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Voronin Grotto (Middle Urals, Russia): Analysis of vertebrate assemblage with taphonomic remarks and reconstruction of the Late Bronze Age and Early Iron Age human environment in the east end of Europe based on small mammals

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ABSTRACT

We present the Voronin Grotto as a new site where numerous remains of vertebrates (total NISP = 12574) and artefacts (N = 46) were found. The grotto is located in Serga River valley at the foot of the western slope of the Middle Urals, i.e., in the east end of continental Europe. The deposits have been accumulating during the last 3310 years. The AMS dates and artefacts indicate that the grotto was periodically visited by human population in the period between 3310 cal BP (the Late Bronze Age) and 1899 cal BP (the Early Iron Age). Recovered vertebrate assemblage included 49 species belonging to 5 classes (Actinopterygii, Amphibia, Reptilia, Aves, and Mammalia). The bones of fish and amphibians were collected by either otters or minks. Prevailing fish sizes between 10 and 15 cm reconstructed by means of bones confirm this. The bones of small mammals accumulated due to the predation of the owls and mustelids. Most identified vertebrate species currently inhabit the vicinity of the grotto, except for the steppe pika. Steppe pika is now disjointed from the Voronin Grotto by approximately 200–300 km to the south. Perhaps between 3310 and 1899 cal BP, steppe pika inhabited the vicinity of the grotto as the Late Pleistocene and Early Holocene relic. Palaeoenvironmental analysis of small mammal assemblage showed the predominance of woodlands with a significant proportion of open mesophytic meadows around the grotto during the last 3310 years. The landscape did not change significantly during this time. This is consistent with high values of the Simpson evenness index (1–D). Between 3310 and 1899 cal BP, the ratio of forests decreased, while the ratio of open meadows increased. Perhaps this was due to anthropic activity. After 1899 cal BP, the relative abundances of taiga small mammal species increased among forest dwellers, which is consistent with palynological data for the Middle Urals. At approximately 3310 cal BP, the climate of area around the grotto was slightly milder, and the winters were warmer than in the present day. At approximately 1899 cal BP, the climate was similar to the modern climate of the region and was cold, without a dry season, and with warm summers (Dfb type according to the Köppen–Geiger classification) as well as that of the previous period. Towards the recent time, the climate became colder and was possibly cold, without a dry season, but with a cold summer (type Dfc).

1. Introduction

According to Dinesman et al. (1979) in the study of the Holocene history of modern ecosystems, it is of great importance to study the history of their components (e.g., plants, invertebrates, vertebrates, soils). The study of vertebrate remains plays an important role in these investigations because vertebrate fossils are a source of information about the palaeoenvironment of an area surrounding a site during the time of deposition of sediments due to habitat preferences of specific taxa (Doukas et al., 2018). The study of small mammal assemblages occupies an important place among these studies because small mammals are opportune objects for palaeoenvironmental reconstructions

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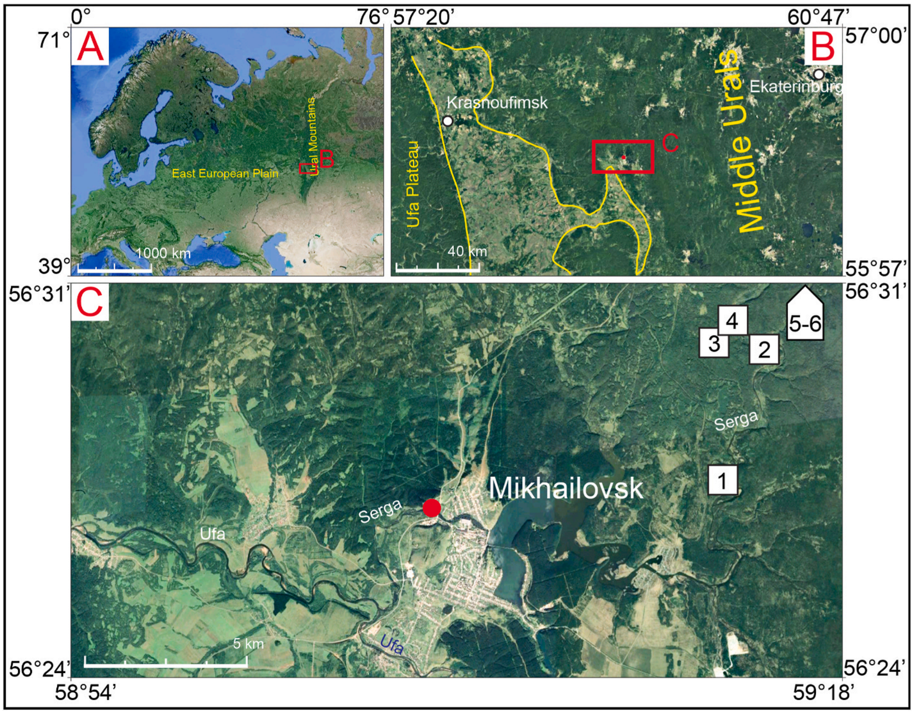

Fig. 1. Geographical location of the Voronin Grotto: A, on the map of Europe; B, in the southwest Middle Urals (yellow line indicates limits of the Krasnoufimsk insular forest according to Gorchakovsky, 1967); C, in the outskirts of the town of Mikhailovsk (a red dot). The numbers (1–6) indicate position of the localities of Late Pleistocene and Holocene vertebrate assemblages in the Serga River valley: 1-Arakaevo-8 Cave; 2-the Smotrovoi Rock shelter; 3-the Svetlyi Rock shelter; 4-the Dyrovatyi Kamen Grotto; 5-the Starik Rock shelter; 6-the Oleniy Grotto. The sites 5 and 6 are located approximately 3–4 km north of the Dyrovatyi Kamen Grotto (4) outside the area C. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

because of their high dependence on vegetation cover changes (Fernández-Jalvo et al., 2016). In additional, small mammal assemblages are a suitable source for palaeoclimate reconstructions (Hernández-Fernández, 2001). Bird assemblages are an equally important source of palaeoecological information (Tomek and Bocheński, 2005; Carrera et al., 2021). Undoubtedly, archaeological localities are of great interest to palaeoecological investigations because in the deposits, apart from vertebrate remains, artefacts have been found. Archaeological sites provide an opportunity to study both the history of ecosystems and the influence of humans on them. Therefore, each new location of vertebrate bone remains and artefacts is a new "piece of the puzzle" that allows us to fill in the gaps in our knowledge of the Holocene history of modern ecosystems. This is especially important for areas that have been poorly studied. An example of a territory of this type is the valley of the Serga River, which is located in the southwest of the Middle Urals in the east end of continental Europe.

Significant time periods, during which significant palaeoclimatic and palaeoenvironmental events and changes in the human material culture and economic activity have occurred, have not been studied in the Serga River valley yet, and therefore, in general, in the south-west of the Middle Urals. This primarily concerns the time span between 4840 ± 109 BP (3619 ± 136 cal BC) and 700 ± 90 BP (1300 ± 71 cal AD), which belongs to the end of Middle Holocene (Northgrippian) and to the Late Holocene (Meghalayan) of Global Quaternary scheme (Cohen and Gibbard, 2019). This time interval also corresponds to the Subboreal (SB: 4700–2500 BP according to Khotinsky, 1987; Arslanov et al., 1999) and most of the Subatlantic (SA1–SA2: 2500–800 BP) of the Blitt–Sernander scheme. In an archaeological scale, this time interval is placed between the Copper Age (4000–2200 BC according to Bogucki, 2008, or 4500–2500 BC according to Marciniak, 2008) and the Middle Ages (400–1550 AD according to O'Keeffe, 2008). In this article, we present the Voronin Grotto as a new site with Upper Holocene deposits containing numerous vertebrates bone remains and artefacts pertaining to cultures of the Late Bronze Age (1300–800 BC according to Marciniak, 2008) and of Early Iron Age (900 BC – 400 AD according to Grakov, 1977, or 800 BC – 400 AD according to Wells, 2008).

The objectives of this study are to describe taphonomy process, vertebrate assemblages of Upper Holocene sediments of the grotto and to carry out a palaeoenvironmental interpretation of the obtained data in context of human presence in this territory during the Late Bronze Age and Early Iron Age.

2. Voronin Grotto

2.1. Regional settings

The valley of the Serga River is located in the northern part of the foothill depression, which is bounded in the east by the Bardymsky ridge (the height of the ridge is on average approximately 500–600 m; the maximum height is up to 650 m). The depression altitude is up to 350 m a.s.l., but in the valley of the Serga River, it drops to 240 m. The depression is composed of Silurian, Devonian, and Lower Carboniferous limestone. The valley of the river is narrow (0.5–0.8 km wide) and is deeply cut into the limestone basement, and bedrock outcrops are found on its steep banks. This area is distinguished by a developed karst (Prokaev, 1963).

The Voronin Grotto is located in the temperate continental climate zone. The climate in this part of the Middle Urals is cold without a dry season and with warm summers (type Dfb according to the Köppen-Geiger classification; Beck et al., 2018). The mean annual temperature (MAT) is 2.3 °C (data for the period from 1989 to 2019). The mean temperatures of the warmest month of the year (MTW) and the coldest month (MTC) are 18.3 °C and −14.4 °C, respectively. The total annual precipitation (P) is approximately 588 mm. Climatic data over the last 30 years for the nearest grid-point to the Voronin Grotto location (56–56.5° N, 59–59.5° E) were obtained from the CRU TS 4.04 (land) 0.5°-resolution gridded dataset for temperature (Harris et al., 2020) and from the spatial statistics from the GPCC analysis v.2020 (land) 0.5°-resolution gridded dataset for precipitation (Schneider et al., 2020). However, the climate in this area was more severe and corresponded to the Dfc type (cold, without a dry season, with a cold summer) in 1881–1935: MAT = 0.1–0.3°C; MTW = 16.0–16.7°C; MTC = −16.6°C; P = 513–585 mm (Prokaev, 1963).

