

Environments of the Russian Plain during the Middle Valdai Briansk Interstade (33,000–24,000 yr B.P.) Indicated by Fossil Mammals and Plants

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Abundant mammal (45 localities) and plant (52 sections) fossil data collected from the Russian Plain deposits of the Middle Valdai Briansk Interstade indicate a period of noticeable warming. These materials were jointly analyzed. The data were organized in the database software PARADOX and then moved to the GIS program ARC/INFO. Mathematical methods as well as traditional research methods were used for the analysis. The reconstructed biogeographical provinces illustrate the specific environmental and climatic conditions of the Briansk Interstade. Analogues of modern natural zones did not exist at this time on the Russian Plain. The Briansk landscapes reflect the moderate-cool climate of this period, when the majority of northern subarctic plant and mammal species extended their ranges considerably to the south to the Central Russian Plain. At the same time, steppe species penetrated farther north and west. This combination shows that the continuous forest zone was destroyed during the Briansk Interstade. Five biogeographical provinces have been reconstructed from the north to the south for the Russian Plain during the Briansk warming on the basis of joint analysis of mammalian and botanical data. © 2002 University of Washington.

Key Words: Late Pleistocene; Briansk Interstade; mammals; plants; database; GIS; reconstructions; biogeographical provinces.

INTRODUCTION

Investigations of Valdai glacial deposits over the past three decades produced a significant paleobiological database that

can be used to evaluate the complicated history of this interval on the Russian Plain. Abundant fossil mammal and plant data collected from deposits of the Middle Valdai Briansk Interstade indicate a period of significant warming with respect to climates associated with the encompassing glacial deposits. Although the Briansk is divided by a short cooling episode, fossils associated with this ~9000-yr interval are interpreted as one event because two warmer phases reflect nearly identical environments. Also, chronological control does not always permit more precise division of fauna and flora fossil remains. The principal goal of this study is an analysis of this extensive Russian Plain database. For this, we used mathematical modeling as well as traditional research methods. Information about mammal and plant species composition, geology and geographical position of the sections, as well as absolute and relative ages of all known localities and their references are included. The data were organized in the database software PARADOX and then moved to the GIS program ARC/INFO, from which a series of electronic maps of indicator mammal and plant ranges were plotted to reconstruct the principal Eastern European biomes during the Valdai.

GEOLOGICAL-GEOGRAPHICAL, PALEOPEDOLOGICAL, AND CHRONOLOGICAL MATERIALS

Briansk (Dunaevo = Dniester) Interstade, which preceded the Late Valdai glaciation, was complicated and included relatively cool and warm phases (Ivanova, 1982; Breslav *et al.*, 1992;

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Shik, 1993; Lavrushin and Spiridonova, 1998). It corresponds to the Upper Karga warming in Siberia, and the Shtilfried B = Denekamp = Grand Bya of Western Europe (Bolikhovskaya, 1995; Velichko *et al.*, 1992; Faustova and Velichko, 1992). The Briansk interval was dated by ^{14}C to 33,000–24,000 ^{14}C yr B.P. (Chichagova, 1992; Chichagova and Cherkinsky, 1993) and is the last in a series of the interstades of the Middle Valdai. The Middle Valdai (~64,000–24,000 yr B.P., oxygen isotope stage 3) was on the whole the warmest period of the entire Valdai Glaciation.

The Briansk periglacial paleosols are distributed between (~55°N) and the Northern Black Sea coast (at ~45°N). Evidence of latitude zonality was not pronounced in Briansk paleosol. All Briansk soil deposits are strongly deformed by cryogenic processes and resemble the pale-colored cryogenic soils of Yakutia (Velichko and Morozova, 1982; Tzatzkin, 1980). As follows from Frenzel's reconstructions based on paleobotanic data (Frenzel *et al.* 1992), mean annual temperatures and rainfall were lower than at present.

The complex nature of the Briansk was documented during detailed excavation of Eastern European Paleolithic sites in the Dniester, Don and Kliazma river basins. Two warm stages, separated by a cooler one, have been distinguished by paleopedological characteristics and by an increase spruce *Picea* in forest coenosis and the appearance of some broadleaf plants (Arslanov and Bakanova, 1972; Kholmovoi and Praslov, 1981; Gurtovaya, 1985; Spiridonova, 1991; Bolikhovskaya, 1995; Lavrushin and Spiridonova, 1998; Sycheva *et al.*, 1999). Usually the dates derived from mammal fossil localities are not as precise as those from palynological samples because of the variety of taphonomic processes by which mammal bones are incorporated into deposits. Therefore, we compare, analyze, and interpret the mammal and plant fossil materials without separating temporal phases of the Briansk Interstade.

MAMMALIAN FOSSIL DATA

The northernmost localities with mammal remains of Briansk age have been found at ~62°N (Pechora River basin); the southernmost were recovered at ~45°N (Crimea). There are 45 Briansk mammal localities, 43 of which are referred to cultural levels of Paleolithic sites and have ^{14}C data. One corresponds to mole borrows of the Briansk soil, another to fluvial deposits. The mammals from five of these sites have been studied by one of the authors (Markova, 1982a, 1985, 1999). Other primary literature sources include the analyses of Guslitser and Kanivets (1965), Tatarinov (1977) Vereschagin and Kuzmina (1977), David (1980), Rogachev *et al.* (1981), Kalinovski (1983), Rekovets (1985) and Alexeeva (1990).

All these data were generalized with the help of the database program PARADOX and the cartographic programs ARC/VIEW and ARC/INFO (Markova *et al.*, 1995). This permits construction of a series of maps for indicative mammal species as well as ecological groups of mammals (steppe, tundra, etc.) and

allows us to characterize the mammal assemblages of Russian Plain for the Briansk Interstade.

