Universiteit Leiden
The Netherlands

Evolution of European ecosystems during pleistocene-holocene transition (24-8 Kyr BP)

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Citation
Markova, A. K., Kolfschoten, T. van, & Puzachenko, A. (2019). *Evolution of European ecosystems during pleistocene-holocene transition (24-8 Kyr BP)*. Moscow: GEOS Press. Retrieved from https://hdl.handle.net/1887/3217445

Version:	Publisher's Version
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Downloaded from:	https://hdl.handle.net/1887/3217445

Note: To cite this publication please use the final published version (if applicable).

INSTITUTE OF GEOGRAPHY OF RUSSIAN ACADEMY OF SCIENCES

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EVOLUTION OF EUROPEAN ECOSYSTEMS DURING PLEISTOCENE–HOLOCENE TRANSITION (24–8 KYR BP)

Collective monograph

Responsible editors:
Anastasia K. Markova, Thijs van Kolfschoten
and Andrey Puzachenko

Moscow
Institute of Geography RAS
GEOS Press
2019

UDK 551.79(4) + 551.807(4)
BBK D432-72-995(4)

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The figure on the cover sheet:
Woolly mammoth *Mammuthus primigenius*.
Painted by *E.O. Pylenkova*

This is the translation of the book published in Russian in 2008 уг / Эволюция экосистем Европы при переходе от плейстоцена к голоцену (24–8 тыс.л.н.). KMK Scientific Press, Moscow, 2008, 556 pp./.

Evolution of the European Ecosystems during Pleistocene–Holocene transition (24–8 куг BP) / Edited by Anastasia Markova, Thijs van Kolfschoten and Andrey Yu. Puzachenko – Moscow, GEOS, 2019. 279 p.
ISBN 978-5-89118-795-5

This book provides detailed reconstructions of mammal assemblages, vegetation communities and ecosystems of Europe during the Pleistocene-Holocene transition. The reconstructions are based on palaeobiological data, united in databases and with help of mathematic methods. Reconstructions are made for the five most successful time intervals. The text is illustrated by numerous maps of mammal and plant ranges, mammal assemblages, plant communities and European ecosystems. The publication is intended for geographers, biologists, and palaeontologists.

ISBN 978-5-89118-795-5

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INTRODUCTION

Thijs van Kolfschoten, Anastasia Markova and Andrey Puzachenko

The transition between the Pleistocene and Holocene, i.e. between the last glaciation and the Holocene interglacial, was characterized by drastic changes in Earth biota, clearly revealed in the Northern Hemisphere. Huge amounts of palaeobiological data, characterizing these changes, have been collected during past few decades. Several extensive databases with palaeobotanical (mainly palynological) data and palaeotheriological data were elaborated in a number of European countries. However, these data are related to separate regions of Europe and do not cover the entire territory of northern Eurasia. The participants of the project called "The evolution of the mammalian fauna and flora in Western, Central and Eastern Europe during the Pleistocene – Holocene transition (25–10 kyr B.P.)" attempted to unite palaeobiological data in a joint database, and to analyze them together and elucidate the peculiarities of the European ecosystems during different temporal intervals of the Late Pleistocene-Holocene transition. Another goal was to distinguish the main trends in ecosystem evolution under climatic changes and to reconstruct their regional peculiarities.

A group of Dutch and Russian scientists carried out this research in the frame of the cooperation between The Netherlands Organization on Scientific Research (NWO) and the Russian fundamental basic research foundation (RFBR). The team of Dutch/ Russian researchers included specialists of different profiles: researchers of fossil mammals (Thijs van Kolfschoten, Anastasia Markova, Nikolai Smirnov, Pavel Kosintsev, and Ilya Golovachev), palynologists (Alexandra Simakova and Sjoerd Bohncke), an archaeologist (Alexander Verpoorte), a specialist in periglacial processes (Joanne Mol) and a specialist in mathematical analysis and electronic mapping (Andrey Puzachenko). Liselotte Takken helped collecting Western European mammalian data. Kelly Fennema and Naomi Prins assisted in editing the English language. Prof. Natalia Leonova from the Moscow State University gives effectual help in editing of Chapter 7 and Dr. Margarita Faustova (Institute of Geography RAS) helps with editing of Chapter 3. We thank them very much.

Data from several Russian and Western European databases, elaborated earlier, were united in a joint database, including the Leiden database, the Cambridge Stage 3 – database, a Western European pollen database and PALEOFAUNA and PALEOFLORA databases for Eastern Europe. The joint database was completed with additional data from recent publications and from recent studies by the participants of the project.

In order to get an idea about biotic changes during the Late Pleistocene-Holocene transition we divided the period between 24 and 8 kyr. BP into 5 intervals: the Last Glacial Maximum (24–17 kyr BP), the Late Glacial Transition (LGT) (17–12,4 kyr BP), the Bølling/Allerød Interstadial complex (BAIC) (12,4–10,9 kyr BP), the Younger Dryas (YD) stadial cooling (10,9–10,2 kyr BP) and the Early Holocene (10,2–8 kyr BP).

Well-dated palaeobiological data of Europe (accompanied by radiocarbon dates) were collected to analyze the ecosystems for the different temporal intervals. These analyses were carried out with help of mathematical methods, excluding subjective interpretations of the dataset. We also carried out electronic mapping of plant and mammal distribution, geographical ranges of mammal assemblages, plant communities and ecosystems for the 5 intervals. This research, for the first time, comprises a detailed reconstruction of European biota, during the dramatic time of transition between periglacial ecosystems of the last glaciation and the forming of zonal ecosystems of the Holocene interglacial. The peculiarities of human occupation and economic activities of Late Paleolithic and Mesolithic people, their dependence on the climate, environmental conditions and game dependency are analyzed in chapter 7.

Reconstructing European ecosystems during the five successive intervals of the Late Pleistocene-Holocene transition permits to elucidate the evolution of biotic changes for the first time and explains their trends, rates and regional peculiarities. The data presented in this book could form the base for models of future European ecosystem changes under predicted climatic alternations of different intensiveness and direction.

This monograph was done in a frame of the Institute of Geography RAS scientific theme No 0148-2019-0007 "Assessment of physical geographic, hydrological and biotic changes in the environments and their consequences for the development of the basis for a sustainable environmental management".

The first version of this book ("Evolution of European Ecosystems during Pleistocene – Holocene transition (24–8 kyr BP", A. Markova and T. van Kolfschoten, eds., KMK Scientific Press, Moscow, 2008) has been published in Russian. Unfortunately this book is not well known in Western European and other countries because of the difficulties with Russian language. So, we decided to publish the English version of this book. We understand very well that a lot of new palaeobiological materials appear during last ten years. We hope to involve them in our future publications

Chapter 1

DATABASES AND GEOGRAPHICAL DISTRIBUTION OF THE LOCALITIES

Anastasia Markova and Ilya Golovachev

In the studies in the framework of the NWO-RFBS project "The evolution of the mammalian fauna and flora in Western, Central and Eastern Europe during the Pleistocene–Holocene transition (24,000–8,000 yrs BP)", two main electronic databases were used: the PALEOFAUNA (Fig. 1.1) database for the mammal data, and the PALEOFLORA (Fig. 1.2) database for the plant data. Eastern European data were collected in these databases (Markova *et al.*, 1995). The structure of these databases was elaborated earlier. To unite the Western and Eastern European information, the mammalian data collected in the Leiden databases and the Cambridge databases were included in a joint database. The pollen data from the European pollen database were also used in this work. New information from literature was analyzed and also input into the joint databases.

The principal information that these databases cover is:

- information on mammal or plant species composition in the locality;
- information on the geographical position of the localities (coordinates, river basins, etc.);
- ^{14}C and TL dates, as well as the results of the relative dating methods (geological position, archaeological cultures, etc.). We used in this study uncalibrated ^{14}C data;
- References.

To reconstruct the principal changes in mammal assemblages and plant communities we defined five temporal intervals covering the Late Pleistocene and Early Holocene, based on more or less uniform climatic conditions (for details, see chapter 3):

I. The Last Glacial Maximum (≤24,000 – >17,000 yrs BP);

II. The Late Glacial Transition (<17,000 – ≥12,400 yrs BP);

III. The Bølling–Allerød Interstadial complex (≥12,400 – <10,900 yrs BP);

IV. The Younger Dryas (<10,900 – ≥10,200 yrs BP);

V. The Preboreal–Boreal periods of the Early Holocene (<10,200 – ≥8,000 yrs BP).

Geographical distribution of the localities

For every interval, the distribution of the localities yielding mammal and plant data is presented in Figs. 1.2–1.11.

The complex information from 362 European mammalian sites and from 831 spore-pollen localities (3741 samples) of Late Pleistocene – Early Holocene age (united in the form of databases), was collected during an in-depth study. The distribution of localities is irregular in most of the intervals due to lack of information. Most of the mammal and plant localities are concentrated in the central part of Europe.

GIS and a number of mathematic methods were used to construct the maps of mammal and plant ranges, mammal assemblages and plant communities, and also to reconstruct palaeoecosystems in Europe during the five Late Pleistocene – Early Holocene intervals, which can be distinguished by their climatic conditions.

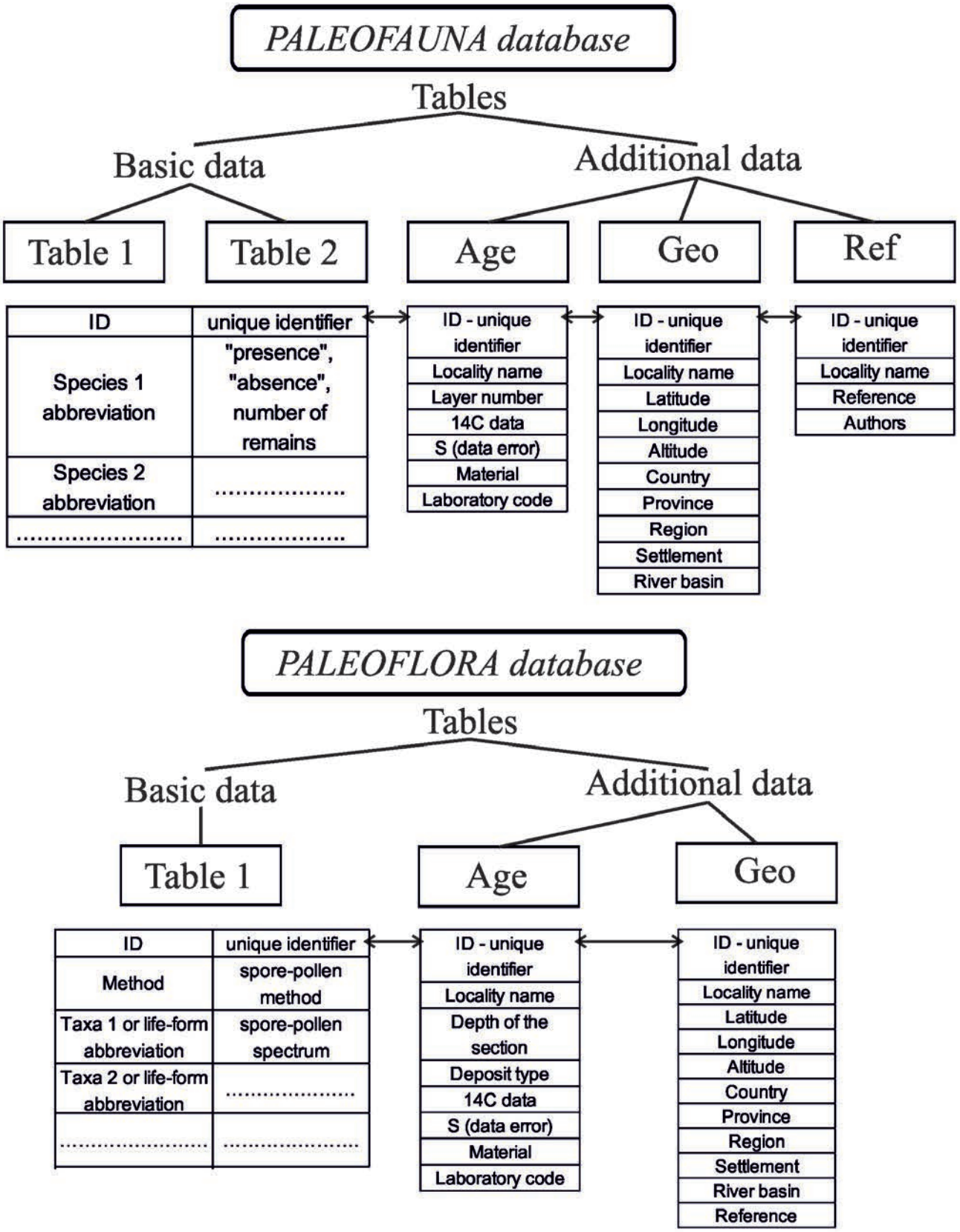

Fig. 1.1. *Structure of the PALEOFAUNA and PALEOFLORA databases*

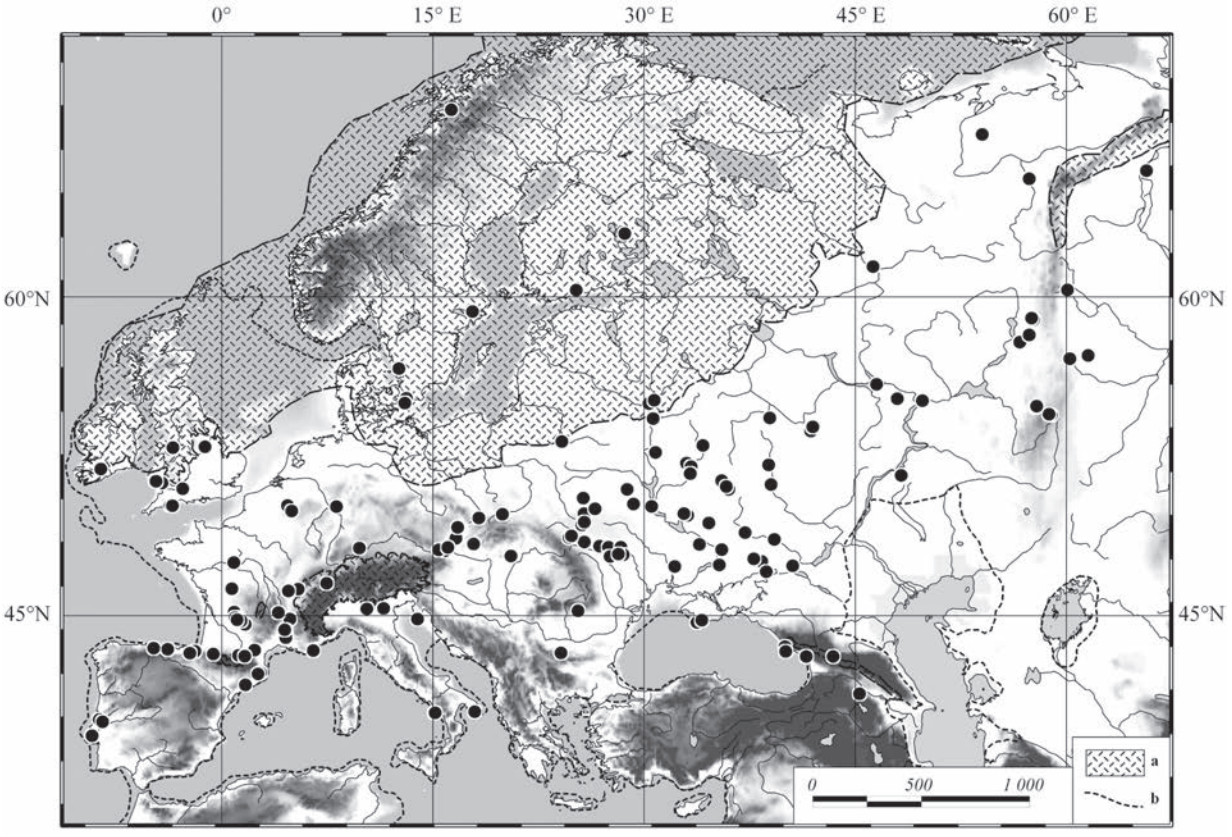

Fig. 1.2. *Last Glacial Maximum (LGM) mammal localities; a – ice sheets; b – coastline*

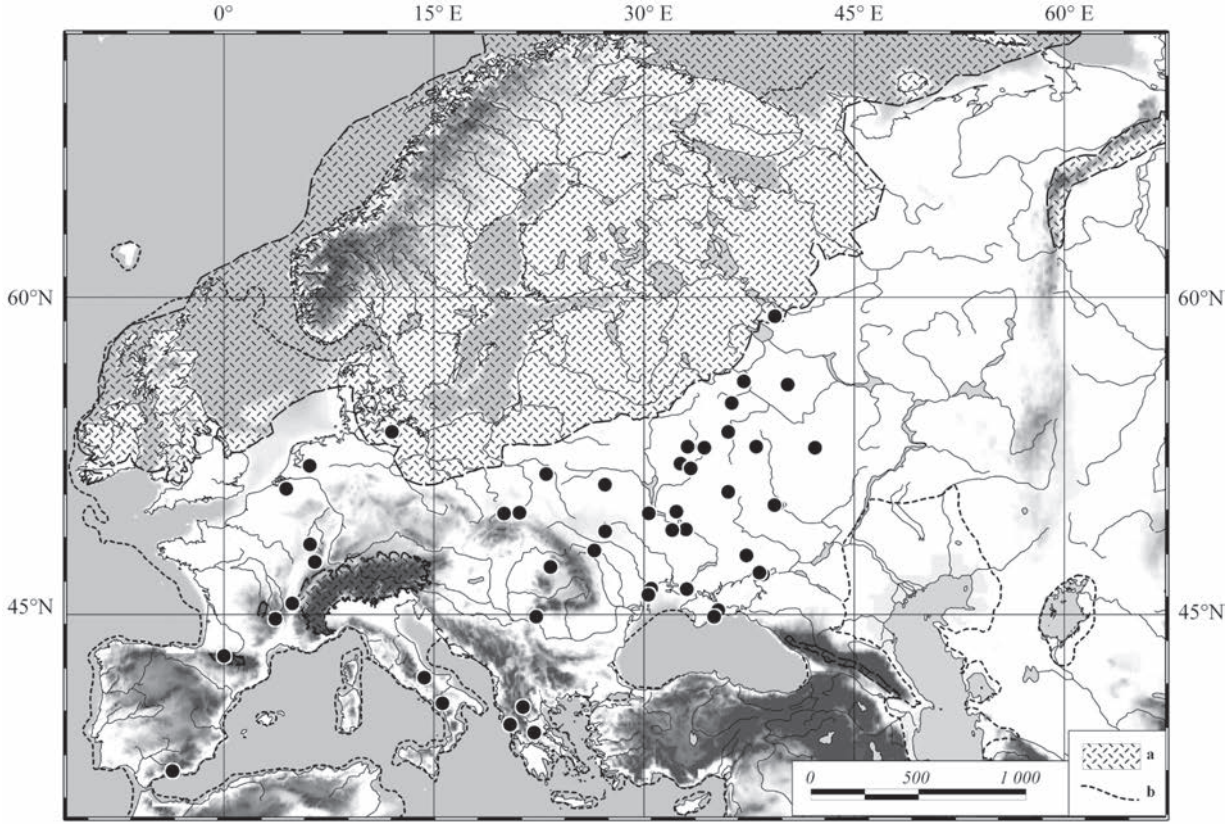

Fig. 1.3. *Last Glacial Maximum (LGM) plant localities; a – ice sheets; b – coastline*

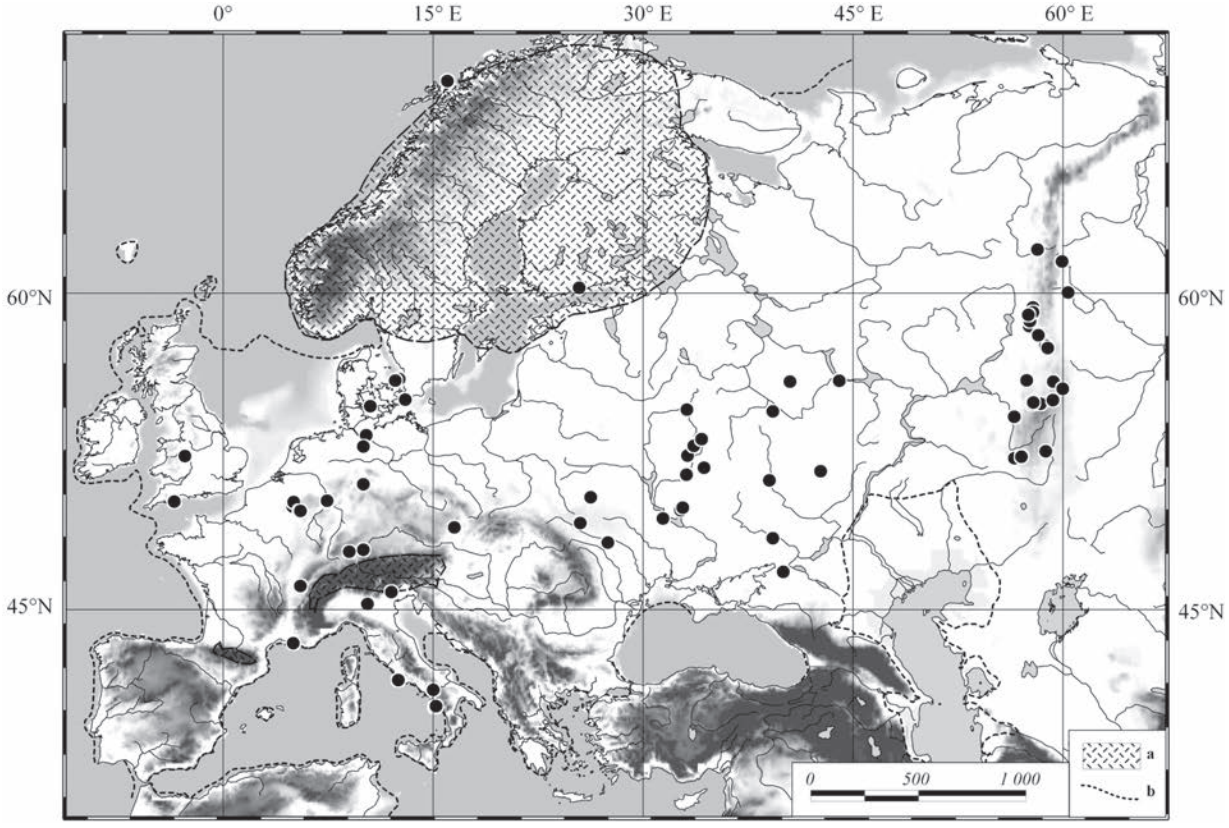

Fig. 1.4. *Late Glacial Transitional (LGT) mammal localities; a – ice sheets; b – coastline*

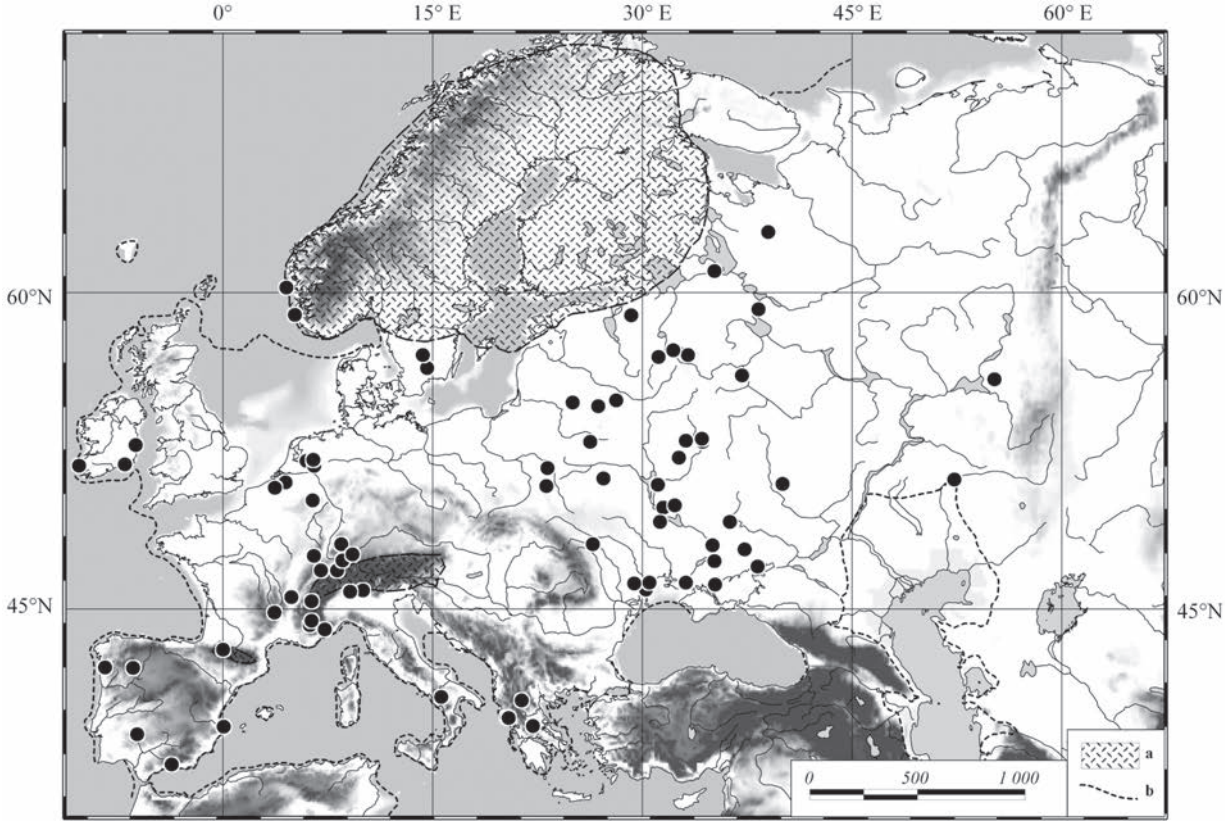

Fig. 1.5. *Late Glacial Transitional (LGT) plant localities; a – ice sheets; b – coastline*

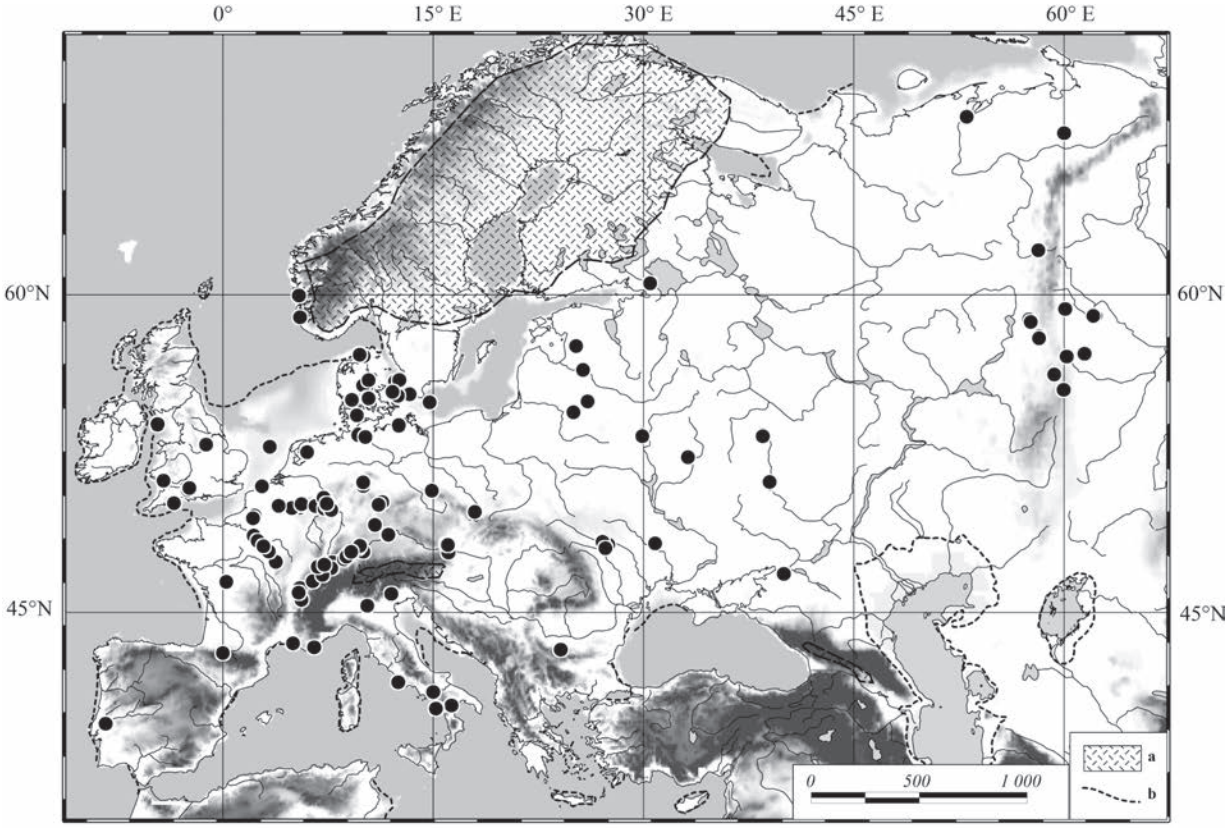

Fig. 1.6. *Bølling-Allerød Interstadial complex (BAIC) mammal localities; a – ice sheets; b – coastline*

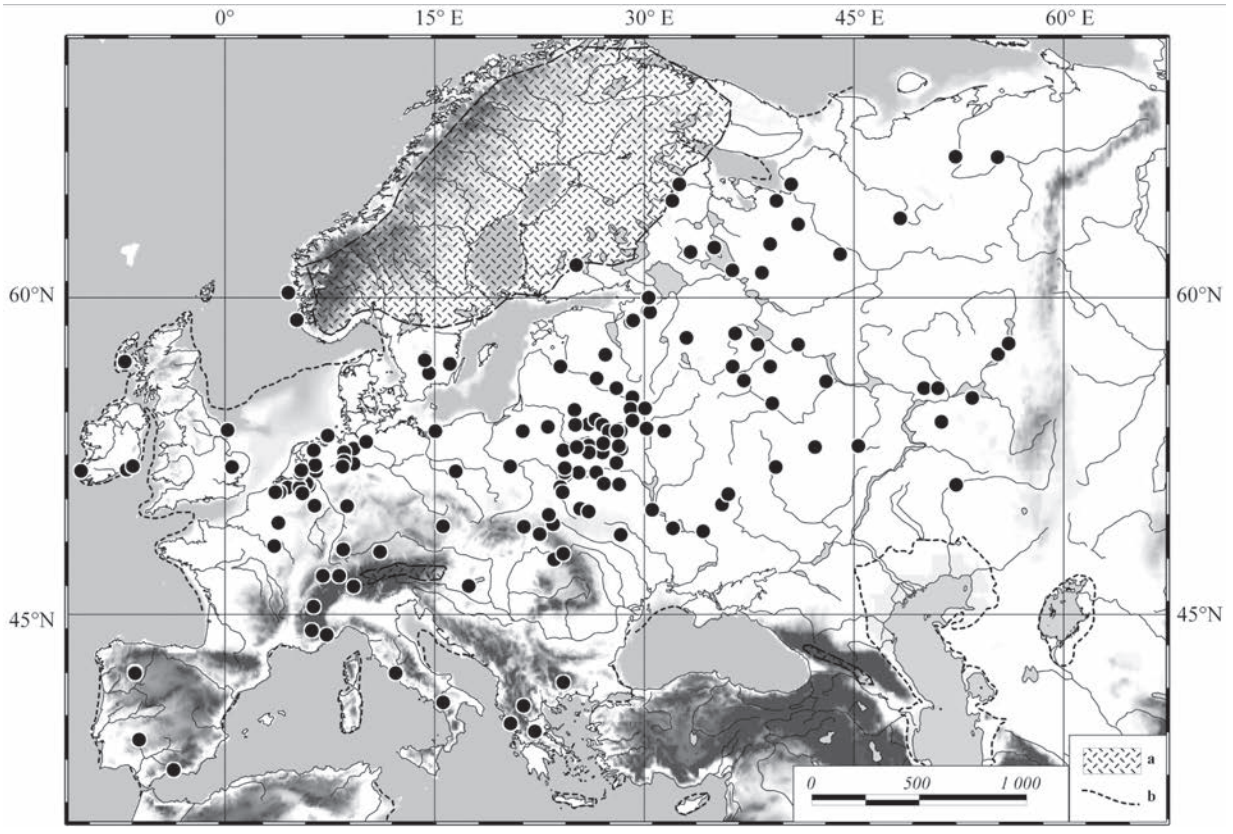

Fig. 1.7. *Bølling-Allerød Interstadial complex (BAIC) plant localities; a – ice sheets; b – coastline*

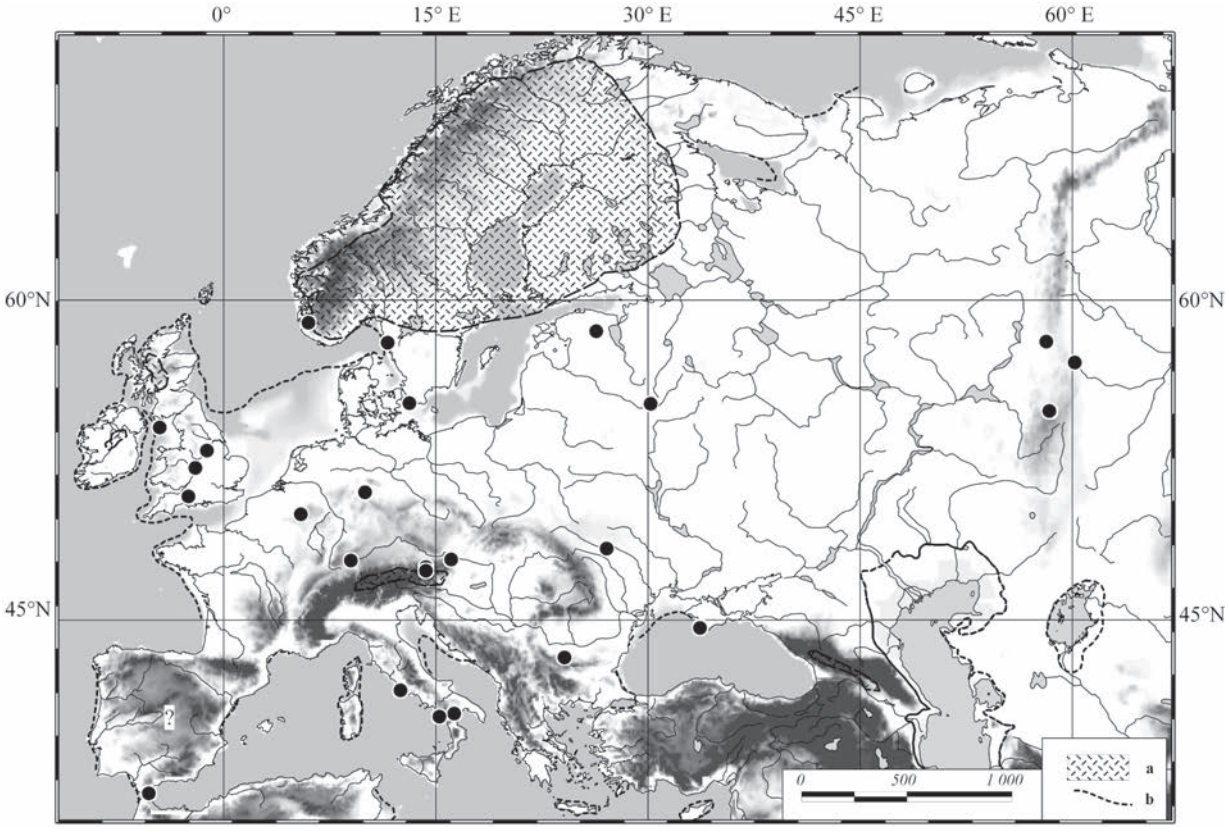

Fig. 1.8. *Younger Dryas mammal localities; a – ice sheets; b – coastline*

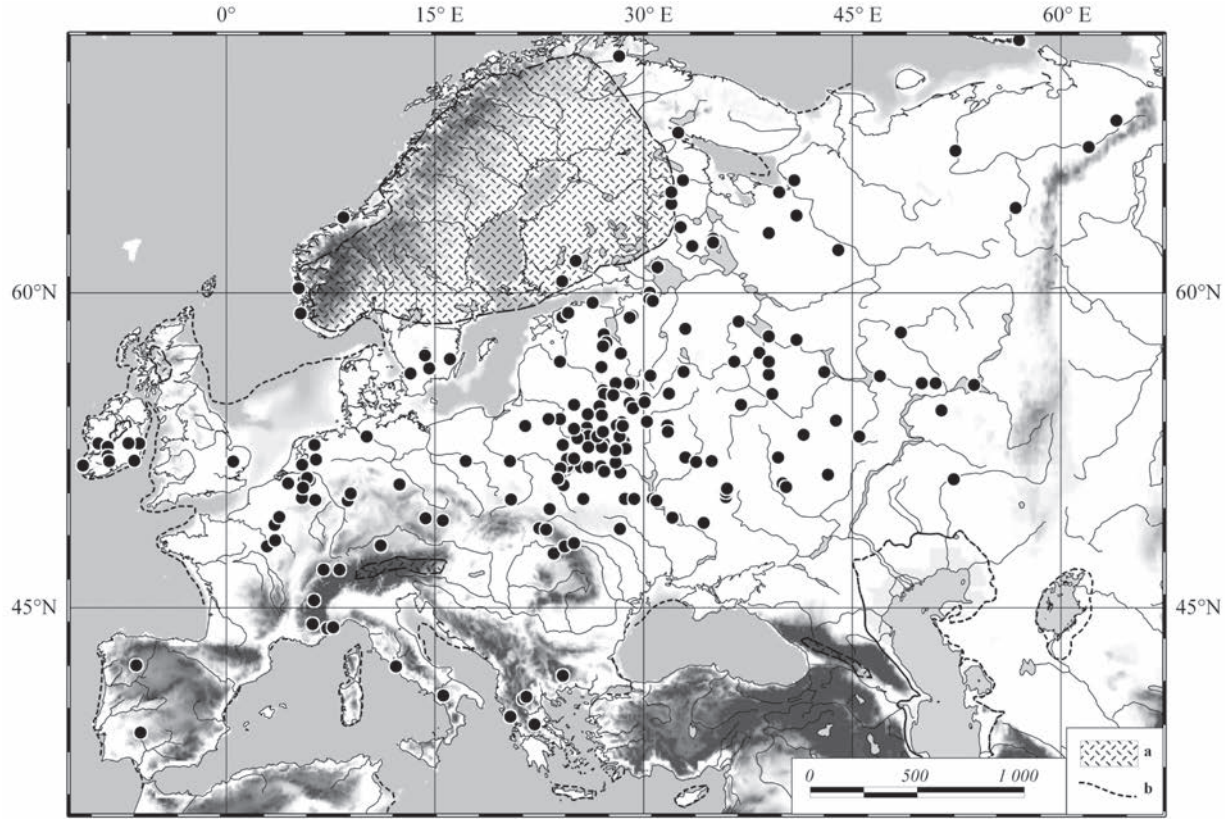

Fig. 1.9. *Younger Dryas plant localities; a – ice sheets; b – coastline*

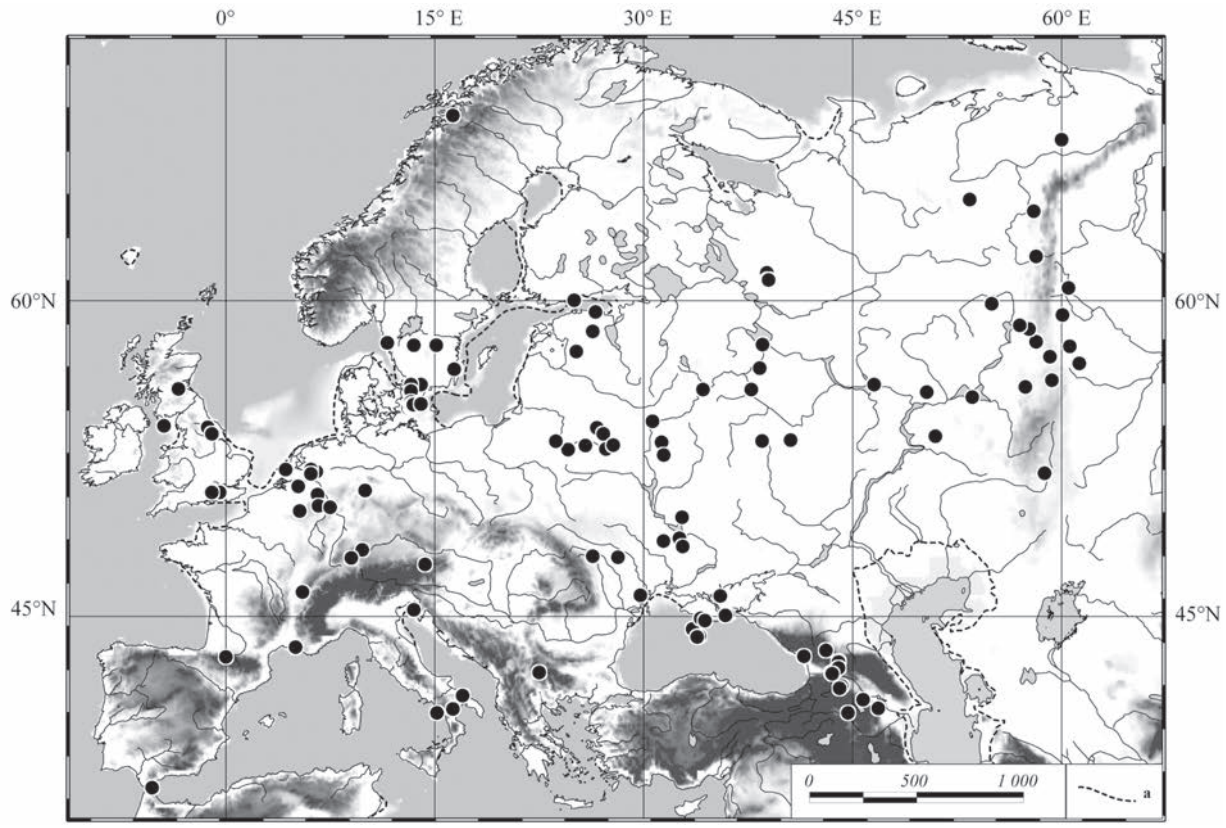

Fig. 1.10. *Preboreal–Boreal (Early Holocene) (PB–BO) mammal localities; a – coastline*

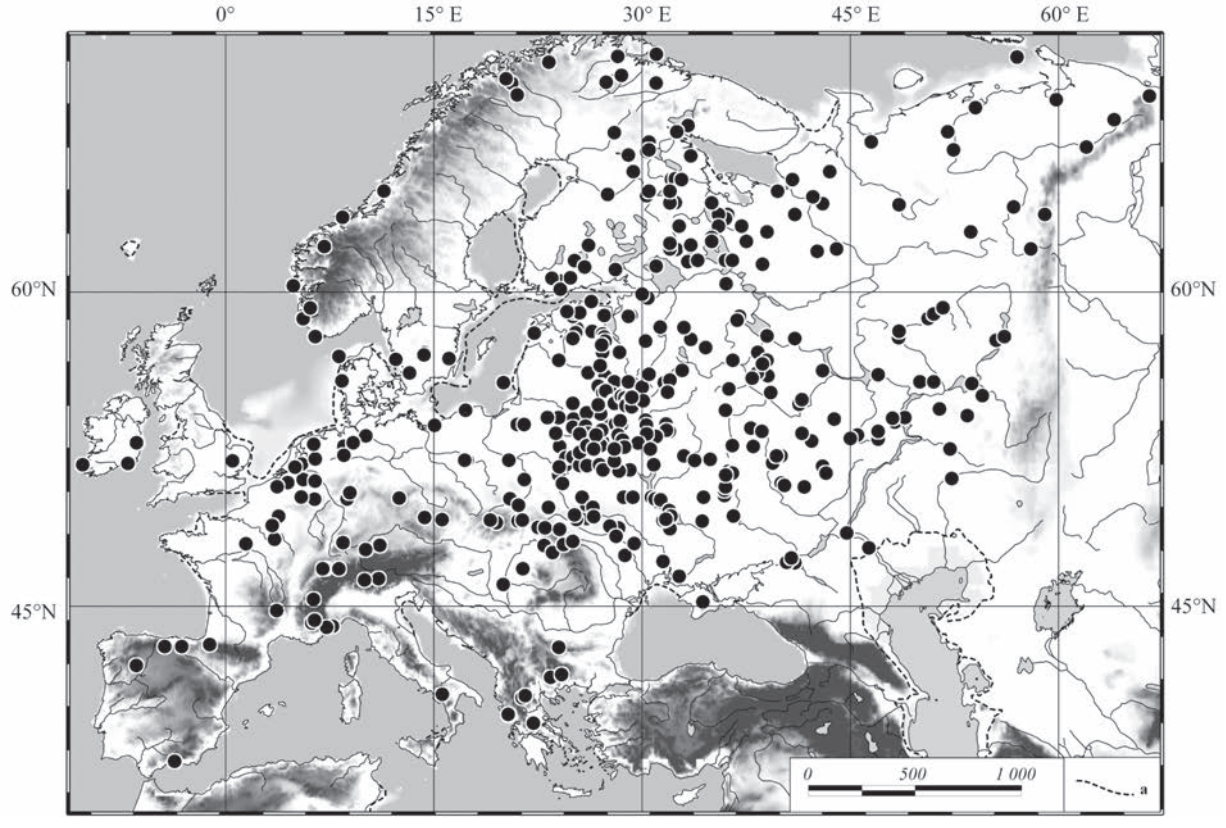

Fig. 1.11. *Preboreal–Boreal (Early Holocene) (PB–BO) plant localities; a – coastline*

Chapter 2
ANALYTICAL APPROACHES

2.1. METHODS TO INTERPRET SPORE-POLLEN ASSEMBLAGES

Sjoerd Bohncke and Alexandra Simakova

Analysis of the collected material was conducted using traditional methods of pollen spectra interpretation based on correlation characteristics between fossil and sub-fossil spectra for different vegetation zones, taking into account the genetic types of deposits (Grichuk and Zaklinskaya, 1948; Fedorova, 1976; Isaeva-Petrova, 1979), as well as using mathematical methods (Markova *et al.*, 2002a,b). Special attention was given to the quantification of non-arboreal taxa from pollen data of peat bog deposits. The sub-fossil pollen spectra from peat deposits located in the forest and forest-steppe zones contain an overrepresentation of spores and an overrepresentation of tree and shrub pollen grains (Nikiforova, 1978; Syrova and Krenke, 1992).

For forest phytocoenoses reconstructions, the high value of tree pollen grains and the presence of forest-indicating plant species in the pollen spectra were taken into account. For example, surface samples from the coniferous forests of North-Eastern Europe (the Mari AR territory and the Kirov area) show that *Picea* pollen constitute 5–51% (Nikiforova, 1977; Shalandina, 1985; Guikova, 2002), and on the southern border of the *Picea* area it constitutes 1–4% of the total arboreal pollen. In the recent spectra of the forest-steppe zone, *Picea* grains are very rare (Chupina, 1970; Isaeva-Petrova, 1979; Fedorova, 1976).

In order to define palaeo-phytocoenoses in the pollen spectra, we used the following criteria:

- as a whole, in the spore and pollen spectra representing forest phytocoenoses more than 60% is pollen of trees and shrubs, and *Picea* pollen reaches more than 4%, and the presence of indicator forest taxa such as *Cornus*, *Lonicera*, *Sorbus*, *Viburnum*, *Euonumus*, *Lycopodium clavatum*, *Lycopodium complanatum*, *Pteridium,* etc. is recorded:
- the following pollen spectra indicate tundra and forest tundra communities: the tree and shrub species amount to less than 40%, while spores vary from 20 to 50%. A presence of hypoarctic plants such as *Alnus verides*, *Selaginella selaginoides*, *Betula nana*, *Salix*, *Dryas*, Saxifragaceae, *Empetrum*, *Lycopodium apressum*, and *Sphagnum* was also recorded in the pollen samples (Grichuk and Zaklinskaya, 1948).
- the steppe and semi-desert pollen spectra are characterized by the presence of *Ephedra*, *Kochia*, *Eurotia ceratoides*, *Helianthemum*, *Artemisia*, Chenopodiaceae, and Poaceae. The phytocoenoses that represents steppe vegetation was determined by the dominance of non-arboreal plants. Thus, *Artemisia* prevails in pollen spectra of herb – grass – herb and wormwood – grass steppes. *Herbetum mixtum* dominates in meadow, feather grass – herb, and sheep's fescue – feather grass – herb

steppes. Poaceae dominate in wormwood – sheep's fescue steppes and are the subdominants of feather grass – sheep's fescue – herb steppes. Chenopodiaceae occur as one of the subdominants of steppe pollen spectra and characterize feather grass – herb, wormwood – grass steppes (Chypina, 1970; Serebriannaya, 1978). Spores of *Sphagnum* in steppe spectra are absent. In semidesert coenosis the amount of Chenopodiaceae constitutes more than 38%, spores are less than 7%, and trees are more than 7% (Grichuk and Zaklinskaya, 1948; Monoszon, 1985; Bolikhovskaya, 1998).

The analysis of collected palynological materials made it possible to reconstruct the vegetation cover for the different time slices and to study the temporal dynamics of palaeophytocoenosis during the Late Pleistocene and early Holocene.

2.2. INDICATOR SPECIES AND ECOLOGICAL GROUPS OF MAMMALS

Anastasia Markova

Morphological similarity of the recent and fossil mammals – the testimony of their ecological similarity

Noting the morphological similarities of Late Pleistocene and Holocene mammal fossils and modern ones, representing different phylogenetic lineages, we could suppose that these similarities reflect an adaptation to specific environments. The structure of the dental apparatus, skulls, and extremities suggest significant specialization and adaptation to specific nutrition and locomotion. It was shown that in the modern interfluvial zonal assemblages, animal population includes species adapted to the environmental conditions of that zone. Such adaptations are the result of the long process of evolution. This fact permits us to use the data of the mammal species composition for the reconstructions of past environments. Most reliable are the reconstructions based on mammals that are still extant.

Main ecological groups of mammals

Modern mammals inhabit all the natural zones of Europe: from the Arctic tundra to deserts and high mountain belts. Many of the mammals are stenobiotic and adapted to very definite environments. Often they inhabit rather restricted territories and could be good indicators of modern as well as past environments. Collared lemming, polar bear, polar fox, musk ox and some others exist only in tundra zones; elk, squirrel, European lynx, the red-backed *Clethrionomys* and pine voles *Terricola* and many others inhabit different types of forests; saiga, corsac-fox, marmot, ground squirrels, steppe and yellow lemmings, common hamster *Cricetus*, dwarf hamster *Cricetulus*, five-toed jerboas *Allactaga*, mole-rat *Spalax*, mole-vole *Ellobius* and others are typical of the open landscapes, such as forest-steppe, steppes and semi-desert; sand rat *Meriones* and great gerbils *Rombomus* are characteristic of deserts; goat *Capra*, chamois *Rupicapra*, argali *Ovis ammon*, snow-vole *Chionomys*, long-clawed mole-vole *Prometheomys* and others inhabit the mountains.

Some other species have large ranges and could inhabit different natural zones. Many carnivores occur in different environments and the main reasons for their distribution is the presence of certain prey. A large group of animals is connected with different bodies of water and could penetrate along rivers far to the north up to the tundra zone, and far to the south up to the steppes. They include water-vole *Arvicola*, root-vole *Microtus oeconomus* and some others. Information about these animals can be used in the reconstruction of past environments, but they carry less information than the first group of stenobiotic mammals (Flint *et al*., 1970; Chernov, 1975; Görner and Hackethal, 1988; Gromov and Erbaeva, 1995; Aristov and Baryshnikov, 2001).

Thus, by using the information on modern adaptations of mammals we could try to reconstruct past environments. As described in Chapter 2, we have collected in the databases extensive information on the Late Pleistocene and Early Holocene mammal species composition and distribution in Europe. The geochronological data helps unite the mammalian data for the defined temporal intervals. To reconstruct the environmental changes, we have used information on the ecological adaptations of modern mammals. We distinguished several principal

ecological groups of mammals, connected with forested (taiga, mixed and broad-leaved forests), open (steppe, forest-steppe and semi-desert and desert), tundra and forest-tundra landscapes, and mountain environments. More than one hundred indicator mammal species were included in Table 2.1. We have excluded from this table the group of ubiquitous animals which inhabited several natural zones, such as *Arvicola*, *Microtus oeconomus*, *Vulpes vulpes*, *Mustela erminea* and some others, because this information does not help much in the environmental reconstructions. We also have not included the list of mammals extinct by the end of the Pleistocene: mammoth, woolly rhinoceros, giant deer, steppe bison, aurochs, cave hyena, cave lion, cave bear and others. The information on their ecology is dependent on the paleontological (theriological, palynological, etc.) data from the same sites. By using this information, we could also reveal the principal characteristics of their adaptations and use them in the environmental reconstructions of the past. Many papers have been devoted to this subject (Vereshchagin, 1971; Vangengeim, 1977; Vereshchagin and Baryshnikov, 1980; Musil, 1985; Graham, 1986; Kuzmina, 1989; Guthrie, 1990; Stuart, 1991; Kahlke, 1994; Baryshnikov, 1995; Lister and Sher, 1995; Markova *et al*., 1995; Baryshnikov and Markova, 2002; and others). The accompanying data indicates the good adaptation of extinct herbivores (mammoth, woolly rhinoceros, giant deer, steppe bison, aurochs, and others) to the different types of open periglacial landscapes of the glacial epoch.

All spectra of this ecological information related to extinct mammals, as well as to mammals which have modern ancestors, help in reconstructions of past environments.

Table 2.1

Ecology of modern indicator mammals

Taxa	Ecological units										
	Arctic desert	Tundra and forest-tundra	Taiga	Mixed and broad-leaved forests	Forest-steppe	Steppe	Semi-desert	Desert	Mountain Forests	Mnt Alpine belt	Mnt steppe
Sorex minutissimus – Eurasian least shrew			+	+	+						
Talpa europaea – European mole			+	+	+						
Lepus tolai – tolai hare						+	+				
Ochotona pusilla – steppe pika					+	+	+				
Pteromys – flying squirrel				+	+						
Eutamius – Siberian chipmunk			+	+	+						
Sciurus vulgaris – red squirrel			+	+	+				+		
Marmota bobak – bobak marmot					+	+					
Spermophilus – suslik (all species)					+	+	+				
Castor fiber – beaver			+	+	+						
Glis glis – fat dormouse				+	+				+		
Eliomys quercinus – garden dormouse				+	+				+		
Muscardinus – dormouse				+	+				+		
Dryomys nitedula – forest dormouse				+	+				+		
Myomimus personatus – musked mouse-tailed dormouse							+				
Cricetus cricetus – European hamster					+	+	+				
Mesocricetus raddei – Ciscaucasian hamster					+	+					+
M. brandti – Brandt's hamster					+						+

Continued table 2.1

Taxa	Ecological units										
	Arctic desert	Tundra and forest-tundra	Taiga	Mixed and broad-leaved forests	Forest-steppe	Steppe	Semi-desert	Desert	Mountain Forests	Mnt Alpine belt	Mnt steppe
Allocricetus eversmanni – Eversmann hamster						+	+	+			
Cricetulus migratorius – grey hamster					+	+	+	+			
Myospalax – zokor						+					
Nannospalax leucodon – lesser mole rat					+	+					+
Spalax microphthalmus – Russian mole rat					+	+					
S. giganteus – giant mole rat							+				
Meriones libycus – Libian jird							+	+			
M. persicus – Persian jird							+	+			
M. vinogradovi – Vinogradov's jird											+
Dicrostonyx torquatus – collared lemming		+								+	
Myopus schisticolor – wood lemming			+								
Lemmus lemmus & *L. sibiricus* – Norway & Siberian lemmings		+								+	
Clethrionomys glareolus – red-backed vole			+	+	+				+		
Clethrionomys rufocanus – grey vole			+	+							
Clethrionomys rutilus – northern red-backed vole			+	+							
Microtus hyperboreus – North Siberian vole		+									
M. middendorffii – Middendorf's vole		+									
M. agrestis – field vole			+	+	+						
M. (Terricola) subterraneus – pine vole				+	+				+		
M. (T.) majori – Minor Asian vole									+		
M. socialis – social vole					+	+	+				+
M. (Stenocranius) gregalis – narrow-skulled vole		+			+	+					
Eolagurus luteus – yellow steppe lemming					+	+	+				
Lagurus lagurus – steppe lemming					+	+					
Ellobius talpinus – northern mole-vole						+	+				
E. lutescens – mountain mole-rat											+
Apodemus speciosus – Asian forest mouse				+	+						
Sylvaemus sylvaticus / S. uralensis – wood mouse / pygmy wood mouse				+	+				+		
Apodemus mystacinus – broad-toothed mouse									+		

Continued table 2.1

Taxa	Ecological units										
	Arctic desert	Tundra and forest-tundra	Taiga	Mixed and broad-leaved forests	Forest-steppe	Steppe	Semi-desert	Desert	Mountain Forests	Mnt Alpine belt	Mnt steppe
Sylvaemus flavicollis – yellow-necked mouse									+		
Sicista subtilis – southern birch mouse					+	+	+				
Sicista betulina – northern birch mouse											
Dipus sagitta – northern three-toed jerboa							+	+			
Scirtopoda telum – thick-tailed three-toed jerboa						+	+	+			
Jaculus – desert jerboa							+	+			
Eremodipus lichtensteini – Lichtenstein's jerboa							+	+			
Allactaga major – great jerboa					+	+	+				
A. severtzovi – Severtzov' jerboa							+	+			
A. williamsi – Williams' jerboa											+
A. bobrinski – Bobrinski's jerboa							+	+			
A. saltator – Mongolian five-toed jerboa						+	+	+			
Pygeretmus pumilio – dwarf fat-tailed jerboa							+	+			
Hystrix leucura – Indian porcupine							+	+			+
Vulpes lagopus – Polar fox		+									
Vulpes corsac – corsac fox						+	+	+			+
Nyctereutes procyonides – raccoon dog				+							
Cuon alpinus – red dog									+		
Ursus arctos – brown bear		+	+	+	+				+		
Ursus maritimus – Polar bear	+	+									
Mustela eversmanni – Russian polecat						+	+				
Mustela erminea – ermine stoat		+	+	+	+	+			+		
M. nivalis – least weasel		+	+	+	+	+			+		
M. sibiricus – Siberian weasel				+	+	+					
M. altaica – mountain weasel				+					+		
Vormela peregusna – marbled polecat						+	+	+			
Martes zibellina – sable				+					+		
M. martes – common marten			+	+	+	+					
M. foina – beech marten									+		
M. flavigula – yellow-throated marten			+	+	+						
Gulo gulo – wolverine		+	+								
Meles meles – badger			+	+	+	+					
Hyaena hyaena – common hyena						+	+	+			+

Continued table 2.1

Taxa	Ecological units										
	Arctic desert	Tundra and forest-tundra	Taiga	Mixed and broad-leaved forests	Forest-steppe	Steppe	Semi-desert	Desert	Mountain Forests	Mnt Alpine belt	Mnt steppe
Felis silvestris – wood cat			+	+	+						
Felis libyca – African wild cat						+					
F. chaus – jungle cat				+	+						
F. pardus – leopard									+		
Lynx lynx – common lynx			+	+	+						
Otocolobus manul – manul						+	+				
Caracal caracal – caracal						+					
Acinonyx jubatus – cheetah						+					
Sus scrofa – wild boar				+	+				+		
Cervus elaphus – red deer				+	+				+		
Cervus dama – fallow deer				+					+		
Alces alces – elk		+	+	+							
Rangifer tarandus – reindeer		+	+								
Capreolus capreolus – roe deer				+	+				+		
Bison bonasus – European bison, wisent				+	+						
Gazella subgutturosa – goitered gazelle						+					
Procarpa gutturosa – Mongolian gazelle						+	+				
Saiga tatarica – saiga					+	+	+				
Ovibos moschatus – muskox	+	+									
Ovis ammon – argali						+	+			+	+

Possible changes of the ecological preferences of mammals during the Late Pleistocene and the early Holocene

An opinion about some changes in mammal adaptations during the Pleistocene and the Holocene was discussed in some papers (Smirnov, 1993). This opinion is based on the changes in accompanying mammal associations. For example, fossil collared lemming in some sites was only found together with tundra mammals, while in other localities steppe and even forest mammals accompanied it. This fact is explained by Smirnov as the ecological changes of this animal in the past. However, other explanations are also possible.

Firstly, a lot of the sites related to the glacial periods are characterized by non-analogue compositions, when tundra and steppe and sometimes forest animals co-occured (Graham, 1985; Faunmap Working Group, 1996; Markova *et al*., 1995). These data are supported by AMS dating (Stafford *et al*., 1999).

Secondly, these arguments are based mainly on data from mountain regions (the Urals). However, we need to take into consideration that concentrations of fossil bones in mountain cave sites occur due to birds of prey activity. These birds have large ranges and hunt mammals in different mountain belts. After all, the mountain landscapes are characterized by numerous local biotopes, connected with different slope orientations, depressions and so on. Thus, mountain regions are characterized by many ecological niches, and mountain localities

very often include mammals of different ecological niches.

By using materials from sites located on the large plains (for example, the Russian Plain), where the natural zones are more uniform in time and space, we could exclude these mistakes. However, in particular cases, we could find the mammal associations indicating specific ecotones. Taking into account all these cases and excluding the possibilities of re-deposition of mammal bones from deposits of different ages, we can analyze the Late Pleistocene and early Holocene mammal faunas based on ecological preferences of the modern ancestors of fossil animals.

Thus, the information about the species composition in the Late Pleistocene and the early Holocene sites indicates the environmental conditions around a locality and together with the data of other paleontological methods (palynological, carpological, malacological, etc.) it forms the basis of the reconstruction of past environments and past palaeoclimate.

2.3. PROBLEMS OF THE TAXONOMIC STATUS OF LATE PLEISTOCENE MAMMALS IN EUROPE

Pavel Kosintsev

The analysis of mammal species recovered at European sites dated to the end of the Late Pleistocene – beginning of the Holocene revealed some problems in defining the taxonomic status of some mammalian genera and species. It is not uncommon that remains of the same species found in different localities are known under different names. Sometimes, there are differences between lists of the species composition from the same locality published at different times. Such inconsistencies may arise for different reasons.

Firstly, the systematic of species and their groups is still being specified and elaborated. Some sibling species have been discovered and as a result new species were identified (for example, in *Microtus* and *Sylvaemus* genera). The taxonomic status of some species have been revised (e.g. cave hyena and cave lion), and faunal remains in some localities have been determined more precisely at species level (the case of cave bear remains from the Caucasus).

Secondly, there are still unsolved problems in the taxonomic ranks of the Late Pleistocene mammals; in particular, there is uncertainty as to the species status of some taxa (for example, that of the so-called Don hare – *Lepus tanaiticus*), or a number of species in the *Dicrostonyx* and *Equus* genera.

Thirdly, non-valid species names are sometimes used in the description of faunas (such as *Ochotona spelaea*).

The problems related to the assignment of a taxonomic rank are serious enough and deserve special consideration. Below we discuss some taxa of uncertain rank and explain the taxa names used in this work.

Moles – *Talpa europaea* L., 1958 – *Talpa minor* Freudenberg, 1914 – *Talpa magna* Woldrich, 1893

By the end of the Late Pleistocene and in the Early Holocene, there were four species of moles inhabiting Europe (including the Caucasus), namely *Talpa europaea* L., 1758, *T. romana* Thomas, 1902, *T. caeca* Savi, 1822, and *T. caucasica* Satunin, 1908; the same species occur there at present (Gureev, 1979). In most of the published fauna lists, however, there is only genus name cited (*Talpa* sp.), so in our work we identify the taxa only to genus level.

Nevertheless, there are two more mole species listed in some faunal assemblages recovered from Late Pleistocene localities – *T. minor* Freudenberg, 1914, and *T. magna* Woldrich, 1893. A mole close to *Talpa minor* (*T.* cf. *minor*) is listed as a member of the assemblage from final Late Pleistocene localities in Central Poland (Rzebik-Kowalska, 2006). The occurrence in Late Pleistocene assemblages is quite uncommon and is not in agreement with our palaeontological and ecological knowledge of the mole. Before, *T. minor* was known in Europe from localities dated to the Pliocene – Middle Pleistocene (Rzebik-Kowalska, 2000; Cleef-Roders and

Van den Hoek Ostende, 2001). It should also be noted that *T.* cf. *minor* and *T. europaea* remains were recovered from the same layers (Rzebik-Kowalska, 2006), so the two species could coexist. Moles are stenobiont animals, so two or more species may coexist only in extremely favorable environments abounding with food – soil-dwelling invertebrates. At present two coexisting mole species are found in the south of Europe and in the Caucasus (Gureev, 1979). Ecologically, Central Poland at the end of the Late Pleistocene was much less favorable for moles than it is at present, so it is hardly believable that two mole species could inhabit the region together at the time because of unfavorable environments. According to the competitive exclusion principle (Gause, 1934), if two species of similar ecological requirements (as is the case of all the mole species) coexist in a territory and compete for limited resources, one of them would be excluded as a result of competition. Therefore, until new finds of *T. minor* are found in the Late Pleistocene localities in Europe, it seems unlikely that this species "survived longer (up to Holocene) in this part of Europe than in the west" (Rzebik-Kowalska, 2006, p. 90).

Another species – *T. magna* has been listed in some localities (Storch, 1974; 1994), but its validity is still to be confirmed.

Shrews – *Sorex arcticus* Kerr, 1792 – *Sorex tundrensis* Merriam, 1900 – *Sorex runtonensis* Hinton, 1911

Sorex tundrensis Merriam, 1900 was formerly included into the species *Sorex arcticus* Kerr, 1792, and described under this name in earlier publications. Later *S. tundrensis* has been proven to be a separate species (Ivanitskaya and Kozlovsky, 1983), so we use the name in this work.

The problem of the relationship between *Sorex tundrensis* Merriam, 1900 and *Sorex runtonensis* Hinton, 1911 is more complicated. The latter species is listed in many faunal assemblages from Central European localities dated to the end of the Late Pleistocene (Rzebik-Kowalska, 2006). Multivariate statistical analysis of *S. runtonensis* remains and modern *S. tundrensis* has revealed the differences between them to be comparable with differences between recent geographically separate populations of *S. tundrensis* (Osipova, 2006; Osipova *et al*., 2006). According to these authors, both species are members of a "tundrensis" complex of a higher – super-species – taxonomic rank (Osipova, 2006; Osipova *et al*., 2006). Their results, however, suggest *S. runtonensis* to be rather a subspecies of *S. tundrensis.* At present it is difficult to define unambiguously the taxonomic status of *S. runtonensis* from the Late Pleistocene localities in Europe.

Hares – *Lepus tanaiticus* Gureev, 1964 – *Lepus timidus* L., 1758

During the Late Pleistocene, Europe was supposedly inhabited by two species of hare, both belonging to the subgenus *Lepus*: Alpine hare – *L. timidus.*, 1758 and Don hare – *L. tanaiticus* Gureev, 1964. The former species was distributed over Western and Central Europe and the Crimea (Koby, 1958, 1960; Lopez, 1980; Fladerer, 1992; Nadachowski *et al*., 1993; Averyanov, 1994; Altuna, 1999; Street and Baales, 1999). The Don hare was confined to Eastern Europe east of the Dnieper River (Rekovets, 1985; Averyanov and Kuzmina, 1993; Averyanov, 1995; Kosintsev, 1996). Hare remains recovered from localities in Moldavia are attributed to *L. timidus* by some specialists (Lozan, 1970), while others consider them to belong to *L.* cf. *tanaiticus* (David, 1999). So attribution of the remains is still to be specified. It should be noted that neither the eastern limit of the *L. timidus* range, nor the western limit of the *L. tanaiticus* range has been clearly determined as yet. It is also unknown whether their ranges overlapped some time in the past. It may be suggested that the boundary of their ranges was between 25° and 30°E. At the beginning of the Holocene, the range of *L. timidus* began to shrink in Western and Central Europe. In Eastern Europe *L. timidus* replaced *L. tanaiticus*, which resulted in extinction of the latter.

A precise species identification of remains of *L. tanaiticus* Gureev, 1964 and *L. timidus* L., 1758, is hampered by two problems. The first is the lack of diagnostic characteristics on the majority of bones found with the exception of the lower mandible (Gureev, 1964; Rekovets, 1985; Rekovets and Topachevsky, 1988; Averyanov, 1993). Postcranial skeleton bones may be determined only with reference to average dimensions calculated from representative samples (Averyanov, 1993). Strictly speaking, in case of rare remains of the postcranial skeleton and scattered fragments of cranial bones, it is hardly possible to distinguish with confidence between taxa belonging to the *L. tanaiticus-timidus* group.

The second problem is the timing of the *L. tanaiticus* disappearance. Until recently, it was believed to have become extinct at the end of the Pleistocene (Gureev, 1981). It has been recently established, however, that in some regions the species persisted until the Holocene. In Moldavia, remains similar to those of Don hare (*L.* cf. *tanaiticus*) are dated to the Early Holocene (David, 1999). In the Urals, *L. tanaiticus* existed as late as the Middle Holocene (Averyanov, 1995; Kosintsev, 2003, 2007). These finds allow the fairly confident conclusion that in some regions of Eastern Europe *L. tanaiticus* persisted until the early Holocene. Therefore the species attribution of hare remains from Early Holocene localities in

Eastern Europe should be revised. In this paper, we assign all those remains to *L. timidus* (in accordance with other publications).

In general, the question of assignment of species status to *L. tanaiticus* is still debatable. Taking this into account and giving due consideration to difficulties involved in the identification of fossil remains, we indicate only one hare species in the tables, namely *L. timidus*, all the hare remains of the *L. timidus-tanaiticus* group being attributed to it.

Ground-squirrels – *Spermophilus superciliosus* Kaup, 1839 – *Spermophilus major* Pallas, 1778

The species *S. superciliosus* existed during the Late Pleistocene – Early Holocene (Gromov, 1981) and was an ancestral form of *S. major* (Gromov, 1965; 1985; Nadachowski, 1982; Gromov and Erbaeva, 1995); the latter appeared later in the Holocene (Gromov, 1965). Some authors attribute remains of ground squirrels from Late Pleistocene localities to *S. major* (e.g. Smirnov, 1993; Kuzmina *et al*., 2001), others think that a synchronous habitation of *S. superciliosus* and *S. major* is possible (e.g. Topachevsky *et al*., 2000). Some assign a species status (*S. birulai* I. Grom., 1961) to the subspecies *S. s. birulai* I. Grom., 1961 (Vereshchagin and Baryshnikov, 1980; Topachevsky *et al*., 2000). All these attributions, however, are given without being duly substantiated. So here we use the name *S. superciliosus* Kaup, 1839 for the Late Pleistocene localities, while the species name *S. major* Pallas, 1778 is applied to the early Holocene ground squirrels. The Biruli ground squirrel is considered to be a subspecies, *S. s. birulai* I. Grom., 1961.

Common dormouse – *Glis glis* L., 1766

After the Myoxidae family had been revised, this species was attributed to the genus *Myoxus* Zimmermann, 1780 – *Myoxus glis* L., 1766 (Pavlinov and Rossolimo, 1987; Wahlertetall, 1993). However, we give its name according to formerly used system (*Glis glis*), as is usually done in publications so far.

Wood mouse group – *Sylvaemus sylvaticus* s.l.

Several forms attributed until recently to *Sylvaemus sylvaticus* L., 1758 have been recognized as separate species; among these are *S. uralensis* Pallas, 1811; *S. ponticus* Sviridenko, 1936; *S. fulpectus* Ognev, 1924; *S. alpicola* Heinrich, 1952 (Mezhzherin and Zagorodnyuk, 1989; Storch and Luth, 1989; Vorontsov *et al*., 1989; Mezhzherin, 1991; Mezhzherin and Zykov, 1991; Zagorodnyuk, 1993; Chelomina, 2005). All the publications, however, refer to remains of that group as *S. sylvaticus*, so we use only this name in the present paper.

Hamsters – *Mesocricetus raddei* Nehring, 1894 – *Mesocricetus planicola* Argyropulo, 1941

Until recently, the Binagady hamster was regarded as a subspecies of the Ciscaucasian hamster – *Mesocricetus raddei planicola* Argyropulo, 1941 (Gromov, 1981). At present, its taxonomic rank has been raised to species level – *Mesocricetus planicola* Argyropulo, 1941. However, the advance in rank has not been substantiated with new data (Baryshnikov *et al*., 1986), so the assignment of a species status to this form calls for additional evidence.

Collared lemmings – genus *Dicrostonyx* Gloger, 1841

Collared lemmings have shown a high rate in the directional evolution of the molar structure in the Pleistocene (Agadjanian, 1976; Agadjanian and Koenigswald, 1977). The phyletic lineage of species and subspecies spanning this time interval illustrates the evolution process (Kochev, 1993; Smirnov *et al*., 1997; Smirnov, 1999). It should be noted, however, that there are two different opinions about the taxonomical status of the Late Pleistocene collared lemmings in Eurasia. According to the first one, the Late Pleistocene lemmings are regarded as a single species – *Dicrostonyx gulielmi* Sanford, 1890 (Agadjanian, 1973; Gromov and Polyakov, 1977). At the Pleistocene/Holocene boundary, a phyletic transformation resulted in its replacement by the newly appeared recent species – *Dicrostonyx torquatus* Pallas, 1779, (Gromov, 1981). In the opinion of other specialists, the only species that existed in the late Pleistocene was *D. torquatus* Pallas, 1779 (Zazhigin, 2003). In this work we hold the first viewpoint as commonly accepted.

It is not always possible, however, to identify at species level collared lemming remains (*D. gulielmi* or *D. torquatus*) recovered from localities dated to the end of the late Pleistocene. That may be attributed to the fact that at the Pleistocene/Holocene transition the *D. torquatus* Pallas, 1779 replaced *D. gulielmi* Sanford, 1869. A reliable identification of the remains and confident attribution to a certain species are possible only in the case of a large enough series of teeth, which are

not available from all localities. Studies performed on large samples of collared lemming teeth from localities dated to a rather narrow time interval (24,000–6,000 yrs BP) and distributed over a large geographical region (the Middle and Northern Urals) permitted to date the replacement to 14,000–13,000 yrs BP (Smirnov, 2002; Smirnov *et al*., 1999). Accordingly, all the remains from localities younger than 13,000 yrs BP (Allerød to the present days) should be considered as *D. torquatus* Pallas, 1779, while those older than 14,000 years should be considered as *D. gulielmi* Sanford, 1869. Here collared lemmings of Younger Dryas and Preboreal–Boreal age are referred to as *D. torquatus* Pallas, 1779, those of the Bølling-Allerød (BAIC) and Late Glacial (LGT) as *Dicrostonyx* sp., and those dated to the maximum cooling (LGM) are attributed to the species *D. gulielmi* Sanford, 1869. However, it should be noted, that the statement formulated above is based on results obtained from a single region only. It is not inconceivable that in Western Europe (where climatic and environmental changes proceeded at a faster rate than in the Urals) *D. gulielmi* populations became extinct rather than evolved into *D. torquatus*. So some relict populations of the species could persist there during the Younger Dryas. A revision of those materials should be done to validate or disprove the hypothesis.

Sibling species – *Microtus arvalis* Pallas, 1779 – *M. rossiaemeridionalis* Ognev, 1924

A sibling species has been described, *M. rossiaemeridionalis* Ognev, 1924, with a range largely overlapping with that of *M. arvalis* Pallas, 1779 (Gromov and Erbayeva, 1995). Differences in skull and teeth structure have been identified only recently (Malygin *et al*., 1996; E. Markova, 2002), so all their fossil remains were described as *M. arvalis* Pallas, 1779. The latter name is used in the present work.

Cave bears – subgenus *Spelaearctos* Geoffroy, 1833

During the Late Pleistocene, the European territory was inhabited by three species of cave bear, namely the large cave bear – *Ursus* (*S.*) *spelaeus* von Rosenmuller, 1794; a small one – *U.* (*S.*) *savini* Andrews, 1922, and Deninger's bear – *U.* (*S.*) *deningeri* von Reichenau, 1904.

Cave bear remains found in the Caucasus have been attributed to *U. spelaeus* Rosenmuller, 1794, until 1987 (Vereshchagin, 1959; Baryshnikov and Dedkova, 1978; Burchak-Abramovich and Burchak, 1982). Later the remains have been revised and appeared to belong to the Deninger's bear – *U.* (*S.*) *deningeri* von Reichenau, 1904 (Baryshnikov, 1987). The species became extinct over the greater part of its range (Europe) at the end of the Middle Pleistocene, while in the Caucasus its relict subspecies – *U. deningeri kudarensis* Baryshnikov, 1980 – probably persisted until the end of the Pleistocene (Baryshnikov, 1987). In the Caucasus, only one find of the large cave bear (*U. spelaeus*) is known, recovered from Mousterian layers of the Erevan site in Armenia (Baryshnikov, 1987), so its presence in this region still needs to be confirmed by additional materials.

Small cave bear remains found in Eastern Europe were described until recently as *U. (S.) rossicus* Borissiak, 1930. A revision of the remains, however, identified them as belonging to *U. (S.) savini* Andrews, 1922 (Baryshnikov, 2003).

Recently a new cave bear species – *Ursus ingressus* Rabeder et al., 2004 – has been recognized on the basis of DNA analysis of cave bear bones recovered from the Potocka zijalka cave (Slovenia) (Rabeder *et al*., 2004). DNA analysis of bone samples from Europe, the Urals and the Altay Mountains revealed the new species inhabiting the Alps, Carpathians, northern coasts of the Black Sea, and the Urals, while *U. spelaeus* occurred in the Pyrenees, Alps, and Altay (Knapp, *et al*., 2009). Without going into further details, we would note two points. Firstly, the two large species coexisting in the Alps are very similar in their environmental requirements. The latter is indicated by a considerable similarity in morphology, first of all in teeth structure. Let us have a look at the ecology of modern bears. At present, two bear species are found only in friendly enough environments, such as those of the Far East and Japan. Bear species living there (*Ursus arctos* and *U. thibetanus*) differ noticeably both in ecology and morphology; that reduces considerably the interspecific competition and permits their coexistence. The Late Pleistocene environments in the Alp region were not very favourable, as is suggested by the fauna composition (Markova *et al*., 2008). According to the competitive exclusion principle (Gause, 1934), it is unlikely that two large animal species of similar ecological characteristics could coexist under those conditions. Secondly, as follows from published data (Knapp *et al*., 2009, fig. 1), the species *U. spelaeus* had a discontinuous range, with one part in Western Europe and another in the Altay Mountains. Some modern mammals are known to have such ranges (for example *Panthera leo* L., 1758). In the case under consideration, however, the area between two parts of the range appears to be filled with a closely related species, *U. ingressus*. Should this be the case, *U. ingressus* would have displaced the ecologically similar species *U. spelaeus* from the great area. Such a situation is unlikely from an ecological point of view. Therefore, in the context of biology and ecology, the *U. ingressus* validity is questionable and needs further substantiation.

Badgers – *Meles meles* L., 1758 – *Meles leucurus* Hodgson, 1847

The boundary between the ranges of the two badger species, the European (*Meles meles* L., 1758) and the Asian badger (*M. leucurus* Hodgson, 1847) lies in the east of Europe (across the Pechora and Volga drainage basins). The Asian badger is referred to as *M. anacuma* Temminck, 1844 by some specialists (Baryshnikov and Aristov, 2001), and as *M. leucurus* Hodgson, 1847 by others (Abramov and Puzachenko, 2006). The latter opinion has been confirmed by results of DNA analysis (Marmi *et al*., 2006) and seems to be most credible. It is only recently that the diagnostic properties of *M. meles* and *M. leucurus* have been described (Baryshnikov and Potapova, 1990; Aristov and Baryshnikov, 2001; Baryshnikov *et al*., 2002), so all the fossil remains found in the east of Europe and in the Urals were identified as *M. meles* L., 1758. It is not improbable that after revision of the remains, part of them may appear to belong to *M. leucurus* Hodgson, 1847. In this work (in common with publications used) we use only one species name – *M. meles*.

Cave hyena – *Crocuta crocuta spelaea* Goldfuss, 1823

Opinions differ as to the taxonomic rank of the Late Pleistocene cave hyena in Europe. Some palaeontologists regard it as a separate species – *Crocuta spelaea* Goldfuss, 1823 (Baryshnikov and Averianov, 1995; Baryshnikov, 1999), others consider it to be a subspecies of the modern *Crocuta crocuta* Erxleben, 1777 (Kurten, 1956; Werdenlin and Solounias, 1991). Analysis of DNA recovered from bones of the modern *Crocuta crocuta* and the fossil *C. c. spelaea* seems to confirm the latter point of view, with which we also agree.

Cave lion – *Panthera spelaea* Goldfuss, 1810

There is no agreement among specialists regarding the taxonomic status of the Late Pleistocene cave lion in Europe. Some of them consider it a subspecies of the modern *Panthera leo* L., 1758 (Kurten, 1968; Hemmer, 1974; Turner and Anton, 1997), while others identify it as a separate species – *Panthera spelaea* Goldfuss, 1810 (Vereshchagin, 1971; Baryshnikov, 1981; Baryshnikov and Boeskorov, 2001). Sometimes it is considered to be a subspecies of a tiger – *Panthera tigris spelaea* (Groiss, 1996). Analysis of DNA from bones of the cave lion in comparison with modern lions dwelling in Africa and Asia produced somewhat controversial results. According to some, the differences revealed are at subspecies level (Burger *et al*., 2004). There are other data, however, obtained from studies of a large sample of palaeo-DNA recovered from cave lion remains from Eurasia and North America; according to these data, the cave lion and modern lion are most likely different species (A. Cooper, personal communication). A comparative analysis of the skull and teeth structure of the cave lion, African lion and tiger allows the definite conclusion that the cave lion is a separate species (Sotnikova and Nikolskiy, 2006). So the data now available permit to assign species status to the cave lion – *P. spelaea* Goldfuss, 1810. That raises another problem as to which species belonged the lions inhabiting the Balkans and the south of Eastern Europe in the Holocene (Bartosiewicz, 1999; Krakhmalnaya, 1999; Ninov, 1999; Sommer and Benecke, 2006).

True horses – subgenus *Equus (Equus)* L., 1758

A large number of horse varieties have been described that inhabited Europe during the Late Pleistocene and Holocene, their taxonomic status (species or subspecies) and phylogenetic relationships being still uncertain. Among them are *Equus germanicus*, *E. gallicus*, *E. arcelini*, *E. transilvanicus*, *E. scythicus*, *E. spelacus*, *E. latipes*, *E. uralensis*, *E. remagensis*, *E. achenheimensis*, *E. caballus*, *E. ferus*, *E. gmelini*, *E. silvaticus*, and even *E. przewalskii* (Gromova, 1949; Prat, 1968; Nobis, 1971; Samson, 1975; Eisenmann, 1988, 1991; Forsten, 1988; Azzaroli, 1990; Kuzmina, 1997; Spassov and Iliev, 1998). Revisions performed on the form remains from different parts of Europe produced inconsistent or partly contradictory results (Eisenmann, 1988, 1991; Kuzmina, 1997; Spassov and Iliev, 1998; Bachura *et al*., 2003). Palaeo-DNA analysis has also not yielded unambiguous results as yet. For example, according to the results, the Przewalski's horse, the domesticated horse of the early Iron Age from the Southern Urals and a horse dated to the Viking epoch in Western Europe appeared to belong to the same clade (Weinstock *et al*., 2005). Therefore, here we do not use species names for true horse remains and indicate only the subgenus – *Equus (Equus*) sp.

Roe deer – *Capreolus capreolus* L., 1758 – *Capreolus pygargus* Pallas, 1771

Until recently the European and Asian roe deer have been regarded as subspecies of a single species – *Cap-*

reolus capreolus capreolus L., 1758 and *C. c. pygargus* Pallas, 1771. Genetic researches, however, provided evidence for species status of both taxa – *C. capreolus* L., 1758 and *C. pygargus* Pallas, 1771 (Sokolov and Gromov, 1990; Korotkevich and Danilkin, 1992). In the Late Holocene, the boundary between the species ranges passed across the Dnieper drainage basin (Danilkin, 1992). As to the early Holocene, the position of the boundary is still unknown, as no revision of the early Holocene roe deer remains has been performed until now. All are tentatively assigned to *C. capreolus*, though some remains recovered from localities in the eastern part of Europe could be in fact *C. pygargus* Pallas, 1771.

Bisons – genus *Bison* H. Smith, 1827

Several species are recognized among the Late Pleistocene bisons: *Bison priscus* Bojanus, 1827; *Bison schoetensacki* Freudenberg, 1910; and *Bison bonasus* L., 1758. Although there does not seem to be a problem in the species identification among the Late Pleistocene remains, there are two hypotheses as to history of the European bisons evolution in the Pleistocene. According to the first, there were two parallel lines in bison evolution (Hilzhaimer, 1918; Flerov, 1979): that of the forest bison evolution from *B. schoetensacki* to the modern *B. bonasus*; and another evolution, namely the development of steppe *B. priscus*. The latter existed until the beginning of the Holocene and then became extinct. In the opinion of N.K. Vereshchagin, it is only in the steppe regions of the southern Russian Plain that they persisted until the Late Holocene (Vereshchagin and Baryshnikov, 1985). The second hypothesis suggests a single lineage of bison evolution: *B. schoetensacki – B. priscus – B. bonasus* (Gromova, 1965). So, if we accept the first hypothesis, bone remains of bisons recovered from Late Pleistocene localities should be described as belonging to two different species: *B. bonasus* and *B. priscus.* All the publications on the subject, however, describe the Late Pleistocene bison remains as *B. priscus.* It seems evident that even in the case of the hypothesis being correct; it is extremely difficult to identify the two species by morphological criteria. It is possible that the problem can be clarified in the future by applying DNA analysis.

Muskox – *Ovibos moschatus* Zimmermann, 1780 – *Ovibos pallantis* Ham.-Smith, 1827

Muskox remains recovered from Late Pleistocene deposits in Eurasia are usually attributed to the species *O. moschatus* Zimmermann, 1780. Sometimes fossil muskox are regarded as a separate subspecies, *O. moschatus pallantis* (Andree, 1931; Gromova, 1935; Baryshnikov, 1981). However, back in 1827 H. Smith attributed extinct muskox to a separate species, *O. pallantis.* Since then, some researchers refer to Late Pleistocene muskox remains as *O. moschatus*, while others refer to them as *O. pallantis.* A comparative analysis of skulls of modern *O. moschatus* Zimmermann, 1780, and of the Late Pleistocene muskox from Eurasia revealed their difference in a number of taxonomically significant features (Ryziewicz, 1955; Sher, 1971; Tikhonov, 1994), and therefore confirmed the validity of *O. pallantis* Ham.-Smith, 1827. Further evidence for the assumption that fossil and modern muskox in Asia and North America belong to a single species was obtained from palaeo-DNA analysis (MacPhee *et al*., 2005). At present it seems impossible to determine unambiguously the species status of the Pleistocene muskox in Eurasia. Most of published fauna lists define the Late Pleistocene muskox of Europe as *O. moschatus* Zimm., 1780. In this work we use the species name of Siberian muskox – *O. moschatus* Zimm., 1780.

The following should be noted in conclusion. Lists of the final Late Pleistocene mammal faunas sometimes contain species of doubtful or unconfirmed validity. For example, we refer to *Canis volgensis* M. Pavlova, 1930–1931 cited as a valid species (Baryshnikov and Vereshchagin, 1981; Vereshchagin, 1985), or *Ochotona spelaea* Owen, 1846 (Rekovets, 1985; Topachevsky *et al*., 2000), the latter being later reduced to the subspecies *Ochotona pusilla spelaea* Pallas, 1773 (Erbajeva and Currant, 2003). Some species are erroneously put into the lists of mammal assemblages in Eastern Europe. Roe deer (*Capreolus capreolus*), for example, has been confidently identified only in the Crimean (Benecke, 1999) and Moldavian (David, 1999) localities dated to the end of the Late Pleistocene. Information on its presence in localities on the Russian Plain (Vereshchagin and Kuzmina, 1977) and in the Urals (Karacharovsky, 1951; Kuzmina, 1971) has not been confirmed (Sablin, 2001; Kosintsev, 2003). Large cave bear (*Ursus spelaeus*), cave hyena (*Crocuta c. spelaea*), wild boar (*Sus scrofa*), giant deer (*Megaloceros giganteus*) have also not been identified in the Russian Plain localities (Sablin, 2001). No reliably identified remains of aurochs (Bibikova, 1975) or cave hyena are known from the final Late Pleistocene localities in Eastern Europe (see section "Extinctions"). Mistakes in identification are related to the difficulty in recognizing species from fragmentary remains and identification of bones of young animals, as well as to taphonomic problems.

2.4. STATISTICAL ANALYSIS OF THE DATABASE

Andrey Puzachenko

The present study requires standardization of the paleontological data, and the analytical methods used by different scientists (theriologists, botanists, geologists, and archaeologists) in order to be able to analyze the multivariate primary data stored in the two databases. The main requirements were to use well-known statistical methods, and if possible, to apply a uniform sequence of operations for the different types of data, and to make a selection of statistical methods according to the statistical 'nature' of the available data. We used statistical methods, which included minimal number of prior statistical hypotheses about the objects of investigation. Furthermore, the principle of «minimal number of prior hypotheses» was used as the basis for our research as a whole and, everywhere, if possible, we used and tested most simple assumptions.

The common goal of the multivariate analysis is the separation of the 'explained variation' of input variables against a background of stochastic variation. The basic claim of multivariate analysis is that 'explained variation' can be reproduced from a set of pairwise independent virtual variables ('factors').

Basic approach

The well-known strict statistical requirements for input data with the restriction on choice of the metrics and algorithms in parametric multivariate analysis were forcible arguments for us to choose nonparametric nonmetric multidimensional scaling (MDS) (Shepard, 1962; Kruskal, 1964) as a basic technique for producing the virtual variables, which describe the 'explained variation' of input data. This multivariate method is one of the most unprejudiced and robust statistical methods to be applied if there is no assumption about the type of multivariate sample distribution and the linear relationships between the variables. That is why MDS has methodological preference over standard principal components analysis (PCA) and other parametric linear methods of multivariate analysis (see James & McCulloch, 1990). The contents of the results of MDS and PCA may be similar when the assumptions for the latter method are correct. In this study initial configuration was calculated according to the classical metric algorithm (Torgerson, 1952). Metric solution was used as a starting configuration for the MDS algorithm (Kruskal, 1964).

Our data analysis consisted of the following steps: testing of the data distribution type (distribution fitting), choice of metrics for different types of data, computation of 'distances' between localities using these metrics, estimation of the optimal number of the virtual variables ('non-metric multidimensional axes') and their interpretation, classification of the localities by cluster analysis using the 'axes' as variables. To illustrate the different steps we used data from the LGM time window (24–17 kyr BP).

Distribution Fitting

The lists of mammalian species contained information about the presence or absence of taxa. An investigation of the distributions of occurrence of mammal species in different time windows showed that only a canonical Binominal distribution approximated the real data (Fig. 2.1).

Spore-pollen spectra required using a different method. Differences in the number of pollen of different species are caused not only by differences in species abundances but also by the specific parameters (e.g. specific spore or pollen production and so on). Because of all that within the subsets corresponding different design methods, the input data were standardized according to the equation: $x^{st}_i = (x_i - x_{\min})/(x_{\max} - x_{\min})$.

It turned out that the standardized numbers of the spore or pollen may be approximated by several canonical distributions: exponential, log-normal, or gamma (Fig. 2.2). From a formal point of view based on the Kolmogorov-Smirnov test, a log-normal distribution fits the observations best. The log-normal distribution is frequently used to describe pollutants propagation, e.g. in the soil (Y. Puzachenko, 2004). Therefore, the 'log-normal model' may reflect some basic properties of spore/pollen accumulation in the deposits. Of course, the other two models would also provide an acceptable fit.

Choice of metrics

As is well known, a metric is the distance or a proxy for estimating this distance between pairs of elements of

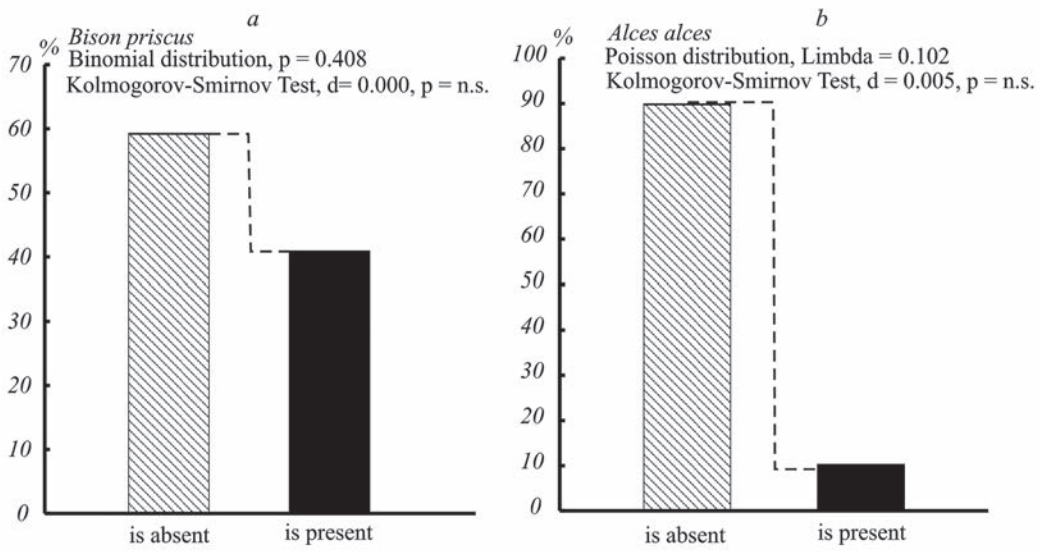

Fig. 2.1. *Distribution of the frequencies of occurrence of widespread Bison priscus (a) and relatively rare Alces alces (b) among localities dating to the LGM*

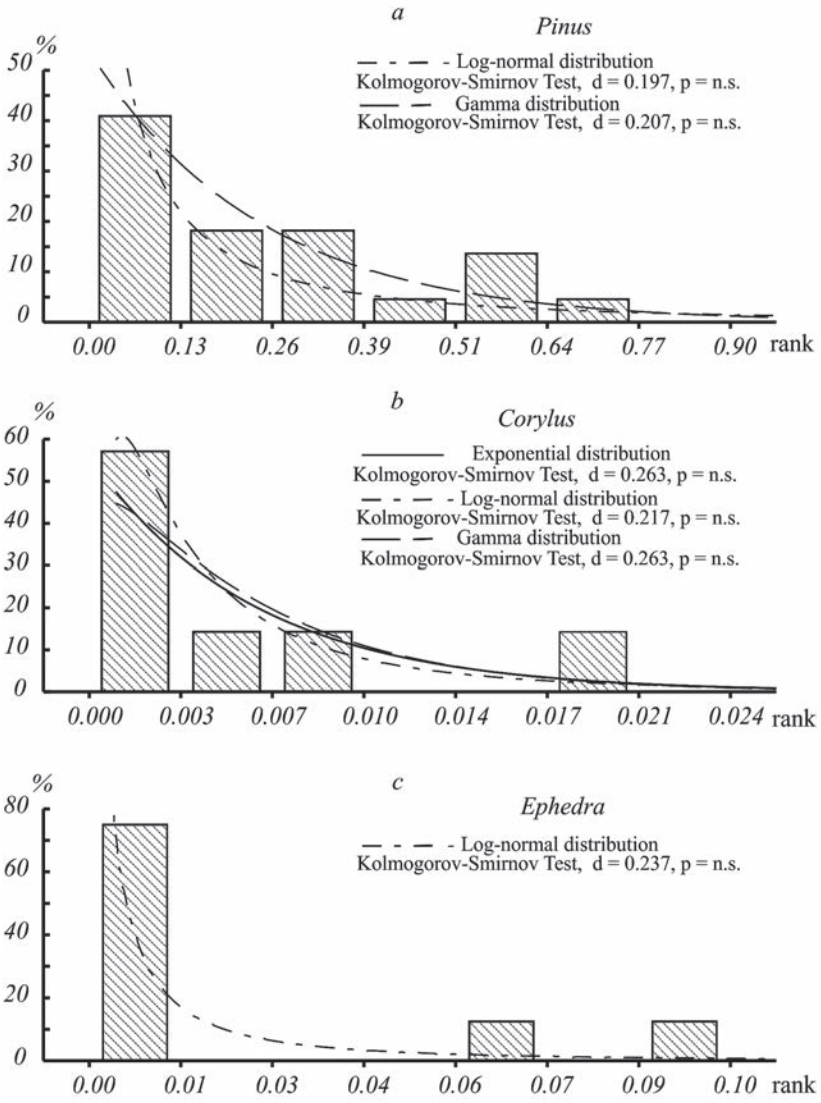

Fig. 2.2. *Distribution (x > 0) of the standardized pollen spectra of the widespread Pinus silvestris (a), common Corylus (b), and relatively rare Ephedra (c) species among localities dating to the LGM*

some set. Both the set of elements and the metric define the metric space. Metric selection may be based on a type of data distribution and knowledge of its use in multivariate analyses. For nominal (binary) variables ('presence' or 'absence'), describing mammals among localities, the simplest and easiest to understand is Jaccard's coefficient: $J(i, j) = a/(a + b + c)$, where a – the number of pairs ('presence-presence') or species is present at both localities; b – the number of pairs ('presence-absence'), c – the number of pairs ('absence-presence'). It is important that this metric does not take into account the variant 'absence-absence' which is not interesting for us because of the relatively low frequency of observations for most species. The choice of the metrics for the botanical data depends on data distribution on the assumption that further multivariate analysis will not substantially skew the distances between localities.

To describe the relationships between localities we need two types of metric. The first one is the metric (distance) reflecting the variation in the number of spore/pollen for all separate species (metric of 'size or volume'). It is reasonable to assume that this metric is one of the Minkovski metric families (*City-block (Manhattan)* distance, *Euclidean distance etc.*).

The second metric must describe the concordance in variation of different species from one locality to another (metric of 'shape'). These distances are based on different correlation coefficients, e.g. rank Kendall *tau* or *Gamma* (when the data contain many tied observations – '0-0'). Let's illustrate the effects of some metrics on an artificial data set (100 'cases', 100 'variables') with a log-normal distribution. As a first step we calculated distances between 'cases' x_i and x_j using *Euclidian* distance (*E*), standardized *Manhattan* distance (Bray-Curtis dissimilarity index, *BC*) and *Kendall tau-b* distance (*K*):

$$E(x_i : x_j) = \sqrt{\sum_{i=1}^{n} (x_i - x_l)^2}; \quad BC(x_i : x_j) = \left(\sum_{i=1}^{n} |x_i - x_j| \right) \Big/ \left(\sum_{i=1}^{n} |x_i + x_j| \right); \quad K(x_i : x_j) = \sqrt{1 - \tau_{i,j}}.$$

Next, a pairwise comparison of the results using 2d-scatterplots was done (Fig. 2.3). According to Figure 2.3, the Bray-Curtis metric results in larger distances than the Euclidian metric for low or medium values and vice versa for large values. Figure 2.3b compares with Kendall *tau* metric. These two metrics stretch the space near the coordinate origin and squeeze it far off that range. The Kendall *tau* metric squeezes the space a little more than the Bray-Curtis metric (Fig. 2.2c)[1]. The metrics transform the space in a, for us desirable, way, because the input data contains many low values and few high ones.

The new Euclidean space originates from a non-metric multidimensional scaling (MDS) procedure. As implied by its name, there is no exact metric. In the most general MDS algorithm, which we use in the present work[2], only a monotonic shape for the function relating input distances to output ones is assumed. Figure 2.3 shows the results of MDS for a model log-normal sample. Because the model variables are not correlated (the dimensionality is equal to the number of variables), we can present the results in the space of any pair of MDS axes.

We see that the Euclidean metric keeps distances according to log-normal law; the Bray-Curtis metric transforms the input distribution into a Gamma distribution; the Kendall *tau* metric transforms the input distribution into a Uniform distribution because there is no order in variability between model variables.

Thus, for further study (classification) the Bray-Curtis metric, as a metric of 'size', and the Kendall *tau* metric, as a metric of 'shape', are preferable to the Euclidean metric.

Dimensionality measure and interpretation

The principal question is "how many virtual variables ('factors') do we need to reproduce 'explained variation' in input multivariate data correctly?" or, in other words, "what is the dimensionality of the simulated space?"

The 'best-minimum' dimension in the MDS model is estimated with Kruskal's Stress formula 1:

$$S_1 = \sqrt{\left[\left(\sum_{ij} (d_{ij} - \bar{d}_{ij})^2 \right) \Big/ \sum_{ij} d_{ij}^2 \right]},$$

where, d_{ij} are the observed distances or measured distances between objects i and j during any step of MDS algorithm, $\bar{d}_{ij}$ are the predicted distances after the next step of the MDS algorithm or after the last step (final configuration). In general, the 'best solution' (best final configuration) in MDS is reached at minimum stress according to convergence criteria (minimum stress value, minimum stress change from one iteration to the next, etc.).

We used a modified 'scree test' (as when plotting the eigenvalues in descending value factor analysis (Cattell, 1966)) of the first 15 stress values for finding the 'minimum number' of MDS axes. It is assumed that if the distribution of the distances in the input matrix is close

[1] Metric based on Gamma coefficient gives the same results.

[2] Kruskal's STRESS formula 1 scaling method was used. Initial configuration for MDS was calculated according to the classic metric algorithm. Metric solution was used as a starting configuration for the nonmetric algorithm.

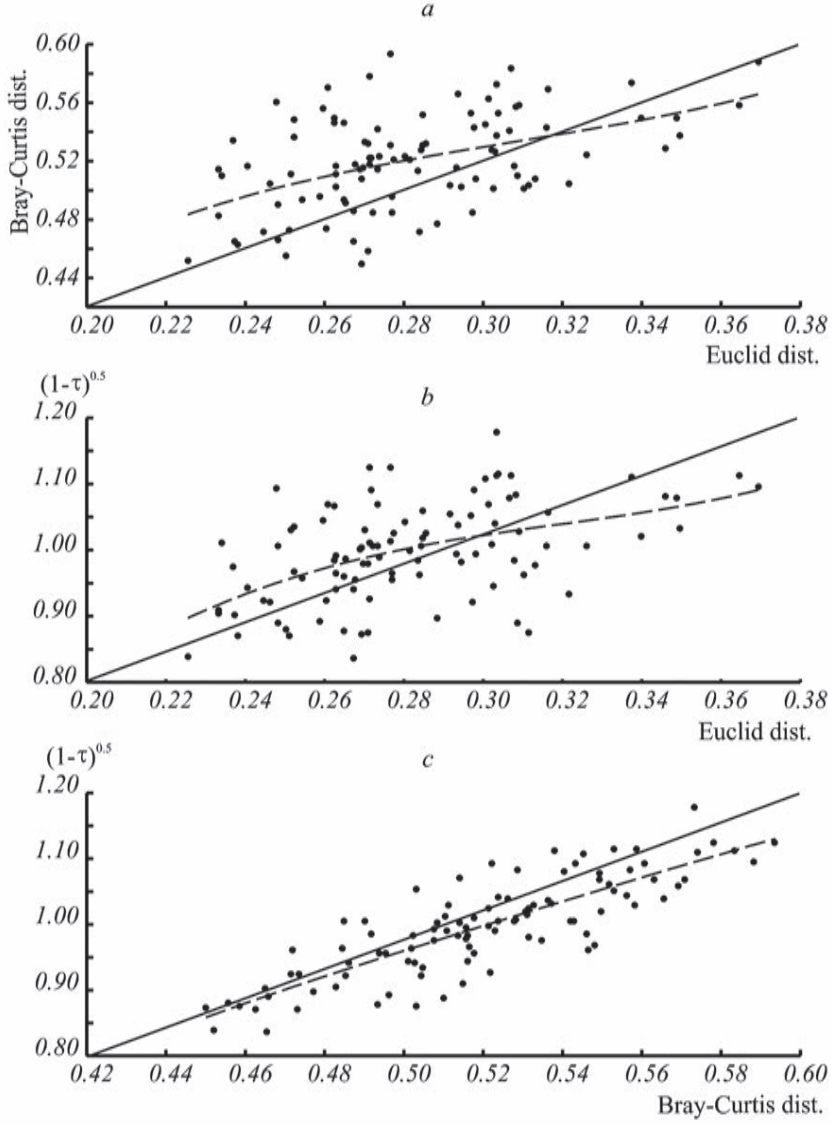

Fig. 2.3. *Results of a pairwise comparison between three metrics: Euclidean – Bray-Curtis (a), Euclidean – Kendall tau (b), Bray-Curtis – Kendall tau (c)*

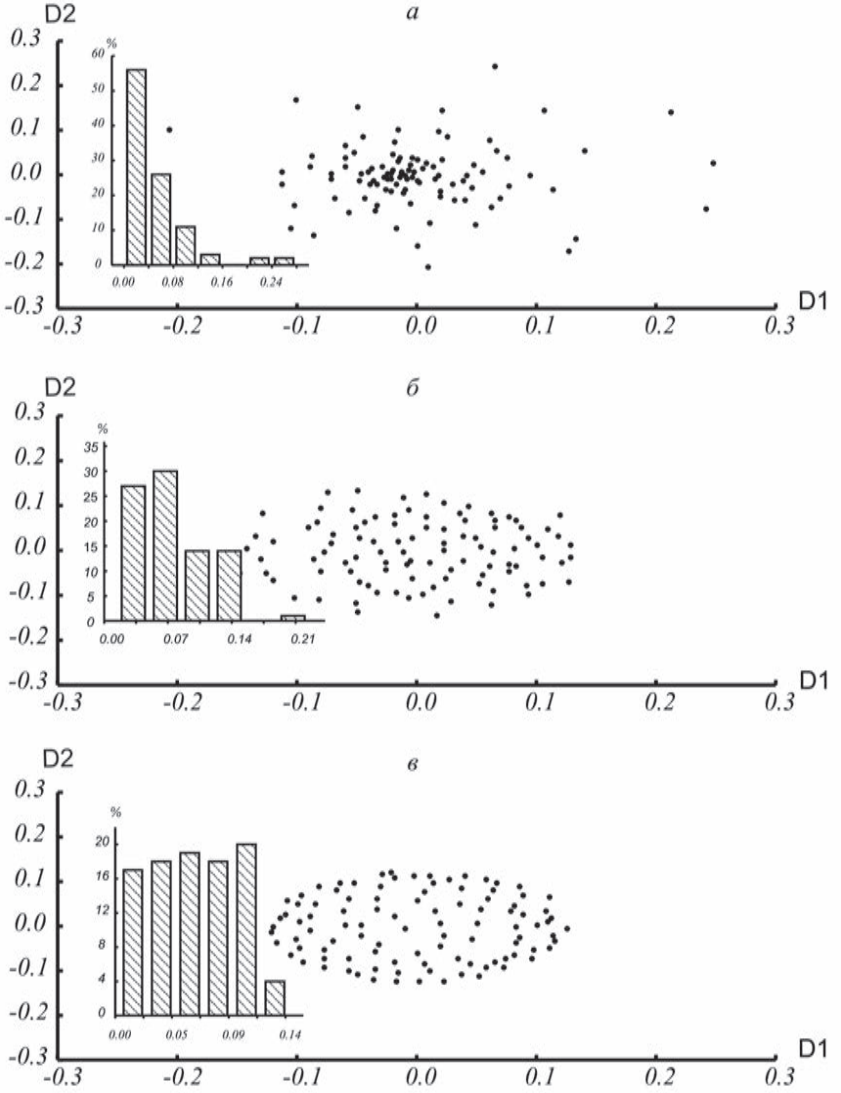

Fig. 2.4. *Ordination of the 100 log-normal distributed objects in the space of two first MDS axes (D1, D2) based on the different input distances matrixes: a – matrix of Euclidean distances, b – matrix of Bray-Curtis distances, c – matrix of Kendall tau distances*

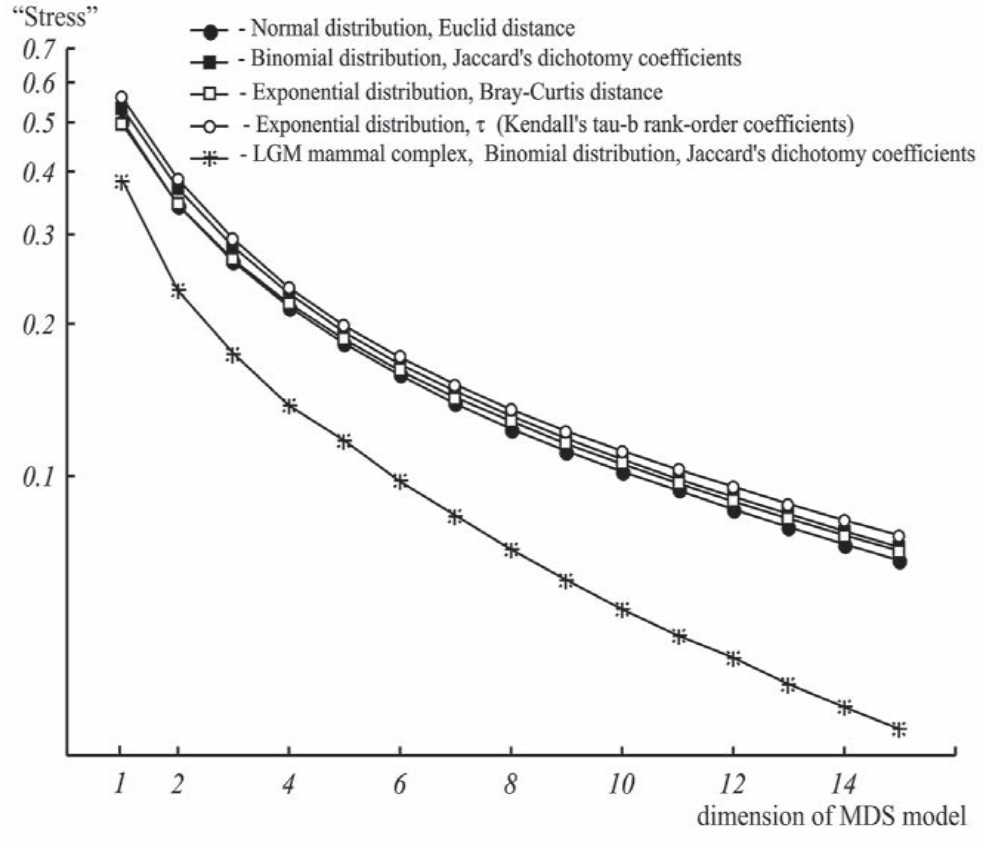

Fig. 2.5. *Stress values for model data sets with different random distributions and observed stress values for the mammalian complex during the LGM against increasing number of MDS axes (dimension)*

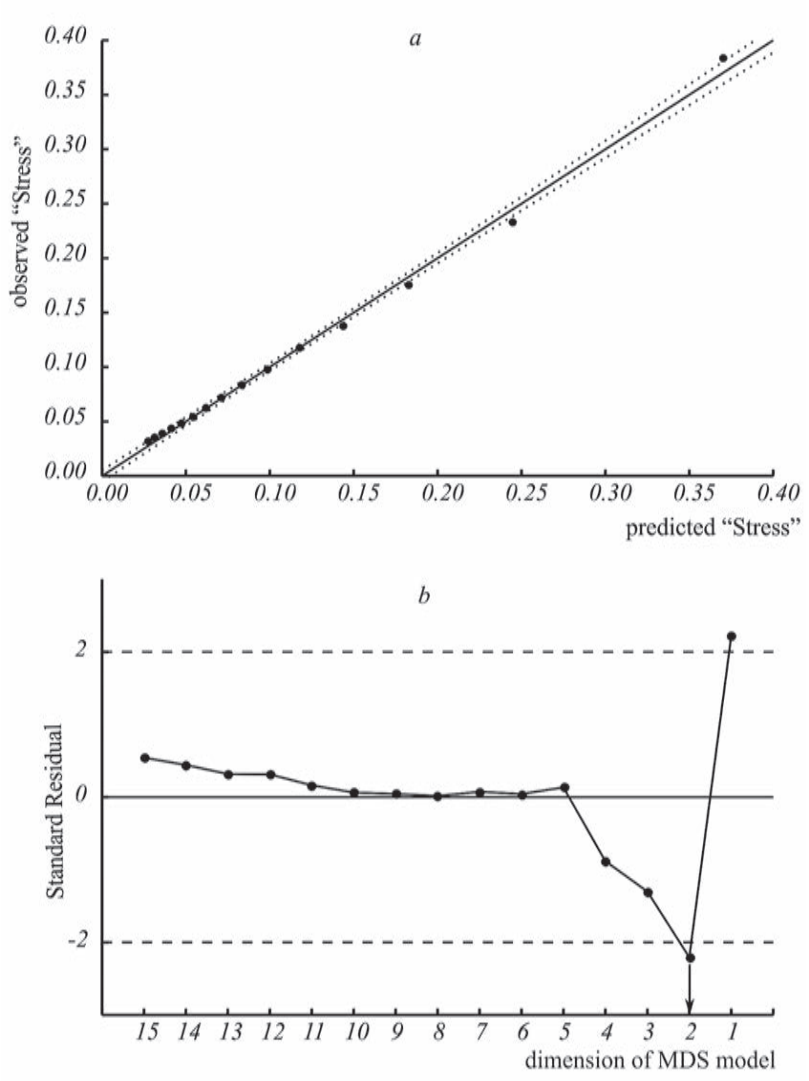

Fig. 2.6. *The results of the regression model for finding the optimal dimension for the mammalian complex during the LGM: a – predicted and observed stresses with 95% confidence interval, b – standard error of the regression model*

to random, initial stress is maximal and must decrease monotonically when increasing the number of MDS axes (dimension) (Fig. 2.5).

In practice, the results are not very dependent on the type of distribution or metric for the same number of MDS axes (= for the same dimension). However, they are determined by the presence of a latent structure ('correlations' between variables) in the input data sample. Under equal circumstances, for the real non-random data, the best MDS solution must be associated with a minimum stress value that (accurate to scaling constant) deviates relatively maximal from the model value. In general, we assume the following linear regression model (Kupriyanova *et al*., 2003): $Stress_i = B \cdot Stress_{i,\mathrm{mod}} - A + \varepsilon_i$, $i = 1, 2, \ldots, 15$; where $Stress_i$ is the value of stress function for real data, i – the number of dimensions in MDS solution, $Stress_{i,\mathrm{mod}}$ is the value of stress function for model random data set (normal distribution), A and B are "scaling" constants, ε_i is error term, with the normal distribution. Furthermore, at the plot of standardized residuals from this regression model the minimum value and corresponding dimensionality can be easily found (Fig. 2.6).

The optimal dimension for the mammalian complex during the LGM equals 2 in the present example. In other words, there were two 'general' linear independent factors, which 'explained' the mammalian distribution.

Non-linear correlation analysis was used to discover the relationship between MDS axes and geographical coordinates of the localities, because one of the main practical goals was to define an ordering of the sites in the geographical space. In correlation analysis, MDS axes are selected for the next classification procedure. In the example presented in Fig. 2.7 two axes, demonstrate sophisticated non-linear correlations with latitude and longitude.

According to this, the main spatial gradient was observed from south to north. Nevertheless, it included two independent components described by the D1 and D2 MDS axes. A general exchange of the components was most likely about 55°N. The longitudinal gradient was expressed relatively weaker and stopped near 30°E. On the whole, as a hypothesis, a relatively simple, energetically powerful 'mechanism' is capable of producing the 'order' in space during the Last Maximum Glaciation. This 'order' is reflected for example in the change of species richness (Fig. 2.8).

Classification

In the next step, for the hierarchical classification of localities we used the UPGMA procedure (Sokal and Sneath, 1973) with a Euclidean distance measure using the MDS axes correlated with their position in geographical space. The number of clusters was determined by specialist decision after mapping the points in GIS (MapInfo 7) for further biogeographical research and interpretation.

In general, when the variability of the distances in a multidimensional space is close to random (normal or uniform) then, on each subsequent step of the UPGMA clustering algorithm, the increase of the distance between new groups ('linkage distance') must be approximately equal and monotonic[3]. Thus, the distribution of linkage distances must tend to normal in the stochastic case as the number of variables increases. It is easy to find on the plot short intervals where the graphic of linkage distance deviates abruptly from the monotonic model (Fig. 2.9).

A more formal approach for uncertainty reduction when choosing the 'cut-off levels' for the tree diagram was based on the comparison of empirical linkage distances with the model ones constructed on the stochastic normal distribution samples with empirical variances. The model takes proper account of the number of variables (MDS axes), volume of the real sample, metrics, and classification method. We generated 100 times a random sample and calculated the linkage distances in the UPGMA classification. Then the means of the distances for each step of classification (N-1) were calculated. We then determined the nonlinear regression model, which most fully reproduced the empirical linkage distances (y), from the simulated linkage distances as independent variable (x). The general mathematical equation searched for as: $y = e^{(A + Bx + C\ln(x))}$ (Fig. 2.10a).

The diagram of the standardized residuals from this regression was used to estimate the number and 'statistical' significance of hierarchical levels in empirical classification. The maximal values of residuals were considered as probable hierarchy indicators, as they reflected a considerable (for example, more than 2 or 2.5 standard deviation) excess of the observed linkage distances over the predicted ones (Fig. 2.10c). These linkage distances were regarded as the most probable 'cut-off levels' (Fig. 2.10b).

Main Possible Sources of Uncorrectable Mistakes

Discussing the results of formal statistical analyses, we must keep in mind possible main sources of 'mistakes'. These are: the incompleteness of the geological record; different quality of species determination (for

[3] The clear linear dependence between the step of classification and the linkage distance should be observed in the case of uniform distribution only.

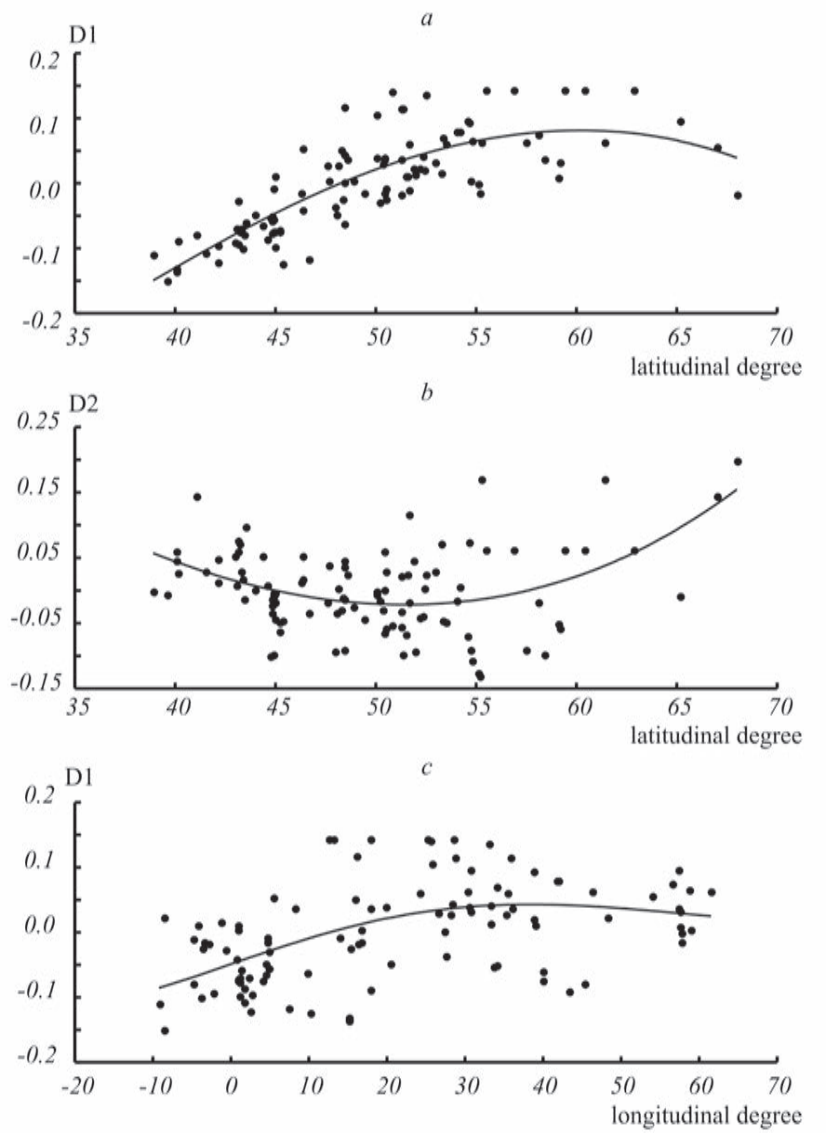

Fig. 2.7. *Non-linear correlation between MDS axes and geographical coordinates of the localities for the mammalian complex in the LGM; a, b – latitude; c – longitude*

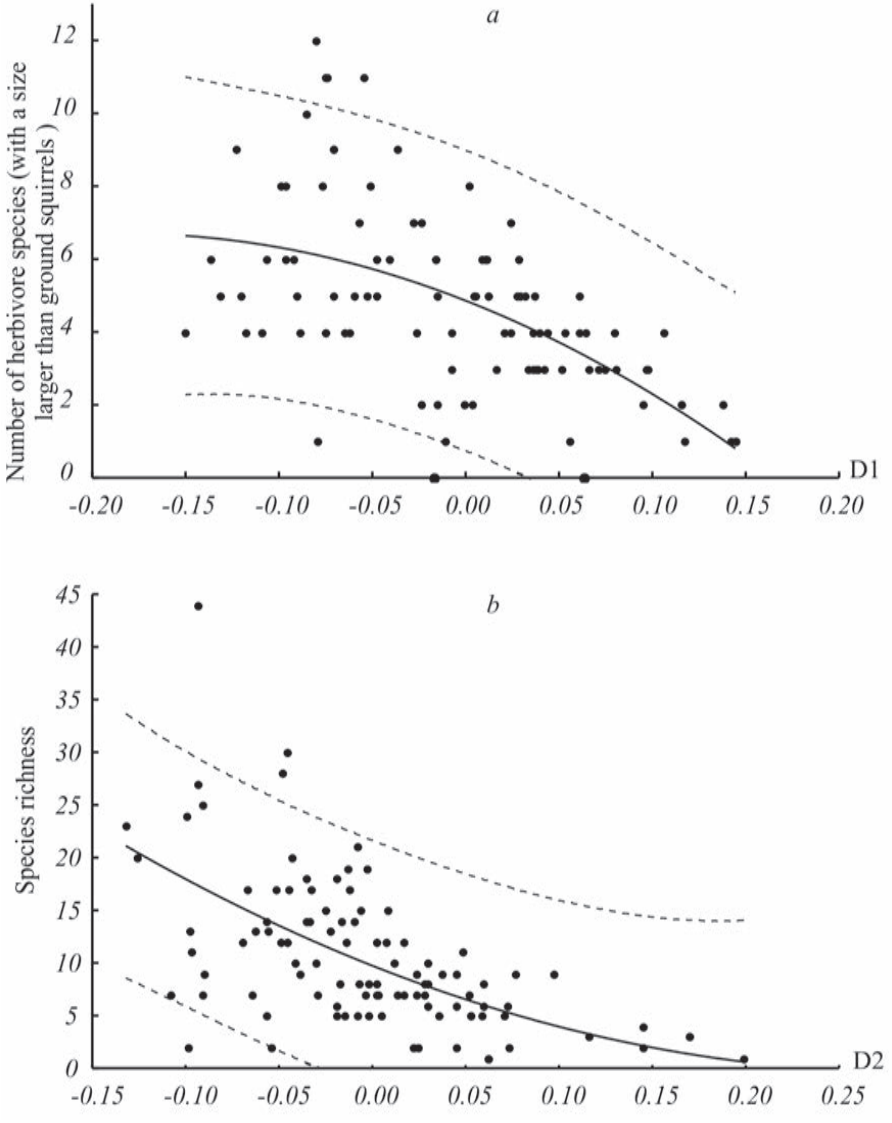

Fig. 2.8. *Regressions between some species richness parameters and MDS axes; a – number of herbivore species with sizes larger than ground squirrel size; b – species richness*

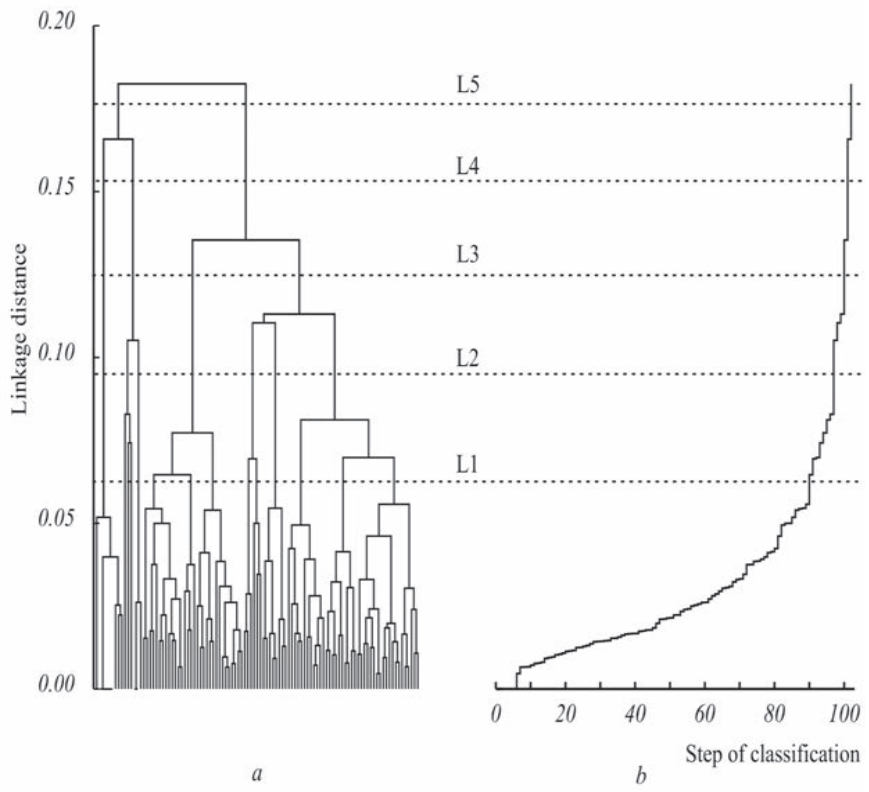

Fig. 2.9. *UPGMA dendrogram (103 LGM mammal localities) constructed using the MDS axes correlated with geographical coordinates: a – dendrogram, b – plot of linkage distances. There are 5 levels (supposed 'hierarchical' levels) with abrupt deviates of linkage distance from monotonic growth*

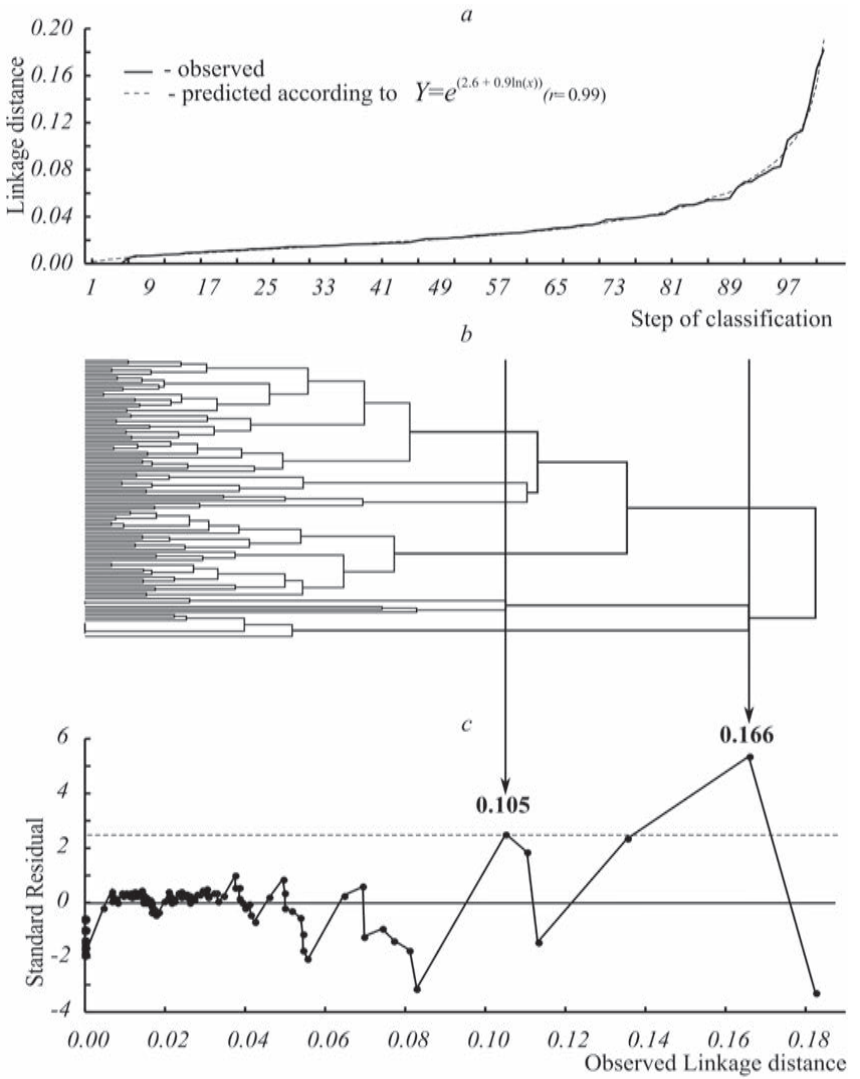

Fig. 2.10. *The comparison between observed (103 LGM mammal localities, two MDS axes) and predicted (two normal distributed variables, N=103) linkage distances of UPGMA dendrograms: a – observed an predicted Euclidian linkage distances, according to nonlinear regression model: y = e(A+Bln(x)); b – observed tree plot; c – standard residuals between observed and predicted linkage distances. Two maximal values (>2.5σ) of standard residuals correspond to 0.166 and 0.105 observed linkage distances. The arrows in Fig. 2.10b fit with the most 'realistic' cut-off levels on the present tree*

instance, *Betula* sec. *nana*/*B. pubescens*; *Bos*/*Bison*, *Alopex*/*Vulpes*, etc.); no clear correspondence in semantic of maximum and minimum between spore-pollen spectra, designed using different methods; incompleteness of taxa lists among different localities. All of them can be sources of error in the final classification of localities. Therefore, only a specialist can decide on the correctness of the statistical results and come up with the final interpretation.

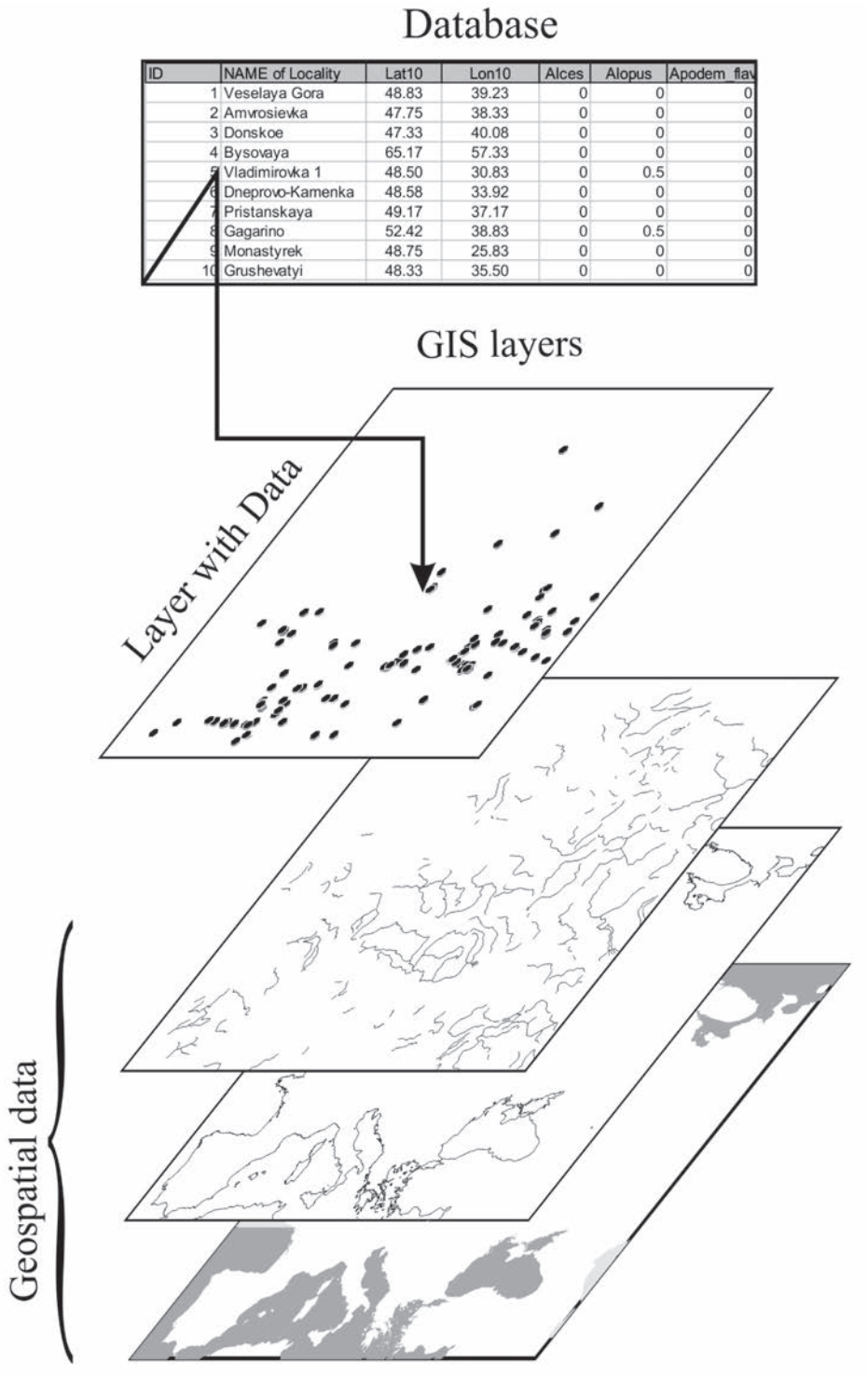

Fig. 2.11. *The principal scheme of the GIS includes several geographical layers and a data layer connected with the database*

Conclusion

In this study we used MapInfo Professional Version 7.0 GIS (MapInfo Corp.) for most of the data presentations. All databases with primary palaeontological materials have fields with geographical coordinates (latitude and longitude in the decimal degree format). As a final step in map preparation and GIS construction, we exported the tables in MapInfo Professional. Four basic geographical GIS layers were formed (Fig. 2.11): oceans and seas, land frontiers, rivers and lakes. In addition, for every time slice there are layers defined with data on a.o. shorelines and ice sheets. Maps of species natural ranges, results of theriological and botanical zonation of Europe across a specific time scale, maps of natural zones and maps of species richness are included in the list of thematic maps. All maps in the text are presented in the Gall projection of the World. For measuring spatial mammalian biodiversity (species richness) variations, we created 5×5 degree grids. The compilation of new GIS tables derived from data and grid layers, was based on the spatial relationship between their geographical objects – grid cells (centroids of the rectangle polygons) and palaeontological sites (points). The sum of species was calculated among all grid cells. The preparation of contour maps for spatial variations in species richness was carried out by means of Surfer Vers. 8.02 (Golden Software Inc.).

Summary

In this research we designed a general formalistic approach to analyse multivariate, primary palaeobotanical and palaeotheriological, data, to use well-known statistical methods, whenever possible to apply a uniform sequence of operations to different types of data and to make a selection of statistical methods according to the statistical "nature" of the input data. We used non-parametric multidimensional scaling, MDS (Shepard, 1962; Kruskal, 1964) as a basic technique for producing the virtual variables, which describe the "ordered variation" of input data. The main steps of data processing included: testing the data distribution (distribution fitting), choice of metrics for different types of data, computation "distances" between localities using these metrics, estimation of both the number of the virtual variables ("factors" – "dimensions"), their calculation and interpretation and classification of the localities in the cluster analyses using the "factors" as the variables. Investigating the distribution of mammal species in different time periods showed that canonical Binominal distribution and Poisson distribution approached real data well. The standardized numbers of spore-pollen data may be approached by lognormal distribution. The simplest and easiest way of understanding nominal (binary) variables (presence or absence) describing mammals among localities is the Jacquard's Coefficient. Calculating the "distances" between any pairs of palaeobotanical localities, we used both the Bray-Curtis metric and the Kendall *tau* coefficient. The "best-minimum dimensionality" in a MDS model (minimal "necessary and sufficient" of the number of the MDS axes) was estimated on behalf of Kruskal's Stress formula 1 according to the technique designed in Kupriyanova *et al*. (2003). Non-linear correlation analysis was used to discover a relation between MDS axes and the geographical coordinates of localities, because one of the main goals was to clarify the geographic distribution of floral and faunal assemblages in a geographical order. During correlation analysis, MDS axes were selected for the following classification procedure. For a hierarchical classification of localities we used the UPGMA procedure (Sneath, Sokal, 1973) with Euclid distance measuring, using the MDS axes in correlation with their position in the geographical range. The probable number of clusters was defined after mapping the points in GIS (MapInfo 7) for further biogeographically research and interpretation.

2.5. GIS TECHNOLOGY

Andrey Puzachenko

We used MapInfo Professional Version 7.0 GIS for most data presentations. In addition, we used the built-in SQL query language for the calculation of several secondary datasets of interest from two or more GIS layers. All databases with primary paleontological information have fields with the geographical coordinates (latitude

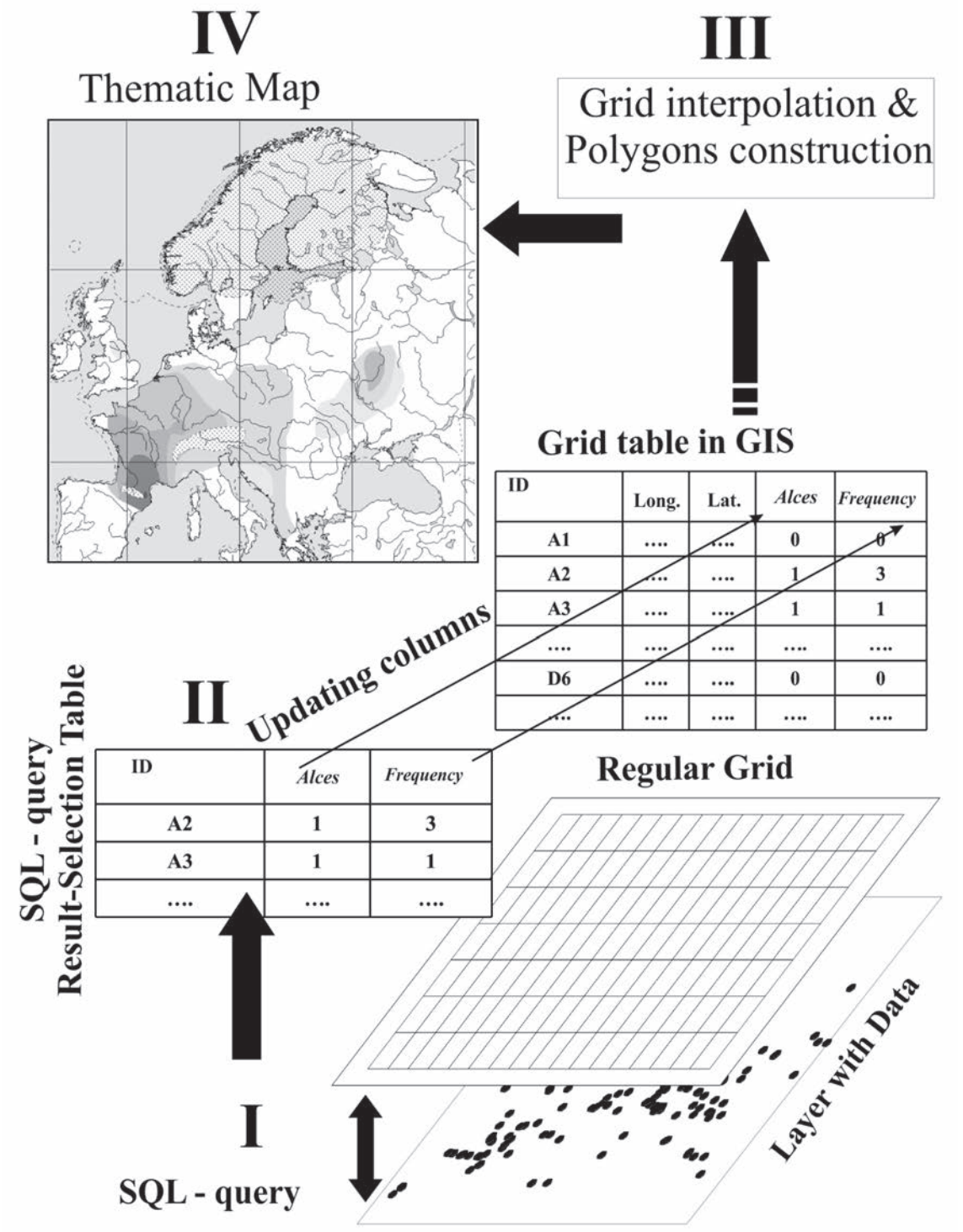

Fig. 2.12. *The scheme of data transformation for building of thematic maps of species richness using grid layer: I – re-calculation of data to the grid using SQL query, II – updating of columns in the grid table, III – preparation of contour map, IV – creation of the thematic map in MapInfo Professional*

and longitude in decimal degree format) (Fig. 1.1). For mapping, the data was transferred to GIS format.

Four basic geographical layers formed the GIS layers (Fig. 2.11): oceans and seas, the outline of the land, rivers, and lakes. All of them were digitized on a 1 : 20 000 000 scale. The western borders coincide with the Atlantic shorelines of Europe. The eastern border of Europe is taken to pass along the Ural Mountains (approximately

60°E) up to approximately 50°N. Thereafter this border turns to the west up to approximately 50°E and further rotates to the south along the western shoreline of the Caspian Sea.

Besides, there were layers with the contour maps of shorelines and ice sheets for each time slice, data layers and different thematic layers. The list of thematic maps includes reconstructions of the species natural ranges, results of theriological and botanical zonings of Europe across time scales, maps of the palaeoecosystems or natural zones, and maps of species richness, etc. All maps in the text are presented in the Gall projection of the World.

Spatial biodiversity (species richness) variation was measured on a 5×5 degree grid. The geographical coordinates (latitude and longitude of the cell's centroid) and the areas were calculated for each grid cell.

The compilation of the new GIS table from the data layer and grid layer was based on the spatial relationship between their geographical objects – grid cells (rectangular polygons) and palaeontological sites (points). The typical MapInfo SQL query has the following structure: Selected Columns: "Grid.Description, Data.Alces; From Tables: Grid, Data; Where Condition: Data.obj within Grid.obj and Data.Alces > 0; Into table Named: Selection".

The field "Description" in the grid table ("Grid") contains unique cell labels, field "Alces" of the "Data" table contains the data about the distribution of elk (present "1"; absence "0";). "Within" is a MapInfo Professional operator indicating the spatial relationship between the geographical objects. The result of such a query is stored in the temporal tables named "Selection". In the present example, this table will include two fields: "Description" and "Alces". In the final step, the sum of the species was calculated over all grid cells. To prepare the maps of spatial variations of the species richness, we used Surfer Vers. 8.02 (Golden Software Inc.). Grids were created by using a modified Shepard's method of data interpolation (Renka, 1988). The resulting contour maps were exported into MapInfo Professional as separate layers for the next edition and incorporation into the GIS. Figure 2.12 illuminates the generalized scheme of data transformations during the procedures described above.

Chapter 3

DEFINITION OF THE TIME SLICES. LANDSCAPE AND CLIMATE CHANGE DURING THE LAST GLACIATION IN EUROPE; A REVIEW

Joanne Mol

The Last Glaciation is a period that experienced major climate changes. The study of isotopes in ice cores identified superimposed on the Milankovitch cycle relatively mild episodes of 500–200 years duration: the Dansgaard-Oescher events (Dansgaard *et al*., 1993).

These short-lived climate changes were also recognized in other high-resolution logs, such as deep sea cores, lake records and the atmospheric dust record in the GRIP and GISP2-ice cores (Fig. 3.1). Similar changes of such short duration have been identified in the eustatic sea level, with changes up to 2 cm per year (Sidall *et al*., 2003). Identification of these events in terrestrial records has proven extremely difficult, due to their short duration.

Climate usually has a large impact on flora and fauna. Stone Age people depended heavily on fauna and were forced to react to changes in the flora and fauna that resulted from climate changes. This joint research deals with the relationship between flora, fauna and human occupation in Western and Eastern Europe. A challenging task, since not only the time lag between vegetation built-up and climate change needs to be taken into account, but also the dating of the sites, with errors sometimes bigger than one single short-term climatic event.

The nature of this multi-disciplinary study resulted in the selection of five very broad time windows, each characterized by its own specific climatic conditions. Their relatively long duration was the only way in which all time windows contained sufficient datapoints for flora, fauna and archaeology to show any regional and temporal changes. Therefore, the short-lived climate changes are not taken into account in this study.

This study provides a general overview of the variations in climate and landscape based on geological proxy data, and provides a framework for understanding the variations in flora and fauna during the time slices used in this study.

Nowadays, continuous permafrost is restricted to the uplands in Scandinavia, the northern Ural Mountains and the northern rim of the Russian Plain (Fig. 1). During the Last Glacial, this permafrost zone was located further south, due to the lower temperatures in Europe. The presence of permafrost depends on the mean annual (air) temperature, while flora depends on the mean summer temperature and the availability of moisture. More-over, information on the presence of permafrost can also be obtained from sites that lack organic material. Therefore, the presence or absence of permafrost is an important parameter, which can be used to explain changes in flora or fauna.

Periglacial landscapes are typified by wet soil conditions, due to the poor infiltration capacity of the frozen subsoil. Moreover, they are usually characterized by braided river systems, which are major sediment sources for aeolian deposition. Aeolian deposition, however, does

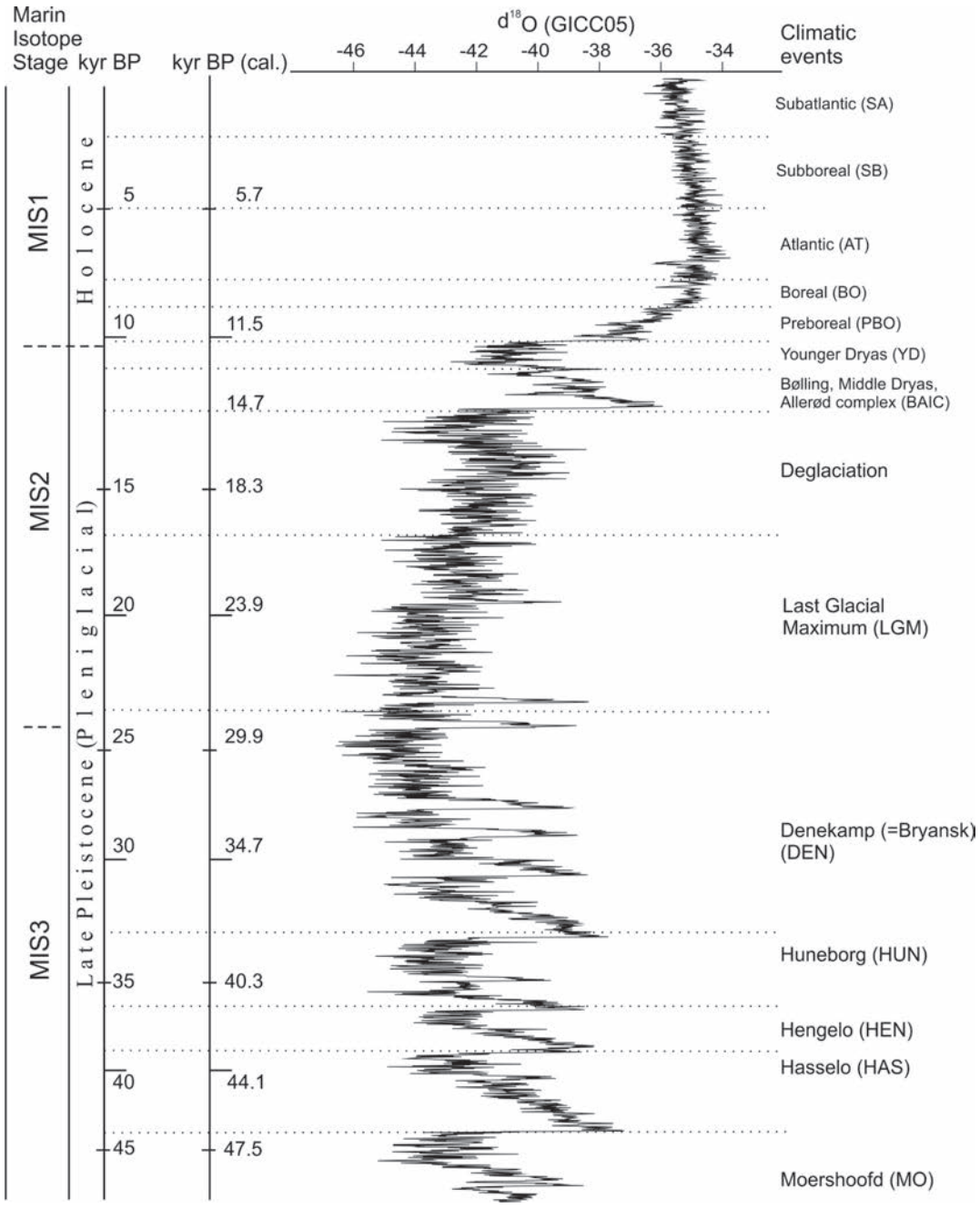

Fig. 3.1. *General climate trend of the last part of the last glacial according to the NGRIP-ice record (Andersen et al., 2004). The wiggles can be translated into oscillations in the growth and decay of the Greenland ice sheet, as a result of changes in temperature. The time windows that are subject of this study are indicated on the right of the curve. Please note that the ages in the y-axe are "ice-core years", which cannot be translated straightforward into the radiocarbon years used in this study*

not reveal any changes in temperature, but points to dry conditions and ample source sediment.

