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Makhnevskaya Ledyanaya Cave (Middle Urals, Russia): Biostratigraphical reconstruction

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ABSTRACT

Pollen and fossil mammals of the terrigenous deposits in the Makhnevskaya Ledyanaya Cave (59°26′ N 57°41′ E), located in the northern part of the Middle Urals and on the border with the Northern Urals, were studied. The spore-and-pollen spectra are divided into four pollen zones. In all the spectra, pollen concentrations of tree species amount to 50–70%. The presence of pollen in thermophilic (*Quercus robur*-type, *Tilia cordata*-type, *Ulmus* sp., *Carpinus betulus, Corylus avellana*-type) and moderate boreal *(Abies, Picea, Pinus, Betula, Alnus)* species and a lack of any tundra flora elements indicate their interglacial nature. The following have been identified as small mammal fauna: 8 taxa of insectivorous mammals, 4 taxa of bats, 2 taxa of lagomorphs, 4 species of carnivores, 16 species of rodents, 1 species of odd-toed ungulates and 4 species of even-toed ungulates. The remains of cryoxerophilous (*Dicrostonyx* sp., *Lasiopodomys gregalis*) and steppe (*Ochotona* sp.) species are scarce in the studied fauna. Species typical of forests (genus *Sorex*, genus *Craseomys*, genus *Myodes*, *Myopus schisticolor*, *Microtus agrestis*) are dominant. Remains of *Erinaceus* sp., *Talpa* sp., *Crocidura leucodon, Sciurus vulgaris*, *Hystrix brachyura*, *Dryomys nitedula*, *Apodemus flavicollis*, *Stephanorhinus kirchbergensis* have been found. The morphology and dimensions of the teeth of *Panthera spelaea fossilis*, *Hystrix brachyura*, *Dryomys nitedula*, *Arvicola amphibius,* mice of genus *Apodemus* are described. The compositions of the palynocomplexes and mammal fauna as well as the SDQ values for m1 of *Arvicola amphibius* allow us to date the deposits from the Makhnevskaya Ledyanaya Cave to the Eemian interglacial period (MIS 5e).

1. Introduction

The western slope of the Urals is a karst area where limestone, gypsum and anhydride are widespread and are formed by various surface and underground karst relief complexes. There are many caves and grottos. Four karst provinces have been identified here, each of which includes several karst areas (Lavrov and Andrejchuk, 1992). The Makhnevskaya Ledyanaya Cave is located in the Kizelovsko-Yayvinsky region of the middle part of the Western Ural speleological province. There are 219 known caves and grottos (Lavrov and Andrejchuk, 1992), most of which have soft deposits of various geneses. A total of 27 caves and grottos were subjected to a palaeontological analysis of their soft deposits. All the caves and grottos yielded bone remains of Quaternary and Holocene vertebrates (Kuzmina, 1975; Kosintsev, 2007; Fadeeva and Smirnov, 2008; Ponomarev et al., 2013). Radiocarbon dating, analysis of the species composition of the fauna, and archaeological materials showed that almost all the sites are dated to MIS 4–1. Only two sites in the Viasherskaya Cave and the Makhnevskaya Ledyanaya Cave may be dated to an earlier period. Both caves yielded remains of the Malayan porcupine, whereas the Makhnevskaya Ledyanaya Cave also had remains of the black bear (*Ursus thibetanus* (G. Cuver, 1823)) (Baryshnikov, 2001, 2003; Kosintsev and Podoprigora, 2003; Fadeeva et al., 2010, 2011). The authors preliminarily dated this fauna to the Eemian interglacial period (MIS 5e).

We have searched for intact zoogenic deposits in the Makhnevskaya Ledyanaya Cave for several years (Fadeeva et al., 2011), but the bone remains from 10 sites subjected to our analysis were of mixed origin. These remains contained bones of the bicoloured white-toothed shrew, yellow-necked mouse, and Malayan porcupine. No such species have been found in numerous examined zoogenic deposits of the Late Pleistocene and Holocene caves within the territory of the Middle and Northern Urals (Bachura and Kosintsev, 2007; Kosintsev, 2007; Fadeeva

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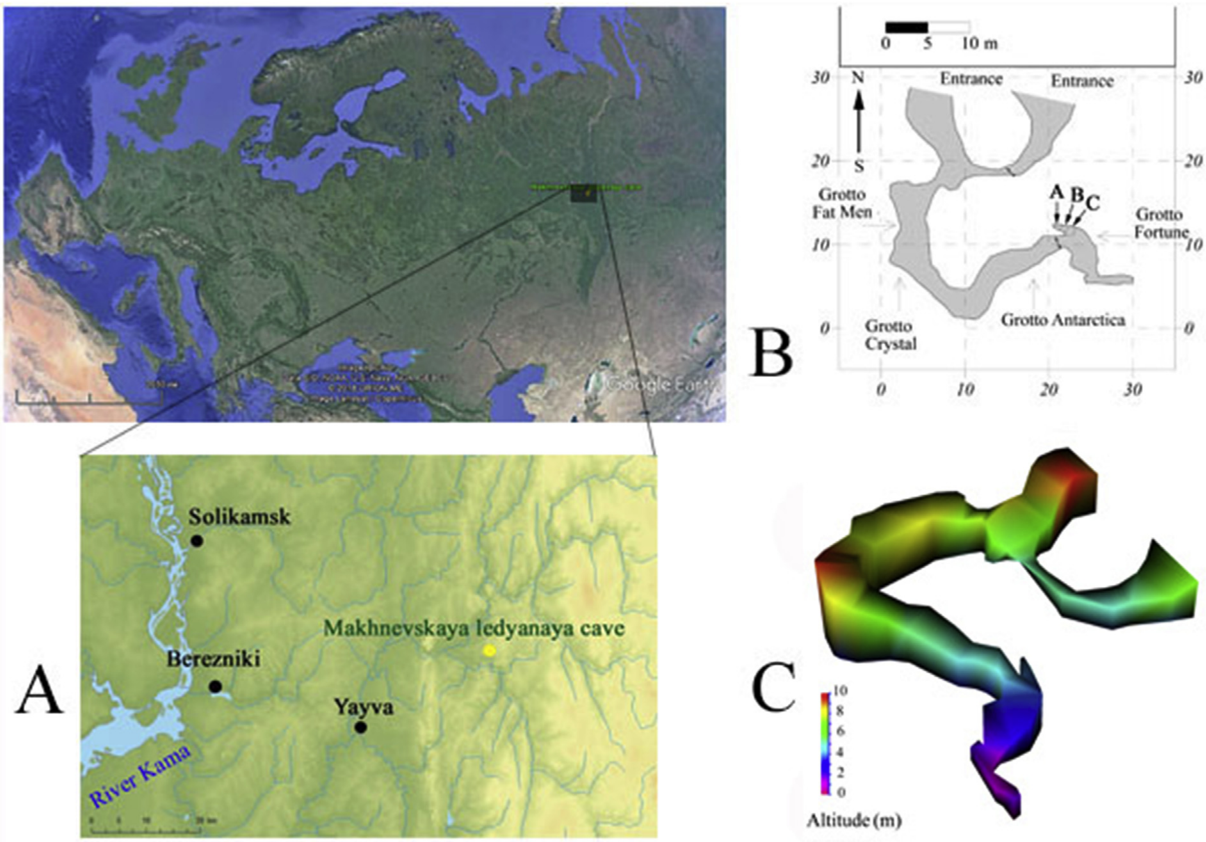

Fig. 1. The geographical position of the Makhnevskaya Ledyanaya Cave (A), the scheme of the cave (B) with the designation of the excavation sectors (A, B, C) and altitude of the cave (C).
B, C – the scheme and altitudes of the cave are given according to O. Shvetsova and I. Gerasimova (08.2019, Mining Institute, Perm, Russia), names of the grottos are given according to E.P. Bliznetsov.

and Smirnov, 2008; Ponomarev et al., 2013). The northern boundaries of their modern ranges are located far to the south of the cave. We first managed to discover intact deposits in 2017. Their excavation took place in 2017 and 2018. This paper covers the results of the palaeontological analysis of these intact zoogenic deposits.

2. Background

The Makhnevskaya Ledyanaya Cave (59°26′ 57,6636” N 57°41’ 16,9152” E) is situated on the northwestern slope of the Middle Urals, on the border with the Northern Urals (Fig. 1A), within the territory of the complex natural reserve “Makhnevskie peshchery” (Makhnevsky Caves). The study area is located in the southern taiga piedmont forests of the western slope of the Middle Urals. These forests are characterized by the presence of nemoral species and diverse grass forests. There, the proportion of Siberian species is high, with the occurrence of larch (*Larix sibirica* (Ledeb., 1833)) and Siberian pine (*Pinus sibirica* (Du Tour, 1803)). Linden (*Tilia cordata* (Miller, 1768)) can be found in the dark coniferous forest, mainly in the understory, and it thus reaches the northern boundary of its range in this area (Ovesnov, 1997).

The average temperature in January ranges from −15°C to −16°C. Average temperature in July is 17–18°C. The average rainfall is 600–700 mm per year (Tartakovskij, 2012).

There are 4 caves within this natural reserve. The Makhnevskaya Ledyanaya Cave is the shortest in terms of its length. The caves were developed from massive Middle Carboniferous limestones. All the caves have zoogenic deposits of varying levels of exploration. The main entrance to the Makhnevskaya Ledyanaya Cave is formed as a wide elliptic arch, and then the height of the ceiling lowers (Fig. 1C). The corridor runs from the main entrance, and then it turns left and leads to a steep slope (about 2 m high) of a remote dead-end grotto. The floor of the corridor is sloping in the direction of the grotto. The corridor in front of the slope was once covered with ice as per the data collected by G. Maksimovich (1947) and historical records made by E. Bliznetsov (Record Services and Archives, Aleksandrovsk, AAO ф96). We observed this cave over several years (August–September), but traces of ice were detected in the corridor only in 2011.

The pit is located in the left part of the remote grotto of the cave (Fig. 1B) and consists of three sectors (A, B, C, 1.0 m × 0.5 m each). The deposits were excavated in horizons of 5–10 cm thick. A total of 17 horizons were identified in sector A, 7 horizons in sector B, and 6 horizons in sector C. The deposits of sectors A and B were studied to the bedrock. The deposits of sector A give the most comprehensive profile and yield the greatest number of palaeontological materials. They consist of two layers. Layer 1, from the surface to a depth of 76 cm, is represented by dark brown light loam with alluvium, ratchel, rock debris and limestone boulders. Layer 2, from 76 cm to 81 cm, contains yellow brown sandy loam with limestone alluvium on the bedrock. The depth of layer 1 of sector B is 55 cm, whereas that of layer 2 is 15 cm. The bedrock surface is even. In sector C, we studied the deposits of layer 1 only to the depth of 45 cm.

In the lower part of the deposit (lower half of layer 1 and entire layer 2) we found calcite-phosphorite pseudomorphs after fragments of limestone. They consist of three layers. Carbonate rock (limestone) is located in the centre, and was only slightly changed. The second layer consists of phosphate materials with a shell-like fracture of light brown colour. The outer layer is represented by dense and finely dispersed or acicular porous carbonate material. These pseudomorphs were formed in the cave soil in a warm humid climate from animal waste and from their bone remains (phosphates) on the limestone fragments (calcium carbonate). The presence of shrinkage cracks on the surface of the phosphate layer caused by the water evaporation indicates their formation from a colloidal solution. As this took place, the solution diffused inside the limestone fragments and the dissolved calcium carbonate was transported through the colloidal membrane of the solution, which caused a fine and acicular structure of the redeposited outer calcite layer.

