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Northern Urals (Russia) quaternary deposits and biostratigraphical record caves and grottoes

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ABSTRACT

Investigations of the unconsolidated Upper Pleistocene – Holocene cave deposits of the Northern Urals resulted in detailed biostratigraphical and palaeoenvironmental data. The article summarizes data from important stratigraphical levels exposed in 19 cave localities, most part of which represent several layers dated to different periods. These data cover the period from the beginning of the Upper Pleistocene (MIS 5-4) to the end of the Upper Holocene. At the beginning of Marine Isotope Stage 3 (MIS 3), open woodlands were distributed, which at the end of MIS 3 were replaced by Forest–steppe landscapes. At the beginning of MIS 2 (LGM), Periglacial steppe landscape was distributed. At the end of MIS 2 and at the beginning of the Holocene (MIS 1), semi-open landscapes were common. At the beginning of the Middle Holocene, they were replaced by taiga landscapes. Fish were present in the fauna of the Northern Urals in the Upper Pleistocene and Holocene. Amphibians in the Upper Pleistocene as part of the fauna of the region appear only at its beginning (MIS 5-4) and end (Bølling – Allerød period). Since the beginning of the Holocene (MIS 1), they have been constantly present in the fauna of the Northern Urals. Reptiles appear in the fauna of the region only in the Middle Holocene. During the Upper Pleistocene, the avifauna and fauna of small mammals were dominated by species of open landscapes, and the fauna of large mammals was dominated by species of open and semi-open landscapes. At the beginning of the Holocene, the avifauna and theriofauna increased the number of species associated with tree and shrub vegetation and near-aquatic species. Since the beginning of the Middle Holocene, the avifauna and theriofauna have been dominated by species of taiga landscapes. Palynological data and data on the fauna of small and large mammals allow us to separate the deposits of the Upper Pleistocene and Holocene. These data also allow us to separate the deposits of the beginning (MIS 5-4), middle (MIS 3), end (MIS 2)) of the Upper Pleistocene, Lower, Middle and Upper Holocene (MIS 1).

1. Introduction

This paper presents biostratigraphical data from the caves and grottoes located in the Northern Urals (approximately 59°–64°N and 58°–60°E) (Fig. 1; Table 1). All studied caves and grottoes occur in limestone and are of karst origin. The caves under study are located on the western and eastern slopes of the Northern Urals. On the western slope, they are located in the Upper Pechora River and its tributaries. On the eastern slope, the caves are located in the Upper Loz'va and Sos'va Rivers. Caves with soft deposits are also known on the Vishera River on the western slope, but there are only preliminary data on the biostratigraphy of their deposits (Melnichuk et al., 2001; Fadeeva, 2002; Kosintsev et al., 2005; Maksimova, 2006; Fadeeva and Smirnov, 2008).

The first biostratigraphical data were obtained in 1847 in the Uninskaya Cave located on a tributary of the Pechora River (Gofman, 1856). Focused studies of the biostratigraphy of the cave deposits on the western slope of the Northern Urals started in the late 1950s and are associated with geological and archaeological research (Kanivets, 1962, 1964; Vereschagin, Kuzmina, 1962; Guslitser and Kanivets, 1965). The researchers continued their studies in 1970–1980s (Kuzmina, 1971; Sukhov, 1976; Guslitser and Pavlov, 1988; 1989; Kochev, 1993), and fresh studies are now under way (Melnichuk et al., 2001; Fadeeva, 2002; Kosintsev et al., 2005; Maksimova, 2006; Fadeeva and Smirnov, 2008; Kryazheva et al., 2019). The studies of the loose deposits in the caves located on the eastern slope began in the late 1970s (Petrin, 1979) and continue with short interruptions to the present day (Smirnov et al.,

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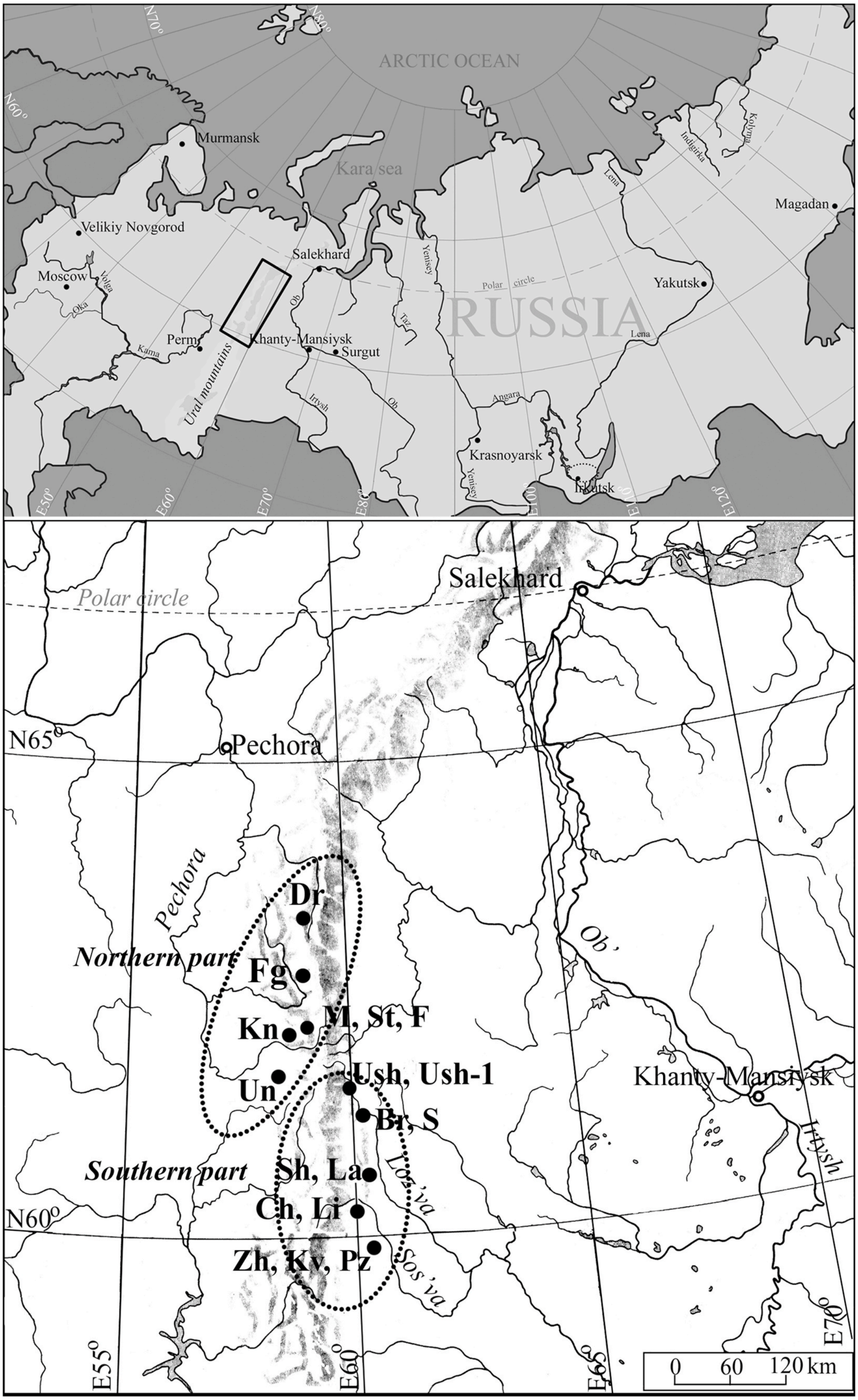

Fig. 1. Studied Norhern-Uralian area with the locations of the caves
Northern part of the study area: Dr – Drovatnitsa grotto; Fg – Figurniy grotto; M – Medvezhaya cave; St–Studenaya cave; Kn – Kaninskaya cave; F – Filin grotto; Un – Uninskaya cave. Southern part of the study area: Ush – Ushminskaya cave; Ush_1 – Ushma-1; S – Severnaya cave; Br – Burmantovo grotto; Sh – Shaytanskaya cave; La – Lakseyskaya cave; Us – Usoltsevskaya cave; Ch – Cheremukhovo cave; Li – Lisia cave; Zh – Zhilische Sokola; Kv – Kakva–4; Pz – Puzan grotto.

Table 1
Biostratigraphically investigated caves are located in the Northern Ural.

Studied areas	Cave index	Object	Coordinates	Cave height abov sea level (m)	Cave height above regional thalweg (m)/ name of the rive	Cave max length (m)	Cave medium height (m)	Thickness of studied Quaternary deposits (m)	Year of a cave discovery/study and an author/year of topographical plan creation	Methods of investigations	Composition of the carbonate deposits/ stratigraphical index	Stratigraphical index of the deposits	References
Western slope	M	Medvezhaya cave	62°02′N 58°38′E	230	40/Pechora	480	2	2.5	1960/Guslitser and Kanivets/1926	b/mm, b/lm, b/sp, C^{14}, a	Limestone/C	Q_3^{3-4}, H_1	Kuzmina, 1971; Kochev, 1993; Smirnov, 1996
Western slope	St	Studenaya cave	62°02′N 58°38′E	220	18/Pechora	8	1	6.6	1960/Guslitser and Kanivets	b/mm, C^{14}	Limestone/C	Q_3^{3-4}	Kochev (1993)
Western slope	Dr	Drovatnitsa grotto	63°47′N 57°53′E	190	9/Podcherem	5	2	2.2	1965/Guslitser/ 1965	b/lm	Limestone/C	Q_3^3, H_3	Ponomarev (2001)
Western slope	Kn	Kaninskaya cave	62°02′N 58°09′E	170	11/Pechora	7	2.2	1.5	1955/Guslitser/ 1947	b/lm, C^{14}, a	Limestone/C	$H_{2\text{-}3}$	Kuzmina (1971)
Western slope	Un	Un'inskaya cave	61°47′N 57°52′E	222	6/Un'ya	17.5	6	0.8	1957/Guslitser	b/lm, a	Limestone/C	Q_3^{3-4}, $H_{2\text{-}3}$	Kuzmina (1971)
Western slope	F	Filin grotto	62°07′N 58°24′E	230	40/Pechora	3	1.5	1.1	1960/Guslitser	b/mm	Limestone/C	M	Kuzmina (1971)
Western slope	Fg	Figurniy grotto	62°50′N 58°26′E	230	41/Ilych	8	4	1.5	1963/Guslitser and Kanivets	b/lm	Limestone/C	Q_3^4	Kuzmina (1971)
Eastern slope	Ch	Cheremukhovo cave	60°24′N 60°03′E	150	5.5/Sos'va	32	5	4.5	1998/Chairkin/ 1998	b/mm, b/lm, b/sp, C^{14}, a	Limestone/D	Q_3^{3-4},$H_{2\text{-}3}$	Teterina, 2002; Strukova et al., 2006
Eastern slope	Li	Lisia cave	60°24′N 60°06′E	150	16/Sos'va	10	1	0.7	1998/Chairkin/ 1998	b/mm, b/lm, b/sp, C^{14}	Limestone/D	H_2	Kosintsev et al., 2000; Teterina, 2002
Eastern slope	Kv	Kakva–4	59°36′N 60°02′E	170	12/Kakva	10	7	1.0	199?/Chairkin	b/mm, b/lm, b/sp, C^{14}, a	Limestone/D	Q_3^4	This work
Eastern slope	Ush	Ushminskaya cave	61°28′N 60°03′E	180	5/Loz'va	30	5	0.8	1991/Chairkin	b/mm, b/lm, b/C^{14}, a	Limestone/D	$H_{2\text{-}3}$	Smirnov (1996)
Eastern slope	Ush_1	Ushma-1	61°33′N 60°00′E	271	15/Loz'va	3	2.5	0.25	2002/Ulitko and Teterina	b/mm	Limestone/D	M	Teterina and Ulitko, 2002
Eastern slope	Sh	Shaytanskaya cave	60°42′N 60°22′E	140	32/Ivdel	29	2	2.0	1978/Petrin/1928	b/mm, b/lm, b/C^{14}, a	Limestone/D	Q_3^{3-4}, $H_{1\text{-}3}$	Smirnov, 1996; Kosintsev (1996)
Eastern slope	S	Severnaya cave	61°14′N 60°04′E	200	12/Vizhay	2250	42	0.2	2009/Tsurikhin and Lavrov/2009	b/lm, C^{14}, a	Limestone/D	Q_3^3	Kosintsev and Bachura, 2015
Eastern slope	La	Lakseyskaya cave	60°43′N 60°17′E	170	6/Ivdel	70	2	2.1	1978/Petrin/1928	b/lm, C^{14}, a	Limestone/D	$H_{1,3}$	Kosintsev and Borodin, 1990
Eastern slope	Us	Usoltsevskaya cave	60°16′N 60°09′E	170	10/Vagran	100	5	1.0	2002/Erokhin	b/mm, b/lm, b/sp	Limestone/D	Q_3^{1-2}	Bachura et al., 2004
Eastern slope	Zh	Zhilische Sokola	59°36′N 60°02′E	170	3/Kakva	180	3	1.5	1990/Chairkin	b/mm, b/lm, C^{14}, a	Limestone/D	Q_3^{1-2}, $H_{1\text{-}3}$	Teterina (2002), Bachura (2008)
Eastern slope	Br	Burmantovo grotto	61°18′N 60°25′E	160	5/Loz'va	13	4	0.7	2001/Chairkin	b/mm, b/lm, C^{14}, a	Limestone/D	H_2	Bachura and Plasteeva, 2005
Eastern slope	Pz	Puzan grotto	59°36′N 60°00′E	170	15/Kakva	2.3	3	0.15	2012/Sadykova	b/mm	Limestone/D	M	Sadykova, 2013a