Relicts of periglacial features which form in permafrost environments, such as thermal contraction cracks, cryoturbations and perennial frost mounds, can be used as proxy data for earlier permafrost distribution and the assessment of the mean annual air temperature (MAAT) (Huijzer and Isarin, 1997). It is generally accepted that the presence of ice wedges and sand wedges and large periglacial involutions point to a MAAT of at least –4°C, while soil wedges (frost cracks) point to higher values: –1°C. Also perennial frost mounds are reliable indicators of permafrost conditions: closed system pingos form below a MAAT of –6°C, while open system pingos and mineral palsas form below –4°C and organic palsas below –1°C.

The present study is based on a database that was initially constructed by Huijzer and Isarin (1997), supplemented with recent data and some data from Russia. The main difficulty in the adaptation of datapoints into climate proxies remains the assessment of the data. Either the time control is poor or the description of the features is not clear. Especially the first two time slices, during Marine Isotope Stage 2, have few sites with good age constraints. This is mainly due to the limited amount of organic deposits during this period and the small number of reliable luminescence dates. In this period, the age control is mainly stratigraphically controlled and can therefore only show crude climate changes.

Time slice I: LGM (24–17 kyr[4])

The onset of time slice I roughly coincides with the boundary between stages 3 and 2 (25 kyr, after Svendssen *et al*., 1999). It starts at c. 24 kyr, after a period in which soil formation took place in Russia (the Bryansk Soil) and ends at the onset of the deglaciation at c. 17 kyr. During this period, between 22–18 kyr, the Scandinavian ice sheets expanded considerably and reached their maximum extents, though well above the maximum Quaternary drift limit. As a result of the ice sheet expansion, the glacioeustatic sea level dropped c. 120 m below the present one at the time of the maximum glaciation (Bard *et al*., 1990; Sidall *et al*., 2003).

During the last decade it has become clear that the exact timing of this maximum ice advance differed geographically, due to variations in ice sheet behaviour (Sejrup *et al*., 1994). The maximum advance to the south is marked by the Brandenburg Moraine in Germany, extending into the Lezno Moraines in Poland and the Bologoe Moraine in Russia (Kozarski, 1983; Lowe and Walker, 1997; Velichko *et al*., 2004). The extent of the ice sheet during oxygen isotope stage 2 is still in debate, but recent fieldwork in North West Siberian and the Russian plains resulted in a new reconstruction for the Eurasian ice sheet and more data on landscape development

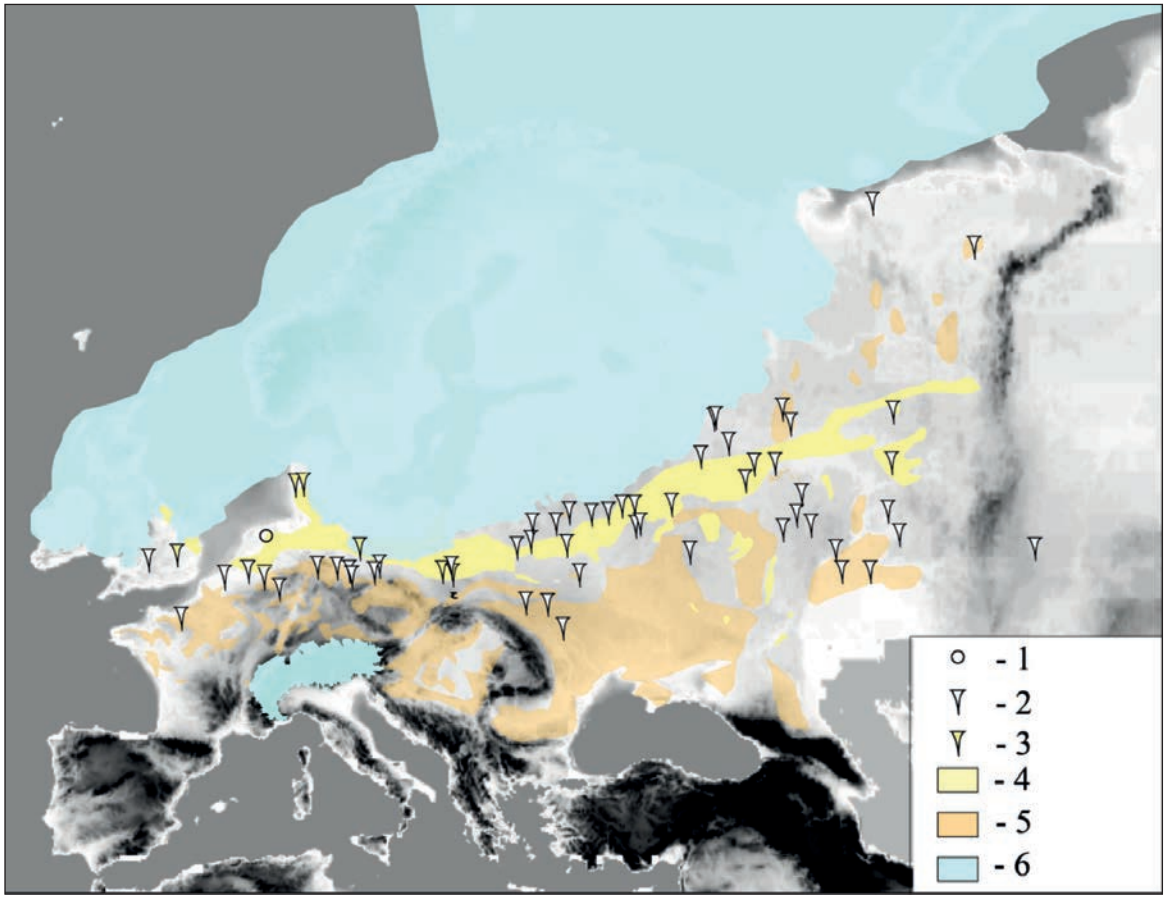

Fig. 3.2. *Time window 1: extent of the ice sheet and permafrost indicators at c. 20 kyr BP including the aeolian coversand and loess belt (adapted from Velichko, Zelikson, 2005 and Koster, 2005): 1 – perennial frost mound, 2 – ice wedge cast, 3 – sand wedge, 4 – cover sand, 5 – losses, 6 – ice extent*

[4] The ages mentioned are radiocarbon ages.

near the Eastern European ice margin (Hubberten *et al*., 2004; Svendssen *et al*., 2004) (Fig. 3.2). In Britain, the maximum ice advance was named the Dimlington Stadial (Rose, 1985). In Russia, timing and limits of the ice sheet expansion are still debatable due to insufficient age constraints (see Velichko, 1997; Grosswald and Hughes, 2002; Mangerud *et al*., 2002). It can confidently be stated, however, that at the LGM the Scandinavian ice sheet expanded onto the northeastern Russian Plain, but left a sizeable portion of the Russian Plain free of ice. Ice sheets centered at the Kara and Barents Sea shelves, as well as that on the Polar Urals, reached their maximum either in the early or in the middle Valdai, and had been considerably reduced by the LGM (Velichko *et al*., 1997; Mangerud *et al*., 2002; Berger *et al*., 2004). There are also significant data on the Alps and British Isles indicative of maximum glacial expansion before the LGM (Bowen *et al*., 2002; Guiter *et al*., 2005).

Whether or not the British and Scandinavian ice sheets coalesced is still in debate. Recent work in Ehlers and Gibbard (2004) shows one large ice sheet covering Europe from Britain up to Siberia (Fig. 3.2).

The largest part of the Russian-European lowlands was not covered with ice. Aeolian action was favoured by the sparsity of vegetation and the presence of large braided river plains that provided potential sediment sources. Locally, sand accumulated, while southward loess-like deposits accumulated in a zone up to Northern France, Southern Germany, Southern Poland, and Russia up to the Ural Mountains (Velichko, 1973, 1982; Mangerud *et al*., 2002; Koster, 2005). Sedimentological investigations of the deposits in the Netherlands and Germany showed that they were frequently reworked by surficial runoff, thus pointing to relatively humid conditions compared to the following deglaciation phase (Vandenberghe and Van Huissteden, 1988; Mol, 1997). This is attributed to the presence of permafrost, which caused poor infiltration and saturation of the active layer. This favoured overland flow and hampered aeolian deposition (Kasse, 1997).

In this aeolian accumulation zone periglacial conditions existed, evidenced by the presence of ice wedge casts and large cryoturbations (Huijzer and Vandenberghe, 1998). Ice wedge casts have been found in Denmark, the Netherlands, Northern France, Germany, Poland, and Northern Russia (Huijzer and Vandenberghe, 1997; Mangerud *et al*., 2001; Hubberten *et al*., 2004). Most of these ice wedge casts were situated in the coversand region, but also in the loess area were ice wedge casts found (Huijzer and Vandenberghe, 1997; Velichko *et al*., 2004; Velichko and Zelikson, 2005). Based on this evidence, Huijzer and Vandenberghe located the boundary of continuous permafrost conditions at c. 50°N (Belgian-French border) and defined a zone of discontinuous permafrost conditions up to Brittany (N. France), which can be extended to the east with data from Bełchatów (Central Poland) (Kasse *et al*., 1997) and the Russian Plain. In the Russian lowlands, continuous permafrost existed north of 57–58°N, while discontinuous to sporadic permafrost reached as far south as the coastal lowlands of the Black and Caspian Seas (48–49°N) (Velichko and Zelikson, 2005). The presence of ice wedge casts points to a MAAT of at least –4°C.

Time slice II: deglaciation (17–12.8 kyr BP)

The second time slice deals with the deglaciation history of Europe. The ice masses gradually melted and sea level rose accordingly from –120 m to c. –95 m at the onset of the Late Glacial (Sidell *et al*., 2003), the next time slice.

Continental Europe deglaciated rapidly. The first deglaciation phase, dated at c. 17 kyr is marked by the Main Stationary Line in Denmark, the Frankfurt Moraine in Germany, the Poznan Moraine in Poland, and the Edrovo or Outer Baltic Moraines in Russia (Kozarski, 1983; Houmark-Nielsen, 1989; Lowe and Walker, 1997; Velichko *et al*., 2004). At c. 13 kyr. almost all of Britain was deglaciated, with a possible exception of the Scottish Highlands. Deglaciation was interrupted by a number of stagnation phases and re-advances, of which the Drumlin re-advance in Ireland (c. 17 kyr) is the most prominent.

The second pronounced recession line is the East Jutland Line in Denmark, the Pommerian Moraine in Germany, the Pomorze moraine in Poland, and the Vepsopo moraine in Russia, dated at c. 15.2 kyr (Kozarski, 1993; Velichko *et al*., 2004).

Permafrost degradation and increased aridity favoured the development of extensive sand sheets and loess across Europe. Deposition occurred mainly during the final stage of the deglaciation phase and was dated to c. 14 kyr up to 12.4 kyr (Late Pleniglacial up to the Bølling) in the Netherlands (Kasse, 1997). In the west, sand sheets had formed, while more eastward mainly dunes had formed during the same period (Manikowska, 1991; Mangerud *et al*., 2002). This may be attributed to differences in vegetation cover, since in Poland and Russia vegetation growth started earlier than in the Netherlands; from 12.3 kyr pine and birch were already present in Poland and on the Russian Plain (Kasse, 1997; Chapters 5 and 6 this volume).

In contrast to the earlier aeolian deposits, the sand sheets were no longer subject to fluvial reworking, suggesting drier conditions than during the previous interval.

Periglacial features included numerous ice wedge casts and sand wedges. In the Netherlands, sand wedges were absent, while ice wedge casts were restricted to the first part of this time window: they were all situated below the Beuningen Gravel Bed, a deflation lag dated

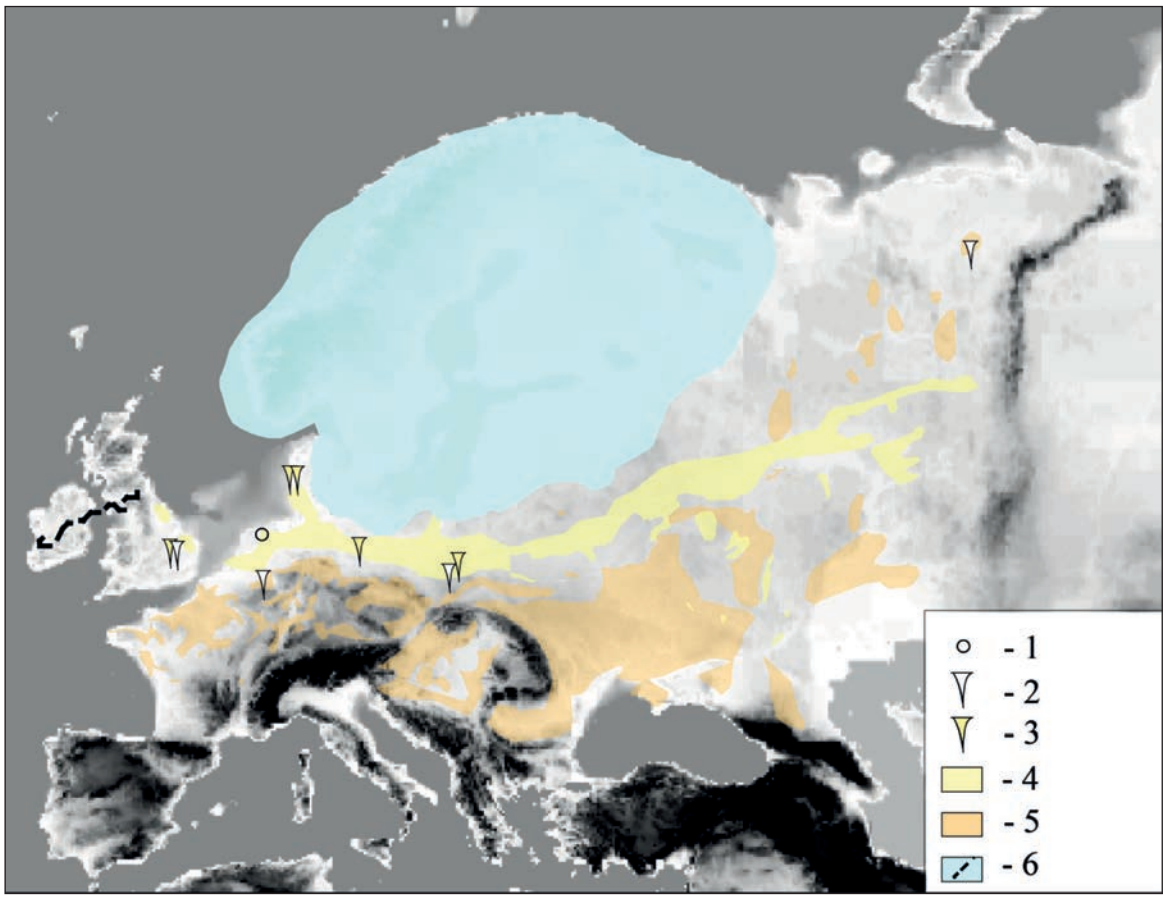

Fig. 3.3. *Time window II: extent of the ice sheet and permafrost indicators at c. 17 ka including the aeolian coversand and loess belt (adapted from Velichko, Zelikson, 2005 and Koster 2005): 1 – perennial frost mound, 2 – ice wedge cast, 3 – sand wedge, 4 – cover sand, 5 – losses, 6 – ice extent*

at c. 14 kyr (Kasse, 1997). Above this deflation lag there were still aeolian deposits, but no indications of permafrost (Van der Hammen and Wijmstra, 1971). The absence of thermal contraction cracks in the final part of this time window suggested a gradual warming to mean annual temperatures above –1°C and a northward shift of the permafrost boundary. In Poland, however, Kozarski (1993) reported sand wedges within the Vistulian (Weichselian) deglaciated till plains, and ice wedge casts within the glacial outwash plains. Their presence pointed to the presence of permafrost after the LGM. They were only sporadically present in till of the Pommerian phase (Godzjik, 1986). This may suggest that after this phase, permafrost diminished rapidly. On the Russian Plain, many ice wedge casts were reported. In the Pechora lowland (NW Russia), permafrost melting started around 13 kyr. Nowadays, this region is characterized by discontinuous permafrost (Henriksen *et al*., 2003).

The ample presence of sand wedges within the till plains in Poland may point to a gradual increase in aridity, although Kozarski stated that this may very well be a local, geomorphological phenomenon. Nevertheless, it coincides with the change in depositional style to aeolian deposits in Northern Europe and therefore a gradual increase in aridity during this time window is assumed.

Time slice III: Lateglacial Bølling-Allerød Interstadial Complex (BAIC) (12.8–10.9 kyr BP)

The Late Glacial is characterized by a rise in the temperature and by continued melting of the ice sheets. The eustatic sea level rose from c. –95 m to –70 m at the onset of the Younger Dryas (Sidell *et al*., 2003).

Britain was totally deglaciated, although some small ice remnants in the Scottish Highlands may have survived (Lowe and Walker, 1997). This period is characterized by extensive peat growth and soil formation in the Netherlands, Northern France, Germany, Poland, and Russia (Van der Hammen and Wijmstra, 1971; Velichko, 1982; 1990; Mol, 1997; Antoine *et al*., 2003). Limited periglacial features were found, the majority of which reflected melting of the permafrost (periglacial involutions). Aeolian deposition ceased gradually and was

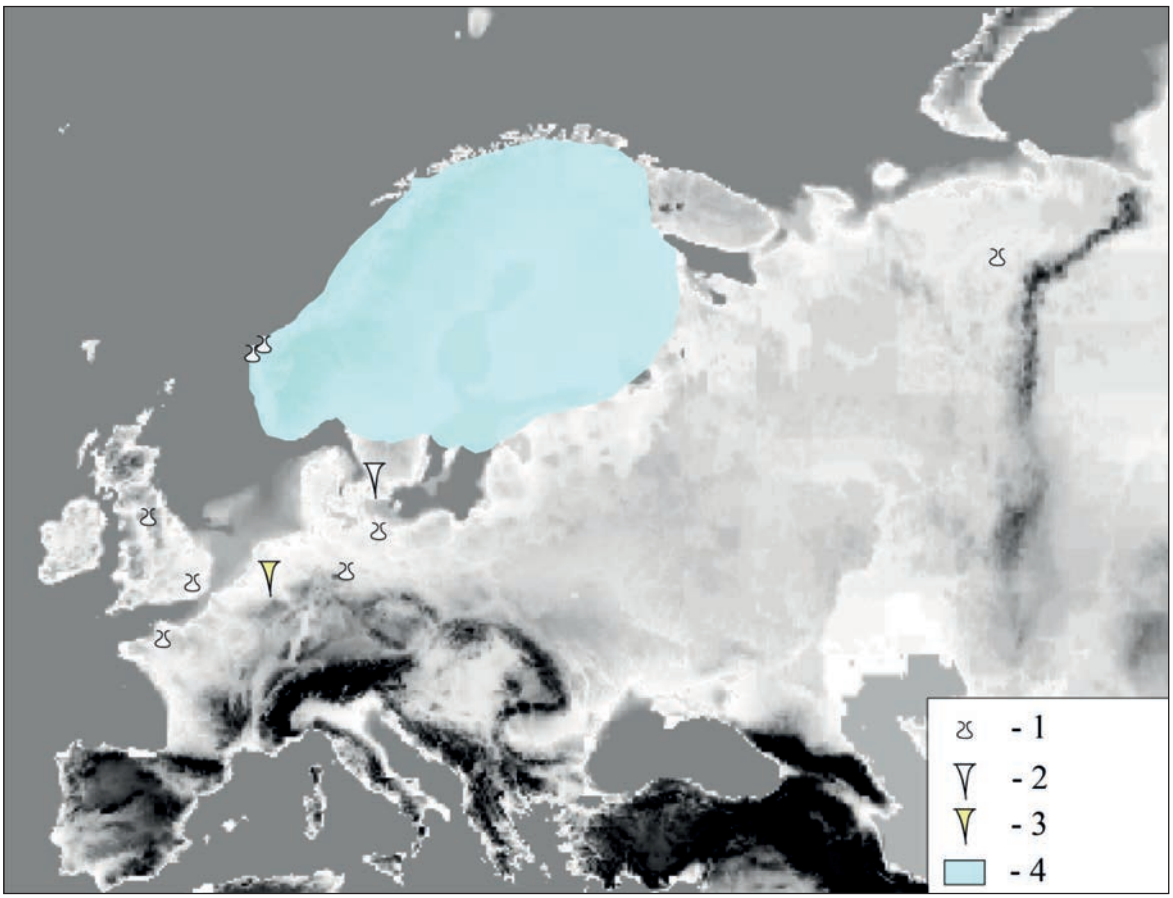

Fig. 3.4. *Time window III: extent of the ice sheet during the Lateglacial interstadial. Permafrost was (almost) absent everywhere: 1 – periglacial involution, 2 – ice wedge cast, 3 – sand wedge, 4 – ice extent*

almost absent during the climax of this period, due to an extensive vegetation cover. Van der Hammen and Wijmstra (1971) identified a period in between the Bølling and Allerød that was chracterized by aeolian deposition. This period, the Older Dryas, may very well be a local phenomenon, reflecting drier conditions instead of colder ones (Hoek, 1997). In the Netherlands the nature of the aeolian deposition was characterized by dune formation, in contrast to the earlier period, during which mainly sand sheets were deposited. The increase in density and height of the vegetation coincided with a change from sand sheet to dune formation (Kasse, 1997). In the east, however, dune formation had started earlier (see above). Periglacial phenomena were absent, which points to a MAAT of more than –1°C.

Time slice IV: Younger Dryas (11–10 kyr BP)

Time slice IV, the Younger Dryas, is a relatively short period during which cold, glacial conditions returned. The eustatic sea level rose from c. –70 m to –60 m.

It is characterized by glacial re-advances in Scandinavia and Britain. In Britain, small ice caps were formed in the Scotttish Highlands (Loch Lomond Stadial), while the advances of the Scandinavian land ice masses created a prominent morainic belt in Southern Norway (Ra Moraines), Sweden (Middle Swedish Moraines), Finland (Salpausselkä Moraines), and NE-Russia (Rugozero and Kalevala Moraines) (Saarnisto and Saarinen, 2001). In the west of Norway, the ice limit is marked by the Herdla Moraines and in the north by the Tromsø-Lyngen moraines (Mangerud, 1979; Vorren *et al*., 1988). However, these outer morainic belts were not completely synchronous, but formed at slightly different intervals during the Younger Dryas (Lundqvist, 1986; Saarnisto and Saarinen, 2001).

Renewed aeolian activity led to the formation of dune fields, sand sheets and remodelling of existing landforms. In the Netherlands, the aeolian landforms are parabolic river dunes, located on the banks of river valleys. Also in Eastern Germany have similar dunes been observed (Mol, 1997). In Poland, however, dune formation was far less intensive; it was characterized by remodelling pre-existing (Older Dryas) river dunes. This difference

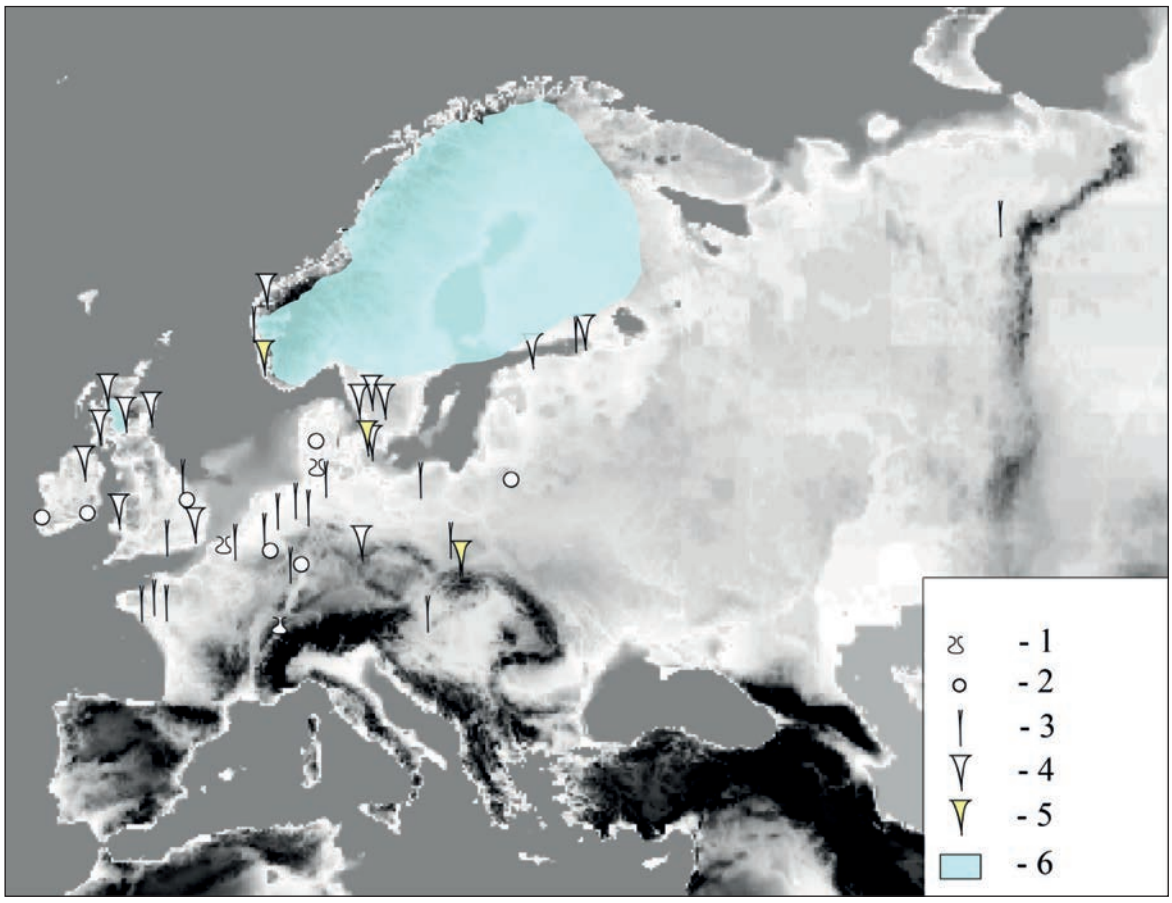

Fig. 3.5. *Time slice IV extent of the ice sheet and permafrost indicators during the Younger Dryas: 1 – periglacial involution, 2 – perennial frost mound, 3 – frost wedge, 4 – ice wedge cast, 5 – sand wedge, 4 – ice extent*

was attributed to differences in river systems, since the major rivers in the Netherlands developed a braided river pattern, which acted as a major sediment source, whereas the Polish rivers remained meandering. Moreover, also differences in vegetation cover may have contributed to the differences: the tree cover was estimated to have reduced by 50% in the Netherlands, and by only 25% in Poland (Isarin *et al*., 1997). Regrettably, in Eastern Europe, including the Russian Plain, we have limited data on the exact nature of the aeolian deposits, though Mangerud *et al*. (2002) report aeolian sand sheet formation in the Pechora basin.

Periglacial features have been found frequently (Isarin, 1997). Ice wedge casts are abundant near the ice margin, and in Ireland and Britain. Generally, there is consensus on the presence of continuous permafrost conditions near the Scandinavian ice margin, and in Northern Ireland and Britain. More eastward, limited datapoints are present, which may either be due to unfavourable conditions or poor chronological control. Periglacial indicators south of the Scandinavian ice margin are restricted to frost cracks and immature ice wedges. This may be caused by a slightly higher annual air temperature, but it may also have been caused by the short duration of formation processes (Vandenberghe, 1987). Locally, at the Haute Fagne (Belgium), in the Northern Netherlands, Ireland, and Britain some well-dated seasonal frost mounds are described, which indicated discontinuous permafrost.

Isarin (1997) concluded that continuous permafrost conditions existed north of 54°N. South of this zone, discontinuous permafrost existed up to Poland, Germany, the Netherlands, Southern England and upland Belgium (54–50°N), while in Northern France sporadic permafrost was present. Although there are no datapoints in the Russian Lowlands, it seems likely that this zone can be extended eastward.

Time slice V: Preboreal and Boreal

During the Early Holocene, melting of the ice sheet continued and at c. 8500 BP, the Scandinavian ice sheet had virtually disappeared (Lundqvist, 1986).

Aeolian deposition continued at the onset of the Holocene. In Germany and Denmark aeolian deposits have

been reported from the Preboreal and Boreal and also in Scandinavia did aeolian deposition occur after the retreat of the Scandinavian ice sheet. Indicators of permafrost have not been reported.

Conclusions

The Weichselian experienced major climatie changes that forced flora and fauna to react. Five broad time slices enabled the assessment of regional variations in flora and fauna and human occupation.

Time slice 1 (24–17 kyr), includes the LGM, during which the ice sheets reached their maximum expansion and permafrost extended to 49°N. A broad zone with aeolian deposits (coversand and loess) was laid down, though they were frequently reworked by overland flow due to poor infiltration.

Time slice 2 (17–12.8 kyr), comprises the deglaciation phase. The ice sheets melted rapidly and permafrost melted accordingly. After 14 kyr, the whole of the Northen Europe experienced dry conditions, envisaged by large-scale aeolian deposition (coversand and loess), that was not reworked.

Time slice 3 (12.8–10.9 kyr), deals with the Lateglacial interstadial, the Bølling/Allerød complex. During this period, the ice sheet had completely melted and permafrost was absent. It is a period characterized by mild conditions, with peat development, and soil formation.

Time slice 4 (10.9-10 kyr), is the Younger Dryas, a short glacial phase, during which ice sheets expanded and permafrost returned. Also aeolian deposition occurred at a large scale, though mainly as dunes, in contrast to the earlier period, in which sand sheets were more frequent.

Time slice 5 (10.0–8 kyr), the Preboreal and Boreal, is the start of the following interglacial period, during which vegetation re-established (including reforestation) and the ice sheet gradually disappeared from Europe.

Regional differences in climatic regime occurred during all time slices. The main variation is north-south, but also east-west climatic differences existed. Similar to the present situation, the marine influence resulted in less severe conditions near the North Sea and slightly higher temperatures as a result. Regional differences in deposition type could not always be related to climatic differences. During the deglaciation phase the difference in aeolian deposition in the west and east was attributed to the difference in vegetation cover, while during the Younger Dryas, the difference was attributed to different river types, resulting in different sediment source opportunities[5].

[5] Chronostratigraphic units within the late Pleistocene and Holocene as given in this chapter are somewhat different from the time intervals we used in Chapter 1 and the rest of the book. When dealing with palaeontological materials, we used the late Pleistocene – Holocene subdivisions indicated in Chapter 1, according to Coope and Lemdahl (1995), Stuiver *et al*. (1995), Hoek (1997), and Bolikhovskaya (2004).

Chapter 4

MAMMAL ASSEMBLAGES OF EUROPE DURING THE PLEISTOCENE–HOLOCENE TRANSITION (⩽24 – ⩾8 KYR BP)

4.1. MAMMAL ASSEMBLAGES DURING THE LAST GLACIAL MAXIMUM (LGM) (⩽24 – ⩾17 KYR BP)

Anastasia Markova and Andrey Puzachenko

The Late Valdai glacial time was marked by the most severe climate in the Pleistocene, with extensive ice sheets and periglacial landscapes widely spread over the extra-tropical regions of the northern hemisphere. In the stratigraphical scheme of the central Russian Plain, the late Valdai sediments are defined as the Ostashkov horizon dated from <25 kyr BP to >10 kyr BP (Breslav *et al.*, 1992) and correlated with Stage 2 of the oxygen isotope scale (Fig. 4.1) (GRIP, 1993; Petit, 1999). This stratigraphic horizon includes glacial deposits (till and glaciofluvial sediments) as well as periglacial alluvium of low terraces and loess-soil series. The latter consists (from the top down) of the Altynov loess (loess I), the Trubchevsk interstadial soil (~17 kyr BP) and the underlying Desna loess (loess II). The time of Desna loess formation is thought to correspond to the maximum Valdai cooling (usually termed LGM, that is the Last Glacial Maximum) (Gerasimov *et al.*, 1980). In the Ural Mountains, the divisions of the Late Pleistocene sequence are not so clear and based mostly on ^{14}C dates. In Western Europe, the Last Glacial Maximum is correlated with the Brandenburg glacial stage, in Northern Europe it is related to the Haugesund stage, and in Central Europe (Poland) to the Leshchinsko-Pomorski (Glowny) Stage (Linder and Marks, 1994; Ber, 2000). The Sartan glaciation correlated with the maximum cooling of the Last Glaciation in Western and Central Siberia (Biryukov *et al.*, 1988).

In this section we concentrate on the analysis of the European mammal fauna and flora of the LGM time interval (24–17 kyr BP). There are a number of reconstructions of late Valdai (=Weichselian) environments, including those of vegetation, mammal fauna, cryogenic phenomena, loess cover, etc. They have been published in monographs and palaeogeographic atlases (Markov *et al.*, 1965; Chebotareva and Makarycheva, 1982; Gerasimov and Velichko, 1982; Markov, 1986; Grichuk, 1989; Atlas of paleoclimates and paleoenvironments of Nor-

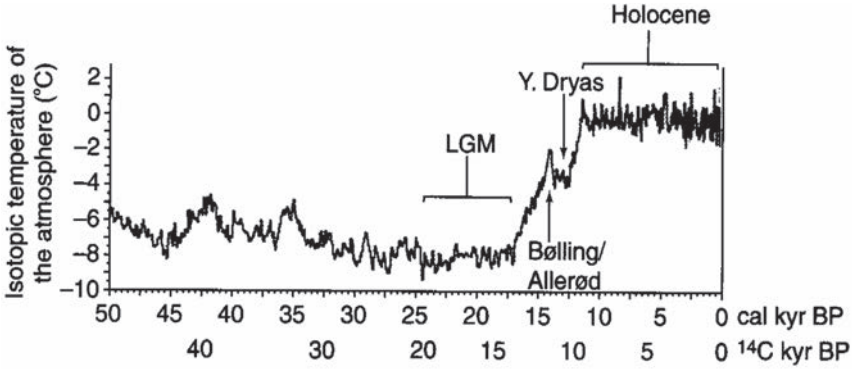

Fig. 4.1. *Global climate change based on oxygen isotope data from the Vostok ice-core, Antarctica (after Petit, 1999)*

thern Hemisphere, 1992; Bolikhovskaya, 1995; Dynamics of landscapes and climates of northern Eurasia, 2002). There are now new data available on the ice sheet limits on the land, as well as in the coastal regions and Arctic shelves (Svensen *et al*., 1999; Siegert *et al*., 2002; Velichko *et al.*, 2002).

Materials and methods

Information from 341 localities dating to the LGM was collected for the territory of Europe (Fig. 4.2). Ninety-one mammal taxa were distinguished from these localities, including 86 mammal species and 5 taxa of higher rank. The data were united in the form of an electronic database, similar to the PALEOFAUNA database, which was elaborated for the Former Soviet Union Late Pleistocene mammal data (Markova *et al*., 1995). The structure of Western European databases (Leiden database, Cambridge database, Pangea database) was transformed to the same form and united with the Russian database. We used the ^{14}C data (not calibrated) as dating sources, which permitted us to unite all European materials. The LGM mammal localities cover the territory of

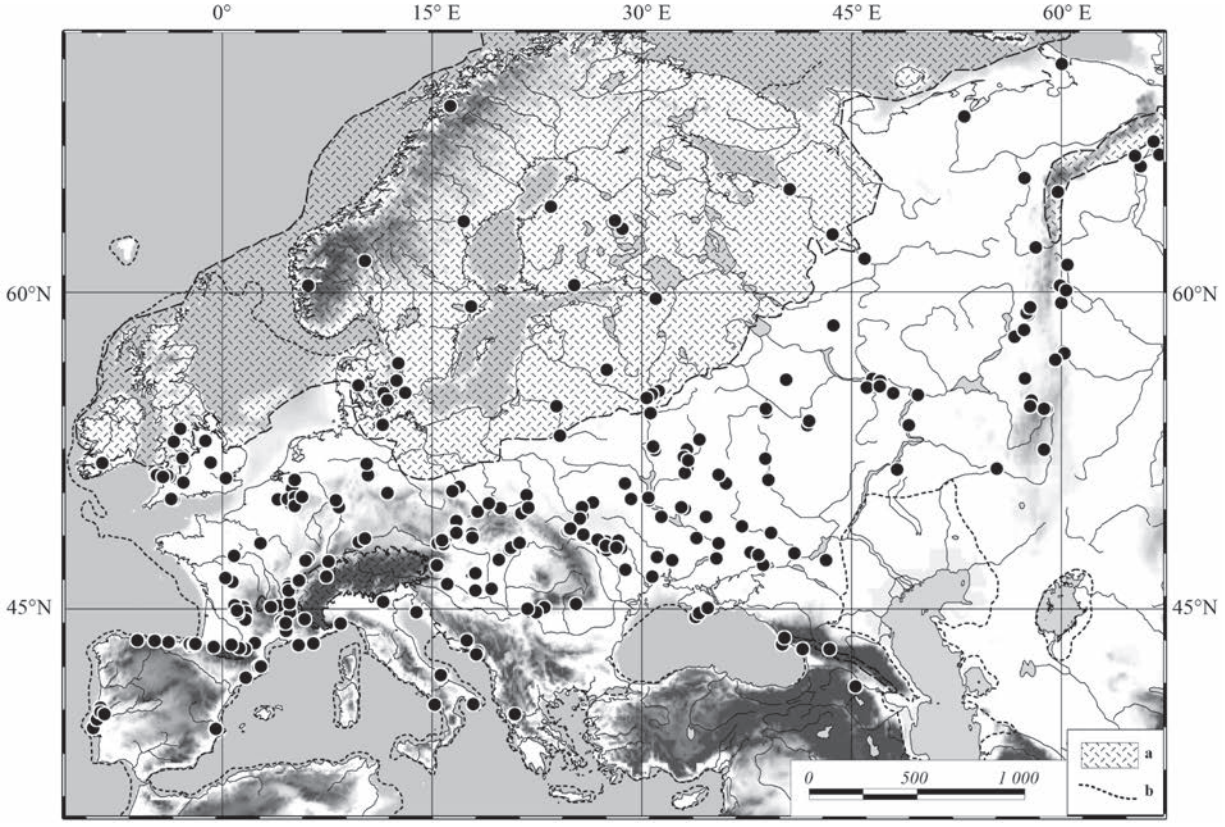

Fig. 4.2. *Last Glacial Maximum mammal localities dated by 14C between >17 – ≤24 kyr BP: a – ice sheets and mountain glaciers; b – coastline*

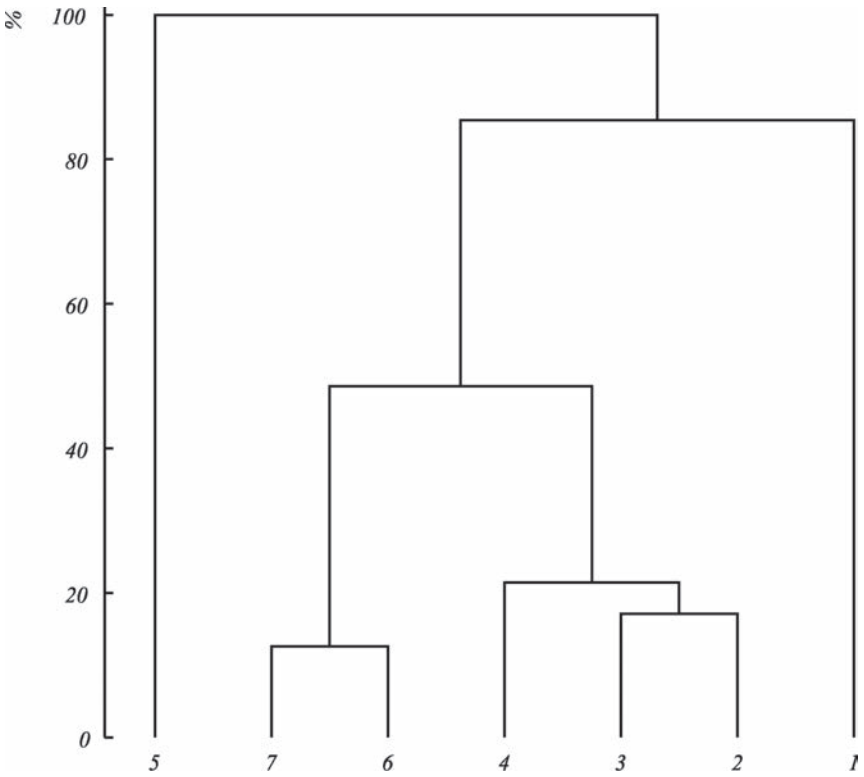

Fig. 4.3. *The result of classification of mammal localities (UPMGA method)*

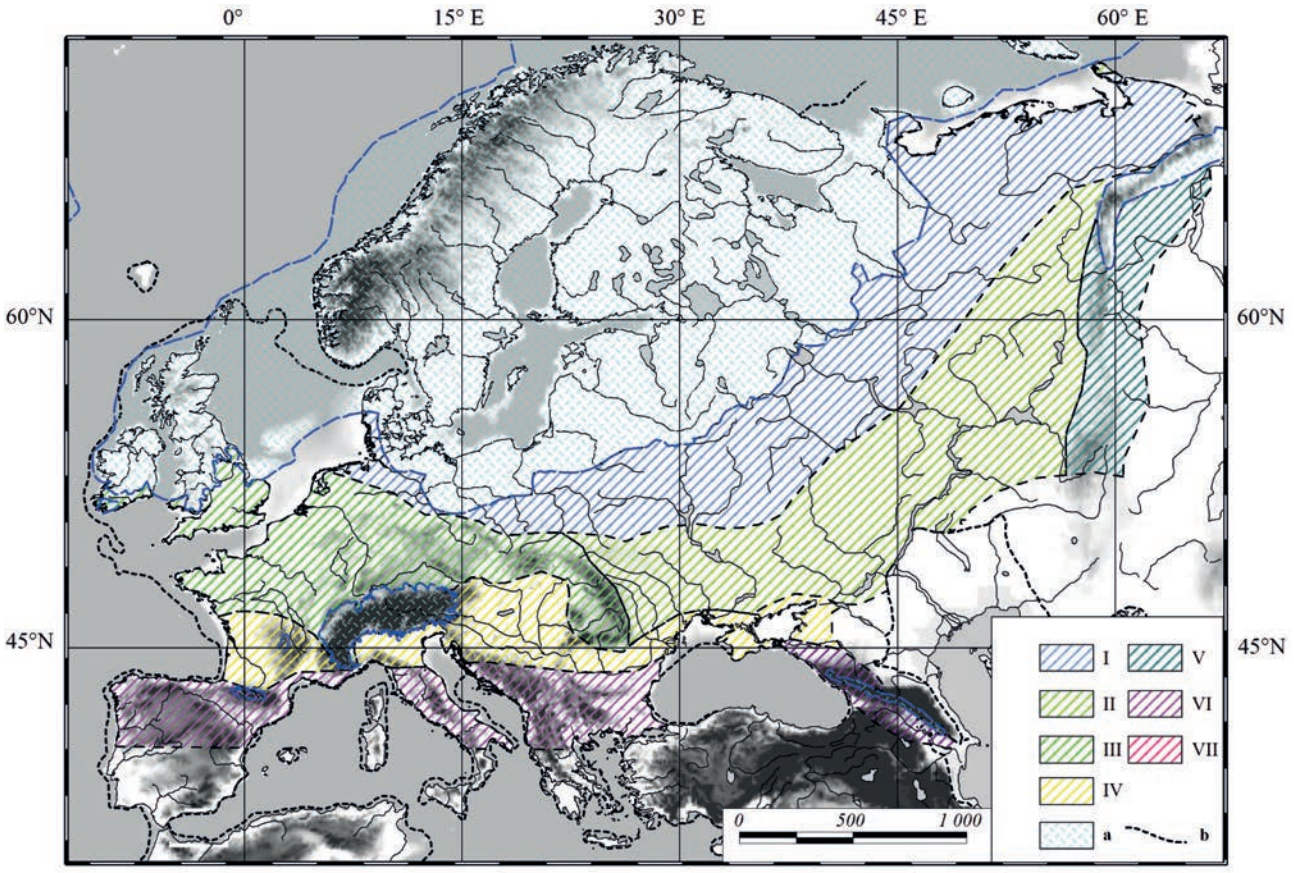

Fig. 4.4. *LGM mammal assemblages – I–VII; a – ice sheet and mountain glaciers; b – coastline*

Europe irregularly. Most of the localities can be found in France, northern Spain, Germany, Great Britain, the Czeck Republic, Hungary, and Eastern Europe. The very north of Europe and also the South is rather empty. Possibly, we have not collected all the data for these regions. The mammal assemblages for the very southern regions of Europe were not reconstructed.

Fossil mammal data was summarized and mapped using MapInfo GIS. Next, the classification of all localities was undertaken. We classified only localities where more than 3 mammal species were found (110 localities). The matrices of pair distances were calculated for mammal localities, after which those localities were clustered (UPGMA method) using multidimensional scale axes. This procedure has been described in chapter 2). This resulted in seven clusters. These clusters are characterized by normal distribution of intra-cluster distances (Fig. 4.3). The location of the mammal localities, belonging to the different clusters, is presented in Figure 4.4.

LGM Mammal assemblages

The occurrence of mammal taxa in the clusters is shown in Table 4.1.

Table 4.1

The indicator species for every cluster (assemblage), in percentages. Maximum credibility based on Chi-square with $p \leqslant 0.05$

Taxa	Clusters (mammal assemblages)							M-L Chi-sq, *p*
	1	2	3	4	5	6	7	
Erinaceus sp. – Eurasian hedgehog	0.0	1.56	0.0	**16.0**	0.0	**16.67**	0.0	0.03
Desmana moschata – Russian desman	0.0	1.56	0.0	0.0	0.0	0.0	0.0	–
Talpa sp. – Eurasian mole	0.0	1.56	0.0	16.0	0.0	5.56	0.0	–
Sorex araneus – common shrew	0.0	1.56	0.0	12.0	12.50	0.0	0.0	–
Sorex arcticus – arctic shrew	0.0	1.56	0.0	0.0	0.0	0.0	0.0	–
Sorex minutus – lesser shrew	0.0	1.56	0.0	12.0	0.0	0.0	0.0	–
Neomys sp. – water shrew	0.0	3.13	0.0	4.0	0.0	0.0	0.0	–
Oryctolagus cuniculus – European rabbit	0.0	0.0	0.0	**20.0**	0.0	11.11	0.0	0.05
Lepus timidus – Polar hare	0.0	10.94	7.69	20.0	**62.50**	0.0	0.0	–
Lepus europaeus – European hare	0.0	1.56	0.0	12.0	0.0	11.11	0.0	–
Ochotona pusilla – steppe pika	0.0	17.19	0.0	8.0	**50.0**	5.56	0.0	0.07
Sciurus vulgaris – red squirrel	0.0	0.0	0.0	4.0	0.0	0.0	**20.0**	–
Spermophilus sp. – suslik	0.0	**20.31**	0.0	8.0	0.0	5.56	0.0	0.02
Marmota bobak – bobak marmot	0.0	9.38	0.0	4.0	**50.0**	0.0	0.0	0.04
Marmota marmota – Alpine marmot	0.0	1.56	0.0	12.0	0.0	0.0	0.0	–
Castor fiber – beaver	0.0	6.25	0.0	4.0	0.0	5.56	0.0	
Eliomys quercinus – garden dormouse	0.0	0.0	0.0	**16.0**	0.0	5.56	0.0	0.03
Glis glis – fat dormouse	0.0	0.0	0.0	4.0	0.0	0.0	0.0	–
Sicista subtilis – southern birch mouse	0.0	1.56	0.0	0.0	0.0	5.56	0.0	–
Sicista betulina – northern birch mouse	0.0	1.56	0.0	0.0	0.0	0.0	0.0	–
Allactaga major – great jerboa	0.0	3.13	0.0	4.0	0.0	0.0	0.0	–
Allactaga pygmaeus – small jerboa	0.0	0.0	0.0	0.0	12.5	0.0	0.0	–
Stylodipus telum – three-toed jerboa	0.0	0.0	0.0	4.0	0.0	0.0	0.0	–
Nannospalax – lesser mole rat	0.0	1.56	0.0	0.0	0.0	0.0	0.0	–
Spalax sp. – mole rat	0.0	4.69	0.0	0.0	0.0	0.0	0.0	–

Continued table 4.1

Taxa	Clusters (mammal assemblages)							M-L Chi-sq, *p*
	1	2	3	4	5	6	7	
Sylvaemus sp. – wood mouse	0.0	3.13	0.0	20.0	0.0	5.56	0.0	–
S. sylvaticus – wood mouse	0.0	3.13	0.0	12.0	0.0	5.56	0.0	–
S. flavicolis – yellow-necked mouse	0.0	1.56	0.0	4.0	0.0	0.0	0.0	–
Ellobius talpinus – northern mole-vole	0.0	0.0	0.0	4.0	0.0	0.0	0.0	–
Allocricetulus eversmanni – Eversmann' hamster	0.0	0.0	0.0	4.0	0.0	0.0	0.0	–
Cricetulus migratorius – grey hamster	0.0	4.69	0.0	0.0	0.0	0.0	0.0	–
Cricetus cricetus – common hamster	0.0	4.69	0.0	4.0	0.0	0.0	0.0	–
Dolomys bogdanovi – Martino's snow vole	0.0	0.0	0.0	4.0	0.0	0.0	0.0	–
Clethrionomys rufocanus – gray red-backed vole	0.0	1.56	0.0	0.0	12.50	0.0	0.0	–
Clethrionomys glareolus – red-backed vole	0.0	4.69	0.0	4.0	12.50	5.56	0.0	–
Clethrionomys rutilus – northern red-backed vole	0.0	3.13	0.0	0.0	0.0	0.0	0.0	–
Lagurus lagurus – steppe lemming	0.0	10.94	0.0	4.0	**25.0**	5.56	0.0	–
Eolagurus luteus – yellow steppe lemming	0.0	3.13	0.0	0.0	0.0	0.0	0.0	–
Dicrostonyx gulielmi – collared lemming	**28.57**	**18.75**	0.0	8.0	**37.50**	0.0	0.0	0.07
Lemmus lemmus – Norway lemming	0.0	**3.13**	0.0	0.0	0.0	0.0	0.0	–
Lemmus sibiricus – Siberian lemming	**28.57**	9.38	0.0	0.0	**37.50**	0.0	0.0	0.02
Arvicola terrestris – water vole	0.0	15.63	0.0	**44.0**	12.50	16.67	0.0	0.01
Terricola sp. – pine vole	0.0	1.56	0.0	4.0	0.0	**16.67**	0.0	–
Microtus gregalis – narrow skull vole	**28.57**	17.19	0.0	12.0	**50.0**	0.0	0.0	0.04
Microtus oeconomus – root vole	0.0	9.38	0.0	12.0	**37.50**	0.0	0.0	0.03
Microtus agrestis – field vole	7.14	6.25	0.0	16.0	12.50	5.56	0.0	–
Microtus arvalis – common vole	0.0	12.50	0.0	**24.0**	0.0	11.11	0.0	0.045
Microtus middendorfii – Middendorf's vole	0.0	1.56	0.0	0.0	12.50	0.0	0.0	–
Chionomys nivalis – snow vole	0.0	1.56	0.0	4.0	0.0	0.0	0.0	–
Canis lupus – common wolf	0.0	37.50	38.46	**76.0**	25.0	16.67	**40.0**	<0.001
Vulpes lagopus – Polar fox	0.0	**35.94**	15.38	**44.0**	**37.50**	0.0	0.0	<0.001
Vulpes vulpes – common red fox	0.0	31.25	7.69	**72.0**	12.50	38.89	20.0	<0.001
Vulpes corsac – corsac fox	0.0	0.0	0.0	8.0	0.0	0.0	0.0	–
Cuon alpinus – red dog	0.0	0.0	0.0	8.0	0.0	0.0	0.0	–
Ursus arctos – brown bear	0.0	23.44	**30.77**	20.0	0.0	0.0	**40.0**	0.03
Ursus spelaeus – cave bear	0.0	12.50	**53.85**	**36.0**	0.0	22.22	**40.0**	0.005
Ursus maritimus – Polar bear	**7.14**	0.0	0.0	0.0	0.0	0.0	0.0	–
Gulo gulo – wolverine	0.0	9.38	**15.38**	**12.0**	0.0	0.0	0.0	–
Mustela erminea – ermine stoat	0.0	14.06	0.0	8.0	**25.0**	0.0	0.0	–
M. nivalis – weasel	10.0	2.44	50.0	11.54	0.0	4.55	9.09	–
M. putorius – polecat	0.0	3.13	0.0	0.0	0.0	0.0	0.0	–
M. eversmanni – Russian polecat	0.0	1.56	0.0	0.0	**25.0**	0.0	0.0	–
Meles meles – badger	0.0	4.69	0.0	**24.0**	0.0	0.0	0.0	0.01
Crocuta crocuta spelaea – cave hyena	0.0	6.25	**53.85**	24.0	0.0	**38.89**	20.0	<0.001

Continued table 4.1

Taxa	Clusters (mammal assemblages)							M-L Chi-sq, *p*
	1	2	3	4	5	6	7	
Panthera spelaea – cave lion	0.0	7.81	23.08	24.0	12.50	0.0	0.0	0.03
Panthera pardus – leopard	0.0	0.0	0.0	4.0	0.0	**11.11**	0.0	–
Felis silvestris – wood cat	0.0	3.13	0.0	**16.0**	0.0	**22.22**	0.0	0.03
Lynx sp. – Lynx	0.0	4.69	0.0	12.0	0.0	**22.22**	0.0	–
Mammuthus primigenius – woolly mammoth	**64.29**	**81.25**	**61.54**	24.0	12.50	0.0	0.0	<0.001
Equus (Equus) sp. – wild horse	7.14	40.63	**84.62**	**72.0**	12.50	**55.56**	40.0	<0.001
Equus hydruntinus – Pleistocene ass	0.0	1.56	0.0	**32.0**	0.0	5.56	0.0	0.006
Coelodonta antiquitatis – woolly rhinoceros	7.14	**51.56**	38.46	16.0	**75.0**	0.0	0.0	<0.001
Sus scrofa – wild boar	0.0	0.0	0.0	36.0	0.0	**50.0**	**60.0**	<0.001
Dama dama – fallow deer	0.0	0.0	0.0	0.0	0.0	0.0	**20.0**	–
Cervus elaphus – red deer	0.0	21.88	7.69	**76.0**	0.0	**88.89**	**40.0**	<0.001
Capreolus capreolus – roe deer	0.0	3.13	0.0	**32.0**	0.0	**44.44**	**60.0**	<0.001
Megaloceros giganteus – giant deer	0.0	9.38	15.38	16.0	0.0	11.11	0.0	–
Alces alces – elk	0.0	14.06	0.0	16.0	0.0	5.56	20.0	–
Rangifer tarandus – reindeer	7.14	**78.13**	**61.54**	**76.0**	**75.0**	22.22	0.0	<0.001
Bos primigenius – aurochs	0.0	15.63	38.46	**64.0**	0.0	**61.11**	**60.0**	<0.001
Bison priscus – steppe bison	7.14	40.63	30.77	**72.0**	**62.50**	27.78	20.0	0.01
Saiga tatarica – saiga	0.0	15.63	0.0	16.0	37.50	0.0	0.0	0.08
Ovibos moschatus – muskox	0.0	3.13	0.0	8.0	**12.50**	0.0	0.0	–
Rupicapra rupicapra – chamois	0.0	1.56	7.69	**60.0**	0.0	**77.78**	0.0	<0.001
Capra sp. – Goat	0.0	1.56	0.0	**72.0**	0.0	**72.22**	**20.0**	<0.001
Capra aegagrus – goat	0.0	0.0	0.0	4.0	0.0	0.0	0.0	–
Capra caucasica – Caucasian goat	0.0	0.0	0.0	0.0	0.0	0.0	**20.0**	–
Capra ibex – mountain goat	0.0	1.56	0.0	**68.0**	0.0	**72.22**	0.0	<0.001
Ovis sp. – mountain sheep	0.0	0.0	0.0	4.0	0.0	0.0	**20.0**	–

Periglacial tundra mammal assemblage (cluster 1)

The 16 localities of the first cluster include only 8 species. Mammoth *Mammuthus primigenius*, collared lemming *Dicrostonyx gulielmi*, Siberian lemming *Lemmus sibiricus*, narrow-skulled vole *Microtus gregalis*, and polar bear *Ursus maritimus* were found in these areas (Figs. 4.5–4.10). These species were indicative of this assemblage.

Besides lemming remains, reindeer *Rangifer tarandus* bones were also found in some of the sites (Table 4.1). *Ursus maritimus* bones were recovered on the coast of Scandinavia (Hufthammer, 2001). The presence of narrow-skulled vole remains in the sites also indicates a severe climatic condition, because this animal was well adapted to the periglacial tundra and tundra-steppe landscapes, and was a member of the "mammoth" assemblage (Baryshnikov and Markova, 1992; 2002). The unique sites in Finland also fall in this cluster, which permit us to reconstruct the ice sheet free areas in Scandinavia (Ukkonen, 2001). Another option could be that the bones were transported by humans after the deglaciation. The southernmost localities are situated in the upper drainage basins of the Dnieper and Don Rivers. But *Dicrostonyx* and *Lemmus* are absent there. *Mammuthus*, *Coelodonta* and *Rangifer* are the principal animals in this assemblage. The southern position of several localities of the first group could be explained by the poor species composition of these sites, which could reflect the different approaches of studies of mammal sites. First of all, in many cases, the small mammal remains have not been collected

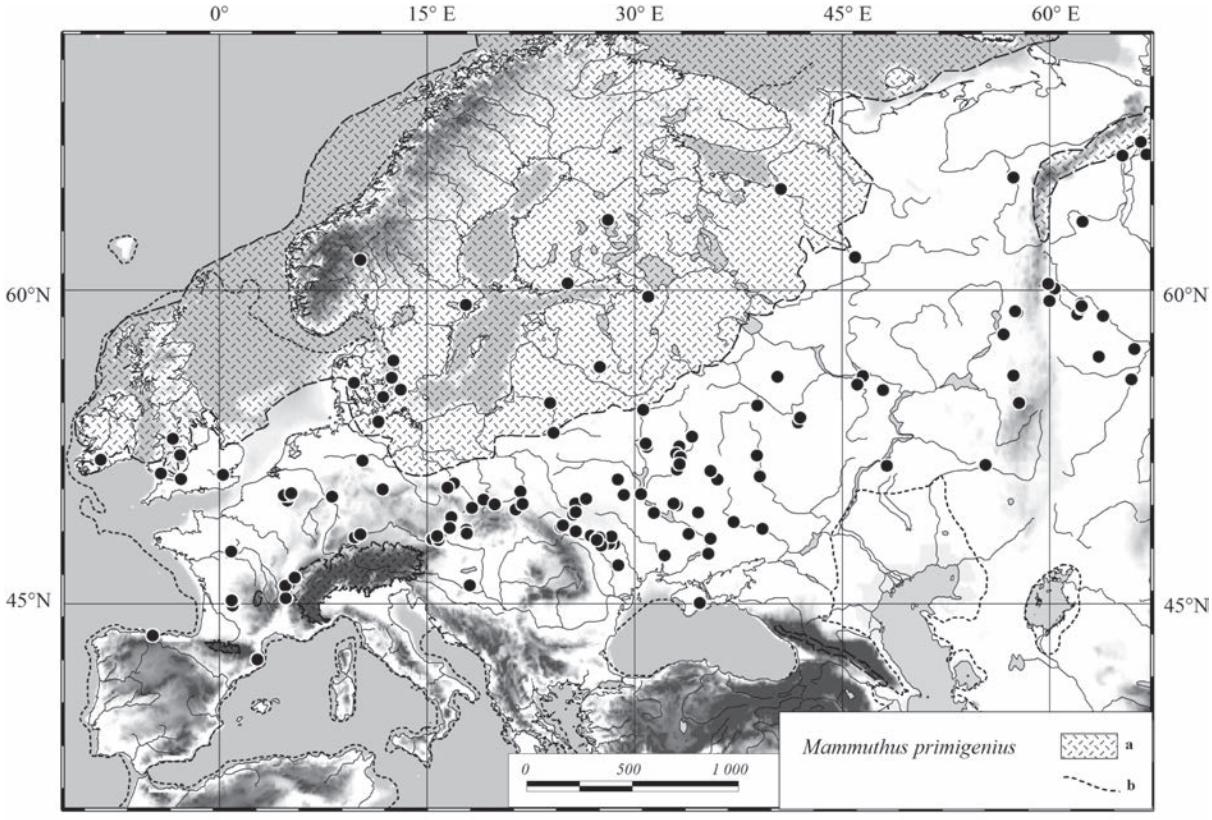

Fig. 4.5. *Mammoth Mammuthus primigenius in LGM localities; a – ice sheets; b – coastline*

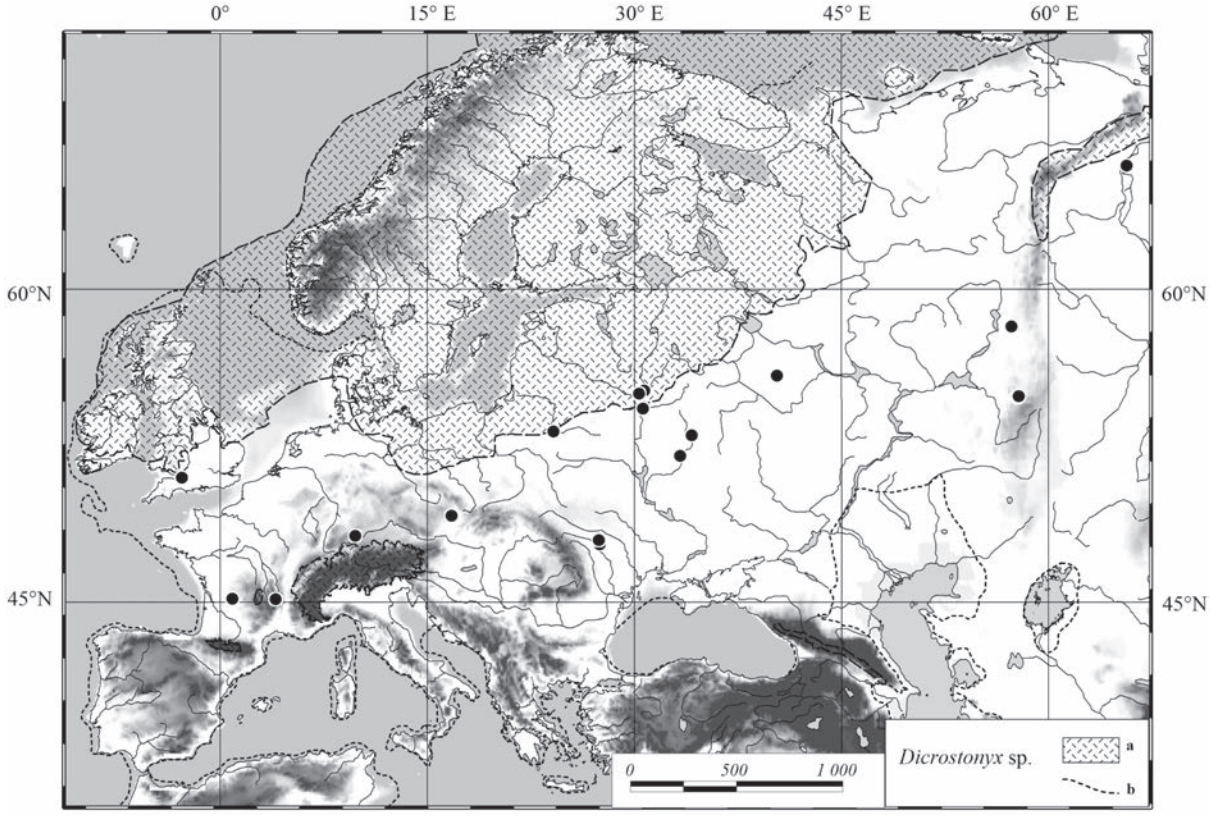

Fig. 4.6. *Collared lemming Dicrostonyx sp. in LGM localities; a – ice sheets; b – coastline*

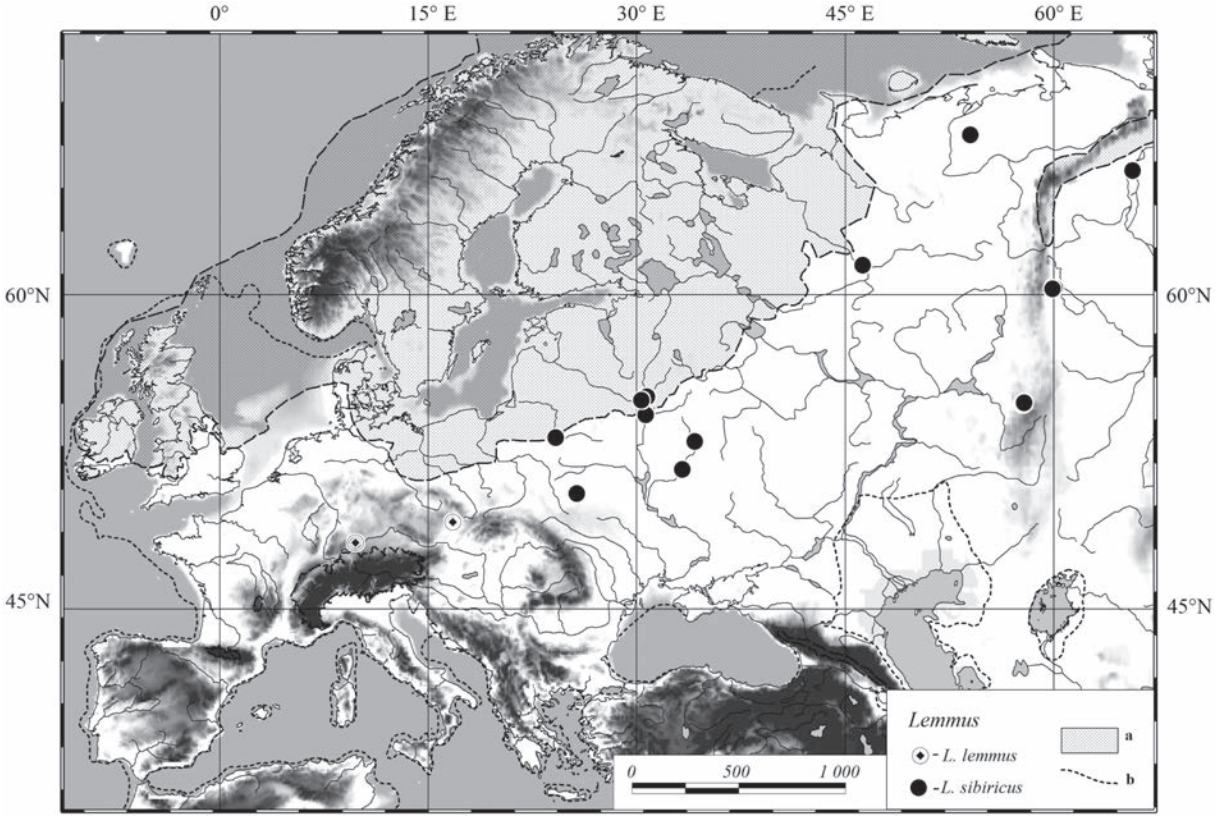

Fig. 4.7. *Siberian lemming Lemmus sibiricus and Norway lemming Lemmus lemmus in LGM localities; a – ice sheets; b – coastline*

and described during the studies from the 1960s to 1990s. These localities may have to be transferred to another assemblage once we have more detailed information about their species composition.

Western Europe is practically devoid of sites of the first assemblage; this shows the uniqueness of the Western European faunas. As a whole the localities of this cluster indicate periglacial tundra environments.

Periglacial tundra-forest-steppe mammal assemblage (cluster 2)

The sites of this assemblage cover almost the whole of Europe (Fig. 4.4). This fact would explain the more than 70 mammal species found in this assemblage (Table 1). We should mention that there was no site where all the species of this cluster were found together.

The dominant species of the second mammal assemblage (cluster) is the mammoth *Mammuthus primigenius.* Polar fox *Vulpes lagopus* and reindeer *Rangifer tarandus* are abundant in this assemblage and indicate tundra-like environments. A large number of localities with woolly rhinoceros *Coelodonta antiquitatis* remains were also found (Fig. 4.8).

Several species, adapted to open landscapes, first of all horse *Equus*, were present in this assemblage (Fig. 4.9). Such steppe animals as *Spermophilus*, *Lagurus lagurus*, *Marmota bobak*, *Ochotona pusilla* and others were also distributed in these areas. The remains of several forest-steppe and forest species (*Alces alces*, *Cervus elaphus*, *Capreolus capreolus*, and *Clethrionomys glareolus*) were found in a few of the localities. The species composition of the localities of the second cluster reflects periglacial tundra-forest-steppe environments. This assemblage occurred in central regions of Eastern and Central Europe. The distribution of these localities reflects non-analogue periglacial ecosystems with a mosaic structure of the biota.

Periglacial forest-steppe mammal assemblage (cluster 3)

The rare localities of this assemblage were distributed in the belt between 47–49°N. Two sites in the British Isles are located further north than other localities (Fig. 4.4). Most of the sites in continental Europe are situated in the foothills and mountains. The species composition amounts to 29 species (Table 1). Cold-adapted

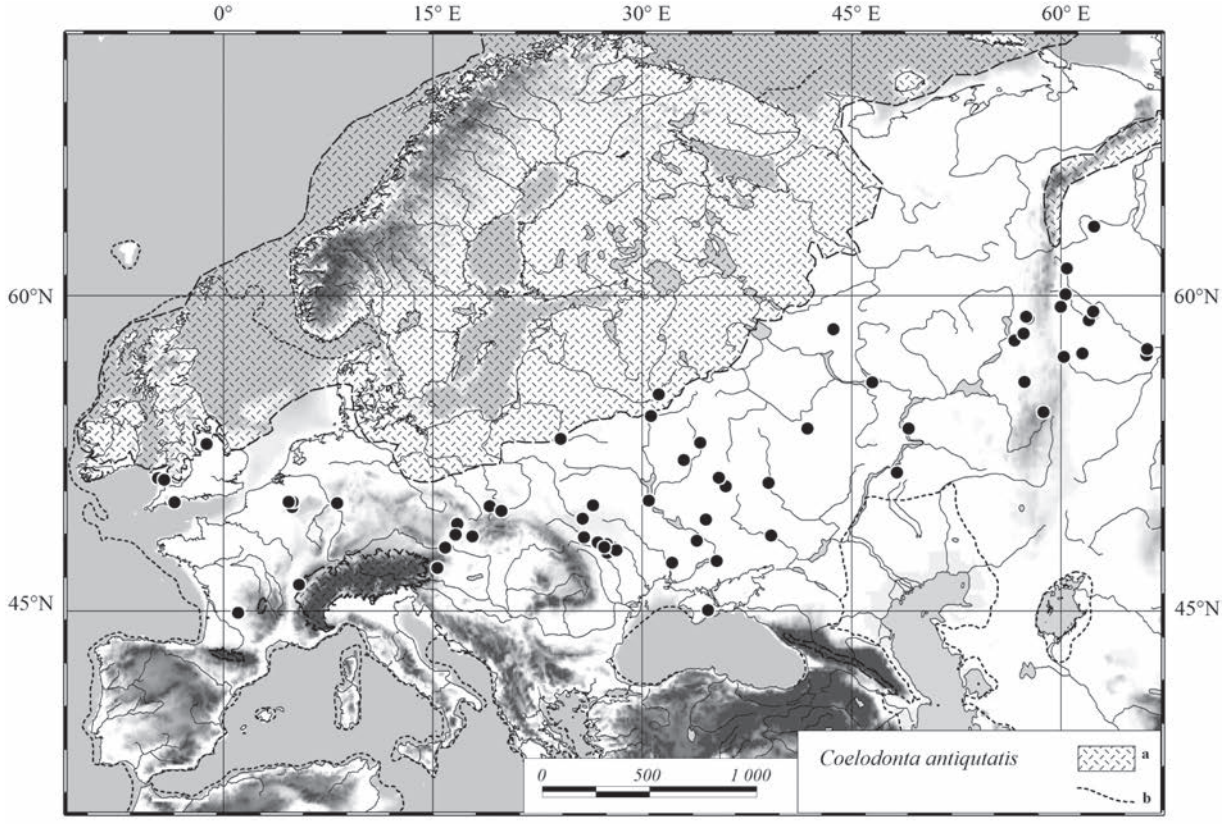

Fig. 4.8. *Woolly rhinoceros Coelodonta antiquitatis in LGM localities; a – ice sheets; b – coastline*

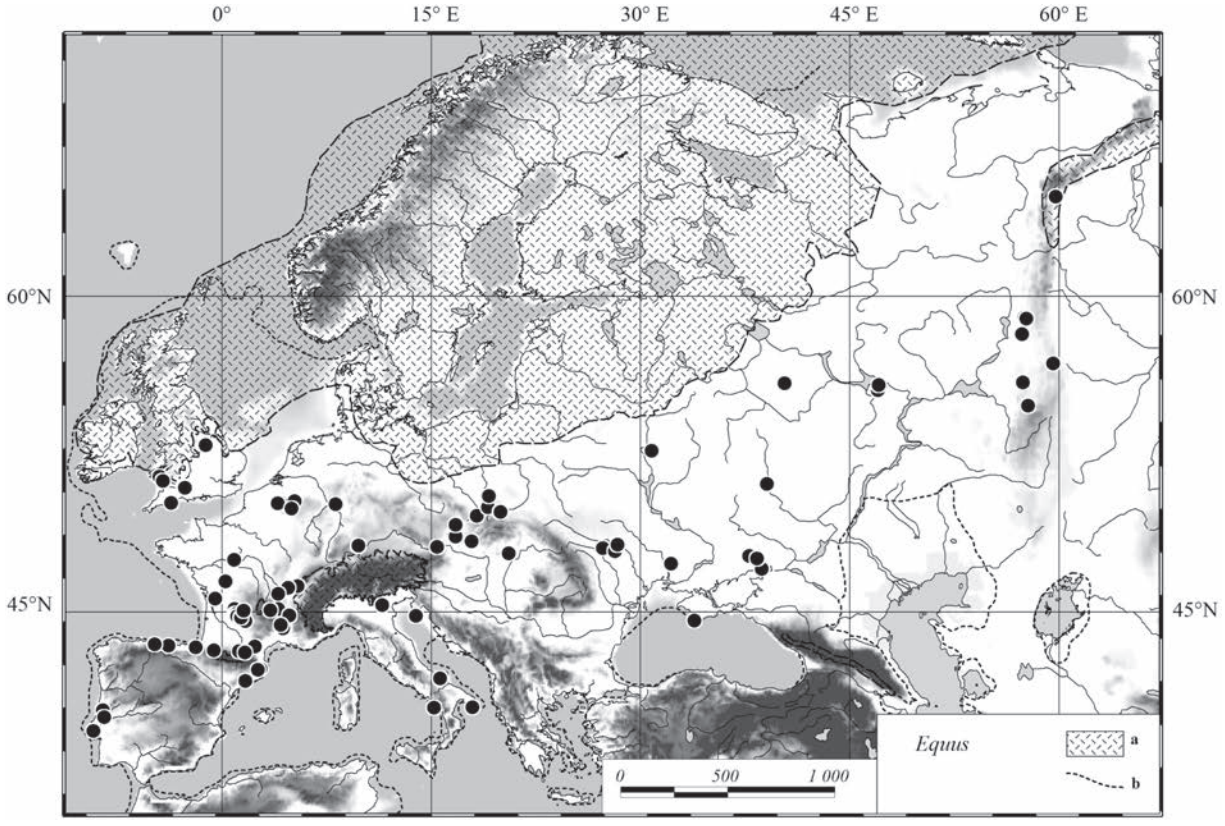

Fig. 4.9. *Horse Equus in LGM localities; a – ice sheets; b – coastline*

species are represented only by polar fox *Vulpes lagopus*. The core of the assemblage includes the large herbivores: mammoth, woolly rhinoceros, steppe bison and aurochs, and wild horse. Giant deer remains were also found here. Carnivores include a high number of animals that became extinct by the end of the Pleistocene (cave bear *Ursus spelaeus*, cave hyena *Crocuta crocuta spelaea*, and cave lion *Panthera spelaea*), and also includes mammals that exist in modern times (brown bear *Ursus arctos*, wolf *Canis lupus* and least weasel *Mustela nivalis*). The abundant quantity of large herbivores, the rather low number of forest animals (only remains of *Gulo gulo* and *Cervus elaphu*s were found), and rare mountain species (*Rupicapra rupicapra*) indicate periglacial forest-steppe conditions, which were more moderate than the ones under which the animals of the previous assemblage existed.

Southern variant of the periglacial forest-steppe (cluster 4)

The sites of this cluster are located mostly in Western Europe (around the Alps, the Massif Central, and the Carpathians). Only two localities of this cluster were found in Eastern Europe, near the mouth of the Don River and in the Crimea. The diversity of this assemblage is very high and the number of mammal species totals 80 species.

The cold-adapted species such as polar fox and reindeer are rather abundant in the localities, but lemmings are practically absent in the sites. The list of forest species is rich and includes elk *Alces alces*, wolverine *Gulo gulo*, wild boar *Sus scrofa*, lynx *Lynx lynx*, wild cat *Felis silvestris*, Eurasian badger *Meles meles*, dormouse *Eliomys* sp., hedgehog *Erinaceus*, beaver *Castor fiber*, and field vole *Microtus agrestis*.

Some of the large herbivores *Bos primigenius*, *Bison priscus*, *Cervus elaphus*, and *Capreolus capreolus* are common in this assemblage, but mammoth, woolly rhinoceros and giant deer finds are rather rare. The high number of *Capra* and *Rupicapra* remains and the presence of *Microtus nivalis* finds indicate foothill and mountain conditions. Steppe species (*Equus* sp., *Equus hydruntinus*, *Saiga tatarica*, *Vulpes corsac*, *Ochotona pusilla*, *Marmota*, *Lagurus lagurus*, and others) were found only in some of the localities.

All the materials together would indicate a high diversity of landscapes, which allowed the living together of animals from different habitats: cold-adapted, forest, steppe and mountain ones. The influence of the glaciation was pronounced weaker than in the previous as-

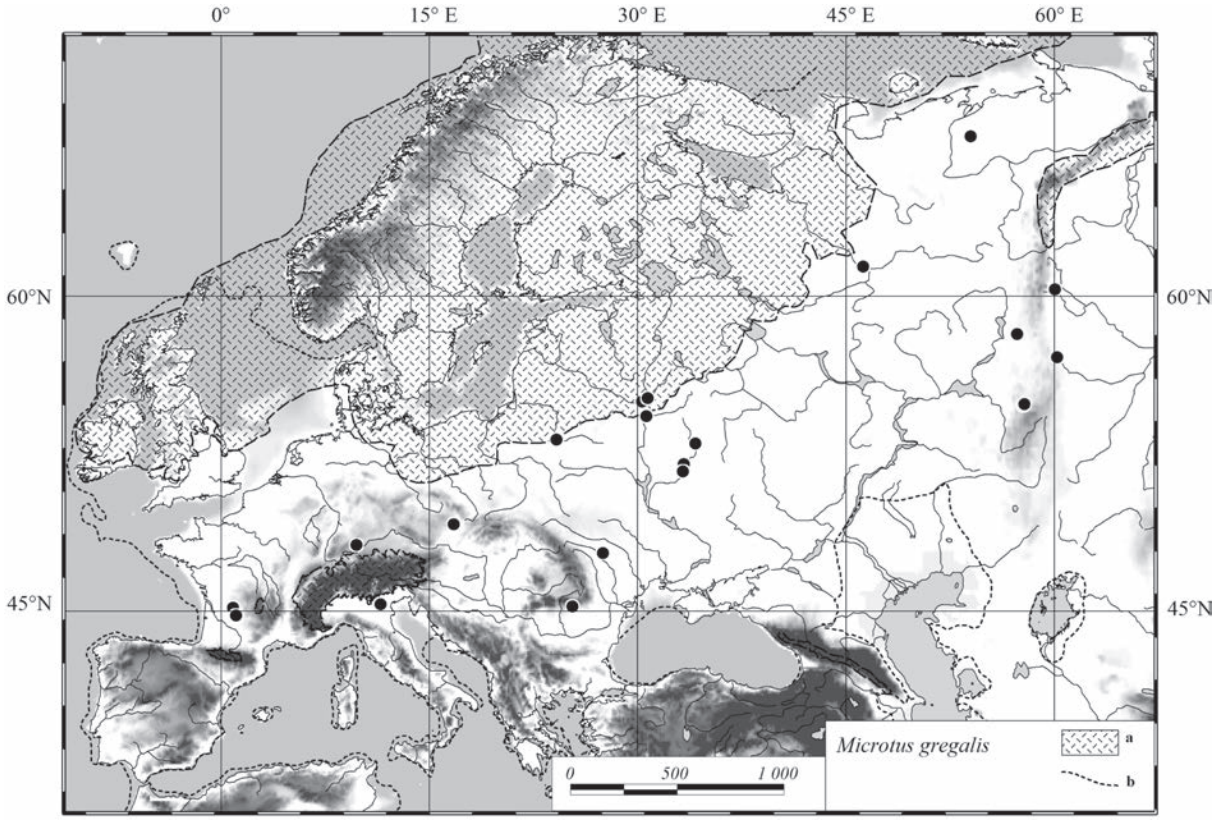

Fig. 4.10. *Microtus gregalis in LGM localities; a – ice sheets; b – coastline*

semblages. The rich grasslands with the forested 'islands' located in the river basins and in the mountains and foothills, supported the high diversity of mammals. From the above data we can reconstruct the south variant of the periglacial forest-steppe.

Periglacial tundra-forest-steppe assemblage (the Urals variant) (cluster 5)

Most of the localities of this assemblage are located in the Ural Mountains (Fig. 4.4). The species composition of the mammal faunas comprises 30 species, including animals of different ecological groups (Table 4.1):

- cold-adapted mammals with *Rangifer tarandus* (many), *Ovibos moschatus*, *Vulpes lagopus* (many), *Dictostonyx torquatis* (many), *Lemmus sibiricus*, *Microtus middendorfii*, *Microtus gregalis* (many);
- steppe mammals with *Saiga tatarica*, *Equus* sp., *Allactaga pygmaeus*, *A. major*, *Lagurus lagurus* (many), *Marmota bobak* (many), *Ochotona pusilla* (many);
- forest mammals with *Alces alces*, *Clethrionomys glareolus*, *Cl. rufocanus*, *Microtus agrestis*, *Mustela erminea* (many), and *Mustela eversmanni* (many);
- large herbivores including rare finds of *Mammuthus primigenius*, and many finds of *Coelodonta antiquitatis* and *Bison priscus*. Such herbivores as *Bos primigenius*, *Cervus elaphus* and *Capreolus capreolus*, which prefer forest-steppe environments, were not found here;
- animals adapted to riverbanks and lakesides (*Microtus oeconomus*, *Arvicola terrestris*) were present in this assemblage.

Thus, the diverse species composition of this assemblage, including the high number of small mammals of different ecology permits us to reconstruct the tundra-forest-steppe assemblage (the Urals variant). The high diversity of local environment of the Ural Mountains supports the requirements of the many different animals.

In their species composition, this assemblage is close to the second assemblage, which also includes tundra, steppe and forest mammals. But the species richness and the ratio of the mammals in the second assemblage was different from the Urals one. Also the dominant species in these two assemblages differ very strongly. If in the second assemblage mammoth was the dominant species (~80%), it was very uncommon in the Ural Mountains (only 12.5%); wild horse *Equus* sp. was typical of the second assemblage (40%), and rare in the Urals (12%); Siberian lemming *Lemmus sibiricus* was rather rare in the second assemblage (9%), and common in the Urals (~40%). These differences can be seen in many cases (Table 1). Thus, we need to distinguish two variants of the tundra-forest-steppe assemblage.

Mediterranean forest assemblage (cluster 6)

The animals of this assemblage were found in Western Europe (southern France, the Iberian, Apennine and Balkan Peninsulas). Thirty-six species were distinguished in this group. Dominant species include *Bison priscus*, *Bos primigenius*, *Rupicapra rupicapra*, *Capra ibex*, *Ovis* sp., *Cervus elaphus*, *Capreolus capreolus*, *Sus scrofa*, *Felis silvestris*, *Panthera pardus*, *Lynx* sp., *Oryctolagus cuniculus*, *Lepus europaeus*, *Erinaceus*, *Eliomys quercinus*, *Microtus (Terricola*) and others. Most of these species inhabited the forest and mountain areas.

Mammoth and woolly rhinoceros were not found in these regions. Cold-adapted animals such as polar fox, collared lemming, Norway lemming and musk ox were absent in these territories during the LGM. Only reindeer remains were found in some of the sites. But this mammal has rather broad ecological preferences and can exist in different types of landscapes, including forested areas.

Pleistocene ass *Equus hydruntinus* and wild horse *Equus* sp. also were typical of this assemblage and indicate the presence of areas with xerophytic grasslands. This assemblage reflects a fundamentally different natural condition from the first five assemblages described earlier in this chapter. Here in the Mediterranean, the influence of the ice sheet was almost absent. The mammal assemblage indicates in the southern regions of Europe the existence of forested areas, including broad-leaved forests, alternating with xerophytic grasslands, where wild horse, Pleistocene ass and steppe bison could exist. Thus, the influence of the ice sheet was insignificant south of 45°N. The reconstructed assemblage can be distinguished as a Mediterranean forest assemblage.

Caucasian mammal assemblage (cluster 7)

From Caucasian localities of the LGM were distinguished about 20 species. Of course it is only part of the Caucasian fauna, because most of the identified animals belong to the large mammals, while the small mammals are represented in the lists only by a few species.

Mammoth and woolly rhinoceros are absent in this assemblage. No cold-adapted animals were found in the Caucasus. The dominant species in this group include steppe bison *Bison priscus*, Caucasian goat *Capra caucasica*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, fallow deer *Dama dama*, wild boar *Sus scrofa*, cave bear *Ursus spelaeus*, and brown bear *Ursus arctos*. The species composition includes also the aurochs *Bos primigenius*, wild horse *Equus* sp., mountain sheep *Ovis* sp., cave hyena *Crocuta crocuta spelaea*, corsac fox

Vulpes corsac, squirrel *Sciurus vulgaris* and some others (Fig. 4.4; Table 1).

The mammal assemblage does not reflect any noticeable influence of the ice sheet, which could be explained by the southern position of the Caucasian Mountains. This assemblage is close to the Mediterranean mammal assemblage, but some endemic Caucasian species (*Capra caucasica*) were also identified in this region. The species composition of this assemblage includes first of all a large number of mountain and forest species and indicates the Caucasian mammal assemblage.

Geographical variation of the mammal species richness

The results of the analysis of the mammal materials permit us to reconstruct the geographical variation of the mammal biodiversity (species richness) during the LGM (Fig. 4.11). Undoubtedly, the numbers submitted in Figure 4.11 are conservative as the real fauna was probably more diverse. But we presume that a positive correlation exists between estimated and real species richness.

The maximal species richness in Europe during the LGM is observed: 1) to the north of the Massif Central, upper reaches of the Seine and Loire Rivers (France), 2) the northern foothills of the Alps – Bavarian tableland (Austria, Germany), 3) the Dniester River and Prut River basins with neighbouring territories (Moldova, Romania, Ukraine), 4) the Desna River (inflow of the Dnieper River) basin (Ukraine). In the most common cases the biodiversity centres were associated with the foothills or tablelands, and in one case with the lowland.

Conclusions

The results of the analysis of the mammal materials, correlated with the Late Glacial Maximum interval, permit us to reconstruct the mammal assemblages during that time for the territory of Europe. The area of Europe located between the Scandinavian ice sheet and ~48°N were covered by different variants of the **"Mammoth complex".** The first five clusters (mammal assemblages) describe the variants of the Mammoth complex: **periglacial tundra, periglacial tundra-forest steppe (2 variants), periglacial forest-steppe (2 variants).** All of these assemblages have a unique structure and have no analogues in modern times. All of them include animals of different ecologies, which now and also during the previous Interglacial (Eemian=Mikulino) inhabit different natural zones. Such an animal composition reflects

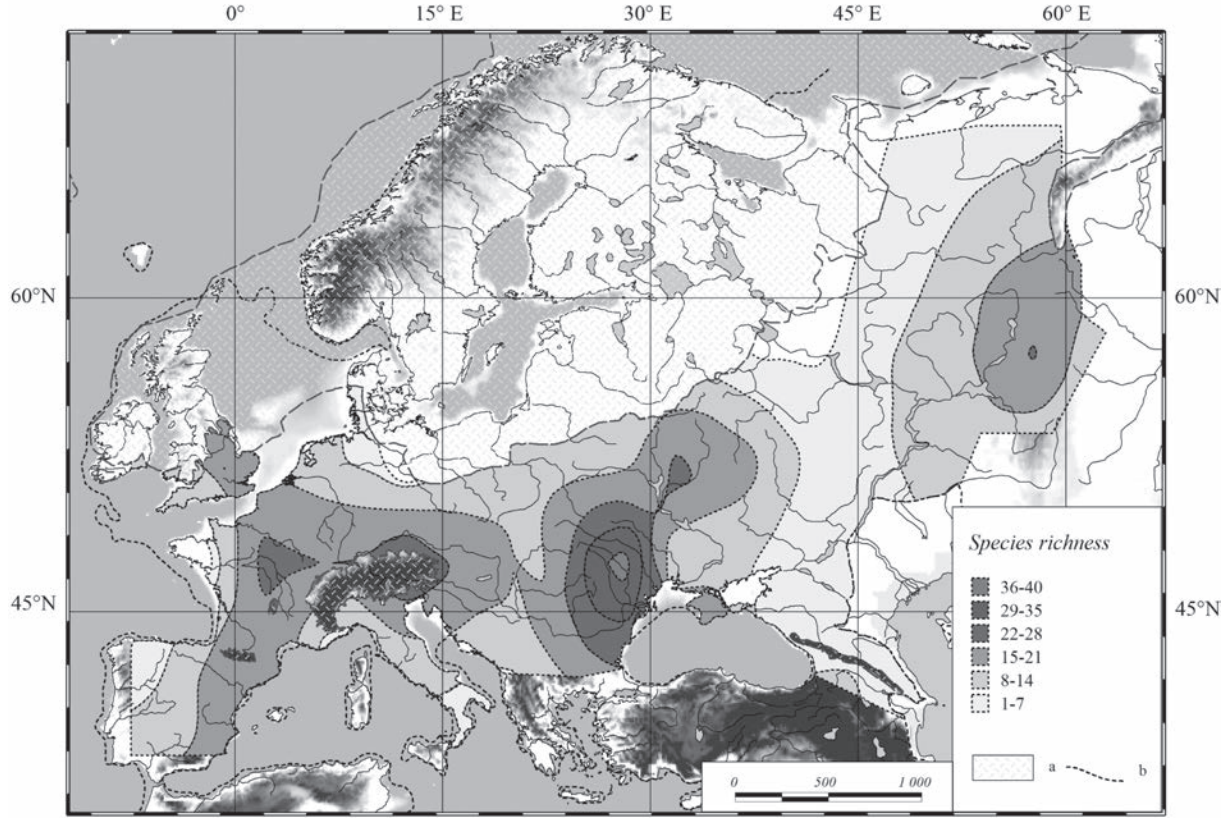

Fig. 4.11. *Reconstruction of the geographical variation of the LGM mammal species richness; a – ice sheets; b – coastline*

the mosaic structure of the European environment during the LGM. A continuous forest zone did not exist in this time. This explains the wide distribution of steppe animals to the north and west in Europe. The influence of the Late Valdai (=Weichselian) ice sheet was very strong, which permitted typical tundra species to penetrate up to 46–48°N. The forest species migrated to the south and survived also in refugia, related to river basins and mountain and uphill regions with a high number of local habitats. The analysis of the mammal distribution shows that the manifestation of the European natural zonality was weak during the LGM. The species composition of localities indicates non-analoguous 'mixed' faunas, and includes mammals from different natural zones. The specific structure of these faunas has earlier been discussed in many papers and they were described as "mammoth", "non-analog", "mixed" or "periglacial" assemblages (Pidoplichko, 1954; Vereshchagin, 1971; Vangengeim, 1977; Vereshchagin and Baryshnikov, 1980; 1985; Markova, 1982; 2004; Flerov, 1985; Graham, 1985; 1986; Musil, 1985; Semken, 1988; Smirnov *et al*., 1990; Lister, 1991; Stuart, 1991; Baryshnikov and Markova, 1992; 2002; Markova *et al*., 1995; 2002 a, b; Smirnov, 1995; Graham *et al*., 1996; Stewart *et al.*, 2003 a, b; Kosintsev, 2003).

South of 45°N, the structure of the mammal assemblages did not reflect the influence of the ice sheet. The forested areas, including the broad-leaved forests, alternating with xerophytic grasslands and Alpine meadows, were distributed on the plains and mountains of these regions (on the Iberian, Apennine, and Balkan Peninsulas, and in the Caucasus Mountains).

The differences between the Western and Eastern European faunas have been established. Eastern European faunas reflect more arid environments than West European faunas. So an Atlantic influence existed during the LGM, but the principal influence was the atmospheric high above the Scandinavian ice sheet.

4.2. MAMMAL ASSEMBLAGES DURING THE LATE GLACIAL TRANSITION (LGT) PERIOD (<17 – ⩾12.4 KYR BP)

Anastasia Markova and Andrey Puzachenko

The beginning of the deglaciation of the Scandinavian ice sheet began after 17 kyr BP. This process went on until the end of the Pleistocene. However, the climate was rather severe between 17 and 12.4 kyr BP and includes several oscillations. The materials of the Russian Plain show that a small advance of the ice sheet interrupted the process of deglaciation dating to about 15.5 kyr BP (Vepsovsk-Krestetsk stage). After the Vepsovsk-Krestetsk advance, a progressive regression of the ice sheet began and continued until ~13 kyr BP, when the next small advance (Luga – Neva stage) took place (Faustova, 1994; Fig. 4.12).

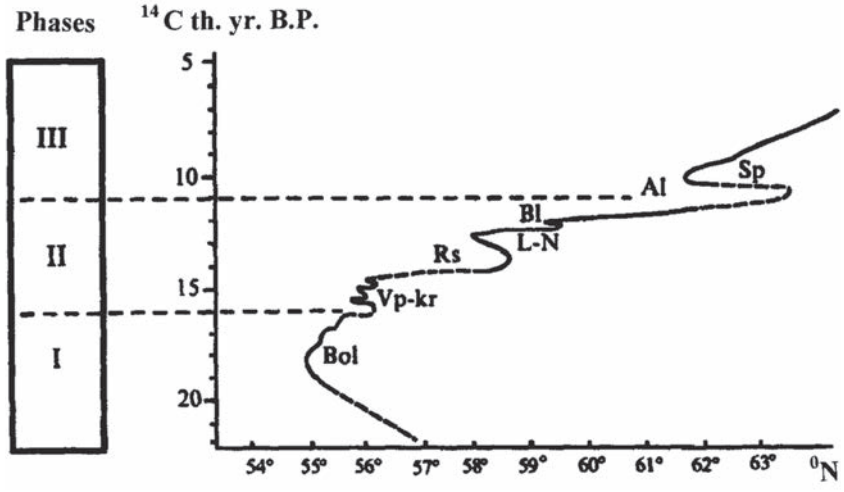

Fig. 4.12. *The main phases and deglaciation stages of the Late Pleistocene glaciation on the Eastern European Plain: Bol – Bologovo; Vp-kr – Vepsovsk-Krestetsk; Rs – Raunissk; L-N – Luga-Neva; Bl – Bølling; Al – Allerød; Sp – Salpausselka (after Faustova, 1994)*

The δO^{18} values and palynological and beetle data indicate the significant warming that took place about 12.4 kyr BP (Bølling Interstadial) (Coope and Lemdahl, 1995; Isarin and Bohncke, 1999; Petit, 1999; and others). Sher also indicates that the significant warming in Northeast Siberia was found only after 12.4 kyr BP (Sher, 1997). So, the climatic conditions between 17 and 12.4 kyr BP were not equal, but remained rather severe during the entire interval. This is the reason why we analyzed the LGT mammalian materials dated between 17 and 12.4 kyr BP together.

Materials and methods

The materials from 79 European mammal localities dated by ^{14}C to between 17 and 12.4 kyr BP were united in the form of an electronic database (Fig. 4.13). These localities include 76 mammal taxa, identified mostly at species level. The structure of the database was described in a previous chapter.

Compared to the LGM, mammal localities are rare in the LGT. But this interval lasted ~ 4.6 kyr, and the LGM ~ 7 kyr. Most of the localities are concentrated in the central and southern parts of Europe. Only a few points are located north of 60°N (in Scandinavia and in the Urals) (Fig. 4.12). The matrices of pair distances were calculated for the mammal sites, after which the data were subjected to cluster analysis (UPGA method), using multidimensional scale axes (Fig. 4.14).

This classification helps to clarify the picture of the mammal distribution and diversity in Europe during 17–12.4 kyr BP. The geographical position of the sites belonging to the different clusters is shown in Figure 4.15.

Mammal ranges and mammal assemblages during the LGT

The materials and the analysis permitted us to map, with the help of the Map/Info program, the principal mammal ranges for this period and also to reconstruct the main European mammal assemblages, using the results of cluster analysis. The not abundant material for this period only permitted us to reveal the main picture of the mammal distribution and diversity during 17–12.4 kyr BP.

Subarctic mammals

The configuration of LGT mammal ranges of typical subarctic (tundra) mammals was very indicative. Such

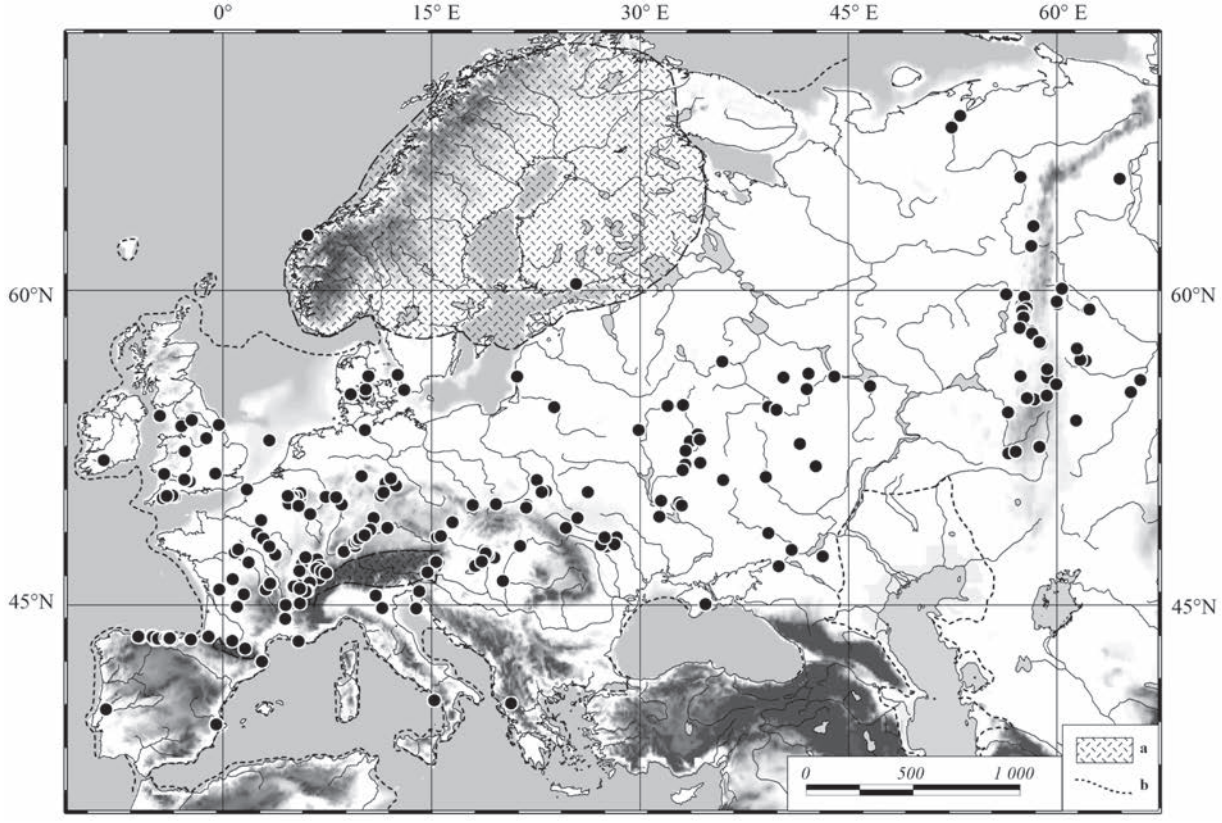

Fig. 4.13. *LGT localities, a – ice sheet and mountain glaciers; b – coastline*

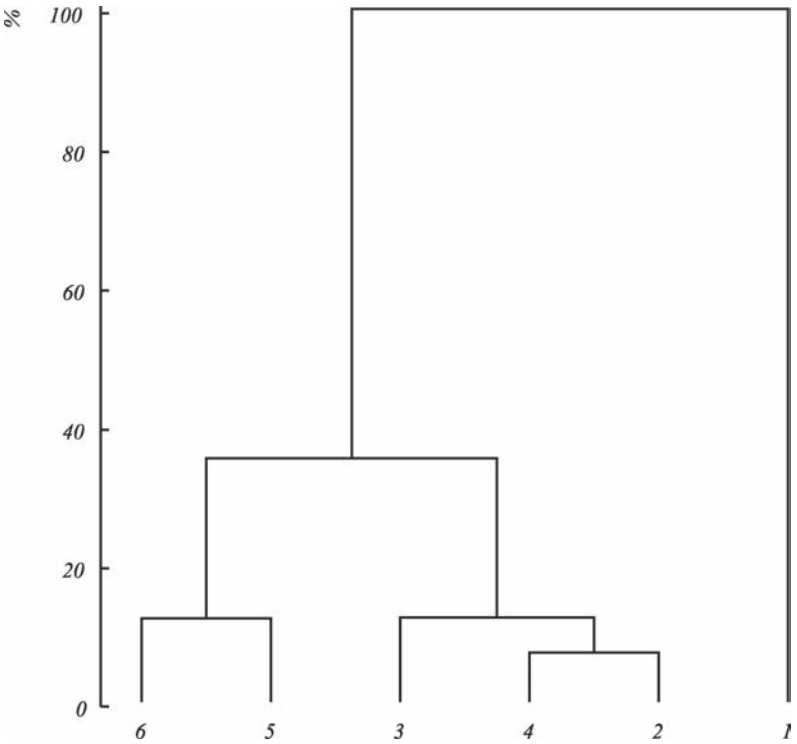

Fig. 4.14. *Six principal clusters, obtained from LGT mammal materials. The seventh cluster comprises only 3 localities and is not shown in the figure*

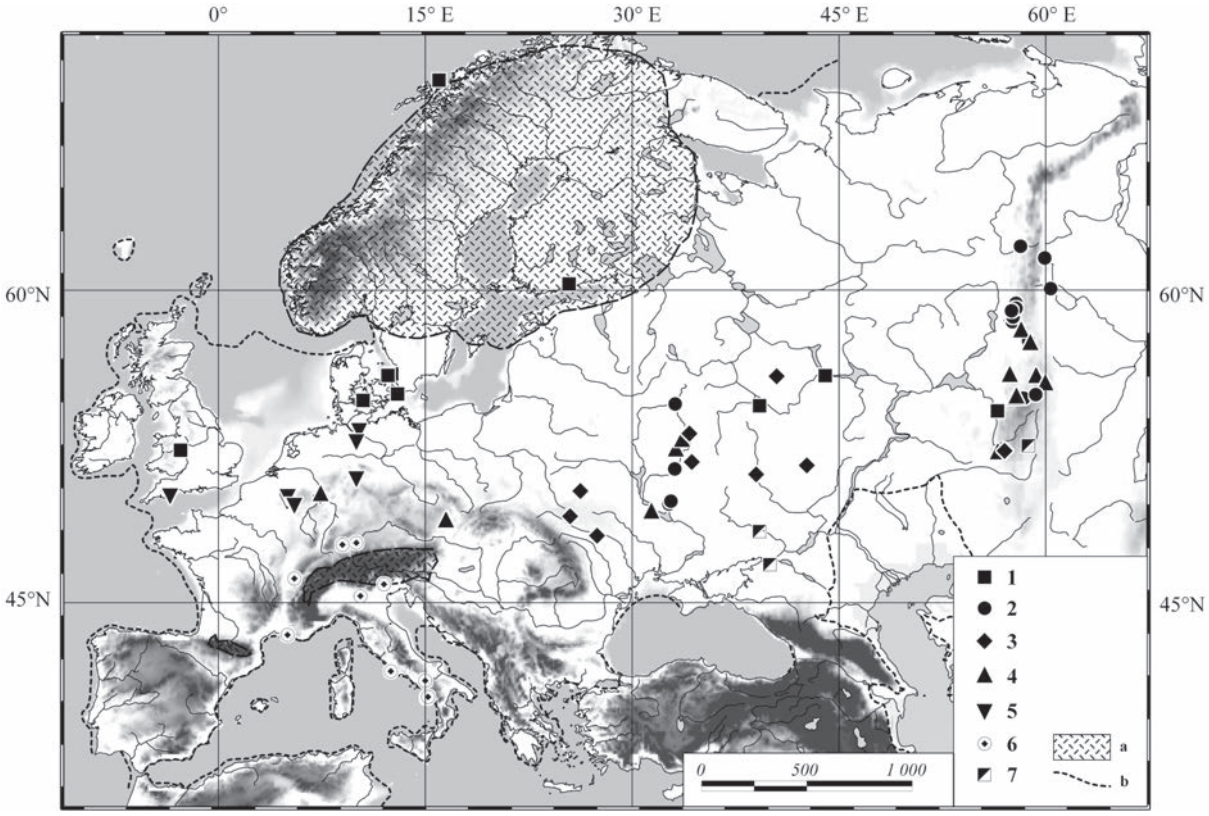

Fig. 4.15. *1–7 – mammal localities belonging to clusters 1 – 7; a – ice sheets; b – coastline*

typical tundra species as collared lemming *Dicrostonyx gulielmi-torquatus* and Siberian lemming *Lemmus sibiricus* significantly widened their ranges further south than their modern distribution. The southernmost localities of lemmings were found ~50°N (Figs. 4.16–4.17).

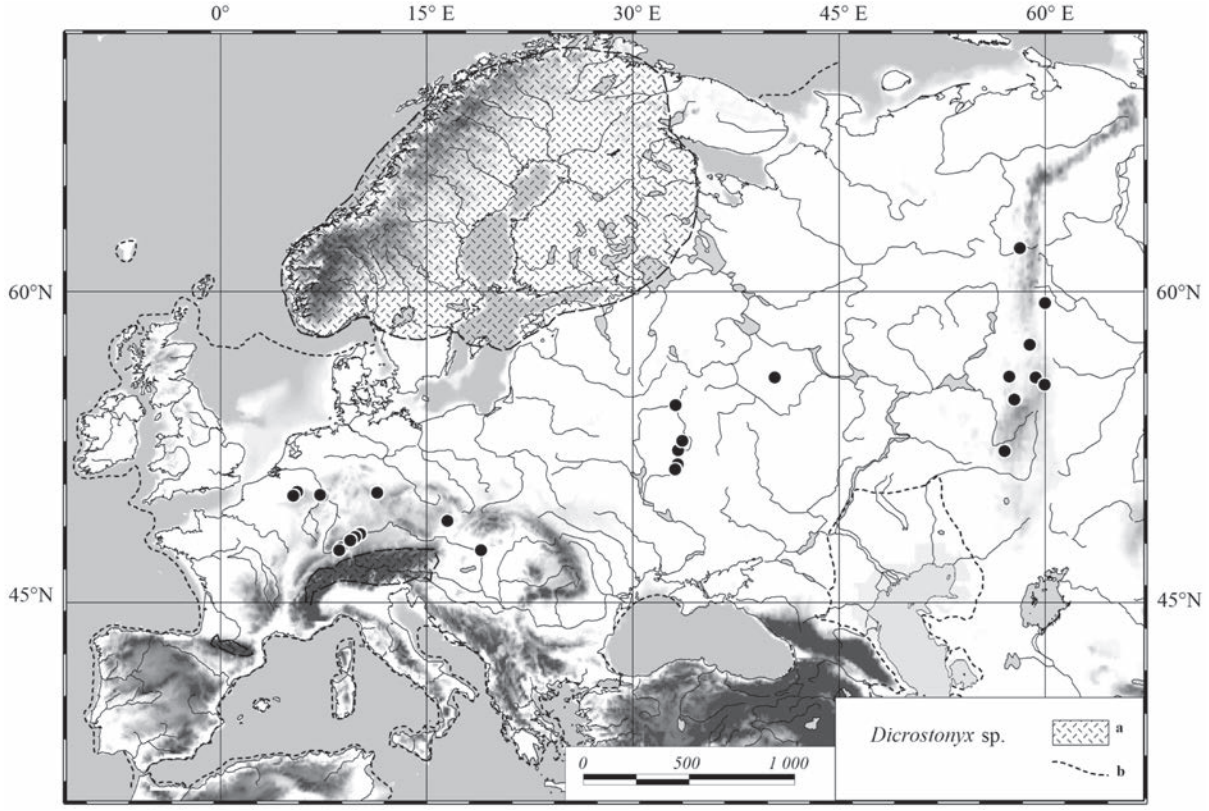

Fig. 4.16. *Collared lemming Dicrostonyx (D. guilielmi and D. torquatus) localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

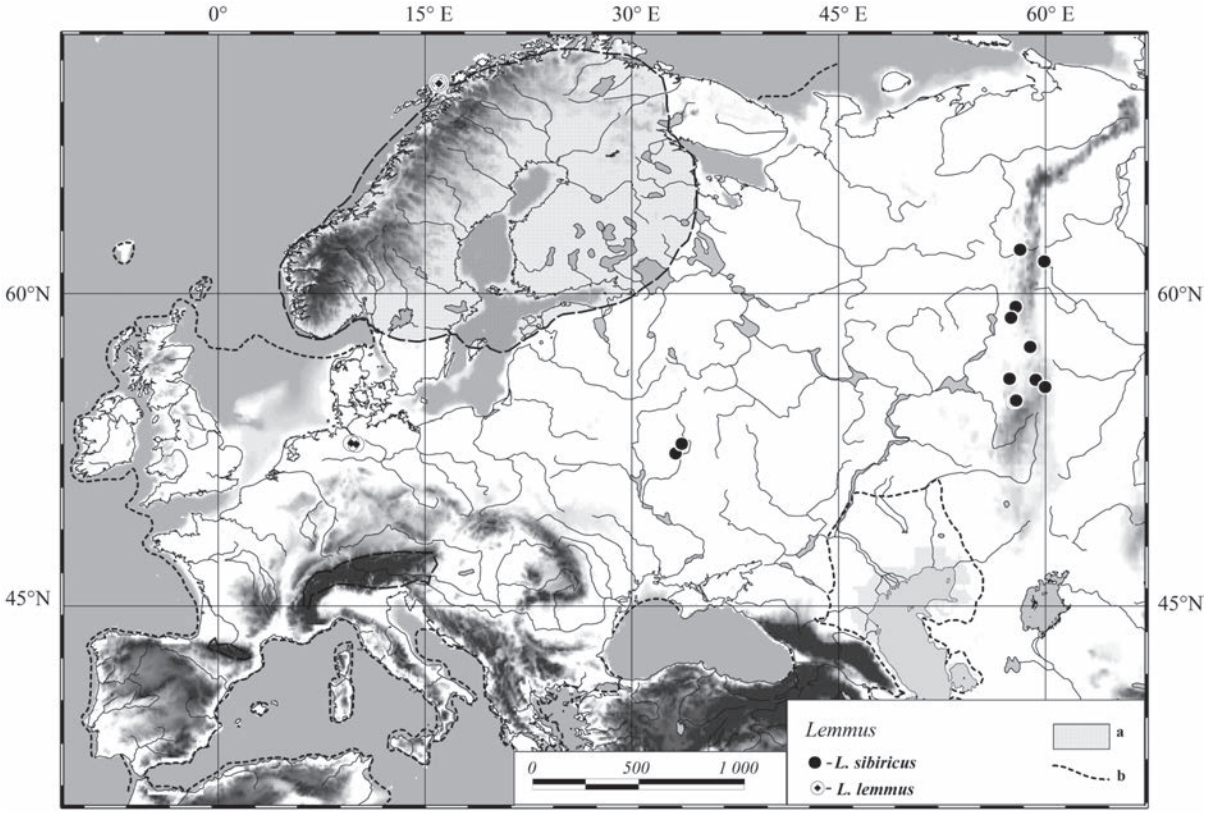

Fig. 4.17. *Lemming Lemmus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

Table 4.2

Indicator species for every cluster (% indicates the value of the species in the cluster)

Taxa	Clusters (mammal assemblages)							M-L Chi-sq, *p*
	1	2	3	4	5	6	7	
	N of localities							
	11	17	13	16	8	11	3	
Erinacaeus sp. – hedgehog	0.0	0.0	0.0	6.25	0.0	9.09	0.0	–
Desmana moschata – Russian desman	0.0	0.0	0.0	0.0	12.50	0.0	0.0	–
Talpa sp. – mole	0.0	0.0	0.0	6.25	0.0	18.18	0.0	–
Sorex minutus – lesser shrew	0.0	0.0	0.0	0.0	0.0	9.09	0.0	–
Sorex sp. – shrew	0.0	0.0	0.0	12.50	25.0	27.27	0.0	0.04
Crocidura sp. – musk white toothed shrew	0.0	0.0	0.0	6.25	0.0	0.0	0.0	–
Lepus timidus – Polar hare	0.0	58.82	23.08	25.0	25.0	18.18	0.0	–
Lepus europaeus – European hare	0.0	0.0	7.69	0.0	0.0	9.09	0.0	–
Ochotona pusilla – steppe pika	0.0	5.88	15.38	**81.25**	12.50	0.0	**33.33**	<0.001
Sciurus vulgaris – red squirrel	0.0	5.88	0.0	0.0	0.0	0.0	0.0	–
Spermophilus suslicus – spotted suslik	0.0	0.0	0.0	18.75	0.0	9.09	0.0	–
Spermophilus superciliosus- suslik “superciliosus”	0.0	5.88	0.0	6.25	0.0	0.0	0.0	–
Spermophilus major – great suslik	0.0	0.0	0.0	**25.0**	0.0	0.0	**33.33**	0.01
Spermophilus sp. – suslik	0.0	5.88	7.69	**56.25**	0.0	9.09	33.33	0.006
Marmota bobak – bobak marmot	0.0	**52.94**	7.69	**43.75**	0.0	0.0	**33.33**	<0.001
Marmota marmota – Alpine marmot	0.0	0.0	0.0	0.0	0.0	**27.27**	0.0	0.05
Castor fiber – beaver	0.0	0.0	0.0	12.50	0.0	9.09	0.0	–
Driomys nitedula – forest dormouse	0.0	5.88	0.0	0.0	0.0	0.0	0.0	–
Eliomys quercinus – garden dormouse	0.0	0.0	0.0	0.0	0.0	9.09	0.0	–
Glis glis – fat dormouse	0.0	0.0	0.0	0.0	0.0	18.18	0.0	–
Sicista betulina – northern birchmouse	0.0	0.0	0.0	6.25	0.0	0.0	33.33	–
Allactaga major – great jerboa	0.0	17.65	0.0	18.75	0.0	0.0	**33.33**	–
Allactaga pygmaeus – small jerboa	0.0	0.0	0.0	6.3	0.0	0.0	0.0	–
Spalax sp. – mole rat	0.0	11.76	0.0	6.25	0.0	0.0	0.0	–
Sylvaemus sylvaticus – common mouse	0.0	0.0	0.0	6.25	0.0	0.0	0.0	–
S. flavicollis – yellow-necked mouse	0.0	0.0	0.0	6.25	12.50	9.09	0.0	–
Sylvaemus sp. – mouse	0.0	0.0	0.0	18.8	0.0	9.09	0.0	–
Ellobius talpinus – northern mole-vole	0.0	0.0	0.0	**25.0**	0.0	0.0	**33.33**	0.02
Allocricetulus eversmani – Eversmann’ hamster	0.0	0.0	0.0	**31.25**	0.0	0.0	**33.33**	0.06
Cricetulus migratorius – grey hamster	0.0	0.0	0.0	**62.50**	0.0	0.0	**33.33**	<0.001
Cricetus cricetus – common hamster	0.0	5.88	0.0	25.0	0.0	0.0	**33.33**	0.04
Clethrionomys rufocanus – gray red-backed vole	0.0	0.0	0.0	**37.50**	12.50	0.0	0.0	0.03
Clethrionomys glareolus – red-backed vole	0.0	0.0	0.0	**50.0**	12.50	18.18	0.0	0.003
Clethrionomys rutilus – northern red-backed vole	0.0	5.88	0.0	**50.0**	0.0	0.0	0.0	0.002
Lagurus lagurus – steppe lemming	0.0	5.88	23.08	**62.50**	0.0	0.0	**33.33**	<0.001

Continued table 4.2

Taxa	Clusters (mammal assemblages)							M-L Chi-sq, *p*
	1	2	3	4	5	6	7	
	N of localities							
	11	17	13	16	8	11	3	
Eolagurus luteus – yellow steppe lemming	0.0	5.88	0.0	**31.25**	0.0	0.0	**33.33**	0.01
Dicrostonyx gulielmi-torquatus – collared lemming	0.0	23.53	23.08	**81.25**	25.0	9.09	0.0	<0.001
Lemmus lemmus – Norway lemming	9.09	0.0	0.0	0.0	12.50	0.0	0.0	–
Lemmus sibiricus – Siberian lemming	0.0	17.65	0.0	**68.75**	0.0	0.0	0.0	<0.001
Myopus sp. – wood lemming	0.0	5.88	0.0	6.25	0.0	0.0	0.0	–
Arvicola terrestris – water vole	0.0	17.65	0.0	**62.50**	25.0	27.27	0.0	0.002
Microtus gregalis – narrow-skulled vole	0.0	17.65	15.38	**93.75**	25.0	9.09	33.33	<0.001
Microtus oeconomus – root vole	0.0	0.0	0.0	**87.50**	25.0	18.18	33.33	<0.001
Microtus agrestis – field vole	0.0	5.88	0.0	**43.75**	0.0	9.09	0.0	0.03
Microtus arvalis –common vole	0.0	5.88	0.0	**43.75**	25.0	9.09	**33.33**	0.05
Microtus middendorfii – Middendorf's vole	0.0	11.76	0.0	6.25	0.0	0.0	0.0	–
Chionomys nivalis – snow vole	0.0	23.53	7.69	37.50	12.50	18.18	0.0	–
Canis lupus – wolf	0.0	**70.59**	30.77	**87.50**	0.0	9.09	0.0	<0.001
Vulpes lagopus – Polar fox	0.0	**70.59**	**46.15**	**81.25**	12.50	0.0	0.0	<0.001
Vulpes vulpes – common red fox	0.0	**47.06**	7.69	**37.50**	25.0	18.18	0.0	0.01
Vulpes corsac – corsac fox	0.0	5.88	0.0	12.50	0.0	0.0	0.0	–
Ursus arctos – brown bear	0.0	**47.06**	15.38	25.0	12.50	18.18	0.0	0.05
Ursus spelaeus – cave bear	0.0	9.9	7.69	0.0	0.0	0.0	0.0	–
Ursus maritimus – Polar bear	**27.27**	0.0	0.0	0.0	0.0	0.0	0.0	0.05
Martes zibellina – sable	0.0	5.88	0.0	0.0	0.0	0.0	0.0	–
Martes martes – common marten	0.0	0.0	0.0	**18.75**	0.0	0.0	0.0	–
Martes foina – beech marten	0.0	0.0	0.0	0.0	0.0	9.09	0.0	–
Martes sp. – marten	0.0	**11.76**	0.0	0.0	0.0	9.09	0.0	–
Gulo gulo – wolverine	0.0	**52.94**	15.38	6.25	12.50	0.0	0.0	0.01
Mustela erminaea –ermine stoat	9.09	11.76	0.0	31.25	0.0	9.09	0.0	–
Mustela nivalis – weasel	0.0	0.0	0.0	0.0	0.0	9.09	0.0	–
Mustela sibirica – Siberian weasel	0.0	0.0	0.0	12.50	0.0	0.0	0.0	–
Mustela putorius – polecat	0.0	0.0	0.0	6.25	0.0	9.09	0.0	–
Mustela eversmanni – Russian polecat	0.0	17.65	0.0	0.0	0.0	0.0	0.0	–
Meles meles – badger	0.0	5.88	7.69	0.0	12.50	18.18	0.0	–
Crocuta crocuta spelaea – cave hyena	0.0	0.0	0.0	6.25	0.0	0.0	0.0	–
Panthera spelaea – cave lion	0.0	**47.06**	0.0	12.50	0.0	0.0	0.0	0.004
Felis silvestris – wood cat	0.0	0.0	0.0	0.0	0.0	18.18	0.0	–
Lynx sp. – lynx	0.0	5.88	0.0	12.50	0.0	9.09	0.0	–
Mammuthus primigenius – woolly mammoth	**63.64**	**70.59**	**100.0**	**50.0**	0.0	0.0	0.0	<0.001
Equus(Equus) sp. – wild horse	0.0	**76.47**	**69.23**	**68.75**	**50.0**	27.27	33.33	0.001

Continued table 4.2

Taxa	Clusters (mammal assemblages)							M-L Chi-sq, *p*
	1	2	3	4	5	6	7	
	N of localities							
	11	17	13	16	8	11	3	
Equus hydruntinus – Pleistocene ass	0.0	0.0	0.0	0.0	0.0	**36.36**	0.0	0.08
Coelodonta antiquitatis – woolly rhinoceros	0.0	**82.35**	23.08	31.25	12.50	0.0	0.0	<0.001
Sus scrofa – wild boar	0.0	0.0	0.0	0.0	0.0	**72.73**	0.0	<0.001
Cervus elaphus – red deer	0.0	5.88	38.46	6.25	12.50	**72.73**	0.0	<0.001
Capreolus capreolus – roe deer	0.0	0.0	0.0	0.0	0.0	**63.64**	0.0	<0.001
Alces alces – elk	0.0	23.53	7.69	6.25	0.0	18.18	0.0	–
Rangifer tarandus – reindeer	0.0	**88.24**	**53.85**	**87.50**	25.0	0.0	33.33	<0.001
Bos primigenius – aurochs	0.0	0.0	**0.0**	6.25	0.0	**54.55**	0.0	0.008
Bison priscus – steppe bison	0.0	**82.35**	23.08	**50.0**	0.0	18.18	**66.67**	<0.001
Saiga tatarica – saiga	9.09	**41.18**	0.0	**31.25**	0.0	9.09	0.0	0.08
Ovibos moschatus – muskox	0.0	**41.18**	0.0	6.25	12.50	0.0	0.0	0.03
Rupicapra rupicapra – chamois	0.0	0.0	0.0	0.0	0.0	**54.55**	0.0	0.001
Capra ibex – mountain goat	0.0	0.0	0.0	0.0	12.50	**63.64**	0.0	<0.001
Ovis sp. – mountain sheep	0.0	0.0	0.0	0.0	0.0	0.0	33.33	–

So, the southern limits of the lemming ranges shifted more than 2000 km southward. A similar picture was reconstructed for the Last Glacial Maximum.

Very typical of modern tundra and forest tundra zones, such mammals as polar fox, reindeer, and musk ox also show a similar reaction to the severe condition of this period (Figs. 4.18– 4.20). This group of cold-tolerant species was widely distributed in Europe. This indicates a persistence of very cold climatic conditions not only during the Late Glacial Maximum, but also during the LGT, and also the absence of continuous forest vegetation (which could be a natural barrier for mammal dispersal events) during the LGT period. These features were elucidated earlier for the mammal faunas of the Former Soviet Union relating to the various intervals of the Valdai Glaciation, including the Late Glacial (Markova *et al*., 1995).

Steppe mammals

The remains of open landscape (steppe, forest-steppe and semi-desert) mammals were widely distributed in Europe during the LGT, similar to their LGM distribution. The limits of their ranges expanded to the north and west of their modern positions. Thus, the remains of typical steppe and semi-desert species saiga *Saiga tatarica* were found in an LGT locality in France (more than 3000 km west from the western limit of their distribution in historical times), and *Saiga* remains dated 14,800 yrs BP were found near Ringe on Fyn Island (55°N; 10.5°E) (Aaris-Sørensen, 2001) (Fig. 4.21). Possibly this species survived there during the LGT in isolated ranges, which represent part of the large Last Glacial Maximum saiga area. On the other hand, maybe we have not sufficient information and there are not enough localities for a reconstruction of the whole saiga range in this interval. Now saiga inhabits Kazakhstan, northern Middle Asia, and the northern Caspian Sea coastal territories (Flint *et al*., 1970).

It is also remarkable that saiga penetrated further north along the Ural Mountains and reached 63–64°N (Fig. 4.21). The position of the Urals localities indicates a restriction of forest vegetation and a distribution of open landscapes in the Urals during the LGT. The steppe pika *Ochotona pusilla* range also widened surprisingly. Its remains were found in France and Denmark (Aaris-Sørensen, 2001), LGT localities which are further west than its modern range (Fig. 4.22). The steppe pika modern range is restricted to the left bank of the Lower Volga drainage basin, the southern Urals, and North and Central Kazakhstan. This species is a typical steppe animal (Flint *et al.*, 1970). During the Pleistocene its area was rather wide and includes the Russian Plain (Gromov and Erbaeva, 1995; Markova *et al*., 1995).

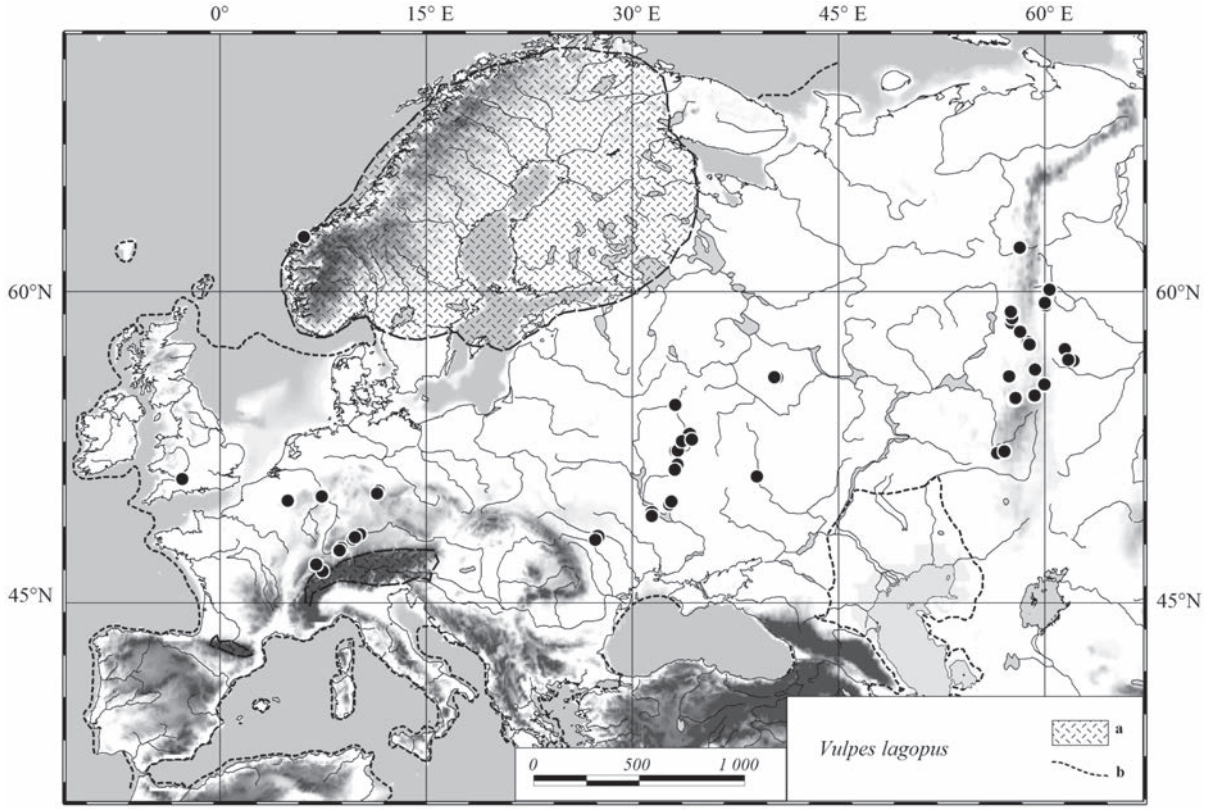

Fig. 4.18. *Polar fox Vulpes lagopus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

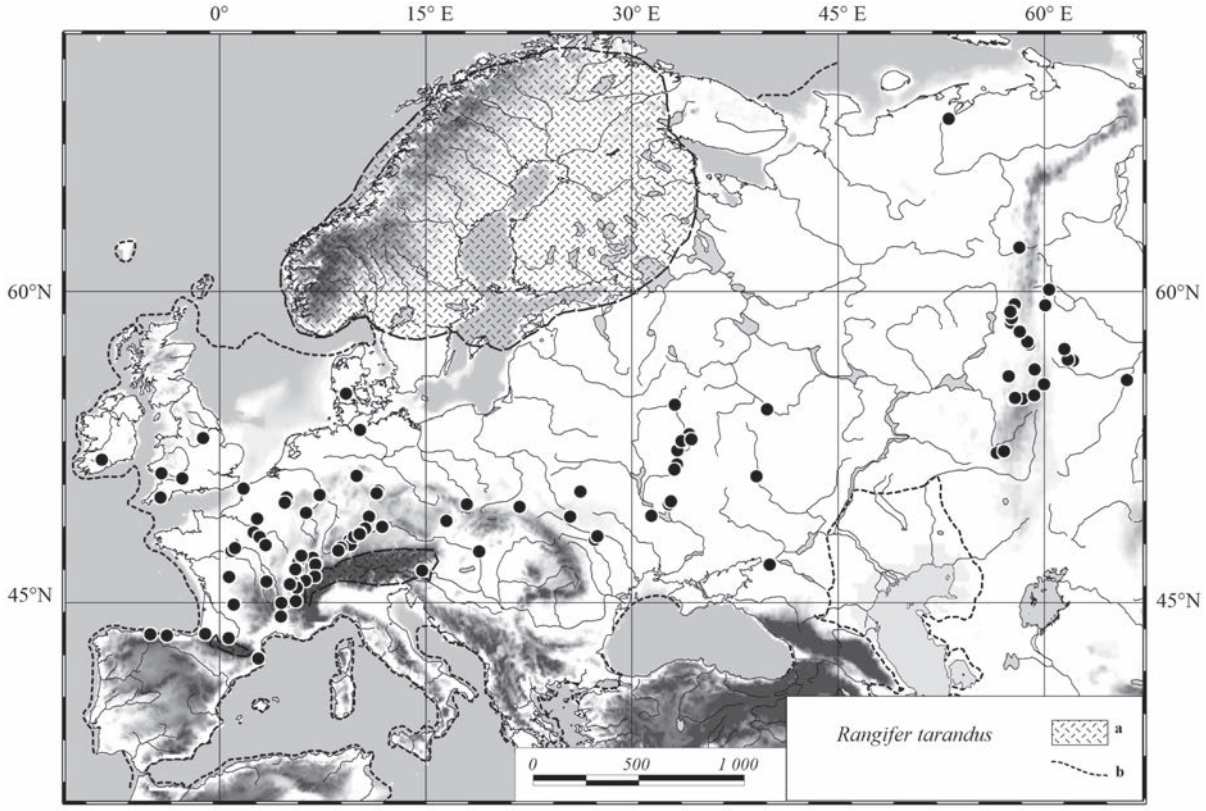

Fig. 4.19. *Reindeer Rangifer tarandus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

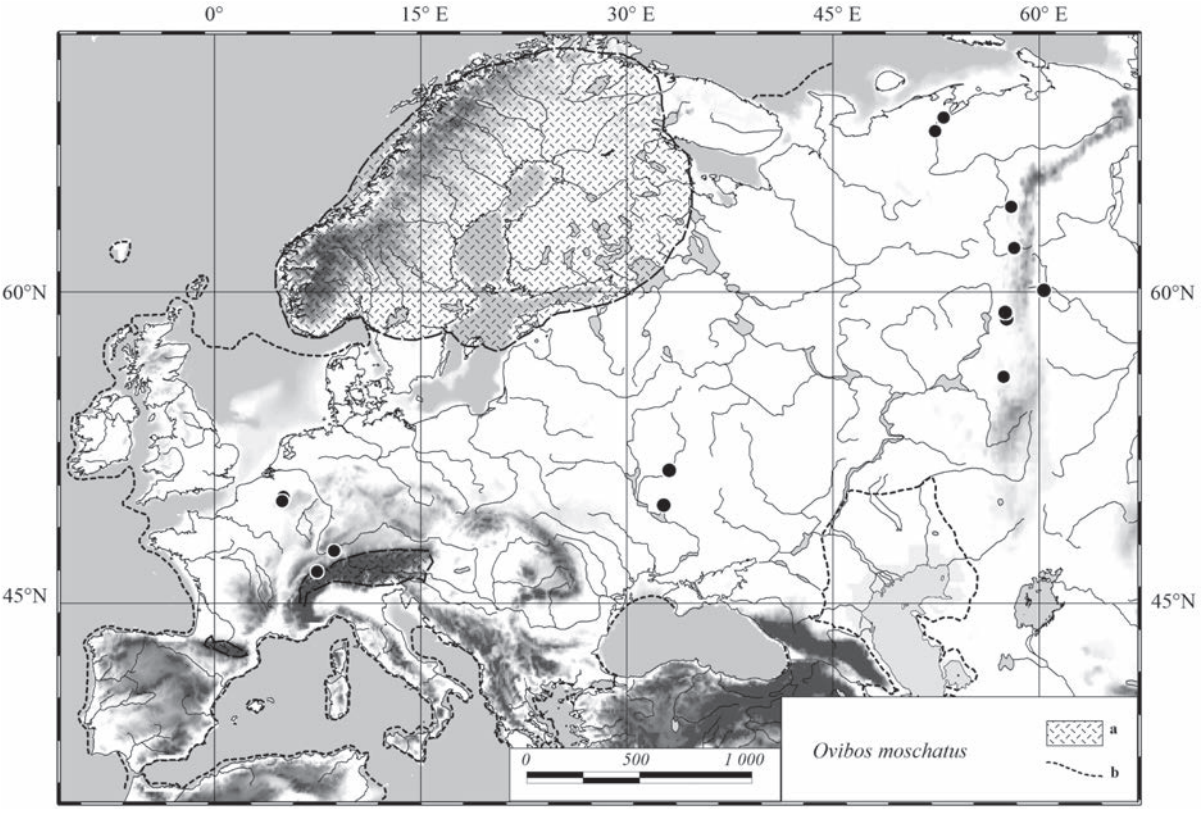

Fig. 4.20. *Muskox Ovibos moschatus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

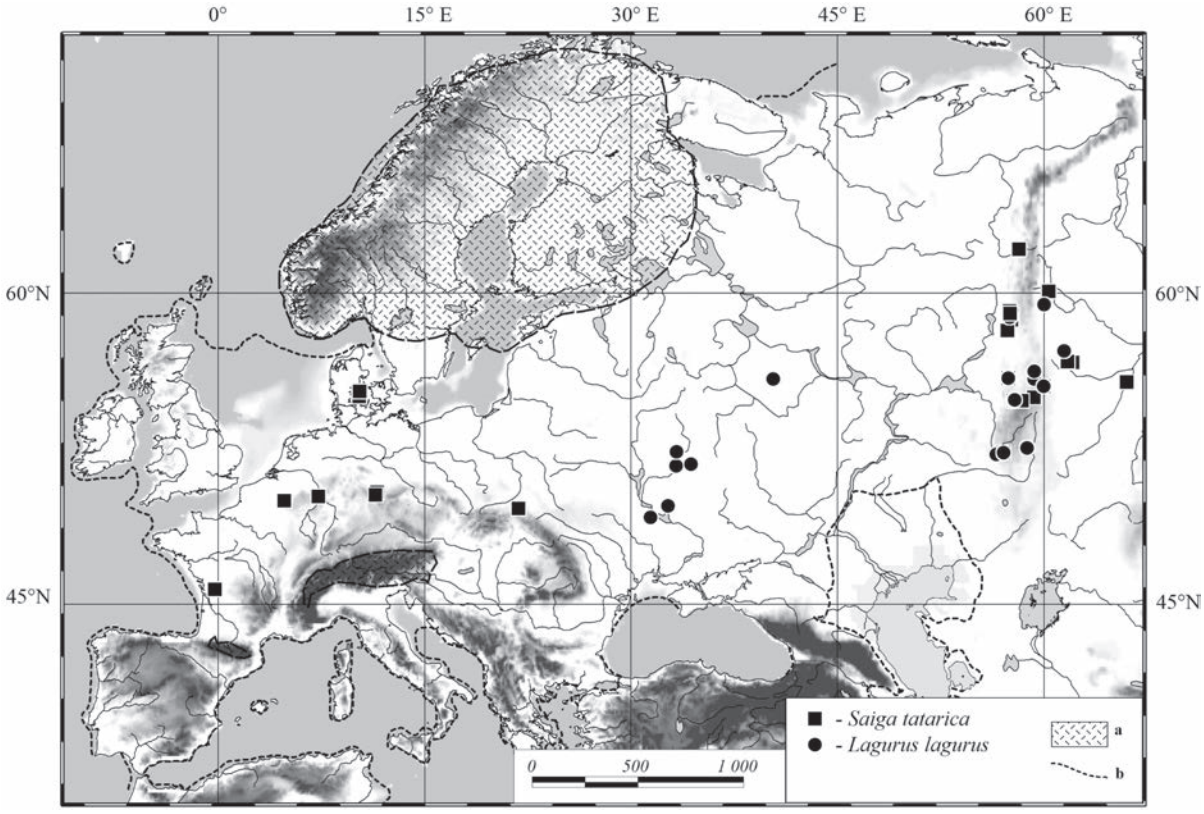

Fig. 4.21. *Saiga tatarica and steppe lemming Lagurus lagurus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

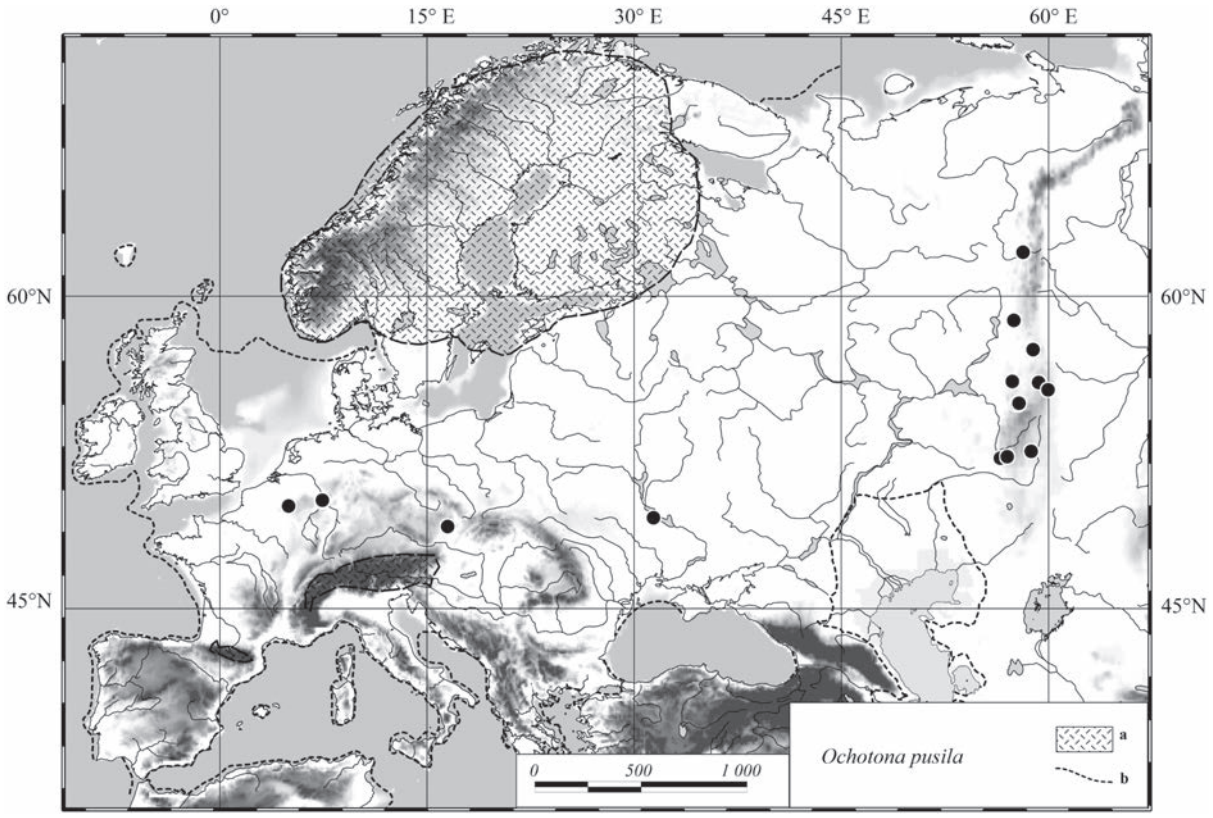

Fig. 4.22. *Steppe pika Ochotona pusilla localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

Other open-landscape animals, including steppe (*Lagurus lagurus*) (Fig. 4.21) and yellow (*Eolagurus luteus*) lemmings, great jerboa *Allactaga major* and others had a similar reaction to the cold climatic conditions. Their areas widened to the north and partly to the west. These animals inhabited the open periglacial forest-steppes and steppes that were distributed over the Russian Plain during the Valdai Glaciation and included in that time the territories of the modern forest zone (Markova *et al*., 2002 a, b).

Forest species

The localities of forest mammals are rather rare during the LGT. Some of these are situated in the mountain and highland areas, which are characterized by numerous local habitats (in the Urals, in the Carpathians, near the Alps and others) (Fig. 4.23). Thus, elk *Alces alces* finds were recovered only in these regions. This species is connected very strongly with forest vegetation, which survived mostly in local biotopes (refugia) in the mountains and along the rivers during glaciation.

The European wood mouse *Sylvaemus sylvaticus* and yellow-necked mouse *S. flavicollis* practically disappeared during the LGT and survived according to our data only in the Southern Urals and in the Sudeten Mountains (Fig. 4.24). Only 4 localities include these animals.

Some of the forest and forest-steppe mammals were more tolerant of periglacial conditions and found their habitats in the forested 'islands' persisting in the 'mosaic' periglacial landscapes. Typical forest-steppe animal red deer *Cervus elaphus* finds were recovered at ~55–48°N in Western, Central and Eastern Europe (Fig. 4.23). Red deer localities also concentrated in the Apennines.

The roe deer *Capreolus* range was more restricted than the *Cervus elaphus* range and is located on the Apennine Peninsula and near the Alps (Fig. 4.23).

Typical forest animal wild boar *Sus scrofa* remains were identified only in the Mediterranean area. The red-backed voles *Clethrionomys glareolus* were tolerant of the cold conditions and could also exist in the forested and shrub 'islands' in 'mammoth' forest-steppes. Their remains were found at the same latitudes where they live nowadays. But the density of their finds is very low, which indicates very scarce forested areas (Fig. 4.24). Only in the Urals and some parts of Western Europe were their localities common.

The field vole *Microtus agrestis* now also prefers to inhabit the forested and shrub areas, mostly in the taiga zone. Only a few localities with remains of this animal were found in the LGT (Fig. 4.25). The low number of

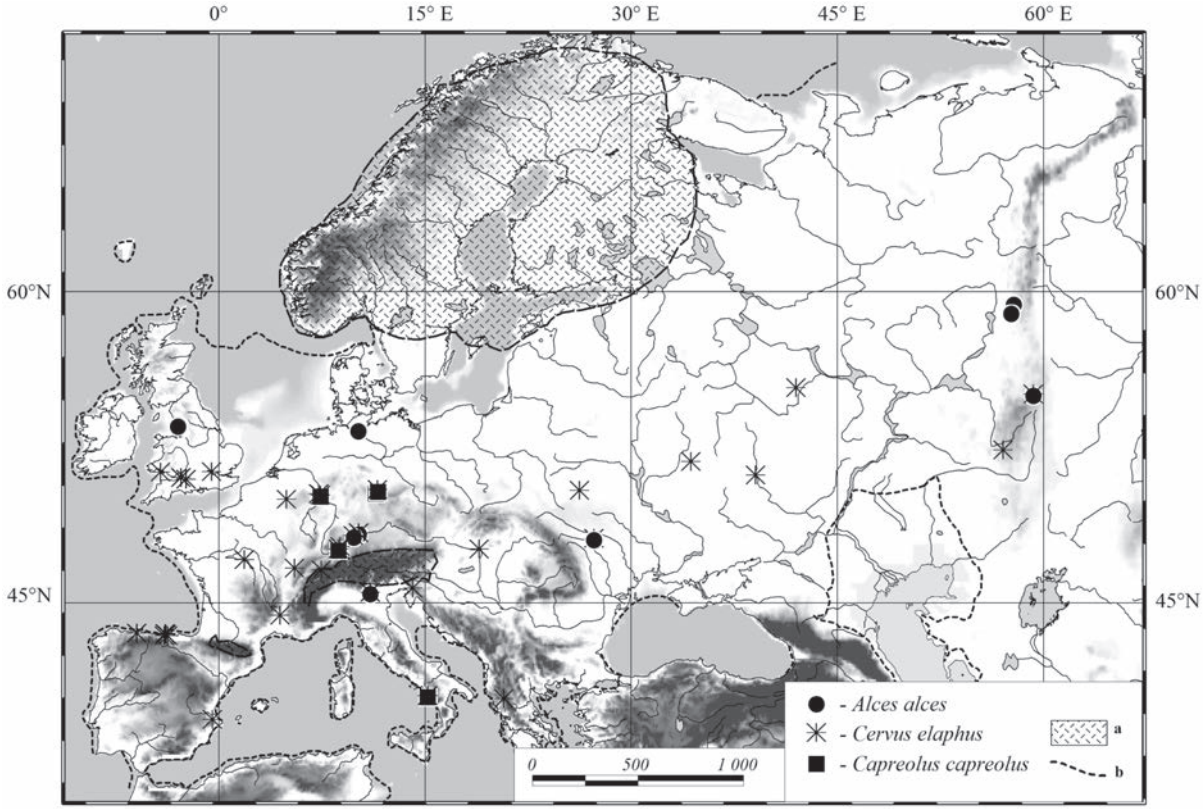

Fig. 4.23. *Elk Alces alces, red deer Cervus elaphus, and roe deer Capreolus capreolus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

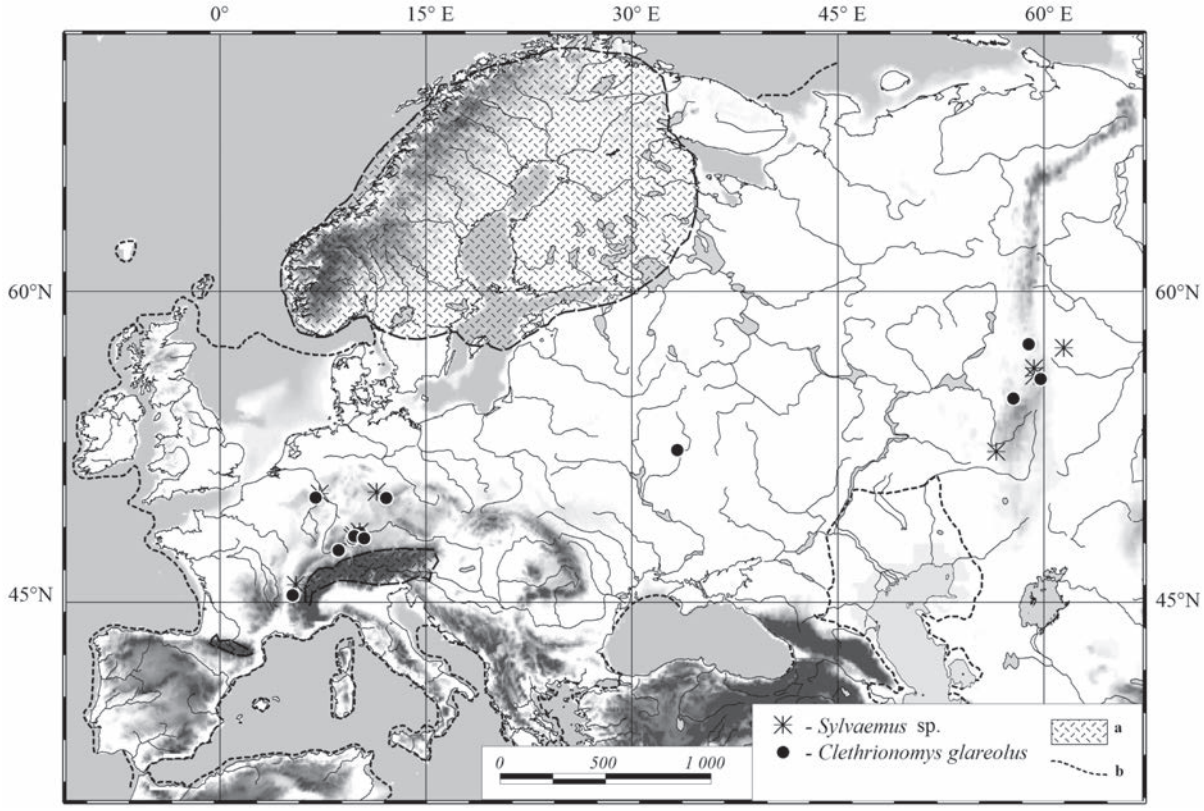

Fig. 4.24. *Mouse Sylvaemus sp. and forest vole Clethrionomys glareolus localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

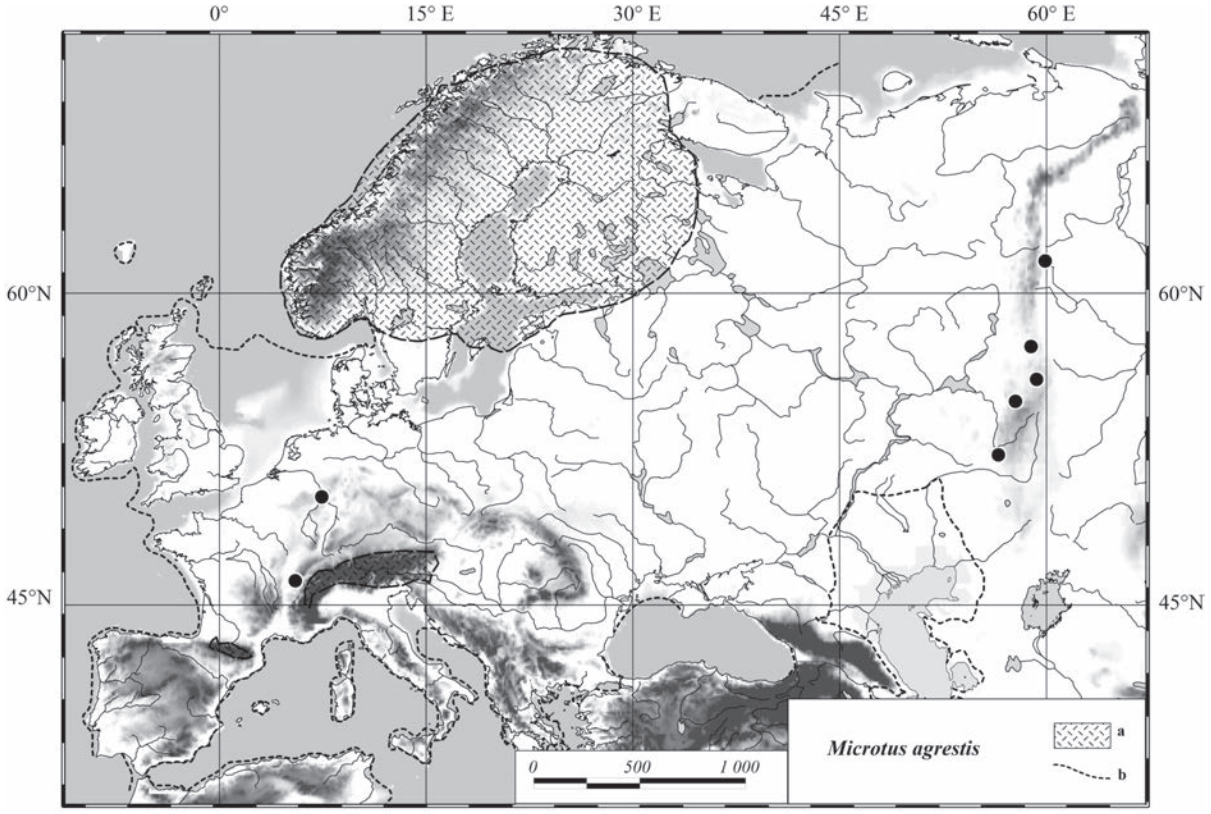

Fig. 4.25. *Field vole Microtus agrestis localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

field voles in LGT sites indicates a cold climatic condition and a prolongation of forest degradation.

