Environmental changes in the Middle Urals during Briansk interstadial: Makhnevskaya-2 cave (MIS 3, Russia)

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ABSTRACT

The results of the comprehensive study of zoogenic deposits in the Makhnevskaya-2 Cave (the north of the Middle Urals) made it possible to reconstruct gradual changes in the flora and fauna of the local territory during the Middle Valdai (Briansk) interstadial (MIS 3). The formation of deposits passed through three stages, which differ in proportions of tundra, steppe, and forest vegetation components as well as in proportions of multiple taxa *Dicrostonyx torquatus*, *Microtus gregalis*, Lemmini *gen.* The dental morphological characteristics of two species of rodents (*Dicrostonyx torquatus*, *Microtus gregalis*) helped identify biostratigraphic markers of the studied period of the Late Pleistocene.

1. Introduction

The Middle Weichselian (Middle Valdai) or MIS 3 (Marine Isotope Stage 3) is a moderate climatic interval between the two cold maxima of the Last Glacial Period (LGP); it is characterized by frequent and abrupt climate shifts (Chebotareva and Makarycheva, 1974; Dansgaard et al., 1993, Van Andel, 2002; Shik et al., 2006; Kindler et al., 2014; etc.). The late part of this period (33-24 thousand years ago) is known as the Briansk interstadial in Eastern Europe (Chichagova and Cherkinsky, 1993), the Denekamp-Interstadial in Western Europe (Holland, Germany), and the Grand Bois interstadial (France) (Van Andel and Tzedakis, 1996).

Within the Briansk interstadial, on the territory of Eurasia, there were identified eight paleo-theriocomplexes, which are characterized by a mixed, non-analogue species composition of mammals (Markova et al., 2010). In various combinations, these complexes include mammals, which currently can be found in different natural zones (tundra, steppe, forest). The Urals hosts "the Urals montane mammoth assemblage", which includes 31 mammal species *Coelodonta antiquitatis, Equus caballus, Rangifer tarandus, Bison priscus, Ovibos pallantis, Saiga tatarica, Panthera spelaea, Alopex lagopus, Canis lupus, Vulpes vulpes, Mustela erminea, Mustela eversmanni, Ursus spelaeus, Spermophilus superciliosus, Marmota bobac, Allocricetulus eversmanni, Arvicola amphibius, Craseomys rufocanus, Myodes glareolus, M. rutilus, Cricetulus migratorius, Dicrostonyx gulielmi, Lemmus sibiricus, Eolagurus luteus, Lagurus lagurus, Microtus*

agrestis, Alexandromys middendorffii, A. oeconomus, Microtus gregalis, Lepus tanaiticus, Ochotona pusilla. The Ural territory extends for more than 2000 km, and each section of this territory has its own distinctive characteristics of the fauna development. In the Northern Trans-Urals (the location of Cheremukhovo), in deposits of the Briansk interglacial period, there were found 10 taxa of small mammals significantly dominated by collared lemmings (Strukova et al., 2006; Teterina, 2009). In the Middle Trans-Urals (Rechkalovo, Nikitino, Nizhnyaya Tavda), there were found faunas (8–14 small mammal species) dating back to the final period of the Briansk interstadial and dominated by steppe lemmings and narrow-skulled voles (Strukova, 2002). In the South Pre-Urals, this period is represented by Uteymullino II deposits, which also demonstrated the dominance of steppe lemmings and narrow-skulled voles (Danukalova et al., 2007; Yakovlev, 2009), as well as Gornovo deposits with multiple fossil bones of root voles, steppe lemmings and narrow-skulled voles (Yakhimovich et al., 1987).

In the north of the Middle Pre-Urals, deposits containing the large number of vertebrate bone remains were found in the Makhnevskaya-2 cave in 2004–2005 (Fadeeva, 2005). The species compositions of the identified mammals and proportions of species' bone remains in the specified reference horizons of the deposits are remarkably similar. According to the results of radiocarbon dating the cave deposits were accumulated during the final stage of MIS 3 of the Late Pleistocene. The core fauna (up to 86% of the total number of bones) is represented by three taxa (*Microtus gregalis* (21.1–29.1%), *Dicrostonyx torquatus*

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(15.3–33.9%), Lemmini *gen.* (18.9–28.4%)). Intrazonal species of rodents account for comparatively smaller proportions in this fauna (*Alexandromys oeconomus* (5.0–15.6%) and *Arvicola amphibius* (0.6–4.5%) и *Alexandromys middendorffii* (1.5–5.5%). The number of other species present in the deposits is insignificant (*Sorex tundrensis*, Chiroptera, *Ochotona* sp., *Spermophillus* sp., *Sicista* sp., *Sciurus vulgaris*, *Craseomys rufocanus*, *Myodes* sp., *Lagurus lagurus*, *Cricetus cricetus*, *Cricetulus migratorius*, *Microtus* ex gr. *arvalis – agrestis*). In 2019–2020, new excavation of zoogenic deposits in the above cave were carried out for detailed analysis of the formation of deposits containing numerous bone remains and for specification of chronological boundaries of the fossil faunal assemblage. The results of the studies are presented in this work.

2. Background

The Makhnevskaya-2 Cave (59° 26′ 59.4″ N 57° 41′ 13.5″E) is located in the nature reserve known as Makhnevskiye caves (Aleksandrovsk Region, Perm Territory, Russia), in a rock area composed of light grey limestone of the Oksk-Serpukhovian layer of the Lower Carboniferous stratum (Fig. 1). The cave has two entrances: The right one leads into a wide and high vaulted grotto smoothly narrowing towards its end; the left entrance opens into a gradually narrowing corridor with occasional pockets. The corridor narrows down abruptly, opening into a large grotto (Fig. 1).

Excavations of deposits in the cave (the archaeological exploration) were performed by Ye. P. Bliznetsov in 1964 (Fig. 1, excavation sectors $A_{1, 2, 3}$). The thickness of loose deposits in the central section of the right-wing grotto is 0.20–0.25 m. Bone remains of animals are scarce; slate equine bones were found. Within the corridor shaft (1.40 × 0.80 m), the explorer identified 2 reference layers (0.35–0.40 m and 0.50 m) containing avian and mammalian bones, tentatively dated back to the

Holocene and the Late Pleistocene. The lower layer contained bones of cave bears and horses. The stratum of large stones and boulders was found at a depth of 0.9 m. No archaeological materials were found (historical records made by Evgeniy Bliznetsov, fund № 96, Record Services and Archives, Aleksandrovsk, Russia).

In 2004–2005, excavations were carried out in the entrance section of the left-wing corridor of the cave (Fig. 1, excavation sector B). The depth of the exposed deposits in the wall shaft (0.6 × 0.75 m) was 0.7 m; their depth in the central shaft (1.2 × 1.05 m) was 1.1 m. The rock is represented by clay-and-sand aggregate; with the depth, the color changes from light grey to brown and yellowish-brown. The blocky layer is located below 1.1 m. Numerous bone remains of animals were found throughout the exposed deposits (Fadeeva, 2005).

In 2019–2020, a new shaft (1.2 × 1.0 m) was excavated 1.3 m away from the southern frontier of the previous shaft (Fig. 1, excavation sector C). The thickness of the reference horizons of deposits is 4–10 cm; a total of 20 sediment samples were extracted. The excavation reached the rocky bed (the depth of 94 cm).

3. Materials and methods

3.1. Radiocarbon dating

AMS dating of the bone and the charcoal from the cave deposits was performed at the Center for Collective Use "Laboratory of Radiocarbon Dating and Electron Microscopy" of the Institute of Geography (IGAN) of the Russian Academy of Sciences and the Center for Applied Isotope Studies of the University of Georgia (The United States of America). Three radiocarbon dates were determined by the Geochronological Laboratory of the Geological Institute (GIN) RAS and the Laboratory for historical ecology of the Institute of Evolutionary Morphology and
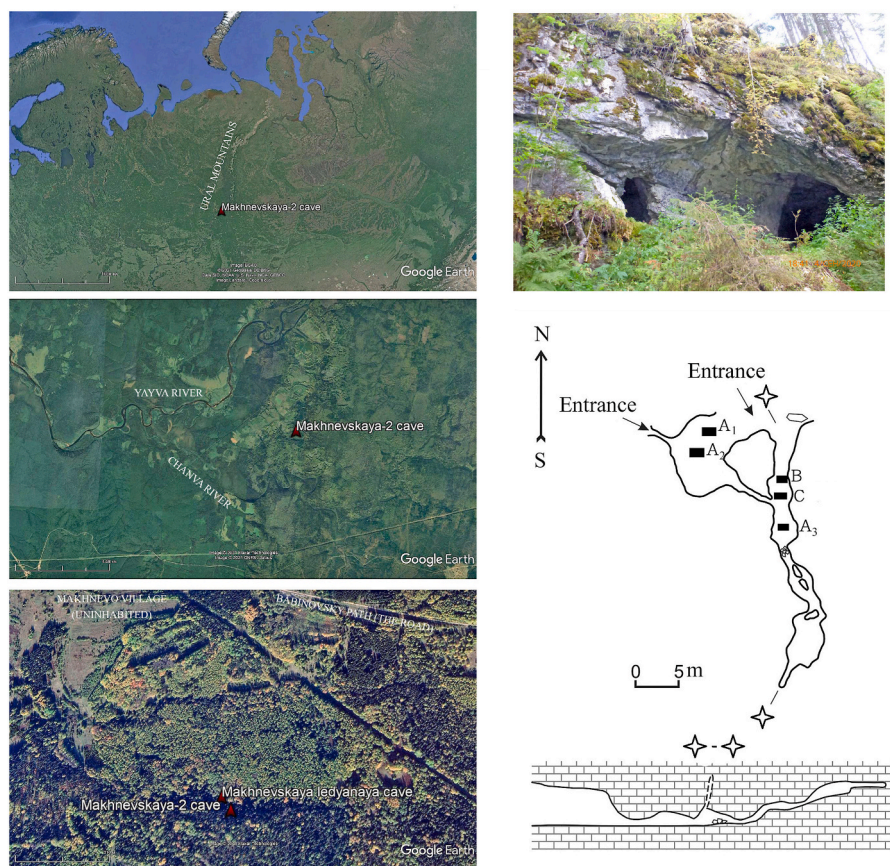

Fig. 1. The geographical position of the Makhnevskaya-2 Cave and the scheme of the cave with the designation of the excavation sectors (A, B, C). The scheme of the cave are given according to data the Bereznikovsky city speleological detachment (1974).

Ecology of Animals (IEMEA) RAS. The original 14C ages were recalibrated using the program OxCal 4.4 (Bronk Ramsey, 2008).

3.2. Lithological analysis

The particle size analysis using a sieving method was conducted for 1.5 kg samples selected within each reference layer of the excavation sector C. Each sample went through preliminary ultrasonic treatment to be further washed over sieves (0.1; 0.25; 0.5; 1.0; 2.0; 5.0; 10.0 mm) and left to dry.

Two different size fractions (>2 mm and 1–0.5 mm) were examined through a complete mineral and lithological analysis for 100 and 300 grains (clasts), respectively, depending on the quantity of fractions. The diagnostics of the rock composition was based on qualitative tests and physical properties.

