The Holocene History of the European Vertebrate Fauna

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Holocene history of small mammals in the Urals

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Abstract

Based on abundant fossil bone remains from many localities in different regions of the Urals, authors discuss problems of transformation of late glacial communities of small mammals into recent zonal assemblages in relation to palaeoenvironmental changes. Particular spatial and temporal features of the process are shown to be related to physiogeographical characteristics of montainous regions exemplified by the Urals. A new term is proposed to describe the disharmonious faunas of the transitional period – faunas of "hyperborean" type.

Keywords: Late Pleistocene, Holocene, Urals, rodents, environmental changes.

Zusammenfassung

Auf der Grundlage eines reichen Fossilmaterials von vielen Fundplätzen in verschiedenen Regionen des Urals diskutieren die Autoren Probleme der Umwandlung spätglazialer in rezente, zonale Kleinsäugergemeinschaften, und zwar in Beziehung zu den Umweltveränderungen der Vergangenheit. Es ließ sich zeigen, daß besondere räumliche und zeitliche Merkmale dieses Prozesses auf physiogeographische Besonderheiten von Gebirgsregionen, exemplifiziert durch das Uralgebirge, zurückzuführen sind. Für die Beschreibung disharmonischer Faunen der Übergangsperiode wird mit "hyperborean" ein neue Begriff vorgeschlagen.

Schlüsselwörter: Spätpleistozän, Holozän, Ural, Nagetiere, Umweltveränderungen.

INTRODUCTION

The Urals represent a mountainous strip about 2000 km long, usually showing middle and low height values. Six geomorphologic (physiogeographical) regions are distinguished within the Urals (Anonymus, 1968). They are: the **Polar Urals** – between 69° and 66° N, from the northern part of the peak of Konstantinov Kamen' to the upper Khulga River, with usual height values of 1300-1400 m; the **Pre-Polar Urals** – from 66° to 64° N, between the rivers Khulga and Shchugor; the highest peaks of the Urals (1600-1800 m) are situated here. The **Northern Urals** is the region situated between 64° and 59° N, from the river of Shchugor down to the peak named Kos'vinsky Stone (Kamen') and Kachkanar hill. The elevation values come to 1400-1600 m, erosive relief with alpine (so-called "gol'tsy") plots is observed at high ridges and massifs. The **Middle Urals** lies between 59° and 56° N, from the Kos'vinsky Kamen' (Stone) down to the Ufaley River valley (tributary of the Ufa River). The region has the lowest elevation values (usually not exceeding 600-800 m). The **South Urals** – between 56° and 50° N, southwards from the Ufaley River, till the latitudinal part of the Belaya ("White") River. The elevations are medium-sized (up to 1500-1600 m height). The **South-Ural Upland** is situated between the rivers of Belaya and Ural, constituting the southernmost region of the montane strip, where heights decrease to 500-600 m. Besides that, the montane system of the Urals is added to by the submontane belt which is rather wide in some places, the western foothills showing hilly and ridge relief up to 550 m high, and the eastern foothills also of hilly relief, not usually over 400–500 m high. The major part of the eastern slope is shorter and steeper than the western one. Further to the south-east of the Ural mountains, lie the elevated plains of the Trans-Urals, with average heights of 200-300 m.

The modern nature of the Urals shows well-defined zonality. The following natural zones are distinguished. The Polar Urals, the Yughor peninsular, and the Pai-Khoi-ridge make up the tundra zone. Then comes a transitional zone of forest-tundra. The taiga zone covers the Pre-Polar, North and Middle Urals, and the taiga Trans-Urals. Deciduous forests occur only on the western slopes of the South Urals. Forest-steppes may be found in some regions of the South Urals and the Trans-Urals. The steppe zone is situated on the South-Urals flat country and in some regions of the Trans-Urals.

