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Quaternary deposits and biostratigraphy in caves and grottoes located in the Southern Urals (Russia)

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A R T I C L E I N F O

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A B S T R A C T

Investigations of the unconsolidated Upper Pleistocene – Holocene cave deposits of the Southern Urals resulted in detailed biostratigraphical and palaeoenvironmental data. Landscapes of this area have a mosaic character. The forests have regional features developed at the transition of Eastern European broadleaved-dark-coniferous taiga and the Southern-Uralian light coniferous forests. The modern mountain mixed forests appeared during the end of the Holocene. The forest-steppes were widespread during Late Neopleistocene – Holocene. The forest vegetation existed during the warm periods (Tabulda, Middle-Late Holocene) and areas covered by forest were reduced during the cold intervals (Kudashevo, Early Holocene). However, refugia of broad-leaved flora existed in the territory of the Southern Urals even during coldest periods. The Late Pleistocene and Holocene mollusc species are Holarctic species that occur in forest-steppe, forest and intrazonal (river banks) ecological biotopes. The Late Pleistocene and Holocene amphibian associations found in caves are characterized by species that prefer forest biotopes. The reptile faunas contain species which inhabited open areas. The Pleistocene and Holocene fish fauna is a characteristic freshwater fauna occurring in a temperate zone: all species currently inhabit the European rivers. The Pleistocene and Holocene avifaunas include species that occur in the modern ornithological faunas of Northern Asia, Central and Northern Europe. The Late Pleistocene fauna was dominated by species that inhabited open and semi-open landscapes whereas, during the Holocene, species that preferred closed biotopes dominated the bird fauna. During the Late Pleistocene and Early Holocene disharmonious small-mammal faunas existed in the central and northern parts of the Southern Urals. These faunas included steppe and semi-desert species; lemmings are rare. In the southern part of the Southern Urals and in the Trans-Urals lemmings are absent. Starting from the Middle Holocene there is a gradual change of small-mammal communities. In the Southern Urals forest species replace the predominance of steppe species, and only in the Trans-Urals the steppe small mammal fauna preserved. The modern small-mammal faunal community appeared in the latitudinal part of the Belaya River valley at the end of the Late Holocene. There were relatively little changes in the Southern Urals large mammal fauna at the end of the Late Neopleistocene – beginning of Holocene. The large mammal fauna consisted of eurybiotic species and species that inhabit open landscapes. Species that prefer forest landscapes appeared at the end of the Early Holocene – beginning of the Middle Holocene. Modern large mammal species appeared during the second half of the Late Holocene.

1. Introduction

This paper presents the biostratigraphical data from the caves and grottoes located in the Southern Urals (approximately 52°–56°N and 56°–59° E) (Fig. 1, Table 1). The area described in this paper was not well-known for a long time because it was difficult to reach the caves in

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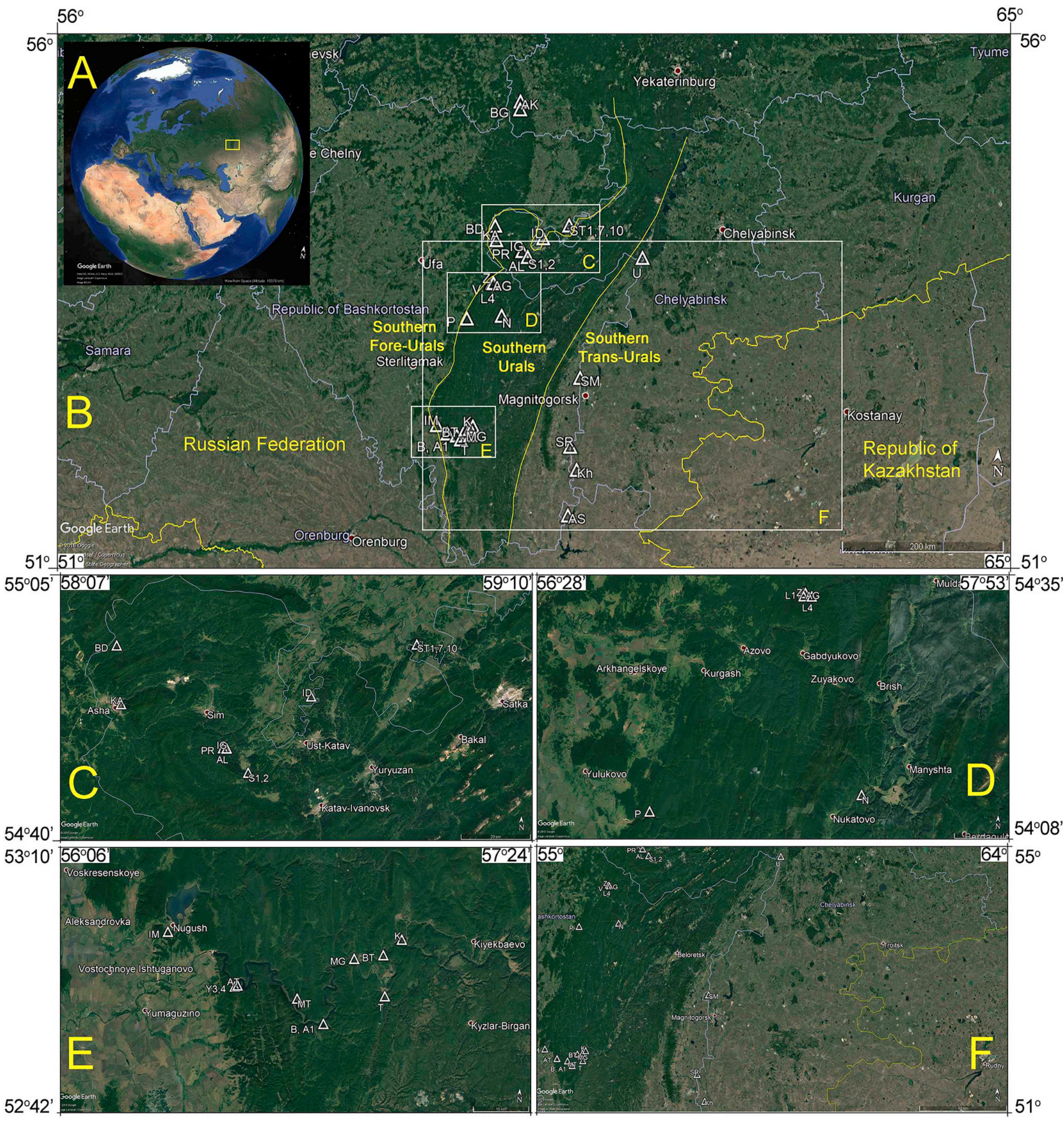

Fig. 1. Studied Southern-Uralian area with the locations of the caves.
Legend: A – general overview; B – locations of the caves discussed in this paper; C – the mountain part of the Southern Urals with the northern group of caves (Yuryuzan, Ai and Sim River valleys); D – the mountain part of the Southern Urals with central group of caves (Lemeza, Inzer, and Zilim River valleys); E – the mountain part of the Southern Urals with southern group of caves (latitudinal stretches of the Belaya and Nugush River valleys); F – the Southern Trans-Uralian area (Miass, Small and Big Kizil, Malaya Urtazymka River valleys). White triangles indicate the caves. For cave identifiers see Table 1. Maps are produced using Google Earth.

the mountainous part of the Urals. Biostratigraphical studies were often associated with archaeological excavations (Karacharovsky, 1951; Yakhemovich et al., 1970; Smirnov et al., 1990; Kuzmina and Abramson, 1997; Yakovlev et al., 2006; Saveliev et al., 2018, etc.) but also road construction works or the construction of water reservoirs offered sometimes the possibilities to a rescue survey of the unconsolidated deposits in the caves (Smirnov et al., 1990; Danukalova et al., 2011).

The Palaeozoic and Riphean sedimentary, metamorphic and magmatic rocks form different geological zones, from west to east: the Eastern part of the Eastern-European platform, the Fore-Uralian foredeep, the western and eastern slopes of the Southern Urals that corresponds to the eastern part of the Eastern-European Plan, the Southern Fore-Urals, the Southern Urals Mountains and the Trans-Urals.

There are several key-areas that yielded in the past biostratigraphical data; areas where the investigations will continue in the future. These areas are: the Southern Fore-Uralian area with the Ufimian Plateau; the mountainous part of the Southern Urals with a northern group of caves (Yuryuzan, Ai and Sim River valleys); the central group of caves (Lemeza, Inzer, and Zilim River valleys) and the southern group of caves (the latitudinal currents of the Belaya and Nugush River valleys); and the Southern Trans-Uralian area (Miass, Small and Big Kizil, Malaya Urtazymka River valleys) (Fig. 2). The elevation of the studied caves above modern thalwegs is shown in Fig. 2.

The caves constitute a natural database that is very informative and can help us to understand the past changes in the area. The main aim of our studies was to reconstruct the Late Pleistocene and Holocene palaeoenvironments based on the obtained biostratigraphical data. This paper presents the results of the biostratigraphical studies of the main localities i.e. the summarised stratigraphic description of the unconsolidated deposits, an overview of the fossil plants, molluscs and vertebrates and the radiocarbon age of the fossils incorporated in the unconsolidated deposits.

Table 1
Biostratigraphically investigated caves located in the Southern Uralian area.

Studied areas	Cave index	Object	Coordinates	Cave heighta-bovesea level (m)	Cave height above regional thalweg (m) / name of the river	Cave max length (m)	Cave volume (m^3)	Cave medium height (m)	Thickness of the studied Quaternary deposits (m)	Year of a cave discovery/study and an author / year of topographic plan creation	Methods of investigations	Composition of the carbonate deposits / stratigraphical index	Stratigraphical index of the unconsolidated deposits	References
Southern Fore-Uralian area	AK	Alikaev Kamen	56°28'N 57°37'E	223	15 / Sarana River	-	No data	No data	0.25	1987: Erokhin, Smirnov / 1987	b/mm; C14	Limestone / P_1	H_1	Izvarin, 2004; Izvarin, Smirnov, 2015
	BG	Bobyliok Grotto	56°23'N 57°37'E	310	7 / Bezymjanyi Stream	56	No data	3*	0.5	1987: Matrenin. 1989: Smirnov, Shirokov, Nekrasov / 1989	b/mm; b/lm; C14	Limestone / P_1	H_1	Smirnov, 1993; Izvarin, 2004; Razhev et al., 2005; Volkov et al., 2007
Southern Uralian Area. Northern part	ST1	Sikiyaz-Tamak 1 Cave	55°11'N 58°36'E	306	50 / Ai River	198	237	8	3	1995-1997, 2000-2002: Yurin / 1954	a, b/mm, b/lm; t	Limestone / C_1v	H, Q_3^4 Palaeolithic, Eneolithic, Bronze Iron, Middle Ages	Kosintsev, Yurin, 2003; Zhitenev, 2009
	ST7	Sikiyaz-Tamak 7 Cave	55°11'N 58°36'E	304	55 / Ai River	51.5	?	8	6	1995-1999, 2001-2003: Yurin / 1954	a, b/sp, b/m, b/mm, b/lm; t; C^{14}	Limestone / C_1v	Q_3-H, Palaeolithic, Bronze, Iron, Middle Ages	Kosintsev, Bachura, 2013; Danukalova et al., 2018
	ST10	Sikiyaz-Tamak 10 Cave	55°11'N 58°36'E	308	48 / Ai River	65	701	8	3	1995,1997, 2000, 2001: Yurin / 1954	a, b/lm; t	Limestone / C_1v	H, Q_3^4 Palaeolithic, Middle Age	Zhitenev, 2009
	ID	Idrisovo Cave	55°02'N 58°9'E	293	42 / Yuryuzan River	93	482	2.6	1.2	1987: Shyrokov / 1971	a; b, C14, b/mm, b/lm	Limestone / C_{1-2}	H_2, H_3, Q_3^3, Palaeolithic	Sokolov (BE); Smirnov et al., 1990; Abdrakhmanov et al., 2002; Smirnov, Sadykova, 2003; Shirokov, 2009; Kosintsev, Bachura, 2013; Kuzmin et al., 2017
	IG	Ignatievska-ya Cave	54°53'N 57°46'E	401	12 / Sim River	635	3100	2	5.2	1981-1984: Petrin; 1985: Smirnov, Kosintsev; 2014: Kosintsev /2014	b, C14, a; b/mm, b/lm, b/f, b/sp	Limestone / D_3fr	Q_2?, Q_3-H, Palaeolithic, Bronze, Iron, Middle Ages	Smirnov et al., 1990; Kosintsev, Bachura, 2013; Shirokov, Petrin, 2013; Smirnov et al., 2014; Fadeeva et al., 2018
	AL	Alenushka Cave	54°54'N 57°47'E	290	22 / Sim River	108	No data	3	0.4	1985: Smirnov, Erokhin / 1976	b, C14, b/mm, b/ml,	Limestone / D_3	H_2 H_3 M	Smirnov et al., 1990; Kosintsev, Bachura, 2013
	BD	Barsuchyi Dol Cave	55°09'N 57°16'E	281	18 / Unnamed creek (Sim River basin)	30	No data		4.2	2005: Yurin; 2013: Kosintsev / 2005	b/mm, b/lm, b/a, b/r	Limestone / D_3-C_1	H, Q_3^1	Kuzmin et al., 2017
	S1	Maiskaya (Serpievska-ya 1)	54°50''N 57°53''E	350	11 / Sim	268	2066	2.2	0.55	1986: Petrin / 1975	b/mm, b/lm, b/sp, C14	Limestone / D_3	Q_3^3 Q_3^4 H_1, M	Smirnov et al., 1990; Kosintsev, Bachura, 2013
	S2	Kolokolnay-a (Serpievska-ya 2)	54°50''N 57°53''E	350	14 / Sim River	344	No data	1.22	3	1986: Petrin / 1980	b/mm, b/lm, b/sp, C14	Limestone / D_3	Q_2, Q_3^4, H_2, H_1	Smirnov et al., 1990; Kosintsev, Bachura, 2013; Shirokov, Petrin, 2013;
	PR	Prizhim 2 Cave	55°59'N 57°46'E	378	4.5 / Sim River	15	No data		0.8	1985: Smirnov / 1987	b/mm, b/lm, b/sp, C14	Limestone / D_3	Q_3^4	Smirnov et al., 1990; Kosintsev, Bachura, 2013
	KA	Kozya (Asha I) Cave	55°00'N 57°18'E	159	17 / Sim River	5	No data		1.42	1980: Kozlov; 2006: Kosintsev / no data	b/mm, b/lm, C14	Limestone / D_3-C_1	H,Q_3^4 ,Q_3^3	Smirnov et al., 1990; Kosintsev, Sataev, 2005

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Table 1 (*continued*)

Studied areas	Cave index	Object	Coordinates	Cave heighta-bovesea level (m)	Cave height above regional thalweg (m) / name of the river	Cave max length (m)	Cave volume (m^3)	Cave medium height (m)	Thickness of the studied Quaternary deposits (m)	Year of a cave discovery/study and an author / year of topographic plan creation	Methods of investigations	Composition of the carbonate deposits / stratigraphical index	Stratigraphical index of the unconsolidated deposits	References
Southern Uralian Area, Central part	V	Verkhnaya Cave	54°33'N 57°16'E	252,2	80 / Atysh River	136	611	6	1	1995: Sataev; 1997: Yakovlev / 1987	b/mm, b/lm; b/sp; t; C^{14}	Limestone / C_1v	Q_2?, Q_3^{3-4}	Abdrakhmanov et al., 2002; Yakovlev et al., 2005; Danukalova et al., 2008
	Z	Zapovedna-ya Cave	54°33'N 57°16'E	235,2	70 / Atysh River	180	900	5	1	1995: Kosintsev; 2009: Kotov / 1991	b/m; b/a, b/r, b/mm, b/lm; b/f; b/sp; t; C^{14}	Limestone / C_1v	Q_3^{3-4}, Palaeolithic	Abdrakhmanov et al., 2002; Yakovlev et al., 2005; Danukalova et al., 2008; Kotov, 2009; Kosintsev, Bachura, 2013
	L4	Lemeza IV cave	54°33'N 57°17'E	179	4 / Lemeza River	10	60	1	0.85	1996: Yakovlev, Yakovleva / 1996	b/a, b/r, b/mm, b/sp; t	Limestone / C_1v	H_3 – M	Danukalova et al., 2008
	AG	Atysh I Grotto	54°33'N 57°16'E	181	6 / Atysh River	6	180	3	Surface of the cave bottom	1992: Yakovlev / 1992	b/a, b/r, b/mm, b/lm; b/f; b/sp; t	Limestone / C_1v	H_3 – M, Middle Ages	Yakovlev et al., 2005; Danukalova et al., 2008
	L1	Lemeza I	54°33'N 57°16'E	232	60 / Atysh River	2.5	21	5	Surface of the cave bottom	1992: Yakovlev / 1992	b/a, b/r, b/mm, b/lm; b/f; b/sp; t	Limestone / C_1v	H_3 – M	Yakovlev et al., 2005; Danukalova et al., 2008
	L2	Lemeza II	54°33'N 57°15'E	179	4 / Atysh River	13	120	1.5	0.55	1992: Yakovlev / 1992	b/a, b/r, b/mm, b/lm; b/f; b/sp; t	Limestone / C_1v	H_3 – M	Yakovlev et al., 2005; Danukalova et al., 2008
	L3	Lemeza III	54°33'N 57°15'E	179	4 / Atysh River	13	60	1	0.75	1992: Yakovlev / 1992	b/a, b/r, b/mm, b/lm; b/f; b/sp; t	Limestone / C_1v	H_3 – M	Yakovlev et al., 2005; Danukalova et al., 2008
	N	Nukatskaya (Zhemchuz-hnaya) Cave	54°12'N 57°28'E	350	30 / Nukat River	260	893	2	1.55	1954: schoolchildren of Inzer village / 1991	b/m, b/a, b/r, b/mm, b/lm; b/f,b/sp; t	Limestone / RF_3mn	H_{2-3}	Yakovlev et al., 2000; Abdrakhmanov et al., 2002;
	P	Kinderlinsk-aya (named by 30th anniversary of Victory) Cave	54°10'N 56°51'E	208	74/ Kinderlya River (Zilim tributary)	9113	245000	55	0.4	1974: Speleologists from Sterlitamak city / 1989	b/mm, b/lm, C14	Limestone / D_3fm	H, Q_3^3	Abdrakhmanov et al., 2002; Kosintsev, Bachura, 2013
	K	Shulgan-Tash (Kapova) Cave	53°2'N 57°3'E	280	8 / Belaya River	3045 / 165	180510	103	3.5	1760: Rychkov / 1990	a, b/m, b/mm, b/lm; b/sp; t; C^{14}	Limestone / C_1v	Q_3^4–H, Palaeolithic	Vakhrushev, 1960; Kudryashov, 1969; Shchelinsky, 1989, 1997; Lyakhnitsky, 2002; Abdrakhmanov et al., 2002; Danukalova et al., 2002, Sokolov, (BE); Yakovlev, 2012; Zhitenev, 2018

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Table 1 (*continued*)

Studied areas	Cave index	Object	Coordinates	Cave heighta-bovesea level (m)	Cave height above regional thalweg (m) / name of the river	Cave max length (m)	Cave volume (m^3)	Cave medium height (m)	Thickness of the studied Quaternary deposits (m)	Year of a cave discovery/study and an author / year of topographic plan creation	Methods of investigations	Composition of the carbonate deposits / stratigraphical index	Stratigraphical index of the unconsolidated deposits	References
Southern Uralian Area. Southern part	KT	Kulyurt-Tamak Cave	53°2' 57°2'E	314	40 / Belaya River	280	-	-	5.7	1960: Ryumin / 1971	b, C14, a	Limestone / C_1	Q_3^4	Yakovlev, 2014; Saveliev et al., 2018
	T	Tashmurun Grotto	52°57'N 57°1'E	287	4 / Irgizla River	12	-	5	4.2	2000: Kotov, Saveliev / 2000	a, b/sp, b/m, b/a, b/r, b/mm, b/lm; t	Limestone / D	H_3, H_2, Eneolithic, Bronze Age, Iron Age, Middle Ages	Danukalova et al., 2002b, 2011, 2017; Kosintsev, 2003; Yakovlev et al., 2004; Saveliev et al., 2018
	MG	Maksyutovo Grotto	53°0'N 56°56'E	278	10 / Belaya River	12	-	-	1	1999: Kotov / 1999	b/mm, b/lm, C14, a	Limestone / D	Q_3^3, H_3	Danukalova et al., 2002b, 2011; Kosintsev, Bachura, 2013; Saveliev et al., 2018
	B	Bajslan-Tash (Ljybimaya) Cave	52°54'N 56°52'E	269	12 / Belaya River	110	1283	4.5	4.5	1770: Lepekhin / 1973	a, b/m, b/a, b/r, b/mm, b/lm; b/f, b/sp; t; C^{14}	Limestone / C_1v	Q_3^4–H	Abdrakhmanov et al., 2002; Yakovlev et al., 2006; Danukalova et al., 2002b, 2011; Kosintsev, Bachura, 2013
	A1	Archaeologists Grotto	52°54'N 56°52'E	287	12 / Belaya River	5	10	1.2	1.7	1999	a, b/sp, b/m, b/mm, b/lm; t	Limestone / C_1v	H_3	Danukalova et al., 2002b, 2011; Yakovlev et al., 2003
	Y3	Yurmash 3 Cave	52°57'N 56°37'25"E	263	12 / Belaya River	-	-	-	-	-	a, b/sp, b/m, b/mm, b/lm; t	Limestone / C_1v	H_3	Danukalova et al., 2002b, 2011
	Y4	Yurmash 4 Cave	52°57'N 56°37'E	263	12 / Belaya River	-	-	-	-	-	a, b/sp, b/m, b/mm, t	Limestone / C_1v	$H_{2\text{-}3}$	Danukalova et al., 2002b, 2011
	AT	Azan-Tash 1 Cave	52°57'N 56°37'E	244	12 / Belaya River	-	-	-	-	-	a, b/sp, b/m, b/mm, t	Limestone / C_1v	H_3	Danukalova et al., 2002b, 2011
	MT	Mujnak-Tash (Teatralnaya) Cave	52°56'N 56°47'E	260	25 / Belaya River	526	6100	2.5	-	No data / 1974		Limestone / D_1	H	Abdrakhmanov et al., 2002
	BT	Balatukai Cave	53°01'N 57°01'E	297	90 / Belaya	70	-	-	1.2	1961: Shokurov / 1999	b/mm, b/lm, b/f, C^{14}, a	Limestone / D	H, Q_3^4	Kosintsev et al., 2018
	IM	Imanai Cave	53°02'N 56°26'E	230	30 / Nugush River	110	-	-	1.2	2010: Almukhametov / no data	b/a, b/r, b/mm, b/lm, b/f, C^{14}, a	Limestone / C_1	H, Q_3^3, Q_3^1 Palaeolithic	Gimranov et al., 2016a, 2016b, 2017a, 2017b; 2018

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Studied areas	Cave index	Object	Coordinates	Cave heightabovesea level (m)	Cave height above regional thalweg (m) / name of the river	Cave max length (m)	Cave volume (m^3)	Cave medium height (m)	Thickness of the studied Quaternary deposits (m)	Year of a cave discovery/study and an author / year of topographic plan creation	Methods of investigations	Composition of the carbonate deposits / stratigraphical index	Stratigraphical index of the unconsolidated deposits	References
Southern Trans-Uralian Area	SM	Smelovskaya 2	53°36'N 58°54'E	373	7 / Malyi Kizil River	30	-	-	3.4	1950: Salnikov / no data	b/mm, b/lm, C^{14}, a	-	H, Q_3^3 Palaeolithic	Kuzmina, 2000; Kosintsev, Bachura, 2013; Kosintsev et al., 2019
	SR	Syrtinskaya	52°52"N 58°45"E	320	7 / Bolshoi Kizil River	14	-	-	1.0	No data	b/mm, b/lm, b/sp C^{14}	-	$Q_3{}^4$, H	Smirnov and Kuzmina, 2001; Kuzmina et al., 2001; Kuzmina, 2002, 2009; Kosintsev, Bachura, 2013
	AS	Alekseevskaya	52°09'N 58°46'E	274	6 / Malyi Urtazym River	10	-	-	0.45	1999: Kuzmina; 2012: Kosintsev /2012	b/mm, b/lm, C^{14}	-	H_1, H_3	Kuzmina et al., 2001; Lapteva, 2006; Kuzmina, 2009; Fadeeva, Kosintsev, 2015
	U	Ustinovo Grotto	54°52'N 59°58'E	358	5.5 / Miass River	5.5	-	-	1.1	1988: Smirnov, Erokhin, Shirokov / 1988	b/mm, b/lm, C^{14}	-	H_2, $Q_3{}^4$, $Q_3{}^3$	Smirnov et al., 1990
	Kh	Khudolaz Caves	52°38"N 58°53"E	300	4.5 / Khudolaz River	15	-	-	0.75	No data	b/mm, b/lm, b/f	-	H_3	Kuzmina, 2009
	Ch	Chernyshevskaya 5 Cave	52°40'N 58°50'E	299.5	4 / Khudolaz River	15	-	-	0.35	No data	b/mm, C^{14}	-	H_3, $Q_3{}^4$	Kuzmina, 2009

Legend: Methods of investigations: biostratigraphical – (b), geochronological (C^{14}); topographical (t), archaeological (a). Detailization of biostratigraphical methods: b/m – molluscs, b/a – amphibians, b/r – reptiles, b/mm – small mammals, b/lm – large mammals; b/f – other fossils; b/sp – palynological investigations. Stratigraphical indices: RF – Upper Neoproterozoic, Riphean; RF_3mn – Upper Riphean, Minyar Suite; D_3fm – Upper Devonian, Famenian Stage; C_1v – Lower Carboniferous, Visean Stage; Q_2 – Middle Neopleistocene; Q_3 – Upper Neopleistocene; $Q_3{}^1$ – Kushnarenkovo Horizon; $Q_3{}^2$ – Saigatka Horizon; $Q_3{}^3$ – Tabulda Horizon; $Q_3{}^4$ – Kudashevo Horizon; H – Holocene; H_1 – Lower Holocene; H_2 – Middle Holocene; H_3 – Upper Holocene; M – Recent time; *– entrance arch' height; – no data.