3.3. Pollen analysis

A total of 20 samples were selected for the pollen analysis from each horizon of the deposits (excavation sector C). The samples were prepared to standard methods (Faegri and Iversen, 1989), with an additional 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 (The Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences – IPAE UB RAS) and the Pollen and Spore Atlas (Beug, 2004). The palynological remains in each sample were counted to 200–400 pollen grains of terrestrial plants, with a parallel record of 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 and non-arboreal pollen were assumed to be 100%. The percentage of spores was calculated from the sum of terrestrial plants pollen.

CONISS stratigraphically constrained cluster analysis was conducted for providing reference for pollen zoning. A square-root transformation was made of the data, thus the implicit dissimilarity coefficient Edwards and Cavalli-Sforza's chord distance (Grimm, 1987).

3.4. Faunistic research

A total of 60,699 mammalian teeth, jaws and bones were identified in the examined deposits (excavation sector C). To measure and study the morphological characteristics of molars and lower jaw bones, we used an MBS-10 binocular microscope and Leica MZ16 stereomicroscope. We used the specific methodology to identify lower jaw bones of representatives of the Soricidae family (Zaitsev, 1998; Fadeeva, 2016). First lower molars of grey voles (*Microtus agrestis, M. arvalis, Alexandromys middendorffii*) were identified with the help of classification functions (Markova and Borodin, 2005). All teeth measurements were taken only on the normally preserved teeth without lateral abrasion facets on prisms and without traces of rounding. All the first lower molars of narrow-skulled voles (*Microtus gregalis*) were divided into three morphotypes (*gregaloid, gregaloid-microtid, microtid*) based on the combination of re-entrant angles on both sides of paraconid complex (Bol'shakov et al., 1980). The species identity of isolated teeth of bank voles (genera *Craseomys, Myodes*) was identified by size characteristics of the second upper molar (M2) that can be diagnosed with the highest accuracy (Borodin et al., 2005; Borodin, 2009). The first and second upper molars (M1, M2) of collared lemmings (*Dicrostonyx torquatus*) were classified as the *simplicior, henseli, torquatus* morphotypes, where differences are manifested in different degrees of development of the enamel cutting edge in the proximal portion of the sixth (M1) and fifth (M2) dentinal triangles (Smirnov et al., 1997). The species identification of teeth of ancient brown lemmings (Lemmini *gen.*) was based on the size and morphological characteristics of third upper molars (Smirnov et al., 1997; Ponomarev et al., 2011, 2015).

The meaning of the term "fossil fauna" was interpreted by A.K. Agadzhanyan (2009) as "a set of species of one particular locality". "Types of fauna" were considered as certain phases of the faunal development, characterized by the quantitative predominance of the certain taxa. The successive stages of the environment evolution in the cave vicinity during the Bryansk interstadial were established on the analysis of the paleoflora and the paleofauna from the deposits of the cave.

4. Results

4.1. Radiocarbon dating

The age of the sediments was determined by radiocarbon dating (Table 1). The cave sediments were accumulated during the second half of Middle Valdai (MIS 3) and the end of the Late Glacial (MIS 2).

4.2. Lithological analysis

The results of the particle size analysis show that rudaceous rocks (>2.0 mm) prevail in the upper and middle section of the deposits. Siltstones prevail at depths of 74 cm and lower. The psammitic fraction of debris (2.0–0.1 mm), together with same-size bone elements, accounts for maximum 20% of the deposit formation (Fig. 2A). This fraction is represented by three lithological zones, the middle one of which (depth 16–74 cm) is characterized by predominance of a very coarse fraction (Fig. 2B).

The composition of samples showed different formations, which were arranged into several groups by their genetic characteristics (Fig. 3). Non-carbonized remains, charcoal, shell and bone fragments were classified as organic remains.

Chemically (and mechanically) stable rocks (brought from outside) include clasts of sericite-quartz schists, silicified limestones and quartz grains. Some of them have a glossy surface and can be classified as gastroliths.

Source rocks include clasts of grey dense fine-grain limestone and fragments of calcite veinlets. Interestingly, in some of the limestone clasts, due to intergranular dissolution, peripheral sections were transformed into a loosely bound powdery aggregate. There were cases of partial and complete replacement (weathering). Hypergene rocks also include limestone clasts, which were replaced with phosphatic materials (from thin rims to complete pseudomorphs). The above group also includes sporadical nodules of iron and manganese hydroxides.

The section-wise distribution analysis of the studied genetic groups shows the following. The proportion of chemically stable rocks and minerals tends to increase from the top downward along the section. Limestone clasts are gradually replaced by weathered and phosphatized types. These data suggest that the studied deposits can be seen as a mature (and undisturbed) profile of the weathering crust, where the source carbonate material is dissolved through a reaction with organic acids (liquids) and replaced with phosphates. It was found that clasts of the fine fraction were transformed more actively. The same fraction demonstrates a few peaks of the increased number of phosphates, thus implying a certain increase in the biological activity.

The lithological analysis was used to identify the following sequence of sediments from the top downward along the section:

1. 0–16 cm light-grey clayey-sandy-grus deposits with inclusions of plant detritus, charcoal, a few fragments of phosphatized limestone. Clasts of the source limestone material prevail. On average, the bone fraction accounts for ~30% in the deposits.
2. 16–74 cm light-brown and dark-brown clayey-coarse-grained-sandy-grus deposits with inclusions of charcoal, clasts of sericite-quartz schists, silicified limestones, quartz grains, and phosphatized limestones. Generally, clasts of weathered limestone prevail. On average, the bone fraction accounts for ~74% in the deposits.

Table 1
Results of dating of Makhnevskaya-2 cave sediments (excavation sectors B, C): radiocarbon dates obtained from mammal bones and charcoal.

| Excavation sector	Depth (cm)	Reference no.	^{14}C yr, BP (1σ)	Cal BP	Material	References
B	20–30	IEMEA-1377	11 146 ± 282	68.3% probability cal BP 11316–11348 (3.6%) 10870–11303 (61.3%) 10821 - 10851 (3.4%) 95.4% probability cal BP 11768–11783 (0.2%) 10662 - 11658 (94.8%) 10550 - 10584 (0.5%)	Bones of small mammals	Fadeeva and Smirnov (2008)
	40–50	GIN-14242	24 760 ± 200	68.3% probability cal BP 26858 - 27212 95.4% probability cal BP 26644 - 27558	Bones of small mammals	This article
	50–70	IEMEA-1376	24 811 ± 426	68.3% probability cal BP 26701–27704 95.4% probability cal BP 26139 - 28060	Bones of small mammals	Fadeeva and Smirnov (2008)
C	20–24	IGAN-9035	34 545 ± 170	68.3% probability cal BP 37514 - 37902 95.4% probability cal BP 37336 - 38162	Bone of *Lepus* sp.	This article
	54–59	IGAN-9038	11 950 ± 40	68.3% probability cal BP 11991–12048 (28.1%) 11880 - 11907 (10.9%) 11818 - 11864 (29.2%) 95.4% probability cal BP 11956–12075 (38.8%) 11800 - 11946 (53.8%) 11712 - 11732 (1.5%) 11664 - 11678 (1.4%)	Vegetable charcoal	This article
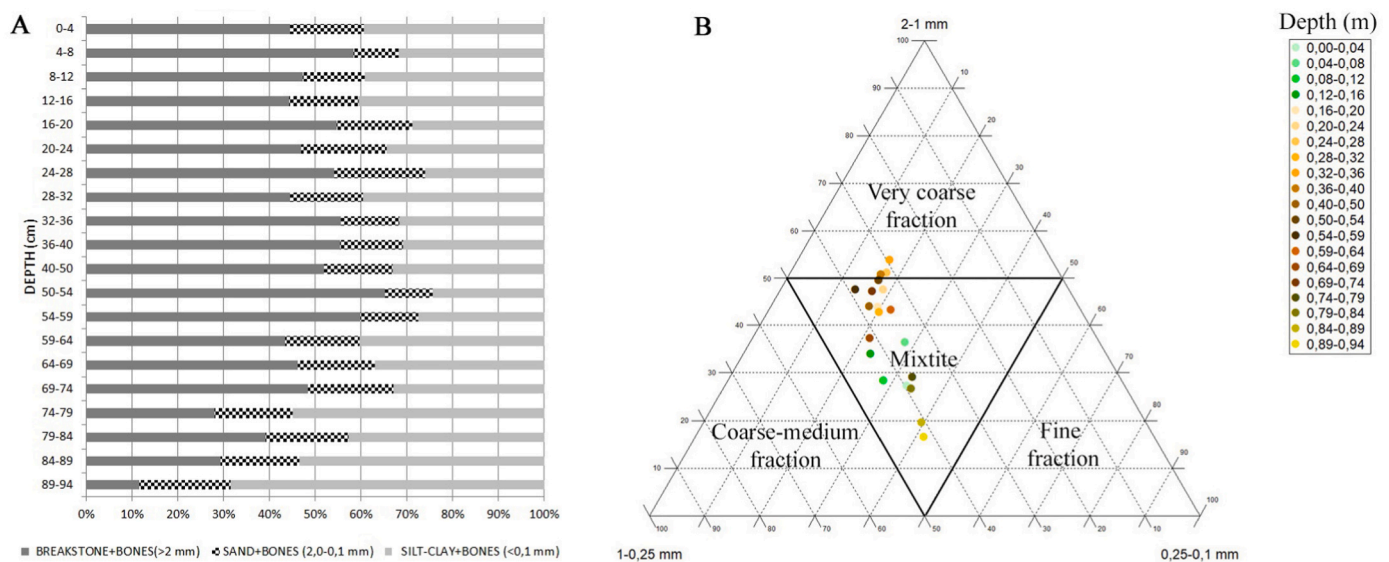
Fig. 2. Characteristics of the sediments of the Makhnevskaya-2 cave (excavation sector C). A – granulometric characteristics of bone-bearing sediments; B – psammite: granulometric classification (fields according to Silaev et al., 2020) and place in them sediments.

3. 74–94 cm yellowish-brown grus-sandy clay with a large number of fragments of sericite-quartz schists, silicified limestones and quartz grains. Clasts of weathered limestone and phosphatized limestone prevail. The proportion of the bone fraction averages ~47% in the deposits.

4.3. Pollen data

Four local pollen zones (LPZs) were identified through the analysis of changes in the content of main dominates in the obtained pollen spectra (Fig. 4).

The LPZ M-1 (the depth of 64–94 cm) combines pollen spectra with dominant non-arboreal pollen (65-55%). The group is well represented by pollen of Polygonaceae (cf. *Polygonum bistorta*) and Poaceae. The spectra demonstrate a variety of mixed-herb pollen: Asteraceae, including *Artemisia*, Apiaceae, Caryophyllaceae, Chenopodiaceae, etc. Among arboreal pollen, the most frequent types are birch pollen (*Betula* sect. Nanae and *B*. sect. Albae accounting for 10–20%) and spruce pollen (*Picea* – 10%). There are a few *Pinus* pollen grains. There is a small

number of spores of Polypodiophyta, *Botrychium*, *Selaginella selaginoides*, *Lycopodium* and *Sphagnum*. The pollen spectra in the bases of the pollen zone at a depth of 64–94 cm are not representative; however, the discovered occasional pollen grains belong to dominant arboreal and non-arboreal pollen groups of the overlying representative pollen spectra of this LPZ.

