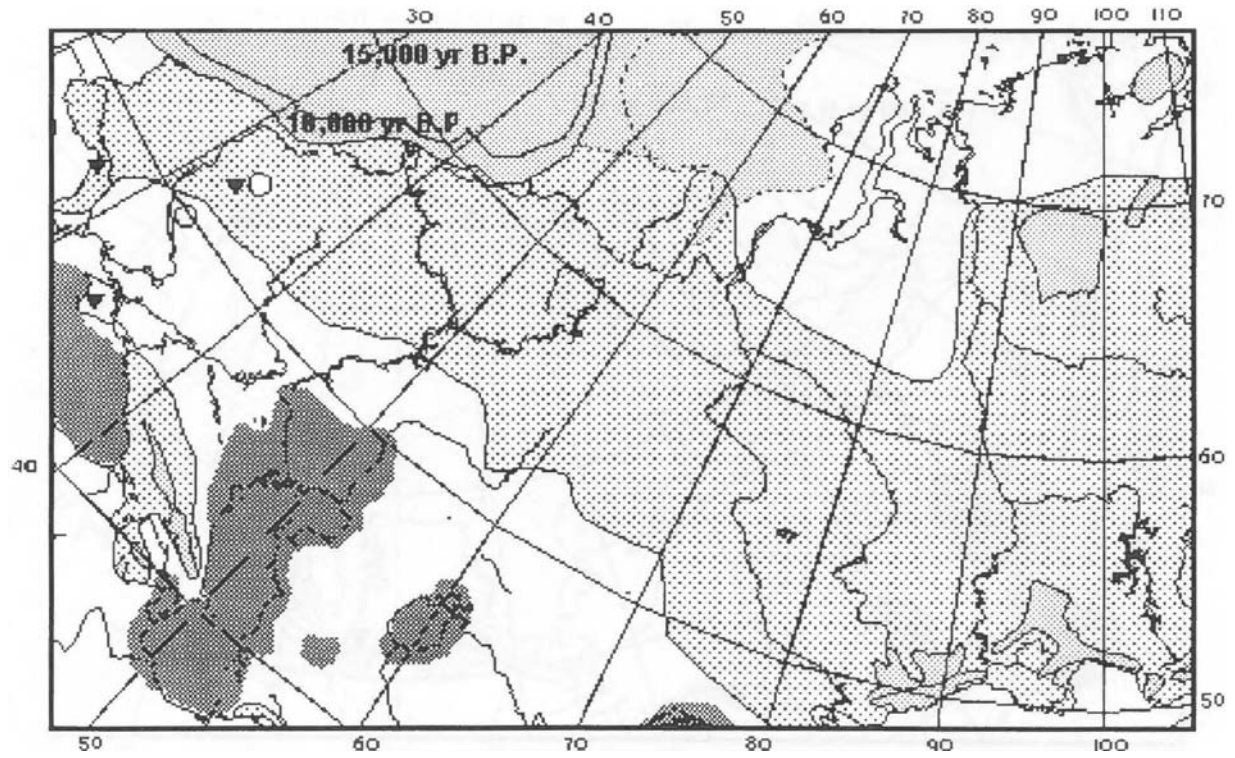


FIGURE 39. Localities of lynx (10,000-24,000 yr B.P.).

ARTIODACTYLA: *Sus scrota*

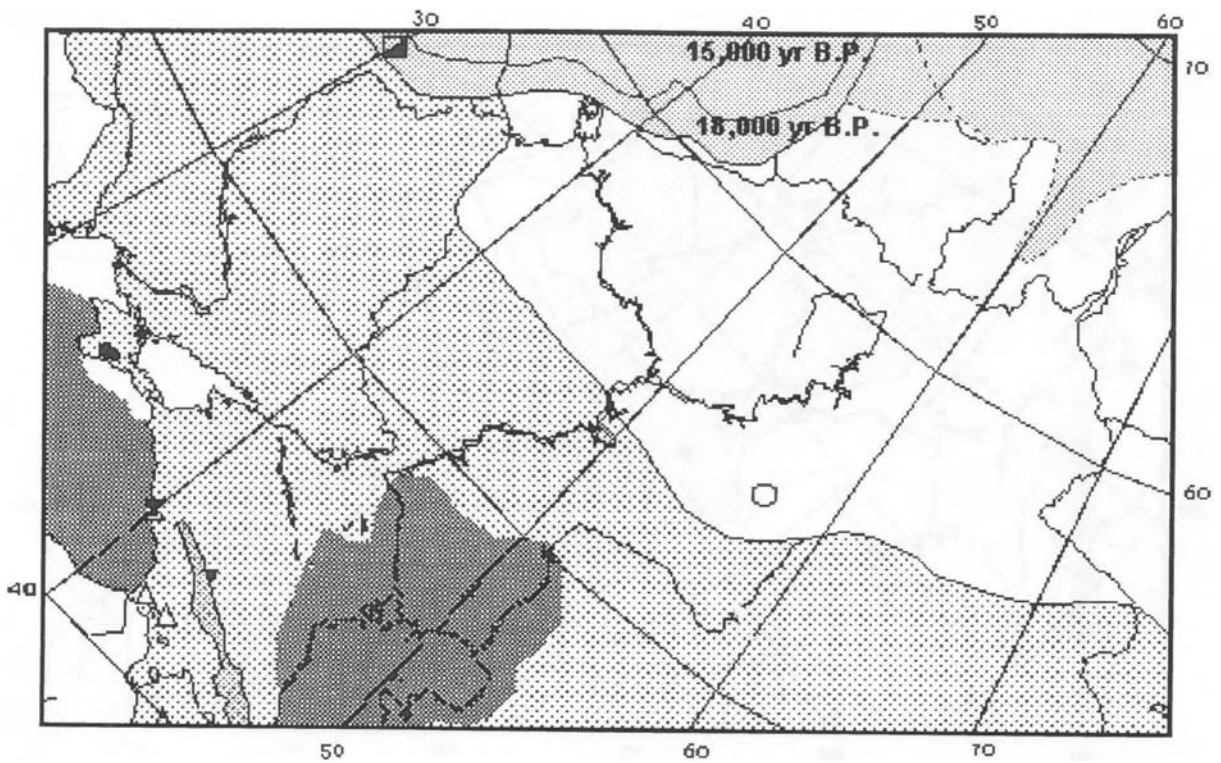


FIGURE 40. Localities of wild boar (pig) (10,000-130,000 yr B.P.).

PERISSODACTYLA: Equus (Hemionus) hemionus

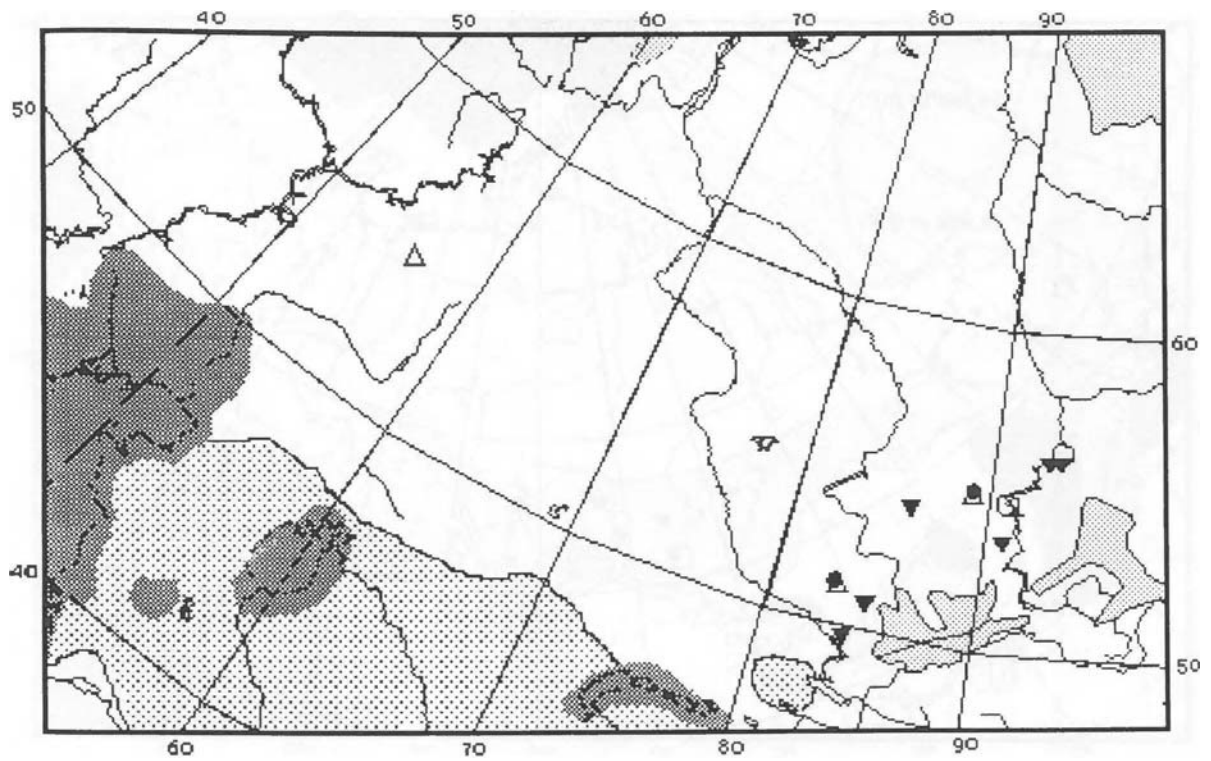


FIGURE 41. Localities of onager (Asiatic wild ass) (10,000-130,000 yr B.P.).

ARTIODACTYLA: Census (Census) elaphus

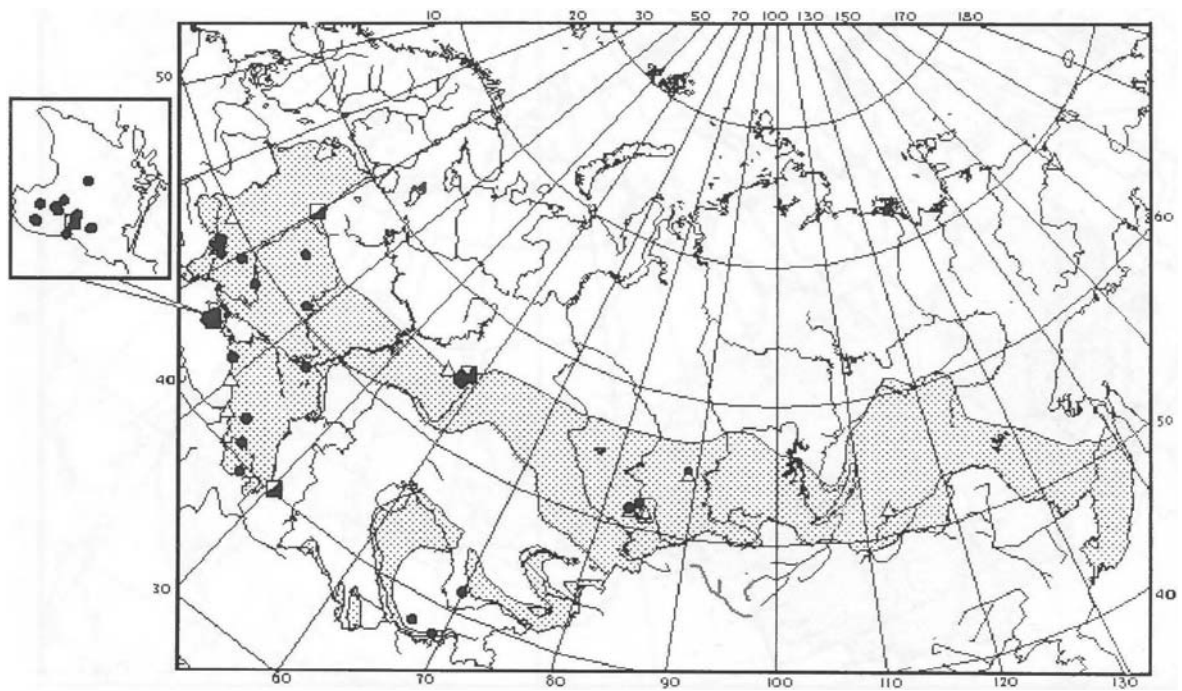


FIGURE 42. Localities of red deer (24,000-130,000 yr B.P.).

ARTIODACTYLA: *Cervus (Cervus) elaphus*

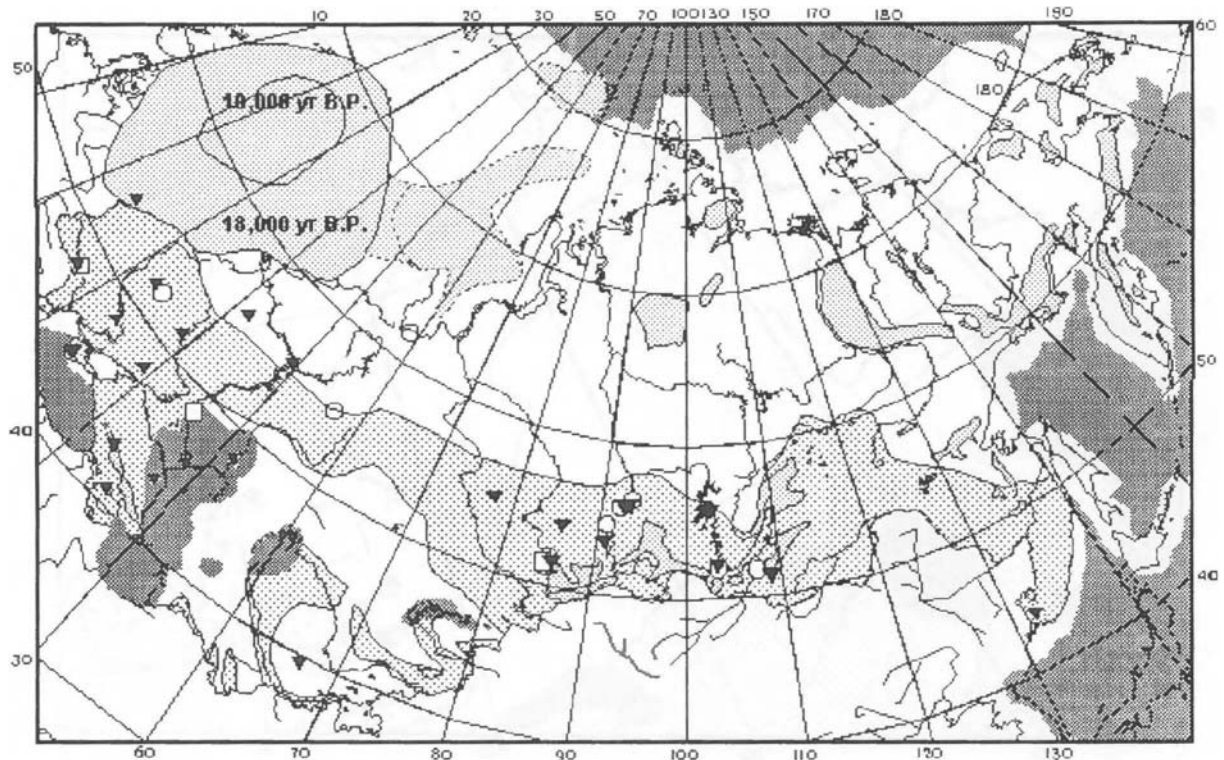


FIGURE 43. Localities of red deer (<math><24,000</math> yr B.P.).

ARTIODACTYLA: *Capreolus capreolus*

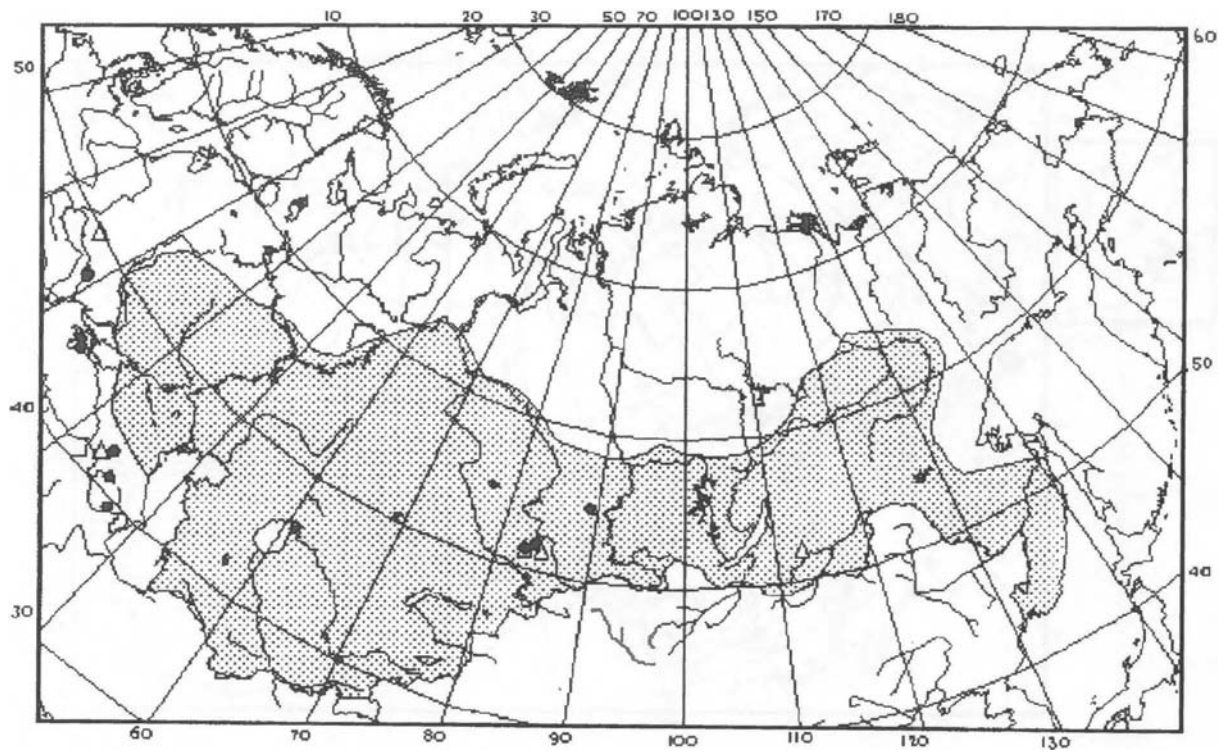


FIGURE 44. Localities of roe deer (24,000-100,000 yr B.P.).

ARTIODACTYLA: *Capreolus capreolus*

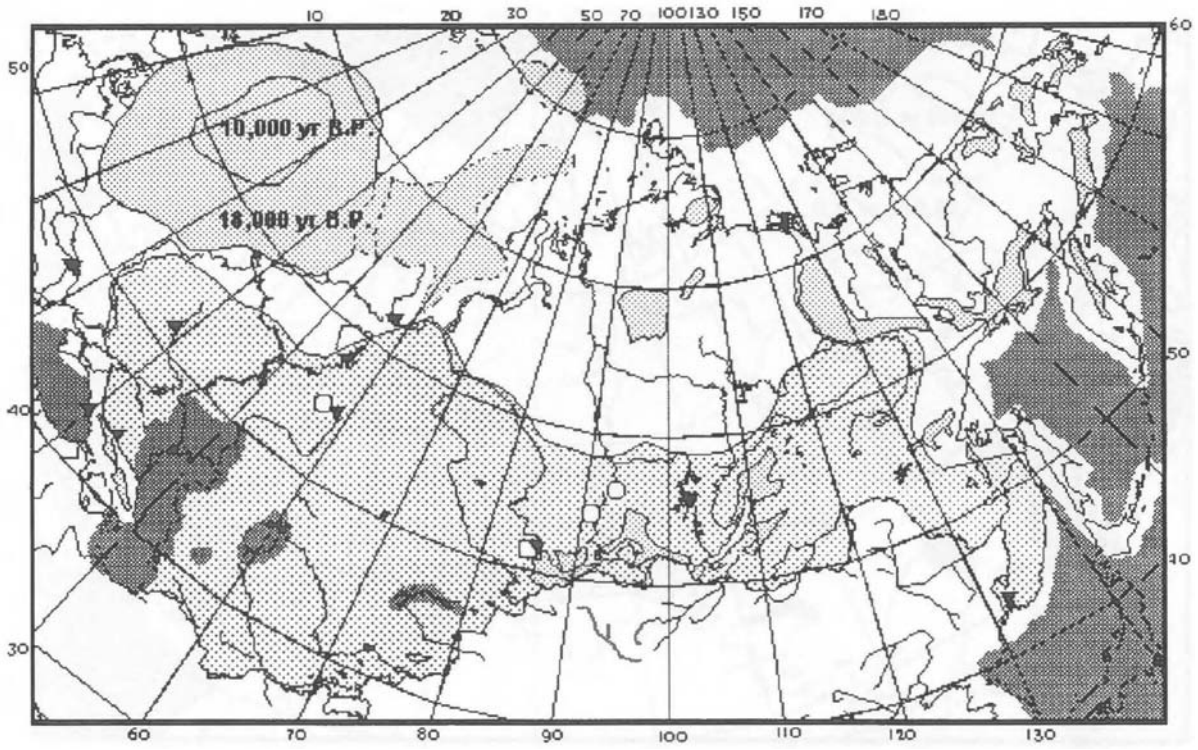


FIGURE 45. Localities of roe deer (<24,000 yr B.P.).

ARTIODACTYLA: *Alces alces*

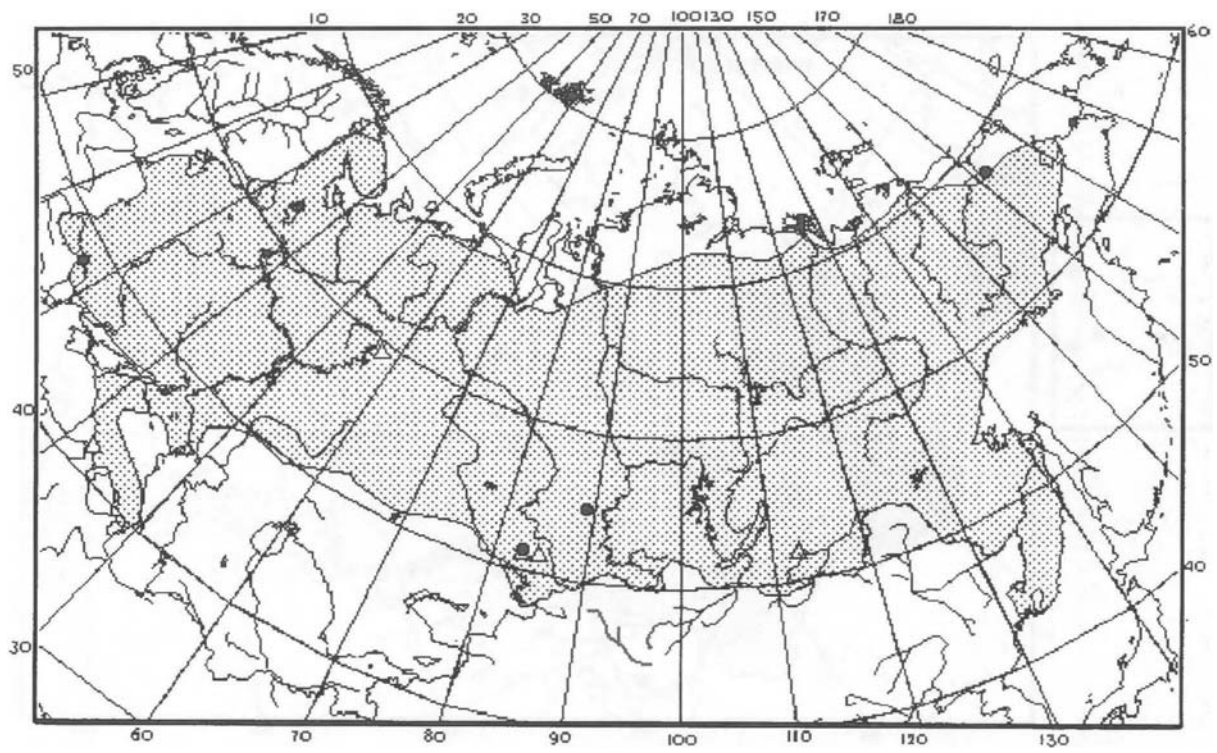


FIGURE 46. Localities of elk (24,000-100,000 yr B.P.).