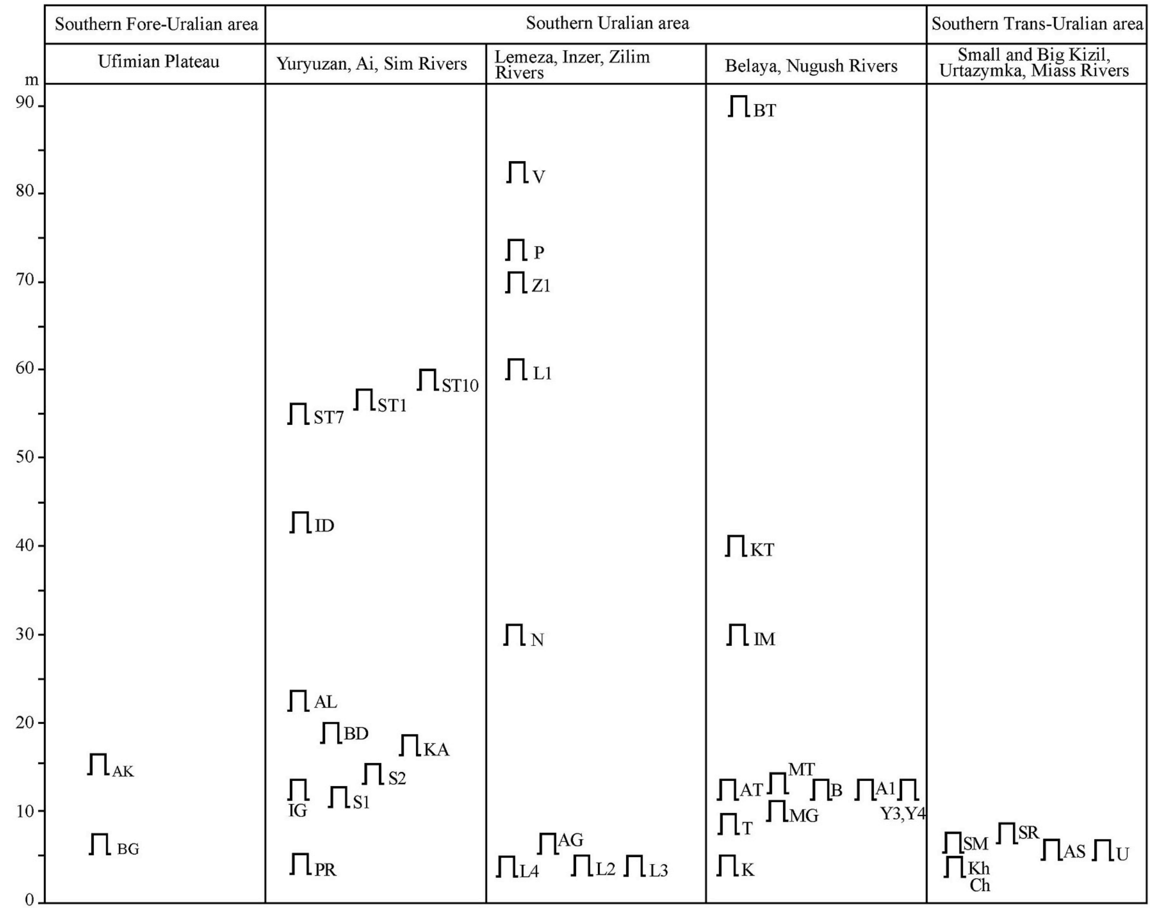

Fig. 2. Topographic position of the studied cave sites (elevations above the local thalweg). The caves are grouped in areas of the Southern Fore-Urals (Ufimian Plateau), the mountain part of the Southern Urals with the northern group of caves (Yuryuzan, Ai and Sim River valleys), the central group of caves (Lemeza, Inzer, and Zilim River valleys), the southern group of caves (latitudinal stretches of the Belaya and Nugush River valleys) and the Southern Trans-Uralian area (Miass, Small and Big Kizil, Malaya Urtazymka River valleys). For cave identifiers see Table 1.

2. General geological background

Based on tectonic features, the investigated area is subdivided, from west to east, into several structural zones – the Eastern margin of the Eastern-European Platform, the Fore-Uralian Foredeep, the Western and Eastern zones of the Central Uralian Uplift, and the Magnitogorsk zone (Puchkov, 2010).

The hills and upland areas of the Eastern margin of the Eastern-European Platform are constituted of the sedimentary rock complex of mainly Permian deposits and Palaeogene-Neogene-Quaternary deposits that occur in the platform depressions. The Fore-Uralian Foredeep sedimentary complex is similar to the Platform Complex. The Upper Palaeozoic deposits form the Western part of the Southern Uralian folded area and the Riphean-Vendian complexes form the Central Uralian Uplifted area. The eastern part of the area consists of Palaeozoic volcanogenic and volcanogenic-sedimentary rocks.

The territory of the Southern Ural region is nowadays characterized by a moderately humid climate with a rainfall of 350–750 mm per year, providing moderate groundwater recharge. In addition, the area demonstrates a dissected relief, where Upper Proterozoic, Devonian, Carboniferous and Permian carbonate rocks, as well as Permian sulphate rocks are widespread. All these features are ideal for the development of the karst forms in about half of the studied territory ("Atlas, Respubliki Bashkortostan Atlas of Bashkortostan Republic," 2005). During the Quaternary, caves and grottoes were accumulating deposits that are the product of weathering processes. At the same time, caves were inhabited by animals and during Late Pleistocene - Holocene – by humans.

3. Archaeological data

The earliest archaeological finds in the caves of the Southern Urals area date back to the Middle Palaeolithic and correspond to the Mousterian epoch. Single artefacts of this age were found in the layer 13 of the Sikiyaz-Tamak 7 cave, which has a radiocarbon date of more than 57.300 years ago (OxA–10916) (Danukalova et al., 2018). A series of bifacial sharp points was found during the excavation of the Imanai cave; the shape of these points is similar to those from the third cultural layer of the Ilskaya Mousterian site in the Fore-Kuban area, Northern Caucasus (Gimranov et al., 2017a). Numerous bone remains of *Ursus savini* Andrews, 1922 and *Pantera (Leo)* ex gr. *fossilis-spelaea* Goldfuss, 1810 were found together with bifacial points (Gimranov et al., 2017a).

Late Palaeolithic archaeological finds from the caves are much more numerous. The archaeological sites in the Smelovskaya II cave (Bader, 1971) and in Idrisovo (Shirokov, 2009) are correlated with the early Late Palaeolithic (Table 2).

The archaeological layers of 23 caves are correlated with the late Late Palaeolithic (Table 2) (Bibikov, 1950a; Bader, 1971; Smirnov et al., 1990; Petrin, 1992; Yakovlev et al., 2006; Volkov et al., 2007; Saveliev et al., 2018; Kosintsev et al., 2018). The deposits in the Prizhim II cave (Smirnov et al., 1990) are correlated with the Last Glacial Maximum; eleven sites are correlated with the Last Glacial Transition and four sites are attributed to the Bolling–Allerød (Table 2). Ten archaeological levels in caves have a late Late Palaeolithic age with

Table 2
The caves in an archaeological and stratigraphical frame.

Stratigraphy / Regional unit		Unformal units	Archaeological data	Caves	References
Late Pleistocene	Saigatka–Tabulda	Glacial / Pleniglacial	Middle Palaeolithic: Mousterian	Imanai, Sikiyaz-Tamak 7	Gimranov et al., 2017a; Danukalova et al., 2018
	Tabulda	Pleniglacial	Late Palaeolithic	Idrisovo, Smelovskaya II	Shirokov, 2009; Bader, 1971
	Kudashevo	Last Glacial Maximum		Prizhim II	Smirnov et al., 1990
		Last Glacial Transition		Ignatievskaya, Solomennaya (Serpievskaya 2), Sikiyaz-Tamak 7, Ustinovo, Zapovednaya, Shulgan-Tash, Kuljurt-Tamak, Balatukai, Maksyutovo gr., Bajslan-Tash, Smelovskaya II, Bobyliok (layer 4)	Smirnov et al., 1990; Danukalova et al., 2018; Kotov, 2009; Bader, 1971; Bibikov, 1950a; Petrin, 1992; Yakovlev et al., 2006; Saveliev et al., 2018; Kosintsev et al., 2018; Volkov et al., 2007
		Bolling–Allerod		Ignatievskaya, Sikiyaz-Tamak 1, Zapovednaya, Balatukai	Petrin, 1992; Kosintsev, Yurin, 2003; Zhitenev, 2009; Kotov, 2009; Kosintsev et al., 2018
		Younger Dryas		No data	
		Last Glacial		Klyuchevaya, Buranovskaya, Smirnovskaya, Sikiyaz-Tamak 10, Mujnak-Tash, Shtabnaya, Tashkelyat, Muradymovskaya I and II, Smelovskaya I	Bibikov, 1950a; Zhitenev, 2009; Saveliev et al., 2018; Kotov, 2009; Bader, 1964
Holocene / Agidel	Lower	Preboreal Boreal	Mesolithic	Shulgan-Tash, Zhemchyuzhnaya, Bajslan-Tash, Alekseevskaya	Bader, 1971; Smirnov et al., 1990; Saveliev et al., 2018;
	Middle	Atlantic	Neolithic Eneolithic	Buranovskaya, Grebnevaya, Ust-Katavskaya II, Kamennoe koltso Gr., Sikiyaz-Tamak 1, Sikiyaz-Tamak 7, Zhemchuzhnaya, Kuallomat, Kutanovo, Balatukai, Tashmurun, Maksyutovo Gr., Bajslan-Tash, Archaeologists Gr., Kargisaar 2, Neolitovaya, Muradymovskaya II	Bibikov, 1950a,b; Smirnov et al., 1990; Kosintsev, Yurin, 2003; Zhitenev, 2009; Kosintsev et al., 2018; Saveliev et al., 2018; Danukalova et al., 2017, 2018
		Subboreal	Late Bronze Age	Buranovskaya, Ust-Katav II, Ignatievskaya, Sikiyaz-Tamak 1, Sikiyaz-Tamak 7; Shulgan-Tash, Kuallomat, Tugai-Chishma, Bajslan-Tash, Archaeologists Gr.; Tashmurun, Neolitovaya	Shorin, 1992; Kosintsev, Yurin, 2003; Zhitenev, 2009; Danukalova et al., 2017, 2018; Saveliev et al., 2018
	Upper	Subatlantic	Iron Age	Buranovskaya, Ust-Katav II, Ignatievskaya, Bolshoi Grot, Solomennaya (Serpievskaya 2), Sikiyaz-Tamak 1, Sikiyaz-Tamak7, Zhemchyuzhnaya, Tashmurun; Balatukai; Bajslan-Tash, Archaeologists Gr., Vorota Arkalyana, Mujnak-Tash, Peschanyi, Azan-Tash 1, Azan-Tash 2, Nadezhda, Yurmash 4, Neolitovaya	Shorin, 1992; Kosintsev, Yurin, 2003; Zhitenev, 2009; Danukalova et al., 2017, 2018; Saveliev et al., 2018
			Middle Ages	Buranovskaya, Ust-Katav II, Ignatievskaya, Solomennaya (Serpievskaya 2), Atysh I, Sikiyaz-Tamak 1, Sikiyaz-Tamak 7, Shulgan-Tash, Tashmurun, Bajslan-Tash, Archaeologists Gr., Yurmash 4, Neolitovaya	Shorin, 1992; Kosintsev and Yurin, 2003; Zhitenev, 2009; Danukalova et al., 2017, 2018; Saveliev et al., 2018

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

Global Quaternary scheme (Cohen et al., 2016; Ravazzi, 2004)			Marine Isotope Stages	Stratigraphic Scheme of Russia (Zhamoida et al., 2006)			Southern Urals region (Danukalova, 2007, 2009)			Regional Stratigraphic scheme of the Eastern European Platform (Shick, 2014)			Urals (Stefanovsky, 1997)		North West European Stages (The Netherlands) (Zagwijn, 1996)		Unformal units
System	Series	Subseries, Stages		Division	Subdivision	Link	Superhorizon	Horizon		Superhorizon	Horizon		Superhorizon	Horizon	Horizon		Units
Quaternary	Holocene	Upper	1	Holocene		Modern		Agidel	Upper		Shuvalovo	Upper		Holocene	Holocene		Subatlantic
		Middle							Middle			Middle					Subboreal
																	Atlantic
		Lower							Lower			Lower					Boreal
																	Preboreal
	Pleistocene	Upper	2	Pleistocene	Neopleistocene	Upper	Valdai	Kudashevo		Valdai	Ostashkov		Northern Uralian	Polar Uralian	Weichselian	Upper	Younger Dryas
																	Allerod
																	Bolling
																	LGT
																	LGM
			3					Tabulda			Leningrad			Nevjansky		Middle	Pleniglacial
			4					Saigatka			Kalinin			Khanmeisky		Lower	
			5a-d					Kushnarenkovo			Chermenino			Streletsky	Eemian		
			5e								Mikulino						
		Middle	6			Middle		Elovka		Middle Russian	Moscow				Saalian		

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

a wide range.

The Mesolithic, which corresponds to the Early Holocene (as well as to Preboreal and Boreal of the Blitt-Sernander scale), is represented by a small number of the artefacts found in six caves (Bader, 1971; Smirnov et al., 1990; Saveliev et al., 2018) (Table 2). In seventeen caves the Neolithic and the Eneolithic, which corresponds to the Middle Holocene, the Atlantic and the beginning of the Subboreal, is represented (Bibikov, 1950a,b; Smirnov et al., 1990; Kosintsev and Yurin, 2003; Zhitenev, 2009; Kosintsev et al., 2018; Saveliev et al., 2018; Danukalova et al., 2018) (Table 2). Burials of this time were found in four of these caves (Buranovskaya, Starichnyi Greben, Ust-Katav II, and the grotto at the Stone Ring) (Bibikov, 1950b).

Bronze Age artefacts (the end of the Middle Holocene; the middle and the end of the Subboreal time) were found in twelve caves (Shorin, 1992; Kosintsev and Yurin, 2003; Zhitenev, 2009; Daanukalova et al., 2018; Saveliev et al., 2018). The artefacts of the early Iron Age are most numerous in the caves of the Southern Urals; they were found in twenty caves (Shorin, 1992; Kosintsev and Yurin, 2003; Zhitenev, 2009; Danukalova et al., 2018; Saveliev et al., 2018). Artefacts of the Middle Ages were found in twelve caves (Shorin, 1992; Kosintsev and Yurin, 2003; Zhitenev, 2009; Danukalova et al., 2018; Saveliev et al., 2018).

Thus, artefacts from all main archaeological epochs, starting with the Mousterian, have been found in the caves of the Southern Urals. The caves were visited most often during the early Iron Age. The Bronze Age, the Early Iron Age and the Middle Ages are represented by several archaeological cultures. A number of caves – Shulgan-Tash, Ignatievskaya, Kolokolnaya (Serpievskaya 2), and Zhemchuzhnaya – have Late Palaeolithic drawings on the walls of the interior halls of the caves (Sčelinskij and Širokov, 1999; Shirokov and Petrin, 2013; Saveliev et al., 2018). Some caves, such as Sikiaz-Tamak 1, were sanctuaries during the Iron Age (Kosintsev and Yurin, 2003).

4. Material and methods

4.1. Stratigraphical and chronological data

The article summarize biostratigraphical and geochronological data from important stratigraphical levels exposed in 35 cave sites, studied by the authors and our colleagues of the Institute of Plant and Animal Ecology of the Ural Branch RAS (Ekaterinburg) (Tables 1 and 4; Fig. 1).

The local stratigraphical units are correlated with the recent stratigraphical scheme of the Neopleistocene and Holocene deposits in the Southern Fore-Urals area; a scheme that is based on biostratigraphic data from key sites in the region, combined with archaeological, radiocarbon dates and palaeofaunal data (Danukalova, 2010). The upper part of the Neopleistocene (= Upper Pleistocene of the International Stratigraphic Chart (Cohen and Gibbard, 2016)) is subdivided into four horizons with local names: Kushnarenkovo (corresponds to MIS 5), Saigatka (MIS 4), Tabulda (MIS 3), Kudashevo (MIS 2) and Agidel Horizon corresponding to the Holocene (MIS 1) (Table 3). The Holocene is subdivided into the Lower (10–8 ka BP), Middle (8–2,5 ka BP) and Upper Holocene (2,5 ka – recent), a subdivision that is traditionally used in Russia during geological survey work (Shick, 2014). The actual data presented and discussed in this paper was collected during the past ca. 50 years by different authors; authors that also used the traditional (Russian) stratigraphical subdivision of the Holocene. We are aware of the fact that the applied subdivision differs from the recently, by the International Union of Geological Sciences ratified, formal subdivision of the Holocene Epoch into three distinct subsections, 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). The 4.2 ky boundary is, however, not well reflected in our region, in contrast to the 2.5 ky boundary, which is rather clear in the palaeobotanical record; a boundary that also correlates with the late Bronze/early Iron Age transition (Khotinsky, 1977). Therefore, for practicle reasons, we decided to use the traditional (Russian) stratigraphical subdivision of the Holocene.

All radiocarbone dates (C^{14}) were obtained, following the standard methodology, in different geochronological laboratories (see Table 4). Part of the large mammal faunas with an age beyond the radiocarbon dating method (i.e. an age beyond ca. 50 ka) are stratigraphically dated on the base of the species composition of the large and small-mammalian assemblages (Smirnov, 1993; Fadeeva et al., 2018; Kosintsev et al., 2013; subchapter 6.7 this paper) and/or on the base of the enamel differentiation coefficient (SDQ) of the *Arvicola terrestris* (Linnaeus, 1758) molars.

4.2. Palynological analysis

Quaternary deposits of 15 caves were studied palynologicaly: Zapovednaya Cave (Alimbekova et al., 1998), Lemeza II, III, IV (Alimbekova et al., 2000; Danukalova et al., 2008), Nukatskaya (Yakovlev et al., 2000), Verkhnyaya (Eremeev, 2003), Bajslan-Tash (Yakovlev et al., 2006), Shulgan-Tash (Eremeev and Kurmanov, 2011), Azan-Tash I, Yurmash 3, 4, Muinak-Tash (Danukalova et al., 2011), Archaeologists and Tashmurun grottoes (Danukalova et al., 2017b) and Sikiyaz-Tamak 7 (Danukalova et al., 2018). Additionally we used in our analyses published palynological data from five caves (Serpievskaya 1 and 2, Ignatievskaya 2, Prizhim 2 and Syrtinskaya) published by Panova (in Smirnov et al., 1990) and Lapteva (2006). The palynological analytic process was done following the standard methods described by Grichuk and Zaklinskaya (1948) with some additions. The basis of the calculation of the percentages for various taxa is the sum of all the grains of pollen and spores (100%) found in a sample. The identification of the pollen and spore species is based on, Kupriyanova and Aleshina (1972, 1978), Bobrov et al. (1983), and the recent spore and pollen collection of the Institute of Geology UFRC RAS (Ufa) has been consulted.

4.3. Palaeofaunal analysis

Molluscs. In total 2111 mollusc shells and identifiable fragments from the unconsolidated deposits of ten caves (Nukatskaya, Bajslan-Tash, Yurmash 4 and 3, Azan-Tash, Sikiyaz-Tamak 7, Zapovednaya caves; Maksyutovo, Archaeologists, and Tashmurun grottoes) were studied by the authors. Traditional methods of dispersal of sediments in water, using sieves with mesh sizes of 0.5 and 1.0 mm, were used to recover the molluscan and small-mammal remains (Zhadin, 1952; Steklov, 1966; Il'ina, 1966; Kaplin, 1987). Zhadin (1952), Likharev and Rammelmeier (1952), Shileyko (1978, 1984), Shileyko and Likharev (1986), Kerney and Cameron (1999), Nederlandse Fauna 2 (1998), Glöer (2002) are used to identify the species. For the malacological taxonomic nomenclature, we used the publication of Falkner et al., 2002).

Vertebrates. In total 7256 amphibian bone remains from eight localities (Bajslan-Tash, Lemeza II, III, IV, and Zapovednaya caves; Maksyutovo, Archaeologists, and Tashmurun grottoes) were identified; 1888 bone remains of reptiles from 9 caves (Bajslan-Tash, Lemeza II, III, IV, Yurmash 4, and Zapovednaya caves; Maksyutovo, Archaeologists, and Tashmurun grottoes) were identified and 27961 small-mammal remains from 13 caves (Bajslan-Tash, Alikaev Kamen', Lemeza II, III, IV, Nukatskaya, Yurmash 4, Azan-Tash 1, and Yurmash 3 caves; Bobyliok, Maksyutovo, Archaeologists, and Tashmurun grottoes) were described. There are fish and birds remains in the caves: fish bones were collected at eight caves (Ignatievskaya, Maiskaya (Serpievskaya 1), Sikiyaz-Tamak 7, Imanai, Prizhim 2, Kolokolnaya (Serpievskaya 2), Zapovednaya, and Nukatskaya caves), bird remains are known from eight caves (Balatukai, Lemeza II, Verkhnaya, Zapovednaya, Nukatskaya, Sikiyaz-Tamak 6 and 10 caves; Atysh I Grotto). In total 63350 large-mammal remains from 25 localities were identified.

Amphibians, reptiles and small-mammal species were identified

Table 4
Radiocarbon dating results.

MIS	Regional unit		Sampling places (locality, layer)	Age[a] in yr BP	Reference of specimen[b]	Material	References
3-4	Upper Pleistocene (Q_3)	Saigatka-Tabulda (Q_3^{2-3})	Sikiyaz-Tamak 7: layer 11	> 57300	OxA–10916	*Mammuthus* sp. bone	Danukalova et al., 2018
			Sikiyaz-Tamak 7: layer 9	> 47600	OxA–10889	*Crocuta* cf. *spelaea* bone	Danukalova et al., 2018
			Bajslan-Tash: layer 4	> 38100	GIN–10855	*Equus ferus* bone	Yakovlev et al., 2006
			Syrtinskaya: layer 4	> 34585	IEMEZ–1373	Mammal indet. bones	Kuzmina, 2009
			Syrtinskaya: layer 4	> 34395	IEMEZ–1377	Mammal indet. bones	Kuzmina, 2009
			Ignatievskaya: pit 5, layer 3	> 27620	IPAE–59	Mammal indet. bones	Smirnov et al., 1990
			Ignatievskaya: pit 5, layer 8	> 27500	IPAE–21	*Ursus spelaeus* bone	Smirnov et al., 1990
			Ignatievskaya: pit 2, layer 3	> 27500	IEMEZ–723	*Ursus spelaeus* bone	Smirnov et al., 1990
3		Tabulda (Q_3^3)	Kozya (Asha 1): layer 2	47100 ± 900	OxA–16959	*Ursus spelaeus* bone	Kosintsev, Bachura, 2013
			Smelovskaya II: layer 3	41000 ± 1800	GIN–8402	Large–mammal bones	Kosintsev, Bachura, 2013
			Sikiyaz-Tamak 1: floor surface	39370 ± 220	GdA–4596	*Cervus elaphus* bone	Kosintsev, Bachura, 2013
			Zapovednaya: pit 2, layers 1, 2	37250	LU–3876	*Ursus spelaeus* bone	Danukalova et al., 2008
			Idrisovo: horizon 8	35820 ± 390	CAMS–35881	*Lagurus lagurus*	Kosintsev, Bachura, 2013
			Idrisovo: horizon 8	32380 ± 610	CAMS–35882	*Dicrostonyx* sp.	Kosintsev, Bachura, 2013
			Smelovskaya II: layer 3	31400 ± 1700	GIN–8401	*Equus ferus* bone	Kosintsev, Bachura, 2013
			Zapovednaya: pit 1, layer 3	28700 ± 1000	LU–3715	*Ursus spelaeus* bone	Danukalova et al., 2008
			Kapova (Shulgan–Tash): cultural layer	28050 ± 250	AAR–20983	Mammal indet. bone	Zhitenev, 2018
			Kinderlinskaya (Pobedy)	27500 ± 350	SOAN–5145	*Ursus spelaeus* Bone	Kosintsev, Bachura, 2013
			Imanai: layer 1	26320 ± 1790	GIN–14244	*Ursus savini* bone	
			Serpievskaya 2 (Maiskaya): layer 3	25200 ± 1800	IPAE–46	Mammal indet. bones	Smirnov et al., 1990
			Smelovskaya II: layer 2	25000 ± 600	GIN–8403	Large–mammal bones	Kosintsev, Bachura, 2013
2		Kudashevo (Q_3^2)	Syrtinskaya: layer 3	23617 ± 267	IEMEZ–1332	Mammal indet. bones	Kuzmina, 2009
			Verkhnya: layer 2	22750 ± 1210	LU–3714	Mammal indet. bones	Danukalova et al., 2008
			Idrisovo: horizon 8	22180 ± 270	CAMS–35884	*Microtus gregalis*	Kosintsev, Bachura, 2013
			Syrtinskaya: layer 3	22050 ± 200	SOAN–5133	Mammal indet. bones	Kuzmina, 2009
			Idrisovo: horizon 8	21970 ± 80	CAMS–35883	*Microtus gregalis*	Kosintsev, Bachura, 2013
			Prizhim 2: horizon 6	21085 ± 630	IPAE–37	Mammal indet. bones	Smirnov et al., 1990
			Nukatskaya	17960 ± 320	SOAN–4805	?	Kosintsev, Bachura, 2013
			Bobyliok: layer 4, lower part	17565 ± 200	SPb–640	*Bison priscus* mandible	Velivetskaya et al., 2016
			Syrtinskaya: layer 3	17160 ± 190	SOAN–5132	Mammal indet. bones	Kuzmina, 2009
			Prizhim 2: horizon 2	17070 ± 1017	IEMEZ–700	Mammal indet. bones	Smirnov et al., 1990
			Bobyliok: layer 4	16720 ± 365	IPAE–142	*Rangifer tarandus* bone	Razhev et al., 2005
			Kapova (Shulgan–Tash): cultural layer	16710 ± 800	Ki–15967	Charcoal	Zhitenev, 2018
			Prizhim 2: horizon 2	16650 ± 400	IPAE–32	Mammal indet. bones	Smirnov et al., 1990
			Serpievskaya 1: layer 3	16585 ± 598	IEMEZ–722	Mammal indet. bones	Smirnov et al., 1990
			Kulyurt-Tamak: cultural layer	15870 ± 390	LE–3350	Charcoal	Saveliev et al., 2018
			Maksyutovo: layer 2	15650 ± 150	SOAN–7755	*Bison priscus* bone	Saveliev et al., 2018
			Sikiyaz–Tamak 7: layer 8	15370 ± 80	OxA–11069	*Coelodonta antiquitatis* bone	Danukalova et al., 2018
			Kapova (Shulgan–Tash): cultural layer	15235 ± 70	AAR–20982	Mammal indet. bone	Zhitenev, 2018
			Kapova (Shulgan–Tash): cultural layer	15100 ± 1300	RGI–505	Charcoal	Zhitenev, 2018
			Kulyurt-Tamak: cultural layer	14920 ± 660	LE–4350	Charcoal	Saveliev et al., 2018
			Kapova (Shulgan–Tash): cultural layer	14680 ± 150	LE–2443	Charcoal	Zhitenev, 2018
			Bobyliok: layer 4	14630 ± 80	OxA–11296	*Coelodonta antiquitatis* bone	Razhev et al., 2005
			Bobyliok: layer 4, upper part	14300 ± 200	GIN–14742	*Bison priscus* mandible	Velivetskaya et al., 2016
			Bobyliok: layer 4	14200 ± 400	IPAE–164	*Coelodonta antiquitatis* bone	Razhev et al., 2005