The pollen spectra of this LPZ represent plant communities of periglacial forest-tundra-steppe communities. This can be proved by the ratio between the pollen of arboreal and herbaceous plants as well as by the presence of pollen grains and spores of boreal (*Picea* and *Betula* sect. Albae), meadow-steppe (grasses and mixed herbs, including *Artemisia*, *Ephedra*, *Knautia*) and subarctic (*Betula* sect. Nanae, Ericales and *Selaginella selaginoides*) elements. Meadow grass-mixed herb communities and brushwood were well represented. Non-grass-covered areas hosted sagebrush-goosefoot communities. Forest outliers of birch trees could be found around watersheds, together with spruce trees in lowland areas or flood plains. Pine tree did not grow within the cave area; occasional pollen grains found in the spectra were imported from afar.

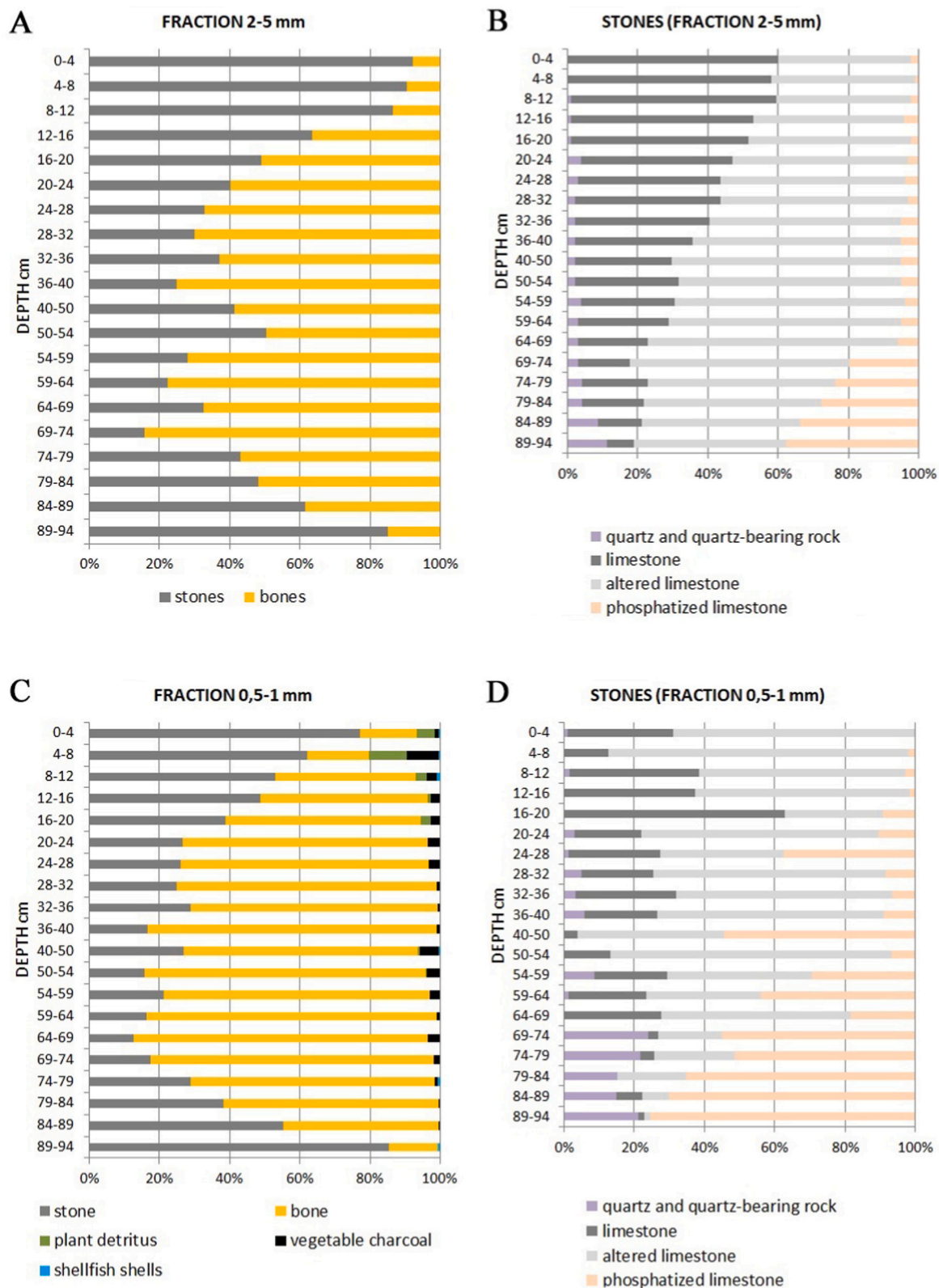The LPZ M-2 (the depth of 40–64 cm) combines pollen spectra

Fig. 3. The material composition of the sediments of the Makhnevskaya-2 cave (excavation sector C): mineral components and inclusions. A, C – the ratio of organic matter and mineral components (fractions 2–5 mm and 0.5–1 mm); B, D – mineral components in the corresponding fractions.

dominated by non-arboreal pollen (70–80%). This group is characterized by a 40–50% increase in the Poaceae pollen proportion and by a 15% increase in the Artemisia pollen proportion. There was still a wide variety of mixed-herb pollen: Asteraceae, Apiaceae, Caryophyllaceae,

Chenopodiaceae, Polygonaceae, etc. *Ephedra*, though in small numbers, can be steadily found in the pollen spectra. Among arboreal pollen, the pollen of birch trees (*Betula* sect. Nanae and *B.* sect. Albae accounting for 10–20%) is well represented, while the pollen of spruce trees is of rare
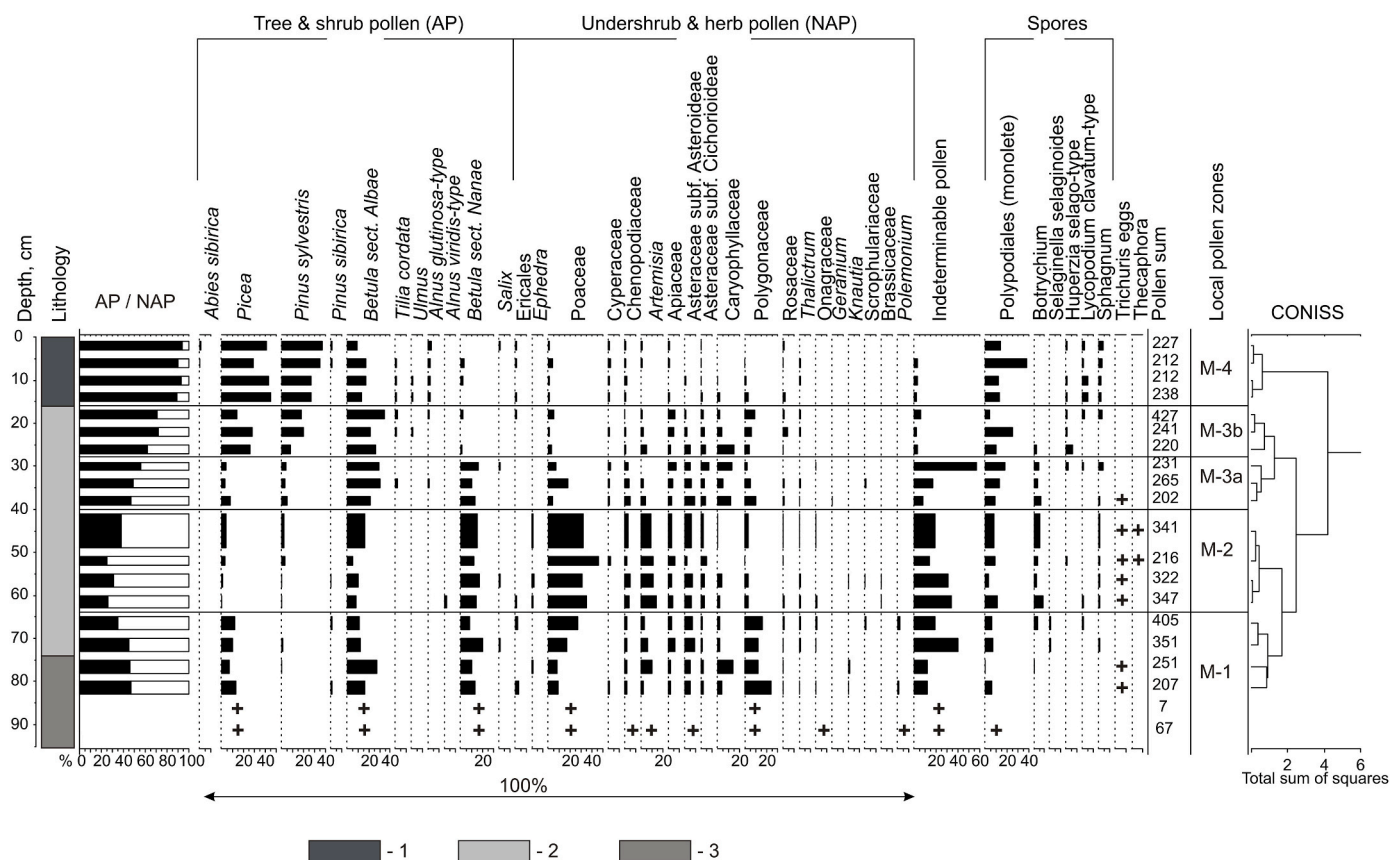
Fig. 4. Percentage pollen diagram. Makhnevskaya-2 Cave (excavation sector C). 1 – light-grey clayey-sandy-grus deposits; 2 – light-brown and dark-brown clayey-coarse-grained-sandy-grus deposits; 3 – yellowish-brown grus-sandy clay.

occurrence. Small amounts of spores of Polypodiophyta, *Botrychium*, *Selaginella selaginoides*, *Lycopodium* and *Sphagnum* were found.

Based on the presence of pollen grains and spores of boreal, meadow-steppe and subarctic elements, pollen spectra are used to describe the periglacial steppe vegetation. The fact of steppification/aridization is supported by the increased proportion of grass pollen and by the presence of ephedra, by the reduced proportion of the arboreal pollen group, including occasional participation of spruce pollen grains. There were mixed-herb and grass communities with participation of sagebrush-goosefoot groups and ephedra as well as brushwood represented by dwarf birch trees. Rare forest outliers were formed by birch trees. Conifer species were not of great significance in the vegetation cover.

The LPZ M-3 (the depth of 16–40 cm) is characterized by a gradually increasing proportion of arboreal pollen from 50% to 70%, dominated by pollen grains of *Betula* sect. Albae – up to 40%. At the same time, the LPZ M-3a pollen spectra demonstrate occasional occurrence of pollen of conifer species and a significant proportion of pollen of the shrub birch. Among non-arboreal pollen, the most representative pollen is that of Poaceae and Caryophyllaceae as well as pollen of a wide variety of mixed herbs. At the same time, *Ephedra* pollen was not found. Then, in the LPZ M-3b, the proportion of pollen of conifer species sharply increases (*Picea* – up to 30% and *Pinus sylvestris* – up to 20%), while pollen grains of the shrub birch are rare. There is pollen of thermophilic species (*Tilia cordata*, *Ulmus*, *Alnus glutinosa*-type), though in small amounts. In the non-arboreal pollen group, the abundant proportion of grass pollen decreases, though a wide variety of pollen of mixed herbs remains unchanged. There is also a gradual increase in the proportion of Polypodiophyta spores up to 20–30%. Spores of *Botrychium* disappear.

