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# The History of Formation of Recent Small Mammal Communities in the Nether-Polar Urals

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**Abstract**—The results of studies on small mammal bone assemblages from seven cave-type sites on the Shchugor and Kozhim rivers are presented. Four stages in the development of small mammal fauna in the Nether-Polar Urals are described, which correspond to the Alleröd, Younger Dryas, Early Holocene, and Subatlantic periods. The moderately cryohydrophilic fauna of the Alleröd was replaced by an atypically "mild" xerophylic community in the Younger Dryas. In the Early Holocene, its structure still included considerable proportions of tundra species, which, along with forest species, were also found in the subfossil assemblage from the Subatlantic. It is shown that the transformation of the small mammal fauna in the above sites had a specific pattern, compared to that in other regions of northeastern Europe and to the dynamics of the natural environment and climate.

*Keywords*: small mammals, Pleistocene, Holocene, Nether-Polar Urals
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Small mammals are traditionally among the most popular objects for paleofaunistic reconstructions used to address various aspects of problems in paleofaunistics and paleoecology. The Urals are also used as a proving ground for such research. These mountains extend for a long distance in a submeridional direction, which provides the possibility to study characteristic features of various living systems in a latitudinal gradient of environmental factors (Smirnov, 2001, 2004). In the Ural foothills, where Paleozoic karst-forming rocks are well developed, late Quaternary vertebrate fossils were found to be accumulated in karst cavities (caves) as a result of life activities of predators and humans. These fossils in cave-type sites occur in especially large amounts, compared to findspots in alluvial or paleosol deposits and archaeological sites, and, as a rule, their assemblage most closely reflect the species composition of the initial natural community. Among all regions of the Ural Mountains, the Nether-Polar Urals is the least studied with respect to its Quaternary fauna of small mammals, even as compared with the Polar Urals (Golovachov and Smirnov, 2009) and Northern Urals (Smirnov, 1996; Kochev, 1993) bordering this region on the north and south, respectively. In particular, published data on late Quaternary small mammals from the Nether-Polar Urals are based on the material found in karst sites on the Shchugor River (Ponomarev and Kryazheva, 2011) and in the Sokolinyi Grotto on the Kozhim River (Ponomarev, 2005). Here, we summarize the results of studies on fossils from seven sites located on these rivers within the territory of the Yugyd Va National Park on the western slope of the Nether-Polar Urals.

## MATERIAL AND METHODS

Sites Shchugor 1, 2, 4, and 5 are within a 50-m carboniferous limestone outcrop in the Verkhnie Vorota cliffs on the right bank of the Shchugor River, 20 m upstream from the mouth of the Veldor Kyrtael' creek (Fig. 1).

Site 1 is a 10-m-long cave open at both ends. One opening (0.8 high and 1.8 m wide) faces the Shchugor River valley, and the other (1 m high and 1.3 m wide), the Veldor Kyrtael' valley. Loose deposits in this cave are stratified into three horizons. The middle horizon contained vertebrate fossils, among which 358 teeth of small mammals were identified (Table 1).

Site Shchugor 2 is under a rock overhang at a distance of 3 m from Shchugor 1. The profile of deposits is reduced to a single soil–plant layer 55 cm deep, where 1415 teeth of small mammals were found and identified (Table 1).

Site Shchugor 4 is a karst grotto 9 m deep, 4 m wide, and 3 m high. Its loose deposits are stratified into four horizons consisting of aleurites, sandy loam, and