Radiocarbon dating does not provide a precise age of the deposits. Two convectional dates of 6121 ± 127 BP (IEMEG-1390) and 30,901 ± 675 BP (IEMEG-1391) were obtained from the long bones of small mammals and the bone fragments of large mammals from mixed deposits, respectively. Accelerator mass spectrometry was used to obtain two dates from two porcupine teeth (> 27,500 BP (AA-90664); 41,800 (+600, −500) BP (GrA-35461)). J. van der Plicht, Head of the Laboratory, believes that the latter tooth is close to the date beyond the method limit. The tooth contained minimal collagen (personal message).

3. Material and methods

3.1. Palynological analysis

A total of 17 specimens were selected for the pollen analysis from each horizon of the deposits in sector A. The specimens were studied in the laboratory of Mesozoic and Cenozoic continental ecosystems of the Tomsk State University (Tomsk city) by the separation method (Grichuk, 1940), with an additional ultrasonic treatment and application of KJ- and CdJ2-based gravity solution. Pollen and spores were identified in temporary glycerine solutions under an Olympus BX51 microscope at × 400 magnification using a reference collection of pollen and spores of modern flora (Institute of Plants and Animals Ecology (IPAE), Ural branch of the Russian Academy of Sciences) and the Pollen and Spore Atlas (Beug, 2004). The palynological remains in each specimen were counted to 250 arboreal pollen grains, with a parallel record of pollen of herbs and spores for higher spore-bearing plants. The data processing and plotting were performed in TILIA software 2.0.41 (Grimm, 2012). The totals for arboreal pollen and herbs were assumed to be 100%. For a more accurate interpretation of palynological data, pollen of Apiaceae was excluded from the pollen total due to its dominance in all the spectra, reflecting the specific local conditions in the vicinity of the cave. The proportion of this pollen was calculated from the total content of pollen grains + Apiaceae. The percentage of spores was calculated from the total content of pollen and spores, taken as 100%.

3.2. Faunistic research

The excavated samples were washed on a sieve with a mesh diameter of 0.7 mm. The following elements were selected from the deposit concentrate obtained from all three sections of A (Table 1), B, C: 6784 teeth and jaws of rodents, insectivorous mammals, bats and lagomorphs, and more than 200 teeth and bones of carnivores, even-toed ungulates and odd-toed ungulates. This material was then additionally cleaned in an ultrasonic cleaner GB-10 LB. Aside from the mammal bones, the deposits are rich in bone remains of amphibians and reptiles, with single bones of birds. The bones were studied using optical (binocular microscope MBS-10, Leica MZ16 stereomicroscope) and electron probe (VEGA 3 LMH Scanning Electron Microscope with energy dispersive X-ray microanalysis Oxford Instruments INCA Energy 250/X-max 20) methods in the laboratory of the Mining Academy, Ural Branch of the Russian Academy of Sciences. The results were graphically visualized in Grafer 13, Strater 5, and Adobe Photoshop Elements 2018. Software Statistika 6 was used for statistical analysis of the results. Evaluation of morphometric differences of the rodent teeth was performed through one-way analysis of variance with a subsequent pairwise comparison following Scheffé's method.

A reference collection of the Mining Academy, Ural Branch of the Russian Academy of Science, was used for species identification of fossil skulls and mandibles of bats. Identification of the mandibles of shrews (Soricidae) followed the methods described by (Zaitsev, 1998; Fadeeva, 2016). Taxonomic nomenclature and classification of rodents follow Wilson et al. (2017). We applied D.J van Weers's method (1990) to determine the identification numbers and dental attrition classes for the porcupine's teeth (genus *Hystrix*). The length (L) and width (W) of the porcupine's teeth were measured along the occlusal surface. Species identifications of mice (genus *Apodemus*) were performed using classification functions indices following respective methods (Lashkova and Dzeverin, 2002). K. Adamczewska-Andrzejewska's method (1973) was applied for determining the age of teeth in mice. Terminology used for the elements of grinding surfaces of molars in voles follows the scheme described by A. van der Meulen (1973). We applied the methods described by Rekovets and Nadachowski, (1995) for the measurement of the first lower molars (m1) in voles. To determine the stratigraphic position of the host deposits, we estimated SDQ (Schmelzband-Differenzierung-Quotient), which is the enamel differentiation quotient for seven triangles of the first lower molar of *Arvicola amphibius* (Heinrich, 1978) as per formula $SDQTn = ebp/eba \times 100$. The enamel thickness of the first lower molars (m1) of water voles was measured on digital images in software tpsDig2. Species identification of isolated teeth of red-backed voles (genuses *Craseomys, Myodes*) is based on dimensional characteristics of the second upper molar (M2), for which the most precise diagnostics are possible (Borodin et al., 2005; Borodin, 2009). Species identification of mandibles and their fragments in the Lemmini species representatives was carried out based on of the position of the alveolar cusp of the incisor (Gromov and Polyakov, 1977). Species identifications of isolated teeth of the fossilized lemmings were based on dimensional and morphological patterns of the third upper molars (Smirnov et al., 1997; Ponomarev et al., 2011, 2015). Species identification of the *Meles* remains was performed based on of a set of patterns of the crown structure in premolars and molars (Baryshnikov et al., 2002) and the morphological and morphometric features of the mandible (Gasilin and Kosintsev, 2012).

4. Results

4.1. Taphonomic observations

The upper horizon yields many bones of post-cranial elements, mandibles and skull fragments, while bones of amphibians were scarce. Bone materials below this horizon are mainly represented by isolated rodent teeth, teeth and mandibles of insectivorous mammals and bats, and numerous bones of amphibians and reptiles. Numerous osteoderms of blindworms (*Anguis fragilis* Linnaeus, 1758) have also been recorded.

Bones and teeth have been divided into four types by their colour characteristics and the presence/absence of mineral and organic formations on the surface. The first type includes whitish and light yellow teeth and bones, many of which have organic remains (fur, skin, muscles) and/or traces of faecal masses of carrion beetles on the surface. The remains of the second type are light, without any organic traces on the surface. Most materials of this type have single black mineral formations (manganese oxides) on the grinding surface of the teeth. Most of these teeth may have remained in the jaws for a long time, and only dental crowns contacted with surrounding rock. Remains of the third type are of different colours; however, they all have dark grey stains on the surface and within deep bone and tooth tissues. The surfaces of most parts of these remains have black mineral formations of various density. Remains of the fourth type are from a dark yellow to brown colour, and their surface is covered with numerous points or dendrite manganese oxides. At a depth of 32–44 cm, the overwhelming majority of the mandibles of red-toothed shrews of the third type have depigmented teeth, which may indicate a long-term contact of the bones with water.

The first type was only found in the upper horizon (21.6% of all the

Table 1
The list of mammal species represented in deposits of the Makhnevskaya Ledyanaya Cave, sector A.

Taxon/Horizons (cm)	0–2	2–12	12–20	20–26	26–32	32–36	36–40	40–44	44–48	48–52	52–56	56–60	60–64	64–68	68–72	72–76	76–81	NISP
Erinaceus sp.	0	0	0	0	0	1	1	0	2	0	0	0	0	2	0	0	0	6
Talpa sp.	2	1	3	1	2	8	2	2	2	1	3	1	8	2	2	3	0	43
Sorex araneus Linnaeus, 1758	28	9	2	4	4	6	4	2	4	2	5	11	19	6	3	5	1	115
Sorex isodon Turov, 1924	48	14	3	1	1	15	3	6	3	3	4	1	5	4	1	0	0	112
Sorex caecutiens Laxmann, 1788	51	7	0	3	0	16	8	8	4	2	0	3	1		0	0	0	103
Sorex minutus Linnaeus, 1766	3	2	2	2	2	0	0	0	0	0	0		2	2		0	0	15
Sorex minutissimus Zimmermann, 1780	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2
Sorex sp.	76	1	6	1	2	0	4	11	5	7	2	5	12	18	1	0	0	151
Eptisicus nilssonii (Keyserling & Blasius, 1839)	128	29	12	8	6	57	18	27	18	11	19	25	33	26	7	6	3	433
Plecotus auritus (Linnaeus, 1758)	6	0	4	2	1	0	1	1	1	2	4	1	6	1	1	2	0	33
Myotis dasycneme (Boie, 1825)	0	0	0	0	0	0	0	0	0	0	0	1	1		2	0	0	4
Myotis sp.	5	1	3	0	0	2	0	0	0	3	2	6	3	2	2	2	0	31
Chiroptera	0	15	2	3	4	32	9	4	8	7	10	9	9	11	1	1	1	126
Lepus sp.	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Ochotona sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2
Ursus savini Andrews, 1922	0	89	37	0	0	0	0	0	2	0	3	3	2	0	7	8	13	164
Gulo gulo (Linnaeus, 1758)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Meles meles (Linnaeus, 1758)	0	2	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	5
Panthera spelaea fossilis (Reichenau, 1906)	0	0	0	0	0	0	0	0	0	0	1	0	0	3	2	1	1	8
Sciurus vulgaris Linnaeus, 1758	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Hystrix brachyura Linnaeus, 1758	0	2	4	1	0	0	0	0	1	0	5	1	1	1	2	1	0	19
Dryomys nitedula (Pallas, 1778)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Sicista betulina (Pallas, 1779)	2	1	0	0	0	0	3	0	0	0	0	1	3	0	0	0	0	10
Myopus schisticolor (Lilljeborg, 1844)	227	114	5	15	12	103	42	47	30	43	11	3	22	0	1	0	0	675
Craseomys rufocanus (Sundevall, 1846) (m1,M2)	43	20	1	2	2	35	9	14	11	9	2	0	4	1	1	1	0	155
Myodes rutilus (Pallas, 1779)(M2)	4	1	5	8	6	4	4	3	4	7	8	15	29	27	5	1	1	132
Myodes glareolus (Schreber, 1780) (M2)	7	5	0	0	0	3	4	3	1	1	1	1	2	0	0	0	0	28
Myodes ex gr. *rutilus-glareolus* (m1)	7	10	9	8	10	13	21	16	14	8	14	28	40	42	12	5	3	260
Craseomys sp., *Myodes* sp.	150	73	24	22	33	99	53	44	65	57	44	76	139	106	23	14	0	1022
Dicrostonyx sp.	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	0	4
Arvicola amphibius (Linnaeus, 1758)	3	30	12	23	8	7	21	12	14	13	28	38	55	44	20	16	5	349
Alexandromys oeconomus (Pallas, 1776) (m1)	11	10	5	2	5	9	5	5	6	14	17	20	26	15	8	0	0	158
Microtus agrestis (Linnaeus, 1761) (m1, M1, M2)	55	35	9	8	8	35	20	20	28	28	23	48	53	24	19	3	8	424
Lasiopodomys gregalis (Pallas, 1779) (m1)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Microtus sp.	108	87	19	22	45	93	50	62	58	55	116	139	200	120	31	3	4	1212
Apodemus uralensis (Pallas, 1811)	0	0	0	0	0	0	0	0	0	0	0	1	3	3	3	2	2	14
Apodemus sylvaticus (Linnaeus, 1758)	0	0	0	1	2	0	1	0	1	0	3	0	6	3	0	0	0	17
Apodemus flavicollis (Melchior, 1834)	0	0	0	0	7	0	0	1	1	0	4	7	3	6	9	3	2	43
Stephanorhinus kirchbergensis (Jäger, 1839)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Cervus elaphus Linnaeus, 1758	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Alces alces (Linnaeus, 1758)	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Rangifer tarandus (Linnaeus, 1758)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Bison priscus Bojanus, 1825	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
NISP[a]	964	565	172	138	161	540	284	289	286	273	330	446	692	470	164	77	44	5895
N[b]	16	22	18	16	16	15	17	15	20	14	19	20	26	18	19	15	9	38

[a] NISP – number of identified specimens.
[b] N – number of taxa.

