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New data on the Holocene history of the rodent fauna in the Pre-Uralian Subarctic (the Chernyshev Ridge, northeastern part of European Russia)

Inna V. Kryazheva, Dmitry V. Ponomarev*, Thijs van Kolfschoten & Johannes van der Plicht

ABSTRACT. In this paper we present the results of the study of rodent faunas from five cave localities in the Chernyshev Ridge located along the Usa and Sharyu Rivers, dated to the Early Holocene, the Late Holocene and "historical" (subrecent) time intervals. The changes in the fauna are correlated with regional alterations in climate and related shifts in the vegetation. Early Holocene faunas consist mainly of forest and intrazonal species; however, there is still a significant portion (10–13%) of tundra species. Late Holocene assemblages are also dominated by forest and intrazonal species but tundra species are less abundant (2.5%). The most recent rodent fauna of the taiga zone in the Chernyshev Ridge area, dated to the last decades, as well as the modern regional fauna, lacks tundra species and consists of forest and intrazonal rodent species.

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KEY WORDS: rodents, mammals, Holocene, northeastern part of European Russia, faunal history, Chernyshev Ridge.

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Новые данные к истории фауны грызунов Приуральской Субарктики (гряда Чернышева, северо-восток европейской части России) в голоцене

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РЕЗЮМЕ. В статье представлены результаты изучения фауны грызунов из пяти пещерных местонахождений гряды Чернышева на реках Уса и Шарью. Описана история формирования фауны грызунов гряды Чернышева в голоцене на трех хроносрезах: раннего голоцена, позднего голоцена и «исторического» (последние десятилетия) периода, которая хорошо сопоставляется с региональной динамикой климата и растительности. Фауна раннего голоцена состояла в основном из лесных и интразональных видов с заметным участием (10–13%) тундровых видов. В сообществах позднего голоцена также преобладали лесные и интразональные виды, но участие тундровых видов было заметно меньше (2.5%). Фауна последних десятилетий таежной зоны гряды Чернышева, как и современная фауна региона, не содержит тундровых видов и состоит из лесных и интразональных видов грызунов.

КЛЮЧЕВЫЕ СЛОВА: грызуны, млекопитающие, голоцен, северо-восток европейской части России, история фауны, гряда Чернышева.

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Introduction

The Holocene history of rodent fauna in the Subarctic Urals has been studied based on materials from a number of cave localities in the Nether-Polar Urals (Kryazheva *et al.*, 2012) and the Polar Urals (Smirnov *et al.*, 1999; Golovachov & Smirnov, 2009). Here we present new data from cave deposits exposed in a poorly studied area of the Uralian Subarctic, the Chernyshev Ridge: a low relief of +200 m above sea level (a.s.l.) parallel to the Nether-Polar and Polar Urals at the edge of the East European Plain, west of the Ural Mountains. The vegetation of the northern part of the Chernyshev Ridge is characterized by a tundra biome, whereas a taiga biome covers the southern part of that ridge (Isachenko, 1964; Ilchukov, 2010), which is the region discussed in this paper. The fossil assemblages from five caves located in the southern part of the Chernyshev Ridge add new information about the Holocene history of the rodent fauna in the Subarctic area.

Stratigraphical and chronological data

The investigated faunal remains originate from five localities, situated on the banks of the Sharyu and Usa Rivers (Fig. 1). The locality Sharyu-1 (66.1531° N., 58.7299° E, 120 m a.s.l.) is a small cave, 1 m high, 0.8 m wide and 2 m long, on the right bank of the Sharyu River, 1.5 km downstream of the natural geological monument Okno in the Silurian limestone outcrop (Fig. 2A, B). The sequence of unconsolidated sediments consists of two layers, silt and loam (Fig. 2C) with abundant fossil remains including fish, small birds, insectivorous mammals, rodents and hares. The fish remains are predominant. The fragmentation of the bones is limited.

The locality of Sharyu-2 (66.1525° N., 58.7325° E, 143 m a.s.l.) is a rock ledge with unconsolidated material that includes bird pellets, skulls and mandibles of voles and moss turf with bone remains under a habitable nest at an altitude of 30 m above the water level, 200 m upstream from the Sharyu-1 grotto (Fig. 3).

Sharyu-3 (66.1645° N, 58.7442° E, 133 a.s.l.) is a small niche (Fig. 4) with an accumulation of 54 bird pellets and unconsolidated moss turf less than 5 cm thick with a small amount of bone remains. The locality is situated on the left bank of the Sharyu River, 2 km upstream from the mouth of the Durnaya River in a rocky outcrop of Carboniferous limestone at an altitude of 20 m above the water level.

The localities of Usa-1 and Usa-2 (66.4969° N, 59.5569° E, 90 m a.s.l.) are located one meter from each other on the left bank of the Usa River, 1.5 km upstream from the mouth of the Bolshoy Adak River in an outcrop of Silurian limestone at an altitude of 11 m above the water level (Fig. 5A). Bone remains of vertebrates were found in sediments of Usa-1 and Usa-2. They include rodents, small mustelids (*Mustela* sp.), shrews (*Sorex* sp.), hare (*Lepus* sp.), small birds, fish and few fragments of unidentified bones of some large mammals.

Usa-1 (Fig. 5A, B) is a grotto 1.3 m high, 2 m wide and 7 m long. The thickness of the unconsolidated deposits

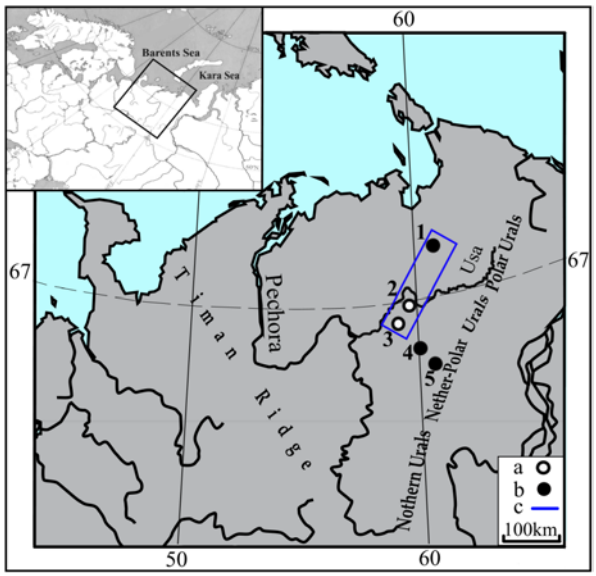


Fig. 1. Map showing the geographical position of the cave localities mentioned in the text. a — new cave localities in the Chernyshev Ridge; b — other cave localities in the Pre-Uralian Subarctic mentioned in the text. The Chernyshev Ridge is indicated with a rectangle.
1 — Pymvashor; 2 — Usa-1, Usa-2; 3 — Sharyu-1, Sharyu-2, Sharyu-3; 4 — Kozhim-1, Kozhim-2, Kozhim-4; 5 — Sokoliny.