Mountain species

A number of typical mountain species such as *Capra ibex* and *Rupicapra rupicapra* has been found in some of LGT localities. They were distributed in the southern-western mountain regions of Europe (Figs. 4.26–4.27). Their preferred habitats are located in the upper part of the mountain forest belt and in Alpine fields in mountains (the Alps, the Apennines, etc.). In the LGT *Capra ibex* also penetrated into the north and was found in the uplands in the De Sèvre Province.

Mammals of the 'mammoth' assemblage, extinct during the end of the Pleistocene and in the Holocene.

A lot of mammal remains, belonging to mammals extinct by the end of the Pleistocene and in the Holocene, were found in LGT localities.

Mammoth *Mammuthus primigenius* was as common during the LGT as during the LGM. The southernmost localities were recovered in the middle and low drainage basins of the Dniester, Dnieper and Don Rivers, and in the Ural Mountains. We have not enough information about mammoth distributions in the very north of Europe, but the existence of this animal in Fennoscandia (Hertoniemi locality), dated by ^{14}C to 15,500±200 (Hel-1074), allows us to assume ice-sheet free areas there (Ukkonen *et al*., 1999). Unique finds of mammoth bones were also recovered in the Pechora River drainage basin, and in the northern part of the Urals.

Unfortunately, there are only a limited number of mammal localities in Western Europe corresponding to this interval, so it is difficult to reconstruct the real mammoth range in this part of Europe. The existence of a mammoth locality in the British Isles indicates the western limit of its distribution.

The large mammoth range during the second part of the last glaciation, including the LGT, indicates the distribution of periglacial open landscapes with some modification of it in different parts of Europe (periglacial tundra, tundra-steppes and tundra-forest-steppes). These ecosystems existed during the LGM, as well as during the LGT. But the density of the mammoth sites during the LGT became lower than during the LGM. For example, there were a lot of LGM mammoth finds in Western Europe (see previous chapter), and only a few LGT finds. The southern limit of the mammoth range shifted to the north in the LGT.

The woolly rhinoceros *Coelodonta antiquitatis* range, it seems, was narrower than the mammoth range. The density of the rhinoceros localities was lower than the mammoth localities (Fig. 4.28). There are also no finds

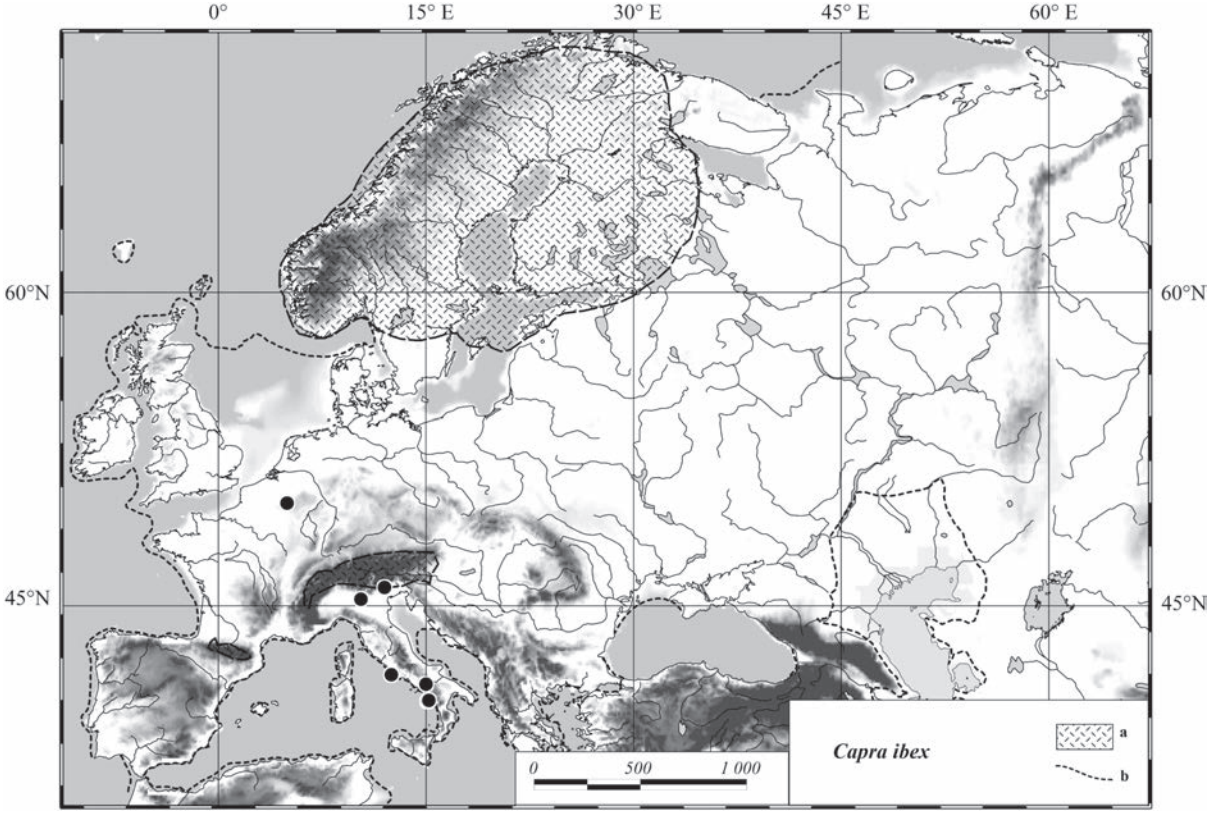

Fig. 4.26. *Mountain goat Capra ibex localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

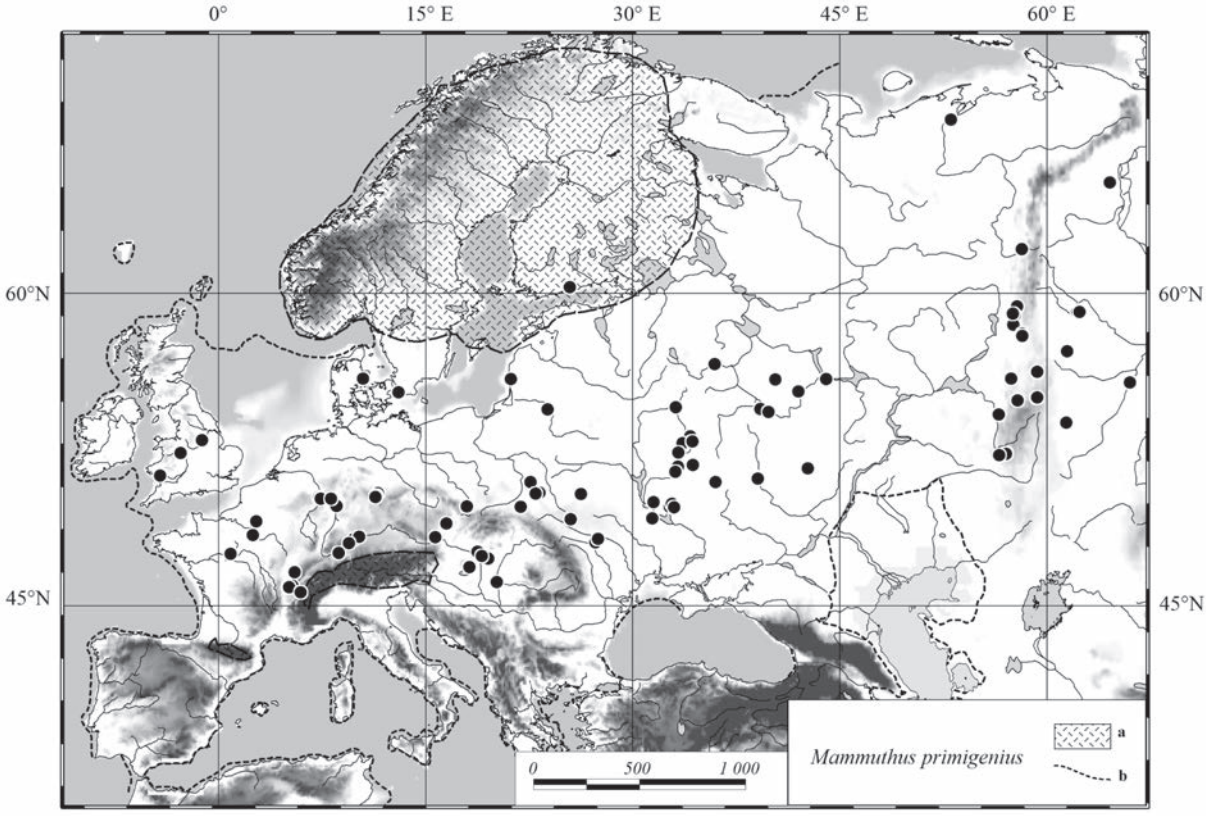

Fig. 4.27. *Mammoth Mammuthus primigenius localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

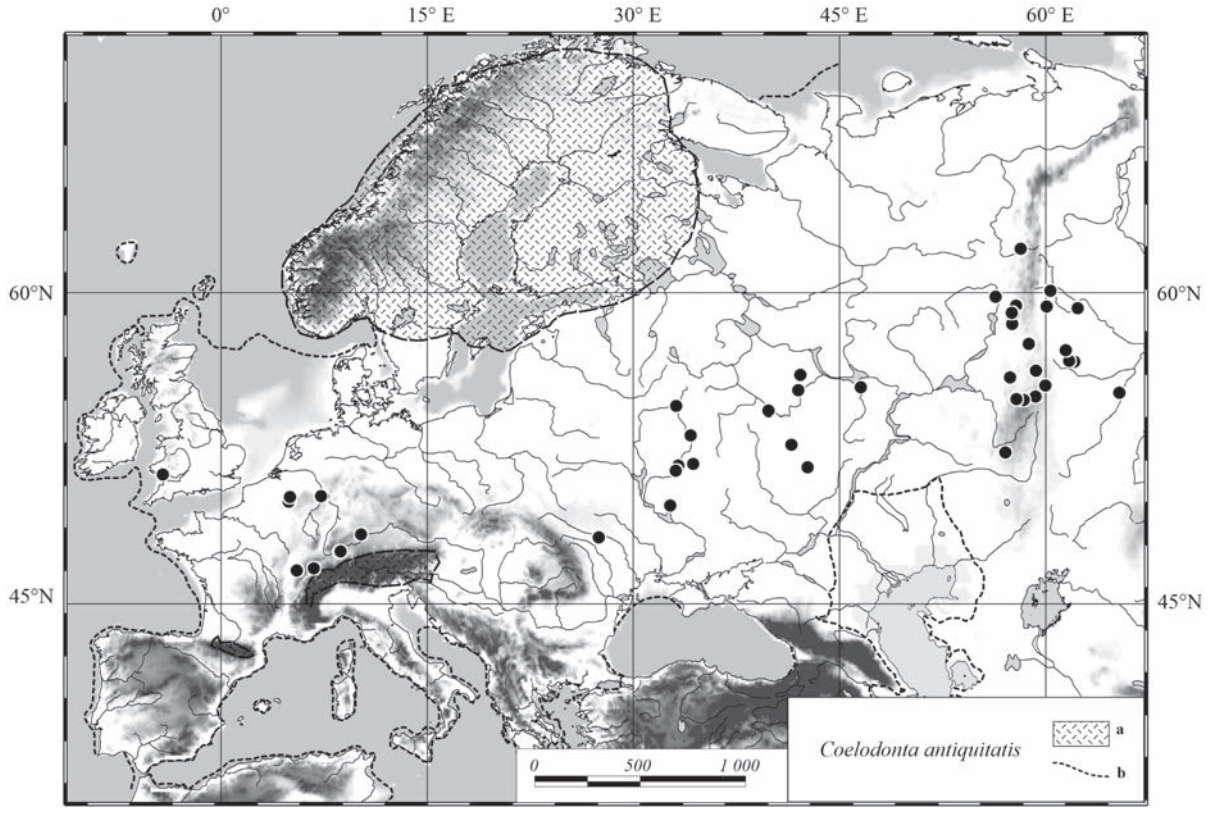

Fig. 4.28. *Woolly rhinoceros Coelodonta antiquitatis localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

of *Coelodonta antiquitatis* in the British Isles, nor in Fennoscandia.

Most of the localities were concentrated in the Urals, on the central Russian Plain, and in France. During the previous interval (LGM), remains of woolly rhinoceros were found in several sites in the British Isles and also in more northern regions than during the LGT. The conclusion about a narrower range of *Coelodonta antiquitatis* during the LGT compared with the LGM could be incorrect and could possibly be explained by the lower number of LGT sites. It could also be the influence of more moderate climatic conditions, which resulted in a restriction of the range of this typical open-landscape animal.

Very characteristic of the 'mammoth' assemblage large herbivores, such as steppe bison and aurochs, were widely distributed during the LGT (Figs. 4.29). Steppe bison was one of the most widely spread species of the Late Pleistocene megafauna, and one of the most important hunted mammals. It occurred in Northern Eurasia until the Holocene. The best habitats for this animal were the steppe landscapes, including the periglacial steppe. It seems that the location of *Bos primigenius* sites was further south than the *Bison priscus* sites. The most optimal conditions to aurochs were to be found in the forest-steppe, where they fed on the herbaceous vegetation. This animal with a body mass of 600–800 kg existed as recent as the 17th century (Tsalkin, 1966). Remains of this important hunted animal were found in the cultural layers of many Late Palaeolithic sites in Northern Eurasia. The species formed part of the boreal variant of the 'mammoth' assemblage (Baryshnikov and Markova, 1992).

Several localities contain the remains of cave lion *Panthera spelaea*, one of the largest cave carnivores, with a body mass of c. 250–300 kg (Fig. 4.30).This species was widely distributed in the southern regions of the Russian Plain during the LGM and was found in the Crimea and in the lower and middle drainage basins of Dniester, Dnieper and Don Rivers (Markova *et al*., 1995). The most complete data on the history, morphology and distribution of the cave lion was presented by N.K. Vereshchagin (1971), who concludes that this predator was perfectly adapted to the cold forest-steppe landscapes. Many LGM localities with cave lion remains have been found in Western Europe (Markova and Puzachenko, previous chapter). It seems that this animal became scarce in the Late Glacial Transition. During the LGT cave lion survived only in the Urals and in the middle Dnieper drainage basin.

The information about 100 mammal species found in LGT localities allows us to reconstruct the characteristics of their ranges during the second part of the last glaciation. The summarizing of this data was done with a help of mathematic methods.

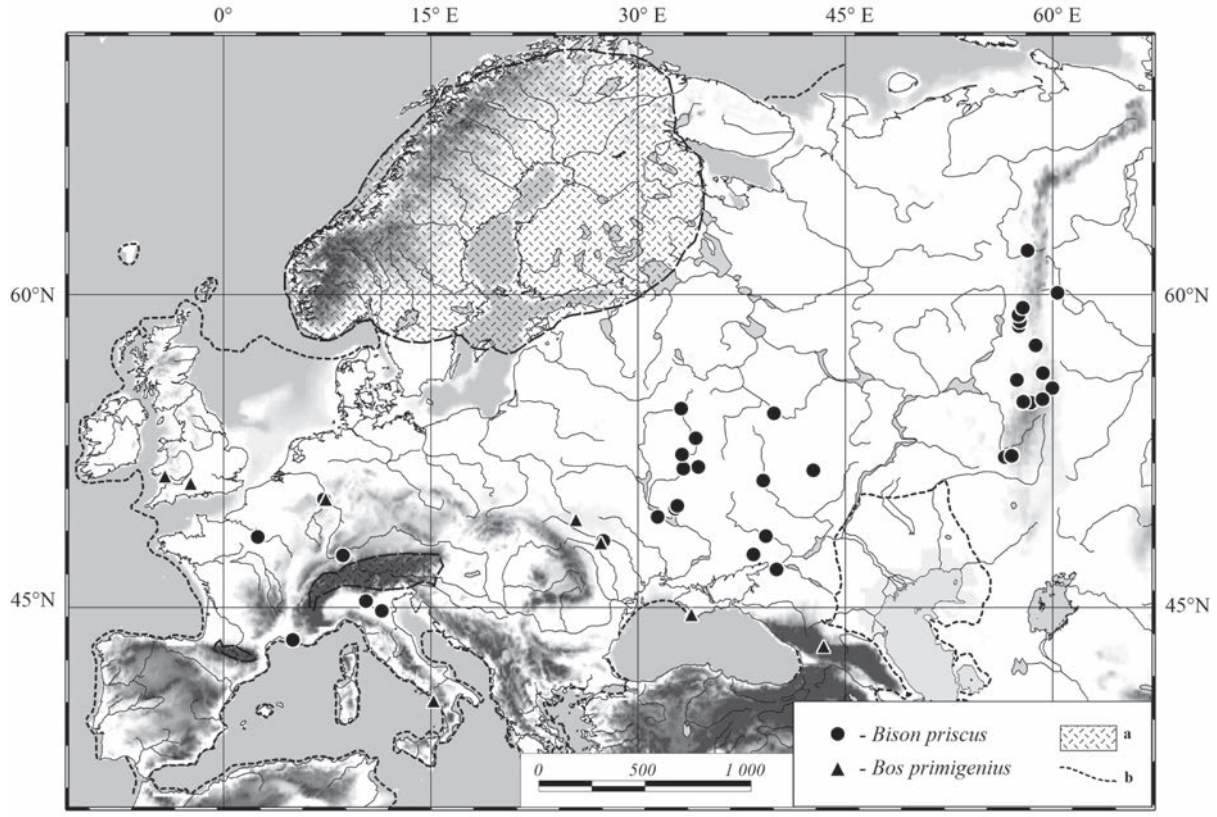

Fig. 4.29. *Steppe bison Bison priscus and Aurochs Bos primigenius localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

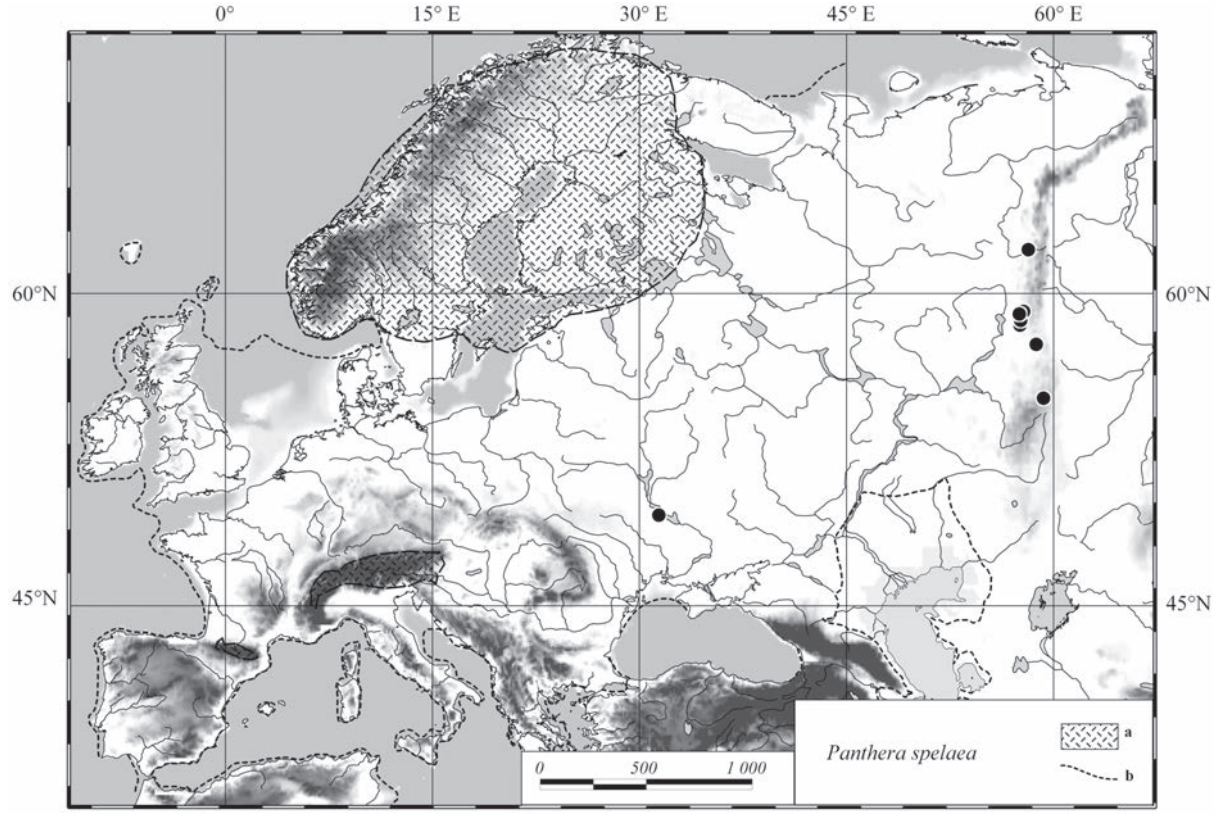

Fig. 4.30. *Cave lion Panthera spelaea localities (17–12.4 kyr BP); a – ice sheets; b – coastline*

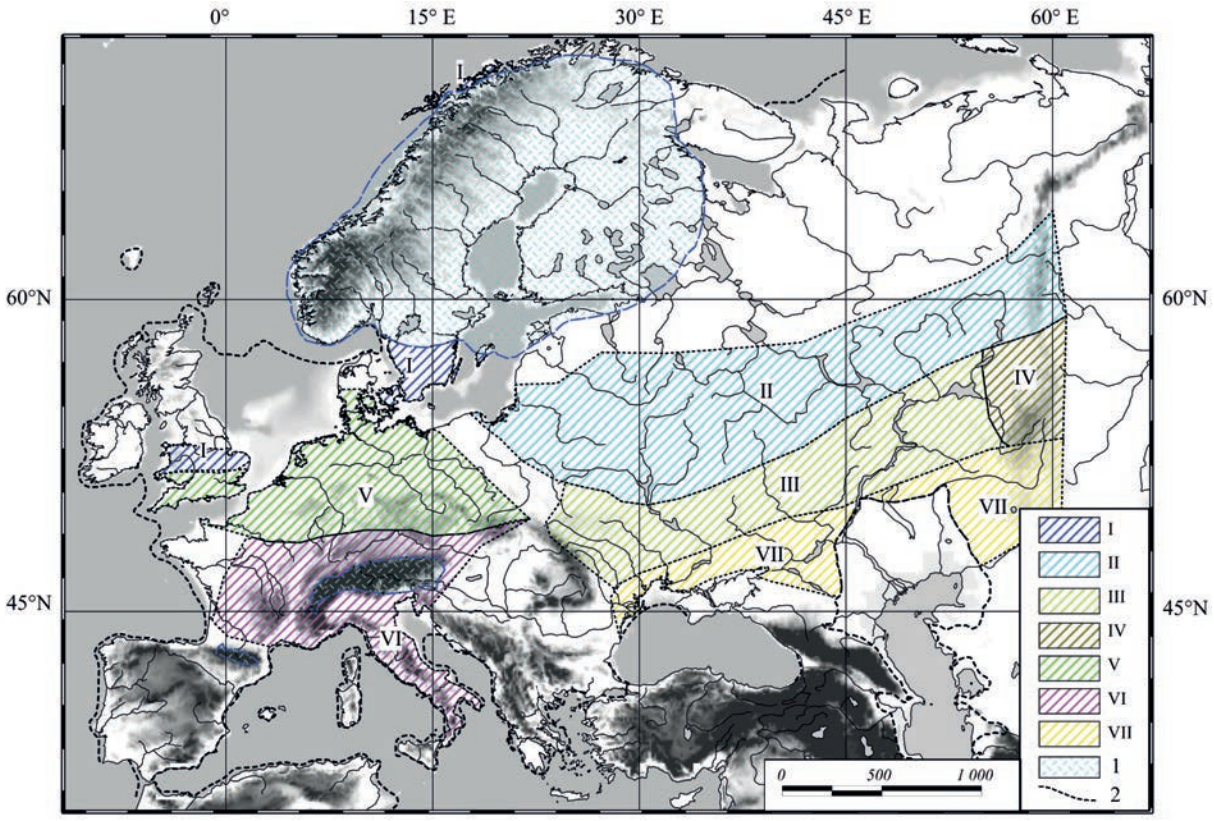

Fig. 4.31. *LGT mammal assemblages: I – periglacial tundra and arctic desert mammal assemblage; II – periglacial tundra-steppe mammal assemblage; III – periglacial tundra-forest-steppe mammal assemblage (eastern variant); IV – Urals tundra-forest-steppe mammal assemblage; V – periglacial tundra-forest steppe mammal assemblage (western variant); VI – mountain forest mammal assemblage; VII – periglacial steppe mammal assemblage, 1 – ice sheets, 2 – coastline*

Principal mammal assemblages during the LGT

The species composition and the geographical position of the principal mammal assemblages were found with the help of mathematical methods (see section 2.4). All the assemblages were mapped with the Map/Info program (Fig. 4.31).

I. Periglacial tundra and arctic desert mammal assemblage

The periglacial tundra and arctic desert mammal assemblage existed on the coasts of Scandinavia, in Fennoscandia, and in the British Isles (Ukkonen *et al*., 1999; Hufthammer, 2001). These sites were attributed to cluster 1 (Table 4.2, Figs. 4.31). Only a few mammals lived here: *Mammuthus primigenius*, *Ursus maritimus*, and *Mustela erminea* (the last species was found on the western-southern coast of Scandinavia) and possibly some others animals. The shrub-tundra vegetation was typical of these areas (Simakova, this volume).

Two points of cluster 1 were distinguished outside the boundaries of these territories, in the Oka River drainage basin. We have ignored these sites, because their relationship to cluster 1 is artificial and is the result of the poor species composition distinguished in these localities.

II. Periglacial tundra-steppe mammal assemblage

This assemblage comprises a high number of mammals. The 17 localities of cluster 2 belonged to this assemblage (Table 4.2, Figs. 4.15 and 4.37). The dominant mammal species include *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Bison priscus*, *Ovibos moschatus*, *Rangifer tarandus*, *Equus* sp., *Saiga tatarica*, *Vulpes lagopus*, *Panthera spelaea*, *Gulo gulo*, *Vulpes vulpes*, *Ursus arctos*, and *Marmota bobak*. Such cold-adapted small mammals as *Dicrostonyx*, *Lemmus*, *Microtus middendorfii*, and *Microtus gregalis* were also distinguished in these sites. Several small mammals are typical steppe dwellers (*Spermophilus*, *Lagurus*, *Eolagurus*, *Ochotona*, etc.) were found in these localities. Most of the animals are typical representatives of the 'mammoth' assemblage

(arctic variant) (Baryshnikov and Markova, 1992; Markova, 2004). Only a few sites include the remains of animals occurring in the shrub and forested areas.

This complex of mammals indicates the wide distribution of periglacial tundra-steppe environments. The tundra-steppe mammal assemblage (including 47 animals) covered large territories: the northern and central parts of the Russian Plain and the northern Urals. These assemblages have not been found in localities in Western Europe.

III. Periglacial tundra-forest-steppe mammal assemblage (eastern variant)

The dominant species of cluster 3 include *Mammuthus primigenius, Rangifer tarandus, Vulpes lagopus, Bos primigenius*, *Cervus elaphus*, and *Equus* sp. The remains of woolly rhinoceros *Coelodonta antiquitatis, Gulo gulo, Ursus arctos, U. spelaeus, Dicrostonyx torquatus, Lagurus lagurus*, *Lepus timidus*, *Microtus gregalis, Ochotona pusilla*, and some other mammals were also found here (Table 4.2, Fig 4.31). The number of cold-adapted species is lower in this assemblage. There are no muskox *Ovibos moschatus*, and Siberian lemming *Lemmus sibiricus* remains in the localities. The number of red deer bones was higher than in cluster 2, it is 38.46% in this third cluster and only 5.88% in the second cluster. All the data indicate a more moderate environmental condition.

Most of the sites in cluster 3 are located further south than the position of the sites in cluster 2. But some of the sites of cluster 3 are situated between the cluster 2 localities. Such a picture could be explained by the wide distribution of the periglacial open environments in Eastern Europe, which changed gradually from north to south. These changes indicate more forested areas in the belt 52–48°N than in the northernmost territories. But the principal picture changed little. At these latitudes, the main environment could be described as periglacial open landscapes with some forested islands in the uplands and in the river basins, but the influence of the ice sheet decreased slightly here.

IV. The Ural tundra-forest-steppe mammal assemblage

The Central Ural Mountains mammal assemblage is distinguished by localities belonging to cluster 4. About 15 sites were found here. The list of dominant species includes *Mammuthus primigenius, Bison priscus, Bos primigenius, Rangifer tarandus, Equus* sp., *Saiga tatarica, Vulpes lagopus, Martes martes, Mustela erminea* and a lot of small mammals of different ecologies: the small steppe mammals include *Allactaga pygmaeus, A. major, Allocricetus eversmanni, Sylvaemus, Arvicola terrestris, Spermophilus* sp., *S. suslicus, S. major, Cricetulus migratorius, Cricetus cricetus, Ellobius talpinus, Eolagurus luteus, Lagurus lagurus, Marmora bobak, Spalax* sp., *Ochotona pusilla* and others; the cold-adapted small mammals include a large quantity of remains of *Dicrostonyx, Lemmus sibiricus,* and *Microtus gregalis*; the forest small mammals were represented by *Sylvaemus, Castor fiber, Clethrionomys glareolus, Cl. rutilis, Cl. rufocanus, Erinaceus* sp., *Microtus agrestis, Myopus* sp., and others.

Many intra-zonal species were also found in these localities, such as *Arvicola terrestris, Microtus oeconomus* and some others. These mammals occupied the banks of rivers and other water bodies.

The mammals represent a large ecological spectrum and therefore indicates the complicated structure of the mammal communities. This depends on the numerous local environments in this mountain region with mountain belts and with different slope exposures. The species richness was very high and reached more than 60 species (Table 4.2). It also important to note that the very detailed studies of the Urals mammal localities were done during the last decades, which allow us to distinguish the high number of small mammals that were usually not distinguished in the sites (Smirnov, 1993; 1996).

V. Periglacial tundra-forest-steppe mammal assemblage (western variant)

The sites of this assemblage are located in the central and northern parts of Western Europe, and in the south of the British Isles. A lot of remains of cold-adapted species including *Vulpes lagopus*, *Dicrostonyx torquatus*, *Lemmus lemmus*, *Microtus gregalis*, *Chionomys nivalis*, *Ovibos moschatus*, and *Rangifer tarandus* have been identified in these localities. Mammoth was not found in most of the sites of the region (only one site with mammoth remains was recovered), but woolly rhinoceros *Coelodonta antiquitatis* did inhabit these territories. The dominant species of this area was *Equus* sp., which was one of the hunted animals. Other steppe species include *Ochotona pusilla* and *Saiga tatarica*, which was found in the middle drainage basin of river Rhine (Fig. 4.21) Some forest-steppe and forest animals were discovered here, including *Cervus elaphus*, *Gulo gulo*, *Meles meles*, *Sylvaemus flavicollis*, and *Clethrionomys glareolus*. The finds of *Capra ibex* indicate mountain regions.

The mammal species composition characterized the typical periglacial faunas with a mixture of cold-adapted, steppe and forest animals. The differences with the Eastern European tundra forest-steppe faunas (assem-

blage III) lay in the presence in Western European faunas of *Lemmus lemmus*, whereas *Lemmus sibiricus* was found in Eastern Europe. Mammoth was very rare in Western Europe, and common in Eastern European faunas. Lagurids were found in Eastern Europe and are absent in assemblage V. We distinguished the faunas of cluster 5 as a periglacial tundra-forest steppe mammal assemblage (western variant).

VI. Mountain forest mammal assemblage

The localities of cluster 6 are distributed near the Alps and on the Apennine Peninsula. Eleven sites were found here. The dominant species of this cluster are Alpine marmot *Marmota marmota*, aurochs *Bos primigenius*, mountain goat *Capra ibex*, roe deer *Capreolus capreolus*, red deer *Cervus elaphus*, chamois *Rupicapra rupicapra*, and wild boar *Sus scrofa*. Most of these animals indicate forest and mountain environments. Such less common species in this cluster as elk *Alces alces*, *Martes foina*, *Mustela erminea*, *M. eversmanni*, *M. nivalis*, *Meles meles*, *Castor fiber*, *Clethrionomys glareolus*, *Glis glis*, *Eliomys quercinus*, *Erinaceus*, *Felis silvestris*, and *Microtus agrestis* also allow us to assume dominance of forest environments.

A unique locality with saiga remains was found on the Mediterranean coast (Fig. 4.21). But steppe animals were very rare here. Only isolated areas with open landscapes could be reconstructed in these regions. Cold-adapted mammal remains are absent in these sites. The remains of mammoth and woolly rhinoceros were also not found here. This assemblage indicates a dominance of mountain forests of different types and could be described as a mountain forest mammal assemblage.

VII. Periglacial steppe mammal assemblage

Only 3 localities belong to cluster 7. They are situated in the Southern Urals, and in the lower Don River drainage basin (Table 4.2). A high number of typical steppe species were discovered in these sites, including *Bison priscus*, *Equus* sp., *Ochotona pusilla*, *Allactaga major*, *Allocricetus eversmanni*, *Marmota bobak*, *Spermophilus major*, *Cricetulus migratorius*, *Cricetus cricetus*, *Ellobius talpinus*, *Lagurus lagurus*, and *Eolagurus luteus*. Forest animals are absent here. Mammoth and woolly rhinoceros remains were not found in the localities of cluster 7. The presence of reindeer *Rangifer tarandus* remains is strange in these localities, but this animal is well adapted to different types of environments. The influence of the ice sheet was very weak in these regions. A periglacial steppe mammal assemblage was reconstructed in the south of the Russian Plain on the basis of these data.

Geographical variation of the mammal species richness

The mammal materials for the LGT were not enough to reconstruct in detail the variation in mammal biodiversity during the LGM (Fig. 4.32). The highest species number was observed in the western foothills of the Ural Mountains (Russia). Other 'centres' of biodiversity occupied the Dnieper River basin with the neighbouring territories (Ukraine) and Central Europe (the foothills of the Alps; the modern basins of the Elbe and Rhine Rivers).

Conclusions

The reconstructions we have made allow us to conclude that the principal structure of mammal assemblages during the LGT was similar to that of the LGM. This indicates the persistence of cold and rather arid climatic conditions in Northern and Central Europe. The main features of LGT assemblages are the occurrence in the huge territory of Europe of mammals belonging in modern times to different natural zones: tundra, forest and steppe zones. The presence of the high number of large herbivores, extinct by the end of the Pleistocene / beginning of the Holocene, also was very typical of these assemblages. The penetration of steppe animals far to the north indicates the absence of a continuous forest zone at that time. Forest animals were rather rare during the LGT and survived in the refugia in the mountain and uphill regions, as well as in the river valleys, with forested and shrub areas.

Many tundra animals had huge ranges in this time, as well as during the LGM, which indicates a cold climatic condition and the distribution of periglacial types of vegetation in Northern and Central Europe. Steppe animals also widened their ranges and penetrated as to the north and to the west. The open landscapes were favourable for such an increase in distribution. The forest mammals concentrated mostly in the southern mountain regions of Europe (in the Apennines, near the Alps, and possibly in the Balkans, the Pyrenees and the Carpathians, from where we have no material yet). Here the influence of the glaciation was rather weak and did not effect the mammal composition and diversity. The studied materials also allow us to reconstruct a large refugium in the Ural Mountains, located northward. Here a high number of both tundra and steppe mammals, and forest ones, were recovered. The numerous local environments supported a distribution of animals of different ecologies in this region.

It is clear that every mammal reacts to the glacial conditions individualistically, some changed their range very

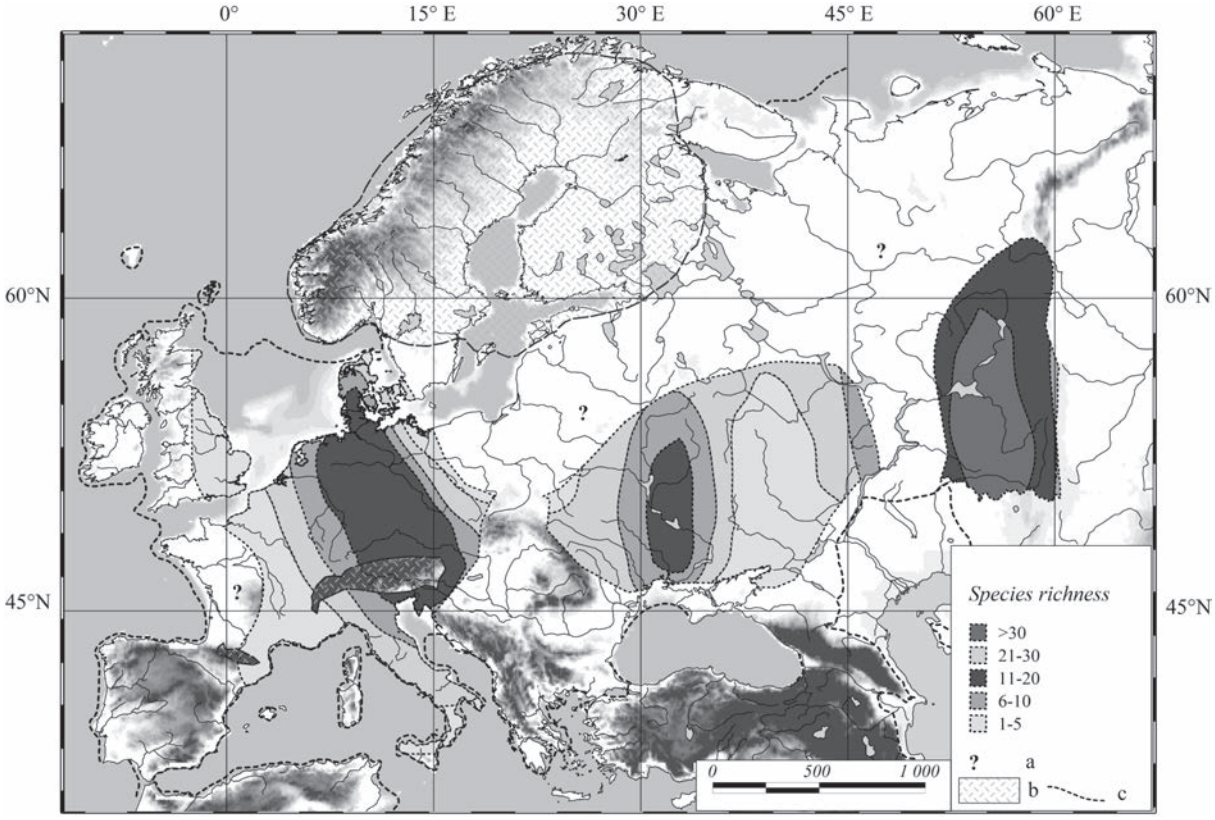

Fig. 4.32. *Geographical variation of the LGT mammal species richness; a – absence of data, b – ice sheets, c – coastline*

significantly; the ranges of others became discontinuous and restricted. These very different mammal reactions resulted in the absolutely new mammal assemblages, which do not have any analogues in modern times. LGT mammal assemblages, belonging to clusters 1–5 could be referred to different types of periglacial habitats. Only assemblages located in the southern regions of Western and Eastern Europe, corresponding to clusters 6 and 7, indicate a very weak influence of the ice sheet.

It should be noted that the principal picture of periglacial non-analogue faunas have been described by many authors and have been attributed as mixed, non-analogue, disharmonious and/or hyperborean faunas. In our opinion the term "disharmonious" should not be used, because the faunas of the glacial period were harmonious despite these severe conditions, and were stable during a long time, including the LGM and the LGT.

4.3. EUROPEAN MAMMAL ASSEMBLAGES DURING THE BØLLING/ALLERØD INTERSTADIAL COMPLEX (BAIC) (<12.4 – ⩾10.8 KYR BP)

Anastasia Markova and Andrey Puzachenko

The materials from the latest interstadials of the last glaciation: Bølling (^{14}C yrs BP 12,400–12,000) and Allerød (^{14}C yrs BP 11,800–10,800) and the intermediate Older Dryas cooling (^{14}C yrs BP 12,000–11,800), were analyzed together. There are two reasons for combining these data: firstly, the duration of the Older Dryas was

very short, about ~200 yrs; secondly, this cooling was weak according to the δ^{18} O values (Coope and Lemdahl, 1995).

Materials and methods

The materials from 53 European mammal localities dated by ^{14}C to between 12,400 yrs BP and 10,800 yrs BP were combined in an electronic database. These localities comprise 76 mammal taxa, identified mostly at species level. The structure of the database has been described in previous chapters.

BAIC mammal localities are rare (Fig. 4.33). Most of the localities were found in the central part of Europe. Only a few sites were found further north than 60°N (Blomva, in Scandinavia and the Medvezhya Cave in the Urals). Another northern location is the Norre Lyngby B site on the Jutland Peninsula (56°N). The southernmost localities are the Picareiro Cave on the Iberian Peninsula and the Grotte de l'Erica, the Serratura, the Grotte du Mezzogiorno and Grotte Paglicci on the Apennine Peninsula (about 40°N) (Fig. 4.33).

A unique site is situated on a small Isle of Man in the Irish Sea, Close-y-Garey at 4.67°W. The matrices of pair distances were calculated for mammal sites, followed by cluster analysis (UPGMA method) of the data, using multidimensional scale axes. Six clusters were distinguished in the mammal data (Fig. 4.34).

The mammal lists for each cluster are present in Table 4.3.

Mammal ranges during the BAIC

The distribution of the localities of the clusters is shown in Figure 4.35. The low number of localities allows us to reconstruct only the very principal features of the mammal distribution and diversity in Europe. A lot of 'white' areas without any information caused difficulties in the reconstructions. The series of maps with index mammal ranges were constructed with the help of the Map/Info program. These maps help us to understand the structure and position of the main mammal assemblages and their origin.

Subarctic mammals

The remains of polar fox *Vulpes lagopus* were found mainly in the Urals and in the west and north of Western Europe and in the British Isles (Fig. 4.36).

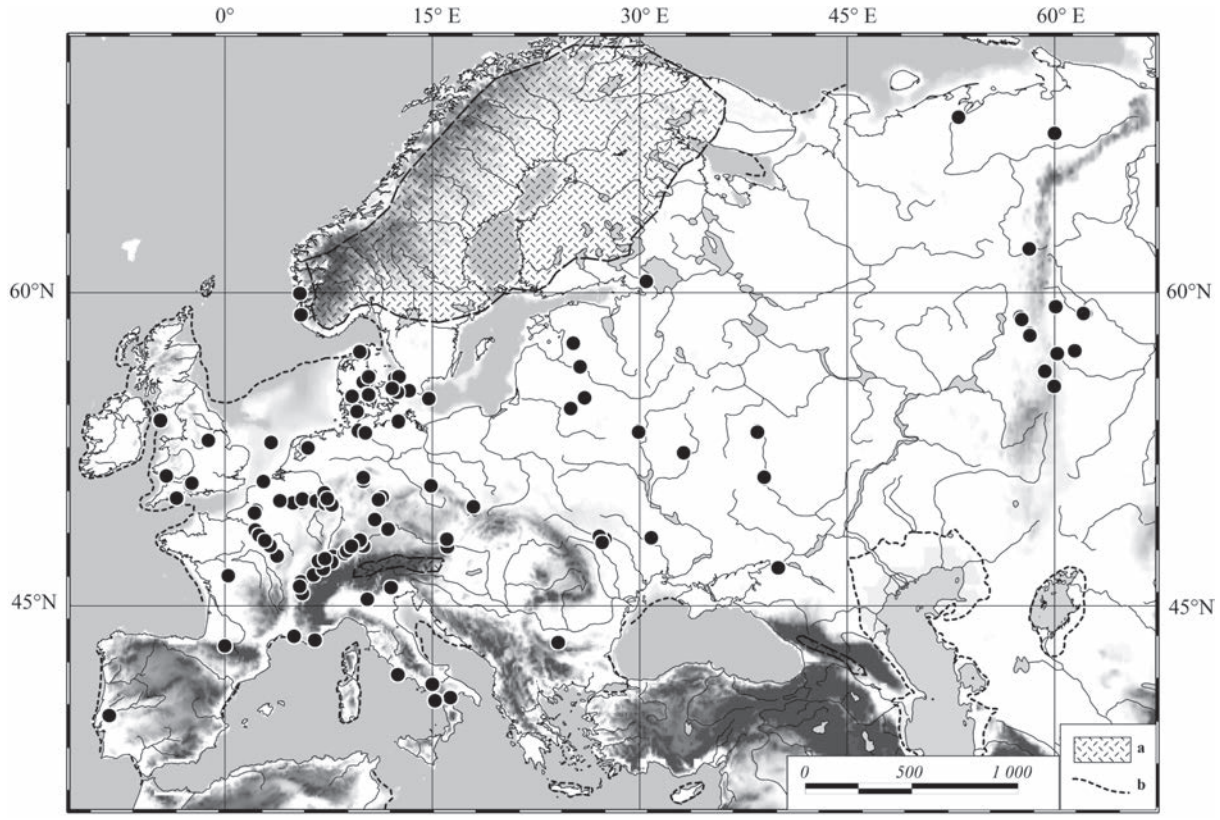

Fig. 4.33. *BAIC mammal localities (12.4–10.8 kyr BP); a – ice sheet; b – coastlines*

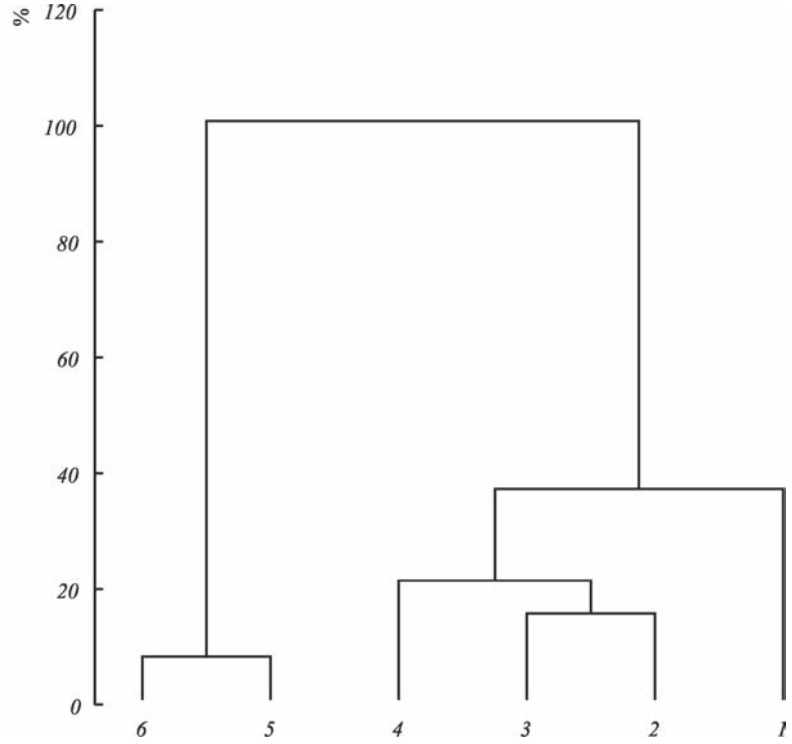

Fig. 4.34. *Clusters distinguished in BAIC mammal data*

Table 4.3

Mammal taxa found in the localities belonging to the different clusters (% indicates the finds in the cluster)

Taxa	Number of clusters (mammal assemblages)						M-L Chi-sq, *p*
	1	2	3	4	5	6	
	Number of localities						
	9	9	9	7	4	15	
Erinacaeus sp. – Eurasian hedgehog	0.0	0.0	0.0	0.0	0.0	6.67	–
Desmana moschata – Russian desman	11.11	11.11	0.0	14.29	0.0	0.0	–
Talpa sp. – Eurasian mole	0.0	0.0	11.11	0.0	25.00	13.33	–
Sorex araneus – common shrew	11.11	0.0	11.11	0.0	0.0	13.33	–
Sorex minutus – lesser shrew	0.0	0.0	11.11	0.0	0.0	0.0	–
Crocidura sp. – white-toothed shrew	0.0	0.0	0.0	0.0	0.0	13.33	–
Oryctolagus cuniculus – European rabbit	0.0	0.0	0.0	0.0	0.0	13.33	–
Lepus timidus – Polar hare	0.0	11.11	**44.44**	14.29	0.0	6.67	–
Lepus europaeus – European hare	0.0	22.22	0.0	**42.86**	0.0	13.33	0.04
Ochotona pusilla – steppe pika	**44.44**	**44.44**	33.33	14.29	0.0	0.0	0.01
Spermophilus superciliosus – suslik "superciliosus"	0.0	0.0	0.0	0.0	0.0	6.67	–
Spermophilus sp. – suslik	11.11	**55.56**	0.0	0.0	0.0	6.67	0.02
Marmota bobak – bobak marmot	0.0	**33.33**	0.0	14.29	0.0	0.0	0.05
Marmota marmota – Alpine marmot	0.0	0.0	0.0	0.0	0.0	**20.0**	–
Castor fiber – beaver	0.0	0.0	11.11	0.0	**50.0**	13.33	–
Eliomys quercinus – garden dormouse	0.0	0.0	0.0	0.0	0.0	26.67	–

Continued table 4.3

Taxa	Number of clusters (mammal assemblages)						M-L Chi-sq, *p*
	1	2	3	4	5	6	
	Number of localities						
	9	9	9	7	4	15	
Glis glis – fat dormouse	0.0	0.0	0.0	0.0	0.0	13.33	–
Allactaga sp. – jerboa	11.11	11.11	0.0	14.29	0.0	0.0	–
Sylvaemus sylvaticus – common mouse	0.0	0.0	0.0	0.0	0.0	**20.0**	–
S. flavicollis – yellow-necked mouse	0.0	0.0	11.11	0.0	0.0	13.33	–
Sylvaemus sp. – mouse	0.0	11.11	22.22	0.0	25.00	**33.33**	–
Ellobius talpinus – northern mole-vole	0.0	11.11	0.0	0.0	0.0	0.0	–
Cricetulus migratorius – grey hamster	0.0	**33.33**	11.11	0.0	0.0	0.0	–
Mesocricetus sp. – golden hamster	0.0	0.0	0.0	14.29	0.0	0.0	–
Cricetus cricetus – common hamster	0.0	0.0	11.11	0.0	0.0	6.67	–
Clethrionomys rufocanus – grey-sided vole	11.11	11.11	0.0	0.0	0.0	0.0	–
Clethrionomys glareolus – red-backed vole	22.22	0.0	22.22	0.0	25.00	13.33	–
Clethrionomys rutilus – northern red-backed vole	**22.22**	0.0	11.11	0.0	0.0	0.0	–
Lagurus lagurus – steppe lemming	11.11	33.33	0.0	14.29	0.0	0.0	–
Eolagurus luteus – yellow steppe lemming	11.11	22.22	0.0	0.0	0.0	0.0	–
Dicrostonyx sp.** – collared lemming	**33.33**	**44.44**	**44.44**	0.0	0.0	6.67	0.02
Lemmus lemmus – Norway lemming	0.0	11.11	**44.44**	0.0	0.0	0.0	0.01
Lemmus sibiricus – Siberian lemming	**22.22**	**33.33**	0.0	0.0	0.0	0.0	0.03
Myopus sp. – wood lemming	11.11	11.11	0.0	0.0	0.0	0.0	–
Arvicola terrestris – water vole	22.22	22.22	**55.56**	0.0	25.00	20.0	
Microtus (Terricola) sp. – pine vole	0.0	0.0	0.0	0.0	0.0	13.33	–
Microtus gregalis – narrow skulled vole	**33.33**	**33.33**	**33.33**	0.0	0.0	6.67	–
Microtus oeconomus – root vole	**44.44**	**33.33**	44.44	0.0	25.00	6.67	0.5
Microtus agrestis – field vole	11.11	0.0	22.22	0.0	0.0	13.33	–
Microtus arvalis – common vole	0.0	11.11	22.22	0.0	0.0	13.33	–
Microtus savii – Savi's pine vole	0.0	0.0	0.0	0.0	0.0	6.67	–
Chionomys nivalis – snow vole	0.0	22.22	22.22	0.0	0.0	20.0	–
Canis lupus – wolf	0.0	22.22	22.22	28.57	**50.0**	26.67	–
Vulpes lagopus – Polar fox	0.0	**44.44**	**33.33**	14.29	0.0	0.0	0.09
Vulpes vulpes – common red fox	0.0	11.11	33.33	14.29	25.00	20.0	–
Ursus arctos – brown bear	0.0	0.0	22.22	14.29	**50.0**	6.67	–
Ursus maritimus – Polar bear	**44.44**	0.0	0.0	0.0	0.0	0.0	0.07
Martes sp. – marten	0.0	11.11	0.0	0.0	25.00	20.0	–
Martes martes – common marten	0.0	0.0	0.0	0.0	0.0	6.67	–
Gulo gulo – wolverine	0.0	11.11	0.0	28.57	0.0	0.0	–
Mustela erminaea – ermine stoat	11.11	22.22	0.0	0.0	0.0	6.67	–
Mustela nivalis – weasel	0.0	0.0	0.0	0.0	0.0	20.0	–
Meles meles – badger	0.0	11.11	0.0	14.29	0.0	6.67	–

Continued table 4.3

Taxa	Number of clusters (mammal assemblages)						M-L Chi-sq, *p*
	1	2	3	4	5	6	
	Number of localities						
	9	9	9	7	4	15	
Lutra lutra – common otter	0.0	0.0	0.0	0.0	0.0	6.67	–
Panthera spelaea – cave lion	0.0	11.11	0.0	0.0	0.0	0.0	–
Felis silvestris – wood cat	0.0	0.0	0.0	0.0	0.0	**13.33**	–
Lynx lynx – European lynx	0.0	0.0	0.0	0.0	0.0	**6.67**	–
Mammuthus primigenius – woolly mammoth	0.0	11.11	11.11	**42.86**	0.0	0.0	0.05
Equus (Equus) sp.* – wild horse	0.0	44.44	33.33	**71.43**	25.00	40.0	0.03
Equus hydruntinus – Pleistocene ass	0.0	0.0	0.0	0.0	0.0	20.0	–
Equus asinus – wild ass	0.0	0.0	0.0	0.0	0.0	6.67	–
Coelodonta antiquitatis – woolly rhinoceros	0.0	**33.33**	**22.22**	0.0	0.0	0.0	0.03
Sus scrofa – wild boar	0.0	0.0	0.0	0.0	0.0	**73.33**	<0.001
Cervus elaphus – red deer	0.0	0.0	33.33	14.29	**100.0**	**66.67**	<0.001
Capreolus capreolus – roe deer	0.0	0.0	0.0	0.0	**50.0**	**73.33**	<0.001
Megaloceros giganteus – giant deer	0.0	22.22	0.0	0.0	0.0	6.67	–
Alces alces – elk	0.0	0.0	11.11	0.0	**50.0**	13.33	–
Rangifer tarandus – reindeer	22.22	**44.44**	33.33	**57.14**	25.00	13.33	–
Bos primigenius – wild ox	0.0	0.0	22.22	14.29	**100.0**	**60.0**	<0.001
Bison priscus – steppe bison	0.0	22.22	11.11	**57.14**	**50.0**	20.0	0.05
Saiga tatarica – saiga	0.0	22.22	11.11	0.0	0.0	6.67	–
Rupicapra rupicapra – chamois	0.0	0.0	11.11	14.29	25.00	**40.0**	0.05
Capra ibex – mountain goat	0.0	0.0	11.11	0.0	0.0	**53.33**	0.007

** Equus sp. unites all horse remains referred to by different names.*
*** Dicrostonyx sp. comprises both D. torquatus and D. gulielmi.*

Only one site with Polar fox remains is located in the middle drainage basin of the Yuzhnyi Bug River (47°N). The position of this single site could indicate the persistence of areas of periglacial tundra-steppe environments during this period, even so far south of the modern Polar fox range. Perhaps these landscapes had an 'island' structure.

The Late Pleistocene collared lemming *Dicrostonyx* (described in the literature as *D. torquatus* and as *D. gulielmi*, but undoubtedly referring to one species, with some archaic features in the morphology) existed also in Europe during the BAIC (Fig. 4.37), but finds of *Dicrostonyx* became rather rare in this period. The southernmost locality was found at 51°N in the Rhine River basin. Collared lemming remains were also found on the Russian Plain in the Upper Don River basin and in the Urals. The rather low number of sites of this typical tundra species indicates the disintegration of the wide periglacial zone during the BAIC transition, and a milder climate.

The Siberian lemming *Lemmus sibiricus* sites were located only in the Ural Mountains (Fig. 4.37). This fact also indicates the warming up during the BAIC. The other representative of the genus *Lemmus* genus, the Norway lemming *Lemmus lemmus*, was discovered in the middle Rhine River drainage basin, on the Jutland Peninsula, and in the British Isles (Fig. 4.37). These two species of the genus *Lemmus* are absent in most of the BAIC localities.

Reindeer *Rangifer tarandus* finds were rather common in this interval (Fig. 4.38). This animal occurred both in Western Europe and Eastern Europe, and its range reached south up to 43°N. Modern reindeer has adapted a wide range of ecological niches and inhabits tundra landscapes as well as forest-tundra and taiga landscapes (Flint *et al*., 1970). This could explain their wide distribution during the BAIC.

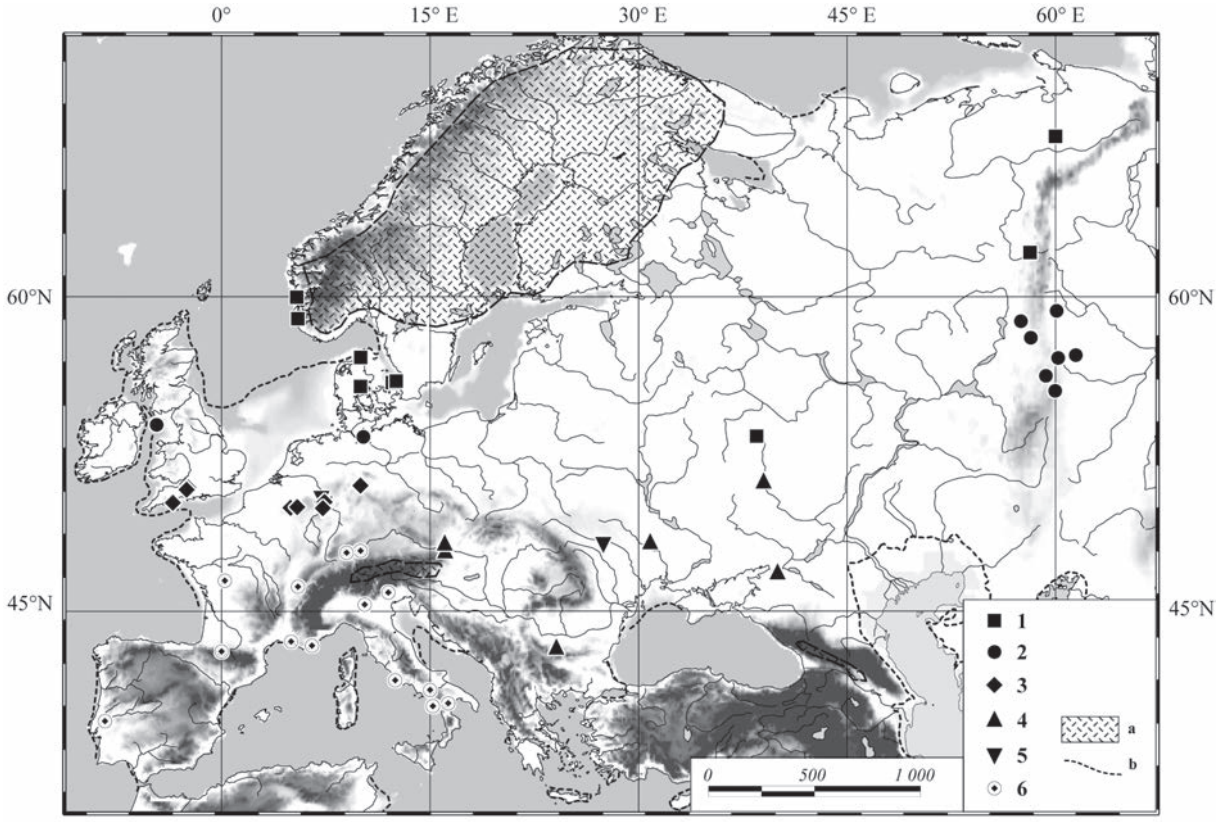

Fig. 4.35. *The distribution of BAIC mammal localities belonging to different clusters: 1–6 – localities of the different clusters; a – ice sheet limits; b – coastlines*

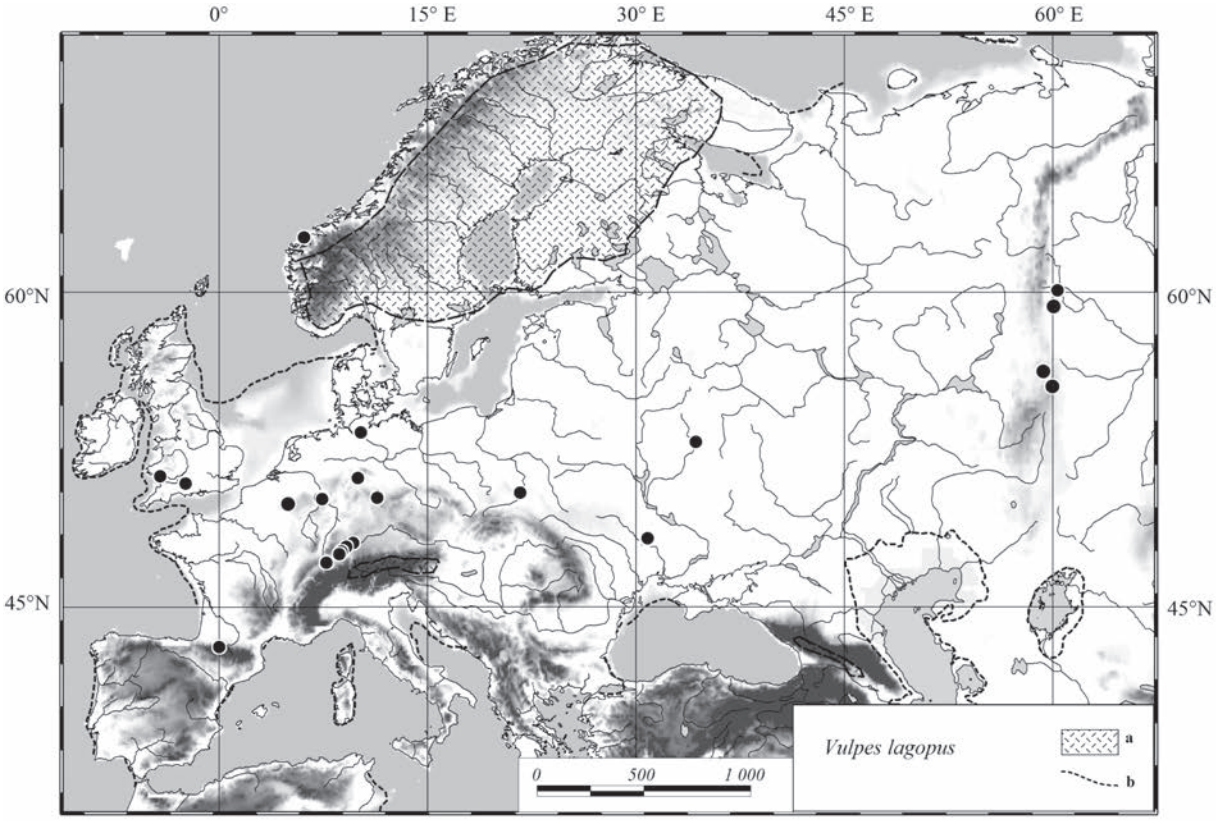

Fig. 4.36. *Polar fox Vulpes lagopus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastlines*

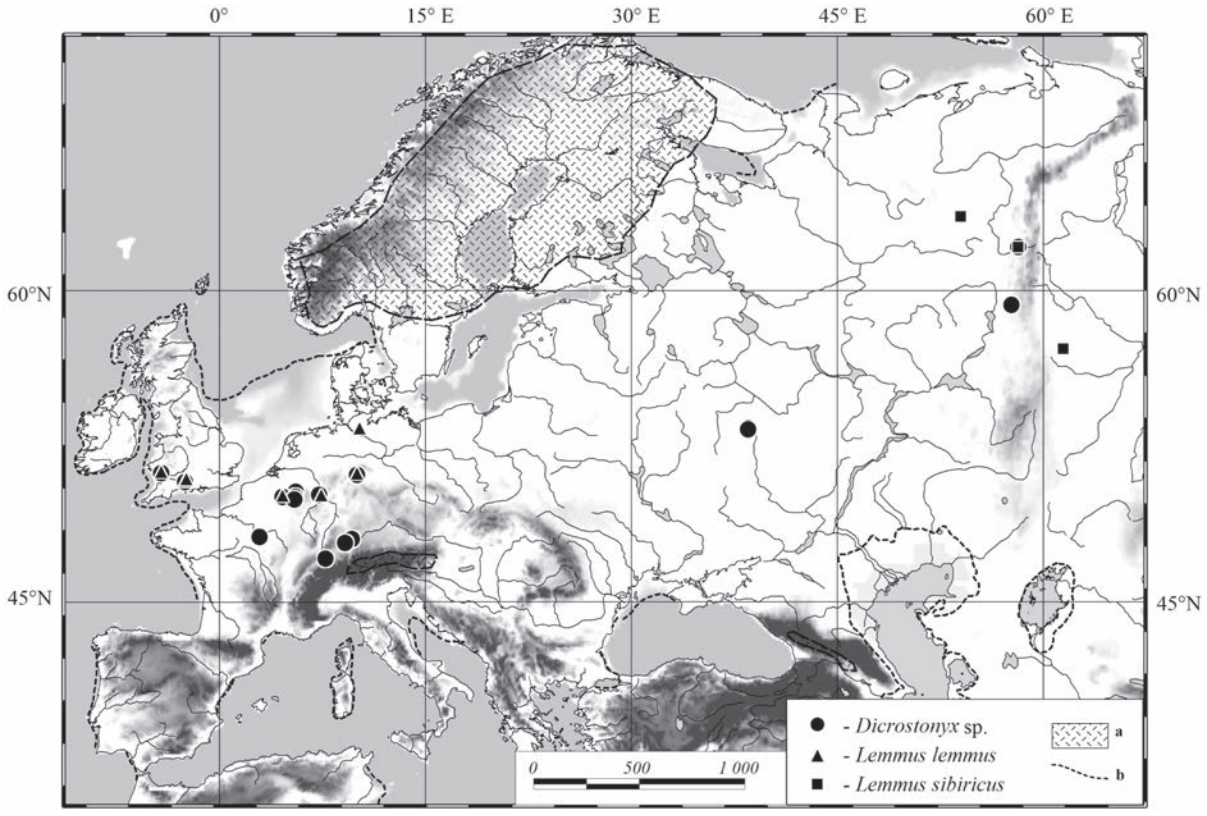

Fig. 4.37. *Collared lemming Dicrostonyx sp., Siberian lemming Lemmus sibiricus and Norway lemming Lemmus lemmus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

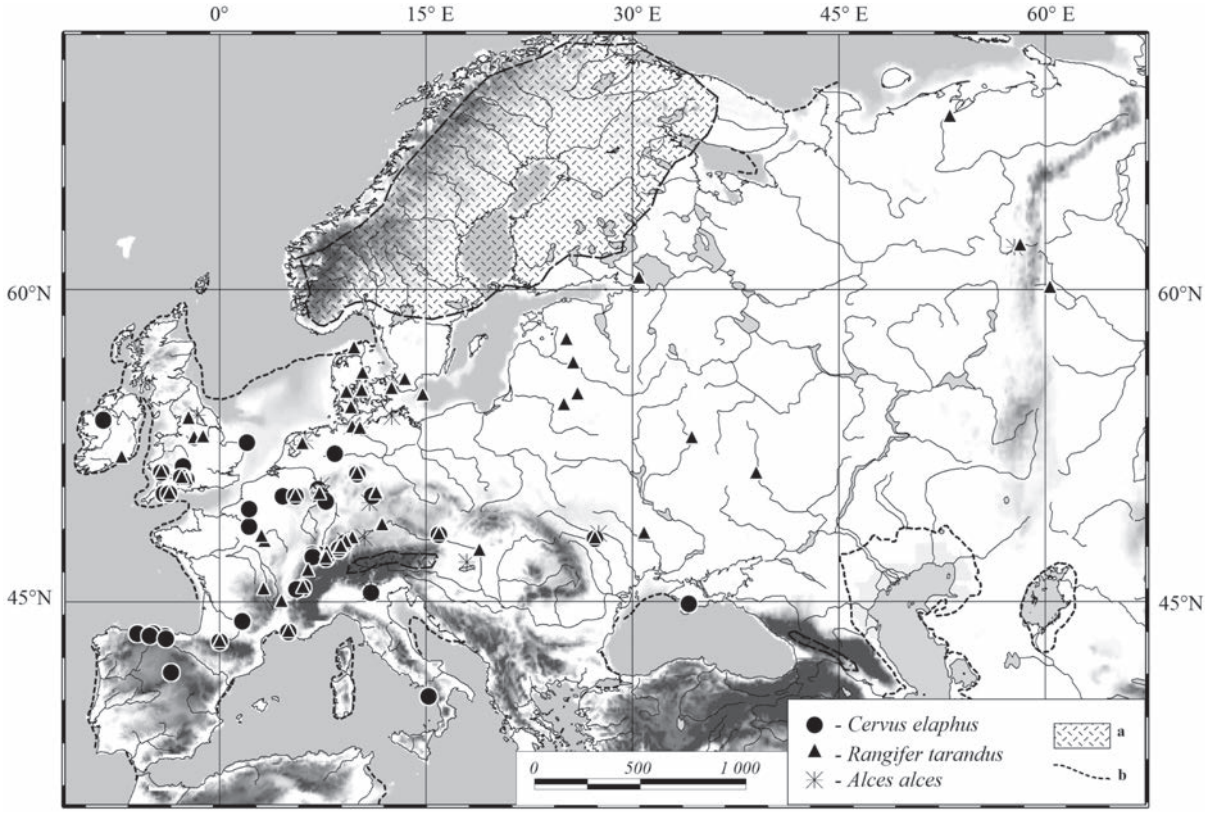

Fig. 4.38. *Red deer Cervus elaphus, reindeer Rangifer tarandus and elk Alces alces localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

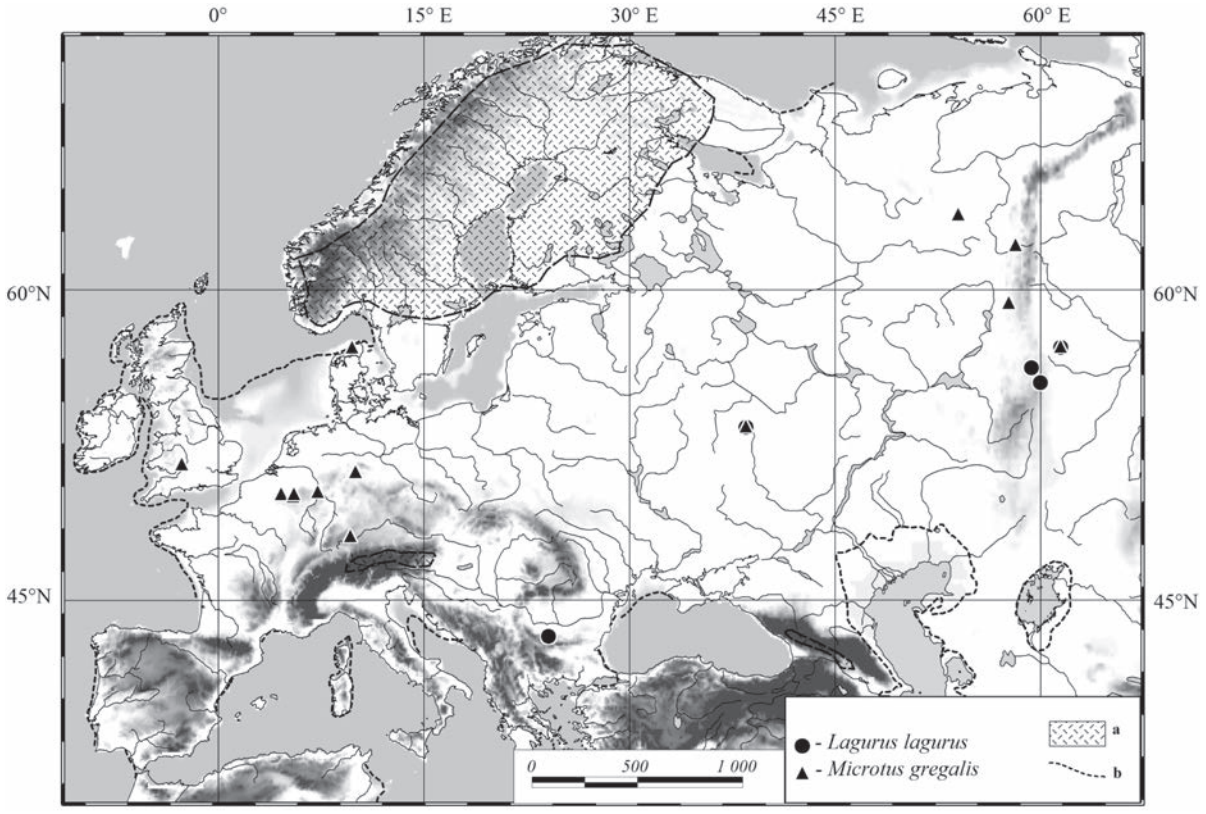

Fig. 4.39. *Narrow-skulled vole Microtus (Stenocranius) gregalis and steppe lemming Lagurus lagurus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

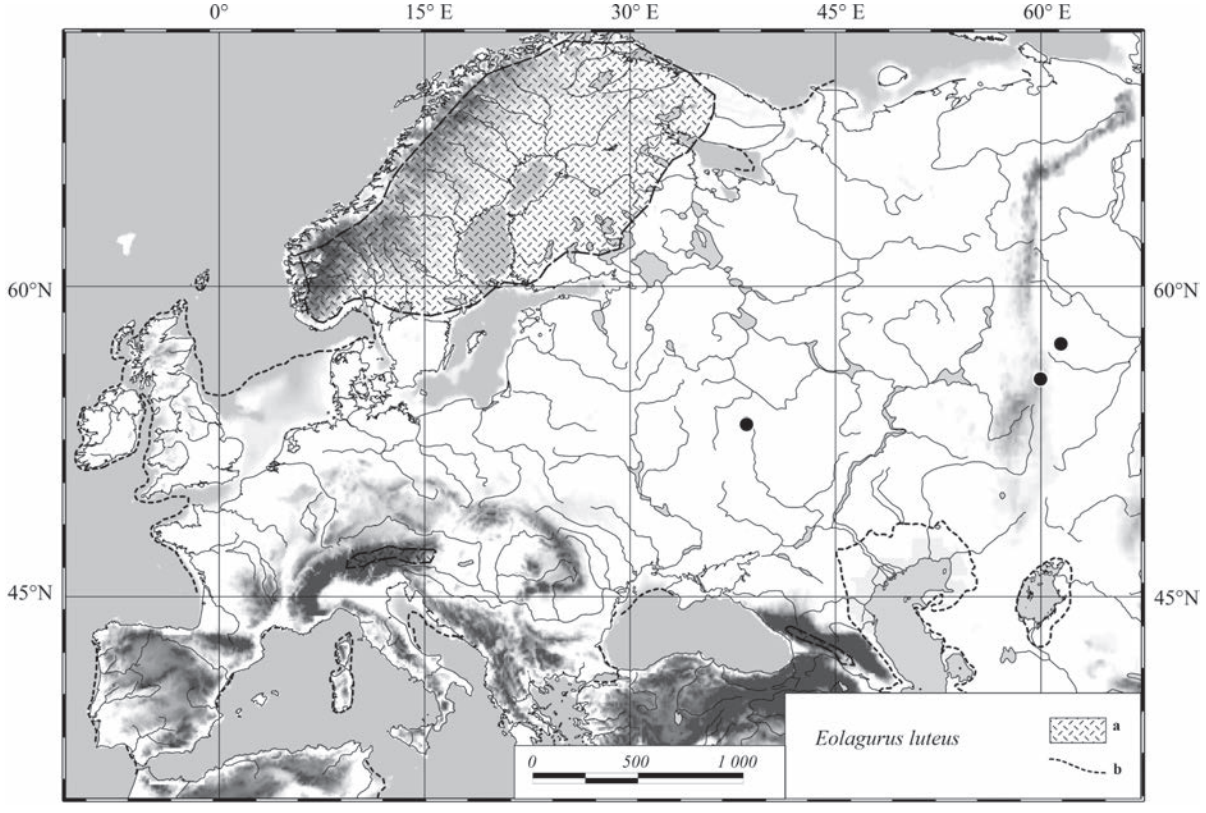

Fig. 4.40. *Yellow steppe lemming Eolagurus luteus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

The narrow-skulled vole *Microtus (Stenocranius) gregalis* was the most common animal in Late Pleistocene glacial faunas. This mammal penetrated far to the west and north during the Last Glaciation (Markova *et al*., 1995). In the BAIC interval, the narrow skulled vole was distributed in the Urals, on the Central Russian Plain, and in Western Europe (in the Rhine basin) (Fig. 4.39).

Steppe mammals

A high number of mammals found in BAIC localities were adapted to open landscapes. Sites with steppe lemming *Lagurus lagurus* are located in the Urals, on the Central Russian Plain and in the Danube lowlands (~41.5°N; 23°E) (Fig. 4.39). These locations indicate the rather wide distribution of open landscapes during the BAIC. However, the steppe lemming range was wider during the Last Glacial Maximum period, when its remains were found as far west as 17°E. The decrease of the steppe lemming range indicates a milder climate during the BAIC and a decline in open landscapes.

The typical steppe and semi-desert yellow lemming species *Eolagurus luteus* was widely distributed during the Last Glaciation and was a representative of the 'mammoth' complex. A tendency to reduction of its range can be observed during the BAIC. In the BAIC yellow lemming remains were not found in Western Europe, and were recovered only on the Central Russian Plain and in the Urals (Fig. 4.40). The saiga *Saiga tatarica* range also became more restricted during the BAIC. Its remains were recovered in the Ural Mountains, on the north coast of the Mediterranean and in the British Isles (Fig. 4.41). The distribution of the saiga most probably became discontinuous in this time interval.

A milder climate and an increase in precipitation restricted the saiga habitats. This species is very sensitive to an increase in the snow cover, which strongly limits the saiga distribution (Nasimovich, 1955; Zhirnov *et al*., 1998). If the snow cover is higher than 10–15 cm during two weeks, the saiga population decreases very strongly because the animal is unable to reach its food. The ice cover, formed on the snow surface during the warmer fluctuations, is traumatic for saiga extremities, and could cause the death of this mammal.

Horse *Equus* sp. remains were found in most of the BAIC localities (Fig. 4.42). This species prefers open landscapes, but its ecology was less restricted than the saiga ecology. During the Last Glaciation, different *Equus* species occurred in Northern Eurasia. Some of these (*E. latipes*) were adapted to forest-steppes, *Equus uralensis* preferred habitats with more continental conditions, and *Equus lenensis* inhabited periglacial tundra landscapes (Kuzmina, 1980; 1989). Thus, the wide distribution of the horse could indicate the existence of both steppe and tundra-steppe areas in Europe, as well as forest-steppe landscapes.

Pleistocene wild ass *Equus hydruntinus* localities, dated by ^{14}C to the BAIC, were recovered only in the Apennines. This animal was adapted to dry steppes and semi-deserts, as were saiga, horse, ground squirrels, steppe and yellow lemmings and other species close to open landscapes. The wild ass became extinct in the Crimea in Mesolithic times (Batyrov and Kuzmina, 1991), and persisted as late as the Middle Holocene in northern regions near the Black Sea (Bibikova, 1975). So, the limited number of the sites with *Equus hydruntinus* remains dated to the BAIC, gives an incomplete picture of its distribution. Undoubtedly, this animal inhabited the south of the Russian Plain and the Crimea during the BAIC interval.

The steppe pika *Ochotona pusilla* also had a large range during the BAIC and its remains were found in Western and Eastern Europe (Fig. 4.43). The modern range of the steppe pika is located on the left bank of the Lower Volga drainage basin, in the South Ural Mountains, and in Northern and Central Kazakhstan, where *Ochotona pusilla* inhabits the steppes (Flint *et al.*, 1970). The unique steppe pika finds on the Jutland Peninsula, and in the Rhine and Upper Danube basins indicate the preservation of open, steppe-like areas in these regions even during the BAIC.

Ground squirrel *Spermophilus* sp. localities were registered on the Jutland Peninsula and in the Urals (Fig. 4.43). These finds together with the pika finds confirm the preservation of some open landscapes on the Jutland Peninsula even during the BAIC.

Some other steppe-adapted mammals were recorded in BAIC localities. Gray hamster *Cricetulus migratorius* sites were found in the Ural Mountains and also in the Rhine drainage basin, far west of its modern range. Northern mole-rat *Ellobius talpinus* remains were recovered in the Middle Urals, and great jerboa *Allactaga major* in the Urals and also on the Balkan Peninsula. Bobak marmot *Marmota bobak* finds were located only on the central Russian Plain in this time. Only one Newtoni hamster *Mesocricetus newtoni* site was recovered, in the Danube middle drainage basin near the Stary Planina Mountains. The modern area of this animal is also located in this region. Thus, the information on the distribution of steppe species indicates the existence of open landscape areas in both Eastern and Western Europe. In Western Europe these areas were more restricted and located on the Jutland Peninsula, in the Rhine and Loire River basins, in the Danube lowlands, on the Iberian Peninsula, and possibly in some other areas. Open landscapes of a different type were more widely distributed in Eastern Europe, which could be explained by its geographical position and more continental climate.

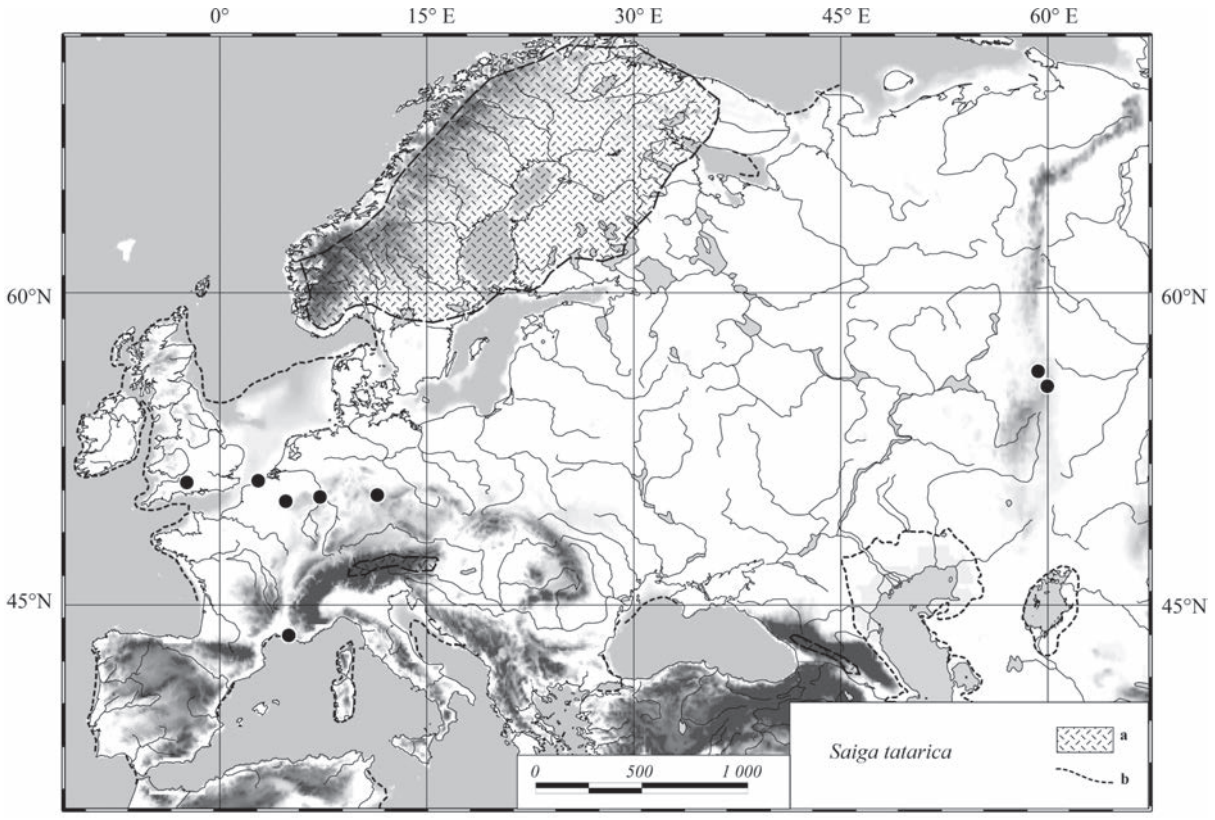

Fig. 4.41. *Saiga Saiga tatarica localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

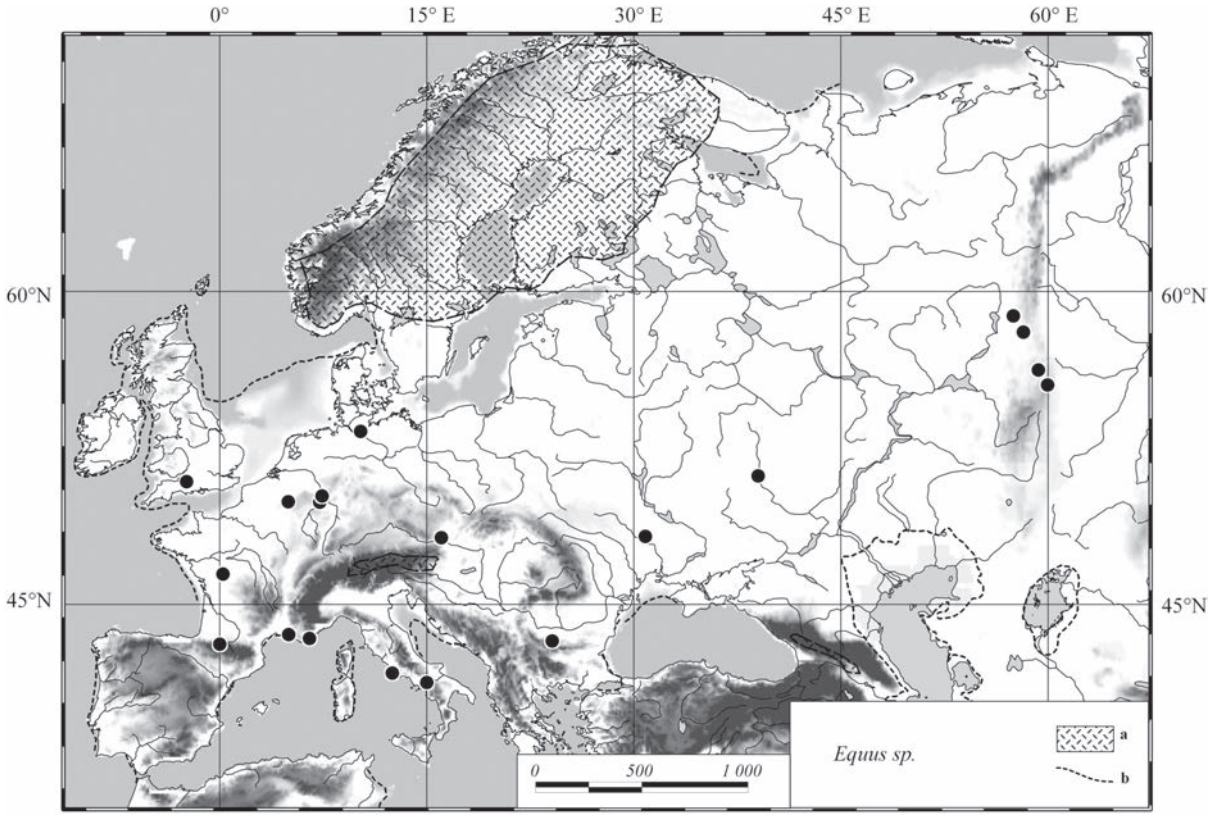

Fig. 4.42. *Horse Equus sp. localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

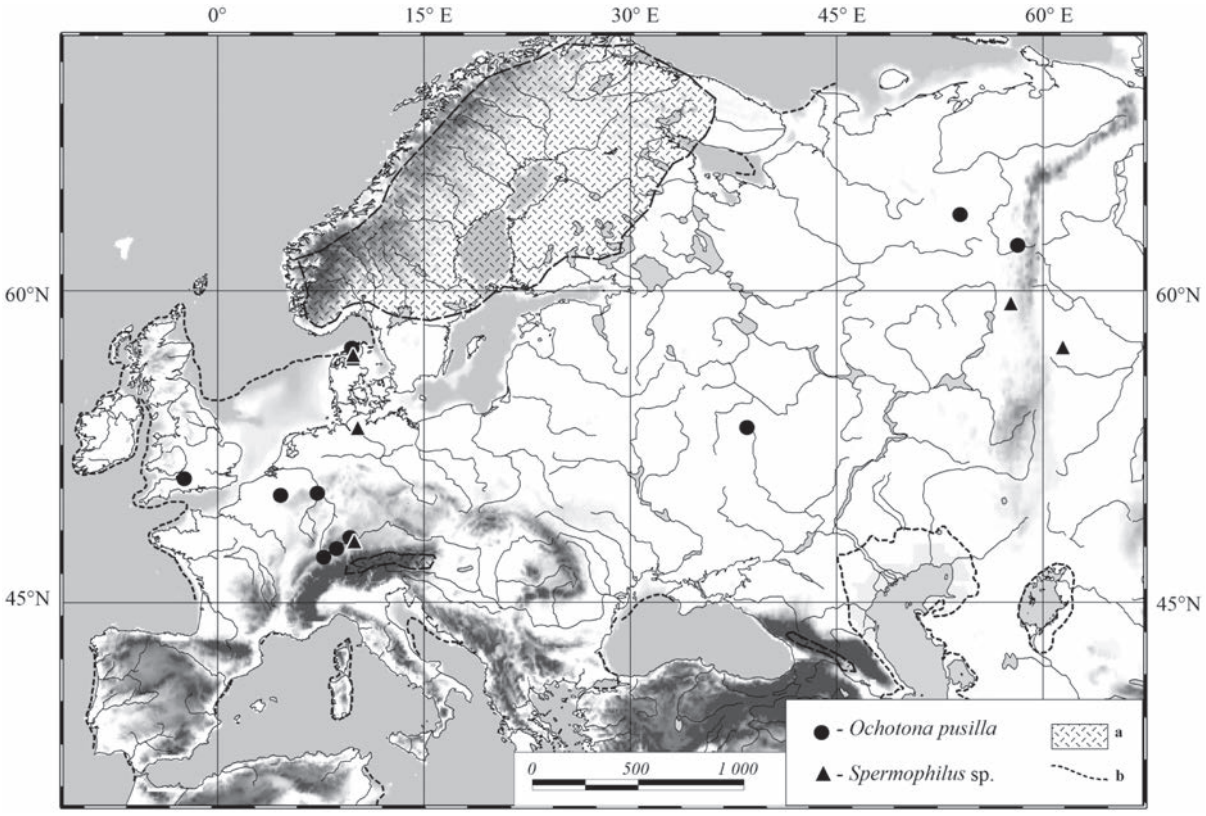

Fig. 4.43. *Steppe pika Ochotona pusilla and ground squirrel Spermophilus sp. localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

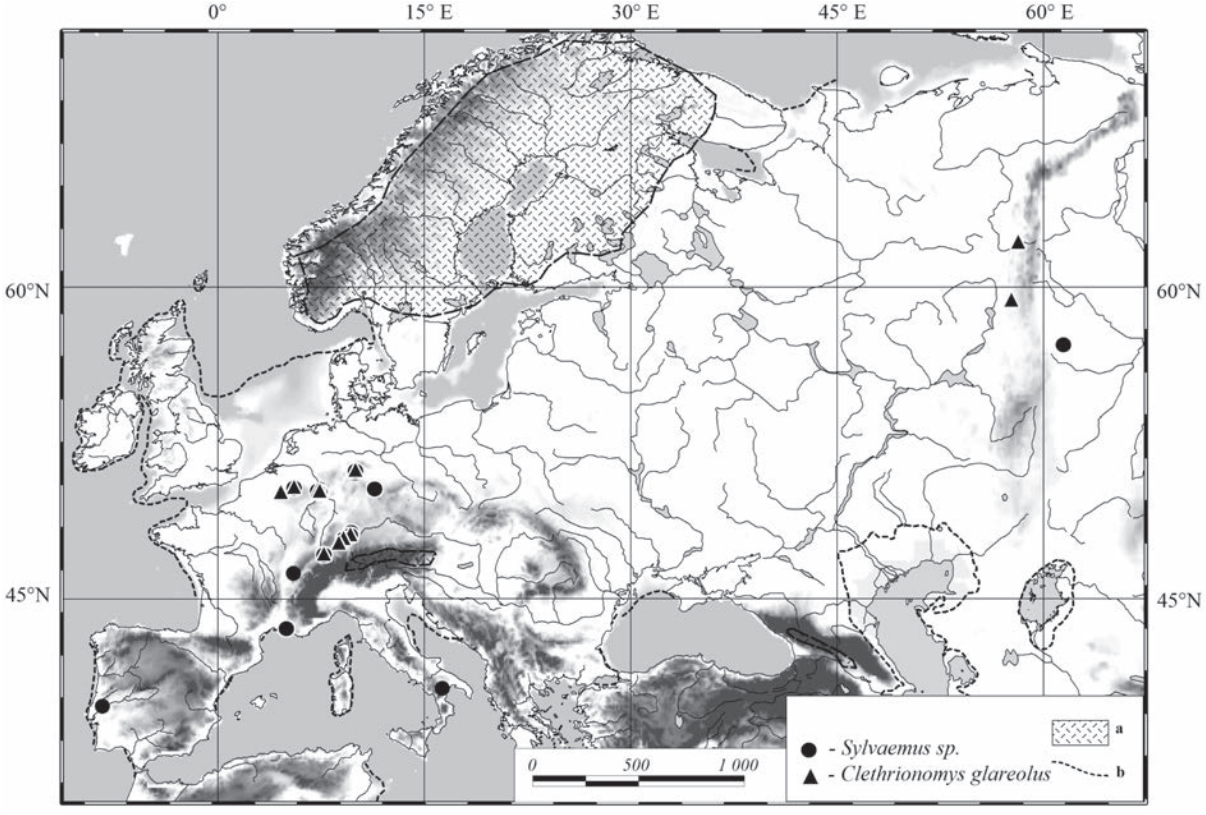

Fig. 4.44. *Wood mouse Sylvaemus sp. and bank vole Clethrionomys glareolus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

Forest mammals

Remains of typical forest species were found in only a few BAIC localities. Elk *Alces alces* sites were recorded only in the Rhine drainage basin, near the Alps, and in the Dniester drainage basin (Fig. 4.38). Elk now inhabits the taiga and mixed forests. It also penetrates into forest-tundra and forest-steppes. Such rare finds indicate a low number of forested areas in Europe during the BAIC, but could also be connected with the low quantity of data for this interval. Only a small number of sites with forest mouse remains *Sylvaemus* sp. were found. They are located mainly in Western Europe (on the Iberian and Apennine Peninsulas, in the Rhine drainage basin), and in the Urals (Fig. 4.44). The genus *Sylvaemus* includes several species. Most of these are adapted to nemoral forests. These locations of *Sylvaemus* finds indicate the absence or low distribution of forests of this type in the BAIC interval.

Several taiga species have been found in BAIC sites. Forest lemming *Myopus schisticolor* localities were found only in the Urals. Forest lemming now inhabits the plain and mountain taiga. Wolverine *Gulo gulo* sites, a typical taiga species, were recovered on the Jutland Peninsula, in the Middle Don River drainage basin, and in the Urals. These finds indicate areas with coniferous forests. Gray red-backed vole *Clethrionomys rufocanus*, the modern ranges of which are connected with taiga forests, were found only in the Urals. The common red-backed vole *Clethrionomys glareolus* has a wider modern range. During the BAIC its remains were recovered in the Urals and also in the Rhine drainage basin (Fig. 4.44).

Some mammal species found in BAIC localities indicate a forest-steppe environment. Thus, red deer *Cervus elaphus* was more common than taiga species during the BAIC and was found mostly in Western Europe (in the Rhine and Danube drainage basins, in the British Isles, in the Apennines), and also in the west of the Russian Plain in the Dniester drainage basin (Fig. 4.38). Earlier studies have shown that this typical forest-steppe animal was well adapted to the periglacial tundra-forest-steppe environments that existed during the LGM and the LGT (Markova *et al*., 1995, 2003). The roe deer *Capreolus capreolus* had a very similar distribution (Fig. 4.45).

The number of localities with forest mammal remains is lower than the number of steppe mammal localities and is comparable with the number of tundra mammal localities. This fact indicates that during the BAIC the distribution of open landscapes was significant. Forested areas were rather restricted in this time and connected with river basins and with mountains, and highlands.

Wild boar *Sus scrofa* finds were discovered only in Southwestern Europe (Fig. 4.46). Nowadays, wild boar lives in different types of forests, and inhabits forest-steppes. It prefers deciduous forests, especially oak and beach forests with wetlands and grasslands. In the mountains the wild boar inhabits mostly the forest belt. According to our data and also the data published earlier (Markova *et al*., 1995), *Sus scrofa* practically disappeared from Northern Eurasia during the last glaciation and survived the cold period in the southern mountain regions. Even in the BAIC interval, the position of wild boar localities indicates the rare occurrence of forests in Europe.

Mountain species

The remains of two typical mountain species were recovered in BAIC sites: chamois *Rupicapra rupicapra* and mountain goat *Capra ibex* (Figs. 4.47 and 4.48).

These animals are now distributed only in the Mediterranean mountains, including the Pyrenees, Massif Central, the Alps, the Balkans and the Caucasus. It seems that the chamois range was wider in the BAIC, because its remains were found in the Rhine basin. *Capra ibex* sites were found also in Western Europe, mostly in the Mediterranean.

Mammals of the 'mammoth' assemblage that became extinct during the Late Pleistocene and the Early Holocene

Mammoth *Mammuthus primigenius* remains were recovered in the central part of Western and Eastern Europe between 56° and 47°N (Fig. 4.49). Its range became more restricted than in the LGM and LGT. The ratio between the mammoth sites and the total number of BAIC localities became lower than during the LGM and LGT. This indicates the mammoth reaction to milder climatic conditions during 12,400–10,800 yrs BP. The southern boundary of the mammoth range retreated northward during the LGT and this tendency continued during the BAIC. Undoubtedly, the catastrophic collapse of the mammoth range was related, first of all, to degradation of the periglacial biome (called "hyperzone" by Velichko, 1972). This biome was characterized by highly productive herbaceous vegetation. During the terminal Pleistocene significant changes took place in the vegetation cover in Northern Eurasia. The mammoth diet changed to include plants of wet biotopes, in which the content of nutritious elements and mineral composition was lower than in a dry biotope vegetation (Ukraintseva, 1991). This change was quite unfavourable for the mammoths and was one of the reasons for a decrease in the mammoth range and resulted in mammoth extinction over vast areas during the terminal Pleistocene – Early Holocene.

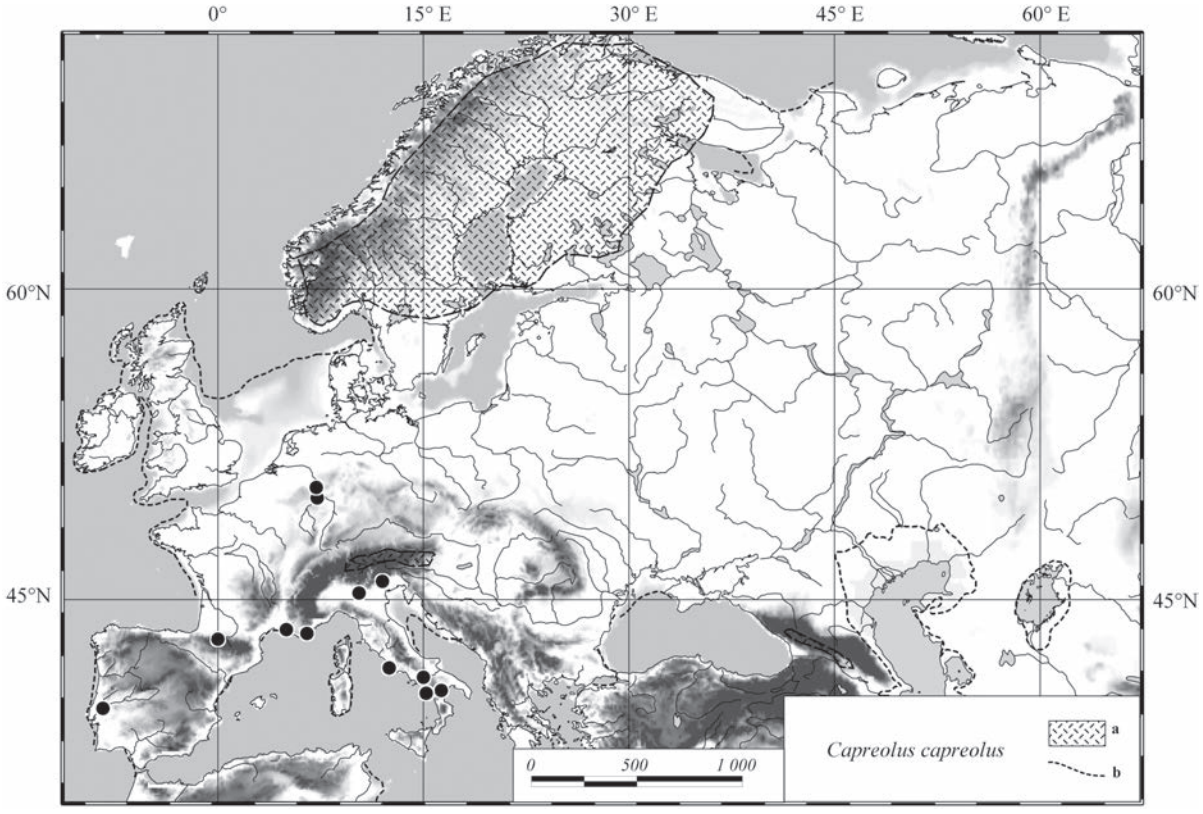

Fig. 4.45. *Roe deer Capreolus capreolus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

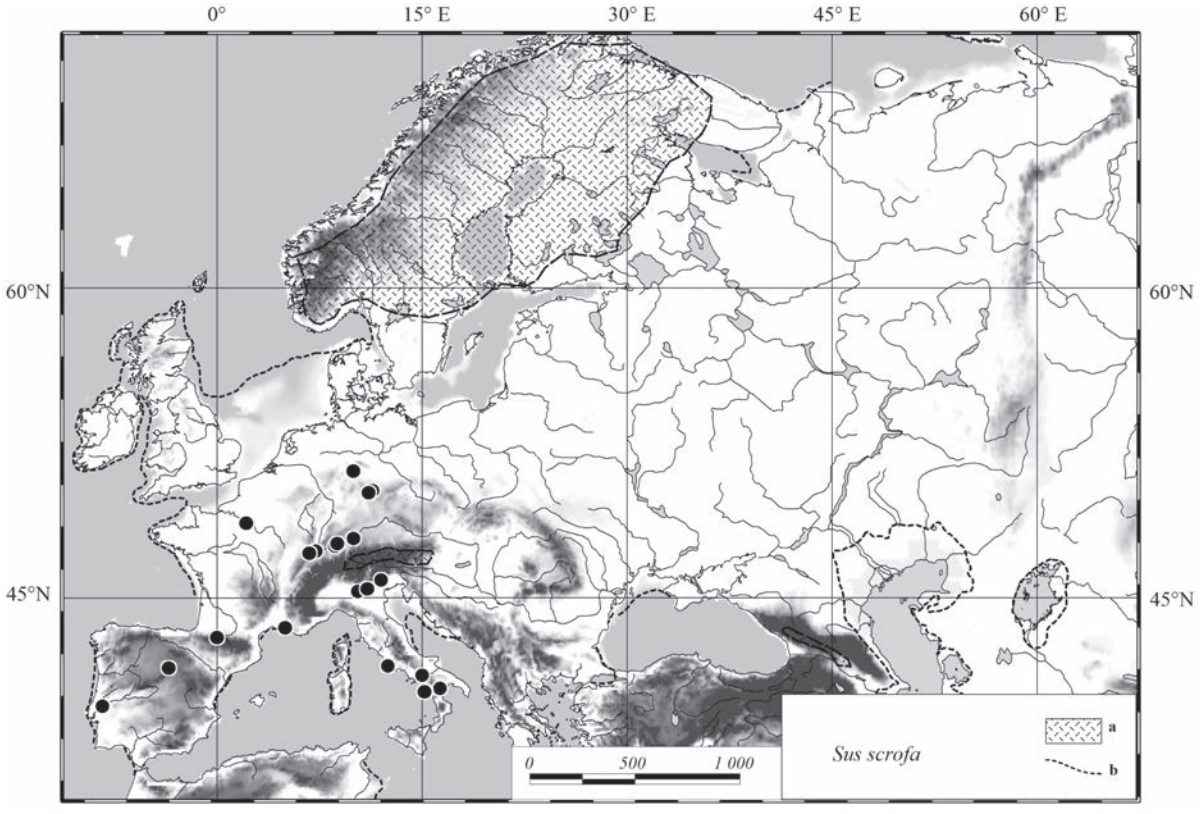

Fig. 4.46. *Wild boar Sus scrofa localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

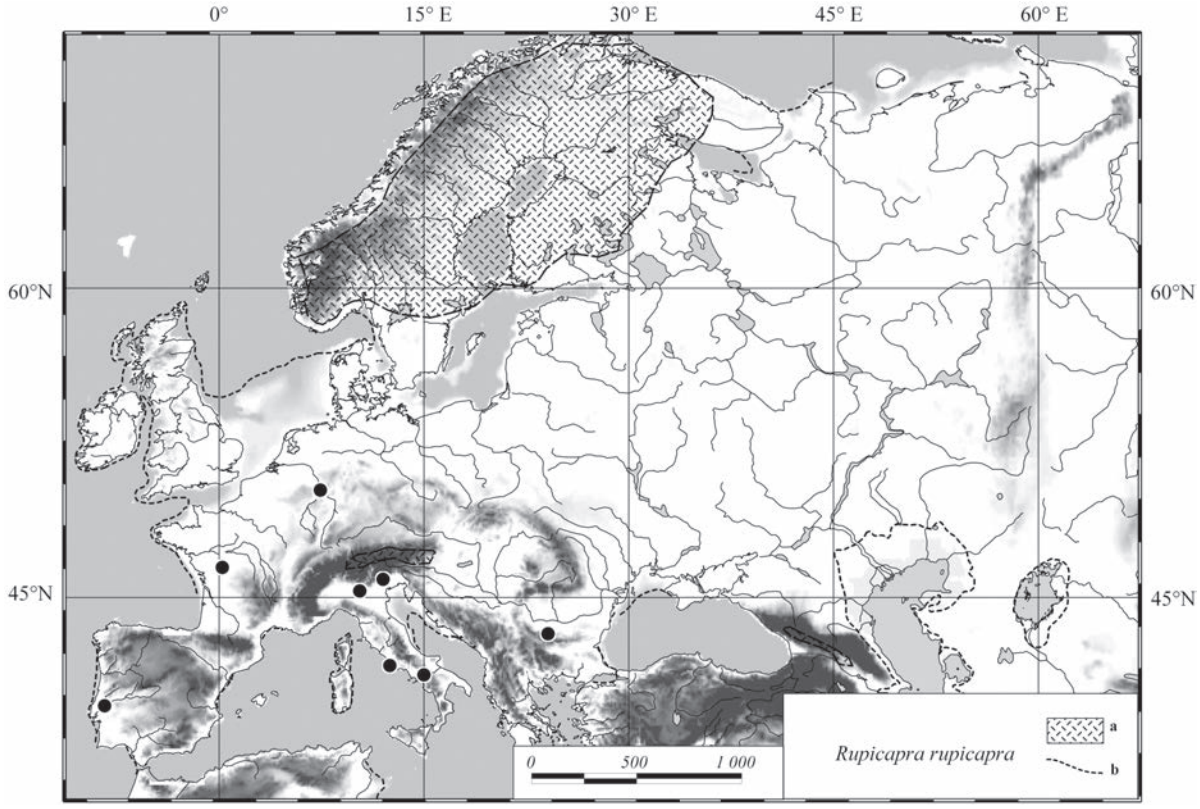

Fig. 4.47. *Chamois Rupicapra rupicapra localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

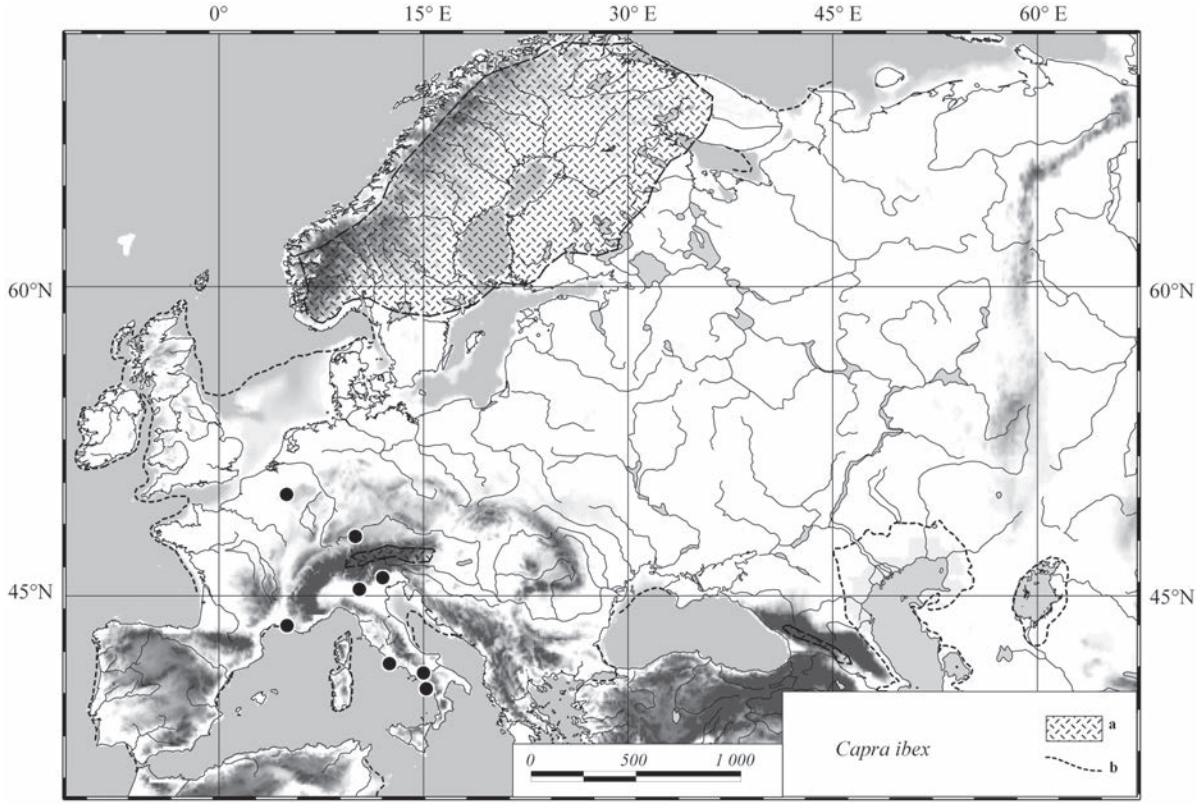

Fig. 4.48. *Mountain goat Capra ibex localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

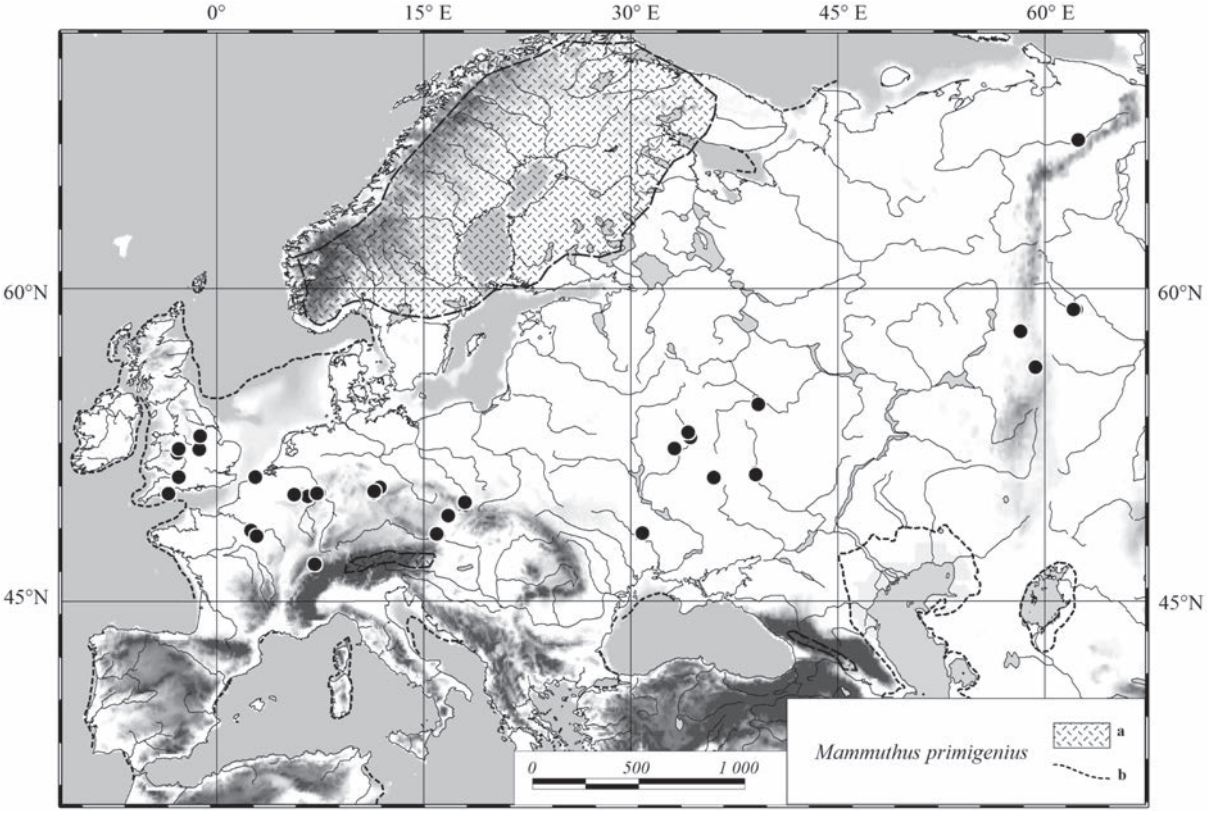

Fig. 4.49. *Mammoth Mammuthus primigenius localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

There are five BAIC sites with remains of woolly rhinoceros *Coelodonta antiquitatis*. They were found in the Urals and in the Rhine drainage basin (Fig. 4.50). The most favourable conditions for woolly rhinoceros probably existed in dry periglacial steppes (Vangengeim, 1977; Vereshchagin and Baryshnikov, 1980; Markova *et al.*, 1995; 2002). This typical 'mammoth complex' animal became rare in the BAIC, which indicates a reorganization of the environments and a decrease in the areas of the periglacial steppes. The rather low number of BAIC localities however prevents us to reconstruct a reliable picture of the woolly rhinoceros distribution.

Giant deer *Megaloceros giganteus* remains were found in several sites: in the Urals, in the British Isles, and on the Jutland Peninsula (Fig. 4.51). This animal was not abundant in the Late Pleistocene and was distributed mostly in the central and southern regions of Northern Eurasia, probably being limited mainly to highly-productive periglacial forest-steppes and grasslands. Its extinction resulted primarily from the devastation of relatively mesic herbaceous formations, and was aggravated by the low reproduction in the species, and hunting pressure by early hominines.

The cave lion *Panthera spelaea* was one of the largest cave carnivores, with a body mass of c. 250–300 kg. This predator was well adapted to periglacial forest-steppes and was widely distributed during the last glaciation (Vereshchagin, 1971). During the BAIC, a cave lion site was found only in the Ural Mountains (Fig. 4.51).

The most favourable conditions for aurochs *Bos primigenius* were those of forest-steppes and probably steppes (see previous chapters). The data of the PALEOFAUNA database indicate its distribution during the BAIC in the central regions of Europe (Fig. 4.52). Steppe bison *Bison priscus* was distributed a little wider and also mainly occupied Western Europe (Fig. 4.52).

Mammal assemblages during the BAIC

The low quantity of mammalian data related to the BAIC diminishes the possibilities of mammal assemblage reconstructions for Europe. However the principal picture of the mammal composition and distribution could be elucidated. Cluster analysis and the maps with index mammal ranges form the basis of these reconstructions. Five principal mammal assemblages were reconstructed for this interval (Fig. 4.53).

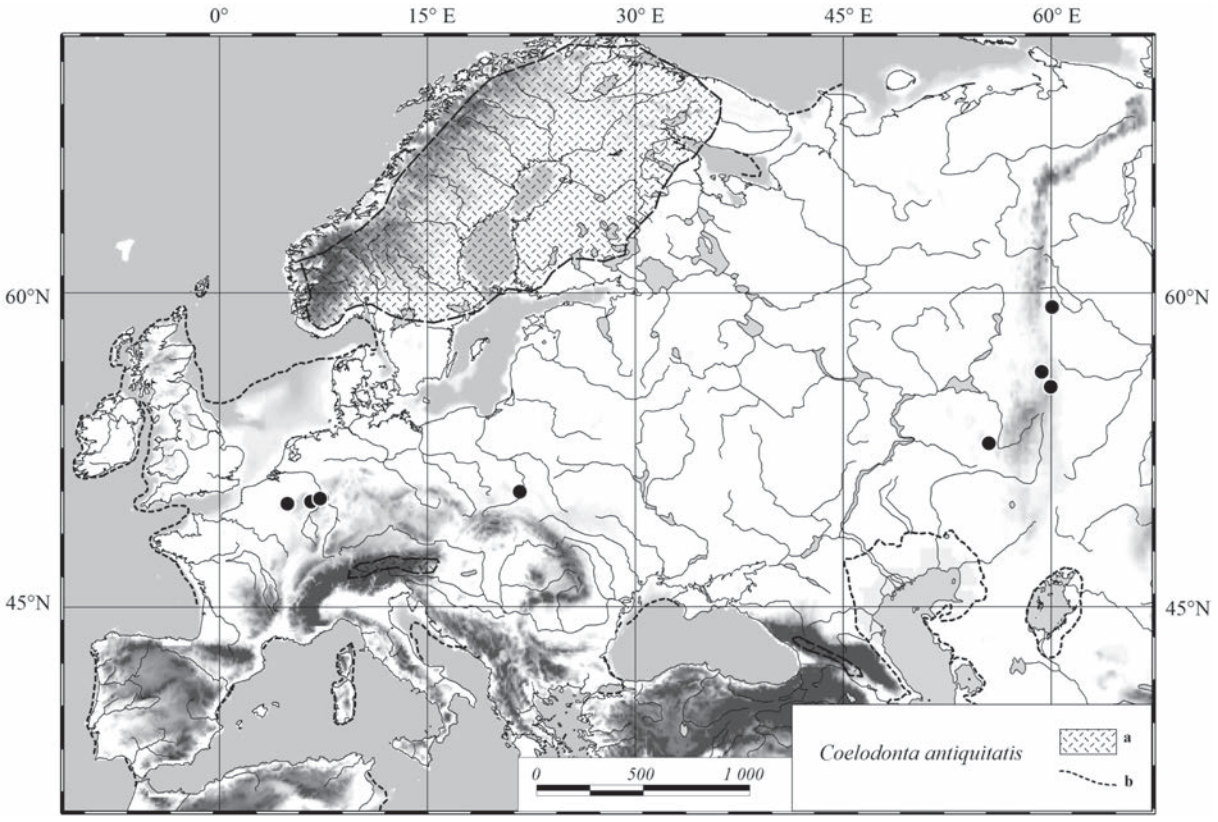

Fig. 4.50. *Woolly rhinoceros Coelodonta antiquitatis localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

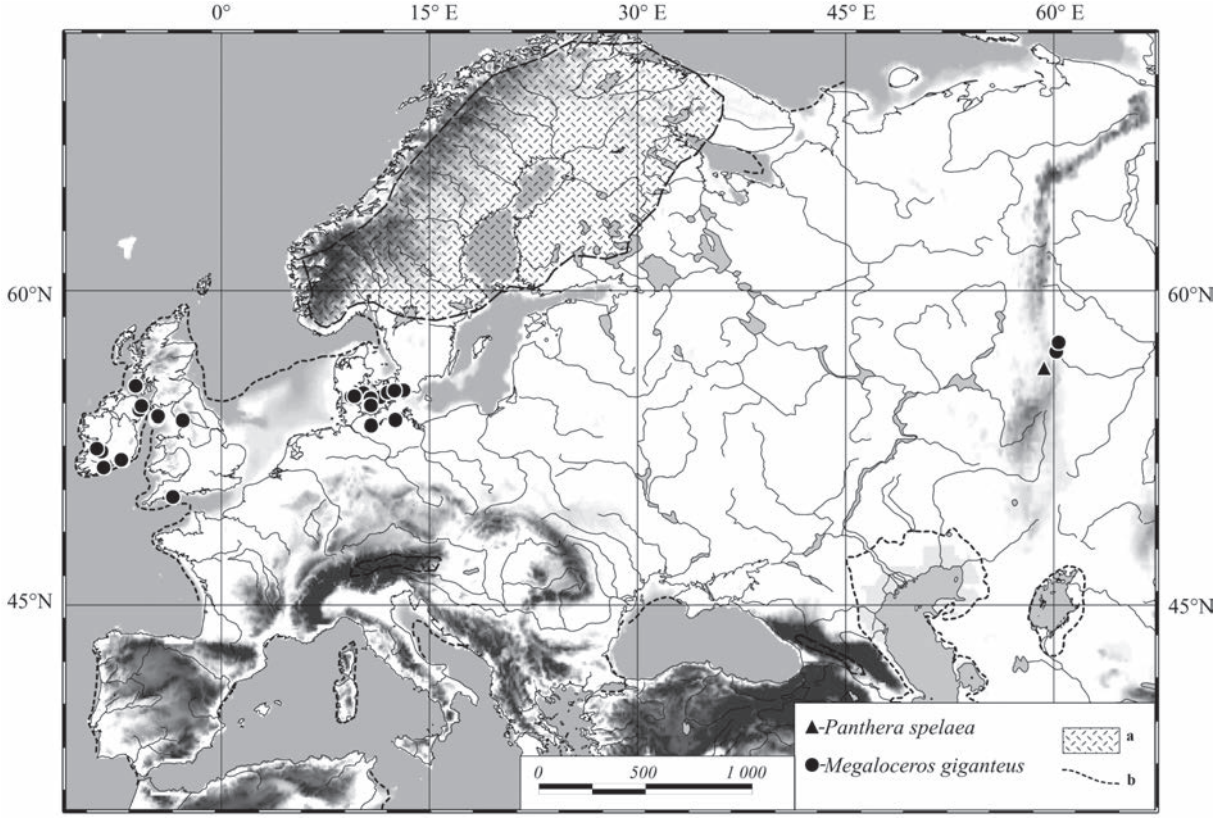

Fig. 4.51. *Giant deer Megaloceros giganteus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

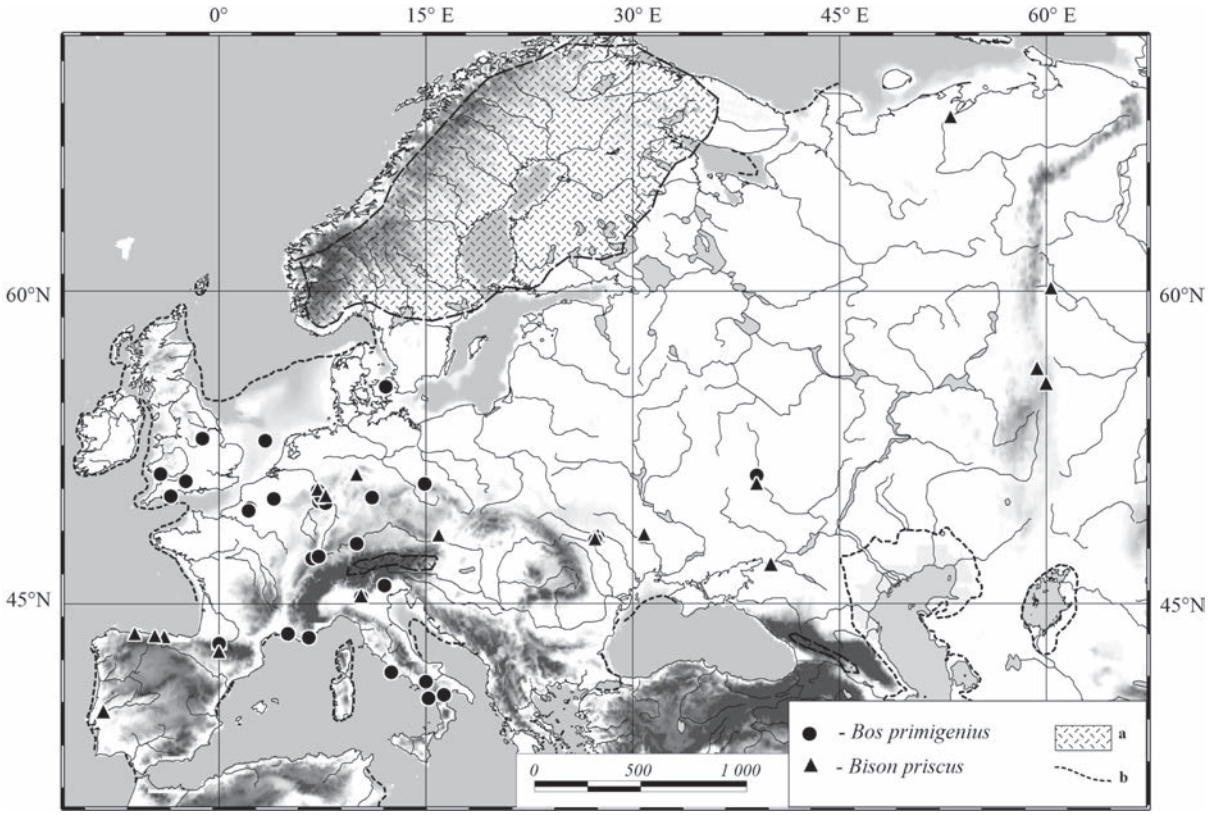

Fig. 4.52. *Aurochs Bos primigenius, steppe bison Bison priscus localities (12.4–10.8 kyr BP); a – ice sheets; b – coastline*

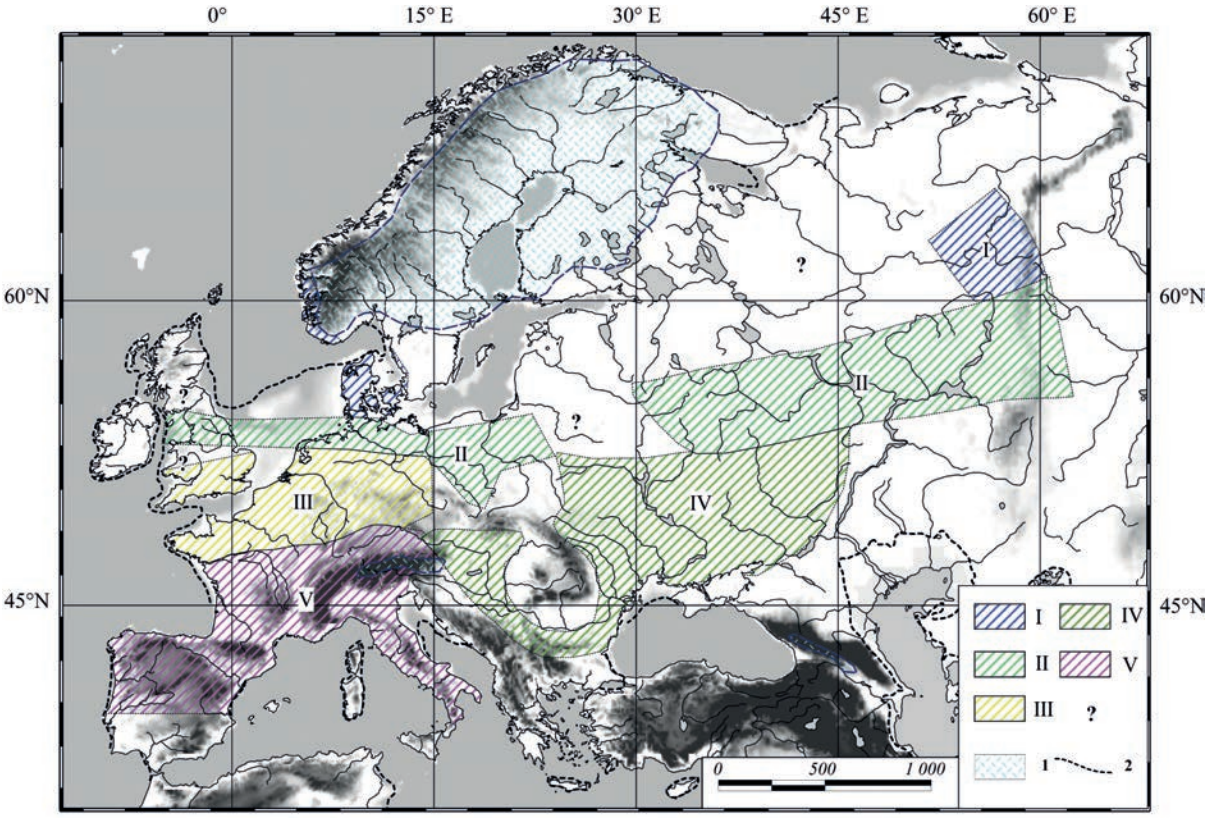

Fig. 4.53. *BAIC mammal assemblages: 1 – periglacial tundra-steppe assemblage; 2 – periglacial tundra-forest-steppe assemblage (north variant); 3 – periglacial tundra-forest-steppe assemblage (West European variant); 4 – periglacial forest-steppe assemblage; 5 – mountain forest and forest-steppe assemblage; a – ice sheet and mountain glacials; b – coastlines; ? – absence of data*

I. Periglacial tundra-steppe mammal assemblage

The assemblage of cluster 1 is based on finds from the Jutland Peninsula, the southwestern coast of Scandinavia, and in the Polar and North Urals. Only one site was found in Eastern Europe, in the Upper Don basin (Fig. 4.41), but this site, it seems, could belong to another assemblage. The absence of large animals there depends only on the taphonomic setting of the locality (Markova, 2000). The dominant species of this assemblage include several typical cold-adapted animals: collared and Siberian lemmings, Polar bear, narrow-skulled vole, and reindeer. The animals of open landscapes also were typical of this assemblage and were represented by steppe and yellow lemmings, the remains of which were found in the Urals. Saiga lived in the North Urals. Wild horse and steppe pika were more common in most localities. Their remains were found both on the Jutland Peninsula and in the Urals.

Mammoth and woolly rhinoceros, as well as aurochs and steppe bison were absent in the localities of this cluster, but this could be explained by the low number of sites in the northern part of Europe. Forest animals were not abundant and were represented only by species adapted to forest-tundra and taiga environments.

The low species richness of these sites shows severe climatic conditions in these areas. The data of cluster 1 are indicative of the tundra-steppe assemblage. The southern limit of this assemblage is undefined because of the few data.

II. Periglacial tundra-forest-steppe mammal assemblage (north variant)

This assemblage is similar in its structure and species composition as the first one (Table 4.3). The species composition includes first of all the sub-arctic and steppe mammals, but its species richness is significantly higher than in the first assemblage and totals 37 species, whereas in the first cluster only 20 taxa were distinguished.

Higher species richness indicates more comfortable environmental conditions for animals in these territories and a more moderate climate. Large herbivores (mammoth, woolly rhinoceros, aurochs, steppe bison, wild horse, and reindeer) were found in the sites. Giant deer also existed here. The *Megaloceros* westernmost site of Close-y-Garey was discovered on an Irish Sea island (which was part of the continent at that time), at 4.67°W.

Some forest species were identified in the assemblages of cluster 2, but they did not include mammals that inhabited broad-leaved forests (wild boar, pine vole, yellow-necked mouse, and others), nor animals typical of the forest steppe (roe and red deer). Thus, this assemblage is typical periglacial and demonstrates a mixture of cold-adapted, steppe and some forest mammals.

III. Periglacial tundra-forest-steppe assemblage (West European variant)

Nine localities belonging to cluster 3 are distributed in the British Isles, in the Rhine drainage basin, in the Ardennes, and the Rhine Shale Mountains (Fig. 4.53). These localities include 36 mammal species (Table 4.3). The most typical animals of these territories were woolly rhinoceros, reindeer, Polar fox, collared lemming, Norway lemming, narrow-skulled vole, water vole, root vole, and Polar hare. Mammoth was found only in the Rhine drainage basin. Large herbivores (steppe bison, aurochs, red deer, and wild horse) were rather common in these areas.

The finds of forest animals (elk, yellow-necked mouse, red-backed vole, field vole, beaver, and some others) indicate the distribution of shrub and forested areas. The mosaic structure of the landscapes is revealed by a persistence of not only tundra and forest animals, but also of typical steppe animals, including saiga (the remains of which were found in the British Isles), wild horse, and steppe pika. Steppe bison also preferred open landscapes.

The influence of the glaciation was strong in these areas, which is indicated by the dominant role of typical cold-adapted mammals (collared and Norway lemmings, Polar fox, reindeer, and narrow-skulled vole).

The specific features of this assemblage are indicated by the presence of Norway lemming, typical only of Western Europe, and chamois and mountain goat, found in the Ardennes. This assemblage also belonged to the non-analogue ones, which were widely distributed during the last glaciation in the Northern Hemisphere, and are characterized by the contemporaneous existence of tundra, forest and steppe animals.

IV. Periglacial forest-steppe mammal assemblage

This mammal complex was reconstructed on the basis of the data of clusters 4 and 5 (Table 4.3). The localities of these clusters can be found in the central and southern parts of Eastern Europe, and in Central Europe (Fig. 4.53). Indicative mammals of this assemblage include mammoth, steppe bison, aurochs, reindeer, red deer, roe deer, wild horse, cave hyena, and European hare.

Cold-adapted animals are few and include Polar fox and reindeer. Lemmings were absent in these areas. A high number of typical steppe animals were distribu-

ted in these areas, including wild horse, steppe pika, bobak marmot, jerboa, golden hamster (in the middle Danube basin), steppe lemming, and others. Forest animals were more typical of the Dniester basin, with high-elevated valleys, where the dominant species were red and roe deer, elk, and beaver.

The absence of the most typical cold-adapted animals, the presence of many steppe and forest animals allows us to reconstruct the periglacial forest-steppe assemblage. The finds of mammoth, cave carnivores, steppe bison and aurochs indicate the unique structure of this assemblage and its difference from the modern forest-steppe mammal assemblage.

V. Mountain forest and forest-steppe mammal assemblage

The dominant species of localities belonging to cluster 6 include wood mouse *Sylvaemus* sp., common mouse *A. sylvaticus*, aurochs, mountain goat, red deer, roe deer, Alpine marmot, wood cat, European lynx, chamois, and wild boar (Table 4.3). The area of this assemblage is located near the Alps, in the Massif Central, and on the Iberian and Apennine Peninsulas (Fig. 4.68). Possibly, this assemblage occupied also most of the Balkan Peninsula, but the BAIC data from this region are missing. The number of localities in cluster 6 is rather high and includes 15 sites.

Cold-adapted animals were not characteristic of this assemblage. Only a single find of *Dicrostonyx* was recovered just north of the Alps. Two sites with reindeer remains were found in the Pyrenees and near the Mediterranean coast. But this animal has high adaptive possibilities, migrating very intensively during the year and could exist in different landscapes.

Large herbivores such as mammoth and woolly rhinoceros were not found here, but giant deer fossils were discovered near the Mediterranean coast. Aurochs remains were found in most of the sites. Steppe bison fossils were encountered to a lesser degree. Wild horse localities concentrated mostly on the Mediterranean coast. The single find of saiga bones is also located in this area.

The list of forest species is very long and includes mouse *Sylvaemus*, red and roe deer, wood cat, common marten, weasel, pine vole, red-backed vole, fat dormouse, and garden dormouse. Wild boar *Sus scrofa* remains are very typical of this assemblage, and were not found in other assemblages of the BAIC. The complex of forest species includes many animals connected with broad-leaved forests (fat dormouse, garden dormouse, pine vole, wild boar and others) and indicates its distribution in some mountain belts of the Massif Central, the Alps, the Apennines, and the mountains of the Iberian Peninsula. Such typical mountain species as chamois *Rupicapra rupicapra* and Alpine goat *Capra ibex* were the index species of this assemblage, which is natural in these mountain regions. Mammals preferring open landscapes were also distributed in this area, and found comfortable biotopes in the unforested belt of the mountains. Wild horse, steppe bison, Alpine marmot, and even saiga remains were recovered in some of the localities. This assemblage we classified as mountain forest and forest-steppe assemblage. It resembles very much the LGT assemblage from the same territories. So, the core of the mammal fauna was rather constant here, and indicates only a very weak influence of the climate change.

Geographical variation of the mammal species richness

We have scant information only for the reconstruction of the mammal biodiversity in the BAIC. With this reservation there were at least 3 large regions with high species richness (Fig. 4.54): the middle and southern Urals, middle Europe, and southern Europe around the Alps. In the BAIC, biodiversity 'centres' were probably arranged approximately similar to the LGT.

Conclusions

The reconstructed picture of the BAIC mammal assemblages indicates the very beginning of the destruction of the 'mammoth' steppes or periglacial hyper-zone during 12.4–10.8 kyr BP, which reflects a climatic warming.

Typical tundra-adapted animals existed southward up to 52–54°N, but their density and ranges decreased compared to the LGM and LGT. The presence of forest species even in the northern part of Europe confirms the increase in forested areas in these regions. They alternated with open tundra-steppe environments, which were also distributed in these areas.

Steppe animals were distributed far to the west during 12.4–10.8 kyr BP, which indicates the existence of open periglacial tundra-forest-steppe, forest-steppe and steppe even in Western Europe, but their areas became smaller after the beginning of the Bølling Interstadial and probable had an 'island' character.

Typical representatives of the 'mammoth' complex were distributed in Europe, including mammoth, woolly rhinoceros, *Bison priscus*, *Bos primigenius*, *Megaloceros giganteus* and others. But their finds became rather rare during the BAIC. Some of these survived only in the mountain regions (cave lion).

The study of BAIC mammal assemblages demonstrates that the non-analogue faunas continued to exist in the central and northern regions of Europe. These assem-

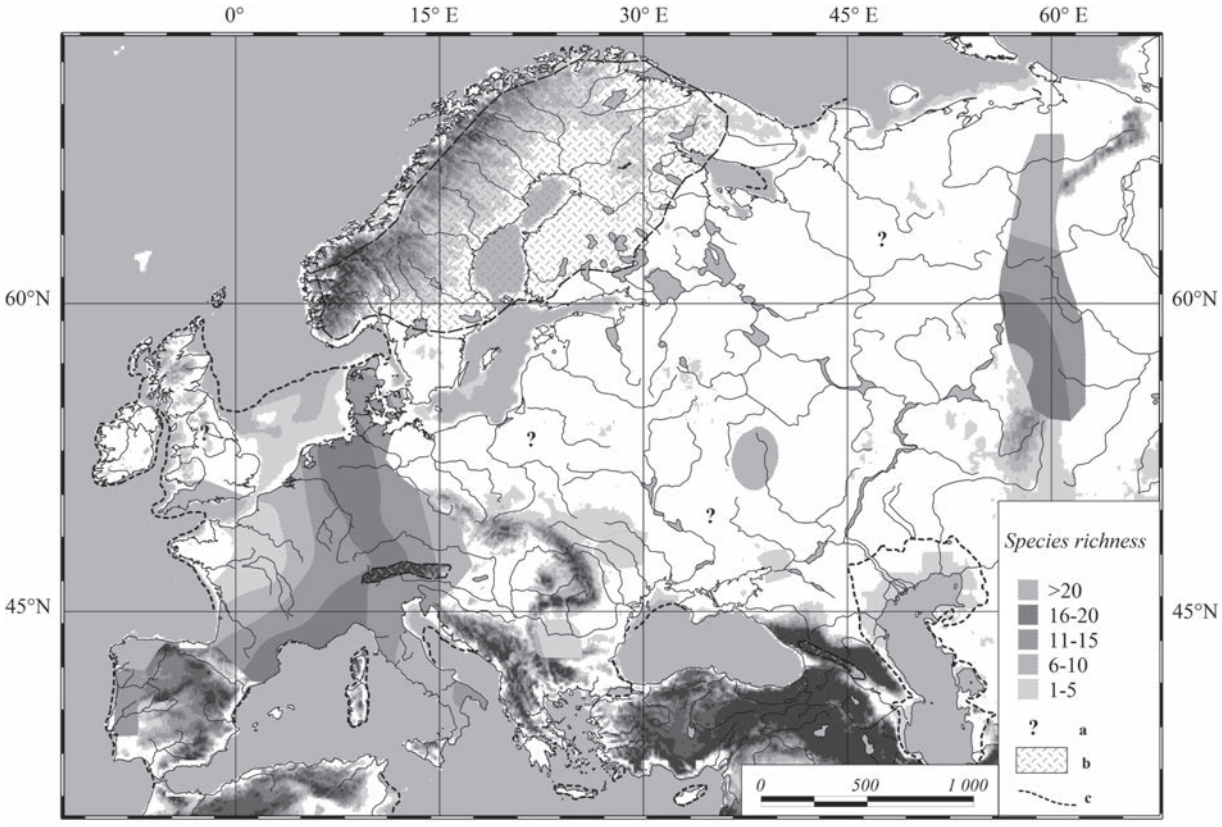

Fig. 4.54. *Reconstruction of geographical variation of the BAIC mammal species richness; a – absence of data, b – ice sheets, c – coastline*

blages were generated earlier and were the result of the rearrangement of the mammal species ranges in different directions and on different scales, which indicates that each mammal responded individually to climatic and environmental changes. Such rearrangements can also be observed in the Late Pleistocene data of North America (FAUNMAP Working Group, 1996; Webb *et al.*, 2003).

The influence of the Scandinavian ice sheet became very insignificant in the Mediterranean. The fauna of the Massif Central, the Apennines and the Iberian Peninsula showed no noticeable traces of the cooling.

4.4. MAMMAL ASSEMBLAGES OF THE YOUNGER DRYAS (YD) (<10.9 – ⩾10.2 KYR BP)

Nikolai Smirnov

The Younger Dryas was a short period lasting about 700 years; however it is of special significance for understanding the process of the dynamics of the mammal communities composition and structures registered during the Pleistocene-Holocene transition. This time span corresponds to the last remarkable climatic oscillation, which was terminated by a return of the cold. Characteristics of the biota during this 700-year interval probably should be regarded not as a rigid single (static) picture, but as that formed by summarized reactions of the dif-

ferent species, caused by previous steep shifts from warm to cold, that resulted in the collapse of the former biota characteristic of the Late Pleistocene. An understanding of the nature of the Younger Dryas is also important as a standpoint to be compared with the beginning of the Holocene.

The database contains 26 sites covering the whole territory of Europe and may be used to characterize mammals of the Younger Dryas (Figs. 4.55–4.71). Among these, only 5 taxa lists include information about 15 (or more) species. Three site lists were composed of 11 species, 10 numbered from 2 to 8 species, whereas in each of the remaining 8 points only 1 mammal species was registered.

Thus, the data on the Younger Dryas period are rather poor. Why? Several answers may be possible. It is probably due to the shortness of the time interval. For example, the LGM period lasted about 7000 years, and 145 sites in the database are dated to it, making 14.5 sites per span of 700 years. For the LGT, the corresponding value is 7.7. That is, the relative number of sites representing the Younger Dryas actually is higher than the number of sites dated to the LGM and LGT. Thus, there does not seem to be a special reason, and the low number of sites dated to the Younger Dryas probably results mainly from the short duration of the period.