The LPZ M-3a pollen spectra are represented by mixed-herb and grass communities with participation of sagebrush-goosefoot groups and dwarf birch shrubs. The role of birch trees increased, but conifer species

were not well represented in the vegetation cover.

The LPZ M-3b pollen spectra demonstrate an increased proportion of boreal elements and a decreased proportion of meadow-steppe and subarctic elements, being indicative of gradual expansion of forest vegetation. The climate warming and increasing humidity are indirectly proved by spruce tree expansion, which can be seen by the increased spruce pollen in the spectra, as well as by the decreased role of birch shrubs. Birch forests with spruce trees and, possibly, sparse spruce forests and grass-mixed-herb meadow communities had frequent occurrence. It should be noted that occasional pollen grains of thermophilic species and spruce trees, which were discovered in the LPZ M-3b pollen spectra, differ in their preservation level from the main stock of the identified pollen and are of younger geological age.

The LPZ M-4 (the depth of 0–16 cm) combines pollen spectra dominated by arboreal pollen (around 90%). Pollen grains of *Picea* and *Pinus sylvestris* conifer species prevail – up to 40% with participation of pollen of *Betula* sect. Albae. Pollen of thermophilic species and shrub birches is present in small numbers. Occasional pollen grains of grasses and mixed herbs are found. Spores of Polypodiophyta, with participation of *Lycopodium* and *Sphagnum* are plentiful. It should be noted that most of the pollen grains in pollen spectra of this zone are well preserved unlike pollen grains in pollen spectra of the above LPZs M-1-3. Most likely, the pollen spectra of this zone are, to a larger extent, representative of Late Glacial and Holocene plant communities.

The studied pollen spectra are typical of forest vegetation. Dark coniferous taiga forests with participation of pine trees prevailed. Thermophilic species were not essential in forests, though their pollen was found in the pollen spectra.

It should be noted that the content of indeterminable pollen exceeds 20% of the total quantity of the identified pollen, sometimes reaching 60% in the pollen spectra ranging from LPZ M-1 to LPZ M-3b. This group

includes deformed, crumpled, or skeletonized pollen grains or grains lacking distinctive morphological features, taxonomic identity of which was not identified. In the LPZ M-3b and LPZ M-4 pollen spectra, the proportion of indeterminable pollen does not exceed 5%.

4.4. Faunistical data

Most of the organic matter inclusions in the cave deposits are represented by isolated teeth and bone fragments of mammals – representatives of the orders Eulipotyphla, Rodentia, Lagomorpha, Carnivora, Artiodactyla (Table 2). Fragments of bones of birds, reptiles and amphibians, fish scale and bones, clamshells were found in all the layers of the deposits. The lower deposits contain a large number of eggs of helminths belonging to the genus *Trichuris*.

Throughout the cave deposits, the teeth of small mammals are dominated by teeth of collared lemmings (*Dicrostonyx torquatus*), narrow-skulled voles (*Microtus gregalis*), and brown lemmings (Lemmini *gen.*). Besides, there are numerous teeth of intrazonal species of the tundra vole (*Alexandromys oeconomus*) and water vole (*Arvicola amphibius*). Among the teeth of red-backed voles, teeth of the grey large-toothed red-backed vole (*Craseomys rufocanus*) prevail. Fragments of lower jawbones of red-toothed shrews were found in all the layers of the deposits, and they are dominated by jawbones of tundra shrews (*Sorex tundrensis*). Teeth of the Middendorf's vole (*Alexandromys middendorffii*) and representatives of the genus *Ochotona* were found in deposits of all the reference horizons. However, the ratios of the number of found teeth of the dominant rodent taxa differ at different depths of the deposits, making it possible to identify three conditional types of fauna (Fig. 5).

The lowest reference horizons (74–94 cm) are characterized by the dominant presence of teeth of Lemmini *gen.* and *Dicrostonyx torquatus* (Fig. 5). The identity of bone remains of 23 mammalian taxa was identified (Table 2). A lower cheek tooth of the red squirrel (*Sciurus vulgaris*) was found in this section of the deposits (Fig. 6, A). First lower molars (n = 7) are provisionally assigned to the extinct species *Microtus malei* Hinton, 1907 (dentine confluence of anteroconid complex fields by the economus pattern, abundant depositions of external cementum in re-entrant angles) (Fig. 6, F). The large number of teeth of brown lemmings implies the existence of well-watered land with moss cover.

The dominant presence of teeth of *Dicrostonyx torquatus* is typical of the reference horizons of cave deposits at a depth of 16–74 cm (Fig. 5). It is in this section of deposits where the concentration of bone remains is the highest (Fig. 3 A, C). *Microtus gregalis* and representatives of the tribe Lemmini are well represented in the deposits and are codominant taxa. The species richness of mammals' representatives is relatively high – 33 taxa were identified (Table 2). There were found bone remains and teeth of northern birch mice (*Sicista betulina*) (Fig. 6, C), the species identity of which is defined by elliptic occlusal contours without pronounced concavity from the buccal side (between the protoconid and the hypoconid) of the first lower molars (Kalthoff et al., 2007) as well as by the presence of extra spurs (Kowalski, 1979). The teeth are of small sizes (m1: L 1.05–1.15 mm [n = 5]; 0.8–0.825 mm [n = 5]), which are within the range of morphometric variations of *Sicista betulina* (Pucek, 1982; Oppliger and Becker, 2010). In their fossilization, teeth of *Mus* sp. (L m1 1.35 mm; 1.4 mm; W m1 1.4 mm; 1.4 mm; Lm2 1.4 mm; W m2 1.4 mm) do not differ from teeth of other species found in the lower and middle deposits of the cave (Fig. 6 B). At the same depth of the deposits, there were also found teeth of representatives of the *Marmota* and *Spermophilus* genera (Fig. D, E). Isolated teeth (m1) of *Microtus malei* were found at the depth of 50–74 cm. The dominance by the cryoxerophilous species of *Dicrostonyx torquatus* and the codominance by the xerophilous species of *Microtus gregalis* is typical of more arid conditions.

The uppermost reference horizons of the deposits (0–16 cm) are mostly represented by teeth of *Microtus gregalis* (Fig. 5); 26 taxa of mammals were identified (Table 2). The proportion of the formerly dominant species *Dicrostonyx torquatus* is the lowest among numerous species. The above proportions of dominant species of rodents may have

resulted from mixing between Middle Valdai and Late Glacial bones.

4.5. Taxonomic notes

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer, 1817
Subfamily Arvicolinae Gray, 1821
Genus *Microtus* Lataste, 1887.
Microtus (Stenocranius) gregalis Pallas, 1779
Fig. 7.
Material: 2,285 first lower molars (m1).

The ratios of the three identified groups of morphotypes of the first lower molars (*gregaloid, gregaloid-microtid* and *microtid*) in the representative samples from the reference horizons of the Makhnevskaya-2 Cave deposits (excavation sector C) show that teeth with a more complex structure (*microtid* morphotype) account for less than half of the total number, which is also quite typical of samples taken from Rasik Grotto (B29-33) and representing the middle of the Late Pleistocene (Fig. 7). The Late-glacial teeth samples from this territory (Rasik Grotto, B15-29c) were characterized by pronounced dominance by teeth of *microtid* morphotype (>50%).

Tribe Lemmini Gray, 1825 (Miller, 1896).
Fig. 8.
Material: 12,939 M, including 2,552 upper third molars (M3).
Morphometric study 176 M3.

Considering the difficulties of specific differentiation of upper third molars of representatives of the tribe Lemmini *gen.*, we focused on the morphometric analysis of the respective material from several reference horizons of the upper, middle and lower sections of the deposits. The analysis of the morphometric data of the samples of upper third molars from reference horizons at different depths (0–16 cm (n = 74), 36–40 cm (n = 32) и 79–84 cm (n = 70)), including the discriminant analysis (Smirnov et al., 1997) and the WM3/LM3 × 100 index (Ponomarev et al., 2011), demonstrated that teeth belonging to *Lemmus sibiricus* prevail in the samples. Most of them belong to morphotype M3/1, some teeth have morphotypes M3/2 and M3/4 (according to classification by Ponomarev et al., 2015). The teeth identified by using the method offered by Smirnov et al. (1997) as *Myopus schisticolor* (posterior probabilities of species identity exceed 75%), in their vast majority, belong to morphotype M3/1. A few teeth from this group have morphotype M3/7, which was found only in representatives of *Myopus schisticolor*. However, the criteria for measuring the extent of flattening and elongation of morphotypes of the posterior unpaired loop M3 are quite subjective and accurate visual differentiation, for example, of M3/1 and M3/7, can be complicated (Ponomarev et al., 2015). In total, indices for teeth of the contemporary *Lemmus sibiricus* and *Myopus schisticolor* from different parts of the habitat overlap within the 52.4–60.9 range (Ponomarev et al., 2011). Based on these summarized data, we can conclude that in the studied fossil samples, most of the teeth have indices with values below the minimum overlap threshold and belong to the Siberian lemming, while the parameters of the other teeth fall within the overlap zone (Fig. 8).

Tribe Dicrostonychini Kretzoi, 1955
Genus *Dicrostonyx* Gloger, 1841
Dicrostonyx torquatus Pallas, 1778
Fig. 9.
Material: 17,864 M. The morphotype is identified for 499 M1 and 428 M2.

The lack of cementum in re-entrant angles of prisms of cheek teeth of collared lemmings contributes to their rapid destruction. Among all the rodents' teeth found in the cave deposits, teeth of collared lemmings were characterized by the highest degree of fragmentation. The completely preserved teeth account for 1.7–8.6% (of the total number of teeth) for M1 and 1.1–5.7% for M2. Therefore, the analysis of ratios of teeth morphotypes was conducted by using combined representative samples from the upper (0–16 cm), middle (16–40 cm и 40–74 cm) and

Table 2
The list of mammal species represented in deposits of the Makhnevskaya-2 Cave (excavation sector C).