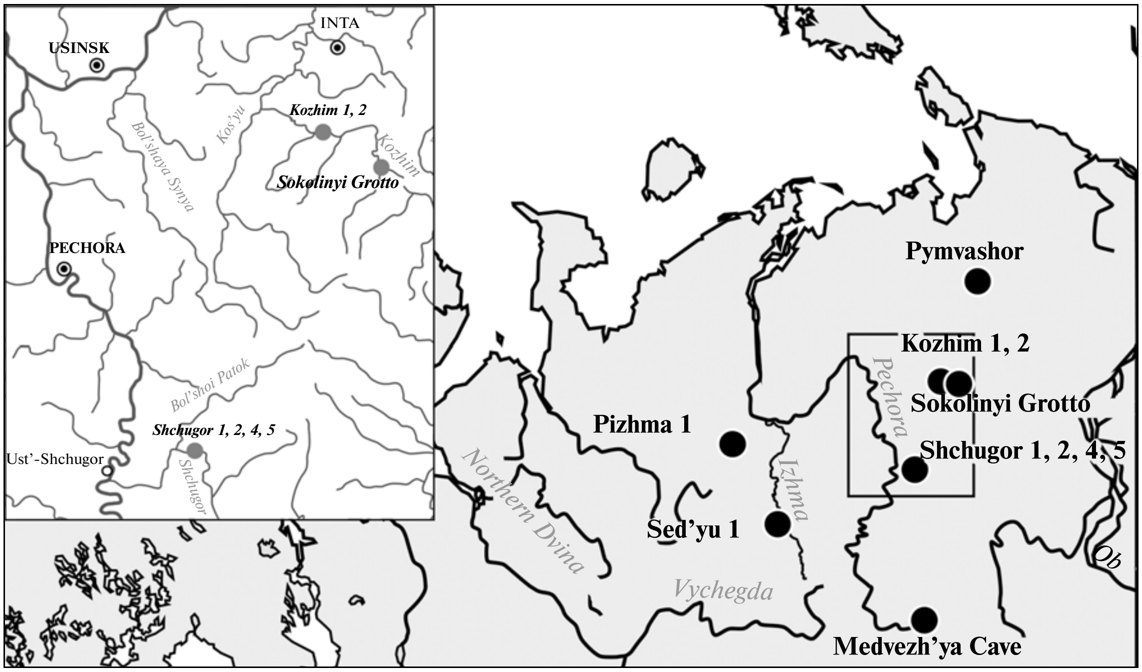


**Fig. 1.** Map of sites with fossils of late Quaternary small mammals in the extreme northeast of Europe.

loam with gravel–gruss rock debris. Three horizons contained bones of vertebrates. More than 4666 teeth of small mammals from this site were identified (Table 1).

Site Shchugor 5 is a grotto 8 m deep, 5 m wide, and 1.5 m high. The profile of loose deposits has three horizons consisting of humic clumpy gravely matter, sandy loam, and sand. A total of 337 teeth of small mammals from the upper two horizons were identified (Table 1).

Hans van der Plicht (Center for Isotope Research, University of Groningen, The Netherlands) determined the age of mammal bones from sites Shchugor 2 and 4 by means of AMS $^{14}C$ dating. The results were as follows: Shchugor 2 (the lower jaw of a squirrel), 950 ± 35 years (GrA 49352); Shchugor 4, horizon 1 (a collared lemming bone), 10090 ± 60 years (GrA 49440); Shchugor 4, horizon 2 (a fragment of the reindeer humeral diaphysis), 9710 ± 45 years (GrA 49351); Shchugor 4, horizon 3 (the skull of a *Lemmus* lemming), 11850 ± 60 years (GrA 49439). Thus, horizon 2 was dated to a slightly earlier period than overlying horizon 2, which was evidence for its contamination with younger carbon from the latter layer. The composition and structure of the small mammal fauna from horizon 2 were almost identical to those of the subfossil assemblage from horizon 3 but markedly differed from the assemblage found in horizon 1. In our opinion, these facts show that the age of horizon 2 is close to that of horizon 3 and, therefore, the assemblages from these two lower horizons represent the same type of community corresponding to a certain stage in the development of theriofauna.

Sites Kozhim 1 and 2 are located at a distance of 50 m from each other in an Ordovician limestone outcrop on the right bank of the Kozhim River, 7 km upstream from the mouth of the Syv'yu River and 1 km downstream from the Kayuk-Nyrd cliffs.

Site Kozhim 1 is a small karst cave 2.4 m deep, 1.1 m wide, and 1.1 m high. Loose deposits are stratified into three horizons: aleurite, loam, and clumpy gravel–gruss deposits. The upper two horizons contained vertebrate fossils, among which 1825 teeth of small mammals were identified Table 2). The material from horizon 2 was AMS dated to 9090 ± 45 years BP (GrA 49353), i.e., to the Late Preboreal–Early Boreal.