Legend: Methods of investigations: biostratigraphical – (b), geochronological (C14); archaeological (a). Detailization of biostratigraphical methods: b/mm – small mammals, b/lm – large mammals; b/sp – palynological investigations. Stratigraphical indices: D – Devonian, C– Carboniferous, Q3 – Upper Pleistocene; Q_3^2 – Khanmei horizon, Q_3^3 – Nev'yansk Horizon, Q_3^4 – Polar Urals Horizon, H – Holocene; H_1 – Lower Holocene; H_2 – Middle Holocene; H_3 – Upper Holocene; M – Recent time.

1981; Petrin, 1987; Kosintsev and Borodin, 1990; Potapova, 1990; Kosintsev, 1996; Smirnov, 1996; Volkov et al., 1996; Borodin et al., 2000a, b; Kosintsev et al., 2000; Bachura and Strukova, 2002; Teterina, 2002, 2009; Teterina and Ulitko, 2002; Bachura and Plasteeva, 2005; Kosintsev and Bachura, 2005; Kosintsev et al., 2005; Strukova et al., 2006; Bachura and Kosintsev, 2007; Kosintsev, 2007; Bachura, 2008; Sadykova, 2013a, b; Kosintsev and Bachura, 2015; Smirnov et al., 2016; Kadebskaya et al., 2019; Kadebskaya, 2020).

Thus, there are two key-areas that yielded biostratigraphical data for the cave deposits. These are the Upper Pechora River (Northern part) and its tributaries on the western slope and the Upper Loz'va and Sos'va Rivers (Southern part) on the eastern slope of the Northern Urals (Fig. 1; Table 1). All studied caves are listed in Table 1 with reference to elevation above modern thalwegs.

The cave deposits constitute a natural database that helps us understand the past changes in the region. This paper presents the results of the biostratigraphical studies of the main localities, i.e. the summarized stratigraphic description of the unconsolidated deposits. It provides a general description of the deposits, an overview of the fossil remains of small and large mammals, birds, amphibians, fish, plants and the radiocarbon age of the fossils incorporated in the unconsolidated deposits. It also describes archaeological materials accompanying fossil remains.

2. General geological background

The Northern Ural region consists of a series of parallel ridges of meridional extension, separated from the East European Plain and the West Siberian Plain by the foothills. The width of the mountains is 50–60 km. Their average height is 700–750 m. The ridges have flat or rounded peaks. They represent Proterozoic, Cambrian and Ordovician metamorphic deposits. In the west, they are separated from the Eastern-European Platform by the wide Fore-Uralian Foredeep that is constituted of Permian and Carboniferous sedimentary rocks. The width of the western foothills is up to 70 km; their average height is 250–350 m. The narrow Tagil Foredeep goes along the eastern slope. It consists of Silurian, Devonian and Carboniferous volcanogenic deposits interbedding with sandstones and limestones dated to the same periods. The width of the eastern foothills does not exceed 30 km. Their average height is 150–250 m. The Palaeogene-Neogene-Quaternary deposits occur in the platform depressions. Neotectonics is poorly represented (Borisevich, 1968).

The caves on the western slope are part of the northern speleological region of the Western Ural speleological province (Lavrov and Andreichuk, 1992). They were formed in the Carboniferous limestones. The caves on the eastern slope are part of the Tagil speleological region of the Tagil-Magnitogorsk speleological province (Lavrov and Andreichuk, 1992). They were formed in the Devonian and Carboniferous limestones.

The Northern Ural territory is nowadays characterized by a continental climate with a rainfall of 700–800 mm per year on the western slope and 600–700 mm per year on the eastern slope (Kuvshinova, 1968). The area demonstrates a dissected relief, where Palaeozoic sedimentary rocks are widespread, while karst rocks (limestones) are locally distributed, therefore, carbonate karst is poorly developed (Lavrov and Andreichuk, 1992). During Quaternary, caves and grottoes accumulated loose deposits as a product of weathering processes. In the Late Pleistocene and Holocene, the majority of caves were inhabited by animals, while some of them - by humans.

3. Archaeological data

The caves in the Northern Urals have been visited by humans starting from the Upper Palaeolithic till present days (Kanivets, 1976; Borodin and Kosintsev, 1997). The earliest archaeological finds in the caves of the Northern Urals date back to the Upper Palaeolithic and correspond to the Middle Upper Palaeolithic. A single artifact of this age was found in the layer 10 of the Cheremukhovo Cave, pit 1(which has a radiocarbon date 31,500 ± 1200 RP (AA-36470), 26,480 ± 840 RP (OxA-10926) and 25,150 ± 500 RP (SOAN-5302) (Strukova et al., 2006), which corresponds to the Marine Isotope Stage 3 (MIS 3) or the end of the Nev'yansk horizon. Finds from the Medvezhaya Cave have a completely different age (16,130 ± 150, LE-3060; 17,980 ± 200, LE-2876; 18,700 ± 180, GIN-8399), indicating that humans were also present along the Urals in the beginning of the Last Glacial Transition, right after the Last Glacial Maximum (Guslitser and Pavlov, 1988; Svendsen et al., 2010), in the beginning of the Polar Urals horizon or in the beginning of MIS 2. Two caves (Uninskaya and Studenaya) yielded rare artifacts dated to the second half of the Upper Palaeolithic (Guslitser and Pavlov, 1988).

The Mesolithic, which corresponds to the Lower Holocene (as well as to Preboreal and Boreal of the Blitt-Sernander scale), is represented by a small number of the artifacts found in four caves - Pervokamennaya Cave (Guslitser and Kanivets, 1965), Cheremukhovo Cave (Borodin et al., 2000a), Shaitanskaya Cave (Petrin, 1987; Volkov et al., 1996) and Lakseiskaya Cave (Chairkin et al., 2005; Chairkin et al., 2005). The Neolithic and the Eneolithic, which correspond to the Middle Holocene, the Atlantic and the beginning of the Subboreal, are represented in five caves (Kanivets, 1962; Guslitser and Kanivets, 1965; Chairkin, 2004a; Chairkina and Kuzmin, 2018). Burials of this time were found in one of these caves (Chairkina and Kuzmin, 2018).

Bronze Age artifacts (the end of the Middle Holocene; the middle and the end of the Subboreal period) were found in five caves (Kanivets, 1961, 1964; Volkov et al., 1996; Chairkin et al., 2005). The artifacts of the early Iron Age (the beginning of the Upper Holocene, the beginning of the Subatlantic period) were found in six caves (Gening, 1951; Kanivets, 1962, 1964; Melnichuk et al., 2001; Chairkin, 2004a, 2004b; Chairkin et al., 2005). The artifacts of the Middle Ages (the middle and the end of the Upper Holocene, the beginning of the Subatlantic period) were found in seven caves (Kanivets, 1961, 1964; Volkov et al., 1996; Chairkin, 2004a, 2004b; Chairkin et al., 2005).

Thus, the caves of the Northern Urals yielded the artifacts of the archaeological periods starting from the middle Upper Palaeolithic. But the artifacts number is very small. In these caves there are no bones with cat mark. This indicates human visited caves very rare during the Upper Paleolithic. Zoogenic factor was practically only one factor of bone accumulation in the Upper Paleolithic. During the Mesolithic, Neolithic, Bronze Age and Early Iron Age, a significant artifacts number accumulated in the caves. There are numerous bones with cut marks. The caves were most frequently visited by humans in the Middle Ages. During the Holocene, man was one of the factors of bone accumulation. Some caves in the early Iron Age (Kaninskaya Cave, Temnaya Cave) (Gening, 1951; Kanivets, 1964; Melnichuk and Kazantsev, 1998) and in the Middle Ages (Kaninskaya Cave, Uninskaya, Ushminskaya, Shaitanskaya, Lakseiskaya, Yurtischenskaya, Zhiliche Sokola) (Kanivets, 1961, 1964; Volkov et al., 1996; Chairkin, 2004a, 2004b; Chairkin et al., 2005) were used as sanctuaries. The *Ursus arctos* was the main sacrificial animal (Kanivets, 1964; Kosintsev et al., 2018). In the Iron Age, Ugrian or Ugro-Samoyedic-speaking populations, who lived in the Northern and Middle Ural had complex of rituals relating to the brown bear. The skull and bones of the bear were buried in caves (Lepekhin, 1780; Pallas, 1786).

4. Material and methods

4.1. Stratigraphical and chronological study

The article summarizes biostratigraphical and geochronological data from important stratigraphical levels exposed in 19 cave localities, most part of which represent several layers dated to different periods (Tables 1 and 2, A.1).

The local stratigraphical units are correlated with the stratigraphical

Table 2
Radiocarbon dates number of different stratigraphical levels in the Northern Urals.

Stratigrafical scheme	Upper Pleistocene			Holocene		
	Nev'yansk (MIS 3)-	Polar Urals (MIS 2)		Gorbunovo (MIS 1)		
Key-areas		LGM – LGT*	LGM – LGT	Lower	Middle	Upper
Northern part of the study area	5	9	16	0	2	2
Southern part of the study area	19	10	4	3	7	8

Legend: * LGM – LGT –Last Glacial Maximum – Late Glacial Time (24–17 kyr BP); BAIC – Bølling – Allerød period (17–10.2 kyr BP).

scheme of the Pleistocene and Holocene Ural deposits (Table 3). The scheme is based on palaeofaunistic and palaeobotanical data, combined with radiocarbon dates of the reference sections (Stefanovsky, 2006). The upper part of the Pleistocene (= Upper Pleistocene of the International Stratigraphic Chart, (Cohen and Gibbard, 2019)) is subdivided into five horizons with local names: Streletsky (=Streletsk) horizon (corresponds to MIS 5), Khanmeysky (=Khanmei) horizon (MIS 4), Nev'yansky (=Nev'yansk) horizon (MIS 3), Polarnouralsky (=Polar Urals) horizon (MIS 2), and Gorbunovsky (=Gorbunovo) horizon (MIS 1) (Table 3). Some material is analyzed based on the division of the Holocene into the Lower, Middle, and Upper Holocene (from 8 to 2.5 ka), a division that is traditionally used in Russia (Shick, 2014). In this paper, we apply the Holocene stratigraphical subdivision based on the Blytta-Sernandera-Posta scheme (Table 3) instead of formal subdivision of the Holocene Epoch into three distinct subsections, ratified by the International Union of Geological Sciences (Greenlandian (11,700 years ago to 8326 years ago), Northgrippian (8326 years ago to 4200 years ago) and Meghalayan (4200 years ago to the present) (Walker et al., 2009). This is our conscious choice due to several reasons. First of all, the boundaries of these subdivisions in the Urals are not stratigraphically justified. Preliminary analysis of the biostratigraphical data showed that the 8326 and 4200 boundaries are not reflected in the Uralian deposits, in contrast to the 8000 and 2500 boundaries, which are rather clear in the palaeobotanical (Khotinsky, 1977) and archaeological records. The 8 ky boundary correlates with the Mesolithic/Neolithic transition, while the 2.5 ky boundary - with the Bronze/early Iron Age transition (Ashikhmina et al., 1997). Besides, the actual data presented and discussed in this paper were collected by different authors who also used the traditional (Russian) stratigraphical subdivision of the Holocene. Therefore, we decided to adhere to it as well.