ARTIODACTYLA: *Alces alces*

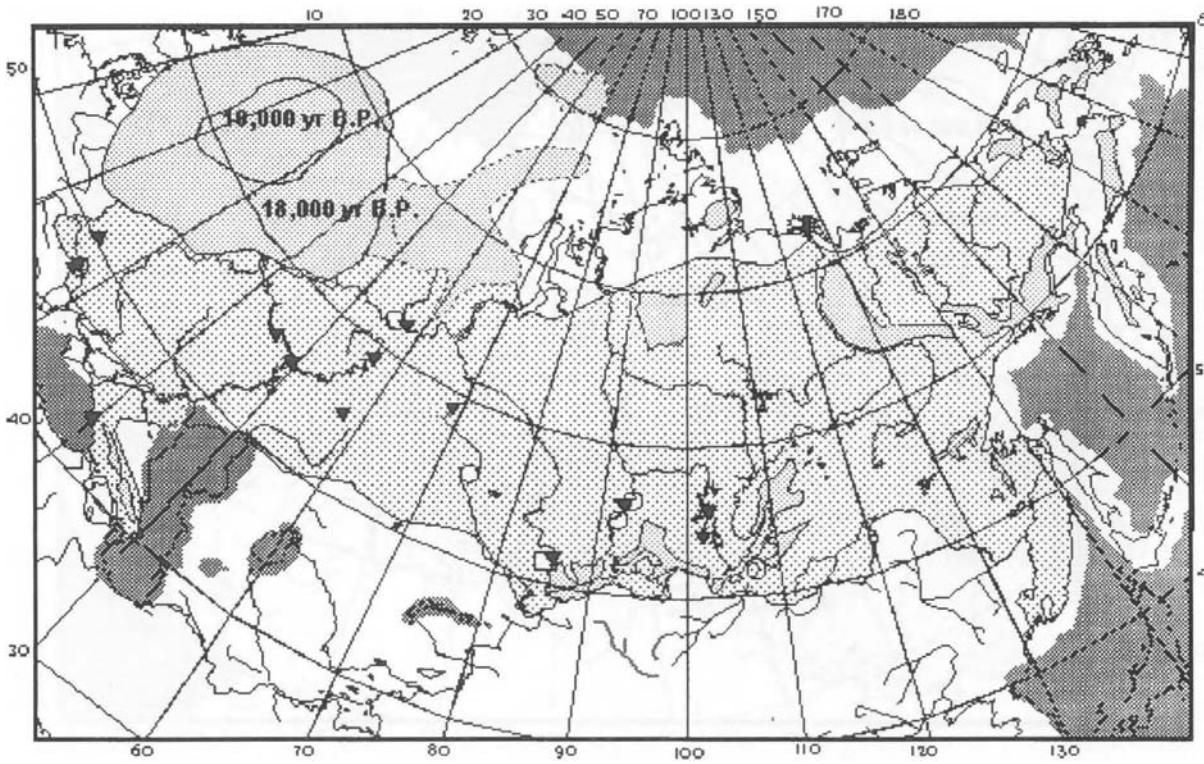


FIGURE 47. Localities of elk (<math><24,000</math> yr B.P.).

CARNIVORA: *Vulpes corsac*

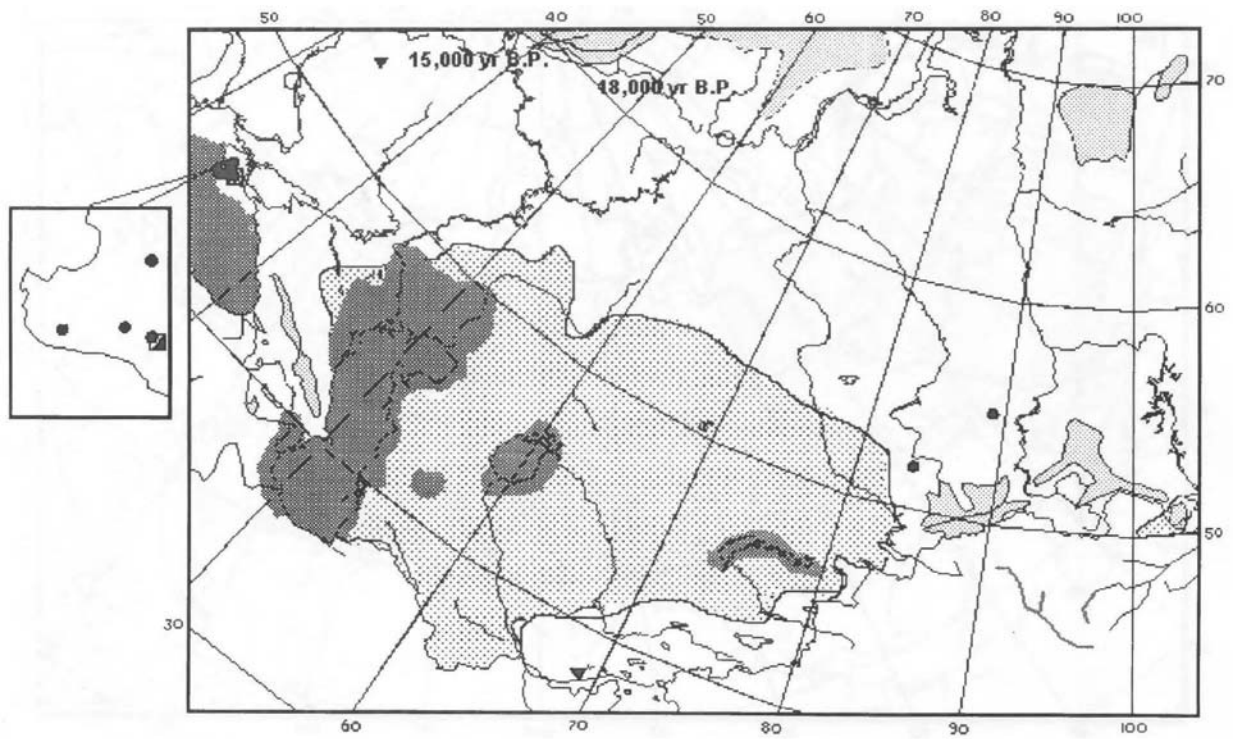


FIGURE 48. Localities of corsac fox (10,000-130,000 yr B.P.).

ARTIODACTYLA: *Saiga tatarica*

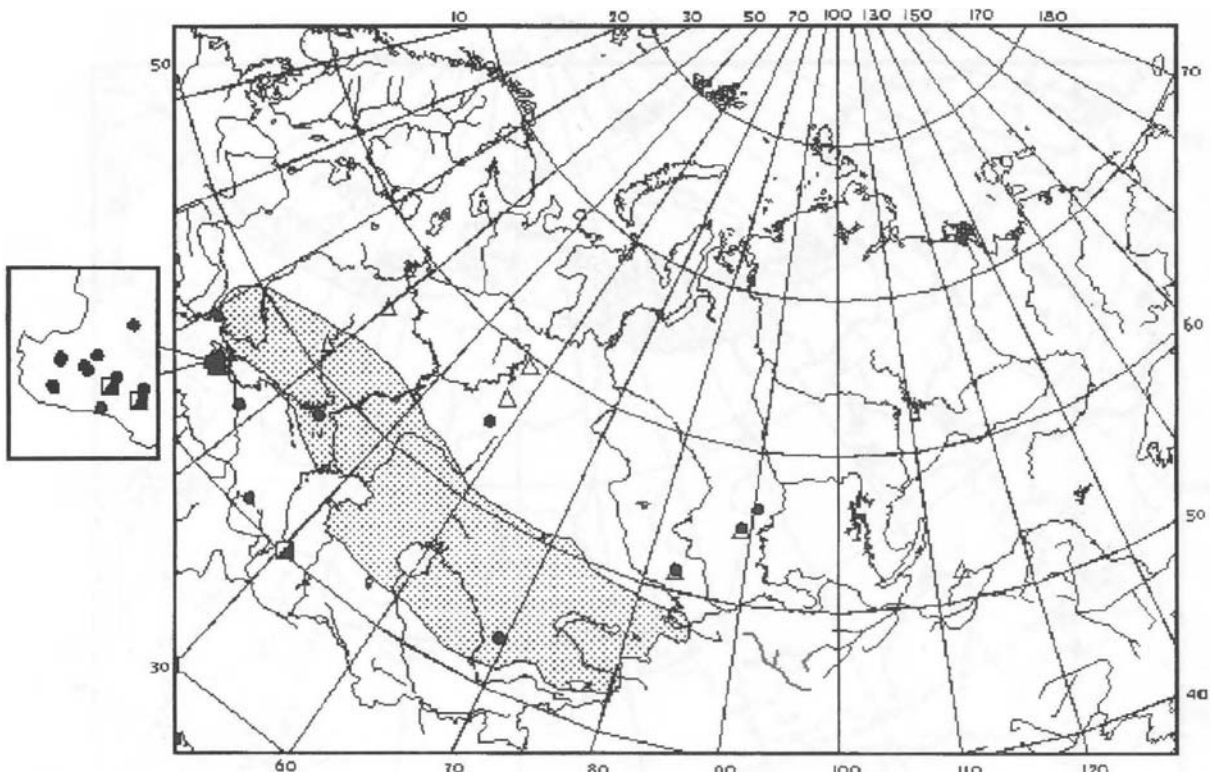


FIGURE 49. Localities of saiga (24,000-130,000 yr B.P.).

ARTIODACTYLA: *Saiga tatarica*

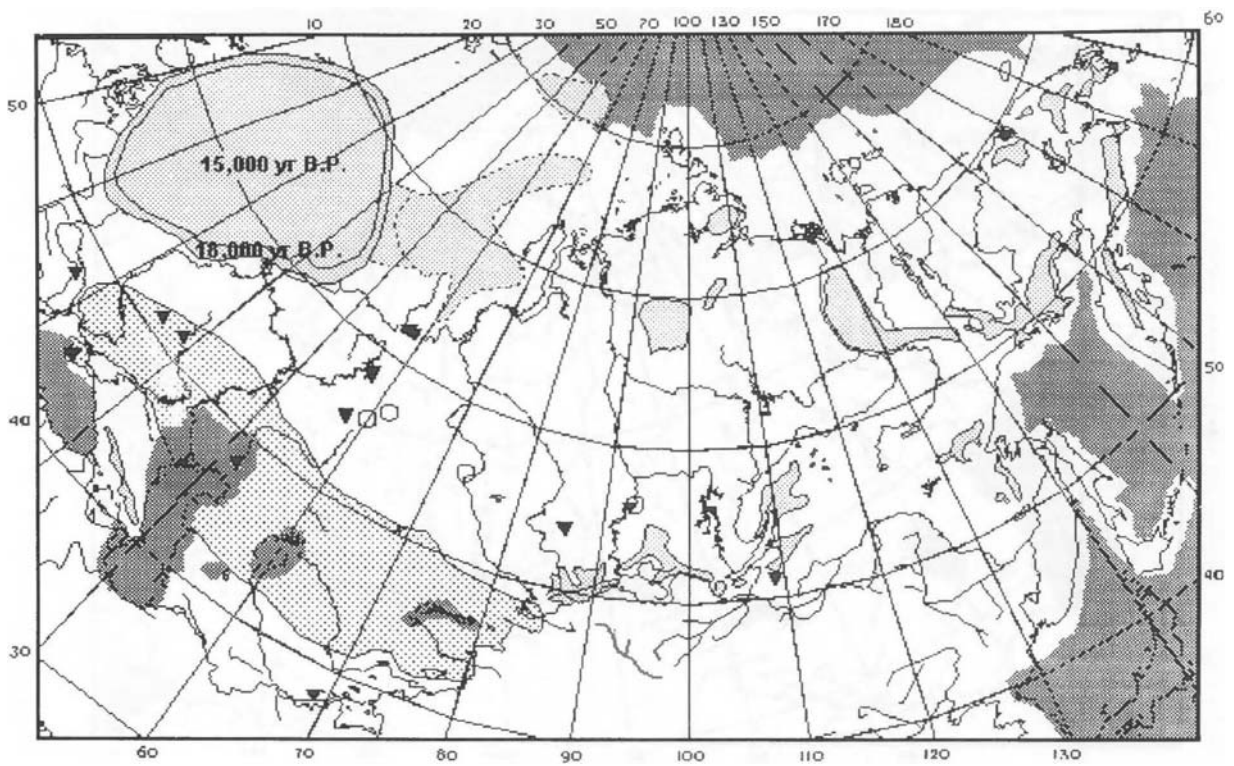


FIGURE 50. Localities of saiga (<24,000 yr B.P.).

MAPS OF SMALL MAMMAL LOCALITIES

RODENTIA: *Discrostonyx*

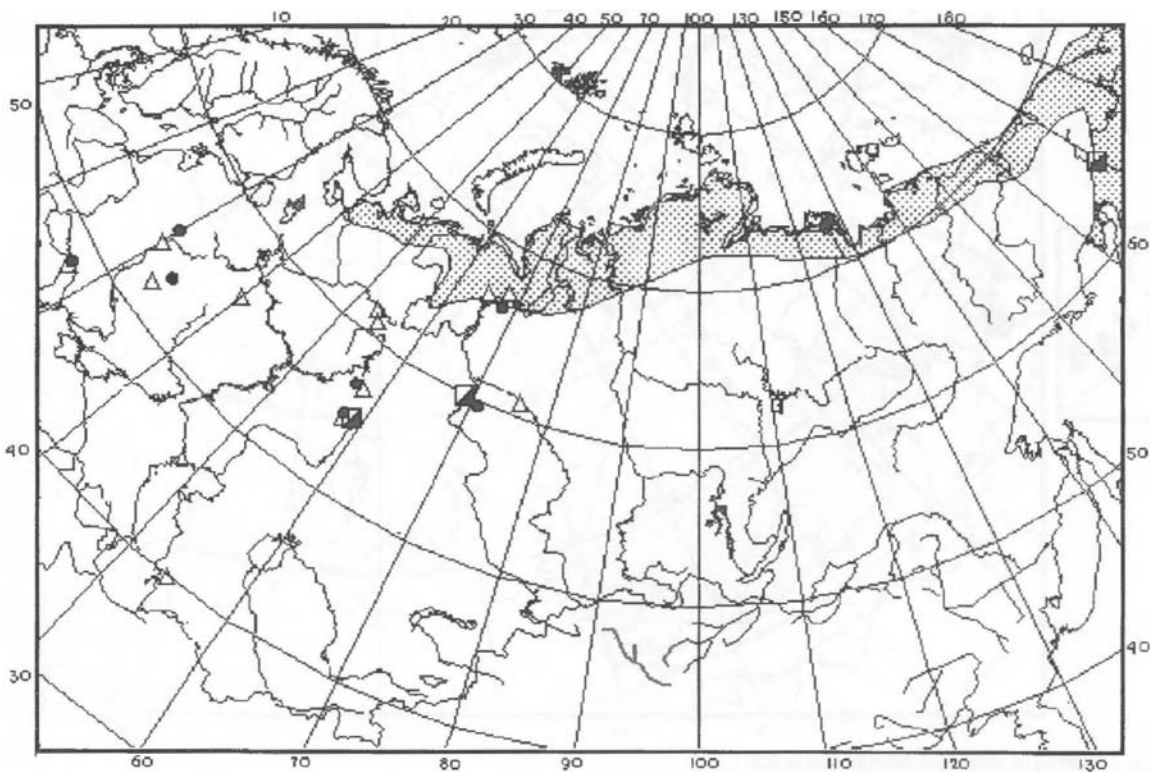


FIGURE 51. Localities of pied lemming (24,000-130,000 yr B.P.).

RODENTIA: *Dicrostonyx*

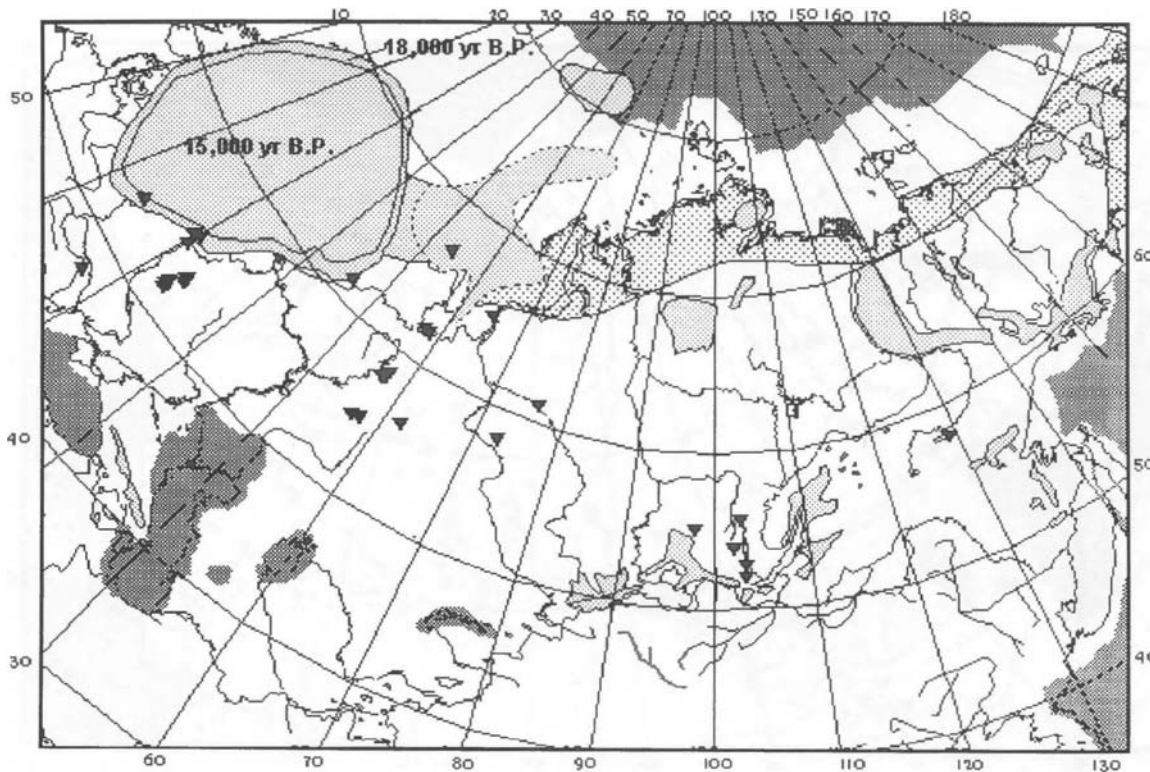


FIGURE 52. Localities of pied lemming (15,000-24,000 yr B.P.).

RODENTIA: *Dicrostonyx*

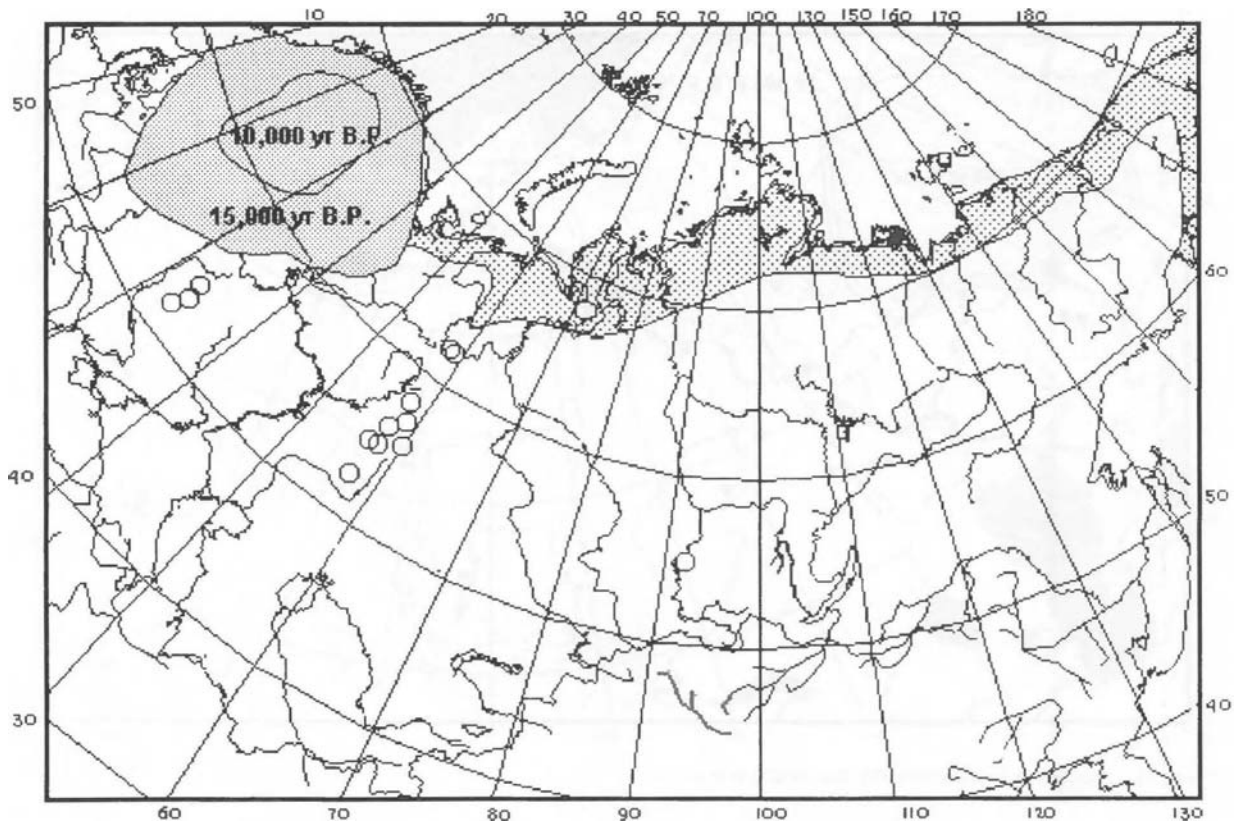


FIGURE 53. Localities of pied lemming (10,000-15,000 yr B.P.).