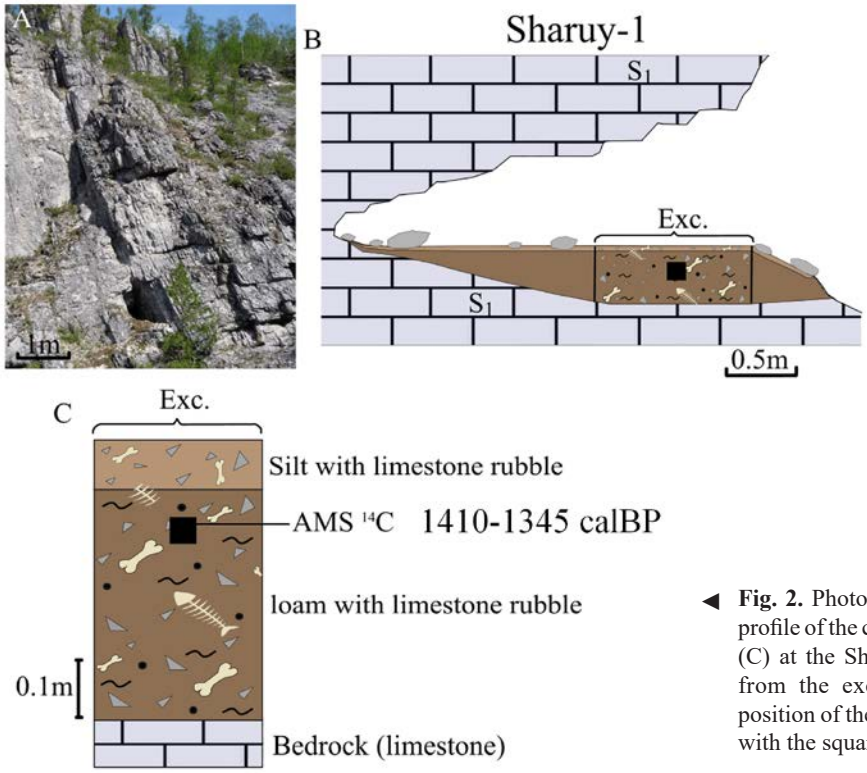
was 0.4 m. Based on the lithological characteristics, the section is divided into two layers: silty sediments (layer 1) and loamy sediments (layer 2) (Fig. 5C). The excavated area is 1 m^2.

Usa-2 (Fig. 5A, B) locality is a grotto 1.1 m high, 1.5 m wide and 7 m long. Based on lithological characteristics, the section of unconsolidated sediments (0.4 m. thick) is divided into two layers with silty (layer 1) and loamy (layer 2) sediments (Fig. 5C). The excavated area was 0.8 m^2.

Dating

Radiocarbon dating was performed by AMS in Groningen, the Netherlands (laboratory code GrA). Our dataset contains one radiocarbon date obtained by radiometry in Moscow, Russia (laboratory code GIN). The ^{14}C dates are reported in BP by convention (Mook & van der Plicht, 1999). Calibrated dates are reported in calBP, i.e. calendar age relative to AD 1950. The 1-sigma range (rounded to 5) of the calibrated dates is reported. Calibration was done using the recommended IntCal20 calibration curve (Reimer *et al.*, 2020). The ^{14}C dates (in BP and calBP) are shown in Table 1.

The oldest radiocarbon date is obtained for rodent bones from Usa-2 layer 2, yielding a calibrated ^{14}C date of 9530–9470 calBP (GrA-66466), which corresponds to the Early Holocene. The youngest radiocarbon date is obtained for rodent bones from locality Sharyu-1 layer 2 (17 cm depth), yielding a calibrated ^{14}C date of 1410–1345 calBP (GrA-66862), which corresponds to the Late Holocene.



◄ **Fig. 2.** Photo of the cave locality Sharyu-1 (A), profile of the cave (B) and of the excavated section (C) at the Sharyu-1. The bones were recovered from the excavated area. The stratigraphical position of the AMS ^{14}C dated sample is indicated with the square.

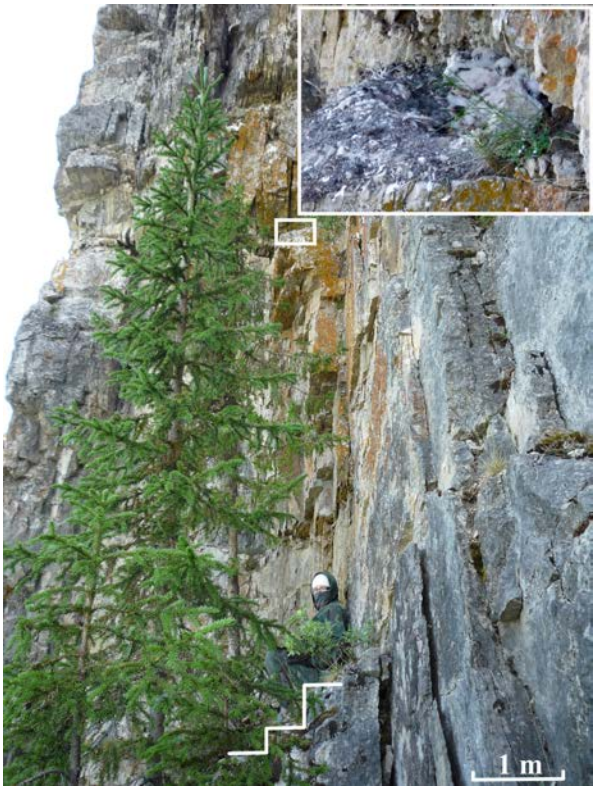


Fig. 3. Photo of the locality Sharyu-2. The bone material felt down from the habitable nest, marked with white rectangle (enlarged image of the nest is shown in the upper right part of the figure), and accumulated on the rock ledge, highlighted with white step line in the lower part of the photo.

Fig. 4. Photo of the locality Sharyu-3. The plastic bag contains pellets that were found at this site.

An indirect age assessment of the fossil assemblages was carried out based on the similarity in fauna composition and the ratio of the remains compared to other local radiocarbon dated faunas in the region, as well as on the stratigraphical position of the bone-bearing layer in the section. When muskrat remains were found in the local fauna, the entire complex was assigned as subrecent. This is due to the fact that the muskrat was introduced to the Usa River basin from the Solovetsky Islands in 1964 and soon after the species became a common element of the regional rodent fauna (Polezhayev, 1994).