Table 2
Skeletal elements of small cave bear (*Ursus savini* Andrews, 1922). Makhnevskaya Ledyanaya Cave, sectors A, B.

Bones	Sector A		Sector B	
	0–76 cm	76–81 cm	0–55 cm	55–70 cm
Cranium	4	1	5	3
Mandibula	2	2	2	2
Dentes	10	9	7	7
Vertebarae	6	4	5	3
Costae	11	2	11	2
Scapula	0	1	0	1
Humerus	2	1	5	0
Radius	1	1	2	1
Ulna	1	0	2	1
Pelvis	4	1	4	2
Femur	2	1	2	1
Tibia	6	0	3	0
Fibula	1	1	2	1
Carpus et tarsus	3	1	2	0
Calcaneus	3	1	2	1
Astragalus	3	0	2	0
Sesamoideum	0	0	0	0
Metapodia	11	1	9	1
Phalanx I	1	0	2	1
Phalanx II	1	1	0	0
Phalanx III	2	1	1	2

remains). This horizon yields numerous faecal masses of small mammals. The material of the first type has been excluded from this analysis as it belongs to modern and Late Holocene mammals.

All the bones of large mammals belong to the fourth group. The vast majority of bone remains of large mammals belong to the small cave bear (*Ursus savini* Andrews, 1922) (Table 1). Its remains include all the skeleton elements with vertebrae, ribs and metapodia being most numerous (Table 2). These elements are most numerous in the skeleton. Milk teeth and bones of new-born individuals were found. This indicates that bears in the cave died during their hibernation, including females with their new-born cubs.

Many bones of large mammals have biting marks, the incisor traces of which have a width indicating that they belonged to porcupines (Fig. 2).

In the Pleistocene, the grotto must have been used as a temporary shelter by four-legged predators, whose diet included amphibians, reptiles and small mammals. The grotto must have also been used by small cave bears for their hibernation. Bones and teeth of the first type from the upper horizon belonged to small mammals that accidently entered the grotto in the Late Holocene. An abrupt slope from the corridor to the grotto to a depth of 2 m might have acted as a trap. Bats died in the grotto in the Pleistocene and Holocene. The animals might have entered the grotto during periods when there was no ice in the corridor, most likely during warm periods.

Fig. 2. Traces of porcupine incisors on the fragment of the large mammal's bone. Makhnevskaya Ledyanaya Cave, sector A (depth 68–72 cm).

4.2. Palynological data

The spore-and-pollen spectra of the deposits from the Makhnevskaya Ledyanaya Cave yield the following pollen grains in various states of preservation: 1) recent-type light pollen grains with no mineralization, imported into the cave recently; 2) pollen grains of a darker colour with traces of mineralization, apparently dated to the Holocene; 3) pollen grains with grey exine, mineralized and presumably dated to the Pleistocene. The most evident taphonomic differentiation is observed in pollen grains of *Tilia* and *Picea*. However, the third type of pollen is quantitatively predominant, and contains sporadic recent and Holocene pollen (not more than 5–6 grains, not more than 1–2% from the total amount of spores and pollen). The results of the palynological analysis of the cave deposits are given in the spore pollen diagram (Fig. 3). The spore-and-pollen spectra form four pollen zones (PZ) addressing the changes in pollen content and composition. While spores of Polypodiophyta and pollen grains of Apiaceae are abundant in all the spectra, the pollen concentration of tree species ranges from 50 to 70%.

PZ–1: (depth of 72–81 cm) unites the pollen spectra of two lower samples with a predominance of *Betula* sect. Albae pollen (30–35%) and sporadic occurrence of pollen grains of coniferous species (*Pinus* s/g Diploxylon and *Picea*). Small forms morphologically close to shrubs (*Betula* sect. Nanae) can be found among the birch pollen grains. The total content of Quercetum mixtum pollen is less than 10%. *Corylus avellana*-type and *Alnus glutinosa*-type pollen grains occur sporadically. In the non-arboreal group, Poaceae and Asteroideae pollen grains are abundant (10–15% each), while Cichorioideae is less frequent (about 5%). Pollen of forbs is diverse but sporadic. The concentration of Polypodiophyta spores is less than 10%, with rare spores of *Lycopodium* and *Sphagnum*.

PZ–2 (depth of 52–72 cm) includes spectra that demonstrate a decrease in the *Betula* sect. Albae pollen concentration to 25%, while *Alnus glutinosa*-type and Quercetum mixtum pollen increase to 15%. The increase in the total content of Quercetum mixtum pollen occurs due to a higher content of the pollen grains of the *Tilia cordata*-type and *Quercus robur*-type with rare occurrences of *Ulmus* and *Carpinus betulus*. *Corylus avellana*-type pollen grains are sporadic. In the non-arboreal group, Asteroideae pollen is abundant, while the concentration of Poaceae pollen does not exceed 10%. The pollen of forbs is diverse. The content of Polypodiophyta spores increases to 30% with a sporadic occurrence of *Lycopodium* and *Sphagnum*.

PZ–3 (32–52 cm) unites the pollen spectra with a predominance of the birch pollen and an increase in the content of pollen grains of *Pinus* s/g Diploxylon and *Picea* to 15–20%. These spectra are characterized by maximum Quercetum mixtum pollen contents. The concentration of alder pollen is reduced. The pollen of herbaceous plants is very diverse, but its concentration is lower. The concentration of spores of ferns is at maximum (up 30–40%).

PZ–4 (0–32 cm) includes spore-and-pollen spectra of the upper part of the test pit. This zone is characterized by a high content of pollen grains of coniferous species, with a spruce pollen concentration of 15% and an alder pollen concentration of 20%. The pollen of broad-leaved species is abundant, but total content is lower in comparison with previous PZ–3. The pollen of forbs is diverse with the increase in the content of *Polemonium* pollen grains. Spores of ferns are also abundant, while those of mosses and sphagnum mosses are rare.

The predominance of arboreal pollen in the spore-and-pollen spectra is indicative of forest-type vegetation (Fig. 3). The deposits in the cave began to form with the spread of birch forests, including broad-leaved and coniferous species (PZ–1). Meadows played an important role in the composition of vegetation, which is documented by the abundance of grasses and diversity of mesophilic forbs. Then, the concentration of birch in the forests started to decrease, while alder and broad-leaved species spread. This is shown by the increase in *Alnus glutinosa*-type and Quercetum mixtum pollen concentrations, including pollen of the *Quercus robur*-type and *Tilia cordata*-type, and the decrease

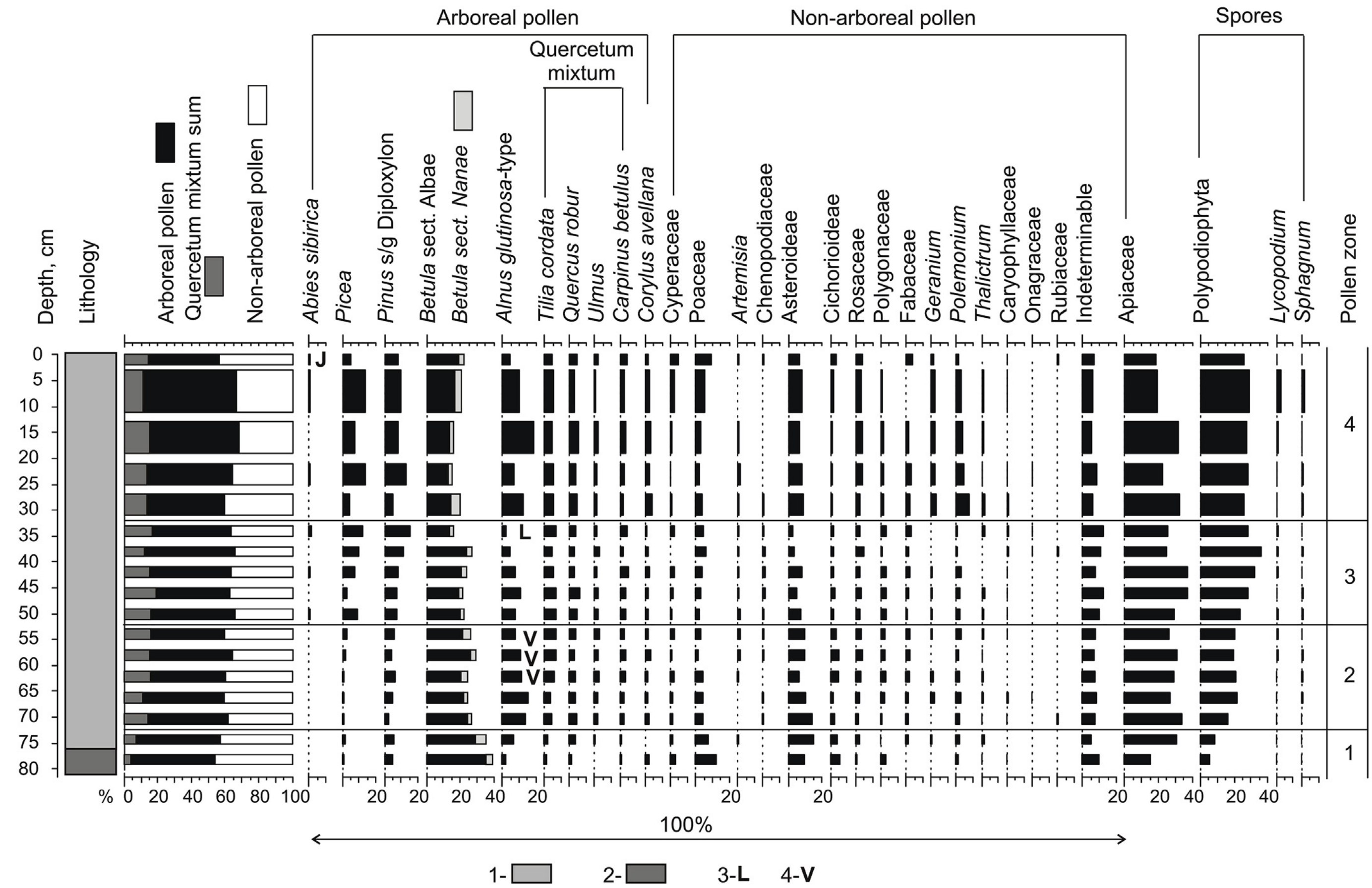

Fig. 3. Spore-pollen diagram. Makhnevskaya Ledyanaya Cave, sector A. 1 – dark-brown light loam, 2 – yellow-brown sandy loam, 3 – *Lonicera* sp., 4 – *Viburnum* sp.

in the *Betula* sect. Albae pollen concentration (PZ–2). Alder grew in swamp forests, while lindens and oaks were found in birch forests. *Viburnum* was found in the forest understory. Later, coniferous species (spruce, pine and probably fir) began to spread in the forests, which is proven by the increase in the concentration of *Picea* sp. and *Pinus* s/g Diploxylon pollen and a sporadic occurrence of *Abies* pollen grains (PZ–3). Alder was also widespread. The total pollen contents of broad-leaved species (linden, oak, elm-tree, horn-beech) and hazel reached their maximum, which is demonstrated by the widespread occurrence of these species in the forests. Broad-leaved coniferous and birch forests prevailed. In the forest understory and in the vicinity of the cave, ferns were wide spread, which is demonstrated by the abundance and diversity of the spores of ferns, including cf. *Osmunda* sp. When the upper part of the deposit was formed, coniferous species and alders predominated in the vicinity of the cave, while the concentrations of horn-beech and elm-tree decreased whereas lindens and oaks increased. This is proven by the abundance of pollen of *Picea* and *Pinus* s/g Diploxylon, a maximum content of *Alnus glutinosa*-type pollen and increases in *Quercus robur*-type and *Tilia cordata*-type pollen with sporadic occurrences of *Ulmus* sp., *Carpinus betulus* and *Corylus avellana*-type pollen (PZ–4). The forests may have started to acquire a southern taiga form, but with a higher proportion of broad-leaved species than in the modern southern taiga.