RODENTIA: *Lemmus*

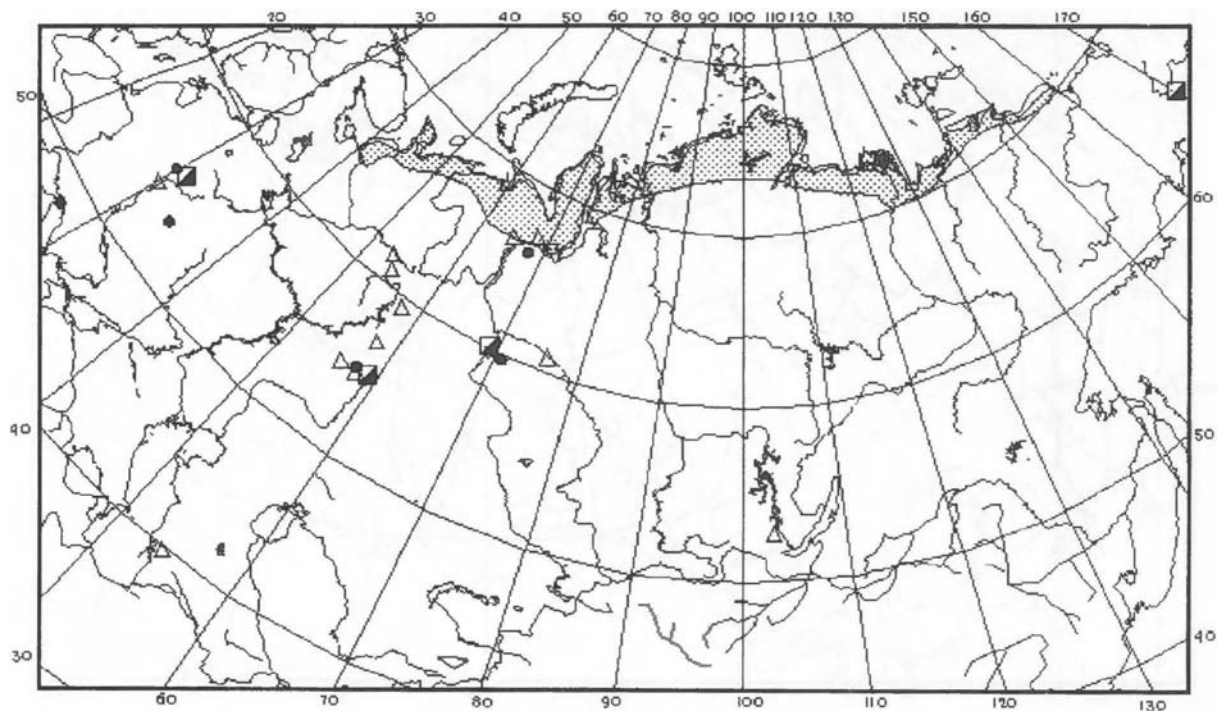


FIGURE 54. Localities of true lemming (24,000-130,000 yr B.P.).

RODENTIA: *Lemmus*

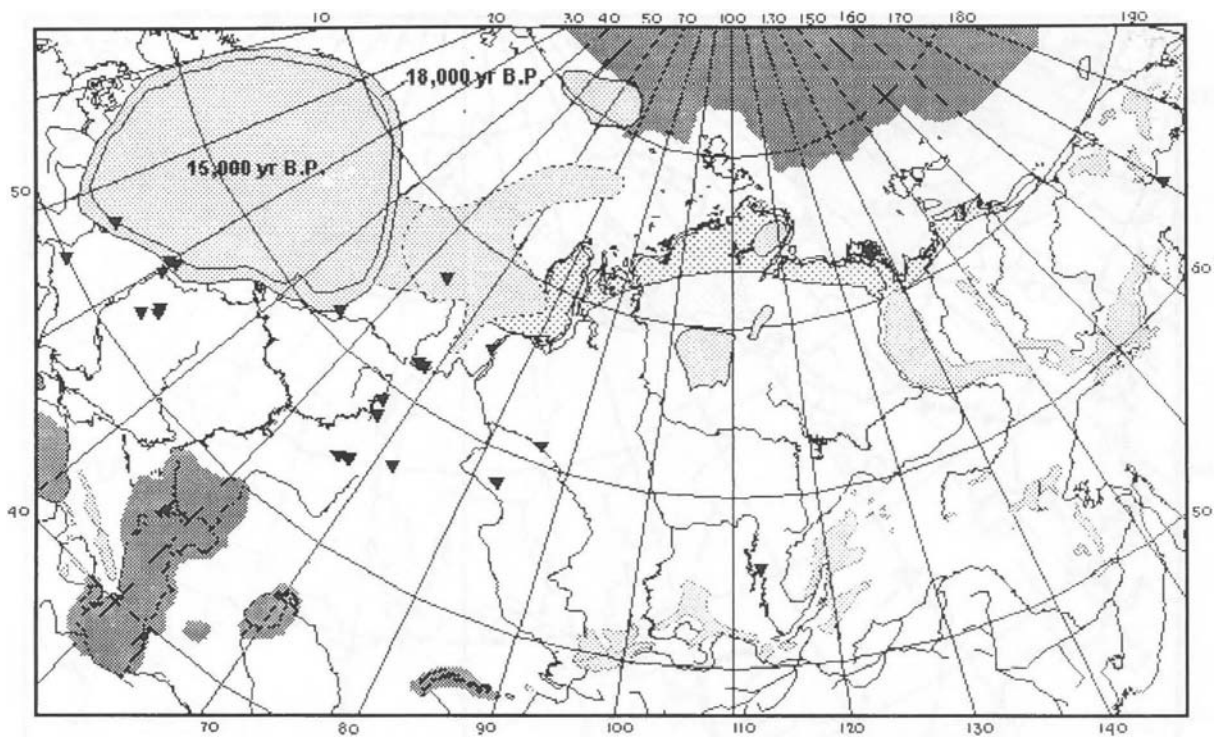


FIGURE 55. Localities of true lemming (15,000-24,000 yr B.P.).

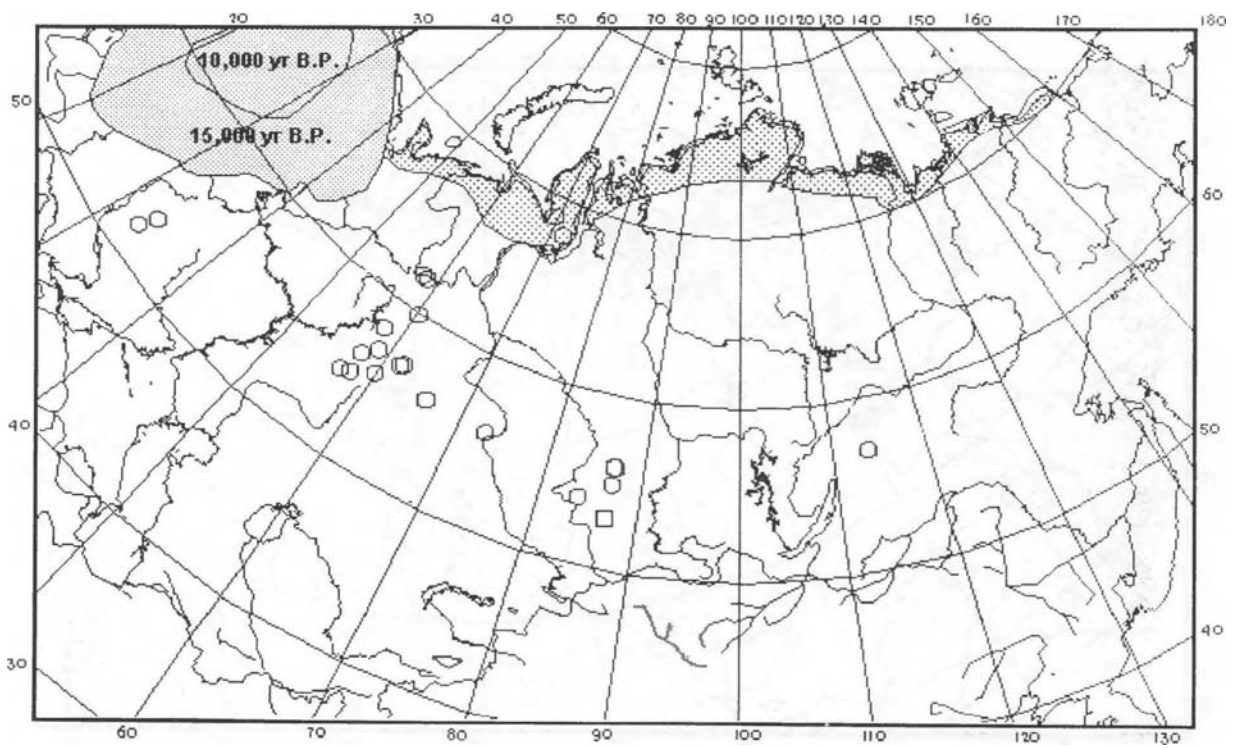


FIGURE 56. Localities of true lemming (<15,000 yr B.P.).

RODENTIA: *Marmota bobac*

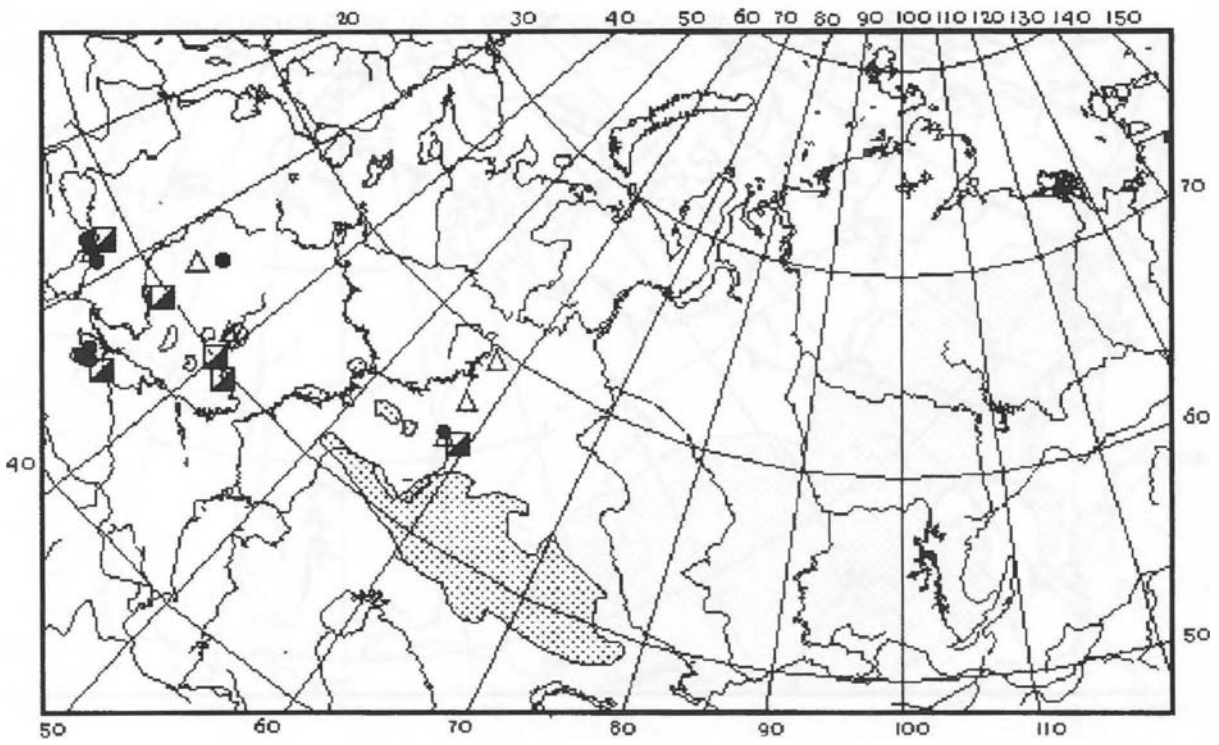


FIGURE 57. Localities of *marmota bobac* (24,000-130,000 yr B.P.).

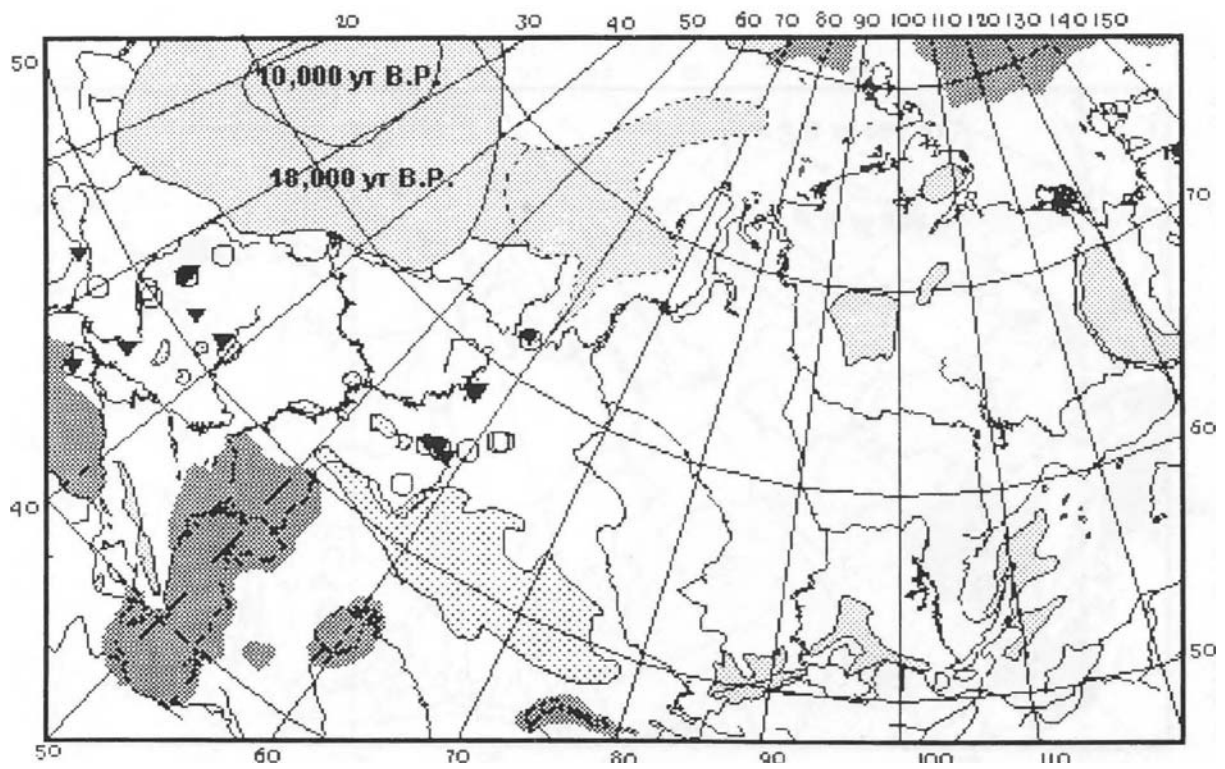


FIGURE 58. Localities of *marmota bobac* (10,000-24,000 yr B.P.).

RODENTA: *Allactaga major*

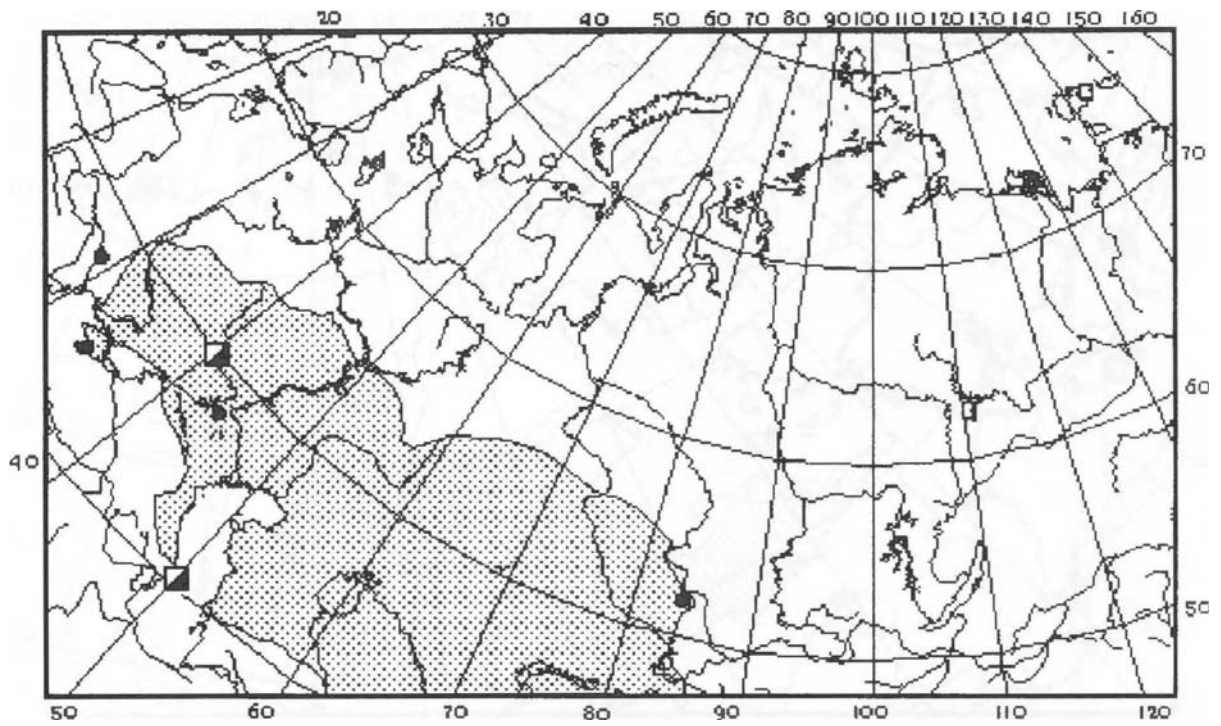


FIGURE 59. Localities of great jerboa (35,000-130,000 yr B.P.).

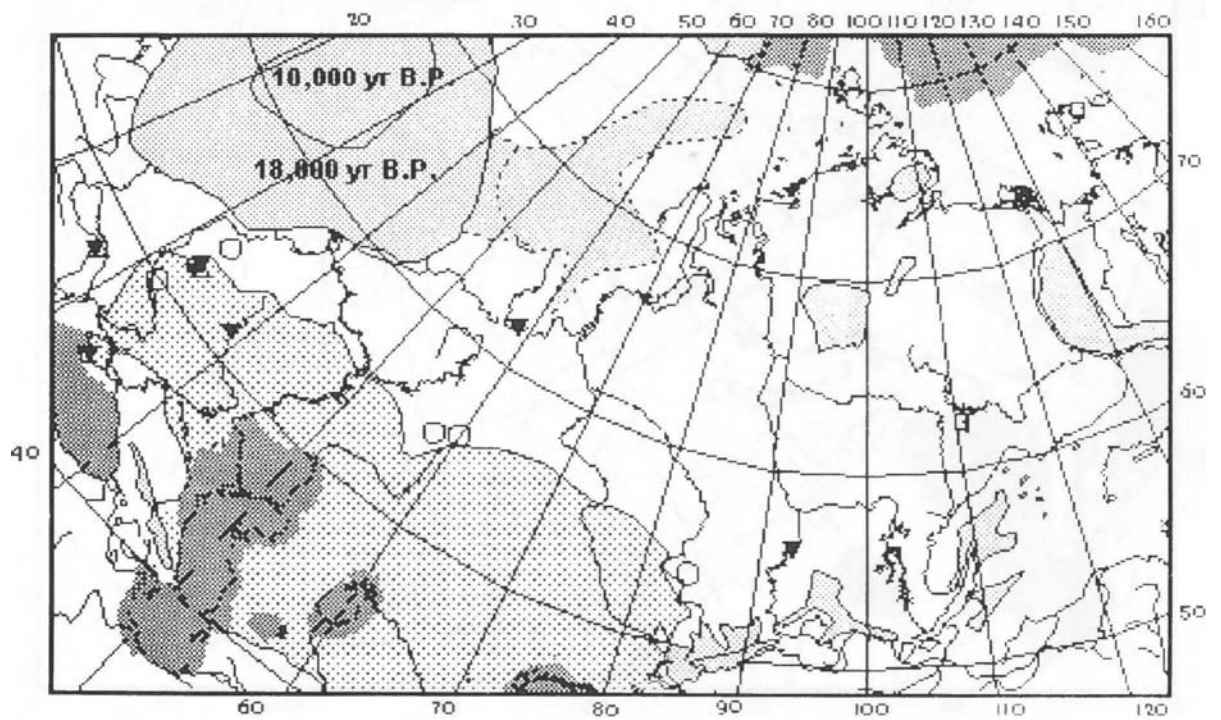


FIGURE 60. Localities of great jerboa (10,000-35,000 yr B.P.).

RODENTIA: *Spalax*

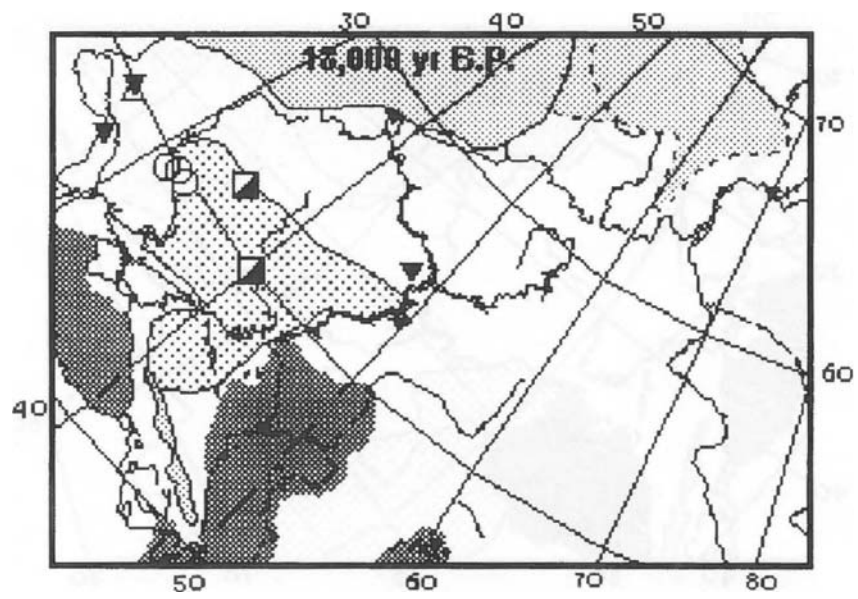


FIGURE 61. Localities of greater mole rat.

RODENTIA: *Myospalax*

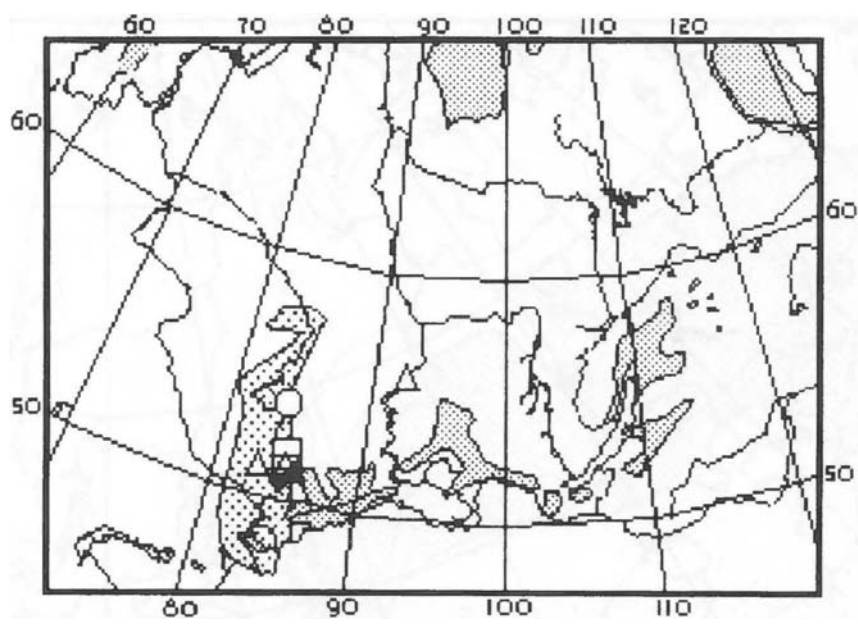


FIGURE 62. Localities of altai zokor.

