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Zoogeography of Holocene mammals in northern Eurasia

Zoogeografie holocénních savců severní Evroasie

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Abstract. Information on about 1600 Holocene mammal localities of the former Soviet Union was generalized in the form of electronic database HOLFAUNA. The computer maps of mammal ranges for the main Holocene intervals were constructed. The main features of the species composition and distribution in mammal assemblages were revealed for the principal Holocene periods (Preboreal, Boreal, Atlantic, Subboreal, and Subatlantic). The reconstructed biomes reflect the specific environmental and climatic conditions of the different Holocene periods. This information allowed also ascertaining the time and places of the first occurrence and further expansion of the domestic animals.

INTRODUCTION

Analysis of changes in the species composition and distribution of mammals, as well as their communities structure influenced by the climate dynamics during the last 10 thousand years provides important information to predict future evolution of the mammal diversity and distribution in relation to the different probable scenarios for climatic changes (warming, cooling). Until the present time, the notion of the Holocene climate and environment based mainly on paleobotanical, paleoentomological, and paleopedological data, and also on the information about sea coast lines changes, and shifts of the mountain glaciers limits (ALEKSANDROVSKIJ 1983, VELIČKO 1989, VELIČKO & KLIMANOV 1990, KLIMANOV 1994a, b, KLIMENKO et al. 1996, NAZAROV 1989, NEJŠTADT 1957, SEREBRJANNYJ & SOLOMINA 1995, SYČEVA 1996, CHOTINSKIJ et al. 1991). However, the significant Holocene theriological information available from literature sources and also data obtained by the authors were not jointly analyzed till the present time. Quantity of the Holocene mammal localities is very large, and for some Holocene intervals their number is significantly higher than that of the paleobotanical ones. Thus, it seemed necessary to involve all these data to reconstructions of the Northern Eurasia Holocene environments. In the present paper au-

thors for the first time revised all available theriological materials as an electronic database HOLFAUNA covering the former Soviet territory. Our database includes information of both wild and domestic mammal localities, what helps to reveal features of distribution, diversity, and structure of mammal Holocene assemblages. HOLFAUNA database permits also to reveal the primary centers of domestication and the ways of secondary expansion of domestic forms.

MAIN OBJECTIVES

The data on the Holocene mammal diversity and distribution in northern Eurasia are very important in concern to the mammal gene pool protection, as numerous animal species are influenced now by heavy anthropogenic pressure and also by natural climatic changes. The analyses of regularities of the northern Eurasian mammal species composition and distribution as well as the evolution of mammal assemblages structure during the last 10,000 years is the basis for prediction of possible mammal diversity and distribution changes in future.

METHODS AND APPROACHES

By now, enormous material on Holocene mammal remains has been accumulated. For the most part, these localities are connected with complexly examined archeological sites. The age of these sites is recognized both by absolute and relative dating methods. However, the analysis of the huge Holocene mammal material was impossible without generalization of these data in the form of electronic database.

Database structure was developed earlier, during generalization and analyses of the Late Pleistocene Northern Eurasian mammals (Markova et al. 1995), with regard to the approaches of American paleontologists that elaborated the structure of FAUNMAP database (FAUNMAP 1994).

Access to the database is provided by two programs: PARADOX V.4 – Database Management Program, and ARC/INFO, which was used to create the GIS.

Information is presented both in text and numeric types. The total number of the fields (parameters) exceeds 500, the whole number of attributers is about 1600. The topographic map of scale 1:8 000 000 was used as a cartographic base. Based on the features of primary materials, the following characters were marked when developing the GIS: (1) sites of mammal remains (points); (2) modern ranges of the mammal species, and (3) ranges of mammal paleoassemblages (lines and polygons).

GIS includes a series of initial specialized maps (covers) and derivative synthetic maps with possibility of quest. This GIS is used as informational-reference system and as an instrument for analysis of spatial-temporal modeling.

The database HOLFAUNA is used as the basis for an automatic mapping. The database includes four information blocks concerning: (1) "GEO" – geographical setting of localities; (2) "AGE" – age of localities; (3) "TAXA" – species composition; (4) "REFER" – references. Each of these blocks (databases) contains the locality number thus providing the possibility of their combined analyses further on.