4.3. Small mammals

Forest species prevail among the bone remains of rodents, whereas intrazonal species form the second largest group (Fig. 4). Bone remains of tundra and steppe species of small mammals (*Dicrostonyx* sp., *Lasiopodomys gregalis* (Pallas, 1779), *Ochotona* sp.) are scarce.

The lower part of the deposit is characterized by an increased species diversity with a predominance of short-tailed field voles (*Microtus agrestis* (Linnaeus, 1761)), root voles (*Alexandromys oeconomus* (Pallas, 1776)), water voles (*Arvicola amphibius* (Linnaeus, 1758)), ruddy voles (*Myodes rutilus* (Pallas, 1779)), and common shrews (*Sorex araneus* Linnaeus, 1758). Teeth of the Malayan porcupine (*Hystrix brachiura* Linnaeus, 1758) and three species of mice (genus *Apodemus*) have been found throughout the depths of all the deposits, except for the upper layers. Teeth of the forest dormouse (*Dryomys nitedula* (Pallas, 1778)), red squirrel (*Sciurus vulgaris* Linnaeus, 1758), least shrew (*Sorex minutissimus* Zimmermann, 1780) and hedgehog (*Erinaceus* sp.) are rare and have mainly been found in the lower half of the studied deposit.

The upper part of the deposit mostly yields wood lemmings (*Myopus schisticolor* (Lilljebog, 1844)), grey red-backed voles (*Craseomys rufocanus* (Sundevall, 1846)), even-toothed shrews (*Sorex isodon* Turov, 1924) and Laxmann's shrews (*Sorex caecutiens* Laxmann, 1788).

Scarce bone remains of bank voles (*Myodes glareolus* (Schreber, 1780)), moles (*Talpa* sp.) and lesser shrews (*Sorex minutus* Linnaeus, 1766) have been recorded throughout all the depths of uncovered deposits, except for the lowest layers.

Bones and teeth of bats occur throughout the depths of all deposits, with a predominance of remains of northern bats (*Eptesicus nilssoni* (Keyserling and Blasius, 1839)), whereas remains of the long-eared bat (*Plecotus auritus* (Linnaeus, 1758)) and small species of common bats (*Myotis* sp.) are less numerous. Single bones of the pond bat (*Myotis dasycneme* (Boie, 1825)) have been found at a depth of 56–72 cm.

In this study, we have analysed the morphologic patterns of the teeth and jaws of some mammal species that were found to describe their morphology and level of evolutionary development.

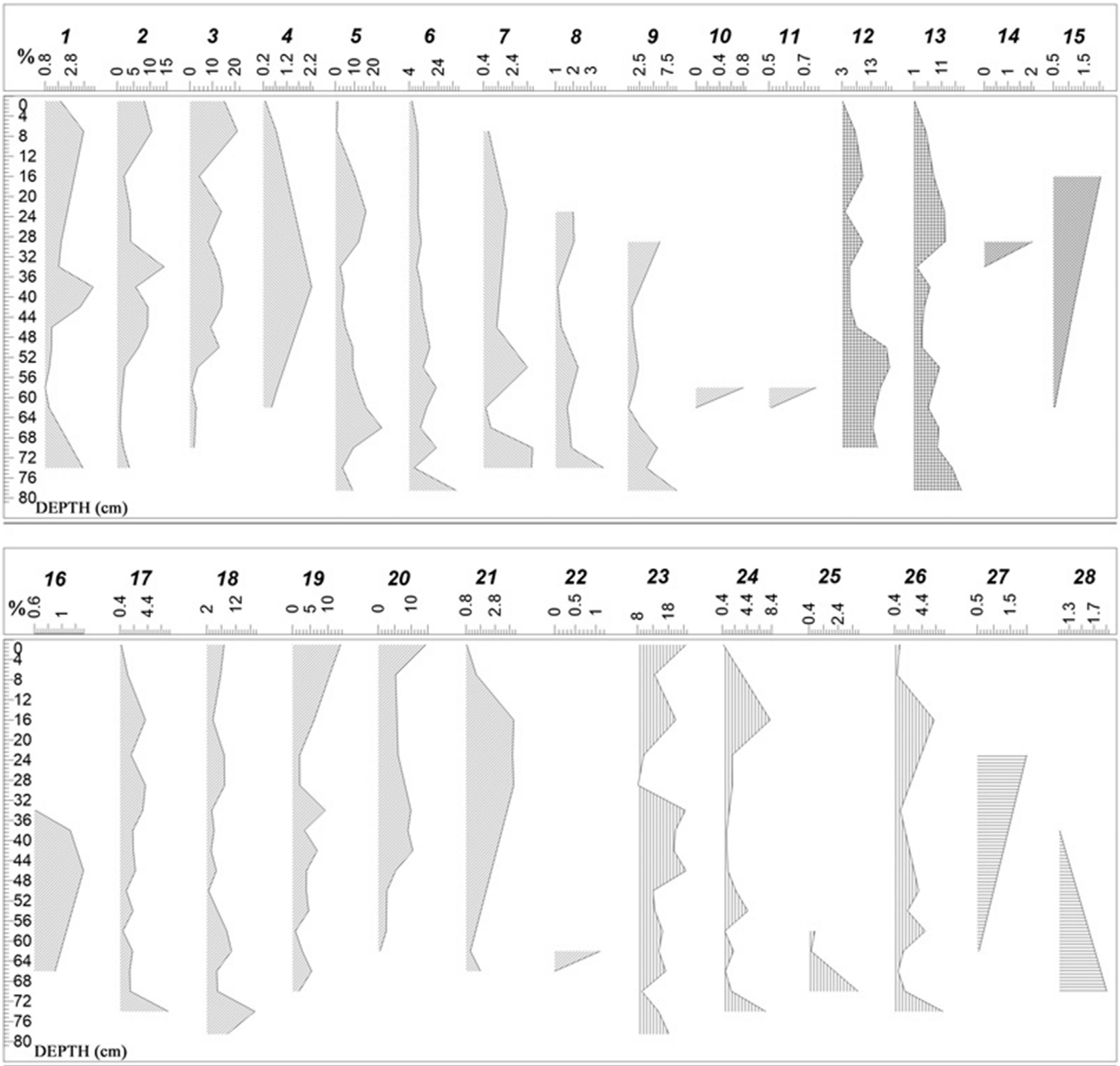

Fig. 4. The species composition and the ratio (%) of the fossil remains of insectivorous mammals, rodents, bats and lagomorphs. Makhnevskaya Ledyanaya Cave, sector A. *1 – Myodes glareolus*, *2 – Craseomys rufocanus*, *3 – Myopus schisticolor*, *4 – Sicista betulina*, *5 – Myodes rutilus*, *6 – Microtus agrestis*, *7 – Hystrix brachyura*, *8 – Apodemus sylvaticus + A. uralensis*, *9 – Apodemus flavicollis*, *10 – Dryomys nitedula*, *11 – Sciurus vulgaris*, *12 – Alexandromys oeconomus*, *13 – Arvicola amphibius*, *14 – Lasiopodomys gregalis*, *15 – Dicrostonyx* sp., *16 – Erinaceus* sp., *17 – Talpa* sp., *18 – Sorex araneus*, *19 – Sorex isodon*, *20 – Sorex caecutiens*, *21 – Sorex minutus*, *22 – Sorex minutissimus*, *23 – Eptesicus nilssonii*, *24 – Plecotus auritus*, *25 – Myotis dasycneme*, *26 – Myotis* sp., *27 – Lepus* sp., *28 – Ochotona* sp.

4.4. Large mammals

Few large mammal remains and taxons were found (sector A, Table 1). There are very few large mammal bones in sectors B and C. The greatest number of remains are of the small cave bear (*Ursus savini* Andrews, 1922), which can be explained through taphonomy, because the cave provided the species with winter shelter. The observed fauna contained species that preferred open landscapes (small cave bear *Ursus savini*, bison *Bison priscus* Bojanus, 1825), semi-open landscapes (cave lion *Panthera spelaea fossilis* (Reichenau, 1906), badger *Meles meles* (Linnaeus, 1758), Merck's rhinoceros *Stephanorhinus kirchbergensis* (Jäger, 1839), and red deer *Cervus elaphus* Linnaeus, 1758), closed landscapes (elk *Alces alces* (Linnaeus, 1758)) and polyzonal examples (wolverine *Gulo gulo* (Linnaeus, 1758), reindeer *Rangifer tarandus* (Linnaeus, 1758)). Among the hoofed animals we observed species that preferred tree and shrub-like vegetation (Merck's rhinoceros, red deer, elk) and herbaceous vegetation (reindeer, bison). However, the paucity of the remains precludes our ability evaluate the ratios of these species and their distribution in the deposits.

The fauna composition contains European badgers (*Meles meles*) whose main food sources were soil invertebrates and amphibians, which are typical inhabitants of deciduous and mixed coniferous-leaved forests and forest-steppes (Heptner et al., 2001). Findings of European badgers are rare in the Pleistocene sites of North Eurasia. In the Urals, these remains were observed exclusively in Eemian sites (MIS 5e) and interstadial Bølling и Allerød sites, as well as in Holocene sites (Kosintsev et al., 2016).

4.5. Taxonomic notes

Order Eulipotyphla Waddel, Okada and Hasegawa, 1999
Family Soricidae Fischer, 1814
Genus *Crocidura* Wagler,1832
Crocidura leucodon (Hermann, 1780)

Fig. 5 (A, B).

Material. Sector C. Mandible with p3, p4, m1 – 1 (sin), mandible with p4, m2, m3 – 1 (dex).

Description and discussion. Preservation type IV. The dimensions and preservation of the mandibles are similar. They apparently belonged to the same individual.

No white-toothed shrews currently inhabit the Middle Urals (Demidov and Demidova, 1990). The ranges of all the representatives of this genus stretch southwards. The range of the lesser white-toothed shrew (*Cr. suaveolens*) is about 700 km south of the cave (Stroganov, 1957), whereas the range of the bicolored white-toothed shrew (*Cr. leucodon*) is located about 1200 km south (Zaitsev et al., 2014). No fossil white-toothed shrew has been found in the Late Pleistocene and Holocene faunas of Perm Pre-Urals (Fadeeva and Smirnov, 2008). However, these shrews have been found on the western slopes of the Southern Urals in the Holocene and Late Pleistocene faunas (Zaitsev, 1992). Both white-toothed shrew species have been found in the Holocene deposits of the Ayu-Yskan Cave (Fadeeva et al., 2018b), whereas *Cr. leucodon* was found in the deposits of the onset of the Late Pleistocene of the Ignatievskaya Cave (Fadeeva et al., 2017, 2019). The range boundary of the Bicolored white-toothed shrew apparently passed substantially northwards during one of the Pleistocene periods.

Dimensions. Table 3.