All site taxa lists numbered in total 60 mammal species, belonging to several orders. There were 2 species of insectivores (*Talpa europaea*, *Sorex araneus*), and 3 lagomorphs (*Ochotona pusilla*, *Lepus timidus*, *Lepus europaeus*). Rodents were represented by 29 species: *Sciurus vulgaris*, *Marmota bobak*, *Spermophilus superciliosus*, *Castor fiber*, *Glis glis*, *Eliomys quercitinus*, *Sylvaemus sylvaticus*, *A. flavicollis*, *Mus mus*, *Ellobius talpinus*, *Cricetus cricetus*, *Cricetulus migratorius*, *Allocricetulus eversmanni*, *Dicrostonyx torquatus*, *Lemmus lemmus*, *Lagurus lagurus*, *Eolagurus luteus*, *Clethrionomys glareolus*, *Cl. rufocanus*, *Cl. rutilus*, *Arvicola terrestris*, *Microtus agrestis*, *M. (Terricola) savii*, *M. oeconomus*, *M. nivalis*, *M. gregalis*, *M. arvalis*, *Allactaga major*, and *Nannospalax leucodon.* Thirteen mammal species were carnivourous: *Canis lupus*, *Vulpes lagopus*, *Vulpes corsac*, *V. vulpes*, *Ursus arctos*, *U. maritimus*, *Mustela erminaea*, *M. nivalis*, *Meles meles*, *Crocuta crocuta spelaea*, *Felis silvestris*, *Lynx lynx*, and *Panthera spelaea*. One proboscidean: *Mammuthus primigenius*, 2 perissodactyles: *Equus hydruntinus* and *Equus* sp. and there were also 10 mammals belonging to the ungulates: *Sus scrofa*, *Megaloceros giganteus*, *Cervus elaphus*, *Rangifer tarandus*, *Capreolus capreolus*, *Bos primigenius*, *Bison priscus*, *Carpa sibirica*, *Rupicarpa rupicarpa*, and *Saiga tatarica.*

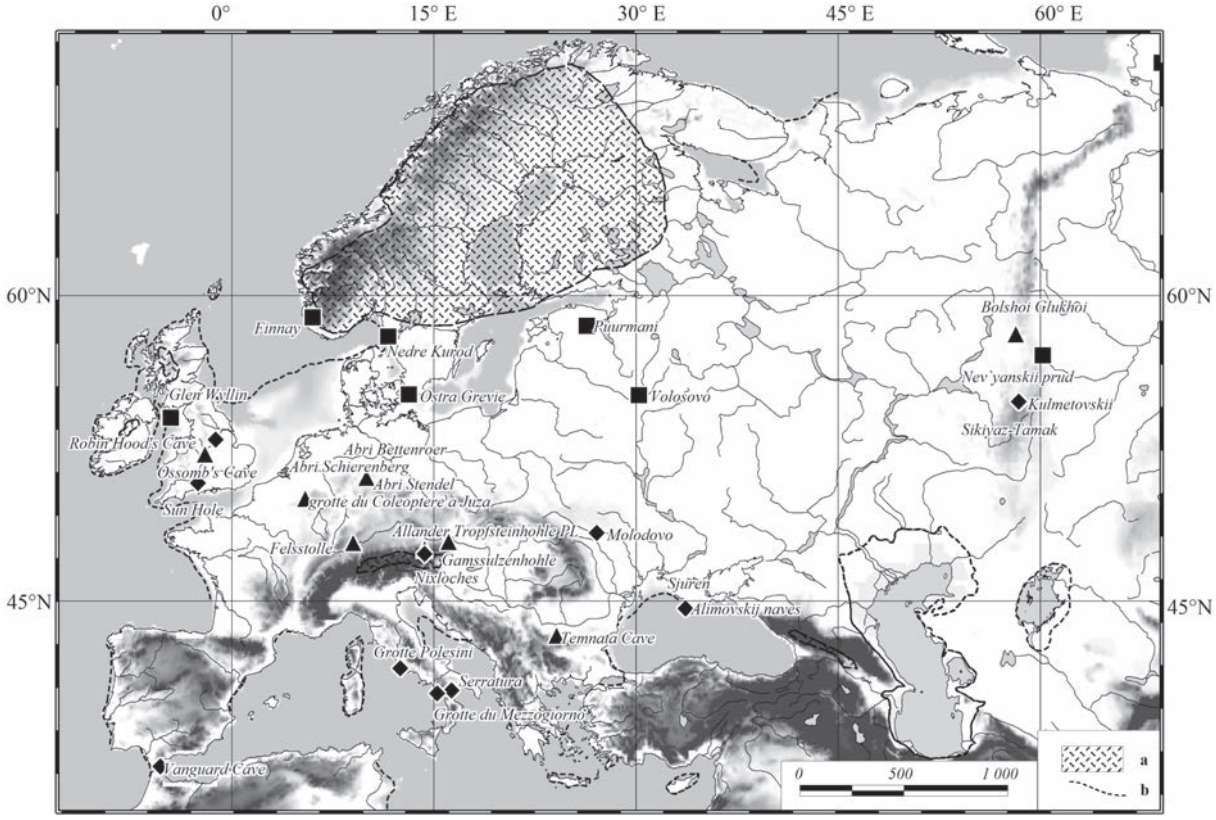

Fig. 4.55. *Mammal localities of the Younger Dryas*

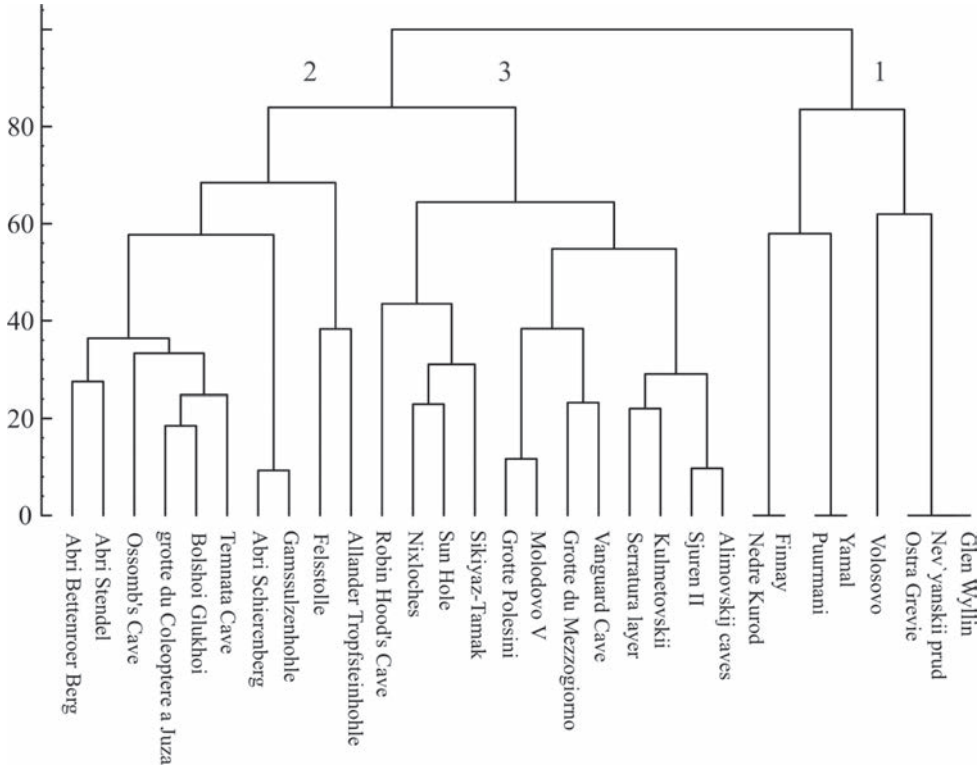

Fig. 4.56. *The results of cluster analysis of mammal localities in the Younger Dryas*[6]

However, the total amount of information is clearly insufficient to present adequate fauna characteristics, even for the main regions of Europe. Cluster analysis was also not very helpful, as it led to the formation of groups reflecting taphonomical characteristics of the sites concerned, but not the nature of the mammal communities. One cluster comprises cave sites with abundant rodent remains; another included sites with numerous bones of ungulates and carnivores, but few rodent remains, whereas a third showed sites containing only ungulates and mammoth fossils. That made us to interpret the species lists taking into account the sites situated relatively near to each other. And the main question discussed for the Younger Dryas was the following: what is the similarity level between the faunas of certain regions. Namely, those dated to the Younger Dryas period, did they maintain the general features of the Late-Pleistocene communities, or did they seem to look similar to the Holocene complexes.

Species, characteristic to the Pleistocene and becoming extinct during the Holocene

Mammuthus primigenius was the most characteristic Late Pleistocene species. However, its fossils were registered only in two sites of the interval, both situated in the north of the territory: one in the Baltic region, another on the Jamal Peninsula (just off the top right corner of the map) (Fig. 4.57).

Other mammal species found in the Younger Dryas sites were *Bison priscus*, *Panthera spelaea*, and *Megaloceros giganteus*. The latter was registered in 4 sites, three of which are situated in the Middle and South Urals, and 1 (Glen Wyllin) in Western Europe (Fig. 4.57). *Bison* remains were found in only one site, in the South Ural Mountains. The cave carnivore *Panthera spelaea* was found also in elevated regions, the first one in the Crimea, and the second in the site of Allander Tropfsteinhohle (Southern Germany).

Tundra mammal species

Mammals, the descendants of which now inhabit the tundra zone, during the Younger Dryas were still found significantly further south than their modern ranges. This group included 4 species. For example, *Dicrostonyx torquatus* fossils were found in the Middle Urals, in the British Isles, in the Ardennes (modern Belgium), and in Germany (Schwabische Alb) (Cordy, 1974; Collcutt *et al*., 1981; Coard and Chamberlain, 1999) (Fig. 4.58).

[6] The statistical and mathematical treatment of YD data and also the maps of mammal finds were done by Andrey Puzachenko.

Table 4.4

Characteristics of the basic site groups (1, 2, 3).
The taxa that are cluster indicators (frequency of occurrence in cluster (%))

Taxon	Complex			Taxon	Complex		
	1	2	3		1	2	3
Sorex sp. – shrew	0	20	0	*Microtus agrestis* – field vole	0	0	20
Talpa sp. – mole	0	0	20	*Microtus arvalis* – common vole	0	0	60
Homo sapiens – modern human	0	20	0	*Microtus oeconomus* – root vole	0	0	20
Ochotona pusilla – steppe pika	0	0	100	*Microtus gregalis* – narrow-skulled vole	0	0	20
Lepus tanaiticus – Don hare	0	20	0	*Sicista betulina* – northern birch mouse	0	0	20
Lepus europaeus – European hare	0	0	60	*Sicista subtilis* – southern birch mouse	0	0	20
Sciurus vulgaris – red squirrel	0	0	20	*Allactaga major* – great jerboa	0	0	60
Marmota bobak – bobak marmot	0	20	20	Nannospalax leucodon – lesser mole rate	0	0	20
Spermophilus superciliosus – suslik "supercilious"	0	0	40	*Canis lupus* – wolf	25	0	20
				Vulpes lagopus – Polar fox	0	20	0
Spermophilus major – great suslik	0	20	0	*Vulpes vulpes* – common red fox	0	0	40
Castor fiber – beaver	0	20	0	*Vulpes corsac* – corsac fox	0	0	20
Allocricetulus eversmanni – Eversmann hamster	0	0	40	*Ursus arctos* – brown bear	0	0	40
				Mustela erminea – ermine stoat	0	20	0
Sylvaemus flavicollis – yellow-necked mouse	0	0	20	*Meles meles* – badger	0	0	20
Sylvaemus sylvaticus – wood mouse	0	0	60	*Crocuta crocuta spelaea* – cave hyena	0	0	20
Mus musculus – house mouse	0	0	20	*Lynx* sp. – lynx	0	0	20
Ellobius talpinus northern mole-vole	0	0	40	Panthera spelaea – cave lion	0	0	20
Cricetus cricetus – common hamster	0	40	80	*Mammuthus primigenius* – woolly mammoth	50	0	0
Cricetulus migratorius – grey hamster	0	0	40				
Mesocricetus newtoni – Rumanian hamster	0	0	20	*Equus* sp. – wild horse	50	20	40
Dicrostonyx torquatus – collared lemming	0	0	20	Equus hydruntinus – Pleistocene ass	0	0	20
Lemmus sibiricus – Siberian lemming	25	0	20	*Sus scrofa* – wild boar	50	0	0
Lagurus lagurus – steppe lemming	0	0	40	*Megaloceros giganteus* – giant deer	0	80	0
Eolagurus luteus – yellow steppe lemming	0	0	40	*Cervus elaphus* – red deer	25	0	40
Chionomys nivalis – snow vole	0	0	20	*Rangifer tarandus* – reindeer	25	20	0
Clethrionomys glareolus – red-backed vole	0	0	60	*Capreolus capreolus* – roe deer	0	20	40
Clethrionomys rutilus northern red-backed vole	0	0	25	*Bison priscus* – steppe bison	0	20	0
				Capra sp. – goat	25	0	20
Clethrionomys rufocanus – grey red-backed vole	0	0	20	*Rupicapra rupicapra* – chmois	0	0	20
Arvicola terrestris – water vole	0	0	60	*Saiga tatarica* – saiga	0	20	40

The site in the Urals included also *Lemmus* bones. In addition, *Lemmus* was found in the site of Volosovo, the northernmost point of the Russian Plain (55°N), which contained mammal remains dated to the examined time interval (Fig. 4.58).

Bones of the reindeer *Rangifer tarandus* were also recorded at the same latitude (in the South Urals), and even further south and west, between the Carpathians and the Dnieper River (49°N) (Fig. 4.59). In Western Europe, reindeer remains were found in Southern

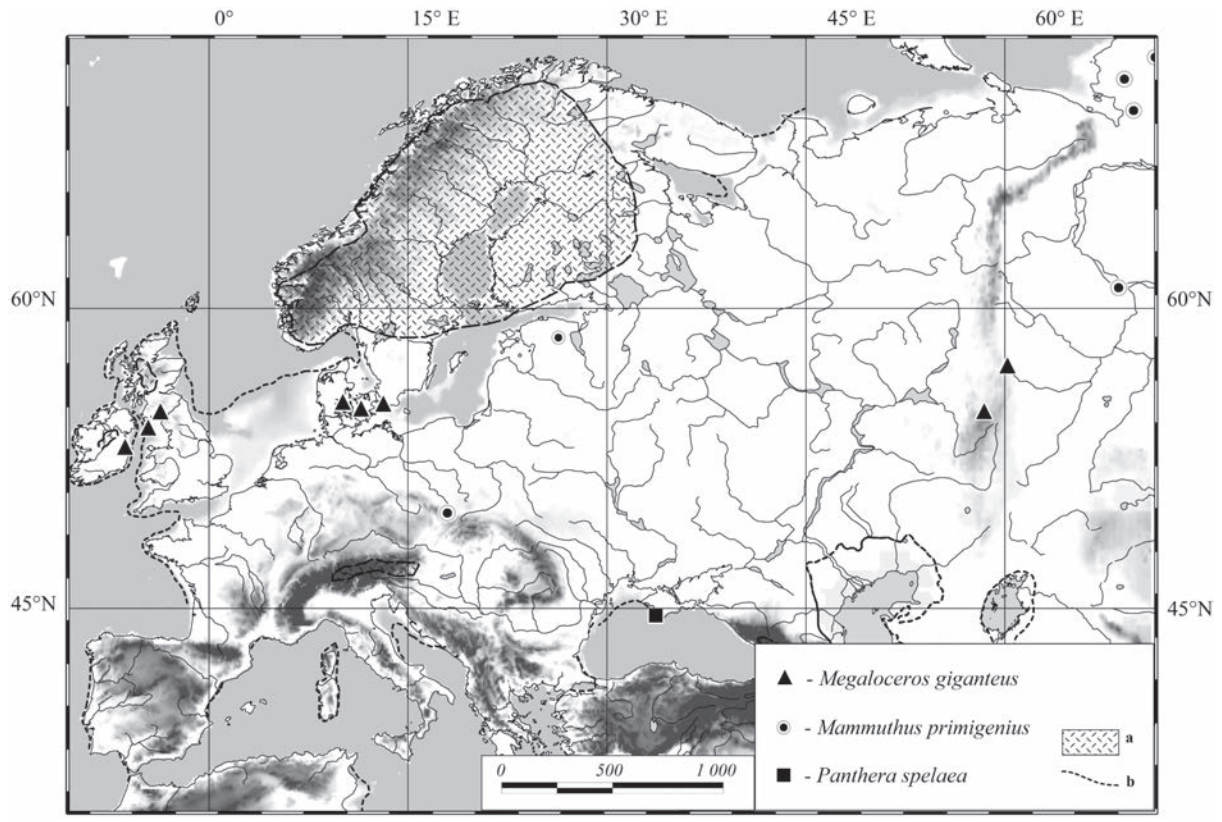

Fig. 4.57. *Woolly mammoth Mammuthus primigenius, cave lion Panthera spelaea, giant deer Megaloceros giganteus localities during the Younger Dryas; a – ice sheets; b – coastline*

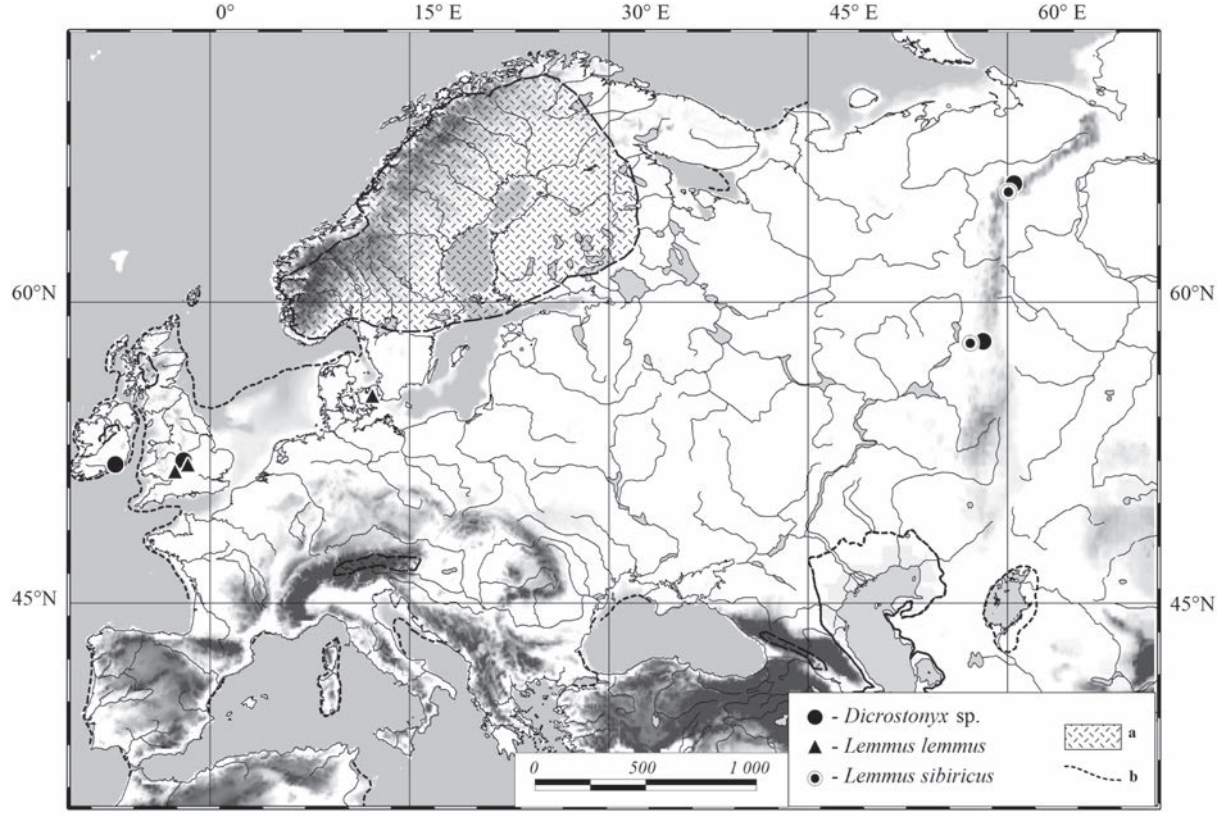

Fig. 4.58. *Collared lemming Dicrostonyx torquatus, Siberian lemming Lemmus sibiricus and Norway lemming Lemmus lemmus localities during the Younger Dryas; a – ice sheets; b – coastline*

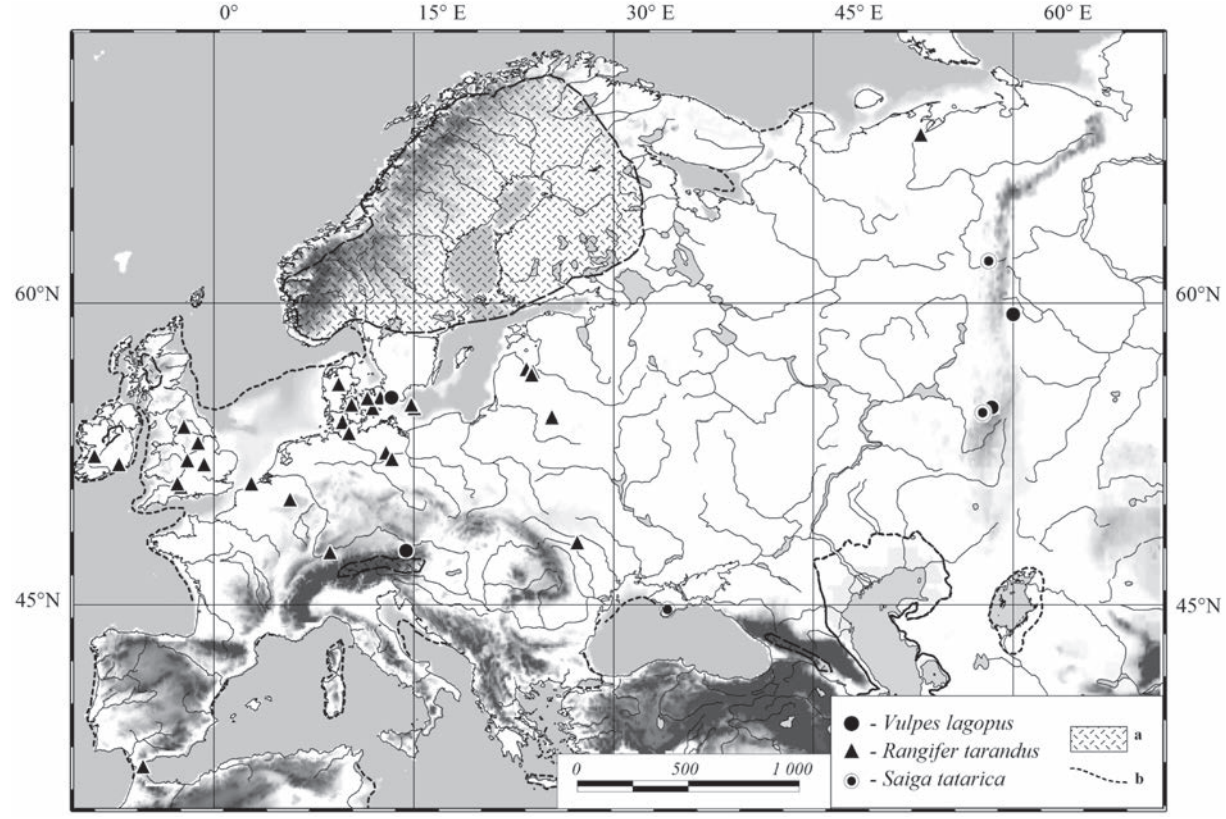

Fig. 4.59. *Reindeer Rangifer tarandus localities during the Younger Dryas; a – ice sheets; b – coastline*

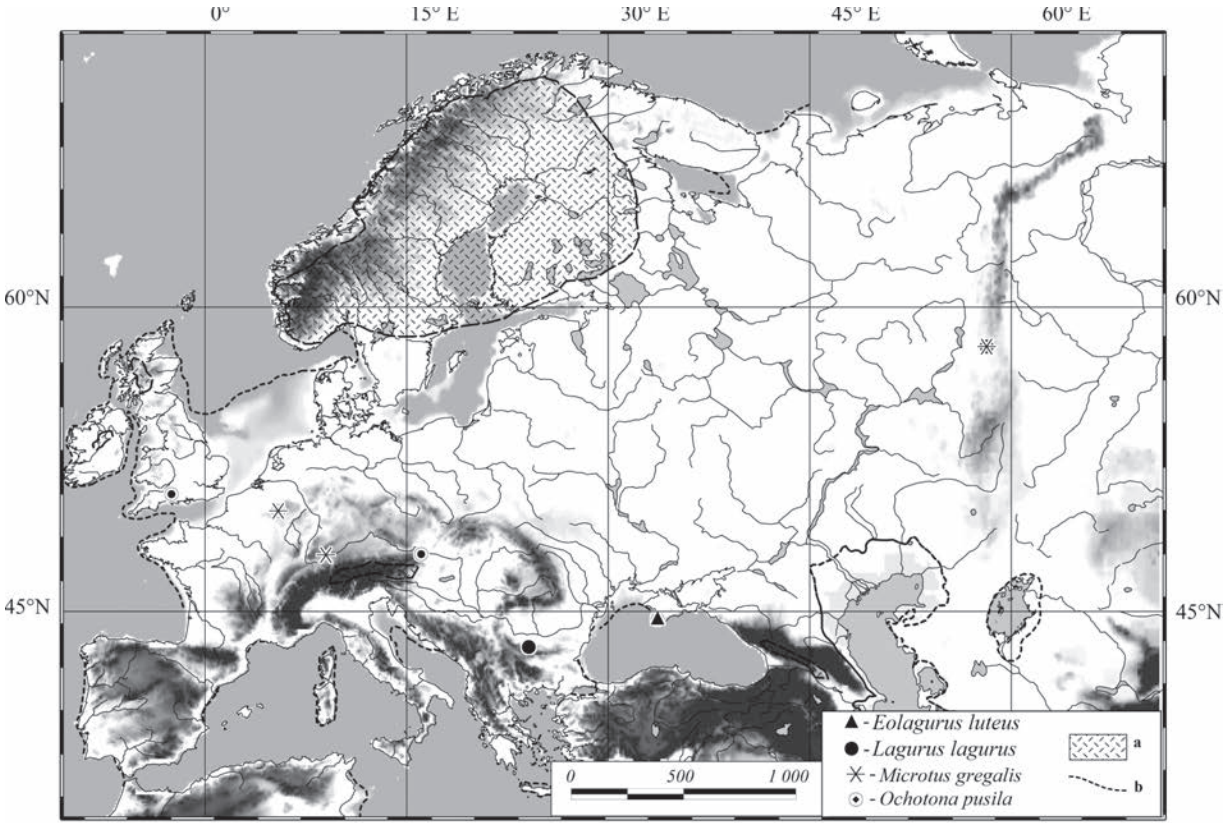

Fig. 4.60. *Steppe pika Ochotona pusilla, steppe lemmings Lagurus lagurus, yellow steppe lemming Eolagurus luteus, and narrow-skulled vole Microtus gregalis localities during the Younger Dryas; a – ice sheets; b – coastline*

England. The Polar fox, *Vulpes lagopus*, was registered in one site of this time situated in the very east of Europe, in the South Ural Mountains, and one site in Austria (Fig. 4.59).

Thus, the species of this group, now regarded as tundra inhabitants, were found in Younger Dryas sites in the British Isles, in the north of Western and Central Europe, and were rare enough in middle Eastern Europe. The majority of the sites including these mammals were situated in the very east of Europe, in the Urals.

Steppe species

Fossils of these species were found in sites of the Younger Dryas situated both west and north of the species modern ranges. This group numbered 13 species, namely *Saiga tatarica*, *Vulpes corsac*, *Ochotona pusilla*, *Microtus gregalis*, *Marmota bobak*, *Spermophilus superciliosus*, *Lagurus lagurus*, *Eolagurus luteus*, *Cricetulus migratorius*, *Allocricetulus eversmanni*, *Allactaga major*, *Equus hydruntinus*, and *Equus* sp. (Fig. 4.60).

The steppe pika *Ochotona pusilla* had a vast range in the Late Pleistocene. It was recorded in all sites of the Younger Dryas period marked for abundant fossils of small mammals: in the British Isles, in Belgium, in the Austrian Alps, the Balkans, the Crimea, and the Middle Urals (Fig. 4.60). Fossils of bobak marmot *Marmota bobak* were marked only in the South Urals and the Crimea.

Steppe lemming *Lagurus lagurus* was one of the most distinctive species, typical of the steppe zonal complexes; its remains were registered in sites in the Balkans and in the Middle Urals. However, we can assert that during the Younger Dryas, the sagebrush vole would have inhabited also many intermediate regions, namely the Urals and Trans-Urals south of the mentioned site in the Middle Urals (Fig. 4.60).

Grey hamster *Cricetulus migratorius*, similar to the sagebrush vole, has been registered in sites in the Balkans and Middle Urals. Probably one should regard these occurrences as relicts of the former Pleistocene vast species range. During the Younger Dryas interval, the grey hamster probably still continued to inhabit some intermediate regions, but without new additional data, it was not possible to make reconstructions of the ranges for the huge and diversified territory between the Balkans and the Urals.

The narrow-skulled vole *Microtus gregalis* was distributed extremely wide during the LGM, but among the sites of the Younger Dryas it was found only in a few locations in Western Europe (Southern England, Belgium, and Germany) and in the Middle Urals. However, we regard this as being due to the fact that sites of this age are not yet known from the South Urals and Trans-Urals. In these areas, the narrow-skulled voles were quite abundant both during the LGM and later, and in the Trans-Ural steppes where they are still present. In the Crimean sites of the Younger Dryas, the species was absent, though it was marked in the region previously (Fig. 4.60).

Fossils of the Younger Dryas identified as *Ellobius talpinus*, *Allocricetulus eversmanni*, *Allactaga major*, *Eolagurus luteus*, *Saiga tatarica*, *Equus hydruntinus*, *Equus* sp. and *Vulpes corsac* were registered only in the Crimea. However, remains of *Ellobius talpinus*, *Allocricetulus eversmanni*, *Allactaga major* and *Eolagurus luteus* were found in the South Trans-Urals, in layers ^{14}C dated to the intervals both preceding and following the Younger Dryas; thus they probably inhabited this region during the period at stake too. Only Balkan sites included remains of *Mesocricetus newtoni* and *Nannospalax leucodon*. Other species, namely *Cricetulus migratorius*, *Allactaga major*, *Lagurus lagurus* and *Ochotona pusilla*, were also registered in the Balkan sites. Judging from the data on Temnata Cave, layer 3, these mammals composed the bulk of the community there, though some forest species were present, too.

Fossils of *Spermophilus superciliosus*, *Ochotona pusilla*, *Ellobius talpinus*, *Marmota bobak*, *Allocricetulus eversmanni*, *Allactaga major*, *Eolagurus luteus*, *Saiga tatarica*, *Equus hydruntinus*, *Equus* sp. and *Vulpes corsac* were described from Crimean locations.

In the Middle Urals, fossils of *Cricetulus migratorius*, *Microtus gregalis*, *Lagurus lagurus* and *Ochotona pusilla* were represented. In the South Urals, *Marmota bobak* and *Spermophilus superciliosus* remains were recorded.

Therefore, mammal species now characteristic of the steppe biota were during the Younger Dryas spread extremely wide, their ranges significantly exceeding those of modern areas; however, the areas of that time seemed to be narrower than those during the previous intervals of the LGM and LGT. In the regions where these species maintained their occurrence, their presence in the fauna complexes was noticed to decrease, and they were replaced by dwellers of mesophitic (meadow) and forest habitats. As compared to other species, the *Ochotona pusilla* range occurred further north and west during the Younger Dryas.

Forest species

Among the forest species registered by fossils found in the Younger Dryas sediments were the following: *Sylvaemus flavicollis*, *Sylvaemus sylvaticus*, *Cervus elaphus*, *Clethrionomys glareolus*, *Clethrionomys rutilus*, *Clethrionomys rufocanus*, *Microtus agrestis*, *Talpa europaea*, *Lynx* sp., *Felis silvestris*, *Eliomys quercinus*, *Glis glis* and *Sciurus vulgaris* (Figs. 4.61–4.62).

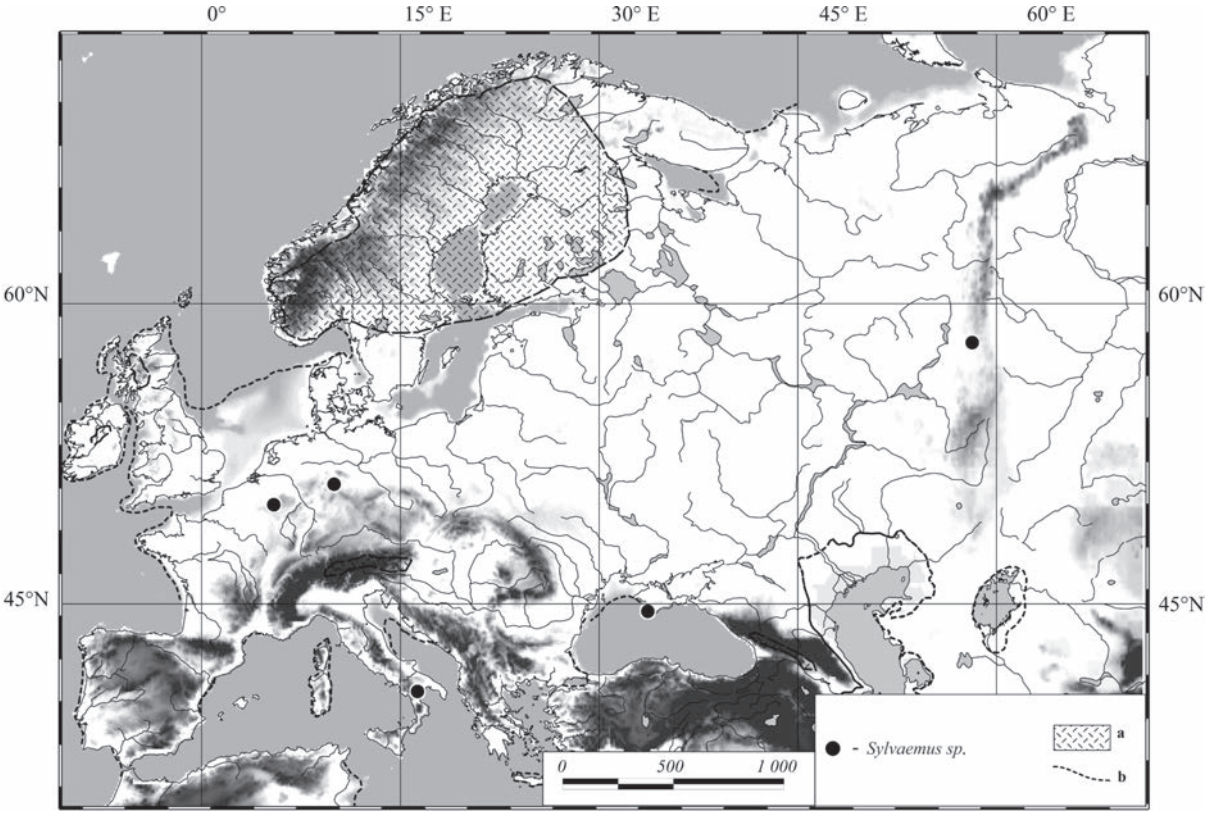

Fig. 4.61. *Wood mouse Sylvaemus sp. localities during the Younger Dryas; a – ice sheets; b – coastline*

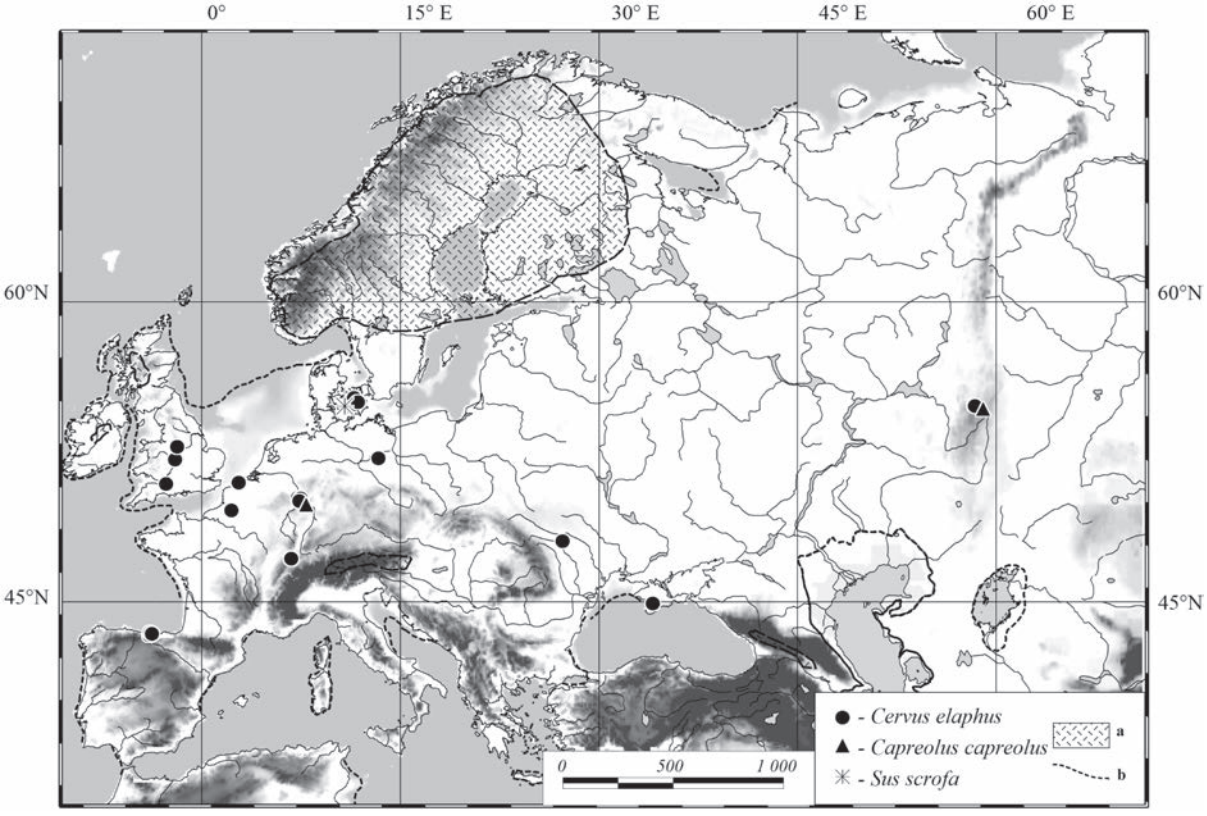

Fig. 4.62. *Wild boar Sus scrofa, red deer Cervus elaphus, and roe deer Capreolus capreolus localities during the Younger Dryas; a – ice sheets; b – coastline*

It was of special importance to analyse features of their distribution, because this enables us to clarify the problem of the refugia, where elements of forest biota could have survived the Late-Pleistocene cold intervals, when forest complexes (both of the taiga and of the broad-leaved type) did not exist as biota zonal components; however, the species forming these complexes found some refugia, spreading from those during the post-glacial warming up. This expansion process became noticeable just during the Younger Dryas. The available data showed that species of forest habitats composed a significant part (both by species quantity and by the number of fossils in oryctocoenoses) in locations of elevated regions of the Apennine Peninsula, in the Crimea and the Middle Urals. Thus, in montane Italy, fossils were found of *Lynx* sp., *Felis silvestris*, *Eliomys quercinus*, *Glis glis*, *Sylvaemus sylvaticus*, and *Cervus elaphus* (Sala, 1983). In the Crimean sites, students recorded the remains of *Sylvaemus flavicollis*, *Sylvaemus sylvaticus*, *Cervus elaphus*, *Clethrionomys glareolus*, *Talpa europaea*, *Lynx* sp.; while *Microtus agrestis*, *Clethrionomys rufocanus*, *Clethrionomys rutilus*, *Clethrionomys glareolus*, and *Sciurus vulgaris* were registered in the Urals. Some forest species, namely *Talpa europaea* and *Clethrionomys glareolus* were also found in Balkan sites (Popov, 1994). Forest species were evidenced also in Western European sites beyond the elevated regions.

Regional features of the mammal fauna composition and structure

On the basis of the available data, we can describe regional peculiarities of the fauna composition and structures during the Younger Dryas, for Southern England, Belgium, Germany, the Middle Urals, the Crimea, and, to a lesser extent, for the Balkans. The locations of Western Europe, including the descriptions of mammal bone remains, added with information on the proportions of different species' remains (i.e., Grotto du Coléoptères à Juzaine, in the Ardennes; the Felsstalle site in the Schwabische Alb) demonstrated similar features in rodent population structure. In all of these, forest, steppe and tundra elements were present, but the number of remains of forest species was however low. Lemmings were still numerous, but they disappeared after the end of the Younger Dryas.

The fauna of this time was described in most detail for the Grotto du Coléoptère in the Ardennes (Codry, 1974). The most abundant among the remains there were those of the *Microtus arvalis-agrestis* group (43.8%), the second place was occupied by *Dicrostonyx* fossils (19.5%), while 5–9% represents bones of the water vole, the narrow-skulled vole, *Clethrionomys glareolus*, and the tundra vole *Microtus oeconomus*. The percentages of *Sylvaemus sylvaticus*, *Cricetus cricetus*, *Mustela erminea*, *Mustela nivalis*, *Ochotona pusilla*, *Sorex araneus*, *Talpa europaea*, *Pitymys subterraneus* and *Microtus nivalis* were significantly lower.

Other Younger Dryas sites in Central Europe, which included smaller amounts of bone remains (as the location Felsstalle in the Schwabische Alb), showed about a similar ratio of the most abundant species.

The sample from the Bolshoi Glukhoi Grotto (horizon 13) situated on the western slope of the Middle Urals included 7295 rodent molars (Smirnov, 1993). They were identified to 17 species of small mammals: *Desmana moschata*, *Ochotona pusilla*, *Sciurus vulgaris*, *Dicrostonyx torquatus*, *Cricetus cricetus*, *Cricetulus migratorius*, *Lagurus lagurus*, *Lemmus sibiricus*, *Sylvaemus sylvaticus*, *Clethrionomys rutilus*, *Clethrionomys glareolus*, *Clethrionomys rufocanus*, *Arvicola terrestris*, *Microtus agrestis*, *M. gregalis*, *M. oeconomus*, and *Sicista* sp. At present, these species or their descendants occur in different zones, namely the tundra, forest and steppe zones. However, when taking into consideration not a simple taxa list, but also the species relative abundance values, and with regard to their zonal ecological preferences (zonal, intrazonal, or extrazonal), we can draw quite another pattern for the interpretation of the data. Thus, the bulk of the animal population is formed by three *Microtus* species: *M. gregalis*, *M. agrestis*, and *M. oeconomus*, and their fossils constitute about 81% of the total amount. Six more species (*Cricetus cricetus*, three *Clethrionomys* voles, *Arvicola terrestris*, and *Ochotona pusilla*) numbered together about 17%, each one of them separately accounted for 1 to 9%. Lastly, fossils of all the remaining 8 species, namely *Sciurus vulgaris*, *Cricetulus migratorius*, *Dicrostonyx torquatus*, *Lemmus sibiricus*, *Sicista* sp., *Lagurus lagurus*, *Sylvaemus sylvaticus*, and *Desmana moschata*, together made up no more than 2% of the total. Thus it becomes clear that the probability of registering every one of these rare enough species would be quite insignificant, if the total quantity of fossils in a sample is not very high. Moreover, low occurrence of some species among the molars probably indicates their rare occurrence in the community, evidently reflecting the corresponding proportions (areas) of the occupied biotopes. These rare species usually do not characterize the proper zonal complex, but they occupy the habitats penetrating into the main zonal landscape from some other zones. In our case, all tundra elements, and some part of the steppe and forest inhabitants, should be regarded in such a way. However, the most abundant species (*Microtus gregalis*, *M. agrestis*, and *M. oeconomus*) also show different zonal preferences. Thus, the tundra vole (*M. oeconomus*) is a polyzonal rodent, inhabiting wet biotopes near water pools in different zones. *M. agrestis* shows the widest distribution within

the forest zone. The narrow-skulled vole (*M. gregalis*) now represents a polyzonal species adapted to cryo-arid conditions and inhabiting open biotopes in different landscapes (tundra, steppe, forest-steppe and forest-tundra ones).

Therefore, one can conclude that the characteristics of the small mammal population structure in the Middle Urals during the Younger Dryas would probably indicate cryo-arid conditions dominated by open-land biotopes, not of the forest type, but including some forest elements and still preserving some tundra components (rare enough and actually relic elements); such a community has no analogues in present-day zonal complexes. On the other hand, no direct analogues can be found for such communities among the Pleistocene complexes either.

A community of this type should be regarded as a transitional one. In the studies of mammal spatial distribution patterns, similar communities are termed as ecotones. When we examine patterns of temporal dynamics, we propose to use the term "temporal ecotone".

The Younger Dryas fauna of the lower mountain region of the Crimea was characterized by the fossils collected in the sites of Sjuren II and Alimovskij Naves (Benecke, 1999). The joint list of mammal species for this region consists of 28 items. The following species have been registered: *Clethrionomys glareolus*, *Spermophilus superciliosus*, *Ochotona pusilla*, *Microtus arvalis*, *Arvicola terrestris*, *Ellobius talpinus*, *Marmota bobak*, *Allocricetulus eversmanni*, *Sylvaemus sylvaticus*, *Sylvaemus flavicollis*, *Mus mus*, *Cricetus cricetus*, *Allactaga major*, *Eolagurus luteus*, *Capra capra*, *Cervus elaphus*, *Saiga tatarica*, *Sus scrofa*, *Lepus europaeus*, *Equus hydruntinus*, *Equus* sp., *Vulpes corsac*, *Vulpes vulpes*, *Canis lupus*, *Lynx lynx*, *Meles meles*, *Panthera spelaea*, and *Ursus arctos*. Eleven of these should be regarded as steppe species, 6 as usual forest inhabitants, 10 as meadow-dwellers and eurytopic forms, and *Panthera spelaea* as a relic of the late Pleistocene complex.

The steppe group shows dominance. Meadow-dwelling *Cricetus cricetus* and forest inhabitant *Sylvaemus sylvaticus* dominate the small mammals; *Saiga tatarica*, *Cervus elaphus*, and *Sus scrofa* in the large mammals.

Analysis of the peculiarities of the mammal fauna composition and structure in the sub-montane Crimea revealed that, as in the Middle Urals, during the Younger Dryas, there existed a community with neither Pleistocene nor Holocene analogues. It is a kind of transitional variant between the Pleistocene and Holocene ones, showing features of an ecotone, embracing elements of different modern zonal complexes, mainly steppe and forest ones.

Conclusion

To conclude, we should return to the main question arising from the studies of mammals dated to the Younger Dryas: whether the mammal communities known from different regions mainly retain the features of the Late-Pleistocene faunas, or that they reveal more similarity to the later Holocene faunas, and how should we reconstruct the picture that might seem general for Europe, based on peculiar features of the different regions.

It is acknowledged that the character of the Pleistocene communities is due to the simultaneous presence of three elements (groups of species), namely: 1) the species that were characteristic only of the Pleistocene (*Mammuthus primigenius*, *Ursus speleaeus*, *Panthera spelaea*, *Bison priscus*, etc.); 2) species now inhabiting the tundra zone; 3) those which now occupy the steppes. Analysis of the available data has shown that none of the associations of the Younger Dryas found all over Europe demonstrate this complex of features. Thus, if we admit that a peculiar biota complex existed during the Pleistocene, we should propose that it had collapsed by the Younger Dryas. However, in some regions, relic populations of the Pleistocene species were found to have been retained. In the north and east of Eastern Europe were recorded unique finds (^{14}C dated) of *Mammuthus primigenius* bones, in the South Urals *Bison priscus* remains, and in the Crimea those of *Panthera spelaea*. *Megaloceros giganteus* was found to have been retained in the north of Europe, and in the Middle and South Urals. A combination of tundra and steppe elements in the faunas was registered only in the north and mountains of Western Europe, and in sites of the Middle Urals, but the tundra species there also showed a decrease in their dominance, becoming rare and very rare. The steppe forms were still found further north than their modern ranges. Forest elements do not yet occur in uninterrupted zones, but their occurrence is noticeable only in the elevated regions.

On the basis of the species composition, the cryo-arid complex changed to look similar to the steppe one, but with the addition of some forest elements, some relic populations of the Pleistocene, and a few arctic elements. All these features of the Younger Dryas mammal communities in Europe can be regarded as representing temporal ecotones, with no analogues in modern zonal associations.

4.5. MAMMAL ASSEMBLAGES DURING THE EARLY HOLOCENE (PREBOREAL–BOREAL – PB–BO) <10.2 – ⩾8.0 KYR BP)

Pavel Kosintsev

According to the Stratigraphic Chart of the Quaternary system, the Holocene starts with the Preboreal with its lower boundary at 10,200 yrs BP. This first Holocene interval is marked by an unstable (variable) climate, with an early Preboreal warming (10,200–10,000 yrs BP) and a late Preboreal cooling (10,000–9,200 years ago). This date of 9200 years BP is regarded as the boundary dividing the Preboreal and Boreal periods. The Boreal climate was warmer and more stable than that of the previous interval. However, some authors distinguish an early warmer period (9200–8900 yrs BP), a median thermal maximum between 8900 and 8300 years ago, and a late-Boreal cooling from 8300 until 8000 years BP; the latter date is considered as the boundary marking the Boreal and the Atlantic period.

During the Preboreal and Boreal intervals, the main modern natural zones were formed. Although some climatic oscillations were registered during this period compared to the previous (Younger Dryas) and the following (Atlantic) intervals, its climate can be described as relatively uniform. The Preboreal and Boreal periods are often regarded as one and the same time interval, namely as the Early Holocene. That is why the fauna complexes from sites dated to the Preboreal and Boreal periods are combined together. The analysis of the theriocomplex of Preboreal – Boreal was previously done for Eastern Europe only (Markova *et al*., 2001). We will here analyse theriocomplexes from in total 142 sites from all over Europe.

The analysis and classification has resulted in two groups of clusters, with three clusters (1–3 and 4–6) in each group (Fig. 4.63). Looking at the geographical positions of the sites indicated that sites of the first three clusters are situated in the northern part of Europe (Fig. 4.64).

Sites forming the fourth cluster are located in the central and southern regions west of the Volga River basin (Fig. 4.71). Sites forming the fifth and sixth clusters are situated in the southern part of Europe and in the Caucasus. Thus, clusters of 'northern', 'southern' and 'middle' European faunas can be distinguished.

An analysis of the groups of faunas forming each cluster has been conducted. Two characters, namely area (Fig. 4.71) and species composition (Table 4.5), were regarded for each group. Three species groups were distinguished in the species list. Indicator species are those species that made the greatest impact on the group formation. Typical species are the species whose remains were recorded in many sites. The other species are species whose remains were found only in a small number of sites. The first two species groups (Table 4.6) served as a basis for analysis of the fauna groups. Description and interpretation of the fauna groups were based on landscape and biotopic preferences of indicator and typical species. The other species were used only in the analysis of the fourth fauna group (cluster 4), due to the low number of species in the first two groups.

The first fauna group (cluster 1) is formed by only two sites in Scandinavia (Fig. 4.71). The indicator species of this group is the polar bear, *Ursus maritimus*, and the group includes only 3 other species (Table 4.5). So, this group is not representative and cannot be distinguished as an independent fauna complex.

The second fauna group (cluster 2) is formed by 11 sites. The indicator species of this group are those related to boreal forests. The presence of polar fox among them may seem inconsistent, but, considering the transitional character of faunas and vegetation at this time, it is quite explainable. It should be noted that the typical species group includes fox, the species that will later replace polar fox in many regions. Sites with faunas of this group cover a restricted territory in the northeast of Europe (Fig. 4.716). This fauna group reflects the early stage of the formation of the coniferous and coniferous – small-leaved forests fauna complex.

The third fauna group (cluster 3) is formed by 21 sites. It is characterized by a large number of indicator species (Table 4.6), which belong to different ecological groups: a group of dry open landscape species: *Ochotona pusilla* (Fig. 4.65), *Lagurus lagurus*, and *Cricetulus migratorius* (Fig. 4.65); a group of cold-tolerant species of open landscapes*: Lemmus* (Fig. 4.66), *Dicrostonyx torquatus* (Fig. 4.66), *Microtus gregalis* (Fig. 4.65), and *Vulpes lagopus* (Fig. 4.77); species of mesothytic steppe and forest-steppe biotopes: *Cricetus cricetus*; a group of taiga and mixed forest zone species: *Clethrionomys*, *Myopus schisticolor*, *Sicista betulina*; and a group of intrazonal species: *Arvicola terrestris*, *Microtus oeconomus*, and *Microtus agrestis*.

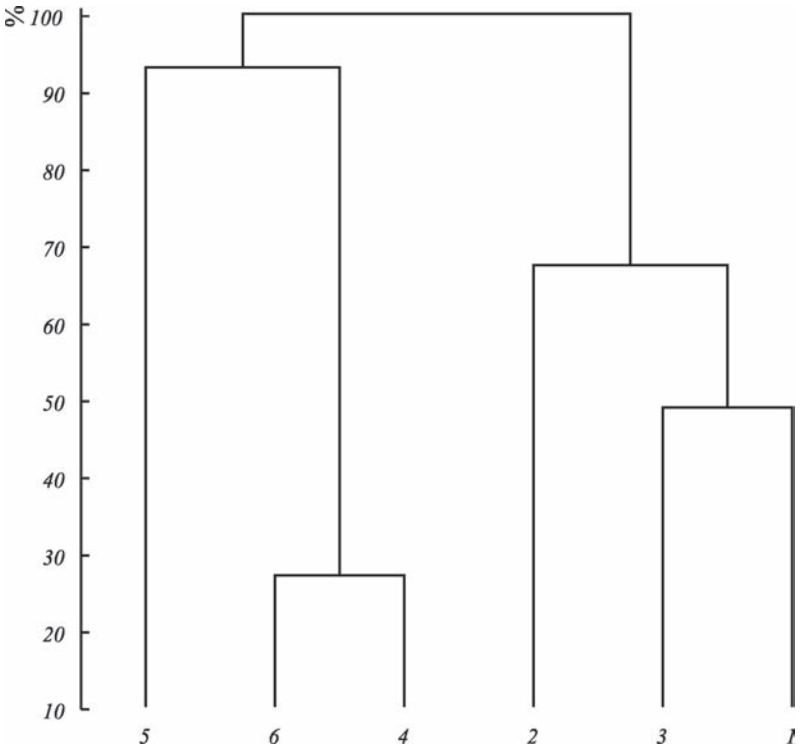

Fig. 4.63. *Scheme of relationships between clusters*[7]

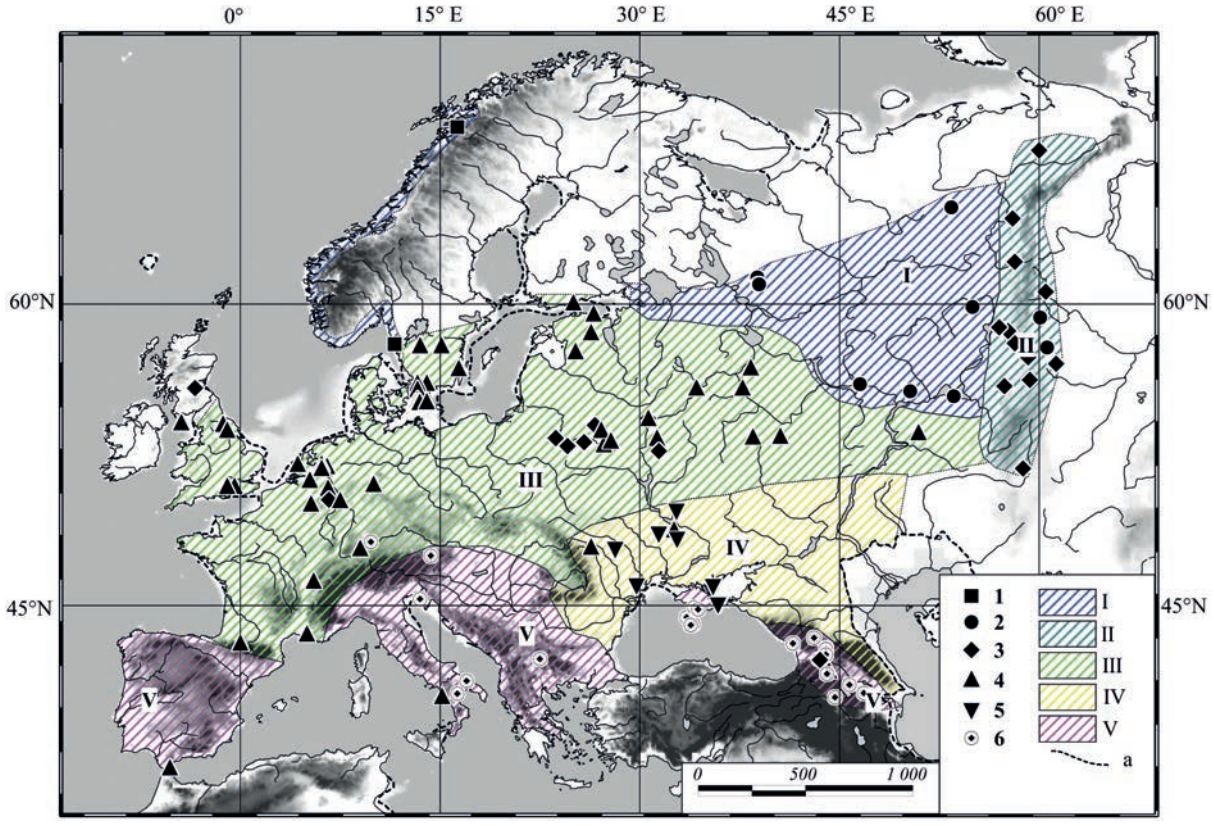

Fig. 4.64. *Preboreal–Boreal mammal assemblages: I – boreal forest and tundra assemblage; II – tundra-forest-steppe assemblage of the Urals; III – assemblage of forest-steppe with "islands" of tundra communities; IV – forest-steppe and steppe assemblage; V – Mediterranean mountain forest assemblage; 1–6 – the localities related to the different clusters; a – coastline*

[7] The statistical and mathematical treatment of PB and BO data was done by Andrey Puzachenko.

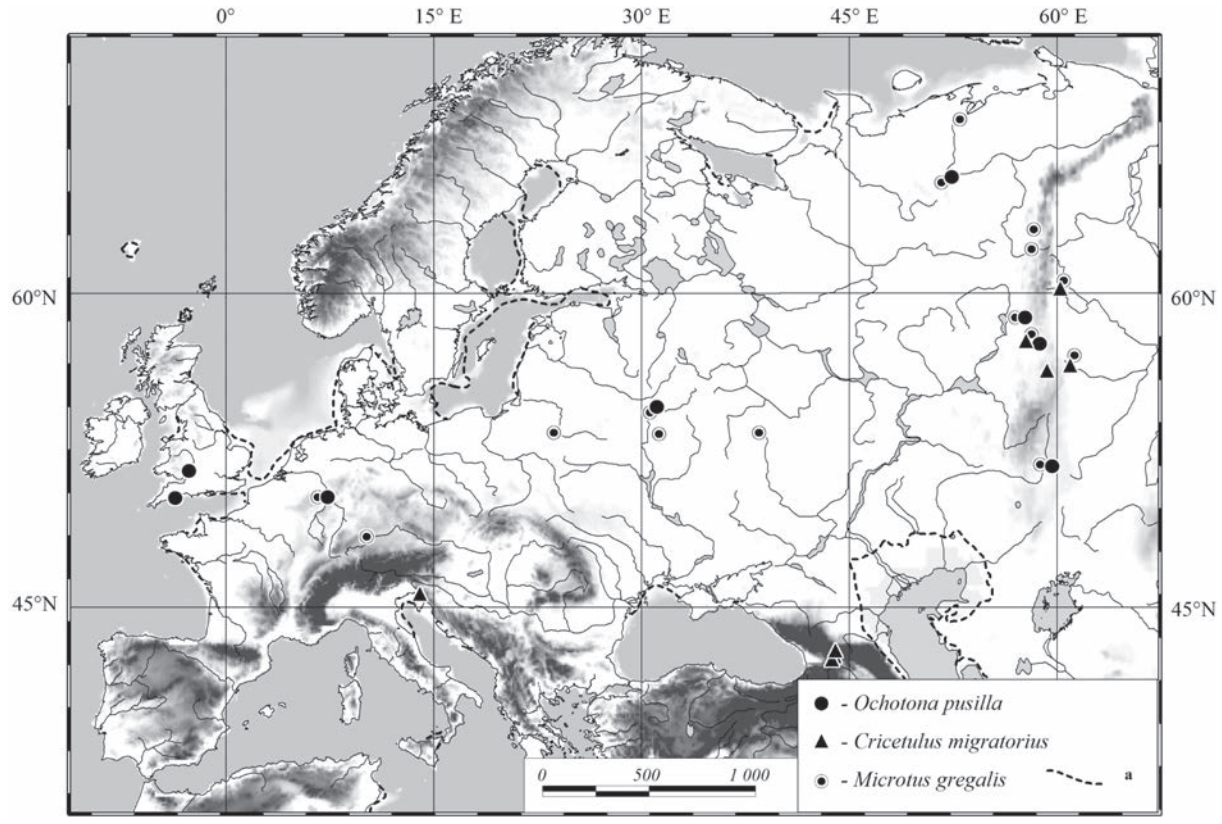

Fig. 4.65. *Steppe pika Ochotona pusilla, grey hamster Cricetulus migratorius, and narrow-skulled vole Microtus gregalis localities during the Preboreal–Boreal; a – coastline*

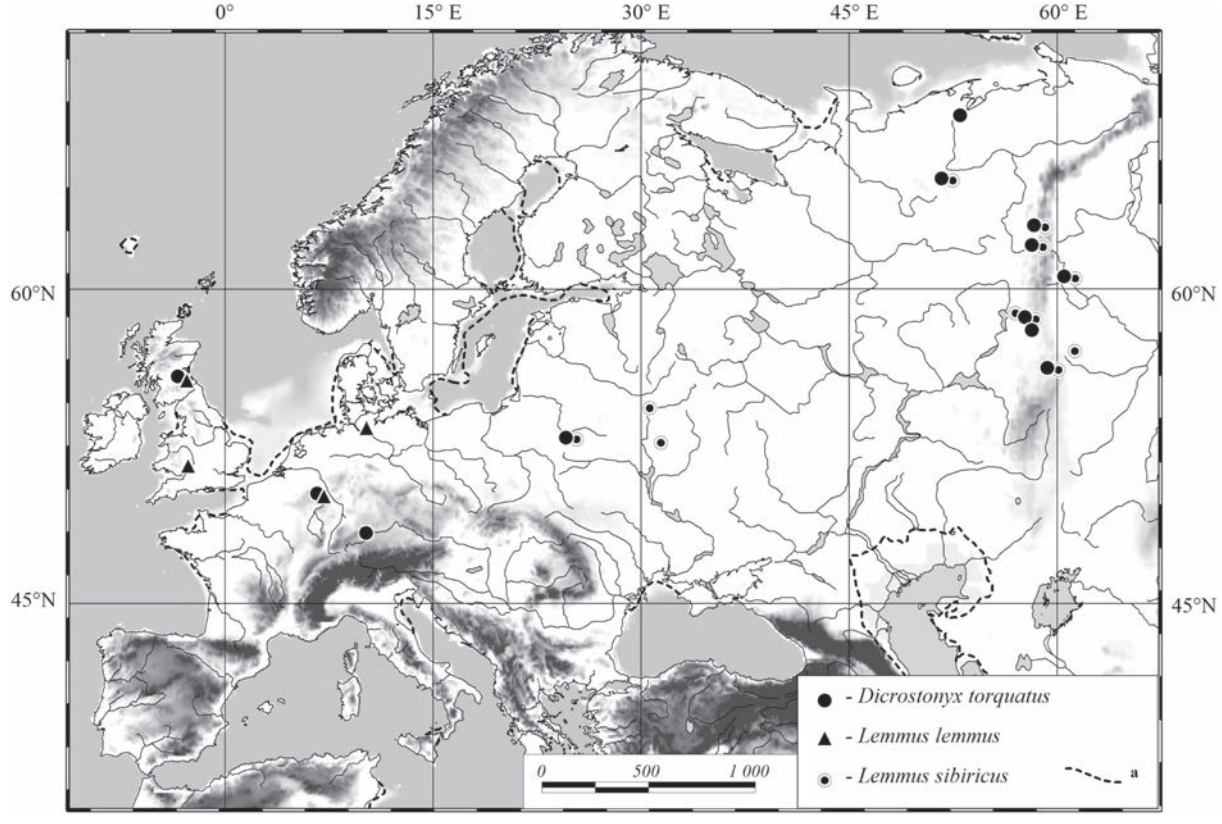

Fig. 4.66. *Siberian lemming Lemmus sibiricus, collared lemming Dicrostonyx torquatus and Norway lemming Lemmus lemmus localities during the Preboreal–Boreal; a – coastline*

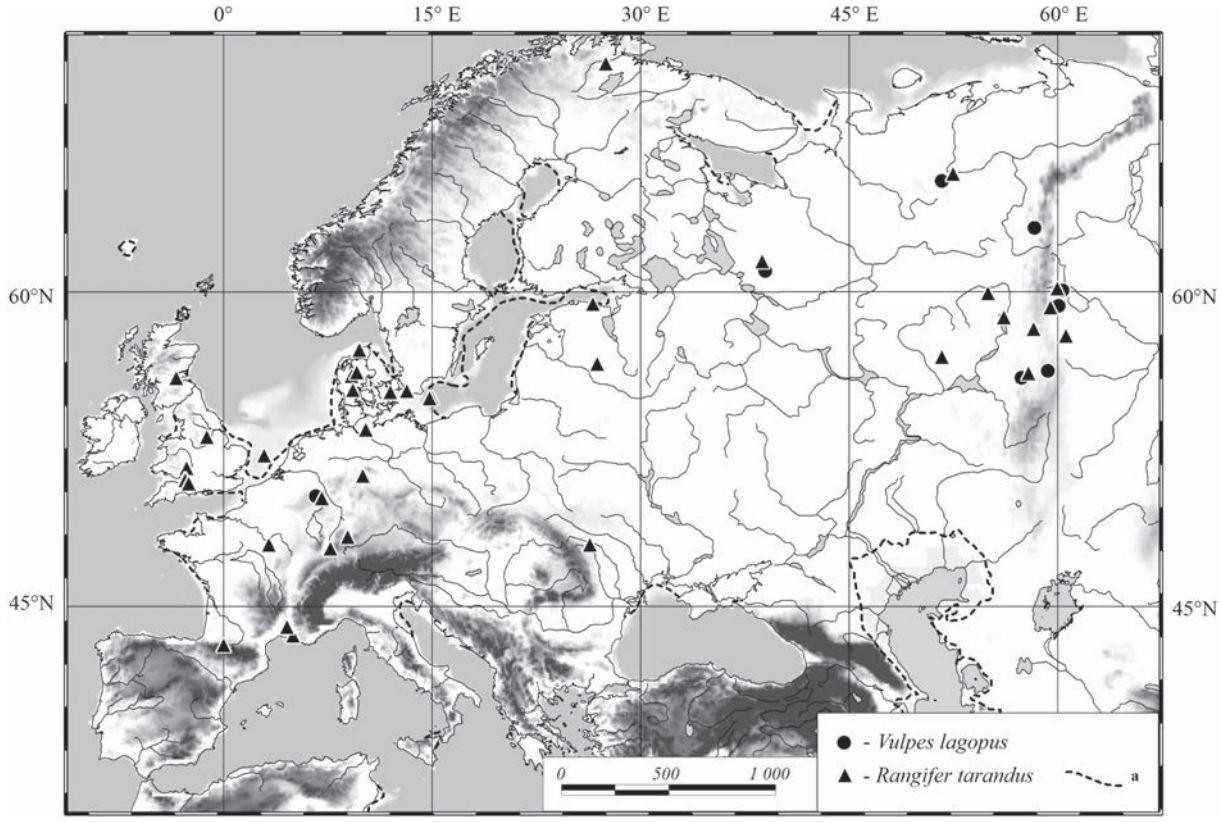

Fig. 4.67. *Polar fox Vulpes lagopus localities during the Preboreal–Boreal; a – coastline*

The area with sites of cluster 3 had a patchy character and stretched from east to west between 50° and 55°N. Only in the Urals do these sites reach the polar circle. On the whole, these are faunas transitional from the Late Pleistocene theriocomplexes to the Holocene ones. The species lists include Late Pleistocene relict species, which later reduce their areas to the northern territories (*Dicrostonyx torquatus*, *Lemmus*, *Microtus gregalis*, and *Vulpes lagopus*) (Fig. 4.67), and to the south (*Ochotona pusilla*, *Lagurus lagurus*, *Cricetulus migratorius*, and *Microtus gregalis*), or become extinct (*Megaloceros giganteus*). Along with these relict species, the fauna lists already include species characteristic of the Holocene fauna complex (*Clethrionomys*, *Cricetus cricetus*, *Arvicola terrestris*, and *Sicista betulina*). Besides, these faunas also include a large group of species that is adapted to forest-steppe and forest landscapes: *Sciurus vulgaris*, *Sylvaemus*, *Lynx*, *Gulo gulo*, *Martes zibellina*, *Sus scrofa*, *Cervus elaphus*, and *Alces alces* (Table 4.6, Figs. 4.68–4.69) characteristic of the Holocene faunal complex. This fauna group reflects a transition that existed for a short period of time and that was soon replaced by the Holocene zonal theriocomplexes.

The fourth fauna group (cluster 4) is formed by 77 sites. It has only two indicator species, *Bos primigenius* and *Mammuthus primigenius* (Table 4.6). The number of typical species is also small: *Castor fiber*, *Sus scrofa*, and *Cervus elaphus* (Table 4.6). But the total number of species is high and most of these are species characteristic for forest-steppe and broad-leaved forests: *Lepus europaeus*, *Sylvaemus*, *Glis glis*, *Eliomys quercinus*, *Martes martes*, *Meles meles*, *Felis sylvestris*, *Lynx*, *Capreolus capreolus*, *Bison bonasus*, and *Equus (Equus)* sp. (Table 4.6). This fauna group occupies the middle part of Europe (Fig. 4.68). The occurrence of *Mammuthus primigenius* distinguishes this fauna group from all others. Only 2 sites, where Holocene remains of mammoth were recorded, are known in Europe, in the north of the Russian Plain and in Estonia (Stuart and Sulerzhitsky, Orlova *et al*., 2002). The extremely rare occurrence of this species recorded in the Holocene determined its inclusion in the group of indicator species. When analyzing the species composition of the faunas of this group (Table 4.6), one can suppose that they characterize the early stages of the formation of broad-leaved forest and forest-steppe theriocomplexes. These theriocomplexes mainly differ not by species composition but by different relative abundances of the same species. The reason why our analysis, based only on species composition, did not differentiate these complexes. Some relict species of the Pleistocene complex still occur (*Microtus gregalis*, *Megaloceros giganteus*, *Rangifer tarandus*,

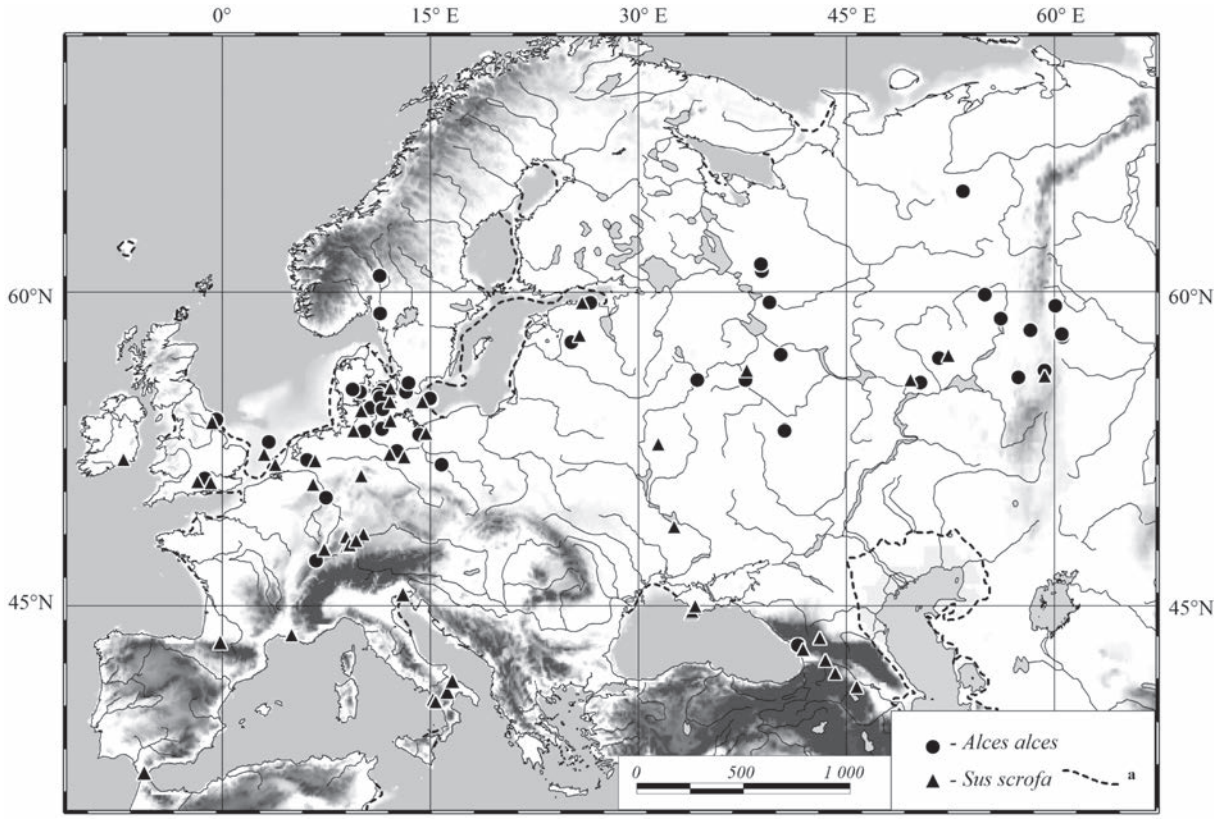

Fig. 4.68. *Elk Alces alces and wild boar Sus scrofa localities during the Preboreal–Boreal; a – coastline*

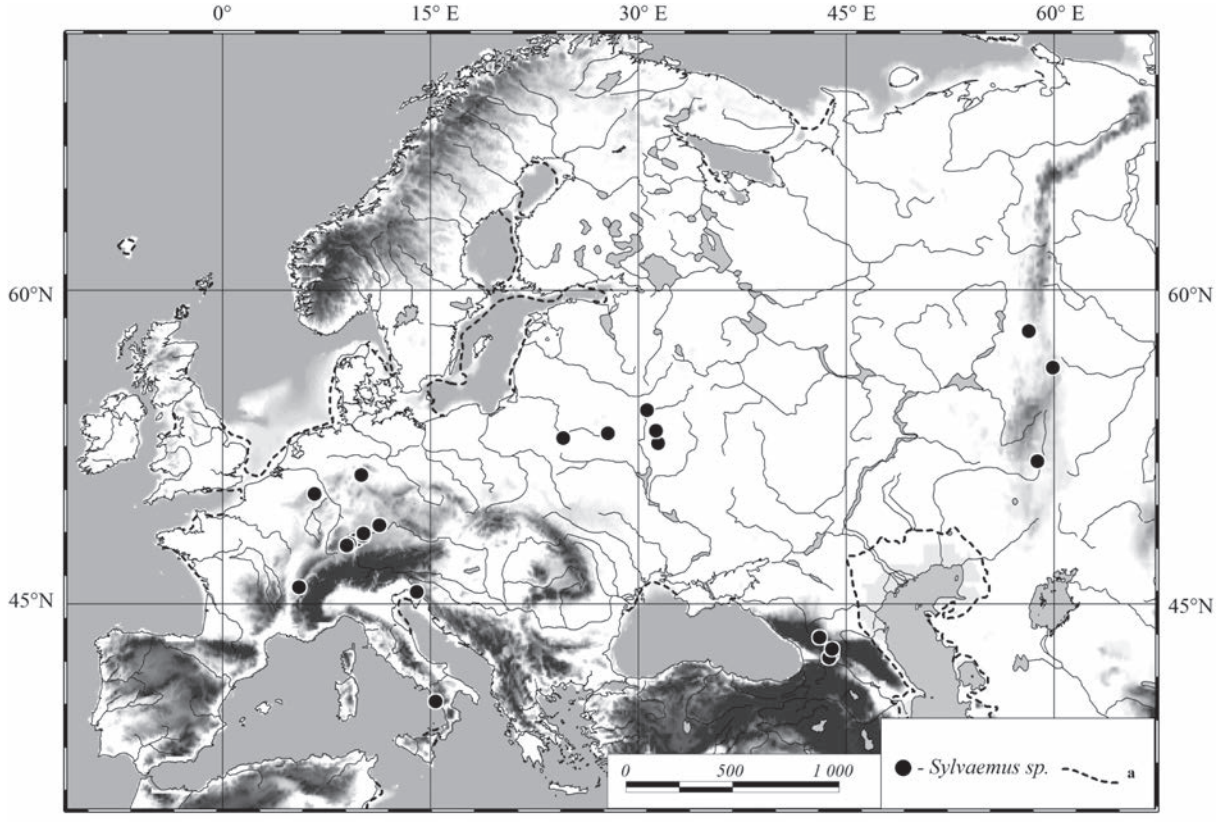

Fig. 4.69. *Wood mouse Sylvaemus localities during the Preboreal–Boreal; a – coastline*

Saiga tatarica, *Equus hydruntinus*, and *E. hemionus*), most of these species are connected to open, periglacial landscapes. But their remains are very scarce and have been recorded only in a few sites.

The fifth fauna group (cluster 5) is formed by 8 sites. It is characterized by the following indicator species: *Bison bonasus*, *Bos primigenius*, *Equus (Equus)* sp., and *Equus hydruntinus.* The group of typical species includes *Castor fiber*, *Sus scrofa*, *Cervus elaphus*, and *Saiga tatarica* (Table 4.6). This group covers the southern part of Eastern Europe (Fig. 4.85). The species list of this fauna group includes species characteristic of steppe landscapes (*Bos primigenius, Equus (Equus)* sp., *E. hydruntinus*, and *Saiga tatarica*) and broad-leaved and lowland forests (*Castor fiber*, *Bison bonasus*, and *Cervus elaphus*). This fauna group characterizes the European steppe theriocomplex, which had already been basically formed by the beginning of the Holocene.

The sixth fauna group (cluster 6) is formed by 23 sites. Lists of indicator and typical species of this fauna group are extensive and diverse (Table 4.6). Sites with faunas belonging to this group are situated in the mountain areas of southern Europe: the Caucasus, the Crimea, the Balkans, the Alps, and the Apennines (Fig. 4.86). Fauna lists consist of species of very different landscapes and biotopic groups. Among the indicator species are species of forest and forest-steppe landscapes: *Ursus arctos*, *Martes martes*, and *Sus scrofa*; forest-steppe landscapes: *Lepus europaeus*, *Cricetus cricetus*, *Meles meles*, *Cervus elaphus*, and *Capreolus capreolus*; steppe landscapes: *Marmota paleocaucasia*, *Cricetulus migratorius*, and *Mesocricetus raddei*; intrazonal species: *Arvicola terrestris*, *Canis lupus*, and *Vulpes vulpes*, and, of course, species connected with mountain landscapes: *Prometheomys schaposchnikovi*, *Chionomys nivalis*, *Microtus major*, *Rupicapra rupicapra*, and *Ovis.* Some of these species are endemics. The only Pleistocene relicts present in faunas of this group are *Marmota paleocaucasica* in the Caucasus and *Equus hydruntinus* in the Balkans, the Apennines and in the Crimea. The large species diversity is connected with the mosaic character of mountain landscapes.

Analysis of the Preboreal-Boreal fauna's composition has revealed the existence of five theriocomplexes in Europe in this time. Three of them are early stages of the main zonal theriocomplexes in Europe during Holocene times: steppe, boreal forest and a complex of broad-leaved forest and forest-steppe, which will differentiate later into two complexes. It is also possible to include in this group the azonal theriocomplex of the Southern European mountains. Faunas of different mountain systems, notwithstanding the presence of endemic species, were united one theriocomplex due to large number of species they have in common. The fifth theriocomplex has a pronounced transitional character between Pleistocene and Holocene faunas, and existed during a relatively short time span. Only in the mountain areas of the Urals was its existence relatively long.

Pleistocene relicts

The character which all of the considered theriocomplexes share is the presence of Pleistocene relicts in their species lists. Species which inhabited Europe at the end of the Pleistocene (Fig. 4.70), survived the transition from the Younger Dryas to the PB, and considerably reduced their distribution later. Most of these species inhabit steppe landscapes: *Ochotona pusilla*, *Marmota bobak*, *Marmota paleocaucasica*, *Spermophillus*, *Allactaga major*, *Allocricetulus eversmanni*, *Cricetulus migratorius*, *Lagurus lagurus*, *Eolagurus luteus*, *Vulpes corsac*, *Mustela eversmanni*, *Saiga tatarica*, *Gazella subgutturosa*, *Equus hydruntinus*, and *E. hemionus*. The number of species that inhabit 'tundra' landscapes: *Dicrostonyx torquatus*, *Lemmus*, *Microtus middendorffii*, *Vulpes lagopus*, *Rangifer tarandus*, and *Ovibos moschatus*, and forest-steppe landscapes: *Lepus tanaiticus*, and *Megaloceros giganteus*, is much lower. A separate group consists of *Microtus gregalis*, *Panthera spelaea* and *Mammuthus primigenius*. The number of relict species was different in different theriocomplexes.

The greatest number, 20 species, is, as can be expected, present in the transitional theriocomplex (fauna group 3). In the non-differentiated theriocomplex of broad-leaved forest and forest-steppe (fauna group 4) are 7 relict species, in the boreal forest theriocomplex (fauna group 2) 4 species, in the steppe theriocomplex (fauna group 5) 2 species and in the mountain theriocomplex of Southern Europe (fauna group 6) 8 species.

The historical fates of the individual relict species were different. The overwhelming majority reduced their areas. A part of the species reduced their areas to the north and northeast (*Dicrostonyx torquatus*, *Lemmus lemmus*, *L. sibiricus*, *Microtus gregalis*, *M. middendorffii*, *Vulpes lagopus*, *Rangifer tarandus*, and *Mammuthus primigenius*), another part to the south and southeast (*Ochotona pusilla*, *Marmota bobak*, *Allactaga major*, *Allocricetulus eversmannii*, *Cricetulus migratorius*, *Lagurus lagurus*, *Eolagurus luteus*, *Microtus gregalis*, *Vulpes corsac*, *Panthera spelaea*, *Mustela eversmannii*, *Saiga tatarica*, *Gazella subgutturosa*, *Equus hydrundinus*, and *E. hemionus*), and yet another to the east (*Lepus tanaiticus* and *Megaloceros giganteus*). The areas of some of these species were reduced beyond the territory of Europe (*Microtus middendorffii*, *Mammuthus primigenius*, *Gazella subgutturosa*, and *Equus hemionus*). Probably the only species in the theriofauna of Europe of this period that became extinct during the Early Holocene is *Ovibos moschatus*.

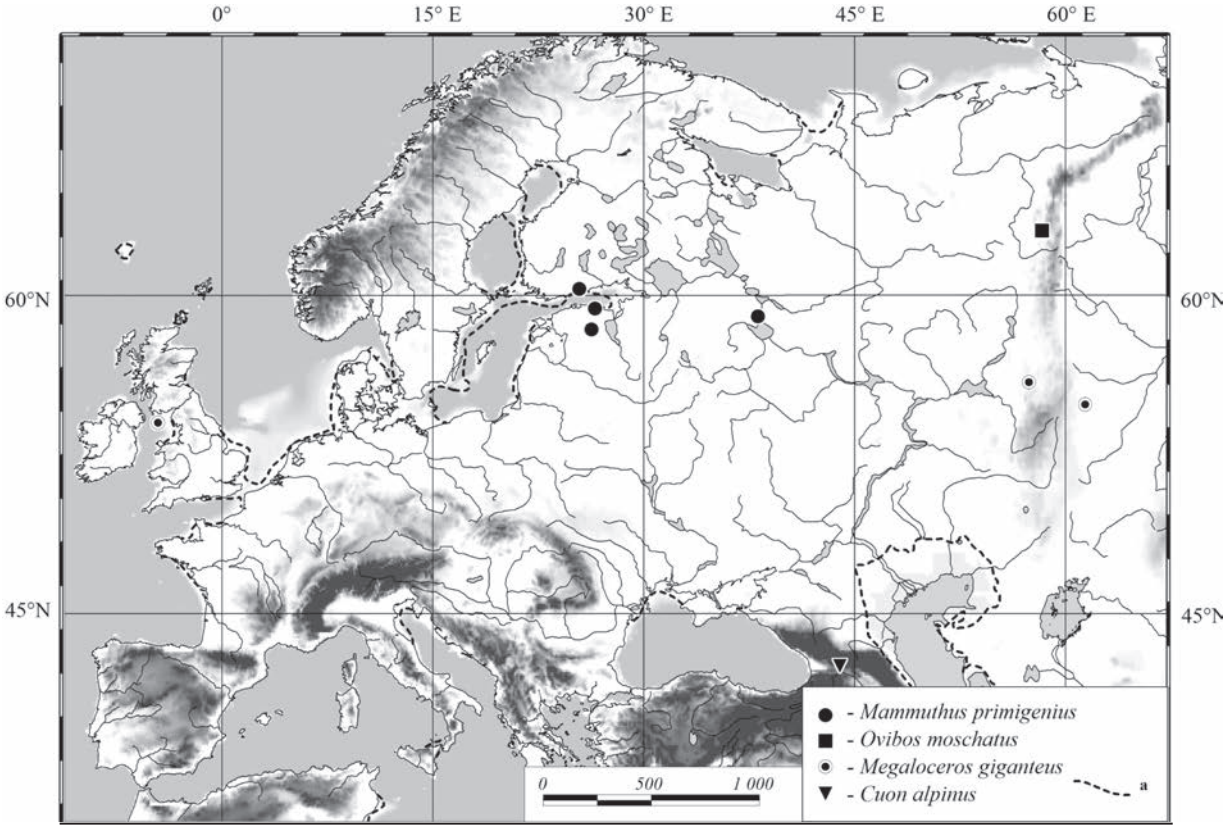

Fig. 4.70. *Mammoth Mammuthus primigenius, musk ox Ovibos moschatus, giant deer Megaloceros giganteus, and red dog Cuon alpinus localities during the Preboreal–Boreal; a – coastline*

Table 4.5

Mammal occurrence in the clusters (%)

Species	Clusters (mammal assemblages)						M-L Chi-sq, *p*
Cluster's number:	1	2	3	4	5	6	
N:	2	11	21	77	8	23	
Erinaceus sp. – Eurasian hedgehog	0.0	9.09	0.0	3.90	0.0	17.39	–
Desmana moschata – Russian desman	0.0	0.0	4.76	0.0	0.0	0.0	–
Sorex araneus – common shrew	0.0	0.0	0.0	6.49	0.0	4.35	–
Sorex minutus – lesser shrew	0.0	0.0	0.0	3.90	0.0	4.35	
Sorex sp. – shrew	0.0	0.0	19.05	6.49	0.0	8.70	–
Crocidura russula – white-toothed shrew	0.0	0.0	0.0	1.30	0.0	0.0	–
Crocidura leucodon – bicoloured white-toothed shrew	0.0	0.0	0.0	1.30	0.0	4.35	–
Neomys fodiens – water shrew	0.0	0.0	4.76	2.60	0.0	8.70	–
Oryctolagus cuniculus – European rabbit	0.0	0.0	0.0	2.60	0.0	0.0	–
Lepus tanaiticus – Tanaitic' hare	0.0	0.0	14.29	0.0	0.0	0.0	
Lepus timidus – Polar hare	0.0	**54.55**	0.0	2.60	0.0	13.04	0.0004
Lepus europaeus – European hare	0.0	9.09	0.0	10.39	0.0	**47.83**	0.0001

Continued table 4.5

Species	Clusters (mammal assemblages)						M-L Chi-sq, *p*
Cluster's number:	1	2	3	4	5	6	
N:	2	11	21	77	8	23	
Ochotona alpina – Altai pika	0.0	0.0	9.52	0.0	0.0	0.0	–
Ochotona pusilla – steppe pika	0.0	0.0	**38.10**	0.0	0.0	0.0	<0.00001
Sciurus vulgaris – red squirrel	0.0	18.18	19.05	7.79	0.0	0.0	–
Spermophilus pygmaeus – little suslik	0.0	0.0	14.29	0.0	0.0	4.35	–
Spermophilus superciliosus – suslik "superciliosus"	0.0	0.0	9.52	0.0	0.0	0.0	–
Spermophilus major – great suslik	0.0	0.0	9.52	0.0	0.0	0.0	–
Marmota bobak – bobak marmot	0.0	0.0	9.52	0.0	0.0	0.0	–
Marmota marmota – Alpine marmot	0.0	0.0	0.0	1.30	0.0	0.0	–
Marmota paleocaucasica – Palaeocaucasian marmot	0.0	0.0	0.0	0.0	0.0	26.09	0.0003
Castor fiber – beaver	0.0	**72.73**	4.76	22.08	12.50	4.35	0.0002
Muscardinus – dormouse	0.0	0.0	0.0	1.30	0.0	8.70	–
Dryomys nitedula – forest dormouse	0.0	0.0	0.0	0.0	0.0	8.70	
Eliomys quercinus – garden dormouse	0.0	0.0	0.0	1.30	0.0	4.35	–
Glis glis – fat dormouse	0.0	0.0	0.0	5.19	0.0	13.04	
Sicista subtilis – southern birch mouse	0.0	0.0	4.76	0.0	0.0	0.0	–
Sicista betulina – northern birch mouse	0.0	0.0	**14.29**	0.0	0.0	8.70	0.03
Allactaga major – great jerboa	0.0	0.0	4.76	0.0	0.0	8.70	–
Pygerethmus platyurus – lesser fat-tailed jerboa	0.0	0.0	4.76	0.0	0.0	0.0	–
Spalax microphthalmus – Russian mole	0.0	0.0	0.0	1.30	0.0	0.0	–
Sylvaemus sylvaticus – wood mouse	0.0	0.0	23.81	7.79	0.0	21.74	–
Apodemus agrarius – striped field mouse	0.0	0.0	4.76	1.30	0.0	0.0	–
Sylvaemus flavicollis – yellow-necked mouse	0.0	0.0	4.76	7.79	0.0	4.35	–
Talpa sp. – mole	0.0	9.09	4.76	9.09	0.0	21.74	–
Mus musculus – house mouse	0.0	0.0	4.76	5.19	0.0	4.35	–
Micromys minutus – harvest mouse	0.0	0.0	4.76	1.30	0.0	0.0	–
Rattus sp. – rat	0.0	0.0	4.76	0.0	0.0	0.0	–
Ellobius talpinus – northern mole-vole	0.0	0.0	9.52	0.0	0.0	8.70	–
Allocricetulus eversmanni – Eversmann' hamster	0.0	0.0	4.76	0.0	0.0	0.0	–
Cricetulus migratorius – grey hamster	0.0	0.0	**23.81**	0.0	0.0	**13.04**	0.0009
Mesocricetus brandti – Brandt's hamster	0.0	0.0	0.0	0.0	0.0	4.35	–
Mesocricetus raddei – Ciscaucasian hamster	0.0	0.0	0.0	0.0	0.0	**21.74**	0.002
Cricetus cricetus – common hamster	0.0	0.0	**28.57**	5.19	0.0	**13.04**	0.03
Prometheomys – long-clawed mole-vole	0.0	0.0	0.0	0.0	0.0	**26.09**	0.0003
Clethrionomys rufocanus – grey red-backed vole	0.0	0.0	**42.86**	0.0	0.0	0.0	<0.00001
Clethrionomys glareolus – red-backed vole	0.0	0.0	**61.90**	11.69	0.0	13.04	0.00001
Clethrionomys rutilus – northern red-backed vole	0.0	0.0	**23.81**	0.0	0.0	0.0	0.001
Lagurus lagurus – steppe lemming	0.0	0.0	**19.05**	0.0	0.0	0.0	0.007

Continued table 4.5

Species	Clusters (mammal assemblages)						M-L Chi-sq, *p*
Cluster's number:	1	2	3	4	5	6	
N:	2	11	21	77	8	23	
Eolagurus luteus – yellow steppe lemming	0.0	0.0	4.76	0.0	0.0	0.0	–
Dicrostonyx torquatus – collared lemming	0.0	0.0	**61.90**	0.0	0.0	0.0	<0.00001
Lemmus lemmus – Norway lemming	0.0	0.0	**14.29**	0.0	0.0	0.0	0.04
Lemmus sibiricus – Siberian lemming	0.0	0.0	**61.90**	0.0	0.0	0.0	<0.00001
Myopus schisticolor – wood lemming	0.0	0.0	**19.05**	0.0	0.0	0.0	0.007
Arvicola terrestris – water vole	0.0	0.0	**80.95**	18.18	0.0	**30.43**	<0.00001
Microtus (Terricola) majori – Minor Asian vole	0.0	0.0	0.0	0.0	0.0	**21.74**	0.002
Microtus (Terricola) daghestanicus – Daghestanian vole	0.0	0.0	0.0	0.0	0.0	13.04	
Microtus (Terricola) subterraneus – pine vole	0.0	0.0	0.0	5.19	0.0	8.70	–
Microtus gregalis – narrow-skulled vole	0.0	0.0	**61.90**	2.60	0.0	0.0	<0.00001
Microtus oeconomus – root vole	0.0	0.0	**80.95**	10.39	0.0	4.35	<0.00001
Microtus agrestis – field vole	50.0	0.0	**66.67**	6.49	0.0	4.35	<0.00001
Microtus arvalis – common vole	0.0	0.0	9.52	5.19	0.0	21.74	–
Microtus middendorfii – Middendorf's vole	0.0	0.0	14.29	0.0	0.0	0.0	0.04
Chionomys nivalis – snow vole	0.0	0.0	0.0	2.60	0.0	**17.39**	0.05
Canis lupus – common wolf	50.0	**54.55**	23.81	14.29	12.50	**39.13**	0.02
Canis aureus – Asiatic jackal	0.0	0.0	0.0	0.0	0.0	4.35	–
Vulpes lagopus – Polar fox	50.0	**18.18**	**19.05**	0.0	0.0	0.0	0.0005
Vulpes vulpes – common red fox	50.0	18.18	23.81	12.99	0.0	**47.83**	0.006
Vulpes corsac – corsac fox	0.0	0.0	9.52	0.0	0.0	0.0	–
Cuon alpinus – red dog	0.0	0.0	0.0	0.0	0.0	4.35	–
Ursus arctos – brown bear	0.0	**63.64**	0.0	7.79	0.0	**21.74**	0.00005
Ursus maritimus – Polar bear	**100.0**	0.0	0.0	0.0	0.0	0.0	0.0008
Ursus sp. – bear	0.0	0.0	0.0	0.0	0.0	8.70	–
Martes zibellina – sable	0.0	0.0	4.76	1.30	0.0	0.0	–
Martes martes – common marten	50.0	**36.36**	0.0	5.19	0.0	**26.09**	0.0009
Martes foina – beech marten	0.0	0.0	0.0	0.0	0.0	8.70	–
Gulo gulo – wolverine	0.0	0.0	4.76	0.0	0.0	4.35	–
Mustela erminea – ermine stoat	0.0	9.09	4.76	0.0	0.0	0.0	–
Mustela nivalis – weasel	0.0	9.09	4.76	0.0	0.0	8.70	–
Mustela sibirica – Siberian weasel	0.0	0.0	4.76	0.0	0.0	0.0	–
Mustela putorius – polecat	0.0	9.09	4.76	0.0	0.0	4.35	–
Mustela eversmanni – Russian polecat	0.0	9.09	0.0	0.0	0.0	0.0	–
Meles meles – badger	0.0	18.18	0.0	11.69	0.0	**30.43**	0.02
Lutra lutra – common otter	0.0	9.09	14.29	3.90	0.0	0.0	–
Panthera pardus – leopard	0.0	0.0	0.0	0.0	0.0	8.70	–

Continued table 4.5

Species	Clusters (mammal assemblages)						M-L Chi-sq, *p*
Cluster's number:	1	2	3	4	5	6	
N:	2	11	21	77	8	23	
Felis silvestris – wood cat	0.0	0.0	0.0	3.90	0.0	17.39	–
Lynx sp. – lynx	0.0	0.0	4.76	2.60	12.50	4.35	–
Mammuthus primigenius – woolly mammoth	0.0	0.0	0.0	**3.90**	0.0	0.0	–
Equus (Equus) sp. – wild horse	0.0	0.0	14.29	9.09	**87.50**	21.74	0.00003
Equus hydruntinus – Pleistocene ass	0.0	0.0	0.0	1.30	50.0	8.70	0.001
Equus hemionus – onager	0.0	0.0	0.0	1.30	0.0	8.70	–
Sus scrofa – wild boar	0.0	18.18	9.52	20.78	12.50	**47.83**	0.05
Cervus elaphus – red deer	0.0	0.0	9.52	24.68	12.50	**73.91**	<0.00001
Capreolus capreolus – roe deer	0.0	0.0	0.0	14.29	0.0	**47.83**	0.00005
Megaloceros – giant deer	0.0	0.0	4.76	1.30	0.0	0.0	–
Alces alces – Elk	0.0	**90.91**	4.76	16.88	0.0	4.35	<0.00001
Rangifer tarandus – reindeer	0.0	**54.55**	9.52	3.90	0.0	0.0	0.0003
Bos primigenius – Aurochs	0.0	0.0	4.76	**53.25**	**75.00**	13.04	<0.00001
Bison bonasus – European bison, wisent	0.0	0.0	0.0	10.39	**50.0**	26.09	0.002
Gazella subgutturosa – goitered gazelle	0.0	0.0	0.0	0.0	0.0	8,70	
Saiga tatarica – saiga	0.0	0.0	0.0	2.60	12.50	8.70	–
Ovibos moschatus – muskox	0.0	0.0	4.76	0.0	0.0	0.0	–
Rupicapra rupicapra – chamois	0.0	0.0	0.0	0.0	0.0	**21.74**	0.002
Capra sp. – goat	0.0	0.0	14.29	2.60	0.0	**34.78**	0.0007
Ovis sp. – sheep	0.0	0.0	0.0	0.0	0.0	**13.04**	0.05

In some areas in Europe, the complex of relict species persisted in the Early Holocene. The Urals was one of these areas (Markova *et al*., 2001; Fadeeva, 2003; Kosintsev, 2003; Teterina, 2003; Yakovlev, 2003). In the North Urals this complex consisted of 14 species, in the Middle Urals of 13 species, and in the South Urals of 6 species (Table 4.7). These are tundra-steppe species characteristic of the Late Pleistocene mammoth steppe fauna. Throughout the end of early – middle Holocene, the distribution areas of these species will be 'drawn apart' by the formation of a forest zone: *Dicrostonyx torquatus*, *Lemmus sibiricus*, *Microtus middendorffii*, and *Vulpes lagopus* will retreat to the north; *Ochotona pusilla*, *Spermophillus*, *Marmota bobak*, *Cricetulus migratorius*, *Lagurus lagurus*, *Eolagurus luteus*, *Mustela eversmannii*, and *Equus (Equus*) will move to the south, and *Microtus gregalis* will disrupt its area and, as a result, two subspecies will emerge, the northern (*M.g. major*) and the southern (*M.g. gregalis*). Three species will become extinct during this period, *Lepus tanaiticus*, *Coleodonta antiquitatis* and *Megaloceros giganteus*.

A small number of Pleistocene relicts persisted in the Early Holocene in other areas of Europe. *Ochotona pusilla*, *Lepus timidus*, *Dicrostonyx torquatus*, *Lemmus lemmus*, and *Rangifer tarandus* inhabited England and Ireland during the Preboreal (Stuart, 1982; Coard and Chamberlain, 1999). *Rangifer tarandus* still persisted in the Preboreal in the north of the Iberian Peninsula (Altuna, 1999), *Equus hydruntinus* (Bartosiewiez, 1999) and *Panthera* in the Carpathians (Ninov, 1999), and *Ochotona pusilla*, *Equus hydruntinus*, and *Saiga tatarica* in the Crimea (Benecke, 1999).

The analysis performed allows us to assume that formation of the Holocene theriocomplexes took place during the Boreal period nearly all over Europe. The exception was the far eastern part of Europe, where a mammal assemblage of transitional character still persisted in the Urals. The Holocene theriocomplex formed there during the Atlantic period.

Table 4.6

Indicator species and typical species composition of mammal assemblages

Mammal assemblages	Indicator species	Typical species
1	*Ursus maritimus*	*Microtus agrestis, Canis lupus, Vulpes vulpes, Vulpes lagopus, Martes martes*
2	*Lepus timidus, Castor fiber, Canis lupus, Vulpes lagopus, Ursus arctos, Martes martes, Alces alces, Rangifer tarandus*	*Sciurus vulgaris, Vulpes vulpes, Meles meles*
3	*Ochotona pusilla, Sicista betulina, Cricetus cricetus, Cricetulus migratorius, Clethrionomys glareolus, Cl. rutilus, Cl. rufocanus, Lagurus lagurus, Dicrostonyx torquatus, Lemmus* sp., *Myopus schisticolor, Arvicola terrestris, Microtus gregalis, M. oeconomus, M. agrestis, Vulpes lagopus*	*Sylvaemus sylvaticus* and *S. uralensis*
4	*Bos primigenius, Mammuthus primigenius*	*Castor fiber, Sus scrofa, Cervus elaphus*
5	*Bison bonasus, Bos primigenius, Equus (Equus*) sp., *Equus hydruntinus*	*Castor fiber, Lynx* sp., *Cervus elaphus, Saiga tatarica*
6	*Lepus europaeus, Cricetulus migratorius, Mesocricetus raddei, Cricetus cricetus, Promethiomys nivalis, Microtus majori, Canis lupus, Vulpes vulpes, Ursus arctos, Martes martes, Meles meles, Sus scrofa, Cervus elaphus, Capreolus capreolus, Rupicarpa rupicarpa, Ovis* sp.	*Marmota paleocaucasica, Glis glis, Sylvaemus, Microtus arvalis, Bison bonasus, Equus (Equus)* sp.

Table 4.7

Mammal taxa list of the Urals in the Early Holocene (Preboreal–Boreal)

Species	The North Urals	The Middle Urals	The South Urals
	2	3	4
Sorex sp.	+	+	+
Ochotona pusilla	+*	+*	+
Lepus tanaiticus	+*	+*	+*
Sciurus vulgaris	+	+	+
Spermophilus sp.	+*	+*	+
Marmota bobak	–	+*	+
Castor fiber	–	+	+
Sicista sp.	–	+	+
Allactaga major	–	–	+
Allactagulus sp.	–	–	+
Sylvaemus sylvaticus – uralensis	–	+	+
Sylvaemus flavicollis	–	–	+
Allocricetulus eversmanii	–	–	+
Cricetulus migratorius	+*	+*	+*
Cricetus cricetus	–	+	+
Clethrionomys ex. gr. *rutilus – glareolus*	+	+	+
Clethrionomys rufocanus	+	+	+
Lagurus lagurus	+*	+*	+
Eolagurus luteus	+*	–	+
Dicrostonyx torquatus	+*	+*	+*
Lemmus sibiricus	+*	+*	–
Myopus schisticolor	+	+	–
Arvicola terrestris	+	+	+
Microtus gregalis	+*	+*	+
Microtus oeconomus	+	+	+
Microtus agrestis	+	+	+

Continued table 4.7

Species	The North Urals	The Middle Urals	The South Urals	Species	The North Urals	The Middle Urals	The South Urals
	2	3	4		2	3	4
Microtus middendorfii	+*	–	–	*Lutra lutra*	+	+	+
Microtus arvalis	–	–	+	*Lynx lynx*	–	+	+
Canis lupus	+	+	+	*Equus (Equus) gmelini*	+*	+*	+
Vulpes lagopus	+*	+*	+*				
Vulpes vulpes	+	+	+	*Coelodonta antiquitatis*	+*	–	–
Vulpes corsac	–	+	+	*Camelus ferus*	–	–	+
Ursus arctos	+	+	+	*Cervus elaphus*	–	+	+
Martes zibellina	+	+	–	*Capreolus pygargus*	–	+	+
Martes martes	–	+	+	*Megaloceros giganteus*	–	+*	+*
Gulo gulo	+	+	+				
Mustela erminea	+	+	+	*Alces alces*	+	+	+
Mustela nivalis	+	+	+	*Rangifer tarandus*	+	+	+
Mustela lutreola	+	+	+	*Bos primigenius*	–	–	+
Mustela eversmanii	+*	+*	+	*Bison* sp.	–	–	+
Meles meles	–	+	+	*Saiga tatarica*	–	–	+

* – Pleistocene relict species.

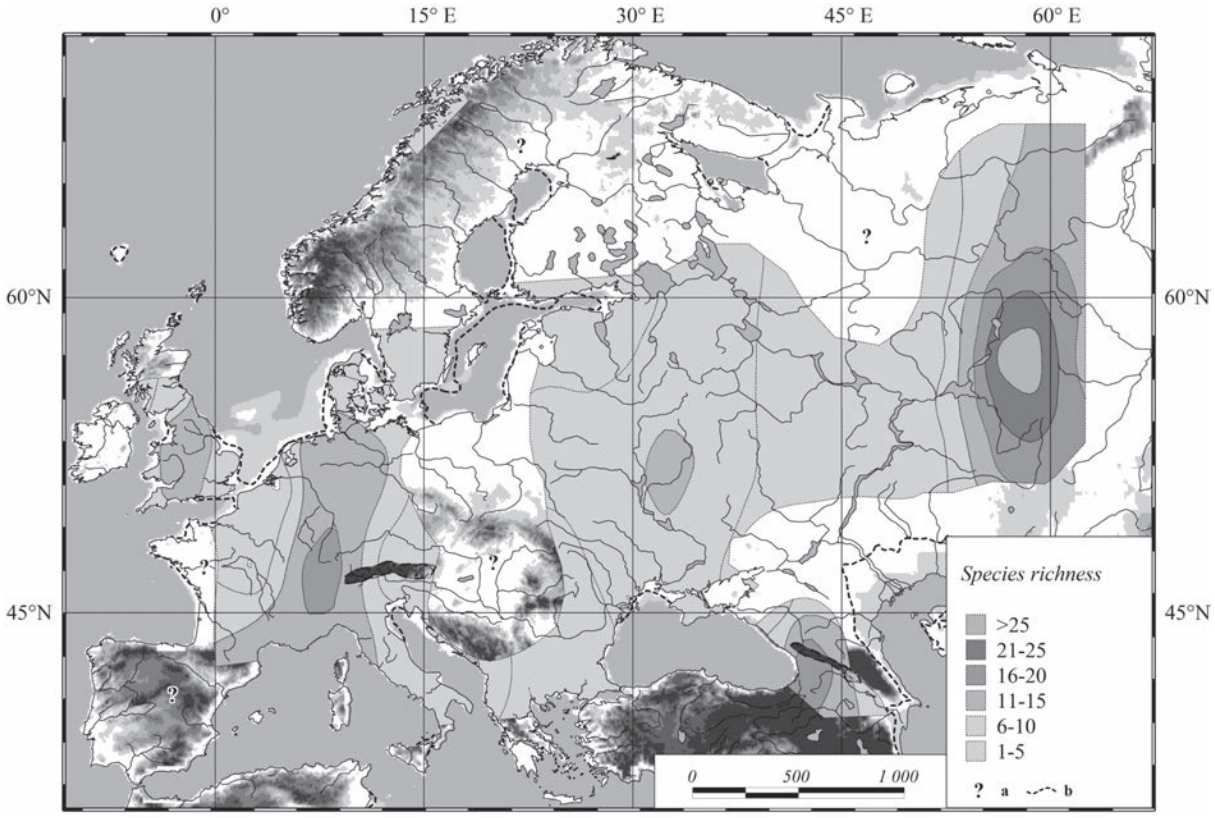

Fig. 4.71. *Species richness of herbivores during Preboreal–Boreal periods; a – absence of data; b – coastline*

Geographical variation of the mammal species richness during Preboreal–Boreal periods[8]

In the Early Holocene we can observe 3 important centres with a high biodiversity (Fig. 4.71). The first one was located in Southeastern Europe in the west of the Caucasus Mountains. This centre most probably existed during the entire Late Pleistocene. According to our data, the maximal species richness was observed in Eastern Europe – in the South Urals and the adjacent territories. The Western Alps were also characterized by a high species richness level. Unfortunately, we have not enough data for the Carpathian Mountains and their foothills. However, we propose that one more centre of mammal diversity was situated in this region as well as in the present time.

4.6. MAMMAL EXTINCTION IN EUROPE AT THE END OF THE PLEISTOCENE – BEGINNING OF THE HOLOCENE

Pavel Kosintsev

The extinction of mammals at the end of the Pleistocene and beginning of the Holocene is unique. Mainly megamammals became extinct, and ecological niches of some extinct species were left unoccupied (Puchkov, 1989a, b). We will not go into the causes, mechanisms or progress and rates of the extinction process, as those problems have been extensively discussed already (Pleistocene extinctions, 1967; Quaternary Extinctions, 1984; Vereshchagin and Baryshnikov, 1985; Puchkov, 1989a, b; Stuart, 1991; 1993; 2005; Putshkov, 1997; Extinction in Near Time, 1999; Zhegallo *et al*., 2001; Stuart *et al*., 2002; Hofreiter, 2007; Stuart and Lister, 2007; 2008).

The date of the extinction of a certain species is determined by the age of the latest find of its fossil remains. The dating involves some methodical problems which will be discussed below.

The process of extinction consists in an irreversible decrease in the number of individuals belonging to the species. As a result, the nearer the date of the complete extinction of a given species, the less probable is finding its remains. The remains of the last surviving individuals are hardly ever found. Therefore, we determine not the time of the last individual dying, but the time when a certain number of the species representatives were still living and their remains could be found.

The most reliable way of determining this time is based on analysis of a large series of radiocarbon dates on bones of that species. There are, however, a limited number of species for which large series of dates are available. The age of a single bone may be taken as the age of the entire faunal assemblage the bone belongs to. But again this date may be erroneous as the fauna could be really a mixture of remains of different ages. The Ustinovo locality provides an example of such a mixture (Smirnov *et al*., 1990). There is a ^{14}C date, 12 400±300 IERiZh, obtained on rodent bones from layer 3, and another date, 50 100±2300 OxA-10930, obtained on a woolly rhinoceros tooth recovered from the overlying layer 2. There are other examples of a similar inconsistency in dates obtained on bones of different species within a single elementary fauna (Smirnov and Sadykova, 2003). In our opinion, applying the age of the entire elementary fauna to dating remains of a single species – participant of the fauna – is admissible only on the condition that there are consistent radiocarbon dates for elementary faunas recovered from overlying and underlying layers. In other words, in the case of a series of consistent dates obtained for elementary faunas recovered from a single locality with a distinct sequence of sediments. Therefore, the time of extinction of the majority of individuals belonging to a certain species may be defined based on radiocarbon dating of its bones as well as on the basis of a series of radiocarbon dates obtained for elementary faunas (of which the species was a constituent) recovered from localities with a stratigraphically unambiguous sequence.

In addition, some dates obtained from associated archaeological materials have been used. In particular, pictures of animals painted by early hominins may also

[8] The analysis of the species richness during the Preboreal–Boreal was done by Andrey Puzachenko.

be used for the determination of the time of the species existence. It is evident that an ancient painter could produce a realistic drawing of only those animals he could see himself. So the dates obtained for such drawings are suitable for dating the pictured species.

The timing of extinction becomes problematic also in case of possible phyletic evolution of the species – can we consider a species to be extinct if it evolved into another species? Especially as we cannot be confident that a phyletic transformation actually took place. For example, we can state with certainty that the Late Pleistocene species *Dicrostonyx gulielmi* Sanford gave rise to the modern species *D. torquatus* Pallas (Smirnov *et al*., 1999). As for another Late Pleistocene species *Spermophilus superciliosus* Kaup, its history is not so clear. Probably it evolved into the modern *S. mayor* Pallas (Gromov, 1981). Below are given some cases of possible phyletic evolution without discussing them in details. In those cases, only the latest finds of ancestral form remains are cited.

Another problem in estimating the number of extinct species rises from uncertainties in the taxonomic status of some fossil forms. For example, there are three mole species listed in the Late Pleistocene faunas in Europe (*Talpa europaea* L., 1958; *Talpa minor* Freudenberg, 1914; *Talpa magna* Woldrich, 1893). If all three are considered as separate species, two of them should be listed as extinct at the end of Pleistocene. But if those species are not valid, no mole species became extinct.

Taking all the above problems into consideration, one cannot but draw a disappointing conclusion: at present it is impossible to answer the question how many species became extinct in Europe at the end of the Pleistocene and beginning of the Holocene.

Below only those species are discussed that disappeared from Europe and the Caucasus at the end of the Pleistocene and beginning of the Holocene. Here are used published radiocarbon dates along with some unpublished ones obtained by the author.

Don hare – *Lepus tanaiticus* Gureev, 1964

In the Late Pleistocene, the range of the Don hare covered Eastern Europe and Northern Asia (Markova *et al*., 1995). In the Early Holocene it was replaced by the alpine hare (*L. timidus* L., 1758) probably over the entire area, with only a few relict populations known from the Urals (Kosintsev, 2003a; Kosintsev, 2007). In the Southern Urals it persisted until the end of the Early Holocene. The radiocarbon age of its bones recovered from the Bayslantash locality (upper reaches of the Ufa River) is 8216±344, IEMEZh-1369. In the Middle Urals its remains were found in the cave of Bobylek, the enclosing layers were dated by archaeological materials to the Atlantic – beginning of the Subboreal period. In the Northern Urals its remains were recovered from localities dated by radiocarbon to 7213±60, IEMEZh-1338 and 5073±173, IEMEZh-1339, as well as from those dated by archaeological evidence as 4000–5000 yrs BP (Bachura and Kosintsev, 2007). So the Don hare may be considered to become extinct in the mid-Subboreal period.

Pleistocene ground-squirrels – *Spermophilus superciliosus* Kayp, 1839

There is no date on bones of this species. The latest finds on the East European Plain are attributed to the Early Holocene on the basis of geological and stratigraphical data (Gromov, 1981). *Spermophilus superciliosus* Kayp is possibly the ancestral species of *S. major* Pallas, 1778 (Gromov, 1981).

Caucasian marmot – *Marmota paleocaucasica* Baryshnikov, 1980

Remains of the species were recovered from localities dated by archaeological materials. The latest finds are attributed to the second half of the Holocene (Baryshnikov, 1979; Baryshnikov *et al*., 1986).

Binagady hamster – *Mesocricetus planicola* Argyropulo, 1939

There are no dated remains of the species. It is known to have inhabited the Caucasus since the Middle Pleistocene and probably persisted until the Middle Holocene (Baryshnikov, 1979; Baryshnikov *et al*., 1986).

Collared lemming – *Dicrostonyx gulielmi* Sanford, 1869

This species evolved into *D. torquatus* Pallas, 1779, probably 13–14 ^{14}C kyr BP (Smirnov *et al*., 1999; Smirnov, 2002). This conclusion is based on a series of 6 radiocarbon dates obtained for elementary faunas with the early form of *D. torquatus* already present (Smirnov *et al*., 1997); in two cases lower mandibles of that form were dated (Stafford *et al*., 1999). It is quite possible, however, that in some regions *D. gulielmi*

became extinct before it had a chance to evolve into *D. torquatus*.

Volga wolf – *Canis volgensis* M. Pavlova, 1930–1931

The species is thought to have become extinct in the Early Holocene (Baryshnikov and Vereshchagin, 1981; Vereshchagin, 1985). Its remains, however, are known only from localities in the middle reaches of the Volga, where they occur in alluvial deposits of uncertain age. So a conclusion on its extinction early in the Holocene seems premature until new reliably dated materials have been obtained.

Red dog – *Cuon alpinus* Pallas, 1811

Red dog remains were discovered in localities of Late Glacial age in the north of the Iberian Peninsula (Altuna, 1973, 1983, 1986) and in the south of France (Bouchud and Bouchud, 1953). It is still uncertain when it existed in the regions. At least, the species is not listed in the Late Glacial faunas in the Pyrenees (Altuna, 1999). According to Kurten, it became extinct in Europe at the end of the Late Pleistocene (Kurten, 1968). It appeared impossible to date the extinction more precisely. In the opinion of some researchers (Sommer and Benecke, 2005), both the range and timing of the species in Europe call for further investigations. Most likely it became extinct at the maximum of the last cooling, or even earlier. In the Caucasus, the red dog persisted until the Early Holocene (Vereshchagin and Baryshnikov, 1980; Baryshnikov and Chistyakov, 1985).

Deninger's bear – *Ursus (Spelaearctos) deningeri* von Reichenau, 1904

Deninger's bear is a characteristic Middle Pleistocene species in Europe (Baryshnikov, 2007). There are no radiocarbon dates on bones, the age of remains being mostly inferred from ^{14}C dates of enclosing layers and archaeological evidence. Archaeological data suggest the Caucasian subspecies extinction (*U. d. kudarensis* Baryshnikov, 1980) took place at the Pleistocene/Holocene boundary (Baryshnikov *et al*., 1986; Baryshnikov, 1987). However, there are a few radiocarbon dates which, when considered together with data on stratigraphy and taphonomy of localities with *U. d. kudarensis* bones, suggest the species' extinction in the Caucasus in the LGM at the latest.

Large cave bear – *Ursus (Spelaearctos) spelaeus* Rosenmüller, 1794

There are about 200 ^{14}C dates on bones of this species, the latest being 18720±350 Ly-2856 in the Pyrenees (Stuart, 1991); 18130±580, VRII-1030 in the Alps (Rabeder, 1999); 15570±310 in the Balkans (Spassov and Raychev, 1997); and 16470±560, COAH-4516 in the Urals (Kosintsev *et al*., 2003). Drawings of cave bear in the Chauvet cave are dated by radiocarbon to 30,000–20,000 yrs BP (Clottes, 1999). All this gives ground to the suggestion that the extinction of the large cave bear took place at the LGM/ Late Glacial boundary, about 15,000–16,000 yrs BP (Markova *et al*., 2008).

Later revision of the dates on large cave bear bones revealed the last populations of *Ursus spelaeus* disappeared from Central Europe about 24 ^{14}C kyr BP, at the beginning of the LGM (Pacher and Stuart, 2008).

Small cave bear – *Ursus (Spelaearctos) savini* Andrews, 1922

Several ^{14}C dates have been obtained on the bones of this species, the youngest one (18 800±340, IGAN-340) being on bones recovered from the Kizelovskaya cave on the western slope of the Middle Urals (Vereshchagin, 1982). A newly performed dating, however, yielded results of more than 30 ^{14}C kyr BP (Pacher and Stuart, 2008). Those results are in reasonable agreement with the remaining dates on bones of that species (Sinitsyn *et al*., 1997; Kosintsev *et al*., 2003; unpublished data of the author).

Cave hyena – *Crocuta crocuta spelaea* Goldfuss, 1823

The cave hyena is regarded as a subspecies of the spotted hyena (*C. crocuta* Erxleben, 1777), and therefore properly speaking it cannot be attributed to extinct species. It is customary, however, to consider its disappearance from Europe as extinction (Stuart, 1993; Stuart and Lister, 2001, 2007).

There are more than 30 radiocarbon dates on cave hyena bones (Stuart, 1991; Currant and Jacobi, 2001; Germonpré, 2004; Hofreiter *et al*., 2004; Jacobi *et al*., 2006; Stuart and Lister, 2007), the latest is 23120±130, OxA-13659 obtained on a bone from Goat's Hole in Great Britain (Jacobi *et al*., 2006). It should be noted that the age of all reliably dated elementary faunas including cave hyena exceeds 20,000 years. A review of

hyena remains found in the former USSR and in Western Europe does not include localities younger than 25,000 yrs BP (Baryshnikov and Vereshchagin, 1996; Baryshnikov, 1999). There are no reliably identified cave hyena remains in faunas younger than 18,000 yrs on the Iberian Peninsula (Altuna, 1994; 1999); in Ireland (McCormic, 1999); Great Britain (Stuart, 1983); in the northwest of Europe (Street and Baales, 1999); in Moldavia (David, 1999); or in the Crimea (Benecke, 1999). In the Urals, all the reliably dated faunas with cave hyena are older than 25,000 yrs BP (Kuzmina *et al*., 1999; Kuzmina, 2000; Kosintsev, 2003; unpublished data of the author). The Chauvet Cave drawings with a picture of a hyena-like animal are radiocarbon-dated between 30,000 and 20,000 yrs BP (Clottes, 1999).

It may be safely concluded that the *Crocuta c. spelaea* became extinct in Europe at the onset of the LGM.

Cave lion – *Panthera (Leo) spelaea* Goldfuss, 1810

Radiocarbon dates on the bones of this species are few in number (Housley, 1991; Stuart, 1991; Burger *et al*., 2004). Some young dates have been recently discussed in a paper by Stuart and Lister (2007), the youngest of them – 12 375±50, OxA-17268 – was obtained on a bone sample from a locality in Germany. In Eastern Europe, a bone from a cave locality in the Middle Urals yielded the youngest date of 13 500±65, OxA-11349 (Stuart and Lister, 2007). In the Middle Urals and the Crimea, cave lion remains were recovered from localities dated to the Bølling-Allerød (Benecke, 1999; the author's data), though the bones themselves have not been dated. No confidently identified remains of cave lion are known from Early Holocene localities. That suggests extinction of the species during the Bølling-Allerød. There are, however, cave lion remains in the materials obtained from settlements in Southeastern Europe, the northern coasts of the Black Sea and in the lower reaches of the Dnieper; the settlements are dated to the second half of the Middle Holocene and beginning of the Late Holocene (Subboreal and Subatlantic periods) (Gromova, 1928; Bibikova, 1973; Zhuravlev, 1973; Vörös, 1983; Krakhmalnaya, 1999; Ninov, 1999; Zuravlëv, 1999). Those finds are attributed to the modern species *Panthera leo* L., 1758, though no special studies of the remains in comparison with cave lion bones have been performed. It is not inconceivable that they belong to cave lion; a relict population of the latter could persist in the south of the Balkan Peninsula and later disperse northwards and northeastwards. So, the timing of the extinction of the cave lion will remain unresolved until the species status of the European lions in the Holocene has finally been established.

Mammoth – *Mammuthus primigenius* Blümenbach, 1799

The process of the mammoth extinction in Europe has been described in detail elsewhere (Stuart *et al*., 2002; Stuart, 2005), so there is no need to repeat it here. We will give only the latest dates obtained for the European mammoths: 10 100±100, Hela-423 and 10 200±200, Hela-425, on two mammoth teeth from Puurmani, Estonia (Lõugas *et al*., 2002); 9760±40, GIN-8885c; 9810±100, GIN-8867a; and 9840±50, GIN-8885b, on skeletal bones recovered from the Zhidikhin swamp in Russia, Vologda region, Cherepovets district (Stuart *et al*., 2002; Yashina, 2002); and 10 000±800, LE-5521 on bones recovered from a quarry in the village of Bolshaya Selmenga (Yashina, 2002). It may be concluded from the above that the last mammoth population in Europe persisted to the beginning of the Preboreal period.

Woolly rhinoceros – *Coelodonta antiquitatis* Blümenbach, 1799

More than 70 ^{14}C dates were obtained on woolly rhinoceros bones from European and Uralian localities (Current, 1986; Stuart, 1991; Erokhin and Chairkin, 1995; Danukalova *et al*., 2002; Kosintsev *et al*., 2005; Stuart and Lister, 2007). The youngest remains were found in the east of Europe. A bone from the Lobva Cave (the Middle Urals) is dated at 12 275±55, KIA-5670 and 9510±260, IRiZh-93, (Erokhin and Chairkin, 1995). Rhinoceros teeth from the Zlatoustovka locality in the Belaya River drainage basin yielded a date of 12 330±120, LU-1668 (Danukalova *et al*., 2002). The species most likely disappeared before 13,000 yrs BP from the greater part of Southern, Central and Western Europe (Stuart, 1983; 1991; Altura, 1999; David, 1999; Street and Baales, 1999; Stuart and Lister, 2007). Nevertheless, its remains are present in faunas from the Verlaine and Goget localities in Belgium dated at 12 870±110, OxA-4014; 12 770±90, GrA-3237; 12 620±90, GrA-3238 (Germonpré, 1997), as well as in the Palaeolithic site of Gönnersdorf in Central Germany; the latter is dated at about 12,500 yrs BP (Bosinski, 1981). It is possible that in some regions of Europe the woolly rhinoceros extinction occurred at about 12, 000 yrs BP.

True horses – *subgenus Equus (Equus)* L., 1758

No less than two horse species of Late Pleistocene age are recognized by palaeontologists in Europe (see above),

while only one species – tarpan (*E. gmelini* Antonius, 1912) – lives through the Holocene. If this is the case, at least one horse species became extinct in Europe at the beginning of the Holocene. The situation may be clarified after the taxonomic problem has been settled.

Giant deer – *Megaloceros giganteus* Blümenbach, 1803

Bone remains of this species yielded more than 40 radiocarbon dates (Gonzales *et al*., 2000; Kosintsev, 2003b; Aaris-Sørensen and Liljegren, 2004; Stuart *et al*., 2004), which allows us to trace the process of its extinction (Stuart *et al*., 2004). The majority of the populations have died by the end of the Younger Dryas, though in the western and eastern parts of its range the giant deer persisted beyond the Pleistocene-Holocene boundary. The giant deer bones recovered from two localities in Ireland were dated at 9430±65, AA-18513 and 9225±85, AA-29744 (Gonzales *et al*., 2004), which corresponds to the Preboreal – beginning of the Boreal periods. Five localities in the Middle Urals produced radiocarbon dates as follows: 10 260±55, OxA-10676; 9960±55, OxA-11063; 7990±45, OxA-11064; 7034±34, OxA-13014; 6968±33, KJA-5668; 6881±38, OxA13015; 6816±35, KJA-5669 (Stuart *et al*., 2004). The dates show the gradual extinction process of the giant deer. It seems possible that the species finally disappear in the mid-Atlantic period.

Bisons – *Bison priscus* Bojanus, 1827; *Bison schoetensacki* Freudenberg, 1910; *Bison bonasus* L., 1758

As was mentioned in the section on the problems of systematics, there are two hypothesis on the bison evolution in Europe. Regardless of which of the hypotheses is true, *Bison priscus* practically disappears from the European faunas at the beginning of the Holocene (Gromova, 1965; Flerov, 1979; Baryshnikov, 1981). This is supported by 42 radiocarbon dates on bison bones recovered from Uralian locations, all of which are older than 12,000 yrs BP. It may have survived until the Preboreal in the Crimea (Bibikova, 1984; Benecke, 1999), and there are indications that *Bison priscus* still lived in the south of the Russian Plain in the Subatlantic period of the Holocene (Vereshchagin and Baryshnikov, 1985). The latter, however, is to be confirmed by convincing evidence. It seems most likely that *Bison priscus* became extinct – or evolved into *Bison bonasus* – during the Preboreal.

Siberian muskox – *Ovibos moschatus* Zimmermann, 1780

As has been noted above, we regard the Eurasian and the North American musk ox as different species. Anyhow, musk ox populations completely disappeared from Europe. After the LGM period, when musk ox was most widely spread in Europe (Cregut-Bonoure, 1984; Altuna, 1994), its range began to reduce and retreat towards the north and northeast. Seven dates have been obatined on its bones from European localities (Stuart, 1991; Germonpré, 1996; Mangerud *et al*., 2002; unpublished data of the author), all of them belong to the Late Glacial interval. The youngest date – 11 450±90 (Ki-14962) – was obtained on bone from the Verchnegubachinskaya cave in the Middle Urals.

The above discussion of the mammal extinction processes in Europe in the period between the last maximum cooling of the late Pleistocene and the Boreal period of the Holocene revealed a number of complicated problems to be solved. The problems arise not only from the above noted difficulty in determining the time when the last animals of the species disappeared. There are also some other methodical complications. First of all (as has been mentioned above), the case of phyletic speciation – may the disappearance of the ancestral species be considered as extinction? On the one hand, the genetic material (genofond) of the ancestral species does not disappear completely, on the other the genofond of the new species is not identical to the former, as speciation leads to a break in the genetic continuity and to development of a new genetic (or, more precisely, ecological-genetic) entity. In our opinion, there is no extinction *s.s.* of the ancestral species in case of phyletic speciation. There is a constructive aspect in such an approach. On the one hand, the phyletic speciation leads to changes in the fauna composition, on the other; it results from some essential changes in the environments and/or the ecological-genetic structure of the ancestral species. This problem is part of the general problem of taxonomic status determination for fossil forms.

In this context we do not discuss forms whose status as a separate species is doubtful. We do not consider cave pika (*Ochotona spelaea* Owen, 1846), as it has not been recognized as a valid species (Erbajeva, Currant, 2003). The species *Talpa magna*, *Cricetus major*, and *Arvicola antiquus*, cited by Storch (1974), are hardly valid (Stuart, 1991). The same is true of the Volga wolf, *Canis volgensis*, M. Pavlova, 1930–1931. The species status of a number of species, including the Don hare (*Lepus tanaiticus*), Binagady hamster (*Mesocricetus planicola*), Siberian muskox (*Ovibos moschatus*), and lion that existed in Europe in the Holocene (*Panthera leo* or *P. spelaea*), has not been conclusively proven. The time of red dog presence in Europe is still not clear. There is

no agreement among the specialists as to the number of species of moles, shrews, horses and bisons inhabiting Europe during the Late Pleistocene. The majority of palaeontologists considers the Late Pleistocene ground squirrel (*Spermophilus superciliosus*) and collared lemming (*Dicrostonyx gulielmi*) to be separate species evolving later into russet (red-cheeked) suslik (*S. major*) and modern collared lemming (*D. torquatus*) respectively (Table 4.8).

Table 4.8

Time of mammal extinctions in Europe in the end of Pleistocene–Holocene

Taxa	Date** ^{14}C	Likely time of extinction	Possible time of extinction
Lepus tanaiticus	5073**	Subboreal	Subboreal
Spermophilus superciliosus		Preboreal–Boreal	Preboreal–Boreal
Marmota paleocaucasica		Preboreal	Preboreal
Mesocricetus planicola		Preboreal	Boreal
Dicrostonyx gulielmi	14200**	Vepsa glacial stage	Vepsa glacial stage
Cuon alpinus		Preboreal	Boreal
Ursus deningeri		Preboreal	Boreal
Ursus spelaeus	15570**	The end of LGM	Younger Dryas
Ursus savini	18800**	LGM	The end of LGM
Crocuta crocuta spelaea	22880**	LGM	LGM
Panthera spelaea	10670**	Younger Dryas	Subatlantic
Mammuthus primigenius	9760**	Preboreal	Preboreal
Coelodonta antiquitatis	9510±260*	Preboreal	Preboreal
Megaloceros giganteus	6816**	Atlantic	Atlantic
Bison priscus		Preboreal	Boreal
Ovibos moschatus		Preboreal	Boreal

* reliable data.
** the dates received by the bones of this species.

Conclusion

Thus, there is possible to reveal two "time of extinction" for every extinct species. The first one is the time of probable dying-out defined by the latest reliably dated find of its remains. Reliability of dating is discussed above. The second time is the time of possible extinction, when the last animals of the given species might have disappeared. The latter is essentially an expert evaluation derived from the totality of dates obtained for associated faunas, as well as from geological, stratigraphical and palaeogeographical evidence. Both times are given in the table. Analysis of the table reveals the species extinction being a rather prolonged process spanning the interval from the LGM to the Atlantic, and probably to the Subboreal period. Two peaks may be recognized in the process. The first falls in the maximum cooling, 24,000 to 17,000 yrs BP, when at least 4 species died out in Europe, among them large and small cave bears, Deninger's bear, cave hyena and possibly red dog. The second peak of extinctions is dated to the end of the Pleistocene and early Holocene (12,000 to 8,000 yrs BP), when as many as 5 species disappeared and 2 or 3 evolved into other species. The given numbers are only approximate due to methodical complications as discussed above. At that time mammoth, woolly rhinoceros, musk ox and Caucasian marmot are likely to disappear, and most probably also cave lion and bison; the Pleistocene ground squirrel, Binagady hamster, and probably bison and horse evolved into other species. Between the two intervals, the Late

Pleistocene collared lemming evolved into the modern collared lemming. Later on, in the Atlantic–Subboreal periods, the giant deer and Don hare also became extinct. It is evident, therefore, that in Europe the mammal fauna underwent major transformations at the Pleistocene/Holocene boundary.

4.7. DOMESTICATION OF MAMMALS

Pavel Kosintsev

In the period under consideration, pioneer domestic mammals appear in Europe: the dog at the end of the Pleistocene, cattle, sheep, goat and pig in the Early Holocene (Shnirelman, 1980, 1989; Davis, 1987; Benecke, 1993, 1999).

Dog – *Canis lupus* f. *familiaris* L., 1758

The wild ancestor of the dog, the wolf (*Canis lupus* L., 1758), has a very extensive area, namely Europe and almost the whole of Asia and North America. In such a large area there probably were several domestication centres of the wolf. One of these was in Europe. It is highly probable that in Europe the wolf could have been domesticated in different regions and at different times. The most ancient bone remains belonging to a dog were found in the settlement of Eliseevichi (Sablin and Khlopachev, 2002). The cultural layer of this settlement was radiocarbon dated on mammoth bones and charcoal. Eleven ^{14}C dates were obtained: four are within the time span 20,570–15,600 yrs BP, five dates within 14,590–14,080

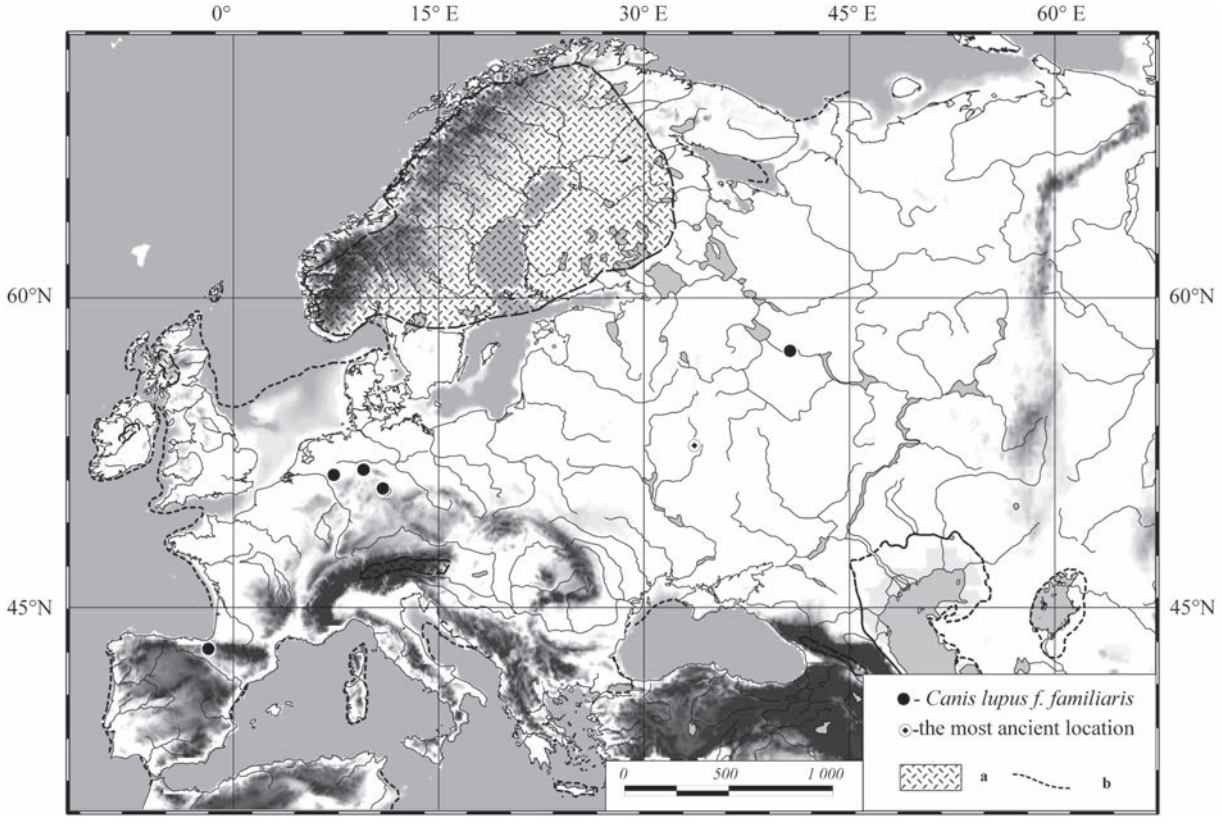

Fig. 4.72. *Dog Canis lupus f. familiaris localities in the Upper Palaeolithic settlements; a – ice sheets; b – coastline*

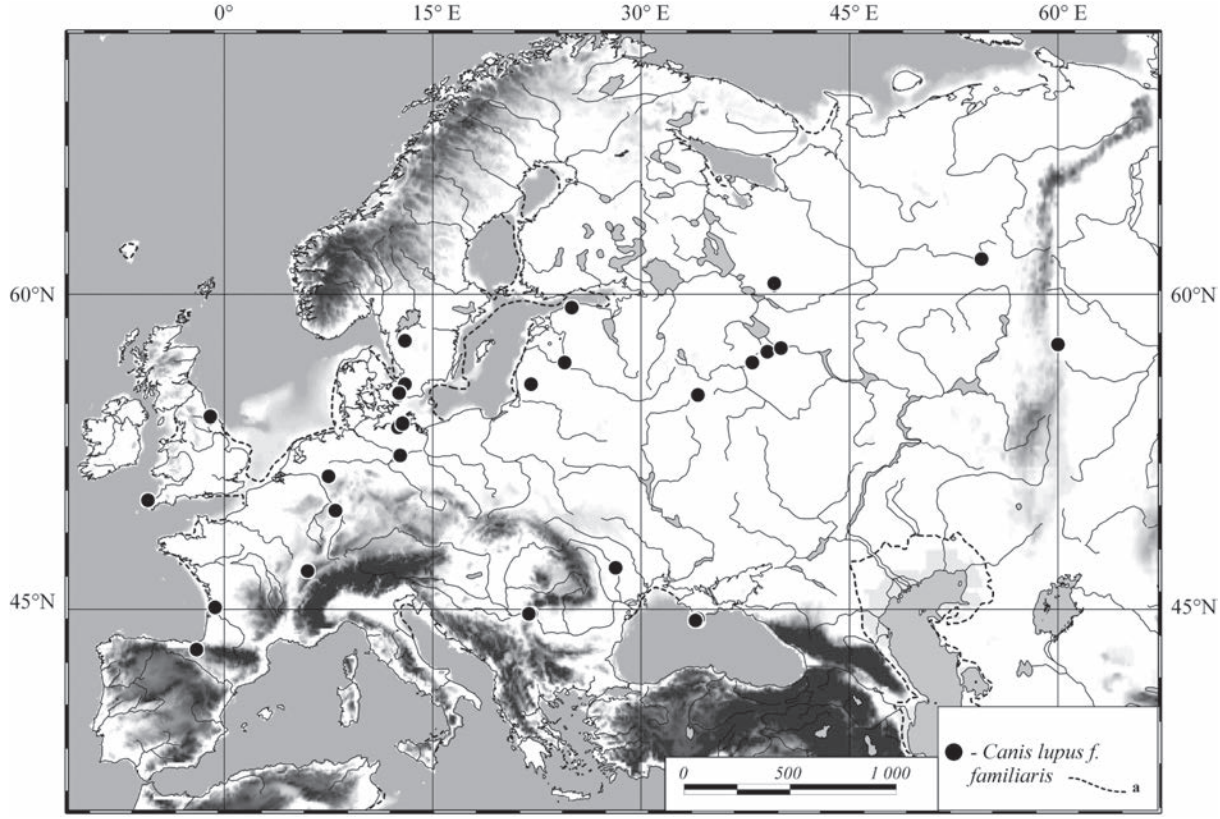

Fig. 4.73. *Dog Canis lupus f. familiaris localities in the Mesolithic settlements; a – coastline*

and two dates within 12,970–12,630 yrs ago (Lisitsin *et al*., 1997). Thus, the most probable age of the cultural layer containing dog's bones is not younger than 14,000 yrs BP. Besides, the remains of dogs were found in 6 other Upper Palaeolithic settlements (Fig. 4.72).

All of these have an age of less than 13 kyr BP (Benecke, 1993). In the Mesolithic period (Preboreal–Boreal), the number of sites containing dog bones is substantially larger (Serikov and Kuzmina, 1985; Benecke, 1993; Oshibkina, 2000). Such sites are located all over Europe (Fig. 4.73).

Cattle – *Bos primigenius* f. *taurus L.,* 1758;

Sheep – *Ovis* ammon f. *aries* L., 1758;

Pig – *Sus scrofa* f. *domestica* L., 1758;

Goat – *Capra aegagrus* f. *hircus* L., 1758.

The earliest findings of these animals in Europe belong to the beginning of the Boreal period. In the Pre-pottery Neolithic settlements (Argissa Magula, Soufli Magula, Sesklo, Nea Nikomedia and others) in the southern part of the Balkan Peninsula, bones of cattle, sheep and pig were found (Bökönyi, 1974; Clutton-Brock, 1981; Uerpmann, 1990; Benecke, 1999). Some researchers suppose that in the Boreal cattle, sheep and goats appeared also in the Northern Caucasus (Davis, 1987). By the end of the Boreal cattle, sheep, goat and pig appear in the Middle Danube area (Uerpmann, 1990).

The first domestic ungulates were brought by farming and cattle-breeding groups of people migrating to Europe from Anatolia (Tringham, 1971). But, it should be noted that wild ancestors of cattle (*Bos primigenius* Bojanus, 1827), pig (*Sus scrofa* L., 1758) and sheep (*Ovis ammon* L., 1758) inhabited Europe, so autochthonous domestication of these species was possible. Some researchers admit the possibility of domestication of aurochs and wild boar (Boessneck, 1961; Rodden, 1962).

As a result, by the end of the Boreal in Southeastern Europe and, probably, in the Northern Caucasus, stable areas of nearly all main domestic animals, cattle, sheep, goat and pig, had formed. Dog by that time was already ranging over the whole of Europe.

4.8. SPATIAL AND TEMPORAL DYNAMICS OF EUROPEAN MAMMAL DIVERSITY DURING THE END OF THE LATE PLEISTOCENE – HOLOCENE

Andrey Puzachenko and Anastasia Markova

Analysis of the pattern of change in species composition, mammal distribution, as well as the structure of their communities due to climate changes over the last 10–25 thousand years has provided information important for forecasting probable evolutionary trends in mammal diversity and distribution in the future, for different scenarios (warming, cooling).

Data on European mammal diversity and distribution in the period of transition from the Pleistocene to the Holocene are also topical in the context of preserving the gene pool of this group, including those being exposed to anthropogenous pressure.

The Last Glacial Maximum (24–17 kyr BP, LGM) was the coldest part of the Valdai (=Weichselian) Glaciation and the time with one of the most severe climates in the Pleistocene. In Europe, it was accompanied by the formation of a significant (but not the most significant one in Pleistocene) ice sheet in the north and northwest of Europe, the development of mountain glaciation and the wide distribution of specific periglacial landscapes. The period from 17 to 10 kyr BP witnessed a gradual warming of the climate, interrupted by periods of a decrease in temperature (Fig. 4.74). According to available data, the difference in mean annual temperatures between the present Holocene and the time of the Late Valdai Glaciation Maximum was about 8 degrees (Petit *et al*., 1999).

There are numerous reconstructions of Europe's natural components for the epoch of the Late Valdai glaciation and the transition period from the Pleistocene to the Holocene: those of climate, vegetation cover, mammal fauna, cryogenic phenomena, loess cover, etc. (Markov *et al*., 1965; Velichko, 1973; Europe's Paleogeography…, 1982; Grichuk, 1989; Klimanov, 1989; Atlas of Paleoclimates and Paleoenvironments, 1992; Kozharinov, 1994; Zelikson, 1994; Markova *et al*., 1995; 2002; 2003; Petit *et al*., 1999; Baryshnikov and Markova, 2002; Landscape Components Dynamics, 2002; Davis *et al*., 2003; Barnosky *et al*., 2004; Markova, 2004; Simakova and Puzachenko, 2005; etc.).

In this period, the territory of Europe was home to a wide representation of the so-called 'mammoth complex' of mammals characterized by the presence of the mammoth (*Mammuthus primigenuis*), woolly rhinoceros (*Coelodonta antiquitatis*), reindeer (*Rangifer tarandus*), muskox (*Ovibos moschatus*), wild horse (*Equus ferus*), and saiga (*Saiga tatarica*). Typical complex representatives among small mammals were: steppe and yellow lemmings (*Lagurus lagurus, Eolagurus luteus*), arctic lemming and brown lemming (*Dicrostonyx gulielmi, Lemmus sibiricus*), narrow-skulled vole (*Microtus (Stenocranius) gregalis*), etc. (Agadjanian, 2001).

It has been found (Markova, 2004) that the mammals' reaction to the Late Valdai cooling (as well as to other Pleistocene coolings) differed in direction and scale, leading to the emergence of original communities with no modern analoguess. Thus, in Eastern Europe (the Russian Plain), tundra species of large and small mammals reached as far south as 48°N. Steppe zone fauna representatives, on the contrary, moved far to the west and north, into the modern forest zone. At the same time, forest and forest-steppe species of flexible ecology and taiga species changed their ranges insignificantly. Mammals of nemoral forests disappeared from the Russian Plain, basically remaining only in the mountain refugia, some uplands and extrazonal habitats located along valleys of big rivers. A similar picture was observed in the west and southwest of Europe where individual representatives of Pleistocene herbivores, adapted to the periglacial landscapes (woolly mammoth, woolly rhinoceros, etc.) moved to the south, down to approximately 45°N. At the same time, mountain areas of Western and Central Europe, as well as regions in the extreme south, southwest and southeast offered possibilities for survival of thermophilic and nemoral forms, which had become extinct in other parts of Eurasia.

The reaction of mammals to global climate warming in post-glacial times was also multidirectional. The 'mammoth complex' disintegration in Europe included extinction or sharp ('catastrophic') shrinkage of habitats of several species (the mammoth, woolly rhinoceros, musk ox, reindeer, steppe bison (*Bison priscus*), and arctic fox (*Vulpes lagopus*)). Due to the formation of the forest zone and modern tundra zone, the habitats of tundra and steppe species were divided. Forest species expanded their distribution ranges extensively. On the

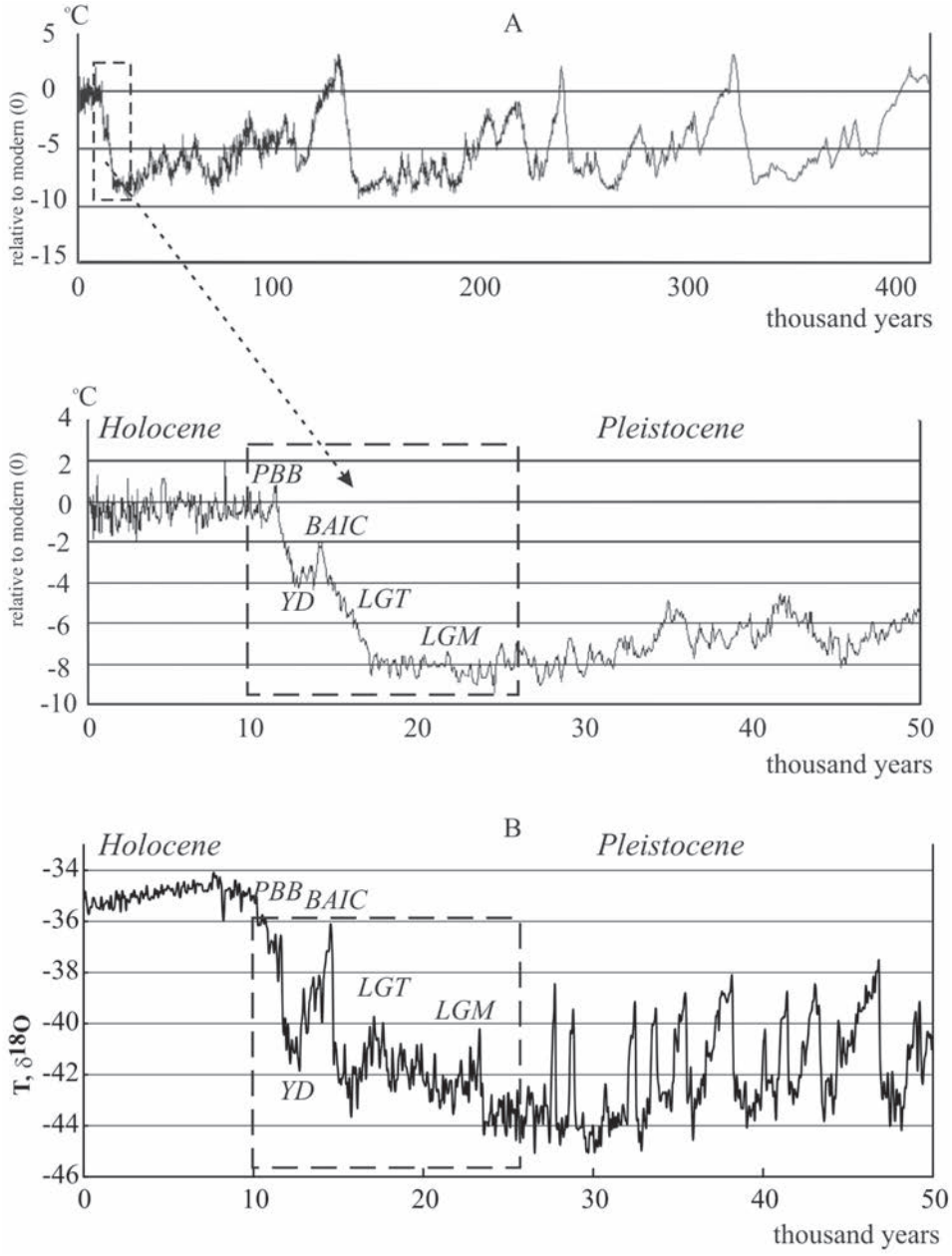

Fig. 4.74. *A – Mean annual temperature dynamics (Southern Hemisphere) over the last 420,000 yrs according to the 'Vostok' station, Antarctica (acc. to Petit et al., 1999)*[9]*. B – NGRIP North Greenland Ice Core Project Oxygen Isotope Data, NGRIP (Andersen et al., 2004)*[10]*. The main stages of transition from the Late Valdai glaciation to the Holocene are: LGM – Last Glacial Maximum, LGT – Late Glacial Transition, BA – Bølling/Allerød warming, YD – Younger Dryas cooling*

whole, the spatial distribution of mammals and mammal assemblages was becoming more and more zonal.