The following generalizations are clear regarding mammal species composition, species richness, and distribution during the Briansk Interstade in comparison with modern assemblages.

There was wide range expansion to the south of subarctic mammals (pied lemming *Dicrostonyx*, true lemming *Lemmus*, polar fox *Alopex*, reindeer *Rangifer*, musk-ox *Ovibos*) to the regions now occupied by taiga, mixed, broad-leaved forests and forest-steppes.

There was widespread northern and western dispersal of the steppe species (including horse *Equus*, saiga *Saiga*, pika *Ochotona*, bobac marmot *Marmota*, ground squirrel *Spermophilus*, yellow lemming *Eolagurus*, steppe lemming *Lagurus*). Their remains have been found in Briansk deposits inside the boundaries of modern forest zone where their ranges overlap with the subarctic mammal ranges to form nonanalogue mammal associations. This confirms the breakdown of the continuous forest zone in the Briansk Interstade.

Ranges of widely distributed forest species (common red-backed vole *Clethrionomys glareolus*) as well as those of taiga and mixed forests (field vole *Microtus agrestis*, wolverine *Gulo gulo*, Russian sable *Martes zibellina*) remained within their present boundaries but were fragmented. Only forested islands persisted where continuous forest zone previously existed. The ranges of some forest-steppe species (red deer *Cervus elaphus*, roe deer *Capreolus capreolus*) changed little; however, their northern boundary moved slightly to the south (200–300 km).

Broad-leaved forest mammals (wild boar *Sus scrofa*, yellow-necked mouse *Apodemus flavicollis*, fat dormouse *Glis*, dormice *Muscardinus*, European vole *Terricola subterraneus* and others) practically disappeared from the Russian Plain and survived only in mountain and upland refugia (the Carpathians, the Crimea, and the Caucasus).

The faunal configuration of Briansk time for the Russian Plain described above can be divided into the following assemblages and biotic zones.

1. The subarctic mammal assemblage—including pied lemming *Dicrostonyx* and true lemming *Lemmus*, polar fox *Alopex lagopus*, reindeer *Rangifer tarandus*, and also narrow-skulled vole *Microtus (Stenocranius) gregalis*, which was well adapted to the tundra conditions—lived on the northern portion of the Russian Plain (Pechora basin). The remains of displaced forest and steppe mammals as well as large herbivores (mammoth, woolly rhinoceros, primitive bison, wild ox) have not been found in this region. Environments close to the modern tundra zone are suggested by the fossil mammal data from the Northern Russian Plain.

2. A unique nonanalogue mammal assemblage was located southward from this near-tundra zone. It included the subarctic mammals (pied lemming *Dicrostonyx gulielmi*, Siberian lemming *Lemmus sibiricus*, polar fox *Alopex lagopus*, reindeer *Rangifer tarandus*), as well as numerous steppic taxa (saiga *Saiga tatarica*, horse *Equus ferus*, northern pika *Ochotona*

pusilla, bobac marmot *Marmota bobac*, ground squirrel *Spermophilus*, great jerboa *Allactaga major*, steppe lemming *Lagurus lagurus*, yellow lemming *Eolagurus luteus*). Forest-steppe (red deer *Cervus elaphus*, roe deer *Capreolus capreolus*), taiga (wolverine *Gulo gulo*, Russian sable *Martes zibellina*), and forest species with plastic ecology (common red-backed vole *Clethrionomys glareolus*, field vole *Microtus agrestis*) were rarely found. The persistence in this assemblage of the large herbivores (woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, primitive bison *Bison priscus*, wild ox *Bos primigenius*) and carnivores, such as cave lion *Panthera (Leo) spelaea*, cave hyena *Crocota spelaea*, large cave bear *Ursus (Spelaeartcos) spelaeus*, added to the peculiarity of this mammalian complex. Mammals associated with broad-leaved forests have not been found in this territory. The southern border of this assemblage is located at 48°N on the West of Russian Plain and at ~52–53°N in the Don basin. The position of this border eastward is not clear because of the absence of data. This assemblage may be attributed to the arctic subassemblage of the Mammoth assemblage previously distinguished for Late Valdai mammal faunas (Baryshnikov and Markova, 1992). The mammal composition of this zone is called as periglacial tundra-forest-steppe. The principal features of such nonanalogue intermingled mammal assemblages were described previously from Northern Eurasia and North America (Vangengeim, 1977; Semken, 1988; Graham, 1986; Markova, 1982b; Markova *et al.*, 1995).

3. A steppe mammal assemblage predominated southward from this zone. The woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, primitive bison *Bison priscus*, wild ox *Bos primigenius*, and cave carnivores also inhabited this zone. No subarctic species except the reindeer lived here. Periglacial steppes are reconstructed here by mammalian data.

4. Two mountain assemblages have been identified during the Briansk: 4a. A diverse mammal assemblage was present in the Carpathian Mountains, Mammals, characteristic of the tundra-forest-steppe periglacial zone, occupied the region along with a few mammals from the broad-leaf forests (wild boar *Sus scrofa*, forest mouse *Apodemus*). This mountain region, characterized by the diversity of local habitats, was the refuge for more temperature mammals during the Valdai Glaciation. The mammal composition of this assemblage is called the southern variant of periglacial mountain forest-steppe (Carpathian variant). 4b. In the Crimea the mammoth was absent during the Briansk Interstade, but the woolly rhinoceros, primitive bison, red deer, and roe deer were widely distributed there. Dry steppe and semidesert mammals prevailed in Crimean assemblage (woolly rhinoceros *Coelodonta antiquitatis*, horse *Equus ferus*, Pleistocene wild ass *Equus hydruntinus*, saiga *Saiga tatarica*, great jerboa *Allactaga major*, small ground squirrel *Spermophilus pygmaeus*, northern mole-vole *Ellobius talpinus*, steppe lemming *Lagurus lagurus*, yellow lemming *Eolagurus luteus*). Remains of reindeer and narrow-skulled vole have also been found. Their appearance obviously suggests a rather cool climate in

the Crimea during the Briansk. Forest species are represented by few remains of wild boar *Sus scrofa* and yellow-necked mouse *Apodemus flavicollis*. The Crimean variant of southern periglacial mountain forest steppe could be reconstructed in the Crimea.