The deposits in most caves were dated using radiocarbon method (C14). All radiocarbon dates were obtained, following the standard methodology, in different geochronological laboratories (Table A1). Part of the large and small mammal faunas with an age beyond the radiocarbon dating method (i.e. an age beyond ca. 50 ka) are stratigraphically dated on the basis of the species composition of the large and small-mammalian assemblages (Smirnov, 1996; Kosintsev, 2007; Kosintsev, 2007; Teterina, 2009; subchapter 6.6 of this paper) and on the base of the morphotype ratio of the teeth of the collared lemming (*Dicrostonyx* sp.) (Smirnov et al., 1997; Ponomarev and Puzachenko, 2015). The radiocarbon dates mentioned in the paper are uncalibrated.

4.2. Palynological analysis

Quaternary deposits of 6 caves were studied palynologically: Medvezhaya, Kaninskaya, Uninskaya (Guslitser and Kanivets, 1965); Shaitanskaya, pit 2 (Smirnov, 1996); Cheremukhovo, pit 1 (Strukova et al., 2006); Cheremukhovo, pit 4; Usoltsevskaya; Lisia, Kakva 4 (Lapteva, 2007, 2008, 2009) (Table 4). The palynological analytic process was done following the standard methods described by Grichuk (1940). The

Table 3
Stratigraphic scheme of the Upper Pleistocene and Holocene deposits from the Northern Urals region in a broader stratigraphical context.

Global Quaternary scheme (Cohen and Gibbard, 2019)			Marine Isotope Stages	Stratigraphic Scheme of Russia (Zhamoida et al., 2006)			Northern Urals region (Zastrozhnov et al., 2018)		Regional Stratigraphic scheme of the Eastern European Platform (Shick, 2014)			North West European Stages (The Netherlands) (Zagwijn, 1996)		Unformal units
System	Series	Subseries, Stages		Division	Subdivision	Link	Superhorizon	Horizon	Superhorizon	Horizon		Horizon		Units
Quaternary	Holocene	Upper Middle Lower	1	Holocene		Modern		Gorbunovo		Shuvalovo	Upper Middle Lower	Holocene		Subatlantic Subboreal Atlantic Boreal Preboreal
	Pleistocene	Upper	2	Pleistocene	Neopleistocene	Upper	Valdai	Polar Urals	Valdai	Ostashkov		Weichselian	Upper	Younger Dryas Allerod Bolling LGT LGM
			3					Nev'yansk		Leningrad			Middle	Pleniglacial
			4					Khanmei		Kalinin			Lower	
			5					Streletsk		Chermenino-Mikulino		Eemian		

Legend: LGT – Last Glacial Transition; LGM – Last Glacial Maximum.

Table 4
The main stages of the vegetation development in the Southern Urals area according to palynological data from caves.

Stratigraphical scale			Westslope (Guslitser and Kanivets, 1965)	East slope (Lapteva, 2009; Strukova et al., 2006)
Division	Horison	Subhorizon		
Holocene		Upper		There was *Betula–Picea–Pinus* forest with *Abies*. Poaceae and Polypodiaceae were numerous (Cheremukhovo, pit 1)
		Middle		In the beginning of period there was *Abies–Picea* forest with *Pinus* and *Betula* (Kakva–4, Usoltsevskaya cave, Lisiya cave). In the end of the period there was *Betula–Pinus* forest with broadleaved trees (*Tilia, Ulmus*) admixture. Grasse were represented mainly by herbage and Polypodiaceae (Cheremukhovo, pit 1).
		Lower		Mixed open woodland with *Betula, Larix, Pinus* and *Picea* dominance. There were mesophilic meadows. Polypodiaceae were numerous (Kakva–4 and Usoltsevskaya cave).
Upper Neopleistocene	Polar Urals		Periglacial steppe landscape with present forest communities by the river (Medvez'ya cave)	Perglacial steppe landscape with present *Betula* forest by the river. There were elements of the tundra shrub assocations and Ephedra and Plumbaginaceae (Cheremukhovo, pit 4)
	Nev'yansk	the end		Forest–steppe landscapes. Artemisia–Chenopodiaceae and Asteracea and Caryophyllaceae assocition and *Betula* and *Pinus –Picea* forest (Cheremukhovo, pit 1).
		the beginning		Open woodland with *Pinus sibirica–Picea–Betula* and *Pinus –Picea* (Cheremukhovo, pit 4).

palynological research was carried out at different times, starting from the mid-1960s. The results of the palynological analysis are represented in different ways: as a word description (Guslitser and Kanivets, 1965; Smirnov, 1996) and as charts (Strukova et al., 2006; Lapteva, 2007, 2008, 2009). Research in recent years (Lapteva, 2007, 2008, 2009) was carried out with an additional ultrasonic treatment and application of KJ- and CdJ2-based gravity solution. Pollen and spores were identified in temporary glycerine solutions under an Olympus BX51 microscope at .400 magnification using a reference collection of pollen and spores of modern flora (Institute of Plants and Animals Ecology (Yekaterinburg, Russia), and the Pollen and Spore Atlas (Beug, 2004). The palynological remains in each specimen were counted to 250 arboreal pollen grains, with a parallel record of pollen of herbs and spores for higher spore-bearing plants. The data processing and plotting were performed in TILIA software 2.0.41 (Grimm, 2012). The totals for arboreal pollen and herbs were assumed to be 100%. For a more accurate interpretation of palynological data, pollen of Apiaceae was excluded from the pollen total due to its dominance in all the spectra, reflecting the specific local conditions in the vicinity of the cave. The proportion of this pollen was calculated from the total content of pollen grains + Apiaceae. The percentage of spores was calculated from the total content of pollen and spores, taken as 100%.

4.3. Palaeofaunal analysis

The bones of fish, amphibians and reptiles were identified only to the class level: Pisces, Amphibia, Reptilia. The fish bones were found in the unconsolidated deposits of ten caves: Medvezhaya (Kuzmina, 1971; Vereshchaghin and Kuzmina, 1962), Kaninskaya (Kuzmina, 1971), Uninskaya (Kuzmina, 1971); Ushminskaya (Kosintsev et al., 2005), Shaitanskaya; Cheremukhovo (Borodin et al., 2000a, 2000b; Strukova et al., 2006); Lisia (Kosintsev et al., 2000), Kakva 4, Zhilische Sokola (Bachura, 2008) and Burmantovo Grotto (Bachura and Plasteeva, 2005). The amphibian bones were found in the deposits of six caves: Ushminskaya (Kosintsev et al., 2005); Shaitanskaya; Cheremukhovo (Borodin et al., 2000a, 2000b; Strukova et al., 2006); Lisia (Kosintsev et al., 2000), Zhilische Sokola (Bachura, 2008) and Burmantovo Grotto (Bachura and Plasteeva, 2005). Bones of reptiles were found in the deposits of the Cheremukhovo Cave (Strukova et al., 2006) and Burmantovo Grotto (Bachura and Plasteeva, 2005). Bones of birds were found in all the caves, but they were identified only in five caves (Table A2). In total, 8631 bird bones were identified in the following caves: Medvezhaya (Potapova, 1990), Kaninskaya (Kuzmina, 1971), Ushminskaya (Kosintsev and Nekrasov, 1996), Shaitanskaya (Nekrasov, 2003), Cheremukhovo (Borodin et al., 2000a). Large and small mammal bones were found in all the caves. In total, 67,530 teeth of small mammals were identified in the Late Pleistocene deposits of six caves (Medvezhaya (Smirnov, 1996), Studenaya (Guslitser et al., 1989; Kochev, 1993; Kryazheva et al., 2019), Shaitanskaya (Smirnov, 1996), Cheremukhovo (Bachura and Strukova, 2002; Teterina, 2002; Strukova et al., 2006); Kakva 4, Zhilische Sokola (Smirnov, 1996; Teterina, 2002). In total, 15, 584 teeth were identified in the Holocene deposits of eight caves: Medvezhaya (Smirnov, 1996), Ushminskaya (Smirnov, 1996) Ushma-1 (Teterina and Ulitko, 2002), Cheremukhovo (Teterina, 2002; Strukova et al., 2006); Lisia (Teterina, 2002), Zhilische Sokola (Bachura, 2008), Puzan (Sadykova, 2013a, 2013b), Filin Grotto (Kuzmina, 1971). A total of 21,479 large mammal bones was identified in the Late Pleistocene deposits of seven caves (Medvezhaya (Kuzmina, 1971), Figurniy grotto (Kuzmina, 1971), Shaitanskaya (Kosintsev, 1996); Cheremukhovo (Borodin et al., 2000a; Bachura and Strukova, 2002; Strukova et al., 2006); Usoltsevskaya, Kakva 4, Zhilische Sokola (Bachura, 2008). A total of 55,623 large mammal bones was identified in the Holocene deposits of eight caves (Medvezhaya (Kuzmina, 1971), Kaninskaya (Kuzmina, 1971), Uninskaya (Kuzmina, 1971); Burmantovo grotto (Bachura and Plasteeva, 2005) Ushminskaya cave (Kosintsev et al., 2005), Shaitanskaya (Kosintsev, 1996); Lakseyskaya (Kosintsev and Borodin, 1990) Cheremukhovo (Borodin et al., 2000a; Strukova et al., 2006); Usoltsevskaya, Lisia (Kosintsev et al., 2000), Zhilische Sokola (Bachura, 2008) (Tables 5–8; Table A.2–6).

Traditional methods of dispersal of sediments in water, using sieves with mesh sizes of 1.0 mm, were applied to recover the fish, amphibians and reptiles, and small-mammal remains. Bones of birds, large and small mammals were identified using a reference collection of skeletons kept at the Zoological Institute, RAS, the Institute of Geology of the Komi Scientific Centre, RAS, and the Museum of the Institute of Plant and Animal Ecology, UB RAS.

5. Results

5.1. Stratigraphy and chronology

Unconsolidated cave deposits in the caves of the Northern Urals are of different genesis, mainly eluvial and landslide. At the cave entrances, the deposits are of eluvial-slope and thermal gravitational genesis. Some caves are of alluvial speleogenesis. Speleothems in the caves of the Northern Urals are poorly represented. Unconsolidated cave deposits consist of brown and light-brown loam and sandy loam. Sometimes grey sandy loam and loam occur in the upper parts of the deposits, while sand and clay can be found in their lower parts. Primitive soil is often formed on the surface of the entrance grottoes. The deposits contain numerous

Table 5
List of species of small mammal bone remains from the Upper Pleistocene cave deposits based on Kochev (1993),Smirnov, 1996, Borodin et al., 2000b, Bachura and Strukova, 2002, Teterina (2002), Strukova et al. (2006).

Stratigraphy	Upper Pleistocene						
	Northern part of the study area			Southern part of the study area			
	Nev'yansk (MIS 3)	Polar Urals (MIS 2)		MIS 5-4	Nev'yansk (MIS 3)	Polar Urals (MIS 2)	
Taxa		LGM – LGT*	BAIC			LGM – LGT	BAIC
Spermophillus sp.	–	–	–	+	+	–	+
Arvicola amphibius (Linnaeus, 1758)	+	–	+	+	–	–	+
Dicrostonyx gulielmi-simplicior	–	–	–	+	–	–	–
Dicrostonyx gulielmi (Hinton, 1910)	+	+	–	–	+	+	–
Dicrostonyx torquatus (Pallas, 1778)	–	–	+	–	–	–	+
Lagurus lagurus (Pallas, 1773)	–	+	–	+	+	+	+
Lasiopodomys gregalis Pallas, 1779	+	+	+	+	+	+	+
Lemmus sibiricus (Kerr, 1792)	+	+	+	+	+	+	+
Microtus agrestis (Linnaeus, 1761)	+	–	+	+	–	–	+
Alexandromys middendorffii (Poljakov, 1881)	+	+	+	+	+	+	+
Alexandromys oeconomus Pallas, 1776	+	+	+	+	+	+	+
Myodes sp.	+	+	+	+	+	–	+
Craseomys rufocanus Sundevall, 1846	–	–	–	+	–	–	+
Myopus schisticolor (Liljeborg, 1844)	–	–	–	–	–	–	+
Cricetulus migratorius (Pallas, 1773)	–	–	–	+	+	–	+
Ochotona pusilla (Pallas, 1769)	+	+	+	+	+	+	+
Sorex sp.	–	–	–	–	+	–	+
Chiroptera	–	–	–	+	+	–	+

Legend: * LGM – LGT –Last Glacial Maximum – Late Glacial Time; BAIC – Bølling – Allerød period.