(*continued on next page*)

Table 4 (*continued*)

MIS	Regional unit		Sampling places (locality, layer)	Age[a] in yr BP	Reference of specimen[b]	Material	References
2	Upper Pleistocene (Q_3)	Kudashevo (Q_3^2)	Ignatievskaya: pit 2, layer 2a	14038 ± 490	IEMEZ–366	Mammal indet. bones	Smirnov et al., 1990
			Syrtinskaya: layer 2	13990 ± 340	SOAN–5134	Mammal indet. bones	Kuzmina, 2009
			Kapova (Shulgan–Tash): cultural layer	13930 ± 300	GIN–4853	Charcoal	Zhitenev, 2018
			Kapova (Shulgan–Tash): cultural layer	13900 ± 190	Ki–15568	Charcoal	Zhitenev, 2018
			Balatukai: horizons 8–9	13770 ± 220	SOAN–7272	Large mammal bones	Kosintsev et al., 2018
			Bajslan-Tash: layer 4	13560 ± 250	GIN–108533	Mammal indet. bones	Yakovlev et al., 2006
			Ignatievskaya: pit 2, layer 2b	13500 ± 1660	IPAE–41	Mammal indet. bones	Smirnov et al., 1990
			Balatukai: horizon 10–13	13450 ± 120	Ki–14960	Small mammal bones	Kosintsev et al., 2018
			Ustinovo: layer 3	12400 ± 300	IPAE–49	Mammal indet. bones	Smirnov et al., 1990
			Zapovednaya: pit 1, layer 1	12380 ± 260	LU–3861	Charcoal	Kotov, 2009
			Sikiyaz-Tamak 9: floor surface	12135 ± 60	OxA–22171	*Cervus elaphus* bone	Kosintsev, Bachura, 2013
			Balatukai: horizons 6–7	11900 ± 130	SOAN–7271	Large mammal bones	Kosintsev et al., 2018
			Sikiyaz-Tamak 7: layer 8	10775 ± 75	OxA–10704	*Cervus elaphus* bone	Danukalova et al., 2018
			Sikiyaz-Tamak 7: ?	10355 ± 45	OxA–12099	*Megaloceros giganteus* bone	Danukalova et al., 2018
1	Holocene (H)	Lower (H_1)	Bobyliok: layer 3	10220 ± 500	IPAE–136	Mammal indet. bones	Razhev et al., 2005
			Alikaev Kamen'	10140 ± 150	SPb–1242	Small–mammal bones	Izvarin, Smirnov, 2015
			Bobyliok: layer 3	9960 ± 50	OxA–11063	*Megaloceros giganteus* tooth	Razhev et al., 2005
			Bajslan-Tash: layer 4	9616 ± 62	IEMEZ–1340	Small–mammal bones	Yakovlev et al., 2006
			Bobyliok: layer 2	8690 ± 66	IEMEZ–1366	Mammal indet. bones	Volkov et al., 2007
			Alexeevskaya: layer 2, horizon 5	8450 ± 200	GIN–11334	Mammal indet. bones	Kuzmina, 2009
			Bajslan–Tash: layer 3	8216 ± 344	IEMEZ–1369	*Lepus timidus* bones	Kosintsev, Bachura, 2013
			Alexeevskaya: layer 2, horizon 4	8100 ± 240	GIN–11333	Mammal indet. bones	Kuzmina, 2009
		Middle (H_2)	Bajslan–Tash: layer 3	7140 ± 170	GIN–10854	Mammal indet. bones	Yakovlev et al., 2006
			Ustinovo: layer 1	4380 ± 170	IPAE–47	Mammal indet. bones	Smirnov et al., 1990
			Bobyliok: layer 1-2	3600 ± 150	IPAE–120	Mammal indet. bones	Razhev et al., 2005
			Bobyliok: layer 1-2	3170 ± 170	IPAE–121	Mammal indet. bones	Razhev et al., 2005
			Alenushka: layer 1	2718 ± 171	IPAE–53	*Capreolus pygargus* bone	Smirnov et al., 1990
			Bobyliok: layer 1-1	2650 ± 365	IPAE–140	*Alces alces* bones	
		Upper (H_3)	Alexeevskaya: layer 1, horizon 2	2550 ± 100	GIN–11331	Mammal indet. bones	Kuzmina, 2009
			Bobyliok: layer 1-1	2490 ± 190	IPAE–123	Mammal indet. bones	Razhev et al., 2005
			Bobyliok: layer 1-1	2260 ± 175	IPAE–125	Mammal indet. bones	Razhev et al., 2005
			Bajslan–Tash: layer 2	2095 ± 28	OxA–22168	*Cervus elaphus* bone	Kosintsev, Bachura, 2013
			Bobyliok: layer 1-1	2050 ± 200	IPAE–124	Mammal indet. bones	Razhev et al., 2005
			Bobyliok: layer 1-1	1713 ± 110	IPAE–140	Mammal indet. bones	Razhev et al., 2005
			Bajslan–Tash: layer 2	1600 ± 50	GIN–10852	Mammal indet. bones	Yakovlev et al., 2006
			Alexeevskaya: layer 1, horizon 1	1470 ± 90	GIN–11330	Mammal indet. bones	Kuzmina, 2009
			Bobyliok: layer 1-1	1215 ± 170	IPAE–123	*Rangifer tarandus* bone	Razhev et al., 2005

MIS – Marine Isotope Stages. A tentative correlation between MIS and other data is shown.

[a] Dates are not calibrated.

[b] Laboratory codes for dates: CAMS – Centre for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, USA; GIN – Geological Institute, Russian Academy of Sciences (RAS); IEMEZ – Institute of Animal Evolution Morphology and Ecology, RAS; IPAE – Institute of Plant and Animal Ecology, Ural branch, RAS; LE – Institute of the History of Material Culture, RAS; LU – St. Petersburg University, RAS; OxA – Oxford Accelerated, University of Oxford, UK; SOAN – Institute of Geology and Geophysics, Siberian Branch, RAS; Ki – Kyiv Radiocarbon laboratory, National Academy of Sciences of Ukraine; RGI – A.P. Vernadsky All-Russian Geological Institute; SPb – Herzen State Pedagogical University of Russia, St.Peterburg; AAR – University of Aarhus AMS Laboratory.

Table 5
Stratigraphical attribution of the unconsolidated deposits in the caves based on the faunal assemblages and the radiocarbon dates.

Studied areas	Cave index	Stratigraphy	Pleistocene					Holocene				
		Stratigraphical Index	Q_2	Q_3^1, Q_3^{1-2}	Q_3^{2-3}	Q_3^3	Q_3^4	H_1	H_{1-2}	H_2	H_3	H
		MIS Object	MIS 6?	MIS 5 MIS 5a-d – 4	MIS 4–3	MIS 3	MIS 2	Preboreal - Boreal; MIS 1	Preboreal - Subboreal; MIS 1	Atlantic - Subboreal; MIS 1	Subatlantic; MIS 1	Holocene not subdivided MIS 1
Southern Fore-Uralian Area	AK	Alikaev Kamen’						10140 ± 150 SPb–1242				
	GB	Bobyliok grotto		MIS 5e Layer 6 Large mammals			Layer 4 16720 ± 365* IPAE–142; 14630 ± 80 OxA–11296; 14200 ± 400 IPAE–142	Layer 3 10220 ± 500 IPAE–136; 9960 ± 80 OxA–11063; Layer 2 8690 ± 66 IEMEZ–1366		Layer 1-1 3600 ± 170 IPAE–121; 3170 ± 150 IPAE–120; 2650 ± 365 IPAE–140	Layer 1-2 2260 ± 175 IPAE–125; 2050 ± 200; IPAE–124; 1713 ± 110; IPAE–140; 1215 ± 170; IPAE–122	
Southern Uralian Area. Northern part	ST	Sikiyaz-Tamak caves		MIS 5e ST7 Layers 15–17 MIS 5a-d – 4 ST6 Layers 12–14	ST7 Layers 9–11 > 57300 OxA–10916; > 47600 OxA–10889	ST1 39370 ± 220 GdA–4596	ST4 Layer 8 15370 ± 80 OxA–11069; 10775 ± 75 OxA–10704; 10355 ± 45 OxA–12099; Floor surface 12135 ± 60 OxA–22171		ST3 Layer 7 Bronze Age artefacts; Late Palaeolithic faunal complex	ST2 Layers 5, 6 Bronze Age artefacts	ST1 Layers 1–4 Early Iron Age artefacts	
	ID	Idrisovo Cave				Horizon 8 35820 ± 390 CAMS–35881; 32380 ± 610 CAMS–35882	Horizon 8 22180 ± 270 CAMS–35884; 21970 ± 80 CAMS–35883					
	IG	Ignatievskaya Cave	Pit 5, layer 10 (1985) Small mammals	MIS 5e Pit 5, layer 10 (2014) Small mammals	Pit 5, layers 3–8 > 27620 IPAE–59; > 27500 IPAE–21; Pit 2, layer 3 > 27500 IEMEZ–723		Pit 2, layer 2a 14038 ± 490 IEMEZ–366; layer 2b 13500 ± 1660 IPAE–41					
	AL	Alenushka Cave									Layer 1 2718 ± 171 IPAE–53	
	BD	Barsuchyi Dol Cave		MIS 5e Large mammals								
	S1	Maiskaya (Serpievskaya 1)	Layer 3 Small mammals				Layer 2 16585 ± 598 IEMEZ–722					
	S2	Kolokolnaya (Serpievskaya 2)				Layer 3 25200 ± 1800 IPAE–46						
	PR	Prizhim 2 Cave					Horizon 2 16650 ± 400 IPAE–32; 17070 ± 1017					

(*continued on next page*)

Table 5 (*continued*)

Studied areas	Cave index	Stratigraphy	Pleistocene					Holocene				
		Stratigraphical Index	Q_2	Q_3^1, $Q_3^{1\text{-}2}$	$Q_3^{2\text{-}3}$	Q_3^3	Q_3^4	H_1	$H_{1\text{-}2}$	H_2	H_3	H
		MIS Object	MIS 6?	MIS 5 MIS 5a-d – 4	MIS 4–3	MIS 3	MIS 2	Preboreal - Boreal; MIS 1	Preboreal - Subboreal; MIS 1	Atlantic - Subboreal; MIS 1	Subatlantic; MIS 1	Holocene not subdivided MIS 1
							IEMEZ–700; horizon 6 21085 ± 630 IPAE–37					
	KA	Kozya (Asha I) Cave			Layer 2 47100 ± 900 OxA–16959							
Southern Uralian Area, Central part	V	Verkhnaya Cave	Deposits are eroded. *Ursus savini*				V2 Layer 2 Mammoth faunal complex 22750 ± 1210 LU–3714					V1 Layer 1 Holocene faunal complex
	Z	Zapovednaya Cave, pit 1				Z2 Pit 1, layers 2, 3. Mammoth faunal complex 28700 ± 1000 LU–3715; 37250 LU–3876	Z1 pit1, layer 1 Mammoth faunal complex 12380 ± 260 LU–3861					
	Z	Zapovednaya Cave, pit 2				Z3 Pit2, layers 1, 2 Mammoth faunal complex						
	Z	Zapovednaya Cave, pit 3									Pit 3: layers 1, 2	
	L4	Lemeza IV cave									L4 Layers 1–3 Modern faunal complex	
	AG	Atysh I Grotto									AG Cave's floor. Late Middle ages artefacts (800–900 years ago), before X century	
	L1	Lemeza I									L1 Cave's floor. Modern faunal complex (250 years ago)	
	L2	Lemeza II								L2a Layer 2: Middle Holocene faunal complex	L2b Layer1: Modern faunal complex	
	L3	Lemeza III						L3a Layers 2–6: Early Holocene faunal complex			L3b Layer 1: Modern faunal complex	
	N	Nukatskaya (Zhemchuzhnaya) Cave					Deposits are eroded 17960 ± 320 SOAN–4805	N2 Layer 2			N1 Layer 1	

(*continued on next page*)

Table 5 (*continued*)

Studied areas	Cave index	Stratigraphy	Pleistocene					Holocene				
		Stratigraphical Index	Q_2	Q_3^1, Q_3^{1-2}	Q_3^{2-3}	Q_3^3	Q_3^4	H_1	H_{1-2}	H_2	H_3	H
		MIS Object	MIS 6?	MIS 5 MIS 5a-d – 4	MIS 4–3	MIS 3	MIS 2	Preboreal - Boreal; MIS 1	Preboreal - Subboreal; MIS 1	Atlantic - Subboreal; MIS 1	Subatlantic; MIS 1	Holocene not subdivided MIS 1
								Early Holocene faunal complex			Modern faunal complex	
	P	Kinderlinskaya Cave			27500 ± 350 SOAN–5145							
Southern Uralian Area, Southern part	K	Shulgan-Tash (Kapova) Cave				Cultural layer 28050 ± 250 AAR–20983	K3 Cultural layer. Late Palaeolithic artefacts. 16710 ± 800 Ki–15967; 15235 ± 70 AAR-20982; 15100 ± 1300 RGI–505; 14680 ± 150 LE–2443; 13930 ± 300 GIN–4853; 13900 ± 190 Ki–15568	K2 layer 6?				K1 Layers 1–5
	KT	Kulyurt-Tamak Cave					Cultural layer. Late Palaeolithic artefacts. 15870 ± 390 LE–3350; 14920 ± 660 LE–4350					
	T	Tashmurun Grotto							T3 Layers 2–3, (1.2–4.2 m)	T2 Layer (0.6–1.2 m) Eneolithic Bronze age (horizons 3–4–5)	T1 Layer 1 (0–0.6 m) Modern faunal complex. Iron Age, Middle Ages (horizons 1–2)	
	MG	Maksyutovo Grotto					MG2 Layer 2 Mammoth faunal complex 15650 ± 150 SOAN–7755			MG1 layer 1 Middle Holocene faunal complex		
Southern Uralian Area. Southern part	B	Bajslan-Tash (Ljybimaya) Cave			B3 Layer 4 > 38100 GIN–10855		B3 Layer 4 13560 ± 250 GIN–108533	B3 Layer 4 9616 ± 62 IEMEZ–1340; layer 3 8216 ± 344 IEMEZ–1369		B2 Layer 3 7140 ± 170 GIN–10854	B1 Layer 1, 2 1600 ± 50 GIN–10852; 2095 ± 25 OxA–222168	
	A	Archaeologists Grotto									A1 Layer 1-4 Modern faunal complex	
	Y3	Yurmash 3 Cave									Layer 1 Modern faunal complex	
	Y4	Yurmash 4 Cave								Y4a Layers 2–3 Middle Holocene faunal complex	Y4b Layer 1 Modern faunal complex	
	AT	Azan-Tash 1 Cave									AT1 Layers 1–3	

(*continued on next page*)

Table 5 (*continued*)

Studied areas	Cave index	Stratigraphy	Pleistocene					Holocene				
		Stratigraphical Index	Q_2	Q_3^1, Q_3^{1-2}	Q_3^{2-3}	Q_3^3	Q_3^4	H_1	H_{1-2}	H_2	H_3	H
		MIS Object	MIS 6?	MIS 5 MIS 5a-d – 4	MIS 4–3	MIS 3	MIS 2	Preboreal - Boreal; MIS 1	Preboreal - Subboreal; MIS 1	Atlantic - Subboreal; MIS 1	Subatlantic; MIS 1	Holocene not subdivided MIS 1
											Modern faunal complex	
	BT	Balatukai Cave					Horizons 6–13 11900 ± 130 COAH–7271; 13770 ± 220 COAH–7272; 13450 ± 120 Ki–14960					
	IM	Imanai Cave				Layer 1 26320 ± 1790 GIN–14244						
Southern Trans-Uralian Area	SM	Smelovskaya 2				Layers 2,3 25000 ± 600 GIN–8403; 31400 ± 1700 GIN–8401; 41000 ± 1800 GIN–8402						
	SR	Syrtinskaya			Layer 4 > 34395 IEMEZ–1375; > 34585 IEMEZ–1373		Layer 2 13990 ± 340 SOAN–5134; Layer 3 23617 ± 267 IEMEZ–1334; 22050 ± 200 SOAN–5133; 17160 ± 190 SOAN–5132					
	AS	Alekseevskaya						Layer 2, horizon 4 8100 ± 240 GIN–11333; Layer 2, horizon 5 8450 ± 200 GIN–11334			Layer 1, horizon 1 1470 ± 90 GIN–11330; layer 1, horizon 2 2550 ± 100 GIN–11331	
	U	Ustinovo Grotto					Layer 3 12400 ± 300 IPAE–49			Layer 1 4380 ± 170 IPAE–47		

Legend: ST1, MG2… – indices of the different stratigraphical levels in caves, which were used in the Tables 7–14.* Data are uncalibrated. A tentative correlation between MIS and other data is shown. See Table 1 for the legend.

using Ratnikov (2002), Agadjanian (2009) and Borodin (2009). The Late Pleistocene and Holocene amphibians and reptiles were studied by Yakovleva (in Danukalova et al., 2008) (valley of the Lemeza River) and (in Danukalova et al., 2011) (valley of the Belaya River); small mammal faunas from the cave sites of the Southern Urals in the northern part of the region (Ufimian Plateau) were studied by Izvarin (2004, 2015, Izvarin, 2017 and Smirnov (1993); fossil remains from the central part of the region they were studied by Smirnov (in Smirnov et al., 1990) (the valley of the Sim River and the Yuryuzan River) and by Yakovlev (in Danukalova et al., 2008) (valley of the Lemeza River). The southern part of the Southern Urals the cave sites with small mammals were studied by Yakovlev (in Danukalova et al., 2011) (valley of the Belaya River). Small mammals from caves in the Southern Trans-Urals were studied by Smirnov (in Smirnov et al., 1990) and Kuzmina, 2003a, 2003b; 2009). Large mammals remains were studied by Kosintsev, additional data of other authors were cited in the text: Kapova Cave (Kuzmina, Abramson, 1997), Smelovskaya 2 Cave (Kuzmina, 2000), Syrtinskaya Cave (Kuzmina, 2003), Atysh I Grotto (Sataev, 2005), Kulyurt-Tamak Cave (Saveliev et al., 2018). Fish and bird remains were summarised by the authors with references listed in the text and the tables.

The shells of molluscs, amphibians, reptiles and partly small mammals were photographed at the Institute of Geology UFRC RAS (Ufa) using a stereomicroscope Motic SMZ-171 TLED with a camera Moticam-10x and/or with a camera Sony ILCE-6000 and a lens Sony SEL35F18.

5. Results

5.1. Stratigraphy and chronology

Unconsolidated cave deposits of eluvial-slope genesis cover the bottom surfaces of the caves and grottoes. They consist of (mainly) light-brown or reddish-brown loam and sandy loam and sometimes sand and clay occur in the lower parts of the deposits. The deposits contain numerous small and big-size limestone debris, as well as floral and faunal remains. Artefacts of different archaeological cultures occur in some levels. The thickness of these deposits differs and depends on the location of the deposit's section in the outer/inner parts of the caves and on the height above thalweg (Table 1). A summarised description of the unconsolidated deposits with their (possible) attribution to the MIS stages and the Western-European stratigraphical units is given below (Tables 3 and 5).

Middle Pleistocene (Upper Saalian? MIS 6?). Deposits of this interval are eroded and only a bone assigned to *Ursus* cf. *deningeri* Reichenau, 1904 discovered in Verkhnya Cave indicate a late Middle Pleistocene age. Deposits of the same age were also discovered inside the cracks in the rocky bottom of the Ignatievskaya (pit V, layer 10, excavation of 1985) and Maiskaya (Serpievskaya 1) (layer 3) Caves.

Kushnarenkovo? Horizon (lower part) (Eemian? MIS 5e?). White loamy sand and yellow clay with rare pebbles (thickness is 0.5 m) were encountered in the lowermost part of a pit in the Sikiyaz-Tamak 7 Cave. Cracks in the rocky floor of the Ignatievskaya Cave (pit V, layer 10, excavation of 2014) at the depth of 3.1–5.2 m were filled with light-brown silty clay and small fragments of limestone.

The Kushnarenkovo-Saigatka Horizons (Lower Weichselian, MIS 5a–d – 4) consist of reddish-brown and yellowish-brown clay (average thickness is 1.75 m) with pebbles and sharp-edge limestone fragments.

The Tabulda Horizon (Middle Weichselian, MIS 3) is represented by yellowish-brown loam with limestone debris (average thickness is 3.2 m) and Upper Palaeolithic large mammal bones (Sikiyaz-Tamak 1, Idrisovo, Serpievskaya 2, Zapovednaya, Ignatievskaya, Imanai, Nukatskaya, Shulgan-Tash, and Smelovskaya 2 Caves).

The Kudashevo Horizon (Upper Weichselian, MIS 2) is represented by yellowish-brown loam with limestone debris (average thickness is 0.8 m) and Upper Palaeolithic large mammal bones and artefacts (Sikiyaz-Tamak 4, Idrisovo, Ignatievskaya, Serpievskaya 1, Prizhim 2, Verkhnaya, Zapovednaya, Nukatskaya, Shulgan-Tash, Kulyurt-Tamak, Bajslan-Tash, Balatukai, Syrtinskaya Caves and Babyliok (layer 4), Maksyutovo and Ustinovo Grottoes).

The Agidel horizon (Holocene, MIS 1) is represented by loamy facies with limestone debris that can be subdivided into Lower, Middle and Upper Subhorizons using geochronological data and based on the composition of the mammalian faunas. The Lower Subhorizons deposits consist of brown loam with limestone debris and blocks. The thickness of these deposits is around 0.8 m. Deposits of this age were described in the localities of Alikaev Kamen', Lemeza III, Nukatskaya, Shulgan-Tash, Bajslan-Tash, Alekseevskaya caves, and Bobyliok Grotto (layers 2 and 3). The Middle subhorizon deposits consist of grayish-brown and brown sandy light loam with limestone debris and blocks. Ash layers and Bronze Age artefacts are known from those deposits. The average thickness is 0.85 m. Deposits of this age were described in the localities Sikiyaz-Tamak 7, Lemeza II, Bajslan-Tash, Yurmash 4 caves, and Tashmurun, Maksyutovo, Ustinovo Grottoes. The Upper subhorizon is characterized by brownish-gray loam (average thickness is 1 m) with limestone debris with ashes and artefacts from the Early Iron age to recent. Deposits of this age are represented in numerous caves distributed all over the studied area.

5.2. Palynology

Analysis of the samples from sediments of 20 caves made it possible to characterize the Late Pleistocene (Tabulda and Kudshevo horizons) and the Holocene flora. The pollen spectra reflect both local (plant communities of rocks, represented in many spectra by a high proportion of Polypodiaceae), and regional vegetation features (forest, forest-steppe, periglacial steppe). The dynamics of landscape changes in the South Urals during the Late Neopleistocene – Holocene are shown in Table 6 and Fig. 3.

5.3. Malacology

Mollusc shells were found in deposits correlated with the second half of the Late Pleistocene (Tabulda and Kudashevo Horizons) and the Holocene (Table 7, Fig. 4).

In total 94 terrestrial mollusc shells representing 5 different taxa were collected from the Tabulda Horizon deposits (Zapovednaya cave, pit 1, layer 3). Only 50 shells and their fragments belonging to ten terrestrial species (eight genera) and five freshwater species (4 genera) were collected from the deposits of Kudashevo Horizon of the Bajslan-Tash cave (see Table 7).

All the Holocene stratigraphical units yielded mollusc shells.

In total 427 shells and their fragments, representing 10 terrestrial gastropod species (9 genera) and 4 freshwater gastropod and bivalve species, were found in the Lower Holocene deposits of the Nukatskaya cave and the Tashmurun Grotto. The Middle Holocene deposits are known from the Bajslan-Tash and Yurmash 4 caves and the Maksyutovo Grotto. Nine terrestrial species (8 genera) and 4 freshwater species were identifies among the 32 extracted shells and their fragments.

The Upper Holocene deposits were recorded in several caves – the Archaeologists and Tashmurun Grotto, Bajslan-Tash, Azan-Tash 1, Yurmash 3 and 4, Nukatskaya and Sikiyaz-Tamak 7 caves. In total 674 mollusc shells and their fragments were discovered representing 13 terrestrial and 10 freshwater species.