In the valley of the Serga River, secondary mixed coniferous and deciduous forests dominate mainly with pine, spruce, fir, birch, and aspen. Pine–larch forests are found in some places. However, in the past,

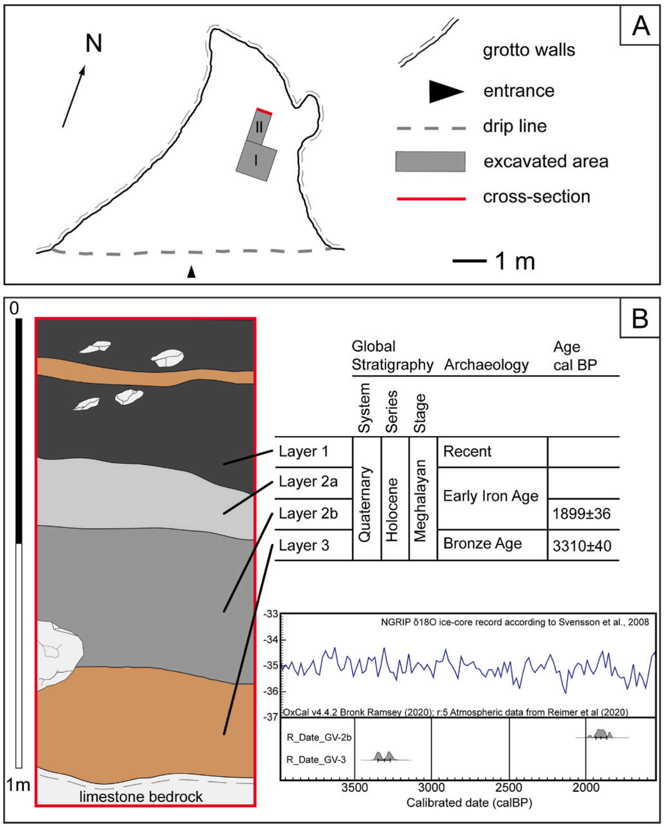

Fig. 2. Voronin Grotto: A, plan of the grotto, I-II – pits; B, stratigraphic profile correlated to the global chronostratigraphic scheme (Cohen and Gibbard, 2019), archaeology, dating of the grotto deposits and palaeoclimate context for deposition performed using OxCal software (Bronk Ramsey, 2009) and a depositional model (Bronk Ramsey, 2008) compared with the North Greenland Ice Core Project (NGRIP) $\delta^{18}O$ ice-core record (Svensson et al., 2008).

broad-leaved fir–spruce forests with linden and, in places, elm and maple prevailed (Kolesnikov et al., 1973). On the southern slopes of the hills in the vicinity of the Mikhailovsk town, on the outskirts of which the grotto was discovered, meadow-steppe herbaceous associations are widespread (Prokaev, 1963). In addition, the Krasnoufimsk insular forest-steppe extends to the west of the grotto in a large tectonic depression of the Fore-Ural Foredeep between the Ufa Plateau and the Ural Mountains (Fig. 1B). The insular forest-steppe is a relic of Late Pleistocene "cold steppes" (Krasheninnikov, 1937; Gorchakovsky, 1967).

2.2. Palaeontological background of the Serga River valley

Serga River valley contains only six localities with Late Pleistocene and Holocene vertebrate assemblages dated by means of the ^{14}C method (Fig. 1C), i.e., the Arakaevo-8 Cave (Smirnov, 1993), the Dyrovatyi Kamen Grotto (Smirnov, 1993; Ulitko, 2006), the Svetlyi Rock shelter (Korkina et al., 2016), the Oleniy Grotto (Smirnov, 1993), the Smotrovoi Rock shelter, and the Starik Rock shelter (Sadykova, 2011). Unfortunately, only mammal remains (mainly small ones) have been identified and described among the bones of vertebrates found in all of the listed above localities. The ancient mammal assemblages in the Serga River valley were obtained from the Upper Pleistocene deposits of the Svetlyi Rock shelter (16400 ± 165 BP) and of the Arakaevo-8 Cave (15739 ± 590 BP). The sediments of the Svetlyi Rock shelter also contained Early – Late Holocene, mammal remains. The mammal assemblages from Middle and Upper Holocene deposits included numerous Late Pleistocene mammal bones, which entranced to the strata during the deposition

Table 1
Results of dating of Voronin Grotto sediments.

Layers	Levels	Method	Reference no.	^{14}C dates ±σ, BP	Calibrated dates ±σ, cal BP
2b	−0.6–0.7 m	AMS	$IGAN_{AMS}$–8646	1970 ± 20	1899 ± 36
3	−0.8–0.9 m	AMS	$IGAN_{AMS}$–8647	3100 ± 20	3310 ± 40

$IGAN_{AMS}$ – the Laboratory of Radiocarbon Dating and Electronic Microscopy, Institute of Geography, Russian Academy of Sciences (Moscow, Russia) and the Centre for Applied Isotope Studies, University of Georgia (Athens, USA).

process and, as a result, these sediments have not been dated (Korkina et al., 2016). The sequence at the Dyrovatyi Kamen Grotto contained Upper Pleistocene (14810 ± 130 BP), Lower Holocene (9327 ± 158 BP), and Middle Holocene (6462 ± 46 BP) layers with the corresponding mammal assemblages. The stratum attributed to the Upper Holocene has not been dated. The Mid-Holocene mammal bone remains were also found in the sediments of the Oleniy Grotto (4840 ± 109 BP, 5122 ± 92 BP, 5440 ± 117 BP). A palynological analysis of the studied layers demonstrated that pine and birch forests dominated near the Oleniy Grotto during sedimentation process (Smirnov, 1993). Sediments of both Smotrovoi and Starik Rock shelters were accumulated during the end of the Late Holocene between 700 ± 90 BP and the present day (Sadykova, 2011) and contained only small mammal bones.

2.3. Site location and description

The Voronin Grotto (56.45°N, 59.1°E) is located on the northern outskirts of Mikhailovsk town (Fig. 1) on the right bank of the Voronin River, which is the right tributary of the Serga River. The grotto is situated in the base of a limestone bed rock at a height of approximately 2 m above the river. The site has a south-eastern exposition (Fig. 2A). The surface of the floor does not have a slope; it bears traces of frequent visits by humans. There are traces of old excavations, which remained, probably because of archaeological work to find new locations that were carried out in this area at the end of the 20th century. However, unfortunately, it was not possible to find exact information about these studies. No bone material was found on the surface. Preliminary data about mammal fauna were published by Izvarin and Ulitko (2019).

2.4. Brief stratigraphical description of the sediments and dating

The grotto sediments sequence contains 4 layers (Fig. 2B). The total maximal thickness of the described deposits was 1.06 m.

Layer 3. Light brown finely dispersed loam with separate limestone blocks (total thickness of up to 0.26 m).

Layer 2b. Grey with a brownish tinge sandy loam with the inclusion of small and middle-sized limestone debris; in the lower part contains debris with rounded edges; significant osteological material and numerous ceramic fragments were found in the layer (thickness of up to 0.32 m).

Layer 2a. Light grey sandy loam with the inclusion of small and middle-sized limestone debris; significant osteological material and ceramic fragment were found in the layer (thickness of up to 0.15 m).

Layer 1. Dark grey humus sandy loam with numerous small and middle-sized limestone debris; in the upper part contains a large amount of charcoal and recent man-made garbage; at a depth of 0.1–0.12 m, there is an intermittent loam sublayer with a thickness of approximately 0.05 m, which was formed as a result of dump sediments from old excavations (total layer thickness of up to 0.4 m).

The age of the sediments was determined by AMS dating (Table 1). The AMS dating of samples was carried out in the Laboratory of Radiocarbon Dating and Electronic Microscopy, Institute of Geography, Russian Academy of Sciences (Moscow, Russia) and in the Centre for

Table 2
Number of artefacts found in the Voronin Grotto sediments.

Layers	Levels	Pottery		Bones	Bone tools	Stone tools	Pebbles	Ochre	Total
		Ornamented	Non-ornamented						
2a	−0.4–0.5 m	1	2	–	–	1	–	–	4
2b	−0.5–0.6 m	4	6	1	–	–	4	–	15
	−0.6–0.7 m	–	3	–	3	–	3	–	9
	−0.7–0.8 m	2	2	1	–	–	–	1	6
3	−0.8–0.9 m	–	–	–	1	–	11	–	12
	Total	7	13	2	4	1	18	1	**46**