So the distribution and composition of mammal assemblages during the Briansk Interstade differed significantly from the present, reflecting the colder climate. Range extensions, contractions, and continuations at different scales resulted in mammalian communities, which differed strongly from the modern ones. The presence of the extinct terminal Pleistocene large herbivores (woolly mammoth, woolly rhinoceros, bovids) and cave carnivores added to their eccentricity.

PALEOBOTANICAL DATA

Detailed Briansk palynological studies supported by radiocarbon dates and by geological data on the Russian Plain have appeared in the last three decades (Artushenko, 1973; Gurtovaya, 1985; Spiridonova, 1991; Bolikhovskaya, 1995; Lavrushin and Spiridonova, 1998). Some localities have not been ¹⁴C dated (e.g., Artushenko and Pashkevich, 1972; Serebriannaya, 1972; Medianik and Mikhailets, 1992). These have been combined into the Briansk as a whole in order to be comparable with the mammalian data. This can be refined into smaller increments in the future. The paleofloristic materials have been united in a palynological database. It includes the data from 52 sections, which were used in the fossil mammal evaluation.

An analysis of recent pollen spectra from tundra and forest-tundra shows that pollen of tree and shrub species amount to less than 40% of total, while spores vary from 20 to 50%. A presence of cold-tolerant plants was also recorded in the samples (Grichuk and Zaklinskaya, 1948).

The palynological data show that tundra and forest-tundra elements were widely distributed on the Russian Plain in the Briansk Interstade. The pollen and spores of arctic and hypoarctic species such as thrift *Armeria*, dryad *Dryas*, cloudberry *Rubus chamaemorus*, Manchurian alder *Alnaster fruticosus*, mountain moss *Selaginella selaginoides*, Chapman's club-moss *Lycopodium appressum*, and spiny club-moss *Lycopodium pungens* were found southward to 53–54°N. So the southern limit of these plants shifted ~1200 km from the modern southern border (64–66°N) of their ranges. This is comparable with the penetration of arctic mammals to the south during the Briansk. Manchurian alder *Alnaster fruticosus*, mountain moss *Selaginella selaginoides*, Arctic birch *Betula nana* have been found in the Southwest on the Russian Plain and into the Carpathians. This is reflected in the significant increase in the ranges of these Arcto-boreal plants. In the Late Valdai these tundra species penetrated even further to the south (>6° or on ~600 km more than in the Briansk Interstade) (Markova and Simakova, 1998).

The tundra-steppe landscapes with the sparse pine-birch forests penetrated southward to 56°–57°N. The distribution of

northern taiga trees (spruce *Picea*, Siberian stone pine *Pinus sibirica*, silver fir *Abies alba*, larch *Larix*) changed significantly. *Picea* pollen was found in every Briansk section, however the quantity dropped to less than 10% in localities situated to the south of 53°N. *Picea* was not the main component in these communities below 53°N, according to the studies of subfossil spectra (Grichuk and Zaklinskaya, 1948).

The Siberian stone pine *Pinus sibirica* and silver fir *Abies alba*, now absent on the Russian plain, expanded their ranges from Siberia to the south and west across the central and eastern parts of the Russian Plain to ~51°N. In south Eastern Europe, *Pinus sibirica* pollen has been found in the Donetsk Kriazh uplands and in the Carpathian Mountains. Larch *Larix* pollen has been recovered from Middle Russian highlands, in the Upper Desna River basin, in Oka River basin, and also in the western part of the Podolsk highlands. This shows a significant expansion of larch to the south during the Briansk Interstade.

Taiga communities did not have a continuous distribution during Briansk time but were restricted to “island” configurations as shown by the mammals. These “islands” continued into the highlands on the Russian Plain (the Valdai, the Middle Russian, the Donetsk highlands, etc.) with well-protected slopes and depressions. Some forested islands with the same composition, were located in more southerly regions, especially in the Dniester basin and the Podolsk highlands.

Birch *Betula*, pine *Pinus*, and spruce *Picea* were the main forest trees in the Briansk and formed the core of forest islands in the periglacial forest-tundra and forest-steppe communities. The scarce forest islands, together with meadow-steppes, tundra communities, and halophytic steppe associations, were located between 54° and 59°N on the Russian Plain. The co-occurrence of grasslands with the forest islands is confirmed by pollen and spores from grasses and mosses associated with the forest pollen. Examples include honeysuckle *Lonicera*, buckthorn *Rhamnus*, dogwood *Cornus* pollen, and common club-moss *Lycopodium clavatum* and bracken *Pteridium* spores, which were recovered in the same area as arboreal plant remains.

Spore and pollen spectra representing the modern steppe zone show that forest elements constitute <30%, grasses and small bushes 40–60%, and *Chenopodiaceae* family pollen varying between 10 and 22.5%. Typical steppe plants have been obtained from the subfossil spectra of the steppe zone, such as joint fir *Ephedra*, summer cypress *Kochia*, and European winter-fat *Eurotia ceratoides*. Spores of sphagnum moss *Shagnum* are absent in these samples (Grichuk and Zaklinskaya, 1948; Monoszon, 1985).

