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Palaeontological description of Nizhneirginsky Grotto Upper Holocene sediments (Ufa Plateau, Fore-Urals) with taphonomic and palaeoenvironmental remarks based on bird and small-mammal assemblages

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A B S T R A C T

Mammal and bird bone remains from Upper Holocene sediments at the Nizhneirginsky Grotto were studied. Nizhneirginsky Grotto is located in the northern part of the Ufa Plateau in the Middle Fore-Urals. The sequence of deposits contains three layers which have been accumulating during the last 4150 years. Identified mammal elements include 9839 bone remains of 29 species belonging to five orders, i.e., Eulipotyphla (435), Chiroptera (1608), Lagomorpha (52), Rodentia (7688), and Carnivora (56). Recovered bird remains include 1946 bones of 38 species. Most identified species currently inhabit the Nizhneirginsky Grotto area. The analysis of alterations in the first lower molars of arvicoline rodent species caused by the digestion showed that eagle owl (*Bubo bubo*, Linnaeus, 1758) is the most possible agent responsible for the accumulation of small mammal assemblages in the grotto sediments. An unusually high number of birch mouse fossils was noted over the entire sediment section of the grotto (MNI on average by layers is 8.1–15.4%). This phenomenon, probably, has a taphonomic origin and is associated with the predation activity of mustelids. Palaeoenvironmental analysis of small mammal assemblages based on the habitat weighting method showed the predominance of open landscapes and woodlands around the grotto during the Late Holocene. This landscape did not change in the last 4150 years. The connection of the history of the yellow-necked mouse in the northeast of its modern range with the palaeogeographic events of the second half of the Holocene was established. The material from the sediments of the Nizhneirginsky Grotto shows that the species was common in the northern part of the Ufa Plateau, in the Irgina River valley, in the period of 4150-3100 cal BP, which coincides with the maximum distribution of broad-leaved trees in the Fore-Urals during the mid-Subboreal thermal maximum (SB-2; 4200-3200 BP). Pika's (*Ochotona*, perhaps *O. pusilla*, Pallas, 1769) sinister mandible was found among osteological material from the upper part of layer 2 which dates to 710 ± 20 cal BP (1240 ± 20 cal AD). This is the first find of the pika's remains of such late age in the Middle Urals and in adjacent territories. The species was common in the northern part of the Ufa Plateau during Late Pleistocene and Early Holocene. Steppe pika is now disjunct from the Nizhneirginsky Grotto by approximately 200–300 km to the south and to the southwest. *O. pusilla* probably inhabited the valley of the Irgina River as a relic of the Late Pleistocene and Early Holocene faunas as early as 12th and 13th centuries AD.

1. Introduction

Vertebrate fossils are a reliable source of information about the fauna that inhabited an area around sites in the past. In addition, due to habitat preferences of specific taxa, wertebrate fossils are a source of information about the palaeoenvironment during the time of deposition of the sediments (Doukas et al., 2018). Furthermore, fossils of small mammals are opportune objects for palaeoenvironmental reconstructions because they are highly dependent on vegetation cover; in addition, small mammals do not migrate over long distances compared to large mammals (Fernández-Jalvo et al., 2016). Therefore, each new location of small-mammal fossils allows us to better understand the Holocene

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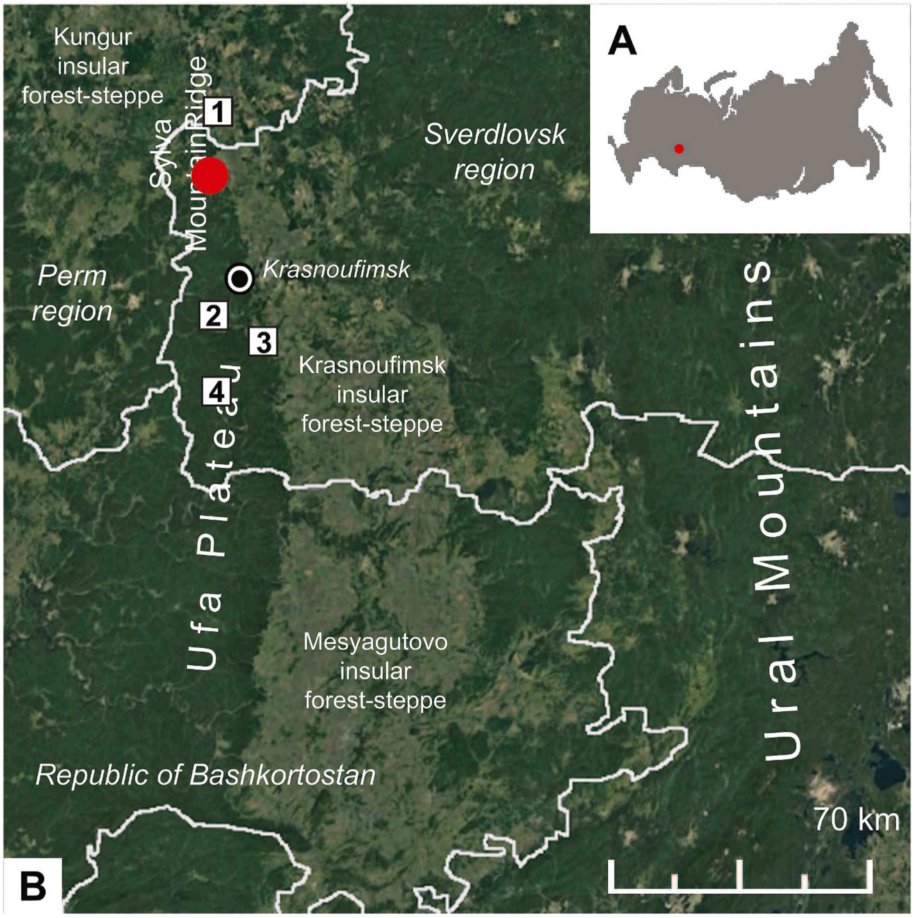

Fig. 1. Geographic location of the Nizhneirginsky Grotto (red circle) on the map of Russia (A) and on the Ufa Plateau (B). Numbering shows location of Ust-Log 5 Site (1), Alikaev Kamen' Site (2), the Sukhorechensky Grotto (3), and the Grotto Bobyliok (4). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

history of modern ecosystems. This is especially important for areas that have not been previously studied at all or that have been poorly studied. In the Fore-Urals region, the Ufa Plateau is a poorly studied territory.