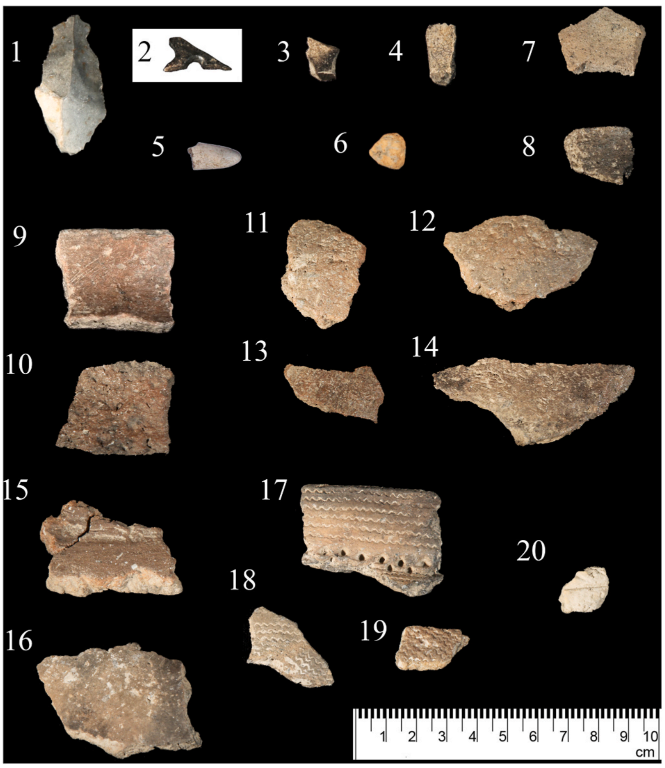

Fig. 3. Artefacts obtained from Voronin Grotto sediments. 1-Flint flake from layer 2a (depth of 0.4–0.5 m); 2-sub-triangular antler pendant from layer 2b (depth of 0.6–0.7 m); 3, 4-two fragments of an arrowhead made of bone from layer 2b (depth of 0.6–0.7 m); 5-polished tip of bone kochedyk from layer 3 (depth of 0.8–0.9 m); 6-rounded ochre fragment from layer 2b (depth of 0.7–0.8 m); 7-potsherd of an Iron Age small vessel from layer 2b (depth of 0.5–0.6 m); 8-fragment of a rim of a small vessel from layer 2b (depth of 0.7–0.8 m); 9-rim of a vessel of the Itkul culture of the Early Iron Age from layer 2a (depth of 0.4–0.5 m); 10-fragment of the neck (?) of the same vessel as the rim No. 9, without the outer surface and found in layer 2b (depth of 0.5–0.6 m); 11–14-undecorated fragments of another vessel of the Itkul culture from layer 2b (depth of 0.5–0.6 m); 15, 16-potsherds of a vessel of the Sargat culture of the Early Iron Age from layer 2b (depth of 0.5–0.6 m); 17, 18-potsherds of a vessel of the Gamayun culture of the finishing Bronze Age from layer 2b (depth of 0.5–0.6 m); 19-fragment of the same vessel of the Gamayun culture but found in the lowest part of layer 2b (depth of 0.7–0.8 m); 20-potsherd with a carved ornament of the Cherkaskul culture of the Bronze Age from layer 2b (depth of 0.7–0.8 m).

Applied Isotope Studies, University of Georgia (Athens, USA). The calibration of radiocarbon dates was performed using the OxCal 4.4.2 software (Bronk Ramsey, 2009) using the atmospheric data from Reimer et al. (2020). Indeterminable fragments of bones of Cetartiodactyla from the upper part of layer 3 (depth of 0.8–0.9 m) and from the middle part of layer 2b (depth of 0.6–0.7 m) were used for dating.

AMS dating on the bone fragment from layer 3 yielded an age of 3100 ± 20 BP (3310 ± 40 cal BP). Layer 2b has been dated to 1970 ± 20 BP (1899 ± 36 cal BP). Layer 1 contained present-day anthropogenic garbage, and it was attributed to the recent time. Thus, the entire thickness of the studied deposits can be attributed to the Late Holocene of the Global chronostratigraphic scheme (Meghalayan Stage, since 4200 cal BP according to Walker et al., 2018; Cohen and Gibbard, 2019) (Fig. 2B). According to these data, grotto sediments have been accumulating during at least the last 3310 ± 40 years, i.e., during the Late Holocene time.

2.5. *Archaeology*

During the excavation of the Voronin Grotto sediments, 46 artefacts were found in layer 2a, at different levels of layer 2b, and at the upper part of layer 3 (Table 2). Archaeological finds were also used to determine chrono-cultural age of the grotto deposits.

2.5.1. *Stone and bone artefacts*

A small rounded ochre fragment was found in the lower part of layer 2b at a depth of 0.7–0.8 m (Fig. 3, no. 6). There are 3 massive natural-shaped pebbles (2 of flint and 1 of chalcedony) without traces of processing or use from a depth of 0.6–0.7 m (layer 2b), which could have been brought into the grotto by humans as mineral raw materials. Only one flint flake found in layer 2a at a depth of 0.4–0.5 m could be classified as an stone artefact (Fig. 3, no. 1). The remaining 15 pebbles of flint and quartzite are too small and, most likely, are gastroliths (Table 2).

In the upper part of layer 3, at a depth of 0.8–0.9 m (Table 2), a polished tip of bone kochedyk was found (Fig. 3, no.5). In layer 2b, at a depth of 0.6–0.7 m, two fragments of an arrowhead made of bone and one fragment of a sub-triangular antler pendant were found (Fig. 3, no. 3, 4, and 2, respectively). Such tools are cultural ascribed to the wide range from the Neolithic (VI–IV millennium BC) to the Early Iron Age (middle of I millennium BC – middle of I millennium AD).

2.5.2. *Pottery*

The dating archaeological material is represented by fragments of ceramic vessels (Fig. 3, no. 7–20). In the lowest part of layer 2b, at a depth of 0.7–0.8 m, a small potsherd with a carved ornament of the Cherkaskul culture of the Bronze Age (2–3rd quarter of the 2nd millennium BC according to Obydennov and Shorin, 1995) was found (Fig. 3, no. 20). Probably one of the earliest visits to the grotto is associated with this time. In the middle and upper parts of layer 2b (depth of 0.5–0.7 m), pottery of the following archaeological cultures was found: Gamayun (the end of Bronze Age, 4th century BC after Borzunov, 1992), Itkul (Early Iron Age, VII–III centuries BC according to Beltikova, 1977), and Sargat (Early Iron Age, from VII–VI centuries BC to III–V centuries AD according to Koryakova, 1988). In layer 2a (depth of 0.4–0.5 m), a rim of a vessel of Itkul culture was noted (Fig. 3, no. 9).

Thus, the discovered artefacts testify to an episodic visit to the grotto during the Bronze Age and the Early Iron Age by the population of the forest and forest-steppe zone of the Urals and Western Siberia.

3. Materials and methods

3.1. Excavation and sampling

Excavations in the Voronin Grotto were conducted in 2007. The total area of the excavated pit was 1.5 m^2 (Fig. 2A). First, a 1 m^2 exploration pit was started (section I). Deposits have been taken in separate 10-cm levels and washed in sieves with a 0.8-mm mesh size to recover small vertebrate remains (Gromov, 1955; Guslitcer, 1979; Agadjanian, 1979). In section I, an old archaeological pit was discovered. The sediments in this area contained almost no vertebrate bones, and there were no archaeological finds at all. The original pit was extended by another 0.5 m^2 (section II). Palaeontological and archaeological materials (12,574 vertebrate bone remains and 46 artefacts, respectively) were found in section II, where intact sediments were uncovered. Osteological material in all the layers is represented by fish bones, vertebrae, and scales (NISP = 2937), by the amphibian bones (NISP = 3646), reptiles (NISP = 1398), and birds (NISP = 544), and by mammal postcranial bones, mandibles, maxillae, and isolated teeth (NISP = 4049). In addition, 119 mollusc shells were found in all layers. In the article, we discuss only archaeological finds and fish, bird, and mammal assemblages.

3.2. Taxonomy and quantification

The taxonomic nomenclature of insectivores, lagomorphs, and rodents was given in accordance with Lissovsky et al. (2019), except genus *Sylvaemus* Ognev, 1924, which is considered as a subgenus within genus *Apodemus* Kaup, 1829, according to Wilson and Reeder (2005). We used the name *Clethrionomys* Tilesius, 1850 for the genus of red-backed voles instead of *Myodes* Pallas, 1779 according to Tesakov et al. (2010) and Kryštufek et al. (2020).

Anatomical elements used for taxonomic determination of small mammal remains included the following: maxillae/mandibles and isolated teeth (except incisors) for sciurids (family Sciuridae Fischer, 1817), murids (family Muridae Illiger, 1811), birch mice (genus *Sicista* Gray, 1827), common hamster (*Cricetus cricetus* Linnaeus, 1758), grey red-backed vole (*Craseomys rufocanus* Sundevall, 1846), and water vole (*Arvicola amphibius* Linnaeus, 1758); M1–M3 and m1–m2 for voles belonging to genus *Clethrionomys* Tilesius, 1850; M1–M2 and m1 for the field vole (*Microtus agrestis* Linnaeus, 1761); m1 for other arvicolines (subfamily Arvicolinae Gray, 1821); and mandibles for soricids (family Soricidae Fischer, 1814).

Species of mammal remains were identified using the etalon collections at the Laboratory of Palaeoecology of the Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences and using special literature. In general, bone remains of Eulipotyphla and Rodentia were determined in accordance with Zaitsev (1998) and Fadeeva (2016) for soricids; Zaitsev et al. (2014) for talpids; Gromov and Polyakov (1977) and Borodin (2009) for arvicolines; and Gromov and Erbajeva (1995) for other rodents. Species identification of fish and bird fossils were carried out using etalon bone collections at the Museum of Institute of Plant and Animal Ecology of the Ural Branch of the Russian Academy of Sciences (Ekaterinburg, Russia).

The number of identified bones (NISP) and a minimum number of individuals (MNI) were used for quantitative analysis. The MNI of mammals was calculated based on the most numerous identifiable elements, taking into account its position in the skeleton on the right or left side. The minimum number of bird individuals was estimated using the number of paired bones of the skeleton. The MNI of fishes was computed either by the number of paired bones of the skull or by the number of first vertebrae, taking into account differences in bone sizes (Poplin, 1976). The reconstruction of the sizes of fish remains was carried out by means of direct comparison with etalon bone collections at the Museum of the Institute of Plant and Animal Ecology (Ekaterinburg, Russia).