RODENTIA: *Allocricetulus eversmanni*

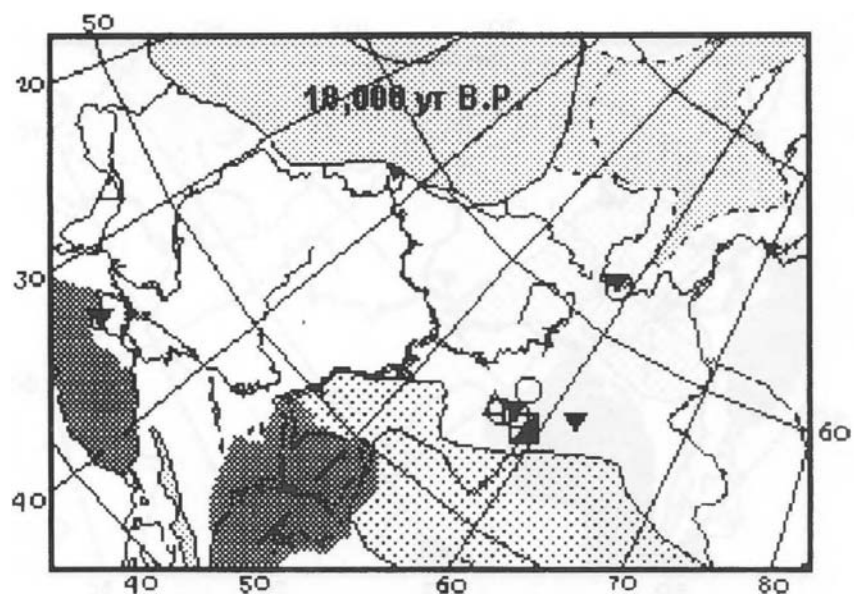


FIGURE 63. Localities of eversmann's hamster.

RODENTIA: *Cricetus cricetus*

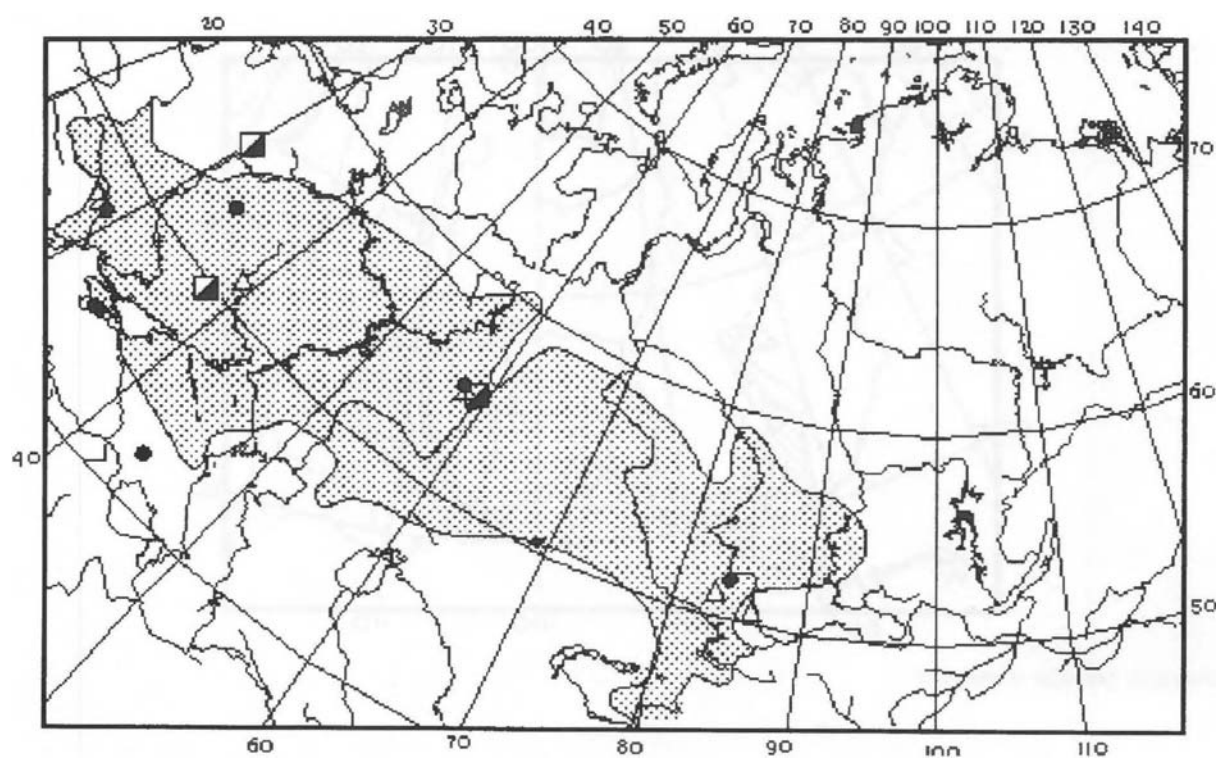


FIGURE 64. Localities of common hamster (24,000-130,000 yrB.P.).

RODENTIA: *Cricetus cricetus*

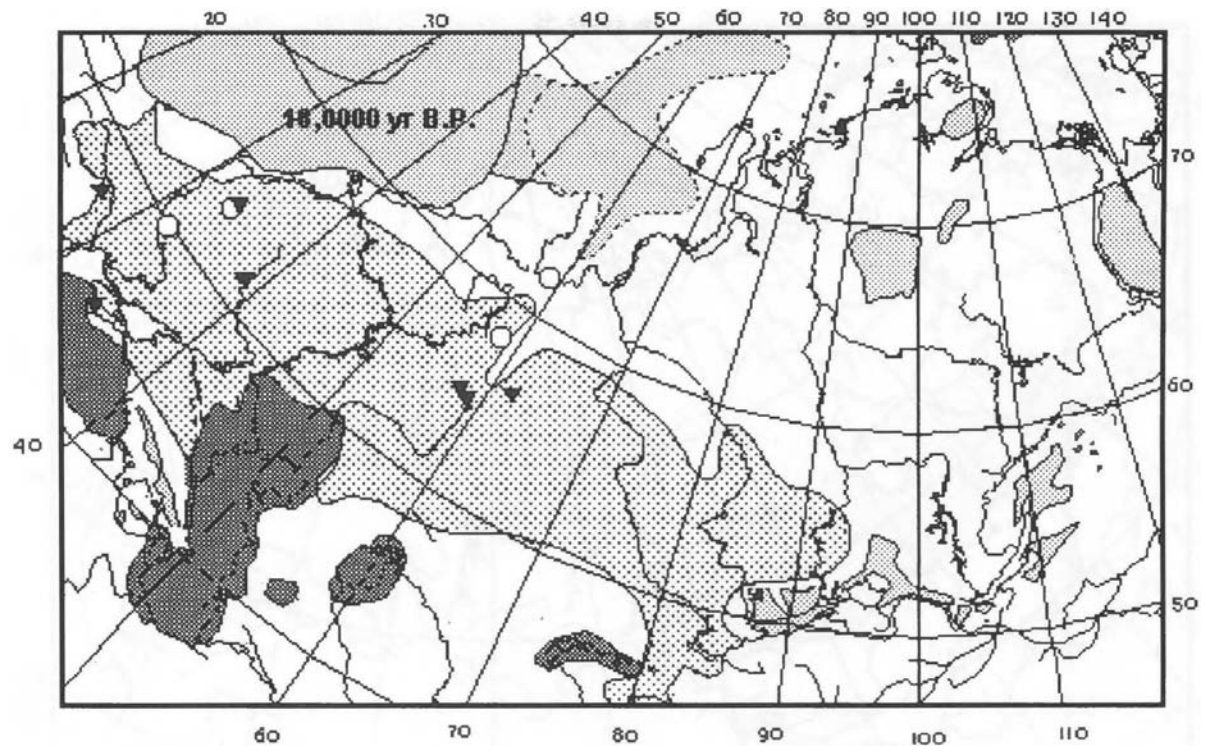


FIGURE 65. Localities of common hamster (10,000-24,000 yr B.P.).

RODENTIA: *Lagurus lagurus*

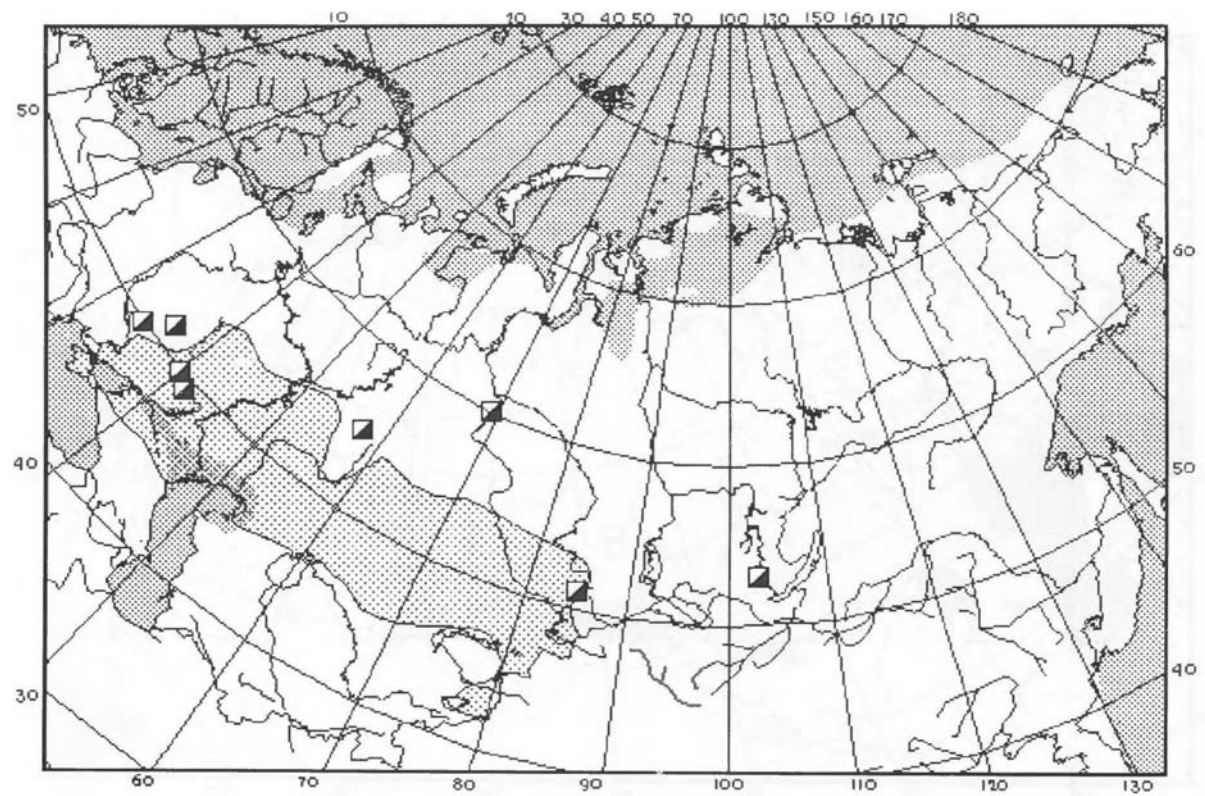


FIGURE 66. Localities of steppe lemming (100,000-130,000 yr B.P.).

RODENTIA: *Lagurus lagurus*

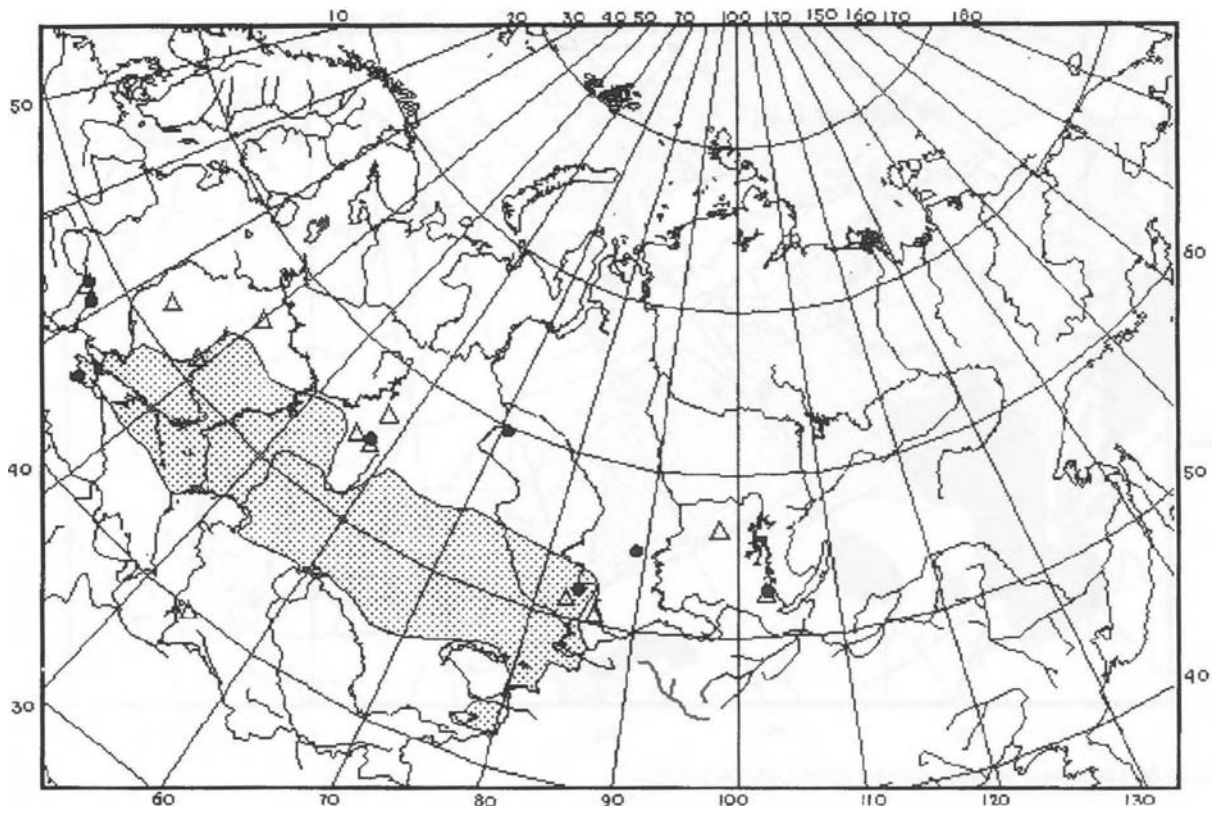


FIGURE 67. Localities of steppe lemming (24,000-100,000 yr B.P.).

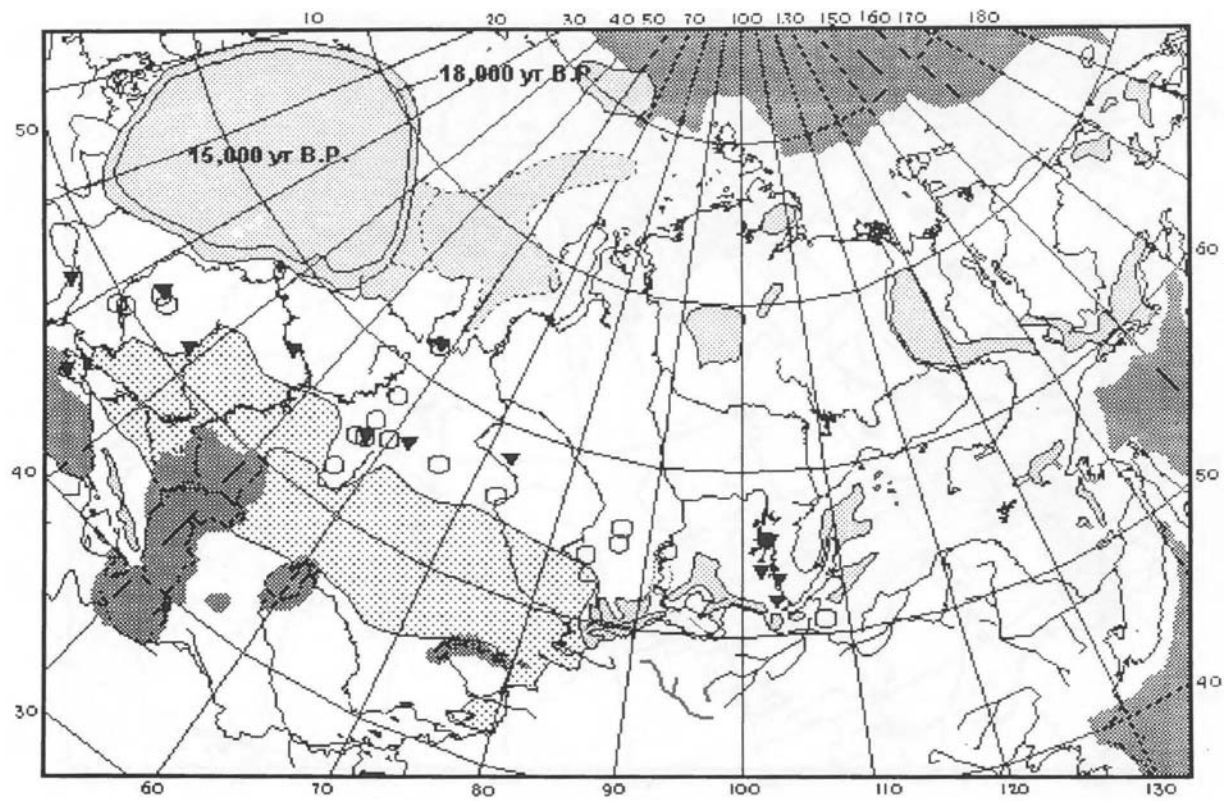


FIGURE 68. Localities of steppe lemming (10,000-24,000 yr B.P.).

RODENTIA: *Eolagurus luteus*

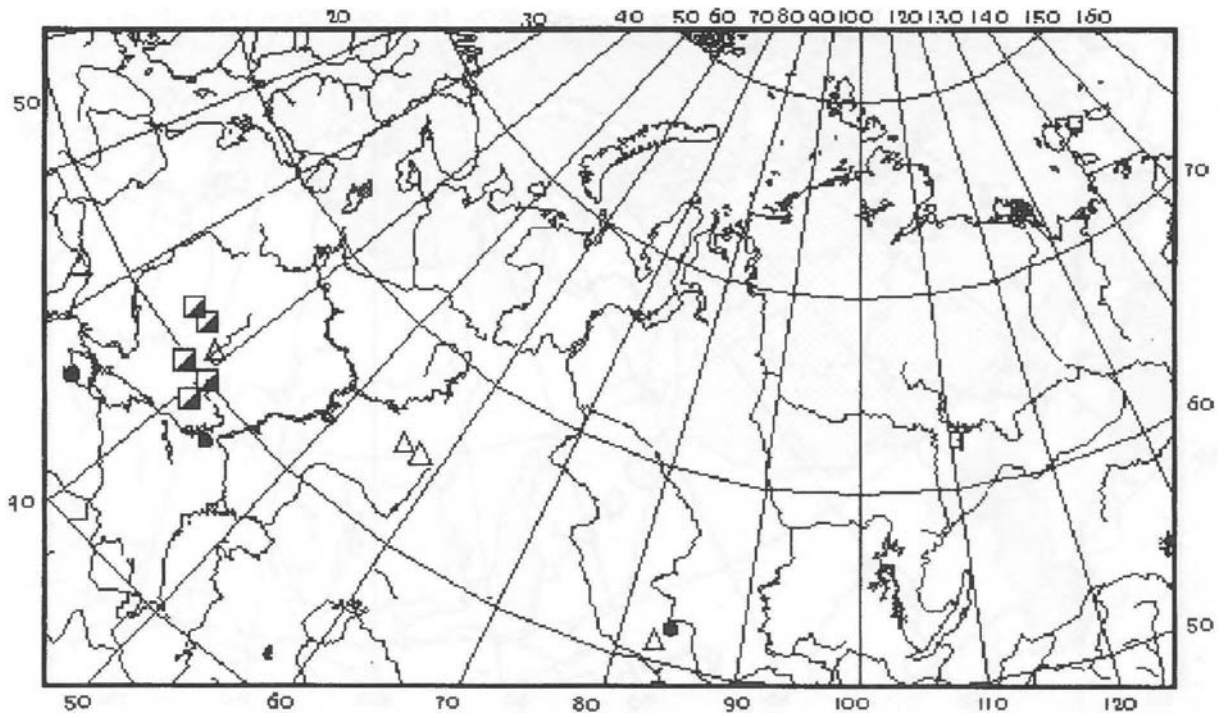


FIGURE 69. Localities of yellow steppe lemming (24,000-130,000 yr B.P.).

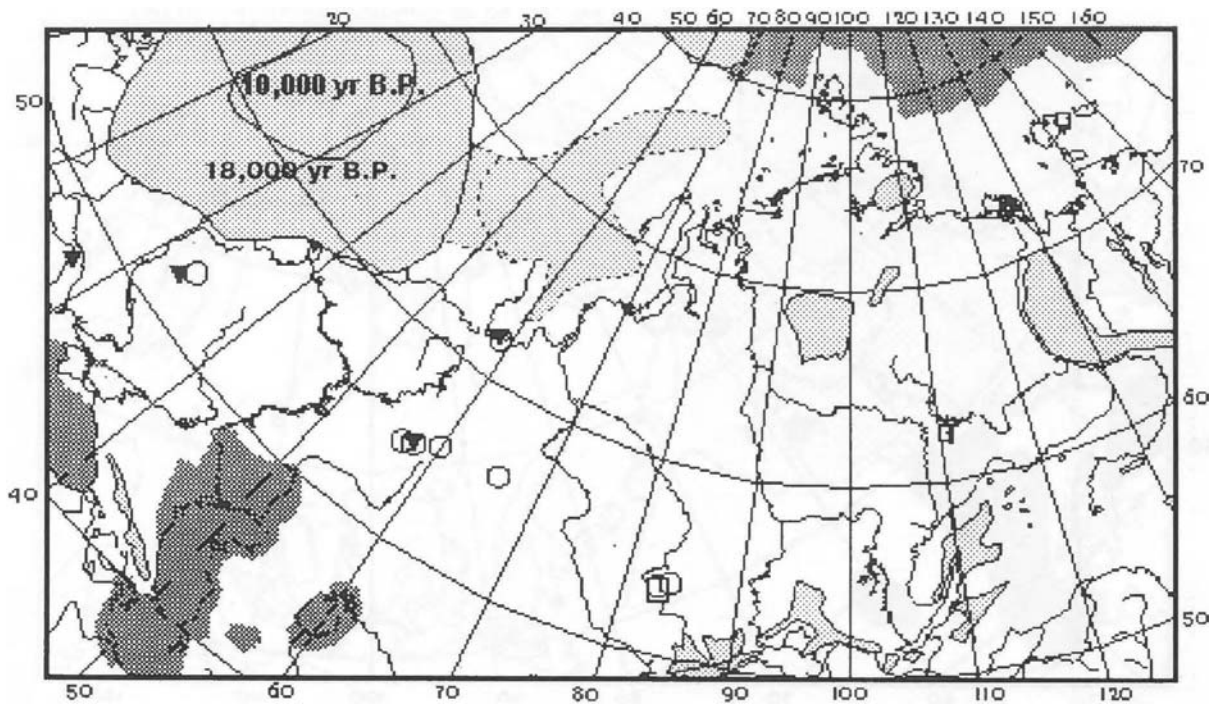


FIGURE 70. Localities of yellow steppe lemming (<24,000 yr B.P.).