SPECIES/DEPTH (cm) Глубина (cM)	89–94	84–89	79–84	74–79	69–74	64–69	59–64	54–59	50–54	40–50
Sorex araneus Linnaeus, 1758	0	0	1	0	2	0	1	2	7	2
Sorex tundrensis Merriam, 1900	1	4	2	0	4	4	15	37	2	14
Sorex minutus Linnaeus, 1766	0	0	0	0	0	0	0	0	0	1
Sorex minutissimus Zimmermann, 1780	0	0	0	0	0	0	0	1	0	0
Sorex sp.	0	0	1	0	9	1	5	21	9	7
Myotis sp.	0	0	0	0	0	0	0	1	1	0
Ochotona sp.	6	17	21	17	110	44	126	265	93	193
Lepus timidus (Linnaeus, 1758)	1	5	0	6	14	14	15	39	19	17
Vulpes lagopus Linnaeus, 1758	0	2	0	0	1	1	1	0	1	2
Vulpes vulpes Linnaeus, 1758	1	0	0	0	0	0	0	0	0	0
Ursus arctos Linnaeus, 1758	0	2	3	2	3	2	4	2	2	2
Martes sp.	0	0	0	0	1	0	2	4	0	0
Meles sp.	0	0	0	0	0	0	1	0	0	0
Mustela nivalis Linnaeus, 1766	0	0	1	3	6	2	4	6	10	12
Mustela erminea Linnaeus, 1758	0	2	2	2	6	6	1	18	1	4
Sciurus vulgaris Linnaeus 1758	0	0	1	0	0	0	0	0	0	0
Marmota sp.	0	0	0	0	0	1	0	0	0	0
Spermophilus sp.	0	0	0	0	1	0	0	2	0	3
Sicista betulina Pallas, 1779	0	0	0	0	0	0	0	2	1	0
Cricetulus migratorius Pallas, 1773	1	0	4	0	4	0	5	3	8	4
Lemmini *gen.*	122	292	239	302	1610	437	1134	1901	754	1248
Dicrostonyx torquatus Pallas, 1778	66	281	291	296	2209	631	1657	3641	1094	1568
Craseomys rufocanus (Sundevall, 1846) (m1, M2)	7	16	4	4	44	18	118	150	27	39
Myodes glareolus (Schreber, 1780) (M2)	2	1	0	1	2	4	10	0	2	0
Myodes rutilus (Pallas, 1779) (M2)	0	0	0	0	3	0	8	20	2	2
Craseomys sp.*, Myodes* sp.	12	35	24	21	117	43	298	482	89	131
Lagurus lagurus Pallas, 1773	0	1	0	1	7	0	2	5	4	4
Arvicola amphibius (Linnaeus, 1758)	0	7	5	14	117	94	350	542	94	107
Alexandromys oeconomus (Pallas, 1776) (m1)	3	13	17	16	104	41	173	321	104	164
Alexandromys middendorffii Poljakov, 1881 (m1)		11	5	2	23	15	15	24	15	23
Microtus (Stenocranius) gregalis Pallas, 1779 (m1)	3	23	14	29	195	69	235	444	176	219
Microtus malei Hinton, 1907 (m1)	1	1	4	1	5	0	1	1	2	0
Microtus agrestis Linnaeus, 1761 (m1)	1	0	0	0	2	0	3	5	6	10
Microtus agrestis Linnaeus, 1761 (M2)	0	0	0	0	0	2	5	14	3	7
Microtus arvalis s.l. (m1)	0	0	0	0	5	1	3	1	0	0
M. agrestis/A. middendorffii/M. arvalis (m1)	8	5	7	5	38	13	34	60	18	37
Microtus sp.	94	327	287	401	1974	553	2385	4052	1140	1159
Mus sp.	0	0	0	0	0	0	0	2	0	0
Rangifer tarandus Linnaeus, 1758	0	0	1	1	3	3	1	2	0	0
NISP (number of identified specimens)	**329**	**1045**	**934**	**1124**	**6619**	**1999**	**6612**	**12070**	**3684**	**4979**
N (number of taxa)	**15**	**18**	**20**	**18**	**27**	**22**	**28**	**30**	**26**	**22**

SPECIES/DEPTH (cm)	**36–40**	**32–36**	**28–32**	**24–28**	**20–24**	**16–20**	**12–16**	**8–12**	**4–8**	**0–4**
Sorex araneus Linnaeus, 1758	0	1	0	0	0	0	2	0	0	0
Sorex tundrensis Merriam, 1900	1	0	10	4	10	3	3	0	1	1
Sorex caecutiens Laxmann, 1788	0	0	0	0	1	0	1	0	0	0
Sorex sp.	1	2	4	9	8	1	0	1	1	5
Ochotona sp.	61	17	109	100	199	65	74	28	8	11
Lepus timidus (Linnaeus, 1758)	4	7	27	12	10	2	7	2	4	7
Vulpes lagopus Linnaeus, 1758	0	0	2	0	1	4	1	0	2	0
Vulpes vulpes Linnaeus, 1758	0	0	1	0	0	0	0	0	0	0
Ursus arctos Linnaeus, 1758	1	1	2	1	0	0	2	0	0	0
Martes sp.	0	0	1	0	0	0	0	0	0	1
Mustela nivalis Linnaeus, 1766	3	1	4	3	1	1	6	0	2	4
Mustela erminea Linnaeus, 1758	3	3	3	5	2	10	1	0	2	0
Spermophilus sp.	3	0	1	1	0	1	2	0	1	0
Sicista betulina Pallas, 1779	0	1	0	3	0	0	0	1	3	0
Cricetulus migratorius Pallas, 1773	0	1	5	3	2	0	1	0	0	0
Lemmini *gen.*	583	191	974	872	1201	447	404	117	48	63
Dicrostonyx torquatus Pallas, 1778	807	296	1280	1115	1553	549	356	110	29	35
Craseomys rufocanus (Sundevall, 1846) (m1,M2)	13	7	21	19	16	21	22	10	6	7
Myodes glareolus (Schreber, 1780) (M2)	0	1	0	0	2	2	1	3	0	0
Myodes rutilus (Pallas, 1779) (M2)	0	1	4	3	0	0	9	0	0	0
Craseomys sp.*, Myodes* sp.	30	25	133	32	82	46	67	42	26	30
Lagurus lagurus Pallas, 1773	3	0	3	1	1	0	0	2	0	0
Arvicola amphibius (Linnaeus, 1758)	25	16	69	42	62	37	33	11	9	11
Alexandromys oeconomus (Pallas, 1776) (m1)	52	34	99	87	96	52	48	35	6	7
Alexandromys middendorffii Poljakov, 1881 (m1)	5	1	5	14	14	7	1	1	1	1
Microtus (Stenocranius) gregalis Pallas, 1779 (m1)	103	48	157	149	203	73	92	27	14	12
Microtus agrestis Linnaeus, 1761 (m1)	3	1	3	2	3	2	3	0	0	0
Microtus agrestis Linnaeus, 1761 (M2)	1	2	6	3	1	7	2	3	2	2
Microtus arvalis c.l. (m1)	0	0	1	1	1	1	1	0	0	0
M. agrestis/A. middendorffii/M.arvalis (m1)	11	11	17	17	27	18	15	8	1	5
Microtus sp.	645	353	1518	1199	1482	455	604	202	109	138

Table 2 (*continued*)

SPECIES/DEPTH (cm) Глубина (cM)	89–94	84–89	79–84	74–79	69–74	64–69	59–64	54–59	50–54	40–50
***Mus* sp.**	0	0	0	0	2	0	0	0	0	0
***Rangifer tarandus* Linnaeus, 1758**	0	0	2	2	2	0	0	0	2	1
NISP (number of identified specimens)	**2358**	**1021**	**4461**	**3699**	**4982**	**1804**	**1758**	**603**	**277**	**341**
N (number of taxa)	**17**	**19**	**24**	**22**	**22**	**18**	**23**	**13**	**17**	**14**
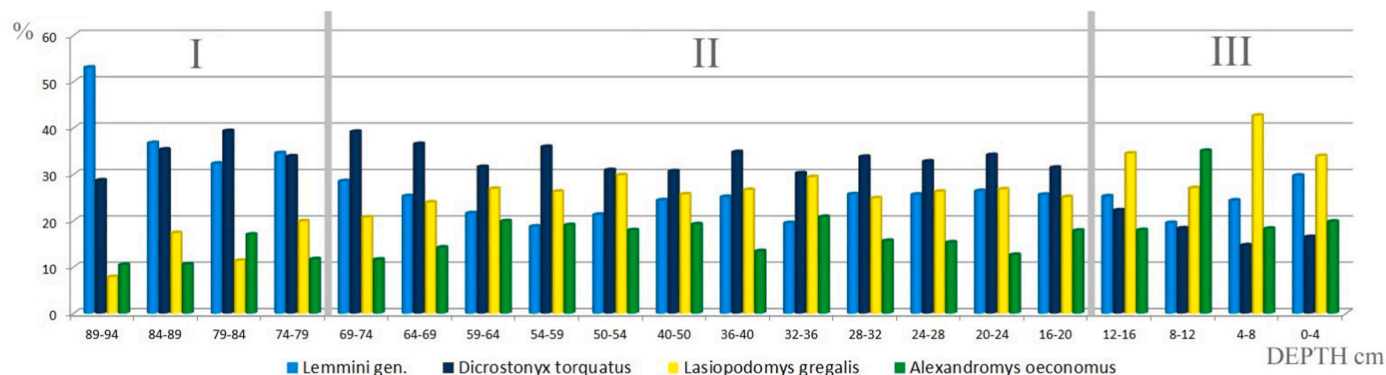
Fig. 5. The ratio of the number of teeth of the dominant rodent species in the identified groups of fossil faunas (I, II, III). Makhnevskaya-2 Cave (excavation sector C).

lower (74–94 cm) reference horizons of the deposits (corresponding to the three identified types of fauna). The analysis showed that molars of the *henseli* morphotype prevailed (Fig. 9). The similar results were shown by the morphotypical analysis of the teeth of collared lemmings from deposits of the excavation sector B. For comparison, the chart presents the proportions of morphotypes of teeth from the Rasik Grotto deposits – the Late-glacial samples demonstrate the dominance by morphs of *torquatus* and *henseli*, the Middle Valdai samples are dominated by *henseli* and *simplicior*. The morphological evolutionary stages of the studied samples are in line with the data of the paleogenetic analysis (mtDNA cytochrome *b*) (Palkopoulou et al., 2016). Most of the collared lemmings' teeth from the Makhnevskaya-2 Cave belong to the chronologically discrete line EA3, the carriers of which existed within the 22.8–32 ky BP interval; two teeth belonged to the EA2 line (42->46 ky BP). The collared lemmings' teeth from the Rasik Grotto deposits belong to the EA1 (42->46 ky BP) and EA5 (0–20,5 ky BP) clusters.

4.6. Archaeological artifact

A flint arrowhead of the late Neolithic Period (Fig. 10) was found for the first time in this location, in the upper layers of the excavated deposits (at a depth of 4–8 cm). Its grey color is typical of flint nodules, which were frequent in Paleozoic carbonate rocks of the western slope of the Urals.

5. Discussion

The abundance of fragmented bone material of vertebrate animals and numerous isolated teeth of mammals as well as the presence of helminths' eggs are indicative of the excremental origin of zoogenic deposits in the Makhnevskaya-2 Cave. Cave dwellers contributed to accumulation of bone detritus; processes of active hypergene transformation of the clastic carbonate material were detected. The small particles of charcoal, which were found in the upper and middles deposits of the cave, can be explained by local fire in the vicinity of the cave (the end of the Late Glacial). Except for an arrowhead, no traces of ancient people's presence were found in the cave.