Against this background, the total number of mammal species in Europe (species richness), apparently, has not undergone significant changes. Europe's modern continental mammal fauna totals at least 190–200 species (Görner and Hackethal, 1987). The number of extinct species in the Late Pleistocene – Early Holocene in relation to their total number is insignificant. It includes large herbivores and also carnivores: mammoth, woolly rhinoceros, musk ox, giant deer (*Megaloceros giganteus*), spotted hyena (*Crocuta crocuta spelaea*), cave lion (*Pan-*

[9] http:// www.clearlight.com / ~ mhieb/WVFossils/last_400k_yrs.html

[10] Andersen, K.K., Azuma, N., Barnola, J.M., Bigler, M. et al., High-resolution record of Northern Hemisphere climate extending into the last interglacial period. Nature, 2004. v. 431, No. 7005, pp. 147–151.

thera spelaea), cave bear (*mainly a plant feeder species*) (*Ursus spelaeus*), etc. (about 10 species in total). Thus, losses of the number of species due to direct and indirect influence of climate reorganization, probably, were about 5%. Hence, the main effect of events accompanying the transition from the Last Ice Age to modern times in Europe was that the mammal ranges drastically changed in geographical space, which was connected with local changes in species diversity. The purpose of this research is to give a quantitative estimation of this process.

Extensive Late Pleistocene – Early Holocene mammal data on Eastern and Western Europe was integrated for the first time, which allowed us to get a complete picture of species diversity evolution in Europe. Initial data includes the lists of mammal species from localities with ^{14}C data and concise coordinates (see chapter 1 of this book).

Methods and Materials

For our analysis, we applied rather general methods and focused on: 1) the detection of meaningful underlying 'virtual factors' reproducing the basic properties of the species occurrence in the deposits of different ages and at different locations (we used nonmetric multidimensional scaling (Shepard, 1962)); 2) the identification of factors reproducing the spatial variability in the local fauna structure; 3) the reconstruction of spatial units with similarity in the characteristics of species diversity (classification of localities); 4) the quantitative characteristics of the diversity changes on the basis of informational indices (Shannon's entropy, degree of 'organization', Kullback's entropy) (Kullback, 1959). The first three research 'program' items are described in detail in the following publications[11] (Markova *et al*., 2002 a,b; Kupriyanova *et al*., 2003; Puzachenko, 2005; Simakova and Puzachenko, 2005).

Quantitative measurements of diversity were carried out on the basis of Shannon's statistical entropy, the value of which was determined for every virtual factor at the number of gradations of the variable, $k = \log_2(N) + 1$ (N – sample size, number of locations): $H = -\sum_{i=1}^{k} p_i \log_2 p_i$ ($p_i = n_i/N$; n_i – number of i-th class locations; $\sum p_i = 1$). Then we calculated the evenness (E, not dependent on the k) $\left[\sum_{j=1}^{m} H_m\right] \Big/ m\log_2 k$, where H_m is the entropy, m is the number of virtual factors which forms the basis of the degree of organization (MO): 1-E. MO varies in the range 0 to 1. The higher the MO value, the greater the degree of restrictions for random occurrence of different species in the same place, and the stronger the influence of factors regulating diversity.

As virtual factors are linearly independent, the final entropy value can be estimated as a simple sum of entropies of all factors. Along with the above parameters, we calculated "relative entropy" or Kullback-Leibler's divergence (Kullbak and Leibler, 1951): $J = \sum_{i=1}^{k} p_i \log_2(p_i/P_i)$, where the P_i are the probabilities of normally distributed random values (with sample average and variance), corresponding to the sample probabilities observed p_i (i = 1, …, k). Kullback-Leibler's divergence gives an assessment of the deviation of the observed distributions from a random normally distributed model. We used a value that is based on the average over all virtual factors.

The data analysis (stages 1–4) was performed separately for the following time slices of the Late Pleistocene and the Early Holocene: Late Valdai Glacial Maximum (24–17 kyr BP; 147 localities); Late Glacial transition (17–12.4 kyr BP; 80 localities); Bølling/Allerød warming (12.4–10.8 kyr BP; 53 localities), Younger Dryas (10.8–10.1 kyr BP; 30 localities), and Preboreal-Boreal (10.1–8 kyr BP; 145 localities). The available information for the various time slices differs significantly, which is inevitably reflected in the quality of palaeoreconstructions. For this reason, we do not produce a reconstruction for the Younger Dryas and Bølling/Allerød mammal assemblages as not enough data were available.

On the basis of modern European mammal distributions (except for the bats, Chiroptera), a similar analysis was carried out. For this study the mammal localities were replaced by conventional 'points' (508 units) located regularly on a 2×2 degrees geographical grid covering the whole of Europe. For each 'point', a qualitative mammal composition was determined.

Results

Modern status of the European mammal diversity

Three virtual factors have been singled out for Europe's modern mammal fauna. The first and most significant factor is correlated with geographical latitude (Spearman's correlation, r_s = 0.94). The third factor reflects longitudinal changes in the fauna composition (r_s = 0.92). The second factor is in non-linear correlation with latitude, but it also reproduces 'azonal' aspects of the spe-

[11] See also Puzachenko Yu. (2004).

cies distribution. All three factors jointly describe about 80% of the species diversity in 'local' faunas (including the carnivorous mammals 64%, the ungulate mammals 28%, rodents and lagomorphs 79%). Thus, the geographical location itself determines about 26% of the diversity variation only.

Figure 4.75 presents a scheme of modern zoogeographical zonation in Europe, obtained from a classification based on three virtual factors. It follows from Figure 4.100 that latitudinal curving of unit borders prevails both in the east and the west of Europe. Alongside with it, latitudinal-meridional gradients are observed in Central Europe.

Figure 4.75 (*a–d*) illustrates the modern diversity of mammal species in Europe. Along with specificity of certain mammal ranges belonging to the different groups (carnivores, herbivores, rodents), it is possible to indicate the areas with a high level of species richness (diversity 'centers'), such as: the Caucasus, the South Urals, the Carpathians, and the Southern Alps. Secondary diversity 'centers' are determined by specificity of the distribution of certain mammal groups. For example, the high distribution of rodents in some regions (in the Desna River basin, in the Volga Uplands); the high diversity of carnivores in the Middle Urals, the Karelian Isthmus; the high species richness of herbivores on the Byelorussian Ridge, and in the mountain regions of Central and Western Europe.

Information parameters of the modern mammal fauna diversity indicate a high level of spatial differentiation (MO = 0.23) and a significant degree of deviation from the 'equilibrium' state (J = 0.37).

Mammal diversity in the Late Glacial Maximum

Only two principal factors influencing mammal diversity have been determined for the LGM. The first factor reflects diversity variability by latitudinal gradient (r_s = 0.80). The second factor mainly by longitude (r_s = 0.85). At the same time, the first and the second factors are in a non-linear connection. Both factors jointly describe about 55% of the species diversity variability. The geographical position of locality itself determines no more than 7% of the diversity variation.

Figure 4.76 presents the zoogeographical zonation during the LGM. In the west of Europe, the unit borders stretch in latitudinal direction, while in the east and northeast of the Europe they stretch in latitudinal-meridional direction. The Carpathian Mountains are the border between the western and eastern sectors of Europe.

Figure 4.76 presents the variation of species diversity in the period under consideration. Information parameters of diversity specify a relatively low level of spatial differentiation (MO = 0.17) and 'equilibrium' of the entire mammal complex (J = 0.17). In other words, 'zonal' borders are less clearly marked than in modern times, and very wide areas are typical of most species.

Mammal Diversity during the Late Glacial transition period (17–12.4 kyr BP)

This period indicates the beginning of progressive climate warming and the degradation of ice sheets. The mammal diversity structure is determined by three factors. There are no factors reflecting its variability by latitude or longitude only. The latitudinal gradient is determined by the first and second factors (r^2 = 0.58); the longitudinal gradient by all three, but to lesser extent (r^2 = 0.45). The factors jointly describe about 78% of the species diversity variability. The 'point's' geographical location determines about 19% of the diversity variation.

The reconstruction of the distribution of mammal assemblages in this period is presented in Figure 4.31. In general, the direction of the zoogeographical borders is similar to that observed in the previous time interval (LGM). Major borders between zoogeographical units are expressed more clearly than in the glacial period (MO = 0.22) and, accordingly, their structure (content) (J = 0.29) is better determined. Figure 4.77 presents the variation of species diversity during the LG.

Mammal diversity in the Bølling/Allerød Warming (12.4–10.8 kyr BP)

The Bølling/Allerød is a short stage of sharp warming against a background of the general trend from the maximum glaciation to the Holocene (Fig. 4.78). The mammal diversity structure is determined by three factors. Only the first, leading factor has shown strong correlation with geographical latitude (r_s = 0.85). It is only the large herbivorous mammal diversity variability (r_2 = 0.33) that is reproduced rather well by the factors in the linear regression model. On the whole, the correlation of the diversity value with the factors is nonlinear and is reproduced by a second order polynomial (quadratic equation). Within the framework of this model, 71% of the species diversity on the whole, 55% of the carnivorous mammal's diversity, 74% of the large herbivorous mammals are described. It is not obviously possible 'to predict' the diversity value on the basis of the geographical location of occurrence.

The primary direction of the Bølling/Allerød zoogeographical borders is a latitudinal one. Information parameters of the diversity specify a relatively low level of spatial differentiation (MO = 0.18) with a relatively

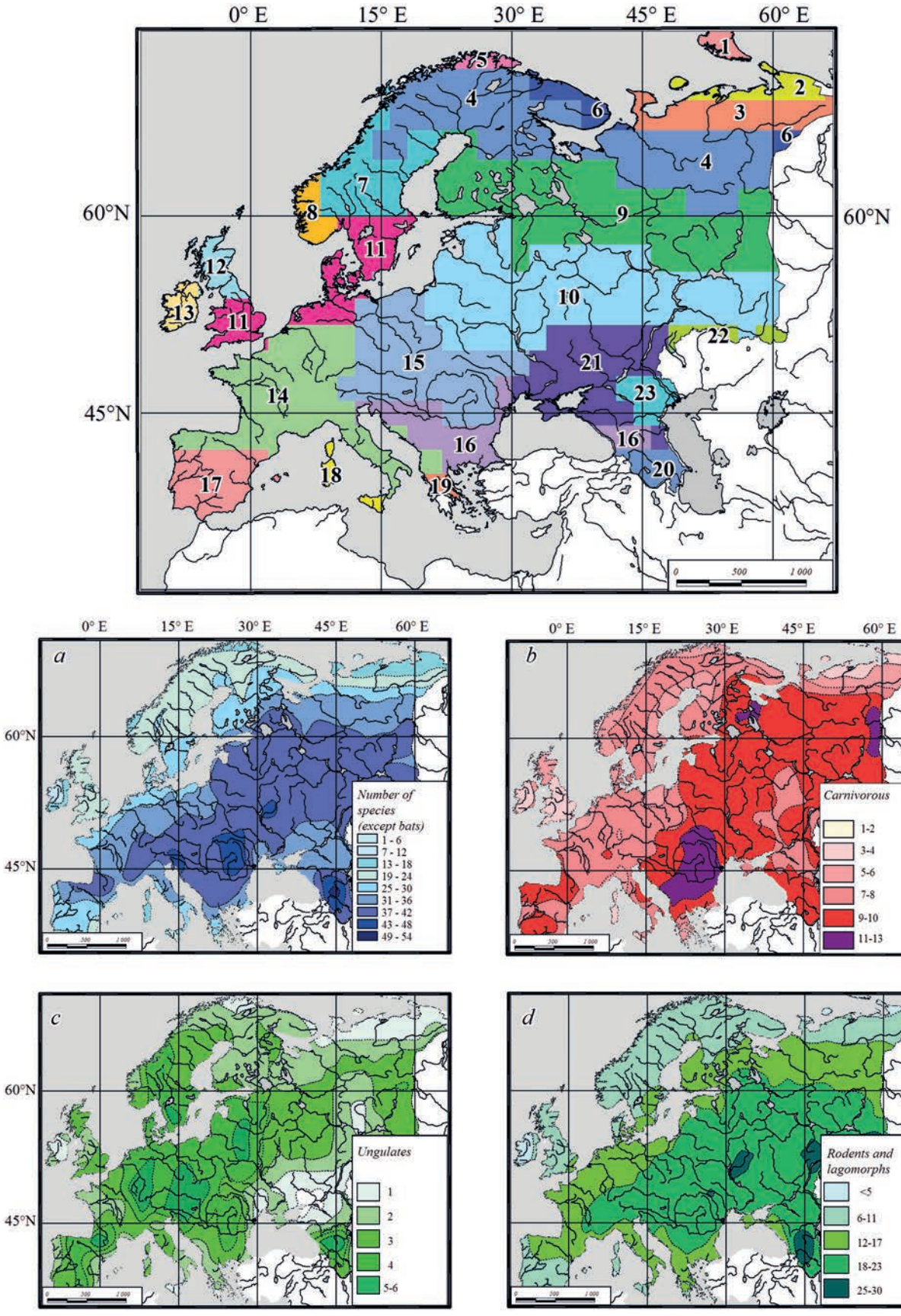

Fig. 4.75. *European biogeographical zonation (23 units) on the basis of modern continental mammal distribution and skeleton maps of species diversity: a – all mammal taxa; b – carnivores, c – ungulates, d – rodents*

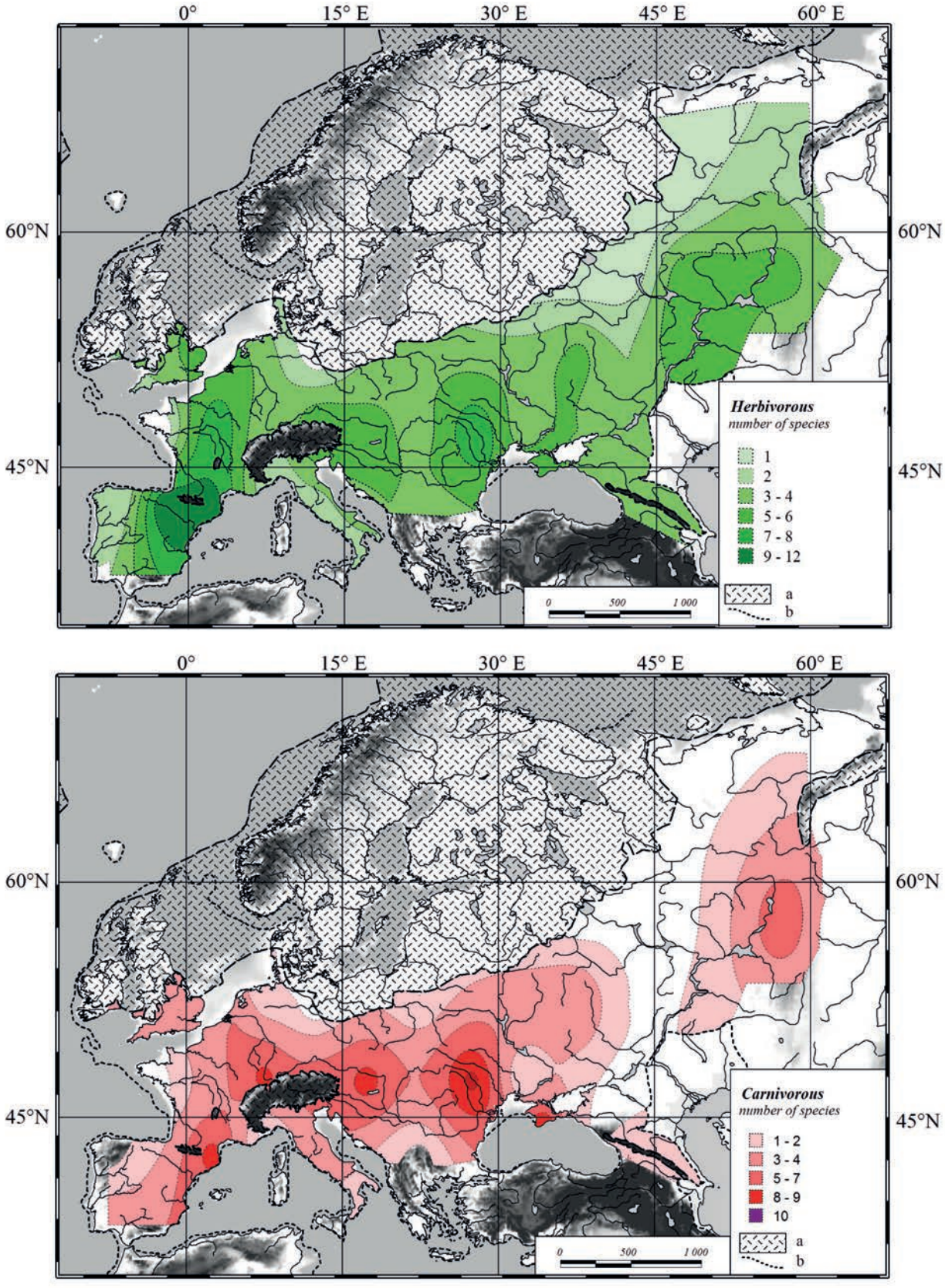

Fig. 4.76. *Herbivorous (upper fig.) and carnivorous (lower fig.) species diversity in Europe between 24–17 kyr BP; a – ice sheets, b – coastline*

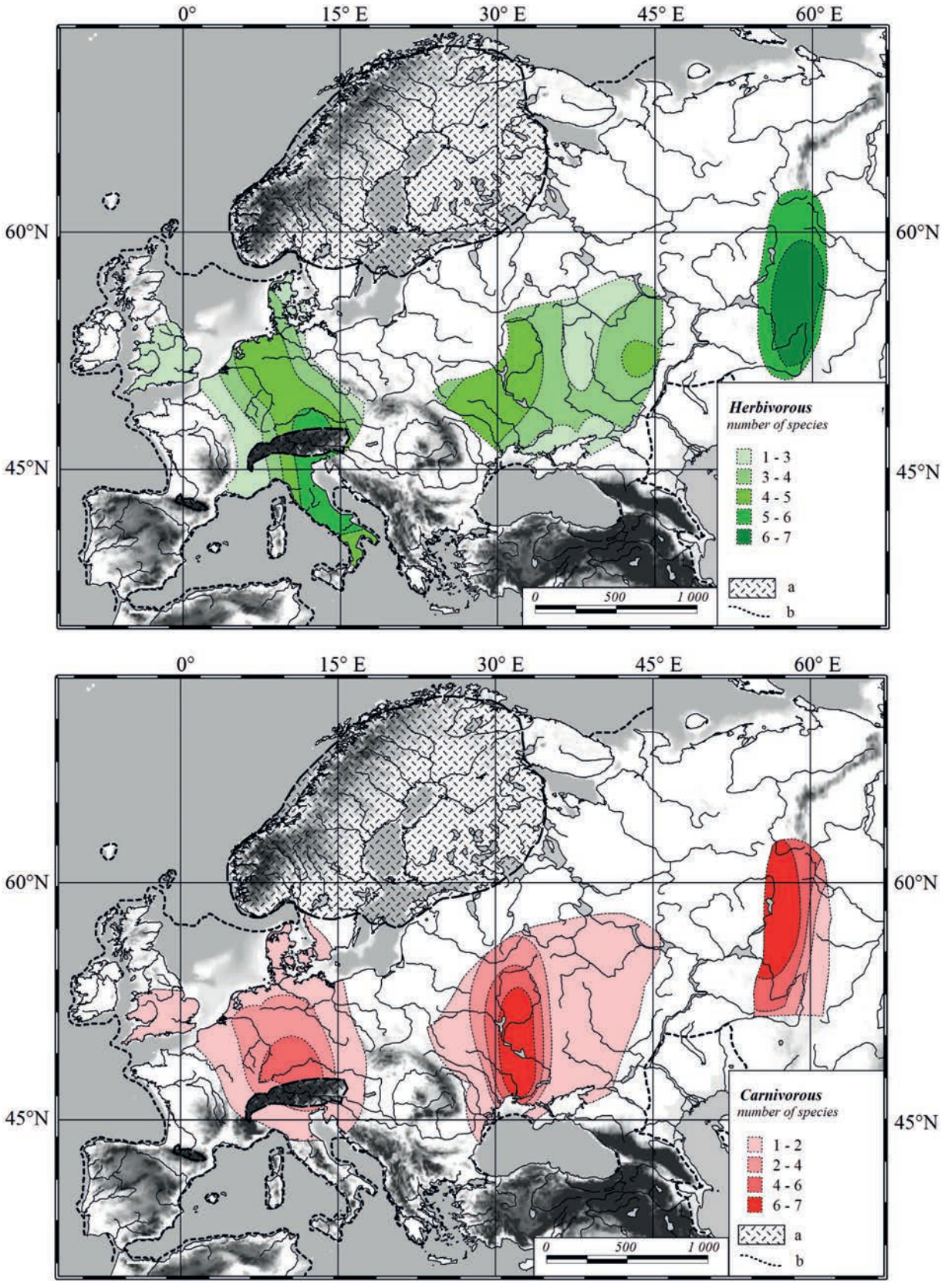

Fig. 4.77. *Herbivorous (upper fig.) and carnivorous (lower fig.) species diversity in Europe between 17–12.4 kyr BP; a – ice sheets, b – coastline*

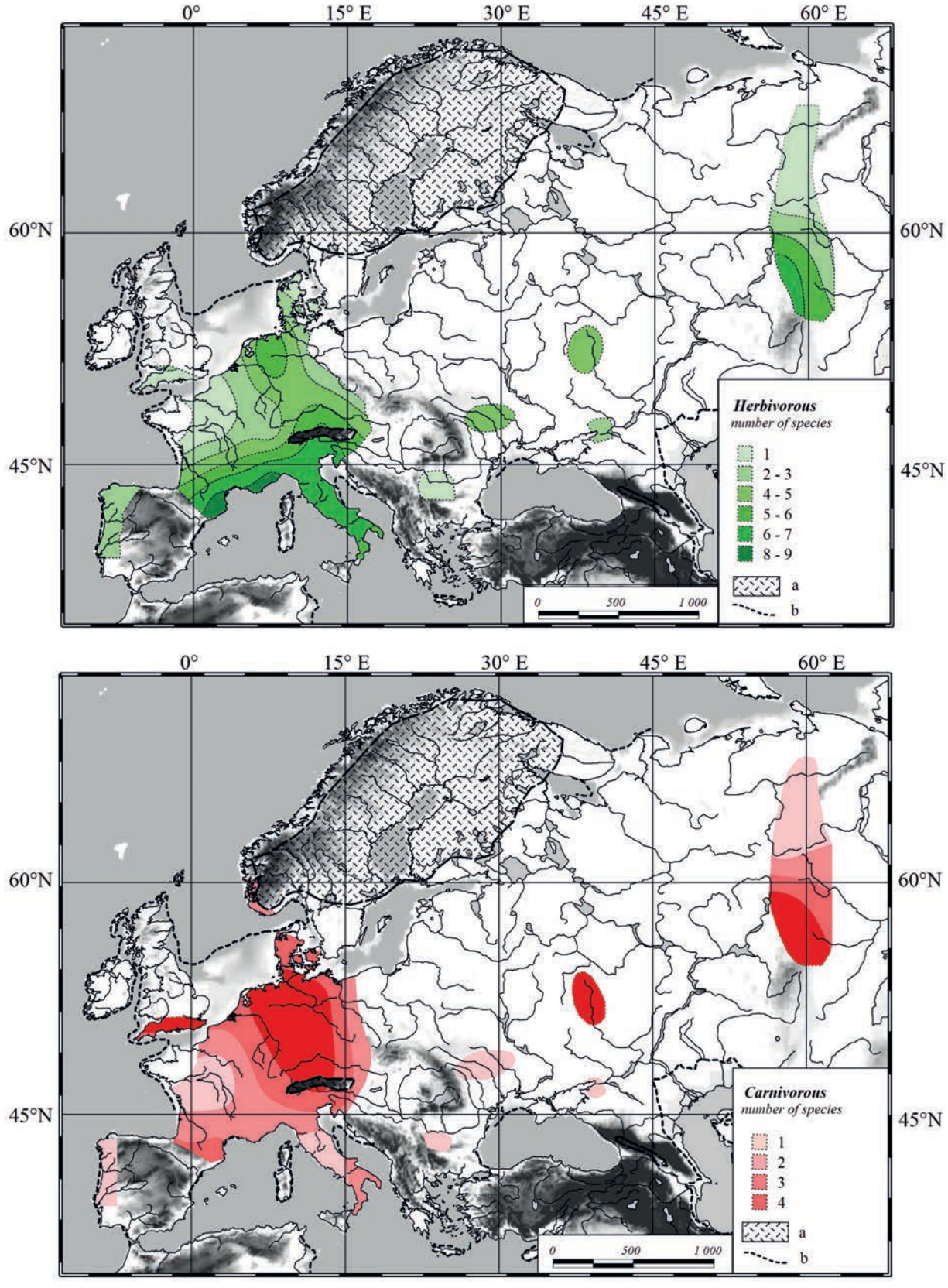

Fig. 4.78. *Herbivorous (upper fig.) and carnivorous (lower fig.) species diversity in Europe between 12.4–10.8 kyr BP; a – ice sheets, b – coastline*

high value of Kullback-Leibler's divergence (0.24). Figure 4.78 provides insight into the variation of herbivorous and carnivorous species diversity during the Bølling/Allerød.

Mammal Diversity during the Early Holocene (10.8–8 kyr BP)

The mammal species diversity in the Preboreal-Boreal is described by three factors. The first and second factors correlate with geographical latitude (r_s = 0.44 and 0.66). The third one is independent of geography.

The three factors within the framework of the linear model reproduce about 56% of the species diversity variability. The second factor contains the information on the ungulates diversity (r^2 = 0.43) mainly, while the first and the third contains information on the carnivorous diversity (r^2 = 0.48). The geographical location of occurrence determines about 12% of the diversity variation.

A total of five large territorial mammal complexes with 'unclearly' marked borders generally going in a latitudinal direction have been successfully singled out for the Holocene stage under consideration. Apparently, there is also a zoogeographical border along the east Carpathian Mountains (a meridional one). Corresponding to this reconstruction are both a very low MO value (0.13) and a low value of Kullback-Leibler's divergence (0.18).

The spatial variation of herbivores and carnivores are presented in Figure 4.79.

Assessment of the relatively stability of the zoogeographical borders and species diversity centers

To summarize the information presented, we shall show that with the conditional character of the reconstructions connected with the incompleteness of palaeontological data and other factors, their joint consideration has allowed us to conclude that a relative stability of mammal diversity exited during the Late Pleistocene – Early Holocene.

If we combine the reconstructions for the different time intervals, it will be clear to see that the lines separating mammal species assemblages lie within quite certain spatial 'corridors' (Fig. 4.91*a*): the 'North European' corridor with an eastern and a western part (Fig. 4.91*a*: 1 and 2); the 'Central Russian' corridor on the Russian Plain along latitude 50°N approximately (Fig. 4.91*a*: 3); the 'Volga-Dniester' or 'South Russian' corridor goes in a latitudinal-meridional direction from the Volga Upland in the east to the lower reaches of the Dniester River in the west (Fig. 4.91*a*: 4); the 'East Carpathian' corridor lies approximately between the 25° and 30° E longitude between the Podolsk Upland in the east and the Carpathian Mountains in the west (Fig. 4.91*a*: 5); the 'French' corridor stretches along the foothills of French Massif Central up to the Ardennes (Fig. 4.91*a*: 6); the 'North Balkan' corridor (Fig. 4.915*a*: 7); the 'Pyrenean' corridor (Fig. 4.91*a*: 8); the 'South Balkan' corridor (Fig. 4.91*a*: 9); the 'North Caucasian' corridor (Fig. 4.91*a*: 10). An overwhelming majority of the specified zoogeographical corridors stretch in a latitudinal direction, while only a few stretch in a latitudinal-meridional direction. Some corridors are definitely caused by orography.

It is essential to note that a significant part of the major modern zoogeographical borders follow the historical corridors (Fig. 4.80*a*). This statement is mostly true for the south of Europe, the 'East Carpathian' and the 'North Caucasian' corridors. Major differences of the present stage manifest themselves in the northeast of Europe, where zoogeographical borders are turned at an angle of 30–50° in relation to those existing in the Late Pleistocene and Early Holocene.

A similar analysis of historical and modern European centres of mammal species diversity has also shown relative spatial stability (Fig. 4.80*b*). A total of 7 mammal biological diversity centres, which are different in character, are singled out. The ones having the highest value are the 'Caucasian', the 'Carpathian' and the 'Ural'. Less valuable are (in decreasing order of importance): the 'Alpine', the 'Upper Dnieper', the 'Pyrenean' and the 'Central Russian' diversity centres. All specified territorial areas with a high biological diversity are connected with mountain ranges or uplands.

Changes in diversity parameters

We have used three diversity parameters in this work: the number of linearly independent virtual factors reproducing the occurrence of species on the level of separate localities; organization measure; and Kullback-Leibler's divergence. The number of factors corresponds to the number of potential physical factors determining elements of 'order' in the spatial distribution of mammal species diversity. Throughout the time period under consideration it remained constant (3 factors), except for the Late Valdai Glacial Maximum (2 factors).

The organization measure (Fig. 4.81*a*) has shown positive correlation with the degree of spatial differentiation in the mammal diversity and 'evidence' of zonal borders. Kullback-Leibler's divergence *(J)* (has shown a positive correlation with the organization measure, r_s = 0.72) (Fig. 4.81*b*) describes formally the measure of the discrepancy between virtual factor values distribution observed and normal distribution. Normal distribution of spatial species occurrence is regarded as a 'standard'

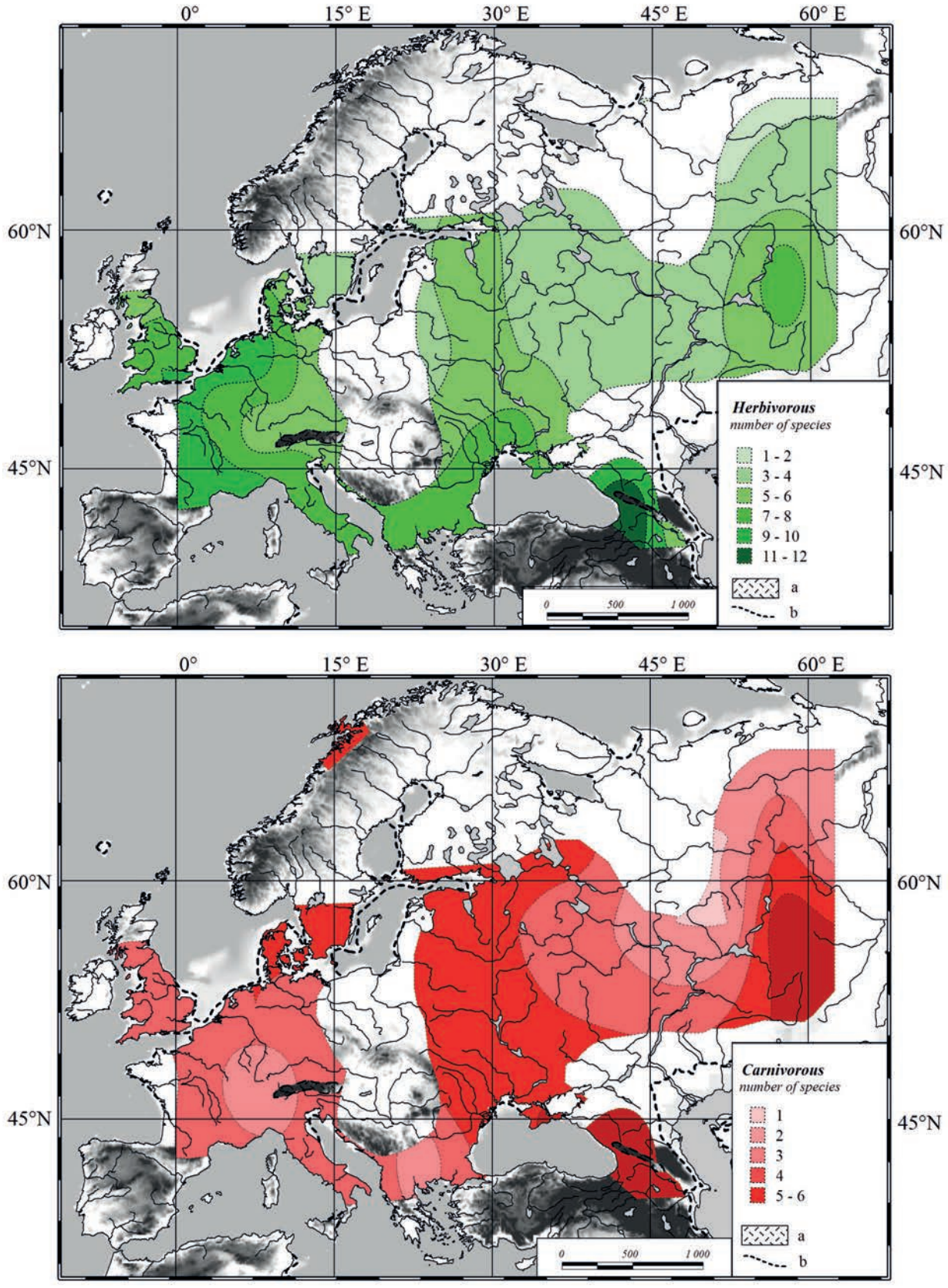

Fig. 4.79. *Herbivorous (upper fig.) and carnivorous (lower fig.) species diversity in Europe between 10.1–8 kyr BP; a – ice sheets, b – coastline*

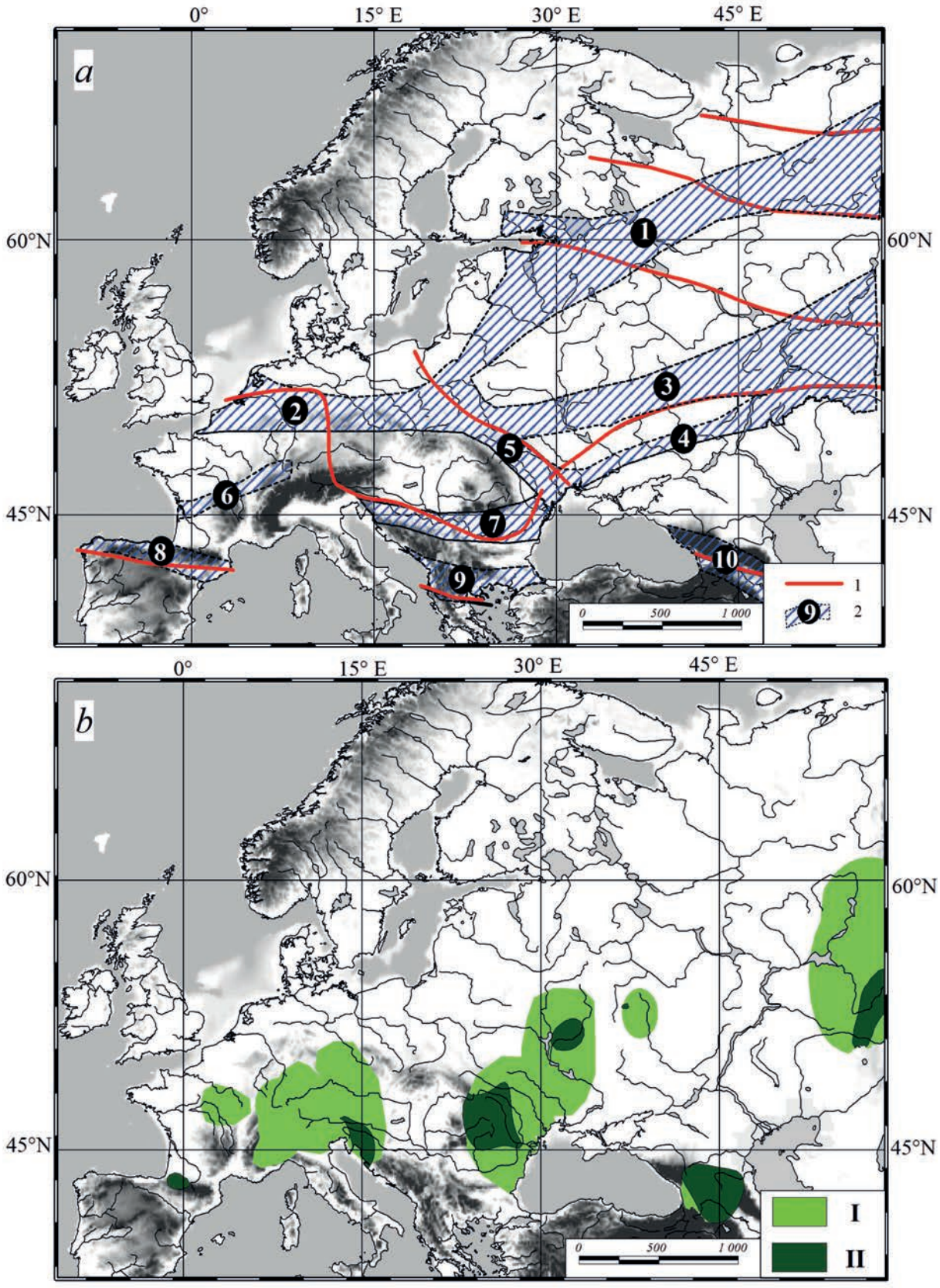

Fig. 4.80. *Stability of zoogeographical borders and geographical location of the centers of mammalian species diversity in Europe during the Pleistocene–Holocene transition: a – main modern zoogeographical borders (1) and historic "corridors" of ancient zoogeographical borders (2); b – location of historic (I) and modern (II) centers of diversity*

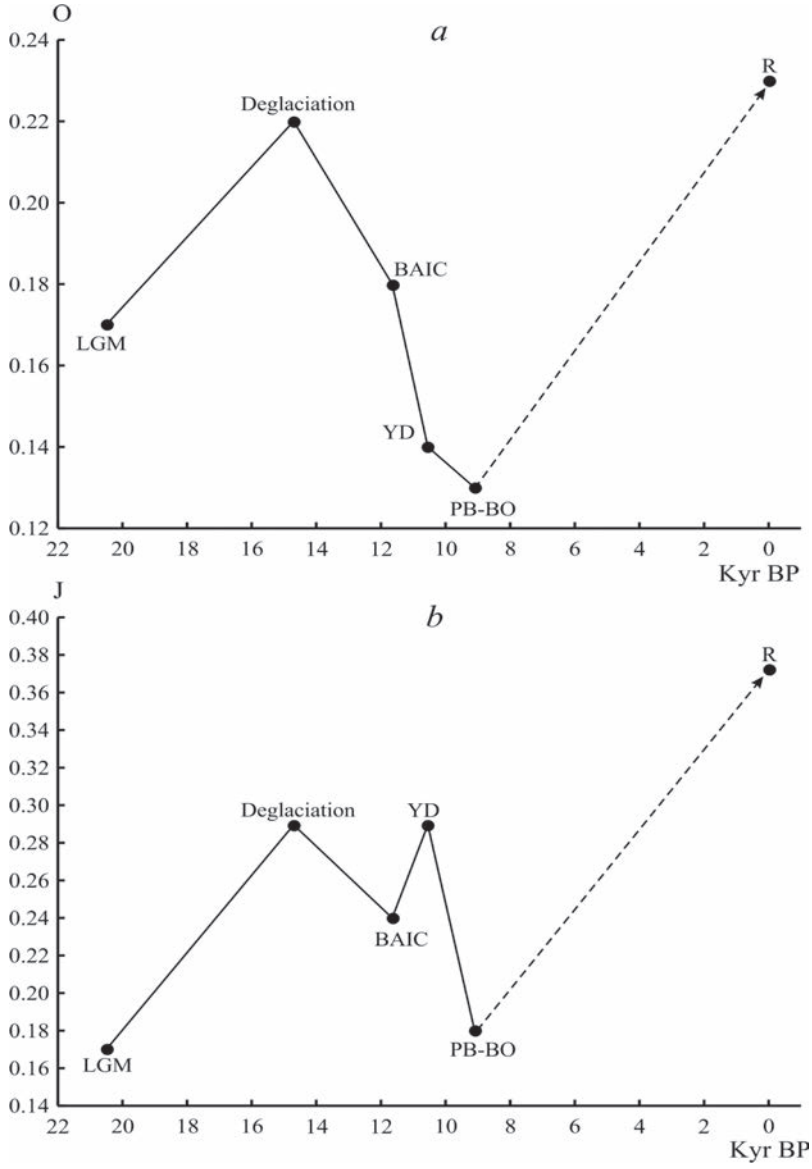

Fig. 4.81. *Dynamics of the mammalian species diversity parameters during the transition from the Pleistocene to the Holocene: a (top) – organization measure O; b (bottom) – Kullback-Leibler measure (J). R – the present time*

of equilibrium state, at which 'mixing' of species reaches some maximum possible level. Accordingly, the higher value of Kullback-Leibler's divergence implies a higher potential migratory gradient at zoogeographical borders.

During the transition from a rough climatic regime in the LGM to a relatively soft climatic regime in the early Holocene, information parameters dynamics, ambiguous in trend, are observed. Equilibrium states of Europe's mammal diversity system (a small number of wide-ranged mammal assemblages with fuzzy space borders) were observed, on the one hand, in the glacial maximum, and on the other hand, at the turn from the Pleistocene to the Holocene. In the LGT time slice, during a steady climatic trend, the complex zonality with clearly marked zonal borders was formed. In addition, during sharp climatic fluctuations, the existing zonality was exposed to destruction and reorganization. The beginning of the Holocene is characterized by a maximal degree of destruction of late Pleistocene theriocomplexes. It was on this basis that a complex zonal structure was generated under climatically favourable conditions in Europe over the last 7000 years. Within the framework of the suggested model, modernity is characterized by a maximal (for the entire period under consideration) degree of zoogeographical zonality display, maximal potential of species migratory activity (fast movements of species area's boundaries, invasions), maximal activity of physical 'factors' limiting diversity of theriocomplexes.

Conclusions

1. The spatial structure dynamics of European mammal species diversity at the turn of the Pleistocene and Holocene was mostly determined by a small number

(2–3) of factors. Most likely, the nature of these factors is primarily a physiographic one (climate, orography, etc.).

2. Against the background of a sharp qualitative reorganization of theriocomplexes structure (including extinction from the territory of Europe), major zoogeographical borders and locations of species diversity centres demonstrated relative stability.

3. During Holocene, theriocomplexes original in structure and having no analogs in the past were formed, and maximal deviation from Late Pleistocene zoogeographical borders curving direction is now observed in the northeast of Europe[12].

It follows from the diagram in Figure 4.99 and other numerous oxygen-isotope researches that temperature fluctuations similar to or having a larger amplitude than those during the transition from the Pleistocene to the Holocene have been repeatedly observed over the last more than 800,000 years. Therefore it is possible to assume that spatial dynamics of zonality display that we have described also had a cyclic character in a more remote past. Thus theriocomplexes transformation itself had an irreversible character.

The mammal diversity spatial structure existing in the current historical period in Europe, characterized by strong differentiation of their zonal complexes, is potentially unstable and will be destroyed both in case of significant global warming and climate cooling.

The following should be pointed out as potential features of this process: a) increase of migrations frequency and intensity (including those of invasive type), b) geographical expansion of ecologically plastic species, c) shrinkage of ecologically specialized species areas, d) amplification of the fluctuation amplitude of population dynamics, and e) local fauna structure simplification.

Human activity in Europe, both in the historical past and at present is objectively 'aimed' at destruction of zonal borders (deforestation, ploughing, creation of artificial ecological corridors, dispersion of adventitious species, etc.). In the context of the considered model of mammal diversity evolution in the Late Pleistocene-Holocene, anthropogenous transformation of the environment on most of the European territory leads objectively to an increase of both entropy and uniformity and its spatial organization measure decreases. Thus, consequences of human activity on a qualitative level coincide with consequences imposed on the biodiversity by natural, primarily climatic, factors (for instance, extinction or sharp reduction of large mammal numbers).

Therefore, under conditions of global reorganization of the climatic situation, fundamentally possible is a synergetic effect that can be expressed in unusually high rates and depth of the biological diversity spatial structure.

4.9. EUROPEAN MAMMAL RANGES AND ASSEMBLAGES' DYNAMICS DURING THE PLEISTOCENE–HOLOCENE TRANSITION (⩽24.0 – ⩾8.0 KYR BP)

Anastasia K. Markova

An analysis of the vast material on mammals in Europe reveals dramatic changes of environments at the transition from the last glaciation to the Holocene interglacial.

Extensive studies based on numerous dated findings of mammals allowed tracing the main trends and rates of transformations of mammal ranges, as well as changes in mammal assemblages, in Europe at the end the Pleistocene – in the Early Holocene.

Mammal's responses to climatic and environmental changes. Shifts of ranges

Earlier studies of faunas in Northern Eurasia and North America elucidated the principal characteristics of mammal assemblages typical of glacial and interglacial epochs (Vereshchagin, 1971; Vangengeim, 1977;

[12] 'New zoogeographical borders have also been formed on the territory occupied by ice sheets in the Late Pleistocene.

Graham, 1985; 1986; Vereshchagin and Baryshnikov, 1985; Semken, 1988; Guthrie, 1990; Baryshnikov and Markova, 1992; Smirnov, 1993; Markova *et al*., 1995; Markova, 1998; 2004; и др.). Analysis of Pleistocene mammal ranges in Eastern Europe (Markova, 1998; Markova *et al*., 2002 a,b; 2003), Siberia (Vangengeim, 1977; Agadjanian, 2001; Borodin and Kosintsev, 2001; a.o.), the Urals (Smirnov, 2001; a.o.), Northern Eurasia and Northern Hemisphere (FAUNMAP, 1994; Markova *et al*., 1995; Baryshnikov and Markova, 2002) permitted to identify the main types of mammal responses to global climatic variations. The present research based on a large volume of data and focused on European mammalian faunas enlarged our understanding of those regularities. The principal kinds of response may be summarized as follows:

1) changes in outlines of mammal ranges;

2) changes in structure and geographic position of mammal assemblages;

3) some mammal species extinction at the transition from one environmental-climatic situation to another;

4) changes in characteristics of mammal faunas diversity.

When reconstructing the chorology of individual mammalian species and their assemblages at certain time intervals in the past, the main constraints imposed on the reconstruction may be defined as follows:

1) materials from individual time intervals of the past are not complete enough;

2) the taphonomy of mammal localities might have affected the composition of bone remains;

3) environmental requirements of mammals could change in the process of evolution.

In the process of analyzing the total volume of data on mammalian assemblages in Europe in the transitional epoch from the Pleistocene to the Holocene, we were confronted by an insufficient volume of palaeontological material from some intervals in this epoch. That is especially true for the Younger Dryas stadial (YD) – probably due to brevity of this interval. Data on Bølling and Allerød interstadials are also rather scarce. The remaining time intervals analyzed in this paper are longer and better provided with data of fossil mammals. In many cases, the scarcity of initial data is attributable to insufficient knowledge about the region under consideration, or to the fact that not all mammalian taxa have been determined. The latter was quite common in earlier studies of the past mammal faunas, when small mammal remains most often were not determined at all.

The taphonomic characteristics of the mammal localities left a noticeable imprint on the species composition of fossil fauna. Here we concentrate mainly on faunas recovered from campsites and settlements of prehistoric hominins, partly because those sites are better substantiated with radiocarbon datings. There are two types of Palaeolithic sites: those of open type and cave sites. In the former the fossil fauna is represented both by animals (mostly small mammals) that inhabited vicinities of the site and by remains of larger animals which were objects of the hunts by the prehistoric hominids. Besides, the fauna composition in open Palaeolithic sites may depend on their position in the landscape. Animal remains recovered from sites located near water bodies (rivers, streams, lakes, etc.) often include those of intrazonal species dwelling near water (beavers, water voles, desmans, a.o.). Contrary to that, sites of high terraces and plateaus mostly contain remains of species characteristic of the given natural zone. In the Palaeolithic settlements located in uplands with an intensively dissected topography, the faunal composition reflects the diversity of local environments, determined by different slope orientation, depressions, etc. As a rule, faunas recovered from the Palaeolithic sites of this type are richer in species than those from settlements on plains.

Cave sites are mostly concentrated in mountains; such regions are distinct for highly diversified biotopes depending both on altitudinal zonality and on slope exposure. Concentration of mammal bone remains in the sites of this kind may result from various causes: it may be due to natural death of animals – cave dwellers (which is the case of Chiroptera and some carnivores); some were brought into the cave as a result of hunting, others are found in excrements of predatory birds. Studies of the material recovered from cave localities brought us to the conclusion that associations of this type contain faunas showing the highest values of species richness. A similar picture is typical of mountain regions at present (Shvarts *et al*., 1996). Those values reflect a diversity of environments within mountain regions (see section 4.8; Markova *et al*., 1995).

Some consideration concerning possible changes in mammals' requirements for their habitats is given in Chapter 2. Undoubtedly, ecological characteristics of mammals' species can undergo transformations – possibly due to evolutionary changes over long time intervals (ecogenesis, after Smirnov, 1993). The changes were governed both by intra-evolutionary transformations (related to mutational processes), and by subsequent fixing of characters in the process of selection. It has been found that phylogenetic changes were not regular, nor uniformly distributed over time. The longer periods of slow smooth phylogenesis alternated with intervals of quick dramatic changes; the different types of evolutionary processes were termed "coherent" and "incoherent", respectively (Krasilov, 1969). The coherent type is controlled by biocoenotic systems, while incoherent phylogenesis may be 'switched on' by abiotic factors, such as climate changes. Accelerated evolutionary changes may take place in case of distinct genetically isolated populations. Therefore, studies of evolutionary rate in diffe-

rent phylogenetic mammal lineage may shed light upon factors accountable for a particular rate of evolutionary transformation.

The evolutionary processes have been proven to gain in speed in case of drastically changed environments, and to proceed much slower in stable ecosystems. The phylogenesis rate increases in unstable environments, when stabilizing factors of selection are attenuated. Under such conditions some populations show an increasing changeability (Zherikhin, 1987).

Changes of climate produced an effect not only on the species ranges; they could also shift the 'norm of their response' to environmental conditions.

We have considered mammal faunas attributed to different climatic types of the past (such as the Last Glacial Maximum, interstadials, stadials, and the beginning of the Holocene Interglacial) in an attempt to establish empirically how various mammalian species and assemblages responded to climatic changes. It appeared in the course of the studies that mammals belonging to different phylogenetic lines responded to climate changes in varying degrees.

Data on fossil mammals allow tracing the evolution of species that differ in their environmental preferences. Palaeontological research provided support for a highly intensive micro-evolution of teeth of cryo-xerophile voles belonging to genus *Dicrostonyx* which is endemic in the Subarctic (Agadjanian, 1976). At the time of drastic restructuring of ecosystems during the Pleistocene glaciations, mammals of this genus enlarged their ranges considerably and occupied newly formed ecological niches. Selection pressure was weakened in the new areas, which in turn was favourable to the populations' conservation and fostered the newly acquired characters to be preserved.

Contrary to this, animals related to stable ecosystems (primarily, to forest and intrazonal ones, such as riverine areas, etc.) show slower rates of evolution; many investigators, however, have noted the progressive character of the latter.

Taxa of open dry landscapes (such as lemmings *Lagurus*, *Eolagurus*) that retained large ranges during both glacial and interglacial epochs, evolved intensively and progressively throughout the Pleistocene. The evolutionary changes left an imprint on their morphology. Numerous studies proved that fossil representatives of those genera, as well as their ancestral forms (*Borsodia*), were dwellers of various open landscapes. They were common both in zonal steppes of interglacials and in various types of open periglacial landscapes since the early Pleistocene (Markova, 1982b; 2004). Considering animals belonging to these phylogenetic lines, it should be noted that the rate of evolutionary processes was heavily influenced by repeated fluctuations of their ranges, the latter expanding in glacial times and shrinking during interglacials.

If principal morphological characters of the mammal skeleton are preserved for a long period, it seems safe to assume that the main environmental requirements of the animal did not change either. And conversely, if bone remains display conspicuous changes, it is not inconceivable that environmental requirements suffered considerable changes too. In the Pleistocene, ecological adaptations of mammals have already been formed. They may be seen in the specific structure of limbs, teeth, and skull, and reflect the species adaptation to certain environmental conditions.

Spatial and temporal dynamics of mammal's ranges

A sizeable quantity of materials on mammals in Europe enabled fossil mammal ranges to be reconstructed in their dynamics at the transition from severe environments of the last glaciation to the interglacial ones of the Holocene. Below we give some examples of how ecologically different groups responded to the transition.

Subarctic mammals

Starting from the Don Glaciation epoch and during all the subsequent Pleistocene glaciations (including the Valdai – Weichselian), the collared lemming *Dicrostonyx* noticeably expanded its range every time; it has been recorded in many local faunas in Europe. Contrary to this, there is no data as yet on the presence of the taxon in the Pleistocene interglacial faunas outside the present-day tundra zone (Markova, 1992; Markova *et al*., 1995; Baryshnikov and Markova, 2002; Markova, 2004). As follows from data on the European faunas, collared lemming remains dated to the Last Glacial Maximum (LGM) were found more than 1500 km south of the southern boundary of its present-day range (see Chapter 4). A similar pattern of the range dynamics is reconstructed for another subarctic species – *Lemmus*, the present-day inhabitant of tundra and forest-tundra. Still wider was the range of reindeer (*Rangifer tarandus*). In the second half of the last glaciation it occurred practically all over Europe except for the Southern Mediterranean. Other subarctic species, such as musk ox and Polar fox, responded in a similar way. Remains of Polar fox, for example, were recovered from Palaeolithic sites in the Crimea.

Therefore, subarctic animals expanded their ranges to the south at the Valdai (Weichselian) Glacial epoch, in common with preceding glaciations. The expansion rate of areas inhabited by those mammals varied from one epoch to another and reflected individual features of the particular animals. When the climate became warmer, the distribution of subarctic species reduced and changed

to the modern natural zones. Occasionally a receding range could not 'keep pace' with warming during the Holocene, and isolated occurrences persisted as 'refugia' in the southern part of its former area, in particular, in upper altitudinal zones in mountains, such as the Urals (Smirnov, 2001).

Steppe mammals

Typical steppe mammal species responded to cooling in a different way. As open periglacial landscapes occupied vast plains, the steppe species expanded their ranges westward and northward. Such an expansion became possible due to decay of the continuous forest zone that had barred steppe species from migrating to the north. During the last phases of the glacial period, many typical steppes taxa occurred all over Europe. Saiga antelope, wild horse, steppe pika, yellow and steppe lemmings, hamsters, ground squirrels (susliks), marmots and many others penetrated westward as far as the British Isles, and northward to the Jutland Peninsula and the Northern Urals. In common with subarctic mammals, the different steppe species responded differently to the global cooling. Under conditions of the Holocene warming and a continuous forest zone formation, the steppe mammal ranges shrank and shifted to the east and south. Some species that initially (in the Early-Middle Pleistocene) were steppe dwellers, such as the narrow-skulled vole *Microtus gregalis*, became fully adapted to periglacial open landscapes. After the forest zone formed in the Holocene, the range of this animal broke into two parts: tundra and steppe, two subspecies being thus formed.

On the whole, individual steppe species varied widely in their response to climatic changes and their ranges changed accordingly.

Forest species with flexible environmental requirements

Some species, such as the common red-backed vole (*Clethrionomys glareolus*), field vole (*Microtus agrestis*), and wolverine (*Gulo gulo*), did not migrate southwards at the time of the Last Glaciation. Their ranges became discontinuous and confined to relict areas of forests.

Forest species related to nemoral vegetation

There are a number of small mammals that inhabit nemoral forests at present (and inhabited them in the earlier interglacials), including yellow-necked field mouse (*Sylvaemus flavicollis*), fat dormouse (*Glis*), garden dormouse (*Eliomys*), pine vole (*Terricola*), wild boar (*Sus scrofa*) and others. During the last phases of the glacial period, these species survived in the forest zone of mountains in Southern Europe. With the beginning of the Holocene Interglacial, their ranges expanded northward and, after broad-leaved and mixed broad-leaved-coniferous forest zones finally developed, they became arranged in accordance with zonal boundaries.

Intrazonal species

The northern boundaries of the intrazonal species (including water vole *Arvicola terrestris*, root vole *Microtus oeconomus* and some others) shifted somewhat to the south during glaciations. After the decay of the ice sheet, they moved back to the north.

The above-listed changes in areas of mammal's occurrence in response to climatic fluctuations suggest an early differentiation of mammals into groups adapted to certain types of environments. Responses of mammals belonging to a particular ecological group to similar climatic changes appear to be alike, as may well be traced in the Pleistocene and Holocene faunas, including those dated to the Pleistocene-Holocene transition (Markova, 2004).

Abundant data permit to state the following:

1. Species belonging to the same ecological group respond to similar changes of climates in a similar way;
2. At the warmings (interglacials) and coolings (glaciations) species of different ecological groups display differently directed shifts of their ranges.

Analysis of faunas not only dated to the end of Pleistocene and early Holocene, but faunas of the entire Pleistocene, revealed a 'convergence' of subarctic and steppe species ranges at glacial epochs and a 'divergence' during warm periods (Markova, 1998). Therefore, spatial changes of range established for typical subarctic mammals and for steppe zone endemics show a cyclicity caused by macro-climatic fluctuations.

A comparison between the ranges of animals endemic to different natural zones reveals the fact that at the time of glaciations (including the second half of the last glaciation) many of them superposed one another; areas of such superposition indicate the existence of specific assemblages typical of periglacial zones of glacial epochs and known as 'mixed', ''hyperborean', 'non-analogue', 'periglacial', etc.

An analysis of the total data on the European mammal faunas between 24 and 8 kyr BP, as well as the series of maps compiled for several chosen time intervals and showing ranges of species, consisting of members of different ecological groups, revealed the whole spectrum of mammal responses to global changes of climate. The different responses were manifested in changes of the

mammal ranges widely varying in direction and scale. Five main groups of mammals have been recognized on the basis of their response to global climatic changes (and primarily to the cooling of the last glacial):

1) subarctic species conspicuously expanded their ranges to the south in glacial periods;

2) typical steppe species expanded their ranges northward and westward in the glacial and penetrated into regions formerly (in interglacial times) occupied by various forest formations;

3) forest species flexible in their environmental requirements did not migrate to the south during glaciations. Their ranges became discontinuous and were confined to remaining patches of forests;

4) the ranges of mammals that are inhabitants of nemoral forests are reduced in area and shifted far southward during glaciations;

5) intrazonal species ranges shifted slightly to the south in glacial times.

In this way, an analysis of the mammal response to climatic and environmental changes reveals it to be highly individual, which agrees well with the Gleason-Ramensky model (Ramensky, 1924; Gleason, 1926).

Another concept developed by Clements early in the 20th century proceeds from the assumption that species assemblages, having attained an equilibrium (which is controlled by biological links and particularly by competition), may persist for a long time (as long as several tens of thousands of years); this is the so-called 'organismic' concept (Clements, 1916). According to Clements, zonal biomes are to shift gradually from north to south and from south to north in response to changes of climate. (It should be noted that by a biome Clements means a totality of plants and animals). As was shown above, having analysed extensive data on European fossil mammals and taking into account the studies of vegetation of the same time (Chapter 5), we cannot see a successive displacement of zonal mammal (and plant) assemblages. To the contrary, all the data lend support to the validity of the model by Gleason and Ramensky (individual response of species to changing environments).

During the cold (glacial) times, ranges of practically all mammal species underwent considerable change, with some of them disintegrating into a number of small areas within the former large one; that resulted in a complete restructuring of the mammal assemblages characteristic of interglacial epochs, and in the formation of completely new ones, different in species composition and geographical distribution, and having no analogues at present. Those assemblages (known as 'mixed', 'disharmonic', 'hyperborean', 'non-analogue', 'periglacial') were stable and long-lived enough, as the duration of Pleistocene glaciations exceeded considerably those of interglacials. To take but one example, the last glaciation was about 100,000 years long, while the Mikulino (Eemian) interglacial only lasted for 15,000 years. The Holocene interglacial has so far lasted 10,000 years.

Dynamics of the European mammal assemblages' during the end of the Pleistocene – the Early Holocene

Reconstructed mammal assemblages of Europe have been analyzed for five successive time intervals between 24 and 8 kyr BP. The intervals differed essentially in climatic characteristics, and the sequential analysis of mammal assemblages elucidated the principal features of their structure and its variations through that dramatic period of the end of the Pleistocene – Early Holocene that is marked by 'revolutionary' changes in climate and landscapes.

Mammal assemblages of the maximum cooling during the last glaciation (LGM) (⩽24 to ⩾17 kyr BP)

At that time in Europe, vast areas located between the Scandinavian ice sheet and ~48°N were occupied by various kinds of 'mammoth steppe assemblages'. There are five variants of the assemblage reconstructed for the LGM: periglacial tundra, periglacial tundra-steppe (two variants), and periglacial forest-steppe (two variants) (see Chapter 4.1 by Markova and Puzachenko); all of them are unique in structure and have no modern analogues. Typically, the mammal assemblages included species of different ecologies that inhabit at present (and inhabited in the past interglacials) different natural zones. Such a composition indicates the specific environments of the LGM were dominated by open treeless landscapes. In the absence of a continuous forest zone, a way was opened to steppe species to penetrate to the north and west of Europe. At the same time, an overwhelming influence of the ice sheets enabled typical tundra mammals to expand their ranges southward as far as 46–48°N. Species of nemoral forests persisted in mountain refugia and, to a lesser extent, in river valleys and on some uplands distinguished by a diversity of local habitats and 'shelters'. Natural zonality appeared only slightly in the LGM. The mammal species composition suggests the existence of so-called 'mixed' faunal assemblages with no analogues at present. They included species that at present live in different natural zones.

Some species disappeared from Europe during this interval. Red dog (*Cuon alpinus*), for example, became extinct in Europe in the LGM and later was found only in the Caucasus. The small cave bear and cave hyena also

died out at that time. The large cave bear became extinct towards the end of the LGM.

The principal boundary between the faunas belonging to the mammoth assemblage and those without noticeable traces of cooling followed roughly 45°N. South of this latitude, the European mammal assemblages are quite different in structure. The ice sheet impact is practically unnoticeable. Widely spread over plains and mountain systems of Southern Europe were forests (including broad-leaved) alternating with open spaces with xerophytes and alpine meadows in high mountains (the Pyrenees, Apennines, Balkans, and Caucasus).

The difference between mammal faunas in Western and Eastern Europe consisted of a larger proportion of open landscape dwellers (typical of steppe and semi-deserts) in the East European region. It may be concluded that though the air mass transfer from the Atlantic exerted a perceptible influence in the LGM, a much greater impact on the biotic structure was made by the anticyclone formed above the Scandinavian ice sheet.

Mammal assemblages of the Late Glacial transition (LGT) (<17 to ⩽12.4 kyr BP)

Mammal assemblages of the Late Glacial (LGT) were not unlike those of the maximum of the last glacial cooling (LGM). This fact indicates that cold and arid enough conditions still persisted in Northern and Central Europe. Late Glacial mammal assemblages were also unique in structure and included species of various ecologies (inhabitants of tundra, steppe and forests) that now occur in different natural zones (see Chaper 4.2 by Markova and Puzachenko). Such assemblages, close to those of the LGM, were dominant over vast areas in Europe. They were distinct for the presence of large herbivores and 'cave' carnivorous animals that became extinct at the end of the Pleistocene – in the early Holocene. From the fact of steppe species occurring far north of their present-day habitation, it may be inferred that a continuous forest zone had not formed yet. Forest mammals still persisted in mountain refugia, in foothills and uplands with diversified habitats, and in river valleys where tree groves and shrub patches existed. The data obtained suggest a large refugium located near the Urals. A considerable number of mammal species – inhabitants of tundra and steppe and forests – were found in this region. Undoubtedly they dwelled in a great number of various local ecotopes.

The position of the southern limit of periglacial mammal assemblages at that time was practically the same as in the LGM, at 45–46°N in Eastern Europe and ~45°N in Western Europe.

The ranges of many tundra species in the LGT were as vast as they were during the LGM, which suggests the persistence of cold climates and a dominance of the periglacial vegetation in Northern and Central Europe. Steppe mammals extended their ranges northward and westward (due to open landscapes prevailing everywhere). Forest mammals concentrated mainly in the mountain systems of Southern Europe (in the Apennines, near the Alps and probably in the Balkans, Pyrenees and Carpathians – unfortunately, we have not yet a sufficient number of dated localities in those regions). With the glacier influence considerably mitigated, many thermophilic forest species could survive there.

It may be stated that the Late Glacial mammal assemblages bear an imprint of severe palaeo-environments that had much in common with those of the previous interval (LGM). It follows, therefore, that cryoarid conditions persisted in Europe from 24 to 12.4 kyr BP.

Mammal assemblages during the Bølling-Allerød interstadial warmings (BAIC) (<12.4 to ⩾10.9 kyr BP)

The assemblages reconstructed for these intervals give an indication of the initial decay of the 'mammoth steppe' landscapes resulting from climatic warming. Subarctic mammal ranges were somewhat reduced and reached only as far south as 52–54°N, while in the LGM and LGT they penetrated to 45°N, and the density of their localities was much greater. Findings of forest species in the north of Europe suggest an increased significance of forest vegetation in those regions. Forested areas alternated with open patches of tundra-steppe.

In common with previous intervals, the ranges of steppe mammals covered western regions of Europe in the Bølling-Allerød and were much more extensive than at present. This may be interpreted as a persistence of periglacial landscapes (tundra-forest-steppe, forest-steppe and steppe) even in Western Europe, though the ranges of species – inhabitants of open landscapes – were in all probability discontinuous.

Typical representatives of the 'mammoth' complex (mammoth, woolly rhinoceros, steppe bison, giant deer and others) still occurred in Europe, though their findings became scarce in the BAIC. Some mammals persisted in mountains only (e.g., the cave lion).

Studies of mammal faunas of Bølling-Allerød age revealed the presence of 'mixed', or 'non-analogue', faunas in the centre and north of Europe even at that interval of the Late Pleistocene. It should be noted, however, that the ranges of the periglacial assemblages were reduced in area and shifted northwards compared to the previous intervals.

At that time woolly rhinoceros died out all over Europe, with the only exception of the Urals.

In the south of Europe, in the Mediterranean region, the cooling influence of the Scandinavian ice sheet was negligible. Mammal faunas of the Bølling-Allerød interstadials (reconstructed from materials of the Massif Central, and the Apennine and Iberian Peninsulas) bear no signs of a cold climate.

On the whole, faunas of this interval permit us to trace the gradual changes in the geographical position and species composition of mammal assemblages; the changes manifested themselves as follows: ranges of the subarctic species are reduced in area and become discontinuous; species belonging to the 'mammoth fauna' occur less frequently, and the density of the findings is noticeably less. However, as may be seen from the data on the mammals, there was no continuous forest zone at that time; judging from fossil mammals, the area of the modern forest zone was occupied by periglacial tundra-steppe assemblages in the north and by those of the periglacial steppe in the south (see Chapter 4.3 by Markova and Puzachenko).

Mammal assemblages during the Younger Dryas stadial cooling (<10.9 to ⩾10.2 kyr BP)

The analyzed data on the Younger Dryas faunas have not revealed anywhere in Europe a simultaneous presence of the following groups of species: 1) species typical of the Pleistocene only (*Mammuthus primigenius, Ursus spelaeus, Panthera spelaea, Bison priscus*); 2) species inhabiting the tundra at present; and 3) those living on the steppes. Therefore, the specific periglacial assemblage ceased to exist by that time (Smirnov, Chapter 4.4).

There were relict populations of Pleistocene species persisting in isolated regions; for example, single dated findings of *Mammuthus primigenius* are known from the north and east of Eastern Europe, *Bison priscus* from the Southern Urals, *Panthera spelaea* from the Crimea (which is the latest findings of this species); giant deer *Megaloceros giganteus* was found in the north of Europe, as well as in the Middle and Southern Urals. A combination of tundra and steppe elements is found in Western Europe only in the north and in mountains, and in the east in the Middle Urals; it should be noted though, that even in those regions, tundra species lose their dominant position and enter the category of rare or even very rare species. Steppe species still lived far to the north of their present ranges. As for forest species, their occurrence does not prove the existence of a continuous forest zone, though they gain in importance, in particular in mountains. The species composition of mammals in the Younger Dryas provides evidence of the cryoarid Pleistocene ('mammoth') assemblage having been transformed into a primarily steppe assemblage, with included forest elements and relict populations of Pleistocene and arctic elements. In common with earlier faunas, the Younger Dryas mammal assemblages cannot be compared with any of the present-day assemblages.

Mammal assemblages during the Early Holocene (Preboreal–Boreal (PB-BO)) (<10.2 to ⩾8 kyr BP)

The Early Holocene (Preboreal and Boreal) was the interval in which the main natural zones began to form. As follows from the performed studies, the zonal structure of the mammal assemblages had not been completely developed in Europe by the end of the Boreal. The development proceeded at different rates in different parts of Europe. At the end of the Boreal, mammal assemblages were formed of steppe and – probably – mixed forests of Eastern Europe, as well as the Caucasian mountain assemblage (Kosintsev, Chapter 4.5). The formation of mammal assemblages of the tundra, taiga, broad-leaved forests and forest-steppe, however, had not yet been completed. In some regions of Europe there still persisted relict populations of species – participants of the 'mammoth' assemblage (such as *Coelodonta antiquitatis* and *Megaloceros giganteus* in the Urals, *Mammuthus primigenius* dated to Preboreal by radiocarbon – in the north of the Russian Plain) that had already disappeared from the rest of Europe.

During the Early-Middle Holocene, some other species practically disappeared from Europe, including steppe bison, musk ox, the Pleistocene suslik, Binagadinian hamster, probably Volgian wolf. Donian hare becomes extinct in the beginning of the Late Holocene (Kosintsev, Chapter 4.5).

There was another Early Holocene mammal assemblage identified in the Southern European mountains. It is known to be the most stable assemblage in the species composition that persisted through the terminal Pleistocene and Early Holocene. Its stability may be attributed to its geographical position in the south.

Therefore, the analysis of the abundant information related to assemblages of the Early Holocene permits us to conclude that zonal mammal assemblages of the Holocene interglacial began to develop at that time.

Conclusion

The studies of European mammal faunas dated to the end of the Pleistocene – Early Holocene makes it possible to trace the process of the transformation of last glacial faunas in the Holocene interglacial faunas. Mammal assemblages related to the maximum cooling of the last glaciation and late glacial interval were distinct

for a specific structure having no analogues at present. They are placed into a category of typical 'mixed', 'hyperborean', 'non-analogue', 'periglacial' faunas. It was only in the Mediterranean that the ice sheet influence was not felt.

The interstadial warmings of the Bølling-Allerød (BAIC) featured a wider distribution of the forest communities (Simakova, Chapter 5.3). Mammal faunas dated to this interval include more forest species than in the LGM and LGT. However, mammals – present-day tundra dwellers, as well as steppe inhabitants – were still widely spread all over Europe. Typical representatives of the mammoth assemblage (mammoth, woolly rhinoceros, steppe bison and others) were as common as before.

A short cooling in the Younger Dryas did not exert a noticeable effect on the mammal fauna (its species composition and ranges). Mammal assemblages dated to that time still include members of the mammoth assemblages, though subarctic animals are reduced in number. A single discovery of mammoth bones attributed to that interval was made in Estonia (the site of Puurmani at ~59°N), the bones being ^{14}C dated to 10,200±100 (Hela-425) (Stuart *et al*., 2002).

In the Early Holocene, the gradual warming of the climate initiated a restructuring of mammal ranges and assemblages in Europe. The process lasted through the Preboreal and Boreal and was completed only in the Middle Holocene, in the Atlantic period. Large herbivores of the mammoth assemblage (mammoth, woolly rhinoceros, giant deer, and others) survived only in a few refugia, mainly in the Ural Mountains and in the north of the Russian Plain (Kosintsev, Chapter 4.5.). The youngest mammoth bones in Europe were found at the town of Cherepovets (59.8°N, 37.55°E), dated between 10.10 kyr BP and 9.76 kyr BP. (Stuart *et al*., 2002). In the Early Holocene (Boreal period), mammal assemblages were formed of steppe and mixed forests. Besides, the Mediterranean mammal assemblage was stable and persisted from 24 to 8 kyr BP. Assemblages of the taiga, broad-leaved forests and forest-steppe had not developed by that time. The Early Holocene mammal assemblages reflect an initial stage of formation of zonal mammal assemblages in Europe.

The LGM and LGT European mammal assemblages could be referred to as typical non-analogue, mixed, periglacial assemblages. Only in the Mediterranean was the influence of the ice sheet very weak.

During the Bølling-Allerød Interstadial warming (BAIC), a more extensive distribution of forest communities reflected more clement climatic conditions (Simakova, Chapter 5.3). BAIC mammal assemblages include more forest animals than those of the LGM and LGT, although tundra and steppe mammals were still rather common in this interval. The modern zonality had not yet developed at that time. Typical representatives of the Mammoth assemblage (mammoth, woolly rhinoceros, steppe bison and others) were recovered in many sites dated to this interstadial.

A short cooling in the YD had not a great influence on the mammal distribution and composition. These assemblages also include animals of the Mammoth assemblage, although subarctic mammals are reduced in number. A single mammoth site related to the Younger Dryas has been found in Estonia (Puurmani site, about 59°N) and is dated to 10,200±100 (Hela-425) (Stuart *et al*., 2002).

A gradual warming induced a reorganization of the mammal assemblages during the Early Holocene all over Europe. This process continued through the Preboreal and Boreal and was completed only in the Atlantic period. Large Pleistocene herbivores (mammoth, wooly rhinoceros, giant deer, and others) survived only in a few sites, mainly located in the Ural Mountains and in the north of the Russian Plain (Kosintsev, Chapter 4.5.). The youngest mammoth bones in Europe were found at the town of Cherepovets (59.8°N, 37.55°E), dated between 10.10 kyr BP and 9.76 kyr BP. (Stuart *et al*., 2002).

The southern borders of the Arctic mammal ranges shifted to the north, the steppe mammal ranges shifted eastward and southward. The presence of forest animals became more conspicuous. The steppe and mixed forests' mammal assemblages were finally formed during the Early Holocene (Boreal). Also the stable Mediterranean mammal assemblage continued to exist in the south of Europe. However the mammal assemblages of the taiga, broad-leaved forests and forest-steppe were not fully developed during this interval. The mammal assemblages of the Early Holocene reflected the initial stage of the formation of a zonal structure of European mammal assemblages.

Chapter 5

PALAEOVEGETATION OF EUROPE DURING PLEISTOCENE–HOLOCENE TRANSITION (24–8 KYR BP)

5.1. EUROPEAN VEGETATION DURING THE LAST GLACIAL MAXIMUM (LGM) (⩽24 – ⩾17 KYR BP)

Alexandra Simakova and Andrey Puzachenko

A drastic reorganization in the biota, both animal and plant life, of Europe and in fact of the whole Northern Hemisphere took place during the Upper Pleniglacial, including its coldest phase, the Last Glacial Maximum (LGM) (≤24 – ≥17 kyr BP). The LGM is especially interesting for the existence of specific vegetation associations. Analogues of the modern natural phytocoenoses did not exist in this time in Northern Europe.

During glacial times, ecological niches of many plants differed from modern ones and, probably, had wider ecological amplitude, creating new plant associations. The changed configuration of the thermal environment resulting in tundra taxa intermingling with steppe taxa, thus creating totally different phytocoenoses from modern ones.

In Northern and Central Europe the reconstructed temperatures based on pollen data were lower than today at 20°/30°C – 10°C for the temperature of the coldest month. South of 45–47°N, January anomalies were 8–15°C (Kolstrup, 1980; Velichko, 1982; Peyron *et al.*, 1998; Tarasov, 2000). The Late Pleniglacial (Late Valdai) deposits are represented by glacial formations (moraine and fluvioglacial deposits), and periglacial alluvial-fan, lake-marsh, cover sands and loess/soil sequences. The Desna Loess unit (Loess II) in the central regions of the Russian Plain (Velichko and Morozova, 1972), and the Bug Loess unit (Loess II) in the southern Russian Plain (Gozhik *et al*., 2001) were formed during the LGM. In the northwestern and central European lowlands, deposition of cover sands took place, sometimes alternating with deflation horizons and formation of a polar desert.

A number of reconstructions of the palaeovegetation and biomes during the last ice sheet distribution period were carried out for Europe (Grichuk, 1982; Zagwijn, 1992; Adams and Faure, 1997; Prentice *et al.*, 2000), and for the Russian Plain (Gerasimov and Velichko, 1984;

Grichuk, 1989, 2002; Markova *et al.*, 2002b). There are reconstructions of the vegetation during the LGM for several territories in Europe (the Netherlands, Hungary, France, Germany, Poland, Romania, Spain, Italy, Ukraine, Russia, etc. (Artiushenko, 1970; Kolstrup, 1980; Grichuk, 1982, 2002; De Beaulieu and Reille, 1984, 1992; Caspers, 1985; Mojski, 1985; Zelikson, 1986; Pons and Reille, 1988a, 1988b; Spiridonova, 1991, 2002; Willis *et al.*, 1995; Bos, 1998; Bjorkman *et al.*, 2002; Gerasimenko, 2004; and others).

For the LGM the pollen records from 64 sections including 196 samples were added into the database (Table 5.1).

Table 5.1

The Last Glacial Maximum pollen sites

ID	Localities	Latitude	Longitute	Age	Reference
1	Molodovo V	48.30	26.45	23 700±235б, GIN-10; 23 000±800, MO-10; 17 100±180, GIN-54; 17 000±180, GIN-62	Pashkevich, 1987
2	Korman IV	49.24	27.22	18 000±400, GIN-719; 18 560±2000, SOAN-145	Pashkevich, 1987
3	Avdeevo	51.15	36.00	22 700±700, GIN-1571; 22 400±500, GIN-1969; 22 200±700, GIN-1970	Velichko et al., 1981
4	Puchka	59.30	39.33	21 880±110, LU-18A; 21 410±150, LU-18B	Khomutova, 1974
5	Karachish	53.25	34.30	Loess II (LGM)	Serebriannaya, 1972
6	Arapovichi	53.30	33.10	Loess II (LGM)	Grichuk et al., 1972
7	Aktash	45.33	35.29	19 130±1040	Pakhomov, 1993
8	Ivanovo	57.00	40.30	Relative±	Grichuk, 1982
9	Khotylevo II	53.30	33.25	23 660±270, LY-359; 24 960±400, IGAS-73	Zelikson, 1986
10	Factory of 1 May	56.35	37.12	21 140±590, LY-348	Semenenko et al., 1081
11	Veselo-Voznesenskii	47.20	38.24	Loess II (LGM)	Agadjanian et al., 1976
12	Mouralovka	47.12	38.48	19 170±120, LE-2947; 18 040±150, LE-2424	Spiridonova, 1991
13	Kostenki 1	50.50	39.48	24 100±500, GIN-2529; 23 500±200, GIN-2527; 23 000±500, GIN-2528; 22 800±200, GIN-2530; 22 300±200, GIN-2538; 21 300±400, GIN-2534; 22 300±230, GIN-1870; 14 020±60, GIN-86	Spiridonova, 1991
14	Kostenki 14	50.51	39.30	22 500±1000, LE-5274; 22 780±250, OxA-4114; 19 700±300, LE-5567; 19 900±50, GIN-8024	Spiridonova, 2002
15	Kostenki 21	50.51	39.30	16 960±300, LE-1043; 22 270±150, GrN-7363	Praslov et al., 1977
16	Yeliesevichi 1	52.5o	32.60	17 340±170, Lu-360	Zelikson, 1986
17	Gdanov	48.05	37.30	Loess II (LGM)	Artiushenko, 1970
18	Primorskoe	46.05	30.25	Loess II (LGM)	Artiushenko, 1970
19	Zagorodnee	49.40	36.25	Loess II (LGM)	Artiushenko, 1970

Continued table 5.1

ID	Localities	Latitude	Longitute	Age	Reference
20	Mironovka	46.35	35.20	Loess II (LGM)	Artiushenko, 1970
21	Kuyalnitskii limen	46.40	30.50	Loess II (LGM)	Artiushenko, 1970
22	Prilyki	50.20	32.30	Loess II (LGM)	Artiushenko, 1970
23	Berislav	46.35	33.10	Loess II (LGM)	Artiushenko, 1970
24	Kruganovka	46.38	33.05	Loess II (LGM)	Artiushenko, 1970
25	Chapyrovo	55.35	36.25	22 430±210, LU-91	Chebotereva&Makarycheva, 1974
26	Mezin	51.50	33.05	Loess II (LGM)	Gubonina, 1969
27	Pushkari	52.25	33.30	17 892 18 690	Velichko, et al., 1999
28	Pogon	52.27	33.32	relative	Velichko, et al., 1999
29	Zaraisk	53.30	38.00	relative	Velichko, et al., 1999
30	Syngir'-87	56.20	40.25	relative	Lavrushin & Spiridonova, 1998
31	Galichskoe 2	59.25	42.20	18 700±100, KIA-7070	Velichko et al., 2001
32	Roksolany	46.10	30.30	Loess II (LGM)	A.N. Simakova
33	Starye Bezradichy (sec.1)	50.11	30.33	Loess II (LGM)	Gozhik et al., 2001
34	Starye Bezradichy (sec. 2)	50.11	30.33	Loess II (LGM)	Gozhik et al., 2001
35	Viazovok	49.33	32.98	Loess II (LGM)	Artiushenko, 1970
36	Chygyrin	49.30	32.00	Loess II (LGM)	Artiushenko, 1970
37	Kabazi II	45.00	35.00	Loess II (LGM)	Gerasimenko, 1987
38	Likhvin	54.00	36.00	Loess II (LGM)	Sudakova et al., 1977
39	Oria	56.17	55.17	18 315±300	Nemkova, 1978
40	Myzuchi	50.10	30.00	Loess II (LGM)	Gerasimenko, 1988
41	Semibalka	47.00	38.45	Loess II (LGM)	A.N. Simakova
42	Prinsenbeek	51.30	4.45	22 460±219, GrN-26744	S.J.P. Bohncke
43	Lourdes	43.00	0.00	19 300±600, GrN-8582; 18 950±400, GrN-8512	Kolstrup, 1980
44	Stapborst	52.40	6.12	23 750±130, GrN-8506; 19 100±180, GrN-8594	Kolstrup, 1980
45	Podglemboke	52.00	23.00	relative	Grichuk, 1982
46	Shipotel'	45.00	22.30	relative	Grichuk, 1982
47	Lago de Ajo	38.6	-6.15	Calculated±±	EPD±±±
48	Lago Grande di Monticchio	40.56	15.6	18 290±290, Beta-9152; 21 200±500, QI-1883; 23 840±60, Beta-7496	EPD
49	Khimaditis	40.37	21.35	calculated	EPD
50	Quaternary de la Sierra	42.0	–3.25	18 250±230	Goni, 1994
51	Wilk Bij Duurstede	51.80	4.30	17 260±105	De Jong, 1995
52	Ioannina	39.45	20.43	calculated	EPD
53	Xinias	45.67	4.89	21 390±430, GrN-6886	EPD
54	Echets	39.03	22.16	21 400±400, Ly-2770; 20 420±380, Ly-2769; 18 030±50, Ly-2768	Beaulieu & Reille, 1984

Continued table 5.1

ID	Localities	Latitude	Longitute	Age	Reference
55	Padul	37.00	3.67	23 600±500, Gif-6009; 19 800±220, Gif-6389; 19 100±160, Gif-6390; 18 300±300, Gif-6390	Pons & .Reille, 1988
56	La Bouchet B5	44.89	3.67	19 400±1300, Gif-5943	Pons &.Reille, 1988
57	La Bouchet B53	44.89	3.67	relative	Pons &.Reille, 1988
58	La Bouchet B60	44.89	3.67	relative	Pons &.Reille, 1988
59	Castiglion	41.89	24.30	relative	Zagvijn, 1992
60	La Grande Pile	47.73	6.50	20000	Beaulieu & Reille, 1992
61	Steregoiu	47.48	23.32	relative	Bjorkman et al., 2002
62	Gross Todtshorn (Tost34)	54.00	12.00	20 530±405, Hv-21214	Caspers, 1997.
63	Podgrodzie	50.10	20.00	22 450±40	Mojski, 1985
64	Nowa Huta	50.15	21.10	18 460±250 20 560±735	Mojski, 1985

* The age of deposits have been identificate on the base of palynological, archaeological and geological data.
** The age of deposits with pollen data have been calculated on the base of 14 C dates existing in this section.
*** The materials were received from the European pollen database /EPD/: www.ncdc.noaa.gov/paleo/epd).

The pollen database “Paleoflora” contains 224 different LGM localities (99 species, 97 genera, and 28 families). Radiocarbon data are available for 28 sections. The age of other sites was determined based on archaeological, biostratigraphical and geological data.

As a result of the mathematical analysis, the palynological material was divided into three basic clusters and 8 sub-clusters (Fig. 5.1; Table. 5.2).

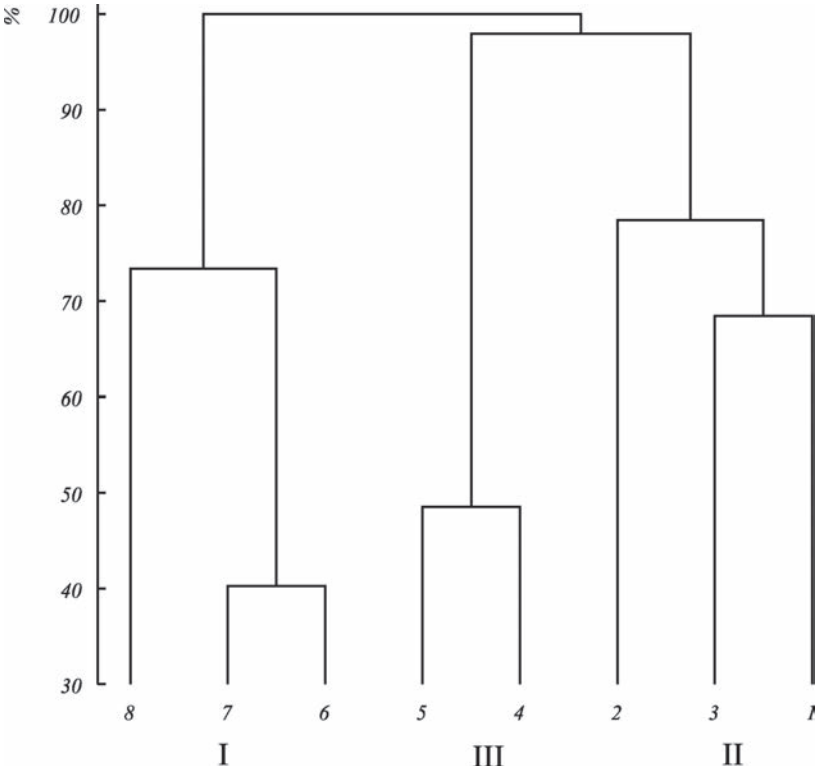

Fig. 5.1. *Dendrogram for LGM pollen assemblages*

Table 5.2

Clusters characteristic in standard units (average value of the cluster)

Taxa	Cluster groups			Clusters							
	I	II	III	1	2	3	4	5	6	7	8
Trees and Shrubs	0.3722	0.467	0.320	0.489	0.537	0.402	0.500	0.370	0.316	0.434	0.186
Herbs	0.4638	0.523	0.609	0.520	0.361	0.624	0.500	0.572	0.501	0.423	0.701
Spores	0.3792	0.179	0.255	0.267	0.333	0.000	0.333	0.292	0.396	0.361	0.175
Fir (Abies)	0.0114	0.009	0.173	0.023	0.000	0.000	0.000	0.235	0.000	0.024	0.143
Cedrus (Cedar)	0.0000	0.096	0.056	0.200	0.083	0.000	0.500	0.000	0.000	0.000	0.000
Juniperus (Juniper)	0.0952	0.187	0.210	0.054	0.344	0.225	0.563	0.241	0.000	0.200	0.070
Larix (Larch)	0.0833	0.158	0.009	0.200	0.333	0.012	0.000	0.018	0.159	0.000	0.000
Picea (Spruce)	0.2182	0.141	0.059	0.217	0.000	0.150	0.000	0.111	0.288	0.141	0.009
Pinus (Pine)	0.3625	0.449	0.312	0.358	0.616	0.441	0.500	0.320	0.308	0.423	0.249
Pinus subsect. Cembrae (Stone pine)	0.0509	0.195	0.006	0.200	0.333	0.107	0.000	0.000	0.000	0.107	0.014
Pinus sibirica (Siberian stone pine)	0.1088	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.184	0.026	0.000
Ta*xus* (Yew)	0.000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tsuga (Hemlock)	0.0000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arceuthobium (Dwarf Mistletoe)	0.0000	0.154	0.000	0.200	0.333	0.000	0.000	0.000	0.000	0.000	0.000
*Alnu*s (Alder)	0.1686	0.261	0.207	0.315	0.021	0.350	0.500	0.271	0.226	0.106	0.041
Alnus fruticosa = Alnus alnobetula subsp. *fruticosa* (green alder)	0.1835	0.088	0.021	0.229	0.000	0.000	0.000	0.000	0.131	0.241	0.054
Betula sect. Albae (Arboreal birch)	0.3438	0.359	0.048	0.361	0.138	0.490	0.000	0.089	0.178	0.526	0.010
Betula sect. Nanae (Dwarf birch)	0.1810	0.275	0.004	0.400	0.190	0.200	0.000	0.000	0.195	0.165	0.010
Buxus (Box)	0.0000	0.077	0.000	0.201	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Carpinus (Hornbeam)	0.1359	0.037	0.064	0.095	0.000	0.000	0.000	0.128	0.168	0.100	0.000
Cornus (Dogwood)	0.0000	0.077	0.056	0.200	0.000	0.000	0.500	0.000	0.000	0.000	0.000
Corylus (Filbert)	0.1375	0.098	0.121	0.256	0.000	0.000	0.500	0.111	0.163	0.109	0.026
Fraxinus (Ash)	0.0000	0.100	0.006	0.260	0.000	0.000	0.000	0.013	0.000	0.000	0.000
Fagus (Beech)	0.0000	0.077	0.056	0.200	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Hippophaë rhamnoides (Sea buckthorn)	0.0476	0.179	0.111	0.165	0.500	0.000	0.500	0.111	0.000	0.100	0.000
Juglans (Walnut)	0.0000	0.077	0.056	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.143
Myrica (Bog-myrtles)	0.0000	0.164	0.000	0.226	0.000	0.200	0.000	0.000	0.000	0.000	0.000
Olea (Olive)	0.0000	0.077	0.056	0.200	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Phillyrea mock privet	0.0000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Populus tremula (Aspen)	0.0000	0.215	0.000	0.200	0.267	0.200	0.000	0.000	0.000	0.000	0.000
Quercus (Oak)	0.1211	0.167	0.165	0.214	0.233	0.080	0.100	0.273	0.038	0.213	0.044
Quercus ilex (Holm oak)	0.0000	0.154	0.056	0.200	0.333	0.000	0.000	0.111	0.000	0.000	0.000
Rhamnus (Buckthorn)	0.0000	0.000	0.056	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Salix (Willow)	0.1444	0.299	0.047	0.205	0.357	0.357	0.000	0.049	0.213	0.069	0.057
Sambucus (Elders)	0.0000	0.130	0.000	0.337	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tilia (Linden)	0.1296	0.000	0.056	0.000	0.000	0.000	0.000	0.111	0.122	0.138	0.000
Ulmus (Elms)	0.2579	0.103	0.052	0.268	0.000	0.000	0.000	0.070	0.213	0.308	0.044

Continued table 5.2

Taxa	Cluster groups			Clusters							
	I	II	III	1	2	3	4	5	6	7	8
Viburnum (Viburnum)	0.0476	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000
Alismataceae (Water-plantain family)	0.000	0.070	0.056	0.183	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Apiaceae (Carrot family)	0.019	0.185	0.132	0.268	0.022	0.200	0.500	0.034	0.006	0.034	0.153
Brassicaceae (Cabbage family)	0.0721	0.335	0.167	0.371	0.667	0.100	0.500	0.111	0.002	0.150	0.143
Campanulaceae (Bellflower family)	0.0476	0.134	0.015	0.349	0.000	0.000	0.000	0.031	0.000	0.100	0.000
Caryophyllaceae (Pink family)	0.1089	0.231	0.131	0.301	0.083	0.250	0.500	0.041	0.114	0.103	0.143
Chenopodiaceae (Goosefoot family)	0.215	0.233	0.373	0.447	0.129	0.083	0.600	0.432	0.258	0.167	0.233
Corispermum (Bugseed)	0.071	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.091	0.050	0.000
Cistaceae (Rock-rose family)	0.0000	0.000	0.056	0.000	0.000	0.000	0.500	0.000	0.000	0.000	0.000
Helianthemum (Rock-rose)	0.049	0.218	0.165	0.328	0.375	0.014	0.536	0.210	0.093	0.000	0.000
Compositae (Compositae family)	0.0435	0.159	0.140	0.200	0.000	0.213	0.000	0.167	0.004	0.087	0.146
Asteraceae (Daisy family)	0.0717	0.238	0.169	0.336	0.474	0.000	0.921	0.004	0.030	0.117	0.167
Asteraceae (Asteraceae family)	0.0959	0.280	0.179	0.379	0.583	0.000	0.500	0.179	0.154	0.032	0.087
Artemisia (Wormwood)	0.3841	0.312	0.397	0.539	0.240	0.128	0.650	0.521	0.432	0.331	0.165
Centaurea (Knapweed)	0.0000	0.088	0.015	0.230	0.000	0.000	0.000	0.029	0.000	0.000	0.000
Convolvulus (Field Bindweed)	0.0000	0.000	0.111	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.143
Cyperaceae (Sedge family)	0.0936	0.291	0.144	0.234	0.114	0.454	0.007	0.175	0.117	0.068	0.143
Dipsacaceae (Teasel family)	0.0476	0.077	0.056	0.200	0.000	0.000	0.500	0.000	0.091	0.000	0.000
Scabiosa (Scabiouses)	0.0476	0.154	0.054	0.200	0.000	0.200	0.000	0.108	0.091	0.000	0.000
Ephedra (Ephedra)	0.1046	0.358	0.171	0.582	0.250	0.200	1.000	0.042	0.099	0.111	0.100
Epilobium (Fireweed)	0.000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ericaceae (Heather family)	0.1010	0.083	0.060	0.215	0.000	0.000	0.000	0.009	0.099	0.103	0.143
Calluna (Heather)	0.000	0.115	0.000	0.000	0.000	0.300	0.000	0.000	0.000	0.000	0.000
Empetrum (Crowberry)	0.0000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Vaccinium (Bilberry)	0.000	0.154	0.000	0.200	0.000	0.200	0.000	0.000	0.000	0.000	0.000
Euphorbia (Spurge)	0.000	0.077	0.004	0.200	0.000	0.000	0.000	0.008	0.000	0.000	0.000
Fabaceae (Pea family)	0.1071	0.198	0.097	0.315	0.333	0.000	0.000	0.080	0.013	0.210	0.146
Hedera (Fir Clubmoss)	0.000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lamiaceae (Dead-nettle family)	0.0568	0.077	0.111	0.000	0.333	0.000	0.500	0.111	0.091	0.119	0.143
Liliaceae (Lily Family)	0.0000	0.130	0.222	0.139	0.333	0.000	0.500	0.222	0.000	0.000	0.143
Linum (Flax)	0.0476	0.154	0.041	0.200	0.000	0.200	0.000	0.082	0.091	0.000	0.000
Malva (Mallow)	0.0000	0.000	0.056	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Menyanthes (Bog-bean)	0.0000	0.000	0.111	0.000	0.000	0.000	0.500	0.111	0.000	0.000	0.000
Myriophyllum (Water-milfoil)	0.0476	0.114	0.162	0.096	0.333	0.000	0.500	0.213	0.000	0.100	0.000
Nymphaea (White Water-lily)	0.0000	0.045	0.167	0.116	0.000	0.000	0.500	0.111	0.000	0.000	0.143
Papaveraceae (Poppy family)	0.000	0.000	0.056	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Pedicularis (Lousewort)	0.0000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Plantago (Plantain)	0.0515	0.238	0.144	0.266	0.256	0.200	0.500	0.065	0.001	0.107	0.143

Continued table 5.2

Taxa	Cluster groups			Clusters							
	I	II	III	1	2	3	4	5	6	7	8
Plumbaginaceae (Thrift family)	0.0000	0.000	0.075	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.194
Armeria (Sea grass)	0.0000	0.274	0.000	0.212	0.333	0.300	0.000	0.000	0.000	0.000	0.000
Poaceae (Grass family)	0.1719	0.363	0.394	0.427	0.329	0.320	0.639	0.516	0.115	0.234	0.168
Polemoniaceae (Jacob's-ladder family)	0.0476	0.077	0.024	0.200	0.000	0.000	0.000	0.000	0.000	0.100	0.061
Polygonaceae (Knotweed family)	0.1965	0.154	0.166	0.200	0.000	0.200	0.500	0.118	0.197	0.196	0.131
Koenigia (Iceland-purslane)	0.000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rumex (Docks)	0.0553	0.228	0.134	0.373	0.007	0.217	0.583	0.027	0.004	0.112	0.143
Primulaceae (Primrose family)	0.0476	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.091	0.000	0.000
Lysimachia (Creeping jenny)	0.0000	0.077	0.037	0.200	0.000	0.000	0.000	0.074	0.000	0.000	0.000
Ranunculaceae (Buttercup family)	0.1067	0.165	0.208	0.018	0.006	0.407	0.000	0.304	0.093	0.121	0.143
Thalictrum (Meadow-rue)	0.0476	0.206	0.099	0.319	0.338	0.015	0.525	0.082	0.000	0.100	0.000
Rosaceae (Rose family)	0.0996	0.226	0.163	0.337	0.417	0.000	0.500	0.103	0.004	0.204	0.144
Dryas octopetala (Mountain Avens)	0.0476	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000
Filipendula (Meadowsweet)	0.000	0.023	0.056	0.060	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Potentilla (Cinquefoil)	0.0000	0.102	0.048	0.265	0.000	0.000	0.000	0.096	0.000	0.000	0.000
Rubiaceae (Bedstraw family)	0.005	0.217	0.111	0.263	0.167	0.200	0.500	0.000	0.000	0.011	0.143
Galium (Bedstraw)	0.0000	0.054	0.111	0.142	0.000	0.000	0.500	0.111	0.000	0.000	0.000
Sanguisorba (Burnet)	0.000	0.080	0.058	0.208	0.000	0.000	0.500	0.004	0.000	0.000	0.000
Saxifragaceae (Saxifrage family)	0.095	0.077	0.111	0.200	0.000	0.000	1.000	0.000	0.182	0.000	0.000
Scrophulariaceae (Scrophulariaceae family)	0.000	0.000	0.056	0.000	0.000	0.000	0.000	0.111	0.000	0.000	0.000
Sparganium (Bur-reed)	0.000	0.091	0.062	0.036	0.333	0.000	0.000	0.123	0.000	0.000	0.000
Typha (Reedmace)	0.000	0.084	0.063	0.017	0.333	0.000	0.000	0.126	0.000	0.000	0.000
Urtica (Nettle)	0.060	0.077	0.056	0.200	0.000	0.000	0.000	0.000	0.002	0.123	0.143
Urticularia (Bladderwort)	0.000	0.077	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Valerianaceae (Valerian family)	0.000	0.077	0.068	0.200	0.000	0.000	0.500	0.024	0.000	0.000	0.000
Botrychium (grape-fern)	0.0900	0.077	0.056	0.200	0.000	0.000	0.000	0.000	0.061	0.122	0.143
Bryales (mosses)	0.3244	0.149	0.157	0.388	0.000	0.000	0.000	0.222	0.325	0.324	0.117
Equisetum (horsetail)	0.0000	0.232	0.056	0.203	0.000	0.400	0.000	0.000	0.000	0.000	0.143
Osmunda (fern royal)	0.0476	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000
Polypodiaceae (Polypody family)	0.3803	0.042	0.083	0.110	0.000	0.000	0.000	0.136	0.566	0.176	0.039
Selaginella (mountain moss)	0.0273	0.077	0.068	0.200	0.000	0.000	0.000	0.025	0.000	0.057	0.143
Sphagnum (sphagnum moss)	0.1273	0.247	0.004	0.241	0.000	0.400	0.000	0.000	0.234	0.010	0.010

In figures 5.2 and 5.3 the geographical distribution of the three main clusters and the eight sub-clusters is depicted.

Cluster 1 indicates the presence of forest-tundra and periglacial forest phytocoenoses; cluster 2 characterizes the distribution of both shrub tundra and forest-steppe communities; and cluster 3 determined the vegetative associations of open (steppe) landscapes (Fig. 5.2). Analysis of the geographical distribution of pollen sites shows that during the LGM Eastern Europe was under more

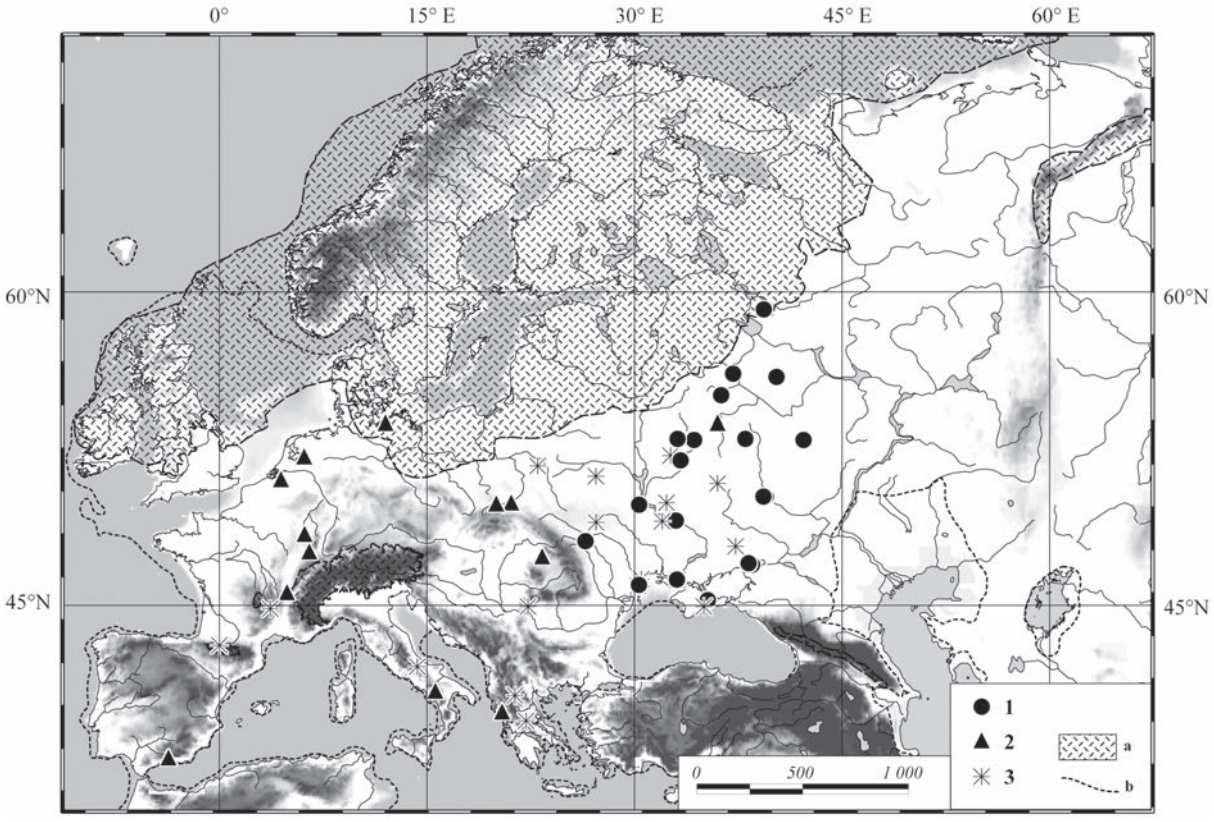

Fig. 5.2. *The geographical distribution of the LGM pollen sites, according to the three main clusters; a – ice sheets and mountain glaciers; b – coastline*

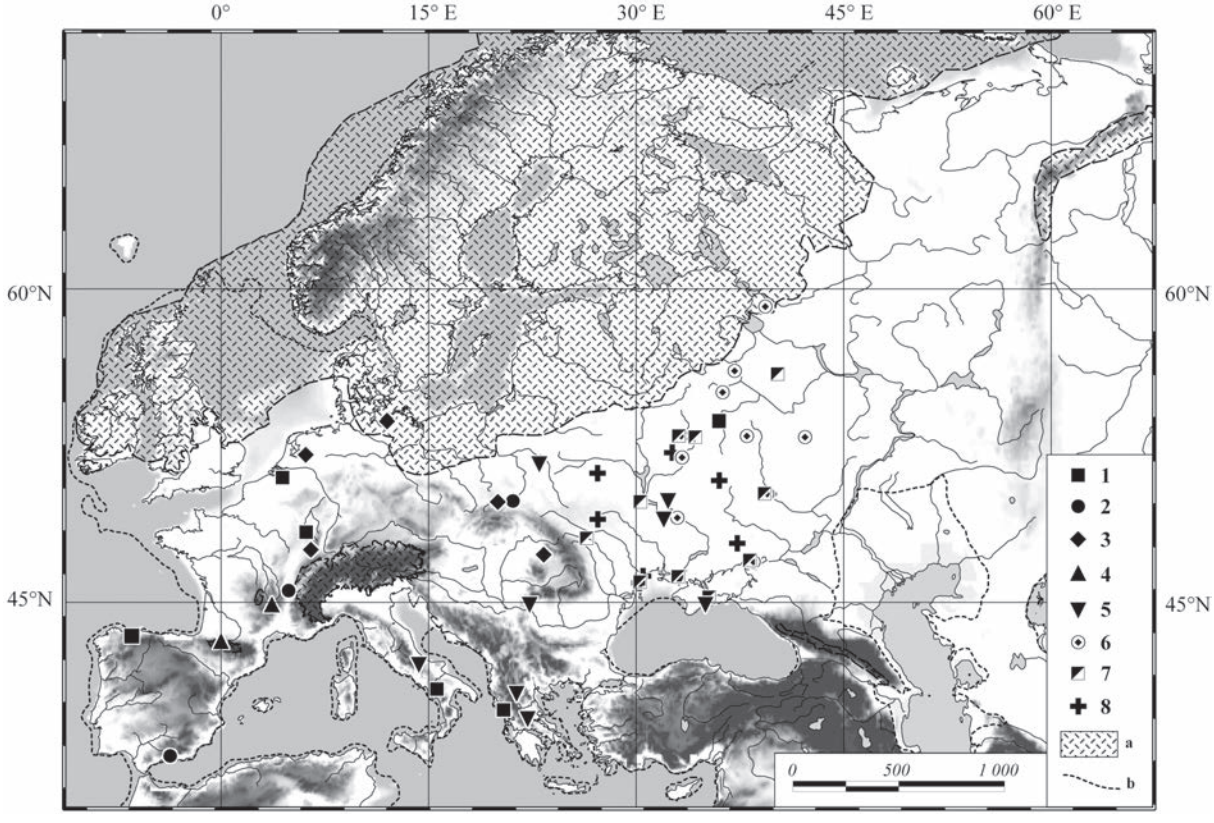

Fig. 5.3. *The geographical distribution of the LGM sites, according to the eight sub-clusters; a – ice sheets and mountain glaciers; b – coastline*

continental climatic conditions than Western Europe and the periglacial vegetation of the Russian Plain differed from the periglacial vegetation of Western Europe.

Dividing the pollen data into 8 sub-clusters gives a more complex and detailed picture of the geographical distribution of the palaeophytocoenoses or biomes. These clusters indicate the distribution of the following vegetation biomes: 1 – both forest-tundra and steppe, 2 – forest-steppe, 3 – both *Pinus-Betula* forest-steppe and tundra; 4 – both forest-steppe and *Artemisia*-Poaceae steppe; 5 – *Artemisia*-Chenopodiaceae steppe; 6 – both forest and tundra-steppe; 7 – both forest-steppe and tundra; 8 – both tundra-steppe and meadow steppe (Table 5.2, Fig. 5.3).

The series of electronic maps of the different indicator plant species, which characterize certain palaeophytocoenoses, and the series of maps of different plant communities determining a landscape as a whole, were constructed using Mapinfo® software.

Analysis of the palynological data shows that tundra and forest-tundra elements had a wide distribution in Europe during the LGM. During the LGM, tundra and forest-tundra vegetation associations were dispersed southward up to 48–49°N on the Russian Plain, and up to 53°N in Western Europe. That means that the southern limit of these tundra plants shifted approximately 1500 km southward compared to its modern south range boundary. The distribution of hipoarctic taxa such as *Alnus fruticosa*, *Selaginella selaginoides*, *Lycopodium appressum*, and *Lycopodium pungens* covered almost the whole of the Russian Plain and were absent in Western Europe. Only *Selaginella* spores have been found in the western Netherlands (Fig. 5.4). At the same time *Armeria* pollen have been found in the north of Western Europe and in the foothill areas of France. *Alnus fruticosa*, *Selaginella selaginoides*, and *Betula nana* have been found in the Dniester River region, the lower basin of Don River, and in the Carpathian foothills. This reflects a significant expansion of the ranges of these hypoarctic plants.

In the north of Europe the pollen spectra contain a significant amount of *Sphagnum* spores, and *Betula* sect. *Nanae*, *Salix*, Ericales, *Empetrum*, and Cyperaceae pollen grains (Figs. 5.4, 5.5). According to the criteria of the mathematical classification (MDS method) the tundra and forest-tundra communities have also shifted south up to 53–54°N.

The representative species of steppe phytocoenoses were also widespread in Europe and entered into vegetational associations of periglacial tundra-steppe, forest-steppe, steppe and semidesert landscapes. *Ephedra* occurred in southern areas of Europe, expanded northward to 48°N in Western Europe and to 62°N in Eastern Europe (Fig. 5.6).

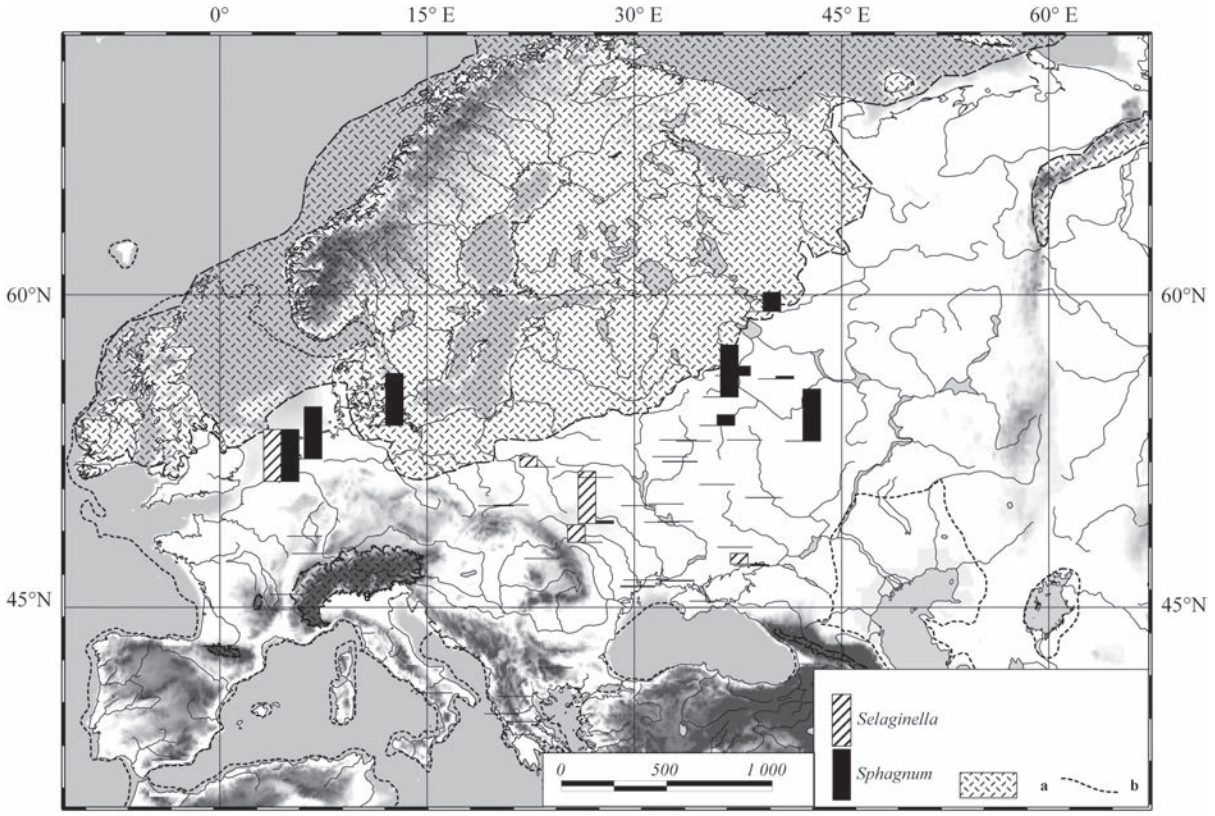

Fig. 5.4. *Selaginella and Sphagnum spores from LGM localities; a – ice sheets; b – coastline*

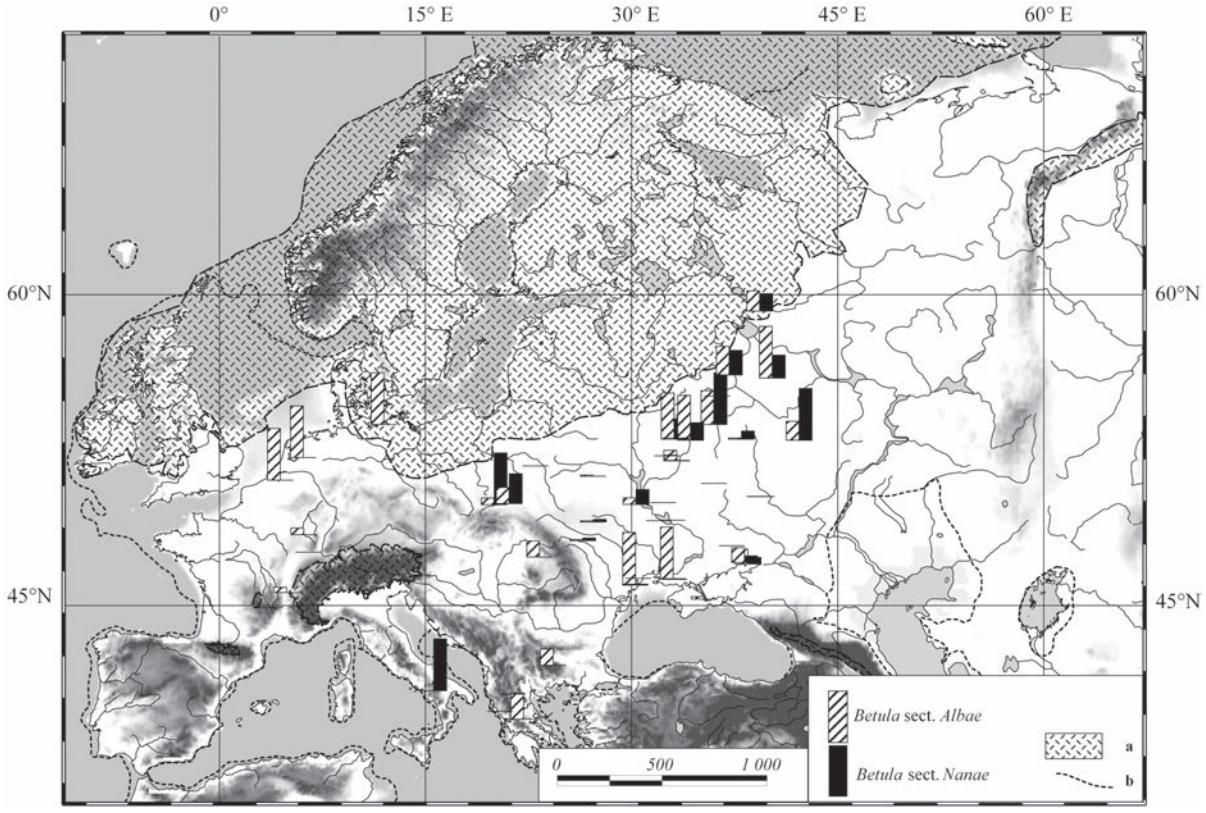

Fig. 5.5. *Betula pollen from LGM localities; a – ice sheets; b – coastline*

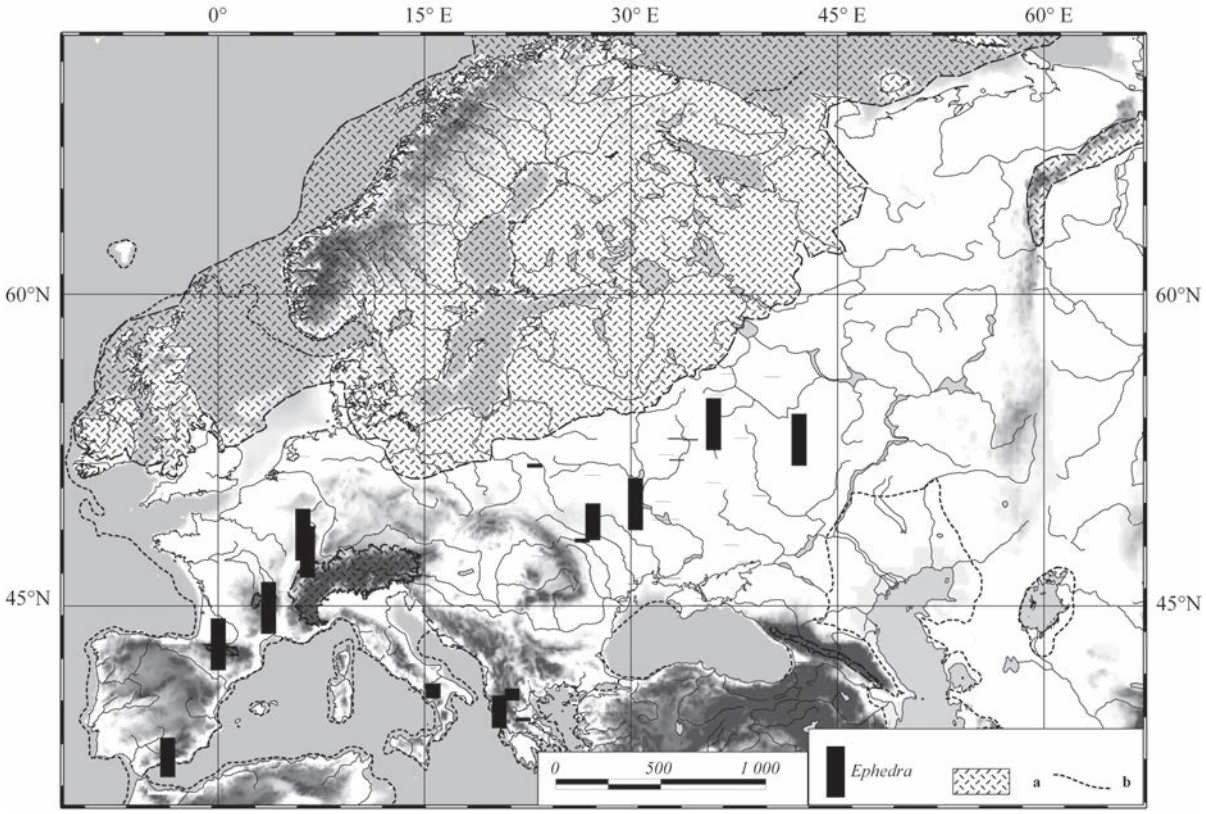

Fig. 5.6. *Ephedra pollen from LGM localities; a – ice sheets; b – coastline*

The range of species that characterize the semidesert and steppe phytocoenoses, like *Eurotia ceratodes*, are extended by more than 1,000 km to the northwest compared to its modern distribution and reached 62°N on the Russian Plain. *Artemisia* and Chenopodiaceae were widely distributed all over Europe. Their pollen is absent in the north of Western Europe and in Poland. The amount of *Artemisia* and Chenopodiaceae pollen in the European spectra gradually increases from west to east (Figs. 5.7, 5.8).The maximum amount of Poaceae pollen was obtained from sections located in the central and southern regions of Europe (Fig. 5.9). The sections with dominance of steppe taxa in the pollen spectra, and characterizing the wide development of periglacial steppes, are basically located south of 48–52°N.

The semidesert vegetation communities are basically distributed along the coast of the Black Sea (at 45–47°N.) at this time, and, fragmentarily, in the south of the Oka-Don Plain. The forest vegetation did not completely disappear during the LGM. A pine, birch and spruce, larch assemblage is part of the periglacial forest-steppe and forest-tundra vegetation associations. *Abies*, *Cedrus*, and *Pinus subsect. Cembrae*, and also representatives of the broad-leaved species remained in the forest refugia, which are associated with mountains, highlands, and large valleys, and the Mediterranean xerophytic forest, where the influence of the glaciation was minimal.

Pinus and *Betula* were widespread in the whole of Europe. The highest values for birch pollen in spectra are found in the sections located in Northern Europe, and in Southern Italy and the Black Sea coast.

Pollen of *Hippophaë rhamnoides* was found south of 48°N and west of 27°E. *Larix* is determined in the sections of Central and Eastern Europe between 50° and 53°N, and also in Western Greece (Fig. 5.10).

During the maximal stage of the Late Pleniglacial, the spruce, a typical representative of the dark coniferous taiga, has penetrated southward from its modern range. *Picea* was most widely distributed in Eastern Europe and in Southern Italy. Rare findings of *Picea* pollen grains are known from the Black Sea coast, the Asov Sea coast, in Poland, in the north of the Netherlands, and in Germany. Pollen of *Picea* was not found in Western Europe (Fig. 5.11).

The distribution of *Pinus subsect. Cembrae* was limited to the Carpathians. Single grains of *Pinus subsect. Cembrae* were found in the Don River middle reaches and in the Dnieper upstream, and on the Black Sea and Azov Sea coasts. Probably, the Carpathians formed the southern centre of the *Pinus subsect. Cembrae* expansion in the cold periods, as the Ural region formed the centre in the east (Fig. 5.12).

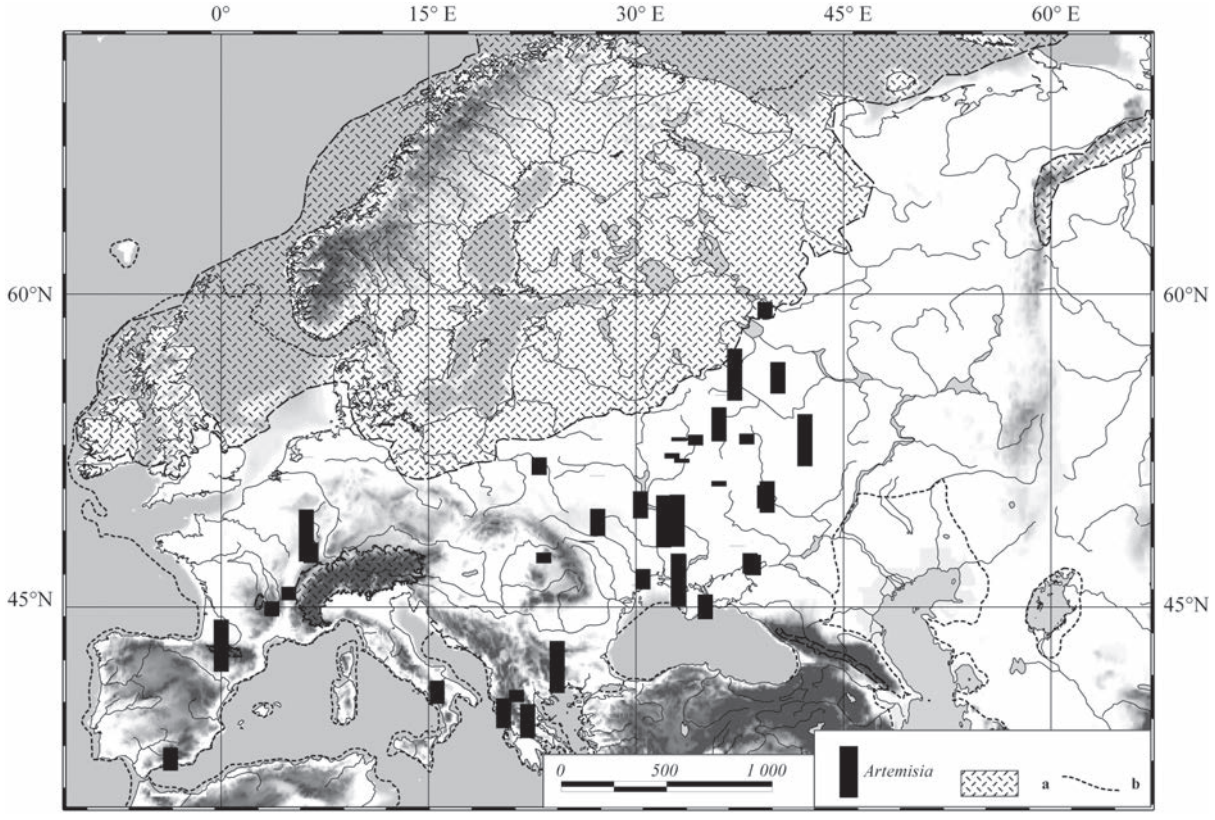

Fig. 5.7. *Artemisia pollen from LGM localities; a – ice sheets; b – coastline*

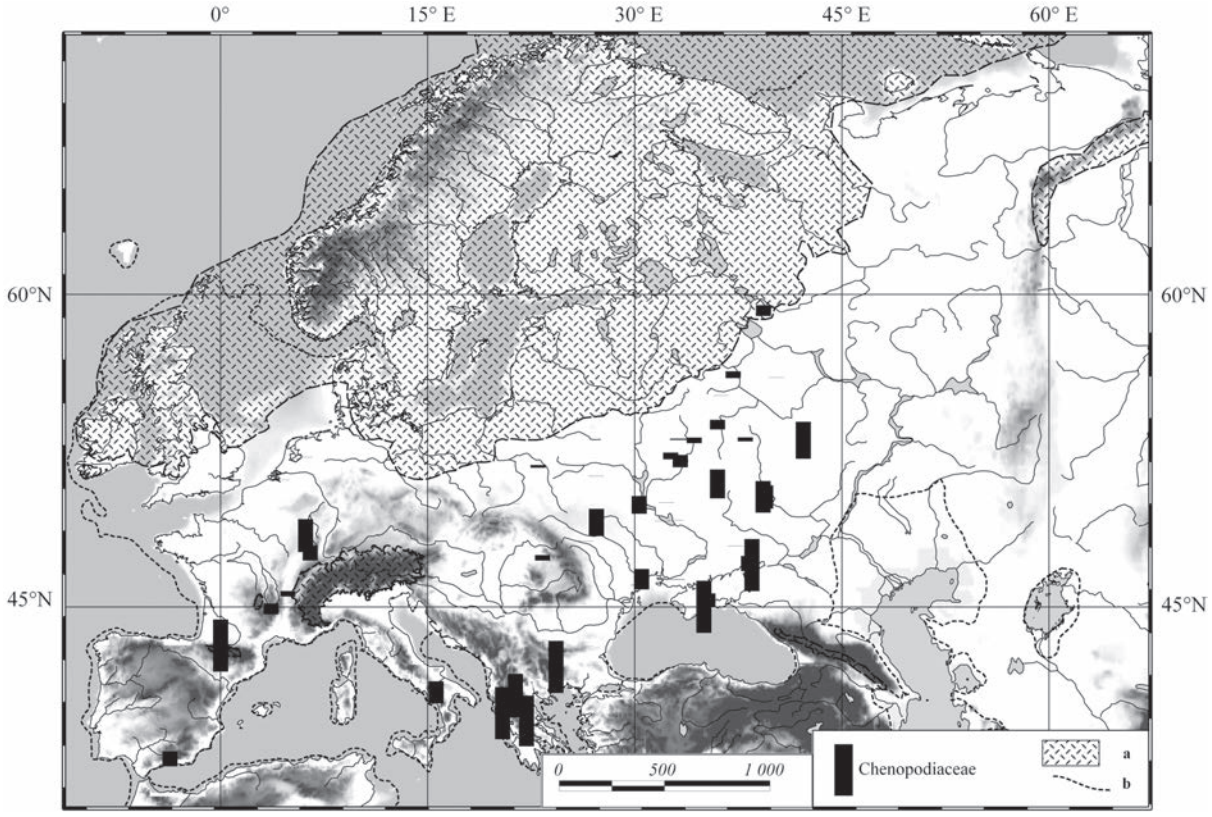

Fig. 5.8. *Chenopodiaceae pollen from LGM localities; a – ice sheets; b – coastline*

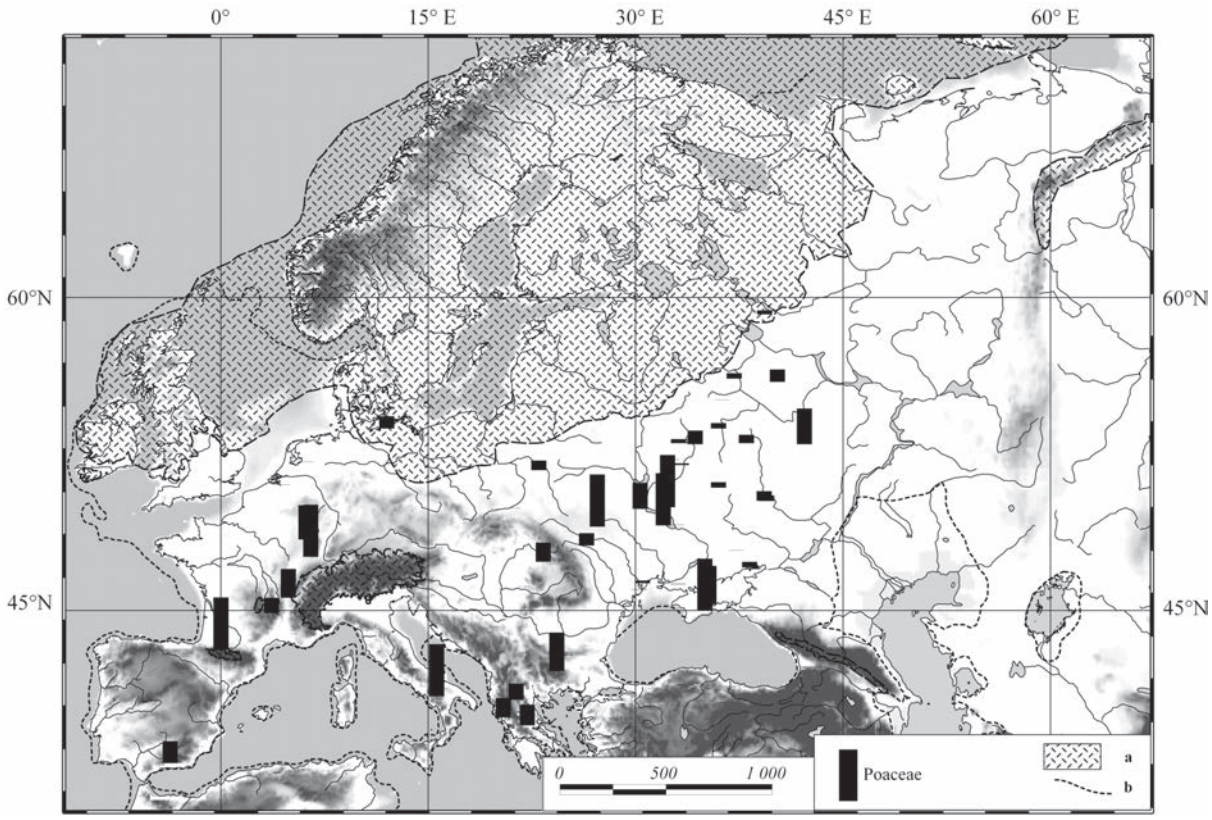

Fig. 5.9. *Poaceae pollen from LGM localities; a – ice sheets; b – coastline*

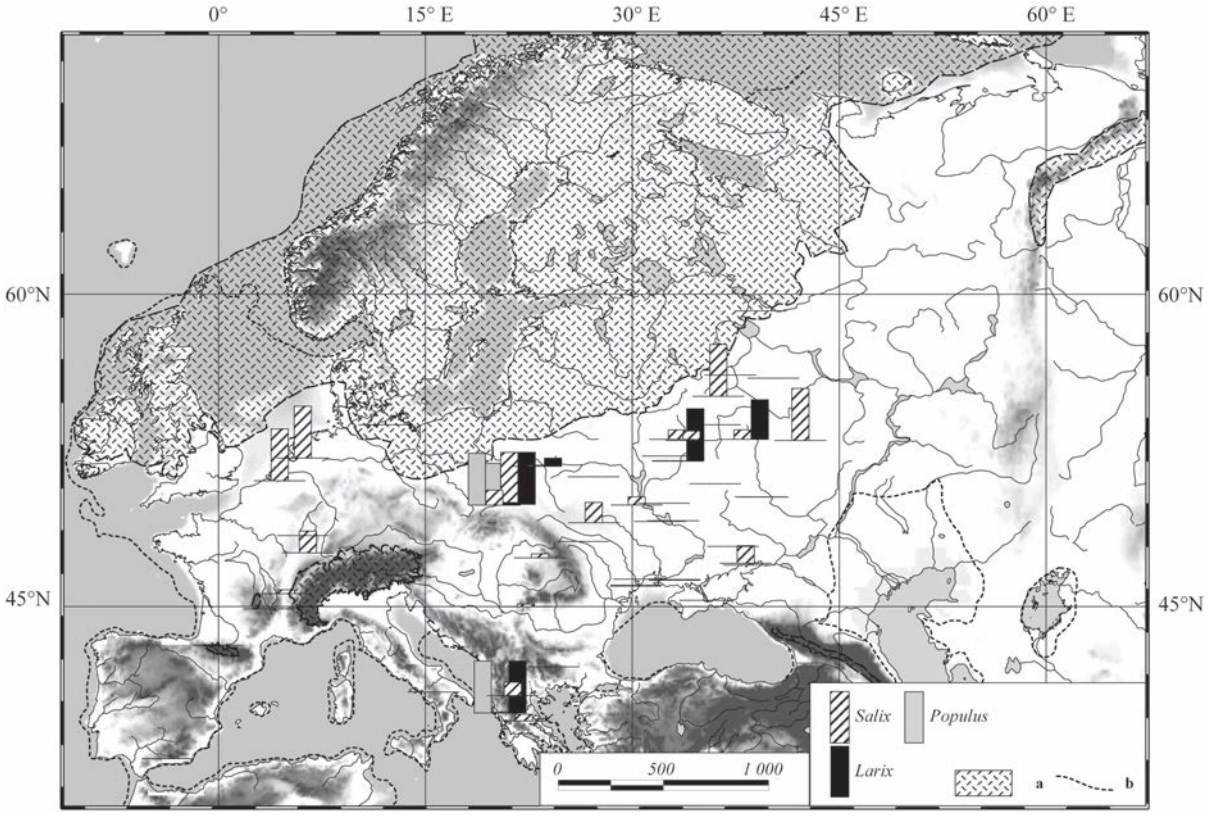

Fig. 5.10. *Populus, Salix, and Larix pollen from LGM localities; a – ice sheets; b – coastline*

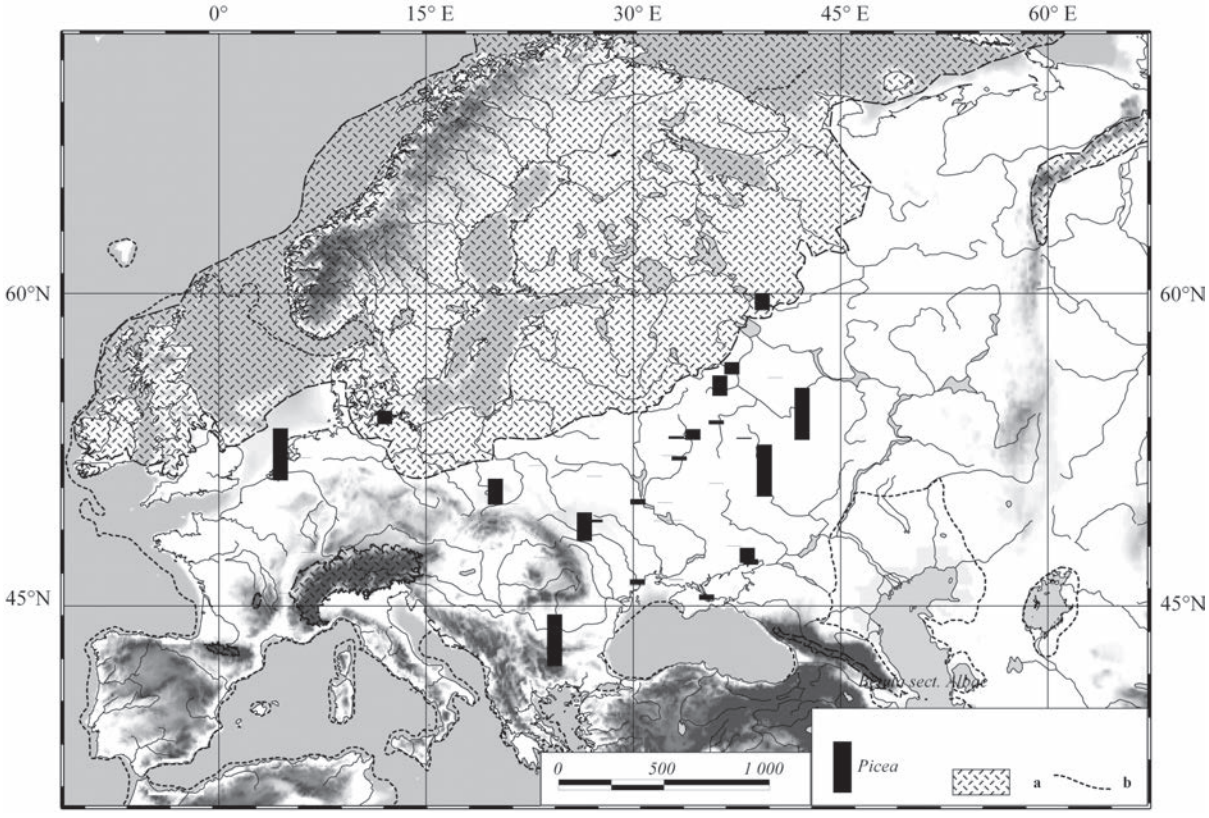

Fig. 5.11. *Picea pollen from LGM localities; a – ice sheets; b – coastline.*

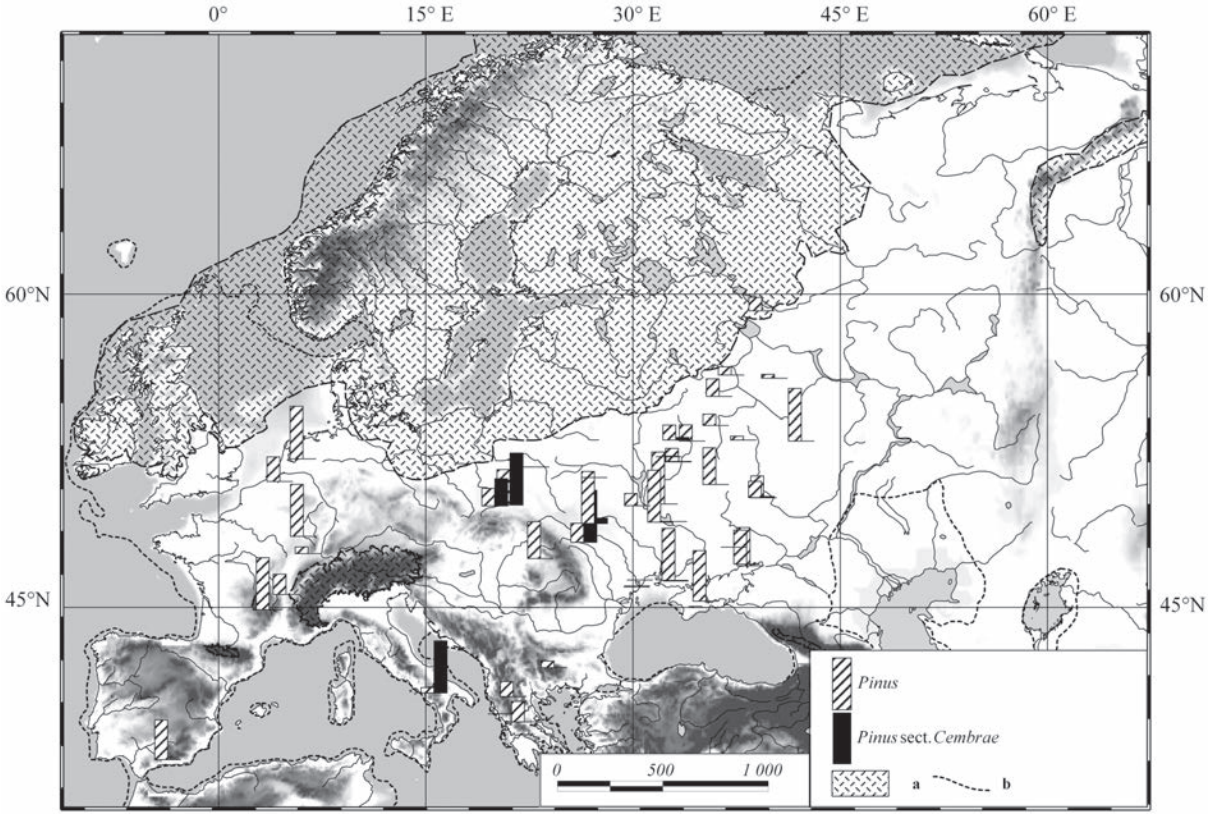

Fig. 5.12. *Pinus pollen from LGM localities; a – ice sheets; b – coastline*

Pollen of *Abies* is practically absent in Western and Central Europe. Single grains of *Abies* were found in the Donetsky Ridge, in the Carpathians, in Southern Italy, and in Greece.

Real forest pollen spectra are derived from the Moscow, Middle Russian, Donetsk, the south of Podolian Upland, in the Carpathians, in southeastern France, in the Crimea, and in Southern Italy and Spain.

The participation of broad-leaved species in the phytocoenoses in Northern and Central Europe during the Upper Pleniglacial remains disputable. Many authors consider the presence of broad-leaved tree pollen in sediments of this age as the result of redeposition (Grichuk *et al*., 1969; Pashkevich, 1977, 1987; Semenenko *et al*., 1981; Deviatova, 1982; Zelikson, 1986). In our opinion, redeposition occurs in the regions situated inside the limits of the ice sheet or near its margins. In other cases we assume that the findings of broad-leaved pollen in spectra are in situ. At the same time, we assume the possibility that the reworking of broad-leaved tree pollen can also occur in fluvial districts, where due to river dynamics, older deposits are being reworked. Another agent is the periglacial process, such as repeated freezing and thawing, which can mobilize sediment and pollen. The analysis of maps showing the occurrence of *Tilia*, *Carpinus*, *Corylus*, *Quercus*, and *Ulmus* pollen has revealed certain conformities, which were taken into account when dealing with palaeovegetation reconstructions in periglacial areas. During the glacial maximum, the pollen of *Fraxinus*, *Carpinus*, *Acer*, and *Cornus* disappeared in most of Europe. The pollen grains of *Tilia*, *Corylus*, *Ulmus*, and *Quercus* occur in the sections located south of 49–51°N, and also in the small areas of central parts of the Russian Plain (Moscow, Middle Russian highland). However, the refugia of the forest phytocoenoses were retained in the Moscow, the Middle Russian, the Donetsk, and the south of Podolsk highlands, in the middle reaches of the Dniester and Dnieper Rivers, in the Carpathians, in Southeastern France, in the Crimea, and in Southern Italy and Spain.

Therefore, the following provinces of three vegetation domains were established in Europe during the LGM (Fig. 5.13).

The East European domain

I. Low shrub tundra with patches of forest-tundra and tundra steppe vegetation (cluster 8) – north of 55°N.

II. Periglacial tundra-forest-steppe (clusters 1, 6, 7, and 8) – the combination of tundra and steppe vegetation communities with light pine-birch forest (53–56°N).

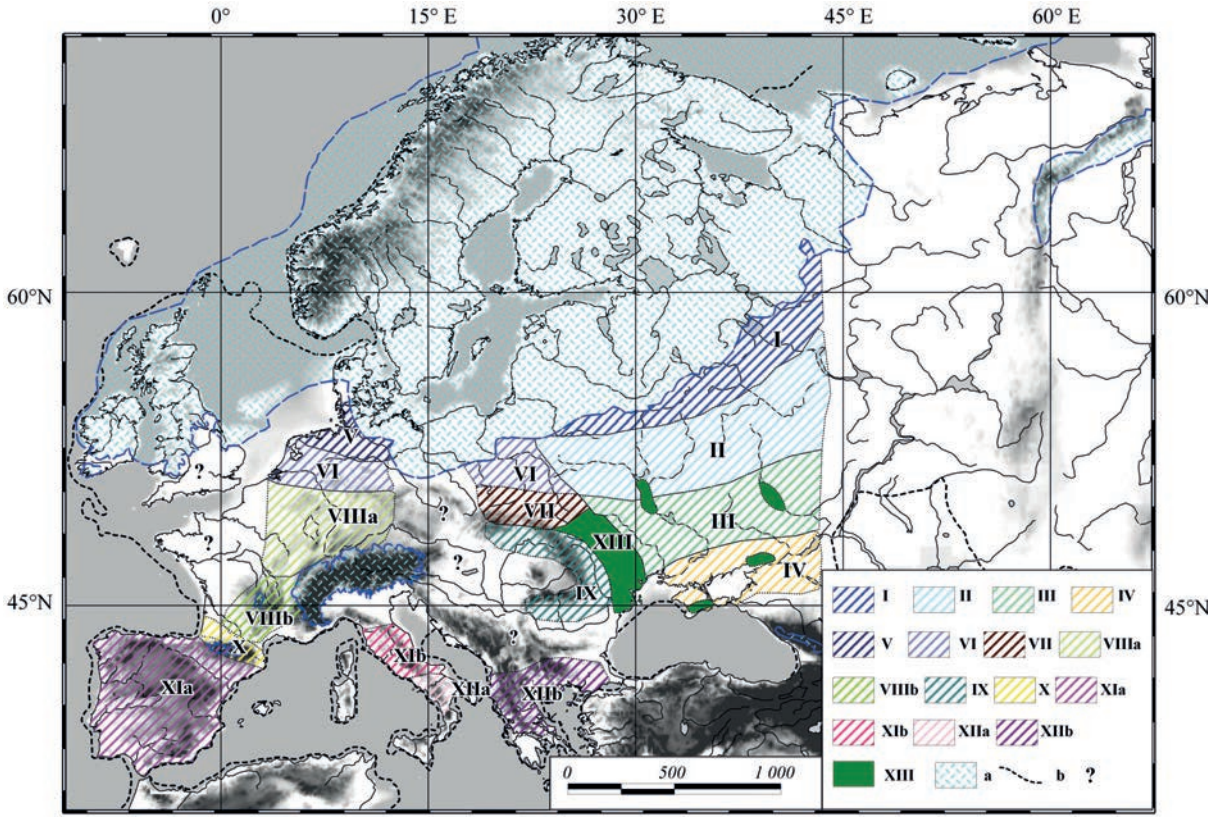

Fig. 5.13. *Palaeovegetation during the LGM: I – Low shrub tundra; II – Periglacial tundra-forest-steppe; III – Periglacial forest steppe; IV – Periglacial steppe; V – Periglacial shrub tundra;VI – Periglacial forest-tundra; VII – Periglacial light forest; VIIIa – Northern periglacial forest-steppe; VIIIb – Southern periglacial forest-steppe; IX – Periglacial pine forest; X – Periglacial steppe; XIa – The combination of coniferous-broad-leaved forest and grass-herb steppes; XIb – The combination of coniferous-broad-leaved forest and steppes both grass-wormwood and wormwood – Chenopodiaceae family; XIIa – Broad-leaved forest with patches of grass-wormwood steppes; XIIb – coniferous-broad-leaved forest with patches of grass-wormwood steppes; XIII – Forest refugia, a – ice sheets, b – coastline, ? – absence of data*

III. Periglacial forest steppe (clusters 5, 6, 7, and 8) – association of steppe, tundra steppe and pine-birch parklands (49–53°N).

IV. Periglacial steppe (clusters 5 and 6) – the combination of *Artemisia*-Chenopodiaceae steppe intermingled with tundra and semidesert plants (45–49°N).

The West European domain

V. Periglacial shrub tundra (cluster 3) – the associations of shrub tundra with *Betula*, *Alnus*, *Salix*, and *Juniperus* participation (north of 51°N).

VI. Periglacial forest-tundra (clusters 3 and 5) – the combination of pine-birch parklands, shrub tundra, and insignificant patches of steppe vegetative associations (50–51°N).

VII. Periglacial light forest (cluster 3) – the light coniferous forest with participation of tundra and meadow phytocoenoses (45–51°N and west of 11°E).

VIII. Periglacial forest-steppe.

VIIIa. Northern periglacial forest-steppe (cluster 3) the combination of pine-birch woodland and grass-cereal-wormwood steppes (45–47° – 51°N and east of 11°E).

VIIIb. Southern periglacial forest-steppe (clusters 2 and 4) – the combination of pine woodlands and herb-wormwood steppes (43–47°N).

IX. Periglacial pine forest of the Carpathians (clusters 3 and 5).

X. Periglacial steppe (cluster 4) – wormwood-grass steppes with participation of mountain pine-birch forests (42–43°N).

The Mediterranean domain

XI. Forest-steppe.

XIa. The combination of coniferous-broad-leaved forest and grass-herb steppes (clusters 1 and 2) – Iberian Peninsula.

XIb. The combination of coniferous-broad-leaved forest and steppes both grass-wormwood and worm-

wood – Chenopodiaceae family (cluster 5) – Northern Italy and Danube lowland.

XII. The Mediterranean xerophytic forest.

XIIa. Broad-leaved forest (with *Acer*, *Quercus*, and *Ulmus*) with patches of grass-wormwood steppes (cluster 1) – Southern Italy and Western Greece.

XIIb. Coniferous-broad-leaved forest with patches of grass-wormwood steppes (clusters 1 and 5) – Greece.

XIII. Forest refugia (birch-pine and spruce forest with broad-leaved trees) located in large river valleys, mountain systems and highlands of Europe.