1.1. Studies of the late quaternary mammal assemblages on the Ufa Plateau

On the Ufa Plateau only four localities of Late Pleistocene and Holocene mammal assemblages are known (Fig. 1), i.e., the Sukhorechensky Grotto (Smirnov et al., 1992), the Bobyliok Grotto (Smirnov, 1993), Alikaev Kamen' (Izvarin, 2004), and Ust-Log 5 (Izvarin and Ulitko, 2016). The Sukhorechensky Grotto is located at the eastern edge of the plateau, 100 m above valley the Ufa River valley. Grotto sediments contained Late Holocene mammal assemblages (Smirnov et al., 1992). Both the Bobyliok Grotto and Alikaev Kamen' localities are located at the centre of the northern part of the Ufa Plateau. The sediments at the Bobyliok Grotto were formed in the time interval from the Late Pleistocene to Late Holocene (Smirnov, 1993). Large mammal remains were studied in the entire sediment sequence (Razhev et al., 2005), but small mammal assemblages were studied only from Upper Pleistocene and Lower Holocene strata (Smirnov, 1993; Izvarin, 2004). Sediments at Alikaev Kamen' contained small mammal fossils from the Early Holocene period (Izvarin, 2004). The Ust-Log 5 locality is a small grotto with a large pre-entry rock-shelter. It is located at the northernmost part of the Ufa Plateau (Sylva Mountain Ridge) on the right bank of the Irgina River (left tributary of the Sylva River, Kama River basin). Sediments under the pre-entry rock-shelter contained mid Holocene and late Holocene mammal assemblages (Izvarin and Ulitko, 2016).

1.2. Nizhneirginsky Grotto

The Nizhneirginsky Grotto (56°52′ N, 57°25′ E) is a site of Late Holocene vertebrate remains. The grotto is located in the northern part of the Ufa Plateau on the left bank of the Irgina River (Fig. 2), 12 km to the south from the Ust-Log 5 locality. The grotto was found by authors in 2009 on the outskirts of the Nizhneirginskoe village. Excavations of the grotto sediments started in 2009 and continued in 2010. Preliminary data about small mammal fauna were published (Izvarin, 2010). However, in the above-mentioned paper, only the presence or absence of species were noted without any indication of the number of identified bones and teeth. Detailed stratigraphy of the grotto sediments was described by A.I. Ulitko (2014).

The goals of this study are to describe taphonomy and mammal and bird assemblages of Upper Holocene sediments in the grotto and to carry out palaeoenvironmental interpretation of palaeontological data.

2. Regional settings

Ufa Plateau is the easternmost part of the East-European platform and is located on the territory of the Sverdlovsk region and the Republic of Bashkortostan and partially in the Perm region (Fig. 1). The northern part of the plateau located to the north of the Krasnoufimsk city is known as Sylva Mountain Ridge. The plateau altitude is 360–480 m a.s.l. Its steep eastern edge rises approximately 100 m above Ai River depression of the Fore-Urals Foredeep. The plateau is mainly composed of Lower Permian limestone and dolomite, where karst processes are active (Verbitskaya, 1964; Sofronitsky, 1969). The plateau is covered with mixed coniferous and broad-leaved forests, and the easternmost geographic range limits of some deciduous plants of European broad-leaved forests pass here: among others European oak (*Quercus robur*, Linnaeus, 1753), Norway maple (*Acer platanoides*, Linnaeus, 1753) and European white elm (*Ulmus laevis*, Pallas, 1784) (Gorchakovsky, 1968). Diverse forest-steppe landscapes are extended in the Ai depression along the eastern border of the Ufa Plateau, i.e., Krasnoufimsk and Mesyagutovo insular forest-steppes. Insular forest-steppes are probably

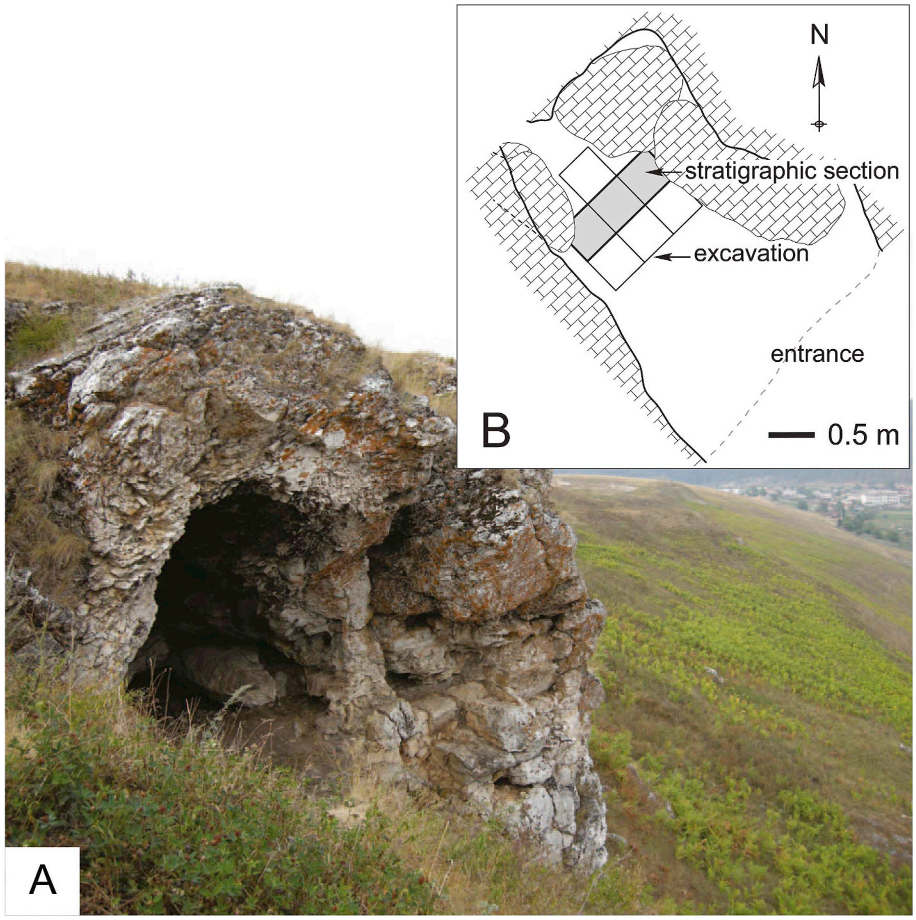

Fig. 2. View of the Nizhneirginsky Grotto entrance (A) and the plan of the grotto (B).

relicts of Late Pleistocene "cold steppes" (Krasheninnikov, 1937). Forest-steppes were cultivated during 19th and 20th centuries AD, and steppe associations were preserved only on the steep stony banks of some rivers (e.g., Irgina River valley) and on the southern slopes of the hills (Gorchakovsky, 1967). Therefore, different landscapes are presented in the Irgina River valley. Mixed dark coniferous and broad-leaved forests cover watersheds (e.g., Nizhneirginsk oak forest) (Gorchakovsky, 1968), and various steppe associations are extended on the slopes of the river valley (Zolotareva and Podgaevskaya, 2012).

3. Brief stratigraphical description of sediments

The grotto sediments sequence contains 3 layers (Fig. 3), in according to A.I. Ulitko (2014).

Upper Holocene:

1. Dark gray humus sandy loam with numerous small and middle-sized debris (thickness of 0.05–0.07 m).
2. Reddish brown sandy loam with small- and middle-sized debris (thickness from 0.07 to 0.12–0.15 m).
3. Light gray with a brownish tinge sandy loam with inclusions of small- and middle-sized debris and large lumps (total thickness is up to 0.25 m); in the western part of the pit, brownish gray sandy loam is replaced by light brown sandy loam (sublayer 3a), which gradually narrows and wedges into layer 3 in the form of a lens.