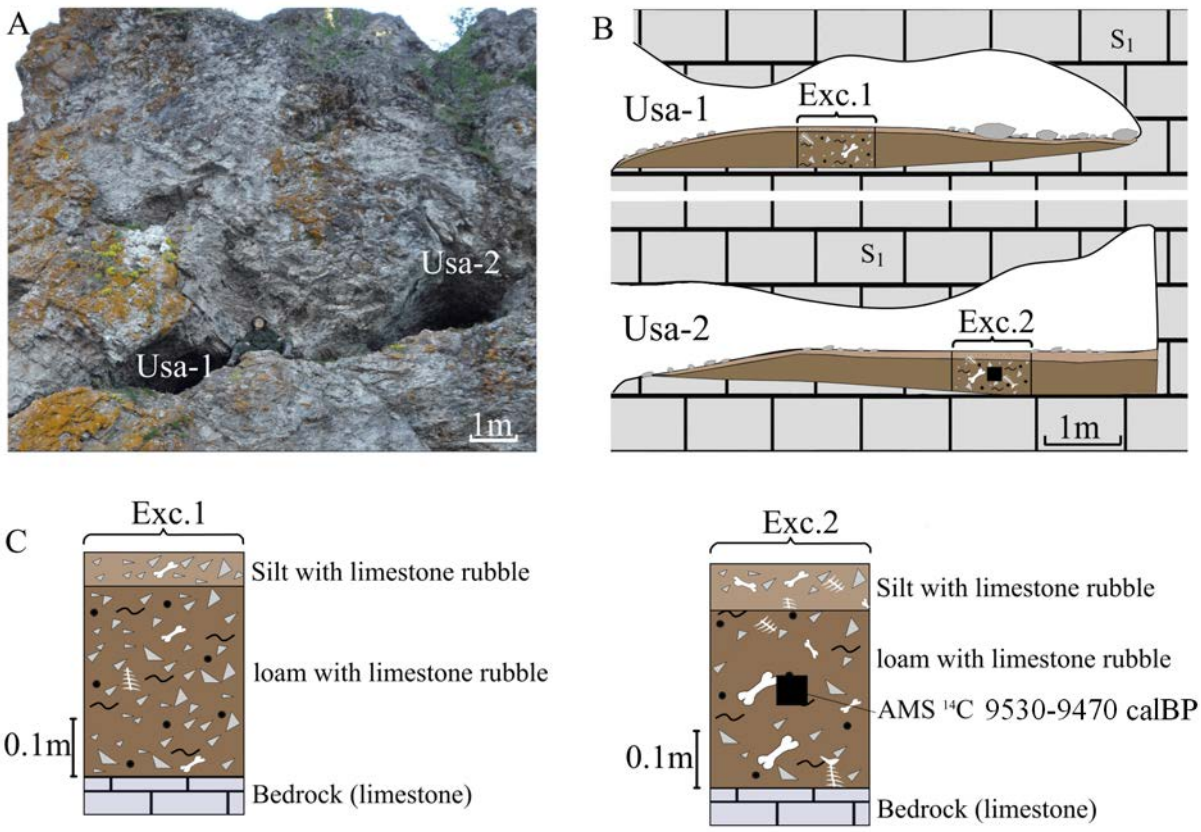


Fig. 5. Photo of the cave localities Usa-1 and Usa-2 (A), profiles of the caves (B) and of the excavated sections (C) at the Usa-1 and Usa-2. The position where the sample was taken for the AMS ^{14}C dating is indicated with the square.

By the terms Early, Middle and Late Holocene we mean subepochs: Early — 11700 years ago to 8200 years ago; Middle — 8200 years ago to 4200 years ago; Late — 4200 years ago to the present (years b2k, before 2000 AD) (Walker *et al.*, 2018).

Materials and methods

The unconsolidated deposits were excavated in layers of up to 10 cm thick and water screened using 0.8 mm sieves. The mixture of bones and rock fragments was dried, and subsequently the vertebrate remains were manually collected. In total, more than 6000 rodent cheek teeth collected from the unconsolidated cave deposits were identified (Tab. 2). The bird pellets were dried and the bone remains (including more than 1800 rodent teeth) were collected manually. In the studied material, remains of 14 different rodent species were found: northern birch mouse (*Sicista betulina* Pallas, 1778), red squirrel (*Sciurus vulgaris* Linnaeus, 1758), wood lemming (*Myopus schisticolor* Lilljeborg, 1844), collared lemming (*Dicrostonyx torquatus* Pallas, 1779) and the Siberian lemming (*Lemmus sibiricus* Kerr, 1792), muskrat (*Ondatra zibethica* Linnaeus, 1766), red-backed voles (*Craseomys rufocanus* Sundervall, 1846; *Clethrionomys glareolus* Schreber, 1780; *Clethrionomys rutilus* Pallas, 1779), water vole (*Arvicola amphibius* Linnaeus, 1758), narrow-headed vole (*Lasiopodomys gregalis* Pallas, 1779), root vole (*Alexandromys oeconomus* Pallas, 1778), Middendorf's vole (*Alexandromys middendorffii* Poljakov, 1881), field vole (*Microtus agrestis* Linnaeus, 1761) (Tab. 2).

The identification of morphologically similar species, such as the Middendorf's vole, field vole, and the Siberian lemming, wood lemming, was carried out using the method proposed by Smirnov *et al.* (1997). The species identification of the remains of the narrow-headed vole, the Middendorf's vole, the root vole and the field vole is based on the first lower molar. All other molars of the "*Microtus*" group were assigned to a species taking into account their relative abundance based on the number of the first lower molars. For the identification of the red-backed voles of the genus *Clethrionomys* the method proposed by Borodin *et al.* (2005) has been used. For the arvicolines taxa we followed the taxonomy proposed by Abramson & Lissovsky (2012), with exception of *Clethrionomys* which should be considered as valid name for red-backed voles according to Kryštufek *et al.* (2020).

By the term local fauna we mean the taxa recovered from one layer or several conventional horizons (Smirnov, 2003).

Table 1. List of radiocarbon dates, indicating sample location, the measured ^{14}C date in BP, the calibrated age range in calBP and the laboratory code (GrA — Center for Isotope Research, Groningen University, Groningen; GIN — Geological Institute, Russian Academy of Sciences (RAS), Moscow).

Locality	Layer	Material	Laboratory ID	^{14}C date (BP±s)	Calibrated age (calBP, 1s range)
Usa-2	2	bone	GrA-66466	8470±45	9530–9470
Sharyu-1		bone	GrA-66862	1510±35	1410–1345
Kozhim-1	2	bone	GrA-66908	9360±190	11065–10275
Sokoliny	1	bone	GrA-66864	4540±50	5315–5050
Kozhim-4		bone	GrA-66465	1620±30	1540–1415
Pymvashor*	3		GIN-9005	8500±250	9130–9890
Kozhim-2		bone	GrA-49355	1655±35	1685–1420

* — data from Golovachov & Smirnov, 2009.

Table 2. Frequencies (%) and total number (n) of rodent's molars from localities of the Chernyshev Ridge as well as other localities mentioned in the text.

Species	Sharyu-1	Sharyu-2	Sharyu-3	Usa-1		Usa-2		Pellets from Usa River	Pymvashor	Kozhim-1	Sokoliny	Kozhim-2	Kozhim-4
				Layer 1	Layer 2	Layer 1	Layer 2						
Northern birch mouse — *Sicista betulina*	0.3	—	—	—	—	+	—	2.4	—	—	—	—	—
Red squirrel — *Sciurus vulgaris*	0.1	—	11.9	—	—	+	—	14.6	—	—	—	—	—
Wood lemming — *Myopus schisticolor*	9.7	—	—	12.6	6.8	8.9	4	3.2	8.8	1.6	8.8	2.9	10.8
Siberian lemming — *Lemmus sibiricus*	1.4	—	—	2.5	6.8	2.7	3.6	—	4.1	10.3	4.1	5	3
Collared lemming — *Dicrostonyx torquatus*	0.7	—	—	—	2	—	2.3	—	4.1	12.8	4.1	—	0.5
Muskrat — *Ondatra zibethicus*	—	—	3.4	—	—	—	—	10.9		—	—	—	—
Grey red-backed vole — *Craseomys rufocanus*	22.3	4.7	1.5	26.8	12.7	25	15.3	3.6	17.7	1.7	17.7	—	13.9
Bank vole — *Clethrionomys glareolus*	4.1	14.4	3.6	7.2	4.8	9	3.6	3	—	0.9	—	13	6.3
Red-backed vole — *Clethrionomys rutilus*	7.2	12.9	6.2	21	6.9	19	3.3	1.8	—	2.9	—	19.5	13.9
Red-backed voles — *Clethrionomys* sp.	—	—	—	—	—	—	—	—	15.6	—	15.6	—	—
Water vole — *Arvicola amphibius*	14.8	—	24.3	6.4	8.3	9.6	6.7	32.9	12.9	30.6	12.9	29.3	16.2
Narrow-headed vole — *Lasiopodomys gregalis*	—	—	—	—	4.4	—	3.6	—	2	12.3	2	2.7	—
Root vole — *Alexandromys oeconomus*	25.3	4.7	3.9	11	35.3	17.9	42.3	12.4	32	16.3	32	5	11.1
Middendorf's vole — *Alexandromys middendorffii*	—	—	—	—	—	—	0.3	—	0.7	—	0.7	—	—
Field vole — *Microtus agrestis*	14.3	63.3	45.2	12	12	7.7	15	15.2	2	10.5	2	15.6	24.3
Total	1024	1161	535	462	340	3553	704	164	170	1611	170	481	835

Taphonomical aspects

The preservation of the small mammal remains from the two localities along the Usa River, such as the pattern of corrosion caused by digestive enzymes and the degree of fragmentation, indicates that the fossil assemblage has been accumulated by birds of prey in the form of pellets. The presence of small fragments of large mammalian bones with gnawing marks reflects an insignificant part of the assemblage that has been accumulated by mammalian carnivores.