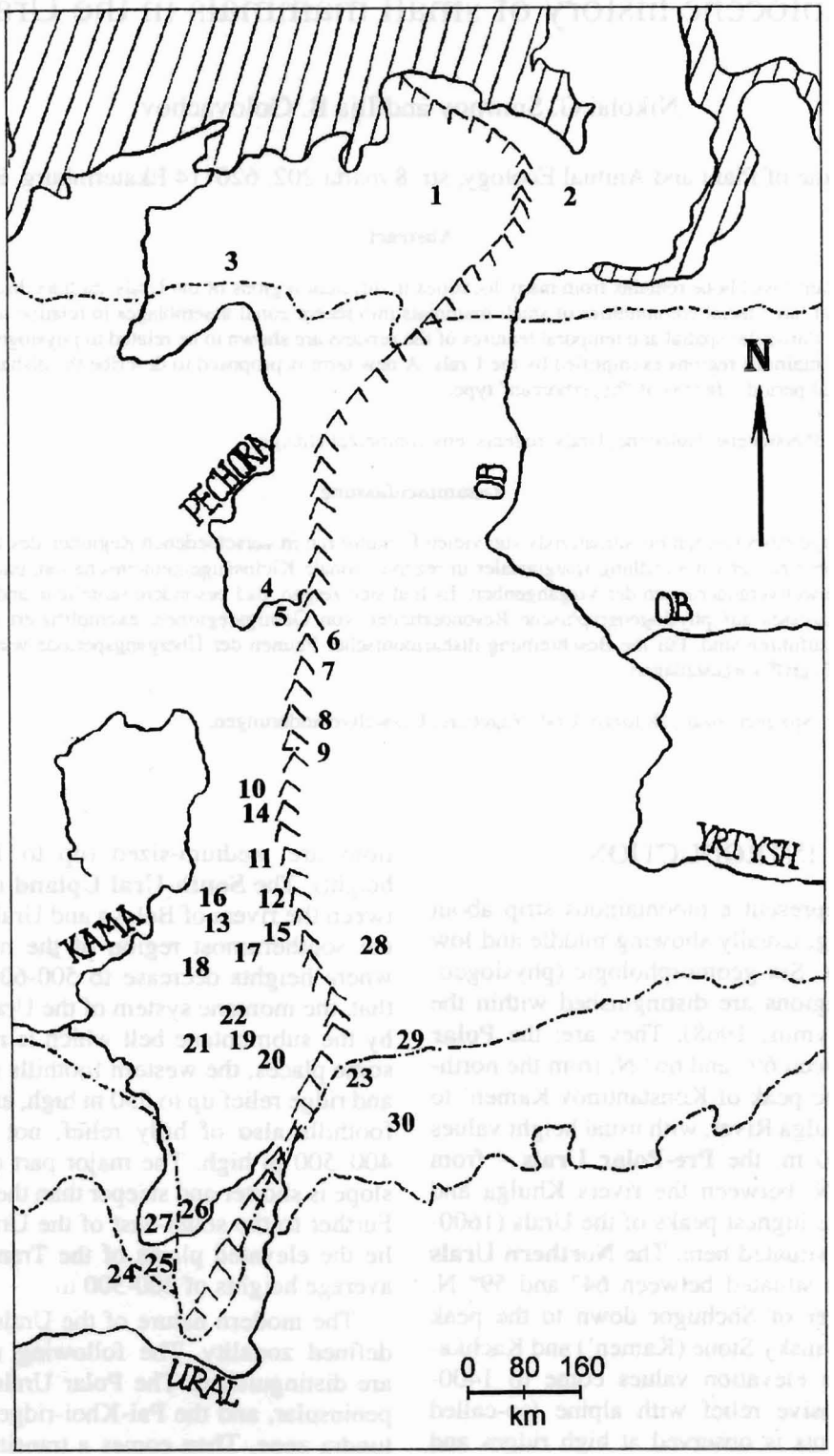

Figure 1: Location of the main sites in the Urals.
1 Pymva-Shor; 2 Zveroboy cave; 3 Shapkina 1108; 4 Medvezh'ya (Bear's) cave; 5. Studenaya cave; 6 Ushminskaya cave; 7 Shaitansky cave; 8 Lobvinsky cave; 9 Kakva-4; 10 Bolshoi Glukhoi cave; 11 Dyrovaty Kamen' on Tchusovaya-river; 12 Dyrovaty Kamen' on Serga-river; 13 Bobyliok cave; 14 Shaitan cave on river Tchusovaya; 15 Oleniy (Deer's) cave; 16 Rock-shelter Sukhorechensky; 17 Bazhukovo III; 18 Tavra shelter; 19 Ignatievsky cave; 20 Serpievsky cave I & II; 21 Prizhim II; 22 Idrisovsky cave; 23 Usminskaya cave; 24 Bolshoi Suren'; 25 Kvadratny (Square) cave; 26 Kapova cave; 27 Kuljurt-Tamak; 28 Zotinsky cave; 29 Sukharysh cave; 30 Kamenka.

The major part of the sites containing small mammal remains *(Figure 1)* are situated within the Middle Urals region, from where 20 Holocene local faunas have been described (Smirnov, 1993, 1995). They are fewer in the North and South Urals. Only four sites have since been found in the Polar Urals, three on the eastern and one on the western slope. No data has yet been obtained from the Pre-Polar Urals. All the sites represent deposits of bone remains in rock-shelters or in caves, which were used as habitats (lairs) by predators or seats for birds of prey; sometimes these are accompanied by archaeological materials. The sites are situated usually 200-400 m above sea level.

Altitude zonality at these elevation marks is observed only in the Polar Urals, whereas in the more southern regions only natural zonality is revealed. However, one should keep in mind that montane character of the relief provides the conditions creating greater mosaic topography structure even when the absolute elevation marks are not so high, thus creating additional conditions for the existence of some extra-zonal faunal elements.

The Urals constitutes an intermediate region between Europe and Asia. Thus, both European and Siberian elements are registered in the flora and fauna lists of the Urals. During the different periods of the region's history, they alternated to show their influence upon the biota formation. During the cold epochs, the Siberian taxa or those from Central Asia expanded, as the case of *Dicrostonyx* lemmings, Middendorf's voles, *Eolagurus luteus* and some others, which occupied the territories far westwards. During the warm periods, the Urals was invaded by European nemoral elements, namely *Glis glis* and *Apodemus flavicollis*.

The background to ensure formation of the Holocene complexes of mammals was the peculiar biota of the late Valdai (Markova *et al.*, 1995). One needs to understand the regional features of that in order to study the Holocene dynamics of the mammal fauna of the Urals. Now, specialists differ in their opinions about the nature of zonal distribution of mammals during the late Valdai, size and boundaries of the zones and sub-zones. Two approaches exist here. One of them concerns the late Valdai spread of mammals being due to a mosaic of biotopes from different zones, leading to a seeming mixture of characters of some modern zonal complexes (tundra-steppe). The second point of view comes from a particular character of the zone, which can not be understood as a "hybrid" of some recent zones (Vangengeim, 1977). Everybody probably now recognises the original pattern of the "mixed" fauna, as definitions indicating to its similarity to forest-tundra or forest-steppe type are now added to the terms "periglacial" or "Pleistocene-dated" for better discrimination from the modern types mentioned. Sometimes, the term "tundra-steppe" too is used. American authors use two more names in order to mark particular features of these faunas, making them dissimilar to all now existing zonal natural complexes: "disharmonious" and "non-analogous" (Graham & Lundelius, 1984; Semken, 1984; etc.). Use of them in Russian publications produced much valid criticism, as the essence was not revealed only reminding one of the fact that they looked different from all recent complexes.

All this caused us to propose a new name for the disharmonious zonal complex when compared to modern zonal communities, having no direct analogies in modern nature, and demonstrating some features which draw it together with both the steppe and tundra communities ("mixed" fauna); the symbol species in it are mammoths among megamammals and *Dicrostonyx* lemmings among small mammals. This complex occupied the major part of the late Valdai hyper-zone, that is, of the northern (boreal) part of Eurasia; thus we consider it appropriate to define it as "hyperborean".

DYNAMICS OF THE RODENT FAUNA IN THE POLAR URALS

The late Valdai arctic complex of mammals was spread over the Polar Urals and the adjacent territories from 20,000 until 13,000 BP. After a very short time interval, it transformed into a fauna looking very similar to that now inhabiting modern forest-tundra and even north taiga regions, which existed during the major part of Holocene. Only about 3000 years ago, the forest elements in it were observed to deteriorate, and the fauna took on the features of modern fauna.