3.3. Predator identification

To identify which predator was involved in the accumulation of small mammal bones, alterations, which are caused by the digestion, on the all molars of arvicoline rodent species were evaluated and described in accordance with Andrews (1990). A total of 741 arvicoline molars from lithological strata of the Voronin Grotto were studied. The studied molars were sorted into 5 categories based on the digestion degree of tooth tissues (absence, light, moderate, heavy, and extreme), following Andrews (1990) and Fernández-Jalvo et al. (2016). The ratios of digested teeth were counted. Furthermore, 95% confident intervals (CI) of the digestion degree ratios were computed based on the Clopper–Pearson method (Clopper and Pearson, 1934) using the PAST 4.05 software (Hammer et al., 2001). According to Suchéras-Marx et al. (2019), the calculation of 95% confident intervals is necessary to evaluate statistical significance of the ratio differences among strata.

3.4. Palaeoenvironment and palaeodiversity

To reconstruct the environment, we used the method of habitat weightings (Andrews, 2006) by distributing each small mammal taxon in the habitat(s) where it can be currently found in the Urals. Habitat preferences of small mammals (Eulipotyphla, Lagomorpha, and Rodentia) in the Urals were obtained from Bolshakov et al. (2006). Habitats were divided into five types in accordance with López-García et al. (2010): open land in which dry (OD) and wet (OH) meadows are distinguished, woodland, forest edge areas and forest patches (Wo), rocky areas (Ro), and habitats related to water (Wa). According to López-García et al. (2019), the categories “Open” and “Woodland” habitats are used in this study to compare the layers of Voronin Grotto sediments. In our opinion, “Open” includes both open dry (xerophytic) meadows, open humid meadows (including mesophytic meadows), and wet herbaceous associations near water that are preferred habitats for water vole (*Arvicola amphibius* Linnaeus, 1758) and to a lesser extent for root vole (*Alexandromys oeconomus* Pallas, 1776), following Markova et al. (2018). “Woodland” includes mature forests, forest edge, and forest patches.

Basing on the small mammal assemblage (Eulipotyphla, Lagomorpha, and Rodentia) from the grotto sequence, we calculated the Simpson evenness index (1–D) to assess the homogeneity of an environment using the formula: $1-\Sigma(n_i/N)^2$, where n_i is the number of individuals of taxon i, and N is the total number of small mammal individuals in the sample (Hammer and Harper, 2006). The Simpson 1–D index varies from 0 to 1 and represents the probability that any two individuals selected at random from the sample belong to different species. If the value of the index approaches 1, the assemblage will be more even, and thus, the environmental conditions will be more homogeneous (Magurran, 2004). The index was obtained using the PAST 4.05 software (Hammer et al., 2001).

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

3.5. Palaeoclimate

For palaeoclimatic interpretation of palaeontological data, the Bioclimatic Model method was used, which is based on a quantitative assessment of the main climatic parameters of modern small mammal communities in different climate zones (Hernández-Fernández, 2001;

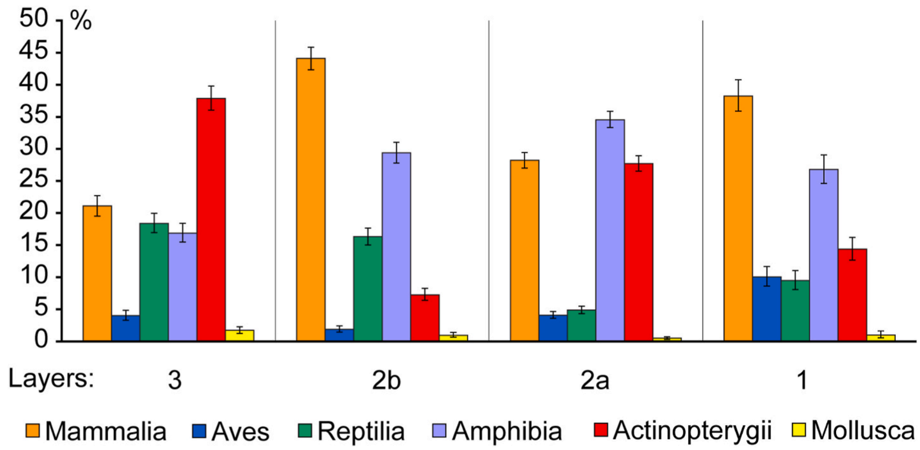

Fig. 4. Proportion (%) of vertebrate bone remains from Voronin Grotto sediments with 95% confident intervals (black whiskers).

Table 3
Proportion (%) of different degrees of digestion with 95% confident intervals (95% CI) estimated on arvicoline molars from Voronin. sediments.

Layer	N	absent	light	moderate	heavy	extreme	Total digested	95% CI
1	120	91.7	5.0	1.7	0.0	1.7	8.3	4.1–14.8
2a	311	88.1	8.0	1.9	1.9	0.0	11.9	8.5–16.0
2b	243	62.6	28.8	4.1	3.7	0.8	37.4	31.3–43.9
3	67	50.7	34.3	9.0	3.0	3.0	49.3	36.8–61.8

Hernández-Fernández and Peláez-Campomanes, 2005). Each species in a climatic zone is assigned a value (Climate Restriction Index, CRI, according to Hernández-Fernández, 2001) from 0, if the species does not occur in this zone, to 1/n, where n is the number of climate zones in which the species is present. Next, for each layer, the Bioclimatic Component (BC) was calculated using the formula: $BC = (\Sigma\ CRIi) \times 100/S$, where i is the climatic zone and S is the number of small mammal species identified in the layer. The obtained values of the bioclimatic components of insectivores and rodents (model "Eulipotyphla-Rodentia" in accordance with Royer et al., 2020) were used to calculate the following climatic parameters by multiple linear regression analysis for each using Microsoft Excel and StatSoft Statistica software: the mean annual temperature (MAT), the mean temperature of the warmest month (MTW), the mean temperature of the coldest month (MTC), and the total annual precipitation (P). The results were compared with present day data over the last 30 years (1989–2019), but the nearest climatic stations are located far from the grotto: WMO station 28434 in Krasnoufimsk (approximately 85 km northwest of the grotto; MAT = 2.2 °C, MTW = 18.3 °C, MTC = −15.1 °C, P = 576 mm) and WMO station 28541 in Verkhnij Ufalei (approximately 80 km southeast of the grotto; MAT = 2.0 °C, MTW = 17.4 °C, MTC = −13.7 °C). However, the values of the total annual precipitation from station 28541 are available only for the period of 1959–1995 (P = 518 mm). Meteorological data from these stations were obtained from the Global Historical Climatology Network Daily Database (Menne et al., 2012). Therefore, the current values of the climatic parameters (MAT = 2.3 °C; MTW = 18.3 °C; MTC = −14.4 °C and P = 588 mm) for the nearest grid-point to the Voronin Grotto location (56–56.5° N, 59–59.5° E) were obtained from the CRU TS 4.04 (land) 0.5°-resolution gridded dataset for temperature (Harris et al., 2020) and from spatial statistics of the GPCC

Table 4
Species composition and the number of identified fish bone remains in Voronin Grotto sediments.

Taxa №	Taxa	Layer 1		Layer 2a		Layer 2b		Layer 3	
		NISP[a]	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Esociformes									
1	*Esox lucius* Linnaeus, 1758	26	2	276	12	9	1	91	4
	Perciformes								
2	*Perca fluviatilis* Linnaeus, 1758	74	2	284	7	45	1	170	3
3	*Gymnocephalus cernuus* Linnaeus, 1758	–	–	7	1	–	–	–	–
	Salmoniformes								
4	*Thymallus thymallus* Linnaeus, 1758	49	2	217	4	42	2	192	5
	Scorpaeniformes								
5	*Cottus gobio* Linnaeus, 1758	9	2	16	3	7	1	–	–
	Gadiformes								
6	*Lota lota* Linnaeus, 1758	25	1	262	5	17	1	148	3
	Cypriniformes								
7	*Squalius cephalus* Linnaeus, 1758	–	–	7	1	–	–	–	–
8	*Phoxinus phoxinus* Linnaeus, 1758	–	–	4	2	–	–	–	–
9	*Gobio gobio* Linnaeus, 1758	–	–	5	1	–	–	–	–
10	Cyprinidae indet.	–	–	106	–	–	–	–	–
	Actinopterygii indet.	44	–	320	–	105	–	380	–
	Total	227	9	1504	36	225	6	981	15

[a] NISP is total number of identified bone remains; MNI is minimum number of individuals.

Table 5
Reconstruction of fish sizes based on bone remains from Voronin Grotto sediments.

Taxa	Size (cm)							Total
	8–10	10–12	12–15	15–20	20–25	25–30	45–50	
Esox lucius L.	1	3	3	1	1	1	1	11
Perca fluviatilis L.	1	2	1	2	–	–	–	6
Gymnocephalus cernuus L.	–	1	–	–	–	–	–	1
Thymallus thymallus L.	2	1	1	–	–	–	–	4
Cottus gobio L.	3	3	–	–	–	–	–	6
Lota lota L.	2	4	4	3	–	–	–	13
Squalius cephalus L.	–	–	1	–	–	–	–	1
Phoxinus phoxinus L.	2	–	–	–	–	–	–	2
Gobio gobio L.	1	–	–	–	–	–	–	1
Total	12	14	10	6	1	1	1	45

Table 6
Species composition and the number of identified bird bone remains in Voronin Grotto sediments and distribution of bird species by habitat(s) in the Urals according to Ryabitsev (2008).