Total maximal thickness of the described deposits is 0.47 m.

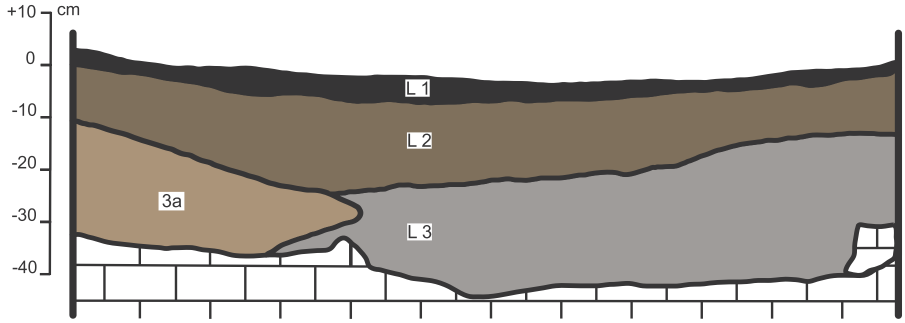

Fig. 3. Stratigraphy of Nizhneirginsky Grotto sediments: L1 – layer 1, L2 – layer 2, L3 – layer 3, 3a – sublayer 3a. Colours indicate colours of the deposits and are explained better in the Chapter Number 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article).

4. Methods and materials

The excavation and sampling of fauna and radiocarbon investigations followed standard methodology (Gromov, 1955; Arslanov, 1987). Deposits were excavated in separate 5-cm levels and washed in sieves with a mesh size of 0.8 mm to recover small vertebrate remains (Gromov, 1948; Guslitcer, 1979; Agadjanian, 1979). Species of mammal remains were identified using the etalon collections at the Laboratory of Palaeoecology of Institute of Plant and Animal Ecology of Ural Branch of the Russian Academy of Science and special literature (Gromov and Polyakov, 1977; Gromov and Erbaeva, 1995; Zaitsev, 1998; Borodin, 2009; Fadeeva, 2016). Species identification of bird fossils were carried out using etalon bone collections at the Museum of Institute of Plant and Animal Ecology of Ural Branch of the Russian Academy of Science. The ratios of species in fossil faunas were calculated on the basis of the minimum number of individuals (MNI). The total number of identified mammal remains (NISP) was 9839. The total number of identified bird remains was 1946.

The taxonomic nomenclature of insectivores, lagomorphs and rodents was given in accordance with Wilson and Reeder (2005) with some exceptions. Insectivores were considered as a single order, i.e., Eulipotyphla, Waddell, Okada et Hasegawa, 1999. We used the name *Clethrionomys* Tilesius, 1850 for the genus of red-backed voles instead of *Myodes* Pallas, 1779 according to Tesakov et al., (2010).

To identify which predator was involved in the accumulation of small mammal bones, alterations, which are caused by the digestion, on the first lower molars (m1) of arvicoline rodent species were evaluated and described in accordance with Fernández-Jalvo et al. (2016). A total of 816 arvicoline m1 from lithological strata of the Nizhneirginsky Grotto were studied.

The radiocarbon age of samples was determined in the Isotope Center of The Herzen State Pedagogical University, St. Petersburg. The calibration of radiocarbon dates was performed by the OxCal 4.3 software using the IntCal13 calibration curve (Reimer et al., 2013).

To reconstruct the environment, we used the method of habitat weightings (Andrews, 2006) by distributing each small-mammal taxon in the habitat(s) where it can be currently found in the Urals. Habitats are divided into five types in accordance with López-García et al. (2010): open land in which dry (OD) and wet (OH) meadows are distinguished, woodland, forest edge areas and forest patches (Wo), rocky areas (Ro) and habitats related to water (Wa). According to López-García et al. (2019), the categories “Open” and “Woodland” habitats are used in this study to compare the layers of Nizhneirginsky Grotto sediments. In our opinion, “Open” includes both open dry (xerophytic) meadows, open humid meadows (including mesophytic meadows), and wet herbaceous associations near water that are preferred habitats for water vole (*Arvicola amphibius* Linnaeus, 1758) and to a lesser extent for root vole (*Microtus oeconomus* Pallas, 1776) (Markova et al., 2017).“Woodland” includes mature forests, forest edge, and forest patches.

Information on the distribution areas and living conditions of different bird species was obtained from ornithological literature (Ryabitsev, 2008). Each established taxon was assigned to one of four main groups of habitats, which differ on the basis of breeding requirements, i.e., “amphibians”, “forest”, “open spaces”, and “ecotone” (Tomek and Bocheński, 2005). Habitats “amphibians” include all types of freshwater lakes, ponds, rivers, swamps, as well as wet meadows. Habitats “forest” include all types of forests, excepting forest edges which were extracted as “ecotone” type. Type of “open spaces” includes dry treeless areas, i.e., dry meadows, steppes, and rocks.

Table 1
Results of dating of Nizhneirginsky Grotto sediments: radiocarbon dates obtained from small mammal bones and their calendar values.

Layer	Samples	Depth (m)	Reference no.	^{14}C dates,BP	Calibrated dates ± σ,cal BP
2	2	0.05–0.1	SPb-971	795 ± 30	710 ± 20
	3	0.1–0.15	SPb-913	2579 ± 70	2640 ± 110
	3		SPb-915	2650 ± 70	2770 ± 90
3-3a	5	0.2–0.25	SPb-809	2945 ± 80	3100 ± 110
	6	0.25–0.3	SPb-808	3120 ± 80	3320 ± 100
	6		SPb-806	3350 ± 100	3600 ± 120
	7	0.3–0.35	SPb-914	3770 ± 100	4150 ± 150

SPb – the Isotope Center of The Herzen State Pedagogical University, St. Petersburg, Russia.

5. Results

5.1. Radiocarbon dating

The age of the sediments was determined by radiocarbon dating (Table 1). According to these data, grotto sediments have been accumulating during the last 4150 years, i.e., during Late Holocene (Meghalayan Age, since 4200 cal BP according to Walker et al., 2018). In accordance with the modified Blytt – Sernander climatic classification (Khotinsky, 1977, 1987), the grotto sediments have been accumulating since Middle Subboreal (SB-2, 4200-3200 BP) up to the end of Subatlantic (SA, 800-0 BP).

5.2. Taphonomical aspects

The preservation analysis of bone material showed that the most of small mammal remains were intact. It is possible that small mammal bones accumulated as a result of the predation activity of birds. Most of large mammal bones are highly fragmented. Perhaps, the grotto was used as a den for carnivorous mammals.