The late Valdai arctic complex showed a poor species content, which can be characterised in the Ural region by the data from a few perfectly-dated sites. Among small mammals, the collared lemming (*Dicrostonyx guilielmi*), dominated clearly. Thus, the site of Pymva-Shor (67° N, 61° E) provided several thousands of molars, and in different layers *Dicrostonyx* molars made up 90-95 %, those of *Lemmus* composed 5-10 %, while the rest (single percents) were des-

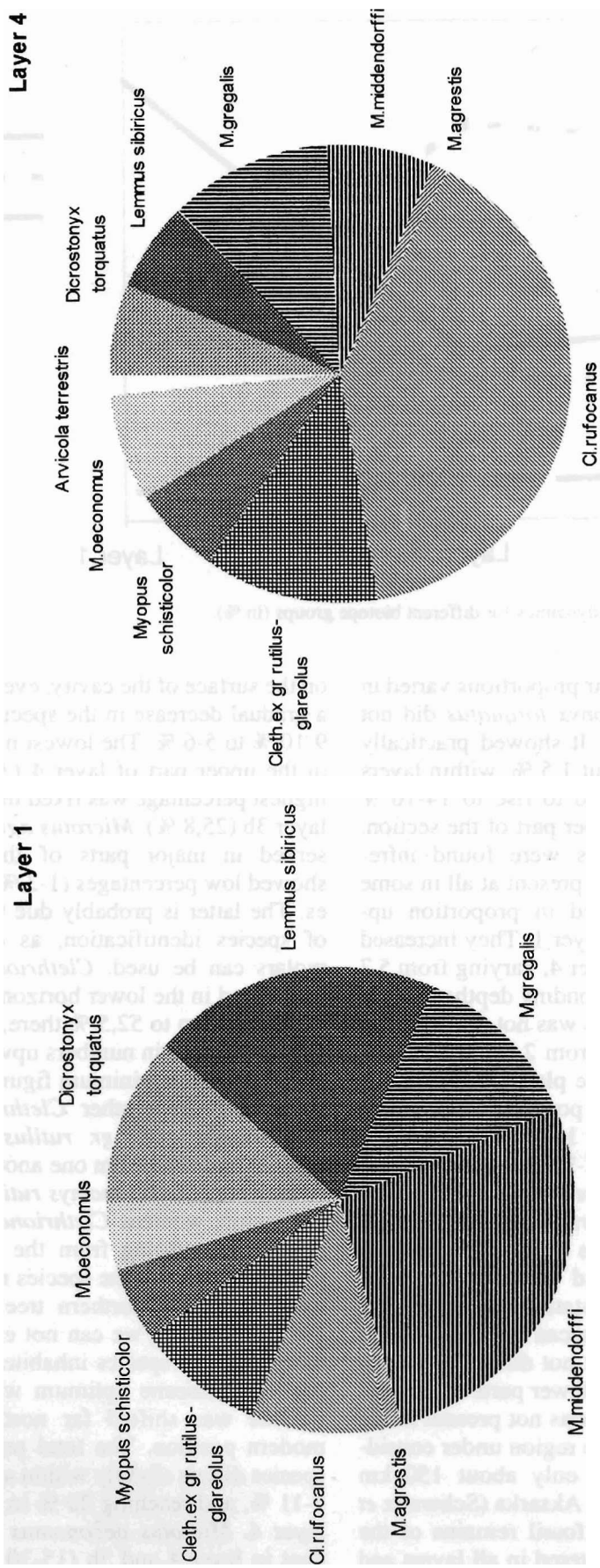

Figure 2: Zveroboy cave. Percentages of rodent species remains in upper (layer 1, left) and lower (layer 4, right) parts of the section (in %).

ignated as the narrow-skulled vole. Collections from the site of Shapkina 1108 (67° N, 54° E) included about 20 % of *Lemmus* molars, no more than 1 % of those from *Microtus gregalis,* whereas the majority of molars represented the collared lemmings. Other sites of the late Valdai, studied from the Pechora-River lower reaches (Kochev, 1993), gave practically the same picture. No remains of other species of small mammals occurred in any of the sites, including those of *Microtus middendorffii.* Following the humidity and rise in temperature, the percentages of the Siberian lemming and narrow-skulled vole remains also increased to some extent. However, even the latter percentage variant differed significantly from all the complexes, which are now observed in the forest-tundra, south-tundra and typical tundra regions, and seems to be most similar to the recent communities of the arctic. The main character of this complex was probably determined both by low temperatures and higher aridity of climate. The complex spread over the glacier edge and the ocean shore in the north, but it is difficult to describe the southern boundary because the territory has hardly been studied. This may become possible to do so if we find and examine the materials from the regions between 63° and 65° N.

The collections from the site of Pymva-Shor reveal that about 12,000 BP the complex was enriched, and about 8,000 BP the fauna looked quite different. The dominating elements there were forest-dwellers. Faunal data does not correspond to the time interval between 8,000 and 4,000 BP. However, pollen data indicates forest vegetation predominance in the region at this time (Surova *et al.*, 1975).

The time interval from 4,000 BP till our time has been studied in terms of bone remains from the rock-shelter of Zveroboy (Golovachov, in press). This site is situated on the eastern foothills of the Polar-Urals ridge, on the upland of Yangana-Pe (67°42' N, 67°50' E). The region is referred to as the south-tundra sub-zone (Chernov, 1978), and altitude belts are observed at the upland. Forest-tundra here is seen to be replaced by the undershrub tundra. Southern slopes are covered with curved larch trees, whereas the northern slopes and peaks look similar to arctic deserts. Modern fauna of small mammals includes nine species (Bolshakov & Balakhonov, 1986; Balakhonov & Shtro, 1995): *Dicrostonyx torquatus* Pallas, 1779; *Lemmus sibiricus* Kerr, 1792; *Microtus middendorffii* Poljakov, 1891; *Microtus gregalis major* Ognev, 1918 (tundra subspecies); *Microtus agrestis* L.,1861; *Microtus oeconomus* Pallas, 1778; *Clethrionomys rufocanus* Sundevall, 1846-1847; *Clethrionomys rutilus* Schreber, 1780; *Arvicola terrestris* L.,1758.

The small rock-shelter of Zveroboy is situated in a gorge south slope of the Yangana-Pe flatland, with a south-facing entrance. The cavity is about 2-3 m deep and wide, and about 1 m high. Loose deposits were 110 cm thick. Four layers were distinguished there: 1 – a humus upper layer, not exceeding 5-8 cm deep, looking like buried soil. The loose layer named 3a was of grey sandy loam and contained abundant bone remains; it laid under the first one near the cavity walls, and in some places was 50 cm thick. Layer 3b of brown sandy loam also laid under layer 1 and in some plots reached the bottom of the site, being up to 1 m thick. The major part of the bottom was covered by layer 4 of more viscid brown loam; at the northern wall of the cavity this layer started at the very surface and reached 110 cm deep at the bottom. All the layers were arranged like overlapping flakes. Layer 4 was thinning out from the northern wall towards the entrance, while layer 1 showed just the opposite picture.