During the LGM three vegetation domains are essentially distinguished based on the structure of the provinces in Europe: East European, West European, and Mediterranean. The increase in climatic continentality, reflected in the vegetation structure occurred from east to west. The subarctic and steppe plants were present almost everywhere. The arctic and northern-taiga species expanded to the south – southeast up to 47°N. The steppe plants distributed to north – northwestern Europe up to 62°N. During the LGM, a destruction of the forest zone took place and a reorganization of the vegetation zones occurred, considerably north of 54°N. The distinctions among the reconstructed vegetation provinces became smoothed, and the existing landscapes had no analogues in modern vegetation. The highest flora diversity is associated with the dissected territories in which variable local habitats occur (uplands, mountain systems, river valleys). These areas played a role in the refugia during the glacial time.

5.2. PALAEOVEGETATION DURING THE LATE GLACIAL TRANSITION (LGT) (⩽17.0 – ⩾12.4 KYR BP)

Alexandra Simakova and Andrey Puzachenko

The Late Glacial Transition (LGT) is the time of the ice sheet melting during the final stages of the Late Pleniglacial, including the Oldest Dryas (Bos *et al*., 2001). The conditions were colder than at present during all months; however the warming trend in the Northern Hemisphere had set in. January temperatures indicate that the deviations from modern temperatures were 11–7°C, July anomalies were about 2–9°C (Velichko and Morozova, 1982; Kutbash *et al.*, 1998). LGT deposits that represent this episode are fluvioglacial formations and periglacial alluvial deposits, lake-sediments and fen peats, cover sands, and loess/soil sequences. The Altyn Loess unit (Loess III) in the central region of the Russian Plain (Morozova and Nechaev, 2002), and the Prichernomorskii Loess unit (Loess III) in the southern Russian Plain (Gozhik *et al*., 2001) were formed during the LGT.

There are reconstructions of the vegetation during the LGT only for several territories in Europe based on pollen records from the Netherlands, France, Germany, Italy, Ireland, Poland, Spain, Switzerland, Norway, Russia, Moldova, Belarus, Ukraine, Estonia, Lithuania, etc. (Grichuk *et al*., 1969; Artushenko, 1970; Verburggen, 1979; Kolstrup, 1980; Velichko *et al*., 1981; Bolikhovskaya, 1982; Veklich, 1982; Vandenberghe and Bohncke, 1985; Pashkevich, 1987; Bohncke *et al*., 1988; Lotter, 1988; Pons and Reille, 1988a; Goslar *et al*., 1991; Beaulieu and Reille, 1992; Iakushko *et al*., 1992; Hoek, 1997; Turner and Goni, 1997; Kremenetskii *et al.*, 1998; Zernitskaya *et al.*, 2001; Pini, 2002; etc.).

For the LGT (17–12.4 kyr BP) the pollen records from 76 sections including 273 samples were put into the database (Table 5.3). In addition, we used the palynological records in the European Pollen Database.

The pollen database includes 222 taxa of pollen and spores (79 species, 116 genera, 38 family identifications) from LGT sites. Radiocarbon data are available for 38 sections. Twelve localities have calculated dates. The ages of the other sites were determined using geological methods taking into account pollen spectra from Loess III formations, formed during melting of the ice sheet. Unfortunately, we have no Late Glacial palynological evidence available from Central Europe, nor from Western France.

The analysis of collected pollen data and palaeovegetation reconstruction for the LGT was carried out with the help of a technique described earlier.

The Late Glacial Transition pollen sites

ND	Localities	Latitude	Longitude	Age	References
1	Meekelermeer	52.4	6.45	relative	Bohncke *et al*., 1988
2	Epe	50.34	5.97	14 000±150, GrN-8509	Kolstrup, 1980
3	Ballybetagh	53.10	–6.25	12 540±80, TO-238	EPD
4	Belle Lake	52.11	–7.03	calculated	EPD
5	Blomoy	60.32	4.53	calculated	EPD
6	Ballinloghig Lake	52.12	–10.18	13 980±460, UB-2685	EPD
7	Spjallsjon	56.68	14.59	12 540±140, Lu-2511a	EPD
8	Tomtabaken	57.29	14.28	12 450±130, Lu-894 12 610±190, Lu-893	EPD
9	Liastemmen	59.10	5.14	12 640±160, T-6333a; 2 780±210, Ua-479; 12 630±130, T-6686a; 13 275±220, Ua-477; 12 720±130, T-6164a; 13 240±210, Ua-478; 13 000±170, T-6684; 12 670±140, T-6165b; 13 000±160, T-6333b	Paus, 1989
10	Notsel	51.32	4.47	12 600±60, GrN-9594	Vandenberghe &.Bohncke, 1985
11	La Grande Pile	47.73	6.5	13 000 15 000	Beaulieu & Reille, 1992
12	Usselo 1	52.11	6.51	12 930±210, Ua-382; 12 840±200, Ua-381; 12 540±110, GrN-1104	Van Geel *et al*., 1989 Hoek, 1997
13	Vinderhoute-Kale	51.05	3.7	12 650±70, GrN-5062	Verburggen, 1979
14	Timonovka II	53.4	34.24	15 110±530, LU-358	Velichko *et al*., 1981
15	Antu Sinijavr	59.08	29.19	calculated	EPD
16	Sitno	57.29	33.25	relative	Kotlykov, 1972
17	Karachish	53.25	34.3	Loess III (LGT)	Serebriannaya, 1972
18	Arapovichi	53.3	33.1	Loess III (LGT)	Grichuk *et al*., 1972
19	Factory of 1 May	56.35	37.12	13 800	Semenenko *et al*., 1981
20	Koposa	57.2	31.15	relative	Grichuk *et al*., 1969
21	Vasilievka	46.4	33.1	Loess III (LGT)	Veklich, 1982
22	Zaporogie	47.47	35.15	Loess III (LGT)	Veklich, 1982
23	Dvorets	57.5	32.2	relative	Grichuk *et al*., 1969
24	Voznesenie	61.05	35.15	relative	Grichuk *et al*., 1969
25	Mezin	51.5	27.2	Loess III (LGT)	Gubonina, 1969
26	Lozoviki	55.2	28.12	13 739±854, IGSB-464	Zernitskaya *et al*., 2001
27	Poteriaevo (700)	59.35	38.3	12 420±150, LU-1947	Gei *et al*., 2000
28	Chernikhovo	53.25	26.26	12 680±110, VS-366	EPD
29	Navarrus	39	0.04	12 665±150, Va-3077	EPD
30	Lac Saint Leger	44.25	6.2	12 520±360, Ly-963	EPD
31	Schusssenquelle	48.3	8.45	13 350, GrO-468	Lang, 1963

Continued table 5.3

ND	Localities	Latitude	Longitude	Age	References
32	Meerfelder	50.45	6.4	relative	Litt & Steblich, 1999
33	Dobranichevka	50.1	31.48	Loess III (LGT)	Shovkoplias *et al*., 1981
34	Mezhirich	49.4	31.25	15 245±1080, JC-900 B	Kornietst *et al*., 1981
35	Yeliesevichi	52.5	32.6	Loess III (LGT)	Zelikson, 1986
36	Gdanov	48.05	37.3	Loess III (LGT)	Artushenko, 1970
37	Primorskoe	46.05	30.25	Loess III (LGT)	Artushenko, 1970
38	Zagorodnee	49.4	36.25	Loess III (LGT)	Artushenko, 1970
39	Mironovka	46.3	35.2	Loess III (LGT)	Artushenko, 1970
40	Kuyalnitskii limen	46.4	30.5	Loess III (LGT)	Artushenko, 1970
41	Prilyki	50.2	32.3	Loess III (LGT)	Artushenko, 1970
42	Berislav	46.35	33.1	Loess III (LGT)	Artushenko, 1970
43	Kryhganovka	46.38	33.05	Loess III (LGT)	Artushenko, 1970
44	Kolkotovskaya balka	46.35	29.4	Loess III (LGT)	Veklich, 1982
45	Kotui	51.2	31.1	Loess III (LGT)	Veklich, 1982
46	Taromskii ovrag	48.25	35	LoessIII (LGT)	Veklich, 1982
47	Gavrilovo II	51.24	40.01	14 170±330, LU-1658; 13 560±200, LU-1654; 13 560±150, LU-1659	Spiridonova, 1991
48	Zarvinos	55.1	25	16 200±640	Kondratene *et al*., 1965
49	Naroch	54.92	26.83	13 110±70, Tln-654	Iakyshko *et al*., 1982
50	Lago Grande di Monticchio	40.56	15.6	calculated	EPD
51	Khimaditis	40.37	21.35	calculated	EPD
52	Ioannina	39.45	20.43	calculated	EPD
53	Xinias	39.03	22.16	calculated	EPD
54	Pobochnoe	51.45	52.3	13 000±600, CS-208	Kremenetskii *et al*., 1998
55	Lago de Ajo	38.6	–6.15	12 610±90, Beta-9157; 14 40±180, Beta-6740	EPD
56	Echets	45.67	4.89	15 050±250, Ly-2060; 17 320±250, Ly-2766; 15 260±290, Ly-2767	EPD
57	Laguna de la Roya	42.13	6.46	12 940±60, CAMS-12618	EPD
58	Col des Lauzes	45.46	6.32	13 060±270, Ly-1209; 13 750±450, Ly-1210	EPD
59	Lac Long Inferieur	44.03	7.27	12 510±370, Ly-1236; 13 460±410, Ly-1253	EPD
60	Sanabria Marsh	42.06	6.44	12 580±100, CAMS-15300; 12 580±330, Beta-9162	EPD
61	Padul 3	37.00	–3.67	13 200±150, Gif-6007; 15 200±190, Gif-6008	Pons & Reille, 1988a
62	ClairveauxPetitlac	47.00	7.00	relative	Bohncke, unpublishted
63	Lourdes	43.00	0.00	13 480±140, GrN-8675; 15 270±140, GrN-8510	Kolstrup, 1980
64	La Bouchet B5	44.89	3.67	15 800±900, Gif-5942	Pons & Reille, 1988b

Continued table 5.3

ND	Localities	Latitude	Longitude	Age	References
65	Lake Tseravinas	39.5	20.3	13 530±130, OxA-966; 14 930±150, OxA-4862; 15 300±160, OxA-4863	Turner, 1997; Goni, 1997
66	Rotsee RL300	47.00	8.15	12 580±170, C-791	Lotter, 1988
67	Rotsee RL305	47.00	8.15	13 350±210, C-805; 13 990±220, C-838; 14 170±230, C-836	Lotter, 1988
68	Lac de Siguret	44.47	6.33	13 190±260, Lv-712	EPD
69	Pian di Gembro	46.00	10.00	calculated	Pini, 2002
70	Lake Perespilno	52.00	23.20	calculated	Goslar *et al*., 1999
71	Molodovo V	48.30	26.45	17 000±180, GIN-62	Pashkevich, 1987
72	Molodovo I	48.30	26.45	Loess III (LGT)	Bolikhovskaya & Pashkevich, 1982
73	Oria	56.17	55.17	relative	Nemkova, 1978
74	Iksa	62.75	39.00	relative	Deviatova, 1969
75	Lake Steissling			calculated	Eusterhues K *et al.*, 2002
76	Froslev	55.00	07.00	calculated	Kolstrup, 1983

Twelve main clusters were distinguished using cluster analysis (Fig. 5.14, Table 5.4). These clusters indicate the distribution of the following vegetation associations: cluster 1 – forest-tundra communities with patches of ruderal perennials; cluster 2 – both shrub tundra and forest-tundra communities; cluster 3 – shrub tundra; cluster 4 – periglacial pine forests with patches of *Artemisia*-herb steppe communities; cluster 5 – pine-birch forest steppe with *Artemisia*-herb steppe communities; cluster 6 – periglacial coniferous-broad-leaved forest steppes; cluster 7 – *Artemisia*- grass steppes; 8 – *Artemisia*-Chenopodiaceae steppes and meadows with participation of coniferous-broad-leaved forest communities; 9 – forest-steppes (the combination of pine-fir forests with *Artemisia* – Chenopodiaceae and grass steppe communities); cluster 10 – meadows; cluster 11 – the combination of *Cedrus-Abies-Pinus* forests and grass steppe communities; cluster 12 – *Artemisia* and grass steppes with patches of pine-broad-leaved forest.

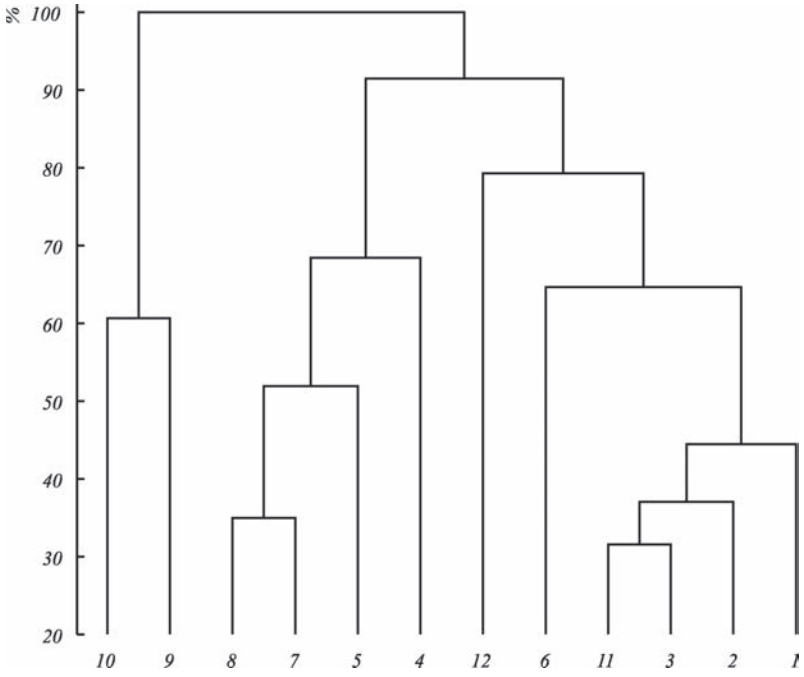

Fig. 5.14. *Dendrogram showing the relationship of LGT pollen assemblages*

Table 5.4

Cluster characteristics in standard units (average value of the cluster)

Taxa	Clusters											
	5	1	2	4	1	7	9	8	12	10	3	11
Abies (Fir)	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.31	0.00	0.04	0.00
Cedrus (Cedar)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.17	0.13
Cupressaceae (Juniper family)	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.13
Juniperus (Juniper)	0.02	0.10	0.52	0.00	0.05	0.00	0.00	0.00	0.01	0.00	0.19	0.04
Picea (Spruce)	0.42	0.01	0.00	0.06	0.00	0.30	0.00	0.00	0.00	0.00	0.00	0.00
Pinus (Pine)	0.47	0.12	0.00	0.22	0.66	0.56	0.01	0.01	0.12	0.01	0.20	0.45
Taxus (Yew)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.03	0.00	0.00	0.05
Acer (Maple)	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.16	0.00	0.00	0.00
Alnus (Alder)	0.20	0.04	0.00	0.26	0.00	0.31	0.01	0.21	0.03	0.01	0.01	0.01
Alnus fruticosa = Alnus alnobetula subsp. *fruticosa* (green alder)	0.20	0.00	0.00	0.06	0.00	0.09	0.00	0.00	0.00	0.01	0.00	0.00
Betula sect. *Albae* (Arboreal birch)	0.49	0.45	0.13	0.06	0.29	0.25	0.01	0.00	0.02	0.01	0.18	0.06
Betula nana (Dwarf birch)	0.44	0.15	0.00	0.06	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.03
Buxus (Box)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.06	0.00	0.00	0.00
Carpinus (Hornbeam)	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.36	0.00	0.00	0.03
Castanea (Chestnut)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.08
Corylus (Filbert)	0.28	0.02	0.00	0.00	0.00	0.14	0.03	0.13	0.04	0.00	0.02	0.13
Fagus (Beech)	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.20	0.03	0.00	0.00	0.00
Frangula (Alder Buckthorn)	0.05	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00
Fraxinus (Ash)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.01	0.00	0.17	0.00
Hippophaë rhamnoides (Sea buckthorn)	0.01	0.06	0.00	0.00	0.60	0.00	0.08	0.00	0.05	0.00	0.24	0.21
Ilex (Winterberry)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.11	0.13
Pistacia (Pistachio)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.28	0.00	0.00	0.00
Populus tremula (Aspen)	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00
Quercus (Oak)	0.04	0.01	0.00	0.00	0.01	0.08	0.01	0.21	0.30	0.00	0.05	0.03
Salix (Willow)	0.03	0.49	0.13	0.01	0.00	0.05	0.02	0.02	0.00	0.00	0.08	0.03
Tilia (Linden)	0.05	0.00	0.00	0.00	0.00	0.40	0.09	0.21	0.05	0.00	0.03	0.01
Ulmus (Elm)	0.11	0.01	0.00	0.00	0.00	0.00	0.01	0.13	0.05	0.00	0.01	0.13
Viburnum (Viburnum)	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00
Alismataceae (Water-plantain family)	0.00	0.01	0.00	0.00	0.00	0.00	0.18	0.00	0.25	0.00	0.00	0.00
Apiaceae (Carrot family)	0.00	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.10	0.36	0.24
Armeria (Sea grass)	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.42	0.05
Brassicaceae (Cabbage family)	0.08	0.03	0.15	0.00	0.02	0.01	0.05	0.00	0.11	0.03	0.15	0.18
Campanulaceae (Bellflower family)	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.10	0.25	0.13	0.05
Caryophyllaceae (Pink family)	0.02	0.17	0.08	0.00	0.00	0.05	0.03	0.00	0.12	0.03	0.45	0.23
Chenopodiaceae (Goosefoot family)	0.19	0.03	0.00	0.00	0.00	0.27	0.07	0.55	0.43	0.01	0.10	0.06
Compositae (Compositae family)	0.26	0.02	0.00	0.00	0.03	0.01	0.01	0.00	0.00	0.03	0.00	0.00
Asteraceae (Daisy family)	0.01	0.01	0.02	0.00	0.00	0.30	0.01	0.46	0.41	0.00	0.19	0.19

Continued table 5.4

Taxa	Clusters											
	5	1	2	4	1	7	9	8	12	10	3	11
Asteraceae (Asteraceae family)	0.00	0.10	0.38	0.00	0.00	0.35	0.00	0.14	0.31	0.00	0.02	0.23
Artemisia (Wormwood)	0.33	0.18	0.02	0.00	0.12	0.43	0.01	0.28	0.41	0.01	0.36	0.42
Centaurea (Knapweed)	0.00	0.02	0.15	0.00	0.02	0.22	0.00	0.00	0.18	0.00	0.07	0.17
Convolvulus (Field Bindweed)	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.14	0.25	0.00	0.13
Cyperaceae (Sedge family)	0.02	0.17	0.15	0.00	0.00	0.01	0.00	0.00	0.21	0.00	0.03	0.13
Dipsacaceae (Teasel family)	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.22	0.08	0.05	0.14
Scabiosa (Scabiouse)	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.50	0.00	0.00	0.00
Ephedra (Ephedra)	0.00	0.01	0.00	0.00	0.00	0.00	0.17	0.07	0.56	0.00	0.16	0.34
Ericaceae (Heather family)	0.15	0.10	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.14	0.05
Euphorbia (Spurge)	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.25	0.00	0.00	0.13
Fabaceae (Pea family)	0.10	0.01	0.00	0.00	0.00	0.03	0.00	0.03	0.09	0.06	0.22	0.13
Helianthemum (Rock-rose)	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.40	0.09
Lamiaceae (Dead-nettle family)	0.08	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.21	0.20
Liliaceae (Lily Family)	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.11	0.00	0.28	0.19
Myriophyllum (Water-milfoil)	0.01	0.09	0.17	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00
Lotus (Bird's-foot-trefoil)	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00
Nymphaea (White Water-lily)	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.00
Plantago (Plantain)	0.01	0.04	0.56	0.00	0.00	0.00	0.00	0.02	0.10	0.01	0.18	0.27
Poaceae (Grass family)	0.14	0.38	0.65	0.00	0.05	0.12	0.03	0.14	0.69	0.00	0.29	0.43
Polemoniaceae (Jacob's-Ladder family)	0.08	0.08	0.48	0.00	0.02	0.00	0.00	0.00	0.06	0.00	0.05	0.12
Polygonaceae (Knotweed family)	0.09	0.05	0.00	0.00	0.00	0.00	0.07	0.00	0.60	0.02	0.07	0.02
Rumex acetosa (Dock)	0.04	0.22	0.59	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.21	0.04
Potamogeton (Pondweed)	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00
Primulaceae (Primrose family)	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.17	0.00
Ranunculaceae (Buttercup family)	0.05	0.02	0.00	0.00	0.00	0.03	0.08	0.00	0.42	0.03	0.28	0.01
Thalictrum (Meadow-rue)	0.02	0.37	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	0.12
Rosaceae (Rose family)	0.07	0.19	0.00	0.00	0.00	0.00	0.12	0.00	0.04	0.06	0.55	0.00
Dryas octopetala (Mountain Avens)	0.00	0.13	0.50	0.00	0.07	0.00	0.00	0.00	0.04	0.00	0.05	0.10
Rubiaceae (Bedstraw family)	0.08	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.10	0.13
Saxifragaceae (Saxifrage family)	0.00	0.11	0.25	0.00	0.00	0.00	0.00	0.08	0.41	0.13	0.39	0.23
Sparganium (Bur-reed)	0.00	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Typha (Reedmace)	0.02	0.28	0.29	0.00	0.00	0.04	0.01	0.00	0.26	0.00	0.02	0.13
Urtica (Nettle)	0.12	0.21	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.00	0.03	0.25
Verbascum (Mullein)	0.00	0.00	0.00	0.00	0.00	0.20	0.00	0.00	0.25	0.00	0.00	0.00
Botrychium (grape-fern)	0.21	0.00	0.43	0.00	0.00	0.08	0.00	0.00	0.00	0.00	0.01	0.07
Bryales (mosses)	0.42	0.06	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.01	0.00	0.13
Huperzia selago (Fir Clubmoss)	0.01	0.13	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Continued table 5.4

Taxa	Clusters											
	5	1	2	4	1	7	9	8	12	10	3	11
Lycopodium (Clubmosses)	0.20	0.05	0.00	0.00	0.00	0.22	0.00	0.01	0.01	0.00	0.00	0.13
Ophioglossum (Adder's-tongue ferns)	0.08	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00
Polypodiaceae (Polypody family)	0.09	0.10	0.61	0.00	0.00	0.04	0.02	0.00	0.08	0.00	0.02	0.00
Selaginella selaginoides (mountain moss)	0.10	0.23	0.00	0.10	0.00	0.08	0.00	0.00	0.00	0.00	0.20	0.00
Sphagnum (sphagnum moss)	0.40	0.14	0.50	0.00	0.00	0.01	0.00	0.00	0.01	0.01	0.00	0.00

The geographical distribution of the twelve clusters is shown in figure 5.15.

The sites with pollen data according to clusters 1 and 2 are basically located in Western Europe north of 47°N. The pollen localities belonging to clusters 6, 3 and 11 occur in more southern areas. Pollen sites of cluster 12 are distributed in Greece. The pollen localities of clusters 4, 5, and 7 are located in Eastern Europe. The pollen localities belonging to the clusters 8, 9, and 10 occur in more southern areas of the Russian Plain.

Analysis of the geographical distribution of pollen sites shows that during the LGT the palaeovegetation of Western Europe differed considerably from the palaeovegetation of Eastern Europe and the Mediterranean.

The pollen spectra indicate that tundra and forest-tundra vegetation communities were widely distributed during the LGT. Their southern limits extended up to 48–49°N on the Russian Plain and more northward to 53°N in Western Europe. The maximum amount of *Sphagnum*, *Betula nana*, *Salix*, Ericaceae, *Empetrum*, Cyperaceae, *Selaginella selaginoides*, *Alnus fruticosa*, and *Huperzia selago* has been found north of 52–53°N (Figs. 5.16–5.18).

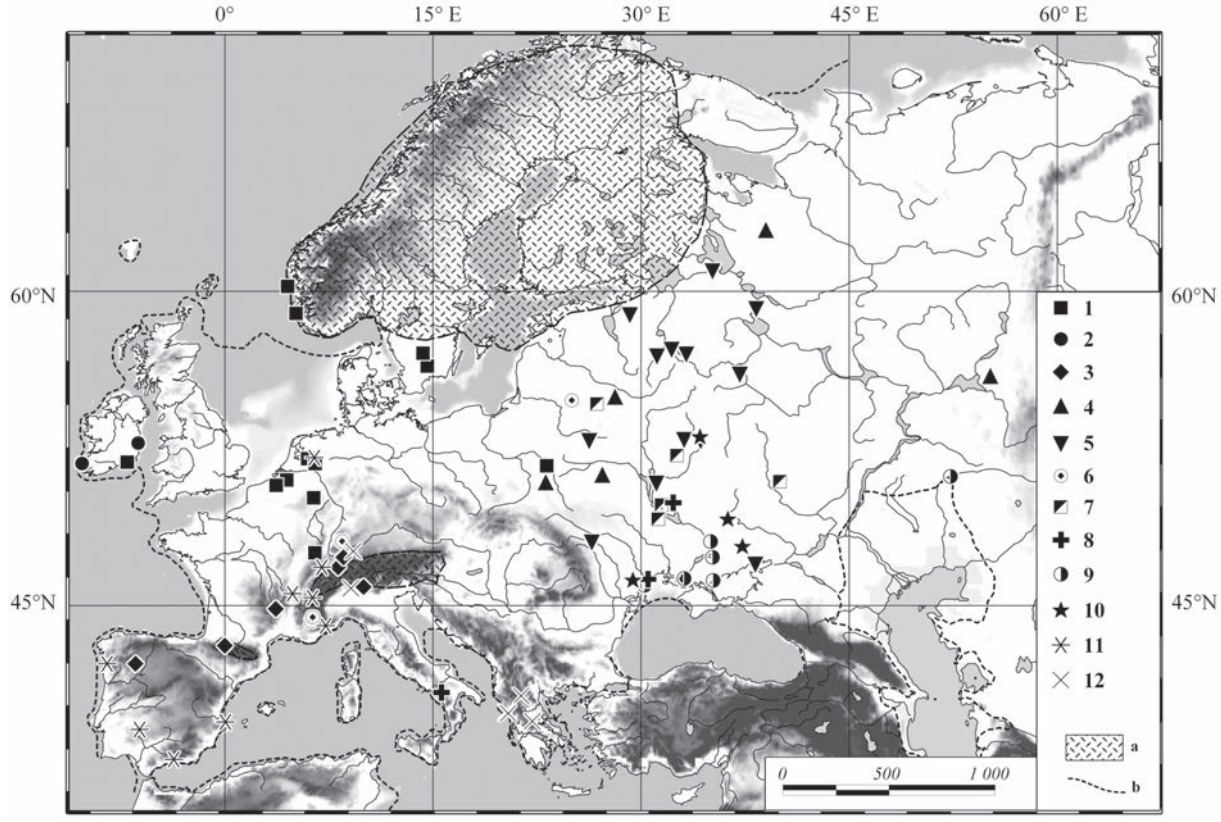

Fig. 5.15. *The geographical distribution of LGT pollen localities belonging to the different clusters (1–12); a – ice sheets; b – coastline*

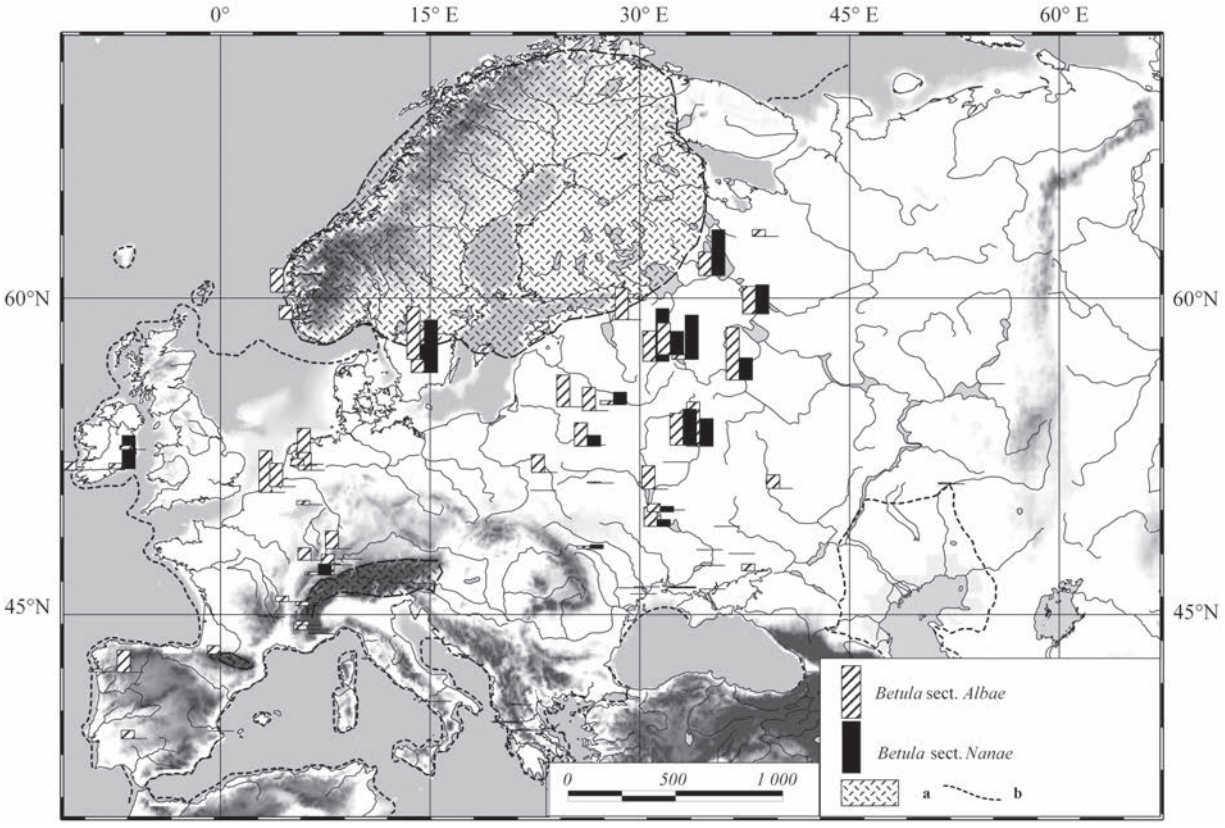

Fig. 5.16. *Betula pollen from LGT localities; a – ice sheets; b – coastline*

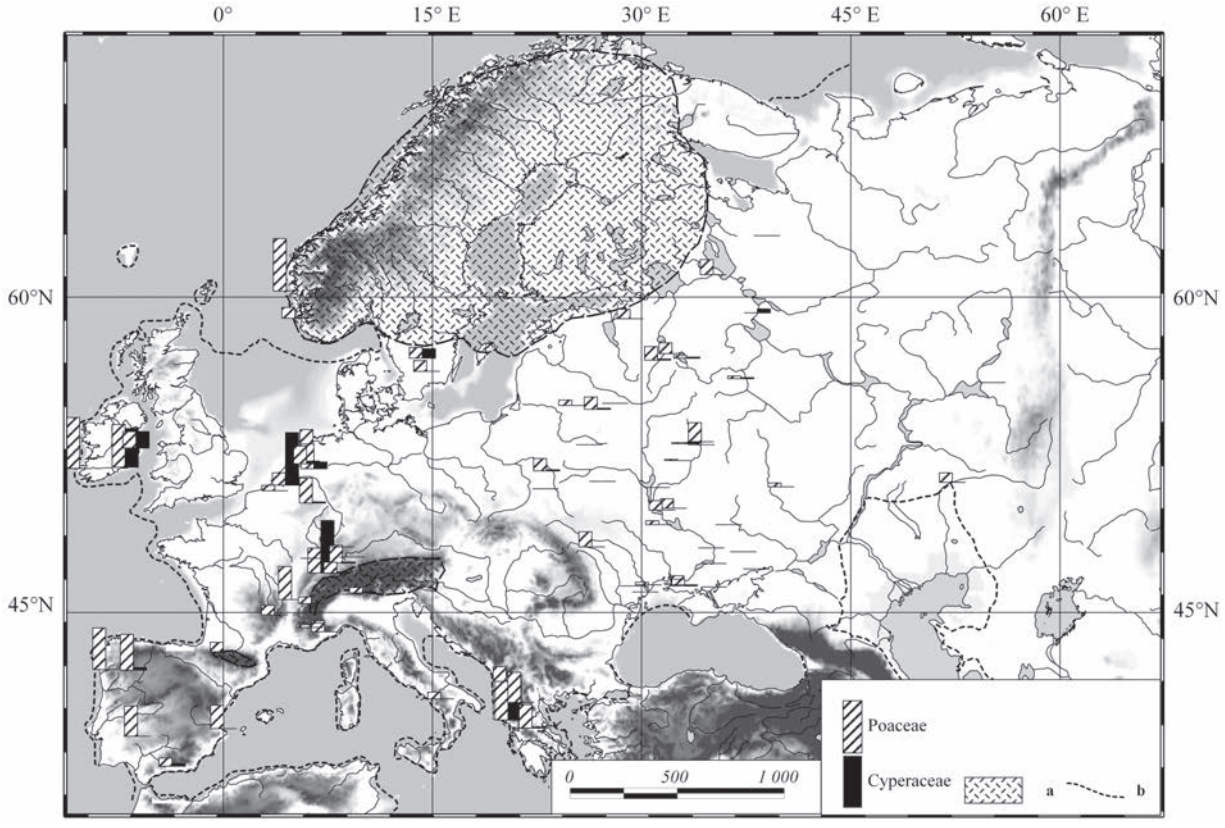

Fig. 5.17. *Poaceae and Cyperaceae pollen from LGT localities; a – ice sheets; b – coastline*

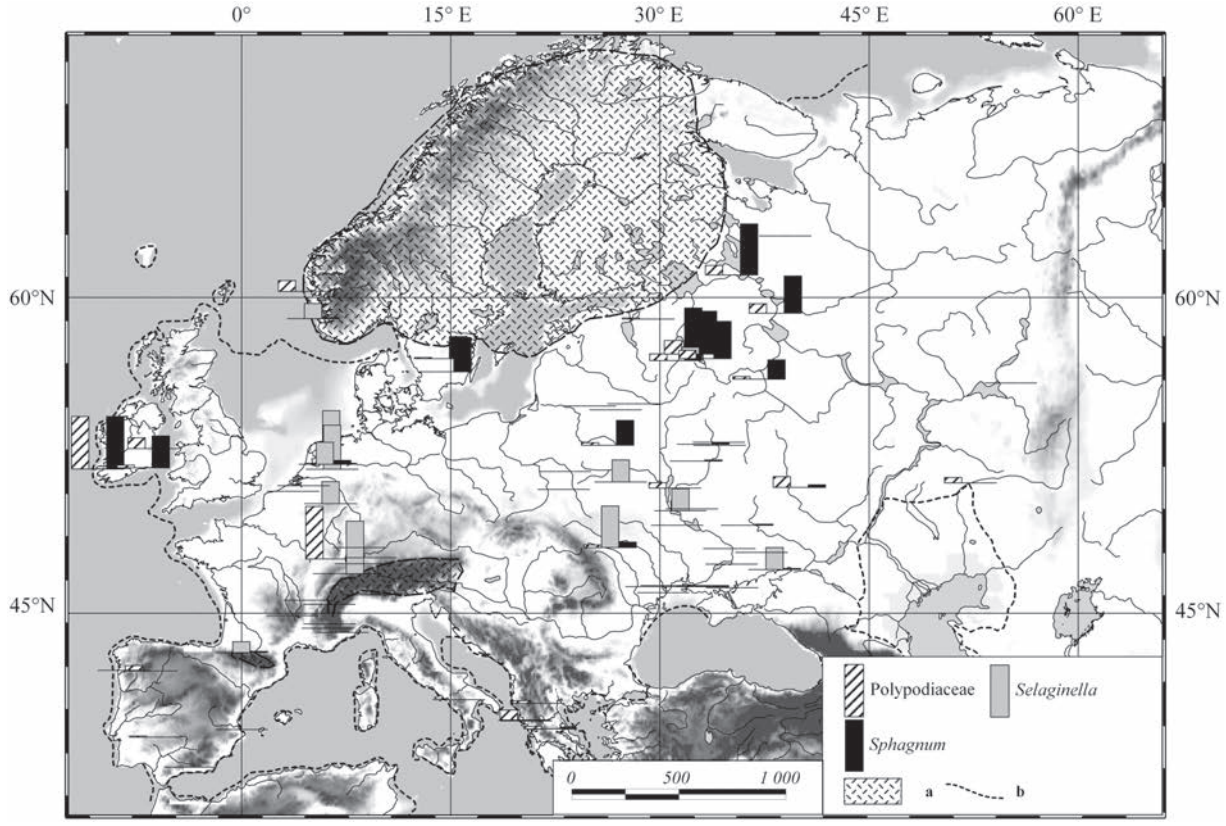

Fig. 5.18. *Selaginella, Sphagnum, and Polypodiaceae spores from LGT localities; a – ice sheets; b – coastline*

During the LGT, the southern boundaries of the *Alnaster fruticosa* and *Betula nana* ranges shifted approximately 6° to the north compared to the LGM time window. The range of *Selaginella selaginoides* did not change. *Armeria* grains were found in the foothills of the Pyrenees, and the Pindus, and in the mountain regions of the Iberian Peninsula (at altitudes of over 1000 m).

The area of tundra and forest tundra increased considerably during the LGT and was restricted to 53°N in Western Europe and 56–57°N in Eastern Europe. The presence of tundra and forest-tundra communities in palaeolandscapes significantly reduced in a southerly direction and are located only in mountain regions and river valleys. These valleys were connected with the development of large meanders during the LGT and formation of back swamps and bayou oxbows in the river valleys of Europe (Panin *et al*., 2001; Sidorchuk *et al.*, 2001).

The representatives of steppe coenoses were still widespread and occurred almost everywhere in Europe. During the deglaciation, *Ephedra* was most widely distributed in the south of Europe (up to 51°N in Eastern Europe and up to 48°N in Western Europe) (Fig. 5.19).

Single grains of *Ephedra* and *Eurotia ceratodes* were found on the northern Russian Plain up to 62°N. *Artemisia*, Poaceae, Chenopodiaceae and *Helianthemum* were widespread all over Europe (Figs. 5.17, 5.20, 5.21). The ranges of these taxa extended into Western Europe and reached 60°N.

Significant amounts of *Ephedra*, Brassicaceae, Polygonaceae, Lamiaceae, and Caryophyllaceae are associated with the central and southern regions of Europe, and of Chenopodiaceae were widespread in Eastern Europe and in the Mediterranean. Rubiaceae, Ranuncullaceae, Umbelliferae, and *Armeria* are mainly located in Western Europe (Figs. 5.22, 5.23). The range of *Centaurea* expanded from southern Europe northward up to 51°N in Western Europe and up to 47°N in Eastern Europe during the deglaciation. Also the ranges of *Plantago*, *Typha*, and Nymphaceae extended north up to 58–59°N.

The dominant presence of steppe and forest steppe indicator species in pollen spectra occurred southward of 47–51°N. This feature characterizes the widespread development of the periglacial steppe and periglacial forest-steppe in these territories. The steppe palaeovegetation was distributed to the southward of Central Europe, south of 47°N in Western Europe, and south of 51°N in Eastern Europe. In the central areas of Western Europe meadow communities were distributed wider than in Eastern Europe and in the Mediterranean. The

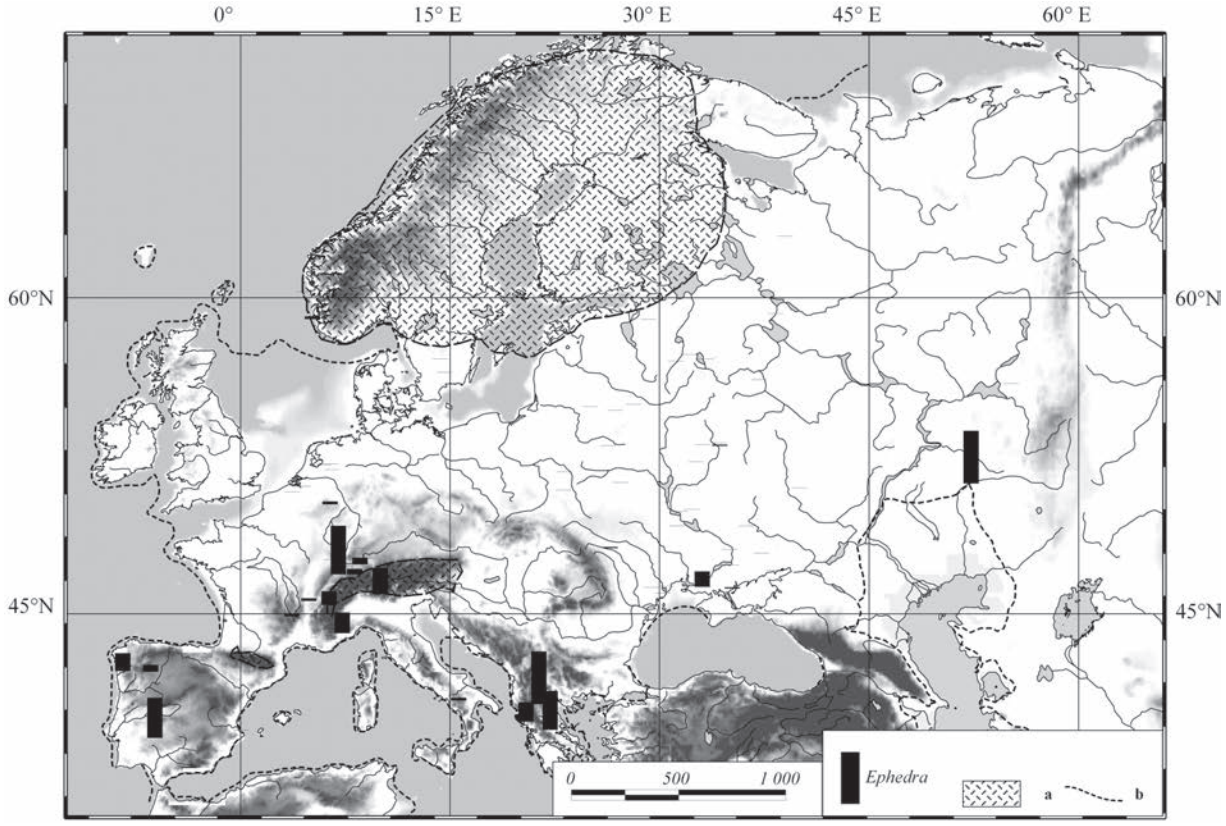

Fig. 5.19. *Ephedra pollen from LGT localities; a – ice sheets; b – coastline*

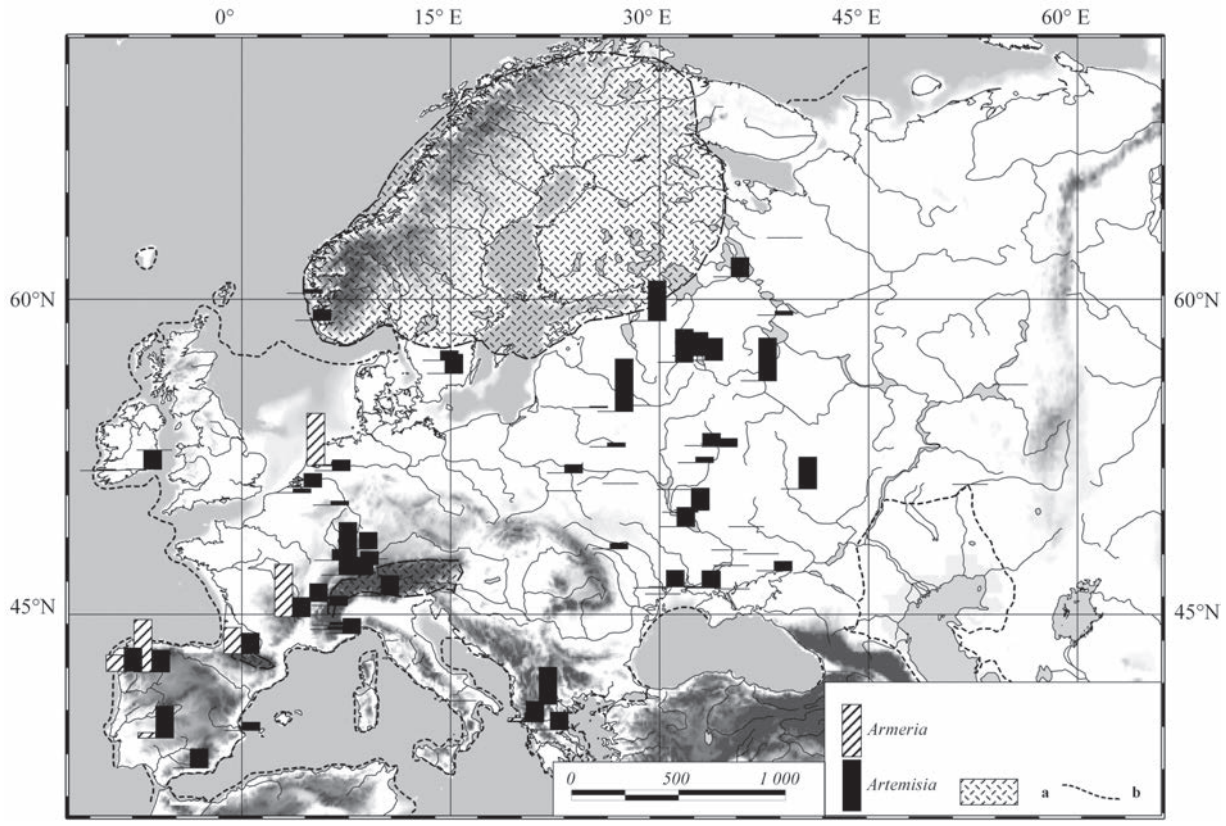

Fig. 5.20. *Armeria and Artemisia pollen from LGT localities; a – ice sheets; b – coastline*

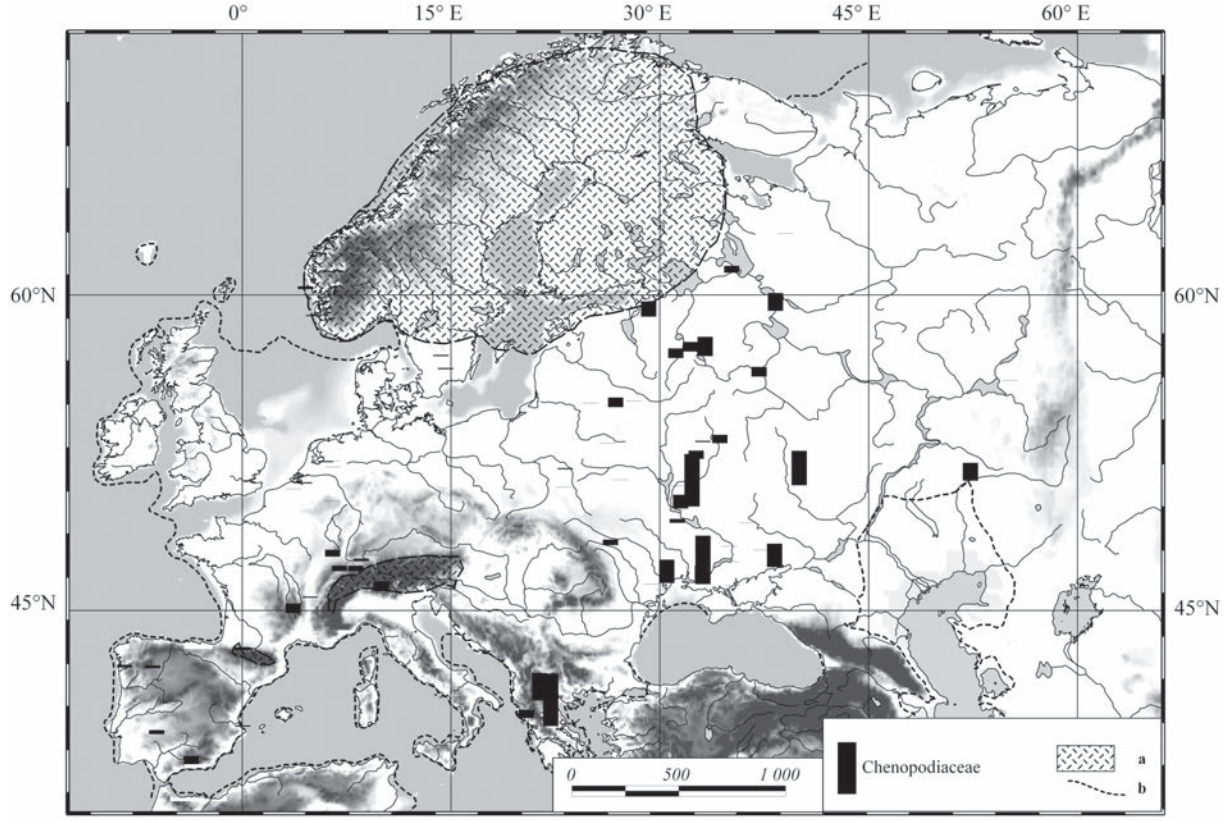

Fig. 5.21. *Chenopodiaceae pollen from LGT localities; a – ice sheets; b – coastline*

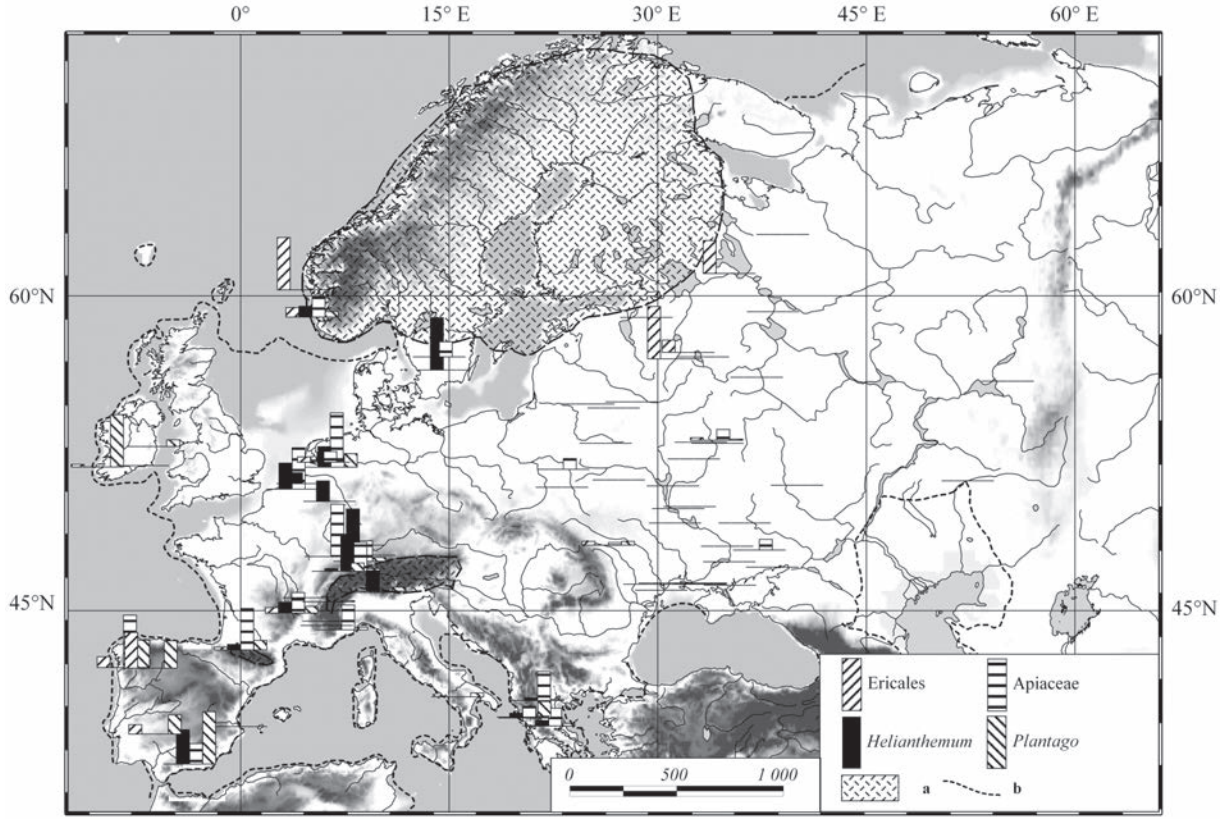

Fig. 5.22. *Ericales, Helianthemum, Apiaceae, and Plantago pollen from LGT localities; a – ice sheets; b – coastline*

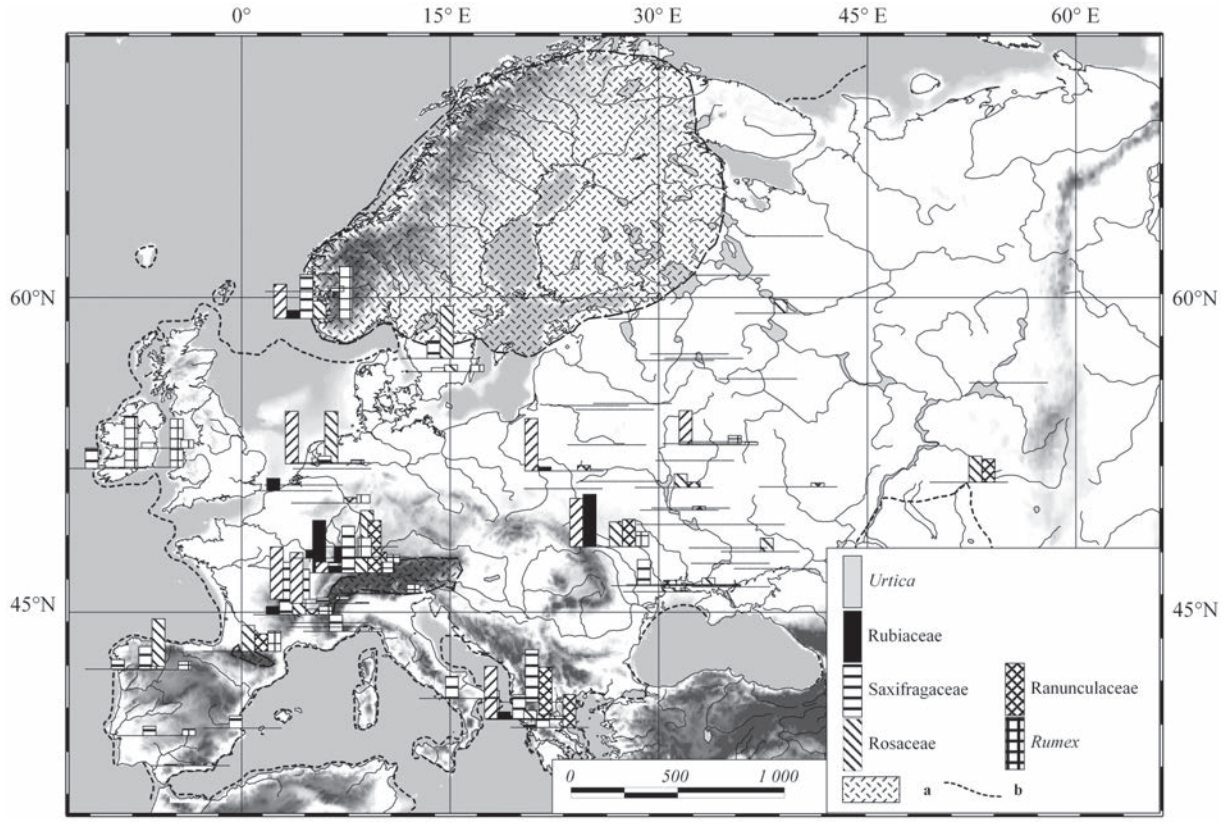

Fig. 5.23. *Urtica, Rubiaceae, Saxifragaceae, Rosaceae, Ranuncullaceae, and Rumex pollen from LGT localities; a – ice sheets; b – coastline*

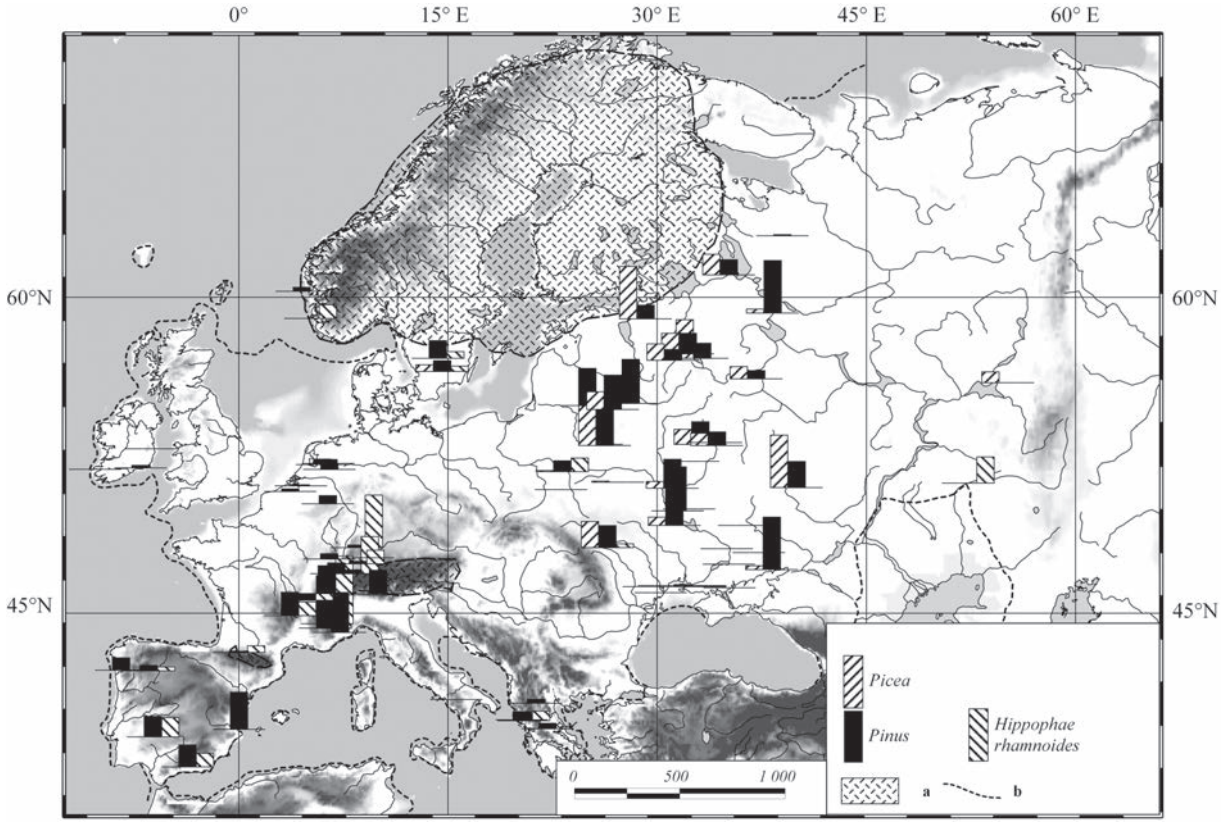

Fig. 5.24. *Picea, Pinus, and Hippophae rhamnoides pollen from LGT localities; a – ice sheets; b – coastline*

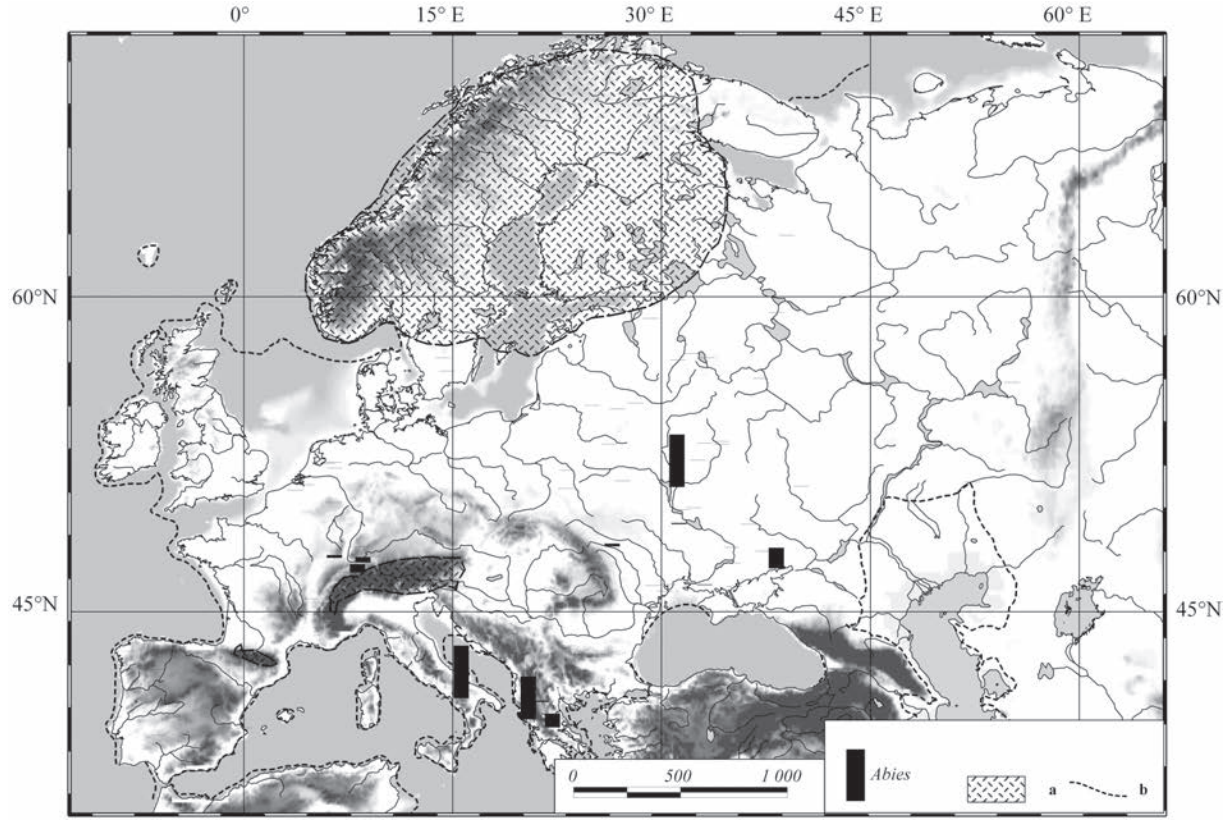

Fig. 5.25. *Abies pollen from LGT localities; a – ice sheets; b – coastline*

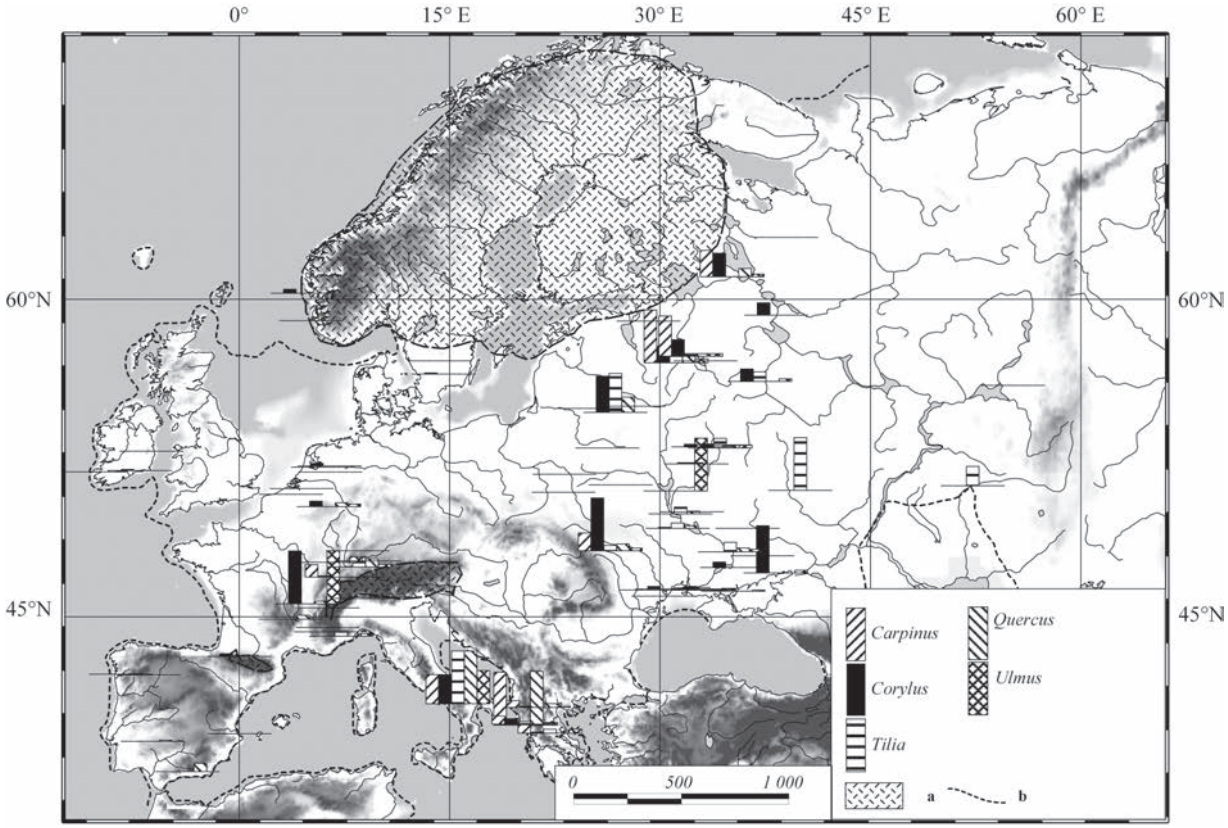

Fig. 5.26. *Carpinus, Corylus, Tilia, Quercus and Ulmus pollen in LGT localities; a – ice sheets; b – coastline*

semidesert landscapes occurred eastward of 43°E. Thus, during the LGT a more arid climate was established in Western Europe than during the LGM.

Forest associations dominated in the mountains and the highlands (the Iberian Peninsula, the Apennine Peninsula, the Carpathians, the Alps, the Pyrenees, the Crimea, the Pindus, the south of Podolian Upland, and the Oshmiansk Highlands).

Pinus and *Betula* were the principal forest formation species in the whole of Europe during the LGT. The highest values of *Betula* pollen in spectra occurred in sites situated south of 47°N. In contrast to the LGM, *Betula* disappeared in the southern regions of Central Europe during the LGT. The ranges of *Hippophaë rhamnoides* and *Juniperus* expanded to the north of Western Europe reaching Scandinavia. Pollen of *Hippophaë rhamnoides* and *Juniperus* are almost absent on the Russian Plain (Fig. 5.24).

Spruce disappeared in the southern part of the Apennine Peninsula and on the northern Black Sea coast during the end of the glaciation. In Western Europe spruce was found in the foothills of Vosges and in the south of the Scandinavian Peninsula. On the Russian Plain *Picea* was distributed northward of 51°N, and occurred in the forest-tundra, open woodland, and in the forest-steppe periglacial vegetation associations. During the LGM, *Pinus subsect. Cembrae* pollen was associated with the Carpathians. During the LGT, *Pinus subsect. Cembrae* was found in the foothills of the Alps, in the Vosges, in the Carpathians, in the Desna middle reaches, and also on the Ilmen Lake coast. *Abies* also expanded and it range penetrated the foothills of the Alps, and the Vosges, and was located also in the Dnieper valley.

Thus, during the Late Glacial Transition the taiga coenoses ratio in the palaeocoenoses structure of the forest-tundra became higher in the north and centre of Europe, penetrated river valleys in the forest-steppe zone (Fig. 5.25). However zones with continuous forests were absent during this time.

Broad-leaved trees gradually started to extend their ranges (Fig. 5.26). They were distributed into the foothills of the Pyrenees (*Quercus* and *Corylus*), in the Alps, in the Vosges, in the Massif Central (*Quercus*, *Ulmus*, *Corylus*, and *Carpinus*), in the Carpathians (*Quercus*, *Tilia*, and *Carpinus*), on coast of the southern seas (*Ulmus*, *Acer*, *Tilia*, *Corylus*, and *Fraxinus*), and along river valleys such as the Dnieper, the Don, and the Desna (*Quercus*, *Ulmus*, *Tilia*, and *Corylus*). *Carpinus* were found only in the low reaches of the Dnieper River.

The problem of an occurrence of broad-leaved elements in the north of Europe is not solved. Most likely their pollens were reworked. The pollen of spruce on the Scandinavian Peninsula is possibly also reworked (Birks, 2003). According to the other opinion, spruce refugia existed in southwestern Sweden (Petit, 2003).

In general, during the Late Glacial Transition periglacial forest-tundra and forest-steppe palaeolandscapes were widespread in Europe. Therefore, the following provinces covering three vegetation domains in Europe during the LGT (17–12.4 kyr BP) were established (Fig. 5.27).

The East European domain

I. Periglacial forest-tundra.

Ia. A combination of shrub tundra and light pine-birch forests with tundra-steppe and pioneer vegetation communities was distributed northward of 56°N.

Ib. Light pine-birch and pine-spruce forest with patches of tundra and meadow coenoses– located between 53–56°N.

II. Periglacial forest-steppe (the combination of *Artemisia*-Chenopodiaceae steppe, light pine-birch forest, and tundra-steppe vegetation – were distributed between 49–53°N.

III. Periglacial *Artemisia* – Chenopodiaceae steppe with patches of tundra associations –located between 45–49°N.

IV. Periglacial semidesert (the combination of *Artemisia*-Chenopodiaceae steppe and semidesert) (cluster 4) – was distributed to the east of 43°E.

V. Periglacial forest (spruce-pine forests located north of 54°N and coniferous-broad-leaved forests were southward reconstructed).

The West European domain

VI. Periglacial forest-tundra (the combination of shrub tundra with participation of *Betula*, *Salix*, and *Juniperus* and patches of light pine-birch forest – located north of 54°N.

VII. Periglacial forest – tundra-steppe (the combination of light pine-birch forest, shrub tundra and tundra-steppe communities) – distributed between 49–54°N.

VIII. Periglacial light pine forest with participation of meadow and meadow-steppe palaeophytocoenoses – located between 45–49°N and west of 11°E.

IX. Periglacial forest-steppe (the combination of pine-birch mountain forest with steppes both wormwood and grass-herb mixed steppe – foothills of the Pyrenees, the Massif Central – between 45–43°N.

X. Periglacial mountain coniferous forest combined with broad-leaved taxa – the Alps, and the Carpathians.

The Mediterranean domain

XI. The Mediterranean xerophytic forest.

XIa. The combination of pine-oak forests with *Juniperus, Hyppophae, Betula*, herb-grass steppes and wormwood steppes – Iberian Peninsula.

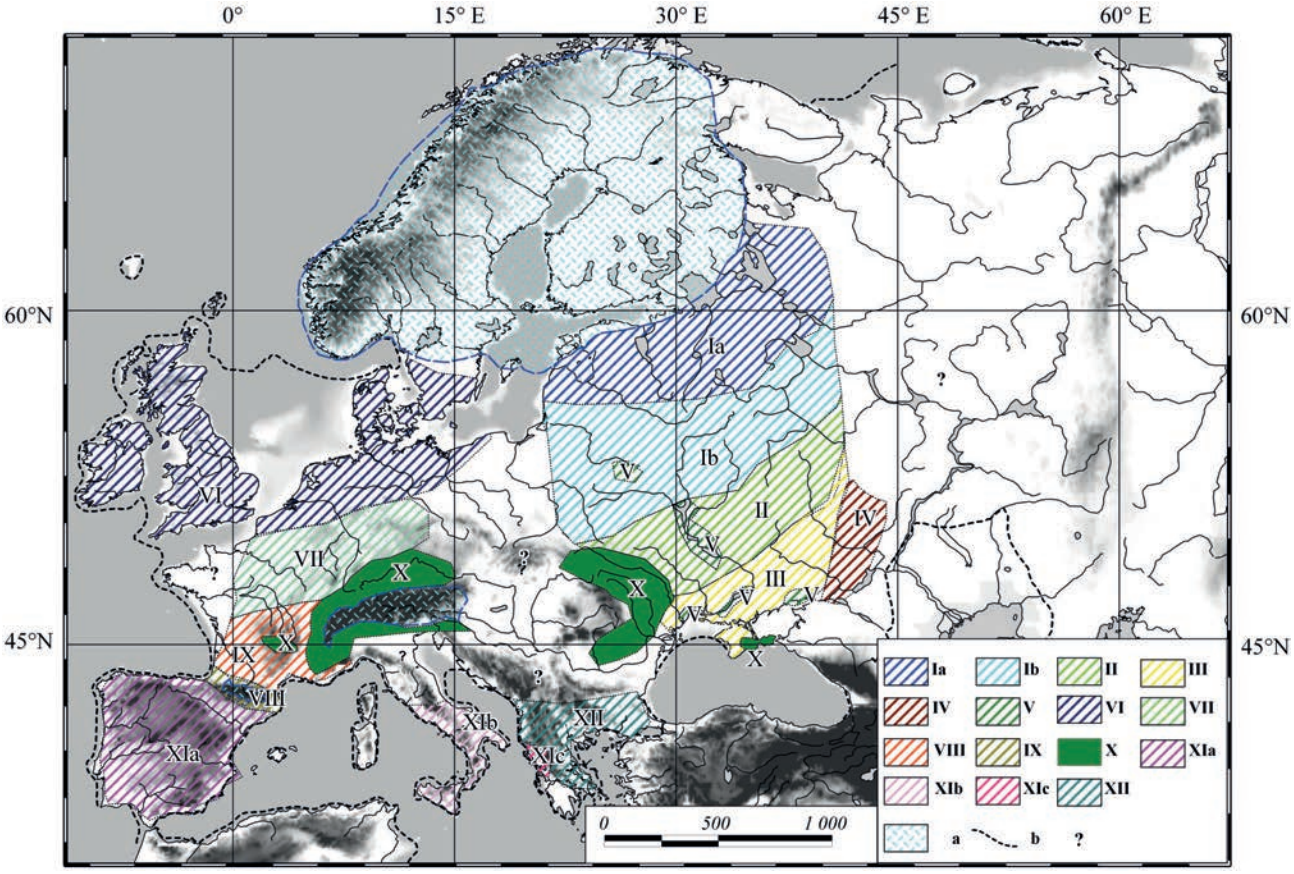

Fig. 5.27. *Palaeovegetation during the LGT. Ia – Shrub tundra and light pine-birch forests with tundra-steppe and pioneer vegetation communities; Ib – Light pine-birch and pine-spruce forest with patches of tundra and meadow coenoses; II – Periglacial forest-steppe; III – Periglacial steppe with patches of tundra associations; IV – Periglacial semidesert; V – Periglacial forest; VI – Periglacial forest-tundra; VII – Periglacial forest-tundra-steppe; VIII – Periglacial light pine forest with participation of meadow and meadow-steppe palaeophytocoenoses; IX – Periglacial mountain forest-steppe; X – Periglacial mountain coniferous forest combined with broad-leaved taxa; XIa – Pine-oak forests with herb-grass steppes and wormwood steppes; XIb – Broad-leaved forests with grass steppes; XIc – Pine-fir –broad-leaved forests and grass-wormwood steppes steppes; XII – Steppes with coniferous-broad-leaved forests. a – ice sheets, b – coastline, ? – absence of data*

XIb. Broad-leaved forests with patches of grass steppes – the Apennines.

XIc. The combination of pine-fir-broad-leaved forests and grass-wormwood steppes and wormwood–Chenopodiaceae family steppes – Western Greece.

XII. Forest-steppe (grass steppes and *Artemisia*-Chenopodiaceae steppes with patches of coniferous-broad-leaved forests – the south of Central Europe.

Thus, principal vegetation provinces have been reconstructed based on LGT materials. Europe was covered with various vegetation, which can be broadly subdivided into three provinces (Eastern European, Western European, and the Mediterranean) based on the palaeophytocoenoses structure. The arctic and northern-taiga species were widespread and reached 47°N. The steppe plants expanded to north-northwestern Europe up to 62°N. In Eastern Europe the participation of steppe communities in palaeolandscapes decreased northward and subarctic plants decreased southward compared to the LGM. On the contrary, in the north of Western Europe the role of tundra-steppe associations increased in the palaeovegetation structure. In Eastern Europe and the Eastern Mediterranean a significant increase in steppe communities in the palaeovegetation cover occurred. According to a continuous pollen record obtained from the southern Tyrrhenian Basin, the wide development of herbaceous and steppe elements in the Mediterranean was confirmed during the LGT (Ermolli and Pasquale, 2002). An increase of forest coenoses in forest-steppe landscapes on the Iberian Peninsula and on the Apennine Peninsula took place.

A continuous forest zone did not exist, but taiga communities started to play a rather significant role in forest-tundra landscapes in Northern and Central Europe. Also

taiga species like *Pinus*, *Picea*, and *Abies* penetrated along river valleys into the forest-steppe zone. Broad-leaved species started to expand their ranges and participated in the palaeocoenose structure of the foothills of the Alps, the Vosges, the Massif Central, the Pyrenees, and the Carpathians. They were distributed also along coasts of southern seas, and the river valleys, like the Dnieper, the Desna, and the Don. Therefore it seems that the river valleys and mountain systems are the most favourable areas for plant migration (Udra, 1988).

During LGT the principal boundaries of the vegetation provinces were similar to LGM boundaries. Towards the end of the LGT, the insignificant reorganization of the palaeophytocoenoses began and distinctions among palaeovegetation provinces become more observable, though still smoothed.

5.3. THE VEGETATION OF EUROPE DURING THE BØLLING/ALLERØD INTERSTADIAL COMPLEX (<12.4 – ⩾10.9 KYR BP)

Alexandra Simakova and Andrey Puzachenko

The Bølling–Allerød Interstadial complex (BAIC) (12.4–10.9 kyr BP) is distinguished as a distinct warming immediately preceding the Younger Dryas cold stage. The pollen data are relating to the latest interstadials Bølling (12,400–12,000 yrs BP) and Allerød (11,800–10,900 yrs BP), and intermediate Older Dryas cooling (12,000–11,800 yrs BP). Though a great volume of palynological data on the BAI complex interval has been published, there are only a few publications providing a synthesis of materials on this interstadial (Grichuk, 1965; Zimenkov and Valchik, 1987; Bohncke *et al.*, 1988; Bohncke, 1993; Berglund *et al.*, 1994; Zelikson, 1994; Hoek and Bohncke, 1997; Bos, 1998). Zelikson (1994) and Quaternary Environments Network (QUEEN) participants gave the most comprehensive descriptions of the Allerød palaeovegetation in Eastern Europe. There are also palaeoclimatic characteristics of this period inferred from palaeobotanic data and coleopteran assemlages. In the north of Central Europe deviations of January temperatures from modern values were –7 to –13°C, and farther south –1°C (Velichko *et al*., 1997) and those of July are no more than –1°C (Zelikson, 1994; Velichko *et al.*, 1997). In the middle reaches of the Volga the mean July temperatures were 2–3°C and the January ones 3 to 4°C below modern values (Kremenetskii *et al*., 1998). In northwestern Europe, both pollen data and plant macroremains suggest temperatures at the BAI interval to be 11–14°C in July and –13.9°C in January (Bohncke *et al*., 1988; Hoek and Bohncke, 1997; Bos, 1998; Coope *et al*., 1998; Lotter *et al*., 2002).

Data on the BAIC interval (12.4–10.9 kyr BP) have been obtained from 91 sections (554 samples altogether), primarily of fluvial-lacustrine and lacustrine-paludal sediments. 279 plant taxa have been identified from the sections (including 67 determined to species level and 179 to genus level) (Table 5.5). Data on another 89 sections (326 samples) have been taken from the palynological database developed by A. Kozharinov (1994). Unfortunately, this database contains mostly information on arboreal pollen and total spectra composition of the central Russian Plain, and no data on non-arboreal pollen and spores. Almost all of the sampled horizons are dated by radiocarbon to the BAIC interval, or alternatively could be dated biostratigraphically.

The results of the classification of the palynological data were analyzed using GIS (Figs. 5.28, 5.29). For the palynological data the correlation between the axes (MDS) and geographical position was established on the basis of a matrix of range coefficients of the Kendall correlations (Markova *et al*., 2002a, 2002b, 2003; Simakova and Puzachenko, 2005). Based on the species composition and diversity of plants, as well as the peculiarities of their ranges, we can establish the palaeovegetation coenoses during the latest Interstadial warming of the final stages of the Late Pleniglacial. Mathematical processing of the palynological database on the Bølling-Allerød Interstadial complex resulted in the data being grouped into 11 clusters. Table 5.6 provides information on the distribution of the taxa and life forms by using cluster analysis; their geographical distribution is shown in figure 5.28.

Table 5.5

The BAIC pollen sites

ID	Localities	Latitude	Longitude	Age	References
1	Grabmuhle	48,19	11,09	11 380±295, Jahre v.h.-16515; 11 325±180, Jahre v.h.-16514	Kortfunke, 1992
2	Core 903 (B)	51,20	5,50	11 500±50, GrN-17139	Kasse & Bohnke, 1992
3	Meekelermeer	52,40	6,45	12 100±200, GrN-10028; 12 380±130, GrN-10029	Bohncke *et al.*, 1988
4	Kostverlon	53,10	0,17	calculated	Bohncke, pers.communic.
5	Bosscher (gully)	51,40	6,00	11 300±60,GrN-13380; 12 100±79, GrN-13381; 12 100±70, GrN-133812; 11 860±120	Bohncke, 1993
6	Lago de Ajo	8,60	–6,15	calculated	EPD
7	Lago Grande di Monticchio	40,56	15,60	calculated	EPD
8	Khimaditis	40,37	21,35	calculated	EPD
9	Ioannina	39,45	20,43	calculated	EPD
10	Xinias	39,03	22,16	10 680±90, GrN-6889	EPD
11	Aholami	61,53	25,13	calculated	EPD
12	Antu sinijarv	59,08	29,19	11 150±150, Ja-2117; 11 280±200, Ja-2118; 10 930±200, Ja-2119	EPD
13	Ballinloghig Lake	52,12	–10,18	11 006±455, UB-2684	EPD
14	Ballybetagh	53,10	–6,15	12 200±90, TO-236; 12 350±140, TO-237	EPD
15	Belle Lake	52,11	–7,02	12235, D-110	EPD
16	Blomoy	60,32	4,53	11 070±190, T-625; 12 070±180, T-672	EPD
17	Le Marais St Boetien (Chivres)	49,61	3,81	11 430±60, GrN-6528	EPD
18	Coolteen	52,35	–6,60	11 800±179, I-5036; 11 940±180, I-5037; 12 020±180, I-5038	EPD
19	Voros-mocsar	46,29	19,11	11 470±85, deb-3924; 11 960±100, deb-3930	EPD
20	Hockham Mere	52,30	0,50	11 160±190, Q-2204	EPD
21	Kamenicky	49,44	15,58	11 070±245, Hv-11536	EPD
22	Kansjon	57,38	14,32	11 120±100, Lu-2917	EPD
23	Kupena	41,59	24,20	11 875±310, UA-1554	EPD
24	Laguna de la Roya	42,13	6,46	calculated	EPD
25	Col des Lauzes	45,46	6,32	11 800±340, Ly-1283	EPD
26	Lac Long Inf,rieur	44,03	7,27	11 270±230, Ly-1208; 10 970±210, Ly-1206; 12 040±370, Ly-1205; 12 170±280, Ly-1237	EPD
27	Lago di Martignano	42,07	12,20	11 640±280, BETA-32008	EPD
28	Niechorze	54,00	15,05	11 880±110, Gd-1107; 11 880±130, Gd-1108; 12 150±100, Gd-1109; 12 010±150, Gd-673	EPD

Continued table 5.5

ID	Localities	Latitude	Longitude	Age	References
29	Sanabria Marsh	42,06	6,44	11 690±100, CAMS-15299	EPD
30	Lac Saint Leger	44,25	6,20	calculated	EPD
31	Hozelec SK-5-A	49,03	28,30	11 010±160, VRI-796	EPD
32	Skvarran	57,12	16,09	109 20±100, Lu-2176; 11 310±110, Lu-2727; 11 610±100, Lu-2175	EPD
33	Bledowo lake	52,33	20,40	11 170-160, Helsinki	EPD
34	Spj„llsj”n	56,41	14,36	11 710±140, Lu-2514a; 12 540±140, Lu-2511a; 11 760±220, Lu-2512	EPD
35	Tarnawa Wyzna	49,06	22,50	11 360±170	EPD
36	Tarnowiec	49,42	21,37	11 190±140, Gd-967	EPD
37	Lake Balaton centre	46,49	17,44	10 960±300	EPD
38	Tomtabaken	57,29	14,28	11 150±110, Lu-896; 11 480±115, Lu-895	EPD
39	Preluca Tiganuli	47,49	23,32	11 515±115, Ua-1634; 11 950±125, Ua-1633; 12 230±105, Ua-16331; 12 250±105, Ua-1630	Bjorkman *et al*., 2002
40	Steregoiu	47,49	23,33	10 910±105, Ua-1624; 12 365±115, Ua-1623	Bjorkman *et al*., 2002
41	Coizard-Joches-II	48,47	3,52	11 780±60, GrN-4717	Zeist & Spoel-Walvius, 1980
42	Liastemmen	59,10	5,14	11 880±220, T-7196a; 11 980±160, T-7103b	Paus, 1989
43	Milheeze D	51,31	5,49	11 010±190, Utr.-1980; 10 940±110, Utr.-1976	Bos, 1988
44	Milheeze C	51,31	5,49	10 940±110, Utr.-1620; 11 700±80, Utr.-1977; 11 190±170, Utr.1622; 11 340±90, Utr.-1621	Bos, 1988
45	Zabinko	52,10	16,50	11 190±170, GrN-16190; 12 040±160, GrN-16189; 12 190±270, GrN-16188	Bohncke *et al*., 1995
46	Oppershofen 5	50,25	8,44	11 550±80, Ucr.-4412; 12 050±90, Ucr.-4412; 12 360±70, Utc.-5739	Bos, 1988
47	Notsel	51,32	4,47	10 970±50, GrN-9595; 11 600±60, GrN-10883; 11 960±60	Vandenberghe & Bohncke, 1985
48	Mariahout	51,32	5,33	11 990±70, GrN-13437; 12 400±60, GrN-13438	Bohncke, 1993
49	Gransmoor	54,05	0,18	11 715±45, SRR-3873; 11 530±50, SRR-3874; 11 820±45, SRR-3875; 11 340±45, SRR-3876; 11 790±45, SRR-3877; 12 660±55, SRR-3873; 12 040±45, SRR-3874; 12 205±45, SRR-3875; 12 805±85, SRR-3876; 12 845±45, SRR-3877	Walker *et al*., 1993

Continued table 5.5

ID	Localities	Latitude	Longitude	Age	References
50	Padul 3	37,00	3,67	12 080±180, Gif-6391	Pons & Reille, 1988
51	Schusssenquelle	48,30	8,45	11 150±110, GRO-2090	Lang, 1963
52	Loch a' Phuinnd	57,22	7,16	12 100±160, Q-2744	Fossitt, 1996
53	Gulickshof 1	51,04	5,53	11 250±140, GrA-4124; 11 730±80, GrA-5239; 12 040±80, GrA-5238; 12 300±70, GrA-5042; 12 480±90, UTC-3196; 12 330±60, GrA-5051	Hoek, 1997
54	Achterberg	52,00	5,36	10 960±60, GrN-17326; 10 940±60, GrN-17327; 11 020±60, GrN-17328; 11 200±60, GrN-17329; 11 130±60, GrN-17330; 11 160±60,GrN-17331; 11 540±70, GrN-17332; 11 260±60, GrN-18339; 11 550±80, GrN-18334; 12 050±90, GrN-18335; 12 110±70, GrN-18337; 12 010±90, GrN-18338; 12 190±60, GrN 8844;	Hoek, 1997
55	Moerbeke (Moervaart)	51,10	3,57	12 065±65, GrN-6376; 11 955±105, GrN-6032	Hoek, 1997
56	Snellegem	51,10	3,90	10 940±60, GrN-6063; 11 780±70, GrN-6061	Hoek, 1997
57	Usselo 1	52,11	6,51	12 070±140, K-542; 11 305±120, GrN-925; 11 710±90, GrN-947; 11 700±140, K-549; 11 300±140, K-552	Hoek, 1997
58	Westrhauderfehn	53,80	7,35	10 940±60, Hv-736-ML	Hoek, 1997
59	Poggensee	53,50	10,10	relative	Kiel, 1987
60	Hamelsee (Lake Hamel 9)	52,46	9,19	12 300±50; 11 990±70; 12 080±50; 11 860±60; 11 770±70; 11 860±60; 11 690±50; 11 660±60; 11 880±60; 11 650±70; 12 210±50	Merkt & Muller, 1999
61	ClairveauxPetitlac	47,00	7,00	calculated	Bohncke
62	Steklin lake	52,58	19,00	11 630±110	Noruskiewicz, 1982
63	Meerfelder	50,45	6,40	calculated	Litt & Stebich, 1999
64	L. Namackanbeg	53,17	9,18	calculated	Andrieu *et al*., 1993
65	Lugra	53,01	8,52	calculated	Andrieu *et al.*, 1993
66	Illaucronan	52,57	8,52	calculated	Andrieu *et al.*, 1993
67	Toty Hill	52,32	8,41	calculated	Andrieu *et al*., 1993
68	St. Andries-Beisbroek	51,10	3,60	10 940±60, GrN-6033	Verburggen, 1979
69	Uddelemeer	52,15	5,46	11 720±90, GrN-9551; 11 980±110, GrN-9552	Bohncke *et al*., 1988
70	Rotsee RL305	47,00	8,15	11 370±180, C-915; 11 740±180, C-920	Lotter, 1988

Continued table 5.5

ID	Localities	Latitude	Longitude	Age	References
71	Rotsee RL300	47,00	8,15	11 440±140, C-784; 11 880±140, C-783	Lotter, 1988
72	Beugen meander scar			relative	Bohncke
73	Factory of 1 May	56,35	37,12	12 400±160, LU-374	Semenenko *et al*., 1981
74	Melekhovo	58,00	38,10	11 975±370; 11370±300	Neishtadt *et al*., 1965
75	Latishy	53,10	24,20	11 600±110, MIG-9; 11 720±140, MIG-10	Vozniachuk & Valchik, 1987
76	Goja	53,05	24,25	11 050±100, Vib-41A;	Vozniachuk & Valchik, 1987
77	Berbykas	54,30	25,05	11 300±300, Vs-20; 11 800±300, Vs-19	Khotinskii, 1977
78	Pobochnoe	51,45	52,30	12 000±600, CS-209	Kremenetskii *et al*., 1988
79	Galichskoe 2	59,25	42,20	11 480±45, KIA-7069	Velichko *et al.*, 2001
80	Sydoble	54,00	27,45	11 500±100, TA-1226; 11 160±100, TA-1225	Iakushko *et al*., 1992
81	Chernikhovo	53,25	26,26	calculated	EPD
82	Starniki	50,16	26,01	11 750±300, Ki-1301	EPD
83	Ivano-Frankovskoye	49,55	23,46	11 250±90, Ki-2350	EPD
84	Vizusti	57,88	27,33	relative	Zelikson, 1994
85	Dolgoe	55,14	28,11	11 500 calculated	Zernitskaya *et al.*, 2001
86	Pian di Gembro	46,00	10,00	11 540-60, UtC-9076; 12 320-60, UtC-9075	Pini, 2002
87	Lake Steissling	47,50	8,55	calculated	Eusterhues *et al.*, 2002
88	Lake Perespilno	52,00	23,2	calculated	Goslar *et al.*, 1999
89	Gerzensee	47,00	7,00	11 000	Wick, 2000
90	Leysin	46,55	7,00	11 200	Wick, 2000
91	Juodonys	55,44	25,26	12 170±180, Ki-10952	Stanĉitaité *et al.*, 2004

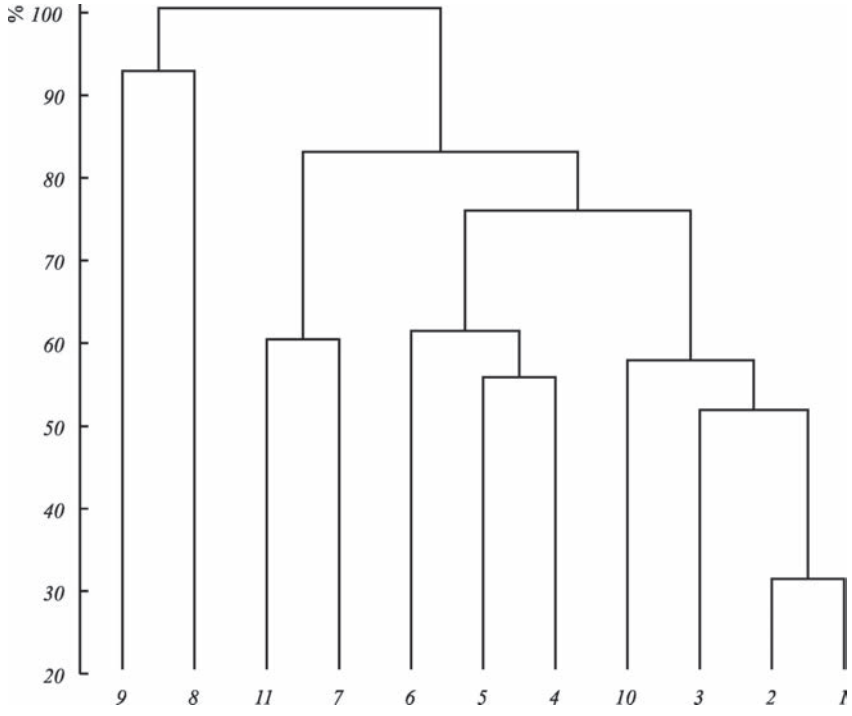

Fig. 5.28. *Dendrogram showing the relationship between the BAIC pollen assemblages*

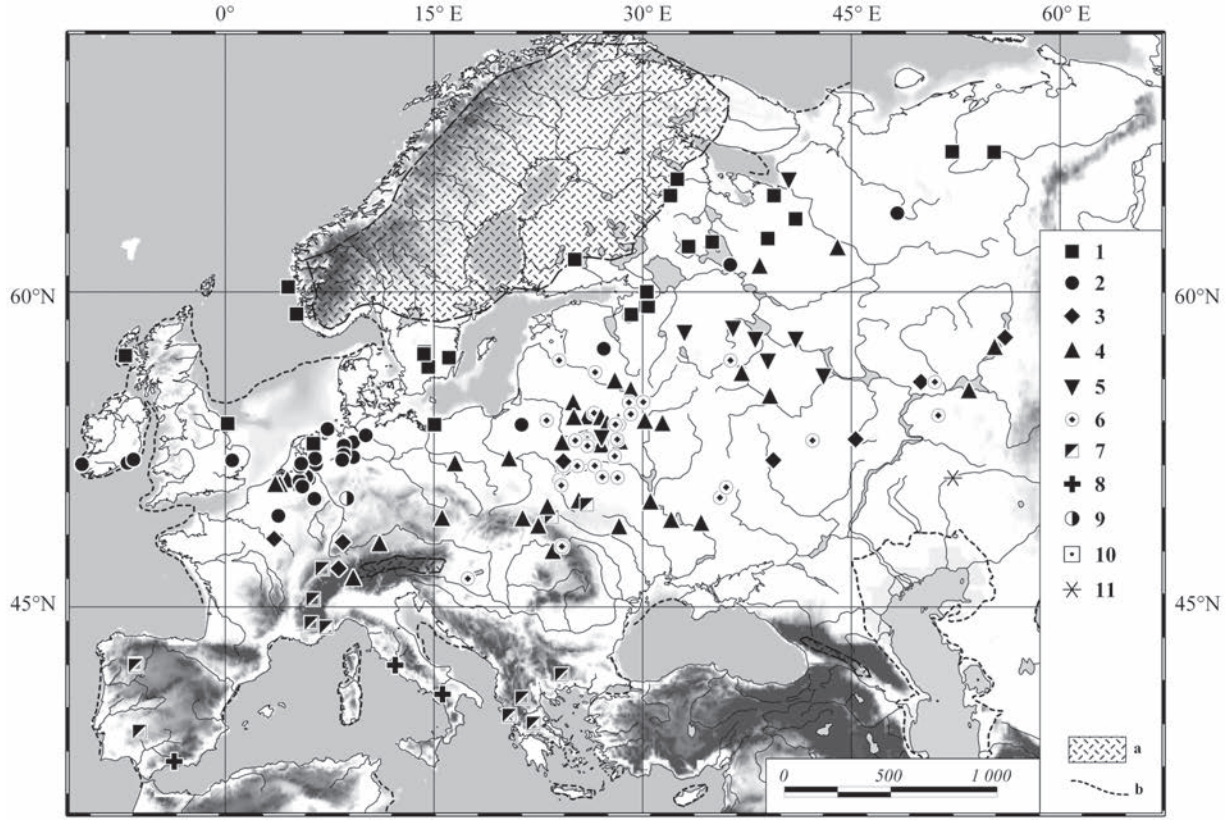

Fig. 5.29. *The geographical distribution of BAIC pollen localities belonging to the different clusters (1–11); a – ice sheets; b – coastline*

The distribution of the coenoses is as follows: cluster 1 – shrub tundra and forest-tundra coenoses; cluster 2 – those of forest-tundra with patches of tundra-steppe; cluster 3 – periglacial birch and pine-birch forests, locally with steppe and tundra plant communities; cluster 4 – periglacial coniferous-broad-leaved forests; cluster 5 – periglacial spruce and spruce-pine forests; cluster 6 – periglacial open pine-birch forests (parklands); cluster 7 – periglacial forest-steppe; cluster 8 – broad-leaved forests; cluster 9 – periglacial forest-tundra-steppe; cluster 10 – periglacial pine-birch forests, with some broad-leaved species; cluster 11 – periglacial grass-herb and Chenopodiaceae steppe.

Table 5.6

Cluster characteristic in standard units (average value of the cluster for BAIC.

Taxa	Clusters										
	1	2	3	4	5	6	7	8	9	10	11
Abies (Fir)	0.001	0.000	0.000	0.006	0.000	0.000	0.048	**0.500**	0.000	0.000	0.000
Cedrus (Cedar)	0.000	0.000	0.000	0.000	0.000	0.000	**0.124**	0.000	0.000	0.000	0.000
Cupressaceae (Juniper family)	0.000	0.000	0.000	0.000	0.000	0.000	**0.134**	0.000	0.000	0.000	0.000
Juniperus (Juniper)	0.062	**0.315**	0.025	0.040	0.000	0.000	0.049	0.046	0.000	0.014	0.000
Larix (Larch)	0.000	0.000	0.000	0.086	0.000	**0.500**	0.005	0.000	0.000	0.000	0.000
Picea (Spruce)	0.039	0.000	0.000	**0.163**	**1.000**	**0.292**	0.003	0.000	0.000	0.016	0.000
Pinus (Pine)	0.168	0.101	0.291	**0.631**	0.162	**0.414**	**0.325**	0.133	0.015	0.210	0.030
Taxodium (Cypress)	0.111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Taxus (Yew)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.000	0.000

Continued table 5.6

Taxa	Clusters										
	1	2	3	4	5	6	7	8	9	10	11
Acer (Maple)	0.000	0.048	0.000	0.000	0.000	0.000	0.060	**0.333**	0.000	0.000	0.000
Alnus (Alder)	0.006	0.004	0.003	0.065	**0.281**	**0.121**	0.009	**0.345**	**0.214**	0.121	0.080
Alnus fruticosa = Alnus alnobetula subsp. *fruticosa* (green alder)	0.000	0.000	0.000	**0.042**	0.000	1.000	0.000	0.000	0.000	0.000	0.000
Betula sect. *Albae* (Arboreal birch)	**0.504**	**0.458**	**0.855**	0.274	**0.801**	0.201	0.128	0.000	0.000	0.792	0.118
Betula nana (Dwarf birch)	0.101	0.046	0.000	0.073	**1.000**	**0.327**	0.014	0.000	0.000	0.000	0.000
Carpinus (Hornbeam)	0.001	0.022	0.000	0.000	0.000	0.000	0.076	**0.561**	**1.000**	**0.197**	0.000
Castanea (Chestnut)	0.000	0.000	0.000	0.000	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Corylus (Filbert)	0.006	0.058	0.000	0.040	0.000	0.000	**0.103**	**0.214**	**1.000**	**0.375**	0.000
Cornus (Dogwood)	0.003	**0.167**	0.000	0.000	0.000	0.000	0.026	0.000	0.000	0.000	0.000
Evonymus (Spindle tree)	0.000	0.000	0.000	0.000	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Fagus (Beech)	0.000	0.000	0.000	0.050	0.000	0.000	0.004	**0.502**	0.000	0.000	0.000
Fraxinus (Ash)	0.012	0.000	0.000	0.050	0.000	0.000	0.024	**0.859**	0.000	0.000	0.000
Hippophaë rhamnoides (Sea buckthorn)	0.148	0.127	**0.479**	0.076	0.000	0.000	0.075	0.000	0.000	0.007	**0.250**
Ilex (Winterberry)	0.000	0.048	0.000	0.000	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Ligustrum (Privet)	**0.111**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Myrica (Waxberry)	0.000	0.000	0.000	0.000	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Olea (Olive)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.500**	0.000	0.000	0.000
Pistacia (Pistachio)	0.000	0.000	0.000	0.000	0.000	0.000	**0.076**	**0.019**	0.000	0.000	0.000
Populus tremula (Aspen)	**0.103**	**0.142**	0.042	0.041	0.000	0.000	0.000	0.000	0.000	**0.242**	0.000
Pterocarya (Wing nut)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000
Quercus (Oak)	0.000	0.004	0.000	0.001	0.021	0.000	**0.193**	**0.604**	0.000	0.021	0.000
Rhamnus (Buckthorn)	0.000	0.000	0.000	0.000	0.000	0.000	0.100	0.000	**1.000**	0.000	0.000
Ribes (Currant)	0.007	0.000	0.000	0.000	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Salix (Willow)	**0.335**	**0.274**	0.071	0.172	0.047	0.118	0.091	0.008	0.016	0.012	0.047
Sorbus (Whitebeam)	0.055	0.000	0.000	0.000	0.000	0.000	0.023	0.000	0.000	**1.000**	0.000
Tilia (Linden)	0.001	0.000	0.000	0.050	**0.500**	0.000	0.095	**0.273**	0.000	0.000	0.000
Ulmus (Elm)	0.005	0.000	0.004	0.028	0.000	0.000	**0.116**	**0.341**	**1.000**	0.000	0.000
Viburnum (Viburnum)	0.000	0.000	0.000	**0.125**	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Alismataceae (Water-plantain family)	0.004	**0.167**	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000
Apiaceae (Carrot family)	0.114	0.143	0.025	0.000	0.000	0.150	0.113	0.000	**1.000**	0.025	0.000
Armeria (Sea grass)	0.087	0.024	0.000	**0.152**	**0.150**	0.050	0.024	0.000	**0.267**	0.025	0.000
Boraginaceae (Forget-me-not family)	0.054	0.000	0.000	0.004	0.000	0.000	0.089	0.000	0.000	0.000	**1.000**
Brassicaceae (Cabbage family)	0.000	0.011	**0.375**	0.005	0.000	0.000	0.096	0.000	**1.000**	0.015	0.000
Campanulaceae (Bellflower family)	0.000	0.000	0.000	0.000	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Cannabis (hemp)	0.032	0.193	0.000	0.072	0.000	0.000	0.014	0.000	0.000	**1.000**	0.000
Caryophyllaceae (Pink family)	0.000	0.000	0.000	0.000	0.000	**0.500**	0.075	0.000	0.000	0.000	0.000
Chenopodiaceae (Goosefoot family)	**0.104**	**0.128**	0.002	0.004	0.000	0.000	**0.100**	0.005	0.010	0.025	0.057
Compositae (Compositae family)	0.042	0.007	0.014	0.082	**0.460**	**0.120**	**0.148**	0.035	0.000	0.001	**1.000**

Continued table 5.6

Taxa	Clusters										
	1	2	3	4	5	6	7	8	9	10	11
Asteraceae (Daisy family)	0.025	0.000	0.000	0.070	0.000	0.000	0.071	0.000	0.000	0.000	0.000
Asteraceae (Asteraceae family)	0.127	0.073	0.090	0.050	0.000	0.000	**0.289**	0.040	**1.000**	0.034	**0.240**
Artemisia (Wormwood)	0.078	0.159	**0.354**	0.093	0.000	0.000	**0.287**	0.000	0.000	**0.368**	0.000
Centaurea (Knapweed)	**0.344**	0.156	0.106	0.194	**0.648**	0.183	**0.353**	0.035	0.012	0.177	0.000
Cyperaceae (Sedge family)	0.014	0.060	0.000	0.039	0.000	0.000	0.070	**0.333**	0.000	**0.511**	0.000
Dipsacaceae (Teasel family)	0.000	**0.067**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scabiosa (Scabiouse**)**	0.038	0.021	0.002	0.011	0.000	0.000	0.191	0.000	**1.000**	0.046	0.054
Ephedra (Ephedra)	**0.072**	**0.108**	0.000	0.000	0.000	0.000	**0.114**	0.000	**0.333**	0.000	0.000
Ericaceae (Heather family)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000
Calluna (Heather)	**0.146**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Empetrum (Crowberry**)**	**0.149**	**0.137**	0.000	0.047	0.000	**0.524**	0.006	0.028	0.000	0.000	0.000
Vaccinium (Bilberry)	**0.207**	0.077	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000
Fabaceae (Pea family)	0.004	0.039	0.000	0.000	0.000	0.000	0.078	0.000	0.000	**0.127**	0.000
Astragalus (Milk-vetch)	0.048	0.045	**0.375**	0.000	0.000	0.000	0.152	0.167	**1.000**	0.000	0.000
Trifolium (Clover)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000
Geranium (Crane's bill)	0.000	**0.230**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.151**	0.000
Hedera (Fir Clubmoss)	0.041	**0.109**	0.000	0.043	0.000	0.000	0.000	0.000	0.014	0.035	0.000
Helianthemum (Rock-rose)	**0.084**	0.000	0.000	0.000	0.000	0.000	**0.071**	**0.059**	0.000	0.000	0.000
Lamiaceae (Dead-nettle family)	0.073	0.000	0.000	0.000	0.000	0.000	**0.154**	0.000	**1.000**	0.000	0.000
Liliaceae (Lily Family)	0.000	0.000	0.000	0.000	0.000	0.000	0.109	0.000	0.000	0.000	0.000
Linum (Flax)	**0.089**	**0.060**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000
Nymphaea (White Waterlily)	0.000	0.020	0.000	0.002	0.000	0.000	**0.071**	0.000	0.000	0.000	0.000
Onagraceae (Willowherb family)	0.019	0.063	0.333	0.059	0.000	0.000	**0.083**	0.000	0.000	0.000	0.000
Epilobium *(Willowherb)*	**0.111**	0.000	0.000	**0.080**	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Papaveraceae (Poppy family)	0.050	0.028	0.000	0.065	0.000	0.000	0.199	0.000	0.000	0.016	**0.500**
Plantago (Plantain**)**	0.000	0.000	0.000	0.000	0.000	0.000	0.071	0.000	**1.000**	0.000	0.000
Poaceae (Grass family)	0.019	0.054	0.042	0.055	0.000	**0.250**	**0.357**	0.000	0.000	0.000	**1.000**
Poaceae (Gramineae plants)	0.176	**0.266**	**0.337**	0.124	0.049	0.052	**0.288**	**0.280**	**0.262**	0.160	0.084
Polemoniaceae (Jacob's-ladder family)	0.050	0.098	**0.188**	0.067	0.000	0.000	**0.222**	**0.485**	0.000	0.074	0.000
Polygonaceae (Knotweed family)	0.005	**0.217**	0.000	0.061	0.000	0.000	0.014	0.000	0.000	0.000	0.000
Oxyria (Oxalis)	0.042	0.010	**0.333**	0.076	0.000	0.000	0.073	0.167	**0.667**	0.004	0.000
Rumex acetosa (Dock)	0.083	**0.262**	0.089	0.048	0.000	0.054	0.050	0.000	0.000	0.054	0.000
Primulaceae (Primrose family)	0.033	0.000	0.000	0.052	0.000	0.000	0.085	0.000	0.000	**0.255**	0.000
Lysimachia (Creeping jenny**)**	0.010	0.079	0.000	0.009	0.000	0.000	0.081	0.000	0.000	**0.533**	0.000
Ranunculaceae (Buttercup family)	0.000	0.000	0.000	**0.125**	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Caltha (Marsh-marigold)	0.045	0.103	0.025	0.102	0.000	0.000	0.061	**0.171**	**0.334**	0.054	0.100
Thalictrum (Meadow-rue)	0.018	0.159	0.000	0.184	0.000	0.000	0.000	0.000	0.000	**0.351**	0.000
Rosaceae (Rose family)	0.159	**0.329**	0.103	0.080	0.000	0.177	0.108	0.059	0.000	**0.222**	0.000

Continued table 5.6

Taxa	Clusters										
	1	2	3	4	5	6	7	8	9	10	11
Dryas octopetala (Mountain Avens)	**0.170**	0.078	0.025	0.006	0.000	0.000	0.019	0.000	0.050	0.034	0.000
Filipendula (Meadowsweet)	0.175	**0.236**	0.103	0.086	0.000	0.000	0.102	**0.335**	0.000	**0.588**	0.177
Potentilla (Cinquefoil)	**0.256**	0.121	**0.368**	0.063	0.000	0.000	0.000	0.000	**0.834**	0.083	0.000
Rubus (Bramble)	**0.353**	0.052	0.000	0.045	0.000	0.000	0.057	0.000	**1.000**	0.000	0.000
Rubiaceae (Bedstraw family)	0.030	0.000	0.000	0.050	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000
Galium (Bedstraw)	**0.113**	0.000	0,000	0.000	0,000	0.000	0.000	0.000	0,000	0.002	0,000
Saxifragaceae (Saxifrage family)	0.008	**0.083**	0.000	0.000	0.000	0.000	0.082	0.000	0.000	**0.202**	0.000
Typha (Reedmace)	0.009	0.027	0.000	0.003	0.000	0.000	0.079	**0.333**	0.000	0.001	0.200
Urtica (Nettle)	0.000	0.048	0.000	0.006	0.000	0.000	0.029	0.000	0.000	**0.500**	0.000
Urticularia (Bladderwort)	0.068	0.151	0.444	0.081	0.000	0.000	0.149	0.112	0.000	**0.516**	0.000
Valerianaceae (Valerian family)	0.033	0.056	0.035	0.050	0.000	0.000	0.025	0.000	0.000	**0.119**	0.000
Botrychium (grape-fern)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000	0.000
Bryales (Mosses)	0.002	**0.142**	0.069	0.011	0.000	0.000	0.081	0.000	**0.556**	0.002	0.000
Diphasiastrum (Alpine Clubmosses)	0.000	0.000	0.000	**0.154**	**0.988**	0.000	0.011	0.000	0.000	0.000	0.000
Equisetum (Horsetail)	**0.333**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.333**	0.000	0.000
Huperzia selago (Fir Clubmoss)	**0.141**	**0.203**	0.003	0.053	**0.137**	0.000	0.031	0.000	0.000	**0.277**	0.000
Lycopodium (Clubmoss)	**0.250**	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ophioglossum (Adder's-tongue ferns)	**0.160**	0.000	0.000	0.085	0.000	0.000	0.000	0.000	**1.000**	0.000	0.000
Polypodiaceae (Polypody family)	0.000	**0.091**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Selaginella selaguinoides (mountain moss)	0.089	0.039	0.011	**0.140**	0.031	0.016	0.051	0.010	0.000	0.000	0.016
Sphagnum (sphagnum moss)	0.007	0.037	0.000	**0.163**	0.000	0.083	**0.115**	0.000	0.000	0.000	0.000

Sections with palynospectra belonging to cluster 1 are confined to the northernmost regions of Europe (north of 59°N in Eastern Europe and north of 53°N in Western Europe). Sections with cluster 2 spectra are located south of this zone. Clusters 7 and 8 spectra correspond to southern areas of Europe (south of 50°N). Clusters 6, 4 and 3 are found in central regions, between 47° and 55°N. Clusters 9 and 10 are limited to northern regions of Western Europe, cluster 5 to the east of the Russian Plain, and cluster 11 occurs in the southeast of the Russian Plain (east of the lower Volga). The geographical distribution of the identified clusters reveals certain features of periglacial zonality in the palaeovegetation of the BAIC period; the zonal pattern, however, was essentially different from interglacial zonality.

The total composition of pollen spectra and analysis of indicator taxa distribution provided evidence of tundra and forest-tundra communities being still quite common in the BAIC, especially north of 51°N in Western Europe and north of 58°N in Eastern Europe; their limit shifted northward by approximately 2° since the second half of the last glaciation. The maximum amount of pollen and spores of *Sphagnum*, *Betula* sect. *Nanae*, *Salix*, *Populus*, Ericaceae, *Empetrum*, *Hippophae rhamnoides*, *Juniperus*, *Selaginella selaginoides*, *Alnus fruticosa*, *Huperzia selago*, *Diphasium*, and *Armeria* is concentrated at these latitudes (Figs. 5.30–5.32, Fig. 5.34).

Southwards the proportion of tundra and forest-tundra communities is noticeably reduced; they are actually found only in the Alpine-Carpathian mountain regions.

The maximum amount of *Sorbus*, Cannabaceae, *Filipendula*, *Hedera*, Rubiaceae, Umbelliferae, Rosaceae, Ranuncullaceae, *Thalictrum*, and *Rumex* pollen is also found in sections of northern European (Fig. 5.30, Fig. 5.32).

Typical representatives of steppe phytocoenoses at the time interval under consideration were still widely spread all over Europe (Fig. 5.33). Chenopodiaceae and *Ephedra* formed part of steppe the palaeophytocoenoses

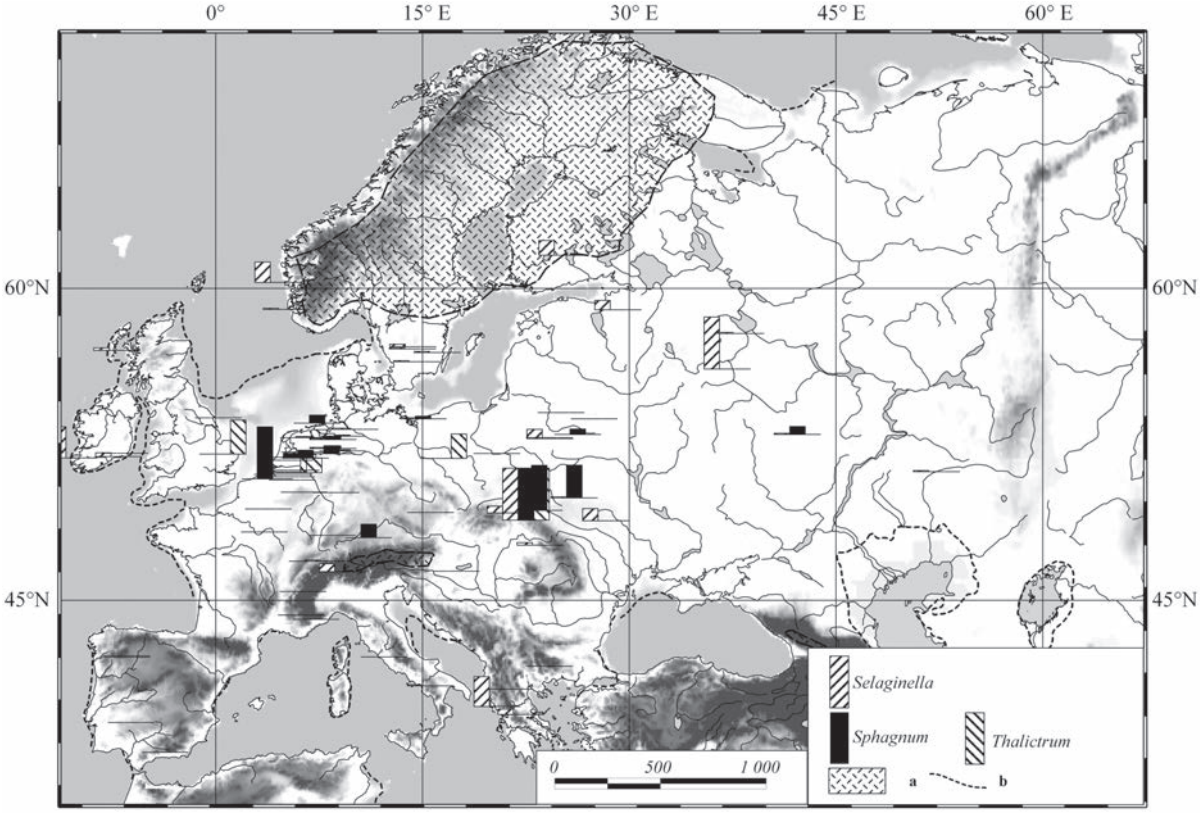

Fig. 5.30. *Selaginella and Sphagnum spores and Thalictrum pollen from BAIC localities; a – ice sheets; b – coastline*

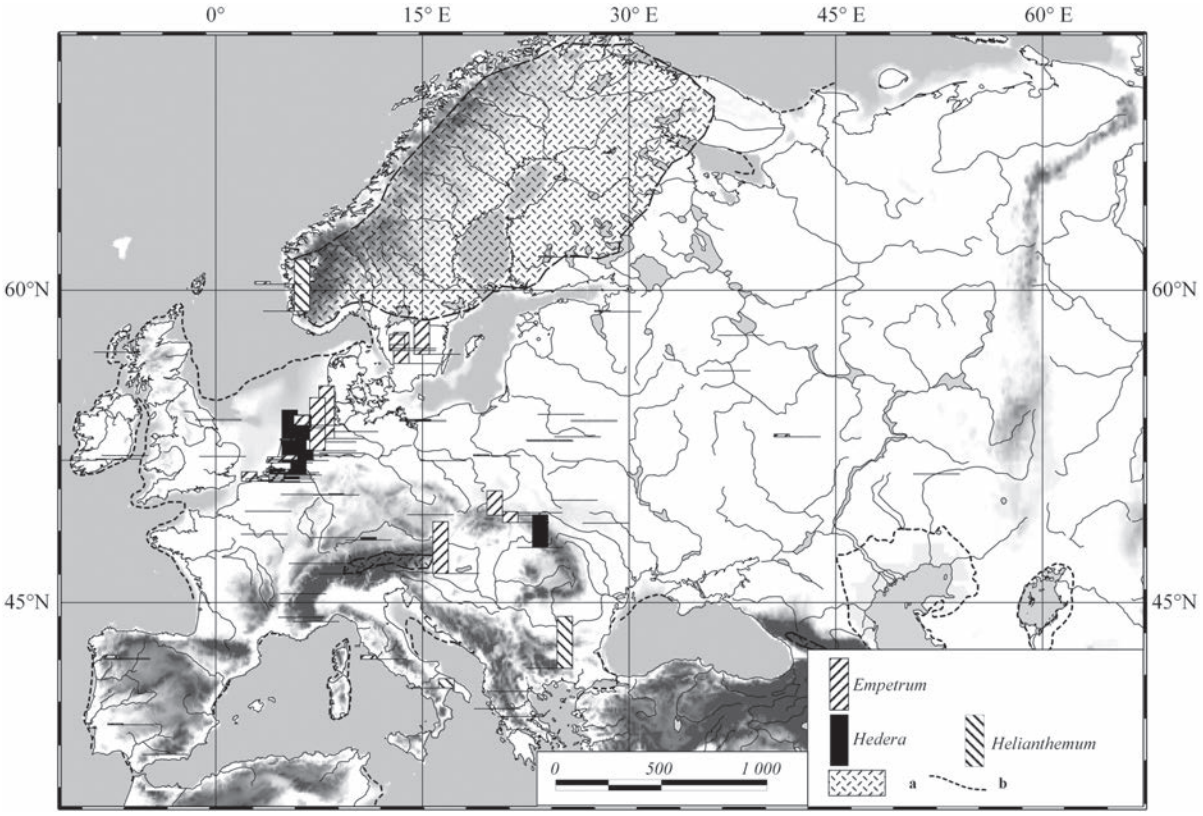

Fig. 5.31. *Empetrum, Hedera, and Helianthemum pollen from BAIC localities; a – ice sheets; b – coastline*

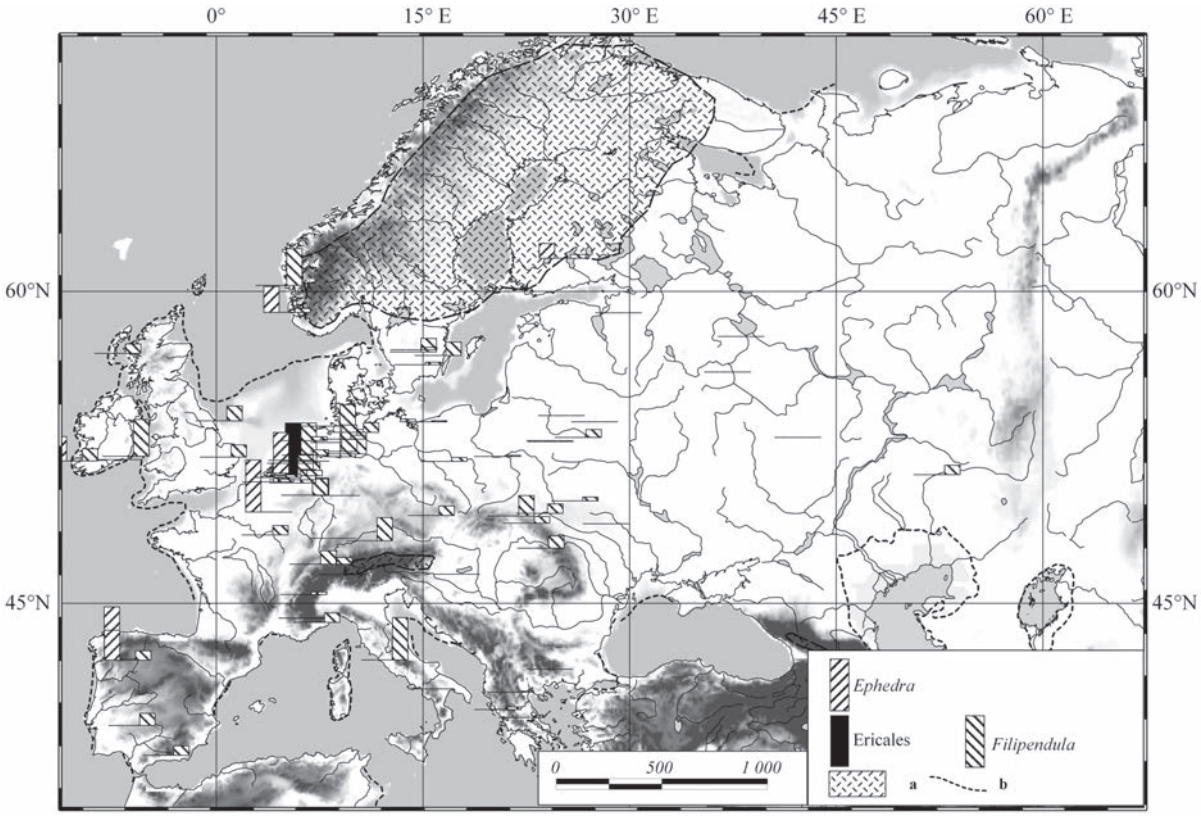

Fig. 5.32. *Ephedra, Ericales and Filipendula pollen from BAIC localities; a – ice sheets; b – coastline*

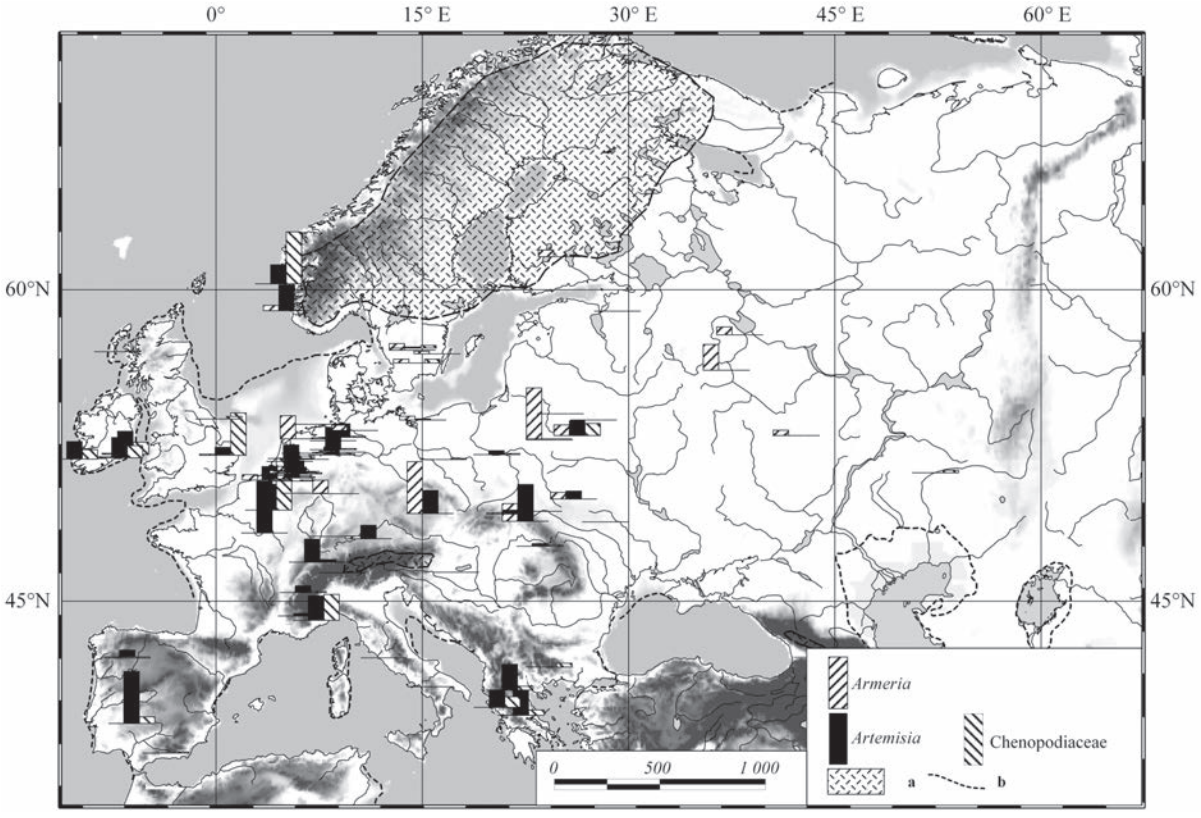

Fig. 5.33. *Armeria, Artemisia, and Chenopodiaceae pollen BAIC localities; a – ice sheets; b – coastline*

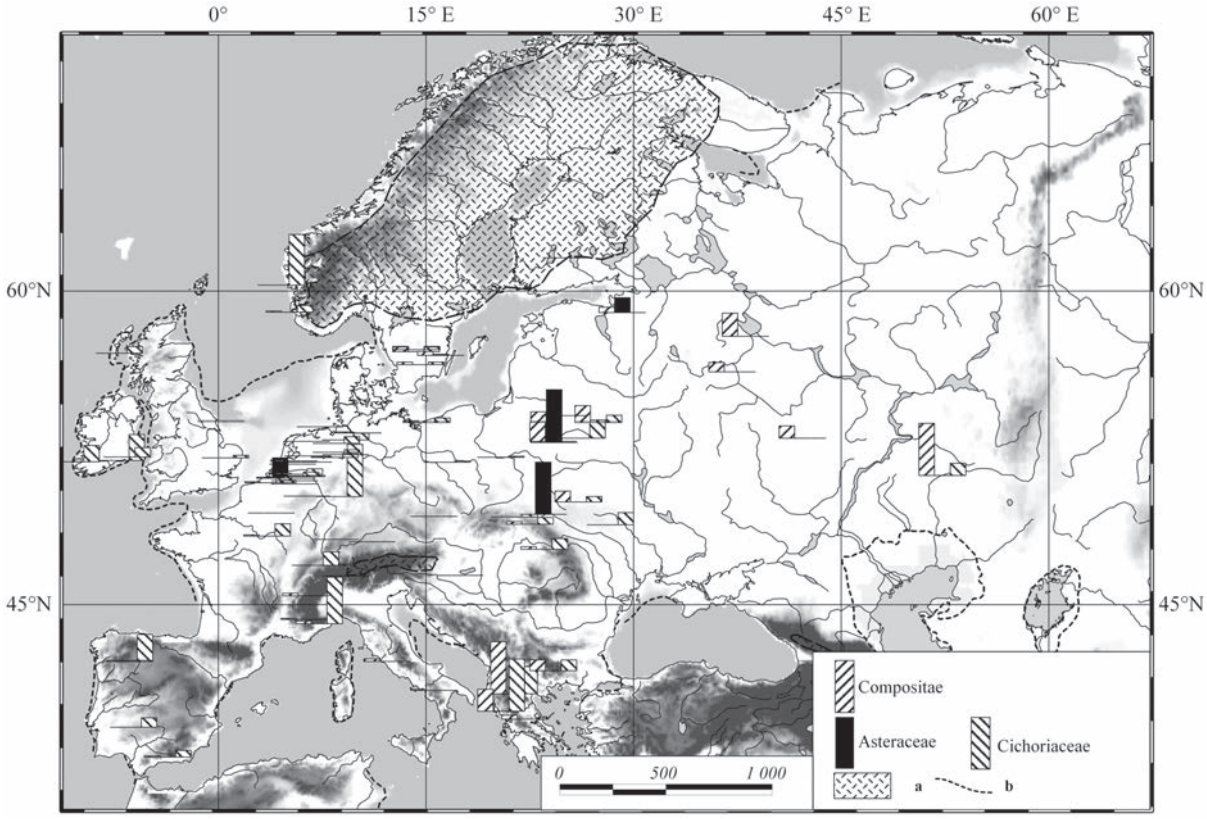

Fig. 5.34. *Compositae, Asteraceae, and Cichoriaceae pollen from BAIC localities; a – ice sheets; b – coastline*

on the Iberian and Balkan peninsulas, in the south of the Russian Plain, and occupied tundra-steppes in the north of Europe. Compared to the preceding time interval (the LGT), the maximum concentrations of Chenopodiaceae and *Ephedra* pollen are found farther north (north of 52°N) during the BAIC.

Pollens of *Helianthemum*, Papaveraceae, *Plantago*, *Sanguisorba*, and Saxifragaceae concentrated in Europe norther of 53°N, as well as in the Mediterranean regions. Sections with considerable amounts of grass pollen are grouped in Central Europe and in the southwestern Mediterranean. Asteraceae pollen is found mostly in Central Europe, while Cichoriaceae is known from Western Europe and the Mediterranean regions (Fig. 5.34).

Therefore, palaeophytocoenoses of open landscapes prevailed in the northern and southern parts of Europe. Steppe communities were dominant south of 50°N.

As follows from the total pollen spectra composition, forest coenoses prevailed in Central Europe and in some mountains (the Apennines, Alps, Carpathians, Crimean mountains, southern part of the Podolian Upland), *Pinus*, *Betula* and *Picea* being the main forest-forming taxa (Figs. 5.34–5.36). The maximum concentrations of *Pinus* pollen were found in spectra from the north of Western Europe, central Eastern Europe, and mountain regions. The amount of pine is noticeably reduced in palaeophytocoenoses from the plains of Europe south of 52°N. The maximum concentrations of birch pollen are found in sections located north of 50°N.

Most of the spruce pollen findings are limited to the eastern regions of the Russian Plain (north of 52°N). As a subdominant species, spruce occurred in forest palaeophytocoenoses in the west of the Russian Plain and in the Alpine-Carpathian mountain regions. Pine-birch forests were widely spread in Europe north of 51°N, and pine-spruce forests north of 53°N, mostly in the east of the Russian Plain.

Broad-leaved species were present in forest communities of the temperate regions of Europe (south of 51°N in Western Europe and south of 57°N in Eastern Europe) and in the Mediterranean regions. Pollen spectra from sections located in the north of Western Europe contain rather low pollen values of *Quercus*, *Ilex*, *Corylus*, *Acer*, *Ulmus*, *Carpinus*, and *Rhamnus*, those from west of the Russian Plain have grains of *Tilia*, *Quercus*, *Corylus*, *Ulmus* and *Carpinus*, and in the central part of the plain of *Tilia*, *Quercus*, *Corylus*, and *Ulmus*. Such genera as *Tilia*, *Fagus*, *Fraxinus*, *Corylus*, *Carpinus* and *Ulmus* grew in the Carpathian Mountains and in the Southern Alps. Pine-birch forests with *Quercus*, *Tilia*, *Corylus*, *Acer*, and *Ulmus* existed in the Dnieper valley. Forests of pine and broad-leaved species (with *Quercus*, *Acer*

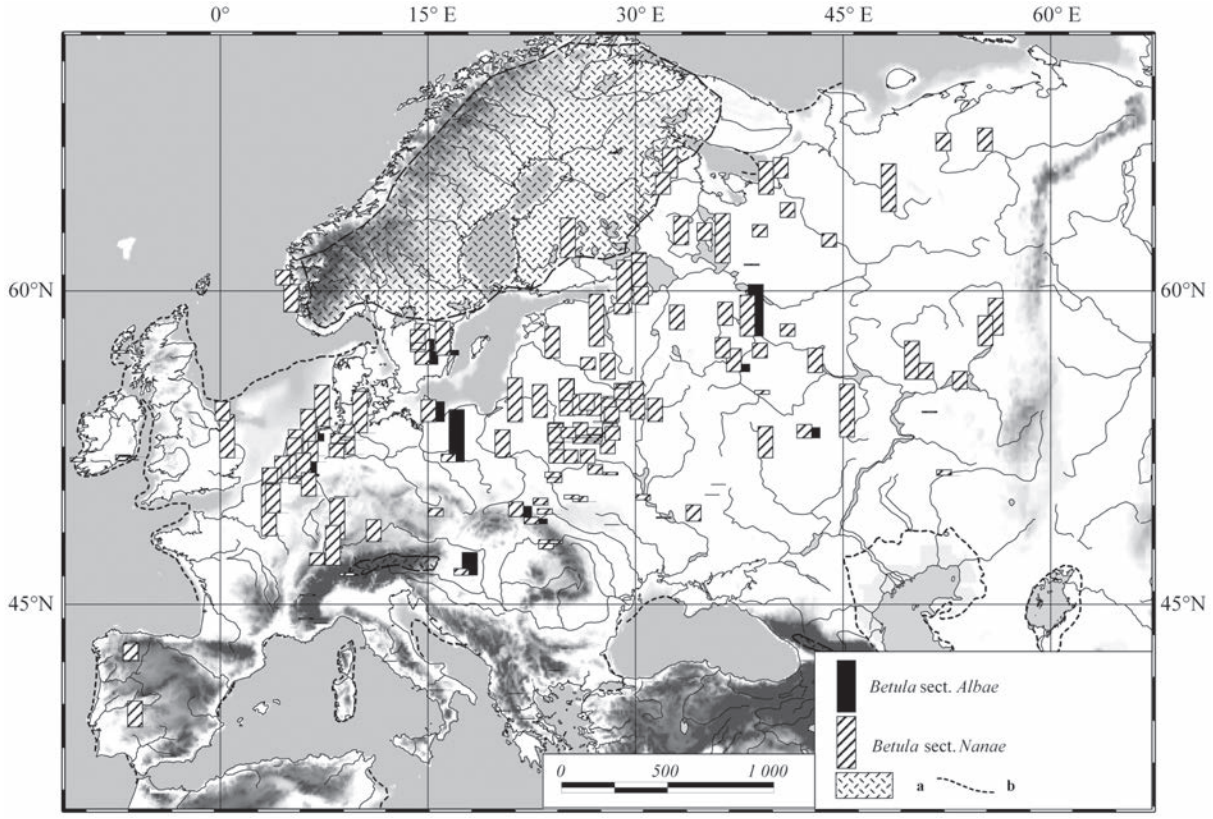

Fig. 5.35. *Betula and Betula nana pollen from BAIC localities; a – ice sheets; b – coastline*

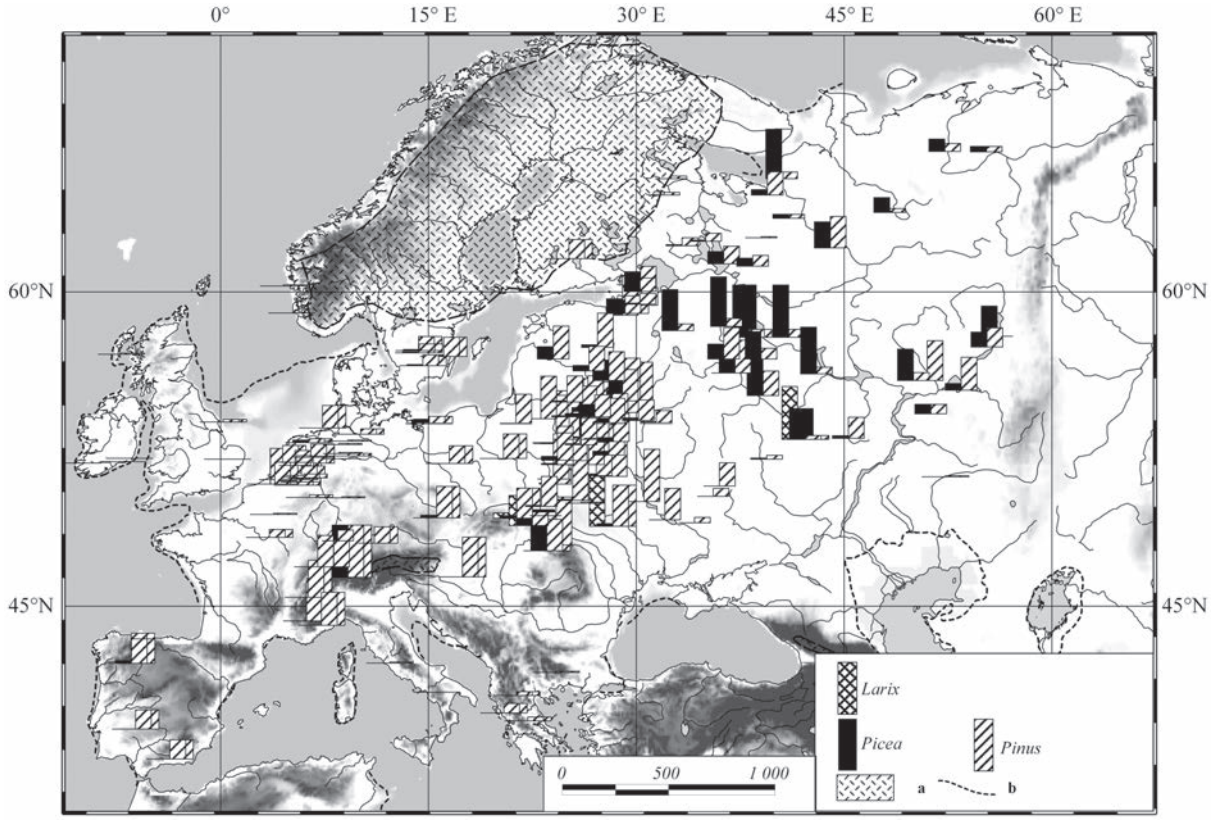

Fig. 5.36. *Larix, Picea, and Pinus from BAIC localities; a – ice sheets; b – coastlin*

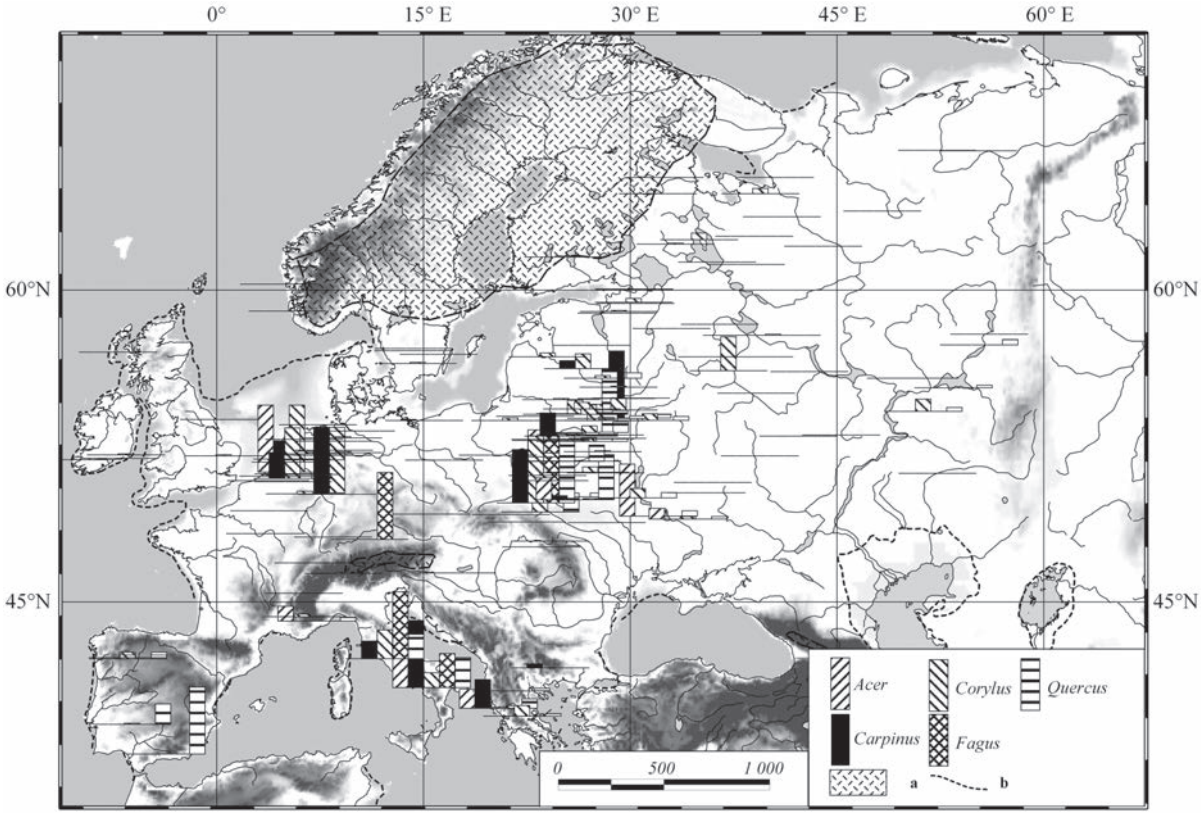

Fig. 5.37. *Acer, Carpinus, Corylus, Fagus, and Quercus pollen from BAIC localities; a – ice sheets; b – coastline*

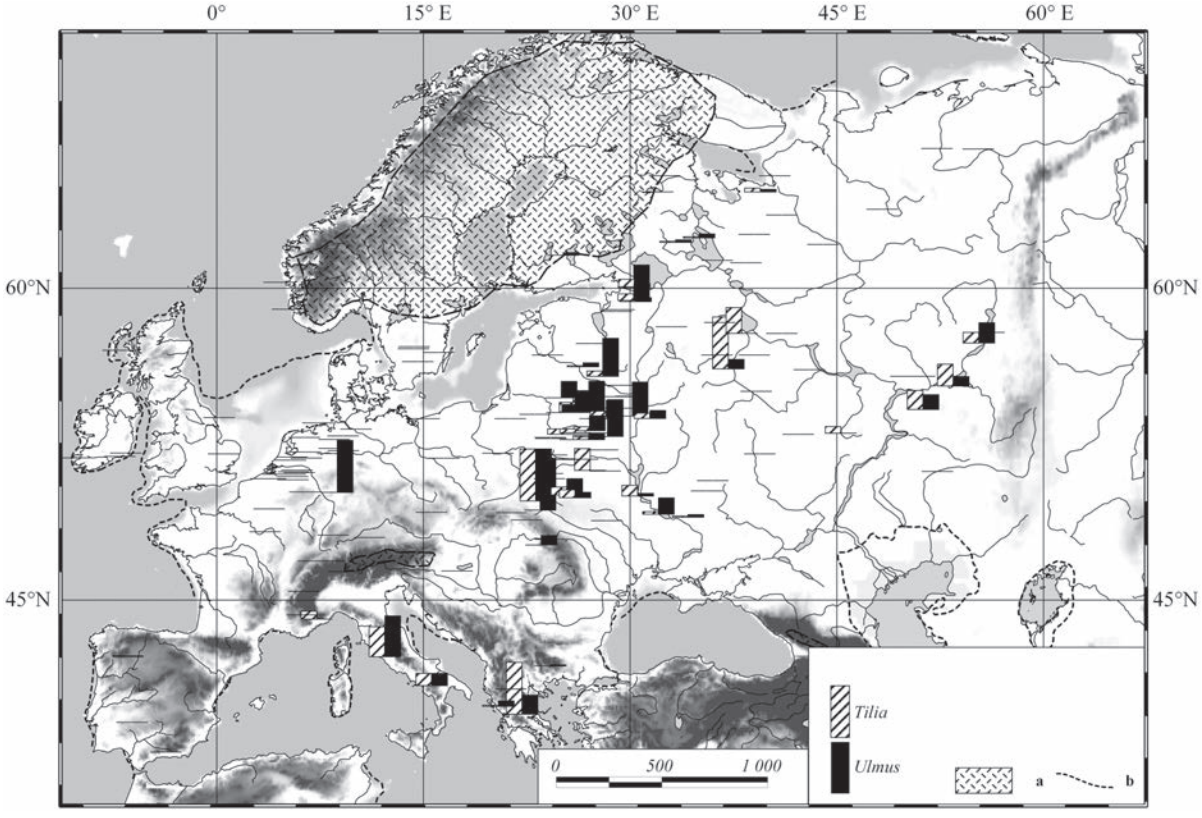

Fig. 5.38. *Tilia and Ulmus from BAIC localities; a – ice sheets; b – coastlin*

and *Ulmus*) grew in the southeast of the Russian Plain (Figs. 5.37, 5.38).

Forest and forest-steppe plant communities of the Mediterranean included *Quercus*, *Rhamnus*, *Castenea*, *Myrica*, *Cedrus*, *Ostrya*, *Taxus*, *Olea*, *Pinus*, *Abies*, *Fagus*, *Fraxinus*, *Ilex*, *Tilia*, *Acer*, *Ulmus*, *Carpinus*, and *Corylus*.

Qualitative and quantitative analyses of pollen and spores permitted to identify 13 provinces (I to XIII) in two main vegetation domains (European and Mediterranean) that existed in Europe during the BAIC interstadial (10.9–12.4 kyr BP) (Fig. 5.39).

European vegetation domain

I. Periglacilal shrub tundra with *Salix*, *Betula nana*, Ericales, *Hippophae*, *Juniperus* and small patches of open pine-birch forests north of 51°N in Western Europe and north of 61–63°N in Eastern Europe.

II. Periglacial forest-tundra-steppe – combination of shrub tundra, pine-birch forests and tundra-steppe plant communities – north of 49–51°N in Western and Central Europe and between 59° and 62°N in Eastern Europe.

III. Periglacial birch forests with tundra-steppe elements (Western Europe) – between 47° and 49°N and west of 15°E.

IV. Periglacial pine-birch forests (northern taiga) between 50°N and 52°N, 15° and 21°E (Central Europe) and in the Middle Danube Lowland.

V. Periglacial forest-steppe of forelands and middle mountains – a combination of light pine forests with broad-leaved species (*Quercus*, *Corylus*, and *Ulmus*) and herb-grass steppes, between 44° and 49°N in Western Europe.

VI. Mountain forests of the Carpathian-Alpine region – pine and spruce forests with some broad-leaved species (the Carpathian Mountains) and pine-birch forests with broad-leaved species (the Alps).

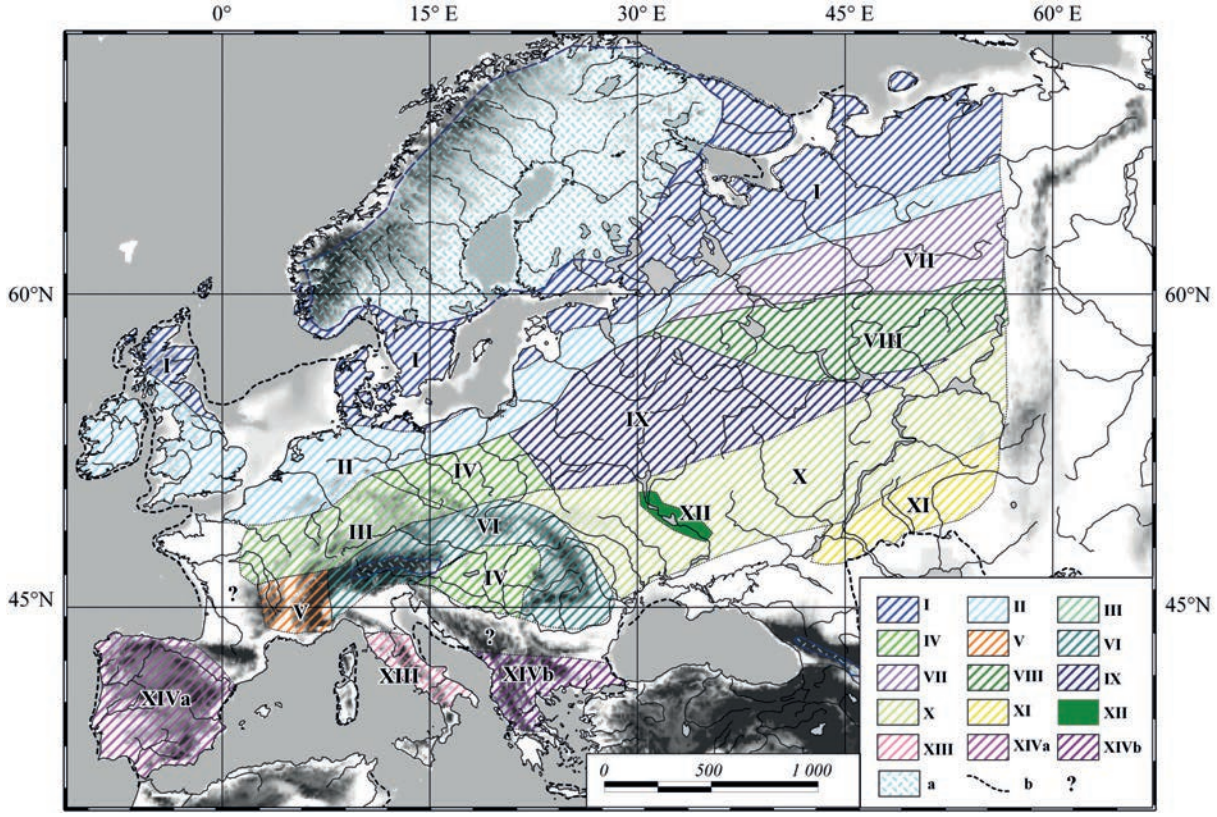

Fig. 5.39. *Palaeovegetation during the BAIC: I – Periglacilal shrub tundra; II – Periglacial forest-tundra-steppe; III – Periglacial birch forests with tundra-steppe elements; IV – Periglacial pine-birch forests; V – Periglacial forest-steppe of forelands and middle mountains; VI – Mountain forests; VII – Periglacial pine-birch forests with some tundra-steppe plant communities; VIII – Periglacial spruce and pine-birch forests with patches of steppe coenoses; IX – Periglacial pine-birch and spruce forests with some nemoral elements, in combination with patches of steppes and shrub tundra; X – Periglacial forest-steppe; XI – Periglacial steppe; XII – Riverine pine and broad-leaved forests; XIII – Pine-broad-leaved forests and hard-leaved shrubs; XIVa – Broad-leaved forests, hard-leaved and herb associations; XIVb – Xerophytic forests with grass plant communities. a – ice sheets, b – coastline, ? – absence of data*

VII. Periglacial pine-birch forests (northern taiga) with some tundra-steppe plant communities – between 60° and 62°N on the Russian Plain.