The malacological study resulted in the identification of terrestrial (15 species) and freshwater (12 species) molluscs which belong to two classes, Gastropoda and Bivalvia. The malacological assemblages consist of species that are widely distributed in the study area. Terrestrial molluscs are inhabitants of forest biotopes, with dense grass cover and leaf litter under shrubs and trees. They could inhabit the rocky well-warmed slopes under the stones. The presence of freshwater molluscs in the collections is due to the presence of nearby water bodies from where the shells were transported by animals. Freshwater molluscs lived in

Table 6
The main stages of the vegetation development in the Southern Urals area according to palynological data from caves

Stratigraphical scale			Southern Uralian area			Southern Trans-Uralian area
Division	Horizon	Subhorizon	Yuryuzan, Sim, Ai River valleys (Smirnov et al., 1990; Alimbekova et. al., 1998; Eremeev, 2003; Danukalova et. al., 2018)	Lemeza River valley (Alimbekova et. al., 2000; Danukalova et. al., 2008) Inzer River valley (Yakovlev et. al., 2000)	Belaya River Valley (Yakovlev et. al., 2006; Danukalova et. al., 2011; Eremeev, Kurmanov, 2011; Danukalova et. al., 2017)	Kizil, Miass, Small Urtazymka (Lapteva, 2006)
Holocene	Agidel	Upper	*Betula-Pinus* forests with broadleaved trees admixture. *Artemisia*-herbage associations covered open spaces (Sikiyaz-Tamak 7 Cave).	*Pinus-Picea* forests with broadleaved and small-leaved trees admixture. Polypodiaceae were numerous (Lemeza 2-4 Caves). *Betula-Pinus* forests with broadleaved trees and *Picea* admixture. Herbaceous meadows (Nukatskaya Cave).	*Pinus-Betula* forests with *Tilia* admixture. Polypodiaceae were numerous (Archaeologists Grotto, Azan-Tash 1, Tashmurun, Bajslan-Tash, and Shulgan-Tash Caves). *Betula* forests with *Pinus, Tilia* and *Ulmus* admixture (Yurmash 3 and Mujnak-Tash Caves).	Forest-steppe landscapes. Poaceae-herbage and *Artemisia*-Chenopodiaceae associations dominated steppe. *Pinus* and *Betula* forests with broad-leaved trees admixture (Syrtinskaya Cave).
		Middle	*Betula-Pinus* forests with broadleaved trees admixture. Grasses were represented mainly by herbage and *Artemisia*. Polypodiaceae were numerous (Sikiyaz-Tamak 7 and Serpievskaya 1 Caves).	Small coniferous-broadleaved forests. Polypodiaceae were numerous (Lemeza 2 Cave).	Forest-steppe landscapes. *Pinus-Betula* forests with broadleaved trees admixture. *Artemisia*-Chenopodiaceae-herbage associations. Polypodiaceae were numerous (Yurmash 4 and Bajslan-Tash Caves).	
		Lower	Forest-steppe landscapes. Mixed forests with *Betula, Pinus* and *Larix* dominance. Polypodiaceae were numerous. Mostly tundra shrub vegetation existed (Sikiyaz-Tamak 7, Serpievskaya 1 Cave).	Mixed forests with *Pinus, Betula, Ulmus* and *Alnus* and with *Picea* and *Tilia* admixture. Polypodiaceae were numerous. Small open spaces were occupied by Poaceae-herbage vegetation (Lemeza 3 Cave). Forest-steppe landscapes. *Artemisia*-Poaceae-herbage associations. Spruce *Picea*-forests (Nukatskaya Cave).	Forest-steppe landscapes. *Artemisia*-Chenopodiaceae and Poaceae-herbage associations dominated open areas. *Betula-Pinus* forests with *Tilia* admixture. Polypodiaceae were numerous (Bajslan-Tash and Shulgan-Tash Caves).	
Neopleistocene	Kudashevo		Forest-steppe landscapes. The areas of *Picea* forests began to decline, the role of *Pinus* increased. Herbage with Chenopodiaceae, *Artemisia* and Poaceae admixture (Sikiyaz-Tamak 7 Cave). Periglacial steppe landscapes with high percent of Asteraceae. Small *Betula* and *Picea* forests. There were elements of the tundra shrub associations (Serpievskaya 1, 2, Ignatievskaya 2, Prizhim 2, Zapovednaya, and Verkhnyaya Caves).		Forest-steppe landscapes. *Betula-Pinus* forests with *Picea, Tilia* and *Ulmus* admixture. Asteraceae and *Artemisia*-Chenopodiaceae associations dominated open spaces (Shulgan-Tash Cave).	Periglacial steppe landscapes. During the humid and arid periods, the proportion of representatives of the tundra, steppe and boreal-forest flora changed (Syrtinskaya Cave).
	Tabulda		Forest-steppe landscapes. *Artemisia*-Chenopodiaceae and Poaceae-herbage associations and *Picea* and *Pinus-Picea* forests with an admixture of deciduous and small-leaved trees (Sikiyaz-Tamak 7, Serpievskaya 1, and Zapovednaya Caves).			Periglacial steppe landscapes with Poaceae dominance. There were *Betula-Pinus* small forests with *Picea* admixture at the beginning of that time and spruce *Picea*-woodland at the end (Syrtinskaya Cave).

flowing waters with a moderate or slow current, and on the banks were heated backwaters with silted bottom and aquatic vegetation occurred.

5.4. Ichthyology

Caves where fish remains were found are located in the basins of the European rivers. The fish remains date to the end of the Middle Neopleistocene, the Late Neopleistocene and the Holocene (Table 8).

The Middle Neopleistocene deposits in the Ignatievskaya and Maiskaya (Serpievskaya 1) Caves yielded 17 fish bones, which belong to 3 different species (Table 8).

Deposits of the lowermost part of the Upper Neopleistocene (MIS 5a-d – 4) from the Sikiyaz-Tamak 7 Cave (layers 12–14) contain only 6 undetermined fish bone remains.

22 bones of 3 species and 29 undetermined fish bone remains were found in the deposits correlated with the middle part of the Upper Neopleistocene (MIS 3) known from Ignatievskaya Cave (1985, pit V, layers 2–9) and Sikiyaz-Tamak 7 Cave (layers 9–11).

Deposits of the uppermost part of the Upper Neopleistocene (MIS 2) from Prizhim 2 Cave, Maiskaya (Serpievskaya 1) Cave (layer 2), Kolokolnaya (Serpievskaya 2) Cave (layers 2–3) and Zapovednaya Cave (layers 1–2) contain 620 bones which belong to 9 different fish species.

The non-stratified Upper Neopleistocene (MIS 5e – 2) deposits of the Imanai Cave contain bones of two fish species – *Esox lucius* Linnaeus, 1758 and *Perca fluviatilis* Linnaeus, 1758 (Table 8).

The Lower Holocene cave deposits from the Nukatskaya cave (layer 2) contain 73 bones which were attributed to six species. The deposits of the Middle Holocene excavated in the Sikiyaz-Tamak 7 Cave (layers 5–6) contain four undetermined fish bones.

In total 169 bones of six species were discovered in the Nukatskaya cave (layer 1) in the Upper Holocene deposits.

The non-stratified Holocene (MIS 1) deposits of the Maiskaya (Serpievskaya 1) Cave (layer 1) yielded 738 bones of seven species.

The best represented species in the different assemblages are *Thymallus thymallus* (Linnaeus, 1758) and *Barbatula barbatula* (Linnaeus, 1758). The bone remnants of *Lota lota* (Linnaeus, 1758) and *Cottus gobio* (Linnaeus, 1758) are not numerous but they are also represented in all the studied deposits (Table 8). The bone remains of the other species are less numerous and the species are not represented in all the assemblages. All the freshwater fish species found in the Middle-Upper Neopleistocene and Holocene cave deposits are widely spread in Europe (Reshetnikov, 1998).

5.5. Herpetology

Bones of amphibians and reptiles are known from the unconsolidated Quaternary cave deposits (Fig. 5).

5.5.1. Amphibians

Amphibian bone remains were found in the Upper Pleistocene and Holocene deposits (Table 9).

The Upper Pleistocene (Kudashevo Horizon) deposits of the Bajslan-Tash Cave contain rare bones, representing only three species and three genera. Bone remains of the forest species *Rana arvalis* Nilsson, 1842 and *R. temporaria* Linnaeus, 1758, dominate the assemblage. Lower Holocene deposits of the Lemeza III Cave contain 520 bones of three species and three genera; the typical forest representatives *Rana temporaria* Linnaeus, 1758 and *Bufo bufo* (Linnaeus, 1758) dominate the assemblage.

The Middle Holocene deposits of the Bajslan-Tash and Lemeza II Caves and the Maksyutovo Grotto yielded in total 189 bones representing five species and three genera. Bone remains of *Rana temporaria* Linnaeus, 1758 are most numerous; bones of *Lissotriton vulgaris* (Linnaeus, 1758) and *Bufo viridis* Laurenti, 1768 are present. The Middle Holocene association is characterized by forest species and species that prefer open areas.

The Upper Holocene deposits of the Bajslan-Tash cave, the Archaeologists and Tashmurun Grottoes, the Lemeza IV and Zapovednaya Caves yielded in total 6503 amphibian bones from four species and five genera. Bone remains of *Rana temporaria* Linnaeus, 1758 and *Bufo bufo* (Linnaeus, 1758) dominate and bone remains of *Triturus cristatus* (Laurenti, 1768), *Bombina* sp. and *Rana arvalis* Nilsson, 1842 are present. This association consists of forest species; *Triturus cristatus* (Laurenti, 1768) and *Bombina* sp. inhabit broad-leaved forests.

5.5.2. Reptiles

Reptiles bone remains were found in the Upper Pleistocene and Holocene deposits (Table 10).

The Upper Pleistocene Kudashevo Horizon deposits of the Bajslan-Tash cave yielded nine species of seven genera. Bone remains of *Lacerta agilis* Linnaeus, 1758, *Vipera ursinii* (Bonaparte, 1835), *Anguis fragilis* Linnaeus, 1758 and *Coronella austriaca* Laurenti, 1768 dominate; species are characteristic of steppe and forest biotopes.

The Lower Holocene deposits of the Lemeza III cave yielded three species that inhabit forest and steppe biotopes. The Middle Holocene deposits of the Maksyutovo Grotto, Bajslan-Tash, Yurmash 4 and Lemeza II caves yielded in total 479 remains of 10 species and eight genera. Bone remains are represented mainly by steppe species. *Anguis fragilis* Linnaeus, 1758, *Lacerta agilis* Linnaeus, 1758, *Vipera ursinii* (Bonaparte, 1835) and *Coronella austriaca* Laurenti, 1768 dominate the assemblages.

The Upper Holocene deposits of the Archaeologists and Tashmurun Grottoes, the Bajslan-Tash, Lemeza IV and Zapovednaya caves yielded in total 519 bone remains of eight species and five genera. Bone remains are represented mainly by forest species. *Anguis fragilis* Linnaeus, 1758, *Natrix natrix* (Linnaeus, 1758), *Vipera berus* (Linnaeus, 1758), *Coronella austriaca* Laurenti, 1768, and *Lacerta agilis* Linnaeus, 1758 dominate the association.

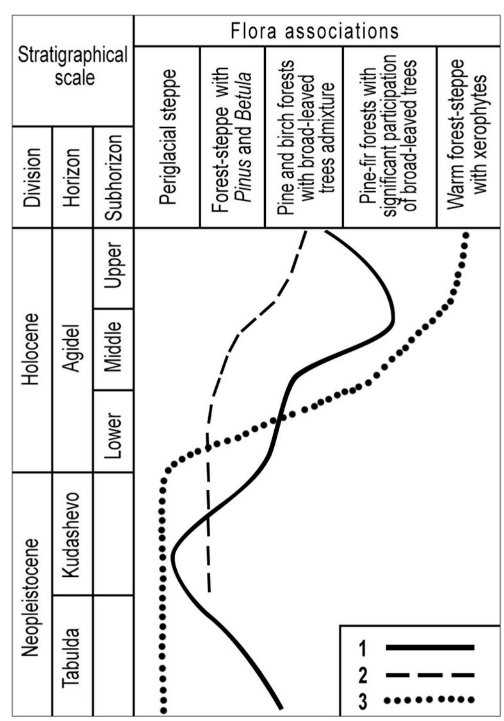

Fig. 3. Reconstruction of the main stages of the development of the flora during the late Late Pleistocene and Holocene in the territory of the Southern Urals and Trans-Urals.

Legend: 1 – the northern zone of the studied Southern Urals mountainous area; 2 – the southern zone of the studed Southern Urals mountainous area; 3 – the Southern Trans-Uralian area.

Table 7
List of species and number of mollusc shell remains from the Upper Neopleistocene – Holocene unconsolidated cave deposits based on Danukalova and Osipova's determinations (Yakovlev et al., 2000; Danukalova et al., 2008, 2011, 2018 and new authors' data).

№	Stratigraphy	Upper Neopleistocene		Holocene												
		Tabulda	Kudashevo	Lower		Middle			Middle-Upper	Upper						
	Taxa/Cave	Z2	B3	N2	T3	B2	Y4a	MG1	T1–2	B1	A1	AT1	Y3	Y4b	N1	ST7
1	*Succinella oblonga* (Draparnaud, 1801)	-	12	-	-	4	-	1	-	6	-	-	-	-	-	-
2	*Succinea* cf. *putris* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	3 fr.	-	-	-	-	-	-
3	*Succinea* sp.	-	1 fr.	-	-	-	-	-	-	-	-	-	-	-	-	-
4	*Cochlicopa lubrica* (Müller, 1774)	7	2	14	-	1	1	-	3	6	28	2	3	8	1	-
5	*Pupilla muscorum* (Linnaeus, 1758)	-	14	7	-	2	-	-	1 fr.	8	8	-	-	-	6	-
6	*Vertigo pygmaea* (Draparnaud, 1801)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
7	*Vallonia costata* (Müller, 1774)	58	15	332	23	8			13	80	93	7	12	1	196	-
8	*Vallonia pulchella* (Müller, 1774)	-	-	-	-	-	-	2	-	1	41	-	-	-	-	-
9	*Vallonia tenuilabris* (Al. Braun, 1842)	-	2	3	-	-	-	-	-	3	-	8	-	-	-	-
10	*Vallonia* sp.	-	-	-	-	3	-	-	-	-	32 fr.	-	-	-	-	-
11	*Perpolita hammonis* (Ström, 1765), *Perpolita* sp.	20	2	15	1		4		1	3	27	2	6	9	94 fr.	-
12	*Euconulus fulvus* (Müller, 1774)	-	1	5	3	-	-	-	4	1	7	4	-	-	-	-
13	*Discus ruderatus* (Hartmann, 1821)	9	-	16	1	-	2	-	-	3	3	-	3	5	6	-
14	*Chondrula tridens* (Müller, 1774)	1 fr.	2 fr.	1 fr.	10 fr.	1 fr.	1 fr.	-	6+1 fr.	31 fr.	119 fr.	25 fr.	-	2 fr.	1 fr.	1+4 fr.
15	*Euomphalia strigella* (Draparnaud, 1801)	-	-	-	-	-	-	-	-	5 fr.	1+9 fr.	-	-	-	-	3
16	*Pseudotrichia rubiginosa* (A. Schmidt, 1853)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
17	*Fruticicola fruticum* (Müller, 1774)	-	1	-	-	17 fr.	13 fr.	-	-	120 fr.	2+113 fr.	1 fr.	32 fr.	11 fr.	-	4+3 fr.
18	*Lymnaea* sp.	-	-	-	1	-	-	2	3 fr.	1 juv.	3 fr.	2	-	-	-	-
19	*Galba* cf. *truncatula* (Müller, 1774)	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
20	*Planorbis planorbis* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
21	*Planorbarius corneus* (Linnaeus, 1758)	-	-	1 juv.	-	-	-	-	-	-	-	-	-	-	-	-
22	*Gyraulus laevis* (Alder, 1838)	-	1	-	-	1	-	-	-	9	-	-	-	-	-	-
23	*Gyraulus albus* (Müller, 1774)	-	-	-	-	-	-	-	-	1 fr.	-	-	-	-	-	-
24	*Gyraulus* sp.	-	2 fr.	-	-	-	-	-	-	-	-	-	-	-	-	-
25	*Ancylus fluviatilis* (Müller, 1774)	-	1	-	-	-	-	-	2	1	2	-	-	-	-	-
26	*Acrolox lacustris* (Linnaeus, 1758)	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-
27	*Pisidium amnicum* (Müller, 1774)	-	-	-	3	-	-	-	1	10	3	3	-	-	-	-
28	*Pisidium* sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
29	*Sphaerium rivicola* (Lamark, 1818)	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
30	*Unio* sp.	-	1 fr.	-	3 fr.	1 fr.	2 fr.	-	6 fr.	16 fr.	67 fr.	-	-	-	-	-
31	*Dreissena polymorpha* (Pallas, 1771)	-	-	-	-	-	-	-	-	1 fr.	-	-	-	-	-	-
32	Gastropoda	fr.	10 fr.	+	-	4 fr.	-	-	-	14 fr.	40 fr.	-	-	-	19 fr.	
	Total:	94/1 fr.	50/18 fr.	393/1fr.	34/13 fr.	19/23 fr.	7/16 fr.	6	33/11 fr.	134/ 191 fr.	215/383 fr.	28/26 fr.	24/32 fr.	23/13 fr.	209/114 fr.	8/7 fr.

Legend: fr – mollusc shells fragments; juv. – juvenile shell; + – fragments were not calculated. Sites: N2 – Nukatskaya Cave, section 2, horizons 1–2; B2 – Bajslan-Tash Cave, layer 3, horizons 11–13; Y4a – Yurmash 4 Cave, layer 2; MG1 – Maksyutovo Grotto, layer 1; B1 – Bajslan-Tash Cave, layer 1–2, horizon 1–10; A1 – Archaeologists Grotto, layers 1–4; T1–2 – Tashmurun Grotto, layer 1; T3 – Tashmurun Grotto, layers 2–3; AT1 – Azan-Tash I Cave, layers 1–3; Y3 – Yurmash 3 Cave, layer 1; Y4b – Yurmash 4 Cave, layer 1; N1 – Nukatskaya Cave, section 2, depth interval 0–5 cm; ST7 – Sikiyaz-Tamak 7 Cave, layer 1; Z2 – Zapovednaya Cave, pit1, layer 3; B3 – Bajslan-Tash Cave, layer 4; 94/1 fr. – number of complete shells/number of shell fragments.

5.6. Ornithology

The studied remains of birds were from sediments of a very small number of caves (Yakovlev et al., 2000; Sataev, 2005; Kosintsev et al., 2018; Danukalova et al., 2018). In total 393 bones of 20 different species were found in sediments of the upper part of the Upper Neopleistocene (MIS 2) in the Balatukai Cave (layer 3) (Table 11). Among them there are 6 bones of 5 different species, all living near water bodies, 319 bones of 6 species that prefer open and semi-open landscapes including *Lagopus lagopus* (Linnaeus, 1758) (the dominant species with 310 records), and 68 bones from 9 species that inhabit enclosed and/or semi-closed landscapes.

The Late Holocene deposits are recorded in Balatukai Cave (layer 1), Atysh Grotto, and Lemeza II Cave (layer 2). These deposits contain 138 bird bones (Table 11) assigned to 13 species that inhabit semi-open landscapes and 22 species that prefer closed habitats. The non-stratified Holocene (MIS 1) deposits recorded in a number of caves (Balatukai Cave, layer 2; Verkhnaya Cave, layer 1; Zapovednaya Cave, layer 1; Nukatskaya Cave, layer 1; Sikiyaz-Tamak 6 Cave, layer 1; Sikiyaz-Tamak 10 Cave, layer 1) yielded 243 bird bones (Table 11): 6 species that prefer to live near water bodies, 11 species that inhabit open and semi-open landscapes and 33 species that prefer enclosed and semi-closed habitats. The bones of *Lyrurus tetrix* (Linnaeus, 1758), *Tetrao urogallus* Linnaeus, 1758, and *Bonasa bonasia* (Linnaeus, 1758) are most numerous. The remaining species are represented by single bones. All bird species found in the cave sediments, except for the ring ouzel *Turdus torquatus* Linnaeus, 1758, inhabit currently the Southern Urals territory.

5.7. Mammalogy

5.7.1. Small mammals

Small-mammal bone remains are known from Upper Pleistocene and Holocene deposits in caves (Table 12, Figs. 6 and 7).

The Upper Pleistocene Kudashevo Horizon deposits in the Bajslan-Tash cave located in the Belaya River valley yielded 31 different taxa including steppe species such as *Lagurus lagurus* (Pallas, 1773), *Microtus gregalis* (Pallas, 1779), *Cricetulus migratorius* (Pallas, 1773), *Allocricetulus eversmanni* (Brandt, 1894), and *Ochotona* sp. (Table 12). The assemblage dates to the end of the Kudashevo time.

Lower Holocene deposits with small-mammal remains were recorded in the central part of the Southern Urals – in the caves located in the Lemeza and Inzer River valleys. The 3191 fossil remains are assigned to 33 taxa (Table 12). The share of steppe species (*Microtus gregalis* (Pallas, 1779), *Lagurus lagurus* (Pallas, 1773), *Ochotona* sp., *Cricetulus migratorius* (Pallas, 1773), and *Alactagulus* sp.) is high in the

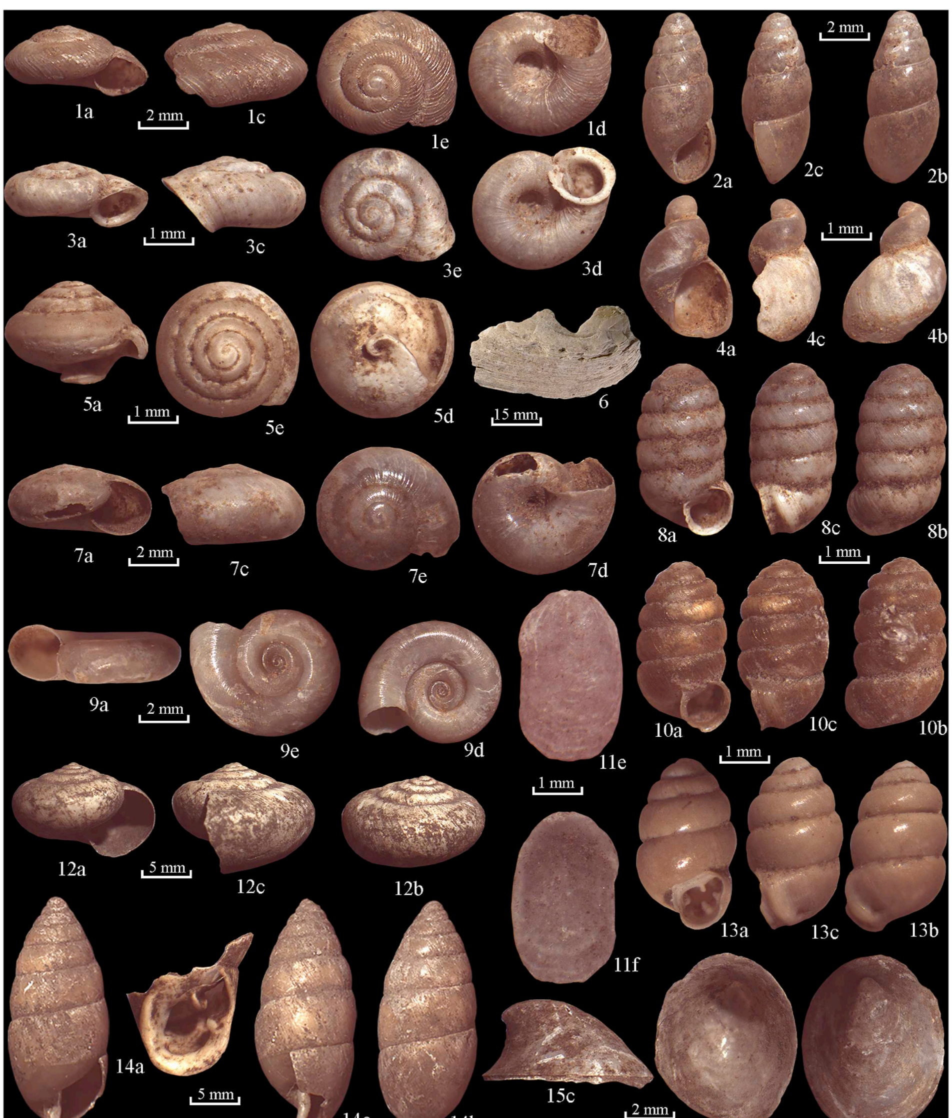

Fig. 4. Key-species of molluscs found in the Upper Pleistocene – Holocene unconsolidated cave deposits, Southern-Urals region, Russia. Legend: 1 – *Discus ruderatus* (Fer.), IG 50/988/2; 2 – *Cochlicopa lubrica* (Müll.), IG 50/988/4; 3 – *Vallonia costata* (Müll.), IG 21/1114/7; 4 – *Succinella oblonga* (Drap.) (juvenile form), IG 21/1117/9; 5 – *Euconulus fulvus* (Müll.), IG 21/1291/6; 6 – *Unio* sp. (shell fragment), IG 21/1114/11; 7 – *Perpolita hammonis* (Ström), IG 22/990/17; 8 – *Pupilla muscorum* (L.), IG 22/989/16; 9 – *Gyraulus laevis* (Alder), IG 21/1112/24; 10 – *Pupilla muscorum* (L.), IG 21/1112/25; 11 – *Limax* sp., IG 68/1285/40; 12 – *Fruticicola* sp. (juvenile form), IG 21/1083/35; 13 – *Vertigo pygmaea* (Drap.), IG 68/1284/39; 14 – *Chondrula tridens* (Müll.), IG 21/1085/36; 15 – *Ancylus fluviatilis* Müll., IG 68/1285/41; a – apertural view; b – abapertural view (view from the opposite side of the aperture); c – lateral view (top right); d – umbilical view; e – apical view; f – basal view (view from the opposite apical side). 1 and 2 – Tabulda Horizon; 3–6 – Kudashevo Horizon; 7 and 8 – Lower Holocene; 9 and 10 – Middle Holocene; 11–15 – Upper Holocene.

Table 8
List of species and number of fish bone remains from the Middle-Upper Neopleistocene and Holocene cave deposits (Nekrasov, 1992; Yakovlev et al., 2000, 2005; Gimranov et al., 2016a; Danukalova et al., 2018).