Information block "GEO" contains the detailed information on the geographic position of each locality. Besides the locality number and name, there are the fields indicating latitudes and longitudes (degrees and minutes); absolute height (meters); the names of the state, province, region; river basin; and the name of the nearest settlement.

Database "AGE" includes information fields concerning geochronological characteristics of each locality, including all available absolute dates, first of all the radiocarbon dates. Data on thermolu-

minescence and paleomagnetic methods found in literature are also comprehended. Materials on relative dating including geological, paleontological, and archeological data are also presented. Maximum and minimum datings of the locality are indicated, too, with remarks on the methods by which they were obtained. Lastly the most reliable age of locality is given as result of the complex of methods.

Database "TAXA", apart from the locality number and name, contains information fields for each mammal species ever inhabiting the former SU territory during the Holocene. Basis to the fields' composition for this database was provided by the materials of "Catalogue of Mammals of the USSR" (GROMOV & BARANOVA 1981). New information in regard to the mammal systematics presented in the latest publications was also taken into account. For the most complete presentation of materials, the fields were introduced also in order to include the remains identified only for the genera or family ranks.

Database "REFER" includes all bibliographic references in regard to each mammal locality, indicating the authors' names, the year, title and place of publication, publishing house, pages; as well as the names of specialists who identified paleontological materials.

MATERIAL

Mammal remains from about 1600 localities were analyzed. The numbers of localities referred to the Holocene main periods are distributed as follows: Preboreal period – 23; Boreal – 69; Atlantic – 289; Subboreal – 466; Subatlantic – 724. Fig. 1 shows geographic distribution of the Holocene mammal sites.

More than 90% of localities are related to cultural layers of archeological sites. Localities, associated with alluvial, cave and other types of sediments without artifacts, are less common. Unfortunately, materials for some groups of mammals are quite deficient. The most part of publications contains information only about large mammals, both wild and domestic. On the other hand, materials on small mammals referred to the orders Rodentia, Lagomorpha, Insectivora, Chiroptera, were seldom

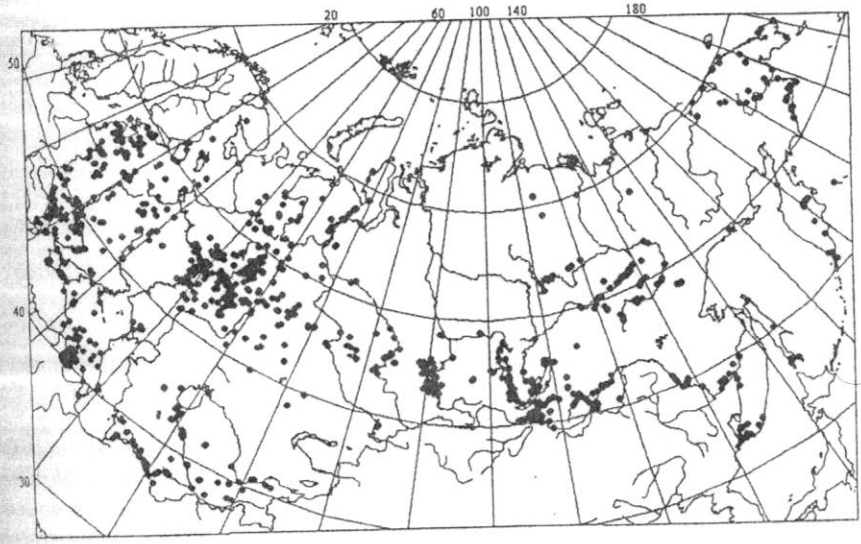

Fig. 1. Holocene mammal localities.

analyzed. This was especially typical for early publications. However, recently this gap has been gradually filled up. The authors of the present paper actively work in this direction. Their original materials were also included to the HOLFAUNA database.

Holocene mammal localities are distributed irregularly throughout the studied territory (Fig. 1). The major part of the localities concentrates in the territories of eastern Europe, the Ural region, and the Baikal area. This is related mainly to the history of archeological and geological investigations. Moreover, in several cases we possess only relative datings of the localities based on the geologic and archeological data.