Steppe indicator taxa were recovered across the whole Russian Plain in Briansk deposits. They expanded southward from 44°N to 61°N. Taking pollen spectra from present-day steppe associations (Grichuk and Zaklinskaya, 1948; Monoszon, 1985), we concluded that the different types of steppes (meadow steppe, forb steppe, etc.) were distributed southward of 48°–49°N during the Briansk Interstade. They were similarly distributed during the Late Valdai period (Grichuk, 1989) and the present day. The periglacial forest-steppe zone was located be-

tween 49° and 54°N in the Briansk. The meadow steppes and islands of *Pinus*–*Betula* forests contained within the steppe were situated there; oak *Quercus*, lime *Tilia*, and other broad-leaf species were rare in these latitudes. Periglacial tundra-forest-steppe communities were further to the North (between 54° and 59°N). The closest analogues of these communities exist as fragmentary association today in northeastern Russia.

The cluster analysis showed strong differences between the vegetation in the southern and northern parts of the Russian Plain during Briansk Interstade. The boundary between the periglacial forest tundra-steppe and periglacial forest steppe with meadow steppes was located at ~54°N. Broad-leaf forests now extend to these latitudes.

Thus, tundra and tundra-forest communities had a significantly wider distribution during the Briansk than at present. The areas of northern taiga plants extended to the south very widely (to 51°N) and the continuous taiga-forest zone was broken down into islands in favorable locations.

The periglacial tundra-forest-steppe community (with the islands of birch *Betula*, pine *Pinus*, and spruce *Picea*, and of meadow-steppes, tundra communities, and halophytic steppe species) was situated between 54° and 59°N.

A few remnants of broad-leaf species have been found among other forest island species in Briansk deposits on the Neman and the Moscow Highlands. More abundant remains of broad-leaf plants have been recovered to the south in the Dniester basin, on the Podolsk and Middle Russian Highlands, and also on the Donetsk Kriazh Highlands. The species practically disappeared in Late Valdai times (Simakova and Kozharinov, 1995). Steppe species penetrated far to the North of their recent range and demonstrate a cool, continental climate during the Briansk Interstade. The climatic conditions of the Briansk were more severe than today, although warmer than during the Late Valdai.

High vegetation diversity on the highlands and mountains, including the Valdai, Middle Russian, Moscow, Neman, Podolsk, Donetsk Kriazh highlands, and the Carpathian and Crimean Mountains, provided refugia during the glaciation. Plant species with different ecological requirements, including a few broad-leaf species, existed in montane regions in a biota of high local environmental diversity.

PALEOBIOGEOGRAPHICAL RECONSTRUCTIONS

Fossil mammal (45 localities) and plant (52 sections) data of the Briansk Interstade were jointly analyzed. Mathematic methods (multidimensional scaling (MDS) (Kruskal, 1964), cluster analysis (Sneath and Sokal, 1973)) were used. The multivariate techniques application to discovering and describing the latent structure of the data set is based on the key concept that in most cases multiple measurements collected on a set of subjects are partly redundant, i.e., correlated in some way (Aivazyan *et al.*, 1989). The basic goal is to search more parsimonious structure of variables, which would remove redundancy in the original set of data while preserving most of information.

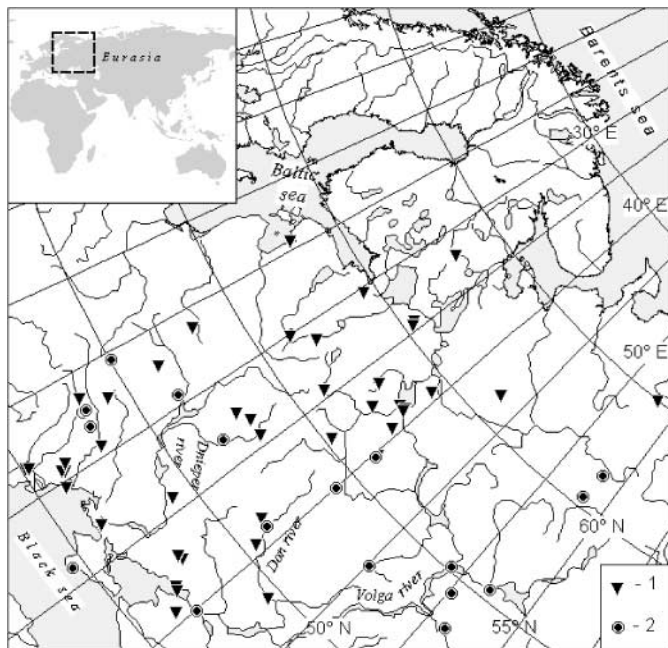


FIG. 1. The geographical position of (1) plant localities (the sites with palynological data) and (2) mammal localities.

At the first stage of analysis the localities were classified by mammalian and botanical composition. Lists of mammals were established for each class of localities. The results of this classification were analyzed in artificial multidimensional space

(MDS), as well as in geographical space according the latitude and longitude. At the first phase of the analysis, the mammalian materials were tabulated as a matrix of “presence-absence” of 46 genera of mammals (58 species) that have been found in Briansk deposits. The squared dissimilarity matrix was calculated (Jakardian distance) for 45 mammalian sites located at 19 geographical points. Where both species were absent, they were ignored during matrix calculation. This matrix was then analyzed for reproducing the distances, based on several underlying dimensions. The paleofloristic data were classified analogously, but based on a Euclidian distance matrix. The distances between the sites calculated for logarithm spectrum. The distinguished classes were characterized by mean values of pollen spectra. The results of pollen analysis reflect their relative abundance (maximum value for the sample in %) for 20 most widely distributed species, genera, or higher taxa (Fig. 1). During the second phase, the limits of biogeographic regions were defined based on the results obtained from the joint analysis of mammals and plants and with special attention to the geographical position of all the site groups.