RODENTIA: *Clethrionomys glareolus*

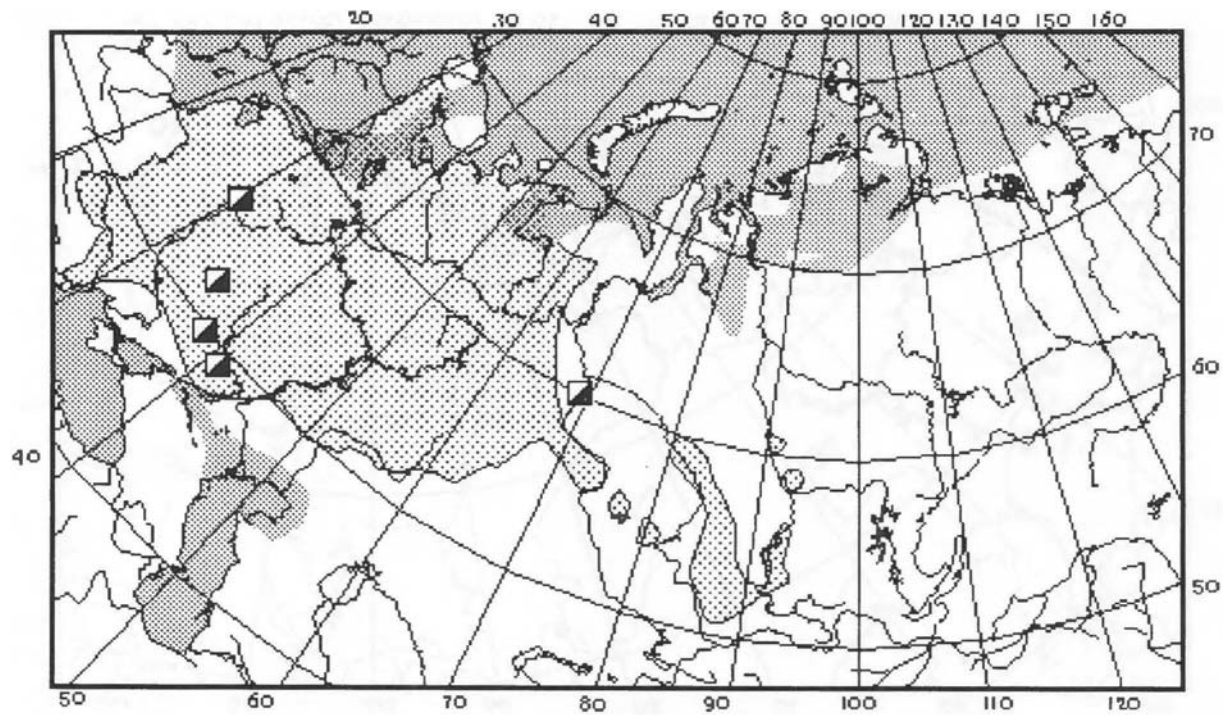


FIGURE 71. Localities of bank (common red-backed) vole (100,000-130,000 yr B.P.).

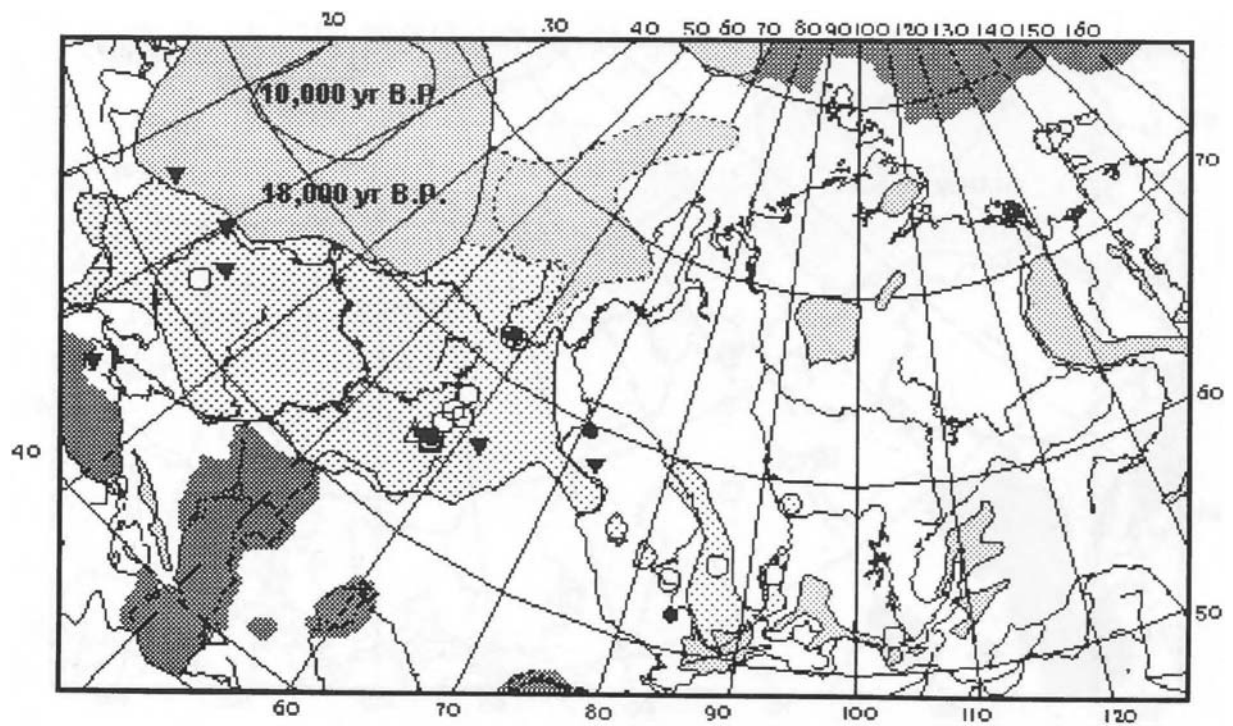


FIGURE 72. Localities of bank (common red-backed) vole (<100,000 yr B.P.).

RODENTIA: *Clethrionomys rutilus*

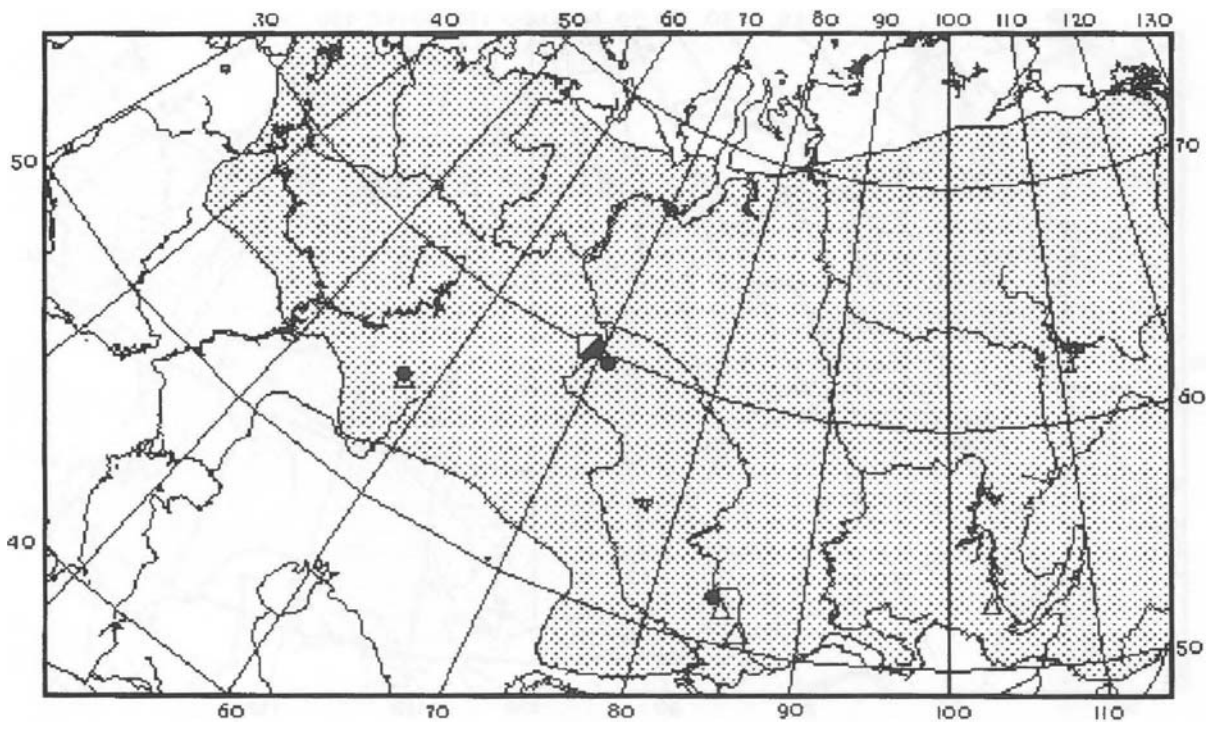


FIGURE 73. Localities of ruddy (northern red-backed) vole (24,000-130,000 yr B.P.).

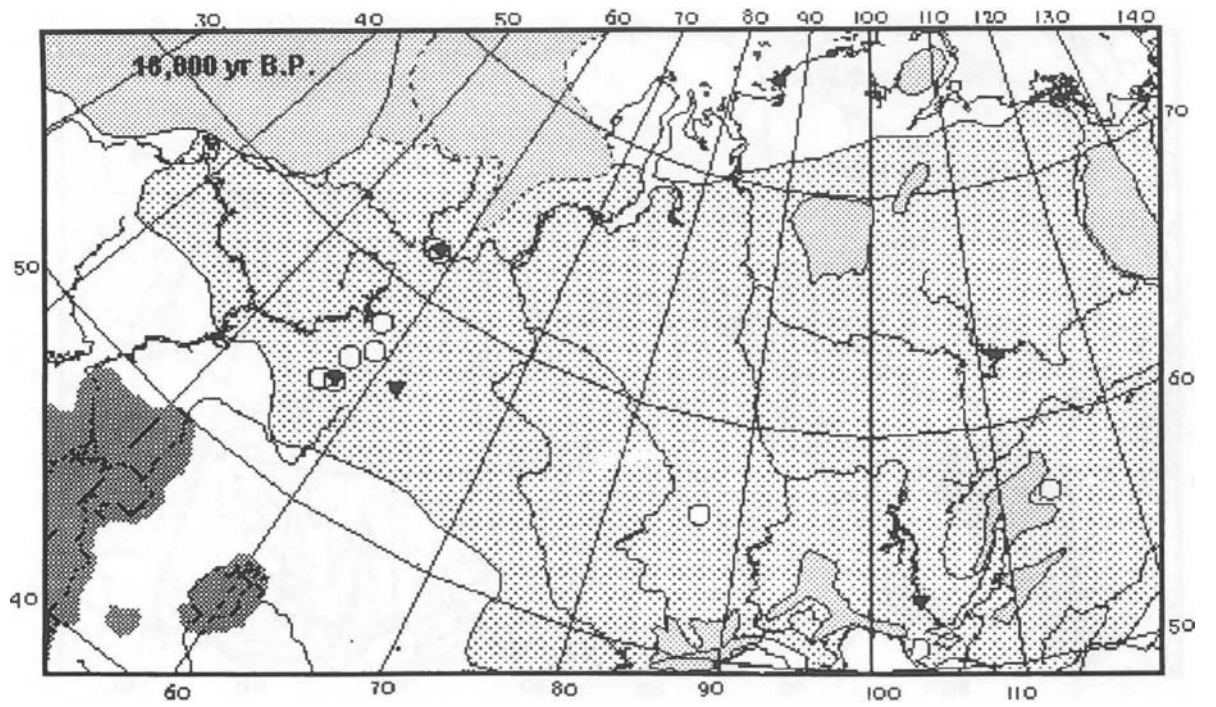


FIGURE 74. Localities of ruddy (northern red-backed) vole (10,000-24,000 yr B.P.).

RODENTIA: *Clethrionomys rufocanus*

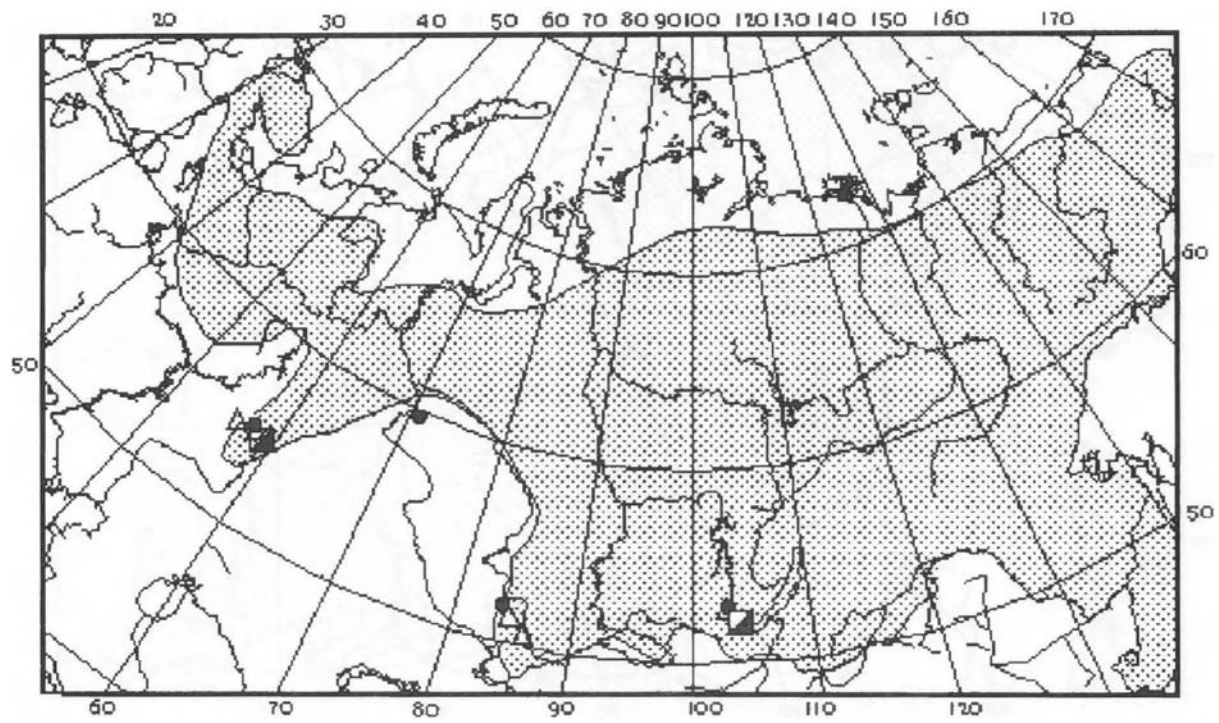


FIGURE 75. Localities of grey red-backed vole (24,000-130,000 yr B.P.).

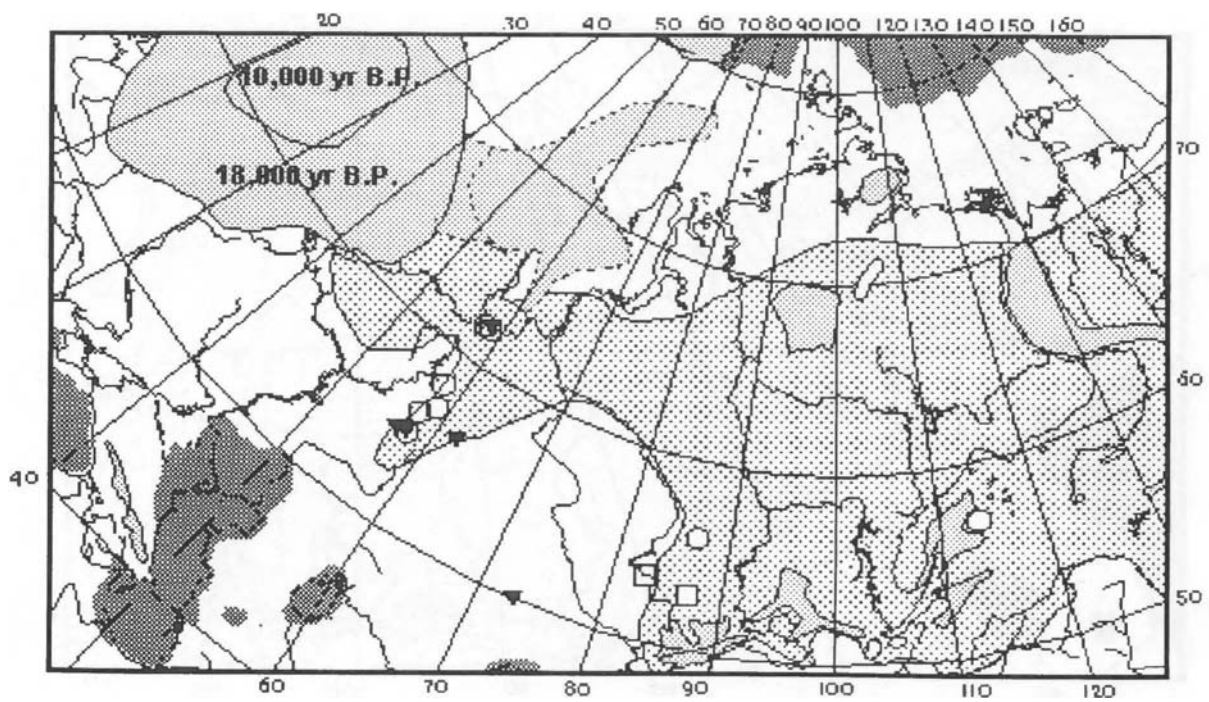


FIGURE 76. Localities of grey red-backed vole (<24,000 yr B.P.).

RODENTIA: *Microtus agrestis*

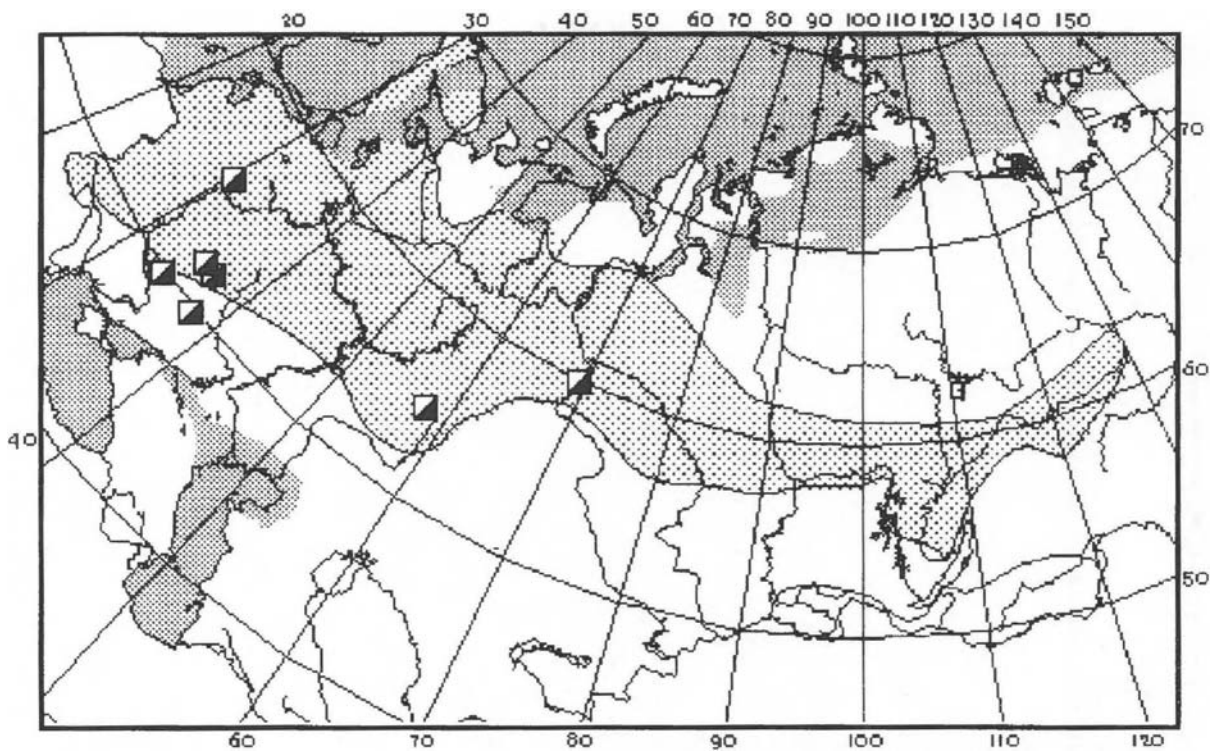


FIGURE 77. Localities of field vole (100,000-130,000 yr B.P.).

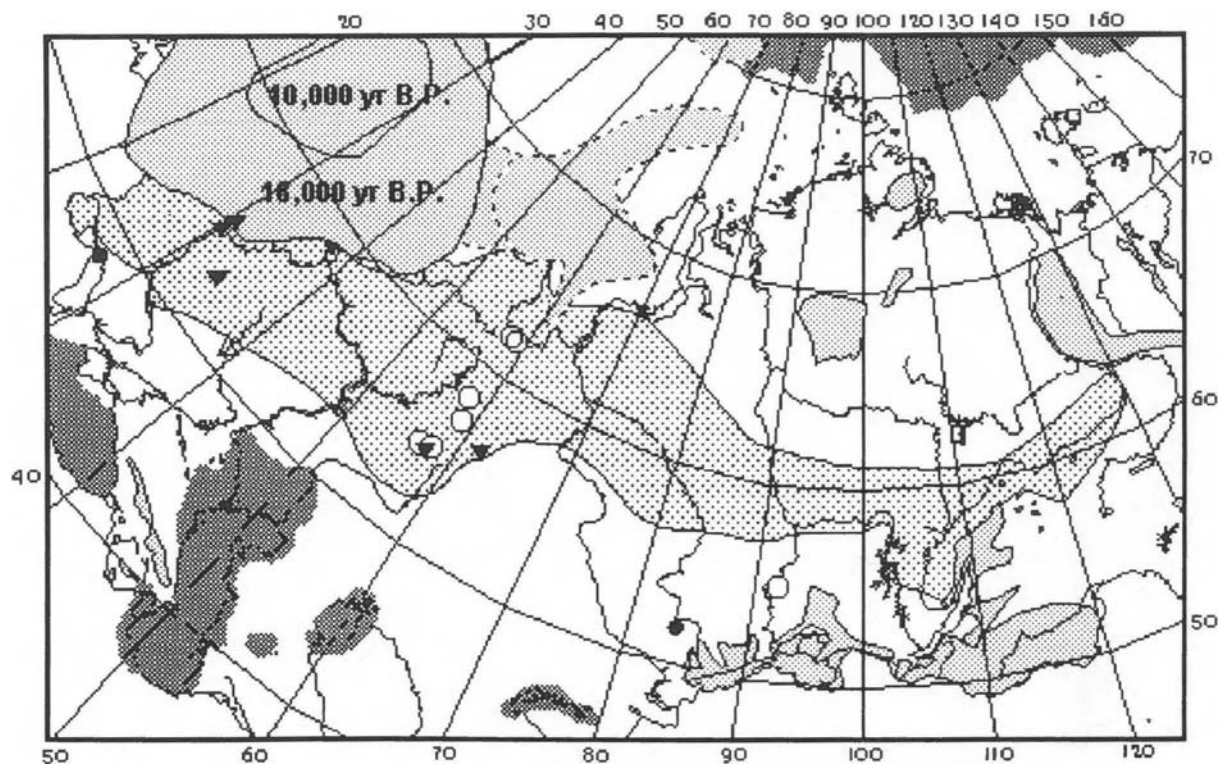


FIGURE 78. Localities of field vole (10,000-100,000 yr B.P.).