N	Stratigraphy	Middle Neopleistocene		Upper Neopleistocene								Holocene				
		Elovka (MIS 6?)		Kushnarenkovo-Saigatka (MIS 5a-d – 4)	Kushnarenkovo-Kudashevo (MIS 5e – 2)	Tabulda (MIS 3)		Kudashevo (MIS 2)				Agidel (MIS 1)				
												H_1	H_2	H_2		$H_{1\text{-}3}$
	Taxa/Cave	IG (1985a)	S1 (3)	ST7 (12-14)	IM	IG (1985b)	ST7 (9-11)	PR	S1 (2)	S2 (2-3)	Z (1-2)	N2	ST7 (5-6)	N1	ST7 (1-4)	S1 (1)
1.	*Hucho taimen* Pallas, 1773	-	-	-	-	-	-	-	-	-	13	-	-	-	-	-
2.	*Salmo trutta* Linnaeus, 1758	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-
3.	*Thymallus thymallus* (Linnaeus, 1758)	5	8	-	-	18	-	68	-	246	28	52	-	150	-	337
4.	*Esox lucius* Linnaeus, 1758	-	-	-	+	-	-	-	-	-	8	4	-	4	-	-
5.	*Squalius cephalus* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	-	-	-	-	5	-	-
6.	*Leuciscus leuciscus* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	-	-	10	-	1	-	-
7.	*Phoxinus phoxinus* (Linnaeus, 1758)	-	-	-	-	-	-	9	1	6	-	-	-	1	-	23
8.	*Gobio gobio* (Linnaeus, 1758)	-	-	-	-	-	-	3	-	-	-	3	-	2	-	7
9.	*Barbatula barbatula* (Linnaeus, 1758)	-	-	-	-	1	-	62	40	53	-	3	-	6	-	247
10.	*Lota lota* (Linnaeus, 1758)	-	3	-	-	3	-	7	1	8	-		-	3	-	31
11.	*Perca fluviatilis* Linnaeus, 1758	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
12.	*Cottus gobio* Linnaeus, 1758	-	1	-	-	-	-	46	3	17		1	-	1	-	94
13.	Pisces indet.	+	+	6	+	+	29	+	+	+	+	+	4	+	1	+

Legend: IG(1985a) – Ignatievskaya Cave, 1985, pit V, layer 10; S1(3) – Maiskaya (Serpievskaya 1) Cave, layer 3; ST7(12–14) – Sikiyaz-Tamak 7 Cave, layers 12–14; IM – Imanai Cave; IG(1985b) – Ignatievskaya Cave, 1985, pit V, layers 2–9; ST7(9–11) – Sikiyaz-Tamak 7 Cave, layers 9–11; PR – Prizhim 2 Cave; S1(2) – Maiskaya (Serpievskaya 1) Cave, layer 2; S2(2–3) – Kolokolnaya (Serpievskaya 2) Cave, layers 2–3; Z(1–2) – Zapovednaya Cave, layers 1–2; N2 – Nukatskaya Cave, layer 2; ST7 (5–6) – Sikiyaz-Tamak 7 Cave, layers 5–6; N1 – Nukatskaya Cave, layer 1; ST7(1–4) – Sikiyaz-Tamak 7 Cave, layers 1–4; S1(1) – Maiskaya (Serpievskaya 1) Cave, layer 1. MIS – Marine Isotope Stages. H – Holocene; $H_{1,\ 2,\ 3}$ – Lower, Middle, Upper Holocene; + – uncounted bone remains.

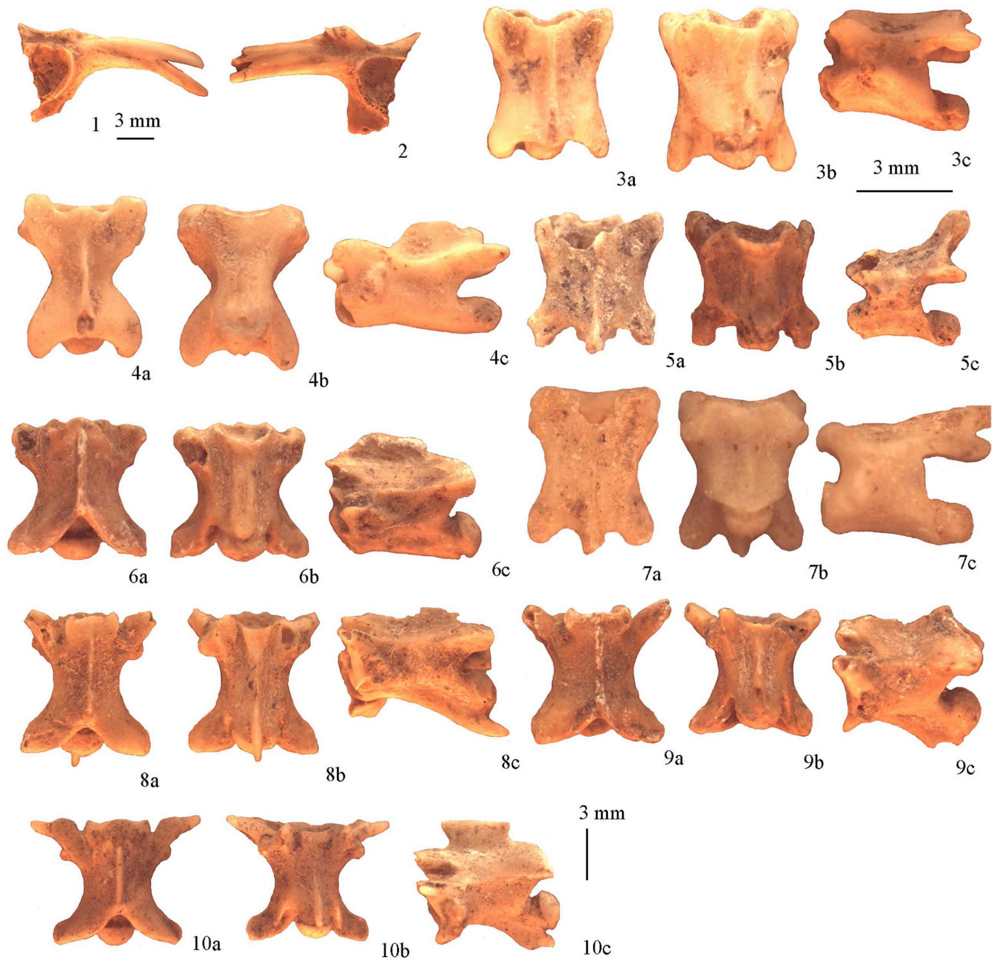

Fig. 5. Key-species of amphibians and reptiles found in the Upper Pleistocene – Holocene unconsolidated cave deposits, Southern-Urals region, Russia.
Legend: 1 – *Bufo bufo* (Linnaeus, 1758), ilium, Lemeza IV cave, layers 1–3; 2 – *Rana temporaria* Linnaeus, 1758, ilium, Lemeza IV cave, layers 1–3; 3 – *Eremias* cf. *arguta* (Pallas, 1773), trunk vertebra, Bajslan-Tash cave, layer 3; 4 – *Anguis fragilis* Linnaeus, 1758, trunk vertebra, Maksyutovo Grotto, layer 1; 5 – *Lacerta agilis* Linnaeus, 1758, trunk vertebra, Bajslan-Tash cave, layers 1–2; 6 – *Coronella austriaca* Laurenti, 1768, trunk vertebra, Bajslan-Tash cave, layers 1–2; 7 – *Zootoca vivipara* (Jacquin, 1787), trunk vertebra, Maksyutovo Grotto, layer 1; 8 – *Vipera ursinii* (Bonaparte, 1835), trunk vertebra, Bajslan-Tash cave, layer 4; 9 – *Vipera berus* (Linnaeus, 1758), trunk vertebra, Bajslan-Tash cave, layers 1–2; 10 – *Natrix natrix* (Linnaeus, 1758), trunk vertebra, Bajslan-Tash cave, layers 1–2; a – top view, b – basal view, c – lateral view. 1, 2, 5, 6, 9, 10 – Upper Holocene; 3, 4, 7 – Middle Holocene, 8 – Upper Pleistocene, Kudashevo Horizon.

Early Holocene mammalian association. *Clethrionomys rufocanus* (Sundevall, 1846) and *Cl.* ex gr. *glareolus-rutilus* prefer forest biotopes whereas *Dicrostonyx torquatus* (Pallas, 1778), which is rare, indicates a tundra environment.

There are two localities in the northern part of the studied region (the Ufimian Plateau) (Alikaev Kamen site and Bobyliok Grotto, layer 2) with unconsolidated deposits that yielded 2261 small-mammalian fossil remains assigned to 27 taxa with steppe (*Microtus gregalis* (Pallas, 1779), *Lagurus lagurus* (Pallas, 1773), *Eolagurus luteus* (Eversmann, 1840), *Cricetulus migratorius* (Pallas, 1773), *Spermophilus* sp.), forest (*Clethrionomys* sp., *Apodemus* sp.) and tundra (*Dicrostonyx* sp.) dwellers.

Middle Holocene deposits with small mammal remains are known from the central and southern parts of the studied area from the Belaya and Lemeza River valleys. The recorded 5854 small mammal remains are from 32 different taxa. Steppe species (*Microtus gregalis* (Pallas, 1779), *Lagurus lagurus* (Pallas, 1773), and *Ochotona* sp.) dominate the assemblage; the share of species that prefer a forested biotope (*Clethrionomys* ex gr. *glareolus-rutilus* and representatives of *Apodemus* sp.) increased.

Upper Holocene deposits are recorded in six caves of the central and southern parts of the Southern Urals – in the Belaya and Lemeza River valleys. The 6114 small mammal remains are attributed to 31 taxa (Table 11). A significant part of the represented species are forest dwellers e.g. *Clethrionomys* ex gr. *glareolus-rutilus, Cl. rufocanus* (Sundevall, 1846), *Microtus agrestis* (Linnaeus, 1761), *Talpa europaea* Linnaeus, 1758 and representatives of *Apodemus* genus. At the end of the Holocene, species that prefer steppe habitats almost disappeared from the mountainous part of the Southern Urals.

5.7.2. Large mammals

The more ancient mammal faunas have been discovered in the Ignatievskaya Cave (1985, pit V, layer 10), Maiskaya (Serpievskaya 1) Cave (layer 3) and Verkhnaya Cave. The faunal assemblage includes Middle Pleistocene key-species: the fossil lemming *Dicrostonyx simplicior* Fejfar, 1966, and the large mammals *Ursus* cf. *deningeri* Richenau, 1904, and *Stephanorhinus* cf. *kirchbergensis* Jäger, 1839 (Smirnov et al., 1990, Table 13). Faunas from the Ignatievskaya and Serpievskaya Caves described as "Serpievskaya" fauna (Smirnov et al., 1990) are dated to the Middle Pleistocene and are correlated with the Middle Neopleistocene Elovka time (MIS 6?) (Table 13).

Mammalian faunas from Ignatievskaya Cave (2014, pit V, layer 10), Barsuchyi Dol Cave and Bobyliok Grotto (layers 5–6) include *Hystrix brachyura* Linnaeus, 1758, *Mustela lutreola* (Linnaeus, 1761), *Stephanorhinus* cf. *kirchbergensis* Jäger, 1839 (Table 13), *Sciurus vulgaris* (Linnaeus, 1758), *Apodemus flavicollis* (Melchior, 1834), *Dryomys nitedula* (Pallas, 1778) (Smirnov, 1993; Fadeeva et al., 2018, 2019), species that indicate interglacial conditions. Other species indicate a Late Neopleistocene age (Smirnov, 1993; Fadeeva et al., 2018, Table 13) and the enamel differentiation coefficient (SDQ) of the *Arvicola terrestris* molars (Heinrich, 1982) suggests a Late Pleistocene age (Fadeeva et al., 2018, 2019). Based on the different features, the faunas are attributed to the first half of the Late Neopleistocene Kushnarenkovo time (MIS 5e).

Faunas from Ignatievskaya Cave (pit V, layers 2–9), Sikiyaz-Tamak 7 Cave (layers 9–11), Kozya (Asha I) Cave, Zapovednaya Cave, Kinderlinskaya Cave, and Smelovskaya 2 Cave include *Ursus spelaeus* Rosenmüller, 1794 and *Crocuta crocuta spelaea* (Goldfuss, 1823) (Table 13); these species dissapeared at the end of MIS 3 (Pacher,

Table 9
List of species and number of amphibian bone remains from the Upper Neopleistocene – Holocene unconsolidated cave deposits; identification by T. Yakovleva (Yakovlev et al., 2003, 2004, 2005; Danukalova et al., 2008, 2011).

№	Stratigraphy	Upper Neopleistocene	Holocene								
		Kudashevo horizon	Lower	Middle			Upper				
	Taxa/Cave	B3	L3a	B2	MG1	L2a	B1	A1	T1-2	L4	Z4
1	*Lissotriton vulgaris* (Linnaeus, 1758)	-	-	-	1	-	-	-	-	-	-
2	*Triturus cristatus* (Laurenti, 1768)	-	-	-	-	-	-	-	-	-	1
3	*Bombina* sp.	-	-	-	-	-	-	-	-	1	-
4	*Pelobates* cf. *fuscus* (Laurenti, 1768)	1	-	-	-	-	1	-	-	-	-
5	*Bufo bufo* (Linnaeus, 1758)	-	24	-	1	9	2	-	-	391	-
6	*B.* cf. *bufo*	-	-	-	-	-	-	-	1	-	-
7	*B. viridis* Laurenti, 1768	-	-	-	1	-	-	-	-	-	-
8	*Bufo* sp.	1	4	-	1	-	1	-	1	-	-
9	*Rana arvalis* Nilsson, 1842	19	2	7	3	-	2	-	2	-	-
10	*R.* cf. *arvalis*	1	-	1	-	-	2	-	-	-	-
11	*R. temporaria* Linnaeus, 1758	8	140	-	14	32	9	1	2	1892	3
12	*R.* cf. *temporaria*	-	-	1	-	-	1	-	-	-	-
13	*Rana* sp.	7	51	4	6	-	3	2	8	-	-
14	Anura indet.	7	299	10	8	90	5	1	8	4150	13
	Total:	44	520	23	35	131	26	4	22	6434	17

Legend: B3 – Bajslan-Tash Cave, layer 4; L3a – Lemeza III Cave, layers 2–6; B2 – Bajslan-Tash Cave, layer 3; MG1 – Maksyutovo Grotto, layer 1; L2a – Lemeza II Cave, layer 2; B1 – Bajslan-Tash Cave, layers 1–2; A1 – Archaeologists Grotto, layers 1–4; T1–2 – Tashmurun Grotto, layers 1, 2; L4 – Lemeza IV Cave, layers 1–3; Z4 – Zapovednaya Cave, pit 3, layers 1–2.

Stuart, 2009; Stuart, Lister, 2014). This fact and the series of the radiocarbon dates (Table 4) permitted to correlate these faunas with the Late Pleistocene Tabulda period (MIS 3). The fauna from the Sikiyaz-Tamak 7 Cave (layers 12–14) includes Late Pleistocene key-species (Kosintsev and Bachura, 2013, Table 13). The age of the fauna is beyond the radiocarbon dating range (Table 4) and is, therefore, attributed to the Late Neopleistocene Kushnarenkovo-Saigatka (MIS 5a-d – 4) time interval.

Table 10
List of species and number of reptile bone remains from the Upper Neopleistocene and Holocene cave deposits; identification by T. Yakovleva (Yakovlev et al., 2003, 2004, 2005; Danukalova et al., 2008, 2011).

№	Stratigraphy	Upper Neopleistocene	Holocene									
		Kudashevo horizon	Lower	Middle				Upper				
	Taxa/Cave	B3	L3a	B2	Y4a	MG1	L2a	B1	A1	T1-2	L4	Z4
1	*Anguis fragilis* Linnaeus, 1758	36		29	4	37		54	2	27	5	4
2	*Anguis* cf. *fragilis*					4						
3	*Eremias* cf. *arguta* (Pallas, 1773)			5								
4	*Lacerta agilis* Linnaeus, 1758	140		48	3			32	4	7		
5	*L.* cf. *agilis*	5	1			1		2				
6	*Zootoca vivipara* (Lichtenstein, 1823)	2		1	1	7				3	1	1
7	*Z.* cf. *vivipara*	1										
8	*Lacerta* sp.			1				3				
9	Lacertidae indet.	14		16				21				
10	Sauria indet.	23		12				9				
11	*Coronella austriaca* Laurenti, 1768	35		7				31	2	13		
12	*Elaphe* cf. *dione* (Pallas, 1773)	1		1								
13	Colubrinae indet.	5		8				10	2	8		
14	*Natrix natrix* (Linnaeus, 1758)	1	2		2	1	6	11	4	18	2	43
15	*Natrix* cf. *natrix*			1								
16	*N. tessellata* (Laurenti, 1768)							1				
17	*N.* cf. *tessellata*	10		6	1	12		6				
18	*Natrix* sp.	89		41		6		41	1			
19	Natricinae indet.	21	1	13				3				
20	*Vipera berus* (Linnaeus, 1758)	11	3	5		8	1	10		2	4	36
21	*V.* cf. *berus*	6						2				
22	*V.* aff. *berus*	1										
23	*V. ursinii* (Bonaparte, 1835).	89		26		1		4				
24	*V.* cf. *ursinii*	80		38		7		27				
25	*Vipera* sp.	286		108				56				
26	Serpentes indet.	27		11				1				6
	Total:	883	7	377	11	84	7	324	15	78	12	90

Legend: B3 – Bajslan-Tash Cave, layer 4; L3a – Lemeza III Cave, layers 2–6; B2 – Bajslan-Tash Cave, layer 3; Y4a – Yurmash 4 Cave, layers 2–3; MG1 – Maksyutovo Grotto, layer 1; L2a – Lemeza II Cave, layer 2; B1 – Bajslan-Tash Cave, layers 1–2; A1 – Archaeologists Grotto, layers 1-4; T1–2 – Tashmurun Grotto, layers 1, 2; L4 – Lemeza IV Cave, layers 1–3; Z4 – Zapovednaya Cave, pit 3, layers 1–2.

Large and small-mammal faunas from a series of caves (Bobyliok Grotto (layer 4), Sikiyaz-Tamak 7 Cave (layer 8), Maiskaya (Serpievskaya 1) Cave (layer 2), Syrtinskaya Cave (layer 3), Prizhim 2 Cave, Shulgan-Tash Cave, Kulyurt-Tamak Cave, Bajslan-Tash Cave (layer 4, lower part), Maksyutovo Grotto, Balatukai Cave, Ustinovo Grotto (layer 3)) do not contain Middle Pleistocene, Kushnarenkovo, Tabulda or Holocene key-species (Kosintsev and Bachura, 2013, Table 13). Based on the radiocarbon dates, these faunas are attributed to the Kudashevo time interval (MIS 2) (Table 4).

Analysis of the composition of large and small mammal faunas from the Idrisovo and Imanai Caves (Kosintsev and Bachura, 2013; Gimranov et al., 2018, Table 13) as well as the radiocarbon dates (Table 4) demonstrate that the deposits from these caves are stratigraphically mixed.

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 caves into the following, regionally defined, time intervals: Middle Pleistocene (possibly MIS 6), Upper Pleistocene with Kushnarenkovo (MIS 5), Saigatka (MIS 4), Tabulda (MIS 3), and Kudashevo (MIS 2) Horizons and the Holocene represented by the Agidel (MIS 1) Horizon. This subdivision corresponds to the subdivision of similar deposits in the Southern Fore-Uralian area with a detailed stratigraphic succession of radiocarbon dated Upper Pleistocene continental deposits with archaeological and palaeontological finds (Danukalova, 2010; Yakovlev et al., 2013c; Danukalova et al., 2014).

6.2. Palynology

The Southern Trans-Urals. During the Late Pleistocene, periglacial steppe landscapes with Poaceae prevailed in the southern part of this area (Tanalyk River valley; Kosintsev et al., 2013) and forest-steppe and forest landscapes dominated in the northern part (Ural, Ui, Bolshoi Kizil, Kumach River valleys; Yakhemovich, 1965). During the Holocene forest-steppe landscapes dominated, with an increase of forested areas.

The same trend is recorded in other areas in the Urals. For example, the Late Pleistocene palynocomplexes of the Tanalyk River valley (Kosintsev et al., 2013) demonstrate the change of the solonchak *Artemisia*-Chenopodiaceae-herbage steppes at the end of the Tabulda time to more mesophilious herbage-*Artemisia*-Chenopodiaceae meadow-steppe associations during the Kudashevo time interval. During the Early and Middle Holocene, a rise in tree pollen is noted, in which *Pinus* pollen gradually begins to predominate, and at the very end of the Middle Holocene pollen sequence broad-leaved species (*Tilia cordata*) appears. During the Late Holocene, the areas of open habitat, *Artemisia* steppes, increased.

The Southern Urals. During the second part of the Late Pleistocene, coniferous-leaved forests existed which were replaced by periglacial steppe and forest-steppe during the Kudashevo time interval. During Holocene time there was a gradual increase of forested areas. It should be noted that during the Middle Holocene the climate was warmer and more humid in the northern zone than in the southern zone, as indicated in the pollen spectra by a higher proportion of pollen of broad-leaved species.

The Southern Fore-Urals. The change of plant associations in the Southern Fore-Urals and in the Southern Urals proceeded in a similar way. Among the differences, it should be noted that during the Holocene, the forestation on the plains was higher than in the mountains.

During the Tabulda time interval, *Picea-Pinus* forests with a significant admixture of *Abies* dominated in the northern part of the territory of the Southern Fore-Urals region, whereas in the southern part forest-steppe dominated. A Chenopodiaceae-*Artemisia*-herbage steppe association covered the water interfluves and a *Picea* forests biocoenosis occupied the river valleys (Danukalova et al., 2016).

The vegetation during the Kudashevo time interval consisted of herbage-*Artemisia*-Chenopodiaceae meadow-steppe associations covering most of the territory, and in the low, more humid places – *Picea* forests with an admixture of birch trees existed (Nemkova, 1976).

During the Early Holocene *Pinus* forests with *Picea, Betula* and broad-leaved trees admixture dominated and *Artemisia*-Chenopodiaceae-herbage meadow-steppe associations covered the open areas. The Middle Holocene pollen spectra indicate coniferous-deciduous forests (dominated by *Pinus, Picea,* and *Betula*) and meadow-steppe associations. Among the trees there is a high proportion of pollen from warm-loving broad-leaved species *(Tilia, Quercus,* and *Ulmus*). The spectrum of grasses becomes, compared to the Early Holocene, more diverse.

During the Late Holocene pollen of *Pinus, Picea*, and *Betula* dominate the spectra; the proportion of pollen of the broad-leaved trees (*Tilia, Quercus,* and *Ulmus*) is, compared to the Middle Holocene time interval, reduced. *Artemisia*-Chenopodiaceae-herbage meadow-steppe associations grew in the open areas (Danukalova et al., 2014).

6.3. Malacology

We would like to compare the data of the malacological complexes from the studied Upper Pleistocene – Holocene subaerial deposits in caves with published data from deposits of the same genesis and the same stratigraphical units from the adjacent territories, however, this kind of information is lacking. Therefore we compared our data with malacological data extracted from the deposits of different genesis (subaerial – loess, or loess-like loam, lacustrine and fluvial clay and sand) from the same Upper Pleistocene – Holocene stratigraphical intervals. The species composition of molluscs from the Southern Uralian caves resembles the malacocomplexes of other regions in the Urals, Trans-Urals and Siberia (Stefanovsky, 2006; Sato et al., 2014; Danukalova et al., 2015; Khenzykhenova et al., 2019; Osipova et al., 2018). The molluscs are represented by modern species, which live under severe continental climate conditions with cold winters and warm summers. Malacocomplexes described from the Central Russian territory (Danilovskyi, 1955), Ukraine (Gozhik, 1965; Veklich and Sirenko, 1972; Kunitsa, 2007; Alexandrowicz, Dmytruk, 2007; Alexandrowicz et al., 2014) and Europe (Monnier, 1980; Alexandrowicz S., 1986; Fükon, 1987; Alexandrowicz S. and Alexandrowicz W., 1995a, b, 2010; Alexandrowicz W., 1999, 2001, 2002, 2009, 2011a, b, 2013a, b, c, 2014, 2018; Lozek, 2000; Sümegi and Krolopp, 2002, Marković et al., 2004, 2006, 2007, 2008; Martin et al., 2005; Dobrowolski, 2005; Moine et al., 2005; Moine, 2008 ; Cieszkowski et al., 2010; Sümegi et al., 2011; Dobrowolski et al., 2012; Alexandrowicz and Rybska, 2013; Danukalova et al., 2013, 2017a) also consist of geographically widely distributed mollusc species but among them there are warm-loving species which are completely absent in Urals because of the more severe climatic conditions.

6.4. Ichthyology

Fish remains were discovered in the deposits assigned to the uppermost part of the Middle Neopleistocene (Elovka Horizon, MIS 6?), the Upper Neopleistocene (Kushnarenkovo-Saigatka Horizons, MIS 5a-d – 4; Tabulda Horizon, MIS 3; Kudashevo Horizon, MIS 2) and to the Holocene (Lower, Middle and Upper Holocene; MIS 1) (Table 10).

In total 13 fish' species were identified. Two species (*Thymallus thymallus* (Linnaeus, 1758), *Lota lota* (Linnaeus, 1758)) were present in all studied deposits. One species (*Barbatula barbatula* (Linnaeus, 1758)) was discovered in the Upper Neopleistocene and the Holocene deposits. Three species (*Esox lucius* Linnaeus, 1758, *Phoxinus phoxinus* (Linnaeus,

Table 11
List of species and number of birds bone remains in the Upper Neopleistocene and Holocene cave deposits (Yakovlev et al., 2000; Sataev, 2005; Kosintsev et al., 2018; Danukalova et al., 2018).