Site Kozhim 2 is a niche 1.7 m deep, 2.5 m wide, and 1.6 m high. There are two horizons of sand–aleurite and sandy loam deposits containing large amounts of coarse rock detritus and mammal bone remains. Among the latter, 1165 teeth of rodents were identified (Table 2).

The Sokolinyi Grotto site is in an Ordovician rock outcrop located 1.5 km from the Limbekhayu River mouth. The grotto is 2.5 m deep, up to 2 m wide, and 1.3 m high. The profile of loose deposits consists of three aleurite and loam horizons containing mammal bone remains, including 3259 identified teeth of small mammals (Table 2). The lower jaw of a Siberian lemming from horizon 2 was AMS dated to 10390 + 50–45 radiocarbon years BC (GrA 42215), i.e., to the Younger Dryas.

The condition of small mammal bone remains from these sites (the pattern of degradation by digestive enzymes, the degree of fragmentation, etc.) indi-

**Table 1.** Numbers of buccal teeth of different species and their proportions (%) among small mammal fossils from sites on the Shchugor

| Species | Shchugor 1, horizon2 | Shchugor 2, horizon 1 | Shchugor 4 | | | Shchugor 5 | |
|---|---|---|---|---|---|---|---|
| | | | Horizon 1 | Horizon 2 | Horizon 3 | Horizon 1 | Horizon 2 |
| Steppe species | | | | | | | |
| *Ochotona pusilla* | – | – | – | 20 (1) | 6 (1.7) | – | – |
| Tundra species | | | | | | | |
| *Dicrostonyx* sp. | 18 (5.1) | – | 234 (13.9) | 416 (15.8) | 53 (15.7) | – | 5 (2.2) |
| *Lemmus sibiricus* | 40 (11) | 46 (3.7) | 318 (18.9) | 954 (36.2) | 139 (43.3) | – | 14 (6.2) |
| *Microtus gregalis* | 78 (21.7) | 17 (1.8) | 407 (24.2) | 666 (25.3) | 99 (29.3) | – | 9 (4) |
| Forest species | | | | | | | |
| *Clethrionomys glareolus* | 19 (5.3) | 66 (4.7) | 44 (2.6) | 18 (0.7) | – | 12 (10) | 9 (4) |
| *Cl. rufocanus* | 32 (9) | 222 (15.7) | 77 (4.6) | 21 (0.8) | – | 22 (19.8) | 52 (23) |
| *Cl. rutilus* | 18 (5.1) | 74 (5.6) | 104 (6.2) | 32 (1.2) | 4 (1.2) | 21 (18.9) | 33 (14.6) |
| *Myopus schisticolor* | 18 (5.1) | 82 (5.7) | 90 (5.4) | 173 (6.4) | 15 (4.4) | 35 (31.5) | 28 (12.4) |
| *Microtus agrestis* | 33 (9.2) | 84 (6.5) | 155 (9.2) | 190 (7.2) | 4 (1.2) | 8 (7.9) | 19 (8.4) |
| *Sciurus vulgaris* | – | 165 (11.6) | – | – | – | 3 (2.7) | 1 (0.5) |
| Intrazonal species | | | | | | | |
| *Arvicola terrestris* | 53 (14.8) | 594 (41) | 130 (7.6) | 49 (1.8) | 2 (1) | 8 (7.4) | 36 (15.9) |
| *Microtus oeconomus* | 49 (13.7) | 65 (3.7) | 122 (7.4) | 95 (3.6) | 8 (2.2) | 2 (1.8) | 20 (8.8) |
| Total | 358 (100) | 1415 (100) | 1680 (100) | 2634 (100) | 337 (100) | 111 (100) | 226 (100) |

cated that they have been mainly deposited with feces, and the presence of large-mammal bone fragments with traces of gnawing indicated that carnivores had also been somewhat involved in the formation of the corresponding orictocenosis.

Excavations and retrieval of mammal remains were performed by the standard procedure. Loose deposits were excavated by conditional horizons (to a depth of no more than 10 cm at a time) and washed on sieves with a mesh size of 0.8–1 mm, and the remaining mixture of bones and rock fragments was dried and sorted manually.