MAPS OF INDICATOR MAMMAL AND PLANT LOCALITIES

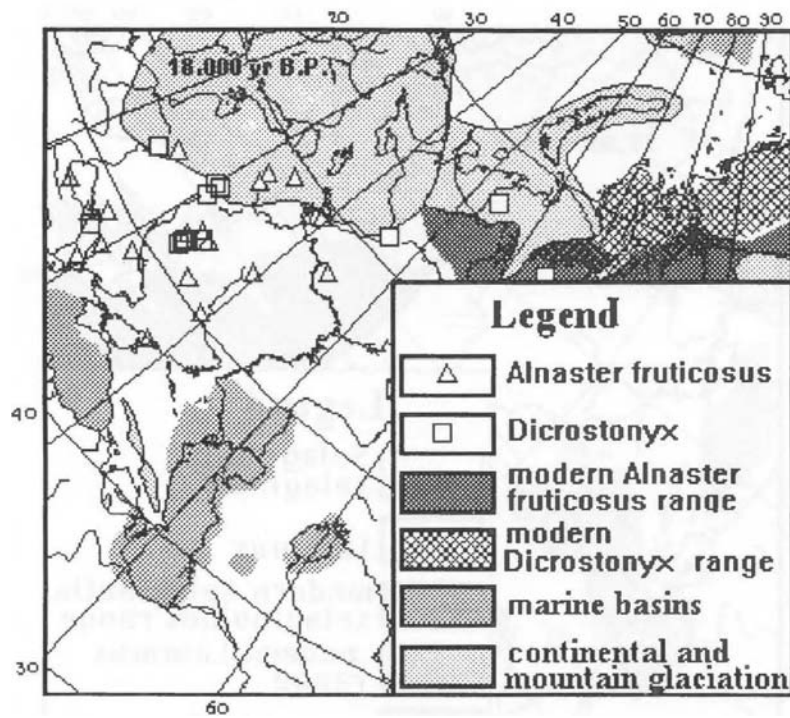


FIGURE 79. Localities of *Dicrostonyx* and *Alnaster fruticosus* (17,000-24,000 yr B.P.).

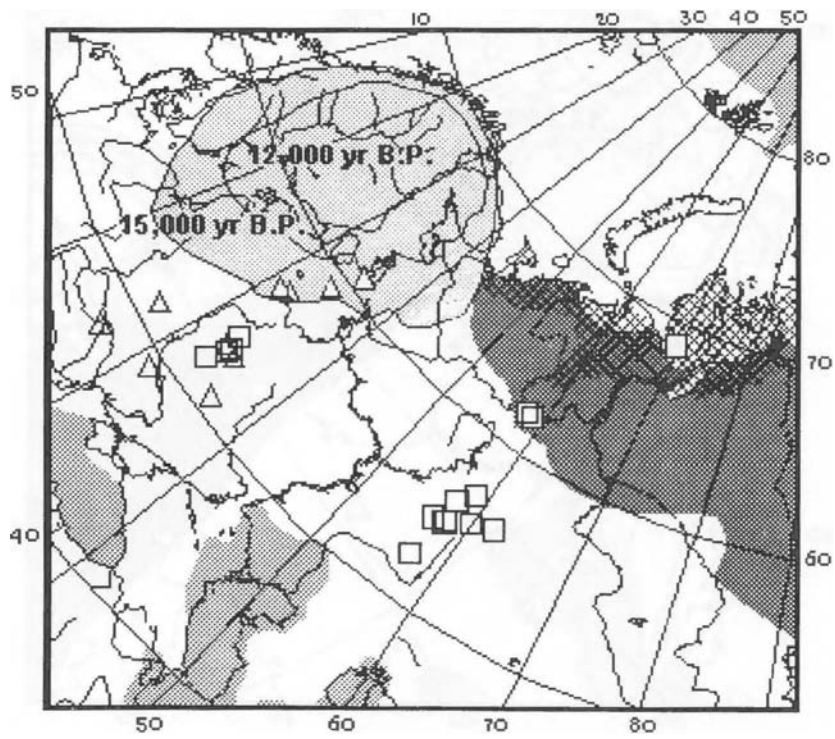


FIGURE 80. Localities of *Dicrostonyx* and *Alnaster fruticosus* (12,000-17,000 yr B.P.)

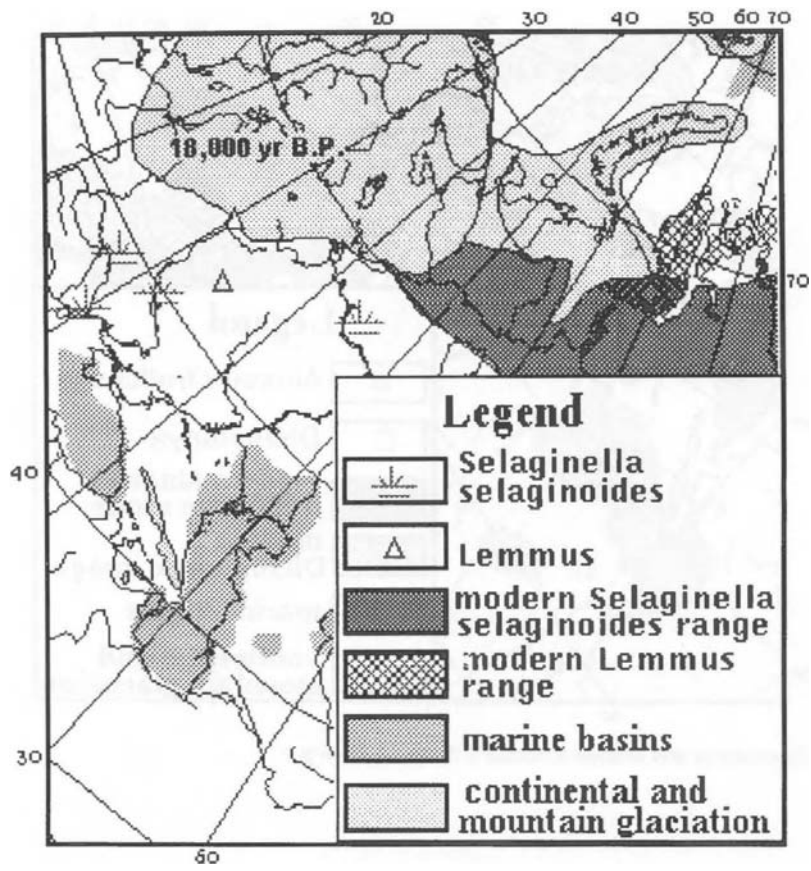


FIGURE 81. Localities of *Lemmus* and *Selaginella selaginoides* (21,000-24,000 yr B.P.).

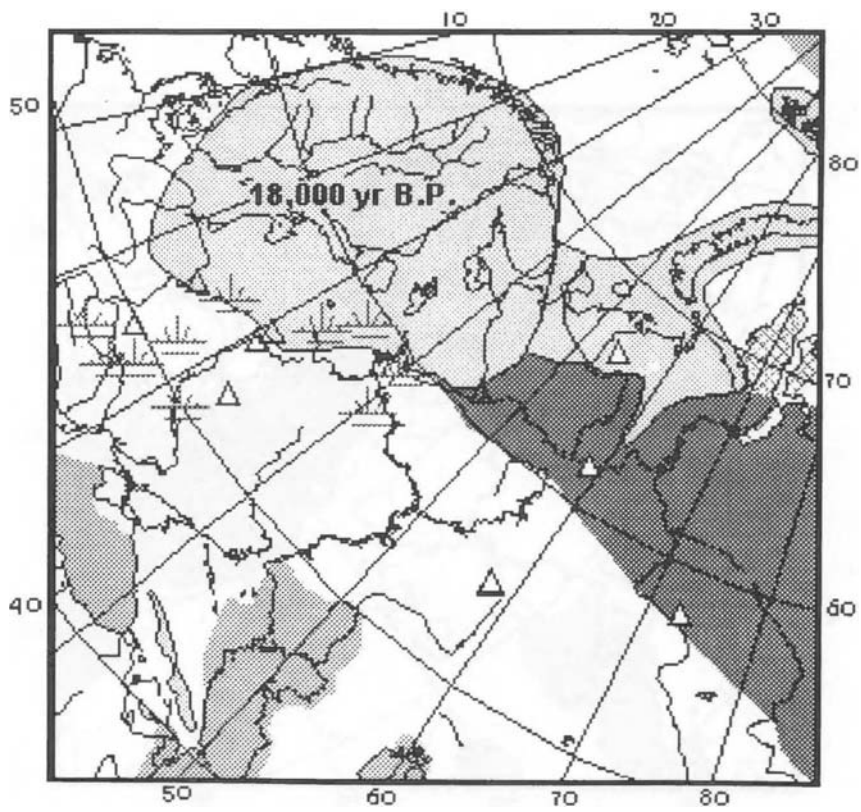


FIGURE 82. Localities of *Lemmus* and *Selaginella selaginoides* (17,000-21,000 yr B.P.).

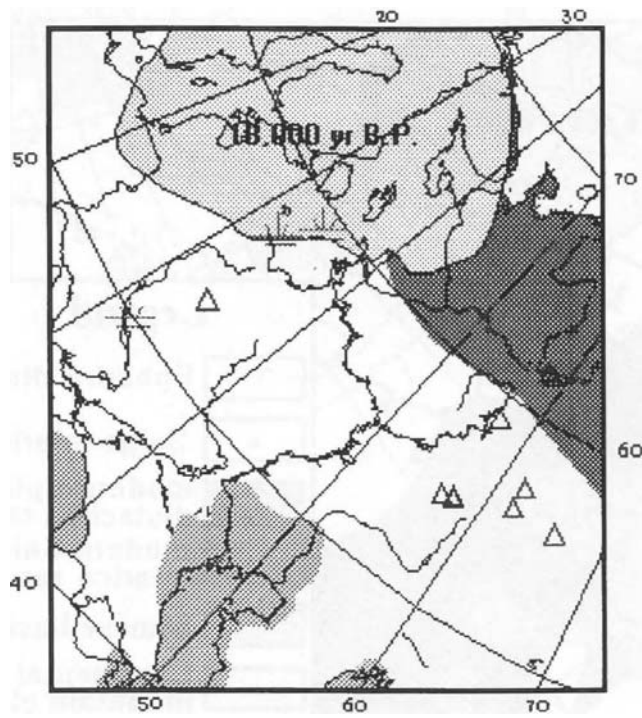


FIGURE 83. Localities of *Lemmus* and *Selaginella selaginoides* (15,000-17,000 yr B.P.).

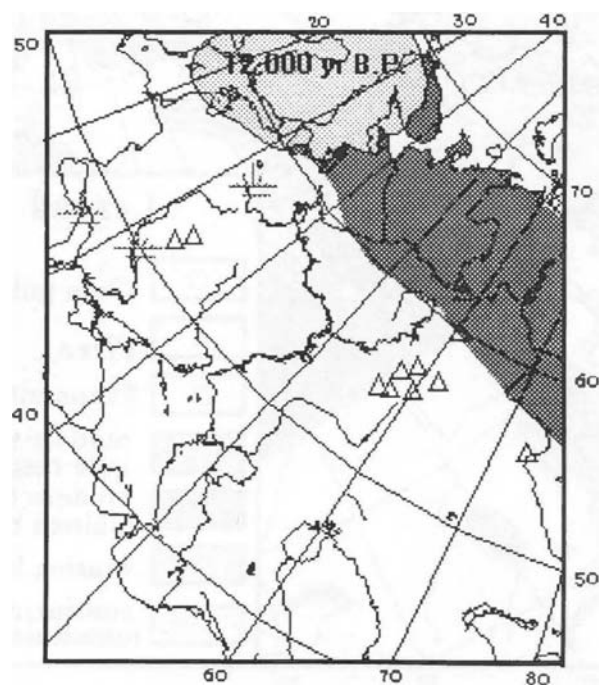


FIGURE 84. Localities of *Lemmus* and *Selaginella selaginoides* (12,000-15,000 yr B.P.).

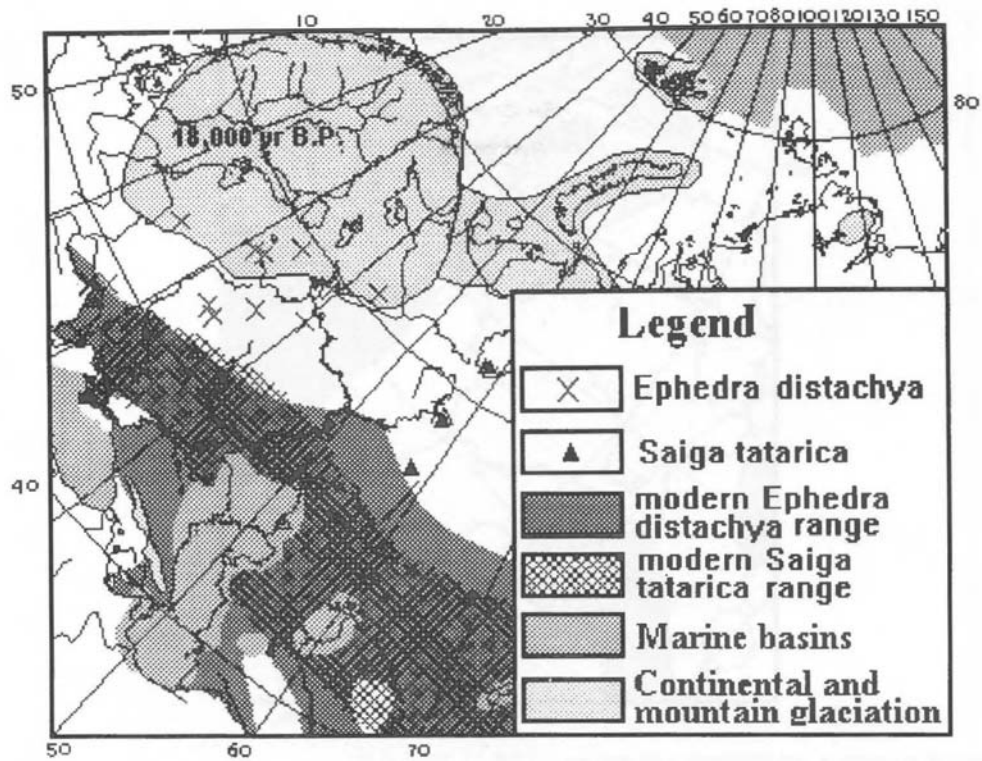


FIGURE 85. Localities of *Saiga tatarica* and *Ephedra distachya* (12,000-24,000 yr B.P.).

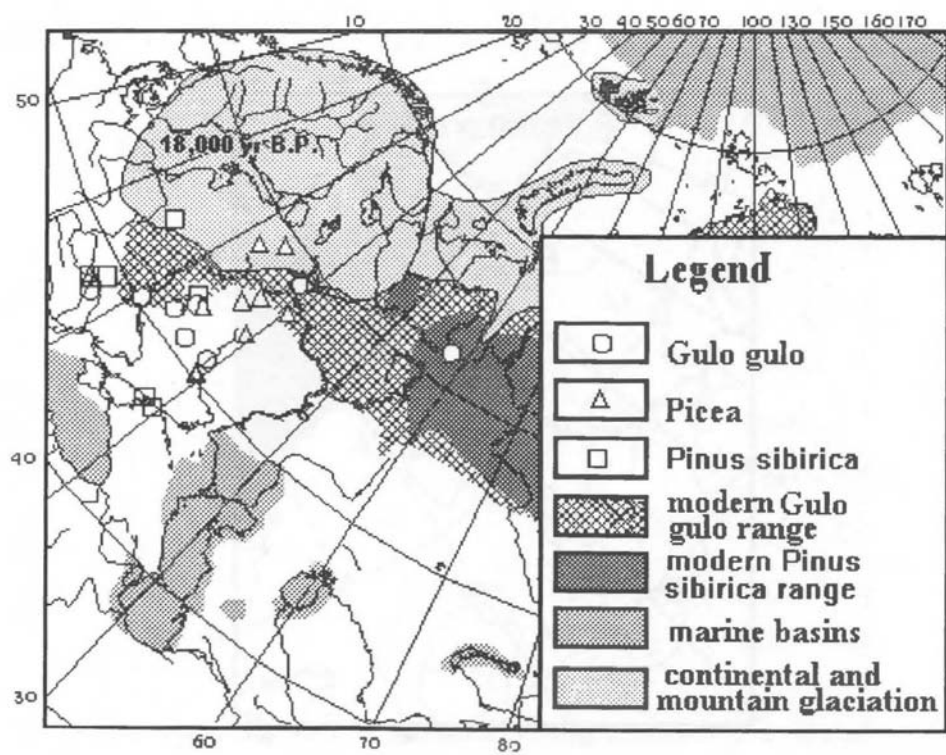


FIGURE 86. Localities of *Gulo gulo* and *Pinus sibirica* (12,000-24,000 yr B.P.).

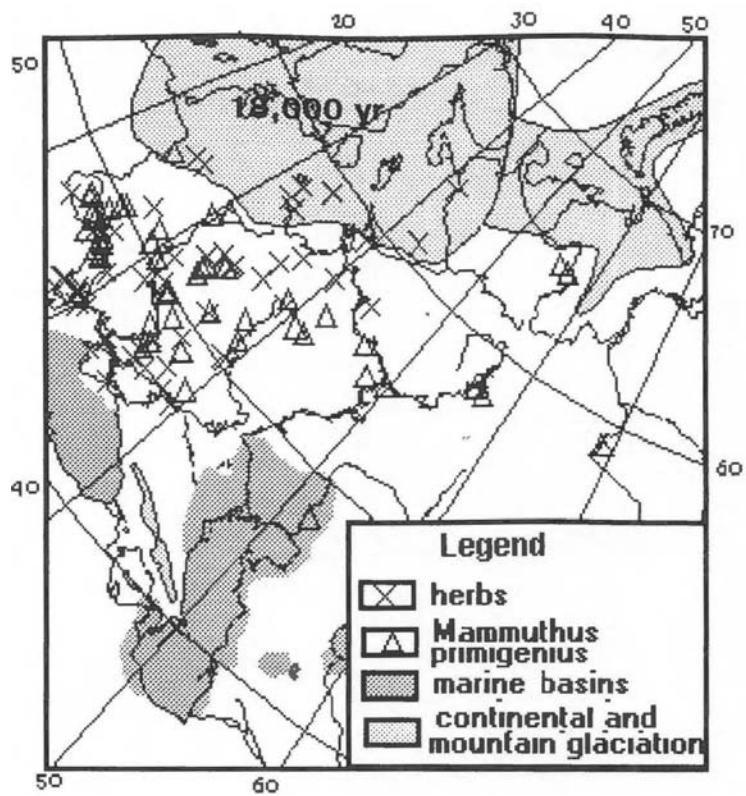


FIGURE 87. Localities of *Mammuthus primigenius* and herb communities (17,000-24,000 yr B.P.).

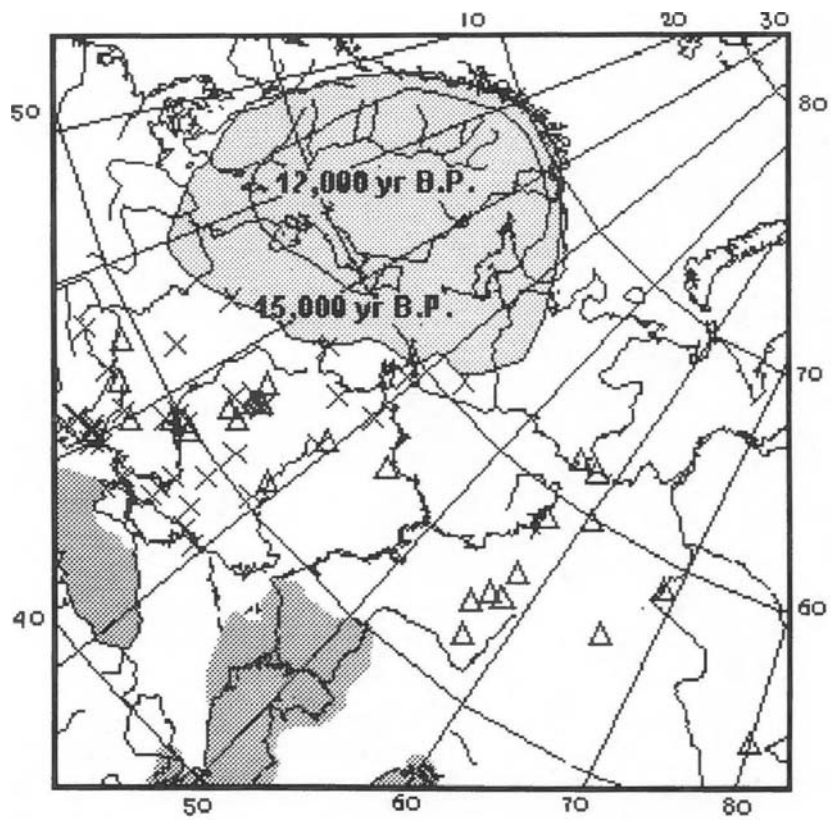


FIGURE 88. Localities of *Mammuthus primigenius* and herb communities (12,000-17,000 yr B.P.).

MAPS OF SPORE-POLLEN LOCALITIES

LEGEND TO THE MAPS OF SPORE-POLLEN LOCALITIES

SPORE-POLLEN LOCALITIES

VALDAI GLACIAL

LATE VALDAI

- a. Late glacial 12,001 - 15,000 yr B.P.
- b. Late glacial 15,001 - 17,000 yr B.P.
- c. Glacial maximum 17,001 - 21,000 yr B.P.
- d. Glacial maximum 21,001 - 24,000 yr B.P.



MODERN SPECIES DISTRIBUTION



CONTINENTAL AND MOUNTAIN GLACIATION



ICE SHEETS BOUNDARIES

- a. proved
- b. approximate



MARINE BASINS OF THE GLACIAL MAXIMUM



Alnaster fruticosus

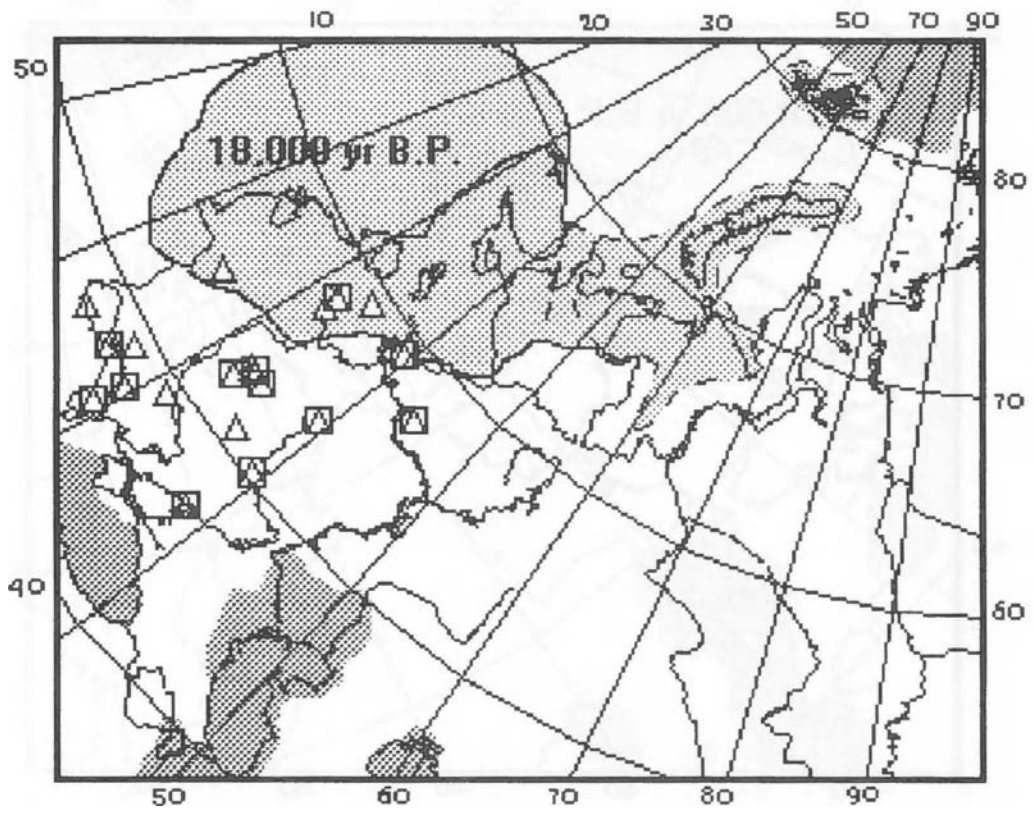


FIGURE 89. Localities of *Alnaster fruticosus* (17,000-24,000 yr B.P.).