Only a part (about 3500) of the undamaged molars collected in the site have been examined at present. Judging from the quality of their preservation, the bone remains of small mammals originate mainly from pellets. However bones of megamammals (reindeer, polar fox, etc.) found in the site indicate that the rock-shelter could also have served as a retreat for predators. Recent collections of small mammal remains from pellets were studied in order to compare modern data on the region with fossil materials. The taxa lists were similar; only the wood lemming (*Myopus schisticolor* Lillijeborg, 1984) was missing in the recent collections; the species proportions were similar to those in the upper part of layer 1.

Rodent species were identified by the molars collected, and the percentages of molars were considered to be proportional to the species ratio in the community. Special methods were developed and applied to provide accurate identification, with special consideration of the forms being difficult in this respect and particular features of the region (Golovachov, 1997; Smirnov *et al.*, 1998). L. D. Sulerzhitsky (Geological Institute RAS, Moscow) carried out C14 datings on some fossil remains. The bottom part of the section is dated to 4100 ± 200 BP (GIN-9006).

The species list obtained for the fossil remains was practically the same as that at present. All the species were found among the remains of

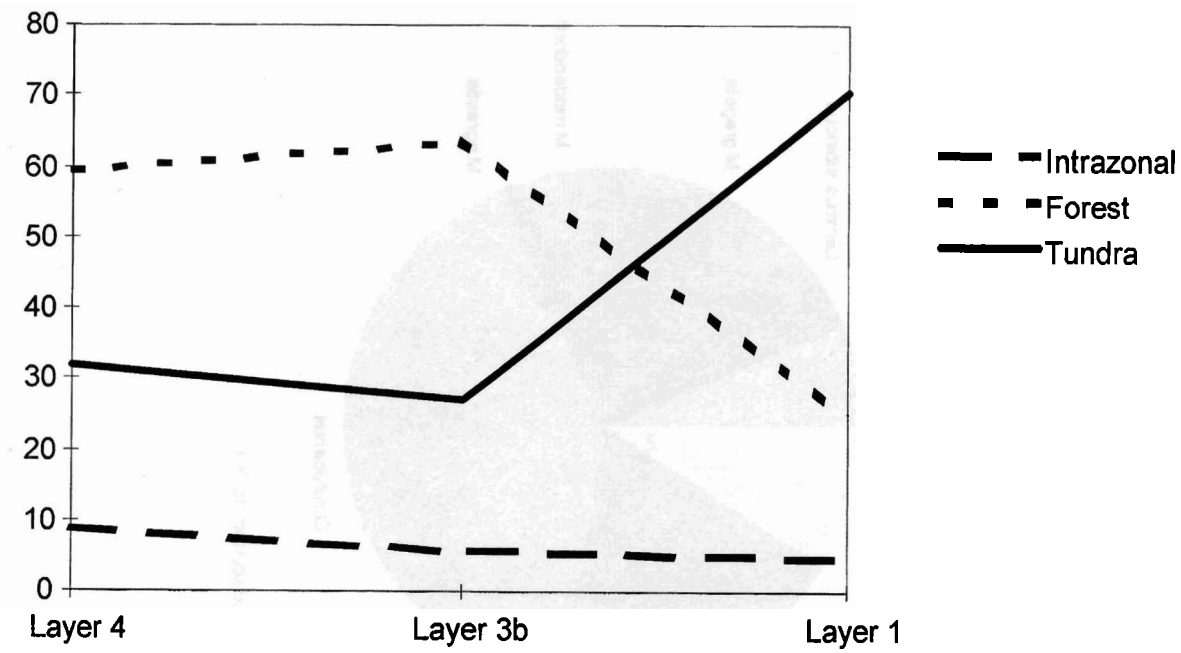

Figure 3: Zveroboy cave. Ratio dynamics for different biotope groups (in %).

the whole section, but their proportions varied in depth and layer. *Dicrostonyx torquatus* did not prevail in either horizon. It showed practically the same percentage, about 1,5 %, within layers 4 and 3b, and was marked to rise to 14-16 % (Max = 18.5 %) in the upper part of the section. *Lemmus sibiricus* remains were found infrequently, and they were not present at all in some plots. They also increased in proportion upwards, reaching 20 % in layer 1. They increased from 0 to 3,3 % within layer 4, varying from 5,7 % to 18,5 % at the corresponding depths of layer 3b. *Microtus middendorffii* was not numerous in layers 4 and 3b, varying from 2 to 6 %, with a maximum of 23,3 % in the plot A2 of layer 3b (18-30 cm deep). Then the portion of the species fell to 5,5 %. Within layer 1, the remains of the species decreased from 22-25 % to 18 % at the very surface. *Microtus gregalis* showed a rise from 2-3 % to 7-11 % upwards within layers 3b and 4. The same trend was observed in layer 1, and the proportion reached 16 % in the upper horizon. The sub-species status of this vole has not been clarified; thus we can not be sure that its taxonomic status might not differ for the remains from the upper and lower parts of the section. *Myopus schisticolor* was not present in the recent collections from the region under consideration; it was observed only about 150 km southwards, at the point of Aksarka (Schwartz *et al.*, 1971). However, the fossil remains of the forest lemming were registered in all layers and on the surface of the cavity, everywhere showing a gradual decrease in the species' remains from 9-10 % to 5-6 %. The lowest number was found in the upper part of layer 4 (3,3 %), while the highest percentage was fixed in the lower part of layer 3b (25,8 %). *Microtus agrestis* was not observed in major parts of the horizons, and showed low percentages (1-3 %) in all other cases. The latter is probably due to the difficulties of species identification, as only undamaged molars can be used. *Clethrionomys rufocanus* dominated in the lower horizons of loose deposits, making up to 52,5 % there, and showed significant decline in numbers upwards in all layers to 20-30 %; the minimum figure made up 3-9 % in layer 1. Two other *Clethrionomys* species (*Clethrionomys ex gr. rutilus-glareolus*) were not distinguished from one another. Only the red forest vole (*Clethrionomys rutilus*) now inhabits the region, whereas *Clethrionomys glareolus* is considered missing from the region, with the northern border of the species range in the Urals lying along the northern treeline (Anonymus, 1981). However, we can not exclude the possibility that this species inhabited the region during the Holocene optimum when the northern treeline was shifted far northwards from its modern position. The total percentage of both species differs slightly within a layer, making up 7-11 %, and reaching 20 % in the upper part of layer 4. *Microtus oeconomus* was more abundant in layer 4 and 3b (15-30 %), and reached

only 1-3 % in layer 1, showing the same trend of decrease within each layer. *Arvicola terrestris* was very rare in all layers (1-4 %). The portion of its remains was registered to rise slightly within layers 3b and 4 (from 1,7 % to 3,3 %). The species was not present in some plots of layer 1, and made up to only about 1 % in the others.