Taxa №	Taxa	Habitat type[a]	Layer 1		Layer 2a		Layer 2b		Layer 3	
			NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Anseriformes										
1	*Anas platyrhynchos* Linnaeus, 1758	A	–	–	1	1	–	–	–	–
2	*Anas crecca* Linnaeus, 1758	A	–	–	1	1	–	–	1	1
3	*Anas* sp.	A	4	–	1	–	–	–	1	–
	Accipitriformes									
4	*Milvus migrans* Boddaert, 1783	E	1	1	–	–	–	–	–	–
Galliformes										
5	*Tetrao tetrix* Linnaeus, 1758	F	1	1	1	1	–	–	–	–
6	*Tetrao urogallus* Linnaeus, 1758	F	1	1	–	–	–	–	–	–
7	*Tetrao* sp.		4	–	5	–	1	–	–	–
Charadriiformes										
8	*Scolopax rusticola* Linnaeus, 1758	F	–	–	1	1	–	–	–	–
9	*Charadrii* indet.		1	–	–	–	–	–	–	–
Strigiformes										
10	*Bubo bubo* Linnaeus, 1758	F	–	–	–	–	–	–	1	1
11	*Aegolius funereus* Linnaeus, 1758	F	2	1	–	–	–	–	–	–
Piciformes										
12	*Dendrocopos major* Linnaeus, 1758	F	2	1	–	–	–	–	–	–
13	*Picidae* indet.		4	–	–	–	–	–	–	–
Passeriformes										
14	*Turdus pilaris* Linnaeus, 1758	E	2	1	–	–	1	1	–	–
15	*Turdus philomelos* Brehm, 1831	F	1	1	–	–	–	–	–	–
16	*Turdus* sp.		6	–	–	–	–	–	–	–
17	Passeriformes (up to *Motacillidae* size)		41	–	48	–	17	–	27	–
	Aves indet.		89	–	164	–	40	–	74	–
	Total		159	7	222	4	59	1	104	2

[a] Habitats are divided into 3 types (A, "amphibians"; E, "ecotone"; F, "forest"), in accordance with Tomek and Bocheński (2005).

analysis v.2020 (land) 0.5°-resolution gridded dataset for precipitation (Schneider et al., 2020).

4. Results

4.1. Taphonomy

In the deposits of the Voronin Grotto, a large number of bone remains of fish (7.3–37.9% throughout the sequence), amphibians (16.9–34.6%), and mammals (21.1–44.1%) were found (Fig. 4). The bones of reptiles and birds were found in significantly smaller amounts at 4.9–18.4% and 1.9–10.1%, respectively. However it should be precise that in layers 3 and 2b reptiles were relatively abundant (18.4 and 16.3%, respectively).

Analysis of digestion traces on 741 arvicoline molars (Table 3; Table A1) revealed significant differences between layers 1–2a and 2b–3, because, according to Suchéras-Marx et al. (2019), their confidence intervals did not overlap. In all layers, the total share of digested teeth was less than 50%, which indicates the accumulation of remains of small mammals could be produced by a nocturnal bird of prey. However, the high proportions of heavy and extreme digested molars in layers 2b–3 indicate that either diurnal bird predators or mammal predators also took part in the accumulation.

4.2. Fish assemblage

A total of 2937 fish bones, vertebrae and scales (23.1% of total NISP) were found in the sediments of the grotto (Table 4), of which 1982 bone remains were identified to species level. The remains of 9 fish species belonging to 6 orders have been identified.

In terms of the number of remains, species belonging to the order Perciformes (NISP = 580) prevailed, and further, in decreasing order, Salmoniformes (NISP = 500), Gadiformes (NISP = 452), Esociformes (NISP = 402), Cypriniformes (NISP = 122) and Scorpaeniformes (NISP = 32). The fish sizes were reconstructed using 45 bones (Table 5). Fish that were a 10–15-cm size prevailed (24 bones in total). Fish with sizes of 8–10 cm and 15–20 cm are represented by fewer bone numbers (12 and 6 bones, respectively). Fish larger than 20 cm are represented only by single bones. In layer 2a, 4 northern pike vertebrae with traces of thermal action (presumably from a fire) were found.

Table 7
Species composition and the number of identified mammal bone remains in Voronin Grotto sediments.

Taxa N°	Taxa	Layer 1		Layer 2a		Layer 2b		Layer 3	
		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Eulipotyphla									
1	*Talpa europaea* Linnaeus, 1758	3	1	11	1	3	1	7	1
2	*Neomys fodiens* Pennant, 1771	2	2	11	2	10	3	1	1
3	*Sorex araneus* Linnaeus, 1758	4	2	8	5	12	7	2	1
4	*S. caecutiens* Laxmann, 1785	3	2	5	2	2	2	–	–
5	*S. isodon* Turov, 1936	–	–	–	–	4	3	–	–
6	*S. minutus* Linnaeus, 1766	3	2	5	4	3	2	–	–
7	*Sorex* sp.	39		83		27		20	
Chiroptera									
8	Chiroptera indet.	21		75		97		45	
	Lagomorpha								
9	*Ochotona* cf. *pusilla* Pallas, 1769	–	–	–	–	1	1	–	–
10	*Lepus timidus* Linnaeus, 1758	2	1	3	1	1	1	3	2
Rodentia									
11	*Pteromys volans* Linnaeus, 1758	1	1	–	–	–	–	–	–
12	*Sciurus vulgaris* Linnaeus, 1758	–	–	3	1	5	1	–	–
13	*Castor fiber* Linnaeus, 1758	–	–	2	1	4	1	1	1
14	*Sicista* cf. *betulina* Pallas, 1779	–	–	3	2	1	1	1	1
15	*Apodemus agrarius* Pallas, 1771	1	1	3	1	6	2	2	1
16	*A. uralensis* Pallas, 1811	4	2	4	1	3	1	1	1
17	*Apodemus* sp.	2		–	–	1		5	
18	*Micromys minutus* Pallas, 1771	1	1	1	1	1	1	–	–
19	*Cricetus cricetus* Linnaeus, 1758	1	1	–	–	20	3	9	1
20	*Craseomys rufocanus* Sundevall, 1846	1	1	3	1	–	–	–	–
21	*Clethrionomys glareolus* Schreber, 1780	30	6	69	13	50	10	18	5
22	*Cl. rutilus* Pallas, 1779	25	7	60	10	14	3	9	3
23	*Cl.* ex gr. *glareolus-rutilus*	15	1	29	3	18	2	6	1
24	*Arvicola amphibius* Linnaeus, 1758	2	1	20	4	26	6	3	1
25	*Alexandromys oeconomus* Pallas, 1776	3	2	5	4	–	–	2	1
26	*Microtus agrestis* Linnaeus, 1761	10	4	13	4	24	8	7	3
27	*M. arvalis* s.l.	6	4	19	12	10	6	–	–
28	*M.* ex gr. *arvalis-agrestis*	–	–	1	1	5	3	–	–
29	*Microtus* s.l. sp.	38		101		96		24	
30	Rodentia indet. (postcranial bones)	386		988		920		373	
Carnivora									
31	*Vulpes vulpes* Linnaeus, 1758	1	1	–	–	–	–	1	1
32	*Mustela nivalis* Linnaeus, 1766	–	–	2	1	–	–	–	–
33	*Mustela erminea* Linnaeus, 1758	–	–	2	1	–	–	–	–
34	*Martes* sp.	–	–	1	1	1	1	–	–
Cetartiodactyla									
35	*Rangifer tarandus* Linnaeus, 1758	–	–	–	–	–	–	3	1
36	*Alces alces* Linnaeus, 1758	–		2	1	1	1	4	1
	Total	**604**	**43**	**1532**	**78**	**1366**	**70**	**547**	**27**

4.3. Bird assemblage

In the sediments of the grotto, 544 bird bones were found (4.3% of total NISP), but only 14 of them were identified to species level. The rest of the bird remains were difficult to identify to the species level due to poor preservation. Therefore, data on the distribution of birds in habitats are given in Table 6 for illustrative purposes only.

Nevertheless, it was possible to identify the bones of 11 bird species belonging to 7 orders. Bones of representatives of the order Passeriformes (NISP = 143) predominated. The following orders are represented by a smaller number of remains, in descending order: Galliformes (NISP = 13), Anseriformes (NISP = 9), Piciformes (NISP = 6), Strigiformes (NISP = 3), Charadriiformes (NISP = 2), and Accipitriformes (NISP = 1).

Only 6% of the total number of bird bones were intact and, therefore, were of pellet origin. The remaining 94% of the bones were highly fragmented and bore the chewing marks characteristic of carnivorous mammals. One radius, belonging to a male western capercaillie from layer 1, had characteristic damaged epiphyses. We previously noted similar damage to the radius bones at a number of archaeological sites in Western Siberia (Poshekhonova et al., 2015, 2018).

4.4. Mammal assemblage

A total of 4049 bone remains (31.9% of total NISP) of 29 mammal species belonging to 6 orders (Eulipotyphla, Chiroptera, Lagomorpha, Rodentia, Carnivora, and Cetartiodactyla) were identified in the grotto sediments (Table 7). Twenty-two identified taxa belong to small mammals (Eulipotyphla, Chiroptera, Lagomorpha: Ochotonidae, and Rodentia) (Fig. 5). Rodents predominate both in the number of remains (NISP = 3515) and in the number of species (15). The orders Eulipotyphla (NISP = 268), Chiroptera (NISP = 238), Lagomorpha (NISP = 10), Carnivora (NISP = 8), and Cetartiodactyla (NISP = 10) are represented by a significantly smaller number of remains.

In all layers of the grotto sequence, the predominant species among small mammals are the forest voles of genus *Clethrionomys* (in total, 22.1–37.5% of MNI) (Table 8). After *Clethrionomys* voles, the field vole *Microtus agrestis* and common vole *M. arvalis* s.l. are the most abundant species (5.4–12.5% and 8.8–16.2%, respectively). However, in contrast to the field vole, the common vole is present only in layers 1–2b, while it is absent in layer 3. The common shrew *Sorex araneus* Linnaeus, 1758 is the most abundant species among insectivores (4.2–10.3%).