The fauna of the studied deposits (sector C) has the composition and proportions of small mammals that are similar to the dated fauna of the deposits from the excavation sector B; the dental morphological

characteristics of dominant species are also identical. Based on the radiocarbon dates (Table 1), the studied zoogenic deposits contain bones of the mammals that lived within the Makhnevskaya-2 Cave area during the Briansk interstadial period and at the end of the Late Glacial period. Late Glacial materials are well-represented in the upper deposits in the cave, which is demonstrated not only by the radiocarbon dates, but also by well-preserved pollen grains of LPZ M-4 (0–16 cm) and LPZ M-3b (16–28 cm) found in palynozones. The comparative analysis of the upper deposit faunas and the dated Late-glacial faunas from Rasik Grotto (59°04′ N, 57°33′ E) (Fadeeva et al., 2000), which is located approximately 45 km to the south of the Makhnevskaya-2 Cave, revealed significant differences. The first half of the Late Glacial period (Rasik grotto, sediment horizons 21, 24, 27) is characterized by the dominance of collared lemmings (42.1–57.4%) and the codominance of narrow-skulled voles (35.6–45.9%), while brown lemmings are poorly represented in this fauna (2.2–4.0%). The end of the Late Glacial period was marked by a sharp change in the proportions of the above three taxa of rodents (Rasik grotto, sediment horizons 17, 18) – narrow-skulled voles became the dominant species (70.3–74.1%), brown lemmings were of rare occurrence (0.6–1.1%) and collared lemmings almost disappeared from the fauna composition (0–0.1%). The upper deposits of the Makhnevskaya-2 Cave are dominated by narrow-skulled voles (22.5–31.1%), though brown lemmings (16.2–20.2%) and collared lemmings (10.7–19.4%) are present in large quantities. The teeth of Middendorf's vole, which were found in the Makhnevskaya-2 Cave, signify the difference between the Late-glacial faunas from Rasik Grotto and the upper deposit fauna of the Makhnevskaya-2 Cave.

The upper deposit fauna of the Makhnevskaya-2 Cave belongs to the same cluster as the faunas from the middle and lower deposits of the cave (Fig. 11), thus being indicative of some interference of Late Glacial materials. Through their digging activities, the mammal predators inhabiting the cave caused mixing between the earlier (the Late Glacial period) and the older (the Briansk interstadial) materials in the upper layers of deposits. The middle and lower cave deposits, the fauna of which is more similar to the faunas of the first half of the Late Pleistocene from the Rasik Grotto deposits (sediment horizon 30), were formed during the Briansk interstadial. The Late Glacial fauna from the Rasik grotto (sediment horizons 17, 20, 21, 24, 27) differs significantly from the fauna of Makhnevskaya-2 cave and is identified as a separate isolated cluster (Fig. 11).
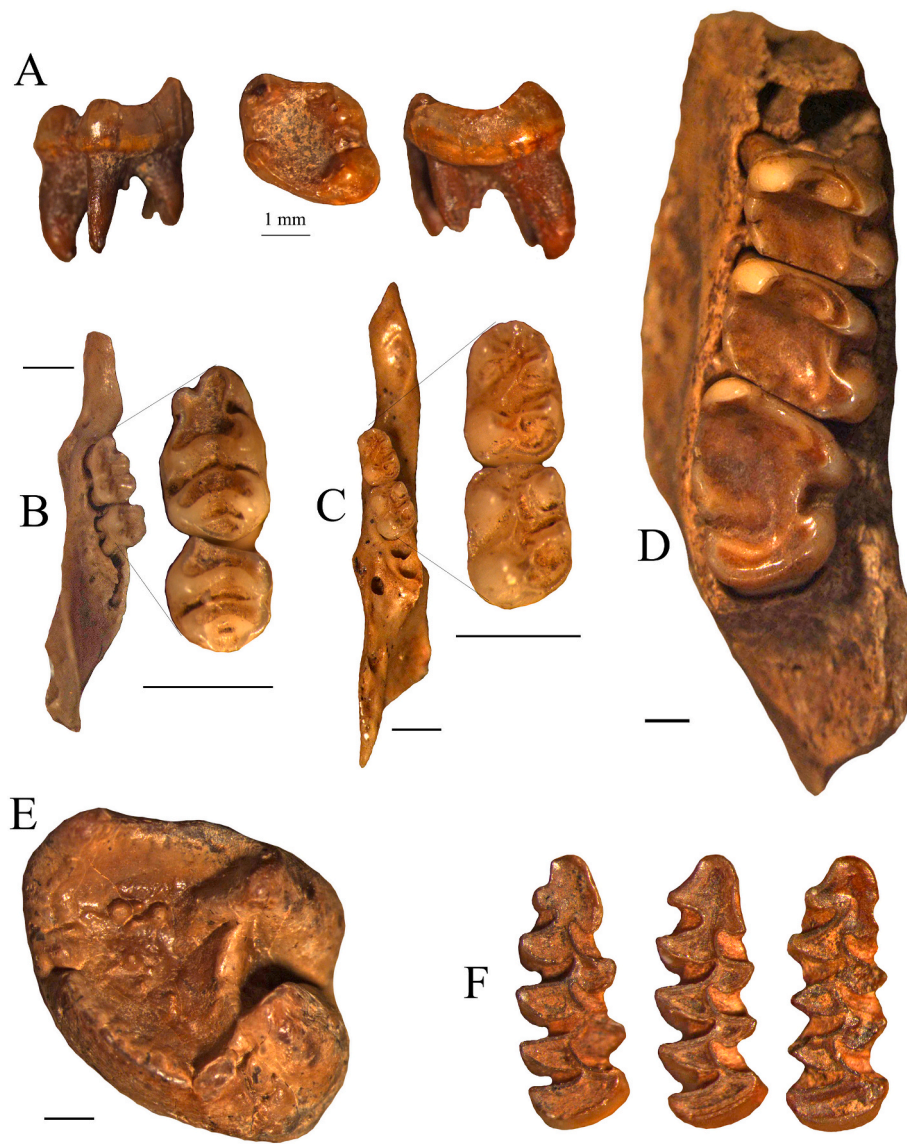
Fig. 6. Rodent teeth from the deposits of the Makhnevskaya-2 cave (excavation sector C). A – m2 dex *Sciurus vulgaris* (depth 79–84 cm); B – fragment of left mandible with m1, m2 *Mus* sp. (54–59 cm); C – fragment of left mandible with m1, m2 *Sicista betulina* (54–59 cm); D – fragment of right mandible with m1, m2, m3 *Spermophilus* sp.(40–50 cm); E – m2 dex *Marmota* sp.; F – m1 dex *Microtus malei* (69–74 cm, 79–84 cm).

By now, the Briansk interstadial is thoroughly described with the help of palynological data and radiocarbon dates from the sections of the East European Plain (Bolikhovskaya, 1995; Markova and Simakova, 1998; Simakova, 2001, 2006; etc.). The comprehensive studies showed that this period was characterized by a convoluted evolution of the vegetation and climate. It was found that the paleoflora of the Briansk interstadial included representatives of arctic and subarctic (*Armeria, Dryas, Rubus chamarmorus, Betula* sect. Nanae, *Alnus viridis*-type, *Selaginella selaginoides* and others), steppe (*Ephedra*, species of Chenopodiaceae, *Artemisia*) and taiga (*Picea, Larix, Pinus sibirica, P. sylvestris, Betula* sect. Albae) elements (Simakova, 2001, 2006).

The LPZs M-1-3a pollen spectra from the deposits of the Makhnevskaya-2 Cave also contain pollen of tundra (*Betula* sect. Nanae, *Alnus viridis*-type, Ericales, *Polemonium,* Polygonaceae и *Selaginella selaginoides*), steppe (*Artemisia, Ephedra, Knautia,* Chenopodiaceae, Poaceae), and forest (*Picea, Pinus sibirica, P. sylvestris, Betula* sect. Albae) coenotic groups. The ratio between these groups in pollen zones tends to change (Fig. 12), being affected by the dynamics in the plant communities and climate during building-up of the deposits.

The analysis of the paleofauna and paleoflora of the lower and middle cave deposits makes it possible to identify three stages that characterize the evolution of the environment in the vicinity of the cave during the Briansk interstadial.

The first stage. The LPZ M-1 pollen spectra from the lower deposits are characterized by the dominance and almost identical proportion of pollen of tundra and steppe species with participation of pollen grains of the forest group (Fig. 12, a). Such proportions are typical of pollen spectra representing periglacial forest-tundra-steppe communities (Bolikhovskaya, 1998). There were meadow grass-mixed-herb communities with steppe and tundra species as well as brushwood combined with birch and spruce forests.

The dominant species such as collared lemmings and brown lemmings were present in the lower deposits nearly in equal proportions, thus being an indirect proof of the moderately humid cold climate during the formation of this layer of deposits. The initial analysis shows that most of the studied third upper molars of lemmings from the Makhnevskaya-2 Cave deposits belong to *Lemmus sibiricus*. The employed methods of specific differentiation of teeth of the tribe Lemmini can be used for diagnosis of fossil teeth only within certain limits, considering the high level of interpopulation variability of tribe
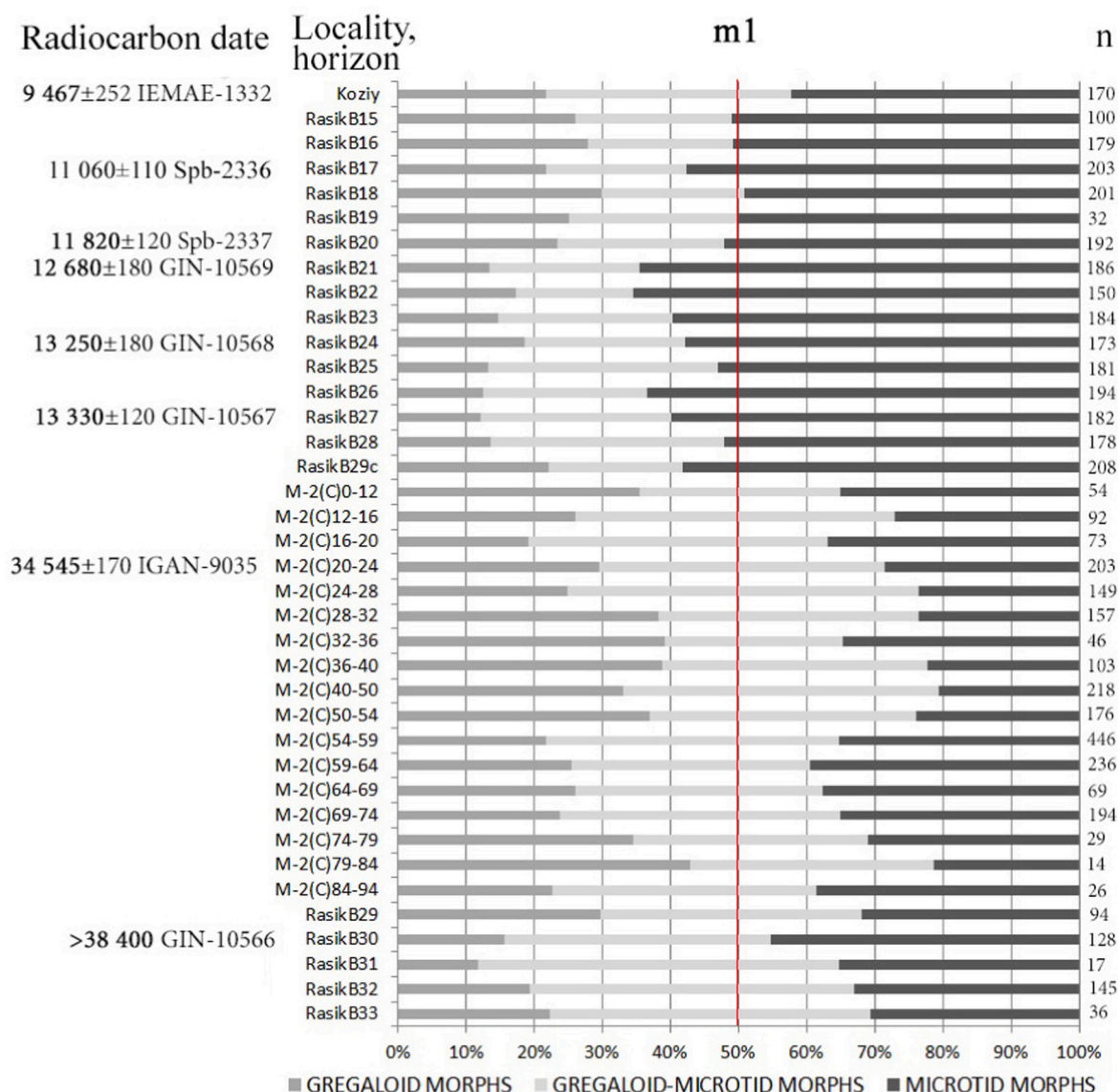
Fig. 7. Frequencies of morphotypical groups (%) of the m1 of *Microtus gregalis* from localities of Perm Pre-Urals, Russia. N – number of first lower molars (m1). Koziy – sub-rock location Koziy (59°10′N 57°31′E). Rasik – Grotto Rasik (59°04′N 57°33′E), square B, 15–33 – sediment horizons (sequential numbers). M-2 – Makhnevskaya-2 Cave (excavation sector C), 0–94 – sediment horizons (cm).