VIII. Periglacial spruce and pine-birch forests with patches of steppe coenoses – between 52° and 60°N and east of 33°E on the Russian Plain.

IX. Periglacial pine-birch and spruce forests with some nemoral elements, in combination with patches of steppes with *Stipa* and *Festuca* and shrub tundra between 50° and 53°N in the western and central regions of the Russian Plain.

X. Periglacial forest-steppe – pine-birch forests in combination with meadow steppe and tundra communities – south of 50°N on the Russian Plain.

XI. Periglacial steppe (east of the Volga River).

XII. Riverine pine and broad-leaved forests with *Quercus, Tilia, Corylus,* and *Acer* (in large river valleys in the central and southern parts of the Russian Plain).

Mediterranean vegetation domain

XIII. Mediterranean pine-broadleaved forests and hard-leaved shrubs with *Taxus, Olea, Ostrya, Tilia, Quercus, Fagus, Fraxinus, Acer, Ulmus,* and *Abies* (the Apennine Peninsula).

XIV. Mediterranean forest-steppe.

XIVa. Combination of broad-leaved forests, hard-leaved shrubs with *Quercus, Fraxinus, Myrica* and sagebrush-herb associations (the Iberian Peninisula).

XIVb. Combination of xerophytic forests with *Abies, Tilia, Carpinus, Pistacia, Myrica, Castanea, Ilex, Fraxinus, Acer, Ulmus,* and *Quercus* and sagebrush-grass plant communities (the Balkan Peninsula).

Conclusion

Performed analysis of extensive palynological material provided evidence of a considerable warming during the BAIC interstadial. In Europe forest provinces expanded their ranges noticeably. In the central regions of the Russian Plain spruce forest were important in the palaeovegetation. Tundra and steppe communities still existed in the periglacial flora. An analysis of indicator taxa distribution suggests that the steppe communities were somewhat reduced in Western Europe, in the Mediterranean regions and in the centre of Eastern Europe. Hypoarctic elements (*Selaginella, Betula nana, Alnaster, Huperzia,* and *Armeria*) were also reduced in their ranges in comparison with the Late Glacial Transition period and occurred in the north of Europe and in the mountains. The highly frequent occurrence of *Hippophae*, Chenopodiaceae, and *Ophyoglossum* in northern regions suggests landscapes with disturbed vegetation cover and some pioneer communities. Broad-leaved species participated in periglacial forests in the south of Western Europe, in Central Europe (forelands and middle mountains) and in the centre of the Russian Plain. In the Mediterranean regions broad-leaved species occurred in the xerophyte forests of the Apennine Peninsula and were present in forest-steppe communities on the Iberian and Balkan peninsulas. Within the limits of the periglacial forest belt, the succession of main coenoses from west to east was as follows: periglacial birch forests – periglacial pine-birch forests – periglacial pine-birch and spruce forests with nemoral elements – periglacial spruce and birch-pine forests. The spatial distribution of palaeophytocoenoses suggests a periglacial zonality of interstadial type in the vegetation. The reconstructed palaeo-vegetation provides support for a noticeably warmer and wetter climate at the Bølling-Allerød interstadial.

5.4. THE VEGETATION OF EUROPE DURING THE YOUNGER DRYAS STADIAL (YD) (⩽10.9 – ⩾10.2 KYR BP)

Sjoerd Bohncke

Altogether 94 sites have been analysed for the Younger Dryas time interval (Table 5.7). Of these sites 60 are absolute dated and 34 sites are dated on biostratigraphical grounds (94 sites in total).

Table 5.7

The Younger Dryas pollen sites

ID	Localities	Latitude	Longitude	Age	References
1	Cospuden	51,18	12,47	10 260±110, GrN-17156	Mol, 1995
2	Zoschen	51,20	12,45	10 370±190, Leipzig 626	Litt, 1992
3	Walda Bakels	48,20	11,10	10 440±95	Kortfunke, 1992
4	Grasheim	48,21	11,10	10 625±295, Jahre v.h.-16324; 10 530±310, Jahre v.h.-16323; 10 240±295, Jahre v.h.-16322	Kortfunke, 1992
5	Meekelermeer	52,40	6,45	10 710±230, GrN-10027	Boncke *et al*., 1988
6	Kostverlon	53,10	6,35	related	Bohncke
7	Gennep	51,40	5,58	related	Bohncke
8	Bosscherheid (gully)	51,40	6,00	10 940±60, GrN-13379	Bohncke, 1993
9	Kingbeek dal	50,55	5,45	related	Bohncke
10	Lago de Ajo	8,60	–6,15	calculated	EPD
11	Lago Grande di Monticchio	40,56	15,60	calculated	EPD
12	Khimaditis	40,37	21,35	calculated	EPD
13	Ioannina	39,45	20,43	calculated	EPD
14	Xinias	39,03	22,16	calculated	EPD
15	Ampoix	48,10	2,56	10 550±160, MBN-330	EPD
16	Aholami	61,53	25,13	calculated	EPD
17	Antu sinijarv	59,08	29,19	calculated	EPD
18	Ballinloghig Lake	52,12	–10,30	10 420±215, UB-2693; 10 020±340, UB-2682; 10 450±360, UB-2683	EPD
19	Ballybetagh	53,10	–6,25	10 600±60, TO-235	EPD
20	Belle Lake	52,11	–7,03	10 590±185, D-111	EPD
21	Blomoy	60,32	4,53	calculated	EPD
22	Bruvatnet	70,11	28,25	10 280±260, Hel-497	EPD
23	Selle di Carnino	44,09	7,41	10 690±140, Ly-729	EPD
24	Le Marais St Boetien (Chivres)	49,61	3,81	calculated	EPD
25	Coolteen	52,35	–6,60	10 880±190, I-5035	EPD
26	Edessa	40,49	21,57	10 645±100, GrN-6189	EPD
27	Grasvatn	63,42	8,42	10 360±100, T-3149a	EPD
28	Hirvilampi	60,37	24,15	calculated	EPD
29	Hockham Mere	52,3	0,50	10 820±900, Q-2205	EPD
30	Kamenicky	49,44	15,58	calculated	EPD
31	Kansjon	57,38	14,32	10 530±90, Lu-2918	EPD
32	Kupena1	41,59	24,20	10 700±64, Tln-1000	EPD
33	Laguna de la Roya	42,13	6,46	10 290±60, CAMS 12617	EPD

Continued table 5.7

ID	Localities	Latitude	Longitude	Age	References
34	Col des Lauzes	45,46	6,32	10 870±300, Ly-1282	EPD
35	Lac Long Inferieur	44,03	7,27	calculated	EPD
36	Lago di Martignano	42,07	12,20	10 550±290, BETA-33224; 10 480±290, BETA-33225	EPD
37	Lake Skvzetuszewskie (87)	52,33	17,21	10 500±140, Gd-2762	EPD
38	Lac Saint L,ger	44,25	6,20	calculated	EPD
39	Hozelec SK-5-A	49,03	28,30	calculated	EPD
40	Skvarran	57,12	16,09	10 320±90, Lu-2482	EPD
41	Bledowo lake	52,33	20,40	calculated	EPD
42	Slopiec	50,47	20,47	10 280±210, Gd-704	EPD
43	Spjallsjon	56,41	14,35	10 420±180, Lu-2515	EPD
44	Tarnawa Wyzna	49,06	22,50	10 340±160; 10 790±160	EPD
45	Tomtabaken	57,29	14,28	10 440±110, Lu-897; 10 500±130, Lu-1090; 10 580±130, Lu-1089	EPD
46	Zbudovska Blata	49,55	14,19	10 341±100, Bln-1482	EPD
47	Preluca Tiganuli	47,48	23,31	10 240±90, Ua-1637; 10 260±115, Ua-636	Bjorkman *et al.*, 2002
48	Steregoiu	47,48	23,32	10 325±150, Ua-1625	Bjorkman *et al.*, 2002
49	Coizard-Joches-II	48,47	3,52	10 520±95, GrN-4715; 10 860±90, GrN-4716	Zeist & Spoel-Walvius, 1980
50	Liastemmen	59,10	5,14	10 420±170, T-6167a; 10 760±130, T-6166a	Paus, 1989
51	Milheeze c	51,30	5,49	10 570±120, Utr. -1618	Bos, 1988
52	Zabinko	52,10	16,50	10 380±170, GrN-16191; 10 380±120, GrN-16192	Bohncke *et al*., 1995
53	Oppershofen 3	50,25	8,44	10 510±110, Utc.-5239; 10 400±289, Utc.-6086	Bos, 1988
54	Mardorf-Schweinsberg	50,45	8,57	10 200-60, Utc.-4848; 10 560-80, Utc.-4874	Bos, 1988
55	Sandsjon	56,45	13,25	10 200±90, Lu-2697	Magnus, 1989
56	Maizy-Cuiry	49,23	3,48	10 480±130	Bakels, 1995
57	Gulickshof 1	51,04	5,53	10 800±90, GrA-4309	Hoek, 1997
58	Poggensee	53,50	10,10	Related	Kiel, 1987
59	ClairveauxPetitlac	47,00	7,00	Related	Bohncke
60	Minderhout	51,25	4,46	Related	Bohncke & Vandenberghe, 1991
61	Meerfelder	50,45	6,40	calibrated	Litt & Stebich, 1999
62	L. Namackanbeg	53,17	–9,18	Related	Andrieu *et al*., 1993
63	Lugra	53,01	–8,52	Related	Andrieu *et al*., 1993
64	Illaucronan	52,57	–8,52	Related	Andrieu *et al*., 1993

Continued table 5.7

ID	Localities	Latitude	Longitude	Age	References
65	Toty Hill	52,32	–8,41	Related	Andrieu *et al*., 1993
66	Uddelemeer	52,15	5,46	10 610±60, GrN-9550	Bohncke *et al*., 1988
67	Rotsee RL305	47,00	8,15	10 450±160, C-901; 10 465±160, C-909	Lotter, 1988
68	Rotsee RL300	47,00	8,15	10 730±150, C-968	Lotter, 1988
69	Beugen meander scar			Related	Bohncke
71	Gavrilovo 84	51,25	40,00	10 220±130, LU-1722; 10 420±140, LU-1664	Spiridonova, 1991
72	Chernaya Ligovka	58,15	39,00	10 070±130, TA-187	Serebriannii, 1978
73	Somino (скв.86)	57,40	38,32	10 535±330; 10260-330	Neishtadt *et al.*, 1965
74	Polovetsko-Kupanskoe boloto	56,40	39,00	10 260±300	Khotinskii *et al*., 1994
75	Latyshy	53,10	24,20	10 870±100,Tln-137	Vozniachuk & Valchik, 1987
76	Volosovo	55,30	30,10	10 650±169, Tln-325	Sanko, 1987
77	Krestovaya	70,08	57,00	10 550±160, LU-1466	Serebryanny & Malyasova, 1998.
78	Senokosnaya balka	55,00	37,00	10 380±110, Ki-6155	Simakova
79	Pobochnoe	51,45	52,30	10 288±435, IGRAS-1573	Kremenetskii *et al.*, '98
80	Naroch	54,92	26,83	10 710±50, Tln-653	Iakushko *et al*., 1992
81	Mire Saviku	58,24	27,14	10 200±90, Ta-328	EPD
82	Lake Jarveotsa	59,02	24,17	10 190±110, Tln-1719; 10 205±80, Tln-1721	EPD
83	Nizhnevartovsk	76,40	62,00	10 600±80, SOAN-172	EPD
84	Chernikhovo	53,25	26,26	calculated	EPD
85	Gass 33 Sig	56,00	9,01	10 060±185, K4288	Kolstrup *et al*., 1990
86	Quintanar de la Sierra	42,00	–3,25	10 120±160	Goni, 1994
87	Urtiaga	43,30	–5,00	10 280±190	Goni, 1994
88	Pian di Gembro	46,00	10,00	Related	Pini, 2002
89	Lake Steissling	47,50	8,55	calculated	Eusterhues et al., 2002
90	Lake Perespilno	52,00	23,20	calibrated	Goslar *et al.*, 1999
91	Gerzensee	47,00	7,00	calibrated	Wick, 2000
92	Leysin	46,55	7,00	calibrated	Wick, 2000
93	Lake Gosciaz	53,00	20,00	calculated	Ralska-Jasiewiczowa, 2003
94	Le Locle,	47,03	6,43	10 220±70, A-22260; 10 420±70, A-22259	Magny *et al.*, 2001

The number of sites taken from the database of Kozharinov is 121 localities (Kozgarinov, 1994). The data from this database were analysed separately because the Kozharinov database includes only tree pollen data (no herbs) from the Russian Plain. Nine clusters were allocated (Fig. 5.40).

Additional data on the occurrence of taxa can be found in Tables 5.8 and 5.9.

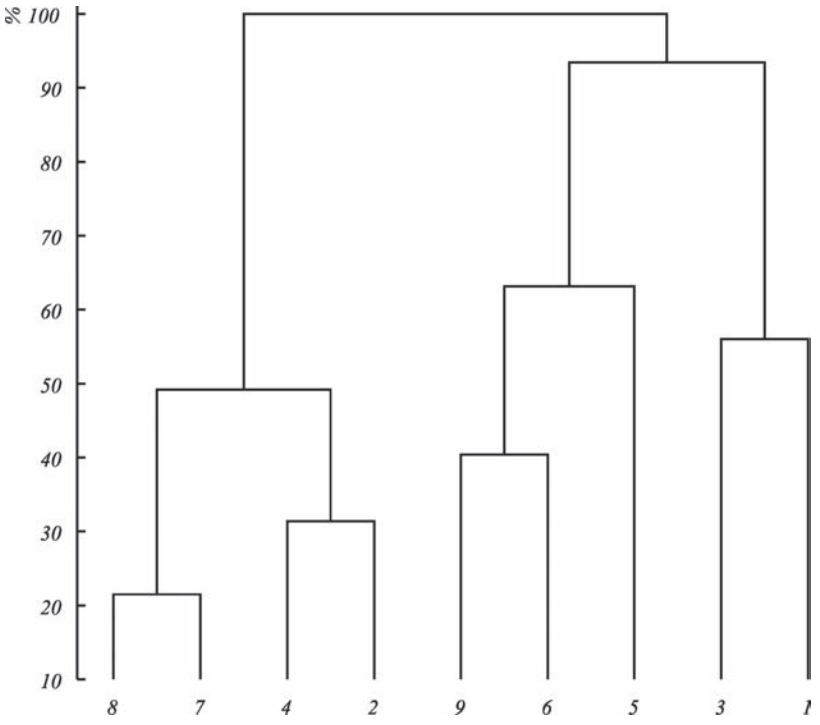

Fig. 5.40. *Dendrogram showing the relationship of the Younger Dryas pollen assemblages*

Table 5.8

Plant taxa occurrence in the different clusters

Taxa	Clusters								
	1	2	3	4	5	6	7	8	9
Abies (Fir)	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.03
Juniperus (Juniper)	0.02	0.23	0.02	0.30	0.05	0.07	0.25	0.59	0.01
Picea (Spruce)	0.13	0.00	0.52	0.01	0.00	0.00	0.00	0.00	0.00
Pinus (Pine)	0.46	0.05	0.32	0.27	0.06	0.35	0.31	0.28	0.07
Alnus (Alder)	0.14	0.05	0.47	0.01	0.39	0.06	0.02	0.00	0.01
Betula sect. *Albae* (Arboreal birch)	0.34	0.10	0.35	0.33	0.01	0.10	0.14	0.23	0.00
Betula sect. *Nanae* (Dwarf birch)	0.16	0.00	0.27	0.20	0.00	0.00	0.00	0.00	0.00
Corylus (Filbert)	0.02	0.00	0.25	0.02	0.44	0.01	0.01	0.00	0.02
Fraxinus (Ash)	0.00	0.00	0.00	0.00	0.54	0.13	0.00	0.00	0.01
Hippophaë rhamnoides (Sea buckthorn)	0.08	0.05	0.00	0.09	0.00	0.08	0.10	0.00	0.00
Populus tremula (Aspen)	0.06	0.00	0.00	0.06	0.00	0.00	0.08	0.13	0.00
Quercus (Oak)	0.00	0.00	0.33	0.01	0.60	0.12	0.01	0.00	0.13
Salix (Willow)	0.18	0.45	0.02	0.17	0.01	0.02	0.23	0.54	0.00
Tilia (Linden)	0.01	0.00	0.73	0.00	0.37	0.06	0.00	0.00	0.01
Ulmus (Elm)	0.03	0.00	0.39	0.06	0.72	0.03	0.00	0.00	0.06
Apiaceae (Carrot family)	0.04	0.05	0.13	0.08	0.05	0.12	0.37	0.75	0.07
Asteraceae (Daisy family)	0.02	0.05	0.18	0.03	0.02	0.14	0.08	0.60	0.36
Cichorium (Chicory)	0.00	0.15	0.25	0.10	0.01	0.05	0.15	0.50	0.34
Artemisia (Wormwood)	0.16	0.37	0.25	0.22	0.05	0.24	0.16	0.13	0.07

Continued table 5.8

Taxa	Clusters								
	1	2	3	4	5	6	7	8	9
Brassicaceae (Cabbage family)	0.00	0.20	0.09	0.04	0.00	0.18	0.16	0.42	0.02
Caryophyllaceae (Pink family)	0.03	0.77	0.25	0.08	0.01	0.06	0.10	0.17	0.03
Chenopodiaceae (Goosefoot family)	0.10	0.16	0.39	0.13	0.07	0.20	0.04	0.02	0.81
Cyperaceae (Sedge family)	0.09	0.13	0.05	0.30	0.03	0.10	0.24	0.54	0.15
Ephedra (Ephedra)	0.00	0.02	0.00	0.02	0.00	0.19	0.04	0.11	0.37
Ericaceae (Heather family)	0.09	0.28	0.00	0.16	0.20	0.05	0.16	0.50	0.00
Empetrum (Crowberry)	0.05	0.15	0.00	0.08	0.00	0.00	0.07	0.50	0.00
Fabaceae (Pea family)	0.01	0.00	0.00	0.01	0.00	0.20	0.01	0.00	0.06
Helianthemum (Rock-rose)	0.01	0.10	0.00	0.12	0.00	0.10	0.17	0.01	0.00
Myriophyllum (Water-milfoil)	0.05	0.03	0.00	0.00	0.01	0.05	0.04	0.50	0.18
Nymphaea (White Water-lily)	0.00	0.00	0.00	0.00	0.33	0.00	0.01	0.00	0.11
Plantago (Plantain)	0.00	0.10	0.00	0.01	0.14	0.31	0.04	0.75	0.01
Poaceae (Grass family)	0.13	0.38	0.12	0.32	0.42	0.19	0.42	0.73	0.48
Polygonaceae (Knotweed family)	0.04	0.00	0.00	0.13	0.00	0.00	0.11	0.50	0.33
Rumex (Dock)	0.02	0.56	0.00	0.06	0.08	0.05	0.14	0.13	0.02
Potamogeton (Pondweed)	0.02	0.00	0.00	0.04	0.00	0.13	0.02	0.53	0.03
Ranunculaceae (Buttercup family)	0.07	0.07	0.03	0.03	0.00	0.16	0.18	0.00	0.02
Thalictrum (Meadow-rue)	0.02	0.42	0.00	0.15	0.00	0.02	0.13	0.09	0.07
Rosaceae (Rose family)	0.06	0.28	0.00	0.02	0.00	0.07	0.04	0.30	0.00
Dryas octopetala (Mountain Avens)	0.0	0.30	0.00	0.12	0.002	0.13	0.00	0.50	0.00
Filipendula (Meadowsweet)	0.05	0.01	0.00	0.13	0.00	0.01	0.10	0.18	0.00
Potentilla (Cinquefoil)	0.03	0.00.	0.07	0.14	0.00	0.00	0.09	0.53	0.12
Rubus (Bramble)	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.50	0.00
Rubiaceae (Bedstraw family)	0.02	0.00	0.00	0.21	0.00	0.03	0.20	0.01	0.00
Galium (Bedstraw)	0.02	0.00	0.00	0.03	0.16	0.11	0.08	0.50	0.52
Sanguisorba (Burnet)	0.00	0.00	0.00	0.08	0.15	0.13	0.00	0.67	0.00
Saxifragaceae (Saxifrage family)	0.03	0.69	0.00	0.09	0.00	0.01	0.03	0.00	0.00
Sparganium (Bur-reed)	0.00	0.00	0.00	0.01	0.01	0.06	0.01	0.88	0.66
Typha (Reedmace)	0.06	0.09	0.00	0.02	0.15	0.05	0.01	0.50	0.09
Valerianaceae (Valerian family)	0.05	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00
Botrychium (grape-fern)	0.09	0.44	0.13	0.06	0.00	0.07	0.07	0.00	0.00
Bryales (mosses)	0.09	0.00	0.44	0.00	0.00	0.13	0.00	0.00	0.00
Dryopteris (Buckler-fern)	0.05	0.21	0.10	0.00	0.00	0.00	0.06	0.00	0.02
Equisetum (horsetail)	0.03	0.01	0.00	0.18	0.05	0.00	0.04	0.45	0.00
Lycopodium (Clubmosses)	0.11	0.00	0.00	0.05	0.00	0.00	0.00	0.75	0.00
Polypodiaceae (Polypody family)	0.12	0.17	0.26	0.03	0.01	0.04	0.06	0.04	0.00
Selaginella (mountain moss)	0.05	0.60	0.00	0.10	0.00	0.00	0.07	0.00	0.00
Sphagnum (sphagnum moss)	0.03	0.00	0.25	0.09	0.00	0.01	0.01	0.10	0.00

Mathematical processing of the palynological database of the Younger Dryas resulted in the data being grouped into 9 clusters. Processing of the palynological data in the database of Kozharinov resulted also in 9 clusters and will be dealt with later.

Compared to the previous Bølling/Allerød interstadial complex some (5) of the The clusters represent different phytocoenoses and based on the ranking, these can be defined as follows: cluster 1 – periglacial birch – pine forests (with small patches of steppe tundra), cluster 2 – open dwarf shrub tundra intermingled with tundra communities, cluster 3 – periglacial open coniferous – broad-leaved forests, cluster 4 – open forest shrub tundra, cluster 5 – open broad-leaved forests intermingled with steppe communities, cluster 6 – periglacial pine – birch forests with some broad-leaved forests, cluster 7 – open pine – birch shrub tundra, cluster 8 – periglacial birch – pine forests intermingled with dwarf shrub tundra, cluster 9 – periglacial grass – herb and Chenopodiaceae steppe. phytocoenoces have disappeared, and 3 new clusters have appeared, namely clusters 4, 7, and 8. The new clusters are characterized by the open structure of the phytocoenose (4 and 7), and cluster 8, the periglacial birch – pine forest, contains open dwarf shrub communities.

The fact that the landscape became more open shows the impact of the Younger Dryas climate on the vegetation and hence on the pollen assemblages during this episode. Moreover the broad-leaved communities are considerably less well represented.

The zonal vegetation that developed during the Bølling/Allerød interstadial complex has disappeared and has been replaced by much more diverse vegetation, consisting of several phytocoenoses.

Instead of a North – Sourth zonation in the vegetation, the Younger Dryas shows a more East – West oriented zonation. Clusters 7 (periglacial forest steppe) and 8 (broad-leaved forest), that dominated the palaeovegetation during the Bølling/Allerød interstadial complex has now been substituted by clusters 5 (open broad-leaved forest), 6 (periglacial pine (-birch) forest intermingled with some broad-leaved forest), and 9 (grass-herb and Chenopodiaceae steppe).

The impact of the YD climate reversal is less severe in the Mediteranean. The periglacial forest steppe (cluster 7) persists on the Iberian Peninsula (cluster 6, periglacial pine (-birch forest) intermingled with some broad-leaved and steppe. Also the broad-leaved forest (cluster 8), that was present in Italy and Greece, persists (cluster 5), but has a much more open character with steppe communities. Whilst in the upland area of Albania and Yugoslavia the forest steppe is replaced by a steppe phytocoenoses (cluster 9).

Cluster 9 is similar to cluster 11 of the Bølling/Allerød interstadial complex, which at that time was located in

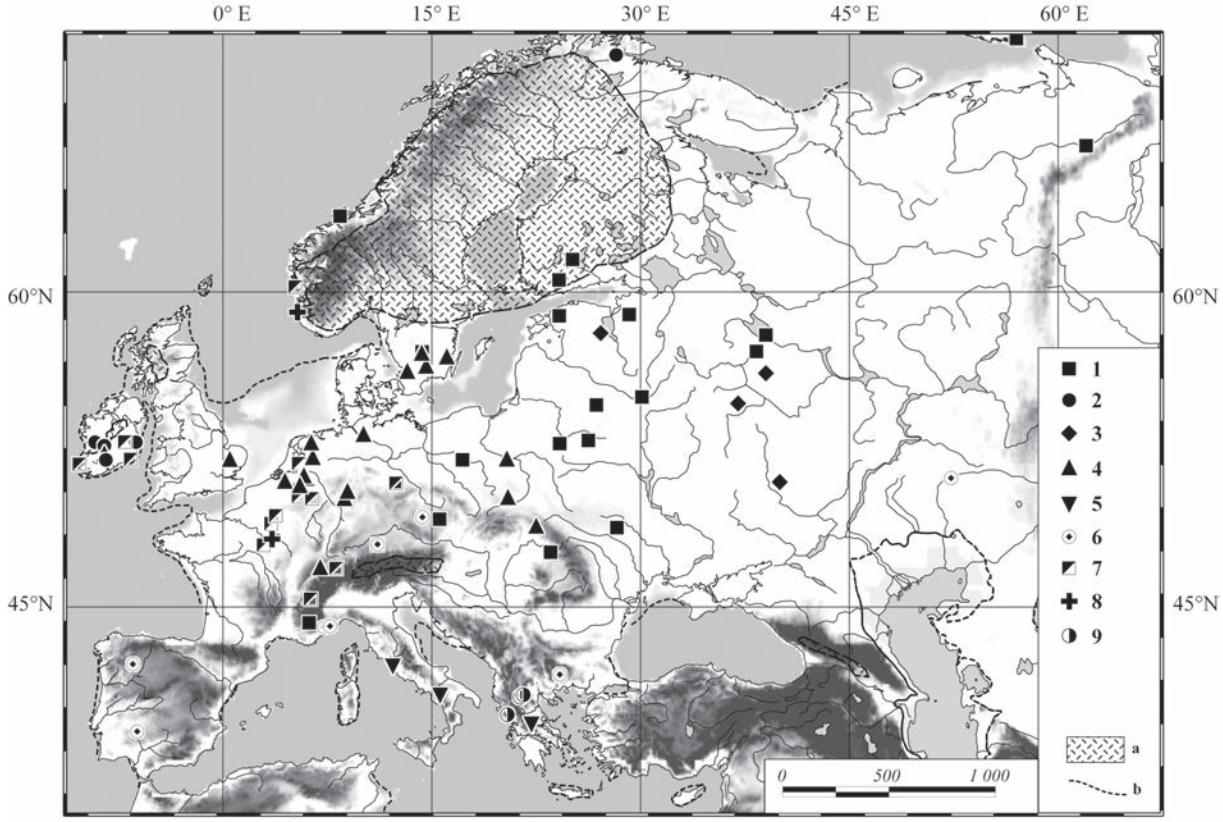

Fig. 5.41. *Geographical distribution of YD pollen localities, belonging to different clusters; a – ice sheets; b – coastline*

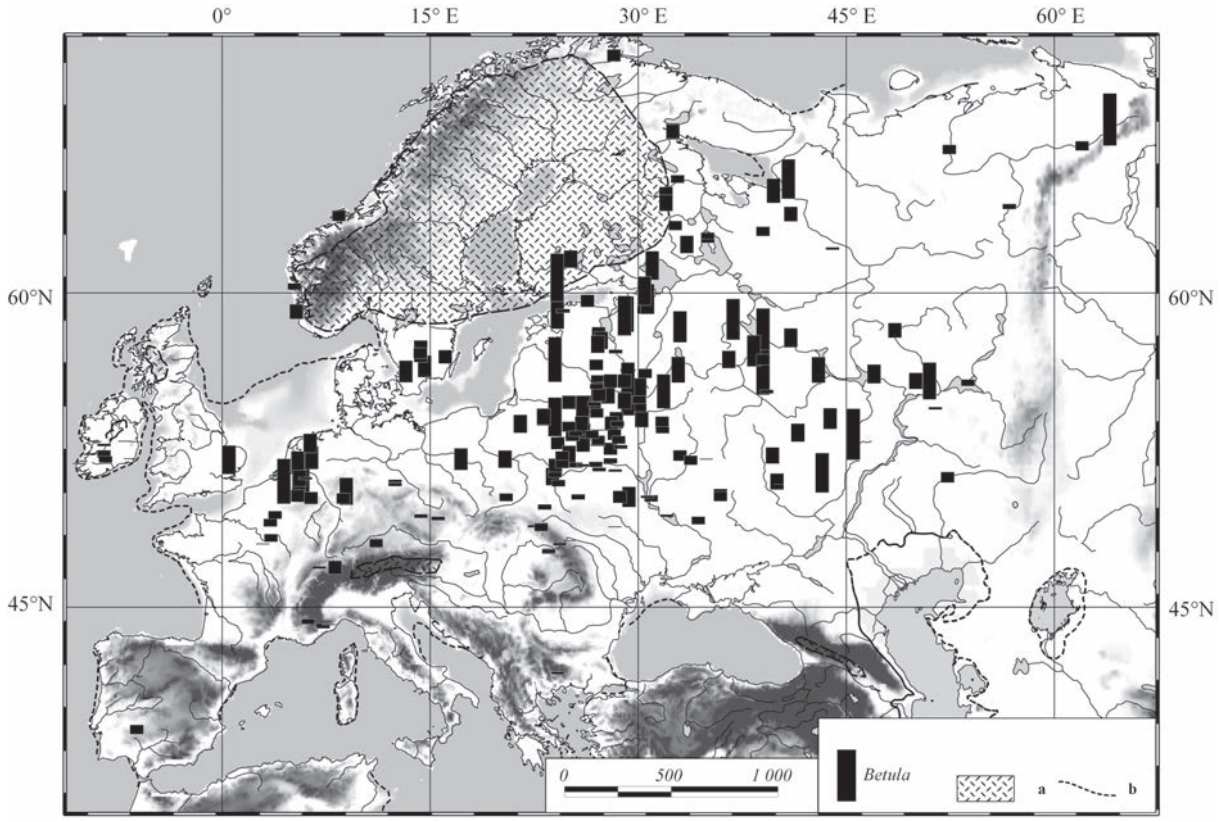

Fig. 5.42. *Betula pollen from YD localities: a – ice-sheets and mountain glaciers; b – coast line*

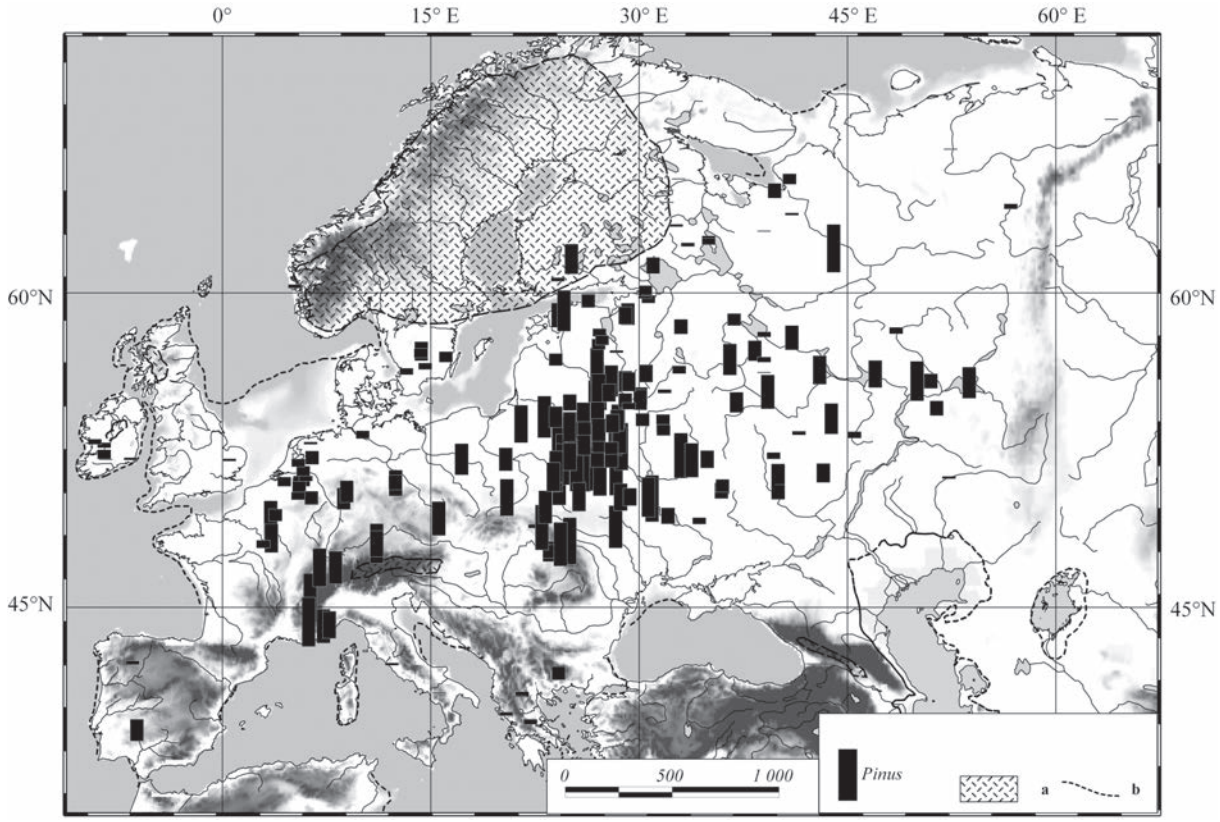

Fig. 5.43. *Pinus pollen from YD localities: a – ice sheets, b – coastline*

the southeast of the Russian Plain. To summarize, we can observe that the steppe communities during the Younger Dryas show a westward shift.

In N.W. Europe three clusters have been designated, namely cluster 7 (pine – birch shrub tundra), cluster 4 (birch – pine shrub tundra) and cluster 2 (dwarf shrub tundra and herbaceous tundra). All clusters have a strong shrub tundra component and a more (7) or less (4) stronger contribution of pine. East of the river Oder this phytocoenose develop into a birch – pine forest with patches of steppe tundra communities (cluster 1). This phytocoenoses extends into the Russian Plain and northwards up to southern Finland and the Baltic Republics. It replaces the open broad-leaved forest intermingled with steppe communities (cluster 5 of the previous Bølling/Allerød interstadial complex).

Towards the eastern boundary, e.g., towards the drainage basin of the Volga and Dnieper Rivers, the pine – birch forest with patches of steppe tundra communities develop into a periglacial open coniferous (*Picea* and *Pinus*) forest intermingled with some broad-leaved elements.

At the southeastern end of our transect, east of the lower Volga, the periglacial grass-herb and Chenopodiaceae steppe (cluster 11), that excised during the Bølling/Allerød interstadial, developed into cluster 6. This cluster still contains steppe elements but this time intermingled with periglacial pine – birch forest and some broad-leaved forest.

Under the influence of the Younger Dryas climatic deterioration, the boreal birch-pine forest extends far into the east and southeast, while the steppe phytocoenose reaches towards the west and southwest. Another major change during the Younger Dryas is that all forested areas become much more open and a tundra or steppe vegetation develops in the open patches. This is most pronounced in Ireland where the birch – pine shrub tundra (cluster 7) contains little tree birch and pine in the pollen assemblages (see individual plots for birch and pine). Similarly at the margins of the Norwegian continent an open birch pine forest with dwarf shrub tundra (cluster 8), a birch pine forest intermingled with steppe tundra communities (cluster 1), and open dwarf shrub tundra with tundra communities develops.

Pollen data from the Kozharinov database contains only tree species and total herb and total spores (Kozarinov, 1994) (Fig. 5.42, Table 5.9).

Although herb taxa characteristic of steppe or tundra cannot be designated, a more global impression of the phytocoenose that is discriminated in the cluster analyses can still be made.

In total 9 clusters could be distinguished in this database. These are;

- Cluster 1, broad-leaved forest intermingled with pine-birch forest;
- Cluster 2, birch – alder (*Alnus* cf. *incana*) spruce forests;
- Cluster 3, open spruce-pine intermingled with birch forest and alder;
- Cluster 4, open birch pine forest with some broad-leaved (*Ulmus*, *Quercus*, and *Corylus*);
- Cluster 5, open birch pine forest;
- Cluster 6, pine forests;
- Cluster 7, pine birch forest intermingled with some hazel;
- Cluster 8, pine birch forest intermingled with some broad-leaved;
- Cluster 9, coniferous pine spruce forest;

In previous analyses the area of the Russian Plain was mainly assigned to the periglacial birch – pine forest (cluster 1) and the periglacial open coniferous – broad-leaved forest (cluster 3). Analyses of the Russian data demonstrate that in detail the vegetation is much more diverse. The periglacial birch – pine forest sensu stricto (cluster 1) is located to the west of the Russian Plain (Baltic Republics, Byelorussia) and the southern part of the Russian Plain. The open coniferous broad-leaved forest (cluster 3) sensu stricto, from the eastern part of the Russian Plain, is represented by clusters 9 and 3. Clusters 5 and 8, which also occur on the Russian Plain, show that forest phytocoenoses, with predominantly pine and birch, are also present. Cluster 1, which shows a considerable contribution of broad-leaved forest, does not show a pattern. There is only one dot on the map and therefore this information point should be omitted.

Although changes in vegetation patterns are evident, no exact approximation of changes in the climate in terms of average July temperatures, January temperatures, annual temperatures or precipitation changes can be deduced. A literature review by Klimanov (1997) concerning Northern Eurasia demonstrates that there are considerable differences in the response of the YD July temperature climate in this area. He distinguishes northwestern regions bordering on Scandinavia with July temperatures that deviate from presentday values by –6°C. Isarin and Bohncke (1999) came to similar values based on the absence or presence of *Typha latifolia* in their palynological database.

For the region of northern Siberia, Klimanov (1997) reconstructed mean July temperatures less than –4°C, southern Siberia where mean July temperatures were at least –10°C lower than presentday values, and the northern part of European Russia and western Europe where the mean July temperatures were at least 4°C lower than at present.

With respect to winter temperatures, the anomalies follow a similar pattern as the summer temperatures. N.W. Europe close to the Scandinavian ice sheet demonstrates the lowest winter temperatures, being more than 14°C lower than at present.

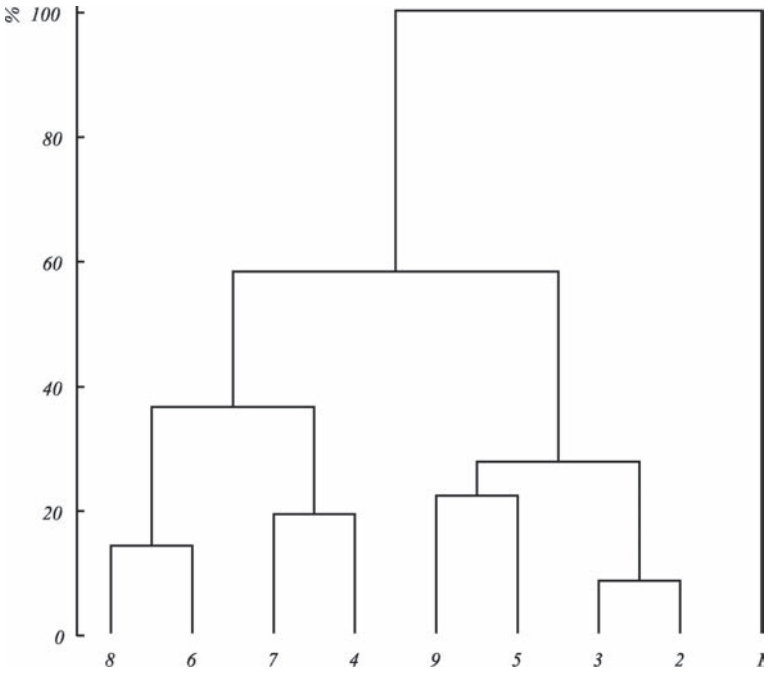

Fig. 5.44. *Dendrogram based on the axes for the YD (according to Kozarinov's database)*

Table 5.9

Plant taxa occurrence in the different clusters (Kozarinov's database)

Taxa	Clusters								
	1	2	3	4	5	6	7	8	9
Trees	**0.68**		0.40	**0.60**	0.51		0.82	0.75	**0.84**
Herbs	0.13		0.33	**0.43**	0.38		0.19	0.28	0.13
Spores	0.30		**0.43**	0.09	0.27		0.04	0.15	0.10
Picea (Spruce)	0.05	**0.12**	**0.27**	0.03	0.08	0.00	0.05	0.05	**0.14**
Pinus (Pine)	0.29	0.05	0.18	**0.30**	**0.31**	**0.95**	**0.78**	**0.58**	**0.84**
Acer (Maple)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
Alnus (Alder)	0.27	**0.46**	0.21	0.03	0.08	0.05	0.02	0.08	0.03
Betula (birch)	0.14	**0.82**	0.35	**0.36**	**0.36**	0.13	0.18	**0.20**	0.11
Carpinus (Hornbeam)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
Corylus (Filbert)	**0.66**	0.00	0.00	0.13	0.08	**0.31**	0.11	0.12	0.00
Fagus (Beech)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00
Fraxinus (Ash)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus (Oak)	0.15	0.00	0.00	0.08	0.00	**0.23**	0.00	**0.31**	0.00
Tilia (Linden)	**0.49**	0.00	0.00	0.01	0.00	0.00	0.06	0.16	0.00
Ulmus (Elms)	**0.49**	0.00	0.00	0.14	0.00	0.10	0.04	0.14	0.00
Lamiaceae (Dead-nettle family)	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00
Oxyria (Oxalis)	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Rubiaceae (Bedstraw family)	0.00	0.00	0.05	0.10	0.01	0.00	0.02	0.00	0.01

At the eastern end of our transect, in southern Siberia (Kazakhstan), these values were more than 12°C less than at present. Deviations diminish towards northern Siberia where temperatures were only 6°C less than at present. Klimanov (1997) suggests therefore the occurrence of an extensive mountain glaciation in Central Asia during the course of the Younger Dryas.

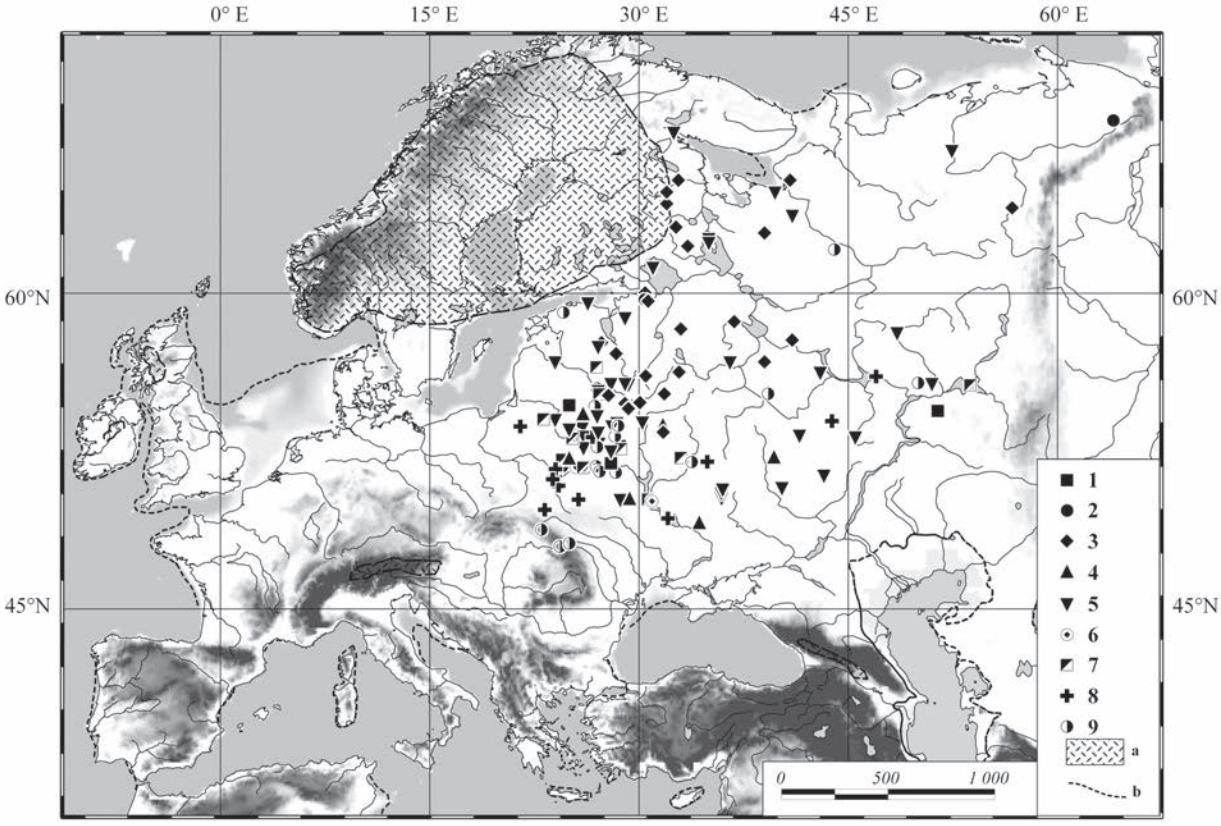

Fig. 5.45. *Geographical distribution of YD pollen localities belonging to different clusters (1–9) (according to Kozarinov's database); a – ice sheets; b – coastline*

It is interesting to see how the Ural mountain ridge acts as a dividing line between different climate regimes controlled by the Scandinavian ice sheet in the northwest and a presumed Central Asian mountain glaciation in the southeast In this respect the rather homogeneous pattern of phytocoenoses on the Russian Plain versus a very diverse pattern of phytocoenoses in N.W. Europe is understandable.

A very broad band that runs between the Scandinavian ice sheet in the northwest and the Central Asian mountain glaciation in the southeast is less severely affected by the Younger Dryas climate deterioration. This band of diminished impact is reflected in the occurrence of a less diverse pattern in the palaeophytocoenoses. Only towards the southeast, the region with presumed mountain glaciations, does a third cluster (6) occur. In this band, possibly in secluded places, broad-leaved trees (*Quercus, Tilia,* and *Alnus)* get the opportunity to gain a place among the coniferous forest (3) and the birch pine forest (1). Summarizing, both progressive forest development and retrogressive developments near the influence of ice sheets take place simultaneously during the Younger Dryas.

An attempt has been made to group the palaeophytocoenoses into vegetation provinces.

Ia. Periglacial shrub tundra at the margins of the West European continent comprising most of Ireland and southwest Norway.

Ib. Shrub tundra with elements of periglacial vegetations and primitive aggregations of halophytes.

IIa. Periglacial dwarf shrub tundra with some tree birch and pine.

Confined to the N.W. European lowlands up to the Vistula drainage basin in the east.

IIb. Pine-birch open woodland combined with steppe communities.

III. Coniferous forests of the central and east European Plain with some broad-leaved forest in the central Russian Plain.

IV. Alpine forelands, pine forests with some birch and steppe communities.

V. Central and Northern France shrub tundra with willow, Juniper, and birch.

VIa. Forest-steppe – meadow and herb steppes with pine and birch forests with broad-leaved participation. West of the Central Urals.

VIb. Boreal pine forest intermingled with steppe communities. Running westwards into southern Yugoslavia, continuing along the Mediterranean coast and into the Iberian Peninsula.

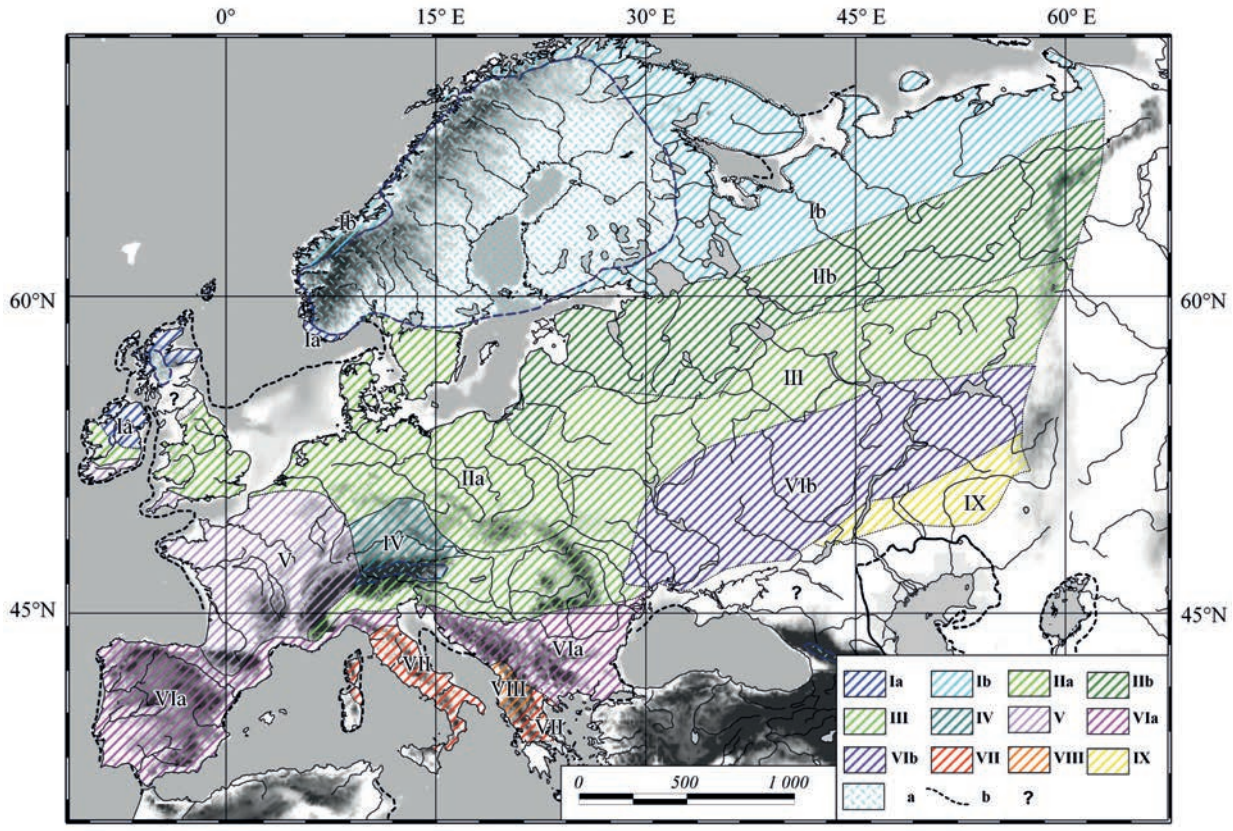

Fig. 5.46. *Palaeovegation provinces during the YD: Ia – Periglacial shrub tundra; Ib – Bush tundra with elements of periglacial vegetations and primitive aggregations of halophytes; IIa – Periglacial dwarf shrub tundra with some tree birch and pine; IIb – Pine-birch open woodland combined with steppe communities; III – Coniferous forests with some broad-leaved forest; IV – mountain pine forests with some birch and steppe communities; V – Shrub tundra with willow, Juniper, and birch; VIa – Meadow and herb steppes with pine and birch forests with broad-leaved participation; VIb – Boreal pine forest intermingled with steppe communities; VII – Open broad-leaved forest with steppe communities; VIII – Grass steppe; IX – Meadow and grass steppe. a – ice sheets, b – coastline, ? – absence of data*

VII. Open broad-leaved forest with steppe communities in central and southern Italy and on the Peloponnesos in Greece.

VIII. Grass steppe with *Ephedra* in southern Albania and N.W. Greece. In between VI and VII.

IX. Meadow and grass steppes.

5.5. THE VEGETATION OF EUROPE DURING THE EARLY HOLOCENE (PREBOREAL AND BOREAL PERIODS) (<10.2 – ⩾8.0 KYR BP) (PB–BO)

Alexandra Simakova and Andrey Puzachenko

The Early Holocene (10.2–8.0 kyr BP) comprises the Preboreal and Boreal periods, and is marked by a considerable increase in mean T-July. On the western end of the transect July temperatures had risen from 10–11°C in the Younger Dryas to 15–17°C in the Preboreal (Bohncke, 1993). The deviations in July temperatures from mo-

dern values varied from 0° to –1°C. Winter temperatures were lagging behind since the lowering of the sea level, as a consequence of the previous glacial period, giving Western Europe a continental setting. In the northwestern part of the Russian Plain, the presence of the Scandinavian ice sheet under the prevailing western circulation still exerts its influence on both summer and winter temperatures. According to Velichko *et al*. (2002), July temperatures were some 2° lower than at present. Winter temperatures were even more suppressed and were 2° to 6° lower than at present in the north of Europe and –6° to –3°C farther south. Annual precipitation in Central Europe was on the whole below the present-day values (Savina and Khotinsky, 1985; Zagwijn, 1994; Coope *et al*., 1998; Velichko *et al*., 2002; Heikkilä and Seppä, 2003; Davis *et al*., 2003; and others).

Nevertheless, the amelioration of the climate that had set in at the beginning of the Holocene led to considerable changes both in the biotic and physical environment. A reorganization of the phytocoenoses led to the development of the zonal vegetation structure of interglacial type. The studied interval included the Preboreal (10.1–9.0 kyr BP) and Boreal (9.0–8.0 kyr BP) periods, each presenting a complicated sequence of climatic fluctuations like the PB–BO (Van der Plicht *et al*., 2004) and the 8.2 kyr event.

The palynological studies thus far performed provided us with extensive material on the Early Holocene of Europe; the sediments have been dated by absolute chronological methods. A few summaries of the Boreal vegetation have recently been published, among which the vegetation map of the former USSR territory (Khotinsky and Klimanov, 2002) and the map of Europe (discussions in the World Wide Web version of the QUEEN review).

Palaeoclimatic reconstructions of the Early Holocene were based on palaeobotanical data obtained from 194 sections (892 samples altogether) of lacustrine-fluvial and lacustrine-paludal sediments (Table 5.10).

Table 5.10

The Early Holocene pollen sites

ID	Localities	Lat.	Long.	Age	References
1	Zwickau	50,50	12,50	Calculated	Wole, 1991
2	Grabmuhle	48,19	11,09	9795±195, Jahre v.h.-16513; 9570±260, Jahre v.h.-16512; 9025±245, Jahre v.h.-16511; 8365±200, Jahre v.h.-16510	Kortfunke, 1992
3	Grasheim	48,21	11,10	10 065±440, Jahre v.h.-16325; 9680±275, Jahre v.h.-16321; 9860±285, Jahre v.h.-16322	Kortfunke, 1992
4	Laich II	48,18	11,11	10 100±470, Jahre v.h.-16319; 10 020±335, Jahre v.h.-16317; 9375±240, Jahre v.h.-16316; 8795±250, Jahre v.h.-16315	Kortfunke, 1992
5	Meekelermeer	52,40	6,45	9410±110, GrN-10026; 9410, GrN-10026	Bohncke *et al*., 1988
6	Kostverlon	53,10	6,35	Calculated	Bohncke
7	Gennep	51,40	5,58	9730±80; 8 910±110; 9660±60; 9730±60; 9 950±50; 9840±80; 9780±60; 9 820±50; 9700±50; 9730±60	Bohncke
8	Kingbeek dal	50,55	5,45	9600	Bohncke
9	Callanish 3	58,12	6,45	Calculated	Bohncke, 1988
10	Lago de Ajo	8,60	–6,15	9650±120, Beta-9156; 9780±80, Beta-6739	EPD
11	Lago Grande di Monticchio	40,56	15,60	Calculated	EPD
12	Khimaditis	40,37	21,35	9340±85, GrN-6598	EPD
13	Ioannina	39,45	20,43	10 190±90, GrN-4875	EPD
14	Xinias	39,03	22,16	Calculated	EPD

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
15	Ampoix	48.10	2.56	8970±115, MBN-343; 9790±175, MBN-325	EPD
16	Akuvaara	69,07	27,41	8840±170, Hel-521	EPD
17	Aholami	61,53	25,13	8030±80, Su-1545	EPD
18	Antu sinijarv	59,08	29,19	8040±120, Ja-2115; 8930±100, Ja-2116	EPD
19	Ballinloghig Lake	52,12	–10,3	9695±465, UB-2696; 9840±295, UB-2686; 9370±315, UB-2692	EPD
20	Ballybetagh	53,10	–6,25	10 070±60, TO-233	EPD
21	Belle Lake	52,11	–7,03	9100±130, D-113; 9600±135, D-112	EPD
22	Blavasstjonn	64,55	11,4	8000±160, T-2845; 8950±260, T-2844	EPD
23	Besbog-2	41,45	23,4	8420±160, VRI-969	EPD
24	Blomoy	60,32	4,53	9340±160, T-623	EPD
25	Bruvatnet	70,11	28,25	8810±190, Hel-498	EPD
26	Selle di Carnino	44,09	7,41	9840±110, Ly-728	EPD
27	Chivres	49,61	3,81	9200±80, GrN-4691	EPD
28	Domsvatnet	70,19	31,02	8570±200, Hel-775	EPD
28	Edessa	40,49	21,57	8050±70, GrN-5262; 9760±58, GrN-6187; 9765±45, GrN-6188	EPD
30	Flaatevatn	59,42	6,10	8000±120, T-5823; 9570±140, T-5824	EPD
31	Grasvatn	63,42	8,42	8130±150, T-3278a; 9210±160, T3277a; 9330±160, T-3277b	EPD
32	Hirvilampi	60,37	24,15	8750±120, Hel-2355; 9450±120, Hel-2356	EPD
33	Hockham Mere	52,3	0,50	8230±150, Q-2217; 8250±80, Q-2216; 8500±80, Q-2215; 8675±60, Q-2214; 8960±95, Q-2213; 9400±110, Q-2212; 9110±115, Q-2211; 9130±600, Q-2210; 9270±150, Q-2209; 9390±140, Q-2208; 9460±100, Q-2207; 9560±95, Q-2206	EPD
34	Kaarkotinlampi	61,25	25,86	8790±120, Hel-1215	EPD
35	Kalsa Mire	58,10	27,27	8160±80, TA-1882	EPD
36	Kamenicky	49,44	15,58	8080±190, Hv-11532; 8145±295, Hv-12962; 7580±315, Hv-11533; 9985±220, Hv-11534	EPD

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
37	Kanjerjoki [Kuusamo]	66,07	29,00	8240±190, Hel-320	EPD
38	Kansjon	57,38	14,32	8580±80, Lu-2930; 9580±90, Lu-2919	EPD
39	Kluki	54,42	17,17	8130±85, Gd-1322; 9370±115, Gd-547; 9110±70, Gd-1329; 9855±315, Hv-9104; 9865±105, Gd-548	EPD
40	Kuivajarvi	60,75	23,50	8990±100, SU-2267	EPD
41	Kupena	41,59	24,20	9320±185, UA-1552 9825±155, UA-1553	EPD
42	Kupena1	41,59	24,20	9000±40, Tln-1004 9700±150, INRNE-100	EPD
43	Col des Lauzes	45,46	6,32	9860±200, Ly-1281	EPD
44	Lake Lednica	52,33	17,39	9060±160, Gd-5034	EPD
45	Lac Long Infrieur	44,03	7,27	8730±220, Ly-1240; 9330±220, Ly-1239	EPD
46	Lobsigensee	47,01	7,17	9500±90, B-4323	EPD
47	Maanselnsuo	65,37	29,36	9150±220, I-1700; 9100±220, I-1699	EPD
48	Masehjavri	69,03	20,59	8260±170, Hel-976; 9690±220, Hel-975	EPD
49	Myrlampi	62,20	26,14	8260±100, Su-1549; 8480±130, Su-1548	EPD
50	Mukkavaara	68,55	21,00	8430±160, Hel-990; 9040±140, Hel-1069; 9960±150, Hel-989; 8890±190, Hel-1070	EPD
51	Niechorze	54,00	15,05	9330±120, Gd-1112	EPD
52	Puscizna Rekowianska	49,29	19,49	8570±90, Gd-1501; 8800±160, Gd-986; 8960±80, Gd-1500	EPD
53	Rattuvarri	69,21	20,19	9460±140, Hel-1082	EPD
54	Rudushskoe Lake	56,30	27,33	8390±150, Lu-1713	EPD
55	Ryonansuo	60,26	24,10	9180±130, Hel-2169	EPD
56	Lake Skvzetuszewskie	52,33	17,21	8390±120, Gd-2796 9110±120, Gd-2797	EPD
57	Lake Skvzetuszewskie (87)	52,33	17,21	9670±130, Gd-2761	EPD
58	Saksunarvatn	62,15	–7,11	8230±100, K-2331; 9180±140, K-2159; 9380±130, K-2332; 9390±150, K-2160	EPD
59	Lake Sambosjon	57,08	12,25	8280±85, Lu-1271; 9190±90, Lu-1269; 9390±95, Lu-1267; 9860±95, Lu-1270	EPD

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
60	Sanabria Marsh	42,06	6,44	10 140±180, CAMS-15296; 9760±90, CAMS-15297; 8200±90, Beta-9160; 9940±100, AMS-15298; 9490±110, Beta-9161	EPD
61	Lac Saint Leger	44,25	6,20	8400±200, Ly-1138	EPD
62	Hozelec SK-5-A	49,03	28,30	9020±120, VRI-795	EPD
63	Skvarran	57,12	16,09	10 080±90, Lu-2483; 10 150±90, Lu-2177	EPD
64	Bledowo lake	52,33	20,40	Calculated	EPD
65	Slopiec	50,47	20,47	9090±100, Gd-776; 9330±145, Gd-703; 9620±120, Gd-700; 10 080±160, Gd-702	EPD
66	Suovalampi	69,35	28,50	8710±240, Hel-540	EPD
67	Syrjlnsuo	61,13	28,07	8550±50, SU-2301	EPD
68	Szymbark	49,38	21,06	8210±150, Lv-661	EPD
69	Tarnawa Wyzna	49,06	22,50	9510±150	EPD
70	Tarnowiec	49,42	21,37	9380±80, Gd-1481; 9840±100, Gd-962	EPD
71	Tomtabaken	57,29	14,28	9120±95, Lu-902; 9530±95, Lu-901; 9860±85, Lu-90; 10 150±115, Lu-899	EPD
72	Trollvatnet	69,52	23,28	8780±130, Hel-1088; 9930±140, Hel-1087	EPD
73	Vallon de Provence	44,23	6,24	9750±200, Lv 1284	EPD
74	Vasikkasuo	64,40	27,52	8610±80, SU-1866	EPD
75	Zbudovska Blata	49,55	14,19	8438±80, Bln-1480	EPD
76	Zsombo-swamp	46,21	19,59	9029±98, deb-3985	EPD
77	Zirbenwaldmoor	46,51	11,01	8600±150, VRI-216; 8540±130, VRI-217	EPD
78	Preluca Tiganuli	47,48	23,31	8565±90, Ua-16341; 9185±100, Ua-6340; 9680±90, Ua-1639; 9685±95, Ua-1638	Bjorkman *et al*., 2002
79	Steregoiu	47,48	23,32	8300±85, Ua-1629; 9130±95, Ua-1628; 9530±85, Ua-1627; 9665±110, Ua-1626	Bjorkman *et al*., 2002
80	Batorliget	47,00	21,40	9339±130, DEB-2660	Willis *et al*., 1995
81	Lake Solso	56,08	8,38	8140±120, K-3854; 8380±120, K-3853; 8800±120, K-3852; 8910±120, K-3851; 9180±130, K-3850	EPD
82	Coizard-Joches-I	48,47	3,52	8490±70, CrN-4714	Zeist & Spoel-Walvius, 1980

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
83	Valler de la Voise	48,25	1,45	9110±80, GrN-6240	Zeist & Spoel-Walvius, 1980
84	Liastemmen	59,10	5,14	9560±160, T-6168a	Paus, 1989
85	Zabinko	52,10	16,50	9950±90, GrN-16193	Bohncke *et al*., 1995
86	Oppershofen 5	50,25	80,44	9330±500, Utc.-4411	Bos, 1988.
87	Oppershofen 3	50,25	8,44	8990±90, Utc.-6085; 840±220, Utc.-6084; 9800±60, Utc.-5206; 10 000±80, Utc.-5207	Bos, 1988
88	Ober-Horgern 2	50,27	8,44	9160±70, Utc.-4403; 9470±70, Utc.-4404; 9520±60, Utc.-4405; 10 180±190, Utc.-4406	Bos, 1988
89	Mardorf-Schweinsberg	50,45	8,57	8720±110, Utc.-6087; 9230±80, Utc.-4875	Bos, 1988
90	Maanselansuo	67,00	28,00	9150±220, I-1 699; 9100±220, I-1 700	Vasari, 1965
91	Nieuwe Weterring	52,00	5,00	8700	Hartman, 1968
92	Padul 3	37,00	3,67	8200±80, Gif-6393; 9300±90, Gif-6392; 10 000±110, Gif-6212; 9930±110, Gif-6006	Pons & Reille, 1988
93	La Bouchet B5	44,89	3,67	8340±150, Gif-5941	Pons & Reille, 1988
94	Panicishte	43?	24?	10 035±65	Bozilova, 1975
95	Le Moura	43,15	–1,15	9960±160, Q 616-17	Oldfield, 1964
96	Schusssenquelle	48,30	8,45	9150±200, H861/971	Lang, 1963
97	Sandsjon	56,45	13,25	8850±80, Lu-2700; 9440±80, Lu-2699; 10 140±90, Lu-2698	Magnus, 1989
98	Bazoches	49,16	3,35	9580±130, GrN-19477	Bakels, 1995
99	Loch Buailaval Beag	58,16	6,46	8175±95, Q 2726; 9730±110, Q 2725	Fossitt, 1996
100	Loch a' Phuinnd	57,22	7,16	8600±100, Q 2745	Fossitt, 1996
101	Dinslaken-Klaranlage	51,33	6,43	9700	Bjorkman *et al*., 2002
102	Gramousti	39,50	20,35	9260±170, 8790±150	Turner & Goni 1997
103	Poggensee	53,50	10,10	8650±120	Kiel, 1987
104	Podgrodzie	50,15	21,10	8000±100, 9160±135, 9915±95	Mojski, 1985
105	Clairveaux Petitlac	47,00	7,00	Calculated	S.J.P. Bohncke
106	Minderhout	51,25	4,46	10 180±90, GrN-10086	Bohncke & Vandenberghe, 1991
107	Meerfelder	50,45	6,40	Calculated	Litt, Stebich, 1999
108	L. Namackanbeg	53,17	9,18	Calculated	Andrieu *et al*., 1993
109	Lugra	53,01	8,52	Calculated	Andrieu *et al*., 1993

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
110	Illaucronan	52,57	8,52	Calculated	Andrieu *et al*., 1993
111	Vinderhoute-Kale	51,05	3,70	9530±55, GrN-6035; 10 085±90, GrN-6034	Verburggen, 1979
112	Uddelemeer	52,15	5,46	9940±90, GrN-9549	Bohncke *et al*., 1988
113	Rotsee RL250	47,00	8,15	8750±50, B 4889; 9800±120, B 4890	Lotter, 1988
114	Rotsee RL305	47,00	8,15	9505±140, C-846; 9760±160, C-848	Lotter, 1988
115	Rotsee RL300	47,00	8,15	9380±130, C-725; 9360±130, C-728	Lotter, 1988
116	Hauterive	46,00	6,30	8165±70, ETH-20718; 9295±75, ETH-20717; 9585±75, ETH-20716; 9790±95, ETH-16722; 10 110±75, ETH-20715; 9985±75, ETH-20714; 9930±75, ETH-29713; 9885±75, ETH-20712	Magny *et al*., 2003
117	Herrestads mosse	55,25	13,52	8560±85, Lu-1228; 9250±90, Lu-1227; 9420±95, Lu-1226; 9620±95, Lu-1225	Hakansson & Kolstrup, 1987
118	Quintanar de la Sierra	43,00	–3,25	8260±140	Goni, 1994
119	Urtiaga	43,30	–5,00	8700±170	Goni, 1994
120	Lake Steissling	47,50	8,55	Calculated	Eusterhues *et al*., 2002
121	Lake Perespilno	52,00	23,2	Calculated	Goslar *et al*., 1999
122	Pian di Gembro	46,00	10,00	8730±70, UtC-9078 9250±50, UtC-9077	Pini, 2002
123	Laihalampi	61,29	26,04	9520±160, Hela-4421	Heikkilä & Seppä, 2003
124	Lipushki II	53,00	38,00	8750±40, GIN-1093	Spiridonova, 1991
125	Gavrilovo 86	51,23	40,01	8750± 40, GIN-1093; 9390±120, GIN-4946; 9270±60, GIN-4945; 9270±20, GIN-4944; 8340±120, GIN-4943	Spiridonova, 1991
126	Chernaya Ligovka	58,15	39,00	10 010±120, TA-186; 9740±80, TA-185; 9470±120, TA-184	Serebryanny, 1978
127	Shuvalovskoe Boloto	59,83	30,42	8720±275; 8770±295; 8600±310	Khotinskii, 1977
128	Osechnoe Boloto	58,00	33,50	9575±305; 9300±215	Neishtadt *et al*., 1965
129	Somino (borehole.86)	57,40	38,32	9430±300	Neishtadt *et al*., 1965
130	Somino (10)	57,40	38,32	9890±300; 9780±315; 9560±345	Neishtadt *et al*., 1965

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
131	Polovetsko-Kupanskoe Boloto	56,40	39,00	8290±430	Khotinskii *et al*., 1994
132	Seb-boloto	64,00	43,00	8800±80	Velichko *et al*., 1994
133	Gel'miazevskoe	49,00	32,00	8210±100, Ku-1291	EPD
134	Zalozhtsy II	49,50	26,00	8840±100, Ku-1284; 8410±100, Ku-1283; 8050±80, Ku-1282	EPD
135	Morino	53,00	24,05	9970±110, Tln-136	Vozniachyk & Valchik, 1987
136	Baiaara	68,51	66,54	8000±125, WAT-2924 8210±110, GIN-7862a 8120±90, GIN-7862б 8090±40, GIN-7862в	Andreev *et al*., 1998
137	Krestovaya	70,08	57,00	8210±90, Lu-1462	Serebryanny & Malyasova, 1998
138	Ivanovskoe III	56,32	39,05	8850±700, GIN-242	Khotinskii, 1977
139	Kalina peat	59,10	25,30	8040±70, TA-152 9130±135, TA-153	Khotinskii, 1977
140	Teosaare	58,50	25,30	8015±80, TA-97 8495±85, TA-98	Khotinskii, 1977
141	Kuiksilla	58,30	25,20	8095±75, TA-69 9080±100, TA-70 9350±250, TA-51	Khotinskii, 1977
142	Berbukas	54,30	25,05	8100±290, Vs-18	Khotinskii, 1977
143	Apatity	67,30	33,30	8030±90; 8470±140	Semenova &, Saveleva, 2002
144	Lozoviki	55,20	28,12	8051±179, IGSB-508; 9190±53, IGSB-509; 9371±95, IGSB-507	Zernitskaya *et al*., 2001
145	Berendeevo III	56,30	39,00	8800±100, GIN-266	Neishtadt *et al*., 1969
146	Isshbulatovo	55,40	54,50	8570±40, BASH.GI-31; 8880±60, BASH.GI-32	Nemkova, 1978
147	Chernaya (escov.1)	55,00	41,30	8190±120, GIN-3893; 8190±120, GIN-3892; 8630±40, GIN-3894; 8630±40, GIN-3891; 8720±200	Kravtsov *et al.*, 1994
148	Chernaya (escov.2)	55,00	41,30	8060±100, GIN-3547; 9770±800, GIN-3548; 8730±300, GIN-3551; 9280±160, GIN-3552; 10 000±400, GIN-3549	Kravtsov *et al*., 1994
149	Razdorskoe	47,33	40,40	9470±310, IGRAS-722	Kremenetskii, 1997
150	Pobochnoe	51,45	52,30	8978±353, IGRAS-1301; 9897±388, IGRAS-1574	Kremenetskii *et al*., 1998
151	Dvurechki-Esaulovo	52,20	39,40	9480±190	Khmelev, 1979
152	Butyrskoe	53,35	47,00	8740±120, KRIL-91	Blagovekshenskii & Blagovekshenskaya, 1978
153	Arkonskaya vpadina	56,00	20,00	8400±120	Kleimenova *et al*., 1984

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
154	Kurino	55,30	30,00	8590±140, MIG-13	Valchik, 1985
155	Berekhovo	54,15	48,20	8170±130, TLN-561	Blagoveshenskaya, 1985
156	Rodnichnoe	64,30	42,30	8760±120	Elovicheva, 1985
157	Ivanovskoe III	56,32	39,05	8850±70, GIN-242	Khotinskii, 1977
158	Galichskoe 1	53,25	42,20	8362±44, KIA-7066	Velichko *et al*., 2001
159	Berestovskaya balka	47,30	41,00	8270±175, MGU-1458	Panin *et al*., 1998
160	Tomitsa	53,25	42,20	8705±70, Tln-89	Koshechkin *et al*., 1977
161	Sudoble	47,30	41,00	8510±70, TA-1223; 9080±90, TA-1224	Yakyshko *et al*., 1992
162	Chernikhovo	60,50	36,05	8690±240, Vs-365	EPD
163	Novolsky	54,00	27,45	8600±170, Tln-585; 9270±150, Tln-586	EPD
164	Starniki	53,25	26,26	8190±160, Ki-1299; 920±200, Ki-1300	EPD
165	Imatu mire	56,46	26,11	9400±120, TA-1805	EPD
166	Kalsa Mire	50,16	26,01	8160±80, TA-1882	EPD
167	Kirikumae	49,40	31,50	9395±75, Tln-1447	EPD
168	Lake Maardu	49,45	25,27	8625±85, Tln-1265	EPD
169	Mire Pelisoo	59,08	27,26	8030±90, Tln-1112; 8980±120, Tln-1104	EPD
170	Rudushskoe Lake	58,10	27,27	8390±50, Lu-1713	EPD
171	Raigastvere lake	57,40	27,15	8180±70, TA-1749; 9800±120, TA-1750	EPD
172	Mire Saviku	59,26	25,00	8090±70, TA-426; 9090±70, TA-327	EPD
173	Baidara	58,28	22,23	8090±40, GIN-7862c; 8000±125, WAT-2924; 8120±90, GIN-7862b; 8210±110, GIN-7862a	EPD
174	Bezdonnoe	56,30	27,33	9085±120, TA-533; 9880±150, TA-535	EPD
175	Gotnavolok	58,36	26,40	8670±80, TA-1185	EPD
176	Kerskoe	58,24	27,14	8995±100, TA-1017	EPD
177	Landshaftnoe	68,51	66,54	8000±100, TA-730	EPD
178	Mustusuo	62,02	32,46	8670±100, TA-579	EPD
179	Nenazvannoe	62,12	33,48	8460±100, TA-838	EPD
180	Nizhnevartovsk	65,05	32,10	8350±45, SOAN-177; 8780±35, SOAN-173	EPD
181	Petrolivo	64,34	30,32	9490±80, Lgu-2291	EPD
182	Ptichje	61,48	33,30	8600±100, TA-1021	EPD
183	Rugozero	61,48	33,29	9230±80, TA-1129	EPD
184	Pervoe Maya	76,40	62,00	9120±90, LU-1350	EPD

Continued table 5.10

ID	Localities	Lat.	Long.	Age	References
185	Sosvyatskoe	56,00	31,59	9500±1 400, Mgu-1108	EPD
186	Zapovednoe	66,21	30,34	8990±100, TA-954	EPD
187	Zaruskoe	64,05	32,38	8360±100, TA-836	EPD
188	Chistoe	58,07	47,30	8052±186, IGRAS-1756	Prokashev *et al*., 2003
189	Prokopievskii	58,51	50,25	9508±266, IGRAS-1766	Prokashev *et al*., 2003
190	Karinskii	58,35	50,20	8697±165, IGRAS-1774	Prokashev *et al*., 2003
191	Solenoe zaimishe	45,00	48,00	8500±100; 9560±60	Bolikhovskaya, 1990
192	Chus	59,45	52,55	9020±50, IGRAS-2630; 8030±30	Pakhomova, 2004
193	Ponor	46,00	24,00	8770±90, Gifa-100157; 8990±80, Gifa-996999	Bodnarius *et al*, 2002
194	Le Locle	47,03	6,43	9355±60, AA-2226; 9425±70, AA-22261	Magny *et al*., 2001

The studied sections provided palynological information of 279 floristic taxa, (including 222 taxa determined to genus level and 77 to species level). Mathematical processing of the palynological database on the Preboreal–Boreal interval permitted to identify 7 clusters (Fig. 5.45). Table 5.11 shows how the taxa cluster.

Cluster 1 indicates widely distributed forest-tundra with patches of northern taiga forest and shrub tundra. Cluster 2 corresponds to shrub tundra coenoses; cluster 3 to periglacial spruce and pine-birch forests, locally with steppe and tundra plant communities; cluster 4 to open pine-birch forests, with patches of steppe plant communities; cluster 5 pine and broad-leaved forests, locally with meadow steppe, cluster 6 forest-steppe coenoses (coniferous-broad-leaved forests in combination with herb and wormwood-grass steppes, cluster 7 forests of fir (*Abies*) and broad-leaved species in combination with grass steppes.

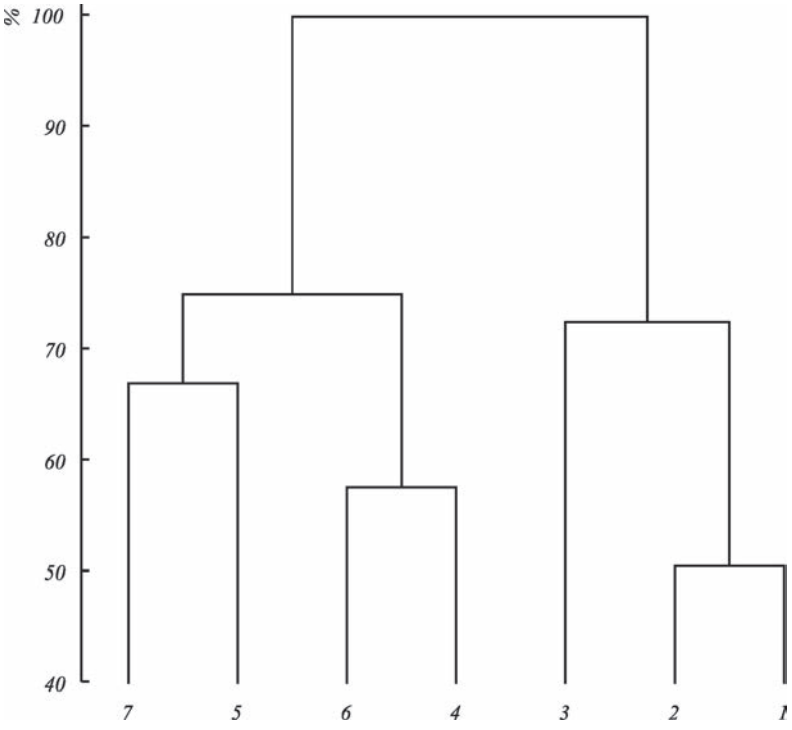

Fig. 5.47. *Dendrogram showing the relationship of the early Holocene pollen assemblages*

Table 5.11

Cluster characteristic in standard units (average value of the cluster) for PB–BO

Taxa	Clusters							
	1	2	3	4	5	6	7	p
Abies (Fir)	0.006	0.000	0.000	0.035	0.034	0.148	0.206	<0.0001
Larix (Larch)	0.032	0.000	0.125	0.038	0.018	0.000	0.000	.10
Picea (Spruce)	0.102	0.028	0.344	0.068	0.022	0.017	0.000	.0002
Pinus (Pine)	0.343	0.258	0.345	0.579	0.459	0.358	0.066	<0.0001
Acer (Maple)	0.027	0.002	0.000	0.092	0.095	0.014	0.294	<0.0001
Alnus (Alder)	0.025	0.078	0.101	0.050	0.092	0.037	0.127	.32
Betula (Birch)	0.384	0.518	0.147	0.108	0.232	0.044	0.007	<0.0001
Betula nana (Dwarf birch)	0.262	0.021	0.264	0.032	0.021	0.000	0.000	<0.0001
Carpinus (Hornbeam)	0.000	0.000	0.000	0.000	0.113	0.063	0.154	<0.0001
Corylus (Filbert)	0.018	0.113	0.023	0.043	0.202	0.012	0.068	<0.0001
Fagus (Beech)	0.003	0.000	0.000	0.001	0.007	0.126	0.155	<0.0001
Fraxinus (Ash)	0.006	0.012	0.000	0.047	0.059	0.004	0.283	<0.0001
Populus tremula (Aspen)	0.003	0.095	0.000	0.007	0.046	0.000	0.008	.0012
Quercus (Oak)	0.004	0.025	0.006	0.035	0.185	0.092	0.521	<0.0001
Salix (Willow)	0.078	0.197	0.113	0.049	0.145	0.046	0.018	<0.0001
Tilia (Linden)	0.018	0.042	0.151	0.034	0.036	0.012	0.062	.17
Ulmus (Elm)	0.029	0.039	0.008	0.122	0.056	0.021	0.034	.16
Apiaceae (Carrot family)	0.010	0.047	0.007	0.069	0.132	0.205	0.186	<0.0001
Asteraceae (Daisy family)	0.004	0.004	0.028	0.074	0.016	0.385	0.053	<0.0001
Cichorium (Chicory)	0.000	0.010	0.000	0.069	0.046	0.387	0.114	<0.0001
Artemisia (Wormwood)	0.024	0.030	0.513	0.173	0.071	0.350	0.041	<0.0001
Brassicaceae (Cabbage family)	0.002	0.030	0.129	0.050	0.037	0.242	0.119	.0002
Caryophyllaceae (Pink family)	0.003	0.008	0.129	0.075	0.019	0.250	0.035	<0.0001
Chenopodiaceae (Goosefoot family)	0.011	0.017	0.313	0.169	0.017	0.345	0.329	<0.0001
Cyperaceae (Sedge family)	0.121	0.104	0.158	0.170	0.062	0.162	0.086	.27
Ephedra (Ephedra)	0.000	0.001	0.138	0.115	0.029	0.390	0.230	<0.0001
Ericaceae (Heather family)	0.023	0.066	0.136	0.000	0.020	0.000	0.000	<0.0001
Calluna (Heather)	0.001	0.048	0.000	0.000	0.096	0.000	0.000	.0001
Fabaceae (Pea family)	0.027	0.001	0.126	0.024	0.061	0.007	0.008	.01
Helianthemum (Rock-rose)	0.000	0.003	0.000	0.077	0.070	0.135	0.069	0.000
Myriophyllum (Water-milfoil)	0.003	0.021	0.011	0.065	0.068	0.058	0.086	.089
Nymphaea (White Water-lily)	0.073	0.032	0.000	0.033	0.011	0.000	0.177	.018
Plantago (Plantain)	0.001	0.002	0.000	0.011	0.077	0.185	0.071	<0.0001
Poaceae (Grass family)	0.114	0.112	0.107	0.186	0.139	0.169	0.463	.017
Ranunculaceae (Buttercup family)	0.041	0.019	0.142	0.053	0.053	0.246	0.004	<0.0001
Thalictrum (Meadow-rue)	0.017	0.050	0.092	0.083	0.087	0.276	0.036	.063

Continued table 5.11

Taxa	Clusters							
	1	2	3	4	5	6	7	p
Rosaceae (Rose family)	0.054	0.080	0.001	0.081	0.164	0.283	0.009	<0.0001
Rubiaceae (Bedstraw family)	0.000	0.011	0.003	0.052	0.136	0.187	0.018	<0.0001
Galium (Bedstraw)	0.016	0.035	0.000	0.022	0.020	0.125	0.307	.001
Rumex acetosa (Dock)	0.002	0.103	0.000	0.039	0.200	0.145	0.184	<0.0001
Saxifragaceae (Saxifrage family)	0.024	0.044	0.063	0.060	0.034	0.077	0.000	.50
Sparganium (Bur-reed)	0.002	0.016	0.006	0.037	0.022	0.027	0.340	.003
Typha (Reedmace)	0.022	0.016	0.302	0.091	0.063	0.005	0.111	.0392
Urtica (Nettle)	0.001	0.071	0.108	0.008	0.095	0.126	0.025	.008
Botrychium (grape-fern)	0.005	0.004	0.281	0.033	0.035	0.000	0.000	.0003
Bryales (Mosses)	0.179	0.013	0.286	0.085	0.000	0.000	0.000	<0.0001
Equisetum (Horsetail)	0.082	0.057	0.004	0.015	0.009	0.006	0.001	.001
Lycopodium (Clubmosses)	0.070	0.041	0.015	0.049	0.000	0.005	0.000	.0001
Polypodiaceae (Polypody family)	0.169	0.065	0.419	0.169	0.007	0.015	0.055	.0001
Selaginella selaguinoides (mountain moss)	0.031	0.042	0.015	0.034	0.000	0.050	0.000	.68
Sphagnum (sphagnum moss)	0.081	0.042	0.397	0.031	0.008	0.001	0.000	<0.0001

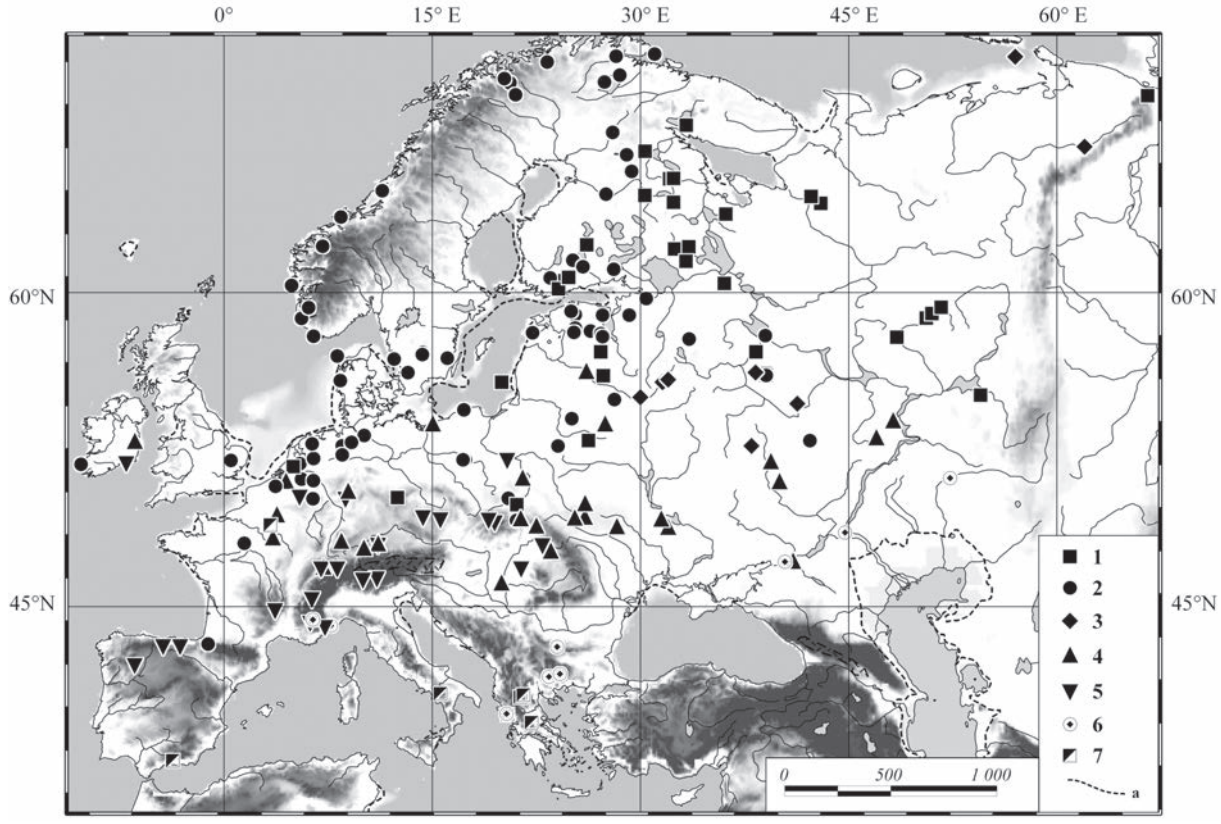

Fig. 5.48. *The geographical distribution of early Holocene pollen localities belonging to the different clusters; a – coastline*

Figure 5.46 illustrates the geographical distribution of the analysed sections and their division into the described seven groups or clusters.

Sections with pollen assemblages attributed to clusters 1 and 2 are located in the northernmost regions of Europe (north of 59°N in Eastern Europe and north of 50°N in Western Europe). Sections with pollen assemblages belonging to cluster 2 are mostly confined to northeastern regions. Sections attributed to cluster 3 are concentrated east of 30°E and north of 53°N. Sections of cluster 5 are found in mid-latitudes of Western Europe (between 42° and 52°N), those of cluster 4 in Central Europe between 46° and 56°N. Pollen assemblages of clusters 6 and 7 occur in southern regions (south of 51°N).

The geographical distribution of the identified clusters suggests a certain latitudinal zonation in vegetation during the early Holocene. Besides, the palaeo-phytocoenoses of Western Europe were somewhat different from those of Eastern Europe; the boundary between the two groups lay approximately at 23°E.

In addition we used some data on tree species from the palynological database developed by Kozharinov (1994); the data are from 1217 samples taken from 229 sections on the Russian Plain (Fig. 5.47).

Mathematical analysis of the pollen database of Kozharinov permits to group the data on the Preboreal-Boreal interval into 6 clusters, which differ in the proportion of tree species in the pollen assemblages (Table 5.12). So, *Picea* and *Betula* are dominant in the AP in cluster 1, *Pinus* and *Betula* in cluster 2; the assemblages of cluster 3 are distinct for a noticeable proportion of *Picea* and *Betula* along with *Ulmus*, *Tilia*, and *Corylus*. *Pinus* is dominant in clusters 4, 5 and 6; cluster 5, however, is noted for a high content of *Ulmus*, *Tilia* and *Corylus* pollen, while cluster 6 is characterized by a high quantity of *Quercus*, *Carpinus*, *Fagus* and *Corylus* values.

The geographical distribution of early Holocene pollen localities belonging to different clusters (based on Kozarinov's database) permits to specify the main species specific for the forest coenoses on the Russian Plain (Fig. 5.47). The total composition of pollen assemblages and the spatial distribution of indicator taxa show tundra and forest-tundra plant communities to be more common in the Early Holocene than at present; they were dominant north of 53°N in Western Europe and north of 61°N in Eastern Europe. The boundary between forest-tundra and taiga was 2° farther north in comparison with the Bølling-Allerød interstadial warming.

In those latitudes, high concentrations of pollen and spores have been recorded of *Sphagnum*, *Betula* sect. *Nanae*, *Salix*, *Populus*, *Alnus*, *Larix*, Ericaceae, *Hippophae rhamnoides*, *Rumex*, Saxifragaceae, Rosaceae, *Selaginella selaginoides*, *Lycopodium*, and *Equisetum* (Figs. 5.48–5.51). The proportion of tundra and forest-tundra coenoses drops noticeably further south; in fact, they occur only in the mountains of Central and Southern Europe.

Table 5.12

Plant taxa occurrence in the different clusters (according to Kozarinov's database)

Taxa	Clusters						
	1	2	3	4	5	6	P
Picea (Spruce)	**0.11**	**0.08**	0.04	0.04	0.04	0.04	.0332
Pinus (Pine)	0.04	0.20	**0.41**	**0.53**	**0.59**	**0.49**	<0.0001
Acer (Maple)	0.00	0.00	0.00	0.01	0.04	0.19	.0008
Alnus (Alder)	0.00	0.06	0.09	0.07	**0.12**	**0.15**	<0.0001
Betula (Birch)	**0.55**	**0.49**	**0.48**	0.16	0.12	0.08	<0.0001
Carpinus (Hornbeam)	0.00	0.00	0.00	0.00	0.04	**0.32**	<0.0001
Corylus (Filbert)	0.00	0.02	**0.08**	0.03	**0.11**	**0.11**	<0.0001
Fagus (Beech)	0.00	0.00	0.00	0.04	0.02	**0.44**	<0.0001
Fraxinus (Ash)	0.00	0.00	0.02	0.00	0.01	0.00	.34
Quercus (Oak)	0.00	0.01	0.07	0.01	**0.10**	**0.25**	<0.0001
Tilia (Linden)	0.00	0.02	**0.21**	0.03	**0.18**	0.07	<0.0001
Ulmus (Elm)	0.00	0.03	**0.24**	0.01	**0.13**	0.02	<0.0001

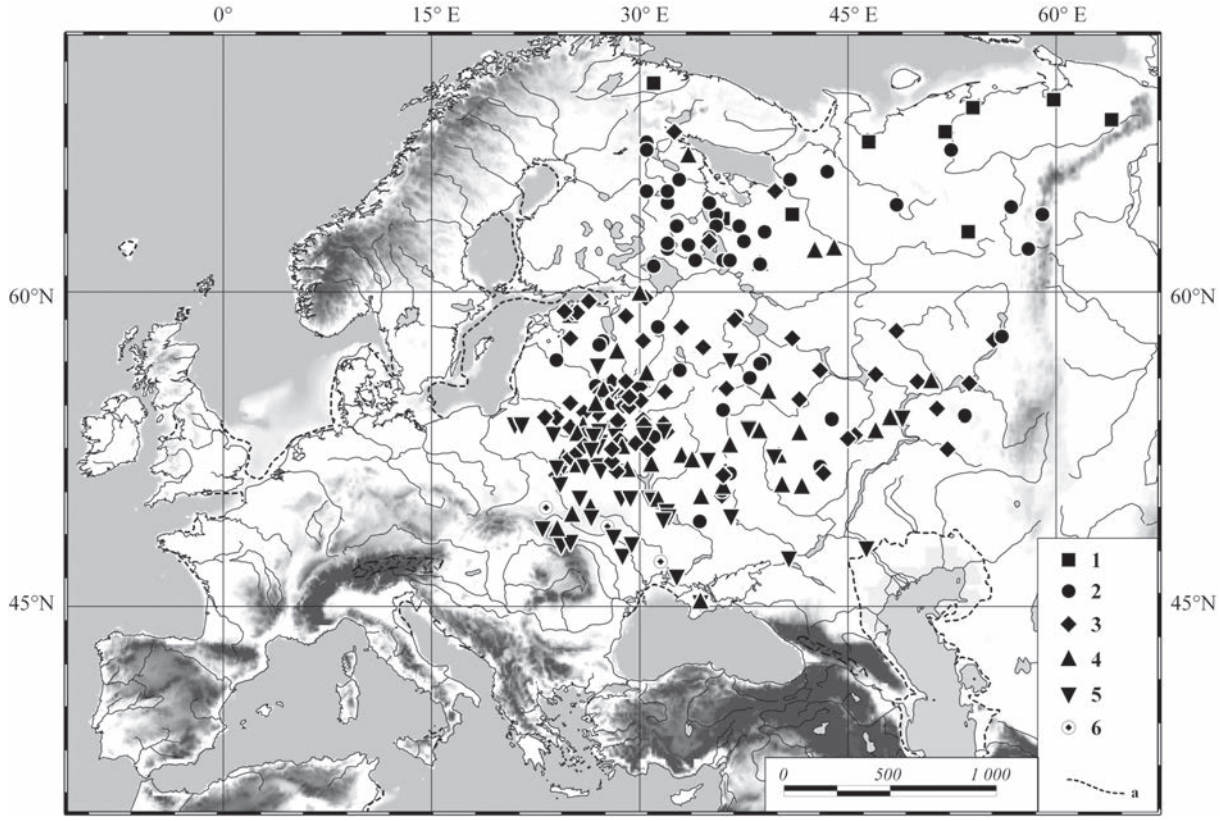

Fig. 5.49. *Geographical distribution of Early Holocene pollen localities belonging to different clusters (Kozarinov's database)(1–6); a – coastline*

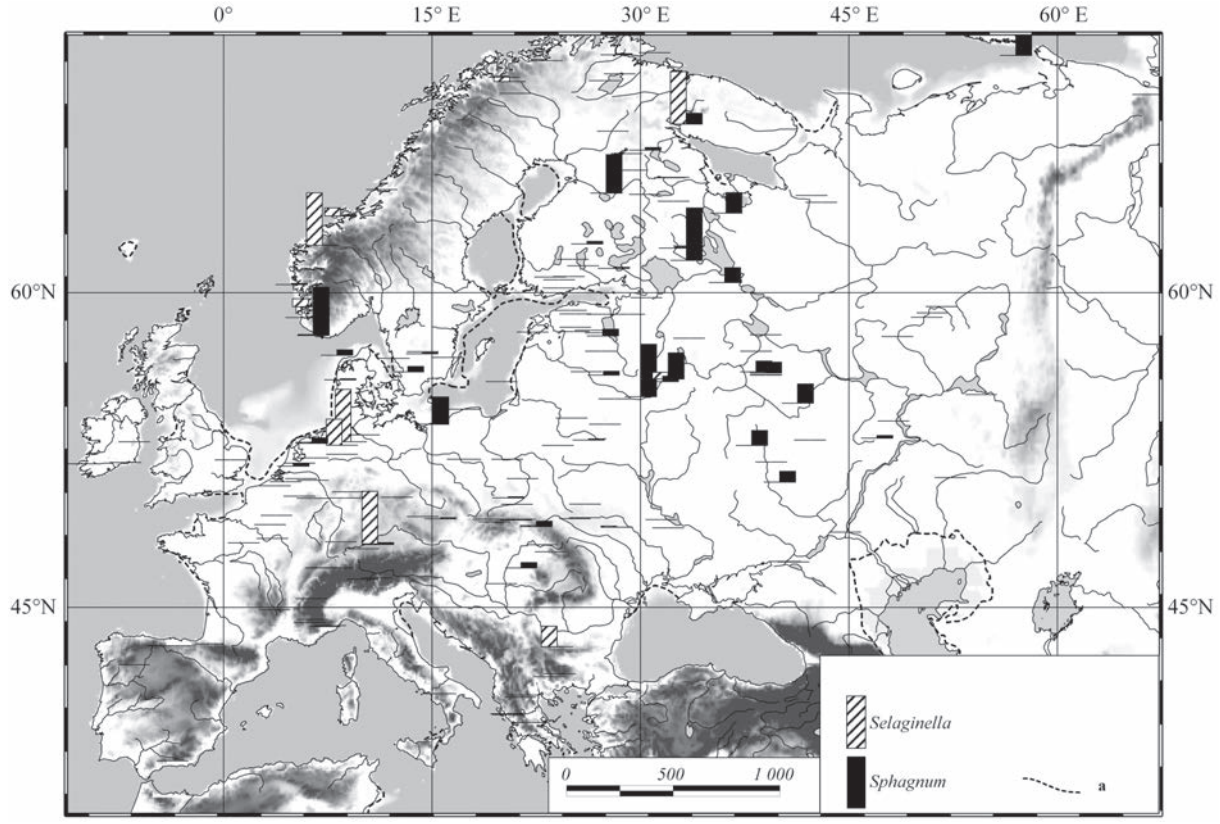

Fig. 5.50. *Selaginella and Sphagnum from Early Holocene localities; a – coastline*

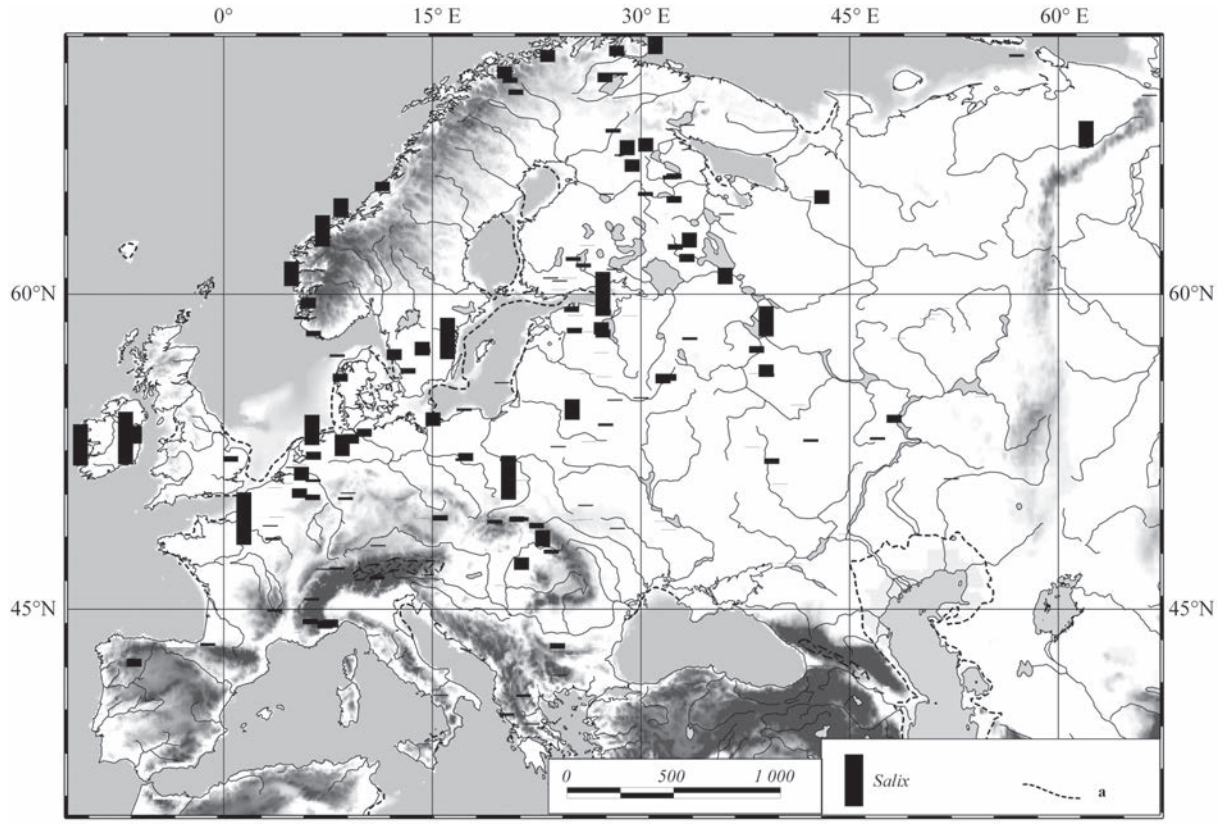

Fig. 5.51. *Salix from the Early Holocene localities; a – coastline*

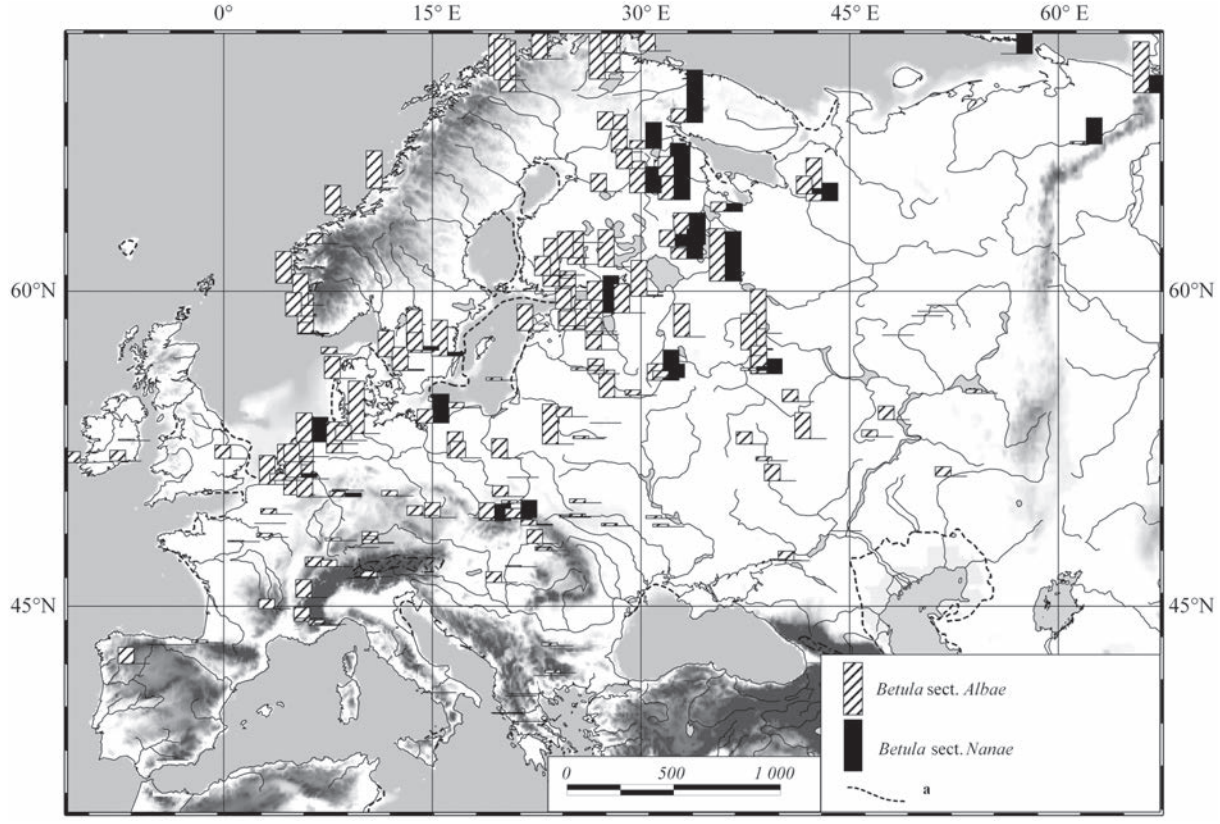

Fig. 5.52. *Betula sect. Albae and Betula sect. Nanae from the Early Holocene localities; a – coastline*

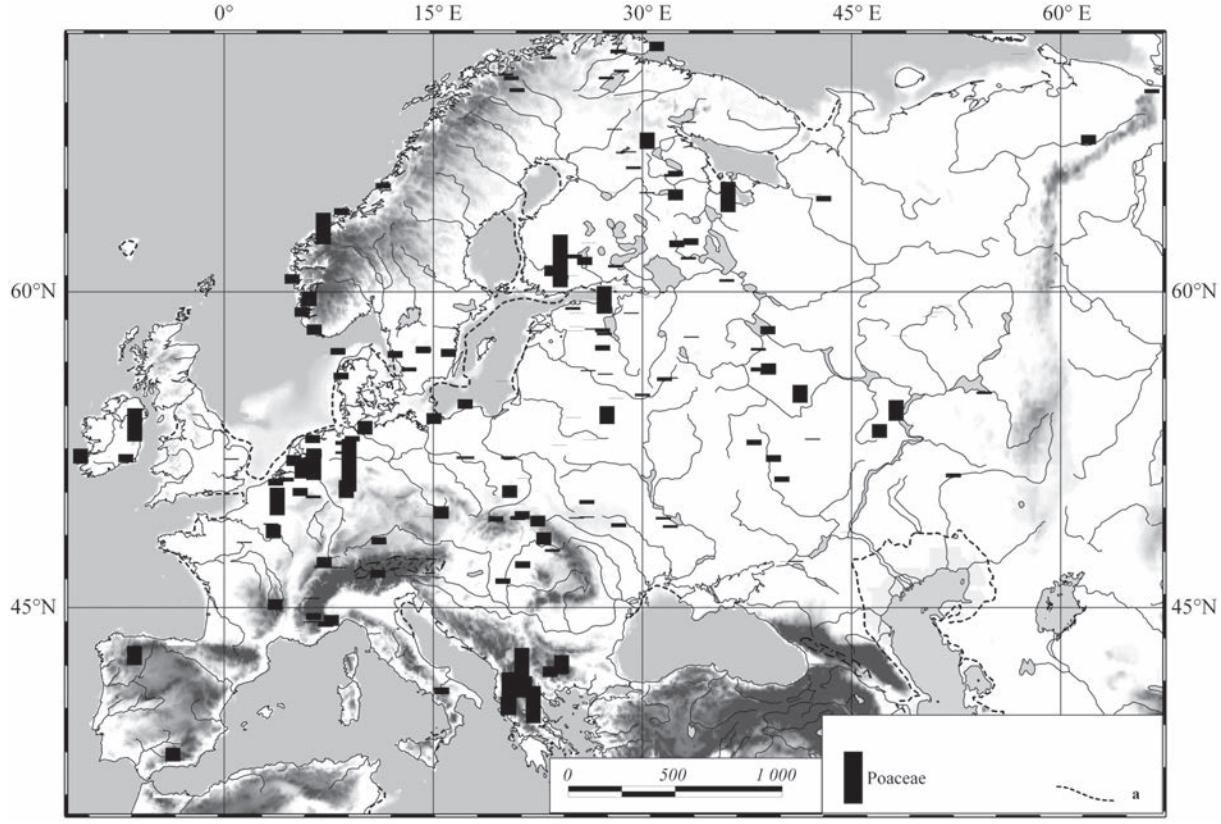

Fig. 5.53. *Poaceae from the Early Holocene localities; a – coastline*

Pollen of *Hellianthemum*, Brassicaceae, Poaceae, Cyperaceae, and *Thalictrum* is found in sizeable amounts in sections located in the north of Europe and in the Mediterranean regions.

Typical representatives of steppe phytocoenoses, such as *Artemisia*, Chenopodiaceae and *Ephedra* reduced their area at the beginning of the Holocene, though they still widely occurred in Europe. *Ephedra* pollen occur mostly in assemblages from sections located south of 50°N. Occasionally it is found in the northeast of the Russian Plain, as well as in the west of the Russian Plain at latitude 56°N (Fig. 5.52). Maximum concentrations of Chenopodiaceae and *Artemisia* pollen are found in sections in central and southern regions of Eastern Europe (south of 53°N), and in the Balkan region. Asteraceae and *Cichorium*, as well as *Helianthemum* pollen have been found in sections all over central and southern regions of Europe except for the Iberian Peninsula; *Plantago*, Rubiaceae, and *Rumex* are restricted to Western Europe (Figs. 5.53, 5.54). Ranunculaceae and Caryophyllaceae occur in considerable amounts in northern and central regions of the Russian Plain, in the Balkan region, and in the south of France and Ireland.

As follows from the analyses above, phytocoenoses of open landscapes were confined to northern and southern regions of Europe. Steppe plant communities were dominant south of 51°N. At the beginning of the Holocene, when the forest zone developed, small areas favourable to steppe communities still existed in the north of Europe; tundra-steppe vegetation, which had been wide-spread during the second half of the last glacial epoch, persisted in the northeast of the Russian Plain.

The total composition of pollen assemblages indicates forest coenoses to be prevalent in Central Europe and in the mountains (the Apennine Peninsula, the Alps, the Carpathians, the Crimea, and the Balkans). The plains of Western Europe, as well as the south and southeast of the Russian Plain, were distinguishable for dominance of boreal forest, forest-steppe and steppe palaeo-phytocoenoses. *Pinus* and *Betula* were the principal forest-forming taxa in Europe north of 43°N (Figs. 5.52 and 5.55).

In the northeast of the Russian Plain and in the Mediterranean regions, the proportion of pine was noticeably reduced. Maximum concentrations of birch pollen are found in sections north of 50°N in Western Europe and north of 56°N in Eastern Europe.

Picea pollen is mostly found in the northern and northeastern regions of the Russian Plain (north of 55–56°N). Spruce was a subdominant component of forest palaeo-phytocoenoses in Central Europe north of 49°N and west of 12°E, as well as in the Alpine-Carpathian mountain region. In Western Europe, in the Mediterranean,

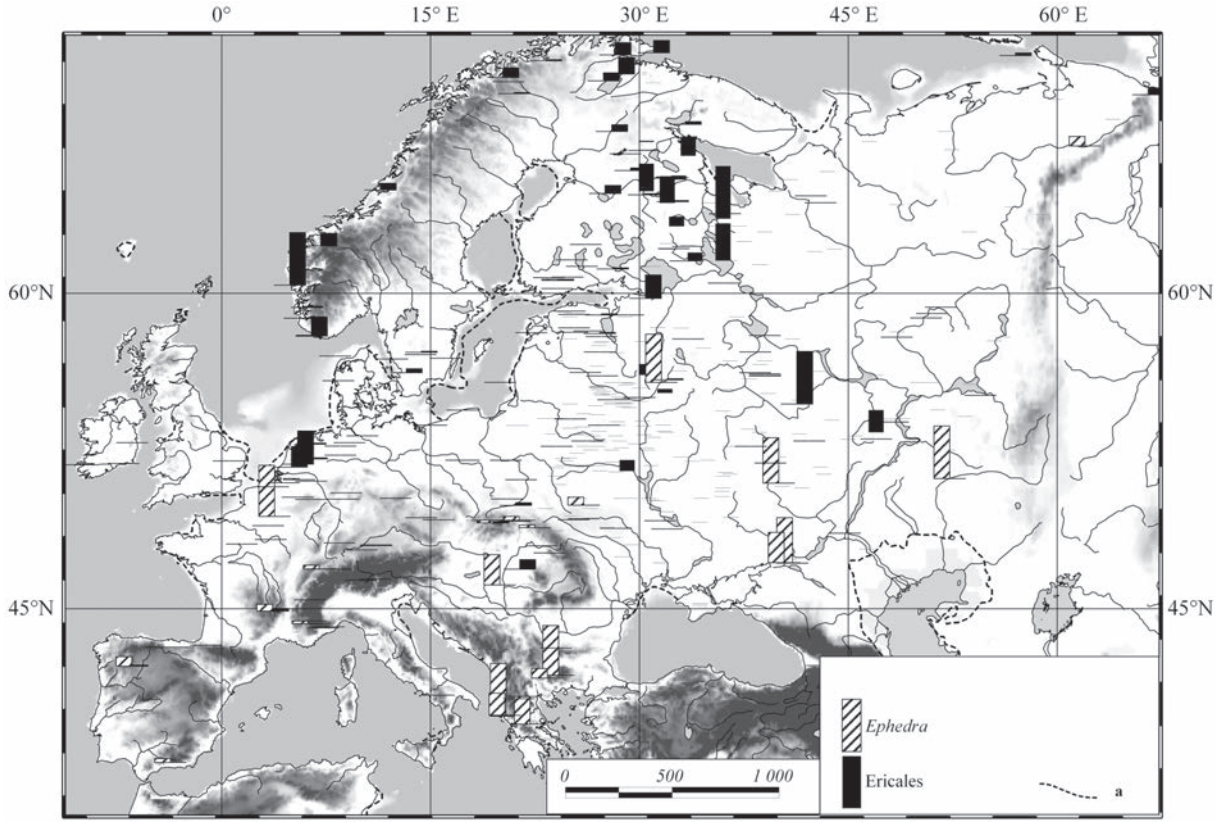

Fig. 5.54. *Ephedra and Ericales from the Early Holocene localities; a – coastline*

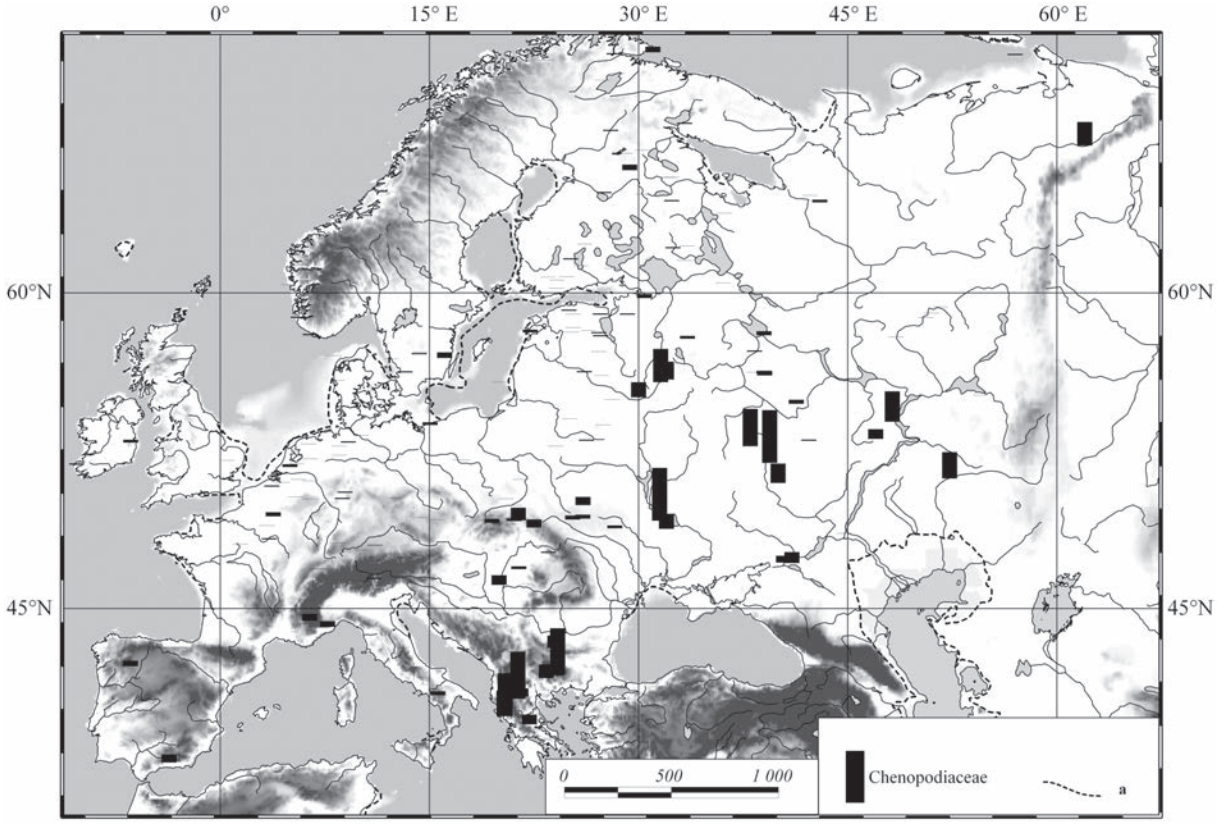

Fig. 5.55. *Chenopodiaceae from the Early Holocene localities; a – coastline*

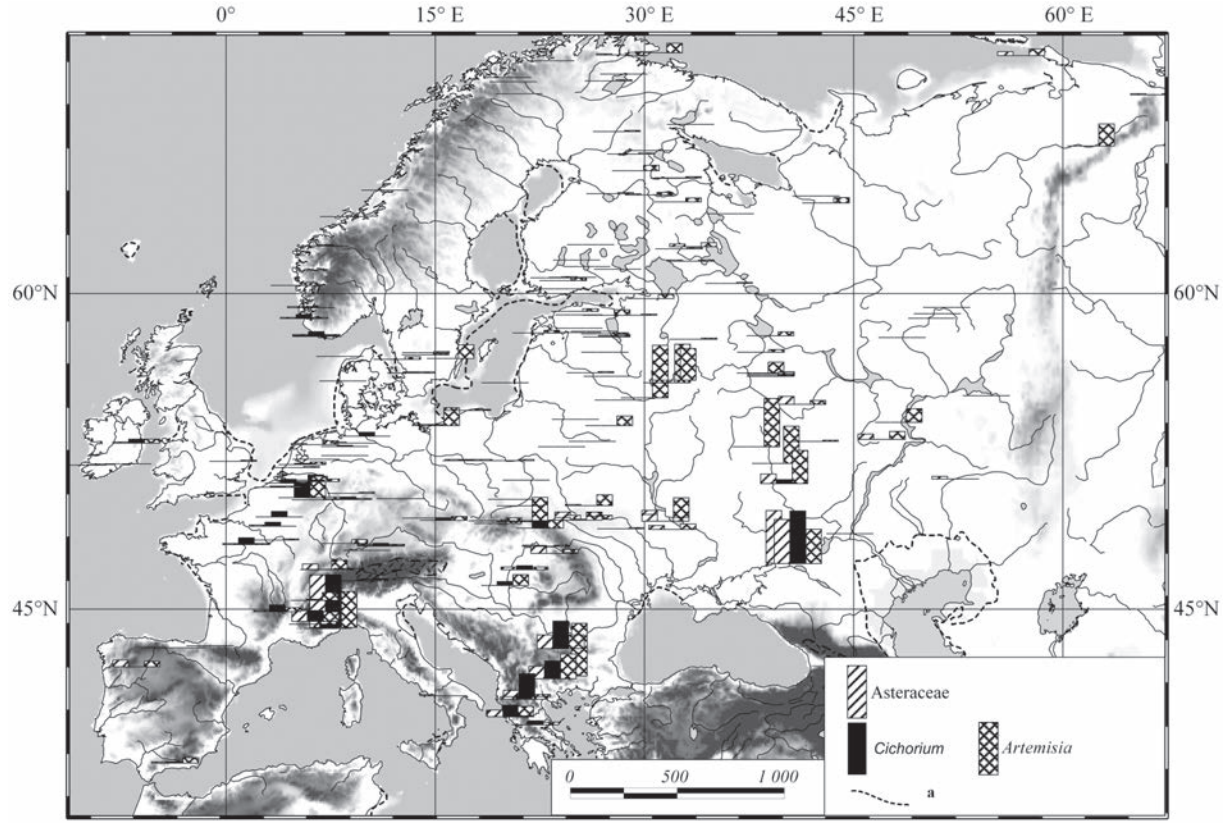

Fig. 5.56. *Asteraceae, Cichorium and Artemisia from the Early Holocene localities; a – coastline*

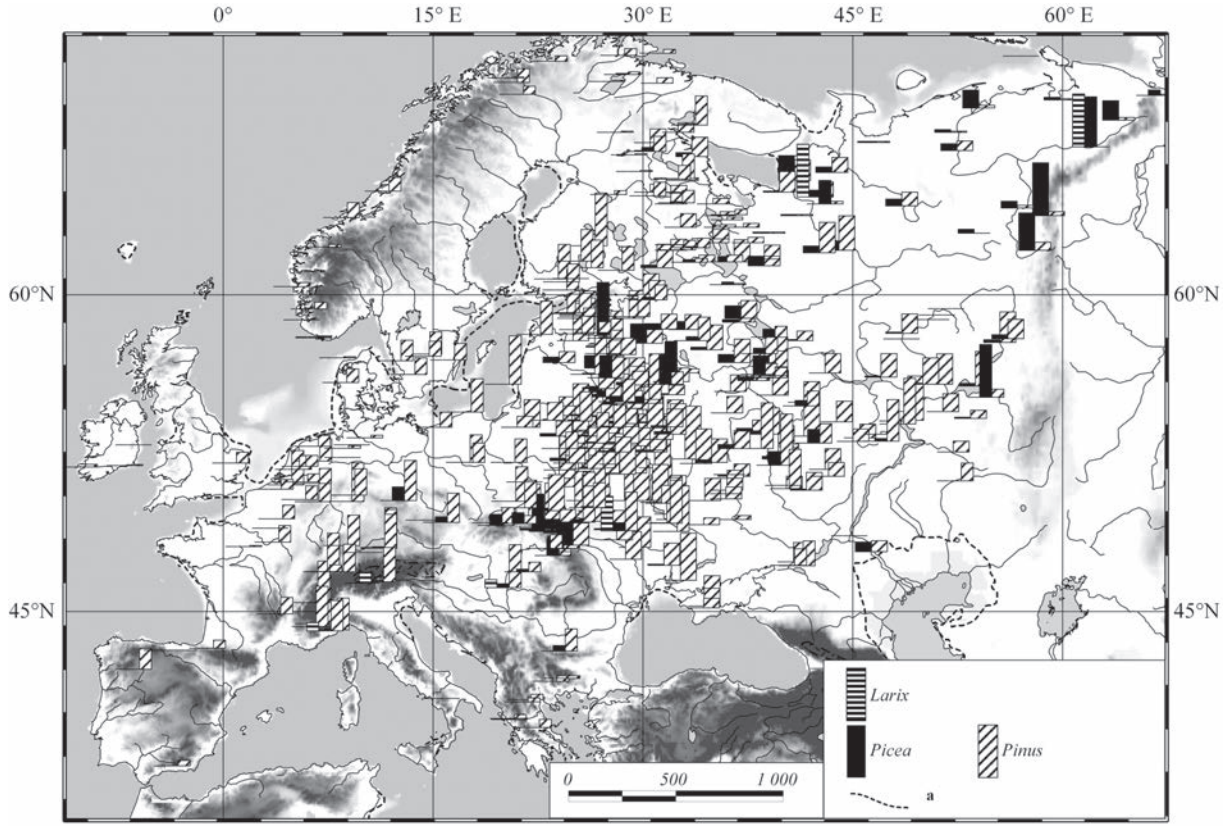

Fig. 5.57. *Larix, Picea and Pinus from the Early Holocene localities; a – coastline*

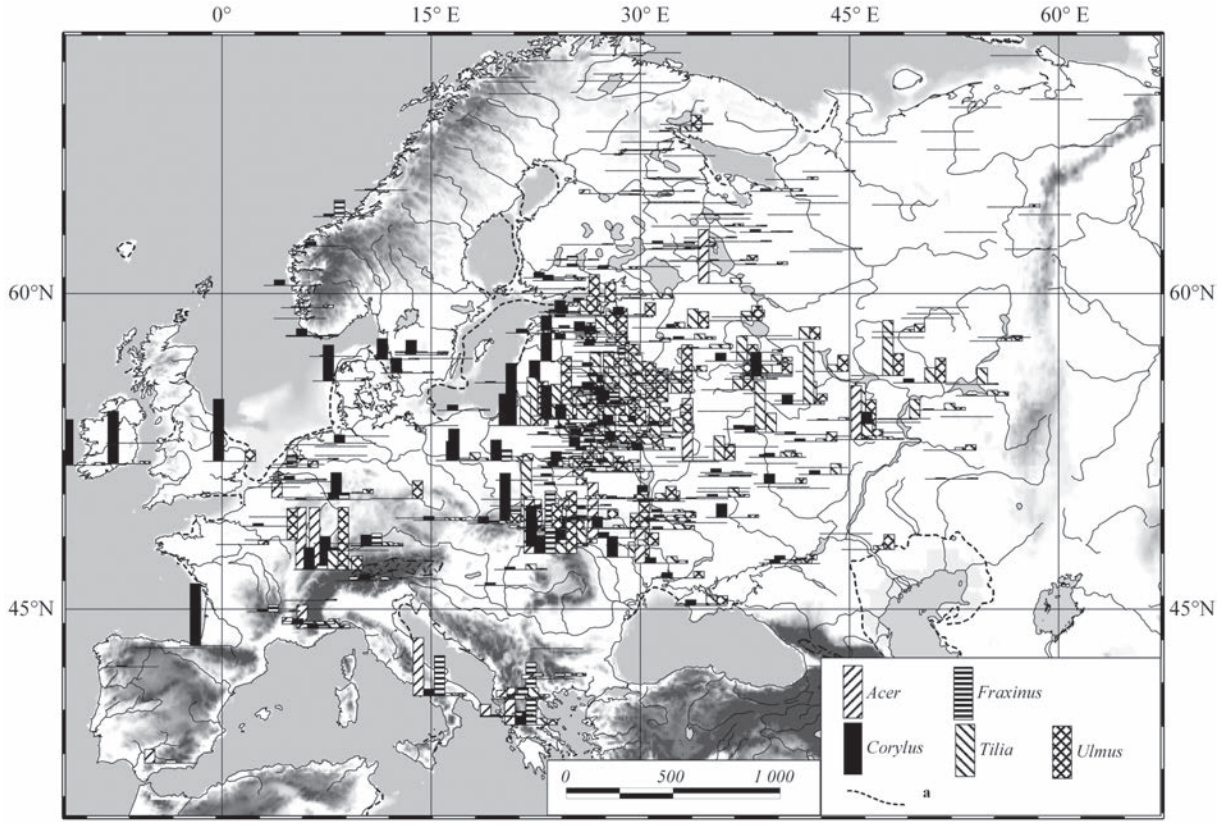

Fig. 5.58. *Acer, Corylus, Fraxinus, Tilia and Ulmus from the Early Holocene localities; a – coastline*

and in the south of the Russian Plain its pollen is practically absent from the Early Holocene sediments. *Abies* has been found in the Alps, Carpathians, and Balkans, on the Apennine Peninsula, in the southeast of France and in the Uralian forelands.

During the Preboreal-Boreal, broad-leaved flora began to spread all over the European territory (Fig. 5.56). Maximum amounts of broad-leaved species in pollen assemblages are recorded between 47° and 60°N. Compared to the last interstadial warming (Bølling-Allerød), the northern limit of broad-leaved trees shifted northward by at least 350 km. South of 53°N, arboreal constituents included *Acer*, *Carpinus*, and *Fagus*. *Carpinus* is found in pollen assemblages of Central Europe, the western Black Sea region, the Crimea, the Apennines and Balkans. *Fagus* pollen occurs in the middle reaches of the Don River, the upper Dnieper, in the western Black Sea region, in the Carpathians and their forelands, in the Apennines and Balkans.

In the north of Europe (in Scandinavia and in the northwest of the Russian Plain) pollen of *Fraxinus*, *Tilia*, *Ulmus*, and *Corylus* is found occasionally (Fig. 5.56). The amount of broad-leaved species is considerably reduced in pollen assemblages of the western Russian Plain, only *Corylus*, *Tilia*, and *Acer* being found there. Pollen of such broad-leaved species as *Tilia, Quercus*, and *Ulmus* is most abundant in sections located between 52° and 58°N on the Russian Plain.

The Early Holocene pollen assemblages recovered from sections of the Iberian Peninsula are dominated by *Quercus* pollen, with occasional pollen of *Fraxinus* and *Corylus.* The eastern Mediterranean pollen assemblages typically contain *Fraxinus*, *Fagus*, and *Carpinus*, as well as smaller amounts of *Tilia*, *Ulmus* and *Corylus.* Among components of forest and forest steppe communities there were such taxa as *Phillyrea*, *Pistacia*, *Castanea*, *Myrica*, *Cedrus*, *Ostrya*, *Taxus*, *Olea* and others.

Qualitative and quantitative analyses of palynological materials permitted to identify the following eight principal provinces (and their varieties), which existed in Europe during the Early Holocene (Fig. 5.59).

In the north of Europe (in Scandinavia and in the northwest of the Russian Plain) pollen of *Fraxinus*, *Tilia*, *Ulmus*, and *Corylus* is found occasionally (Fig. 5.56). The amount of broad-leaved species is considerably reduced in pollen assemblages of the western Russian Plain, only *Corylus*, *Tilia*, and *Acer* being found there. Pollen of such broad-leaved species as *Tilia, Quercus*, and *Ulmus* is most abundant in sections located between 52° and 58°N on the Russian Plain.

The Early Holocene pollen assemblages recovered from sections of the Iberian Peninsula are dominated by

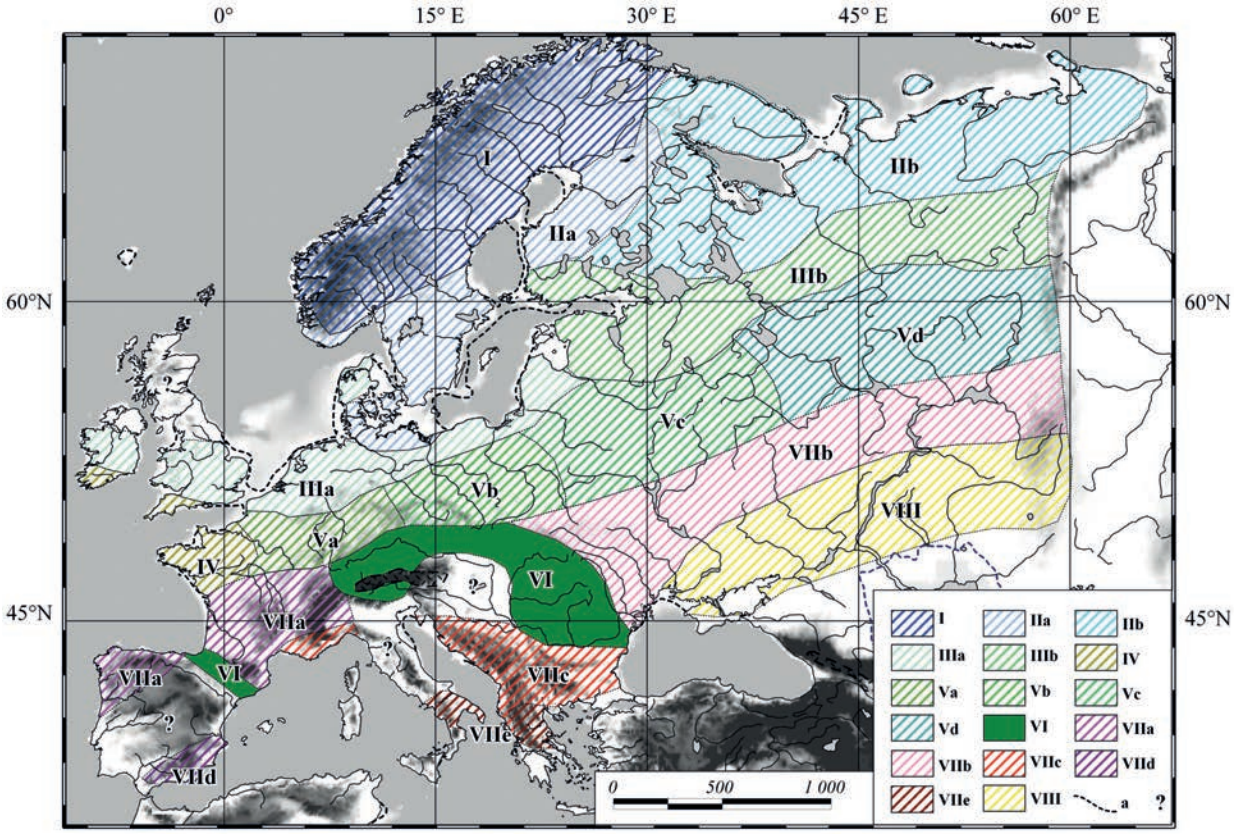

Fig. 5.59. *Palaeovegetation during the Early Holocene: I – Shrub tundra; IIa – Pine and birch boreal forests in combination with tundra communities; IIb – Combination of pine and birch forests (with spruce) with tundra-steppe communities; IIIa – Pine and birch forests with some tundra phytocoenoses; IIIb – Pine and birch forests with admixture of spruce and some tundra plant communities; IV – Small-leaved forests; Va – Forest of pine with broad-leaved species; Vb – Forests of pine and small-leaved species, with some broad-leaved species; Vc – Forests of pine, spruce and birch, with broad-leaved species, locally with forest-steppe phytocoenoses; Vd – Forests of pine, spruce and birch, with broad-leaved species and small patches of tundra-steppe plant communities; VI – Coniferous-broad-leaved forests of mountain regions; VIIa – Oak and pine forests in combination with grass and herb steppes; VIIb – Pine-broad-leaved forests in combination with grass-herb steppes; VIIc – Pine-broad-leaved forests in combination with herb steppes and with steppes of Artemisia and Chenopodiaceae; VIId – Forests of oak and other broad-leaved species in combination with grass-herb steppes; VIIe – Forests of spruce and broad-leaved species in combination with grass steppes; VIII – Steppe. a – coastline, ? – absence of data*

Quercus pollen, with occasional pollen of *Fraxinus* and *Corylus.* The eastern Mediterranean pollen assemblages typically contain *Fraxinus*, *Fagus*, and *Carpinus*, as well as smaller amounts of *Tilia*, *Ulmus* and *Corylus.* Among components of forest and forest steppe communities there were such taxa as *Phillyrea*, *Pistacia*, *Castanea*, *Myrica*, *Cedrus*, *Ostrya*, *Taxus*, *Olea* and others.

Qualitative and quantitative analyses of palynological materials permitted to identify the following eight principal provinces (and their varieties), which existed in Europe during the Early Holocene (Fig. 5.59).

I. Shrub tundra

With *Salix*, *Betula nana*, *Ericales*, *Lycopodium*, *Sphagnum*, and *Bryales*, and small patches of pine and birch open woodlands – the Scandinavian Peninsula (north of 58°N) and the northern Russian Plain (north of 68°N).

II. Forest-tundra

A. Pine and birch boreal forests with *Populus*, *Juniperus*, and *Hippophae rhamnoides* in combination with tundra communities – northwest Europe (53–58°N) and the southern part of Scandinavia (61–67°N);

B. Combination of pine and birch forests (with spruce) with tundra-steppe plant communities – Eastern Europe (61–64°N to 68°N).

III. Open forests of pine and birch

A. Pine and birch forests with some tundra phytocoenoses – Western Europe (51–53°N);

B. Pine and birch forests with an admixture of spruce and some tundra plant communities (clusters 1, 2, and 3) – Central Europe and Eastern Europe (59° to 66°N and east of 25°E).

IV. Small-leaved forests

With *Salix*, *Alnus*, *Betula*, and *Populus* – Western Europe and the southern part of the British Isles (Ireland and Great Britain, 46–52°N and west of 2°E).

V. Coniferous-broad-leaved forests

A. Forest of pine with broad-leaved species (*Ulmus*, *Fraxinus*, and *Corylus*) – Western Europe (48–51°N, 2–12°E);

B. Forests of pine and small-leaved species, with some broad-leaved species (*Quercus*, *Ulmus*, *Tilia*, *Corylus*, *Alnus*, and *Populus*) – Central Europe (50–52°N; 12–21°E);

C. Forests of pine, spruce and birch, with broad-leaved species (*Corylus*, *Tilia*, *Ulmus*, and smaller proportions of *Quercus* and *Fraxinus*), locally with forest-steppe phytocoenoses – western regions of the Russian Plain (54–57°N, 21–38°E);

D. Forests of pine, spruce and birch, with an insignificant admixture of broad-leaved species – *Tilia*, *Corylus*, and *Ulmus*, and small patches of tundra-steppe plant communities – eastern Russian Plain, between 55° and 59°N, west of 38°E).

VI. Coniferous-broad-leaved forests of mountain regions

The Alps and Carpathians (*Carpinus*, *Corylus*, *Quercus*, *Fagus*, *Abies*, *Pinus*, and *Picea*); the Pyrenees (*Pinus*, *Quercus*, and *Corylus*); the Crimea (*Pinus*, *Ulmus*, *Corylus*, *Quercus*, and *Tilia*).

VII. Forest-steppe – combinations of meadow-steppe phytocoenoses

A. Oak and pine forests in combination with grass and herb steppes – Western Europe (42–45°N to 48°N);

B. Pine-broad-leaved forests with *Corylus*, *Quercus*, *Tilia*, and *Ulmus* in combination with grass-herb steppes and those of *Artemisia* and Chenopodiaceae – Eastern Europe (50–55°N) and locally southeast of the Russian Plain;

C. Pine-broad-leaved forests in combination with herb steppes and with steppes of *Artemisia* and Chenopodiaceae – southeast of Western Europe, the Balkan region;

D. Forests of oak and other broad-leaved species in combination with grass-herb steppes – south of the Pyrenees, the Iberian Peninsula;

E. Forests of spruce and broad-leaved species in combination with grass steppes – south of the Apennines and the Balkan region.

VIII. Steppe

Phytocoenoses of grass and *Artemisia* or *Artemisia* and Chenopodiaceae – southern regions of the Russian Plain (south of 50–51°N).

The performed analysis of the extensive palynological materials permitted to identify 8 prevailing provinces, which evolved in the Early Holocene (during the Preboreal–Boreal interval). Tundra elements were reduced in area at that time, while broad-leaved species were gaining in importance in forest phytocoenoses. It was during this period that the vegetation finally reached a zonal pattern on the European continent. Tundra and forest-tundra communities became dominant in Scandinavia and in the northernmost regions of Europe. South of this, a differentiated forest zone developed by the end of the Boreal, with forests of pine and birch prevailing in the north and pine-broad-leaved forests in mid-latitudes. Spruce forests were of secondary importance. Pine and birch were the main forest-forming taxa. In the coniferous-broad-leaved forest zone *Ulmus*, *Corylus* and *Tilia* were important in the north and *Quercus*, *Carpinus* and *Fagus* in the south. Forest-steppe was widely spread in the south of Western Europe and in the Mediterranean region. Steppes of Gramineae and *Artemisia* or of *Artemisia* and Chenopodiaceae occupied the south of the Russian Plain.

The position of the tundra zone was close to that of today, while the southern limit of forest-tundra was about 6° south of its modern position. In Eastern Europe forest-steppes occupied the territory of modern broad-leaved forests and forest-steppes. The northern limit of the former steppe zone coincided with that of the modern herb and bunchgrass steppe. Southern regions of Western Europe were dominated by forest-steppes (which occupied the place of modern broad-leaved forests).

The performed reconstructions of dominant plant assemblages suggest a drier and perhaps somewhat cooler climate in Europe during the Preboreal-Boreal interval compared to the present-day climate.

5.6. VEGETATION DYNAMICS DURING THE PLEISTOCENE–HOLOCENE TRANSITION (⩽24 – >8 KYR BP)

Alexandra Simakova

In Chapter 5 we analysed the palaeovegetation changes during the 5 time slices: Last Glacial Maximum, the Late Glacial Transition period, the Bølling–Allerød Interstadial complex, the Younger Dryas stadial, and the early Holocene. That permitted to reconstruct the evolution of the plant communites and the peculiarities of the geographical position of the vegetation zones over Europe during the end of Late Pleistocene – the beginning of the Holocene (24–8 kyr BP).

The Late Glacial Maximum (LGM) (⩾24 – ⩽17 kyr BP)

The character of the palaeocoenoses was first of all defined by the presence of the Scandinavian ice sheet, and the mountain glaciation in central and southern regions of Europe. During the LGM, the periglacial palaeovegetation was widespread in Europe. Periglacial tundras, periglacial forest-tundras and periglacial forest-steppes were the main types of landscapes.

Periglacial shrub tundra dominated in the territories adjacent to the ice sheet boundary (north of 51°N in Western Europe and north of 55–56°N in Eastern Europe) with *Betula, Alnus, Salix, Juniperus, Helianthemum, Armeria,* Brassicaceae, Poaceae, Cyperaceae, and *Sphagnum.* In Eastern Europe shrub tundra landscapes had a more mosaic structure, where tundra vegetative associations combined with small forest-tundra patches, steppe coenoses, and also pioneer plant groupings with *Alnus fruticosae, Pinus, Picea,* Ericales, Chenopodiaceae, and *Artemisia* were developed.

To the south (between 50–51°N in Western Europe, and between 51–56°N in Eastern Europe), the periglacial tundra-forest-steppes zone occurred, represented the combination of the light pine-birch forests, shrub tundra, meadow and steppe phytocoenoses. *Ephedra* and Chenopodiaceae dominated in plant associations on the east of Europe, and *Armeria* and *Empetrum* prevailed in Western Europe. The role of the forest components in the palaeolandscape structure decreased from west to east in Europe.

Further south in Western Europe (between 43° and 50°N) and on the Russian Plain (between 49° and 51°N), forest-steppe landscapes dominated. In Western Europe pine and pine-birch forest in combination with wormwood – grass and herb-grass associations developed widely. *Pinus, Betula, Hippophäe, Juniperus, Salix, Larix,* sometimes *Quercus* and *Ulmus* occupied the periglacial forest landscapes. On the Iberian Peninsula and in the north of the Apennine Peninsula xerophytic coniferous-broad-leaved forests with *Pinus, Picea, Abies, Corylus, Fagus, Quercus,* non-decidious *Quercus, Tilia, Buxus,* and *Olea* alternated with patches of meadow and steppe vegetation with Brassicaceae, Poaceae, *Ephedra* and *Artemisia*.

Forest-steppe landscapes of the Russian Plain included areas of pine-birch light forests herb steppes, meadow steppes and tundra-steppe vegetative communities with *Betula nana,* Poaceae, Chenopodiaceae, Asteraceae, and Plumbaginaceae. In the Danube Lowlands, coniferous-broad-leaved forest (*Abies, Pinus, Alnus, Carpinus, Quercus,* non-decidious *Quercus,* and *Fraxinus*) combined with grass-wormwood and wormwood – Goosefoot family steppe associations with Asteraceae, Campanulaceae, Rosaceae, and *Thalictrum*.

On the seaside territories of the Russian Plain (45–49°N) wormwood – Goosefoot family steppes developed widely, with participation of tundra species and semi-desert elements, rare with *Pinus, Betula, Alnus* and *Carpinus* along the river valleys.

The role of the representatives of steppe coenoses in the landscapes was more significant in Eastern Europe than in Western Europe as a result of a more continental climate during the glaciation. A typical steppe vegetation, reconstructed on the basis of palynological data occurred only in the south of the Russian Plain.

The coniferous forest with boreal elements such as *Quercus, Corylus, Ulmus, Tilia, Acer, Fraxinus,* and *Cornus* survived the cooling time in the Alps, the Carpathians, the Massif Central, the Crimea, the Apennines, in the mountain systems and the highlands of the southeast of the Iberian Peninsula and Balkan region.

Broad-leaved species took significant participation in the Mediterranean forest coenoses, especially in the south of the Apennine Peninsula. Here *Phillyrea, Olea, Quercus, Ulmus, Carpinus,* and *Buxus,* and some other

forest species survived the cooling. On landscapes of the plains, forest refugia were associated with the dissected territories such as the Moscow, Middle Russian, Donetsk, Neman, Privolgsk, and the south of the Podolsk highlands, and with the large river valleys.

During the LGM three vegetation provinces were distinguished in Europe: East European, West European, and Mediterranean. The distinctions between the reconstructed vegetation zones became smoothed.

The Late Glacial Transition period (LGT) (⩽17 – ⩾12.4 kyr BP)

During the second half of the last glaciation (LGT), the snow-line of the ice sheet receded, approximately by 350 km. The periglacial forest-tundra vegetation began to prevail in the glacial territories free from glacial cover and on the territories occupied by shrub tundra communities during the LGM.

In Western Europe (north of 51°N), the combination of the shrub tundra with dwarf birch, willow, and juniper and small patches of open pine-birch forests occurred. These palaeophytocoenoses included *Populus*, *Hippophae ramnoides*, Saxifragaceae, *Rumex*, *Thalictrum*, Rosaceae, *Dryas*, *Helianthemum*, *Armeria*, *Artemisia*, Caryophyllaceae, Cyperaceae, Plumbaginceae, Plantago, Lamiaceae, Umbelliferae, *Sphagnum*, Bryales, *Selaginella*, and *Huperzia selago.* In Eastern Europe (north of 55°N), shrub tundra intermingled with open pine-birch forest and tundra-steppe communities with *Alnus*, *Betula nana*, *Picea*, Ericales, *Artemisia*, *Ephedra*, Chenopodiaceae, *Selaginella* and *Sphagnum* are widespread.

To the south (53–56°N), the tundra-forest-steppe which existed on the Russian Plain during the LGM transformed into the forest-tundra-steppe – light pine-birch and pine- spruce forests, in combination with patches of tundra and meadow-steppe communities, including *Alnus*, *Betula nana*, *Artemisia*, Chenopodiaceae, Poaceae, *Ephedra*, *Selaginella* and *Botrichium*.

Further south, the periglacial forest-steppe was located in Eastern Europe (between 49° and 53°N) representing a combination of light pine-birch forests with herb and *Artemisia*-Chenopodiaceae steppes associations, and also meadow and tundra plant communities (*Alnus*, *Picea*, Fabaceae, Asteraceae, *Cichorium*, Dipsacaceae, *Selaginella*, *Sphagnum*, Polypodiaceae, *Quercus* and *Ulmus*. At the same time, in Western Europe between 49–50°N, light pine-birch forest alternated with shrub tundra and tundra-steppes associations including widespread *Salix*, *Juniperus*, *Thalictrum*, *Rumex*, *Helianthemum*, *Ephedra*, Poaceae, Umbelliferae, *Botrichium* and *Quercus*. To the south (between 43–49°N), pine forest with meadow and steppe coenoses dominated.

In the northern Black Sea and Sea of Azov coastal areas continued to prevail *Artemisia*-Chenopodiaceae steppe associations with participation of tundra elements. During the LGT, the participation of the arctic and northern taiga elements in the palaeolandscapes in Northern Europe and the steppe species in the south decreases compared to the LGM. The forest-tundra vegetation expanded their ranges to the north, where shrub tundra coenoses dominated earlier.