Approximately 25–43.1% of the analysed m1 have an alteration on enamel owing to digestion (see Table 2), which confirms that the accumulation is related to predation by nocturnal raptors. The amount of m1 with digestion traces in each stratum is less than 50%. In each separate layer, the total number of molars with significant degrees of digestion (i.e., moderate, heavy, and extreme) is a minimum of 9.2% (layer 3-3a) and a maximum of 13.1% (layer 2), which means that the agent responsible for the accumulation of small mammal assemblages in these grotto sediments is a predator of category 3, in accordance with Fernández-Jalvo et al. (2016), possibly an eagle owl (*Bubo bubo* Linnaeus, 1758). The presence of eagle owl suggests that the landscape was dominated by open and/or open-woodland environmental conditions around the Nizhneirginsky Grotto, as at present. This is also confirmed by the species composition of the most abundant species (see below) that are rather large-sized and/or the most available preys (Gromov and Parfyenova, 1950), except for birch mouse remains (*Sicista*, perhaps *Sicista betulina* Pallas, 1779). The abundance of the teeth of this species in the Nizhneirginsky Grotto sediments is a taphonomic phenomenon because, typically, the remains of the birch mice are rare in the pellets and in the localities accumulated by bird predators. However, according to Shenbrot et al. (1995), mustelid predators often successfully feed on northern birch mice. Is it possible that some part of studied osteological material, including birch mouse remains, was accumulated due to predation activity of mustelids. However, palaeoenvironmental interpretations based on osteological material of small mammals from studied strata are quite reasonable.

Table 2
Number of arvicoline first lower molars from Nizhneirginsky Grotto sediments showing different degrees of digestion (according to Fernández-Jalvo et al., 2016).

Layer	Degree of digestion	*Clethrionomys rufocanus* Sundevall, 1846	*Cl. glareolus* Schreber, 1780	*Cl. rutilus* Pallas, 1779	*Cl.* ex gr. *glareolus-rutilus*	*Arvicola amphibius* Linnaeus, 1758	*Microtus* sp.	*M. oeconomus* Pallas, 1776	*M. agrestis* Linnaeus, 1761	*M. arvalis* s.l.	*M.* ex gr. *arvalis-agrestis*	Total	%
1	absence	0	0	0	0	3	0	0	0	3	0	6	75.0
	light	0	0	0	0	1	0	0	0	0	0	1	12.5
	moderate	0	0	0	0	0	0	0	1	0	0	1	12.5
	heavy	0	0	0	0	0	0	0	0	0	0	0	0.0
	extreme	0	0	0	0	0	0	0	0	0	0	0	0.0
	Total	**0**	**0**	**0**	**0**	**4**	**0**	**0**	**1**	**3**	**0**	**8**	**100.0**
2	absence	2	5	4	0	53	35	1	6	45	20	171	57.4
	light	2	4	1	1	31	20	1	6	13	9	88	29.5
	moderate	0	2	3	1	3	4	0	0	5	4	22	7.4
	heavy	1	0	0	0	3	2	0	1	3	0	10	3.4
	extreme	0	0	0	0	3	0	0	0	4	0	7	2.3
	Total	**5**	**11**	**8**	**2**	**93**	**61**	**2**	**13**	**70**	**33**	**298**	**100.0**
3-3a	absence	10	13	17	2	160	5	2	16	64	1	290	56.9
	light	6	7	9	1	88	3	1	5	52	1	173	33.9
	moderate	2	2	2	0	11	3	0	0	16	1	37	7.3
	heavy	1	1	0	0	3	1	0	1	1	0	8	1.6
	extreme	0	0	0	0	2	0	0	0	0	0	2	0.4
	Total	**19**	**23**	**28**	**3**	**264**	**12**	**3**	**22**	**133**	**3**	**510**	**100.0**

5.3. Description of mammal fauna

A total of 9839 bone remains of 29 mammal species were identified in the grotto sediments (Table 3). Twenty-three identified taxa belong to small mammals (Eulipotyphla, Chiroptera, Lagomorpha: Ochotonidae, Rodentia) (Fig. 4). An abundance of osteological material was found in layers 2 and 3-3a (Table 3). The remains of 24 species are the same for both layers 2 and 3-3a. In these layers, the predominant species among rodents are water vole (*Arvicola amphibius* Linnaeus, 1758), common hamster (*Cricetus cricetus* Linnaeus, 1758), field vole (*Microtus arvalis* Pallas, 1778) and birch mouse (*Sicista* cf. *betulina* Pallas, 1779). Layer 1 contains scarce osteological material.

Almost all species determined in these layers currently inhabit the vicinity of the grotto. The obtained data are consistent with the data from the deposits of the Ust-Log 5 locality (Irgina River valley, 10–12 km to the north from the grotto), where the remains of these species were also found (Izvarin and Ulitko, 2016). However, in the grotto sediments, the bone remains of *Apodemus flavicollis* Melchior, 1834 (yellow-necked mouse) were found in layer 3-3a, and *Ochotona pusilla* Pallas, 1769 (steppe pika) remains were found in both layers 2 and 3-3a (Table 3). Yellow-necked mouse is a convenient indicator of habitats associated with deciduous tree species (e.g., linden, oak, hazel, beech, and elm) at palaeoecological interpretations because the seeds of these trees form the basis of the species diet (Popov, 1960; Juškaitis, 2002). The distribution of steppe pika is related to steppe habitats (Sokolov et al., 1994). Owing to the large number of identified yellow-necked mouse elements, the presence of steppe pika remains, and the abnormally high number of birch mouse bones and teeth, the fauna of small mammals from the Nizhneirginsky Grotto sediments is unique among others localities in the northern part of the Ufa Plateau.

5.4. Description of bird fauna

Bones of birds were found in all levels of the Nizhneirginsky Grotto sediments (Table 4). Recovered bird remains include 1946 bones of 38 species which currently inhabit the Middle Urals and the adjacent territories (Ryabitsev, 2008). Most of the bones belong to the Galliformes family. However, remains belonging to families Anseriformes, Gruiformes, and Charadriiformes, and to the genus *Turdus* Linnaeus, 1758, are relatively numerous.

The identified bird taxa indicate a mosaic of landscapes in the vicinity of the Nizhneirginsky Grotto. *Tetrao tetrix* Linnaeus, 1758 was the most abundant among species inhabiting woodlands. Both *Anas platyrhynchos* Linnaeus, 1758 and *Anas querquedula* Linnaeus, 1758 were abundant among species living in pond and swamp habitats. *Crex crex* Linnaeus, 1758 and *Vanellus vanellus* Linnaeus, 1758 prevailed among species which inhabited flood meadows. All these species inhabited the Nizhneirginsky Grotto surroundings during the entire time of the sediment accumulation.

6. Discussion

6.1. Palaeoenvironmental remarks

Considering rodent species habitat preferences, it is important to note that open habitat species prevail in each stratum of Nizhneiginsky Grotto sediments (Fig. 5). Only insignificant shifts are observed towards one or another type of habitat throughout the sediment sequence. In addition, there are no clear changes in the structure of the small mammal assemblages between the strata of the grotto. It is possible that the landscape around the grotto and, therefore, the structure of the small mammal community remained stable during the period of accumulation of the sediments, i.e. during approximately 4150 yrs.

The obtained data agree with the data from the Ust-Log 5 site (Izvarin and Ulitko, 2016), which is located in the Irgina River valley 10 km north of the grotto. In Ust-Log 5, deposits accumulated over the past 7150 years cal BP, i.e. from Middle Holocene, and no shifts in the composition and structure of the community of small mammals was observed. Thus, in the vicinity of the Nizhneirginsky Grotto forest-steppe landscape remained stable for the last 4150 years, and in general in the Irgina River valley for at least 7150 years.