Table 6
List of species of small mammal bone remains from the Holocene cave deposits based on Smirnov, 1996, Teterina (2002), Strukova et al. (2006); Sadykova, 2013b

Stratigraphy	Holocene (MIS1)				
	Northern part of the study area		Southern part of the study area		
Taxa	Lower	Upper	Lower	Middle	Upper
Sciurus vulgaris Linnaeus, 1758	+	+	–	+	+
Pteromys volans (Linnaeus, 1758)	–	–	–	–	+
Spermophillus sp.	–	–	–	+	–
Tamias sibiricus Laxmann, 1769	–	–	–	+	+
Sicista betulina (Pallas, 1779)	–	–	–	+	+
Sylvaemus sylvaticus	–	–	–	+	–
Arvicola amphibius (Linnaeus, 1758)	+	+	–	+	+
Micromus minutus (Pallas, 1771)	–	–	–	+	–
Dicrostonyx torquatus (Pallas, 1778)	+	–	+	+	+
Lagurus lagurus (Pallas, 1773)	–	–	–	+	–
Lasiopodomys gregalis Pallas, 1779	+	+	+	+	+
Lemmus sibiricus (Kerr, 1792)	+	–	+	+	–
Microtus agrestis (Linnaeus, 1761)	+	+	+	+	+
Alexandromys middendorffii (Poljakov, 1881)	–	–	–	+	–
Alexandromys oeconomus Pallas, 1776	+	+	+	+	+
Myodes rutilus (Pallas, 1779)	–	–	+	+	+
Myodes sp.	+	–	–	+	+
Craseomys rufocanus Sundevall, 1846	+	+	+	+	+
Myopus schisticolor (Liljeborg, 1844)	+	–	–	+	+
Ondatra zibetica (Linnaeus, 1766)	–	+	–	–	+
Cricetulus migratorius (Pallas, 1773)	–	–	–	+	–
Ochotona pusilla (Pallas, 1769)	–	–	+	+	–
Sorex sp.	–	–	–	+	–
Talpa europaea Linnaeus, 1758	–	+	–	+	+
Chiroptera	–	–	+	+	+

small and big-size limestone debris, and sometimes faunal remains. The thickness of these deposits differs and depends on the location of the deposit's section in the cave and on the height above thalweg. A summarized description of the unconsolidated deposits with their (possible) correlation with the MIS stages and the Western-European stratigraphical units is given below.

Streletsk-Khanmei horizons (Lower Weichselian, MIS 5a–d – 4). The deposits are represented by reddish-brown clay with pebbles and sharp-edge limestone fragments (Zhilische Sokola Cave (pit 2), average thickness is 0.75 m; Usoltsevskaya Cave, average thickness is 1.45 m). Zhilische Sokola Cave (pit 2) yielded small and large mammal fauna which provides only approximate radiocarbon age (Table 2; A.2). Based on the morphotype ratio of the teeth of the collared lemming, this fauna was dated to the first half of the Upper Pleistocene (Smirnov et al., 1997; Teterina, 2003). The fauna can be dated as early or late MIS 5, or as early or late MIS 4.

Nev'yansk horizon (Middle Weichselian, MIS 3). The horizon consists of yellowish-brown loam with limestone debris, grey clay and limestone debris with humus (Studenaya Cave, average thickness is 4.2 m); brown loam with limestone debris and yellow sand (Shaitanskaya Cave (pit 1), layers 4–5, average thickness is 0.65 m); brown polymict sand with limestone debris (Cheremukhovo Cave (pit 1), layers 9–12, average thickness is 2.6 m), brown loam with some limestone debris (Cheremukhovo Cave (pit 2), layer 3, average thickness is 0.7 m; Cheremukhovo Cave (pit 4), layer 2, horizons 3–4, average thickness is 0.25 m). The deposits contain numerous bones of large and small mammals. The mammal bones from the deposits of this horizon gave a series of radiocarbon dates (Table 2).

Polar Urals horizon (Upper Weichselian, MIS 2). The horizon is represented by brown loam with limestone debris (Medvezhaya Cave, average thickness is 1.5 m), yellowish-brown loam with limestone debris (Studenaya Cave, average thickness is 1.0 m); yellow loam with limestone debris (Figurniy Grotto, average thickness is 1.5 m); grey-brown clay with large limestone debris (Shaitanskaya Cave, pit 2, layer 5b, average thickness is 0.35 m); polymict grey sand with fine limestone debris (Cheremukhovo Cave (pit 1), layer 6, average thickness is 0.7 m); light grey clay with some limestone debris (Cheremukhovo Cave (pit 2), layers 1–2, average thickness is 0.15 m); grey loam with limestone debris (Kakva 4, average thickness is 0.4 m; Zhilische Sokola (pit 1), average thickness is 0.2 m); grey-brown clay with large limestone debris

Table 7
List of species of large mammal bone remains from the Upper Pleistocene cave deposits based on Kuzmina (1971), Kosintsev (1996), Borodin et al., 2000b, Bachura and Strukova, 2002, Bachura et al., 2004, Strukova et al. (2006), Bachura (2008).

Stratigraphy	Upper Pleistocene						
	Northern part of the study area			Southern part of the study area			
	Nev'yansk (MIS 3)	Polar Urals (MIS 2)		MIS 5-4	Nev'yansk (MIS 3)	Polar Urals (MIS 2)	
Taxa		LGM – LGT*	BAIC			LGM – LGT	BAIC
Mammuthus primigenius (Blumenbach, 1799)	+	+		+	+	+	–
Marmota bobak (Müller, 1776)	–	–		+	+	+	+
Lepus timidus Linnaeus, 1758	+	+		+	+	+	+
Panthera leo spelaea Goldfuss, 1810	+	+		+	+	+	–
Canis lupus Linnaeus, 1758	+	+		+	+	+	+
Vulpes lagopus (Linnaeus, 1758)	+	+		+	+	+	+
V. vulpes (Linnaeus, 1758)	–	+	+	+	+	+	+
Ursus kanivetz Vereshchagin, 1973	+	–	–	–	–	–	–
U. ex gr. *savini-rossicus*	+	–	–	–	–	–	–
U. arctos Linnaeus, 1758	+	–	+	+	+	+	+
Gulo gulo (Linnaeus, 1758)	–	+	–	–	+	+	+
Martes zibellina (Linnaeus, 1758)	+	+	+	+	+	+	+
Meles meles (Linnaeus, 1758)	–	–	–	+	–	–	–
Mustela erminea Linnaeus, 1758	–	+	–	+	+	+	+
M. eversmanni (Lesson, 1827)	–	+	+	+	+	+	+
M. nivalis Linnaeus, 1766	–	+	+	+	+	+	+
Equus ferus Boddaert, 1785	-+	+	+	+	+	+	+
Coelodonta antiquitatis (Blumenbach, 1799)	+	+	+	+	+	+	–
Alces alces Linnaeus, 1758	–	–	+	+	–	–	–
Rangifer tarandus Linnaeus, 1758	+	+		+	+	+	+
Cervus elaphus Linnaeus, 1758	–	–	–	+	+	–	–
Saiga tatarica Linnaeus, 1766	+	+	+	+	+	+	+
Bison priscus Bojanus, 1827	–	+	+	+	+	+	+
Ovibos moschatus (Zimmermann, 1780)	+	+	+	–	+	+	+

Legend: * LGM – LGT –Last Glacial Maximum – Late Glacial Time (24–17 kyr BP); BAIC – Bølling – Allerød period (17–10.2 kyr BP).

Table 8
List of species of large mammal bone remains in the Holocene cave deposits based on Kosintsev and Borodin, 1990; Kosintsev (1996); Kosintsev et al. (2000); Bachura and Plasteeva, 2005, Kuzmina (1971); Strukova et al. (2006).

Stratigraphy	Holocene (MIS1)				
	Northern part of the study area		Southern part of the study area		
Taxa	Middle	Upper	Lower	Middle	Upper
Castor fiber Linnaeus, 1758	+	+	+	+	+
Lepus timidus Linnaeus, 1758	+	+	+	+	+
Lynx lynx (Linnaeus, 1758)	+	+	–	+	–
Canis lupus Linnaeus, 1758	+	+	+	+	+
Vulpes lagopus (Linnaeus, 1758)	+	+	–	+	–
V. vulpes (Linnaeus, 1758)	+	+	–	+	+
Ursus arctos Linnaeus, 1758	+	+	+	+	+
Lutra lutra (Linnaeus, 1758)	+	+	–	+	+
Gulo gulo (Linnaeus, 1758)	+	+	+	+	+
Martes zibellina (Linnaeus, 1758)	+	+	+	+	+
Meles meles (Linnaeus, 1758)	+	–	–	+	–
Meles leucurus (Hodgson, 847)	–	+	–	–	–
Mustela erminea Linnaeus, 1758	–	–	–	+	+
M. eversmanni (Lesson, 1827)	–	–	–	+	–
M. lutreola (Linnaeus, 1761)	+	–	–	–	–
M. nivalis Linnaeus, 1766	–	–	–	+	–
Alces alces Linnaeus, 1758	+	+	+	+	+
Rangifer tarandus Linnaeus, 1758	+	+	+	+	+
Equus caballus Linnaeus, 1758	–	+	–	–	–
Sus scrofa domestica Linnaeus, 1758	–	+	–	–	–
Bos taurus Linnaeus, 1758	–	+	–	–	–
Ovis aries Linnaeus, 1758	–	+	–	–	–

(Shaitanskaya Cave (pit 2), layer 5b, average thickness is 0.35 m). The deposits of all the caves contain the Upper Pleistocene mammal bones, and the deposits from three caves (Medvezhaya, Uninskaya and Studenaya) yield Upper Palaeolithic artifacts.

Gorbunovo horizon (Holocene, MIS 1). The Holocene deposits are represented by loamy and sandy loam facies with limestone debris. Based on radiocarbon dates, mammal fauna composition and archaeological materials, they can be subdivided into Lower, Middle and Upper Subhorizons.

Lower Subhorizon. The deposits are represented by green sandy loam (Medvezhaya Cave, layer 3, average thickness is 0.25 m); grey sandy loam with numerous limestone blocks (Lakseyskaya Cave, layer 4, average thickness is 0.20 m) and light brown clay with numerous limestone debris (Cheremukhovo Cave (pit 1), layer 7, average thickness is 0.45 m).

Middle Subhorizon. The deposits consist of grey-brown loam with numerous limestone debris (Burmantovo Grotto, average thickness is 0.7 m); grey-brown clay with some limestone gravel (Lisia Cave, average thickness is 0.5 m); grey loam with limestone debris (Kaninskaya Cave, layer 5, average thickness is 0.95 m; Zhilische Sokola (pit 1), average thickness is 1.1 m). The Neolithic, Eneolithic and Bronze Age artifacts are known from these deposits.

Upper Subhorizon. The deposits are represented by limestone debris with humus (Uninskaya Cave, layer 18, average thickness is 1.0 m; Ushma1, average thickness is 1.0 m); grey sandy loam with humus and fine limestone gravel (Kaninskaya Cave, layer 6, average thickness is 0.45 m; Ushminskaya Cave, average thickness is 1.0 m); grey sand with clay and fine limestone gravel (Cheremukhovo Cave (pit 1), layer 3–4, average thickness is 0.45 m; Cheremukhovo Cave (pit 1), layer 2, average thickness is 0.15 m). The artifacts from the early Iron Age to recent times were found in these deposits.