The taphocenoses of fossil rodent assemblages in caves is in most cases the result of the activity of predators (mainly raptors) which use karst cavities as shelters and nesting places. As a rule, such localities are well accessible for excavations and often contain an extensive amount of vertebrate remains. The dietary selection made by the predators determines the faunal composition of the accumulated assemblage. However, the ability of the predators to thoroughly hunt over the territory around the temporary nest or shelter as well as the fact that many predators are very selective, allows an accurate reconstruction of the regional animal population during the past, based on the remains encountered today.

Ecological analyzes

To analyze the fauna dynamics in detail, it is necessary to classify the rodent species according to their biological and ecological requirements: their biotopes, climatic preference and their distribution in the modern natural zones. This information is taken from various sources (Ognev, 1950; Gromov & Polyakov, 1977; Gromov & Erbajeva, 1995; Anufriev, 1994a, b, c; Anufriev & Bobretsov, 1994; Petrov, 1994a, b, c, 2007; Pystin, 1994).

Based on the main climatic factors (temperature and humidity), the rodent species are combined as follows: 1) cryoxerophilous species — collared lemming (*Dicrostonyx*); 2) mesothermic-xerophilous — narrow-headed vole (*Lasiopodomys gregalis*); 3) mesophilous species preferring temperate conditions — *Craseomys* and *Clethrionomys* species, field vole (*Microtus agrestis*), squirrel (*Sciurus vulgaris*) and northern birch mouse (*Sicista betulina*); 4) mesothermic-hydrophilous species — root vole (*Alexandromys oeconomus*) and wood lemming (*Myopus schisticolor*); 5) eurythermic-hydrophilous species — water vole (*Arvicola amphibius*) and muskrat (*Ondatra zibethicus*); 6) cryohydrophilous species — Siberian brown lemming (*Lemmus sibiricus*) and Middendorf's vole (*Alexandromys middendorffii*).

One of the most essential ecological properties is the specific biotope. Rodents prefer certain biotopes, and according to this parameter they can be divided into five groups: 1) typical tundra biotopes except for wet habitats — collared lemming (*Dicrostonyx torquatus*) and partly narrow-headed vole (*Lasiopodomys gregalis*) which is also abundant in grasslands, shrubs and floodplains; 2) wet tundra biotopes — Siberian brown lemming (*Lemmus sibiricus*) and Middendorf's vole (*Alexandromys middendorffii*); 3) semi-aquatic (riparian) habitats — water vole (*Arvicola amphibius*) and muskrat (*Ondatra zibethicus*); 4) different forest habitats — all *Craseomys-Clethrionomys* voles; 5) various forest and grassland habitats — field vole (*Microtus agrestis*) and northern birch mouse (*Sicista betulina*). In the tundra, field vole inhabits patches with willow trees in shrub tundra and on floodplains. The water vole *Arvicola* prefers the riparian habitats mainly in summer whereas in wintertime, it occupies elevated areas far from water bodies. The root vole (*Alexandromys oeconomus*) can also be assigned, to some extent, to the third group. However, it prefers shrubby highly productive lush riparian vegetation along shores of small rivers and springs.

According to their preferred natural zone (tundra, forest-tundra or forest), all identified species were grouped as follows: tundra species (collared lemming, Siberian lemming, Middendorff's vole), forest species (red squirrel, wood lemming, red-backed voles, field vole, northern birch mouse), tundra and steppe species (narrow-headed vole) and intrazonal species (root vole, water vole, muskrat). To some extent field vole may also be referred as intrazonal species since it prefers intrazonal habitats and it is quite common in forest-tundra and tundra.

The present-day mammal population inhabiting the different natural zones (tundra, forest-tundra and taiga) in the northeastern part of European Russia is known quite well (Ognev, 1950; Kulik, 1972; Turyeva *et al.*, 1977; Turyeva & Balibasov, 1982; Gromov & Erbaeva, 1995; Petrov, 2002, 2007; Bobretsov *et al.*, 2005; Petrov & Poroshin, 2005). However, it should be noted that the narrow-headed vole is a species that at present inhabits two natural zones — tundra and steppe. The narrow-headed vole should therefore probably be considered as a species adapted to a specific biome — "tundra-steppe" or the so-called "mammoth steppe" — biome, a non-analogue biome that existed in the northern parts of Eurasia and North America during the Quaternary.

In the tundra zone, intrazonal species are present in addition to the tundra animals and in the south some species of the taiga faunal assemblage (*Sicista betulina*, *Microtus agrestis*, *Clethrionomys rutilus*, *Clethrionomys glareolus*) occur. Different investigations, such as the trapping of wild animals and the analysis of pellets of the rough-legged buzzard (*Buteo lagopus*) show that the most abundant mammals in this zone are *Dicrostonyx torquatus*, *Lemmus sibiricus* and *Lasiopodomys gregalis* (Kulik, 1972; Voronin, 1995; Petrov, 2002, 2007). *Arvicola amphibius* and *Clethrionomys rutilus* are also common and *Cl. rutilus* sometimes even dominates (Petrov, 2007).

Mammals of the forest-tundra zone usually belong to the taiga faunal assemblage; there are also some intrazonal species and only one tundra rodent — *Lemmus sibiricus*. The taiga zone is inhabited by taxa of the taiga faunal assemblage and some intrazonal species (Turyeva *et al.* 1977; Turyeva & Balibasov, 1982; Bobretsov *et al.*, 2005; Petrov & Poroshin, 2005).

Results

Early Holocene

The fossil assemblages from Usa-1 layer 2 and Usa-2 layer 2 are very similar in the species composition and the proportions of remains. Both assemblages are dominated by forest and intrazonal species with a noticeable portion of tundra species (10–13%) (Tab. 2, Fig. 6).

Late Holocene

Our collection includes three rodent faunas that are correlated with the Late-, and possibly Middle Holocene: Sharyu-1, Usa-1 (layer 1) and Usa-2 (layer 1). The Sharyu-1 assemblage is a typically forest community with the presence of tundra species — collared and Siberian lemmings (2% together) (Tab. 2, Fig. 7).