In voles of the genus *Microtus*, only the first lower molars can be identified to species. Therefore, to estimate the proportions of different *Microtus* species in the fossil assemblage, the species distribution ratio of the first lower molars was first determined, and then all teeth attributed to this genus were divided by species in the same ratio. Species poorly distinguishable morphologically, such as the Middendorf's vole (*Microtus middendorffii*)–field vole (*M. agrestis*) or the wood lemming (*Myopus schisticolor*)–Siberian brown lemming (*Lemmus sibiricus*), were discriminated as described (Smirnov et al., 1997). The molars of three vole species of the genus *Clethrionomys* were identified by the method proposed by Borodin (2009).

The radiocarbon dates were calibrated using the Calib program (http://calib.qub.ac.uk/calib/) with the IntCal09 data set (Reimer et al., 2009).

## RESULTS AND DISCUSSION

The recent fauna of the Nether-Polar Urals includes 12 species of rodents and small lagomorphs: the pica *Ochotona pusilla* (in the mountain forest belt); forest voles *Clethrionomys rutilus*, *Cl. glareolus*, and *Cl. rufocanus*; root vole *Microtus oeconomus*; water vole *Arvicola terrestris*; wood lemming *Myopus schisticolor*; northern birch mouse (*Sicista betulina*); red squirrel (*Sciurus vulgaris*); Siberian chipmunk (*Tamias sibiricus*); and Siberian flying squirrel (*Pteromys volans*) (Tur'eva, 1977; *Fauna* ..., 1994; Bobretsov et al., 2004). All these species are generally common in the taiga zone. Dominance by abundance in almost all taiga habitats belongs to the northern red-backed vole (*Cl. rutilus*). In droppings collected in the Shchugor valley, we identified the teeth of *M. schisticolor*, *L. sibiricus*, *Cl. glareolus*, *Cl. rutilus*, *M. agrestis*, *A. terrestris*, *M. oeconomus*, and *Sc. vulgaris*, with prevalence of the last two species.

The most ancient small mammal remains were found in horizons 2 and 3 from Shchugor 4 site. This moderately cryohydrophilic assemblage with a slight prevalence of *L. sibiricus* remains was dated from the Alleröd. Faunas of more or less the same age, dating from the Bölling–Alleröd interstadial, are known from sites in the Polar and Northern Urals and Southern Timan. Horizon 5 from the Pymvashor area, the Polar Urals, was found to contain the remains of only tundra species: *Dicrostonyx* sp. (46%), *L. sibiricus* (36%), and *M. gregalis* (19%) (Smirnov et al., 1999).

**Table 2.** Numbers of buccal teeth of different species and their proportions (%) among small mammal fossils from sites on the Kozhim