Palaeornithological data agree with the data inferred from small mammal assemblages (Fig. 6). Bird fauna from Subboreal stratum (3-3a) includes species belonging to all four habitat types (Table 4). Approximately 43% of bones belong to the species inhabiting different woodlands (combine “forest” and “ecotone” types). Among birds from Subatlantic strata (1-2), species of “forest” and “ecotone” types prevail (in total 60%). Apparently closer to the present, the territories occupied by forests increased due to the reduction of open spaces.

6.2. Zoogeographical considerations

6.2.1. Yellow-necked mouse

Prior to our studies of osteological material from the Nizhneirginsky Grotto, there were no data on the distribution of yellow-necked mouse in the Middle Urals and the adjacent territory of the Ufa Plateau. The nearest limits of the species distribution were recorded only in the

Table 3
Species composition and the number of identified mammal bone remains in Nizhneirginsky Grotto sediments and distribution of small mammal species by habitat(s) (Bolshakov et al., 2006).

Taxa №	Layers	1	2		2/3-3a	3-3a			Habitats[b]				
	Taxa	samples (depth, cm)											
		1 (0–5)	2 (5–10)	3 (10–15)	4 (15–20)	5 (20–25)	6 (25–30)	7 (30–35)	OD	OH	Wo	Ro	Wa
	Eulipotyphla												
1	*Talpa europaea* Linnaeus, 1758	3	78/6[a]	50/5	53/3	105/6	25/3	22/3		0.5	0.5		
2	*Neomys fodiens* Pennant, 1771	-	2/1	-	-	-	-	-		0.25			0.75
3	*Sorex* sp.	-	37	14	7	9	2	2					
4	*S. araneus* Linnaeus, 1758	-	4/2	4/1	2/1	-	2/1	2/2		0.5	0.5		
5	*S. caecutiens* Laxmann, 1785	-	-	1/1	1/1	-	-	-		0.5	0.5		
6	*S.* cf. *isodon* Turov, 1936	-	1/1	-	-	-	-	-		0.25	0.75		
7	*S. minutus* Linnaeus, 1766	-	1/1	2/2	1/1	4/1	-	1/1		0.25	0.5	0.25	
	Chiroptera												
8	Chiroptera indet.	7	527	339	285	293	98	59					
	Lagomorpha												
9	*Ochotona* cf. *pusilla* Pallas, 1769	-	1/1	-	-	1/1	-	-	1				
10	*Lepus timidus* Linnaeus, 1758	2/1	10/2	11/2	5/1	10/3	5/2	7/2			1		
	Rodentia												
11	*Pteromys volans* Linnaeus, 1758	1/1	4/1	1/1	-	2/1	-	-			1		
12	*Sciurus vulgaris* Linnaeus, 1758	-	5/1	4/1	8/2	4/1	7/2	6/1			1		
13	*Castor fiber* Linnaeus, 1758	-	2/1	2/1	3/1	12/3	7/2	8/2			0.5		0.5
14	*Sicista* cf. *betulina* Pallas, 1779	2/1	48/11	61/10	117/22	306/52	129/27	81/16		0.25	0.75		
15	*Apodemus agrarius* Pallas, 1771	-	7/2	6/1	15/7	43/12	46/10	11/4		0.5	0.5		
16	*A. flavicollis* Melchior, 1834	-	-	-	11/3	36/6	16/4	5/1			1		
17	*A. uralensis* Pallas, 1811	-	10/3	5/2	2/1	3/2	-	-		0.25	0.75		
18	*A.* ex gr. *agrarius-uralensis*	-	4	1	1	21	28	6					
19	*Micromys minutus* Pallas, 1771	-	-	-	-	1/1	-	2/1		0.75	0.25		
20	*Cricetus cricetus* Linnaeus, 1758	14/2	102/24	227/28	380/47	653/75	259/29	120/18	0.5	0.5			
21	*Clethrionomys rufocanus* Sundevall, 1846	1/1	12/2	17/3	32/6	46/8	28/6	11/2			0.5	0.5	
22	*Cl. glareolus* Schreber, 1780	4/2	13/3	17/5	24/5	59/9	15/4	6/2			1		
23	*Cl. rutilus* Pallas, 1779	1/1	24/7	20/6	32/6	35/7	29/8	9/2			1		
24	*Cl.* ex gr. *glareolus-rutilus*	-	12/1	4/1	17/2	32/2	14/2	7/1			1		
25	*Arvicola amphibius* Linnaeus, 1758	11/3	260/26	254/23	384/35	911/85	462/46	289/31		0.75			0.25
26	*Microtus* sp.	12	308	212	231	262	227	143					
27	*M. oeconomus* Pallas, 1776	-	1/1	1/1	1/1	2/2	-	1/1		0.5	0.25		0.25
28	*M. agrestis* Linnaeus, 1761	-	11/4	14/6	13/5	21/8	11/4	4/2		0.5	0.5		
29	*M. arvalis* s.l.	1/1	45/27	25/17	51/29	75/38	33/19	27/14	0.5		0.5		
30	*M.* ex gr. *arvalis-agrestis*	1/1	2/1	3/3	-	-	-	3/2	0.333	0.333	0.333		
	Carnivora												
31	*Canis lupus* Linnaeus, 1758	-	-	-	-	3/1	-	-					
32	*Vulpes vulpes* Linnaeus, 1758	1/1	2/2	8/3	5/2	3/1	2/1	3/2					
33	*Martes martes* Linnaeus, 1758	-	-	1/1	-	2/1	-	2/2					
34	*Mustela nivalis* Linnaeus, 1766	-	-	-	-	4/1	-	3/1					
35	*M. erminea* Linnaeus, 1758	-	1/1	4/2	3/1	2/2	1/1	6/4					
	Total:	**61/16**	**1534/132**	**1308/126**	**1684/182**	**2960/329**	**1446/171**	**846/117**					

[a] Numerator is total number of identified bone remains (NISP); denominator is minimum number of individuals (MNI).
[b] Habitats are divided into five types (OD, open dry; OH, open humid; Wo, woodland/woodland-edge; Ro, rocky; Wa, water), in accordance with López-García et al. (2010).

Bashkir Fore-Urals and in the South Urals more than 200 km to the south of the grotto. After we found yellow-necked mouse fossils in the sediments of the grotto, we discover the modern population of the species on the territory of the closed coniferous-broad-leaved forest "Nizhneirginskaya dubrava" ['Nizneirginsk oak forest'], which is located approximately 8–10 km to the north of the site (Izvarin et al., 2013).