All species of small mammals identified in the deposits of the Zveroboy rock-shelter may be divided into three groups, according to their zonal relationship. The first one includes the **tundra species**: both collared and Siberian lemmings, which are regarded as eu-arctic species, being wide-spread in the whole tundra zone, but not dominating in the subarctic south (Chernov, 1978); Middendorf's vole inhabits the southern part of the sub-zone of typical tundra, and is regarded as a hypoarctic species (Chernov, 1978); and the tundra subspecies of the narrow-skulled vole *Microtus gregalis major.* The second group comprises the **forest species**: wood lemming (*Myopus schisticolor*), red-backed voles (genus *Clethrionomys*), and the field vole (*Microtus agrestis*). The third group is composed of **intrazonal species**, which inhabit grasslands and by-water biotopes in different natural zones: the water vole (*Arvicola terrestris*) and the root (tundra) vole *Microtus oeconomus.*

Ratio of bone remains of different species was noted to vary between the layers, and in different horizons within each layer. The lower parts of the Zveroboy section showed a dominance of forest species remains. Upwards, both within a layer and within the whole section, the ratio was observed to change with the percentage of forest species declining. The share of intrazonal species revealed a similar trend: it also decreased towards the upper horizons. The percentage of tundra species changed in the opposite way, making up 80 % of the total number in the upper horizons of the section *(Figure 2)*. The picture described does not conflict with the existing concept about climate and related vegetation changes in the Polar Urals during the second half of the Holocene, which considers that the Holocene optimum (the warmest period) in the Polar Urals began about 8,000 BP (Surova *et al.*, 1975). At that time, the northern treeline shifted northwards as compared to its modern position, reaching the mid-Yamal regions. In the Polar Urals, forests of spruce and birch were spread mostly during the Atlantic period, which revealed three stages there. The first and third of these were marked by the most extensive development of spruce forests, and the second one was distinguished by the broadest expansion of birches (Surova & Troitsky, 1971; Surova *et al.*, 1975). Then, at the boundary of Atlantic and Sub-Boreal periods, there occurred a colder interval, which caused deterioration of the forest vegetation which continued during the Sub-Atlantic. The picture registered by ratio variations of different species in the section studied *(Figure 3)* seems to correlate with climatic and vegetation changes which took place after the Holocene optimum period.

As well as the temperature, one can also regard humidity as another factor to influence the species combination and ratio in a fauna, though no accurate criteria to classify the species by this factor have since been elaborated. According to the character of xerophily, two species may be easily distinguished from the others. One of them is the collared lemming, showing cryo-xerophily to be an inhabitant of dry and cold areas (Chernyavsky & Tkachev, 1982), while the second includes all sub-species of the narrow-skulled vole, which all prefer dry places with grasses, both in tundra and in steppes (Pavlinin & Schwartz, 1953). We regarded these two species as a group of **xerophilic** animals. On the contrary, the water vole, the root vole, and Middendorf's vole all inhabit more moist biotopes, and thus we considered them to be a group of **hygrophilic** species. All the other species observed in the site were regarded as **mesophilic** animals. The analysis of data grouped in this way *(Figure 4)* revealed some decline in the percentage of mesophilic species remains, whereas the corresponding number of xerophilic and hygrophilic animals increased nearer to the surface. However, we previously saw that the share of the forest species also decreased towards the upper layers. Thus, both these trends together probably indicate more continental climatic conditions. Pollen analysis also confirms this suggestion. Besides, valid data is known which suggests that climate changes to colder and more continental conditions after 4,000 BP did not only occur in some local places. Thus, based on the data concerning abrupt climatic changes in Scotland 3900-3500 BP, and on data from other world regions, some scientists proposed that these alterations may not be regional or even continental, but perhaps global-scale climate changes (Anderson *et al.*, 1998).

The data from the Yangana-Pe site was compared to that from the above-mentioned site of Pymva-Shor *(Figure 5)*, situated at the same latitude. A series of C14-dates characterising Holocene deposits in both sites made it possible to

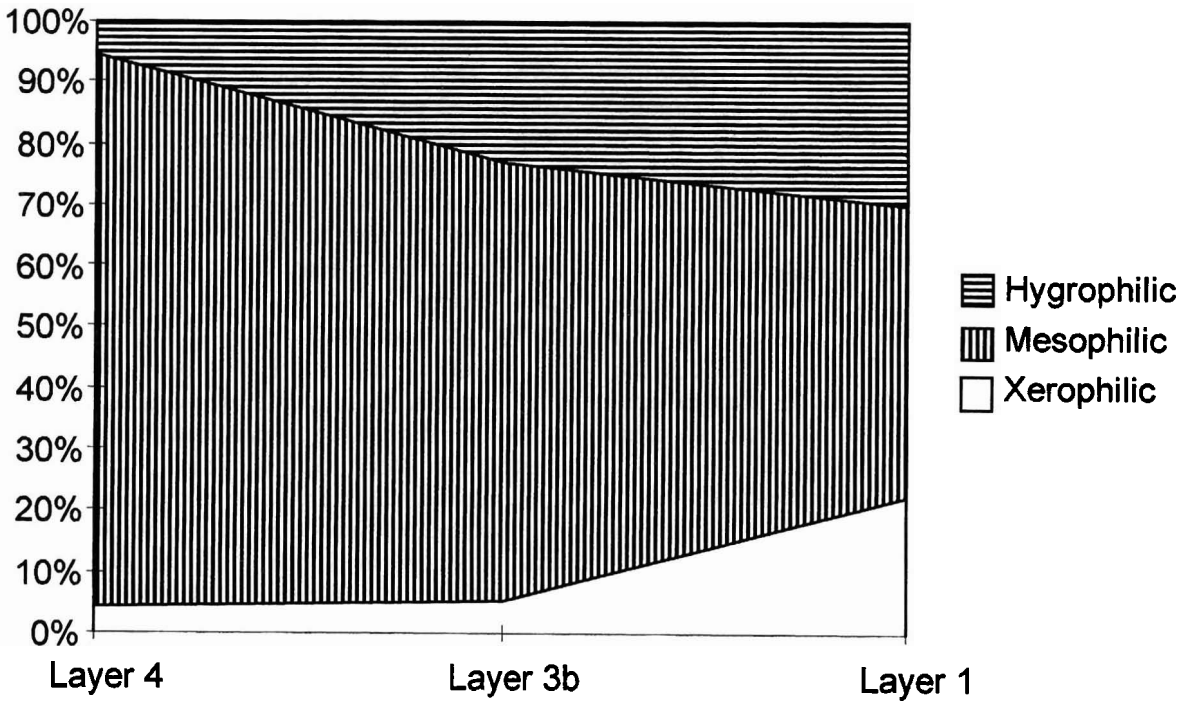

Figure 4: Zveroboy cave. Ratio of xerophilic, mesophilic and hygrophilic fauna elements (in %).