Different layers in the caves were attributed to the beginning of the Late Pleistocene – possibly Streletsk (MIS 5) and Khanmei horizons (MIS 4), as well as to Nev'yansk (MIS 3), Polar Urals horizon (MIS 2) intervals of the Late Pleistocene and Gorbunovo (MIS 1) interval in Holocene. This attribution to the stratigraphical units and geochronological equivalents is based on the radiocarbon dates, faunal complexes and archaeological materials that are listed in Table 2 and 9

5.2. Palynology

The palynological spectra were obtained from the deposits of nine caves. The data from three caves of the western slope (Guslitser and Kanivets, 1965) make it possible to reconstruct vegetation of the Polar Urals horizon only (Table 4). Periglacial steppes with forest communities were spread in the river valleys. The analysis of the deposits from 6 caves of the eastern slope (Strukova et al., 2006; Lapteva, 2009) enabled us to characterize the Late Pleistocene (Nev'yansk and Polar Urals horizons) and Holocene (Gorbunovo horizon) vegetation. The landscape dynamics of the eastern slope of the Northern Urals during the Upper Pleistocene-Holocene is represented in Table 4.

5.3. Ichthyology

Fish remains were found in the deposits of all the Upper Pleistocene and Holocene stratigraphical horizons (Table 9). They are rare in the Upper Pleistocene deposits but abundant (some localities yielding numerous remains) in the Holocene deposits. Fish bones were studied only from the Nev'yansk horizon deposits (pit 2, layer 3) of the Cheremukhovo Cave (Borodin et al., 2000a). Three graying (*Thymallus thymallus*) bones and fifteen pike (*Esox lucius*) bones were identified here.

5.4. Herpetology

Some amphibian bones were found in the Streletsk (MIS 5)–Khanmei (MIS 4) horizons deposits and in the deposits dated to the end of the Polar Urals horizon (MIS 2). They were found in the deposits of all the Gorbunovo horizon (MIS 1) periods (Table 9). The Holocene deposits yield more bones than the Pleistocene ones.

The reptile bones were found only in the Middle and Upper Holocene deposits. No reptile bones were found in the Pleistocene and Lower Holocene deposits (Table 9).

The bones of amphibians and reptiles were identified to the class level only.

5.5. Ornithology

Bird bones were found in the deposits of all the horizons (Table A2). The deposits dated to the end of the Polar Urals horizon (MIS 2) and the Gorbunovo horizon (MIS 1) deposits yield most numerous remains. However, bird bone remains in the majority of the localities were identified to the class level only. The studied remains of birds were from a very small number of caves, which was done intentionally (Kuzmina, 1971; Potapova, 1990; Kosintsev and Nekrasov, 1996; Borodin et al., 2000a; Nekrasov, 2003). The most ancient bird fauna was found in the Nev'yansk horizon (MIS 3) deposits (pit 2, layer 3) of the Cheremukhovo Cave (Borodin et al., 2000a). Fifty-six bones were identified here. The fauna is dominated by the species that prefer open (*Lagopus lagopus*) and semi-open (*Lyrurus tetrix*, *Buteo buteo*) landscapes, while species living near water bodies (*Cygnus cygnus*, *Anser* sp., *Anas* sp.) are not numerous (Table A2). The Medvezhaya Cave yielded most numerous bird remains in the deposits dated to the middle period of the Polar Urals horizon (mid-MIS 2) (Potapova, 1990) (Table A2). The fauna is dominated by the species of the open landscape - ptarmigan (*Lagopus lagopus*, *L. mutus*) (more than 94%), while species living near water bodies (Anseriformes, Charadriiformes) represent about 4%, species of the semi-open landscapes about 2%, and forest species about 0.2%. The Medvezhaya Cave also yielded 435 bird bones from the deposits dated to the end of the Polar Urals horizon (the end of MIS 2). The fauna is dominated by the ptarmigan (74%), and species from the open landscapes amount to 76%. Species that live near water bodies comprise about 20%, while species of the semi-open landscapes about 3%, and species that inhabit closed landscapes about 1%.

The Lower Holocene deposits (the beginning of the Gorbunovo horizon (MIS 1) in the Medvezhaya Cave contain 52 bird bones (Table), 55% of which were assigned to ptarmigan, 25% to species living near water bodies, and 20% to species of the semi-open and closed landscapes. The Middle Holocene deposits of the Kaninskaya Cave yielded 35 bones (Table A2) identified as the ptarmigan (63%), species living near water bodies (about 29%), and taiga species of the capercaillie (*Tetrao urogallus*) (about 9%). The Upper Holocene deposits at four localities gave 1962 bird remains, of which 1370 bones were identified (Table A2). These are dominated by bones assigned to the capercaillie (*Tetrao urogallus*) (776 bones or 57%). In total, the species of the closed landscapes amount to about 60%. The proportion of the ptarmigan bones amounts to 8%, while species of semi-open landscapes and species living near water bodies represent about 16% each. All the bird species identified in the cave deposits inhabit modern Northern Urals.

5.6. Mammals

Bone remains of small and large mammals were found in the Upper Pleistocene and Holocene unconsolidated deposits of the caves from both key areas, namely the Upper Pechora River and its tributaries on the western slope and the Upper Loz'va and Sos'va Rivers on the eastern slope of the Northern Urals (Fig. 1, Tables 6–9). These deposits in all the caves, except for the Drovatnitsa Grotto, Burmantovo Grotto, Lisia Cave and Usoltsevskaya Cave, are represented by several lithological layers dated to different periods.

5.6.1. Small mammals

The most ancient faunas were identified in the deposits from the Zhilische Sokola Cave (pit 2) and Usoltsevskaya Cave. These yield 13 species (Table 5), including steppe ones (*Spermophillus* sp., *Lagurus lagurus, Cricetulus migratorius, Ochotona pusilla*), species that live near water bodies (*Arvicola amphibius, Alexandromys oeconomus*), and species of the closed landscapes (*Craseomys rufocanus, Myodes* sp.). The faunas are dominated by the tundra species (*Dicrostonyx gulielmi-simplicior, Lemmus sibiricus*, *Alexandromys middendorffii, Lasiopodomys gregalis*). The age of the fauna from the Zhilische Sokola Cave (pit 2) is beyond the radiocarbon dating range. The teeth samples of palaearctic collared lemming from the Zhilische Sokola Cave (pit 2) and Usoltsevskaya Cave comprise a high percentage of morphotypes of transitional nature (transition from *D. simplicior* to *D. gulielmi* though the faunas' composition does not include species typical of the Middle Pleistocene. Due to this reason, the faunas from the Zhilische Sokola Cave (pit 2) and Usoltsevskaya Cave were correlated with the Streletsk (MIS 5) or Khanmei (MIS 4) horizons. Seven faunas from the Nev'yansk horizon deposits were studied. The fauna from the northern part of the study area includes 9 species, whereas those from the southern part comprise 14 species (Table 5). The faunas from both parts are dominated by the tundra species. At the same time, these are represented by small proportions of the species that live near water bodies (*A. amphibius, A. oeconomus*). The northern faunas differ from the southern ones by the presence of *Microtus agrestis* in the north, and by the proportion of steppe and forest species. In the northern fauna, these are represented by the *Ochotona pusilla* and *Myodes* sp., while the southern faunas also include the *Spermophilus* sp., *Lagurus lagurus*, *Cricetulus migratorius* and *C. rufocanus*. Six faunas were studied in the Polar Urals horizon deposits (three faunas in the north, and three in the south, Fig. 1, Table 5). Nine species were identified in the northern faunas, while thirteen in the southern ones. Remains of the tundra species are most abundant in the fauna composition of both parts of the study area. Remains of *A. oeconomus*, *M. agrestis*, *Myodes* sp., *O. pusilla* were also found in the faunas of both parts of the study area. Remains of *Sorex* sp., *Spermophilus* sp., *Lagurus lagurus, C. migratorius*, *C. rufocanus* and *Myopus schisticolor* were found in the southern faunas only. The southern faunas lack the remains of the *A. amphibius* due to taphonomic reasons.

Changes in the teeth morphology of the collared lemming occurred during the Upper Pleistocene. In the beginning of the Upper Pleistocene (Streletsk–Khanmei horizons, MIS 5-4), the teeth were identified as

Table 9
Summarizing data of different faunal and floral complexes.

Time, Ka	MIS	Stratigraphical scheme			Fish	Aves	Small mammals	Large mammals	Amphibians	Reptilies	Vegetation
2,5	1	Holocene	Gorbunovo	Upper	Fish	Aves	*Chiroptera, Talpa europaea, Sorex* sp., *Ochotona pusilla, Sciurus vulgaris, Pteromys volans, Tamias sibiricus, Sicista betulina, Craseomys rufocanus, Myodes* sp., *Lagurus lagurus, Dicrostonyx torquatus, Myopus schisticolor, Arvicola amphibius, Lasiopodomys gregalis, Alexandromys oeconomus, Microtus agrestis, Alexandromys middendorffi*	*Lepus timidus, Castor fiber, Canis lupus, Vulpes vulpes, Ursus arctos, Meles leucurus, Martes zibellina, Martes martes, Gulo gulo, Mustela erminea, M. nivalis, M. lutreola, Meles leucurus, Lutra lutra, Lynx lynx, Alces alces, Capreolus pigargus, Rangifer tarandus, Equus caballus, Sus scrofa domestica, Bos taurus, Ovis aries*	Amphibians	Reptilies	There was *Betula–Picea–Pinus* forest with *Abies*. Poaceae and Polypodiaceae were numerous
8				Middle	Fish	Aves	*Chiroptera, Talpa europaea, Sorex* sp., *Ochotona pusilla, Sciurus vulgaris, Tamias sibiricus, Spermophillus* sp., *Sicista betulina, Sylvaemus sylvaticus, Micromus minutus, Craseomys rufocanus, Myodes* sp., *Lagurus lagurus, Dicrostonyx torquatus, Lemmus sibiricus, Myopus schisticolor, Arvicola amphibius, Lasiopodomys gregalis, Alexandromys oeconomus, Microtus agrestis, Alexandromys middendorffi*	*Lepus timidus, Castor fiber, Canis lupus, Vulpes lagopus, V. vulpes, Ursus arctos, Martes zibellina, Gulo gulo, Mustela erminea, M. nivalis, M. lutreola, M. eversmanni, Meles meles, Lutra lutra, Lynx lynx, Alces alces, Rangifer tarandus*	Amphibians	Reptilies	In the beginning of period there was *Abies–Picea* forest with *Pinus* and *Betula* In the end of the period there was *Betula–Pinus* forest with broadleaved trees admixture. Grasse were represented mainly by herbage and Polypodiaceae.
10				Lower	Fish	Aves	*Chiroptera, Sorex* sp., *Ochotona pusilla, Sciurus vulgaris, Spermophillus* sp.,*Craseomys rufocanus, Myodes* sp., *Lagurus lagurus, Dicrostonyx*	*Lepus timidus, Castor fiber, Canis lupus, Vulpes lagopus, V. vulpes, Ursus arctos, Martes zibellina, Gulo gulo, Mustela erminea, M. nivalis, M.*	Amphibians		Mixed open woodland with *Betula, Larix, Pinus* and *Picea* dominance. There were mesophilic meadows. Polypodiaceae were numerous

(*continued on next page*)

Table 9 (*continued*)