A total of 68 molars belonging to yellow-necked mouse identified in layer 3-3a showed that the species was common in the Irgina River valley during the period 4150-3100 cal BP, which coincides in time with the mid-Subboreal thermal maximum (SB-2; 4200-3200 BP). At this time, coniferous-deciduous forests with oak, elm, maple, hazel, hornbeam were widespread in the Middle Urals and at the adjacent area of Fore-Urals (Panova and Antipina, 2016; Lapteva et al., 2017). However, bone remains of the yellow-necked mouse were not found in layers 1 and 2. We assume the age of layer 1 to be modern due to the presence of modern anthropogenic trash such as fragments of broken glass. Layer 2 was dated to the Subatlantic period of the Holocene (top of the layer is 710 ± 20 cal BP, bottom of the layer is 2640 ± 110 and 2770 ± 90 cal BP). Clearly, the yellow-necked mouse in the time span between 3100 and 2640 cal BP (corresponds to the Late Subboreal cooling of the Holocene – SB-3; 3200-2500 BP according to Khotinsky, 1987) disappeared from the area around the grotto and never appeared here again.

According to the data of palynological studies, the late-Subboreal reduction of mixed coniferous and broad-leaved forests occurred in the Fore-Ural region between 3400 and 2600 cal BP (Lapteva et al., 2017) and in the Middle Urals between 3700 and 2700 cal BP (Panova and Antipina, 2016), and the vegetation of the region acquired a taiga appearance. However, mixed coniferous and broad-leaved forests have survived on the Ufa Plateau to the present day, e.g., Nizhneyirginsky oak forest (Gorchakovsky, 1968). Unfortunately, later sediments with remnants of this species in the valley of river Irgina were not found; therefore, nothing can be said about the history of the species here during the Subatlantic period (SA; 2500-0 BP according to Khotinsky, 1987). However, it was previously established (Smirnov, 1993) that yellow-necked mouse lived on the Ufa Plateau in the 12–15 centuries AD approximately 50 km south-east of the Nizhneirginsky Grotto.

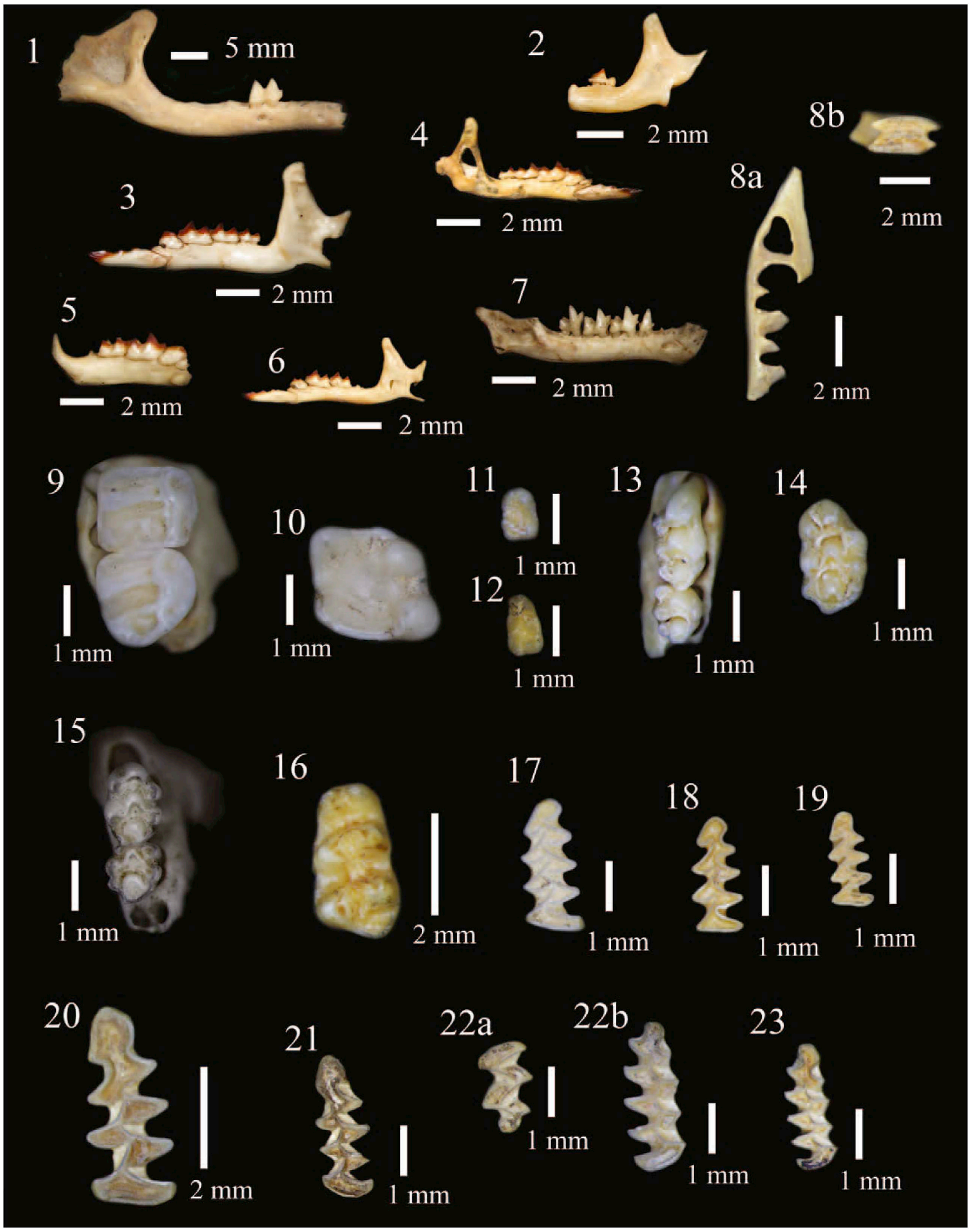

Fig. 4. Small mammal remains from Nizhneirginsky Grotto sediments. 1-*Talpa europaea* Linnaeus, 1758: dex mandible wit m1; 2-*Neomys fodiens* Pennant, 1771: fragment of sin mandible with m3; 3-*Sorex araneus* Linnaeus, 1758: sin mandible; 4-*S. caecutiens* Laxmann, 1785: dex mandible; 5-*S.* cf. *isodon* Turov, 1936: fragment of dex mandible; 6.-*S. minutus* Linnaeus, 1766: sin mandible. 7-Chiroptera: dex mandible; 8-*Ochotona* cf. *pusilla* Pallas, 1769: a. fragment of sin mandible; b. M1 dex; 9-*Pteromys volans* Linnaeus, 1758: fragment of dex maxilla with M2 and M3; 10-*Sciurus vulgaris* Linnaeus, 1758: m1 dex; 11-*Sicista* cf. *betulina* Pallas, 1779: m1 dex; 12-*Micromys minutus* Pallas, 1771: m1 dex; 13-*Apodemus agrarius* Pallas, 1771: fragment of sin maxilla with M1 and M2. 14-A. *flavicollis* Melchior, 1834: M1 dex; 15-A. *uralensis* Pallas, 1811: fragment of dex maxilla with M1 and M2; 16-*Cricetus cricetus* Linnaeus, 1758: m1 sin; 17-*Clethrionomys rufocanus* Sundevall, 1846: m1 sin; 18-Cl. *glareolus* Schreber, 1780: m1 sin; 19-Cl. *rutilus* Pallas, 1779: m1 sin; 20-*Arvicola amphibius* Linnaeus, 1758: m1 sin; 21-*Microtus oeconomus* Pallas, 1776: m1 sin; 22-*M. agrestis* Linnaeus, 1761: a. M2 sin; b. m1 dex; 23-*M. arvalis* s.l.: m1 dex.