arrange all the data by chronology, and to describe some faunal types of the late glacial and Holocene times. The late Valdai complex from the Pymva-Shor cave was described as an arctic one. The first Holocene fauna type (tundra xerophilic one) dated to about 10,000 BP was distinct in the dominance of tundra species, namely the collared and Siberian lemming and the narrow-skulled vole, together making up 85-87 % of the total sample. It was regarded as tundra and xerophilic, as the portion of *Microtus gregalis* remains in it was the highest for the whole period. The rest of the species of this complex represented groups of forest and by-water inhabitants, including wood lemming, *Clethrionomys* and *Microtus* voles (*M. middendorffii-hyperboreus*, *M. agrestis*, *M. oeconomus*), *Arvicola terrestris*. The later fauna types exhibited the same taxa lists, but differed in proportions of the biotope groups. Thus, ca. 8,000 BP the "north-taiga" fauna type showed a heavy decline in the tundra species portion (to 10 %), with equal proportions of forest and by-water animals. Neither material has been found yet which dated to the interval between 8,000 and 4,000 BP. The fauna from the period of about 4,000 BP reflected the similar "north-taiga" appearance. Tundra species revealed the same low percentage, forest species dominated (65 %), with the main elements in it represented by *Clethrionomys rufocanus* and *Myopus schisticolor*. The third fauna type of the late Holocene ("forest-tundra" type) was distinct in its increased share of tundra species (65 %) with the Siberian lemming prevailing. This latter variant corresponds to the modern forest-tundra pattern, and has no direct analogies in the past.

FORMATION PATTERNS OF MODERN FAUNA TYPES IN THE TAIGA, FOREST AND FOREST-STEPPE ZONES

During the late Valdai, the whole vast territory now covered by the modern taiga zone, those of mixed forests and forest-steppes, was occupied by the *hyperborean complex of mammals*. The main feature of this complex was high species diversity showing maximum values in the central part of the zone. High species diversity was formed due to the presence of a series of zonal species characteristic of this peculiar biota (as mammoth, woolly rhinoceros, cave bear, etc.), and many polyzonal animals species. After the hyperborean zone vanished, and the animal complex came to degenerate, a major part of the first group appeared to die out (mammoth, woolly rhinoceros, bison, cave bear, cave hyena, etc.). The development of the polyzonal species continued in different ways. In the course of an ecological crisis at the Pleistocene/Holocene boundary, some of them modified their ranges, others changed their ecological strategies, and

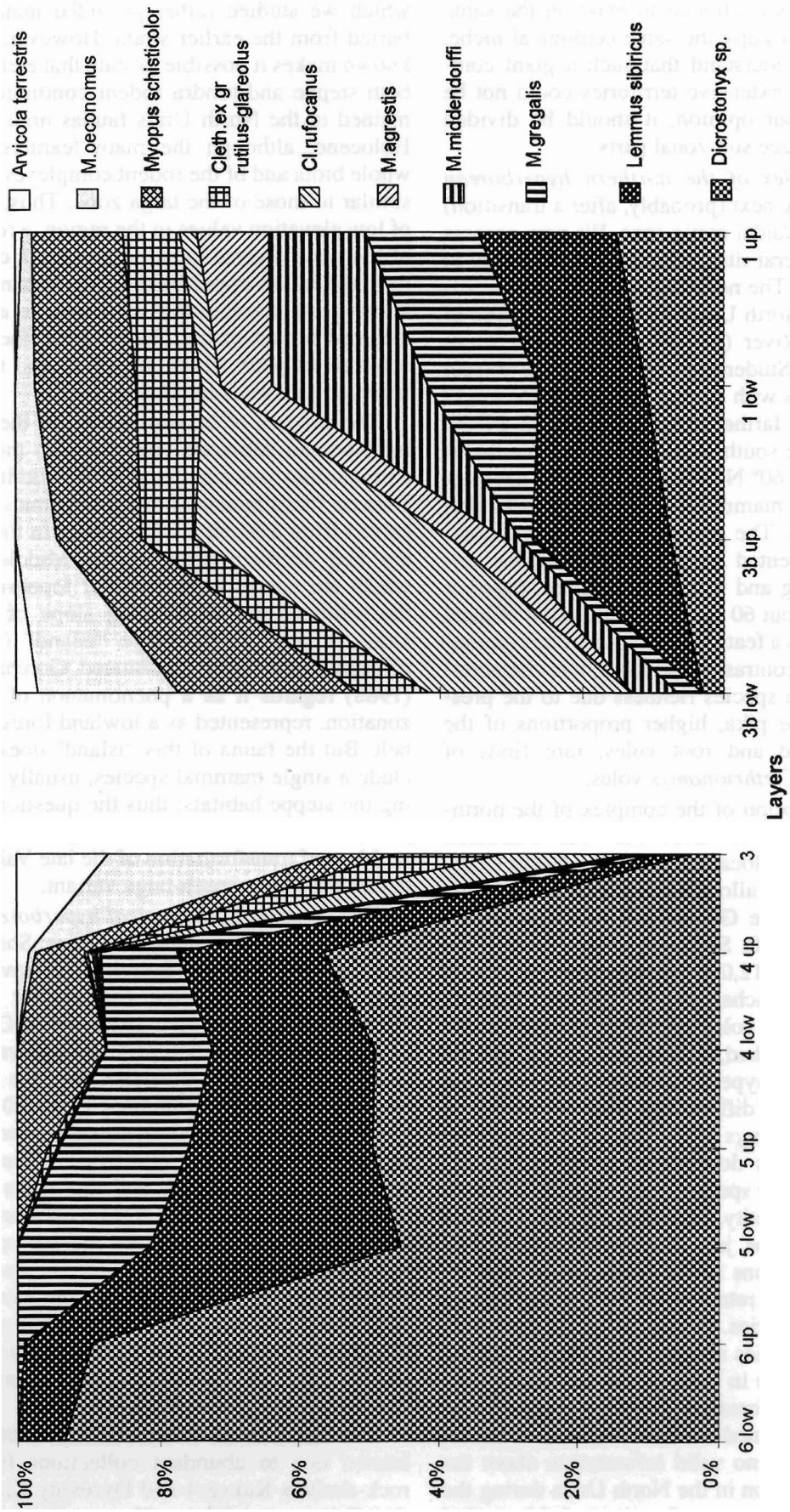

Figure 5: Correlated dynamics of the species ratio within biotope groups for Pymva-Shor (left) and Zveroboy cave (right).

several species continued to exist on the same territory and occupy the same ecological niche. One should understand that such a giant complex covering extensive territories could not be uniform. In our opinion, it should be divided into at least three sub-zonal parts.