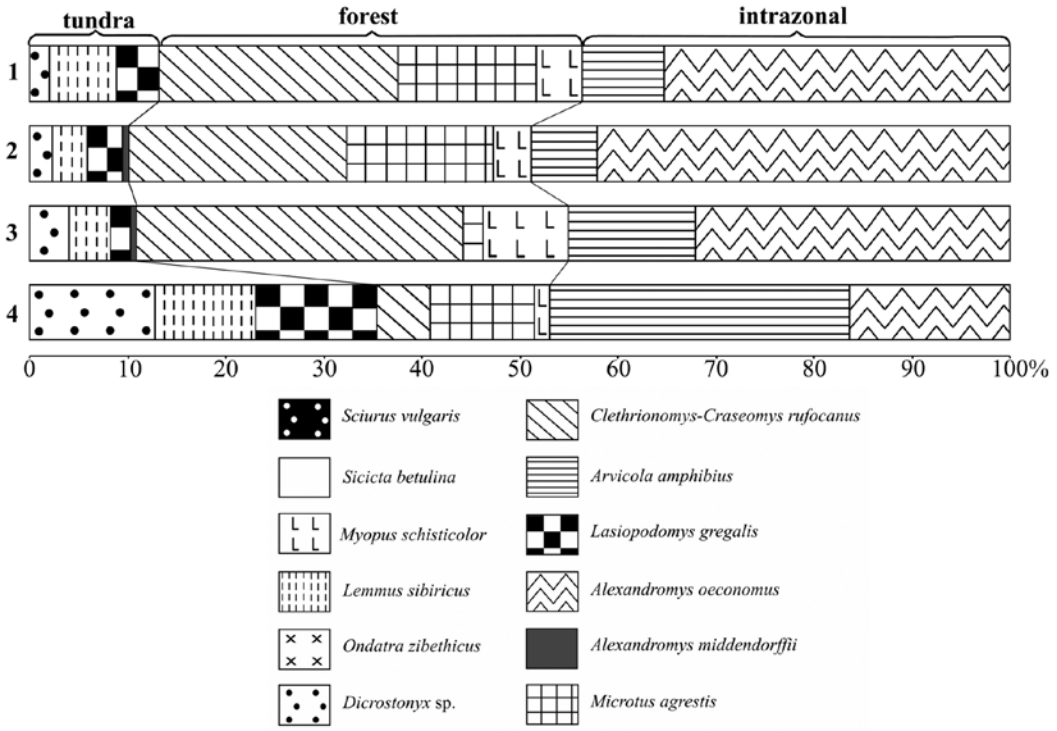


Fig. 6. Composition of the rodent fauna (%) from the Early Holocene localities of the Chernyshev Ridge and the Nether-Polar Urals. 1 — Usa-1, layer 2; 2 — Usa-2, layer 2; 3 — Pymvashor, layer 3; 4 — Kozhim-1.

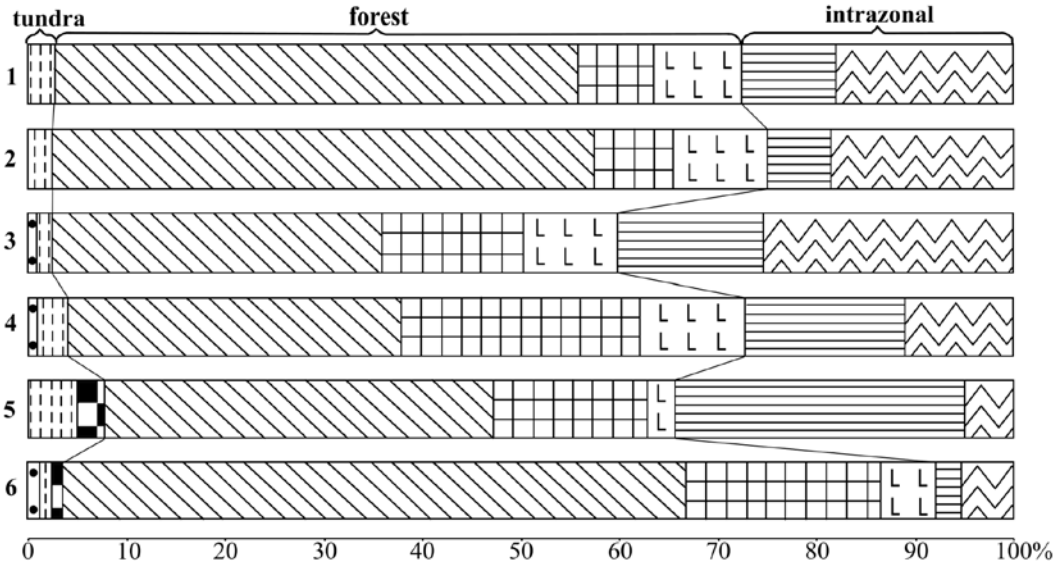


Fig. 7. Composition of the rodent fauna (%) from the Late Holocene localities of the Chernyshev Ridge and the Nether-Polar Urals and Middle Holocene localities of the Nether-Polar Urals. 1 — Usa-1, layer 1; 2 — Usa-2, layer 1; 3 — Sharyu-1; 4 — Kozhim-4, layer 2; 5 — Kozhim-2, layer 2; 6 — Sokoliny, layer 1. For figure legend see Figure 6.

The fossil assemblages from the upper layers of the Usa-1 and Usa-2 localities were not ^{14}C dated. These faunas are, compared to the dated assemblage of Sharyu-1, slightly different in composition (Tab. 2). The Sharyu-1 assemblage has a larger portion of remains of forest species such as the red-backed voles and a minor share of the Siberian lemming. Based on the stratigraphic position of the layers and the characteristics of the fauna, it can be assumed that the Usa-1 and Usa-2 faunas most likely date back to the Late Holocene. However, a Middle Holocene age cannot be excluded. For example, in the Nether-Polar Urals, an assemblage corresponding to the end of the Middle Holocene is known from the uppermost part of the section (layer 1) of the locality Sokoliny (Fig. 7). This locality (65.845° N, 60.037° E) is situated on the western slope of the Ural Mountains, on the right bank of the Kozhim River, approximately 120 km southeast from localities of Usa-1 and Usa-2 (Fig. 1). It is a small karst cavity filled with unconsolidated sediments (from top to bottom): sandy silt (layer 1), sandy loam (layer 2) and loamy sediments (layer 3). Three fossil assemblages dating to the Bølling-Allerød Interstadial Complex (layer 3), Younger Dryas (layer 2) and the very end of the Middle Holocene (layer 1) were collected at the locality Sokoliny (Ponomarev, 2005) (Tab. 1, 2). The rodent fauna from layer 1 represents a typically forest community (Fig. 7) with tundra species including the Middendorf's vole, a species that has not been observed in the fauna of the Chernyshev Ridge (Ponomarev, 2005).

Subrecent

Pellet clusters found along the bank of Sharyu River (two localities Sharyu-2 and Sharyu-3) and the bank of the Usa River give insight in the subrecent rodent fauna in the region. In the Sharyu-2 assemblage, only remains of quite small-sized mammals were found: field vole, northern red-backed vole and bank vole, and the root vole (Tab. 2, Fig. 8). In the Sharyu-3 fauna, the species composition is more diverse: field vole, water vole, red squirrel, northern red-backed vole and bank vole, root vole and muskrat (Tab. 2, Fig. 8).

The significant differences in the composition of the two assemblages with approximately the same age, found close to each other, are most likely the result of the fact that pellets were accumulated by different raptor species which hunt on different rodent prey species. This idea is supported by the difference in size and the morphology of pellets, as well as by the amount and preservation of bone material extracted from pellets. The pellets from Sharyu-2 were regurgitated by diurnal raptors, most likely the common kestrel *Falco tinnunculus* (Linnaeus, 1758) (identification by S.K. Kochanov). Despite the small size of the pellets (2 to 4 cm), they contained teeth from two or more rodent individuals, including a high number of isolated teeth. It should also be noted that the enamel of the teeth is partially dissolved and eroded, and the portion of bones is relatively small. Such preservation of remains in pellets is typical for diurnal raptors. The presence of remains of different prey species in one pellet and the low content of bone remains are connected with the way the raptor feeds. Using a hooked beak and powerful neck muscles, the raptor tears its prey into small pieces, which leads to a partial consumption of their prey and the loss of bones. The small size of some pellets is likely because they were regurgitated by chicks (Mayhew, 1977; Andrews, 1990).

The pellets from Sharyu-3 are large (4 to 6 cm), dense, with a gray-brown to black color and a greasy shine. They contain bone remains from one or two individuals. In pellets with remains of only one individual, the remains belonged to a red squirrel, muskrat or water vole. A large number of intact facial parts of skulls with teeth, mandibles and articulated skeletal elements were found in the pellets from Sharyu-3. A small number of isolated teeth were also observed. The enamel on the teeth remained smooth and shiny. In general, the bone remains do not show distinct signs of digestion. All these features indicate that the pellets are most likely produced by a large owl (family Strigiformes), which rarely decapitate their prey and most often swallow it completely, except when feeding recently hatched chicks (Glue, 1971; Mayhew, 1977; Andrews, 1990; Smirnov & Kropacheva, 2019).