representatives. The geometric morphometric method may be more efficient for accurate identification of the species identity of fossil teeth of lemmings. This analysis helped establish the fact that *Myopus schisticolor* lived during the Late Pleistocene (MIS3) – the early Holocene in Western Europe (Arbez et al., 2021). The cohabitation of *Lemmus sibiricus* and *Myopus schisticolor* during the Late Pleistocene and the Holocene in the Perm Pre-Urals remains unclear. Most of the collared lemmings from this section of deposits, by their dental structure, can be assigned to the morph *henseli* (the stage of morphological development "*D. guilielmi* morph II" based on the classification offered by Smirnov et al. (1997)). Such fossils of the Late Pleistocene fauna where proportion of teeth of *Lemmus sibiricus* and teeth of *Dicrostonyx torquatus* are almost identical were found in Zilishche Sokola, North Trans-Urals (the first half of the Late Pleistocene), Studyonaya Cave, North Pre-Urals (Middle Valdai), Rasik Grotto, Perm Pre-Urals (Middle Valdai) (Kochev, 1993; Fadeeva et al., 2000; Teterina, 2002).

In the lower deposits, the found isolated teeth of *Microtus malei* are of special interest. First lower molars having the same morphology and previously assigned to the *Alexandromys oeconomus* species ("complex" morphotypes) were also found in other locations in Perm Pre-Urals; the

largest number of them was found in the most ancient samples within the above territory (Fadeeva, 2003). Molars assigned to *Microtus malei* were found in several middle Pleistocene locations along the Lower Irtysh in the north of Western Siberia (Smirnov et al., 1986). Teeth of this fossil species occur within the Holarctic from the Early Pleistocene to the Late Pleistocene (Gromov and Polyakov, 1977).

The found tooth of *Sciurus vulgaris* supports the data of the palynological analysis regarding the presence of spruce forests during the formation of lower deposits of the cave. This species had not been found in any known late Pleistocene faunas of the Urals. Bone remains of this species were found in interglacial deposits in the East European Plain and Urals (Yakhimovich et al., 1988; Sanko and Motuzko, 1991; Fadeeva et al., 2018).

The second stage. While the middle layer of the deposits was built up, forest areas, especially those with spruce forests, shrank, giving way to steppe elements, which had an increasing role in the communities. This is demonstrated by the reduced proportion of the forest group, especially due to the decreased content of spruce pollen, and the increased proportion of the steppe group due to the increased content of Poaceae pollen grains and steady presence of ephedra in the LPZ M-2
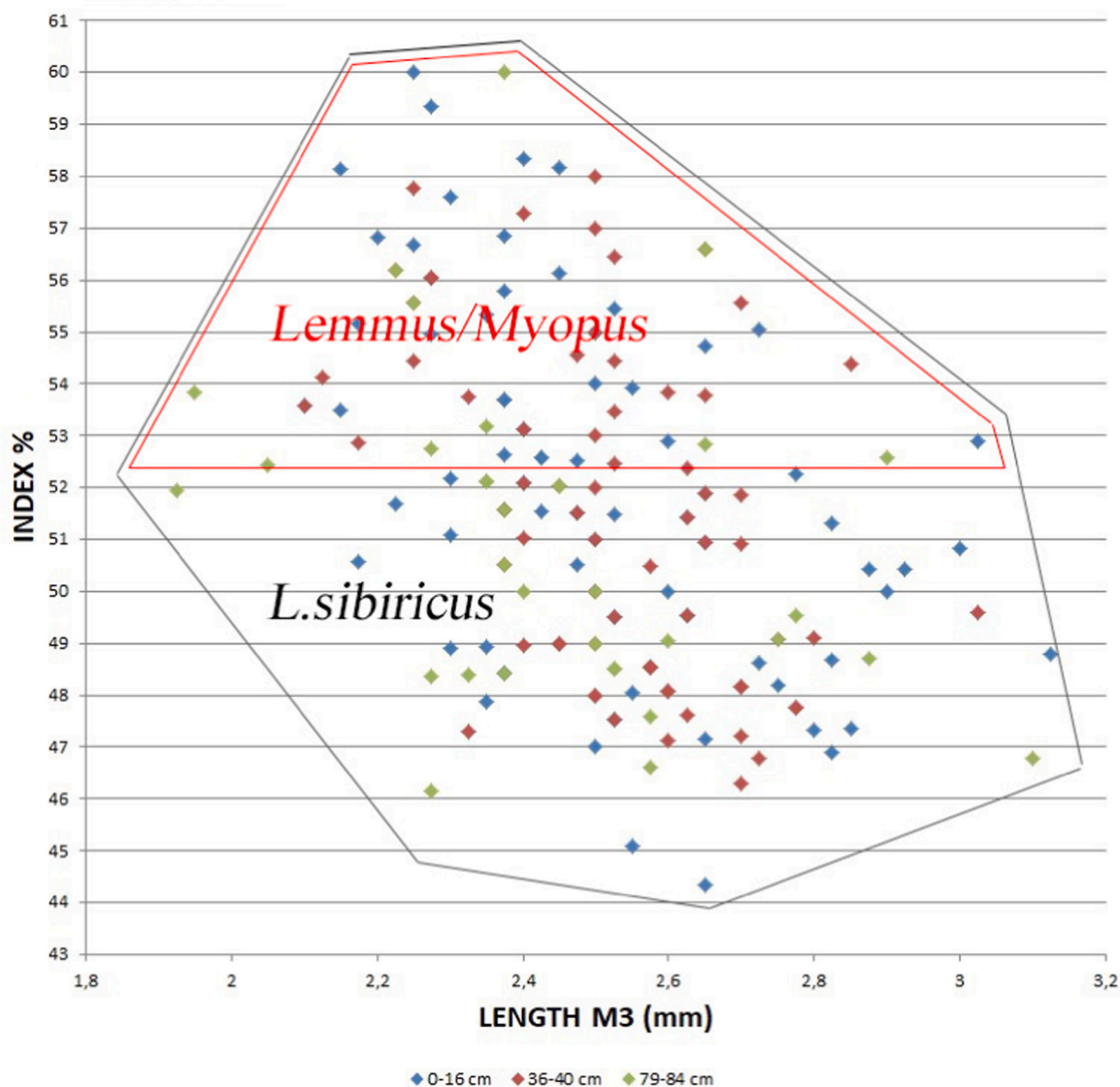
Fig. 8. Dimensions and proportions (ratio of width to length,%) M3 lemmings (Lemmini *gen.*) from the deposits. Makhnevskaya-2 Cave (excavation sector C).

pollen spectra (Figs. 4 and 12, b). Such proportions of pollen of three coenotic groups are typical of pollen spectra of tundra-steppe communities (Bolikhovskaya, 1998). Well-represented communities included mixed-herb-grass and ephedra communities with participation of birch forest, including a combination of tundra and steppe species. Most likely, such changes in the vegetation are associated with lower temperatures and climate aridization.

The third stage. Subsequently, the proportion of pollen of the forest group increases and the proportion of the steppe group decreases in the LPZ M-3a pollen spectra. However, the quantitative ratios of the pollen in three main coenotic groups are almost equivalent (Fig. 12, c). The role of forest elements increased due to the increased proportion of birch tree pollen (*Betula* sect. Albae), while the steppe group demonstrated a decrease in grass pollen, along with disappearing pollen grains of ephedra (Fig. 4). Equal pollen proportions in coenotic groups are typical of periglacial forest-tundra-steppe communities (Bolikhovskaya, 1995). Periglacial communities became widespread, including meadow grass-mixed-herb communities with participation of steppe and tundra species and brushwood combined with birch forests. Conifer species were not of great significance in the vegetation cover. The decreasing significance of steppe elements can be indicative of the increased

humidity of the climate.

Similar communities for the Briansk interstadial were reconstructed for the latitude 59°N of the East European Plain, westward of the exploration area: 1) periglacial forest tundra steppe where a combination of birch-pine and spruce forest intermingled with meadow steppe formations, tundra communities and steppe halophyte species; 2) a combination of tundra and steppe plant communities with pine-birch light forest (Simakova, 2001, 2006). It should be noted that the pine tree plays an essential role in western areas of the East European Plain, being well represented in the forest communities of periglacial vegetation. Based on the pollen data of the Makhnevskaya-2 Cave, the pine tree was poorly represented in the vegetation cover. Most likely, its occasional pollen in the pollen spectra was imported from afar.