Family Sciuridae Fischer, 1817

Genus *Sciurus* Linnaeus, 1758

Sciurus vulgaris Linnaeus, 1758

Fig. 5 (C, D, F).

Material. Sectors A, B. Lower teeth: isolated m2 – 1 (sin), isolated incisor −1 (sin); upper tooth: isolated M1 – 1 (sin).

Description and discussion. The incisor and the first upper molar are of the fourth type of preservation, while the second lower molar is of the third type of preservation. The incisor is strongly compressed from the sides; m2 has four roots; M1 is a tri-rooted tooth.

The squirrel remains are very rare for the Pleistocene sites of Eastern Europe and Urals. They have been found only at one site in Eastern Europe (Motuzko, 2007), at two sites of the Middle Urals (Yakhimovich et al., 1988; Smirnov, 1993) and at one site of the Southern Urals (Fadeeva et al., 2018a). The fauna of these sites are dated to the late interglacial period or the period close to it. However, the Holocene sites, including those in the Middle Urals, yield abundant squirrel remains. This species is currently widespread in the Urals.

Dimensions. m2: L 2.4 mm, W2.7 mm; M1: L 2.2 mm, W 5.3 mm; incisor: W 3.55 mm.

Family Myoxidae Gray, 1821

Genus *Dryomys* Thomas, 1906

Dryomys nitedula (Pallas, 1778)

Fig. 5 (E).

Material. Sector A. Lower tooth: fragment of mandible with m1 – 1 (dex).

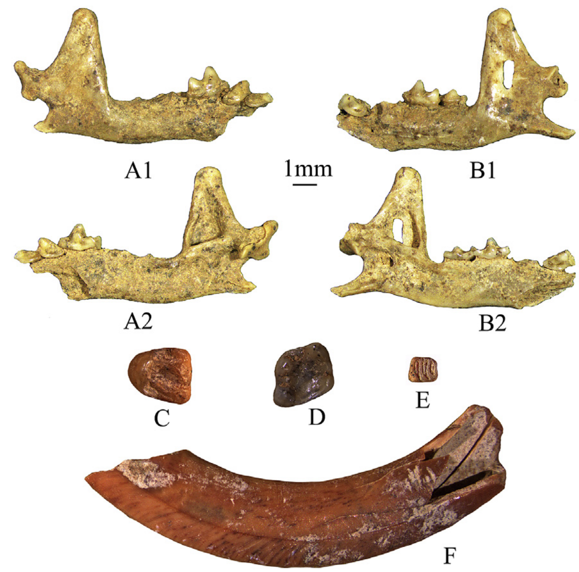

Fig. 5. Fossil remains of *Crocidura leucodon*, *Sciurus vulgaris*, *Dryomys nitedula*. Makhnevskaya Ledyanaya Cave. Right and left mandibles of *Cr. leucodon* (A1, B1 – buccal side, A2, B2 – lingual side), sector C; M1 sin, m2 sin of *Sc. vulgaris* (C, D), sector A; m1 dex of *Dr. nitedula* (E), sector A; the fragment of the low incisor (sin) of *Sc. vulgaris* (F), sector B.

Description and discussion. At the depth of 56–60 cm we found a fragment of a right mandible with a bi-rooted molar (m1) of the fourth type of preservation.

The tooth is slightly larger than m1 of the European fossil and recent forest dormouse with a recorded maximum length of 1.15 mm (Daams, 1981; Daoud, 1993). The tooth width is within the size variation limit typical of this species. The tooth dimensions are smaller than those of m1 in the garden dormouse (*Eliomys quercinus* L., 1758) (Daoud, 1993). The tooth form is trapezoidal, and its grinding surface is slightly concave. The tooth has 5 main ridges (anterolophid, metalophid, centrolophid, mesolophid and posterolophid) and two additional ridges (anterior extra ridge between the anterolophid and metalophid, and a posterior extra ridge between the mesolophid and posterolophid). This is a new m1 morphotype of *Dryomys nitedula,* as previously there has been only one known morphotype with one posterior extra ridge (Daoud, 1993).

Finding a tooth of the forest dormouse is the first evidence proving its existence within the territory of the Middle Urals in the past. There is no reliable data available on modern habitation of the forest dormouse within the territory of the Middle Urals (Perm Pre-Urals). In the literature there are only some facts on the purchase of pelts of another species, garden dormouse, in the southern Perm Territory (Pavlinin and Shvarts, 1957). However, other researchers believe that this data is

Table 3
Measurements (mm) of lower molars (m) and mandibles (*Crocidura leucodon, Cr. suaveolens*).

Species/measurements	Length m1	Length m1-m3	Height of the mandible under m3
Cr. leucodon[1]	–	–	1.75
Cr. leucodon[2]	1.8	–	1.75
Cr.leucodon[3]	1.77 ± 0.04 (1.70–1.85) [3][a]	3.93 ± 0.09 (3.75–4.05) [3]	1.55 ± 0.04 (1.45–1.65) [4]
Cr.leucodon[4]	1.73 ± 0.03 (1.65–1.80) [4]	3.86 ± 0.08 (3.70–4.00) [4]	1.55 ± 0.08 (1.35–1.75) [4]
Cr.leucodon[5]	1.75 ± 0.00 [4]	3.90 ± 0.03 (3.90–4.05) [4]	1.49 ± 0.07 (1.35–1.65) [4]
Cr. suaveolens[6]	1.6	3.75	1.4

[1, 2]Makhnevskaya Ledyanaya Cave, sector C, Middle Urals; [3] Ignatievskaya Cave (excavation V, 2014), depth 3.20–3.90 m (MIS 5e), Southern Urals; [4]Au-Yskan Cave (2017), upper deposits (MIS 1), Southern Urals; [5]Kashkuk, Orenburg region, Southern Urals (Modern Time); [6]Aydar-Arnasay, Uzbekistan (Modern Time).

[a] Hereinafter in the tables and text: mean ± standard error (minimum–maximum) [quantity].

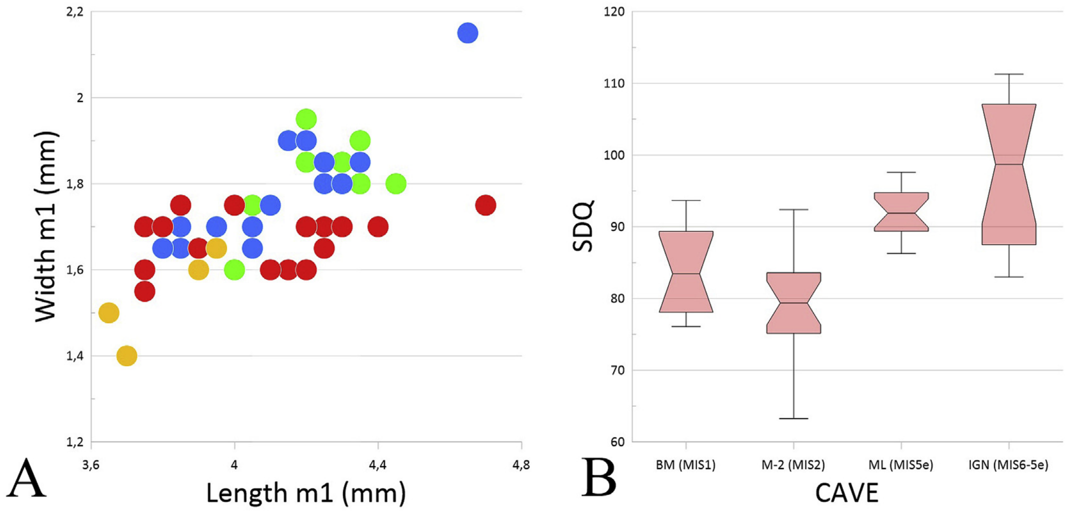

Fig. 6. Sizes of the first lower tooth (A) and SDQ m1 (B) of *Arvicola amphibius* from four caves.
Green circles – Bolshaya Makhnevskaya Cave (BM) (MIS 1); blue circles – Makhnevskaya-2 Cave (M-2) (MIS 2); red circles – Makhnevskaya Ledyanaya Cave (ML) (MIS 5e); yellow circles – Ignatievskaya Cave (IGN) (MIS 6-5e), Southern Ural. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

erroneous (Demidov and Demidova, 1990). According to V. Popov (1960), the modern eastern range boundary of the forest dormouse is located within the territory of Middle Povolzhye (the Volga river region, Tatarstan).

Dormouse remains are very rare for the Pleistocene sites of Northern Asia and Eastern Europe. They were found at four sites of the East-European Plain. Two sites yielded common dormouse (*Glis* sp.) remains (Motuzko, 2007; Agadzhanyan, 2009), one site, contained forest dormouse (*Dryomys* sp.) remains (Agadzhanyan, 2009) and another containing hazel dormouse (*Muscardinus avellanarius* Linnaeus, 1758) remains (Yakhimovich et al., 1988). The forest dormouse (*Dryomys nitedula*) remains were found in the lower layer of pit V of the Ignatievskaya Cave (Southern Urals), the fauna of which is presumably related to the transition time (MIS6-MIS 5e) (Fadeeva et al., 2018a).

Dimensions. m1: L 1.2 mm, W 1.05 mm.
Family Cricetidae Fischer, 1817
Genus *Arvicola* Lacepede, 1799
Arvicola amphibius (Linnaeus, 1758)
Fig. 6.
Material. Sectors A, B, C. Lower teeth: isolated m1 – 82, isolated m2-3 –141; upper teeth: isolated M1 – 87, isolated M2 – 54, isolated M3 – 67.
Description and discussion. All the teeth from the deposits of sectors B and C are of the fourth type of preservation. The overwhelming majority of the teeth from the deposits of sector A are of the same type (only five teeth are of the second type, and six teeth of the third).

The widths of the first lower molars of water voles from the Makhnevskaya Ledyanaya Cave (Fig. 6A) are less than those of m1 from the deposits of the neighbouring caves (Makhnevskaya-2 Cave (MIS2) and Bolshaya Makhnevskaya Cave (MIS1). No significant differences were identified for the length of m1 in all the samples. The mean SDQ value for m1 from the Makhnevskaya Ledyanaya Cave is higher than that for m1 from these caves (Fig. 6B). The widths of the first lower teeth from the lower part of the deposit (3.10–4.00 m) of the Ignatievskaya Cave (Southern Urals) which are preliminary dated to the period between the end of the Middle Pleistocene (MIS6) and the onset of the Late Pleistocene (MIS 5e) (Fadeeva et al., 2018a, 2019) are even smaller and significantly differ from all three samples from the Perm Pre-Urals caves. However, the m1 samples from the Ignatievskaya Cave (96.7) and the Makhnevskaya Ledyanaya Cave (91.9) do not differ in terms of SDQ values. The SDQ values around 100 are typical of the Eemian and the early Weichselian localities (Koenigswald and Heinrich, 1999). A. Markova (2006) believes that though the tendency of the SDQ values to decrease from the Middle to the Late Pleistocene is apparent, this quotient cannot be regarded as the only decisive argument in favour of a certain age of the Late Pleistocene fauna due to significant variation within one and the same locality. E. Escude et al. (2008) do not consider the SDQ to be a reliable indicator for stratigraphic interpretation. At the same time, this quotient makes it possible to approximately estimate the time of formation of a fossil sample.