Therefore, we can assume after 2640 cal BP (in the Subatlantic) the yellow-necked mouse did not inhabit the vicinity of the grotto because the relevant habitats disappeared there between 3100 and 2640 cal BP. However, in general, the species survived in the region up to present day.

6.2.2. Steppe pika

Currently, steppe pika inhabits shrubs of steppe slopes of the Obshchyi Syrt Range, foothills of the South Urals and West Altai Mountains (Lissovsky, 2012) more than 200–300 km to the south and to the south-east of the grotto. However, steppe pika was widespread in the Urals at the end of the Late Pleistocene between 25000 and 10500 BP and during both Preboreal (PB; 10500-9000 BP according to Khotinsky, 1987) and Boreal (BO; 9000-8000 BP) periods of the Holocene (Smirnov et al., 2016). Finally, the species disappeared over most of this territory during the Atlantic (AT; 8000-4500 BP). Then, steppe pika still existed in the Krasnoufimsk insular forest-steppe on the border with the Ufa Plateau in the vicinity of the Sukhorechensky Grotto (Fig. 1) between 2863 ± 143 BP and 3208 ± 171 BP (Smirnov, 1993), i.e., at the end of the Subboreal. One upper molar of this species was found in the upper part of the layer 3 of the Nizhneirginsky Grotto sediments dated 3100 ± 110 cal BP, which confirms these data and moved the Subboreal distribution limits of steppe pika 50 km to the north. In addition, a mandible of this species was found in the upper part of layer 2 dated 710 ± 20 cal BP (1240 ± 20 cal AD); thus, we can assume that steppe pika inhabited the valley of the Irgina River as a relic of the Late Pleistocene and early-Holocene faunas as early as the 12th and 13th centuries AD. This is the first find of the pika's remains of such late age in the Middle Urals and in the adjacent territory of the Fore-Urals. Unfortunately, we do not have enough data yet to identify the detailed history of this species on this territory.

7. Conclusions

The Nizhneirginsky Grotto is currently the only source of taphonomic, palaeoenvironmental, and palaeoecological data in the northern part of the Ufa Plateau where mixed coniferous-broad-leaved forests of the plateau are associated with steppe landscapes of Krasnoufimsk

Table 4
Species composition and the number of identified bird bone remains in Nizhneirginsky Grotto sediments and distribution of bird species by habitat(s) (Ryabitsev, 2008).

Taxa №	Taxa	Habitat type	**Subatlantic**				Subboreal		
			Samples (deph, cm)						
			1 (0–5)	**2 (5–10)**	**3 (10–15)**	**4 (15–20)**	5 (20–25)	**6 (25–30)**	**7 (30–35)**
	Anseriformes								
1	*Anas platyrhynchos* Linnaeus, 1758	A[a]	-	4/1[b]	4/1	3/1	12/1	7/2	1
2	*Anas querquedula* Linnaeus, 1758	A	1	3/2	6/2	2/1	9/2	4/3	2/1
3	*Anas crecca* Linnaeus, 1758	A	-	-	1	-	1	2/1	-
4	*Anas clypeata* Linnaeus, 1758	A	-	1	1	1	8/2	-	-
5	*Anas penelope* Linnaeus, 1758	A	-	-	1	-	1	-	-
6	*Anas* sp.		-	3	7	5	3	4	-
7	*Aythya fuligula* Linnaeus, 1758	A	-	-	1	-	1	-	1
8	*Mergellus albellus* Linnaeus, 1758	A	-	-	-	-	1	-	-
9	Anatinae indet.	A	2	2	1	7	3	2	-
	Falconiformes								
10	*Circus* sp.		-	-	-	-	2	-	-
11	*Accipiter gentilis* Linnaeus, 1758	E	-	-	-	1	-	-	-
12	*Buteo buteo* Linnaeus, 1758	E	1	2/1	3/1	2/1	5/1	2/1	1
13	*Milvus migrans* Boddaert, 1783	E	-	-	2/1	2/1	-	2/1	-
14	*Falco tinnunculus* Linnaeus, 1758	O	-	-	-	2/1	-	-	-
	Galliformes								
15	*Tetrao tetrix* Linnaeus, 1758	F	-	23/2	34/5	49/4	84/4	40/4	18/3
16	*Tetrao urogallus* Linnaeus, 1758	F	-	-	1	-	3/2	-	-
17	*Tetrao* sp.		-	10	6	35	48	12	23
18	*Perdix perdix* Linnaeus 1758	O	-	1	1	-	3/2	1	5/1
19	*Coturnix coturnix* Linnaeus, 1758	O	-	-	-	3/1	1	1	1
	Gruiformes								
20	*Fulica atra* Linnaeus, 1758	A	-	-	-	1	-	-	-
21	*Gallinula chloropus* Linnaeus, 1758	A	-	-	-	-	1	-	-
22	*Porzana porzana* Linnaeus, 1766	A	-	-	1	-	-	-	-
23	*Crex crex* Linnaeus, 1758	A	1	9/1	22/2	31/3	60/4	19/2	11/1
	Charadriiformes								
24	*Vanellus vanellus* Linnaeus, 1758	A	-	-	2/1	1	6/2	3/1	5/2
25	*Philomachus pugnax* Linnaeus, 1758	A	-	-	-	1	15/1	4/1	-
26	*Actitis hypoleucos* Linnaeus, 1758	A	-	-	1	1	2/1	1	1
27	*Scolopax rusticola* Linnaeus, 1758	F	-	3/1	10/2	22/1	51/1	-	1
28	*Tringa stagnatilis* Bechstein, 1803	A	-	-	-	-	-	1	-
29	*Tringa totanus* Linnaeus, 1758	A	-	-	-	1	-	-	-
30	*Charadriiformes* indet.		1	-	-	7	-	-	-
	Strigiformes								
31	*Bubo bubo* Linnaeus, 1758	F	-	3/1	1	-	-	-	-
32	*Strix uralensis Pallas, 1771*	F	-	2/1	-	6/1	1	-	-
33	*Aegolius funereus* Linnaeus, 1758	F	-	3/1	1	-	-	-	-
34	*Asio otus* Linnaeus, 1758	A	1	4/1	-	-	9/2	2/1	1
35	Strigiformes small size		-	-	3	-	-	-	3
	Piciformes								
36	*Dryocopus martius* Linnaeus, 1758	F	-	-	1	-	2/1	-	1
37	*Dendrocopos major* Linnaeus, 1758	F	2	-	2/1	-	6/1	-	1
	Passeriformes								
38	*Turdus philomelos* Brehm, 1831	F	-	1	-	-	1	-	-
39	*Turdus iliacus* Linnaeus, 1766	F	-	1	1	-	-	-	-
40	*Turdus pilaris* Linnaeus, 1758	E	-	6/1	5/1	2/1	8/1	3/1	-
41	*Turdus* sp.		-	8	4	4	10	2	-
42	*Coccothraustes coccothraustes* Linnaeus, 1758	F	-	-	-	1	-	-	-
43	*Pica pica* Linnaeus, 1758	E	-	3/1	2/1	-	5/1	-	-
44	*Corvus corax* Linnaeus, 1758	F	-	-	2/1	-	1	-	1
45	Passeriformes indet.		3	8	9	14	16	4	9
46	Aves indet.		6	55	75	135	568	41	33
	Total		**18**	**155**	**211**	**339**	**947**	**157**	**119**

[a] Habitats are divided into four types (A, “amphibians”; O, “Open spaces”; E, “ecotone”; F, “Forest”), in accordance with Tomek and Bocheński (2005).
[b] Numerator is total number of identified bone remains (NISP); denominator is minimum number of individuals (MNI).

insular forest-steppe in the valley of Irgina River.