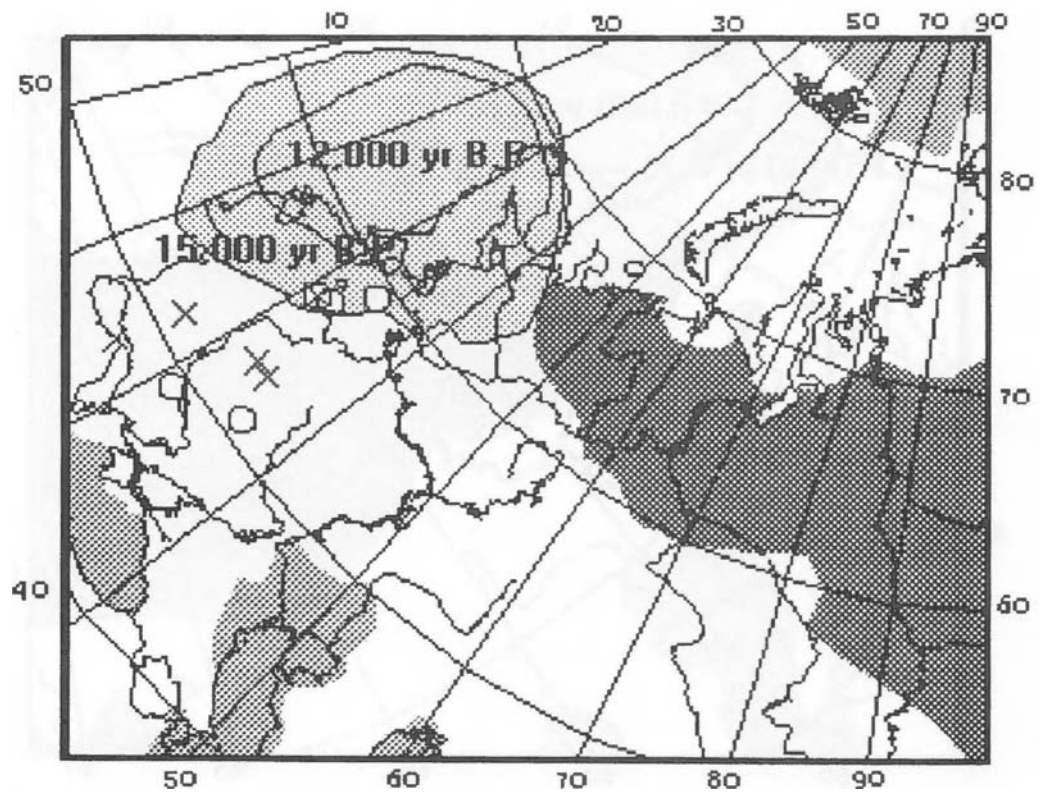


FIGURE 90. Localities of *Alnaster fruticosus* (12,000-17,000 yr B.P.).

Betula nana

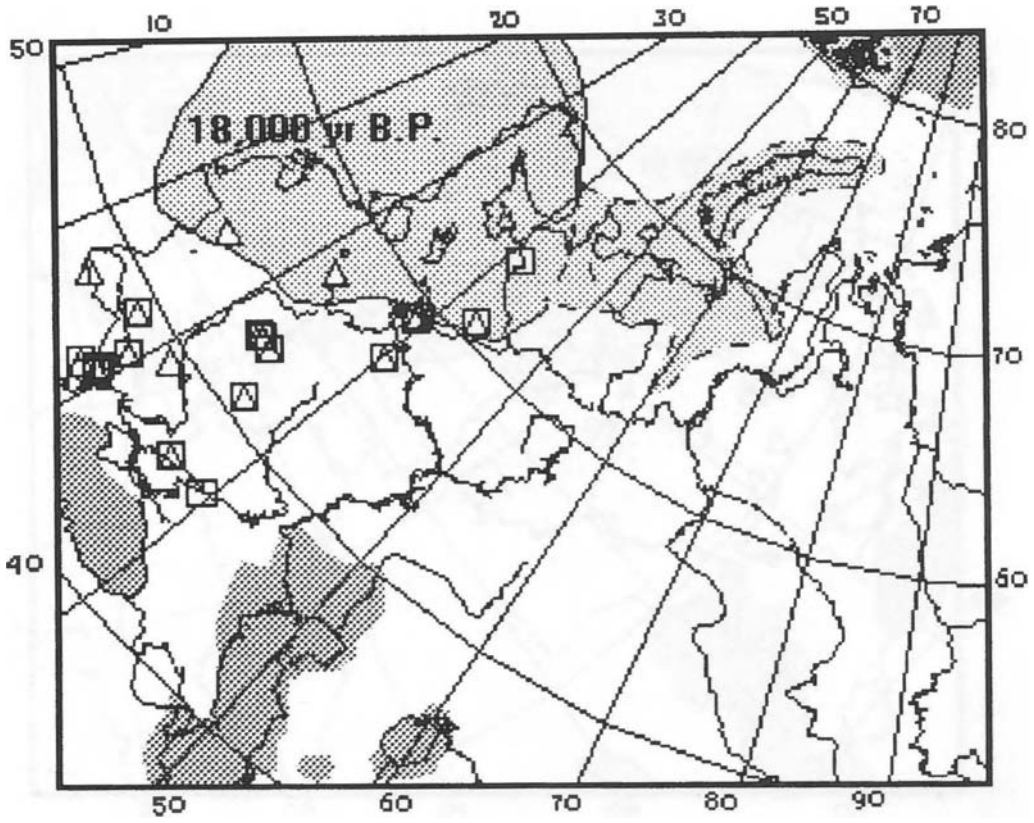


FIGURE 91. Localities of *Betula nana* (17,000-24,000 yr B.P.).

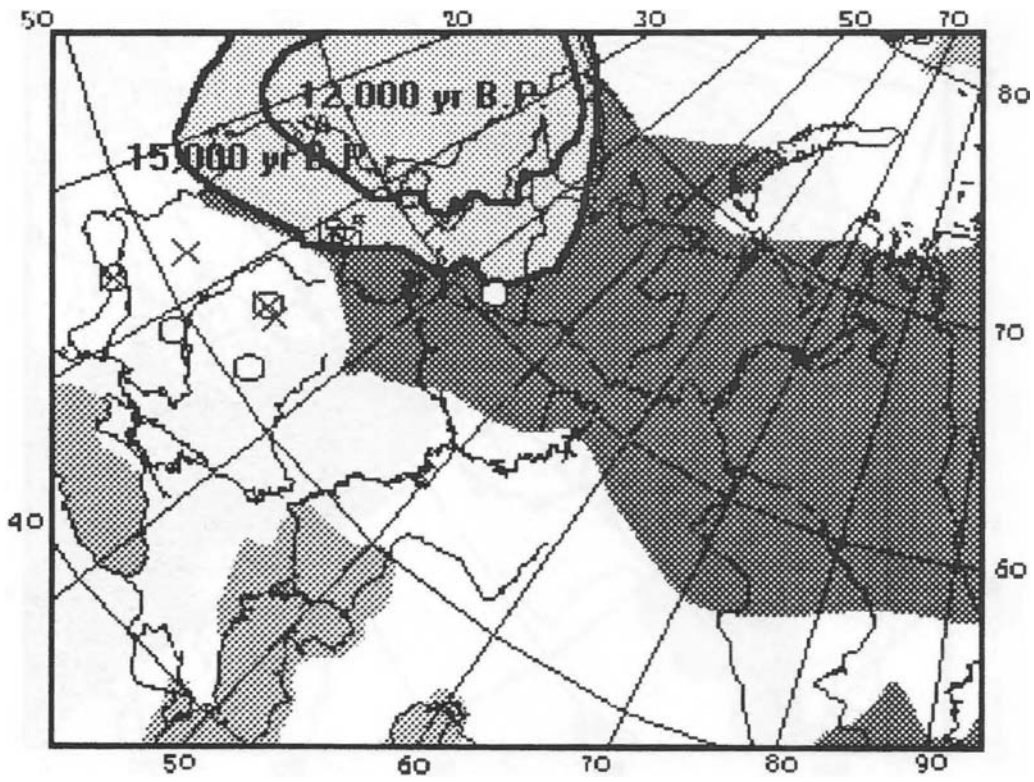


FIGURE 92. Localities of *Betula nana* (12,000-17,000 yr B.P.).

Selaginella selaginoides

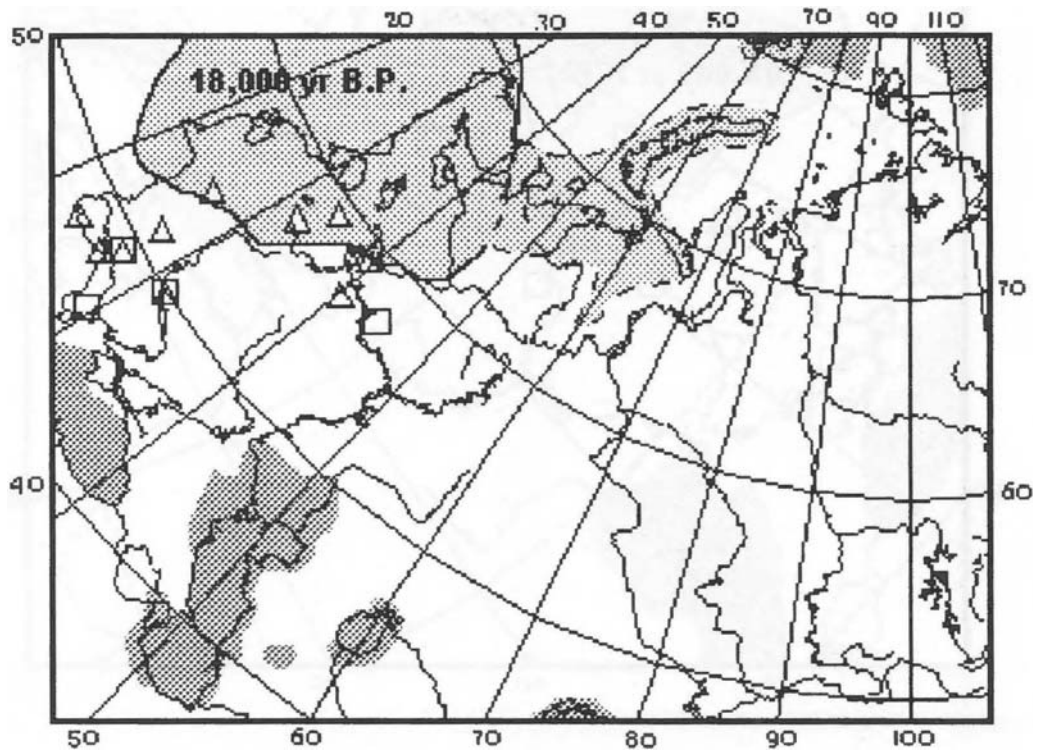


FIGURE 93. Localities of *Selaginella selaginoides* (17,000-24,000 yr B.P.).

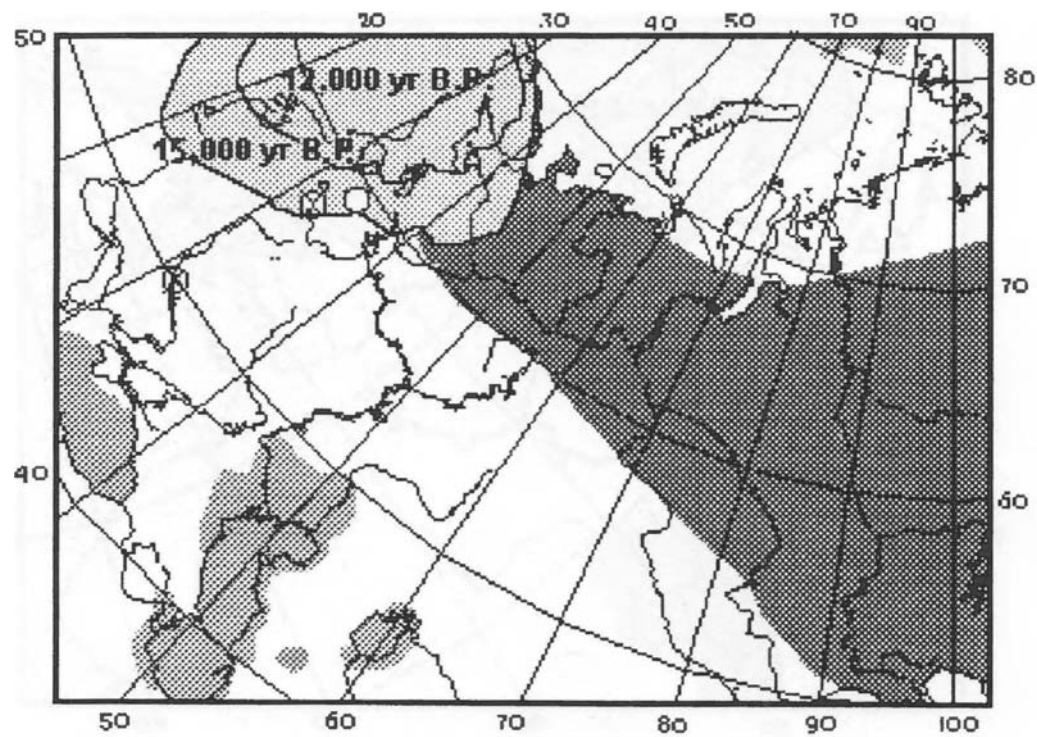


FIGURE 94. Localities of *Selaginella selaginoides* (12,000-17,000 yr B.P.).

Picea

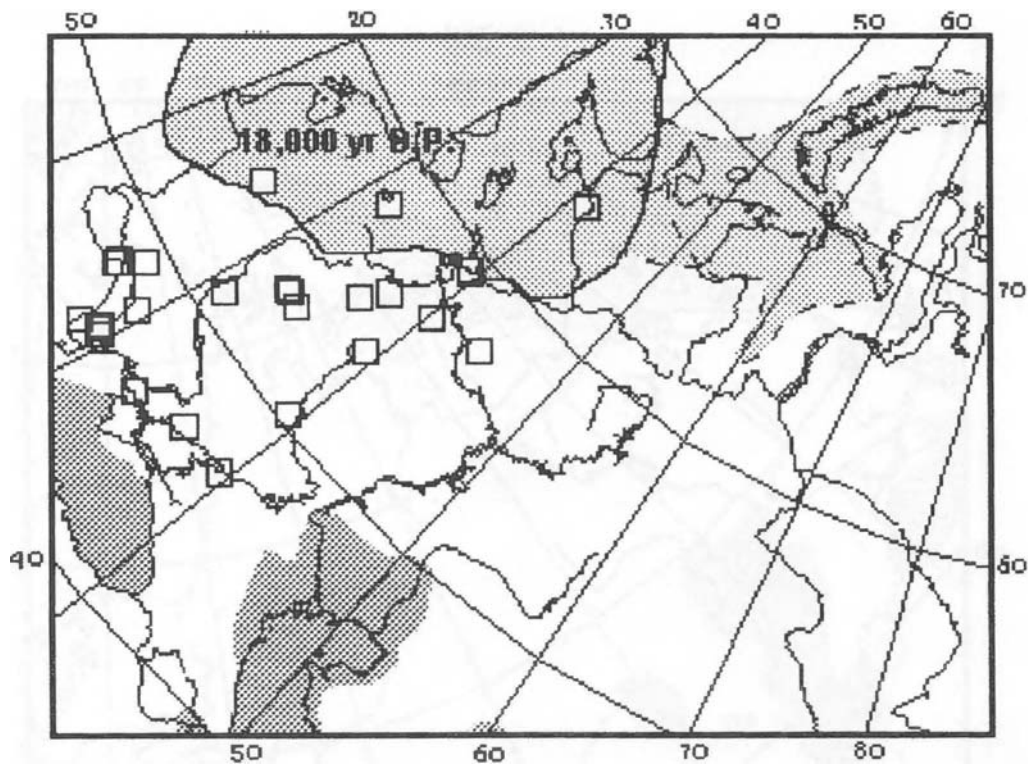


FIGURE 95. Localities of *Picea* (21,000-24,000 yr B.P.).

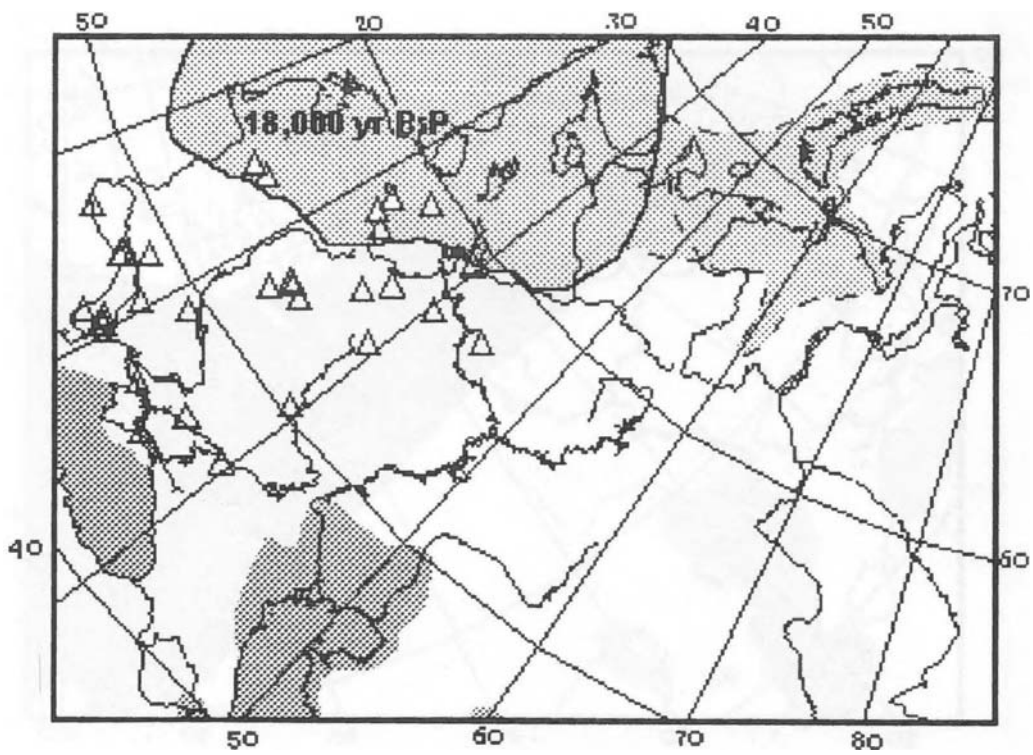


FIGURE 96. Localities of *Picea* (17,000-21,000 yr B.P.).

Picea

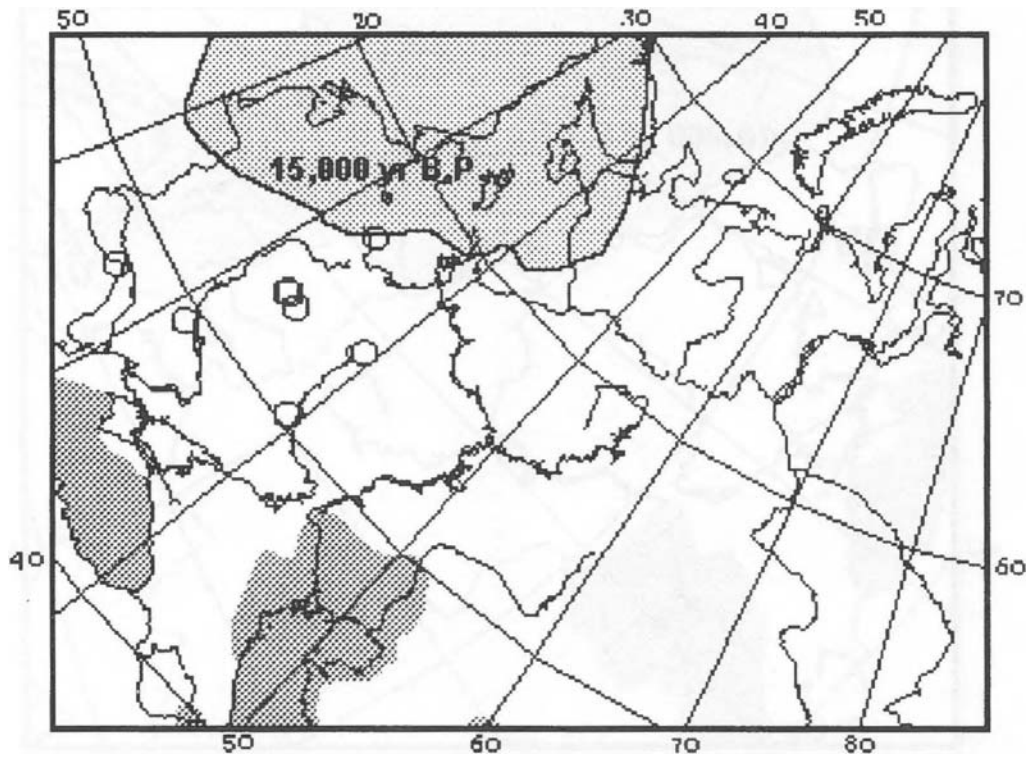


FIGURE 97. Localities of *Picea* (15,000-17,001 yr B.P.).