TIME INTERVALS

In order to analyze the dynamics of key mammal ranges, mapping of the localities was made for the different Holocene periods. In this paper we used the mean chronological dates for the principal Holocene intervals: Preboreal (PB, = <10300 = >9300 years ago); Boreal (BO, <9300 = <8000 years ago); optimum of Atlantic period (AT3, = <6200 = >5000 years ago); the beginning of Subboreal period (SB1, <4600 = >4200 years ago); the middle of Subboreal period (SB2, <4200 = >3200 years ago); terminal of Subboreal period (SB3, <3200 = >2600 years ago); the early, middle and late Subatlantic period (SA1, SA2, SA3, <2600 = >1800, <1800 = >800, <800 = >200 years ago respectively). The materials referring to the last 200 years were not analyzed, because of significant changes of the mammals' spatial distribution in this time. This event was caused by remarkable transformations of the animal' natural habitats due to gradually increasing anthropogenic pressure during the XIXth and XXth centuries.

ECOLOGICAL GROUPS OF MAMMALS

In order to reveal the influence of climatic changes on mammal assemblages hundreds of range maps were constructed showing the localities position of different ecological groups of mammals referred to main Holocene periods. It is impossible to present all these maps here. However, we used them in analysis of mammal distribution dynamics, with regard to different ecological groups and for each time span. This also helped to establish main features of the species composition and chorology for the Holocene mammal assemblages.

Mammals, which are now widely distributed through all the main natural zones of northern Eurasia, have been excluded from the analysis (for example, such species as water vole, root vole, wolf, fox and some others). These animals inhabit intrazonal (mostly peri-aquatic) landscapes where influence of environmental and climatic factors smoothed out. Mammals of this group can penetrate far northwards and southwards using these habitats.

Seasonal migrations of some animals, in relation to the fossil material, are more difficult to take into consideration. For example, it is known that modern areas of the reindeer, saiga and many other mammals vary significantly by season. One has two possible ways to account for findings of their fossil remains far beyond their modern ranges: (1) as being due to seasonal migrations; (2) as resulting from the mammal range shifts caused by changing global climate. We regarded localities of such mammals found far away from their present ranges (including seasonal migration areas) as influenced by changing global climate. In reconstructing past mammal faunas and environments, we paid main attention to the records of stenotopic mammal remains, because these animals occupy limited habitats. This mammal group includes mostly the subarctic species, many steppe animals, forest dwellers characteristic to the different forest types, and numerous mammals inhabiting semi-deserts and deserts.

Reviewing the mammal fossil remains we took into consideration features of the species ecology and distribution. Thus, certain forest mammals inhabit different types of forests and their finding made it possible to elucidate the distribution of forest communities in the broad sense. Among such species, one can mark the forest vole (*Clethrionomys glareolus*) and the field vole (*Microtus agrestis*). Other forest species are closely related to special vegetation types. For example, ranges of the yellow-necked mouse, fat dormouse, forest and garden dormouse, pine vole, wildboar and some other animals are associated with nemoral forests. Their records would testify the existence of broad-leaved and mixed forests during the formation of a sediment. Such approaches were used also in the analyses of finds of other ecological groups of mammals (subarctic, steppe, semidesert, desert, etc.).

As mentioned above, elucidation of characteristics of the species composition, diversity and chorology of the Holocene mammal assemblages was based on the analysis of bone remains designated to the species referred to the following ecological groups:

(1) tundra species (*Sorex arcticus*, *Dicrostonyx torquatus*, *Lemmus sibiricus*, *Alopex lagopus*, *Rangifer tarandus*, etc.);

(2) forest species (*Pteromys volans*, *Sciuruis vulgaris*, *Castor fiber*, *Apodemus flavicollis*, *Glis*, *Dryomys*, *Eliomys*, *Muscardinus*, *Myopus*, *Clethrionomys*, *Microtus* (*Terricola*) *subterraneus*, *M.* (*Microtus*) *agrestis*, *Mustela sibirica*, *Martes*, *Gulo*, *Felis lynx*, *Sus*, *Moschus*, *Capreolus*, *Cervus*, *Alces*, etc.);

(3) steppe species (*Diplomesodon*, *Ochotona*, *Spermophilopsis*, *Sicista subtilis*, *Allactaga*, *Spalax*, *Cricetus*, *Ellobius*, *Lagurus*, *Eolagurus*, *Microtus* (*Stenocranius*) *gregalis*, *M.* (*Sumerionnus*) *socialis*, *Myospalax*, *Vulpes corsak*, *Putorius eversmanni*, *Felis*, *Saiga tatarica*, etc.);