In the pellets collected in the valley of the Usa River, in the vicinity of the Usa-1 and Usa-2 localities, 10 forest and intrazonal rodent species were identified (Tab. 2, Fig. 8).

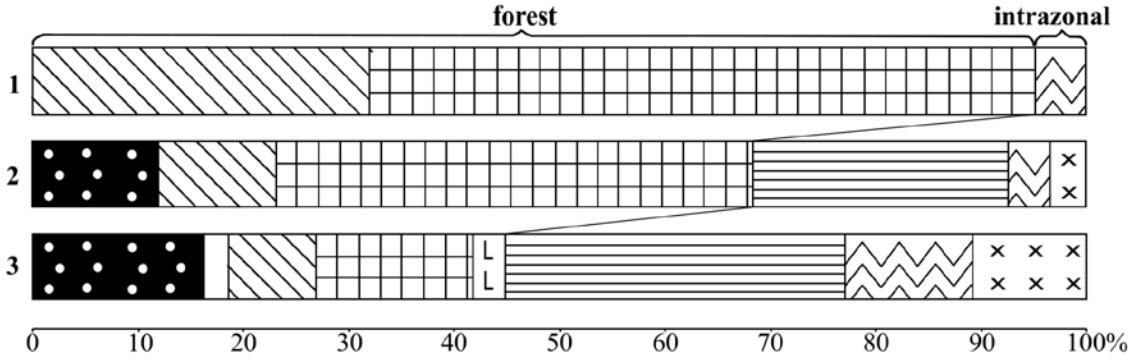


Fig. 8. Composition of the rodent fauna(%) from localities of the Chernyshev Ridge dated with last decades. 1 — Sharyu-2; 2 — Sharyu-3; 3 — Usa. For figure legend see Figure 6.

Discussion

Early Holocene faunas are also known from the localities Kozhim-1 (the Nether-Polar Urals) and Pymvashor (northern part of the Chernyshev Ridge) (Fig. 6).

The Kozhim-1 locality (65.845° N, 60.037° E) is situated on the western slope of the Ural Mountains, on the right bank of the Kozhim River, approximately 100 km to south-southeast of the localities Usa-1 and Usa-2 (Fig. 1). It is a small karst cavity filled with unconsolidated sediments (from top to bottom): sandy silt (layer 1), loamy sediments (layer 2) and limestone rubble (layer 3). Two rodent assemblages (of Early Holocene age (layer 2) and of Late Holocene age (layer 1)) have been described from this locality (Tab. 2) (Kryazheva *et al.*, 2012). Both the radiocarbon date (Tab. 1) and the proportion of rodent remains (with predominance of tundra species) indicate that Kozhim-1 local fauna dates to the earliest cold part of the Early Holocene.

The Usa-2 Early Holocene assemblage differs quite significantly from the local fauna of layer 2 of the Kozhim-1 grotto located 100 km to the southeast (Fig. 6). The Kozhim-1 local fauna has a more "tundra-like" appearance with a significant and equal portions of the Siberian lemming, the collared lemming and the narrow-headed vole (together 35%) and a relatively low proportion of forest species (17.6%) (Kryazheva, 2012; Kryazheva & Ponomarev, 2014).

The Pymvashor locality (69.7808° N, 74.4908° E) is situated in the northern part of the Chernyshev Ridge about 100 km northeast of the localities Usa-1 and Usa-2. It is located in the tundra zone along the right bank of the stream Pymvashor, a small tributary of the Adzva River that flows into the Usa River (Fig. 1) (Smirnov *et al.*, 1999; Golovachov & Smirnov, 2009; Svendsen *et al.*, 2010). The section is lithologically subdivided into six layers: peat (layer 1), limestone rubble (layer 2), humic loam (layer 3), sandy loam (layer 4), sand (aeolian) (layer 5) and limestone rubble (weathered) (layer 6). Three fossil assemblages, corresponding to the Last Glacial Maximum (lower part of layer 6), the Deglaciation and Lateglacial (layers 6–4) and the Early Holocene (layer 3) are known from the locality Pymvashor (Golovachov & Smirnov, 2009).

Layer 3 of the Pymvashor locality has a radiocarbon date of 8500±250 BP (GIN-9005; Smirnov *et al.*, 1999). We have calibrated this conventional date now with the latest calibration curve IntCal20 (Reimer *et al.*, 2020), resulting in 9130–9890 calBP (see Tab. 1). The layer yielded an assemblage where forest and intrazonal species dominate, whereas tundra and tundra-steppe species account for only 10% (Smirnov *et al.*, 1999) (Tab. 2). The species composition and the relative proportion of the remains in this fossil assemblage are very similar to the faunal assemblage from layer 2 of Usa-2 locality (Fig. 6).

Palynological data show that during the Early Holocene, taiga forests dominated the entire territory in the north of Eastern Europe up to the coast of the Barents Sea. However, it is also important to note, that the vegetation includes periglacial tundra-steppe elements until the middle part of the Early Holocene (Arslanov *et al.*, 1981; Nikiforova, 1982; Velichko *et al.*, 1997, 2002; Kremenetsky *et al.*, 1998; Kaakinen & Eronen, 2000; Kultti *et al.*, 2003; Golubeva, 2008; Golubeva & Kryazheva, 2020).

Our paleofaunal data are in agreement with palynological data, showing that tundra species were present in the rodent fauna of the study area until the middle part of the Early Holocene (about 9500 calBP).

Late Holocene faunas are also known from the localities Kozhim-2 and Kozhim-4 (the Nether-Polar Urals) (65.6975° N, 59.7702° E) (Fig. 7). They are situated on the western slope of the Ural Mountains, on the right bank of the Kozhim River, approximately 100 km south-southeast of the localities of Usa-1 and Usa-2 (Fig. 1). Kozhim-2 and Kozhim-4 are small karst cavities filled with unconsolidated sediments. Kozhim-2 is filled with sandy loam deposits; Kozhim-4 is filled with humic loam and sandy loam. The Kozhim-2 and Kozhim-4 ^{14}C dated fossil assemblages include taiga and intrazonal species with admixture of tundra species (7.7% and 3.5% respectively) (Tables 1, 2) (Kryazheva, 2012; Kryazheva *et al.*, 2012; Kryazheva & Ponomarev, 2014).

Based on palynological data (Nikiforova, 1982; Golubeva, 2008; Andreicheva *et al.*, 2015; Golubeva & Kryazheva, 2020) it can be concluded that dark coniferous forests, dominated by spruce with a significant admixture of pine, developed during the Late Holocene in both the plain and mountainous parts of the northeastern sector of Eastern Europe. However, spore-pollen data also show that the climate of the last 2500 calBP was not stable. There were cool phases, when the northern limit of forest vegetation shifted up to 150 km to the south. In addition, the share of spruce decreased whereas the portion of pine and birch increased. During the warm intervals, there were opposite changes in vegetation similar to, for example, climate changes during the Medieval Warm Period.

The materials show, that during the Late Holocene, the rodent fauna of the Chernyshev Ridge had a typical forest appearance but with small portion (2–3%) of tundra species, being almost identical to the small mammal communities of the Nether-Polar Urals. In general, it can be assumed that the vegetation dynamics could be the reason for the Late Holocene occurrence of tundra species in the rodent assemblages from the northeastern part of Eastern Europe.