N	Stratigraphy	Upper Neopleistocene	Holocene (MIS 1)								
		Kudashevo (MIS 2)	Lower-Middle	Lower-Upper					Upper		
	Taxa/Cave	BT3(3)	BT(2)	V(1)	Z(1)	N(1)	ST6(1)	ST10(1)	BT(1)	AG	L2a
1	*Podiceps cristatus* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	-	+
2	*Podiceps auritus* (Linnaeus, 1758)	1*	-	-	-	-	-	-	-	-	-
3	*Podiceps* sp.	-	-						1		
4	*Anas platyrhynchos* Linnaeus, 1758	1	-	-	-	-	+	-	-	-	-
5	*Anas crecca* Linnaeus, 1758	-	-	-	-	-	+	-	-	-	-
6	*Anas* ex gr. *crecca-querquedula*	-	-	-	-	+	-	-	-	-	-
7	*Anas acuta* (Linnaeus, 1758)	-	-	-	-	-	-	-	1	-	-
8	*Anas querquedula* (Linnaeus, 1758)	1	-	-	+	-	-	-	-	-	-
9	*Anas strepera* (Linnaeus, 1758)	-	-	-	-	-	+	-	-	-	+
10	*Bucephala clangula* (Linnaeus, 1758)	1	-	-	-	-	-	-	-	-	-
11	Anatidae indet.	-	-	-	-	-	-	+	2	-	-
12	*Accipiter nisus* (Linnaeus, 1758)	-	-	-	-	-	+	-	-	+	+
13	*Buteo buteo* (Linnaeus, 1758)	-	-	-	-	-	-	+	-	-	-
14	*Buteo* sp.	-	1	-	-	-	-	-	-	-	-
15	*Circus pygargus* (Linnaeus, 1758)	1	-	-	-	-	-	-	-	-	-
16	*Falco* ex gr. *rusticolus-cherrug*	-	-	-	-	-	+	-	-	-	-
17	*Falco subbuteo* Linnaeus, 1758	-	-	-	-	-	+	+	-	+	-
18	*Cerchneis tinnunculus* Linnaeus, 1758	8	1	-	-	-	-	-	1	-	-
19	Falconidae indet.	2	-	+	+	-	-	-	-	-	-
20	*Perdix perdix* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	+	+
21	*Lagopus lagopus* (Linnaeus, 1758)	310	57	-	-	-	+	+	2	-	-
22	*Lagopus muta* (Montin, 1776)	-	1	-	-	-	-	-	-	-	-
23	*Lagopus* sp.	-	6						-		
24	*Lyrurus tetrix* (Linnaeus, 1758)	19	46	-	-	+	+	+	118	-	-
25	*Tetrao urogallus* Linnaeus, 1758	2	31	-	-	+	+	-	35	-	-
26	*Bonasia bonasia* (Linnaeus, 1758)	4	43	-	-	-	-	-	64	-	-
27	Tetraonidae indet.	1	-	-	+	-	-	-	1	-	-
28	*Coturnix coturnix* (Linnaeus, 1758)	-	-	-	-	-	-	-	1	-	-
29	Galliformes indet.	-	-	-	-	-	-	-	6	-	-
30	*Crex crex* (Linnaeus, 1758)	1	3	-	-	-	-	+	5	-	-
31	*Tringa ochropus* Linnaeus, 1758	-	-	-	-	-	-	-	1	-	-
32	*Scolopax rusticolus* Linnaeus, 1758	3	1	-	-	-	+	-	4	-	+
33	*Philomachus pugnax* (Linnaeus, 1758)	4	-	-	-	-	-	-	2	-	-
34	*Calidris canutus* (Linnaeus, 1758)	2	-	-	-	-	-	-	-	-	-
35	Limicolae indet.	6	2	-	-	-	-	-	2	-	-
36	*Larus* sp.	-	1	-	-	-	-	-	-	-	-
37	Charadriiformes indet.	1	-	-	-	-	-	-	-	-	-
38	*Columba oenas* Linnaeus, 1758	-	-	-	-	-	+	-	-	-	-
39	*Cuculus canorus* Linnaeus, 1758	-	-	-	-	-	-	-	1	-	-
40	*Otus scops* (Linnaeus, 1758)	-	-	-	-	-	-	-	2	-	-
41	*Strix aluco* Linnaeus, 1758	-	1	-	-	-	-	-	-	+	-
42	*Strix uralensis* Pallas, 1771	-	-	-	-	-	-	-	2	-	-
43	*Asio otus* (Linnaeus, 1758)	-	-	-	-	-	-	+	-	-	-
44	*Asio flammeus* (Pontoppidan, 1763)	-	1	-	-	-	-	-	-	-	-
45	*Asio* sp.	-	1	-	-	-	-	-	-	-	-
46	*Aegolius funereus* (Linnaeus, 1758)	2	1	-	-	-	-	-	2	-	-
47	*Dryocopus martius* (Linnaeus, 1758)	-	-	-	-	-	-	-	1	-	-
48	*Dendrocopos minor* (Linnaeus, 1758)	-	-	-	-	-	+	-	-	-	-
49	*Dendrocopos major* (Linnaeus, 1758)	-	1	-	-	-	-	-	12	-	-
50	*Dendrocopos leucotos* (Bechstein, 1802)	-	1	-	-	-	-	-	1	-	-
51	*Dendrocopos* sp.	-	-	-	-	-	-	-	3	-	-
52	*Picoides tridactylus* (Linnaeus, 1758)	-	-	-	-	-	-	-	1	-	-
53	*Melanocorypha yeltoniensis* (J.R. Forster, 1768)	1	-	-	-	-	-	-	-	-	-
54	*Hirundo rustica* Linnaeus, 1758	1	-	-	-	-	-	-	1	-	-
55	*Delichon urbica* (Linnaeus, 1758)	-	1	-	-	-	-	-	1	-	-
56	*Lanius excubitor* Linnaeus, 1758	-	-	-	-	-	-	-	2	-	-
57	*Bombycilla garrulus* (Linnaeus, 1758)	-	1	-	-	-	-	-	-	-	-
58	*Luscinia luscinia* (Linnaeus, 1758)	-	-	-	-	-	-	-	1	-	-
59	*Tarsiger cyanurus* (Pallas, 1773)	-	-	-	-	-	-	-	1	-	-
60	*Turdus torquatus* Linnaeus, 1758	3	1	-	-	-	-	-	1	-	-
61	*Turdus pilaris* Linnaeus, 1758	4	1	-	-	-	-	+	1	-	+
62	*Turdus viscivorus* Linnaeus, 1758	2	3	-	-	-	+	-	2	+	-
63	*Turdus philomelos* Brehm, 1831	-	1	-	-	+	+	-	2	-	+
64	*Turdus* sp.	13	9	-	-	-	-	-	8	-	-
65	*Sitta europaea* Linnaeus, 1758	-	-	-	-	-	-	-	1	-	-
66	*Carpodacus erythrinus* (Pallas, 1770)	-	1	-	-	-	-	-	-	-	-
67	*Pyrrhula pyrrhula* (Linnaeus, 1758)	-	-	-	-	-	-	-	2	-	-
68	*Coccothraustes coccothraustes* (Linnaeus, 1758)	-	-	-	-	-	-	-	1	-	-
69	Fringillidae indet.	-	1	-	-	-	-	-	-	-	-

(*continued on next page*)

Table 11 (*continued*)

N	Stratigraphy	Upper Neopleistocene	Holocene (MIS 1)								
		Kudashevo (MIS 2)	Lower-Middle	Lower-Upper					Upper		
	Taxa/Cave	BT3(3)	BT(2)	V(1)	Z(1)	N(1)	ST6(1)	ST10(1)	BT(1)	AG	L2a
70	*Garrulus glandarius* (Linnaeus, 1758)	-	4	-	-	-	+	-	8	-	-
71	*Nucifraga caryocatactes* (Linnaeus, 1758)	-	-	-	-	-	-	-	2	-	-
72	*Pica pica* (Linnaeus, 1758)	3	2	-	-	-	+	-	5	-	-
73	*Corvus monedula* (Linnaeus, 1758)	-	1	-	-	-	+	-		-	-
74	*Corvus cornix (corone)* (Linnaeus, 1758)	-	-	-	-	+	+	-	-	-	-
75	Corvidae indet.	-	-	-	-	-	-	-	2	-	-
76	Passeriformes indet.	3	5	-	-	-	-	-	4	-	-
77	Aves indet.	124	119	-	-	-	-	-	138	-	-

Legend: * – number of determined remains; + – uncounted bone remains; BT(3) – Balatukai Cave; layer 3; BT(2) – Balatukai Cave; layer 2; BT(1) – Balatukai Cave; layer 1; AG – Atysh I Grotto; L2a – Lemeza II Cave, layer 2; V(1) – Verkhnaya Cave, layer 1; Z(1) – Zapovednaya Cave, layer 1; N(1) – Nukatskaya Cave, layer 1; ST6(1) – Sikiyaz-Tamak 6 Cave, layer 1; ST10 (1) – Sikiyaz-Tamak 10 Cave, layer 1. MIS – Marine Isotope Stages.

1758), and *Gobio gobio* (Linnaeus, 1758)) were identified in the deposits assigned to the upper part of the Upper Neopleistocene and to the Holocene. The other species were only discovered in the Upper Neopleistocene deposits (*Hucho taimen* (Pallas, 1773), *Salmo trutta* Linnaeus, 1758, and *Perca fluviatilis* Linnaeus, 1758) or only in the Holocene deposits (*Squalius cephalus* (Linnaeus, 1758), *Leuciscus idus* (Linnaeus, 1758), and *Leuciscus leuciscus* (Linnaeus, 1758)). In sediments of different periods, the amount of bones varies significantly (Table 10).

All the fossil bone remains belong to modern freshwater species. A number of species (*Hucho taimen* Pallas, 1773, *Salmo trutta* Linnaeus, 1758, *Thymallus thymallus* (Linnaeus, 1758), *Squalius cephalus* (Linnaeus, 1758), *Barbatula barbatula* (Linnaeus, 1758), *Cottus gobio* Linnaeus, 1758) prefers fast flowing rivers. Most species inhabit the modern waters of Northern Asia and Europe and five species (*Salmo trutta* Linnaeus, 1758, *Thymallus thymallus* (Linnaeus, 1758), *Squalius cephalus* (Linnaeus, 1758), *Barbatula barbatula* (Linnaeus, 1758), *Cottus gobio* Linnaeus, 1758) inhabit only European rivers (Reshetnikov, 1998). There are no thermophilic species in the ichthyofauna. All the identified fish species were also discovered in the Middle Neopleistocene, Upper Neopleistocene and Holocene localities of Europe (Lebedev, 1960).

6.5. *Herpetology*

6.5.1. *Amphibians*

The Late Pleistocene and Holocene amphibian data from caves in the mountainous part of the Southern Urals allow us to characterize the amphibian communities of the Kudashevo Horizon and the Holocene time intervals. During end of the Kudashevo time until the Late Holocene, species that prefer forest habitats – *Bufo bufo* (Linnaeus, 1758), *Rana arvalis* Nilsson, 1842 and *Rana temporaria* Linnaeus, 1758 dominated. These faunas contain also warm-loving species such as *Bufo viridis* Laurenti, 1768 (Middle Holocene) which prefer open steppe habitats as well as *Triturus cristatus* (Laurenti, 1768) and *Bombina* sp. (Late Holocene) – inhabitants of the broad-leaved forests.

6.5.2. *Reptiles*

The Late Pleistocene and Holocene reptile data from caves in the mountainous part of the Southern Urals characterize the communities of the Kudashevo Horizon and the Lower, Middle and Upper Holocene. Starting from the end of the Kudashevo time interval until recent time, there were in the reptilian faunas species living in open habitats (meadow and steppe biotopes) – *Lacerta agilis* Linnaeus, 1758 and *Vipera ursinii* (Bonaparte, 1835), as well as species that occur in forest and near-water habitats – *Anguis fragilis* Linnaeus, 1758, *Zootoca vivipara* (Lichtenstein, 1823), *Coronella austriaca* Laurenti, 1768, *Natrix natrix* (Linnaeus, 1758) and *Vipera berus* (Linnaeus, 1758). In the faunas there were single species represented by *Eremias* cf. *arguta* (Pallas, 1773) (Middle Holocene), *Elaphe* cf. *dione* (Pallas, 1773) (end of Kudashevo time and Middle Holocene), and *Natrix tessellata* (Laurenti, 1768) (Late Holocene) which prefer warm and dry habitats.

The eastern margin of the Eastern-European Plain is, in contrast to the rest of Eastern Europe, herpetologically insufficiently studied. Several localities in the middle reaches of the Volga River are known to contain Late Pleistocene and Holocene reptiles and amphibians: Bolshie Tigany, Krasnyi Bor, Domashkinskie Vershiny, Strelnenskaya cave and Vovanova cave (Ratnikov, 2002, 2009; Yakovlev et al., 2013, b; Yakovleva et al., 2014). The species composition of the herpetofauna from these localities is similar to that of the studied sites from the mountainous part of the Southern Urals, but in the Volga River faunal associations, species of open biotopes prevail.

6.6. *Ornithology*

Remains of birds are only found in deposits of the younger part of the Upper Neopleistocene (MIS 2) and in Holocene (MIS 1). The end-Late Neopleistocene fauna includes species that occur near water bodies, inhabit open and semi-open landscapes and closed and semi-closed landscapes. The dominant species is *Lagopus lagopus* (Linnaeus, 1758) which inhabits open landscapes. The species composition shows that at the end of the Late Neopleistocene open landscapes dominated in the Southern Urals; however, also closed and semi-closed landscapes covered large areas.

Species of the Holocene avifauna belong to the same landscape-biotope groups as the Late Pleistocene species: species living near water bodies, in open and semi-open landscapes and in closed and semi-closed landscapes. An increase in the number of species during the Holocene was due an increase of closed and semi-closed biotopes. Species that inhabit forest appeared (*Dryocopus martius* (Linnaeus, 1758), *D. minor* (Linnaeus, 1758), *D. major* (Linnaeus, 1758), *D. leucotos* (Bechstein, 1802), and *Picoides tridactylus* (Linnaeus, 1758)) in the Southern Urals Holocene avifauna assemblage which is due to a significant increase of areas with a forest vegetation. All the recorded Holocene species occur currently the Southern Urals.

6.7. *Mammalogy*

6.7.1. *Small mammals*

The central part of the Southern Urals mountains

During the beginning of the Late Pleistocene (Kushnarenkovo time, MIS 5; Idrisovo, Ignatievskaya caves) *Microtus gregalis* (Pallas, 1779) dominated (see Table 12) whereas other species, for example *Cricetulus migratorius* (Pallas, 1773), *Apodemus uralensis* (Pallas, 1811) and *Myopus schisticolor* (Lilljeborg, 1844) were rare. The fauna from the Kushnarenkovo deposits is a non-analogue fauna occurring under moderate

Table 12
List of species and number of small mammal bone remains from the Upper Neopleistocene and Holocene cave deposits based on Yakovlev et al. (2000, 2003, 2004, 2005, 2006), Danukalova et al. (2008, 2011), Izvarin (2004, 2017), Izvarin and Smirnov (2015).

N	Stratigraphy	Upper Neopleistocene	Holocene (MIS 1)													
		Kudashevo (MIS 2)	Lower				Middle				Upper					
	Taxa/Cave	B3	AK	GB2	L3a	N2	B2	Y4a	MG1	L2a	B1	A1	T1-2	AT1	Y3	L4
1	Chiroptera	92/56*	1/1			10/5	35/19	15/14	95/42		205/123	53/40	19/6	3/2	1/1	24/15
2	*Talpa europaea* Linnaeus, 1758			4/1	1/1	4/3		3/1	10/5			18/2	10/1		1/1	57/19
3	*Talpa* sp.	8/5					6/3				19/12					
4	*Sorex* sp.	236/169	8/6	13/6	6/2	9/4	53/39	5/5	53/31	4/2	112/91	41/35	13/10	1/1	3/3	6/5
5	*Crocidura* sp.	7/5				1/1	4/3				3/3		1/1			
6	Erinaceinae	1/1										1/1				
7	*Lepus* sp.	20/5	2/1	8/1	6/2	4/1	4/2			17/3	4/3		1/1			3/2
8	*Ochotona sp.*	1124/129	6/1	123/15	120/14	51/5	820/90	15/3	16/4	6/2	235/26	2/1	3/1	2/1	2/1	
9	*Sciurus vulgaris* Linnaeus, 1758			1/1		2/1					1/1	1/1				
10	*Spermophilus* sp.	10/3		3/1	6/2	24/4	1/1		5/2	2/1						
11	*Marmota* sp.	5/1														
12	*Sicista* sp.	26/11	2/1	2/2		1/1	8/6			3/1	4/2	1/1		1/1		1/1
13	*Allactaga major* (Kerr, 1792)	3/1			1/1	1/1			1/1		1/1					
14	*Alactagulus* sp.	1/1				13/3			1/1							
15	*Apodemus uralensis* (Pallas, 1811)	22/22		2/2			7/7		2/2		9/9		5/5	2/1	1/1	
16	*A. agrarius* (Pallas, 1771)												1/1			
17	*A.* ex gr. *uralensis-agrarius*	158/100				2/2	42/28	1/1	18/11	1/1	54/38	8/6	19/13			2/2
18	*A. flavicollis* (Melchior, 1834)	2/2	1/1			1/1	3/3		3/2		12/9	10/3			4/3	
19	*Ellobius talpinus* (Pallas, 1770)	156/25			1/1		83/14	1/1		1/1	68/16	2/1	3/3			
20	*Cricetulus migratorius* (Pallas, 1773)	40/19	6/4	34/12	5/2	19/8	17/7		3/1		7/6					
21	*Allocricetulus eversmanni* (Brandt, 1894)	78/23				6/3	20/6	1/1	6/3		12/5			1/1		
22	*Cricetus cricetus* (Linnaeus, 1758)	175/37	1/1	3/1	1/1	11/3	46/10	11/2	2/2		31/13	14/3	7/3	4/2	1/1	15/3
23	*Clethrionomys rufocanus* (Sundevall, 1846)	41/11	1/1	5/3		32/3	8/5	5/2	20/5	1/1	30/14	59/14	1/1	4/1	5/2	13/7
24	*Cl.* ex gr. *glareolus-rutilus*	661/133	13/5	41/9	1/1	58/18	342/87	48/9	111/30	24/4	1145/306	696/210	77/23	37/12	47/19	53/28
25	*Lagurus lagurus* (Pallas, 1773)	1643/377	110/24	193/41	10/4	56/12	788/157		143/36	8/3	252/67	5/1		7/1	1/1	
26	*Eolagurus luteus* (Everssmann, 1840)	23/9		1/1		5/3		7/3			2/2					
27	*Dicrostonyx torquatus* (Pallas, 1778)				3/2											
28	*Dicrostonyx* sp.		33/14	134/37		2/1										
29	Lemmini gen.		2/1	3/1												
30	*Arvicola terrestris* (Linnaeus, 1758)	208/41	1/1	1/1	15/3	50/8	56/12	6/1	4/3	19/5	49/17	30/3	74/14	1/1	1/1	12/3
31	*Microtus gregalis* (Pallas, 1779)	763/763	119/119	137/137	45/45	202/202	245/245	12/12	112/112	36/36	113/113	6/6		4/4		
32	*M. oeconomus* (Pallas, 1776)	198/198	21/21	14/14	75/75	102/102	52/52	1/1	17/17	23/23	27/27	1/1	1/1			9/9
33	*M. agrestis* (Linnaeus, 1761)	197/121	5/4	12/7		18/4	57/53	5/5	1/1	6/5	85/46	36/19	15/8	2/1	4/4	14/5
34	*M. arvalis* (Pallas, 1778)	220/220		2/2	3/3	10/10	93/93	10/10	4/4	1/1	193/193	34/34	41/41	1/1	2/2	13/13
34	*M.* ex gr. *arvalis-agrestis*		3/3	1/1		8/8		3/3				7/7			6/6	16/16
36	*Microtus* sp.	4410	494	695	485		1399	74	500	158	1182	236	112	18	21	165
37	*Mustela nivalis* Linnaeus, 1766	11/5			1/1		3/2				4/3					
38	*Mustela erminea* Linnaeus, 1758	2/2					2/2									
	Total:	10541/2495	830/210	1432/296	785/160	2406/417	4194/946	223/74	1127/315	310/89	3859/1146	1261/389	403/133	88/30	100/46	403/128

Legend: * – number of determined remains/number of individuals; B3 – Bajslan-Tash Cave, layer 4; AK – Alikaev Kamen' site; GB2 –Bobyliok Grotto, layer 2; L3a – Lemeza III Cave, layers 2–6; N2 – Nukatskaya Cave, layer 2; B2 – Bajslan-Tash Cave, layer 3, horizons 11–13; Y4a – Yurmash 4 Cave, layers 2–3; MG1 – MG1 – Maksyutovo Grotto, layer 1; L2a – Lemeza II Cave, layer 2; B1 – Bajslan-Tash Cave, layers 1–2, horizons 1–10; A1 – Archaeologists Grotto, layer 1–4; T1–2 – Tashmurun Grotto, layers 1, 2; AT1 – Azan-Tash 1 Cave, layers 1–3; Y3 – Yurmash 3 Cave, layer 1; L4 – Lemeza IV Cave, layers 1–3. MIS – Marine Isotope Stages.

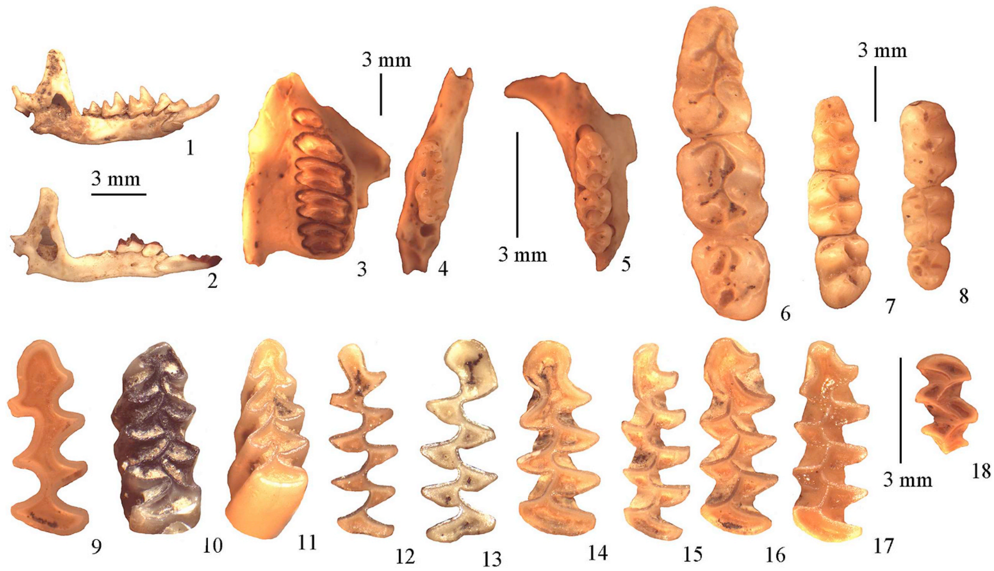

Fig. 6. Key-species of small mammals found in the Upper Pleistocene (Kudashevo Horizon) unconsolidated deposits of the Bajslan-Tash Cave, Southern-Urals region, Russia.
Legend: 1 – *Crocidura* sp., right mandibula; 2 – *Sorex* sp., right mandibula; 3 – *Ochotona* sp., fragment of maxilla; 4 – *Sicista* sp., fragment of mandibula; 5 – *Apodemus uralensis* (Pallas, 1811), fragment of maxilla; 6 – *Cricetus cricetus* (Linnaeus, 1758), m1–m3; 7 – *Allocricetulus eversmanni* (Brandt, 1894), m1–m3; 8 – *Cricetulus migratorius* (Pallas, 1773), M1–M3; 9 – *Ellobius talpinus* (Pallas, 1770), m1; 10 – *Clethrionomys rufocanus* (Sundevall, 1846), m1; 11 – *Clethrionomys* ex gr. *glareolus-rutilus*, m1; 12 – *Lagurus lagurus* (Pallas, 1773), m1; 13 – *Eolagurus luteus* (Eversmann, 1840); 14 – *Arvicola terrestris* (Linnaeus, 1758), m1; 15 – *Microtus gregalis* (Pallas, 1779), m1; 16 – *Microtus oeconomus* (Pallas, 1776), m1; 17 – *Microtus arvalis* (Pallas, 1778), m1; 18 – *Microtus agrestis* (Linnaeus, 1761), M2. 1, 2 – lateral view; 3–18 – top view.

climatic conditions.

During the Tabulda time interval (MIS 3; Idrisovo and Ignatievskaya caves) *Microtus gregalis* (Pallas, 1779) and *M. oeconomus* (Pallas, 1776) formed the main part in the small-mammal associations (see Table 12) whereas *Apodemus flavicollis* (Melchior, 1834) and *Cricetus cricetus* (Linnaeus, 1758) were very rare.

The small-mammal fauna from the Kudashevo Horizon (MIS 2; Prizhim Grotto, Ignatievskaya, Serpievskaya 1 and 2 caves) reflects cold climatic conditions; *Eolagurus luteus* (Eversmann, 1840) *Allactaga major* (Kerr, 1792), *Lagurus lagurus* (Pallas, 1773) and *Dicrostonyx guilielmi* Sanford, 1870 are common. In the central part of the Southern Urals the Late Neopleistocene small mammal fauna was periglacial, both in the warm and cold periods. At the end of the Kudashevo time interval lemmings did not occur in southern part of the Southern Urals (Bajslan-Tash cave in the valley of the Belaya River); the fauna was composed of steppe and semi-desert species (Table 12).

Upper Holocene deposits were recorded in the Sim River valley (Sim I, II and III Grottoes; Serpievskaya 1 cave). During the Upper Holocene *Microtus arvalis* (Pallas, 1778), *Microtus agrestis* (Linnaeus, 1761), *Arvicola terrestris* (Linnaeus, 1758), *Clethrionomys rutilus* (Pallas, 1779), were numerous and *Apodemus flavicollis* (Melchior, 1834), *Eliomys quercinus* (Linnaeus, 1766), *Microtus gregalis* (Pallas, 1779) and *Lagurus lagurus* (Pallas, 1773) were rare (Table 12). The fauna is similar to the small mammal fauna from the Lemeza River valley. Upper Holocene small mammal assemblages from the Belaya River valley contain a larger part of steppe species.