Time, Ka	MIS	Stratigraphical scheme			Fish	Aves	Small mammals	Large mammals	Amphibians	Reptilies	Vegetation
							torquatus, Lemmus sibiricus, Myopus schisticolor, Arvicola amphibius, Lasiopodomys gregalis, Alexandromys oeconomus, Microtus agrestis, Alexandromys middendorffi	*eversmanni, Equus ferus, Cervus elaphus, Alces alces, Rangifer tarandus*			
24	2	Upper Neopleistocene	Polar Urals		Fish	Aves	*Chiroptera, Sorex* sp., *Ochotona pusilla, Spermophillus* sp., *Cricetulus migratorius, Craseomys rufocanus, Myodes* sp., *Lagurus lagurus, Dicrostonyx torquatus, Lemmus sibiricus, Myopus schisticolor, Arvicola amphibius, Lasiopodomys gregalis, Alexandromys oeconomus, Microtus agrestis, Alexandromys middendorffi*	*Lepus timidus, Marmota bobak, Canis lupus, Vulpes lagopus, V. vulpes, Ursus arctos, Martes zibellina, Gulo gulo, Mustela erminea, M. nivalis, M. eversmanni, Panthera leo spelaea, Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Alces alces, Rangifer tarandus, Bison priscus, Saiga tatarica, Ovibos moschatus*	Amphibians		Periglacial steppe landscape with present *Betula* forest by the river. There were elements of the tundra shrub associtions and Ephedra and Plumbaginaceae
37	3		Nev'yansk	the end	Fish	Aves	*Chiroptera, Sorex* sp., *Ochotona pusilla, Spermophillus* sp., *Cricetulus migratorius, Myodes* sp., *Lagurus lagurus, Dicrostonyx gulielmi, Lemmus sibiricus, Lasiopodomys gregalis, Alexandromys oeconomus, Alexandromys middendorffi*	*Lepus timidus, Marmota bobak, Canis lupus, Vulpes lagopus, V. vulpes, Ursus arctos, U. spelaeus, Martes zibellina, Gulo gulo, Mustela erminea, M. nivalis, M. eversmanni, Panthera leo spelaea, Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Rangifer tarandus, Bison priscus, Saiga tatarica, Ovibos moschatus*			Forest–steppe landscapes. Artemisia–Chenopodiaceae and Asteracea and Caryophyllaceae assocition and *Betula* and *Pinus –Picea* forest
50				the beginning	Fish	Aves	*Chiroptera, Sorex* sp., *Ochotona pusilla, Spermophillus* sp., *Cricetulus migratorius, Myodes* sp.,	*Lepus timidus, Marmota bobak, Canis lupus, Vulpes lagopus, V. vulpes, Ursus arctos, U. spelaeus,*			Open woodland with *Pinus sibirica–Picea–Betula* and *Pinus –Picea*

(*continued on next page*)

Table 9 (*continued*)

Time, Ka	MIS	Stratigraphical scheme	Fish	Aves	Small mammals	Large mammals	Amphibians	Reptilies	Vegetation
					Lagurus lagurus, Dicrostonyx gulielmi, Lemmus sibiricus, Arvicola amphibius, Lasiopodomys gregalis, Alexandromys oeconomus, Microtus agrestis, Alexandromys middendorffi	*Martes zibellina, Gulo gulo, Mustela erminea, M. nivalis, M. eversmanni, Panthera leo spelaea, Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Cervus elaphus, Rangifer tarandus, Bison priscus, Saiga tatarica, Ovibos moschatus*			
127	4–5	Streletsk-Khanmei	Fish	Aves	*Chiroptera, Sorex* sp., *Ochotona pusilla, Spermophillus* sp., *Cricetulus migratorius, Craseomys rufocanus, Myodes* sp., *Lagurus lagurus, Dicrostonyx gulielmi-simplicior, Lemmus sibiricus, Arvicola amphibius, Lasiopodomys gregalis, Alexandromys oeconomus, Microtus agrestis, Alexandromys middendorffi*	*Lepus timidus, Marmota bobak, Canis lupus, Vulpes lagopus, V. vulpes, Ursus arctos, U. spelaeus, Martes zibellina, Gulo gulo, Mustela erminea, M. nivalis, M. eversmanni, Meles meles, Panthera leo spelaea, Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Cervus elaphus, Alces alces, Rangifer tarandus, Bison priscus, Saiga tatarica*	Amphibians		

Dicrostonyx gulielmi-simplicior, while throughout the Upper Pleistocene (Nev'yansk horizon (MIS 3) and Polar Urals horizon (MIS 2) till the beginning of the Bølling – Allerød period) as *D. gulielmi*, and starting from the beginning of the Bølling – Allerød period as *D. torquatus*. Similar changes occurred in other parts of the collared lemming's range (Smirnov et al., 1997; Ponomarev and Puzachenko, 2015).

The Lower Holocene deposits with small mammal remains are known from one locality (Medvezhaya cave, layer green sandy loam) in the northern key area and one locality (Cheremukhovo cave, pit 1, layer 8) in the southern key area (Fig., Table 6). The lack of the *A. amphibious, Sciurus vulgaris* in the southern fauna is attributed to taphonomic reasons. The Middle Holocene deposits with small mammal remains were studied in the southern part of the study area only (Table 6). At least 21 species were identified for three faunas. These include tundra species (*D. torquatus*, *L. sibiricus, A. middendorffii*), steppe species (*O. pusilla, Spermophillus* sp., *L. lagurus*), forest species (*S. vulgaris, Tamias sibiricus, Sicista betulina, M. agrestis*, *C. rufocanus*, *Myodes* sp., *M. schisticolor, Micromys minutus, Sylvaemus sylvaticus*), and species that live near water bodies. The Upper Holocene deposits with small mammal remains were studied in two caves in the northern key area and in three caves in the southern key area (Table 6). Fourteen species were identified in the northern faunas, and fifteen in the southern ones. The composition of the faunas of both parts of the study area is dominated by the forest species (*S. vulgaris Pteromys volans*, *Tamias sibiricus*, *S. betulina, M. agrestis*, *C. rufocanus*, *Myodes* sp., *M. schisticolor, Talpa europaea*) and species that live near water bodies (*A. amphibious, A. oeconomus*). The tundra species are also represented here. This is the *Lasiopodomys gregalis* in the north; and *Dicrostonyx torquatus*, *Lasiopodomys gregalis* and *Alexandromys middendorffii* in the south. The steppe species is represented by the *O. pusilla*. Different proportions of these species are attributed to the natural conditions of the northern and southern parts of the study area in the Upper Holocene. The latest Upper Holocene deposits yield the remains of the *Ondatra zibetica* which was acclimatized in Eurasia in the 20th century. Nowadays, only *Lasiopodomys gregalis* among the tundra and steppe species can still be found in the northern part of the Northern Urals (Bobretsov et al., 2012).

5.6.2. Large mammals

The most ancient faunas were found in the unconsolidated Streletsk (MIS 5) and Khanmei (MIS 4) horizons deposits in the Zhilische Sokola

Cave (pit 2) and Usoltsevskaya Cave located in the southern part of the key area. They include some typical mammoth faunal complex species, i. e. *Lepus timidus tanaiticus*, *Panhtera spelaea*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus ferus*, *Bison priscus*. Five faunas were studied in the Nev'yansk horizon deposits from the Drovatnitsa Grotto, Shaytnaskaya Cave (pit 1, layer 4) and Cheremukhovo Cave (pit 1, layer 9–12; pit 2, layer 3; pit 4, layer 2). The Drovatnitsa Grotto is located in the northern part of the study area. It includes 9 species, among which there is *Ursus kanivetz*, *Mammuthus primigenius, Coelodonta antiquitatis, Equus ferus*, *Ovibos moschatus* (Table 7). The fauna from the Drovatnitsa Grotto includes *Ursus kanivetz* (Table 7); this species disappeared at the end of MIS 3 (Pacher and Stuart, 2009). This fact permitted to correlate this fauna with the Upper Pleistocene Nev'yansk horizon (MIS 3). The faunas from the Shaytnaskaya Cave (pit 1, layer 4) and Cheremukhovo Cave (pit 1, layer 9–12; pit 2, layer 3; pit 4, layer 2) are correlated with the Nev'yansk horizon (MIS 3) based on a series of radiocarbon dates (Table 2). The faunas southern part include 20 species, which is significantly more than can be found in the faunas of the northern part of the area. This is explained by a noticeably larger bone sample from the southern localities (Table 7). Eight faunas from the Polar Urals horizon (MIS 2) deposits were studied. These are two faunas from the Medvezhaya Cave (layer grayish–brown "B" loamy soil; layer grayish–brown "A" loamy soil) in the northern part of the area, and six faunas (Zhilische Sokola Cave, pit 1; Cheremukhovo Cave, pit 2, layer 1–2; Shaytnaskaya Cave, pit 1, layer 3; Shaytnaskaya Cave, pit 2, layer 5b; Kakva–4, horizon 7–9) located in the southern part of the area. They include the mammoth fauna species (*Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus ferus*, *Bison priscus*, *Ovibos moschatus*) and give a series of radiocarbon dates correlated with MIS 2 (Table A1). The northern faunas include 18 species, while the southern faunas are composed of 19 species (Table 7). The faunas differ from each other by the presence of the steppe species *Marmota bobak* in the southern fauna.

Eleven faunas were identified in the unconsolidated Gorbunovo horizon (MIS 1) deposits. One fauna (Lakseyskaya cave, layer 4) from the southern part of the study area is dated to the Lower Holocene (Table 8). It includes 8 species only as it is represented by a small amount of bone sampling. One fauna from the northern part of the study area (Kaninskaya Cave, layer 1) and four faunas from the southern area (Lisia Cave; Burmantovo Grotto; Zhilische Sokola, pit 1; Cheremukhovo Cave, pit 1, layer 5) are dated to the Middle Holocene (Table 8). Fourteen species were identified in the northern fauna, and fifteen in the southern ones. Two faunas from the northern part of the study area (Kaninskaya Cave, layer 2; Uninskaya Cave) and three faunas from the southern part (Kaninskaya Cave, layer 2; Uninskaya Cave) are dated to the Upper Holocene (Table 8). The northern faunas include 18 species, while southern faunas are comprised of 12 species. The scope and composition of the faunas are different due to taphonomic reasons.

6. Discussion and palaeoenvironment reconstructions

6.1. Stratigraphy and chronology

The lithology of the deposits combined with the radiocarbon dates (this paper, sections 4.1 and 5.1) form the base of the subdivision of the studied unconsolidated deposits in the caves into the following, regionally defined, time intervals: the Upper Pleistocene (possibly with Streletsk (MIS 5) and Khanmei horizons and Nev'yansk (MIS 3), Polar Urals (MIS 2) and Gorbunovo (MIS 1) horizons. This subdivision corresponds to the subdivision of similar deposits in the Middle Urals (Smirnov et al., 2014) and is correlated with similar deposits in the Southern Urals (Danukalova et al., 2020).

6.2. Palynology

Western slope of the Northern Urals. In the middle and at the end of the Polar Urals horizon (MIS 2) time interval, periglacial steppe landscapes with forest communities were widespread in the river valleys. Herbaceous vegetation included grasses, sagebrush and forbs. Arboreal vegetation was represented by spruce (*Picea* sp.), Siberian pine (*Pinus sibirica*) and birch (*Betula* sect. *Alba*) (Guslitser and Kanivets, 1965). In contrast to the eastern slope (Lapteva, 2008), more open landscapes existed here at that time (Table 4).

Eastern slope of the Northern Urals. In the beginning of the Nev'yansk time interval, periglacial open woodland with *Picea* – *Larix* and *Betula* – *Pinus* with participation of the tundra flora elements was typical of this area. In the middle of this period, it was replaced by open woodland with *Pinus sibirica*–*Picea* and *Pinus* – *Betula* and more widespread meadow communities, and later on by periglacial forest-tundra communities with meadows (Lapteva, 2009) (Table 4). At the end of this time interval, spruce and spruce-birch forests with mesophilic meadows existed here (Strukova et al., 2006). In the beginning of the Polar Urals (LGM) time interval, periglacial tundra/forest tundra expanded with participation of dwarf birch (*Betula* sect. *Nana*), large proportion of the steppe vegetation and birch thickets (*Betula* sect. *Alba*) in the river valleys. At the end of the Polar Urals time interval, periglacial forest-steppe existed here (Lapteva, 2008) (Table 4). In the beginning of the Gorbunovo time interval (Lower Holocene), open woodland with *Betula, Larix, Pinus* and *Picea* dominance formed in the area. There were mesophilic meadows (Strukova et al., 2006; Lapteva, 2007). In the middle of the Gorbunovsky time interval (Middle Holocene), spruce and pine forests expanded with participation of broad-leaved species (*Tilia*, *Ulmus*) (Lapteva, 2007), which, at the end of this time interval (Upper Holocene), were replaced by birch-pine and pine forests (Lapteva, 2009; Antipina et al., 2014).