Dimensions. m1 (mm): L 4.10 ± 0.05 (3.75–4.70) [22], W 1.67 ± 0.01 (1.55–1.75) [20].
Family Muridae Illiger, 1811
Genus *Apodemus* Kaup, 1829
Fig. 7.
Apodemus flavicollis (Melchior, 1834)

Material. Sectors A, B, C. Lower teeth: mandibles with m1, m2, m3 – 3 (1sin, 2dex); mandibles with m1, m3 – 1 (sin); mandibles with m1, m2 – 1 (sin); isolated m1 – 3 (1sin, 2dex); isolated m2 – 2 (dex); isolated m3 – 2 (1sin, 1dex). Upper teeth: maxillae with M1, M2, M3 – 6 (4 sin, 2 dex); maxillae with M1, M2 – 2 (sin); isolated M1 – 2 (1sin, 1 dex); isolated M2 – 2 (1sin, 1 dex); isolated M3 – 1 (dex).

Apodemus sylvaticus (Linnaeus, 1758)

Material. Sectors A, B. Lower teeth: mandibles with m1, m2 – 5 (3sin, 2dex); mandibles with m1 – 1 (dex); isolated m1 – 4 (2sin, 2dex); isolated m2 – 2 (dex). Upper teeth: isolated M1 – 4 (2sin, 1 dex); isolated M2 – 1 (sin).

Apodemus uralensis (Pallas, 1811)

Material. Sectors A, B. Lower teeth: mandibles with m1, m2 – 2 (sin); isolated m1 – 2 (dex); isolated m2 – 2 (dex); isolated m3 – 2 (1sin, 1dex). Upper teeth: maxillae with M1, M2, M3 – 2 (dex); maxillae with M2, M3 – 1 (dex); isolated M1 – 1 (dex); isolated M2 – 1 (dex).

Description and discussion. All the bone remains and teeth of the representatives from the Muridae family are of the fourth type of preservation. The morphology of the first lower molar (m1) and the second

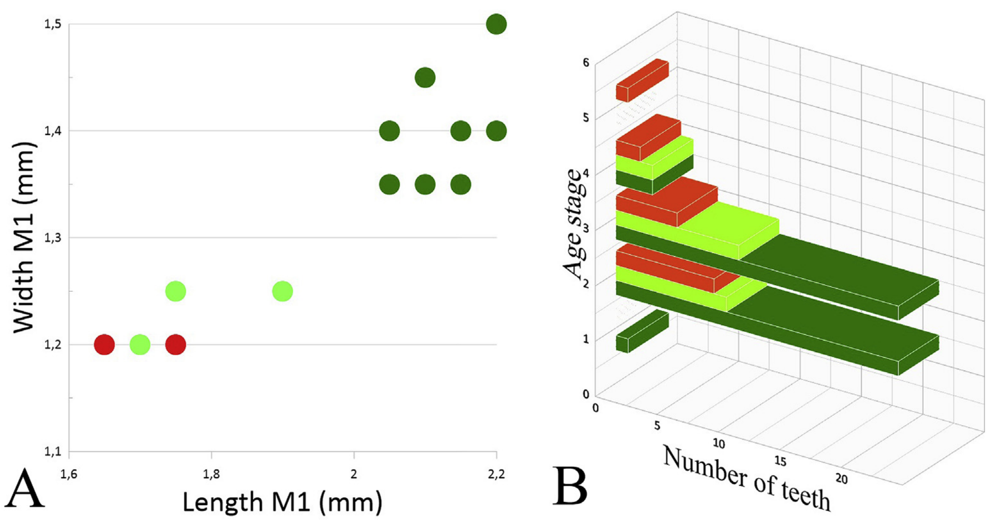

Fig. 7. Sizes of the first upper tooth (A) and number of teeth by age stages (B) of three species of mice. Makhnevskaya Ledyanaya Cave, sectors A, B, and C.
Dark green – *Apodemus flavicollis*; light green – *A. sylvaticus*; red – *A. uralensis*. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

upper molar (M2) is typical of wood mice genus *Apodemus*. The labial cingulum on m1 has additional cusps (from 2 to 4). All the M2 samples have an anteroexternal cusp (tb1). The morphometric analysis showed that the first upper molars (M1) of *A. flavicollis* differ considerably from other species by their size (Fig. 7A). The teeth of the second and third age groups prevail in the samples of all three species. The age composition of the teeth (Fig. 7B) sample gives enough evidence to posit that the mice entered the remote grotto of the cave during the summer-autumn period.

These are the first findings of the wood mouse in the northern Middle Urals in the Pleistocene fauna. Bone remains of mice within this territory were found only in the Holocene fauna (Smirnov, 1993; Fadeeva and Smirnov, 2008). These are the northernmost findings of the fossil wood mouse in the Urals so far. No such findings have been found further north than this location (Bachura and Kosintsev, 2007; Ponomarev et al., 2013). The wood mouse bone remains were found in the Late Pleistocene localities in the southern Middle Urals (Smirnov, 1993) and in the Southern Urals (Kosintsev and Bachura, 2013). The Pleistocene and Holocene faunas have yielded only remains of *Apodemus flavicollis, Apodemus uralensis* and *Apodemus* ex gr. *uralensis-sylvaticus* so far (Smirnov, 1993; Fadeeva and Smirnov, 2008; Kosintsev and Bachura, 2013; Fadeeva et al., 2019). The remains of *A. sylvaticus* were found in the Urals for the first time ever.

The Middle Urals are presently inhabited by the herb wood mouse (*Apodemus uralensis*) (Pavlinov and Lisovskiy, 2012). The yellow-necked mouse (*Apodemus flavicollis*) has been found in the southern Middle Urals (Demidov and Demidova, 1990; Izvarin et al., 2013). The range of the long-tailed wood mouse (*A. sylvaticus*) currently extends considerably westward, through the territory of the Baltic states, Belarus, and the Ukraine (Mezhzherin, 1997; Pavlinov and Lisovskiy, 2012). Finding three wood mouse species in the deposits of the Makhnevskaya Ledyanaya Cave demonstrates that in certain Pleistocene periods the range of the long-tailed wood mouse was significantly larger than its current range, extending to the east as far as the Urals.

Dimensions: Table 4.
Order Rodentia Bowdich, 1821
Family Hystricidae Fischer, 1817
Genus *Hystrix* Linnaeus, 1758
Hystrix brachyura Linnaeus, 1758
Fig. 8
Material. Sector A. Lower teeth: isolated p4 – 2 (sin); isolated m1-2 – 3 (dex); isolated incisors (fragment) – 2. Upper teeth: isolated M1-2 – 4 (1 sin, 3 dex).

Description and discussion. All the teeth are isolated, and are of the third and fourth type of preservation. They were found only in the deposits of sector A. The teeth lack the traces of digestive corrosion. The upper tri-rooted teeth belonged to adults. The left upper molar (Fig. 8A) has a pronounced left lingual fold; there are three enamel islands (attrition class E). The other upper teeth (Fig. 8 (B, C, D)) lack any lingual fold; there are 5–6 enamel islands (attrition class G). The lower teeth (3–4 underdeveloped roots) belong to animals from two age groups: subadults (attrition class P), the enamel islands of which have not been formed yet (Fig. 8H and I), and adults (attrition class T), who have enamel islands only without any lingual folds (Fig. 8 (F, G, J)). The sample provides an upper molar of a large adult (attrition class G) (Fig. 8B), which is comparable to *H. cristata* teeth (Montoya, 1993). However, most of the examined teeth apparently belong to a small porcupine (Table 5). Analysis of dimensional characteristics of a porcupine skull from this cave indicated that it belongs to fossil subspecies *H. brachyura vinogradovi* Argyropulo, 1941 (Baryshnikov, 2003).

The teeth of a small porcupine (one undamaged p4 dex (L 8.0 mm, W 5.3 mm) and a tooth fragment) have also been found in the deposits from Viasherskaya Cave within the territory of the Middle Urals (Fadeeva et al., 2010). The porcupine remains were discovered in the caves of the Southern Urals. Bone remains of *H. brachyura vinogradovi* were also found in the MIS3 deposits of the Altai caves (Strashnaya, Razboynichiya and Ust-Kanskaya) (Kuzmin et al., 2017). In the Palaearctic the majority of the fossil porcupine sites are located outside its modern range (Tong, 2008; Kuzmin et al., 2017). Currently, the Makhnevskaya Ledyanaya Cave is the most northern site where the porcupine remains have been discovered. If we consider the modern ranges of the Eurasian porcupines, this site is close to the northern boundary of the Indian porcupine (*Hystrix indica)* habitat. However, small dimensions of the skull from the Makhnevskaya Ledyanaya Cave (Baryshnikov, 2003) identify it as *Hystrix brachiura.*

Cohabiting Malayan and Indian porcupines (North-East of India) prefer humid tropical broad-leaved and evergreen forests, and have a wide temperature tolerance range(from 0° to 38°C) (Talukdar et al., 2019). Based on the modern geographic distribution of representatives of the family Hystricidae, fossil remains of the Pleistocene porcupines can be used as indicators of a warm climate (Tong, 2008).

Dimensions: Table 5.
Order Carnivora Bowdich, 1821
Family Felidae G. Fisher, 1817
Genus *Panthera* Oken, 1816
Panthera spelaea fossilis (v. Reichenau, 1906)
Fig. 9.

Table 4
Measurements (mm) of the upper (M) and lower (m) molars of three species of mice. Makhnevskaya Ledyanaya Cave, sectors A, B, C.

Measurements/species	*Apodemus flavicollis*	*Apodemus sylvaticus*	*Apodemus uralensis*
L* m1	1.97 ± 0.03 (1.80–2.05) [8]***	1.75 ± 0.05 (1.50–1.95) [10]	1.54 ± 0.01 (1.50–1.55) [4]
W**m1	1.21 ± 0.02 (1.15–1.30) [8]	1.07 ± 0.03 (0.95–1.20) [10]	0.95 ± 0.00 (0.95) [4]
L m2	1.38 ± 0.02 (1.30–1.40) [6]	1.24 ± 0.04 (1.05–1.35) [7]	1.13 ± 0.08 (1.05–1.20) [2]
W m2	1.20 ± 0.03 (1.15–1.35) [6]	1.11 ± 0.04 (0.90–1.25) [7]	0.98 ± 0.03 (0.95–1.00) [2]
L m3	1.17 ± 0.02 (1.10–1.20) [6]	–	–
W m3	1.05 ± 0.02 (0.95–1.10) [6]	–	–
L m1-3	4.44 ± 0.03 (4.35–4.50) [4]	–	–
L M1	2.14 ± 0.02 (2.05–2.20) [10]	1.78 ± 0.04 (1.70–1.90) [4]	1.68 ± 0.03 (1.65–1.75) [3]
W M1	1.40 ± 0.02 (1.35–1.50) [10]	1.23 ± 0.01 (1.20–1.25) [4]	1.20 ± 0.00 (1.20) [3]
L M2	1.40 ± 0.02 (1.30–1.50) [10]	1.25 [1]	1.23 ± 0.05 (1.10–1.35) [4]
W M2	1.29 ± 0.02 (1.20–1.40) [10]	1.29 [1]	1.11 ± 0.07 (1.00–1.30) [4]
L M3	1.08 ± 0.02 (1.00–1.15) [7]	–	0.95 ± 0.05 (0.85–1.00) [3]
W M3	0.97 ± 0.02 (0.90–1.05) [7]	–	0.87 ± 0.04 (0.80–0.95) [3]
L M1-3	4.36 ± 0.04 (4.20–4.45) [6]	–	3.58 ± 0.07 (3.50–3.65) [2]

L* – length of the molar, W** – width of the molar, *** for the legend see Table 3.

Material. Sector A. Lower teeth: p4 – 1 (dex).