The Results of the Classification of Paleofloristic Data

The localities with palynological materials were subdivided into two groups (I, II), each divided in two subgroups (1–4, Fig. 2a). Their ordination in the space of MDS axes, with consideration to data from Tables 1 and 2, could be interpreted as follows: the sites of group I (subgroups 1 and 2) are marked by a relatively high quantity of cold-tolerant and moisture-loving

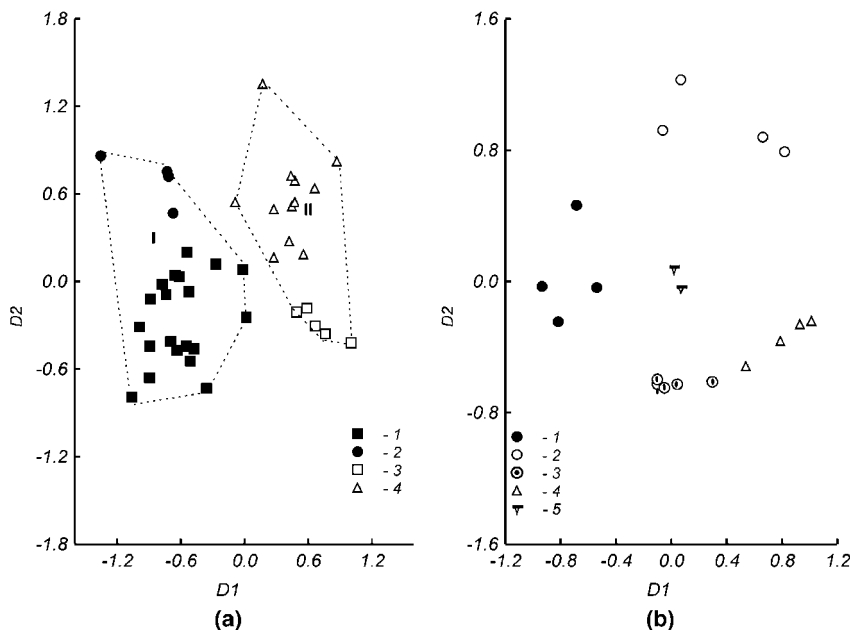


FIG. 2. The position of locality groups in the space of two first multidimensional space axes (D1, D2): (a) plants (1–4, subgroups of plant sites): (1) group I, subgroup 1 (periglacial forest tundra steppe; combination of *Betula*, *Pinus* and *Picea* forest island with meadow steppe formations, tundra communities, and steppe halophyte species). (2) group I, subgroup 2 (periglacial forest-steppe (*Artemisia* and *Graminae* meadow steppe areas with *Betula*–*Pinus* forest islands); (3) group II, subgroup 3 (periglacial forb steppe); (4) group II, subgroup 4 (periglacial forest-steppe; combination of *Artemisia*–*Chenopodiaceae* steppe areas *Betula*–*Pinus* forest islands with some broad-leaf trees). (b) Mammals (1–5, groups of mammal localities): (1) group 1 (periglacial mammal community with tundra, steppe, and forest-steppe species); (2) group 2 (periglacial tundra-steppe mammal community); (3) group 3 (mammal community, including mostly the widespread species); (4) group 4 (periglacial steppe mammal community, including some forest and semidesert species); (5) group 5 (periglacial forest-steppe mammal community).

TABLE 1

Spearman's Correlation Coefficient between Two First Multidimensional Space Axes (D1, D2; see Fig. 1a) and the Abundance of Pollen and Spores of Significant Plant Taxa

Taxa	D1	D2	Taxa	D1	D2
<i>Picea</i>	-0.57	-0.06	<i>Cyperaceae</i>	-0.77	-0.30
<i>Pinus</i>	-0.23	0.60	<i>Gramineae</i>	-0.72	0.21
<i>Betula sp.</i>	-0.65	-0.05	<i>Varia</i>	-0.56	0.48
<i>Betula nana</i>	-0.40	0.12	<i>Botrichium</i>	-0.59	-0.01
<i>Alnus</i>	-0.50	-0.13	<i>Lycopodium</i>	-0.66	-0.19
<i>Alnaster</i>	-0.31	0.16	<i>Polypodiaceae</i>	-0.79	-0.28
<i>Tilia</i>	-0.09	0.40	<i>Bryales</i>	-0.81	-0.19
<i>Ulmus</i>	0.02	0.42	<i>Sphagnum</i>	-0.74	-0.12
<i>Artemisia</i>	-0.61	0.41	<i>Selaginela</i>	-0.46	-0.23
<i>Chenopodiaceae</i>	-0.28	0.62	<i>selaginoides</i>		
<i>Asteraceae</i>	0.07	0.54			

Note. Statistically significant values are bold.

forest taxa. The sites in the group II (subgroups 3 and 4) feature a relatively high proportion of xerophytic taxa typical of steppe and semidesert, with some broad-leaf trees (subgroup 4).