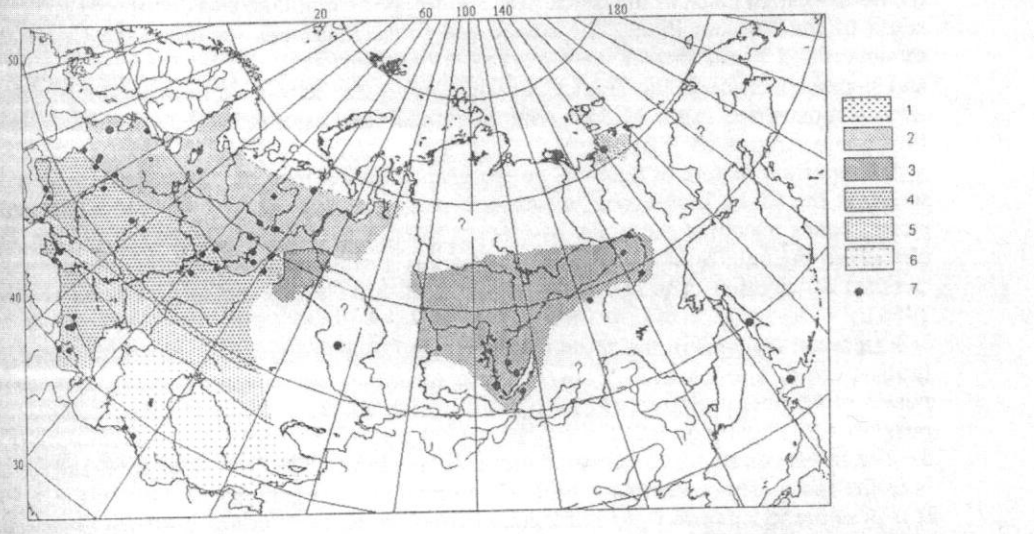

Fig. 2. Mammal assemblages of the Boreal Period: *1* – tundra; *2* – forest-tundra; *3* – forest; *4* – forest-steppe; *5* – steppe; *6* – desert and semi-desert; *7* – mammal localities.

(4) desert and semi-desert inhabitants (*Hemiechinus*, *Lepus tolai*, *Ochotona daurica*, *Spermophilus* (*Colobotus*) *fulvus*, *Pygerethmus*, *Dipus*, *Paradipus*, *Scirtopoda tellum*, *Meriones*, *Rhombomys*, *Hyaena hyaena*, *Felis caracal*, *F. margarita*, *Gazella subgutturoza*, etc.).

Range dynamics of these mammals during the past 10,000 years allowed to reveal their reactions on the climate changes and to elucidate the spatial-temporal reorganizations of the mammal assemblages' structure during the Holocene.

PRINCIPAL FEATURES OF THE ZOOGEOGRAPHY OF HOLOCENE MAMMALS

Distribution of the Holocene mammals of different ecology was analyzed, what allowed to distinguish peculiarities of the mammal assemblages' structure and chorology during the last 10,000 years.

Several assemblages were reconstructed for the beginning of the **Holocene (Preboreal period);** the major part of the materials came from Eastern Europe. The far north of the eastern Europe was occupied by tundra mammal assemblage; southward to 53–58° N, the vast area with tundra and forest mammals was reconstructed. To the south from this zone, the territory was inhabited by numerous steppe and rare forest mammals making us to reconstruct a forest-steppe biome here. Only steppe species were distributed in the northern Black Sea and the Sea of Azov coastal regions. Forest and steppe mammals inhabited the Crimea Mountains. The desert and semi-desert species were distributed in the Middle Asia south.

During the **Boreal period,** just as in the previous interval, the forest-tundra assemblage was also widely ranged in Eastern Europe and the Urals (Fig. 2). The forest-tundra biome stretched from the Arctic Ocean coastline to 54–58° N in the south. Further southward, the area of forest-steppe mammal assemblage was situated, occupying the vast territories till the northwestern coast of the Black Sea. The steppe assemblage was distributed in the very south of the Russian Plain. The steppe and forest mammals inhabited the Crimea; the mountain and forest species were marked in the Caucasus, whereas the mountain, forest and steppe species – in the Trans-Caucasus. Desert and semi-desert mammal assemblages were reconstructed in the Middle Asia; forest mammal assemblage was distributed in the Enisej and Angara river basins.