The analysis of the pollen spectra from the unconsolidated deposits from the northern Uralian caves demonstrates the predominance of the open and semi-open landscapes in the Upper Pleistocene and their rapid replacement by closed landscapes in the Lower Holocene (Fig. 2). This correlates well with the changes demonstrated at that time by the landscapes of the adjacent territories, namely Nether-Polar Urals (Kultti et al., 2003; Golubeva and Kryazheva, 2020), Middle Urals (Panova and Antipina, 2016) and Southern Urals (Danukalova et al., 2020). In the Lower Holocene and in the beginning of the Middle Holocene, some semi-open landscapes could still be found in the Northern Urals, however, these disappeared by the end of the Middle Holocene (Strukova et al., 2006; Lapteva, 2007, 2009; Antipina et al., 2014) (Fig. 2). Adjacent territories demonstrated similar changes in the landscapes in the Holocene (Zaretskaya et al., 2014).

6.3. Ichthyology

Fish remains were discovered in the most ancient Streletsk (MIS 5) or Khanmei (MIS 4) horizons deposits in the Zhilische Sokola Cave (pit 2) located in the southern part of the key area (Table 9). These were also found in the Nev'yansk horizon (MIS 3) deposits in the caves of the southern area, in the Polar Urals horizon (MIS 2) deposits in the caves of both northern and southern parts of the study area, as well as in the Gorbunovo horizon (MIS 1) deposits in the northern and southern parts of the area (Table 9). Fish bones were identified only in the Nev'yansk horizon deposits of the Cheremukhovo Cave (pit 2, layer 3) (Borodin et al., 2000b). The grayling (*Thymallus thymallus*) and pike (*Esox lucius*) remains, that are known from the deposits dated to this time in the southern Uralian caves, were found here (Danukalova et al., 2020). Currently, both species inhabit the Northern Urals. The amount of fish bones in the Gorbunovo horizon deposits is significantly higher than that of the Pleistocene deposits. This is attributed to a more humid Holocene climate and, respectively, to a large number of water bodies and their greater water reserves at that time.

6.4. Herpetology

In the Pleistocene deposits, the amphibian remains were discovered

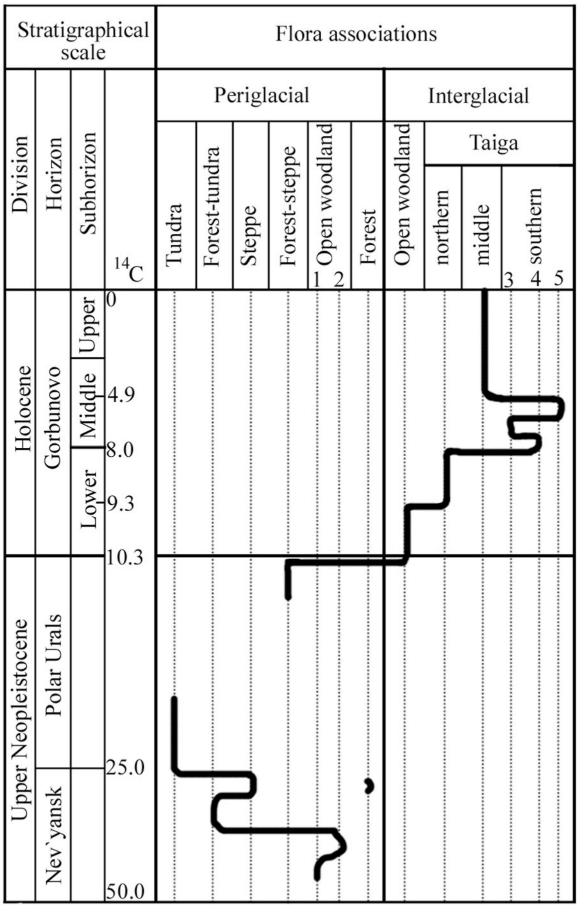

Fig. 2. Reconstruction of the main stages of the development of the flora during the late Upper Pleistocene and Holocene in the territory of the Northern Urals.

only in the earliest Streletsk (MIS 5) or Khanmeiy (MIS 4) horizons deposits in the Zhilische Sokola Cave (pit 2) located in the southern part of the key area, as well as in the deposits assigned to the end of the Polar Urals time interval (MIS 2) in Shaitanskaya cave (pit 2, layer 5b) dated to the Bølling – Allerød period (Table 9). Amphibian remains were found in the Gorbunovo (MIS 1) horizon deposits assigned to the Lower, Middle and Upper Holocene (Table 9) in the localities of the northern and southern parts of the study area. This is attributed to a more humid Holocene climate and, respectively, to a large number of water bodies and their greater water reserves at that time. The Southern Urals demonstrates similar scenario: amphibian remains were discovered only in the deposits dated to the Bølling – Allerød period (Danukalova et al., 2020).

No reptile remains were found in the Pleistocene deposits. The earliest finds were discovered in the Middle Holocene deposits (Table 9). The warmest climate in the northern Urals over the last 50,000 years was reconstructed for this period (Lapteva, 2009). This made it possible for the reptiles to inhabit the Northern Urals.

6.5. *Ornithology*

Bird remains were found in the deposits of all the Upper Pleistocene and Holocene horizons (Table 9). The greatest amount of the remains was found in the deposits dated to the second half of the Polar Urals (MIS 2) time interval and Upper Holocene (MIS 1) (Table A2). The end-Upper Pleistocene fauna includes species that occur near water bodies, inhabit open and semi-open landscapes. Species of the closed landscapes amount to less than 1%. The dominant species is *Lagopus lagopus* which inhabits open landscapes. The species composition shows that at the end of the Upper Pleistocene open landscapes dominated in the Northern Urals, while semi-closed landscapes covered only small areas, and closed landscapes were practically absent.

Species of the Holocene avifauna belong to the same landscape biotope groups as the Upper Pleistocene species: species living near water bodies, in open and semi-open landscapes and in closed landscapes. An increase in the number of species during the Holocene was due to an increase in closed biotopes. New species inhabiting forests (*Tetrastes bonasia*, *Dendrocopos major*) appeared. Holocene avifauna assemblage which is due to a significant increase in areas with forest vegetation. The changes in the structure of the avifauna assemblage that occurred in the Northern Urals during the transition from the Pleistocene to the Holocene are similar to the changes that occurred at that time in the Southern Urals (Danukalova et al., 2020). All the recorded Holocene species occur currently in the Northern Urals.

6.6. *Mammalogy*

6.6.1. *Small mammals*

We investigated the small mammal faunas from the cave deposits of the stratigraphical units exposed in the northern part of the study area and dated to the middle (Nev'yansk horizon, MIS 3) and the end (Polar Urals horizon, MIS 2) of the Upper Pleistocene, Lower Holocene (MIS 1), and Upper Holocene (MIS 1). In the southern part of the study area, we investigated the small mammal faunas from the cave deposits of all the stratigraphical units exposed there and dated from the beginning of the Upper Pleistocene (Streletsk–Khanmei horizon, MIS 5-4?) to the Upper Holocene (Tables 6 and 7).

6.6.1.1. Northern part of the study area. The small mammal fauna from the Nev'yansk horizon deposits (MIS 3) is dominated by tundra species (*Dicrostonyx gulielmi*, *Lemmus sibiricus*, *Lasiopodomys gregalis*, and *Alexandromys middendorffii*). Steppe species (*Ochotona pusilla*), forest species (*Myodes* sp., *Microtus agrestis*), and species that live near water bodies (*Arvicola amphibius* and *Alexandromys oeconomus*) were rare (Table 5). The Polar Urals horizon (MIS 2) fauna was still dominated by tundra species (*Dicrostonyx gulielmi*, *Lemmus sibiricus*, *Lasiopodomys gregalis*, *Alexandromys middendorffii*), while steppe (*Ochotona pusilla*), and forest species (*Microtus agrestis, Myodes* sp.) remained rare. In the end of the Polar Urals time interval, the brown lemming (*Lemmus sibiricus*) became dominant, while the *Dicrostonyx gulielmi*, *Lasiopodomys gregalis* and *Ochotona pusilla* were numerous. Other species (*Arvicola amphibius*; *Microtus agrestis*, *Alexandromys middendorffii*, *Alexandromys oeconomus*, *Myodes* sp.) were rare or very rare (Table 5). During the second half of the Upper Pleistocene (MIS 3 and MIS 2), tundra species dominated the small mammal faunas of the northern part of the study area, while steppe and forest species, as well as species that live near water bodies were small in numbers (Table 9). The Upper Pleistocene small mammal fauna of the northern part of the Northern Urals was a periglacial landscape fauna that reflects cold and dry climatic conditions.

The share of forest species (*Sciurus vulgaris*, *Microtus agrestis*, *Myodes* sp., *Craseomys rufocanus*, *Myopus schisticolor*) and species that live near water bodies (*Arvicola amphibius*; *Alexandromys oeconomus*) significantly increased in the fauna from the beginning of the Gorbunovo time interval (Lower Holocene, MIS 1) (Table 6). Nevertheless, tundra species (*Dicrostonyx gulielmi*, *Lemmus sibiricus*, *Lasiopodomys gregalis*) were still numerous, and the steppe species *Ochotona pusilla* could still be found there (Table 6). The faunas from the end of the Gorbunovo time interval (Upper Holocene, MIS 1) were dominated by forest species, while tundra species were represented only by the very rare *Lasiopodomys gregalis*. The latest deposits yield the remains of *Ondatra zibetica* acclimatized in the 20th century (Table 6). The Holocene small mammal fauna was a forest fauna that reflects moderately warm and humid climatic conditions.

The small mammal fauna of the northern part of the study area demonstrates fast changes in the predominance of tundra species that were replaced by forest species, as well as the increase in the share of species that live near water bodies in the Lower Holocene (Table 9). Vast open landscapes were still preserved in the Lower Holocene.

6.6.1.2. Southern part of the study area. The fauna from the beginning of the Upper Pleistocene deposits (Streletsk-Khanmei time interval, MIS 5-4) is dominated by tundra species (*Dicrostonyx gulielmi-simplicior*, *Lemmus sibiricus*, *Lasiopodomys gregalis* and *Alexandromys middendorffii*). Steppe species (*Spermophillus* sp., *Lagurus lagurus*, *Cricetulus migratorius*, *Ochotona pusilla*), forest species (*Myodes* sp., *Craseomys rufocanus*, *Microtus agrestis*) and species that live near water bodies (*Arvicola amphibius* and *Alexandromys oeconomus*) were rare (Table 5). The Nev'yansk horizon (MIS 3) fauna demonstrates the increased predominance of tundra species (*Dicrostonyx gulielmi, Lemmus sibiricus*, *Lasiopodomys gregalis*, *Alexandromys middendorffii*) and the reduction of forest species (*Myodes* sp.; *Craseomys rufocanus*), steppe species (*Spermophillus* sp.; *Lagurus lagurus*, *Cricetulus migratorius*, *Ochotona pusilla*) and species that live near water bodies (*Alexandromys oeconomus*) (Table 5). The faunas from the Polar Urals horizon (MIS 2) deposits preserve the dominance of tundra species. The occurrence of forest species slightly increased only at the very end of the Polar Urals time interval, in the Bølling – Allerød period, due to the appearance of *Craseomys rufocanus* and *Microtus agrestis*) in the fauna (Table 5). Steppe species and species that live near water bodies remain quite rare. At the same time, *Dicrostonyx torquatus* replaced species *Dicrostonyx gulielmi* (Table 9). During the Nev'yansk and Polar Urals time intervals, the fauna of the southern part of the study area was a periglacial landscape fauna that reflects cold climatic conditions.