The *complex of the northern hyperborean sub-zone* is the next (probably, after a transition) after the late Valdai arctic zone. We now possess data from several sites, which may be referred to this complex. The northernmost of them are situated in the North Urals, in the upper course of the Pechora-River (62° N; the caves of Medvezh'ya and Studenaya). However, we expect that some sites with similar fauna remains might be found even farther to the north, ca. 63-64° N. We regard the south line of this sub-zone to be situated about 60° N, where the Shaitan cave deposits showed mammal complexes of the kind in bottom layers. The core of this sub-zone complex is represented by the late Pleistocene collared lemming and Siberian lemming, together making up about 60 % of the population of local faunas. This is a feature similar to arctic communities. But in contrast to the latter, it is characterised by a high species richness due to the presence of steppe pika, higher proportions of the narrow-skulled and root voles, rare finds of *Lagurus* and *Clethrionomys* voles.

Transformation of the complex of the northern hyperborean sub-zone has been examined using data of 18 local faunas in the North Urals. These materials allow us to characterise some stages of the late Glacial and Holocene (Guslitzer *et al.*, 1990; Smirnov, 1996). During the late Glacial, ca. 12,000 BP, the fauna of rodents was somewhat richer with 11 species included. Water and field voles appeared in it, Middendorf's vole perished, and the rest of the species of the northern hyperborean sub-zone remained the same. More differences were registered in the relative numbers of the species. The collared lemming lost its dominating position and became an ordinary species, making up about 20 % of the total quantity. *Microtus gregalis* became the dominant type, just then having achieved its highest proportions in the North Urals. The Siberian lemming retained its significant role in rodent communities. During the early Holocene, the ratio of species and biotope groups was observed to change in view of the increasing proportion of taiga foresters; but the steppe and tundra forms remained on the taxa lists. Unfortunately, we have no valid information about the fauna composition in the North Urals during the Holocene optimum, as the sites of this period which we studied rather provided material reburied from the earlier strata. However, what is known makes it possible to state that elements of both steppe and tundra rodent communities remained in the North Urals faunas until the late Holocene, although the main features of the whole biota and of the rodent complexes became similar to those of the taiga zone. Thus, in spite of low elevation values in the region, a residuum of the once diverse hyperborean biota could be reserved in the upper belts of the mountains. It seems quite possible that even now in a certain elevated region of the North Urals, there exist some relict plots which are small and thus not regarded as a separate altitude belt.

The process of transformation of the typical hyperborean sub-zone complex into the recent communities was examined in the Middle Urals. Data on fossil faunas of small mammals was received from a number of localities in the southern and northern parts of the Middle Urals, which are not uniform for their topography. In the south of the west-facing slope of Middle Urals, a large forest-steppe "island" (Krasnoufimsky forest-steppe) is situated. Gorchakovsky (1968) regards it as a phenomenon of altitude zonation, represented as a lowland forest-steppe belt. But the fauna of this "island" does not include a single mammal species, usually inhabiting the steppe habitats; thus the question of this plot genesis will be discussed together with the problem of transformation of the late Valdai biota into the recent south-taiga variant.

The *complex of the typical hyperborean sub-zone* is known from many localities: Shaitansky and Lobvinsky caves, Bobyliok, Dyrovaty Kamen' on the Serga-river, rock-shelter Bolshoi Glukhoi (Smirnov, 1994, 1995, 1996; Guslitzer *et al.*, 1990). This complex demonstrated extremely high species diversity, with the narrow-skulled vole as the dominant type (30-40 %). Collared lemmings also remained numerous and sometimes extremely numerous. Three more species, namely *Lagurus* and root voles and Siberian lemming, showed significant numbers in different local faunas, usually making up 5-8 %, but sometimes increasing to 20 %. Permanent members of the local faunas in the whole sub-zone were field, water, and *Clethrionomys* voles, the grey hamster and steppe pika. At the contact with the southern sub-zone, there occurred rare finds of jerboas and *Eolagurus luteus*.

The **late Glacial** fauna (12,000-7,000 BP) is known due to abundant collections from the rock-shelters Kakva-4 and Dyrovaty Kamen' at the Tchusovaya-River. Narrow-skulled voles

were still dominating there, and collared lemmings were also numerous. To the previously noted forest species, the squirrel can be added. However, the most prominent feature of this fauna is probably the number of steppe-dwelling species (the highest number for the region), combined with their largest portion in the communities during the whole interval of the late Valdai and Holocene.

During the **Pre-Boreal**, the fauna of small mammals began to change significantly. In the Middle Urals, this period is represented by fossil data from two sites. One of them is a rock-shelter named Bolshoi Glukhoi (horizons 12, 13; north of the Middle Urals), dated by radiocarbon analysis to ca. 10,000 BP, where more than 7500 molars have been designated to 15 species of rodents and pikas. The second site is the grotto Dyrovaty Kamen' on the Serga-River (horizon 11; south of the Middle Urals), with a C14-age of ca. 9,000 BP; about 18000 molars were designated to 16 rodent species. When compared to the post-glacial faunas, those of the Pre-Boreal in the Middle Urals reveal similar features and several peculiar characteristics. Features in common concern the significant similarity of the taxa lists and great number of steppe forms. But the species ratio changed. The proportion of collared and Siberian lemmings continued to decrease. The steppe forms occupied first place in the communities by their total relative numbers; the foresters were represented by smaller portion of remains, and inhabitants of grasslands remained in third place.