The Southern Trans-Urals

The small mammal fauna from the Kudashevo Horizon (Syrtinskaya and Smelovskaya 2 caves) contains predominant species such as *Lagurus lagurus* (Pallas, 1773), *Eolagurus luteus* (Everssmann, 1840) and *Microtus gregalis* (Pallas, 1779) whereas in the Lower Holocene deposits (Alekseevskaya, Chernyshevskaya V and Syrtinskaya caves) *Microtus gregalis* (Pallas, 1779), *Lagurus lagurus* (Pallas, 1773) and *Ellobius talpinus* (Pallas, 1770) are most numerous (Table 12).

The Middle Holocene deposits in the Alekseevskaya and Syrtinskaya caves yieled numerous remains of *Microtus gregalis* (Pallas, 1779) and *Lagurus lagurus* (Pallas, 1773) and less numerous *Microtus* ex gr. *arvalis* (Pallas, 1778) and *Ellobius talpinus* (Pallas, 1770) (Table 12).

During Late Holocene (Syrtinskaya, Khudolaz, Alekseevskaya and Chernorechka caves) *Microtus gregalis* (Pallas, 1779), *M.* ex gr. *arvalis* (Pallas, 1778) dominated and *Ellobius talpinus* (Pallas, 1770), *Lagurus lagurus* (Pallas, 1773) and *Arvicola terrestris* (Linnaeus, 1758) were common.

The small mammal species composition of the Trans-Urals area changed unsignificantly – *Eolagurus luteus* (Everssmann, 1840) and *Alactagulus pumilio* (Kerr, 1790) disappeared during the Late Holocene. The Trans-Urals small-mammal fauna in general is represented by species that prefer to inhabit steppe biotopes (Smirnov and Kuzmina, 2001).

Late Pleistocene and Holocene small-mammal faunas from the Southern Trans-Urals are most similar to the contemporaneous faunas from the Southern part of the Southern Urals (The Belaya River valley), in which the proportion of forest and near-water habitats is larger.

6.7.2. Large mammals

The central part of the Southern Urals mountains

The large mammal fauna from cave sediments of almost all the stratigraphical units exposed in the central part of the Southern Urals and dated to the end of the Middle Pleistocene (Elovka Horizon, MIS 6?) to the Upper Holocene (MIS 1) (Tables 13 and 14) were investigated.

Species that inhabit open landscapes (*Marmota bobak* (Müller, 1776), *Vulpes lagopus* (Linnaeus, 1758), *Ursus spelaeus* Rosenmüller, 1794, *U. savini* Andrews, 1922, *Mustela eversmanni* (Lesson, 1827), *Equus ferus* Boddaert, 1785, *Coelodonta antiquitatis* (Blumenbach, 1799), *Rangifer tarandus* (Linnaeus, 1758), and *Bison priscus* Bojanus, 1827) and intrazonal species (*Lepus timidus* Linnaeus, 1758, *Canis lupus* Linnaeus, 1758, *V. vulpes* Linnaeus, 1758, *Mustela erminea* Linnaeus, 1758, *M. nivalis* Linnaeus, 1766, and *Gulo gulo* (Linnaeus, 1758)) are most numerous in the faunas of the end of the Middle Pleistocene. There are very few species associated with tree-shrub vegetation (*Martes* sp., *Stephanorhinus* cf. *kirchbergensis* (Jäger, 1839), *Cervus elaphus* Linnaeus, 1758). The fauna indicates the dominance of the open landscapes with a small amount of trees and shrubs.

At the beginning of the Late Pleistocene (Kushnarenkovo, MIS 5e), open landscape species continue to dominate (*Marmota bobak* (Müller, 1776), *Vulpes lagopus* (Linnaeus, 1758), *Ursus savini* Andrews, 1922, *U. spelaeus* Rosenmüller, 1794, *M. eversmannii* (Lesson, 1827), *Equus ferus* Boddaert, 1785, *Coelodonta antiquitatis* Blumenbach, 1799, *Rangifer tarandus* (Linnaeus, 1758), *Bison priscus* Bojanus, 1827, *Saiga tatarica* (Linnaeus, 1766), and *Ovis ammon* Linnaeus, 1758), but there were more species associated with trees and shrubs (*Hystrix brachyura*

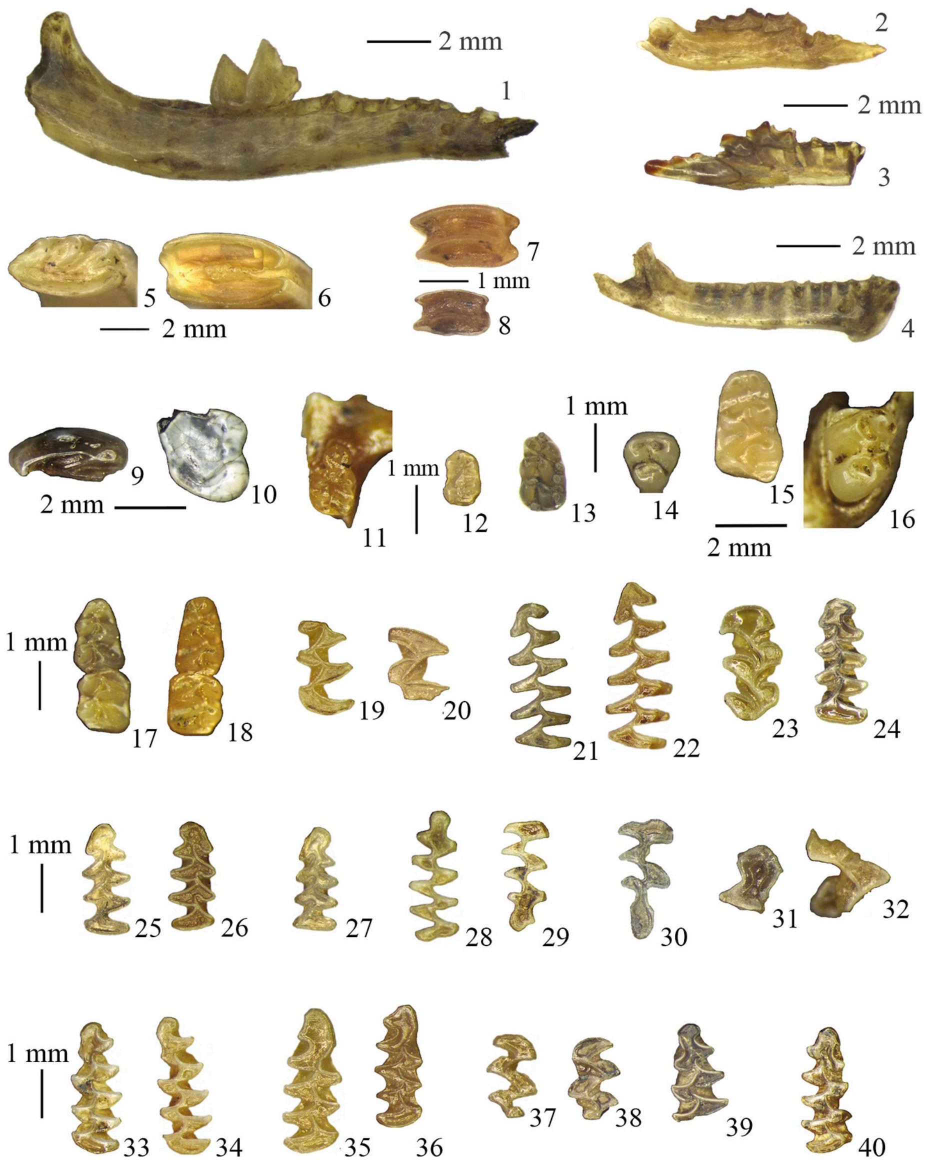

Fig. 7. Key-species of small mammals found in the early-Holocene sediments of Grotto Bobyliok and Alikaev Kamen' site, Southern Fore-Urals region, Russia.

Legend: 1 – *Talpa europaea* Linnaeus, 1758: descending branch of dexter mandibula with m2; 2–3 – *Sorex* sp.: descending branch of dexter mandibula with i1 and m1–m3; fragment of descending branch of sinister mandibula with i1, p4 and m1; 4 – Chiroptera: descending branch of dexter mandibula without teeth; 5–6 – *Lepus* sp.: P2 dexter; dexter upper tooth; 7–8 – *Ochotona* sp.: upper sinister teeth P4–M2; 9 – *Spermophilus* sp.: fragment of M1 dexter; 10 – *Sciurus vulgaris* Linnaeus, 1758: m3 dexter; 11–12 – *Sicista* sp.: fragment of sinister maxilla with P4 and M1; m1 sinister; 13 – *Apodemus uralensis* (Pallas, 1811): m1 dexter; 14 – *A.* cf. *flavicollis* (Melchior, 1834): m3 dexter; 15–16 – *Cricetus cricetus* (Linnaeus, 1758): m1 sinister; fragment of sinister mandibula with m3; 17–18 – *Cricetulus migratorius* (Pallas, 1773): m1 and m2 dexter; m1 and m2 sinister; 19–20 – Lemmini gen.: m2 sinister; fragment of sinister m1 or m2; 21–22 – *Dicrostonyx* sp.: m1 sinister; 23–24 – *Clethrionomys rufocanus* (Sundevall, 1846): M1 dexter; m1 sinister; 25–26 – *Cl. glareolus* (Schreber, 1780): m1 sinister; m1 dexter; 27 – *Cl. rutilus* (Pallas, 1779): m1 sinister; 28–29 – *Lagurus lagurus* (Pallas, 1773): m1 dexter; M3 dexter; 30. *Eolagurus luteus* (Eversmann, 1840): M3 dexter; 31–32 – *Arvicola terrestris* (Linnaeus, 1758): fragment of sinister m1; fragment of sinister M2; 33–34 – *Microtus gregalis* (Pallas, 1779): m1 sinister; 35–36 – *M. oeconomus* (Pallas, 1776): m1 dexter; 37–39 – *M. agrestis* Linnaeus, 1761: M2 dexter; M2 sinister; fragment of sinister m1; 40 – *M. arvalis* s.l.: m1 dexter. Grotto Bobyliok, layer 2 (1, 3, 5, 7, 9, 10, 12, 13, 15, 17, 20, 21, 24, 25, 27, 29–31, 33, 36, 38–40) and Alikaev Kamen' site (2, 4, 6, 8, 11, 14, 16, 18, 19, 22, 23, 26, 28, 32, 34, 35, 37).

Linnaeus, 1758, *Dryomys nitedula* (Pallas, 1778), *Ursus arctos* Linnaeus, 1758, *Martes* sp., *Stephanorhinus* cf. *kirchbergensis* Jäger, 1839, and *Cervus elaphus* Linnaeus, 1758). In addition, typical forest species (*Sciurus vulgaris* Linnaeus, 1758, *Apodemus flavicollis* (Melchior, 1834), and *Lynx lynx* Linnaeus, 1758) were part of the fauna. It should be noted that the fauna includes "thermophilic" species characteristic of interglacials: *Hystrix brachyuran* Linnaeus, 1758, *Dryomys nitedula* (Pallas, 1778), *Meles meles* (Linnaeus, 1758). In the composition of taphonomically mixed bone remains from the Imanai cave (Kushnarenkovo-Kudashevo, MIS 5e – 2), the Asiatic black bear (*Ursus thibetanus* (G. Cuvier, 1823) and the wild boar (*Sus scrofa* Linnaeus, 1758) occur. They were part of the central Southern Urals fauna during the Kushnarenkovo period when open landscapes with large forests were wide-spread in the mountainous part of the Southern Urals.

The larger mammal fauna of the Saigatka horizon (MIS 4) is unknown so far.

The Tabulda fauna (MIS 3) lacks the Merck rhinoceros (*Stephanorhinus* cf. *kirchbergensis* Jäger, 1839), characteristic of the Middle and early Late Pleistocene, and there are no "thermophilic" species such as *Hystrix brachyura* Linnaeus, 1758, *Dryomys nitedula* (Pallas, 1778), and *Meles meles* (Linnaeus, 1758). The fauna includes open landscape species: *Marmota bobak* (Müller, 1776), *Vulpes lagopus* (Linnaeus, 1758), *V. corsac* Linnaeus, 1768, *Ursus spelaeus* Rosenmüller, 1794, *M. eversmannii* Lesson, 1827, *Equus ferus* Boddaert, 1785, *Coelodonta antiquitatis* (Blumenbach, 1799), *Rangifer tarandus* (Linnaeus, 1758), *Bison priscus* Bojanus, 1827, *Saiga tatarica* (Linnaeus, 1766), and *Ovis ammon* (Linnaeus, 1758) (Table 13).

There are few species that are associated with tree-shrub vegetation (*Cuon alpinus* (Pallas, 1811), *Ursus arctos* Linnaeus, 1758, *Martes zibellina* (Linnaeus, 1758), *Lynx lynx* (Linnaeus, 1758), and *Cervus elaphus* Linnaeus, 1758). By the end of this period, cave bears (*Ursus spelaeus* Rosenmüller, 1794), cave hyena (*Crocuta crocuta spelaea* Goldfuss, 1823), dhole (*Cuon alpinus* (Pallas, 1811) and mufflon (*Ovis ammon* (Linnaeus, 1758)) disappeared from the fauna.

Open landscapes with small tracts of forest vegetation dominated during the Tabulda time interval. At the end of the Late Pleistocene (Kudashevo, MIS 2), open landscape and intrazonal species still dominated (Table 13). This indicates the predominance of open landscapes and limited distribution of forest vegetation.

At the beginning of the Holocene, changes occur in the fauna – for the first time a roe deer (*Capreolus pygargus* (Pallas, 1771)) appears, which was absent in the Pleistocene faunas (Tables 13 and 14). Open landscape species (*Marmota bobak* (Müller, 1776), *Vulpes lagopus* (Linnaeus, 1758), *V. corsac* (Linnaeus, 1768), *Mustela eversmannii* (Lesson,

Table 13
List of species and number of large mammal bone remains in the Middle-Upper Neopleistocene cave deposits based on Kosintsev et al. (2013, 2019), Kuzmin et al. (2017), Gimranov et al. (2017a, b) and new authors' data.

N	Stratigraphy	Middle Neopleistocene			Upper Neopleistocene								
		Elovka (MIS 6?)			Kushnarenkovo (MIS 5e)			Kushnarenkovo-Saigatka (MIS 5a-d – 4)	Kushnarenkovo-Tabulda (MIS 5e – 3)	Kushnarenkovo-Kudashevo(MIS 5e – 2)	Tabulda (MIS 3)		
	Taxa/Cave	IG (1985a)	S1(3)	V	IG (2014)	BD	BG(5–6)	ST7 (12-14)	ID	IM	IG (1985b)	ST7 (9-11)	KA
1.	*Lepus timidus* Linnaeus, 1758	160	60	-	98	24	90	39	32	+	526	272	6
2.	*Castor fiber* Linnaeus, 1758	-	1	-	-	-	-	-	1	+	-	-	-
3.	*Marmota bobak* (Müller, 1776)	7	21	-	51	6	267	26	360	+	189	245	7
4.	*Hystrix brachyura* Linnaeus, 1758	-	-	-	-	3	-	-	1	+	-	-	-
5.	*Canis lupus* Linnaeus, 1758	85	2	-	298		20	3	12	+	164	25	16
6.	*Cuon alpinus* (Pallas, 1811)	-	-	-	-	-	-	-	-	+	1	-	-
7.	*Vulpes lagopus* (Linnaeus, 1758)	8	-	-	126	-	47	1	131	+	58	72	-
8.	*V. corsac* Linnaeus, 1768	-	-	-	-	-	-	-	7	+	-	7	-
9.	*V. vulpes* (Linnaeus, 1758)	8	5	-	3	9	14	7	17	+	47	18	9
10.	*Ursus arctos* Linnaeus, 1758	-	-	-	-	2	-	-	-	-	-	-	-
11.	*U. thibetanus* (G. Cuvier, 1823)	-	-	-	-	-	-	-	-	+	-	-	-
12.	*U. spelaeus* Rosenmüller, 1794	-	39	-	-	653	955	30	53	+	3991	82	333
13.	*U.* cf. *deningeri* Richenau, 1904	-	-	172	-	-	-	-	-	-	-	-	-
14.	*U. savini* Andrews, 1922	47	-	-	4	12	-	-	-	+	-	-	-
15.	*Martes zibellina* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	-	-	2	-
16.	*Martes* sp.	3	9	-	8	-	21	-	-	-	-	-	-
17.	*Gulo gulo* (Linnaeus, 1758)	4	-	-	48		1	-	-	+	1	-	-
18.	*Mustela erminea* Linnaeus, 1758	2	4	-	6		-	4	12	+	5	8	2
19.	*M. nivalis* Linnaeus, 1766	5	1	-	23	3	-	5	52	+	1	21	-
20.	*M. lutreola* (Linnaeus, 1761)	-	-	-	-	1	-	-	-	-	-	-	-
21.	*M. eversmanni* (Lesson, 1827)	1	4	-	-		-	-	4	+	3	1	-
22.	*Meles meles* (Linnaeus, 1758)	-	-	-	-	1	13	-	-	+	-	-	-
23.	*Lutra lutra* (Linnaeus, 1758)	-	1	-	-	-	-	-	-	-	-	-	-
24.	*Crocuta crocuta spelaea* Goldfuss, 1823	-	-	-	-	-	-	-	-	-	15	2	-

Table 13 (*continued*)

N	Stratigraphy	Middle Neopleistocene			Upper Neopleistocene								
		Elovka (MIS 6?)			Kushnarenkovo (MIS 5e)			Kushnarenkovo-Saigatka (MIS 5a-d – 4)	Kushnarenkovo-Tabulda (MIS 5e – 3)	Kushnarenkovo-Kudashevo(MIS 5e – 2)	Tabulda (MIS 3)		
	Taxa/Cave	IG (1985a)	S1(3)	V	IG (2014)	BD	BG(5–6)	ST7 (12-14)	ID	IM	IG (1985b)	ST7 (9-11)	KA
25.	*Panthera leo spelaea* Goldfuss, 1810	-	-	-	1	-	-	-	-	+	12	2	-
26.	*Lynx lynx* (Linnaeus, 1758)	-	-	-	-	1	-	-	-	-	-	-	1
27.	*Mammuthus primigenius* (Blumenbach, 1799)	-	-	-	-	-	16	-	-	+	1	2	-
28.	*Equus ferus* Boddaert, 1785	-	5	-	-	-	42	5	9	+	84	66	-
29.	*Stephanorhinus* cf. *kirchbergensis* Jäger, 1839		1	1	-	3	-	-	1	-	-	-	-
30.	*Coelodonta antiquitatis* (Blumenbach, 1799)	2	-	-	-	-	25	1	4	+	43	5	-
31.	*Elasmotherium sibiricum* Fisher, 1809	-	-	-	-	-	-	-	-	-	-	-	-
32.	*Camelus ferus* Przewalski, 1878	-	-	-	-	-	-	-	-	-	-	-	-
33.	*Sus scrofa* Linnaeus, 1758	-	-	-	-	-	-	-	-	+	-	-	-
34.	*Cervus elaphus* Linnaeus, 1758	4	5	3	-	2	11	5	6	+	43	9	1
35.	*Megaloceros giganteus* Blumenbach, 1799	-	-	-	-	-	-	3	-	-	-	-	-
36.	*Alces alces* Linnaeus, 1758	-	-	-	-	-	-	-	-	+	-	-	-
37.	*Rangifer tarandus* Linnaeus, 1758	8	2	-	-	1	191	17	15	+	71	128	-
38.	*Bison priscus* Bojanus, 1827	2	-	-	-	1	80	4	-	+	11	21	-
39.	*Saiga tatarica* Linnaeus, 1766	-	-	-	-	1	16	1	12	+	8	17	-
40.	*Ovis ammon* Linnaeus, 1758	-	-	-	3	-	-	-	-	+	-	1	-
	Total:	346	160	176	669	723	1754	151	718	+	5274	1872	375

N	Upper Neopleistocene													
	Tabulda (MIS 3)			Kudashevo (MIS 2)										
	Z (1-2)	P	SM	BG (3-4)	ST 7 (8)	S1 (2)	SR (3)	PR	K	KT	B (4a)	MG	BT	U (3)
1.	1	9	57	2312	102	15	44	264	79	3	155	74	492	125
2.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3.	5	12	446	46	39	14	871	72	8	1	34	27	75	178
4.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5.	17	126	19	46	-	11	2	3	-	1	1	5	-	4

Table 13 (*continued*)

N	Upper Neopleistocene													
	Tabulda (MIS 3)			Kudashevo (MIS 2)										
	Z (1-2)	P	SM	BG (3-4)	ST 7 (8)	S1 (2)	SR (3)	PR	K	KT	B (4a)	MG	BT	U (3)
6.	-	1	-	-	-	-	-	-	-	-	-	-	-	-
7.	-	2	46	124	12	1	23	11	2	1	-	1	4	5
8.	-	-	7	-	2	-	24	-	-	-	-	-	1	-
9.	32	24	33	15	-	1	28	4	2	-	1	10	2	-
10.	-	1	6	3	-	-	7	3	-	-	-	1	3	-
11.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12.	15667	5743	-	-	-	-	-	-	-	-	-	-	-	-
13.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15.	-	2	-	-	1	-		-	-	-	1	1	-	-
16.	-	12	-	17	-	-	-	-	-	-	-	-	-	-
17.	-	4	-	6	-	3	1	-	-	-	-	-	-	-
18.	-	2	-	24	1	-	4	1	-	-	33	1	24	-
19.	-	-	-	3	-	-	3	1	-	-	21	1	4	-
20.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21.	7	3	2	-	-	-	5	-	-	-	-	1	1	-
22.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24.	-	2	94	-	-	-	-	-	-	-	-	-	-	-
25.	6	14	7	-	-	-	-	-	-	1	-	4	-	-
26.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27.	-	-	10	4	-	1	-	-	-	1	-	-	-	-
28.	1	-	784	265	-	58	90	1	-	1	5	3	24	4
29.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30.	-	-	204	63	2	9	5	-	-	1	-	4	2	5
31.	-	-	1	-	-	-	-	-	-	-	-	-	-	-
32.	-	-	1	-	-	-	-	-	-	-	-	-	-	-
33.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34.	-	-	3	-	2	-	3	-	-	-	-	2	1	
35.	-	-	2	1	-	-	-	-	-	-	-	-	-	-
36.	-	-	-	1	-	-	-	-	-	-	-	-	-	-
37.	-	-	2	1066	18	34	1	8	-	-	1	2	22	19
38.	3	-	152	99	5	20	3	-	-	1	4	15	4	4
39.	-	-	57	150	5	-	45	1	-	-	-	1	1	8
40.	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	15739	5955	1932	4208	189	167	1159	369	91	11	256	153	660	352

Legend: IG(1985a) – Ignatievskaya Cave, 1985, pit V, layer 10; S1–3 – Maiskaya (Serpievskaya 1) Cave, layer 3; V – Verkhnaya Cave; IG(2014) – Ignatievskaya Cave, 2014, pit V, layer 10; BD – Barsuchyi Dol Cave; BG – Bobyliok Grotto, layers 5–6; ST7(12–14) – Sikiyaz-Tamak 7 Cave, layers 12–14; ID – Idrisovo Cave; IM – Imanai Cave; IG(1985b) – Ignatievskaya Cave, 1985, pit V, layers 2–9; ST7(9–11) – Sikiyaz-Tamak 7 Cave, layers 9–11; K – Kozya (Asha I) Cave; Z – Zapovednaya Cave; P – Kinderlinskaya Cave; SM – Smelovskaya 2 Cave; BG(3–4) – Bobyliok Grotto, layers 3–4; ST7(8) – Sikiyaz-Tamak 7 Cave, layer 8; S1(2) – Maiskaya (Serpievskaya 1) Cave, layer 2; SR(3) – Syrtinskaya Cave, layer 3; PR – Prizhim 2 Cave; K – Shulgan-Tash (Kapova) Cave; KT – Kulyurt-Tamak Cave; B(4a) – Bajslan-Tash Cave, layer 4, lower part; MG – Maksyutovo Grotto; BT – Balatukai Cave; U – Ustinovo Grotto. MIS – Marine Isotope Stages. + – uncounted bone remains.

1827)*,* *Equus ferus* Boddaert, 1785*,* *Rangifer tarandus* (Linnaeus, 1758)*,* *Bison priscus* Bojanus, 1827*,* and *Saiga tatarica* (Linnaeus, 1766)) are still numerous (Table 14). At the beginning of the Holocene, open landscapes continue to occupy large areas in the central part of the Southern Urals Mountains, but there was an increase in the areas of semi-open landscapes.

During the Middle Holocene, the number of open landscape species was decreasing – *Vulpes lagopus* (Linnaeus, 1758)*,* *V. corsac* (Linnaeus, 1768)*,* *Mustela eversmannii* Lesson, 1827*,* and *Rangifer tarandus* (Linnaeus, 1758) disappeared. The fauna includes *Castor fiber* Linnaeus, 1758*,* *Lutra lutra* (Linnaeus, 1758)*,* *Meles meles* (Linnaeus, 1758)*,* *Sus scrofa* Linnaeus, 1758, which were absent in the fauna from the Tabulda (MIS 3) and Kudashevo (MIS 2) time intervals. The number of bone remains of *V. vulpes* (Linnaeus, 1758)*,* *Ursus arctos* Linnaeus, 1758*,* *Martes sp.,* *Capreolus pygargus* (Pallas 1771)*,* and *Alces alces* (Linnaeus, 1758) (Table 14) highly increased. At the end of the Middle Holocene (end of Subboreal) domestic ungulates (*Equus caballus* Linnaeus, 1758*,* *Ovis aries* Linnaeus, 1758) appeared. During the Middle Holocene, forest landscapes begin to dominate, but open landscapes still occupy relatively large areas.