An important feature of mammal zoogeography during the Preboreal and Boreal periods was that the forest biome was not marked in eastern Europe. Forest-tundra and forest-steppe zones occupied the range of modern forest zone during the early Holocene. This phenomenon could be attributed to a cooling effect of the Scandinavian ice-sheet and also the vast distribution of permafrost regions in eastern Europe and West Siberia (Velichko 1989).

Significant changes in the structure of mammal assemblages took place during the **Atlantic period**. The materials from the northern part of the territory at study, dated to the period of Atlantic optimum, allowed to distinguish not only tundra-forest complexes (and possibly some tundra ones in the very north) but also assemblages of forest mammals (Fig. 3). The forest communities occupied vast areas between 65–70° N in the north and 52–54° N in the south. This assemblage probably formed at the beginning of the Atlantic period. It is possible to suppose that tundra zone existed in the far north of northern Eurasia, but we have not enough material from these regions. Southward from the forest zone, steppe and forest mammals were distributed, occupying even the northern Black Sea coastal regi-

on, and the forest-steppe biome can be reconstructed by these data. The steppe biome was distinguished only in the Caspian Sea coastal region, in southern West Siberia, and in the Transbaikalia. So, the theriological data reflect a significant growth of temperature and humidity during the Atlantic period. This picture is in good agreement with the data obtained by other methods.

Some changes in chorology of mammalian assemblages occurred during the first part of the **Subboreal period**. Judging by mammal fossil remains dated to this interval, the forest-tundra zone broadened, while the forested area decreased. The steppe belt was distinguished for the Russian Plain south (Fig. 4). Such changes in disposition of mammal assemblages probably reflect some cooling.

The decrease of forest-tundra zone is marked in the end of the Subboreal period indicates some warming at that time. The chorology of other natural zones during the Subboreal terminal showed no significant changes.

The same types of mammal assemblages were characteristic of the first part of the **Subatlantic period**. Geographical position of their ranges practically did not change.

So, the analysis of the numerous Holocene theriological data from a large part of northern Eurasia permitted to distinguish the principal changes in mammal assemblage structure, which reflected the main global climatic fluctuations. The mammal assemblages of the Preboreal and Boreal periods still showed some features of periglacial faunas. The forest biome was not formed at that time. The forest-tundra and forest-steppe mammal communities occupied the territory of modern forest zone. The mammal assemblages dated to the Atlantic optimum time demonstrate the existence of vast forest zone. The range of the steppe zone decreased in this time. These data permit to speak about the considerable growth of temperature and humidity during 6,500–5,000 yr. B.P. The principal biomes

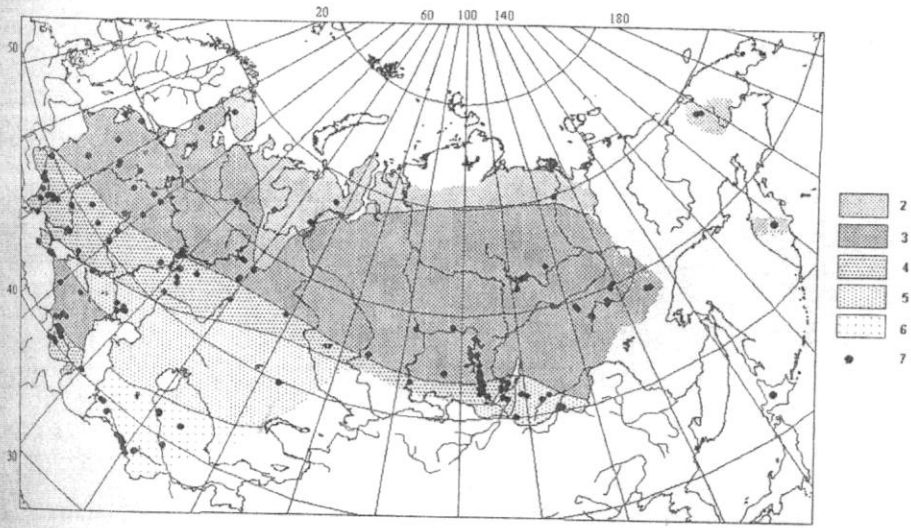

Fig. 3. Mammal assemblages of the Atlantic Period optimum (see captions to Fig. 2).

persisted during the Subboreal and Subatlantic periods with no significant alteration of their ranges.