| Species | Sokolinyi Grotto | | | Kozhim 1 | | Kozhim 2 | |
|---|---|---|---|---|---|---|---|
| | Horizon 1 | Horizon 2 | Horizon 3 | Horizon 1 | Horizon 2 | Horizon 1 | Horizon 2 |
| Steppe species | | | | | | | |
| *Ochotona pusilla* | – | – | – | – | 1 (0.1) | – | – |
| Tundra species | | | | | | | |
| *Dicrostonyx* sp. | 10 (0.4) | 38 (5.4) | 14 (12.4) | 3 (1.5) | 205 (12.8) | – | – |
| *Lemmus sibiricus* | – | 103 (14.6) | 44 (38.9) | 6 (2.8) | 163 (10.3) | 11 (1.6) | 24 (5) |
| *Microtus gregalis* | 8 (0.3) | 239 (33.9) | 38 (33.6) | 13 (6) | 198 (12.3) | 7 (1) | 13 (2.7) |
| Forest species | | | | | | | |
| *Clethrionomys glareolus* | 400 (16.4) | 31 (4.4) | 3 (2.6) | 15 (7.3) | 15 (0.9) | 46 (6.7) | 62 (13) |
| *Cl. rufocanus* | 652 (26.7) | 70 (9.9) | 4 (3.5) | 14 (6.5) | 28 (1.7) | 43 (6.2) | 34 (7) |
| *Cl. rutilus* | 488 (20) | 42 (6) | 4 (3.6) | 19 (8.9) | 48 (2.9) | 78 (11.4) | 94 (19.5) |
| *Myopus schisticolor* | 141 (5.8) | 27 (3.8) | – | 13 (6) | 27 (1.6) | 34 (5) | 14 (2.9) |
| *Microtus agrestis* | 549 (22.5) | 80 (11.4) | 4 (3.5) | 23 (10.7) | 170 (10.5) | 289 (42.2) | 75 (15.6) |
| *Sicista betulina* | – | – | – | – | – | 5 (1) | – |
| *Sciurus vulgaris* | – | – | – | 4 (1.8) | – | 3 (0.5) | – |
| Intrazonal species | | | | | | | |
| *Arvicola terrestris* | 64 (2.6) | 1 (0.1) | 2 (1.8) | 83 (38.7) | 493 (30.6) | 85 (12.3) | 141 (29.3) |
| *Microtus oeconomus* | 130 (5.3) | 73 (10.4) | – | 21 (9.8) | 263 (16.3) | 83 (12.1) | 24 (5) |
| Total | 2442 (100) | 704 (100.03) | 113 (100.01) | 214 (100) | 1611 (100) | 684 (100) | 481 (100) |

The assemblage from the brown loam horizon A in the Medvezh'ya Cave, the Northern Urals, included the remains of *M. gregalis* (32.5%), *L. sibiricus* (30%), *Dicrostonyx guilielmi* (17%), *M. agrestis* (7%), *M. oeconomus* (6.5%), *M. schisticolor* (3.5%), voles of the genus *Clethrionomys* (2.5%), and *A. terrestris* (1%) (Smirnov, 1996). *Dicrostonyx* sp., *L. sibiricus*, and *M. gregalis* were codominant (a total of 79%), with the assemblage containing the remains of forest and riparian species (13.3 and 7.5%, respectively). It can be seen that the fauna from the Medvezh'ya Cave, located close to the study sites, had similar composition and structure, whereas the assemblage from Pymvashor was slightly more cryophilic. This difference is well explained by the latitudinal gradient of environmental conditions. The same-age local fauna from site Sed'yu 1 (the Southern Timan) had a more different structure with distinct dominance of *L. sibiricus* (52%) (Ponomarev, 2006). It appears that a slightly more hydrophilic structure of the small mammal fauna was typical for the Bölling–Alleröd interstadial warming not only in the Nether-Polar Urals but also in northeastern Europe in general.

The local fauna from horizon 1 of Shchugor 4 and horizon 2 of the Sokolinyi Grotto characterizes the Younger Dryas stage in the history of small mammal fauna formation. Horizon 1 was dated from the early Preboreal, but the calibrated date (11 860 years BP) is indicative of its Younger Dryas age (Rasmussen et al., 2006). The structure of the fauna from this layer does not contradict this conclusion: the remains of tundra species account for less than half of all remains. Dominance belongs either to three tundra species (Shchugor 4, horizon 1) or to *M. gregalis* (the Sokolinyi Grotto, horizon 2). Younger Dryas assemblages are known from horizon 5 of the Pizhma 1 Grotto (The Middle Timan), and a similar date corresponding to the Preboreal period of the Holocene was determined for horizon 4 from Pymvashor (the Polar Urals). In horizon 5 from Pizhma 1, almost 96% of all remains were those of *Dicrostonyx* sp. (46.4%), *L. sibiricus* (18.6%) and *M. gregalis* (30.7%) (Ponomarev et al., 2005). In addition, there were few remains of *M. schisticolor* (2%), *Cl. glareolus*, *M, agrestis*, *A. terrestris*, and *M. oeconomus* (no more than 0.6% each. The assemblage from horizon 4 of Pymvashor proved to be closely similar to that from horizon 5 of Pizhma 1: it included the remains of *Dicrostonyx* sp. (49.1%), *L. sibiricus* (21.2%), *M. gregalis* (10.6%), *M. schisticolor* (6.7%), *M. oeconomus* (1.1%), *A. terrestris* (1.7%), *Cl. glareolus*, and *M. agrestis* (0.6% each) (Smirnov et al., 1999).