4.5. Palaeoenvironment and palaeodiversity

Analysis of the distribution of the eulipotyphlan, lagomorph, and

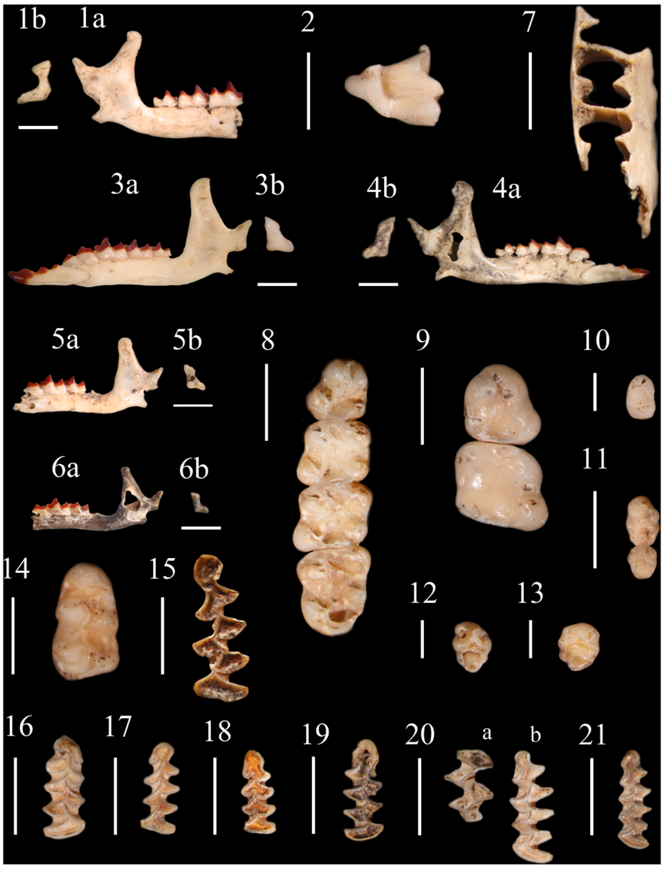

Fig. 5. Small mammal assemblage from the Voronin Grotto sediments. 1-*Neomys fodiens* Pennant, 1771: fragment of right mandible with m1–m3 from layer 2b in labial view (a) and articular process (b); 2-*Talpa europaea* Linnaeus, 1758: left M2 from layer 2a in occlusal view; 3-*Sorex araneus* Linnaeus, 1758: left mandible with i–m3 from layer 3 in labial view (a) and articular process (b); 4-*S. isodon* Turov, 1936: right mandible with i and p4–m3 from layer 2b in labial view (a) and articular process (b); 5-*S. caecutiens* Laxmann, 1785: left mandible with p4–m2 from layer 2b in labial view (a) and articular process (b); 6-*S. minutus* Linnaeus, 1766: fragment of left mandible with p4–m2 from layer 2b in labial view (a) and articular process (b); 7-*Ochotona* cf. *pusilla* Pallas, 1769: fragment of right mandible without teeth from layer 2b in alveolar view; 8-*Pteromys volans* Linnaeus, 1758: left p4–m3 from layer 1 in occlusal view; 9-*Sciurus vulgaris* Linnaeus, 1758: right p4–m1 from layer 2b in occlusal view; 10-*Sicista* cf. *betulina* Pallas, 1779: right m1 from layer 3 in occlusal view; 11-*Micromys minutus* Pallas, 1771: right M1–M2 from layer 1 in occlusal view; 12-*Apodemus agrarius* Pallas, 1771: left M2 from layer 2a in occlusal view; 13-*A. uralensis* Pallas, 1811: right M2 from layer 2a in occlusal view; 14-*Cricetus cricetus* Linnaeus, 1758: right m1 from layer 2b in occlusal view; 15-*Arvicola amphibius* Linnaeus, 1758: left m1 from layer 2a in occlusal view; 16-*Craseomys rufocanus* Sundevall, 1846: right m1 from layer 2a in occlusal view; 17-*Clethrionomys glareolus* Schreber, 1780: left m1 from layer 2a in occlusal view; 18-Cl. *rutilus* Pallas, 1779: left m1 from layer 2a in occlusal view; 19-*Alexandromys oeconomus* Pallas, 1776: right m1 from layer 2a in occlusal view; 20-*Microtus agrestis* Linnaeus, 1761: right M2 (a) and left m1 (b) from layer 2b in occlusal view; 21-*M. arvalis* s.l.: left m1 from layer 1 in occlusal view. Scale bars are 2 mm (numbers 1–9, 11, 14–21) and 1 mm (numbers 10, 12, 13).

rodent taxa relative abundance by the 5 types of habitats in each layer of the Voronin Grotto sequence showed that the landscape was dominated by forests (Wo: 52.2–63.5%), with a significant proportion of open mesophytic meadows (OH: 25.0–29.8%), with abundant near-water and steppe areas (Wa: 6.5–10.7%, and OD: 2.1–3.6%, respectively), and with scarce rocky habitats (Ro: 0.7–2.4%) (Table 9).

The lowest species richness of small mammals was noted in layer 3 of the grotto sequence, which was apparently associated with the smallest number of individuals found in the layer. Values of species richness in layers 2a and 2b were approximately the same, whereas in layer 1 it decreased again, which was also associated with a smaller number of individuals in this layer compared to those found in layers 2a and 2b. The Simpson evenness index (1-D) values varied slightly from bottom to top of the sequence without any significant shifts (Table 9).

4.6. Palaeoclimate

The mean annual temperatures (MAT) inferred by means of the Bioclimatic Model (Table 10; Tables B1–B2) for layers 2b and 3 were warmer than the present-day data by 0.2 and 1.3 °C, respectively. MAT values of layers 1 and 2a were colder than current data by 1.9 and 0.7 °C, respectively. However, the mean annual temperatures established for layers 2a and 2b only slightly differed from the current values. The mean temperatures of the warmest month (MTW) estimated for layers 2b and 3 correspond to the current value, and the values obtained for layers 1 and 2a were colder than present-day MTW by 1.7 and 0.5 °C, respectively. The greatest differences were observed in the mean temperatures of the coldest month (MTC), which were between 2.7 °C warmer (layer 3) and 2.5 °C colder (layer 1) than present-day data. Values of the total annual precipitation (P) were, overall, less than the current P and ranged between 508 mm (layer 1) and 528 mm (layer 3).

5. Discussion

5.1. Palaeobiogeographical considerations

Almost all species of studied vertebrate assemblages determined in the layers of the Voronin Grotto sequence currently inhabit the vicinity of the grotto, except for steppe pika *Ochotona pusilla* Pallas, 1769 (Bolshakov et al., 2006; Ryabitsev, 2008; Kizhevatov, 2017). A pika right mandible (Fig. 5, no. 7) was found in the lowest part of layer 2b. The distribution of steppe pika is related to steppe habitats (Sokolov et al., 1994). Among the known localities of the small mammal remains in the Serga River valley, this is the first evidence of a pika remains from between 3310 ± 40 and 1899 ± 36 cal BP. The latest remains of this species in this area were found in the Lower and Middle Holocene sediments of the Dyrovaty Kamen Cave and were dated to between 7370 ± 40 and 10590 ± 240 cal BP (Smirnov, 1993). The earliest fossils of the species were found in the sediments of the Upper Pleistocene of the Svetly Rock shelter and were aged at 19800 ± 120 cal BP (Korkina et al., 2016). Consequently, steppe pika was widespread in this territory during the Late Pleistocene and Early Holocene time between 19800 and 10590 cal BP. Finally, the species disappeared over most of this territory during the Middle Holocene after 7370 cal BP. Currently, the nearest habitats of the steppe pika are located more than 200–300 km to the south of the grotto in the steppes of the Obshchyi Syrt Range and South Urals (Lissovsky, 2012). Thus, we can assume that steppe pika inhabited the vicinity of the Voronin Grotto as a relic of the Late Pleistocene and Early Holocene faunas between 3310 ± 40 and 1899 ± 36 cal BP. In our opinion, this is possible only due to the location of the grotto on the north-eastern edge of the Krasnoufimsk insular forest-steppe, which is a relic of the Late Pleistocene "cold steppes" (Krasheninnikov, 1937). Late Holocene remains of steppe pika were also found by us in the sediments of the Nizhneirginsky Grotto (Izvarin et al., 2020), which is located on the north-western edge of the insular forest-steppe approximately 100 km to the northwest of the Voronin Grotto.

5.2. Taphonomy notes and predator identification

The osteological collection from the Voronin Grotto deposits is distinguished by a high proportion of remains of fish (23.1% of total NISP), amphibians (28.7%) and mammals (31.9%). High proportion of fish (70–90% or more) was noted in the diet of the otter *Lutra lutra* Linnaeus, 1758 (Abelentsev, 1968; Tyurnin, 1998; Palazón et al., 2008; Hung and Law, 2016). The proportion of amphibian remains in the

Table 8
Relative abundance (%) of Eulipotyphla, Lagomorpha, and Rodentia taxa per level of Voronin Grotto sequence counted via MNI and their distribution by habitat(s) in the Urals according to Bolshakov et al. (2006).