DOMESTIC MAMMALS

The appearance of domestic mammals was an important event in the formation Holocene mammal faunas. These species gradually spread from the places of their first domestication to the adjacent areas. The process of autochthon domestication took place in some regions. In many cases domestic animals enriched the mammal diversity. However, in some other regions, domestic forms ousted native mammals, and the species richness decreased. Studies of the processes of domestication and distribution of domestic mammals imply certain difficulties, first of all in regard to the method. Actually, one can examine domestication processes only on the basis of archaeozoological materials, whereas the differences between wild and domestic forms of mammals are quite insignificant, especially at the early stages of domestication. Thus one cannot point the exact time when domestic forms first appeared in a region. The interval when the domestic form was marked for the first time can be fixed exactly enough only in places of the secondary occupation, where the aboriginal fauna missed the corresponding wild form.

The literature materials show that the dog was domesticated in the Mesolithic (may be even earlier). Sheep and goat were domesticated during the Neolithic at the territory of Turkey, Iran and Iraq. Cows were domesticated about 8,000–7,000 yr. B.P. at the Anatolian Plateau (Nobis 1968). The first domestic pig appeared about 9,000–8,000 yr. B. P. in the territory of the Near East. The wild horse (*Equus przewalskii*) was domesticated in steppes and forest-steppes at the plain regions adjoining the southern Urals and northern coastal regions of the Black and Caspian Seas about 7,000–5,000 yr. B.P.; the donkey about 8,000–

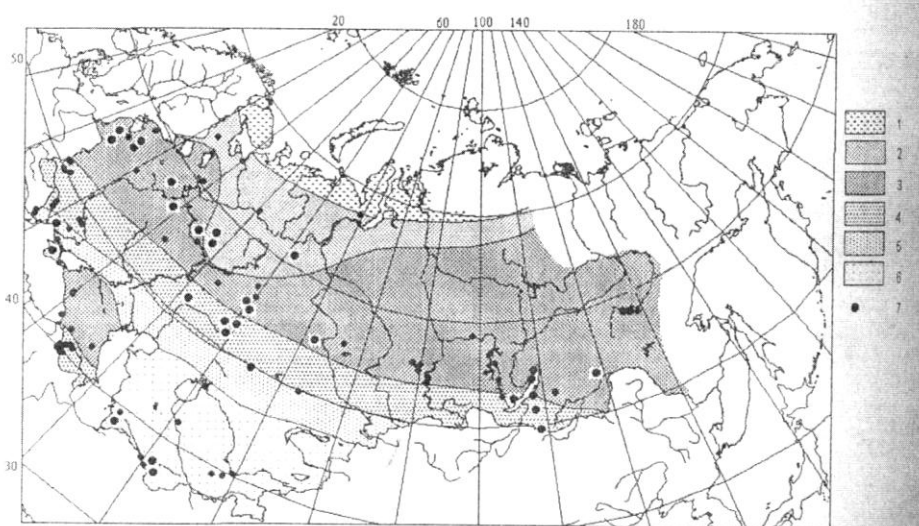

Fig. 4. Mammal assemblages of the early Subboreal Period (see captions to Fig. 2).