The fauna from horizon 3 of the Sokolinyi Grotto differs from that from horizon 2 in a greater proportion of tundra species and smaller proportions of forest and intrazonal species. Its structure is closer to that of the fauna from brown loam horizon A of the Medvezh'ya Cave dated from the Alleröd. Thus, the fossil assemblage of horizon 3, judging from its composition, structure, and location in the profile (below the Younger Dryas horizon 2), was in the late glacial period, probably during the Bölling–Alleröd interstadial. A large proportion of *L. sibiricus* remains in this fossil assemblage is noteworthy as a characteristic feature of assemblages from the Bölling–Alleröd of northeastern Europe.

It is of interest that the fauna from horizon 2 of the Sokolinyi Grotto is similar to that from horizon 1 of Shchugor 4 but differs from the assemblages found in Pizhma 1 and Pymvashor. The remains of tundra species also dominate in this fauna, but their proportion is only 57.8%, and most of them are the remains of *M. gregalis* (34%). The proportions of forest and meadow species are 31.7 and 10.5%, respectively. Apparently, such similarity between the faunas from sites located in the same region is not accidental and can be explained by local specificity of landscape–climatic conditions in the Nether-Polar Urals during the Younger Dryas.

The fossil assemblage from horizon 2 of site Kozhim 1 provides an idea of the Early Holocene fauna of the Nether-Polar Urals. According to radiocarbon dating, this assemblage was formed during the Late Preboreal to Early Boreal periods of the Holocene. The composition and structure of this local fauna have a "hyperboreal," tundra–steppe pattern characterized by considerable and almost equal proportions of *Dicrostonyx* sp., *L. sibiricus*, and *M. gregalis* (a total of 35%) and a small proportion of forest species (17.6%). A fairly cryophilic structure of this assemblage makes it different from the later (boreal) subfossil assemblage from horizon 3 of Pymvashor (Smirnov et al., 1999), which was found to include the remains of *Cl. glareolus* (33.3%), *M. oeconomus* (32%), *A. terrestris* (12.9%), *M. schisticolor* (8.8%), *Dicrostonyx* sp. (4.1%), *L. sibiricus* (4.1%), *M. gregalis* (2%), *M. agrestis* (2%), *M. middendorffii* (0.7%), and *S. betulina*. Thus, the assemblage from horizon 3 represented a typical forest fauna with prevalence of forest and riparian species and an insignificant proportion of tundra species.

The assemblage of forest mammals from Shchugor 2 and Kozhim 2 provides an idea of the Late Holocene (Subatlantic) fauna of the study region, which is also typical for many other sites in northeastern Europe. A basic feature differentiating it from assemblages described in the Northern Urals (Smirnov and Sadykova, 2003) is the presence of tundra species, *M. gregalis* (up to 2.7%) and *L. sibiricus* (up to 5%), while the absence of *Dicrostonyx* sp. and small proportions of tundra species in general make it different from faunistic complexes of the Polar Urals (Smirnov et al., 1999). A considerable proportion of the remains of species characteristic of riparian habitats is probably explained by taphonomic factors, mainly by food specialization of predators.

It is interesting to compare the course of fauna transformation in the sites studied with the history of vegetation and landscapes. According to palynological data (Arslanov, Orlov, and Nikiforova, 1981; Grichuk, 1982; Nikiforova, 1982; Borisova and Zilikson, 1995; Velichko et al., 1997, 2002; Simakova and Puzachenko, 2008a), the periglacial shrub tundras (north of 61°–63°N) and forest– tundra (59°–62°N) with tundra–steppe areas were widespread in northeastern Europe during the Bölling–Alleröd interstadial. Plant associations consisted of *Betula nana*, *Salix* spp., plants of the order Ericales, *Hippophae rhamnoides*, and species of the genera *Juniperus*, *Rubus*, *Helianthemum*, *Armeria*, *Sphagnum*, and *Selaginella*; there also was a certain proportion of pine–birch and spruce forests.