The share of forest species (*Sciurus vulgaris*, *Microtus agrestis*, *Myodes* sp.; *Craseomys rufocanus*, *Myopus schisticolor*) and species that live near water bodies (*Arvicola amphibius*; *Alexandromys oeconomus*) increased in the fauna from the beginning of the Gorbunovo time interval (Lower Holocene, MIS1). Nevertheless, tundra species (*Dicrostonyx torquatus*, *Lasiopodomys gregalis*, *Lemmus sibiricus*) were still numerous, and steppe species could still be found there (Table 6). The faunas from the deposits dated to the middle of the Gorbunovo time interval (Middle Holocene) demonstrate the predominance of forest species (*Sciurus vulgaris*, *Tamias sibiricus*, *Sicista betulina*, *Microtus agrestis*, *Myodes* sp.; *Craseomys rufocanus Myopus schisticolor*). The share of species that live near water bodies (*Arvicola amphibius* and *Alexandromys oeconomus*) increases, though tundra species (*Dicrostonyx torquatus*, *Lasiopodomys gregalis*, *Lemmus sibiricus*, *Alexandromys middendorffii*) and steppe species (*Spermophillus* sp., *Lagurus lagurus*, *Ochotona pusilla*) still occur here (Table 6). Forest species started to dominate in the faunas from the end of the Gorbunovo time interval (Upper Holocene), while tundra species were represented only by the very rare *Dicrostonyx torquatus* and *Lasiopodomys gregalis* (Table 6). Species that live near water bodies remained numerous. The small mammal fauna of the southern part of the study area demonstrates fast changes in the predominance of tundra species that were replaced by forest species, as well as the increase in the share of species that live near water bodies, and gradual reduction of tundra species throughout the Holocene.

The small mammal faunas of the northern and southern parts of the study area were of similar composition and structure in the Upper Pleistocene. During the transition from the Upper Pleistocene to the Holocene and throughout the Holocene, these faunas demonstrated similar changes. The share of forest species and species that live near water bodies significantly increased, while that of tundra species reduced (Table 8).

6.6.2. Large mammals

We investigated the large mammal faunas from the cave deposits of the stratigraphical units exposed in the northern part of the study area and dated to the middle (Nev'yansk horizon, MIS 3) and the end (Polar Urals horizon, MIS 2) of the Upper Pleistocene, Middle Holocene (MIS 1), and Upper Holocene (MIS 1) (Tables 7 and 8). In the southern part of the study area, we investigated the large mammal faunas from the cave deposits of all the stratigraphical units exposed there and dated from the beginning of the Upper Pleistocene (Streletsk−Khanmei horizons, MIS 5-4?) to the Upper Holocene (MIS 1) (Tables 7 and 8).

6.6.2.1. Northern part of the study area. The fauna from the Nev'yansk horizon (MIS 3) does not include many species and consists of species that inhabit open landscapes (*Vulpes lagopus*, *U. kanivetz*, *Mammuthus primigenius*, *Equus ferus, Coelodonta antiquitatis*, *Rangifer tarandus*, *Ovibos moschatus*; species associated with tree vegetation *Martes zibellina*, as well as intrazonal species *Lepus timidus*, *Canis lupus* (Table 7). In the non-stratified deposits dated to this time interval in the Medvezhaya Cave we found the remains of one more open landscape species, namely the small cave bear (*U.* ex gr. *savini-rossicus*) (Gimranov and Kosintsev, 2022). The fauna of the Nev'yansk period indicates the dominance of open landscapes with a small amount of trees. By the end of this period, cave bears (*U. kanivetz*, *U.* ex gr. *savini-rossicus*) had disappeared from the fauna composition. In the Polar Urals horizon (MIS 2) deposits, species that inhabit open landscapes still predominated (*Panthera leo spelaea*, *V. lagopus*, *Mustela eversmanni*, *M. primigenius*, *E. ferus*, *C. antiquitatis, R. tarandus*, *Saiga tatarica, Bison priscus*, *O. moschatus*). Intrazonal species were numerous (*L. timidus*, *V. vulpes*, *C. lupus*, *Ursus arctos*, *Gulo gulo*, *Mustela erminea*, *Mustela nivalis*), while species associated with tree-shrub vegetation were rare (*M. zibellina*, *Alces alces*) (Table 9). This indicates the predominance of open landscapes and limited distribution of tree vegetation. The fauna from the Gorbunovo horizon deposits (Middle and Upper Holocene, MIS 1) is represented by species of closed landscapes, including species that were absent in the Upper Pleistocene *Lynx lynx*, *Meles meles*, *Meles leucurus*; species that live near water bodies (*Castor fiber*, *Lutra lutra*, *Mustela lutreola*) and intrazonal species. Open landscape species are represented by *Vulpes lagopus*. At the end of the Holocene, domestic ungulates (*Equus caballus*, *Sus scrofa domesticus*, *Bos taurus*, *Ovis aries*) appeared (Table 9). At least from the Middle Holocene, forest landscapes were common for the territories of the northern part of the study area.

6.6.2.2. Southern part of the study area. The fauna from the beginning of the Upper Pleistocene deposits (Streletsk-Khanmei time interval, MIS 5-4) includes a large species number of open landscapes (*Marmota bobak, P. L. spelaea, V. lagopus, M. eversmanni, M. primigenius, E. ferus, C. antiquitatis, R. tarandus, Saiga tatarica, Bison priscus*), species associated with woody vegetation (*M. zibellina, M. meles, A. alces, Cervus elaphus*), as well as intrazonal species (*L. timidus, V. vulpes, C. lupus,U. arctos, G. gulo, M. ermine, M. nivalis*) (Table 7). At the beginning of the Upper Pleistocene, open landscapes with large areas of woody vegetation were spread out. The Nev'yansk horizon (MIS 3) fauna include species that inhabit open landscapes and intrazonal species (Table 7). Species associated with tree vegetation (*M. zibellina, Cervus elaphus*) were small in numbers. In the Nev'yansk period, open landscapes with small areas of arboreal vegetation prevailed. The Polar Urals horizon (MIS 2) fauna is dominated by open landscapes and intrazonal species (Table 7). This fauna include only two species (*Martes zibellina, Alces alces*) associated with tree-shrub vegetation. This indicates the predominance of open landscapes and limited distribution of tree vegetation. The fauna from the Gorbunovo horizon deposits (Middle and Upper Holocene, MIS1) is represented by species of closed landscapes, intrazonal species and species that live near water bodies (*Castor fiber, Lutra lutra, M. lutreola*), including species that were absent in the Upper Pleistocene (*Lynx lynx, Meles meles, Meles leucurus*). Open landscape species are represented by *Vulpes lagopus*. At the end of the Holocene, domestic ungulates (*Equus caballus*, *Sus scrofa domesticus*, *Bos taurus*, *Ovis aries*) appeared (Table 8).

7. Extinction

The time of species extinction of particular region is an important biostratigraphic marker. In the Northern Urals, as well as throughout Eurasia, *P. leo spelaea, Ursus kanivetz, U. ex gr. savini-rossicus, M. primigenius*, *C. antiquitatis*, *B. priscus* and *O. moschatus* have become extinct (Stuart, 2021). Some radiocarbon dates on bones of these species were obtained from cave deposits (Table A1). Additionally dates on bones from alluvial localities were involved in order to determine the time of extinction of these species more exactly (Kosintsev et al., 2005). Data on the extinction of these species in neighboring territories were also included (Svendsen et al., 2010; Gimranov and Kosintsev, 2022). *U. ex gr. savini-rossicus* became extinct in the middle of the Upper Pleistocene (the end of the Nev'yansk horizon, MIS 3) (Fig. 3). *Ursus kanivetz* became extinct in at the turn of MIS3 and MIS2 (Fig. 3). *C. antiquitatis* became extinct in the middle of Polar Urals time (Fig. 3). *P. leo spelaea, M. primigenius and B. priscus* became extinct at the end of the Upper Pleistocene (Fig. 3). Probably *O. moschatus* became extinct already at the beginning of the Holocene (Fig. 3).

8. Conclusions

The area of the Northern Urals is characterized by local distribution of the Palaeozoic carbonate rocks on the eastern slope and their relatively wide distribution on the western slope. Thus, karst caves and grottoes are numerous on the western slope and rare on the eastern slope. Series of unconsolidated deposits with a thickness ranging from 0.4 to 6.6 m dated at least to the beginning of the Upper Pleistocene were formed in these caves and grottoes.

Investigations of the unconsolidated deposits resulted in detailed biostratigraphical and palaeoenvironmental data (Table 9). The data indicate the changes in the landscape and fauna composition in the Upper Pleistocene and Holocene. In the beginning of the Nev'yansk time interval (MIS 3), open woodland with *Pinus sibirica–Picea–Betula* and *Pinus –Picea* was typical of the area but by the end of this period it was replaced by forest-steppe landscapes. In the beginning of the Polar Urals time interval (MIS 2, LGM), periglacial steppe landscape with participation of *Betula* forest by the river was widespread; there were elements of the tundra shrub associations and Ephedra and Plumbaginaceae. Semi-open landscapes were typical of this area in the Bølling – Allerød period (the end of the Polar Urals time interval (MIS2)) and in the beginning of the Holocene (Lower Gorbunovo horizon (MIS 1)). Semi-open landscapes included small amounts of *Betula, Larix, Pinus,* and *Picea*. In the beginning of the Middle Holocene (Middle Gorbunovo horizon (MIS 1), these were replaced by the taiga landscapes.

The changes in landscapes provoked the changes in ornithofauna and theriofauna. The Upper Pleistocene ornithofauna and small mammal fauna were dominated by species that inhabit open landscapes, whereas species that prefer open and semi-open landscapes dominated the large mammal fauna. In the beginning of the Holocene, ornithofauna and theriofauna were characterized by an increase in species that live near the water bodies and species associated with tree-shrub vegetation. The Upper Pleistocene and Holocene theriofauna was characterized by permanent presence of the eurybiotic species.

Changes in the mammal faunal composition occurred due to species extinction and changes of their range. At the end of the Nev'yansk time interval, the large (*Ursus kanivetz*) and small (*U.* ex gr. *savini-rossicus*) cave bears became extinct, whereas the *Mammuthus primigenius, Coelodonta antiquitatis* and *Bison priscus* died out at the end of the Polar Urals time interval. At the end of the Pleistocene and the beginning of the Holocene (Gorbunovo horizon (MIS 1), the ranges of some species contracted north, while ranges of other species contracted south. The Pleistocene and Holocene bird faunas found in the cave sediments of the Northern Urals included species that occur in the modern ornithological faunas of Northern Asia and Northern Europe. All Upper Pleistocene and Holocene bird species still occur in the modern fauna of the Northern

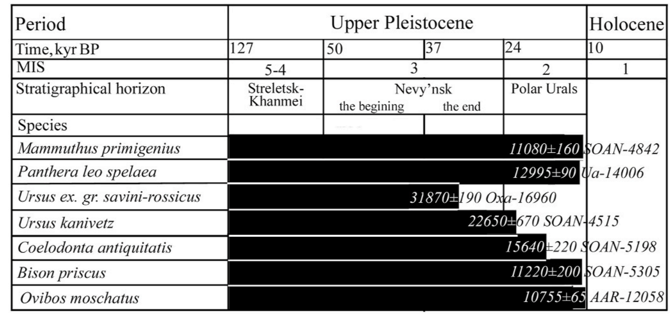

Fig. 3. The timing of Pleistocene mammal extinctions in the Northern Urals.

Urals.

Amphibians appear in the faunal composition of this area in the Upper Pleistocene only during relatively warm periods, i.e. in the beginning (Streletsk-Khanmei horizons, MIS 5-4) and at the end (Bølling – Allerød period). From the beginning of the Holocene (Gorbunovo horizon (MIS 1) they are permanently present in the faunal composition of the Northern Urals. Reptiles appear in the faunal composition of this area only in the Middle Holocene. Fishes were always present in the Northern Urals fauna though there is little data available on their species composition.

Palynological data in combination with the data on small and large mammal faunas can be used to date deposits of the Northern Urals caves. These data make it possible to distinguish the Upper Pleistocene and Holocene deposits, as well as the deposits dated to the beginning (Streletsk-Khanmei horizons, MIS 5-4), middle (Nev'yansk horizon (MIS 3), and the end (Polar Urals horizon (MIS 2)) of the Upper Pleistocene, and Lower, Middle and Upper Holocene (Gorbunovo horizon (MIS 1).

Author contributions

Pavel Kosintsev: Conceptualization, Methodology, Analyze or Synthesize study data, Writing - original draft. Olga Bachura: Analyze or Synthesize study data, Writing - original draft.

Data availability

The authors declare that all data of this research are available within the paper. The palaeontological collections are kept at the Museum of the Institute of Plant and Animal Ecology UB RAS.

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

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