Description and discussion. The cave lion, which was found along with a skull of the Asiatic black bear (*Ursus thibetanus permjak* (Baryshnikov, 2001)), was listed in the fauna composition previously (Baryshnikov, 2001). A giant skull (condylobasal length of 422 mm, zygomatic breadth of 312 mm) was found. These dimensions made it possible to identify the cave lion as *Panthera spelaea fossilis*, but no special analysis has been performed yet (Baryshnikov, 2001). Our test pit, sector A, yielded the bones and teeth of a large lion, including one intact p4. Its dimensions have been compared to p4 samples of two subspecies of the cave lion, namely *Panthera s. spelaea* Goldfuss 1810 and *Panthera s. fossilis* v. Reichenau, 1906 (Barycka, 2008; Ovodov and Tarasov, 2009; Marciszak, 2014). These features make the tooth from the Makhnevskaya Ledyanaya Cave appear similar to teeth from Mosbach, Za Hajovnou Cave, Wierzchowska Gorna Cave, and Aze Cave, which are *Panthera s. fossilis* (Sotnikova and Foronova, 2014). We may thus identify the tooth from the Makhnevskaya Ledyanaya Cave as *Panthera s. fossilis* as well.

Dimension. p4: L 30.9, W 15.9 mm.

5. Discussion

5.1. Palynological data

A total of 30 taxa of different ranks have been identified within the obtained palynoflora. Arboreal pollen is found within at least 14 taxa: *Abies* sp., *Picea* sp., *Pinus* s/g Diploxylon, *Betula* sect. Albae, *B.* sect. Nanae, *Alnus glutinosa*-type, *Quercus robur*-type, *Tilia cordata*-type, *Ulmus* sp., *Carpinus betulus*, *Corylus avellana*-type, *Lonicera* sp., *Viburnum* sp., and *Juniperus* sp. Eighteen taxa of different ranks have been identified in the groups of herbs and shrubs, assigned mainly to the family rank. Spores of prolifically spore-bearing plants – Polypodiophyta, *Lycopodium* sp. and *Sphagnum* sp. – are less diverse. Monolete spores without perispores prevail among the spores of ferns, although some spores of *Asplenium* sp., *Athyrium filix-femina*, *Dryopteris filix-mas*, *Pteridium aquilinum* have also been found.

The presence of pollen of thermophilic (*Quercus robur*-type, *Tilia cordata*-type, *Ulmus* sp., *Carpinus betulus*, *Corylus avellana*-type) and moderate boreal (*Abies*, *Picea*, *Pinus*, *Betula*, *Alnus*) species, and a lack of any tundra flora elements in the obtained spore-and-pollen spectra may indicate their interglacial nature; a clear exception is *Betula* sect. Nanae pollen. The sole presence of pollen grains of dwarf birches, with a lack of any other Arctic and Arctic-boreal flora elements, cannot indicate the glacial nature of the obtained spore-and-pollen spectra. The flora of the study area currently includes dwarf birch *Betula humilis* Schrank. that grows, among other things, on limestone rocks (Ovesnov, 1997). At the same time, pollen grains of taxa that are exotic to the modern dendroflora of the study area have been found: *Quercus robur*-type, *Carpinus betulus*, *Corylus avellana*-type.

Currently, oak (*Quercus robur* L.) and hazel (*Corylus avellana* L.) grow on the southern slopes of sloping hills and in mixed pine forests, as well as broad-leaved and coniferous-broad-leaved forests, around 150 km south of the study area (Ovesnov, 1997). Common hornbeam (*Carpinus betulus* L.) is widespread in Western Europe, the Baltic states, Belarus, Ukraine, and Moldova. The closest hornbeam habitat in Russia is in Bryanskaya Oblast, at 1500 km south-west of the study area. Hornbeam forms the second layer in the mixed broad-leaved forests and is thermophilic and shade tolerant. It prefers lime-containing hover soil (Gubanov et al., 2003).

No *Carpinus betulus* pollen has been found in the sub-recent spore-and-pollen spectra of plant communities of the southern taiga, coniferous-broad-leaved and broad-leaved forests of the Middle and Southern Urals, while single pollen grains of the *Quercus robur*-type and *Corylus avellana*-type are found within the oak and hazel ranges (Lapteva, 2013). Spore-and-pollen spectra containing pollen grains of coniferous and broad-leaved tree species of modern flora and taxa exotic to the study area (*Quercus robur*-type, *Carpinus betulus*, *Corylus avellana*-type) are indicative of warm phases of the Atlantic and Subboreal Holocene periods (Lapteva et al., 2017). However, in the Holocene, the spore-and-pollen spectra of Quercetum mixtum pollen does not exceed 10%, whereas *Tilia cordata*-type is predominant, and the pollen grains of *Quercus robur*-type, *Carpinus betulus*, *Corylus avellana*-type are singular. Spore-and-pollen spectra obtained from the cave demonstrate the abundance of Quercetum mixtum pollen reaching 20% on average, while the maximum content of each exotic taxon reaches 5%. Given a higher proportions of pollen for Quercetum mixtum and the *Quercus robur*-type, *Carpinus betulus*, *Corylus avellana*-type taxa, we can assume that the deposits in the cave were accumulated at an earlier interglacial period than the Holocene. At the same time, the obtained spore-and-pollen spectra lack pollen of taxa typical of interglacial periods of the Early and Middle Pleistocene. Thus, the taxonomic composition and percentage of pollen grains in the obtained spore-and-pollen spectra make it possible to assume that the studied cave deposits accumulated in the Late Pleistocene during the Eemian interglacial period.

Numerous detailed studies of the Eemian interglacial deposits within the territory of the East-European Plain (Grichuk, 1989; Velichko et al., 1983, 2004; 2005; Borisova, 2005; Borisova et al., 2007; Chepurnaya, 2009; Novenko and Zuganova, 2010; etc.) reveal a change of vegetation development phases that were characterized by the presence of a certain zonal type during this period. The spore-pollen diagrams of stratotypic sections of the Eemian interglacial deposits in

Fig. 8. Fossil teeth of *Hystrix brachyura*. Makhnevskaya Ledyanaya Cave, sector A. 1 – occlusal views, 2 – posterior views. M1-2 sin (A); M1-2 sin (B); M1-2 dex (C); M1-2 dex (D); the fragment of low incisor sin, lingual side (E); p4 sin (F); p4 sin (G); m1-2 dex (H); m1-2 dex (I); m1-2 dex (J); the fragment of low incisor, labial side (K).

Table 5
Measurements (mm) of the occlusal surface (lower premolars (p) and lower and upper molars (m, M)) of *Hystrix brachiura.*

Tooth, depth (cm)	p4 (2–12)	p4 (64–68)	m1-2 (20–26)	m1-2 (52–56)	m1-2 (52–56)	M1-2 (2–12)	M1-2 (44–48)	M1-2 (68–72)	M1-2 (72–76)
Class of wear	T		P		T	E	G		
L^1	7.2	7.4	7.7	6.5	7.2	6.7	6.5	6.6	7.7
W^1	5.2	4.9	5.2	5.6	5.5	5.4	6.3	6.4	7.0
L^2	6.4–7.9–9.0 [18]*		7.0–7.6–8.4 [3]		4.6–6.3–7.4 [26]	7.0–7.2–7.9 [6]	4.8–7.1–8.5 [25]		
W^2	4.7–6.2–7.1 [16]		5.2–5.7–6.4 [3]		5.6–6.6–7.6 [26]	5.3–6.1–6.8 [6]	4.9–6.2–6.9 [25]		
L^3	–		–		–	6.1 (ZIN 21918-1)	7.0 (ZIN 87577)		
W^3	–		–		–	5.9 (ZIN 21918-1)	7.6 (ZIN 87577)		

[1]Makhnevskaya Ledyanaya Cave, sector A; [2]according to Weers (1990); [3]according to Baryshnikov (2003).
* minimum-mean-maximum [quantity].

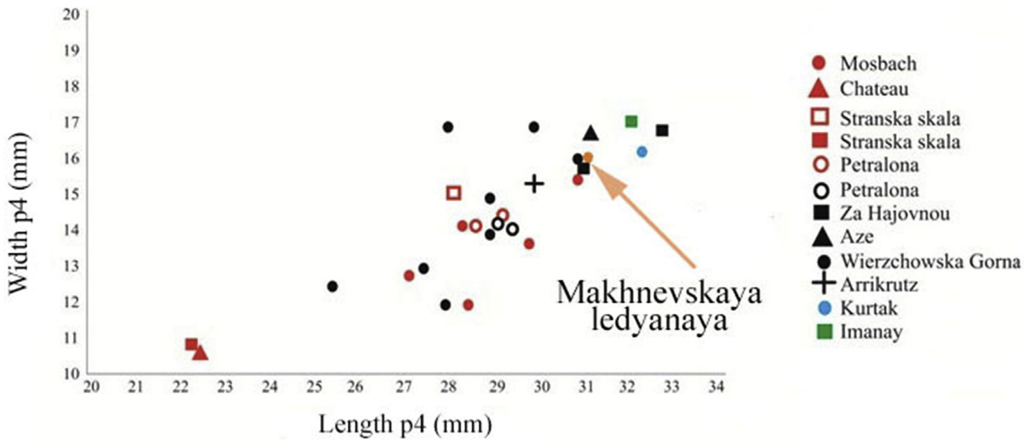

Fig. 9. Scatter diagram of length and width of p4 of *Panthera spelaea* from Pleistocene of Europe and Northern Asia sites.

Eastern Europe, for example Mikulino (Eemian) (~55°02′ North latitude) and Nizhnaya Boyarshchina (~55°19′ North latitude) in Smolenskaya Oblast (Fig. 10, Correlation A), reflect the phases demonstrating the successive changes in the forests and associated zonal types of vegetation in this area throughout the interglacial period. The previously mentioned sections of the Eemian interglacial deposits are characterized by a) a lack of spruce pollen in the optimal interglacial phases, which indicates a total disappearance of spruce forests at that time; b) the successive change in the maximum content of pollen of nemoral flora components, including *Tilia platyphyllos* and *Quercus petraea*, the abundance of which is typical of broad-leaved forests; c) maximum content of hazel pollen, etc.

To the north-east, on the eastern outskirts of Eastern Europe, the spore-and-pollen diagrams of the sections of the Eemian interglacial deposits of Suvodi (~58°04′North latitude) in Kirovskaya Oblast and Sludka (~56°28′North latitude) in Permsky Kray (Fig. 10) demonstrate a predominance of pollen of Boreal flora; specifically, *Picea*, *Pinus sylvestris*, and *Betula.* At the same time, spruce pollen can be found in all the spore-and-pollen spectra, which indicates the presence of spruce forests in the optimal phase of the Eemian interglacial period. Pollen of the representatives of the nemoral flora belongs only to *Quercus robur*, *Tilia cordata, Carpinus betulus* and *Ulmus*, the total maximum content of which is 16%. This indicates that boreal forests with nemoral components dominated this area during the Eemian interglacial period (Grichuk, 1989).

Unlike sections from the central part of Eastern Europe, the spore-and-pollen spectra obtained from the Makhnevskaya Ledyanaya Cave (Fig. 10, Correlation D) are predominated by pollen of the boreal taxa, while pollen of the nemoral flora belongs to *Quercus robur*, *Tilia cordata, Carpinus betulus* and *Ulmus*. The total content of Quercetum mixtum pollen is 15–20%. At the same time, linden pollen grains prevail among the components of the nemoral group, which makes them similar to the sections of the Eemian deposits in the Southern Urals (Yakhimovich et al., 1973, 1988). The palynological material from the Makhnevskaya Ledyanaya Cave enables us to trace the replacement of birch forests with coniferous and broad-leaved species by spruce forests with occurrences of birch, fir tree and broad-leaved species. Birch forests may have prevailed in the cryoxerotic stage, while mixed coniferous-broad-leaved forests with a predominance of spruce may have spread in the thermohygrotic stage.