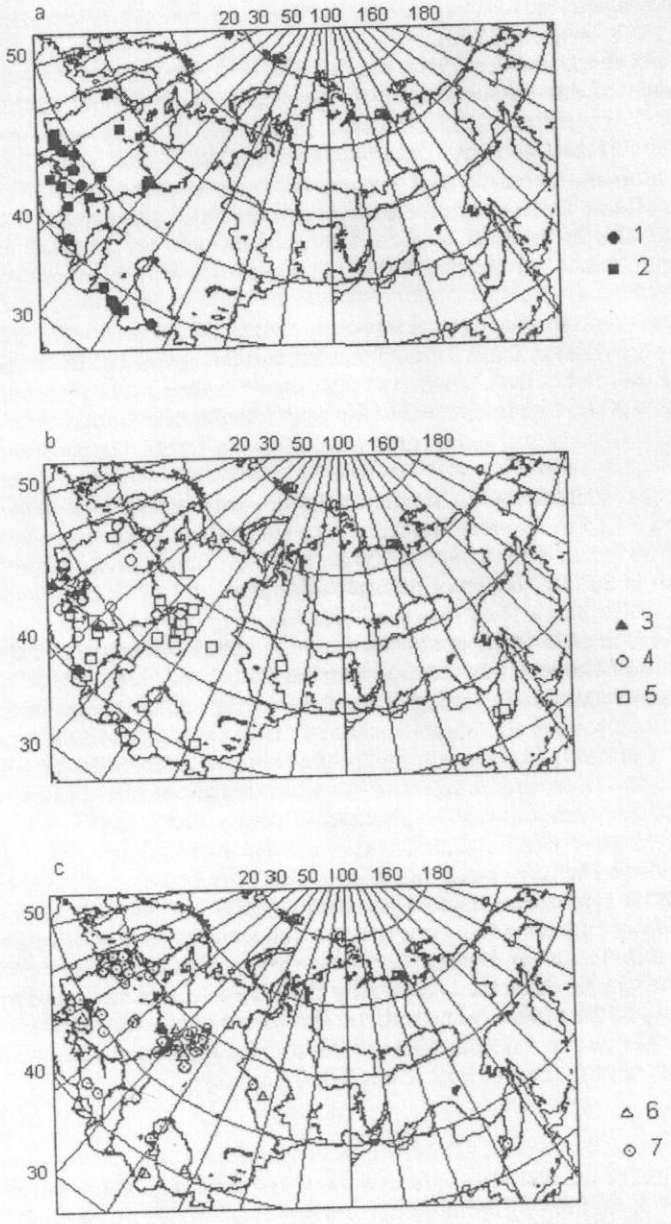

Fig. 5. Domestic pig *Sus scrofa domestica* remains in the localities of: a – Atlantic Period (*1* – AT1-2; *2* – AT3); b – Subboreal Period (*3* – SB1; *4* – SB2; *5* – SB3); c – Subbatlantic Period (*6* – SA1; *7* – SA2).

6,000 years ago in the territory of the Near East and in northeastern Africa (Bibikova 1963, Tzalkin 1972, Bökönyi 1990).

Sites with fossil remains of the pig *Sus scrofa domestica* are shown in Fig. 5. The earliest records of this domestic form in the studied territory and from human settlements date back to the early Atlantic. These localities are situated in the south of the Russian Plain, in the Trans-Caucasus, and in the south of the Middle Asia (Fig. 5a). Later, in the Atlanic optimum, the remains of *Sus scrofa domestica* were found in settlements situated along the Middle Dniestr, Middle Dniepr, and the Don rivers, in the middle reaches of the Volga, and also in the Middle Asia. The northernmost localities of this time containing domestic pig bones are located in the Baltic region and in the upper reaches of the Volga (Fig. 5a).

In the early and middle Subboreal period, bones of *Sus scrofa domestica* were found in the same regions as in the Atlantic optimum, but the density of these finds increased (Fig. 5b). In the late Subboreal, remains of this domestic form were found also in the Far East. As regards middle Subatlanic sites, pig bone remains are known from practically all human settlements situated southwards from 60° N in Eastern Europe and 55° N in Siberia (Fig. 5c).

The earliest localities with fossils of the domestic sheep *Ovis aries* and goat *Capra hircus* were found in the early Holocene sites situated in the lower reaches of the Syr-Darya river (Middle Asia). The remains of *Ovis aries* and *Capra hircus* of the early Atlantic age were found in cultural layers of human settlements in the Middle Asia, the Trans-Caucasus, lower Volga basin, the Crimea and the Azov coastal region. During the Atlantic optimum, these domestic animals appeared also in the northern part of the Caspian coastal region, in the Middle Urals, central Russian Plain, and even in the eastern part of the Baltic region. From the beginning of the Subboreal period, remains of the domestic sheep and goat were found in the lower reaches of the upper Volga and Enisej rivers, and in the western part of the Baikal region. Their range became even wider in the early and middle Subatlantic period when the remains of these animals were recovered also in the Transbaikalia, in the Far East, and on the Kamchatka peninsula.