The taiga communities began to play a rather significant role in the structure of periglacial phytocoenoses. It penetrated along river valleys into the forest-tundra and forest-steppe zones. The participation of broad-leaved elements gradually increases in the mountain areas and in the lowland refugias. Broad-leaved species took significant participation in forest communities of the Mediterranean region where a general tendency in the increase of the steppe palaeovegetation in the southern areas of Europe can be observed.

During the LGT, the northern forest-steppe zone boundary on the Russian Plain shifted approximately 250–300 km and the northern steppe boundary 50 km northward, basically due to the reduction of tundra elements in the palaeolandscape structure. In Western Europe, the reorganization of the periglacial forest-steppe which existed during the LGM was expressed in an increase of forest assemblages in palaeolandscapes. The Mediterranean palaeovegetation had a more steppic character than in the LGM. Distinctions between vegetation provinces become more clear, though still smoothed. Towards the end of the LGT, the differentiation of the vegetation into the three plant regions, namely East European, West European, and Mediterranean, continued to exist.

The Bølling/Allerød Interstadial complex (BAIC) (<12 – ⩾10,9 kyr BP)

During the BAIC a further reduction of the glacial cover occurred on the Scandinavian Peninsula.

In the ice sheet free areas, vegetation appeared, forming periglacial shrub tundra coenoses. In Northern Europe and in northern Great Britain (north of 55–60°N) mainly shrub tundra became widespread, including *Betula nana*, *Salix*, Ericales, *Hippophae rhmnoides*, *Juniperus*, *Rubus*, *Helianthemum*, *Armeria*, *Sphagnum*, *Selaginella*, and *Lycopodium*. Small patches of light pine-birch forests are reconstructed in the southern areas of the Scandinavian Peninsula.

A specific periglacial forest-tundra-steppe was formed on the territory where forest-tundra coenoses existed during the LGT, north of 49–51°N in Western Europe and between 59–62° and 60–63°N in Eastern Europe.

At these latitudes mosaic biocoenoses – the combination of pine-birch forest shrub tundra with *Betula nana*, *Populus*, *Salix*, *Sangiusorba*, *Vassinium*, *Rumex*, and *Rubus*, and tundra-steppe plant associations including *Ephedra*, *Armeria*, Saxifragaceae, Rosaceae, Onograceae, *Lycopodium*, *Huperzia selago* and *Selaginella* were widespread.

To the south the periglacial open pine-birch forests with patches of steppe and tundra communities replaced the periglacial forest-tundra-steppe landscape of the LGT. In Western Europe, between 47° and 49°N and to the west of 15°E, birch forests with tundra-steppe elements occurred. In Central Europe (between 50° and 52°N and between 15° and 21°E) and in the Middle Danube Lowlands pine-birch forest widespread. Open pine-birch forest with tundra and steppe vegetation association dominated on the Russian Plain between 60° and 62°N. Spruce forest occurred in the coniferous forest coenoses of Eastern Europe between 53–60°N. Pine-birch and spruce forest with small proportion of boreal elements such as *Ulmus*, *Tilia*, *Quercus* and *Corylus* in a combination with steppes with *Stipa* and *Festuca* and shrub tundra are reconstructed in the western and central regions of the Russian Plain (50–53°N).

Further south, periglacial forest-steppe vegetation continued to dominate in Europe. On the Russian Plain between 47° and 50°N (in the eastern part of the Russian Plain between 51° and 58°N), forest-steppe landscapes represented the combination of herb steppes, tundra associations and 'islands' of pine-birch forests with widespread *Larix*, *Quercus*, *Tilia*, *Artemisia*, *Centaurea*, *Armeria*, *Cichorium*, Poaceae, *Sphagnum*, *Selaginella* and *Huperzia selago*. In Western Europe (44–49°N), pine forest with broad-leaved species (*Quercus*, *Corylus*, and *Ulmus*) and herb-grass steppes occurred.

Steppe phytocoenoses dominated in the south and the southeast of the Russian Plain. The *Artemisia*-Chenopodiaceae steppes of the LGT were replaced by herb-grass steppes with Boraginaceae, Asteraceae, *Cichorium*, Poaceae, Papaveraceae, and *Scabiosa*. In the river valleys were thickets of willow, birches, pines, alder, and sallow-thorn.

Coniferous-broad-leaved and pine-birch forest with broad-leaved elements were characteristic of the mountain regions of the Alps, the Massif Central, the Jura, the Carpathians, the Crimea, the Balkans, the Pyrenees, the Caucasus, etc. with *Pinus*, *Larix*, *Picea*, *Abies*, *Betula*, *Fagus*, *Juniperus*, *Quercus*, *Ulmus*, *Tilia*, *Corylus* and *Larix* participation.

The BAIC warming in the Mediterranean region was expressed by the increase of a forest coenoses in the palaeolandscape structure represented by the coniferous broad-leaved forest, sclerophyllous shrubs and xerophytic herb communities. A xerophytic broad-leaved forest with *Taxus*, *Olea*, *Ostrya*, *Tilia*, *Quercus*, *Fagus*, *Fraxinus*, *Acer*, *Ulmus*, and *Abies* dominated on the Apennine Peninsula**.** The combination of xerophytic forests with *Quercus*, *Fraxinus*, *Myrica* and sagebrush-herb steppes was widespread on the Iberian Peninisula.

In the Balkan region, forest with *Abies*, *Tilia*, *Carpinus*, *Pistacia*, *Myrica*, *Castenea*, *Ilex*, *Fraxinus*, *Acer*, *Ulmus*, and *Quercus* participation and sagebrush-grass steppes associations occurred.

Thus, during the BAIC in Europe forest phytocoenoses expanded their ranges noticeably. In the central regions of the Russian Plain spruce forest was important in the palaeovegetation. Tundra and steppe communities still existed in the periglacial flora. Hypoarctic elements were reduced in their ranges and occurred in the north of Europe and in the mountains. The steppe communities were reduced in Western Europe, in the Mediterranean regions and in the centre of Eastern Europe.

Broad-leaved species participated in the periglacial forests in the south of Western Europe, in Central Europe (forelands and middle mountains) and in the centre of the Russian Plain. In the Mediterranean regions, broad-leaved species occurred in the xerophytic forests of the Apennine Peninsula and were present in forest-steppe communities on the Iberian Peninsula and in the Balkan region. The spatial distribution of palaeophytocoenoses suggests a periglacial zonality of interstadial character in the vegetation.

The Younger Dryas Stadial (YD) (⩾10.2 ~ ⩽10.9 kyr BP)

The short Younger Dryas Stadial cooling resulted in the changes in the vegetation cover of the European continent.

Tundra with subarctic meadow formation, influenced by the Atlantic Ocean, occurred widespread in the north of Great Britain and in Ireland, and also on the northwest coast of the Scandinavian Peninsula. The dwarf shrub tundra phytocoenoses with *Juniperus* and *Betula* occurred in the south of Ireland and almost all over France. Earlier (during the BAIC) periglacial birch forests coverd these territories.

During the DR3 in Western Europe, the tundra-forest-steppes (the combination of shrub tundra with 'islands' of pine-birch light forests) replaced the forest-tundra-steppe of the BAIC and were distributed in the highlands of Great Britain, and also became widely present in the south of the Scandinavian Peninsula and in the seaside lowlands of Central Europe.

Further south (between 45–49°N) the pine forest intermingled with meadow and wormwood-herb steppe dominated communities. The amount of broad-leaved elements in forest assemblages noticeably increased in pollen spectra only in the western Mediterranean.

On the Russian Plain north of 62°N, shrub tundra with patches of tundra-steppe communities and larch-birch open woodlands, and pine-spruce riverine forests occurred. Forest-tundra – the combination of pine-birch forest with tundra, meadow-steppe and pioneer plant communities – dominated between 58° and 63°N. To the south up to 53°N open pine-birch forests were widespread. On the western Russian Plain and in Central Europe (to the east of the River Oder) open pine-birch forest with insignificant participation of spruce and broad-leaved species occurred. Forest-steppe extended toward the south and was transformed into steppe in the Black Sea and Azov Sea coasts and in the east of the Russian Plain (along the Kama River).

In the Middle Danube Lowlands and in the south of the Balkan region the vegetation of steppe type was also widespread. Palaeophytocoenoses of meadow, grass-herb, and *Artemisia*-Chenopodiaceae steppes with patches of mixed forest with *Betula*, *Pinus*, *Corylus*, *Quercus*, *Tilia* and *Fraxinus* occurred here.

The BAIC forest-steppes of the plain territories of Albania and Yugoslavia were replaced by steppe coenoses during the DR3. The dominating landscape of the Iberian Peninsula remained the forest-steppes. The forests of Italy and Greece have a more xerophytic character due to the expansion of steppe vegetation.

Thus, during the DR3 Stadial cooling the differentiation of the vegetation cover in Western Europe, Eastern Europe, and the Mediterranean was again obvious, though not so expressed as during the LGM and LGT. Tundra and steppe communities have expanded their areas in the northern and southern areas of continent. The participation of forest coenoses in the landscape structure was reduced. But, the basic vegetation zone boundary did not change in the lowland territories, however, in the area an essential transformation of palaeophytocoenoses occurred.

The Early Holocene (Preboreal and Boreal periods) (PB–BO) (<10.2 – ⩾8.0 kyr BP)

After the ice sheet melting draft, shrub tundra with *Salix*, *Betula nana*, Ericales, *Lycopodium*, *Sphagnum* intermingled with small patches of open pine-birch forests dominated the Scandinavian Peninsula and in Northern Europe (north of 58°N in Western Europe and north of 68°N in Eastern Europe).

Instead of the shrubtundra of the DR3, forest-tundra communities were widespread during the Early Holocene. The southern boundary of the forest-tundra vegetation moved 300 km further north than in DR3, basically due to an increase of forest and decrease of tundra associations in the vegetative cover structure.

The combination of pine-birch forests with *Populus*, *Juniperus*, *Hippophae rhämnoides* participation and tundra plant associations prevailed in Northwestern Europe (north of 53°N) and in the south of the Scandinavian Peninsula. In Eastern Europe (between 61–64° and 68°N), pine-birch and pine-spruce forest intermingled with tundra-steppe communities. In Western Europe the birch forest-tundra of the DR3 was transformed into pine-birch forest with participation of tundra coenoses. The small-leaved forest with participation of alder, willow, birch, and aspen replaced shrub tundra of the last stadial in Southern Ireland and Great Britain, and also in Western France. Due to an increase in the amount of broad-leaved trees in the forest structure, Western European pine forests were transformed into a coniferous-broad-leaved forests. During the Early Holocene, pine-small-leaved forests with broad-leaved species dominated in Central Europe. Pine-spruce and pine-birch forests with broad-leaved species such as *Corylus*, *Tilia*, and *Ulmus*, and a small amount of *Quercus* intermingled with small patches of tundra-steppe communities were widespread in Eastern Europe. By the end of the Boreal, the forest zone had expanded it southern boundary approximately 300 km south, up to 48–50°N in Europe. Further south, forest-steppe landscapes prevailed.

In Western Europe, palaeophytocoenoses of oak-pine forests intermingled with grass-herb steppes, and in Eastern Europe landscapes of pine-broad-leaved forests with grass-herb and *Artemisia*-Chenopodiaceae steppes occurred.

In the Middle Danube Lowlands, the Balkan steppes of the DR3 were transformed into forest-steppe coenoses – pine-broad-leaved forest in combination with herb and wormwood-grass steppes. On the Iberian Peninsula, forest-steppe (oak-broad-leaved forest with grass-herb steppes) continued to remain the dominating type of the landscape. In the south of the Apennine Peninsula, silver fir forest intermingled with grass steppes. Steppe of grass and *Artemisia*- Chenopodiaceae phytocoenoses occupied the southern regions of the Russian Plain.

So, during the BP–BO the ranges of the distribution of tundra communities became close to the modern ranges, and the southern boundary of the forest-tundra vegetation moved approximately 6° further south than at present. A differentiated forest zone developed by the end of the Boreal, with forests of pine and birch prevailing in the north, and pine-broad-leaved forests at midlatitudes. In Eastern Europe forest-steppe landscapes occupied the territory of the modern broad-leaved forest and forest-steppe distribution. The northern boundary of the steppe zone coincided with the northern boundary of the modern grass-herb steppe. In the south of Western Europe, forest-steppe landscapes dominated in the areas of modern broad-leaved forest ranges. During the PB–BO the formation of the interglacial vegetation zonality in Europe continent began.

Conclusion

Thus, during the end of the Pleistocene the abrupt climatic fluctuations have caused radical changes in the structure and distribution of palaeophytocoenoses, and the reorganization of the vegetative zones. The differentiation of vegetative zones was minimal during the LGM and LGT, more appreciable in the DR3, and significant in the BAIC and PB–BO.

The distinctions between plant provinces of Eastern and Western Europe were significant during the LGM, LGT, and DR3 time slices. The periglacial zonality took place during the BAIC warming, and during the PB–BO, the interglacial vegetative zonality was formed. The considerable transformations of the vegetative cover structure took place in Northern Europe, northward to 50°N.

The reorganization of the vegetative zones occurred due to a reduction of forest coenoses, and a possibility of tundra and steppe elements migrating accordingly to the south and to the north of the continent during the cold periods in the forest free territories, formed new vegetative associations. So, periglacial plant communities were widespread in Europe until the Boreal period.

To the south of 50°N in the lowland territories of Europe, the boundary of the reconstructed vegetation provinces shifted slightly and was rather conservative. However, the significant reorganization of the palaeovegetation structure occurred within the limits of the reconstructed ecosystem during the different periods of the Late Pleistocene – Early Holocene geological history.

The forest refugia were associated with the dissected territories (the highlands, the mountain systems, and the large river valleys) in which variable local habitats occurred. These territories were the centres of high biodiversity both in cold, and in warm periods. The presence of forest refugia during all the intervals was revealed.

Chapter 6

THE EUROPEAN ECOSYSTEMS DURING THE PLEISTOCENE–HOLOCENE TRANSITION

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The main challenge of the project is to integrate the fossil mammalian data presented in Chapter 4 and the fossil floral data described and listed in Chapter 5. The two databases (flora and fauna) have not been merged and analysed using computer programs trying to compile statistically founded maps showing the extensions of the different ecosystems during the Pleistocene Holocene transition. We preferred a manual comparison of the two biotic components because both datasets have their limitations and strengths. The number of plant taxa generally exceeds the number of animal taxa. However, it is in several cases difficult to identify fossil plant remains to species level which restricts a detailed ecological reconstruction despite the large number of taxa. The animal fossils, although less diverse, can often be referred to single species and the palaeo-ecological information can, hence, be more specific.

By combining the two datasets we will be able to produce maps showing the geographical distribution of the defined ecosystems. It is important to realise that the maps are schematic and present for some regions only a general picture because the number of data points in a specific region is still rather low. The ecological reconstructions are first of all based on the species compositions of both plant and mammal assemblages and their common characteristics. The geographical distribution of the vegetation community and/or mammal assemblage as well as e.g. taphonomical aspects such as the possibility of re-deposition of material and so on has been taking into account.

In some cases we have in one of the time intervals from a specific area only floral or faunal data. The reconstruction is than only based on one component. The reconstructions of the ecosystems, is however, in most cases based of both biotic components that are often consistent in their ecological indications. When inconsistency occurs the entire dataset is analysed in detail. For instance if the plant remains indicate a mainly forested environment and the mammal assemblage contains also steppe dwellers or animals that prefer subarctic conditions, it is concluded that we are dealing with a forest-steppe ecosystem instead of a dominantly forested environment.

6.1. LAST GLACIAL MAXIMUM ECOSYSTEMS (⩽24 – ⩾17 KYR BP)

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The materials from 144 mammal localities and 63 sections with pollen-spore data, including 196 samples, correlated with the Last Glacial Maximum (LGM) interval, were analysed jointly (Fig. 6.1).

Ia. Shrub tundra (western variant)

With *Betula*, *Alnus*, *Salix*, *Juniperus*, Brassicaceae, *Helianthemum*, *Armeria*, Poaceae, Cyperaceae, and *Sphagnum*, and with *Mammuthus primigenius*, *Bos primigenius*, *Rangifer tarandus*, *Vulpes lagopus*, *Ochotona pusilla*, *Lemmus lemmus*, *Clethrionomys glareolus* and *Microtus gregalis*.

Ib. Shrub tundra (eastern variant)

With patches of forest-tundra and tundra-steppe communities with *Betula nana*, *Alnaster fruticosus*, *Salix*, Ericales, *Pinus*, *Picea*, Poaceae, Chenopodiaceae, *Artemisia*, Cyperaceae, and *Sphagnum*, and with *Mammuthus primigenius*, *Bos primigenius*, *Rangifer tarandus*, *Vulpes lagopus*, *Ochotona pusilla*, *Lemmus sibiricus*, *Clethrionomys glareolus* and *Microtus gregalis*.

II. Periglacial tundra-forest-steppe

With a combination of tundra and steppe plant communities with *Pinus-Betula* 'islands', and with *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Megaloceros giganteus*, *Ovibos moschatus*, *Bos primigenius*, *Bison priscus*, and *Alces alces* (in the west), *Saiga tatarica*, *Vulpes lagopus*, *Vulpes vulpes*, *Gulo gulo*, *Lynx* sp., *Panthera spelaea*, *Crocuta crocuta spelaea*, *Ochotona pusilla*, *Lepus timidus*, and *Marmota bobak* (in the east), *Spermophilus* sp., *Lemmus sibiricus*, *Dicrostonyx gulielmi*, *Microtus gregalis*, *M. arvalis*, and *Larix* (in the east), *Picea*, *Pinus*, *Alnus*, Ericales, Gramineae, Saxifragaceae, and Chenopodiaceae (in the east), *Ephedra* (in the east), *Armeria* (in the west) and *Empetrum* (in the west).

III. Periglacial forest-steppe (western variant)

With a combination of *Pinus-Betula* forests with participation of *Pinus*, *Betula*, Hippophae, *Juniperus*, *Salix*, *Larix*, *Quercus*, *Ulmus* and cereal-wormwood steppe and mixed-herb steppe communities Brassicaceae, *Ephedra*, Poaceae, and *Artemisia*, with *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Capreolus capreolus*, *Ovibos moschatus*, *Bos primigenius*, *Bison priscus*, *Saiga tatarica*, *Vulpes lagopus*, *Vulpes vulpes*, *Gulo gulo*, *Lynx* sp., *Panthera spelaea*, *Crocuta crocuta spelaea*, *Sus scrofa*, *Ochotona pusilla*, and *Lepus timidus* (in the north), *Lepus europaeus* (in the south), *Marmota marmota* (in the east), *Spermophilus* sp., and *Sylvaemus* sp. (in the south), *Lemmus lemmus*, *Dicrostonyx gulielmi*, *Lagurus lagurus*, *Microtus gregalis* and *M. arvalis*.

IV. Periglacial forest-steppe (eastern variant)

The combination of *Artemisia*-Chenopodiacae steppe with *Pinus-Betula* 'islands' and with tundra communities, and with *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* sp., *Rangifer tarandus*, *Cervus elaphus*, *Bos primigenius*, *Bison priscus*, *Saiga tatarica*, *Vulpes vulpes*, *Panthera spelaea*, *Crocuta crocuta spelaea*, *Sus scrofa*, *Lepus europaeus*, *Marmota bobak*, *Spermophilus* sp., *Lagurus lagurus* and *Eolagurus luteus*.

V. Periglacial steppe

The combination of *Artemisia*-Chenopodiacae steppe with restricted areas of tundra and semi-desert com-

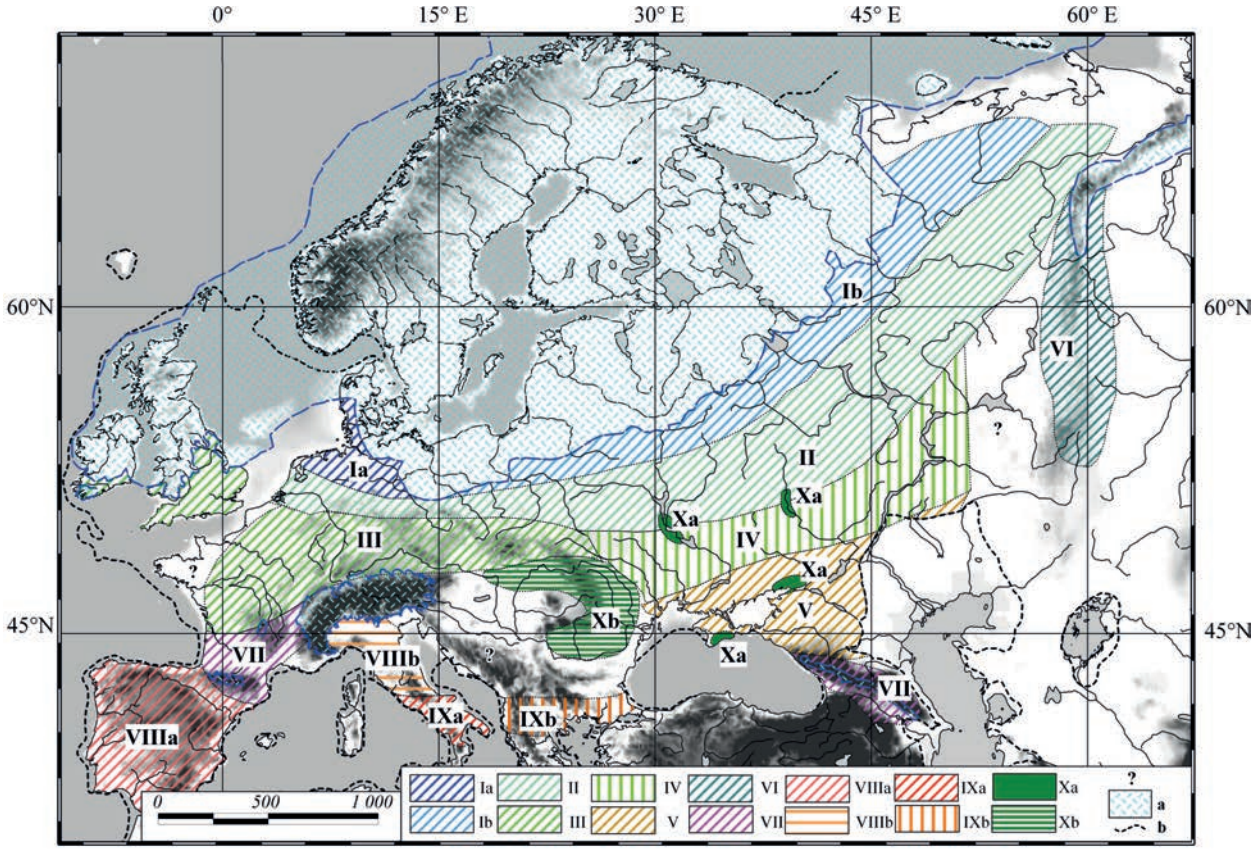

Fig. 6.1. *LGM ecosystems: Ia – shrub tundra (western variant); Ib – shrub tundra (eastern variant); II – periglacial tundra-forest-steppe; III – periglacial forest steppe (western variant); IV – periglacial forest-steppe (eastern variant); V – periglacial steppe; VI – the Ural mountains tundra-forest-steppe; VII – the mountain and plain periglacial forest-steppe; VIIIa – Mediterranean mountain and plain forest-steppe (Iberian variant); VIIIb – Mediterranean mountain and plain forest-steppe (Apennine variant); IXa – Mediterranean xerophytic forests (south Appenine and south Balkan variant); IXb – Mediterranean xerophytic forest (north Balkan variant); Xa – forest refugee; Xb – periglacial pine forests of the Carpathians; 1 – the regions without palaeontological data; 2 – ice sheets; 3 – coastline.*

munities, and with *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* sp., *E. hydruntinus*, *Rangifer tarandus*, *Bos primigenius*, *Bison priscus*, *Saiga tatarica*, and *Vulpes lagopus* (in the Crimea), *Vulpes vulpes* and *V. corsac* (in the south), *Panthera spelaea*, *Crocuta crocuta spelaea*, *Marmota bobak*, *Spermophilus* sp., *Lagurus lagurus* and *Eolagurus luteus*.

VI. The Ural Mountains tundra-forest-steppe

With *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus* sp., *Rangifer tarandus*, and *Capreolus* sp. (in the south of the Urals), *Alces alces*, *Bison priscus*, *Saiga tatarica*, *Vulpes lagopus*, *Vulpes vulpes*, *Panthera spelaea*, *Ochotona pusilla*, *Lepus timidus*, *Spermophilus* sp., *Clethrionomys glareolus*, *Cl. rufocanus*, *Cl. rutilis*, *Lemmus sibiricus*, *Dicrostonyx gulielmi*, *Lagurus lagurus*, *Eolagurus luteus* and *Microtus gregalis*. Plant data are absent.

VII. The mountain and plain periglacial forest-steppe

A combination of mixed – herb – *Artemisia* steppe with the coniferous forest 'islands' (*Cedrus*, *Juniperus*, *Pinus*, Hippophae, and with an admixture of some broad-leaved plants *Quercus*, *Corylus*, and *Cornus*), with *Mammuthus primigenius*, *Equus* sp., *Equus hydruntinus*, *Rupicapra rupicapra*, *Capra ibex*, *Rangifer tarandus*, *Megaloceros giganteus*, *Capreolus capreolus*, *Bos primigenius*, *Bison priscus*, *Ovibos moschatus*, *Saiga tatarica*, *Sus scrofa*, *Vulpes lagopus*, *Vulpes vulpes*, *Felis sylvestris*, *Lynx* sp., *Panthera spelaea*, *Crocuta cocuta spelaea*, *Marmota marmota*, *Spermophilus* sp., *Sylvaemus* sp., and *Microtus gregalis*.

VIIIa. Mediterranean mountain and plain forest-steppe (Iberian variant)

On the Iberian Peninsula: the combination of mixed coniferous-broad-leaved forests (*Pinus*, *Cedrus*, *Juniperus*, *Picea*, *Quercus*, *Ulmus*, and *Corylus*) with mixed-herb and cereal steppes (Poaceae, Caryophyllaceae, Lamiaceae, Helianthemum, Fabaceae, *Plantago*, *Ephedra*, *Artemisia*, Chenopodiaceae, Campanullaceae, and Centaurea), with *Orictolagus cuniculus*, *Galemys*, *Microtus (Terricola) duodecimcostatis*, *M.* (*T.) cabrerae*, *Sylvaemus* sp., *Rupicapra rupicapra*, *Felis sylvestris* and others.

VIIIb. Mediterranean mountain and plain forest-steppe (Apennine variant)

In the north of the Apennine Peninsula: the combination of coniferous-broad-leaved forests (*Pinus*, *Picea*, *Abies*, *Corylus*, *Fagus*, *Quercus*, *Tilia*, *Buxus*, and *Olea*) and cereal-wormwood and wormwood-Chenopodiaceae steppes (Poaceae, *Artemisia*, and Chenopodiaceae).

IXa. The Mediterranean xerophytic forests (south Appenine and south Balkan variant)

In the south of the Apennine Peninsula and in the southwest of Greece: broad-leaved forest (with *Acer*, *Cornus*, *Fagus*, Phillyrea, *Olea*, *Quercus*, *Ulmus*, *Carpinus*, *Pinus*, *Taxus*, *Abies*, and *Buxus*) with patches of cereal-wormwood steppes (Poaceae, *Artemisia*, Chenopodiaceae, Caryophyllaceae, *Ephedra*, *Thalictrum*, Sanguisorba, and Umbelliferae), and with *Bos primigenius*, *Cervus elaphus*, *Capreolus capreolus*, *Rupicapra rupicapra*, *Sus scrofa* and others.

IXb. The Mediterranean xerophytic forest (north Balkan variant)

In the north of the Balkan Peninsula: coniferous-broad-leaved forest (*Abies*, *Pinus*, *Alnus*, *Carpinus*, *Quercus*, and *Fraxinus*) with patches of cereal-wormwood steppes (*Artemisia*, Poaceae, Chenopodiaceae, Asteraceae, Campanulaceae, *Thalictrum*, and Rosaceae).

Xa. Forest refugia

Birch-pine and spruce forests with an admixture of broad-leaved trees (*Abies*, *Alnus*, *Quercus*, *Corylus*, *Ulmus*, *Acer*, and *Tilia*) in large river valleys, highlands and mountain systems of Eastern Europe.

Xb. Periglacial pine forests of the Carpathians

With a mixture of *Juniperus*, *Betula*, *Salix*, *Picea*, Gramineae, Cypeaceae, and *Artemisia*.

Conclusion

The results of the analysis of the plant and mammal materials, correlated with the Late Glacial Maximum interval (≤24 – ≥17 kyr BP), permit to reveal the principal features of the ecosystems during that time for Europe. The joint materials indicate that the huge territories of Europe located between the Scandinavian ice sheet and ~45°N in Eastern Europe and up to 44°N in Western Europe were covered by different variants of periglacial ecosystems. All of these ecosystems were under the influence of the Scandinavian ice sheet. This influence decreased from north to south. Shrub tundra, periglacial tundra-forest-steppe, periglacial forest-steppe (eastern variant), and periglacial steppe existed in Eastern Europe during the LGM. The first two ecosystems were present in Western Europe also and located in the north of the territory. The western variant of the periglacial forest steppe was distributed in Western Europe south of the periglacial tundra-forest-steppe, and occupied the Loire River and Seine River drainage basins, the Rhine middle basin, and the belt of Central European low mountains (the Ardennes, the Vosges, the Sudeten Mountains and others). The mountain and plain periglacial forest-steppes existed in the Massif Central and in the Garonne basin.

All of these ecosystems of Northern and Central Europe have a unique structure and have no analogues in modern times. They include plants and animals of different ecologies, which are now distributed in different natural zones. Such plant and mammal compositions reflect the mosaic structure of the European environment during the LGM. The continuous forest zone does not exist at this time. This explains the wide distribution of steppe animals in the north and west of Europe. The influence of the Late Valdai (=Weichselian) ice sheet was very strong, which permitted typical tundra species to penetrate up to 46–48°N. The forest species migrated to the south and survived also in refugia, related to the river basins and mountain and uphill regions with a high number of local habitats. The analysis of plant and mammal distributions shows that the manifestation of the natural zonality in Northern and Central Europe was weak during the LGM.

The southern regions of Europe practically did not feel the influence of the last glacial ice sheet. The different types of Mediterranean forests and open landscapes with xerophytic herbaceous communities existed on the Iberian, the Apennine and Balkan Peninsulas. The forest-adapted and mountain mammals inhabited mostly these territories. Many endemic animals existed on the Iberian Peninsula.

The differences between the Western and Eastern European ecosystems were established. Eastern European faunas reflect more arid environments than West European faunas. So the Atlantic influence existed during the LGM, but the principal influence was the atmospheric high above the Scandinavian ice sheet.

6.2. THE LATE GLACIAL TRANSITION PERIOD (LGT) ECOSYSTEMS (<17 – ⩾12.4 KYR BP)

Thijs van Kolfschoten, Anastasia Markova, Alexandra Simakova, and Andrey Puzachenko

The analyses of mammal and plant materials from the LGT time (<17 – ≥12.4 kyr BP) and the succeeding reconstructions of the mammal assemblages and plant communities, permitted to reveal the principal palaeoecosystems of this time.

The data from 78 sections, which include 277 spore-pollen samples, and the data from 79 mammal localities were analysed together. In most cases there were no disagreements between the LGT plant and mammal data, but very often we have the situation where for certain territories we have only plant or only mammal data. For example we have only mammal materials for the Ural Mountains. There were no dated pollen spectra from this region.

On the other hand we have mostly plant data for Southern Europe. Thus, the palaeoecosystems reconstructions are in some cases based on materials of both plant and mammal data, in other cases they are based only on data of one biotic component (plants or mammals). From the northern regions of Eastern Europe, as well as from the southern European ones, there is a lack of data. The results of joint analyses are presented in the form of a schematic map in Figure 6.2.

LGT Ecosystems

I. Tundra and arctic desert

Distribution of shrub tundra vegetation and with Polar bear *Ursus maritimus* on the western-northern coast, with *Mustela erminea* on the western-southern coast of the Scandinavian Peninsula, and with the mammoth *Mammuthus primigenius* in southern Scandinavia.

II. Shrub tundra and tundra steppe

The western province (II a) is located on the British Isles. There *Betula nana*, *Salix*, *Populus*, *Hippophae rhamnoides*, *Juniperus*, Saxifragaceae, *Rumex*, *Thalictrum*, Rosaceae, *Dryas*, *Heliantherium*, *Armeria*, Caryophyllaceae, Cyperaceae, Plumbaginaceae, *Plantago*, Labiatae, Umbelliferae, *Bryales*, *Sphagnum*, *Selaginella* and *Huperzia selago* remains were found here. *Mammuthus primigenius* inhabited these territories.

The eastern province (II b) covered the north of continental Europe. Here the combination of shrub tundra vegetation including *Alnaster*, *Alnus*, *Betula nana*, *Picea*, Ericales, *Artemisia*, Chenopodiaceae, *Ephedra*, *Selaginella*, and *Sphagnum*, and with *Mammuthus primigenius*, *Rangifer tarandus*, *Saiga tatarica*, *Equus* sp., *Vulpes lagopus*, *Spermophilus*, *Dicrostonyx*, *Lemmus* and *Ochotona* were reconstructed. *Desmana* was discovered on the south of the Jutland Peninsula; unique are the *Saiga* remains dated to 14,800 yrs BP, on Fyn Island (55°N; 10.5°E).

III. Periglacial tundra-forest-steppe

The combination of light pine-birch forest, shrub tundra and tundra-steppe communities with *Salix*, *Juniperus*, *Thalictrum*, *Rumex*, *Helianthemum*, *Ephedra*, Poaceae,

Umbelliferae, *Botrichium*, and rare *Quercus* were characteristic to the western province (IIIa). Mammals include *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Alces alces*, *Rangifer tarandus*, *Cervus elaphus*, *Saiga tatarica*, *Vulpes lagopus*, *Dicrostonyx*, *Clethrionomys glareolus*, *Microtus agrestis*, and others.

Eastern province (IIIb) includes light pine-birch and pine-spruce forests with patches of tundra and herb-steppe associations with *Alnus*, *Betula nana*, *Picea*, *Artemisia*, Chenopodiaceae, Poaceae, *Ephedra*, *Selaginella*, *Botrichium*, and rare *Tilia*, and with *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Bison priscus*, *Alces alces*, *Rangifer tarandus*, rare *Cervus elaphus*, *Equus* sp., *Ovibos moschatus*, *Gulo gulo*, *Vulpes lagopus*, *Canis lupus*, *Ursus arctos*, *Vulpes corsac*, *Vulpes vulpes*, *Lepus timidus*, *Marmota bobak*, *Dicrostonyx*, *Lemmus sibiricus*, *Lagurus lagurus*, *Eolagurus luteus*, *Clethrionomys glareolus*, *Microtus gregalis* and others.

IV. Periglacial forest-steppe

The combination of *Artemisia* – Chenopodiaceae steppe, light pine birch forest, and tundra-steppe vegetation with *Alnus*, *Picea*, Fabaceae, Asteraceae, *Cichorium*, Dipsacaceae, *Selaginella*, with rare *Sphagnum*, Polypodiaceae and with *Quercus* and *Ulmus* in the drainage basins of big rivers. *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Bison priscus*, *Rangifer tarandus*, *Equus* sp., *Saiga tatarica*, *Panthera spelaea*, *Ursus arctos*, *Vulpes corsac*, *Vulpes vulpes*, *Vulpes lagopus*, *Ochotona pusilla*, *Spermophilus*, *Spalax microphtalmus*, *Dicrostonyx*, *Lemmus*, *Alces*, *Gulo gulo*, *Clethrionomys glareolus*, *Lagurus lagurus*, *Eolagurus luteus*, *Microtus gregalis*, *M. arvalis*, *M. oeconomus* and others inhabited these territories.

V. Periglacial steppe

The periglacial *Artemisia* – Chenopodiaceae steppe with patches of tundra associations with participation of Asteraceae, *Cichorium*, *Convolvulus*, *Labiatae*, *Ephedra*, with rare *Sphagnum*, Polypodiaceae, and with *rare Tilia*. Reindeer *Rangifer*, wild horse *Equus*, aurochs *Bos primigenius*, ground squirrel *Spermophilus* and others inhabited these territories.

VI. The Urals mountain periglacial tundra-forest-steppe

The LGT plant data are absent for the Urals. The mammals include about 60 species of different ecological groups adapted to arctic, steppe, and forest environments: *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Crocuta crocuta spelaea*, *Panthera spelaea*, *Ursus spelaeus*, *Ursus arctos*, *Vulpes vulpes*, *Vulpes corsac*, *Mustela sibirica*, *Mustela putorius*, *Gulo gulo*, *Bison priscus*, *Equus* sp., *Saiga tatarica*, *Alces alces*, *Rangifer tarandus*, *Cervus elaphus*, *Ovibos moschatus*, *Ochotona pusilla*, *Spermophilus*, *Sciurus*, *Marmota bobak*, *Cricetus cricetus*, *Allocricetus eversmanni*, *Cricetulus migratorius*, *Sylvaemus*, *Allactaga major*, *Dicrostonyx gulielmi*, *Lemmus sibiricus*, *Clethrionomys glareolus*, *Cl. rufocanus*, *Cl. rutilus*, *Lagurus lagurus*, *Eolagurus luteus*, *Microtus gregalis*, *M. arvalis*, *M. agrestis*, *M. oeconomus* and others.

VII. The Mediterranean xerophytic forest

The combination of pine-oak forests, grass-herb and wormwood steppes in the north of the Iberian Peninsula; broad-leaved forests with patches of grasses steppes in the Apennines and the combination of pine-fir – broad-leaved forests and Poaceae-*Artemisia* steppes, and *Artemisia*-Chenopodiaceae steppes in the southern part of Balkan Peninsula. The communities of this ecosystem include *Ilex*, *Pistacia*, *Taxus*, Saxifragaceae, *Populus*, *Tilia*, *Ulmus*, *Quercus*, *Carpinus*, *Cedrus*, *Corylus*, *Fagus*, *Pinus*, *Acer*, *Fraxinus*, *Abies*, Saxifragaceae, Umbelliferae, Fabaceae, Poaceae, Asteraceae and *Cichorium*. Mammals include mostly the forest and mountain species *Bos primigenius*, *Cervus elaphus*, *Capreolus capreolus*, *Capra ibex*, *Rupicapra rupicapra* and *Sus scrofa*.

VIII. Periglacial light pine forests with patches of herb steppes

This ecosystem includes the combination of pine-birch mountain forest with herb steppe in the foothills of the Pyrenees, and in the Massif Central with *Corylus*, *Cedrus*, *Juniperus*, *Ulmus*, *Armeria*, *Artemisia*, *Ephedra*, Caryophyllaceae, Saxifragaceae, Umbelliiferae, *Convolvulus*, Rosaceae, *Rumex* and *Thalictrum*. The mammal data are absent.

IX. Erophytic grass communities with patches of open coniferous-broad-leaved forests

Grass steppes and *Artemisia*-Chenopodiaceae steppe with patches of coniferous-broad-leaved forests including Asteraceae, *Cichorium*, Poaceae, *Ephedra*, Polygonaceae, *Carpinus*, *Castenea*, with rare *Quercus* and *Ulmus* were distributed on the Balkan Peninsula. The mammal data for this interval are absent.

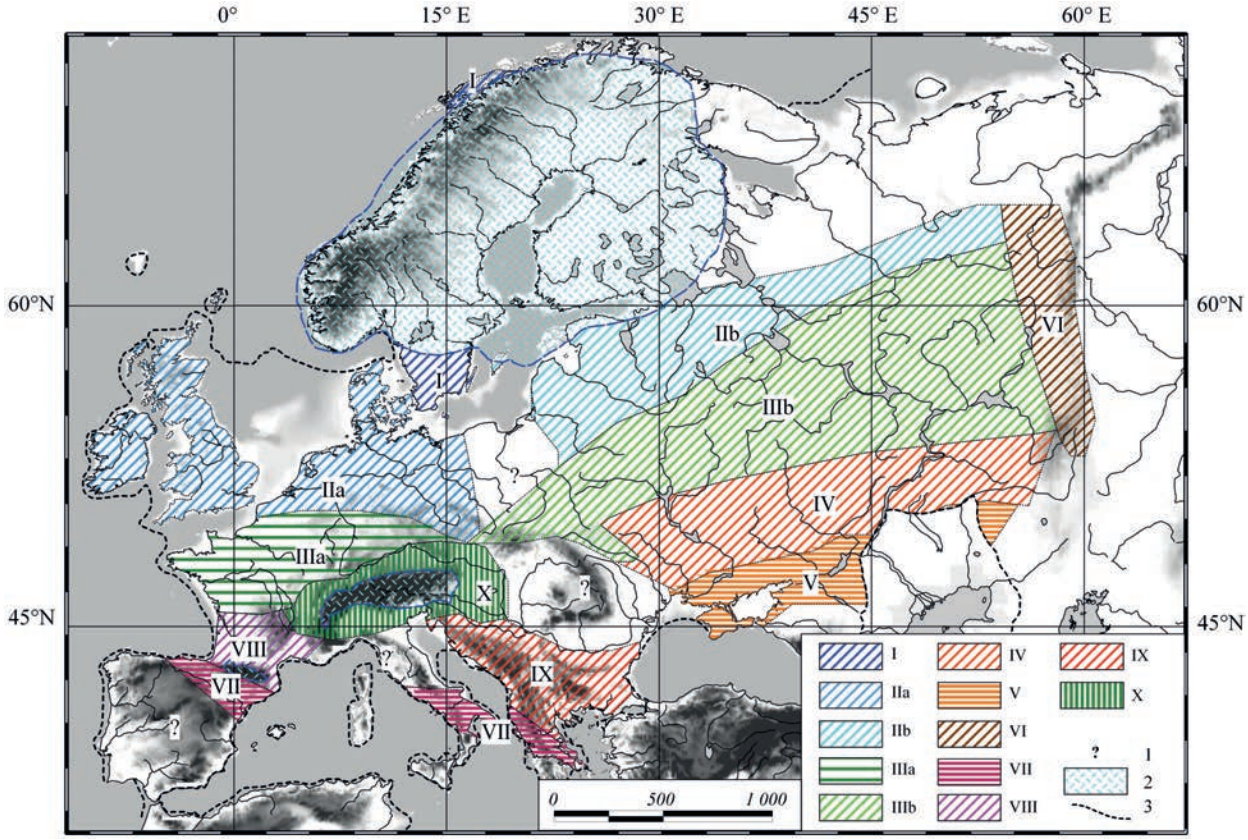

Fig. 6.2. *Late Glacial transitional period ecosystems (1 – tundra and arctic desert; II – shrub tundra and tundra steppe (a – western province; b – eastern province); III – periglacial tundra-forest-steppe (a – western province; b – eastern province); IV – periglacial forest-steppe; V – periglacial steppe; VI – the Urals periglacial mountain tundra-forest-steppe; VII – Mediterranean xerophytic forest; VIII – periglacial light pine forest with meadow-steppe communities; IX – combination of open forest with Artemisia – Chenopodiaceae steppe; X – mountain coniferous forest with admixture of broad-leaved trees; 1 – regions without palaeontological data; 2 – ice sheets; 3 – coastline*

X. Mountain coniferous forest with admixture of broad-leaved taxa

Pine-fir-ash forest was located around the Alps (with *Pinus*, *Abies*, *Fraxinus*, *Quercus*, *Ulmus*, *Artemisia*, Careophyllaceae, *Hippophae rhamnoides*, *Thalictrum*, Lamiaceae, *Botrichium* and others). Mammals include mostly forest species *Capreolus capreolus*, *Cervus elaphus*, *Lutra lutra*, *Martes foina*, *Meles meles*, *Mustela putorius*, *Ursus spelaeus*, *Ursus arctos* and others.

Conclusion

The reconstructions of LGT ecosystems based on plant and mammal data permit to reveal the principal structure of the European biota during <17 – ≥12.4 kyr BP. The characteristics of plant communities and mammal assemblages indicate the cold and rather arid climatic condition in Northern and Central Europe. The huge territories of Europe were covered by different types of periglacial ecosystems, where the species of different ecologies, which in modern times belong to different natural zones (tundra, forest and steppe) occurred together. In addition to these species, the presence of a large number of large herbivores, extinct by the end of the Pleistocene – beginning of the Holocene, was also very typical of these ecosystems.

The penetration of steppe plants and mammals far to the north indicates the absence of a continuous forest zone at that time. The steppe species also penetrated far to the west, which permits us to speak also in these territories of open periglacial landscapes. Forest plants and mammals were rather rare during the LGT in Northern and Central Europe. In the northern areas, the forest plants were represented mostly by pine, birch and spruce.

Forest mammals and plants survived in the refugia in mountain and uphill regions, and also in river valleys, where forested and shrub areas occurred. The forest mammals connected with the broad-leaved forests concentrated mostly in the southern mountain regions

of Europe (in the Apennines, near the Alps, possibly, in the Balkans, Pyrenees and Carpathians, from where we have no materials yet).

Tundra plants and animals were very widely distributed during this time, as well as during the LGM. This indicates cold climatic conditions in Northern and Central Europe.

In the southern regions (south of 48–46°N), the influence of glaciation was rather weak and did not effect the mammal composition and diversity.

It is clear that every mammal and plant individually responds to the glacial condition, some of them widened their range very significantly, the ranges of others became discontinuous and restricted. These very different mammal and plant reactions led to the establishment of a new ecosystems, which have no analogues in modern times.

Thus, the reconstructed ecosystems differ very strongly from modern ones. All the ecosystems located in the northern and central part of Europe reflected the strong influence of the ice sheet. This influence is well pronounced up to 48–46°N. In the southernmost regions the change in the ecosystems was rather weak. Thus, different types of forests existed in the Mediterranean (on the Iberian, Apennine, and Balkan Peninsulas, and around the Alps). These regions together with the northernmost mountain and uphill regions were the refugia for many warm-adapted mammal species.

6.3. THE EUROPEAN ECOSYSTEMS DURING THE BØLLING–ALLERØD INTERSTADIAL COMPLEX (BAIC) (<12.4 – ⩾10.9 KYR BP)[13]

Thijs van Kolfschoten, Anastasia Markova, Alexandra Simakova, and Andrey Puzachenko

A large amount of European palaeobotanical data were collected for the Bølling–Allerød Interstadial complex (BAIC). 186 sections (896 samples) with spore-pollen were used in the analysis. Mammal data are rather rare, only 53 mammal localities dated by ^{14}C to between 12,400 yrs BP and 10,800 yrs BP were united in the form of an electronic database. These localities include 53 mammal taxa. The geographical distribution of the BAIC localities and the schematic position of the ecosystems are shown in Figure 6.3.

Principal BAIC ecosystems

I. Periglacial shrub tundra

With *Betula nana*, *Salix*, Ericales, *Hippophae rhämnoides*, *Juniperus*, *Rubus*, *Helianthemum*, *Armeria*, *Sphagnum*, *Selaginella* and *Lycopodium* in the south of the Scandinavian Peninsula with areas of pine-birch open forests. With *Rangifer tarandus* and *Phoca* in western South Scandinavia.

II. Periglacial forest-tundra-steppe

With *Pinus*, *Betula*, *Betula nana*, *Populus*, *Salix*, *Sangiusorba*, *Vassinium*, *Rumex*, *Rubus*, *Ephedra*, *Armeria*, Saxifragaceae, Rosaceae, Onograceae, *Lycopodium*, *Huperzia selago* and *Selaginella*. The mammal assemblage includes *Bos primigenius*, *Cervus elaphus*, *Saiga tatarica*, *Vulpes lagopus*, *Ursus arctos*, *Vulpes vulpes*, *Ochotona pusilla*, *Lepus timidus*, *Castor fiber*, *Arvicola terrestris*, *Dicrostonyx torquatus*, *Lemmus lemmus*, *Microtus agrestis* and *M. oeconomus* in the British Isles; with *Bos primigenius*, *Rangifer tarandus*, *Megaloceros giganteus*, *Equus* sp., *Ochotona pusilla*, *Spermophilus* sp., *Dicrostonyx torquatus*, *Lemmus* sp. and *Clethrionomys glareolus* in continental Western and Eastern Europe. The presence in these territories of *Mammuthus* and *Coelodonta* are not supported by finds yet.

[13] The paper is supported by RFBS grant N 03-04-48406.

III. Light pine-birch forests with patches of steppe and tundra communities

With *Pinus*, *Betula*, *Picea* (on the Russian Plain), with an admixture of *Betula nana* and rare *Ulmus*, *Tilia*, *Quercus*, *Corylus* and *Armeria*. Mammals include *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Bos primigenius*, *Rangifer tarandus*, *Cervus elaphus*, *Alces alces*, *Equus* sp., *Ochotona pusilla*, *Spermophilus* sp., *Sorex araneus*, *Talpa europaea*, *Dicrostonyx torquatus*, *Lemmus*, *Clethrionomys glareolus*, *Microtus gregalis* and *M. oeconomus*. In Eastern Europe with *Lagurus lagurus* and *Eolagurus luteus*; in Western Europe with *Rupicapra rupicapra*, *Capra ibex* and *Sylvaemus* sp.

IV. Periglacial forest-steppe

The combination of grass steppe areas with tundra communities and pine-birch forest 'islands' with *Pinus*, *Betula*, *Larix*, *Quercus*, *Tilia*, *Artemisia*, *Centaurea*, *Armeria*, *Cichorium*, Poaceae, *Sphagnum*, *Selaginella* and *Huperzia selago*. The mammal assemblage includes *Mammuthus primigenius*, *Bos primigenius*, *Bison priscus*, *Rangifer tarandus*, *Cervus elaphus*, *Alces alces*, *Equus* sp., *Crocuta crocuta spelaea*, *Vulpes lagopus*, *Microtus gregalis* and others. *Eolagurus luteus* and *Lagurus lagurus* were distributed in Eastern Europe.

V. The Urals mountain tundra-forest-steppe

Plant data are absent. The mammal assemblages include *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Rangifer tarandus*, *Megaloceros giganteus*, *Saiga tatarica*, *Equus* sp., *Panthera spelaea*, *Vulpes lagopus*, *Ursus arctos*, *Vulpes vulpes*, *Spermophilus*, *Sylvaemus* sp., *Dicrostonyx torquatus*, *Lemmus sibiricus*, different species of the *Clethrionomys* genus, *Eolagurus luteus*, *Lagurus lagurus*, different species of the *Microtus* genus and others.

VI. Periglacial steppe

With Chenopodiaceae, Boraginaceae, Asteraceaee, *Cichorium*, Poaceae, Papaveraceae, Scabiosa and others;

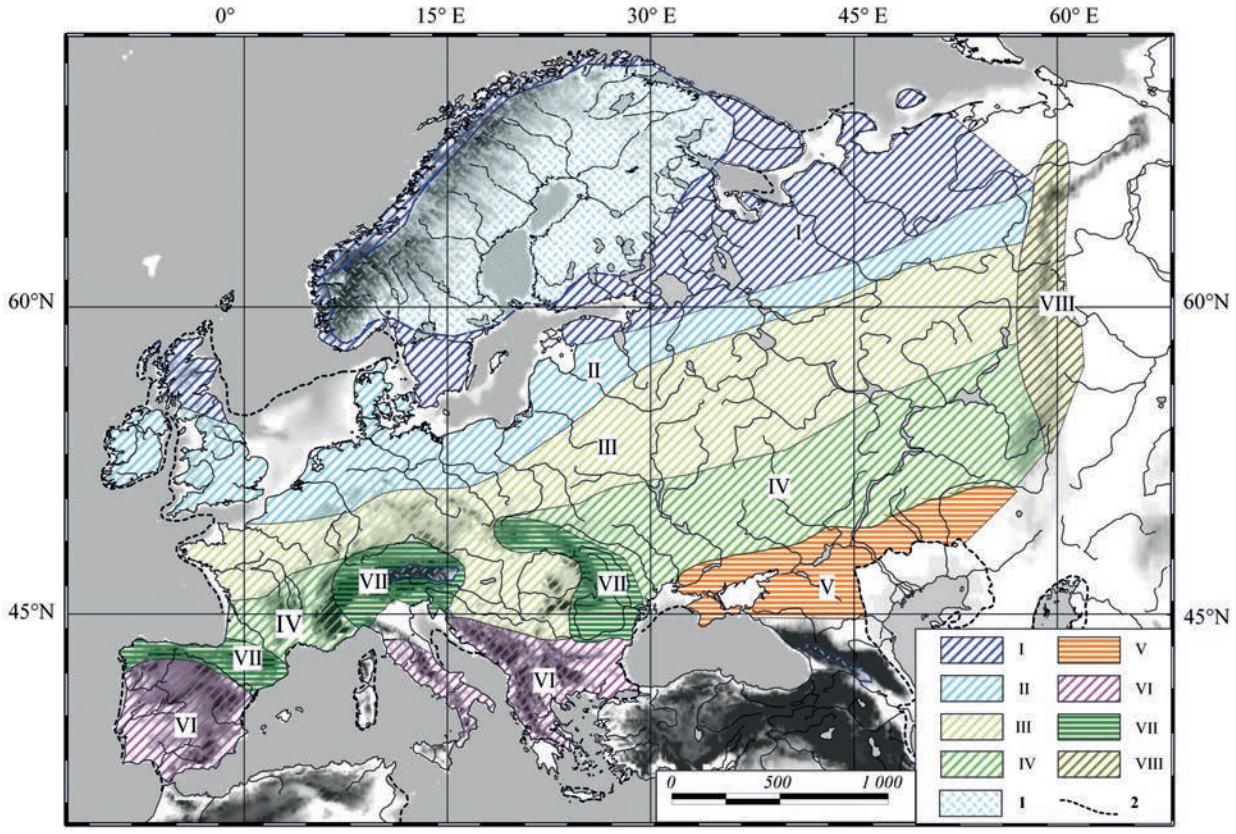

Fig. 6.3. *BAIC ecosystems: I – periglacial shrub tundra; II – periglacial forest-tundra-steppe; III – light pine-birch forests with patches of steppe and tundra communities; IV – periglacial forest-steppe; V – the Ural Mountains tundra-forest-steppe; VI – periglacial steppe; VII – mountain coniferous-broad-leaved forests; VIII – Mediterranean coniferous-broad-leaved forests and hard-leaved shrubs with xerophytic herbaceous communities; 1 – ice sheet; 2 – coastline*

with *Salix*, *Betula*, *Pinus*, *Alnus* and *Hippophae rhämnoides* along the river drainage basins (eastern part of the Russian Plain). The mammals include *Bison priscus*, *Rangifer tarandus*, *Equus* sp., *Spermophilus*, *Eolagurus luteus*, *Lagurus lagurus* and others.

VII. Mountain coniferous-broad-leaved forests

With *Pinus*, *Larix*, *Picea*, *Abies*, *Betula*, *Fagus*, *Juniperus*, *Quercus*, *Ulmus*, *Tilia*, *Corylus*, *Larix*, *Artemisia*, Poaceae, Centaurea, Rosaceae, Ranuncullaceae, *Armeria*, *Selaginella* and others. The mammals including *Bos primigenius*, *Capreolus capreolus*, *Cervus elaphus*, *Felix lynx*, *Canis lupus*, *Ursus arctos*, *Vulpes vulpes*, *Martes* sp., *Talpa europaea*, *Castor fiber* and others inhabited these territories.

VIII. Mediterranean coniferous-broad-leaved forests and hard-leaved shrubs with xerophytic herbaceous communities

With *Pinus*, *Abies*, *Taxus*, *Fagus*, *Quercus*, *Quercus ilex*, *Fraxinus*, *Acer*, *Ulmus*, *Ostrya*, *Olea*, *Pistacia*, *Ilex*, *Myrica*, *Tilia*, *Artemisia*, Chenopodiaceae, Poaceae, *Ephedra*, *Cichorium*, *Helianthemum*, and Papaveraceae. Mammals include *Terricola duodecimcostatus*, *Microtus cabrerae*, *Microtus agrestis*, *Arvicola sapidus*, *Galemys pyrenaicus*, *Rupicapra rupicapra*, *Capreolus capreolus*, *Cervus elaphus*, *Erinaceus europaeus*, *Eliomys quercinus*, *Sylvaemus sylvaticus*, *Crocidura suaveolens*, *C. russula* and *Oryctolagus cuniculus* on the Iberian Peninsula; *Bos primigenius*, *Cervus elaphus*, *Capreolus capreolus*, *Capra ibex*, *Rupicapra rupicapra* and *Sus scrofa* on the Apennine Peninsula; *Allactaga major*, *Mesocricetus newtoni*, *Lagurus lagurus* and others inhabited the north of the Balkan Peninsula.

Conclusion

The Bølling–Allerød Interstadial complex ecosystems reflect the noticeable warming comparing to the previous LGT. At latitudes where the forest-tundra was distributed during the LGT, open pine-birch forests appeared in the BAIC interval. The forest-steppe ecosystem occurred more widely and during the BAIC covered the southernmost territories.

On the other hand, the arctic cold-adapted mammals and plants were also widely distributed in this time interval. However, their density became lower. For example there are no known finds with *Dicrostonyx* and *Lemmus* remains south of 50°N in Eastern Europe during the BAIC, but these species penetrated southward up to 48°N during the LGM. The density of large herbivores such as mammoth, woolly rhinoceros, giant deer and others became lower in this interval, but the reindeer was widely distributed in the Bølling–Allerød Interstadial period.

Thus, the ecosystems of this interval reflected some warming, but this warming was not very significant and had an interstadial character. The definite influence of the Scandinavian ice sheet was pronounced at this time. This influence was noticeable up to 50–48°N. In the South European regions (on the Iberian, Apennine and Balkan Peninsulas), this influence was practically absent. Here the complex of forest adapted mammals and forest plants (broad-leaved and coniferous) were distributed very widely. These territories were refugia in the previous intervals of the Late Glacial period. The species composition of plants and mammals of the South European regions indicates the stable character of the ecosystems in these territories during the entire second part of the last glaciation.

6.4. THE EUROPEAN ECOSYSTEMS DURING THE YOUNGER DRYAS (YD) (<10.9 – ⩾10.2 KYR BP)

The Younger Dryas (YD) is a period of about 700 years and is a relatively short in compare to the other intervals we discuss in this chapter. Despite of the short duration of this interval the amount of biotic data is impressive. In total 94 sites yielded information about the vegetation during the Younger Dryas and there are 26 sites with mammalian data. The botanical record appeared to be extensive enough to produce a map showing the geo-

graphical distribution of the palaeovegetation provinces during the Younger Dryas (see Chapter 5, section 5.4 & Fig. 5.44). The mammalian data are, however, too limited to reconstruct mammal assemblages and to produce reliable maps showing their geographical distribution. Due to the lack of sufficient information on the distribution of the different mammalian taxa it is not useful merge the botanical and mammalian data to compile maps that show the geographical distribution of the different ecosystems during the Younger Dryas. The palaeovegetation map (Fig. 5.4) is the most detailed and reliable picture that can be produced on the basis of the available data.

6.5. EARLY HOLOCENE (PREBOREAL–BOREAL) ECOSYSTEMS (10.2–8.0 KYR BP)

Pavel Kosintsev, Alexandra Simakova, Andrey Puzachenko and Thijs van Kolfschoten

There are fewer theriological (142 localities) than palynological (423 sites, 2108 samples) data, considering both the number of sites and their distribution in Europe dated by ^{14}C to between 10.2 and 8.0 kyr BP. Consequently, the degrees exactness of the territorial reconstructions of mammal assemblages and palaeophythocoenoses are different. The geographical distribution of sites with pollen data in Europe is even. Mammal localities are absent on the Scandinavian Peninsula, in Central Europe, in Western France, and on the southern Russian Plain. But using the same method of analysis for fauna and palynological data makes it possible to conduct a combined analysis of results of these reconstructions. The geographical distribution of Preboreal-Boreal localities and the schematic position of the ecosystems are shown in Figure 6.4.

PB–BO Ecosystems

I. Shrub tundra

Distribution of shrub tundra vegetation with small patches of pine and birch open woodlands *Alnus*, *Betula*, *Pinus*, *Salix*, Ericales, Cyperaceae, Rosaceae, Chenopodiaceae, *Selaginella*, Polypodiaceae, *Lycopodium*, *Equisetum*, and Bryales in Scandinavia. The mammal data are absent for these territories.

II. Forest-tundra

Pine and birch boreal forests with *Populus*, *Juniperus*, and *Hippophae rhamnoides* in combination with tundra communities widespread in the southern part of Scandinavia, and a combination of *Pinus* and *Betula* forests, sometimes with *Picea* participation with tundra-steppe plant communities in the northern part of Eastern Europe. The mammal data are absent for these territories.

III. Light pine-birch forests with patches of tundra communities

Open *Pinus* and *Betula* forests with *Populus*, *Juniperus*, *Hippophae rhamnoides* and some tundra phytocoenoses covered the northern part of Western and Central Europe and with *Picea* participation in Eastern Europe (61–67°N), with an insignificant admixture of broad-leaved species (*Acer*, *Fraxinus*, *Tilia*, *Corulus*, and *Ulmus*), and small patches of tundra-steppe plant communities (*Artemisia*, Chenopodiaceae, Cyperaceae, Poaceae, Rosaceae, *Ericales*, *Rumex*, and *Thalictrum*). The mammal assemblage included four groups of species. The first group consisted of species that inhabited open landscapes from the Pleistocene: *Microtus gregalis*, *Vulpes lagopus*, *Equus* (*Equus*) sp. and *Rangifer tarandus*. The second group consisted of semi-open and forest landscape species: *Lepus timidus*, *Sciurus vulgaris*, *Clethrionomys glareolus*, *Martes martes*, *Ursus arctos*, and *Alces alces*. The third group consisted of widespread azonal species: *Castor fiber*, *Arvicola terrestris*, *Canis lupus* and *Vulpes vulpes*. The forth group included one species, *Mammuthus primigenius*, the last population of which inhabited in the Preboreal the eastern regions of that zone. The theriofauna of western and eastern parts of that zone had some differences in their compositions.

Present in the mammal composition of the western part of that zone were: *Talpa europaea*, *Meles meles*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, and absent were: *Microtus gregalis*, *Vulpes lagopus* and *Rangifer tarandus*. The majority of species in this mammalian assemblage are connected with deciduous forests and semi-open landscapes.

IV. Pine-birch and pine-spruce forests with broad-leaved elements and patches of forest-steppe communities

This ecosystem covered the territory lying approximately between 50–55°N in Western Europe and between 50–62°N in Eastern Europe, and has a character that is transitional between the Late Pleistocene periglacial complex and the Holocene forest complexes, with *Abies*, *Pinus*, *Picea*, *Ulmus*, *Fraxinus*, *Corylus*, *Quercus*, *Tilia*, *Alnus*, *Populus*, Chenopodiaceae, *Artemisia*, Poaceae and Ericales. These were the landscapes of pine, spruce and birch forests with broad-leaved species (*Corylus*, *Tilia*, *Ulmus* and smaller proportions of *Quercus* and *Fraxinus*), locally with forest-steppe phytocoenoses and sometimes with small patches of tundra-steppe plant communities. The mammal assemblage included three groups of species. The first group consisted of species of open landscapes that lived there from the Pleistocene: *Ochotona pusilla*, *Microtus gregalis*, *Vulpes lagopus*, *Equus* (*Equus*) sp. and *Rangifer tarandus*. The second group consisted of sparse forests and forest landscape species*: Talpa europaea, Lepus timidus*, *Sciurus vulgaris*, *Sicista betulina*, *S. subtilis*, *Mus musculus*, *Apodemus agrarius*, *S. flavicolis*, *S. sylvaticus*, *Microtus agrestis*, *M. arvalis*, *Clethrionomys glareolus*, *Cricetus cricetus*, *Martes martes*, *M. zibellina*, *Ursus arctos*, *Meles meles*, *Lynx lynx*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus*, *Alces alces*, *Bos primigenius* and *Bison bonasus.* This group also included species connected with broad-leaved forests: *Muscardinus avellanarius*, *Eliomys quercinus*, and *Glis glis.* The third group consisted of widespread azonal species: *Castor fiber*, *Arvicola terrestris*, *Canis lupus* and *Vulpes vulpes*.

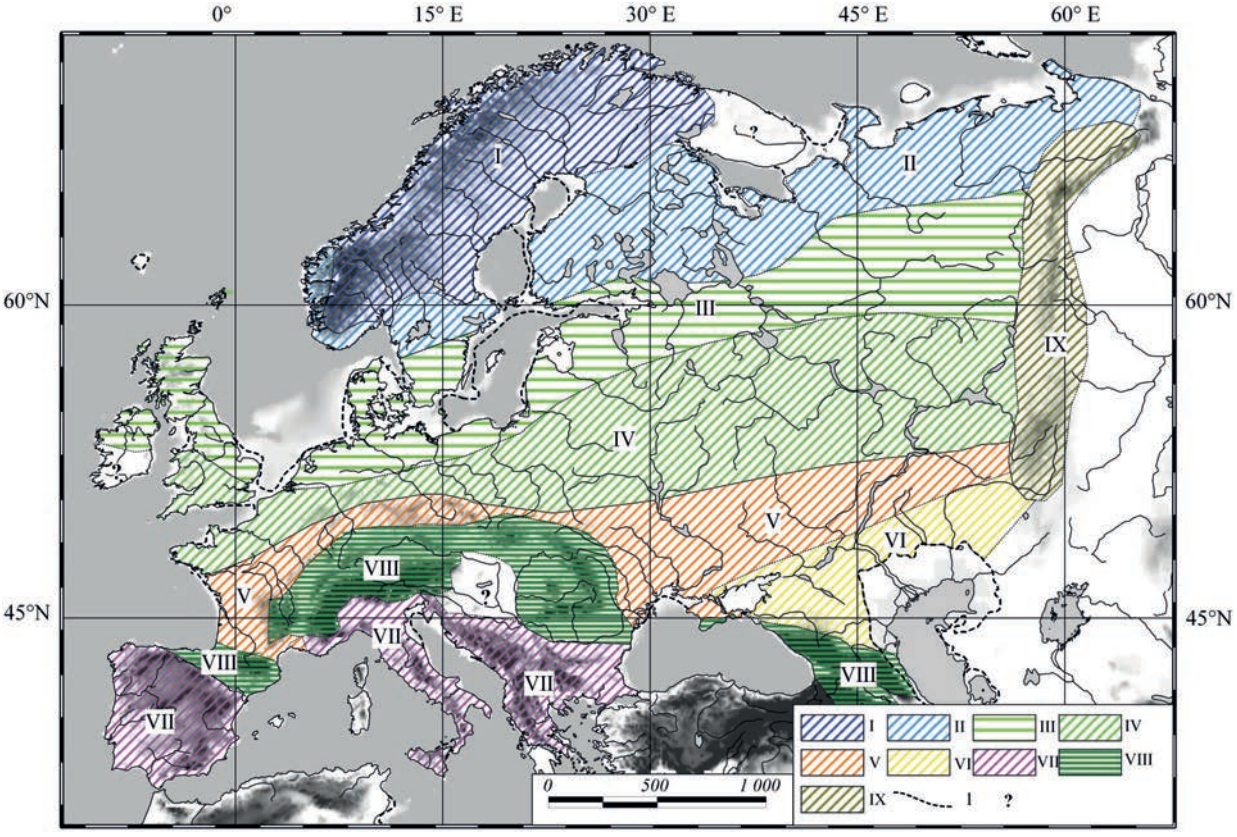

Fig. 6.4. *Preboreal-Boreal ecosystems: I – shrub tundra with patches of forest-tundra; II – forest-tundra; III – light pine-birch forests with patches of tundra communities; IV – pine-birch and pine-spruce forest with broad-leaved elements and patches of forest-steppe communities; V – forest-steppe; VI – steppe; VII – Mediterranean xerophytic coniferous-broad-leaved forests with herbaceous communities; VIII – mountain coniferous-broad-leaved forests; IX – The Ural Mountains forest with patches of tundra-steppe communities; ? – absence of data;1 – coastline*

V. Forest-steppe

Another complex occupied the larger part of Western and Central Europe, except for the mountain regions. It is characterized by well differentiated from each other forest and forest-steppe palaeophytocoenoses with *Pinus*, *Corylus*, *Quercus*, *Tilia*, *Ulmus*, *Carpinus*, *Artemisia*, *Ephedra*, Chenopodiaceae, Poaceae and others. The mammal assemblages included two species groups: the semi-open landscape species group with *Lepus europaeus*, *Apodemus agrarius*, *S. flavicolis*, *S. sylvaticus*, *Microtus agrestis*, *M. arvalis*, *Cricetus cricetus*, *Meles meles*, *Equus (Equus)* sp., *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, and *Bison bonasus*, and a widespread species group with *Castor fiber*, *Arvicola terrestris*, *Canis lupus* and *Vulpes vulpes*. *Microtus gregalis* inhabited the eastern part of this zone. Two causes for this may exist. Either the differentiation rate of the vegetation cover is higher than that of the mammal fauna, or a large degree of the vegetation cover is mosaic as a result of retention of open spaces in the forming forest communities. We are apt to hold the second cause of noted inconsistency between the degrees of differentiation of the vegetation cover and theriofauna in the early Holocene in Europe.

VI. Steppe

The phytocoenoses of grass and *Artemisia* or *Artemisia* and Chenopodiaceae are widespread in the southern regions of the Russian Plain. The mammal data are absent for these territories.

VII. Mediterranean xerophytic coniferous-broadleaved forests with herbaceous communities

During the PB–BO, natural complexes of forest-steppe and mountain forests of pine – broad-leaved species (*Abies*, *Alnus*, *Acer*, *Corylus*, *Fraxinus*, *Fagus*, *Tilia*, *Quercus*, *Ulmus*, and *Carpinus*), in combination with grass steppes (Poaceae, *Artemisia*, Chenopodiaceae, *Ephedra*, and Asteraceae *Plantago*) (south of the Apennine and Balkan Peninsulas) were reconstructed in southern Europe. The mammal assemblage of this zone included: *Oryctolagus cuniculus*, *Marmota marmota*, *Sus scrofa*, *Capreolus capreolus*, *Cervus elaphus*, *Bos primigenius*, *Canis lupus*, and *Vulpes vulpes*, and different species of dormice and mice. These assemblages can be considered as relict assemblages. Their areas, species compositions of mammals and higher plants changed insignificantly after the Pleistocene–Holocene transition. Probably, one of the main changes in their composition was the increase in the number of species connected with forest vegetation.

VIII. Mountain coniferous-broadleaved forests

The mammal assemblage is connected with the mountain systems of southern Europe and occupies the territory where coniferous-broad-leaved forests occur in mountain regions (in the Alps and Carpathians, with *Carpinus*, *Corylus*, *Quercus*, *Fagus*, *Abies*, *Pinus*, and *Picea*; in the Pyrenees *Pinus*, *Quercu ofs*, and *Corylus*, and in the Crimea with *Pinus*, *Ulmus*, *Corylus*, *Quercus* and *Tilia* participation). The mammal assemblage of this zone, as in the Pleistocene, was characterized by a high diversity. This was connected with highly mosaic biotopes in the mountains. Three groups of species can be distinguished in that mammal assemblage composition. The first group consists of mountain species: *Marmota paleocaucasica*, *Mesocricetulus brandti*, *M. raddei*, *Prometheomys schaposchnikovi*, *Microtus daghestanicus*, *M. majori*, *Chionomys nivalis*, *Cuon alpinus*, *Rupicapra rupicapra*, *Ovis* ssp. and *Capra* ssp. The second group consisted of species connected with forest-shrub plants: *Lepus europaeus*, *Martes martes*, *M. foina*, *Meles meles*, *Ursus arctos*, *Sus scrofa*, *Cervus elaphus*, *Capreolus capreolus* and *Bison bonasus*. The third group consisted of widespread azonal species: *Arvicola terrestris*, *Canis lupus*, and *Vulpes vulpes*.

IX. The Ural Mountain's forest with patches of tundra-steppe communities

The PB–BO plant data are absent for the Urals. Remarkable for the PB–BO mammal assemblage in the Urals is the conservation of species of the mammoth assemblage: *Lepus tanaiticus*, *Coelodonta antiquitatis*, and *Megaloceros giganteus*. The mammals included species of different ecological groups adapted to arctic, steppe, and forest environments. The arctic species group included: *Dicrostonyx torquatus*, *Lemmus sibiricus*, *Microtus gregalis*, *Vulpes lagopus* and *Rangifer tarandus*. The steppe species group included: *Ochotona pusilla*, *Marmota bobak*, *Spermophilus major*, *Cricetulus migratorius*, *Lagurus lagurus* and *Eolagurus luteus*. The forest species and forest-steppe species groups include: *Sciurus vulgaris*, *Sylvaemus sylvaticus*, *Clethrionomys rufocanus*, *C. rutilus*, *C. glareolus*, *Microtus oeconomus*, *M. agrestis*, *Martes zibellina*, *M. martes*, *Meles meles*, *Ursus arctos*, *Cervus elaphus* and *Alces alces*. The group of widespread species includes: *Castor fiber*, *Arvicola*

terrestris, *Canis lupus*, *Vulpes vulpes*, *Mustela nivalis* and *M. erminea*.

It should be noted that a large number of sites containing this complex is situated in the Urals, the territory where no reconstructions of palaeophytocoenoses were done. Here, large plots of steppe phytocoenoses could probably exist in the low mountain areas. As a result, a large group of steppe species is present among the indicator species. The assemblage composition and structure show that very different landscapes and biotopes occurred in the Preboreal–Boreal of the Urals.

Conclusion

The combined analysis of mammal assemblages and palaeophytocoenoses of Europe in the Preboreal–Boreal allows us to make general reconstructions of the ecosystems of that time. The natural complex of Northeastern Europe is the boreal forest ecosystem, which includes also some relict elements of the Late Pleistocene periglacial complex. At the middle latitudes, the ecosystem has a character transitional between the Late Pleistocene periglacial complex and the Holocene forest complexes. It was during this period that the ecosystems reached a zonal pattern on the European continent. As a whole, a good ecological correlation between the species composition of distinguished mammal assemblages and corresponding palaeophytocoenoses in the Preboreal–Boreal in Europe should be noted. Probably, in the most parts of Europe, the main natural Holocene complexes were formed between the middle and the end of the Boreal.

Chapter 7

THE GEOGRAPHIC RANGE OF MODERN HUMANS: DYNAMICS OF THE NORTHERN RANGE LIMIT AT THE PLEISTOCENE–HOLOCENE BOUNDARY (<25 – ⩾8 KYR BP)

Alexander Verpoorte

Introduction

The Pleistocene–Holocene transition is characterized by a major transformation in the ecosystems of Eurasia. It involves tremendous shifts in vegetation, changes in faunal associations and the extinction of numerous species (Chapters 4–5). In an elegant paper on North America, Guthrie (1990) has summarized the Late Pleistocene faunal revolution in four aspects:

1) shifts in geographic ranges;
2) community reorganizations, in this case fractionation;
3) evolutionary spurts;
4) extinctions.

The largest shift in geographic range of all species concerns the geographic range of humans. Anatomically modern humans reached a near-global distribution in the early Holocene. How did this range expansion take place? How is it related to the climatic changes in the Pleistocene–Holocene transition? What is the role of human range expansion in the Late Pleistocene faunal revolution? This chapter provides a main outline of the geographic range of modern humans in Europe between 25,000 and 8,000 years ago. This period covers two major climatic 'events':

1) the Last Glacial Maximum (LGM) with the maximum extent of the continental ice sheet in Europe
2) the rise in temperature and precipitation towards the Holocene, interrupted by the Younger Dryas cold spike.

These 'events' had a major impact on human populations, but their effect on the range limit is different across Europe. The focus of this chapter is on the description of the dynamics of the northern range limit in relation to these main climatic 'events', but I will first introduce the principal character of the story, the anatomically modern human making a living by hunting and gathering.

Hunter-gatherers: general characteristics and main trends

Analysis of the few remaining hunter-gatherer societies of the modern world provides some general expectations for the way of life of the humans populating Late Pleistocene and early Holocene Europe. We can expect them to be mainly dependent on the exploitation of animal resources, to use a mobility strategy of frequently shifting camps to exploit the environment, and to live at low population densities. Archaeology generally supports these expectations, but provides a much more subtle picture of variations and change. I will try to sketch the main developments in the archaeological record from 25,000 to 8,000 years ago in Europe north of the Alps.

In archaeological terms, the period covers the transition from the Middle Upper Palaeolithic to the Early Mesolithic. What happened?

The only species of *Homo* left in the period between 25,000 and 8,000 years ago is the one to which both the author and reader belong: *Homo sapiens sapiens*; anatomically modern humans. The last of the Neanderthals died a few thousand years earlier in southern Spain and maybe in Croatia. Few changes seem to occur in the anatomy of modern humans in this time period, though Holliday (1997) reports differences in body shape, body size and stature between early modern humans before the LGM and later modern humans (Late Palaeolithic and Mesolithic). Holliday (1997) interprets these changes as adaptations of modern humans of African decent to the colder conditions in Late Pleistocene Europe.

These modern humans make use of a common cultural repertoire, including the use of fire, clothing and shelters. Control of fire, known for at least 250,000 years, provided protection against the cold and against predators, options for preparing food, and a focus of social life of the group. Fireplaces of different type are known throughout the period and often form the focal point of find distribution patterns. Clothing can be inferred from the position of ornamentation in burial contexts. It provided protection as well as a means to display identity. The first clear evidence of clothing comes from Middle Upper Palaeolithic burials in Italy, the Czech Republic and Russia. Fine needles, found frequently from the Middle Upper Palaeolithic onwards, were probably used in the making of clothes. Shelters such as tents, huts or yurt-like structures provided protection against rain, wind and cold, and offered a home to return to with goods to share among the group. The archaeological record is generally sparse in good evidence for dwellings, but the first convincing examples date to 30–25 thousand years ago. In addition to these features, common to the whole period at stake, some trends are visible in subsistence, mobility strategy, and related technologies.

Generally, the subsistence changes at the Pleistocene-Holocene transition are seen as a transition from specialized big game hunting to a broader resource base including more plant foods as well as marine and freshwater resources. The Late Palaeolithic specialized reindeer hunter was replaced by the Mesolithic solitary hunter, fisher and gatherer of hazelnuts. The transition was characterized as the broad-spectrum revolution. Recent studies of Upper Paleolithic subsistence have added some nuances to this picture. The degree of specialization on a single species differs considerably from site to site and period to period. Small game had been largely overlooked and seems to play a more important role in subsistence than previously acknowledged (Stiner *et al.*, 2000).

Studies of the stable isotope signatures of human bone, indicating the overall diet of roughly the last decade of life, provide an additional line of evidence and have caused considerable debate. Richards *et al*. (2001) report a substantial input of freshwater fish in the diet of 25,000-year-old hunters in Kostienki on the Russian Plain. They suggest a broad-spectrum revolution in the Upper Palaeolithic related to a larger population size. Aldhouse-Green and Pettitt (1998) note stable isotope levels that indicate 15 to 20% marine resources in the diet of Paviland man (Wales) 26,000 years ago. Similar levels were reported from a 12,000 year old skeleton from Cap Blanc in France (Hayden *et al.*, 1987). Studies of Late Palaeolithic human remains in Great Britain show a lot of variation with one group being strongly dependent on marine resources and a close-by group relying almost completely on terrestrial herbivores (Richards *et al.*, 2000). These data all indicate, as expected, a high dependence on animal food, whether from the land or from water. Plant foods are virtually invisible in the Upper Palaeolithic record.

The plant foods become more visible in the early Holocene with better preservation in wetland conditions. However, the stable isotope signatures of English and Danish material do not show a significant increase of plant food in the overall diet. Rather than subsistence types replacing each other over time, the present picture shows a range of subsistence strategies in relation to changing environmental conditions.

One aspect of these subsistence strategies is mobility. Upper Palaeolithic hunter-gatherers *grosso modo* operate from a campsite occupied for a long time that is strategically located with respect to mobile and aggregated food resources. Small groups may procure resources at relatively long distances from the central campsite. In the course of the Late Palaeolithic and Mesolithic, this logistical strategy (‘collectors’) grades into a strategy of frequent relocation of campsites towards more localised resource patches (‘foragers’). This gradation in mobility strategies is translated in the archaeological record. At the ‘collector’ extreme are the substantial living structures with pits and long-lived fireplaces, known from the Middle Upper Palaeolithic of Central and Eastern Europe. Towards the ‘forager’ extreme is the early Mesolithic record of small scatters of stone artefacts, bone fragments and a fireplace.

The trend in mobility strategy is accompanied by a trend in the size of the territory covered by a group of hunter-gatherers. In general, territory size and annual range size increases with latitude. At similar latitudes, the annual range is expected to decrease from the Upper Palaeolithic to the Mesolithic due to changing environmental conditions. Transport distances of raw materials and stylistic ‘provinces’ provide support to this expected trend. There are also other, more direct indications of mobility. Stress features in the locomotive apparatus, e.g. in the lower limbs of the Sungir (Russia) remains, indi-

cate long-distance movements with considerable loads (Mednikova and Trinkaus, 2001). The find of skis at the early Holocene site of Vis in Northern Russia indicate a technological innovation to lower mobility and transport costs in winter snow.

Characteristic from the Early Upper Palaeolithic onwards is the widespread use of organic materials (bone, antler, ivory, wood) for all sorts of tools. The use of composite tools with stone insets seems to become more important. The transition from the Middle Upper Palaeolithic to the early Mesolithic is marked by a number of subsistence-related technological developments in these sorts of tools. The first positive evidence of the use of a spearthrower is about 22,000 years old from the Solutrean in France. Harpoons were first made around 18,000 years ago, also in France. The use of bow-and-arrow is heavily debated, but the first direct evidence in the form of arrows dates to 11,000 years ago at the Ahrensburgian levels of Stellmoor in Northern Germany. Specialized fishing gear occurs for the first time in the early Holocene. Early Holocene sites such as Star Carr in England, Friesack in Germany and Vis in Northern Russia demonstrate the extensive use of plant-derived materials for a wide range of tools, from lining and digging sticks to nets and baskets to skis. These technological innovations affect a variety of foraging costs: search time, hunting success, transport possibilities, etc.

A special case is the domestication of the dog, with the oldest evidence in Eliseevich (15,000 years old) on the Russian Plain and in Bonn-Oberkassel (11,000 years old) in Germany (Sablin and Khlopachev, 2002). These dogs could play a role in tracking, pursuing and collecting game. Other domesticates enter the European scene at a later date in the Holocene and are beyond our interest here.

Though population densities must have been low, estimating population size and density on the basis of archaeological data remains highly problematic. Site size, the number of sites, the number of radiocarbon dates and evidence of resource depletion have all been used as approximations for population size, but their relation to population size is far from straightforward. Many other factors are involved. Simulations of population dynamics at different densities indicate the potential importance of trends in population density. Boone (2002) shows that the amplitude of fluctuations in size and the possibility of population crashes change with population density levels. These population density levels are dependent on the productivity of the environment, in particular prey availability. Therefore changes in the productivity of the environment at the Pleistocene-Holocene transition are expected to have population effects influencing regional settlement systems.

This short overview of the Palaeolithic between 25,000 and 8,000 years ago sets the stage for the main focus of this chapter. The range shifts are taken here as evolutionary and ecological responses of modern humans depending on the mentioned qualities and strategies to the changes taking place in their environment.

Archaeological approaches to the human geographic range

In the preface to his bestseller *'Timewalkers: the prehistory of global colonization'*, Clive Gamble describes that the question of *why* humans have a near-global – and since the International Space Station even beyond-global – distribution is a recent one: *"The fact that people were almost everywhere raised no eyebrows, even when discovered on remote islands, across inhospitable deserts, and up rugged mountains. While the great voyages of discovery that began with Columbus gradually uncovered the near totality of prehistoric colonization, this was rarely seen as an issue requiring the attention of the new science of human prehistory which appeared in the middle of the nineteenth century when the adventure of global empires had reached maturity." (1993, ix)*

Archaeological approaches to why humans are almost everywhere have focused on the question of first colonization: the first wanderings out of Africa, the first colonizations of northern latitudes, the first modern humans in Europe, the first occupation of the Americas and Australia, and so forth. A major emphasis is on chronology as debates centre on the timing and speed of colonizations. There have been recent advances in dating techniques for the period at stake, in particular the use of AMS-dating on bone. The number of dates is now considerable, especially for rich parts of the world like Western Europe. The increased chronological control allows for comparisons of archaeological patterning with high-resolution environmental records such as long pollen sequences and ice-core data.

Other issues have been addressed as well. For example, how does colonization take place? In recent studies the attention has shifted to the *process* of expansion and its archaeological 'signature'. A study of the recolonization of Northwest Europe after the last glacial maximum proposes a twofold process (Housley *et al*., 1997). The initial, so-called pioneer phase consists of seasonal exploitation of a region. The seasonal exploration paves the way for the establishment of a year-round settlement system later on. Another frequently used division is that between wave-of-advance-models, where a front of occupation gradually moves into new territories, and directional models, where a propagule moves over long distances to a suitable location for settlement and the founding of a new population.

The focus on first colonizations seems to suppose that colonization results in continued presence, but does

it? First of all, an ebb-and-flow-model is more realistic. Second, continuity is dependent on the geographical and temporal scale of study. Continuous settlement in one millennium maybe part of discontinuity at both the scale of ten millennia and of centuries. Settlement can be continuous at a 200×200 kilometre grid, but discontinuous at a grid size of 50×50 kilometres.

In fact, colonizations can be taken as a specific case of the more general phenomenon of range limit shifts in dynamic biogeography. The questions concerning chronology, process and continuity concern three aspects of the range limit in general: its structure in space, its dynamics over time, and the factors controlling its structure and dynamics, i.e. the relationship of the biological (including cultural) attributes of a species and the spatio-temperal variation in its environment. The main aims of this chapter are to describe the range limit position over time and space and to identify patterning in regional range trajectories. As mentioned before I restrict myself to the northern range limit only.

Data and methods

The study area is the European continent north of the main mountain chains (Alps and Pyrenees) and main water bodies (the Mediterranean and Black Sea). I have divided this middle and high latitudinal part of Europe into four sections: Western Europe, Central Europe, Eastern Europe, and the Urals. Two sorts of data have been included in this study:

1) archaeological sites, that is findspots of artefacts
2) human remains, frequently burials at archaeological sites.

In comparison with the palaeontological data used in the other chapters in this volume, the record for modern humans has several advantages:

1) the archaeological record consists of artefacts rather than the humans themselves; these artefacts are much more frequently discarded than human and animal skeletons

2) among these artefacts are stone artefacts that preserve much better than organic materials such as skeletons; stone artefacts are preserved under a wider range of depositional circumstances

3) the archaeological record contains information on behavioural traits that are more indirectly preserved in the record of other animals.

The comparison of the records for modern humans and other animal species is therefore not straightforward. They are the result of different taphonomic histories and processes. The methodology applied to identify the range limit is simple. First, I collected site information (in particular coordinates and dates) for each country involved. Second, these sites were attributed to the time-windows (discussed in Chapter 3). However, in order to get a good view of the dynamics of the human range, I had to make a slight modification in the time frame. I include an earlier time-window for the period of 29,000 to 24,000 years ago as a base-line and I divide the time-window of 17,000 to 12,400 years into two phases: before and after 14,000 years. Third, maps were created with locations for each time-window. Fourth, the northern-most locations were connected with a line, forming the northern range limit for the time-window. Fifth, the time-windows were compared to create a trajectory of latitudinal shifts for each geographical section.

The data have been collected from the scientific literature, in particular national overviews and catalogues, recent collections of papers on the periods at stake, and available datelists. This has introduced a bias due to the accessibility of information in terms of language and availability. This bias is limited due to two selection criteria: the focus on sites relevant for the reconstruction of the northern range limit rather than a representative overall distribution pattern, and a preference for sites dated by radiocarbon because of the publication of many radiocarbon dates in datelists and overviews.

A crucial aspect of the data used is the attribution of the archaeological site to one of the time-windows used in this project. The assignment of a data point to a time-window is based on the available radiocarbon dates, interpreted with additional information on archaeology, biostratigraphy and geology (Table 7.1).

Table 7.1

Overview of data per time-window

Time-window	N site	%	Certainty of age attribution (%)			N/1.000 ^{14}C yrs
			Low	Medium	High	
29–24 kyr	80	14.4	21.3	32.5	**46.2**	16
24–17 kyr	118	21.3	5.1	37.3	**57.6**	16.9
17–12.4 kyr	99	17.9	12.1	**47.5**	40.4	21.5
12.4–10.2 kyr	114	20.6	33.3	**42.1**	24.6	51.8
10.2–8.0 kyr	143	25.8	35.0	**35.7**	29.3	65
Total	554	100				

Note: High certainty: reliable radiocarbon dates supported by typochronology and/or stratigraphy.

Medium certainty: mainly typochronological indicators.

Low certainty: limited information and/or inconsistencies between age indicators.

The age attribution can come with several complications that are worth some consideration. These com-

plications are the quality and quantity of dates and the association of dates with human activity. Having multiple age estimates for one archaeological site can be preferred over a single date, but it is not always a blessing. Take for example the series of dates on the site of Paviland in Wales (Aldhouse-Green and Pettitt, 1998). The dates range from 29,000 to 21,000 years radiocarbon (Fig. 7.1.). The oldest dates fit in the earliest time-window of 29,000 to 24,000 years ago and the younger ones in the window of 24,000 to 17,000 years ago. However, a closer look reveals that the age estimates are associated with different dated materials. The older ones are on burned bones, the younger ones on ivory and bone tools, and the middle ones on human bone from the burial for which the site is renowned. Because the younger dates could be the result of contamination by preservation agents, I put the site in the earlier time-window on the basis of the dates on human bone. Another example comes from the site of Moravany-Zakovska in Slovakia where three radiocarbon dates are available: 18,100 years on charcoal, 24,230 years on charcoal and 22,340 years on bone (Fig. 7.2). Two different laboratories produced the two charcoal dates. Accepting one or the other puts the site in a different time-window. On the basis of the bone date and dated sites in the wider region I have assigned the site to the younger time-window, though I regard the 18,000 year date as less reliable than the older ones (Verpoorte, 2002). Sinitsyn and Praslov (1997) have shown

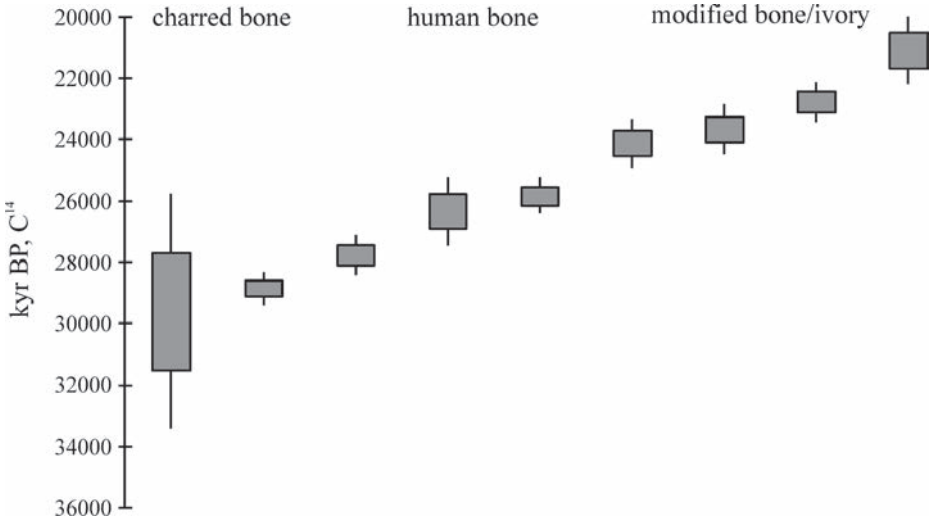

Fig. 7.1. *Radiocarbon dates for Paviland cave, Great Britain (after Aldhouse-Green, Pettitt, 1998)*

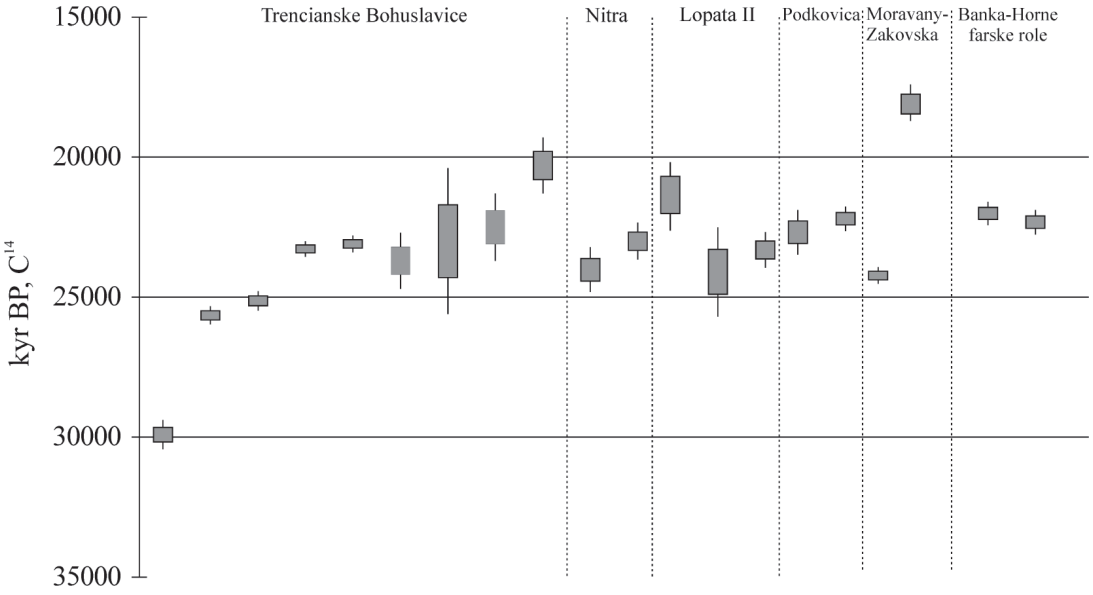

Fig. 7.2. *Radiocarbon dates for Upper Palaeolithic sites in the Slovak Republic*

similar problems with series of dates from the Russian Plain. In describing the range limit position I will discuss crucial assignments of northern sites where necessary.

A second complication is the association of dates with human activity. An illuminating example comes from the Belgian Ardennes (Charles, 1996). A series of dates is available for Magdalenian sites ranging from 16,000 to 12,000 years ago (Fig. 7.3). However, the systematic dating of cut-marked bones failed to produce dates older than 12,800 years ago. The older dates are not associated with human presence in an unambiguous way and are therefore not included in the picture.

A third complication is that the standard deviation of the radiocarbon dates may be such that attribution to more than one time-window is possible. This is particularly problematic in the case of the Younger Dryas. Assigning sites to the Younger Dryas on the basis of a date is virtually impossible and therefore this time-window is not treated separately as too few reliable data are available.

Finally, another problem arises in the Late Palaeolithic and Early Mesolithic. Many sites are known as surface scatters of stone artefacts only, in particular in cover sand regions. The numerous sites in Belarus, the Baltic states, Russia and the northern Ukraine are an example of this. No organic materials are preserved and therefore no radiocarbon dates are available. Assignment to a time-window must then be based on typochronology, the chronological 'value' of specific artefact types.

The complications of attributing sites to time-windows is most crucial for the northern-most locations, but two other biases need to be mentioned that have a more general influence. On the one hand research intensity and on the other hand geological processes of erosion and sedimentation. Even a cursory look at Palaeolithic and Early Mesolithic research in Europe shows a contrast in the number of excavations, number of researchers and number of radiocarbon dates between Western Europe and the other three sections. As a result the information is more dense in Western Europe and that picture could be more refined than I will sketch it in the next paragraphs. It is impossible to judge whether the difference in research intensity influences the main outline of what happens to the northern range limit at the Late Pleistocene-Holocene transition, but it certainly limits the detail at which regional trajectories can be compared.

The second bias is the geological history of Europe. The major advances of the continental ice sheets at the last glacial maximum have overrun potential traces of previous occupation in areas such as Denmark, Southern Sweden, Northern Poland and the Baltic states. Widespread coversand deposits of the Late Glacial cover possible archaeological sites of the late Pleniglacial, particularly on the northern European Plain and northern Russia. These two processes have a direct impact on the visibility of the northern range limit in the period before the last glacial maximum. The preservation and find chances of traces are diminished.

In addition other geological processes have done their eroding or covering work. Drowning of the North Sea basin, Holocene deposits at the margins of the North Sea, the Baltic Sea and in large river basins such as the Middle Danube (Hungary) and Pripjat (Ukraine) make Late Pleistocene deposits largely inaccessible for investigations in these areas. Large-scale soil erosion in the early and late Holocene may have removed Upper Palaeolithic and Mesolithic open-air sites in many higher parts of Europe. These processes do influence the overall picture, but have only limited influence on the reconstruction of the northern range limit.

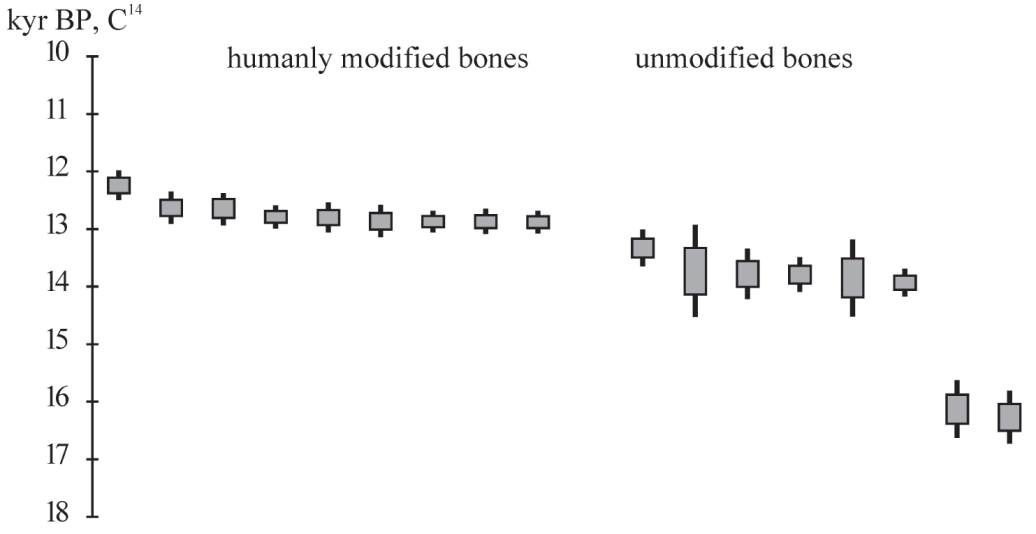

Fig. 7.3. *Radiocarbon dates for the Magdalenian in the Belgian Ardennes*

Defining the range limit

What is actually the range limit? Hunter-gatherer groups can move to the north in summer and south in winter. Small groups can move widely dispersed and far away from more densely occupied regions. They can use a far-away region once in several decades or for a few decades in the course of many centuries or even millennia. Gorodkov (in Gaston, 2003) has made a useful division of the range limit structure. He distinguishes between five zones (Fig. 7.4):

1) the zone of continuous distribution leaving only small lacunae of unsettled space;

2) the zone of disjunct distribution with more isolated populations;

3) the zone of periodic extinction where populations only exist temporarily;

4) the zone of sterile invasion where individuals are unable to sustain themselves;

5) the zone of corpse removal where only skeletons can be found removed by geological processes from the zone of sterile invasion.

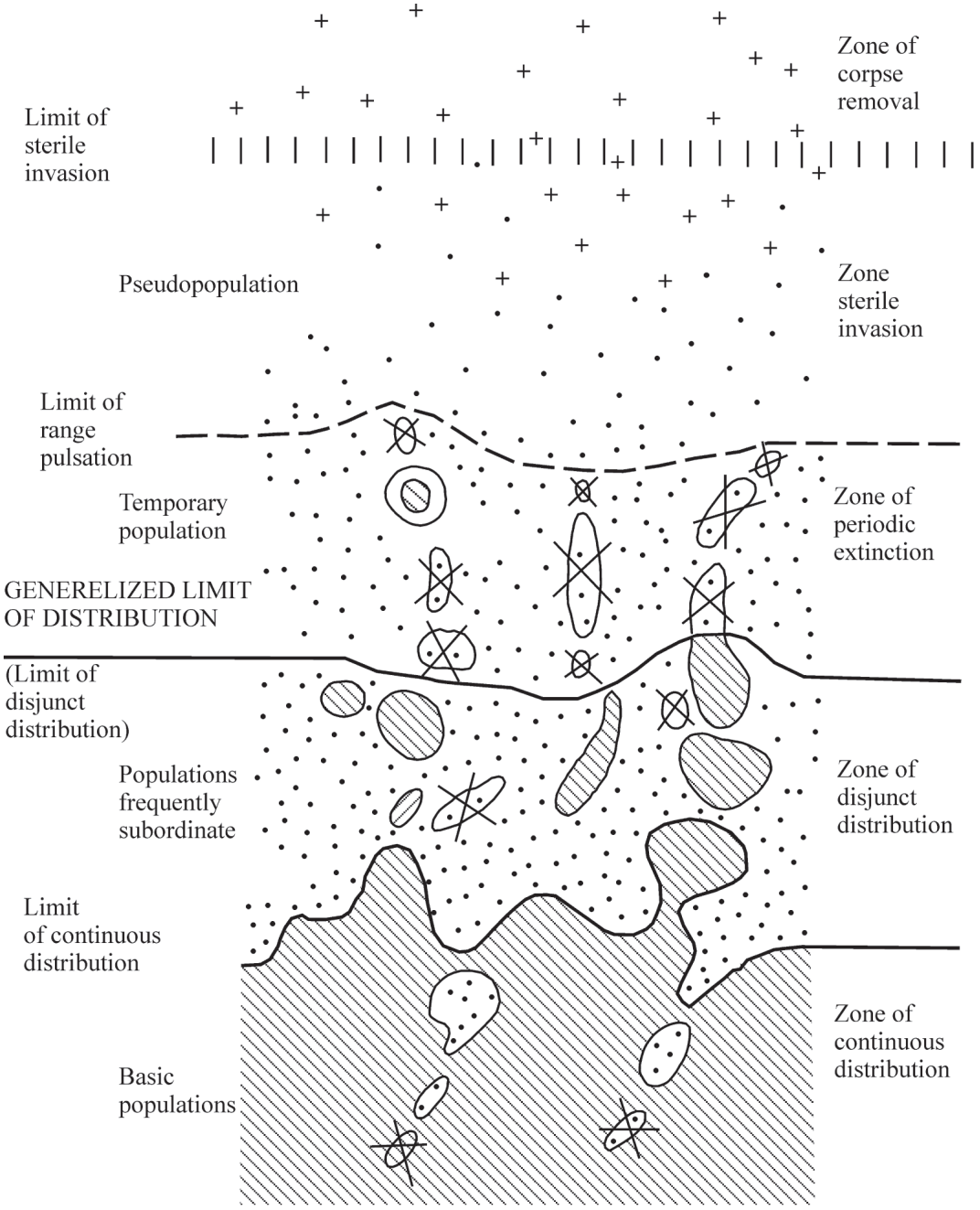

Fig. 7.4. *Schematic representation of the structure of the limit of the geographical range. From Gorodsov (1986)*

Gorodkov defines the generalised limit of distribution as the boundary between the zone of disjunct distribution (2) and the zone of periodic extinction (3). The limit of continuous distribution could be defined as the limit of the habitat of *preference*, whereas the boundary of the zones of periodic extinction and sterile invasion could be defined as the limit of *tolerance* beyond which an individual of the species cannot survive.

But which limit is visible in the archaeological record? Are the most northern sites evidence of temporary populations, disjunct populations, or even visits to the zone of sterile invasion? In theory, the most northern finds could be artefacts left by individuals wandering into the zone of sterile invasion. However, the northern sites included in this study usually indicate temporary presence of a group. These sites can be seasonal camps, short occupational episodes or the only surviving traces of a regional settlement system. Data to distinguish these interpretations are usually lacking. Therefore the limit visible in the archaeological record can best be seen as the boundary between the zones of periodic extinction and sterile invasion, defined by Gorodkov as the limit of range pulsation. What happens to the limit of range pulsation over time?

The northern range limit during the Pleistocene–Holocene transition

How far south did people move in the coldest phases of the last glacial? How far north did they get as soon as the climate was warming up to the present interglacial? In this section I will discuss the position of the range limit for each time window going from east to west (see Fig. 7.5–7.10).

Time window: 29–24 kyr BP (Fig. 7.5)

The maximum extension of the Fennoscandinavian ice-sheet was not reached until 20–18 kyr BP. The growth of the ice sheet seems to have been fast, as mammoths roamed the ice-free south of Sweden until about 24/23 kyr BP. The most northern traces of human presence in this time period have been found on the western slopes of the Ural Mountains. At Byzovaya, located at 65°N on the bank of the Pechora River, a layer of reworked till includes numerous bones (mainly mammoth) as well as palaeolithic artefacts. Radiocarbon dates on bone range from 25.5 to 33.2 kyr BP, mostly around 28 kyr BP. The reworked sediments are covered by a series of aeolian sands. The Palaeolithic artefacts include leaf-like bifacial tools and scrapers. Whether Neanderthals or early modern humans made these artefacts cannot be said. Other northern sites in the Urals are Medvezhya cave (62°N), Garchi I (59°N) and Talitsky (58°N) (Pavlov and Indrelid, 2000).

In the central parts of European Russia, human settlement did not reach as far north. The site of Sungir is located at 56°N, northeast of Moscow. Age estimates differ from about 28 kyr BP to 24/23 kyr BP. Sungir is a large Upper Palaeolithic locality with several burials. The burials include thousands of ivory beads and other ornamentation, probably sewn on clothing. Very few other localities are known and more to the west of Moscow, on the Russian Plain, no sites are located further north than 54°N (Soffer, 1985).

In Central and Western Europe, no trace of humans has been found above 52°N. Research in Polish Silesia, just north of the Sudeten Mountains, has uncovered Gravettian sites near Henrykow and Wojcice (Plonka and Wisniewski, 2002). The site of Bilzingsleben, Germany, is only known from surface collections. The stone tools include some typical Font Robert points (Otte, 1981). Small sites in the north of the Belgian Ardennes and a single find of a Font Robert point in the Meuse valley in the Netherlands form the northern fringe of Gravettian 'settlement' in Western Europe. The site of Paviland in southern Wales is another trace of this range limit. The cave site contained the burial of a red-stained skeleton. It became known as "the Red Lady", but recent anthropological research has shown that the human remains are actually from a man. Few artefacts are attributed to the occupational episode that is associated with the burial, but among them is another Font Robert point.

Though no special attention is paid to a representative sample of sites across Europe, the Hungarian Basin deserves a short remark. In this area, no sites have been found except in the mountainous margins of the basin. This pattern can be explained by geological processes. The centre of the basin is filled with later, Holocene deposits, covering Late Pleistocene sediments. The sediments and the palaeolithic artefacts in them are only accessible for research at the edges of the basin.

Time window: 24–17 kyr BP (Fig. 7.6)

Global climate deteriorates quickly after 24 kyr BP. The continental ice sheets can expand fast, due to the available moisture in the Baltic Sea, and moves onto the northern European Plain. Mountain glaciers in the Carpathians grow larger, flowing further downslope, and the Alpine ice sheet expands more towards the Danube valley. Large parts of the northern ranges are deserted under these climatic and environmental conditions and human populations retreat largely to the Mediterranean zone. Where the evidence is sufficiently detailed, it can be

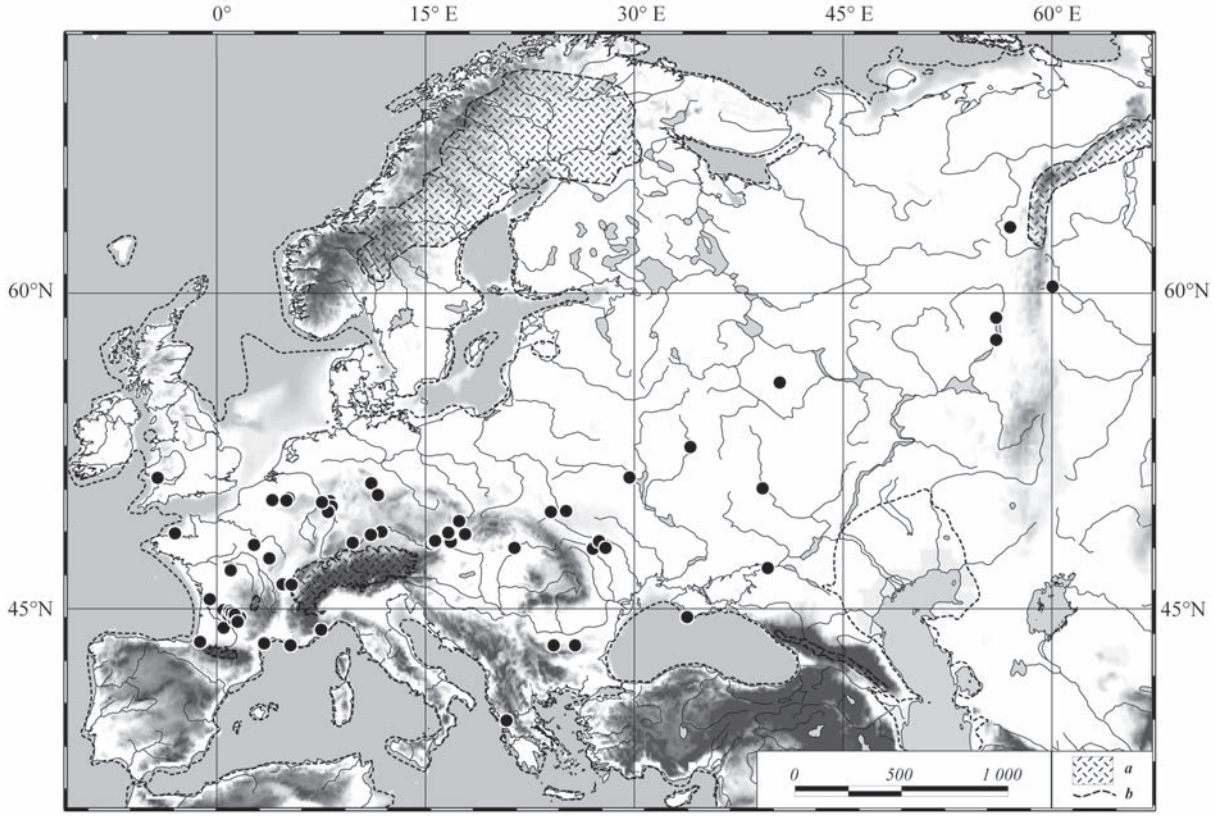

Fig. 7.5. *Human sites corresponding to 29–24 kyr BP: • – human sites, a – ice sheet, b – coastline*

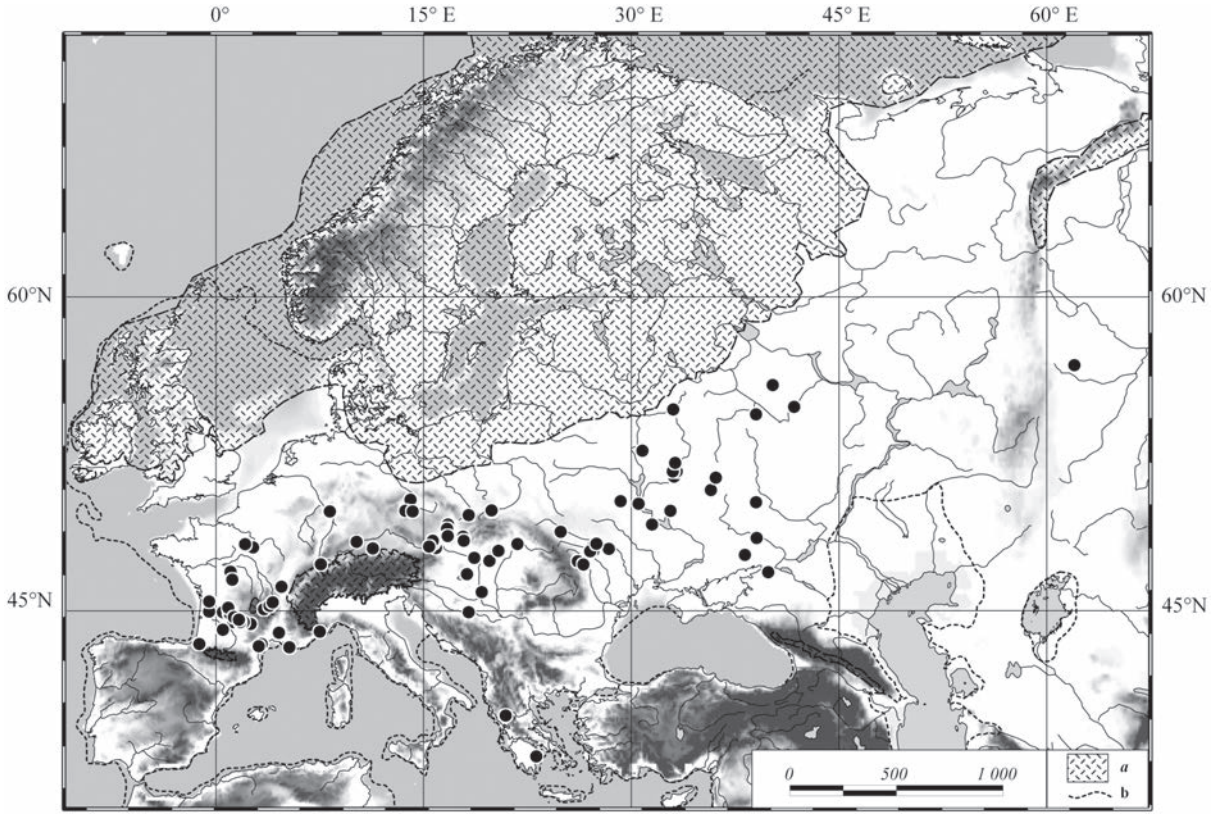

Fig. 7.6. *Human sites corresponding to 24–17 kyr BP: • – human sites, a – ice sheet, b – coastline*

shown that the range contracts in a diverse and sometimes complex pattern.

Occupation in the Urals retreats to the middle and southern Urals. The traces at Bezimannaya cave are the most northern at 57°N. Northern sites in Eastern Europe, such as Sungir and Zaraysk, may have been occupied until about 20,000 years ago, but the data are less clear for the period after 20,000 years. Possibly human occupation was restricted to more southern regions. Central Europe presents a similar picture: traces of human occupation in Southern Poland and Bohemia until 21/20 thousand years and afterwards a move southward to the Middle Danube Basin in Hungary and Austria. The northern ranges of Western Europe seem to be deserted after 24,000 years ago, with the northern limit at the southern edge of the Paris Basin. A surprising deviation from this pattern are several dates of about 19,000 years old for Wiesbaden-Igstadt and Mittlere Klause in Germany and Kastelhöhle-Nord in Switzerland. They suggest a short-lived occupational episode just north of the Alps at 19,000 years ago (Street and Terberger, 2000).

Time window: 17–14 kyr BP
(Fig. 7.7)

The maximum extent of the ice sheets is reached at about 18/17 thousand years ago. Large parts of Europe are deserted under the cold and dry conditions of this period. Human populations are largely limited to the Mediterranean zone (Iberia, Italy, Greece). Artefacts from the cave sites of Dirovati Kamen and Naves Ustinovo and some others indicate presence of humans in the middle Urals. Some data are available for occupation in Eastern Europe; Mezirich and Gontsy in the Ukraine (50 N) with the dates of 15/14.5 kyr BP, several sites in Dnieper, Desna, Don rivers basins also have been found.. Central Europe is virtually deserted after 18/17 thousand years ago. Brno-Videnska in the Czech Republic and Maszycka cave in Poland may be traces of a short-lived, exploratory occupational episode around 15/14.5 thousand years ago (Verpoorte, 2004). In Western Europe, the record shows continued presence of humans in the southwestern part of France (south of the Paris Basin).

Time window: 14–12.4 kyr BP
(Fig. 7.8)

The northern shift of the range limit after the Last Glacial Maximum takes place from about 14,000 years onward. The process of range expansion is not absolutely clear in the Urals and Eastern Europe.. The presence of humans is indicated in Desna, Dniepr, and Don river basins, and also in the Middle Urals. The presence of humans is indicated at the end of the period as far north as the polar circle at the site of Pymva shor (67°N) (we have not this site on the map). Recolonization of Central Europe dates around 13,000 years in Hungary and around 12,800 years in the Czech Republic and Poland. The sites in the Czech Republic and Poland are attributed to the late Magdalenian with many similarities in Western Europe. Housley *et al.* (1997) have drawn a detailed picture of the range expansion out of southwestern France, showing recolonization of the Belgian Ardennes and the middle part of Germany by 12,800 years ago. England and northern Germany (and probably parts of Denmark) were recolonized by the end of the period by the so-called Creswellian and Hamburgian respectively. It is important to note that the range expansion is under way *before* the Bølling-Allerød interstadial complex.

Time window: 12.4–10.2 kyr BP
(Fig. 7.9)

In the Late Glacial only few changes take place in the range limit position. Most important are the traces of occupation in the Polish lowlands. Due to the lack of chronological resolution for most of the database, the impact of the Younger Dryas cold spike cannot be described in detail. The best evidence comes from Northwestern Europe and suggests a retreat from the North Sea Basin region, but hardly any impact further south- and eastwards (also Stuart *et al.*, 2004).

Time window: 10.2–8.0 kyr BP
(Fig. 7.10)

In the early Holocene, the human range expands further northward. Sites in the Russian north and polar Urals are located far above the polar circle. Several sites are located on the northern coast of Norway. In Western Europe, the expansion seems to be slower with sites in Scotland by 9,000 years ago and the first evidence of occupation in Ireland by 9/8.5 ka ago. By 8,000 years ago, modern humans dwelled in the whole of mid- and high latitude Europe.

Regional range trajectories

Three basic processes can be distinguished in the dynamics of the range limit: contraction, stasis, and expansion. As mentioned above, the range limit defined by archaeological data is the limit of range pulsation. The dynamics identified are the shifts in the limit of range pulsation. The data presented above indicate regional differences in the sequence and timing of the range limit

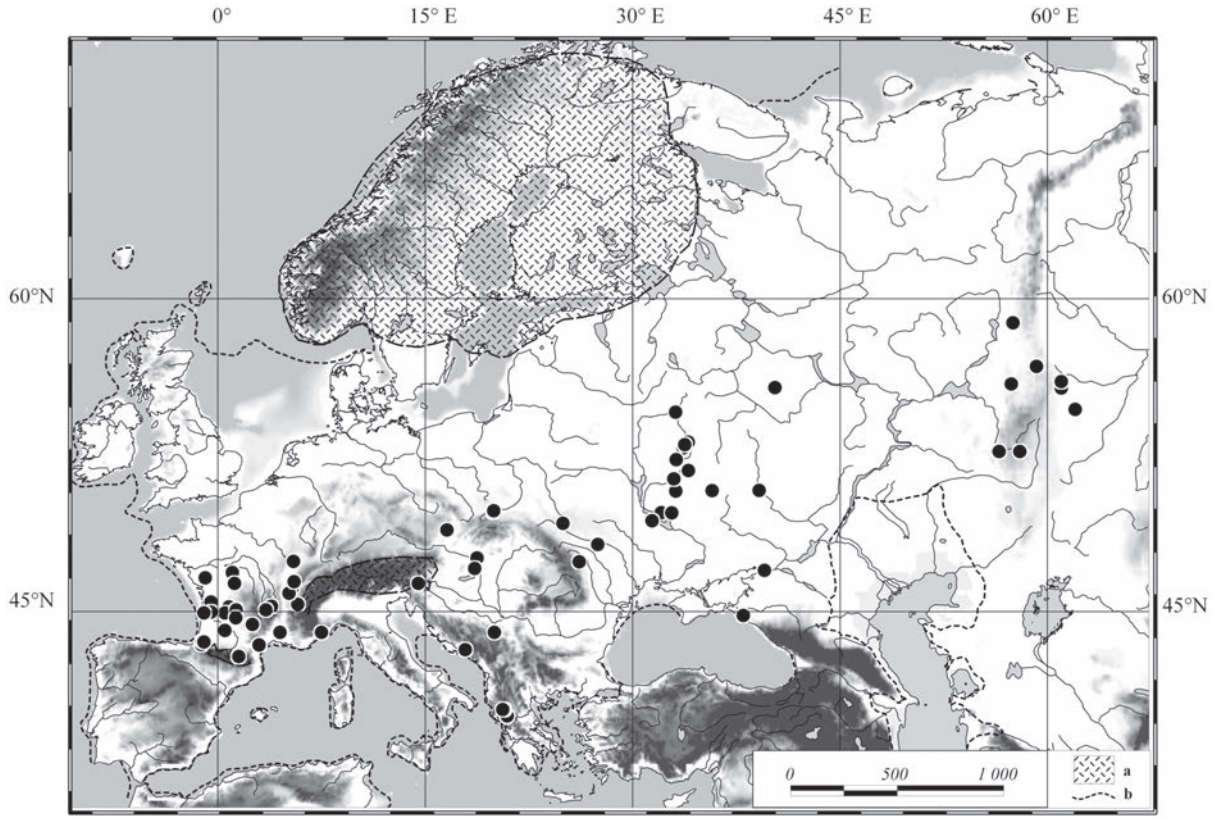

Fig. 7.7. *Human sites corresponding to 17–14 kyr BP: • – human sites, a – ice sheet, b – coastline*

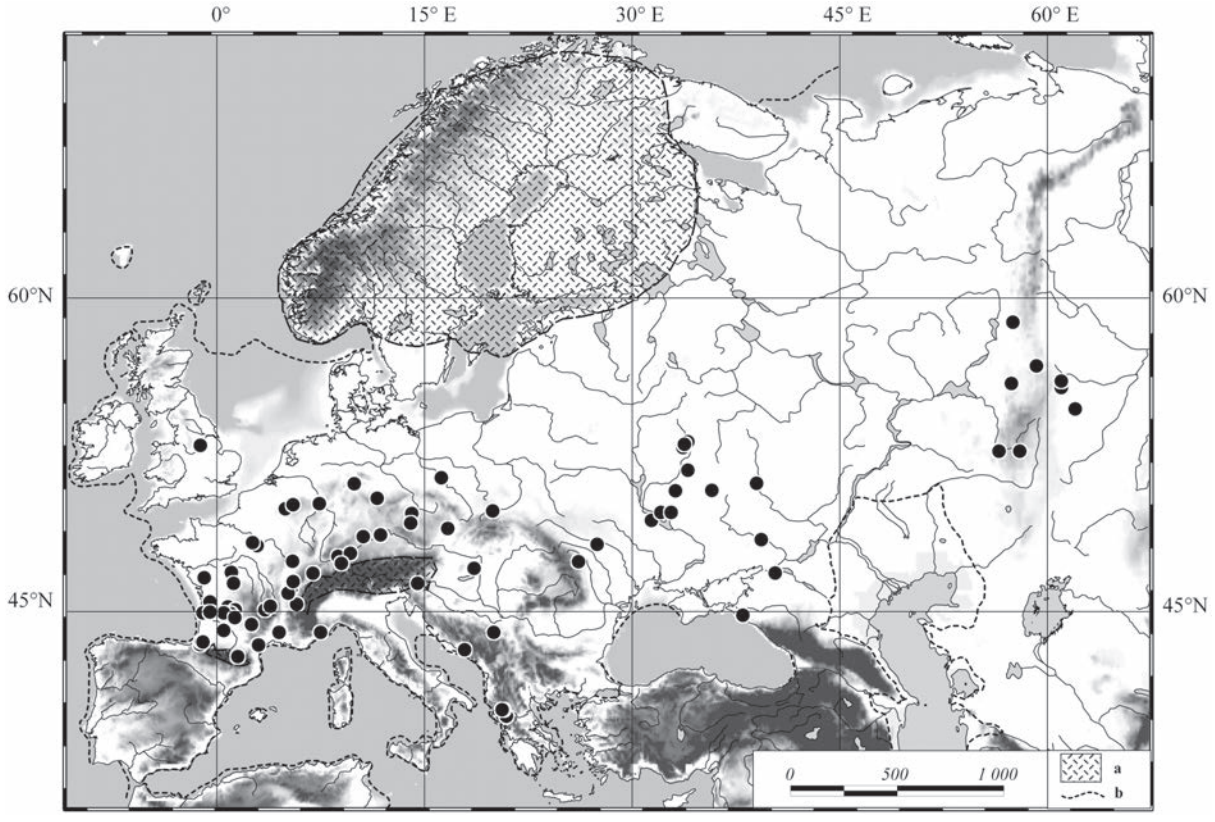

Fig. 7.8. *Human sites corresponding to 14–12.4 kyr BP: • – human sites, a – ice sheet, b – coastline*

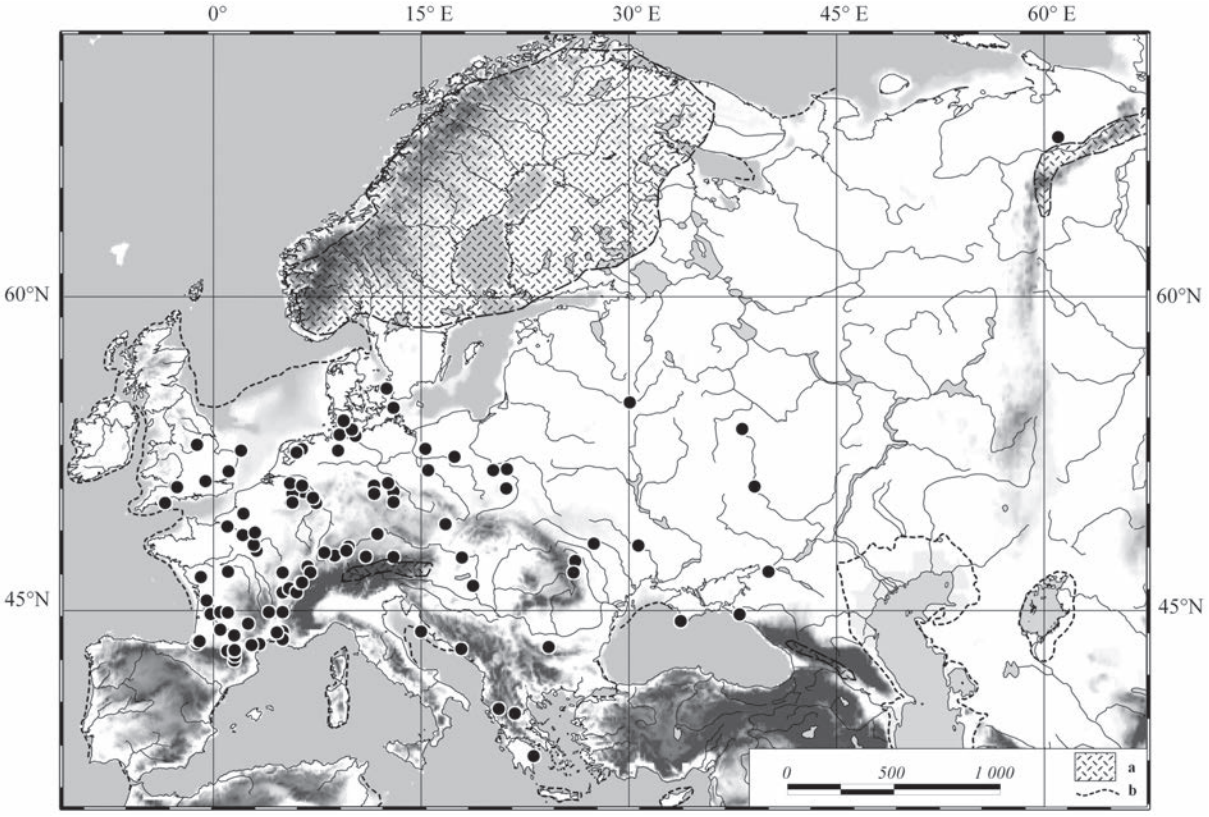

Fig. 7.9. *Human sites corresponding to 12.4–10.2 kyr BP: • – human sites, a – ice sheet, b – coastline*

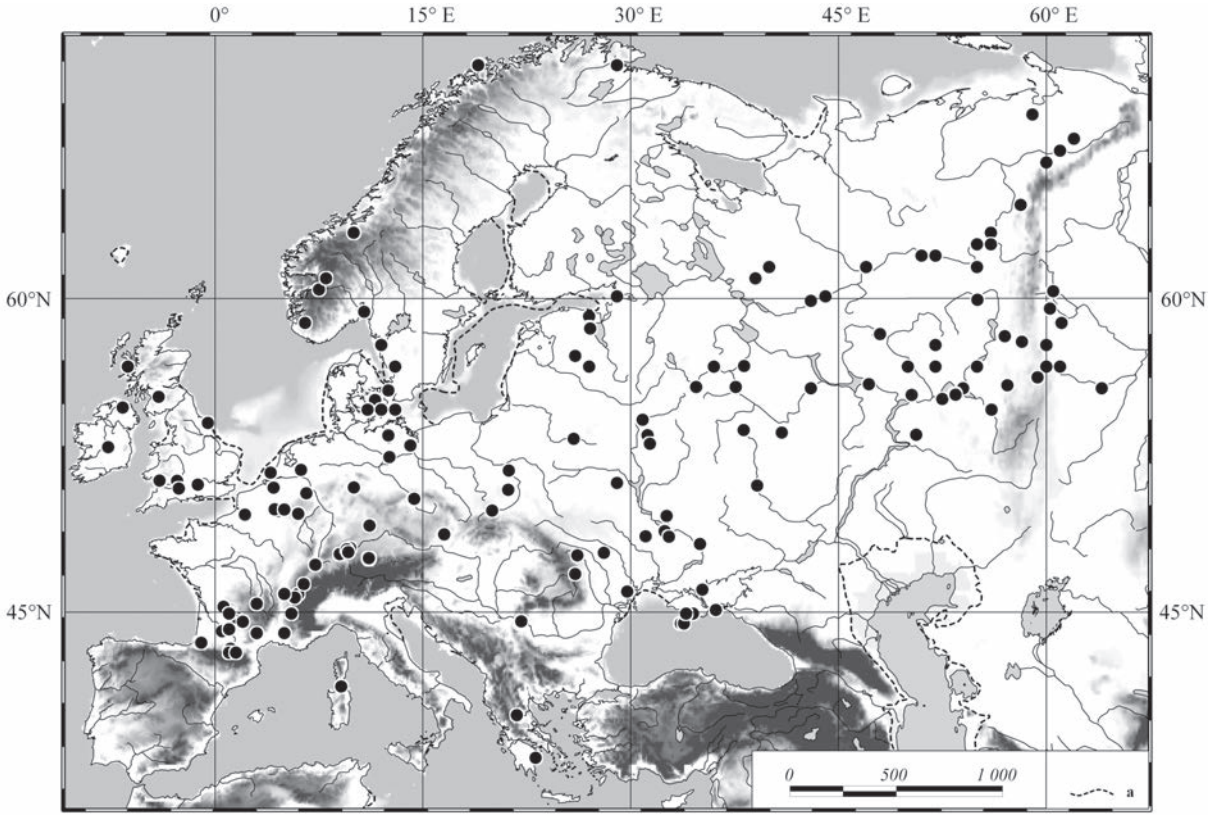

Fig. 7.10. *Human sites corresponding to 10.2–8 kyr BP: • – human sites, a – ice sheet, b – coastline*

dynamics. The regional range trajectories are summarized in the following table 7.2.

These trajectories describe the dynamics of the northern limit of range pulsation. This does not necessarily mean a change of the total range (measured in square kilometres). For example, the rise of sea levels at the Pleistocene–Holocene transition drowned the continental flats of the Atlantic coast of France. Whereas the northern limit expands, the western limit contracts. However on the European scale, the northern range limit is also affecting the total range. A second note is that the range changes do not necessarily mean changes in population size. Range expansion can be accompanied by increasing population size leaving the density relatively constant, or by decreasing population size decreasing the population density as well.

The trajectories share more or less the same pattern: all regions show a contraction of the range in a southerly direction between 25,000 and about 17,000 years ago, a shorter or longer period of stasis (or absence in the case of Central Europe), and a gradual range expansion northward from about 14,000 years onwards. The regional range trajectories also differ in several respects:

1. The spatio-temporal resolution decreases from west to east, and therefore the detail and accuracy;
2. The timing of the contraction in response to the onset of the Last Glacial Maximum; contraction takes place later from west to east, with the exception of the far north in the Urals;
3. The continuity of presence through the 17–14 kyr period with an occupational hiatus in Central Europe;
4. The latitude at which occupation continues through the Last Glacial Maximum and its aftermath, from 48°N in the west to 57°N in the Urals.

In contrast, the timing of range expansion does not seem to vary regionally. It starts everywhere at about 14,000 years ago, though the data are insufficient for Eastern Europe and the Urals.

What factors can explain the overall pattern and the regional differences?

Exploring explanations

It is clear that the overall pattern of range contraction and expansion is a response to the global climate changes at the end of the Weichselian. Deteriorating climate towards the Last Glacial Maximum led to the desertion of large parts of the northern and middle latitudes and a retreat of human populations to Southwestern France, the Mediterranean zone, the Black Sea region in the Ukraine and Russia, and the Urals. With the climatic upturn towards the Holocene, these refugia formed the source areas for recolonization of more northern latitudes. Geneticists have argued that the effects of the contraction of human populations in southern refuge areas and their subsequent expansion can be seen in the genetic diversity of the European gene pool. For example, Semino *et al.* (2000) correlate some differences in the Y chromosome with range expansions from refugia in the Last Glacial Maximum. They interpret the two types (Eu18 and Eu19) as the 'signatures of expansions from isolated population nuclei on the Iberian Peninsula and the present Ukraine, following the Last Glacial Maximum' (Semino *et al.*, 2000: 1156).

Global climate change, however, cannot explain the regional differences in the range trajectories or identify the mechanism by which the range limit responds to climate change. Why, for example, did the range of modern humans contract in Western Europe by 24 kyr and in Eastern Europe by 20–17 kyr? Suppose that an area is left due to a lack of resources. In the case of glacial Europe, it can reasonably be argued that this concerns animal resources and larger herbivore species in particular. Is there any evidence that large herbivores are lacking in Northwestern Europe, while still present in Eastern

Table 7.2

Regional features of human' range dynamics in Europe

Time window	Western Europe	Central Europe	Eastern Europe	Urals
29–24 kyr	Contraction 52°N > 48°N	Stasis	Stasis	Contraction 66°N > 57°N
24–17 kyr	Stasis (+excursion)	Contraction 51°N > 49°N	Stasis?	Stasis
17–14 kyr	Stasis	Hiatus (+episode)	Contraction? 57°N < 53°N?	Stasis
14–12.4 kyr	Expansion 48°N > 54°N	Expansion 48°>	Expansion 53°>	Expansion 57°N > 67°N
12.4–10.9 kyr	Stasis	Expansion	Expansion	?
10.9–10.2 kyr	Contraction (locally)	?	?	?
10.2–8.0 kyr	Expansion 54°N > 58°N	Expansion >71°N	Expansion >70°N	Expansion >70°N

Note: the numbers refer to degrees north and indicate the latitudinal shifts involved in the contraction or expansion.

Europe? Radiocarbon dates of faunal remains from the British Isles show a hiatus for the period of 23 to 13 kyr BP, suggesting very low numbers of herbivores (Stuart, 1982). Part of this picture may however be a taphonomic bias. Archaeological sites are a main source of information on the fauna. Therefore, if humans are not present, a main accumulator of bones is missing and information will be more scarce. The animals may have been around and humans may have been absent for other reasons than lack of animal resources. Some animals do seem to be absent though. Stuart *et al*. (2004) have shown by direct dating of fossil material that both mammoth and giant deer go extinct in Western and Central Europe around the Last Glacial Maximum, whereas they manage to survive in the southern parts of Eastern Europe. Modern humans seem to follow more or less the same pattern.

My hypothesis is that decreasing numbers and decreasing diversity of herbivores is causing a decline of the predators depending on them including modern humans. The question is: why should herbivore diversity and density decrease more drastically in Northwestern Europe than in Eastern Europe? Herbivores depend on available plant foods, in particular the above-ground biomass of grasses. If this becomes less abundant, for example due to extreme aridity and/or lower CO_2-levels, both herbivore density and diversity are likely to decrease. Subsequently, life will get more difficult for predators. However, why should available plant food remain large enough in Eastern Europe, but insufficient in Northwestern Europe? CO_2-levels are probably global and aridity is expected to be more severe in the continental east than near the Atlantic Ocean. Another factor influencing available plant food is the availability of nutrients. It is possible that the widespread loess blankets in Eastern Europe provided more nutrients for more extensive grasslands than the more patchy loess in Northwestern Europe.

Though the decreasing prey numbers may have played a role, it does not seem to be a sufficient explanation. Rather than food, the limiting factor may have been related to temperature. Modern humans are, as Guthrie (1990a) expressed, unwoolly humans. In order to keep their body temperature at a constant level of 37°C, humans do not rely on woolly hair, but on external heat sources (fire), clothing for isolation, and shelter for heat conservation. Of vital importance is the presence of sufficient firewood. Was Northwestern Europe abandoned because there was too little wood available, whereas sufficient amounts of wood could be collected in Eastern Europe? Palaeobotanical data do suggest a difference in this respect. In Northwestern Europe, trees are rare and restricted to sheltered locations. The evidence from Eastern Europe indicates a persistent presence of tree species along the large rivers such as the Dniestr, Dniepr and Don. The availability of (fire-) wood may also be important for other questions, such as the survival of modern humans through the 17–14 kyr period in Southwestern France and the Urals, but not in Central Europe, and survival up to 57°N in the Urals, but only until 48°N in France.

Another way of looking at the issue of abandonment or continued occupation is to consider the necessary technology as the limiting factor. Humans rely on technological aides to sustain themselves. It may be necessary to store foods to survive the lean season or to build huts as protection against the cold and the wind. A worsening of conditions could have been countered by increased investment in the technological aides. The question of abandonment or continued presence could be approached as an optimization problem between the increased investments in technology and technological innovation and their payoff. In the abandoned areas, the benefits of increased investment in technology did not suffice to pay the increased costs of continued occupation.

The above explorations are concerned with the reasons of *abandonment*. Why did humans *not* survive through worsening climatic conditions? Another question is: why did humans migrate north and (re-) colonized the middle and northern latitudes? Why did they not stay in the refuge areas? Suppose the following situation: area 1 has good conditions and area 2 has half as good conditions. However, not all individuals in area 1 will profit equally from the good conditions. For the individuals doing less well, there is a chance of doing better in area 2. With the conditions in area 2 ameliorating, the sooner moving into area 2 will be profitable. This scenario presupposes that individuals have information about the other areas. Initially, however, they cannot have this information. Here, another trade-off comes into play: staying in the area with changing conditions or exploratory (non-calculated) migration into the unknown. Exploratory migration beyond the area may not be much more costly than the exploration within the area in relation to the degree of unpredictable variation in resource availability.

Therefore we should expect the colonization process to take different shapes: exploratory, non-calculated migration, sometimes followed by calculated migration of either the 'return' type (back and forth between two areas) or the 'removal' type (where a part of the population moves to another area). From an archaeological point of view, the question is whether these different types of migration can be distinguished in the archaeological record.

Effects of range shifts in modern humans

Geneticists have argued that the effects of range shifts can be traced in the European gene pool and some physical anthropologists have suggested effects in cold-adapted anatomy, but aspects of the cultural repertoire

of modern humans may have been affected as well. The aspect that I like to mention in this respect is the cultural geography of the Upper Palaeolithic at about the Last Glacial Maximum. There seems to be a difference in the rate of change between the refugia in Western Europe and the southern realms of Eastern Europe. The cultural sequence in Eastern Europe is formed by gradually changing industries identified as eastern Gravettian, gravettoid, or epi-Gravettian: a sequence of 'Gravettian'-derived traces. In Western Europe, the sequence follows another track: the Perigordian/Gravettian is succeeded by the Aurignacian V, Solutrean, Badegoulian and finally the Magdalenian. Diversity in stone tool typology and technology seems to be larger in the west. Innovations like the spearthrower and the harpoon occur in this sequence. Supposing that the difference in archaeological classifications is not just reflecting differences between archaeologists but also differences between the material cultures, how can the difference be explained?

One way of thinking about this is to consider the different sequences as the result of alternative capital investments. Differences in investments are expected to be in response to different problems. For example, the problem in Western Europe could have been to secure the kill with diminishing prey densities; it is beneficial to increase the chance of killing an animal when it is encountered. In Eastern Europe, the problem could be being at the right place at the right time to encounter, kill and process animal resources, whose migratory behaviour becomes less predictable. Whereas the Western European sequence involved increased investments in technological systems directed at foraging costs such as pursuit time, killing and processing efficiency, the Eastern European sequence invested in strategic mobility and information gathering. Different investment strategies may have been selected for in the two main refuge areas from which repopulation of northern latitudes took place in Europe.

Recolonization gradually took place from about 14,000 years onwards. The recolonization of Central Europe is an interesting issue with regard to the biogeographical effects in modern humans. The distribution patterns of many species show a suture zone in Central Europe, where populations from different source areas meet. A similar pattern can be discerned in the archaeological record. First, the locality of Maszycka cave dated to about 15/14.5 kyr is associated with western, middle Magdalenian sites (bone tools) and with the eastern, Ukrainian part (flint source). Later on, the Magdalenian spreads from the west into the Czech Republic and Southern Poland. Southeastern connections seem to predominate in Eastern Slovakia and Hungary. The historic coincidence of who happens to arrive first determines the cultural geography of the Late Upper Palaeolithic in Europe.

These two examples show that the biogeography during the Last Glacial Maximum may have affected both the cultural evolution and the cultural geography of Late Upper Palaeolithic hunter-gatherers.

The role of humans in the Late Pleistocene faunal revolution

The dramatic range shift in modern humans is just one of the faunal changes taking place at the Pleistocene–Holocene boundary. Others are the fractionation of faunal communities, extinctions and evolutionary spurts. All of these aspects can be identified in the European record (Chapter 4). Guthrie (1990) has described this complex of

Table 7.3

Generalized regional cultural sequences from Western Europe to the Urals (29–8 kyr BP)

<table>
<tr><th>Kyr BP</th><th>Western Europe</th><th>Central Europe</th><th>Eastern Europe</th><th>The Urals</th></tr>
<tr><td rowspan="2">10</td><td colspan="3">Mezolithic</td><td rowspan="4">Late
Upper Paleolithic</td></tr>
<tr><td colspan="3">Late Palaeolithic</td></tr>
<tr><td>15</td><td>Magdalenian</td><td>Magdalenian</td><td rowspan="2">epi-Gravettian</td></tr>
<tr><td>20</td><td>Solutrean</td><td>? (Badegoulian /Kazhov culture)</td></tr>
<tr><td>25</td><td rowspan="2">Perigordian/Gravettian</td><td rowspan="2">Gravettian</td><td rowspan="2">Eastern Gravettian</td><td rowspan="2">Early Upper Paleolithic</td></tr>
<tr><td>30</td><td>Aurignacian</td><td>Aurignacian</td><td>Early Upper Paleolithic</td></tr>
</table>

changes as a Late Pleistocene faunal revolution. But what is the role of modern humans in this faunal revolution?

Potentially, humans could take on different roles in this process. Humans are rather general predators on a variety of prey species. Human hunting could drive already declining species into increased extinction risk. Humans compete with other species for resources. The competitive edge of humans could lead to range shifts in other species. Humans can also help species to disperse into new areas by providing a more suitable environment for the arriving species. Finally, domestication of animals and plants can be interpreted as a human role in an evolutionary spurt of these species.

The evidence for any of these roles in Europe is thin. Extinctions take place without clear human involvement. Giant deer, for example, goes extinct in Ireland before any human has arrived. Communities are reorganized without humans playing a part. The separation of saiga and reindeer ranges at the end of the Pleistocene is an example of this. Range shifts are explained by ecological conditions, dispersal ability and the historic coincidence of who gets where first. Evolutionary spurts occur in small mammal species with which humans have little involvement. It seems that the climatic changes of the Late Pleistocene–Holocene transition in Europe created new conditions on the battlefield both for competition between species and for predator-prey arms races. Humans were among the species that took advantage of the changing conditions to expand their range.

Conclusion

The overall pattern of range dynamics of modern human hunter-gatherers in Europe is in close relation to the main climatic shifts at the Pleistocene-Holocene boundary. The range of modern humans contracts in response to the Last Glacial Maximum. The hunter-gatherers retreat to the refuge zone of the Mediterranean with more northern refuge areas in Southwestern France, the Ukraine/Southern Russia and the middle/southern Urals. With the climatic upturn after 14,000 years ago, the range of modern humans starts to expand from southwestern and southeastern refugia. By 8,000 years ago settlement has reached the outer limits of the continent and the British Isles.

The contraction pattern is regionally different in timing and range of latitudinal shift. Northwestern Europe is deserted by about 24,000 years ago and the northern range limit shifts to the south of the Paris Basin (48°N). Central Europe is only deserted by about 17,000 years ago, whereas modern humans survive through the Last Glacial Maximum at latitudes up to 57°N in the middle Urals.

Expansion starts more or less simultaneously from the different refuge areas across Europe. Explanation of range shifts needs more thorough exploration, both in terms of limiting factors such as resource availability, wood for fuel, building and tools, and in terms of the ecology of alternative investment strategies. One should expect variation in time and space. The limiting factor explaining range contraction at one time and in one region is likely to be different from the factors involved in range expansion.

The view is still necessarily rather coarse-grained. On the one hand, because the European subcontintent is substantial, as is the period covered. On the other hand, because of limitations in the spatial and temporal resolution of the data.

CONCLUSION

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Research devoted to the reconstruction of ecosystems of Europe during the Late Pleistocene-Holocene transition permitted to elucidate dramatic biotic changes during 24–8 kyr B.P. This generalization became possible as a result of complex investigations, which have been carried out by Russian and Dutch researchers of different specialization. A huge amount of palaeobiological material from different Western and Eastern European databases was also included in the investigation. This research was carried out for the first time for the entire territory of Europe. Previous work on similar studies related to biotic components of the end of the last glaciation – the beginning of the Holocene were carried out only for some parts of Europe, or for one index temporal interval.

In the present publication we attempted to study evolutional changes of mammal assemblages, vegetation communities, stages of human occupation, dynamics of mammal species richness and dynamics of ecosystems of Europe gradually, by means of five time windows. These time windows reflect the main climatic changes during 24–8 kyr BP and include the last glacial maximum (LGM), the late glacial transition, the Bølling – Allerød Interstadial warming, Younger Dryas stadial cooling and the beginning of the Holocene interglacial.

For the first time mathematical methods were involved in analyzing the collected data. In earlier studies they were not used for reconstructing past environments. The application of mathematical methods increased the comprehensibility of the distribution of flora and fauna including hominids. Involving mathematical methods helped optimizing the joint analyses of a huge palaeobiological dataset and reduced subjective interpretations of the palaeodata (Chapter 2: 2.4, 2.5). The usage of MapInfo and ArcView GIS programs gave the possibility to construct a high amount of maps with mammal, plant and human distribution, mammalian assemblages and vegetation community ranges during the different time windows. For the first time we united the results of mammalian and plant studies and constructed ecosystem maps for the entire territory of Europe during five principal temporal intervals (between 24–8 kyr BP).

Chapter 3 is devoted to the periglacial processes, which took place on the territory of Europe during the Late Pleistocene – Holocene transition, the stages of ice-sheet degradation and oxygen isotope studies, which helped dating the principal time windows of the Late Pleistocene and Holocene. Analysis of all the collected data has been carried out taking into account most recent publications.

Important information about disputable questions on mammal systematic was described in Chapter 2 (2.3). Peculiarities of ecological requirements to environmental conditions of mammals were considered in Chapter 2 (2.2). Special attention was paid to the different types of mammal and plant responses to climatic and environmental changes, to principal characteristics of mammalian assemblages and to vegetation communities formed during glacial and interglacial periods.

The significant volume of mammalian data permits to reconstruct the species composition, species richness and geographical position of the mammal assemblages for five time windows, distinguished by their climatic conditions. The specifity of European mammal assemblages of LGM, LGT, BAIC, YD and PB–BO were revealed (Chapter 4).

The mammalian extinction during the Late Pleistocene – Early Holocene was analyzed by means of significant data, well dated by means of C^{14}. The definite information about the time and place of the last appearance of mammal species were presented in (Chapter 4: 4.6). Information on time and place of mammal domestication has been described too (Chapter 4: 4.7).

The important reconstructions have been obtained by rich palynological data. They permit to analyze the

species composition, geographical position and dynamics of the vegetation communities during 24–8 kyr BP (Chapter 5).

The complex analysis of the palaeofloristic and palaeotheriological data give the possibility to reconstruct the principal types of European ecosystems during five time windows and to present them cartographically (Chapter 6).

The main peculiarities of distribution, migrations, cultures, and economics of past humans were presented in Chapter 7. Attention was paid to the relationship between past humans and game mammals. The gradual changes in human cultures during the Late Paleolithic and Mesolithic were illustrated with examples derived from different parts of Europe.

Undoubtedly, the reconstructions of palaeoecosystems during the different climatic intervals of the Late Pleistocene and Holocene period could be used as models of possible future biotic changes on the territory of Europe under predicted climatic fluctuation.

The authors of the book hope that the research carried out will be interesting for a broad scientific audience: geographers, biologists, archaeologists and paleontologists.

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EVOLUTION OF EUROPEAN ECOSYSTEMS DURING PLEISTOCENE–HOLOCENE TRANSITION (24–8 KYR BP)

Collective monograph

ООО «Издательство ГЕОС»
119017, Москва, Пыжевский пер., 7, к. 332
Тел./факс: (495) 959-35-16; 8-926-222-30-91
e-mail: geos-books@yandex.ru
www.geos-books.ru

Подписано в печать 01.10.2019
Формат 60×90 $^{1}/_{8}$. Бумага офсетная
Гарнитура Таймс. Печать офсетная. Усл.-печ. л. 35
Тираж 100 экз.

Отпечатано с готового оригинал-макета в ПИК «Идел-Пресс»
420066, Республика Татарстан, г. Казань, ул. Декабристов, 2.