The Results of Classification of Fossil Mammal Data

Five groups of mammal localities have been distinguished. Their position in the coordinate space of MDS axes is illus-

trated in Figure 2b. The first group of sites is the most isolated and includes a nonanalogue complex of arctic, steppe, and forest-steppe species. The second group, including tundra and steppe mammals, and the fourth group, with several forest and numerous steppe and even semidesert species, are most distant from the first group. The third group, including mostly widespread species of mammals stands close to the fourth one and well away from the second group. The fifth group occupies an intermediate position between all of the groups and includes steppe, forest, and intrazonal species (Table 3).

The geographical location of plant localities is presented in Figure 3a. The sites in the first group usually are situated mostly to the northern and central Russian Plain (north of 55°N). They are distributed in the Upper Desna basin, the Don basin, and in the Carpathians. The second class of localities is located to the south and southeastern parts of Russian Plain. The position of mammalian sites in the different groups is shown in Figure 3b.

BIOGEOGRAPHICAL PROVINCES ON THE RUSSIAN PLAIN AND IN THE CRIMEA DURING THE BRIANSK INTERSTADE

The following biogeographical provinces (divisions) were reconstructed from the north to the south for the Russian Plain during the Briansk warming (Fig. 4).

TABLE 2

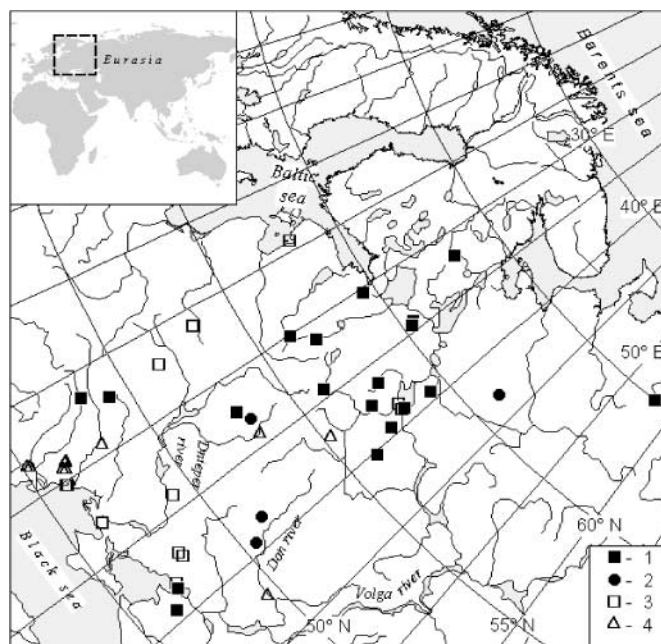
Mean Values of Pollen and Spore Abundance (%) of Several Plant Taxa in Classes (I, II) and Subclasses (1–4) of Plant Localities

Group Subgroup taxa	I		II		Group Subgroup taxa	I		II	
	1	2	3	4		1	2	3	4
<i>Picea</i>		25.4		10.9	<i>Asteraceae</i>		4.5		8.6
	25.2	26.3	11.1	10.8		2.8	13	0	17.2
<i>Pinus</i>		51.1		43.7	<i>Cyperaceae</i>		29.0		0.5
	47.5	69.5	16.1	67.1		34.1	3.3	0	1.0
<i>Betula sp.</i>		36.4		15.2	<i>Ephedra</i>		0.8		0.2
	37.6	30.7	7.7	22.7		0.9	0.3	0.2	0.18
<i>Betula nana</i>		8.2		2.6	<i>Gramineae</i>		27.8		8.7
	6.1	18.5	0.2	5.0		24.9	42.6	0.1	17.4
<i>Alnus</i>		13.5		7.3	<i>Varia</i>		24.9		12.7
	14.5	8.6	7.6	7.0		21.7	40.8	0	25.4
<i>Alnaster</i>		0.80		0.30	<i>Botrichium</i>		8.6		0.0
	0.71	1.3	0.0	0.6		2.1	41.3	0	0
<i>Corylus</i>		4.8		2.1	<i>Lycopodium</i>		2.7		0.0
	5.7	0.7	0.78	3.5		3.16	0.53	0	0.03
<i>Quercus</i>		1.2		1.5	<i>Polypodiaceae</i>		28.1		1.6
	1.2	1.2	0.22	2.9		28.8	24.2	0.6	2.6
<i>Tilia</i>		0.7		1.9	<i>Bryales</i>		64.8		0.2
	0.5	1.4	0.62	3.2		65.6	60.9	0.5	0
<i>Ulmus</i>		0.7		1.6	<i>Sphagnum</i>		18.8		6.8
	0.7	0.6	0.2	2.9		19.6	14.7	7.2	6.3
<i>Artemisia</i>		26.4		10.8	<i>Selaginela</i>		0.43		0.01
	21.3	51.4	0.1	21.6	<i>selaginoides</i>		0.46	0.25	0.0
<i>Chenopodiaceae</i>		12.4		22.3					0.20
	11.5	16.9	0.1	44.5					

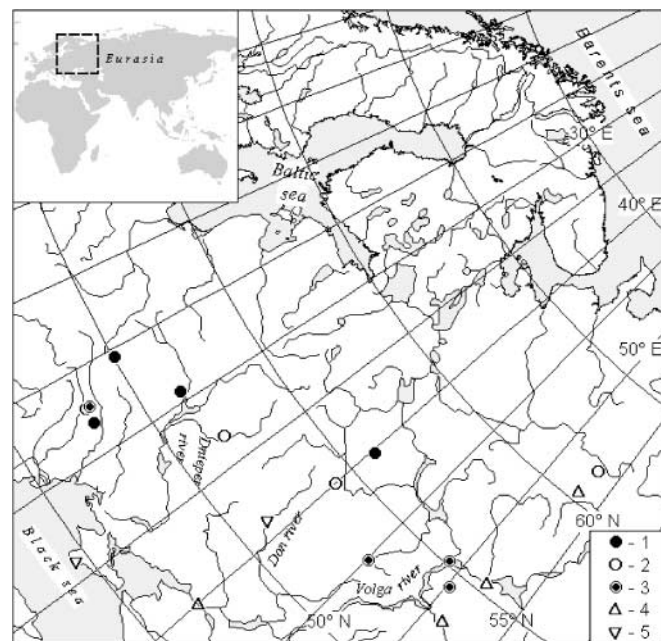
TABLE 3
Locality Classes Characterized by the Species Composition of Their Mammalian Assemblages