Taxa №	Taxa	Layers				Habitats[a] according to López-García et al. (2010)				
		1	2a	2b	3					
		%MNI	%MNI	%MNI	%MNI	OD	OH	Wo	Ro	Wa
1	*Talpa europaea* Linnaeus, 1758	2.4	1.4	1.5	4.2		0.5	0.5		
2	*Neomys fodiens* Pennant, 1771	4.8	2.7	4.4	4.2		0.25			0.75
3	*Sorex araneus* Linnaeus, 1758	4.8	6.8	10.3	4.2		0.25	0.75		
4	*S. caecutiens* Laxmann, 1785	4.8	2.7	2.9	0		0.5	0.5		
5	*S. isodon* Turov, 1936	0	0	4.4	0			1		
6	*S. minutus* Linnaeus, 1766	4.8	5.4	2.9	0		0.25	0.5	0.25	
7	*Ochotona* cf. *pusilla* Pallas, 1769	0	0	1.5	0	1				
8	*Lepus timidus* Linnaeus, 1758	2.4	1.4	1.5	8.3		0.5	0.5		
9	*Pteromys volans* Linnaeus, 1758	2.4	0	0	0			1		
10	*Sciurus vulgaris* Linnaeus, 1758	0	1.4	1.5	0			1		
11	*Castor fiber* Linnaeus, 1758	0	1.4	1.5	4.2			0.5		0.5
12	*Sicista* cf. *betulina* Pallas, 1779	0	2.7	1.5	4.2		0.25	0.75		
13	*Apodemus agrarius* Pallas, 1771	2.4	1.4	2.9	4.2		0.5	0.5		
14	*A. uralensis* Pallas, 1811	4.8	1.4	1.5	4.2		0.25	0.75		
15	*Micromys minutus* Pallas, 1771	2.4	1.4	1.5	0		0.75	0.25		
16	*Cricetus cricetus* Linnaeus, 1758	2.4	0	4.4	4.2	0.5	0.5			
17	*Craseomys rufocanus* Sundevall, 1846	2.4	1.4	0	0			0.5	0.5	
18	*Clethrionomys glareolus* Schreber, 1780	14.3	17.6	14.7	20.8			1		
19	*Cl. rutilus* Pallas, 1779	16.7	13.5	4.4	12.5			1		
20	*Cl.* ex gr. *glareolus-rutilus*	2.4	4.1	2.9	4.2			1		
21	*Arvicola amphibius* Linnaeus, 1758	2.4	5.4	8.8	4.2		0.25			0.75
22	*Alexandromys oeconomus* Pallas, 1776	4.8	5.4	0	4.2		0.75			0.25
23	*Microtus agrestis* Linnaeus, 1761	9.5	5.4	11.8	12.5		0.5	0.5		
24	*M. arvalis* s.l.	9.5	16.2	8.8	0	0.25	0.75			
25	*M.* ex gr. *arvalis-agrestis*	0	1.4	4.4	0	0.333	0.333	0.333		
	Total MNI	**42**	**74**	**68**	**24**					

[a] Habitats are divided into five types (OD, open dry; OH, open humid; Wo, woodland/woodland-edge; Ro, rocky; Wa, water), in accordance with López-García et al. (2010).

Table 9
Palaeoenvironment and palaeodiversity reconstructions based on small mammal assemblage from the Voronin Grotto sequence: weighted (%) small mammal habitat[a] preferences with 95% confidence intervals (95% CI), Simpson evenness index (1-D) with 95% CI, and number of small mammal taxa.

Layers	MNI	Number of taxa	1–D (95% CI)	OD (95% CI)	OH (95% CI)	Wo (95% CI)	Ro (95% CI)	Wa (95% CI)
1	42	19	0.915 (0.891–0.934)	3.6 (0.6–16.2)	29.8 (17.6–47.1)	57.2 (41.0–72.3)	2.4 (0.1–12.6)	6.5 (1.5–19.5)
2 a	74	21	0.903 (0.883–0.928)	4.5 (0.8–11.4)	29.8 (19.7–41.5)	55.5 (43.4–67.0)	2.0 (0.0–7.3)	8.1 (3.0–16.8)
2b	68	22	0.923 (0.903–0.938)	7.4 (2.4–16.3)	29.0 (19.0–41.7)	52.2 (39.0–63.8)	0.7 (0.0–5.3)	10.7 (4.2–20.1)
3	24	15	0.899 (0.865–0.924)	2.1 (0.1–21.1)	25.0 (9.8–46.7)	63.5 (40.6–81.2)	0.0 (0.0–14.2)	9.4 (1.0–27.0)

[a] OD, open dry; OH, open humid; Wo, woodland; Ro, rocky; Wa, water.

Table 10
Temperature and precipitation values[a] estimated for the Voronin Grotto sediments using the Bioclimatic Model.

	Current values	Layer 1	Layer 2a	Layer 2b	Layer 3
MAT (°C)	2.3	0.4	1.6	2.5	3.6
SE		3.1	3.1	3.1	3.2
Δ		−1.9	−0.7	0.2	1.3
MTW (°C)	18.3	17.1	17.8	18.2	18.0
SE		2.5	2.5	2.5	2.6
Δ		−1.2	−0.5	−0.1	−0.3
MTC (°C)	−14.4	−16.9	−15.2	−13.9	−11.7
SE		7.0	7.1	7.1	7.3
Δ		−2.5	−0.8	0.5	2.7
P (mm)	588	528	525	515	508
SE		298	287	286	285
Δ		−60	−63	−73	−80

[a] Mean annual temperature in °C (MAT); mean temperature of the warmest month in °C (MTW); mean temperature of the coldest month in °C (MTC); total annual precipitation in mm (P); standard error of the predicted values (SE); difference (Δ) between the values obtained for each layer and present-day data.

stomachs and excrements of this species ranges from 1.1% (Palazón et al., 2008) to 30–40% (Abelentsev, 1968; Tyurnin, 1998; Hung and Law, 2016). The percentage of small mammals in the otter's diet is on average 10–12% (Abelentsev, 1968; Hung and Law, 2016), but in winter, it can reach more than 20% (Tyurnin, 1998). In addition to the otter, high proportions of fish, amphibians, and mammals were noted in the diet of the European mink *Mustela lutreola* Linnaeus, 1758 (Abelentsev, 1968; Maran et al., 1998; Palazón et al., 2008). Fish sizes between 10 and 15 cm reconstructed for fish assemblage from Voronin Grotto sediments are typical for otter and mink prey (Palazón et al., 2008; Hung and Law, 2016).

The proportions of digested arvicoline molars in layers 1 and 2a (8.3 and 11.9%, respectively) are typical of European eagle owl *Bubo bubo* Linnaeus, 1758 (Fig. 6A), belonging to the 3rd digestion category of predators in accordance with Andrews (1990) and Fernández-Jalvo et al. (2016).

In layers 2b and 3, the total proportion of digested teeth were 37.4 and 49.3%, respectively (Table 3, Fig. 6B), which were close to the values of the predator category 4. According to Andrews (1990) and Fernández-Jalvo et al. (2016), this category includes little owl *Athene noctua* Scopoli, 1769, the kestrel *Falco tinnunculus* Linnaeus, 1758, and mustelids (pine marten *Martes martes* Linnaeus, 1758, for example).

Obviously, the bones of fish and amphibians were collected as a result of the predatory activity of an otter or mink. Various predators participated in the accumulation of bones of small mammals, but in layers 1 and 2a, the remains were accumulated mainly because of the

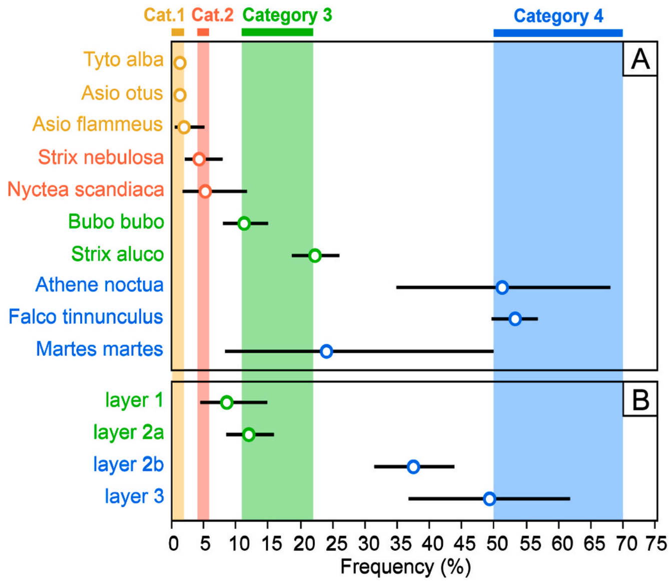

Fig. 6. Digestion categories of predators defined following Fernández-Jalvo et al. (2016). A, Proportion (%) of digested molars of arvicolines obtained from pellets of nocturnal and diurnal predators and from excrements of mammal predator (Andrews, 1990; Fernández-Jalvo et al., 2016). B, Proportion (%) of digested molars obtained from Voronin Grotto sediments. Horizontal black lines are the 95% confident intervals.