During the 2nd and 3rd stages of deposit formation, the fauna of small mammals was more diverse and dominated by *Dicrostonyx torquatus*. No analogs of this fauna have been found in the northern Middle Urals. Most of the molars of dominant species belong to the morph *henseli* (the stage of morphological development "*D. guilielmi* morph III"). During the formation of middle deposits, the cave was used by mammal predators most intensively, which can be seen from a very high concentration of bone material. Most likely, the wide diversity of prey
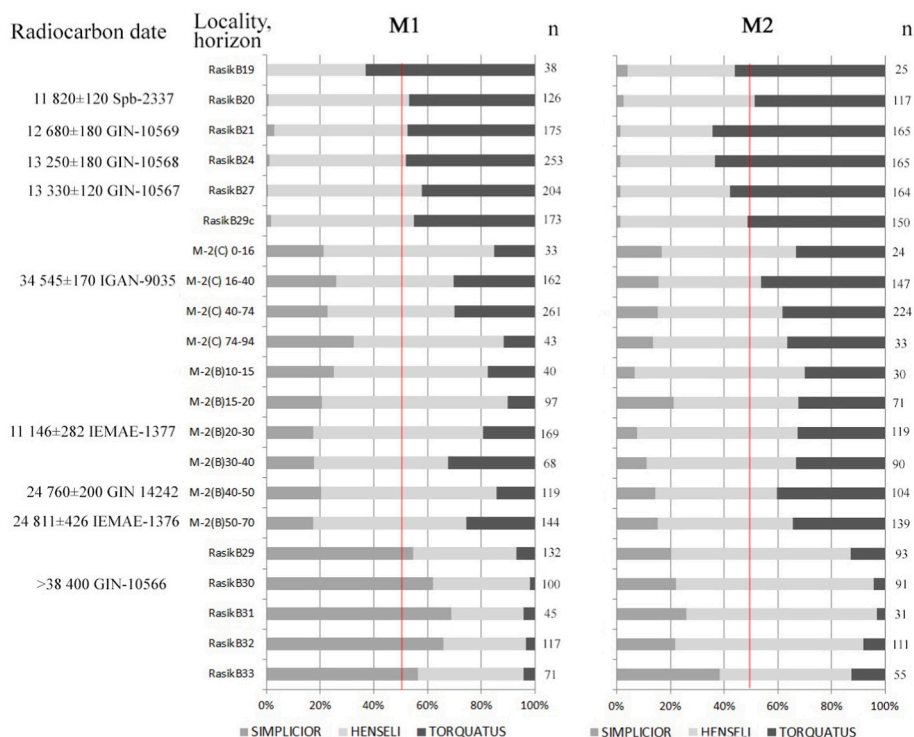
Fig. 9. Frequencies of morphotypical groups (%) of the M1 and M2 of *Dicrostonyx torquatus* from localities of Perm Pre-Urals, Russia. For the legend see Fig. 7.

Fig. 10. Arrowhead in Chert. Different views of the same specimen. Size: 37,7x17,8x4,9 mm. Stage: Later Neolithic Later Neolithic (6000–5000 years BP). Makhnevskaya-2 Cave (excavation sector C), depth 4–8 cm.

species can be explained by the above factor. The remains of insectivorous mammals are dominated by bone remains of tundra shrews. Contemporary representatives of *Sorex tundrensis* are adapted to arid environments; they are commonly found in open landscapes; the species range extends to the tundra zone (Zaitsev et al., 2014). This species is

well represented in "cold" faunas of the late Pleistocene – the early Holocene in the Perm Pre-Urals (Fadeeva, 2016) and is dominant among representatives of the genus *Sorex* in the early Holocene of the South Urals (Zaitsev, 1998).

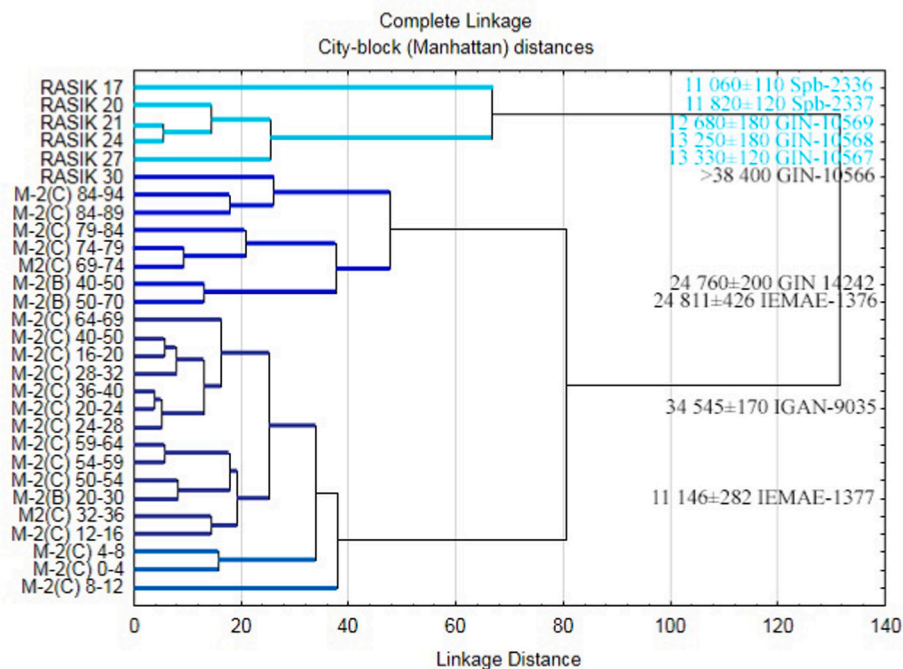In the Urals, there are not any known Late Pleistocene locations with

Fig. 11. Cluster analysis (city-block (Manhattan) distances) of fossil assemblages from two localities of the Middle Urals. M-2 – Makhnevskaya-2 cave (excavation sectors B, C), 0–94 – sediment horizons (cm); RASIK - Rasik Grotto, square B, 17, 20, 21, 24, 27, 30 - sediment horizons (sequential numbers).

bones of species from genus *Mus*. The lower jawbones of *Mus* sp., which were found in the middle section of the cave deposits, have dark-yellow color and pinpoint mineral buildups (iron-manganese oxides) on the surface. These signs are typical of the Late Pleistocene bone material from the lower and middle deposits of the cave. Therefore, bone remains of the mouse belonged to representatives of the aboriginal mouse species – *Mus* sp.

The upper reference horizons of the deposits are characterized by the decreasing number of tundra species' teeth and the dominance of *Microtus gregalis*. However, most likely, this change can be explained by the presence of Late-glacial inclusions. The samples of the first lower molars of narrow-skulled voles from all the reference horizons of the cave deposits are characterized by a low proportion of teeth of the microtid morphotype as compared to the Late-glacial and early Holocene samples of species' teeth from the regional locations. In the upper deposits, the teeth of collared lemmings correspond to the stage of morphological development "*D. guilielmi* morph II". The species composition of small mammals and the morphology of teeth of the dominant rodent species give no grounds for expecting large proportions of Late-glacial and Holocene bone materials in the upper deposits of the cave.

The inconsistency of transitional morphs of collared lemmings (*D. guilielmi* morph II (74–94 cm) – *D. guilielmi* morph III (16–74 cm) – *D. guilielmi* morph II (0–16 cm)) in the Makhnevskaya-2 Cave deposits (differences in teeth morphs within the same location over time) can be explained by different sample sizes or by the impact of external environmental conditions and/or epigenetic processes. Populations of collared lemmings with these both morphs existed concurrently within the territory of European North East 23 thousand calendar years ago (differences in the teeth morphs in samples from locations of the same age), thus being indicative of the mosaic pattern of morphotypical variability in species populations (Ponomarev and Puzachenko, 2015; Ponomarev, 2020).

6. Conclusion

The comprehensive study of the deposits in the Makhnevskaya-2

Cave makes it possible to reconstruct the paleoenvironment of the final stage of the middle of the Late Pleistocene (the Briansk interstadial). Three successive stages of environmental changes were identified; all of them are characterized by moderately cold climate, prevalence of open landscapes and dominance by three taxa of small mammals (*Dicrostonyx torquatus*, *Microtus gregalis*, Lemmini gen.). The first (the lower section of the deposits) and the third (the upper half of the middle section of the deposits) stages are characterized by higher humidity and mosaic landscape with tundra-steppe and birch-spruce formations. The cave was used by predators as a den, especially intensely during the second stage distinguished by high aridity, dominance of mixed-herb-grass and ephedra communities and reduced forest formations in periglacial landscapes. The identified morphological characteristics of teeth of *Dicrostonyx torquatus* (teeth of the morph *henseli* prevail), *Microtus gregalis* (teeth of the *gregaloid-microtid* morphotype prevail) are instrumental for using these data as stratigraphic markers for deposits of the Briansk interstadial of the north-east area of the Middle Urals.

Author contributions

Tatyana Fadeeva: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - original draft. **Pavel Kosintsev**: Investigation, Resources, Writing - original draft. **Elena Lapteva**: Formal analysis, Investigation, Writing - original draft. **Ilya Chaikovskiy**: Formal analysis, Investigation, Writing - original draft. **Elena Chirkova**: Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence
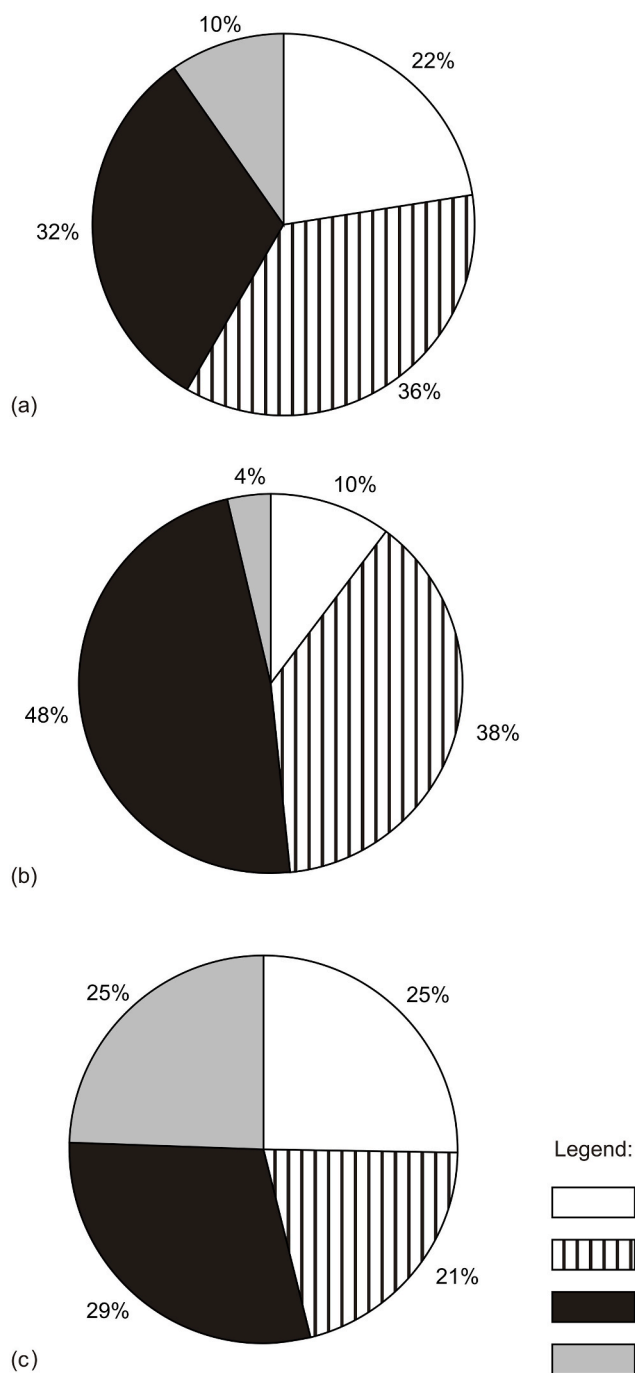
Fig. 12. Average proportions of coenotic groups in local pollen zones (LPZs) of the Makhnevskaya-2 Cave deposits (excavation sector C) representing the Briansk interstadial. (a) LPZ M-1, (b) LPZ M-2, (c) LPZ M-3a. Coenotic groups: 1 – forest, 2 – tundra, 3 – steppe, 4 – other.

the work reported in this paper.

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