Taxa	1	2	3	4	5	Taxa	1	2	3	4	5
Insectivora						Rodentia					
<i>Talpa</i>		+				<i>Selevinia</i>					+
<i>Sorex</i>		+		+		<i>Allactaga</i>		+		+	
Carnivora						<i>Sciurus</i>					+
<i>Canis</i>	+			+		<i>Spermophilus</i>		+			
<i>Alopex</i>	+			+		<i>Marmota</i>				+	+
<i>Vulpes vulpes</i>			+	+		<i>Coelodonta</i>	+	+		+	
<i>V. corsac</i>				+		<i>Allocricetus</i>		+		+	
<i>Martes</i>				+		<i>Cricetulus</i>		+		+	
<i>Mustela</i>				+		<i>Cricetus</i>	+	+		+	
<i>Gulo</i>				+		<i>Eolagurus</i>	+	+		+	
<i>Lutra</i>				+		<i>Lagurus</i>	+	+		+	
<i>Crocuta</i>	+			+		<i>Dicrostonyx</i>	+	+			
<i>Panthera leo</i>				+		<i>Lemmus</i>		+			
<i>Ursus</i>		+	+	+	+	<i>Microtus</i>				+	+
Proboscidae						<i>oeconomus</i>					
<i>Mammuthus</i>	+	+	+	+	+	<i>Microtus agrestis</i>				+	+
Equidae						<i>Microtus gregalis</i>		+		+	+
<i>Equus</i>	+		+	+		<i>Microtus arvalis</i>		+		+	
Cervidae						<i>Ellobius</i>					+
<i>Cervus</i>	+		+	+		<i>Clethrionomys</i>		+			
<i>Rangifer</i>	+		+	+	+	<i>Arvicola</i>	+	+		+	
<i>Megaloceros</i>				+	+	<i>Apodemus</i>		+		+	
<i>Capreolus</i>	+			+		<i>flavicollis</i>					
Bovidae						<i>Apodemus</i>		+		+	
<i>Bison</i>	+			+		<i>sylvaticus</i>					
<i>Bos</i>	+		+	+		<i>Mus</i>					+
<i>Saiga</i>		+	+	+	+	<i>Nannospalax</i>				+	+
Suidae						<i>Spalax</i>			+	+	
<i>Sus</i>		+		+	+						
Lagomorpha											
<i>Ochotona</i>				+	+						
<i>Lepus</i>	+		+	+							

rels *Spermophilus*, common hamster *Cricetus*, pied lemming *Dicrostonyx*, true lemmings *Lemmus*, narrow-skulled vole *Microtus gregalis*, common red-backed vole *Clethrionomys glareolus*, and field vole *Microtus agrestis*).



(a)



(b)

FIG. 3. Geographical location of sites. (a) Plant locality groups and subgroups (1–4 subgroups of plant sites; see captions to Fig. 2a). (b) Groups of mammal localities (1–5; see captions to Fig. 2b).

I. Forest-Tundra

A combination of tundra and steppe plant communities together with scarce *Pinus–Betula* forest “islands” associated with subarctic mammals (e.g., reindeer *Rangifer tarandus*, polar fox *Alopex lagopus*, pied lemming *Dicrostonyx*, true lemming *Lemmus*, and narrow-skulled vole *Microtus (Stenocranius) gregalis*).

II. Periglacial Forest-Tundra-Steppe

A mosaic of plant communities, including forested areas with *Pinus–Betula* and *Picea*, meadow and halophytes steppes, and tundra vegetation elements with a mammalian fauna of tundra and forest-steppe species (e.g., woolly mammoth *Mammuthus primigenius*, primitive bison *Bison priscus*, wild ox *Bos primigenius*, reindeer *Rangifer tarandus*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, horse *Equus*, saiga *Saiga tatarica*, wolverine *Gulo gulo*, polar fox *Alopex lagopus*, ground squir-

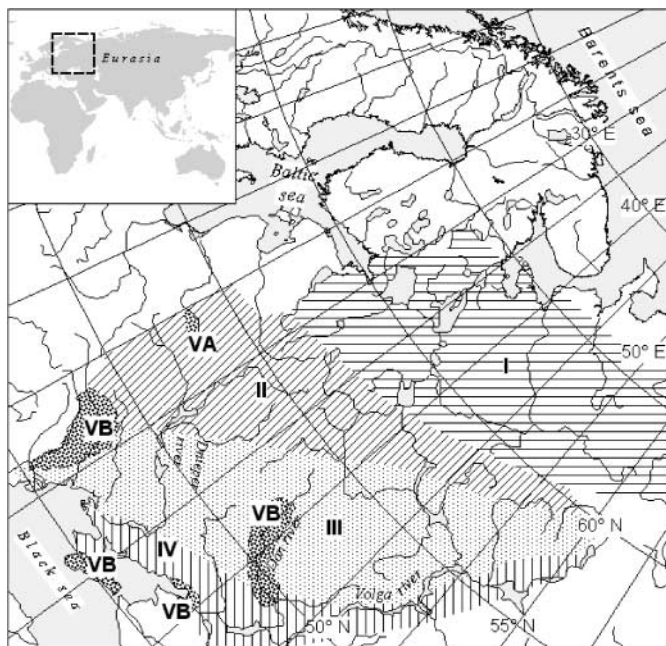


FIG. 4. Biogeographical provinces on the Russian Plain and the Crimea during the Briansk Interstade by defined plant and mammal data: I. Forest-tundra, II. Periglacial forest-tundra-steppe, III. Periglacial forest-steppe, IV. Periglacial steppe, and V. Forest-steppe of plains (A) and highlands and mountains (B).