Conclusions concerning the considerable presence of tree plants in the Bölling–Alleröd vegetation of northern Europe, especially in river valleys and other protected habitats, are confirmed by the analysis of macrofossils and palynological data on the dynamics of tree vegetation boundary during the late glacial period and Holocene in northwestern Europe (Latalowa and van der Knaap, 2006), the central and northwestern parts of the East European Plain (Novenko et al., 2009), northern Eurasia (Binney et al., 2009), Scandinavia (Kullman, 2008), and Karelia (Wolhfarth, Lacourse, and Bennike, 2007).

The idea that tree vegetation in northeastern Europe had expanded up to the Barents Sea coast (Nikiforova, 1982; Arslanov, Lavrov, and Nikiforova, 1981), was not confirmed in subsequent studies based on the material from pits located near the Barents Sea coast (Paus, Svendsen, and Matiouchkov, 2003) and on the Kara Sea coast (Andreev et al., 2001). They showed that vegetation in these regions was represented by dwarf birch tundras (Paus, Svendsen, and Matiouchkov, 2003) and associations with Poaceae, Cyperaceae, *Salix, Saxifraga*, and xerophytes (Andreev et al., 2001), with the weather being slightly colder than today.

According to palynological data, the Younger Dryas cooling resulted in the thinning of forests, with vacant areas being occupied by expanding tundra and steppe plant associations (Arslanov, Orlov, and Nikiforova, 1981; Nikiforova, 1982; Velichko et al., 1997, 2002; Kremenetski, Sulerzhitsky, and Hantemirov, 1998; Kaakinen and Eronen, 2000; Bohncke, 2008; Golubeva, 2008), and in the development of shrub tundras and larch–pine–birch forests with steppe plant communities.

During the Preboreal period, shrub tundras were replaced by forest–tundra plant associations in the form of pine–birch forests with spruce and tundra–steppe communities, but periglacial tundra–steppe elements in northeastern Europe remained an essential component of vegetation until the Boreal period (9000 years BP) (Arslanov, Orlov, and Nikiforova, 1981; Nikiforova, 1982; Velichko et al., 1997, 2002; Kremenetski, Sulerzhitsky, and Hantemirov, 1998;