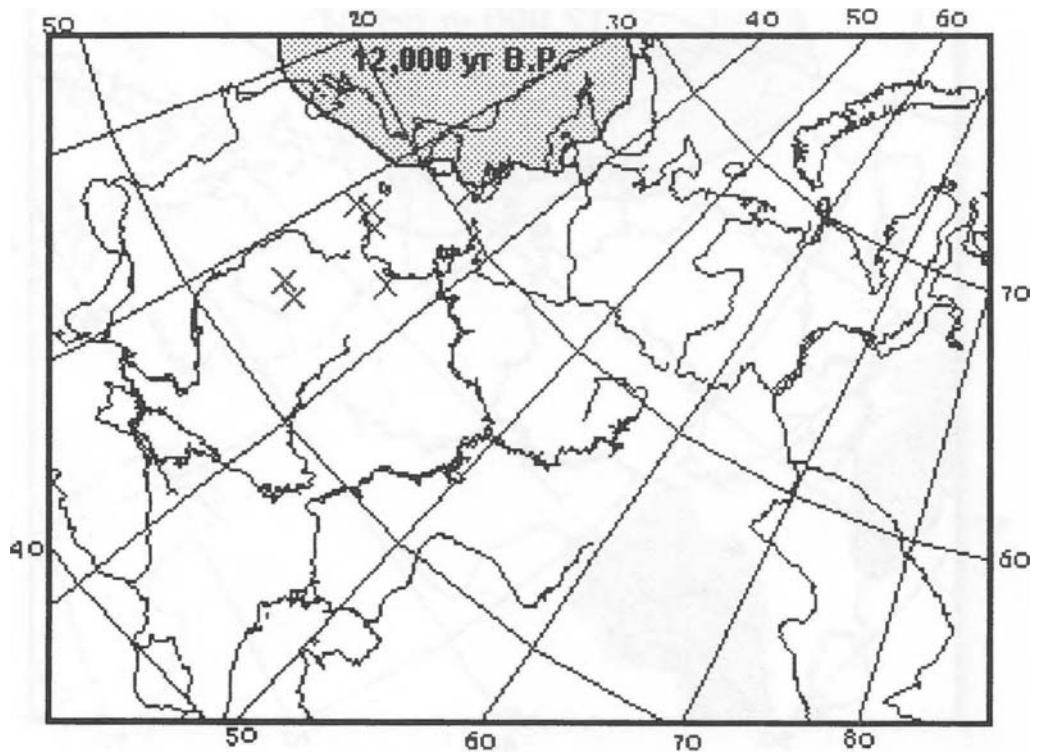


FIGURE 98. Localities of *Picea* (12,000-15,001 yr B.P.).

Abies

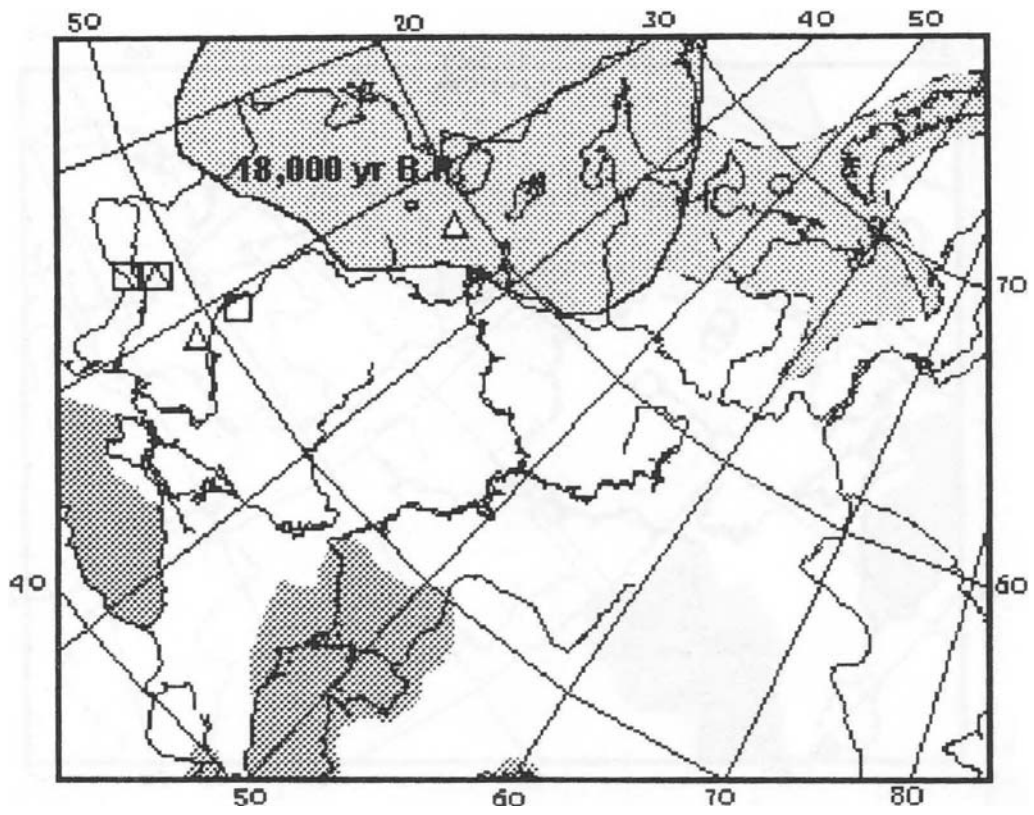


FIGURE 99. Localities of *Abies* (17,000-24,000 yr B.P.).

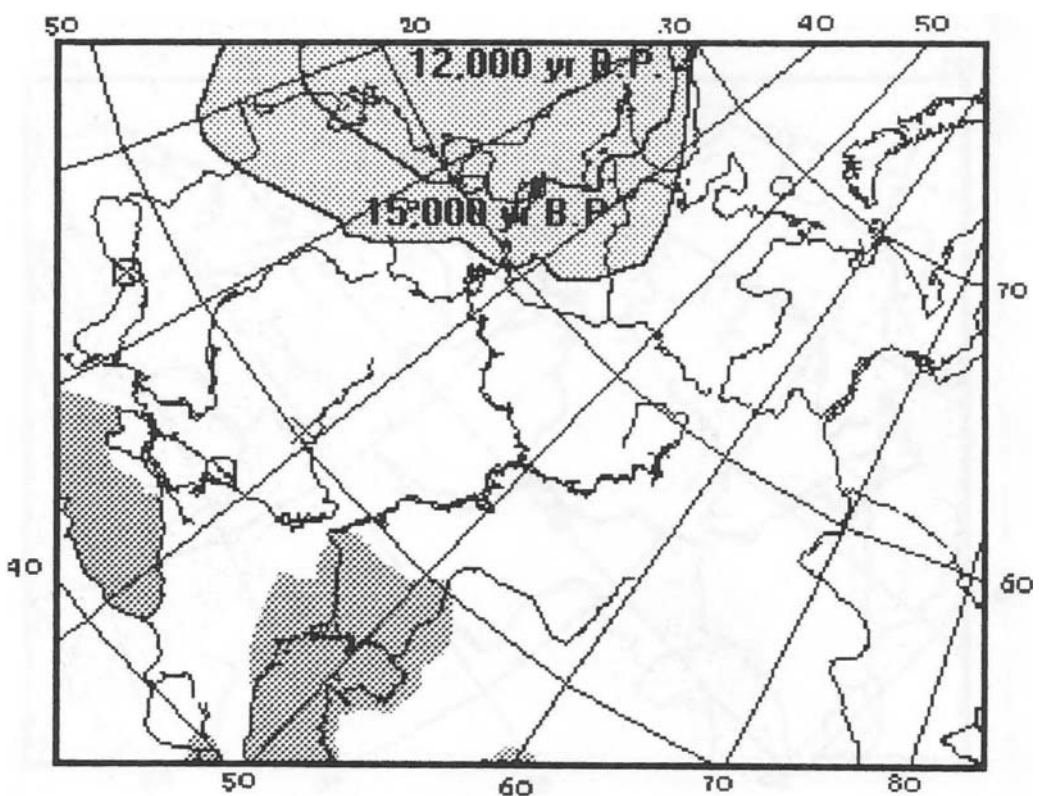


FIGURE 100. Localities of *Abies* (12,000-17,000 yr B.P.).

Pinus sibirica

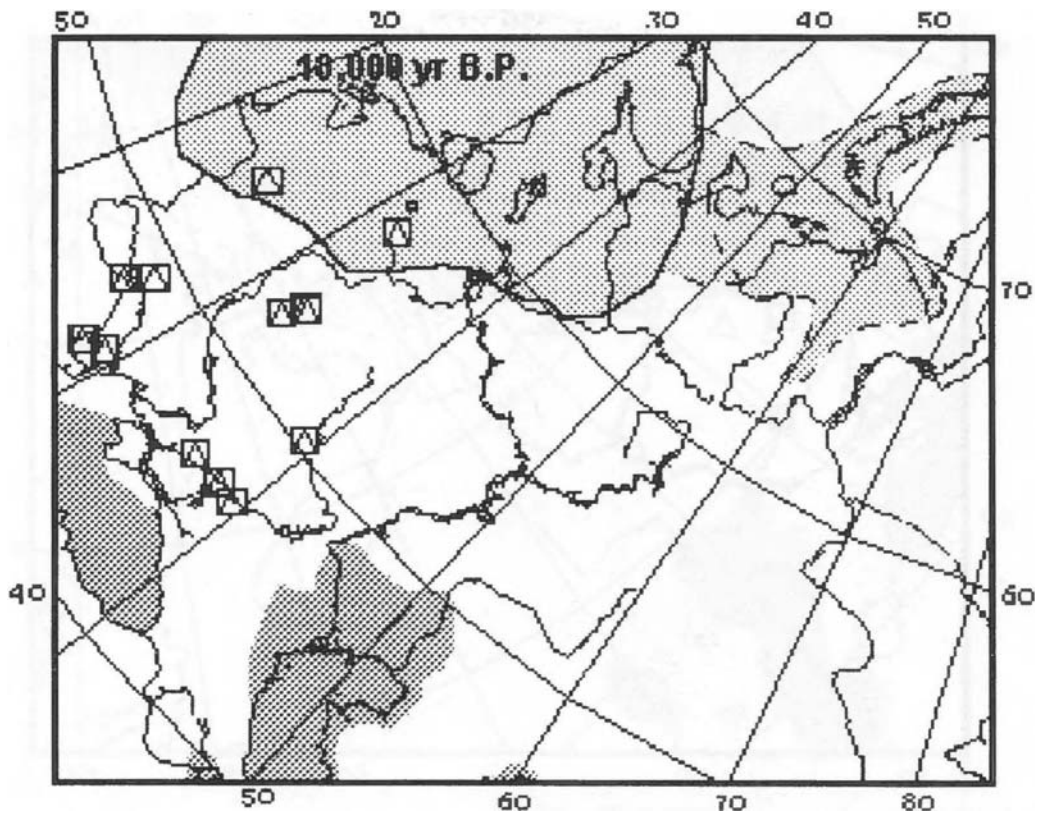


FIGURE 101. Localities of *Pinus sibirica* (17,000-24,000 yr B.P.).

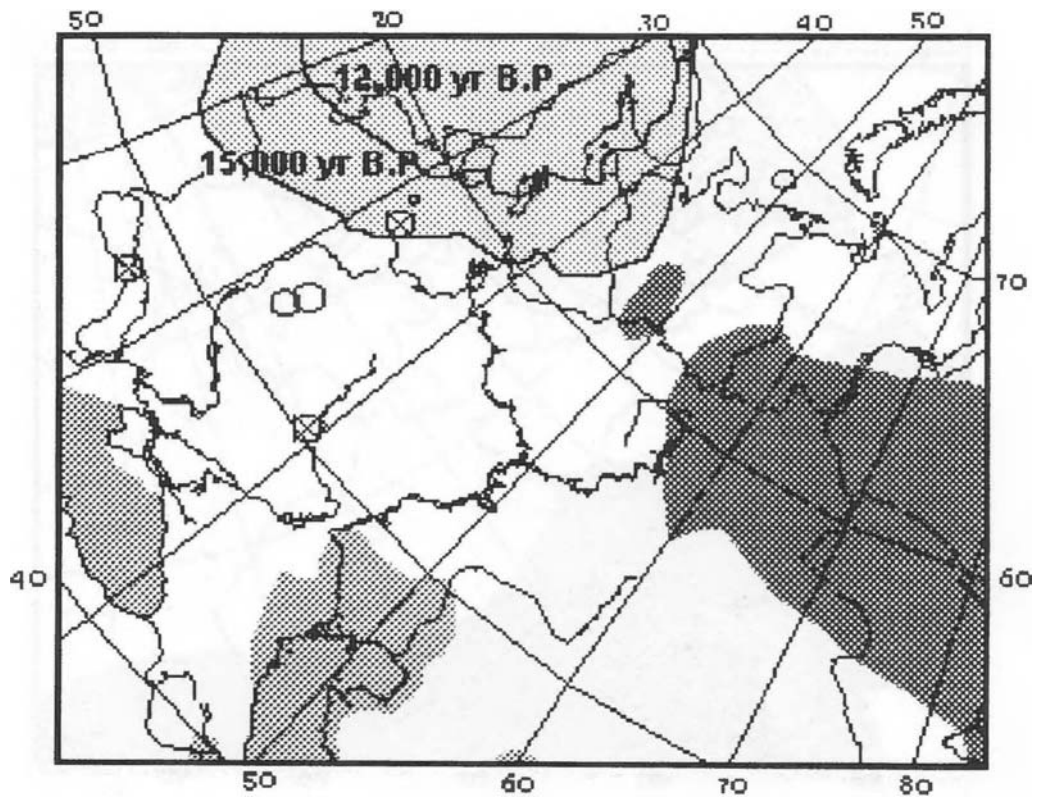


FIGURE 102. Localities of *Pinus sibirica* (12,000-17,000 yr B.P.).

Ephedra distachya

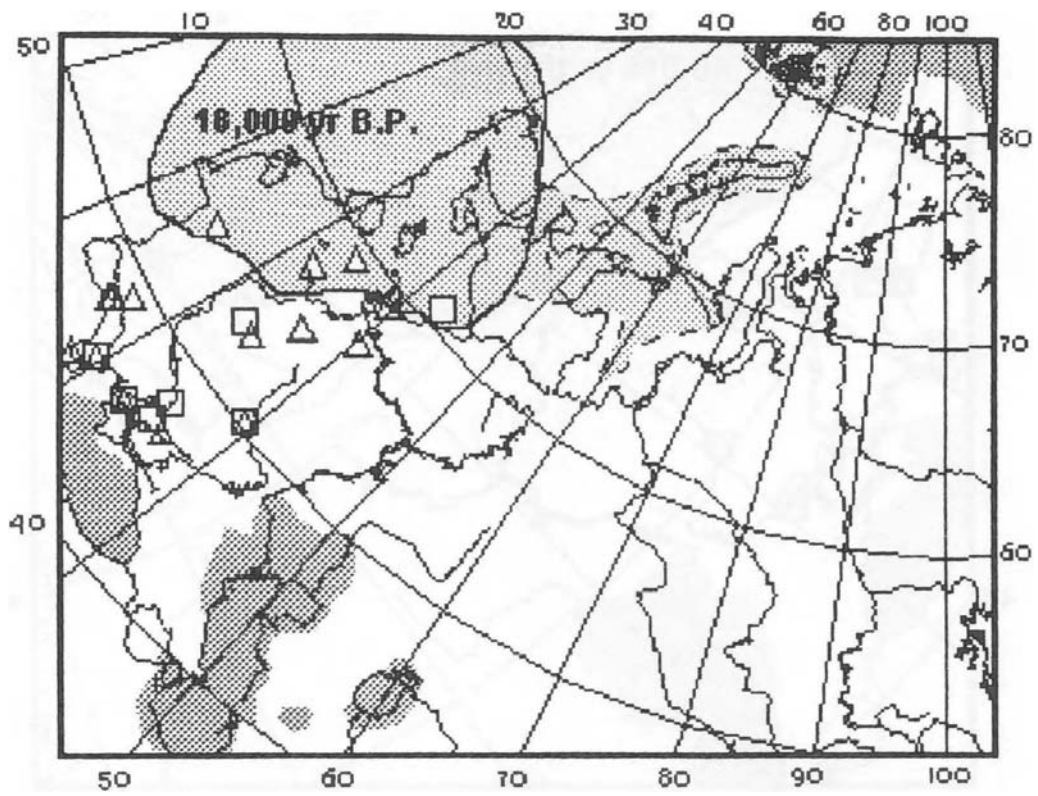


FIGURE 103. Localities of *Ephedra distachya* (17,000-24,000 yr B.P.).

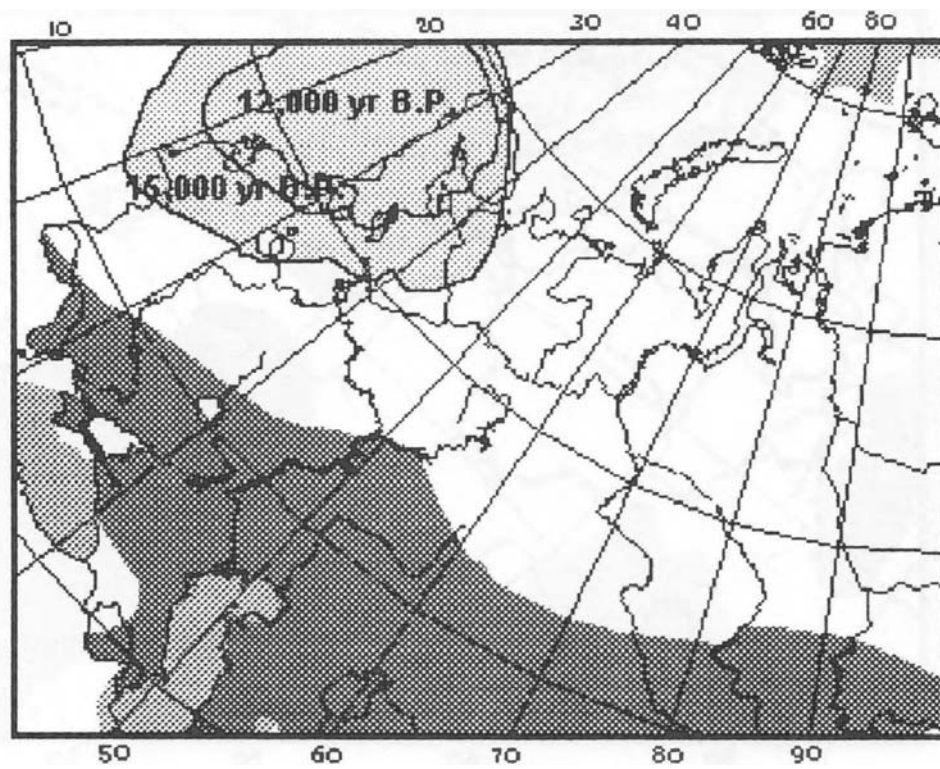


FIGURE 104. Localities of *Ephedra distachya* (12,000-17,000 yr B.P.).

Eurotia ceratoides

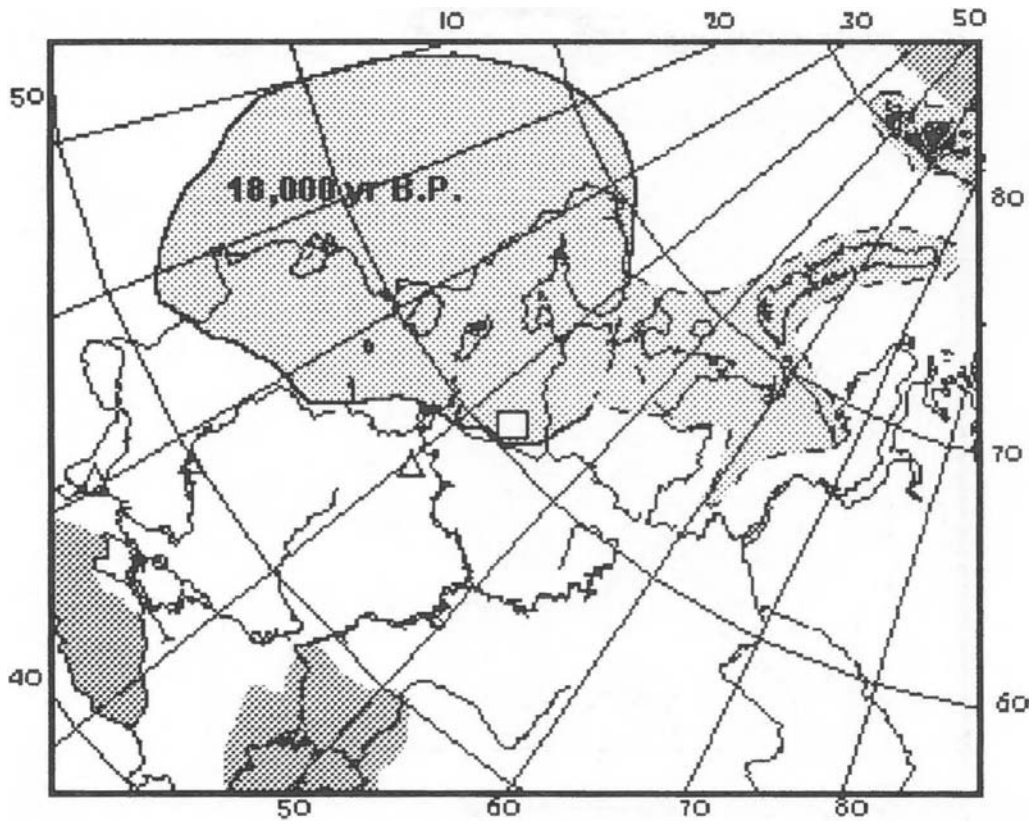


FIGURE 105. Localities of *Eurotia ceratoides* (17,000-24,000 yr B.P.).

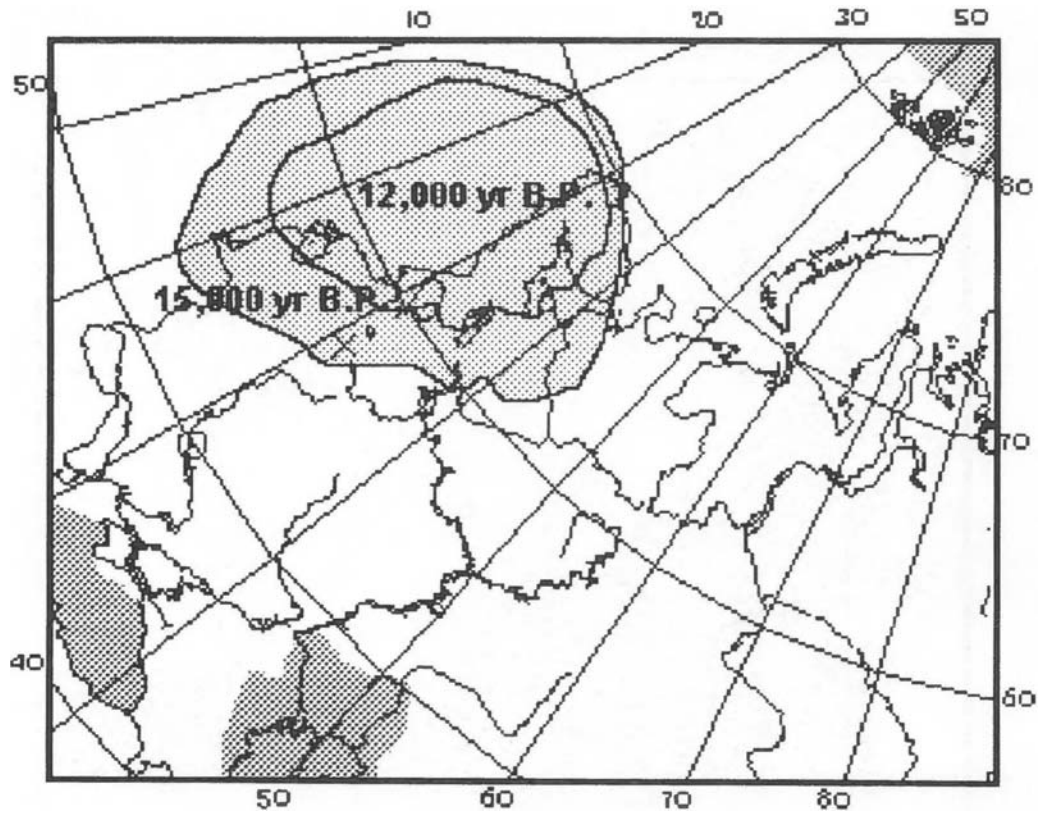


FIGURE 106. Localities of *Eurotia ceratoides* (12,000-17,000 yr B.P.).