III. Periglacia Forest-Steppe

Meadow-steppes with *Pinus–Betula* forest “islands” and with occasional stands of broad-leaved trees. This forest-steppe was inhabited by the woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, primitive bison *Bison priscus*, wild ox *Bos primigenius*, reindeer *Rangifer tarandus*, red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, horse *Equus*, saiga *Saiga tatarica*, cave carnivores, bobac marmot *Marmota bobac*, ground squirrels *Spermophilus*, great jerboa *Alactaga jaculus*, narrow-skulled vole *Microtus gregalis*, and field vole *Microtus agrestis* amongst others.

IV. Periglacial Steppe

Forb steppes with the steppic mammal fauna (woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, horse *Equus*, saiga *Saiga tatarica*, bobac marmot *Marmota bobac*, ground squirrels *Spermophilus*, great jerboa *Alactaga jaculus*, greater mole rat *Spalax microphthalmus*, northern mole-vole *Ellobius talpinus*, yellow lemming *Eolagurus luteus*, steppe lemming *Lagurus lagurus*, reindeer *Rangifer tarandus*, and others).

V. The Plain (A) and Mountain (B) Forest-steppe

Betula–Pinus forests with few broad-leaf trees and mammals of south periglacial forest-steppe (e.g., woolly mammoth *Mammuthus primigenius*, woolly rhinoceros *Coelodonta antiquitatis*, primitive bison *Bison priscus*, wild ox *Bos primigenius*, horse *Equus*, saiga *Saiga tatarica*, giant deer *Megaloceros giganteus*,

red deer *Cervus elaphus*, reindeer *Rangifer tarandus*, wild boar *Sus scrofa*, yellow lemming *Eolagurus luteus*, steppe lemming *Lagurus lagurus*, yellow-necked mouse *Apodemus flavicollis*, field vole *Microtus agrestis*, and common vole *Microtus arvalis*; in the Crimea, mammoth is missing, but Pleistocene wild ass *Equus hydruntinus* and “obscure” vole *Microtus obscurus* are present.

CONCLUSIONS

The reconstructed biogeographical provinces illustrate the specific environmental and climatic conditions of the Briansk Interstade. Analogues of the modern natural zones did not exist at this time on the Russian Plain. The reconstructed landscapes reflect the moderately cool (cold with respect to today) climate of this period, when the majority of northern subarctic plant and mammal species extended their ranges considerably to the south to the Central Russian Plain. At the same time steppic species penetrated farther north and west. This combination shows that the continuous forest zone was destroyed during the Briansk Interstade. The fragmented forested islands were maintained in the territories with highly diverse relief giving many local habitats.

The differences between biogeographical provinces were not severe at time; subarctic plants and mammals were present in practically all of them while forest species, more sensitive to cold, dry conditions, were not particularly abundant on the Russian Plain. However, both the periglacial forest-steppe and forest-tundra steppes were more extensive in Briansk time than during the Late Valdai glaciation. The Briansk Interstade therefore had a more moderate climate than what followed. The composition of Briansk mammal and plant communities shows that all the species have responded to climatic conditions in a Gleasonian manner. Species dispersed in different directions and in different scales influenced the appearance of radically new communities and biomes. This was found also when compiling and analyzing the Late Pleistocene mammal database for the territory of the former Soviet Union (Markova *et al.*, 1995). In that paper we outlined ranges of ecologically important taxa during four principal time intervals of Valdai Glaciation and compared them with the modern areas of the same taxa. Similar results have been received for Western and Central Europe (Musil, 1985). The main part of Western and Central Europe features a very complicated topographic structure and abounds in mountains and uplands and therefore local habitats; that resulted in higher species richness than that of the Russian Plain. A huge amount of data on the Late Pleistocene and Holocene mammal of the United States are compiled in Faunmap database (Faunmap Working Group, 1996). As follows from the data, mammals dispersed diachronically, in different directions and at different rates under climatic changes. The nonanalogue mammal communities of complicated structure existed in North America during the Last Glaciation. Their main difference from the European faunal provinces is the peculiarity of their taxonomic structure. In addition, North American mammal communities are distinguished by a longitudinal arrangement, which may be attributed

to the Rocky Mountains' barrier influence on the temperature and moisture gradients in North America, as well as to the fact that the Wisconsin ice sheet spread farther south as compared the Valdai glacier on the Russian Plain.

The Briansk climate undoubtedly was more severe than that of the Holocene, with lower winter temperatures and low precipitation (Frenzel, 1992). Several factors contributed to this effect: the existence of a small ice sheet in Scandinavia; significant volumes of marine ice, which influenced the continental precipitation deficit; the wide distribution of permafrost; and decreased air mass transfer from the west to the east (Markov *et al.*, 1965; Velichko, 1973; Shackleton and Opdyke, 1977; Markov, 1986; van Andel and Tzedakis, 1996). These climatic conditions influenced the appearance and wide distribution of different types of periglacial vegetation and the "mixed" mammalian communities of the Russian Plain, which do not have modern analogues.

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