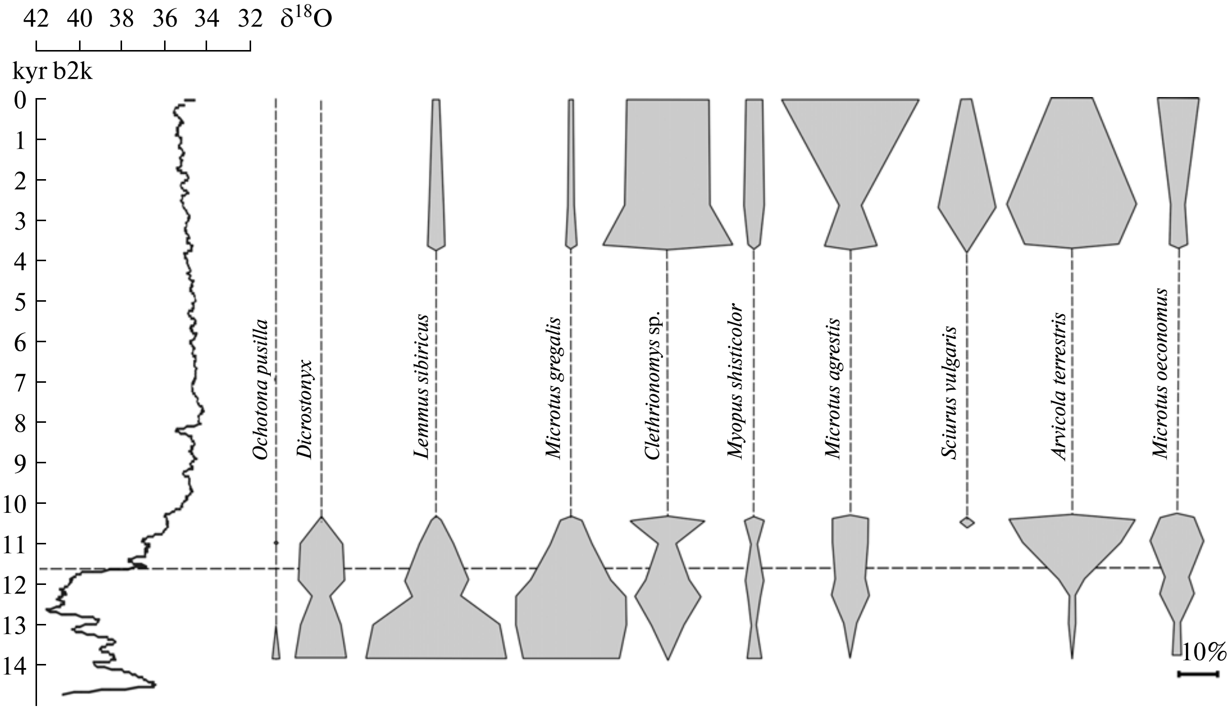


**Fig. 2.** Dynamics of the composition and structure of local faunas in the Nether-Polar Urals during the Late Pleistocene and Holocene. The climatic curve based on the NGRIP ice core data ($\delta^{18}O$) is shown on the GICCO5 time scale (Svensson et al., 2008) graded in kyr b2k (here, b2k means before AD 1950).

Kaakinen and Eronen, 2000; Golubeva, 2008; Simakova and Puzachenko, 2008b).

In the Boreal period of the Holocene, taiga forests were dominant and expanded throughout northwestern Europe to the northern sea coasts (Arslanov, Orlov, and Nikiforova, 1981; Nikiforova, 1982; Velichko et al., 1997, 2002; Kremenetski, Sulerzhitsky, and Hantemirov, 1998; Kaakinen and Eronen, 2000; Golubeva, 2008; Simakova and Puzachenko, 2008b; etc.).

Of interest are data on climate dynamics in the Nether-Polar Urals during the postglacial period (Kultti et al, 2003). The climate optimum in this region occurred in the Early Holocene (9500–9000 radiocarbon years BP), where summer temperatures were about 2°C higher than today and the climate was generally more humic. This warming provided for the expansion of forest vegetation and continued until 5500–4500 uncalibrated years ago.

Thus, transformations of the small mammal fauna in the Nether-Polar Urals arrear to be as follows. The Bölling–Alleröd interstadial warming provided for the expansion of moderately hydrophilic communities dominated by *L. sibiricus* not only in this region but also throughout northeastern Europe (Fig. 2). As a result of the Younger Dryas cooling, the proportion of tundra species slightly decreased in favor of forest species. Among tundra species in a broad sense, this period was marked by an increase in the proportion of *M. gregalis*, a moderately cryophilic and xerophylic species. It should also be noted that the fossil assemblages from horizon 1 of Shchugor 4 and horizon 2 of the Sokolinyi Grotto, having a relatively "mild," steppificated structure, differ from other Younger Dryas and Early Preboreal assemblages described in northern Europe, in particular, those from sites Pizhma 1 (the Middle Timan) and Pymvashor (the Polar Urals), which have a more cryophilic pattern and include considerable proportions of tundra species dominated by *Dicrostonyx* sp. It may well be that the specificity of fossil small mammal communities from the Nether-Polar Urals is not accidental but is explained by as yet unknown local features of landscape–climatic conditions in this region during the Younger Dryas.

As a result of the Preboreal warming, the proportion of tundra species in small mammal communities decreased by half, while that of intrazonal species increased. However, the small mammal fauna of the Nether-Polar Urals generally retained a mixed tundra–steppe pattern, in contrast to the material from horizon 3 of Pymvashor (the Polar Urals) and the results of climatic reconstructions, according to which taiga landscapes existed in the north of the Ural Mountains 9000 years ago. Apparently, the radical structural transformation of small mammal communities, with the replacement of dominants, took place between 9000 and 8500 years BP. Factors due to which the small mammal fauna could retain its tundra–steppe pattern also include the diversity of habitats characteristic of the Ural foothills and the presence of periglacial components in the vegetation until the Boreal period.

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