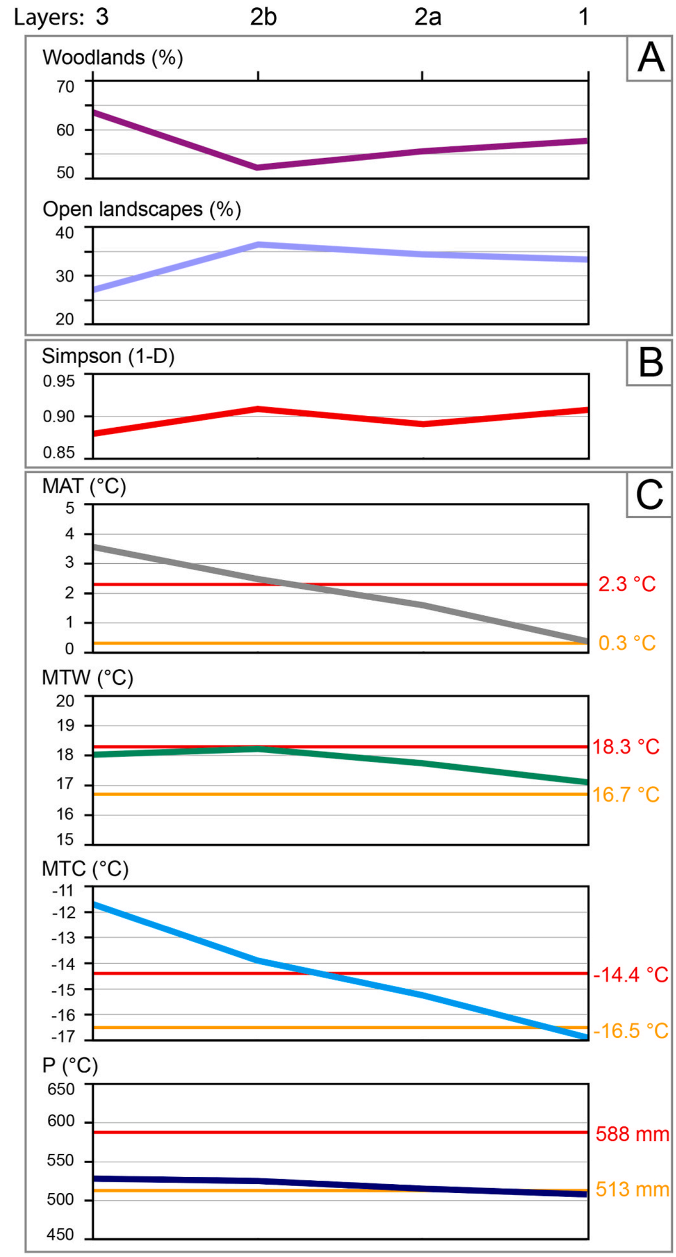

Fig. 7. Palaeoenvironment, palaeodiversity and palaeoclimate reconstructions based on small mammal assemblage from the Voronin Grotto sequence. A, Landscape types inferred through the Habitat Weighting method for the surroundings of the Voronin Grotto at each layer. B, Simpson evenness index (1–D). C, Climatic parameters estimated for the Voronin Grotto sediments using the Bioclimatic Model "Eulipotyphla-Rodentia": MAT, mean annual temperature in °C; MTW, mean temperature of the warmest month in °C; MTC, mean temperature of the coldest month in °C; P, total annual precipitation in mm. Coloured numbers demonstrate the current values of climatic parameters (red) and the values obtained at the territory of the Serga River valley in 1881–1935 (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

predatory activity of the eagle owl. In layers 2b and 3, mustelids (possibly an otter or mink) prevailed in accumulation of small mammal bones. However, given that in these layers the relative abundance of small mammal remains is rather high (up to 44.1%) and this is not typical for the diet of either the otter or the mink, it should be assumed that owls also took part in the accumulation of small mammals. Therefore, palaeoenvironmental interpretations based on osteological material of small mammals from studied strata are quite reasonable.

5.3. Palaeoenvironmental and palaeoclimate remarks

It has been established that the Voronin Grotto was periodically visited by human population in the period between the Late Bronze Age and the Early Iron Age, and bonfire marks on the surface of the sediments and modern anthropogenic garbage in the upper part of layer 1 indicates that people visit the grotto in the present time.

Palaeoenvironmental analysis of small mammal assemblage for each grotto stratum revealed the predominance of woodlands (Fig. 7A) surrounding the grotto during at least the last 3310 yrs. Only insignificant shifts were observed towards "woodland" or "open" habitat types throughout the sediment sequence. In general, this is consistent with the data for birds, among which forest species predominate (Table 6).

However, changes in the proportions of some indicator species remnants between the strata, in our opinion, may be associated with changes in the landscape in the vicinity of the grotto during the period of sediment accumulation. From layer 3 to layer 2b, the relative abundances of forest species (*Talpa europaea*, *Sicista* cf. *betulina*, *Apodemus uralensis*, voles of the genus *Clethrionomys*) decreased (Table 8). However, the proportion of remains of the common vole (*Microtus arvalis* s.l.) increased from 0 to 8.8%. The common vole, being an inhabitant of open mesophytic meadows (Markova et al., 2018), gained maximum distribution at least in the territory of Russia due to the destruction of natural ecosystems by humans for various economic needs (e.g. felling of forests or ploughing of steppes), and as a result, it was able to move deep into taiga and steppe biomes (Bobrov et al., 2008). At the same time, there was a slight shift in the ratio of open and woodland habitats (Fig. 7A) towards an increase in the former (from 26 to 33.8%) and a decrease in the latter (from 63.5 to 52.2%). Perhaps this was due to human activity, because archaeological cultures, artefacts of which were found in layers 2a–3, were characterized by metallurgy, which requires a large amount of charcoal and, consequently, intensive forest cutting. Furthermore, from layer 2b to layer 1, the proportion of forest habitats again increased (from 52.2 to 57.7%). Moreover, the relative abundances of taiga species (*Craseomys rufocanus*, *Clethrionomys rutilus*) increased among forest dwellers. This is consistent with palynological data (Khotinsky, 1977;

Panova and Antipina, 2016; Lapteva et al., 2017) in which, in the Middle Urals after 3400 cal BP, the role of boreal coniferous trees in the forests gradually increased and forests acquired a present-day taiga pattern.

Nevertheless, the landscape around the grotto and, therefore, the structure of the small mammal community remained mainly stable during the period of accumulation of the sediments, i.e., for approximately 3310 yrs. In addition, the values of the Simpson 1–D index are near to 1 throughout the section (Fig. 7B). This indicates rather homogeneous environmental conditions near the grotto during the period of sedimentation.

Palaeoclimate analysis of the insectivore and rodent fauna (Bioclimatic Model "Eulipotyphla-Rodentia") showed a decrease in the mean annual temperature (MAT) since at least 3310 ± 40 cal BP, which was mainly due to cooling in the winter months (Table 10; Fig. 7C). It is possible this could be attributed to the "Subboreal cooling" in 3400–2600 cal BP (Panova and Antipina, 2016; Lapteva et al., 2017). The climate at approximately 3310 ± 40 cal BP (the Late Bronze Age) was milder than in the present day, and the winters were warmer. At approximately 1899 ± 36 cal BP (the Early Iron Age) and a little later, the climate was similar to the present-day climate of the region. At the same time, values of the climatic parameters estimated for that time differed slightly from the present-day values. Perhaps between 3310 and 1899 cal BP, the climate of the south-west Middle Urals belonged to the same Dfb type according to the Köppen–Geiger classification (cold, without a dry season, and with warm summers; Beck et al., 2018) like the present-day climate of the region. By the time of the formation of layer 1, temperatures had decreased to values lower than modern ones, especially in winter, and the climate became noticeably more severe than at the present day. Nevertheless, according to Prokaev (1963), the temperature and precipitation values (MAT, MTW, MTC, and P) reconstructed for layer 1 (Fig. 7C) correspond to the values of the climatic parameters obtained at the territory of the Serga River valley in 1881–1935 (MAT = 0.1–0.3 °C; MTW = 16.0–16.7 °C; MTC = −16.6 °C; P = 513–585 mm). According to these data, the climate at that time was cold, without a dry season, but with a cold summer (type Dfc according to the Köppen–Geiger classification).

6. Conclusions

The Voronin Grotto sediments were accumulated over approximately 3310 ± 40 cal BP, i.e., during the Late Holocene. The grotto was periodically visited by humans between 3310 ± 40 cal BP (Late Bronze Age) and 1899 ± 36 cal BP (Early Iron Age) and is being visited by people currently.

The vertebrates bone remains identified in the sediments were accumulated by different predators. The bones of fish and amphibians were collected as a result of the predatory activity of the otter or mink. Bone remains of small mammals were accumulated due to predation activity of the eagle owl and mustelids (possibly the otter or mink).

Almost all species of the studied vertebrate assemblages currently inhabit the vicinity of the grotto, as well as throughout the Middle Urals, with the exception of the steppe pika. Steppe pika was widespread in the Urals at the end of the Late Pleistocene – Early Holocene. The species became extinct during the Middle Holocene in the most of the Urals and adjacent territories, with the exception of its southern regions. Perhaps between 3310 and 1899 cal BP steppe pika inhabited the vicinity of the grotto as the Late Pleistocene – Early-Holocene relic, which was possible only due to the location of the grotto at the edge of the Krasnoufimsk insular forest-steppe (which itself is a relic of the Late Pleistocene "cold steppes").

Landscape and fauna of small mammals near the grotto remained stable during the period of accumulation of the sediments, i.e. for approximately 3310 yrs. This is consistent with high values (close to 1) of the Simpson evenness index (1−D) based on small mammal assemblage from the grotto sequence. The landscape was dominated by forests with a significant proportion of open mesophytic meadows. However, between 3310 and 1899 cal BP, the ratio of forests in the landscape decreased, whereas the ratio of open meadows increased. Perhaps this was due to human activity because those Bronze Age and early Iron Age cultures, the artefacts of which were found in layers 2a–3, were characterized by metallurgy, which requires a large amount of charcoal and, consequently, intensive deforestation. After 1899 cal BP, the relative abundances of taiga small mammal species increased among forest dwellers, which is consistent with palynological data from the Middle Urals.

At approximately 3310 ± 40 cal BP, the climate of the south-west Middle Urals, where the grotto is located, was milder, and the winters were warmer than in the present day. At approximately 1899 ± 36 cal BP, the climate was similar to the modern climate of the region and was of the Dfb type (cold, without a dry season, and with warm summers) according to the Köppen–Geiger classification as well as in the previous period. Towards the recent time, the climate became colder and was possibly of the Dfc type according to the Köppen–Geiger classification.

Author contributions

Evgeniy Izvarin: Conceptualization, Investigation (excavation; study of small mammal assemblage), Formal analysis (quantitative, taphonomic and palaeoenvironmental analyzes), Writing–Original Draft, Writing–Review & Editing, Visualization, Project administration. **Anatoliy Ulitko:** Conceptualization, Investigation (excavation; stratigraphical description; identification of large mammal remains), Formal analysis (quantitative analysis), Writing–Original Draft, Project administration. **Svetlana Panina:** Investigation (study of archaeological collection), Formal analysis (quantitative analysis), Writing–Original Draft. **Elya Zazovskaya:** Investigation (radiocarbon analysis). **Aleksey Nekrasov:** Investigation (species identification of fish and bird remains), Formal analysis (quantitative analysis), Writing–Original Draft.

Data availability

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

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2022.02.031.

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