It should be noted, that tundra and tundra-steppe rodent species are absent in the subrecent assemblages from the Chernyshev Ridge. This is in agreement with the characteristics of the modern vegetation of the area. The Chernyshev Ridge is nowadays mainly a plain territory with flat hills covered by the spruce forests in the south and by the sparse birch-spruce forests alternating with treeless tundra valleys in the north (Isachenko, 1964; Ilchukov, 2010).

Conclusions

The analyses of the rodent assemblages collected at five localities allow us to describe the distinctive features of the Holocene development of the rodent fauna in the area of the Chernyshev Ridge during three time intervals. These intervals correspond to the Early Holocene, the Late Holocene and to a subrecent time interval. Five faunal assemblages reflect differences in climate and vegetation.

The Early Holocene fauna consisted mainly of forest species (red-backed voles, field vole, wood lemming) and intrazonal (root vole, water vole) species, with a significant portion (10%) of tundra species (narrow-headed vole, Siberian and collared lemmings, as well as single remains of Middendorf's vole). An important and interesting result of this research is the evidence that tundra species remained present in the rodent fauna until the middle of the Early Holocene (about 9500 calBP).

It is important to note that the Late Holocene faunas are dominated by forest and intrazonal species but also include a small (2–3%) proportion of tundra species. The studied localities are nowadays situated within the northern taiga natural zone and tundra species do not occur that far to the south. For the presence of remains of tundra species during the Late Holocene period (about 1500 calBP) there might be two explanations. First, it is possible that the presence of tundra species to some extent can be explained by population booms of rodents and their subsequent migrations. Second, it is also possible that even in a relatively short period of time (the last 1500–2000 years) there were significant fluctuations in climate and vegetation, which led to an expansion of tundra biotopes quite far to the south, into the northern taiga zone.

The subrecent and modern taiga zone fauna inhabiting the southern part of the Chernyshev Ridge region did not include tundra species (in contrast to the rodent fauna with a Late Holocene age) and consists of forest and intrazonal species. It is also characterized by the presence of remains of an introduced species: the muskrat.

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References

Abramson N.I. & Lissovsky A.A. 2012. Subfamily Arvicolinae // Pavlinov I.Ya. & Lissovsky A.A. (eds.). The Mammals of Russia: A Taxonomic and Geographic Reference. Archive of the Zoological Museum of MSU. Vol.52. Moscow: KMK Scientific Press. P.220–276.

Andreicheva L.N., Marchenko-Vagapova T.I., Buravskaya M.N. & Golubeva Yu.V. 2015. [Neopleistocene and Holocene Natural Environment in the European Northeast of Russia]. Moscow: GEOS. 224 p. [in Russian]

Andrews P. 1990. Owls, Caves And Fossils: Predation, Preservation and Accumulation of Small Mammal Bones in Caves, With an Analysis of the Pleistocene Cave Faunas from Westbury-sub-Mendip, Somerset, UK. Chicago: University of Chicago Press. 231 p.

Anufriev V.M. & Bobretsov A.V. 1994. [Grey red-backed vole] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol2. Part 1]. Saint Petersburg: Nauka. P.167–172 [in Russian].

Anufriev V.M. 1994a. [European bank vole] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint Petersburg: Nauka. P.173–185 [in Russian].

Anufriev V.M. 1994b. [Root vole] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint Petersburg: Nauka. P.242–251 [in Russian].

Anufriev V.M. 1994c. [Field vole] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint Petersburg: Nauka. P.252–262 [in Russian].

Arslanov H.A., Lavrov A.S. & Nikiforova L.D. 1981. [About stratigraphy, geochronology and climate changes in the Late Pleistocene and Holocene of the north-east of the Russian Plain] // Velichko A.A. & Faustova M.A. (eds.). Pleistocenovye Oledeneniya Vostochno-Evropeiskoi Ravniny. Moscow: Nauka. P.37–52 [in Russian].

Bobretsov A.V., Lukyanova L.E. & Poroshin E.A. 2005. [Structure and dynamics of small mammals population of the Northern Urals foothills] // Estafyev A.A. (ed.). [Regularities of Zonal Organization of Animal Population Complexes in the European North-East of Russia]. Syktyvkar: Komi SC UB RAS. P.5–20 [in Russian].

Borodin A.V., Kourova T.P. & Markova E.A. 2005. [Dimensional characteristics of molar teeth in *Clethrionomys* (*Craseomys*) *rufocanus*, *Cl. (Clethrionomys) glareolus, Cl. (Cl.) rutilus* (Arvicolinae, Rodentia) and their use for species identification] // Zoologichesky Zhurnal. Vol.84. No.2. P.236–244 [in Russian].

Glue D.E. 1971. Avian predator pellet analysis and the mammalogist // Mammal Review. Vol.1. P.53–62.

Golovachov I.B. & Smirnov N.G. 2009. The Late Pleistocene and Holocene rodents of the Pre-Urals Subarctic // Quaternary International. Vol.201. P.37–42.

Golubeva Ju.V. & Kryazheva I.V. 2020. Vegetation and microtheriofauna dynamics during the Late Glaciation and Holocene in the Yugyd-Va National Park // Stratigraphy and Geological Correlation. Vol.28. No.4. P.445–456.

Golubeva Ju.V. 2008. [Climate and vegetation of the Holocene on the territory of Komi Republic] // Litosfera. Vol.2. P.124–132 [in Russian].

Gromov I.M. & Erbaeva M.A. 1995. [The Mammals of Russia and Adjacent Territories. Lagomorphs and Rodents]. Saint Petersburg: ZIN RAN. 522 p. [in Russian]

Gromov I.M. & Polyakov I.Y. 1977. [Fauna of USSR. Vol.3. No.2. Mammals]. Leningrad: Nauka. 504 p. [in Russian].

Ilchukov S.V. 2010. [Landscapes of Komi Republic]. Ekaterinburg: Izdatel'stvo UrO RAN. 198 p. [in Russian].

Isachenko A.G. 1964. [Landscape map and physical zoning] // Kolesnik S.V. *et al.* (eds.). Atlas of Komi ASSR. Moscow. P.57–64 [in Russian].

Kaakinen A. & Eronen M. 2000. Holocene pollen stratigraphy indicating climatic and tree line changes derived from a peat section at Ortino, in the Pechora lowland, northern Russia // The Holocene. Vol.10. P.611–620.

Kremenetsky C.V., Sulerzhitsky L.D. & Hantemirov R.M. 1998. Holocene history of the northern range limits of some trees and shrubs in Russia // Arctic and Alpine Research. Vol.30. P.317–333.

Kryazheva I.V. & Ponomarev D.V. 2014. [Microteriofauna of the western slope of the Subpolar Urals in the Late Pleistocene and Holocene (Kozhym River)] // Vestnik of Institute of Geology of Komi SC UB RAS. Vol.5. P.3–9 [in Russian].

Kryazheva I.V. 2012. [Small mammals of the late Pleistocene and Holocene of the Nether-Polar Urals]. PhD Thesis. Syktyvkar: Institute of Geology of the Komi SC UB RAS. 18 p. [in Russian]

Kryazheva I.V., Ponomarev D.V., van Kolfschoten T. & van der Plicht J. 2012. History of formation of modern communities of micromammals of the Nether-Polar Urals // Russian Journal of Ecology. Vol.6. P.434–441.

Kryštufek B., Tesakov A.S., Lebedev V.S., Bannikova A.A., Abramson N.I. & Shenbrot G. 2020. Back to the future: the proper name for red-backed voles is *Clethrionomys* Tilesius and not *Myodes* Pallas // Mammalia. Vol.84. No.2. P.214–217.

Kulik I.L. 1972. [Taiga fauna complex of mammals of Eurasia] // Bulletin MOIP. Vol.37. No.4. P.11–24 [in Russian].