The earliest records of the domestic cow *Bos taurus* came from the region between Syr-Darya and Amu-Darya rivers, in the Kopet-Dag Mountains, in the steppe part of the Crimea and in the Trans-Caucasus. They were referred to the late Boreal – early Atlantic period. Abundant bones of *Bos taurus* were collected in numerous settlements of the Atlantic optimum. In eastern Europe, the northernmost sites are situated at 58° N. In Siberia, remains of domestic cows are known only from the sites younger than 5,000 yr BP. From the beginning of the Subboreal period, *Bos taurus* remains were found in the lower reaches of the Ob' river and in the Enisej basin. This animal appeared in Transbaikalia only about 3,000 yr. BP., and in the Far East about 2,000 years ago.

SUMMARY

Generalization of the abundant information on the Holocene mammals distribution throughout the large territory of northern Eurasia has been carried out for the first time, and the HOLFAUNA database was developed. This database includes information on 1600 Holocene mammal localities that allowed to analyze the features of the species composition and

chorology of mammal assemblages in the main stages of the Holocene, which differed in climatic conditions.

The theriological data showed, that formation of the modern natural zones in northern Eurasia went on during a long time. During the Preboreal and the Boreal periods, no well-developed forest biome existed yet. Territories, which are now covered by forests, were occupied at that time by the forest-tundra mammal assemblages (in the northern part) and forest-steppe mammal complexes in the southern regions, forming the appropriate natural zones. Thus, one can state certain inertia in formation of the landscapes' zonal structure in northern Eurasia after the end of the Valdai glaciation. This inertia probably was caused by the influence of the ice sheets preserved during the early Holocene in Scandinavia, and also by the significant permafrost areas in eastern Europe and Siberia. Occurrence of widespread forest mammal assemblages was registered only from the beginning of the Atlantic period onwards. Fossil data indicate the decrease of steppe mammal communities at that time, reflecting significant growth of temperature and humidity. During the late Holocene, natural zones got their modern features, but they also underwent some alterations influenced by climatic changes. In particular, mammal fossils revealed some expansion of forest-tundra zone, decline of forest biome and existence of steppe landscapes at the beginning of the Subboreal period. Such data reflect that climate became cooler during SB-1.

The review of the Holocene mammal data from northern Eurasia allowed in some cases to estimate the time and places of the first appearance of domestic species in the territory of the former Soviet Union, as well as the stages of their secondary distribution. These data were presented in the cartographic form. Thus, the earliest dog remains were found in the Mesolithic sites (by some data, even in the Late Paleolithic sites), the earliest domestic cow bones were registered in the settlements of the Boreal period, the earliest remains of the domestic forms of sheep and goat in the Preboreal and Boreal localities, and the first domestic horse and pig bones were found in the settlements dated to the early Neolithic.

Thus, the accomplished analysis of the abundant mammal Holocene fossils registered throughout the former SU territory showed the importance of these data for the reconstruction of species composition of mammal assemblages, distribution patterns of fossil mammals, and past environments during the principal stages of the Holocene. Previously, such reconstructions were based mainly upon plant macrofossils and pollen evidence. The use of the theriological material for the reconstruction of the past environment allowed to develop a more reliable view in regard to the temporal-spatial changes in the nature.

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SOUHRN

Údaje o zhruba 1600 holocénních savčích lokalit z území bývalého Sovětského svazu byly analysovány s pomocí elektronické database HOLFAUNA. Na jejím základě byly počítačově zpracovány mapy areálů rozšíření savčích taxonů v hlavních obdobích holocénu (preboreál, boreál, atlantik, subboreál, a subatlantik), na jejichž základě byly popsány hlavní znaky druhového složení a rozšíření v savčích společenstvech pro uvedené hlavní periody holocénu. Rekonstruované biomy odpovídají specifickým podnebním a biotopovým podmínkám různých holocénních období. Tyto údaje umožňují také zjistit období a místo prvního výskytu a dalšího šíření domestikovaných druhů zvířat.

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