During the Upper Holocene, the *Marmota bobak* (Müller, 1776) and *Mustela eversmannii* Lesson, 1827 remain in the fauna, but the number of their remains significantly reduced. Forest and semi-open landscape species were dominant and open landscapes occupy small areas, probably located on the top of the mountains.

The Southern Trans-Urals

The large mammal fauna from the unconsolidated sediments of the three caves in the Southern Trans-Urals (Smelovskaya 2 Cave, Ustinovo Grotto (Table 13) and Alekseevskaya Cave) (Table 14) include during the Tabulda time interval (MIS 3) a. o. *Elasmotherium sibiricum* J. Fisher, 1809 and *Camelus ferus* Przewalski, 1878; species that did not occur in the fauna of the central part of the Southern Urals Mountains (Table 13). Their occurrence indicates the almost complete absence of forest vegetation in this area. The fauna of the late Late Pleistocene (Kudashevo, MIS 2) and the Early Holocene (MIS 1) lacks species that are associated with tree-shrub vegetation (Tables 13 and 14). Open landscapes are still preserved in the Southern Trans-Urals.

7. Conclusions

The area of the Southern Urals is characterized by a wide distribution of the Proterozoic and Palaeozoic carbonate rocks which contain numerous big and small caves; the result of karst process related to the humid and temperate climate conditions in the region. Series of unconsolidated deposits with a thickness ranging from 0.5 to 5 m were formed in these caves.

Investigations of the unconsolidated the Late Neopleistocene and Holocene cave deposits resulted in detailed biostratigraphical and palaeoenvironmental data (Fig. 8). The data indicate that the Southern Urals landscapes have a mosaic character. Due to the relief in a limited area, various plant communities (coniferous, deciduous, small-leaved and mixed forests, meadow, steppe and vegetation of the rocky slopes) occur. The forest vegetation, in turn, has unique regional features related to the fact that it was formed at the transition of Eastern European broadleaved, southern dark coniferous taiga and South-Uralian light coniferous forests. The modern mountain mixed forests of the Southern Urals appeared only during the latest Holocene. The forest-steppes were in general widespread during the Late Neopleistocene – Holocene. Forest vegetation occurred at higher altitudes during the warm periods (Tabulda, Middle-Late Holocene); forested areas reduced during the cold intervals (Kudashevo, Early Holocene). However, it should be noted that even during the coldest periods refugia of broad-leaved flora existed in the territory of the Southern Urals.

The late Neopleistocene and Holocene mollusc species are Holarctic species that occur in different ecological biotopes such as forest-steppe, forest and intrazonal (river banks) areas.

The Late Pleistocene and Holocene amphibian associations found in caves of the Southern Urals are characterized by species that prefer forest biotopes. The reptile faunas contain more species which inhabited open areas. This difference is related to the ecological features of the Amphibians which prefer biotopes with constant humidity and of the Reptiles which inhabit opened dry and warm areas on the hill slopes as well as meadows and even in forest biotopes.

The Pleistocene and Holocene fish fauna found in the caves of the Southern Urals is a characteristic freshwater fauna occurring in a temperate zone. All species currently inhabit the rivers of Europe. The ichthyofauna of the Southern Urals during the Late Pleistocene and Holocene did not show significant differences.

The Pleistocene and Holocene bird faunas found in the cave sediments of the Southern Urals included species that occur in the modern ornithological faunas of Northern Asia, Central and Northern Europe. The Late Pleistocene fauna was dominated by species that inhabit open and semi-open landscapes whereas, during the Holocene, species that prefer closed biotopes dominated the bird fauna indicating a change in the landscape during the Holocene. All Late Pleistocene and Holocene bird species still occur in the modern fauna of the Southern Urals.

The small-mammal data from the Late Pleistocene and Holocene cave deposits in the Southern Urals can be used, in association with other biostratigraphical data, to date the cave deposits from the late Glacial (Kudashevo interval) to the Early, Middle and Late Holocene. During the Late Pleistocene and Early Holocene disharmonious/non-analogue faunas of the small mammals existed in the central and northern parts of the Southern Urals (Ufimian Plateau, Sim and Lemeza River valleys). These faunas included steppe, semi-desert species and rare lemmings. In the southern part of the Southern Urals and Trans-Urals, lemmings were absent. In the Southern Urals, starting from the Middle Holocene, there was gradual change of small-mammal communities with predominance of steppe species to predominance of forest species, and only in the Trans-Urals the steppe small-mammal fauna preserved. Modern small-mammal faunas appeared in the latitudinal section of the Belaya River valley at the end of the Late Holocene.

There were relatively little changes in the large-mammal fauna in the Southern Urals at the end of the Late Neopleistocene – beginning of Holocene. The relict population of Don hare (*Lepus tanaiticus* Gureev, 1964) was living in the Southern Urals during the Early Holocene. The large-mammal fauna during the end of the Late Neopleistocene and Early Holocene consisted of eurybiotic species and species of the open landscapes. Species that preferred forest landscapes, appeared at the end of the Early Holocene – beginning of the Middle Holocene. Modern species of the large-mammal fauna appeared in the second half of the Late Holocene.

Data availability

The palaeontological collections (molluscs and vertebrates) are kept at the Institute of Geology UFRC RAS (Ufa, Russian Federation) and Institute of Plant and Animal Ecology of UB RAS (Ekaterinburg, Russian Federation).

Declaration of competing interest

There are no conflict of interests in our manuscript.

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Table 14
List of species and number of large mammal bone remains from the Holocene cave deposits based on Razhev et al. (2005), Kosintsev et al. (2013, 2019), Danukalova et al. (2018) and new authors' data.

N	Stratigraphy	Holocene MIS 1															
		Early-Middle	Early (BO		Middle	Middle (AT)	Middle (SB)				Upper (SA)						
	Taxa/Cave	ST7 (7)	AS (2)	B (4b)	ST 7 (5-6)	B (3)	BG (1b)	AL	T (2)	Al (2)	BG (1a)	ST7 (1-4)	S1 (1)	AG	T (1)	Al (1)	B (1)
1.	*Lepus timidus* Linnaeus, 1758	1	12	465	19	42	11	4	9	8	83	10	34	16	10	31	10
2.	*Castor fiber* Linnaeus, 1758	-	-	-	2	1	4	-	77	2	77	-	-	-	317	8	1
3.	*Marmota bobak* (Müller, 1776)	-	41	32	-	12	-	-	9	2	-	-	-	-	3	-	10
4.	*Canis lupus* Linnaeus, 1758	-	-	1	-	1	2	-	8	-	26	-	1	-	6	1	-
5.	*Vulpes lagopus* (Linnaeus, 1758)	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6.	*V. corsac* Linnaeus, 1768	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
7.	*V. vulpes* (Linnaeus, 1758)	-	1	3	1	-	3	1	3	4	15	-	11	4	8	16	-
8.	*Ursus arctos* Linnaeus, 1758	-	-	-	-	-	8	-	185	2	95	-	1	-	597	19	8
9.	*M. martes* (Linnaeus, 1758)	-	-	36	-	1	-	-	55	2	-	-	-	315	946	39	1
10.	*Martes* sp.	-	-	-	-	-	26	-	-	-	1214	-	1	-	-	-	-
11.	*Gulo gulo* (Linnaeus, 1758)	-	-		-	-	1	-	3		1	-	-	-	7	-	-
12.	*Mustela erminea* Linnaeus, 1758	-	-	41	-	24	2	-	-	-	4	-	3	-	-	-	8
13.	*M. nivalis* Linnaeus, 1766	-	-	13	-	32	-	-	-	1	1	-	-	-	-	6	2
14.	*M. lutreola* (Linnaeus, 1761)	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	
15.	*M. eversmanni* (Lesson, 1827)	-	1	1	-	1	-	-	-	10	-	-	-	-	-	-	4
16.	*Meles meles* (Linnaeus, 1758)	-	-	-	-	-		-	19	-	-	-	2	-	65	5	1
17.	*M. leucurus* Hodgson, 1847	-	-	-	-	-	-	-	-	-	4	-	-	-		-	1
18.	*Lutra lutra* (Linnaeus, 1758)	-	-	-	1	-	-	-	-	2	11	-	-	1	3	9	-
19.	*Lynx lynx* (Linnaeus, 1758)	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
20.	*Equus ferus* Boddaert, 1785	-	5	8	-	1	-	-	-	-	-	-	-	-	-	-	-
21.	*Sus scrofa* Linnaeus, 1758	-	-	-	-	-	1	2	2	-	1	-	-	-	-	-	-
22.	*Cervus elaphus* Linnaeus, 1758	-	-	-	-	-	-	-	2	-	-	-	-	-	39	-	-
23.	*Capreolus pygargus* (Pallas 1771)	3	-	-	25	2	8	23	256	95	163	18	8	107	1285	12	149
24.	*Alces alces* (Linnaeus, 1758)	-	-	-	-	-	292	-	15	8	3874	1	-	43	99	43	2
25.	*Rangifer tarandus* (Linnaeus, 1758)	-	-	1	1	-	138	-	-	-	7176	-	-	-	2	-	-
26.	*Bison priscus* Bojanus, 1827	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
27.	*Saiga tatarica* (Linnaeus, 1766)	-	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28.	*Equus caballus* Linnaeus, 1758	-	-	-	6	-	-	-	-		39	12	1	-	-	-	-
	Total:	7	70	602	56	117	496	30	643	136	12786	41	62	486	3388	189	61

Legend: ST7(7) – Sikiyaz-Tamak 7 Cave, layer 7; AS(2) – Alekseevskaya Cave, layer 2; B(4b) – Bajslan-Tash Cave, layer 4, upper part; ST7(5–6) – Sikiyaz-Tamak 7 Cave, layers 5–6; B(3) – Bajslan-Tash Cave, layer 3; BG(1b) – Bobyliok Grotto, layer 1, lower part; AL – Alenushka; T(2) – Tashmurun Grotto, layer 2; Al(2) – Archaeologists Grotto, layer 2; BG(1b) – Bobyliok Grotto, layer 1, upper part; ST7 (1–4) – Sikiyaz-Tamak 7 Cave, layers 1–4; S1(1) – Maiskaya (Serpievskaya 1) Cave, layer 1; AG – Atysh I Grotto; T(1) – Tashmurun Grotto, layer 1; Al(1) – Archaeologists Grotto, layer 1; B(1) – Bajslan-Tash Cave, layer 1. Indices of Blitt-Sernander scale: BO – Boreal; AT – Atlantic; SB – Subboreal; SA – Subatlantic. MIS – Marine Isotope Stages.

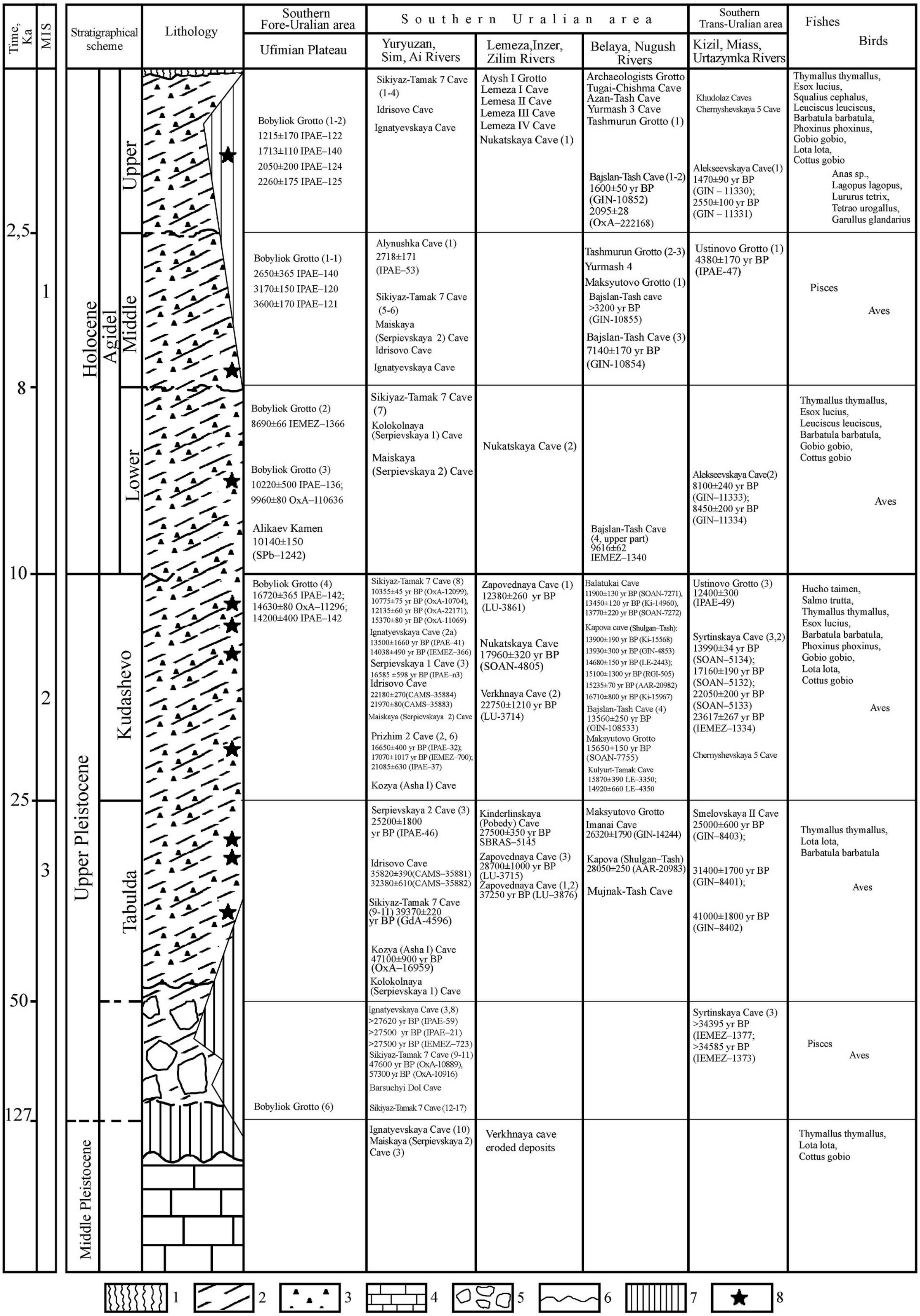

Fig. 8. Summarizing figure with stratigraphical units and the correlation of the different faunal and floral complexes.
Legend: 1 – soil; 2 – loam; 3 – small limestone debrises; 4 – limestone; 5 – blocks of rocks; 6 – erosion levels; 7 – erosion of the deposits; 8 – dated levels. MIS – Marine Isotope Stages. A tentative correlation between MIS and other data is shown.

Time, Ka	MIS	Stratigraphical scheme	Small mammals	Large mammals	Amphibians Reptililes	Molluscs	Vegetation
2,5	1	Holocene, Agidel, Upper	Chiroptera, Erinaceus sp., Talpa europaea, Crocidura sp., Sorex minutus, Sorex araneus, Sorex sp., Neomys sp., Ochotona sp., Pteromus volans, Sciurus vulgaris, Tamias sibiricus, Sicista betulina, Sicista sp., Allactaga major, Apodemus uralensis, A. flavicollis, A. ex gr. uralensis-agrarius, A. agrarius, Rattus sp., Eliomys quercinus, Cricetulus migratorius, Allocricetulus eversmanni, Cricetus cricetus, Ellobius talpinus, Ellobius sp., Clethrionomys rufocanus, C. glareolus, Cl. rutilus, C.. ex gr. glareolus-rutilus, Ondatra zibethicus, Eolagurus luteus, Lagurus lagurus, Arvicola terrestris, Microtus gregalis, M. oeconomus, M. agrestis, M. ex gr. arvalis-agrestis, M. arvalis, Mustela nivalis, M. erminea	Lepus timidus, Marmota bobak, Castor fiber, Ursus arctos, Vulpes corsac, V. vulpes, Martes martes, Mustela putorius, Meles leucurus, Lutra lutra, Alces alces, Cervus elaphus, Capreolus pygargus, Rangifer tarandus, Domestic animals	Triturus cristatus, Pelobates cf. fuscus, Bombina sp., Bufo bufo, Rana arvalis, R. temporaria, Anura indet. Anguis fragilis, Lacerta agilis, L. vivipara, Lacertidae indet., Sauria indet., Coronella austriaca, Colubrinae indet., Natrix natrix, N. tesselata, Natricinae indet., Vipera berus, V. ursinii, Serpentes indet.	Succinella oblonga, Succinea cf. putris, Cochlicopa lubrica, Pupilla muscorum, Vertigo pygmaea, Vallonia costata, V. pulchella, V. tenuilabris, Perpolita hammonis, Euconulus fulvus, Discus ruderatus, Chondrula tridens, Euomphalia strigella, Pseudotrichia rubiginosa, Fruticicola fruticum, Lymnaea sp., Planorbis planorbis, Gyraulus laevis, G. albus, Acrolox lacustris, Ancylus fluviatilis, Pisidium amnicum, Sphaerium rivicola, Unio sp., Dreissena polymorpha	Forest and forest-steppe landscapes. Mixed Pinus-Betula forests with broadleaved trees admixture. Artemisia-herbage associations covered open landscapes. Warm and humid climate.
8	1	Holocene, Agidel, Middle	Chiroptera, Desmana sp., Talpa europaea, Sorex sp., Crocidura sp., Ochotona sp., Spermophilus sp., Sicista sp., Allactaga major, Apodemus uralensis, A. flavicollis, A. ex gr. uralensis-agrarius, Allocricetulus eversmanni, Cricetulus migratorius, Cricetus cricetus, Ellobius talpinus, Ellobius sp., Clethrionomys rufocanus, C. ex gr. glareolus-rutilus, Lagurus lagurus, Eolagurus luteus, Arvicola terrestris, Microtus gregalis, M. oeconomus, M. agrestis, M. ex gr. arvalis-agrestis, M. arvalis	Lepus timidus, Marmota bobak, Castor fiber, Ursus arctos, V. vulpes, Martes martes, Mustela eversmanii, Meles meles, Lutra lutra,Sus scrofa, Alces alces, Cervus elaphus, Capreolus pygargus, Rangifer tarandus, Canis familiaris	Lissotriton vulgaris, Bufo bufo, B. viridis, Rana arvalis, R. cf. ridibunda, R. temporaria, Anura indet. Anguis fragilis, Eremias cf. argute, Lacerta agilis, L. vivipara, Lacertidae indet., Sauria indet., Coronella austriaca, Elaphe dione, Colubrinae indet., Natrix natrix, N. cf. tesselata, Natricinae indet., Vipera berus, V. ursinii, Serpentes indet.	Succinella oblonga, Cochlicopa lubrica, Pupilla muscorum, Vallonia costata, V. tenuilabris, Chondrula tridens, Discus ruderatus, Perpolita hammonis, Fruticicola fruticum, Lymnaea sp., Galba cf. truncatula, Gyraulus laevis, Unio sp.	Forest and forest-steppe landscapes. Mixed Pinus-Betula forests with broadleaved trees admixture. High percentage of Polypodiaceae. Coniferous-broadleaved forests in local places. Artemisia-Cenopodiaceae-herbage associations covered open landscapes. Warm and humid climate.
10	1	Holocene, Agidel, Lower	Chiroptera, Erinaceus sp., Talpa europaea, Crocidura sp., Sorex sp., Ochotona sp., Sciurus vulgaris, Spermophilus sp., Sicista sp., Allactaga major, Alactagulus sp., Apodemus uralensis, Apodemus ex gr. uralensis-agrarius Apodemus flavicollis, Cricetulus migratorius, Allocricetulus eversmanni, Cricetus cricetus, Ellobius talpinus, Clethrionomys rufocanus, Clethrionomys ex gr. glareolus-rutilus Eolagurus luteus, Lagurus lagurus, Dicrostonyx torquatus, Arvicola terrestris, Microtus gregalis, M. agrestis, M. oeconomus, M. arvalis, Microtus ex gr. arvalis-agrestis	Lepus timidus, Marmota bobak, Castor fiber, Ursus arctos, Vulpes corsac, V. vulpes, Martes martes, Mustela eversmanii, Meles meles, Lutra lutra, Equus ferus, Alces alces, Cervus elaphus, Capreolus pygargus, Rangifer tarandus, Megaloceros giganteus, Saiga tatarica	Pelobates fuscus, Bufo bufo, Rana arvalis, R. temporaria, Anura indet. Lacerta cf. agilis, Natrix natrix, Natricinae indet., Vipera berus	Cochlicopa lubrica, Pupilla muscorum, Vallonia costata, V. tenuilabris, Chondrula tridens, Discus ruderatus, Perpolita hammonis, Euconulus fulvus, Planorbarius corneus	Urals (north): Forest and forest-steppe landscapes. Mixed Pinus-Betula forests with broadleaved trees admixture. High percentage of Polypodiaceae. Trans-Urals and Urals (south): Artemisia-Cenopodiaceae and Poaceae-herbage associations covered open landscapes. Cool and dry climate.
25	2	Upper Pleistocene, Kudashevo	Chiroptera, Talpa sp., Sorex sp., Crocidura sp., Neomys sp., Erinaceinae, Ochotona sp., Spermophilus sp., Sicista sp., Allactaga major, Alactagulus sp., Allocricetulus eversmanni, Apodemus uralensis, A.ex gr. uralensis-agrarius, A.flavicollis, Ellobius talpinus, Cricetulus migratorius, Allocricetulus eversmanni, Cricetus cricetus, Clethrionomys rufocanus, Cl. rutilus, Cl.ex gr.glareolus-rutilus, Lagurus lagurus, Eolagurus luteus, Dicrostonyx guilielmi, Lemmus sibiricus, Arvicola terrestris, Microtus gregalis, M. oeconomus, M. agrestis, M. arvalis	Lepus timidus, Marmota bobak, Canis lupus, Vulpes corsac, V. vulpes, Martes sp., Ursus arctos, Panhtera spelaea, Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Megaloceros giganteus, Cervus elaphus, Rangifer tarandus, Bison priscus, Saiga tatarica	Pelobates fuscus, Bufo sp., Rana arvalis, R. temporaria, Anura indet. Anguis fragilis, Lacerta agilis, L. vivipara, Lacertidae indet., Sauria indet., Coronella austriaca, Elaphe dione, Colubrinae indet., Natrix natrix, N. cf. tesselata, Natricinae indet., Vipera berus, V. ursinii, Serpentes indet.	Succinella oblonga, Cochlicopa lubrica, Vallonia costata, V. tenuilabris, Pupilla muscorum, Perpolita hammonis, Euconulus fulvus, Chondrula tridens, Fruticicola fruticum, Gyraulus laevis, Ancylus fluviatilis, Pisidium sp., Unio sp.	Periglacial steppe landscapes with Asteraceae, Chenopodiaceae and Artemisia predominance. Deterioration of the species composition of plant communities. Cold and dry climate.
50	3	Upper Pleistocene, Tabulda	Talpa sp., Sorex sp., Neomys sp., Ochotona sp., Spermophilus sp., Apodemus uralensis, A. flavicollis, Cricetulus migratorius, Cricetus cricetus, Clethrionomys rufocanus, Cl. glareolus, Cl. rutilus, Lagurus lagurus, Dicrostonyx guilielmi, Lemmus sibiricus, Arvicola terrestris, Microtus gregalis, M. oeconomus, M. agrestis	Lepus timidus, Marmota bobak, Canis lupus, Cuon alpinus, Vulpes corsac, V. vulpes, Martes sp., Lynx lynx, Panhtera spelaea, Ursus arctos, U. spelaeus, U. savini, Crocuta c. spelaea, Mammuthus primigenius, Equus ferus, Coelodonta antiquitatis, Elasmotherium sibiricum, Alces alces, Ovis ammon, Megaloceros giganteus, Cervus elaphus, Rangifer tarandus, Bison priscus, Saiga tatarica		Chondrula tridens, Cochlicopa lubrica, Vallonia costata, Discus ruderatus, Perpolita hammonis	Urals (north): forest-steppe landscapes. Picea and Picea-Pinus forests with broadleaved and small-leaved trees admixture. Artemisia-Cenopodiaceae and Poaceae-herbage associations covered open landscapes. Trans-Urals: Periglacial steppe l andscapes with Poaceae. Moderate-warm and humid climate.
127		Upper Pleistocene	Erinaceus sp., Talpa sp., Sorex sp., Crocidura sp.,Eptesicus sp., Plecotus sp., Myotis sp., Ochotona sp., Sciurus vulgaris, Cricetulus migratorius, Dryomys nitedula, Apodemus flavicollis, A. ex gr. uralensis-sylvaticus, Clethrionomys sp., Lagurus lagurus, Dicrostonyx sp., Arvicola terrestris, Microtus oeconomus, M. agrestis, M. gregalis	Lepus sp., Hystrix brachyuran, Marmota bobak, Canis lupus, Vulpes lagopus, V. vulpes, Ursus thibetanus, U. spelaeus, U. savini, Gulo gulo, Stephanorhinus kirchbergensis, Cervus elaphus, Rangifer tarandus, Bison priscus, Ovis ammon			
		Middle Pleistocene	Ochotona sp., Allocricetulus eversmanni, Cricetulus migratorius, Lagurus lagurus, Dicrostonyx simplicior, Arvicola sp., Clethrionomys rufocanus, Cl. ex gr rutilus-glareolus, M. oeconomus, M. agrestis, Microtus gregalis, Apodemus uralensis, A. flavicollis	Lepus sp., Marmota bobak, Canis lupus, Vulpes lagopus, V. vulpes, Ursus savini, Martes sp., Cervus elaphus, Rangifer tarandus, Bison priscus			

Zapovednaya (1-2) - cave name and number of layers in brackets

Fig. 8. (*continued*)

00270mol_a (Russian Federation) A and Russian Goverement Program of Competitive Growth of Kazan Federal University. This paper deals with Quaternary key-sites of the Southern Fore-Urals and Southern Urals region in the frame of the DATESTRA (*Database of Terrestrial European Stratigraphy*) project (grant INQUA-SACCOM: 1612F). This paper mentioned objects of two geoparks: Idrisovo Cave is located on the territory of the "Yangan-Tau" Geopark, the first Russian geopark under umbrella of the Global Geoparks Nework UNESCO; Kinderlinskaya Cave – on the territory of the "Toratau" Geopark.

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