The grotto sediments were accumulated over approximately 4150 ± 150 cal BP, i.e. during the Late Holocene.

The analysis of alterations on first lower molars of arvicoline rodent species caused by the digestion showed that eagle owl (*Bubo bubo* Linnaeus, 1758) is the most possible agent responsible for the accumulation of small mammal assemblages in these grotto sediments. The abundant number of the teeth of birch mouse in grotto sediments is a taphonomic phenomenon, which shows that a part of studied osteological material, including birch mouse remains, was accumulated owing to the predation activity of mustelids.

Palaeoenvironmental analysis based on the habitat weighting method showed that the landscape and, accordingly, the fauna of rodents in the vicinity of the grotto remained almost unchanged during this time. Moreover, both forest and open meadow habitats were common in the northern part of the Ufa Plateau in the Irgina River valley for the last 7150 years, as at present.

The connection between the history of the yellow-necked mouse in

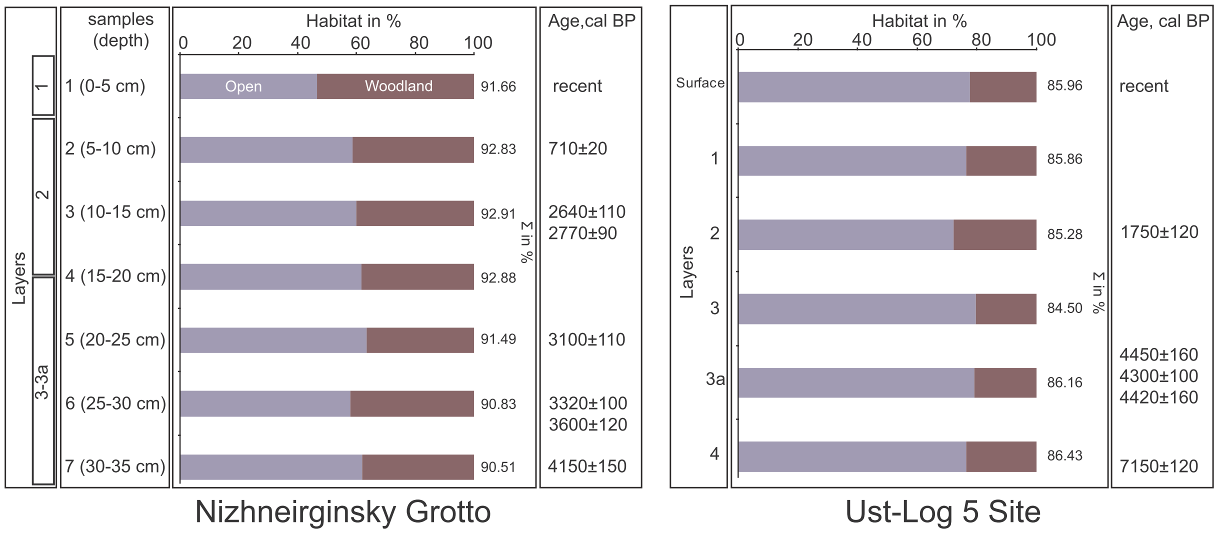

Fig. 5. Environmental comparison between the different layers of the studied sediments from the Nizhneirginsky Grotto and different layers from the Ust-Log 5 locality (data from Izvarin and Ulitko, 2016) based on the habitat weighting method in accordance with López-García et al. (2019).

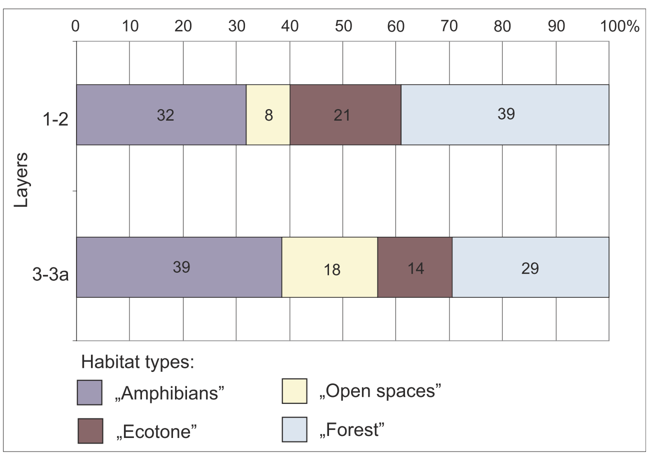

Fig. 6. The ratio of bird remains (MNI) from the Nizhneirginsky Grotto sediments according to habitat preferences of species. Habitats are divided into four types ("Amphibians"; "Open spaces"; "Ecotone"; "Forest"), in accordance with Tomek and Bocheński (2005).

the northeast of its modern range with the palaeogeographic events of the second half of the Holocene was established. The material from the sediments of the Nizhneirginsky grotto shows that the species was common in the Irgina river valley during the period of 4150-3100 cal BP, which coincides in time with the maximum distribution of broad-leaved trees in the Fore-Urals during the mid-Subboreal thermal maximum (SB-2; 4200-3200 BP). As a result of the late-Subboreal cooling in the Late Holocene (SB-3; 3200-2500 BP), following the reduction in coniferous-deciduous forests, the area of yellow-necked mouse decreased; since between 3100 and 2640 cal BP, the species disappeared from the vicinity of the grotto. However, the isolated population of the species was preserved in the Nizhneirginsky oak forest (7–8 km to the northeast of the grotto), where the yellow-necked mouse currently lives.

It has also been established that the steppe pika was widespread throughout the Urals at the end of the Late Pleistocene and in the Early Holocene and became extinct during the Atlantic period of the Holocene in the greater territory of the Urals and adjacent territories, except for its southern regions; steppe pika inhabited the Krasnoufimsk insular forest-steppe as early as the 12th and 13th centuries AD as a relict species of the Late Pleistocene fauna. The modern range of steppe pika is located more than 200–250 km to the south and southeast of the Nizhneirginsky Grotto.

Data availability

The palaeontological collections are kept at the Laboratory of palaeoecology of Institute of Plant and Animal Ecology of Ural Branch of the Russian Academy of Science.

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