The **Boreal** biota of the Middle Urals was also represented by data from several localities, both from the northern and southern parts of the region. About 2000 molars representing 14 species were collected in horizon 10 of the abovementioned grotto Dyrovaty Kamen' on the Serga-River (south of the Middle Urals; age of the layer about 8,000-7,000 BP). The already mentioned rock-shelter Bolshoi Glukhoi (the lower part of the white calciferous sandy loam layer) and horizon 7 of the Shaitan-grotto, both in the northern part of the Middle Urals, supplied a collection of 914 molars. As compared to the Pre-Boreal communities, this fauna showed the foresters' domination in numbers, though the maximum species diversity had not yet been reached. Remains of the steppe forms were still numerous, though the number of species in this group decreased. Proportions of animals inhabiting grasslands were observed to increase, yet they retained the third place in the ratio.

The **Atlantic** was characterised by the warmest climate, which caused the northernmost expansion of broad-leaved forests. In the Middle Urals, the later part of the period is represented by one site in the south of the region, the local fauna of layer 2 from the rock-shelter Oleniy, with a C14-age of about 5,000 BP (Smirnov, 1993). Ca. 5700 molars were designated to 17 species of rodents and steppe pika. Similar to the faunas of the earlier periods, this fossil community contained species of the forest, grassland and steppe biotopes, and, besides, remains of the collared and Siberian lemmings. The group of steppe inhabitants included the steppe pika, grey hamster, *Lagurus* and narrow-skulled voles. Such a mosaic of biotope groups here was probably related to local conditions of the insular Krasnoufimsky forest-steppe periphery.

The **Sub-Boreal** fauna is represented by the collection from horizons 9-12 of the Sukhorechensky grotto (Smirnov *et al.*, 1992), dated to ca. 3,000 BP. The foresters' percentage in the fauna increased by up to 80 %, while the portion of grassland species was about 15 %. However, one ought not to regard this fauna as typical for the taiga zone, as the narrow-skulled vole and steppe pika were registered in it. This variant probably corresponds to the very last stage of transformation of the forest- and grassland-preferring rodent communities into those of the taiga type, which were registered to form at the periphery of the Krasnoufimsky forest-steppe.

The **Sub-Atlantic** was studied using collections from southern and northern parts of the Middle Urals. Two local faunas were described from the southern part. The first half of the Sub-Atlantic is represented by horizons 3 and 5 of the grotto Sukhorechensky which date to a period of about 800-900 years BP. About 4500 molars were designated to 16 rodent species, three of which are missing in the modern rodent communities of the region (*Apodemus flavicollis, Myopus schisticolor, Microtus gregalis*), and one synanthropic species (*Rattus norvegicus*). Forest species dominated the taxa list, whereas the largest portion of remains was represented by inhabitants of grasslands. Only one steppe species, the narrow-skulled vole, was identified in the collection. The fauna showed signs of human influences such as the presence of the Norway rat and high numbers of the common vole (*Microtus arvalis*), the latter being common in ploughed fields. The second half of the Sub-Atlantic is represented by horizons 1 and 2 of the Sukhorechensky grotto, upper horizons of the shelter Bazhukovo III, and horizons 1-3 of the Tavra shel-

ter. About 42000 molars were designated to 16 species, which inhabited the region until now. Not a single steppe form was found. The species diversity was reduced, and the common vole prevailed in abundance, which is characteristic of regions with developed agriculture.

The Shaitan grotto (three upper horizons) in the northern part of the Middle Urals provided a limited collection of 293 molars, among which *Clethrionomys* voles showed dominance, and the wood lemming increased in number (Smirnov, 1995). The features of this fauna were similar to those which depict the modern state of the fauna from the Middle Urals taiga regions.

The *complex of the south hyperborean sub-zone* was found in many cave sites of the South Urals (Smirnov *et al.*, 1990). It was situated adjacent to the southern edge of the typical hyperborean sub-zone, but its south boundary position is not clear, as only scarce localities were found in the region. This variant of the hyperborean micromammalian complex showed the dominance of the narrow-skulled vole (up to 70 %), abundant remains of both root vole and *Lagurus lagurus,* the permanent presence of the grey hamster and collared lemming (up to 10 %), and rarer Siberian lemming. Besides these, there occurred *Clethrionomys* remains, *Eolagurus luteus*, several jerboa and *Citellus* species, with additionally the mole vole on the eastern slope. The Holocene transformation of this complex has been less well documented than that in the Middle Urals for the present. However, it seems probable that during the whole Holocene species of the steppe complex were very slow to retreat from the territories now occupied by the zone of broad-leaved forests with forest-steppe islands, and this process came to an end only some centuries ago. In the upper montane belts of the South Urals, steppe relict species are not represented among rodents, and the montane tundra there omit true tundra species, whose place is now occupied by *Clethrionomys rufocanus.*

CONCLUSIONS

Considering the Holocene as an interglacial period following the most severe cold epoch, suggests the study of the biota history of that period. The response of each living element of the biosphere to a climatic signal is determined by its nature. Small mammals are demonstrative of this. Due to their wide adaptive abilities and significant tolerance for unfavourable abiotic factors, the dynamics of the group under extraordinary conditions is first of all limited by the quality and availability of forage plants. Thanks to the small dimensions of the animals, relatively small areas might appear sufficient for survival of some isolated populations. Thus, the transition between the late Glacial and Holocene periods probably fulfilled the role as a kind of a "bottle-neck" for the mammals of the late Valdai hyperborean complexes. All small mammals and some of the larger ones but none of the giants succeeded in passing through. The transformation of the megamammal fauna proceeded very quickly and dramatically, although some regional differences were registered, too (Sher, 1997). Communities of small mammals revealed different latitude-related patterns when changing their composition and structure, from the late Glacial until the present, which was clearly exemplified by fossil data from the Urals. First of all, this concerned the time of the primary formation of real taiga complexes, and, also, the duration of the interval, when tundra and steppe forms coexisted as some extra-zonal elements in the taiga and broad-leaved forests or forest-steppes. Actually, in the Urals, this long process of transition from the poorly differentiated late Valdai complexes to the high arrangement of the Holocene zonal communities of small mammals was terminated only some centuries ago, when human activity led to the extinction of the last habitats of steppe animals in the forest zone.

Another important phenomenon is that, during the different periods (late Valdai, late Glacial, Holocene), several rodent species showed a change in status, representing either polyzonal species or strictly zonal forms, and thus entering different biotope groups. These characteristics are probably intrinsic to the montane regions, namely the Urals, where a large variety of factors and combination of these might be realised, which is impossible on a plain.

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