5.2. Faunal data

Remains of the representatives of the following orders have been found in the mammal fauna: Eulipotyphla, Chiroptera, Lagomorpha, Rodentia, Carnivora, Perissodactyla and Artiodactyla. Bones of large mammals are inconsiderable in number, and certain horizons lack them at all. For other vertebrates, numerous fragments of amphibian bones have been found. The teeth of small mammals are abundant (insectivorous mammals, chiropterans and rodents), and have been found in all the horizons (Table 1). The following elements have been identified for the small mammal fauna: 16 rodent species (of which 12 are typical forest inhabitants), 8 species of insectivorous mammals, 4 taxa of bats and 2 taxa of lagomorphs. Red-toothed shrews (genus *Sorex*) are abundant among insectivorous mammals, northern Bats (*Eptisicus nilssonii*) are the most common bat type, whereas red-backed voles (genus *Craseomys,* genus *Myodes*) and field voles (genus *Microtus*) are the most common rodents. Bones and teeth of the small cave bear (*Ursus savini*) are the most abundant among large mammals.

In the lowest horizons of the deposits from sector A, corresponding to palynological zone PZ–1 (72–81 cm), the total sample of small mammal remains is minimum (98 specimens), which results in the lowest species diversity (7–13 species). The deposits corresponding to PZ–2 (52–72 cm) contain 2079 isolated teeth and jaws of small mammals with taxa ranging from 16 to 24. The following species dominate these deposits: short-tailed vole *Microtus agrestis* (13.6–22.6% of total sampled bone remains), root vole *Alexandromys oeconomus* (13.5–19.3%), northern red-backed vole *Myodes rutilus* (9.1–24.3%) and common shrew *Sorex araneus* (5.4–10.5%). Teeth of the forest dormouse *Dryomys nitedula*, red squirrel *Sciurus vulgaris*, least shrew *Sorex minutissimus* and the bulk of teeth of wood mice, Eurasian water vole *Arvicola amphibius* and porcupine *Hystrix brachyura* have been found at this depth. At a depth of 32–52 cm (PZ–3), we have discovered 1665 remains of small mammals and recorded the lowest taxonomic diversity (14–17 taxa). Short-tailed voles (9.3–18.1%) and root voles (5.6–18.1%) remain the dominant species. However, grey red-backed voles *Craseomys rufocanus* (5.6–14.2%) have become the most numerous among forest voles, while taiga shrew *Sorex isodon* (3.4–9.3%) and Laxmann's shrew *Sorex caecutiens* (2.6–9.9%) are most common among red-toothed shrews. The proportion of wood lemming *Myopus schisticolor* remains (9.2–14.6%) has significantly increased. These species are also dominant in the most upper deposits of the cave (PZ–1) (1863 remains and 15–16 taxa). Bones of forest species prevail among the remains of small mammals, which is confirmed by the palynological analysis indicating the predominance of forests of different types during the formation of deposits in the cave. Thus, palynological and faunistic analyses generally present similar results in terms of the criteria for selecting biostratigraphic zones. Poor species composition and low abundances of small mammals are typical of this period, as birch forests and meadows prevailed in the area surrounding the cave. The next period with a higher proportion of broad-leaved forests is characterized by a maximum species diversity, with occurrences of exotic thermophilic mammal species (yellow-necked wood mouse, forest dormouse, porcupine). With further growths of coniferous forests, the species

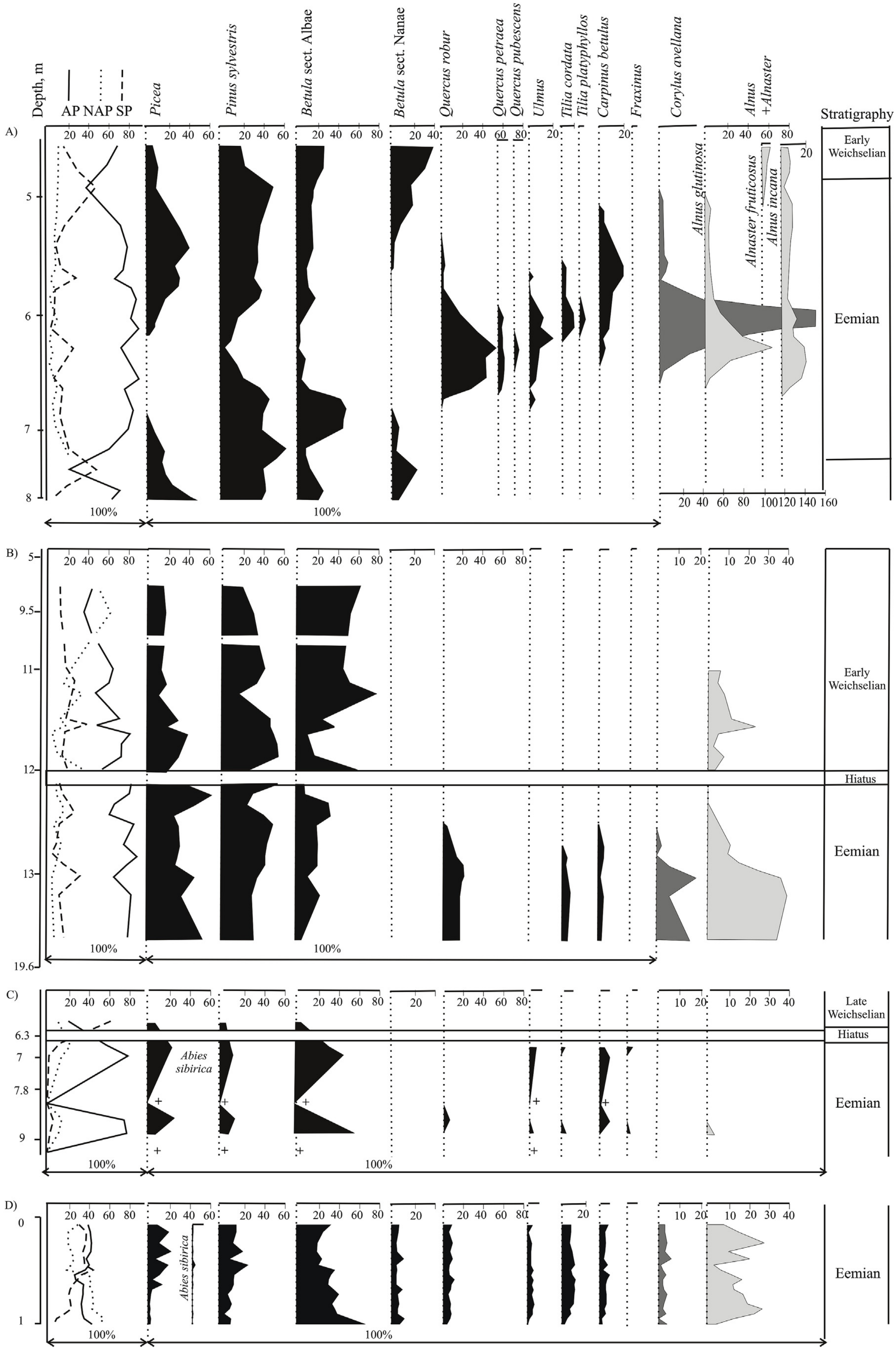

Fig. 10. Changes in the pollen content of the main forest-forming species in the spore-pollen diagrams of sections of sediments of the Mikulino interglacial of the East – European Plain. Geological section Nizhnyaya Boyarshchina (by: Grichuk, 1989) – A; the section Suvod (by: Grichuk, 1989) – B; the section Sludka (by: Yakhimovich et al., 1988) – C; Makhnevskaya Ledyanaya Cave – D.

diversity decreases and prevailing mammal species change, among which typical inhabitants of spruce-fir green moss forests as grey red-backed voles and wood lemmings have been recorded.

Cryoxerophilous species, namely Palaearctic collared lemmings and narrow-headed voles, that dominate the vast majority of the Late Pleistocene – Early Holocene Middle Ural faunas (Smirnov, 1993; Fadeeva and Smirnov, 2008) are extremely rare in the studied fauna. Remains of the steppe species Pica are inconsiderable in number. Certain mammal species that are exotic to the north of the Middle Urals, namely the bicolored white-toothed shrew, porcupine, forest dormouse, yellow-necked mouse, wood mouse and European badger, have been identified. Their modern ranges extend hundreds to thousands of kilometers from the cave. Generally, the mammal fauna of the cave deposits is typical of the forests with broad-leaved species.

A total fifteen locations are indicated for the territory of Eastern Europe in the review of the Eemian faunas of mammals (Markova and Puzachenko, 2018). The analogues of the studied small mammal fauna are faunas from the localities from Eastern Europe, namely Timoshkovichi (Motuzko, 1985), Borisova Gora (Sanko and Motuzko, 1991), Cheremoshnik (Agadzhanyan and Erbaeva, 1983) and Krasny Bor (Yakovlev, 1996); these areas yield a wide assortment of small mammal species (Eurasian red squirrel *S. vulgaris,* wood mouse/yellow necked mouse *Apodemus* ex gr. *sylvaticus-flavicollis*, bank vole *Myodes glareolus*, field vole *Microtus agrestis* and others) that are indicative of the forest zone, but very few steppe species. Regarding Western Europe, the Makhnevskaya Ledyanaya fauna is very similar to the small mammal fauna from layer 14 of the Biśnik Cave (Poland), dated to the boundary between the Middle and Late Pleistocene (Socha, 2014). Finding the analogues of the area's large mammal fauna is difficult due to the taphonomic peculiarities of the locality. The presence of extinct species (*Ursus savini*, *Panthera spelaea fossilis*, *Stephanorhinus kirchbergensis, Bison priscus*) make it possible to date deposits of the Makhnevskaya Ledyanaya Cave to the Pleistocene.

Palynological data and the taxonomic composition of the mammal fauna indicate that during the formation of deposits and accumulation of bone remains, forests with broad-leaved species were widespread in this area. This finding represents an Interglacial landscape. Open and semi-open landscapes were typical of the territory of Eastern Europe and the Urals in the glacial period (Grichuk, 1989). SDQ values of the teeth of Eurasian water voles correspond to those of water voles from the localities dated to the end of the Middle Pleistocene and the Late Pleistocene (Kolfschoten, 1990; Koenigswald and Heinrich, 1999; Kalthoff et al., 2007). There was only one interglacial instance, namely the Eemian (MIS 5e), during this period (MIS 6-2) (Cohen and Gibbard, 2019).

6. Conclusion

The cross-disciplinary research allowed us to correlate palynological and faunistic data and reliably reconstruct the environmental conditions for when the deposits of the remote grotto of the Makhnevskaya Ledyanaya Cave (north of the Middle Urals) were formed. A predominance of forest rodent species (including thermophilic porcupine, forest dormouse, yellow-necked mouse), abundances of insectivorous mammals (including hedgehog and bicoloured white-toothed shrew), amphibians and reptiles, and the presence of taxa (oak, hazel, hornbeam) exotic to this area in the palynological spectra allow us to reliably date the host deposits to the Eemian interglacial period (Mikulino, Kazantsevo, MIS 5e). Currently, the study area is the northernmost locality in the world dated to this period that includes numerous remains of vertebrates and rich spore-and-pollen complexes.

Declaration of competing interest

The authors confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

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