Kultti S., Väliranta M., Sarmaja-Korjonen K., Solovieva N., Virtanen T., Kauppila T. & Eronen M. 2003. Palaeoecological evidence of changes in vegetation and climate during the Holocene in the pre-Polar Urals, northeast European Russia // Journal of Quaternary Science. Vol.18. P.503–520.

Mayhew D.F. 1977. Avian predators as accumulators of fossil mammal material // Boreas. Vol.6. No.1. P.25–31.

Mook W.G. & van der Plicht J. 1999. Reporting ^{14}C activities and concentrations // Radiocarbon. Vol.41. P.227–239.

Nikiforova L.D. 1982. [Dynamics of Holocene biomes in north-east of European part of USSR] // Pokrovskaya I.M. (ed.). Razvitie prirody territorii SSSR v pozdnem pleistocene i golocene. Moscow: Nauka. P.57–64 [in Russian].

Ognev S.I. 1950. [Mammals of USSR and Adjacent Countries. Rodents. Vol.7.]. Moscow-Leningrad: Izdatel'stvo AN SSSR. 380 p. [in Russian].

Petrov A.N. & Poroshin E.A. 2005. [Small mammals of southern taiga subzone in the European north-east] // Estafyev A.A. (ed.). [Regularities of Zonal Organization Of Animal Population Complexes in the European North-East of Russia]. Syktyvkar: Komi SC UB RAS. P.21–29 [in Russian].

Petrov A.N. 1994a. [Collared lemming] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint Petersburg: Nauka. P.202–212 [in Russian].

Petrov A.N. 1994b. [Ob' (Siberian) lemming] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint-Petersburg: Nauka. P.213–219 [in Russian].

Petrov A.N. 1994c. [Narrow-headed vole] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint-Petersburg: Nauka. P.236–241 [in Russian].

Petrov A.N. 2002. [Small mammals of transformed and intact territories of eastern European tundra] // Roschevsky M.P. (ed.). Vestnik Komi nauchnogo centra UrO RAN. Iss.22. Syktyvkar: Izdatel'stvo Komi naychnogo tsentra. P.48–71 [in Russian].

Petrov A.N. 2007. [Small Mammals (Insectivora, Rodentia) of the Transformed and Undisturbed Territories of the Eastern European Tundra]. Saint Petersburg: Nauka. 178 p. [in Russian].

Polezhayev N.M. 1994. [Muskrat] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint-Petersburg: Nauka. P.155–167 [in Russian].

Ponomarev D.V. 2005. [Small mammal remains from Sokoliny grotto (the Nether-Polar Urals)] // Yushkin N.P., Andreicheva L.N., Marchenko-Vagapova T.I., Bratuschak Yu.V., Borintseva N.A. & Ponomarev D.V. (eds.). Materialy IV Vserossiyskogo soveschaniya po izucheniyu chetvertichnogo perioda. Kvarter-2005. Syktyvkar: Geoprint. P.334–336 [in Russian].

Pystin A.G. 1994. [Northern red-backed vole] // Estafyev A.A. (ed.). [Fauna of European North-east of Russia. Mammals. Vol.2. Part 1]. Saint Petersburg: Nauka. P.186–201 [in Russian].

Reimer P.J., Austin W.E.N., Bard E., Bayliss A., Blackwell P.G., Bronk Ramsey C., Butzin M., Cheng H., Edwards R.L., Friedrich M., Grootes P.M., Guilderson T.P., Hajdas I., Heaton T.J., Hogg A.G., Hughen K. A., Kromer B., Manning S. W., Muscheler R., Palmer J.G., Pearson C., van der Plicht J., Reimer R.W., Richards D.A., Scott E.M., Southon J.R., Turney C.S.M., Wacker L., Adolphi F., Büntgen U., Capano M., Fahrni S.M., Fogtmann-Schulz A., Friedrich R., Köhler P., Kudsk S., Miyake F., Olsen J., Reinig F., Sakamoto M., Sookdeo A. & Talamo S. 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 calkBP) // Radiocarbon. Vol.62. P.725–757.

Smirnov N.G. 2003. [Essay on development of Quaternary paleozoology in Ural region] // Smirnov N.G. (ed.) [Quaternary Paleozoology in the Urals: Scientific Papers]. Ekaterinburg: Izdatelstvo Uralskogo Universiteta. P.24–54 [in Russian].

Smirnov N.G., Andreicheva L.N., Korona O.M., Zinov'ev E.V., Golovachev I.B., Pavlov P.Ju. & Hufthammer A.-K. 1999. [Materials to characterize biota of the Pre-Uralian Subarctic during the Holocene optimum] // Golovachov I.B. (ed.). Biota Priural'skoi Subarktiki v pozdnemplejstocene i golocene. Ekaterinburg: Izdatelstvo Ekaterinburg. P.23–60 [in Russian].

Smirnov N.G., Golovachev I.B., Bachura O.P., Kuznetsova I.A. & Cheprakov M.I. 1997. [Complicated cases of identifying rodent teeth from Late Pleistocene and Holocene deposits of tundra regions of Northern Eurasia] // Kosintsev P.A. (ed.). Materialy po istorii I sovremennomu sostojaniju fauny severa Zapadnoj Sibiri. Chelyabinsk: Riphey. P.60–90 [in Russian].

Smirnov N.G. & Kropacheva Y.E. 2019. Main and concomitant prey of the eagle owl (*Bubo bubo*) in problems of historical ecology // Russian Journal of Ecology. Vol.50. No.5. P.491–495.

Svendsen J.I., Heggen H.P., Hufthammer A.K., Mangerud J., Pavlov P. & Roebroeks W. 2010. Geo-archaeological

investigations of Palaeolithic sites along the Ural Mountains — on the northern presence of humans during the last Ice Age // Quaternary Science Reviews. Vol.29. P.3138–3156.

Turyeva V.V. & Balibasov V.P. 1982. [On the characteristics of small mammal fauna of northern taiga] // Estafyev A.A. (ed.). [Fauna and Ecology of Birds and Mammals in the European Northeast of USSR]. Syktyvkar. P.67–73 [in Russian].

Turyeva V.V., Voronin R.N., Estafyev A.A., Novozhilova E.N., Polezhaev N.M. & Yushkov V.F. 1977. [Distribution and abundance of Timan taiga animals] // Zaboeva I.V. (ed.). [Ecological Research of Natural Resources in the North of the Non-Chernozem Zone]. Syktyvkar. P.85–97 [in Russian].

Velichko A.A., Andreev A.A. & Klimanov V.A. 1997. Climate and vegetation dynamics in the Tundra and Forest Zone during the Late glacial and Holocene // Quaternary International. Vol.41/42. P.71–96.

Velichko A.A., Catto N., Drenova A.N., Klimanov V.A., Kremenetski K.V. & Nechaev V.P. 2002. Climate changes in East Europe and Siberia at the Late Glacial–Holocene transition // Quaternary International. Vol.91. P.75–99.

Voronin R.N. 1995. [Rough-legged buzzard (*Buteo lagopus*)] // Potapov R.L. (ed.). [Fauna of European North-east of Russia. Birds. Vol.1. Part 1]. Saint Petersburg: Nauka. P.77–86 [in Russian].

Walker M., Head M.J., Berkelhammer M., Björck S., Cheng H., Cwynar L., Fisher D., Gkinis V., Long A., Lowe J., Newnham R., Rasmussen S.O. & Weiss H. 2018. Formal ratification of the subdivision of the Holocene Series/Epoch (Quaternary System/Period): two new Global Boundary Stratotype Sections and Points (GSSPs) and three new stages/subseries // Episodes. Vol.41. No.4. P.213–223.